

University of Groningen

Auditory mechanics of the frog basilar papilla

Schoffelen, Richard Leonard Maria

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version

Publisher's PDF, also known as Version of record

Publication date:

2009

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Schoffelen, R. L. M. (2009). *Auditory mechanics of the frog basilar papilla*. s.n.

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

CHAPTER 1

Introduction

Even in their simplest form, biological sensory systems depend on complex physiology in order to function. From a physical and engineering standpoint, the vertebrate auditory system may very well be the most intriguing sensory system: In the inner ear, fluid dynamics are generally combined with the mechanics of coupled membranes, adaptive detection thresholds and active amplification, to form a non-linear acoustic detector. It is testament to the complexity of this system that almost half a century has passed since Georg von Békésy published his landmark work ‘Experiments in hearing’ (1960) and won the Nobel prize for Physiology or Medicine for his ‘fundamental discoveries concerning the dynamics of the inner ear’ (1961), yet a complete physiological model of the inner ear remains illusive despite the efforts of many great investigators.

1.1 The vertebrate inner ear

In general, the vertebrate peripheral auditory system consists of three parts: the outer ear, the middle ear, and the inner ear. The system functions to pick up sound –air-pressure fluctuations– from the environment, and transform it into neural signals (Yost 2000). The specific area of interest in this dissertation is the inner ear. The inner-ear anatomy shows wide variations across vertebrate species, but there are a number of shared features (Lewis et al. 1985; Manley and Clack 2003).

All known vertebrate species have two inner ears, located on either side of the skull. They are fluid-filled cavities containing two membranous labyrinths: the endolymphatic space and the perilymphatic space. The sensory organs of hearing and balance are located within the endolymphatic space. Depending on the species, these senses are distributed across four to nine separate end organs. In terrestrial and amphibian species, one or two of the end organs are dedicated to the detection of airborne sound (Lewis et al. 1985).

All the inner-ear end organs have hair cells as their sensory cells. On their apical side, these cells have hair-like protrusions –stereovilli– which extend into the fluid-filled space of the inner ear. Deflection of the stereovilli initiates a bioelectrical response, that ultimately triggers neural activity in the nerve fibers connecting to the basal side of the cell (Pickles 1988; Yost 2000). In essence, the hair cells are mechano-electrical transducers, and they have been compared to strain gauges (Lewis et al. 1985).

The primary point of entry for auditory signals into the inner ear is generally the oval window. Here, the membranous wall of the perilymphatic space connects to the bony middle-ear ossicles to receive the acoustic signals from the environment. The acoustic energy then passes through the fluids of the inner ear, to its detection site at the hair cells of the auditory end organ.

The hair cells of the auditory end organs are set on a flexible basilar membrane (BM) in most classes of terrestrial vertebrates –the one exception being anuran amphibians–. The stereovillar bundles of the hair cells protrude into the endolymphatic space. The hair bundles are often covered by a continuous tectorial membrane (TM), while in some species the TM is not continuous, or lacking altogether (e.g. Lewis et al. 1985; Manley 2006; Manley and Köppl 2008).

The afferent neurons connecting to the auditory epithelium exhibit a frequency-selective response, characterized by a characteristic frequency and a tuning sharpness. The characteristic frequency in many vertebrate hearing organs, among which the mammalian cochlea,

changes with the location at which the afferents connect to the epithelium. This implies that sound frequencies in these organs are detected at a specific place; this relationship between frequency and location of detection in the sensory epithelium is called tonotopy. Throughout the vertebrate species, the sharpness of tuning and the sensitivity are generally similar to those in mammals (Evans 1975b). Thus, a range of structurally different ears apparently have functionally very similar receptors.

In the mammalian cochlea, the frequency selectivity is reflected in the mechanical response of the BM (Ruggero et al. 1992; Narayan et al. 1998). The response of the BM at a specific location in the cochlea matches the properties of the neural-tuning curves. Von Békésy (1960) was the first to establish the mechanical basis for the frequency-selective response by showing a frequency-dependent mechanical response of the BM in the post-mortem inner ear. Later measurements significantly altered the picture presented by these classical experiments. Specifically, the active contribution of the outer hair cells was found to shape the mechanical response of the membrane (Johnstone et al. 1986); their active somatic motility contributes directly to the mechanical response of the BM (Robles and Ruggero 2001). This contribution results in a significant sharpening of the tuning curves, which is of obvious importance to the ability to distinguish between frequencies.

Mammalian outer hair cells have the ability to actively change their soma length. Interestingly, this specific active process seems to be restricted to the mammalian cochlea, and appears to be absent non-mammalian vertebrates. Rather, active hair-bundle motility, as observed in the amphibian saccular hair cells, may serve as a mechanism for active amplifications of sound signals (Martin and Hudspeth 1999; Hudspeth 2008). Recently, this mechanism was suggested to exist in mammalian hair cells as well (Fettiplace 2006).

The response of the BM has only been studied in a few species. Manley et al. (1988) found no mechanical tuning of the BM response in the lizard *Tiliqua*. In such cases, the frequency-selective response, and thus the tonotopic organization, may be based on the mechanical properties of the tectorial membrane. Also, mechanical properties of the hair bundles (Freeman and Weiss 1990) and electrical properties of the cell bodies (Ashmore and Attwell 1985) may contribute to the frequency selectivity.

In conclusion, various vertebrate inner ears show a number of shared features, and a large range of anatomical and functional variations. It is expected that the functional significance of the various substructures in the vertebrate inner ear may be determined from the comparative study of the relation between structure and function across species.

1.2 Auditory mechanics of the basilar papilla

The term *auditory mechanics* refers to the mechanics of the entire peripheral auditory system. The work presented in this dissertation was aimed at understanding the auditory mechanics of the basilar papilla in the frog inner ear. In particular, the focus was on the mechanical response of the tectorial membrane to acoustic stimulation of the oval window.

The basilar papilla is one of the frog's two auditory end organs. It covers the high-frequency part of the frog's auditory range, and is tuned to a single frequency (Ronken 1990, chapter 2). It lacks a BM. The hair cells of the relatively small sensory epithelium are set on the cartilaginous wall of its tubular lumen. A tectorial membrane is suspended over the epithelium (Wever 1985, chapter 3).

Acoustic energy stimulating the basilar papilla enters the lumen on the lateral side, and

exits through the contact membrane on the medial end (Purgue and Narins 2000b). It presumably deflects the hair bundles of the epithelium, with the tectorial membrane playing a role in conveying the fluid displacement to the hair bundles.

1.2.1 Outline of this dissertation

In **chapter 2**, we present a review of the state of knowledge of the frog inner ear. This review is focused on the inner-ear mechanics, rather than the physiology of the sensory end-organs. In order to form hypotheses about the mechanics in the frog inner ear, this chapter combines a model from literature, and a report on direct measurements of inner-ear structures with anatomical observations on frog auditory end organs and literature on measurements of nerve-fiber responses and otoacoustic emissions.

Chapter 3 describes the results of detailed exploration of the anatomy of the basilar papilla and its lumen in the northern leopard frog, *Rana pipiens pipiens*. The use of scanning electron microscopy and light microscopy led to the most extensive description of the organ in this species, to date.

Chapter 4 reports on measurements of the frequency selectivity of the tectorial-membrane response in the frog basilar papilla. We investigated the response of the tectorial membrane to displacement of the oval window, using light microscopy and optical-flow analysis.

For **chapter 5**, the same techniques were used to investigate the input-output characteristics between the oval-window displacement and the tectorial-membrane response.

Chapter 6 reflects on the findings of the preceding chapters, and discusses to what extent the aim of understanding the auditory mechanics of the frog basilar papilla was achieved.

1.2.2 Relation to published work

Chapter 2 through 5 were written as individual research papers. Three of these four chapters have been published in, or submitted to scientific journals. The differences between these papers and the chapters here are limited to the numbering of the chapters and sections, and the addition of cross-references between the chapters.

Chapter 2 was published in the May 2008 issue of the Journal of Comparative Physiology A as "R.L.M. Schoffelen, J.M. Segenhout, P. Van Dijk. Mechanics of the exceptional anuran ear." (Volume 194 (5), pages 417-428).

Chapter 4 was published in the September 2009 issue of the Journal of the Association for Research in Otolaryngology as "R.L.M. Schoffelen, J.M. Segenhout, P. Van Dijk. Tuning of the tectorial membrane in the basilar papilla of the northern leopard frog" (Volume 10 (3), pages 309-320).

Chapter 5 was submitted to Hearing Research as "R.L.M. Schoffelen, J.M. Segenhout, P. Van Dijk. Input-output characteristics of the tectorial membrane in the frog basilar papilla" in April 2009.