Hearing

The active process

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Physics 141
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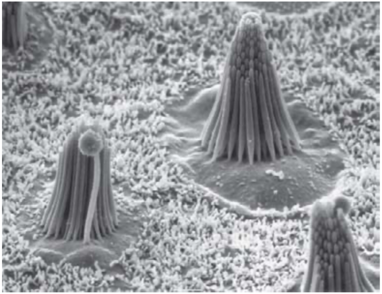
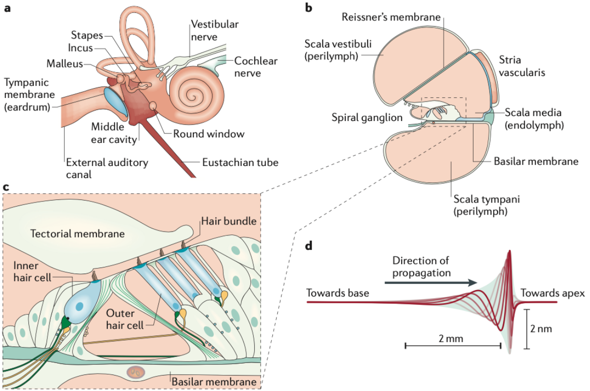
Week 11

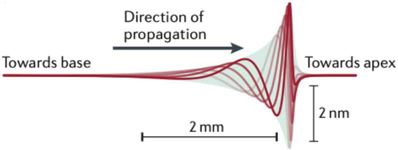


- We can hear vibrations of the eardrum that are as small as 1 picometer
- We hear from 20 Hz to 20kHz, and can distinguish sounds 1/30th of the interval between notes on the piano
- We hear amplitudes ranging a trillion-fold in intensity
- Normal hearing actively amplifies sound intensities by hundredfold
- Active process enhances frequency sensitivity
- The normal cochlea can produce otoacoustic emissions because of the positive feedback that produces spontaneous oscillations

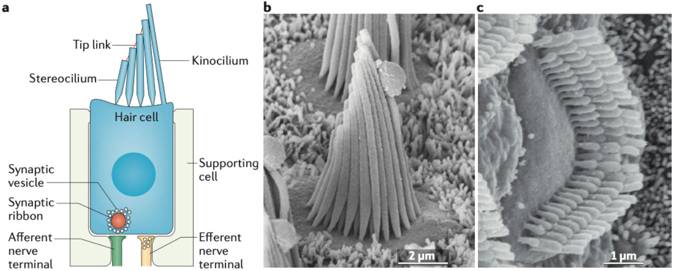
The cochlea and organ of Corti



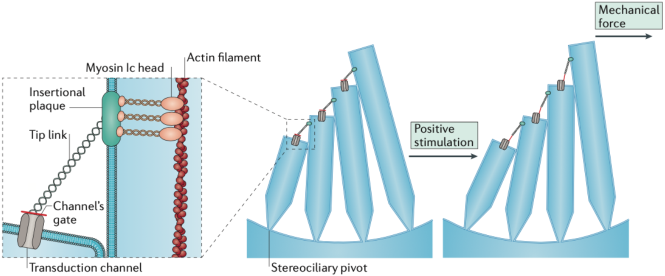
- The receptor for sound in the human ear is the organ of Corti, a strip of sensory epithelium running some 33 mm along the spiral cochlea
- 3,500 inner hair cells are arranged in a single row, forming synapses with afferent nerve terminals.
- 12,000 outer hair cells mediate the active process Their principal role is mechanical



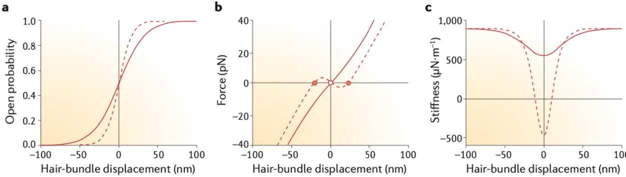
- When a mammalian cochlea receives a pure-tone acoustic stimulus, pressure differences between its liquid-filled compartments set the basilar membrane into oscillation at the frequency of stimulation.
- As each wave progresses, it grows in amplitude, decreases in wavelength, and then abruptly vanishes
- Most of the energy associated with sound of any particular frequency is deposited at a specific position along the basilar membrane, beyond which propagation ceases and the travelling wave collapses
- High frequencies (up to 20 kHz) are represented at the cochlear base
- Low frequencies, down to 20 Hz, excite the apex.
- In the mammalian cochlea, the active process of outer hair cells amplifies the vibration of each increment of the basilar membrane, contributing energy that sustains a travelling wave
- Active hair-bundle motility, constitutes the entire active process of amphibians and some reptiles



- Transduction commences when a stimulus deflects the hair cell's elegant mechanoreceptive organelle, the hair bundle.
- The hair bundle transduces a stimulus force into an electrical response, the receptor potential, which is a change in the voltage across the cell's membrane
- The receptor potential in turn modulates the release of the neurotransmitter from synapses at the hair cell's base and thus transmits the response to the brain

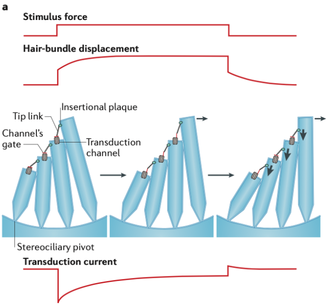


- Movement of a hair bundle's top within its plane of bilateral symmetry, as occurs when a bundle is stimulated by sound, causes the largest electrical response
- Displacement towards the bundle's tall edge, which is defined as a positive stimulus, opens transduction channels and causes depolarization.
- Deflection in the opposite direction closes channels and evokes hyperpolarization.
- Channels appear to be asymmetrically located at the links' lower insertions

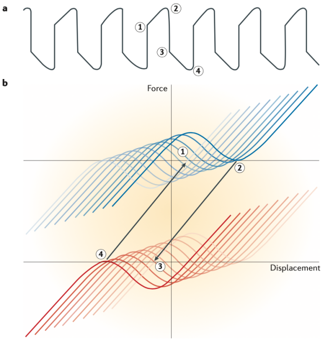


- If a hair cell's transduction channels are gated directly by the force applied to the hair bundle, the opening and closing of the channels should reciprocally influence the bundle's mechanical properties.
- The demonstration of this decrease in hair-bundle stiffness, termed the gating compliance, provides evidence in support of the gating-spring theory
- The gating compliance can become so great that it outweighs the stiffness of a hair bundle's other components, whereupon the bundle's total stiffness becomes negative
- a hair bundle displaying negative stiffness does not oppose an applied stimulus force but instead augments the stimulus by contributing additional force in the same direction
- a hair bundle cannot reside stably near the region of negative stiffness because a thermal deflection in either direction drives the bundle into a region of positive stiffness

Adaptation



- Because auditory transduction does not proceed through a biochemical signalling cascade such as those characteristic of vision, smell and taste, a novel mechanism is required to effect adaptation to sustained stimulation
- If a hair bundle is experimentally displaced from its resting position, the locus of mechanical sensitivity migrates towards its new position with a time constant of a few tens of milliseconds
- When responding to a positive force, a bundle initially moves a distance that is inversely proportional to its stiffness, but then the bundle sags farther in the same direction.



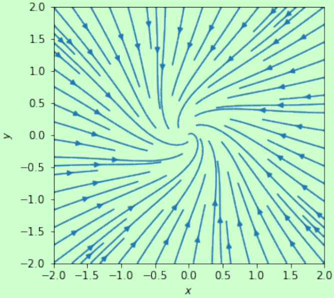
- the hair bundles of many species exhibit spontaneous movements that reflect their capacity to participate in the active process
- Spontaneous hair-bundle oscillations emerge from the combination of negative hair-bundle stiffness and adaptation.
- Suppose that such a bundle starts with a small open probability for its transduction channels
- Acting through the ascent of tip link motors, adaptation begins to increase the open probability towards the steady-state set point
- This progressively shifts the displace- ment–force relation to the left and downwards.
- the region of positive slope vanishes abruptly and the hair bundle must leap to a new fixed point on the curve's opposite limb
- the open probability is high, so the tip link insertions begin to descend
- When mechanical stability again vanishes, the hair bundle jerks back in the negative direction.

Normal form of a dynamical system with a Hopf bifurcation:

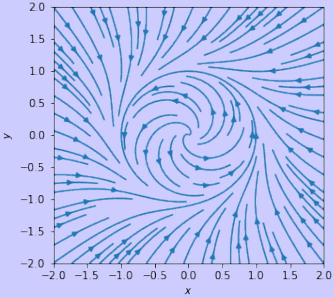
$$\dot{z} = (\mu - i\omega_0)z - \left|z^2\right| z$$

Limit-cycle oscillations when $\mu > 0$, stable fixed point at $x = 0, y = 0$ when $\mu < 0$

$\mu = -1$



$\mu = +1$



Normal form of a dynamical system with a Hopf bifurcation:

$$\dot{z} = (\mu - i\omega_0)z - \left|z^2\right| z$$

- When μ becomes positive, the solution $z \equiv 0$ becomes unstable, and a stable oscillatory solution appears

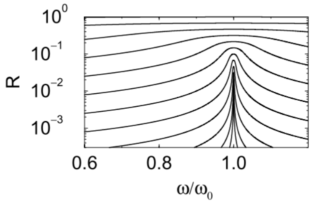
$$z = \sqrt{\mu}\exp\left(i\omega_0 t\right)$$

- If the system is subjected to periodic forcing, the force balance equation becomes

$$\dot{z} = (\mu - i\omega_0)z - \left|z^2\right| z + Fe^{i\omega t}$$

- Assuming a 1:1 locked form $z = Re^{i\omega t + i\phi}$:

$$F^2 = R^6 - 2\mu R^4 + \left[\mu^2 + (\omega - \omega_0)^2\right] R^2$$



Hopf resonance ($\mu = 0$)

At the center of resonance, where $\omega = \omega_0$, $R \approx F^{1/3}$.
No matter how small F might be, the response is nonlinear.