The sense of hearing

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In terms of performance, hearing is the most remarkable of our senses

Frequency analysis: responds selectively to frequencies in range 20–20,000 Hz

Sensitivity: faintest audible sounds impart no more energy than thermal noise: 4 zJ per cycle

Dynamic range: responds and adapts over 12 orders of magnitude of energy: 0–120 dB

Dynamic range

20µPa
20Pa

0dB  30dB  60dB  90dB  120dB

whisper  conversation  motorcycle  pneumatic drill  rifle

Displacement of air molecule at threshold of hearing ~ 0.1nm

The ear

auditory nerve

external  middle  inner
Middle ear

- Impedance matches the air-filled ear canal with the fluid-filled cochlea
- Provides an acoustic gain owing to different areas of eardrum and stapes footplate

Cochlea

- Organ of Corti

- Basilar membrane

- Tectorial Membrane

- To section of cochlea

- Basilar Membrane
Detection apparatus consists of a set of strings of differing length which vibrate in resonance with the incoming sound.

The following table gives the maximum values of $Q$ which a string of density 1 and diameter $0.1$ mm. could have when immersed in water:

<table>
<thead>
<tr>
<th>Frequency (c./sec.)</th>
<th>$Q$</th>
</tr>
</thead>
<tbody>
<tr>
<td>300</td>
<td>1.9</td>
</tr>
<tr>
<td>1,000</td>
<td>1.3</td>
</tr>
<tr>
<td>5,000</td>
<td>0.8</td>
</tr>
<tr>
<td>20,000</td>
<td>0.3</td>
</tr>
</tbody>
</table>

Argued that damping by the fluid in the cochlea would not permit resonant oscillation and proposed that the ear is powered.

Careful experiments on cadavers showed that a wave travels along the basilar membrane, and reaches a peak amplitude at a position that depends on frequency.

Notion of place code.
Gold's regeneration hypothesis

Regeneration hypothesis: An energy supply provides a feedback proportional to velocity, and in phase with it

\[ m \frac{\partial^2 x}{\partial t^2} + \gamma \frac{\partial x}{\partial t} + k x = F + F_{\text{active}} \]

\[ \lambda \frac{\partial x}{\partial t} \]

Critical point \( \lambda_c = \gamma \)

→ near critical point, sharply tuned response at frequency \( \omega_x = \sqrt{\frac{k}{m}} \)

The magnitude of the feedback we require is so large as to come precariously close to cancelling the resistive losses. Some sort of self-regulating device would have to exist

Otoacoustic emissions

The ear in not just a sound receiver; it also spontaneously emits sounds at a very low level

Detection apparatus

Hair bundle is composed of ~50 'stereocilia', which lean against each other. Each stereocilium is a bundle of actin filaments, surrounded by the cell membrane, which tapers at the base. Adjacent stereocilia are connected by a fine filament — the 'tip link'

Hair cells in the bullfrog sacculus

source: Hudspeth
Detection apparatus

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Mechano-chemo-electrical transduction

When bundle is pushed in direction of tallest stereocilium, increased tension in tip links pulls open transduction channels & admits K+

which depolarizes the membrane & opens voltage-gated channels at the base of the cell to nerve synapse

Rapidity of transduction process preserves information about timing of the signal

Transduction current

Active detection by hair bundles
Active bundle movement
Crawford & Fettiplace '86; Howard & Hudspeth '87; Benser, Marquis & Hudspeth '96

Spontaneous hair-bundle oscillations
In the correct physiological conditions, hair bundles actively oscillate

Self-tuned critical oscillators
Camale, Duke, Jülicher & Prost '00

Building a critical oscillator: inertial system
Gold '48

\[ m\ddot{x} = -\lambda \dot{x} - kx + f_a \]
\[ f_a = (C - Bx^2)\dot{x} \]

Vibration sensor is a nonlinear mechanical system which can generate self-sustained oscillations at a characteristic frequency

A feedback control mechanism maintains it on the verge of oscillating

internal active force

remarkable response properties at critical point

critical point: \[ C_c = \lambda \]

characteristic frequency: \[ \omega_c = (k/m)^{1/2} \]
**Building a critical oscillator: non-inertial system**

An internal active process can cause a heavily damped mechanical system to oscillate.

\[ \lambda \ddot{x} = -k(x)x + f_a \]

active force with its own dynamics, coupled to displacement

\[ \tau \dot{f}_a = -f_a - \dot{k}x \]

Suppose effective elasticity can be made negative by changing control parameter \( C \)

\[ \lambda \ddot{x} = -(k - C + B x^2)x + f_a \]

Critical point at

\[ C_c = k + \lambda / \tau \]

**Characteristic frequency**

\[ \omega_c^2 = k / \lambda - 1 / \tau^2 \]

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**Hopf resonance**

**force:** \( F(t) = F_1 e^{i \omega t} \)

\[ F_1 \simeq A x_1 + B |x_1|^2 x_1 + \ldots \]

**displacement:** \( x(t) = x_1 e^{i \omega t} \)

**control parameter:** \( C \)  

**bifurcation point:** \( A(\omega_c, C_c) = 0 \)

- stimulus at characteristic frequency:

\[ |x_1| \simeq \frac{|F_1|^{1/3}}{|B|^{1/3}} \]

**gain diverges for weak stimuli**

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**Critical Hopf resonance: single tone response**

Gain and active bandwidth depend on level of stimulus

- if \( |\omega - \omega_c| \gg \Delta \omega_a \equiv \frac{|B|^{1/3}}{|A|} |F_1|^{2/3} \)

\[ |x_1| \simeq \frac{|F_1|}{(|\omega - \omega_c| A)} \]

**active bandwidth**
Canonical equation

\[
\frac{dz}{dt} = (\epsilon + i\omega_c)z - |z|^2 z + f e^{i\omega t}
\]

\[
z = r e^{i\omega t}, \quad r = r_1 + i r_2
\]

Response at \( \omega = \omega_c \)

for different \( f \)

\[
\begin{array}{c|c|c|c|c|c}
 r & 10^0 & 10^{-1} & 10^{-2} & 10^{-3} \\
 \hline
 \omega / \omega_c & 0.6 & 0.8 & 1.0 \\
\end{array}
\]

Self-adjustment to critical point

Slow dynamics of control parameter, coupled to displacement, provides negative feedback which automatically adjusts system to the critical point

\[
\frac{dC}{dt} = (1 - x \frac{\partial^2}{\partial C^2})(C_{\text{max}} - C) / \tau_a
\]

Eg. Ca\(^{2+}\) concentration is control parameter

Critical Hopf resonance: response in presence of noise

Camalet, Duke, Jülicher & Prost '00

Self-tuned critical oscillations

stimulus

Eg. Ca\(^{2+}\) concentration is control parameter
Spontaneous fluctuations

Martin, Hudspeth & Julicher '01

Auto-correlation function

\[ C(t) = \langle X(t + t_0)X(t_0) \rangle \]

\[ \tilde{C}(\omega) = \int_{-\infty}^{\infty} C(t) e^{i\omega t} dt \]

10 nm 200 nm

20 µm

Response of a frog hair bundle forced by a microneedle

At thermal equilibrium, the linear response is related to the fluctuations

\[ \chi(t) = -\frac{1}{k_B T} \frac{dC(t)}{dt} \]

\[ \tilde{C}(\omega) = 2k_B T \tilde{\chi}(\omega) \]

Test of fluctuation-dissipation relation

Martin, Hudspeth & Julicher '01

Response function \( \chi \) defined by:

\[ \langle X(t) \rangle = \int_{-\infty}^{t} \chi(t - t')f(t')dt' \]

\[ \langle \tilde{X}(\omega) \rangle = \tilde{\chi}(\omega)\tilde{f}(\omega) \]
Hair bundle response

Two adaptation mechanisms

Fast process

$\text{Ca}^{2+}$ binding to transduction channel

$\sim 1 \text{ ms}$

Slow process

movement of myosin-1C motors

$\sim 100 \text{ ms}$

Negative elasticity

Instantaneous force response to an applied displacement

Channel gating compliance

Suppose channel incorporates a lever arm

- opening of channel can substantially reduce the tension in the tip link

- negative elasticity if

$$K_{\text{TL}}d_O^2 > 4k_B T$$

$$d_O > 6 \text{ nm}$$
Channel gating compliance

Influence of motors

Ca\(^{2+}\) binds to motors; causes them to produce less force

Ca\(^{2+}\) released from motors; causes them to produce more force

Physical basis of oscillations

Self-tuning mechanism?

Maybe Ca\(^{2+}\) affects rigidity of tip-links, or size of channel movement
Alternative physical basis of self-tuned oscillations

- Oscillations generated by interaction of Ca\(^{2+}\) with transduction channels

\[ f_c = \sqrt{\frac{1}{R_{\text{mch}} \tau_{\text{m}}}} \]

- Self-tuning accomplished by movement of molecular motors, regulated by Ca\(^{2+}\)

An active role for the kinocilium?

- Kinocilium is motile (Rüsch & Thurm '90)
- Axoneme can vibrate at \(~1000\) Hz (Kamimura & Kamiya '89)
- But spontaneous oscillations of frog hair bundles still occur when the bundle is knocked down (Martin)

Hearing in fruit flies

The antenna of mosquitoes sense both odorants and sounds
Spontaneous oscillations and nonlinear response of antennae

Göpfert '03

Spontaneous otoacoustic emissions in reptiles

Köppl & Manley '93

Reptilian inner ear

Köppl & Manley '93

Coupled critical oscillators

Vilfan & Duke

\( \frac{\partial z_i}{\partial t} = (\varepsilon_i + i\omega_i)z_i - B|z_i|^2z_i + g_i(z_{i+1} - 2z_i + z_{i-1}) \)

real for dissipative coupling
Spontaneous oscillations of a coupled chain

\[ N_{\text{sync}} \sim \sqrt{\frac{g}{\Delta \omega}} \]

Ermentrout & Koppel ’84

Cochlear mechanics

Incoming sound excites a slow travelling wave on the basilar membrane

- location of peak depends on frequency

Place code
Cochlear travelling wave

- sound sets fluid into motion
- variation in flow rate is accommodated by movement of membrane
- membrane acceleration is caused by difference in fluid pressure

Travelling wave: one-dimensional model

- fluid flow
  \[ \rho \frac{\partial j}{\partial t} = -b \ell \frac{\partial p}{\partial x} \]
- incompressibility
  \[ 2b \frac{\partial h}{\partial t} - \frac{\partial j}{\partial x} = 0 \]
- membrane response
  \[ p(x,t) = K(x)h(x,t) \]
  wave velocity
  \[ c(x) = \sqrt{\frac{K(x)}{2\rho}} \]

Travelling wave: damped dispersive waves

Stiffness \( K \) decreases by two orders of magnitude from base to apex

\[ c(x) = \sqrt{\frac{K(x)}{\rho}} \]

- as wave propagates, it slows down & its amplitude increases

Wave peaks when damping becomes significant

\[ \hat{p}(x,\omega) = (K(x) + i\gamma\omega)\hat{h}(x,\omega) \]

Location of peak depends on frequency

\[ \omega_c = \frac{K(x)}{\gamma} \]

Tuning curve

Sound level required to see an observable response at a given place

<table>
<thead>
<tr>
<th>Frequency (kHz)</th>
<th>Level (dB)</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.6</td>
<td>40</td>
</tr>
<tr>
<td>1.3</td>
<td>0.1</td>
</tr>
<tr>
<td>370</td>
<td></td>
</tr>
</tbody>
</table>
In order to obtain a very localized peak, require:

- only waves with frequency lower than \( \omega_c(x) \) carry energy past point \( x \)
- as wave approaches characteristic place, velocity of energy transport falls to zero
- velocity drops so fast that there is time to dissipate all energy before wave reaches characteristic place

\[ \text{energy piles up at characteristic place} \]

Critical oscillators are ranged along basilar membrane, and are positioned so that they can drive its motion

- characteristic frequency diminishes from base to apex, spanning the audible range

\[ \omega_c(x) = \omega_0 e^{-x/d} \]

\[ \hat{p} \propto A(x, \omega)\hat{h} + B|\hat{h}|^2\hat{h} \]

- active oscillators negate friction and damping at the characteristic place where the oscillator frequency matches the sound frequency
Active travelling wave: waveforms

4.6 kHz 40 dB
1.3 kHz 1 nm
370 Hz 5 nm

Basilar membrane motion
Rhode '71; Ruggero et al. '97; Russell & Nilsen '97

BM response is nonlinear

Energy flow in the cochlea
Lighthill '81

Cochlea is an unusual type of waveguide:

- only waves with frequency lower than \( \omega_c(x) \) carry energy past point \( x \)
- as wave approaches characteristic place, velocity of energy transport falls to zero
- velocity drops so fast that there is time to dissipate all energy before wave reaches characteristic place

→ energy piles up at characteristic place
Nonlinearities due to active amplification

A critical oscillator is ideal for detecting a single tone …
… but it causes tones of different frequency to interfere.

Response to multiple tones:

\[ F_{\omega_k} = A(\omega_k)X_{\omega_k} + \sum_{\rho_k,\gamma_k} B(\omega_k, \omega_{\rho_k}, \omega_{\gamma_k})X_{\omega_{\rho_k}}X_{\omega_{\gamma_k}} \]

Psychoacoustic effects & their physical origin

Two-tone suppression

Two-tone suppression

presence of a second tone diminishes the neural response to the first tone

suppression is greater if frequencies are close

Psychoacoustics & auditory illusions

Range of phenomena associated with multiple tones: \( f_1, f_2, \ldots \)

Combination tones:

Tartini 1714

frequencies not present in the stimulus can be heard, most prominently \( 2f_1 - f_2 \)

Residue pitch:

Schouten 1938

frequencies close to, but not necessarily equal to \( \Delta f = f_2 - f_1 \) can be heard

Consonance:

Pythagoras

two musical notes whose frequencies are in a simple integer ratio sound pleasant

basis of diatonic scale
Two-tone suppression

Presence of second tone can extinguish the nonlinear amplification

\[ F_{\omega_1} = A(\omega_1)X_{\omega_1} + B(\omega_1)|X_{\omega_1}|^2X_{\omega_1} + B(\omega_1, \omega_2)|X_{\omega_2}|^2X_{\omega_1} \]

\[ \uparrow = 0 \]

\[ \uparrow \neq 0 \]

Distortion products

Nonlinearities create a characteristic spectrum of distortion products

\[ 0 = A(2\omega_2 - \omega_1)X_{2\omega_2 - \omega_1} + B(2\omega_2 - \omega_1)|X_{2\omega_2 - \omega_1}|^2X_{\omega_2} \]

\[ \Delta f = 50 \text{ Hz} \]

Active travelling wave: two-tone response

Andor
Neural representation of pitch and level

Two competing theories:

**Place code**  pitch represented by the place in the cochlea where nerves fire most frequently

level represented by firing rate at that place

**Time code**  pitch represented by time interval between spikes

level represented by number of nerves firing at an elevated rate

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Inference of pitch and level

**Model**
- A spike is elicited whenever the hair bundle deflection traverses a threshold
- There are hair cells with a wide range of thresholds for each characteristic frequency

**Algorithm**
- Construct histogram of inter-spike intervals $T$, summing over all hair cells in the cochlea
- Perceived tones correspond to peaks in histogram and are assigned pitch $1/T$
- Perceived level corresponds to height of peak

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Auditory nerve: spontaneous activity

Temporal coding permits detection of stimuli 20 dB below rate-threshold

First passage time to traversal of threshold
First passage time to traversal of threshold

Temporal coding permits detection of stimuli 20 dB below rate-threshold

Distortion products: spectra & waveforms

Spontaneous high level stimulus

Spike timings: two tones

$\text{Two-tone stochastic resonance}$

Two-tone stochastic resonance

$\text{Chialvo et al. '02}$

$\text{Chialvo et al. '02}$

$0.009s \sim 110 \text{ Hz}$

$0.045s \sim 22 \text{ Hz}$
Nature of dissonance

Helmholtz ascribed dissonance to close mis-matches in frequency between harmonics

\[
\begin{align*}
5:4 & & & & \text{log}(\text{frequency}) \\
4:3 & & & & \\
\sqrt{2}:1 & & & & \\
\end{align*}
\]

Dissonance: psychophysical experiments

Integer ratios of frequencies are preferred when notes are played on musical instruments.

For pure tones, there is no such preference, but only a dislike of close frequencies.

Dissonance: a physical interpretation

Close frequency mis-matches generate complicated hair bundle responses.

The difficulty of inferring frequency components from partial information about a complex waveform results in an indeterminacy of pitch.

'What distinguishes dissonances from consonances is not a greater or lesser degree of beauty, but a greater or lesser degree of comprehensibility.'

Arnold Schoenberg