Auditory Periphery

- Sound causes air pressure to increase at eardrum.
- Eardrum is pushed inward, moving the middle ear bones.
- Stapes movement initiates a pressure wave in cochlear fluid.
- Fluid-borne mechanical signals are transduced into a neural code.
- VIIIth nerve conveys neural signal to cochlear nucleus.
Central pathways
Non-Periodic Sounds

- single pulse, white noise, brief tone, non-harmonic complex tones

Periodic Sounds

- pure tone, square wave, pulse train, harmonic complex tones
Periodic Sounds

Harmonic Complex Sounds
Each component frequency is an integral multiple of a common fundamental. 
*The complex waveform has a repetition rate equal to the fundamental frequency.*

Perception reflects analysis of sound into Fourier components. 
*We hear pitches related to each component of a complex tone — Ohm’s Acoustical Law.* 
(In contrast, color vision reflects a summed mix of wavelengths)
Spectrum

measured
instantaneously

Spectrogram

captures change in the
sound spectrum over time
Acoustics

Sound travels through air at \( \sim 331.4 + 0.6T_c \) ms\(^{-1} \)
(where \( T_c \) is Temperature in deg C)

\( \sim \) one mile every 5 seconds

Sound Pressure Level  \( = 20 \log (P/P_{\text{ref}}) \)

For hearing threshold measurement,
the Reference pressure is 20 \( \mu \text{Pa} \)
# Pressure Levels of Common Sounds

<table>
<thead>
<tr>
<th>Sound Environment</th>
<th>Sound Pressure Level (dB)</th>
<th>Approximate loudness re normal conversation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Threshold of hearing</td>
<td>0</td>
<td>inaudible</td>
</tr>
<tr>
<td>Broadcast studio interior; rustling leaves</td>
<td>10</td>
<td>1/32nd</td>
</tr>
<tr>
<td>Quiet house interior; rural nighttime</td>
<td>20</td>
<td>1/16th</td>
</tr>
<tr>
<td>Quiet office interior; watch ticking</td>
<td>30</td>
<td>1/8th</td>
</tr>
<tr>
<td>Quiet rural area; small theater</td>
<td>40</td>
<td>1/4th</td>
</tr>
<tr>
<td>Quiet suburban area; dishwasher in next room</td>
<td>50</td>
<td>1/2 as loud</td>
</tr>
<tr>
<td><strong>Office interior; normal conversation</strong></td>
<td><strong>60</strong></td>
<td>normal conversation</td>
</tr>
<tr>
<td>Vacuum cleaner at 10 ft.</td>
<td>70</td>
<td>2x louder</td>
</tr>
<tr>
<td>Passing car at 10 ft; garbage disposal at 3 ft</td>
<td>80</td>
<td>4x</td>
</tr>
<tr>
<td>Passing truck at 10 ft; food blender at 3 ft.</td>
<td>90</td>
<td>8x</td>
</tr>
<tr>
<td>Passing subway train at 10 ft; mower at 3 ft.</td>
<td>100</td>
<td>16x</td>
</tr>
<tr>
<td>Night club with band playing</td>
<td>110</td>
<td>32x</td>
</tr>
<tr>
<td>Threshold of pain</td>
<td>120</td>
<td>64x (2x louder than night club)</td>
</tr>
</tbody>
</table>
Hearing Sensitivity
Hearing Sensitivity

![Graph showing hearing sensitivity across different species.](image-url)
Outer Ear Function
Outer ear amplifies sound pressure

But this filtering differs as a function of signal spectrum and source direction

At 3kHz, final amplification reaches 20 dB
(10 times the free field level)

Møller 2000
“Head-related” acoustic filtering

Head Related Impulse Response

HRIR_021 Left @ 0 el 0 az

HRIR_021 Right @ 0 el 0 az

Azimuth (deg) vs Time (ms)

Left: 0 Elev  
Right: 0 Elev
Head-Related Filtering: Azimuth

Head-Related Transfer Functions across azimuth @ zero elevation

Theoretical HRTFs (spherical head model)

Measured HRTFs
Head-Related Filtering: Elevation

Head Related Transfer Functions across elevation @ zero azimuth

Theoretical HRTFs (spherical head model)  Measured HRTFs

Left  Right  Left  Right

Magnitude Response in relative dB

Frequency in Hz x 10^6

0 0.5 1 1.5 2 2.5
HRTFs

Measured

Theoretical

Grayscale in dB. Each contour line represents a .67 dB change in HRTF magnitude.
Because the inner ear is not organized spatially, sound localization relies on the neural processing of implicit acoustic cues. To determine a sound’s position, the brain must learn and calibrate these cues, using accurate spatial feedback from other sensorimotor systems. Experimental evidence for such a system has been demonstrated in barn owls, but not in humans. Here, we demonstrate the existence of ongoing spatial calibration in the adult human auditory system. The spectral elevation cues of human subjects were disrupted by modifying their outer ears (pinnae) with molds. Although localization of sound elevation was dramatically degraded immediately after the modification, accurate performance was steadily reacquired. Interestingly, learning the new spectral cues did not interfere with the neural representation of the original cues, as subjects could localize sounds with both normal and modified pinnae.
Ear fine structure affects HRTFs

*mid-sagittal plane (azimuth 0°)*

![Diagram showing the effect of ear fine structure on HRTFs](image)

Legend:
- **Attenuation**
- **Amplification**

Original

Modified
Fig. 3. Summary of the results for all four subjects. Adaptation curves for azimuth and elevation gain (defined as the slope of the best-fit regression line through the data of each recording day), as a function of time from the start of the adaptation experiment (in days). Standard deviations in the gains were obtained by bootstrapping the data 100 times. Results for the pre- and post-adaptation control conditions are also shown for comparison (symbols C, elevation data only for clarity; control azimuth gains fell in the range 1.0–1.2 pre- and 1.2–1.3 post-adaptation).
Relearning Sound Localization with a New Ear

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Human sound localization results primarily from the processing of binaural differences in sound level and arrival time for locations in the horizontal plane (azimuth) and of spectral shape cues generated by the head and pinnae for positions in the vertical plane (elevation). The latter mechanism incorporates two processing stages: a spectral-to-spatial mapping stage and a binaural weighting stage that determines the contribution of each ear to perceived elevation as function of sound azimuth. We demonstrated recently that binaural pinna molds virtually abolish the ability to localize sound-source elevation, but, after several weeks, subjects regained normal localization performance. It is not clear which processing stage underlies this remarkable plasticity, because the auditory system could have learned the new spectral cues separately for each ear (spectral-mapping adaptation) or for one ear only, while extending its contribution into the contralateral hemifield (binaural-weighting adaptation). To dissociate these possibilities, we applied a long-term monaural spectral perturbation in 13 subjects. Our results show that, in eight experiments, listeners learned to localize accurately with new spectral cues that differed substantially from those provided by their own ears. Interestingly, five subjects, whose spectral cues were not sufficiently perturbed, never yielded stable localization performance. Our findings indicate that the analysis of spectral cues may involve a correlation process between the sensory input and a stored spectral representation of the subject’s ears and that learning acts predominantly at a spectral-to-spatial mapping level rather than at the level of binaural weighting.

Key words: human; monaural; spectral cues; pinna; directional hearing; plasticity
Subjects adapted well to a test of long-term monaural spectral perturbations, so plasticity acts predominantly at the spectral-to-spatial mapping stage.
Middle Ear Function
Cerumen (ear wax) is good for the ear

- Repels water
- Traps dust, micro-organisms, other debris
- Moisturizes epithelium in ear canal
- Odor discourages insects
- Antibiotic, antifungal properties
Middle Ear

Eustachian Tube

- connects the middle ear with the nasopharynx
- opens during swallowing & yawning
  
  - This equalizes the pressure on either side of the eardrum, improving the efficiency of sound transmission to the inner ear.
Impedance Problem: 99.9% sound is reflected due to high impedance of fluid in the cochlea

(30 dB loss)

Solution: Middle ear ossicles overcome impedance mismatch by increasing sound pressure

(34 dB gain)
Mechanisms for middle ear impedance matching

- Lever action of the ossicles (1.3:1)
  \[20 \log(1.3/1) = +2 \text{ dB}\]

- Buckling of ear drum (x2 pressure increase)
  \[20 \log(2/1) = +6 \text{ dB}\]

- Area ratio of ear drum to stapes footplate (20:1)
  \[20 \log (20/1) = +26 \text{ dB}\]
  * Basic concept: \( p = f/a \)
Middle ear gain is larger in animals with significant air space in the middle ear

Ravicz et al. 1992
Effects of middle ear muscle contractions

Tensor Tympani
- pulls manubrium, TM inward
- increases middle ear pressure (*helps open eustacian tube*)

Stapedius
- pulls incudostapedial joint sideways (*perpendicular to stapes motion*)
- reduces low-frequency middle ear gain

Acoustic Reflex
Inner Ear Function

Diagram showing the anatomy and function of the inner ear.

- Gross division: Outer ear, Middle ear, Inner ear
- Anatomy: malleus, incus, stapes, semicircular canals, vestibule, vestibular n.
- Mode of operation: air vibration, mechanical vibration, mechanical, hydrodynamic, electrochemical
- Function: protection, amplification, localization, impedance matching, selective oval window stim., pressure equalization, filtering distribution, transduction

Diagram highlights the structure of the ear with labels for each component.
Cochlear Partition:
*Basilar Membrane, Tectorial Membrane, & Organ of Corti*
Organ of Corti

hair cells & supporting cells on the basilar membrane.
Cochlear processing is 1000x faster than retinal processing

Retinal photoreceptors depend on a series of intricate interactions with a G protein and a 2nd messenger before their ion channels close, sending a signal to the brain. This would be much too slow for processing sounds.

Cochlear hair cells must open and close ion channels more rapidly. Their mechanism is like a spring that opens channels when the cilia bend, without a time-consuming chemical exchange.
Movement of hair cell cilia bundle opens ion channels at cilia tips

cilia on a hair cell in bullfrog cochlea.

Pickles and Corey (1992)

tip links from higher cilia pull up ion channel gates on adjoining cilia.

Hudspeth
Neurotransmitter Release at the Inner Hair Cell

Movement of hair cell cilia bundle opens ion channels…

• Deflecting the bundle towards the tallest stereocilium stretches the tip links, increasing the probability of the transducer channel opening to allow selective entry of cations (K⁺).

• Deflection in the opposite direction decreases the tension and closes the channels.

- the mechanically-gated current depolarizes the membrane
- voltage-gated Ca²⁺ channels open in the basolateral membrane
- Ca²⁺ influx induces neurotransmitter release, thus stimulating AN fibers
- Ca²⁺ influx also increases the conductance via calcium-dependent potassium channels, repolarizing the membrane due to K⁺ efflux

Glutamate is thought to be the afferent transmitter between the cochlear IHCs and auditory nerve fibers
The hair cell is a mechanoreceptor, producing an electrical signal (receptor potential) when the hair bundle is moved. The resting membrane potential is somewhat hyperpolarized (~ -45mV for IHCs and -70mV for OHCs).

In contrast the stereocilia bundle is bathed in endolymph, a potassium-rich fluid with a potential of about +80mV relative to the potential of the fluid in the other parts of the cochlea (perilymph, which is like CSF).

So the battery for driving the hair cell potential is the 125mV difference between endolymph and the IHC resting potential (150mV for OHCs).
Generation of the cochlear receptor potential

Each tone cycle depolarizes then hyperpolarizes the hair cell potential, following the up-down motion of the BM. Ultimately this leads to phase-related changes in auditory nerve discharges.
Auditory nerve fiber discharge is a sigmoidal function of SPL. Similarly, the hair cell receptor potential (i.e., the probability of cation channel opening) is a sigmoidal function of bundle displacement.

The AC component: The receptor potential changes in sync with the input signal, almost replicating the tone’s sinusoidal nature.

But the membrane potential is modified more by the bundle’s movement towards depolarization, giving rise in addition to a DC component.
The hyperpolarizing current does not compensate fully for the depolarizing current. Each back and forth movement of the hair bundle creates a rising and falling hair cell potential, but the changes in potential are symmetric about a voltage that is higher than the normal resting potential.
Cochlear hair cell damage

- loss of OHCs
  - partial deafness

- loss of all HCs
  - complete deafness

- ototoxic drugs
  - aminoglycoside antibiotics
  - antimitotic agents

- noise trauma

- presbycusis
Cochlear implant (prosthesis)
Resonance of Basilar Membrane

Base is narrow & taut: 
**most sensitive to high pitch.**

Apex is broad & soft: 
**most sensitive to low pitch**
Basilar Membrane Traveling Wave

Human cochlea is ~35mm long; audible frequency range is ~ 20 Hz - 16 kHz.
The first measurements of the vibrational response to sound of the BM were carried out by Georg von Békésy, for which he was awarded the 1961 Nobel Prize for Physiology or Medicine.

Working in the ears of human cadavers, Békésy showed that the cochlea performs a kind of spatial Fourier analysis, mapping frequencies upon longitudinal position along the BM.

He described a displacement wave that travels on the BM from base to apex of the cochlea at speeds much slower than that of sound in water. As it propagates, the traveling wave grows in amplitude, reaches a maximum, and then decays.

The location of the maximum is a function of stimulus frequency: high-frequency vibrations reach a peak near the base of the cochlea, whereas low-frequency waves travel all the way to the cochlear apex.
Békésy’s mechanical model of the inner ear included a water-filled plastic tube and a 30 cm membrane.

Vibration elicited traveling waves mimicking those in the normal human ear. Usable frequency range was two octaves.

“I decided to make a model of the inner ear with a nerve supply. An attempt to use a frog skin as a nerve supply had at an earlier time proved to be impractical, and so I simply placed my arm against the model. To my surprise, although the traveling waves ran along the whole length of the membrane with almost the same amplitude, and only a quite flat maximum at one spot, the sensations along my arm were completely different. I had the impression that only a section of the membrane, 2 to 3 cm long, was vibrating. When the frequency of vibration was increased, the section of sensed vibrations travelled toward the piston (at the right of the figure), which represents the staples footplate of the ear; and when the frequency was lowered, the area of sensation moved in the opposite direction.

The model had all the properties of a neuromechanical frequency-analyzing system, in support of our earlier view of the frequency analysis of the ear. My surprise was even greater when it turned out that two cycles of sinusoidal vibration are enough to produce a sharply localized sensation on the skin, just as sharp as for continuous stimulation. This was in complete agreement with the observations of Savart, who found that two cycles of tone provide enough cue to determine the pitch of the tone.”

“Concerning the pleasures of observing, and the mechanics of the inner ear”

Nobel Lecture, December 11, 1961
Békésy measured BM displacement as a function of frequency and place.

Thus the century-old problem of how the ear performs a frequency analysis -- whether mechanically or neurally -- could be solved; from these experiments it was evident that the ear contains a neuro-mechanical frequency analyzer, combining a preliminary mechanical frequency analysis with a subsequent sharpening of the sensation area.”
Hearing. II. The physical basis of the action of the cochlea

BY T. GOLD, The Zoological Laboratory, University of Cambridge

(Communicated by J. Gray, F.R.S.—Received 27 April 1948)

An attempt is made to discover the physical processes in the cochlea which would yield results in agreement with observations. It is shown that the assumption of a ‘passive’ cochlea, where elements are brought into mechanical oscillation solely by means of the incident sound, is not tenable.

The degree of resonance of the elements of the cochlea can be measured, and the results are not compatible with the very heavy damping which must arise from the viscosity of the liquid. For this reason the ‘regeneration hypothesis’ is put forward, and it is suggested that an electromechanical action takes place whereby a supply of electrical energy is employed to counteract the damping.

The circumstantial evidence for such a process is considered, and it appears that the cochlea microphonic potential, hitherto an unexplained by-product of the action, forms an important link in the chain of events. Some implications of the theory are discussed, and ways of testing it are suggested.

Evolving Concepts in Cochlear Mechanics

• In 1971 Rhode demonstrated that BM vibrations in live squirrel monkeys exhibit a compressive nonlinearity occurring only at or near CF, and disappearing after death.

• Rhode’s discoveries were eventually confirmed (LePage & Johnstone 1980, Robles et al 1986, Sellick et al. 1982), after several unsuccessful attempts.

• But by that time Kemp (1978) had discovered otoacoustic emissions — sounds emitted by the cochlea which grow at compressive rates with stimulus intensity.

• Kemp revived Gold’s 1948 notion of a positive electromechanical feedback to boost BM vibrations to compensate for the viscous damping exerted by the cochlear fluids.

• In 1985, Brownell et al. identified a possible origin for both otoacoustic emissions and the hypothetical electromechanical feedback: they showed that outer hair cells change their length under electrical stimulation.
Frequency tuning in cochlear vibrations and auditory nerve fibers

Tuning curve for an AN fiber (solid) compared with isoresponse curves at a BM site with identical CF (9.5 kHz) recorded in the same ear.

At fiber CF threshold, BM peak displacement was used to plot BM isodisplacement and isovelocity tuning curves (dotted and dashed lines, respectively).

isodisplacement (solid) and isovelocity tuning curves (dotted and dashed) for TM vibrations compared with neural tuning based on averaged responses from many auditory-nerve fibers.
Auditory tuning curves

inner hair-cell damage

outer hair-cell damage

Log Frequency

dB SPL

Characteristic Frequency

Normal threshold

Abnormal threshold

Normal bandwidth

Abnormal bandwidth
Role of Outer Hair Cells in Cochlear Mechanics

1985  Brownell et al. identified a possible origin for both otoacoustic emissions and the hypothetical electromechanical feedback: outer hair cells change their length under electrical stimulation.

Evoked Mechanical Responses of Isolated Cochlear Outer Hair Cells

Abstract. Intracellular current administration evokes rapid, graded, and bidirectional mechanical responses of isolated outer hair cells from the mammalian inner ear. The cells become shorter in response to depolarizing and longer in response to hyperpolarizing currents in the synaptic end of the cell. The cells respond with either an increase or decrease in length to transcellular alternating current stimulation. The direction of the movement with transcellular stimuli appears to be frequency dependent. Iontophoretic application of acetylcholine to the synaptic end of the cell decreases its length. The microarchitecture of the organ of Corti permits length changes of outer hair cells in a manner that could significantly influence the mechanics of the cochlear partition and thereby contribute to the exquisite sensitivity of mammalian hearing.


(A) OHC isolated from guinea pig. Some mechanoreceptive stereocilia can be seen emerging from the cuticular plate.

(B) Microarchitectural features of the organ of Corti permit free movement of OHCs along their length.

(C) A decrease in OHC length results in a decrease in the separation between the basilar membrane and reticular lamina.
Nonlinear Amplifier  

**outer hair cell motion & cochlear micromechanics**

BM is deflected by pressure gradients in surrounding fluid. Hair bundles on IHC and OHCs are deflected by shear displacement between RL and TM.

BM motion without OHC motility: cochlear output is proportional to input.

OHCs contract in-phase with upward deflection of BM, absorbing BM motion, and minimizing shear.

OHC contraction lags BM displacement by 90°. BM forces create negative damping and pump energy into the mechanical system. Energy from OHC motility improves cochlear sensitivity to low-level sounds.
OHC activity

- Increases sensitivity (*lowers thresholds*)
- Increases selectivity (*reduces bandwidth of auditory filter*)
- Gives ear a logarithmic (*non-linear*) amplitude response
- Produces oto-acoustic emissions

*OHCs are relatively more active for quiet sounds than for loud sounds.*

*They only amplify sounds at the CF matching their cochlear place.*
Change in receptor potential with current shows compressive nonlinearity
Compressive nonlinearity near CF in BM Velocity-Intensity functions

- linear growth of responses to tones lower or higher than CF
- highly compressive growth of responses to CF tones (i.e., response magnitude grows by only 28 dB with stimulus increase of 96 dB).

Chinchilla cochlea CF = 10 kHz
Ruggero et al.
BM becomes linear without OHCs
(furosemide injection)
Amplification greater and tuning more selective at low levels

Otoacoustic Emissions
low level sounds produced by the inner ear

Stimulated acoustic emissions from within the human auditory system

D. T. Kemp

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(Received 5 April 1978; revised 10 July 1978)

A new auditory phenomenon has been identified in the acoustic impulse response of the human ear. Using a signal averaging technique, a study has been made of the response of the closed external acoustic meatus to acoustic impulses near to the threshold of audibility. Particular attention has been paid to the waveform of the response at post excitation times in excess of 5 ms. No previous worker appears to have extended observations into this region. The response observed after about 5 ms is not a simple extension of the initial response attributable to the middle ear. The oscillatory response decay time constant was found to change from approximately 1 ms to over 12 ms at about this time. The slowly decaying response component was present in all normal ears tested, but was not present in ears with cochlear deafness. This component of the response appears to have its origin in some nonlinear mechanism probably located in the cochlea, responding mechanically to auditory stimulation, and dependent upon the normal functioning of the cochlea transduction process. A cochlear reflection hypothesis received some support from these results.

J. Acoust. Soc. Am. 64(5), Nov. 1978
Otoacoustic Emissions

low level sounds produced by the inner ear

D.T. Kemp

People often ask what prompted the first OAE measurement. It was to explain a set of complex and little known psychoacoustic phenomena. Spontaneous subjective pure tones had been cited by Gold in 1948 as potential evidence for a 'cochlear amplifier'. Anomalous aural combination tone generation had been reported by Ward in 1952 involving mysterious internal tones. Finally in 1958 Elliot reported a periodic ripple pattern in the fine structure of the auditory threshold in normal ears. All three were systematically linked together but no rational explanation could be found. Only one physical model seemed to fit the facts. It was that near to threshold levels the healthy cochlea behaved like a reverberating and resonating auditorium enhanced by a strange PA system prone to feedback howl and distortion! It was an incredibly long shot but in June of 1977 I put a microphone into my ear canal just to check. Through the microphone came distortion products, spontaneous tones and echoes! The incredible turned out to be true!
Theory of Otoacoustic Emissions

The sensitivity and resolution of the ear depends on two things:

(1) the size and sharpness of cochlear travelling wave peaks.

(2) the efficiency of transduction to the auditory nerve.

Without active OHC function, sound energy is lost from the traveling wave before it peaks. OHCs generate replacement vibration which sustains and amplifies the traveling wave, resulting in higher and sharper peaks of excitation to the IHCs.

Most of the sound vibration generated by OHCs becomes part of the forward travelling wave, but a fraction travels back out of the cochlea to cause secondary vibrations of the middle ear and the ear drum. The whole sequence can take 3 - 15 ms. These cochlear driven vibrations are the source of Otoacoustic Emissions.
Sound is filtered as it passes through the pinna and ear canal. This **acoustic energy** vibrates the tympanic membrane like a drum...

...setting the ossicles in motion, mechanically amplifying sound and changing acoustic energy to **mechanical energy**. The middle ear compensates for an air/fluid impedance loss.

The stapes displaces the oval window, **hydrodynamic energy** causes cochlear membranes to shear against hair cell bundles. An **electrochemical signal** is sent via auditory nerve to brain.