

# Thus, there evolved the major types of functions of the neocortical mantle:

## ■ Location sense

- This set the stage for more and more anticipation of inputs

## ■ Object sense

- This also set the stage for more and more anticipation of inputs, involving both social and non-social objects

## ■ Functions of the prefrontal elaborations of motor cortex:

- Cortical elaboration of complex movement abilities
- More and more **planning** for future actions became possible:
  - Initially the immediate future, later the more distant future as well

## *Questions, chapter 32*

- 6) Discussion question: How does the hippocampal system facilitate the ability to anticipate the stimuli that an animal or person is about to encounter? What neocortical areas are primarily involved?
  
- 7) Contrast the anticipatory activity of the neocortical areas rostral to the primary motor cortex with the anticipatory activity of the multimodal association areas of the parietal and temporal lobes.

# Why neocortex? **Anticipation: The major innovation**

*Evidence from physiology & from brain damage effects*

- **For location sense:** Need for projections from neocortex to and from hippocampal formation (classes 28 and 30)
  1. Head direction information for anticipating changes
  2. Multiple frames of reference retained in multimodal association cortex, especially posterior parietal: Imposed on hippocampus
- **For object sense,** neocortical connections to and from amygdala/ventral striatum, and to dorsal striatum. *Object perception allows prediction/ anticipation of inputs.*
  1. Social objects: living beings that move about
  2. Non-social objects: both moving and fixed
- **Planning: Prefrontal elaborations of motor cortex**
  1. Premotor, supplementary motor: learned movement patterns
  2. Lateral prefrontal: Anticipatory eye movements and other movements, longer-range intentions
  3. Orbital prefrontal: Anticipatory and learned motivations

# Neocortex as anticipator and planner: *Theory*

*with evidence from electrical stimulation and recording, and lesion effects in humans*

- Evolution of anticipatory activity in posterior neocortex, behind the central fissure:
  - The **central model** of expected inputs: Images of objects at specific locations
  - Novelty (unexpected input) causes arousal and orienting responses, with attraction of attention: when the model does not match the inputs.
    - Lab studies by Eugene Sokolov, Moscow, 1960s: Novelty & the “orienting reflex”
  - Suppression of this arousal when inputs are familiar
- Anterior to motor cortex, the same kind of **central model** corresponds to anticipation and planning of actions
  - The model can control **endogenous generation of actions** (what we call **voluntary actions**)
  - The activity of prefrontal cortex affects not only the premotor and motor cortex, but also the posterior association areas, **activating the images relevant to the planned actions**

This kind of view of neocortex was presented by D.M. MacKay in the 1960s, and has been updated more recently.

In computational terms, we can say that the central model of the world (of expected inputs) is a kind of simulation. This is what generates the imagery of lucid dreams (as in hypnogogic imagery/ dream state).

# Ideas about CNS evolution:

## Multiple parallel pathways acting simultaneously

- **Expansions of both striatum and neocortex occurred:**  
They could operate relatively independently
  - However, the striatum in mammals became increasingly dependent on neocortex for inputs.
  - Neocortex expanded more.
- **Distinct expansions of segregated neocortical regions occurred (mosaic evolution of functional modules)**
  - Example: expansion of visual areas in primates (See next slide and class 23.) These areas all act simultaneously.
  - Example: expansions of subregions of somatosensory cortex representing fingers and tongue, with expansion of corresponding regions of motor cortex

**From  
class 23**

## **Evolutionary multiplications of cortical representations of the retina, especially in primates**

Figure removed due to copyright restrictions. Please see course textbook or:  
Allman, John M., and Jon H. Kaas. "Representation of the Visual Field on the Medical Wall  
of Occipital-parietal Cortex in the Owl Monkey." *Science* 191, no. 4227 (1976): 572-5.

**(Left) Microelectrode mapping of visual area M of the owl monkey.**

**(Right) All visual areas thus mapped seen from the lateral side, including areas in  
the posterior parietal, temporoparietal, and inferotemporal neocortex.**

## *Questions, chapter 32*

8) What was probably the earliest parcellation of the pallium in chordates?

*or olfactory and non-olfactory  
" " multimodal*

9) Discuss factors that must have influenced thalamic parcellation during brain evolution.

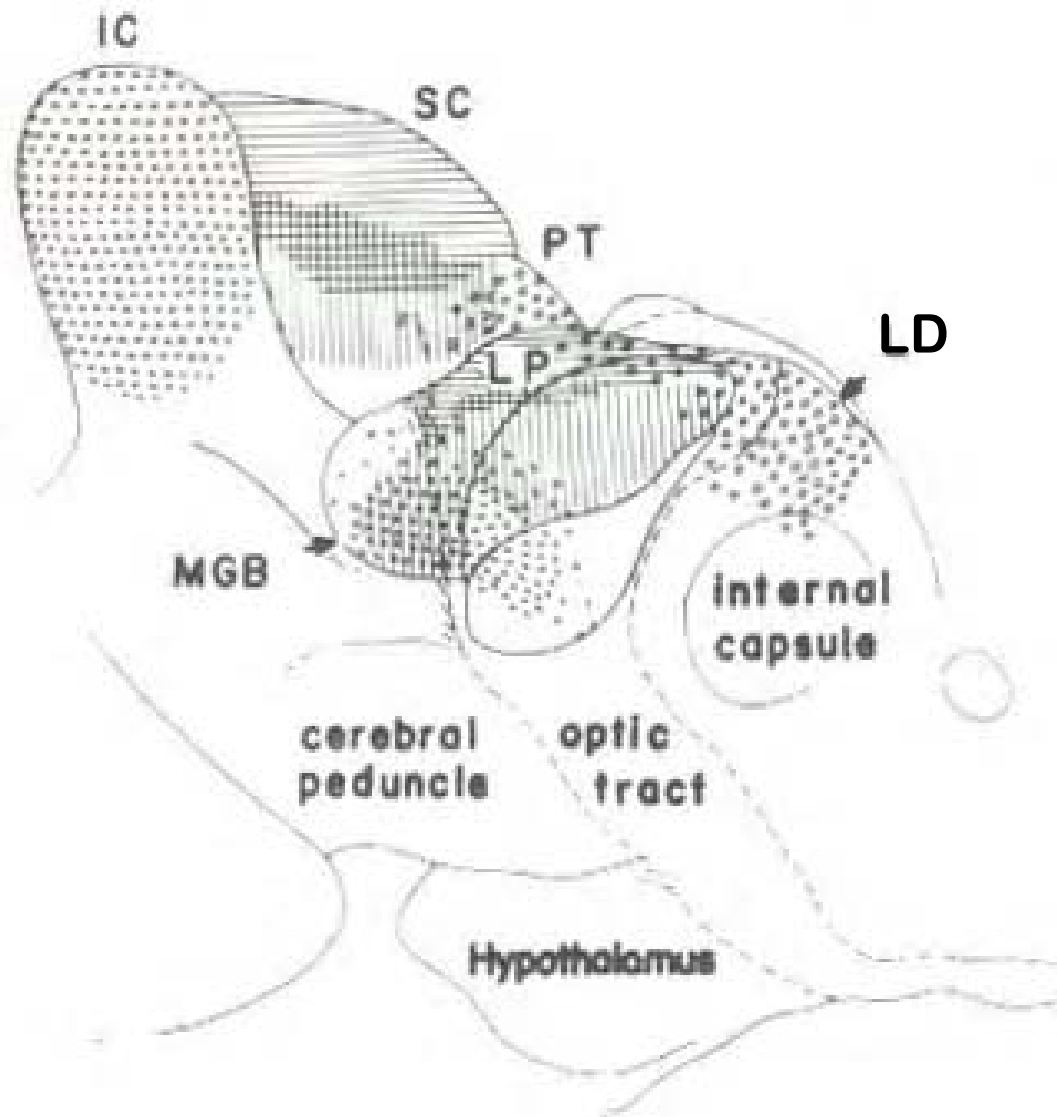
10) Discuss the common belief that the multimodal association areas of the neocortex, including the posterior parietal areas and prefrontal areas, are recent products of brain evolution.

# Ideas about forebrain evolution:

## Suggested major steps reviewed and extended

1. Hagfish-like olfactory dominance of endbrain
2. Invasion of other modalities to give multimodal areas
3. Early dominance of the midbrain tectum—critical for rapid reactions to non-olfactory stimuli:
  - It became the major source of non-olfactory inputs to endbrain
    - *Via* multimodal neurons of paleothalamus and portions of caudal neothalamus
    - *Via* unimodal projections:
      - The spatial pattern in lateral thalamus corresponds to the segregation of modalities in dorsal midbrain (*next slide*).



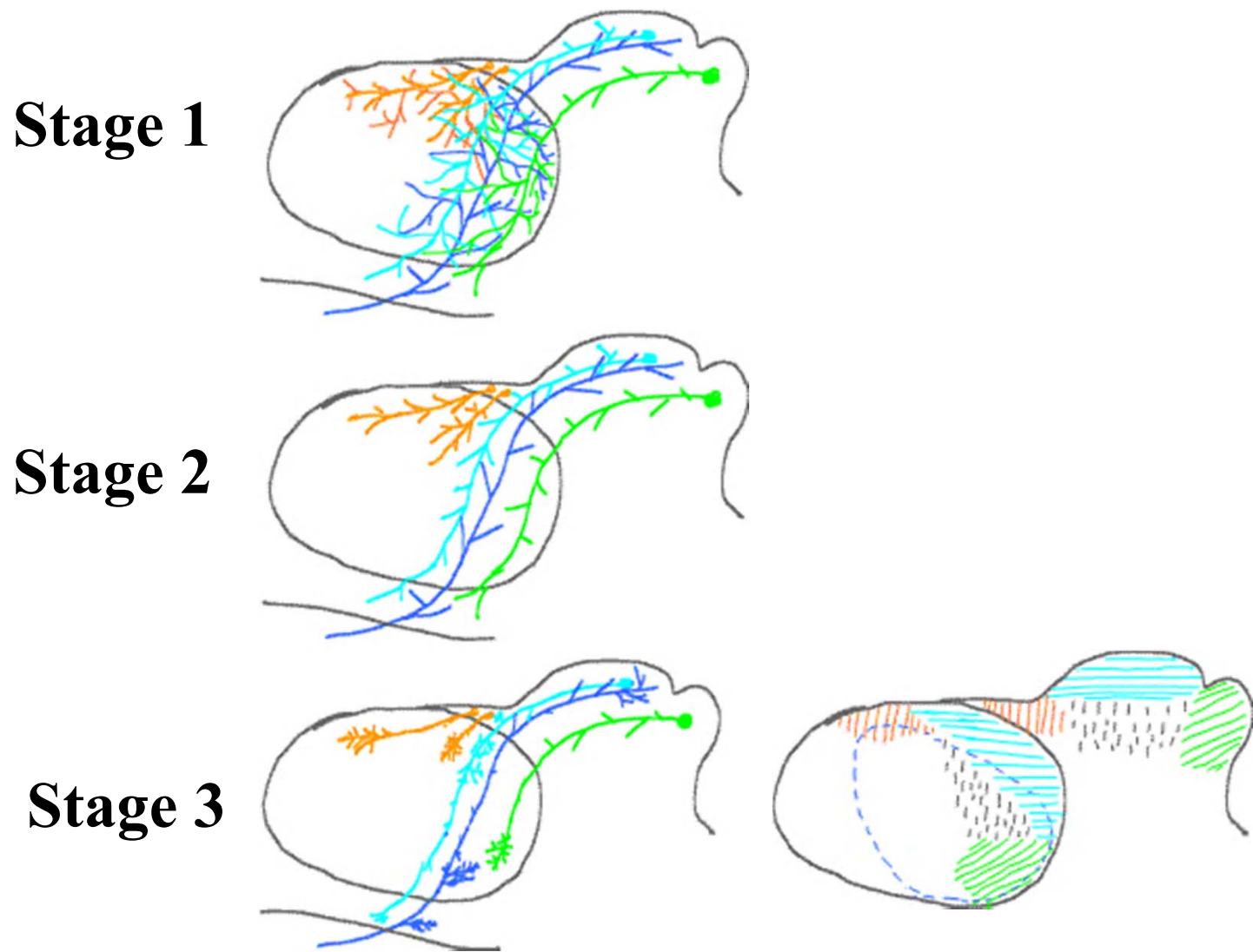


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 Schneider, G. E. *Brain Structure and its Origins: In the Development and in Evolution of Behavior and the Mind*. MIT Press, 2014. ISBN: 9780262026734.

**Fig 32-4**

## Midbrain tectal and pretectal projections to lateral thalamic nucleus

# Thalamic evolution: proposed parcellation of lateral nucleus by competition



**Fig 22-1**

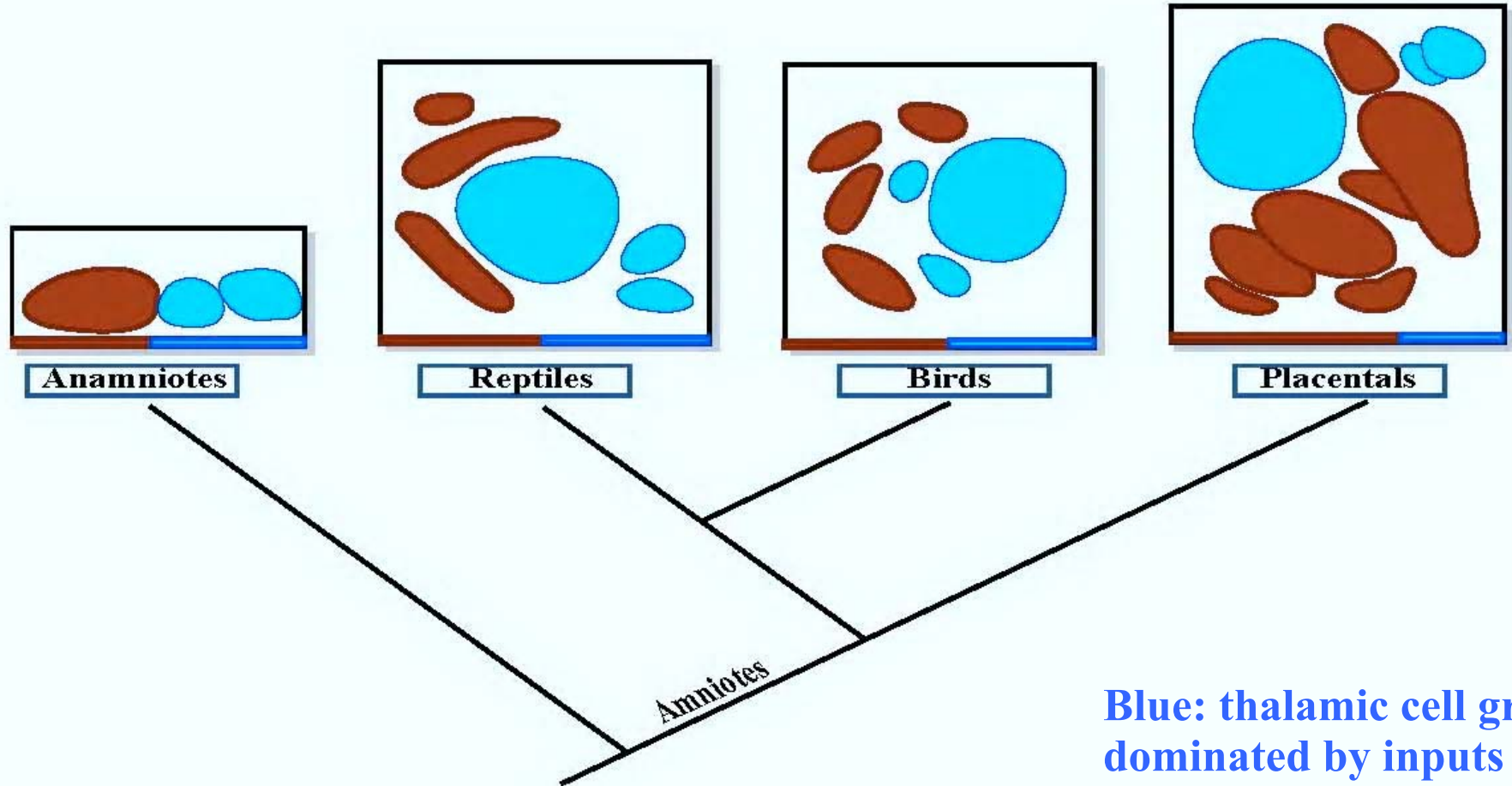
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Schneider, G. E. *Brain Structure and its Origins: In the Development and in Evolution of Behavior and the Mind*. MIT Press, 2014. ISBN: 9780262026734.

# Ideas about CNS evolution:

## Suggested major steps, continued

### 4. Segregation of modalities within multimodal cell groups in forebrain

- Thalamus: Posterior nuclear group and ventral part of LP remain multimodal in modern mammals, abutting unimodal regions. *non-olfactory*
- Proposal: Multimodal convergence was the primitive state of most or all of the thalamus. Then parcellation occurred.
- Correlated changes occurred within neocortex
  - Multimodal thalamus to multimodal association cortex
  - Unimodal thalamus to primary sensory areas and to unimodal association cortex



**Blue: thalamic cell groups dominated by inputs from midbrain tectum**

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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 32-5 Segregation of distinct cell groups in the dorsal thalamus in major vertebrate groups**

## Ideas about CNS evolution:

### Suggested major steps, continued

#### 5. Evolution of pathways to neocortex not synapsing in midbrain

- **VISUAL:** Appearance of a lateral geniculate body within lateral posterior thalamus was very early in evolution, and was probably independent of the route from midbrain tectum to lateral thalamus.
- **SOMATOSENSORY:** Direct pathways from spinal cord and from hindbrain trigeminal nuclei to thalamus probably occurred very early.
- **AUDITORY:** In the auditory system, pathways bypassing the midbrain exist but are not well developed.

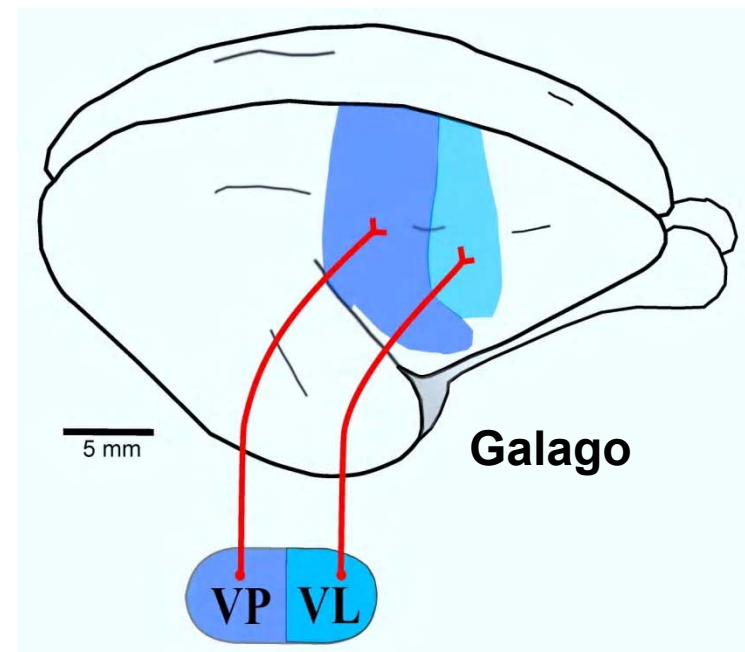
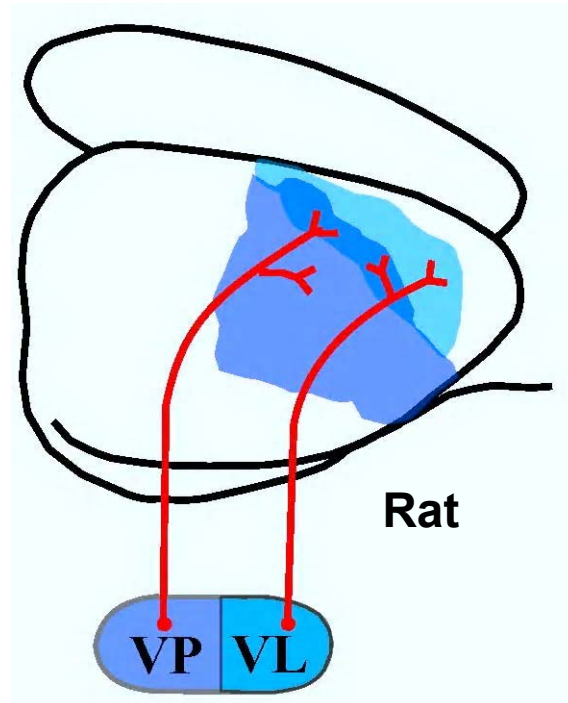
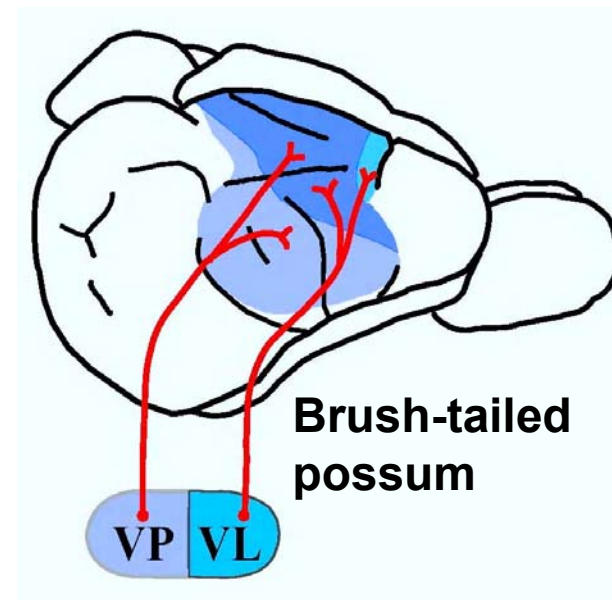
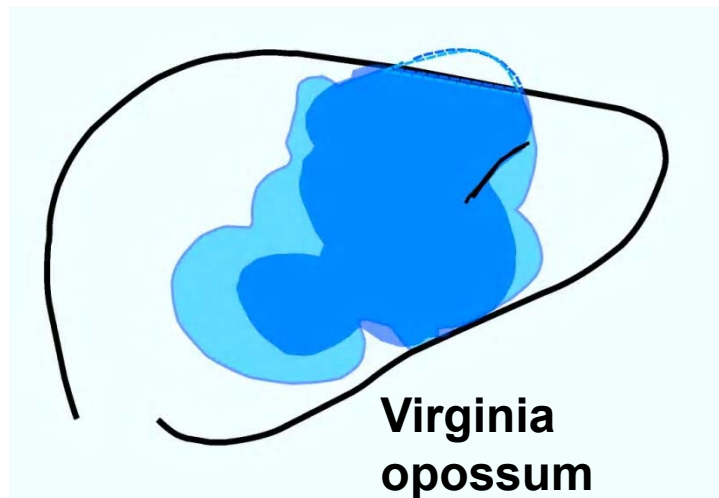
Next: evolution of somatosensory and visual cortical areas.

## **Review: from chapter 15**

### **Parcellation of sensorimotor cortex into distinct motor and sensory areas (the “sensorimotor amalgam” hypothesis)**

In evolution, parcellation probably occurred first in the thalamus, and later in neocortex.

Remember the figure from an earlier class:



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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 15-6**

**VP to somatosensory cortex. VL to motor cortex.**

# Phylogenetic tree of visual neocortical areas

A geniculostriate projection appears to have arisen by the time of the transition to mammals. At least its precursor probably existed much earlier.

*(based on Rosa, 1999)*

Figure removed due to copyright restrictions. Please see course textbook or: Rosa, Marcello G. P, and Leah A. Krubitzer. "The Evolution of Visual Cortex: Where is V2?" *Trends in Neurosciences* 22, no. 6 (1999): 242-8.

Primary visual cortex and adjacent unimodal visual area probably appeared very early in evolution, as all extant mammals have



# **Evolutionary expansions of sensory neocortex by two different means**

- By expansion of total area
- By multiplication of distinct representations of sensory surfaces

# “Old” and “new” neocortical areas (*Striedter p 205*)

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

**All extant mammals studied show the same primary sensory neocortical areas.**

# What the previous picture fails to show:

1. Multimodal regions do exist in between the major sensory areas in hedgehog, hamster, vole.
  - Well studied in voles
  - Unimodal and multimodal association areas are not as distinguishable as in primates. *They are usually all multimodal.*
2. Multimodal inputs<sup>even</sup> to the primary sensory areas, e.g., auditory input to area 17.
  - Parcellation of different sensory areas is not complete

Importance? These neglected facts give us clues about the evolution of the neocortex. Ideas about this evolution have varied, and they continue to be developed as new data are obtained.

# Evolutionary changes in thalamocortical axon trajectories

- Comparative neuroanatomical studies give indications of which pathways are more “primitive” and which are more recent in evolution.

# Amphibian and reptilian dorsal cortex (multimodal)

Image removed due to copyright restrictions. Please see:  
Allman, John Morgan. *Evolving Brains*. Scientific American Library:  
Distributed by W. H. Freeman and Co., 1999. ISBN: 9780716750765.

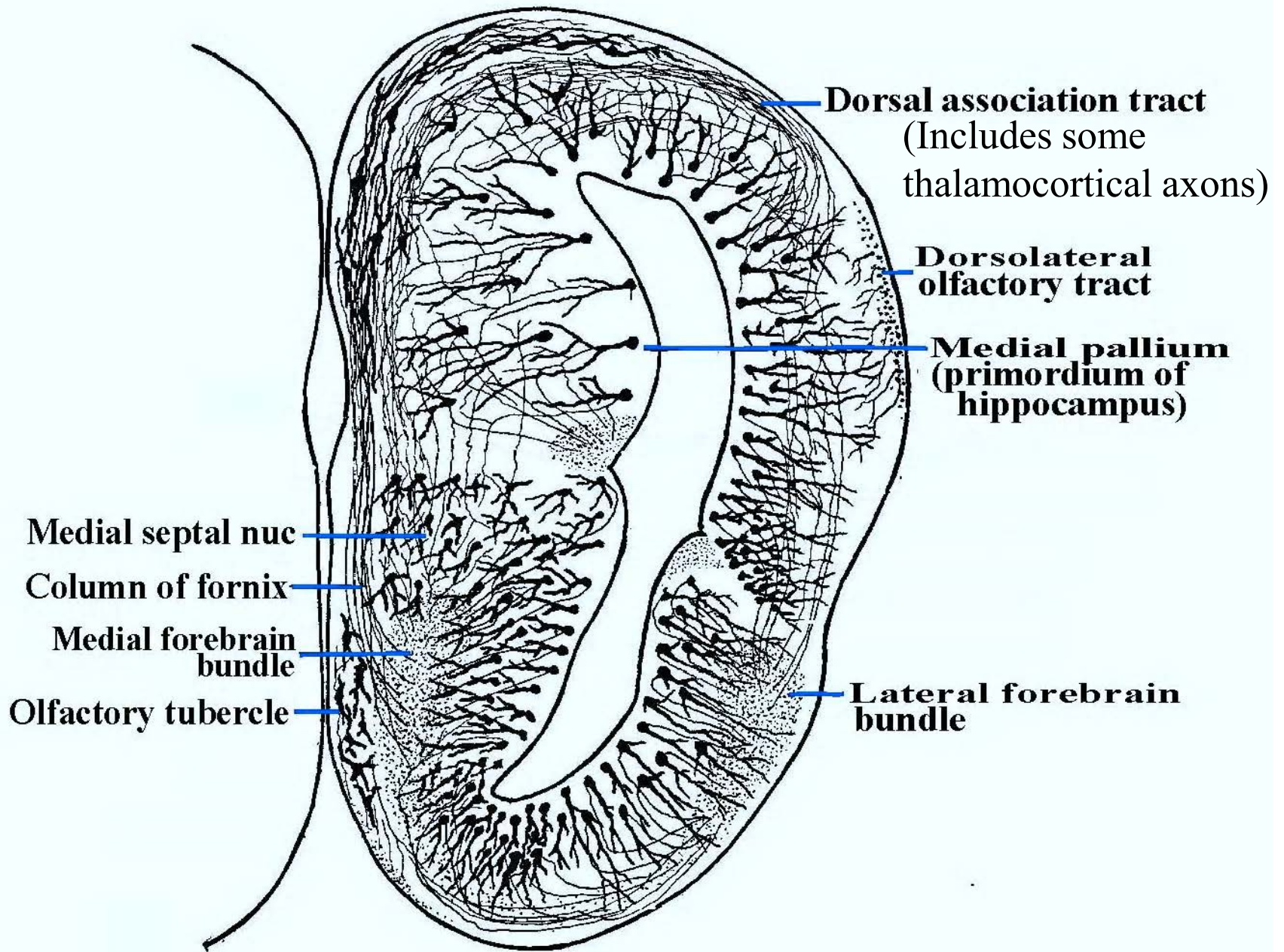


Image is in public domain. Herrick, C. Judson. "The Morphology of the Forebrain in Amphibia and Reptilia." *Journal of Comparative Neurology and Psychology* 20, no. 5 (1910): 413-547.

**Fig 32-6**

## **Frog endbrain, frontal section, Golgi stain**

**Hedgehog neocortex,  
salamander dorsal pallium,  
turtle dorsal cortex**

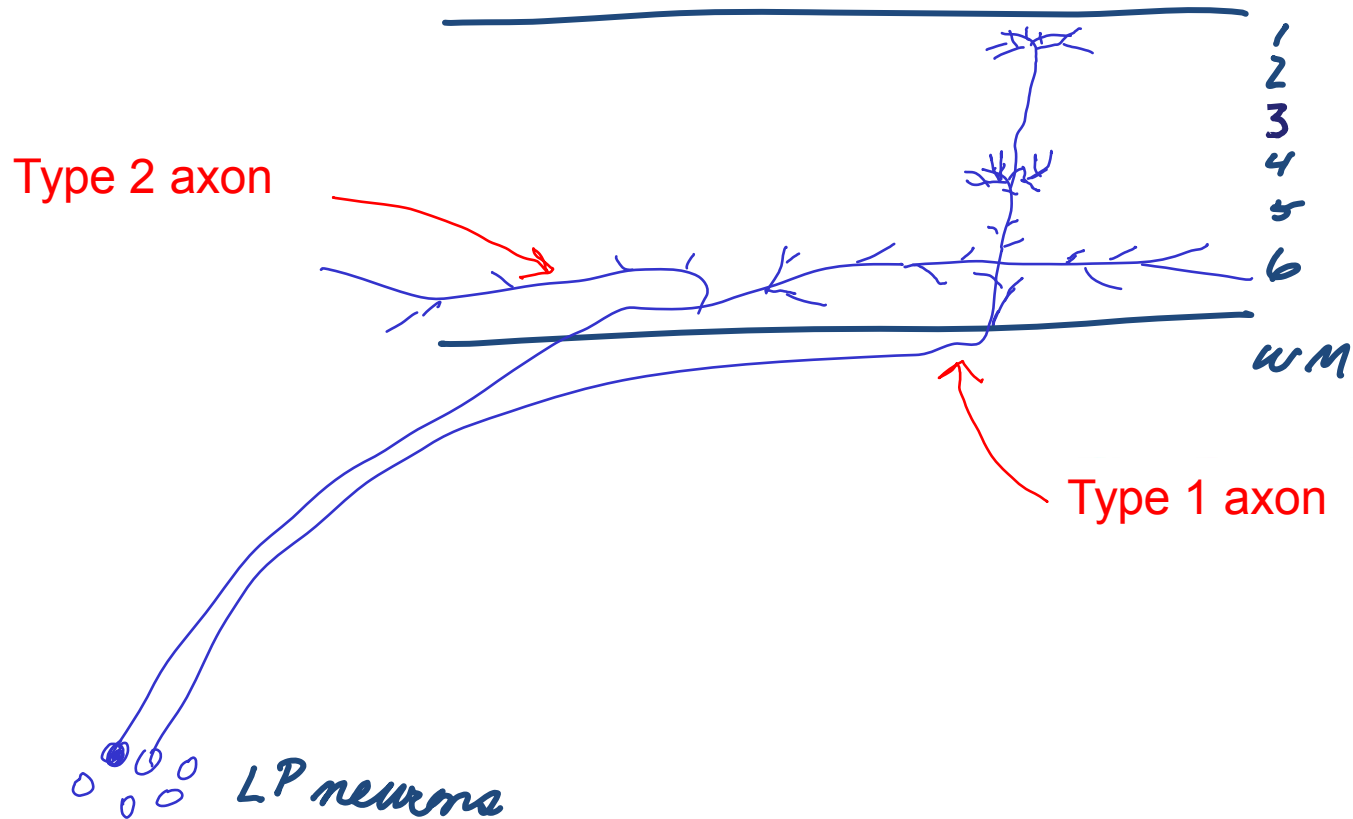
*(Striedter p 270)*

*Note the differences in  
trajectories of axons from  
the thalamus (in red).*

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

*For comparison:*

Trajectories of axons from thalamic nucleus LP in hamster:  
Possible significance for evolution



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**Fig 32-8**



# **Brain structure and its origins**

**MIT 9.14 Class 36**

G. E. Schneider

2014

**Neuronal arrangements of the neopallium, major cortical  
regions and axonal pathways**

*Chapter 33 issues and questions*

# Topics

- ✓ Session 1
  - Evolution and functions of endbrain structures (introduction with review)
  - Introduction to neocortical cell arrangements
  - Comparisons to avian Wulst
- **Session 2**
  - ✓ **Cell types and their connections**
    - **Regions of the expanding neocortex**
    - **Major fiber routes in and out of endbrain**
- Sessions 3-4
  - Thalamocortical connections
  - Association cortex and transcortical connections
  - Thalamic evolution
- Sessions 4-5
  - Cortical development
  - Cortical plasticity with effects of activity

## *Questions, chapter 33*

- 1) Contrast some of the major neuronal cell types of the neocortex: first the spiny excitatory neurons, and second the non-spiny inhibitory neurons. What are the main neurotransmitters? What other characteristics can be used to differentiate them?

What are the names of the two most commonly encountered classes of cortical cells?

Contrast and compare them.

Classifying anything depends on the criteria used. In this case, do you use just morphological characteristics? Neurotransmitters and physiological effects? Molecular specificity of other kinds?

Figure removed due to copyright restrictions. Please see course textbook or:  
Kwan, Kenneth Y., Nenad Šestan, et al. "Transcriptional Co-regulation of Neuronal Migration and Laminar Identity in the Neocortex." *Development* 139, no. 9 (2012): 1535-46.

**Fig 33-1**

The two major shapes of cortical neurons:

Pyramidal & stellate cells (*Nauta & Feirtag, fig. 109 & 110*)

Figure removed due to copyright restrictions. Please see:  
Nauta, Walle J. H., and Michael Feirtag. *Fundamental Neuroanatomy*. Freeman, 1986. ISBN: 9780716717232.

**Neocortical  
interneurons,  
mostly stellate  
in shape:  
Examples of  
specializations**

*Brodal fig. 20.6*

Figure removed due to copyright restrictions. Please see figure 20.6 of:  
Brodal, Per. *The Central Nervous System, Structure and Function*. 3rd ed.  
Oxford University Press, 2003. ISBN: 9780195165609.

There are many more types of interneurons, especially if neurotransmitters and peptides in these cells are considered.

Not all local interconnections within the neocortex are made by the short-axon interneurons:



Figure removed due to copyright restrictions.

Please see course textbook or:

Scheibel, Madge E., and A. B. Scheibel. "Elementary Processes in Selected Thalamic and Cortical Subsystems—the Structural Substrates." *The Neurosciences. Second Study Program* (1970): 443-57.

**Fig 33-2**

**The extent of axon collaterals and dendritic arbors  
in 60-day cat cortex** (drawing from Rapid Golgi sections by  
the Scheibels (1970))

## What are the major **morphological** characteristics of the neocortex?

### *Questions, chapter 33*

- 2) How have neuroscientists defined cortical layers and cortical columns? Name the most common methods.

*Distinguish anatomical and physiological methods*

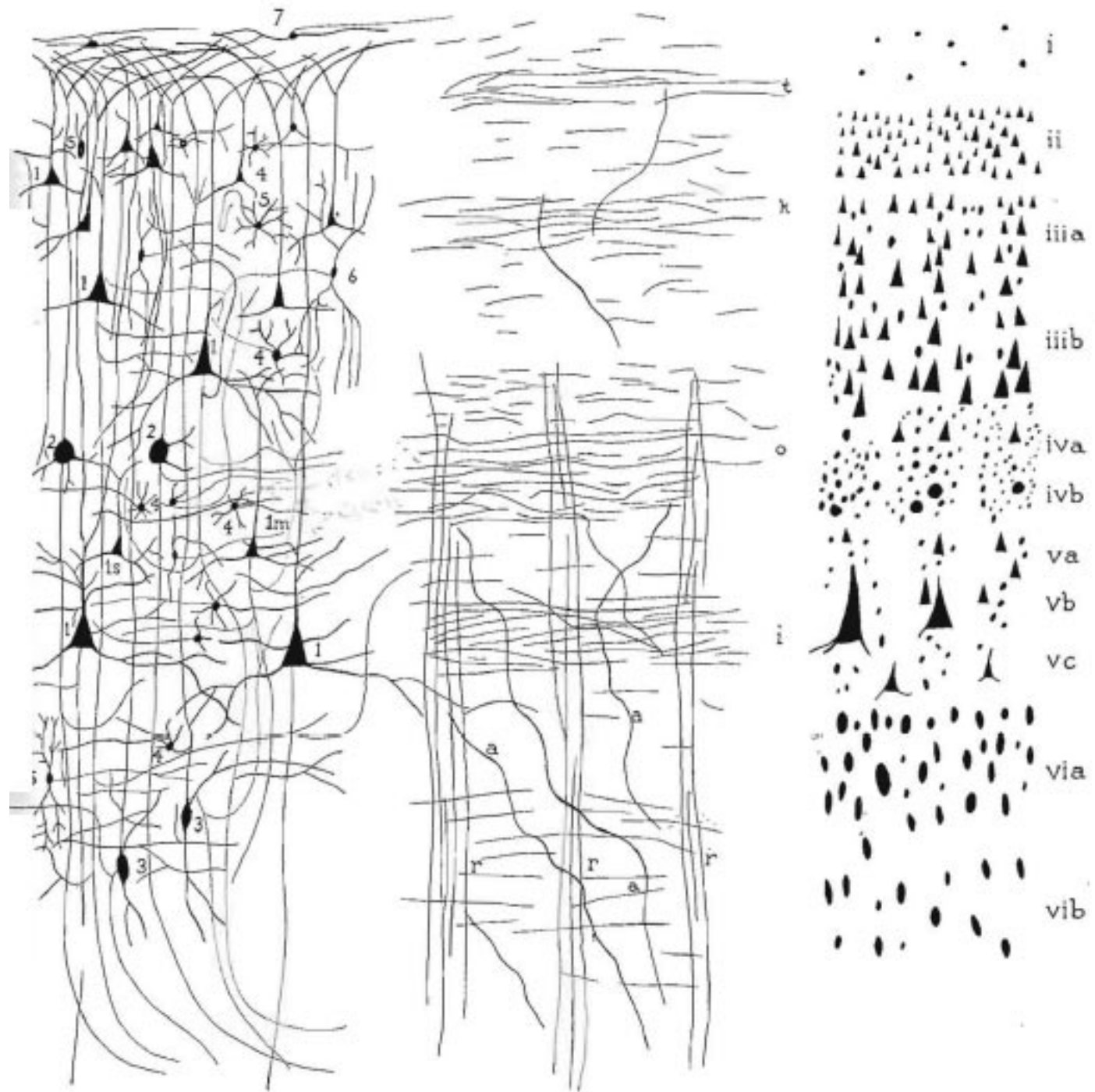
- 3) Describe different methods for differentiating different areas of the mammalian neocortex. How did Brodmann do it?

*Nissl stain for cell bodies*

**(From previous class)**  
**Human neocortex:**  
**3 cytoarchitectural**  
**methods:**

**The dominant cell**  
**type is the pyramidal**  
**cell.**

Is there a consistent  
pattern of connections  
of these neocortical  
cells? See fig 32.2  
(and later in this class)



**Fig 32-1a**

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*From*

*Brodal,*

*2<sup>nd</sup> ed. fig 20.1;*

*3<sup>rd</sup> ed. Fig 21.1*

*Note the names  
of the layers--  
named for cell  
types rather  
than for axonal  
stratification.*

Figure removed due to copyright restrictions. Please see figure 21.1 of:  
Brodal, Per. *The Central Nervous System, Structure and Function*. 3rd ed.  
Oxford University Press, 2003. ISBN: 9780195165609.

Note: The source of this particular figure  
is usually not cited accurately!

## Question on cortical fiber architecture:

What are the **radial fascicles** of the neocortex (*Nauta & Feirtag p. 293-295*)? What are three major groups of cortical output axons found in these fascicles?

...and what are their destinations?

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<http://ocw.mit.edu>

## 9.14 Brain Structure and Its Origins

Spring 2014

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