Doctoral Thesis

Fluid flow in the cochlea
numerical investigation of steady streaming and rocking stapes motions

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FLUID FLOW IN THE COCHLEA: NUMERICAL INVESTIGATION OF STEADY STREAMING AND ROCKING STAPES MOTIONS

A dissertation submitted to

ETH ZURICH

for the degree of

Doctor of Sciences

presented by

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2013
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Abstract

The cochlea is part of the inner ear and of the human hearing organ. The sense of hearing is of great importance for humans because it affects communication, independence, safety and well-being.

The present work investigates the processes in the cochlea from a fluid-dynamical point of view. The movements of the fluid and the basilar membrane are studied by means of numerical simulations using a two-dimensional box model of the passive cochlea. The fluid flow is described by the Navier-Stokes equations and the motion of the basilar membrane by elastic oscillators. The fluid-structure interaction is modelled with the immersed boundary method. The resulting cochlea model reproduces the characteristic properties of cochlear mechanics.

The investigation focusses on two phenomena, the steady streaming and the rocking stapes motions.

The term steady streaming denotes a mean fluid motion which is induced by non-linear effects of an oscillating primary flow. The present investigation shows that steady streaming in the cochlea exists and that its velocities amount to up to several millimetres per second for loud acoustic stimulation. The work shows Eulerian and Lagrangian mean flow fields as well as the Stokes drift. In a comparison between simulation results and Lighthill’s analytical solutions (J. Lighthill, Acoustic streaming in the ear itself, J. Fluid Mech., 1992) good agreement is observed. Further, the processes which generate the steady streaming in the cochlea are investigated. Not only the Reynolds stresses of the fluid flow but also the oscillations of the basilar membrane induce the mean flow. This second source of steady streaming has not been considered by Lighthill. Next it is shown that non-linear effects are present also in the axial component of the basilar membrane motion. Further the dependence of the steady streaming velocity on the frequency and intensity of the stimulation is studied. It is found that medium to low frequencies below 1000 Hz lead to larger streaming velocities than high frequencies.

Concerning the implications of steady streaming for the hearing essentially two possible consequences result. The mean flow might influence the generation of neural signals in a direct way by bending the hair cell stereocilia as it has been pointed out by Lighthill. In addition the steady streaming might influence the neural signals in an indirect way by intensifying the transport of ions which are necessary for the hearing.

The second aspect which is studied in the present work regards the rocking stapes motions, i.e., rotational movements of the stapes. This
middle ear ossicle transduces the sound signal to the fluid in the cochlea. The investigation shows that the rotational component of the stapes motion induces movements of the fluid and of the basilar membrane but to a lesser extent than the traditionally considered translational or piston-like motion component. The differences in the membrane response to both components are investigated in detail. The study shows that a tone which is transmitted to the cochlea only by the rotational stapes motion is perceived as softer by at least 20 dB compared to a tone which stimulates the cochlea by the translational component. Further the translational stapes motion proves to evoke the oscillations of the basilar membrane by a different mechanism than the rotational component.

In a healthy cochlea the basilar membrane oscillation due to rocking stapes motions has nearly no influence on the hearing because the oscillations due to the translational stimulation dominate. In pathological situations which prevent the piston-like stapes motion (e.g. for round window atresia, the ossification of the round window), in contrast, the rocking stapes motion can lead to hearing. Thereby the present work explains results of clinical and experimental studies.
Kurzfassung


Im Vordergrund der Untersuchung stehen zwei Phänomene: das so genannte Steady Streaming und die Anregung durch „Rocking Stapes Motions“.


Hinsichtlich der Auswirkungen des Steady Streaming auf das Hören ergeben sich im Wesentlichen zwei mögliche Folgen. Die stetige Fluidströmung kann über eine Auslenkung der Sterezilien der Haarsinnes-
zellen die Erzeugung von Nervensignalen direkt beeinflussen, wie bereits Lighthill ausführt. Ferner kann die stetige Strömung die Nervensignale indirekt beeinflussen indem sie den Transport von Ionen intensiviert, die für den Hörprozess notwendig sind.


In einer gesunden Cochlea haben die Membranbewegungen infolge der rotatorischen Stimulation fast keinen Effekt auf das Hören, da die Schwingungen infolge der translatorischen Anregung überwiegen. In pathologischen Situationen hingegen, in denen die kolbenähnliche Bewegung nicht möglich ist (z.B. bei Verknöcherung des runden Fensters, „Round Window Atresia“), kann die Rocking-Stapes-Bewegung zum Hören führen. Damit erklärt die vorliegende Untersuchung Resultate klinischer und experimenteller Studien.
Acknowledgements

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Finally I would like to address some words to my family:


Ebenfalls sehr herzlich danke ich meinem Freund Robert: Danke für Deine Hilfe und Unterstützung, für Deine Ermutigungen und für die schöne gemeinsam verbrachte Zeit.

Zürich, December 2013

Elisabeth Edom

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Nomenclature

Roman symbols

\( A \) a constant
\( a \) complex multiplier of \( \zeta \) in the active model of the basilar membrane motion
\( b \) complex multiplier of the non-linearity of the oscillator with Hopf bifurcation
\( c_{ph} \) phase velocity
\( dB \) decibel, measure for the sound pressure level with respect to the hearing threshold
\( f \) stimulation frequency
\( f_{DP} \) distortion product frequency
\( Hz \) Hertz
\( h \) hour
\( i \) imaginary unit, \( i^2 = -1 \)
\( K \) basilar membrane stiffness
\( K \) a constant
\( k \) wave number
\( kg \) kilogram
\( L \) typical length scale
\( L_c \) length of the cochlea
\( m \) metre
\( m \) basilar membrane mass
\( N \) Newton
\( Pa \) Pascal
\( p \) pressure
\( q \) force density
\( R \) basilar membrane damping
\( Re \) Reynolds number, \( Re = \frac{U^*L^*}{\nu^*} \)
\( r \) multiplier in the bifurcation parameter \( \beta \)
\( Str \) Strouhal number, \( Str = \frac{f^*L^*}{U^*} \)
\( s \) second
\( s \) ratio between the active and the passive basilar membrane deflection
\( T \) period of the stimulation frequency, \( T = \frac{1}{f} \)
\( t \) time
\( U \) typical velocity scale
### IV Nomenclature

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>$U_{in}$</td>
<td>maximum inflow velocity at the stapes</td>
</tr>
<tr>
<td>$u$</td>
<td>velocity vector</td>
</tr>
<tr>
<td>$u$</td>
<td>axial velocity</td>
</tr>
<tr>
<td>$u_s$</td>
<td>slip velocity</td>
</tr>
<tr>
<td>$V$</td>
<td>fluid volume</td>
</tr>
<tr>
<td>$v$</td>
<td>transversal velocity</td>
</tr>
<tr>
<td>$x$</td>
<td>coordinate vector</td>
</tr>
<tr>
<td>$x$</td>
<td>axial coordinate</td>
</tr>
<tr>
<td>$x_s$</td>
<td>axial coordinate of the stapes footplate centre</td>
</tr>
<tr>
<td>$y_s$</td>
<td>transversal coordinate of the stapes footplate centre</td>
</tr>
<tr>
<td>$\bar{y}$</td>
<td>shifted transversal coordinate, $y(\bar{y} = 0) = 0.24$</td>
</tr>
</tbody>
</table>

### Greek symbols

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha$</td>
<td>Womersley number, $\alpha = L^* \sqrt{2\pi f^<em>/\nu^</em>}$</td>
</tr>
<tr>
<td>$\beta$</td>
<td>bifurcation parameter</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>complex multiplier of the external forcing of the oscillator with Hopf bifurcation</td>
</tr>
<tr>
<td>$\Delta$</td>
<td>difference</td>
</tr>
<tr>
<td>$\Delta_x$</td>
<td>axial shift</td>
</tr>
<tr>
<td>$\zeta$</td>
<td>oscillation amplitude of the oscillator with Hopf bifurcation</td>
</tr>
<tr>
<td>$\eta$</td>
<td>basilar membrane displacement</td>
</tr>
<tr>
<td>$</td>
<td>\eta</td>
</tr>
<tr>
<td>$\eta_x$</td>
<td>transversal displacement of the basilar membrane</td>
</tr>
<tr>
<td>$\eta_y$</td>
<td>axial displacement of the basilar membrane</td>
</tr>
<tr>
<td>$\kappa_x$</td>
<td>axial membrane stiffness</td>
</tr>
<tr>
<td>$\kappa_y$</td>
<td>transversal membrane stiffness</td>
</tr>
<tr>
<td>$\lambda$</td>
<td>wave length</td>
</tr>
<tr>
<td>$\lambda_{\text{base}}$</td>
<td>eigenfrequency of the passive cochlea model at the base of the cochlea</td>
</tr>
<tr>
<td>$\mu$</td>
<td>dipole intensity</td>
</tr>
<tr>
<td>$\nu$</td>
<td>kinematic viscosity</td>
</tr>
<tr>
<td>$\rho$</td>
<td>density</td>
</tr>
<tr>
<td>$\Phi$</td>
<td>potential</td>
</tr>
<tr>
<td>$\phi$</td>
<td>multiplier of $a$</td>
</tr>
<tr>
<td>$\Omega$</td>
<td>eigenfrequency of the oscillator with Hopf bifurcation</td>
</tr>
<tr>
<td>$\omega$</td>
<td>angular frequency</td>
</tr>
</tbody>
</table>
Nomenclature

Subscripts

\( \cdot \)\text{apex} at the apex (far end of the cochlea, \( x = 12 \))
\( \cdot \)\text{base} at the base (front end of the cochlea, \( x = 0 \))
\( \cdot \)\text{BM} at the basilar membrane
\( \cdot \)\text{BL} at the boundary layer edge
\( \cdot \)\text{EC} in the ear canal
\( \cdot \)\text{E} Eulerian mean
\( \cdot \)\text{L} Lagrangian mean
\( \cdot \)\text{M} Stokes drift
\( \cdot \)\text{OW} at the oval window
\( \cdot \)\text{RW} at the round window
\( \cdot \)\Delta difference
\( \cdot \)\ast at the characteristic place

Superscripts

\( \cdot \)\text{BM} induced by the basilar membrane
\( \cdot \)\text{Re} induced by the Reynolds stresses
\( \cdot \)\text{C} according to Lighthill (1992)
\( \cdot \)\ast dimensional quantity
\( \cdot \) steady part or average over time, typically one period of the stimulation frequency
\( \cdot \)\prime oscillatory part
\( \cdot \)\hat{\cdot} eigenfunction amplitude of a wave ansatz
\( \cdot \)\tilde{\cdot} complex conjugate
\( \cdot \)\dagger complex conjugate (used for longer expressions)
Chapter 1

Introduction

It is a hard matter, my fellow citizens, to argue with the belly, since it has no ears.
Marcus Porcius Cato

1.1 Motivation

The cochlea is the human hearing organ and part of the inner ear. The hearing is one of the five senses and of great significance for humans. While Cato the Elder obviously points at a more subtle implication of hearing than the pure perception of sound, the ability to transduce sound waves into nerve signals is of great importance.

It is substantial for personal communication by influencing to a great extent the integration into social life as well as into professional life. Likewise, personal safety depends strongly on the ability to perceive auditory warning signals. Another aspect of the relevance of hearing is the subjective well-being. While being improved by listening to music, the well-being suffers in case of hearing impairment or deafness. These disabilities restrict the autonomy and self-dependence of patients and might in some cases even lead to depression.

Hearing aids allow to ease hearing loss or even specific types of deafness. However, the technical means are limited and further research and development is required. This aspect gains in importance by the fact that the number of hearing-impaired is increasing.

Investigation of the auditory system has a long history. Already in the 1820s, scientific studies on this topic have been published (e.g. Wollaston, 1820) and man started much earlier to investigate the ability of hearing. Substantial progress in the research on the hearing sense was obtained by von Békésy who was awarded the Nobel prize in medicine “for his discoveries of the physical mechanism of stimulation

---

within the cochlea”\(^2\) in 1961. His monograph “Experiments in Hearing” (von Békésy, 1960) is still one of the most often cited references. A further milestone was the discovery of the active amplification in the cochlea, which has already been suspected by Gold in 1948 (Gold, 1948) and experimentally confirmed by Kemp in 1978 (Kemp, 1978). Despite this long research tradition, there are still many open questions.

Research on the hearing is complicated by the small size of the cochlea. Experimentally the hearing organ is difficult to access and can practically not be explored without damage to itself or to neighbouring structures. If the signal processing in the brain is to be investigated, one faces even bigger difficulties. Furthermore, experimental studies encounter most often ethical issues.

Regarding the enhanced difficulties of experimental measurements, numerical simulations offer a good possibility to study the hearing sense and to improve hearing aids.

The present work aims at contributing to the investigation of the processes in the cochlea from a fluid dynamical point of view. Priority is given to fluid motions in the cochlea which are induced by the displacements of the stapes, the last of the auditory ossicles in the middle ear, and the interaction of the cochlear fluid with the cochlear partition, i.e., the mechanical structures in the cochlea. Two phenomena are examined in detail: the steady streaming and the rocking stapes motion.

Steady streaming denotes a mean fluid motion which is induced by a periodical external forcing of zero mean and which is present additionally to this oscillating primary flow. The steady streaming is a non-linear effect. Popular examples are the Rayleigh or acoustic streaming and the quartz wind (Riley, 2001). These streaming phenomena are generated by higher frequencies and velocities of the primary wave than those stimulating the cochlea. The existence of steady streaming in the cochlea has already been suspected by von Békésy (1960) and Lesser & Berkley (1972), and shown analytically by Lighthill (1992). This phenomenon has been pointed out to possibly stimulate the sensory cells inside the cochlea (Lighthill, 1992) which would affect the hearing. Further, it might influence the transport of solutes in the cochlear fluids. However, both the existence and the relevance of steady streaming in the cochlea

is discussed controversially (cf. Böhnke & Scharff (2009), containing a transcript of a follow-up discussion after presentation at the conference “Mechanics of Hearing” in 2009).

The term “rocking stapes motion” describes a specific displacement of the stapes. The stapes motion is known to exhibit translational as well as rotational components (Stuhlman, 1937). Most of the times the classical theory of hearing accounts only for the translational, the so-called piston-like motion, i.e., a motion which follows the axis perpendicular to the stapes footplate. In contrast, the rotational or rocking components of the stapes motion, in which the stapes footplate rotates around its long or short axis, are regarded as irrelevant for the hearing process. However, experimental studies have shown that these rocking motions can provoke hearing (Huber et al., 2008).

The present work investigates the steady streaming and the rocking stapes motion by means of a two-dimensional box model of the cochlea with one membrane representing the cochlear partition. The fluid motion is described by the Navier-Stokes equations, i.e., in a transient, nonlinear, and viscous way. The membrane is modelled by a set of oscillators and the fluid-structure interaction is realised by an immersed-boundary approach. The model is based on first principles and makes as few assumptions as possible. The idealisations of this model do not allow for exact predictions for the motion of the fluid and the cochlear partition in the real cochlea. For more specific quantifications, further details of the organ would have to be modelled, as well as further processes such as the so-called active amplification. Nevertheless, this work illustrates if the effects discussed above are present in the cochlea and provides estimates to what extent they might affect the hearing.

The structure of the present chapter is the following: Sec. 1.2 explains the anatomy and physiology of the cochlea. Section 1.3 discusses the state of the art of cochlear modelling. The outline of this thesis and its objectives are presented in Sec. 1.4.

### 1.2 Anatomy and physiology of the cochlea

This section addresses the anatomy and physiology of the cochlea. The main emphasis is placed on the aspects which are related more closely to the investigation in the present thesis. More detailed information can be found in, e.g., Dallos et al. (1996, esp. Chap. 3 for the cochlear cell struc-
Figure 1.1: The ear (©Encyclopedia Britannica, Inc.).

The cochlea is the central part of the mammalian hearing organ. It is carved into the temporal bone and part of the inner ear (Fig. 1.1). The dimensions of the cochlea are indicated in the end of the present section. The cochlea (greek κόχλος, kóchlos, snail) is a coiled system of membraneous structures and of several tubes filled with lymphatic liquids. The cross-section of the cochlea (Fig. 1.2) shows two ducts filled with perilymphatic fluid (scala vestibuli and scala tympani) and one duct (scala media/cochlear duct) in between which contains endolymphatic fluid. The perilymphatic ducts are connected by the so-called helicotrema at the far end (apex) of the cochlea. The scalae media and vestibuli are separated by a very thin membrane (Reissner’s membrane). The scalae media and tympani, in contrast, are divided by a structure consisting of the basilar membrane, the organ of Corti and the tectorial membrane. These parts, often referred to as cochlear compartment (Fig. 1.3), are crucial for the actual hearing process, as will be explained in the following.
During hearing (Fig. 1.4), sound signals which reach the outer ear are converted into movements of the tympanic membrane and of the auditory ossicles in the middle ear (Fig. 1.1). The last one of these small bones, the stapes, is connected to the oval window, a small hole in the temporal bone which links the middle ear with the cochlea. It is covered by a supple membrane which allows the stapes to move into the cochlea and out of it. The net displacements of the stapes are compensated at the round window. This additional small hole in the temporal bone opens the cochlea to the middle ear cavity. It is covered by a supple membrane which moves as the stapes is displaced.

The movements of the stapes lead to a travelling wave of the lymphatic fluids inside the cochlea and of the cochlear compartment. The amplitude of the travelling wave increases until the so-called characteristic place is reached while it decreases steeply behind it. At the characteristic place resonance between the stimulation frequency and the eigenfrequency of the cochlear compartment occurs. Thereby each frequency
reaches maximum amplitudes at a specific location along the cochlear partition (Fig. 1.5). This is mainly due to the structure of the basilar membrane which determines the stiffness and mass of the cochlear partition. The membrane stiffness decreases toward the apex while its mass
increases (Dallos et al., 1996), therefore high frequencies yield large oscillation amplitudes in the beginning of the cochlea, and lower frequencies in the end.

The motion of the cochlear compartment induced by the basilar membrane motion leads to the generation of neural signals in the sensory cells (inner and outer hair cells) of the organ of Corti (Fig. 1.3). The cells at the characteristic place show the most intense neural activity and therefore the connected nerve fibers as well. The brain (more precisely the auditory nuclei of the brain stem) detects from the neural signals which nerve fibers are responding and analyses the rate and time pattern of the spikes, which leads to the hearing sensation.

During the hearing process, the so-called active amplification plays an important role. The oscillation amplitudes of the cochlear compartment are not only generated by mechanical resonance, but also by the activity of the outer hair cells. These cells lengthen due to stimulation and thereby increase the oscillation amplitudes of the cochlear compartment by up to a factor of 100 compared to the purely mechanical (“passive”) cochlear response (Dallos et al., 1996). Further, this process enhances the frequency tuning by an increased frequency selectivity. Thus, the active amplification enables to perceive softer tones and smaller frequency differences. There are two further characteristics of the active process, first, the compressive non-linearity which yields less amplification for
louder input signals, and second, otoacoustic emissions which are sounds emanated by the cochlea. Otoacoustic emissions are generated either without stimulation (spontaneous otoacoustic emissions) or after a specific stimulation (e.g., distortion-product otoacoustic emissions) (Fuchs, 2010).

A few details of the physiology of the cochlea shall be addressed. One point is that the size of the cochlear cross-section is not constant but tapered. While the scalae vestibuli and tympani are smaller at the apical than at the basal end, the organ of Corti becomes larger toward the apex. Thereby, the cross-section shape of the basilar membrane changes from narrow and thick at the base of the cochlea to wide and thin at the apex (Dallos et al., 1996).

Next, the structure of the basilar membrane shall be pointed out. The basilar membrane consists of fibres, embedded in a more homogeneous substance. These fibres show specific orientations in the inner and outer regions of the cochlear snail, i.e., in radial direction. While the fibres are arranged transversely in the inner region, i.e., parallel to the long axis of the membrane, they are grouped into bundles and oriented radially in the outer region (Dallos et al., 1996). This zone (pars pectinata) spans about two thirds of the membrane width.

Another detail regards the stapes. This ossicle is attached to the oval window by the annular ligament which allows only for specific motions of the stapes. Therefore, the stapes motion shows only three degrees of freedom instead of six. The remaining motion components are a single translational one perpendicular to the stapes footplate and two rotational components around the long and short axes of the footplate.

Furthermore, the dependence of the hearing on ion processes is to be addressed. Shearing of the basilar and tectorial membranes causes a deflection of the hair cell stereocilia which opens ion channels such that K$^+$ ions enter the hair cell. The resulting depolarisation enables the influx of Cl$^-$ ions. These regulate the intracellular Ca$^{2+}$ concentration. The depolarisation and a specific Ca$^{2+}$ concentration activate the generation of afferent neural signals. These lead to the sensation of hearing. On the side walls of the hair cells, the K$^+$ ions flow back into the lymphatic fluids and the cell repolarises (Lehnhardt & Laszig, 2001). These and other ions influence many further processes in the cochlea, especially during active amplification. The literature cited in the beginning of this section provides detailed information on this.
Finally, a few numbers shall be mentioned here. The human cochlea is coiled with about $2\frac{5}{8}$ turns (Yost, 2007). The height of the coiled system is about 4.5 mm and the longest, orthogonal axes of the ground area measure about 7 mm and 9 mm (Escudé et al., 2006; Mori & Chang, 2012; Rask-Andersen et al., 2012). When uncoiled, the cochlea is about 35 mm long Yost (2007). It is able to detect frequencies between 20 and 20,000 Hz and distinguishes frequencies which are only 0.2% apart. In comparison, two semitones in Western tonal music are about 6% apart in frequency (Dallos et al., 1996). The processable intensity range spans from 0 to more than 120 dB which is more than a million-fold change in energy. Depending on the language the human speech comprises frequencies between 250 Hz and 4000 Hz or even above and below Lehnhardt & Laszig (2001) and sound pressure levels of 30 to 80 dB (Fig. 1.6(a), dark yellow region). Thereby, the loudness (measured in phones) of identical sound pressure levels (SPL, measured in dB) is perceived differently for different frequencies (Fig. 1.6(b)).

1.3 Cochlear modelling

This section gives an overview of analytical and numerical models of cochlear mechanics which include the fluid flow. Further model types such as in-vivo or in-vitro models are not taken into account. The class of analytical and numerical models can be grouped according to:
• the geometric description (box geometry, coiled geometry),

• the dimensional description (1D, 2D, 3D),

• the physical description of the fluid flow (inviscid, viscous; linear, non-linear; stationary, transient),

• the description of the active amplification (passive, active; type of model for the active process),

• the described length scales (macro scale, micro scale),

• the method of solution (analytical, numerical).

This list is ordered arbitrarily and can be extended (e.g., according to the processes which are included, i.e., mechanical, electrical, biological, chemical). The body of literature on cochlear modelling is quite vast as the list above implies. Below only models are discussed which are of higher importance for the development of cochlear modelling or for the model used in this work. Broader overviews of cochlear models can be found in, e.g., Steele et al. (1995), de Boer (1996) and Patuzzi (1996).

From a historical point of view, at least two early studies have to be mentioned, the works by Peterson & Bogert (1950) and by Lesser & Berkley (1972). The transmission-line model by Peterson & Bogert (1950) is one of the first models to represent the basic characteristics of cochlear mechanics. It reproduces the travelling wave but it is limited to a one-dimensional inviscid description of the flow field and to long wave-lengths. The model by Lesser & Berkley (1972) is another important contribution. They describe the flow field by a two-dimensional potential flow and are thus not restricted to long wave-lengths. However, viscous effects are not taken into account.

Amongst the more recent models, three major lines of development can be detected. One is that of models aiming at a more detailed description of the fluid flow. A second trend is that of models striving for a representation of the three-dimensional coiled geometry. Finally, there are models seeking to capture the effects of active amplification. Below models of each of these groups are addressed.

Concerning the description of the fluid flow, the work by Beyer (1992) can be regarded as a milestone because the cochlear fluid flow is described as transient, viscous, non-linear and two-dimensional. Most other models simplify the fluid dynamics using an inviscid and/or stationary and/or
1.3 Cochlear modelling

linear description. Beyer (1992) uses a two-dimensional box model and solves the fluid equations using a finite-difference method according to Bell et al. (1989). The fluid-structure interaction in is modelled with the immersed boundary method by Peskin (1977, 2002). The cochlear partition is represented by an elastic membrane. This model is closest to the one used within the present thesis which, as well, solves the Navier-Stokes equations in a two-dimensional box geometry. Regarding the results of Beyer, he reports having been limited by the computational power available at that time.

Although the present overview of cochlea models concentrates on the three above-mentioned lines of development, some further two-dimensional models shall be briefly adhere. LeVeque et al. (1985, 1988) use a two-dimensional linear model, describing the fluid as inviscid in the first publication and as viscous in the second one. Pozrikidis (2007, 2008) describes the fluid flow by linearised Navier-Stokes equations. The model by Gerstenberger (2013) is addressed below and discussed later in this work (Chap. 4).

The three-dimensional cochlea is modelled by, e.g., Böhnke & Arnold (1999), Parthasarathi et al. (2000) and Givelberg & Bunn (2003). These models study both the coiled system and three-dimensional box models. The coiling of the cochlea is subject of several numerical studies of the micro-mechanical behaviour of the cochlea. While the coiling has long been supposed to serve as a space-saving packaging, it is nowadays believed that the coiling influences the wave energy distribution in such a way that low frequency sounds are amplified (Cai et al., 2005; Chadwick et al., 2006; Manoussaki & Chadwick, 2000; Manoussaki et al., 2008, 2006).

Böhnke & Arnold (1999) present a model of the coiled cochlea with an inviscid and incompressible flow description. The equations are discretised using the finite-element method. According to the authors this model is the first one to represent the cochlear partition and the oval and round windows in a three-dimensional way.

Parthasarathi et al. (2000) use a three-dimensional box model. The flow is treated as incompressible and inviscid and the cochlear partition is modelled by an elastic membrane with damping. Hybrid modal-finite-element and boundary-element methods are used. The modal-finite-element method allows to solve the fluid flow on a two-dimensional computational mesh while for the third dimension a modal expansion is used, resulting in less computational effort. This model is extended by Cheng
et al. (2008) to a fully three-dimensional description of the fluid flow.

The model by Givelberg & Bunn (2003) represents a coiled system with a few geometric simplifications (e.g., position of the oval and round windows). The flow is described by the Navier-Stokes equations which are discretised by finite differences. The cochlear partition is represented by a single membrane which is modelled as an elastic shell, using the immersed boundary method by Peskin (2002).

These three models are shown to reproduce the travelling wave of the cochlear fluid and of the cochlear partition. Results on the three-dimensional character of cochlear mechanics are reported to a rather limited extent. Possibilities to extend the models are pointed out in all of these publications, e.g., by including the organ of Corti. Therefore, it seems that the publications have been meant to serve as starting points for more elaborate descriptions of the cochlea. Nonetheless, the author is not aware of follow-up studies with the respective models apart from the one by Cheng et al. (2008). Besides the challenges of developing a three-dimensional multi-scale model, a reason might be the large amount of computational power which is necessary to perform such simulations. Further three-dimensional models are among the models discussed below.

The third line of development mentioned above regards models which include the active amplification. In this field, many recent publications exist. As pointed out before, this section concentrates on models which include the fluid flow. Therefore, the models by Lim & Steele (2002), Kern (2003) (cf. also Kern & Stoop, 2003), Meaud & Grosh (2011) (or Meaud & Grosh, 2012), and Gerstenberger (2013) are addressed in more detail in this third group. It shall be mentioned that models exist which study subsystems of the active cochlea, e.g., models studying the organ of Corti (e.g. Steele et al., 2009) or the motion of the hair bundles (e.g. Baumgart, 2010).

Lim & Steele (2002) present a multi-scale model in a three-dimensional tapered box with viscous flow. The non-linear active processes in the organ of Corti are described in detail. This model is probably the most elaborated one and reproduces most characteristics of non-linear active processes (compression of response with stimulus level, two-tone suppression, distortion products). To solve the equations, a hybrid asymptotic and numerical method is used. The problem is divided into a macroscopic model, which is based on the WKB method, and a non-linear microscopic model. The combination of both yields a coupled system of non-linear equations which is solved iteratively. This
procedure enables to solve the equations in an efficient way, but reduces
the original problem to a pseudo-local problem (Obrist, 2011).

The characteristics of the active process have been shown to agree
(Camalet et al., 2000; Choe et al., 1998; Eguíluz et al., 2000) with those of
a Hopf bifurcation, a particular bifurcation of dynamical systems (Mars-
den & McCracken, 1976). Reviews on modelling of active amplification
with the Hopf bifurcation can be found in Duke & Jülicher (2008) and
Hudspeth et al. (2010).

of the organ of Corti by a non-linear oscillator with Hopf bifurcation.
Instead of modelling the active amplification on the micro-scale level
they use this quite different ansatz. This model with its refined versions
Stoop & Kern (2004); Stoop et al. (2005) reproduces key features of non-
linear active processes as well. The fluid flow description remains limited
to an analogy with surface water waves.

Another three-dimensional active cochlea model is proposed by
Meaud & Grosh (2011, 2012). It describes the active amplification by
the six-state-channel reclosure model by Choe et al. (1998). This model
for the hair cell kinematics couples the hair cell activity to calcium ion
concentrations and has been shown to reveal Hopf bifurcations. The
active cochlea model by Meaud and Grosh also accounts for electrical
conduction and the micromechanics of the organ of Corti. The fluid
flow is modelled as incompressible and inviscid. This elaborated model
includes many of the cochlear processes. It reproduces effects such as
compressive non-linearity and harmonic distortion. Further information
is given in the publications cited above and in related ones, e.g., Li et al.
(2011); Meaud et al. (2011); Ramamoorthy et al. (2007).

The models above capture the effects of active amplification success-
fully. They do not focus on the description of the fluid flow and model it
as inviscid and linear. Therefore, phenomena such as energy dissipation
in the viscous boundary layers cannot be accounted for. Many are also
restricted to the steady state of the system and have to neglect transient
phenomena.

One further model shall be addressed here, Gerstenberger (2013). He
studies a two-dimensional, tapered box-model of the active cochlea. The
active amplification is modelled by an oscillating system according to
Mammano & Nobili (1993) and Nobili & Mammano (1996), without a
Hopf bifurcation. The system is linearised such that certain phenomena
of active amplification are not captured, e.g., compression of response
with stimulus level. The peak of the membrane displacement shows, however, an amplitude amplification and narrowing. This cochlea model focuses on a study of the steady streaming in the cochlea. The obtained results are discussed in Sec. 4.1.3.

1.4 Objectives and outline

The present work investigates two processes in the cochlea whose influence on the hearing is discussed controversially.

First, the steady streaming in the cochlea is studied. As already pointed out by Lighthill (1992), the streaming motion might lead to a force on the hair cell stereocilia and thereby play a role in the generation of nerve signals. Despite the possible physiological relevance of this phenomenon, only little interest has been shown for this topic until recently and there remain open questions. The present work investigates the velocity fields of steady streaming solving the non-linear viscous Navier-Stokes equations numerically. The steady streaming fields are compared to Lighthill’s analytical predictions. The mechanisms leading to steady streaming are presented and a source of steady streaming which has not been considered by Lighthill is investigated. Possible physiological consequences of the steady streaming in the cochlea are pointed out.

Second, the influence of rocking stapes motions on the deflections of the basilar membrane is investigated. Experimental results suggest that these stimulations of the cochlea lead to hearing, whereas other publications doubt this effect. The present work studies the cochlear fluid flow due to such rotational movements of the stapes and points out the differences to the fluid flow induced by the conventional piston-like motion. The basilar membrane displacements are assessed in detail. The amplitude scaling behaviour along the cochlea is studied and explained for both stimulation types, making use of potential flow theory. The possible impact of rocking stapes motions on the hearing is discussed.

This work is structured as follows: Chapter 2 presents the computational model which is used in this work. It introduces the setup of the model, the governing equations and the numerical solver IMPACT. The immersed boundary approach which is used to model the fluid-structure interaction is presented.

The results are presented and assessed in Chaps. 3 to 5. Chapter 3 addresses the mechanics of the cochlea. To this end, the primary wave
system is presented, i.e., the travelling waves in the fluid and on the basilar membrane which are induced by the conventional piston-like motion of the stapes. The simulated results are compared to the analytical predictions by Lighthill (1992). The peak amplitudes of the basilar membrane displacement due to different stimulation conditions regarding frequency, stapes velocity and ear canal pressure are shown. Chapter 3 also provides a validation of the cochlear model by demonstrating that the characteristics of the well-known travelling wave phenomenon in the cochlea are reproduced.

The steady streaming in the cochlea is addressed in Chap. 4. An introduction into the steady streaming is followed by the simulation results. Thereby, the different fields of steady streaming – Eulerian streaming, Lagrangian streaming and the Stokes drift – are assessed. Effects on the basilar membrane motion due to steady streaming are studied. The simulation results are compared to the analytical predictions by Lighthill (1992). The mechanisms which lead to steady streaming in the cochlea are investigated. It is shown that the basilar membrane is a source of steady streaming, in addition to the Reynolds stresses. The chapter is closed by discussing possible physiological consequences of steady streaming in the cochlea.

Chapter 5 addresses the influence of rocking stapes motions on the travelling wave in the fluid and on the basilar membrane. It gives an overview of motion patterns of the stapes which is followed by the presentation of simulation results. The rocking stapes motion leads to a travelling wave in the fluid and on the basilar membrane. Peak amplitudes of the basilar membrane deflection due to pure rocking stapes motion are shown and compared to those for the conventional piston-like stimulation. Amplitudes due to a combination of rocking and piston-like stapes motions are investigated. Further, the influence of the stapes position on the peak amplitudes is assessed. It is shown that the peak amplitudes due to rocking stapes stimulation can be approximated by means of potential flow theory and that different modes of membrane excitation act due to the different stimulation types. The chapter is closed by a discussion of the influence of rocking stapes motion on the hearing.

The work is concluded in Chap. 6 by summarizing the major findings and by suggesting possible future investigations.
Chapter 2

Methods and Modelling

This chapter introduces the cochlea model used within this thesis. Section 2.1 addresses the model geometry and discusses the assumptions of the model. The equations which describe the motion of the fluid and of the cochlear compartment are presented in Sec. 2.2. The numerical solver IMPACT is addressed in Sec. 2.3 and Sec. 2.4 presents the immersed boundary approach which is used to model the fluid-structure interaction.

2.1 Cochlea model

This section introduces the geometry of the cochlea model and the assumptions on material parameters. All equations which are solved are presented in Sec. 2.2 and information on the fluid-structure interaction is given in Sec. 2.4.

In the present thesis, a two-dimensional box model of the cochlea is used (Fig. 2.1). The term box model refers to a rectangular geometry which represents an uncoiled cochlea. These models idealise the tapering of the cochlea (Sec. 1.2, Fig. 1.5) by a constant height of the fluid-filled channels. It is assumed that both coiling and tapering can be neglected because the curvature radius of the cochlea is small compared to the width of the cochlear ducts and because the angle of the tapering is small compared to the channel height.

The cochlear compartment, i.e., the structure consisting of the basilar membrane, the organ of Corti, and the tectorial membrane (Sec. 1.2, Figs. 1.2 and 1.3), is represented by a single membrane. This is justified because in a macro-scale view of the cochlea, the height of the cochlear compartment is negligible compared to the channel height. The membrane which models the cochlear compartment is most often called basilar membrane. This terminology is also used throughout this thesis.

The basilar membrane divides the cochlea in two fluid-filled compartments which are referred to as scalae vestibuli and tympani. Thus, Reissner’s membrane (Sec. 1.2, Figs. 1.2) is neglected, the membrane
which splits the fluid space above the cochlear compartment into the scalae media and vestibuli. Since this membrane consists of only two cell layers, it is very thin and supple. Therefore it is assumed that it moves passively with the fluid.

These geometric simplifications result in a two-compartment box model. The outer dimensions of the box model are indicated in Fig. 2.1. The length compares to that of a human cochlea and the height has been chosen according to Lighthill (1981).

Further, Fig. 2.1 illustrates the positions of the round and oval windows. The oval window, which corresponds to the position of the stapes, is located in the upper wall of the scala vestibuli at the top-left end of the box. It is oriented parallel to the basilar membrane. The round window is situated at the left-side end of the scala tympani and is oriented perpendicular to the basilar membrane.

The complicated three-dimensional geometry of the cochlea in the high frequency region (hook region) also allows for a different positioning of both windows. Often, both the oval and the round window are modelled at the left-side end of the scala vestibuli at $x = 0$ such that they are oriented orthogonal to the basilar membrane. This results in a symmetric set-up which allows to compute the processes in only one of the scalae vestibuli and tympani. Anatomical investigations of human temporal bones (Eaton-Peabody Laboratory of Auditory Physiology, Boston, 2009), however, show that the oval window position indicated in Fig. 2.1 is favourable. The alternative oval window location would also require
that the size of this opening is reduced to the scala vestibuli height. Since the oval window measures about $1.2 \times 3 \text{ mm}$ to $2.0 \times 3.7 \text{ mm}$ in human (Yost, 2007) while the scala vestibuli height has been chosen to $0.72 \text{ mm}$ according to Lighthill (1981), this is not recommendable.

The best position of the round window is not obvious. The scala media terminates at the posterior edge of the round window (Li et al., 2007; Nager, 1993; Stidham & Roberson, 1999). Therefore it is located at the front side of the scala tympani in this model. Another possibility is to position it in the bottom wall of the scala tympani because it is oriented primarily parallel to the basilar membrane.

The location of these inflow/outflow regions can be assumed to influence the fluid flow and the membrane motion only in the front region of the cochlea. It has to be taken into account that in this area the box geometry differs from the real geometry to a greater extent and that therefore the results for this part of the cochlea should be handled with care.

In the following, the assumptions on the models for the lymphatic fluid and for the basilar membrane are discussed. The equations of motion for the fluid and for the membrane are addressed in Sec. 2.2. The motion of the oval and round windows is modelled by inflow and outflow velocities of the fluid. The membranes covering these openings are not modelled as mechanical structures.

The fluid flow is described as transient, incompressible, viscous and non-linear. The density and the viscosity of the cochlear fluids are known to be similar to water (Steele et al., 1995), therefore these parameters are chosen as $\rho = 10^3 \text{ kg/m}^3$ and $\nu = 10^{-6} \text{ m}^2/\text{s}$, respectively. The fluid motion is assumed incompressible because the shortest acoustic wavelength in the cochlea, present at $20 \text{ kHz}$, is about $7.5 \text{ cm}$. Since this is much longer than the cochlea the propagation of acoustic waves in the fluid may be neglected.

The basilar membrane is modelled by an array of independent oscillators which are positioned in a line along the membrane (Fig. 2.2). Sections 2.2 and 2.4 present more details on the modelling of the membrane and of the fluid-structure interaction. It shall be noted here, however, that the oscillators are connected to their resting positions but not to their neighbouring oscillators (Fig. 2.2) such that they move independently from each other; only the fluid motion leads to a coupled motion. This refers to the fact that the fibres inside the real basilar membrane are oriented in radial direction in most of the membrane (cf. Sec. 1.2),
i.e., perpendicularly to the $x$-$y$-plane of this model. Therefore, the real basilar membrane is not a mechanical membrane but rather an array of individually supported cantilever beams which are oriented perpendicular to the $x$-$y$-plane.

The material properties of the modelled basilar membrane, i.e., mass, damping, and stiffness, are chosen such that as little assumptions as possible are made. The basilar membrane inertia is dominated by the inertia of the fluid which is moved by the membrane. Only for exceedingly high values for the membrane mass an effect on its motion is observed. This is in accordance with de la Rochefoucauld & Olson (2007). They find that only for high frequencies resonance from the cochlear compartment applies, i.e., when only a small fluid volume is moved by the membrane such that the ratio between the fluid mass and the membrane mass is smaller. Therefore, the membrane mass is chosen to be zero in the present model.

The major energy dissipation is assumed to take place in the Stokes boundary layers on the basilar membrane. Therefore, no structural damping of the membrane is modelled.

The reasoning above leaves the membrane stiffness as the only physical parameter which needs to be modelled. The present model assumes a stiffness $\kappa_y^*$ in transversal direction which yields the distribution of resonance frequencies along the basilar membrane. Further, a stiffness $\kappa_x^*$ in axial direction is assumed which can be understood as bending stiffness of the individual cantilever beams against forces in axial direction. In agreement with the distribution of resonance frequencies in the real cochlea, the transversal stiffness is assumed to decay exponentially along the membrane. To achieve resonance with the stimulation frequency $f^* = 20$ kHz at the front end (base) of the cochlea, the stiffness at this location is chosen as $\kappa_y|_{\text{base}} = 6.25 \cdot 10^{11}$ N/m$^3$. The stiffness decays exponentially to a value of $\kappa_y|_{\text{apex}} = 6.25 \cdot 10^5$ N/m$^3$ at the far
end (apex) of the cochlea such that a resonance frequency of $f^\ast = 20 \text{Hz}$ is occurs here This compares well to values by J.H. Sim (private communication) from the University Hospital Zurich. The axial stiffness is more difficult to assess. It has been discussed contradictorily whether there exists a non-negligible axial stiffness or not and whether it increases or decays along the cochlea (e.g. von Békésy, 1960; Naidu & Mountain, 1998, 2001; Voldřich, 1978). Emadi et al. (2004) measure the stiffness of the gerbil basilar membrane and observe a longitudinal stiffness which decays from the base to the apex and approximate it with a logarithmic gradient along the cochlea. In the present model, the axial stiffness has been chosen as $\kappa_x = 0.01 \cdot \kappa_y$. The resulting decay in axial stiffness along the cochlea reflects the fact that the real basilar membrane widens toward the apex (Sec. 1.2). The widening results in longer cantilever beams which are more easily deflected.

The governing equations presented in the subsequent section are solved on a Cartesian computational grid (cf. Sec. 2.3 for the discretisation scheme). The grid is evenly spaced in $x$-direction and locally refined in $y$-direction to resolve the boundary layers at the basilar membrane and at the bounding walls. An example for such a grid is shown in Fig. 2.3 and more information is presented in the following sections (especially Fig. 2.6).

Typical simulations for the results present in Chaps. 3 and 5 are carried out on personal computers with Xeon E5-2643 processors (3.3 GHz, 32 GB Memory) and on personal computers with Intel i7-2600
processors (3.4 GHz, 16 GB Memory) with typical turn-around times of about 1.5 h (for stimulation at $f^* = 1000 \text{Hz}$ on a grid with $96 \times 3072$ points, using four cores) to about 58 h (for stimulation at $f^* = 4000 \text{Hz}$ on a grid with $320 \times 9216$ points, using four cores).

For the steady streaming investigated in Chap. 4 finer spacial resolution is required. Typical simulations are carried out on personal computers with Xeon E5-2643 processors (3.3 GHz, 32 GB Memory) with turn-around times of about 400 h (for stimulations at $f^* = 1000 \text{Hz}$ on a grid with $320 \times 9216$ points, using eight cores).

2.2 Governing equations and boundary conditions

This section presents the equations which describe the motion of the fluid and of the basilar membrane.

The fluid motion is described by the Navier-Stokes equations for an incompressible flow,

$$\nabla \cdot \mathbf{u} = 0,$$

$$\frac{\partial \mathbf{u}}{\partial t} + (\mathbf{u} \cdot \nabla) \mathbf{u} = -\nabla p + \frac{1}{Re} \nabla^2 \mathbf{u} + \mathbf{q},$$

which are given here in dimensionless form and where $\mathbf{u} = (u, v)$ denotes the velocity vector, $t$ the time, $p$ the pressure, and $\mathbf{q}$ a force density representing the effect of the basilar membrane on the fluid motion. The coordinate directions $x$ and $y$ are oriented along the membrane (axial direction) and perpendicular to it (transversal direction), respectively, with the origin located in the lower left corner of the cochlear box (cf. Fig. 2.1). The Reynolds number $Re$ is given by

$$Re = \frac{u^* L^*}{\nu^*},$$

with the maximum velocity $u^*$ of the stapes motion, the length $L^*$ of the stapes footplate, and the kinematic viscosity $\nu^*$. The superscript $*$ denotes a dimensional quantity throughout the present thesis.

At the outer walls and at the basilar membrane no-slip boundary conditions are imposed. At the bounding walls zero velocity is prescribed and at the oval and round windows inflow and outflow velocities. These velocities model the motion of the membranes covering the windows, where the oval window moves due to the stapes displacements. The velocities are imposed normal to the resting positions of the windows.
This approximation is accurate to the order of \( y_s^2 \) where \( y_s \) is the stapes displacement in \( y \)-direction. The characteristic length \( L^* \), i.e., the stapes footplate length, is much larger than \( y_s \), hence \( y_s \) does not influence the travelling wave in the cochlea. This justifies the usage of the present inflow and outflow conditions.

The basilar membrane is modelled by an array of independent oscillators which are governed by

\[
m \frac{\partial^2 \eta}{\partial t^2} + R \frac{\partial \eta}{\partial t} + K \eta = -\Delta p \cdot \frac{\eta}{|\eta|}.
\]

(2.4)

Here \( \eta = (\eta_x, \eta_y) \) denotes the displacement of the basilar membrane with respect to its resting position. The parameters \( m, R \) and \( K \) describe the membrane mass, damping and stiffness, respectively, and \( \Delta p \) the pressure difference across the basilar membrane. As discussed in Sec. 2.1, the model used within this thesis chooses

\[
m = 0, \quad R = 0,
\]

(2.5)

and only the stiffness

\[
K = \begin{pmatrix} \kappa_x & 0 \\ 0 & \kappa_y \end{pmatrix}
\]

(2.6)

remains, resulting in an elastic membrane behaviour.

The membrane displacement in Eq. (2.4) follows from the fluid motion at the basilar membrane because the no-slip boundary condition at the membrane links the two velocities,

\[
\frac{\partial \eta}{\partial t} = u_{|BM}.
\]

(2.7)

The force density \( q_{|BM} \) at the basilar membrane is computed from the elastic reaction force (Eq. (2.4)) of the displaced membrane. With \( q = q(\Delta p(\eta)) \) it follows as

\[
q_{|BM} = - \begin{pmatrix} \kappa_x & 0 \\ 0 & \kappa_y \end{pmatrix} \begin{pmatrix} \eta_x \\ \eta_y \end{pmatrix}.
\]

(2.8)

Section 2.4 addresses the fluid-structure interaction in more detail.
2.3 High-order Navier-Stokes solver IMPACT

This section gives a short introduction to the numerical solver IMPACT which is used for the simulations presented in this thesis.

IMPACT is a high-order solver for the Navier-Stokes equations which has been developed at the Institute of Fluid Dynamics of ETH Zurich (Henniger, 2011; Henniger et al., 2010b). The solver has been designed for the evaluation of large three-dimensional flow problems which are governed by the Navier-Stokes equations. It is optimised for simulations on massively-parallel supercomputers and features both high scalability and high discretisation accuracy to achieve high efficiency. It has been successfully applied to simulations of turbulent particle-laden flows (Henniger & Kleiser, 2012; Henniger et al., 2010a) and to flow stability problems (Obrist et al., 2012).

IMPACT solves the governing equations iteratively on staggered Cartesian grids. The momentum equations are solved on the velocity grids (one per component) and the continuity equation on the pressure grid. The iterative solver is applied to the sub-problems of the original system of matrices. These sub-problems are a pressure Poisson problem and Helmholtz problems for the velocities. The pressure equation is solved with the Krylov subspace method BiCGstab (van der Vorst, 1992) and with a V-cycle multigrid preconditioner (Hackbusch, 1985). The Helmholtz equation for the velocities is not preconditioned and solved with BiCGstab. Henniger (2011) and Henniger et al. (2010b) describe the numerical solution of the Navier-Stokes equations in detail.

In the application studied in the present thesis, the Navier-Stokes equations are discretised by a sixth-order finite-difference scheme in space and an explicit three-stage, third-order Runge-Kutta scheme in time (Wray, 1986).

By applying IMPACT to the fluid flow in the cochlea, the solver is put into practice in a flow regime with two characteristic properties: the immersed boundary of the oscillating basilar membrane, which exerts periodic forces on the fluid, and Reynolds numbers below unity, while IMPACT has been designed for the description of turbulent flows at large Reynolds numbers.

To evaluate the influence of the forces due to the basilar membrane motion on the performance of IMPACT a standard case simulation, including the basilar membrane, is compared to a simulation in the same set-up without membrane. This standard case is characterised as follows:
2.3 High-order Navier-Stokes solver IMPACT

The computational domain sketched in Fig. 2.1 is discretised using a computational grid (cf. Fig. 2.3) of $3072 \times 96$ grid points with stretching in $y$-direction ($\Delta y_{\text{min}} \approx 2 \cdot 10^{-3}$, $\Delta y_{\text{max}} \approx 8 \cdot 10^{-3}$, relative to $L^*=3\text{mm}$) and with equidistant spacing in $x$-direction ($\Delta x \approx 3.9 \cdot 10^{-3}$). The time step is limited by a CFL-criterion (Henniger, 2011) to $\Delta t_{\text{max}} \approx 3.1 \cdot 10^{-8}$. The fluid flow is stimulated by a maximum inflow velocity of $U_{\text{in}} = 1$ relative to the dimensionful velocity $U_{\text{in}}^* = 3 \cdot 10^{-5}$ m/s oscillating at 1000 Hz. This stimulation yields a Reynolds number of $Re = 0.09$ (cf. Eq. (2.3)) and corresponds to an ear canal pressure of about 76 dB according to measurements by Sim et al. (2010). Twenty-five inflow cycles of the acoustic stimulation are simulated, where the inflow velocity is smoothly ramped up to $U_{\text{in}} = 1$ during the first 12 periods. The simulation with basilar membrane runs for about 100 minutes wall clock time\(^1\), using 3 iterations per time step in the pressure solver. The same simulation without the membrane takes about 50 minutes, using 1 to 2 iterations per time step with the same time step size. The runtime of the simulation and the number of iterations suggest that the presence of the basilar membrane increases the computational effort by a factor of two. However, when comparing these numbers it has to be taken into account that the oscillations of the basilar membrane lead to large fluid velocities of $v_{\text{max}} \approx 35$ in regions of the computational domain where a small grid spacing is present. If the simulation without membrane is influenced by altering the inflow velocity such that the fluid velocities in the same region amount to $v_{\text{max}} \approx 35$, as well, the wall clock time increases to about 85 minutes and the number of iterations increases to 3 per time step. This shows that the computational effort due to the presence of the basilar membrane is limited. During the simulations with the fluid-structure interaction the equations for the membrane motion have to be solved. This might explain the increased runtime compared to the simulations without the basilar membrane. Further, the immersed boundary of the basilar membrane introduces a structure which is stiff at least in the front end of the cochlea. This might limit the time step size and hence increase the computational effort. On the other hand, the fact that the number of iterations per time step in the membrane-less simulation is the same as in the simulation with the membrane shows that the stiffness of the equations does not remarkably influence the performance of the solver. Concluding, the immersed boundary seems to

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\(^1\)All simulations compared in the present section are carried out on a personal computer with Intel i7-2600 cores (3.40GHz, 16 GB Memory) using four cores.
influence the performance of IMPACT rather by considerably increasing local fluid velocities than by creating local forces on the fluid.

The second particularity of applying IMPACT to the cochlear fluid flow is the low Reynolds number. A typical value for this quantity is \( Re = 0.09 \), i.e., \( Re \ll 1 \). This might have the effect that the stability limit of the viscous term dominates the advective stability limit which would result in small time steps. Two further simulations without membrane at larger Reynolds numbers, \( Re = 9 \) and \( Re = 90 \), are performed. They run about 50 minutes each, i.e., as long as the first above-mentioned low-Reynolds number simulation without membrane. The time-step size is identical as well as the number of iterations per time step. This suggests that the performance of IMPACT is not decreased by the Reynolds numbers below unity. Reynolds numbers below unity are present in the cochlear fluid flow for stimulations below 100 dB. Reynolds numbers beyond 100 are reached in the cochlea only for exceedingly loud sound signals beyond the pain threshold of about 130 dB.

As pointed out by Henniger (2011), the time step in IMPACT might be increased by applying a semi-implicit time-integration scheme. Further, Choi & Moin (1994) have shown that the computational effort of fully implicit time-integration schemes might be lower than for explicit ones. However, performance tests with IMPACT for different cases (Henniger, 2011; Henniger et al., 2010b) show that fully explicit time-integration is more efficient overall for the studied configuration. The study by Choi & Moin (1994) has been carried out for turbulent channel flows.

### 2.4 Immersed boundary approach for the basilar membrane

This section introduces the immersed boundary approach which is used to model the interaction between the fluid and the basilar membrane. The solution strategy is explained and information on the convergence of the numerical method are given.

The immersed boundary method (Peskin, 2002) has already been applied to the field of cochlear mechanics by Beyer (1992) and Givelberg & Bunn (2003). In the approach used here, the mobility formulation of Eqs. (2.7) and (2.8) is implemented.

The basilar membrane is discretised by an immersed one-dimensional grid. The number of membrane grid points is the same as for the fluid.
2.4 Immersed boundary approach

Figure 2.4: Mobility formulation of the fluid-structure interaction: (a) The membrane velocity is induced by the local flow velocities, (b) integration in time of the membrane velocity yields the displacements, (c) the displacement leads to a pressure difference across the BM, eq. (2.4), (d) the pressure difference affects the fluid as a field force, eq. (2.2).

in axial direction. The membrane acts on the fluid through the force density $q$ which is computed in the following way (Fig. 2.4): The membrane velocity is evaluated (Fig. 2.4(a)) by interpolating the fluid velocity onto the grid of the basilar membrane using a bi-linear scheme. Integration in time solves Eq. (2.7), yielding the membrane displacement $\eta$ (Fig. 2.4(b)). For this step, the same Runge-Kutta method as for the Navier-Stokes equations is used. The deflected membrane points lead to a pressure difference across the basilar membrane, Eq. (2.4) (Fig. 2.4(c)). With Eq. (2.8) the deflection is transformed into a force density $q$ which acts on the fluid (Fig. 2.4(d)). $q$ is distributed to the surrounding fluid grid points through a bi-linear interpolation.

The bi-linear interpolation of the fluid velocity and of the force density is first-order accurate in space and thus limits the overall order of convergence of the numerical method (Sec. 2.3). The error of the membrane motion has been analyzed to increase with the square of the spatial mesh width. This is illustrated in Fig. 2.5 which shows the overall convergence behaviour for the spatial discretisation. On the ordinate, the relative root-mean-square error of the instantaneous membrane displacement at one instant in time is displayed, normalised by the instantaneous membrane displacement. As reference displacement for computing the error, the simulation result for the finest grid resolution has been taken. The abscissa of Fig. 2.5 shows the number of grid points in $y$-direction (Fig. 2.1). The grid (cf. Fig. 2.3) is equidistant in $x$-direction, and stretched in $y$-direction refining toward the rigid walls and the basi-
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Figure 2.5: Relative root-mean-square-error of the instantaneous membrane displacement for different discretisations (— —: error in the simulations; – – –: indicates scaling $\sim N_y^{-1}$; – · –: indicates scaling $\sim N_y^{-2}$).

Figure 2.6: Discretisation in $y$-direction (— —) for the spatial convergence study: (a) distribution of grid points along $y$; (b) grid spacing along $y$. For the simulations presented in the Secs. 3 to 5, mainly two discretisations are used, the finest one, $N_y=320$, and the one indicated by – – –.

For the convergence study the reference grid is coarsened by omitting consecutively every other point. The stimulation frequency is $f^* = 1000$ Hz and the inflow velocity $u_{in} = 3 \cdot 10^{-5}$ m/s. The time step size is kept constant at $\Delta t = 4.1 \cdot 10^{-9}$. Length scales are non-dimensionalised with the length of the stapes footplate, $L^* = 3$ mm.

The immersed boundary method is known to suffer from volume leakage problems (Givelberg, 2012; Peskin & Printz, 1993). However, it has to be noted that in the implementation used in the present thesis only the basilar membrane is modelled as an immersed boundary. The rigid
2.4 Immersed boundary approach

Figure 2.7: Comparison of the fluid volumes $V^{\text{osc}}_{\text{BM}}$ (— —) and $V_{\text{RW}}$ (- - -), sum of both (- - -) during 5 cycles of steady state: (a) linear scaling; (b) logarithmic scaling of the ordinate axis.

Bony walls, in contrast, are treated as outer bounds of the computational domain where Dirichlet boundary conditions are applied. In the model presented here, no significant volume leakage is observed. As is shown in the following, the fluid volume below the basilar membrane remains constant over time.

Figure 2.7 evaluates the change in fluid volume in a simulation which is representative for those presented in the following chapters. Length scales are non-dimensionalised with the length of the stapes footplate, $L^* = 3 \text{ mm}$, and the time scales with $t^* = L^*/U^* = 0.01 \text{ s}$. The figure compares two fluid volumes. One fluid volume is bounded by the rigid walls of the box and by the basilar membrane ($0 \leq x \leq 12, 0 \leq y \leq y_{\text{BM}}$). This volume changes with time because the basilar membrane is deflected by the inflow/outflow at the oval window. This oscillatory part of the fluid body below the basilar membrane, $V^{\text{osc}}_{\text{BM}}$, is the first fluid volume considered in Fig. 2.7. The second is the fluid volume which passes through the round window, $V_{\text{RW}}$. During stimulation at the oval window, a certain fluid volume $V_{\text{OW}}$ enters the box and leads to a deflection of the basilar membrane. If the membrane is impermeable and no volume leakage occurs, the membrane deflection exactly balances the fluid volume which enters through the oval window, $V^{\text{osc}}_{\text{BM}} = V_{\text{OW}}$. At the same time, the membrane deflection pushes the fluid volume $V_{\text{RW}}$ through the round window which has to equal the volume which entered through the oval window, $V_{\text{OW}} = V_{\text{RW}}$. Consequently, the two volumes
regarded in Fig. 2.7 must equal if no losses occur, $V_{BM}^{osc} = V_{RW}$.

Figure 2.7 shows the oscillation of the two volumes during five stimulation cycles in the steady state. They amount to $V_{BM}^{osc} \approx 1.5 \cdot 10^{-6}$ and $V_{RW} \approx 1.5 \cdot 10^{-6}$. As Fig. 2.7(b) shows, they sum up to a net volume loss of $V_\Delta \approx 4 \cdot 10^{-9}$. This volume error remains below the accuracy of the iterative pressure solver. Reduction of the mesh width leads to further reduction of the volume error such that the immersed boundary model for the basilar membrane shows good convergence behaviour.
Chapter 3

Cochlear Mechanics

This chapter presents the simulation results for the travelling wave motion of the basilar membrane and of the fluid. Section 3.1 addresses the primary wave system, investigating the instantaneous travelling wave (Sec. 3.1.1) and comparing the simulated results to the analytical predictions by Lighthill (Sec. 3.1.2). While these sections concentrate on one exemplary stimulation condition, Sec. 3.2 presents the peak amplitudes of the basilar membrane for varying frequencies. The findings of this chapter are summarised in Chap. 6.

The results presented in this chapter are partially published in Edom et al. (2013) and Edom et al. (2014).

All results of this chapter are obtained from simulations which are started from zero initial conditions, i.e., with the flow field and the basilar membrane at rest. The presented results show the steady state which is reached to a sufficient level of accuracy after 25 periods of the harmonic stimulation. The results figures are given in non-dimensional numbers with length scales relative to $L^*$, velocities relative to $U^*$ and time scales relative to $L^*/U^*$ indicated below.

Typical turn-around times of simulations are indicated in Sec. 2.1.

3.1 Primary wave system

In the present work the travelling wave in the fluid and on the basilar membrane oscillating at the stimulation frequency is denoted as primary wave. The term is used in order to distinct this fluid motion from the mean motion of the steady streaming (Chap. 4) and from movements oscillating at higher harmonics of the stimulation frequency (Sec. 4.2.2).

This section shows the primary wave of the transversal membrane displacement. The instantaneous fluid motion is presented and compared to the analytical predictions by Lighthill (1992).

Unless stated otherwise, the results are obtained for a harmonic stimulation with frequency $f^* = 1000\,\text{Hz}$ and inflow velocity $U_{\text{in}}^* = 3 \cdot 10^{-5}\,\text{m/s}$ at the oval window. According to the measurements by
Sim et al. (2010) this is equivalent to a sound signal of about 76 dB ear canal pressure. The values lead to a Reynolds number of $Re = 0.09$ and a Womersley number of $\alpha = 238$; thereby the length of the stapes footplate is used as typical length scale, $L^* = 3 \text{ mm}$, and the inflow velocity at the oval window as typical velocity, $U^* = U_{in}^*$. For this stimulation, the characteristic place is situated at $x^*_s = 4.8$. Apart from a longitudinal shift of the characteristic place the primary wave shows quantitatively no decisive differences for other frequencies or inflow velocities.

3.1.1 Travelling wave

The travelling wave on the basilar membrane (Fig. 3.1(a)) is characterised by an increase in the amplitudes of the transversal deflection $\eta_y$ as the characteristic place is approached. After passing $x_s$, the amplitudes decrease steeply. The wave-length $\lambda$ and the phase velocity $c_{ph}$ decrease as the wave propagates along the cochlea and vanish behind the characteristic place (Fig. 3.1(b)). The longitudinal membrane motion $\eta_x$ is discussed in Sec. 4.2.2.

The fluid velocities (Fig. 3.2) increase as the wave propagates along the cochlea. The largest velocities are present at the characteristic place, either at the edges of the boundary layers which form at the basilar membrane ($x$-component) or on the membrane resting position ($y$-component). These maximum amplitudes are about 30 times larger
than the inflow velocity at the oval window. Behind the characteristic place, the fluid is practically at rest. Fig. 3.3 illustrates the streamlines of the instantaneous fluid motion and the amplitudes of the local velocity vector. The vorticity of the flow field vanishes away from the boundary layers at the membrane (Fig. 3.3) such that the bulk flow of the primary wave is irrotational and can be described by a velocity potential.

Passive tracer particles in the cochlea (Fig. 3.4) move on circular
trajectories. Their diameters increase toward the characteristic place and toward the basilar membrane due to the increasing fluid velocities. The closer the particles are to the membrane, the more their path becomes an oblate ellipse with nearly exclusively transversal motion (cf. inset in Fig. 3.4).

The travelling wave of the pressure field is shown in Fig. 3.5. The pressure is set to zero at the round window. The pressure wave exhibits maximum values in the inflow/outflow region of the scala vestibuli. The amplitudes decrease toward the characteristic place from whereon they are constant. The amplitudes in the scala tympani first increase away from the round window and then decrease to reach behind the characteristic place the same constant value as in the scala vestibuli. During one inflow period, the constant pressure value oscillates (Fig. 3.6(a) for
3.1 Primary wave system

Figure 3.5: Pressure field of the travelling wave at 1000 Hz, \( p = 0 \) at the round window: instantaneous pressure field when the stapes is moving out of the cochlea (\( \cdots \cdots \) exaggerated basilar membrane displacement).

\[
\begin{array}{ll}
\text{(a)} & \\
\text{(b)} & 
\end{array}
\]

Figure 3.6: Pressure field of the travelling wave at 1000 Hz, \( p = 0 \) at the round window: (a) amplitudes (\( \cdots \cdots \)) and instantaneous values (\( \cdots \cdots \)) of the pressure waves in the middle of the scalae vestibuli (black) and tympani (blue); (b) amplitude (\( \cdots \cdots \)) and instantaneous value (\( \cdots \cdots \)) of the vertical pressure difference \( \Delta p \) across the basilar membrane.

\( x \gtrsim 5 \). The pressure difference across the basilar membrane (Fig. 3.6(b)) is maximal beneath the stapes (\( x \lesssim 1.2 \)) and decays toward the characteristic place. Behind \( x_* \) it approaches steeply zero difference, \( \Delta p = 0 \).

3.1.2 Comparison with Lighthill’s analytical predictions

Lighthill (1992) solves the flow field of the primary wave system analytically. To evaluate these predictions, the wave number \( k(x) \) and the transversal velocity amplitude \( V(x) \) of the membrane motion are necessary, in the subsequent comparison they are taken from the simulations. Lighthill assumes only small changes in \( k \) or in \( x \) and writes
Figure 3.7: Comparison of the simulation results with Lighthill’s predictions: instantaneous velocity profiles for $u$ and $v$ at the characteristic place at different instants of time (— — —, blue: simulation, – – –: analytical prediction, Eq. [A4]) .

the wave ansatz as $\exp\{i(\omega t - k x)\}$. Because the wave number increases exponentially with $x$ (cf. Fig. 3.1 b), the original term is rewritten as $\exp\{i(\omega t - \int_0^x k(\tilde{x}) d\tilde{x})\}$. Lighthill’s solution [A4] (brackets $\lbrack$ indicate equations in Lighthill (1992)) then reads

$$u^L = i A(x) e^{i(\omega t - \int_0^x k(\tilde{x}) d\tilde{x})} (e^{-k(x)\tilde{y}} - e^{-K(x)\tilde{y}}),$$

$$v^L = A(x) e^{i(\omega t - \int_0^x k(\tilde{x}) d\tilde{x})} (e^{-k(x)\tilde{y}} - k(x)K(x)^{-1} e^{-K(x)\tilde{y}}),$$

(3.1)

where the vertical axis $\tilde{y}$ originates at the basilar membrane at $y = 0.24$ and with the constants $A$ and $K$ satisfying [A5],

$$A(1 - k(x)K(x)^{-1}) = V(x), \quad K(x)^2 = k(x)^2 + i\omega\nu^{-1}. \quad (3.2)$$

The first and the second terms in the expressions (3.1) divide the fluid velocities into an irrotational motion outside the boundary layer and a flow inside the Stokes boundary layers, respectively.

The simulated velocity profiles compare well to the analytical predictions in the vicinity of the characteristic place (Fig. 3.7). Since Lighthill assumes a semi-infinite domain, the bounding walls of the cochlea lead to small differences (insets in Fig. 3.7).

Away from the characteristic place and from the membrane, the differences between the simulated velocities and the analytical predictions increase. This can be explained by effects of the geometrical setup, i.e., by the influence of the bounding walls and of the inflow/outflow regions.
3.1 Primary wave system

The instantaneous travelling waves (Fig. 3.8) show a slight phase shift in the boundary layers when compared to the bulk flow. This is in agreement with theoretical fluid dynamics. Differences for $x \leq 2$ can be explained by effects of the inflow and outflow at the round and oval windows. These are not present in Lighthill (1992) and influence the local fluid directions. The amplitudes of the travelling wave are shown in Figs. 3.9 and 3.10. The simulated axial component is larger than the analytical prediction in the upper half of the scala in front of the characteristic place which again can be explained by the inflow/outflow region. The simulated transversal velocities are smaller than the prediction by Lighthill towards the upper wall due to the zero-velocity boundary condition.
Figure 3.8: Comparison of the simulation results with Lighthill’s predictions: instantaneous travelling wave at different positions $y$, amplitudes normalised (– – –: simulation; – – –, coloured: analytical prediction, Eq. [A4]; – – –, coloured: indicates the $y$-position of the respective velocity profile; — —: maximum velocity amplitudes at the characteristic place).
3.1 Primary wave system

Figure 3.9: Comparison of the simulation results with Lighthill’s predictions: travelling wave amplitudes at different positions $y$, amplitudes normalised (-- --: simulation; ..., coloured: analytical prediction Eq. [A4] (normalised to compare the shape); ..., coloured: analytical prediction, Eq. [A4] (normalised to compare the peak amplitude); ..., coloured: indicates the $y$-position of the respective velocity profile; — —: maximum velocity amplitudes at the characteristic place).
Figure 3.10: Comparison of the simulation results with Lighthill’s predictions: travelling wave amplitudes at different positions $x$, amplitudes normalised (– – –: simulation; — —, coloured: analytical prediction, Eq. [A4] (normalised to compare the shape); – – –, coloured: analytical prediction, Eq. [A4] (normalised to compare the peak amplitude); — —: maximum amplitudes of the basilar membrane deflection).
3.2 Basilar membrane peak amplitudes for piston-like stapes motion

Section 3.1 studies the primary wave system in the cochlea for one exemplary stimulation condition \( f^* = 1000 \text{ Hz}, U_{in}^* = 3 \cdot 10^{-5} \text{ m/s} \). The present section summarises the simulation results for other frequencies and inflow velocities in terms of the amplitudes of the basilar membrane deflection. The characteristic places of such frequencies are shown in Fig. 3.11 in the tonotopic map of the present cochlea model. The places of resonance are distributed exponentially along the cochlear length.

The travelling wave amplitudes increase as the stimulation frequency decreases (Fig. 3.12 a). The shape of the travelling wave envelopes is the same for all frequencies when the peak amplitudes are normalised and when the curves are shifted along \( x \) such that the characteristic places overlap (Fig. 3.12 (b)). Figure 3.13 (a) shows the peak amplitudes for different frequencies due to stimulation with \( U_{in}^* = 3 \cdot 10^{-5} \text{ m/s} \). Further, the graph indicates isolines of the peak amplitudes for reduced inflow velocities. Figure 3.13 (b) indicates the peak amplitudes for a constant maximum ear canal pressure of \( p_{EC} = 1 \text{ Pa} = 94 \text{ dB} \) for all frequencies along with isolines for reduced stimulation intensities. The stapes velocities (Fig. 3.14) for these stimulations correspond to the measurements by Sim et al. (2010).

The maximum deflection at 94 dB is about 1.5 \( \mu \text{m} \) and thus remains several orders of magnitudes below the dimensions of the cochlea.

![Figure 3.11: Tonotopic map of the cochlea model of the present thesis.](image-url)
Figure 3.12: Travelling wave amplitudes of the basilar membrane deflection $\eta_y$ due to rocking stapes stimulation at different frequencies: (a) amplitudes, (b) normalised amplitudes, vertical lines for the high frequencies are present because the travelling wave reaches the left-hand bound of the cochlear box.

Figure 3.13: Peak amplitudes of the basilar membrane deflection $\eta_y$: (a) for constant maximum inflow velocity $U_{in}^* = 3 \cdot 10^{-5} \text{ m/s}$; (b) for constant maximum ear canal pressure $p_{EC} = 1 \text{ Pa}$; peak amplitudes due to piston-like stimulation (■) and isolines for reduced inflow velocities at $-10 \text{ dB}$ each (— —, coloured).
3.2 Basilar membrane peak amplitudes

Figure 3.14: Velocities of the piston-like stapes motion for different frequencies at 1 Pa ear canal pressure from Sim et al. (2010) (— —), value for constant-velocity simulation (— — —).
Chapter 4

Steady Streaming in a Cochlea

This chapter examines the steady streaming in the cochlea. Section 4.1 familiarises the reader with basic aspects of the steady streaming. The different velocity fields of steady streaming are introduced (Sec. 4.1.1). Further, various streaming phenomena are addressed and characteristic properties of the cochlea are pointed out which distinguish this system from more classical ones which induce steady streaming (Sec. 4.1.2). Studies of steady streaming in the cochlea are pointed out and briefly summarised (4.1.3).

Section 4.2 presents the simulated flow fields of steady streaming in the cochlea, i.e., the Eulerian and Lagrangian streaming and the Stokes drift (Sec. 4.2.1), and phenomena related to the steady streaming which influence the basilar membrane displacement (Sec. 4.2.2). The simulation results are compared to Lighthill’s analytical predictions (Sec. 4.2.3).

Sources of steady streaming in the cochlea are investigated in Sec. 4.3. One component of the steady streaming is generated by the basilar membrane motion (Sec. 4.3.1) and a second component by the Reynolds stresses of the flow field (Sec. 4.3.2). The basilar membrane as a source of steady streaming explains differences between the numerical results and the analytical prediction by Lighthill (Sec. 4.3.2).

Section 4.4 indicates the steady streaming velocities for stimulations at different frequencies and intensities. The chapter is concluded by Sec. 4.5 pointing out possible physiological consequences of the steady streaming in the inner ear.

The findings of this chapter are summarised in Chap. 6.

The results presented in this chapter are partially published in Edom et al. (2014).

All results of this chapter are obtained from simulations which are started from zero initial conditions, i.e., with the flow field and the basilar membrane at rest. The presented results show the steady state which is reached to a sufficient level of accuracy after 25 periods of the harmonic stimulation. The results figures are given in non-dimensional numbers.
with length scales relative to $L^*$, velocities relative to $U^*$ and time scales relative to $L^*/U^*$ indicated in this chapter.

Typical turn-around times of simulations are indicated in Sec. 2.1.

4.1 Aspects of steady streaming

This section introduces the different velocity fields of steady streaming (Sec. 4.1.1). Further an overview of systems which generate steady streaming is given and it is pointed out how the cochlea is characterised in comparison to classical streaming-generating systems (Sec. 4.1.2). Previous studies on the steady streaming in the cochlea are addressed (Sec. 4.1.3).

4.1.1 Velocity fields of steady streaming

Steady streaming is a time-averaged fluid motion which is generated by an external oscillatory primary flow of zero mean. It is a non-linear phenomenon, i.e., it is induced by non-linear effects of the fluid motion such as Reynolds stresses.

The steady streaming is also known as acoustic streaming. Riley (2001) points this out as "misleading because it implies a degree of compressibility in the fluid, and many of the streaming phenomena of interest are associated with incompressible flows" (Riley, 2001, p. 43). To assess the steady streaming often the instantaneous flow field is averaged in time. Therefore the steady streaming is also referred to as mean flow. This terminology is also used in the present work.

When investigating steady streaming it is important to distinguish between Eulerian and Lagrangian mean motions. The Eulerian mean flow field $\mathbf{u}_E = (u_E, v_E)$ is the temporal average of the instantaneous fluid velocities at fixed positions in space over one stimulation period $T = 1/f$,

$$\mathbf{u}_E(x) = \overline{\mathbf{u}(x)} = \frac{1}{T} \int_{t-T}^{t} \mathbf{u}(\mathbf{x}, \tilde{t}) \, d\tilde{t}. \quad (4.1)$$

The Lagrangian mean velocity $\mathbf{u}_L = (u_L, v_L)$ is the temporal average over $T$ of the instantaneous velocities of moving fluid particles. This mean velocity can also be obtained by regarding the distance

$$\Delta \mathbf{x}(t) = \mathbf{x}_p(t) - \mathbf{x}_p(t - T) \quad (4.2)$$
Figure 4.1: Trajectory of a fluid particle illustrating the displacement of the particle during one period of the stimulation frequency from the point $\mathbf{x}_p(t)$ to the point $\mathbf{x}_p(t + T)$. 

which a particle travels during one period of the stimulation frequency (Fig. 4.1). The location $\mathbf{x}_p(t)$ can be obtained from

$$\mathbf{x}_p(t) = \mathbf{x}_p(0) + \int_0^t \mathbf{u}(\mathbf{x}_p(\tilde{t}), \tilde{t}) \, d\tilde{t}. \quad (4.3)$$

The Lagrangian mean velocity follows from

$$\mathbf{u}_L = \Delta \mathbf{x}/T. \quad (4.4)$$

In this work also the well-known Stokes drift $\mathbf{u}_M = (u_M, v_M)$ is considered as a steady streaming flow despite its kinematic nature. In the present work the term Stokes drift denotes the difference between the Eulerian and Lagrangian mean velocities, $\mathbf{u}_M = \mathbf{u}_L - \mathbf{u}_E$. The following approximation illustrate the kinematic character of the Stokes drift. The instantaneous Eulerian velocity is assumed as $\mathbf{u}(\mathbf{x}, t) = \mathbf{u}(\mathbf{x}) + \text{Re} \{ \hat{\mathbf{u}}(\mathbf{x}) \exp(i\omega t) \}$. From (4.3) then follows for sufficiently small velocity magnitudes, as it is the case in the investigation of the present work, that

$$\mathbf{u}_M = -\text{Re} \frac{i(\nabla \hat{\mathbf{u}})^\dagger \hat{\mathbf{u}}}{2\omega}, \quad (4.5)$$

where the superscript $\dagger$ denotes the conjugate complex. This expression illustrates that the Stokes drift is generated by local gradients of the primary wave.
4.1.2 Systems of steady streaming

There exist different types of steady streaming according to different situations in which this mean flow is induced. This section points out some of these steady streaming types. Detailed introductions into various steady streaming phenomena are given in Boluriaan & Morris (2003); Lighthill (1978); Riley (1998, 2001).

The Rayleigh streaming is a steady motion induced by standing sound waves between plane walls (standing wave resonator). Another popular streaming phenomenon is the quartz wind which is induced by a high-intensity beam of sound in a body of fluid. Further, jet driven streaming flows are known. Here a viscous fluid is sucked in and ejected through an orifice. Vortices in the jet shear layer lead then to the mean motion.

There are two situations in which steady streaming is observed and which are more similar to the set-up of the cochlea than the systems pointed out above. One involves travelling waves and the other one vibrating walls. These are characteristics of the basilar membrane motion in the cochlea.

An example for steady streaming in the presence of travelling waves is the Stokes drift phenomenon which originally has been described for waves propagating along the free surface of deep water (Stokes, 1847). Further, for free-surface waves travelling over a circular cylinder, which is immersed into the water, a steady flow is reported which is not induced by viscosity and which is present on top of a Stokes drift (Riley & Yan, 1996).

Next, steady streaming is known to be induced by vibrating walls. Examples are the studies by Bradley (1996), Nguyen & White (2000) and Lucchini & Charru (2005). The first two publications are of special interest for the steady streaming in the cochlea. Bradley (1996), studying the steady streaming in an acoustic radiator, points out a contribution to the steady streaming by the vibration of the wall itself. Nguyen & White (2000) examine the steady streaming generated in a microfluidic flexural plate wave device. Here waves on a flexible plate induce the steady streaming and are hence used to pump fluid through a channel.

The present work studies the steady streaming in the cochlea. In this system a membrane which is immersed into fluid is moved by a travelling wave. The fact that the wave is induced by acoustic stimulation might lead to the wrong assumption that acoustic waves are relevant in the cochlea which is not the case (cf. Sec. 2.1). Consequently, acoustic
phenomena do not play a role in the steady streaming of the cochlea.

The oscillatory motion in the cochlea exhibits low frequencies (20 Hz to 20 kHz) compared to the fluctuating flows in system which generate quartz wind. Also the phase speeds of the wave are small compared to the cases mentioned above. In contrast to the free surface waves referred to previously, the waves of the basilar membrane exhibit Stokes boundary layers in which Reynolds stresses are present as a source of steady streaming.

The fluctuating flow in the cochlea is further characterised by its steep decrease in wave speed and wave-length as the wave travels toward the characteristic place. The wave amplitude and wave velocity, in contrast, increase along the cochlea. Once the characteristic place has been passed, the wave vanishes nearly instantaneously. Altogether, these properties render the cochlea a system which differs considerably from the classical set-ups in which steady streaming has been studied.

4.1.3 Previous studies on steady streaming in the cochlea

The presence of steady streaming in the cochlea has already been suspected by von Békésy (1960) and Lesser & Berkley (1972) and a few more recent publications investigate this mean flow. The approaches and outcomes of these studies are addressed in this section.

Lighthill (1992) studies the cochlear mean motion analytically. Solutions for the Stokes drift and for a so-called slip velocity of the Eulerian mean motion are derived which will be discussed in further detail in the subsequent sections. Some assumptions differ from the cochlea model of the present thesis: Lighthill assumes a semi-infinite domain, as mentioned in Sec. 3.1.2. Further, the basilar membrane of the model used in the present thesis performs a two-dimensional motion whereas Lighthill assumes a one-dimensional motion. Finally, Lighthill uses a wave ansatz in time and in one spatial direction and solves the fluid motion locally in the vicinity of the characteristic place.

The contribution Böhnke & Scharff (2009) for the conference “Mechanics of Hearing” (2009, Keele, England) presents a modelling approach to study the steady streaming numerically in a finite element framework. The authors report that preliminary simulations exist but cannot show results for the mean motion.

The work Gerstenberger (2013) studies the steady streaming in the cochlea numerically in a two-dimensional tapered box geometry. A finite
element model is used. Within a two-stage approach with a perturbation expansion a first-order system of the linear fluid flow and of the fluid-structure interaction is solved and the second-order problem of the steady streaming is computed in a second step. The model includes the active amplification of the membrane motion through a linearisation of the approach by Mammano & Nobili (1993) and Nobili & Mammano (1996). Thereby sharper and higher membrane deflection peaks for active simulations than for passive ones are reproduced while the stimulation intensity dependent compressive non-linearity of the amplitude is not captured.

The Eulerian and Lagrangian mean flow fields presented by Gerstenberger (2013) are qualitatively very similar to those which are obtained with the model of the present thesis. Also the scaling of maximum mean velocities with the stimulation amplitudes seems to be the same. Because it is not clear which stimulation intensities are used in Gerstenberger (2013), the actual streaming velocities cannot be compared.

Gerstenberger (2013) compares some simulation results with the analytical predictions by Lighthill (1992). His comparison shows for the instantaneous velocity profiles small differences which are similar to the ones in the comparison presented in Sec. 3.1.2 of the present thesis. Further Gerstenberger (2013) investigates the simulated Reynolds stresses and compares them to Lighthill's solutions, reporting small deviations. Finally, Gerstenberger considers the slip velocity which is introduced by Lighthill (1992). He observes that the velocity he obtains from his simulations is larger than the analytically predicted one by Lighthill. Also in the present thesis the simulated slip velocity is larger than the one according to Lighthill (1992) (Sec. 4.3.2). An explanation for this difference is given in Sec. 4.3. Lighthill (1992) also provides a solution for the Stokes drift in the cochlea. For this quantity, Gerstenberger does not draw a comparison.

### 4.2 Steady streaming fields and phenomena

This section presents the fields of steady streaming in the cochlea, addressing the Eulerian and Lagrangian mean velocities and the Stokes drift (Sec. 4.2.1). Effects of the steady streaming on the basilar membrane motion are investigated (Sec. 4.2.2) and the simulation results are compared to the analytical solution by Lighthill (1992) (Sec. 4.2.3).

The simulated results are obtained for a harmonic stimulation with
piston-like stapes motion $f^* = 1000$ Hz and with an inflow velocity $U_{in}^* = 3 \cdot 10^{-5}$ m/s, corresponding to a sound signal of about 76 dB ear canal pressure (Sim et al., 2010). The same parameters are used in Sec. 3.1. They yield a Reynolds number of $Re = 0.09$ and a Womersley number of $\alpha = 238$. The characteristic place is situated at $x^* = 4.8$. Results for other stimulation frequencies and intensities are summarised in Sec. 4.4 in terms of maximum Eulerian streaming velocities.

4.2.1 Eulerian streaming, Lagrangian streaming and Stokes drift in the cochlea

The Eulerian mean flow field is shown in Fig. 4.2(a) and the Lagrangian mean flow in Fig. 4.3(a). Both fluid motions show a large vortex pair where one vortex is situated above the basilar membrane and one below it. The vortex centres are situated at the characteristic place in $x$-direction and outside the boundary layer in $y$-direction. The vortex below the basilar membrane rotates in clockwise direction and, consequently, the vortex above the membrane in counter-clockwise direction. Therefore the flow direction in the basilar membrane region points in the positive $x$-direction.

The maximum Eulerian streaming velocities are present in $x$-direction at the characteristic place and in $y$-direction at the resting position of the basilar membrane. For the chosen stimulation the maximum Eulerian mean velocity reaches about 15% of the inflow velocity at the stapes or about 4.75 $\mu$m/s. The axial velocity $u_E$ at the characteristic place (Fig. 4.2(b)) shows a steep decrease from the maximum velocity at $y = 0.24$ to $u_E \approx 0$ in the region of the boundary layer edge. In the bulk of the flow field, small negative velocities are present.

The Lagrangian mean flow exhibits maximum velocities in $x$-direction at the characteristic place, as well, but in $y$-direction within the boundary layer. The amplitude is smaller than for the Eulerian mean flow and amounts to about 4% of the chosen inflow velocity or 1 $\mu$m/s. The mean motion at the resting position of the basilar membrane is zero, $u_{L,BM} = 0$. This can be explained by the elastic coupling of the membrane elements to fixed places: As soon as the steady state has been reached, the elements oscillate around their resting position of this steady state. In the Lagrangian mean the instantaneous velocities of each membrane element are averaged over time such that the steady state oscillation yields a zero Lagrangian streaming velocity at the basilar membrane resting position.
In the Eulerian average, in contrast, the mean fluid velocities at the fixed position $y = 0.24$ are considered. The membrane oscillation induces at this position velocities which point in the same direction during most of the oscillation cycle such that they are not averaged to zero. This effect is explained in more detail in Sec. 4.3.1.

The axial velocity $u_L$ at the characteristic place (Fig. 4.3(b)) increases from zero at the membrane resting position to a maximum within the boundary layer and decreases outside the boundary layer to approx-
The Stokes drift \( \mathbf{u}_M = \mathbf{u}_L - \mathbf{u}_E \) in shown in Fig. 4.4 (a). This flow field exhibits a vortex pair, as well. Since the Eulerian mean flow is faster than the Lagrangian one, the Stokes drift vortices rotate in the opposite direction compared to the vortices of the other mean flow fields. The centres of the rather flat Stokes drift vortices are situated in \( y \)-direction in the boundary layer and in \( x \)-direction approximately at the characteristic place.

The maximum velocity amplitude of the Stokes drift is present in \( x \)-direction at the characteristic place and in \( y \)-direction at the resting position of the basilar membrane. Because the Lagrangian mean at the membrane resting position is zero, \( \mathbf{u}_{L,\text{BM}} = 0 \), the Stokes drift at \( y = 0.24 \) equals the negative Eulerian mean at this position, \( \mathbf{u}_{M,\text{BM}} = -\mathbf{u}_{E,\text{BM}} \). This signifies that the Stokes drift cancels the Eulerian mean flow at this location. The axial velocity \( u_M \) at the characteristic place (Fig. 4.4(b)) increases from the minimum at the basilar membrane to a positive value approximately at the boundary layer edge and decreases to \( u_M \approx 0 \) away from the boundary layer. Consequently the Eulerian and Lagrangian streaming velocities are of nearly equal magnitude in the bulk of the flow.

The transversal components \( v_E \) and \( v_L \) of the Eulerian and Lagrangian mean velocities reach values on the order of \( 10^{-4} \) relative to the...
inflow velocity and the transversal component $v_M$ of the Stokes drift values on the order of $10^{-3}$. Therefore all streaming velocities in y-direction are two to three orders of magnitudes smaller than the corresponding axial velocities which can be regarded as a significant difference. The reason for the small amplitudes of the transversal steady streaming components is that the mean flow is induced mostly in axial direction by the streaming-generating non-linear phenomena. Further, the vertical walls of the box model deflect the axial streaming and thereby induce the small transversal component of the mean flow. The transversal streaming velocities are not further addressed in the present thesis due to their small amplitudes.

4.2.2 Effects of steady streaming on the basilar membrane motion

The membrane motion exhibits two characteristic properties in its axial component $\eta_x$ due to the steady streaming (Fig. 4.5(a)). This membrane motion can be divided into a steady part $\eta_x$, which is the temporal mean of $\eta_x$ over one period of the stimulation frequency, and an oscillatory part $\eta'_x$ which is present on top of the steady part such that $\eta_x = \eta^s_x + \eta'_x$. Both of these components are affected by non-linear effects which are related to the steady streaming.

The steady part $\eta^s_x$ of the axial motion (Fig. 4.5(b)) is not zero,
4.2 Steady streaming fields and phenomena

Figure 4.6: Trajectories of basilar membrane elements (— —) during one inflow cycle in the steady state and their starting positions (●); amplitude of the axial membrane motion \( \eta_x \) (— —, right axis). Arrows indicate directions of the steady axial membrane displacement. The axial membrane displacement \( \eta_x \) is exaggerated in the trajectories for visibility. In Fig. 3.4 the correct aspect ratio of \( \eta_x / \eta_y \) is maintained.

Unlike the temporal mean of the transversal oscillation \( \eta_y \), but shows a stretching of the basilar membrane at the characteristic place. The amplitude of this stretching is about \( 4.5 \cdot 10^{-7} = 1.35 \text{ nm} \) and thus just beyond the sensing threshold of the hair cells which is about \( 0.3 \text{ nm} \) (Dallos et al., 1996).

From the steady deflection results a steady axial restoring force which points toward the characteristic place. The stretching is inversely proportional to the axial membrane stiffness \( \kappa_x \), hence the axial restoring force is independent of the choice of \( \kappa_x \). Therefore the particular choice of the ratio \( \kappa_y / \kappa_x \) does not influence the presence of the stretching and the restoring force.

The steady displacement \( \bar{\eta}_x \) is induced by the transversal oscillation \( \eta_y \) of the basilar membrane as is addressed in more detail in Sec. 4.3.

The oscillatory part \( \eta'_x \) of the axial membrane motion (Fig. 4.5(b)) reaches maximum amplitudes at the characteristic place and beneath the stapes at \( x \approx 0.5 \). The maximum at the characteristic place is induced by the resonance between the stimulation frequency and the local eigenfrequency of the membrane. Here, the instantaneous deflections \( \eta_x \) do not cancel over one stimulation period. The maximum amplitudes at \( x \approx 0.5 \) are generated by the oscillating inflow and outflow at the round and oval windows. Here the instantaneous displacements \( \eta_x \) do cancel over one period and the steady part \( \bar{\eta}_x \) of the deflection is zero.

The component \( \eta'_x \) oscillates at twice the stimulation frequency. The
reason for this frequency doubling is that the non-linear phenomena which lead to the steady streaming inject energy into a higher harmonic and not only into the zero harmonic, i.e., the steady part of the membrane and fluid motion in the cochlea. The higher harmonic is generated by the quadratic non-linear term of the Navier-Stokes equations. The amplitudes of the higher harmonic are much smaller than those of the primary motion which dominates in the bulk of the flow. In the symmetric set-up of the present box model, however, the primary motion cancels in the symmetry plane at $y = 0.24$ such that the presence of the higher harmonic becomes visible in the membrane motion $\eta_x$.

As a consequence of the frequency doubling of the axial membrane oscillation the path of each membrane element looks like a Lissajous figure with a frequency ratio of 2:1 and a phase shift of $-\pi/4$, or a bent eight (Figs. 4.6 and 4.7). The similarity with the Lissajous figures is illustrated in Fig. 4.7 in a comparison of Lissajous curves for different frequency ratios and phase shifts.
4.2.3 Comparison with Lighthill’s analytical predictions

In Sec. 3.1.2 analytical solutions by Lighthill (1992) for the instantaneous flow field are used for comparison with the simulation results. Lighthill (1992) also derives analytical solutions for aspects of the steady streaming in the cochlea, i.e., for the Stokes drift and for a so-called slip velocity. The slip velocity can be understood as a non-zero boundary condition for the bulk flow and is derived from the effects of the Reynolds stresses on the flow. In the following, the simulation results are compared to these analytical predictions. As in Sec. 3.1.2 the wave number $k$ and the velocity amplitude $V$ of the transversal membrane motion are taken from the simulations to evaluate Lighthill’s solutions.

The Stokes drift $u_{M,BM}$ on the basilar membrane resting position is derived by Lighthill as (Eq. [75]; the brackets [·] indicate equations in Lighthill (1992))

$$u_{M,BM}^L = -\frac{V^2}{\sqrt{8\nu\omega}}. \quad (4.6)$$

The simulated result agrees well with this prediction (Fig. 4.8); the curves are nearly identical.

Further, Lighthill gives a solution for the Stokes drift in the flow field
Figure 4.9: Comparison of the simulation results with Lighthill’s predictions for the axial Stokes drift $u_M$: (a) profiles of the Stokes drift at different positions $y$, amplitudes normalised ($\ldots \ldots$: simulation; $\ldots \ldots$, coloured: analytical prediction, Eq. [B 13]; $\ldots \ldots$, coloured: indicates the $y$-position of the respective velocity profile; $\ldots \ldots$: maximum amplitudes of $u_M$ at the characteristic place); (b) profiles of the Stokes drift at different positions $x$, amplitudes normalised ($\ldots \ldots$: simulation; $\ldots \ldots$, coloured: analytical prediction, Eq. [B 13]; $\ldots \ldots$: maximum amplitudes of $u_M$ at the resting position of the basilar membrane); the simulated and analytically predicted velocities are normalised to compare the shape of the curves.
4.2 Steady streaming fields and phenomena

\[
\begin{align*}
\text{(Eq. [B13]),} \\
\quad u_M = & \frac{1}{2} \text{Re} \left\{ \frac{A}{\omega} \left( e^{-k\tilde{y}} - e^{-K\tilde{y}} \right) \hat{A}\hat{k} \left( e^{-\tilde{k}\tilde{y}} - e^{-\tilde{K}\tilde{y}} \right) \\
& + iA \left( -ke^{-k\tilde{y}} + Ke^{-K\tilde{y}} \right) \hat{A}(-i\omega)^{-1} \left( e^{-\tilde{k}\tilde{y}} - \tilde{k}\tilde{K}^{-1}e^{-\tilde{K}\tilde{y}} \right) \right\}, \\
\quad \text{(4.7)}
\end{align*}
\]

where \( \tilde{y} \) is the vertical axis and parallel to the \( y \)-axis of the present model but originating at \( y_{BM} \) such that \( y(\tilde{y} = 0) = 0.24 \). The tilde \( \tilde{\cdot} \) denotes in Eq. (4.7) the complex conjugate and the coefficients \( A, k \) and \( K \) are defined by Eq. (3.2) or [A5]. Figure 4.9 shows good agreement between the Stokes drift in the bulk of the flow and the analytical solution. As discussed in Sec. 3.1.2 for the instantaneous velocity fields, small differences arise due to the presence of the bounding walls and of the inflow/outflow region because both are neglected in Lighthill (1992).

The \( y \)-component of the Stokes drift vanishes in Lighthills solution (Eq. [B17]),

\[
v_M^L = 0. \\
\quad \text{(4.8)}
\]

The simulated transversal velocities of the Stokes drift are on the order of \( 10^{-3} \) relative to the inflow velocity as mentioned previously. A possible reason for this deviation between the simulated and the analytically predicted solutions is that Lighthill (1992) considers an unbounded domain whereas in the present simulations the bounding walls and the position of the inflow and outflow regions might influence the fluid flow such that the steady streaming is two-dimensional.

Besides the Stokes drift, Lighthill gives an analytical solution for an Eulerian streaming velocity by defining a slip velocity (Eq. [92]),

\[
\quad u_s^E = \frac{1}{4} \frac{V^2 k}{\omega} - \frac{3}{4} \frac{V(dV/dx)}{\omega}. \\
\quad \text{(4.9)}
\]

The first term and one third of the second term of this expression are contributed by the Reynolds shear stresses \( -\rho\overline{u'v'} \) and the remaining two thirds of the second term by the Reynolds normal stresses \( -\rho\overline{u'u'} \) (the contributions \( -\rho\overline{v'u'} \) and \( -\rho\overline{v'v'} \) drop out because of the one-dimensional steady streaming in the unbounded domain). The prime \( ' \) denotes the fluctuating part of the velocity field, \( (u, v) = (\overline{u}, \overline{v}) + (u', v') \). The simulated Eulerian flow field does not compare well to the analytical solution Eq. (4.9). Examination of the Eulerian flow profile Fig. 4.2(b) shows
that it is difficult to detect a distinct edge of the Stokes boundary layer where the slip velocity could apply. The reason for the discrepancy between the simulated Eulerian mean flow and $u_s'$ is that, in addition to the Reynolds stresses considered by Lighthill, a second mechanism leads to the steady streaming. The contribution of this streaming component is missing in Eq. (4.9). The simulation results compare better to the analytical prediction if the second source of streaming is accounted for and if a corrected slip velocity is considered. This is shown in the following section.

4.3 Sources of steady streaming in the cochlea

Two mechanisms lead to the steady streaming in the cochlea, first, the Reynolds stresses, which have been considered by Lighthill (1992), and second, the oscillations of the basilar membrane. This section points out how the steady streaming is induced by the two mechanisms and visualises their contributions to the mean flow. The sum of these components yields the streaming flow field shown in Sec. 4.2.1.

This section concentrates on the Eulerian flow fields of the steady streaming.

4.3.1 Membrane-induced streaming

To investigate the effect of the membrane motion on the steady streaming, the unsteady Stokes equations are solved in the simulations instead of the Navier-Stokes equations. This modified model neglects the non-linear advective term and therefore no Reynolds-stress-induced steady streaming is generated. The primary wave system of this modified model is practically identical to the one discussed in Sec. 3. This implicates two things: that the travelling wave is governed by the unsteady Stokes equations and that the Stokes drift is not affected by this change in the model.

Although the equations for the fluid motion which are solved in this modified model contain no apparent non-linearities, the Eulerian mean of the flow field is not zero (Fig. 4.10(a)). It consists of a pair of large vortices, as the original system shown in Fig. 4.2. Again one vortex is located above the basilar membrane and the other one below it. The vortex centres are aligned with the characteristic place and lay outside the boundary layer. The vortex below the basilar membrane rotates
4.3 Sources of steady streaming in the cochlea

Figure 4.10: Eulerian mean flow field induced by the oscillating basilar membrane at 1000 Hz: (a) magnitudes and streamlines, (b) axial velocity profile at the characteristic place. (The small wiggles in (a) at \( x > 5.75 \) are a numerical artefact due to the very slow convergence of the steady state oscillations.)

in clockwise direction. Maximum streaming velocities are present in \( x \)-direction at the characteristic place and in \( y \)-direction at the resting position of the basilar membrane. The maximum Eulerian velocity is the same as in the original system. Because of \( u_M = -u_E \) at the resting position of the basilar membrane the maximum velocity amplitudes are also identical to the maximum amplitudes of the Stokes drift shown in Fig. 4.4.

The axial velocity of the membrane-induced steady streaming \( u_{BM}^E \) at the characteristic place (Fig. 4.10(b)) decreases away from the resting position of the basilar membrane. During decreasing, this mean velocity does not exhibit any influence of the boundary layers at the membrane, i.e., the velocity continuously approaches zero at the bounding walls taking negative values about 0.06 length units away from the membrane due to the vortex system. This indicates that the steady streaming due to the membrane motion contains no boundary layer length scales.

The \( y \)-component of the steady streaming in this modified model reaches values up to 0.009 and is therefore significantly smaller than the axial component. Similar to the transversal streaming velocities discussed before (Sec. 4.2.1) this component might be induced by a deflection of the axial mean flow at the bounding walls. Due to the small velocity amplitudes \( u_{BM}^E \) is not further investigated.

The Eulerian mean flow field in Fig. 4.10 is different from zero because the basilar membrane induces steady streaming. The underlying
mechanism is illustrated in Fig. 4.11. When the membrane is deflected in positive $y$-direction, the travelling wave exhibits fluid velocities in positive $x$-direction below the membrane and therefore also on the resting position of the membrane. When the membrane is displaced into negative $y$-direction, the fluid velocities on the resting position (which is now situated above the basilar membrane) point again in positive $x$-direction. Therefore the instantaneous velocity at $y = 0.24$ is positive during most of the oscillation cycle and non-zero Eulerian mean flow velocities result.

The membrane-induced steady streaming can also be investigated analytically. Lighthill (1992) computes the instantaneous axial velocity in the boundary layer as (according to Eq. [63])

$$u_{\text{BL}}(x, \ddot{y}, t) = \text{Re} \left\{ iV(x) \left( 1 - e^{-\ddot{y}\sqrt{i\omega/\nu}} \right) e^{i(\omega t - kx)} \right\}.$$  

(4.10)

This expression neglects the transversal membrane deflection by assuming that the membrane remains at $\ddot{y} = 0$ during the oscillation cycle. Because consequently Eq. (4.10) yields at $\ddot{y} = 0$ instantaneous axial velocities of $u_{\text{BL}}(x, 0, t) = 0$ during the oscillation cycle, a Eulerian mean flow of $u_{E,\text{BM}} = 0$ results at the resting position of the basilar membrane. If instead the membrane displacement is approximated as a transversal shift $\eta_y$, the instantaneous velocity profiles are shifted in $y$-direction by $\eta_y$. Figure 4.11 illustrates that this shift in $y$-direction induces at the resting position of the membrane instantaneous velocities of $u_{\text{BL}}(x, 0, t) \neq 0$ throughout most of the oscillation cycle. The Eulerian mean velocity at

Figure 4.11: Instantaneous velocity profiles at the transversally deflected basilar membrane: the axial velocities at the resting position of the basilar membrane (---) are positive during most of the stimulation cycle (bold arrows).
4.3 Sources of steady streaming in the cochlea

\( \ddot{y} = 0 \) can be obtained by linearising \( u_{BL}(x, \ddot{y} - \eta_y, t) \) about \( \ddot{y} = 0 \),

\[
\left. u_E \right|_{\ddot{y}=0} = \frac{1}{T} \int_{t}^{t+T} u_{BL}(x, \ddot{y} - \eta_y, \tilde{t}) \, d\tilde{t}
\approx \frac{1}{T} \int_{t}^{t+T} \left( u_{BL} - \eta_y \frac{\partial u_{BL}}{\partial \ddot{y}} \right) \bigg|_{\ddot{y}=0} \, d\tilde{t}.
\]  

(4.11)

The first term of the last line in Eq. (4.11) is zero, as pointed out above. The second term, in contrast, contributes to the Eulerian streaming. If the transversal membrane displacement is approximated by

\[
\eta_y = \text{Re} \left\{ -i V(x) / \omega \exp \{ i(\omega t - kx) \} \right\},
\]  

(4.12)

Eq. (4.11) yields

\[
\left. u_E \right|_{\ddot{y}=0} \approx \frac{V^2}{\sqrt{8\nu \omega}}.
\]  

(4.13)

This is identical to Lighthill’s solution [75] for the Stokes drift, reproduced in Eq. (4.6), with an inverse sign because of \( u_M = u_L - u_E \) where \( u_L = 0 \). Further Eq. (4.13) shows that the Eulerian streaming due to the membrane motion cancels the Stokes drift at \( \ddot{y} = 0 \).

The mechanism addressed above explains the steady streaming shown in Fig. 4.10. It is generated by a non-linearity induced by the moving membrane: The basilar membrane exerts a force on the fluid which oscillates both in amplitude, due to the dependence of the force on the membrane deflection, and in space, due to the membrane oscillation around its resting position.

This non-linearity also leads to the steady part of the axial membrane deflection \( \eta_x \) (Fig. 4.5). When a membrane element is deflected, it is pulled back to its resting position by an elastic reaction force. This induces a flow field as schematically drawn in Fig. 4.12. During the oscillation cycle the transversal component of the induced velocity cancels while the axial component points always in the same direction. This induces on the left of the element a flow in negative \( x \)-direction and a flow in positive \( x \)-direction on the right of the element. When considering two neighbouring elements, the induced flow cancels partially because the velocities between the elements point in opposite directions. During the oscillation of the basilar membrane, however, neighbouring membrane elements show different deflection amplitudes which induce different velocity amplitudes. If of two neighbouring membrane elements the one on
the right-hand side exerts a larger elastic reaction force due to its larger deflection, the element induces larger axial velocities such that the resulting velocity between the elements points in negative $x$-direction. If the left-hand side element is stronger deflected, the resulting velocity between the elements is positive. The amplitude distribution of $\eta_y$ along the cochlea (Fig. 3.1) then makes clear that on the left of the characteristic place a resulting mean velocity in negative $x$-direction is present and a positive mean velocity on the right of the characteristic place. These velocities explain the steady axial displacement away from the characteristic place and the observed membrane stretching.

4.3.2 Reynolds-stress-induced streaming

The Reynolds stresses which act in the boundary layers lead to steady streaming. To evaluate the contribution of this Reynolds-stress-induced steady streaming to the mean flow shown in Fig. 4.2 the model is modified such that the Navier-Stokes equations are solved, hence the non-linear advective terms which generate the Reynolds stresses are present, and such that the membrane-induced streaming is prevented. The latter is achieved by neglecting the displacements of the membrane during evaluation of the fluid-structure interaction. In the immersed boundary approach used in the present work (Sec. 2.4) this signifies that in this modified model the forces which the membrane exerts on the fluid are applied at the fixed position $y = 0.24$ during the complete oscillation cycle. Also the membrane velocity which yields the displacements $\eta$ is evaluated at this position. Despite these alterations nearly the same
Figure 4.13: Eulerian mean flow field induced by the Reynolds stresses at 1000 Hz: (a) magnitudes and streamlines, (b) axial velocity profile at the characteristic place. (The small wiggles in (a) at $x > 5.75$ are a numerical artefact due to the very slow convergence of the steady state oscillations.)

membrane oscillations as in the original model are computed. Also the primary wave system and the Stokes drift of this modified model remain practically unchanged compared to the original set-up.

The Eulerian mean flow of this modified model (Fig. 4.13(a)) shows again a vortex pair, one above and one below the basilar membrane. Their centres are situated at the characteristic place in $x$-direction and outside the boundary layer in $y$-direction. The vortex below the membrane rotates in counter-clockwise direction and therefore opposite to the previously investigated ones. Maximum amplitudes of the streaming velocities are present at the boundary layer edge and reach about 11% of the inflow velocity or $3.3 \, \mu m/s$. The mean velocity is zero on the resting position of the membrane, $u_{E,BM}^{Re} = 0$, because the forces due to the moving membrane are applied at $y = 0.24$ throughout the oscillation cycle and the no-slip boundary condition at the membrane prescribes $u_{BM} = 0$.

The steady streaming is governed by the linear Stokes equations. Therefore, the streaming fields shown in Figs. 4.10 and 4.13 which are generated by the membrane motion and the Reynolds stresses, respectively, can be added. The sum yields the streaming motion of the complete system (Fig. 4.2). The contributions of the two mechanisms which lead to steady streaming cancel each other partially because of the counter-rotating vortices such that the resulting mean velocities of the original model are rather small in the bulk of the flow.
The modified model of the present section explains the differences observed in Sec. 4.2.3 for the Eulerian slip velocity (4.9). Contrarily to the previously shown velocity profiles (Figs. 4.2(b), 4.3(b), 4.4(b), and 4.10(b)) the profile of the axial streaming velocity $u_{Re}$ at the characteristic place (Fig. 4.13(b)) for this modified model shows a clear influence of the boundary layers at the basilar membrane. The velocity at the boundary layer edge present in Fig. 4.13(b) can be identified as the slip velocity which Lighthill (1992) defines. However, this simulated velocity differs from the analytical prediction. The reason is that Lighthill imposes at the resting position of the basilar membrane an Eulerian streaming velocity of $u_{E,BM}^L = V^2/\sqrt{8\nu\omega}$ (Eq. [80]) as a boundary condition to compensate for the Stokes drift at the same position, $u_{M,BM}^L = -V^2/\sqrt{8\nu\omega}$ (cf. Eq. (4.6)), in order to fulfil the zero Lagrangian mean velocity $u_{L,BM} = 0$. The previous section shows that at $y_{BM}$ the Eulerian mean flow due to the membrane motion equals the Stokes drift and thus cancels it. The Eulerian streaming generated by the Reynolds stresses, in contrast, is zero at the basilar membrane resting position such that Lighthill’s above-mentioned boundary condition is not correct. Consequently Lighthill’s prediction for the slip velocity of Eq. (4.9) has to be corrected to

$$u_s = \frac{1}{4} \frac{V^2k}{\omega} - \frac{3}{4} \frac{V(dV/dx)}{\omega} - \frac{V^2}{\sqrt{8\nu\omega}},$$  

where the last term is new. As Fig. 4.14 shows the corrected slip velocity approximates the velocity on the boundary layer of the modified model.
much better than expression (4.9). The remaining differences might be due to the fact that Lighthill neglects the membrane deflection and hence the transversal shifting of the velocity profiles as discussed in Sec. 4.3.1.

To complete the investigation of the Reynolds stress-induced streaming Fig. 4.15 shows the gradients of the Reynolds stresses which are present in the flow field. They can be regarded as force densities which lead to the Eulerian streaming of the modified model.

The largest contribution to the streaming is made by the axial shear stress component $-\rho v' \partial u'/\partial y$ (Fig. 4.15(b)) while the axial normal stress component $-\rho u' \partial u'/\partial x$ (Fig. 4.15(a)) is smaller by more than two orders of magnitude and therefore negligible. The transversal contributions $-\rho u' \partial v'/\partial x$ and $-\rho v' \partial v'/\partial y$ (Fig. 4.15(c,d)) are nearly one order of magnitude smaller than the main component and show approximately the same amplitudes.
4.4 Amplitudes of steady streaming

The previous sections study the steady streaming for an exemplary stimulation condition with the frequency $f^* = 1000$ Hz and at a sound pressure level of 76 dB. The present section addresses the maximum Eulerian streaming velocities for other frequencies and stimulation intensities.

The maximum streaming velocity is found in all cases on the resting position of the basilar membrane and at the characteristic place. The flow fields show the same qualitative properties as the one presented in Fig. 4.2.

Figure 4.16 shows the maximum amplitudes of the Eulerian streaming for different stimulation frequencies. In Fig. 4.16(a) the same maximum inflow velocity $U_{in}^* = 3 \cdot 10^{-5}$ m/s is used for all frequencies and in
4.4 Amplitudes of steady streaming

Figure 4.16: Maximum simulated Eulerian streaming velocities (○) and maximum absolute values of the three terms of the corrected slip velocity (—: $\max_x |V^2/\sqrt{8\nu \omega}|$, -- --: $\max_x |V^2k/(4\omega)|$, - · -: $\max_x |3V(dV/dx)/(4\omega)|$, cf. Eq. 4.14): (a) for a constant maximum inflow velocity of $U^*_{in} = 3 \cdot 10^{-5}$ m/s (corresponds to 76 dB ear canal pressure at $f^* = 1000$ Hz), velocities given in dimensionless values; (b) for a constant maximum ear canal pressure of 94 dB, velocities given in dimensional values. The dotted lines ⋯ indicate a decay rate of (a) $1/f^2$ and (b) $1/f^5$, respectively.

Fig. 4.16(b) the same maximum ear canal pressure $p_{EC} = 1$ Pa is used such that the inflow velocity changes with the stimulation frequencies (cf. Fig. 3.14, p. 43). Because this implies that different characteristic velocities $U^*$ would have to be used for non-dimensionalisation, Fig. 4.16(b) shows the steady streaming velocities in dimensional numbers.

The influence of the frequency on the streaming velocities is not obvious. High frequencies lead to smaller streaming velocities and the largest mean velocities are present for lower frequencies, $250 \leq f^* \leq 1000$. Equation (4.14) illustrates that the streaming velocity depends with different scalings on the frequency because both the expressions $1/\omega$ and $1/\sqrt{\omega}$ are present. For the exemplary stimulation discussed in Secs. 4.2 and 4.3, $f^* = 1000$ Hz and $U^*_{in} = 3 \cdot 10^{-5}$ m/s, the maximum streaming velocity is dominated by the last term of Eq. (4.14), which scales with $1/\sqrt{\omega}$. Since it is possible that the other terms become dominant for different frequencies, Fig. 4.16 shows the amplitudes of the individual terms in Eq. (4.14). The term $V^2/\sqrt{8\nu \omega}$ dominates the streaming velocity for all frequencies and the other terms are at least one order of magnitude smaller.

Figure 4.16 indicates approximations for the decay of the maximum streaming velocities with frequency. For the constant stapes velocity
amplitudes the streaming velocities decrease for high frequencies roughly like $1/f^2$. The decay is steeper for constant ear canal pressure and is approximated by $1/f^5$. This indicates that the steady streaming is most relevant for moderate to low frequencies.

Figure 4.16(b) shows that the largest mean flow velocity is present at 1000 Hz and that it amounts to about 0.3 mm/s for a sound pressure level of 94 dB. The scaling of the streaming velocities with the inflow velocity at the stapes is addressed in Fig. 4.17. Here the maximum Eulerian velocities for different frequencies are indicated, comparing the stapes velocities $U_{in}^* = 3 \cdot 10^{-5}$ m/s (for the upper line) and $U_{in}^* = 3 \cdot 10^{-6}$ m/s (for the bottom one). The maximum Eulerian mean velocity scales with the square of the inflow velocity (since the values in Fig. 4.17 are normalised with the respective $U_{in}^*$, the difference between the curves for the two inflow velocities amounts to only one order of magnitude in this graph).

4.5 Possible physiological consequences

The simulation results presented in the previous sections show that steady streaming in the cochlea is existent and that it can reach velocities on the order of millimetres per second for loud acoustical stimulation. This section discusses how the steady streaming might influence the physiological processes in the cochlea.
Lighthill (1992) points out that the steady streaming might result in an additional deflecting force on the hair cell stereocilia (Fig. 1.3). It is known that the stereocilia deflection polarises or depolarises the cell. Evidence suggests (Fuchs, 2010, p. 8) that the deflection opens mechanically gated ion channels and thus initialise the influx of $K^+$ and $Ca^{2+}$ ions into the hair cells. The force-induced changes in cell potential stimulate processes which are crucial for the hearing and which are determined by the innervation of the inner and outer hair cells. Inner hair cells are connected to afferent neurons which transmit the sound-induced response of the cell (and of the nerve fibre) to the brain. Outer hair cells are able to change their length by voltage dependent protein motors and can thus give mechanical energy into the movement of the cochlear membranes. This is controlled by efferent innervation. The stereocilia of the outer hair cells are directly connected to the tectorial membrane (Fuchs, 2010, p. 6) such that the shearing motion between the basilar and tectorial membranes exert the force which deflect the stereocilia. The activity of these cells is probably not affected by the steady streaming. The inner hair cell stereocilia, in contrast, are not connected to the tectorial membrane but immersed into the fluid. They are possibly deflected by the steady streaming. This fluid flow might exert a steady bending force which probably is superposed to the oscillating bending force which is generated by the primary flow. A steady deflection might lead to a more efficient depolarization or polarization of the cell which might affect the triggering of the signal in the afferent nerve.

Because the present investigation considers a two-dimensional box model with only one membrane, the results will be altered for the real cochlear geometry. Especially the steady streaming in the organ of Corti is difficult to predict because of the influence of the mechanical structures. It has also to be taken into account that the travelling wave of an active cochlea differs from that of a passive one. The active amplification leads to larger amplitudes of the membrane motion and to sharper peaks at the characteristic place. The increase in the membrane deflection reaches 40 to 60 dB for low sound intensities (Hudspeth, 2008) and decreases for louder ones. The larger membrane motion probably leads to a stronger steady streaming. The sharpening of the peak affects only the second term in Eq. (4.14) which scales with the gradient of the membrane amplitude and which does not dominate the streaming velocity.

The real cochlea allows for three-dimensional steady streaming; the character of this motion is not precisely predictable. The three-
dimensional steady streaming is of specific interest for the bending of the hair cell stereocilia because the mechanically gated ion channels respond to deflections along an axis perpendicular to the $x$-$y$-plane of the model used in this thesis (Fuchs, 2010, p. 8).

Because it is not possible to estimate the influence of these effects (structures of the organ of Corti, active amplification, three-dimensional character) on the streaming velocities, no approximation of additional stereocilia bending forces based on the simulation results is given.

The steady streaming might not only influence the bending of the hair cell stereocilia. Another effect might be the transport of solutes in the cochlea. The presented investigation shows that net transport occurs. Therefore, ions present in the cochlea ($\text{Na}^+$, $\text{K}^+$, $\text{Ca}^{2+}$, $\text{Cl}^-$, $\text{HCO}_3^-$) could be transported by advection and not only by molecular diffusion. This could help to re-establish concentration gradients and electrochemical gradients. Since those gradients are necessary for the ion transport via transduction or ion channels, an additional mechanism for ion transport would help to maintain the cell processes which generate the nerve signals.

Further, an additional mechanism for ion transport might reduce the required number of blood vessels in the cochlea and in direct proximity of the organ of Corti. These vessels supply the cochlear fluids with oxygen and ions and carry away metabolism products. An effect of advective
transport of solutes might be an improved energy supply. Further, if less blood vessels are necessary, less mechanical noise due to blood flow is generated. This noise interferes with the hearing process.

Finally it shall be pointed out here that not only solutes inherent to the cochlea could be transported by steady streaming but also solutes which are applied for medical reasons. Under specific pathological conditions drugs are injected into the cochlea, e.g., via the round window or the scalae. Such techniques have been discussed in terms of their invasiveness and of the concentration distribution of the drug (Kingma et al., 1992). Steady streaming might be used to spread medical agents, e.g., by stimulating the cochlea in a defined manner and during specific time spans. Less invasive injection techniques would benefit from such enhanced distribution. Probably also specific non-harmonic acoustic stimulations could be used for this purpose which may reach higher Lagrangian transport velocities.
In this chapter the influence of the rocking stapes motions on the oscillation of the basilar membrane is investigated.

Section 5.1 addresses the different motion components of the stapes oscillation. Section 5.2 presents the simulated travelling wave for the purely rocking stimulation. The peak amplitudes are investigated in Sec. 5.3. To this end, the frequency distribution of the peak amplitudes is studied (Sec. 5.3.1), addressing two different stimulation conditions: on the one hand constant maximum inflow velocity at the stapes for all frequencies, and on the other hand constant maximum ear canal pressure for all frequencies which results in different stapes velocities. The amplitudes due to the rocking stapes motions are compared to those presented in Chap. 3 for the piston-like stimulation. Further, the membrane motion under combined stimulation is examined (Sec. 5.3.2), i.e., the deflection of the membrane when the stapes moves translationally and rotationally at the same time. Because the box model of the present thesis simplifies the real cochlea geometry especially in the high-frequency region, the stapes position of the model is varied and the resulting peak amplitudes of the membrane deflection are investigated (Sec. 5.3.3).

Section 5.4 studies the scaling behaviour of the simulated peak amplitudes due to rocking stapes motions by means of potential flow theory. Different mechanisms evoke the membrane displacements due to the two stapes motions. These stimulation processes are explained in Sec. 5.4, as well. Section 5.5 concludes the chapter discussing possible physiological consequences of the rocking stapes motion for the hearing.

The findings of the present chapter are summarised in Chap. 6.

The results presented in this chapter are partially published in Edom et al. (2013).

All results of this chapter are obtained from simulations which are started from zero initial conditions, i.e., with the flow field and the basilar membrane at rest. The presented results show the steady state which is reached to a sufficient level of accuracy after 25 periods of the harmonic
stimulation. The results figures are given in non-dimensional numbers with length scales relative to $L^*$, velocities relative to $U^*$ and time scales relative to $L^*/U^*$ indicated in this chapter.

The basilar membrane motion induced by the rocking stapes motion is studied in terms of the transversal membrane deflection $\eta_y$. The influence of the rocking stapes motion on effects studied in Chap. 4, the steady streaming in the cochlea and the axial membrane motion $\eta_x$, is not investigated in the present chapter because these non-linear effects are regarded as not essential for cochlear activation by the rocking stapes motion. However, both a mean motion of the fluid and an axial membrane stretching are induced by the rotational stimulation and exhibit nearly no qualitative differences to the results presented in Chap. 4.

Typical turn-around times of simulations are indicated in Sec. 2.1.

5.1 Motion patterns of the stapes

The stapes is connected to the oval window and transduces through its oscillations the sound signal to the cochlea. The stapes motion pattern has proven to be complex and is subject of continuous studies. These extend from the work by Stuhlman (1937) to recent publications such as Hato et al. (2003) and Sim et al. (2010).

The stapes motion shows one translational and two rotational components (Fig. 5.1). In the translational or piston-like motion the stapes moves along an axis perpendicular to its footplate into and out of the cochlea (Fig. 5.1(a)). In the rotational or rocking motion the stapes is displaced around the short (Fig. 5.1(b)) and long (Fig. 5.1(c)) axes of its footplate. Motions in the remaining degrees of freedom are prevented by the annular ligament. The rotational components are present especially at frequencies above 1000 Hz (Hato et al., 2003).

The piston-like displacement evokes a net fluid flow and pressure differences which stimulate the basilar membrane oscillation and lead to the perception of sound. During purely rotational motions, in contrast, the stapes pushes the same fluid volume out of the cochlea as into it. Therefore is it doubted whether these components of the stapes displacement generate fluid flow and pressure differences in the cochlea. Consequently, any contribution of the rocking stapes motion to the hearing is put in question (Decraemer et al., 2007; Voss et al., 1996).

Experiments, however, show that the rotational motion components stimulate the cochlea. Huber et al. (2008) and Eiber et al. (2012) mea-
5.1 Motion patterns of the stapes

![Motion components of the stapes: (a) piston-like displacement (translational); (b) rocking displacement around the short axis of the footplate (rotational); (c) rocking displacement around the long axis of the footplate (rotational).](image)

Figure 5.1: Motion components of the stapes: (a) piston-like displacement (translational); (b) rocking displacement around the short axis of the footplate (rotational); (c) rocking displacement around the long axis of the footplate (rotational).

sure compound action potentials in guinea pigs due to controlled stapes motions. They report that neuronal activity evoked by rotational displacements of the stapes is clearly observed.

Several studies discuss the effects on the fluid flow in the cochlea which originates from the rocking stapes motion. Decraemer et al. (2007) suspect that the rotational component causes a forth and back movement of the fluid in a small volume behind the footplate and that the generated pressure wave does not propagate further into the cochlea. Hato et al. (2003), who examine the three-dimensional stapes motion in human temporal bones, conclude that the rotational motion generates no net fluid shift but a local fluid flow in a region close to the footplate and that it is unknown whether this motion component affects the hearing. In a study of the numerical modelling of cochlea hydrodynamics Pozrikidis (2008) computes the basilar membrane response to rocking stapes motions. The membrane deflections due to the rotational stimulation component are shown to be significantly smaller than those which are induced by the piston-like motion.

The present work studies the effect of rocking stapes motions around the short axis of the footplate (Fig. 5.1(b)). This rotational component displaces more fluid than the one rotating around the long stapes footplate axis. Further, it fits naturally into the set-up of the present cochlea model shown in Fig. 2.1.
Figure 5.2: Travelling wave on the basilar membrane due to rocking stapes stimulation (----) compared to the membrane motion due to piston-like stimulation (— —): (a) instantaneous deflection and amplitude of the transversal membrane displacement \( \eta_y \) at 1000 Hz, maximum amplitudes are normalised; (b) amplitudes of the transversal membrane deflection at different frequencies, maximum amplitudes are normalised.

5.2 Primary travelling wave system due to rocking stapes motions

The rocking stimulation component generates, just as the piston-like component, a travelling wave in the cochlear fluids and on the basilar membrane. Comparison of the normalised instantaneous travelling waves on the basilar membrane due to both stimulation modes (Fig. 5.2(a)) shows that the membrane deflections are identical to each other. The only difference is present in the inflow/outflow region for \( x \leq 1.5 \) where the rotational stimulation generates slightly larger relative amplitudes. The waves due to both stimulations exhibit no phase shift and the wavelengths decay in the same manner along the cochlea. Accordingly the maximum amplitudes of both travelling waves differ only in the region below the stapes. This can also be seen from Fig. 5.2(b), a comparison of normalised envelopes for different frequencies. The curves for the rocking stapes motion differ from those for the piston-like motion only for high-frequency stimulation. The reason for these differences are interactions between the wave on the basilar membrane and the inflow and outflow at the round and oval window. These interactions become visible especially for high frequencies because these generate larger membrane displacements close to the inflow/outflow region.

The fluid flow generated by the rocking stapes motion differs in the
basal region from the fluid motion due to translational motion. Figure 5.3 shows the instantaneous flow directions due to both stimulations. Under piston-like stapes movements (Fig. 5.3(a), when the stapes is moving out of the cochlea) the fluid flows through the oval and round windows and the velocities in the scala tympani are not negligible. The rocking motion of the stapes (Fig. 5.3(b), when the right edge of the stapes moves into the cochlea), in contrast, leads only at the oval window to a fluid flow while nearly no motion is present at the round window and in the basal part of the scala tympani. The flow directions beneath the oval window oscillate during the stimulation period between a clockwise and an anti-clockwise fluid motion.

The instantaneous flow fields due to rocking stimulation (Fig. 5.4) show practically no qualitative differences to the flow fields induced by the piston-like stapes motion (Fig. 3.2, p. 33) apart from the basal region. At the characteristic place, maximum velocities are present either at the boundary layer edges (x-component) or at the resting position of the basilar membrane (y-component). This is also the case for the translational stimulation. In contrast there exist quantitative differences in the flow field. The rocking movement of the stapes yields lower maximum fluid velocities for comparable inflow velocities at the oval window. Depending on the stimulation intensity and frequency the maximum velocities at the characteristic place can be so small that the fluid motion beneath the oval window is nearly equally fast. In this case local maxima are present not only at the characteristic place but also in the inflow/outflow region (Fig. 5.4).
Figure 5.4: Instantaneous flow field in the cochlea due to rocking stapes stimulation at 1000 Hz: velocity components when the right edge of the stapes moves into the cochlea at instantaneous maximum velocity of $U_{in} = 1$.

### 5.3 Peak amplitudes for rocking stapes motion

While Sec. 5.2 focusses on the fluid motion due to stimulation at $f^* = 1000$ Hz, the present section addresses the amplitudes of the basilar membrane deflection for different stimulation frequencies. Also the stimulation intensity is varied by considering both the cochlear responses to a constant maximum inflow velocity of $U_{in}^* = 3 \cdot 10^{-5}$ m/s and those to frequency-dependent inflow velocities at constant maximum ear canal pressure. For the stimulation at constant ear canal pressure the stapes velocities measured by Sim et al. (2010) are used (Fig. 5.5).

This section studies the basilar membrane deflection under different aspects. The peak amplitudes due to rocking stapes stimulation are investigated and compared to those due to the piston-like stapes displacement (Sec. 5.3.1). Further, the membrane deflection due to both stimulation types present at the same time (“combined motion”) is studied (Sec. 5.3.2). Finally, the influence of the stapes position is studied (Sec. 5.3.3).
5.3 Peak amplitudes for rocking stapes motion

The maximum amplitudes of the membrane deflection due to the rocking stapes motion (Fig. 5.6(a)) decrease as the frequency decreases for $f^* < 2000\,\text{Hz}$. Only for larger stimulation frequencies an increase of the peak amplitudes with frequency is present. Piston-like stapes motions, in contrast, lead for the complete frequency range to increasing peak amplitudes as the frequency decreases (Fig. 3.12(a), p. 42).

The shape of the travelling wave envelopes generated by the piston-like displacement is nearly the same for all frequencies when the max-
Figure 5.7: Peak amplitudes of the basilar membrane deflection $\eta_y$: (a) for constant maximum inflow velocity $U_{\text{in}}^* = 3 \cdot 10^{-5}$ m/s; (b) for constant maximum ear canal pressure $p_{\text{EC}} = 1$ Pa; peak amplitudes due to piston-like stimulation (■) and isolines for reduced inflow velocities at $-10$ dB each (— —, coloured), peak amplitudes due to rocking stimulation (●).

The maximum amplitude is normalised and when the curves are shifted in $x$-direction such that the characteristic places overlap (Fig. 3.12(b), p. 42). This is also the case for the rocking stapes motion (Fig. 5.6(b)) with the exception of the envelopes for high frequencies $f^* \geq 6000$ Hz. These stimulations lead for $x < x^*$ to irregularities in the membrane deflections. This can be explained by the previously mentioned interactions of the travelling wave on the basilar membrane with the inflow and outflow of the fluid at the oval and round windows.

Figure 5.7 shows the peak amplitudes of the membrane deflection evoked by rocking stapes motions at different inflow frequencies in comparison to the peak amplitudes due to piston-like displacements of the stapes (the latter maximum deflections are the same as in Fig. 3.13, p. 42). In Fig. 5.7(a) the maximum inflow velocity amplitude is constant for all frequencies ($U_{\text{in}}^* = 3 \cdot 10^{-5}$ m/s), in Fig. 5.7(b) $U_{\text{in}}^*$ varies at constant maximum ear canal pressure ($p_{\text{EC}} = 1$ Pa $\cong 94$ dB sound pressure level) according to the measurements by Sim et al. (2010) (Fig. 5.5). The graphs indicate isolines of the peak amplitudes for decreased inflow velocities (cf. Fig. 3.13). The data points for the maximum deflection due to rocking stapes movements illustrate how much softer these tones are perceived compared to a tone which is generated by a purely piston-like stapes motion, assuming that the stapes velocity scales linearly with the stimulation intensity.
5.3 Peak amplitudes for rocking stapes motion

The rocking motion of the stapes leads for all stimulation frequencies to smaller deflection amplitudes than the piston-like motion. In the case of constant inflow velocities (Fig. 5.7(a)) the smallest difference between both stimulation modes is present at about $f^* = 4000$ Hz, amounting to about 10 dB. If the cochlea is stimulated with lower frequencies, the difference increases by about 12 dB per octave and reaches about 70 dB at 100 Hz.

If instead of the inflow velocity the sound pressure level is kept constant (Fig. 5.7(b)), larger differences between both stimulation modes are present because the rocking component shows for all frequencies smaller stapes velocities than the piston-like motion (Fig. 5.5). The smallest difference in the membrane deflection is about 20 dB at about 2000 to 4000 Hz.

5.3.2 Peak amplitudes for combined stapes motion

Figure 5.8(b) shows the amplitudes of the membrane deflection for simulations with purely piston-like, with purely rocking and with combined stapes motions. The latter signifies that the stapes moves translationally and rotationally at the same time. This combined stapes displacement increases or decreases the membrane amplitudes compared to the purely piston-like stimulation, depending on the phase shift between the two motion components. As discussed previously (Sec. 5.2), the travelling waves generated by the rotational displacement of the stapes are identical to the waves due to the translational movement. Therefore the maximum amplification due to the combined stimulation is evoked if the waves on the basilar membranes are in phase. The maximum reduction occurs if the travelling waves due to the two components are inversely phased. In-phase waves result if the piston-like component moves synchronously with the left stapes edge of the rocking component (case AA in Fig. 5.8(b)). If the piston-like motion is in phase with the right edge of the rocking motion (case AB in Fig. 5.8(b)) instead, the minimum amplitude results.

The maximum differences between the combined and the purely piston-like stapes movement equals the maximum amplitude of the rocking stapes stimulation. The amplitudes of the combined stapes motion can be obtained by linear superposition of the deflection amplitudes for the single-mode stimulations (Fig. 5.8(c)).

Figure 5.8 shows the effect of the combined stapes motion on the
Figure 5.8: Travelling wave amplitudes of the basilar membrane deflection $\eta_y$ due to combined stapes motion: (a) stapes motion components and velocity of point A for combined stapes motion if point A of the piston-like component is in phase with point A of the rocking component (case AA); (b) amplitudes at $f^* = 1000$ Hz for stimulation with purely piston-like (——) and purely rocking (— —, green) stapes motion and for combined stapes motion: case AA, point A of piston-like motion in phase with point A of rocking motion (— — —, blue), case AB, point A of piston-like motion in phase with point B of rocking motion (— — · —, red); (c) amplitudes from a simulation with combined stapes motion (— — —, green) and amplitudes by linear superposition of the membrane motions of purely piston-like and purely rocking stimulation( — —). .

membrane amplitudes for stimulation at $f^* = 1000$ Hz and with equal inflow velocity amplitudes for both motion components. Figure 5.9 extends this investigation to further stimulations. The maximum and minimum membrane deflections due to combined stimulation are indicated for different frequencies at constant maximum inflow velocity (Fig. 5.9(a)) and at constant maximum ear canal pressure (Fig. 5.9(b)). If the maximum stapes velocity is constant and identical for both stimulation modes the membrane displacement is increased or decreased by up to 3 dB (at $f^* = 4000$ Hz) compared to the purely piston-like stimulation. If the same ear canal pressure is present for both components, the maximum difference is smaller and amounts to about 1 dB for most of the frequencies. (The influence of the rocking stapes motion on the hearing is discussed in Sec. 5.5.)
5.3 Peak amplitudes for rocking stapes motion

Figure 5.9: Peak amplitudes of the basilar membrane deflection $\eta_y$: (a) for constant maximum inflow velocity $U_{in}^* = 3 \cdot 10^{-5} \, m/s$; (b) for constant maximum ear canal pressure $p_{EC} = 1 \, Pa$; peak amplitudes due to piston-like stimulation (---, *) and isolines for reduced inflow velocities at $\pm 1 \, dB$ each (-----, coloured), peak amplitudes due to combined stimulation for case AA (-----, ◦) and case AB (-----, □), cf. Fig. 5.8.

5.3.3 Influence of the stapes position

The cochlea geometry is highly three-dimensional in the high-frequency region and the two-dimensional box model is limited in reflecting the real shape of the cochlea in this part. To estimate the influence of a differing geometry in the basal region of the cochlea the present section presents results for the membrane deflection under slight modifications of the box geometry. First, the stapes is shifted in the positive $x$-direction by one length unit ($L^* = 3 \, mm$) such that it is situated at $x_s = 1.7$, $y_s = 0.48$ (Fig. 5.10(b), upper panel). Second, the transversal distance between the stapes and the basilar membrane is increased by a factor of two through doubling the height of the scala vestibuli. This results in a stapes position of $x_s = 0.7$, $y_s = 0.72$ (Fig. 5.10(b), lower panel).

The resulting peak amplitudes of the membrane displacement are shown in Fig. 5.10(a) in comparison to the previously discussed results. The longitudinal shift of the stapes position leads to unchanged or slightly decreased peak amplitudes in case of the piston-like stimulation. For the rocking stapes motion, in contrast, the amplitudes clearly increase. The difference between the results for both stimulation modes decreases therefore by more than $10 \, dB$ for frequencies $f^* \leq 1000 \, Hz$. Simulations at higher frequencies have not been performed because of the above-mentioned interactions between the travelling wave on the
5.4 Different modes of membrane excitation

The results presented in Sec. 5.3 show that the peak amplitudes of the membrane deflection due to the rocking stapes motion decrease with decreasing frequencies whereas they increase for such frequencies if the cochlea is stimulated by the piston-like stapes motion. Changes in the stapes position lead to nearly unchanged peak amplitudes for the translational stimulation while the results for the rocking stapes motion are more sensitive to alterations of the model geometry.

The present section gives a potential flow approximation for the maximum amplitudes due to the rocking stapes displacement. Further, the section explains two different mechanisms which evoke the travelling

basilar membrane and the inflow/outflow.

If the height of the scala vestibuli is doubled, the membrane amplitudes due to piston-like stapes displacements remain practically the same as in the original model. The rocking stimulation, in contrast, leads to smaller amplitudes with a loss of approximately 6 dB.

Figure 5.10: Influence of the stapes positions indicated in (b) on the peak amplitudes of the basilar membrane deflection $\eta_y$: (a) peak amplitudes for constant maximum inflow velocity $U_{in}^* = 3 \cdot 10^{-5}$ m/s, peak amplitudes due to piston-like stimulation (■, ▼, ▲) and isolines for reduced inflow velocities at $-10$ dB each (-----, coloured), peak amplitudes due to rocking stimulation (●, ◆, ▼); stapes positions: (■, ●): stapes footplate centred at $(x_s, y_s) = (0.7, 0.48)$, (▼, ◆, blue): stapes footplate centred at $(x_s, y_s) = (1.7, 0.48)$, (▲, ◆, green): stapes footplate centred at $(x_s, y_s) = (0.7, 0.72)$; (b) indicates the stapes position for the different test cases graphically.
wave on the basilar membrane in the two stimulation cases.

The fluid flow in the cochlea can be approximated as potential flow because the boundary layers are thin and the bulk of the flow is irrotational (Fig. 3.3(b) and Lesser & Berkley, 1972). Therefore the velocity field $\mathbf{u}$ can be described by

$$\mathbf{u} = \nabla \Phi$$  \hspace{1cm} (5.1)

with the potential $\Phi$. The pressure field then follows by the unsteady Bernoulli equation

$$Str \frac{\partial \Phi}{\partial t} + \frac{1}{2} |\nabla \Phi|^2 + p = 0.$$  \hspace{1cm} (5.2)

For an oscillating flow field, the first term in Eq. (5.2) scales with the Strouhal number

$$Str = f^* \frac{L^*}{U^*}.$$  \hspace{1cm} (5.3)

The second term remains of order 1 in the bulk of the flow field. Therefore, the pressure $p$ can be approximated to first order for high frequencies by

$$\dot{p} = i Str \hat{\Phi}$$  \hspace{1cm} (5.4)

where $i^2 = -1$ and

$$(p, \Phi) = (\dot{p}, \hat{\Phi}) \exp\{i t\}.$$  \hspace{1cm} (5.5)

Equation (5.4) shows that the amplitude of the pressure oscillation depends linearly on the stimulation frequency. The potential $\Phi$ is independent of the frequency and therefore the velocity field $\mathbf{u}$ is frequency independent as well.

In the framework of potential flow theory, the cochlear fluid flow under piston-like stimulation can be modelled by the flow which is generated by a source and a sink of oscillating intensity at the positions of the oval and round windows, respectively. The rocking motion of the stapes can be described by an oscillating dipole at the oval window (Pozrikidis, 2008).

The potential of a dipole is given by

$$\Phi_{\text{dipole}} = \mu \frac{X}{X^2 + Y^2}$$  \hspace{1cm} (5.6)

with the dipole intensity $\mu$ and where the origin of the coordinates $(X, Y)$ is situated at the stapes. To model the fluid flow in the cochlea the
presence of the cochlear walls and of the basilar membrane would have to be accounted for. Although the potential (5.6) does not reflect these structures, the potential is sufficient to investigate the scaling of the pressure in the very slender scala vestibuli.

Equation (5.6) shows that the pressure due to the rocking stapes motion decays like $1/X$ along the cochlea while the velocity decays like $1/X^2$ due to (5.1) and therefore more rapidly.

It follows from Eqs. (5.4) and (5.6) that the pressure along the basilar membrane due to the rotational stimulation of the cochlea is

$$\hat{p}_{BM}(x) = i \text{Str} \mu \frac{x - x_s}{(x - x_s)^2 + H^2}$$

(5.7)

where $x_s$ indicates the longitudinal position of the stapes footplate center and where $H$ is the height of the scala vestibuli.

The pressure in the scala tympani induced by the rocking stapes motion is very small and approximately equals the middle ear pressure. Therefore the pressure $\hat{p}_{BM}$ (5.7) is an approximation for the pressure difference $\Delta p$ across the basilar membrane. Hence the spatial maximum of this pressure difference scales like

$$\max_x \hat{p}_{BM} \propto \text{Str}/H.$$  

(5.8)

This finding can be used to explain the scaling of the maximum basilar membrane amplitudes shown in Fig. 5.10. In the present model the basilar membrane displacement $\eta_y$ depends only on the membrane stiffness $\kappa_y$ and on the force which acts on the membrane. Because this force scales with the pressure difference across the membrane, the peak amplitudes can be approximated by

$$\hat{\eta}_y \propto \frac{\text{Str}}{H\kappa_y(x_s)}.$$ 

(5.9)

Figure 5.11 shows the peak amplitudes due to the rocking stapes motion together with the approximation (5.9). This approximation predicts the amplitudes for the original model well and captures the increase of the membrane deflections with increasing frequency. Further, the amplitudes for the modified model geometry are well approximated. For frequencies $f^* \geq 1000$ Hz, when the characteristic place approaches the stapes, differences between the scaling (5.9) and the simulated results can be seen which increase as the frequency increases. As stated before,
5.4 Different modes of membrane excitation

Figure 5.11: Scaling of the peak amplitudes of $\eta_y$ due to rocking stapes stimulation at different stapes positions: simulated peak amplitudes for constant maximum inflow velocity $U^*_in = 3 \cdot 10^{-5}$ m/s (---), scaling $\hat{\eta}_y \propto \text{Str}/\{H\kappa_y(x_s)\}$ (---, cf. Eq. (5.9)); stapes positions: (●, ○): stapes footplate centred at $(x_s, y_s) = (0.7, 0.48)$, (◆, ◆, blue): stapes footplate centred at $(x_s, y_s) = (1.7, 0.48)$, (◇, ◇, green): stapes footplate centred at $(x_s, y_s) = (0.7, 0.72)$, cf. Fig. 5.10(b).

Figure 5.12: Instantaneous pressure field of the travelling wave due to rocking stapes stimulation at 1000 Hz, $p = 0$ at the round window, instant when the left stapes edge has reached the maximum deflection out of the cochlea and starts moving into the cochlea (--- exaggerated basilar membrane displacement).

The inflow/outflow beneath the stapes interacts with the oscillation of the basilar membrane such that the travelling wave of the membrane is disturbed. This is supported by the fact that the deviations begin at lower frequencies for the longitudinally shifted stapes position.

Section 5.3.3 shows that the peak amplitudes due to the piston-like stapes motion are practically not affected by the changes in the stapes position in contrast to the amplitudes due the rotational stimulation. The reason for this behaviour is that the membrane oscillation is evoked by two different mechanisms for the two stapes motion components.

Figure 5.12 depicts the instantaneous pressure field in the cochlea due to rocking stapes movements at a time of maximum pressure. Com-
Comparison with the pressure field due to piston-like stimulation (Fig. 3.5, p. 35) shows that the pressure wave of the rotational stapes displacement reaches the characteristic place with significantly smaller relative amplitudes. The pressure field evoked by the rocking stimulation exhibits relatively large pressures beneath the stapes but only a weak pressure wave. This can also be seen in Fig. 5.13 which displays the amplitudes of the pressure differences across the basilar membrane for both stapes motion components. The pressure difference due to the rocking motion decays rapidly beneath the stapes which is in accordance with potential flow theory (5.7). For $x \geq 1$ the travelling wave dominates the pressure field such that the curve corresponds to the one for the piston-like stimulation with an amplitude shift.

The rocking stapes motion initialise the travelling wave on the basilar membrane only beneath the stapes. The wave then travels due to this local activation along the cochlea and reaches peak amplitudes at the eigenfrequency of the stimulation. As shown in Figs. 5.12 and 5.13 the pressure amplitudes decay along the cochlea. Therefore the lower frequencies lead to smaller peak amplitudes of the membrane deflection. In contrast the characteristic places of higher frequencies, which are less distant to the stapes, are reached with smaller losses in pressure difference across the basilar membrane. The results for the changed stapes positions are in agreement with this mechanism. For the longitudinally shifted stapes position the distance between the stapes and the characteristic place is shortened such that the decay in the pressure difference

Figure 5.13: Amplitudes of normalised vertical pressure differences across the basilar membrane due to piston-like (— —) and rocking stapes (– – –) stimulation at $f^* = 1000$ Hz, $p = 0$ at the round window.
across the membrane is smaller. This leads to larger amplitudes. If the distance between the stapes and the basilar membrane is increased, the excitation of the membrane motion beneath the stapes is less intense which leads to smaller deflection amplitudes.

The piston-like stapes motion excites the basilar membrane along the complete length between the stapes and the characteristic place. This is shown by the considerably larger pressure difference across the membrane compared to the pressure differences due to the rocking stapes motion. The peak amplitude of the deflection increases for lower frequencies because softer membrane sections are activated.

Also the little influence of the stapes position on the membrane displacement can be explained by a non-local stimulation of the membrane movement. Between the stapes and the characteristic place a fluid column oscillates and thereby deflects the basilar membrane. The oscillation intensity in this column, i.e., the fluid velocity, depends on the net fluid displacement due to the piston-like stapes motion but not on the position of the stapes. Nonetheless interactions between the oscillation of the basilar membrane and the inflow beneath the stapes are present. They influence the peak amplitudes for higher frequencies. This explains the slight amplitude difference which can be seen in Fig. 5.10 for the piston-like stimulation at \( f^* = 1000 \text{ Hz} \) between the data points for the original geometry and those for the longitudinally shifted stapes position.

### 5.5 Possible physiological consequences

The presented results for the membrane motion due to rocking stapes displacements (Sec. 5.3) indicate that this stimulation can lead to hearing. The results for the combined stapes motion (Sec. 5.3.2), however, show that the travelling wave on the basilar membrane is dominated by the piston-like motion component and that the rocking component has almost no influence on the peak amplitudes of the membrane deflections.

Under pathological conditions the piston-like component of the stapes motion can be prevented. Round window atresia is a condition in which the round window is covered by solid bone instead of a deformable membrane. This inhibits net volume displacements of the fluid and thereby any piston-like stapes motion. The rotational motion component, in contrast is possible in this situation because it pushes the same fluid volume
out of the cochlea as into it and does not require displacements of the round window.

Studies of the hearing ability of patients suffering from round window atresia (Linder et al., 2003) show that these hearing-impaired are not affected by a total conductive hearing loss. Instead, mixed hearing losses with air-bone gaps\(^1\) of 15–30dB are observed. If the piston-like stapes motion is the only effective stimulus of the cochlea, the hearing ability of patients with round window atresia cannot be explained. Therefore the observations by Linder et al. (2003) suggest that rocking stapes motions stimulate the basilar membrane and lead to the reported sound perception.

Alternative explanations for the observed hearing ability are cochlear receptors which are sensitive to the pressure inside the cochlea. Further, the third window effect, the fluid flow out of the cochlea through the perilymphatic or endolymphatic ducts, might enable the observed hearing. Also the compressibility of tissue is a possible explication. These effects have been shows to be small in normal ears (Shera & Zweig, 1992; Voss et al., 1996), but they might be more relevant in pathological situations.

Another situation besides the round window atresia in which no net fluid displacement in the cochlea is possible is that of patients with middle ear prostheses on the round window and with fixed stapes. Beltrame et al. (2009) investigate the hearing ability of patients with such prostheses which have been implanted because of conductive or mixed hearing loss. Also for patients with additionally a fixed stapes hearing recovery is reported, although with smaller functional gain than for other patients. This indicates that the cochlea can be activated without net fluid volume displacement. Again the stimulation by rocking stapes movements is a possible explanation for the observations.

\(^{1}\)The air-bone gap measures the loss of air-conductive sound transmission. It is the threshold difference between the sound perception by air and by bone conduction.
Chapter 6

Summary, Conclusions and Future Investigations

The present thesis studies the fluid flow and basilar membrane motion in the cochlea by means of a two-dimensional passive box model. The fluid flow in the scala vestibuli and the scala tympani is described as transient, non-linear and viscous by the solving Navier-Stokes equations. The cochlear partition, referred to as basilar membrane in this thesis, is modelled as an array of independent oscillators using the immersed boundary method. The investigation focuses on the steady streaming in the cochlea and on the influence of the rocking stapes motion on the basilar membrane oscillations.

This chapter summarises the major findings (Sec. 6.1) and suggests possible future investigations (Sec. 6.2).

6.1 Summary and conclusions

6.1.1 Primary wave

The primary wave system is presented in Chap. 3. Along the cochlea the travelling wave on the basilar membrane increases in amplitude until it reaches the frequency dependent characteristic place. Thereby, the wave length and the phase velocity decrease. Behind the characteristic place, the travelling wave decays rapidly. The maximum amplitudes of the membrane deflection increase as the stimulation frequency decreases for the conventional, piston-like, stapes motion whereas the amplitudes decrease as the frequency decreases for the rocking stapes motion (Sec. 6.1.3). The envelopes for all stimulation frequencies are nearly identical when normalised by their maximum amplitude and shifted along the cochlear length such that the characteristic places overlap. The fluid motion is fastest at the characteristic place in the vicinity of the basilar membrane. It exhibits along the bounding walls and the membrane Stokes boundary layers whose thickness is known to be frequency dependent. The pressure difference across the basilar membrane
decays toward the characteristic place and vanishes behind this location. Passive tracer particles in the cochlea move on circular trajectories in the bulk of the flow field. In direct proximity to the basilar membrane the circles become increasingly slender ellipses.

Lighthill (1992) describes the primary wave motion of the fluid analytically as a function of the amplitudes of the basilar membrane velocity and the wave number. Inserting the present simulation results for the velocity amplitude and the wave number yields good agreement between the simulated primary wave motion and the analytical predictions. Differences arise in the inflow/outflow region and due to the bounding walls. These are not taken into account in Lighthill’s analytical treatment.

6.1.2 Steady streaming

Chapter 4 presents the results on the steady streaming in the cochlea model. The Eulerian mean motion $u_E$ and the Lagrangian mean motion $u_L$ consist both of a vortex pair, one on either side of the basilar membrane. The vortex above the basilar membrane rotates in counterclockwise direction in both streaming fields. The maximum Eulerian mean velocity is present at the resting position of the basilar membrane at the location of the characteristic place. For sinusoidal stimulation with 1000 Hz at about 76 dB sound pressure level in the ear canal, this maximum velocity reaches about 15% of the stapes velocity. The Lagrangian maximum mean velocity is present at the edge of the boundary layer and no fluid motion is present at the resting position of the basilar membrane. The maximum velocity for the same stimulation as mentioned previously is about 4% of the stapes velocity. The Stokes drift $u_M = u_L - u_E$ shows, as well, a vortex pair which rotates in the opposite direction compared to the Eulerian and Lagrangian streaming fields.

The basilar membrane motion in axial direction shows that higher harmonics are present, i.e., there is a frequency doubling of the axial membrane motion with respect to the stimulation frequency. In the transversal direction the membrane oscillates at the stimulation frequency such that each point of the membrane describes a Lissajous figure of the shape of an eight. Only a little bit away from the symmetry plane at the basilar membrane the amplitudes of the higher harmonics are much smaller than the amplitudes of the fundamental frequency such that frequency doubling not visible in the motion of passive tracer particles in the fluid domain.
A comparison of the simulation results for the Stokes drift with the analytical ones by Lighthill (1992) shows good agreement. In addition, Lighthill (1992) gives a solution for an Eulerian slip velocity at the basilar membrane which corresponds to a non-zero boundary condition for the bulk flow. The simulated velocities differ from this prediction. The difference can be explained by an additional source of steady streaming which has not been taken into account by Lighthill. His solution considers solely Reynolds stress-induced streaming motions while an additional streaming is generated by the moving membrane. The membrane shifts the axial velocity profiles in the vertical direction in such a way that a positive axial velocity is induced at the resting position of the basilar membrane during the stimulation cycle. The resulting Eulerian streaming velocity is independent of boundary layer effects and leads to the maximum mean velocities at the resting position of the basilar membrane. The steady streaming which is generated by the Reynolds stresses, in contrast, shows zero Eulerian mean velocity at this position and is concentrated within the Stokes boundary layers at the characteristic place. The streaming fields due to the two mechanisms together yield the steady streaming of the original, full system. Thereby the streaming due to the individual mechanisms can be added because the streaming motion can be described by the linear Stokes equations.

The membrane-induced streaming results from a non-linearity which is introduced by the oscillations of the basilar membrane together with its periodic reaction forces. This non-linearity also leads to a steady axial displacement of the basilar membrane which consists of a stretching away from the characteristic place.

The maximum velocities of the steady streaming scale with the square of the stapes velocity. Therefore they increase as the sound pressure level increases. With increasing frequency, the maximum streaming velocity decreases. Largest streaming velocities are present in a frequency range between 250 and 1000 Hz for constant maximum inflow velocities. For constant maximum ear canal pressure the largest streaming velocities are reached at about 1000 Hz, amounting to about 0.3 mm/s at 94 dB for the Eulerian mean flow.

The maximum Eulerian streaming velocities are well predicted by the expression $V^2/\sqrt{8\nu\omega}$ by Lighthill (1992) where $V$ is the basilar membrane velocity amplitude that has been obtained from simulation results in the present work.

As a physiological consequence, the steady streaming might induce
bending forces on the hair cell stereocilia, as has already been pointed out by Lighthill (1992). Further, it might enhance the transport of ions in the cochlear fluids. This could assist the processes which re-establish the gradients in ion concentration. Steady streaming might also constitute a mechanism to reduce the number of blood vessels which are necessary to provide the lymphatic solutes. Blood flow in the cochlea is related to mechanical noise which could be reduced by an additional transport mechanism. Finally, steady streaming could be useful in the targeted medication of pathological conditions.

6.1.3 Rocking stapes motion

Chapter 5 investigates the movement of the fluid and the basilar membrane due to stimulation with a rocking stapes motion. Qualitatively, the primary wave of the basilar membrane is the same as for the piston-like stimulation. The primary wave of the fluid exhibits differences in the region close to the oval and round windows. The rocking displacement of the stapes leads to smaller peak amplitudes of the basilar membrane deflection than the piston-like stimulation for comparable stimulation intensities. The maximum deflection amplitudes decrease as the frequency decreases whereas they increase for the piston-like stapes motion. If identical inflow velocities for all frequencies are considered, the difference in basilar membrane peak amplitudes between both stapes motions is smallest at about 4000 Hz. The amplitude difference amounts to about 10 dB at this frequency and increases by about 12 dB per octave towards lower frequencies. The maximum difference of 70 dB is found at 100 Hz. For constant maximum ear canal pressure, and therefore for frequency dependent inflow stapes velocities, the difference between the two stimulation modes is larger. The minimum difference is again present at 4000 Hz with 20 dB.

The oscillation of the basilar membrane is evoked differently for the two stimulation modes which also explains the differing frequency dependencies of the peak amplitudes. The rocking stapes motion initiates the membrane oscillation only locally beneath the oval window. This can be seen from the pressure difference across the basilar membrane which decays steeply behind the inflow region. For the piston-like stapes motion, in contrast, the decay is much slower and relatively large pressure differences are present at the characteristic place. Therefore the membrane motion is induced along the complete length between the
6.2 Future Investigations

The presented cochlea model can be extended in different ways in order to study further aspects of cochlear mechanics. In the long run a detailed model of the cochlea can be developed which accounts for active amplification, the structures in the organ of Corti and the complex cochlear geometry. Obrist (2011) discusses in detail the option of a multi-physics and multi-scale “virtual cochlea” which extends the present model and points out how to meet the upcoming challenges in modelling, implementation and computation.

The suggestions by Obrist (2011) shall not be repeated here. Instead, this section presents extensions which may be realised in the medium term and which can be added to the model of the present work without

stapes and the characteristic place. Potential flow theory shows that for the rocking stapes motion the pressure difference across the membrane scales with the Strouhal number, which leads to lower membrane amplitudes for lower frequencies. In addition, the pressure difference depends on the distance between the stapes and the characteristic place. This explains the stronger influence of the stapes position on the membrane peak amplitudes in the case of the rocking stimulation in comparison to the piston-like stimulations. Larger channel widths generate smaller peak amplitudes while the amplitudes increase if the stapes is moved toward the apex, the far end of the cochlea.

Under combined stimulation, when both stapes movements are present at the same time, the rocking component increases or decreases the membrane amplitudes compared to stimulation with purely piston-like stapes displacement. The enhancement or reduction depends on the phase shift between both stimulations. The difference is rather small and amounts at most to the peak amplitude of the purely rocking stimulation. The peak amplitudes of the combined stimulation can be determined by linear superposition of the single-mode stimulations.

The influence of the rocking stapes motion on the hearing is small under healthy conditions because the membrane amplitudes are dominated by the piston-like component. Under pathological conditions, however, the rocking motion can lead to hearing when piston-like displacements of the stapes are not possible. This is most probably the case for patients suffering from round window atresia. Clinical (Linder et al., 2003) and experimental (Huber et al., 2008) studies support this finding.
using modules outside of the computational code IMPACT. Some of these options have been addressed in student projects.

An important property of the cochlea is the active amplification (Sec. 1.2) of the oscillation of the cochlear partition. This mechanism is included in recent cochlea models in different ways (Sec. 1.3). In the framework of the present cochlea model, the non-linear oscillator with Hopf bifurcation can be regarded as the best description of active amplification. This bifurcation has been shown to reflect the important characteristics of the physiological process (Hudspeth et al., 2010). In student projects, active amplification by a system of oscillators with Hopf bifurcation has been successfully modelled in a potential flow model of the cochlea (Benner, 2011; Koch, 2012; Müller, 2010). Effects such as the compressive non-linearity and distortion products have been reproduced. The same model for the active amplification can be included into the present immersed boundary implementation in a straightforward manner. It adds an array of non-linear oscillators to the present array which represents the basilar membrane. Each oscillator of the second array has a proper eigenfrequency and features a Hopf bifurcation. It exerts an additional force on the cochlear fluid which directly depends on the membrane deflection. This extension to the cochlea model demands a careful implementation of the time integration of the second oscillator array. Special attention has to be paid to the numerical stability of the simulation.

Different effects of active amplification can be studied. Active amplification leads to sharper peak amplitudes of the basilar membrane. The larger gradients of the travelling wave affect the steady streaming. Since the active amplification depends on the stimulation intensity, the streaming velocities as function of frequency and stapes velocity are of interest. Further, the generation of evoked otoacoustic emissions (OAEs) can be studied, making use of different stimulation types such as clicks (click-evoked OAEs) and frequency pairs (distortion-product OAEs). Additional effects are the two-tone suppression (2TS) and spontaneous otoacoustic emissions (SOAEs).

The present model reduces the cochlear partition to a single membrane. Simulations with a second one, the tectorial membrane, have been performed and analysed (Gander, 2012). Further investigations are possible. As Gander (2012) has shown an improvement of the bi-linear
interpolation in the immersed boundary approach is recommendable for future works. In a model with the basilar and the tectorial membrane the motion of both membranes and the steady streaming in the gap between them are of interest.

In some areas, such as the hook region (the high-frequency region of the cochlea), the cochlear geometry is highly three-dimensional. While the present thesis studies a two-dimensional box model of the cochlea, the model can be extended to three dimensions in space. This allows to improve the modelling of the round and oval window positions. Also the distribution of the basilar membrane stiffness (Sec. 1.3) in the radial direction (z-direction in the present Cartesian framework) can be represented. Such a model allows to investigate the three-dimensional travelling wave of the basilar membrane and of the fluid flow. Further, the three-dimensional steady streaming can be studied. Especially in a model which comprises a basilar and a tectorial membrane, insight into the shearing motion between the membranes can be gained. The influence of the steady streaming on the hair cell stimulation could be studied in more detail.

Further, the cochlea model can be extended by changing its geometry. The usage of the immersed boundary approach allows to adapt the outer geometry of the model as well as the resting positions of its mechanical structures toward a more realistic model.

An option towards a more realistic representation of the high-frequency region is to alter the resting position of the basilar membrane. In Spirito (2013) a curved resting position in the front region of the cochlea has been tested together a positioning of the round window in the bottom wall of the scala tympani. Further investigations of the basilar membrane movements for this model geometry are possible. Of special interest is the membrane motion at high frequencies.

Alterations of the outer geometry allow to account for the tapering of the cochlea and for its widening in the hook region. The immersed boundary approach can be used to model the cochlear walls by damped, nearly non-moving, oscillators instead of the current representation by Dirichlet boundary conditions. This allows to position the outer bounds of the cochlea within the computational domain. In this case, the accuracy of the model has to be monitored thoroughly because volume leakage problems are possible (Givelberg, 2012; Peskin & Printz, 1993). Special
interest should also be paid to the computational stability because of the stiffer system of equations. The simulations can be expected to be significantly more expensive and the insight which results from the change in geometry should be weighed up against the computational costs.

When changing the outer geometry by immersed boundaries in a three-dimensional system, several options are possible. One interesting option is to realise the widening in the high-frequency region and the actual positions of the oval and round windows. Probably the high-frequency hearing can be studied best in such a model. Since the cochlea cavity is largest in the basal region, this option implies that stiff immersed boundaries are to be added along the cochlea. The tapering of the cochlea could be accounted for with the implications pointed out above.

Another option is to model the coiled cochlea. In the Cartesian coordinate system which is inherent to the fluid solver IMPACT, the spatial resolution of this geometry is demanding. Obrist (2011) points out more details for such a representation which involves the use of curvilinear coordinates.

The suggestions above concentrate on representing the cochlea in a more realistic way in order to gain more insight into cochlear fluid flow, into the interplay between the fluid and the membranes and into the membrane motion. A further area of application is the development and improvement of hearing aids. Many of these devices directly affect the fluid flow in the cochlea, e.g., by replacing the stapes (middle ear prostheses) or by inserting electrodes (cochlear implants) or probes (cochlear microphone) into the cochlea. Thereby they influence the fluid flow in the cochlea as well as the membrane motion which affects the sound signal transmission to the nerve cells.

By means of the immersed boundary method, the cochlea model can be used to evaluate the effect of such objects as mentioned above on the hearing. Also the shape and placement of these parts of hearing devices can be optimised with the model. First steps into this direction have already been made Spirito (2013).

Apart from the extensions pointed out above, the present model can be improved by altering aspects of the numerical treatment of the basilar membrane with the aim to increase the stability, accuracy and/or efficiency of the computations. The spatial discretisation of the membrane can be refined by increasing the number of oscillators which model
it. This has already been implemented by Spirito (2013). Further, the currently used bi-linear interpolation scheme of the immersed-boundary approach can be changed to a wider stencil with higher convergence order.

In the case that the active amplification of the basilar membrane is added, the time-integration scheme of the membrane might have to be changed or extended. The model for the active amplification pointed out above uses oscillators with Hopf-bifurcation. This implies that a non-linear, time-dependent equation is solved at each membrane point. The oscillators give an additional deflection to the membrane (or an additional force to the fluid) which depends on several parameters, *inter alia* the stimulation frequency, an oscillator eigenfrequency and a bifurcation parameter. Müller (2010) uses a combined implicit-explicit time-integration scheme to circumvent stability problems due to the non-linear equation for the active amplification.

To close the present work, the opening citation on p. 1 by Cato the Elder shall be revisited. Research continues to make progress in explaining the hearing and in enabling to hear – but one task remains with the listener: to understand the things heard.

*We do not hear because we have ears, but we have ears and are able to have ears because we hear.*

Martin Heidegger

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Appendix A

A Model for the Fluid Flow and Basilar Membrane Motion in the Active Cochlea

The present appendix chapter introduces a computational model for the fluid flow and basilar membrane motion in the active cochlea. The active amplification has not been included into the passive cochlea model of the Chaps. 2 to 5 but into a transient inviscid linear model of the passive cochlea extending the one by Lesser & Berkley (1972). The passive model and the modelling approach for the active amplification are described in Sec. A.1. Simulation results of the active model are presented in Sec. A.2. These results have been obtained in student projects at the Institute of Fluid Dynamics of ETH Zurich supervised by the author of the present thesis and by Dr. Dominik Obrist, now Professor at the University of Bern.

A.1 Active cochlea model

The present section describes the model for the inviscid linear fluid flow in the cochlea and for the passive basilar membrane motion (Sec. A.1.1) and the modelling approach for the active amplification (Sec. A.1.2). The resulting active cochlea model has been developed in student projects at the Institute of Fluid Dynamics of ETH Zurich (Benner, 2011; Gorji, 2008; Koch, 2012; Müller, 2010; Piehl, 2007). Section A.1.2 indicates parameter choices for the simulation results presented in Sec. A.2.

For the ease of reading the superscript * denoting dimensional quantities is omitted throughout the present chapter.

A.1.1 Inviscid model for the fluid flow in the cochlea and the passive basilar membrane motion

The fluid flow in the cochlea and the motion of the passive basilar membrane are described extending the model by Lesser & Berkley (1972). The motion of the cochlear fluid is modelled as two-dimensional poten-
tial flow,
\[
\frac{\partial^2 \Phi}{\partial x^2} + \frac{\partial^2 \Phi}{\partial y^2} = 0,
\] (A.1)

with the potential \( \Phi(x, y, t) \) and where \( x \) and \( y \) are directed along the cochlea and perpendicular to it, respectively (Fig. A.1). Non-linear effects such as the steady streaming discussed in Sec. 4 are neglected; further the flow is considered as inviscid which is motivated by large Womersley numbers present in the cochlea for medium to large stimulation frequencies.

The pressure is governed by the linearised unsteady Bernoulli equation (Lesser & Berkley, 1972)
\[
\rho \frac{\partial \Phi}{\partial t} + p = 0.
\] (A.2)

The passive basilar membrane is modelled by an array of independent damped oscillators,
\[
m \frac{\partial^2 \eta}{\partial t^2} + R \frac{\partial \eta}{\partial t} + K \eta = -2p|_{y=0},
\] (A.3)

where \( \eta \) denotes the transversal displacement of the basilar membrane with respect to its resting position at \( y = 0 \). In the present model only the wall-normal membrane displacement is considered. The parameters \( m \), \( R \) and \( K \) describe the membrane mass, damping and stiffness and are chosen according to Lesser & Berkley (1972) as
\[
m(x) = 0.05 \text{ g/cm}^2,
R(x) = 3 \times 10^3 e^{-1.5x/L_c} \text{ g/(cm}^2\text{s)},
K(x) = 1 \times 10^9 e^{-3x/L_c} \text{ g/(cm}^2\text{s}^2)
\] (A.4)
with $L_c$ as the length of the cochlea.

Unlike in the non-linear viscous model addressed in the Chaps. 2 to 5 the damping of the present system is not provided by the fluid flow and needs to be modelled through the membrane motion. Further, the mass is assumed as constant along the membrane. The parameter choices (A.4) yield practically the same tonotopic map as the one obtained by Lesser & Berkley (1972).

The governing equations are solved in a two-dimensional box (Fig. A.1) of 3.5 cm length and of 1 mm height for each of the scalae vestibuli and tympani. The stapes is positioned at the front end of the scala vestibuli. Because the round window is located at the front end of the scala tympani a symmetric domain results such that only the fluid motion in the scala vestibuli is computed.

At the walls, wall-normal velocity boundary conditions are prescribed, using the velocities of the stapes and of the basilar membrane at $x = 0$ and at $y = 0$, respectively. All other boundaries are modelled as solid walls with zero wall-normal velocity. Lesser & Berkley (1972) provide an analytical solution for the potential $\Phi$ for the steady state using a spatial series expansion. This solution fulfils the boundary conditions at the solid walls and at the stapes. The motion of the basilar membrane, expressed in dependence of the material parameters and the potential $\Phi$, needs to be solved numerically which yields the coefficients of the series expansion. The steady state solution by Lesser & Berkley (1972) has been extended to the transient case by Piehl (2007) and Gorji (2008).

### A.1.2 Model for the active amplification

As pointed out in Sec. 6.2 the Hopf bifurcation has been found to reflect the characteristics of the active amplification in the cochlea (Hudspeth et al., 2010). The normal form of an oscillator with Hopf bifurcation stimulated by a harmonic forcing $F e^{i\omega t}$ reads

$$\frac{\partial \zeta}{\partial t} = (\beta + i\Omega)\zeta - b|\zeta|^2 \zeta + \gamma F e^{i\omega t}$$  \hspace{1cm} (A.5)

where $\zeta$ denotes the oscillation amplitude, $\beta$ the bifurcation parameter and $\Omega$ the eigenfrequency of the system. The parameters $b$ and $\gamma$ are complex multipliers of the non-linearity of the system and of the external forcing, respectively.

In a two-way coupling each of the oscillators (A.3) modelling the
A Model for the Active Cochlea

The active basilar membrane is connected to one oscillator with Hopf bifurcation (A.5) in order to model the active basilar membrane motion,

$$\frac{m}{\partial t^2} + R \frac{\partial \eta}{\partial t} + K \eta = -2p + a \zeta, \quad (A.6)$$

$$\frac{\partial \zeta}{\partial t} = (\beta + i\Omega) \zeta - b |\zeta|^2 \zeta + \gamma \frac{\partial \eta}{\partial t}. \quad (A.7)$$

Here the velocity of the oscillating basilar membrane, $\partial \eta/\partial t$, stimulates the active amplification and replaces the harmonic forcing in Eq. (A.5). The displacement of the oscillator with Hopf bifurcation, in turn, acts as an additional forcing on the mass-spring-damper system of the passive membrane.

The resulting system of equations to model the fluid flow and active basilar membrane motion in the cochlea is solved numerically using the analytical solution by Lesser & Berkley (1972). The equations are discretised in space on equidistant collocation points along $x$. In time, a combined implicit-explicit integration scheme is used with an explicit three-step third order Runge-Kutta scheme for the non-linear terms and with an implicit second order Cranck-Nicolson scheme for the linear terms (Müller, 2010).

The model for the active amplification introduces different parameters which are interdependent because the system is over-determined. Müller (2010) derives expressions for these parameters; the results are given in the following.

The Hopf-eigenfrequency $\Omega(x)$ governs the tonotopic map of the Hopf-bifurcation-based amplifiers (A.7). It is assumed that this tonotopic map equals the tonotopic map of the passive system when shifted along the membrane by $\Delta x$,

$$\Omega(x) = \lambda_{\text{base}} e^{-1.5(x + \Delta x)/L_c}, \quad (A.8)$$

where $\lambda_{\text{base}}$ denotes the eigenfrequency of the passive system at the base ($x = 0$), $\lambda_{\text{base}} \approx 76 \text{kHz}$. The choice of the axial shift $\Delta x$ is varied in Sec. A.2.1; here simulation results are given for $\Delta x = 0.126 \text{cm}$ and for $\Delta x = 0.0835 \text{cm}$.

The bifurcation parameter $\beta$ influences, together with the choice for $\Omega$, the spatial bandwidth of the basilar membrane response and the location of the peak of the basilar membrane deflection. The bifurcation parameter is chosen as

$$\beta(x) = r \Omega(x), \quad r = \text{const.} \quad (A.9)$$
with \( r = -1/15 \). For constant \( r \) the spatial bandwidth of the Hopf-amplifier is independent of \( x \).

The multiplier \( b \) of the non-linearity of the oscillator with Hopf-bifurcation is chosen as \( b = 1 \) because this parameter can be shown to be compensated by the choices of \( a \) and \( \gamma \), the multipliers of the coupling between the Hopf-amplifier and the passive mass-spring-damper system.

The multiplier \( a \) of the forcing of the mass-spring-damper system (A.6) due to active amplification is given by

\[
a(x) = \phi \frac{s(x) - 1}{s(x)} \frac{2|\beta(x)|R(x)}{\gamma(x)}
\]

(A.10)

with

\[
s(x) = \frac{\eta_{0 \text{ dB, active}}}{\eta_{0 \text{ dB, passive}}}
\]

(A.11)

For the simulation results shown in Sec. A.2 \( \phi \) and \( s \) are chosen as \( \phi = 4.5 \) and \( s = 1000 \).

The parameter \( \gamma \) multiplying the forcing of the Hopf-amplifier (A.7) is chosen such that the basilar membrane motion is linear for very small sound stimulations (below 10 dB) and compressive non-linear for signals louder than 20 dB. This parameter can be shown to equal

\[
\gamma(x) = \frac{2|\beta(x)| (\beta(x)^2 + \Omega(x)^2)^{1/4}}{\sqrt{b}\Omega(x)|\eta|_{\text{crit}}}
\]

(A.12)

where \( |\eta|_{\text{crit}} \) defines the amplitude of the basilar membrane deflection at 20 dB. In the simulation results shown in Sec. A.2 this value is assumed as 100 times the amplitude of the basilar membrane deflection in a passive simulation with a stimulation intensity of 20 dB, yielding \( |\eta|_{\text{crit}} = 8.45 \cdot 10^{-9} \text{ cm} \).

### A.2 Motion of the active basilar membrane

The active cochlea model captures different properties of the active amplification in the cochlea. The present section presents simulation results of the basilar membrane deflection for different stimulation conditions. Section A.2.1 shows the basilar membrane response to stimulation with one frequency at different stimulation intensities. Two different values for the model parameter \( \Delta x \) are chosen to illustrate the influence of this
parameter on the simulation results. All other parameters are chosen as indicated in Sec. A.1.2. Section A.2.2 presents simulation results for stimulation with two frequencies at the same time leading to distortion products. Stimulation with a chord of three frequencies evokes Rameau’s fundamental bass as shown in Sec. A.2.3.

The simulation results have been taken from the student projects Müller (2010), Benner (2011) and Koch (2012) at the Institute of Fluid Dynamics of ETH Zurich. When considering the actual values for the simulated membrane deflections it has to be noted that the parameter choices of the model have not been optimised in order to match experimental data.

A.2.1 Stimulation with one frequency at different sound signal intensities

Figures A.2 and A.3 show the maximum amplitudes of the basilar membrane deflection for a stimulation frequency of $f = 5000$ Hz at increasing sound signal intensities. In comparison to the passive membrane motion (Fig. A.2) the active amplification leads to significantly sharper peaks which are shifted in the axial direction. The bandwidth increases for louder stimulation. Further the peaks of the active basilar membrane show increased amplitudes.

The active amplification of the model is compressive non-linear as can be seen from Figs. A.4 and A.5 which illustrate the gain (basilar
A.2 Motion of the active basilar membrane

Figure A.3: Amplitudes of the basilar membrane deflection for different stimulation intensities at $f = 5000$ Hz: (a) $\Delta x = 0.126$ cm, (b) $\Delta x = 0.0835$ cm. (Figure adapted from Müller (2010).)

Figure A.4: Gain of the basilar membrane deflection for different stimulation intensities at $f = 5000$ Hz: (a) $\Delta x = 0.126$ cm, (b) $\Delta x = 0.0835$ cm. (Figure adapted from Müller (2010).)

membrane amplitude relative to the ear canal pressure) of the membrane motion. The compressive non-linearity begins at stimulation intensities between 10 and 20 dB (Fig. A.5(a)).

The basilar membrane deflection amplitudes are qualitatively similar to those obtained in experimental studies (e.g. Ruggero, 1992). The compressive non-linearity (Fig. A.5(a)), however, is more pronounced in experimental data (cf. Ruggero, 1992).

The results depicted in Figs. A.2 to A.5 show the effect of $\Delta x$ on
the active amplification. This parameter governs the tonotopic map of
the Hopf-bifurcation-based amplifiers (Eq. (A.8)) and thereby the shift
of the membrane deflection peak due to active amplification. Further
\( \Delta x \) influences the amplification and the gain of the membrane deflection.
For smaller values of \( \Delta x \) the amplification is increased (Fig. A.2) and
consequently also the gain (Fig. A.5(b)).

The effect of \( |\eta|_{\text{crit}} \), which influences the coupling parameter \( \gamma \)
(Eq. (A.12)), is shown by comparison of Fig. A.6(b) with Fig. A.3(a).
A.2 Motion of the active basilar membrane

Figure A.7: Amplitudes of the basilar membrane deflection exhibiting distortion products: (a) $f_1 = 10$ kHz, $f_2 = 12$ kHz; (b) $f_1 = 5000$ Hz, $f_2 = 5700$ Hz. All frequencies are stimulated with the same intensity. (The wiggles at $x > 2.75$ are a numerical artefact due to the very slow convergence of the steady state oscillations. Figure adapted from Benner (2011).)

Figure A.6(b) shows the maximum amplitudes of the basilar membrane deflection for increasing sound signal intensities for stimulation at $f = 1000$ Hz. The active amplification becomes compressive non-linear for lower sound pressure levels than for stimulation at $f = 5000$ Hz which is an effect of the choice of $|\eta|_{\text{crit}}$. In the presented simulation results the same value $|\eta|_{\text{crit}} = 8.45 \cdot 10^{-9}$ cm is used for both stimulation frequencies. Since $|\eta|_{\text{crit}}$ is the amplitude of the basilar membrane deflection at 20 dB, this parameter needs to be increased for lower stimulation frequencies.

A.2.2 Simulation of distortion product otoacoustic emissions

When exposed to two stimulation frequencies at the same time, the active basilar membrane is known to show large oscillation amplitudes not only at the characteristic places of the stimulation frequencies but also at the characteristic places of frequencies which are harmonically related to the presented tones. These distortion products lead to evoked otoacoustic emissions, the distortion product otoacoustic emissions (DPOAEs).

Distortion products simulated with the present active cochlea model are illustrated in Fig. A.7 where the membrane deflection amplitudes along the cochlea are shown for two stimulation frequency pairs. The distortion product of the frequency $f_{\text{DP}} = 2f_1 - f_2$ is clearly visible in both cases and reaches about 10% of the stimulation intensity. While
the distortion product \( f_{DP} = 3f_1 - 2f_2 \) shows a distinct peak for both stimulation cases, the product \( f_{DP} = 4f_1 - 3f_2 \) is visible only for the high-frequency stimulation \( (f_1 = 10 \text{ kHz}, f_2 = 12 \text{ kHz}) \).

A frequency analysis of the membrane motion directly behind the stapes \( (x = 0.1 \text{ cm}) \) shows that the distortion tones propagate along the cochlea (Fig. A.8). This indicates the presence of backwards travelling waves.

### A.2.3 Simulation of Rameau’s fundamental bass

The term Rameau’s fundamental bass denotes a low frequency \( f_0 \) present in the basilar membrane motion due to stimulation at a chord of three higher frequencies with the frequency ratio \( f_1 : f_2 : f_3 = 4 : 5 : 6 \) relative to the fundamental bass frequency. The phenomenon of the fundamental bass is similar to that of the distortion products discussed in the previous section.

Rameau’s fundamental bass simulated with the active cochlea model is shown in Figs. A.9 and A.10 using two different stimulating chords. In both cases the fundamental frequency and its higher harmonics are present in the basilar membrane deflection. The periodograms of the passive and of the active basilar membrane motion presented in Fig. A.10 visualise the effect of the active amplification in the cochlea model.
Figure A.9: Amplitudes of the basilar membrane deflection exhibiting Rameau’s fundamental bass for different sound pressure levels ($f_1 = 1000$ Hz, $f_2 = 1200$ Hz, $f_3 = 1500$ Hz). (The small wiggles in (a) at $x > 3$ are a numerical artefact due to the very slow convergence of the steady state oscillations. Figure adapted from Koch (2012).)

Figure A.10: Periodogram of the basilar membrane deflection for stimulation with $f_1 = 8$ kHz, $f_2 = 10$ kHz, $f_3 = 12$ kHz: (a) simulation of the passive cochlea; (b) simulation of the active cochlea (red colours indicate large, blue colours low power spectral densities). All frequencies are stimulated with the same intensity. (Figure adapted from Koch (2012).)


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**Publications**


**Curriculum vitae**

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