CNS pathways

topics

- The auditory nerve, and the cochlear nuclei of the hindbrain
- Sensory channels of information flow in CNS
- Pathways to medial geniculate body of thalamus
  - Functional categorization of two major ascending pathways
Lateral tegmental axons
Auditory radiations (thalamo-cortical)
Lateral lemniscus (ll)
Brachium of inferior colliculus (bic)
Auditory radiations (thalamo-cortical)
Lateral tegmental axons

Fig 23-10
Auditory pathways in the mammalian brain
(a less compact bundle)

Courtesy of MIT Press. Used with permission.
Note the sensory channels of conduction into the CNS

1. Local reflex
2. Cerebellar
3. Lemniscal:
   - Two main routes to IC; from there to MGB
   - One smaller route directly to MGB from the dorsal cochlear nucleus (larger in large primates)
     - A less compact bundle traversing the lateral midbrain reticular formation.

NEXT: Before we go to the higher levels of the auditory system, we have to return to the 8th nerve axons and the cells of the ventral cochlear nucleus.
The auditory nerve (axons of primary sensory neurons) → cells of the cochlear nuclei

• Single axons with multiple branches
  – to the ventral cochlear nucleus: anteroventral and posteroverentral
  – to the dorsal cochlear nucleus

• Topographic representation of basilar membrane positions:
  – Various cell types in cochlear nuclei
REVIEW:

Tonotopic organization in the cochlear nuclei results from the topographic organization of projections from the cochlea via the 8th nerve to the axonal endings. The branches of the primary sensory axons terminate on different secondary sensory cell types along their A-P trajectory. These cell types have different response characteristics.

**DCN**, dorsal cochlear nucleus
**VCN**, ventral cochlear nucleus
Cochlear nuclei: Correlation of connections and response properties

DorsalCN
PosteroVentralCN
AnteroVentralCN
PosteroVentralCN
VentralCN

Image by MIT OpenCourseWare.
Questions:

• How can a secondary sensory neuron’s axon have a “primary-like” response? To answer this, you need to know the answer to the following anatomical question.

• What is the nature of an “Endbulb of Held” – the endings of 8th nerve axons on certain cells in the ventral cochlear nucleus?
Schematic section through an Endbulb of Held
Ascending projections to thalamus

REVIEW

• Direct, from cochlear nucleus to medial geniculate body (MGB) of thalamus, discovered in chimpanzees and later found in other species as well (e.g., rats, ferrets)
• A less direct connection to MGB is larger:
  – Cochlear nuclei to “trapezoid body” of ventral hindbrain (including the “superior olive”)
  – Then to Inferior Colliculus of the midbrain and the nearby “nuclei of the lateral lemniscus”
  – DCN also projects directly to IC
• Less direct connections to Po (the posterior nucleus of the caudal thalamus): the “lateral tegmental system” of Morest
Thalamic projections
to auditory cortex and to limbic system

• From medial geniculate body (via internal capsule) to auditory areas of neocortex -- in temporal lobe.
• Also from adjacent posterior nucleus of thalamus to several auditory areas.
• In addition, the MGB projects directly to the limbic endbrain – the amygdala.
  – It is likely that this projection evolved very early, along with multimodal projections to striatum and cortex from the posterior nucleus and ventral part of the lateral posterior nucleus of the thalamus
REVIEW:
Auditory thalamus projections to limbic endbrain

Figure removed due to copyright restrictions. Please see course textbook or:

*Striedter p282, from Frost & Masterton (1982).*
A sketch of the central nervous system and its origins

G. E. Schneider 2014
Part 7: Sensory systems

MIT  9.14  Classes 24-25
Sensory systems 3: Auditory systems
continued
First, a review of the pathways beginning at the cochlear nuclei:

```plaintext
Lateral tegmental axons
Auditory radiations (thalamo-cortical)
Lateral lemniscus (ll)
Brachium of inferior colliculus (bic)
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**Fig 23-10**

Auditory pathways in the mammalian brain

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Courtesy of MIT Press. Used with permission.
Note the sensory channels of conduction into the CNS

1. Local reflex
2. Cerebellar
3. Lemniscal
   - Two main routes to IC; from there to MGB
   - One smaller route directly to MGB from the dorsal cochlear nucleus (larger in large primates)
   - Lateral tegmental axons, terminating in other posterior thalamic areas near MGB

NEXT: Before we go to the higher levels of the auditory system, we have to return to the 8th nerve axons and the cells of the ventral cochlear nucleus.
The auditory nerve (axons of primary sensory neurons) \(\rightarrow\) cells of the cochlear nuclei

- Single axons with multiple branches
  - to the ventral cochlear nucleus: anteroventral and posteroverentral
  - to the dorsal cochlear nucleus

- Topographic representation of basilar membrane positions:
  - Positions correspond to best frequencies for activating the neurons. Result: “Tonotopic” maps.
  - Various cell types in cochlear nuclei
**REVIEW:**

Tonotopic organization in the cochlear nuclei results from the topographic organization of projections from the cochlea via the 8th nerve to the axonal endings.

**DCN**, dorsal cochlear nucleus
**VCN**, ventral cochlear nucleus
Cochlear nuclei: Correlation of connections and response properties
Questions, chapter 23

5) Why do some of the auditory nerve axons that terminate in the ventral cochlear nucleus end in a giant terminal enlargement, the endbulb of Held? Answer with a description of the distribution of synapses formed by such axons. (Note the importance of spatial summation and convergence in the triggering of action potentials.)

6) What is the trapezoid body? Describe one important function of a trapezoid body cell group in extracting information from the auditory input.
Schematic section through an Endbulb of Held

We will return to this picture shortly.
REVIEW: Multiple auditory routes to thalamus

| CN = Cochlear nuclei | nLL = Nuclei of the lateral lemniscus |
| DCN = Dorsal cochlear nucleus | MGB = Medial geniculate body |
| VCN = Ventral cochlear nucleus | Po = Posterior nucleus, or group of nuclei, of thalamus |
| IC = Inferior Colliculus | |

- **DCN to midbrain to MGB**
  - Midbrain: IC & nuclei of lateral lemniscus (nLL)

- **VCN to “trapezoid body” to midbrain to MGB**
  - Trapezoid body includes the “superior olive”
  - Midbrain: not only IC but also middle layers of the superior colliculus, which project to posterior portions of lateral nucleus of thalamus

- **CN to reticular formation and/or nLL to Po (posterior nucleus of thalamus) and medial part of MGB**
  - These are components of the “lateral tegmental system” of Morest

- **DCN directly to MGB**
  - Found first in chimpanzee, but later in ferret, rat and other species

These structure are shown in the schematic pictures of the auditory pathways.
Thalamic projections in mammals: to auditory cortex and to limbic system

- From medial geniculate body (via internal capsule) to auditory areas of neocortex -- in temporal region.
- From adjacent posterior nucleus of thalamus, and from medial nucleus of MGB, to several auditory cortical areas.
- In addition, the MGB projects directly to the limbic endbrain – the amygdala. (See illustration.)
  - It is likely that this projection evolved very early along with multimodal projections from posterior thalamic neurons to the corpus striatum.
REVIEW:
Auditory thalamus projections to limbic endbrain

*Striedter p 282, from Frost & Masterton (1982).* (Blue lines have been added to indicate the major axon pathways. LA=lateral nuc of amygdala)
Auditory system

✓ Sensory systems of the dorsolateral placodes and their evolution
✓ Auditory specializations:
  – For antipredator & defensive behaviors
  – For predator abilities
✓ Cochlear nuclei and connected structures
  – Transduction and initial coding
  – Channels of conduction into the CNS

• Two functions, with two ascending pathways
  – Sound localization (“Where is it?”)
  – Auditory pattern detection (“What is it?”)

• Specializations:
  – Echolocation
  – Birdsong
  – Speech
Functional categorization of two major ascending pathways

- **Spatial localization** pathway
  - Connections with superior colliculus for control of orienting movements, and also escape movements.
  - Connections to thalamus, and hence to neocortex of the endbrain

- **Pattern identification** pathway
  - Goes more directly to thalamus, and hence to the endbrain.
Ascending auditory pathways 1: location specificity

Primary sensory neuron of the spiral ganglion

-----Hindbrain---------- ----Midbrain--- Thalamus- Neocortex-

Courtesy of MIT Press. Used with permission.
Spatial localization:

_Hindbrain and midbrain mechanisms summarized_

- **Medial superior olive**: Sensitive to precise time-of-arrival at the two ears $\rightarrow$ azimuthal position
- **Lateral superior olive**: Sensitive to relative amplitude at the two ears $\rightarrow$ azimuthal position
- Location in the vertical axis: Several cues
  - Location information reaches **superior colliculus**
    - Ablation of superior colliculus $\rightarrow$ defective orienting to sounds
  - Location information also reaches neocortex
    - *Via* areas caudolateral and caudomedial to A1, thence to frontal lobe

**How does the medial superior olive compute azimuthal position?**

The best information has come from studies of chickens.
Use of precise time-of-arrival at the two ears for calculating azimuthal position

- **Studies in chicken:**
  - Preservation of timing information through the cochlear nucleus: the Endbulb of Held and the magnocellular nucleus.
  - Coincidence detection in the "nucleus laminaris" (see next figures)

- **In mammals:**
  - The medial superior olive is similar to *nucleus laminaris*. 
Location in the auditory pathways:

Coincidence detection in the “nucleus laminaris” of birds.

In mammals, the medial superior olive is similar to nucleus laminaris of birds.

---------Hindbrain-------------  -Midbrain-  -Thalamus-  -Neocortex------------

Courtesy of MIT Press. Used with permission.
REVIEW:

Endbulb of Held
Axon of 8th nerve in chicken ends on a neuron of nucleus magnocellularis, part of the cochlear nucleus.

Many such neurons exist on both sides; their axons project to dendrites of nucleus laminaris on both sides of the brain. The neurons there appear to act as coincidence detectors. They are activated when inputs from the two sides arrive simultaneously.

RESULT: With simple assumptions about conduction rates of axons from all of the nuc. magnocellularis neurons, one can see how a map of azimuthal positions could be present in nuc. laminaris.

→ The axons of that nucleus project to the midbrain.
Spatial localization:

*How did it evolve? Speculation*

- Diffuse connections from a primitive cochlea to the hindbrain
- Secondary sensory neurons that projected to both sides of hindbrain
- Assume variations in fiber size $\sim$ conduction times
- Some cells received convergence of inputs from two sides. Consider the effects of sounds arising from the right side or from the left side. Certain cells fired more when a sound came from one side rather than the other.
- The resulting crude localization effect was exploited in evolution, and became much more precise.
2nd mechanism for sound localization

• A related mechanism uses relative amplitude at the two ears

• Involves another cell group in the trapezoid body: the lateral superior olive

The superior olive (lateral and medial parts) projects to midbrain, carrying information on spatial location.
Location in the vertical axis is a different problem

• Different frequencies are attenuated differently according to elevation.

• In the owl: External ear mechanics result in amplitude differences in the two ears, depending on elevation.

• Head movements in many animals are used to aid vertical localization.
Questions, chapter 23

7) Distinguish between two prominent pathways of the auditory system: the lateral lemniscus and the brachium of the inferior colliculus.  

8) Where does information about location of sounds and sights converge in the subcortical structures of the CNS? What happens if the auditory and visual maps get out of register?

9) Characterize two separate functions of auditory system pathways ascending through the brainstem. How is the separation of these two functions expressed in the endbrain—in transcortical pathways?
Hamster brain with hemispheres & Cb removed, seen from right side

Courtesy of MIT Press. Used with permission.
Hamster brain with hemispheres & Cb removed, seen from right side

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Questions, chapter 23

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Auditory radiations (thalamo-cortical)
Lateral lemniscus (ll)
Brachium of inferior colliculus (bic)
Auditory radiations (thalamo-cortical)
Lateral tegmental axons

Fig 23-10
Auditory pathways in the mammalian brain

Courtesy of MIT Press. Used with permission.
Location information reaches superior colliculus

- A map of auditory space is found by electrophysiology. It is in register with visual and somatosensory maps.

- The auditory map has been found to be plastic:
  - It can change to match the overlying map of visual space (i.e., map of retinal positions).
  - Experiments: prism displacement of visual inputs causes such a change.
Ablation of superior colliculus

• Experiments with hamster and with cat: Lesions affect not only visual orienting.
• Ablation causes large defects in orienting towards sounds as well.
Information on location of sounds also reaches the neocortex

- Studies of connections and of functional activation patterns in monkeys show distinct cortical regions reached by sound location information.
- These regions are in posterior parietal cortex and in prefrontal cortex. (See next slide.)

Distinct cortical pathways appear to represent location information and information about the identity of sound sources.

These two auditory pathways are similar to the two transcortical visual pathways.
Pathways for object localization and identification in primates

Courtesy of MIT Press. Used with permission.

Fig 23-18
Auditory system

- Sensory systems of the dorsolateral placodes and their evolution
- Auditory specializations:
  - For antipredator & defensive behaviors
  - For predator abilities
- Cochlear nuclei and connected structures
  - Transduction and initial coding
  - Channels of conduction into the CNS
- **Two functions, with two ascending pathways**
  - Sound localization (“Where?”)
  - **Auditory pattern detection & discrimination (“What?”)**
- Specializations:
  - Echolocation
  - Birdsong
  - Speech
Ascending auditory pathways 2:
pattern selectivity

Courtesy of MIT Press. Used with permission.
Auditory neocortex in mammals

topics

• Multiple tonotopic maps define auditory cortical areas
• Unit response properties in cat auditory cortex
• Ablation studies
Questions, chapter 23

10) Describe several properties that have enabled investigators to distinguish multiple neocortical auditory areas in the cat.
Multiple tonotopic maps

• Characteristic frequencies of neurons in A1 of the cat: illustration
• There are at 4 other such maps in cat neocortex, plus other areas that are less tonotopic
• However: Frequency discrimination is not the major function of the auditory neocortex.
Characteristic Frequencies in A1

Graph points at one position along the abscissa show units located at one neo-cortical location; the cells are mostly at different depths in one electrode penetration.

Figure removed due to copyright restrictions. Please see course textbook or: Evans, E. F. "Cortical Representation." In Hearing Mechanisms in Vertebrates; a Ciba Foundation Symposium. Little, Brown, 1968.
Auditory neocortical areas in cat

The ectosylvian cortex:

13 auditory cortical areas:

5 tonotopic areas including A1
3 non-tonotopic areas including A2
3 multi-sensory areas
2 limbic areas

Figure removed due to copyright restrictions. Please see course textbook or:
Tonotopic & columnar organization in cat auditory cortex

• At right angles to the tonotopic (frequency) axis, there are alternating columns where cells in one column respond to both ears, and in adjacent columns to one ear with inhibition from the other ear.

• *See Butler & Hodos (2005), fig 28-7*
Questions, chapter 23

11) How are ablation effects in auditory cortex of the cat related to “word deafness” after certain cortical lesions in humans?

Temporal patterns
Temporal pattern selectivities

• **Early electrophysiological studies** (*Whitfield and Evans in England*)
  – An auditory cortex neuron sensitive to frequency modulation
  – Temporal pattern detection

• Ablation of auditory cortex in cats
  – Support for its importance for temporal pattern discrimination

• Other unit recording studies
An auditory cortex neuron sensitive to frequency modulation

Figure removed due to copyright restrictions.
Other examples of temporal pattern detection

Habituation

Response only to repeated presentations

Off responses, brief & prolonged, to short or to long tones

Off responses only to brief tones
Model:

Connections for tuning to upward frequency sweeps

Fig 23-16

Courtesy of MIT Press. Used with permission.
Ablation of cat auditory cortex

• Frequency and loudness discrimination preserved
• Discrimination of temporal patterns is disturbed or abolished

• Similar results with habituation to novel sounds
• 

*Cf.* humans with “word deafness”
Auditory unit responses with complex temporal pattern selectivities

• Units in bullfrog auditory system specifically tuned to respond to the splash of a bullfrog leaping into the water.

• Selectivity to vocalizations of conspecifics
  – in squirrel monkeys
  – in macaques (2008) [Next slide]

• Units selectively tuned to phonemes are postulated for human auditory cortex.

• There are right-left hemisphere differences in humans
Selectivity to vocalizations of conspecifics

Christopher Petkov and Nikos Logothetis et al. (2008)
“A voice region in the monkey brain”

• “A small region of the monkeys' temporal lobes became active in response to monkey voices but not to other sounds”.

• “This brain region can distinguish the voices of individual monkeys: Responses diminished when the researchers played one monkey's voice repeatedly but perked up again when a new voice was played.”

[Quoted from news report, 11 Feb 2008 online, based on article in Nature Neuroscience]
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  – Auditory pattern detection

• **Specializations:**
  – Echolocation
  – Birdsong
  – Speech
9.14 Brain Structure and Its Origins
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