RETINA, PRIMARY VISUAL PATHWAY AND PRIMARY VISUAL CORTEX

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- Literature: Siegel and Sapru “Essential neuroscience”, chapters 16 and 26.
- Kandel, chapter 28.

VISUAL SYSTEM

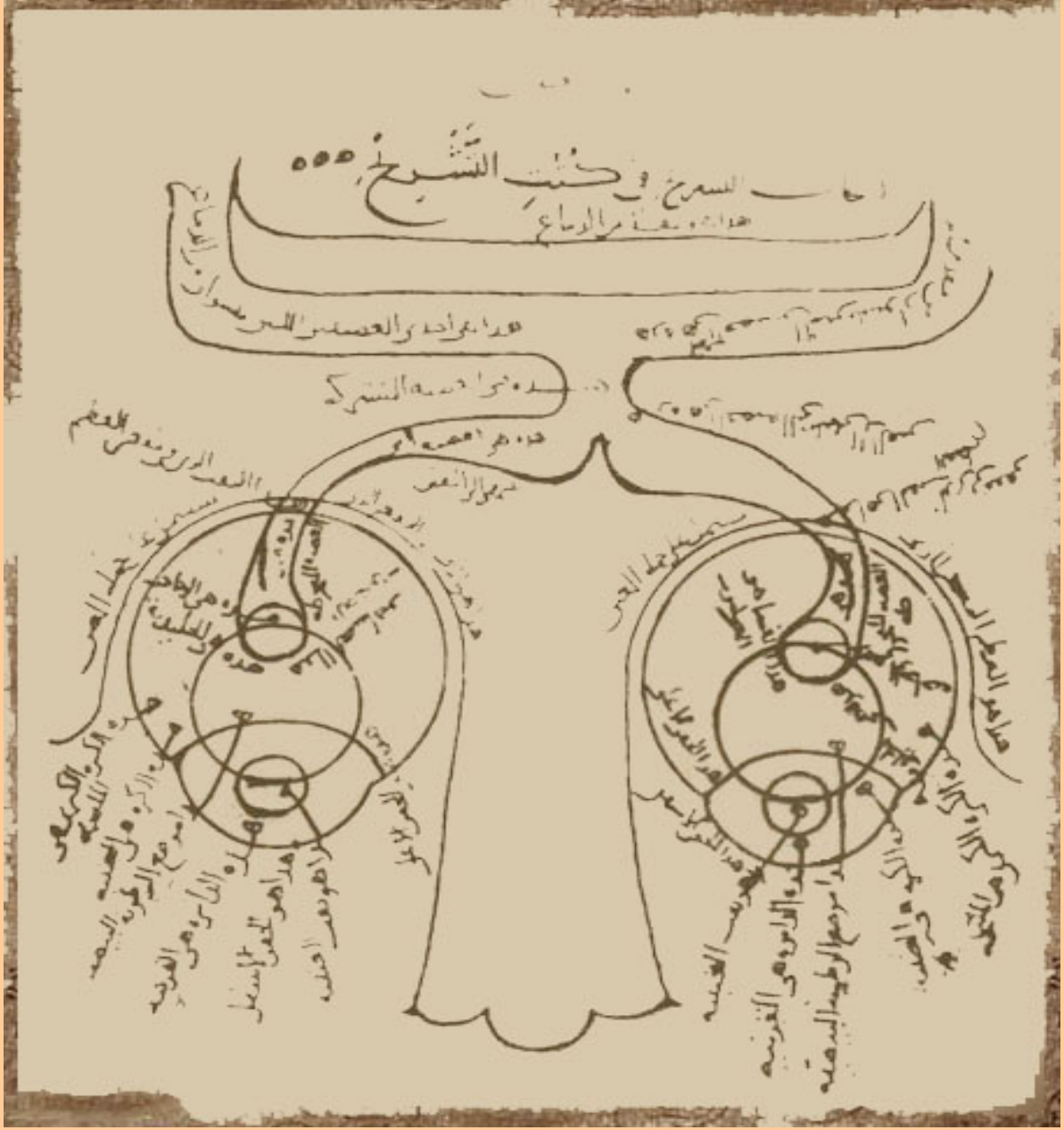
1) PRIMARY VISUAL PATHWAY (retina – primary visual cortex)

- Infranuclear (*retina*, *n. opticus*, *chiasma*, *tractus*)
- Nuclear(*colliculi superiores and thalamic nuclei*)
- Supranuclear (*radiatio optica*, *area striata*)

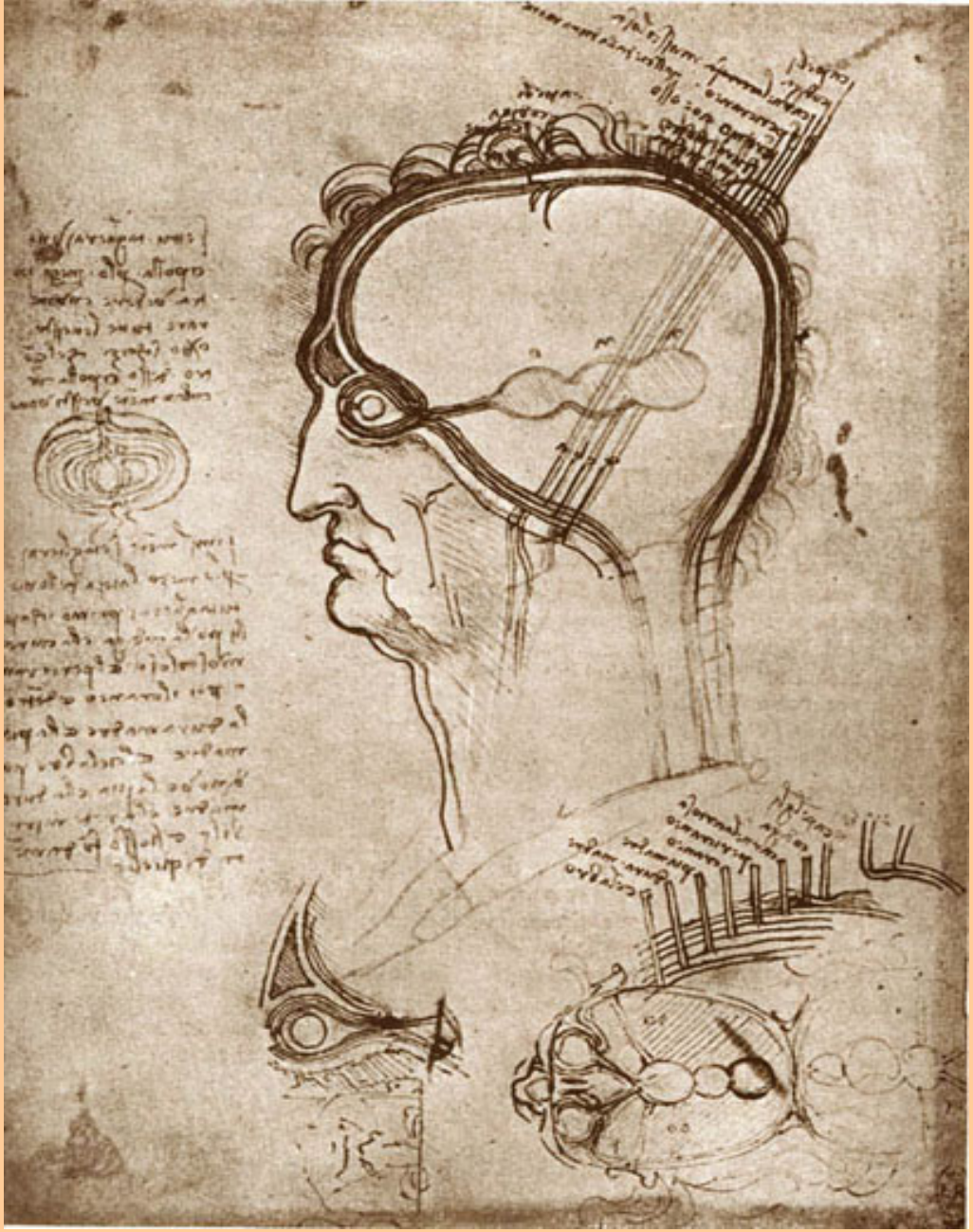
2) VISUAL-MOTORIC PATHWAY (retina – upper colliculi)

3) PATHWAY OF VISUAL-AUTONOMIC REFLEXIS (retina – pretectal area)

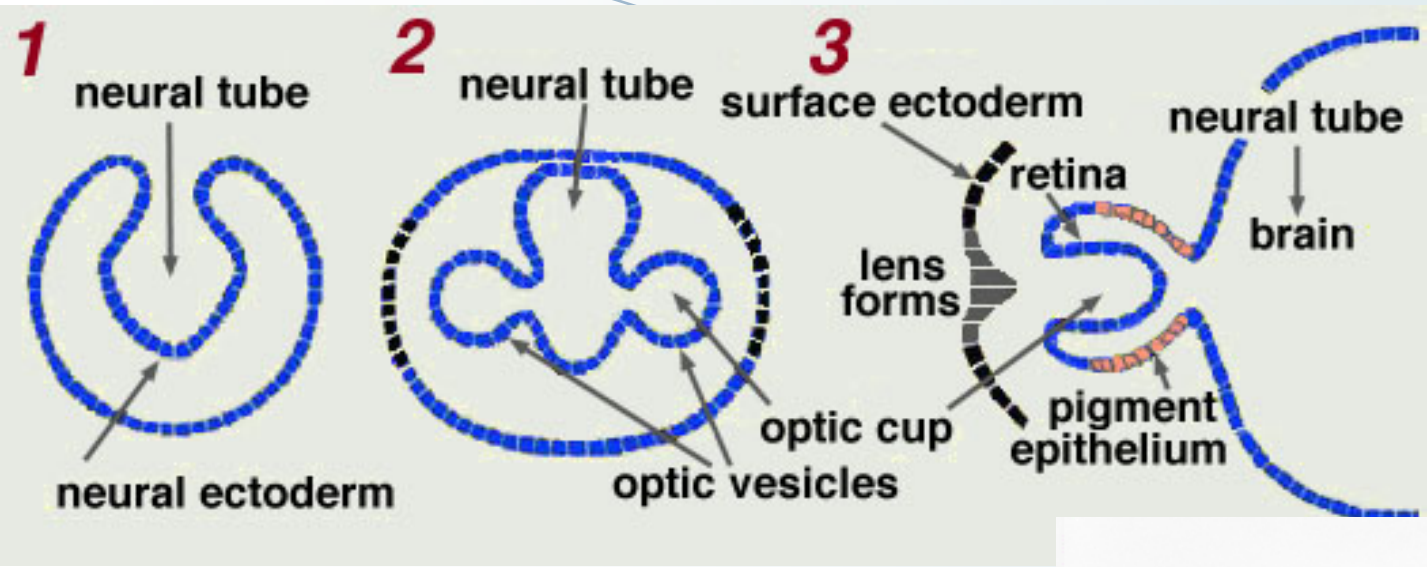
4) PATHWAY TO THE HYPOTHALAMUS



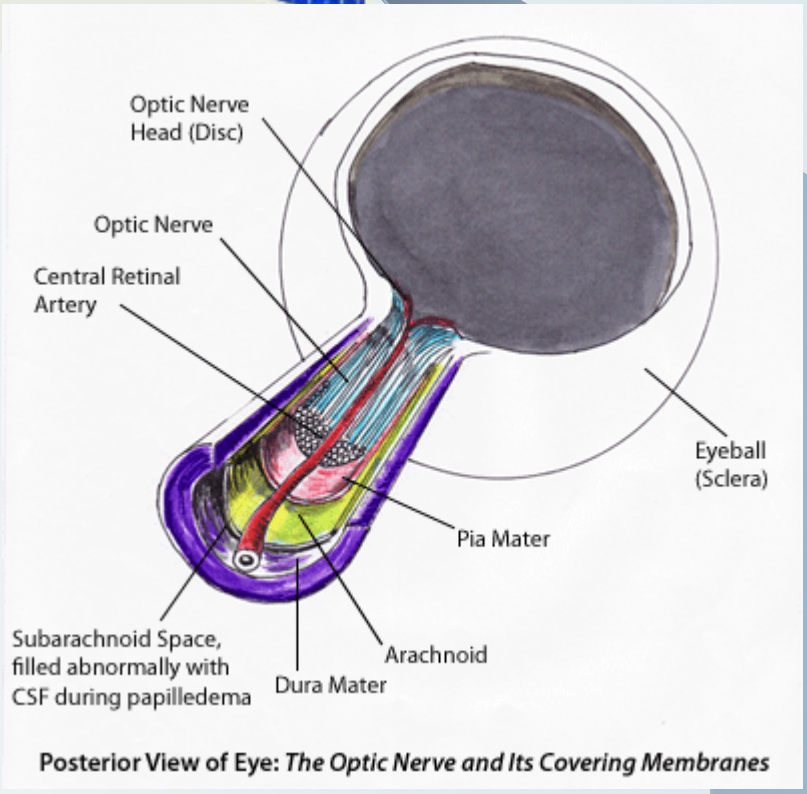
Diagramatic presentation of visual system from the old “Book of optics”, written in 11th century AD (from Polak 1957)



Leonardo daVinci: projection from the eyes to the brain (from Polyak, 1957)



Development of the retina from neural ectoderm.
n. opticus – cranial nerve (part of real cranial pathway), surrounded by cerebral meninges.



Anatomy of the eye

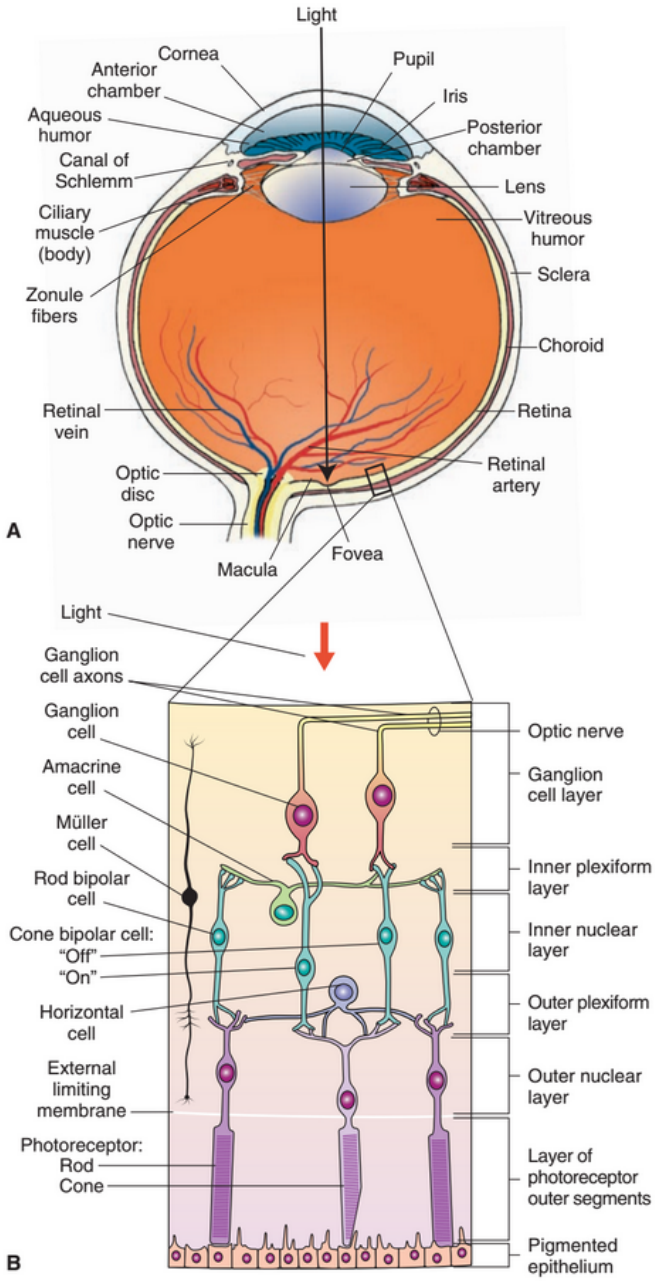
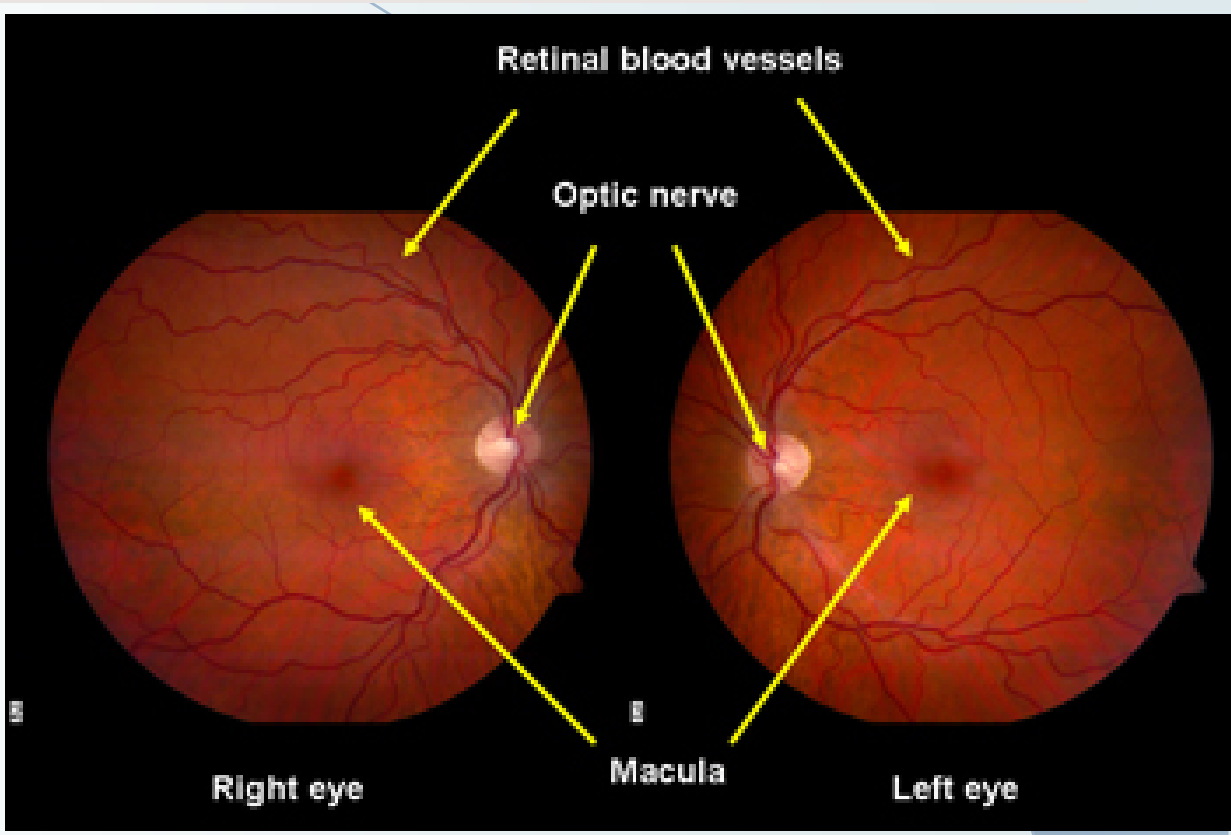
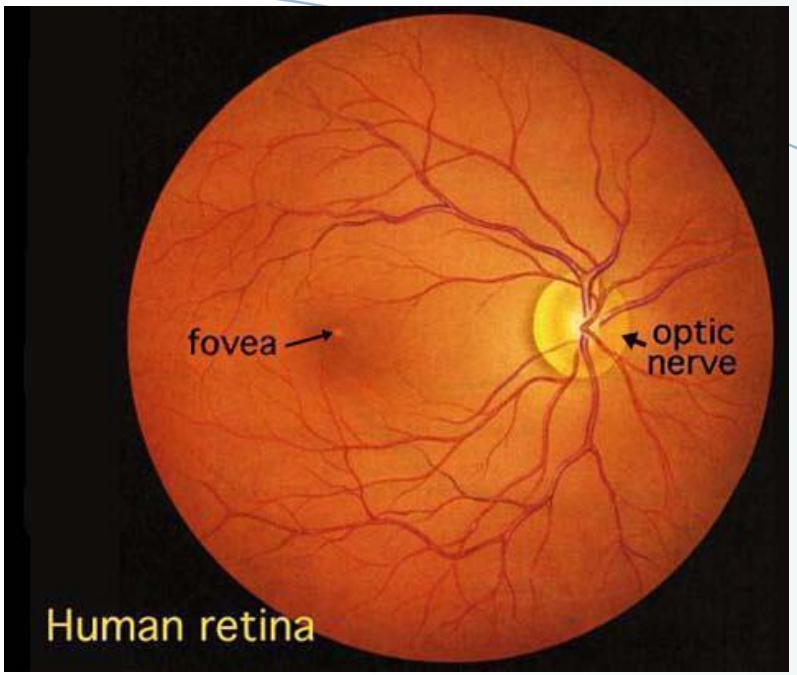


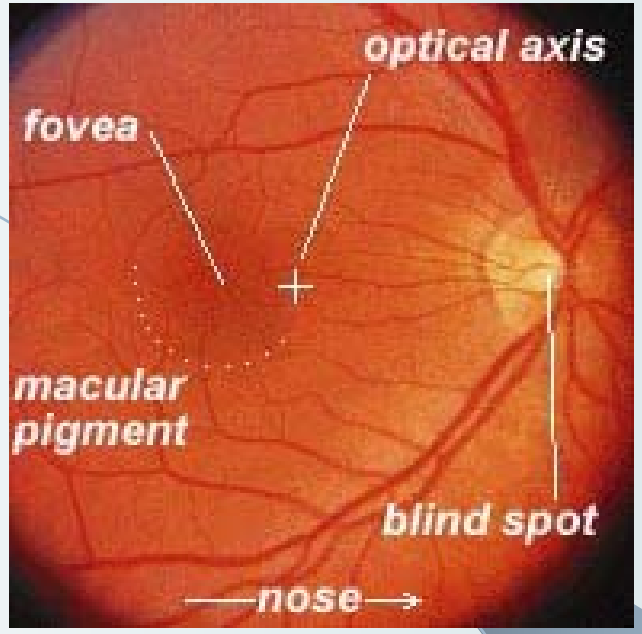
FIGURE 15.1 Structure of the eye and retina. **(A)** Different components of the eye. **(B)** Different layers of the human retina (only a few cells are shown for clarity of their connections).

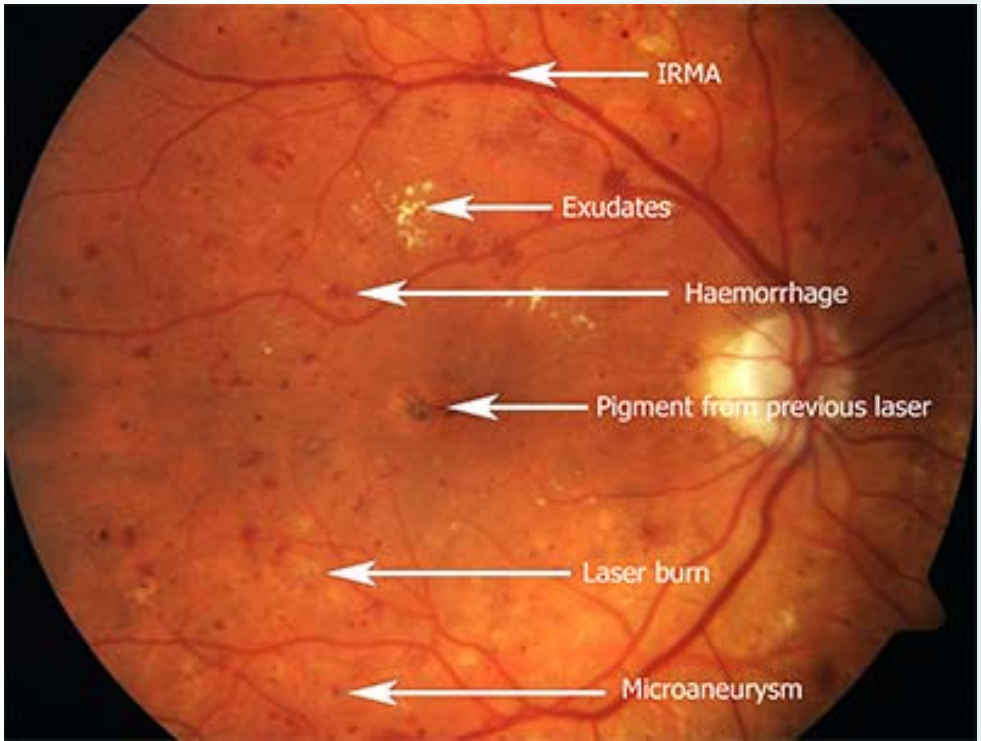
The Background of the Eye fundus

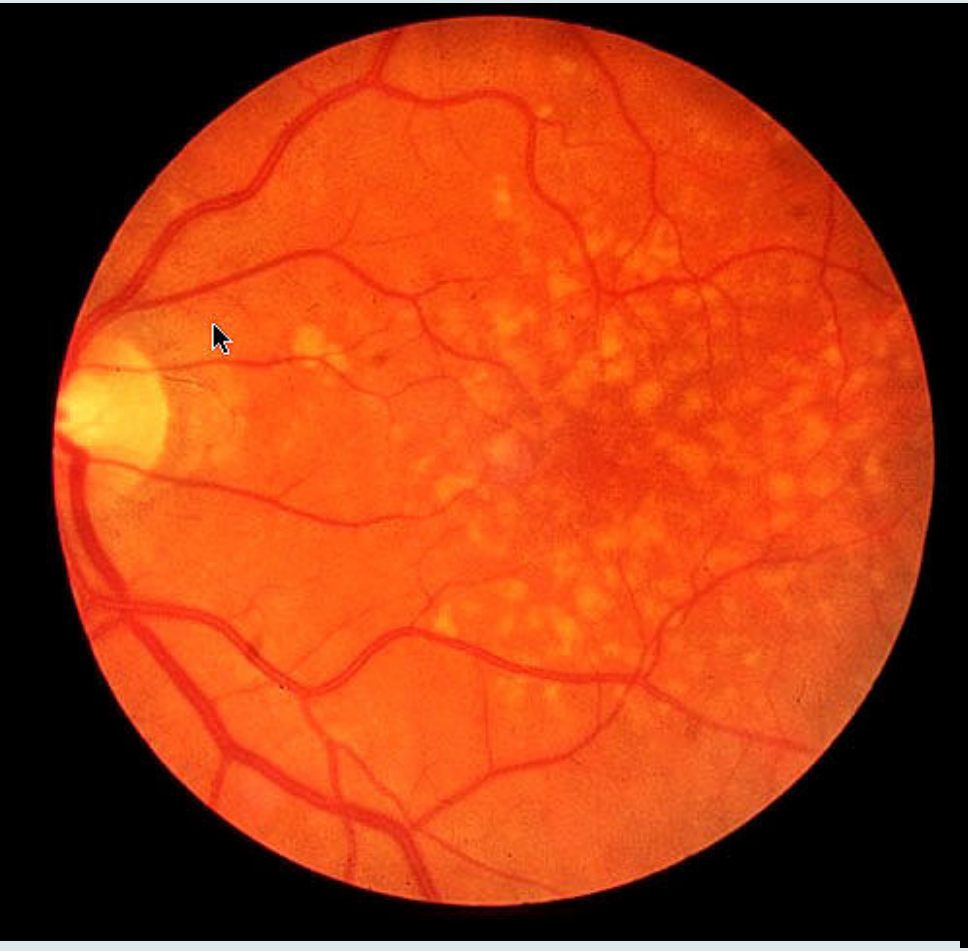
- Ophtalmoskop
- Macula lutea, fovea centralis, discus opticus- papilla nervi optici
- Excavatio papillae
- Lamina cribrosa

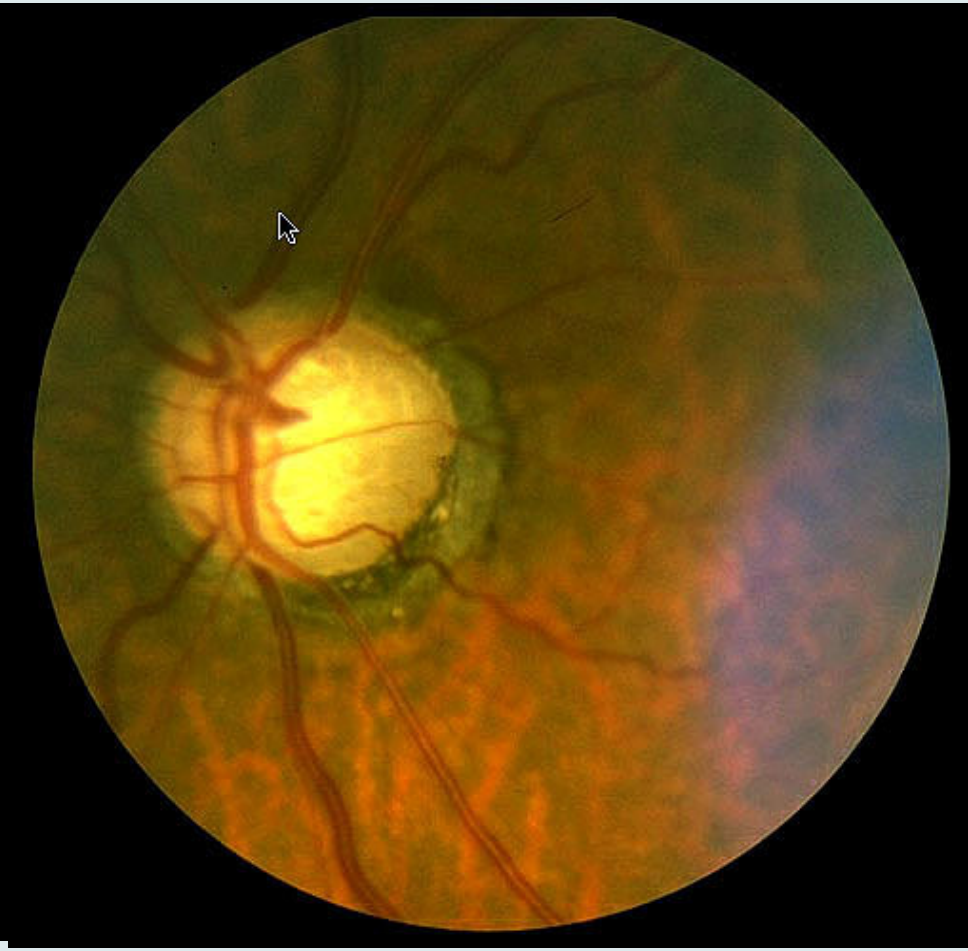



fovea
optic nerve
Human retina


optical axis
fovea
macular pigment
blind spot
nose

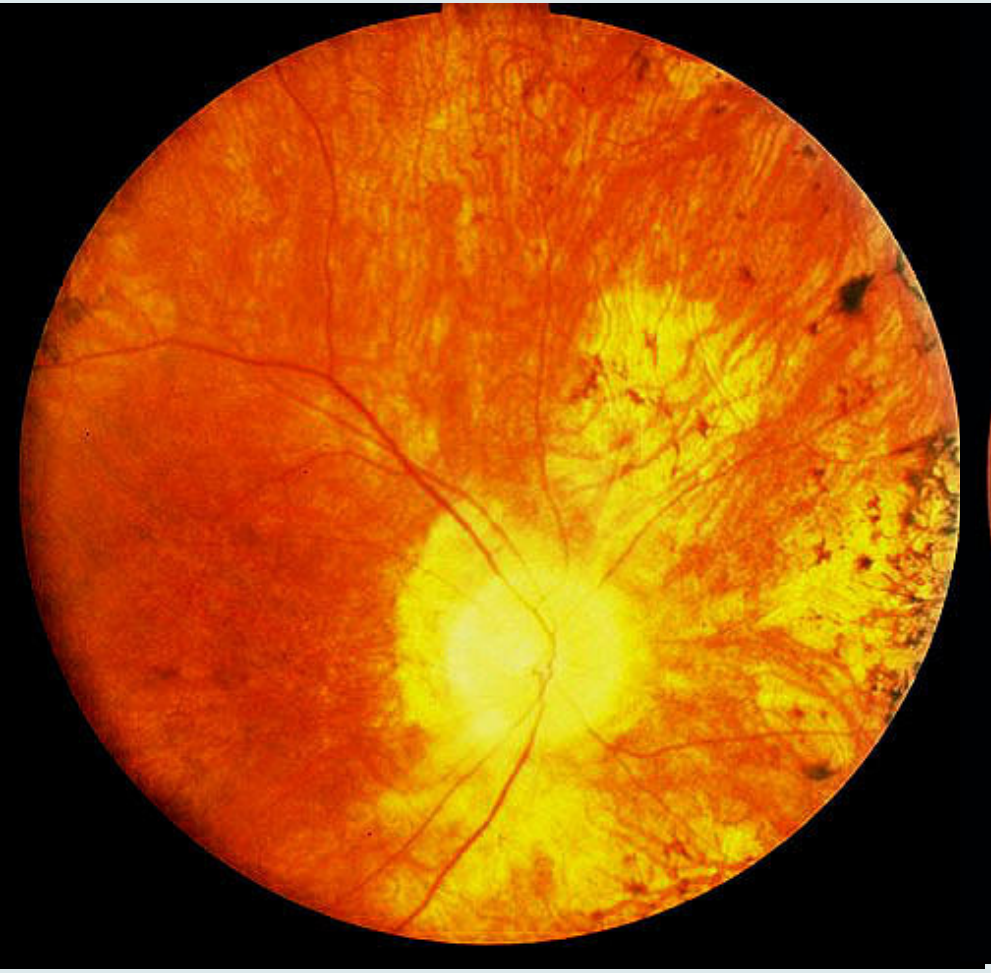

IRMA
Exudates
Haemorrhage
Pigment from previous laser
Laser burn
Microaneurysm



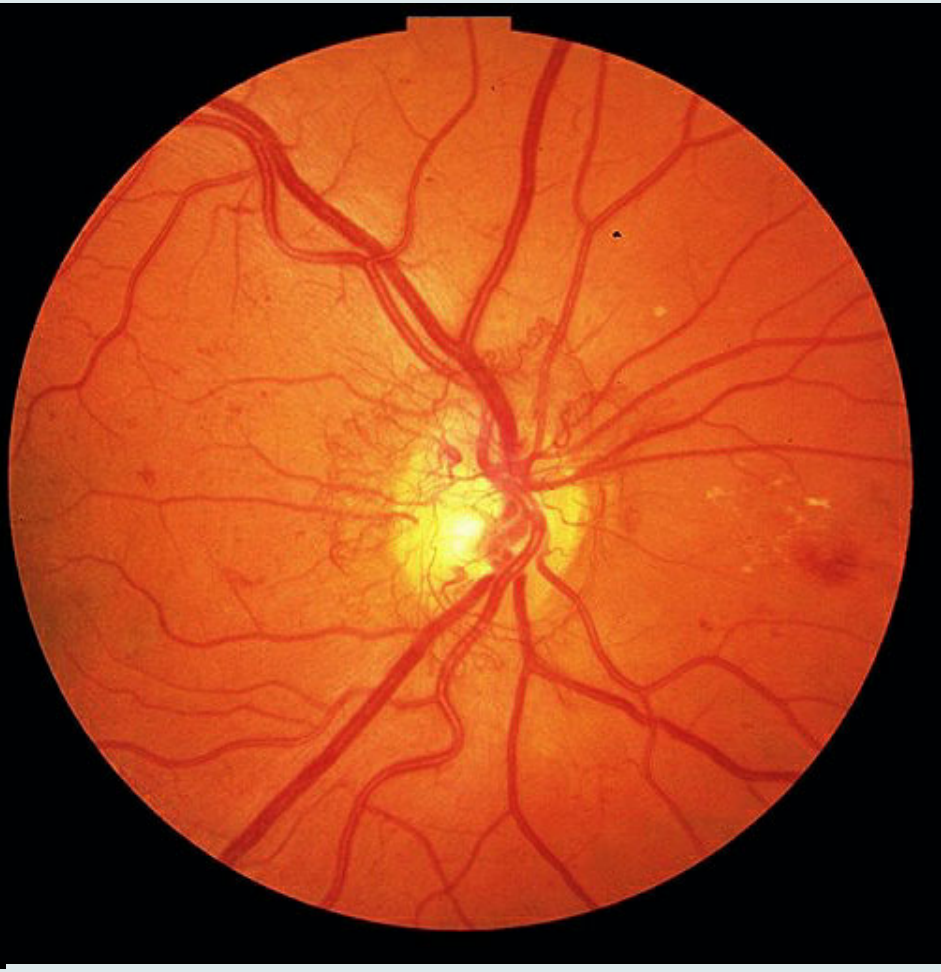


Macular degeneration

Late-stage glaucoma

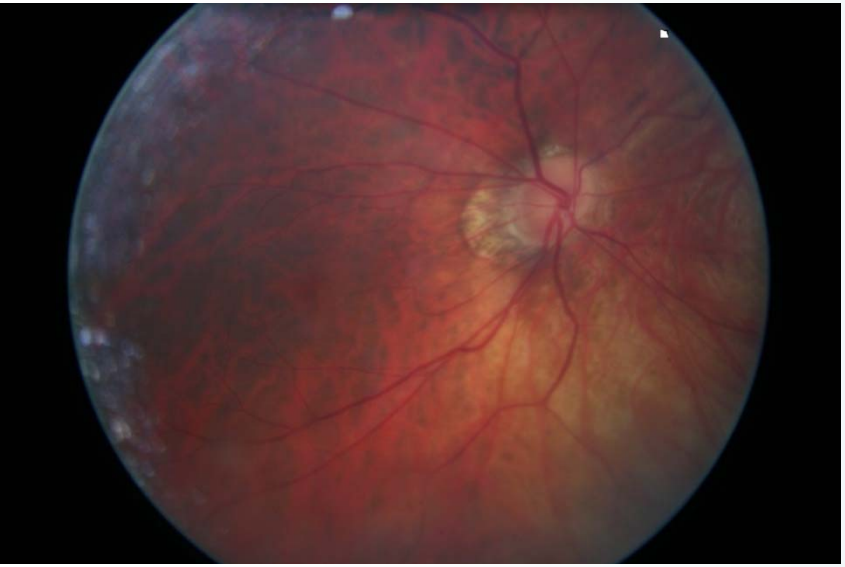


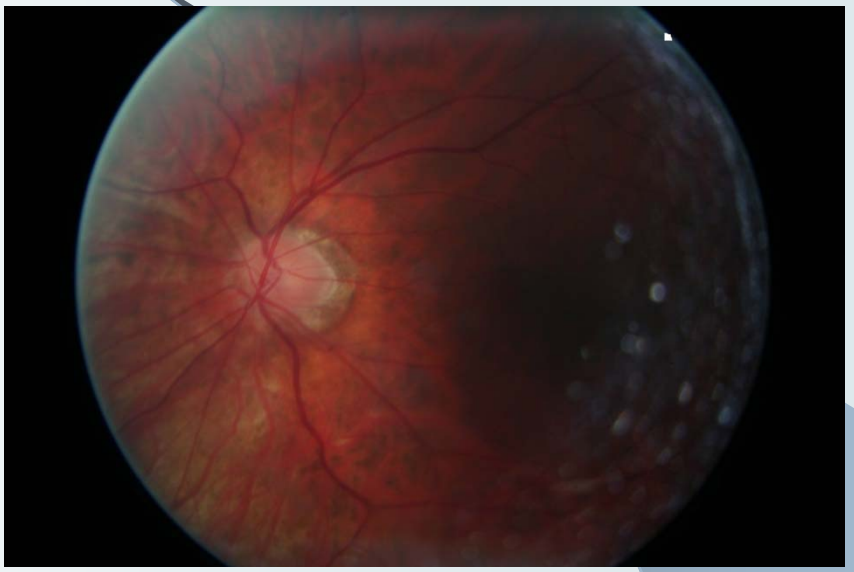
Retinitis pigmentosa



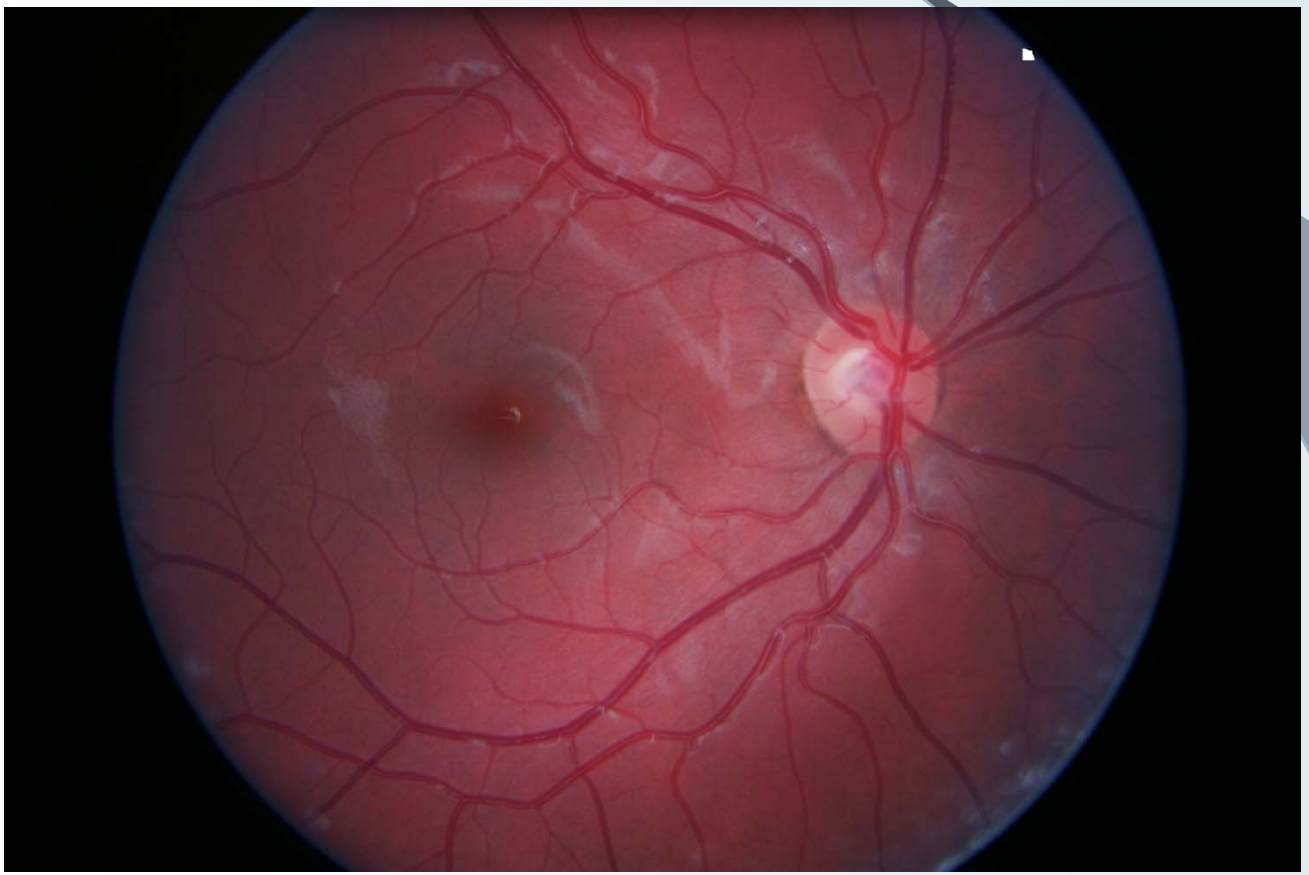
Diabetic retinopathy

Malignant myopia

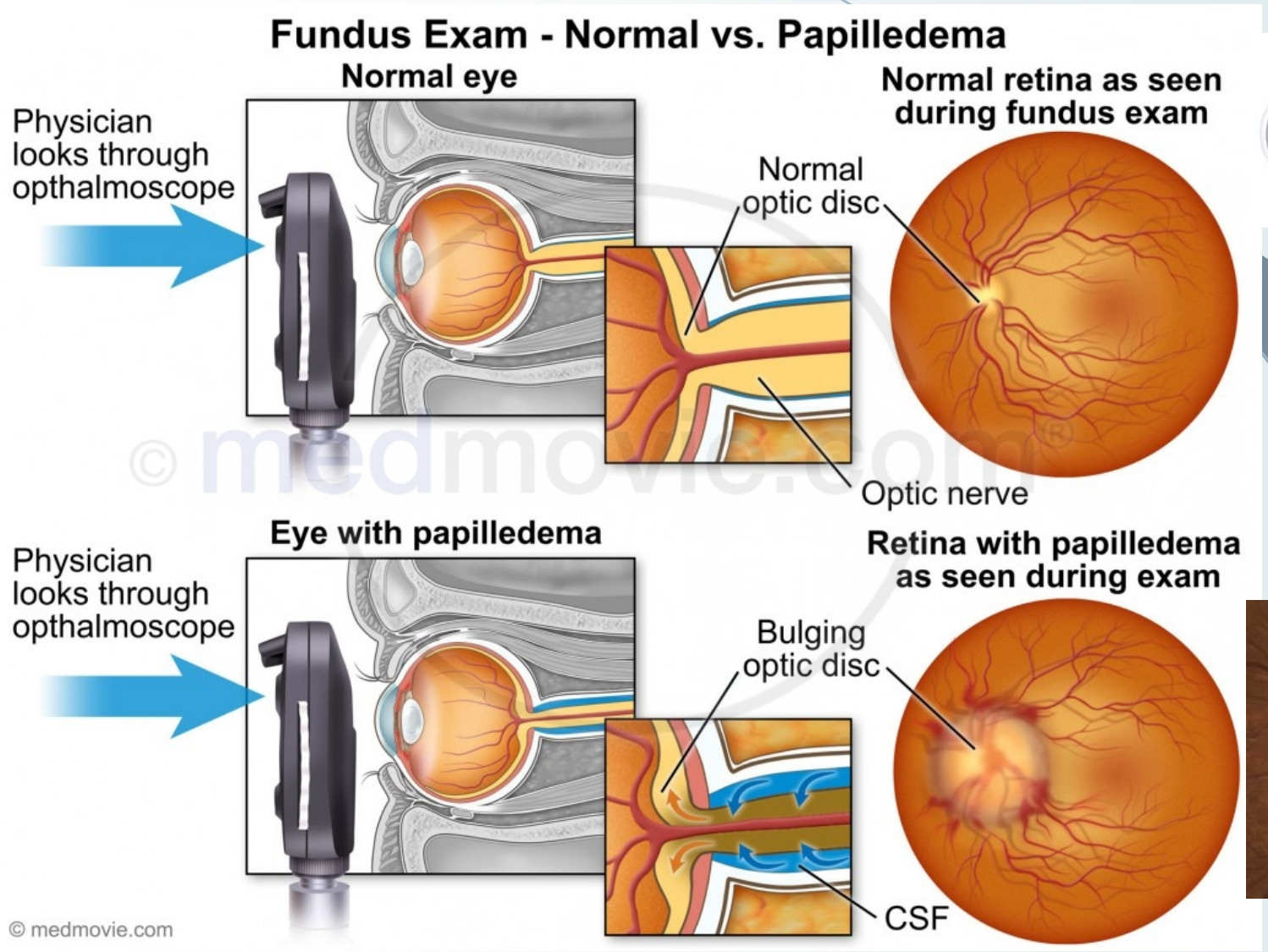


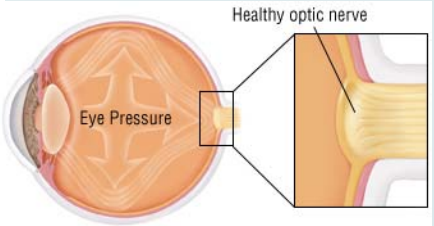


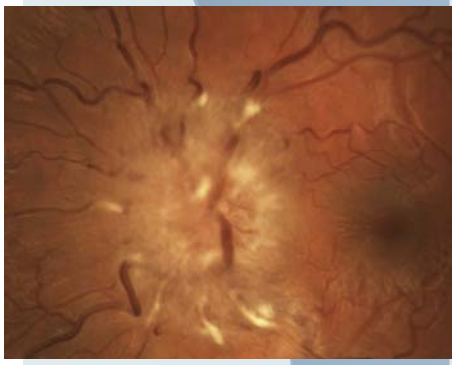
Healthy, young fundus of the eye



Long-term increase of intracranial pressure can be seen at the background of the eye – Papilledema = edema of the optic disk.

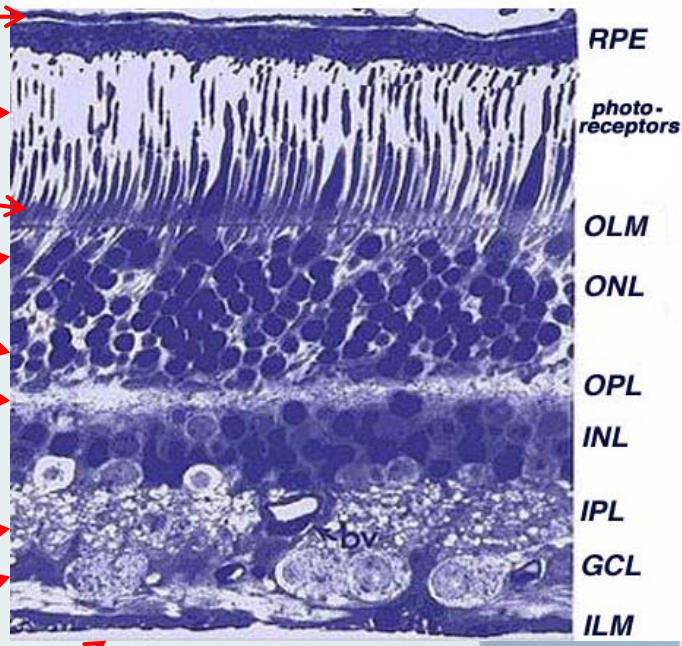


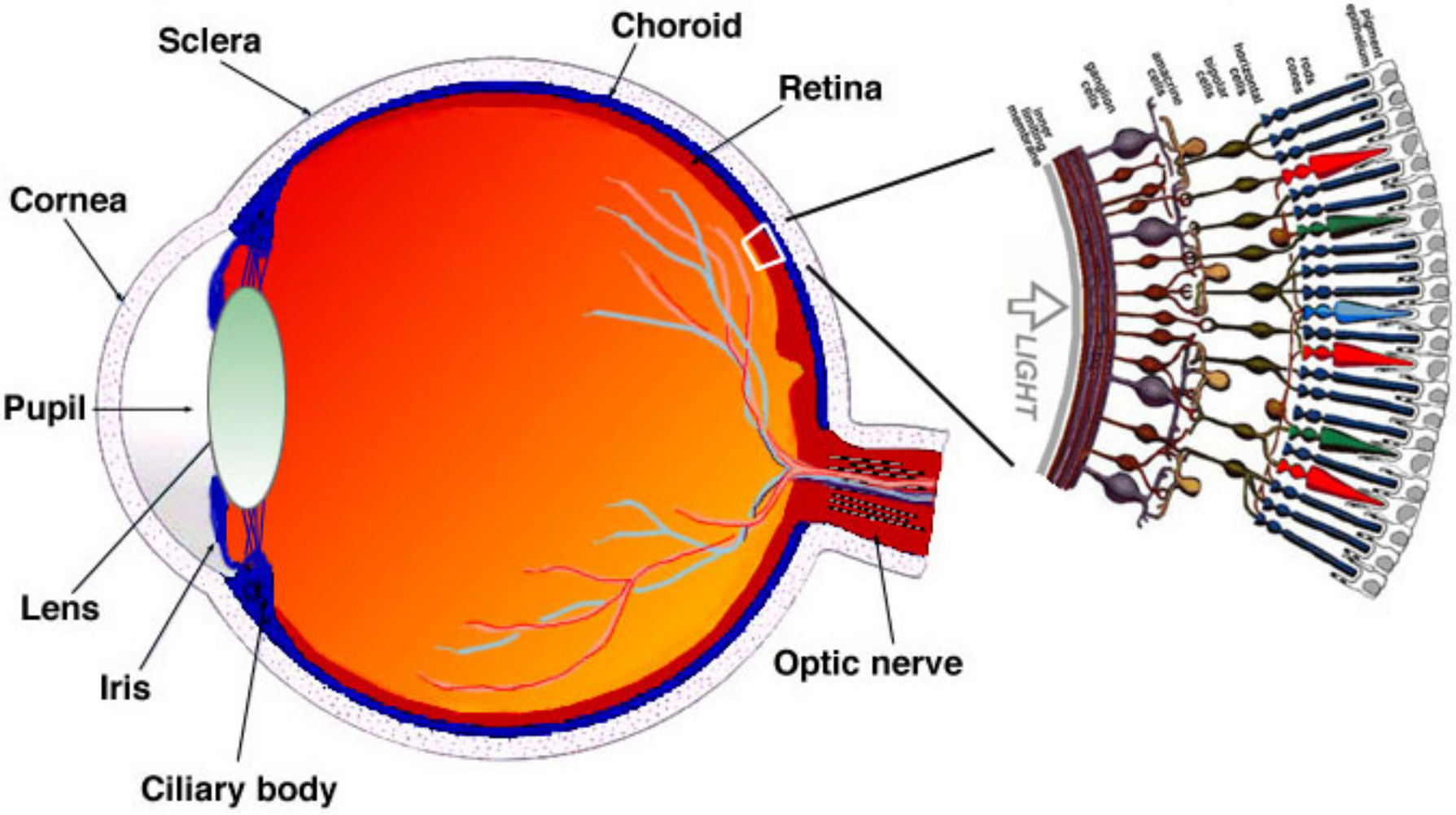


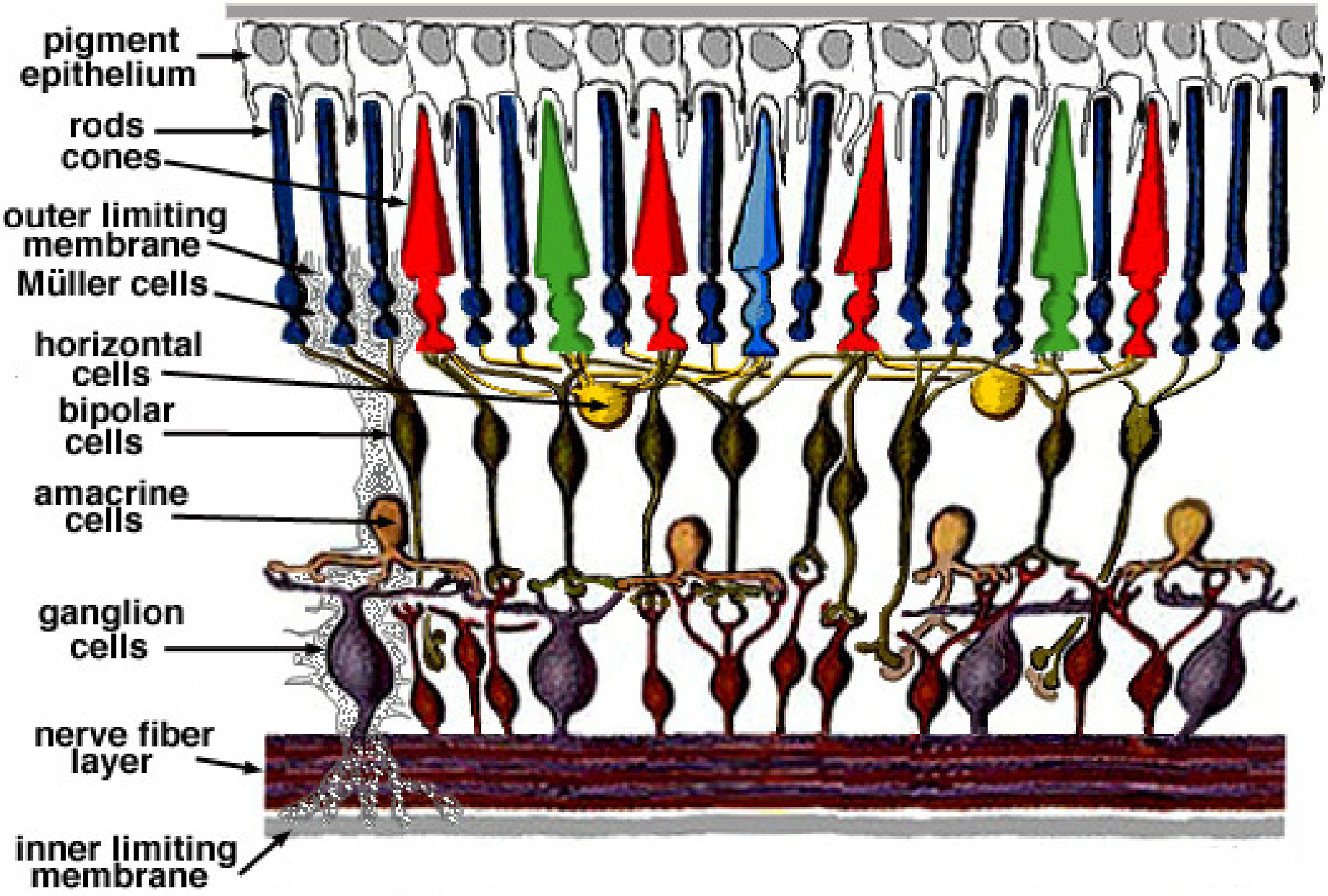


DIFFERENT LAYERS OF THE RETINA

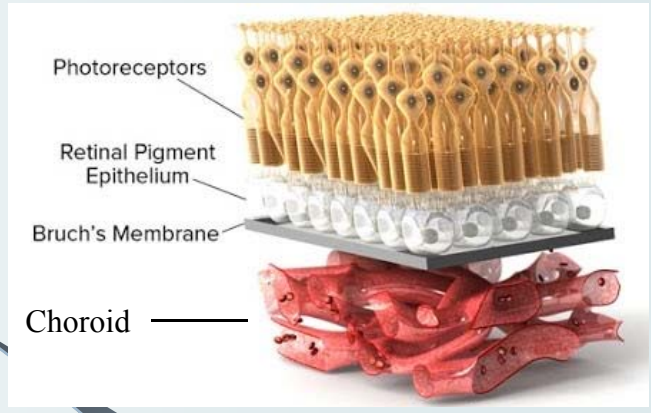
1. The Pigment Epithelium Layer
2. The Layer of Rods and Cones
3. The External Limiting Membrane
4. The Outer Nuclear Layer
5. The Outer Plexiform Layer
6. The Inner Nuclear Layer
7. The Inner Plexiform Layer
8. The Layer of Ganglion Cells
9. The Optic Nerve Layer
10. Internal Limiting Membrane




Sclera
Choroid
Retina
Cornea
Pupil
Lens
Iris
Ciliary body
Optic nerve
LIGHT


pigment epithelium
rods
cones
outer limiting membrane
Müller cells
horizontal cells
bipolar cells
amacrine cells
ganglion cells
nerve fiber layer
inner limiting membrane

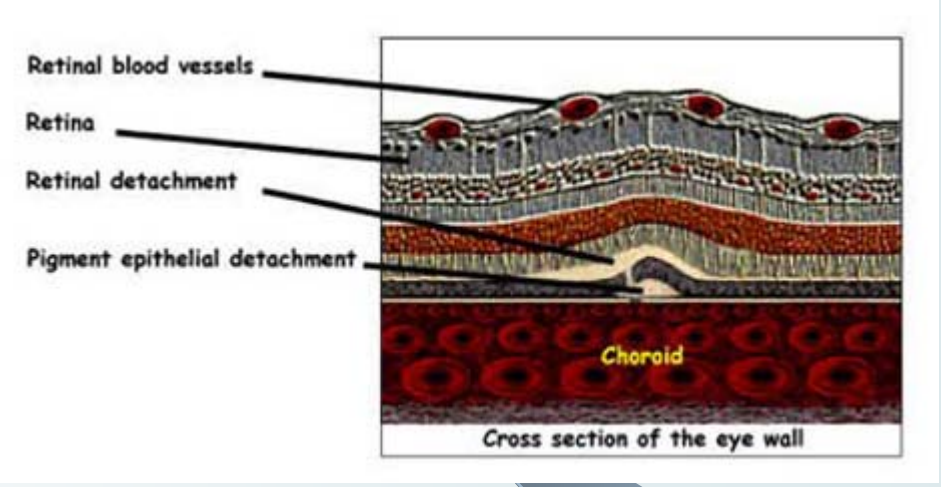
1. The Pigment Epithelium Layer



- the outermost layer of the retina
- consisting of pigmented cuboidal cells that contain **melanin**
- cells are **firmly attached to the choroidal layer** of the eye located outside the retina.
- The cuboidal cells have microvilli at their apical regions which interdigitate with photoreceptors

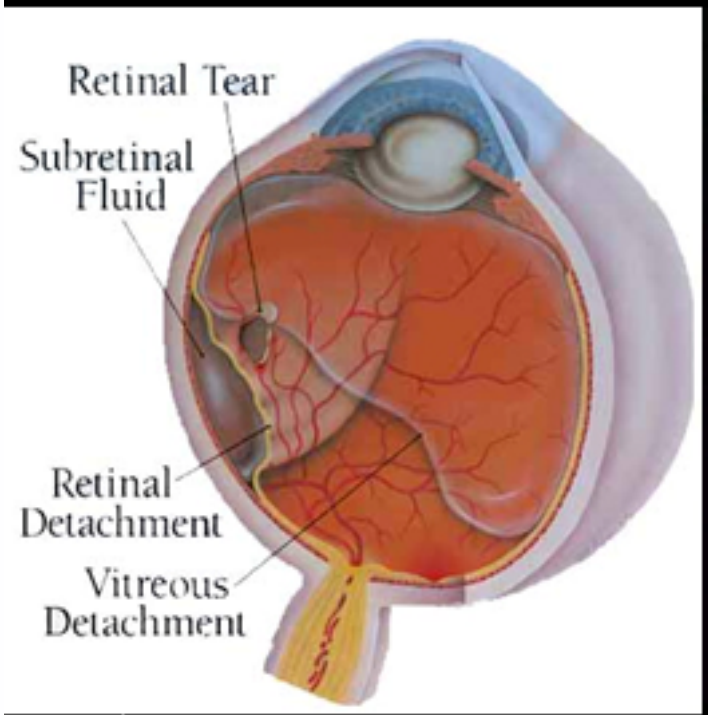
- The pigmented epithelium cells provide **nutrition** (glucose and essential ions) to photoreceptors
- **melanin** absorbs any light that is not captured by the retina and prevents it from reflecting back to the retina,
- **protects the photoreceptors** from damaging levels of light.

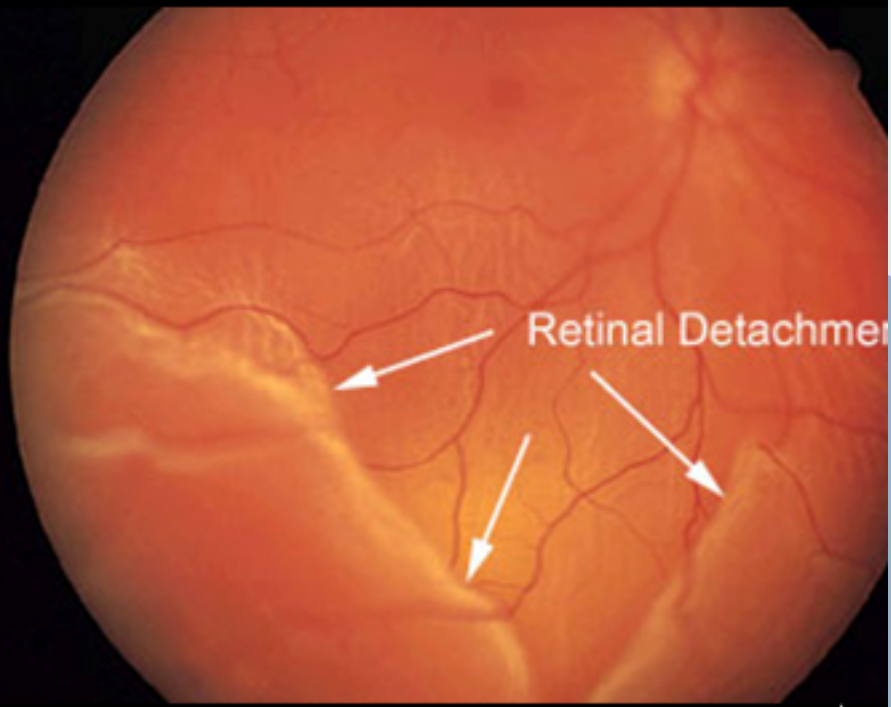
Retinal detachment



- the pigment epithelium layer sometimes detaches from the neural retina - **retinal detachment**
- the photoreceptors can be damaged because they may not receive the nutrition that is normally provided by the pigment epithelium layer.
- Retinal detachment is now repaired by laser surgery.

Retinal Detachment





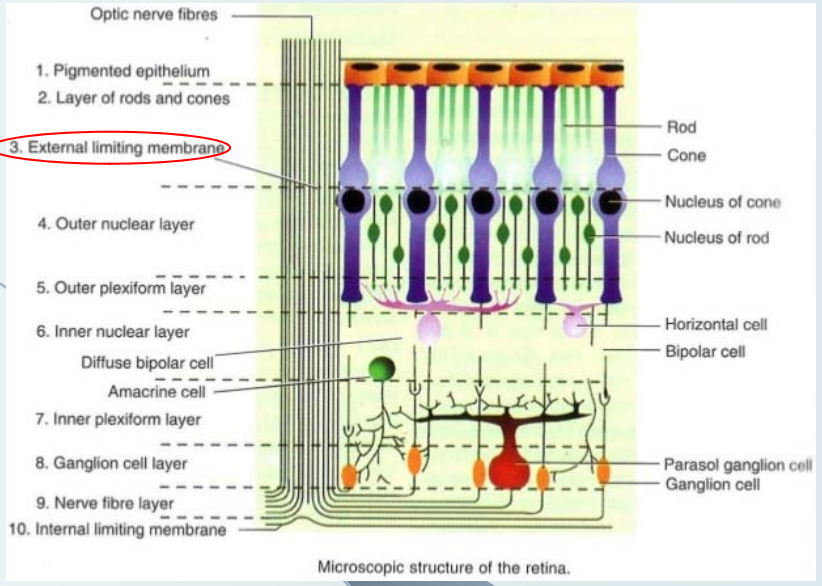
Ablatio retinae – retinal detachment

- **Retinal detachment** -retina peels away from its underlying layer of support tissue. Initial detachment may be localized, but without rapid treatment the entire retina may detach, leading to vision loss and blindness. It is a medical emergency.
- TREATMANT: Cryotherapy (freezing) or laser are used to wall off a small area of retinal detachment so that the detachment does not spread.

2. The Layer of Rods and Cones

- containes the lightsensitive portions of photoreceptors
- the rods outnumber the cones
- One exception to this rule is the region of greatest visual acuity, the fovea (a depression in the center of the macula).
- The fovea contains only cones

3. The External Limiting Membrane

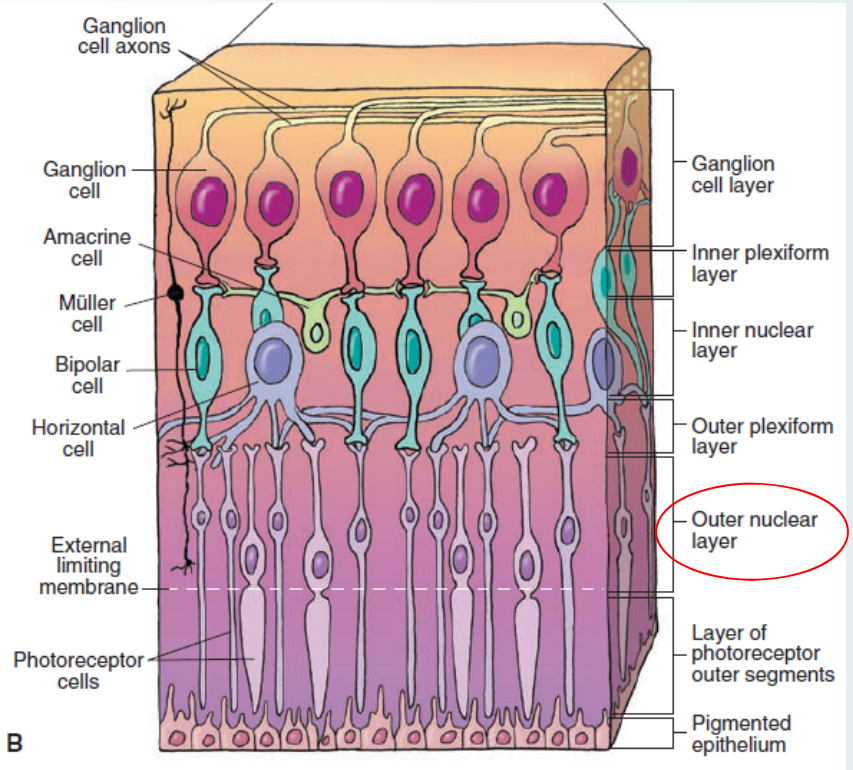


Microscopic structure of the retina.

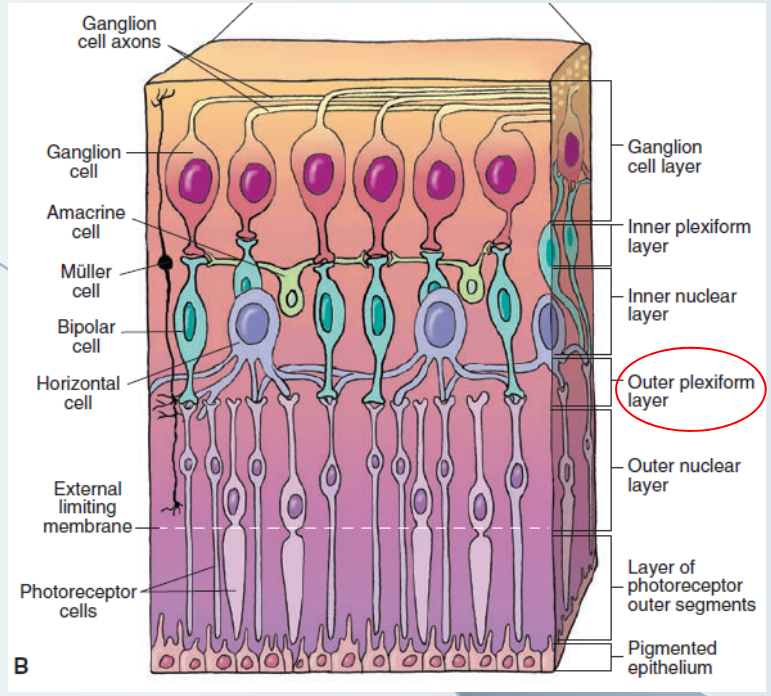
- The photosensitive processes of rods and cones pass through the **external limiting membrane** in order to be connected with their cell bodies.
- This region contains processes of **Müller cells (**these cells are homologous to the glial cells)

4. The Outer Nuclear Layer

- contains the cell bodies of rods and cones



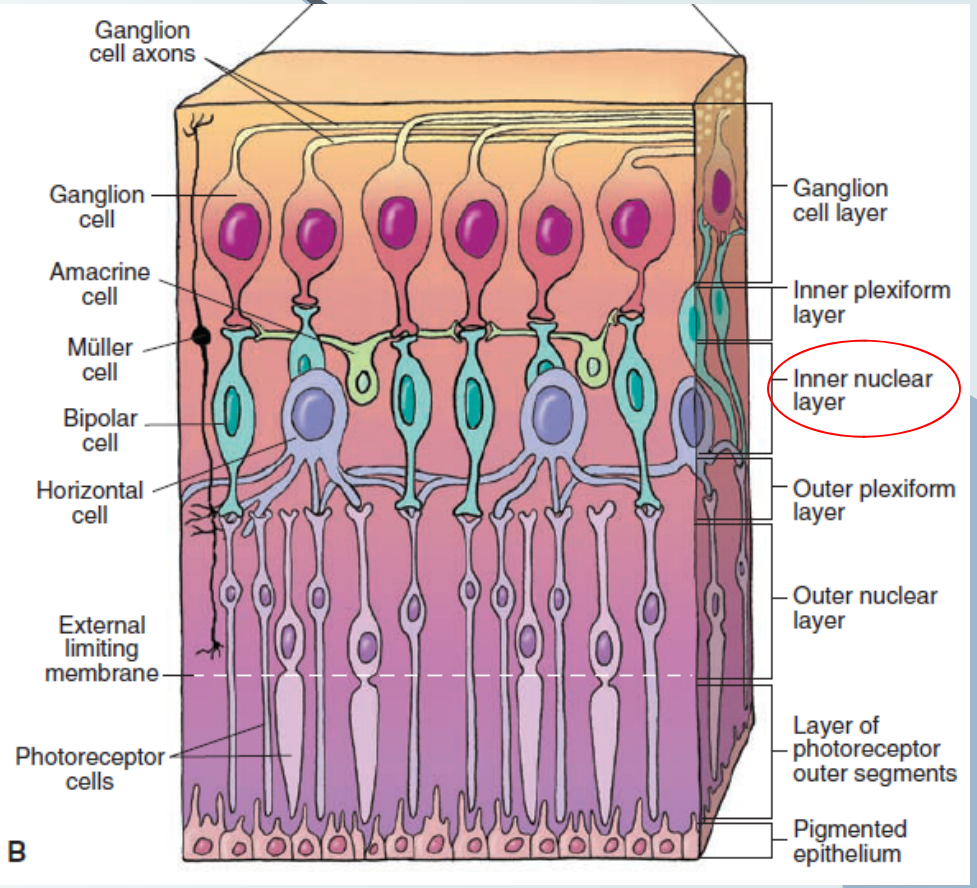
5. The Outer Plexiform Layer



- **Contains:**
- the axonal processes of rods and cones,
- processes of horizontal cells,
- dendrites of bipolar cells.
- **synaptic interaction** between photoreceptors and horizontal and bipolar cells takes place

6. The Inner Nuclear Layer

- contains the cell bodies of amacrine cells, horizontal cells, and bipolar cells
- Amacrine and horizontal cells, or *association cells*, function as interneurons
- Amacrine cells are interposed between the bipolar and ganglion cells and serve as modulators of the activity of ganglion cells



7. The Inner Plexiform Layer

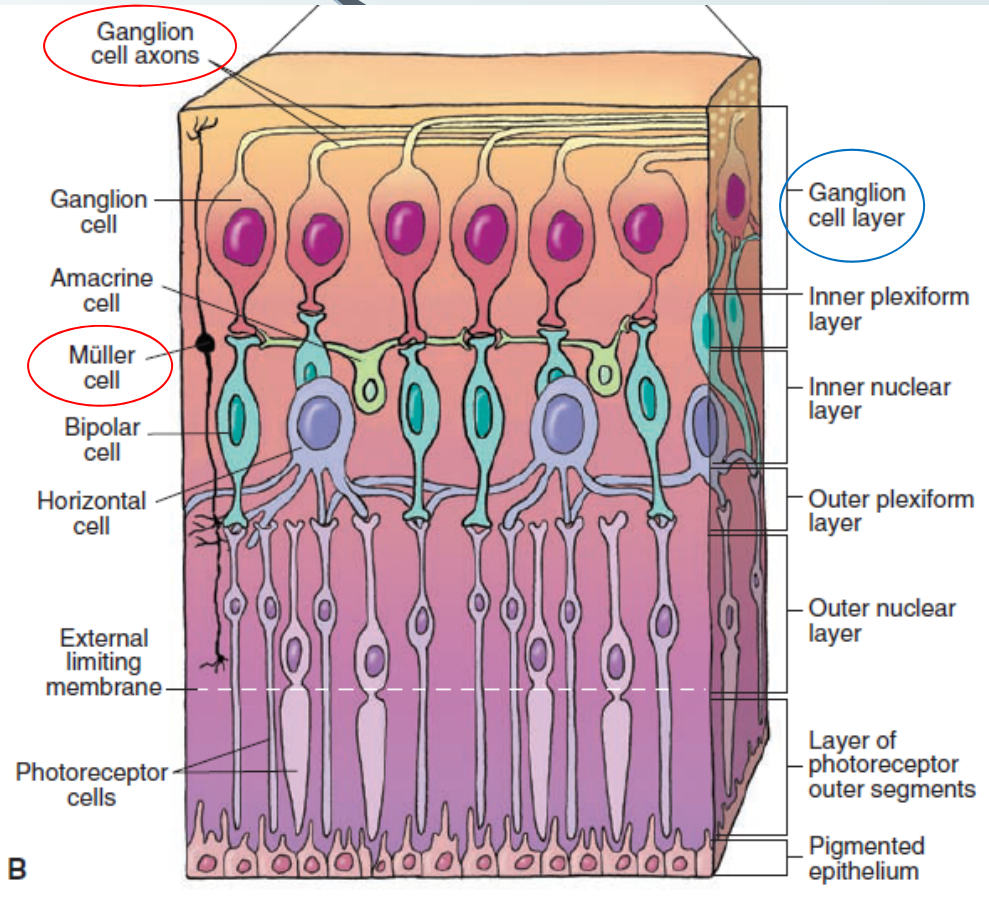
- contains the axons of bipolar cells, processes of amacrine cells, and dendrites of ganglion cells.
- synaptic interaction between different retinal cells takes place.

8. The Layer of Ganglion Cells

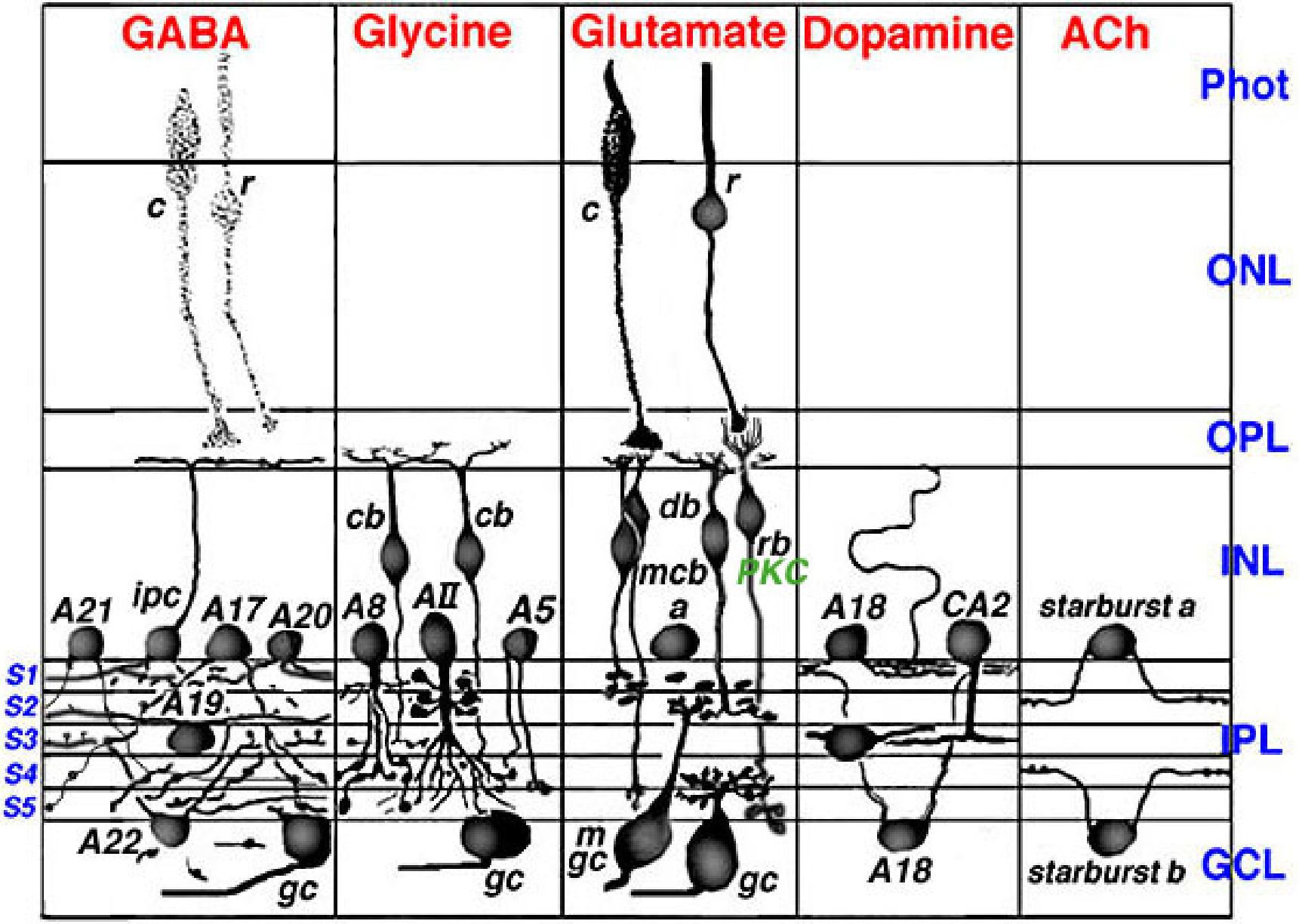
- contains the cell bodies of multipolar **ganglion cells**
- The fovea centralis of retina has the greatest density of ganglion cells
- visual stimulation is transmitted to the CNS via their axons in the **optic nerve**. The ganglion cells are the only retinal cells that are capable of firing action potentials.

9. The Optic Nerve Layer

- contains the axons of ganglion cells and processes of **Müller cells**



Neurotransmitters of retina



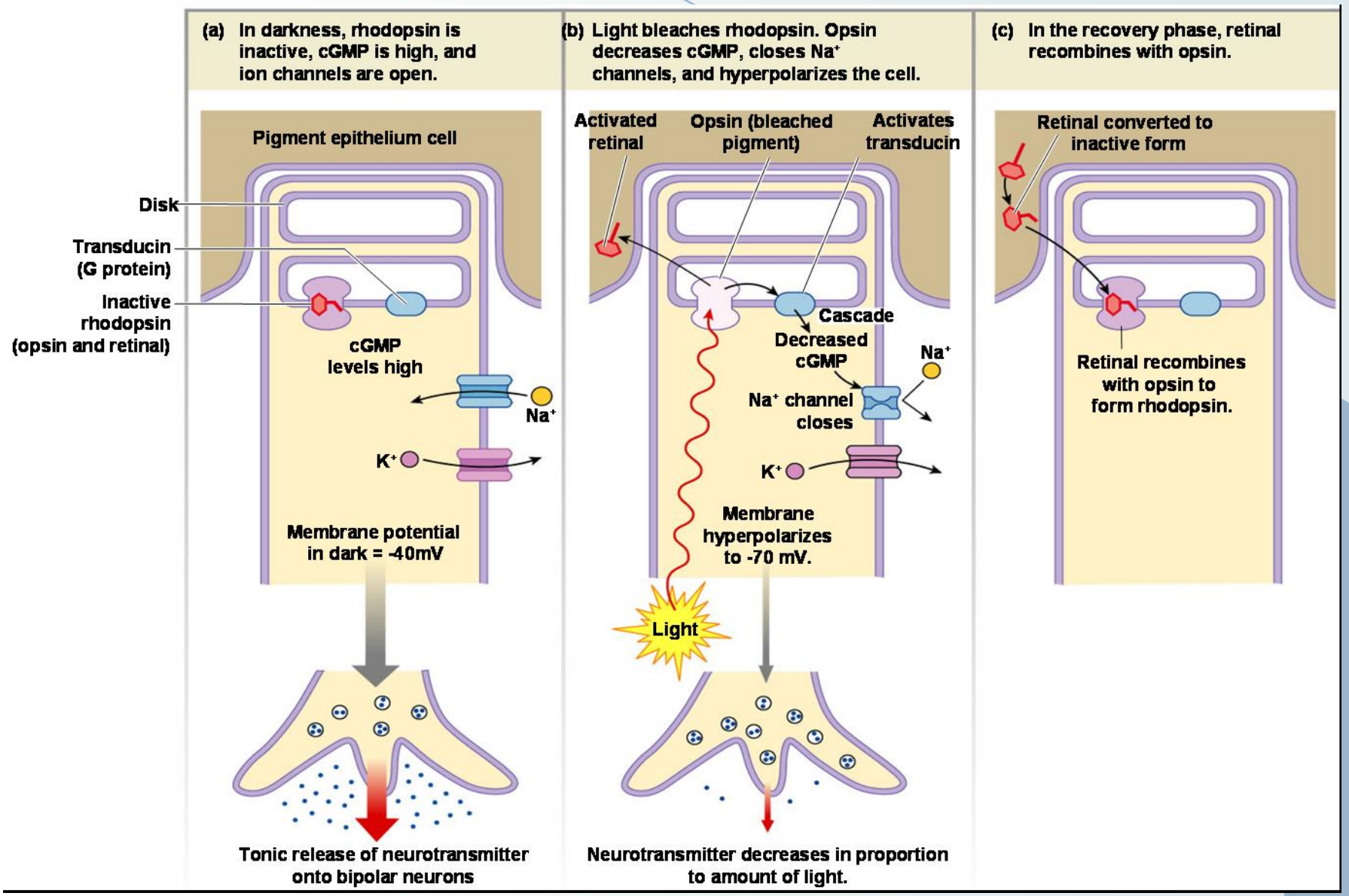
Neurotransmitters of retina

- **Glutamate**: photoreceptors, bipolar cells, horizontal cells, some amacrine cells, ganglion cells, projections to the brain
- **GABA**: interneurons, horizontal cells

Receptor and action potentials in the retina

- **receptor potential** (graded potential): photoreceptors, bipolar cells, amacrine cells
- **action potential**: ganglion cells

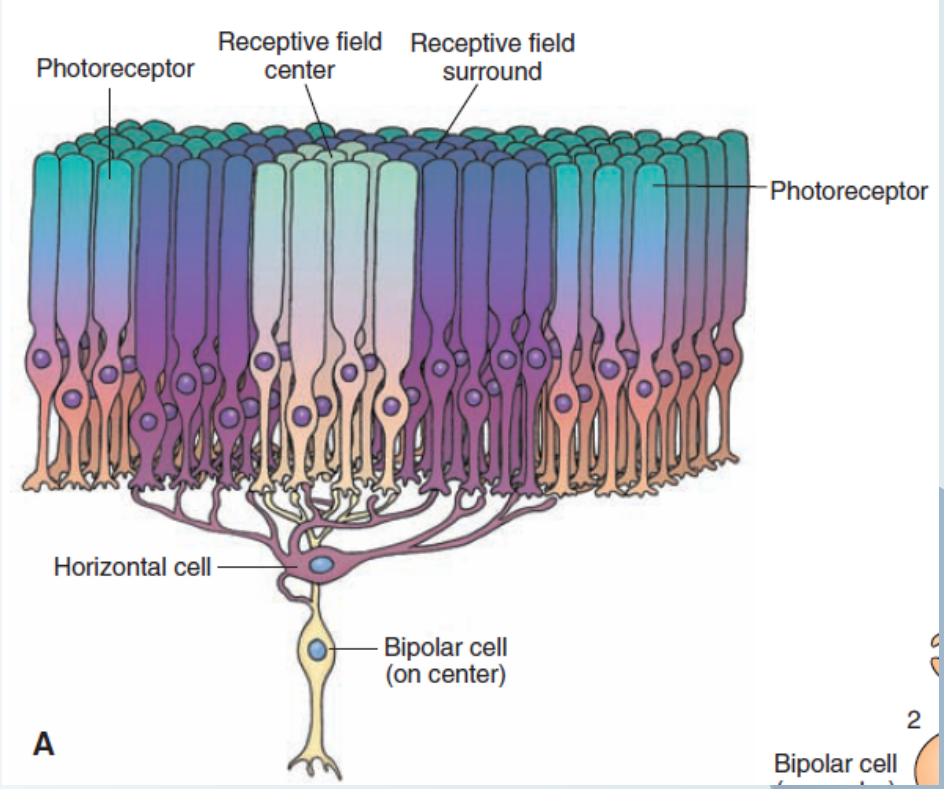
Phototransduction



PROCESSING OF SIGNALS FROM THE PHOTORECEPTORS BY DIFFERENT RETINAL CELLS

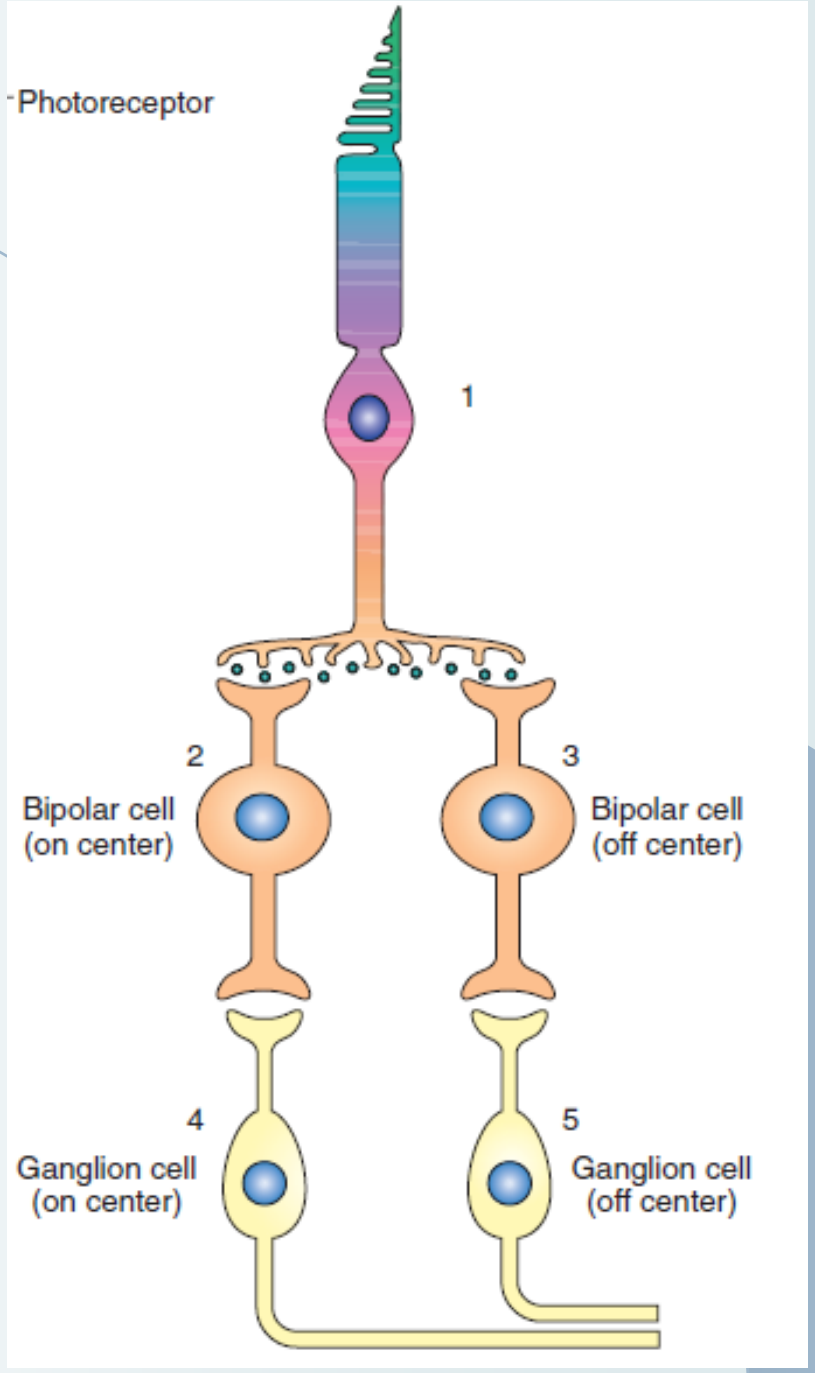
- **Bipolar, Horizontal, and Ganglion Cells**
- Bipolar cells constitute the main link in the transmission of visual signals from rods and cones to ganglion cells.
- The **receptive field** of a bipolar cell (and of ganglion cell) is a circular area that changes the membrane potential when stimulated by light stimulus.

- the ***receptive field center*** provides a **direct input** from the photoreceptors to the bipolar cells
- ***receptive field surround*** provides an indirect input from the photoreceptors to the bipolar cells **via horizontal cells**



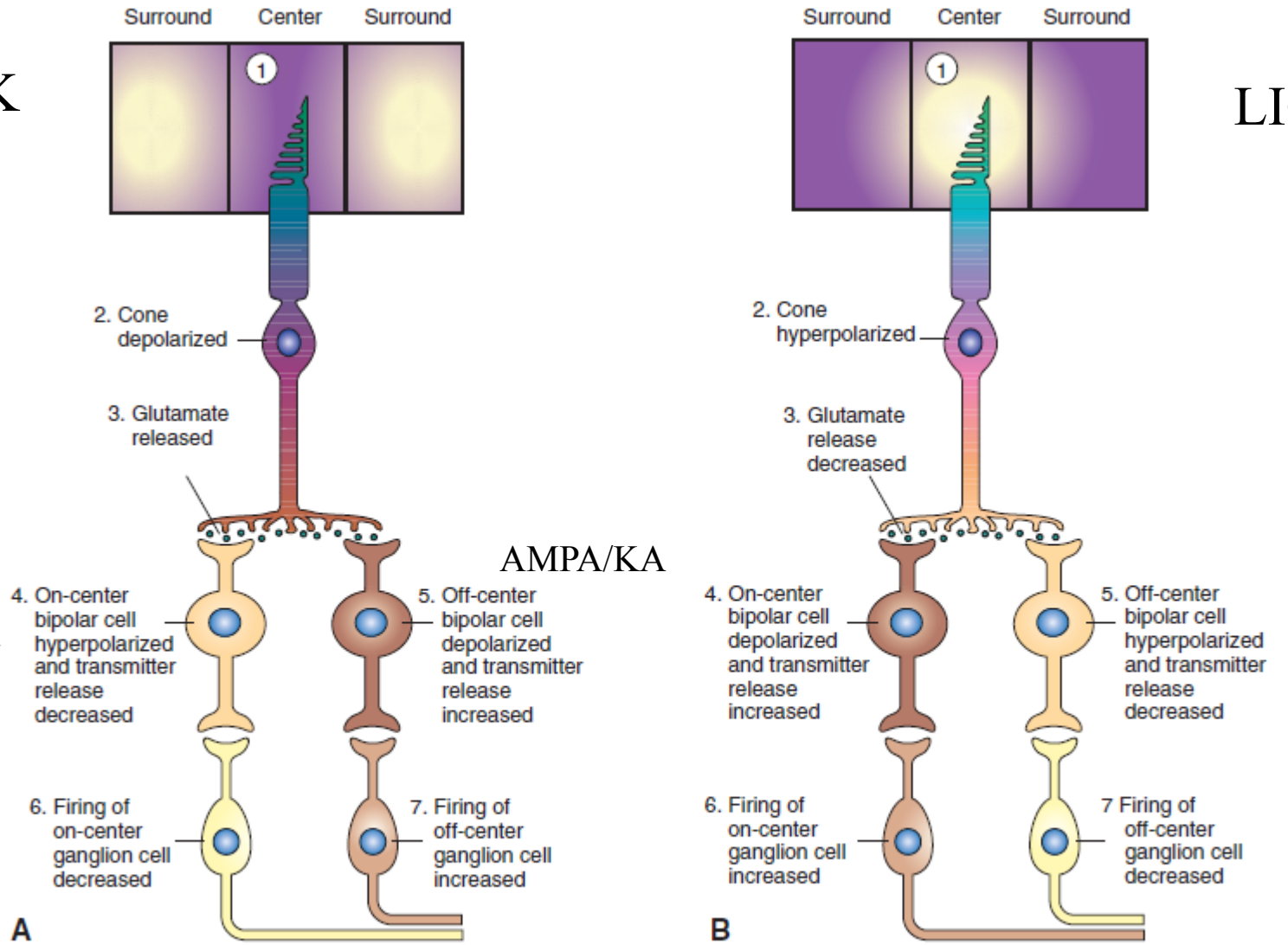
- **two populations of bipolar cells**
- *"ON"-center*
- *"OFF"-center bipolar cells*
- bipolar cells exhibit graded potentials (EPSP) rather than action potentials

- Each cone photoreceptor cell (1) synapses on an ON- (2) and an OFF-bipolar cell (3).
- Each ON-bipolar cell synapses with an ON-ganglion cell (4)
- and each OFF-bipolar cell synapses with an OFF-ganglion cell (5).



DARK

LIGHT

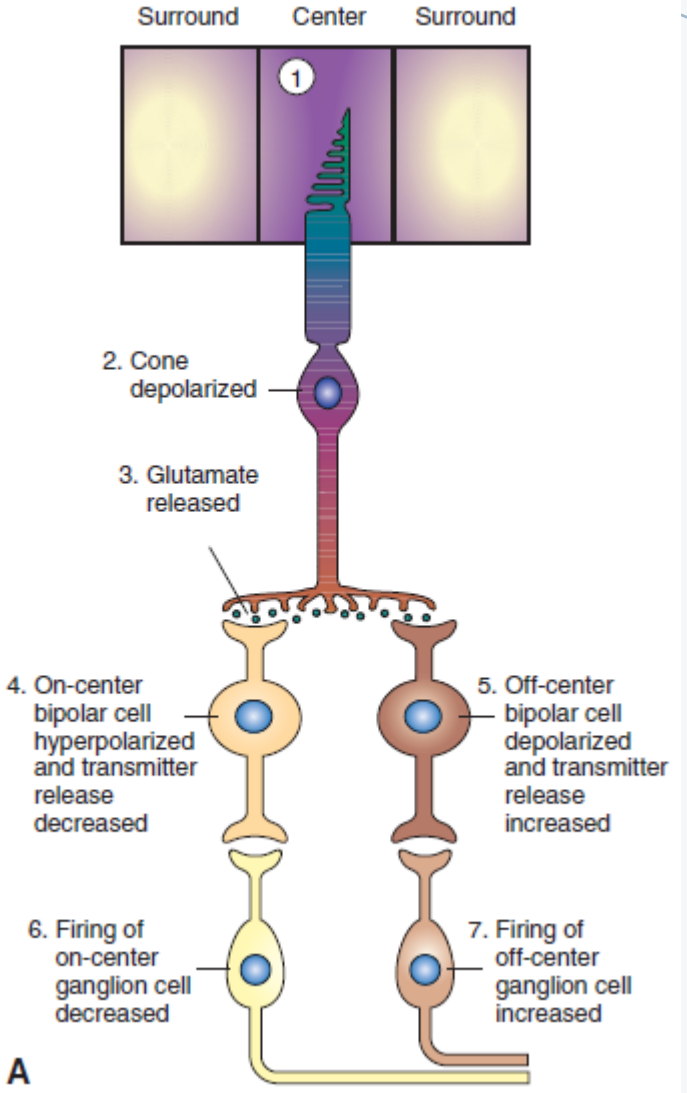


AMPA/KA

mGLUr

FIGURE 16–5 Responses of retinal bipolar and ganglion cells to darkness and illumination in the receptive field center. (A) Changes in the electrical activity of the photoreceptor and on-center and off-center bipolar and ganglion cells when the photoreceptor receptive field center is in the dark. (B) Changes in the electrical activity of the photoreceptor and on-center and off-center bipolar and ganglion cells when the photoreceptor receptive field center is illuminated. See text for details.

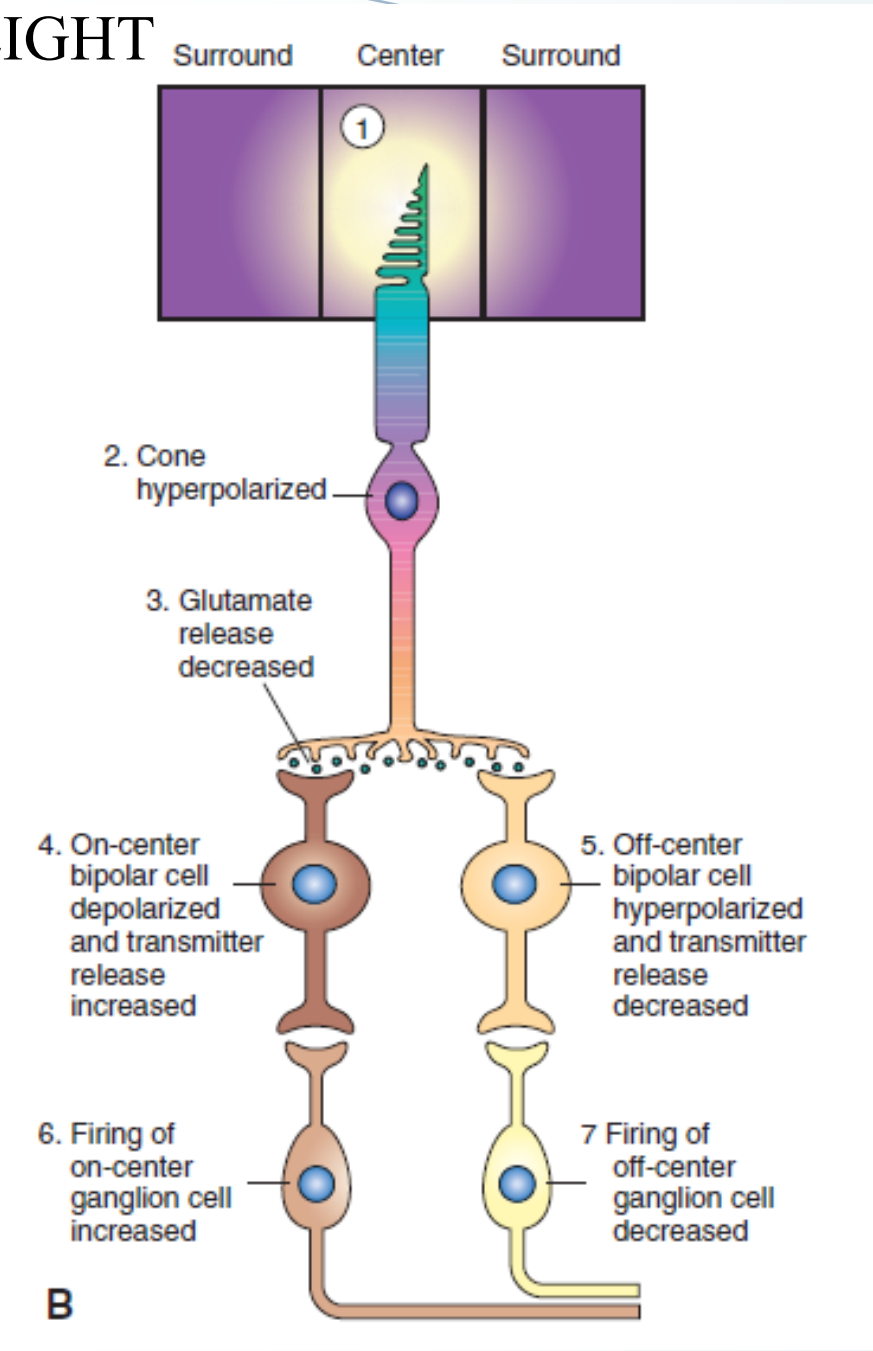
DARK



- receptive field center is in dark (1)
- photoreceptors are depolarized (2)
- they release glutamate constantly (3)
- *metabotropic glutamate receptors* on the ON-center bipolar cells are opening the K^+ (potassium) channels and ON-center bipolar cell is *hyperpolarized* (4)
- *ionotropic glutamate receptors* on the OFF-center bipolar cells stimulate Na^+ channels to open – OFF-center bipolar cell is *depolarized* (5)

- **A**: fotoreceptor in dark
- When the receptive field center is in dark (1), the photoreceptors are depolarized (2)
- they release glutamate constantly (3)
- Glutamate released from the photoreceptor terminal stimulates *metabotropic glutamate receptors* on the ON-center bipolar cells, K^+ (potassium) channels are opened, there is an efflux of K^+, the ON-center bipolar cell is *hyperpolarized*, and the release of its transmitter (probably glutamate) is decreased (4).

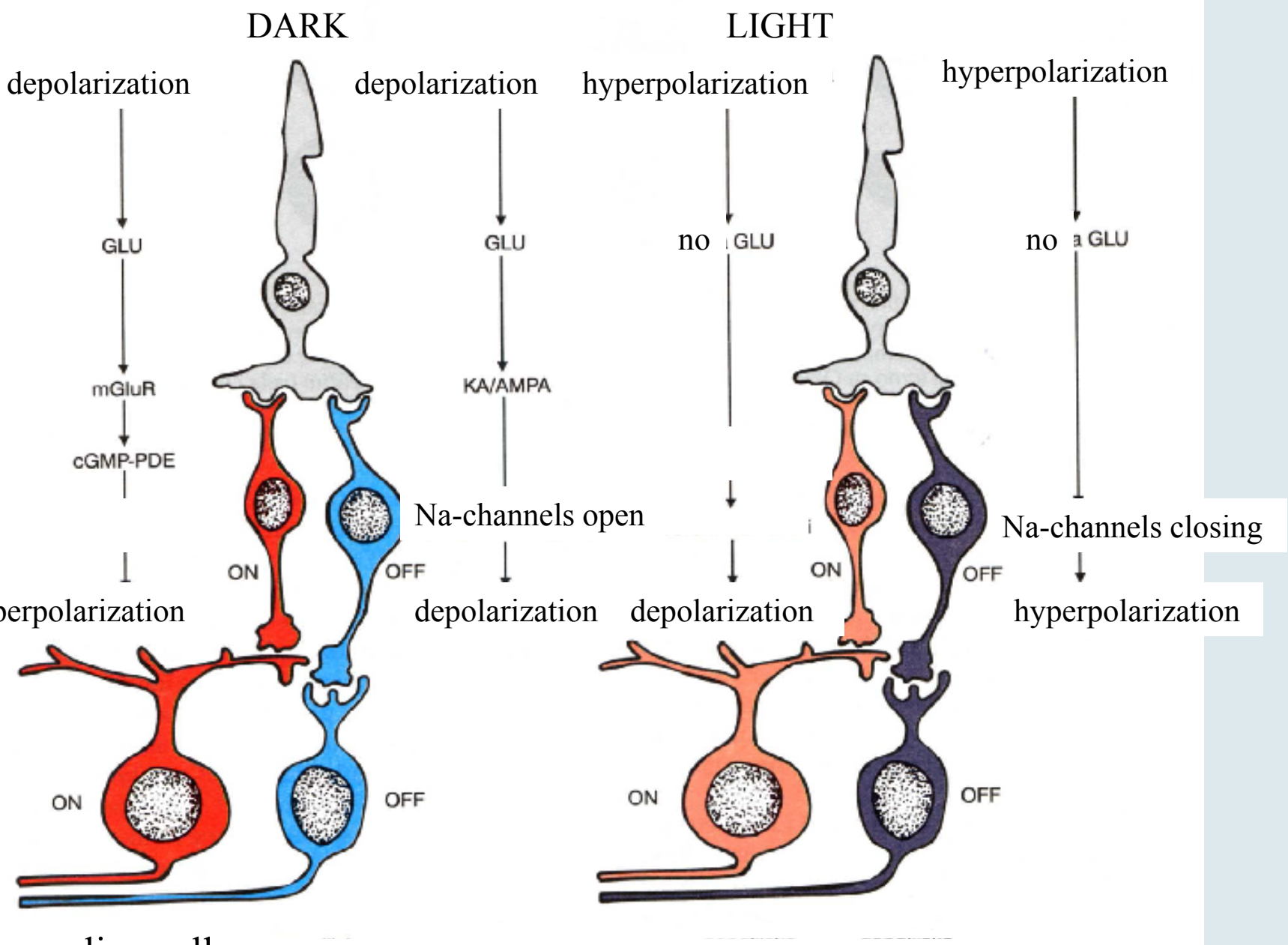
- On the other hand, glutamate released from the photoreceptor terminals stimulates *ionotropic glutamate receptors* on the OFF-center bipolar cells, Na^+ channels are opened, Na^+ flows into the cell, the OFF-center bipolar cell is *depolarized, and the* release of its transmitter (probably glutamate) is increased (5).



a light stimulus (1)
fotoreceptor is hyperpolarized (2)
glutamate release is decreased (3)
depolarization of the ON-center bipolar cell (4)
the OFF-center bipolar cell is hyperpolarized (5)
increase in the firing of the corresponding ON-center ganglion cells (6)
decrease in the firing of the corresponding OFF-center ganglion cells (7)

- **B**: fotoreceptor in light
- When the photoreceptor in the receptive field center receives a light stimulus (1), it is hyperpolarized (2).
- glutamate release from its terminals is decreased (3).
- The reduction in the release of glutamate from the photoreceptor terminals causes depolarization of the ON-center bipolar cell and an
- increase in its transmitter release (4),

- the OFF-center bipolar cell is hyperpolarized, and there is a decrease in its transmitter release (5).
- Depolarization of ON-center bipolar cells (4) results in an increase in the release of their transmitter, which, results in an increase in the firing of the corresponding ON-center ganglion cells (6).
- Hyperpolarization of OFF-center bipolar cells (5) results in a decrease in the release of their transmitter
- results in a decrease in the firing of the corresponding OFF-center ganglion cells (7)


DARK
LIGHT
depolarization
GLU
mGluR
cGMP-PDE
hyperpolarization
depolarization
GLU
KA/AMPA
Na-channels open
depolarization
hyperpolarization
no GLU
depolarization
hyperpolarization
no GLU
Na-channels closing
hyperpolarization
ON
OFF
ON
OFF
ON
OFF
ON
OFF
ON-ganglion cell inhibited
OFF-ganglion cell stimulated
ON-ganglion cell stimulated
OFF-ganglion cell inhibited

LATERAL INHIBITION

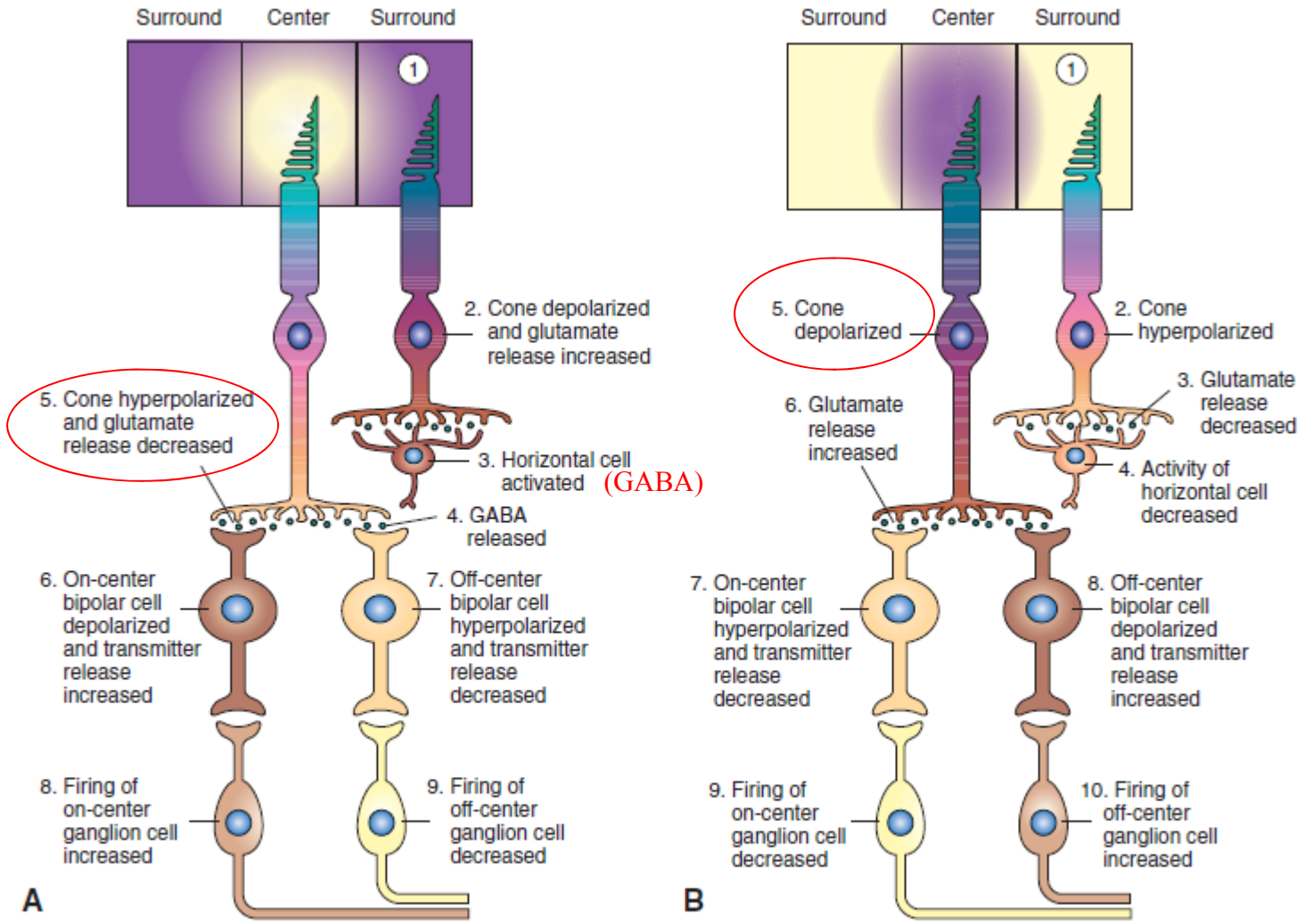
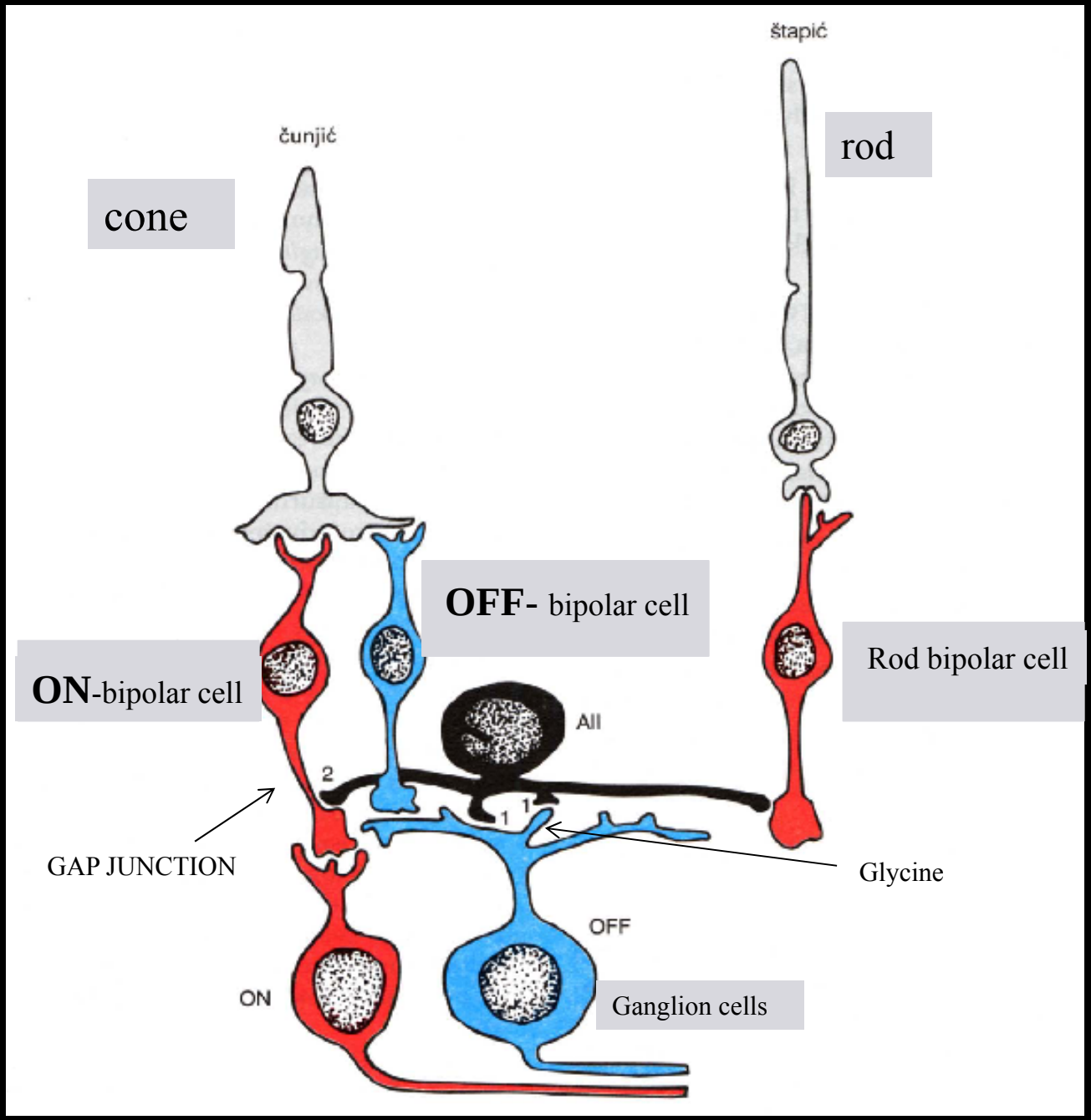


FIGURE 16–6 Responses of retinal bipolar and ganglion cells to darkness and illumination in the receptive field surround. (**A**) Changes in the electrical activity of the photoreceptor and on-center and off-center bipolar and ganglion cells when the photoreceptor receptive field surround is in the dark. (**B**) Changes in the electrical activity of the photoreceptor and on-center and off-center bipolar and ganglion cells when the photoreceptor receptive field surround is illuminated. See text for details. GABA = gamma aminobutyric acid.



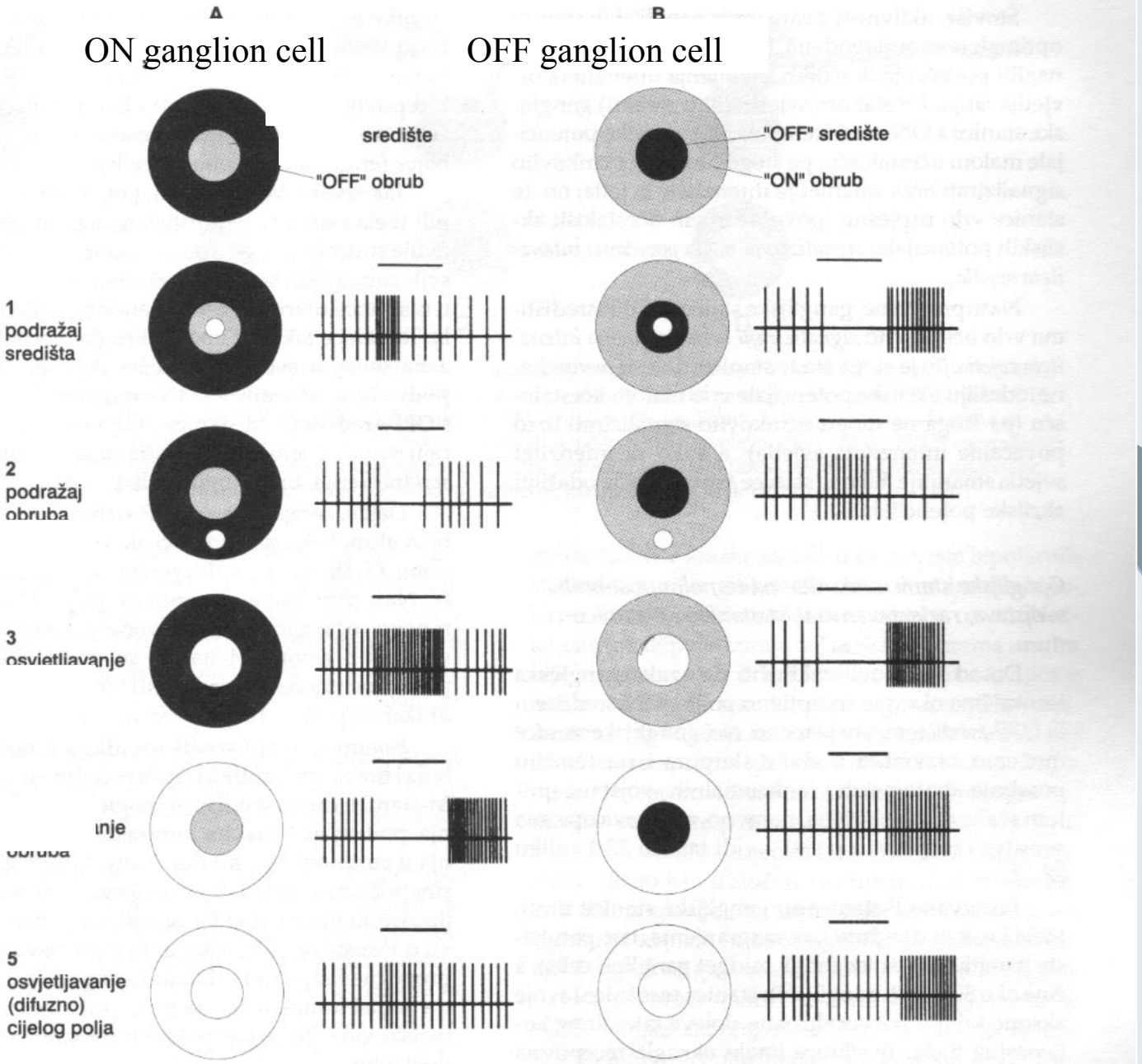
Adaptation to dark

Significance of Changes in On-Center and Off-Center Bipolar and Ganglion Cell Activities

- the changes in membrane potential of ON and OFF bipolar cells and corresponding ganglion are opposite.
- cells sensitive to contrast in illumination
- The sensitivity to the contrast properties, rather than to an absolute level of illumination, renders brightness or darkness of objects constant over a wide range of lighting conditions.

GANGLION CELLS

- 3rd neuron of the visual pathway
- Make optic nerve, project to the Corpus Genuculatum Laterale, colicullus superior, pretectal area and hypothalamus
- RECEPTIVE FIELD
  - Round, the smallest in the fovea centralis
  - **ON** or **OFF** center
  - Information about brightness and darkness of objects in a visual field is transmitted to the brain by on-center and off-center ganglion cells, respectively.


A
B
ON ganglion cell
OFF ganglion cell
središte
"OFF" obrub
"OFF" središte
"ON" obrub
1
podražaj
središta
2
podražaj
obruba
3
osvjetljavanje
5
osvjetljavanje
(difuzno)
cijelog polja

P-cells

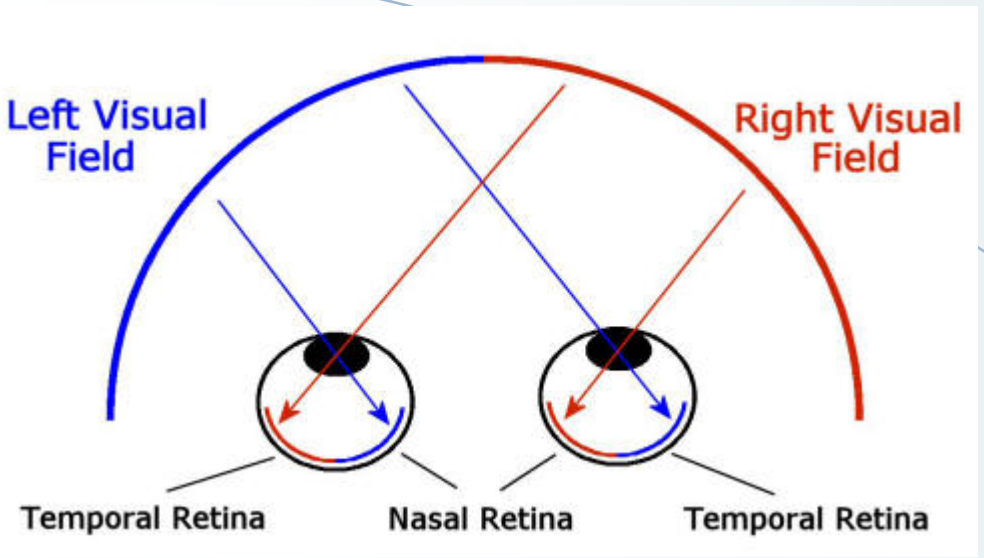
- "midget" cells
- 80% of all ganglion cells
- **ON** and **OFF** cells
- Project to the parvocelullar layers of the CGL
- sensitive to differences in wavelengths "narrow spectrum"
- Connected to cones
- Small receptive fields
- Sustained response
- transmit information
- about color and details

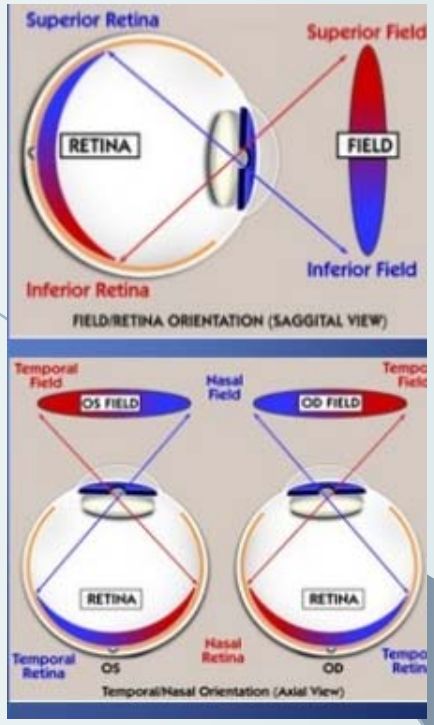
M-cells

- "parasol" cells - larger cell bodies, dendritic fields, and axons
- 10% of all ganglion cells
- **ON** and **OFF** cells
- Project to the magnocelullar layers of the CGL
- "wide spectrum"
- Big receptive fields
- Transient response
- Perception of movement
- Perception of low contrast in dark

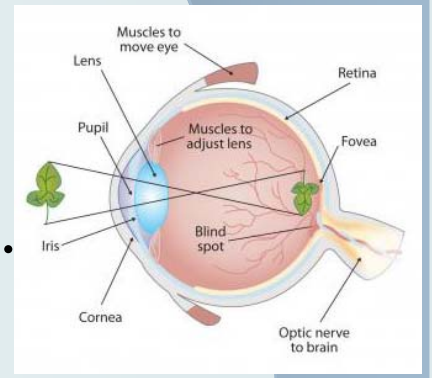
VISUAL AND RETINAL FIELDS

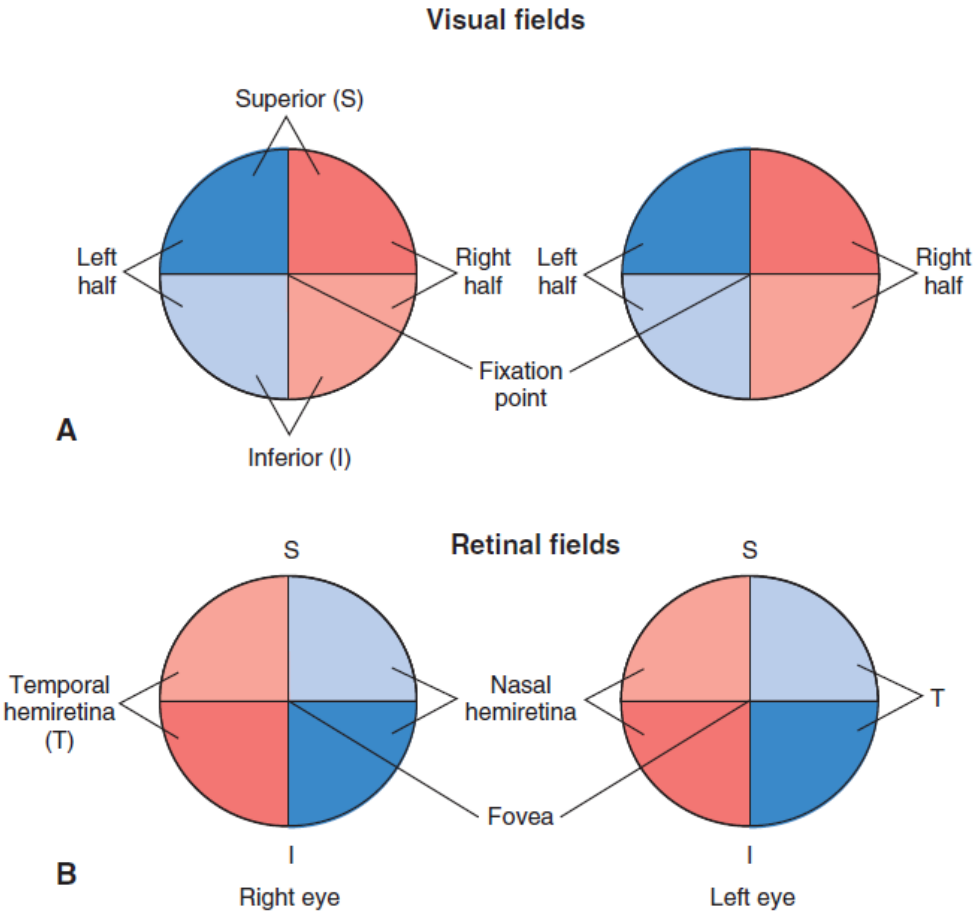
- The **visual field** of each eye is the region of space that the eye can see looking straight ahead without movement of the head.
- The fovea of each retina is aligned with a point, called the **fixation point.**
- left-half field and right-half field
- superior and inferior halves





- **retina** may be divided into:
- **nasal hemiretina** that lies medial to the fovea
- **temporal hemiretina** that is located lateral to the fovea.
- **superior** and **inferior** halves
- The images of objects in the visual field are right-left reversed and inverted on the retina.





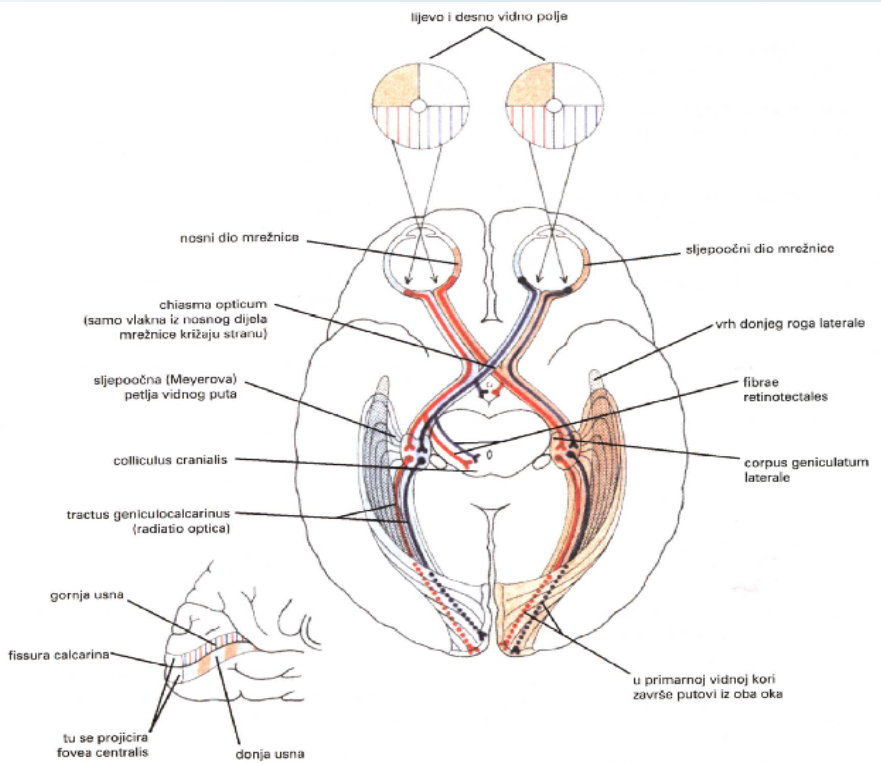
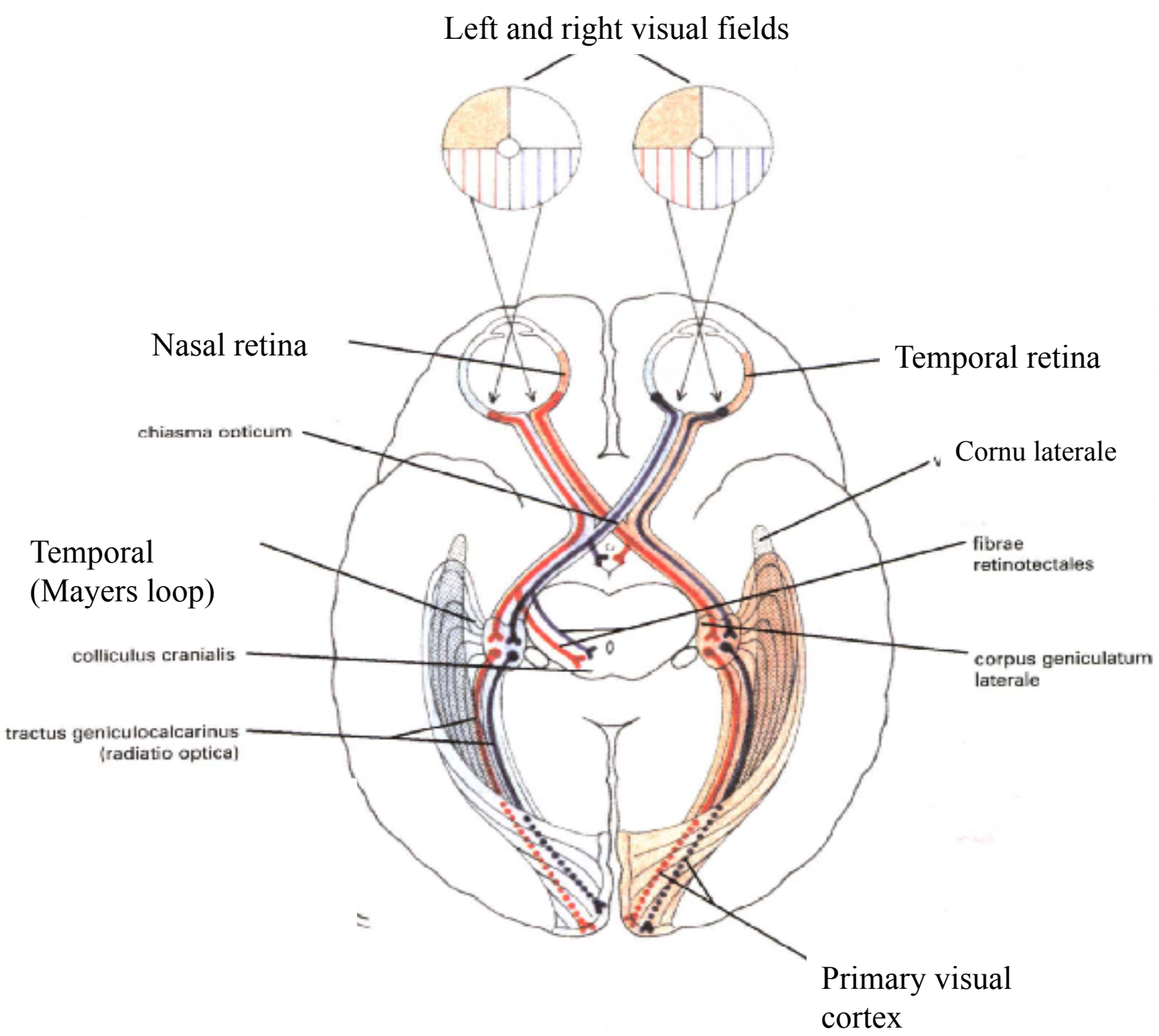
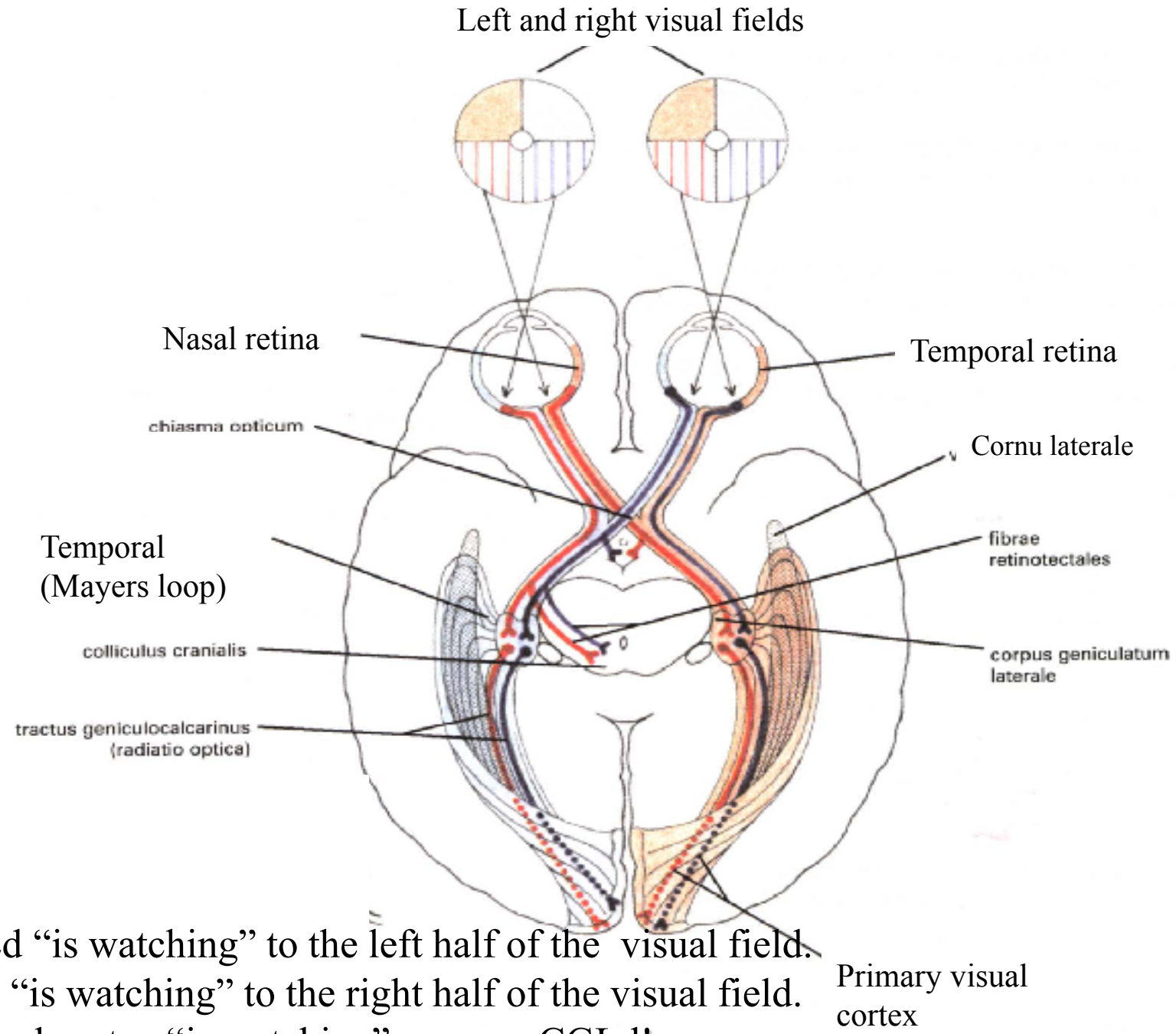


FIGURE 16–7 Visual and retinal fields. (A) Vertical lines divide the visual field of each eye in space into right and left halves. Horizontal lines divide the visual field of each eye into superior and inferior halves. These lines intersect at the fixation point. (B) Vertical lines divide the retina of each eye into temporal and nasal hemiretinae. Horizontal lines divide the retina of each eye into superior and inferior halves. These lines intersect at the fovea.


Left and right visual fields
Nasal retina
Temporal retina
chiasma opticum
Cornu laterale
Temporal
(Mayers loop)
fibrae
retinotectales
colliculus cranialis
corpus geniculatum
laterale
tractus geniculocalcarinus
(radiatio optica)
Primary visual
cortex



Right CGLd “is watching” to the left half of the visual field.
Left CGLd “is watching” to the right half of the visual field.
Primay visual cortex “is watching” same as CGLd!

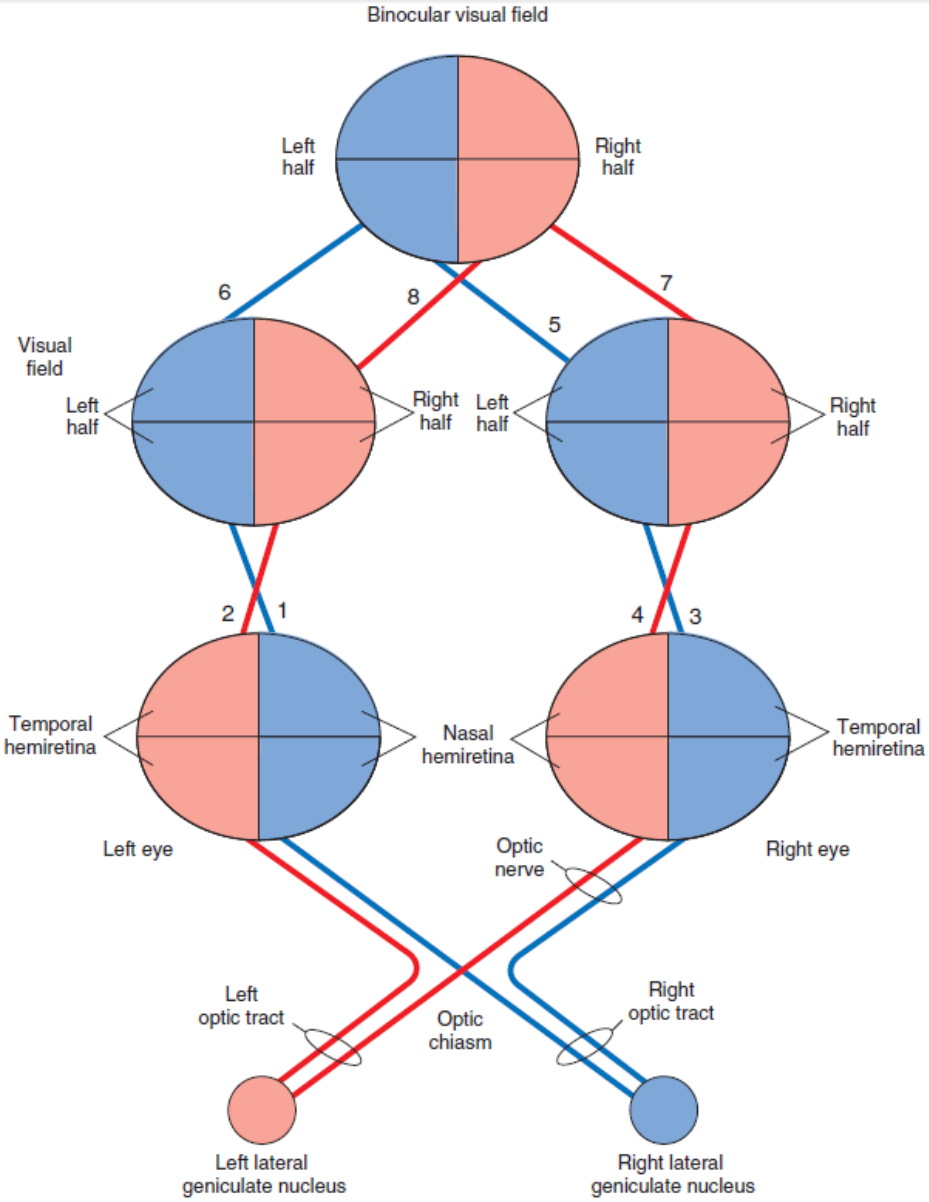


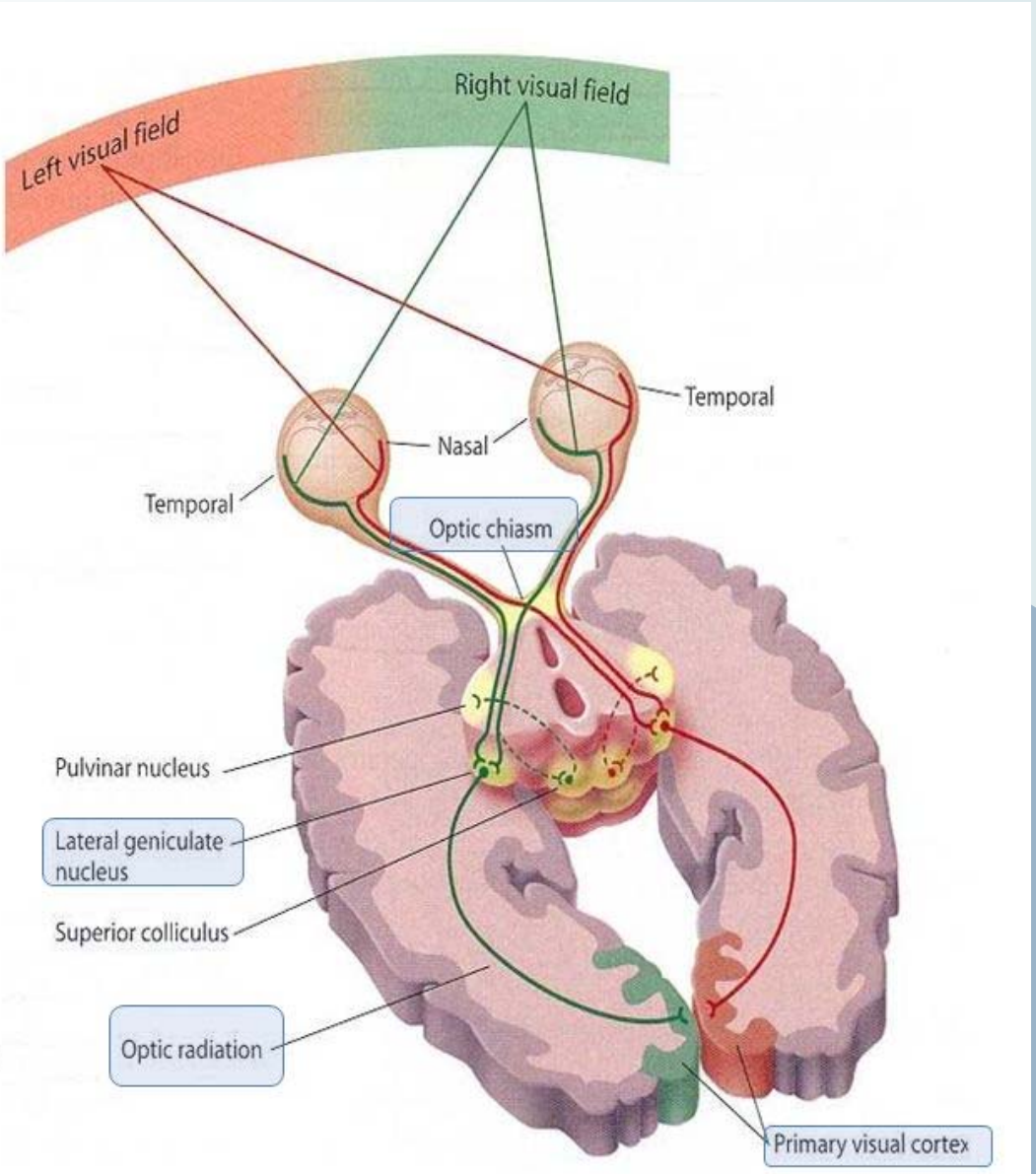
FIGURE 16–8 Relationship between the visual fields and retinae. 1 and 2: The nasal half of the left eye sees objects in the left half of the visual field of the left eye (*shown in blue*) and the temporal half of the left eye sees objects in the right half of the visual field of the left eye *(shown in red)*. 3 and 4: Relationship between the visual fields and hemiretinae of the right eye is similar to that of the left eye. 5 and 6: When the visual fields of the two eyes are superimposed, the left halves of the two eyes coincide to form the left half of the binocular visual field (*shown in blue*). 7 and 8: When the visual fields of the two eyes are superimposed, the right halves of the two eyes coincide to form the right half of the binocular visual field *(shown in red)*. Each optic nerve contains axons from the nasal and temporal hemiretinae. At the optic chiasm, the axons from the nasal hemiretinae cross to the contralateral side, whereas the axons from the temporal retinae remain uncrossed. The crossed and uncrossed axons on each side form the optic tracts.

VISUAL PATHWAYS

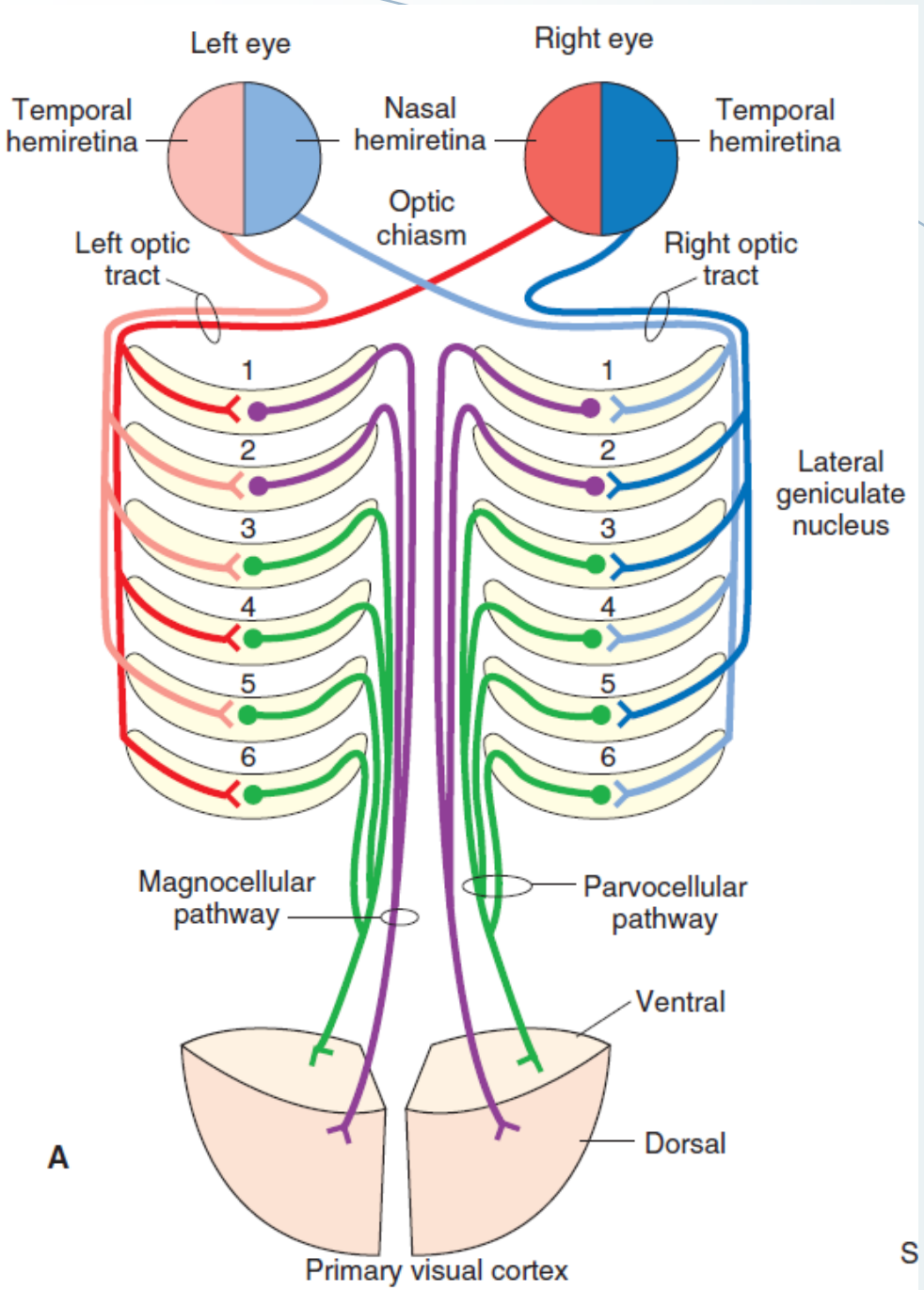
- The axons of ganglion cells travel towards the posterior pole of the eye where the **optic disc** is located.
- When the optic nerves of the two eyes reach the brain, they join to form the **optic chiasm.**
- the fibers representing the nasal half of the retina of each eye cross to the contralateral side
- fibers on each side join to form the **optic tracts.**
- The optic tracts project to the **lateral geniculate nucleus** of the thalamus

Visual Pathway

1. Cones
2. Bipolar neurons
3. Ganglion cell's axon forms the optic nerve
4. Optic nerve to the Optic Chiasm
5. Optic tract
6. Lateral geniculate nuclei of the thalamus
7. Optic Radiations
8. Primary visual areas of the occipital lobes



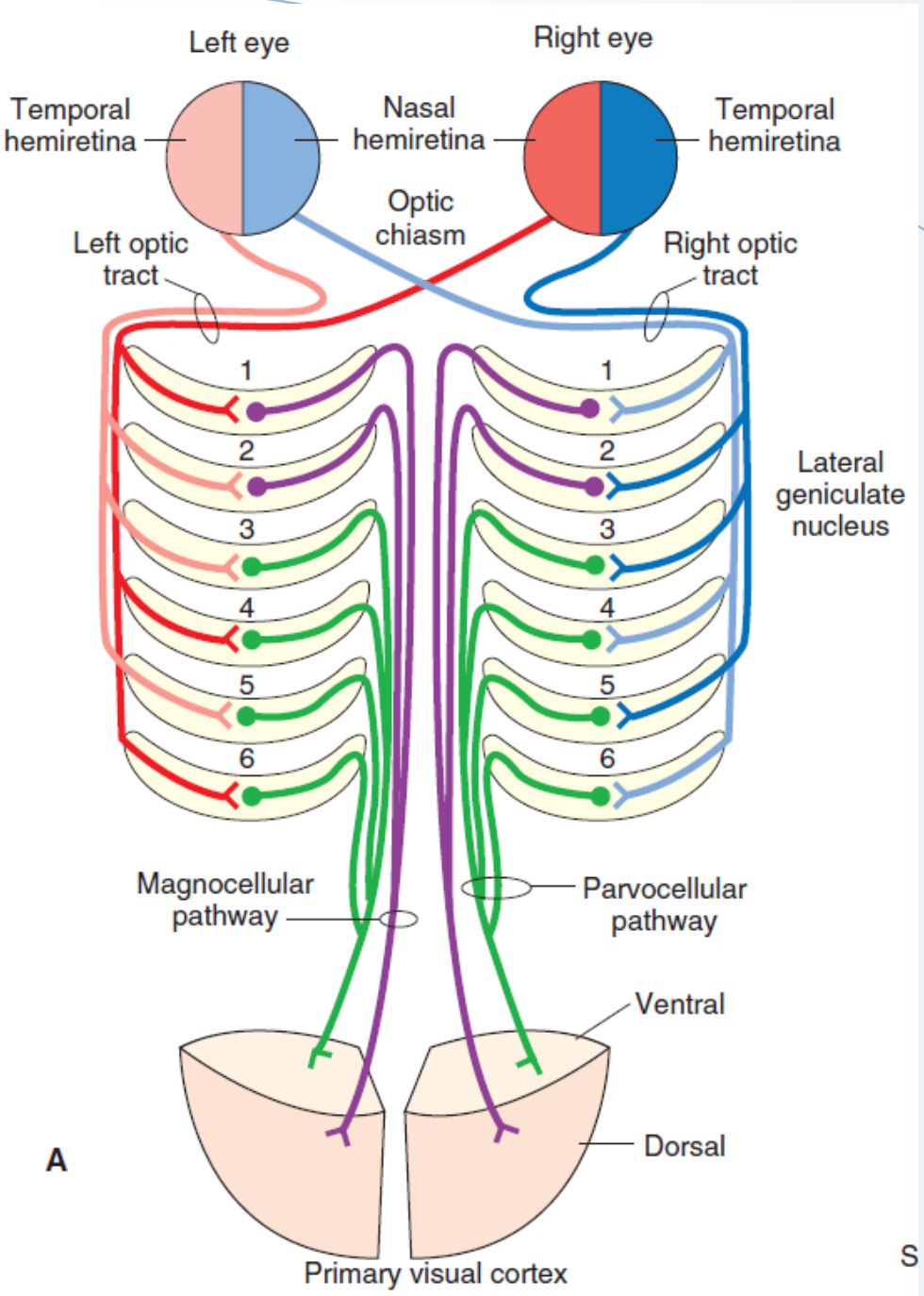
The Lateral Geniculate Nucleus of Thalamus (Corpus geniculatum laterale, CGL)



consists of 6 layers

The ventral layers (layers 1 and 2) are called **magnocellular** layers because they contain large cells. Injury reduces the ability to detect fast-moving visual stimuli.

projects to more dorsal portions (superficial regions, 4Cα) of the **primary visual cortex.**

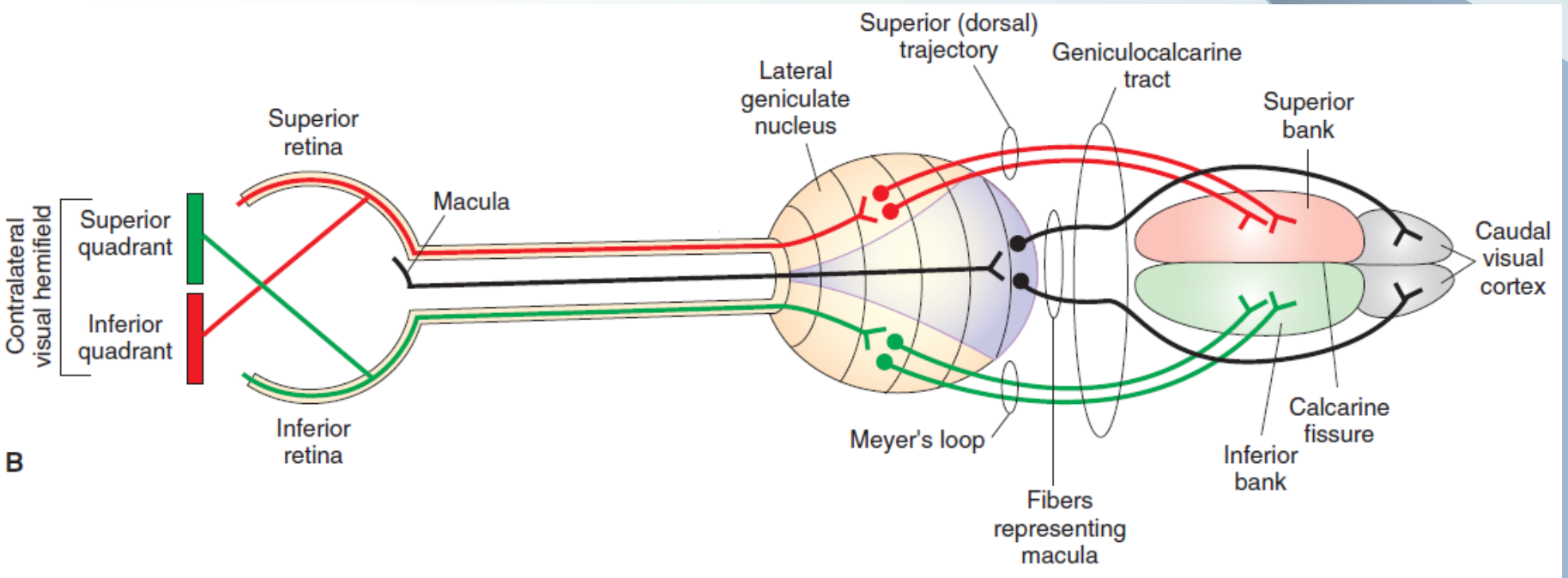


The Lateral Geniculate Nucleus of Thalamus (Corpus geniculatum laterale, CGL)

the dorsal layers (layers 3, 4, 5, and 6) are called **parvocellular** layers because they contain cells of smaller size. Damage eliminates color vision and impairs visual acuity.
projects to more ventral portions (deeper regions, 4A and 4Cβ) of the **primary visual cortex.**
Axons from the contralateral nasal hemiretina project to layers 1, 4, and 6
Axons from the ipsilateral temporal hemiretina project to layers 2, 3, and 5

The Geniculocalcarine Tract

- **geniculocalcarine tract** (also known as **optic radiations)** projects to the **primary visual cortex** (medial aspect of the occipital lobe of the cortex).



- Claudia Krebs Visual pathway:
- **https://www.youtube.com/watch?v=TbDFrbXiz2s**

Visual Cortex

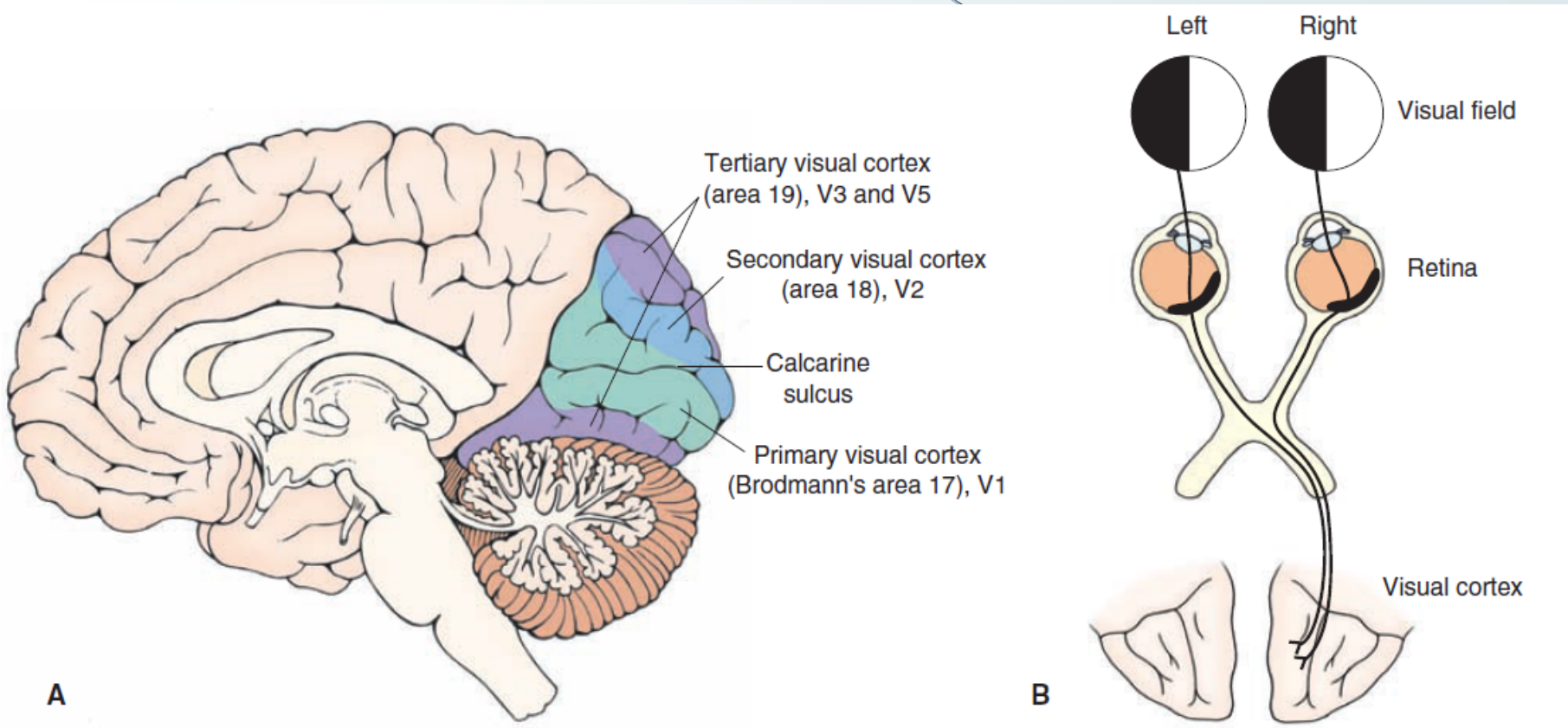


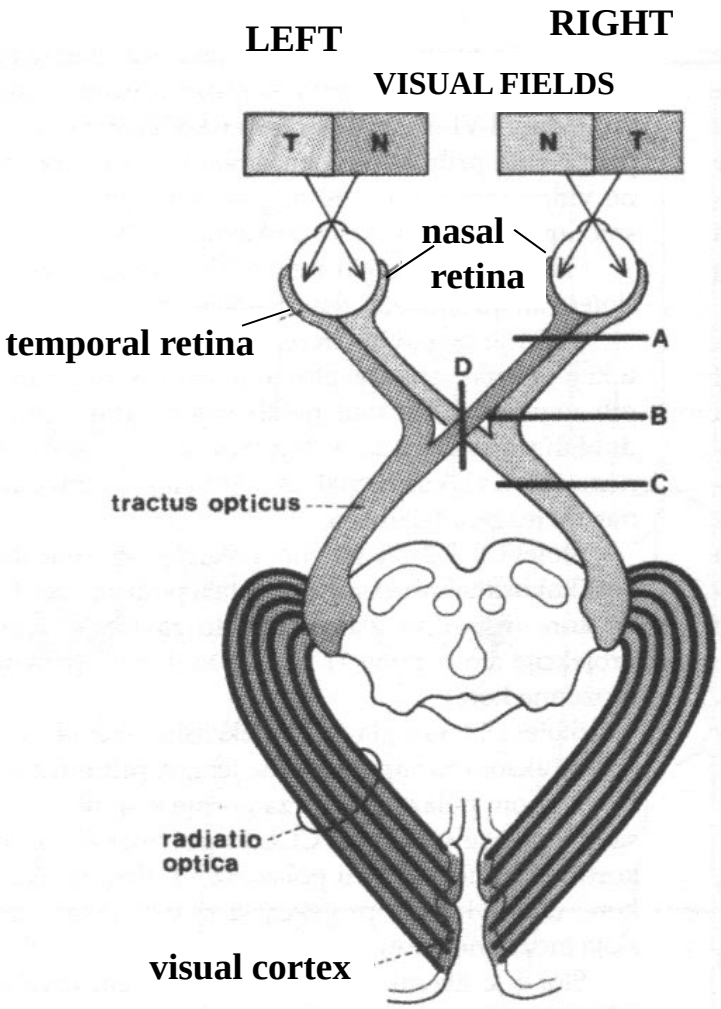
FIGURE 16–10 The visual cortex. (A) Note the location of the primary visual cortex ([V1] Brodmann's area 17), the secondary visual cortex ([V2] Brodmann's area 18), and the visual areas V3 and V5 (Brodmann's area 19). (B) Information from the nasal retina of the left eye and temporal retina of the right eye (representing the left visual field of both eyes) is directed to the right visual cortex. Likewise, information from the nasal retina of the right eye and temporal retina of the left eye (representing the right visual field of both eyes) is directed to the left visual cortex (not shown).

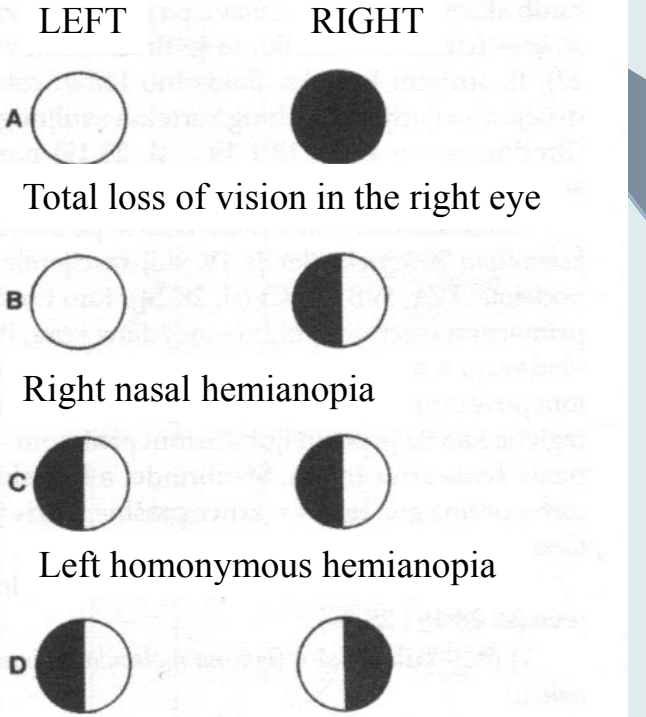
- The primary visual cortex (V1, **Brodmann's area 17)** receives projections from the lateral geniculate nucleus of the thalamus.
- The secondary visual cortex **(association, extrastriate,** or **prestriate areas)** (V2 **Brodmann's area 18) and tertiary visual cortex** (V3 (form) and V5 (motion) **Brodmann's area 19)**
- Visual area V4 (color) is located in the inferior occipitotemporal area
- The primary visual cortex sends projections to the secondary visual cortex; from here, this information is relayed to the tertiary visual cortex

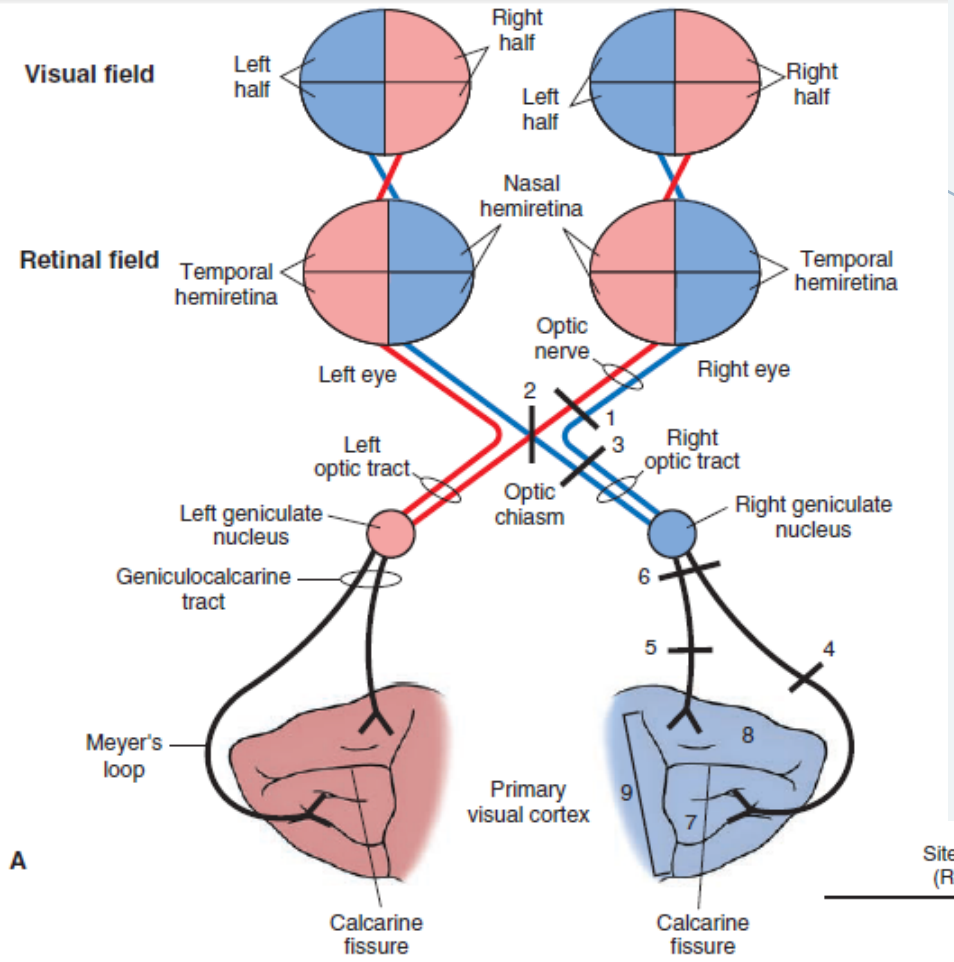
The Superior Colliculus

- controls **saccadic (high velocity)** eye movements
- Colliculus receive converging inputs from: the retina, the visual cortex, somatic sensory and auditory systems.
- the deeper layers of the superior colliculus control motor mechanisms responsible for saccadic movements and orientation of the eyes towards the stimulus

DEFICITS AFTER A LESION AT DIFFERENT SITES IN THE VISUAL PATHWAY







A

Site of Lesion (Right side)	Deficit in the visual field: Left eye	Deficit in the visual field: Right eye	Name of the disorder
Optic nerve: 1			a. Total loss of vision in the right eye
Optic chiasm (midline): 2			b. Non-homonymous bitemporal hemianopia
Optic tract: 3			c. Contralateral (left) homonymous hemianopia
Temporal lobe (Meyer's loop); 4			d. Superior left homonymous quadrantanopia (pie in the sky disorder)
Parietal lobe: 5			e. Inferior left homonymous quadrantanopia (pie in the floor disorder)
Geniculocalcarine tract: 6			f. Contralateral (left) homonymous hemianopia
Inferior bank of calcarine fissure: 7			g. Superior left homonymous quadrantanopia (with macular sparing)
Superior bank of calcarine fissure: 8			h. Inferior left homonymous quadrantanopia (with macular sparing)
Both banks of calcarine fissure: 9			i. Contralateral (left) homonymous hemianopia (with macular sparing)

B

Primary visual cortex

- is located on the superior and inferior banks of the **calcarine sulcus** on the medial side of the occipital lobe
- The secondary and tertiary visual cortex (V2, **18, 19)** are located adjacent to the primary visual cortex
- Visual area V4 is located in the inferior occipito-temporal area

Molecular layer

External Granular layer

External pyramidal layer

(A, B)

Internal granular layer

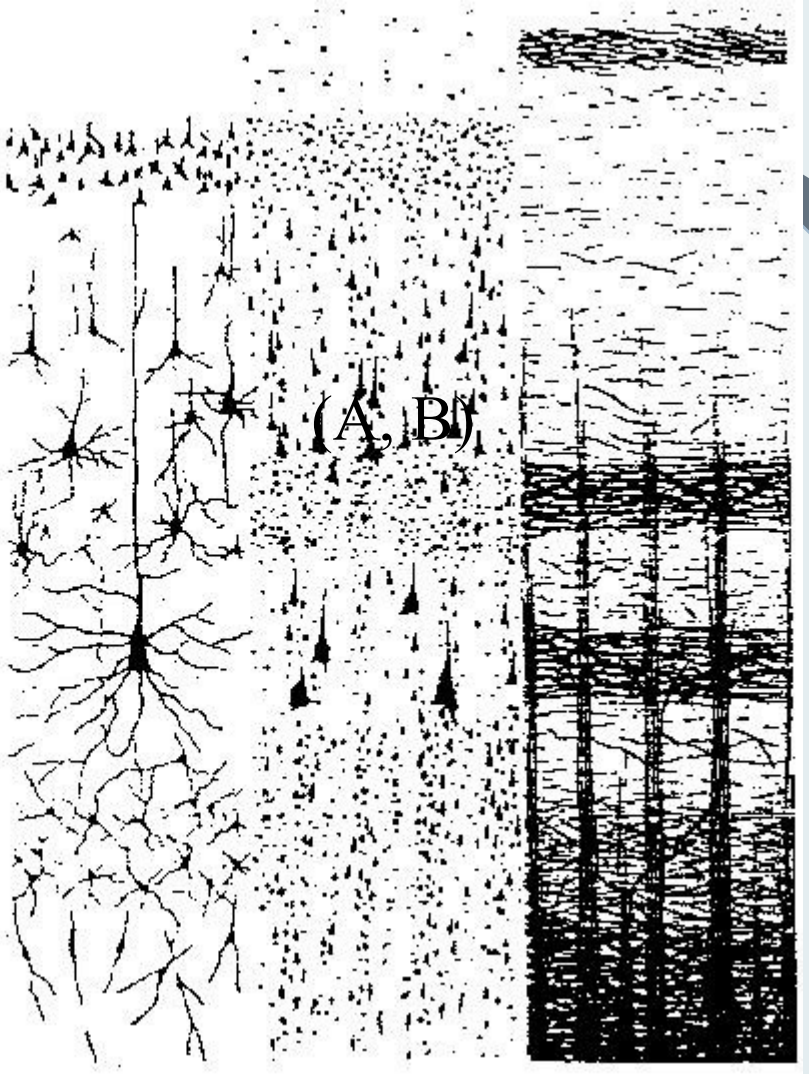
(A, B, Cα, Cβ)

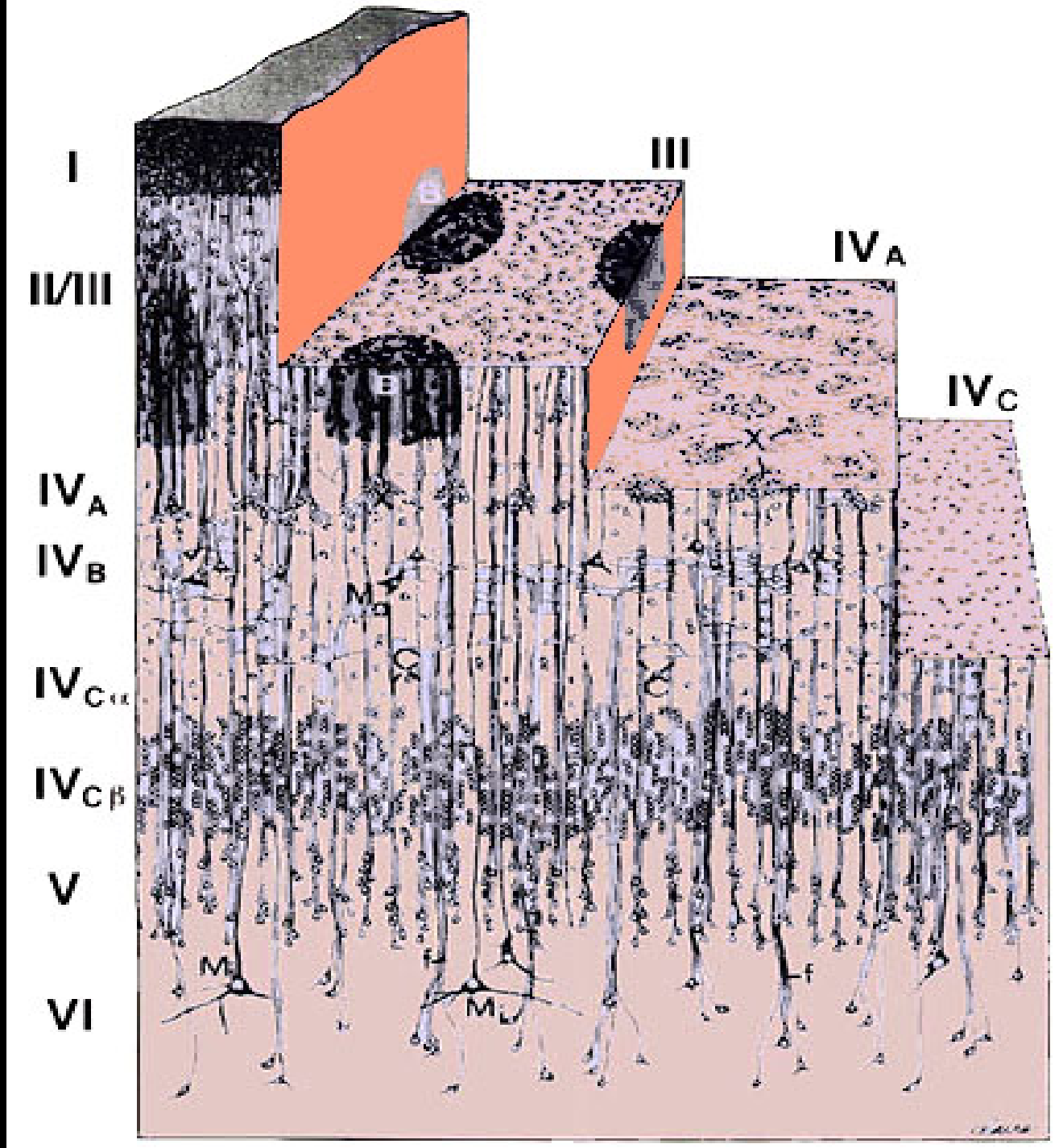
Internal pyramidal layer

(A, B)

Mutiform layer

(A, B)




I
II/III
III
IV A
IV C
IV A
IV B
IV C α
IV C β
V
VI
B
B
X
M
C
C
M
M
f
f
L f

- Layer 1: afferent polysinaptic area
- Layer 2: source of asociative cortico-cortical aksons
- Layer 5 i 6: projection aksons to the subcortical nuclei (layer 5 for The Superior Colliculus, layer 6 for CGLd and Pulvinar)
- Layer 4: main afferent layer: P pathway into the 4A and 4Cβ, M pathway into the 4Cα.

- **color** processing takes place in the blob areas
- whereas the interblob areas contain **orientation columns**

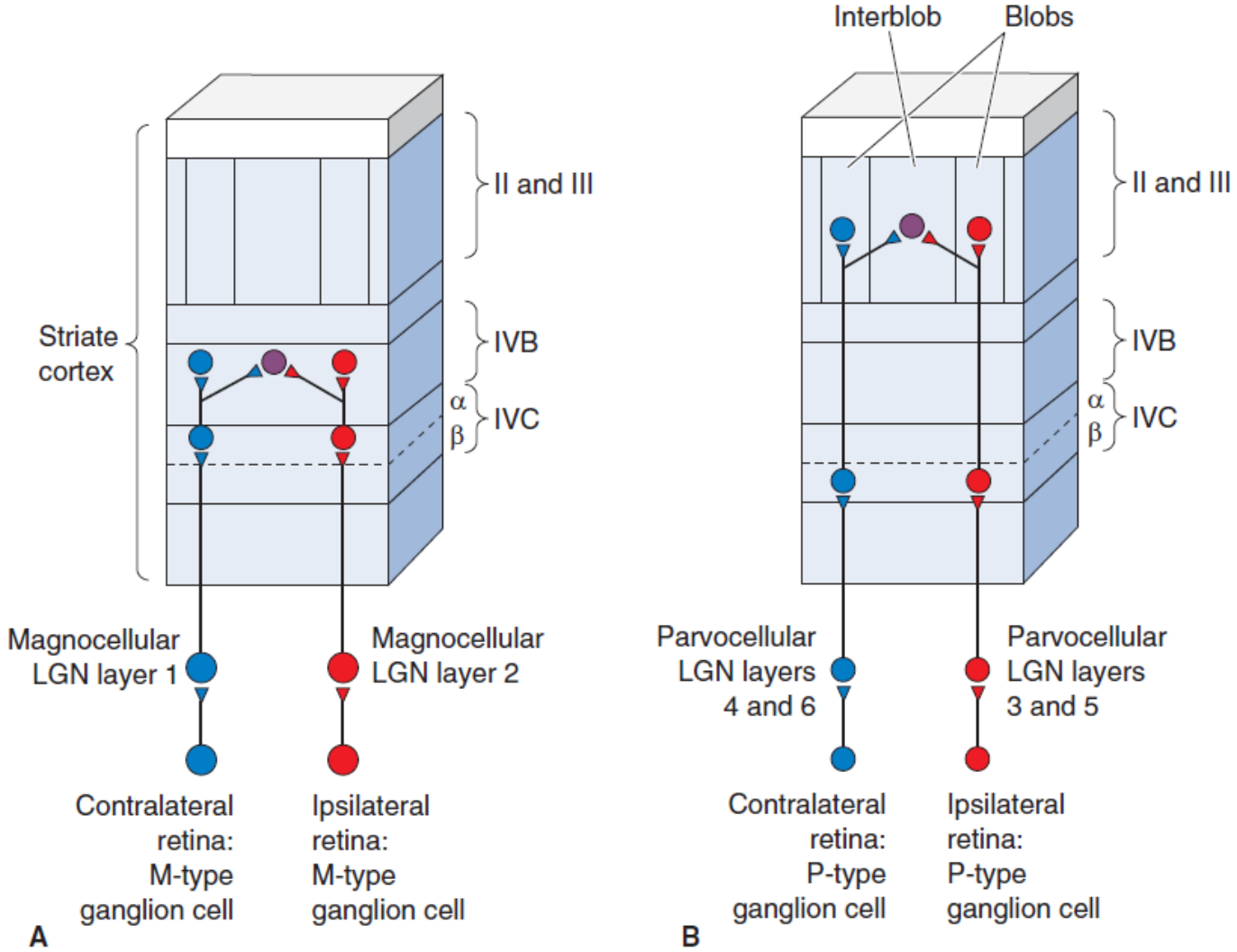
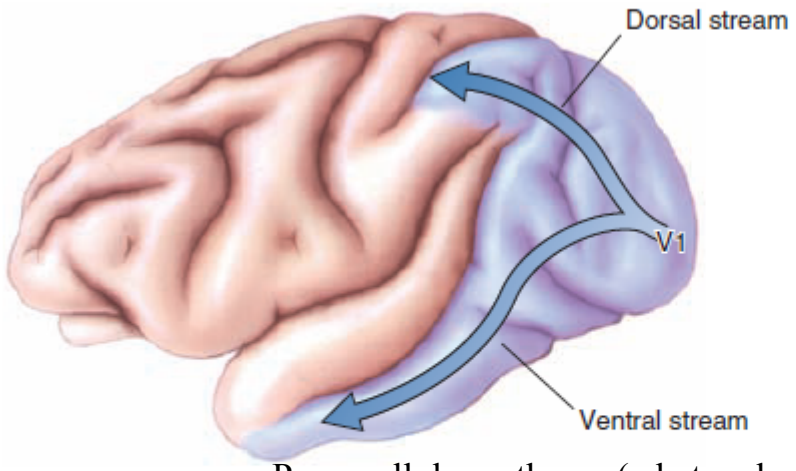
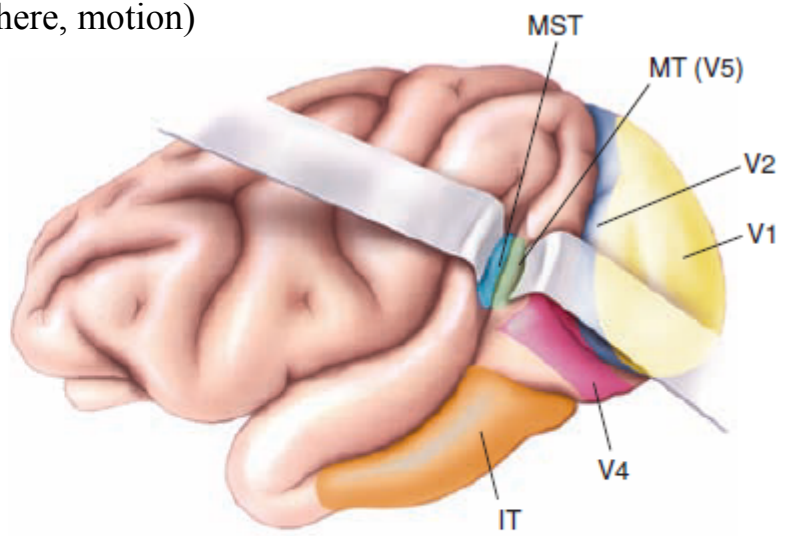


FIGURE 26–13 Retinal projections to the visual (striate) cortex. (A) Projections of the magnocellular pathway, which is associated with identification of the visual image, to upper parts of layer IV. (B) Parvocellular pathway, which is associated with form and color, to lower parts of layer IV. LGN = lateral geniculate nucleus; IVB = layer IVB of visual cortex; IVC = layer IVC of visual cortex. (From Bear MF, et al.: Neuroscience: Exploring the Brain, 2nd ed. Philadelphia: Lippincott Williams & Wilkins, 2001, p. 331.)

Magnocellular pathway (how, where, motion)



Parvocellular pathway (what, color)



A B

FIGURE 26–14 Processing of visual information outside the visual cortex. (A) Fibers mediating visual information pass both dorsally and ventrally from the primary visual cortex to both the parietal and temporal lobes. (B) The dorsal pathway also supplies neurons of the temporal and neighboring parietal cortices (labeled as MT [middle temporal gyrus] and MST [medial superior temporal gyrus]) that respond to specific directional properties of movement of objects. The ventral pathway supplies neurons of the inferotemporal (IT) aspect of the temporal lobe, which respond to faces. (From Bear MF, et al.: Neuroscience: Exploring the Brain, 3rd ed. Philadelphia: Lippincott Williams & Wilkins, 2007, p. 333.)

- different classes of neurons in the visual cortex respond to bars (linear properties) of light and their orientations.
- **simple cell:** receptive fields of the simple cells are considerably larger than stellate cells
- simple cells are rectangular in form and have specific excitatory foci and inhibitory surrounds.
- different groups of cells can respond to various orientations of light

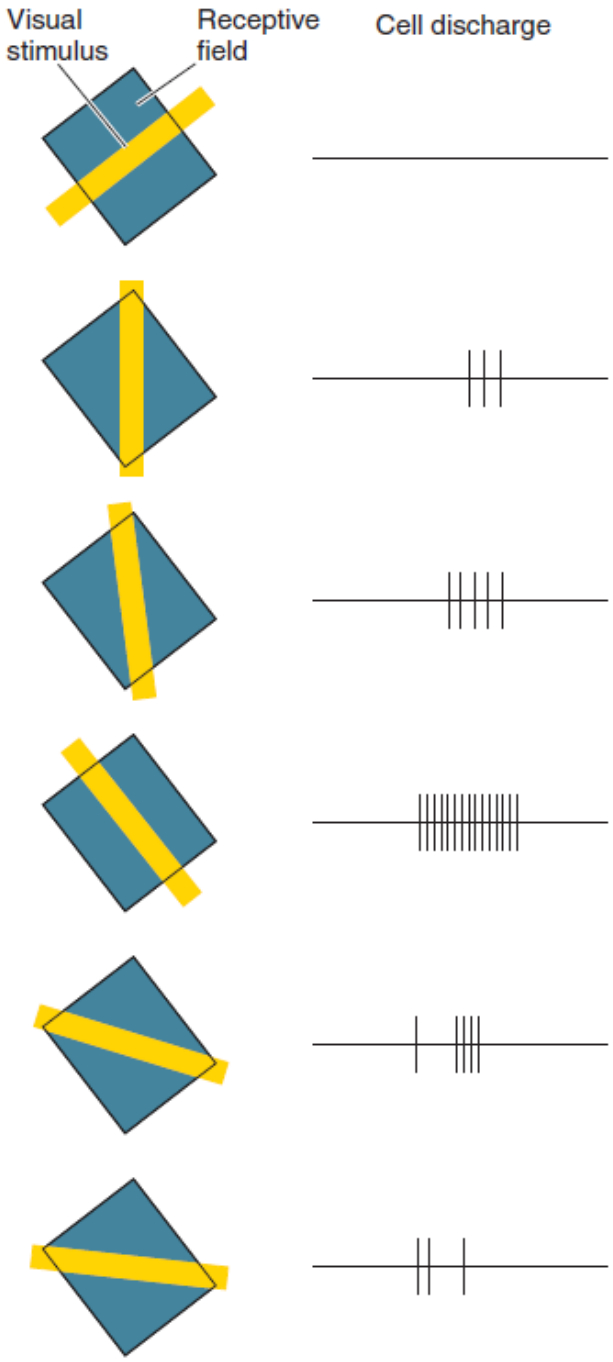


FIGURE 26–15 Orientation-sensitive simple cell. Illustration demonstrates that a simple cell in the primary visual cortex responds maximally to a bar of light oriented approximately 45° to the vertical. Bars of light oriented differently evoke a much weaker neuronal response, especially if the orientation is opposite of that which evokes a maximal response. When spots of light are presented, the response of the cortical neuron is much weaker and diffuses light. The basic concept involves the notion of a convergence of similar center-surround organizations that are simultaneously excited when light falls along a straight line in the retina and, thus, strikes the receptive fields of these cells. These cells then converge upon a single cell in the visual cortex, thereby establishing an excitatory region that is elongated. (From Bear MF, et al.: Neuroscience: Exploring the Brain, 3rd ed. Philadelphia: Lippincott Williams & Wilkins, 2007, p. 325.)

- **Complex cells** differ from simple cells in that complex cells have larger receptive fields
- the “on” and “off” zones are not clearly defined
- complex cell will respond to the same orientation of the beam but will extend to different receptive fields

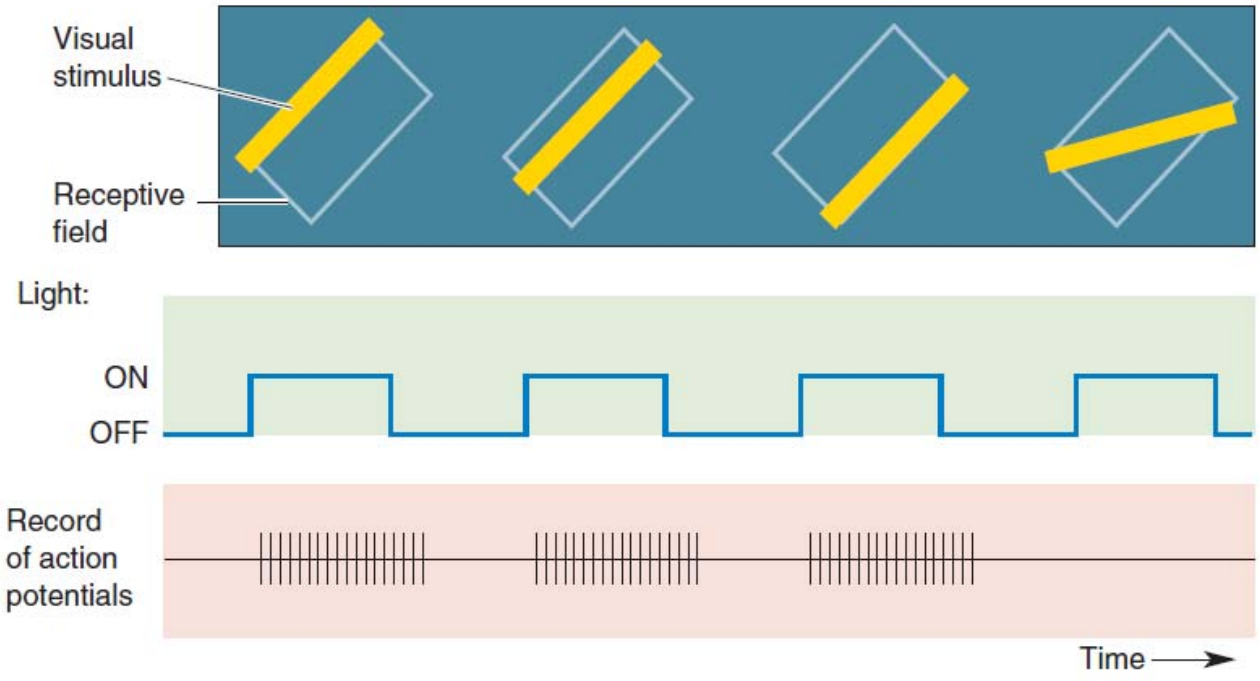
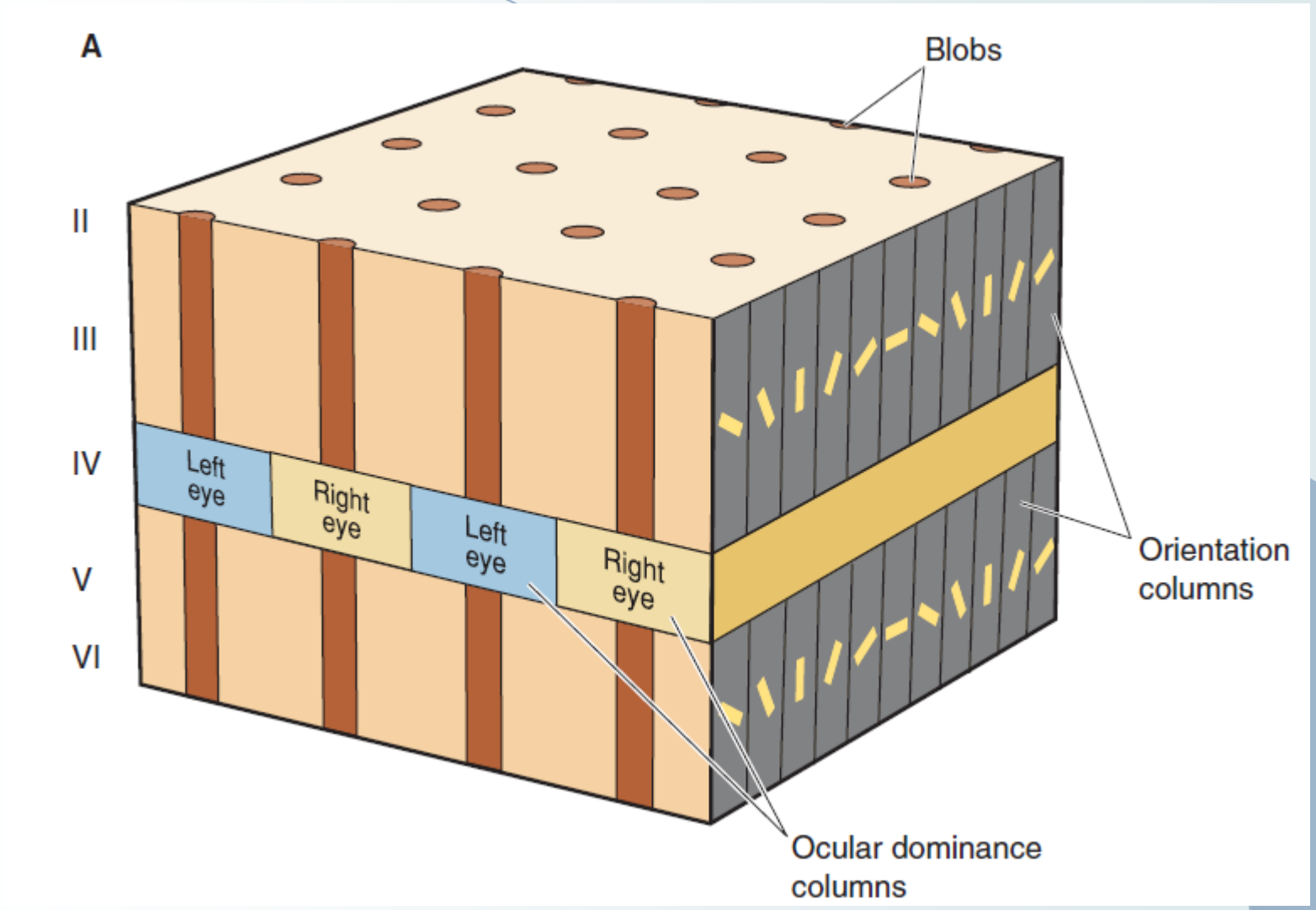


FIGURE 26–16 Complex cells. These neurons respond best to a bar oriented in a specific direction, but they also respond to different positions of the bar within the visual field. (From Bear MF, et al.: Neuroscience: Exploring the Brain, 3rd ed. Philadelphia: Lippincott Williams & Wilkins, 2007, p. 329.)

- **End-stopped cells** are believed to receive inputs from groups of complex cells and possibly signal the length of a line of an object as well as its borders and curvatures.

Features of Cortical Columns Within the Occipital Cortex

- neurons located in the columns
- The **orientation column** contains complex and simple cells, providing the basis for higher levels of integration and abstraction to take place within the column.
- An **ocular dominance column** receives inputs from one eye and the inputs are arranged in patterns of alternate columns for each eye.


A
Blobs
II
III
IV
V
VI
Left eye
Right eye
Left eye
Right eye
Orientation columns
Ocular dominance columns

Hypercolumn

- Collectively, sets of orientation columns (20+20) coupled with blob areas (for color vision) and sets of ocular dominance (2) columns form a unit referred to as a **hypercolumn.**
- The hypercolumn is responsible for analyzing a single point on the retina.
- Hypercolumns are capable of communicating with each other by virtue of short, horizontally arranged axons.