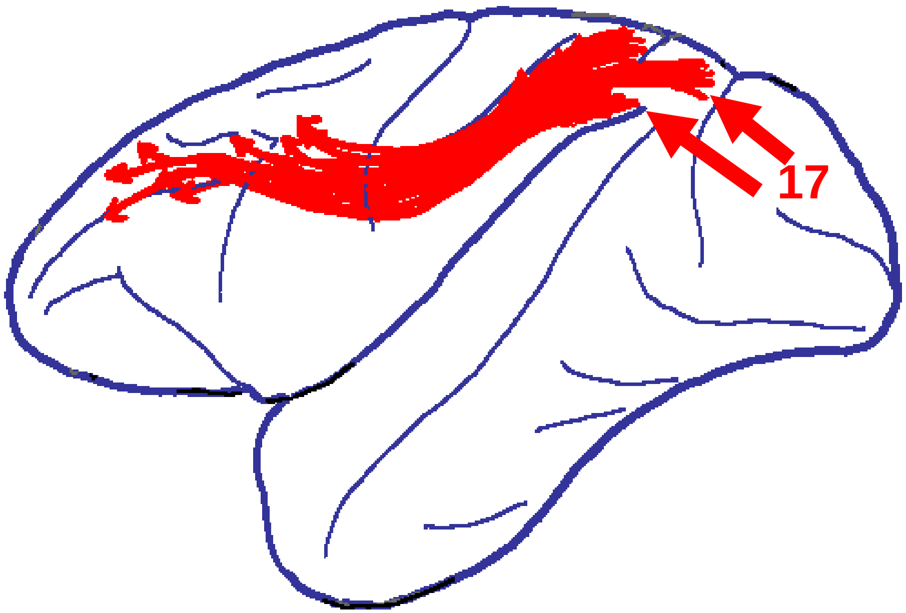
Transcortical connections

- As neocortical area and neuron number increase in evolution, the amount of white matter increases also, at a slightly greater rate.
- Specific long transcortical connections have received special emphasis in neuropsychology because of their importance in understanding functions of the neocortex in humans.

Questions, chapter 22

11) Contrast the functions of the three transcortical pathways, described in chapter 22, from primary visual cortex in primates and probably in other mammals as well. Also describe major anatomical differences in these pathways.

Visual pathway 1: "Where is it?" (object localization)



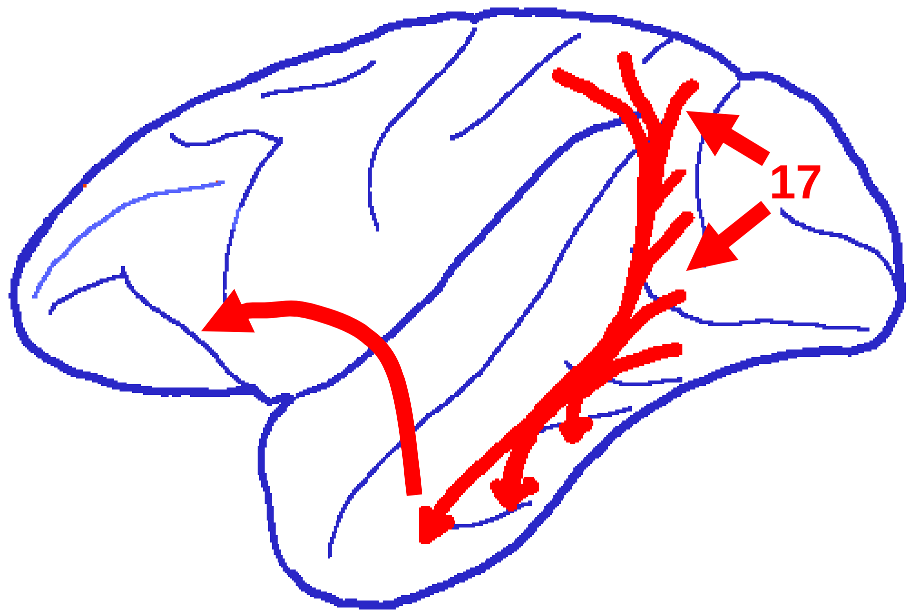
Schneider, G. E. *Brain Structure and its Origins: In the Development and in Evolution of Behavior and the Mind*. MIT Press, 2014. ISBN: 9780262026734.

Transcortical pathways carry information from visual cortex to posterior parietal areas. Information on object location goes from there to premotor and prefrontal cortex.

Fig 22-13

egocentric localization
(w.r.t. head)

Visual pathway 2: "What is it?" (object identification)



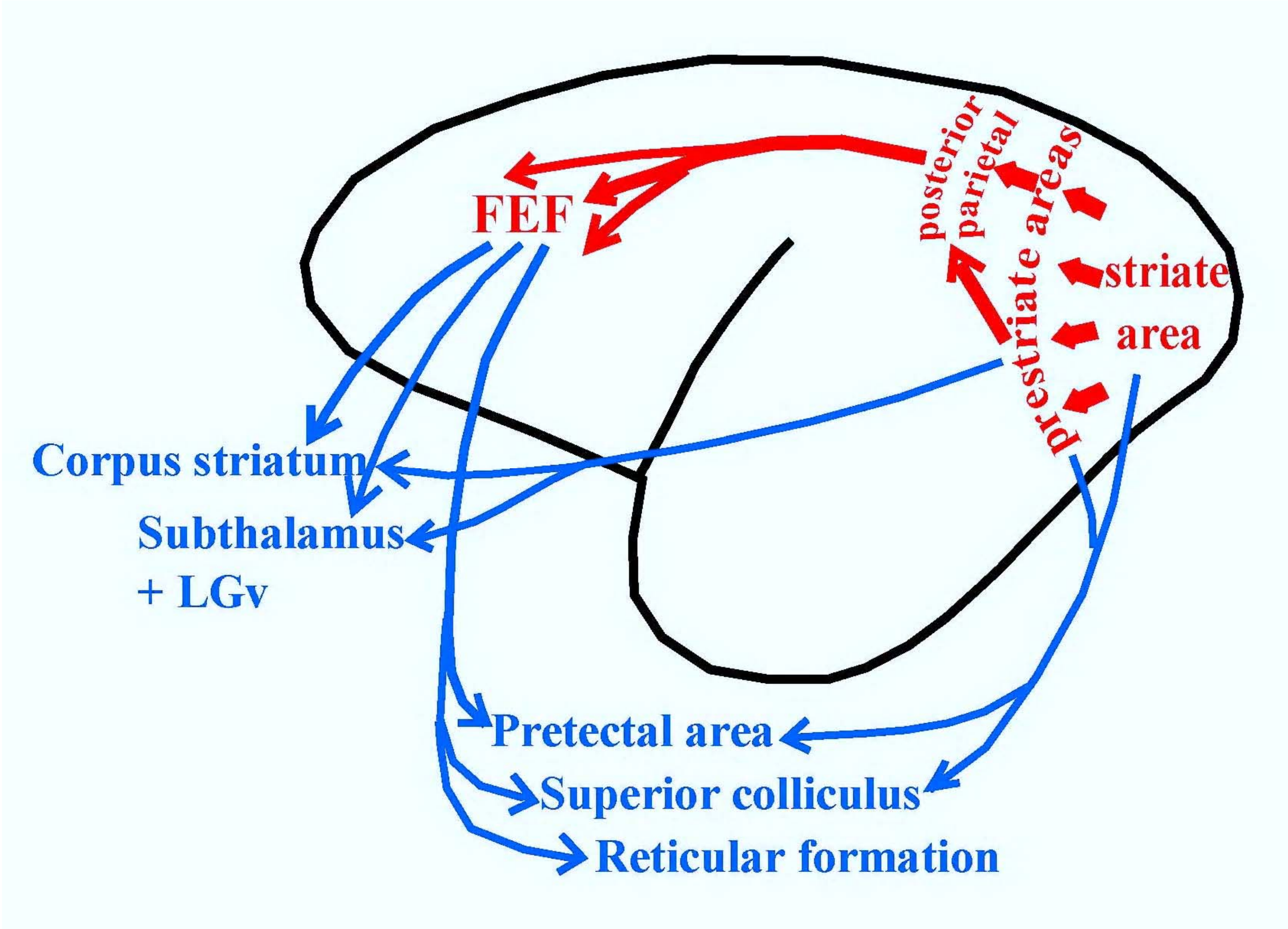
Schneider, G. E. *Brain Structure and its Origins: In the Development and in Evolution of Behavior and the Mind*. MIT Press, 2014. ISBN: 9780262026734.

Transcortical pathways carry information from visual cortex to inferior temporal cortex by way of prestriate and posterior parietal areas. A pathway from the IT cortex leads to ventral prefrontal areas.

Discrimination between objects, faces, etc.

object constancy

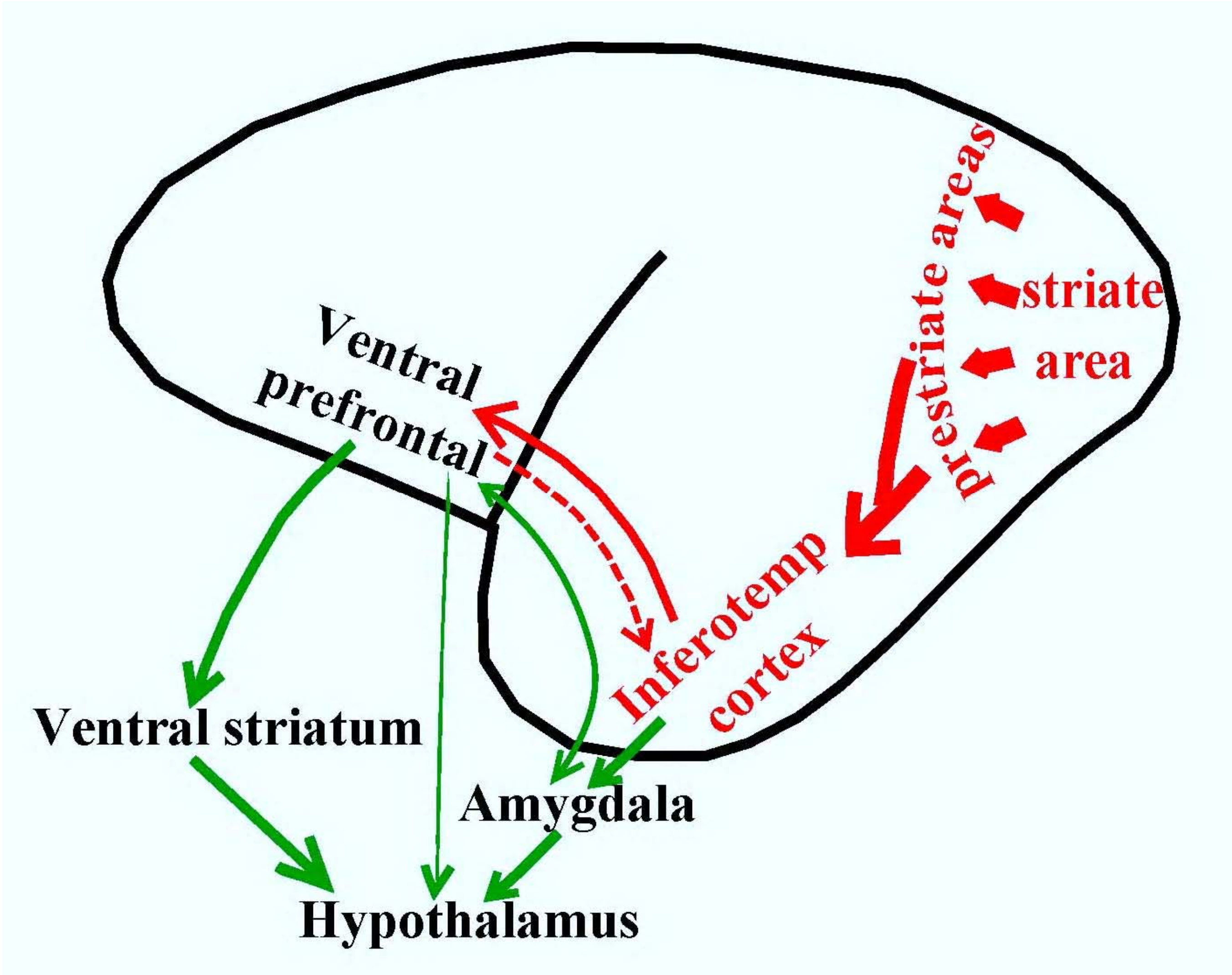
Fig 22-14



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

Some neocortical outputs from structures of the dorsal pathway

Fig 22-15



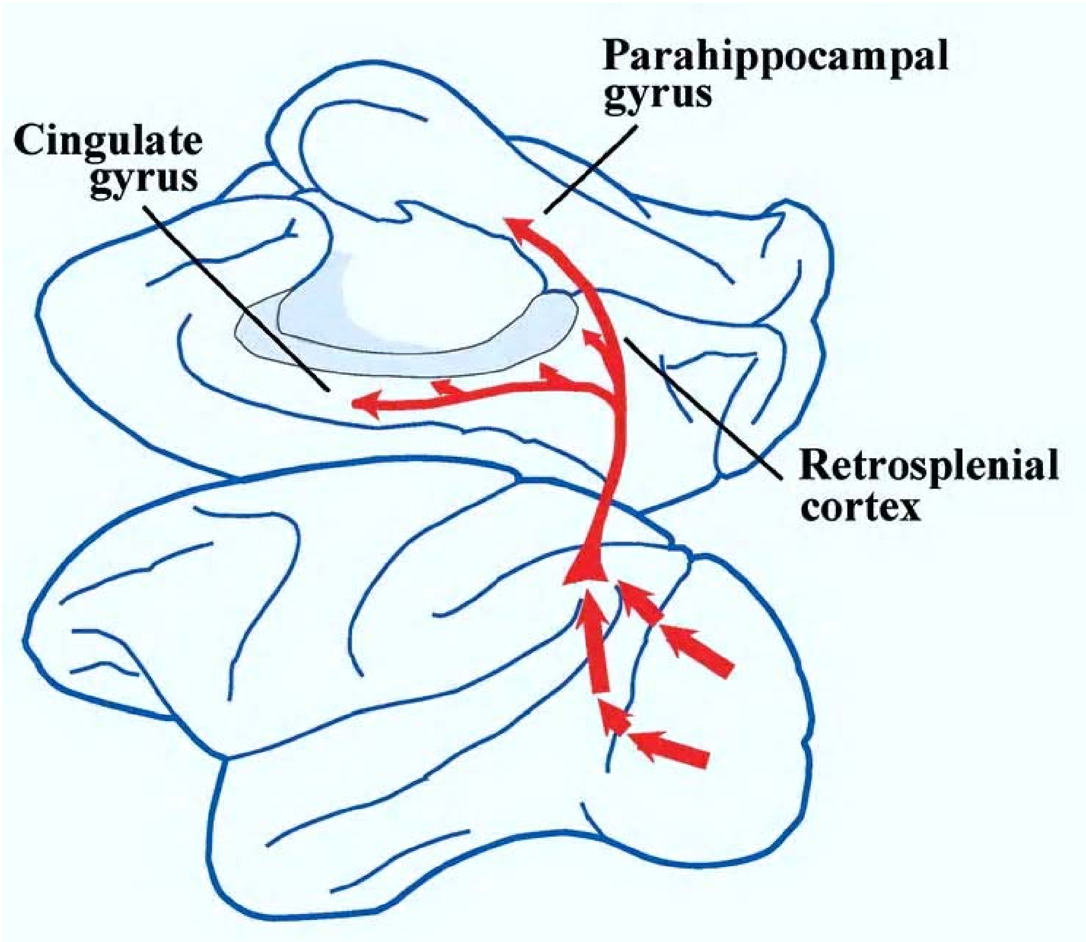
Schneider, G. E. *Brain Structure and its Origins: In the Development and in Evolution of Behavior and the Mind*. MIT Press, 2014. ISBN: 9780262026734.

Outputs from structures of the ventral pathway

Fig 22-16

A third transcortical pathway, carrying visual information to the hippocampal formation

Visual pathway 3: "Where am I?"



Allocentric localization – animal's current location w.r.t visual landmarks

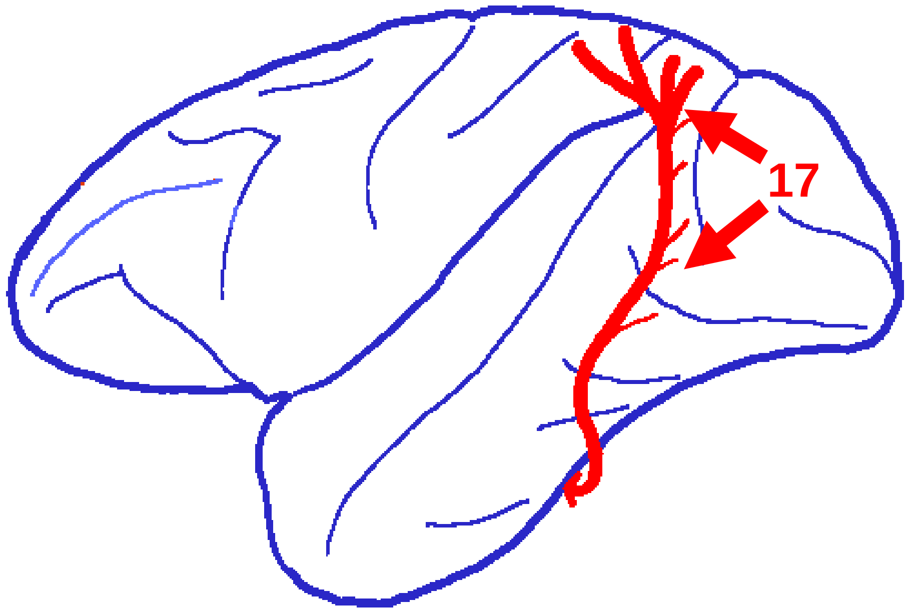
Schneider, G. E. *Brain Structure and its Origins: In the Development and in Evolution of Behavior and the Mind*. MIT Press, 2014. ISBN: 9780262026734.

Transcortical pathways from visual cortex to prestriate and posterior parietal areas to part of the parahippocampal gyrus (area TF; postsubiculum of rat), which projects to the entorhinal area and hippocampus ***Based on figures published by WJH Nauta***

Fig 22-17

Another version of the figure, based on illustrations of Pandya:

Visual pathway 3: "Where am I?"



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

Transcortical pathways from visual cortex to prestriate and posterior parietal areas to part of the parahippocampal gyrus (area TF; postsubiculum of rat), which projects to the entorhinal area and hippocampus

Fig 22-17

Supplementary slides: theoretical considerations

About the interconnections of multiple representations of the visual field *(Striedter fig 4.16)*

Figure removed due to copyright restrictions. Please see course textbook or:
Striedter, Georg F. *Principles of Brain Evolution*. Sinauer Associates, 2004. ISBN: 9780878938209.

Neocortical neuron density, number, and connectivity

(Striedter fig. 4.17)

Mammalian brains tend to maintain absolute connectivity rather than proportional connectivity.

Types of connectivity among cell groups such as multiple neocortical areas:

1. **Regular** (absolute; connections only with nearby cells)
2. **"Small world"** architecture (regular plus some randomly placed longer connections)
3. **Random**

Note how separation comes down with randomness.

Note also the quantity of axons required.

(from Striedter p. 249)

Figure removed due to copyright restrictions. Please see course textbook or:
Striedter, Georg F. *Principles of Brain Evolution*. Sinauer Associates, 2004. ISBN: 9780878938209.

Visual cortex is a "small world" network in macaque monkey (also in cat), achieved with minimum axon length.

[30 interconnected areas]

Figure removed due to copyright restrictions. Please see course textbook or:
Striedter, Georg F. *Principles of Brain Evolution*. Sinauer Associates, 2004. ISBN: 9780878938209.

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

Book chapter 23

Auditory system topics

- Class 1
  - Sensory systems of the dorsolateral placodes and their evolution
  - Why did audition evolve as it did?
    - For antipredator & defensive behaviors
    - For special abilities needed for predation (& also for other functions)
  - Cochlear nuclei and connected structures
    - Transduction and initial coding
    - Channels of conduction into the CNS
- Class 2
  - Two functions, two ascending pathways
    - Sound localization
    - Auditory pattern detection
  - Specializations:
    - Echolocation
    - Birdsong
    - Speech

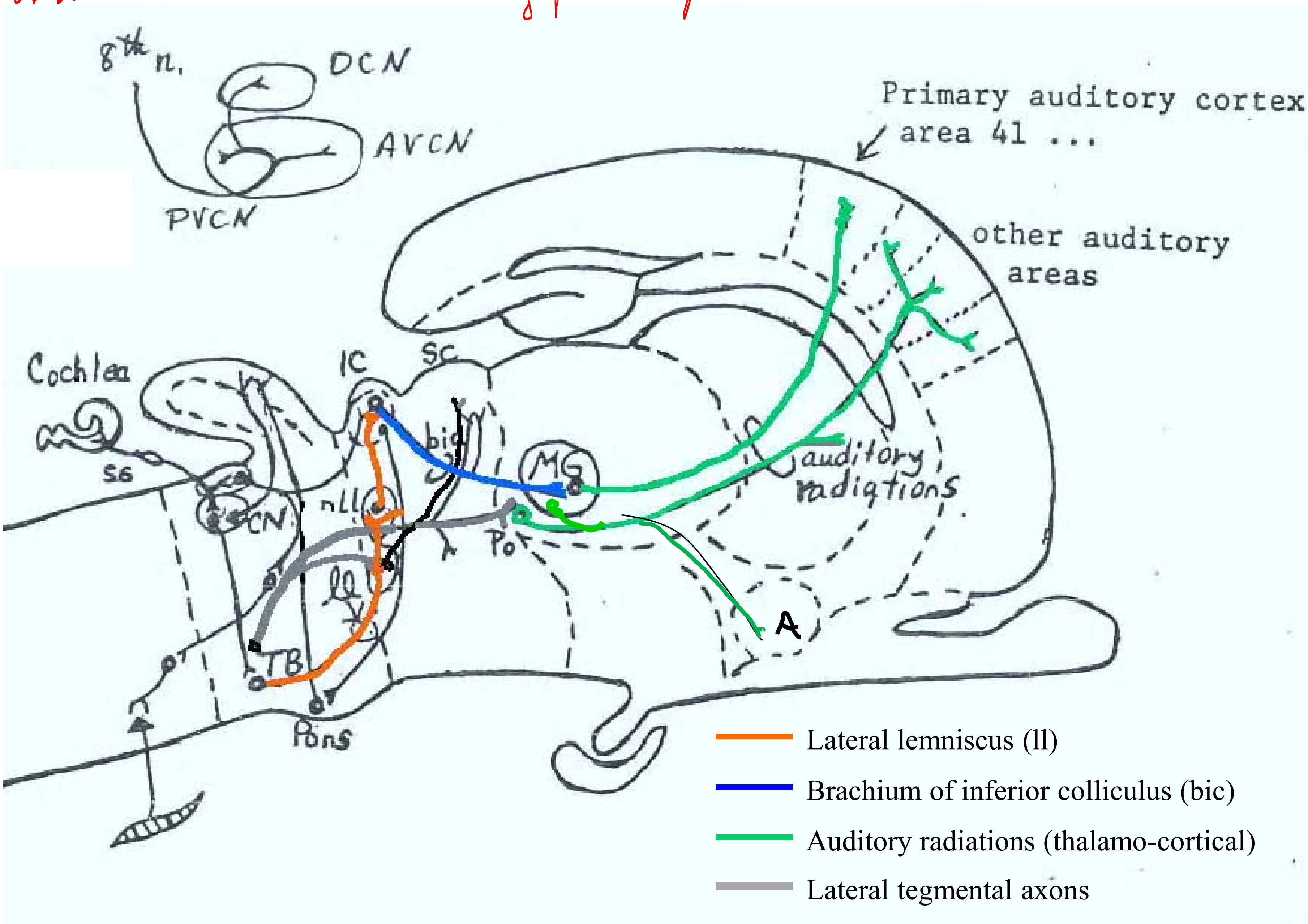
The dorsolateral placodes give rise to multiple sensory cranial nerves

- Sensory categories
  - Mechanosensory lateral line
    - Present in earliest vertebrates; absent in terrestrial vertebrates
  - Electrosensory lateral line
    - Present in fewer species, all aquatic
  - Octaval system: auditory and vestibular
    - Present in all vertebrate groups
- Lateral line receptors are innervated by up to six separate cranial nerves.
- Auditory and vestibular receptors are innervated by two branches of the eighth cranial nerve.

Ascending auditory-system pathways

- The following summary figure of the mammalian brain depicts these pathways.
  - It looks very complicated, and we will leave it until later.
- A simplified summary follows.

First view of central auditory pathways

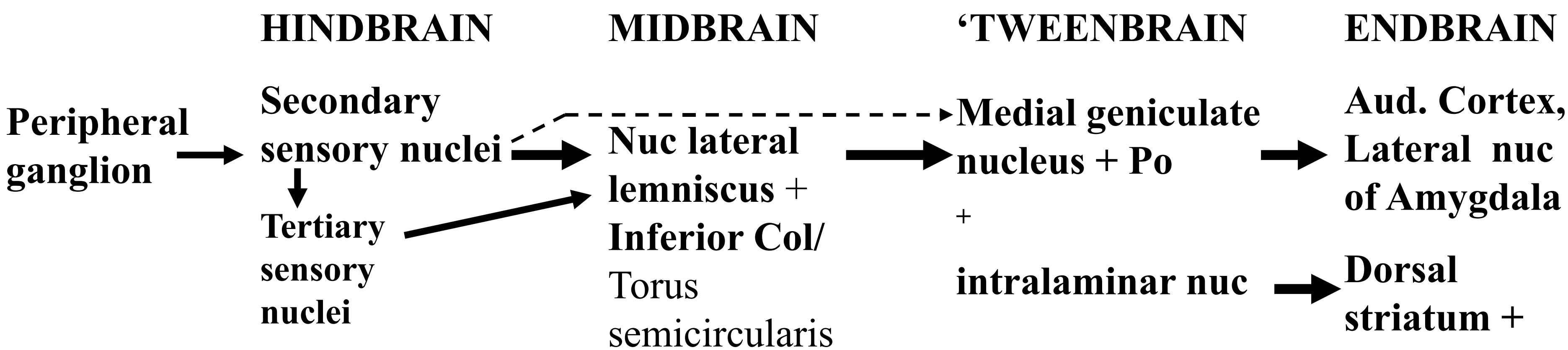


Schneider, G. E. *Brain Structure and its Origins: In the Development and in Evolution of Behavior and the Mind*. MIT Press, 2014. ISBN: 9780262026734.

Fig 23-10

Auditory pathways in the mammalian brain

Simplified diagram



Ascending pathways of auditory systems
simplified

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 23-1

Auditory system

- Sensory systems of the dorsolateral placodes and their evolution
- Why did audition evolve as it did?
  - **For antipredator & defensive behaviors**
  - For predator abilities
- Cochlear nuclei and connected structures
  - Transduction and initial coding
  - Channels of conduction into the CNS
  - Sound localization
- Auditory pattern detection
- Specializations:
  - Echolocation
  - Birdsong
  - Speech

Questions, chapter 23

1) As in the case of the visual system, an important function early in evolution of audition must have been avoidance and escape from predators. Describe an example of a fixed action pattern triggered in a small mammal by sounds of a predator. Freezing, running, specialized actions

2) Two closely related questions on ascending connections of the auditory system:

Instinctive fear/ escape

a) Instinctive aversive behavior in response to loud noise, and learned fear responses to specific sounds, depend on different ascending connections. Contrast the connections.

Learned fear/ escape

b) Fear in response to detection of specific auditory stimuli, even if very low in amplitude, can be learned. Such learning in rodents appears to depend on a pathway from the medial geniculate body of the thalamus direct to a subcortical structure. What structure? (This pathway may be considerably larger in mammals with a relatively smaller neocortex.)

Antipredator and defensive behavior in response to sounds

- Introduction: Critical FAPs
  - Invertebrate example: moth's diving response to bat cries
- Hindbrain circuits for escape behavior
  - Quick escape is critical for survival, hence a high priority in evolution.
  - Fish & tadpole Mauthner cells for rapid escape from sources of vibrations
  - Amphibian hearing can trigger escape behavior, probably *via* same hindbrain mechanisms also used for visually elicited escape behavior
- Mammalian examples of escape & avoidance behavior:
  - Kangaroo rat's escape from rattlesnake attack: sound triggers FAP
  - Hamster escape behavior in response to novel sounds (and similar behavior in many other small mammals): FAPs
  - Rat's unlearned aversion to loud noise depends on midbrain "limbic" area, and not on forebrain. **[Following slides]**
  - Learned fear responses (commonly used in lab studies of learning). **[Following slide]**

unlearned

Aversiveness of noise and role of limbic system

- Auditory intensity thresholds are very difficult to affect permanently by CNS lesions, including ablation of the inferior colliculus or of the entire auditory cortex.
- Study of rats trained to press a lever to turn off aversive noise found evidence for the importance of midbrain's Central Gray Area. (Next 3 slides)

Study of rats trained to press a lever to turn off aversive noise

- No loss of this function after lesions of entire inferior colliculus.
- No loss if ablation of superior colliculus is added.
- These rats can still discriminate different intensities of sound in a test of bar pressing for food.
- However, if lesion includes the ventral part of the **midbrain CGA (central gray area)** and adjacent reticular formation: then there is a loss of noise aversion with preservation of auditory thresholds.

The area is involved in pain perception and responses.

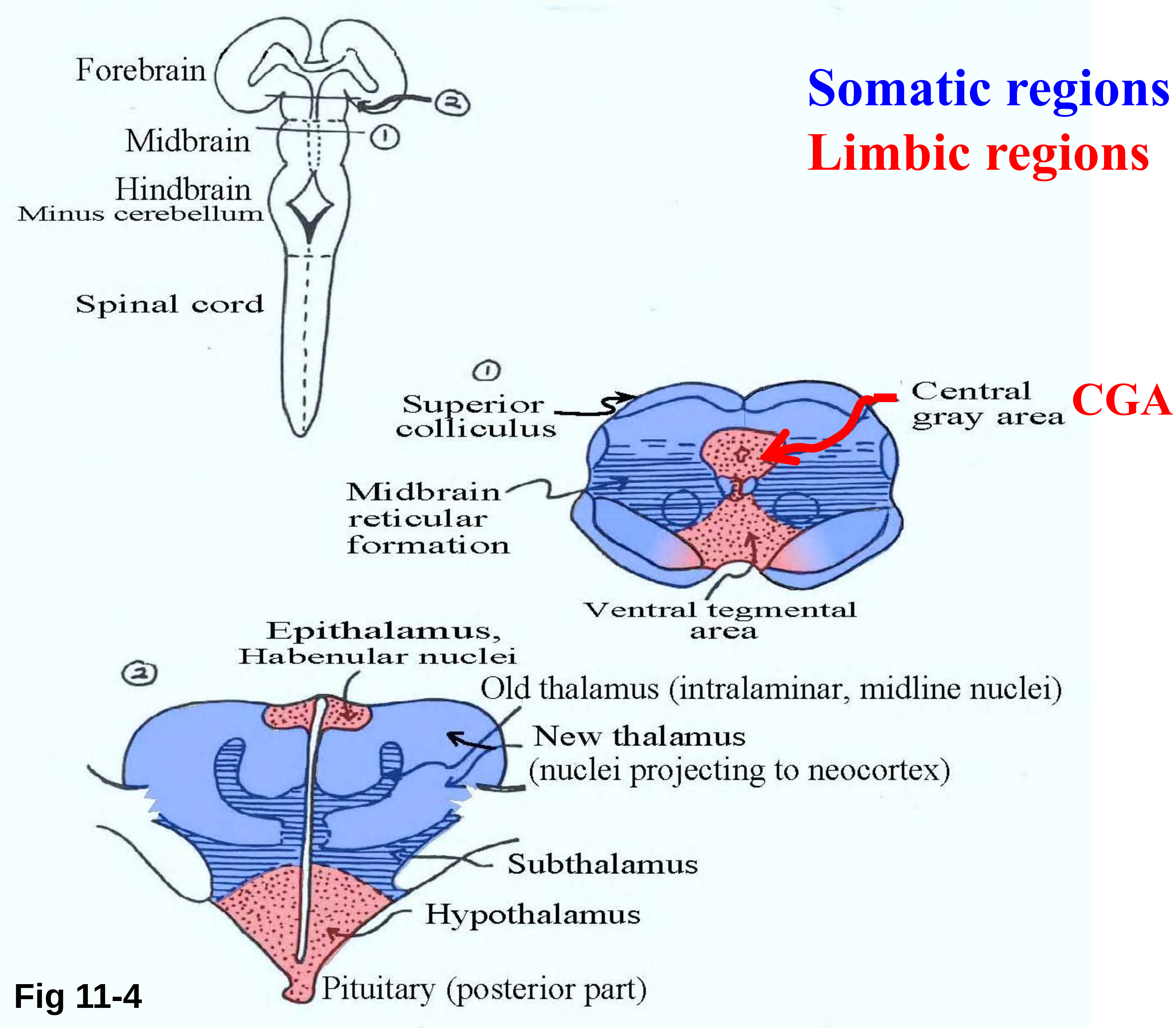
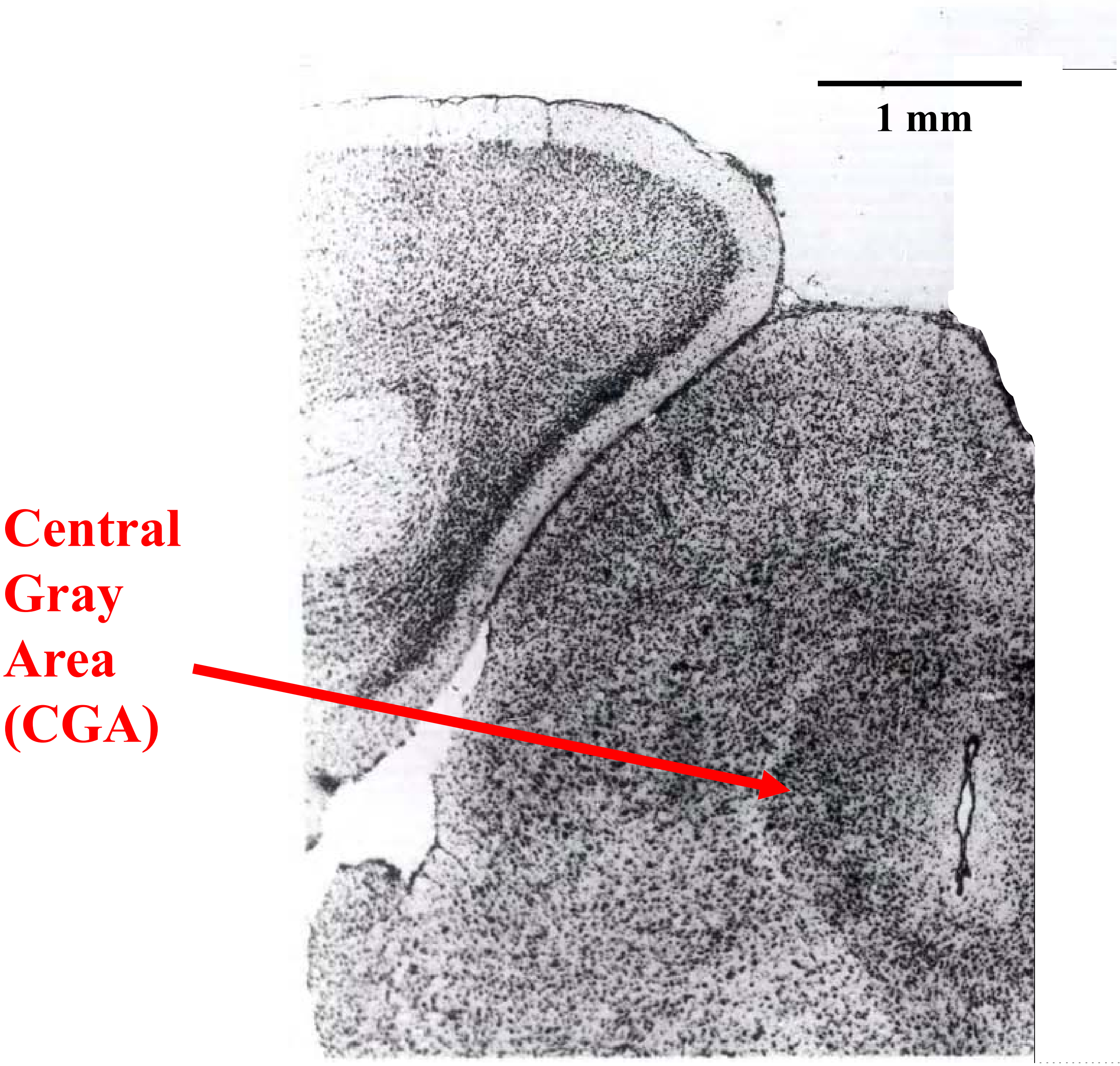


Fig 11-4

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

Hamster Midbrain (left half)



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

Antipredator and defensive behavior

- ✓ Introduction: Moths' diving response to bat cries
- ✓ Hindbrain circuits for escape behavior
  - Fish & tadpole Mauthner cells for rapid escape from sources of vibrations
  - Amphibian hearing can trigger escape behavior, probably *via* same hindbrain mechanisms also used for visually elicited escape behavior
- ✓ Mammalian examples:
  - Hamster escape behavior in response to novel sounds (and similar behavior in many other small mammals)
  - Rat's aversion to loud noise depends on midbrain "limbic" area, and not on forebrain.
  - **Learned fear responses** (commonly used in lab studies of learning): **ROLE OF AMYGDALA, which projects to CGA**
    - **Pathway to amygdala**, in the limbic endbrain: Critical for learned fear responses to sounds (experiments by LeDoux et al., and by Weinberger et al.)
    - **Following slide: Pathways from auditory thalamus to endbrain—auditory neocortex and amygdala**

Neuroanatomical experiments: MGB projects to lateral amygdala and to neocortex.

Figure removed due to copyright restrictions. Please see course textbook or:
Frost, S. B., and B. Masterson. "Origin of Auditory Cortex." In *The Evolutionary Biology of Hearing*. Springer-Verlag, 1992.

Abilities needed especially by predators

1. Need to **identify** prey animals
2. Need to **localize** prey

These two requirements were served by evolution of distinct ascending pathways from hindbrain. We will review the major pathways. (different for the two functions)

These abilities serve other functions as well, and have evolved in prey animals also.

How were these two requirements met?

1. ***Need to identify prey***
2. ***Need to localize prey***

1. Neural equipment for discrimination of differences in sound frequency led to brain circuits for detection of sound patterns.
2. Distinct auditory cues for spatial localization led to neural apparatus for using these cues.

Other abilities that audition serves: various types of communication

Auditory system

- ✓ Sensory systems of the dorsolateral placodes and their evolution
- ✓ Why did audition evolve as it did?
  - 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
  - Auditory pattern detection
- Specializations:
  - Echolocation
  - Birdsong
  - Speech

Transduction and initial coding

- Transduction of mechanical energy to nerve impulses in 8^{th} nerve
- Frequency coding in topographic maps
- Intensity coding

Questions, chapter 23

3) What transformation of the middle ear apparatus occurred in very early mammals that gave them an advantage in avoiding reptilian predators? What did the evolution of these changes accomplish for auditory function?

Transduction of mechanical energy to nerve impulses in 8^{th} nerve

- **The middle ear** efficient
  - The problem of impedance matching: how to transform variations in sound pressure level in external auditory meatus to vibrations in the fluid of the cochlea
  - To achieve better transfer of vibrations to the cochlear fluid, in the mammals there was an evolutionary change in the middle ear bones. (See next slides)
- **The basilar membrane** of the inner ear (later slides)
  - Tiny movements produce shearing forces in hair cells; this leads to action potentials in the axons of the spiral ganglion cells (of the 8^{th} nerve).
  - An additional population of hair cells—the outer hair cells—appeared in mammals.

Evolution of jaw bones into the ossicles of the middle ear in mammals

The changes in the middle ear bones enabled mammals to hear higher frequencies

Figure removed due to copyright restrictions. Please see course textbook or:
Dooling, R. J. "Behavior and Psychophysics of Hearing in Birds." In *Comparative Studies of Hearing in Vertebrates*. Springer-Verlag, 1980.

Fig 23-6 **Absolute threshold curves showing auditory sensitivity in a turtle and two mammals compared with a median curve for birds**

Human Ear

Image by MIT OpenCourseWare.

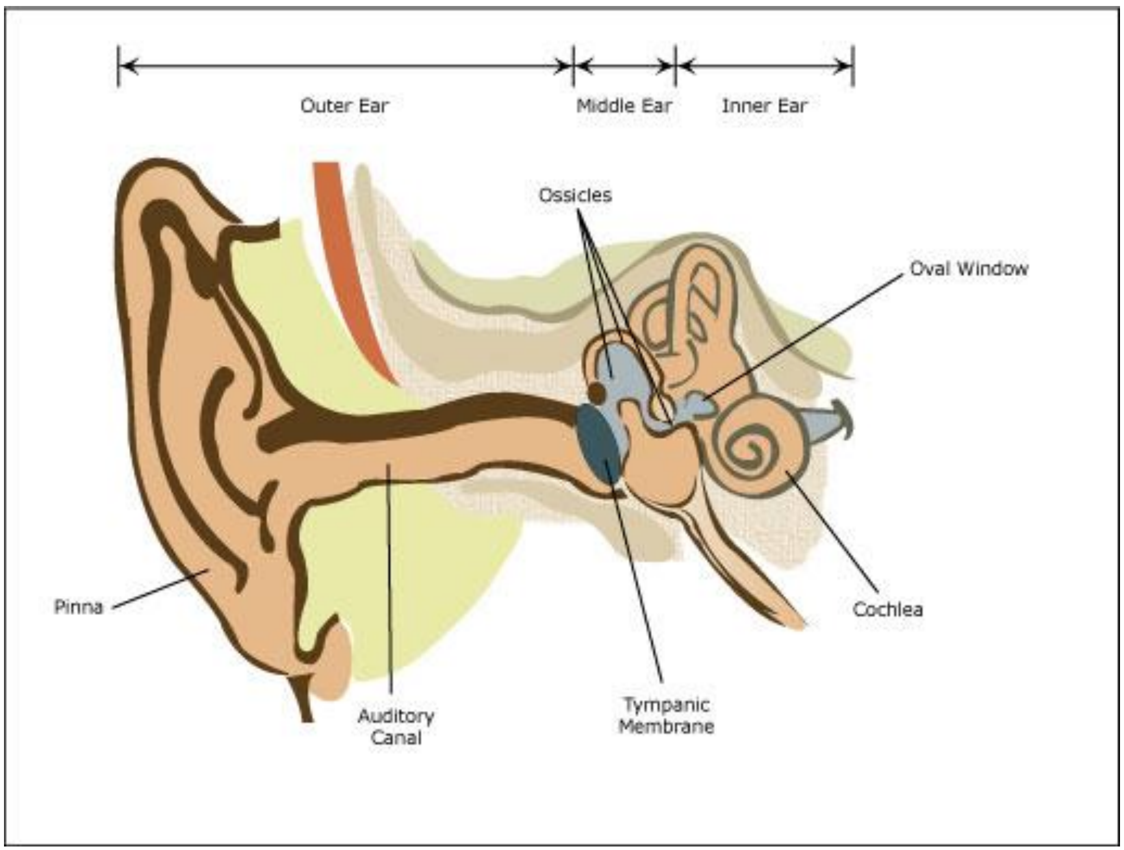
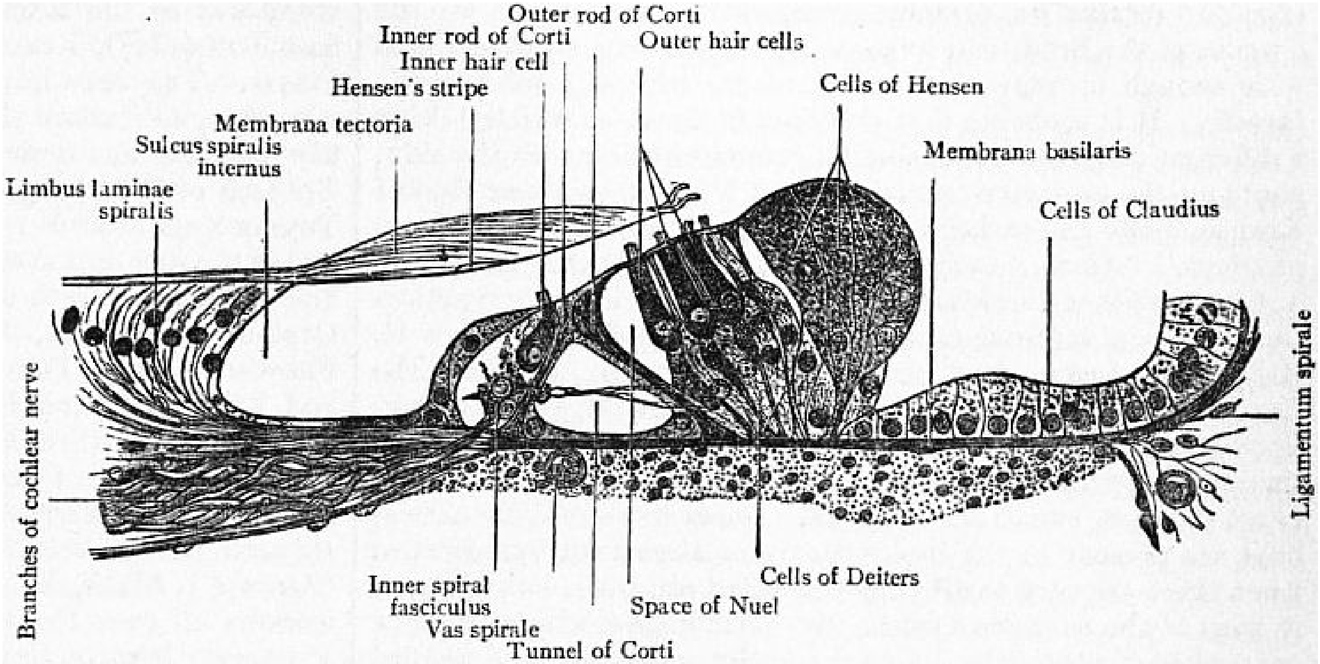


Image by MIT OpenCourseWare. After Figure 11.3 in: Bear, Mark F., Barry W.Connors, and Michael A. Paradiso. *Neuroscience: Exploring the Brain*. 2nd ed. Lippincott Williams & Wilkins, 2001. ISBN: 0683305964.



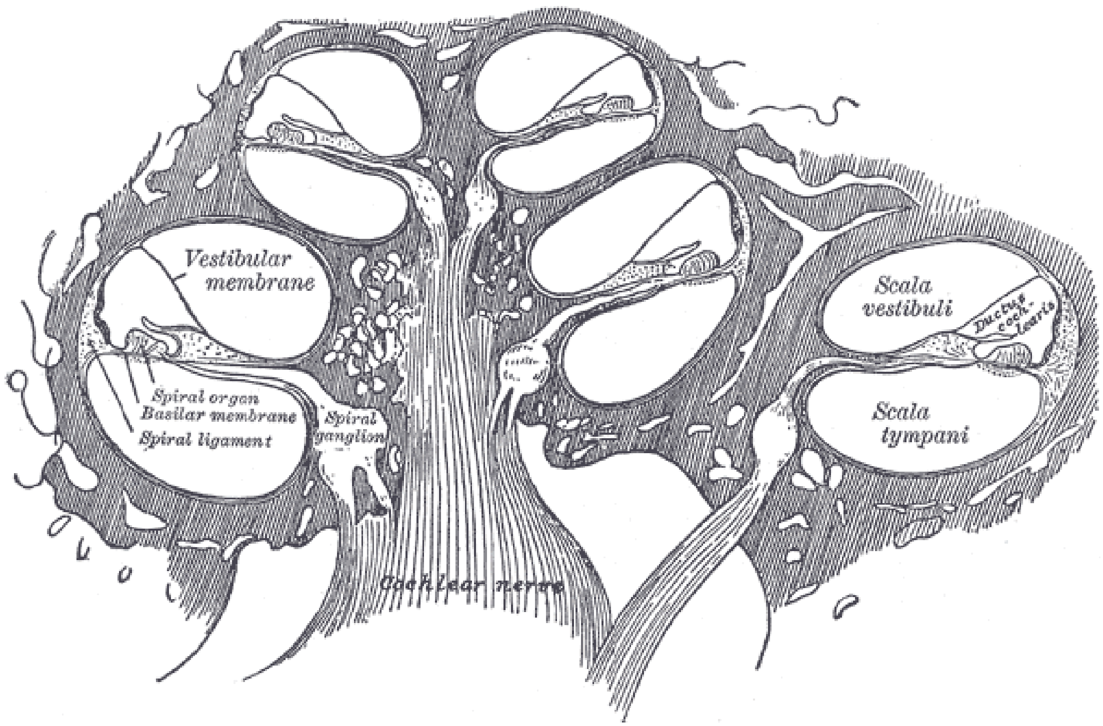


Fig 23-7

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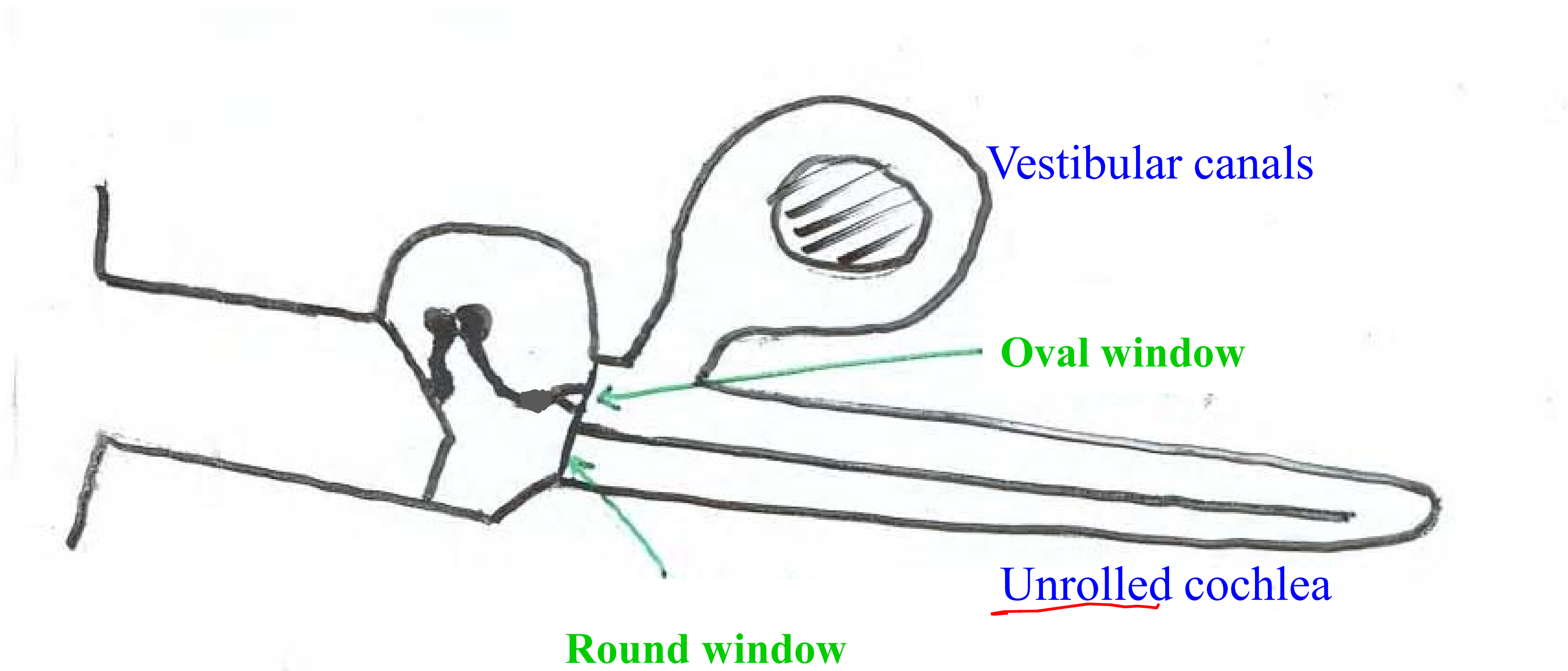
The Organ of Corti

Ear structures, simplified:



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 23-8

Questions, chapter 23

4) How is a “place code” used for encoding of sound frequency information? Describe the apparatus at the level of the periphery and at the level of the secondary sensory neurons.

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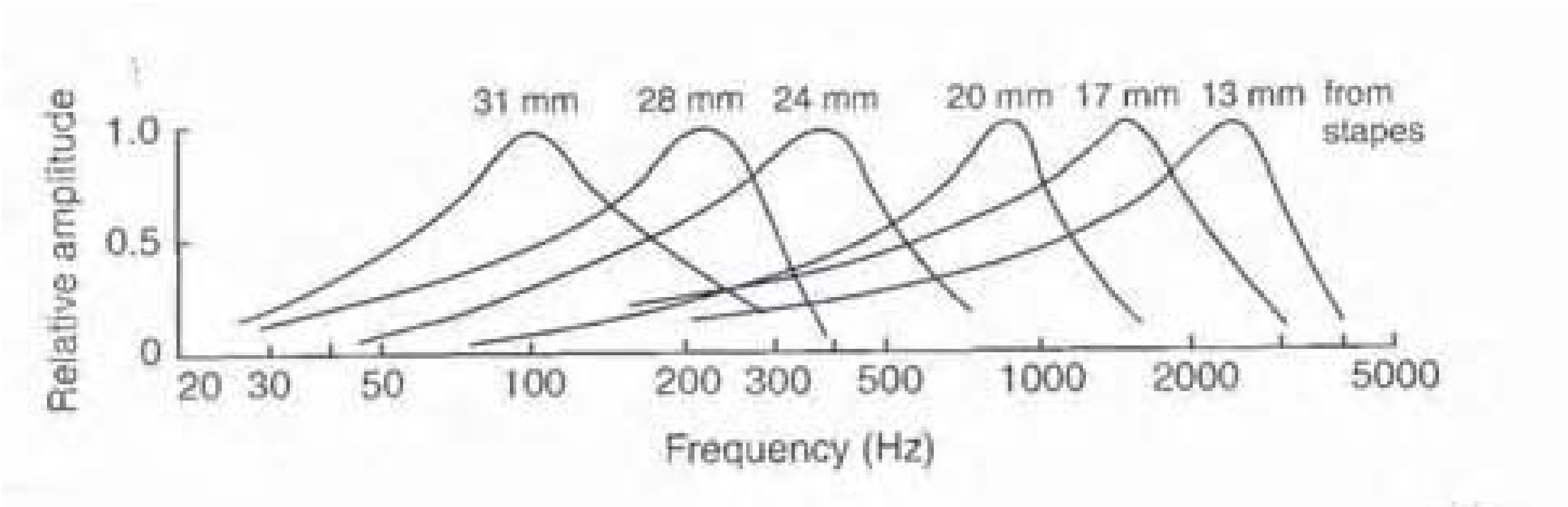


Schneider, G. E. *Brain Structure and its Origins: In the Development and in Evolution of Behavior and the Mind*. MIT Press, 2014. ISBN: 9780262026734.

Basilar membrane dynamics:

Relative amplitude of movement at different positions for tones of different frequencies (data initially obtained by von Bekesy, 1949)

Fig 23-9

Transduction and initial coding

- Transduction of mechanical energy to nerve impulses in 8th nerve
- Frequency coding
- Intensity coding: two major means

Frequency coding

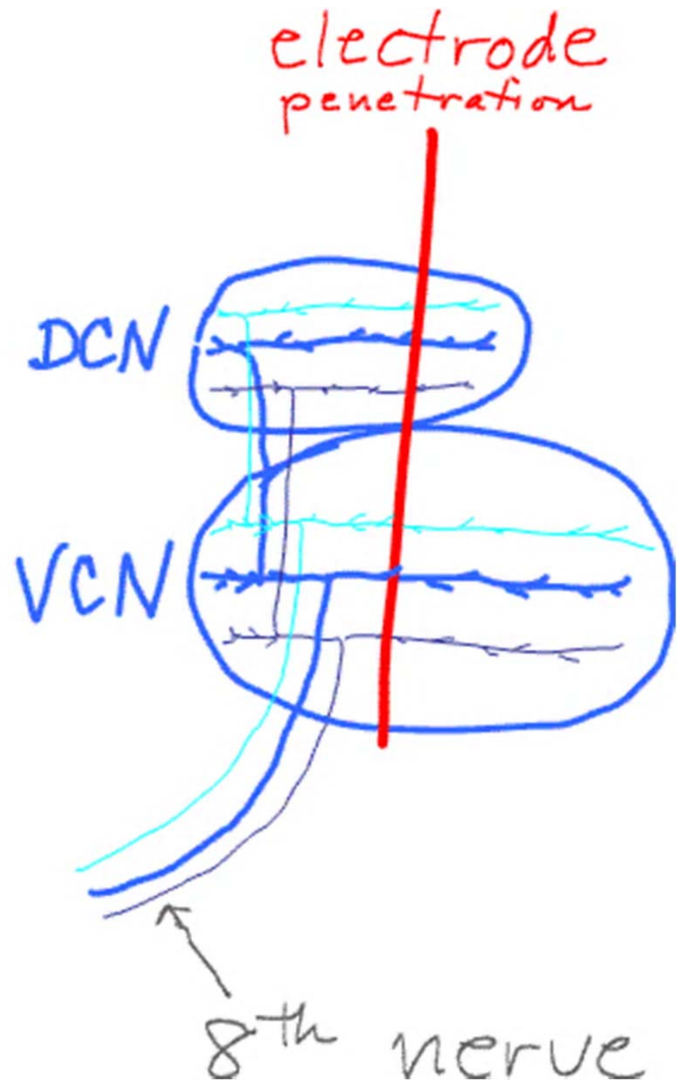
- Standing waves in the basilar membrane
  → a place code for the frequency spectrum in the 8th nerve and the cochlear nuclei

Topographic organization, cochlear nucleus

Figure removed due to copyright restrictions.

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 coclear nucleus

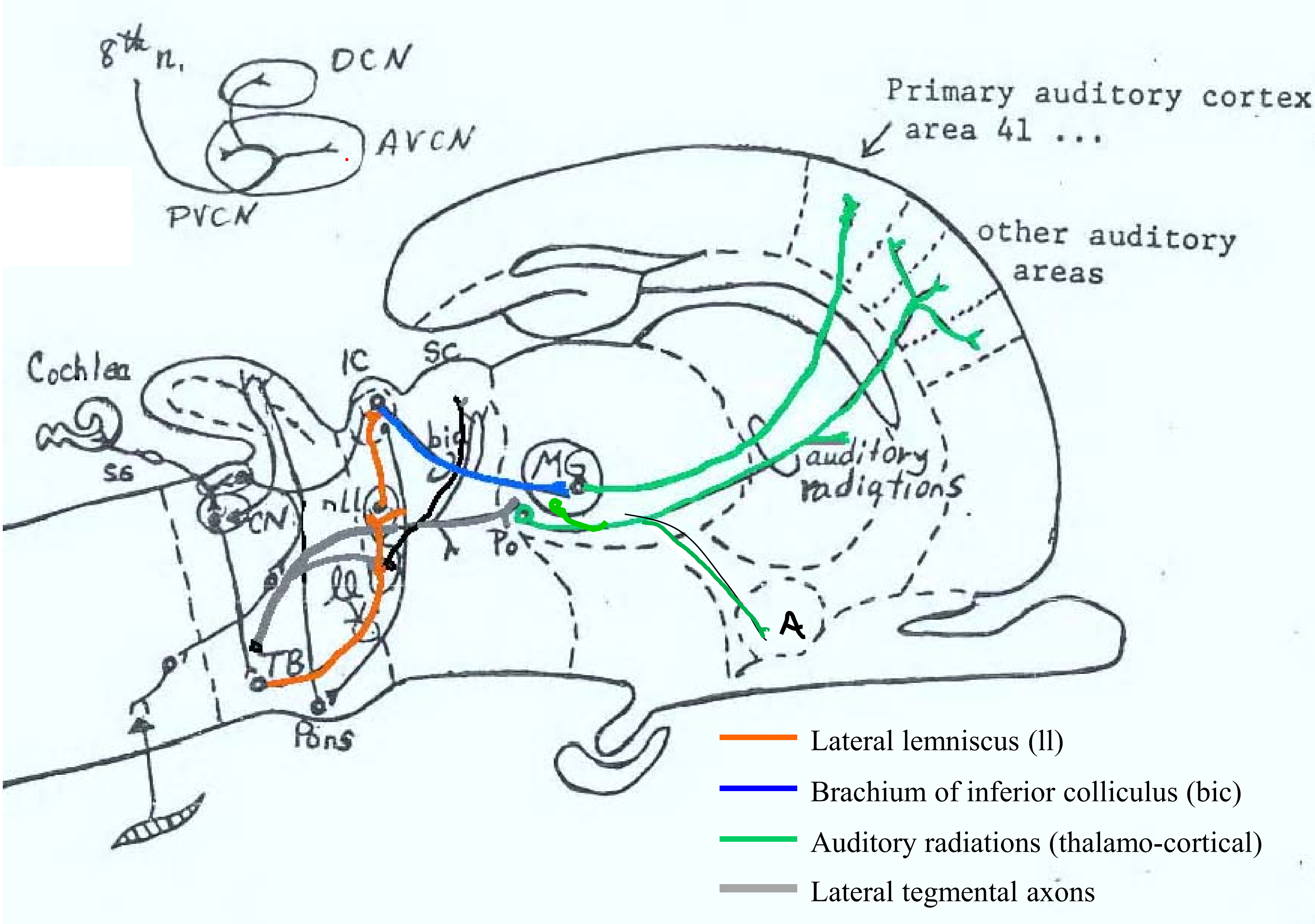


Coding in cochlear nucleus, *continued*

- ✓ How is this precise tonotopic organization achieved?
  - ✓ By topographic mapping in the connections from cochlea to secondary sensory cells in hindbrain (the cochlear nuclei)
- How is intensity coding achieved?
  - – Fibers with different thresholds
  - – Fibers with different best intensities

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



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