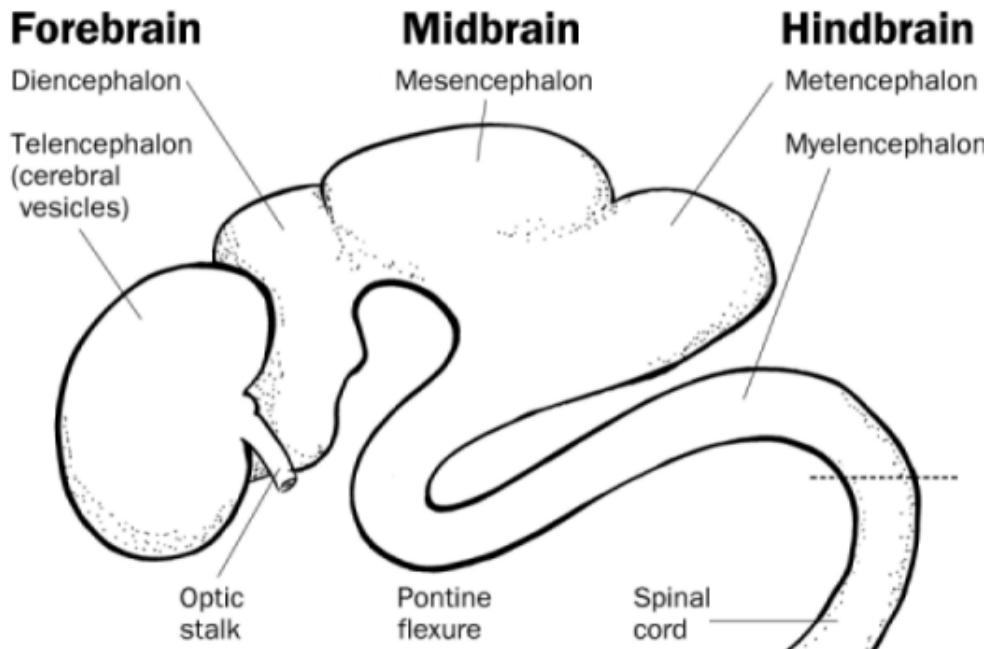
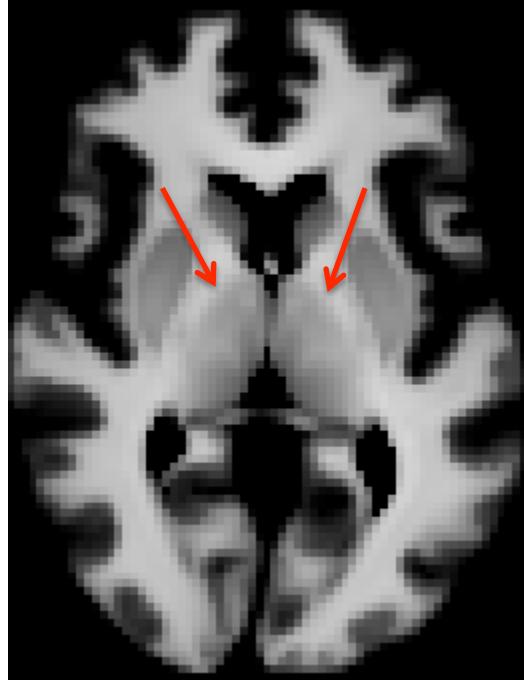


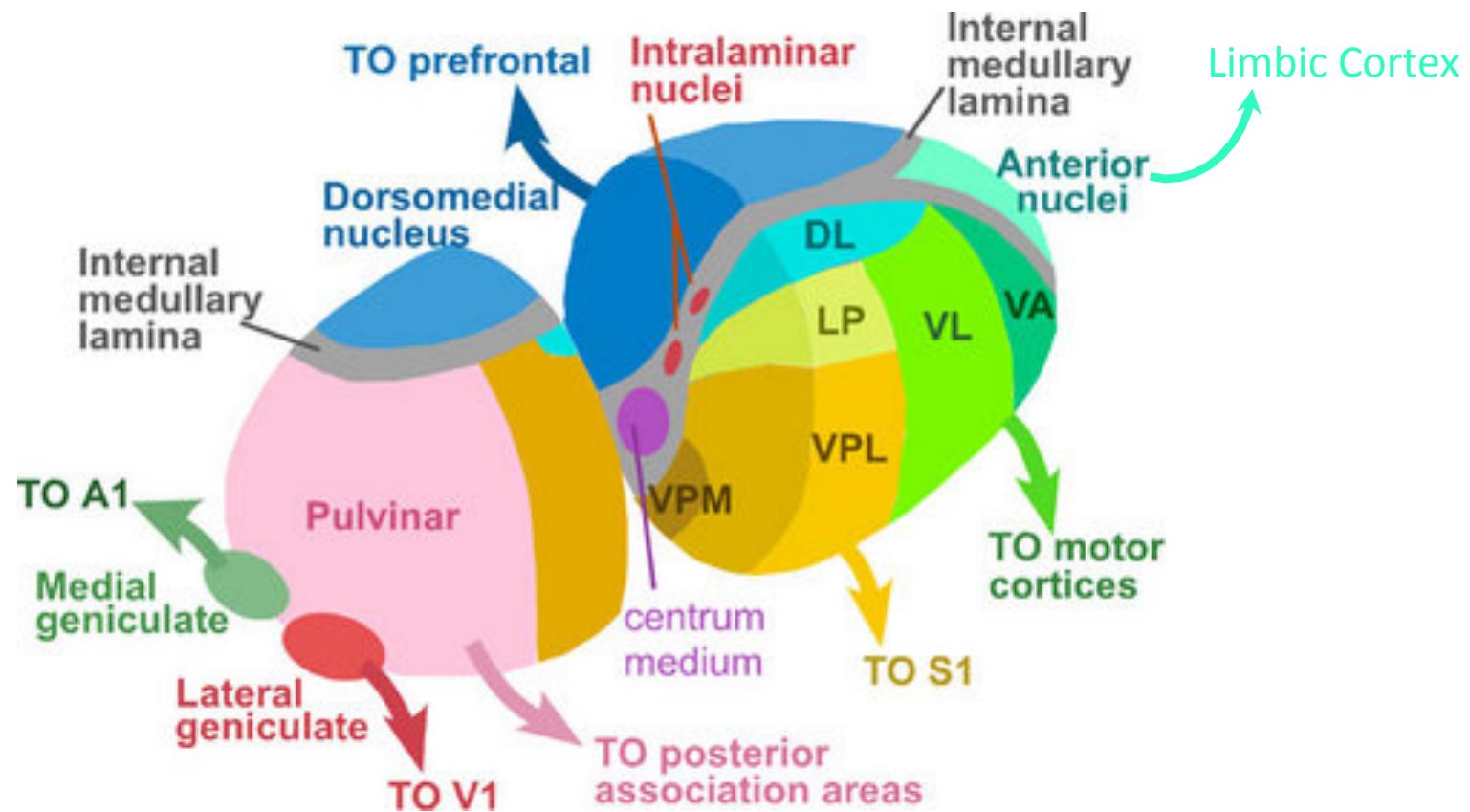
# Organization of Thalamic Connectivity in Monkeys

B.T. Thomas Yeo

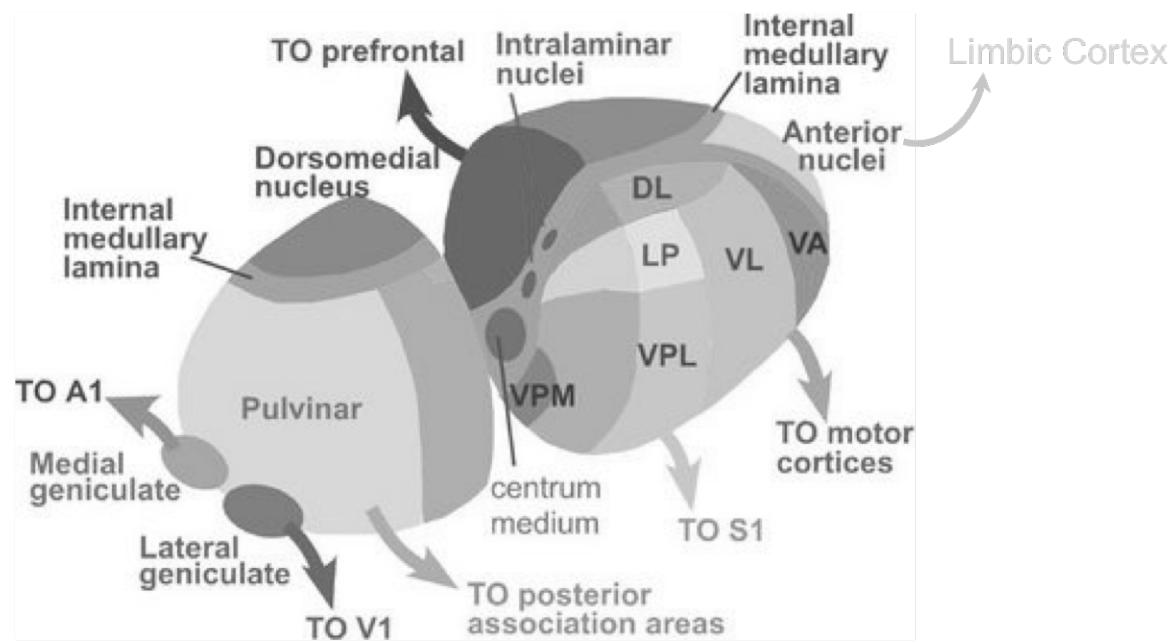
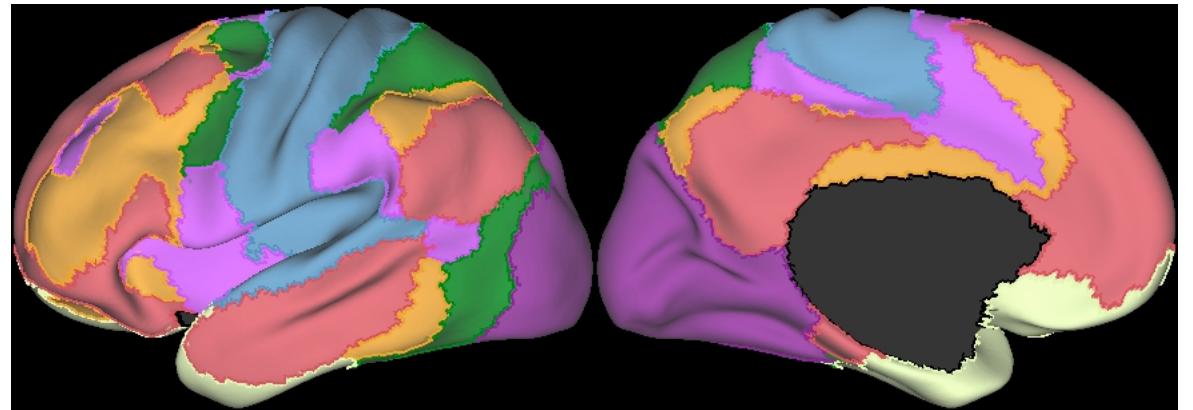


Forebrain	Telencephalon	Cerebral Cortex, Basal Ganglia, Hippocampus, ...
	Diencephalon	Thalamus, Epithalamus, Ventral Thalamus, Hypothalamus, ...
Midbrain	Mesencephalon	Tectum, Tegmentum, Cerebral Peduncles, ...
Hindbrain	Metencephalon	Pons, Cerebellum, ...
	Myelencephalon	Medulla Oblongata, ...

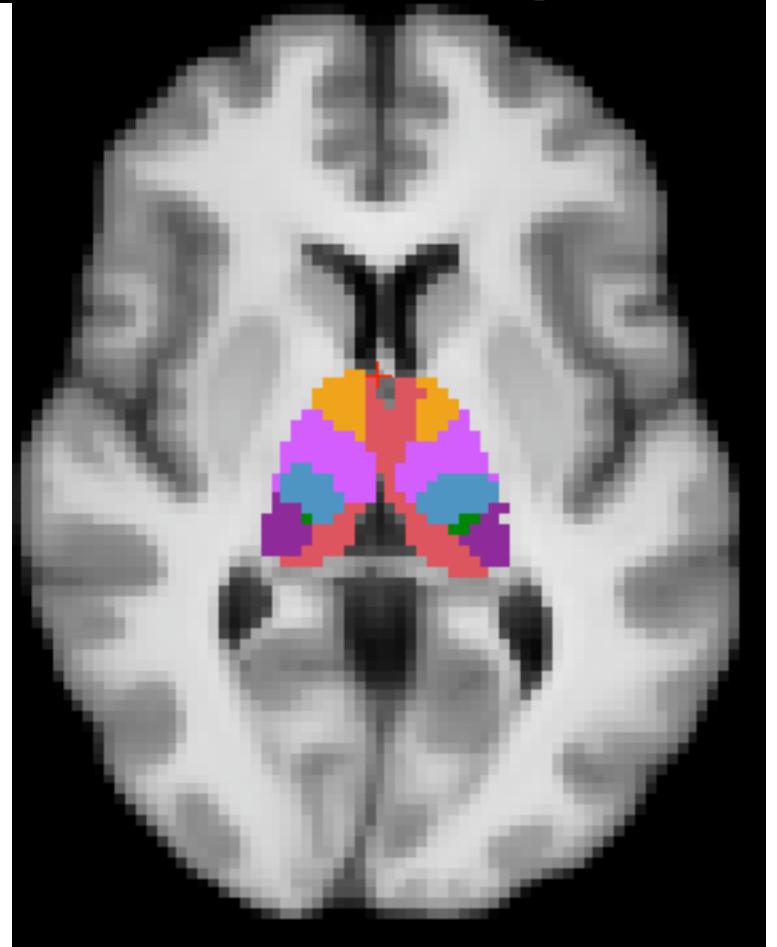
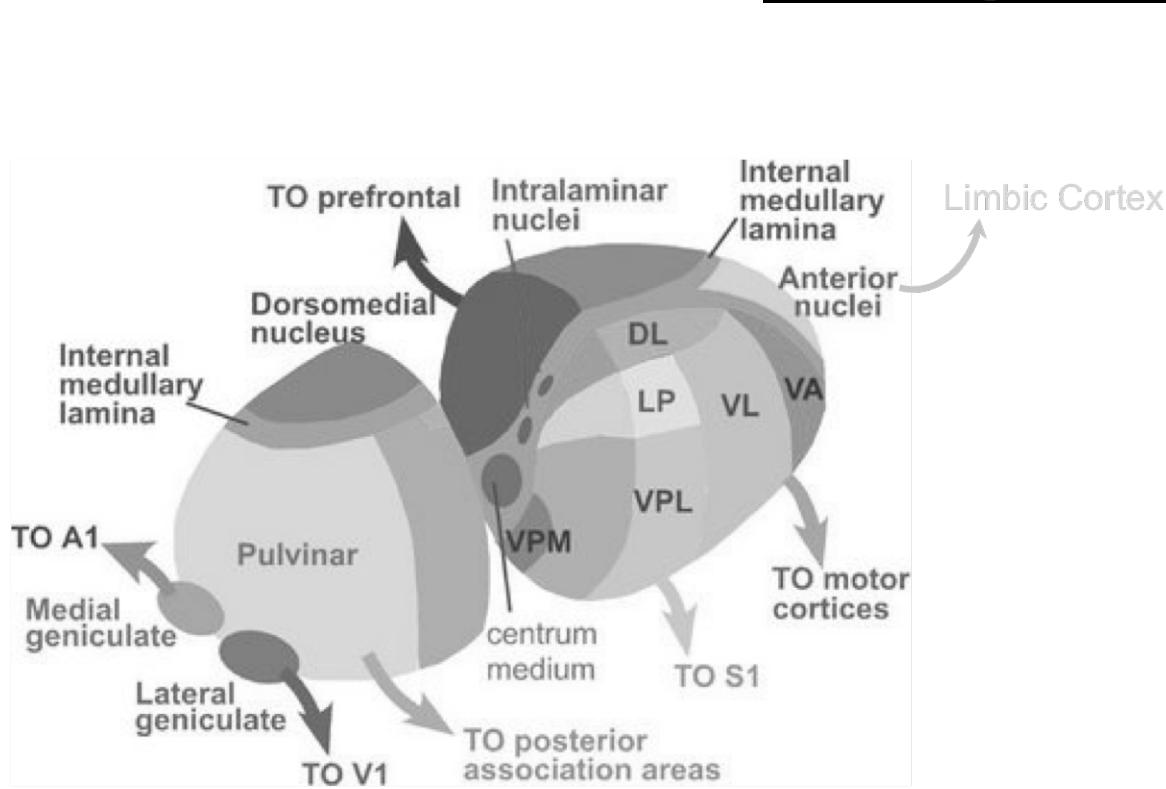
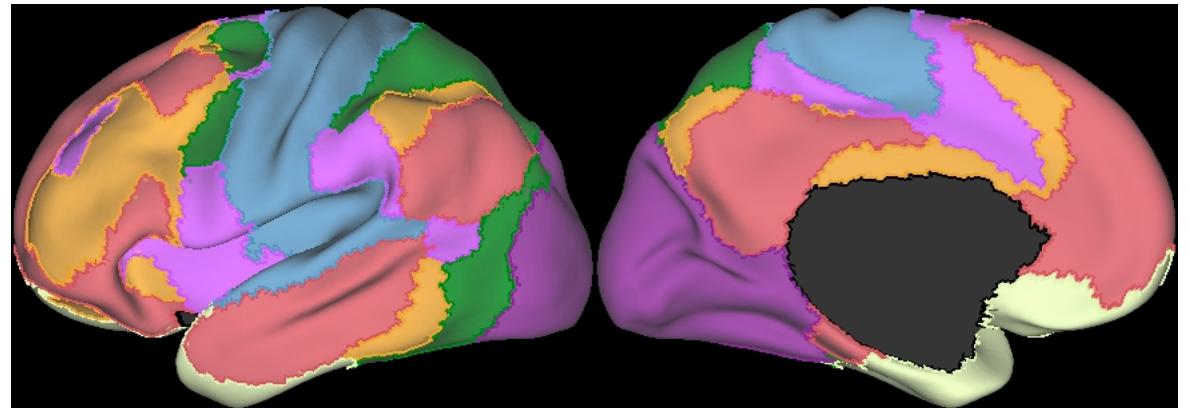
# Cartoon Model of Thalamocortical Connectivity



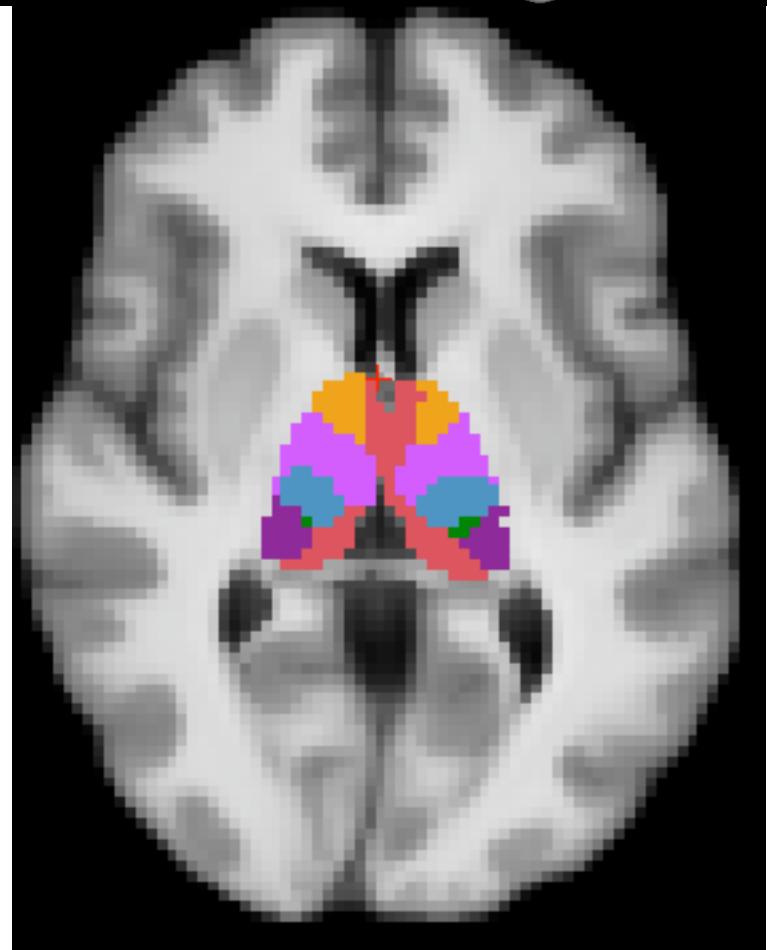
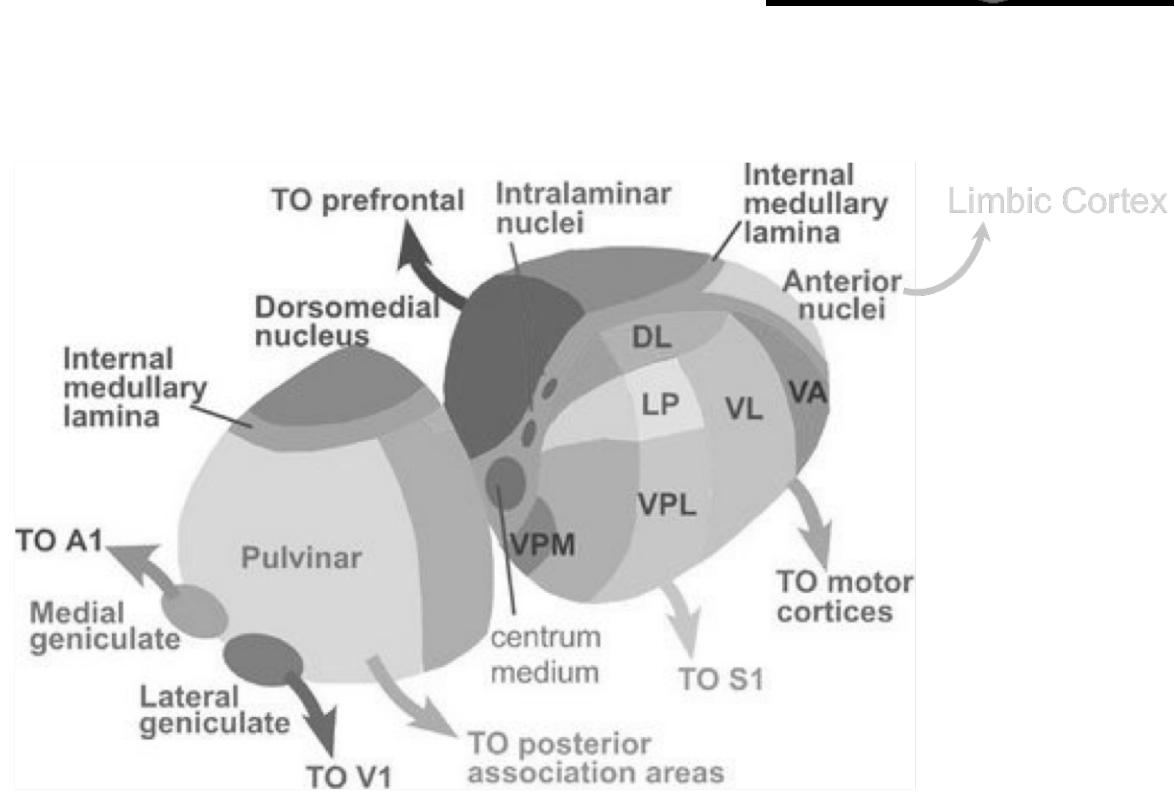
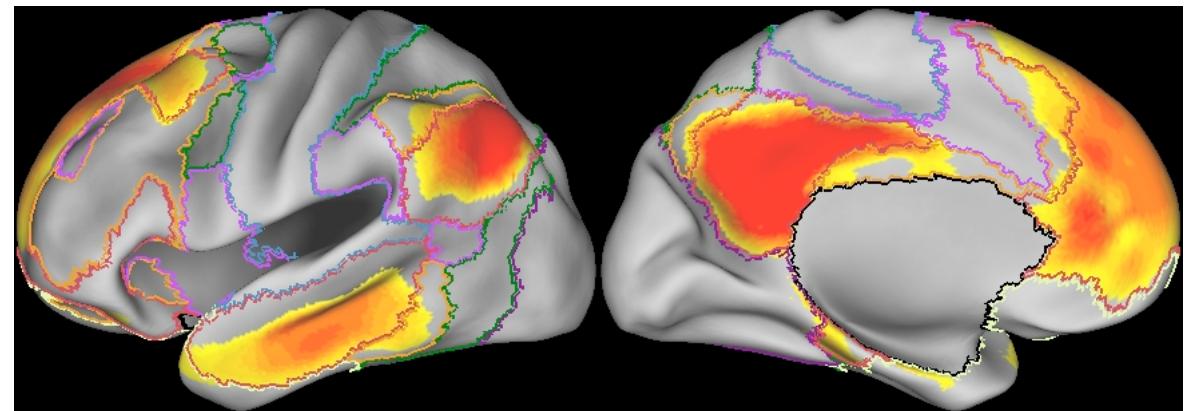
# 7 networks



# 7 networks



# 7 networks



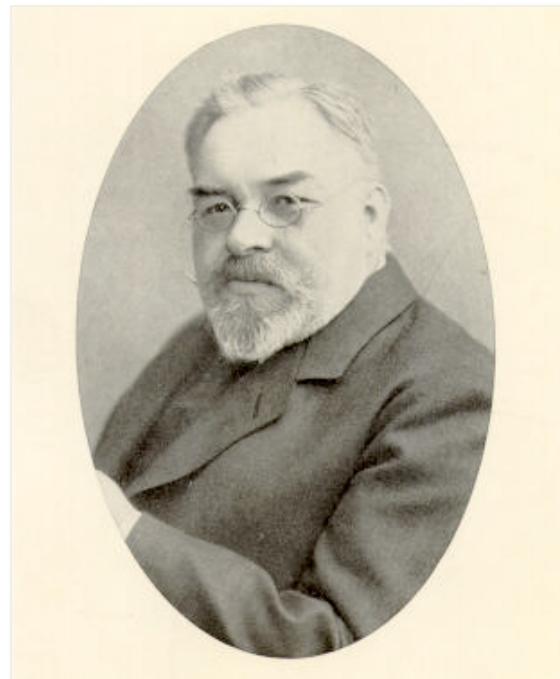
# Outline

- Thalamus: Past to Present
- Modern Tract Tracing

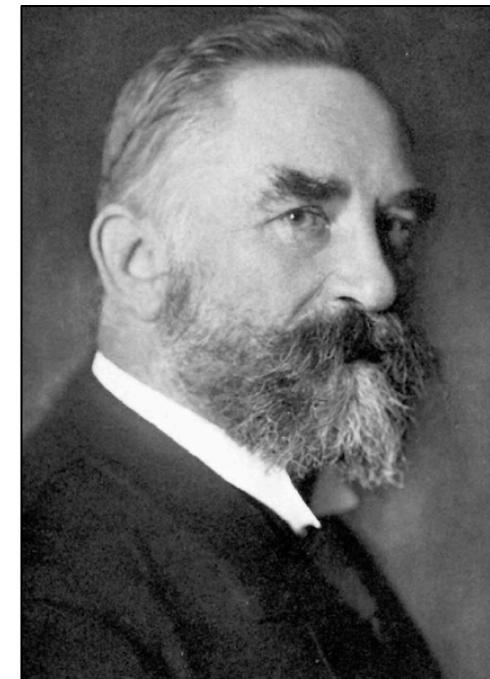
# Early Histology & Tract Tracing



Bernhard von Gudden

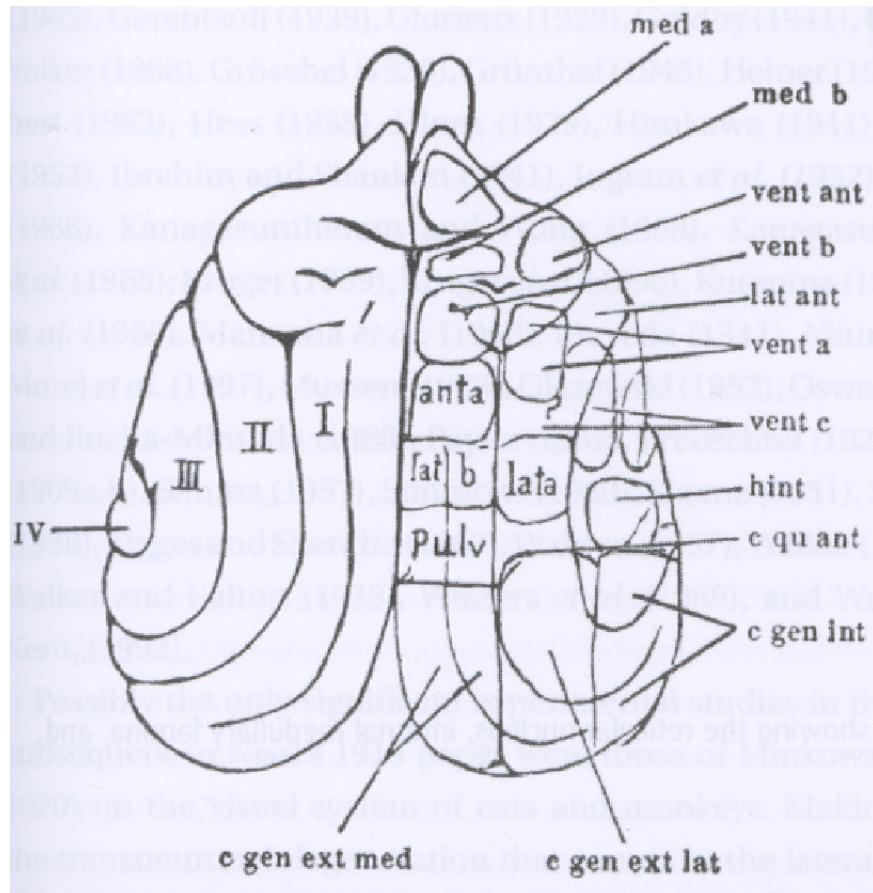


Franz Nissl

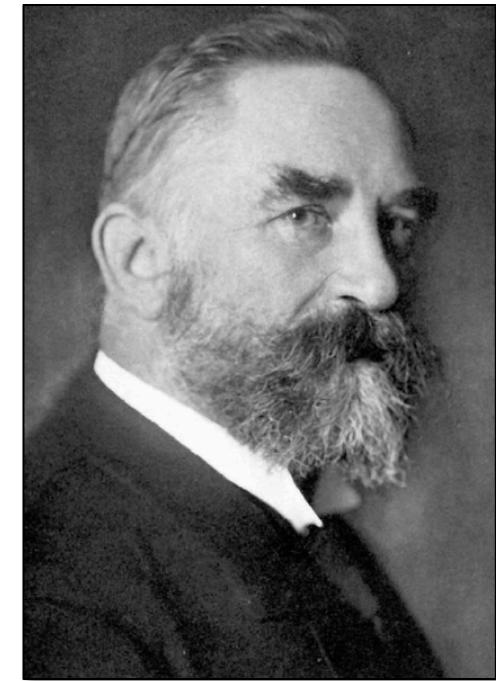


Constantine von Monakow

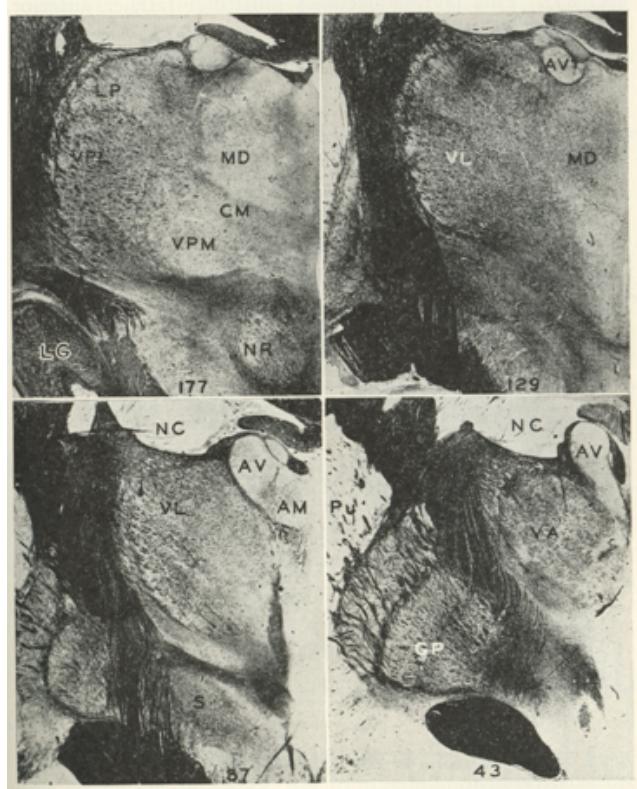
# Early Histology & Tract Tracing



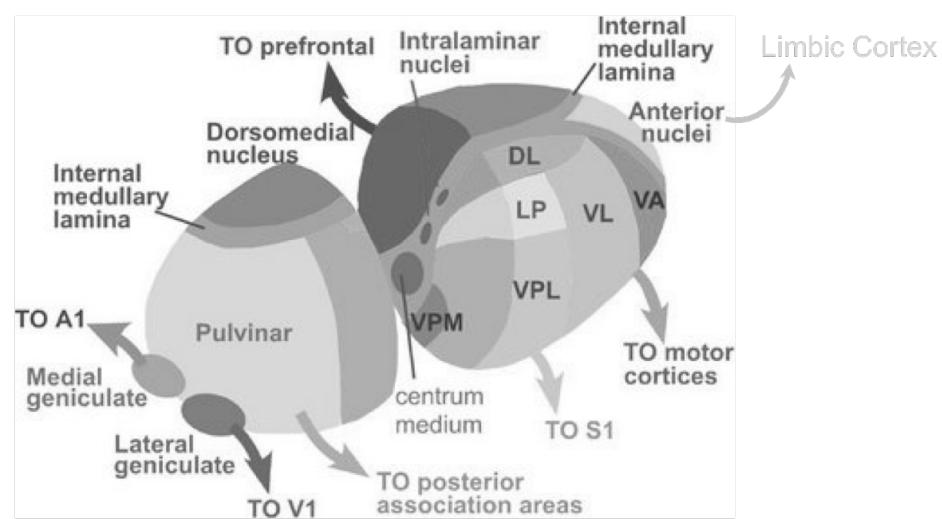
Thalamocortical Projections of Cat Cortex  
von Monakow, 1895

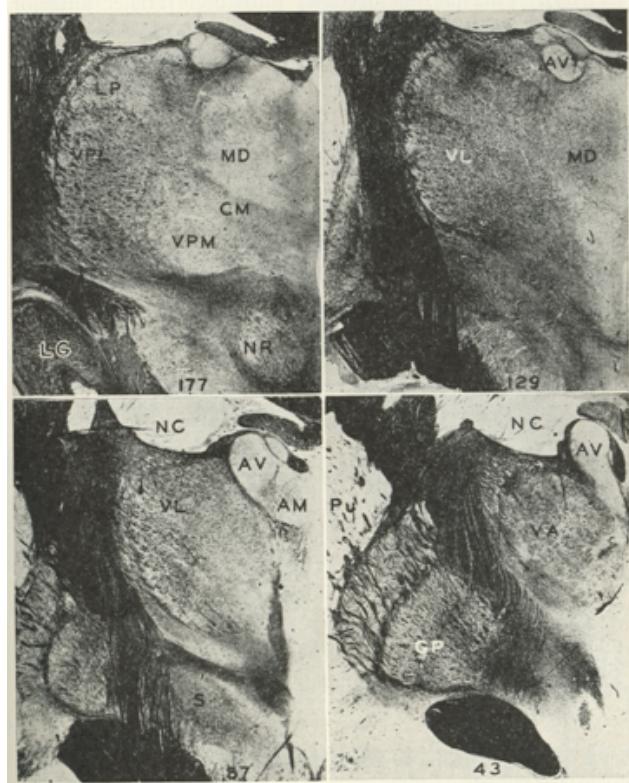


Constantine von Monakow

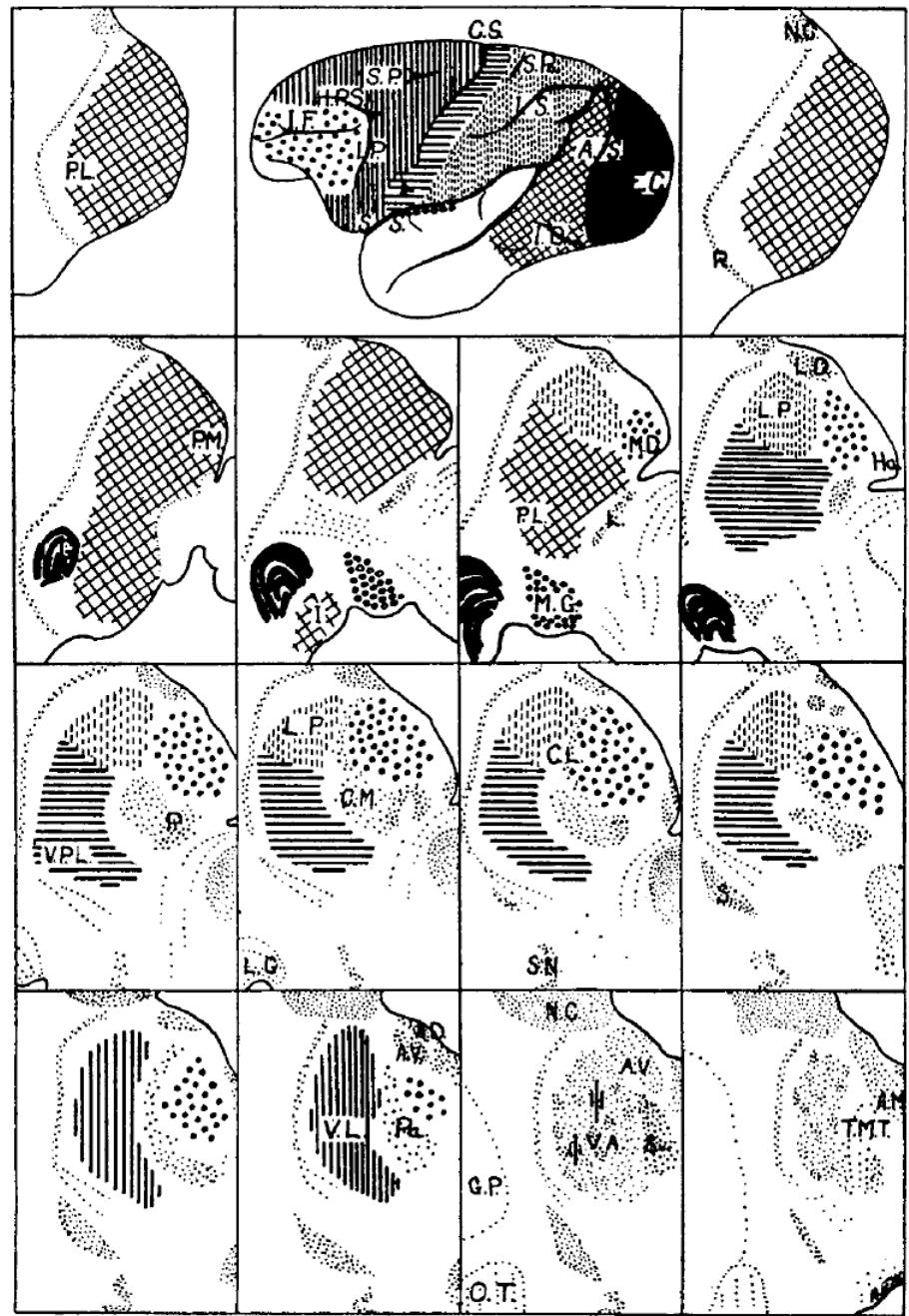
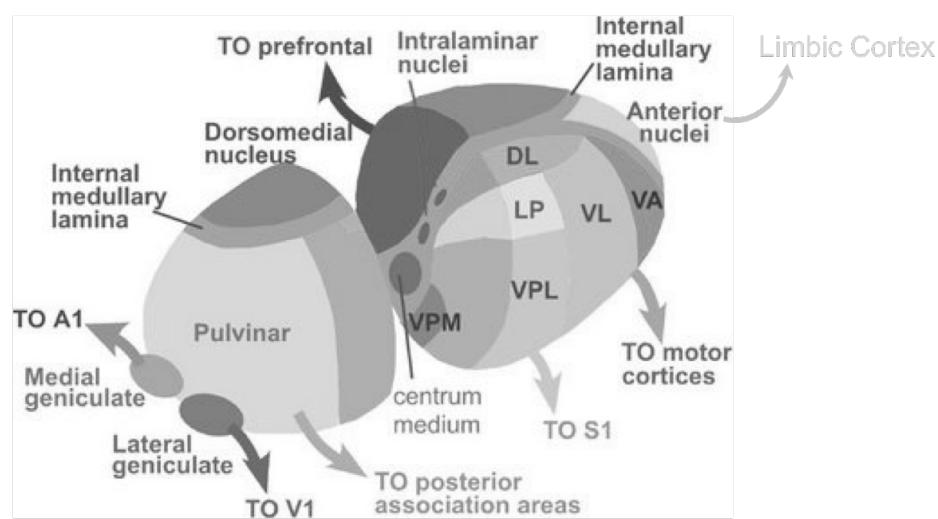


Walker 1938

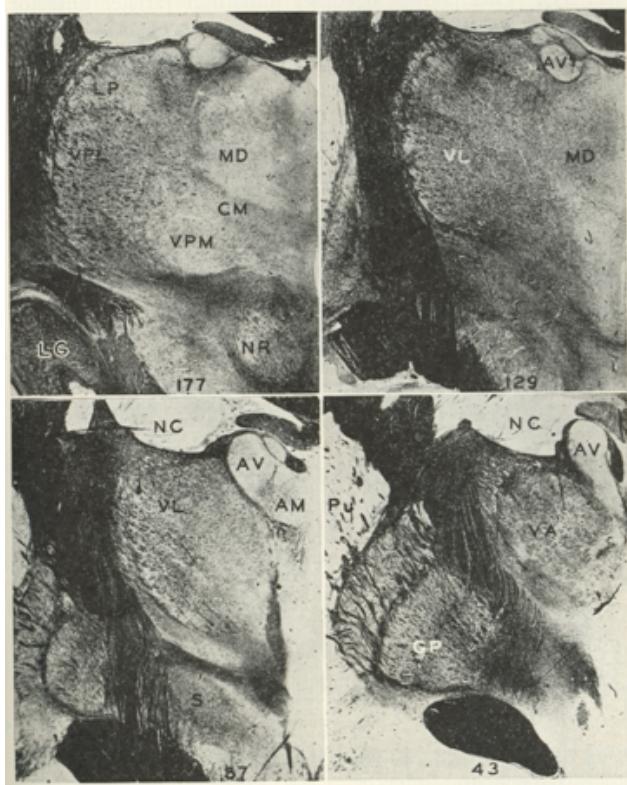




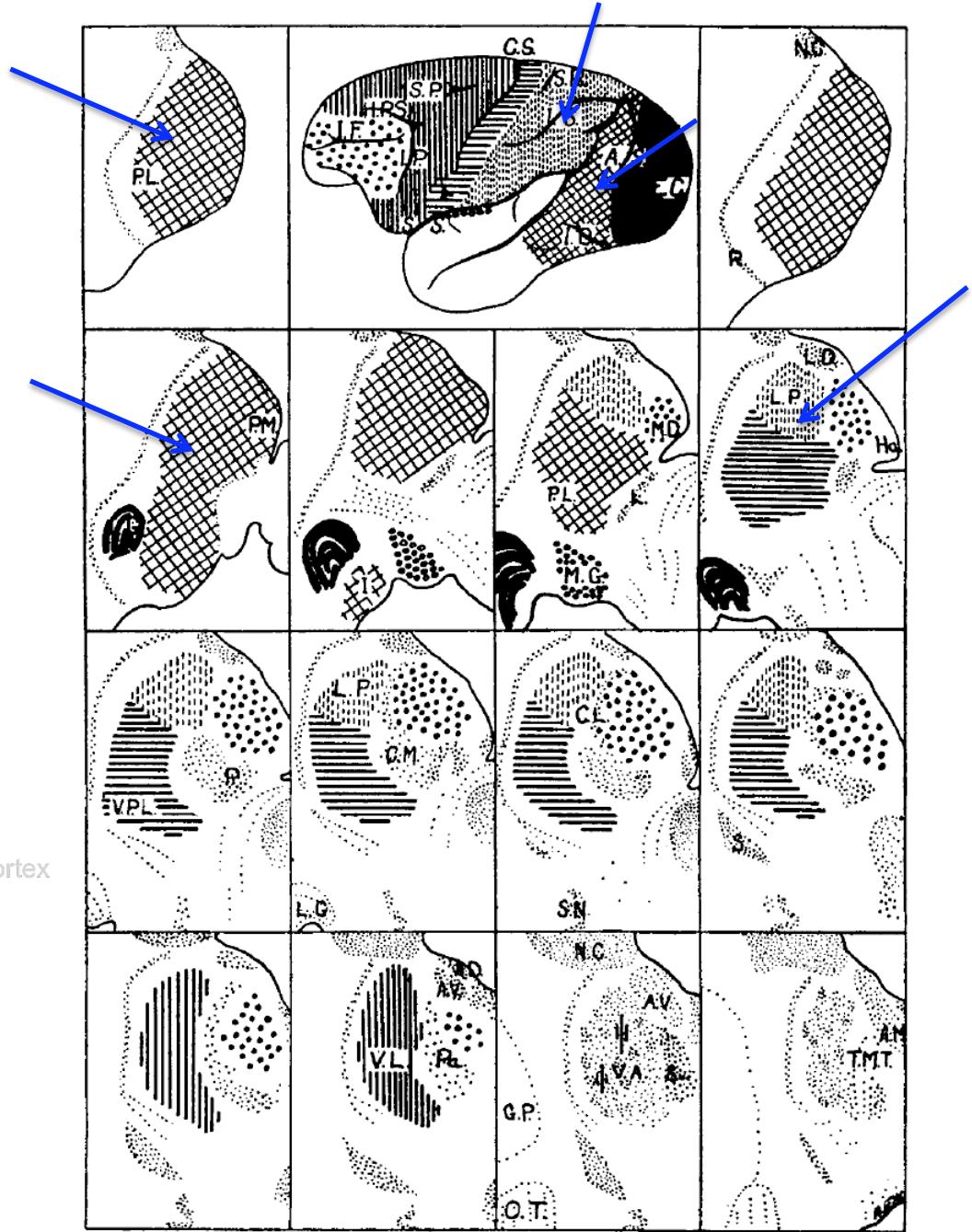
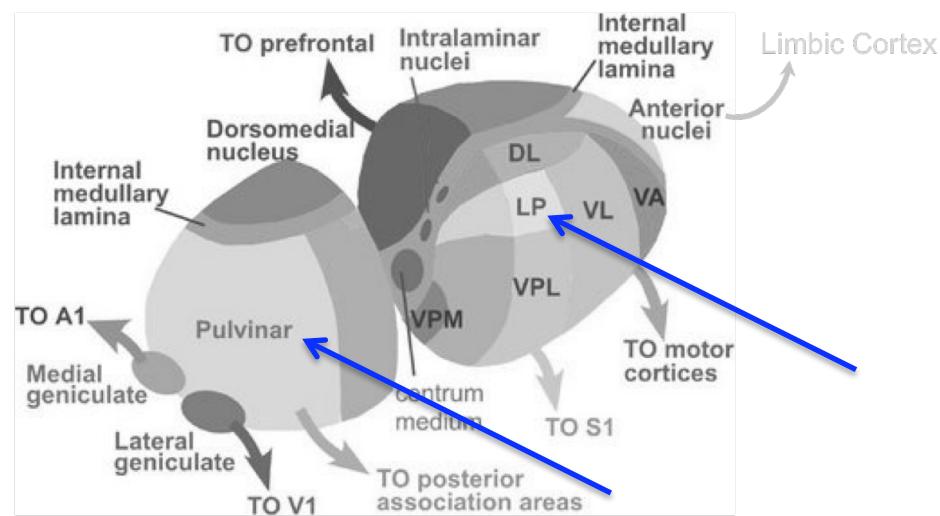
Walker 1938



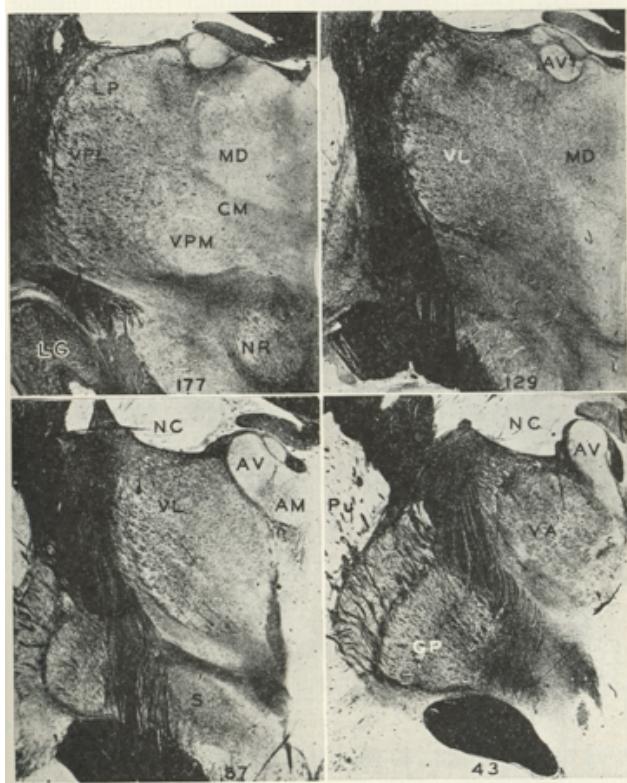
Walker 1936



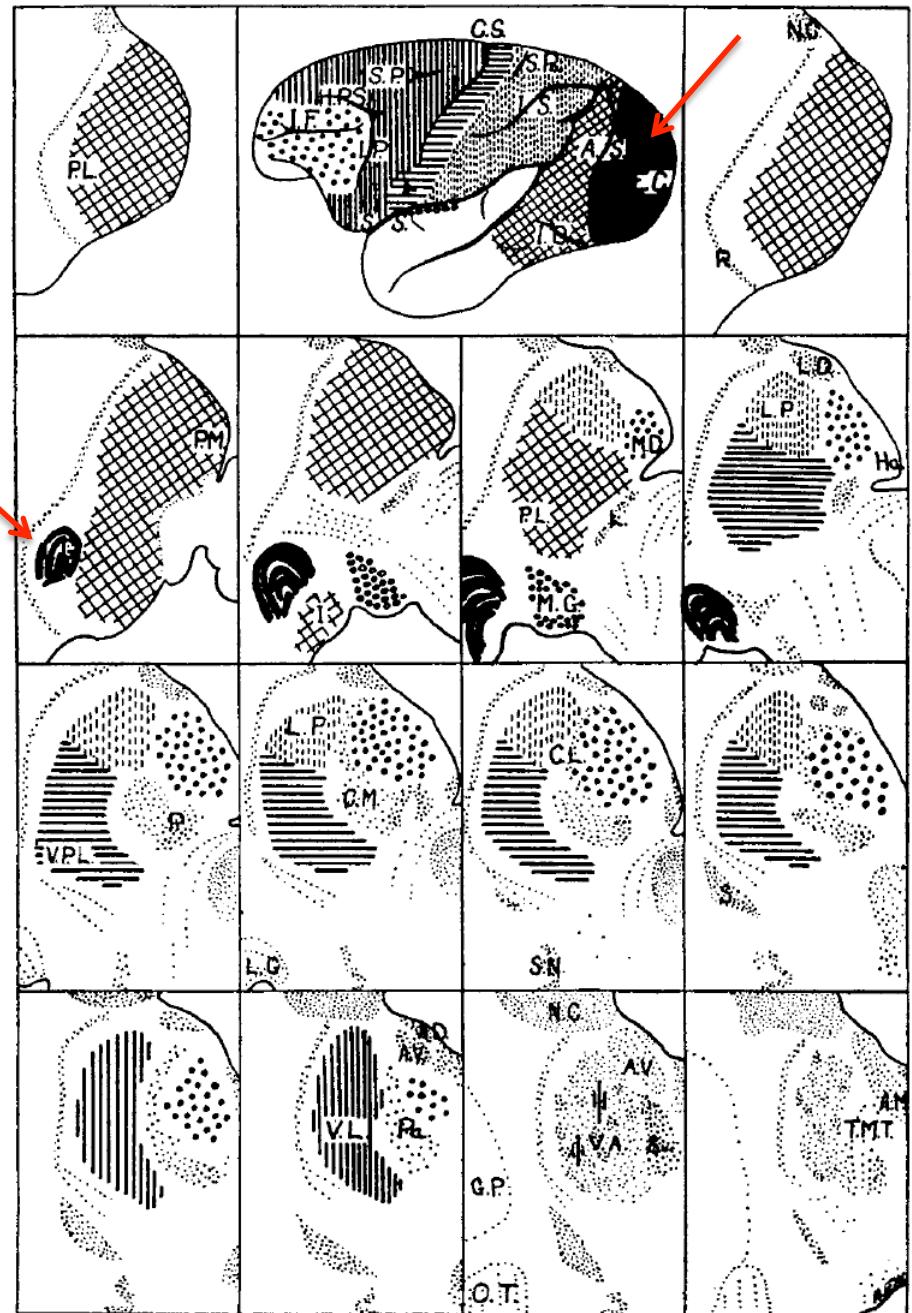
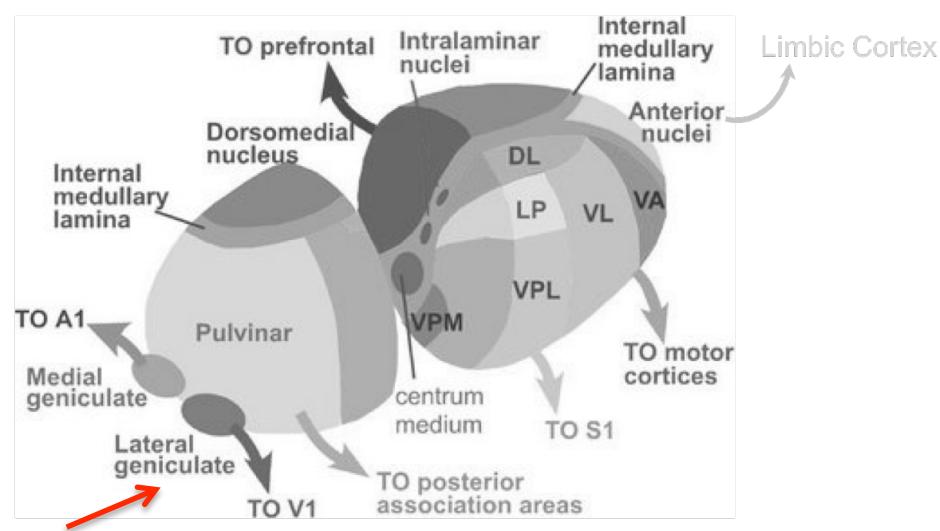
Walker 1938



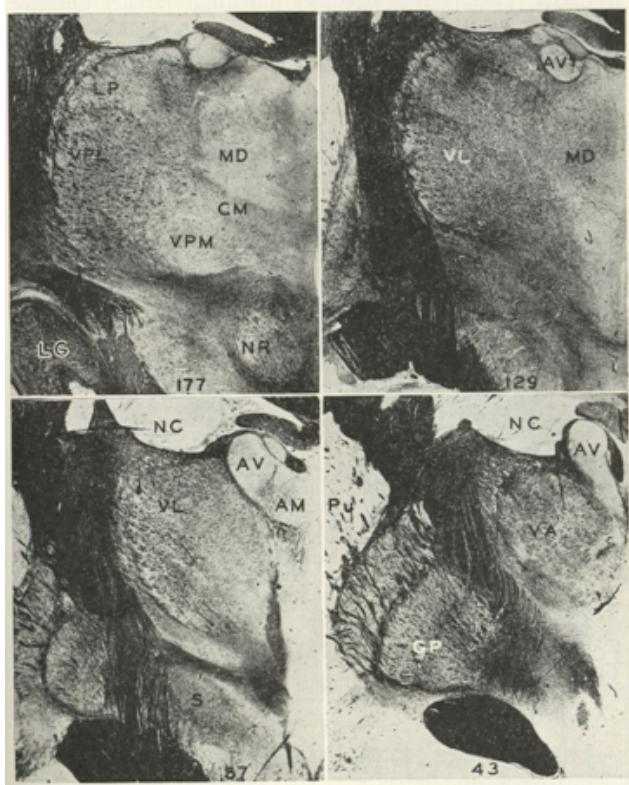
Walker 1936



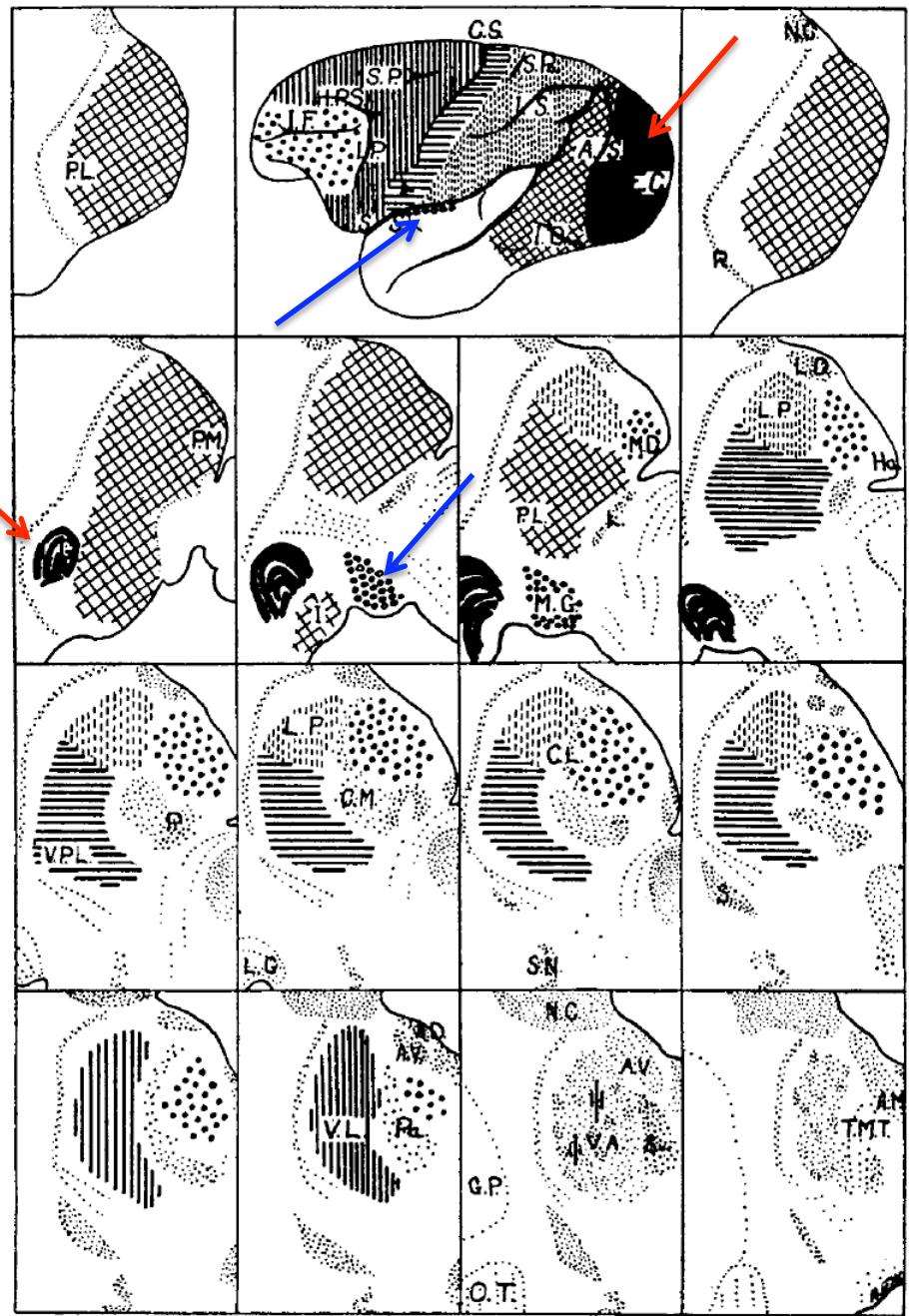
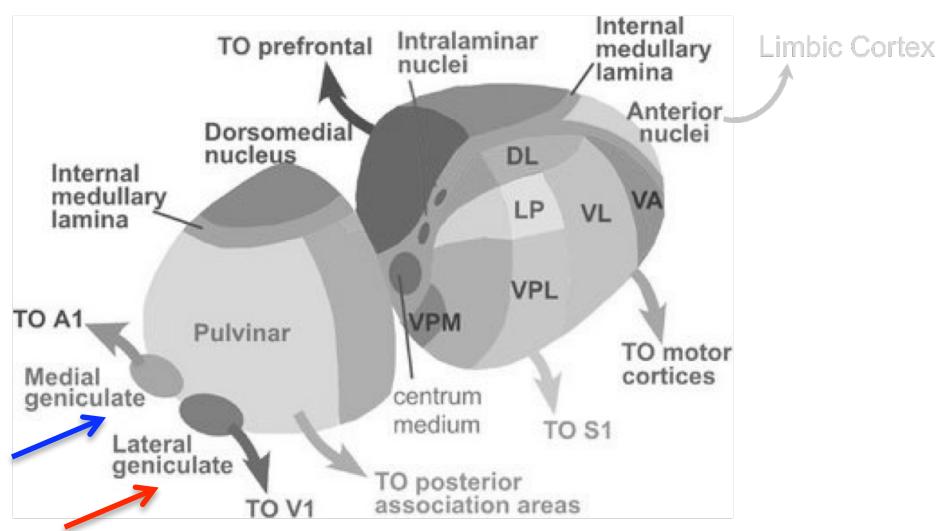
Walker 1938



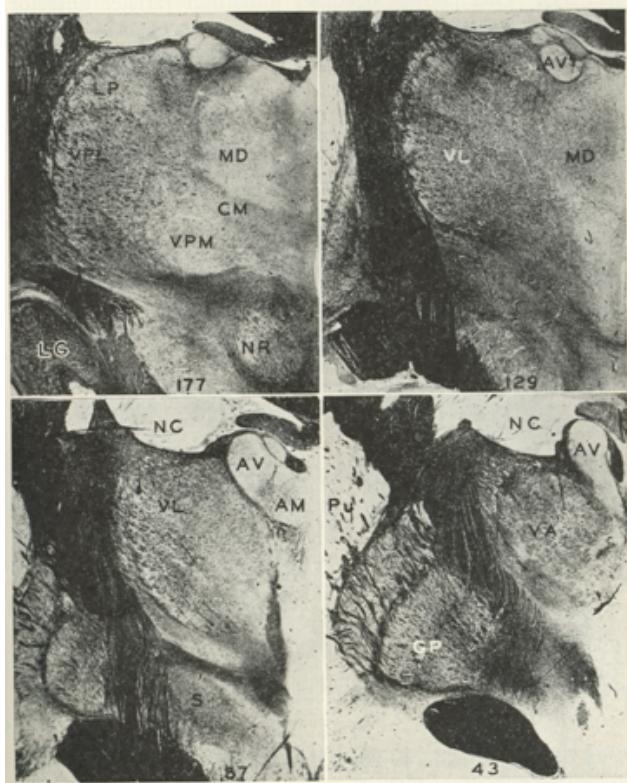
Walker 1936



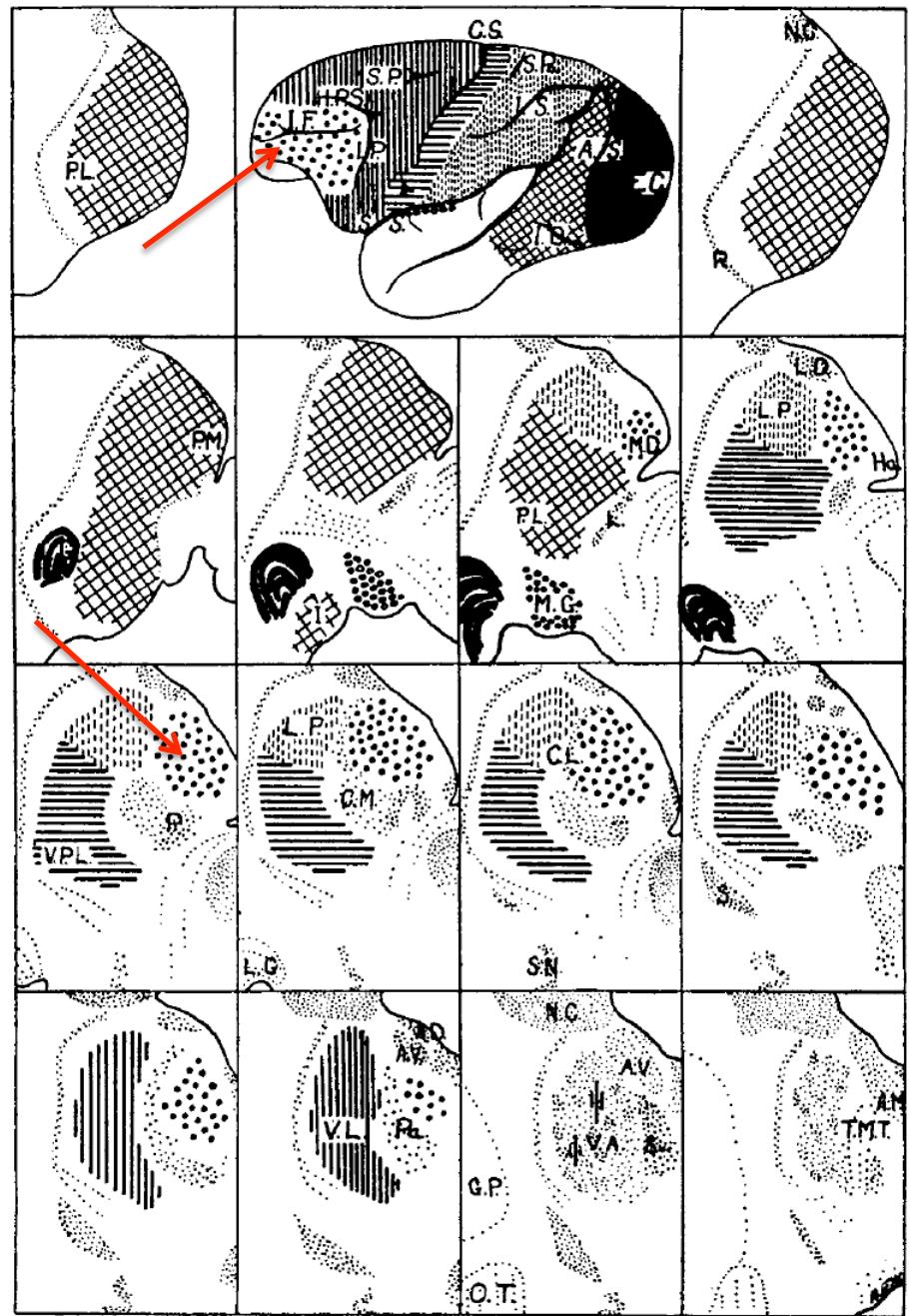
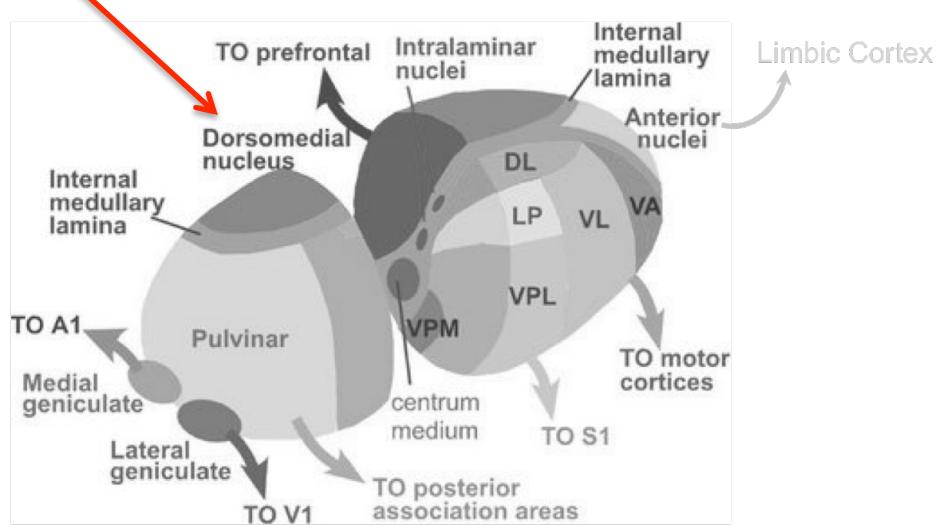
Walker 1938



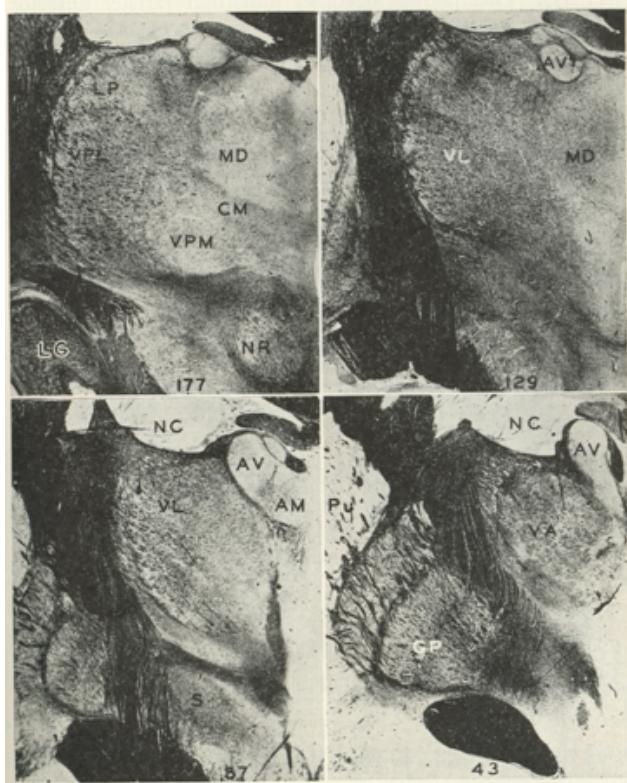
Walker 1936



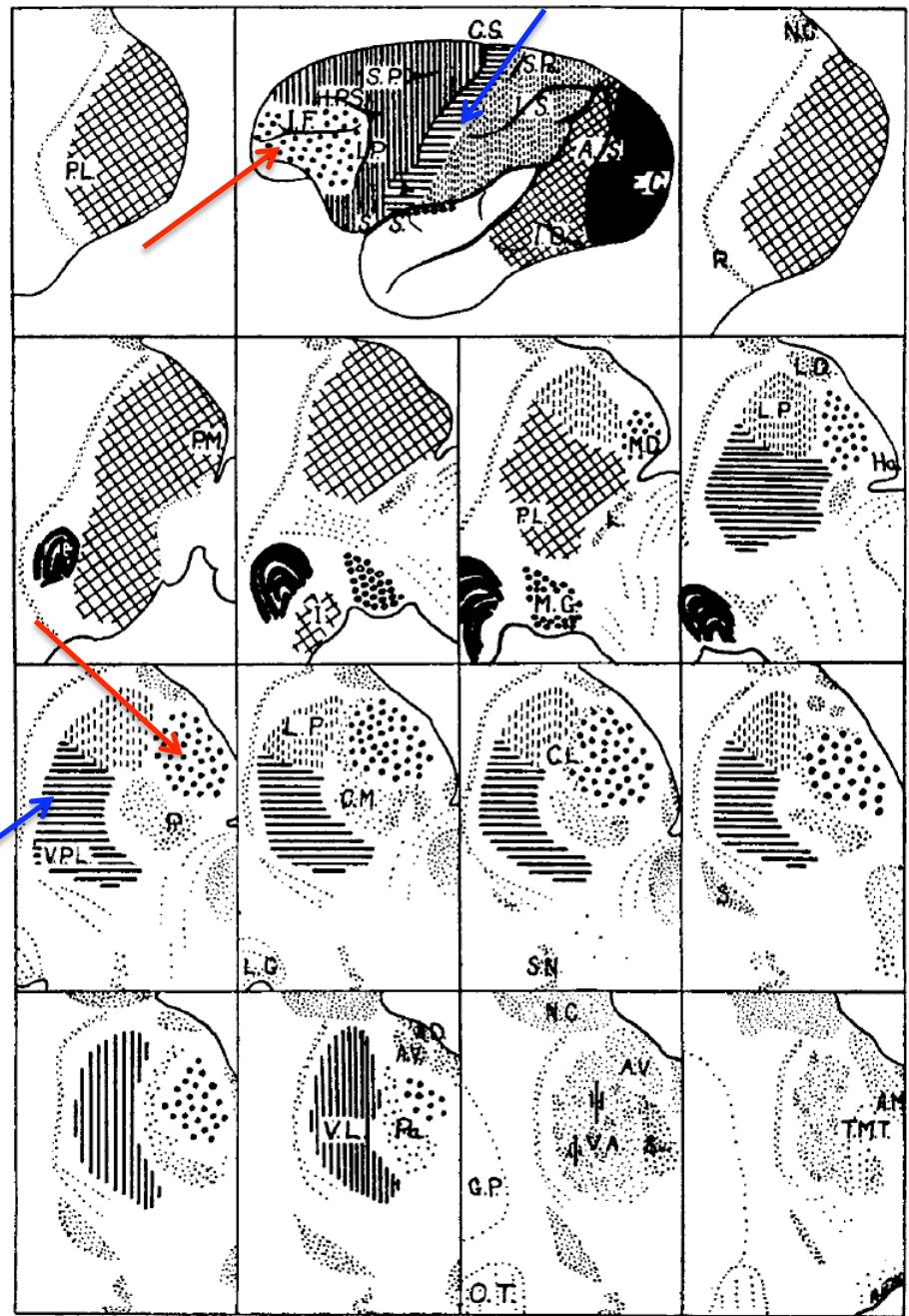
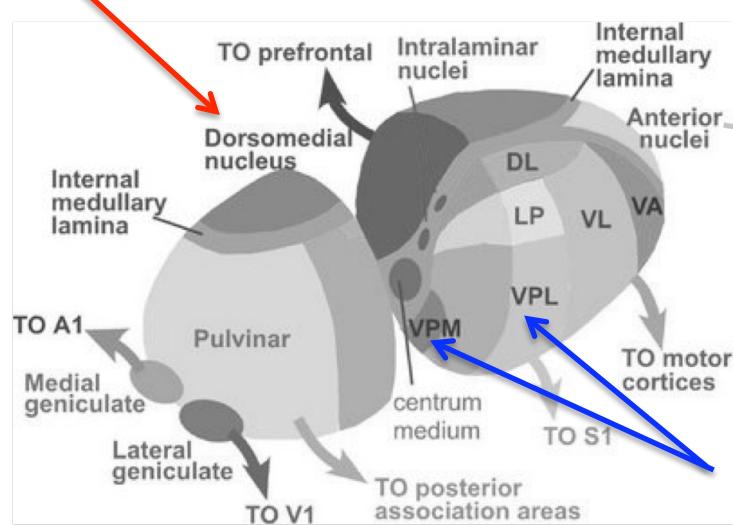
Walker 1938



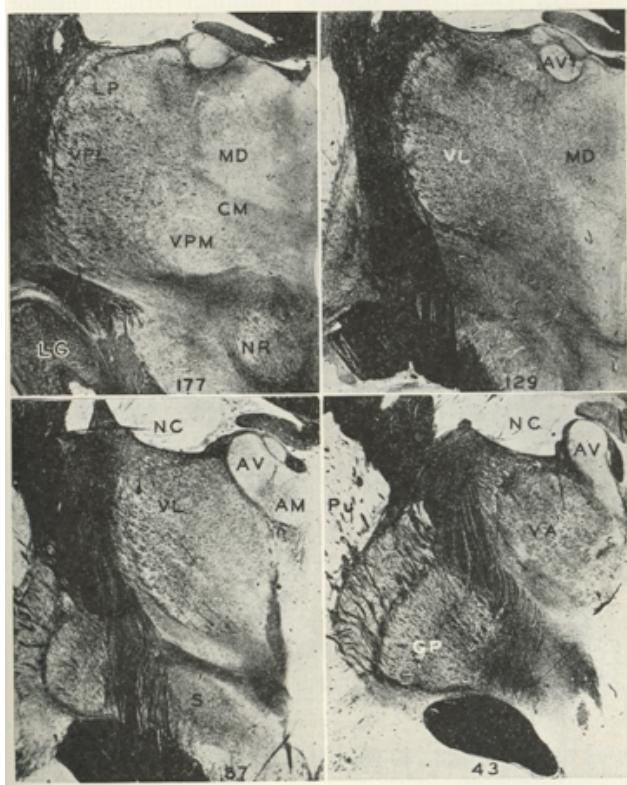
Walker 1936



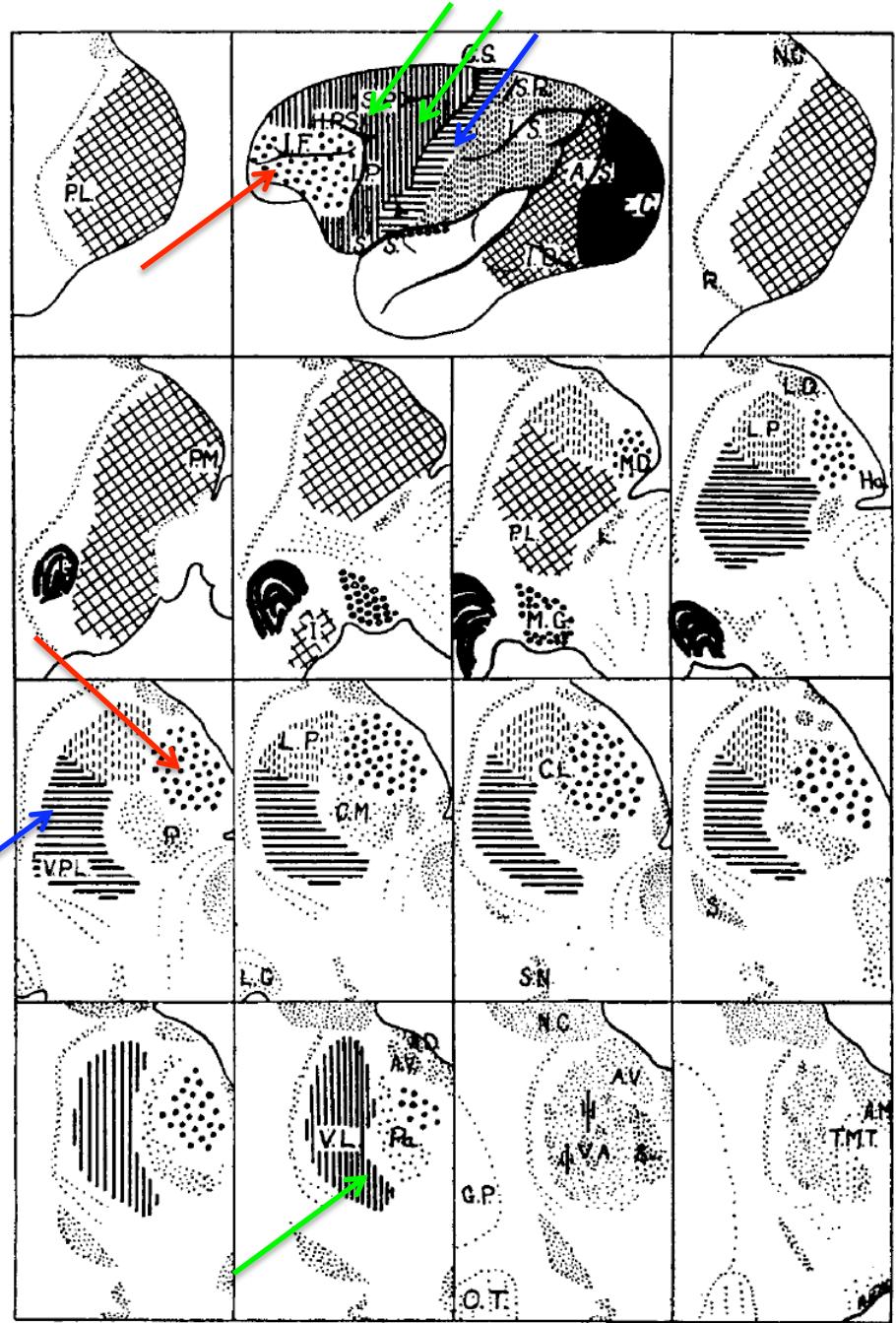
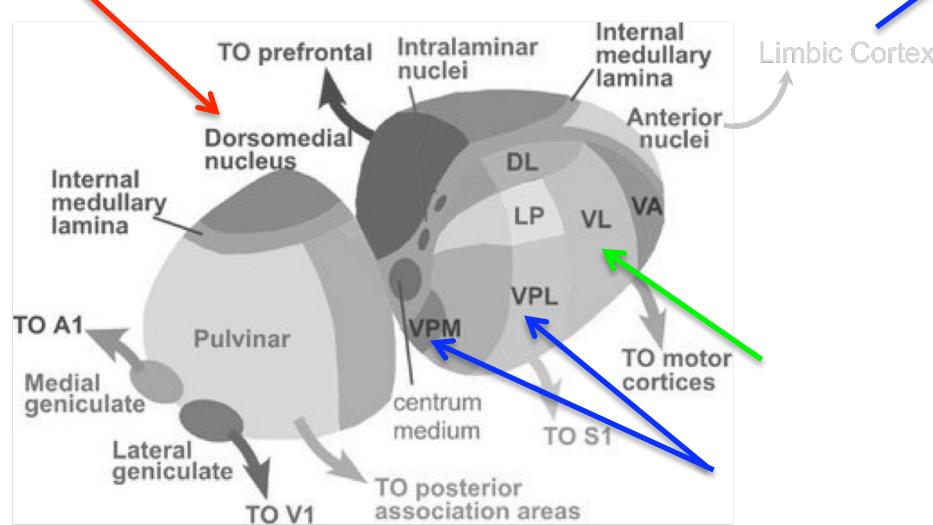
Walker 1938



Walker 1936



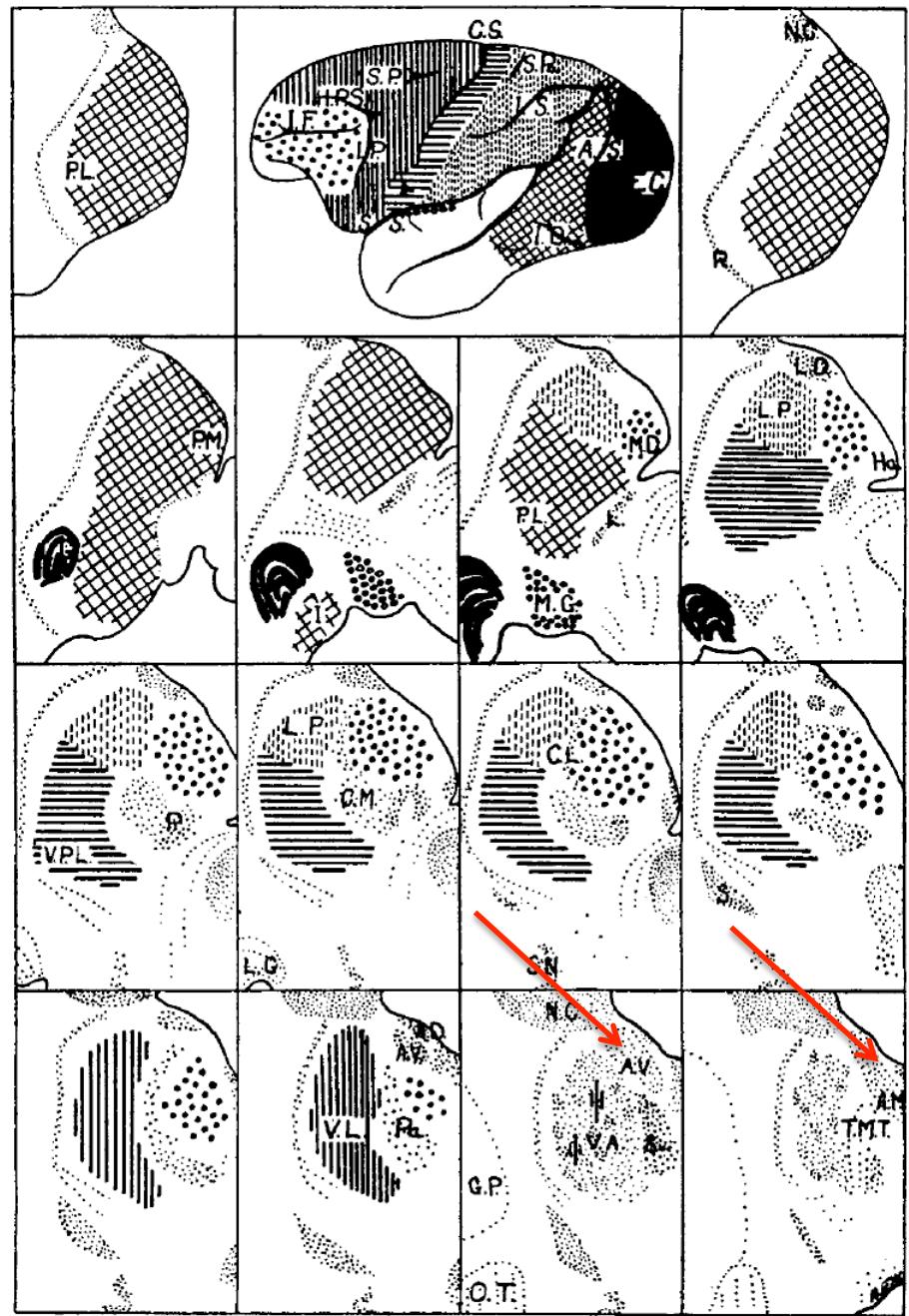
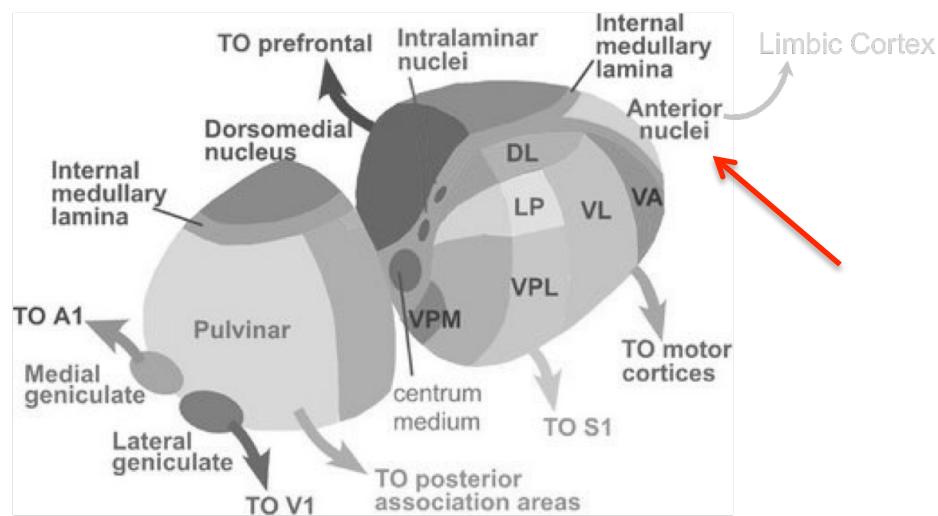
Walker 1938



Walker 1936



Walker 1938



Walker 1936

STRUCTURE AND RELATIONS OF LIMBIC CORTEX  
AND ANTERIOR THALAMIC NUCLEI  
IN RABBIT AND CAT

JERZY E. ROSE AND CLINTON N. WOOLSEY

*Department of Physiology and the Henry Phipps Psychiatric Clinic,  
Johns Hopkins University, School of Medicine<sup>1</sup>*

SIXTY FIGURES

INTRODUCTION

It may be considered as well established, at least for most of them, that the dorsal thalamic nuclei project to specific sectors of the cortex. The specificity has been agreed upon by all workers, although the projection areas of some of the nuclei are still in dispute and others are known only in vague outline.

Since this is so the question arises: does a cortical area which receives projection fibers from a specific thalamic element possess structural characteristics which permit its morphological delimitation? In other words, can such a projection area be regarded as a cortical field? Strangely enough no such studies have ever been attempted. Some correlations of thalamic projection areas with known architectonic fields have been made, of course, and many probably valid relationships have been established. However, the reported correlations always have been arrived at by the simple method of comparing architectonic charts with cortical lesions known to produce some degeneration in the thalamic nuclei. The lesions usually have been placed without any regard for cortical structure and the extent of the actual destruction has seldom been controlled. Furthermore, with the exception of

1-1 relations of  
the Thalamus

Rose & Woolsey, 1948  
52 rabbit hemispheres,  
36 cat hemispheres

## Implications for models of thalamic organization

The general rules that have been suggested to govern the relationship of a thalamic nucleus to the cortex may be evaluated on the basis of the present findings. Two basic models have been proposed concerning this relationship. The first, implicit in the work of Rose (Rose, '49; Rose and Woolsey, '49) and of Jones and his collaborators (e.g., Burton and Jones, '76, see Fig. 17; Jones and Burton, '76; Jones, '81; see also Frost and Caviness, '80), suggests that a one-to-one relationship exists between a given thalamic nucleus and a given cortical field. The second model, which has been summarized by Diamond (Diamond, '79; see also Diamond et al., '69; Winer et al., '77), suggests that this specific relationship may exist only between the primary sensory relay nuclei (i.e., VPLc, LGN, and MGv) and the koniocortical fields to which they project (area 3b of S1, V1, and A1).

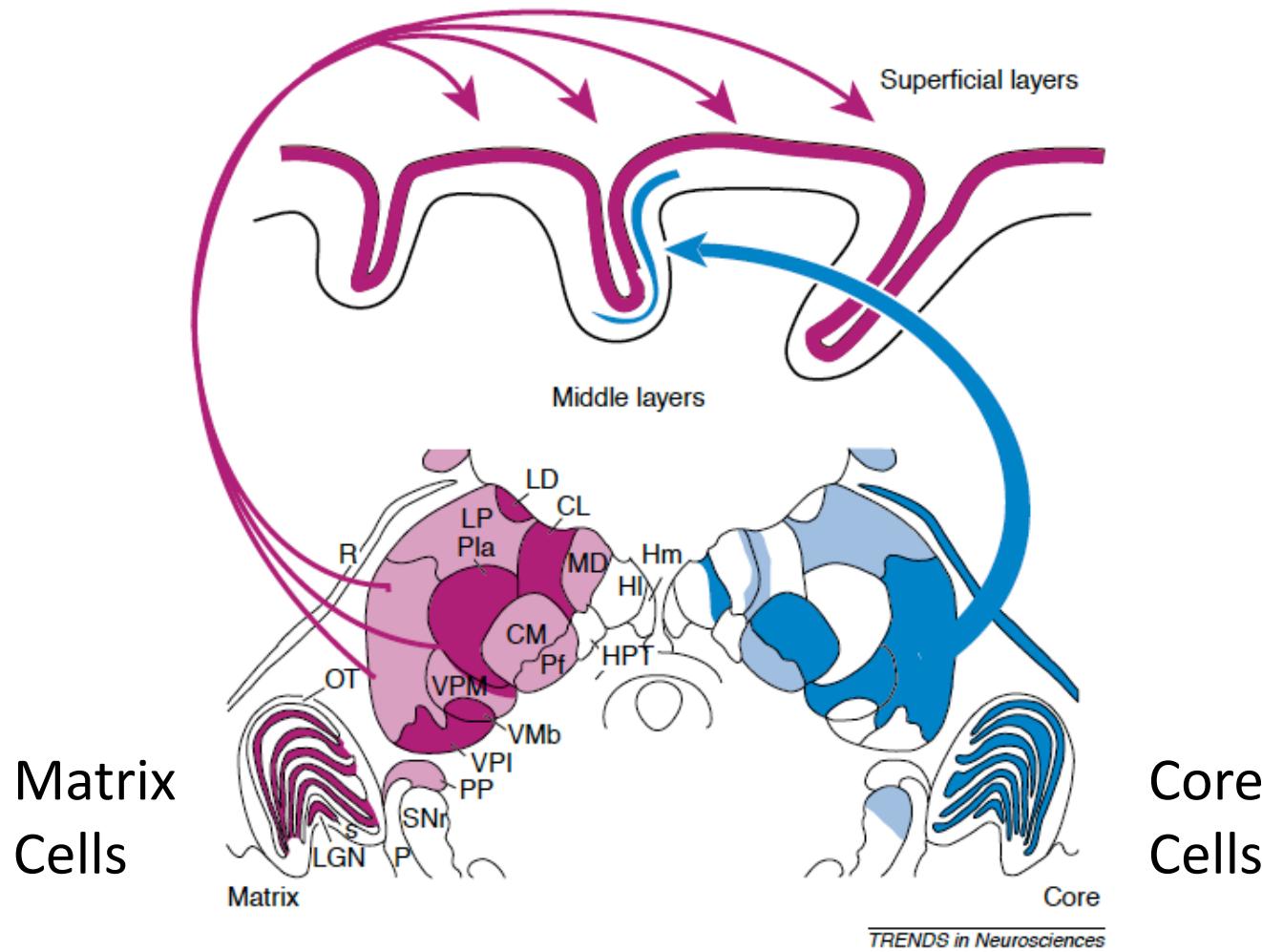
:

Despite general support for the underlying principle of Diamond's proposal ('79), several aspects of the model are not supported by data obtained from the monkey. For example, no single nucleus has yet been demonstrated to project to only one cortical field. In the somatosensory system, VPLc, if it is considered to be a single nucleus, may project to five cortical fields: areas 3a, 3b, 1, 2, and S2. In the visual system, the lateral geniculate nucleus, which projects to V1, has now been shown to project to prestriate areas as well (Benevento and Yoshida, '81; Yukie and Iwai, '81). In the auditory system of the cat, A1, A2, and the anterior auditory field are all reported to receive projections from MGv (Andersen et al., '80). In the present study, two

# Many-to-Many Relations of the Thalamus

Friedman & Murray, 1986

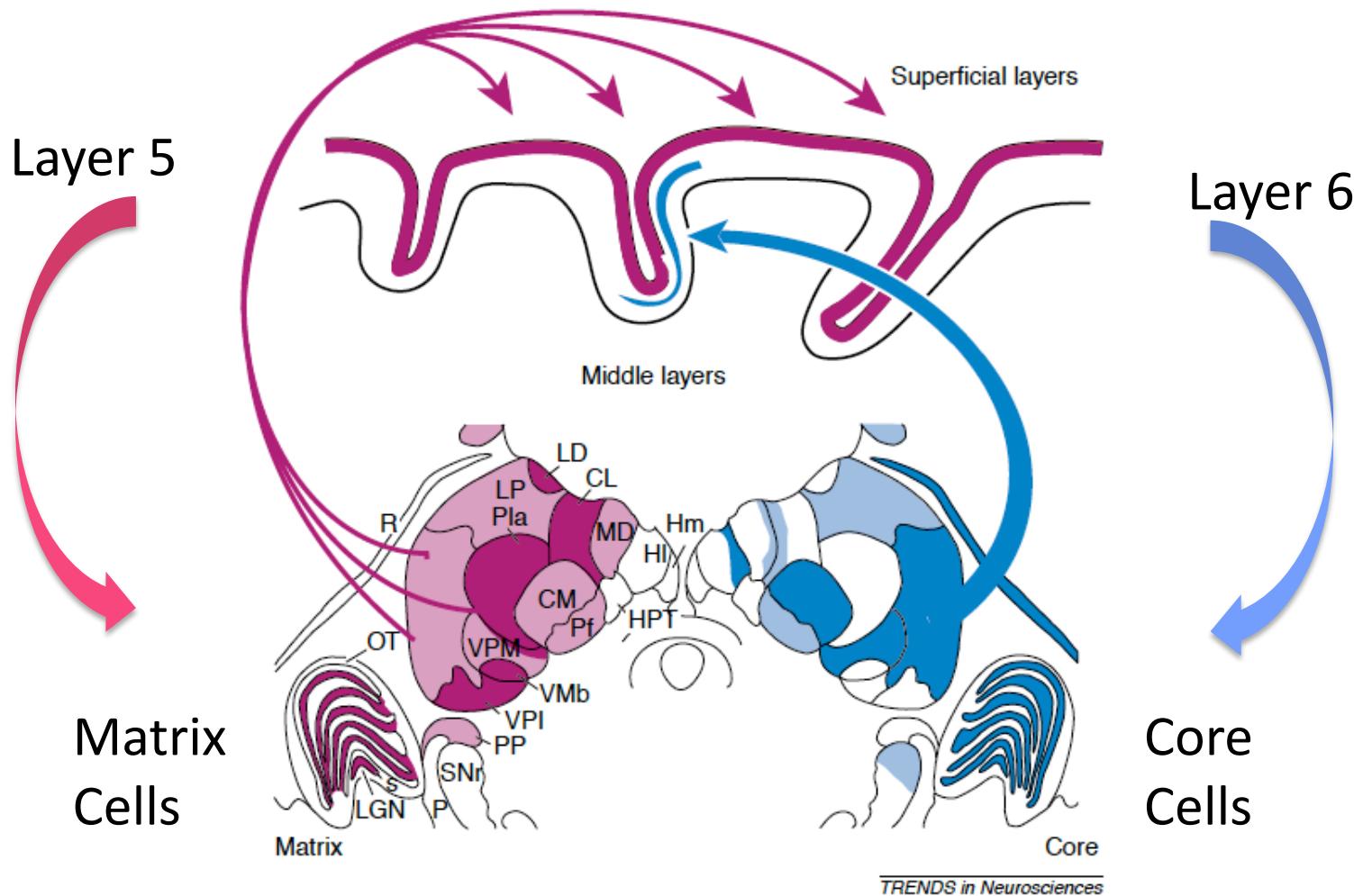
# Specific vs Non-Specific Connections



*TRENDS in Neurosciences*

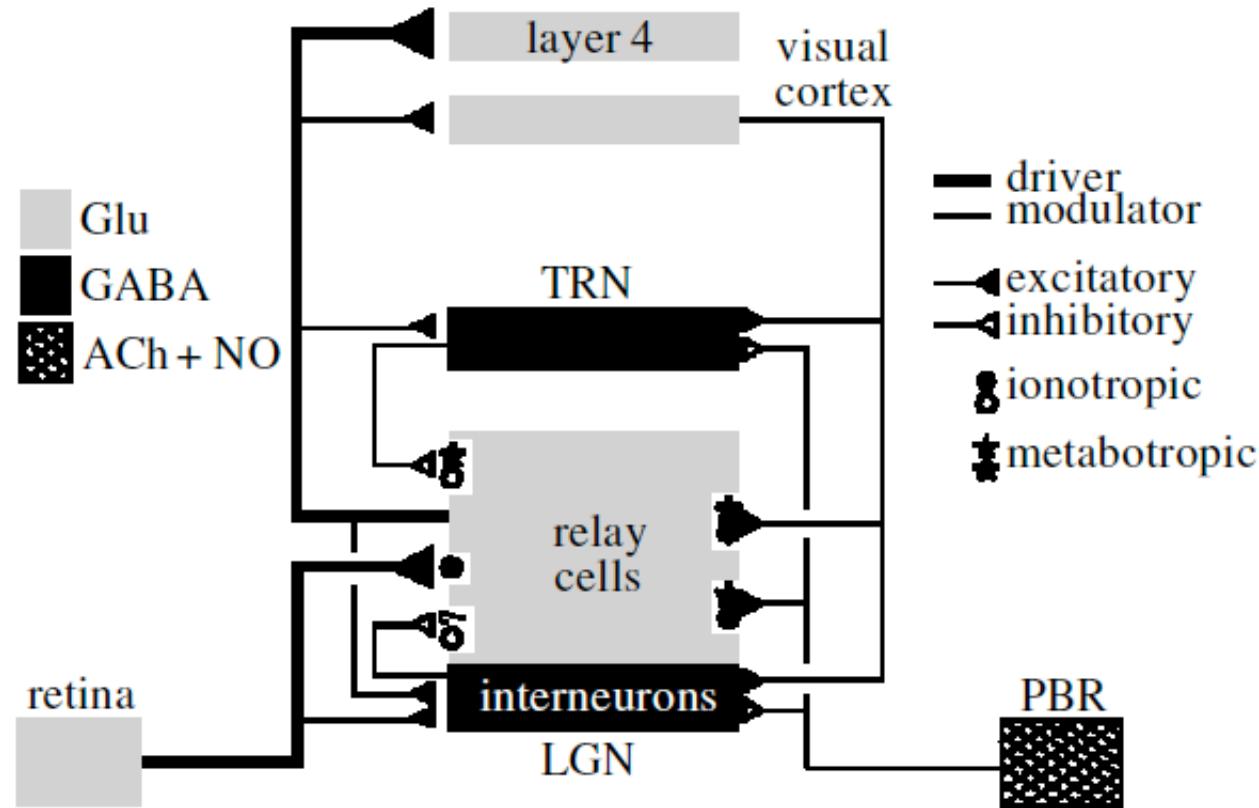
Jones, 2001

# Specific vs Non-Specific Connections



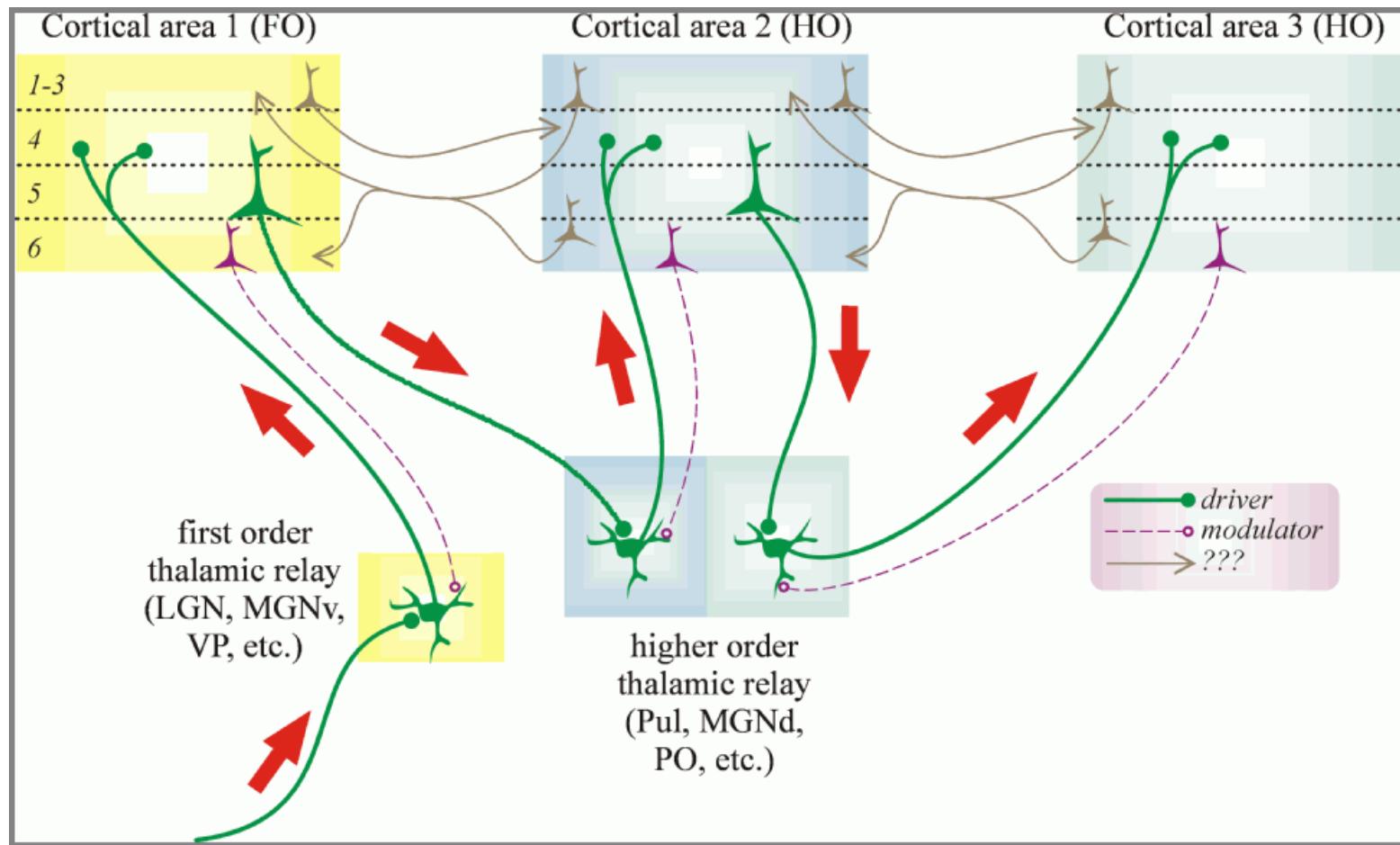
Jones, 2001

# Driving vs Modulating Inputs



Sherman & Guillery, 2002; Guillery & Sherman, 2002

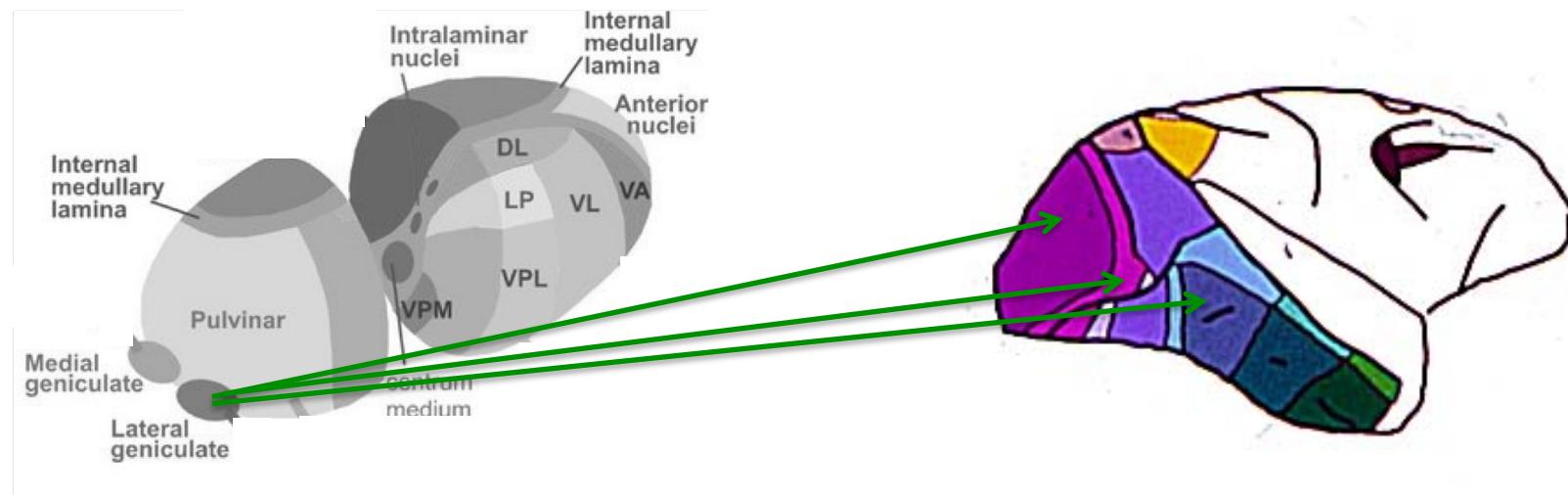
# Thalamus provides alternative pathway for corticocortical communication



Sherman & Guillery, 2002; Guillery & Sherman, 2002

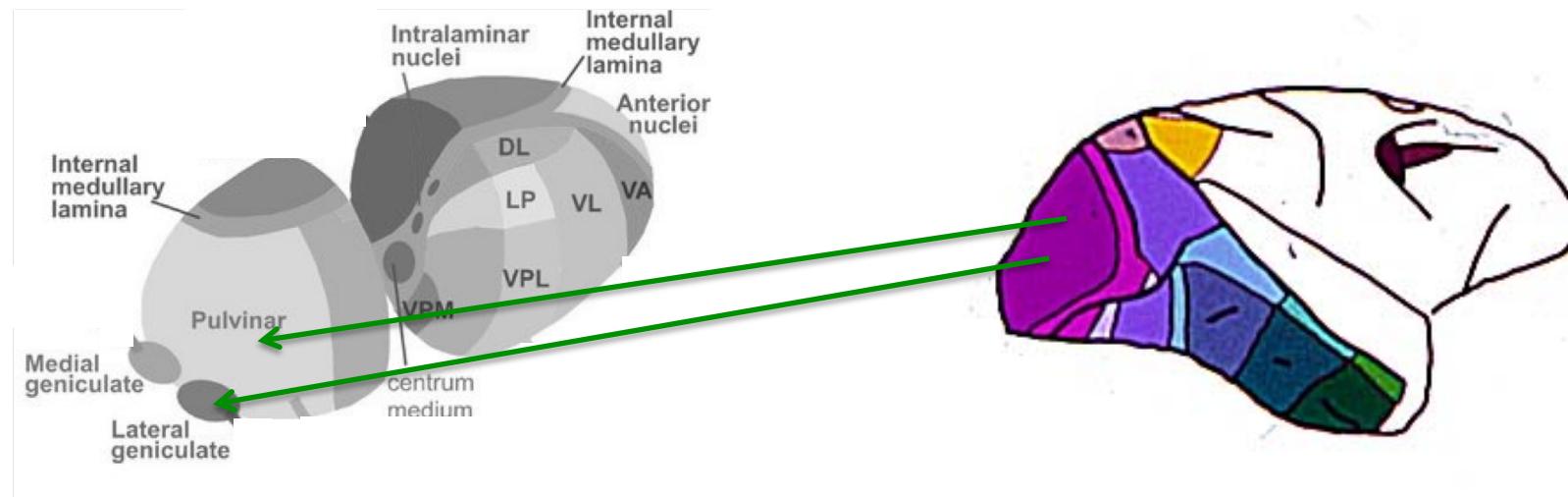
# The Modern View

- Every nucleus → multiple cortical fields
  - Many nuclei → multiple cortical lobes



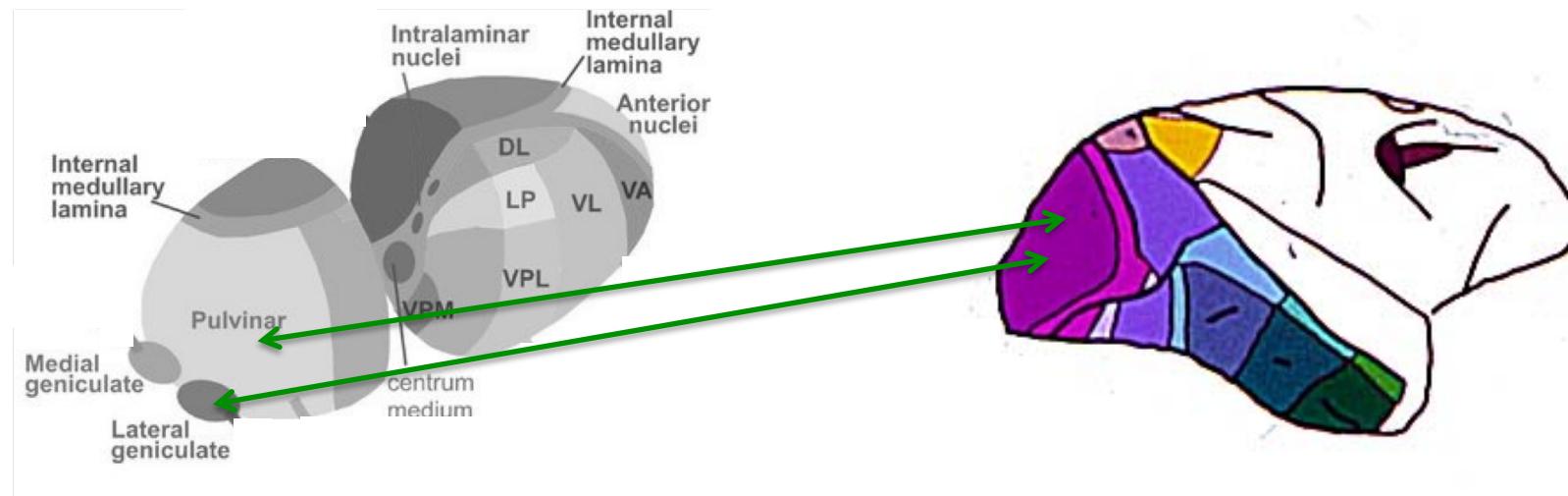
# The Modern View

- Every nucleus → multiple cortical fields
  - Many nuclei → multiple cortical lobes
- Every cortical field (except maybe areas 3, 1) → multiple thalamic nuclei



# The Modern View

- Every nucleus → multiple cortical fields
  - Many nuclei → multiple cortical lobes
- Every cortical field (except maybe areas 3, 1) → multiple thalamic nuclei
- (mostly) Reciprocal connections



# The Modern View

- Every nucleus → multiple cortical fields
  - Many nuclei → multiple cortical lobes
- Every cortical field (except maybe areas 3, 1) → multiple thalamic nuclei
- (mostly) Reciprocal connections
- Every nucleus has subcortical inputs

# The Modern View

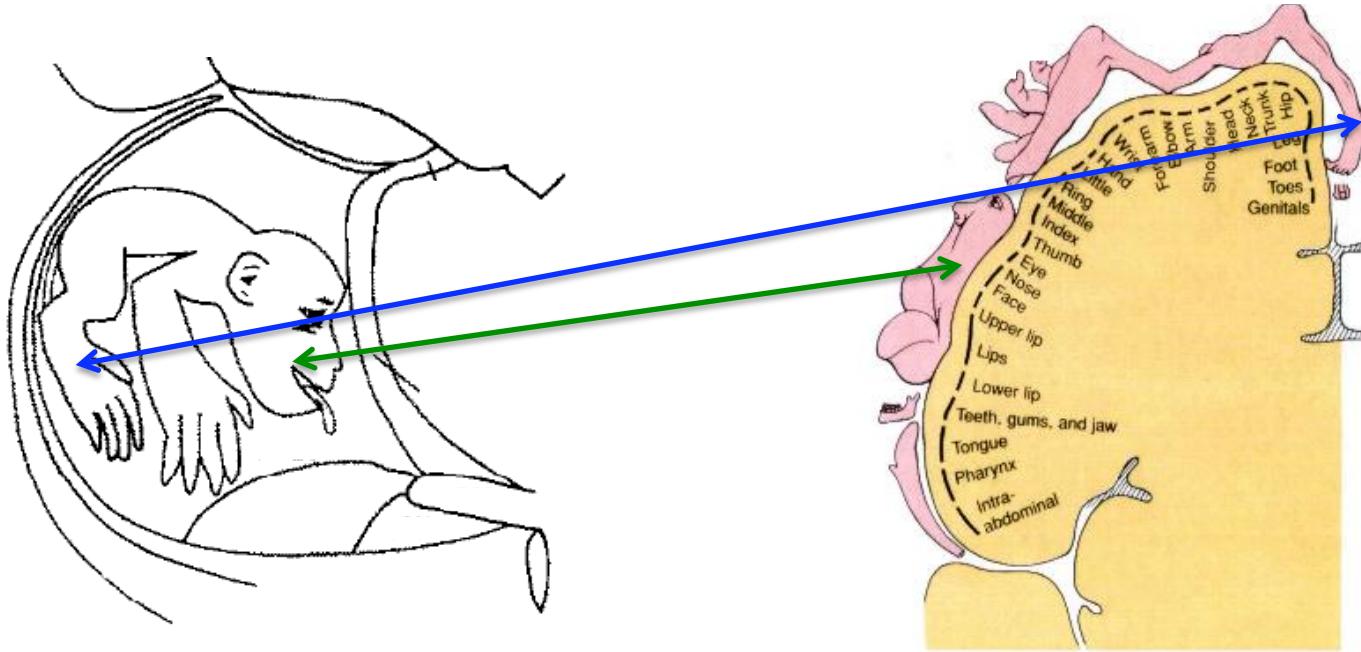
- Every nucleus → multiple cortical fields
  - Many nuclei → multiple cortical lobes
- Every cortical field (except maybe areas 3, 1) → multiple thalamic nuclei
- (mostly) Reciprocal connections
- Every nucleus has subcortical inputs
- Connections (mostly) ipsilateral



# The Modern View

- Every nucleus → multiple cortical fields
  - Many nuclei → multiple cortical lobes
- Every cortical field (except maybe areas 3, 1) → multiple thalamic nuclei
- (mostly) Reciprocal connections
- Every nucleus has subcortical inputs
- Connections (mostly) ipsilateral
- Thalamic receptive field properties generally consistent with connections

# The Modern View



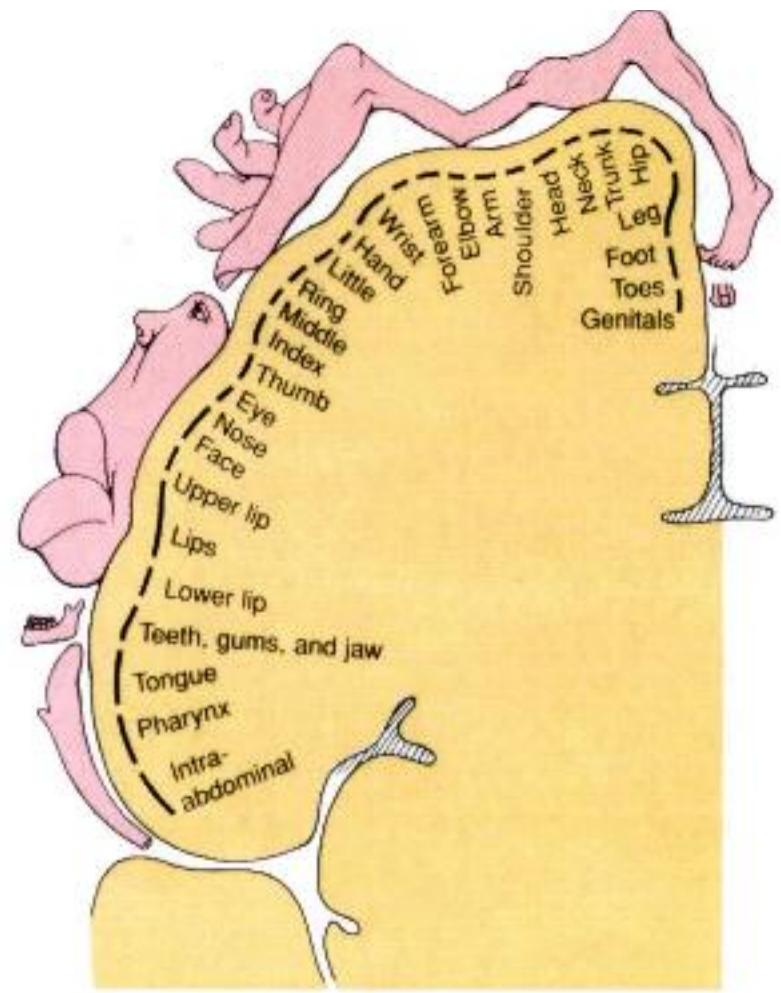
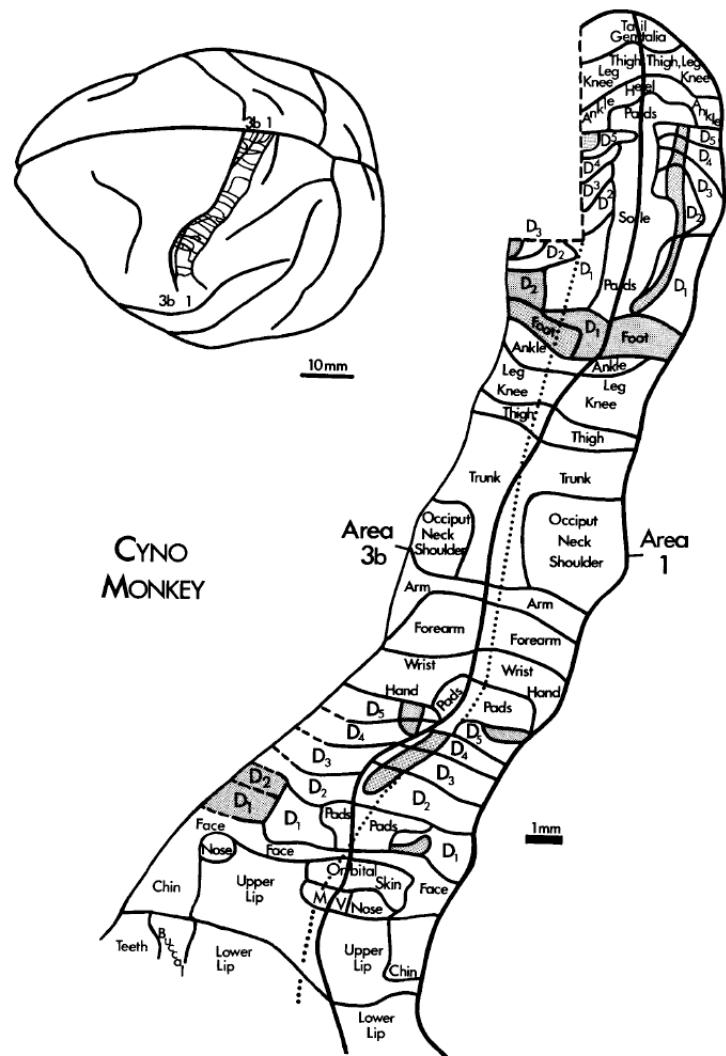
- Thalamic receptive field properties generally consistent with connections

# The Modern View

- Every nucleus → multiple cortical fields
  - Many nuclei → multiple cortical lobes
- Every cortical field (except maybe areas 3, 1) → multiple thalamic nuclei
- (mostly) Reciprocal connections
- Every nucleus has subcortical inputs
- Connections (mostly) ipsilateral
- Thalamic receptive field properties generally consistent with connections

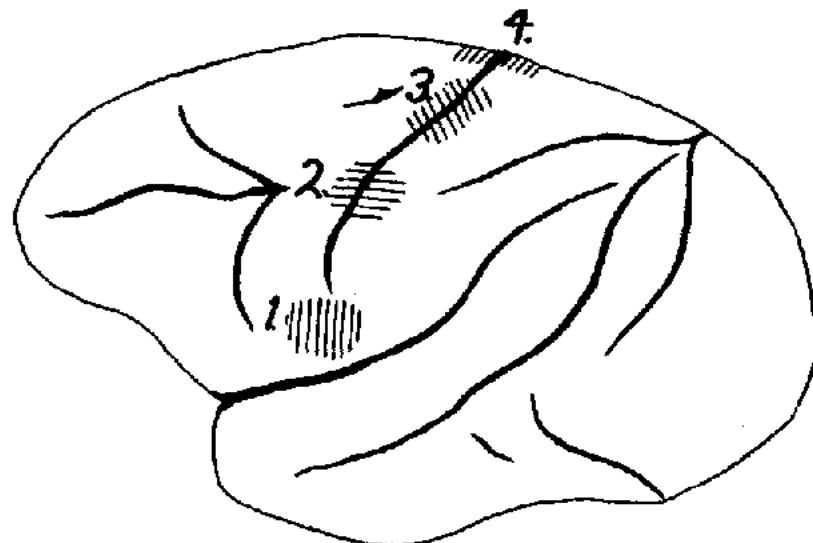
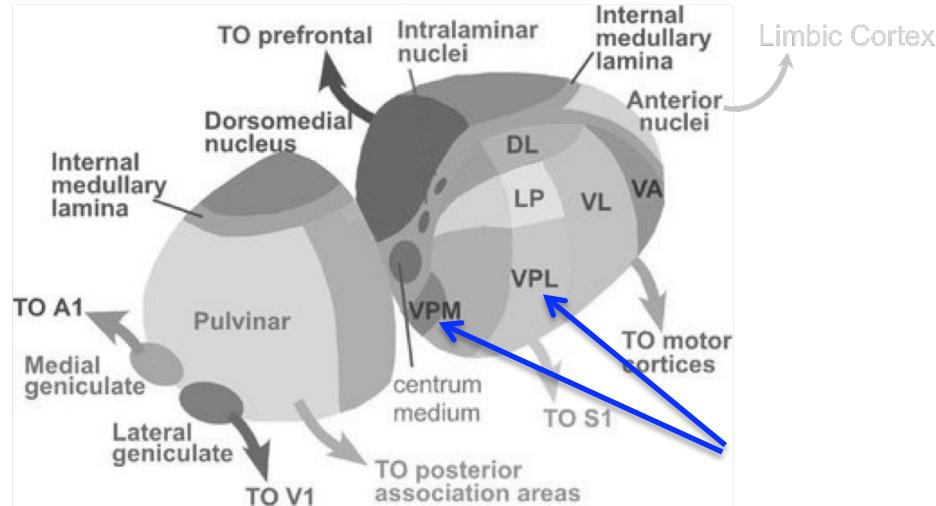
# Modern Tract Tracing: Somatotopy / Motor Map

# SI: Primary Somatosensory Area



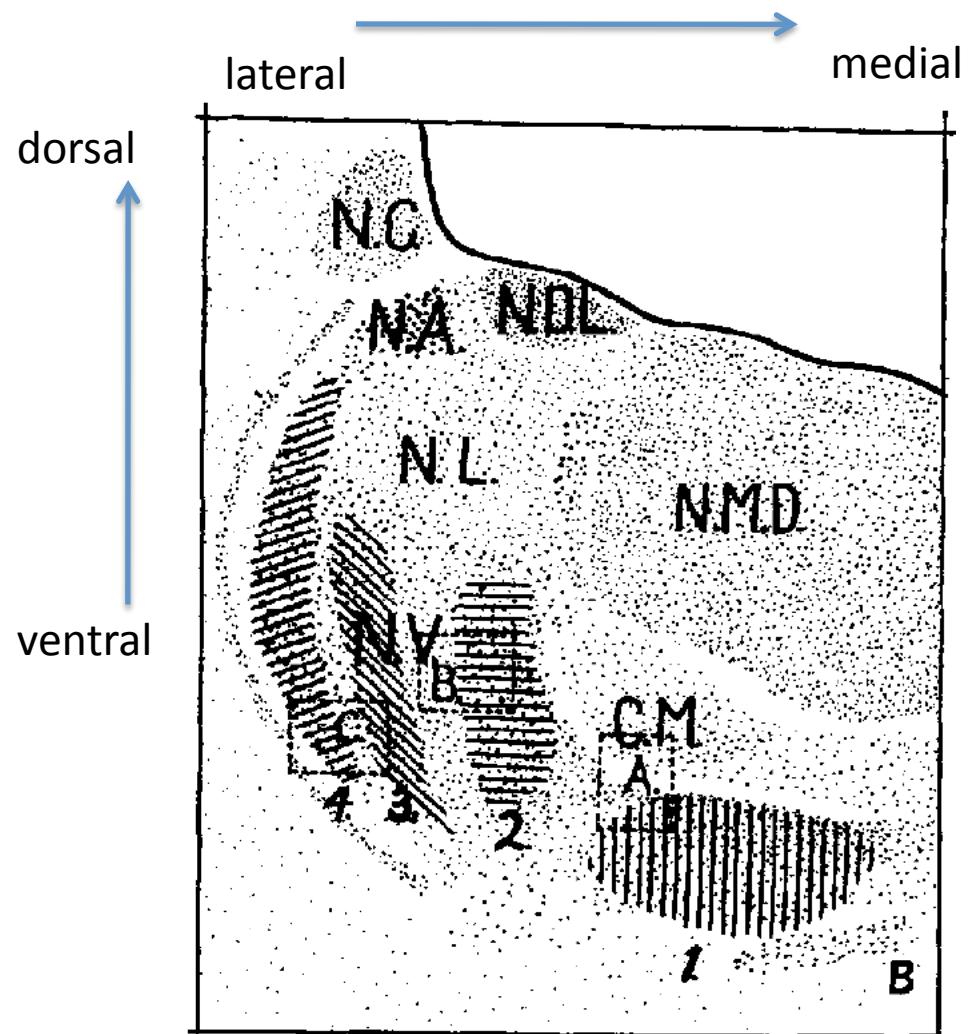
Nelson et al. 1980

# VPL vs VPM



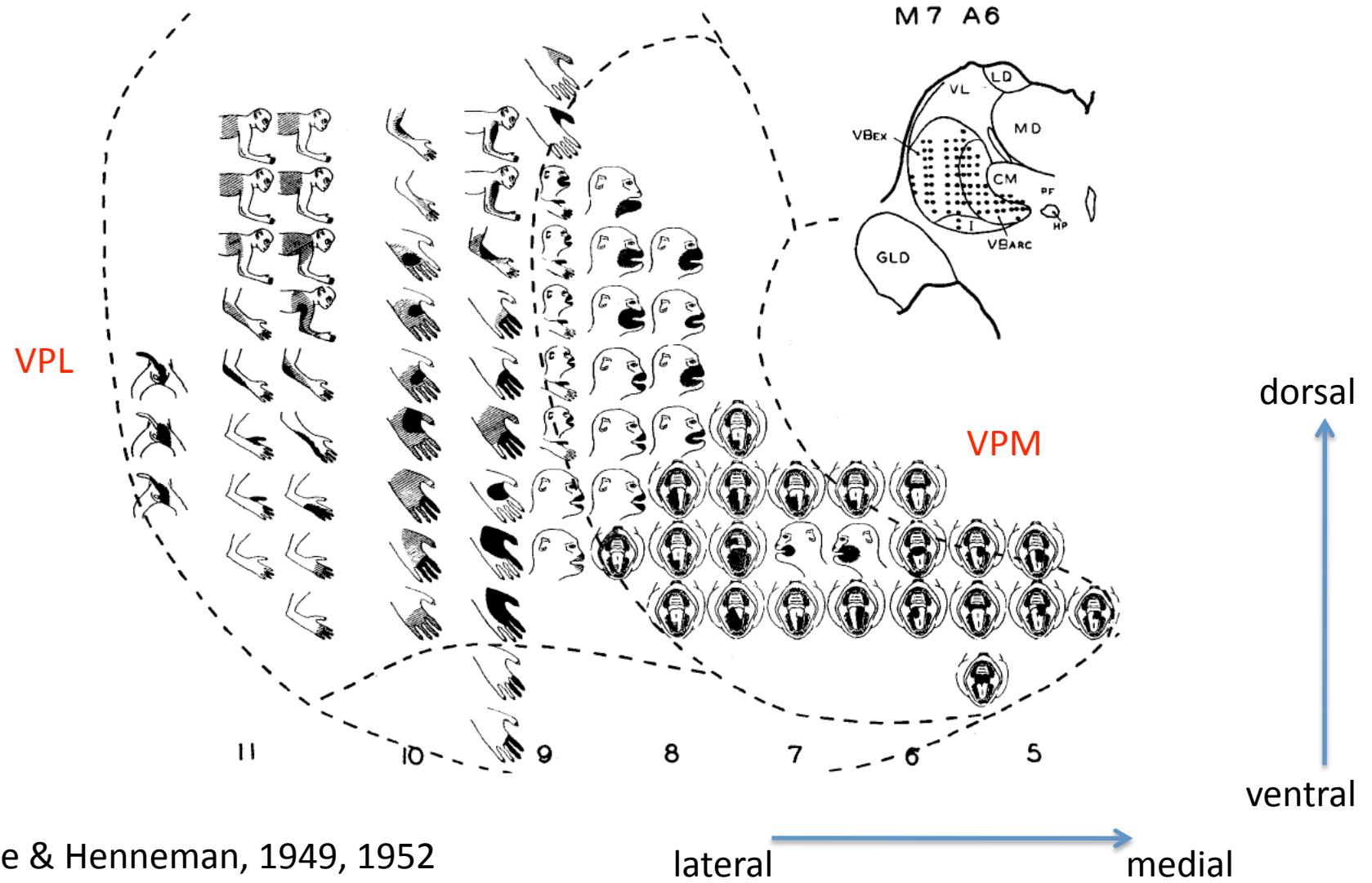
A

Walker, 1934



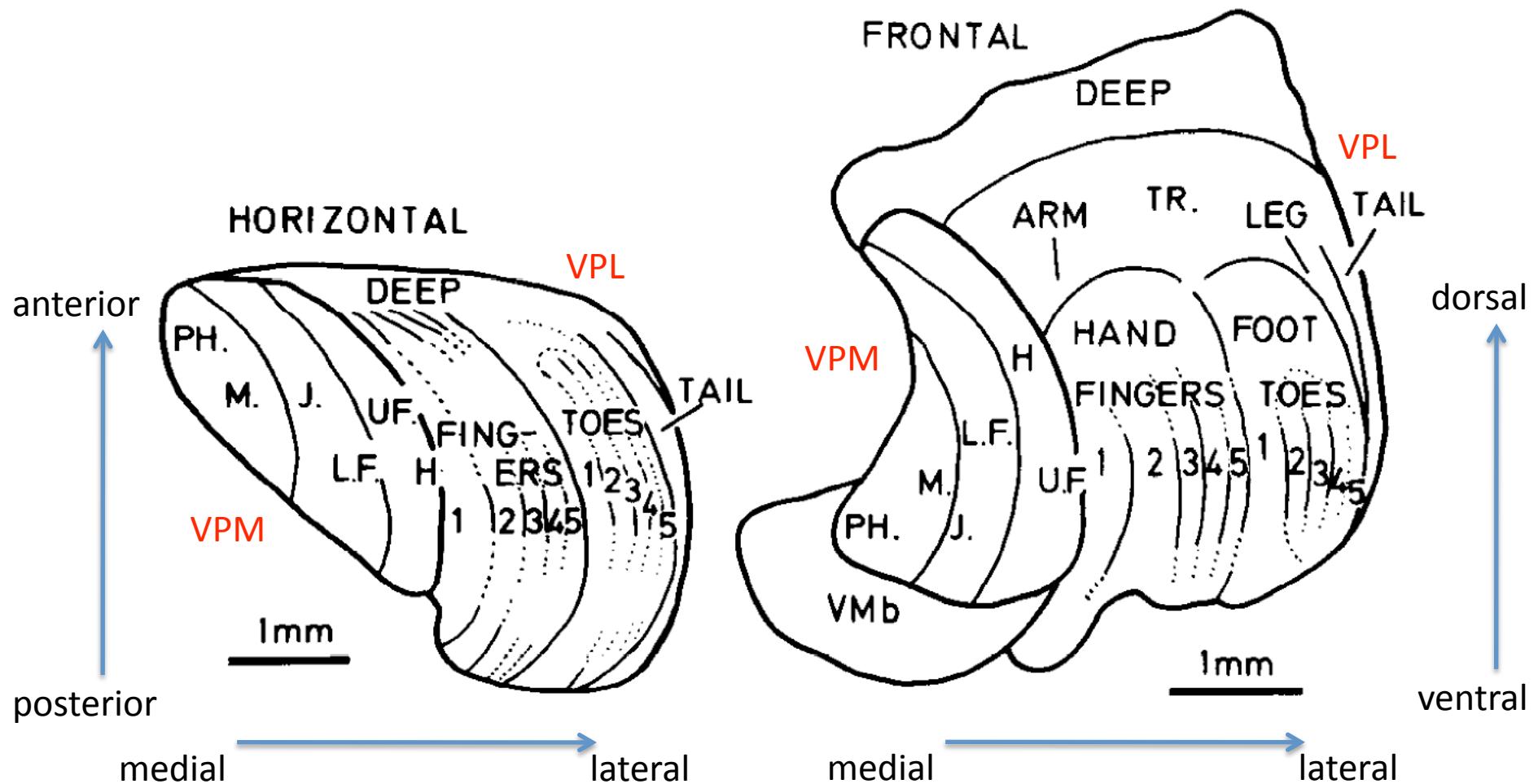
B

# VPL vs VPM



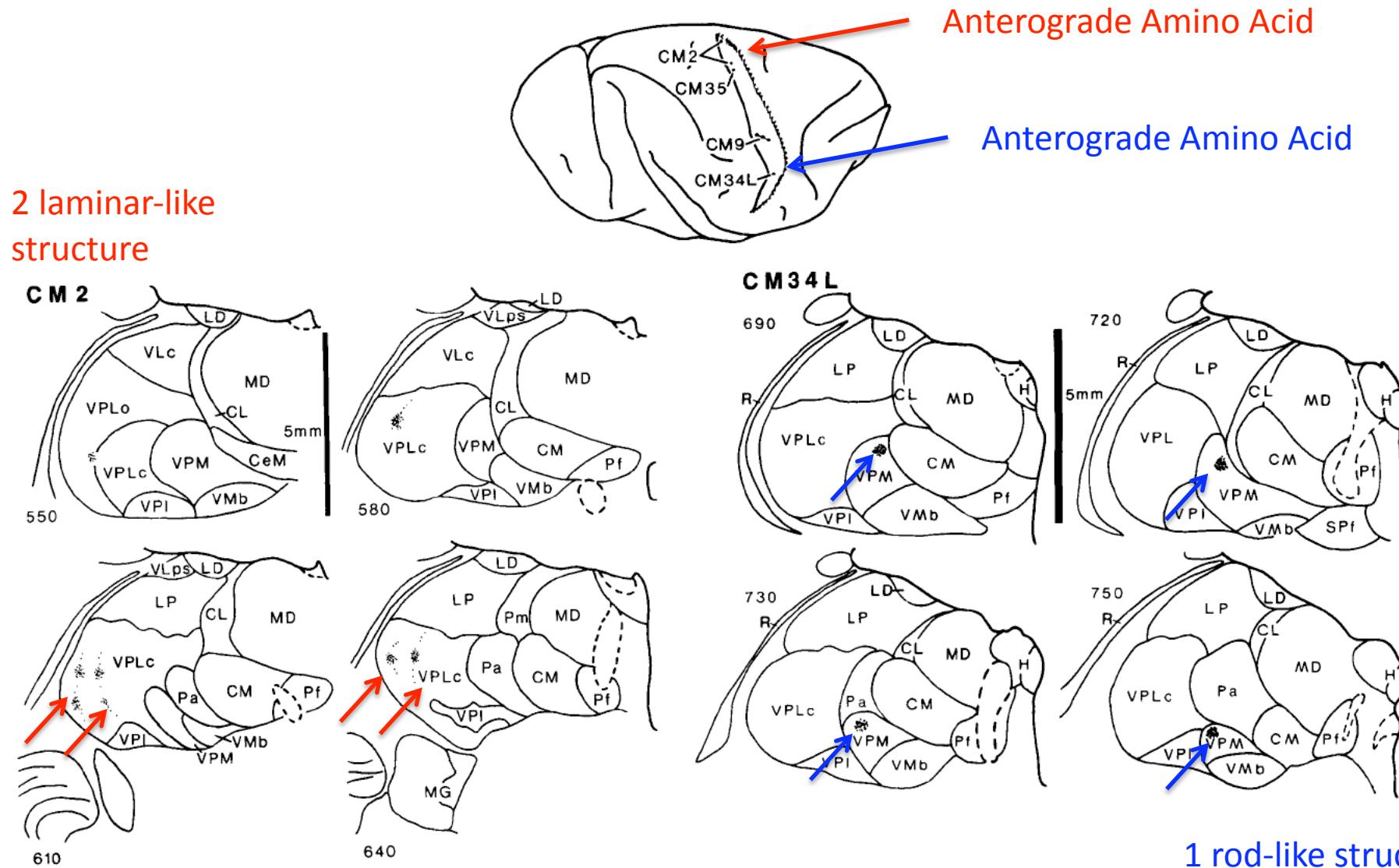
Mountcastle & Henneman, 1949, 1952  
Rose & Mountcastle 1952

# VPL vs VPM



Jones & Friedman, 1982

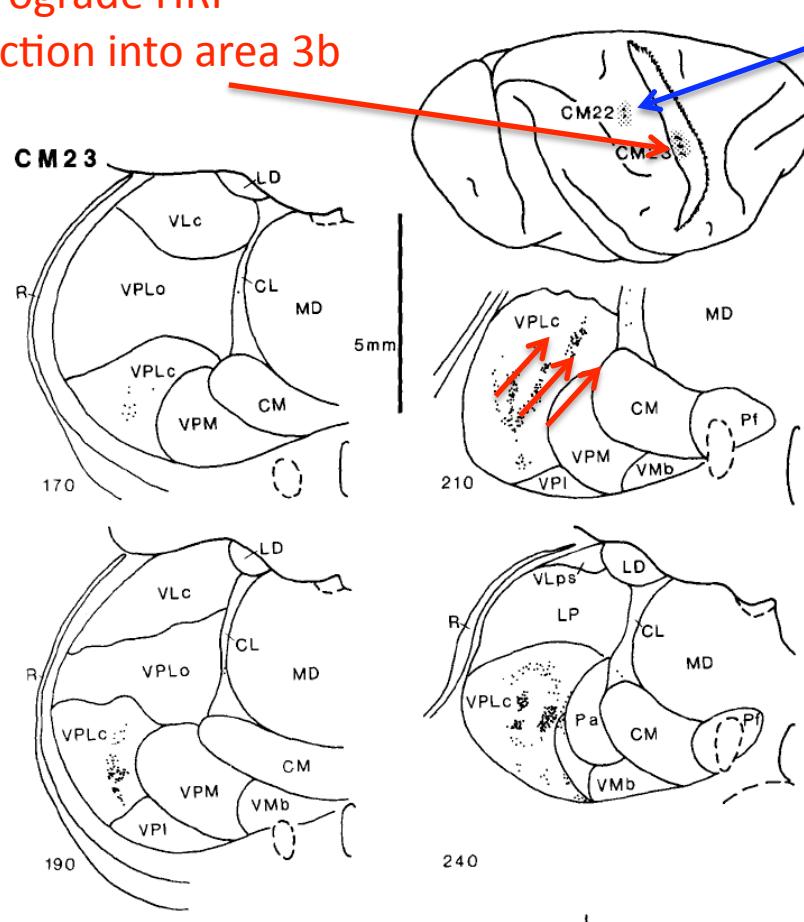
# BA 3b project to VPL, VPM in a topographic fashion



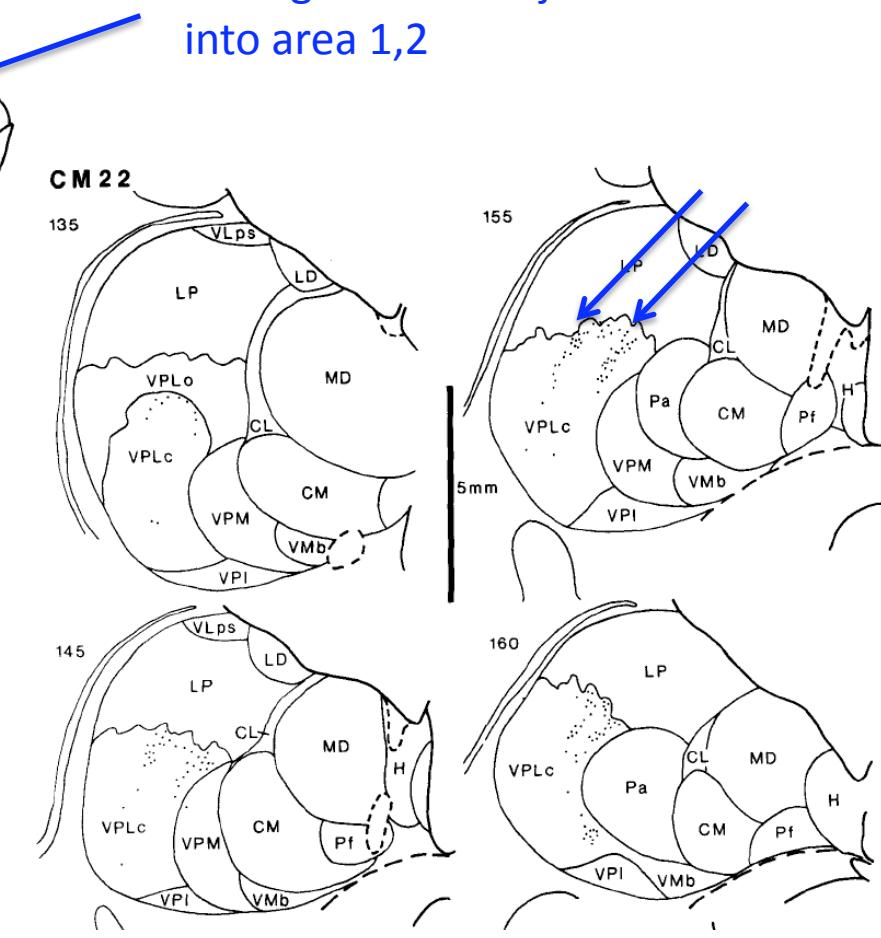
Jones et al. 1979: 30 cynomolgus, 27 rhesus, 31 squirrel

# VPL projects to Areas 3, 1, 2 in a topographic fashion

Retrograde HRP  
injection into area 3b



Retrograde HRP injection  
into area 1,2

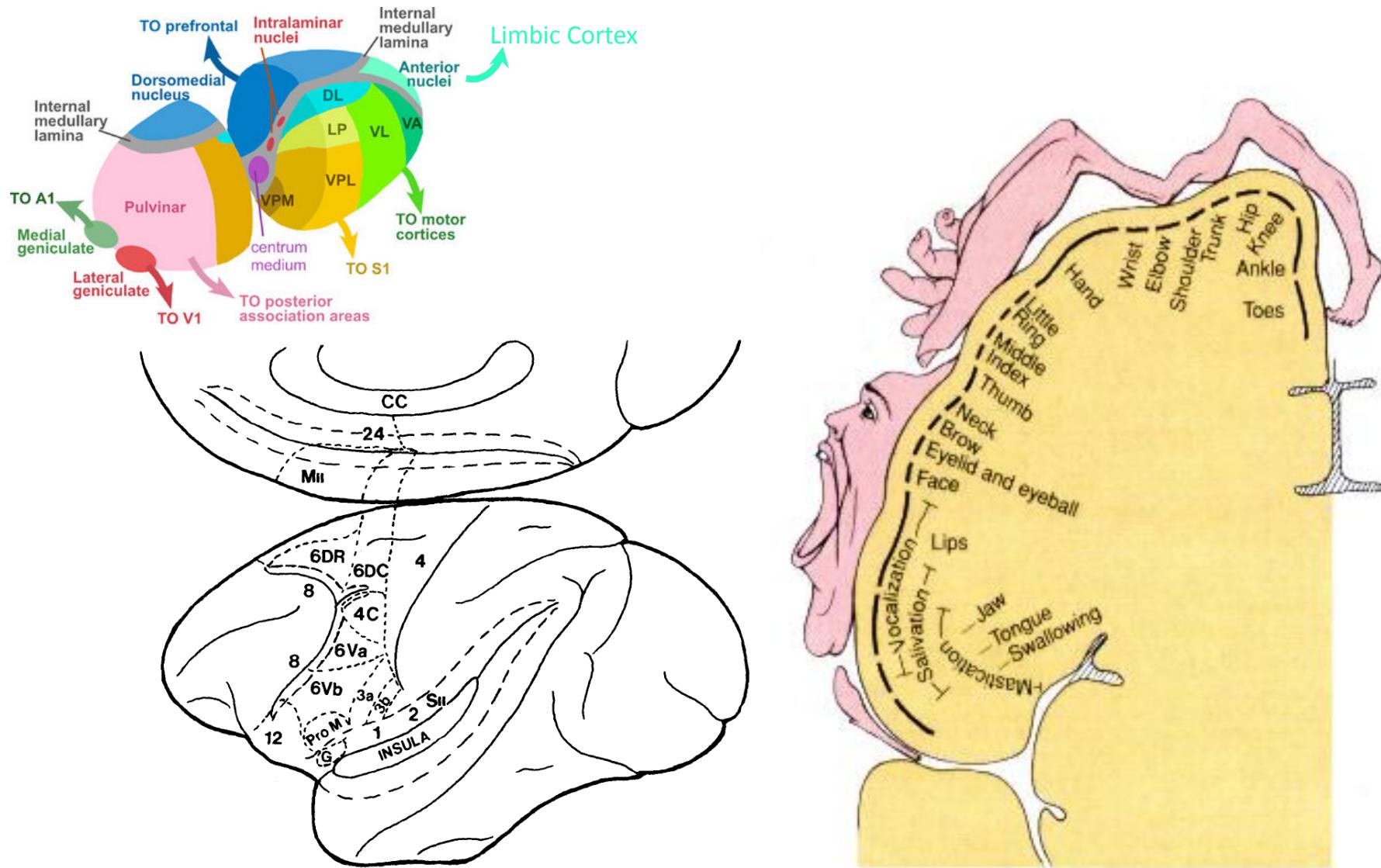


3 "laminar"- like structure

Jones et al. 1979: 30 cynomolgus, 27 rhesus, 31 squirrel

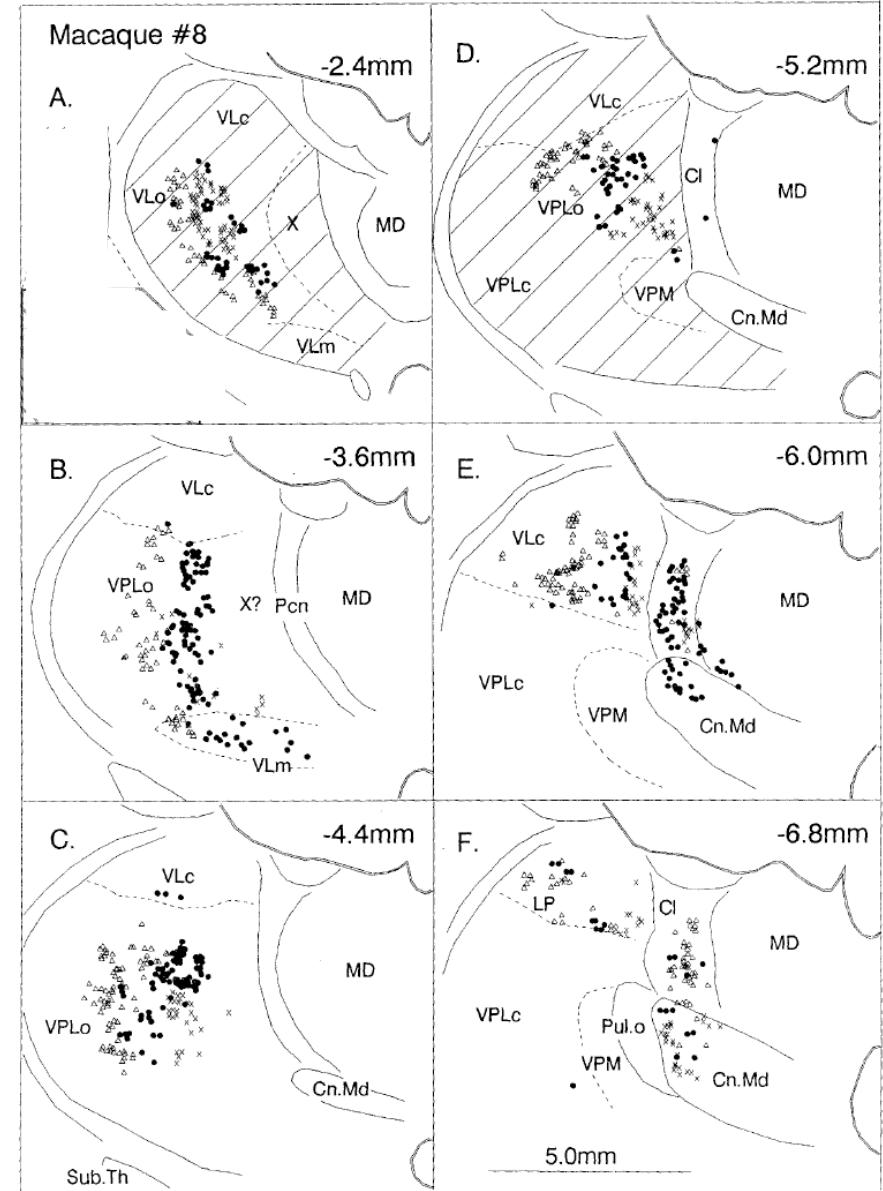
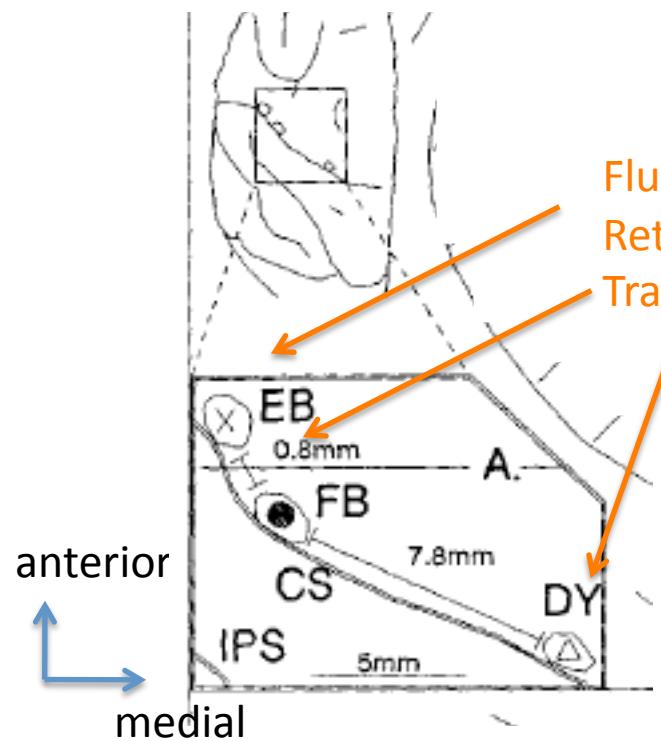
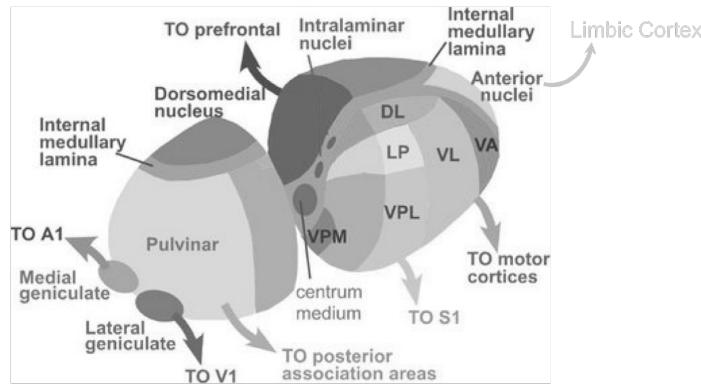
2 laminar-like structure

# M1 / F1 / BA4: Primary Motor Cortex

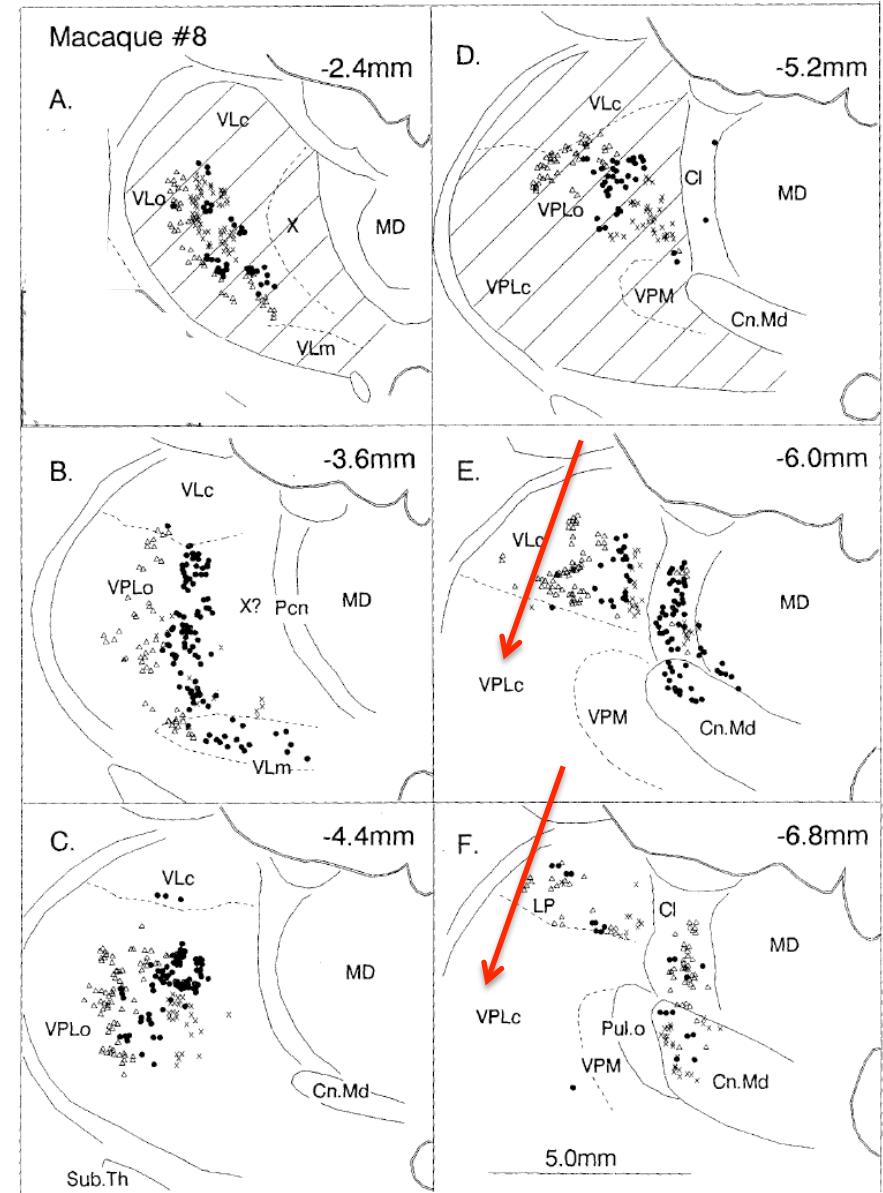
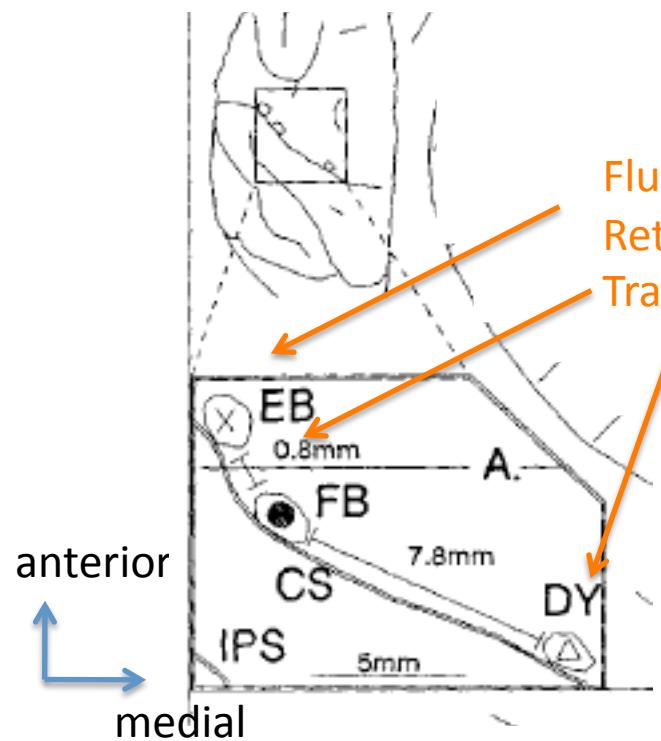
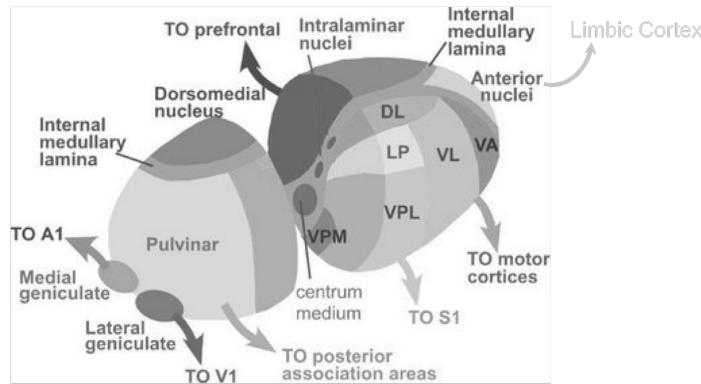


Barbas & Pandya, 1987

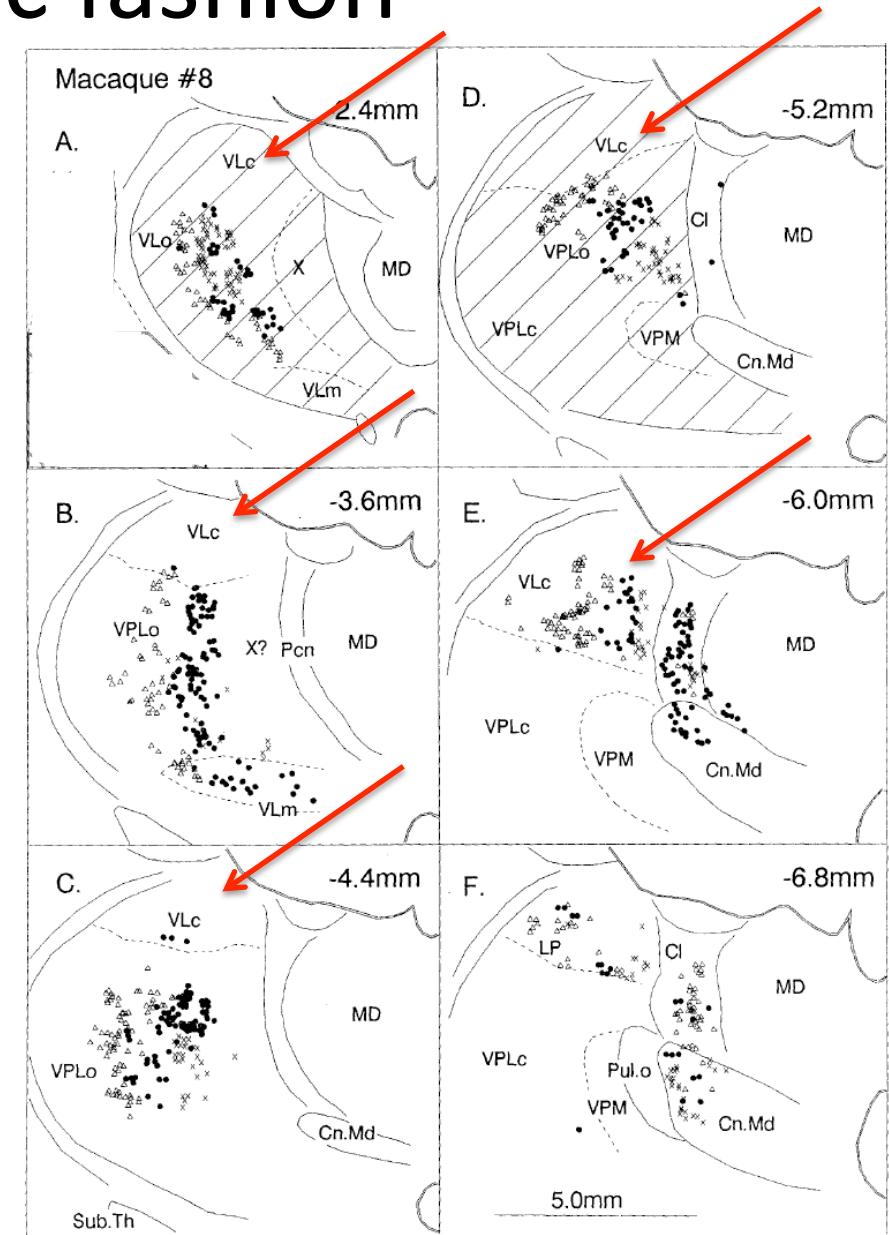
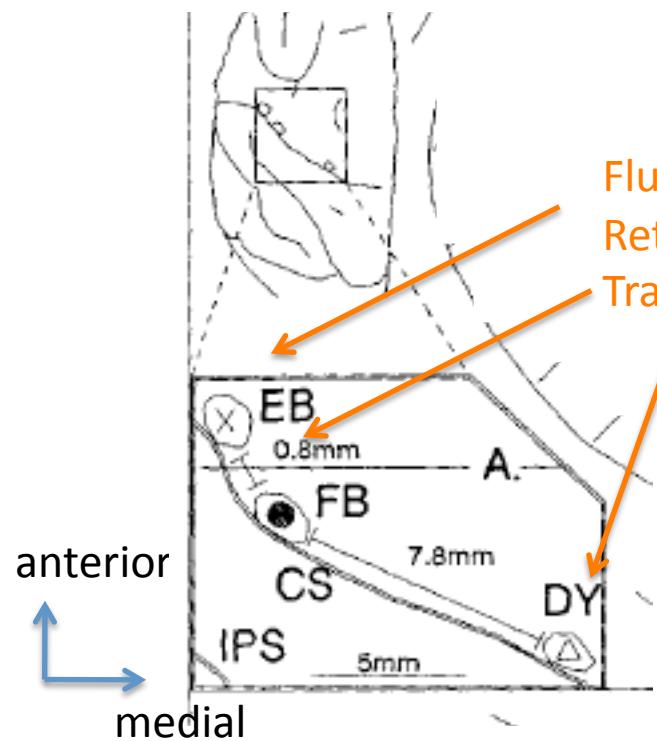
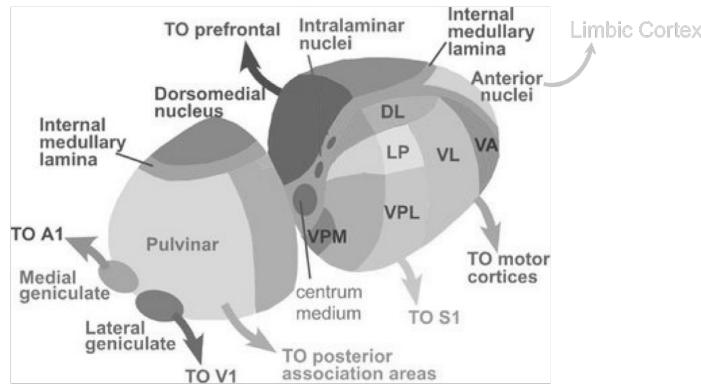
# M1 is innervated by multiple nuclei in a topographic fashion



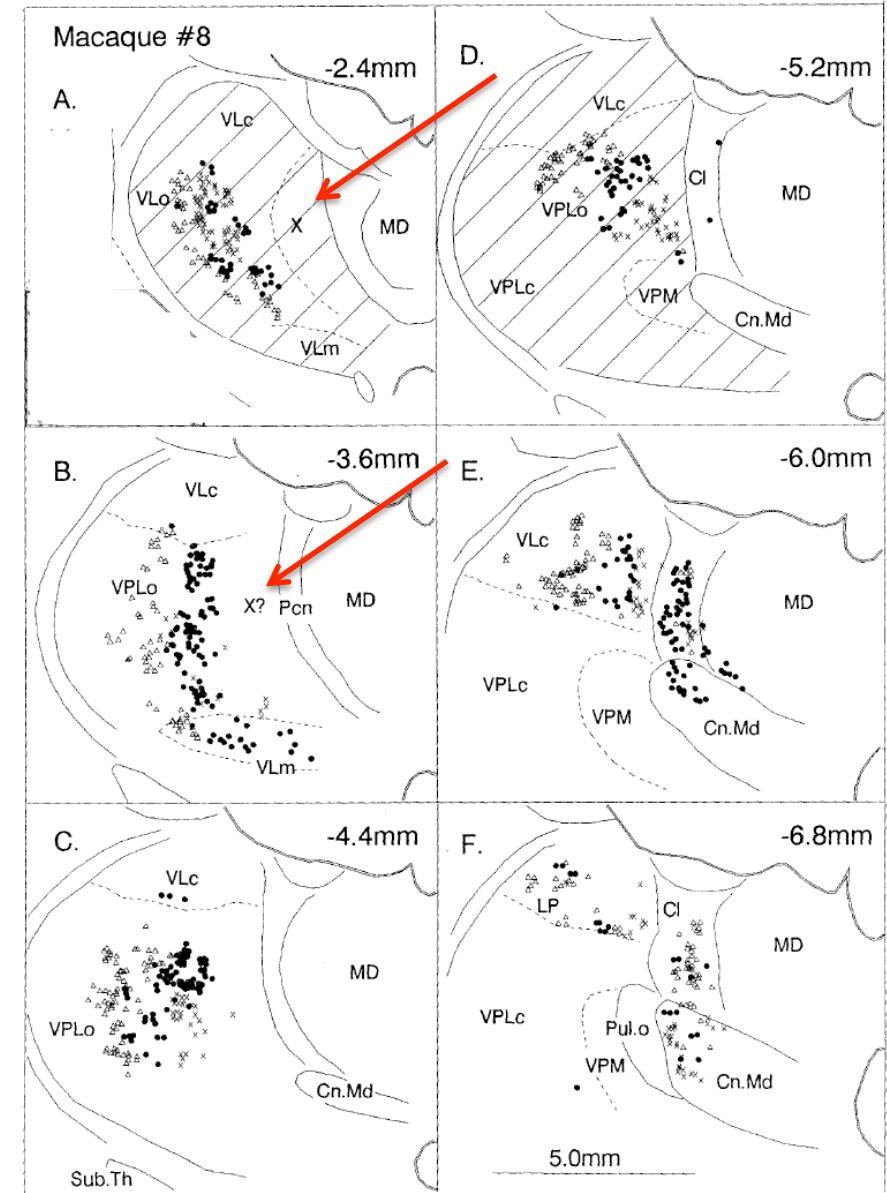
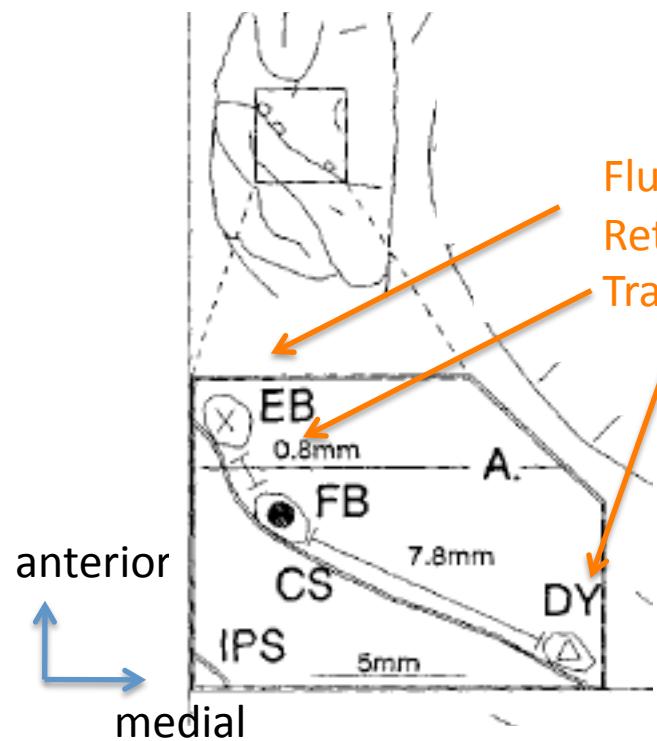
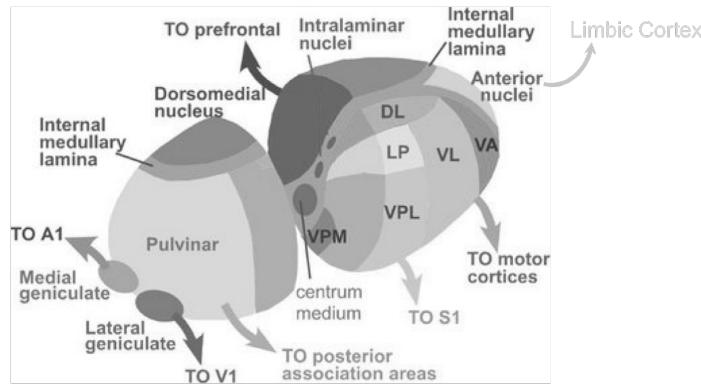
# M1 is innervated by multiple nuclei in a topographic fashion



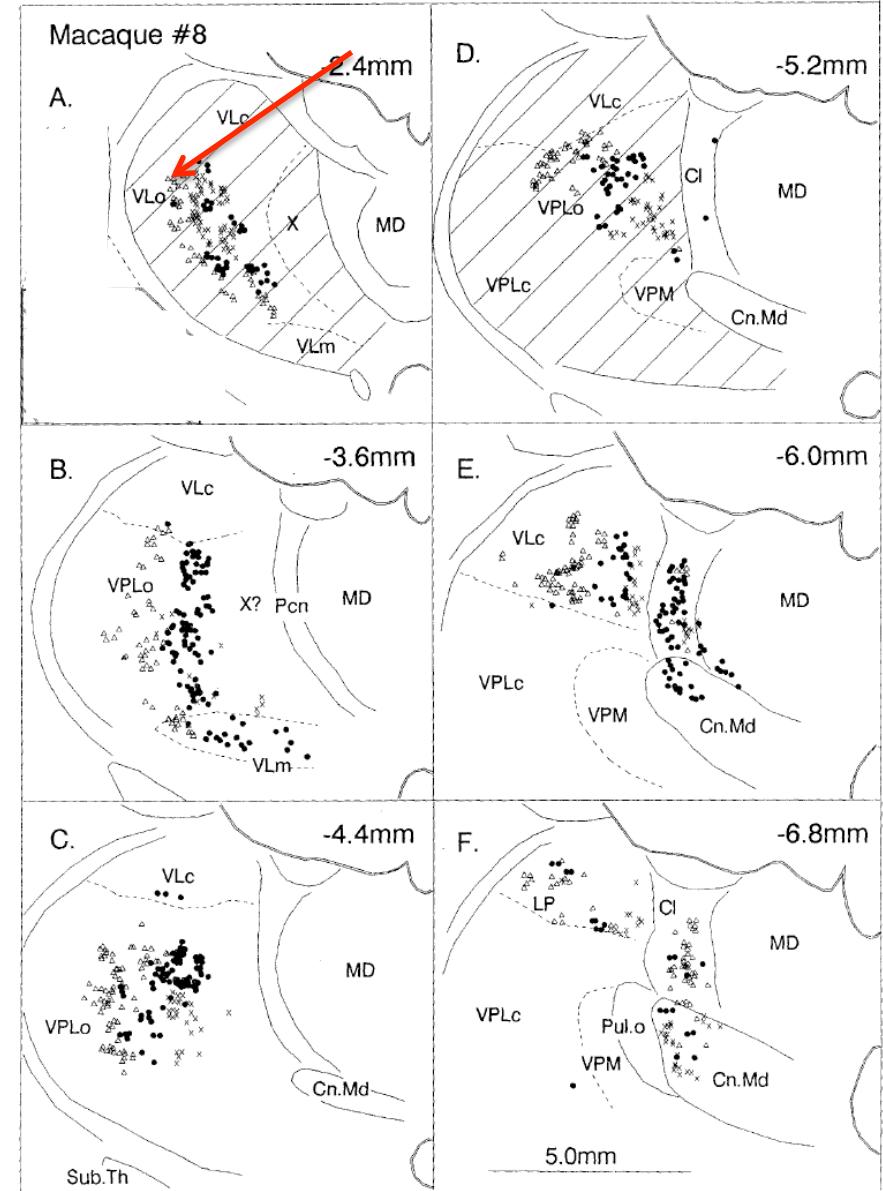
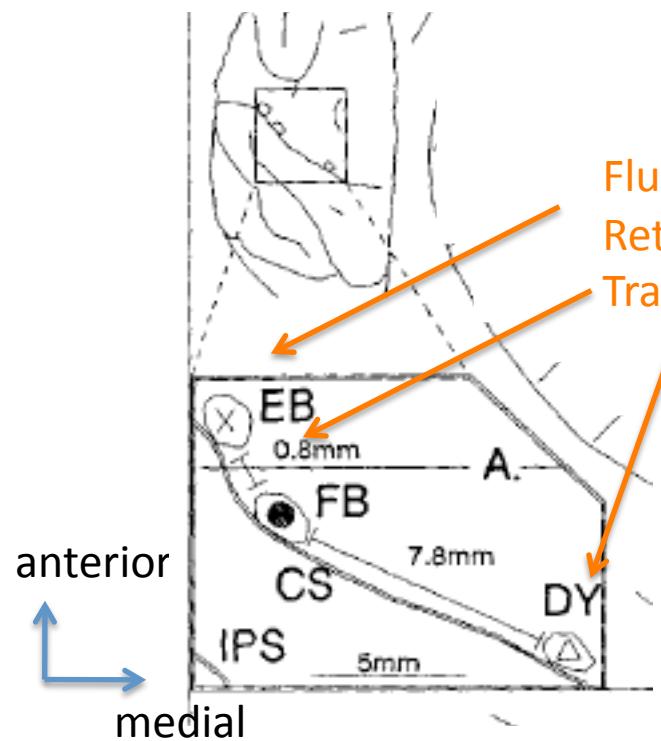
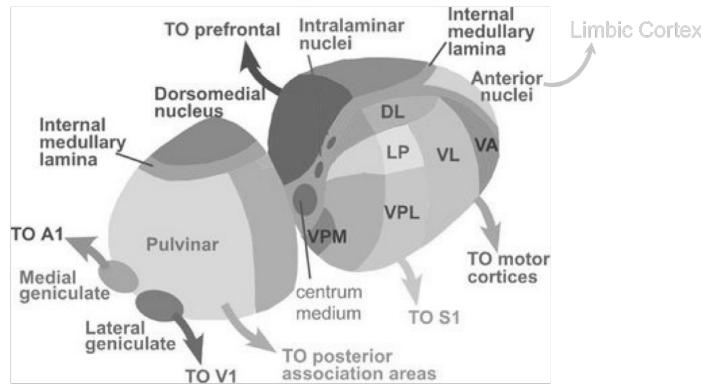
# M1 is innervated by multiple nuclei in a topographic fashion



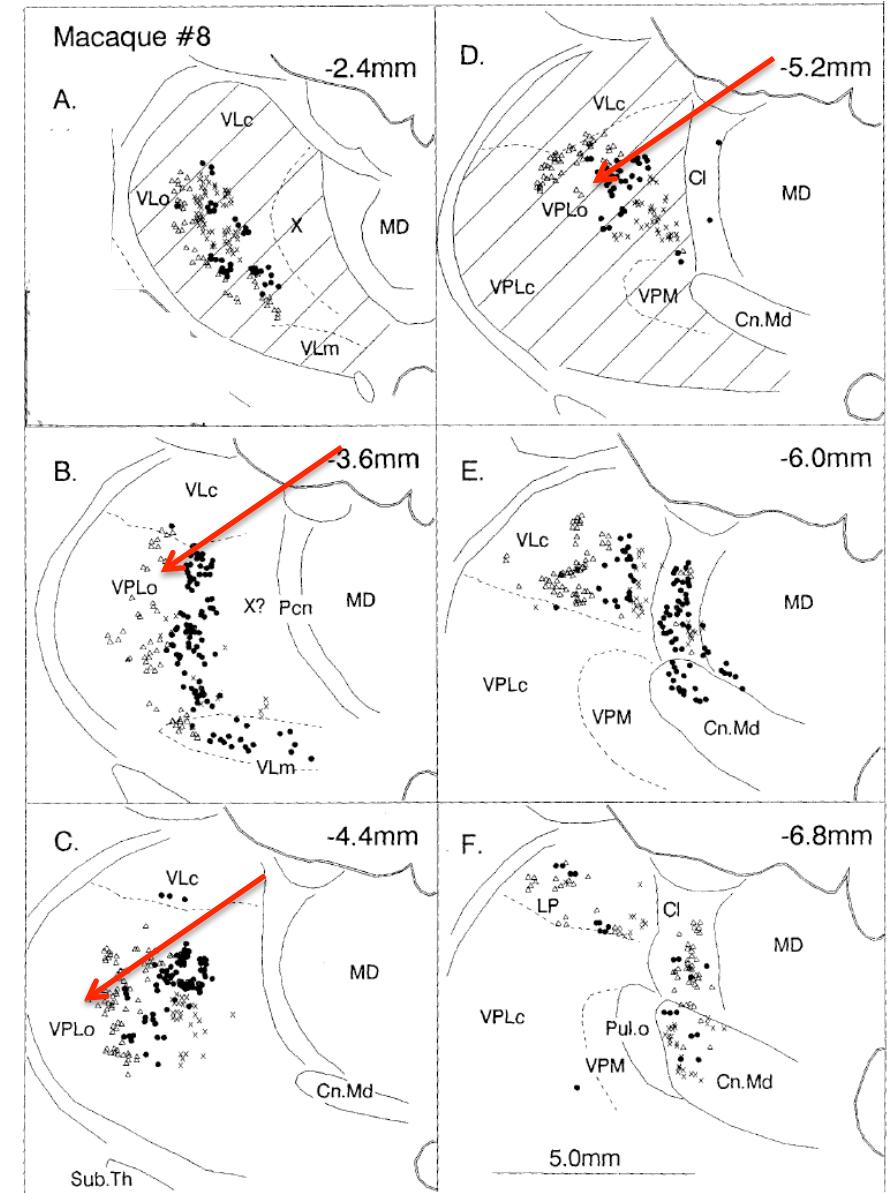
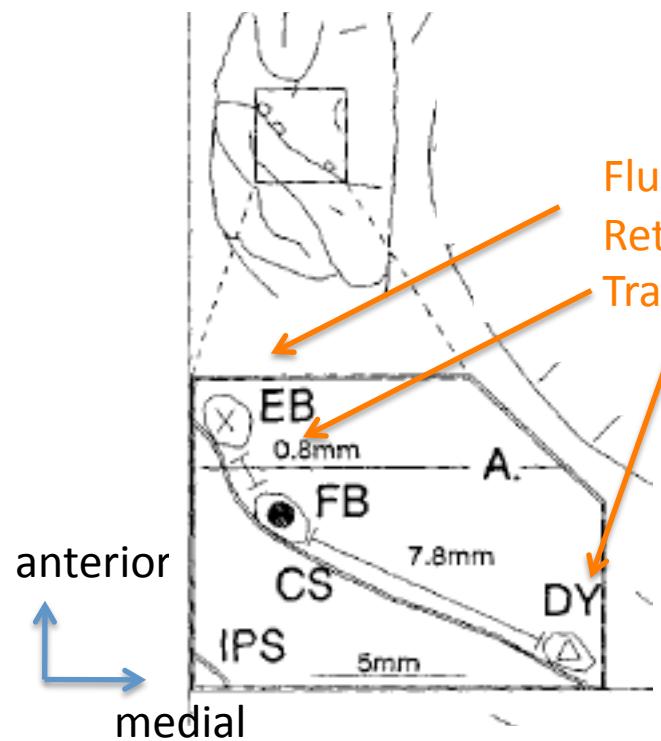
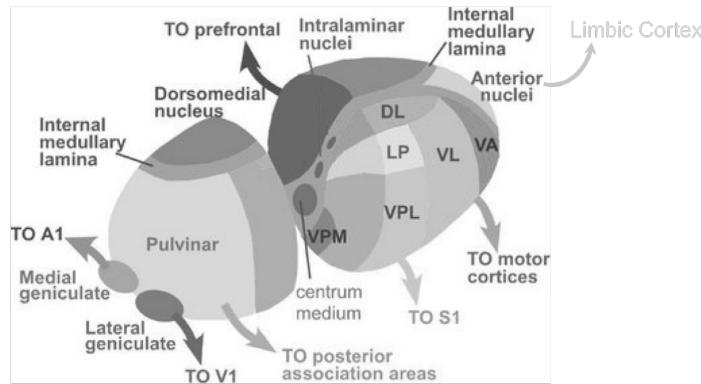
# M1 is innervated by multiple nuclei in a topographic fashion



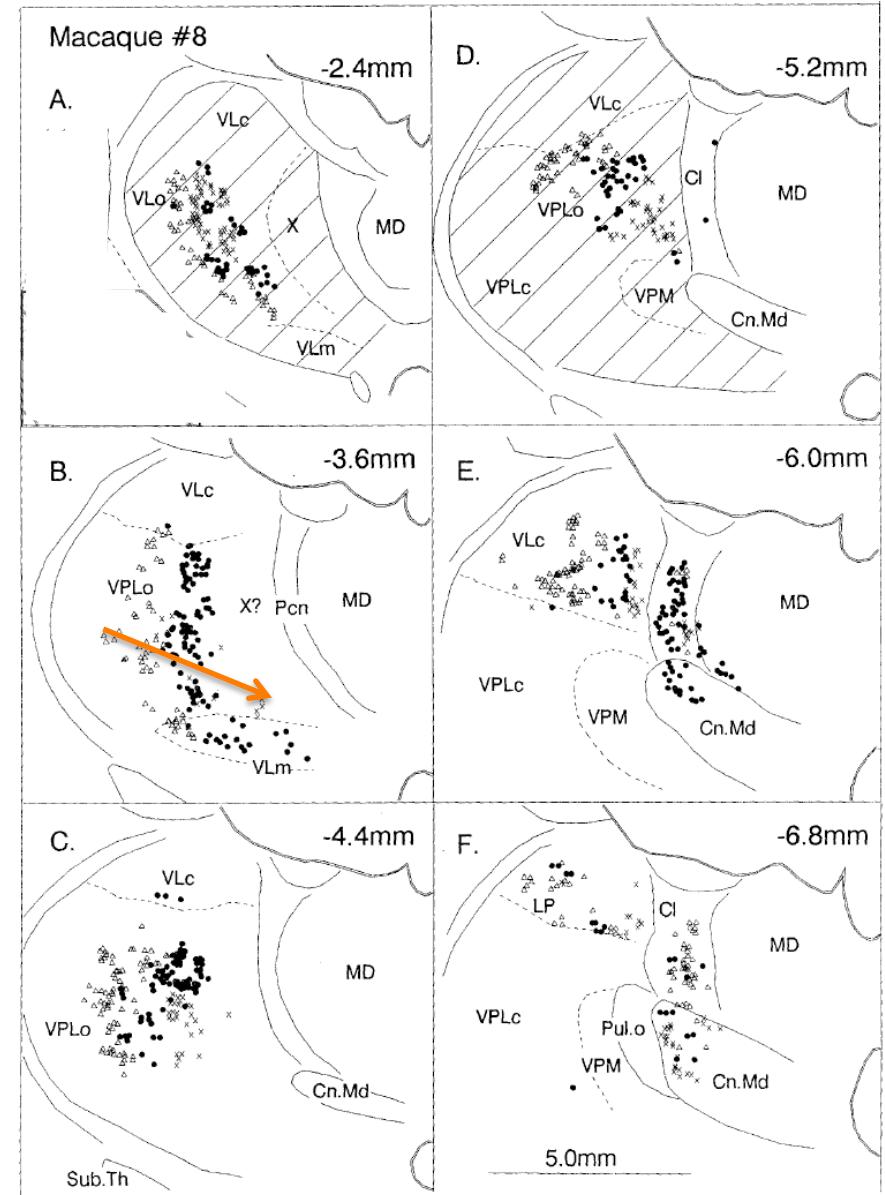
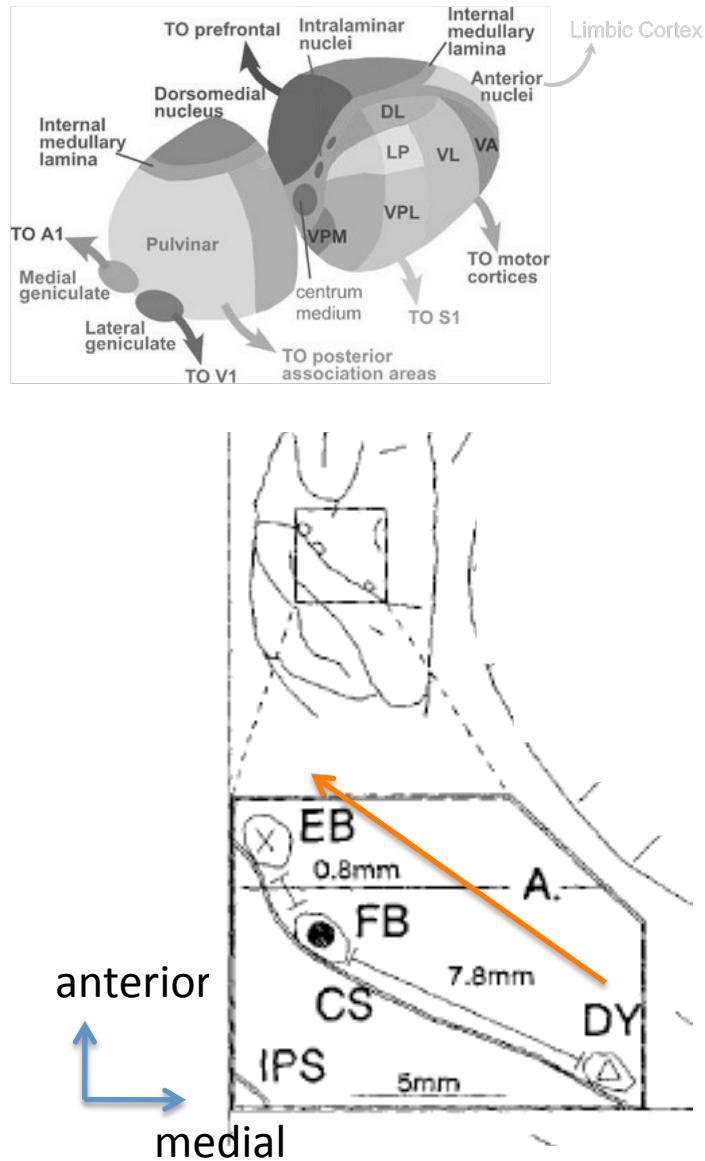
# M1 is innervated by multiple nuclei in a topographic fashion



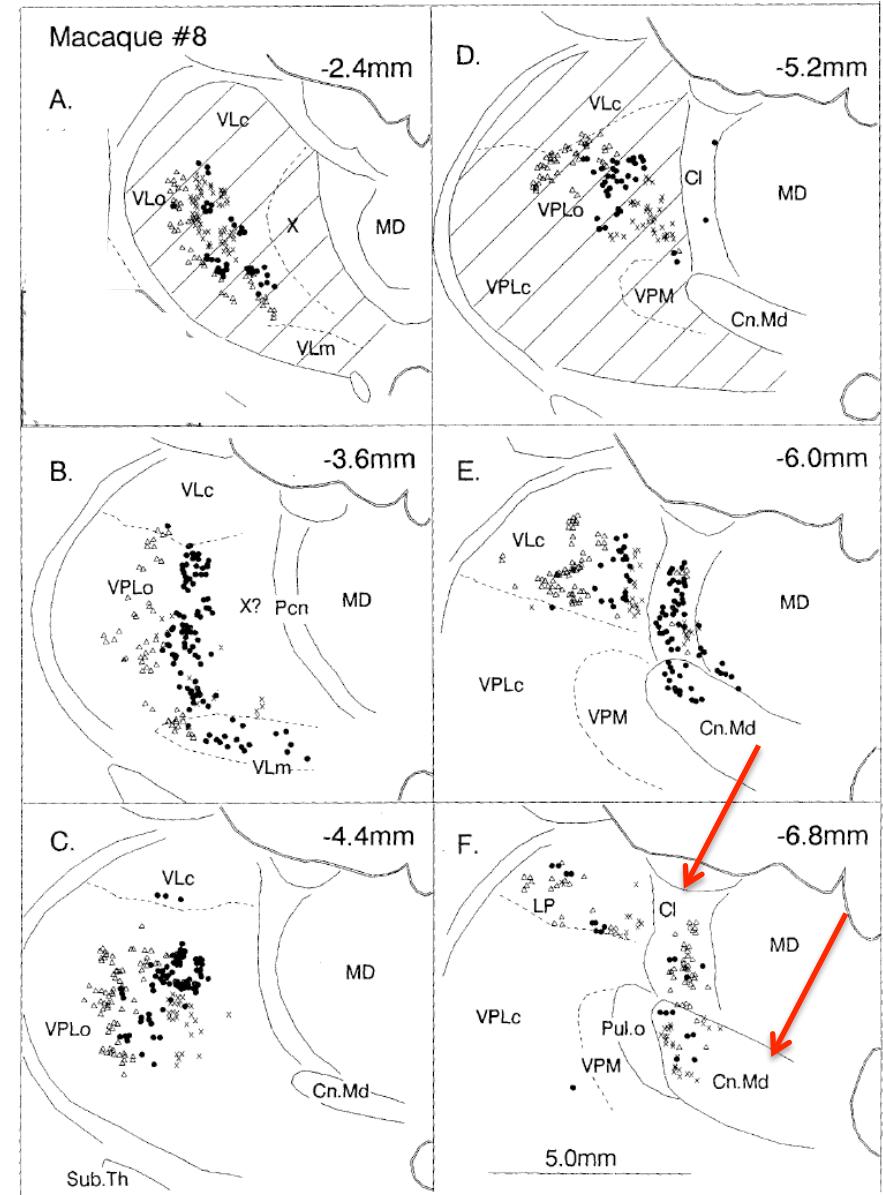
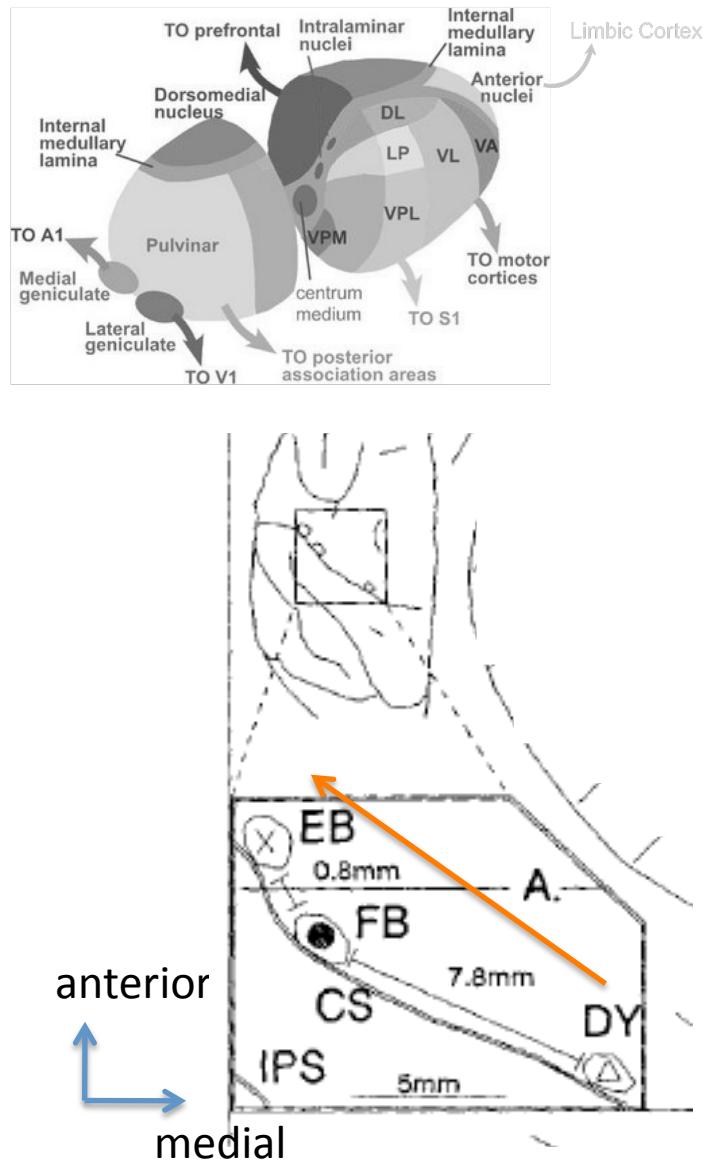
# M1 is innervated by multiple nuclei in a topographic fashion



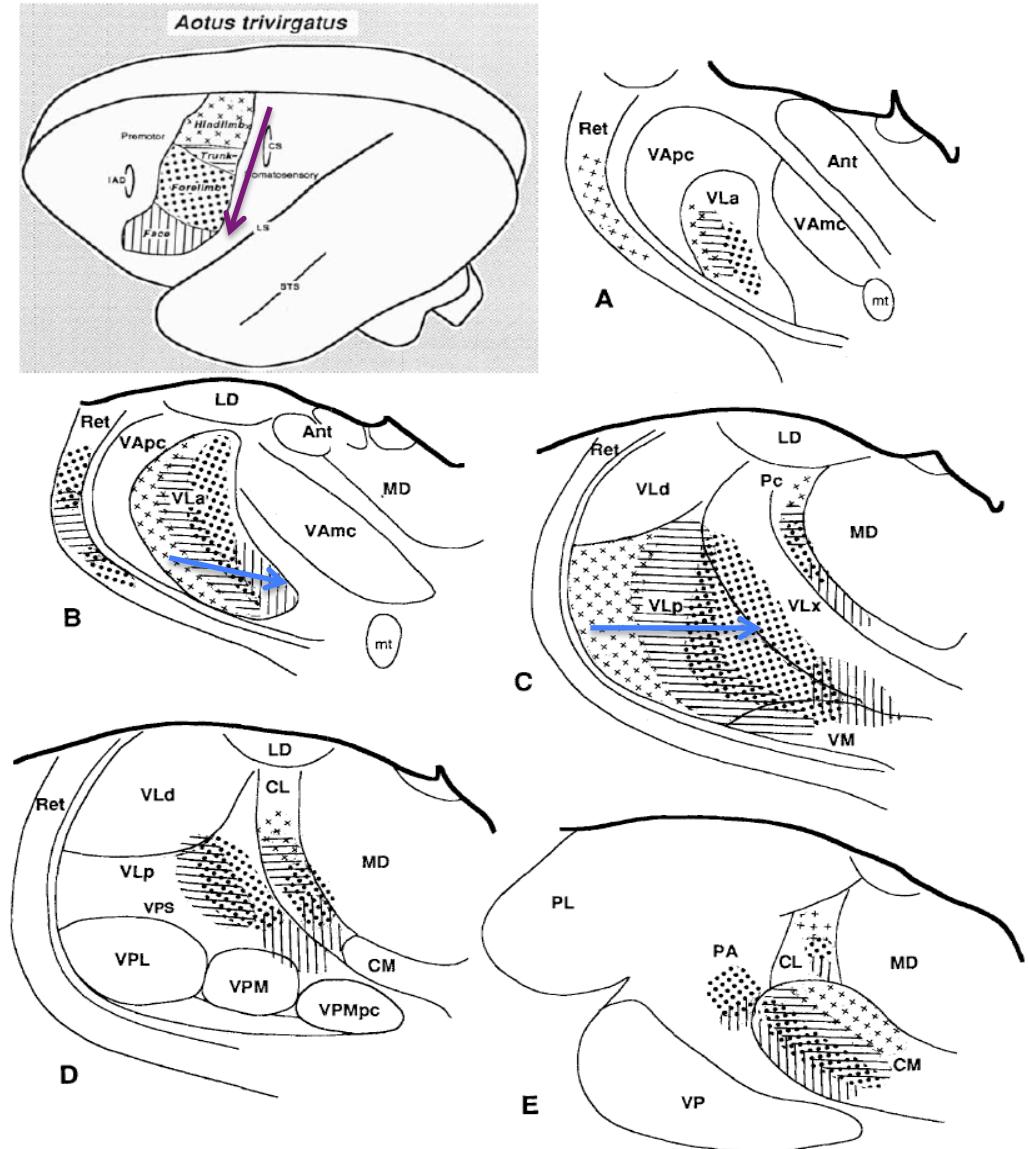
# M1 is innervated by multiple nuclei in a topographic fashion



# M1 is innervated by multiple nuclei in a topographic fashion

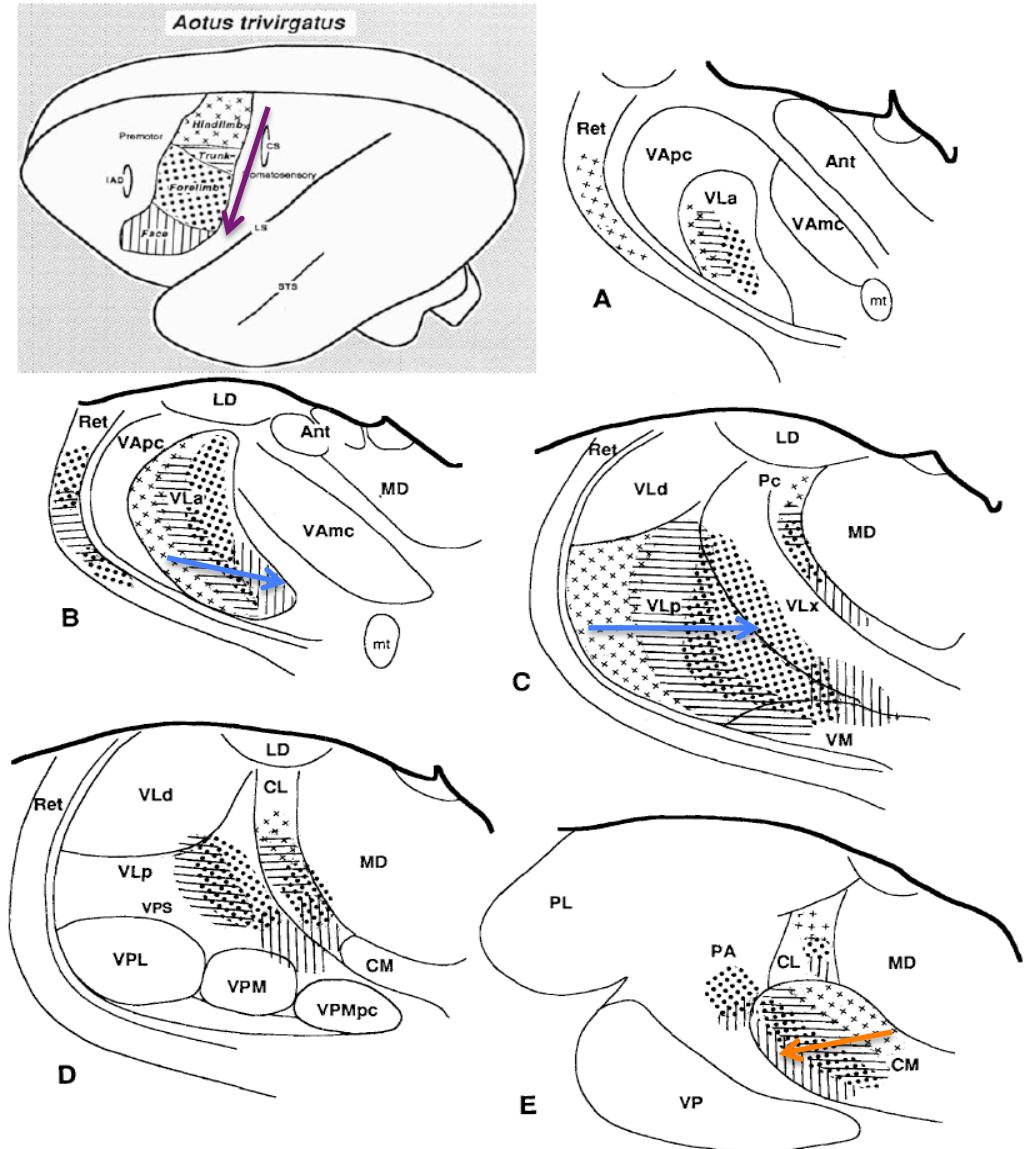


# M1 is reciprocally connected with multiple nuclei in a topographic fashion



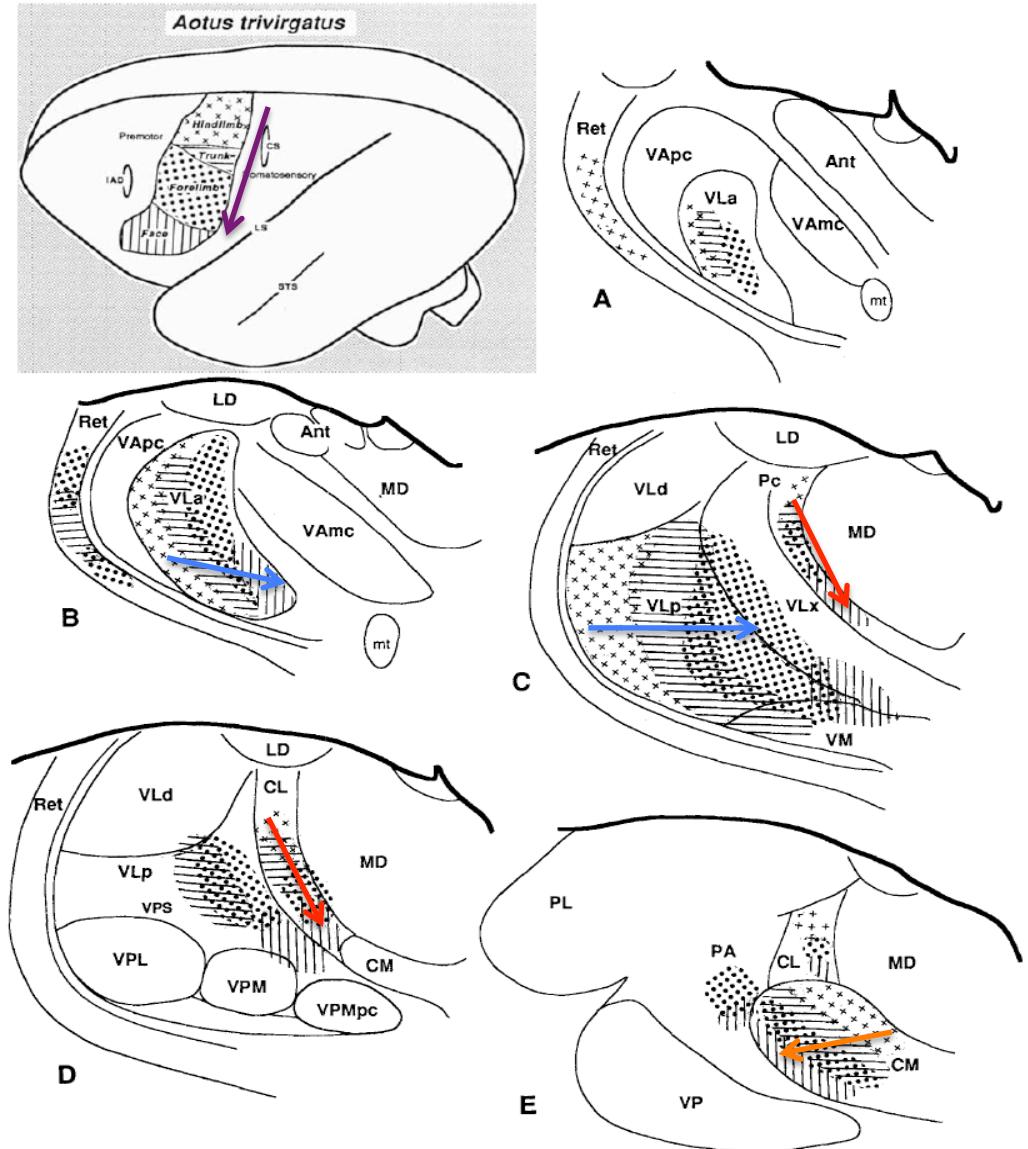
Stepniewska et al., 1994; 7 owl monkeys;  
Bidirectional WGA-HRP; retrograde FRT

# M1 is reciprocally connected with multiple nuclei in a topographic fashion



Stepniewska et al., 1994; 7 owl monkeys;  
Bidirectional WGA-HRP; retrograde FRT

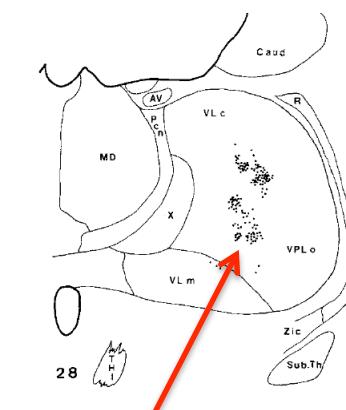
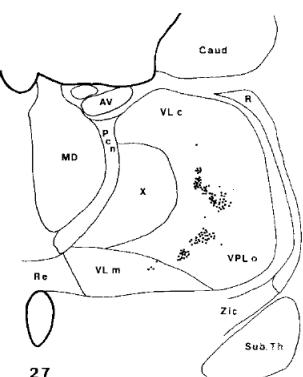
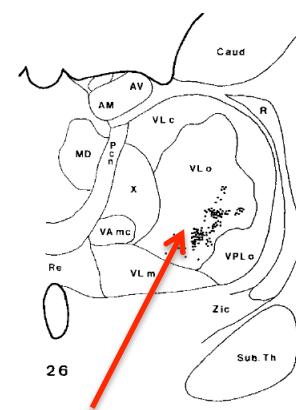
# M1 is reciprocally connected with multiple nuclei in a topographic fashion



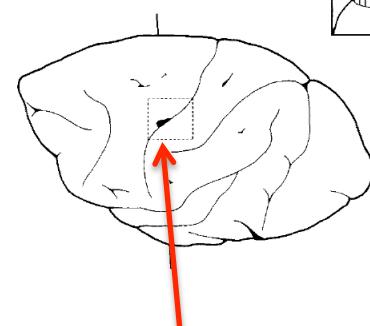
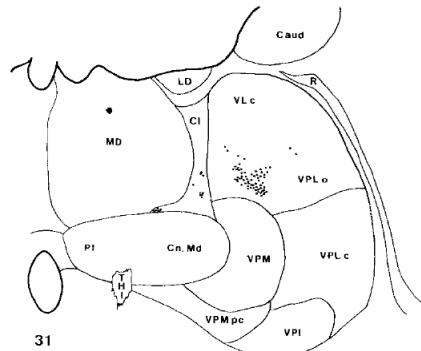
Stepniewska et al., 1994; 7 owl monkeys;  
Bidirectional WGA-HRP; retrograde FRT

# VLo, VPLo project to both F1 (M1) & F3 (SMA)

medial      lateral

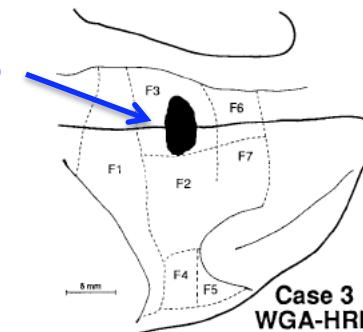


IT4-3

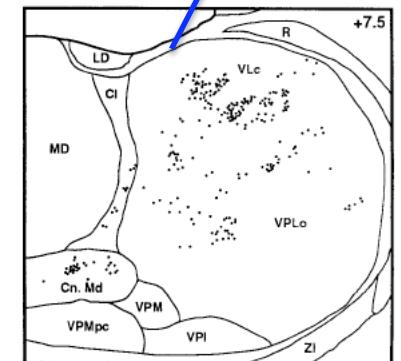
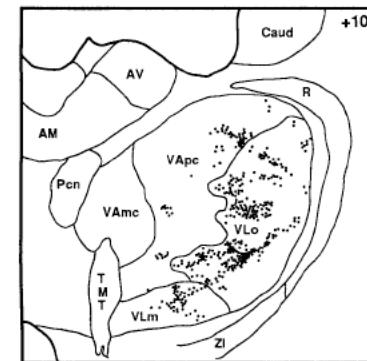
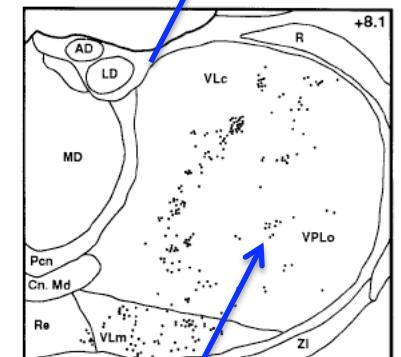
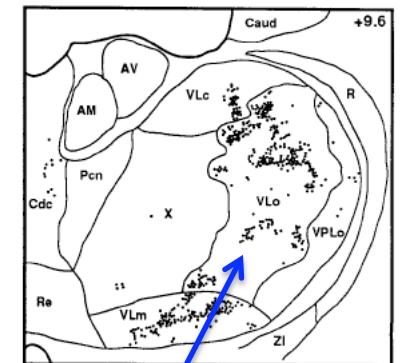
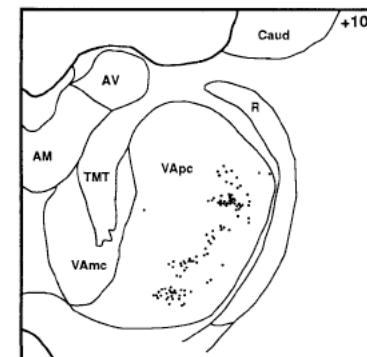


Retrograde WGA-HRP

Retrograde WGA-HRP



Case 3  
WGA-HRP



Matelli et al., 1989

Matelli & Luppino, 1996

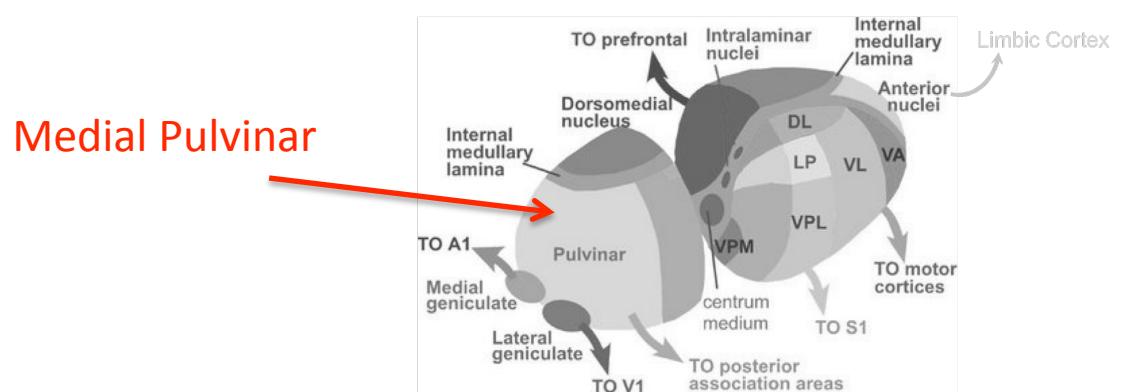
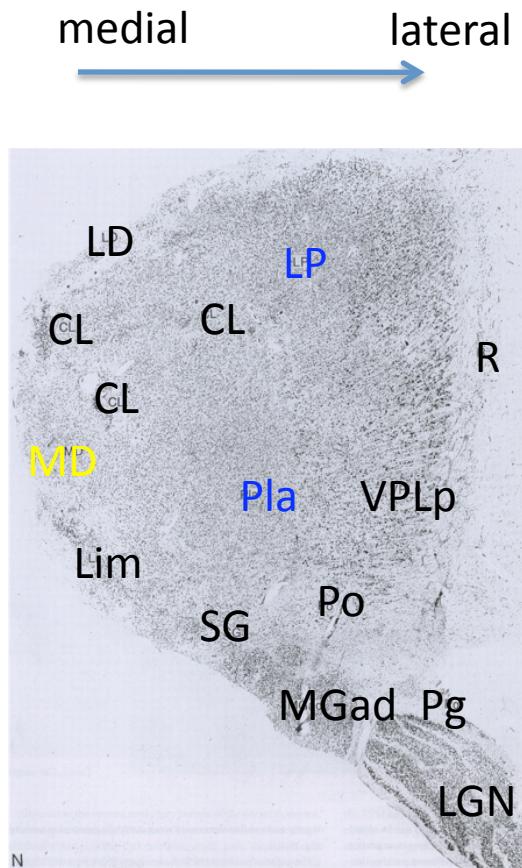
# The Modern View

- Every nucleus → multiple cortical fields
  - VLo, VPLo → M1, SMA
- Every cortical field (except maybe areas 3, 1) → multiple thalamic nuclei
  - M1 → VLo, VPLo, CL, CM
- (mostly) Reciprocal connections
- Somatotopy consistent with connections

# Modern Tract Tracing:

Medial Pulvinar has reciprocal connections with  
Prefrontal, Cingulate, Temporal & Parietal Cortices

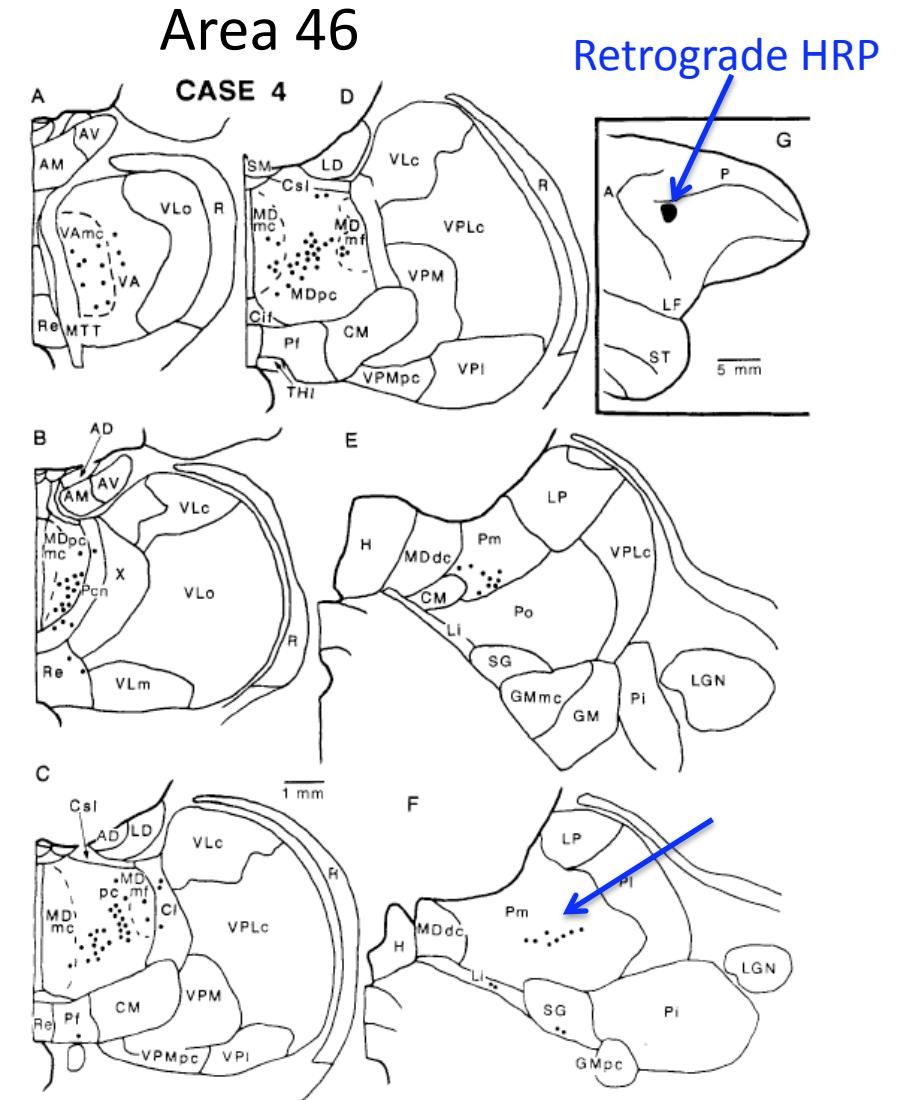
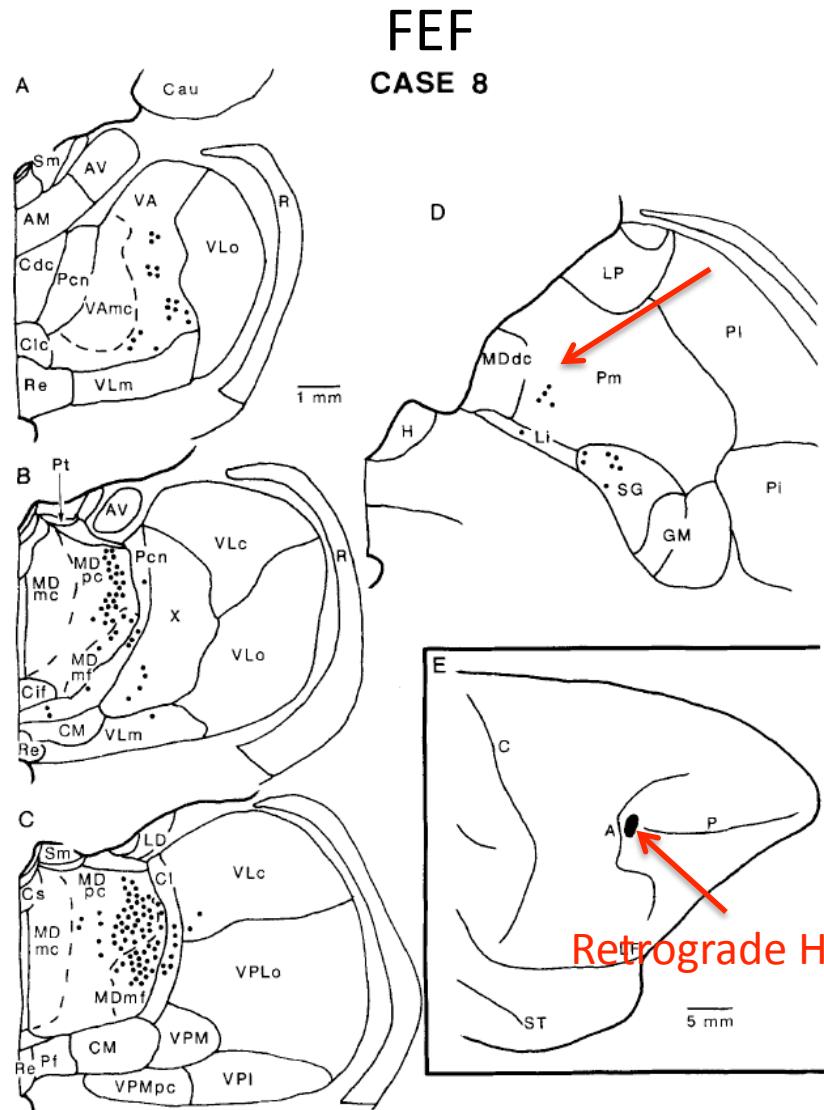
# Medial Pulvinar



# Modern Tract Tracing:

Medial Pulvinar has reciprocal connections with  
Prefrontal Cortex

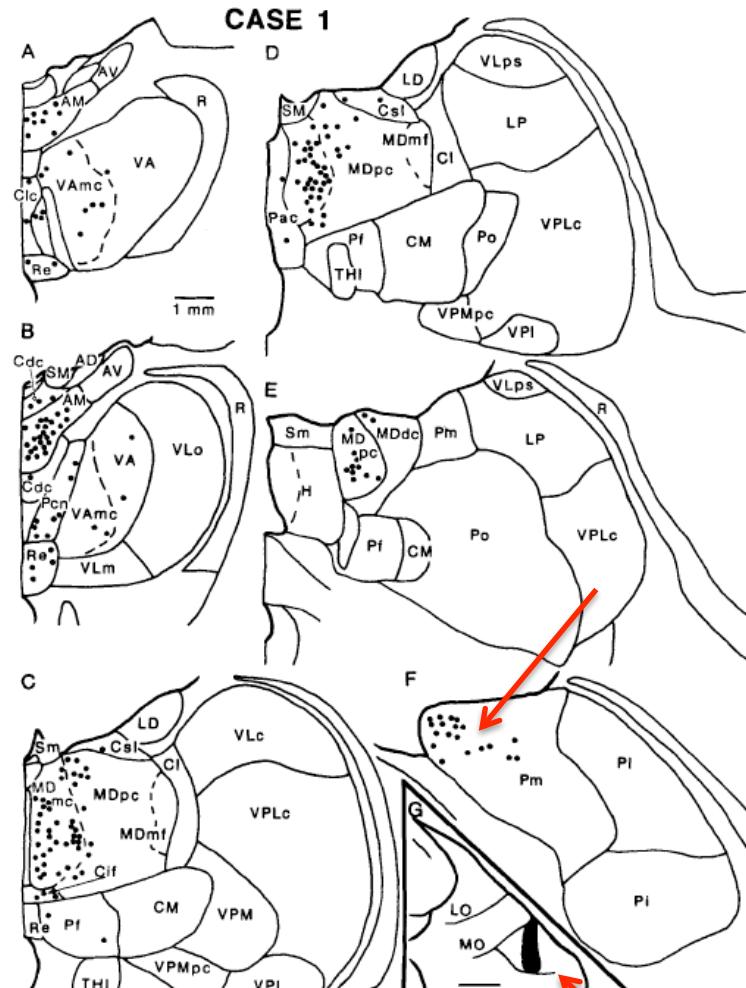
# Medial Pulvinar projects to LPFC



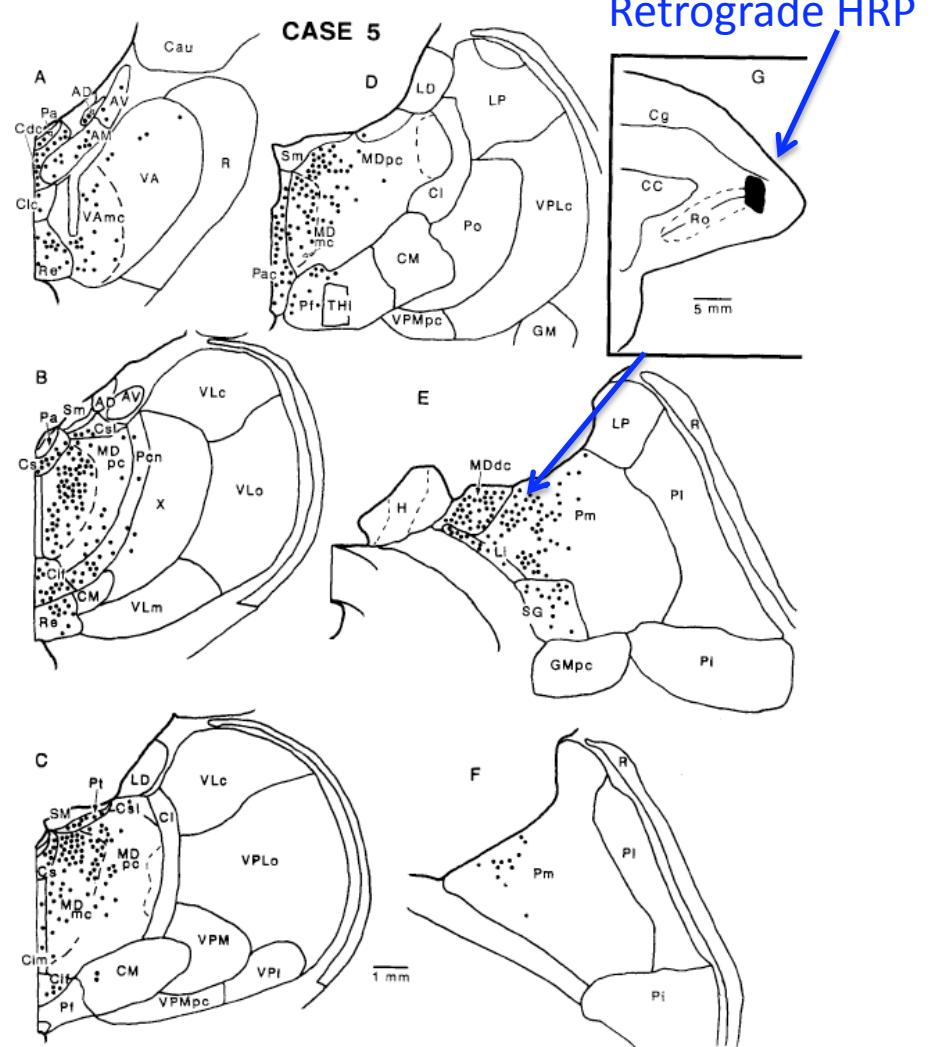
Barbas et al. 1991, 9 monkeys,

# Medial Pulvinar projects to OPFC & MPFC

Area 11



Area 32

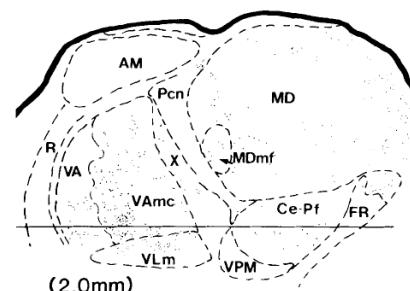
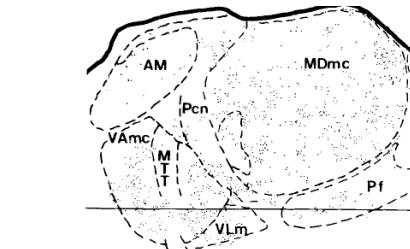
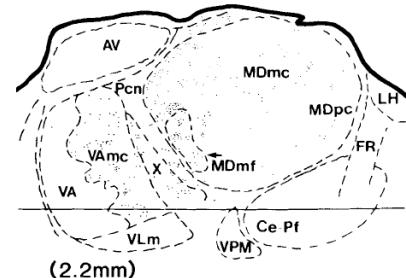
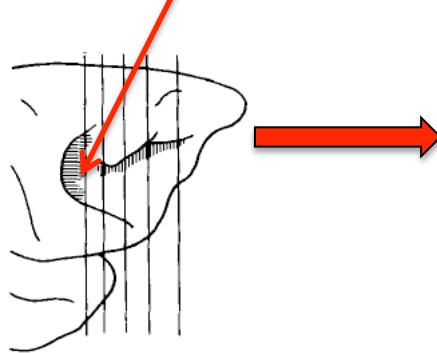


Barbas et al. 1991, 9 monkeys,

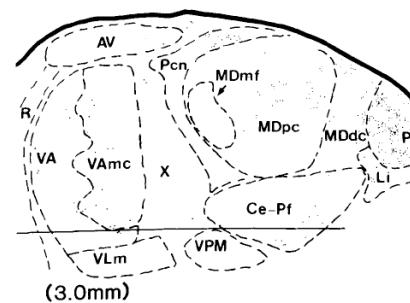
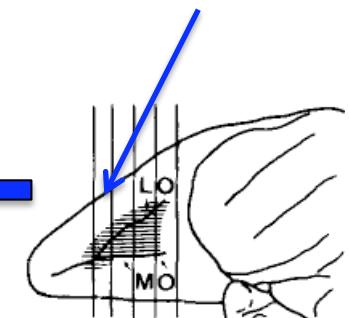
Retrograde HRP

# LPFC → OPFC; Thalamic Stains Lateral → Medial

Fluorescent  
Retrograde  
Tracers

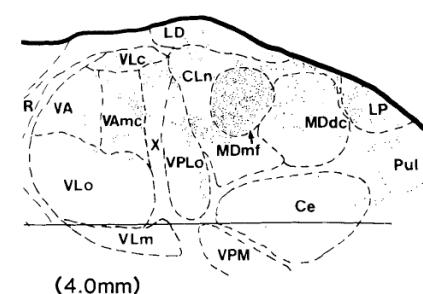


Fluorescent  
Retrograde  
Tracers



medial

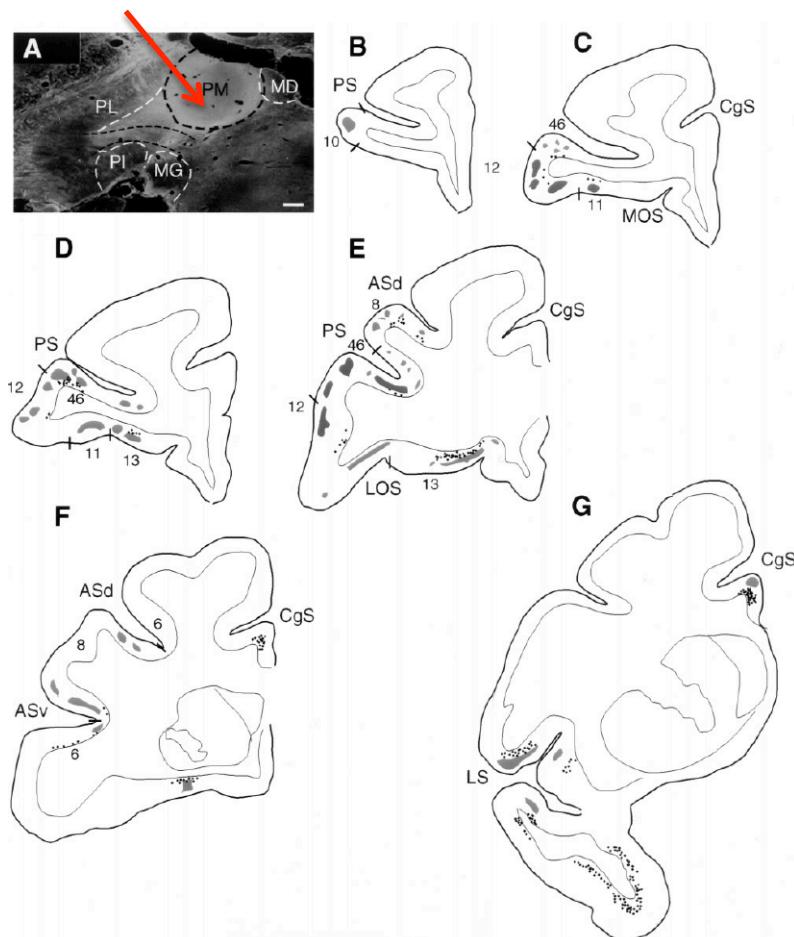
lateral



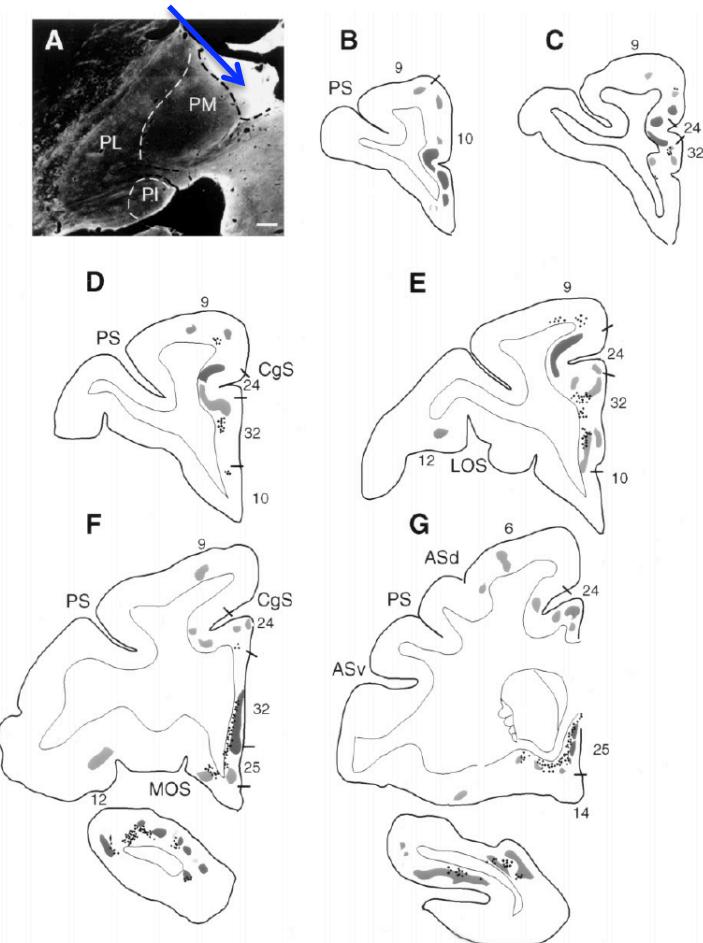
Illinsky et al. 1985.  
9 Rhesus Monkeys

# Lateral Medial Pulvinar reciprocally connected to LPFC, OPFC Medial Medial Pulvinar reciprocally connected to MPFC, OPFC

Bidirectional WGA-HRP into  
lateral medial Pulvinar



Bidirectional WGA-HRP into  
medial medial Pulvinar



Romanski et al. 1997; 15 rhesus.

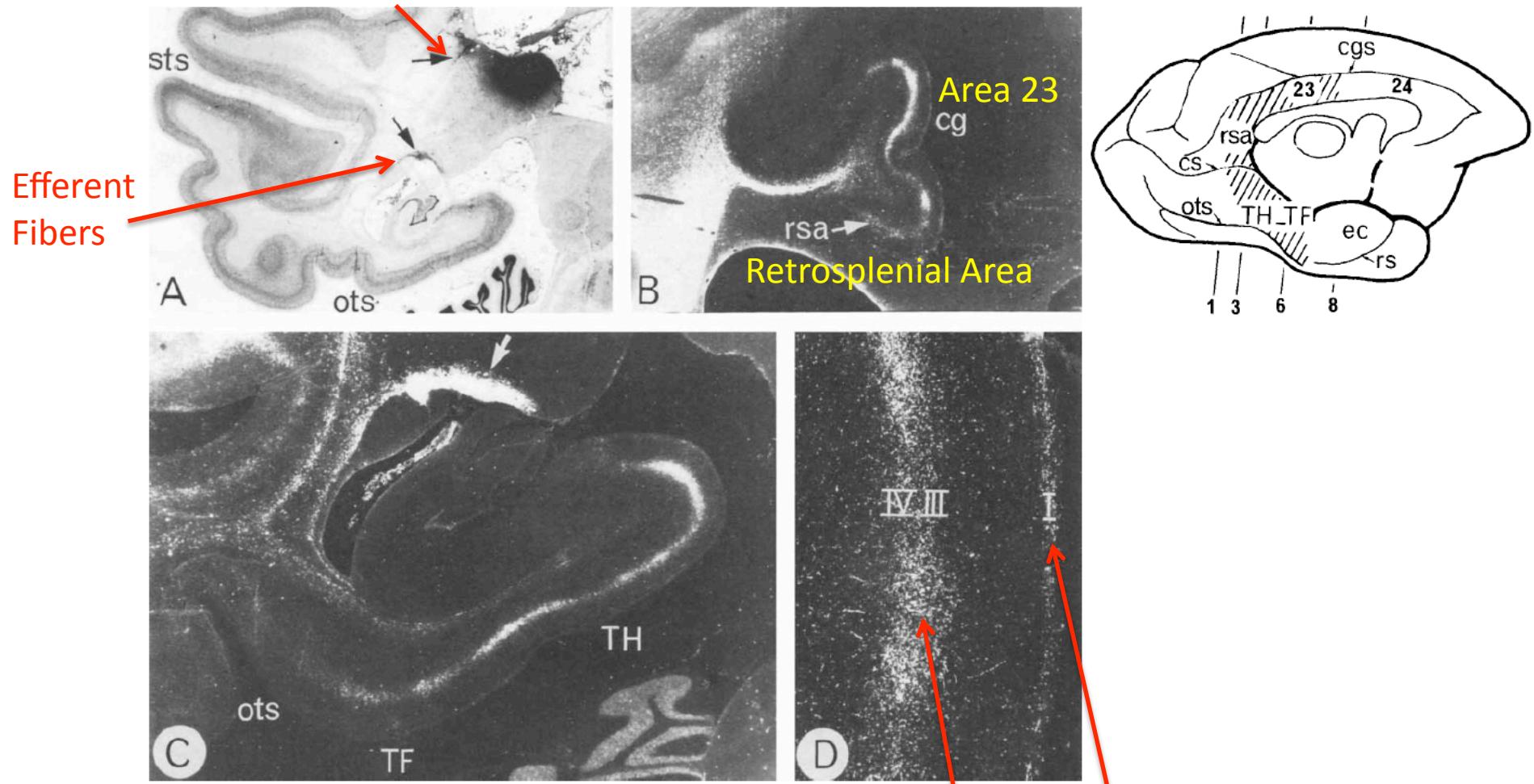
Retrograde: black Circles; Anterograde: Gray Patches

# Modern Tract Tracing:

Medial Pulvinar has reciprocal connections with  
Posterior Cingulate, Retrosplenial Cortex &  
Parahippocampal Cortex

# Medial Pulvinar projects to PCC, Rsp, TH, TF

Anterograde Amino Acid into medial Pulvinar

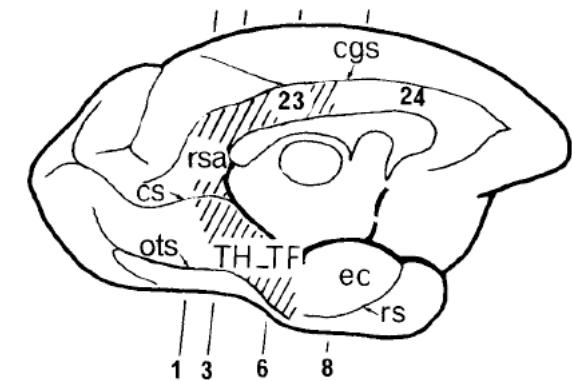
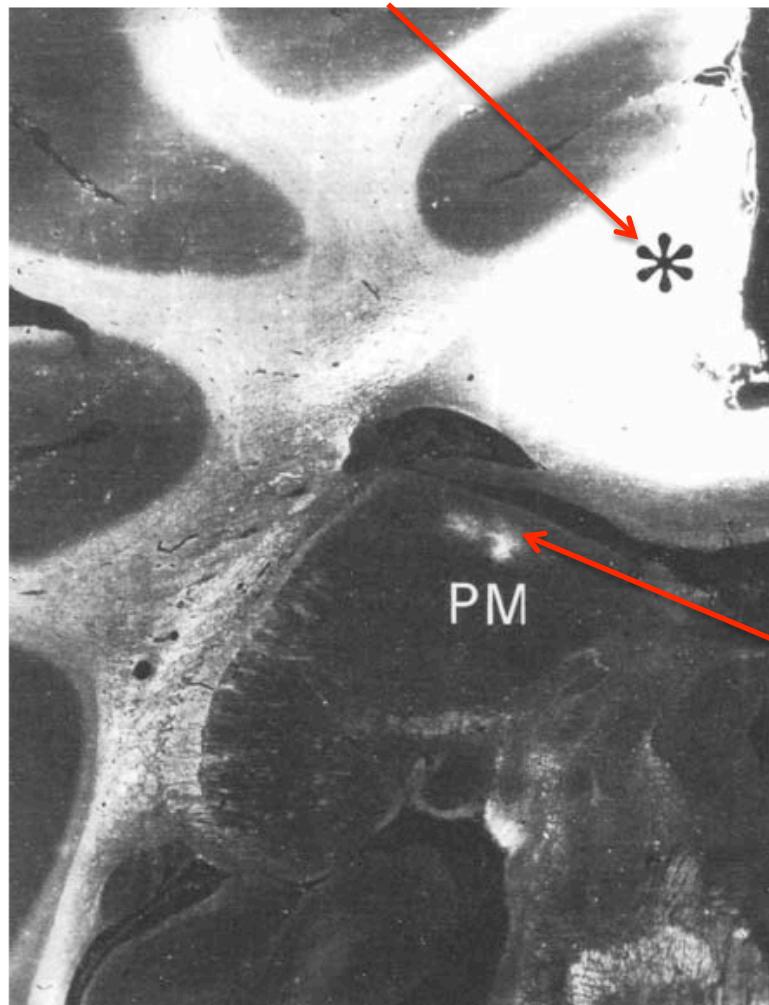


Baleydier & Mauguiere. 1985  
3 baboons, 2 Macaque

Parahippocampal gyrus:  
terminals in layer III, IV and I

# PCC projects to medial Pulvinar

Anterograde Amino Acid into PCC

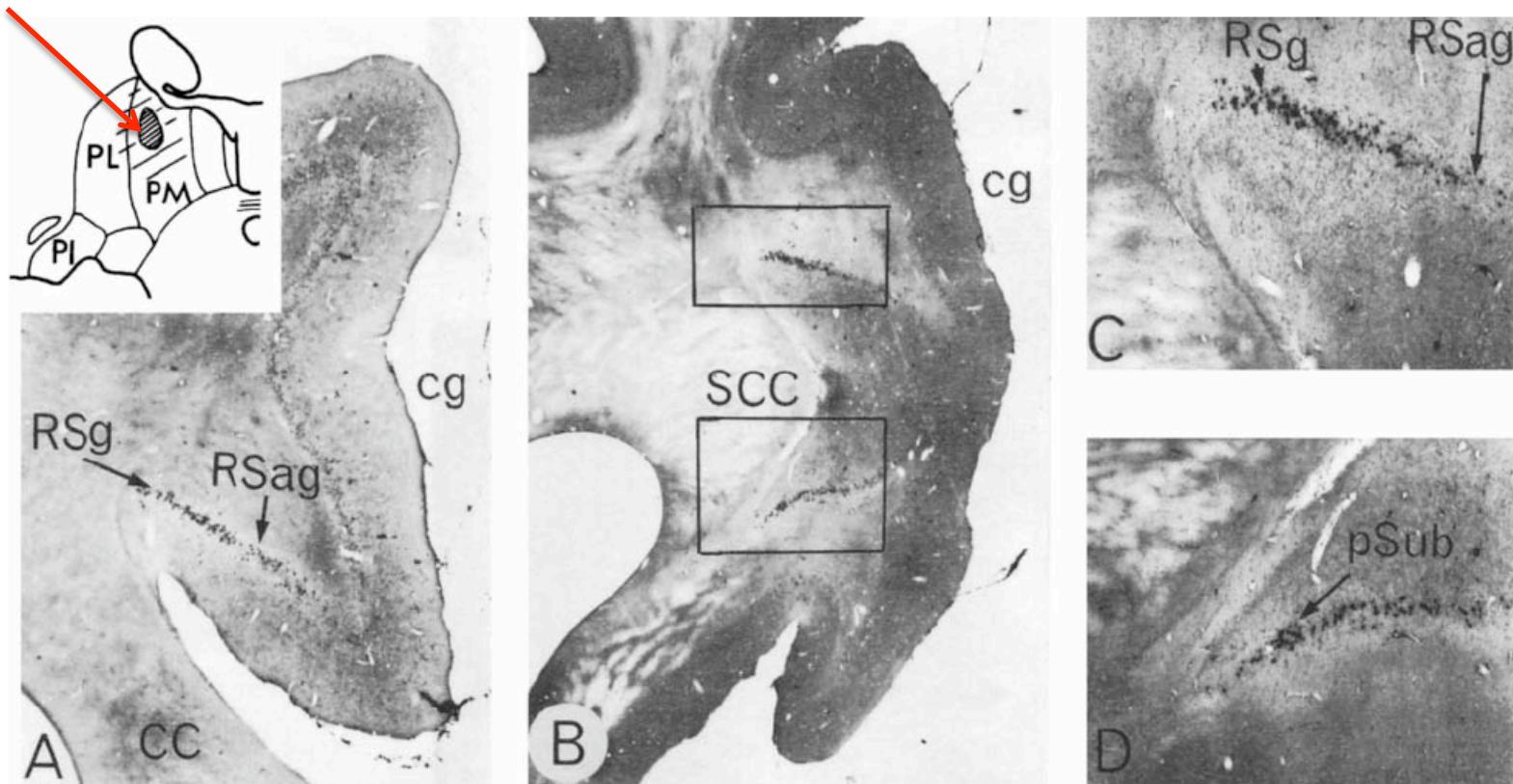


Silver grains in medial Pulvinar

Baleydier & Mauguiere. 1985  
3 baboons, 2 Macaque

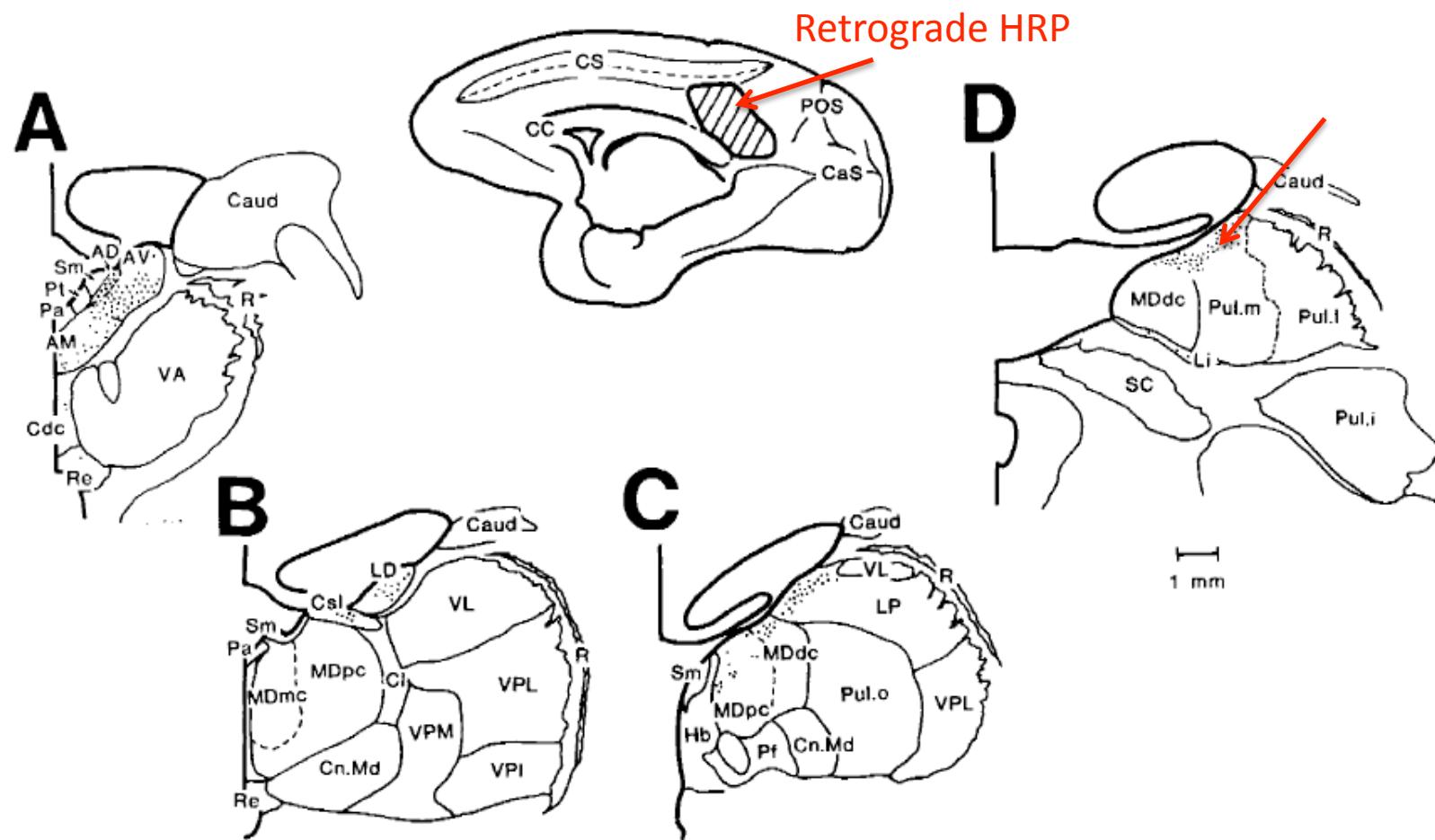
# Rsp, Pre-subiculum project to medial Pulvinar

Retrograde HRP into medial Pulvinar



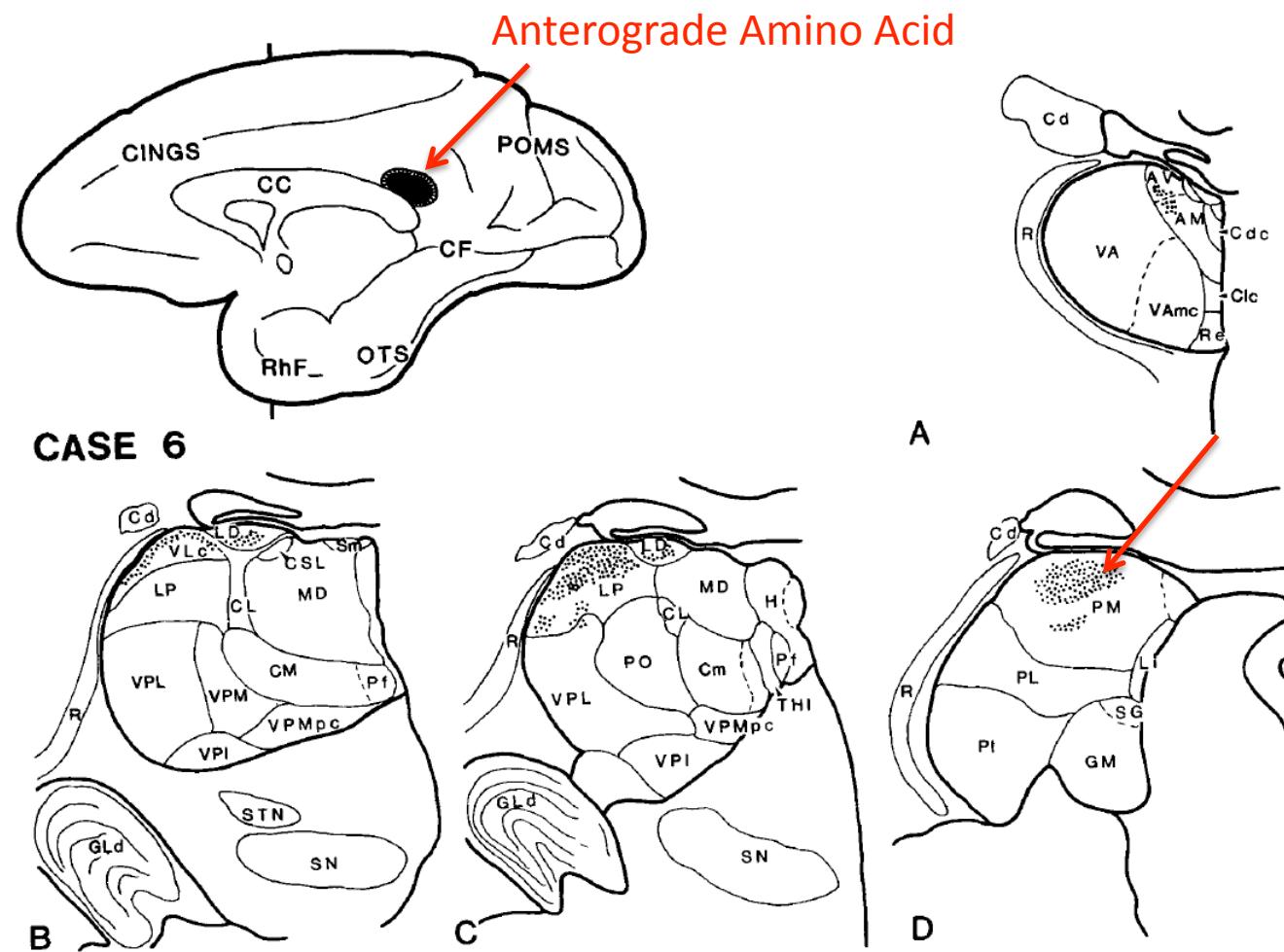
Baleydier & Mauguiere. 1985  
3 baboons, 2 Macaque

# Medial Pulvinar projects to PCC



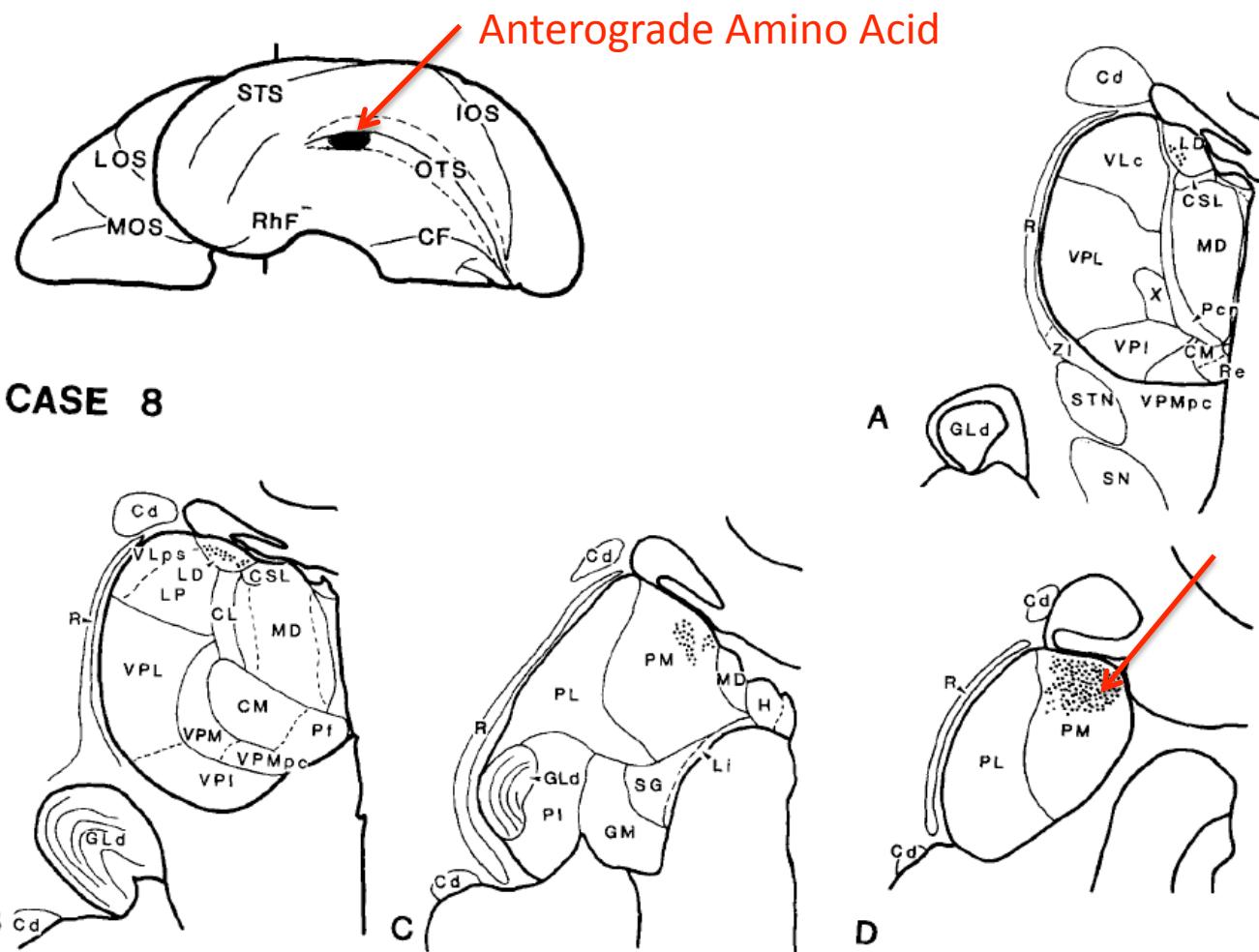
Vogt et al. 1987. 15 Rhesus

# Area 23 projects to medial Pulvinar

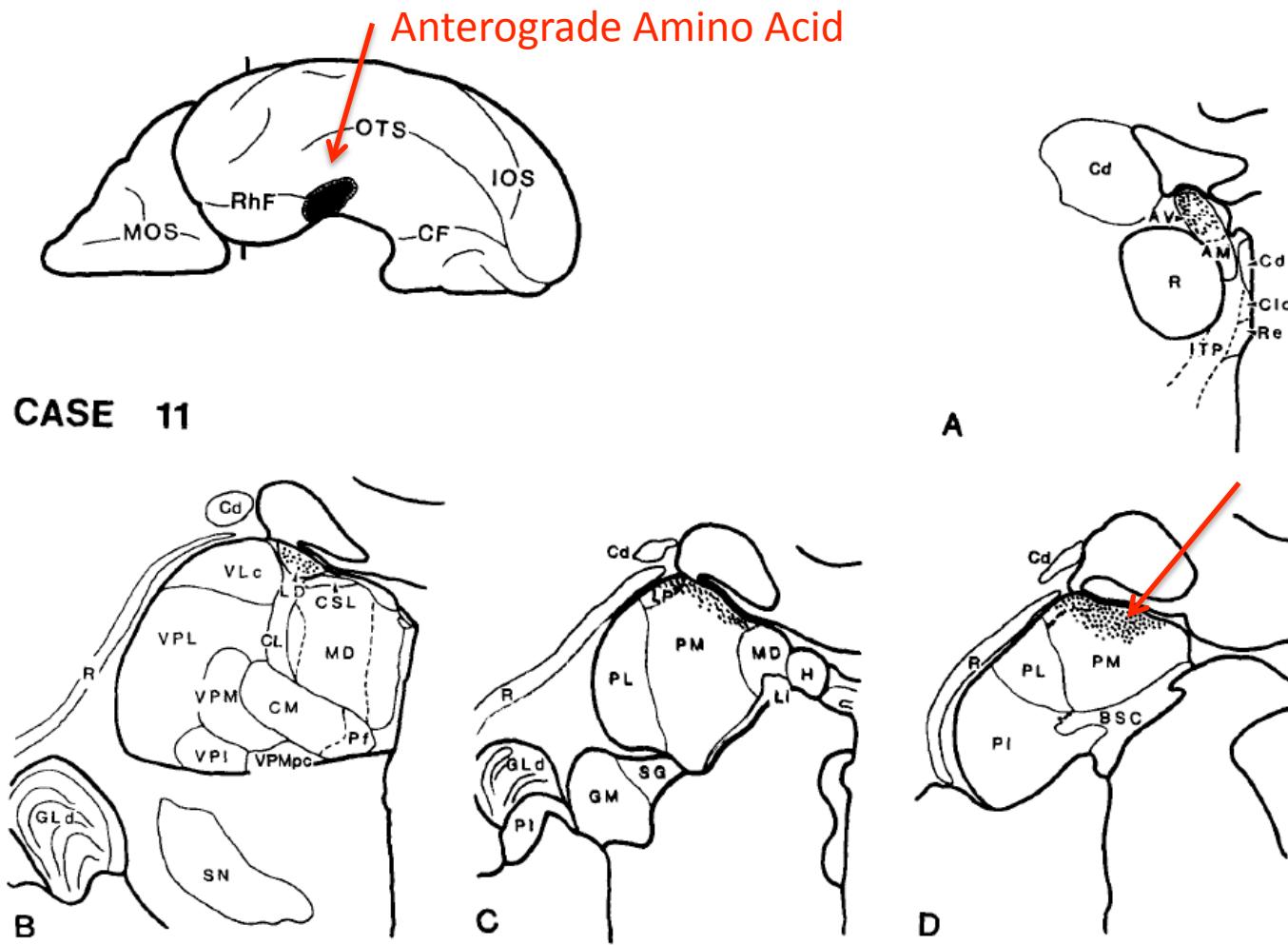


Yeterian & Pandya. 1988. 13 Rhesus

# Parahippocampal TF projects to medial Pulvinar



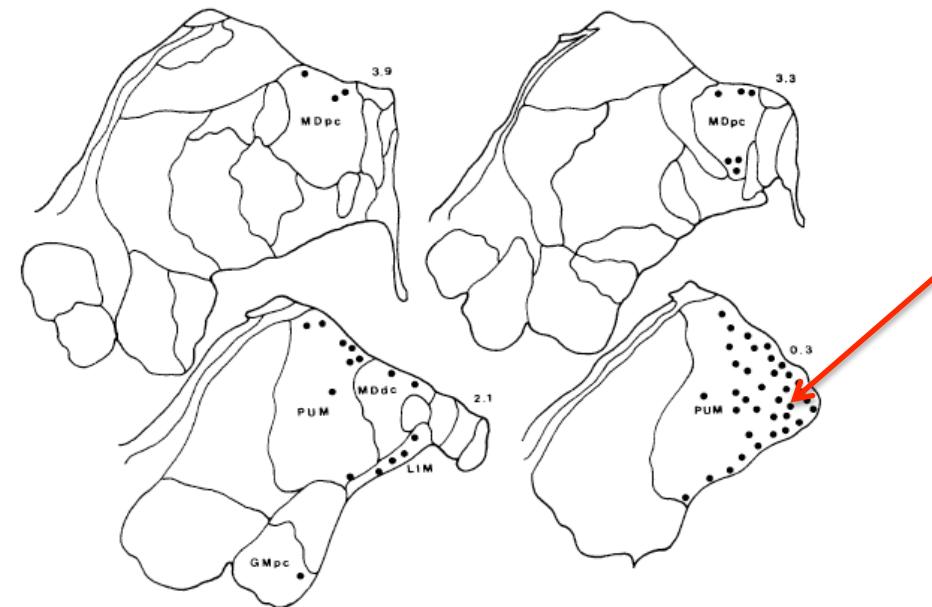
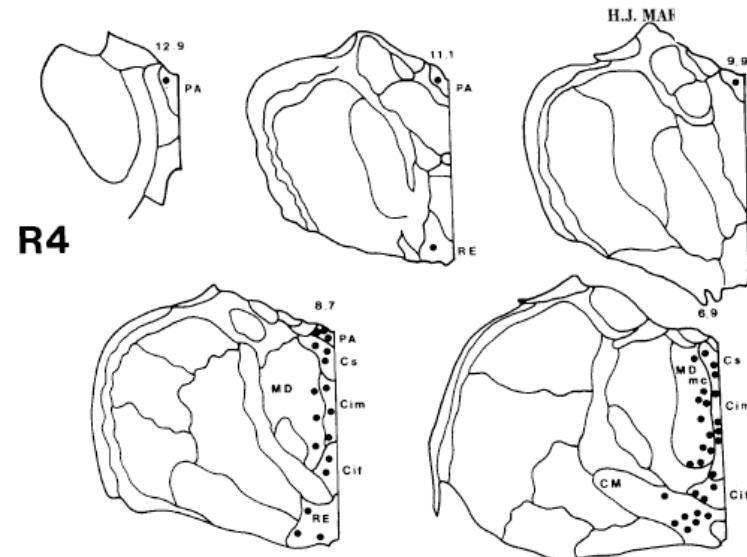
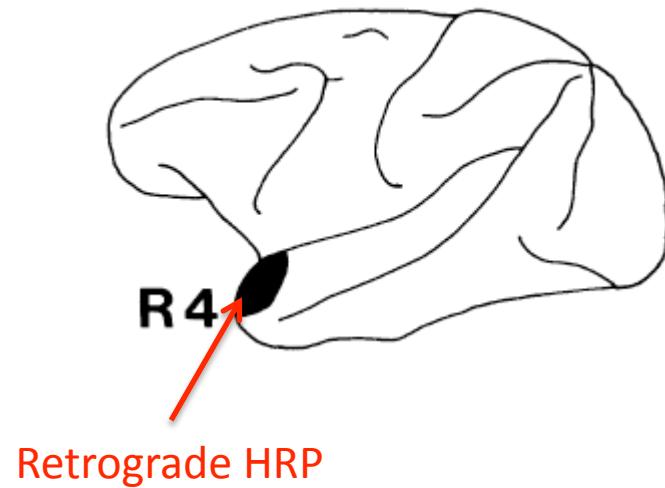
# Parahippocampal TH projects to medial Pulvinar



# Modern Tract Tracing:

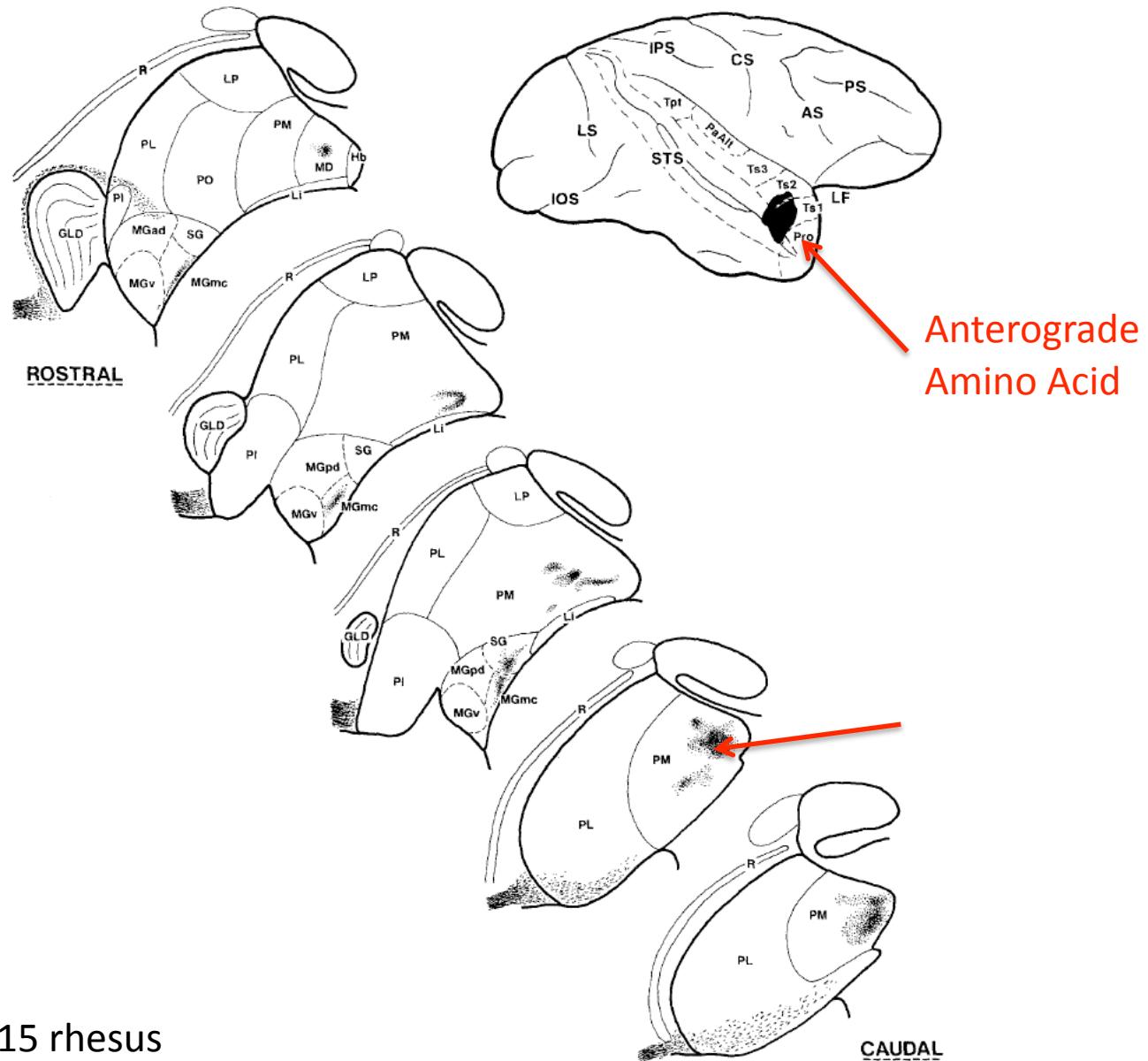
Medial Pulvinar has reciprocal connections with  
Temporal Pole & Superior Temporal Gyrus

# Medial Pulvinar projects to Temporal Pole



Markowitsch et al. 1985.  
6 rhesus, 2 squirrel monkeys, 2 marmosets

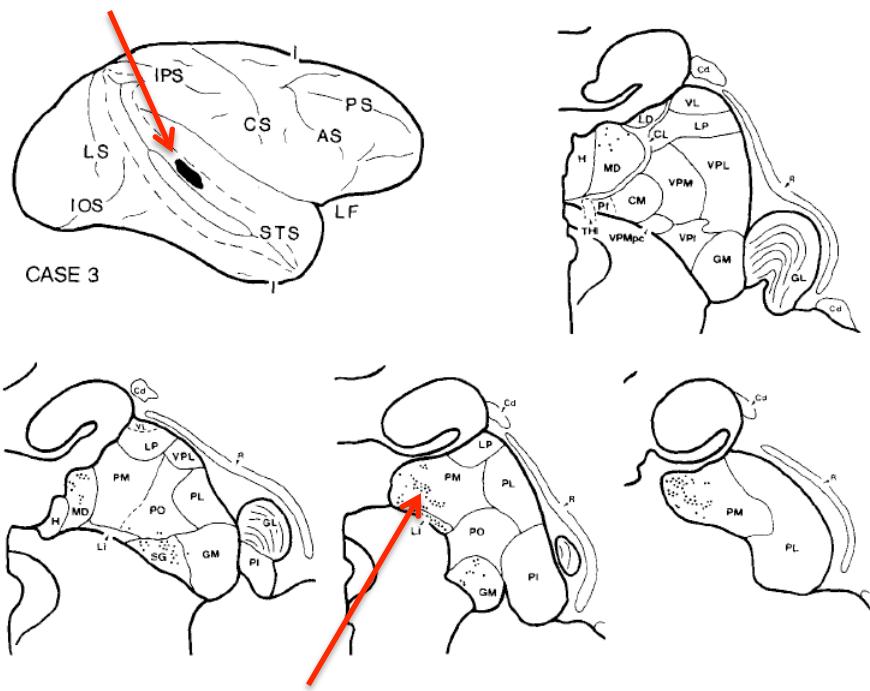
# Temporal Pole projects to medial Pulvinar



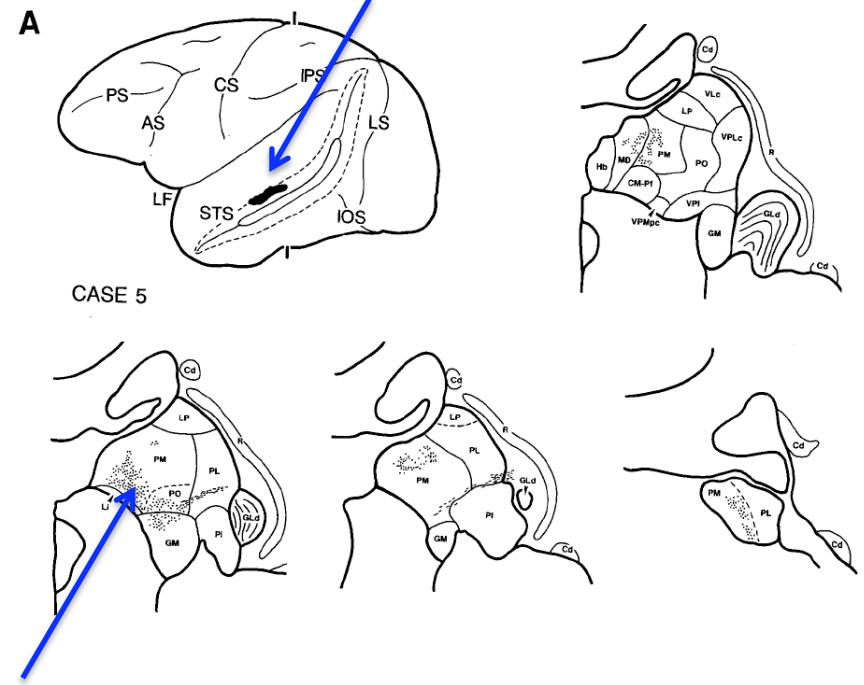
Pandya et al. 1994; 15 rhesus

# Medial Pulvinar is reciprocally connected to dorsal STS

Retrograde HRP



Anterograde Amino Acid



Yeterian & Pandya 1989. 11 Rhesus.

Yeterian & Pandya 1991. 16 Rhesus.

# Medial Pulvinar projects to dorsal STS



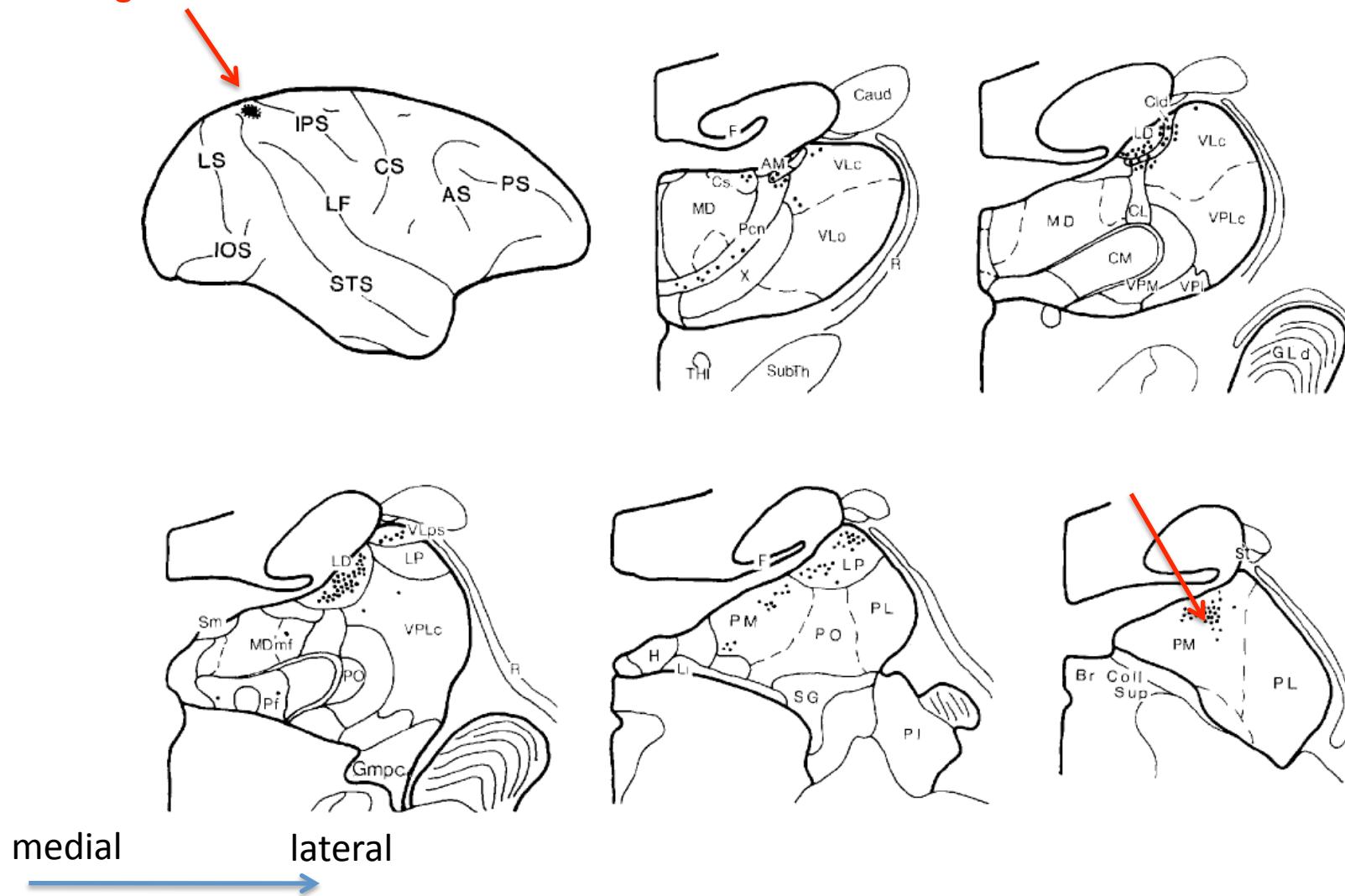
Baleydier & Mauguiere. 1985  
3 baboons, 2 Macaque

# Modern Tract Tracing:

Medial Pulvinar has reciprocal connections with  
Inferior Parietal Cortex

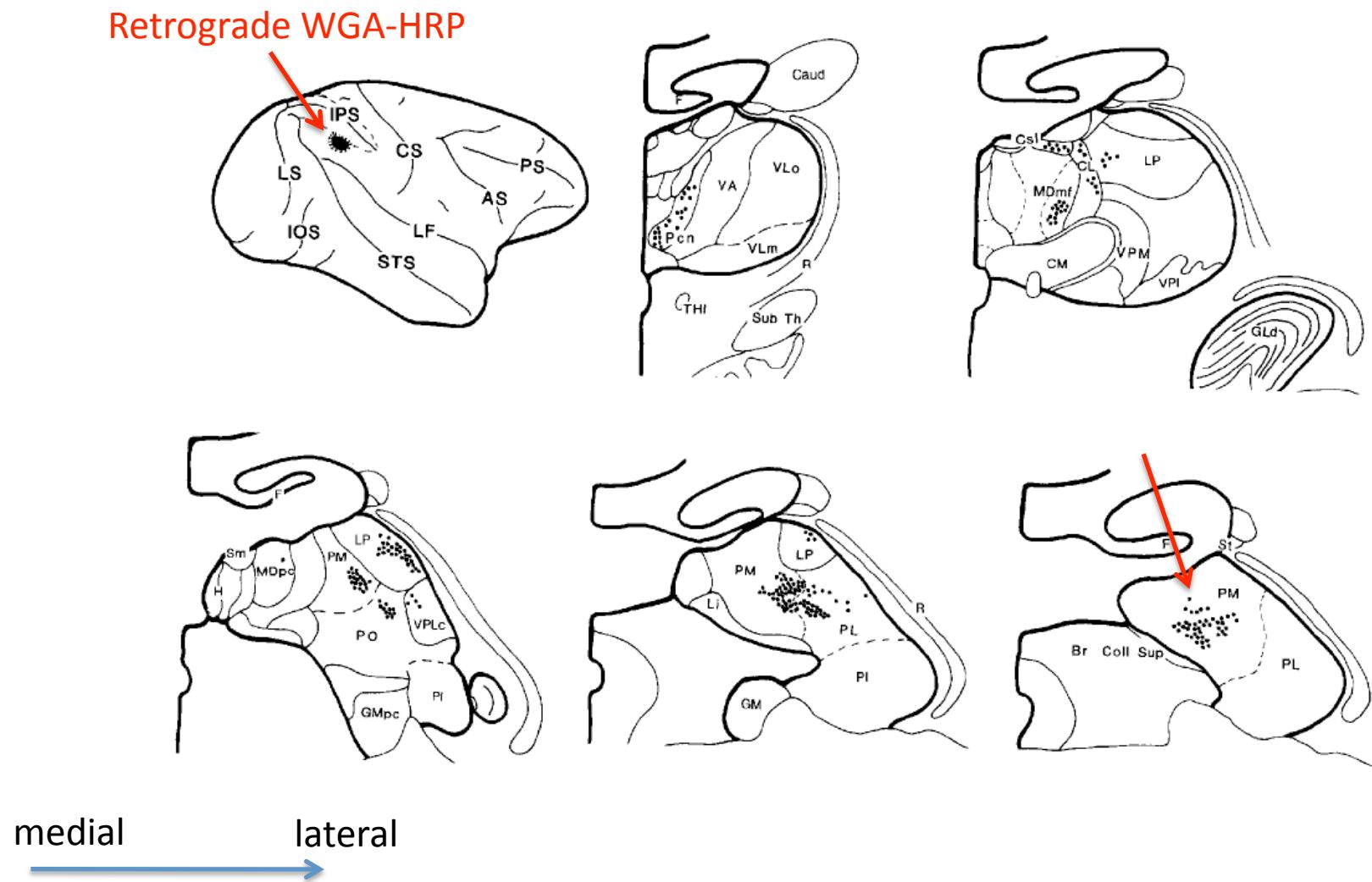
# Medial Pulvinar projects to Opt

Retrograde WGA-HRP



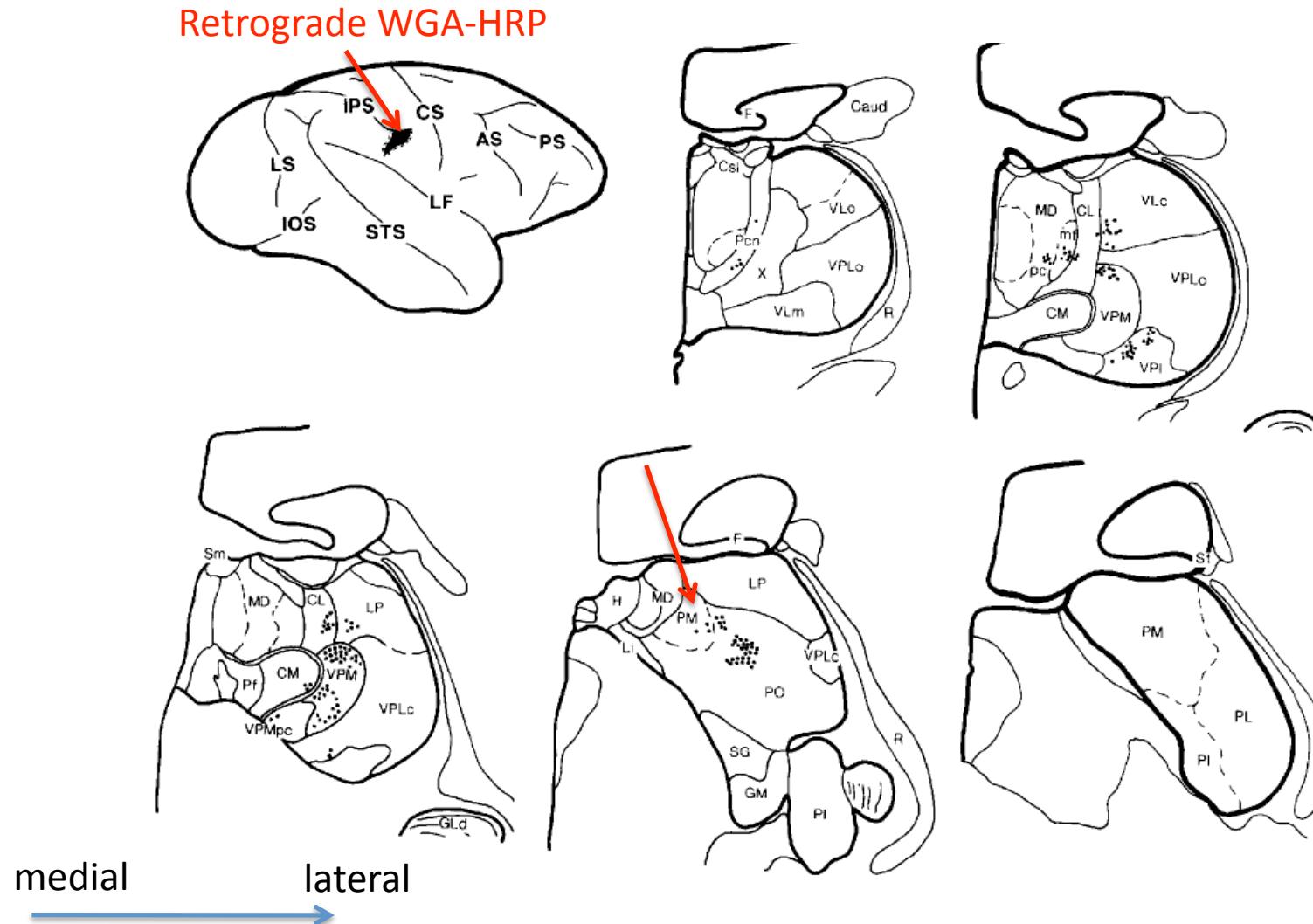
Schmahmann & Pandya. 1990. 12 rhesus.

# Medial Pulvinar projects to PFG



Schmahmann & Pandya. 1990. 12 rhesus

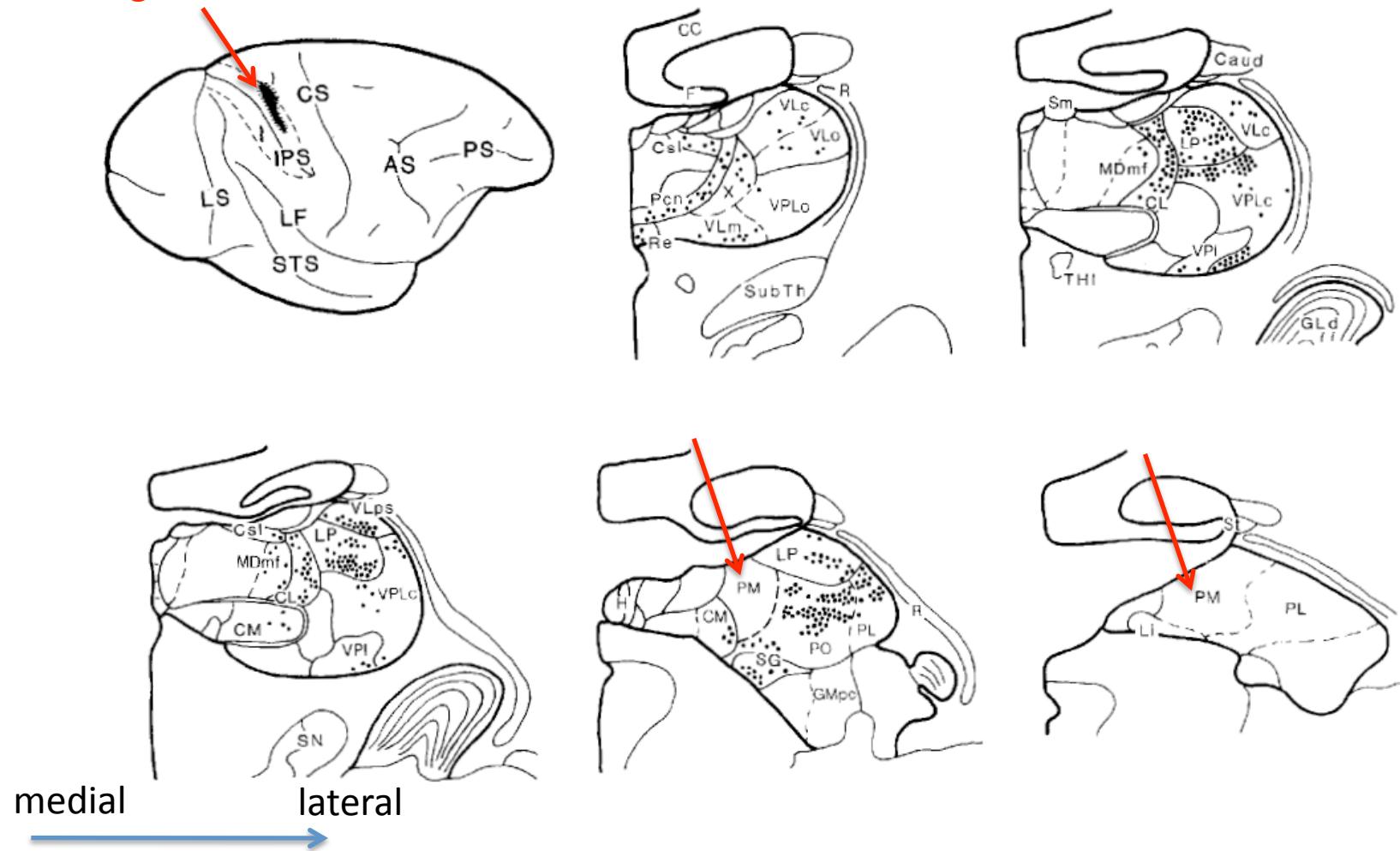
# Medial Pulvinar at most weak projection to PF



Schmahmann & Pandya. 1990. 12 rhesus

# Medial Pulvinar at most weak projection to Superior Parietal Lobe

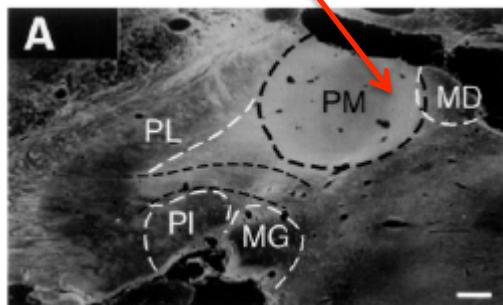
Retrograde WGA-HRP



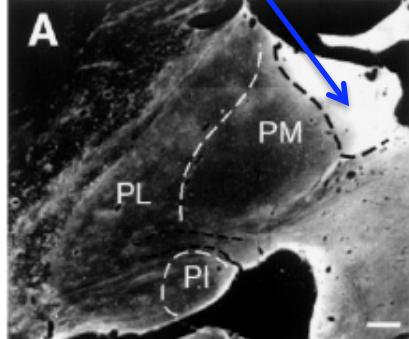
Schmahmann & Pandya. 1990. 12 rhesus

# Medial Pulvinar is reciprocally connected with dorsal STS, PCC, Area 7

Bidirectional WGA-HRP



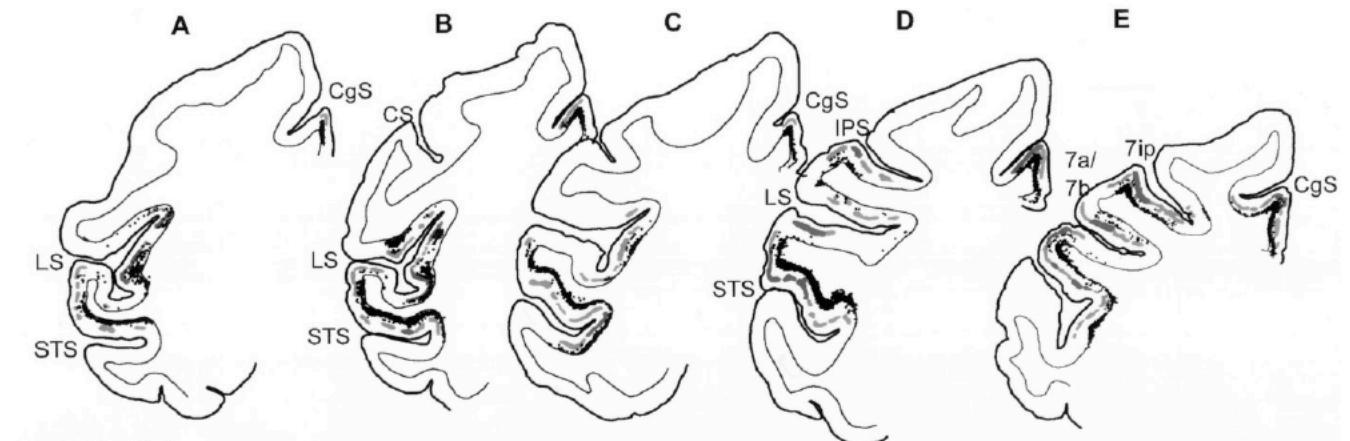
Bidirectional WGA-HRP



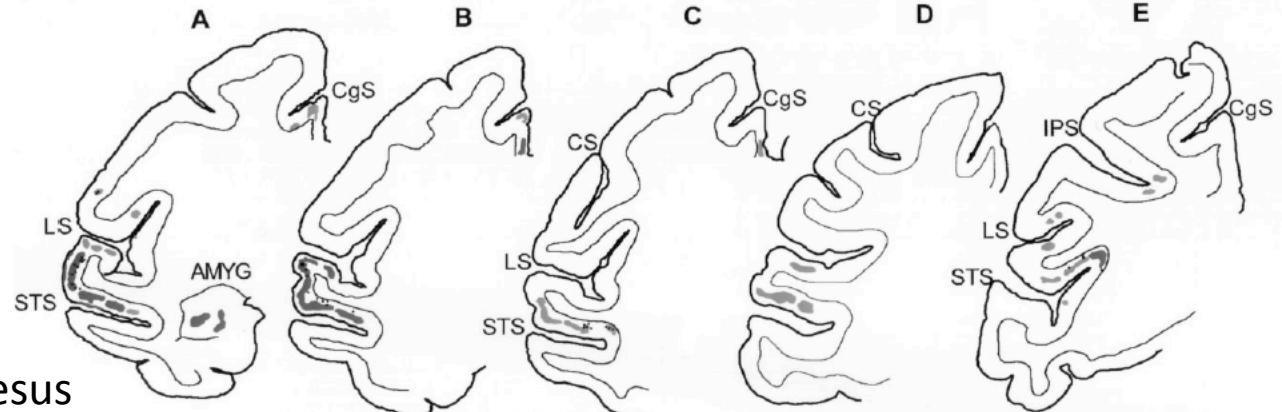
Romanski et al. 1997. 15 rhesus

Retrograde: Black Circles  
Anterograde: Gray Patches

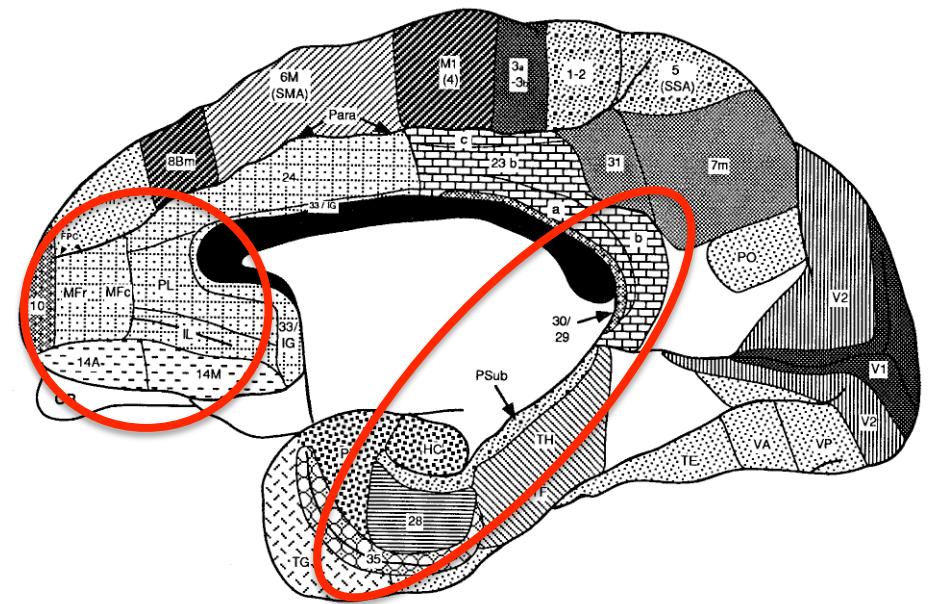
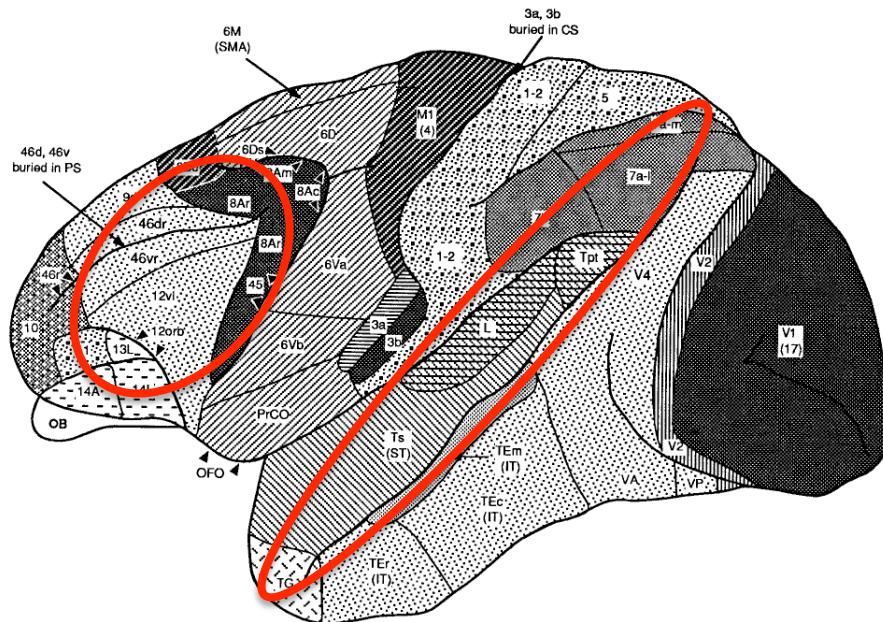
CENTRAL/LATERAL PM



MEDIAL PM



# Medial Pulvinar



Preuss & Goldman-Rakic, 1991

# The Modern View

- Many nuclei → multiple cortical lobes
  - Medial Pulvinar → Prefrontal, Cingulate, Parietal, Temporal
- Every cortical field (except maybe areas 3, 1) → multiple thalamic nuclei
- (mostly) Reciprocal connections

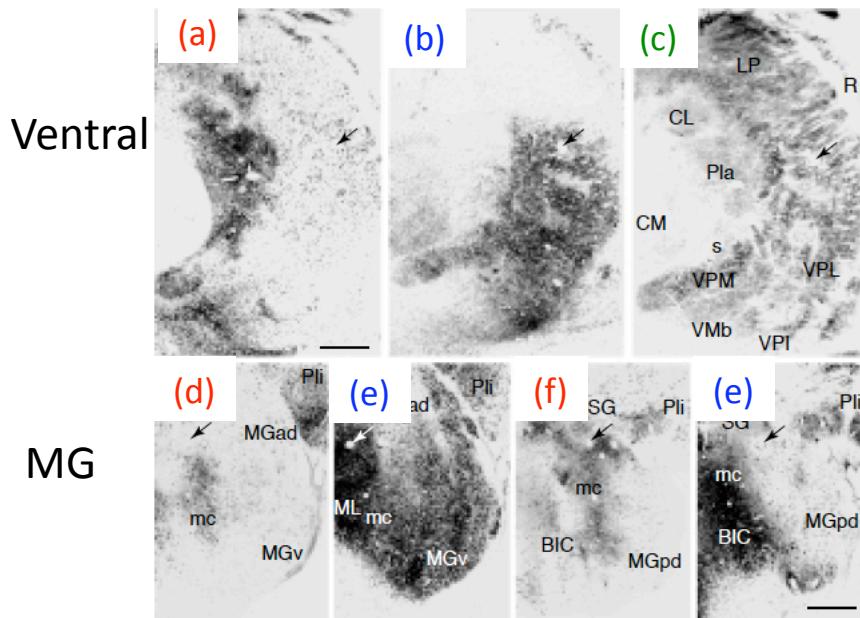
# The Modern View

- Every nucleus → multiple cortical fields
  - Many nuclei → multiple cortical lobes
- Every cortical field (except maybe areas 3, 1) → multiple thalamic nuclei
- (mostly) Reciprocal connections
- Every nucleus has subcortical inputs
- Connections (mostly) ipsilateral
- Thalamic receptive field properties generally consistent with connections

# The Modern View

- Every nucleus → multiple cortical fields
  - Many nuclei → multiple cortical lobes
- Every cortical field (except maybe areas 3, 1) → multiple thalamic nuclei
- (mostly) Reciprocal connections
- Every nucleus has subcortical inputs
- Connections (mostly) ipsilateral
- Thalamic receptive field properties generally consistent with connections

# Matrix vs Core Cells



Frontal Sections

(a), (d), (f): Calbindin

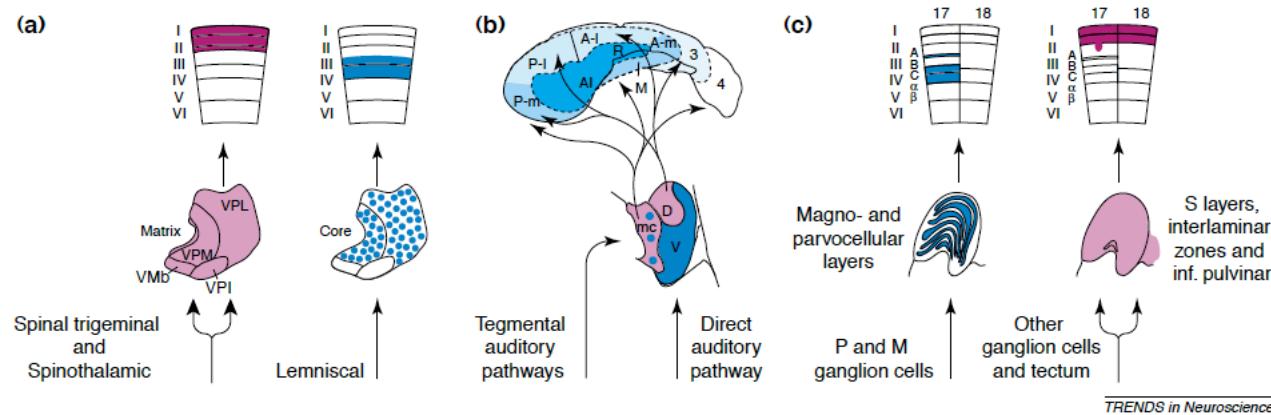
(b), (e), (g): Parvalbumin

(c): cytochrome oxidase

Neurons immunoreactive for the  $\text{Ca}^{2+}$ -binding protein, 28 kDa calbindin, are distributed throughout the dorsal thalamus, unconstrained by nuclear borders or by distinctions between intralaminar, relay or other nuclei<sup>19</sup>. These form a matrix to the whole thalamus. In certain nuclei only, a core of slightly larger neurons that are immunoreactive for a different  $\text{Ca}^{2+}$ -binding protein, parvalbumin, are inserted into the matrix<sup>20</sup>. Parvalbumin-containing cells are particularly prominent in the sensory and motor relay nuclei, but can also be found in specific nuclei of the pulvinar and intralaminar group. Every thalamic nucleus, therefore, contains calbindin-positive matrix cells, but only some also contain parvalbumin-positive core cells. Typically, where core cells are absent, there is an elaboration of the matrix with more calbindin-positive cells being present

# Matrix vs Core Cells

- Subcortical Inputs



- Oscillations

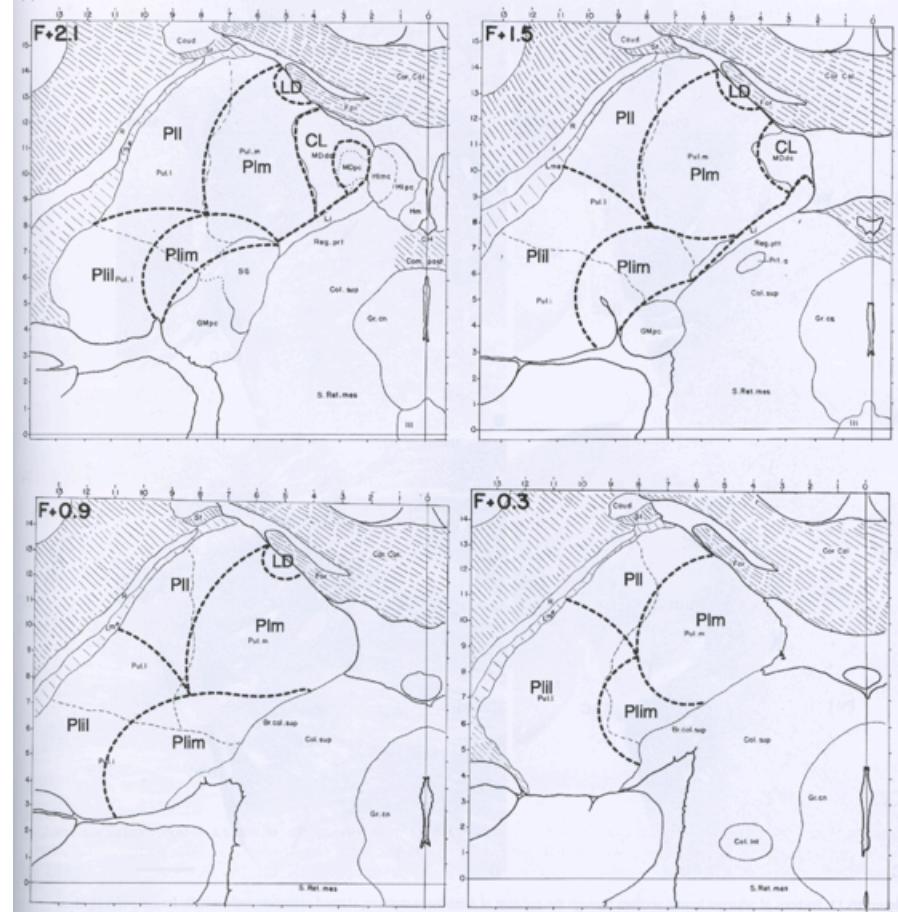
- Relay nucleus / Intra-cortical → Cortical layer III, IV
- Cortical layer VI → relay nucleus
- Cortical layer V → diffuse projections to other thalamic nuclei with Calbindin-positive cells

# First-order vs Higher-order

- Overlap with Jones' matrix-core framework
- First-order relay: sensory → cortex
- Higher-order relay: cortex → cortex
  - Layer VI inputs to thalamus are modulators
  - Layer V inputs to thalamus are drivers
    - Well localized in thalamus and not diffuse (contrary to Jones)

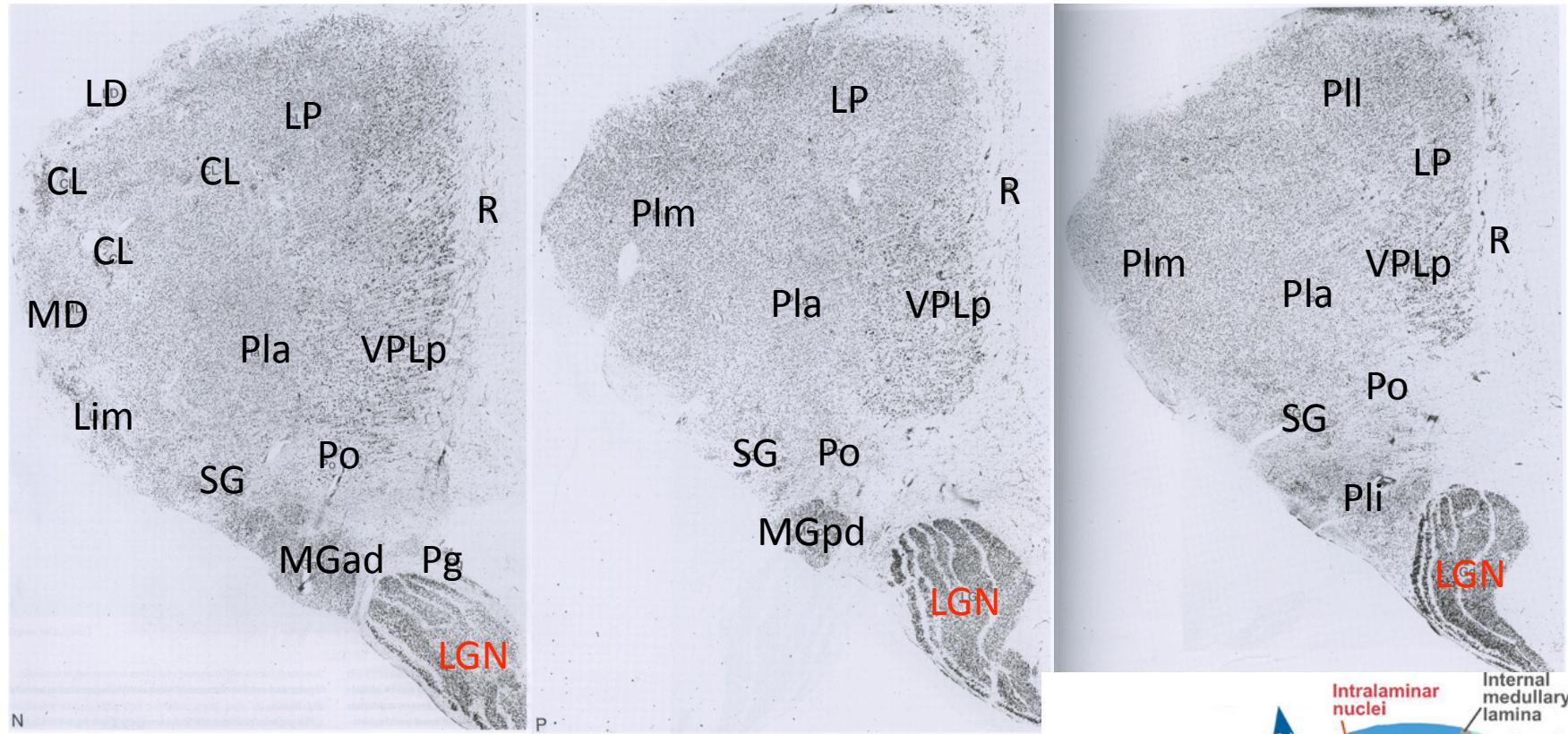
# Factors Influencing Our Understanding of the Thalamus

- Methodologies
  - Staining
  - Tract Tracing
- Our understanding of Cortex

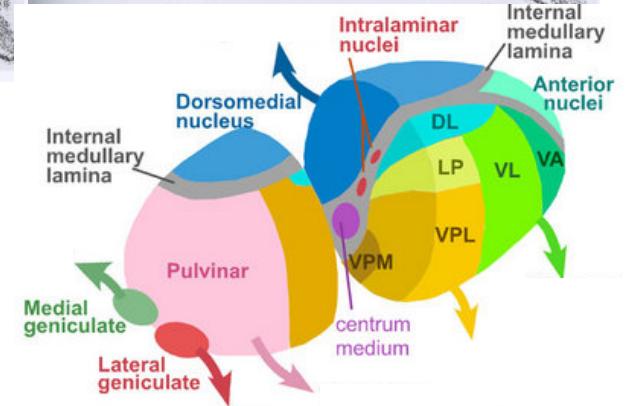


Jones, 2007 modification of Olszewski (1952) atlas of Rhesus monkey pulvinar nuclei, using staining for cytochrome oxidase, acetylcholinesterase, Calbindin, Parvalbumin, 29 kDa Calretinin, CAMKII- $\alpha$ , CAT 301, SMI32 (etc) for Old and New World Monkeys

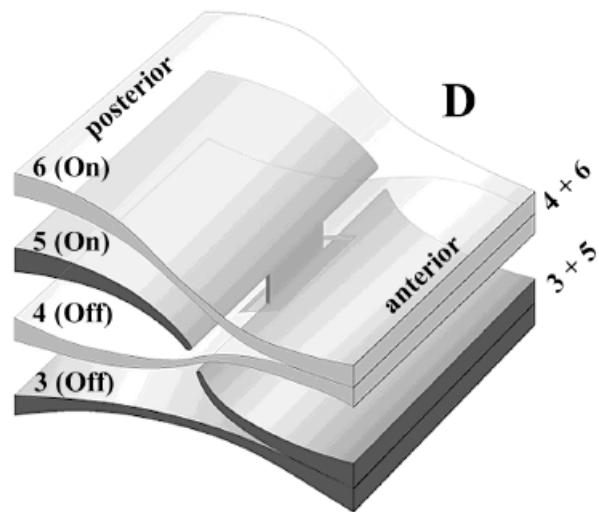
# Dorsal Lateral Geniculate Nucleus



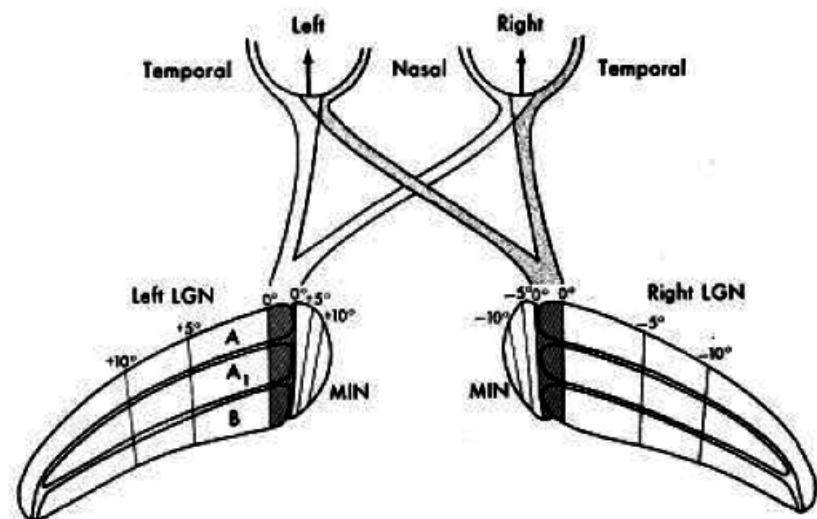
6 layers: magnocellular (1, 2), parvocellular (3-6)  
Retina, SC, Brain Stem Reticular → LGNd



# Retina → LGNd



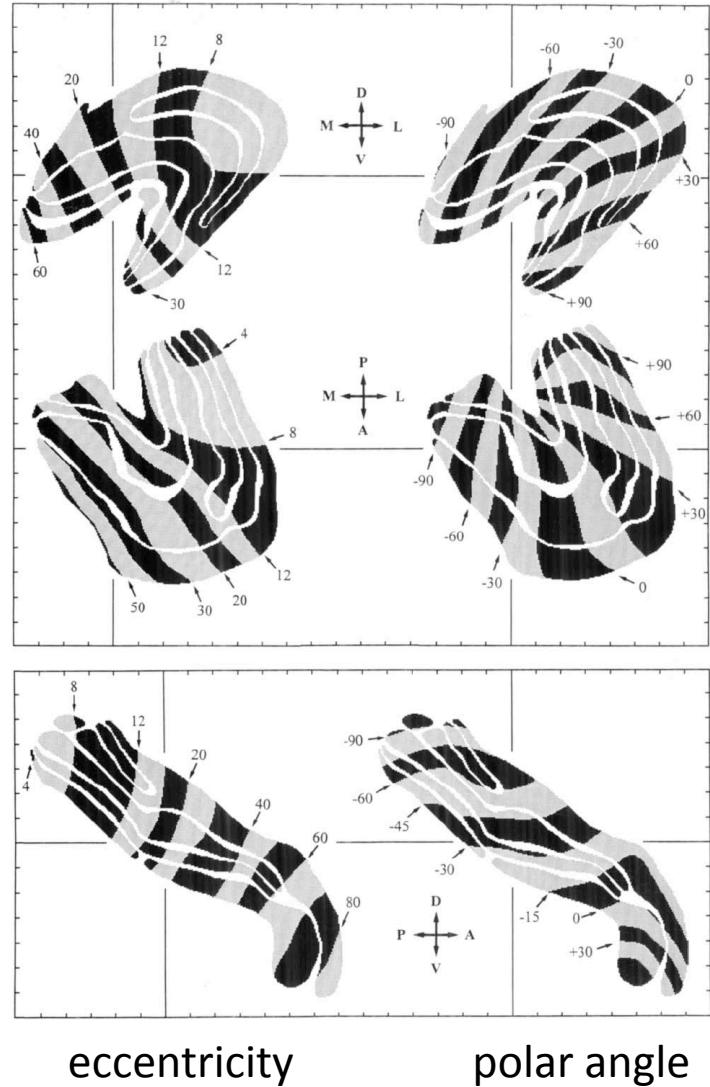
Erwin et al. 1999



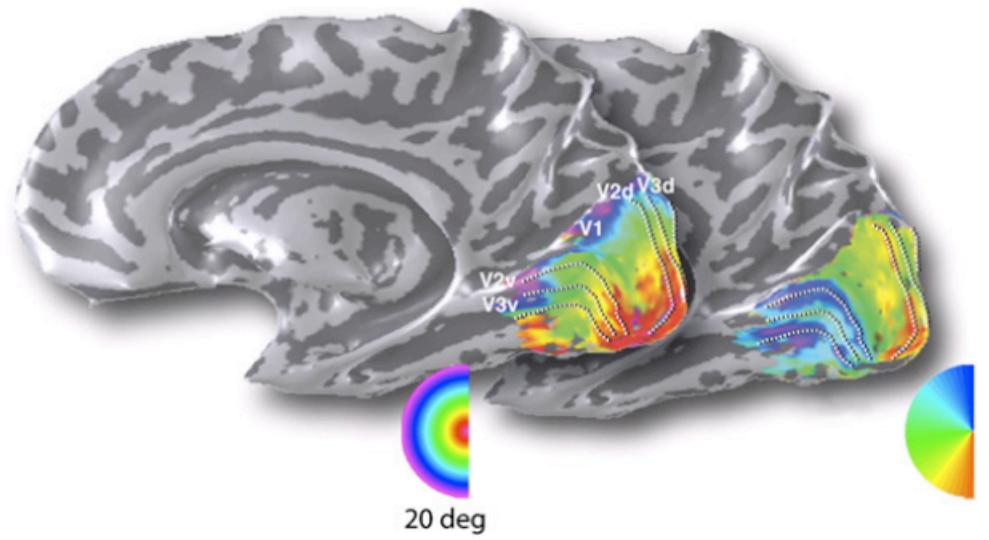
Sanderson & Sherman 1971

Layers 1, 4, 6 from contralateral eye. Layer 2, 3, 5 from ipsilateral. In anterior part of nucleus, layers 4, 6 and 3, 5 fuse  
Left LGNd receive projections from right visual field from both eyes  
Right LGNd receives projections from left visual field from both eyes

# Visual Field Representation LGN



Observe different folding of LGNd in humans and rhesus

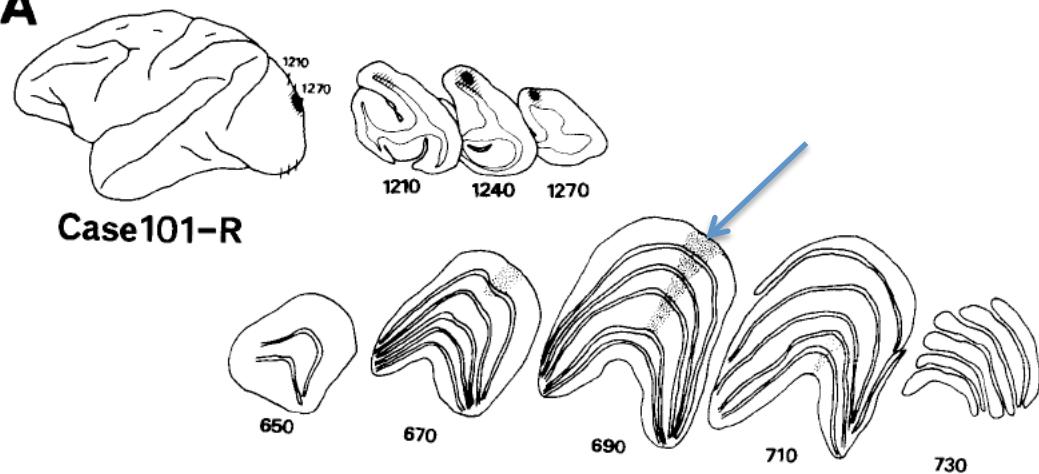


Wandelt et al., 2007

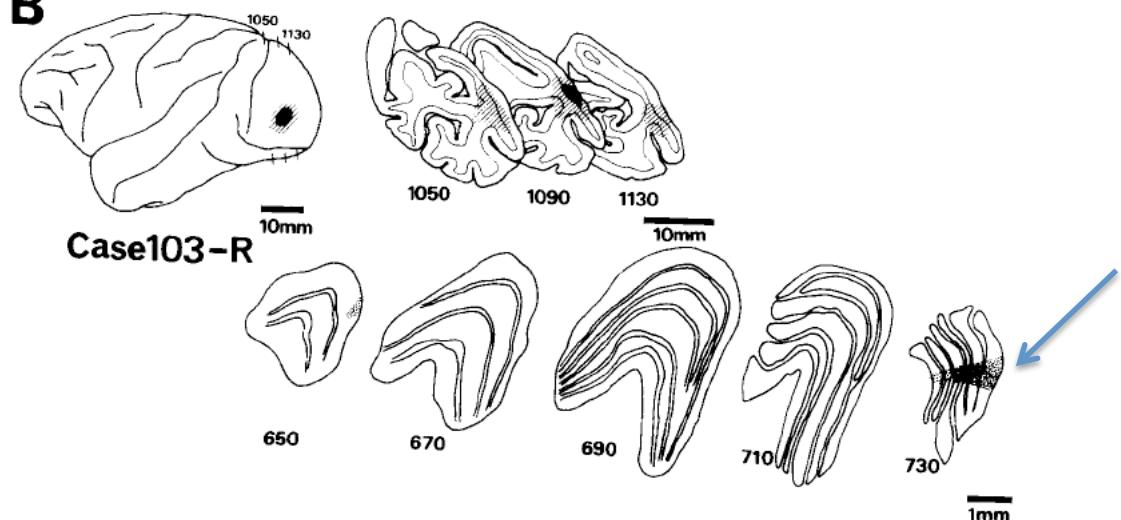
Malpeli et al. 1996

# V1 + LGNd

**A**

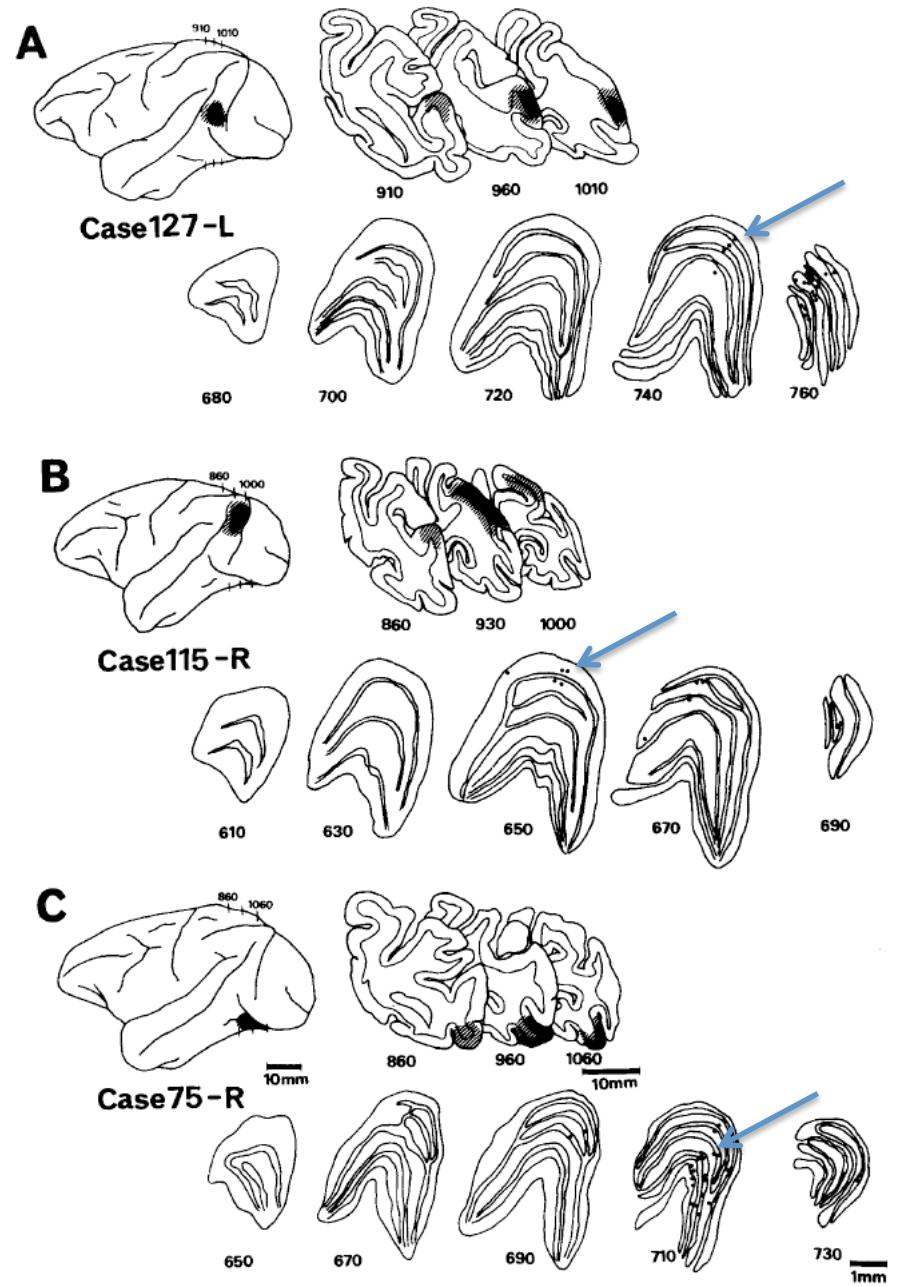
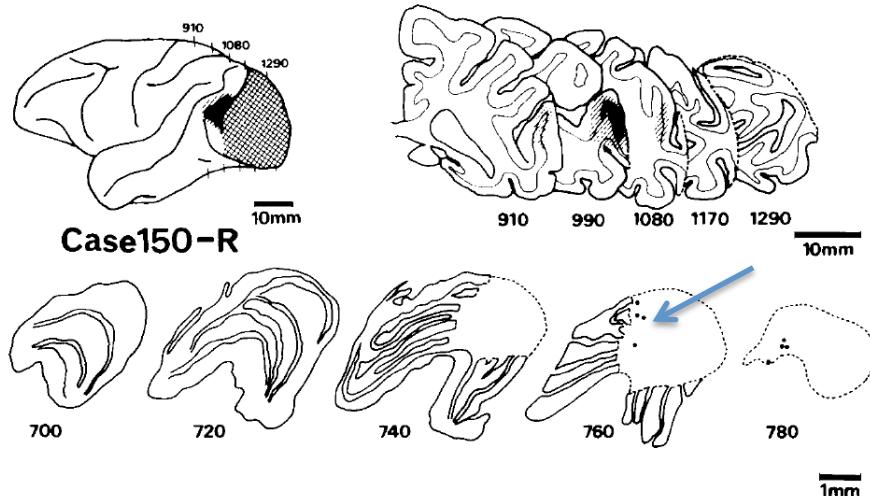


**B**



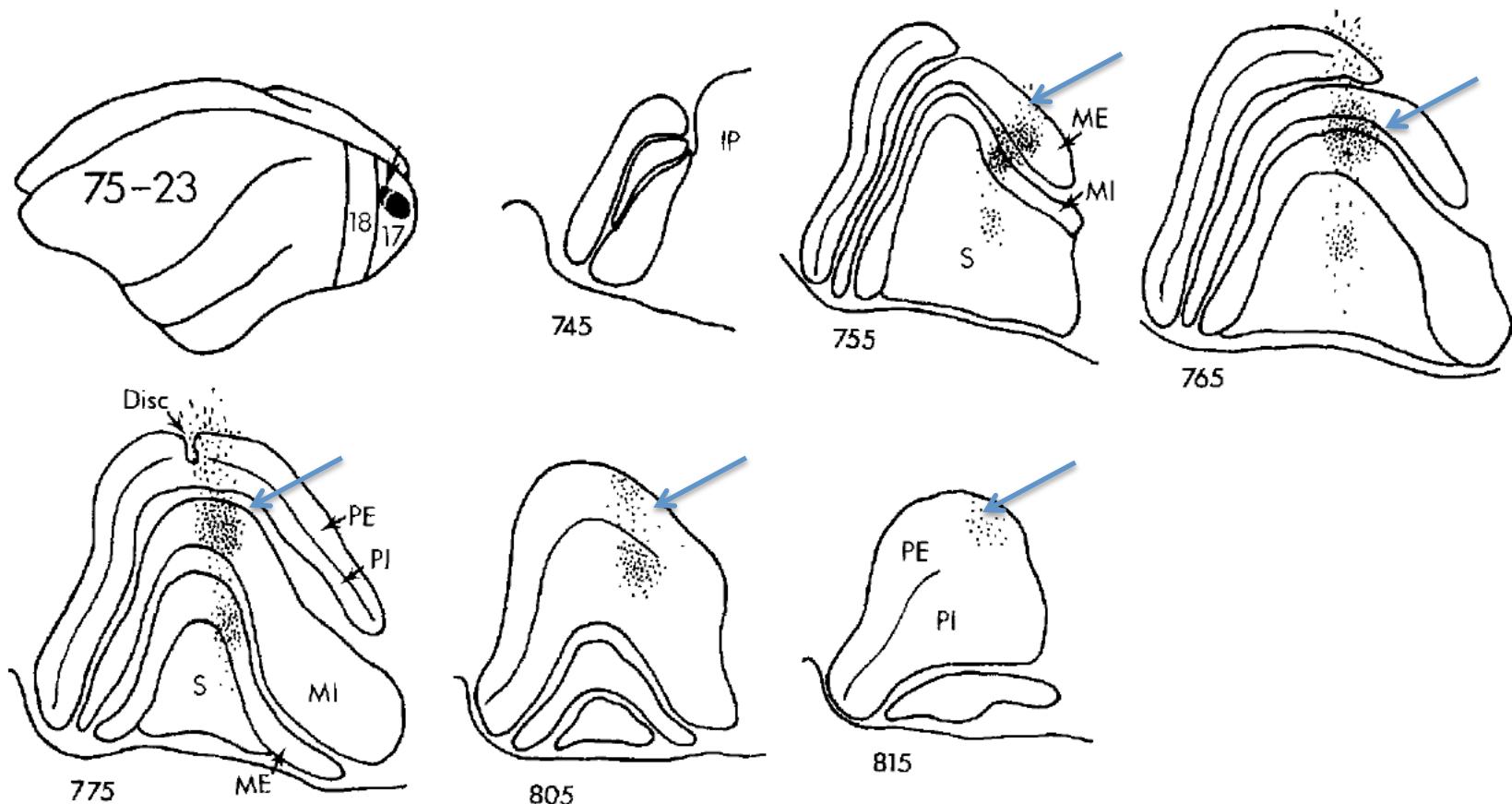
Yukie & Iwai, 1981; HRP,  
16 rhesus, 3 Japanese monkeys (*macaca fuscata*)

# Prestriate + LGNd



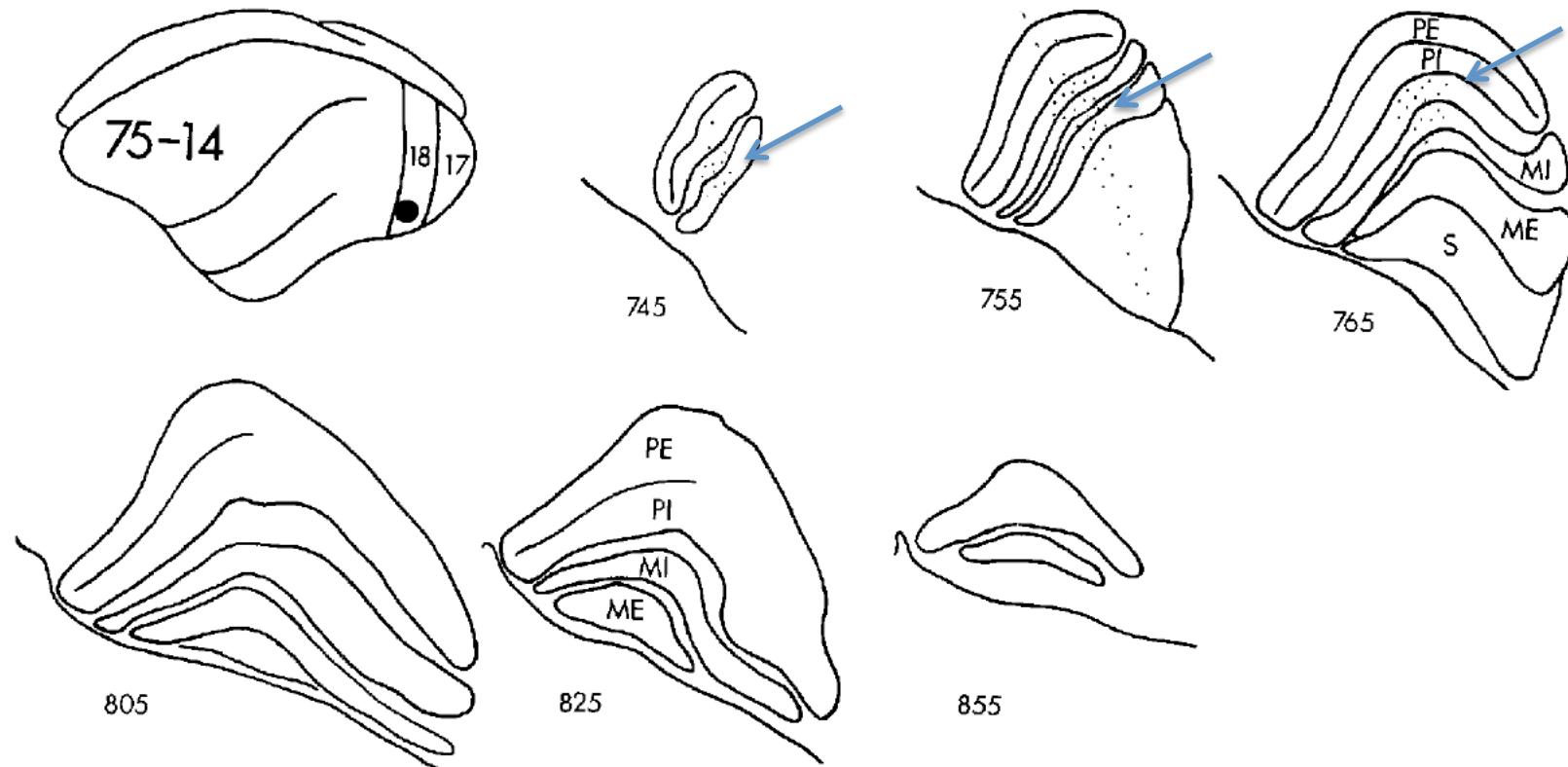
Yukie & Iwai, 1981; HRP,  
16 rhesus, 3 Japanese monkeys (*macaca fuscata*)

# V1 + LGNd



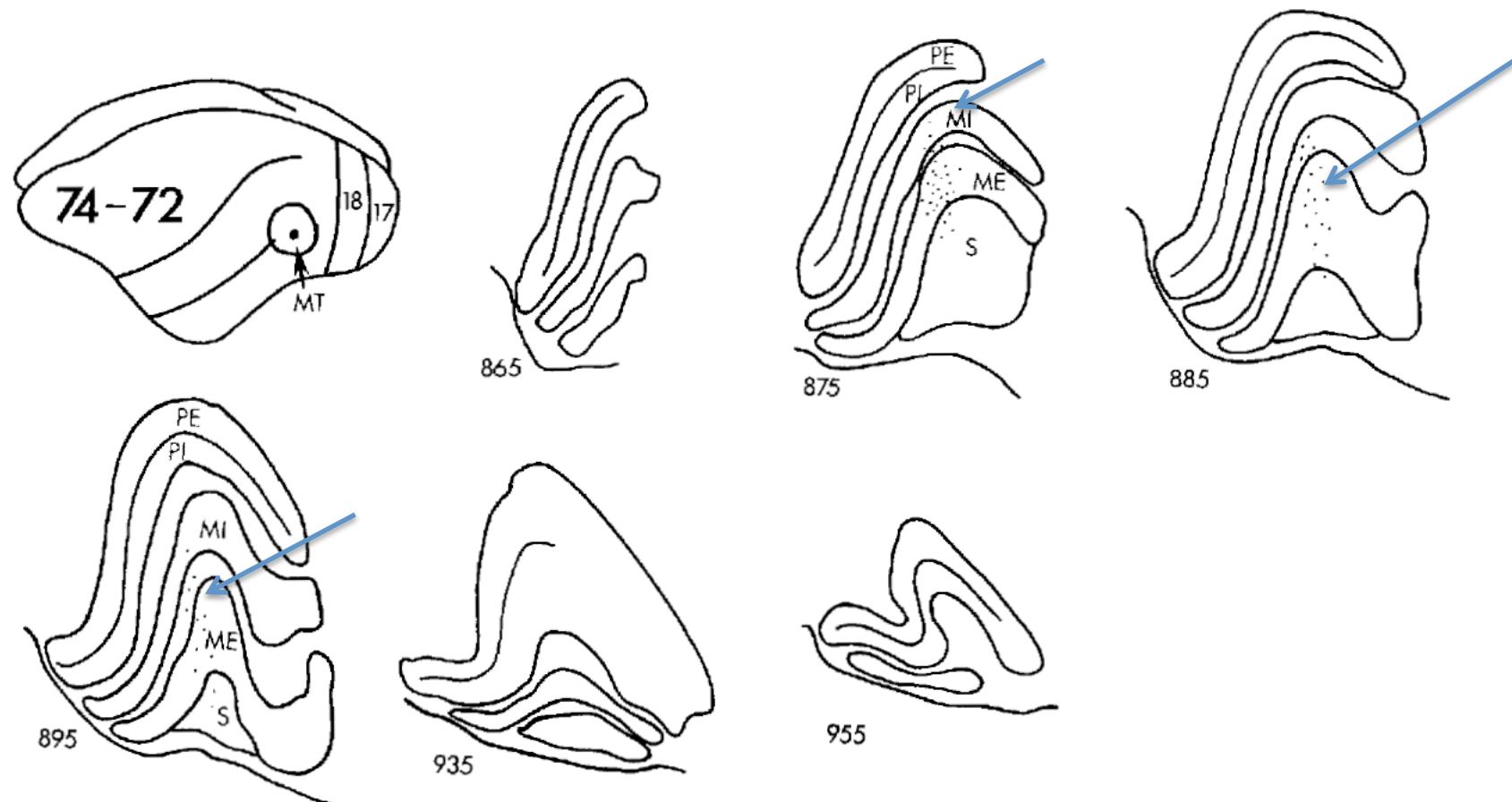
Lin & Kaas, 1977; TAA  
10 owl monkeys

# Area 18 + LGNd



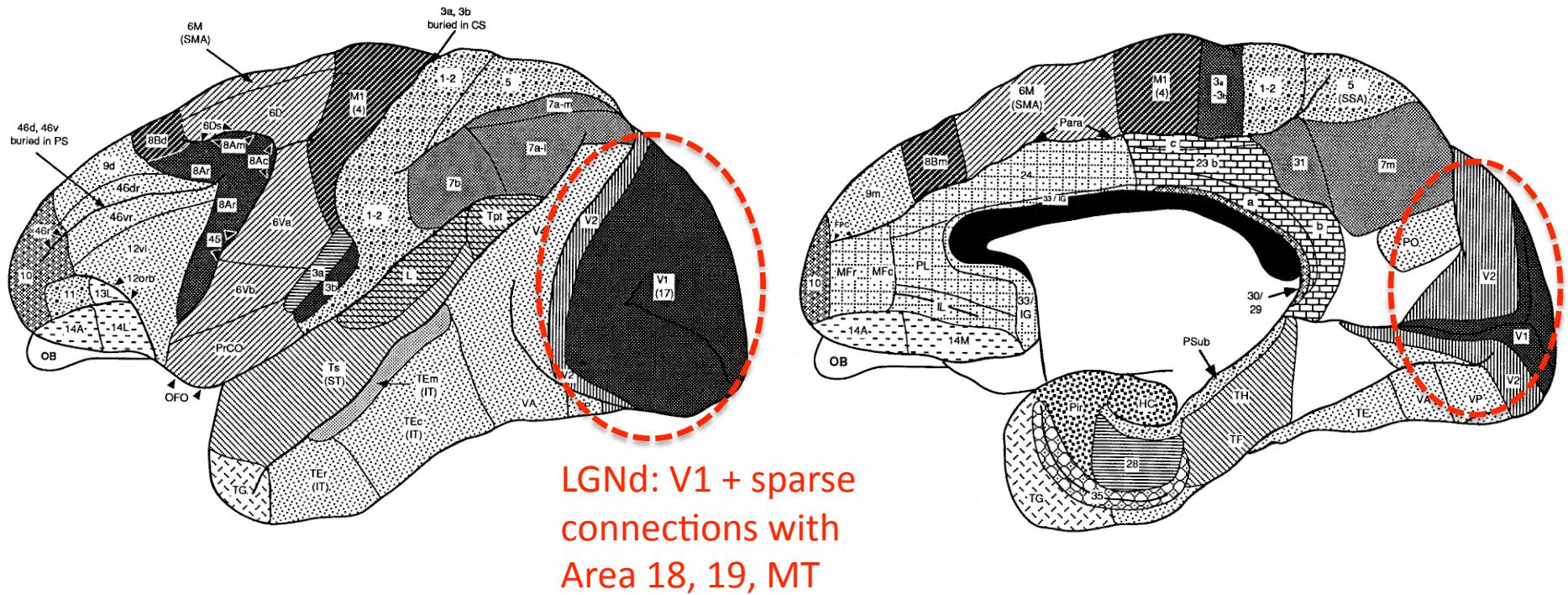
Lin & Kaas, 1977; TAA  
10 owl monkeys

# MT + LGNd



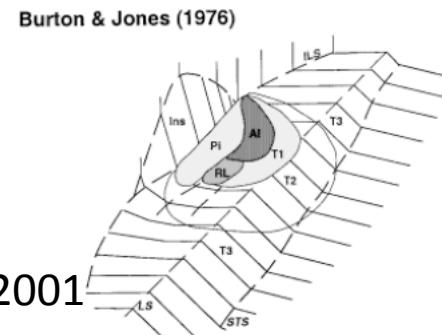
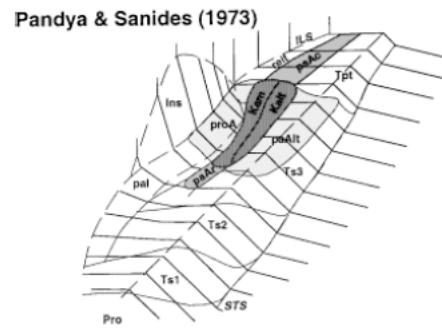
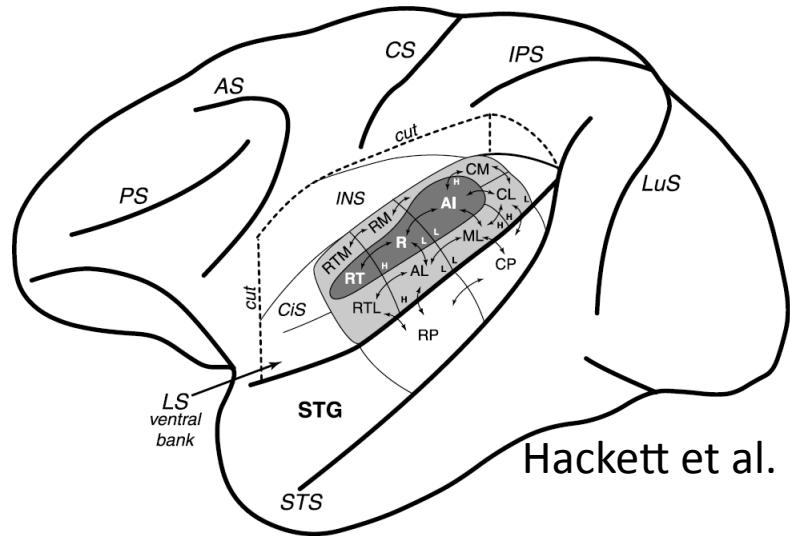
Lin & Kaas, 1977; TAA  
10 owl monkeys

# Dorsal Lateral Geniculate Nucleus

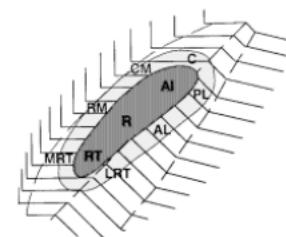


Preuss & Goldman-Rakic, 1991

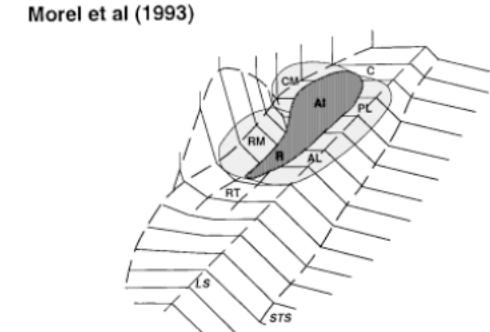
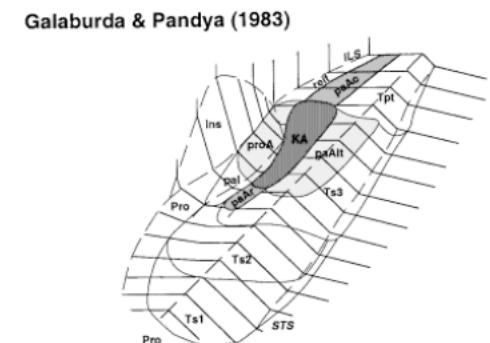
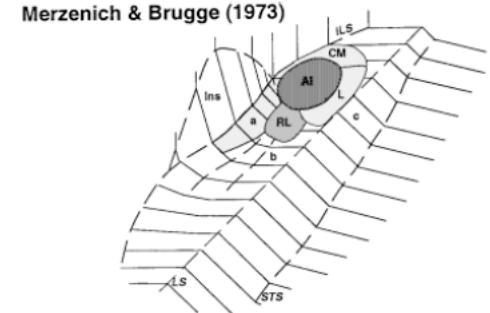
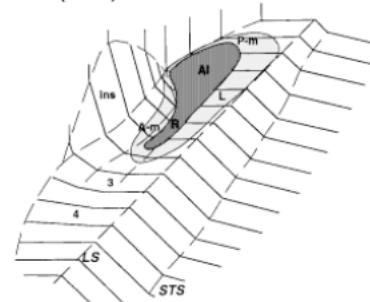
# Auditory Cortex



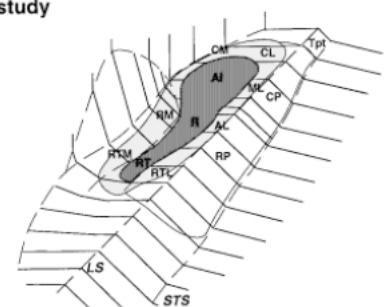
Morel & Kaas (1992) (Owl Monkey)



Jones et al (1995)

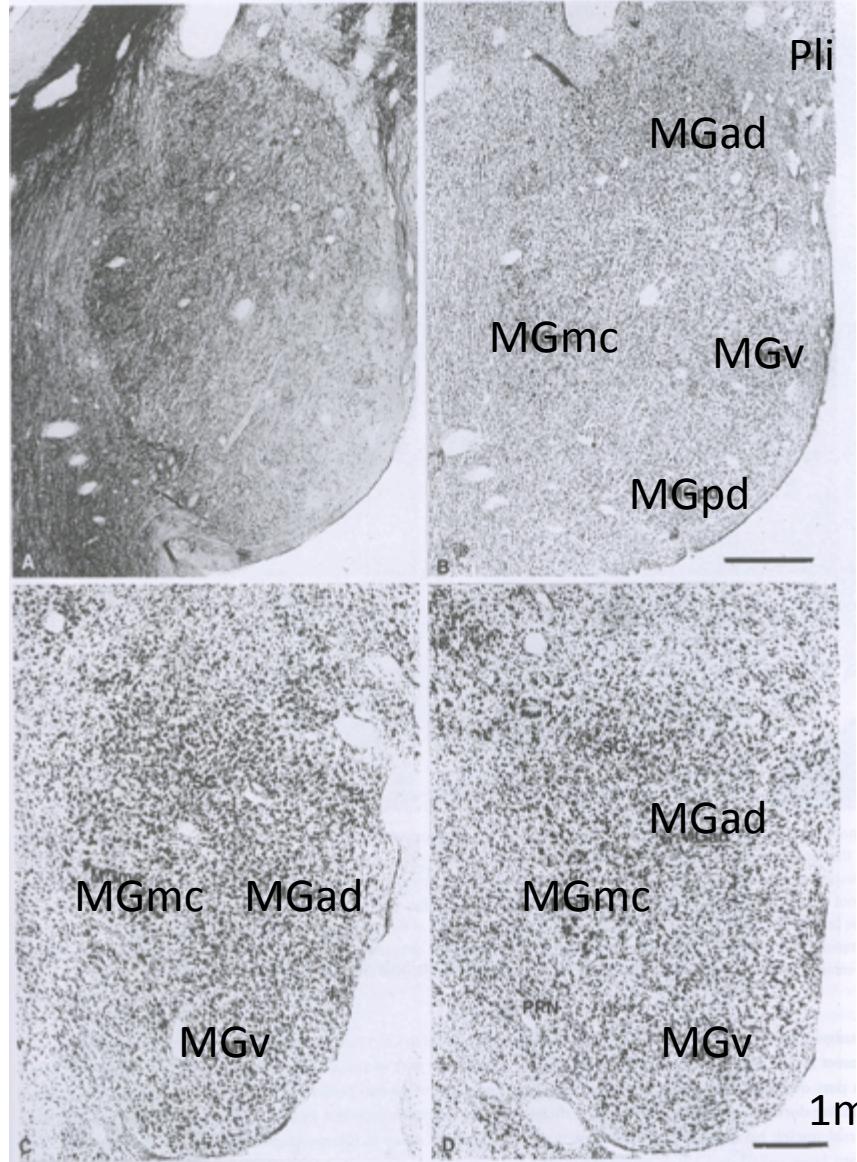


Current study



Hackett et al. 1998

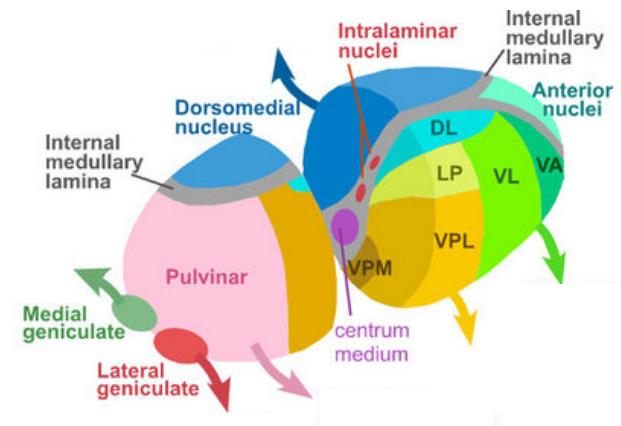
# Medial Geniculate Nuclei



Central nucleus (inferior colliculus) → MGv  
Pericentral, external nuclei (inferior colliculus) → MGd  
Definitely inferior & deep layers superior SC; Maybe:  
medial lemniscal, spinothalamic, vestibular → MGmc

MGmc → amygdala, striatum

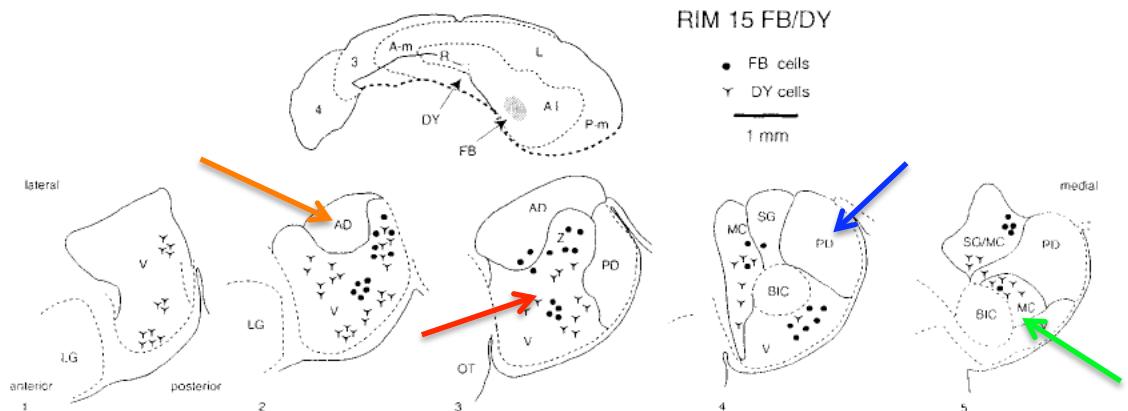
Human: A  
(acetylchoinesterase), B  
(Thionin)



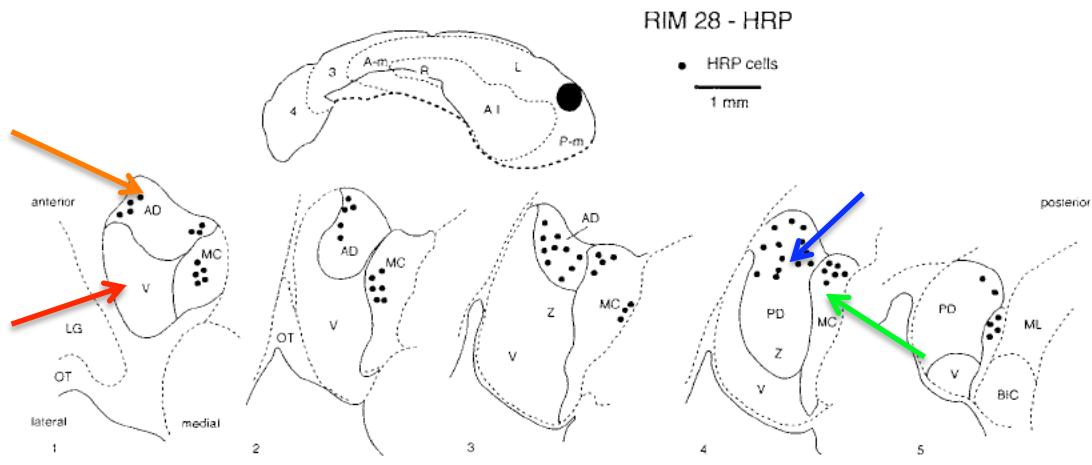
Titi Monkey (Thionin):  
C(anterior), D(posterior)

**MGv**  
**MGad**  
**MGpd**  
**MGmc**

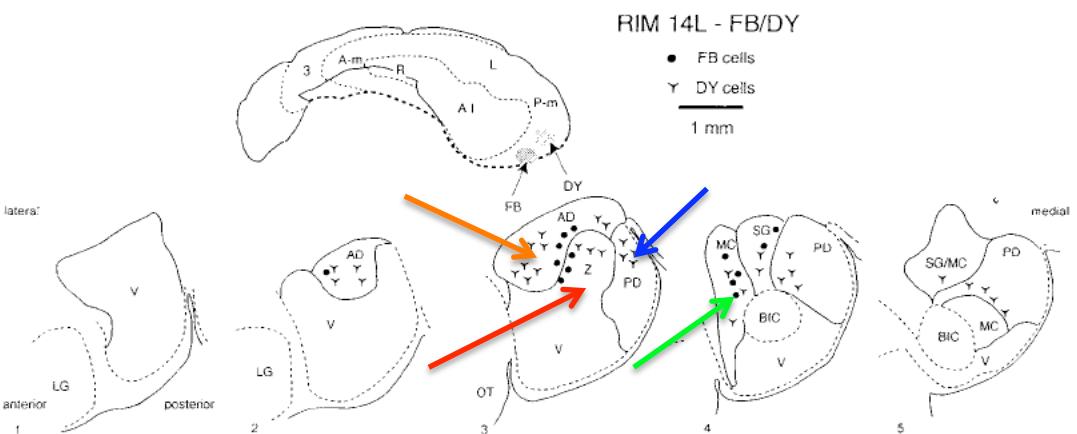
Core



Belt

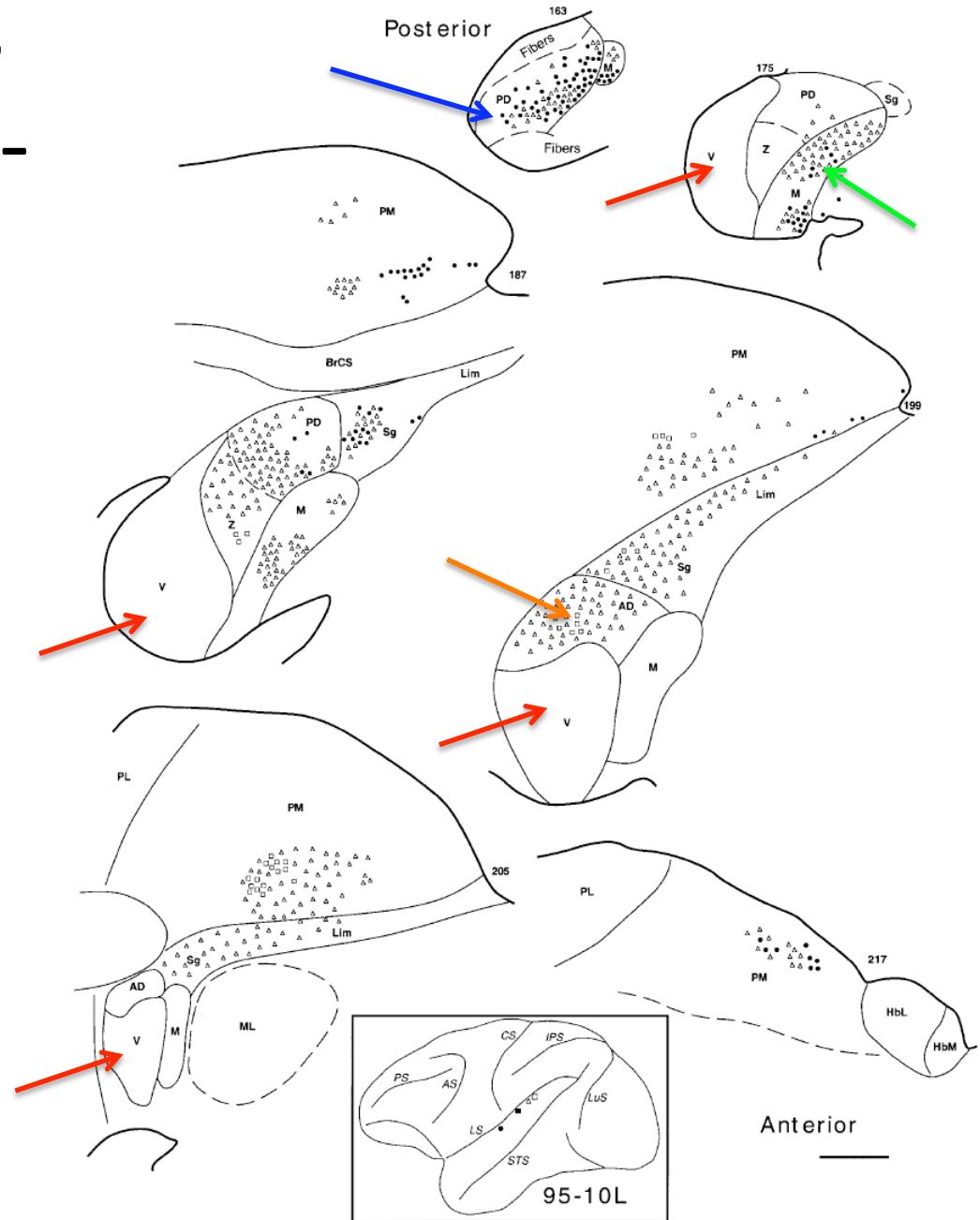


Belt



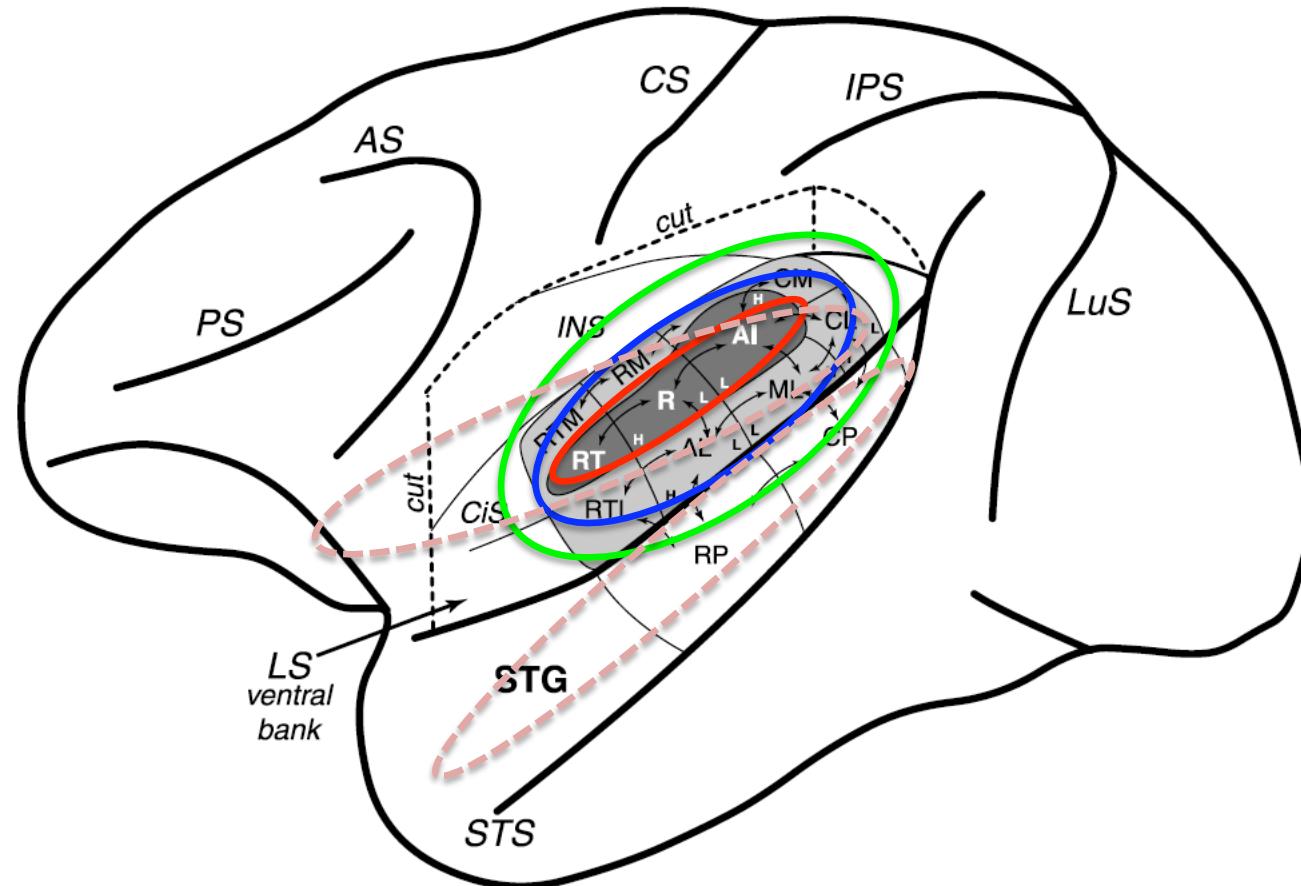
Molinari et al. 1995  
 24 Macaca fuscata  
 HRP, FRT

# Parabelt + MGpd, MGad, MGmc, SG- lim, Plm



Hackett et al. 1994; FRT  
3 macaca mulatta, 3 macaca nemestrina

# Medial Geniculate Nuclei



MGv: Auditory core, sparsely with belt

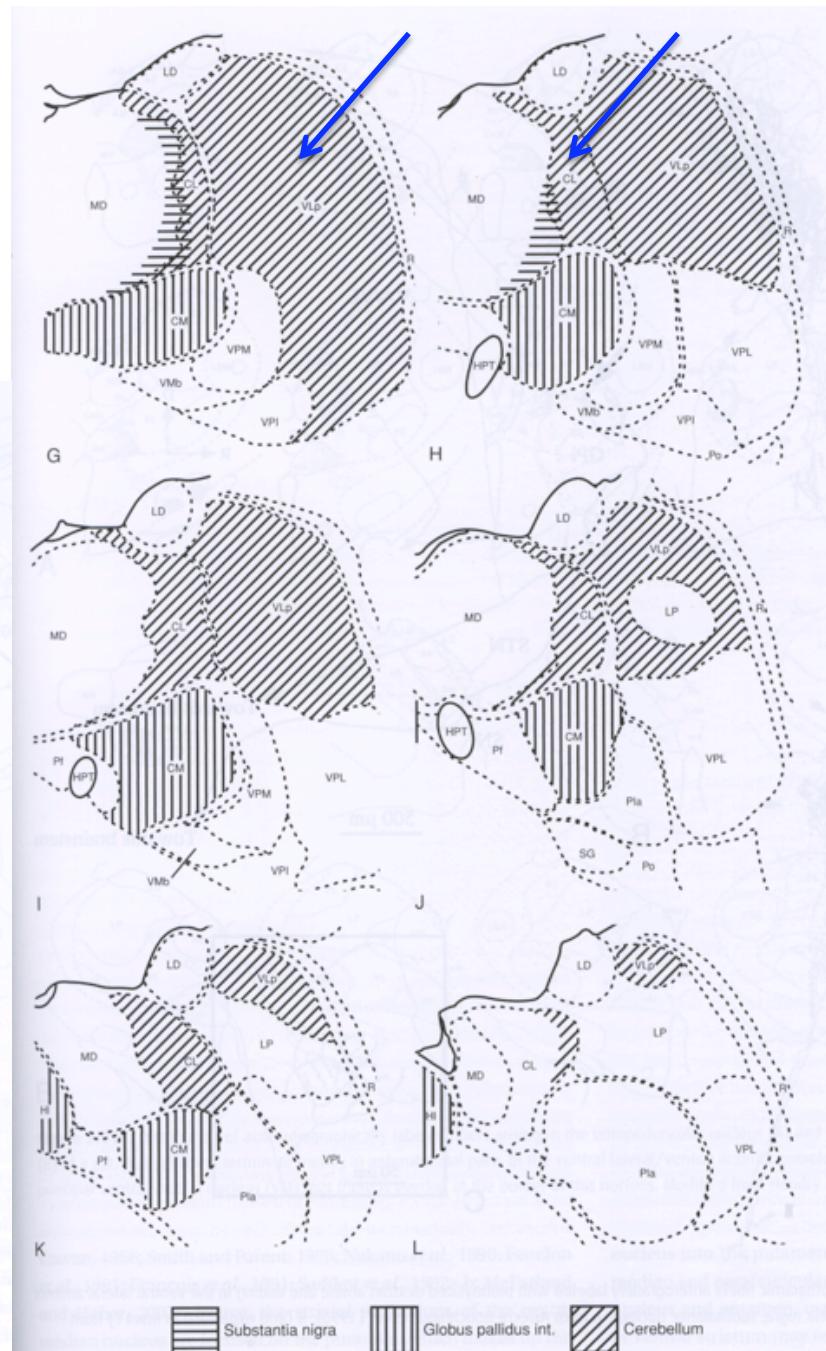
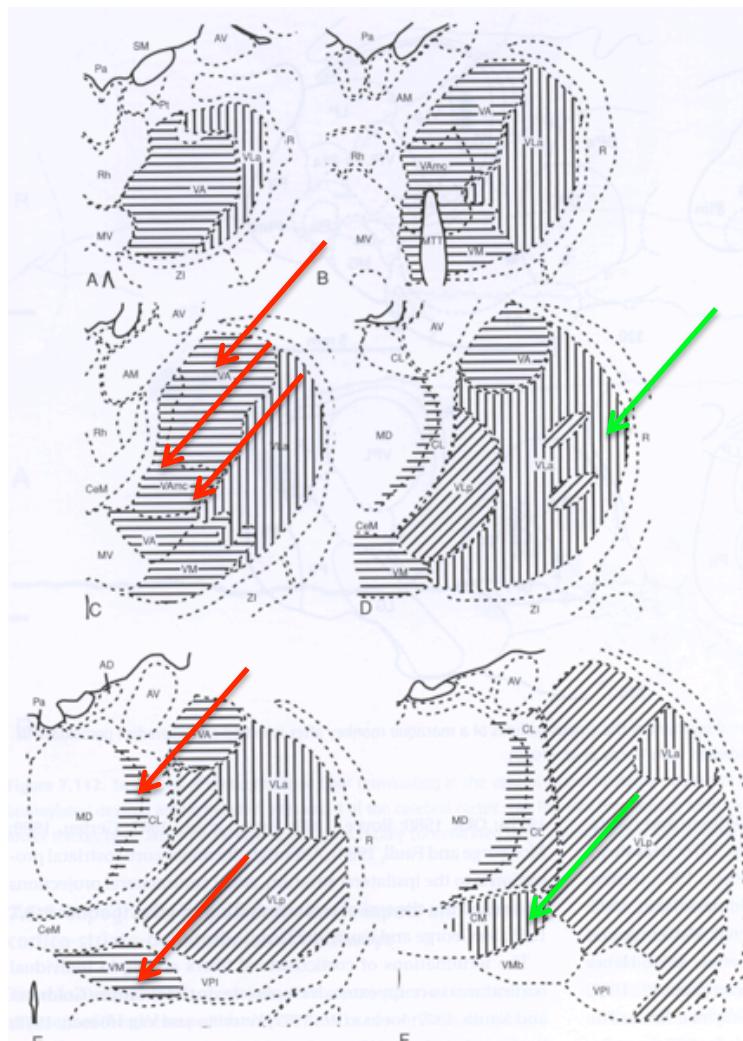
MGd: Auditory belt, parabelt, sparse with core

MGmc: Auditory cortex and surrounding areas

MG: sparse reports of connections in insula and superior temporal areas

Hackett et al. 2001

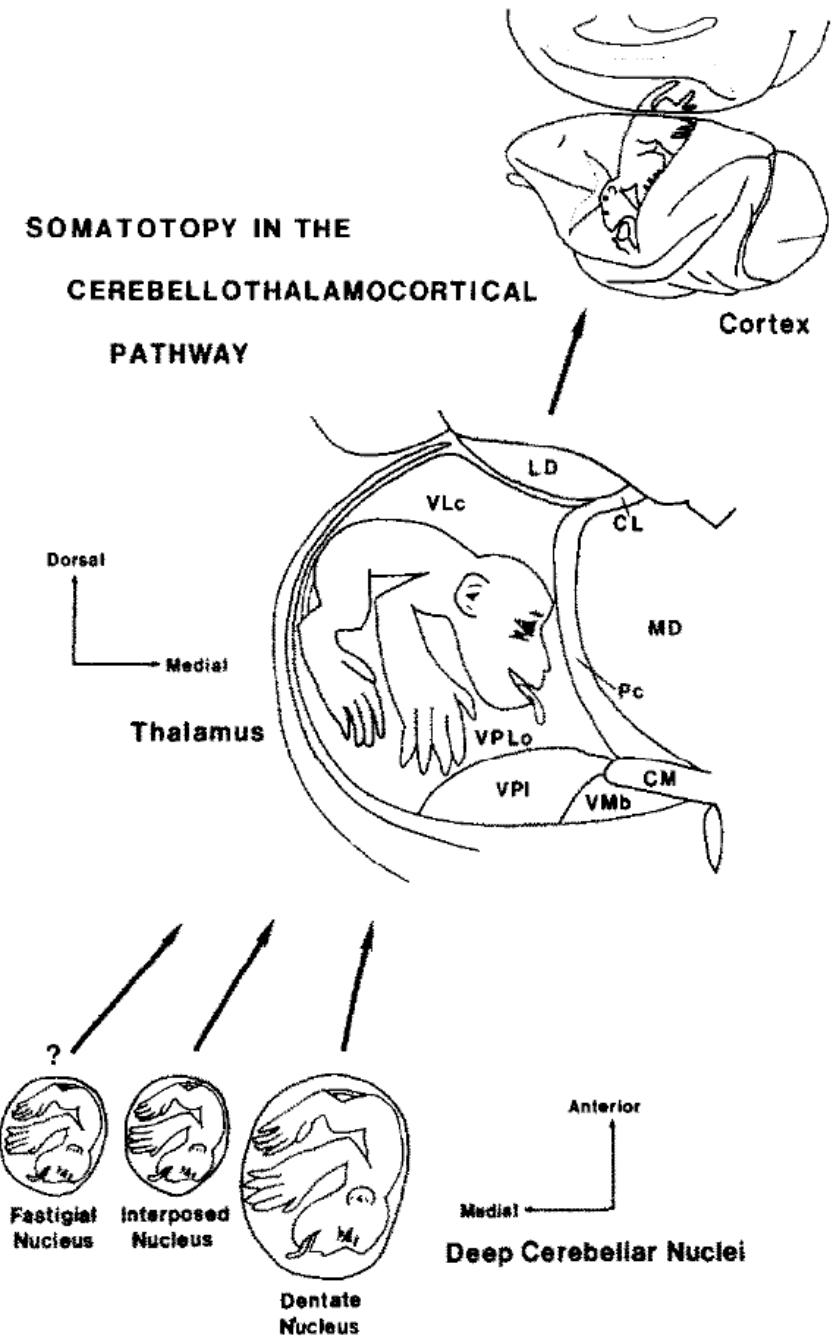
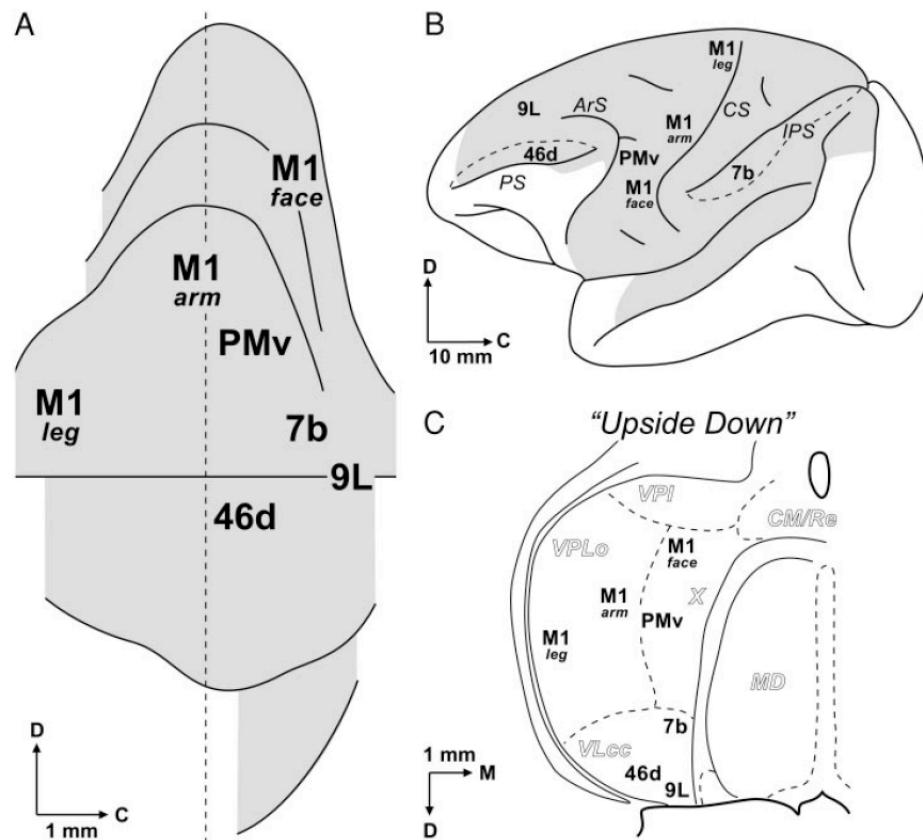
# Substantia Nigra, Globus Pallidus, Cerebellar projections to thalamus



**Figure 7.114.** (cont.)

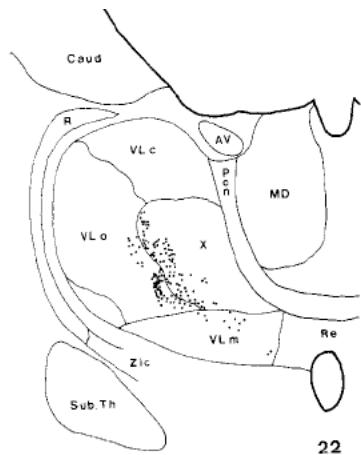
Jones, 2007

# Somatotopy in Cerebellothalamicocortical pathway

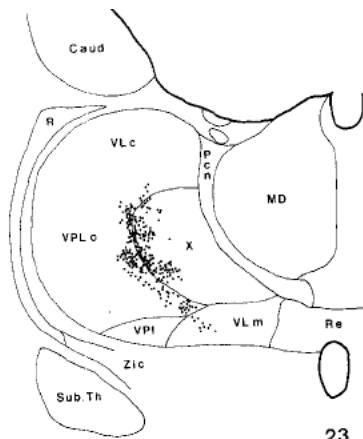


Dum & Strick, 2003

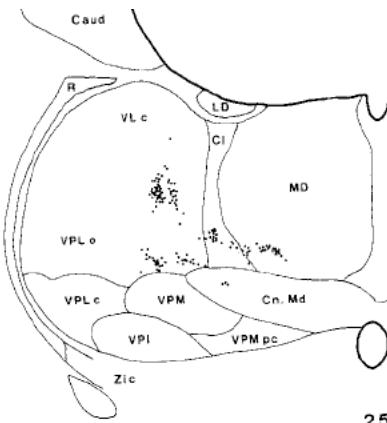
Asanuma et al. 1983



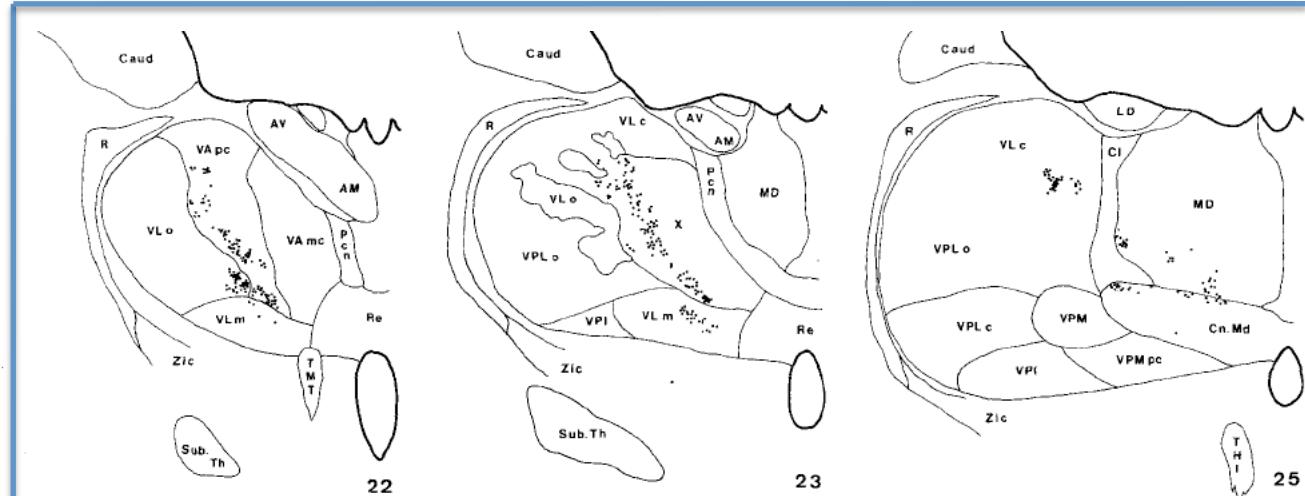
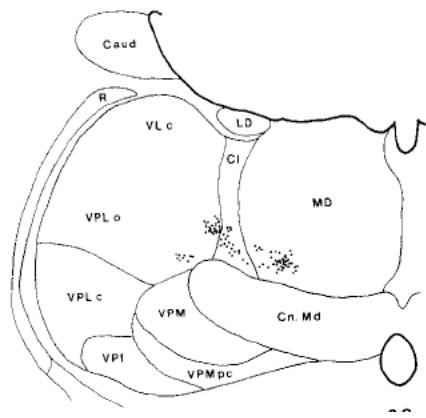
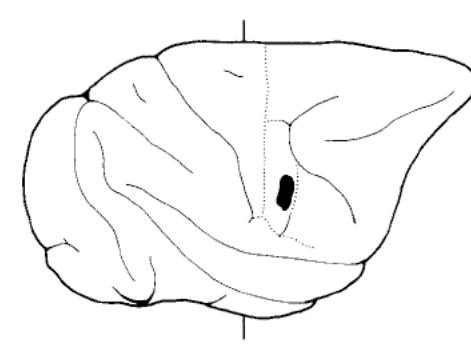
22



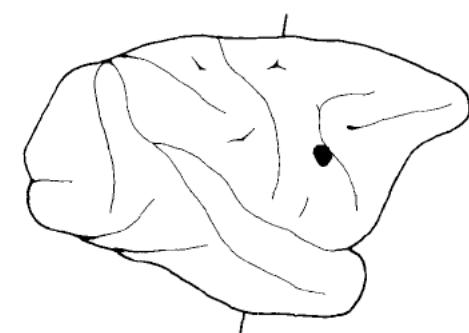
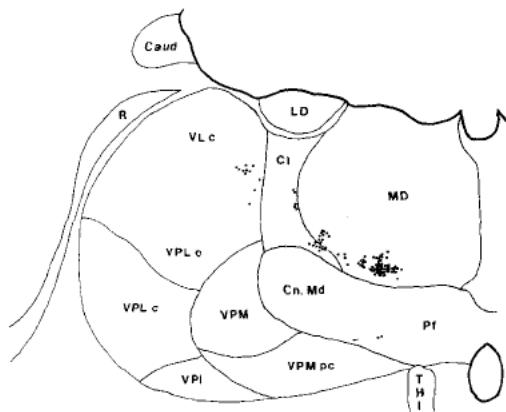
23



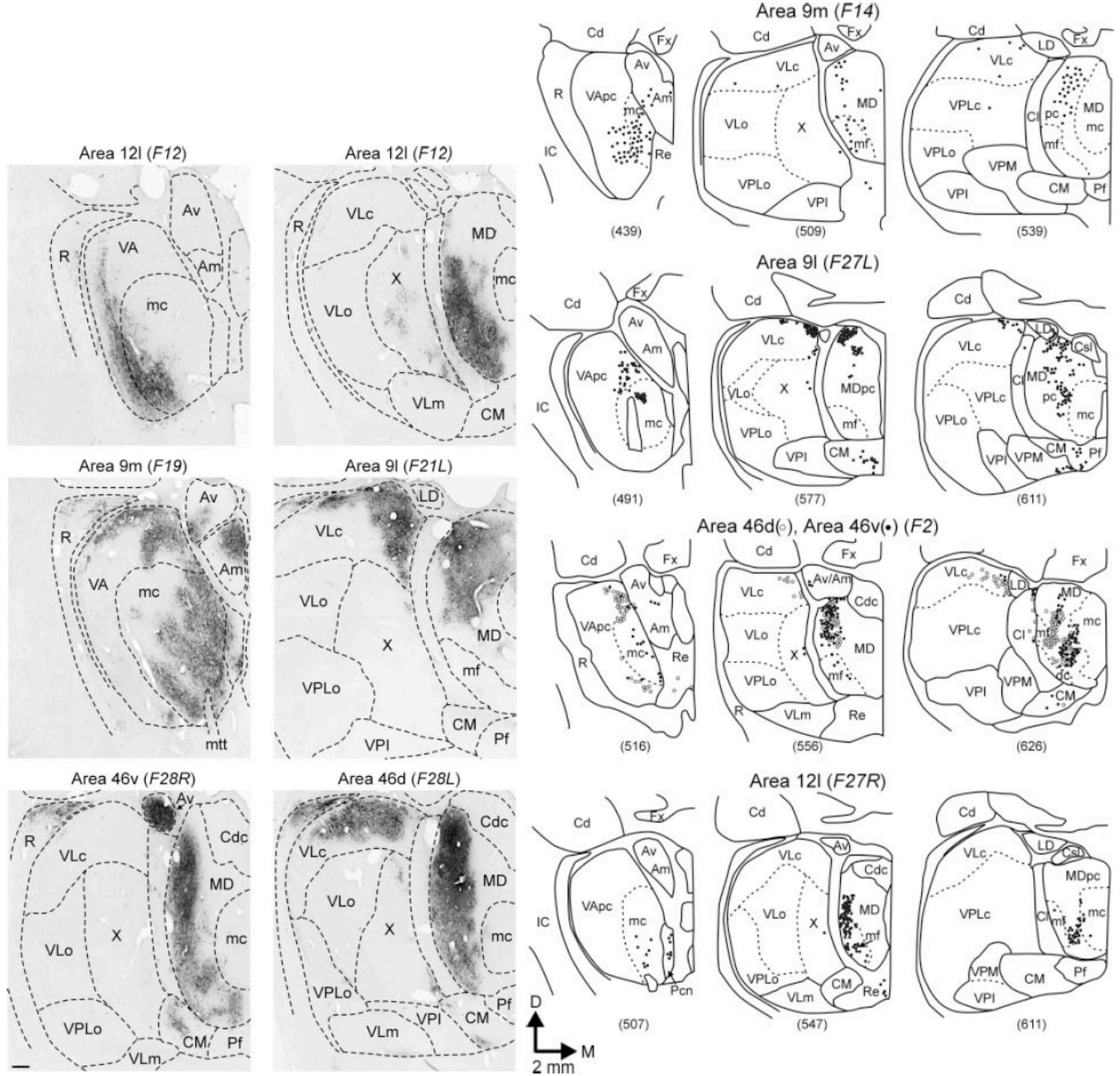
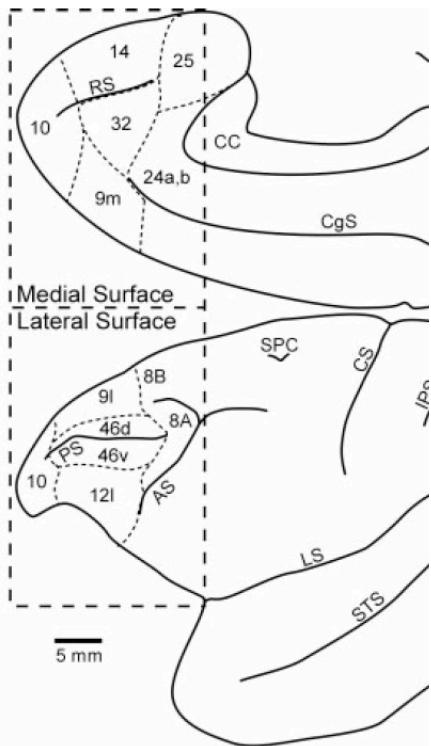
25



IT6-2



Matelli et al., 1989;  
12 *macaca fascicularis*  
& *macaca nemestrina*; FRT



Middleton & Strick,  
2001; 12 cebus  
monkeys, FRT, HSV1