Modelling the micromechanics of the cochlea in Femlab

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Traineeship report

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Abstract

The micromechanics of the cochlea, describing the relative motion of the structures within the organ of Corti, can be modeled as an array of lumped parameters systems spanning the length of the cochlea. These lumped parameter systems form a frequency-place mapping and are coupled via the cochlear fluids. An active process taking place within the organ of Corti is thought to be responsible for the remarkable dynamic range and frequency selectivity of the human ear. This active process, called the cochlear amplifier, can be seen as an energy source enhancing the vibration of the cochlear partition in a manner which is both frequency and place specific. The only candidate capable of fulfilling the activity-source discovered so far is the electromotility of the outer hair cells, a term referring to the cells ability of rapidly changing their shape as a response to a change in the cells potential. The dynamic representation of this electromotility is an important issue in audiology. Two micromechanical models of the cochlea, which have different representations of the cochlear amplifier, are considered here and modelled in Femlab. The cochlear amplifier is implemented as a feedback loop which is driven by the deflection of the stereocilia. The system has to be close to instability in order to get high the amplifications observed in measurements. Frequency response simulations are carried out to analyze the dynamic behaviour of the cochlear partition in both models.
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Chapter 1

Introduction

The performance of the human auditory system is astonishing. It enables us to hear both faint whispers and loud cries, while the difference in energy carried by these signals can be over 12 orders of magnitude. At the same time, two successively played tones can be distinguished by humans if the difference in frequency is only a fraction of a per cent. These extraordinary characteristics of the human ear, a vast dynamic range and excellent frequency selectivity, are achieved thanks to the cochlea.

This snail-shaped organ of hearing is located in the inner ear, deeply embedded in the hardest bone of the body. Although human hearing has always been a subject of interest, progress in understanding the function of the tiny cochlea has been slow. Today we know that the cochlea is a key element in the transduction of mechanical energy of sound into electrical signals to the brain and that an active process within the cochlea is responsible for its remarkable performance. This active process is known as the cochlear amplifier. However, the actual mechanics underlying this active process are, despite all research already carried out, still not totally understood. This is mainly due to the relatively inaccessibility and vulnerability of the cochlea. In order to help us understanding the complex functioning of the cochlea, mathematical models of the cochlea are built. These models can contribute in a greater understanding of hearing disorders. The cochlear amplifier is modeled as a feedback loop, resulting in a system close to instability to get high amplifications. In reality, however, most people’s cochlea’s appear to be unstable, resulting in sounds produced by the cochlea which can be measured in the ear canal.

Two micromechanical models of the cochlea are made in Femlab, with which frequency response simulations will be carried out to provide insight into the dynamics. The models differ in the way in which the cochlear amplifier is implemented, namely as active force or as a active displacement. This report is organized as follows: section 2 describes the basic knowledge of the anatomy of the human auditory system, which is followed by the principles of cochlear modeling in section 3. Section 4 and 5 describe the micromechanical models of the cochlea with the cochlear amplifier implemented as an active force or an active displacement respectively. This is followed by section 6 in which an attempt is made to combine the merits of both models into a new model. Finally, section 7 summarizes the approach and gives the conclusions.
Chapter 2

The cochlea

The chapter will deal with the anatomy of the human auditory system and the mechanics of the cochlea. Section 2.1.1 will briefly outline the main parts of the human ear, after which section 2.1.2 and 2.1.3 will zoom in on the anatomy of the cochlea and the organ of Corti respectively. After that, the mechanics of the cochlea responsible for the transduction process of a mechanical vibration into a nervous pulse are described in two parts. Section 2.2.1 will cover the so-called macromechanics, that is to say the vibration of the basilar membrane and the organ of Corti relative to the surrounding bony structures. Finally, the relative motion of the structures within the organ of Corti, better known as the micromechanics of the cochlea, are discussed in section 2.2.2.

Although an attempt is made to give an clear overview of the anatomy of the human auditory system and its functioning sufficient for a good understanding of the following chapters of this report, it is explicitly not the intention to describe this matter to the minutest detail here. If the reader would desire more detailed knowledge than the basics provided in this chapter, many good resources exist that can fulfill that need better than this report [Pic82] [Dal96].

2.1 The anatomy of the ear

2.1.1 Main structures in the human ear

The human ear comprises three parts, the outer, middle and inner ears. The outer ear consists of the ear flap and the ear canal, which is leading to the eardrum. This eardrum, also called the tympanic membrane, is the border between the outer and the middle ears.

The middle ear is made up of three small bones, known as the ossicles. The so-called malleus, incus and stapes or stirrup can be seen in figure 2.1 from left to right. Together these ossicles transmit the sound from the eardrum to the cochlea, acting as an impedance transformer. Figure 2.1 shows that the stapes is connected to the oval window on the cochlea, enabling the ossicles to apply a force on the cochlea. Besides the cochlea, the inner ear also includes the vestibular organs which is involved in the sense of balance.

2.1.2 The anatomy of the cochlea

The cochlea is shaped like a snail (a long tube which is wound around in a spiral) and is embedded in the temporal bone of the skull. It coiled dimensions are about 1 cm wide and 5 mm from base to apex.
Figure 2.1: Overview of the main structures in the human auditory system. The figure shows that the external auditory canal leads to the eardrum, which is connected to the ossicles. The stirrup is shown, touching the oval window of the cochlea. In addition to the cochlea, the semicircular canals involved in the sense of balance are shown in the inner ear. Taken from [Pic82].

The uncoiled length of the cochlea amounts to approximately 35 mm in the human ear. Furthermore, the structure tapers slightly along its length from the base to the apex. Two membranes subdivide the cochlea in longitudinal direction into three chambers, called scalae. Figure 2.2 shows the location of the scala vestibuli, scala media and scala tympani in a cross-section of the whole cochlea. The scala tympani and scala vestibuli contain a fluid called perilymph, while the scala media is filled with endolymph. Both fluids differ in their chemical composition, since the main components of perilymph and endolymph are sodium and potassium respectively.

The two membranes that cause the subdivision of the cochlea are called the Reissner’s membrane and basilar membrane (BM) and run through almost the entire length of the cochlea. However, a small opening is located at the apex of the cochlea connecting the upper (scala vestibuli) and the lower channel (scala tympani) in the cochlea. Moreover, the scala vestibuli is closed by the so-called oval window, which is touched by the stapes or stirrup as can be seen in figure 2.1. The lower channel, scala tympani, is closed by the round window, which opens onto the air cavity of the middle ear. The central chamber, scala media or cochlear duct, contains the organ of Corti in which motion of the cochlear fluids is converted into a nerve impulse. Figure 2.3 shows the cochlear duct in one single turn of the cochlea.

2.1.3 The anatomy of the organ of Corti

The organ of Corti is resting on the basilar membrane and it consists of several different types of cells as can be seen in figure 2.4(a), from which the most important ones will be described here. The walls of the Corti tunnel and the reticular lamina (RL) form a rigid structure, as shown in figure 2.4(a) with the thick black lines. All the sensory cells, better known as hair cells, can be seen to be located under the reticular lamina. Two types of hair cells exist, inner and outer hair cells distinguished by their position in the organ of Corti. The inner hair cells are flask-shaped and positioned in one row along the cochlea, resulting in one visible inner hair cell in the cross-section shown in figure 2.4(a). In total, approximately 3500 inner hair cells are located along the length of the cochlea. A bundle of hairs, called stereocilia, projects from the surface of the inner hair cell. Moreover, figure 2.4(a) shows that the nerve
Figure 2.2: Cross-section of the whole cochlea, showing the subdivision into the cochlear duct (1), scala vestibuli (2) and the scala tympani (3). The scala vestibuli and the scala tympani contain endolymph, while the cochlear duct contains perilymph. The arrows show the direction of the flow in the cochlea. Reproduced from [Z1].

Figure 2.3: Cross-section of one single turn of the cochlea. The basilar membrane (5) and the Reissner’s membrane (4) can be clearly seen to separate the cochlear duct (1) from the scala tympani (3) and the scala vestibuli (2). Moreover, the organ of Corti is visible, resting on the basilar membrane and covered by the tectorial membrane (6) on top. Finally, the stria vascularis (7), the bony spiral lamina (9) and the fibres (8) are shown. Reproduced from [Z1].
fibers that carry information to the brain contact the inner hair cells. The cylindrically shaped outer hair cells are over three times more numerous than inner hair cells and also the outer hair cells have stereocilia projecting towards the tectorial membrane, a gelatinous mass which is attached only on one side and positioned on top of the organ of Corti. The tips of these stereocilia are probably imbedded in the tectorial membrane, in contrast to the stereocilia of the inner hair cells. Tight bundles are formed by the cilia on top of the apical surface of the hair cells, with so called tip-links providing a connection with adjacent cilia. Figure 2.4(b) is a photo of a bundle stereocilia from a turtle, in which a pyramidal structure can be recognized. In addition, ion channels, through which ions are able to enter or leave the outer hair cells body, are located in the stereocilia walls [Pic82]. The narrow gap in between the reticular lamina and the tectorial membrane is called the sub-tectorial space, and is filled with perilymph.

Figure 2.4: Subfigure (a):Overview of the structures within the organ of Corti. The thick black lines indicate the relatively stiff structure resting on the basilar membrane formed by the rods of Corti and the reticular lamina. Several cell types are shown, the most interesting ones being the inner and outer hair cell. The figure shows that for every inner hair cell approximately three outer hair cells are present in the organ of Corti. In addition, the nerve fibers connected to these hair cells are shown. The tectorial membrane is fixed at one side only and is covering the top of the cochlear partition. The narrow gap between the reticular lamina and the tectorial membrane is called the sub-tectorial space and is filled with perilymph. Taken from [All01].

Subfigure (b): A photo of a bundle stereocilia from a turtle, in which a pyramidal structure can be recognized. Taken from [Duk02].

2.2 Cochlear transduction

Having dealt with the anatomy of the ear in general and the cochlea in particular, the transduction process that converts sound into neural impulses to the brain is discussed. This process can be subdivided into two parts. Firstly, the macromechanics of the cochlea will be discussed which cover the interaction between the motion of the cochlear fluids and the cochlear partition. These macromechanical vibrations, however, are not sufficient to explain the sharp frequency response as observed in a living cochlea. The so-called micromechanics of the cochlea together with the cochlear amplifier are thought to be responsible for this sharp response. Therefore the micromechanics of the cochlea, describing the relative motion of the structures within the organ of Corti, is discussed in 2.2.2. This is
followed by a brief discussion about the cochlear amplifier.

An important final remark that has to be made here. Diverse opinions exist in the literature about certain issues regarding the micromechanics of the cochlea. In the first place, different opinions exist about how the structures within the organ of Corti exactly interact during motion and, in the second place, how the supply of energy to the system around the characteristic position needed to give the sharp response as measured in a living cochlea can be explained. The reader should be aware of the uncertainty present in the field, which arises because of the extreme difficulty of detailed measurements on individual parts of the living cochlea.

### 2.2.1 Macromechanics

When a sound wave reaches the ear drum, the vibrations are transmitted by the ossicles to the oval window on the cochlea as discussed in section 2.1.1. This results in a motion of the perilymph in scala vestibuli towards the round window. The movement of the cochlear fluid towards the round window involves transverse displacement of the cochlear partition, known as the traveling wave.

For a vibration of particular frequency, the amplitude of the displacement of the basilar membrane increases as the wave travels towards the apex and the amplitude peaks at a certain characteristic longitudinal position in the cochlea, before it rapidly dies out. The higher the frequency of the sound, the closer the corresponding characteristic position is located to the base of the cochlea. Consequently, high frequency tones won’t propagate through the helicotrema back to the round window, as low frequency tones do. This place-frequency relation is often expressed as a cochlear map function [All80], which is specific for a certain species. Moreover, since the wave speed varies with the frequency, the traveling wave is a dispersive wave.

### 2.2.2 Micromechanics

The propagation of the travelling wave causes a pressure difference between the cochlear fluids in the scala tympani and the scala vestibuli. This pressure difference results in a vibration of the basilar membrane and the organ of Corti in the transverse direction. The pillars in figure 2.4(a) are fairly rigid and this is where the organ of Corti is thought to pivot about. The tectorial membrane is only fixed at one point and thought to be able to pivot about this hinge. In addition, stiffness of the tectorial
membrane in radial direction is not infinite and has to be taken into account here. Consequently, the transverse motion of the basilar membrane and the organ of Corti causes a relative radial displacement of the tectorial membrane with respect to the basilar membrane. The stereocilia of the outer hair cells, protruding from the apical surface at the reticular lamina and embedded in the tectorial membrane, are forced to deflect in the radial direction.

This deflection of the outer hair cells is thought to open the ion channels of the cilia, resulting in a flow of potassium ions from the perilymph into the body of the outer hair cell. The potassium flow changes the voltage of the cell, which was discovered in 1985 to give rise to a shortening of the cell's length up to 5 per cent [WBdR85]. The ability of the outer hair cells to rapidly change their shape in response to a depolarization of the cell is called the electromotility of the cells, and it is this electromotility that is thought to act as an amplifier of the mechanical response of the cochlea. The electromotility of the outer hair cells leads to contractile forces, increasing the displacement of the basilar membrane towards the scala vestibuli. If the pressure difference between the upper and lower scala in the cochlea changes sign, the basilar membrane moves downwards, compressing the stereocilia and closing the ion channels. During this period of no ion flow in or out the outer hair cells body, the potential of the outer hair cells is restored to its original value leading to an elongation of the cell. Similarly as in the first half part of this cycle, this elongation enhances the response of the cochlear partition. This complicated process, with the shearing motion of the tectorial membrane with respect to the reticular lamina as a key element, is repeated when the basilar membrane is back at its original position. The concept of a cycle-by-cycle amplification of the intracochlear vibrations leading to an enhancement of the mechanical response of the cochlea is known as the cochlear amplifier. This cochlear amplifier can be seen as a mechanism pumping energy into the system at a certain longitudinal position in the cochlea, however, only if the frequency of the traveling wave is close to the characteristic frequency corresponding to this particular position.

**Cochlear amplifier**

The origin of this cochlear amplifier and its exact functioning is the topic of many recent studies in auditory mechanics. The only physiological mechanism to fulfill this role discovered so far, however, is the electromotility of the outer hair cells leading to an increase in the attention to the mechanics of these outer hair cells. This concept is, together with the micromechanics of the organ of Corti, thought to be responsible for the significant difference in the responses measured in a live and dead cochlea. The magnitude of the response measured in a dead cochlea are much broader and are not consistent with the extraordinary frequency selectivity of the human ear [Pie07].

A remarkable consequence of an active process present in the cochlea, is that oscillations can be produced without energy entering the cochlea via the outer ear. This results in sound vibrations called spontaneous otoacoustic emissions, which can be measured in the ear canal. Again this indication of an active process is only measured in living ears, which is explained by the fact that the potential difference between the cochlear fluids dies out and the electromotility of the outer hair cells is not functioning anymore. It should be noted, however, that the details of this mechanism responsible for the amplification are not totally understood yet. The electromotility is a new phenomenon and different from other known cellular or molecular motors [Dal92].
Chapter 3

Basics of Cochlear modeling

The cochlea is modeled to help us understanding the complex functioning of the human auditory system on the one hand, and on the other hand to represent the results from a large variety of physical experiments. To set the framework in which the micromechanics of the cochlea can be seen, the macromechanics have to be modeled first. A macromechanical model describes the interaction between the motion of the cochlear fluids and the cochlear partition as a whole, while micromechanical models cover the interaction of the structures within the cochlear partition. Lumped parameter models are used which model the micromechanics of the cochlea either as an array of mass-spring-damper systems or as an array of electrical circuits. In this report, the focus will be on the mass-spring-damper presentation, since these models offer a good physical insight into the dynamics involved in the hearing system.

3.1 Macromechanical models

The macromechanics involves the wave propagation of the traveling wave in the cochlear fluids, assuming that the organ of Corti and the basilar membrane are considered to move in unison. A few important modeling assumptions can be distinguished.

The complex spiral shape is simplified to a rectangular box and the mechanical influence of the Reissner’s membrane is neglected, leaving two remaining fluid channels which are terminated by the oval and round windows. The pressure of the cochlear fluid at both sides of the cochlear partition consists of a symmetrical and anti-symmetrical component, from which the symmetrical component is the same in both channels. The anti-symmetrical component causes the actual motion of the basilar membrane and the organ of Corti. The cochlear partition is discretised into a number of mass-spring-damper systems, and due to negligible rigidity of the basilar membrane in longitudinal direction, considered to be independent. So, the only coupling between these lumped parameter systems is provided via the cochlear fluids.

Another important assumption usually made is the so-called long wave assumption: the wavelength of the motion of the organ of Corti is assumed to be much greater than the typical height of a cochlear channel. This assumption leads to a pressure difference between the fluids in the two channels which is a function of the longitudinal position \(x\) in the cochlea only. So the variation of pressure in the \(y\) and \(z\) direction in figure 3.1 are neglected here, which leads to the wave equation describing the macromechanics of the cochlea.

\[
\frac{\partial^2 p_d(x, \omega)}{\partial x^2} - \frac{2j\omega p}{Z_{cp}(x, w)H} p_d(x, \omega) = 0
\]  

(3.1)
Figure 3.1: Schematic drawing of the assumed shape of the cochlea in macromechanical modelling. The cochlear partition can be seen to divide the cochlea into two channels, which are terminated by the oval and round window. The antisymmetric pressure $p_d$ is indicated in the figure, acting upon the cochlear partition. $H$ denotes the height of the upper channel.

where $p_d(x, \omega)$ is the pressure difference across the cochlear partition, $x$ the longitudinal position in the cochlea, $\omega$ the frequency, $\rho$ the density of the cochlear fluid, $H$ the height of the upper cochlear channel and $Z_{cp}(x, \omega)$ denotes the impedance of the cochlear partition [dB91]. A key element in (3.1) required to calculate the coupled response of the cochlea is the impedance of the cochlear partition $Z_{cp}$, and it is this impedance that is derived using models for the micromechanics of the cochlea. The basic assumptions made in modeling these micromechanics of the cochlea will be explained in the next section.

### 3.2 Micromechanical models

The micromechanics of the cochlea describe the relative motion of the structures within the organ of Corti, using mass-spring-damper systems to represent the mechanical properties of the involved structures and eventually leading to an expression for the cochlear partition impedance $Z_{cp}(x, \omega)$. The number of degrees of freedom of the micromechanical model varies appears to vary in literature, as does the definition of the of the cochlear partition impedance. Therefore, in this report, this cochlear partition impedance is unambiguously defined as

$$Z_{cp}(x, \omega) = \frac{f_{cochlearpartition}}{\dot{w}_{cp}}$$  \hspace{1cm} (3.2)

where $f_{cochlearpartition}$ is the force acting at the basilar membrane with the organ of Corti on top and $\dot{w}_{cp}$ is the velocity of the cochlear partition in transverse direction as indicated in figure 3.1. This impedance will be a function solely of the longitudinal position $x$ and radian frequency $\omega$.

In addition, the mobility of the cochlear partition is defined as

$$Y_{cp}(x, \omega) = Z_{cp}^{-1}$$  \hspace{1cm} (3.3)

Experimental measures of the mechanical properties of the organ’s components are difficult to perform, mainly due to the location of the organ -deeply embedded in one of the hardest bones of the human body-, but also due to the vulnerability of the processes taking place in the organ of Corti. Consequently,
empirically obtained data is rare and not always reliable since measurements prove to be dependent on the methodology of the measurement [Dal96]. Therefore, the parameters describing the dynamic behaviour of the structures within the organ of Corti are usually fitted to match the measured response. Some general qualitative remarks about the mechanic properties can be made here.

The stiffness of the basilar membrane is large at the base and decreases very fast with increasing $x$. This property is often expressed by an exponential function. The mass of the basilar membrane is usually lumped with the mass of the organ of Corti and often assumed to be constant. Since the cochlear fluids are assumed to be inviscid and incompressible, the damping properties of the basilar membrane are thought to be the only mechanism to dissipate energy and are usually expressed in the same exponential form as the stiffness. Both micromechanical models considered in this report are not solely made up of the lumped mass of the basilar membrane and the organ of Corti, but also include the mass of the tectorial membrane as a second degree of freedom. An often made assumption is that both the basilar membrane and the tectorial membrane are able to rotate about a connection to the bone of the modiolus [Dal96]. This leads to an important concept in cochlear micromechanical modeling, namely the definition of the so-called shear gain $g$ [All80].

This shear gain is defined as the relation between the radial deflection of the cilia and the transverse motion of the basilar membrane, i.e.

$$g = \frac{\Delta}{w} = \frac{h}{l}$$

with $\Delta$ the radial deflection of the cilia, $w$ the transverse displacement of the basilar membrane, $h$ the distance between the hinges and $l$ the distance from a hinge to the mass of the basilar membrane.

The second degree of freedom arises if the tectorial membrane is assumed to slide in radial direction with respect to the basilar membrane, thereby influencing the definition of $\Delta_C$. This quantity, which physically can be seen as deflection of the cilia, appears to be crucial in modeling the micromechanics since it is used as a triggering mechanism for the cochlear amplifier. How this cochlear amplifier is exactly defined varies with micromechanical models, but its underlying principle is often similar. The cochlear amplifier is modeled as a feedback loop enhancing the motion of the cochlear partition around the characteristic frequency.

Figure 3.2: Geometry of micromechanical model with one degree of freedom in which the two right hand triangles can be seen to be similar, and thus the shear gain $g = \frac{\Delta}{w} = \frac{h}{l}$. 
Chapter 4

Micromechanical model with active force

The first model of the cochlear micromechanics that will be analyzed here is a two degree of freedom model proposed in [NK86]. Figure 4.1 compares the model in physical form with the model with all motion transformed into equivalent radial motion. The lower mass represents the basilar membrane and the upper mass represents the tectorial membrane in this system. The tectorial membrane is able to move independently in the radial direction, whereas the basilar and tectorial membrane move as a locked system in transverse direction. The motion of the tectorial membrane causes shearing forces between the tectorial membrane and the membrane at the top of the basilar membrane, called the reticular lamina. The stereocilia of the outer hair cells are deflected by this relative radial motion and this deflection is assumed to be triggering the motile action of the outer hair cells. This deflection of the stereocilia is thought to change the electrochemical potential of the outer hair cell by opening the ion channels in the cell, which again leads to the generation of a mechanical force acting on the basilar membrane. So the outer hair cells are modeled as mechanical force generators that are powered by electrochemical energy of the cochlear endolymph.

4.1 Multi-axis and single-axis motion model

It can be seen in the left hand side of figure 4.1 that the force acting on the basilar membrane causes a rotational motion around a fixed point. The roller connection between the basilar and the tectorial membrane indicates that the height in between the reticular lamina and the tectorial membrane remains constant, but sliding of the tectorial membrane with respect to the basilar membrane is possible. The lower subsystem in the left hand side of figure 4.1 consisting of mass $M_b$, spring $K_b$ and damper $C_b$ represent the mass, stiffness and damping of the basilar membrane. The upper subsystem is made up of a mass $M_t$ and two springs $K_t$ and $K_c$ and two dampers $C_b$ and $C_t$. This mass $M_t$ represents the tectorial membrane, which is connected to the reticular lamina via the cilia of the outer hair cells. The dynamic behaviour of these cilia is modeled by spring $K_c$ and damper $C_c$, which are orientated in radial direction and control the relative shear motion between the organ of Corti and the tectorial membrane. Moreover, the tectorial membrane is able to pivot around a hinge and able to vibrate in radial direction due to the presence of spring $K_t$ and damper $C_t$ which connect the tectorial membrane to rigid bone. All these stiffnesses and damping constants are only a function of the longitudinal position in the cochlea in this model due to the long wave assumption described in section 3.1, and the corresponding expressions are taken from [NK86] and given in table 4.1 as a function of $x$.

Transforming the model in physical form into a model with all motion in one direction significantly
Figure 4.1: Micromechanical model in physical form (left) compared with the model with all motion transformed into equivalent radial motion (right).

Table 4.1: Parameters as a function of $x$ in micromechanical model with active force, taken from [NK86], but corrected for typological errors and transformed into SI units.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M_b/A_p$</td>
<td>$2.5 \times 10^{-2}$ [kgm$^{-2}$]</td>
</tr>
<tr>
<td>$M_t/A_p$</td>
<td>$5 \times 10^{-3}$ [kgm$^{-2}$]</td>
</tr>
<tr>
<td>$K_b/A_p$</td>
<td>$1.1 \times 10^{10} e^{-400x}$ [Nm$^{-3}$]</td>
</tr>
<tr>
<td>$C_b/A_p$</td>
<td>$200 + 15 \times 10^4 e^{-200x}$ [Nsm$^{-3}$]</td>
</tr>
<tr>
<td>$K_c/A_p$</td>
<td>$10^5 \times e^{400x}$ [Nm$^{-3}$]</td>
</tr>
<tr>
<td>$C_c/A_p$</td>
<td>$20 \times e^{-80x}$ [Nsm$^{-3}$]</td>
</tr>
<tr>
<td>$K_t/A_p$</td>
<td>$7 \times 10^7 e^{-140x}$ [Nm$^{-3}$]</td>
</tr>
<tr>
<td>$C_t/A_p$</td>
<td>$10^2 \times e^{200x}$ [Nsm$^{-3}$]</td>
</tr>
<tr>
<td>$K_{active}/A_p$</td>
<td>$6.15 \times 10^9 e^{-400x}$ [Nm$^{-3}$]</td>
</tr>
<tr>
<td>$C_{active}/A_p$</td>
<td>$1.04 \times 10^4 e^{-200x}$ [Nsm$^{-3}$]</td>
</tr>
<tr>
<td>$a$</td>
<td>1</td>
</tr>
<tr>
<td>$b$</td>
<td>0.4</td>
</tr>
</tbody>
</table>
simplifies the analysis of the motion, however, physical insight into the actual motion of the components of the cochlea is lost. This transformation is elaborated in [EPL06], where using the shear gain \( g \) the relations between all transverse variables and their radial equivalents are derived as a function of \( g \).

4.1.1 Active force

The relative motion between the two masses represents the hair bundle displacement, which leads to the generation of an active force acting on the basilar membrane. The origin of this active force is thought to be in the depolarization of vestibular hair cells when the outer hair cell cilia are forced to bend due to the shearing motion of the tectorial membrane with respect to the basilar membrane. In vitro observation of the outer hair cell’s motility shows a shortening of the outer hair cells when the vestibular hair cell is depolarized [WBdR85]. This shortening of the outer hair cell height is interpreted to be the result of an internal pressure decrease in the outer hair cell. Assuming the fluid surrounding the outer hair cell is incompressible, internal pressure changes are transmitted isometrically to the surrounding fluid, leading to a force acting on the basilar membrane. So in this model, the conversion of electrochemical energy of the cochlear endolymph into a mechanical force which is acting on the basilar membrane is the source of activity.

In order to be able to use the parameters proposed in [NK86], consistency with the definition of the active force has to be ensured. The active pressure source is defined in [NK86] as

\[
p_{\text{active}}(x) = -\gamma Z_{\text{active}}(x) \Delta C \cdot i\omega \tag{4.1}
\]

where \( Z_{\text{active}}(x) \) represents the impedance of the active source. Please note that in the original notation in [NK86], the active pressure was acting in opposite direction of the passive force. In this report however, to be consistent with [EPL06], the active pressure is acting in positive radial direction, as is shown in figure 4.1. Another remark that has to be made here is that the parameters in table 4.1 are all given per unit area. Provided these values per area are used in this model, the active pressure becomes an active force. These two considerations result in the definition for the active force in this report as

\[
f_{\text{active}}(x) = \gamma Z_{\text{active}}(x) \Delta C \cdot i\omega \tag{4.2}
\]

The impedance \( Z_{\text{active}}(x) \) is expressed as

\[
Z_{\text{active}} = \frac{K_{\text{active}}(x)}{i\omega} + C_{\text{active}}(x) \tag{4.3}
\]

Although \( Z_{\text{active}} \) is a function of \( x \), this dependency will not be explicitly mentioned from now on. Combining (4.2) and (4.3) gives

\[
f_{\text{active}} = \gamma \left( K_{\text{active}} \Delta C + C_{\text{active}} \Delta C \cdot i\omega \right) \tag{4.4}
\]

This can be converted back into the time domain, so

\[
f_{\text{active}} = \gamma \left( K_{\text{active}} \Delta C + C_{\text{active}} \frac{d\Delta C}{dt} \right) \tag{4.5}
\]

Equation (4.5) shows that the cochlear amplifier is modeled as a spring and a damper in parallel which are elongated or compressed by the cilia displacement \( \Delta C \). In order to implement the active force in the model, \( \Delta C \) has to be expressed in terms of the variables depicted in figure 4.1. The shearing displacement of the cilia is in the model with all motion in radial direction equal to

\[
\Delta C^{SA} = \Delta BM^E - \Delta TM. \tag{4.6}
\]
In the model with multi-axis motion the definition of the cilia displacement changes to
\[ \Delta C_{MA} = \Delta_{BM} - \Delta_{TM}. \]  
(4.7)

Using the shear gain as defined by (3.4) in section 3.1 shows that \( \Delta C_{MA} \) becomes
\[ \Delta C_{MA} = g w_{BM} - \Delta_{TM}. \]  
(4.8)

Now the expressions for the active force can be given in the time domain for both the model in physical form and the model with all motion converted into radial motion respectively as
\[
\begin{align*}
    f_{active}^{MA} &= \gamma \cdot \left\{ K_{active} (g w_{BM} - \Delta_{TM}) + C_{active} \left( g \frac{d(w_{BM})}{dt} - \frac{d(\Delta_{TM})}{dt} \right) \right\} \\
    f_{active}^{SA} &= \gamma \cdot \left\{ K_{active} (\Delta_{BM}^E - \Delta_{TM}) + C_{active} \left( \frac{d(\Delta_{BM}^E)}{dt} - \frac{d(\Delta_{TM})}{dt} \right) \right\}
\end{align*}
\]  
(4.9) (4.10)

### 4.2 Implementation in Femlab

The mass-spring-damper systems will now be implemented in Femlab to analyze its dynamics. The area of a cross-section, the Young’s modulus, the length and the area moment of inertia of the used beam-elements will be tuned to match the corresponding radial and transverse stiffness for each element at each position \( x \). Appendix A provides a clear overview of the modeling strategy in Femlab to model linear springs, viscous dampers and point masses. In addition, the total stiffness matrix of a beam element under axial and lateral loading is also given in this appendix.

To realize the desired rotational motion of the basilar membrane about a fixed hinge, a concession has to be made in the Femlab model in physical form. This is due to the fact that the point mass representing the basilar membrane requires some flexibility in radial direction in order to rotate freely. This can be achieved in two different ways. Firstly, the stiffness of spring \( K_b \) could be decreased in radial direction. However, doing so introduces many new undesired eigenfrequencies into the dynamics of the system. Therefore, a second and better option is to release the constraint in \( x \) and \( \theta \)-direction at the point where the spring \( K_b \) is attached to rigid bone.

### 4.3 Simulation results of model with single-axis motion

In this section the results of the simulations carried out with the model with single-axis motion in Femlab will be discussed. Firstly, the results of the undamped passive system will be shown.

#### 4.3.1 Undamped passive system

Both resonances of the system will be clearly visible when the damping in the system is neglected. When a transverse force \( f_{BM} \) is acting at the basilar membrane and the transverse displacements of the basilar and tectorial membrane are denoted as \( w_{bm} \) and \( w_{tm} \) respectively, then the point and transfer mobility of the basilar and tectorial membrane are defined respectively as
\[
\begin{align*}
Y_{point,BM} &= \frac{1}{f_b^E} \frac{d(\Delta_{BM}^E)}{dt} \\
Y_{transfer,TM} &= \frac{1}{f_b^E} \frac{d(\Delta_{TM}^E)}{dt}
\end{align*}
\]  
(4.11) (4.12)
Figure 4.2(a) shows these mobilities at a longitudinal position in the cochlea of \( x = 0.0186 \text{ m} \). The resonance of the tectorial membrane and the basilar membrane are both clearly visible at approximately 621.5 Hz and 2325 Hz respectively. Both mobility-curves show these two resonances to some extent. In addition, the solid line, representing the mobility of the basilar membrane, also shows an anti-resonance immediately after the first resonance. The expected phase-lag of 90 degrees immediately followed by a phase-lead of 90 degrees in the response of the basilar membrane is not visible here due to the small amplitude of this resonance and anti-resonance. A comparison of this undamped frequency response for two different positions in the cochlea can be seen in figure 4.2(a). The solid line represents the mobility of the basilar membrane at a longitudinal position of \( x = 0.0186 \text{ m} \), while the dotted line shows this mobility at \( x = 0.0093 \text{ m} \). The resonance frequency of both the basilar and tectorial membrane are shifted towards higher frequency when the longitudinal coordinate in the cochlea is halved. This is in agreement with figure 2.5. Furthermore, the resonance of the tectorial membrane again results in a resonance followed by an anti-resonance of the basilar membrane. At \( x = 0.0093 \text{ m} \), however, the magnitude of this resonance appears to be large enough to make the 90 degrees phase lag immediately followed by 90 degrees phase lead visible. The displacements of both the basilar and the tectorial membrane can also be plotted so give more insight in the motion of the system around the resonance frequencies. In this case, the basilar membrane is exerted by a harmonic unit force with a frequency equal to either the resonance frequency of the basilar membrane \( \omega_{bm} \) or the resonance frequency of the tectorial membrane \( \omega_{tm} \). For \( x = 0.0186 \text{ m} \) the displacements of both membranes are depicted in figure 4.3. This figure indicates that both membranes are moving in phase at \( \omega_{tm} \). Furthermore, it is apparent from this figure that the amplitude of the tectorial membrane is much higher compared with the the amplitude of the basilar membrane at \( \omega_{tm} \). In fact, the amplitude of the basilar membrane at \( \omega_{tm} \) is scaled with a factor 10 in figure 4.3. At the resonance frequency of the basilar membrane \( \omega_{bm} \), however, the amplitude of the basilar membrane displacement is much higher than the amplitude of the tectorial membrane displacement.
Figure 4.3: The displacement of the basilar (solid line) and tectorial membrane (dashed line) at $\omega_{tm}$ (upper part) and $\omega_{bm}$ (lower part) at $x = 0.0186 \text{ m}$, the amplitude of the basilar membrane is scaled with a factor 10 to enable comparison.

### 4.3.2 Damped passive model

Rayleigh damping is now implemented in the Femlab model, for more information about the implementation of Rayleigh damping in the Femlab-code, please refer to appendix A. For the same position in the cochlea, $x = 0.0186 \text{ m}$, the point-mobility of the basilar membrane and the transfer-mobility of the tectorial membrane are shown in figure 4.4. Interestingly, the phase of the tectorial membrane in this damped system doesn’t drop to $-270^\circ$ degrees as in figure 4.2(a) but reaches $-180^\circ$ degrees eventually. Furthermore, although heavily damped, the point-mobility curve of the basilar membrane still shows the resonance at $\omega_{bm}$, while the transfer-mobility curve of the tectorial membrane still shows the resonance at $\omega_{tm}$. The resonance of the tectorial membrane, however, isn’t visible anymore in the point-mobility of the basilar membrane and similarly, the resonance of the basilar membrane can’t be seen anymore in the transfer-mobility of the tectorial membrane due to the implemented damping.

### 4.3.3 Damped active model

A feedback-loop is implemented in the Femlab-model as described in section 4.1.1 to represent the effect of the cochlear amplifier. Figure 4.5(a) shows (4.10) as it is applied on the passive system. It is apparent from this figure that the magnitude of the active force starts to decrease around 200 Hz to have a minimum value around 600 Hz and after that increases suddenly to have a maximum value just before 1 kHz. The results of applying this active force at the passive system are shown in figures 4.6(a),4.6(b) and 4.5(b). Figure 4.6(a) shows the cochlear partition mobility for the passive ($\gamma = 0$) and the fully active ($\gamma = 1$) case and a clear peak is visible in the magnitude of the active system around 1 kHz at $x = 0.0186 \text{ m}$ in the cochlea. The slope of the magnitude-curve is fading around the resonance frequency of the tectorial membrane, before it starts to rise to reach its maximum value of approximately $-45 \text{ dB}$ at the characteristic frequency of 1 kHz. Moreover, the curve representing the phase in the lower part of figure 4.6(a) shows a significant phase-lead in the frequency range 0.3 – 1 kHz, indicating the presence of negative damping in this frequency range. After the characteristic frequency, the phase falls, to reach $-90^\circ$ at 25 kHz.

The active response of the transfer-mobility of the tectorial membrane can be compared with the passive response in figure 4.6(b). Again, a difference between the passive and active response is visible in the frequency range 0.4 – 1.3 kHz. The peak of the magnitude-curve of the tectorial
membrane is shifted towards the characteristic frequency and the phase starts to fall for slightly higher frequency than in the passive system. Finally, figure 4.5(b) shows interesting results about the real and imaginary parts of the cochlear partition mobility in this active model compared with the results of the passive model. It can be seen that the real part of the cochlear partition mobility in this model becomes negative in the frequency range $0.4 - 1.0\ \text{kHz}$, while the real part of this point-mobility remains positive in a passive system. The real part passes zero at the characteristic frequency, after which the real part remains positive for approximately another $300\ \text{Hz}$. In the active system, the imaginary part of this mobility rises quickly to show a peak at the characteristic frequency and falls with the same slope to become negative, before it shows the same response as the passive system from $10\ \text{kHz}$ onwards.

Figure 4.5: Subfigure a: Magnitude and phase of normalized active force as a function of frequency as it is applied to the passive system. Subfigure b: Real and imaginary part of the point-mobility of the basilar membrane in a damped active model at $x = 0.0186\ m$. 
Figure 4.6: Magnitude and phase of the mobility of the basilar membrane (a) and the tectorial membrane (b) in a damped active (dashed line) model compared with a damped passive (solid line) model. Both curves represent the response at the same position $x = 0.0186\, m$ in the cochlea.

### 4.4 Simulation results of model in physical form

Having seen the results of the micromechanical model with all motion transformed into equivalent radial motion, now the results of the model in physical form will be presented. Creating the model in physical form can help to imagine the relative motion of the structures within the organ of Corti. The longitudinal position in the cochlea is again taken equal to $x = 0.0186\, m$.

Figure 4.7 shows that the model in physical form motion indeed gives predicted partition mobilities that are equivalent to the model with all motion in radial direction used to generate the results in section 4.3. Four curves are actually shown, of which the curves of the single-axis motion system are covered by the curves of the model in physical form. In addition, the motion of the cochlear partition and the tectorial membrane in radial $x$-direction can be analyzed. Therefore, the $x$-mobilities of the basilar and tectorial membrane are here defined as

$$Y_{x,\text{point,BM}} = \frac{1}{f_b} \frac{d(\Delta_{BM}^{\text{abs}})}{dt}$$

$$Y_{x,\text{transfer,TM}} = \frac{1}{f_b} \frac{d(\Delta_{TM}^{\text{abs}})}{dt}$$

with $f_b$ the force acting on the basilar membrane and $\Delta_{BM}^{\text{abs}}$ and $\Delta_{TM}^{\text{abs}}$ the absolute radial displacement of the basilar and tectorial membrane respectively. The results of the simulations carried out with Femlab are shown in figure 4.8. The magnitude and the phase of the point-mobility of the basilar membrane are shown in (a). Since the basilar membrane is only able to pivot around a fixed hinge and not as the tectorial membrane capable of vibrating in radial direction, a significant difference in magnitude can be seen by comparing the vertical axes of subfigure (a) and (b). The point-mobility of the basilar membrane shows an anti-resonance at approximately 0.3 kHz, leading to phase lead for both the passive (solid line) and active (dashed line) system. In addition, it is apparent from this figure that making this system fully active ($\gamma = 1$), results in a clear peak at the characteristic frequency of 1 kHz and a phase-lead that lasts longer. The frequency response of the upper subsystem, which is in addition to pivoting around a fixed hinge also capable of vibrating in radial direction, is depicted in
Figure 4.7: Frequency response of cochlear partition in passive and active model in physical form compared with the passive and active model with all motion transformed into equivalent radial motion. The curves of the single-axis motion system are covered by the multi-axis motion system.

Figure 4.8: The passive (solid lines) and active (dashed lines) x-mobilities of the basilar (figure a) and tectorial (figure b) membrane as defined in (4.13) and (4.14) at a cochlear site of $x = 0.186 \text{ m}$. 
Figure 4.9: Influence of active gain $\gamma$ on response. Magnitude and phase for different values of $\gamma$: fully passive $\gamma = 0$ (solid line), $\gamma = 0.6$ (dotted line), $\gamma = 0.8$ (dash-dotted line) and fully active $\gamma = 1.0$ (dashed line).

subfigure (b). Comparing this response with figure 4.6(b) learns that this response is exactly the same as the response of the upper subsystem with all motion transformed into radial direction. Nonetheless, due to a sign convention and the fact that for low frequencies the basilar and tectorial membrane are moving out of phase, the phase of this transfer-mobility starts at $-90$ degrees.

### 4.4.1 Influence of the active gain

Changing the active gain $\gamma$ is used to represent the effect of impaired outer hair cells. Figure 4.9 shows the magnitude and phase of the cochlear partition mobility for different values of the active gain $\gamma$: $\gamma = 0$, $\gamma = 0.6$, $\gamma = 0.8$ and $\gamma = 1.0$. Reducing the active gain clearly leads to significant loss of sensitivity, which occurs if the outer hair cells are damaged.

To sum up, this first micromechanical model implements the cochlear amplifier as an active force acting at the basilar membrane. Frequency response simulations are carried out in Femlab with the model in physical form and with the model with all motion transformed into equivalent radial motion. The results of implementing the damping and the active force are discussed and it is demonstrated that the active gain can be used to represent the effect of impaired outer hair cells. A similar micromechanical model with another active mechanism will be treated in the next section.
Chapter 5

Micromechanical model with internal active displacement

In this chapter another micromechanical model will be discussed. This model adopts other assumptions about the effect of the somatic motility of the outer hair cells on the dynamics of the structures within the organ of Corti. In the model discussed in chapter 4, the effect of the motility of the outer hair cells was presented as a force, which was a function of the deflection of the stereocilia embedded in the tectorial membrane. It is, however, difficult to visualise in figure 2.4(a) where this active force would react off, since the outer hair cell body is not connected to rigid bone. Therefore, a more physically plausible model of the micromechanics of the cochlea would include the organ of Corti flexing internally as the outer hair cells change their length. This assumption would lead to a three degree of freedom system. If the internal stiffness of the organ of Corti is assumed to be significantly larger than all the other stiffnesses present in the system, however, then an active force gives rise to an active displacement of the reticular lamina. If the mass of the reticular lamina is assumed to be negligible, no new resonances are introduced to the system and a two-degree of freedom model can be retained [EPL06]. Neely [Nee93] proposed these assumptions about the somatic motility and the dynamics of the organ of Corti in 1993, so the model that ensues from these assumptions is referred to as the N’93 model.

5.1 Multi-axis motion model

Figure 5.1 shows the two degree of freedom model in physical form. The basilar membrane is exerted by a force $f_b$ caused by the traveling wave pressure of the perilymph. The stiffness and damping properties of the basilar membrane are represented by a spring $k_b$ and a damper $c_b$ in parallel, which are connected to rigid bone at the bottom. The basilar and tectorial membrane can rotate separately about a fixed hinge and the tectorial membrane is also able to move in radial direction. The lateral motion of the tectorial membrane is controlled by two spring-damper combinations in series, as is shown in figure 5.1. Spring $k_c$ and damper $c_c$ represent the stiffness and the damping properties of the stereocilia of the outer hair cells, which control the relative shearing motion of the tectorial membrane. Both membranes are represented by a point mass, while the mass of the reticular lamina is neglected, as indicated by the line in figure 5.1. The active displacement $w_a$ is acting at the reticular lamina within the organ of Corti. Finally, a slider is inserted in between the reticular lamina and the tectorial membrane to show that the reticular lamina and tectorial membrane have the same transverse displacement, but are able to slide in radial direction.
5.2 Parameters

Parameters are only specified at three longitudinal positions in the cochlea in [Nee93], namely \( x = 0 \), \( x = \frac{L}{2} \) and \( x = L \). In order to compare simulation results with the results in chapter 4, however, parameters at the same cochlear site \( x = 18.6 \times 10^{-3} \) are required. Values at other locations are interpolated by fitting a quadratic polynomial to the log of the parameter values at the specified locations, a procedure elaborated in [Pie07]. In table 5.1 the resulting parameters are given at the cochlear site \( x = 18.6 \times 10^{-3} \) m.

5.3 Active displacement

If the parameters of [Nee93] are used, consistency with the definition of the active displacement \( w_a \) has to be ensured. This active displacement \( w_a \) is defined as

\[
w_a = H_c \cdot \Delta C
\]

with \( \Delta C \) the cilia displacement and \( H_c \) the outer hair cell gain equal to

\[
H_C = \gamma T_f T_r
\]

with \( \gamma \) representing the activity of the model, i.e. \( \gamma = 0 \) denotes a fully passive model and \( \gamma = 1 \) implies a fully active model. Moreover, \( T_f \) and \( T_r \) are defined as the following first-order low-pass filters

\[
T_f = \frac{g_f}{1 + i\omega \tau_f}
\]
Table 5.1: Parameters used in the micromechanical model with active displacement at \( x = 18.6 \cdot 10^{-3} \text{m} \), taken from [Nee93] but converted into SI units.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>( M_b/A_p )</td>
<td>( 1.00 \cdot 10^{-4} ) [kgm^{-2}]</td>
</tr>
<tr>
<td>( M_t/A_p )</td>
<td>( 2.59 \cdot 10^{-2} ) [kgm^{-2}]</td>
</tr>
<tr>
<td>( K_b/A_p )</td>
<td>( 5.83 \cdot 10^{9} ) [Nm^{-3}]</td>
</tr>
<tr>
<td>( C_b/A_p )</td>
<td>( 1.97 \cdot 10^{-1} ) [Ns^{-1}m]</td>
</tr>
<tr>
<td>( K_c/A_p )</td>
<td>( 1.02 \cdot 10^{9} ) [Nm^{-3}]</td>
</tr>
<tr>
<td>( C_c/A_p )</td>
<td>( 1.06 \cdot 10^{3} ) [Ns^{-1}m]</td>
</tr>
<tr>
<td>( K_t/A_p )</td>
<td>( 2.55 \cdot 10^{9} ) [Nm^{-3}]</td>
</tr>
<tr>
<td>( C_t/A_p )</td>
<td>( 4.17 \cdot 10^{9} ) [Ns^{-1}m]</td>
</tr>
<tr>
<td>( g_f )</td>
<td>( 2.22 \cdot 10^{1} ) [mVnm^{-1}]</td>
</tr>
<tr>
<td>( g_r )</td>
<td>0.1 [nmmV^{-1}]</td>
</tr>
<tr>
<td>( \tau_f )</td>
<td>( 1.78 \cdot 10^{-3} ) [s]</td>
</tr>
<tr>
<td>( \tau_r )</td>
<td>( 8.30 \cdot 10^{-4} ) [s]</td>
</tr>
<tr>
<td>( A_p )</td>
<td>( 5 \cdot 10^{-9} ) [m^2]</td>
</tr>
<tr>
<td>( g )</td>
<td>1</td>
</tr>
</tbody>
</table>

and

\[ T_r = \frac{g_r}{1 + i\omega\tau_r} \quad (5.4) \]

The mechanoelectric transduction \( T_f \) describes the ratio of outer hair cells body potential to stereocilia displacement, while the electromechanic transduction \( T_r \) describes the ratio of outer hair cells length contraction to outer hair cells potential [Nee93]. However, \( H_c \) is defined in [Nee93] as the relation between the lateral deflection of the hair bundle and the amount of contraction of the outer hair cell, while here this outer hair cell gain is seen as the relation between the lateral deflection of the hair bundle and the elongation of the outer hair cell. So, a minus sign has to be added to compensate for this difference in definition:

\[ w_a = -\gamma T_f T_r \cdot \Delta C. \quad (5.5) \]

5.4 Transformation to single-axis motion model

The micromechanical model in physical form as shown in figure 5.1 can be transformed to a model with all the vibration in transverse direction as depicted in figure 5.2(b) by re-formulating the equations of motion using the shear gain \( g \). From [EPL06] however, it appears that in [Nee93] the electrical circuit equivalent to the mass-spring-damper system as depicted in figure 5.2(a) is analyzed, leading to a different expression for the volume velocity over the exerted force. In order to demonstrate the equivalence between the mechanical system depicted in figure 5.2(a) and Neely’s electrical circuit, the equations of motion for both the system with and without the extra mass are derived and compared with the expression for the mobility in [Nee93]. These equations of motion can be found in appendix B, leading to the expressions for the mobility of the cochlear partition in both systems. For the mechanical system shown in figure 5.2(b) the cochlear partition impedance becomes

\[ Z_{cp} = Z_{pass} + \frac{\gamma T_{OHC} T_{shear}}{1 - \gamma T_{OHC} T_{shear}} (Z_{add}) \quad (5.6) \]

with \( Z_{pass} \) is now equal to

\[ Z_{pass} = \frac{K_b}{s} + C_b + s(M_b + M_t) + \frac{gK_c T_{shear}}{s} + gC_c T_{shear} \quad (5.7) \]
Figure 5.2: Comparison of the micromechanical model as shown in figure 5.1 with all motion transferred into equivalent transverse motion (a) with the micromechanical model equivalent to the electrical circuit used in [Nee93](b). The notation $^E$ represents equivalent parameters as results of the transformation.
and \( Z_{add} \) becomes
\[
Z_{add} = sM_t + \frac{gK_c T_{shear}}{s} + gC_c T_{shear}. \tag{5.8}
\]
Combining (B.26), (B.27), (B.28) and (3.3) gives for the cochlear partition mobility
\[
Y_{cp} = \left( \frac{K_b}{s} + C_b + s(M_b + M_t) + sM_t \Upsilon + \frac{gK_c T_{shear}}{s} (1 + \Upsilon) + gC_c T_{shear}(1 + \Upsilon) \right)^{-1}. \tag{5.9}
\]
It can be seen from appendix B that for the system without the inertia loading of the tectorial membrane, which is thought to be equivalent to Neely’s electrical circuit, this expression becomes
\[
Y_{cp,Neely} = \left( \frac{K_b}{s} + C_b + s(M_b) + \frac{gK_c T_{shear}}{s} (1 + \Upsilon) + gC_c T_{shear}(1 + \Upsilon) \right)^{-1} \tag{5.10}
\]
This (5.10) can now be compared with the expression in [Nee93]. It should be noted, however, that a difference in definition of the mobility has to be compensated for, since Neely defines mobility as volume-velocity over force. Figure 5.3 shows that (5.10) for the mobility of cochlear partition gives exactly the same results as \( \frac{Y_{cp,Neely}}{A_p} \) if the transverse inertial force due to the mass of the tectorial membrane is ignored.

### 5.5 Influence of extra mass-inertia

It is interesting to see how including the transverse force influences the mobility of the cochlear partition. Equation (5.9) includes this term and by setting \( \gamma \) either equal to 0 or equal to 1 in (5.9) it is possible to investigate the passive and active response of this system with the inertia term included. For the passive case, the effect of taking this inertia of the tectorial membrane into account can be seen in figure 5.4(a). It is apparent from this figure that the resonance is shifted towards lower frequency if the transverse inertia term of the tectorial membrane is included. In addition, the phase drop appears to increase. The results for a fully active model are illustrated in figure 5.4(b). What is interesting in this figure is that the peak of the mobility curve is decreased in amplitude and shifted towards higher

![Figure 5.3: Cochlear partition mobility in model with active displacement: comparison of expression of Neely for cochlear partition mobility based on his electrical analogy (passive and active) and (5.10)(passive and active) in this report, both at a position \( x = 18.6 \cdot 10^{-3} m \). The curves corresponding to (5.10) are covered by the curves corresponding to the the electrical analogy of Neely.](https://example.com/figure5.3.png)
frequency if the transverse inertia term of the tectorial membrane is taken into account. However, the phase of the active system rapidly increases and no longer shows the same development as in the Neely expression. In fact, the phase rises from 90 degrees to more than 270 degrees before it remains slightly above the 270 degrees. So the conclusion can be drawn that using the parameters of [Nee93] in the correct equations of motion yields a local instable system. It will be demonstrated later in this report that decreasing the active gain restores the local stability of the cochlea. It should be noted that the overall response of the cochlea could, however, still be stable due to the influence of the coupling of these local systems via the cochlear fluids.

Figure 5.4: The effect of including the additional inertia term due to the mass of the TM for a passive system (a) and an active system (b) at a position \(x = 18.6 \cdot 10^{-3}\). Solid lines represent the mobility of the system without the extra inertia of the TM (Neely’s expression), whereas the dashed line stands for the mobility of the system with the transverse inertia of the TM included.

5.6 Implementation in Femlab

Implementing an active displacement in Femlab as shown by \(w_a\) in figure 5.6 turned out to be rather difficult. To connect the reticular lamina and the basilar membrane, an extra beam with stiffness \(k_{add}\) is required in Femlab. A point force equal in magnitude to

\[
f_a = k_{add} \cdot w_a\]

is also added, acting in positive transverse direction at the reticular lamina and in negative transverse direction at the basilar membrane. If the stiffness of the spring \(k_{add}\), which can be seen as the internal stiffness of the organ of Corti, is a few orders of magnitude larger than all the other stiffnesses in the model, this will lead to the desired active relative displacement \(w_a\) of the reticular lamina with respect to the basilar membrane. This method of implementing the active displacement can be motivated by the introductory explanation for this section. Although the principle of the implementation of the active internal displacement in the model with multi-axis motion is similar to the implementation of the active displacement in the model with all motion in one direction, difficulties arise due to the rotational motion involved in the model in physical form. A first requirement for the extra spring \(k_{add}\) is a significant larger axial stiffness than all the other stiffnesses in the model. In addition, a lateral and rotational degree of freedom of the reticular lamina with respect to the basilar membrane should be
Figure 5.5: Comparison of the mechanical equivalent model of Neely’s electrical circuit and the implementation of this model in the Femlab-code.
avoided. In order to retain the geometry and to prevent the length of this extra spring from influencing the transverse displacement of the reticular lamina or the shear gain $g$, the length of this spring should be minimized. It should be noted that the active displacement $w_a$ depends on the transverse displacement of the reticular lamina.

5.7 Femlab Simulation results

Frequency response simulations can be carried out with the micromechanical model with the active displacement implemented. This can be done for every position in the cochlea, here again the position $x = 18.6 \cdot 10^{-3}$m will be used, of which the characteristic frequency is equal to 1 kHz. Section 5.7.1 deals with the results of the model with single-axis motion if loading of the inertia of the tectorial membrane on the lower subsystem is ignored, while section 5.7.2 discusses the results when this loading is taken into account. Finally, section 5.7.3 describes the results of the model with multi-axis motion.

5.7.1 Single-axis motion model without the additional inertia included

Initially, in order to check the Femlab implementation this program has been used to simulate the single-axis motion of the system shown in figure 5.3. Figure 5.7(a) shows the magnitude and phase of the mobility for the passive and the active model depicted in figure 5.2(a). Again, a clear peak in the magnitude is visible at the characteristic frequency for this cochlear site, together with significant phase lead in the frequency range basal to the characteristic frequency. It should be noted that this result obtained using Femlab is the same as those produced from (5.10) and shown in figure 5.3, and to the expression given in [Nee93] based on a equivalent electrical circuit. In addition, figure 5.7(b) shows the response of the tectorial membrane in a passive and active system. The magnitude of the active system also shows the peak at the characteristic frequency, together with significant phase-lead for the phase in this frequency-range. The real and imaginary part of the cochlear partition mobility are depicted in figure 5.8. The real part can be seen to become negative in the frequency range 0, 3 – 1 kHz, while the imaginary part remains positive in this frequency range, leading to a mobility in the upper left half plane. Furthermore, figure 5.9(a) shows the influence of the gain $\gamma$. Changing this gain $\gamma$ represents the consequences of impaired outer hair cells. It is apparent from figure 5.9(a)that reducing this gain gives a less sensitive response of the cochlear partition. In addition, the peak in the magnitude is lowered and shifted towards a lower frequency. These three effects are reported in [PSJ82] based on experimental data.

5.7.2 Single-axis motion model with the additional inertia included

In order to make the model with all motion transformed into transverse motion equivalent the model in physical form, the influence of the loading of the tectorial membrane on the transverse motion of the lower subsystem has to be taken into account. So, adding a point mass equal to $m_t$ at the reticular lamina in the single-axis Femlab model should give the same frequency response as (5.9). In figure 5.9(b), the cochlear partition mobility is plotted for increasing values of $\gamma$, that is $\gamma = 0, \gamma = 0.6, \gamma = 0.8$ and $\gamma = 1$. The curve corresponding to an active model, i.e. $\gamma = 1$, can be seen to be the same as the dashed line in 5.4(b), which was generated using the equations of motion. Figure 5.9(a) shows the effect of increasing the active gain $\gamma$ for the model without the additional inertia term included. The loss of sensitivity as a consequence of impaired outer hair cells is less in this model, if compared with figure 4.9 in section 4.

Interestingly, it appears by comparing figure 5.9(a) with 5.9(b) that implementing this extra mass in the Femlab model has significant consequences. Figure 5.9(b) shows that increasing the gain $\gamma$ from
Figure 5.6: Implementation of the model with an active displacement generated within the organ of Corti with motion in two directions in Femlab. An extra spring with stiffness $k_{add}$ is introduced to generate the active displacement from the active force $f_a$. The length of this spring is minimized in order to avoid influence of this spring on the geometry of the system. $f_a = k_{add} H_c \cdot (w_{RL} - \Delta_{TM})$, $h = 1$, $l = 1$, $l_{add} = 1 \cdot 10^{-2}$. 
Figure 5.7: Active (dashed lines) and passive (solid lines) response of the model with internal active displacement without additional inertia at $x = 18.6 \cdot 10^{-3}$ m for the basilar membrane (a) and the tectorial membrane (b).

Figure 5.8: Real and imaginary part of the cochlear partition mobility in a passive (solid line) and active (dashed line) micromechanical model at $x = 18.6 \cdot 10^{-3}$ m with an internal active displacement.
Figure 5.9: Comparison of the effect of varying the active gain $\gamma$ on the cochlear partition mobility in the single-axis motion systems without (a) and with (b) the additional inertia term at a position $x = 18.6 \cdot 10^{-3} m$. The used values of $\gamma$ are $\gamma = 0$ (solid line), $\gamma = 0.6$ (dash-dotted line), $\gamma = 0.8$ (dotted line) and $\gamma = 1$ (dashed line).

$\gamma = 0.8$ to $\gamma = 1$ does hardly result in a higher magnitude or a sharper response (compare with figure 5.9(a)). The lower part of figure 5.9(b) shows that the phase of the fully active model (dashed line) rapidly rises towards 270 degrees, indicating the local instability of the model. Therefore, the gain will be decreased to $\gamma = 0.8$ to ensure local stability.

5.7.3 Multi-axis motion model

The micromechanical model with an active displacement will now be modeled in physical form as depicted in 5.6. The gain used in the simulation will be reduced from $\gamma = 1$ to $\gamma = 0.6$ to ensure local stability. Initially, the length of the beam with axial stiffness $k_{a,dd}$ is minimized to avoid significant changes to the geometry, which could effect the shear gain and the active displacement. Figure 5.10(a) compares the simulation results for the multi- and single-axis motion model (with additional inertia term) in passive and active form. Figure 5.10(b) shows the active displacement for the multi-axis motion model (dashed line) and the equivalent single-axis motion model (solid line). The two lines cover each other, which proves that the active displacement is implemented correctly in the multi-axis motion model. The animation reveals the cause of the different response, which is that the beam in the active frequency range remains in its rest orientation. Figure 5.11 compares the position of the total model in Femlab for a passive and an active model. The position is shown for a frequency of $f = 1060$ Hz, which is the characteristic frequency of the single-axis motion model. The phase is chosen to be 180, since the extra beam is elongated (instead of compressed) for this phase which improves the visibility. This problem in the geometry of the active model could be overcome by increasing the length of the extra beam and thereby reducing the longitudinal strain component in the beam. The length of the cilia could be adjusted to remain a shear gain equal to 1, however, this will lead to a new geometry and thus to a different active response.

So, another micromechanical model of the cochlea is made in Femlab and used to carry out frequency response functions, having a physically more plausible active mechanism to represent the cochlear amplifier. It is demonstrated that an important inertia term is missing in [Nee93], which could explain some peculiarities in the set of parameters corresponding to this model.
Figure 5.10: Subfigure (a): Comparison between the simulation results of the passive (solid line) and active (dashed line) equivalent single-axis motion model including the extra inertia term (figure 5.2(b)) and the passive (dotted line) and active (dash-dotted line) multi-axis model (figure 5.6) obtained with Femlab with the active gain $\gamma = 0.6$. Both passive responses can be seen to cover each other and the ratio of $l_{add} = 100$.

Subfigure (b): Comparison of the magnitude and phase of the active displacement $w_a$ in the equivalent single-axis motion model including the extra inertia term (solid line) with the magnitude and phase of the active displacement $w_a$ in the multi-axis motion model (dashed line). The active gain $\gamma$ is equal to 0.6, the cochlear site is $18.6 \cdot 10^{-3}$ m and the basilar membrane is exerted with a unit force $F_b$. The curves can be seen to cover each other.

Figure 5.11: Passive (left) and active (right) response of the multi-axis motion system in Femlab for the frequency $f = 1060$ Hz. The lines represent the beams, while the red, blue and green dot denote the basilar membrane, reticular lamina and tectorial membrane respectively. The phase corresponding to this position is 180, which represents one of the two extreme positions.
Chapter 6

New model

Both models discussed so far both have strong and weak points. The merits of both models will be combined here to propose a new model.

To begin with, the model with the somatic motility of the outer hair cells modeled as an active force has an apparently realistic set of physical parameters. The ratio of the masses, defined as

$$i_{\text{masses}} = \frac{M_b}{M_t},$$ (6.1)

is equal to 5. From figure 2.4(a) we can see that this ratio, assuming a density of the same order, seems to be reasonable. In comparing the volumes in figure 2.4(a) for the basilar and tectorial membrane it should be remembered that the point mass $M_b$ also includes the mass of the organ of Corti. In the set of parameters tuned for the model with the internal active displacement taken from [Nee93], however, the mass of the tectorial membrane $M_t$ is higher than the mass of the basilar membrane $M_b$ by about two orders of magnitude at the base and three orders of magnitude at the apex. Obviously, these values for $M_b$ and $M_t$ are not very likely from a physiological point of view, and the set of parameters of the model with the active force as discussed in chapter 4 is preferable. The implementation of the cochlear amplifier as an active force acting on the basilar membrane, however, is questionable from a dynamical point of view. Since no rigid structure is present within the organ of Corti for this force to react off, a force acting within the organ of Corti leading to an active displacement of the reticular lamina seems to be more plausible physically. An attempt will be made here to combine the more likely parameters of the model described in chapter 4 with the more physically plausible active mechanism of the model described in chapter 5, taking into account the forgotten tectorial membrane inertia. The parameters governing the active source in the model of chapter 4, however, cannot be used in this new model due to the different implementation of the activity here. Therefore, the active parameters of [Nee93] are used to simulate the active response of the new micromechanical model.

6.1 Effect of implementing the more likely parameters

To begin with, the response of this new micromechanical model is compared with the micromechanical model with the active displacement including the tectorial membrane inertia in figure 6.1, showing the effect of introducing the passive parameters from [NK86]. Figures 6.1(a) and 6.1(b) compare both passive systems, while figure 6.1(c) and 6.1(d) show the active responses. Introducing the more realistic parameters prevents the active system from getting locally unstable. In addition, the peak in the magnitude curve in figure 6.1(b) is decreased significantly and shifted towards higher frequency, while
the real part of the cochlear partition mobility remains positive for this new system. So, negative damp-
ing is no longer introduced to this new model by the active displacement.

Figure 6.1: Effect on the cochlear partition mobility of using the parameters of [NK86] in the active displacement model of Section 5. The upper two graphs compare the magnitude and phase in the model with an active displacement using the parameters of [Nee93] and the additional inertia included (solid lines) with the model with the same active displacement but using the parameters of [NK86] (dashed lines). The lower two graphs compare the real and imaginary part of the mobility for the same two models. In addition, the figures at the left hand side and the right hand side cover the passive and the active responses respectively.

Clearly, the parameters of this new model have to be adjusted to make the model active before the resonance. It is, however, rather complicated to tune this system with 12 parameters. Therefore, as much as possible parameters will remain their original values here. Since the influence of the parameters of the upper subsystem on the mobility of the cochlear partition appears to be relatively small, the damping of the basilar membrane will be tuned here make this new system active before the characteristic frequency.
6.2 Tuning the damping of the basilar membrane

The left and right hand side of figure 6.2 show the effect of decreasing the basilar membrane damping on the passive and active response respectively. It is visible that the new model becomes active if the damping-parameter per area of the basilar membrane is decreased from $5.6 \times 10^2 \text{[Nsm}^{-3}\text{]}$ (dashed line) to $1.7 \times 10^2 \text{[Nsm}^{-3}\text{]}$ at $x = 18.6 \times 10^{-3} \text{m}$. The most striking features to emerge from the figures are in the first place a clearly visible negative real part combined with a positive imaginary part in the model with the basilar membrane damping tuned (solid line) in the the frequency-range basal to the characteristic frequency, which gives negative damping. Secondly, it is apparent from the phase of the new tuned model (solid line) in subfigure (b) that this new model becomes locally unstable if the basilar membrane damping is decreased. Although most humans cochlea’s are unstable, a locally stable cochlear model is desired. Therefore, a following logical step is to adjust the parameters governing the active component in this new model to ensure local stability.

Figure 6.2: Comparison between the passive (left) and active (right) response of the new model without the damping of the basilar membrane decreased (dashed lines, same as the dashed lines in figure 6.1) and the new model with the basilar membrane damping reduced from $5.6 \times 10^2$ to $1.7 \times 10^2 \text{[Nsm}^{-3}\text{]}$ (solid lines).
6.3 Adjusting the active parameters of the new model

The relation between the amount of contraction of the outer hair cell and the deflection of the cilia was defined in section 5.3 as

\[ T_{OHC} = -\gamma T_f T_r \]  

(6.2)

with \( \gamma \) a multiplier representing the activity of the model, and \( T_f \) and \( T_r \) representing two separate transducer functions. A stable system for the whole range of \( 0 < \gamma < 1 \) is preferable, so one of the two transducer functions will be adjusted here to ensure local stability. Both transducer functions are, as said in section 5.3 modeled as first-order low-pass filters representing the mechanoelectric \( (T_f) \) and electromechanic \( (T_g) \) transduction in the outer hair cells.

Figure 6.3 shows the new model if \( g_f \) is set to \( 1.79 \cdot 10^3 \) at \( x = 18.6 \cdot 10^{-3} \) in the mechanoelectric transduction for the passive (solid line) and the active case (dashed line). It can be seen that the system remains stable and still has negative real part in the frequency range basal to the characteristic frequency combined with positive imaginary part. So, negative damping is introduced in this new model in the frequency range basal to the characteristic frequency resulting in the sharp response observed in live cochlea, as can be seen in subfigure (a). The agreement with the frequency-place map can be restored by a relatively simple change in the ratio of the stiffness over the mass distribution along the cochlea.

Figure 6.3: Magnitude and phase (a) and real and imaginary part (b) of the passive (solid lines) and active (dashed lines) cochlear partition mobility in the new micromechanical model proposed in this section.

The response of the cochlear mobility in this new micromechanical model is similar to the response of the models proposed in [NK86] and [Nee93], that is to say a phase lead and sharp response for a fully active model and a more flat response combined with a slightly higher resonance frequency for a passive model. This new model combines the correct dynamic interpretation of the multi-axis motion model [EPLo6] with the physically more plausible active mechanism [Nee93] and the most likely available set of parameters for the mechanical properties of the components of the organ of Corti [NK86].
Chapter 7

Conclusions and Recommendations

The micromechanics of the cochlea are analyzed, in which an active process known as the cochlear amplifier enhances the motion of the cochlear partition around the characteristic position. Two micromechanical models of the cochlea are made in Femlab, using beam elements to model linear springs and viscous dampers. These micromechanical models are two-degree-of-freedom systems which describe the relative motion of the structures within the organ of Corti. The electromobility of the outer hair cells is modeled here as an active force acting at the basilar membrane or as an active internal displacement within the organ of Corti respectively. These active elements are modeled as feedback loops in Femlab, resulting in a system close to instability.

Frequency response simulations are carried out to provide insight into the dynamics. The characteristic cochlear partition mobility is obtained: a sharp response of the magnitude at and phase-lead before the characteristic frequency, caused by negative damping introduced in the active frequency range. The active gain $\gamma$ was used to simulate impaired outer hair cells: reducing the active gain resulted in a significant loss in sensitivity. In addition, it was demonstrated that an incorrect interpretation of the model with multi-axis motion is used in [Nee93], since the transverse loading of the tectorial membrane is ignored here. Interestingly, the correct interpretation was seen to be unstable for $\gamma = 1$.

A new model was proposed in section 6, combining the merits of both models considered so far. Since it is hard to visualize where an active force acting at the basilar membrane would react off, the active mechanism of an internal active displacement within the organ of Corti is preferable. In addition, the ratio of the masses of both membranes shows that the set of parameters in [NK86] is more likely from a physical point of view. Therefore, this new micromechanical model combines the correct dynamic interpretation of the micromechanical model with an internal active displacement with the most likely available set of passive parameters. It is shown that with only a minor redefinition of two parameters a response similar to the response of previous models can be obtained.

Interesting future work includes the development of more complete micromechanical models, for instance a model which allows independent transverse motion of the tectorial membrane together with shearing with respect to the reticular lamina. Unfortunately, a number of new parameters are required for such a three degree of freedom model. Therefore, very reliable and accurate measurements are needed of the mechanic properties of the components of the organ of Corti at several places along the cochlea. In addition, it would be interesting to analyze the coupled response of the whole cochlea by implementing the effect of the cochlear fluids, while using a three degree of freedom micromechanical model. This will lead to a better understanding of the dynamics of the organ of Corti and thus to more insight into the complex functioning of the cochlea.
Appendix A

Modeling lumped parameter models in Femlab

The micromechanics of the cochlea has been modeled using Comsol Multiphysics, until recently known as Femlab. To avoid confusion, the term Femlab is used to refer to the package throughout this report. Femlab is an Finite Element Modeling package consisting of several modules, each module suited for a specific area of physics. The structural mechanics module will be used for this application. This module is specialized in the analysis of components and subsystems where it is necessary to evaluate structural deformations. It contains special application modes for the modeling of shells, plates and beams. This latter beam mode will be used to create the two-dimensional models of the cochlea. This chapter describes how to use this beam application mode in Femlab to create all the components of the lumped parameters models representing the cochlea: point masses, massless linear springs and massless viscous dampers.

This beam mode assumes plane stress and uses the well-known Euler Bernoulli beam theory for bending. In addition, the rod theory is adopted for axial loading of the element. These two cases of either pure axial deformation or bending of elements will be described in more detail in section section A.1.1 and A.1.2 respectively, resulting in the required axial and lateral stiffness-matrices of a beam for certain boundary conditions. The complete stiffness matrix for elements under axial as well as transverse loading can be found in A.1.3.

An important advantage of using the beam mode over any other application mode in Femlab is the availability of point masses. Moreover, also point mass moments of inertia can be used in this application mode. Viscous dampers are also required to be able to simulate the dynamic behaviour of the cochlea. Therefore, section A.2 deals with modeling a massless viscous damper in the beam application mode.

Femlab offers two opportunities to create models: either via the standalone graphical user interface or using the Femlab script programming within the Matlab language. In practice, a combination of both methods will be used in the modeling process. Section A.3 gives some tips concerning the graphical user-interface in Femlab, while appendix C is an m-file of the multi-axis motion model with an active force which carries out a frequency sweep using the Matlab language.
A.1 Elements under loading

A.1.1 Axial loading of elements

If an one sided pinned element is loaded by an axial force, the stiffness of the element will be equal to the stiffness of an uniform rod, namely

$$k = \frac{E \cdot A}{l}$$  \hspace{1cm} (A.1)

where $E$ is the Young’s modulus, $A$ is the surface of the cross-section and $l$ is the length of the element.

Figure A.1 shows an axial element with axial displacements $u_1$ and $u_2$ and forces $F_1$ and $F_2$ at its endpoints, all in the positive sense.

By assuming that the displacements in this figure A.1 are alternatively equal to zero, so assuming that the beam is fixed at one of both sides, the whole stiffness matrix can easily be determined. Using this stiffness matrix, the relationship between the forces and the displacements of the nodes of this element can be expressed as

$$\begin{pmatrix} F_1 \\ F_2 \end{pmatrix} = \frac{E \cdot A}{l} \begin{pmatrix} 1 & -1 \\ -1 & 1 \end{pmatrix} \begin{pmatrix} u_1 \\ u_2 \end{pmatrix},$$  \hspace{1cm} (A.2)

regardless of the orientation of the element.

A.1.2 Transverse loading of elements: bending

A beam is a slender structure, which mechanics are assumed to be fully described by the properties area, moments of inertia and density of the cross section. The elementary or classical beam theory assumes that the transverse shear strains are negligible and plane cross-sections before bending remain plane and normal to the axis of the beam after bending. The assumption of neglecting shear strains is valid if the thickness $h$ is small relative to the length of the beam [JA04]. In general, the relative axial displacement $u_2 - u_1$ will be small compared to the lateral displacement $v$ of the beam and can be assumed to be zero [Tho88]. Thus, the degrees of freedom of a beam element are the lateral displacements and rotations at the two ends as indicated in figure A.2.

These assumptions lead after a short derivation to the so-called deflection equation of a beam [Ast92]

$$\frac{d^2 v}{dx^2} = -\frac{M(x)}{EI}$$  \hspace{1cm} (A.3)

where $v$, $x$, $M$, $E$, and $I$ are the lateral deflection, longitudinal coordinate, moment, Young’s modulus
and area moment of inertia respectively. Please note that both the Young’s modulus and the area moment of inertia are assumed to be independent of the longitudinal coordinate \( x \) here.

Integrating \( A.3 \) for a given moment distribution \( M(x) \) and taking into account the boundary conditions at the end points of the beam yield the lateral deflection as a function of \( x \). Several examples of this procedure can be found in textbooks as [PBA96] and [Bic94].

If the ends of an element are rigidly connected to the adjoining structure, the element will act like a beam with moments and lateral forces applied at the joints. Solving this general case using \( A.3 \) leads to the stiffness matrix relating the lateral forces and moments at the joints to the displacements and rotations.

\[
\begin{bmatrix}
F_{1x} \\
F_{1y} \\
M_1 \\
F_{2x} \\
F_{2y} \\
M_2
\end{bmatrix} = \frac{E \cdot I}{l^3} \begin{bmatrix}
12 & 6l & -12 & 6l & 0 & 0 \\
6l & 4l^2 & -6l & 2l^2 & 0 & 0 \\
-12 & -6l & 12 & -6l & 0 & 0 \\
6l & 2l^2 & -6l & 4l^2 & 0 & 0 \\
-12 & -6l & 12 & -6l & 0 & 0 \\
6l & 2l^2 & -6l & 4l^2 & 0 & 0
\end{bmatrix}
\begin{bmatrix}
v_1 \\
v_2 \\
\theta_1 \\
\theta_2
\end{bmatrix},
\]

(A.4)

### A.1.3 Modeling springs using Femlab-elements

The total stiffness matrix for a Femlab element rigidly connected to the adjoining structure can be obtained by simply adding up the axial components of the stiffness matrix in (A.2) by the stiffness matrix for bending in (A.4). This total 6 by 6 stiffness matrix for a beam rigidly connected at both sides to the adjoining structure can be written as

\[
\begin{bmatrix}
F_{1x} \\
F_{1y} \\
M_1 \\
F_{2x} \\
F_{2y} \\
M_2
\end{bmatrix} = \frac{E \cdot I}{l^3} \begin{bmatrix}
Q & 0 & 0 & -Q & 0 & 0 \\
0 & 12 & 6l & 0 & -12 & 6l \\
0 & 6l & 4l^2 & 0 & -6l & 2l^2 \\
0 & -12 & -6l & 0 & 12 & -6l \\
0 & 6l & 2l^2 & 0 & -6l & 4l^2
\end{bmatrix}
\begin{bmatrix}
u_1 \\
v_2 \\
\theta_1 \\
\theta_2
\end{bmatrix},
\]

(A.5)

where \( Q \) is equal to

\[
Q = \left( \frac{EA}{L} \right) \left( \frac{l^3}{EI} \right) = \frac{Al^2}{l}
\]

(A.6)

Now that the stiffness of the elements under all types of loading is known, important conclusions can be drawn on how to make the dynamic behaviour of the beams in Femlab equivalent to the springs in the lumped parameter models of the cochlea. A close look at the total stiffness-matrix in (A.5) shows that four parameters of the beam determine its stiffness: the Young’s modulus \( E \), the area of the cross-section \( A \), the length \( l \) and the area moment of inertia of the cross-section \( I \). The area moment of inertia, however, is a function of the dimensions of the cross-section, what would reduce the number
of independent parameters from four to three since the area of the cross-section is also directly related to the dimensions of the cross-section. Nevertheless, in Femlab the area of the cross-section $A$ and the area moment of inertia of the cross-section $I$ can be implemented independently, what keeps the number of adjustable parameters equal to four in Femlab. Since the axial stiffness in matrix A.5 does not depend on the area moment of inertia $I$, and on the other hand the transverse stiffness in this same matrix A.5 does not depend on the area of the cross-section, tuning $A$ and $I$ is an easy way to tune the axial and transverse stiffness of a beam independently in Femlab. Consequently, the stiffness matrix of a Femlab-element can be made equivalent to the stiffness matrix of two springs positioned perpendicular to each other in a lumped parameter model.

### A.2 Damping

Viscous damping is modeled in the structural mechanics module using Rayleigh damping [mul04]. In Rayleigh damping the damping is assumed to be proportional to a linear combination of the stiffness- and the mass-matrix. So, if the damping-matrix, mass-matrix and stiffness-matrix are equal to $C$, $M$, and $K$ respectively, then the damping-matrix $C$ can be expressed as:

$$ C = \alpha \cdot M + \beta \cdot K $$

where $\alpha$ and $\beta$ are the mass and stiffness damping parameter respectively.

The lumped parameter models of the cochlea, however, consist of massless springs, massless dampers and point masses. So, the mass-matrix of the beam elements $M$ will be made equal to zero and (A.7) is simplified to become

$$ C = \beta \cdot K $$

In other words, the damping properties of the used element in Femlab can be made equal to those of a viscous damper by tuning the stiffness damping parameter according to (A.8).

### A.3 Tips and tricks in Femlab

Although the Femlab-documentations on the whole is very extensive, the chapters regarding the two-dimensional beam application mode are quite concise. Therefore, some points regarding this particular application of Femlab are worth mentioning for the interest of future use. The following remarks concern the experience of the present author with Femlab 3.0.0.181 in combination with Matlab 6.5 R13.

- A feedback loop can be modeled in Femlab by using the beam application mode variables as given at page 263 and onwards in [mul04]. However, these variables are initially only available at the considered point in the model and have to be available at the point in the model where the feedback-loop is acting. This can be achieved in this manner if using the graphical user-interface: Options $\rightarrow$ Integration Coupling Variables $\rightarrow$ Point Variables. Select the point which is the source of the variable and type a name in the left column, then enter the correct expression for the variable using page 263 from [mul04] and make sure that global destination is selected. The variable can now be entered using the chosen name in any expression involving constraints and loads at any point in the model. It should be noted that no warning message is shown before running a simulation if the expression field is left empty.
• The expressions for the used parameters can be defined in the field
  Options → Constants
  Although not explicitly written in [mul04], attention has to be paid to the naming of the ex-
  pressions. Using a name that is also used by Femlab itself in the solving procedure results in a
  misleading and useless visualization without any warning. Generally speaking, names consisting
  of only one letter from the alphabet should be avoided.

• The definition Femlab uses for computation of the variables at page 263 of [mul04] can be seen
  for each point separately and, if required, adjusted via
  Physics → Equation System → Point Settings
Appendix B

Equations of motion model with active displacement

In this appendix the equations of motions are derived for both mechanical systems depicted in figure 5.2, resulting in two expressions in which the parameters of [Nee93] can be implemented to compare the two systems in figure 5.2 with the expression of Neely in [Nee93]. The following analysis of the equations of motion of the model of figure 5.1 is analogous to the analysis in [EPL06].

The equation of motion for the basilar membrane in figure 5.1 is in the frequency domain

\[ f_b = K_b w_{BM} + sC_b w_{BM} + s^2 M_b w_{BM} + s^2 M_t (w_{BM} + w_a) + f_{CT} \]  

(B.1)

where \( f_{CT} \) is equal to

\[ f_{CT} = gK_c \Delta C + sgC_c \Delta C \]  

(B.2)

The definition of \( \Delta C \) in (B.2) includes the active displacement:

\[ \Delta C = T_{shear} (w_{BM} + w_a) \]  

(B.3)

with \( w_a \) representing the active displacement. Substituting (B.3) in (B.2) gives

\[ f_{CT} = gK_c T_{shear} (w_{BM} + w_a) + sgC_c T_{shear} (w_{BM} + w_a) \]  

(B.4)

The relation between \( w_a \) and \( w_{BM} \) is given for a system without damping in (5.11) of [EPL06] and can be derived using the assumption that the active displacement of the reticular lamina is proportional to the shear displacement of the cilia, via the frequency-dependent response \( T_{OHC} \) and the the gain \( \gamma \), so

\[ w_a = \gamma T_{OHC} \Delta C \]  

(B.5)
Substituting (B.3) in (B.6) yields

\[ w_a = \gamma_{OHC} T_{shear}(w_{BM} + w_a) \]  \hspace{1cm} \text{(B.6)}

or

\[ w_a = \left[ \frac{\gamma_{OHC} T_{shear}}{1 - \gamma_{OHC} T_{shear}} \right] w_{BM} \]  \hspace{1cm} \text{(B.7)}

Introducing a new dimensionless variable \( \Upsilon \) as

\[ \Upsilon = \left[ \frac{\gamma_{OHC} T_{shear}}{1 - \gamma_{OHC} T_{shear}} \right] \]  \hspace{1cm} \text{(B.8)}

simplifies (B.7) to

\[ w_a = \Upsilon w_{BM} \]  \hspace{1cm} \text{(B.9)}

By substituting (B.4) and (B.9) in (B.1), the motion of the basilar membrane can be rewritten as

\[ f_b = \left[ K_b + sC_b + s^2(M_b + M_t) + s^2 M_t \Upsilon + gK_c T_{shear}(1 + \Upsilon) + g s C_c T_{shear}(1 + \Upsilon) \right] \cdot w_{BM} \]  \hspace{1cm} \text{(B.10)}

In order to plot the mobility of the basilar membrane based on (B.10) and the parameters in the Neely paper, expressions for \( T_{ohc} \) as well as \( T_{shear} \) are required. To begin with, \( T_{OHC} \) is a frequency dependent function relating the active displacement \( w_a \) to the shear displacement of the cilia \( \Delta C \). This shear gain is defined by equation (22) in the paper of Neely [Nee93]

\[ H_C = \gamma T_f T_r \]  \hspace{1cm} \text{(B.11)}

However, Neely defines \( H_C \) as the relation between the lateral deflection of the hair bundle and the amount of contraction of the outer hair cell, while here the outer hair cell gain \( T_{OHC} \) is defined as the relation between the lateral deflection of the hair bundle and the elongation of the outer hair cell. So, a minus sign has to be added to compensate for this difference in definition, making the outer hair cell gain \( T_{ohc} \) equal to

\[ T_{OHC} = -\gamma T_f T_r \]  \hspace{1cm} \text{(B.12)}

with \( \gamma \) representing the activity of the model, i.e. \( \gamma = 0 \) denotes a fully passive model and \( \gamma = 1 \) implies a fully active model. Moreover, \( T_f \) and \( T_r \) are defined in equation (20) and (21) of his paper as the following first-order low-pass filters

\[ T_f = \frac{g_f}{1 + i\omega T_f} \]  \hspace{1cm} \text{(B.13)}

and
respectively.

An expression for $T_{shear}$ is derived in [EPL06], ((3.9)), relating the relative shear motion experience by the cilia $\Delta C$ to the transverse displacement of the basilar membrane $w_{BM}$ for an undamped system. The derivation of this expression will be repeated here leading to a slightly extended expression here to include the damping present in the system.

The transverse motion of the basilar membrane and the tectorial membrane to an external force $f_b$ is described by

$$f_b = K_b w_{BM} + sC_b w_{BM} + s^2(M_b + M_t)(w_{BM}) + f_{CT}$$

(B.15)

The transverse and radial force relation is

$$f_{CT} = g f_{CR}$$

(B.16)

where $g$ is the lever gain.

The equation of motion for the radial motion of the tectorial membrane in figure 5.1 due to the force $f_{CR}$ is

$$f_{CR} = K_c \Delta_{TM} + sC_c \Delta_{TM} + s^2 M_t \Delta_{TM}$$

(B.17)

while $f_{CR}$ is also equal to

$$f_{CR} = K_c (\Delta_{BM} - \Delta_{TM}) + sC_c (\Delta_{BM} - \Delta_{TM})$$

(B.18)

Equating B.17 and B.18 gives

$$\Delta_{TM} = \frac{K_c + sC_c}{K_t + sC_t + s^2 M_t + K_c + sC_c}$$

(B.19)

With the relative shear motion experienced by the cilia for the passive case defined as

$$\Delta C = \Delta_{BM} - \Delta_{TM}$$

(B.20)

and the shear displacement of the basilar membrane equal to

$$\Delta_{BM} = gw_{BM}$$

(B.21)

(B.19) can be written in the form of

$$T_{shear} = \frac{\Delta C}{w_{BM}}$$

(B.22)

as

$$T_{shear} = g \frac{K_t + sC_t + s^2 M_t}{K_t + sC_t + s^2 M_t + K_c + sC_c}$$

(B.23)
When the impedance of the cochlear partition is defined as
\[ Z_{cp} = \frac{f_b}{sw_{BM}}, \]  
(B.24)
this impedance can be expressed, using (B.10) as
\[ Z_{cp} = K_b s + C_b + s(M_b + M_t) + sM_t \Upsilon + \frac{gK_c T_{shear}}{s}(1 + \Upsilon) + gC_c T_{shear}(1 + \Upsilon) \]  
(B.25)
where \( \Upsilon \) is given by (B.8), \( T_{shear} \) by B.23 and \( T_{OHC} \) by B.12. This expression can be rewritten to facilitate comparison with (5.16) of [EPLo6]:
\[ Z_{cp} = Z_{pass} + \frac{\gamma T_{OHC} T_{shear}}{1 - \gamma T_{OHC} T_{shear}} (Z_{add}) \]  
(B.26)
with \( Z_{pass} \) is now equal to
\[ Z_{pass} = K_b s + C_b + s(M_b + M_t) + \frac{gK_c T_{shear}}{s} + gC_c T_{shear} \]  
(B.27)
and \( Z_{add} \) becomes
\[ Z_{add} = sM_t + \frac{gK_c T_{shear}}{s} + gC_c T_{shear} \]  
(B.28)
All the parameters in (B.26) are given in [Nee93] and can be found in table 5.1.

Interestingly, it appears that Neely ignores the term \( s^2 M_t (w_{BM} + wa) \) in the equation of motion of the basilar membrane. If this transverse inertial force due to the mass of the tectorial membrane is ignored in B.1, the expression for the impedance of the basilar membrane becomes
\[ Z_{Neely cp} = K_b s + C_b + s(M_b + M_t) + \frac{gK_c T_{shear}}{s}(1 + \Upsilon) + gC_c T_{shear}(1 + \Upsilon) \]  
(B.29)

This impedance of the system without the inertial force due to the mass of the tectorial membrane included can also be rewritten in the form of (B.26) as
\[ Z_{Neely cp} = Z_{pass} + \frac{\gamma T_{OHC} T_{shear}}{1 - \gamma T_{OHC} T_{shear}} (Z_{add}) \]  
(B.30)
with \( Z_{pass} \) is now equal to
\[ Z_{Neely pass} = K_b s + C_b + sM_b + \frac{gK_c T_{shear}}{s} + gC_c T_{shear} \]  
(B.31)
and \( Z_{add} \) becomes
\[ Z_{Neely add} = \frac{gK_c T_{shear}}{s} + gC_c T_{shear} \]  
(B.32)
The point-mobility of the cochlear partition is given by

\[ Y_{CP} = Z_{CP}^{-1}, \]  

(B.33)

so substituting (B.25) in (B.33) leads to

\[ Y_{cp} = \left( \frac{K_b}{s} + C_b + s(M_b + M_t) + sM_t \Upsilon + \frac{gK_c T_{\text{shear}}}{s} (1 + \Upsilon) + gC_c T_{\text{shear}} (1 + \Upsilon) \right)^{-1} \]  

(B.34)

Similarly, the mobility of the cochlear partition can be determined for the system with the transverse inertial force due to the mass of the tectorial membrane ignored by substituting (B.29) in (B.33). Doing so gives

\[ Y_{\text{Neely}}_{cp} = \left( \frac{K_b}{s} + C_b + s(M_b) + \frac{gK_c T_{\text{shear}}}{s} (1 + \Upsilon) + gC_c T_{\text{shear}} (1 + \Upsilon) \right)^{-1} \]  

(B.35)
Appendix C

M-file of Micromechanical model with multi-axis motion

% M-file of multi-axis motion model with somatic motility modeled as an active force.
% Created by Ruud van Doorn, 11-06
% Compatible with Matlab 6.5 R13

% This file carries out a frequency sweep from 0-25.000 Hz, resulting position is shown afterwards for characteristic frequency = 1 kHz
% Parameters from Neely and Kim, corrected for typo’s and converted to SI units.
% Cochlear Site $x=18.646 \times 10^{-3}$ m.

% Results are stored in structure fem.sol for every frequency

f1clear fem
% Define the geometry

carr={curve2([5,5],[0,1],[1,1])};
g2=geomcoerce('curve',carr);
carr={curve2([5,4],[1,1],[1,1])};
g3=geomcoerce('curve',carr);
carr={curve2([5,5],[1,2],[1,1])};
g4=geomcoerce('curve',carr);
carr={curve2([5,4],[2,2],[1,1])};
g5=geomcoerce('curve',carr);
clear c
c.objs={g2,g3,g4,g5};
c.name={'B1','B2','B3','B4'};
c.tags={'g2','g3','g4','g5'};

fem.draw=struct('c',c);
fem.geom=geomcsg(fem);

% Define constants in the model
fem.const = {'Mt','0.005','r','18.646e-3','Kbeq','g^-2*1.1e10*exp(-400*r)',
'Kt','7e7*exp(-440*r)','Kc','1e8*exp(-400*r)',
'Kactive','6.15e9*exp(-400*r)','Cb','200+15000*exp(-200*r)',
'Ct','100*exp(-220*r)','Cc','20*exp(-80*r)',
'rho','1e-9','Ab','1','At','1','Ac','1','Lb','1','Lc','1','Lt','1',
'Eb','(Lb*Kbeq)/(Ab)','Et','(Lt*Kt)/(At)','Ec','(Lc*Kc)/(Ac)',
'beta_b','Cb/Kbeq','beta_t','Ct/Kt','beta_c','Cc/Kc','Fb','1',
'Ibar','1e0*(20/56)',
'Ec','1e14','Icc','(Lc^3*Ec)/(12*Ecc)',
'Mb_Mteq','0.03','Mb_Mteq*g^-2-Mt','g','1'};

% Initialize mesh
fem.mesh=meshinit(fem);

% Application mode 1
clear appl
appl.mode.class = 'SmeInPlaneEulerBeam';

%Defining the element-type
appl.assignsuffix = '_eulip';
clear prop
prop.analysis='freq';

% Defining the kind of analysis
appl.prop = prop;
clear pnt
pnt.m = {0,0,'Mt','Mb'};

%Defining the properties for various points: mass
pnt.Fy = {0,0,0,'Fb+Kactive*(v+u_tm)+Cactive*(v_t+ut_tm)'};

%Defining the properties for various points: forces
pnt.Hx = {1,0,0,0};
pnt.Ry = {0,0,'v_bm','v_tm'};
pnt.Hy = 1;
pnt.ind = [1,1,2,4,3];
appl.pnt = pnt;
clear bnd
bnd.E = {'Ecc','Eb','Et','Ebar'};

%Defining the properties for various boundaries: Youngs modulus E
bnd.rho = 'rho';
bnd.alphadM = 0;
bnd.betadK = {'beta_c','beta_b','beta_t',0};

%Defining the properties for various boundaries: damping
bnd.alpha = 0;
bnd.A = {'Ac','Ab','At','Abar'};
bnd.Iyy = {'Icc','Ib','It','Ibar'};
% Defining the properties for various boundaries: I
bnd.heightz = 0;
bnd.ind = [4,3,2,1];
appl.bnd = bnd;
appl.var = {'freq','1'};
fem.appl{1} = appl;

% Feedback loop requires the global availability of point-properties!!
clear elem
elem{1} = struct('elem',{'elcplscalar'},'var',{{'ut_bm','u_bm','v_bm','vt_bm','ut_tm','v_tm','vt_tm'}},'g',{{'1'}},'src',{ {struct('expr',{{'u_t',{}},'u',{}},'v',{}},'v_t',{}},'u',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}},'v_t',{}},'u',{}},'v',{}},'u_t',{}],'ind',{{{'1','2','3'},{'4'},{'5'}}}),{},{}}},'geomdim',{{}}},'global',{{'1','2','3','4','5','6','7','8'}});
fem.elemcpl = elem;

% Multiphysics
fem=multiphysics(fem);

% Extend mesh
fem=xmesh=meshextend(fem);

% Solving the problem: choosing the kind of solver and variables of the
% solution, defining the desired frequency range
fem.sol=femlin(fem,'solcomp',{'u','th','v'},...
   'outcomp',{'u','th','v'},...
   'pname','freq_eulip','plist',[0:20:2.5e4],...
   'nonlin','off');

% Save current fem structure
fem0=fem;

% Plotting solution for the characteristic frequency = element 51 of frequency range!
postplot(fem,'lindata','disp_eulip','linmap','jet(1024)',...
   'deformbnd',{'u','v'},'solnum',...
   51,'cont','internal','refine',...
   0,'geom','off');
Appendix D

Relative shear and transverse tectorial membrane motion

In [AGZ96], the acoustically induced tectorial membrane motion is measured in two orthogonal directions. This data is used here to determine the relative shear and transverse tectorial membrane motion $\Delta_{TM}$. Equilibrium of forces in the upper subsystem gives

$$gK_{C}w_{TM} = (K_{T} + K_{C} - (\omega)^2 \cdot M_{T}) \cdot \Delta_{TM}$$  \hspace{1cm} (D.1)

So the relation between the shear and transverse motion of the tectorial membrane is

$$\frac{\Delta_{TM}}{\omega_{TM}} = \frac{gK_{C}}{K_{T} + K_{C} - \omega^2 \cdot M_{T}}$$  \hspace{1cm} (D.2)

The experimental data has to be replotted in the transverse and the shear direction using figure 3 in [AGZ96], given that the spatial angle of 150° is approximately parallel to the reticular lamina in the conducted measurements. This procedure eventually leads to the transfer function between the transverse and shear motion depicted in figure D.2.
Figure D.1: The set-up used in [AGZ96] to carry out the measurements (left) and the magnitude and phase of the orthogonal components of acoustical induced tectorial membrane motion. (right)
Figure D.2: Resulting relation between the shear and transverse motion of the tectorial membrane after the data is replotted for the correct directions.
Appendix E

Femlab-visualization

Figure E.1 shows the motion of the micromechanical model of chapter 4 as calculated with Femlab at its characteristic frequency. The cochlear site is $x = 18, 6 \cdot 10^{-3}$ m. $M_b$ and $M_t$ represent the point mass of the basilar membrane with the organ of Corti resting on top and the tectorial membrane respectively. The two extreme positions and the rest position are shown, represented by the indices 1, 2 and 3. The colors indicate the absolute displacement, defined as $\sqrt{u^2 + v^2}$, which is scaled with a factor $1 \cdot 10^5$. 
Figure E.1: Frequency response of model with motion in two directions if exerted by a unit force with frequency of 1 kHz.
Bibliography


