A sketch of the central nervous system and its origins

G. E. Schneider 2014

Part 3: Specializations in the evolving CNS; introduction to connection patterns

MIT 9.14 Class 6

Interlude:

Some specializations involving head receptors and brain expansions

with questions on book chapter 6

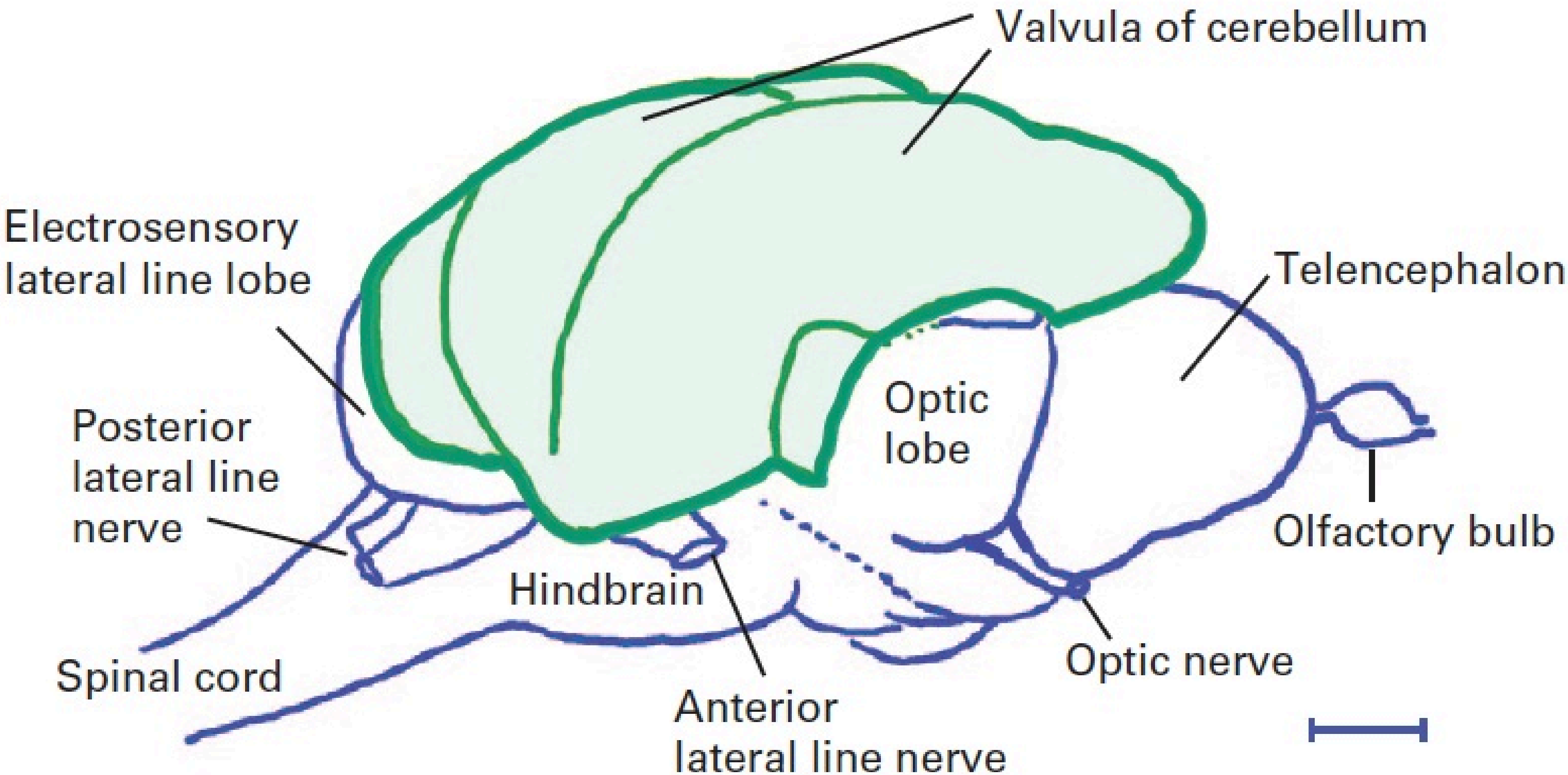
Examples of evolution of non-olfactory sensory specializations (*Most, if not all, led to expansions of brain representations*)

- Electro-reception in some fish → Cerebellar expansion in Mormyrid fish
- Infra-red detectors in the pit vipers → specialized trigeminal nerve (5^{th} cranial nerve) inputs
- Echo-location in bats and porpoises → specialized auditory system
- High visual acuity and learned object recognition in primates → expansion of visual cortical areas
- Vibrissal sensitivity in rodents →specialized somatosensory system

Questions, chapter 6

1. What cranial nerves carry information from electroreceptors in certain fish? Why is electroreception so useful for these fish? Why is their visual sense not adequate?

Lateral line nerves (cranial nerves, up to six of them)



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Questions, chapter 6

2. No placental mammals have electrosensory abilities, but one non-placental mammal does have such an ability. Which one? How are this animal's electroreceptive inputs different from electrosensory fish in the cranial nerves involved?

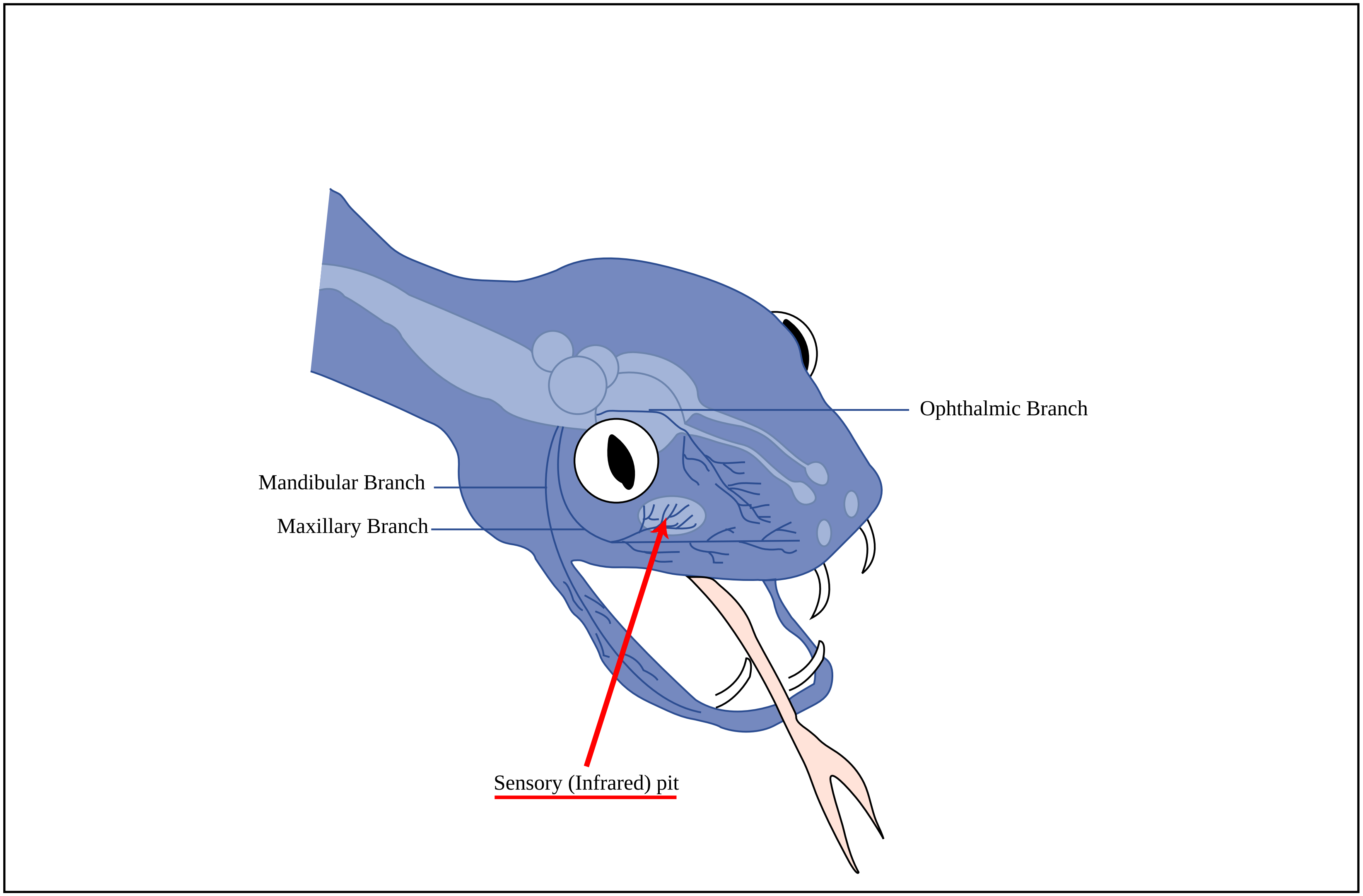
Duck-billed platypus -- a monotreme.

A branch of the trigeminal nerve (the 5th cranial nerve) that innervates the bill.

Questions, chapter 6

3. Another sense that is not highly developed in mammals is infra-red detection. In what animals is this particularly important? Which cranial nerve is involved?

Next



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Rattlesnake trigeminal nerve: innervation of a specialized distance sense

Questions, chapter 6

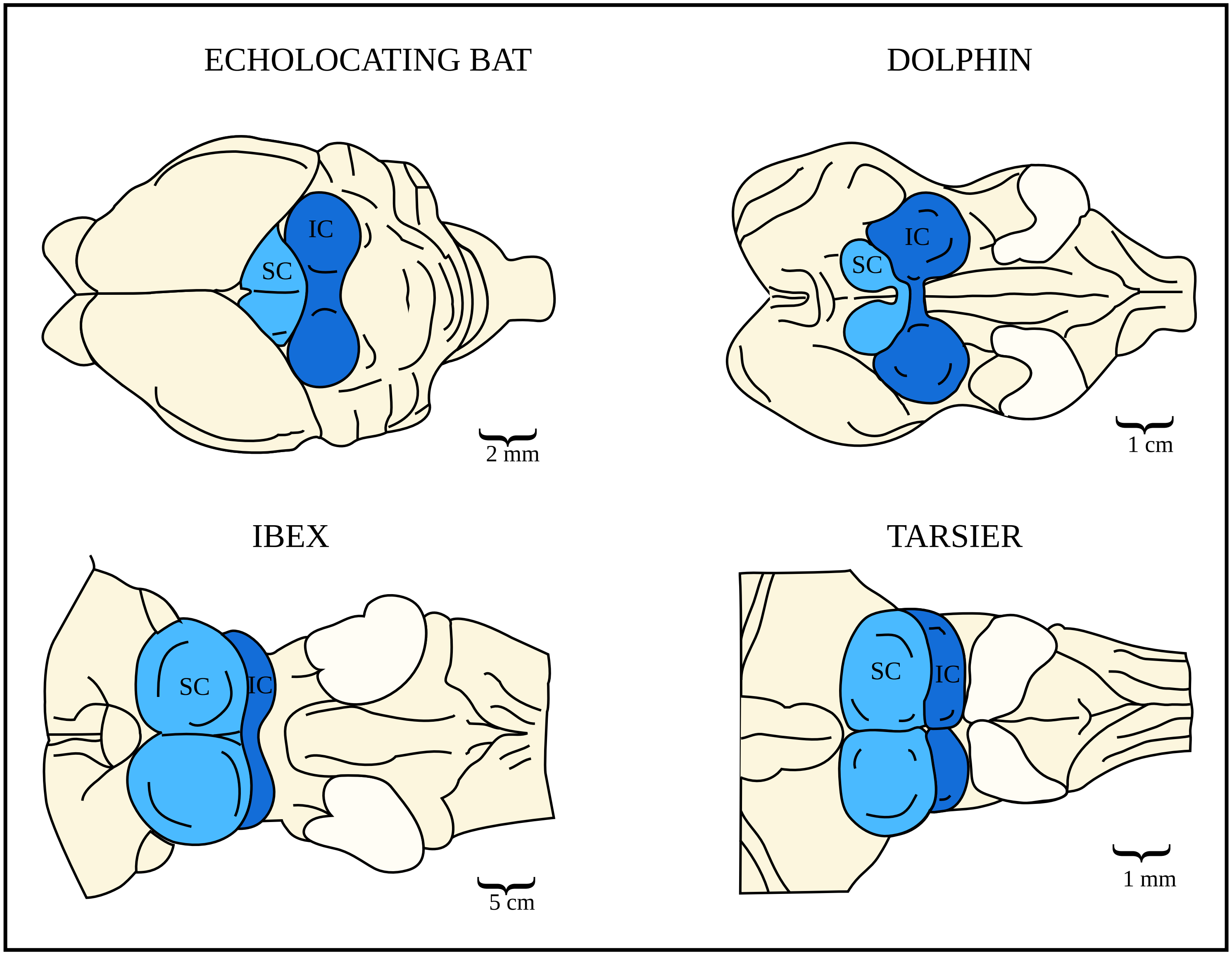
4. Bats are not the only mammal with echolocation ability. In what other mammal is it found? Which cranial nerve is greatly enlarged in that animal?

8th nerve

Next slide

Ibex: a wild goat

Tarsier: a prosimian primate



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From Georg Striedter (2005), p. 166

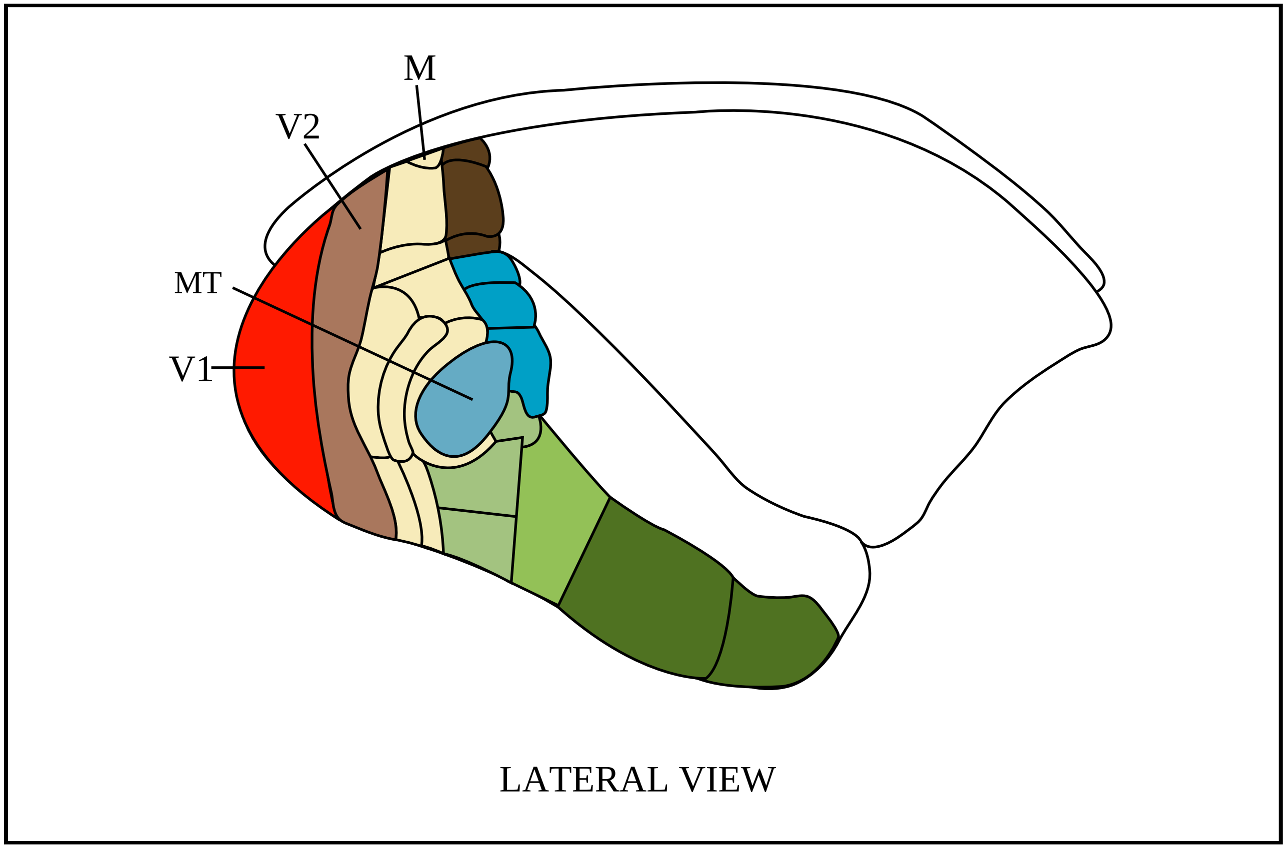
Midbrain roof: the colliculi in four mammals

IC = inferior colliculus. SC = superior colliculus

Questions, chapter 6

5. What is a brain manifestation of the specialization of primates for vision?

Visual areas, owl monkey neocortex



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Questions, chapter 6

6. What is a brain manifestation of the specialization of small rodents for using their vibrissae (whiskers) so well? Describe other somatosensory specializations in some mammals.

Three successive tangential sections of rat hemisphere, Nissl stain, showing the "barrel fields":

Figure removed due to copyright restrictions.
Please see course textbook or:
Woolsey, Thomas A., and Hendrik Van der Loos. "The Structural Organization of Layer IV in the Somatosensory Region (SI) of Mouse Cerebral Cortex: The Description of a Cortical Field Composed of Discrete Cytoarchitectonic Units." *Brain Research* 17, no. 2 (1970): 205-42.

Each barrel represents one whisker

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Please see course textbook.
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Barrel field in 4-day-old rat: axons from thalamus

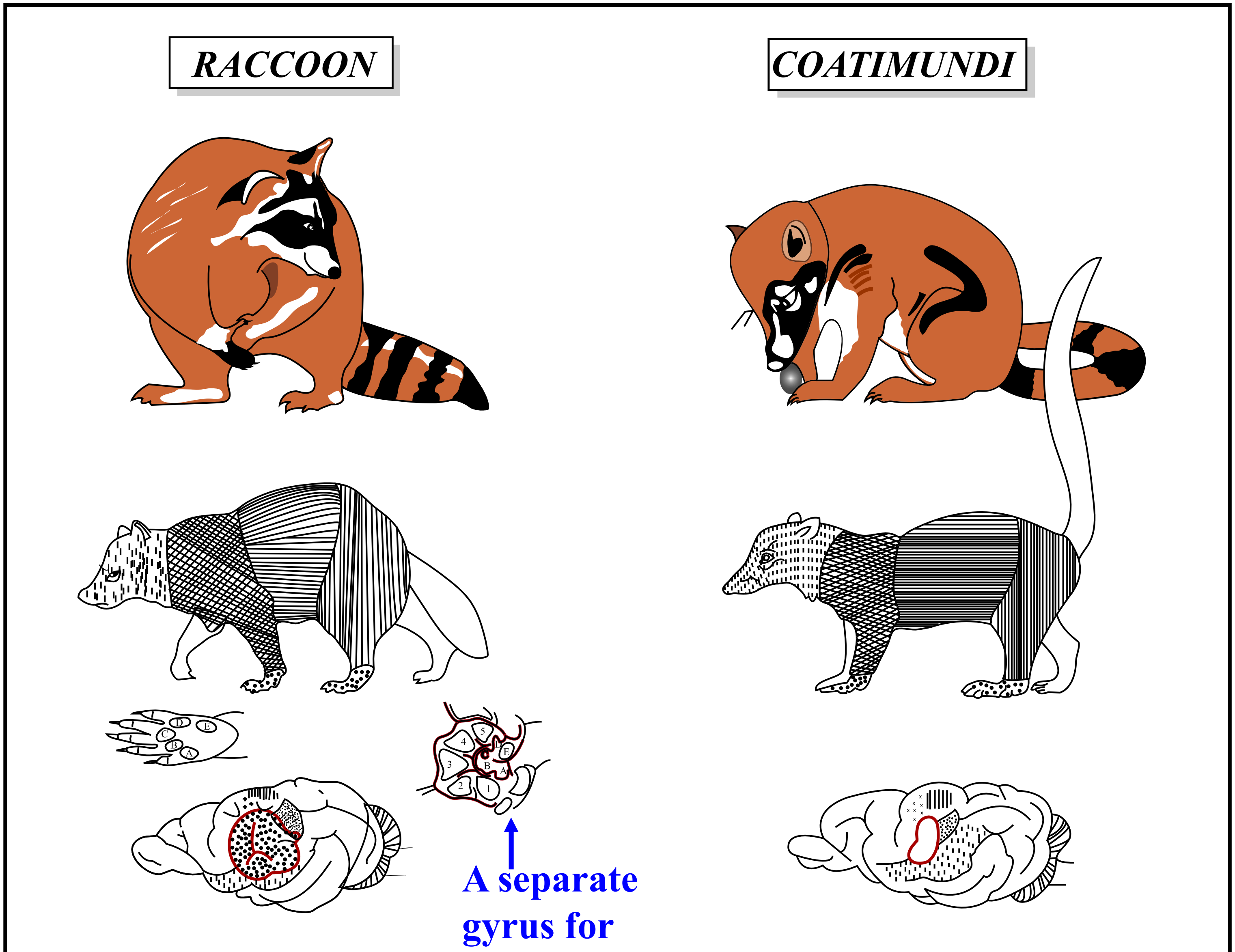
Fig.6-5b

Other somatosensory specializations

- The hand in apes, raccoons and, especially, humans (with high tactile acuity & fine motor control)→ expansions of somatic sensory-motor cortex and of cerebellar hemispheres *[See next slide]*

- Prehensile tail in spider monkey → expanded tail representations in sensory & motor neocortex

Somatosensory neocortex, hand area of two species



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Questions, chapter 6

7. What may be a brain manifestation of the human abilities for complex social interactions?

8. What is a striking specialization (specific function unclear) in the brain of the Echidna (the spiny anteater of Australia)?

Other behavioral specializations

- Elaborate social organization in primates, with planning and problem solving →expanded prefrontal neocortical areas

Brain of an Echidna, the spiny anteater—an Australian monotreme showing an enlarged prefrontal neocortex

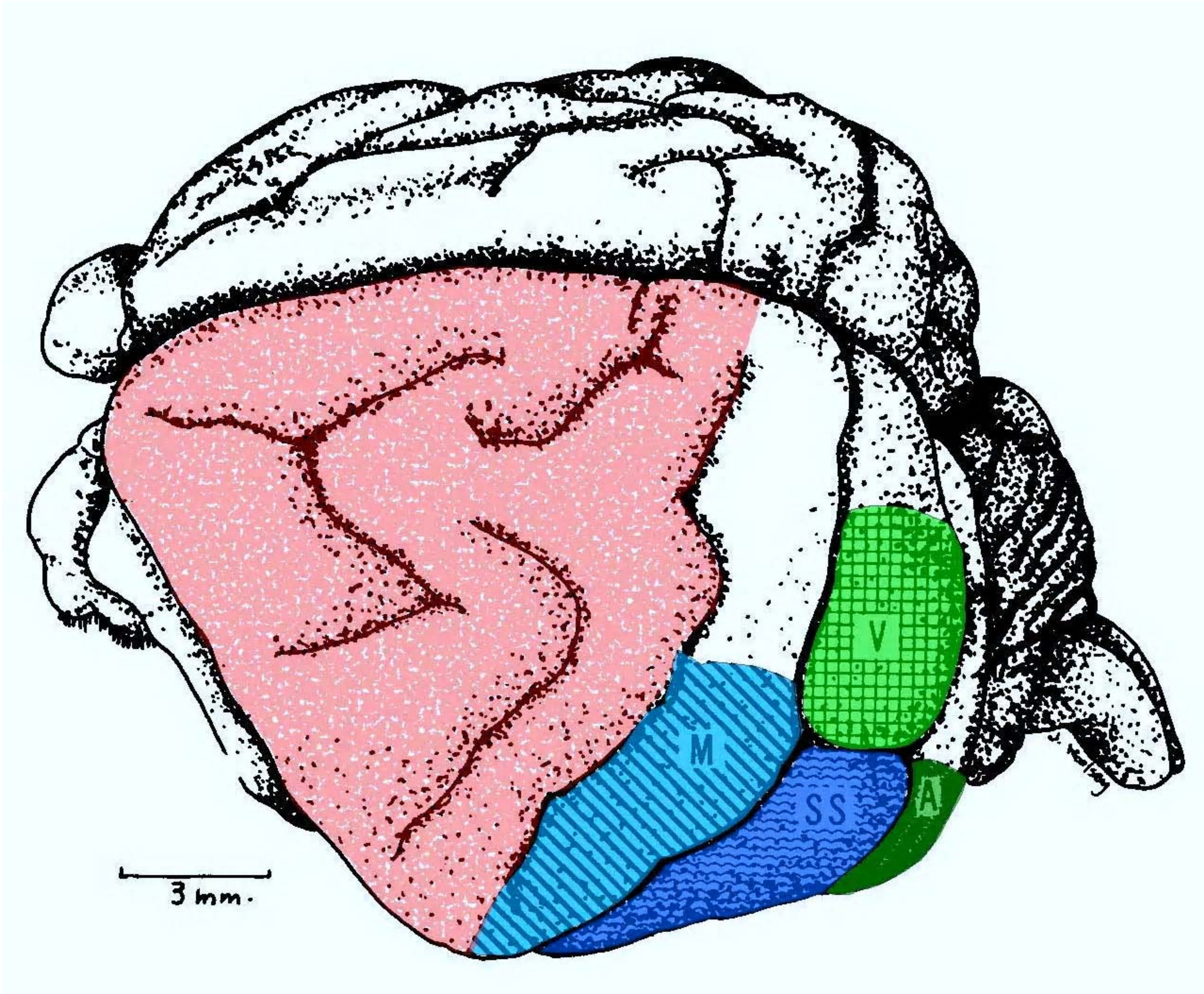

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Fig. 6-7

Questions, chapter 6

9. What other specializations might have noticeable brain manifestations? Try to think of something not mentioned in chapter 6.

Class discussion:

Humans with specially developed abilities may have greater development of certain brain areas. Examples: blind people can have some echolocation abilities; London taxi drivers have unusually large parietal cortical areas -- were they like that from early development, or did these areas enlarge as a result of repeated activity?

Specialized noses: the star-nosed mole; the elephant's trunk

Class session 6 was organized in 2 parts:

1. Some specializations involving head receptors and brain expansions, which correspond with Chapter 6 of the course textbook and were covered in the previous slides.

2. Overview of forebrain structures in vertebrates and an introduction to the neocortex, which correspond with Chapter 7 of the course textbook and are covered in the proceeding slides.

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MIT 9.14 Class 6b

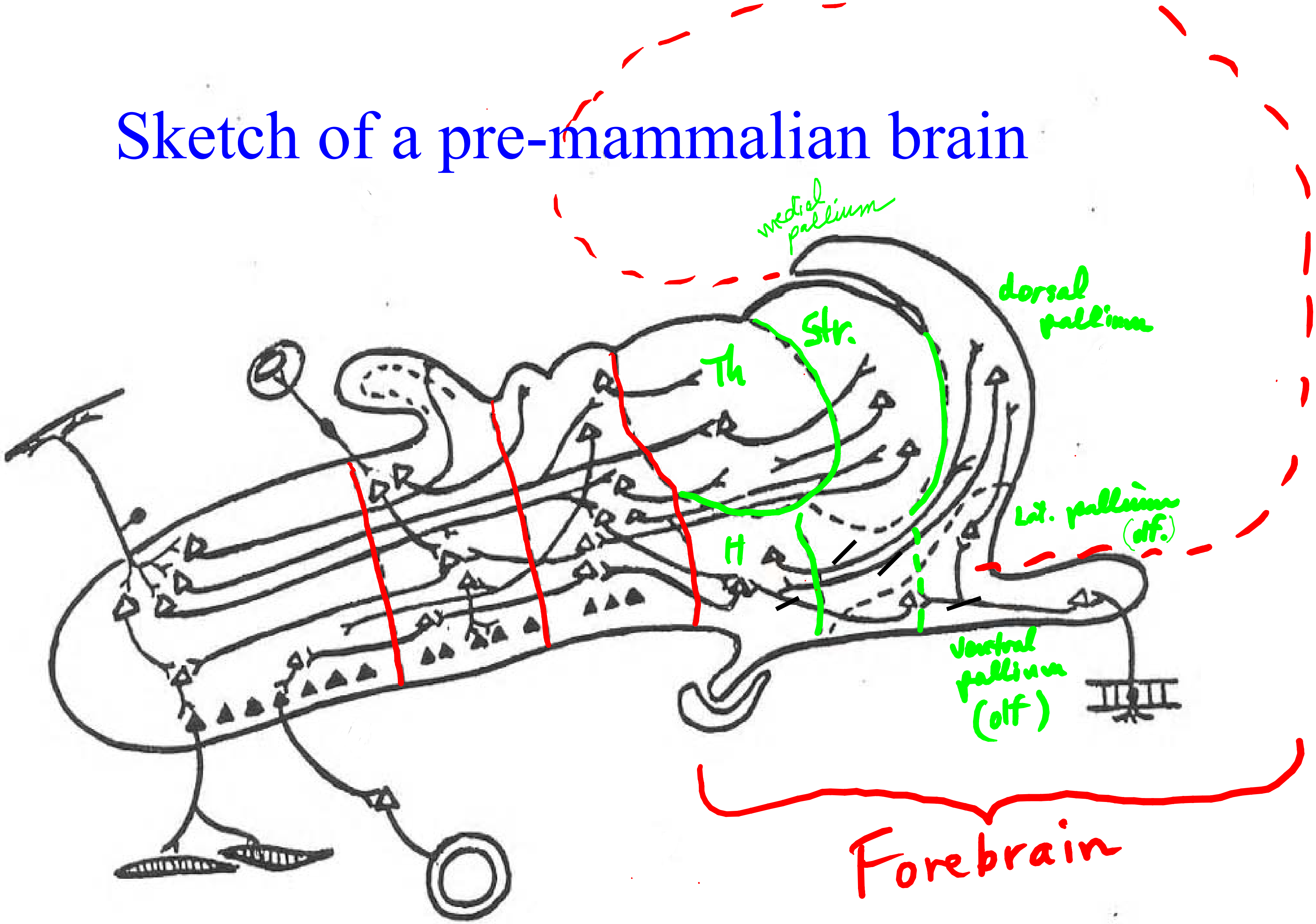
Overview of forebrain structures in vertebrates; neocortex introduced

Questions on chapter 7 of book

Functional overview of cephalic structures

- What can an animal do without a forebrain? Behavior of chronic decerebrate cats, rats and pigeons.
  - Decerebration: removal of cerebral hemispheres (surgical removal of all or most of the forebrain)
- Contributions of forebrain components
  - Diencephalon (‘tweenbrain)
  - Corpus striatum
  - “Limbic” system
  - Neocortex

Sketch of a pre-mammalian brain



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Note: Almost all axons were much more widely branching than shown in this schematic. Dendrites, also highly branched, are omitted

Questions, chapter 7

1. What is the major reason for the very different effects of forebrain removal in cats and rats?

the **number** of connections disrupted

Questions, chapter 7

2. Why was forced feeding required to keep decerebrate cats alive after the surgery?

They had lost normal hunger motivation.

Cats: decerebration effects

- See the conclusion of Bard & Macht (1958) about reflex animals.

- What can such an animal actually do?
- Is it able to learn?

Bard & Macht, 1958; Emmers, Chun & Wang, 1965; Markel & Adam, 1965.

Decerebrate cat behavior, 1

- Anosmic and blind, with loss of cranial nerves 1 and 2
- Failure to eat spontaneously; licking & chewing responses to food placed in the mouth (Forced feeding keeps cats alive.)
- Failure to groom
- No spontaneous sexual or other social behavior; sexual reflexes elicited by genital stimulation

Decerebrate cat behavior, 2

- Good standing, sitting, righting, walking, but abnormal posture & gait; failure to reposition limbs
- Rage responses—e.g., to tail pinching—but failure to bite or strike out
- Autonomic responses: piloerection, thermoregulatory responses but only to extreme temperatures unless hypothalamus left attached
  - A hypothalamic island was usually spared because of need for crucial visceral regulation, e.g., water balance. The island was attached to the posterior pituitary.
- Minimal learning: Conditioned eye blink or respiratory changes occur but there is a rapid loss of the learning.

Questions, chapter 7

3. Describe the behavior that shows how a cat without a forebrain shows no hunger motivation and yet will eat when food is placed in its mouth.

Eating reflexes

Chronic decerebrate **rats** *(Woods, 1964)*

- Similar to the decerebrate cats in many respects, but more rapid recovery of righting reflexes and locomotion
- More eating & drinking responses, but no seeking of food (hence, the damage was fatal without special interventions)
- Grooming occurred. (Thus, they showed a “series of reflexes” – more accurately described as a fixed action pattern.)
- Typical rodent defensive behavior (vocalizations, escape attempts, clawing & biting)
- Some auditory localization in space (shown by orienting towards sounds)

Questions, chapter 7

4. Is it true to say that the cat's forebrain has "taken over" more functions than the rat's forebrain? Is this the best way to describe the results of experiments?

This would imply that there is a **qualitative** difference between the species. It is more accurate to describe the results as indicating **quantitative** differences.

Questions, chapter 7

5. What are some of the unlearned behavior patterns exhibited by pigeons that had suffered a disconnection of the forebrain from the midbrain, except for the connections from the eyes to the dorsal midbrain.

Next slide

Pigeons with forebrain removed, sparing the optic tracts *(Visser & Rademacher, 1935, 1937)*

- They showed a basic repertoire of "unlearned" reactions:
  - Thrown into the air, they flew, avoided vertical sticks, and landed on horizontal sticks.
  - But they also landed on the backs of dogs and cats!
- They lost many more complicated behavior patterns that seemed to depend to some degree on learning.

Pigeons with forebrain removed: Learning?

- Have they lost learned behavior and retained unlearned behavior?
  - This is too extreme, although they did lose many learned responses.
  - Even spinal animals can show conditioned leg withdrawal. Other types of conditioning occur without forebrain.
- **Hypothesis: The forebrain is important in linking together, by learning, species-typical action patterns ("fixed action patterns") which are built in (genetically determined).**

Questions, chapter 7

6. What is meant by “stability in time” and “stability in space”? In which of these is the forebrain most important?

Conclusion: Behavior without forebrain

- Summary in terms of fundamental stabilities (as expressed by W.J.H. Nauta)
  - Stability in space is maintained (at a crude level).
  - Stability of the internal mileau is OK, but best if hypothalamus is left intact.
  - **Very poor "stability in time"**
    - Behavior determined by current inputs
    - Little or no motivation-initiated behavior
    - Little or no long-term memory.
- In addition, without a forebrain a mammal has **major losses in sensory and motor acuity**

Decortication, with sparing of corpus striatum

- Compared with decerebrates, cats show more behavior sequences, e.g., grooming, spontaneous eating, mating.
- But remember, decerebrate rats show grooming even without sparing of the striatum.
- **Why the species difference?**

Neocortex removals in various species compared

- The greater the amount of neocortex removed,
  - the longer lasting the resulting defects*,
  - and the more likely some of those defects will be permanent.
- Again, how do we account for these species differences? slides 4, 11.

*The "defects": The immediately noticeable deficiencies in motor control. Many sensory and cognitive defects occur as well.

Questions, chapter 7

7. What, in a simple phrase, is meant by diaschisis? Describe an example. Why is an understanding of this phenomenon so important in the interpretation of species differences in brain lesion effects?

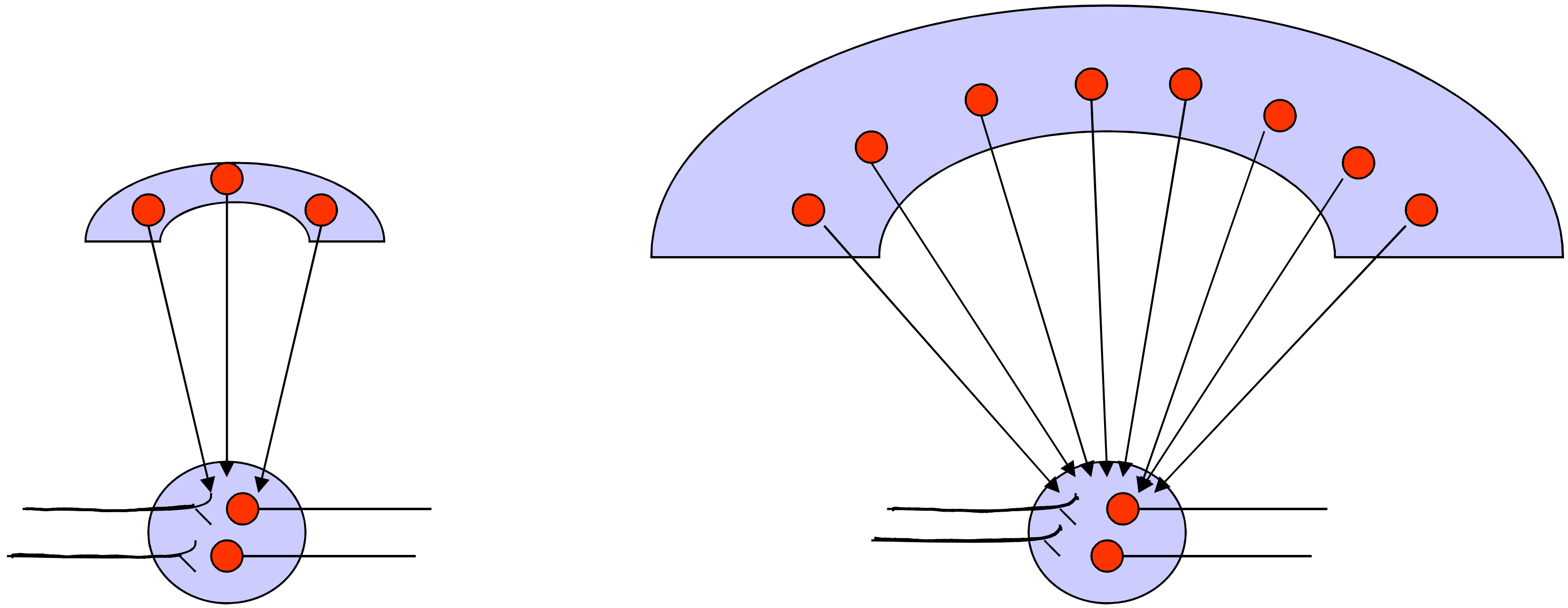
Next slide

“Diaschisis” phenomena

- Term refers to quantitative effects of lesions, usually large lesions, on the functions of other structures not directly damaged
- Defined as **deafferentation depression**
- Example: “spinal shock” in different species

- Next:
  - Von Monikow’s “corticospinal diaschisis”
  - Recovery phenomena: possible mechanisms

Diaschisis: basis



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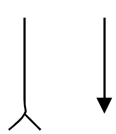
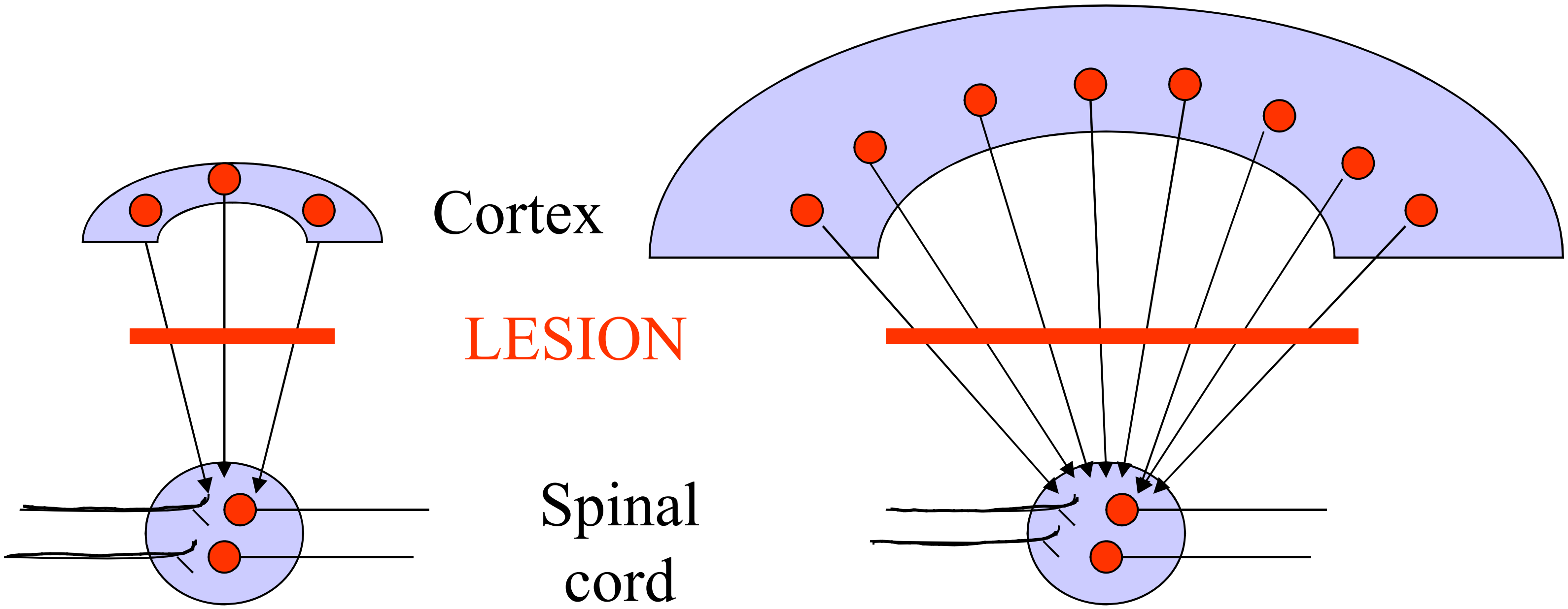
 = excitatory connections

Corticospinal Diaschisis: concept



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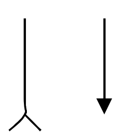
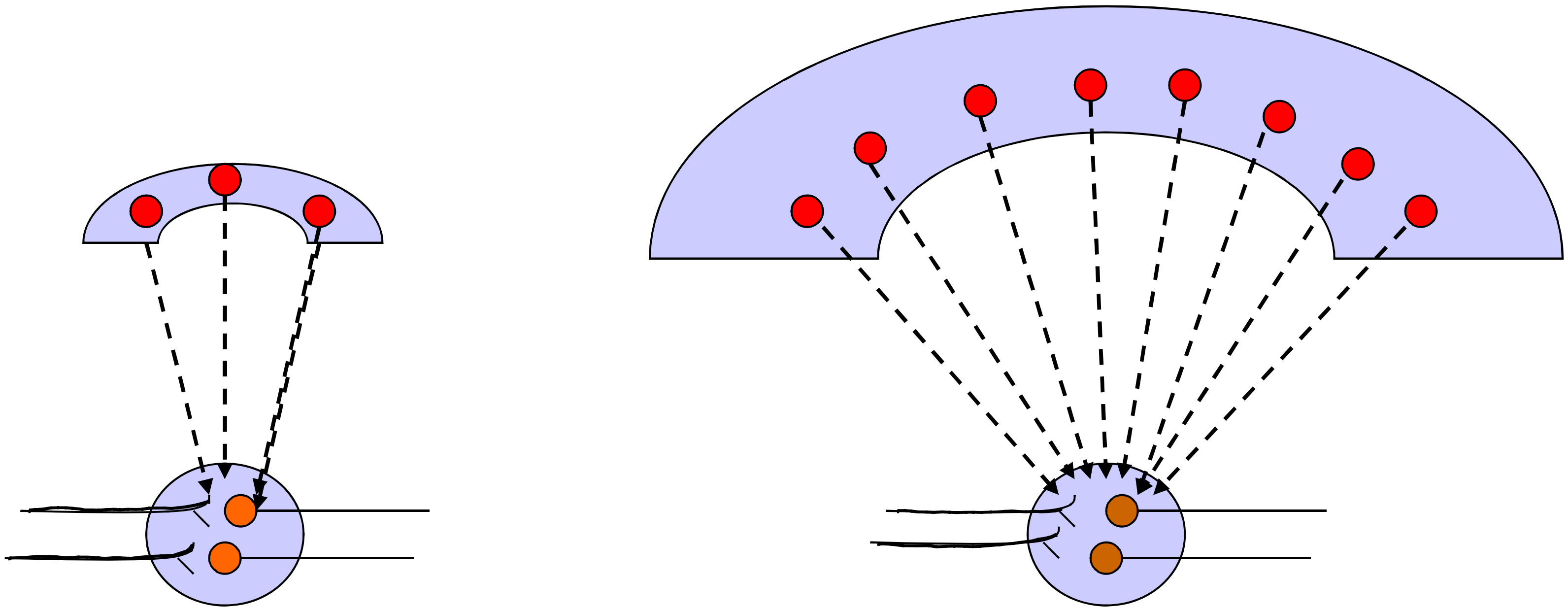
 = excitatory connections

Diaschisis: **the denervation depression phenomenon**



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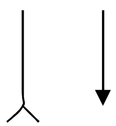
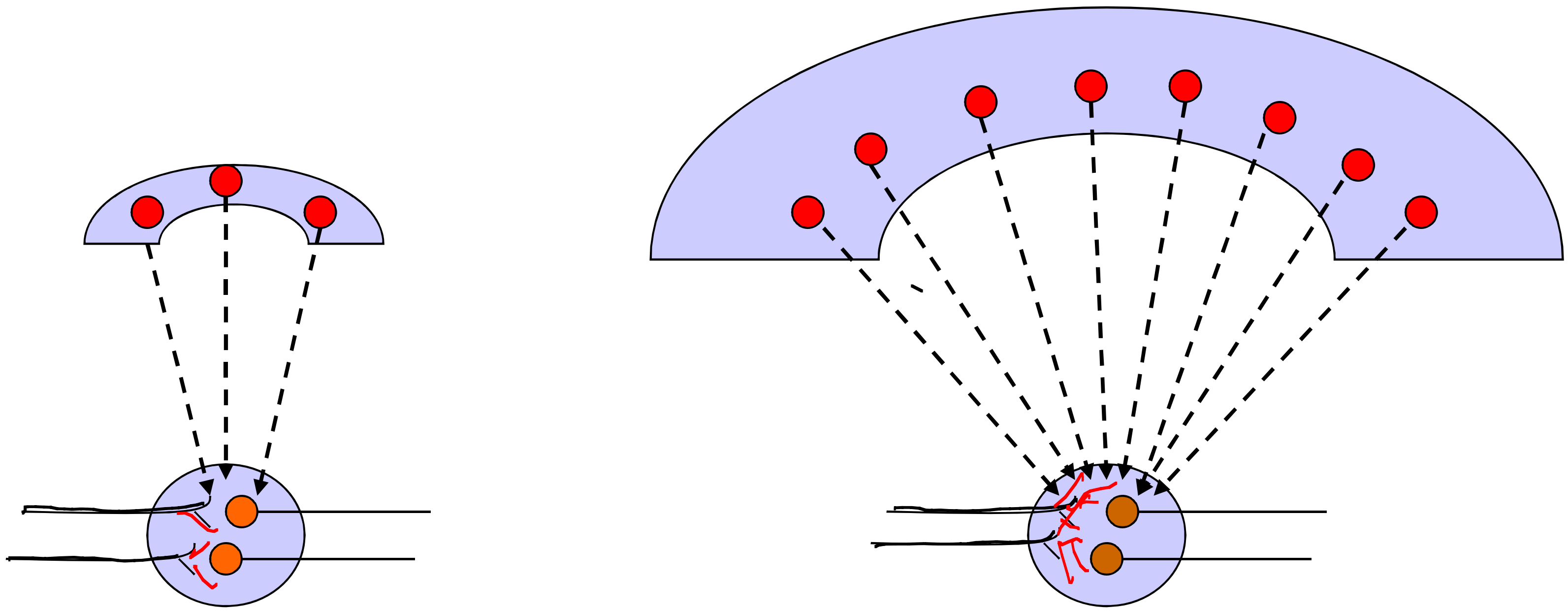
 = excitatory connections

Greater deafferentation (more connections have been removed)

Recovery of excitability after denervation depression

- Collateral sprouting
- Denervation supersensitivity

Diaschisis: **the denervation depression phenomenon**



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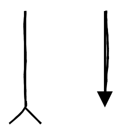
 = excitatory connections

Sketch the predicted collateral sprouting. How can one test for collateral sprouting? Or for denervation supersensitivity?

Greater response to neurotransmitter

Conclusion about brain lesion effects

- Brain lesions cannot be considered as mere subtractions of functions of the removed tissue.
- Quantitative effects of lesions have to be considered.
- Now we return to a functional overview of forebrain structures

Questions, chapter 7

8. What part of the forebrain is most involved in the changes that occur during habit formation, or procedural learning (implicit learning)?

Next slide

Functional overview of forebrain structures, *continued:*

- **Corpus striatum** contributions:
  - The Bard & Macht study indicates that one aspect may be the (learned) linking of components of instinctive behavior patterns during development, as described by Paul Leyhausen in his behavioral studies of kittens and cats.
  - Experimental studies have found that striatum is crucial for habit formation – “procedural learning” or “implicit learning”.
  - Anatomical connections of the striatum fit these functions.
  - Human pathologies of the striatum and its connections raise many additional issues.

We will return to these issues later.

Contributions of forebrain components based on other studies, both anatomical and functional

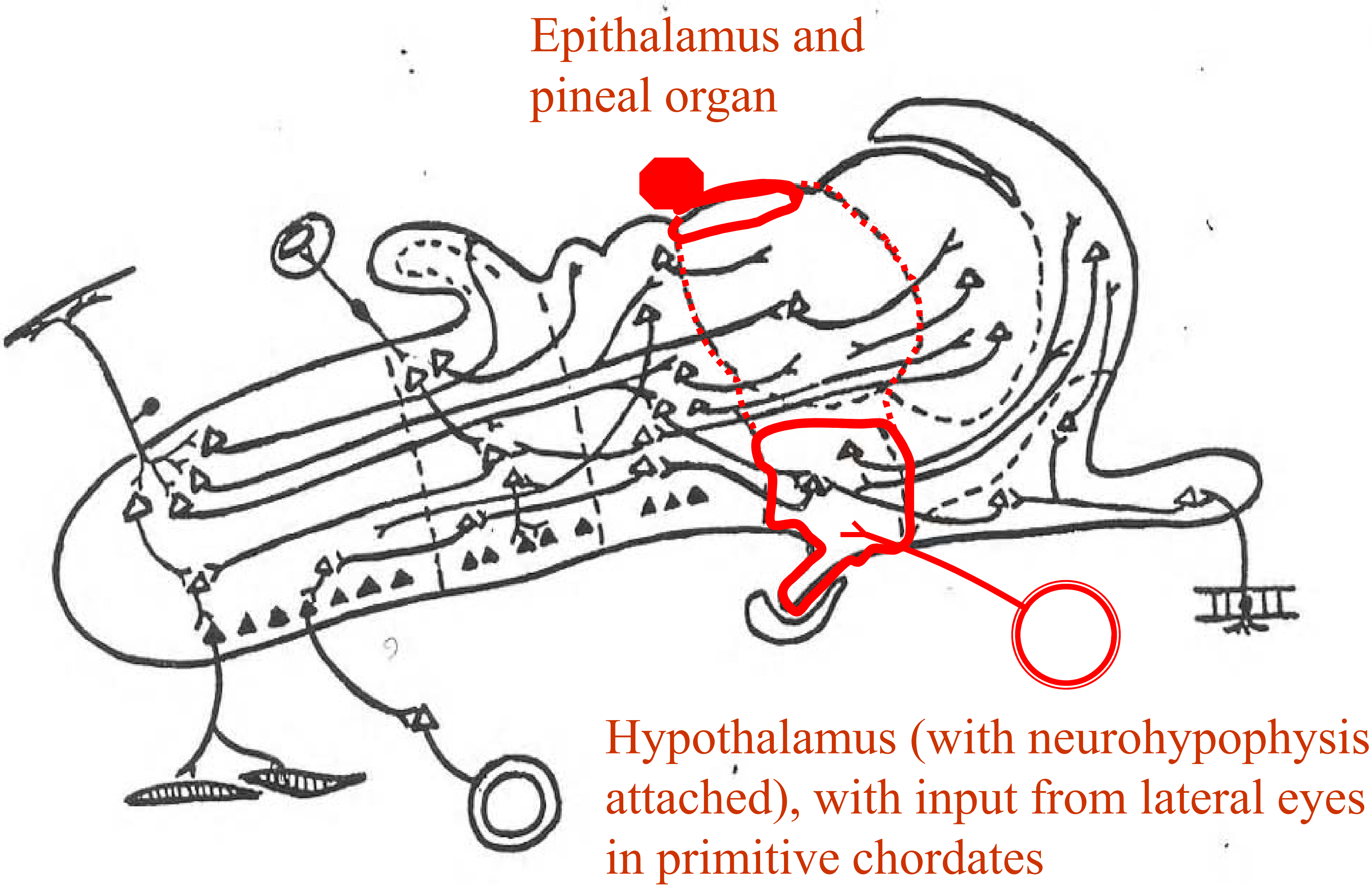
- ✓ Corpus striatum
- **Diencephalon** (‘tweenbrain, so named because it is between the hemispheres of the endbrain)
- Limbic endbrain
- Neocortex

Questions, chapter 7

9. According to the suggestions in this chapter, what is a reason why sensory pathways ascending to the forebrain almost always have a connection in the thalamus?

Diencephalon ('tweenbrain)

- Optic inputs were very early
- They play a special role in organizing the daily rhythm of activity, which is so different during day and night, and also when light levels vary during the daytime.
  - Hypothalamic and epithalamic afferents from the lateral eyes and from the parietal eye **entrain** the endogenous circadian activity rhythm.
  - This rhythm, the biological clock, and these visual inputs, **modulate the behavior of the entire system**.



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Diencephalon, *continued*:
Hypothalamus & pituitary

- Other system-wide modulations occur *via* the endocrine system's diencephalic component: the pituitary.
- Widespread modulation of the CNS is accomplished by the hypothalamus (called by Sherrington "the head ganglion of the autonomic nervous system"), which controls major motivational states in addition to sleep and waking.

Hypothalamic gating/modulation of neuronal activity in thalamus and subthalamus

- Indicated by studies of projections of the hypothalamus
- Demonstrated by electrophysiological studies of biting attack behavior by cats (*John Flynn and students at Yale, 1960s & 1970s*)
  - Electrical stimulation of lateral hypothalamus can cause an altered state: the predator mood.
  - Such stimulation also causes changes in neuronal firing patterns in thalamus and neocortex (as well as elsewhere).
- **In the evolution of sensory pathways ascending to the endbrain, this hypothalamic function may have been a major reason why a connection to thalamus, rather than more direct pathways, was almost always retained.**

Gating of information flowing to the neocortex
(more on this later)

Contributions of forebrain components based on other studies, both anatomical and functional

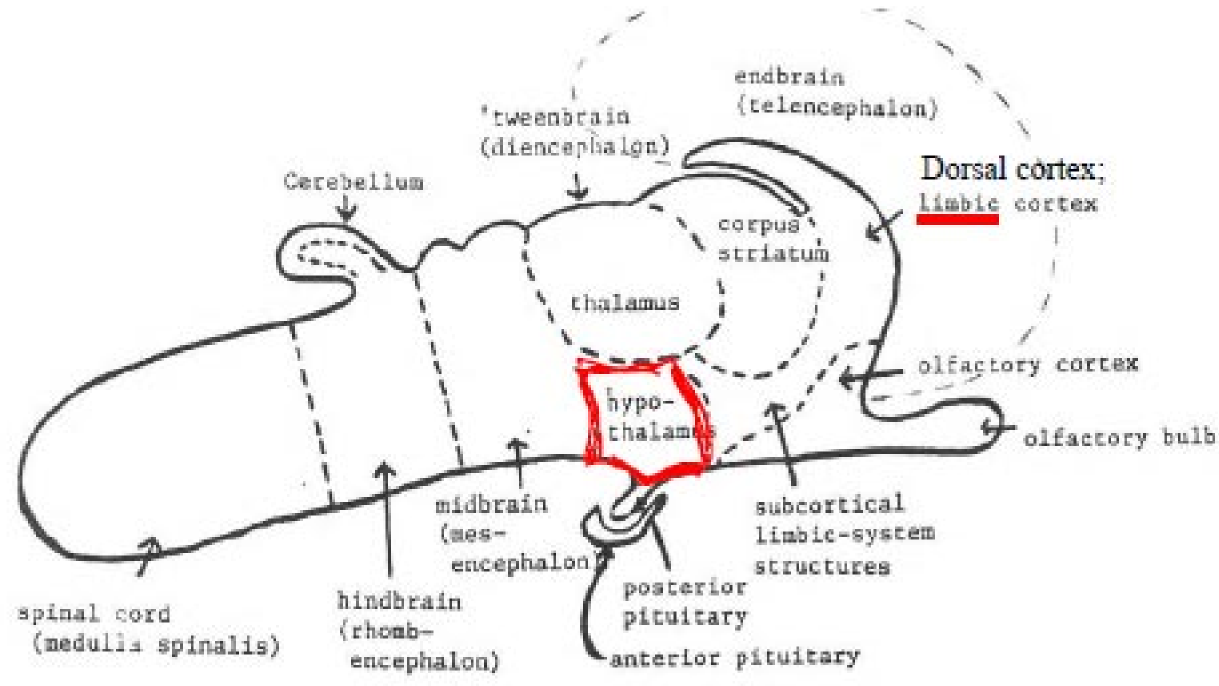
- ✓ Corpus striatum
- ✓ Diencephalon (‘tweenbrain, so named because it is between the hemispheres of the endbrain)
- **Limbic endbrain**
- Neocortex

Questions, chapter 7

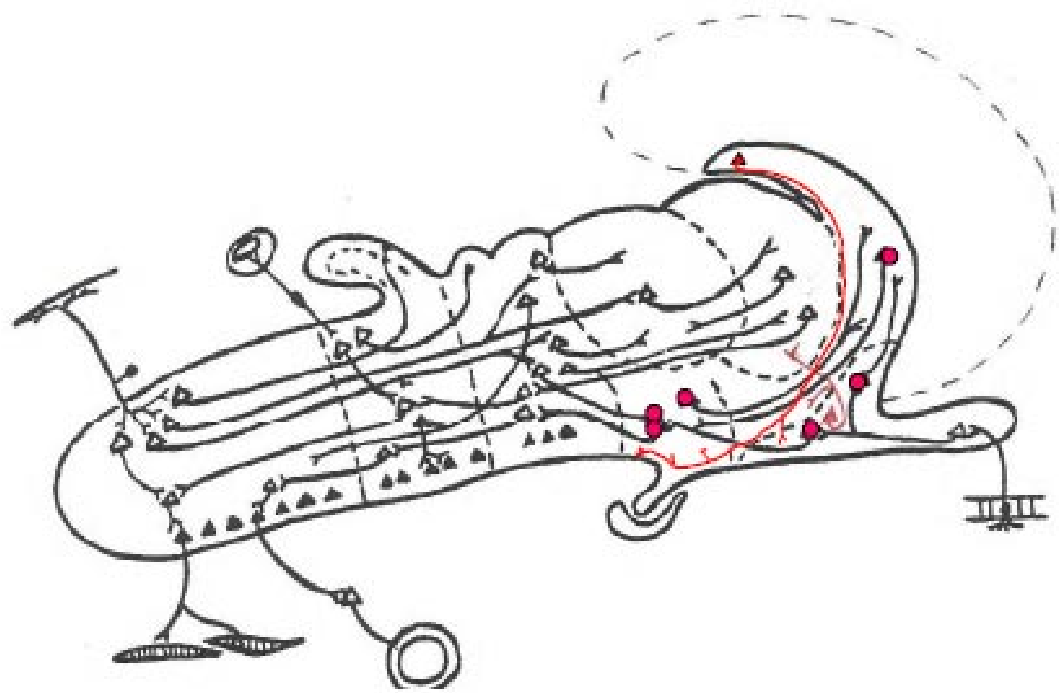
10. The limbic system is characterized by close interconnections with what portion of the upper brainstem?

The hypothalamus

Some "Limbic" connections



(Note definition of limbic system)



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