Mechanical Properties of the Cochlea

Reading: Yost Ch. 7
The Cochlea

- Inner ear contains auditory and vestibular sensory organs.
- Cochlea is a coiled tri-partite tube about 35 mm long.
- Basilar membrane, supporting the Organ of Corti, runs along entire length of cochlea. Its mechanical properties change as a function of distance from the stapes: designed to analyze frequency components in complex sounds.
- Hair cells receptors in Organ of Corti of two types: inner (single row) and outer (3/4 rows)
- Stereocilia are rigid rods interconnected on their flanks, and at their tips.
- Tip links critical to transduction.
Traveling Wave

- **Stapes** vibration generates **pressure waves** in fluids of cochlea.
- Pressure waves generate **vibrations of the basilar membrane** that propagate from base to apex along the basilar membrane as a **traveling wave** (von Békésy 1961)
- BM vibrates **at the same frequency as the simple sound stimulus** wherever the basilar membrane is set in motion by the TW.
- **Amplitude** of the TW differs at different locations, depending on frequency and amplitude (acoustic energy) of the stimulus.
Traveling Wave Motion

The vibratory motion of the basilar membrane is a traveling wave. A traveling wave moves longitudinally from one place (stapes) to another place (helicotrema) (like that in a rope with the far end free).

- Top (a): snapshot of basilar membrane model showing *instantaneous vibration pattern* and shape of traveling wave (as seen from the side).
- Bottom (b): More accurate view of pattern, with membrane attached at sides.

Note that different regions of membrane are out of phase, with a greater phase difference ahead of the peak of the wavefront (apical) than behind it (basal).
For a given traveling wave, basilar membrane displacement changes as a function of distance from apex to base.

If a line is drawn through the points of maximum displacement for a specific traveling wave, then the resulting curve is called the envelope of the traveling wave.

- Numbered curves: freeze-frames of TW for a sustained pure tone stimulus taken at different instants in time.
- Different locations along the membrane displaced in opposite directions (called a local phase difference).

For pure tone stimulus, the TW envelope shows a single maximum of displacement.
Traveling wave peak shifts from base to apex as stimulus frequency is varied from high to low (von Bekesy 1947).

TW for low frequencies stretches over a long distance, can vibrate nearly entire basilar membrane if sound sufficiently intense.

TW for high frequencies more confined, only stimulates the base.
Why do Sounds Generate a TW?

Each point along the basilar membrane that is set in motion vibrates at the same frequency as the stimulus. However, different frequencies will cause maximum vibration amplitude at different points and times along the membrane.

A number of factors vary along the length of the cochlea. In particular, moving from base to apex:

• BM width increases (higher mass)
• BM becomes thinner (less stiffness)
• Stereocilia get longer (higher mass, less stiffness).

→ These changes reduce the resonant frequency of the basilar membrane with distance from the stapes ($F_r \propto \sqrt{s/m}$), and thus increase time to peak response.
Complex sounds create complex traveling wave patterns, with multiple vibration maxima.

**Pattern of excitation** provides information about

- **Frequency**
- **Amplitude**
- **Temporal variation**

Note that due to the traveling wave, low frequency components of a sound are transduced after high frequency components ... ➔ The TW introduces temporal distortions (absolute time and relative phase delays)!

Envelope of basilar membrane displacement to 50 Hz or 100 Hz alone, and combined as $F_0$ and $F_1$ of a harmonic series.
Mechanical Tuning in Organ of Corti

- Mechanical tuning of any point along BM resembles **bandpass filter**, with a steep high-frequency roll-off, and a shallow low-frequency roll-off.

- **Characteristic frequency (CF):** Frequency at which the sound level reaches a minimum to obtain a criterion displacement for that position on the BM.

- Thus, the organ of Corti **topographically decomposes the spectrum of the sound** with frequency-selective bandpass filters (channels).

*Iso-sensitivity curve* of basilar membrane plotted as equal-displacement function re 19 Ångstroms (1.9 x 10^{-8} cm) CF = 8350 Hz.
The higher the stimulus level, the greater the amplitude of basilar membrane displacement.

**Displacement of BM is not linear** as a function of stimulus level near the peak of the TW.

Consequence: Near CF, range of BM motion is less than the range of sound levels, i.e. the **dynamic range shows “compressive non-linearity”**.

Compressive nonlinearity generates *distortion products* (e.g., harmonics, difference tones).

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**Basilar Membrane Nonlinearity**

Input-output ("transfer") function: BM velocity vs sound level. (CF =9000 Hz)
Traveling wave causes up-and-down motion of *basilar membrane and tectorial membrane* (at same frequency as stimulus).

Displacement sets up *transverse shearing force* that deflects hair cell stereocilia.
Tips of OHC stereocilia are \textit{embedded} in tectorial membrane.

BM pivots around inner pillar cell attachment to spiral lamina when stimulated.

Stereocilia deflected by \textit{mechanical shearing}: tectorial membrane pushes and pulls as hair cells move back and forth.

\textbf{Figure 6.7.} Mechanism thought to deflect the cilia of the outer hair cells. As the outer hair cell (OHC) is moved away from (toward) the spiral limbus by the vibrating basilar membrane, the tectorial membrane pulls (pushes) on the retreating (advancing) cilia.

\textit{Geisler 1998}
Model of putative fluid shearing mechanism of stereocilia bundle deflection and excitation in IHCs.
Excitation of inner ear gives rise to traveling wave along the basilar membrane, due to longitudinal changes in the basilar membrane (principally, compliance – stiffness)

Changes in sound frequency shift the location of the traveling wave peak along the basilar membrane, creating a **place code for frequency (tonotopy)**.

Hair cells are stimulated by basilar membrane traveling wave(s): they are mechanically tuned to a single CF according to their location on the BM; and the amplitude of their vibration is related to stimulus level.

**Summary**