Auditory Systems

Slides: www.auditorybrain.com/downloads

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Aims

- Describe key anatomical features and physiological functions of the outer, middle and inner ear
- Outline the major components of the central auditory pathway, and briefly describe their structure and function
- Outline major principles of auditory cortical organisation.
Overview of peripheral auditory system

- Gross division
  - Outer ear
    - pinna
    - concha
  - Middle ear
    - malleus
    - incus
    - stapes
  - Inner ear
    - semicircular canals
    - vestibule
    - vestibular n.
  - Central auditory nervous system
    - facial nerve
    - internal auditory canal
    - cochlear nerve

- Anatomy
  - external auditory meatus
  - external auditory canal
  - eustachian tube
  - cochlea
  - round window

- 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
  - information processing
1. Sound amplification: pinna collects and funnels sound to the eardrum
2. Sound Localization: pinna filters sound in a direction-dependent way
Incoming sounds are filtered by the outer ear in a way that depends upon the location of the sound. This is how we judge the elevation of a sound, and whether a sound is in front of us or behind us.
The diagram illustrates the anatomy of the ear and its function. The outer ear includes the pinna and concha, which house the external auditory meatus. The middle ear contains the malleus, incus, and stapes, connected by the eustachian tube and round window. The inner ear comprises the semicircular canals, vestibule, vestibular n., facial nerve, and cochlea. The central auditory nervous system includes the internal auditory canal and cochlear nerve. The mode of operation for the outer ear is air vibration, for the middle ear, it is mechanical vibration, and for the inner ear, it is mechanical, hydrodynamic, and electrochemical. The functions include protection, amplification, localization, impedance matching, selective oval window stimulation, pressure equalization, filtering and distribution, transduction, and information processing.
The Middle Ear

Without the middle ear, 99.9% of sound would be reflected due to high impedance of fluid in the cochlea (relative to air).

How does the middle ear increase pressure?

1. Lever action of the ossicles (increases force)
2. Footplate of stapes has much smaller area than tympanic membrane (reduces area)

Pressure = Force/Area
Middle ear enhances the amount of sound transmitted to the inner ear, but in a controllable way.
Stiffness is higher at the base

To produce movement at the base, you need to move less fluid (so less mass)

\[ \omega^2 = \frac{k}{m} \]

Frequency (\( \omega \)) increases with stiffness (\( k \)) and decreases with mass (\( m \))
Up-down movement of the basilar membrane causes the stereocilia of hair cells to be displaced in different directions.

Steriocilia of a single hair cell
- The stereocilia of each hair cell are connected by “tip links”.

- Movement of the stereocilia changes the tension on the tip links. This opens or closes stretch-sensitive K+ channels.

- When K+ channels open, there is an influx of K+. This depolarises the hair cell membrane, which opens voltage-gated Ca++ channels and increases the probability of transmitter release.
OHCs actively amplify movement of the basilar membrane. This makes the basilar membrane more sensitive to sound and more frequency-selective.

Active (normal) process:
- higher amplitude in response to same sound
- narrower peak
  (more sharply tuned)

Neely and Kim (1983)
Auditory nerve fibres (spiral ganglion cells)

Responses of auditory nerve fibres (ANFs) vary depending on:

1. Frequency
2. Timing (phase locking)
3. Intensity
Auditory nerve fibres: frequency tuning

**Frequency tuning curve:** at each frequency, what is the minimum sound intensity that will produce a response?

Threshold: the minimum sound intensity at any frequency that produces a response (lower threshold = more sensitive)

Bandwidth: at a particular intensity, how wide is the band of frequencies that produces a response? (narrower = more frequency selective)
Auditory nerve fibres: frequency tuning
Some auditory nerve fibres fire phase-locked to sound wave. Phase-locking decreases with sound frequency, and is strongest in fibres tuned below 3000 Hz.
Peripheral auditory system converts vibration of air into electrical activity

Cochlear implants can do this artificially by directly stimulating ANFs
How does a cochlear implant work?
The Cochlear Nucleus (CN)

Division of labour (DCN/VCN)

First site of convergence/divergence of input

First inhibitory synapses
Tonotopic projections from Cochlea to CN
Cochlear Nucleus: ventral and dorsal

Two major processing streams:

Ventral cochlear nucleus:
- fast, precise
- projects to superior olive

Dorsal cochlear nucleus:
- complex responses
- projects to inferior colliculus
Neurons of the Cochlear Nucleus

AVCN
- Spherical
- Bushy
- Stellate
- Globular
- Bushy

PV CN
- Stellate

DCN
- Fusiform

Novel neurons and their characteristics are illustrated in the diagram.
The Superior Olivary Complex

Convergence of input from the two ears

Important for sound localization

Sends projections back to the cochlea
Binaural Sound Localization Cues

Interaural Level Differences (ILD): most useful at high frequencies

Interaural Time Differences (ITD): most useful at low frequencies
Superior Olive and sound localization

Information streams from the two ears converge in the lateral superior olive (LSO) and medial superior olive (MSO).

LSO extracts Interaural Level Differences (ILDs).

*mechanism:* *ipsi* excitation, *contra* inhibition

MSO extracts Interaural Time Differences (ITDs).

*mechanism:* *different in birds and mammals!*

Grothe and Koch (2011)
The Inferior Colliculus

Site of convergence from ascending and descending pathways

Obligatory station in ascending pathway
Inferior Colliculus: Integration Centre

- almost all ascending auditory pathways go through inferior colliculus!
- primary “core” nucleus surrounded by dorsal cortex and lateral nucleus
- integrates MSO input (low-freq ITD) with LSO input (high-freq ILD)
- integrates auditory input with other sensory inputs
Human Inferior and Superior Colliculi

Figure 4
Superior Colliculus: a map of auditory space

Central Nucleus of the IC

External Nucleus (IC)

Auditory Cortex

Frontal Eye Fields

Superior Colliculus

Bajo et al., 2010
The Auditory Thalamus (MGB)
MGN: Thalamic Gate to Forebrain

MGN

**Dorsal MGN**
- plasticity and learning?

**Medial MGN**
- auditory attention and arousal?
- polysensory integration?

**Ventral MGN**
- primary auditory information transmission
Primary auditory cortex in humans is located in Heschl's gyri.
Functional MRI imaging reveals more complex tonotopic organization.
Auditory Cortex: multiple tonotopic and non-tonotopic areas

Bizley and Cohen 2013
Multiple frequency maps exist in Auditory Cortex

Bizley et al. 2005
Multiple auditory cortical areas

1. Hierarchical: core, belt and parabelt

2. Specialized processing streams
   • Hemispheric specialization and lateralization
   • Sensory-memory and sensory-motor pathways

3. Descending (feedback) connections
Core, Belt and Parabelt

**Core:**
- primary thalamic input
- tonotopically organised
- connects to core and belt

**Belt:**
- thalamic input
- non-tonotopic
- connects to core, belt and parabelt

**Parabelt:**
- no thalamic input
- non-tonotopic
- connects to belt, parabelt and beyond

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Kaas and Hackett (2000)
Simple sounds activate core areas best (e.g. lateralised sounds, noise bursts).

Complex sounds activate progressively more distant belt and parabelt areas (e.g. moving sounds, sounds with pitch, sequences of tones).

E.g., Patterson et al. (2002)
Multiple auditory cortical areas

1. Hierarchical: core, belt and parabelt

2. Specialized processing streams
   • Hemispheric specialization and lateralization
   • Sensory-memory and sensory-motor pathways

3. Descending (feedback) connections
Right hemisphere dominant for processing pitch direction; left hemisphere dominant for processing sound duration.

Figure: fMRI of brain activation when subjects asked either to discriminate pitch direction or sound duration in the same sounds.

Brechman and Scheich (2005)
Hemispheric lateralization of spatial processing

• No map of auditory space exists within Auditory Cortex
• Neurons are broadly tuned to sound location and typically respond to contralateral space.
Left auditory cortex represents primarily right auditory space. Right auditory cortex represents primarily left auditory space.

Figure: fMRI of brain activation by moving or static sounds on left or right vs centre.

Krumbholz et al. (2005)
Lesions of Auditory Cortex in primates (including humans), cats and ferrets impair sound source localisation.

Reversible inactivation or permanent lesion of Primary Auditory Cortex impairs localisation in both horizontal and vertical space (only PAF, not AAF).

Specialization within each hemisphere

Lomber and Malhotra
Nat. Neurosci. 2008
Processing Streams within Auditory Cortex?

Division of function between auditory cortical fields for localizing and identifying sounds?

Rauschecker and Scott (2009)
Not all non-spatial tasks activate only ventral stream, and not all spatial tasks activate only dorsal stream.

More accurate distinction is between sensory-memory and sensory motor pathways.

Arnott et al. (2004)
Specialization within streams: speech

a

Via higher-order frontal networks

Articulatory network
pIFG, PM, anterior insula (left dominant)

Sensorimotor interface
Parietal–temporal Spt (left dominant)

Input from other sensory modalities

Dorsal stream

Spectrotemporal analysis
Dorsal STG (bilateral)

Phonological network
Mid-post STS (bilateral)

Conceptual network
Widely distributed

Ventral stream

Combinatorial network
aMTG, aITS (left dominant?)

Lexical interface
pMTG, pITS (weak left-hemisphere bias)

b

Nature Reviews Neuroscience
Most abilities require multiple brain regions to work together.
Multiple auditory cortical areas

1. Hierarchical: core, belt and parabelt

2. Specialized processing streams
   • Hemispheric specialization and lateralization
   • Sensory-memory and sensory-motor pathways

3. Descending (feedback) connections
Descending Auditory Pathways

Auditory Cortex

Medial Geniculate Body

Inferior Colliculus

Lateral Lemniscus

Superior Olivary Complex

Cochlear Nucleus

Cochlea (Left Ear)

Auditory Cortex

Medial Geniculate Body

Inferior Colliculus

Lateral Lemniscus

Superior Olivary Complex

Cochlear Nucleus

Cochlea (Right Ear)
Descending connections I

- Descending connections exist from Auditory Cortex to the thalamus (cortico-thalamic pathway) and Inferior Colliculus (cortico-collicular pathway).
- Descending connections play a role in learning and plasticity (e.g. adapting to altered sound localisation cues).

Baio et al., Nat. Neuro, 2010
Descending connections II

- Descending connections exist from the brainstem (superior olive) to the cochlea: the Olivo-Cochlear Efferent System

The cochlear efferent system is divided into the medial and lateral systems

Lateral olivo-cochlear fibres (LOC) can modulate the sensitivity of auditory nerve fibres

Medial olivo-cochlear fibres (MOC) can modulate cochlear amplification

This was the first descending sensory system to be discovered
Changing the sensitivity of auditory nerve fibres (i.e. increases the dynamic range of ANFs)
Multiple auditory cortical areas

1. Hierarchical: core, belt and parabelt

2. Specialized processing streams
   • Sensory-memory and sensory-motor pathways
   • Hemispheric lateralisation and specialisation

3. Descending (feedback) connections
Further Reading

General reference:
- See also the accompanying website, which has lots of interesting videos/demos etc. at www.auditoryneuroscience.com

Additional references and reviews:
Suggested textbooks