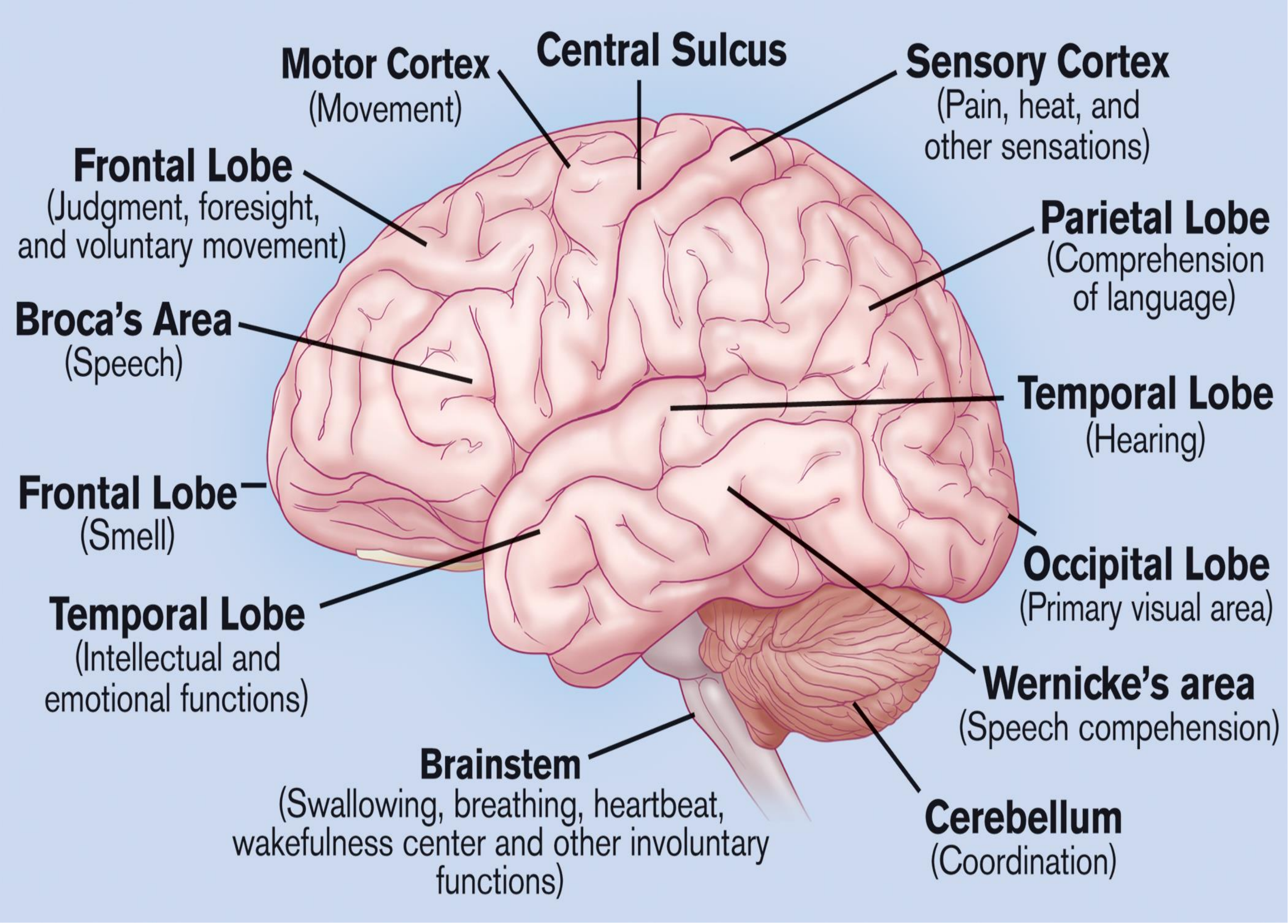
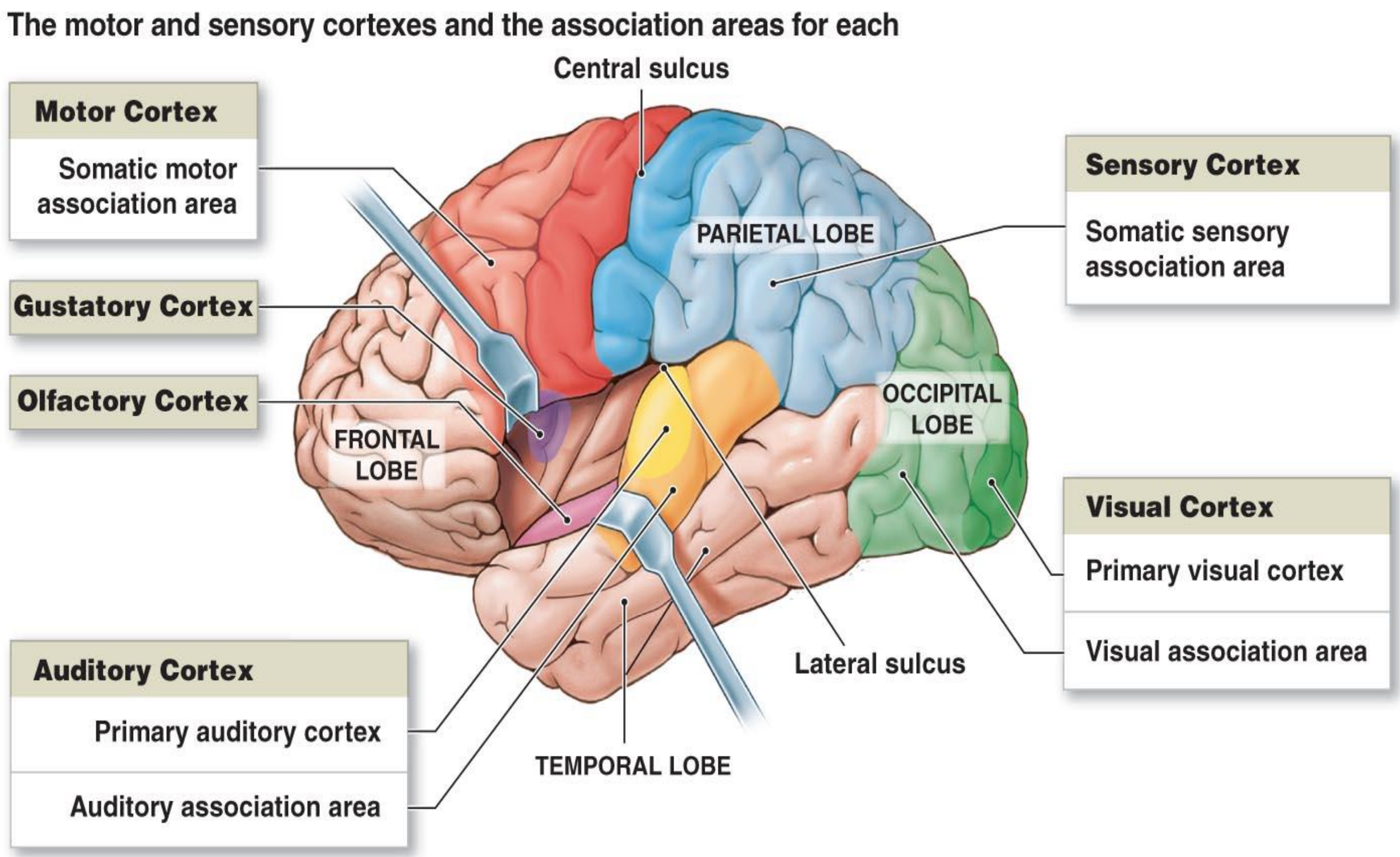
ستون های عملکردی قشر مخ

رضا مقدسی

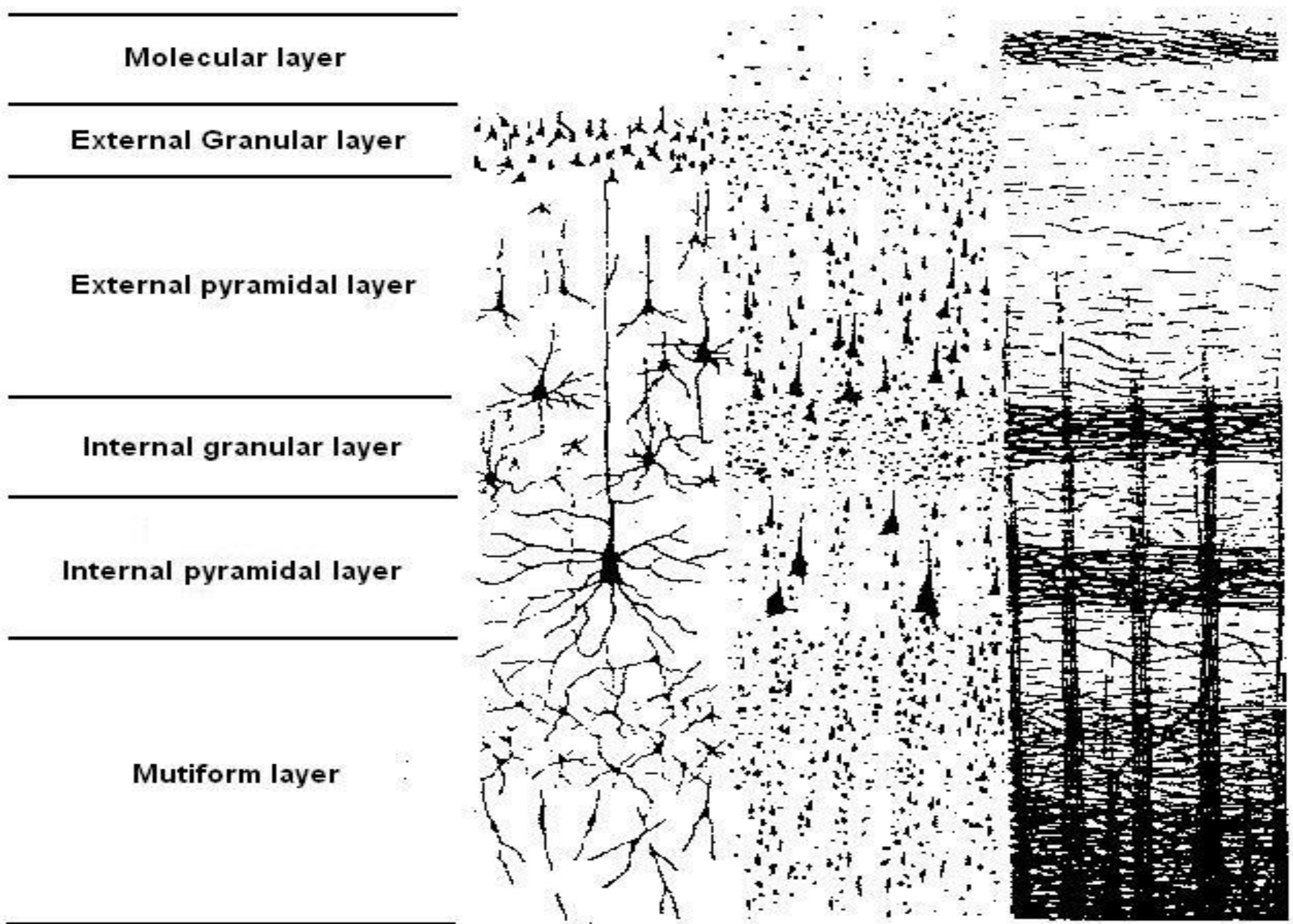
Cerebral cortex



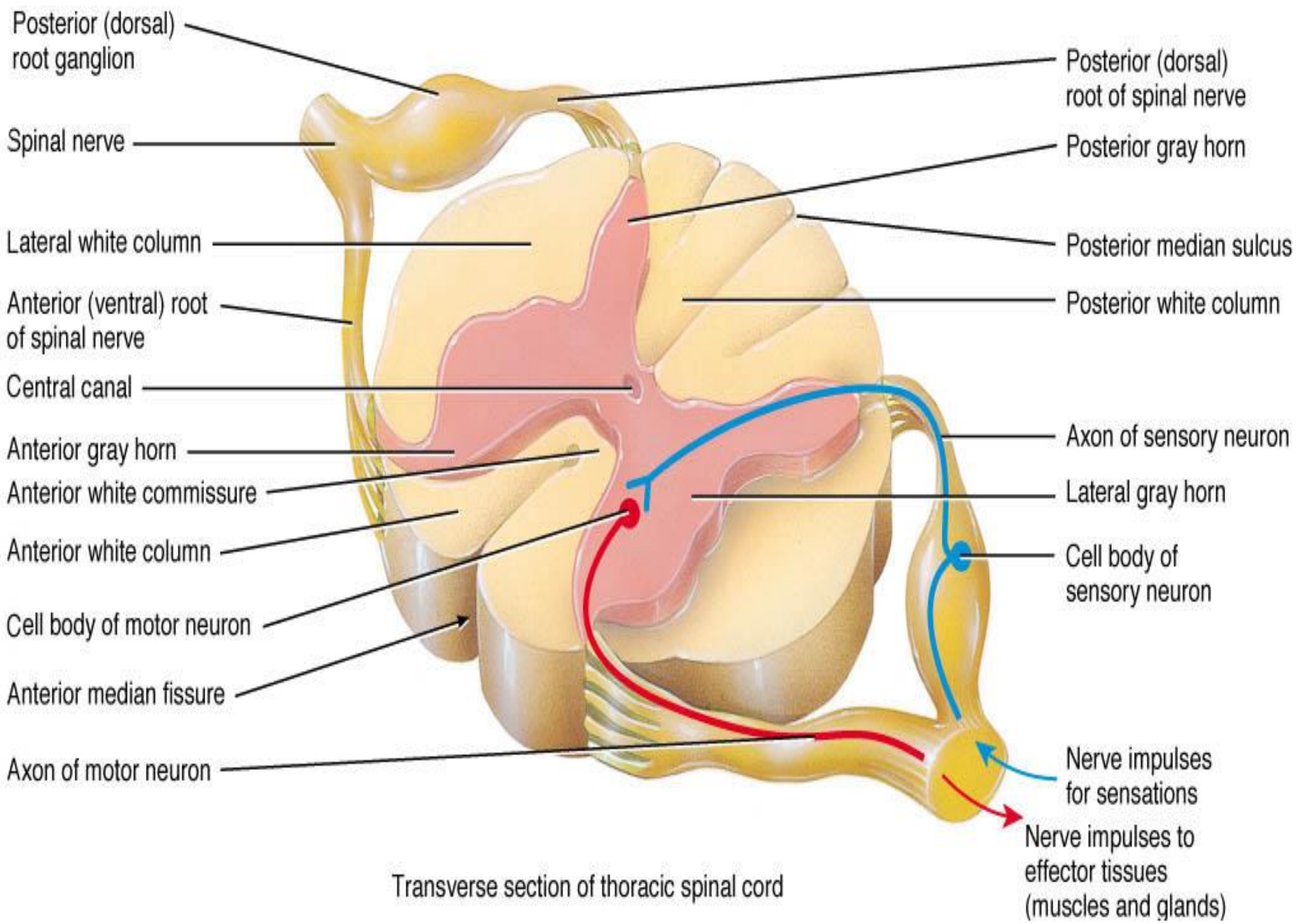
Motor & sensory cortex



فراساختار قشر مخ

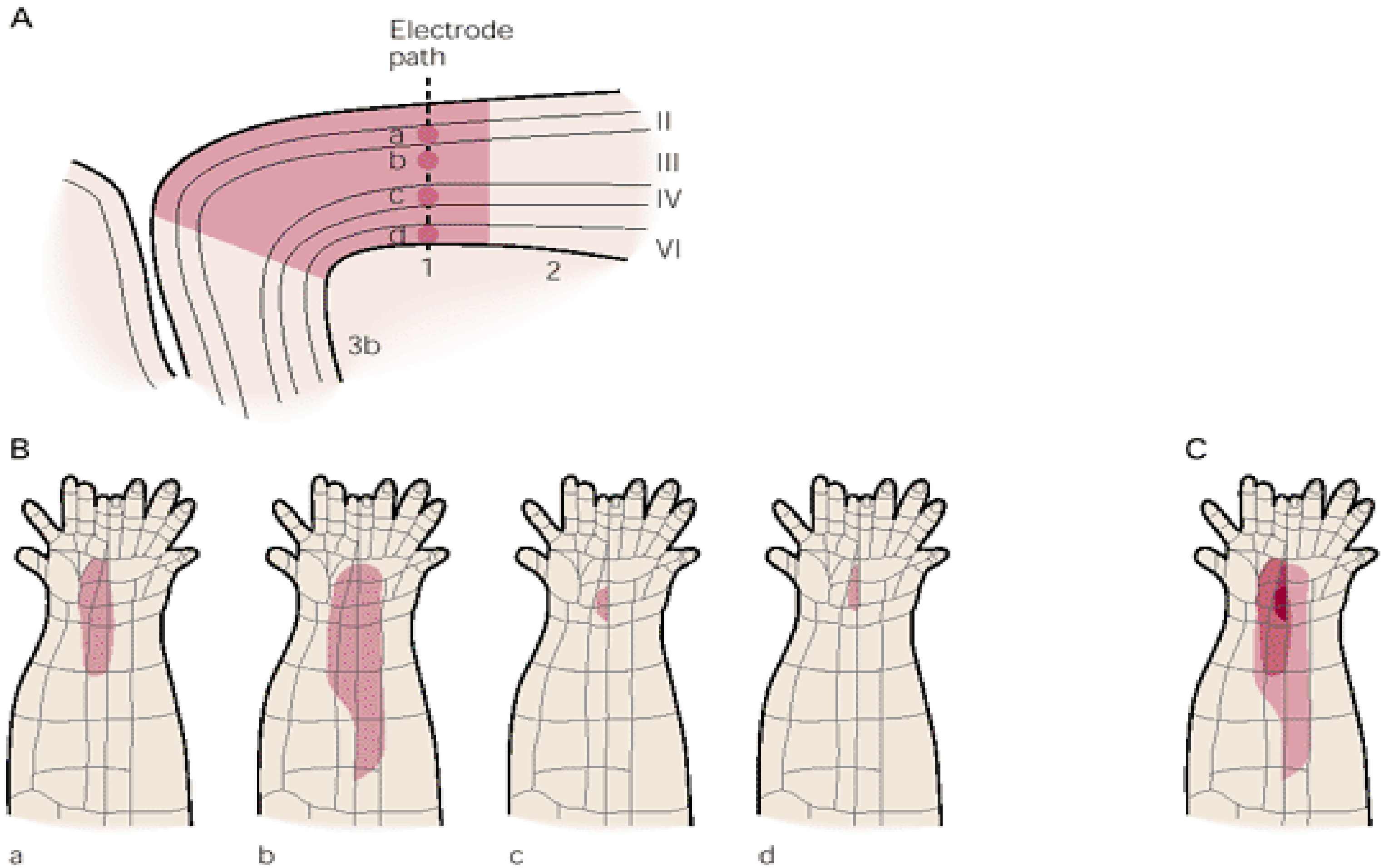


ساختار نخاع

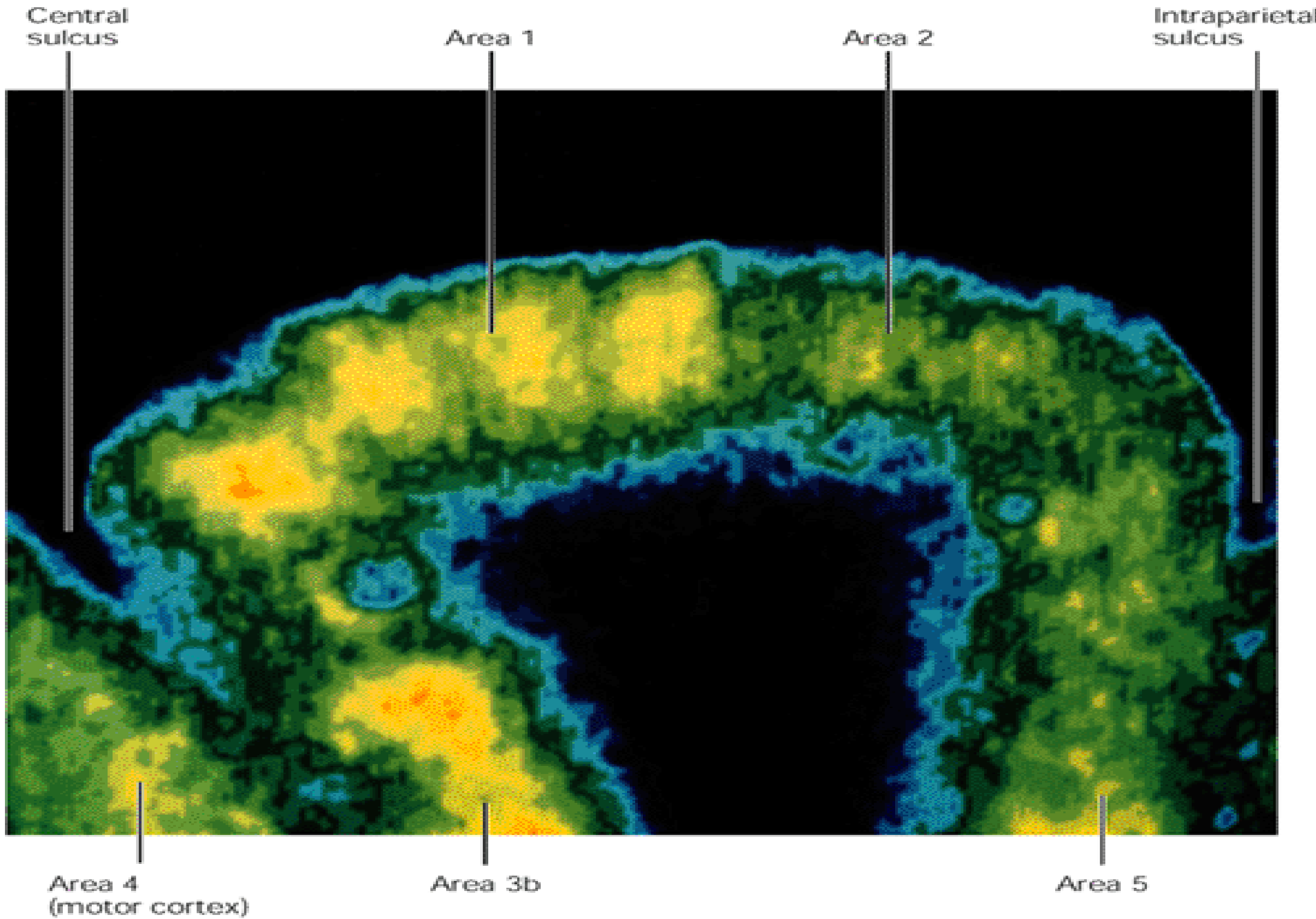


Transverse section of thoracic spinal cord

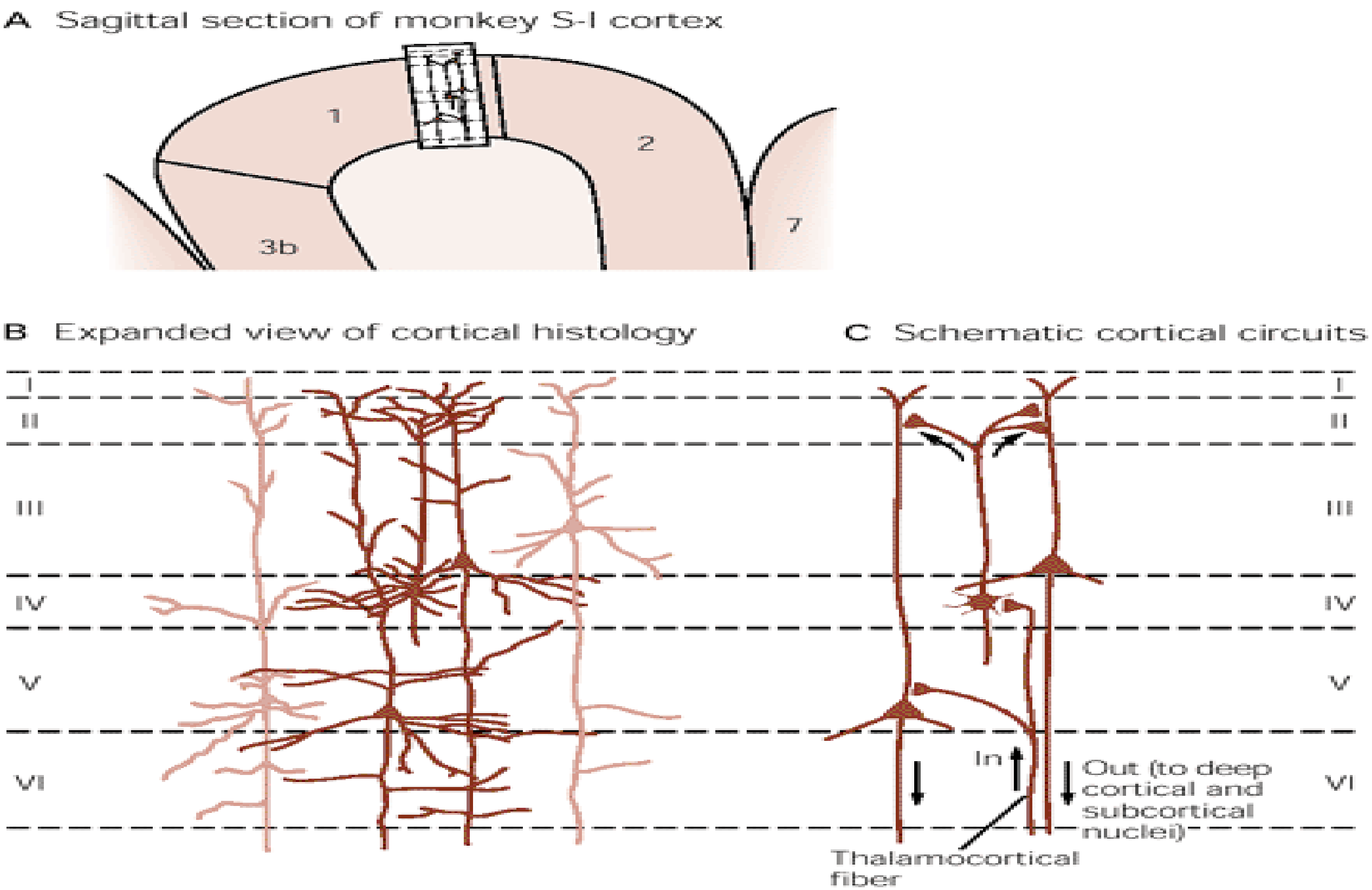
The receptive fields of cells in a column in Brodmann's area 1 share a common central location on the skin. The columns representing a given skin location are approximately 300-600 µm wide. (Adapted from Favorov and Whitsel 1988.)



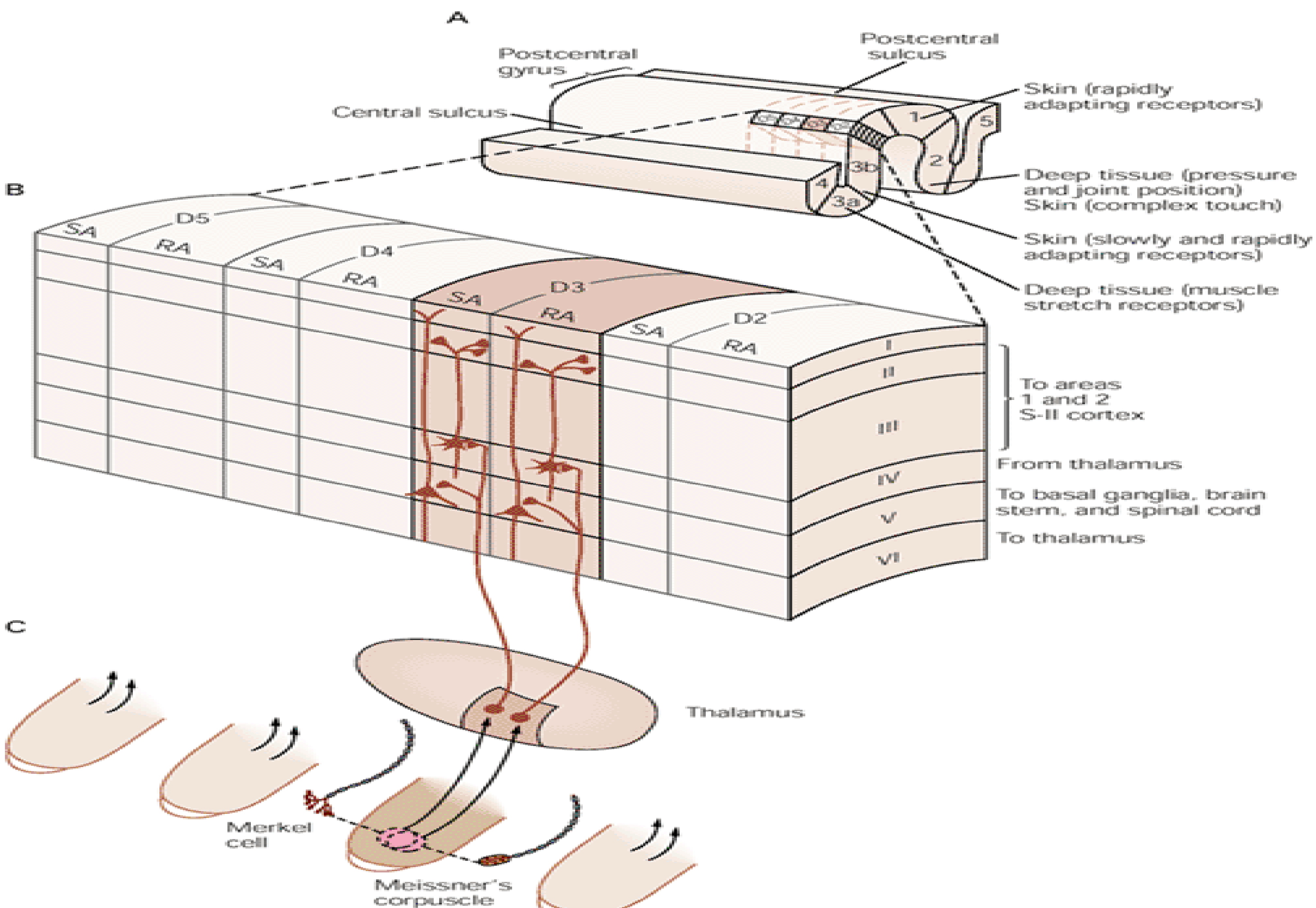
Columns of neurons in the primary somatic sensory cortex comprise the elementary functional modules of cortical processing of somatosensory information



The columnar organization of cortical neurons is a consequence of the pattern of connections between neurons in different layers of cortex. (Modified from Jones 1981.)

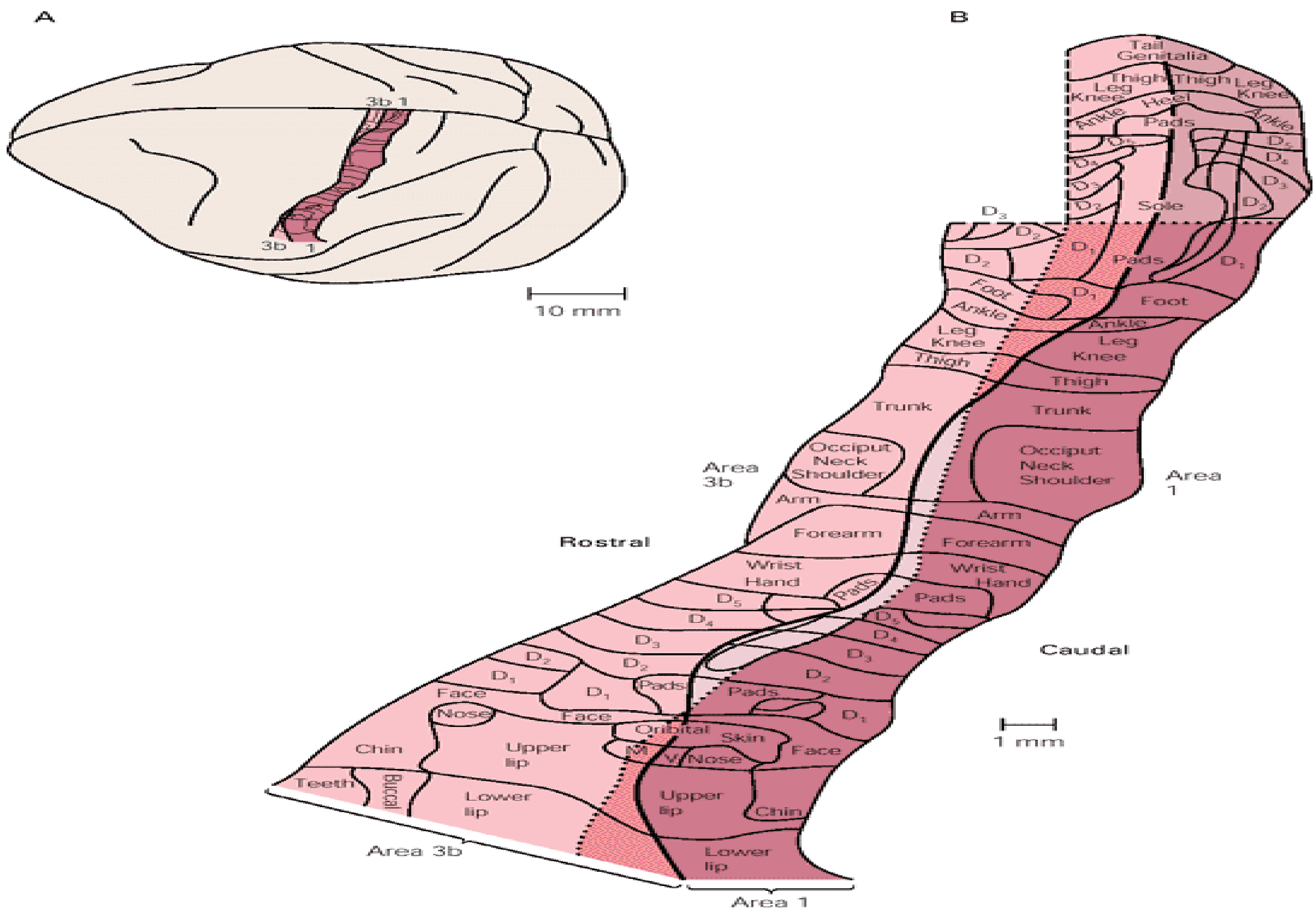


Each region of the somatic sensory cortex receives inputs from primarily one type of receptor

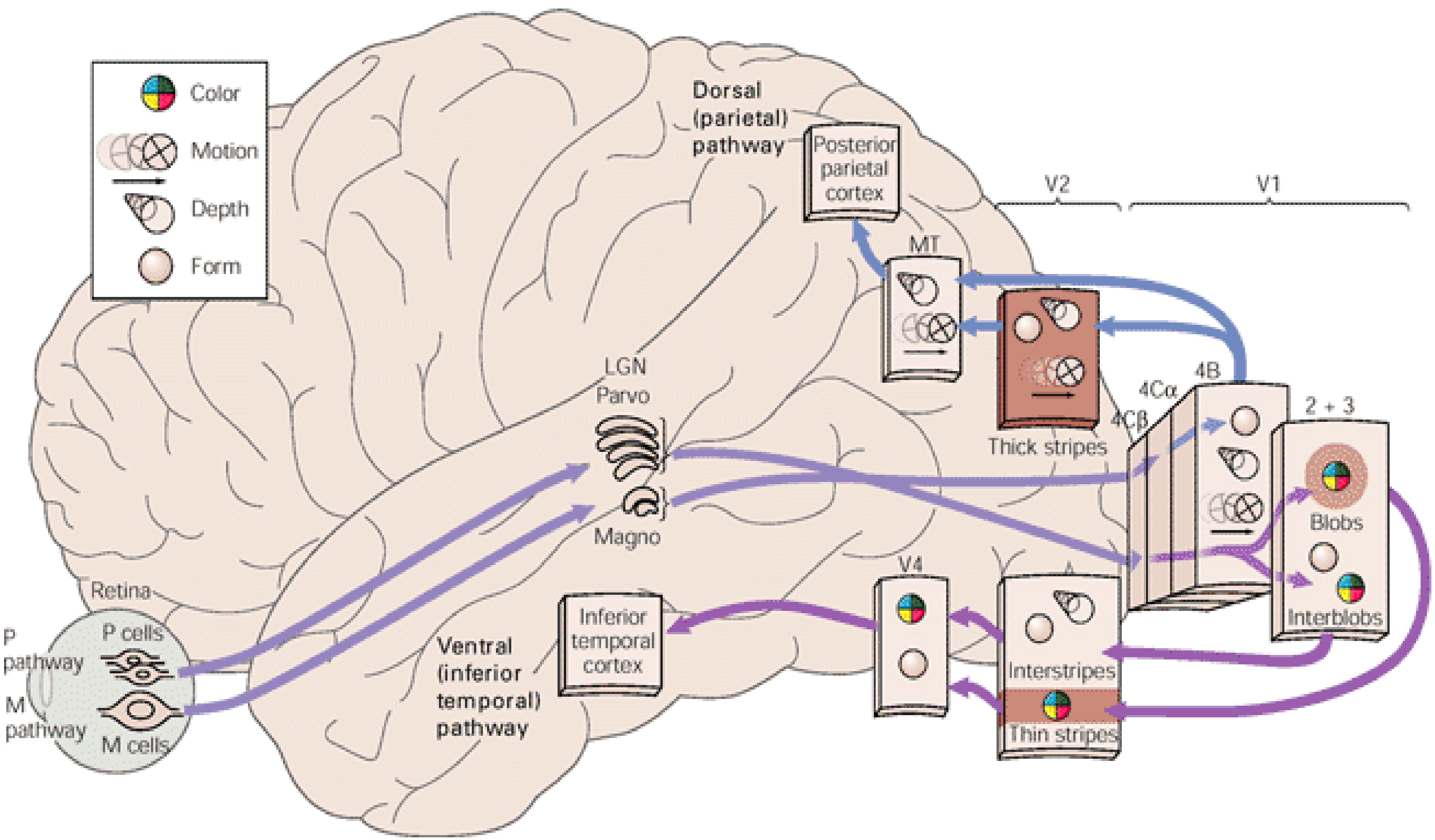


Each of the four regions of the primary somatic sensory cortex contains a complete map of the body surface.

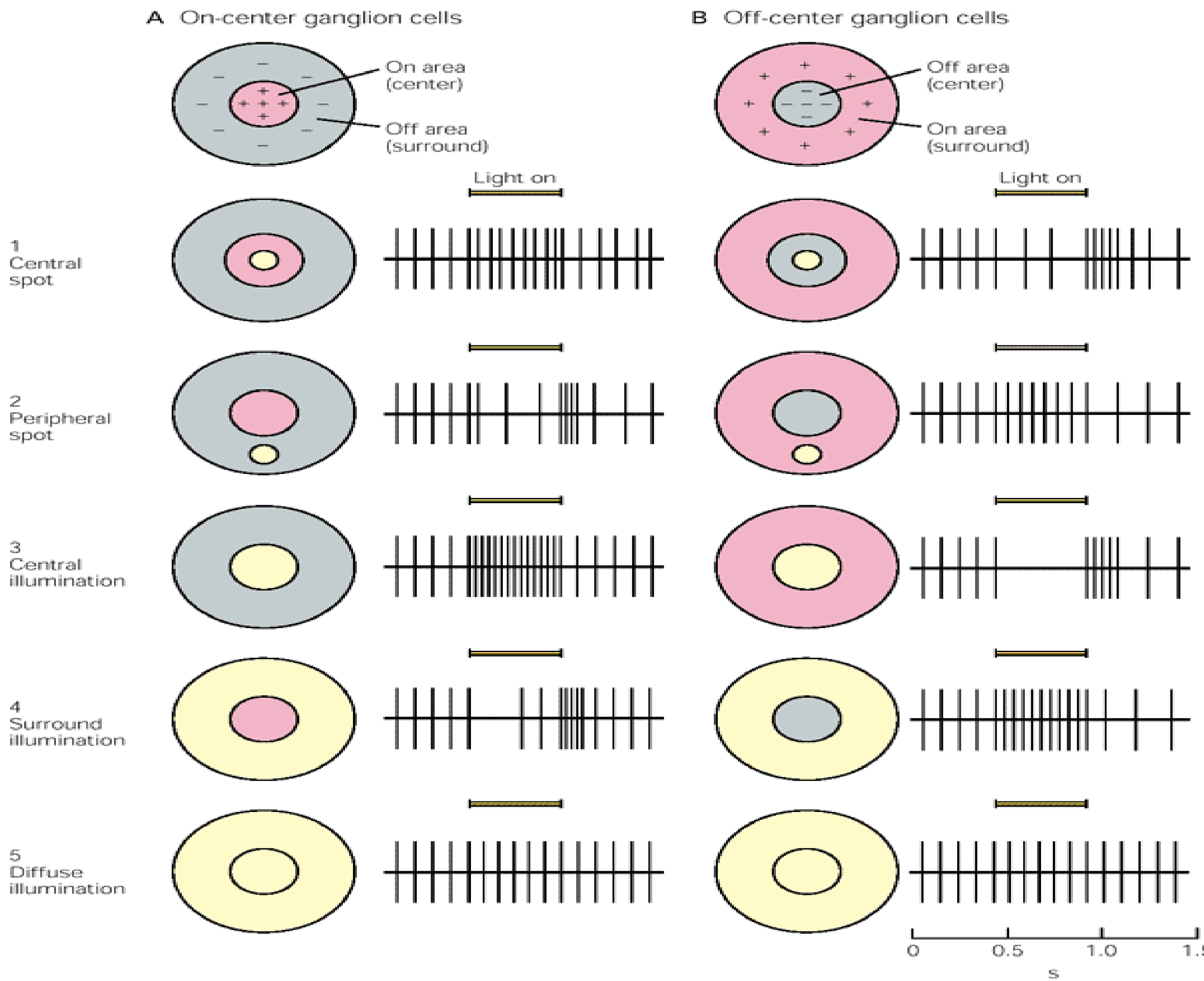
(Adapted from Nelson et al. 1980.)



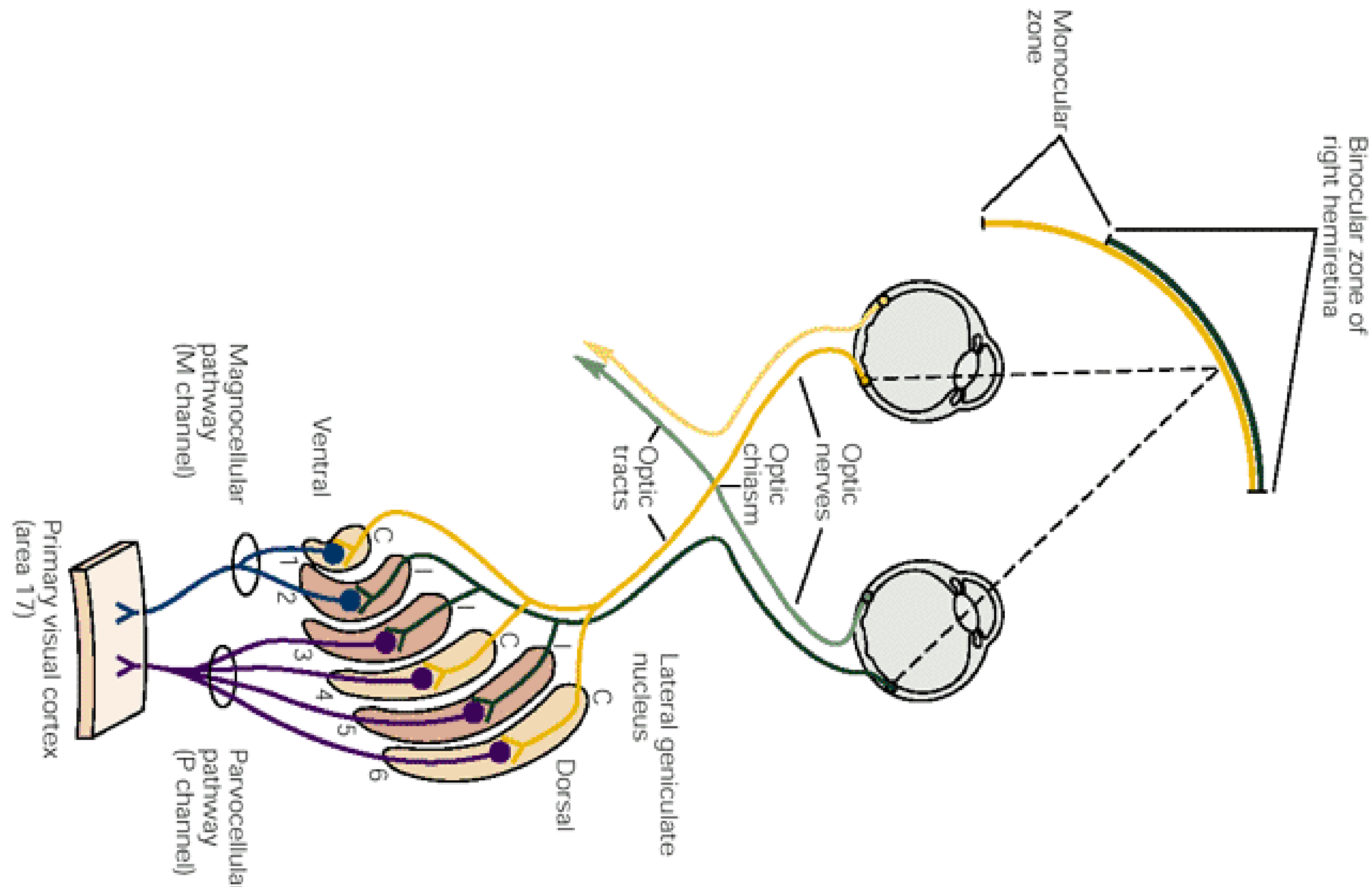
Possible functions mediated by the two pathways connecting visual processing centers in the cerebral cortex



Retinal ganglion cells respond optimally to contrast in their receptive fields.

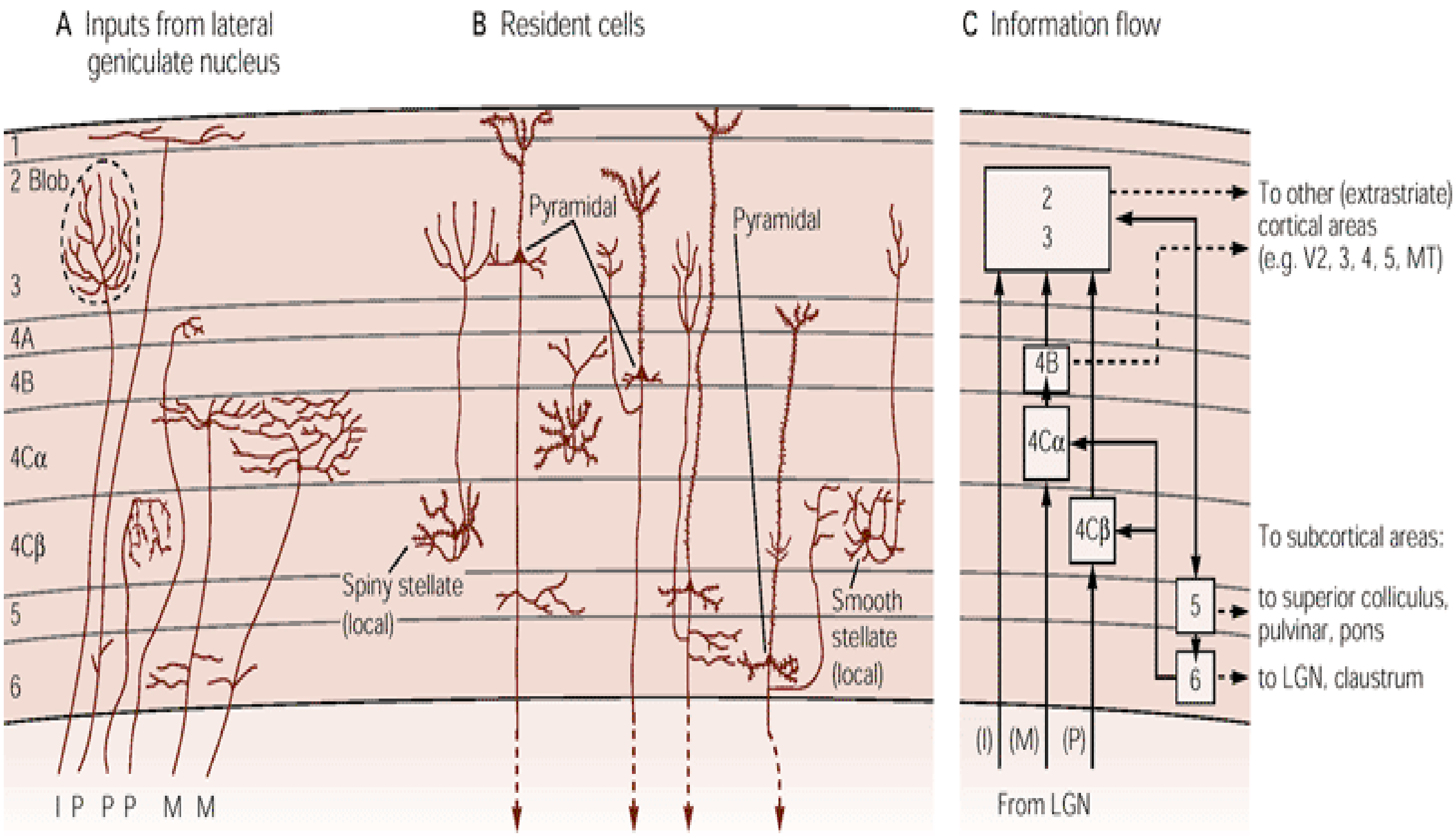


The lateral geniculate nucleus is the principal subcortical site for processing visual information

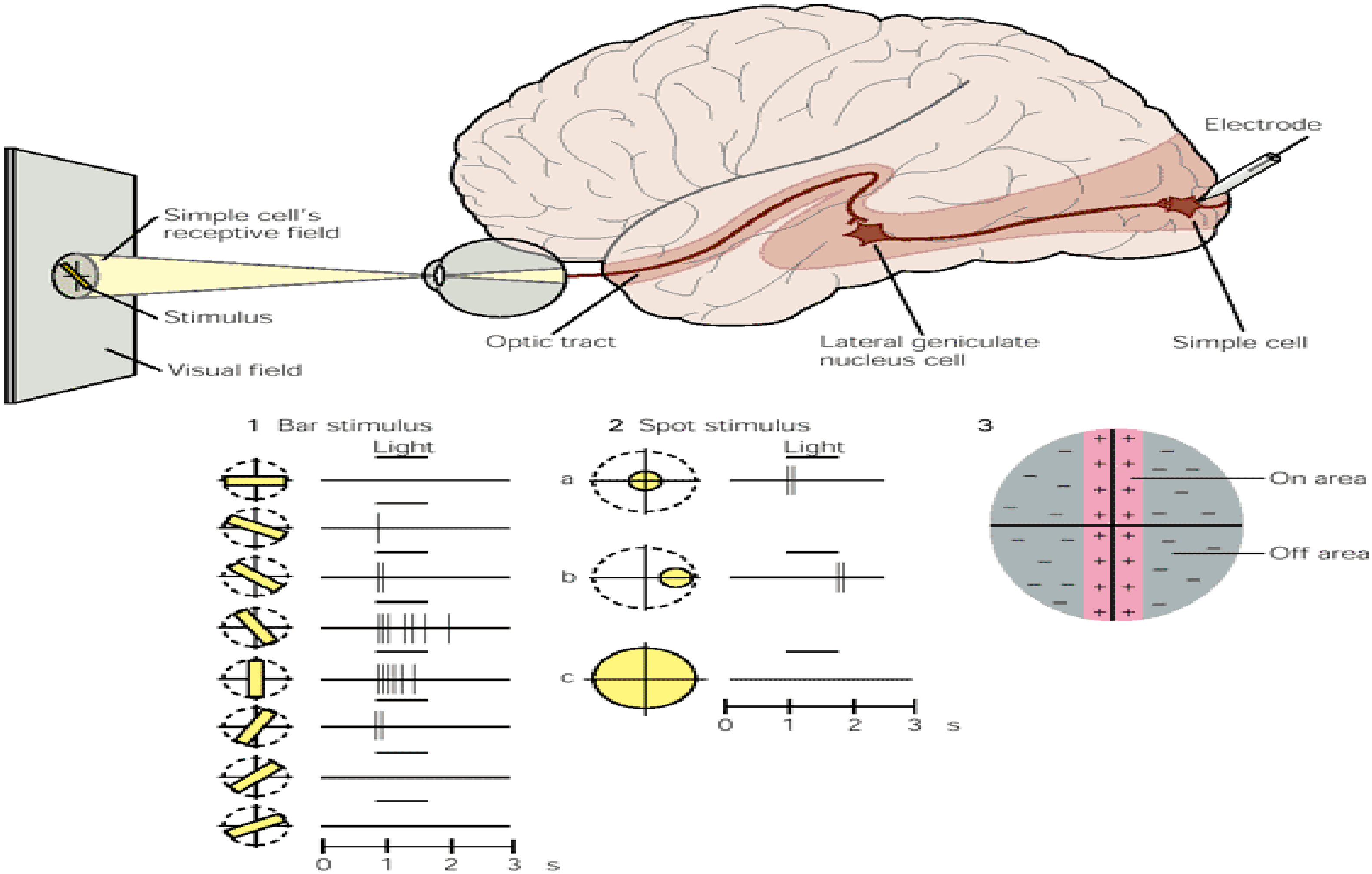


The primary visual cortex has distinct anatomical layers, each with characteristic synaptic connections.

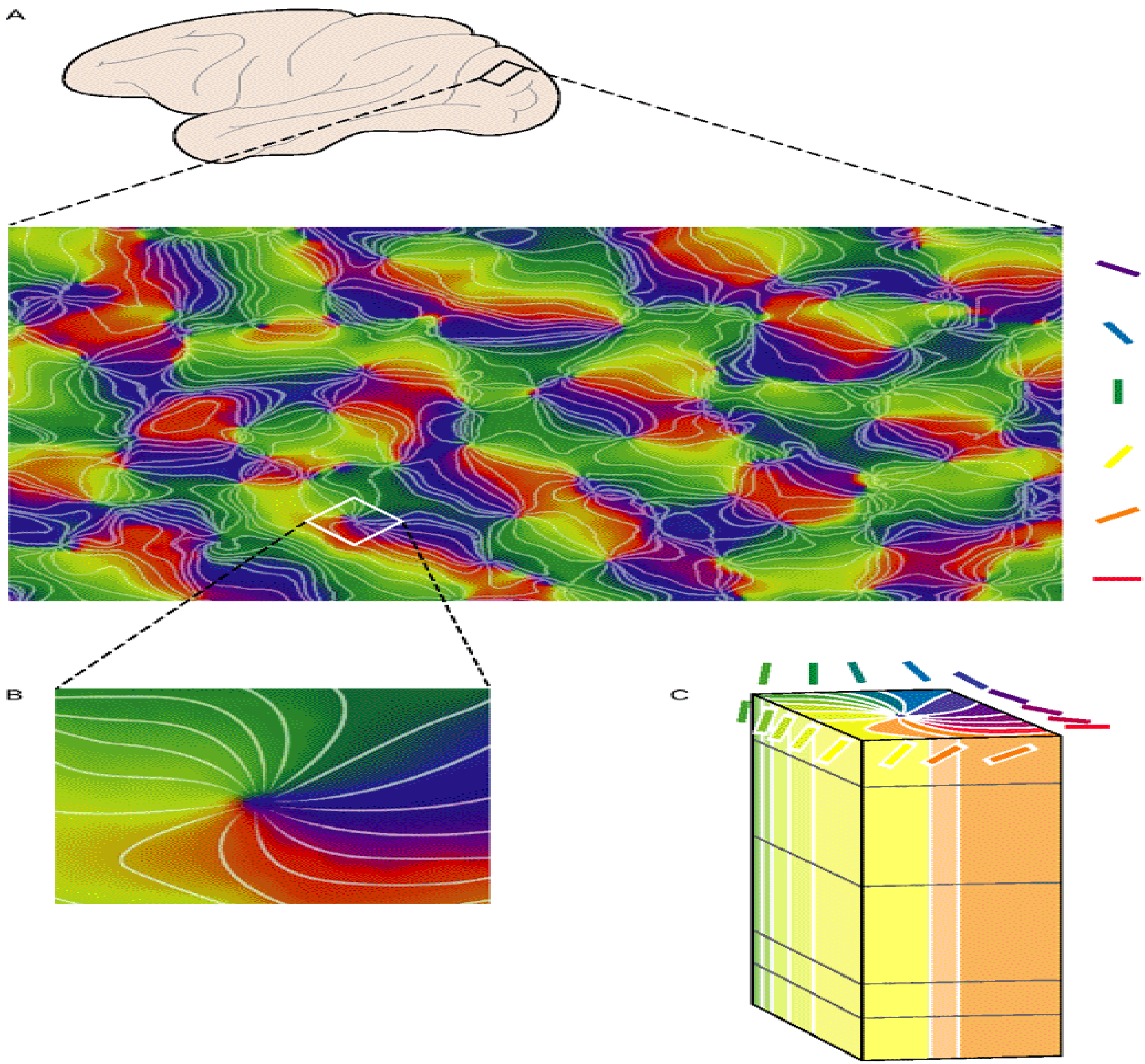
(Adapted from Lund 1988.)



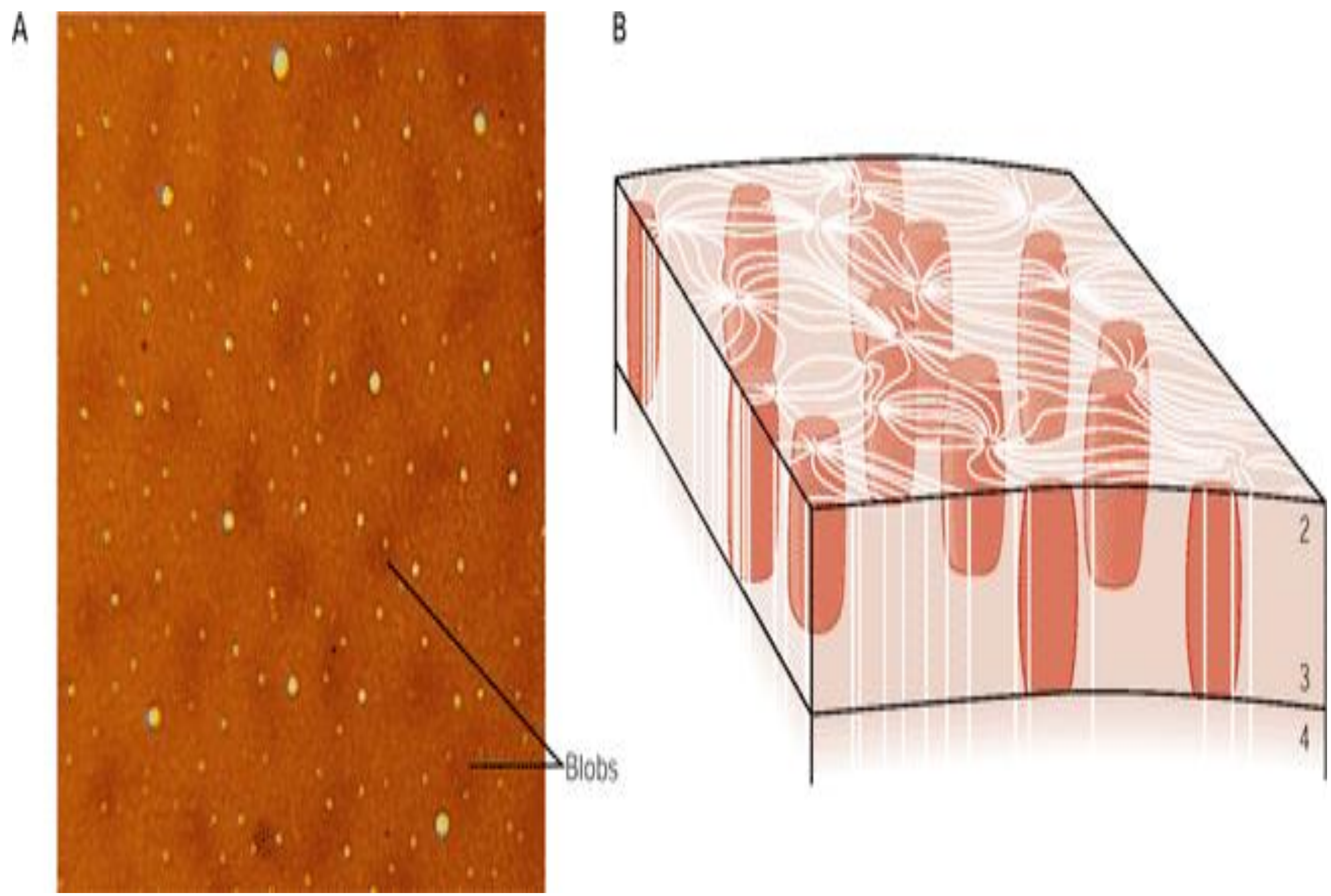
Receptive field of a simple cell in the primary visual cortex



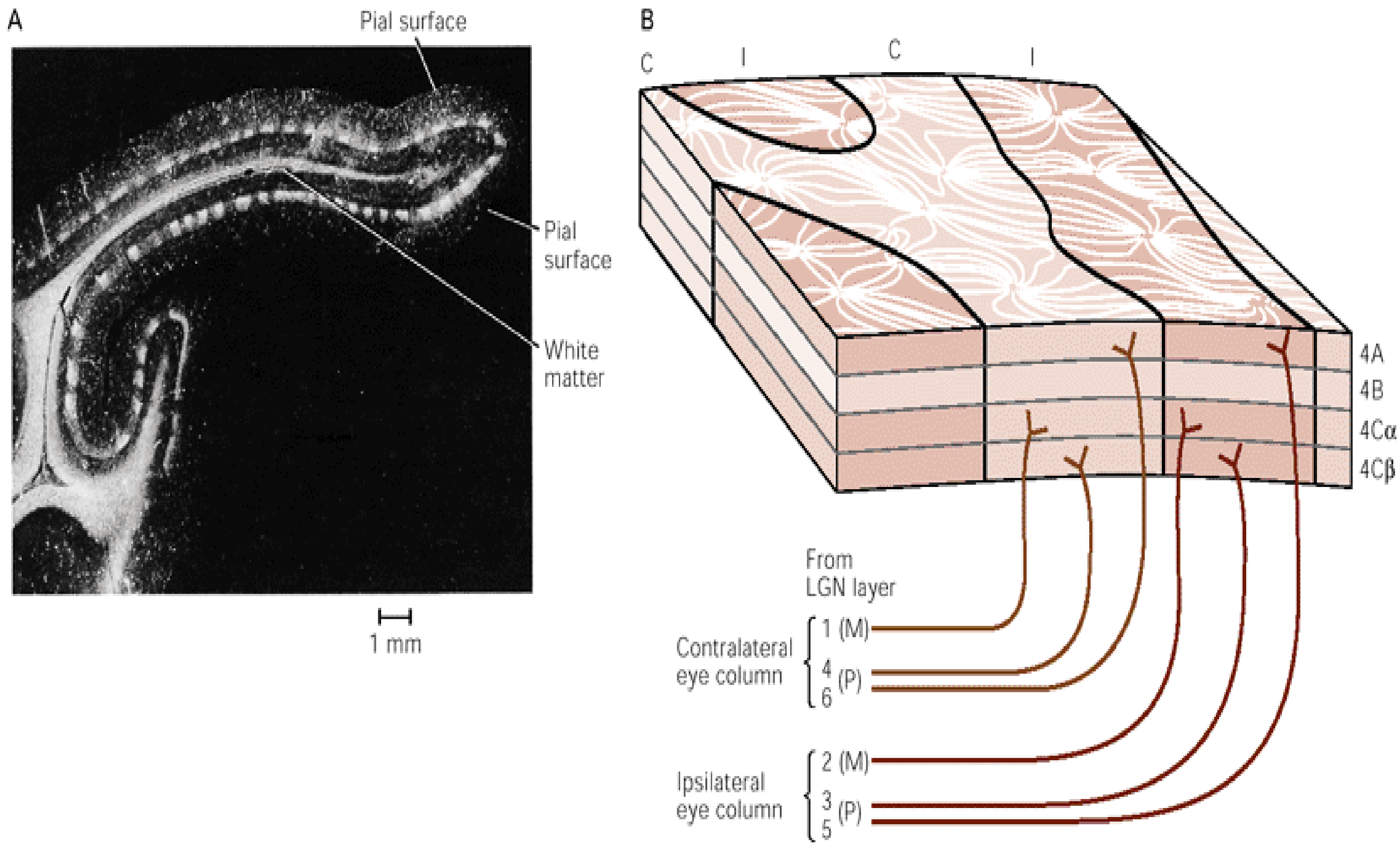
Orientation columns in the visual cortex of the monkey.
(Courtesy of Gary Blasdel.)



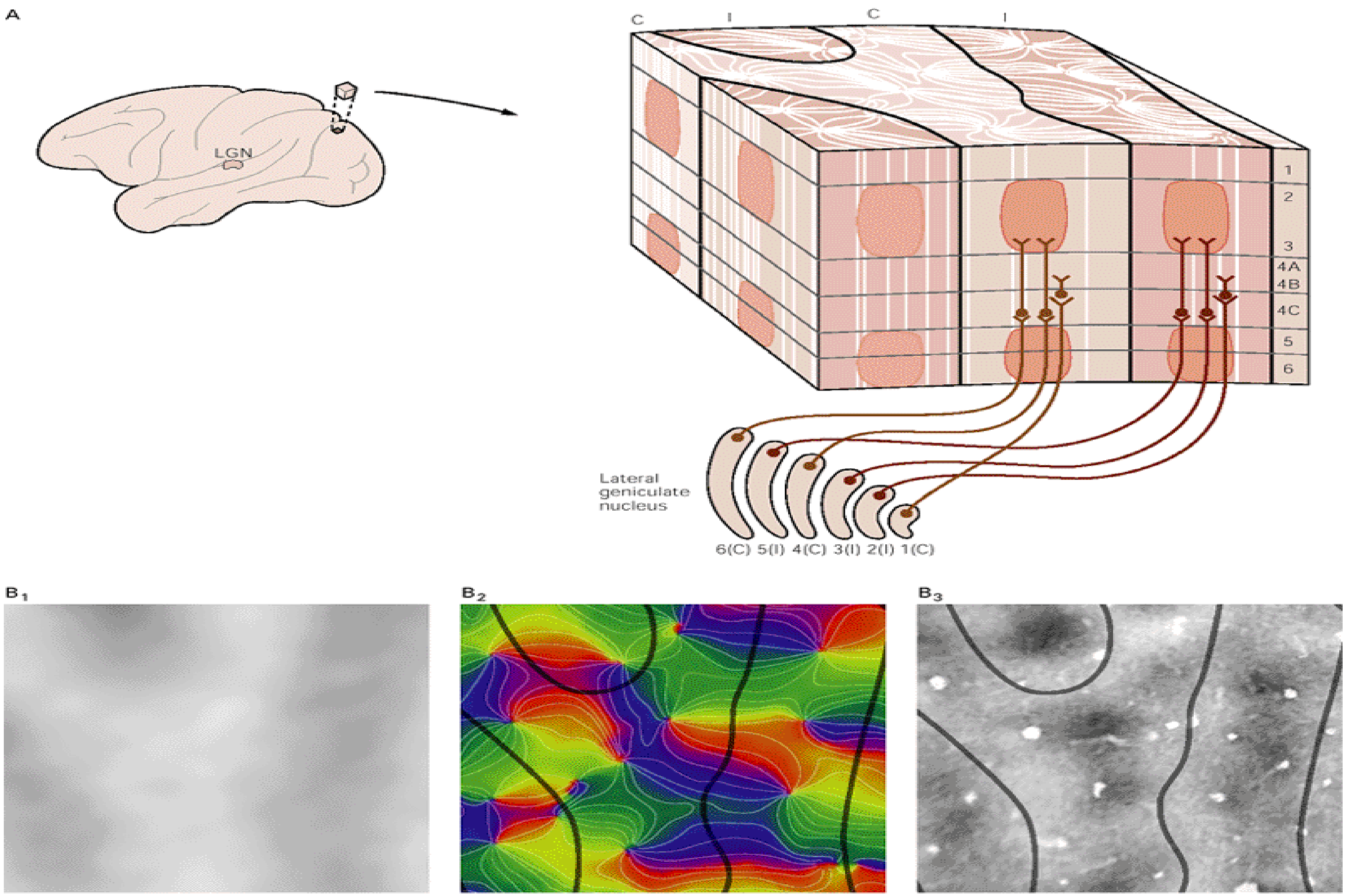
Organization of blobs in the visual cortex



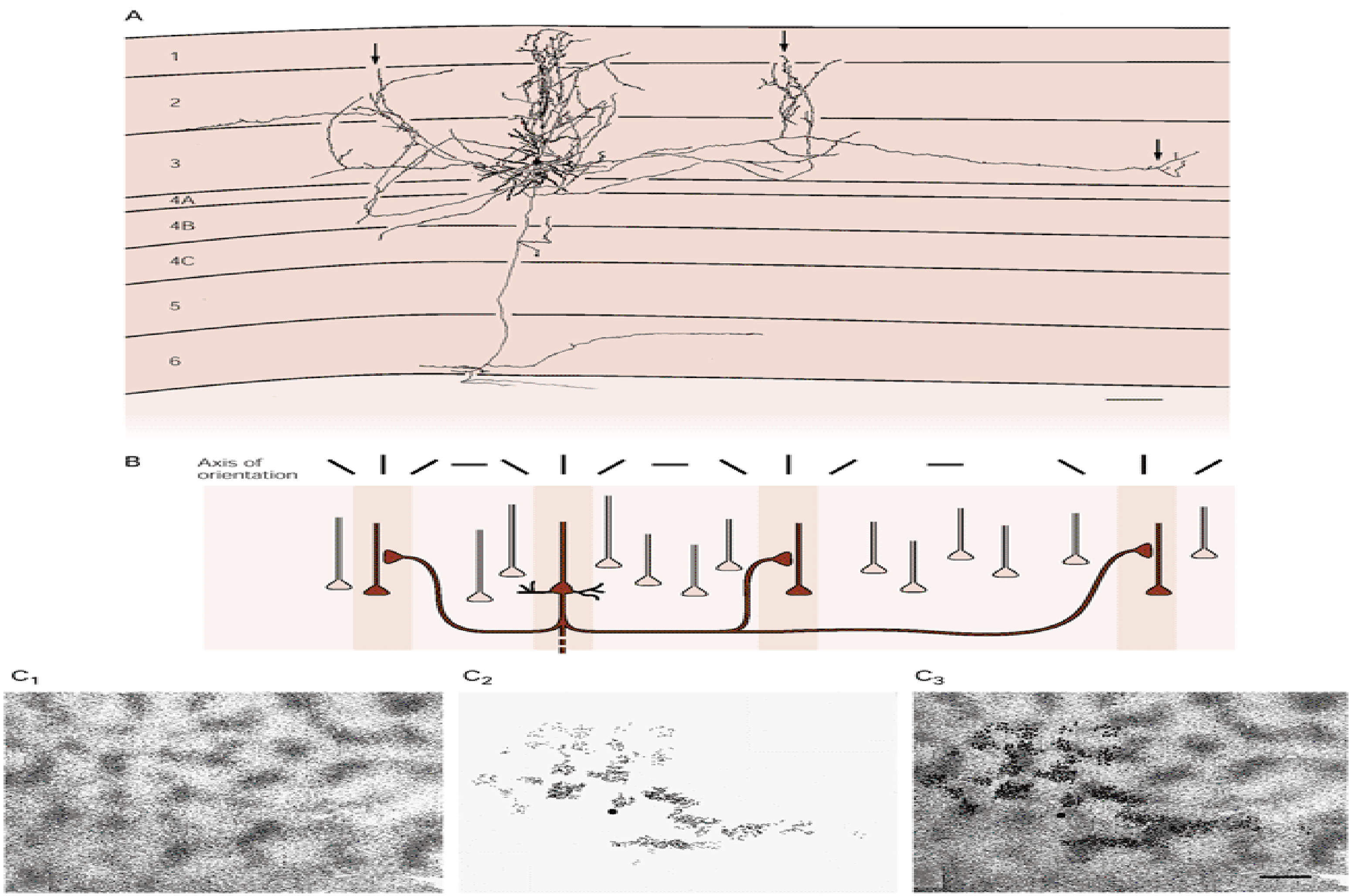
The ocular dominance columns



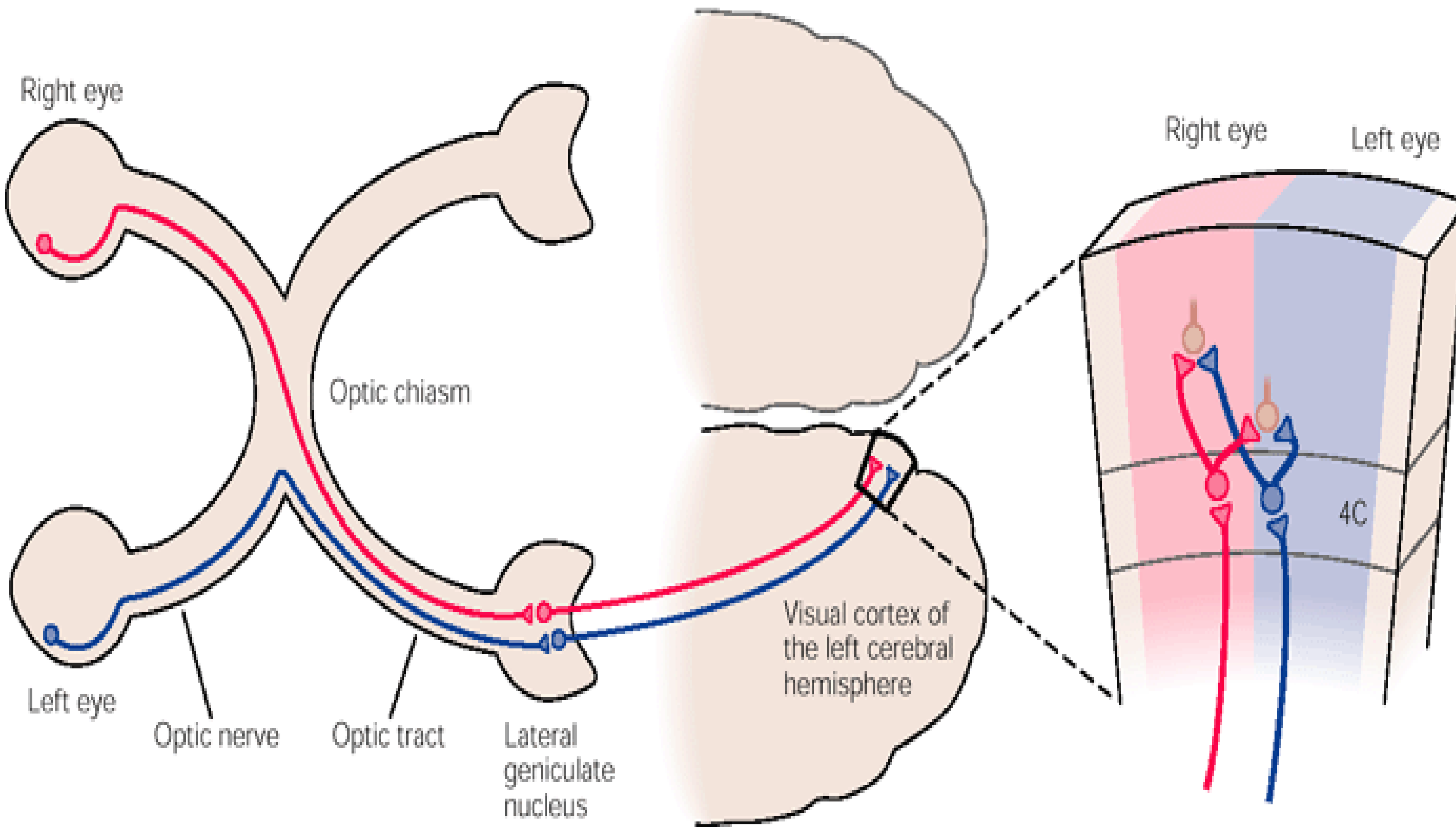
Organization of orientation columns, ocular dominance columns, and blobs in primary visual cortex



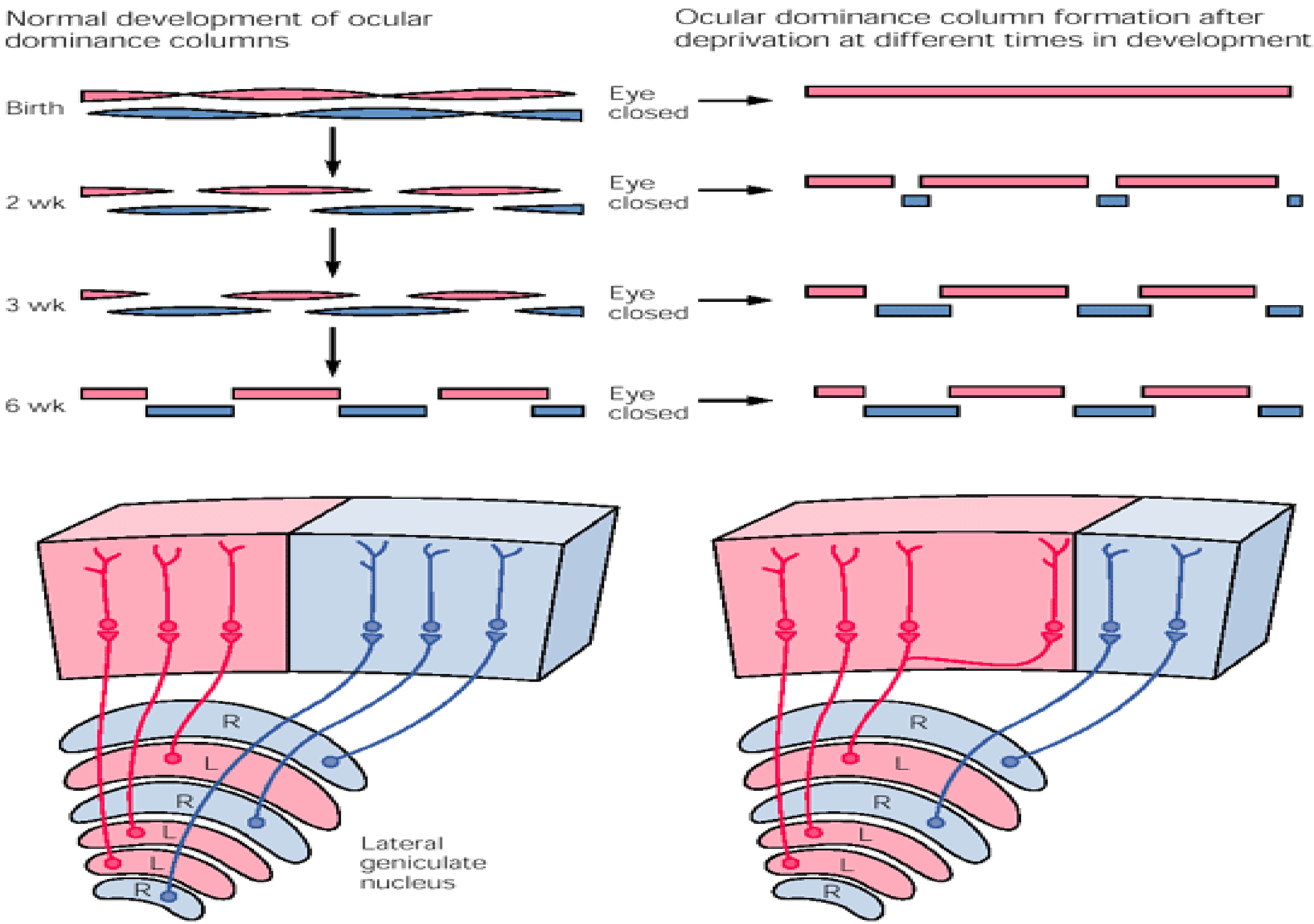
Columns of cells in the visual cortex with similar function are linked through horizontal connections



Afferent pathways from the two eyes remain segregated as they project to the visual cortex. .



The effects of eye closure on the formation of ocular dominance columns in layer 4C

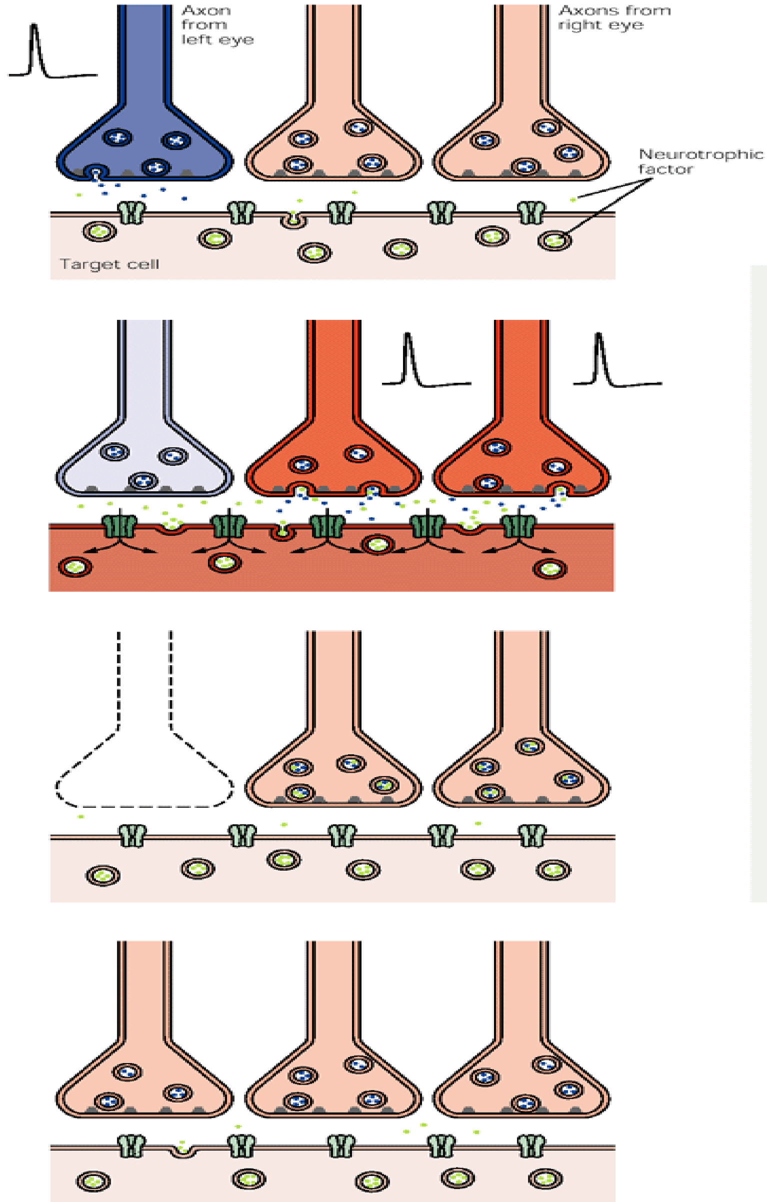


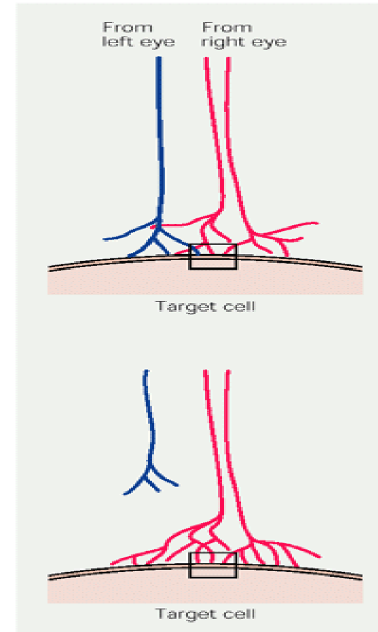
Axon from left eye fires alone, leading to a small depolarization of the target cell which is inadequate to activate the NMDA receptors. Small amounts of neurotrophic factor normally available do not sustain the axon.

Axons from right eye fire synchronously, leading to a larger depolarization of the target cell and activation of the NMDA receptors. This causes the target cell to release increased amounts of neurotrophic factor which is taken up by the active presynaptic terminals from the left eye during endocytic retrieval of the plasma membrane.

The inactive axon from the left eye, which has not taken up neurotrophic factor, retracts.

Axon branches from the right eye, stimulated by the neurotrophic factor, sprout and occupy the vacated target site.





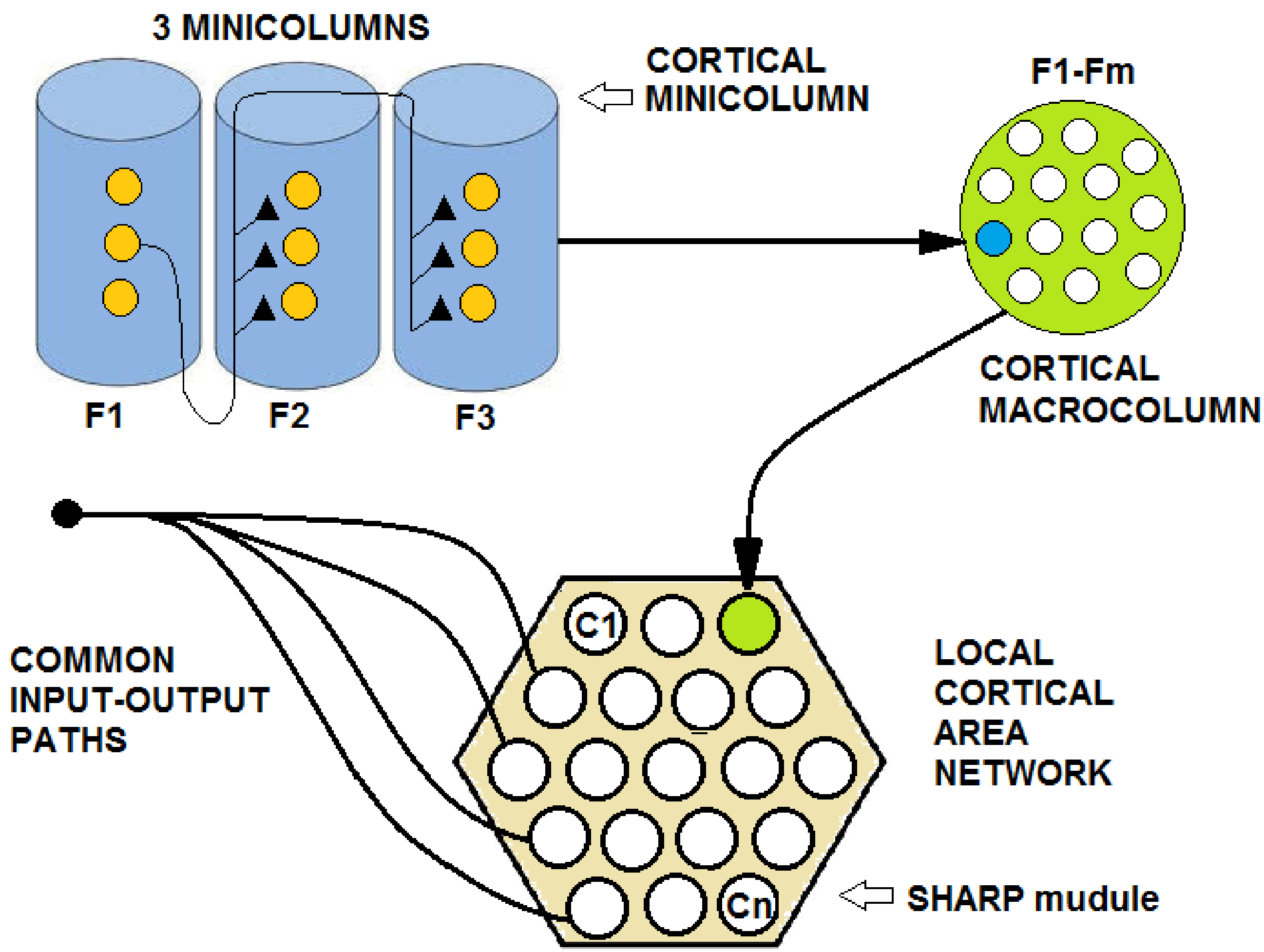
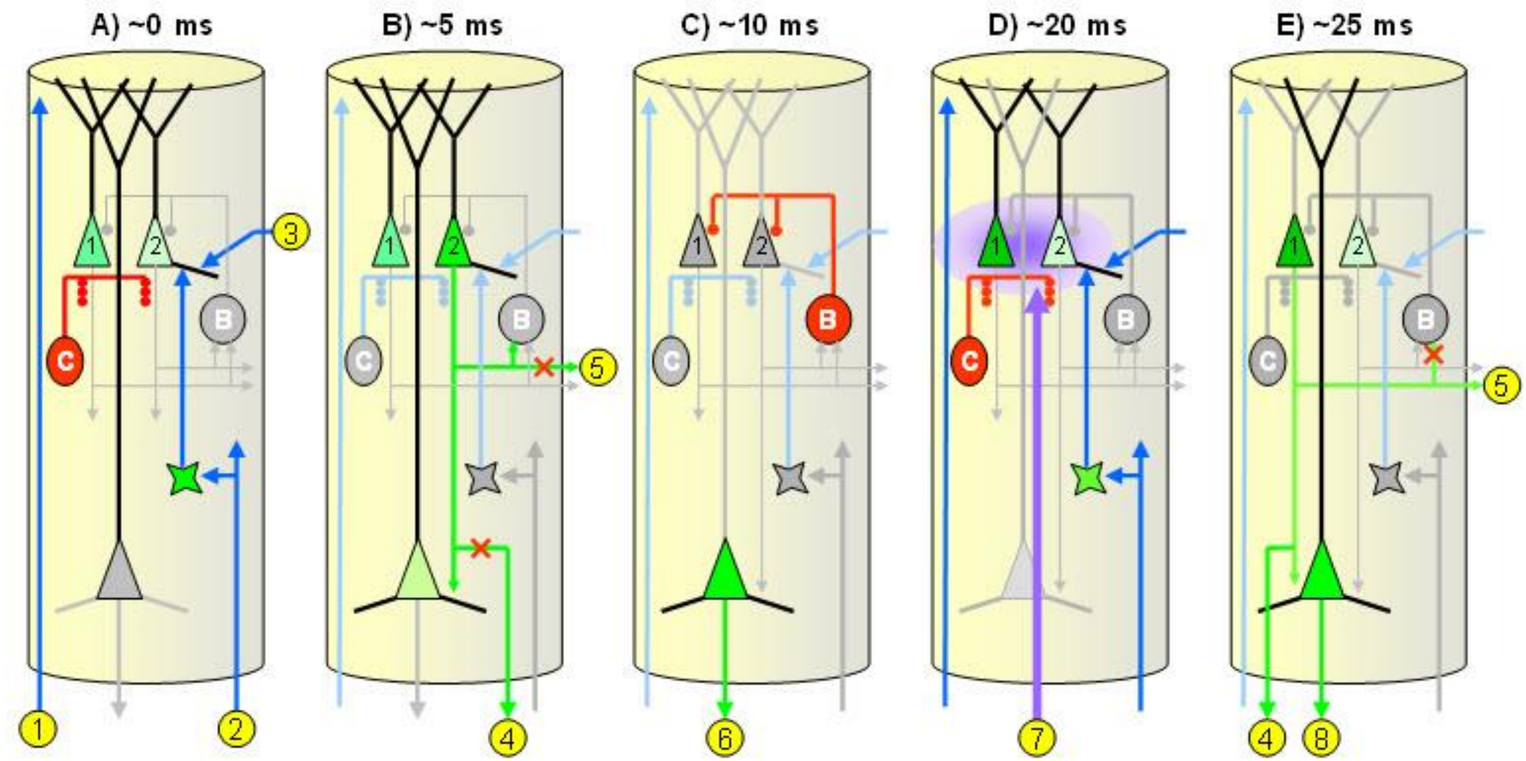
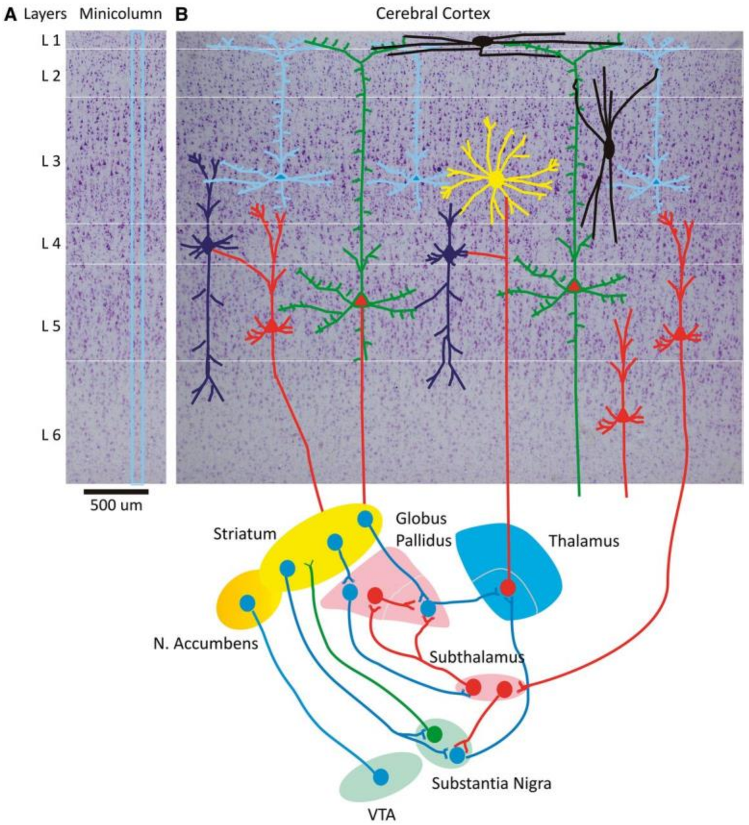
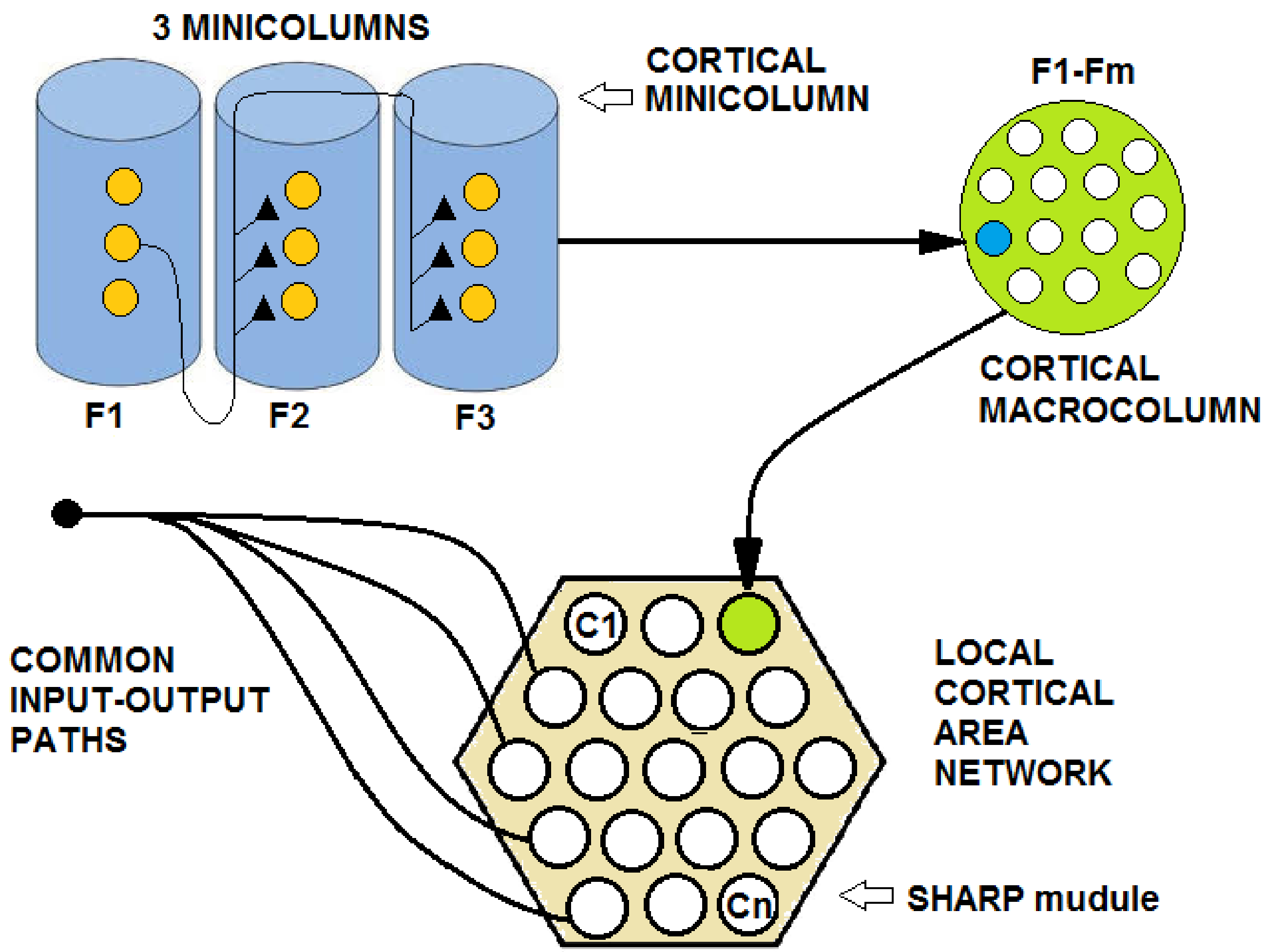

3 MINICOLUMNS
CORTICAL
MINICOLUMN
F1-Fm
F1
F2
F3
CORTICAL
MACROCOLUMN
COMMON
INPUT-OUTPUT
PATHS
C1
Cn
LOCAL
CORTICAL
AREA
NETWORK
SHARP mudule

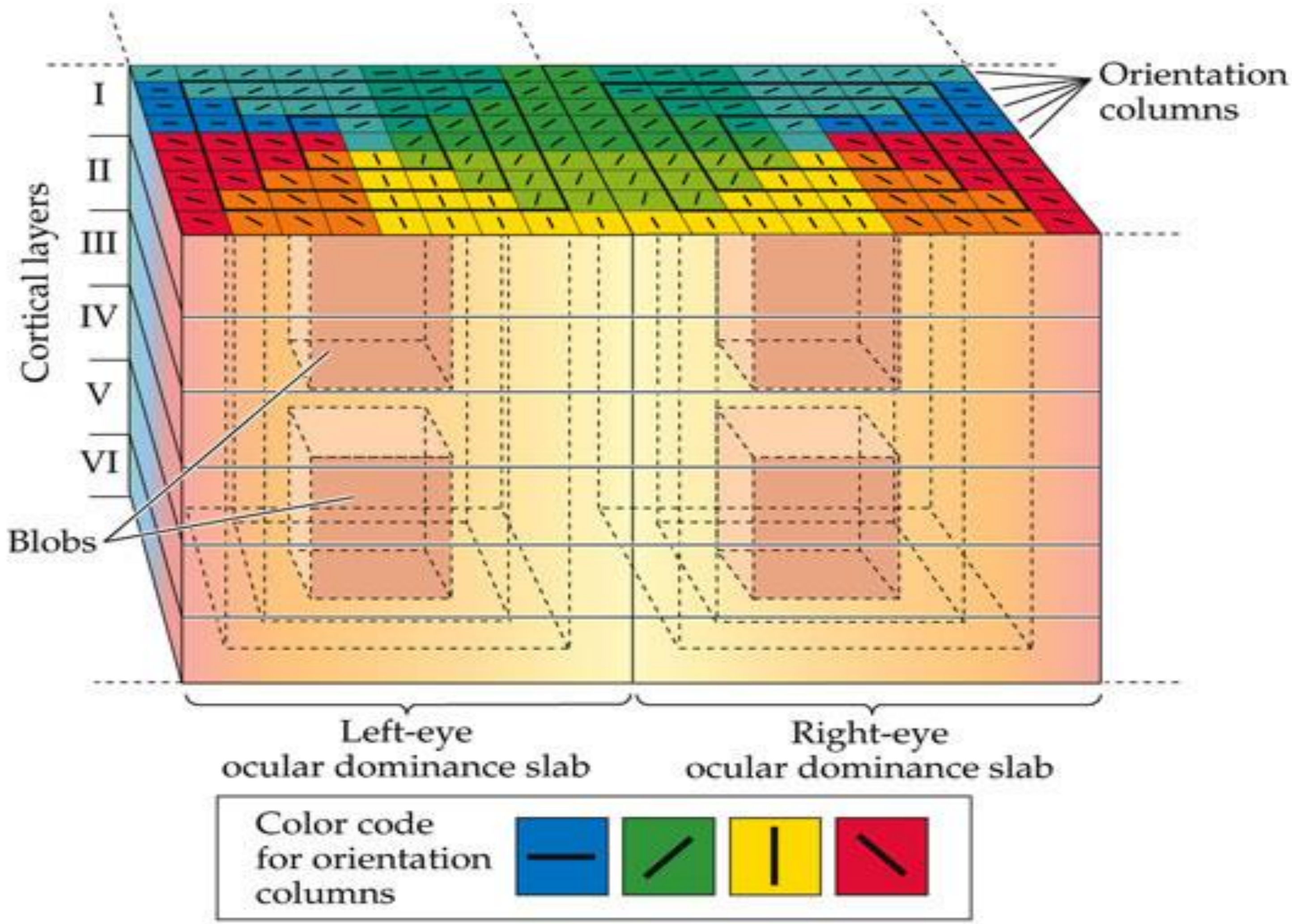
Figure: Hypothetical minicolumnar circuit. Panels A-E depict critical events transpiring in a single minicolumn at five points in time during the CSA's computational cycle, which I propose corresponds to one gamma cycle: approximate timings relative to start of CSA cycle are shown across top. The units labeled "C" ("B") represent the local chandelier (basket cell) populations, respectively; See paper for detailed explanation. Gerard (Rod) Rinkus,



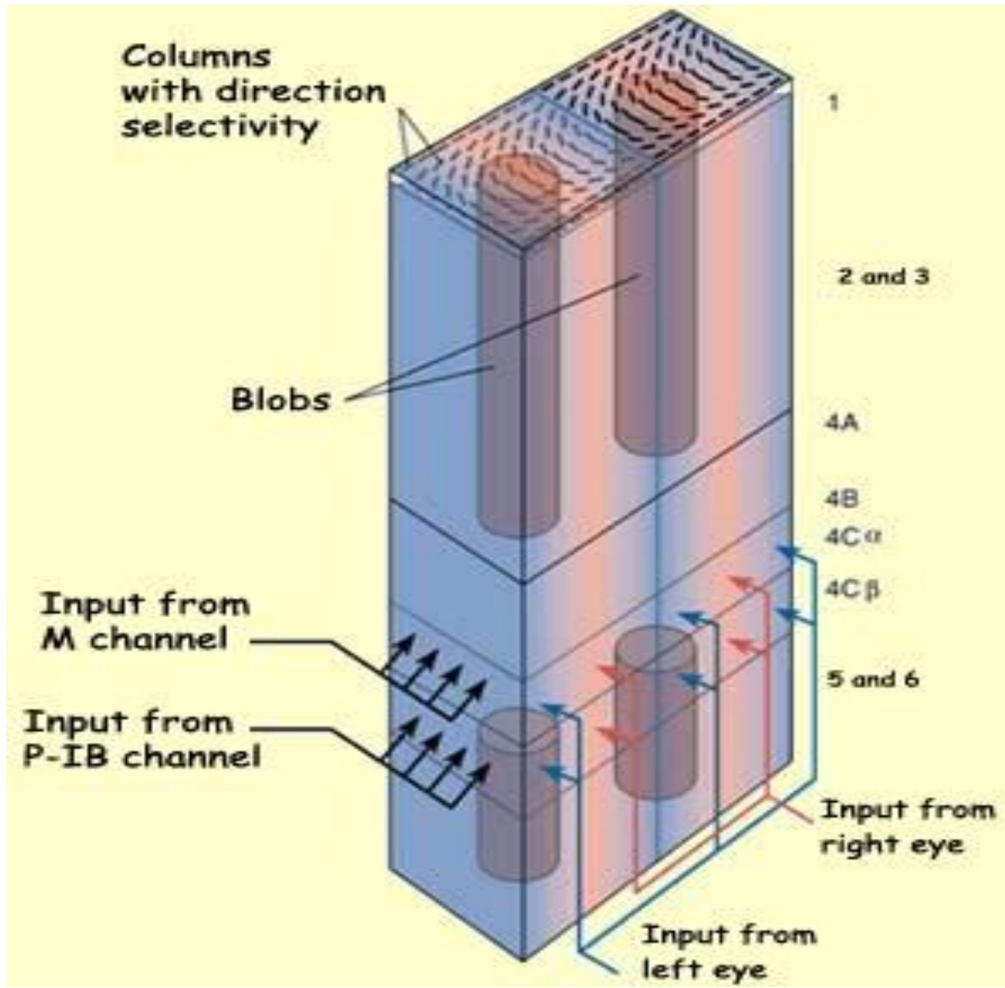


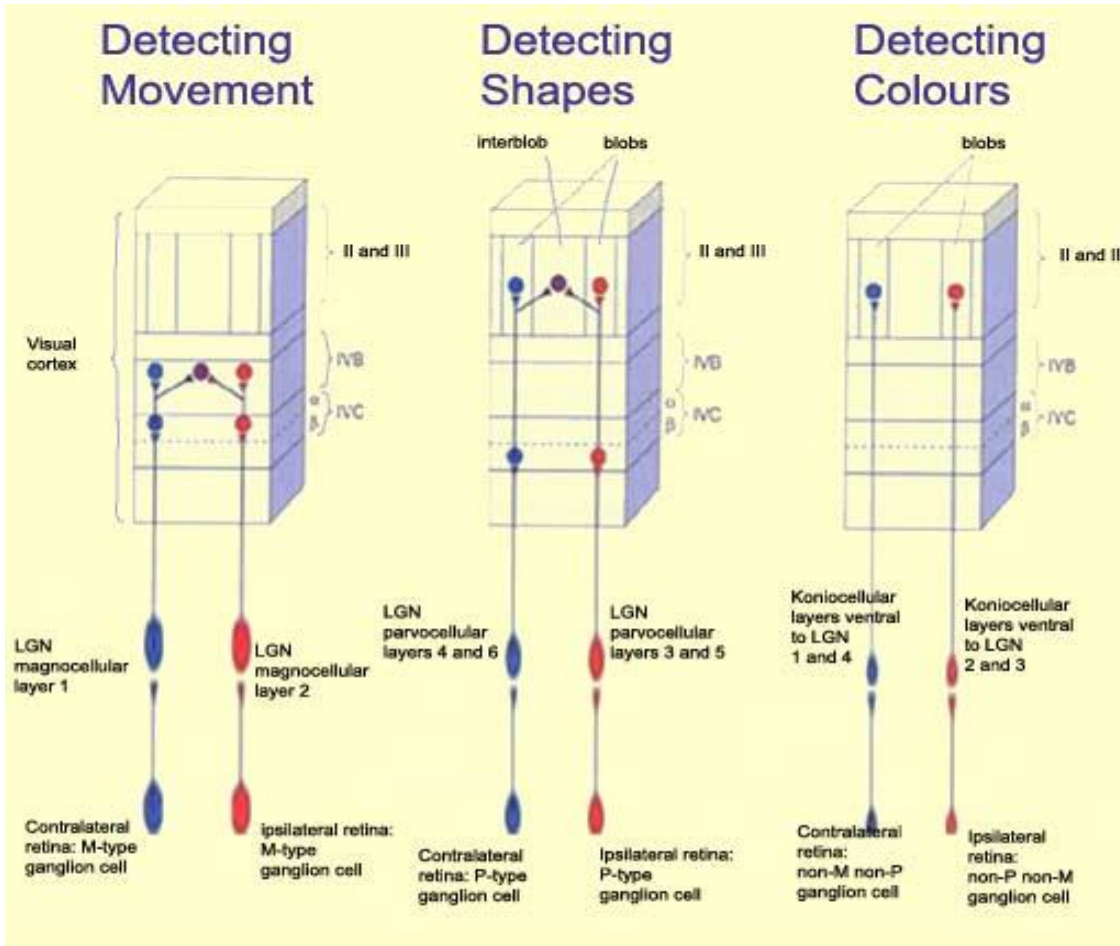
A Layers Minicolumn
B Cerebral Cortex
L 1
L 2
L 3
L 4
L 5
L 6
500 um
Striatum
Globus Pallidus
Thalamus
N. Accumbens
Subthalamus
Substantia Nigra
VTA


3 MINICOLUMNS
CORTICAL MINICOLUMN
F1-Fm
F1
F2
F3
CORTICAL MACROCOLUMN
COMMON INPUT-OUTPUT PATHS
C1
Cn
LOCAL CORTICAL AREA NETWORK
SHARP mudule

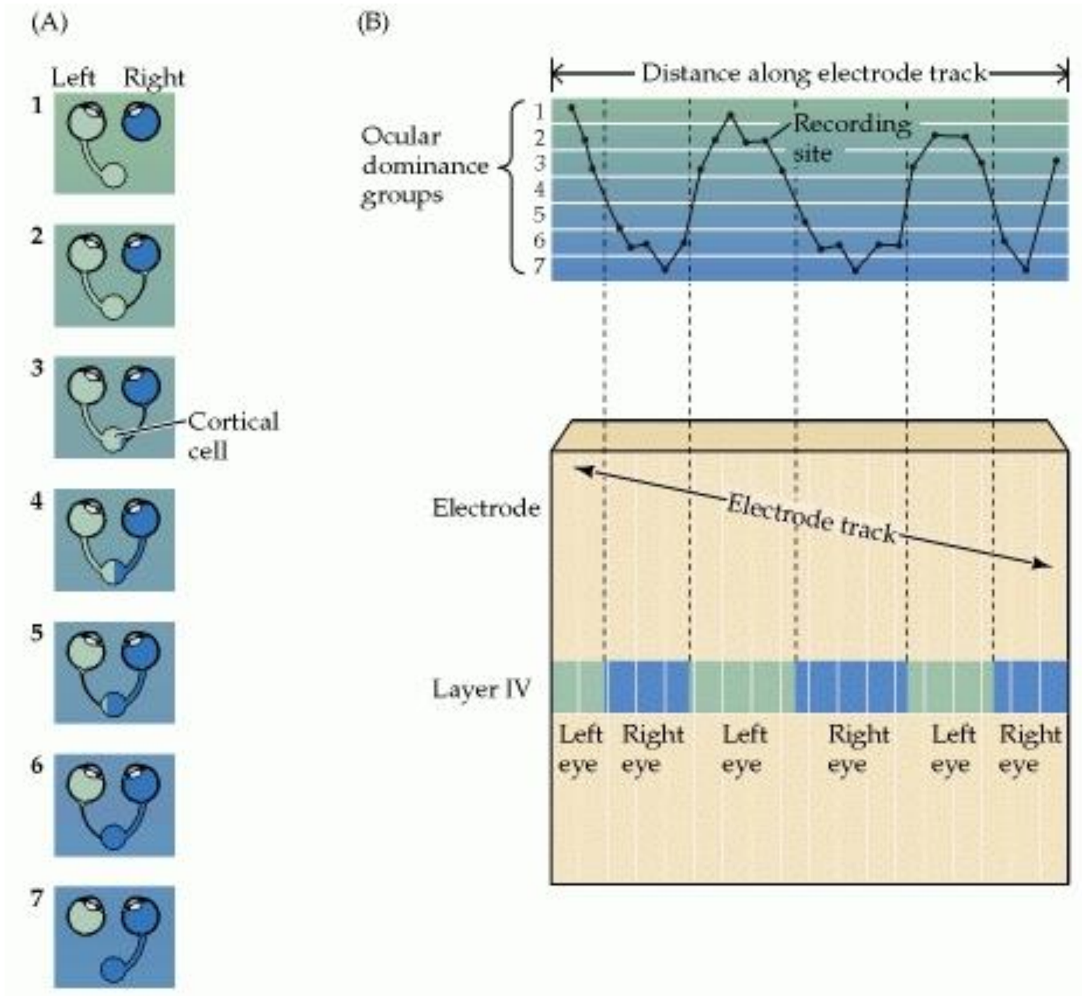


Orientation columns
I
II
III
IV
V
VI
Cortical layers
Blobs
Left-eye ocular dominance slab
Right-eye ocular dominance slab
Color code for orientation columns

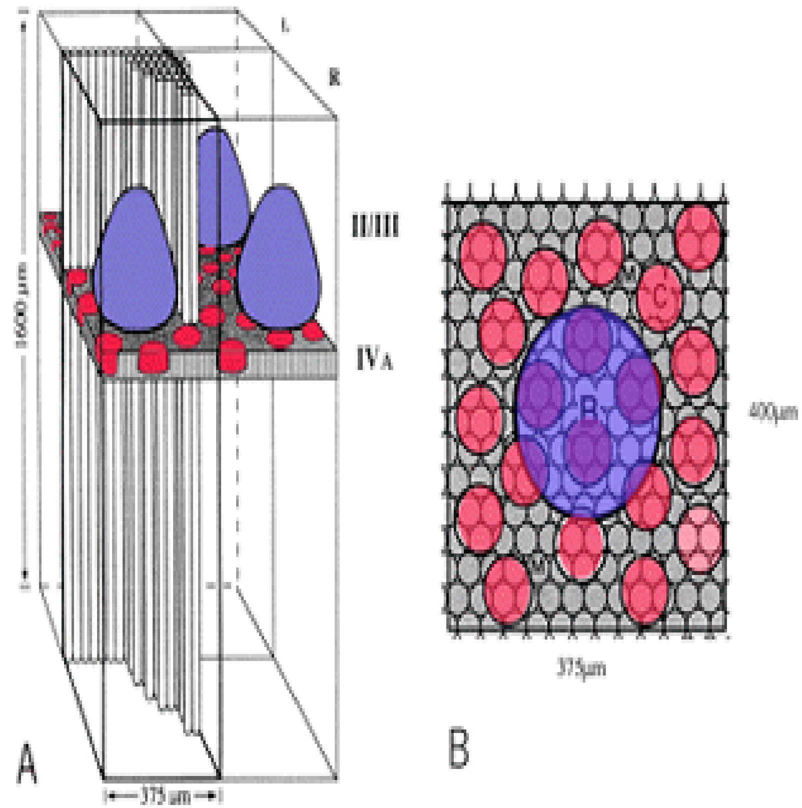

Columns
with direction
selectivity
Blobs
Input from
M channel
Input from
P-IB channel
1
2 and 3
4A
4B
4Cα
4Cβ
5 and 6
Input from
right eye
Input from
left eye



Detecting Movement
Detecting Shapes
Detecting Colours
interblob
blobs
blobs
II and III
II and III
II and III
Visual cortex
IVB
IVB
IVB
IVC
IVC
IVC
LGN magnocellular layer 1
LGN magnocellular layer 2
LGN parvocellular layers 4 and 6
LGN parvocellular layers 3 and 5
Koniocellular layers ventral to LGN 1 and 4
Koniocellular layers ventral to LGN 2 and 3
Contralateral retina: M-type ganglion cell
ipsilateral retina: M-type ganglion cell
Contralateral retina: P-type ganglion cell
Ipsilateral retina: P-type ganglion cell
Contralateral retina: non-M non-P ganglion cell
Ipsilateral retina: non-P non-M ganglion cell



(A)
Left
Right
1
2
3
Cortical cell
4
5
6
7
(B)
Distance along electrode track
Ocular dominance groups
1
2
3
4
5
6
7
Recording site
Electrode
Electrode track
Layer IV
Left eye
Right eye
Left eye
Right eye
Left eye
Right eye


L
R
II/III
IVA
1600 μm
375 μm
A
400μm
375μm
B

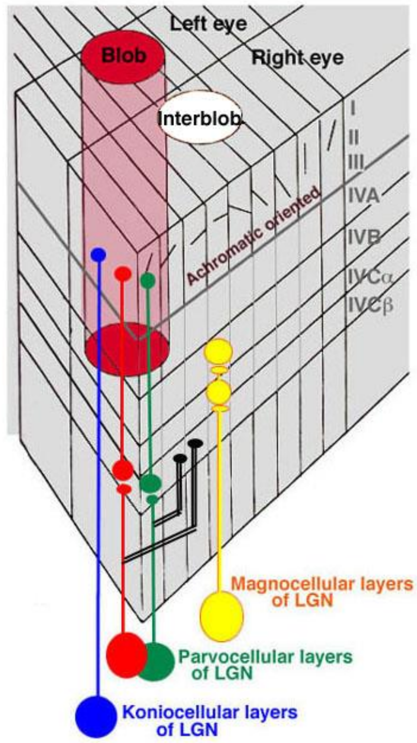


Fig. 24 shows where S cone on and off cells of the koniocellular layers and the four varieties of L and M midget-like cells of the parvo-cellular layers of the LGN target different layers of striate cortex. The midget system must project to both the achromatic interblob areas as well as the "blobs" involved in chromatic vision. The parasol cells from the magno-cellular layers of the LGN target a different layer than the previous cells.

Figure 27-19 Projection of input from the retina to the visual cortex.
A. Fibers from the lateral geniculate nucleus sweep around the lateral ventricle in the *optic radiation to reach the primary visual cortex. Fibers that relay inputs from the inferior half of the retina loop rostrally around the temporal horn of the lateral ventricle, forming Meyer's loop. (Adapted from Brodal 1981.)*
B. A cross section through the primary visual cortex in the occipital lobe. Fibers that relay input from the inferior half of the retina terminate in the inferior bank of the visual cortex, below the calcarine fissure. Those that relay input from the superior half of the retina terminate in the superior bank.

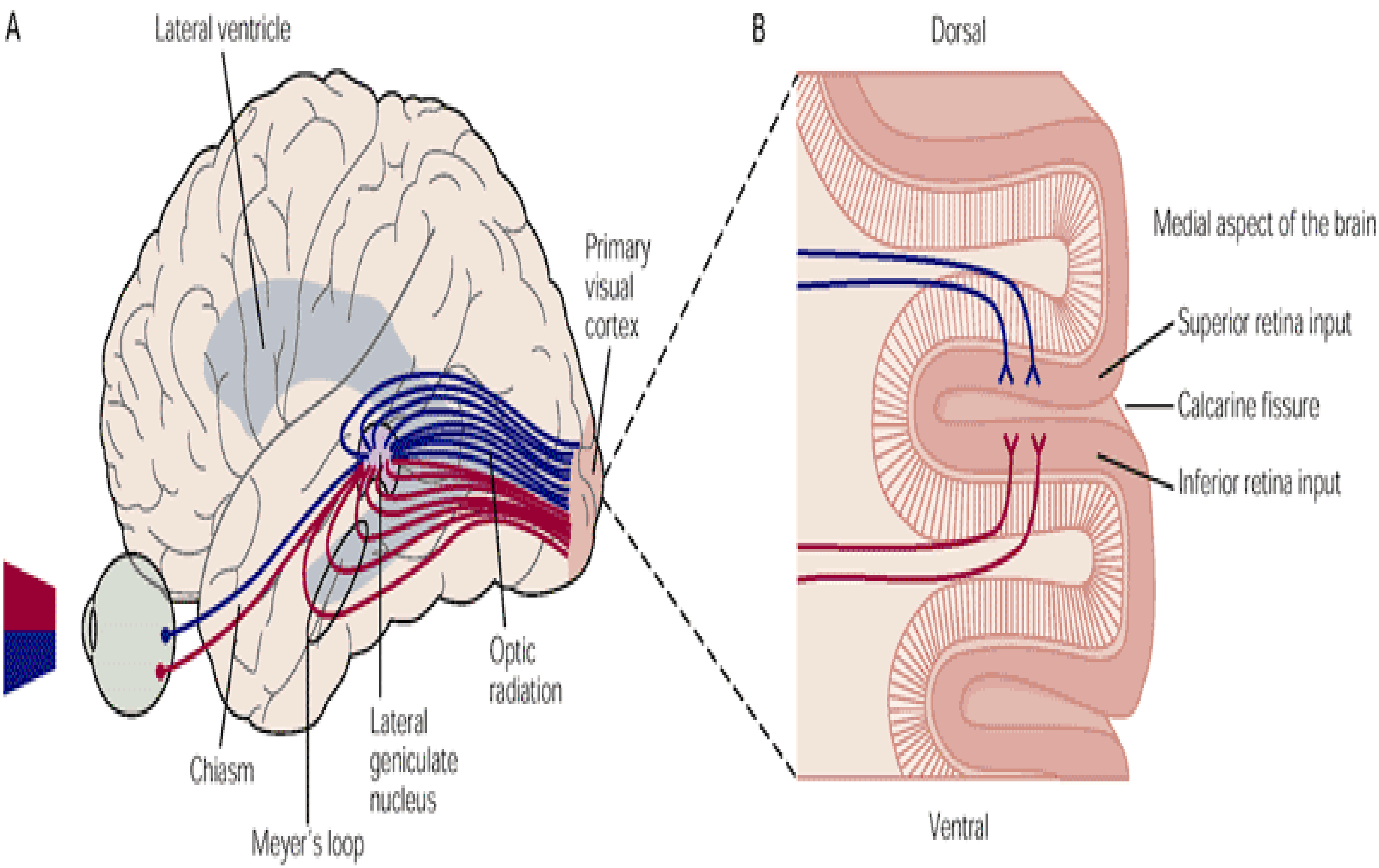


Figure 28-1 Organization of V1 and V2.
A. Subregions in V1 (area 17) and V2 (area 18). This section from the occipital lobe of a squirrel monkey at the border of areas 17 and 18 was reacted with cytochrome oxidase. The cytochrome oxidase stains the blobs in V1 and the thick and thin stripes in V2. (Courtesy of M. Livingstone.)
B. Connections between V1 and V2. The blobs in V1 connect primarily to the thin stripes in V2, while the interblobs in V1 connect to interstripes in V2. Layer 4B projects to the thick stripes in V2 and to the middle temporal area (MT). Both thin and interstripes project to V4. Thick stripes in V2 also project to MT.

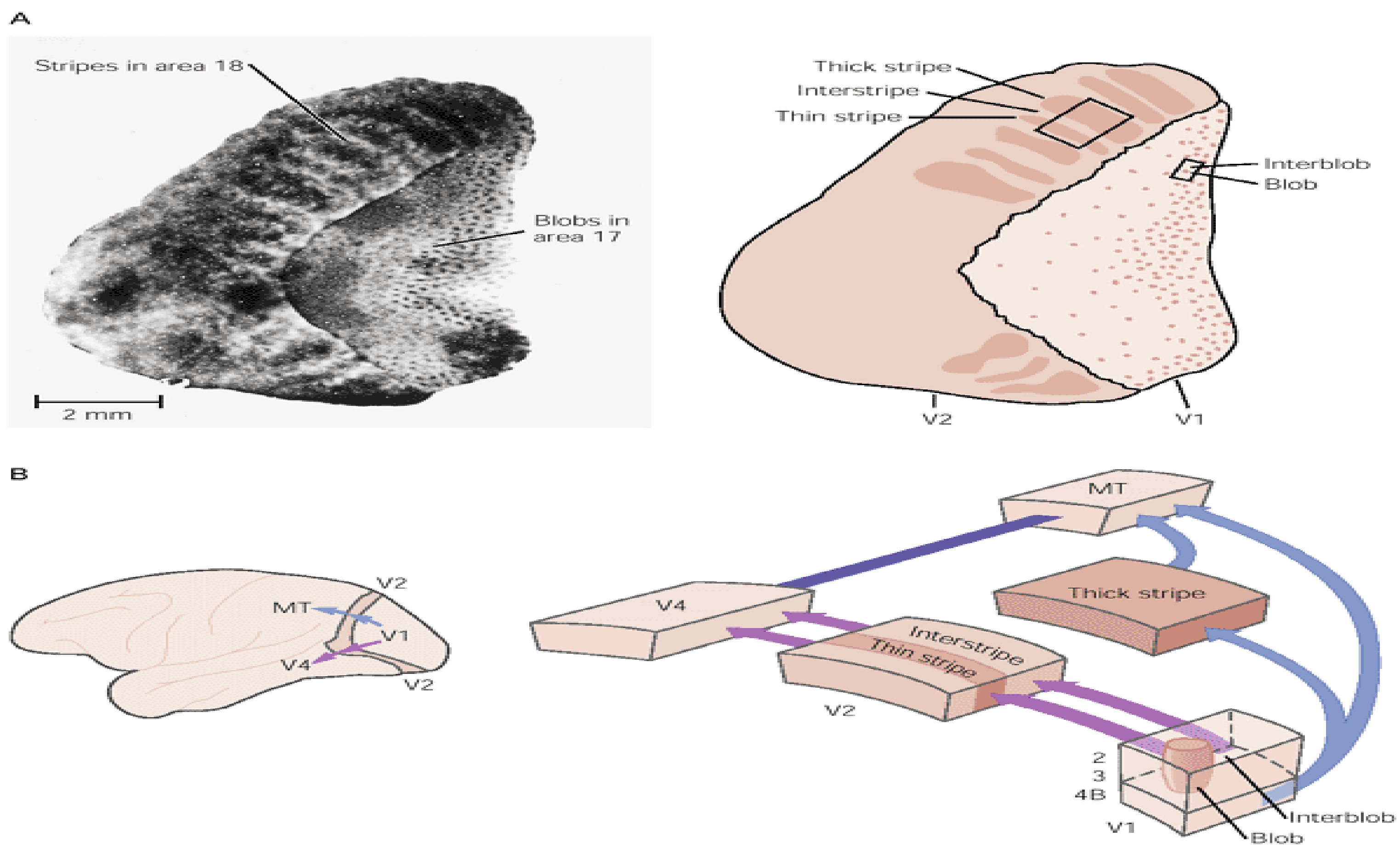
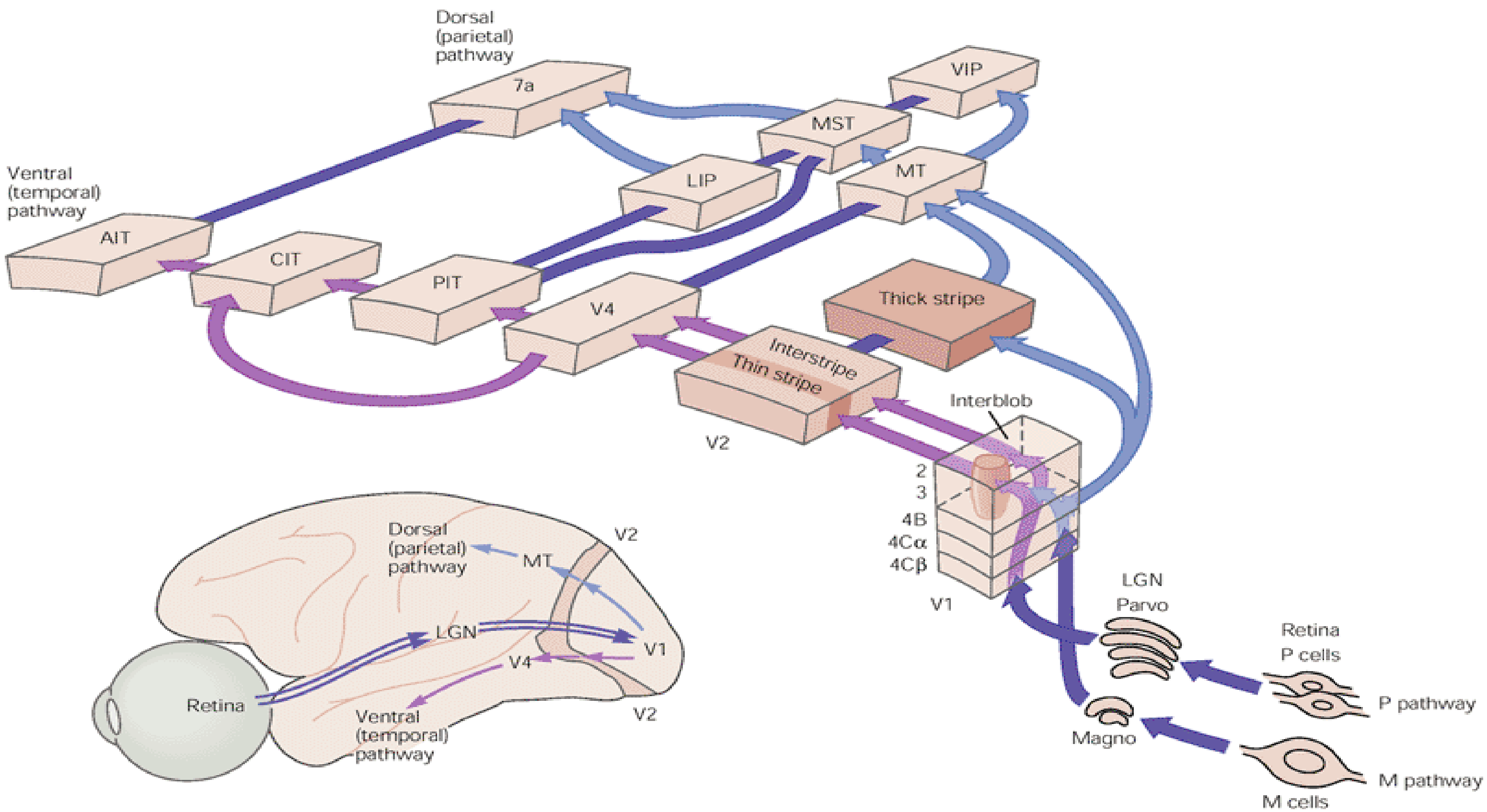
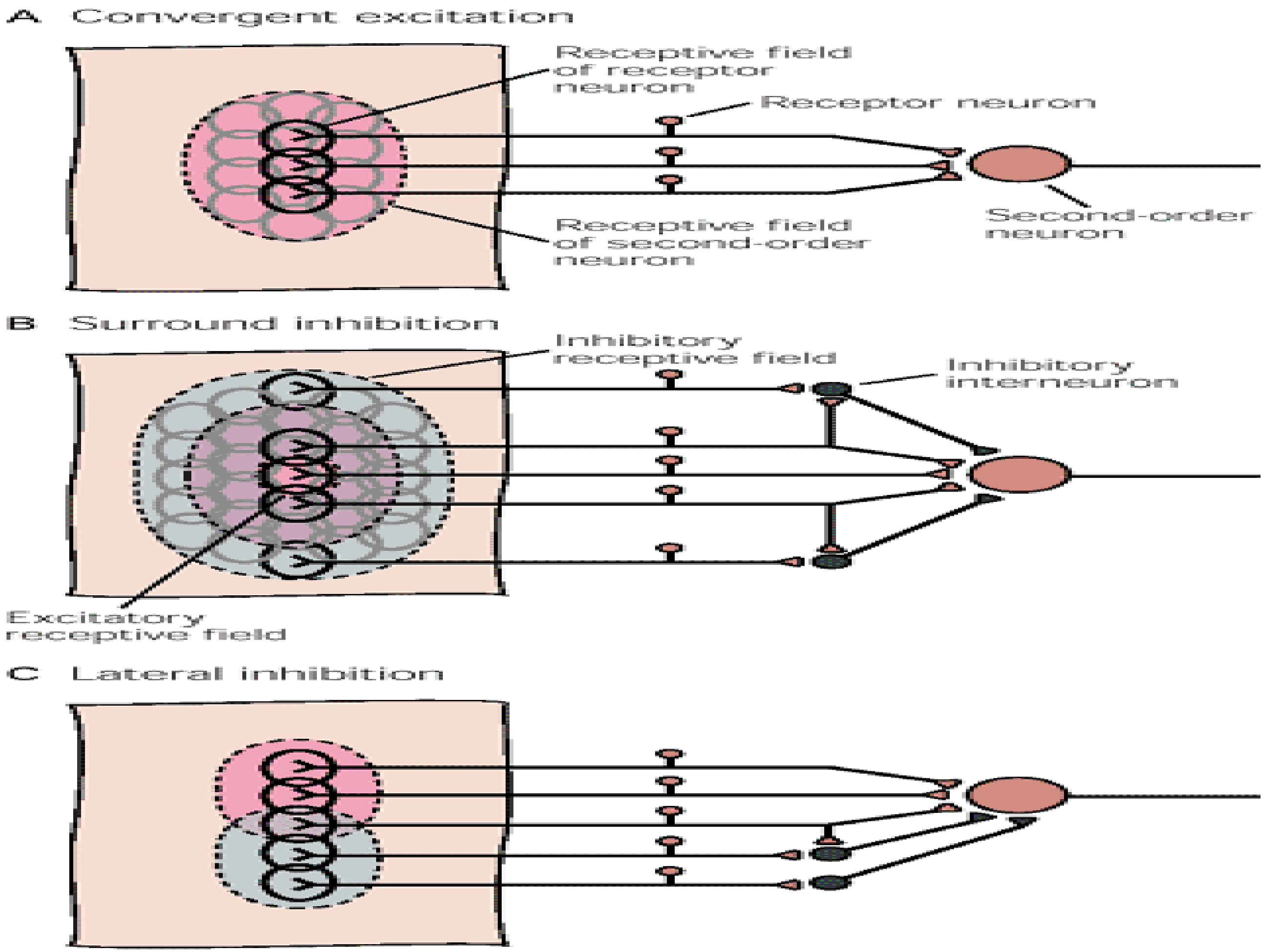


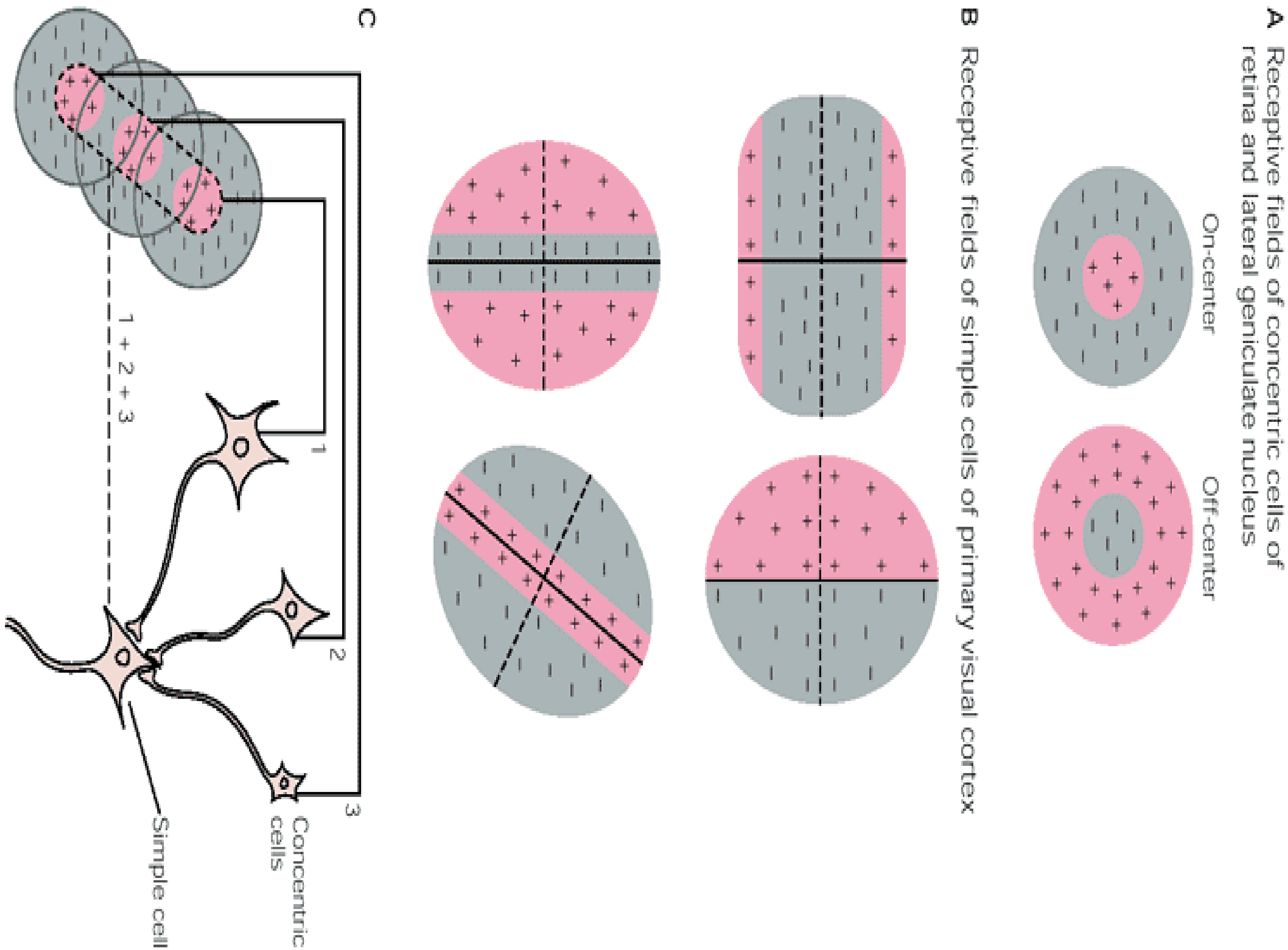
Figure 28-2 The magnocellular (M) and parvocellular (P) pathways from the retina project through the lateral geniculate nucleus (LGN) to V1. Separate pathways to the temporal and parietal cortices course through the extrastriate cortex beginning in V2. The connections shown in the figure are based on established anatomical connections, but only selected connections are shown and many cortical areas are omitted (compare Figure 25-9). Note the cross connections between the two pathways in several cortical areas. The parietal pathway receives input from the M pathway but only the temporal pathway receives input from both the M and P pathways. (Abbreviations: AIT = anterior inferior temporal area; CIT = central inferior temporal area; LIP = lateral intraparietal area; Magno = magnocellular layers of the lateral geniculate nucleus; MST = medial superior temporal area; MT = middle temporal area; Parvo = parvocellular layers of the lateral geniculate nucleus; PIT = posterior inferior temporal area; VIP = ventral intraparietal area.) (Based on Merigan and Maunsell 1993.)



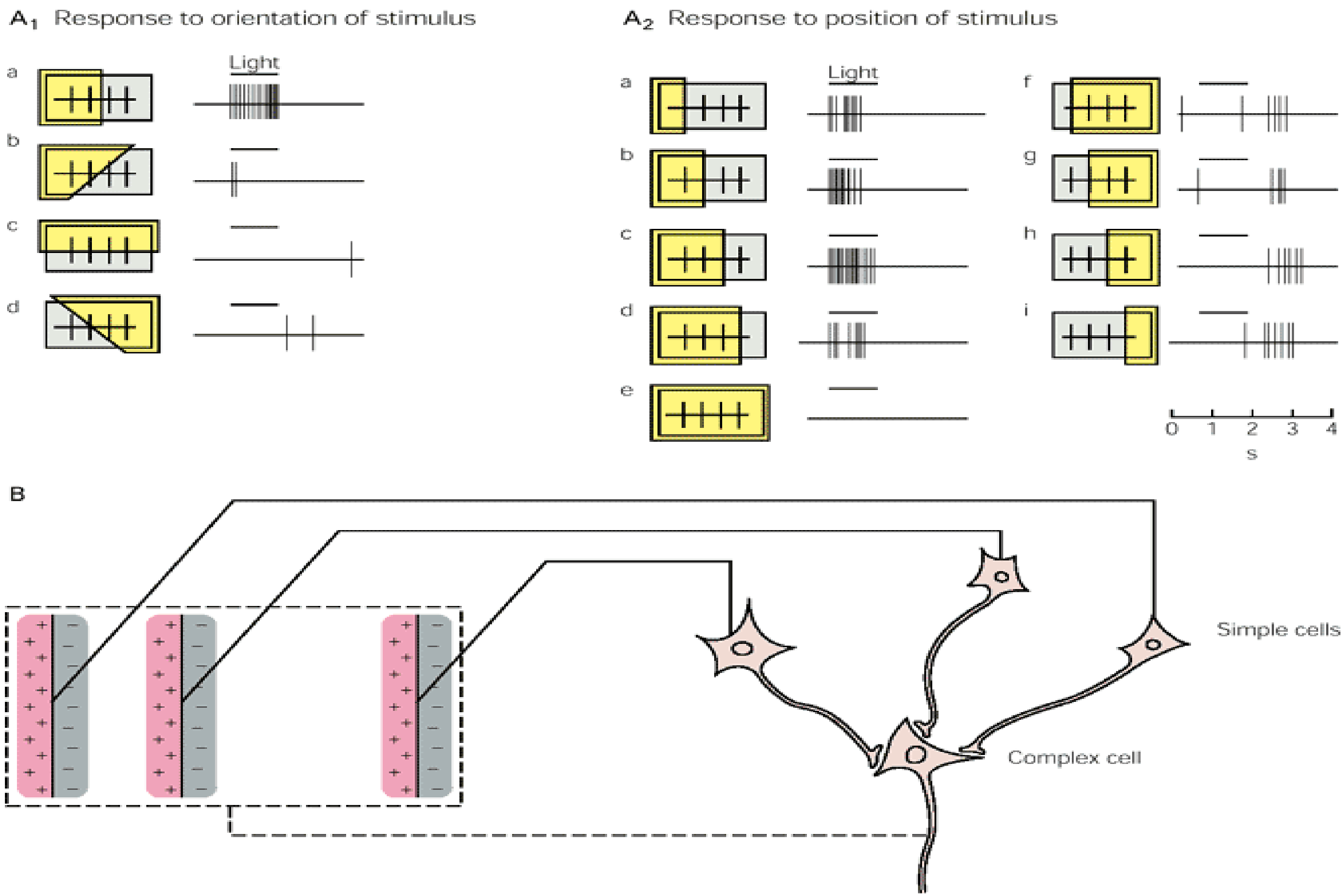
The receptive field of a higher-order neuron in the dorsal column nuclei has a characteristic pattern of excitation and inhibition that increases spatial resolution



The receptive fields of simple cells in the primary visual cortex are different and more varied than those of the neurons in the retina and lateral geniculate nucleus



The receptive field of a complex cell in the primary visual cortex has no clearly excitatory or inhibitory zones



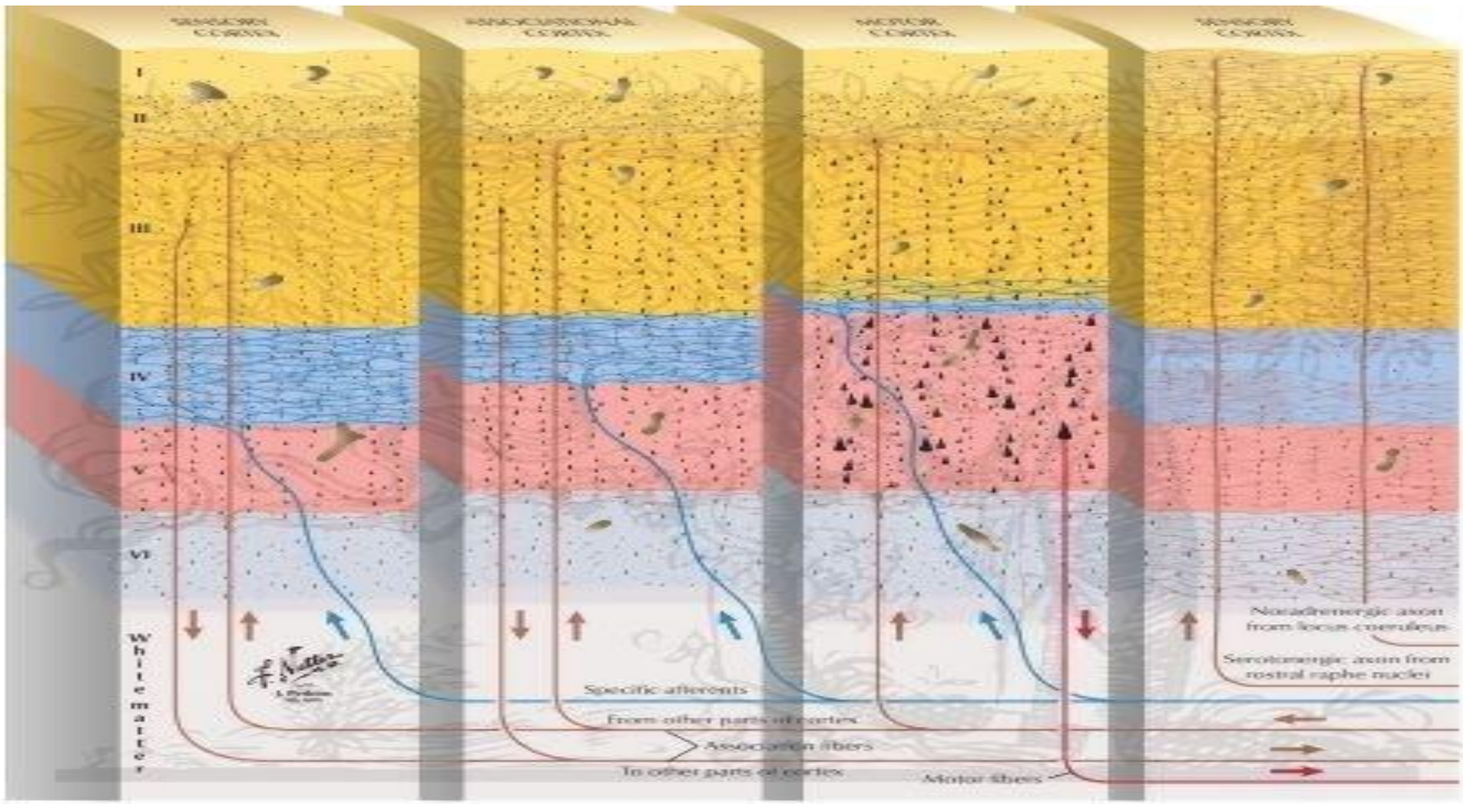

I
II
III
IV
V
VI
White matter
Specific afferents
Association fibers
To other parts of cortex
Motor fibers
Noradrenergic axon from locus coeruleus
Serotonergic axon from rostral raphe nuclei

Figure 1 | Connectional building blocks: feedforward (FF), feedback (FB), and intrinsic (int) connections. (A) Feedforward (red) and intrinsic (blue arrow) connections are both modular ("columnar"). Pyramidal neurons postsynaptic to feedforward connections presumably are themselves interconnected, but how these extrinsic and intrinsic connections interact is poorly understood. Feedback connections (green) are typically divergent, presumably crossing over a territory corresponding to multiple columns. Modified from Rockland and Drash (1996). Ad=apical dendrite; ig=infragranular. (B) Pyramidal neuron in layer 2 of rat visual cortex (intracellularly filled with biocytin *in vitro*). *Arrowhead indicates descending axon (truncated in the slice preparation), and vertical arrow points to distal part of an intrinsic axon collateral in layer 2, 600 μm from the cell body (courtesy of Dr. Tohru Kurotani). Scale bar = 100 μm.*

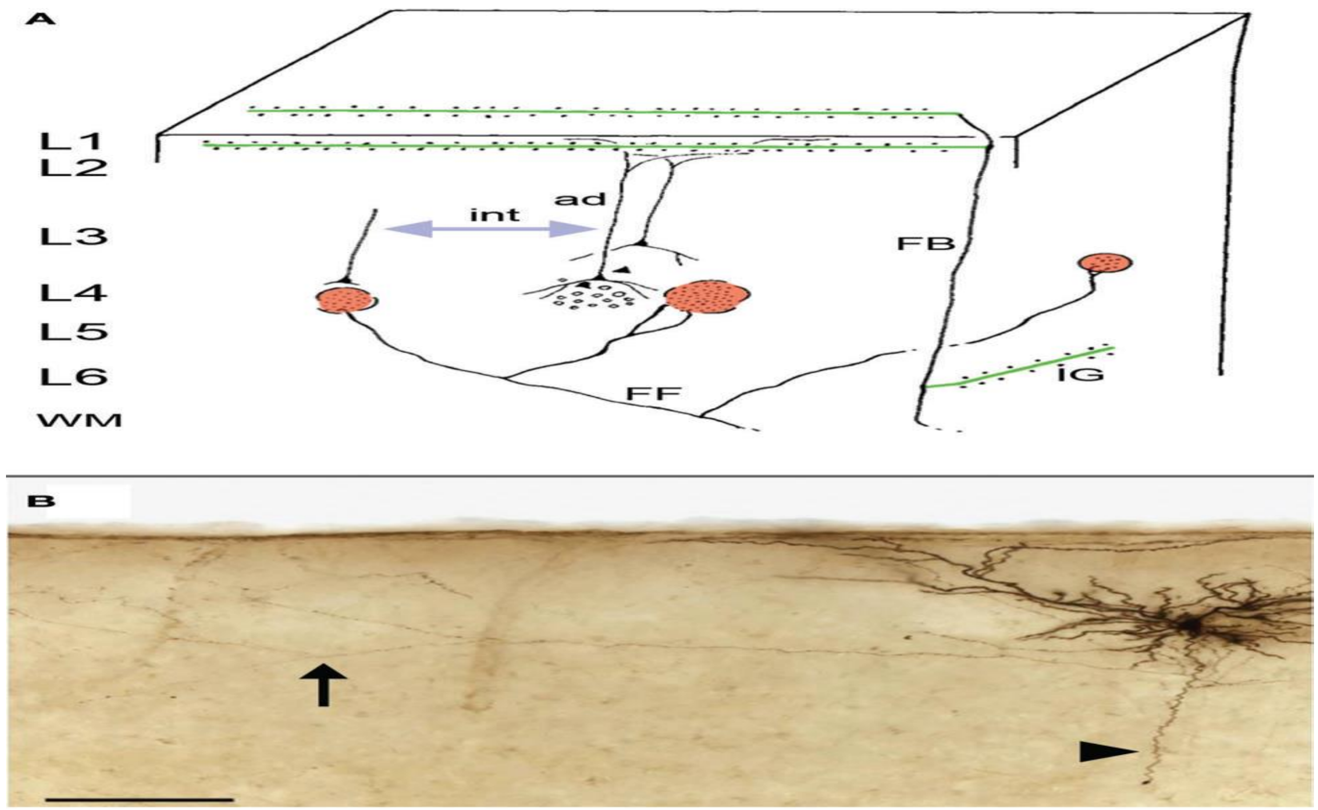


Figure 2 | Columns are not solid structures. (A) Cell stain of layer 4 and adjacent layer 3 (macaque temporal association cortex; coronal section). Three distinct cellular rows are apparent in layer 4 (arrows). However, these will be interpenetrated by dendritic and axonal neutrophil; for example, basal dendrites of layer 3 pyramidal neurons, as drawn schematically. (B) A large patch of neurons in anterior temporal cortex, retrogradely labeled by an injection of EGFP-adenovirus (immunoreacted for DAB) in posterior temporal cortex. A layer 2 neuron (horizontal arrow) has a laterally divergent apical dendrite (vertical arrow) extending over 250 µm from the soma. Scale bar = 40 µm in (A), 500 µm for (B), and 100 µm for inset.

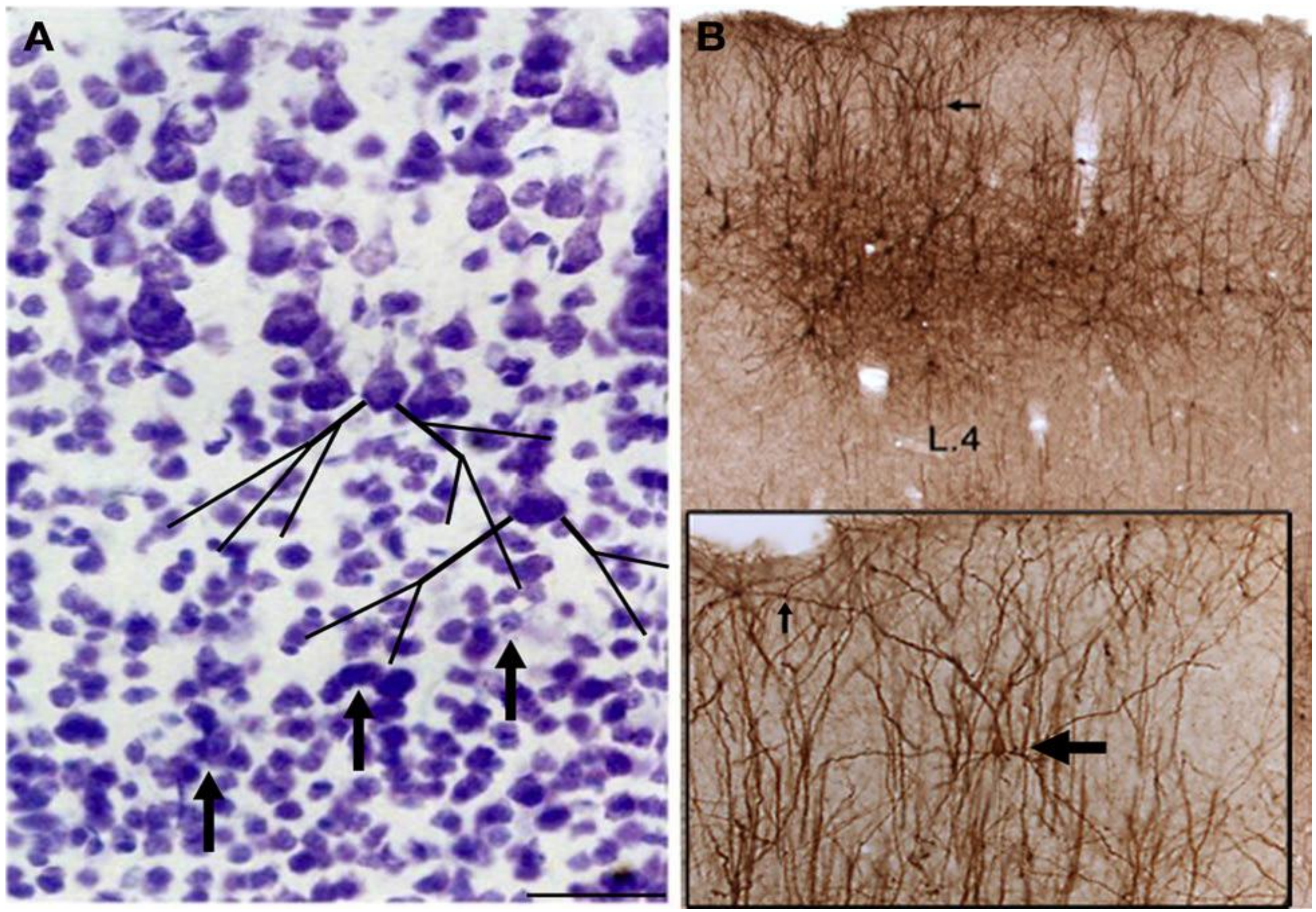


Figure 3 | Interdigitating systems. (A) Tangential section through monkey primary visual cortex, reacted for cytochrome oxidase (CO). Obvious patches correspond to thalamocortical terminations. (B) Adjacent section reacted for synaptic zinc, where patches correspond to a subset of corticocortical terminations. The top of the photo is cut tangential through layer 4A. The zinc-positive patches are complementary to the CO-patches in layer 3 (see arrows), and layer 4A. (C) Coronal section through the posterior orbitofrontal cortex of macaque, where MAP2 immunohistochemistry reveals distinct clusters of apical dendrites at the border of layers 1 and 2. These are likely to co-localize with zinc-positive terminations. (D) Higher magnification of C, where three dendritic clusters are indicated by arrowheads. (C) and (D) are modified from Figure 3 of Ichinohe and Rockland (2004). Scale bar in (C) = 1.0 mm, 160 μm for (D), and 600μm for (A) and (B).

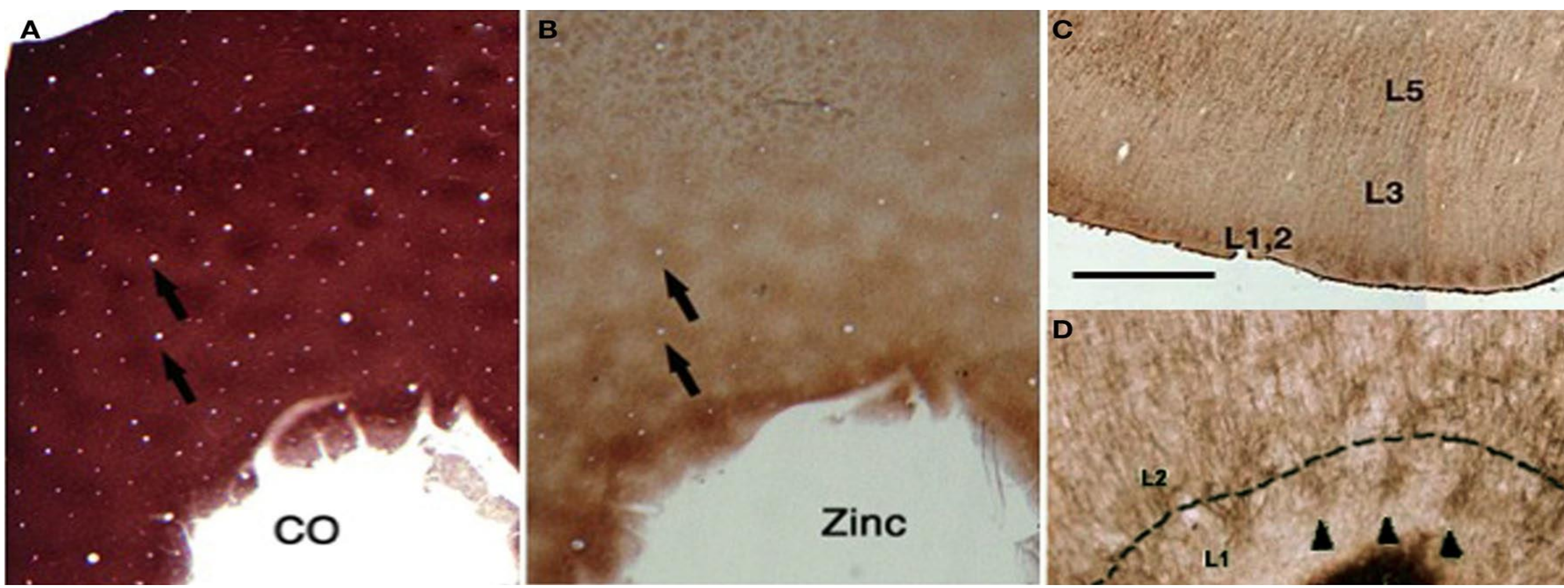


Figure 4 | Columns are part of distributed networks. (A) Top: Meynert cells in area V1 project to extrastriate area MT where they form multiple arbors in layers 4 and 6. One axon with five arbors (arb.) is illustrated. Large numbers = number of terminal specializations (boutons, b); and smaller numbers indicate individual tissue sections, where larger numbers are more anterior. Bottom: The same neurons form extensive intrinsic connections within area V1. For this neuron, four extended collaterals (I–IV) were identified. The anterior–posterior position of three coronal sections is indicated by lines on the schematic of the posterior half of the cerebral hemisphere, and the approximate position of the collaterals is indicated by I–IV. A BDA injection site is indicated by the shaded oval. Terminal specializations in MT are illustrated in the inset. Modified from Figure 1 of Rockland (2002). (B) A neuron anterogradely labeled by an injection of PHA-L in macaque area TEav has four arbors in adjoining parts of area 36, and two additional arbors in the amygdala. Arbors were followed to denser projection patches (color-coded in selected coronal sections) in different sections. Sections correspond to the numbered lines on the schematic of the monkey hemisphere. **Modified from Figure 12 of Cheng et al. (1997).**

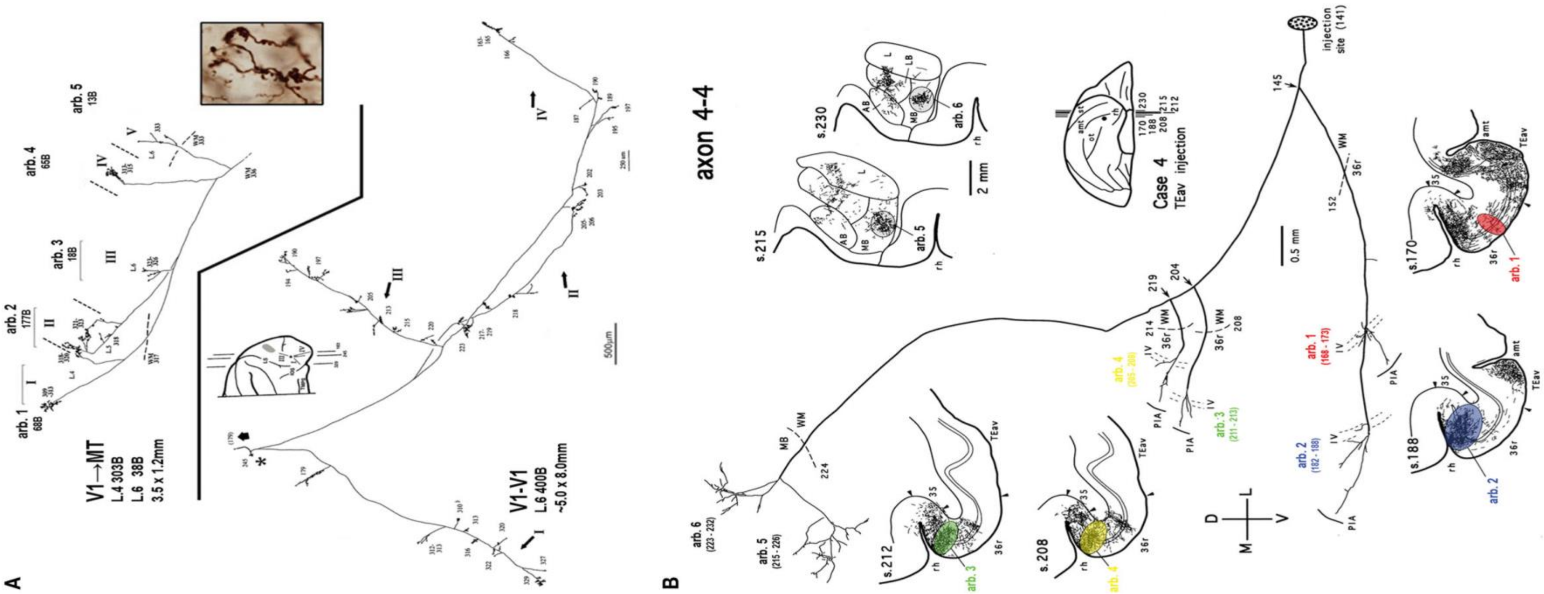


Figure 5 | Distributed terminations shown by retrograde tracers. (A) Small injections of two retrograde tracers in monkey temporal cortex result in large patches of red or green projection neurons, which converge to the respective injection sites. (B) Schematic of the monkey right hemisphere with the two injections (cholera toxin subunit B conjugated with alexa 488 (green fluorescence) or alexa 555 (red fluorescence). The line indicates the level of the coronal section illustrated in (A). (C) Small clusters occur where single-colored neurons are intermixed and where there are also double-labeled neurons. (D) The interpretation, consistent with analysis of anterogradely labeled single axons, is that neurons have branched arbors. Three neurons are represented schematically by colored triangles, and their branched axons by corresponding colored lines. Only some of the arbors (solid lines) will be labeled by a given injection, while others will fall outside the injected area (dashed lines). Modified from Figure 5, Borra et al. (2010).

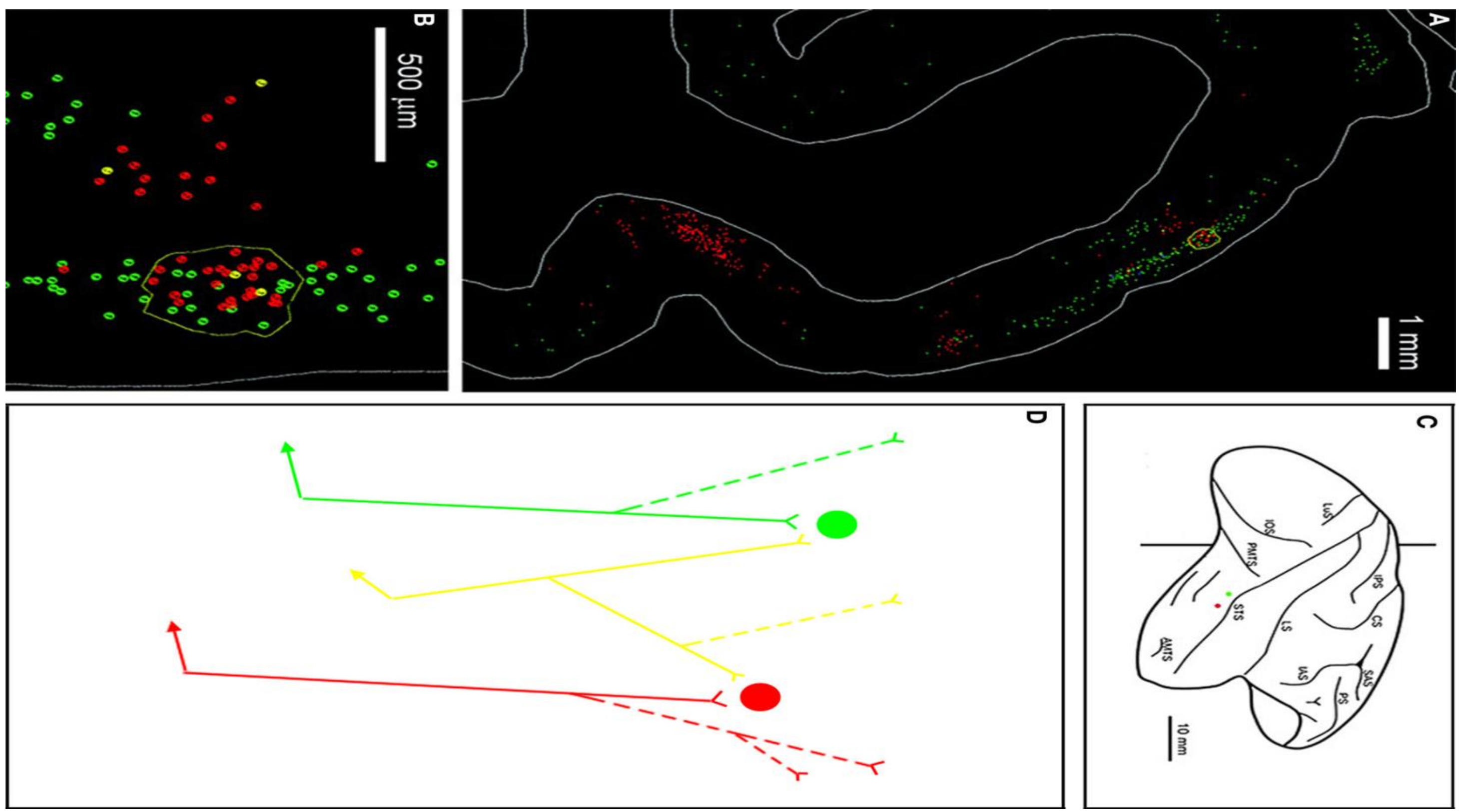


Figure 6 | Columns are not obligatory to all cortical areas. Nissl stains of three areas with low overall columnarity and accentuated layer 2. (A) Posterior orbitofrontal cortex in monkey. (B) Perirhinal cortex, adjacent to posterior entorhinal cortex. Entorhinal cortex (EC) is remarkable for conspicuous lamination, as well as cell islands in layer 2. Coronal section outlines at the right show the areas (arrows) from which the photos were taken. Modified from Figure 4, Ichinohe and Rockland (2004). AMT, anterior middle temporal sulcus; AON, anterior olfactory nucleus; OT, occipitotemporal; WM, white matter. Scale bars = 1 mm for photomicrographs, 5 mm for section outlines.

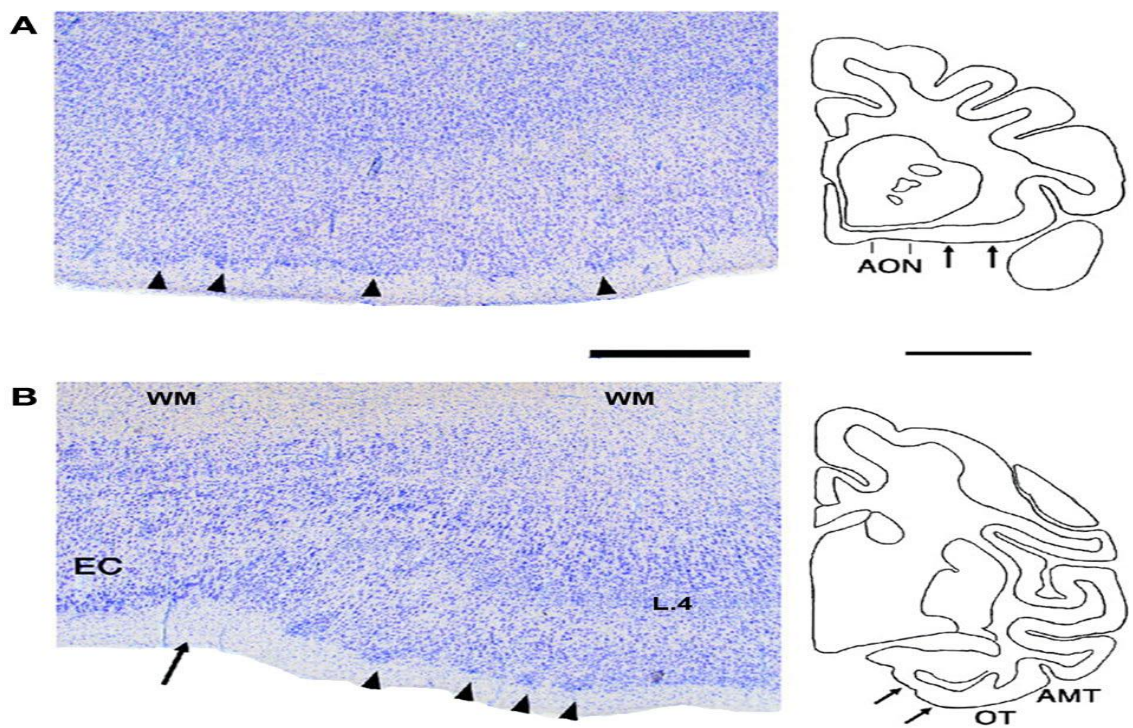


Figure 7 | Columns, as "modules", exist outside cerebral cortex. Three coronal sections (rat) to illustrate injection of WGA-HRP in visual cortex. This results (at right, tangential view of the superior colliculus) in a honeycomb pattern of cortical terminations (Oc2), which overlaps with a similar pattern shown by histochemistry for acetylcholinesterase (AChE). A, anterior; m, medial. Modified from Figure 1 from Mana and Chevalier, 2001. Scale bars = 1 mm for section outlines; 500 µm for tangential colliculus.

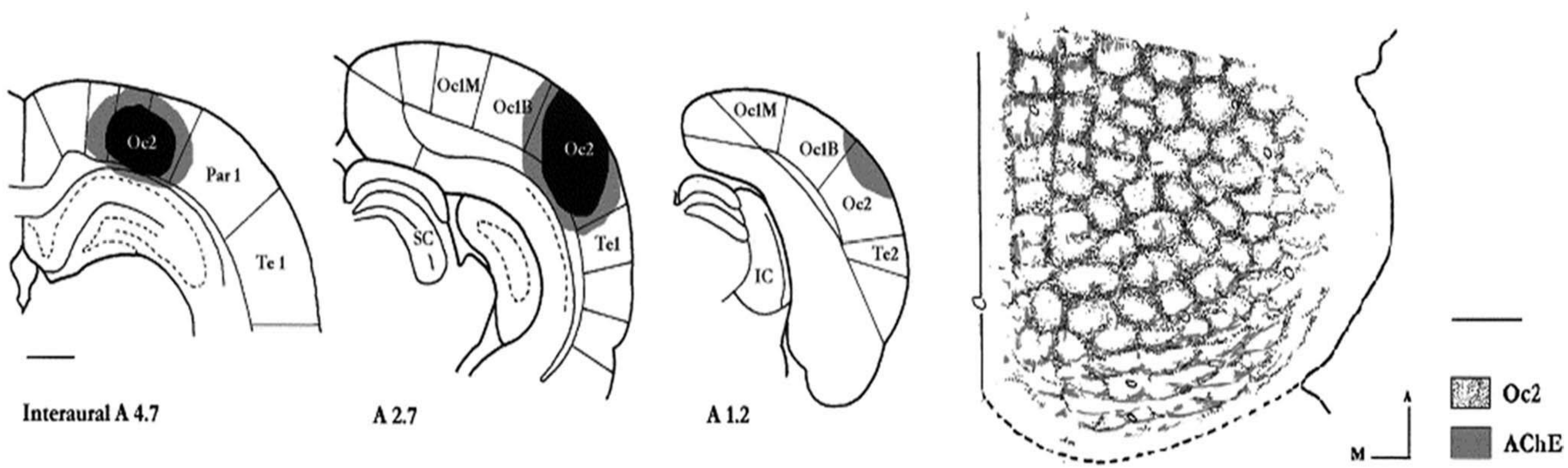
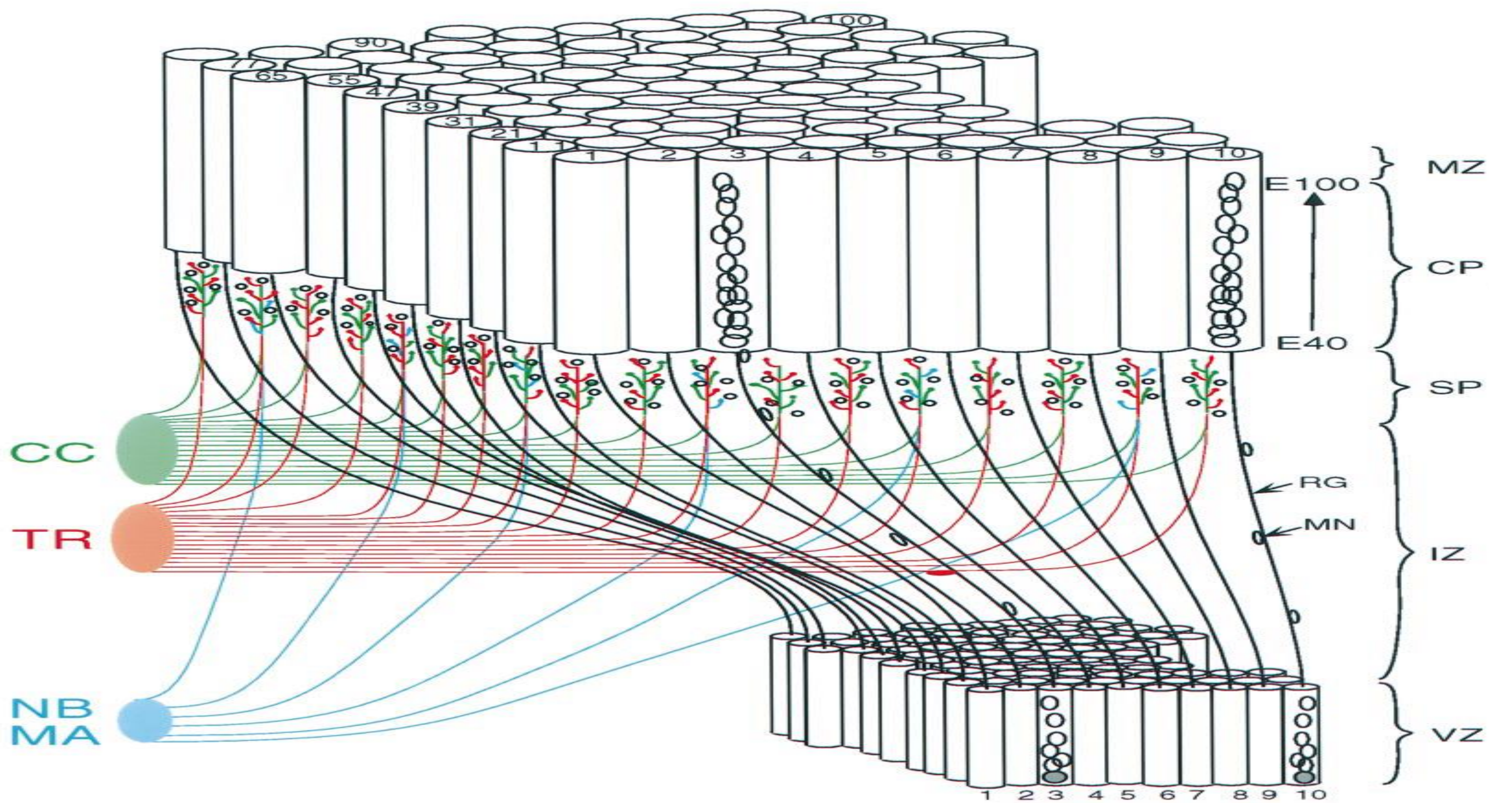
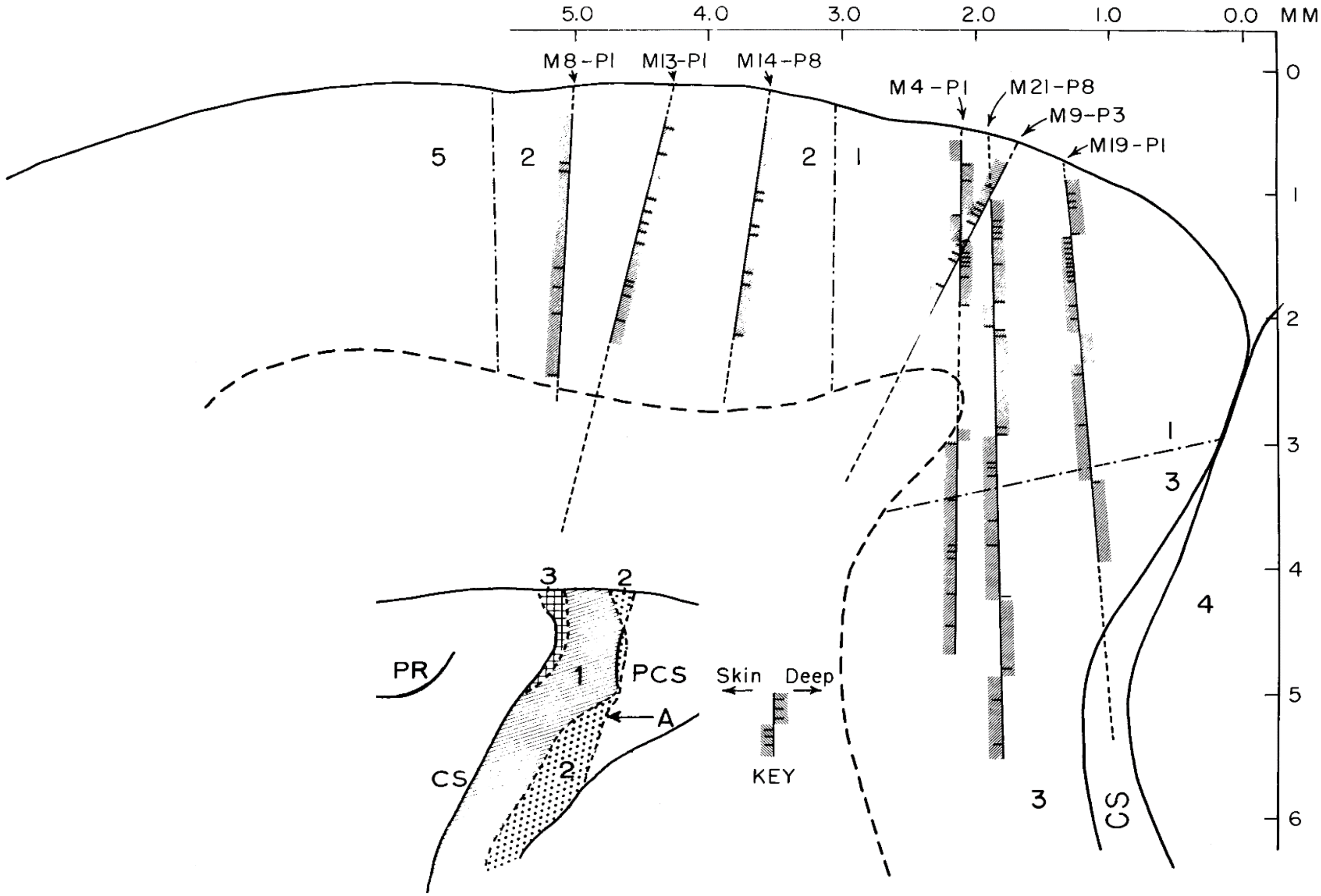
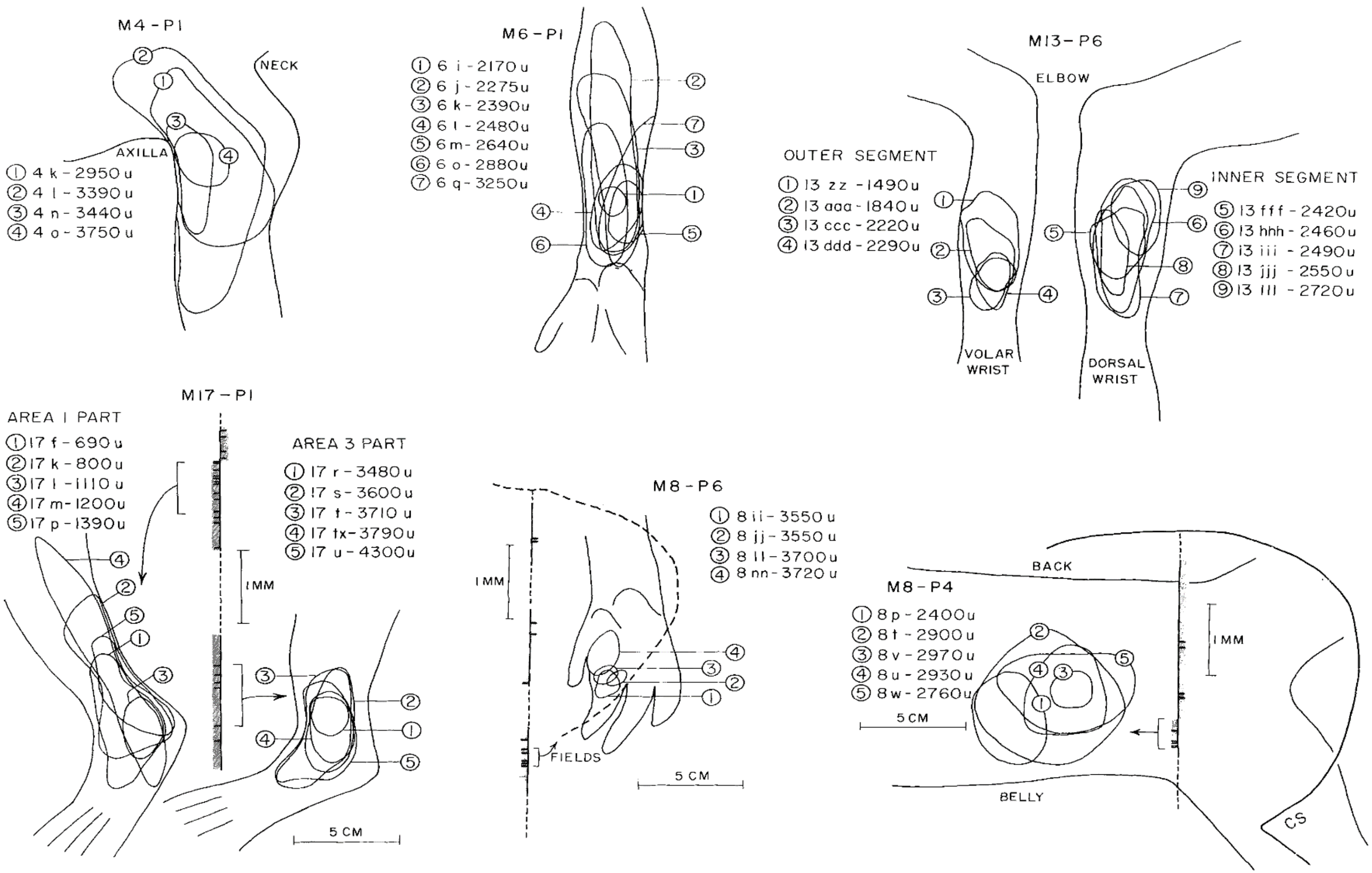


Fig A three-dimensional illustration of the developmental events occurring during early stages of corticognesis in the monkey. The drawing illustrates radial migration, the predominant mode of neuronal movement, which in primates underlies its columnar organization. After their last division, cohorts of migrating neurons (MN) traverse the intermediate zone (IZ) and the subplate (SP) where they may interact with afferents arriving sequentially from the nucleus basalis (NB), the monamine nuclei of the brainstem (MA), from the thalamic radiation (TR), and from several ipsilateral and contralateral corticocortical bundles (CC). Newly generated neurons bypass those generated earlier, which are situated in the deep cortical layers, and settle at the interface between the developing cortical plate (CP) and the marginal zone (MZ). Eventually they form a radial stack of cells that share a common site of origin but are generated at different times. Although some, presumably neurophilic, cells may detach from the cohort and move laterally, guided by an axonal bundle, most are gliophilic, have affinity for the glial surface, and obey the constraints imposed by transient radial glial (RG) cell scaffolding. This cellular arrangement preserves the relationship between the proliferative mosaic of the ventricular zone (VZ) and the corresponding map within the SP and CP, even though the cortical surface in primates shifts considerably during the massive cerebral growth in the mid-gestational period. The numerals refer to corresponding units in the VZ and CP. (From Rakic, 1995, with permission from Elsevier Siem Publishers.)

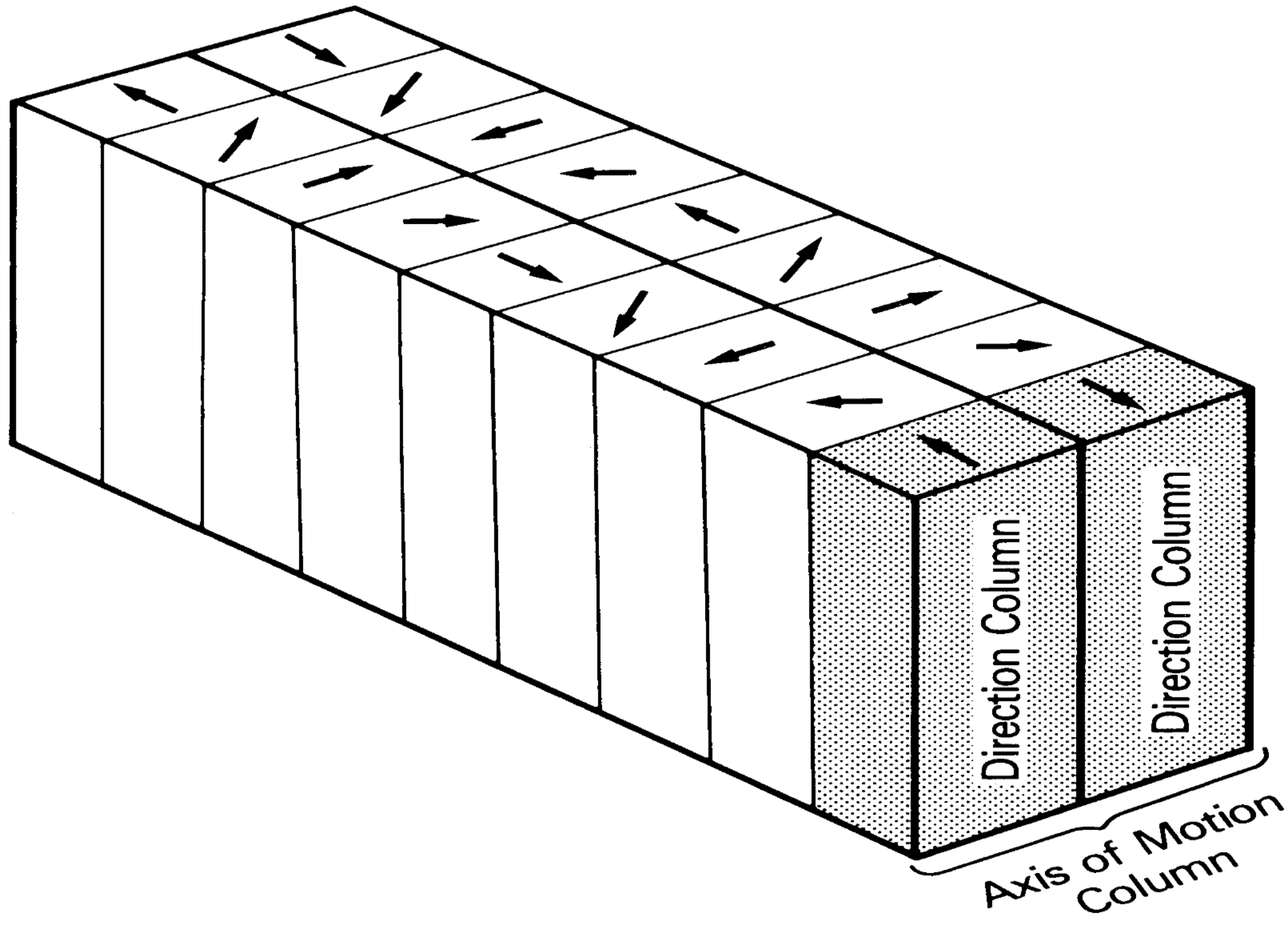




5.0
4.0
3.0
2.0
1.0
0.0
MM
0
1
2
3
4
5
6
M8-P1
M13-P1
M14-P8
M4-P1
M21-P8
M9-P3
M19-P1
5
2
2
1
1
3
4
3
CS
3
2
1
PR
PCS
A
CS
2
Skin
Deep
KEY

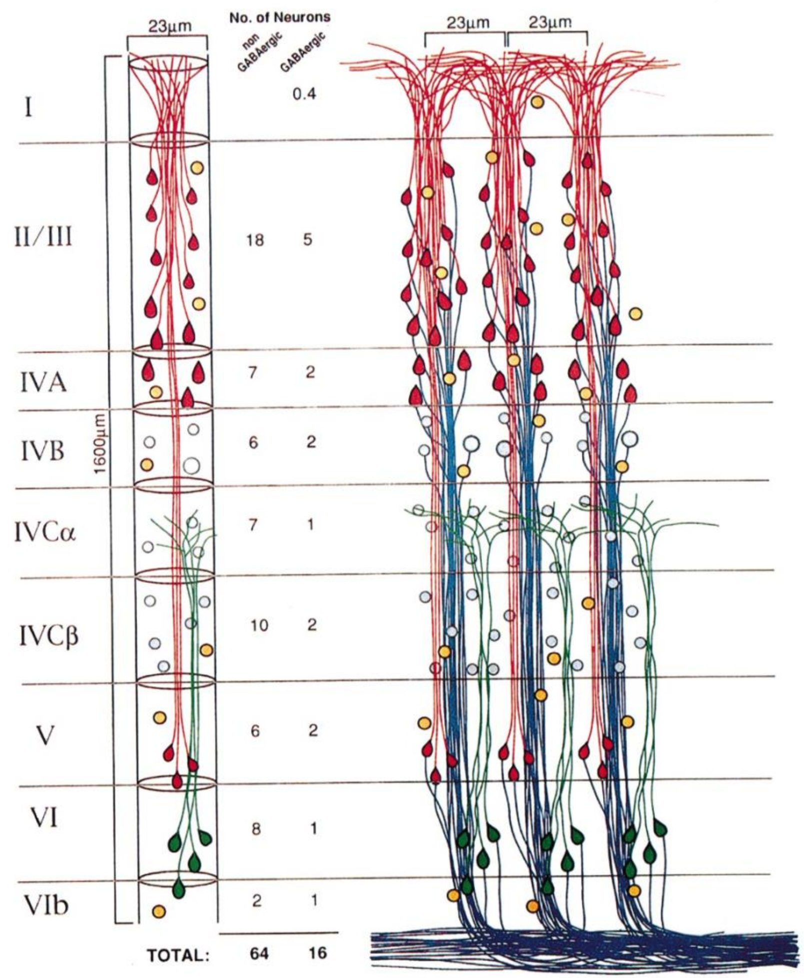


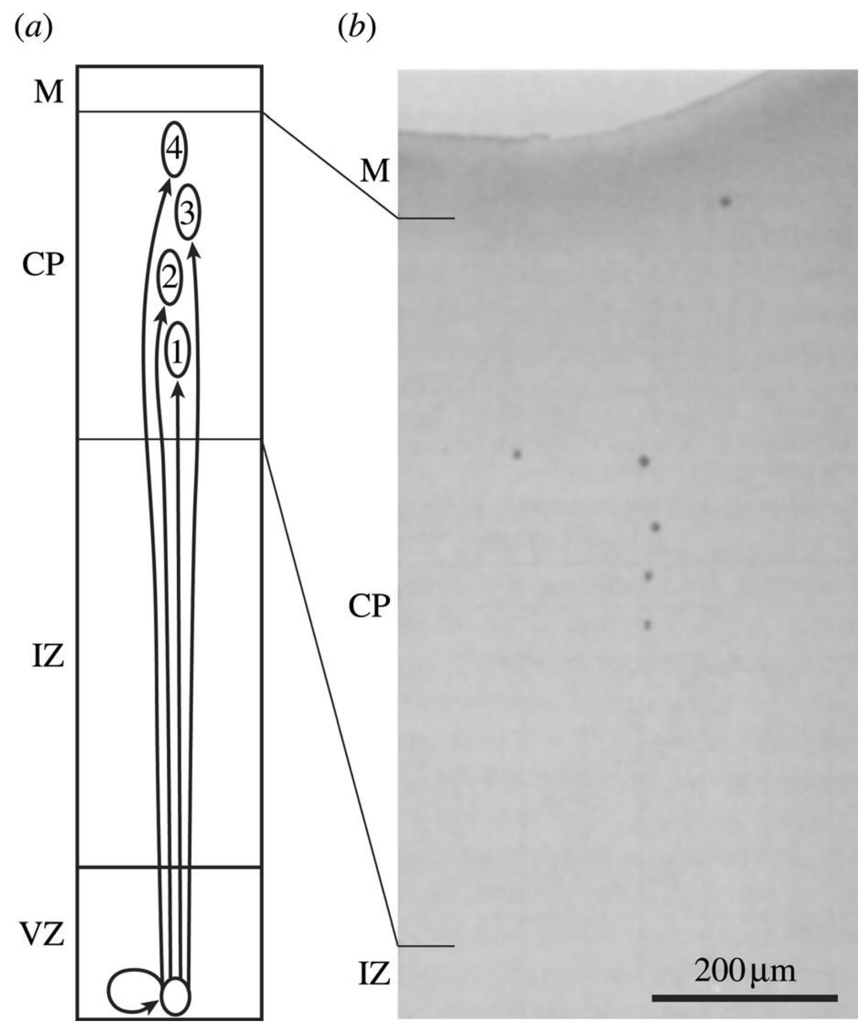
M4 - P1
NECK
AXILLA
① 4 k - 2950 u
② 4 l - 3390 u
③ 4 n - 3440 u
④ 4 o - 3750 u
M6 - P1
① 6 i - 2170 u
② 6 j - 2275 u
③ 6 k - 2390 u
④ 6 l - 2480 u
⑤ 6 m - 2640 u
⑥ 6 o - 2880 u
⑦ 6 q - 3250 u
M13 - P6
ELBOW
OUTER SEGMENT
① 13 zz - 1490 u
② 13 aaa - 1840 u
③ 13 ccc - 2220 u
④ 13 ddd - 2290 u
INNER SEGMENT
⑤ 13 fff - 2420 u
⑥ 13 hhh - 2460 u
⑦ 13 iii - 2490 u
⑧ 13 jjj - 2550 u
⑨ 13 lll - 2720 u
VOLAR WRIST
DORSAL WRIST
M17 - P1
AREA 1 PART
① 17 f - 690 u
② 17 k - 800 u
③ 17 l - 1110 u
④ 17 m - 1200 u
⑤ 17 p - 1390 u
AREA 3 PART
① 17 r - 3480 u
② 17 s - 3600 u
③ 17 t - 3710 u
④ 17 tx - 3790 u
⑤ 17 u - 4300 u
1 MM
5 CM
M8 - P6
① 8 ii - 3550 u
② 8 jj - 3550 u
③ 8 ll - 3700 u
④ 8 nn - 3720 u
1 MM
FIELDS
5 CM
M8 - P4
BACK
① 8 p - 2400 u
② 8 t - 2900 u
③ 8 v - 2970 u
④ 8 u - 2930 u
⑤ 8 w - 2760 u
5 CM
1 MM
BELLY
CS

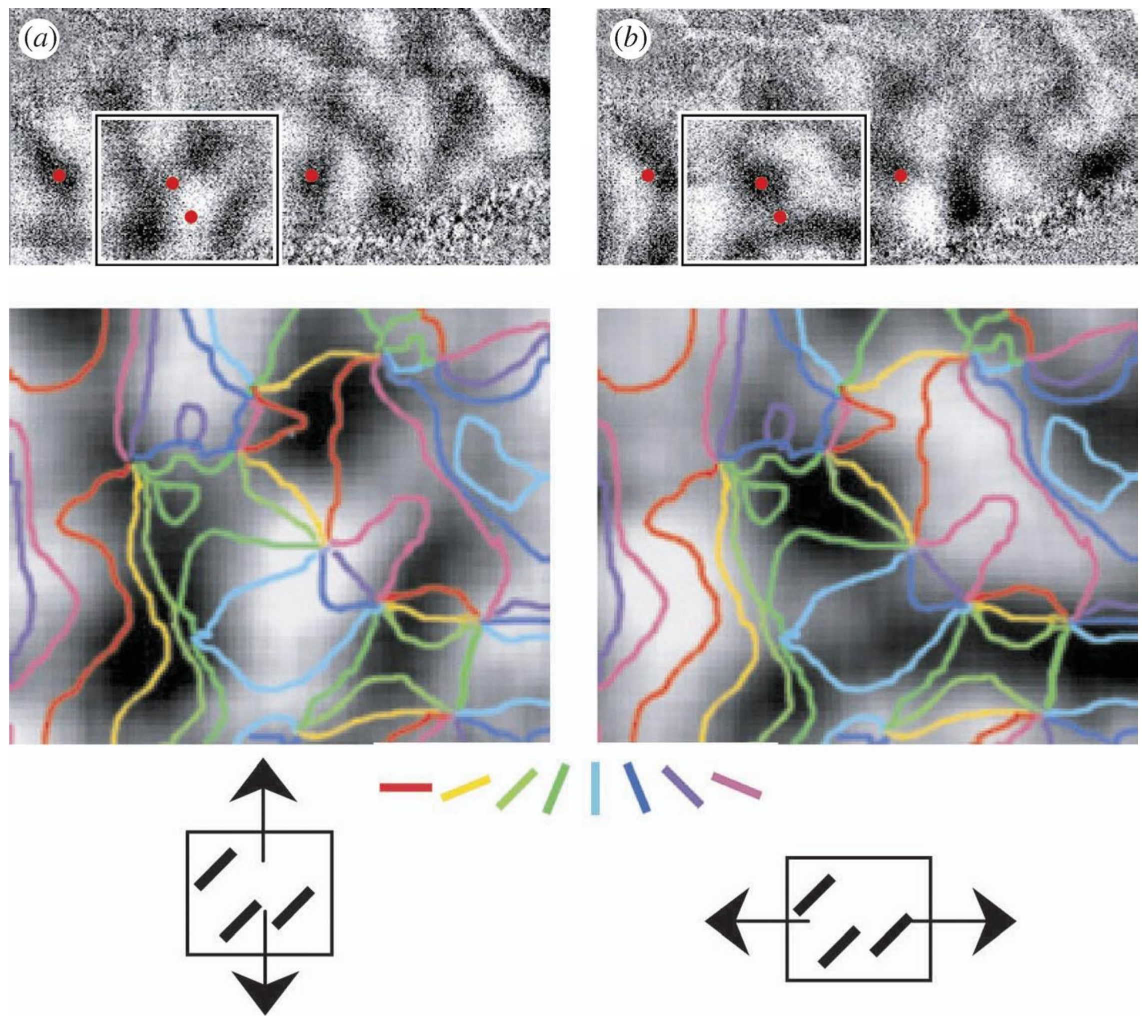


Direction Column
Direction Column
Axis of Motion Column

diagram of the arrangement of neurons, dendrites and axons in vertical modules of the striate cortex of the macaque monkey. *Left*. A drawing to show the arrangement of the apical dendrites of pyramidal cells; for clarity, only one-half of the neurons present are shown. The pyramidal cells in layers II/III, IVA and V are shown in red, those in layer VI in green. Neurons of IVB and IVC are shown without dendrites, in grey; GABAergic neurons in azure. Total numbers of GABAErgic and non-GABAergic cells are given to the right of the drawing. *Right*. A drawing to represent the pyramidal cell modules (columns) showing the arrangement of dendrites and axons. Colour scheme the same as for the left, pyramidal cell axons are shown in blue. (From Peters and Sethares, 1996, with permission from Wiley-Liss.)




(a)
(b)
M
CP
IZ
VZ
4
3
2
1
M
CP
IZ
200 µm


(a)
(b)