1 Introduction

Hearing research

Mammalian hearing is a complicated process which involves many steps. An acoustic pressure wave propagating through air is received by the pinna and channelled to the ear-drum by the external auditory canal. Hereafter, the stimulus is transferred from air to labyrinthine fluid. The medium mismatch is compensated by the middle ear. After this, the stimulus reaches a snail-shell like spiral tube, called the cochlea. The moving structures and the hydrodynamics within the cochlea form an electromechanical structure which enables frequency-, spatial- and temporal analysis. The transduction of the mechanical stimulus to nerve impulses is performed by the mechano-sensory hair cells housed inside the organ of Corti. These electrical impulses are "heard" by the brain as sound.

Just from this simple overview alone, it is clear that understanding the complete hearing process involves knowledge of many disciplines. Hence research into hearing has been divided into many specialisations, each investigating a particular part of the auditory organs in order to understand the specific functions of each part. Present research involves both practical measurements and computer modelling. Measurements supply the necessary data for the development of the cochlea models. In return, the models are used to verify the measurements or to give an insight into what is important to measure. The knowledge obtained from hearing research may lead to improvements in e.g. hearing aids and speech recognition programs.

Besides the complexity of the mammalian cochlea structure, the organ is encased in thick protective temporal bone. This makes it difficult to conduct measurements in the internal structures of the cochlea without disturbing the natural conditions. The complexity of hearing motivates scientists to expand their studies to include birds, reptiles, amphibians and fish. In fact, when it comes to studying the transductional and physical properties of the sensory hair cells it is far easier to conduct the research on fish and amphibians. They possess a far simpler and more easily accessible sensory hair cell organ, the lateral line organ.
Lateral line sensory organ

The ancestors of all jawed vertebrates emerged in the warm waters of the earth's vast primordial sea around 500 million years ago (Litman, 1996). These animals are believed to resemble certain members of a later group of fish, known as the placoderms. These ancestors evolved to more advanced fishes, including those which eventually crawled onto land and evolved further into amphibians, reptiles, birds and mammals.

The lateral line organ, which is unique to fish and amphibians, has been known since ancient times. The first ever (accurate) description of the lateral line organ appears to be given by Stenonis in 1664 (Walker, 1967). At that time, the lateral line organ was thought to be responsible for producing slime. It was not until the early nineteenth century before it was recognised to be a sensory organ (Jacobson, 1813; Walker, 1967), specifically for water motion (Knox, 1825; Walker, 1967). With improvements in measuring techniques, our knowledge of this organ has advanced immeasurably in terms of anatomy, physiology and lateral line mechanics.

The structure of the lateral line organ is relatively simple in comparison with the mammalian cochlea. If we take for example the lateral line organ of the animal used for these studies, the ruffe (*Acerina cernua* L.) a common freshwater fish, it basically consists of a number of neuromasts contained in a bony canal (see Fig. 1). The neuromast comprises of a cluster of sensory hair cells surrounded by supporting cells and a cupula.

![Figure 1: A diagram of the lateral line organs found on the ruffe's head. Part of the supraorbital lateral line organ is also shown with the skin removed.](image)
The stereocilia of the sensory hair cells are embedded in the matrix structure of the cupula (Kelly and van Netten, 1991). Thus, any mechanical stimulus experienced by the cupula is directly coupled to the hair cells. Although the structure of the lateral line organ is relatively simple, it is nevertheless extremely sensitive. For the ruffe, the threshold displacement sensitivity is in the order of 1 nm at 100 Hz (Kuiper, 1956).

The lateral line organ plays a major role in the detection and positioning for striking at the prey (Janssen and Corcoran, 1993), avoiding predators, avoiding obstacles (Dijkgraaf, 1963) and for schooling (Partridge and Pitcher, 1980). This remarkable organ may be a factor in explaining the success fishes and amphibians have in colonising a wide variety of habitats, ranging from clear to dark murky water.

**Labyrinthine fluid**

Bárány's work (1907) on the endolymph, a fluid with suitable density and viscosity, led to the conclusion that it was responsible for the stimulation of the hair cells (Dohlman, 1967). A little more than half a century later, interest in the properties of the labyrinthine fluids and vestibular organs reached new heights. During the early stages of the space race, there was a lot of interest from NASA in the vestibular organs with regard to the problems faced by astronauts during space exploration. The vestibular organs, which evolved to operate within the gravitational forces of earth, are exposed to unique gravitoinertial forces encountered in the exploration of space. This made it necessary to understand the sensory information, which may differ quantitatively and qualitatively from what is experienced on earth, in order to cope and adjust to the extra-terrestrial conditions.

Due to the important roles played by the labyrinthine fluids, there has been much research into the physical properties of these fluids. Physical properties such as viscosity, density, thermal coefficient of viscosity and coefficient of thermal expansion were measured by Steer et al. (1967).

The stimulation of the sensory hair cells of the lateral line organ is analogous to that found in the vestibular system of mammals. In this case, the role of the endolymph is taken by the lateral line fluid which drives the cupula by a combination of viscous and inertial fluid forces (van Netten, 1991). Unlike the multitude of studies on endolymph and perilymph, research carried out on the lateral line canal fluid is very modest in comparison.

In the eighties and early nineties, Denton and Gray devised many novel
measuring techniques to conduct in vivo studies in the lateral line canal. Lateral line canal fluid flow (Denton and Gray, 1983, 1988, 1993) and the interactions with different types of lateral line canal geometry were measured in physical models (Denton and Gray, 1988). With aid of a model, the viscosity of the lateral line canal fluid was estimated to be 1.7 mPa s for a simple canal with pores (Denton and Gray, 1988). A higher value of 5.1 mPa s (van Netten, 1991) was calculated for the lateral line canal fluid of the ruffe.

The flow profiles in the lateral line canal have long been assumed (Denton and Gray, 1988; van Netten, 1991) to resemble the flow profiles found in a closed tube (see e.g. Sexl, 1930; Schlichting, 1960). Although the lateral line canal fluid flow was measured by Denton and Gray (1988), it was limited to single points in space and no flow profiles could be deduced. The lack of measurements in this area of lateral line research needs to be filled to advance our understanding of this organ.

This research

The study presented in this thesis is a continuation of the research carried out on the lateral line organ of the ruffe (Acerina cernua L.) at the Biophysics department of the University of Groningen. Much of the previous research has been concentrated on the morphology and the mechanics of the lateral line, from the cupula down to the level of the sensory hair cells; see e.g. Wubbels (1990), van Maarseveen (1994), van Netten and Kroese (1987), and van Netten (1991). Surprisingly, very little detailed research has been conducted on the lateral line canal fluid which surrounds the neuromasts. The importance of this fluid has long been recognised for the role it plays in driving the cupula. However, research in this field has been limited due to the fact that specialised measurement techniques are required to carry out a comprehensive study on the physical and flow properties of this fluid in vivo.

This thesis consist of several parts, all dealing with different aspects of the lateral line fluid. The first part (chapter 2) deals with measuring the viscosity of a small volume (0.04 ml) of lateral line canal fluid as a function of temperature. For this purpose a novel viscometer was developed. This viscometer has the capability to measure the viscosity of biological fluids in vivo or in vitro over the full, physiologically relevant temperature range. It consists of a laser interferometer closely related to the one described by van Netten (1988), which was used to track the motion of a driven pendulum submerged in the sample fluid. The viscosity of the sample fluid can thus be worked out from the resonance characteristics exhibited by the oscillating pendulum.
The second part (chapter 3) focuses on the flow characteristics of the lateral line canal fluid. In this chapter, the flow measurements in a lateral line canal with the cupula removed are described. The removal of the cupula is necessary to investigate the influence of the lateral line canal on the stimulus received by the cupula. As with the viscosity measurements, a specialised measurement technique was developed. A micro sense probe, constructed from a tapered glass fibre with a \( \varnothing 50 \mu m \) sphere cemented on, is used for tracking the fluid flow. This micro sense probe has the advantage that it can be placed nearly anywhere in 3-D space within the lateral line canal and allows velocity profiles to be made with a high spatial resolution (= 50 \( \mu m \)) and a vibrational velocity sensitivity down to the \( \mu m/s \) range.

In chapter 4, longitudinal and radial profiles measured with the cupula in place are presented. Included in this chapter is an extended version of the hydrodynamic model for cupular motion (van Netten, 1991) to describe the flow caudal to the cupula.

In conjunction with the flow measurements, the flow in the lateral line canal is also computed with a finite element package, SEPRAN (SEPRA-analysis, Delft, the Netherlands). The models' formulation and the computed results are presented in chapter 5. The limited 3-D capabilities of SEPRAN restrict the lateral line models (with and without cupula) to 2-D. The models mimic the conditions as encountered in the measurements described in chapters 3 and 4. These models are in fact first attempts at modelling the influence of a partially open canal on the flow of the lateral line canal fluid in the region of the cupula, with the aim of gaining some insight into the flow in areas which are inaccessible to the micro sense probe.

References


