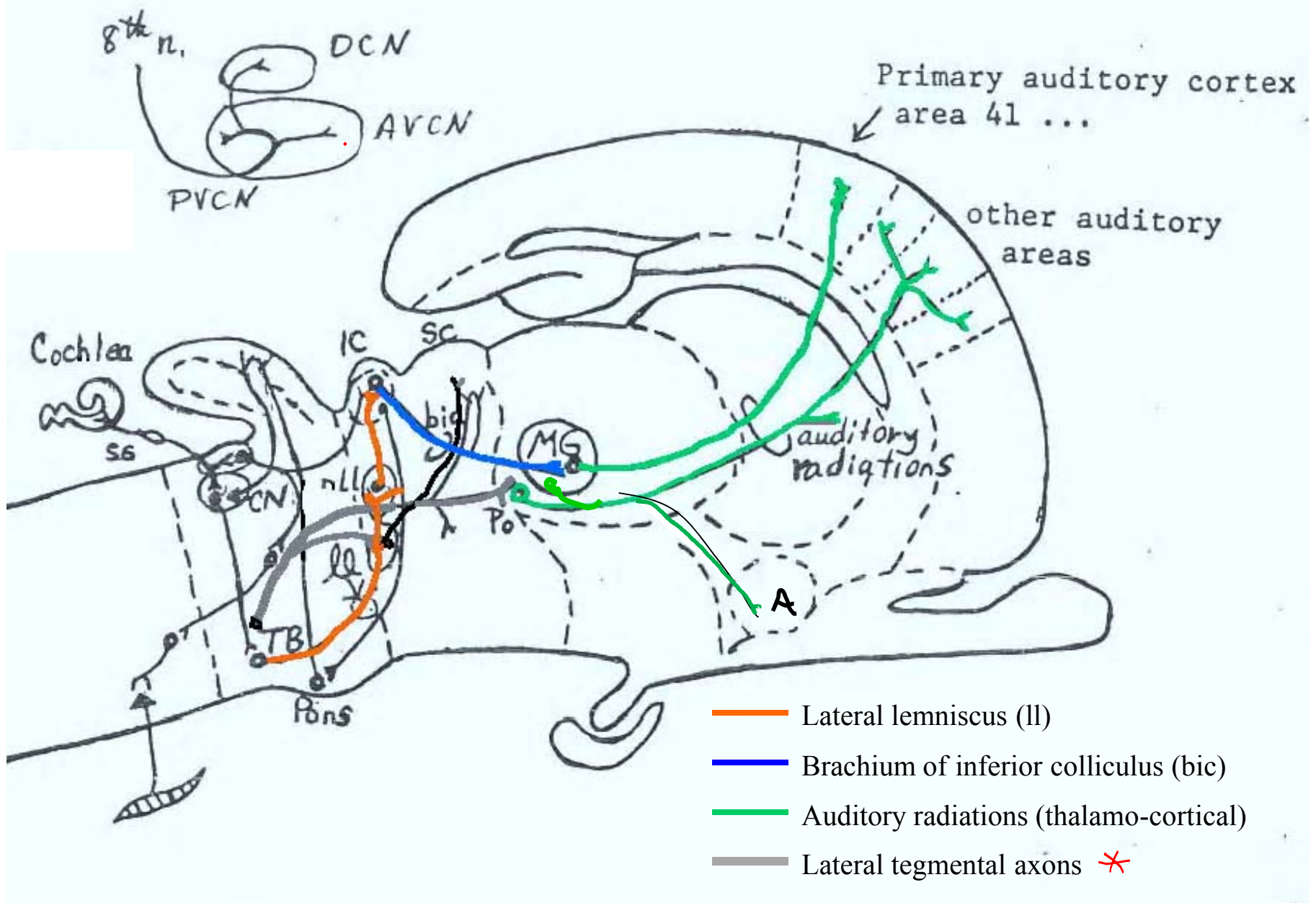


CNS pathways

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



Courtesy of MIT Press. Used with permission.
 Schneider, G. E. *Brain Structure and its Origins: In the Development and in Evolution of Behavior and the Mind*. MIT Press, 2014. ISBN: 9780262026734.

Fig 23-10

Auditory pathways in the mammalian brain

* (a less compact bundle)

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

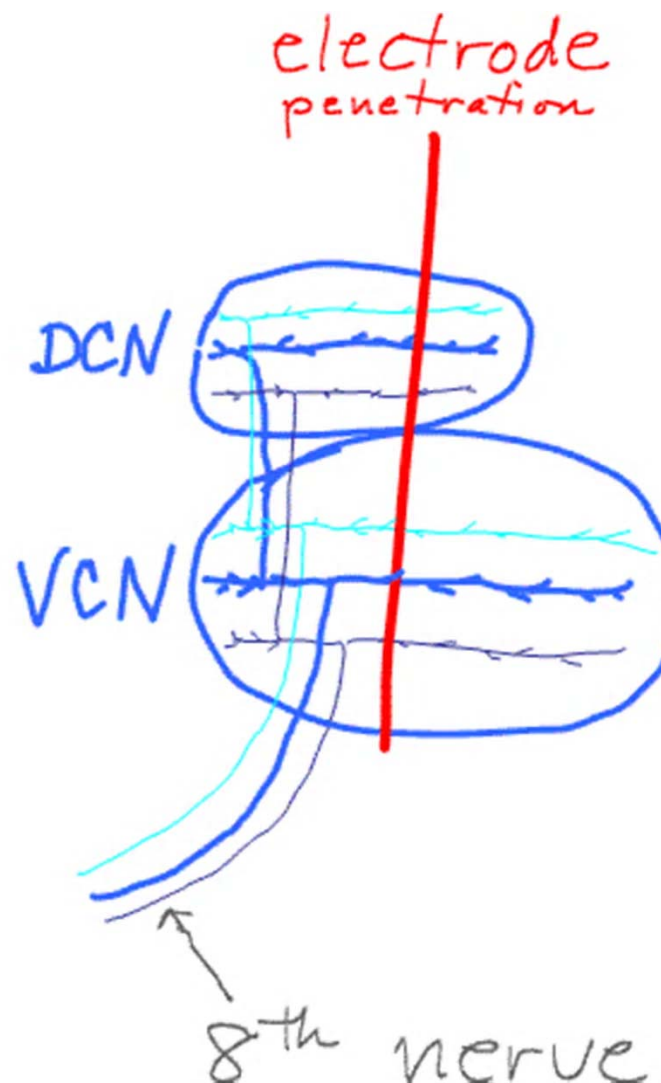
- Single axons with multiple branches
 - to the ventral cochlear nucleus: anteroventral and posteroventral
 - to the dorsal cochlear nucleus
- Topographic representation of basilar membrane positions:
 - Positions correspond to best frequencies for activating the neurons. Result: “Tonotopic” maps.
 - 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.

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

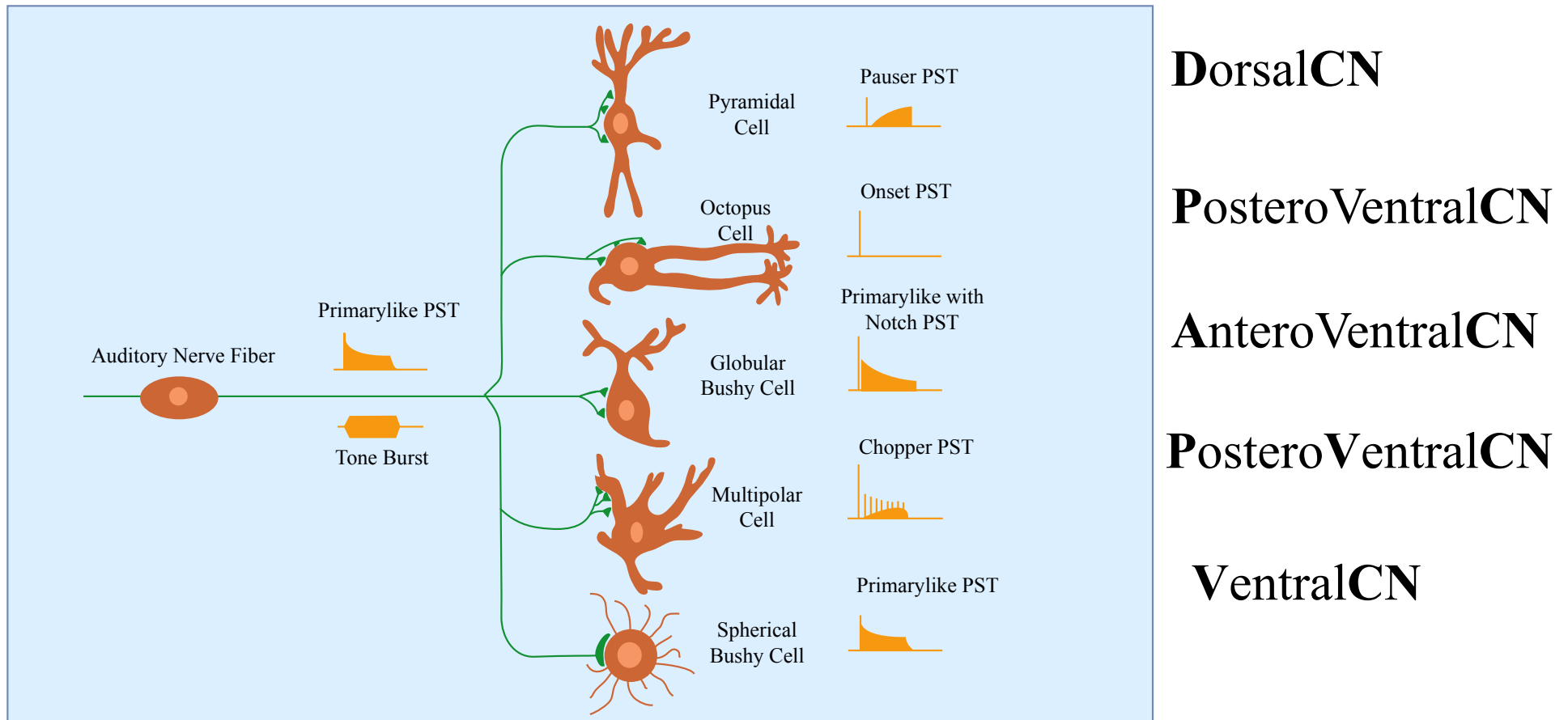
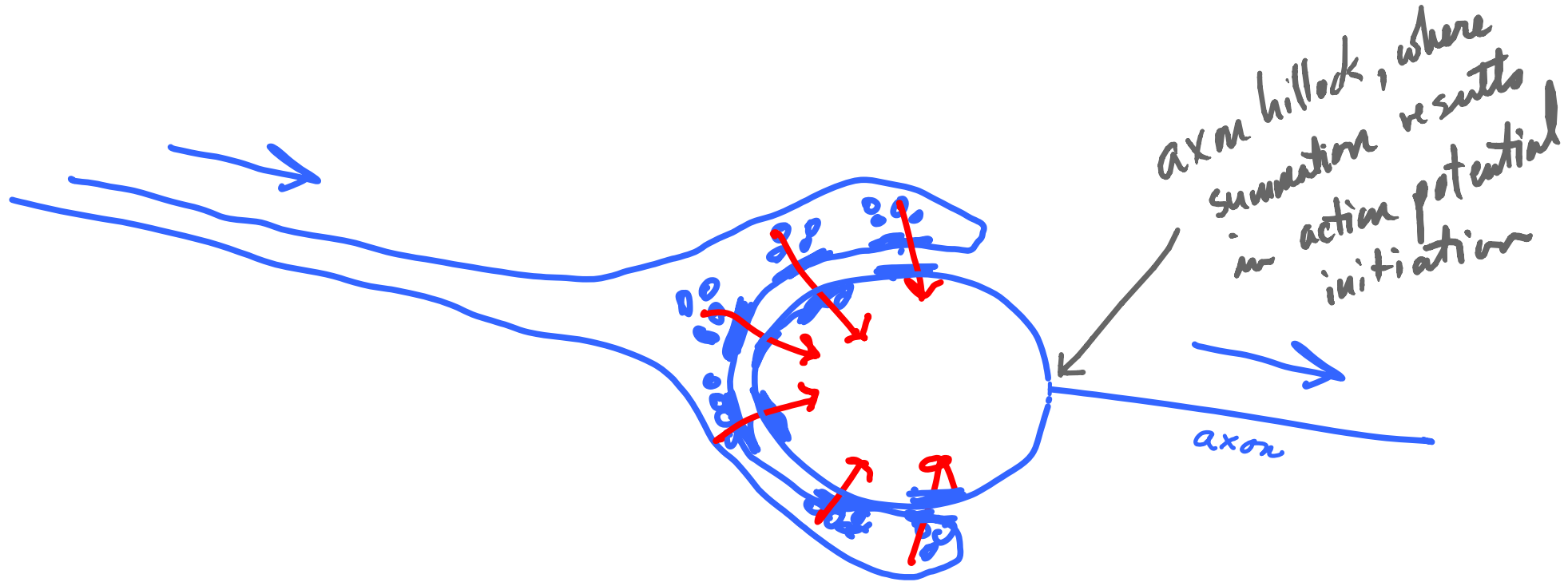


Image by MIT OpenCourseWare.

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:
Frost, Douglas O. "Anomalous Visual Connections to Somatosensory and Auditory Systems
Following Brain Lesions in Early Life." *Developmental Brain Research* 3, no. 4 (1982): 627-35.

Striedter p282, from Frost & Masterton (1982).

A sketch of the central nervous system and its origins

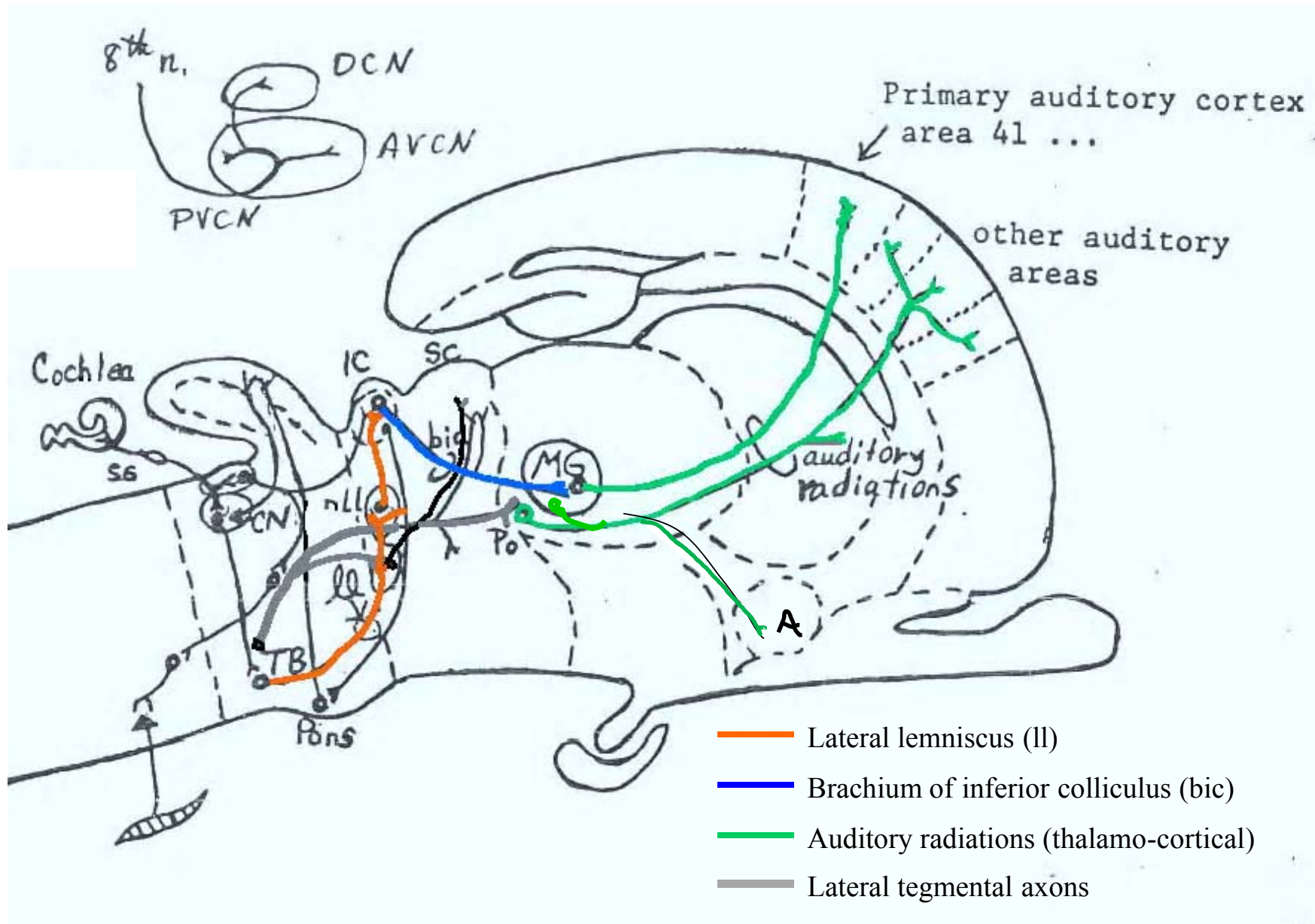
G. E. Schneider 2014
Part 7: Sensory systems

MIT 9.14 Classes 24-25

Sensory systems 3: Auditory systems
continued

First, a review of the pathways beginning at the cochlear nuclei:

X



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Schneider, G. E. *Brain Structure and its Origins: In the Development and in Evolution of Behavior and the Mind*. MIT Press, 2014. ISBN: 9780262026734.

Fig 23-10

Auditory pathways in the mammalian brain

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) → cells of the cochlear nuclei

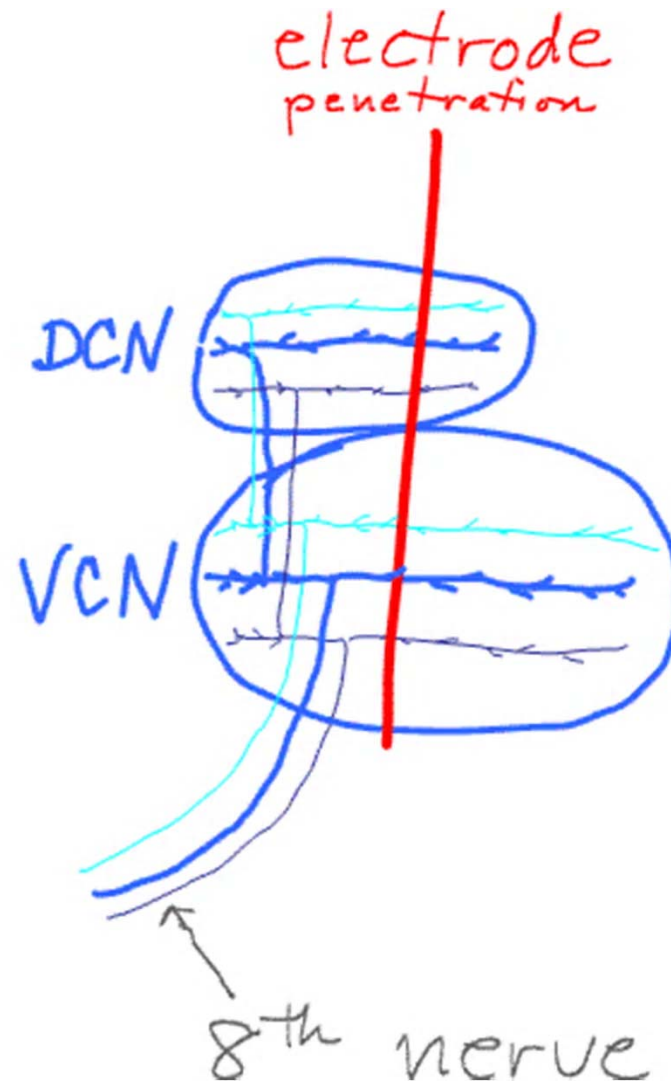
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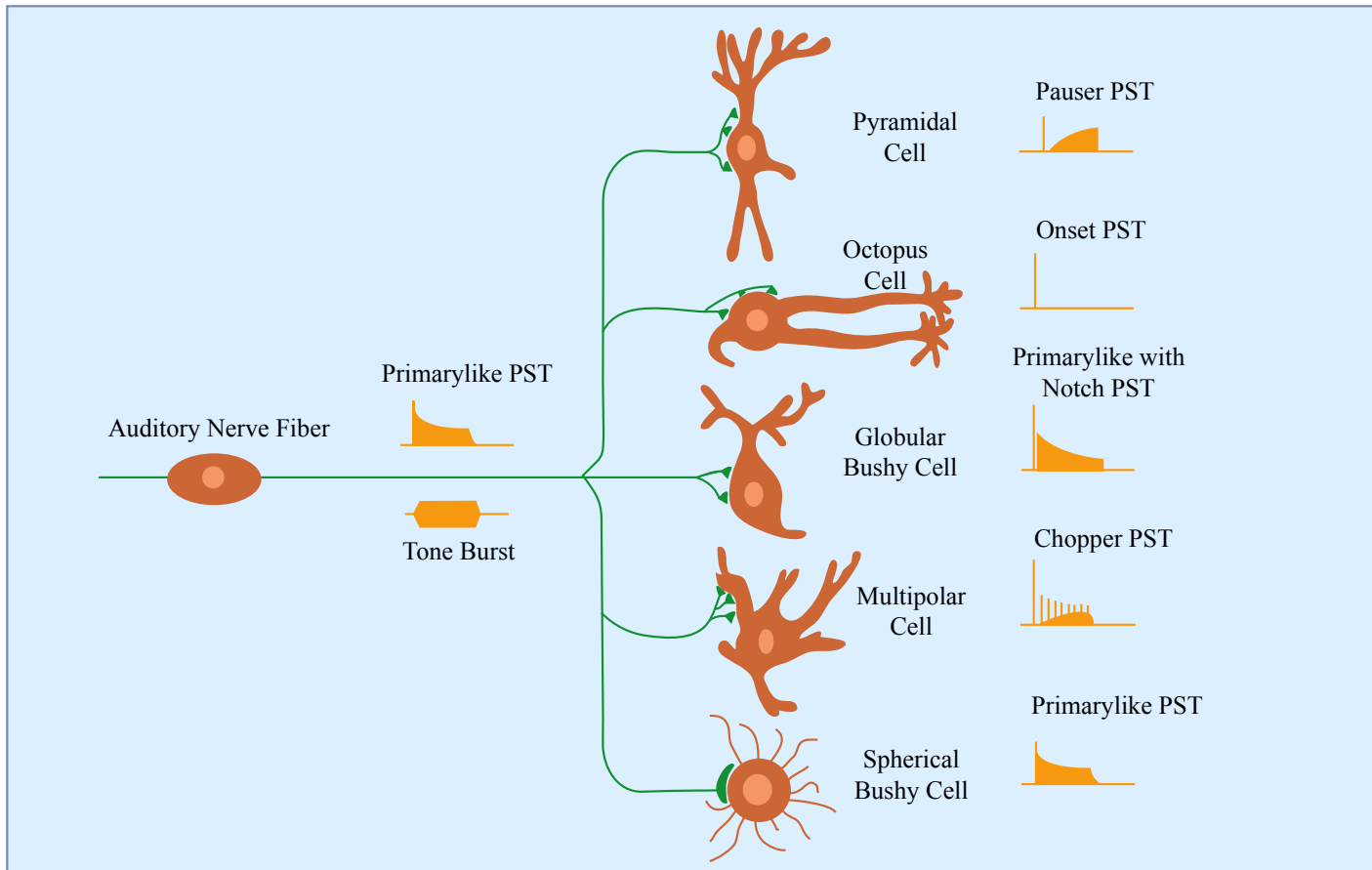
DCN, dorsal cochlear nucleus

VCN, ventral cochlear nucleus



Cochlear nuclei:

Correlation of connections and response properties



DorsalCN

PosteroVentralCN

AnteroVentralCN

PosteroVentralCN

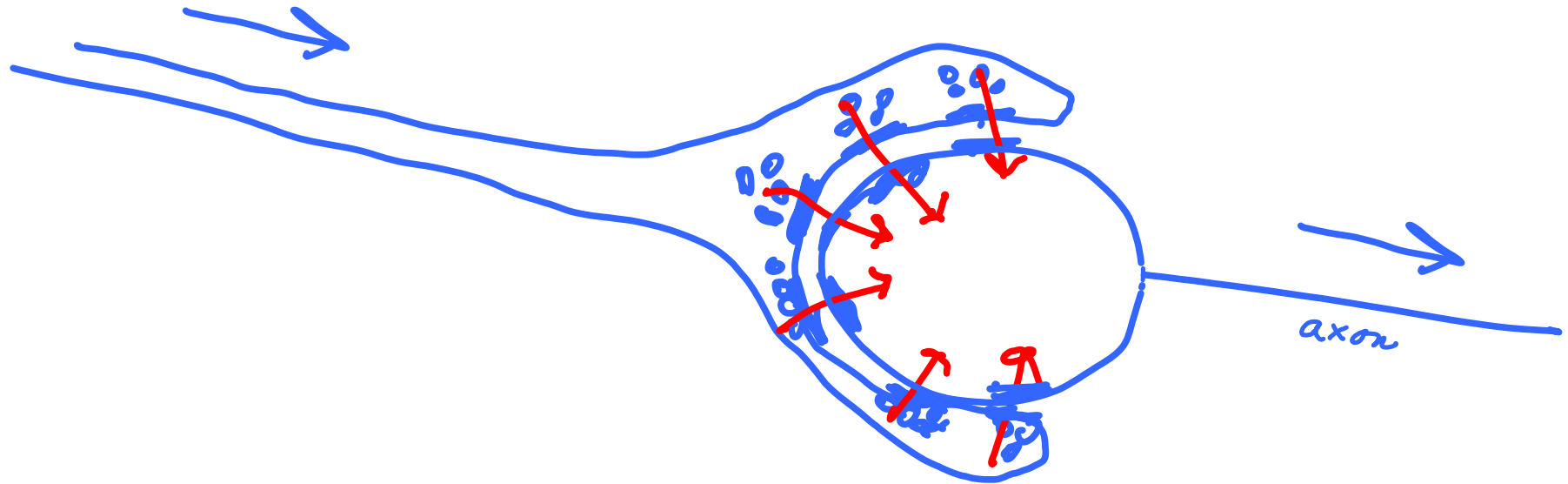
VentralCN

Image by MIT OpenCourseWare.

Questions, 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.

x

REVIEW: Multiple auditory routes to thalamus

CN = Cochlear nuclei

DCN = Dorsal cochlear nucleus

VCN = Ventral cochlear nucleus

IC = Inferior Colliculus

nLL = Nuclei of the lateral lemniscus

MGB = Medial geniculate body

Po = Posterior nucleus, or group of nuclei, of thalamus

- **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.](#)

x REVIEW

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

Figure removed due to copyright restrictions. Please see course textbook or:
Frost, Douglas O. "Anomalous Visual Connections to Somatosensory and Auditory Systems Following Brain Lesions in Early Life." *Developmental Brain Research* 3, no. 4 (1982): 627-35.

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

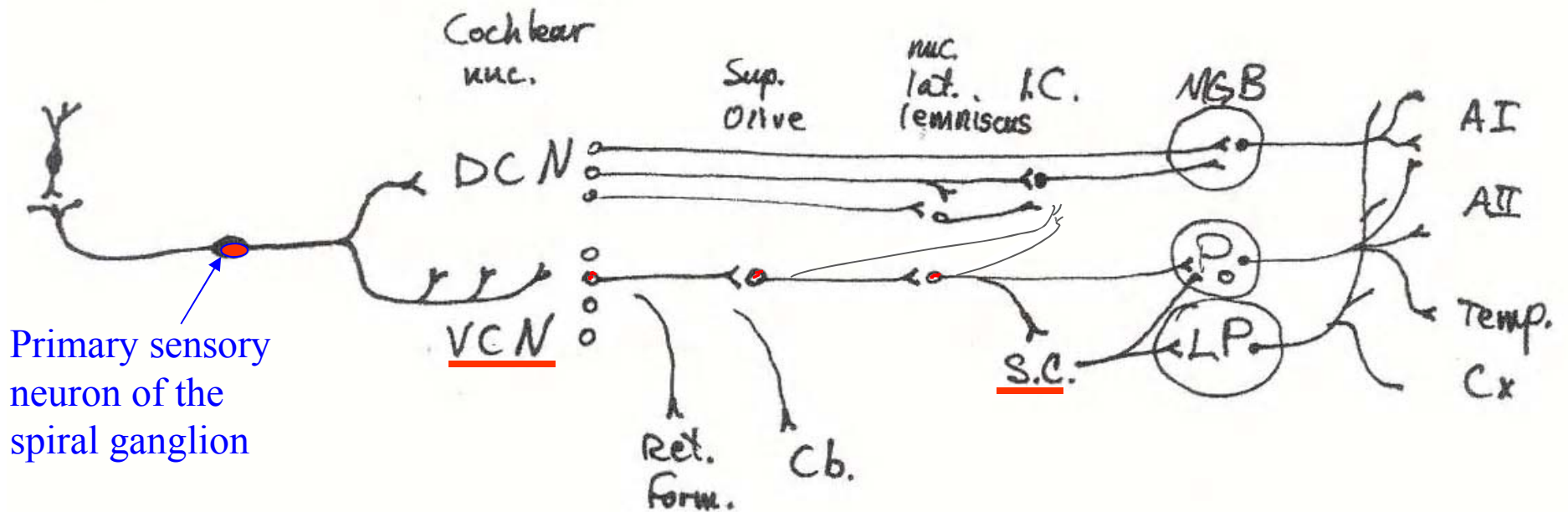
Spatial localization pathway

- 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



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

Courtesy of MIT Press. Used with permission.

Schneider, G. E. *Brain Structure and its Origins: In the Development and in Evolution of Behavior and the Mind*. MIT Press, 2014. ISBN: 9780262026734.

Spatial localization:

Hindbrain and midbrain mechanisms summarized

- **Medial superior olive:** Sensitive to precise time-of-arrival at the two ears → azimuthal position
- **Lateral superior olive:** Sensitive to relative amplitude at the two ears → azimuthal position
- Location in the vertical axis: Several cues
- Location information reaches **superior colliculus**
 - Ablation of superior colliculus → 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.

next

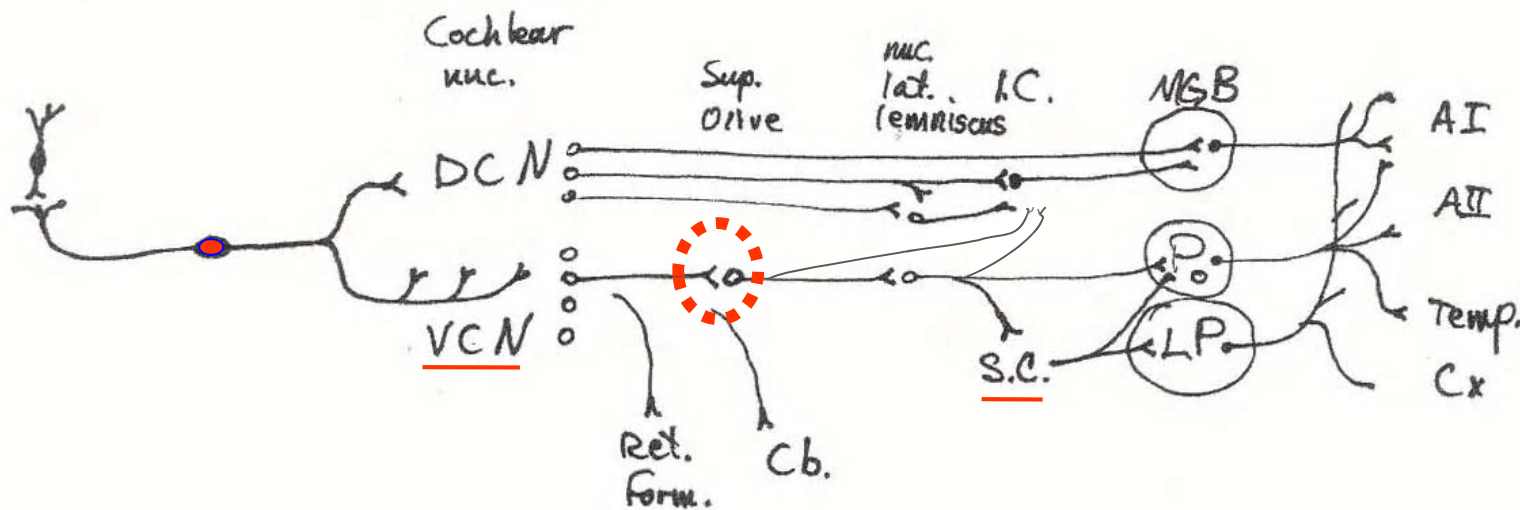
Use of precise time-of-arrival at the two ears for calculating azimuthal position

- 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.



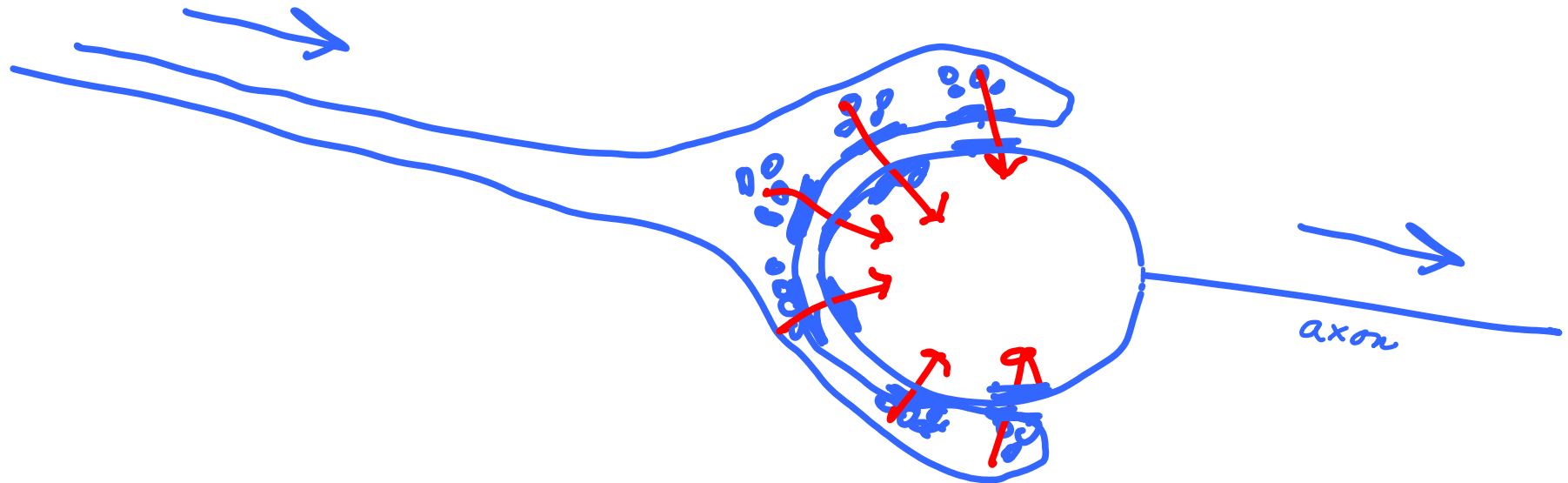
-----Hindbrain----- -Midbrain- -Thalamus- -Neocortex-

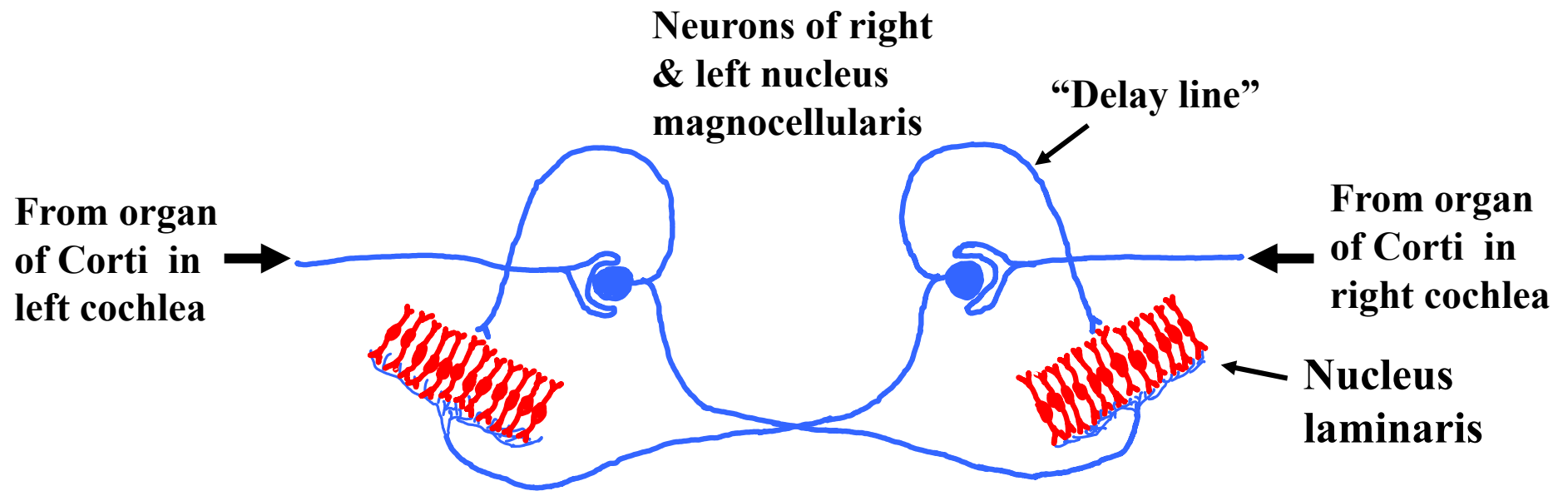
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Schneider, G. E. *Brain Structure and its Origins: In the Development and in Evolution of Behavior and the Mind*. MIT Press, 2014. ISBN: 9780262026734.

REVIEW:

Endbulb of Held





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 Schneider, G. E. *Brain Structure and its Origins: In the Development and in Evolution of Behavior and the Mind*. MIT Press, 2014. ISBN: 9780262026734.

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.

x

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 ~ 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.

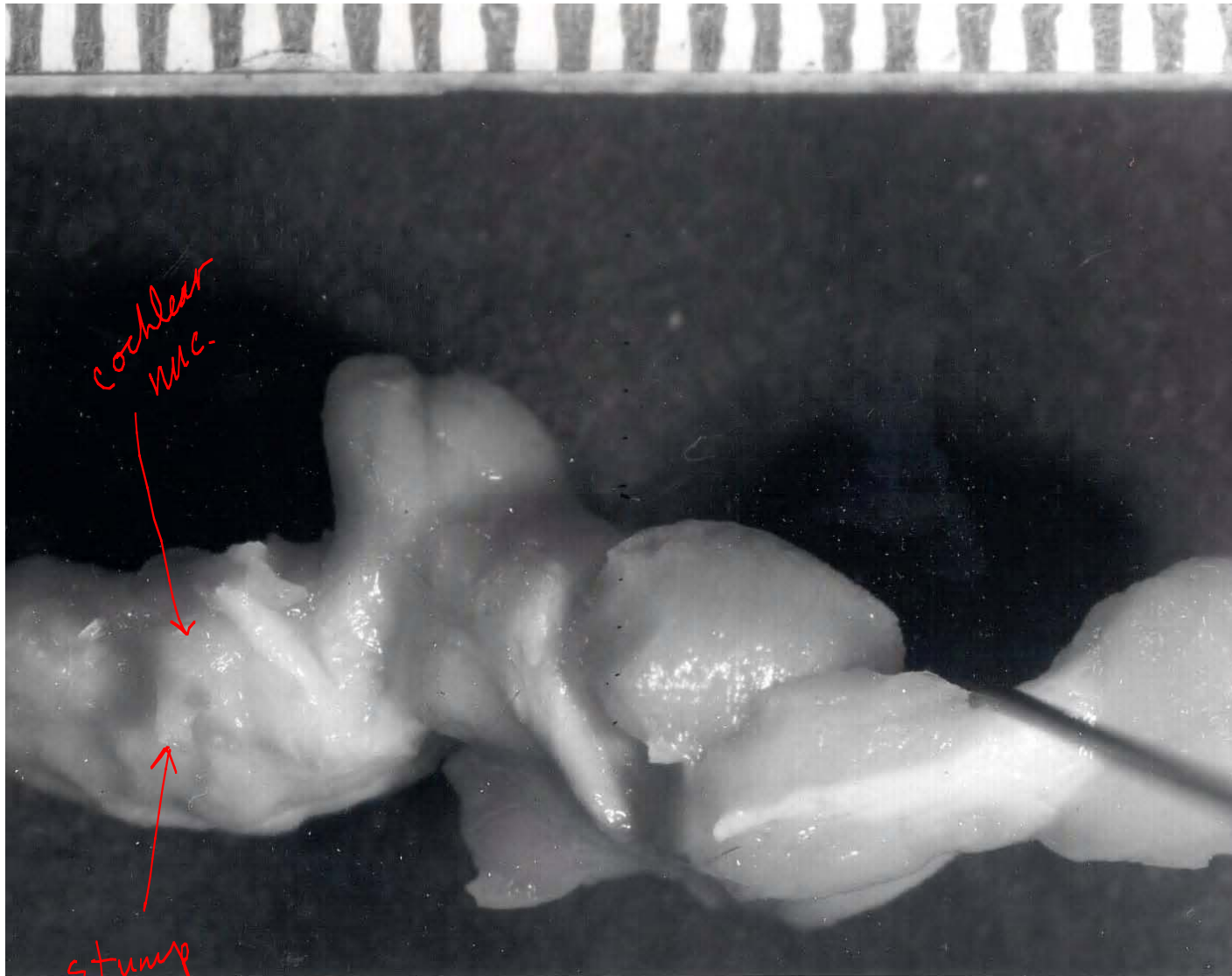
Location in the vertical axis is a different problem

- 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. *Find them in the photo of hamster brainstem (next 2 slides)*
- 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?

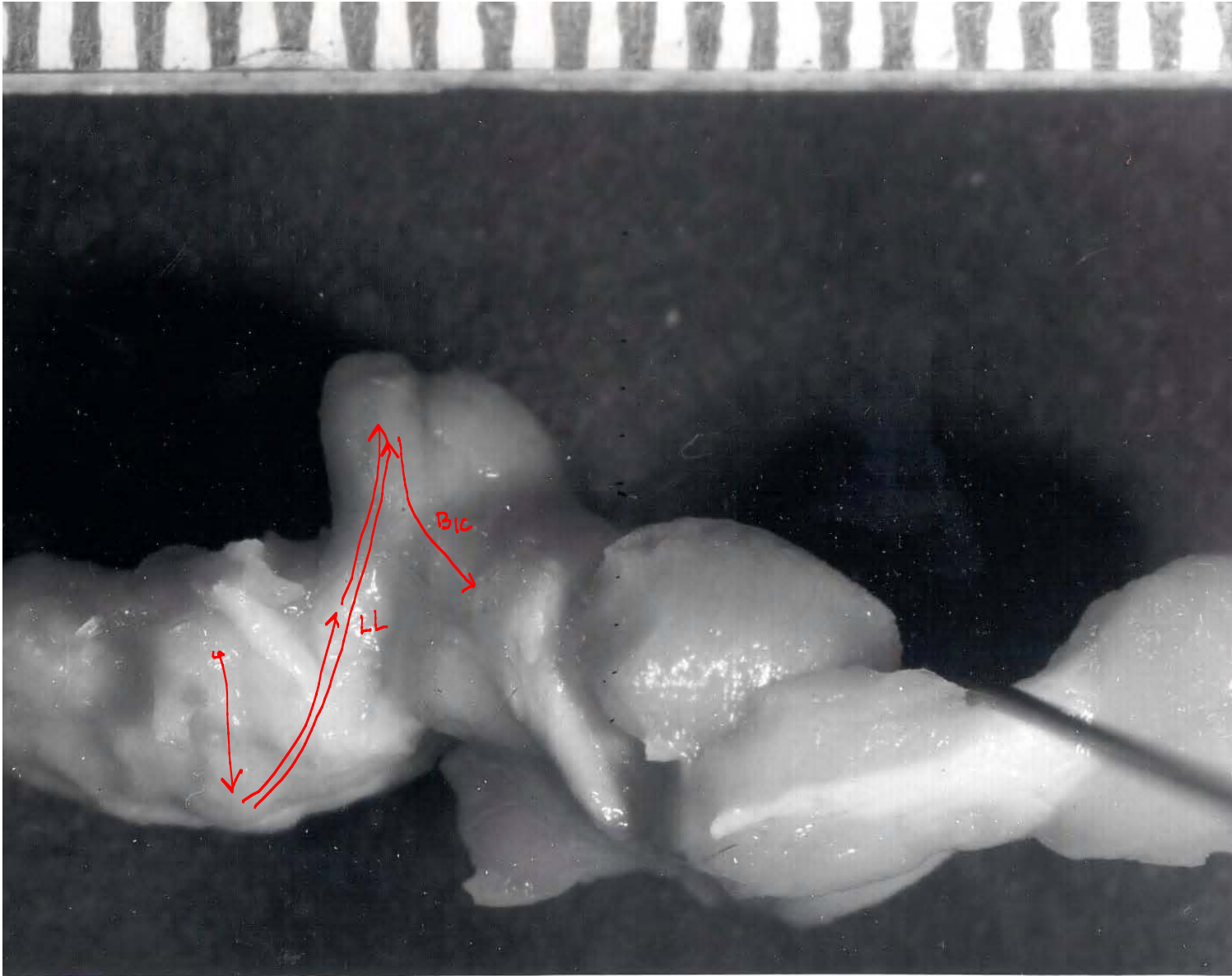
Hamster brain with hemispheres & Cb removed, seen from right side



cochlear
nuc.
stump
of 8th n.

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Schneider, G. E. *Brain Structure and its Origins: In the Development and in Evolution
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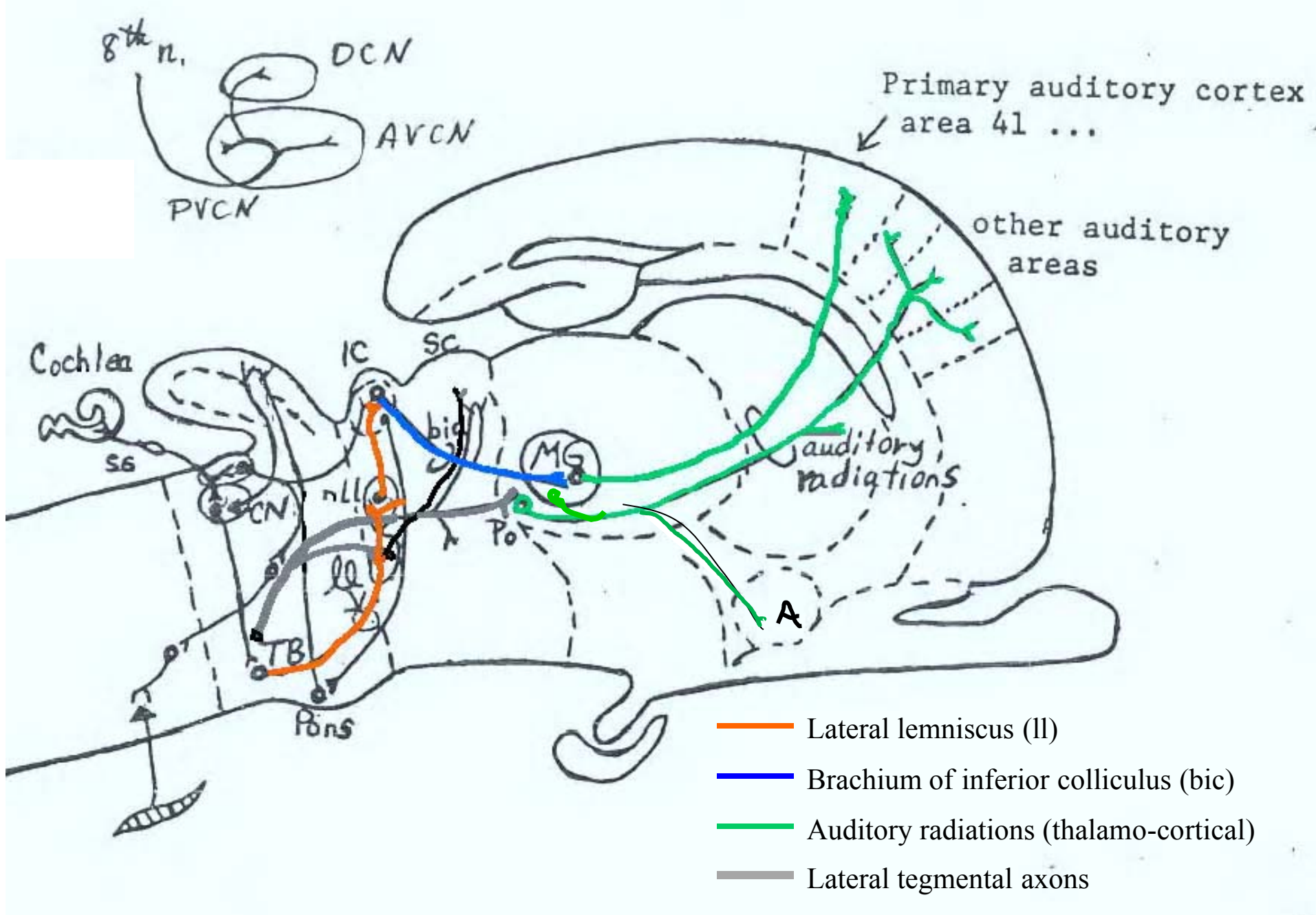
Hamster brain with hemispheres & Cb removed, seen from right side



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Fig 23-10

Auditory pathways in the mammalian brain

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

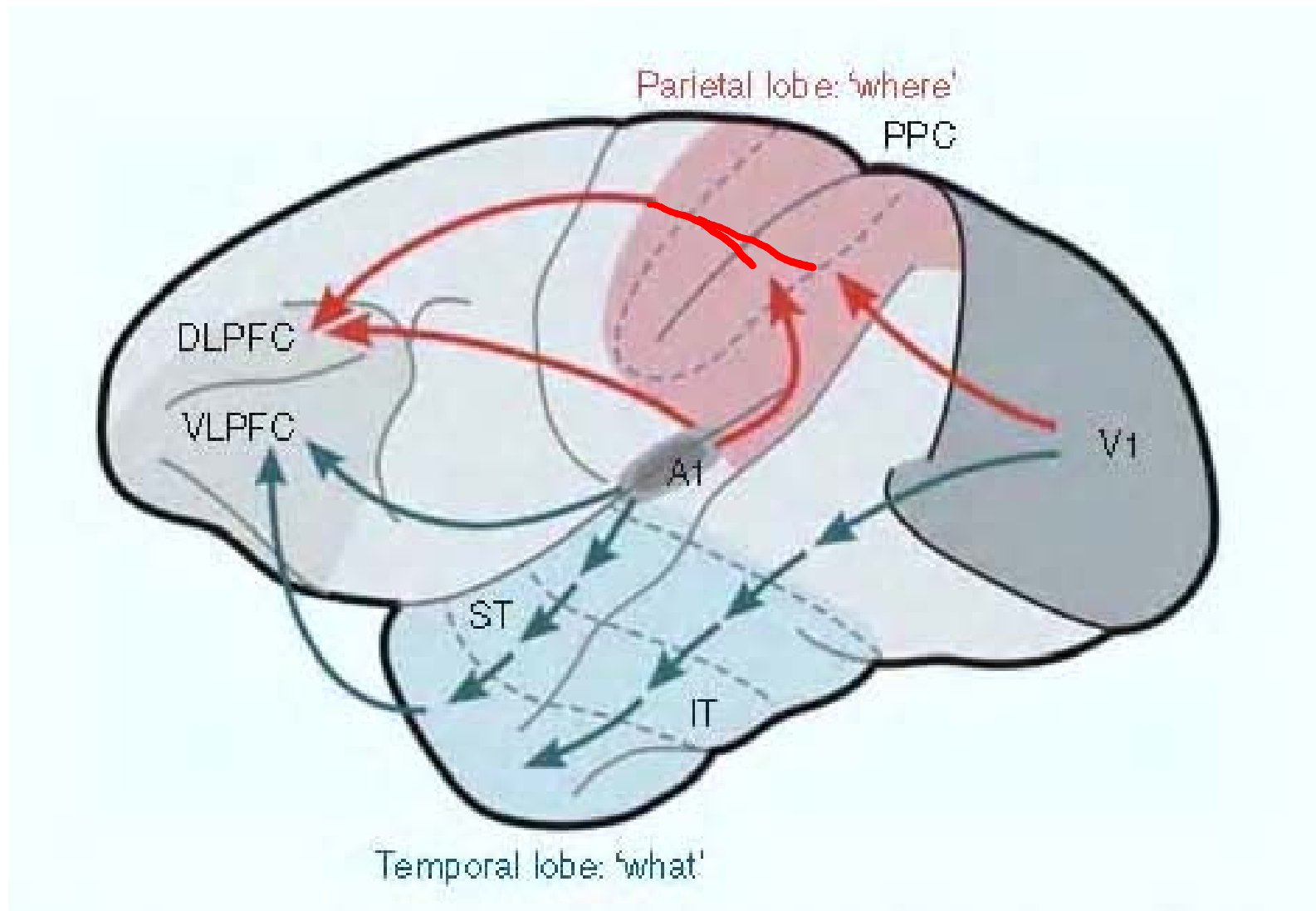
- Experiments with hamster and with cat:
Lesions affect not only visual orienting.
- Ablation causes large defects in orienting
towards sounds as well.

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

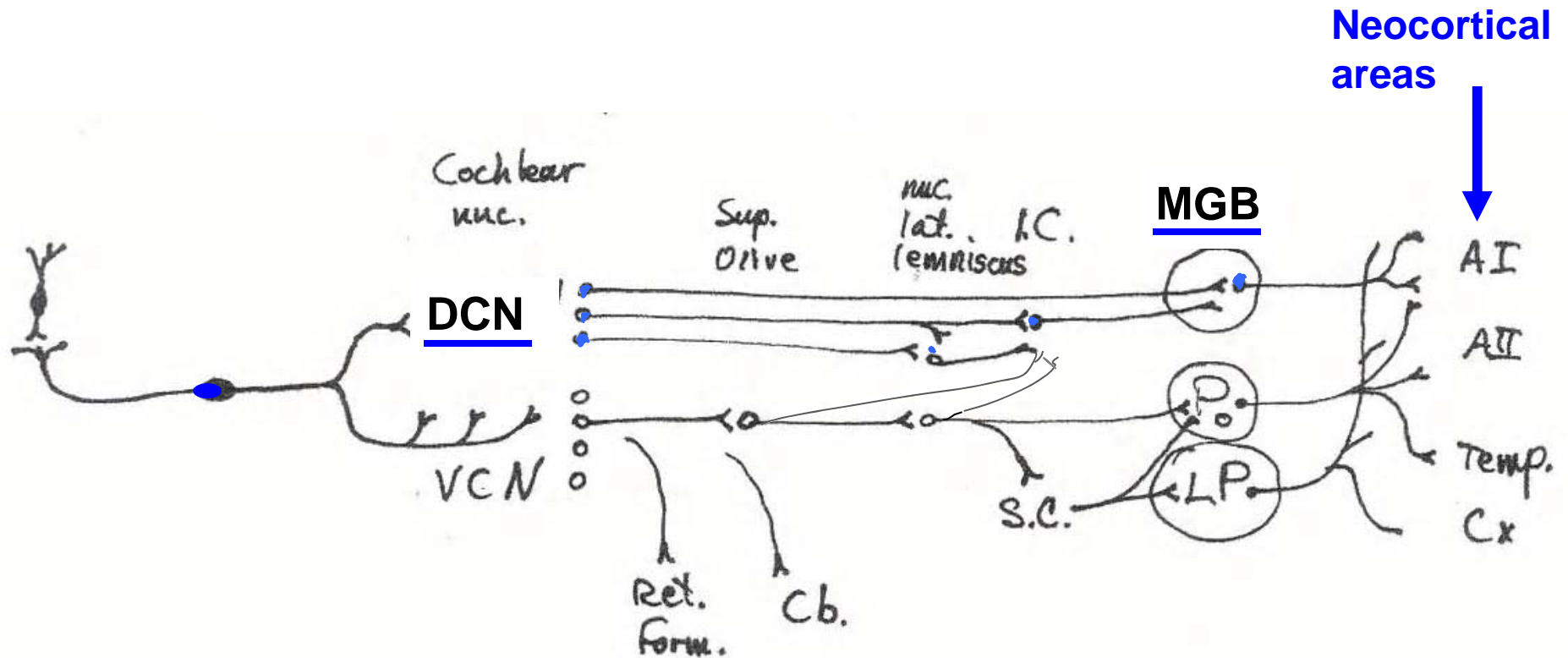
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 Schneider, G. E. *Brain Structure and its Origins: In the Development and in Evolution of Behavior and the Mind*. MIT Press, 2014. ISBN: 9780262026734.

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



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Auditory neocortex in mammals

topics

- Multiple tonotopic maps define ^{a number of} 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

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.

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.

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:
Lee, Charles C., and Jeffery A. Winer. "Connections of Cat Auditory Cortex: I. Thalamocortical System." *Journal of Comparative Neurology* 507, no. 6 (2008): 1879-900.

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

Figure removed due to copyright restrictions.

Model:

Connections for
tuning to upward
frequency
sweeps

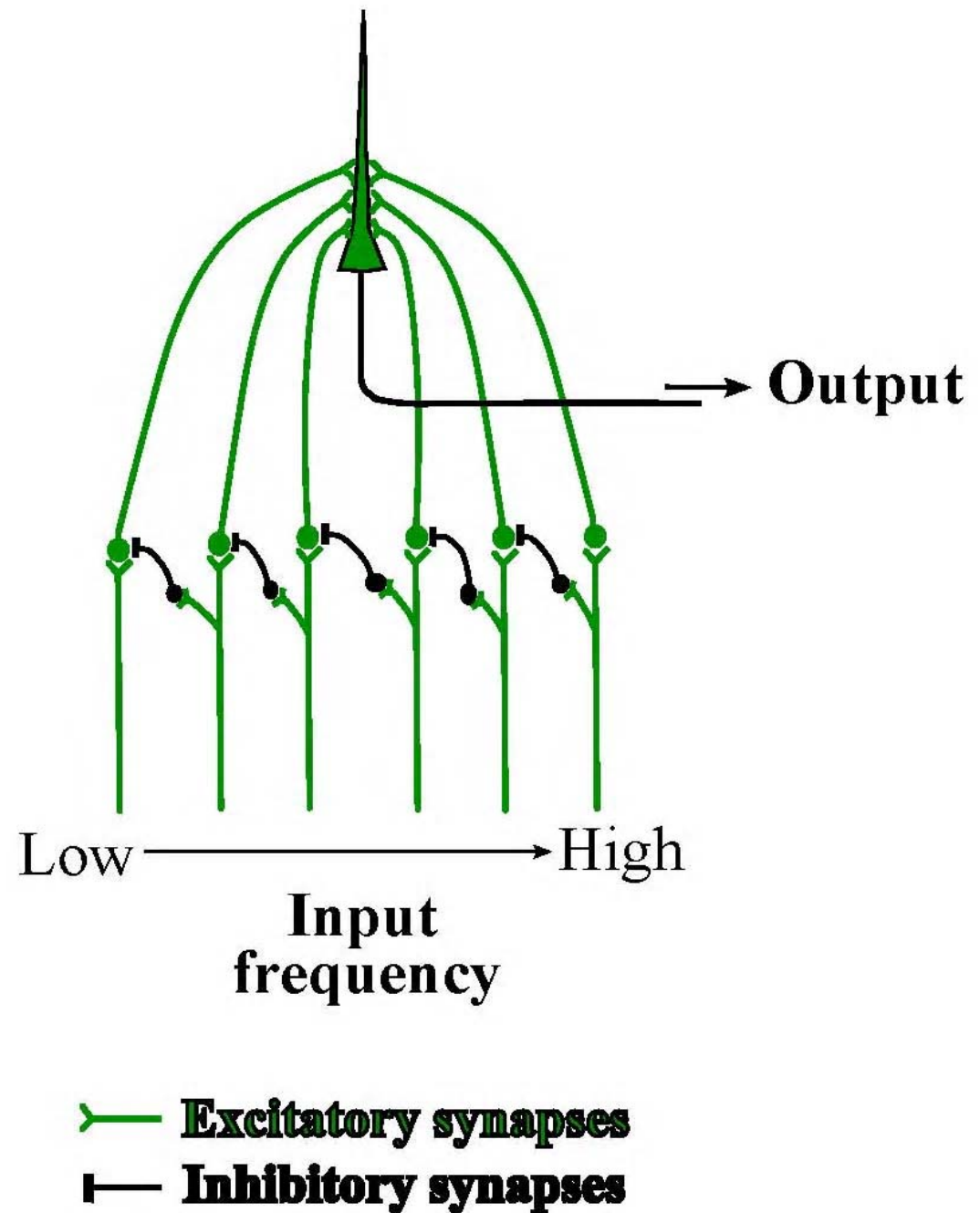


Fig 23-16

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Schneider, G. E. *Brain Structure and its Origins: In the Development and in Evolution of Behavior and the Mind*. MIT Press, 2014. ISBN: 9780262026734.

Ablation of cat auditory cortex

- Frequency and loudness discrimination preserved
- Discrimination of temporal patterns is disturbed or abolished *after partial or complete damage*
- 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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 - **Speech**

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9.14 Brain Structure and Its Origins

Spring 2014

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