

Questions, chapter 24

- 5) Contrast the suggested early functional roles of the medial pallium and the corpus striatum.

- 7) What, in evolution, was the major cause of the differentiation of dorsal and ventral parts of the corpus striatum?

Next: How did the olfactory inputs influence behavior?

1) A likely scenario for the origins of Corpus Striatum

1. Olfactory epithelium → olfactory bulbs → caudally adjacent endbrain.
2. The ventral part of this projection area became the striatum, including parts of what became the amygdala.
 - The striatum had links to output control *via* 'tweenbrain (endocrine & autonomic control, motivational states) and midbrain (for locomotion and orienting)
3. The striatal links were plastic, responding to reward so that conditioned responses (habits) could be formed.
 - These habits were initially simple approach and avoidance responses
4. Later, there was an invasion of non-olfactory projections, and the dorsal striatum differentiated from the ventral striatum.
 - The non-olfactory systems thereby took advantage of the endbrain apparatus for plastic connections (resulting in habit learning).
 - Visual, auditory and somatosensory information reached the paleothalamus and subthalamus, which project to corpus striatum.
 - Projections of the auditory thalamus to the amygdala in mammals (especially primitive mammals) also fit with this idea.

REVIEW:

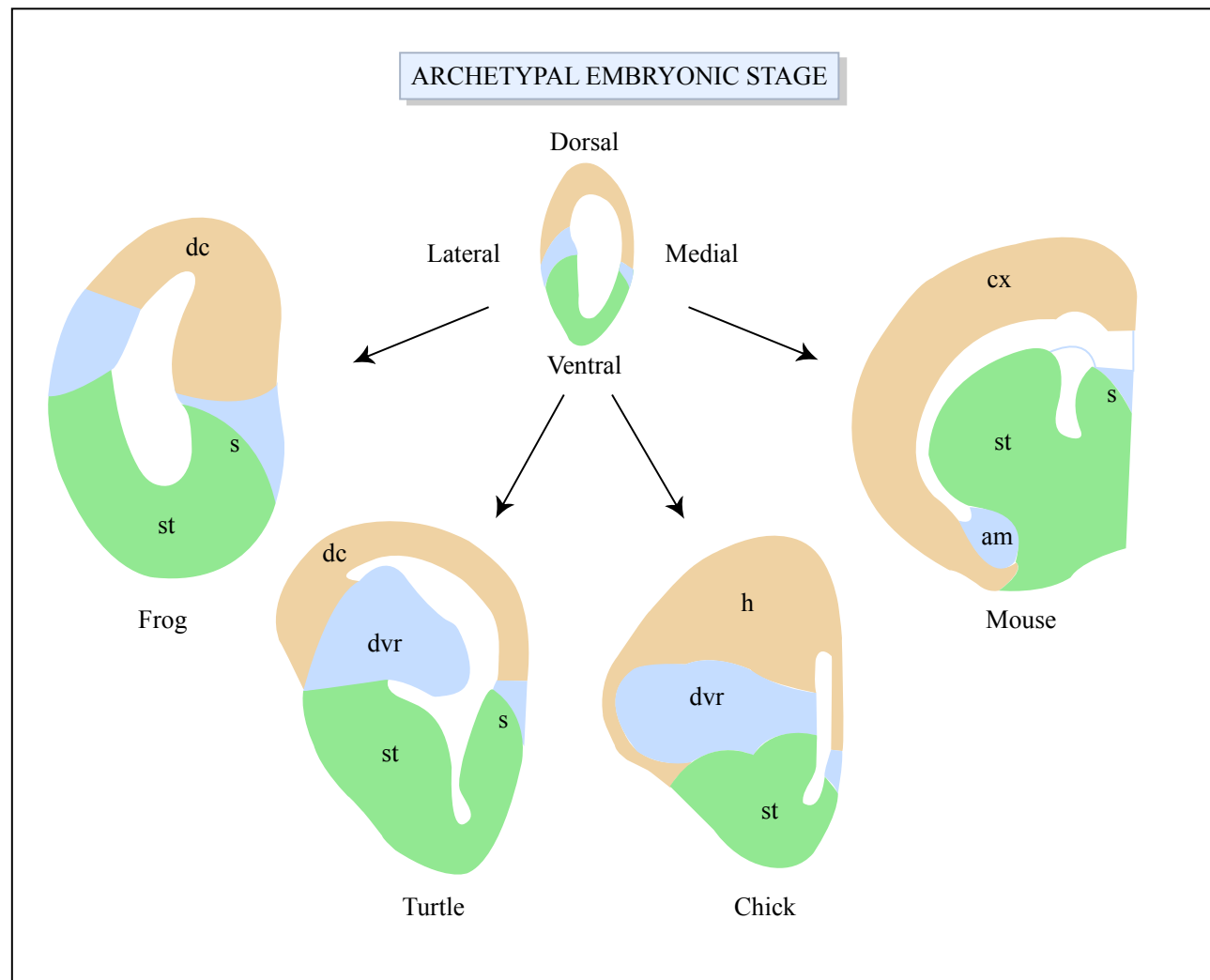


Image by MIT OpenCourseWare.

dc = dorsal cortex

cx = cortex

dvr = dorsal ventricular ridge

st = striatum

s = septum

h = hyperstriatum

Evolution of telencephalon based on expression patterns of regulatory genes during development.

The previous study was based on three genes. With addition of two more, some details have been added, but the main picture is the same:

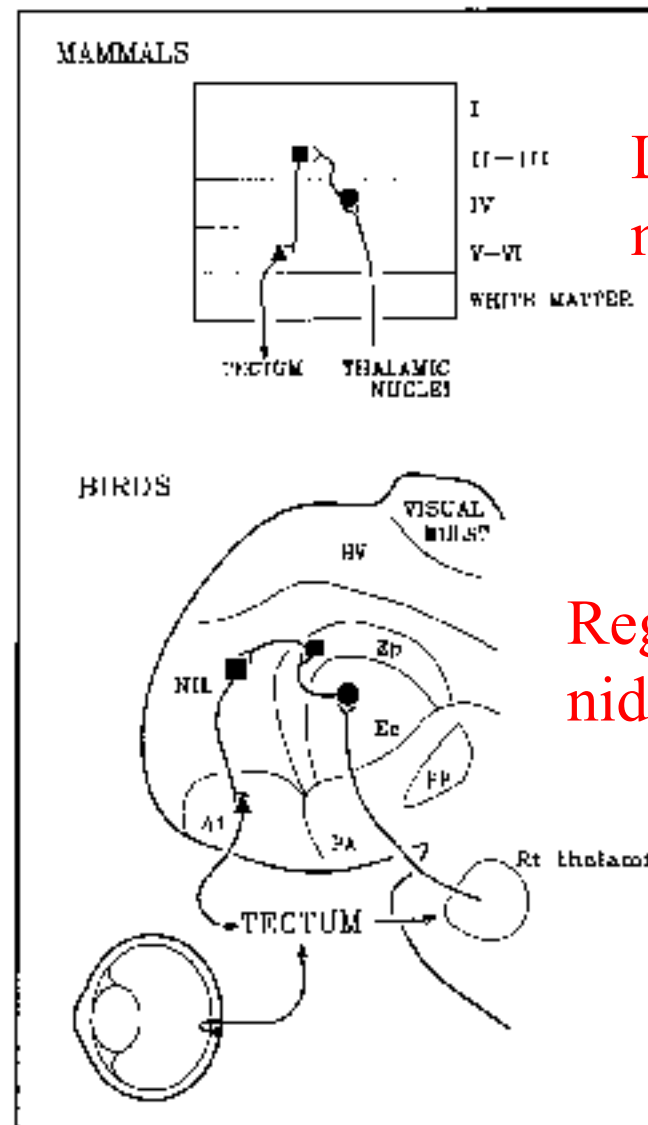
Puelles et al. (2000)
Pallial and subpallial derivatives in the embryonic chick and mouse telencephalon, traced by the expression of the genes Dlx-2, Emx-1, Nkx-2.1, Pax-6, and Tbr-1.

Figure removed due to copyright restrictions.

Please see or: Puelles, Luis, Ellen Kuwana, et al. "Pallial and Subpallial Derivatives in the Embryonic Chick and Mouse Telencephalon, Traced by the Expression of the Genes Dlx-2, Emx-1, Nkx-2.1, Pax-6, and Tbr-1." *Journal of Comparative Neurology* 424, no. 3 (2000): 409-438.

Karten and his collaborators have stressed connection patterns more than gene expression patterns, and have proposed a different pattern of migration of precursor cells from the embryonic DVR region.

From Karten & Shimizu (1989)
 The origins of neocortex:
 Connections and lamination as
 distinct events in evolution.



Layers of
neocortex

Regions of
nidopallium

Figure 3. A comparison of visual-innervation circuits between the mammalian and avian brains. Circles indicate thalamic recipient neurons; squares indicate intrinsic neurons; triangles indicate neurons sending efferents to the optic tectum. Roman numerals indicate cortical layers. Ai = archistriatum intermedium; Ep = periaqueductal belt; HV = hyperstriatum ventrale; NTL = neostriatum intermedium laterale; PA = paleostriatum augmentatum (avian equivalent of caudate-putamen); PP = paleostriatum primitivum (equivalent of globus pallidus).

Courtesy of MIT Press Journals.

Source:Karten, H., and Toru Shimizu. "The Origins of Neocortex: Connections and Lamination as Distinct Events in Evolution." *Journal of Cognitive Neuroscience* 1, no. 4 (1989): 291-301. © 1989 by the Massachusetts Institute of Technology. Used with permission.

2) The early pallium: a second endbrain source of influence on behavior

- Early dominance of olfaction
- A precursor of limbic pallial structures of mammals
- Evolutionary Invasion of non-olfactory projections (as in striatum)
- **Differentiation of medial pallium** (dorsomedial to the striatal portion of the neural tube)
 - It has strong olfactory afferents in Hagfish and other primitive vertebrates
 - Medial pallium of early vertebrates **became the hippocampal formation.**
 - In mammals, only the most rostral hippocampus—the most rostral part of the “hippocampal rudiment”—receives direct olfactory projections.
- A major function: **Memory for locations in space**
 - In primitive chordates: Remembering good vs bad places by their odors
 - Evidence from ablation studies and unit recording studies of mammals
 - Evidence from species variations: Correlations between size of hippocampus and hoarding abilities in birds and mammals [**next slide**]

Relative size of
hippocampus in
passerine birds that
store food in
remembered places
(filled symbols) and
birds that do not store
food (open symbols)

Figure removed due to copyright restrictions.

Please see course textbook or: Sherry, D., and S. Duff. "Behavioural and Neural Bases of Orientation in Food-storing Birds." *Journal of Experimental Biology* 199, no. 1 (1996): 165-72.

Fig 24-5

The primitive endbrain:

Parallel evolution of pallium and subpallium

- **Each evolved non-olfactory portions.** The original olfactory parts of the cortex became “limbic”: pushed to the “fringe” by the non-olfactory areas.
- **Adaptive advantages of the non-olfactory modalities:**
 - **Striatum**: habit learning, involving locomotion, orienting, reaching
 - Non-olfactory inputs initially came from paleothalamus (midline and intralaminar nuclei).
 - Later, non-olfactory inputs came mainly from neocortex.
 - Outputs to ventral ‘tweenbrain and to midbrain (for control of locomotion, orienting, grasping)
 - **Pallium**: Neocortex appeared, and expanded in mammals, after non-olfactory information reached the dorsal cortex.
 - Increasing sophistication of sensory analysis and object discrimination
 - Outputs to striatum, medial pallium, ‘tweenbrain, midbrain. (Later, also to hindbrain and cord)

Questions, chapter 24

8) From what part of the primitive endbrain did the neocortex evolve? What kinds of data support this?

dorsal pallidum/cortex. Gene expression data, also, anatomical position,

9) Name several mammals now living that have a very small neocortex. *Next →*

Pallium began small:

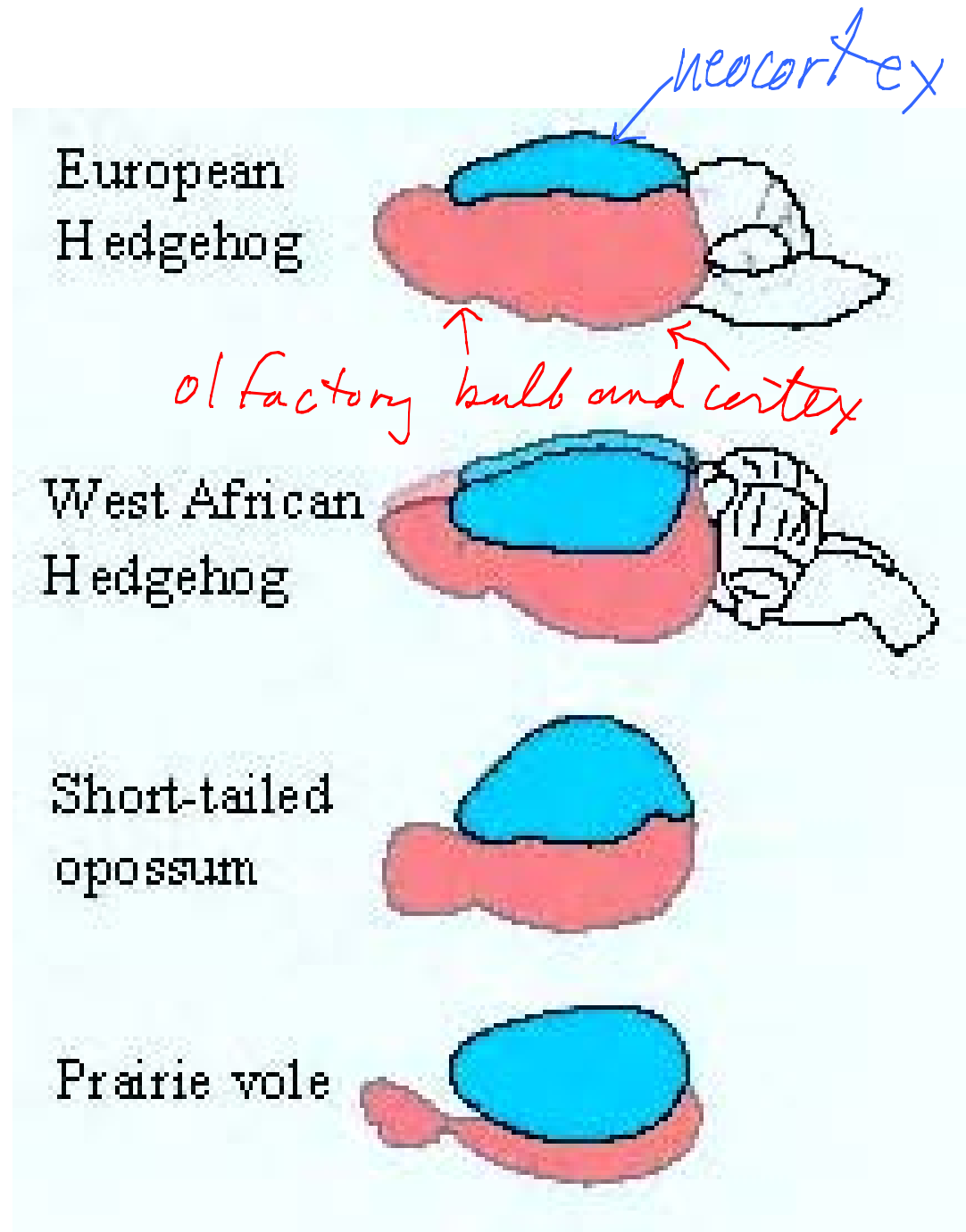


Fig 24-6

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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.

**Pallium begins to expand:
Represented by present-day small mammalian insectivores**

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The ideas about origins in a series of pictures

Evolution of corpus striatum and rest of endbrain: speculations

1. Beginnings: a link between olfactory inputs and motor control: The link becomes “Ventral striatum”.

2. Non-olfactory inputs invade the striatal integrating mechanisms (*via* paleothalamic structures).

3. Early expansions of endbrain: striatal and pallial. Non-olfactory inputs to pallium

4. Pre-mammalian & then mammalian expansions of cortex and striatum: For the striatum, the earlier outputs and inputs remain as connections with neocortex expand.

Figure 1. Postulated beginnings in primitive chordates

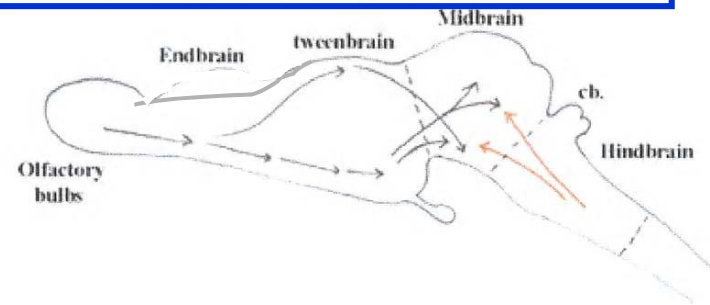


Figure 2 Other inputs reached the striatum

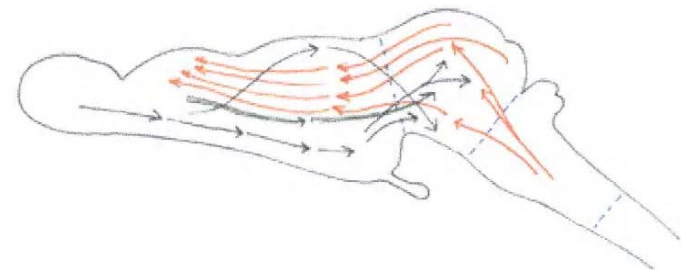


Figure 3. Early expansion of striatal and adjacent "limbic" areas

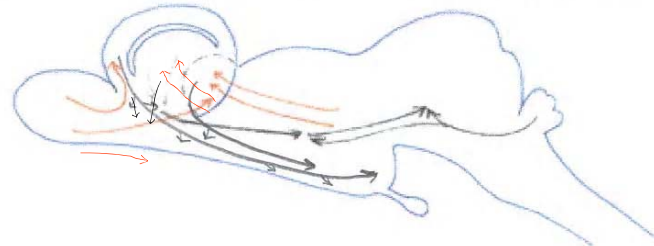
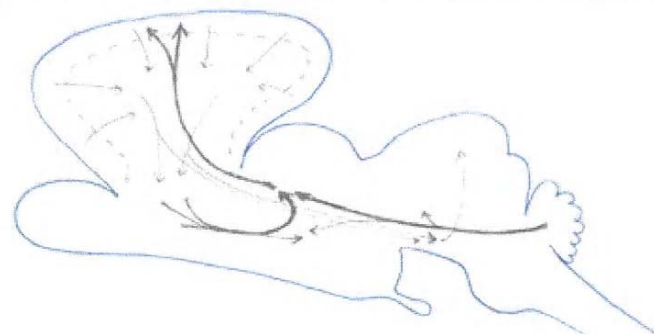


Figure 4. Pre-mammalian, and then mammalian expansions



What are the primitive outputs?

- Earliest projections to hypothalamus and epithalamus
- Evolution of those projections as striatum evolved
 - To ventral thalamus (subthalamus), and
 - To midbrain for major types of motor control
 - Locomotion (towards or away from something)
 - Orienting
 - A third type: manipulation and grasping (Grasping by limbs probably evolved later.)

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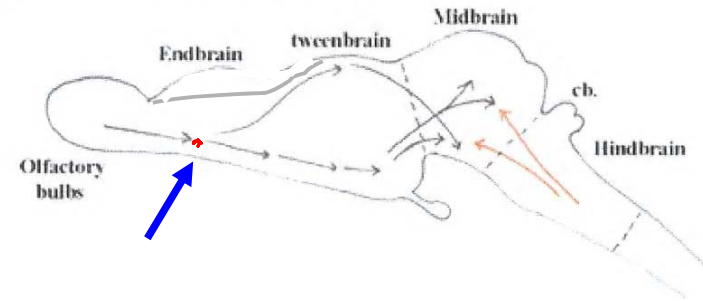


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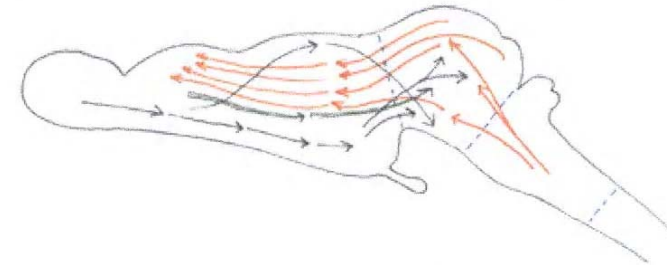


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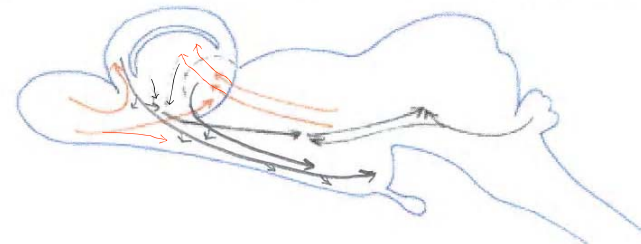
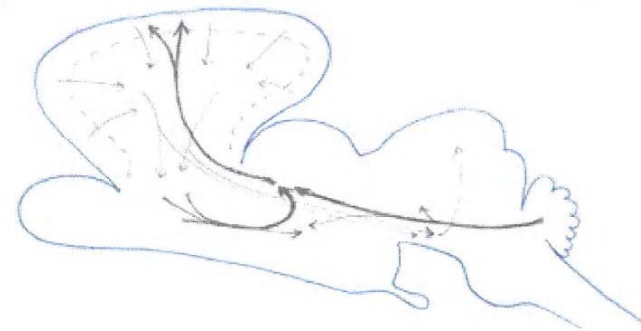


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Plasticity of the links to the output systems: How?

- Feedback from sensory systems monitoring the consequences of the outputs
- Origins of the dopamine pathways from brainstem into striatum, involved in reward mechanisms in mammals:
 - **From posterior tuberculum** and hypothalamus in most vertebrates (lampreys, cartilaginous fishes, ray-finned fishes, lungfishes, amphibians)
 - **From ventral tegmental area and substantia nigra** in the amniotes and in sharks, skates and rays.
- There is evidence that an input to these dopamine cells comes from the taste system—an obvious source of feedback that was probably more prominent early in evolution.

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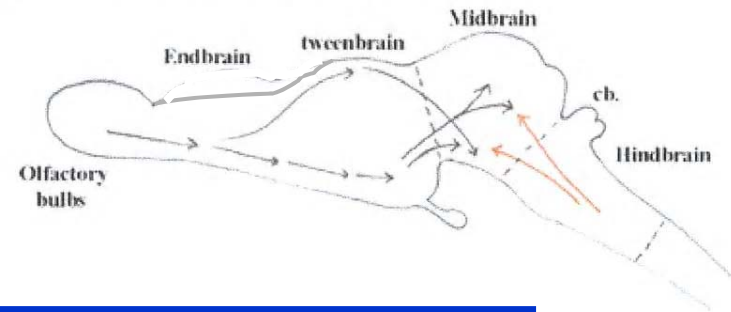


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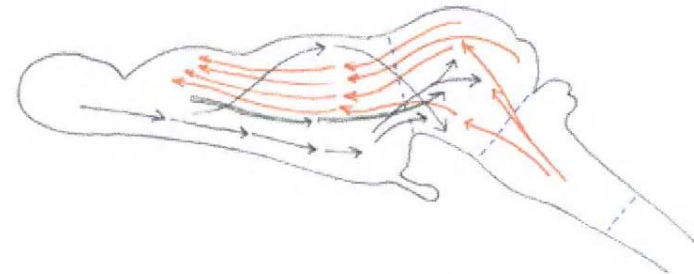


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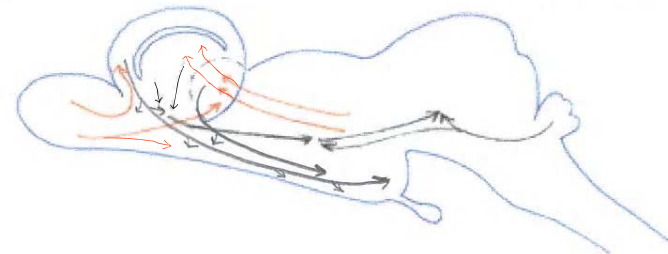
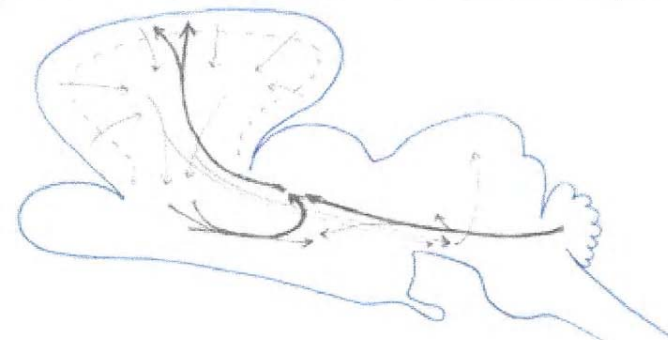


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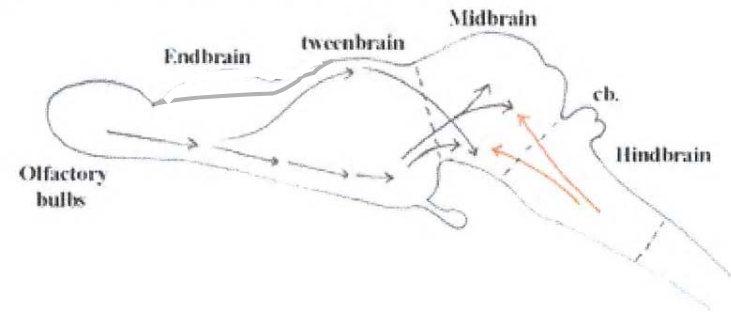


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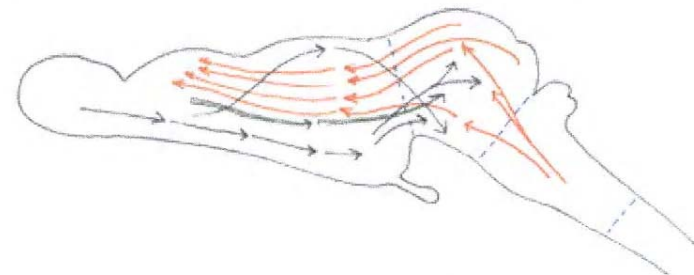


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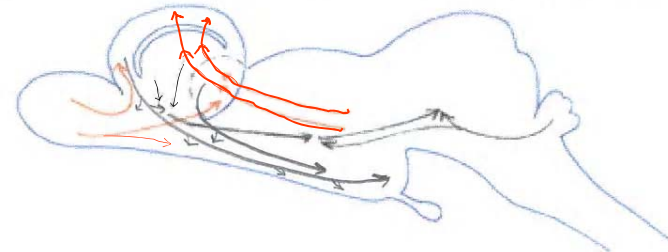
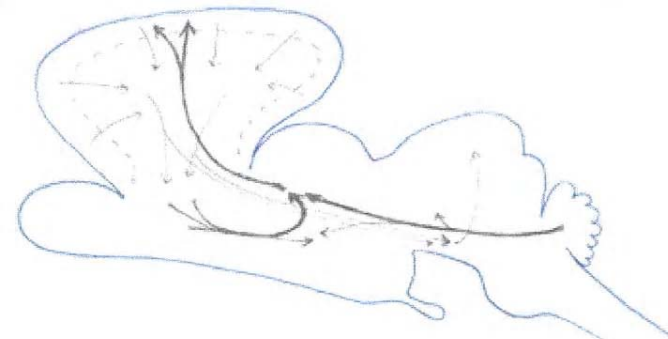


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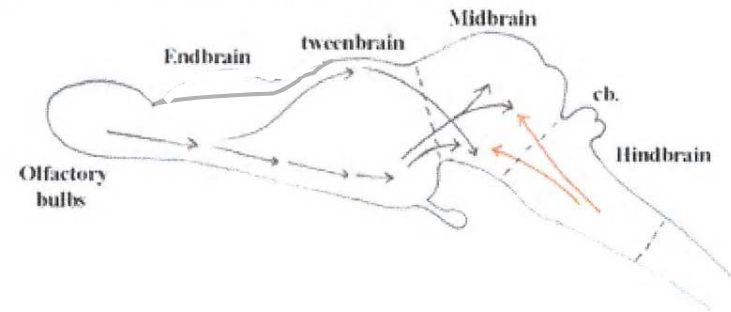


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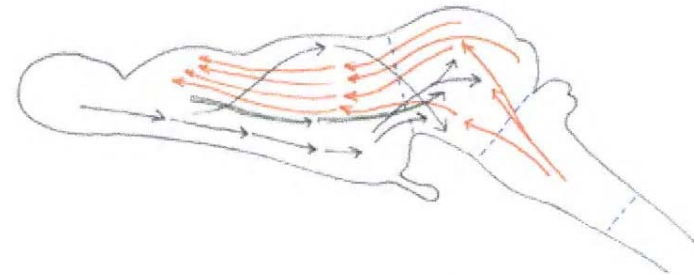


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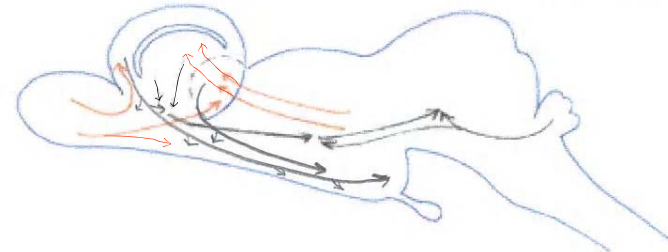
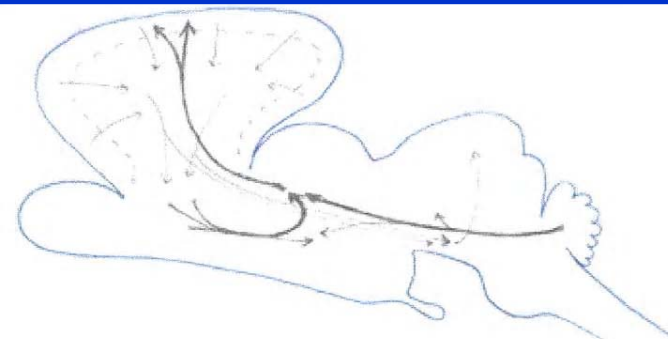


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Next topics:

Part 9: Hypothalamus & Limbic System

Classes 27-32

Part 10: Corpus striatum

Classes 33-34

Part 11: *The crown of the CNS*: The neocortex

Classes 35-39

A sketch of the central nervous system and its origins

G. E. Schneider 2014

Part 9: Hypothalamus & Limbic System

MIT 9.14 Class 27

Regulating the internal milieu and the basic instincts
(Limbic system 1)

Chapter 25

The “**limbic system**”:

Hypothalamus and associated midbrain,
‘tweenbrain, and endbrain structures

These are the interconnected structures underlying motivational and emotional states as well as endocrine and visceral control.

We begin with evolutionary origins and functions and give some definitions.

Initial evolution of forebrain

- With its control of secretory functions, the anterior end of the neural tube (forebrain vesicle) was very probably dominated by the predecessors of the hypothalamus and epithalamus.
- This region of the neural tube became diencephalon.
- The differentiation of a telencephalon must have resulted from olfactory inputs, which—through the primitive striatum and pallium—were closely connected to the hypothalamus.

Functions of hypothalamus and affiliated structures (limbic system)

- 1) The hypothalamus was called the “**head ganglion of the autonomic nervous system**” by C.S. Sherrington, the famous British physiologist working at the time of Cajal (beginning of 20th c).
- 2) Hypothalamus and closely connected structures are involved in the control of motivated behaviors (e.g., ingestive, reproductive, defensive); their activities underlie **drives** and associated affects.
- 3) The hypothalamic cell groups function as “central pattern controllers” acting by connections to the midbrain, and to a lesser extent to the hindbrain and the spinal cord.
 - Such a controller does not organize a movement
 - It makes a movement more or less likely

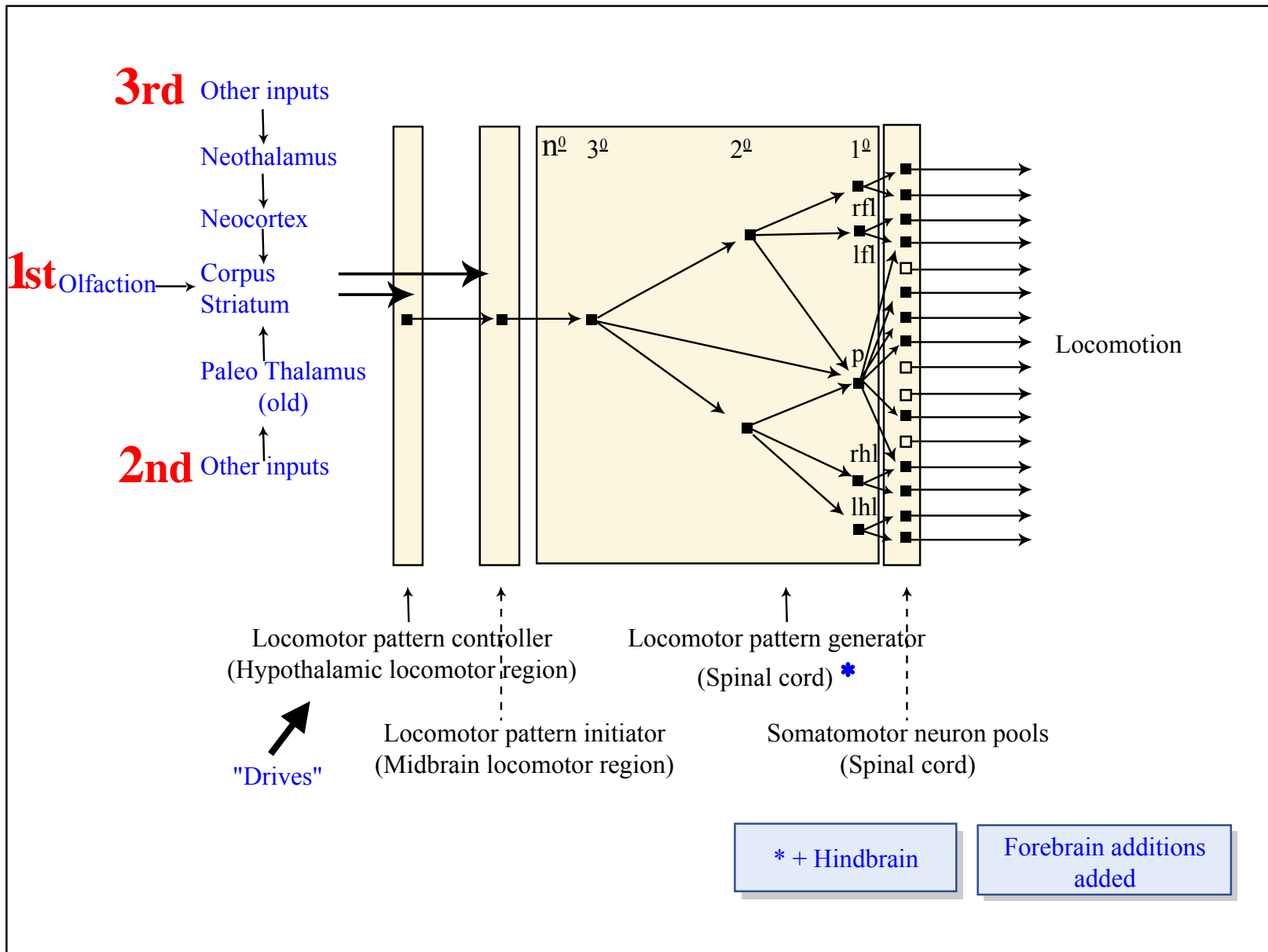


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Hierarchic control of locomotor behavior

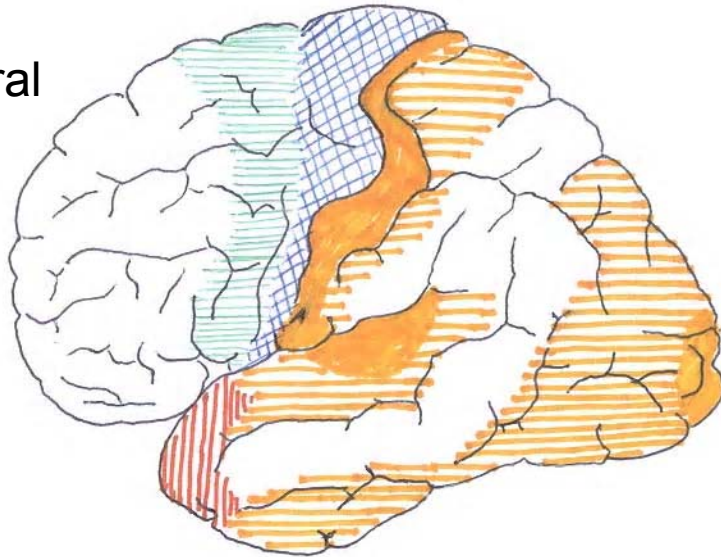
Questions, chapter 25

- 1) Where are the cortical areas that are grouped together as part of the limbic endbrain found in the cerebral hemispheres?

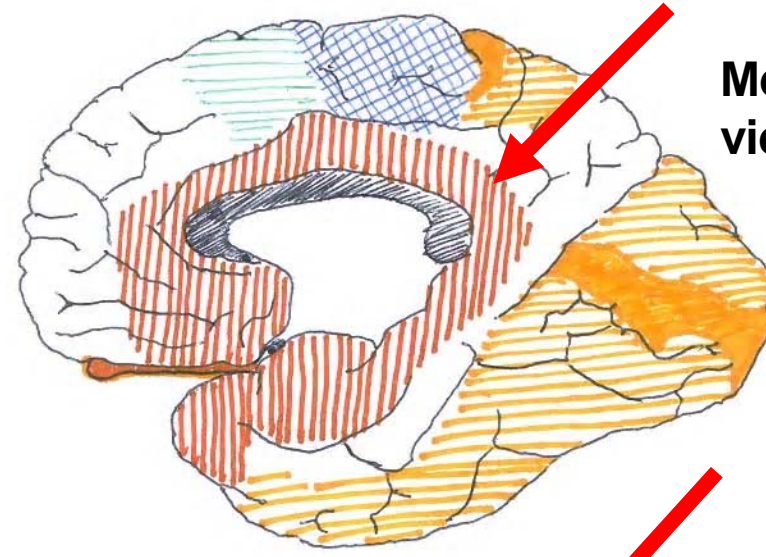
Origin of term “limbic system”

- These structures and their interconnections are often called the “limbic system”, because in the endbrain of mammals, they are located at the fringe or margin (the limbus) of the hemispheres.
- The term came from a phrase used by Pierre Paul Broca, in his phrase “le grand lobe limbique” (1878) in the human brain. See the medial view of the human cerebral hemisphere on the next slide.

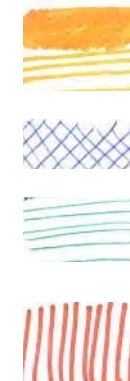
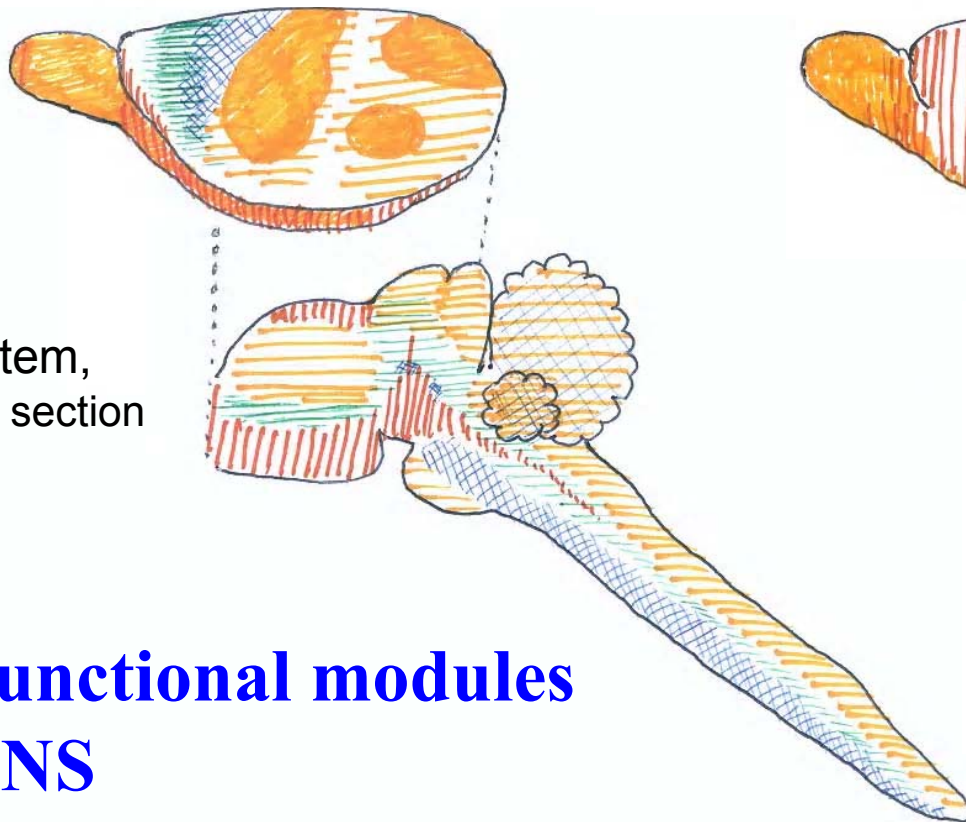
Lateral view



Medial view



Brainstem, sagittal section



Sensory-Perceptual

Motor

Behavior

Motivation

Major functional modules of the CNS

Limbic System

Introductory topics

1. **Two arousal systems in the midbrain:**
limbic and **non-limbic**
2. Hypothalamus: What specific functions?
3. Consummatory and appetitive behavior distinguished
4. Feeding, hunger and other basic drives; electrically elicited aggression in cats
5. Drive and reward involve distinct axons.

Approaching the limbic system from below: Two arousal systems in the midbrain

- The ascending reticular activating system (ARAS)
 - arousal type 1 (non-limbic)
- Limbic midbrain areas
 - arousal type 2
- Both systems, when stimulated, cause sympathetic nervous system arousal

Historical note: The ARAS was discovered by electrical stimulation of the reticular formation of cats by Moruzzi & Magoun (1949). The limbic midbrain areas were defined by Nauta (1950s & 1960s) from neuroanatomical studies.

Somatic regions: arousal type 1

Limbic regions: arousal type 2

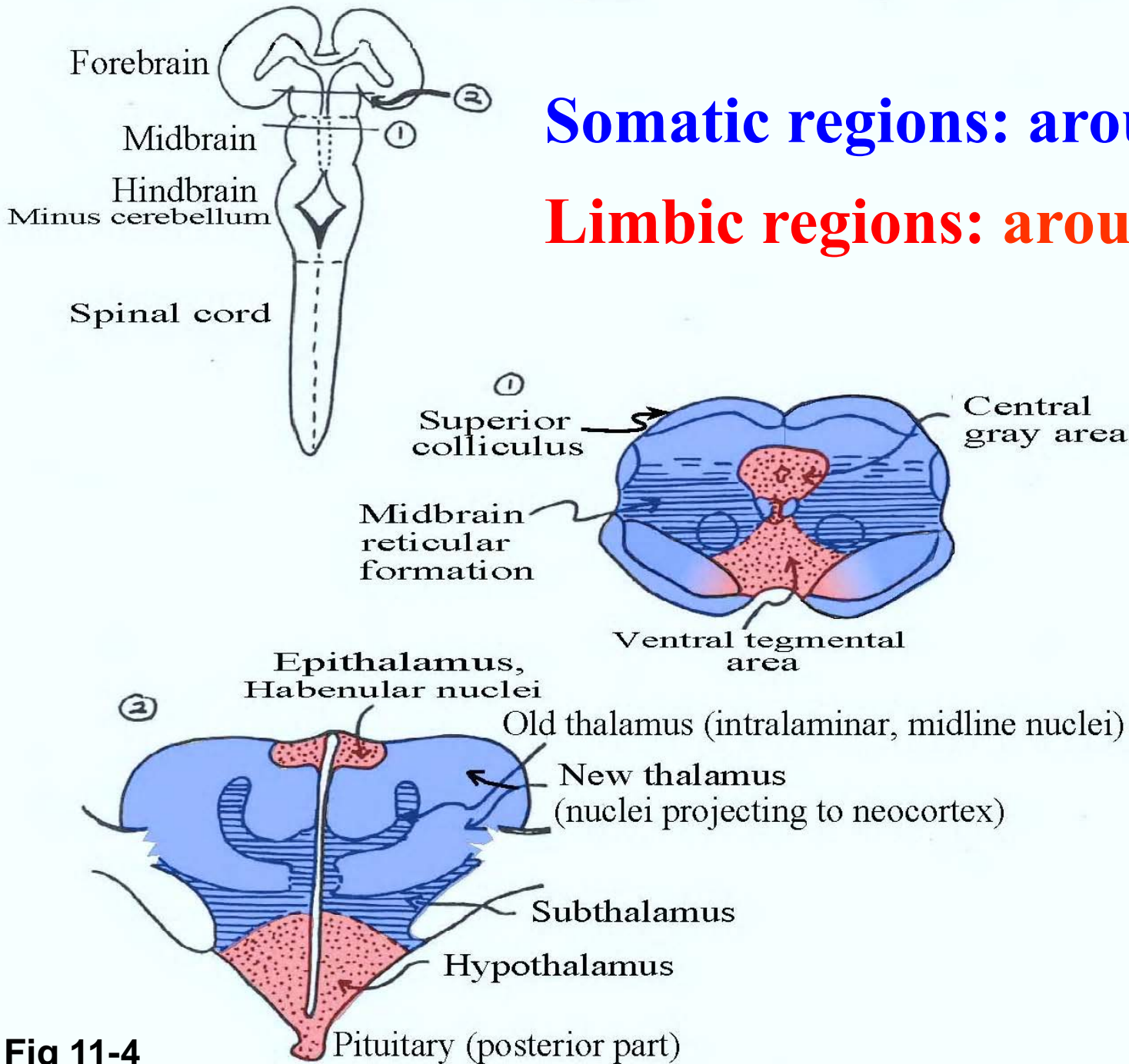


Fig 11-4

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Questions, chapter 25

- 2) Compare the two arousal systems of the midbrain. What structures are involved? What are the major types of connections to these structures? What are the effects of electrical stimulation? Is there habituation to repeated stimulation?

How are these two systems different?

1. Different effects of activation, according to results of electrical stimulation experiments.
2. Different anatomy:
 - locations,
 - types of inputs,
 - types of outputs.

Many of the differences are as you would expect from the midbrain locations: **SOMATIC** and **LIMBIC**

The ascending reticular activating system: Arousal type 1

- Electrical stimulation →
 - EEG arousal.
 - Effects show habituation. *unless electrode is moved*
 - Forced turning often occurs.
 - Rewarding/punishing effects are slight (not very rewarding or punishing in studies of electrical “self-stimulation”).
- Ascending connections:
 - especially from vestibular, somatosensory, auditory and visual systems; inputs also from cerebellum.
- Descending connections:
 - especially from neocortex, corpus striatum, “old thalamus” and subthalamus.

Limbic midbrain areas:

Arousal type 2

- Anatomical locations: Central gray area (CGA); ventral tegmental area (VTA)
- Electrical stimulation →
 - EEG arousal
 - **Resistant to habituation**
 - **Strong self-stimulation effects** at low thresholds
 - Negative dorsally in CGA (Central Gray Area)
 - Positive ventrolaterally in VTA (Ventral Tegmental Area)
- Connections from more caudal structures:
 - Visceral sensory
- Connections from rostral structures of limbic forebrain
 - **Hypothalamus**; septal area and basal forebrain, hippocampal formation, amygdala.

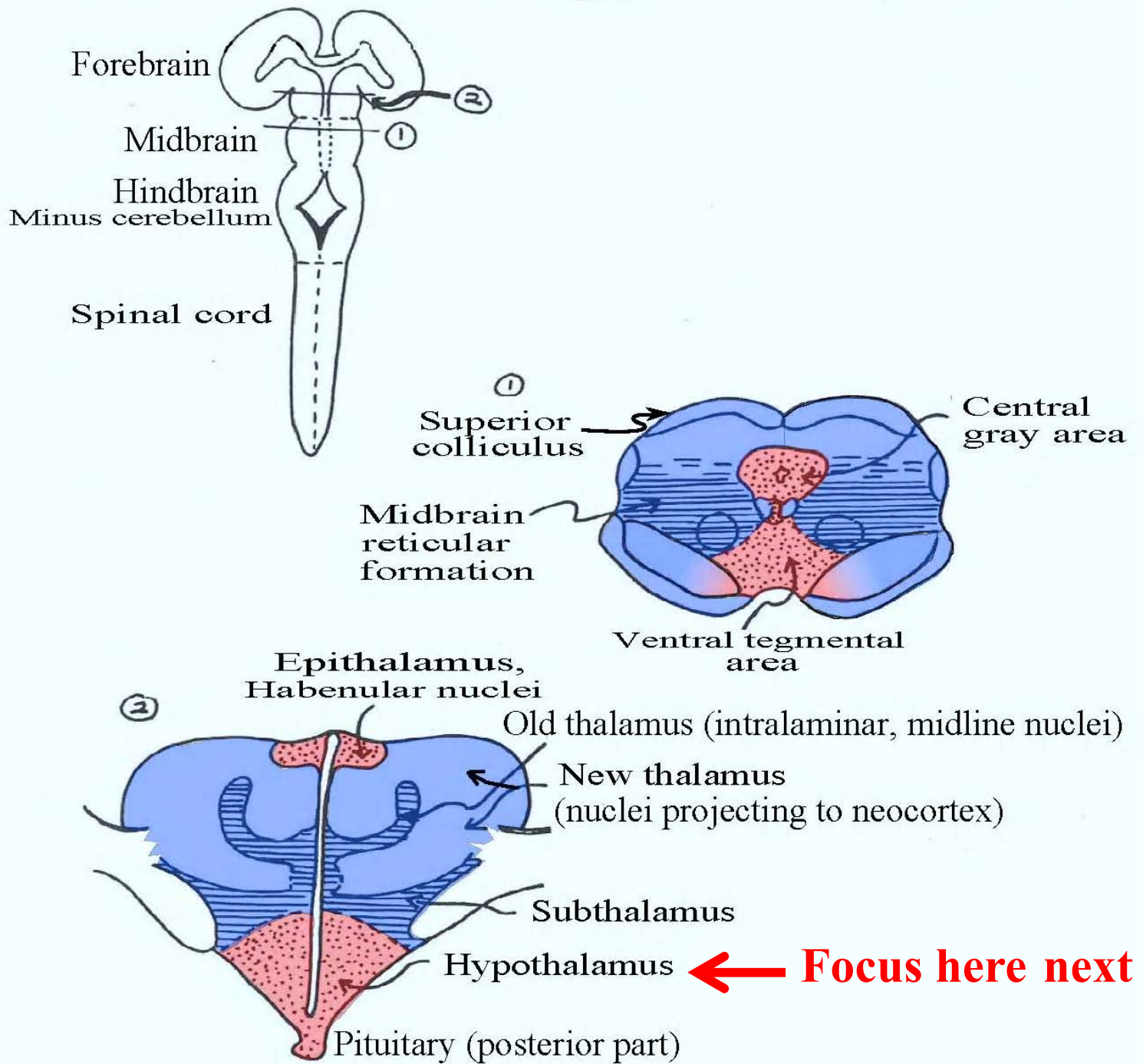


Fig 11-4

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Limbic System

topics

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limbic and non-limbic
- 2. Hypothalamus: What specific functions?**
3. Consummatory and appetitive behavior distinguished
4. Feeding, hunger and other basic drives;
electrically elicited aggression in cats
5. Drive and reward involve distinct axons.

Hypothalamus: What functions?

- **Control of autonomic nervous system and endocrine system**
 - Sherrington’s characterization: The hypothalamus is the “head ganglion of the autonomic nervous system”.
 - Control of endocrine system via the pituitary
- Homeostatic mechanisms
 - e.g., temperature regulation with input from hypothalamic neurons that detect temperature of blood
- Regulation of cyclic behaviors
 - Examples: Sleeping and waking, feeding, drinking, predatory attack
 - These behaviors fit into a daily cycle of activity
 - This activity cycle is regulated by the endogenous clock, synchronized by the daily light-dark cycle
 - These all show species-typical patterns.

Questions, chapter 25

- 3) Describe how hypothalamic neurons control secretions from each of the two divisions of the pituitary organ (the hypophysis).

Hypothalamus and pituitary in a small rodent

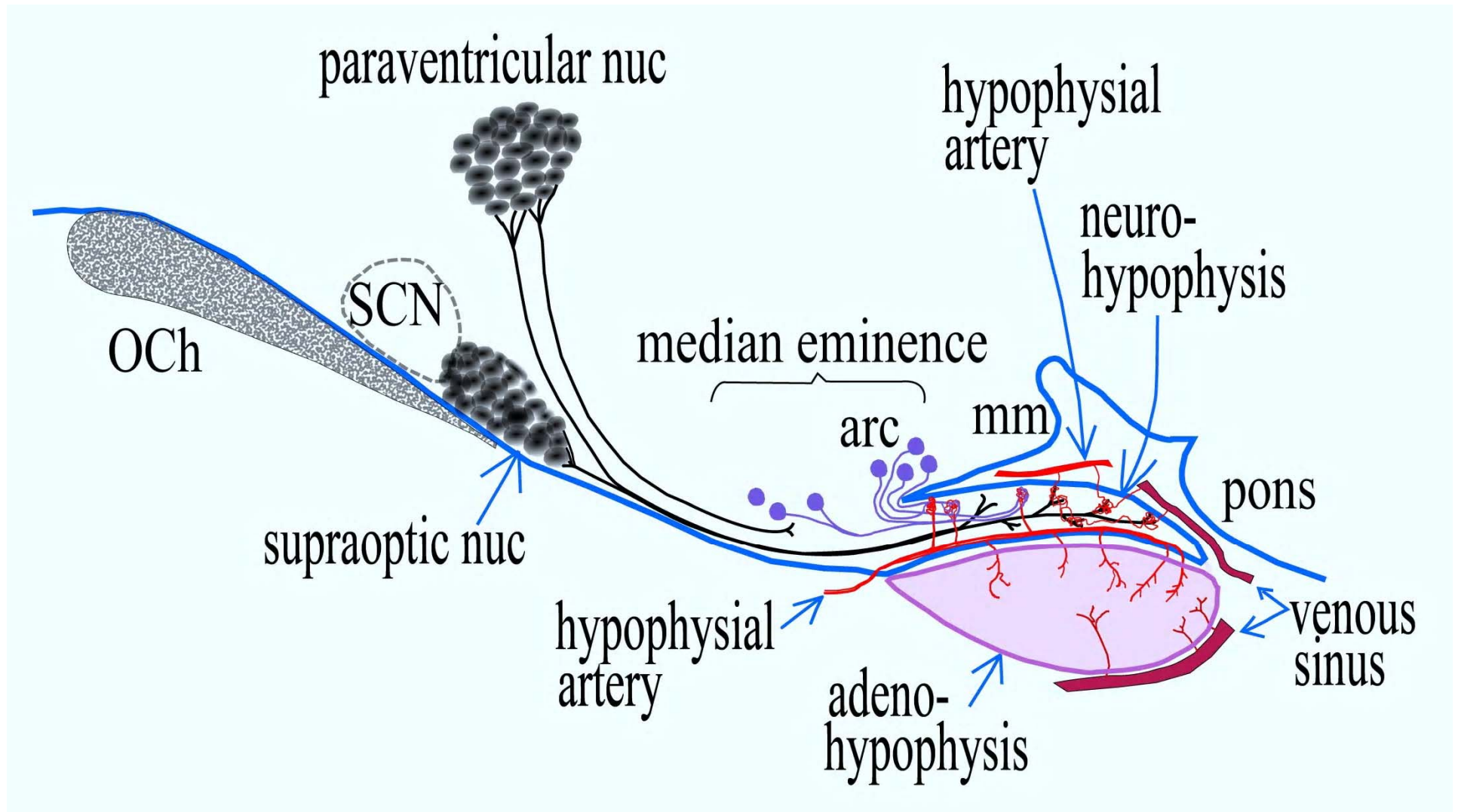


Fig 25-2

SCN = suprachiasmatic nucleus
arc = arcuate nucleus

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Human pituitary

(Illustrations similar to those in Nauta and Feirtag.)

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Please see figure 19.6 of: Brodal, Per. *The Central Nervous System, Structure and Function*. 3rd ed. Oxford University Press, 2003. ISBN: 9780195165609.

Fig 25-2

Questions, chapter 25

Oxytocin
Vasopressin (Anti-diuretic)

4) What hormones are secreted into the bloodstream in the posterior pituitary (neurohypophysis)? Give examples of hormones secreted in the anterior pituitary (adenohypophysis).

Gonadotrophins
Growth hormone
Adrenocorticotrophic hormone (ACTH)

5) What is diabetes insipidus?

Effects of damage to the stalk of the pituitary or to the neurohypophysis, blocking ADH secretion: Symptoms include polyuria and polydipsia.

6) What homeostatic mechanisms are associated with the hypothalamus? (Give examples.)

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9.14 Brain Structure and Its Origins

Spring 2014

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