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Auditory mechanics of the frog basilar papilla

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Summary

The work presented in this thesis 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.

Chapter 1 gives a brief introduction into the general inner-ear anatomy and mechanics in vertebrates, as well as an outline of the following chapters.

The two inner ears in each vertebrate contain the end organs of hearing and balance, one or two of which are generally dedicated to the detection of airborne sound. Although their anatomy varies widely across species, the functioning of the receptor in terms of sharpness of tuning is remarkably similar.

Frequency selectivity in most vertebrate auditory end organs exhibits tonotopy: the characteristic frequency of the afferents connecting to the sensory hair cells changes systematically with the location in the epithelium. The tuning generally results from the passive mechanics of the inner ear and active amplification processes. In mammals, the mechanical response of the basilar membrane and the somatic motility of the outer hair cells provide the most important contributions to the tuning. Where it is studied in other species, the basilar membrane does not seem to be tuned. In these species, the mechanical properties of the hair bundles and the electrical properties of the hair-cell bodies are presumably the basis of the frequency-selective response.

The rationale to perform comparative research is the notion that the functional significance of various substructures in the inner ear may be determined from studying the various auditory organs across species.

In **chapter 2**, a review is presented of the literature concerning the functioning of the frog inner ear. It focuses on the mechanics of the frog's two dedicated auditory end organs, the amphibian papilla and the basilar papilla. The knowledge of and hypotheses about the functioning of these organs are primarily based on anatomical descriptions, models, recordings of neural responses from the auditory nerve and measurements of otoacoustic emissions.

The auditory range is divided between the frog's two auditory end organs. The low-frequency part is detected in the amphibian papilla (~ 100 - 1000 Hz, in *Ranidae*), while the high-frequency portion is detected in the basilar papilla (between ~ 1200 and 2500 Hz, in *Ranidae*). The amphibian papilla consists of multiple, tonotopically organized auditory filters, that have a tuning sharpness similar to that of other vertebrates. By contrast, the basilar papilla functions as a single broadly tuned auditory filter.

Functionally, three distinct regions could be identified within the two auditory end organs: one in the basilar papilla and two in the amphibian papilla. The low-frequency half of the amphibian papilla contains hair cells that exhibit electrical tuning and that are most sensitive to deflection along the tonotopic axis. In the high-frequency portion of the amphibian

papilla, the hair-cell polarization is perpendicular to the tonotopic axis, and there is no known electrical tuning of the hair cells. The presence of spontaneous otoacoustic emissions in this region's frequency range suggests that it functions as an active hearing organ.

Chapter 3 gives a detailed description of the basilar papilla's anatomy in the northern leopard frog, based on scanning-electron-microscopy images, and light-microscopy images in both fixated and non-fixated preparations. Our findings for the size and shape of the basilar papilla's lumen in the northern leopard frog were in line with those determined in related species. Also, the number of hair cells (average = 76) in the epithelium was similar to that in related species. We identified four types of hair cells in the leopard frog's basilar papilla; one more than was reported in the bullfrog. The hair-bundle orientation was uniformly from the saccular (lateral) side to the contact-membrane (medial) side of the epithelium, in correspondence with other derived anuran basilar papillae. The size of the tectorial membrane and its connection to the sensory epithelium led us to the conclusion that a considerable portion of the hair cells in the basilar papilla is most likely not directly connected to the tectorium. Only the hair cells on the medial side of the epithelium appear to connect directly to the overlying tectorial membrane. Their stereovilli protrude into holes in the membrane. The cells are placed in a dense and highly regular pattern, in contrast with the free-standing hair cells.

For the northern leopard frog, the data presented in this chapter form the most extensive description of the basilar papilla in its lumen. The results are not markedly different from reports in related species, and they provide a frame of reference for the interpretation of the results in the following chapters.

Chapters 4 and 5 report on measurements of the tectorial-membrane response to displacement of the oval window. The operculum in the oval window was sinusoidally displaced with mechanical stimulator. Under a light microscope, the response of the TM was captured in a 3D movie, using a digital camera and a stroboscopic illumination scheme. Amplitude and phase of the tectorial-membrane response were then analyzed with optical-flow algorithms.

These measurements were conducted in isolated preparations of the frog inner ear. Any active involvement of the hair cells had presumably ended before the experiments started. There was no evidence of degradation of the preparation during the experiment.

In **chapter 4**, the stimulus frequency was varied between 0.5 kHz and 3.0 kHz, while the stimulus amplitude was kept constant. The tectorial membrane's displacement amplitude in the basilar papilla was largest near the connection to the epithelium, and almost zero near the suspended free edge opposite the hair cells. The phase was constant throughout the membrane. Therefore the motion could be likened to that of a two-dimensional pendulum.

The maximum displacement of the tectorial membrane surpassed the operculum displacement by approximately 15 dB, making the amplitude amplification in the inner ear of the frog similar to that between the oval window and the basilar membrane in mammals.

The tectorial-membrane response was frequency selective with a best frequency of 2.2 kHz, corresponding to the neural peak sensitivity in the basilar papilla of the northern leopard frog. The tuning sharpness, Q_{10dB} , of the tectorial-membrane response was similar to the neural tuning sharpness. This led to the conclusion, that the basilar papilla of frog is an auditory receptor in which the frequency selectivity is based on the mechanical response of the tectorial membrane.

Chapter 5 discusses the input-output characteristics between the operculum displacement and the tectorial membrane response in the basilar papilla, at a stimulus frequency of 2.0

kHz. The tectorial membrane response increased linearly with increasing stimulus levels, and exhibited saturation for high stimulus amplitudes. However the saturation of the mechanical response occurred only at about 100 dB SPL, while neural response saturates approximately 20 dB below that level. Therefore, the mechanical response of the tectorial membrane does not determine the upper limit of the neural response.

The phase differences between the three orthogonal spatial components of the tectorial membrane response were either approximately 0° or approximately 180° , indicating that the motion of the tectorial membrane is predominantly rectilinear. The amplitude ratios and phase differences between the spatial components led to the conclusion that the tectorial membrane most likely moves along the surface of the sensory epithelium.

Finally, **chapter 6** gives a concise discussion of the main findings of the preceding chapters, and relates them to each other and to relevant literature.

Overall, the anatomy and the mechanics of the frog basilar papilla are simple and unique when compared to other vertebrate auditory end organs. The size and structure of the basilar papilla are exceptional due to the lack of a basilar membrane and because of the anatomy of the tectorial membrane. Functionally, it appears to be the only known passive auditory receptor in a vertebrate animal. The frequency selectivity of the basilar papilla is based on the mechanical response of the tectorial membrane, while the saturation of the neural response is based on the physiology of the hair cells and/or the connecting nerve fibers.

