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Auditory mechanics of the frog basilar papilla

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General discussion and outlook

Relation between the anuran and mammalian auditory end organs

The anuran inner ear is unique among terrestrial vertebrates in that it contains two dedicated auditory end organs, which both lack a basilar membrane (BM) as a flexible substrate for their sensory hair cells. The basilar papilla (BP) is considered to be the homologue of the mammalian cochlea (Lewis and Narins 1999; Smotherman and Narins 2003). However, from the literature reviewed in chapter 2 it becomes apparent that the second auditory end-organ, the amphibian papilla (AP), shows a greater anatomical and functional correspondence to the mammalian cochlea, especially its higher-frequency part caudal to the tectorial curtain.

This dissertation focuses on the anatomy and functioning of the BP. In contrast with other vertebrate hearing organs, the majority of neurons connecting to the BP have nearly identical tuning characteristics (Ronken 1990). This, in combination with its relatively simple anatomy, makes the anuran BP a truly unique vertebrate hearing organ.

Anatomy of the BP

The anuran BP is anatomically exceptional among terrestrial vertebrates (chapters 2 and 3). Its sensory epithelium resides in a lumen that opens into the saccular space on the lateral side. The lumen tapers towards a thin contact membrane on the medial end. The contact membrane separates the endolymph within the lumen from the perilymph on the medial side of it. The tectorial membrane (TM) is half-moon shaped with part of its circular edge connecting to the stereovilli of the sensory hair cells. The approximately straight edge of the TM spans the width of the BP lumen, and is firmly connected to the lumen boundary on both sides.

Our study of the BP anatomy in the northern leopard frog (*Rana pipiens pipiens*, chapter 3) confirmed earlier results in related species (e.g. Frishkopf and Flock 1974). The added value of this work lies mainly in the detailed description of the BP's lumen, and the epithelium's position in it. The lumen's taper may function to focus acoustic energy onto the epithelium and the TM at its narrow end. The knowledge gained about the size and shape of the BP's lumen proved to be of value for the interpretation of the mechanical measurements chapters 4 and 5, and may, in future, be used as a basis for modeling the response of the BP based on the hydrodynamics of the endolymph.

Preparations

The measurements of the mechanical response of the BP's TM (chapters 4 and 5) were performed on excised inner-ear preparations, which were kept in amphibian Ringer solution. The preparations were structurally stable, as far as could be determined from the light-microscopy images. However any active hair-cell involvement had presumably ceased before the start of the measurements (see discussion chapter 4). The presented data were, therefore, obtained from structurally sound and presumably functionally passive preparations of the BP.

The relatively simple anatomy of the frog inner ear was beneficial to the mechanical response measurements (chapters 4 and 5). The BP was optically accessible with limited damage to the perilymphatic space, and without opening the endolymphatic space. This, in combination with the used measurement technique, provided the opportunity to study the response of the BP's TM in situ. Presumably the in-situ response of the TM is influenced by the effects of other inner-ear structures on the stimulus signal (Purgue and Narins 2000b), and by its connection to the lumen boundary and the epithelium.

Motion of the TM

The results in chapters 4 and 5 showed that the motion of the TM in response to displacement of the oval window can be likened to a two-dimensional pendulum. The highest displacement amplitudes were recorded near the epithelium, while the TM edge opposite the hair cells was hardly displaced at all. The phase was approximately constant throughout the displaced area of the membrane.

In both mechanical-response studies, the phase differences between the orthogonal spatial components of the TM motion were either approximately 0° or 180° . This indicates, that the displacement of the TM in response to auditory stimuli was approximately rectilinear. In our optical measurements, we did not have the possibility to control the orientation of the viewing direction relative to the BP's epithelium. However, the anatomical data (chapter 3) and the relative amplitudes of the orthogonal motion components (chapters 4 and 5) strongly suggested that the TM displacement was along the sensory epithelium and parallel to the hair-cell polarization (chapter 5).

Filtering and non-linearity

From the experiments described in chapters 4 and 5, characteristics of the BP's TM response became evident. The mechanical response was tuned, on average, to a frequency of 2.2 kHz. The tuned response had a filter quality factor, Q_{10dB} of about 2 (chapter 4). Also, the mechanical response depended linearly on the stimulus amplitude up to a input level estimated to be approximately 100 dB SPL (chapter 5).

Above stimulus levels estimated to correspond to about 100 dB SPL (chapter 5), the mechanical response of the TM saturated. Neural responses in the afferents connecting to the BP saturate at levels about 20 dB below that (Ronken 1990). Apparently, the saturation of the neural response must be based on the physiology of the hair cells and/or the auditory nerve fibers.

The tuning characteristics correspond to those recorded from auditory nerve-fibers connecting to the BP (Ronken 1990; Ronken 1991). This correspondence is remarkable since we performed our measurements on dead and presumably passive preparations. Apparently, the recorded tuning characteristics do not critically depend on the metabolic state of the animal.

Several other studies suggest a similar independence of the BP's function from the animal's metabolic state. The tuning characteristics of the BP's afferent nerve fibers are independent of the animal's body temperature, while those of the AP's nerve fibers are not (Stiebler and Narins 1990; Van Dijk et al. 1990). The temperature dependence of distortion-product otoacoustic emission (DPOAEs) exhibits a similar behavior: they are temperature dependent in the AP's frequency range, while they are not in the BP's range (Meenderink and Van Dijk 2006). A more dramatic physiological insult, the discontinuation of the oxygen supply, rapidly reduces the amplitudes of the DPOAEs in the AP's frequency range, while those in the BP's range disappear over an average time span of about half an hour (Van Dijk et al. 2003). Thus both our data, and earlier studies suggest that the BP's functioning is relatively insensitive to the animal's overall metabolism.

We found the post-mortem tuning TM tuning characteristics to be similar to the in-vivo neural tuning. These findings are consistent with Meenderink and Van Dijk (2006), who suggest that the BP may not use active feedback amplification for enhancing the frequency selectivity, and thus may depend on passive frequency filtering.

By contrast, the tuned response of the basilar membrane (BM) in the mammalian cochlea strongly depends on the animal's metabolism. The post-mortem BM response has a significantly lower amplitude and a lower tuning sharpness, compared to the in-vivo response (Robles and Ruggero 2001; Ren and Nuttall 2001), due to the abolishment of outer hair cell activity (Ruggero and Rich 1991). This dependence on the animal's metabolism combined with the presence of spontaneous otoacoustic emissions (Probst et al. 1991; Hudspeth 2008) are a clear indication of an active feedback-amplification mechanism to exist in the mammalian cochlea.

It must be assumed that active filtering, and the resulting increase in frequency-selectivity, had an evolutionary advantage for mammals. Meenderink and Van Dijk (2006) note that an ectothermic animal, such as the frog, could gain a benefit from possessing a passive hearing organ of which the tuning is not temperature dependent. Such an organ could provide a temperature-independent reference for the frequency content of ambient sound. This benefit may have served as the evolutionary pressure behind the development of the BP.

Concluding remarks and outlook

When starting the work presented in chapters 2 through 5, our aim was to understand the auditory mechanics of the frog BP. The number of reported direct measurements on structures in the frog inner ear associated with the dedicated auditory end organs, the AP and the BP, was limited to one (i.e. Purgue and Narins 2000a). Most of our understanding of the frog's auditory mechanics was based on anatomical studies and the resulting models, or on the measurements of the neural responses and otoacoustic emissions (reviewed in Lewis and Narins 1999; Simmons et al. 2007; Schoffelen et al. 2008, chapter 2). Our measurements of the TM response have taken the knowledge of the mechanics of the frog BP considerably closer to the detection point of acoustic signal, the sensory hair cells.

The results presented in this dissertation are consistent with the idea that the frog's basilar papilla is a passive auditory filter. This in itself makes it unique among the known vertebrate hearing organs. On one hand, chapters 4 and 5 explain a large portion of the auditory mechanics in this 'simple' organ. On the other hand, the BP's anatomy (chapter 3) raises a lot of questions yet unanswered. Most conspicuous in this respect, is the function of the extremely elaborate connections between the TM and the lumen boundary. Also, the variety of hair-cell types in the BP epithelium remains intriguing, just like the percentage of apparently free-standing hair-bundles in this relatively low-frequency detector.

Although, the experimental work described here concentrated exclusively on the mechanics of the BP, the techniques that were implemented are expected to be applicable for studying the AP as well. As described in chapter 2, the presence of tonotopy, the hair-cell orientation in the AP, and the elaborate tectorial structure indicate that there may be a range of different mechanical responses to various auditory frequencies.

The study of the AP mechanics promises to provide a considerable challenge, due to the greater complexity and dimensions of the organ. From a surgical standpoint, gaining visual access to the AP without critically damaging the epithelium and the associated structures will most likely be more complicated than it was for the BP. However, if such a surgical technique were developed, the TM's modes of motion would probably have dominant components within the microscope's plane of focus (chapter 2), which would enhance the effectiveness and accuracy of the motion detection techniques.

The hair-cell polarization in the AP suggests that the modes of motion of the TM may be

complex. Various portions of the membrane may move in different directions under acoustic stimulation. For such structures, the measurement and analysis techniques used in this dissertation (chapters 4 and 5; see also Davis and Freeman 1998) have the advantage that they do not require a-priori knowledge or assumptions about the modes of motion.

In conclusion, the work described in this dissertation represents a considerable stride towards understanding the mechanics of the frog basilar papilla. For the understanding of the mechanics of the anuran auditory end organs, the amphibian papilla still provides an intriguing and challenging opportunity to make the next stride.

