

A few questions on the content of the
previous lecture

slido



Sulci represent...on the surface of the brain, while gyri represent...

ⓘ Start presenting to display the poll results on this slide.

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Cerebral hemispheres control the...side of our body.

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**The sympathetic and parasympathetic
branches belong to the...**

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Any questions/remarks before we begin
today's lecture?



Visual Neuroscience

Dr. Lavinia Carmen Uscătescu

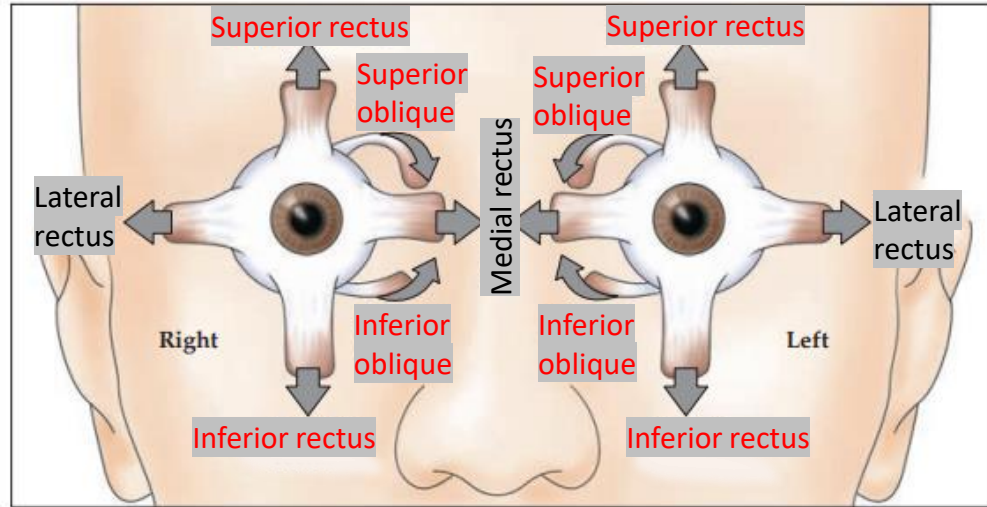
November 27th 2023

Outline

1. The eye
2. The retina
3. The visual pathway
4. The lateral geniculate nucleus
5. The visual cortex

The eye

Eye movements



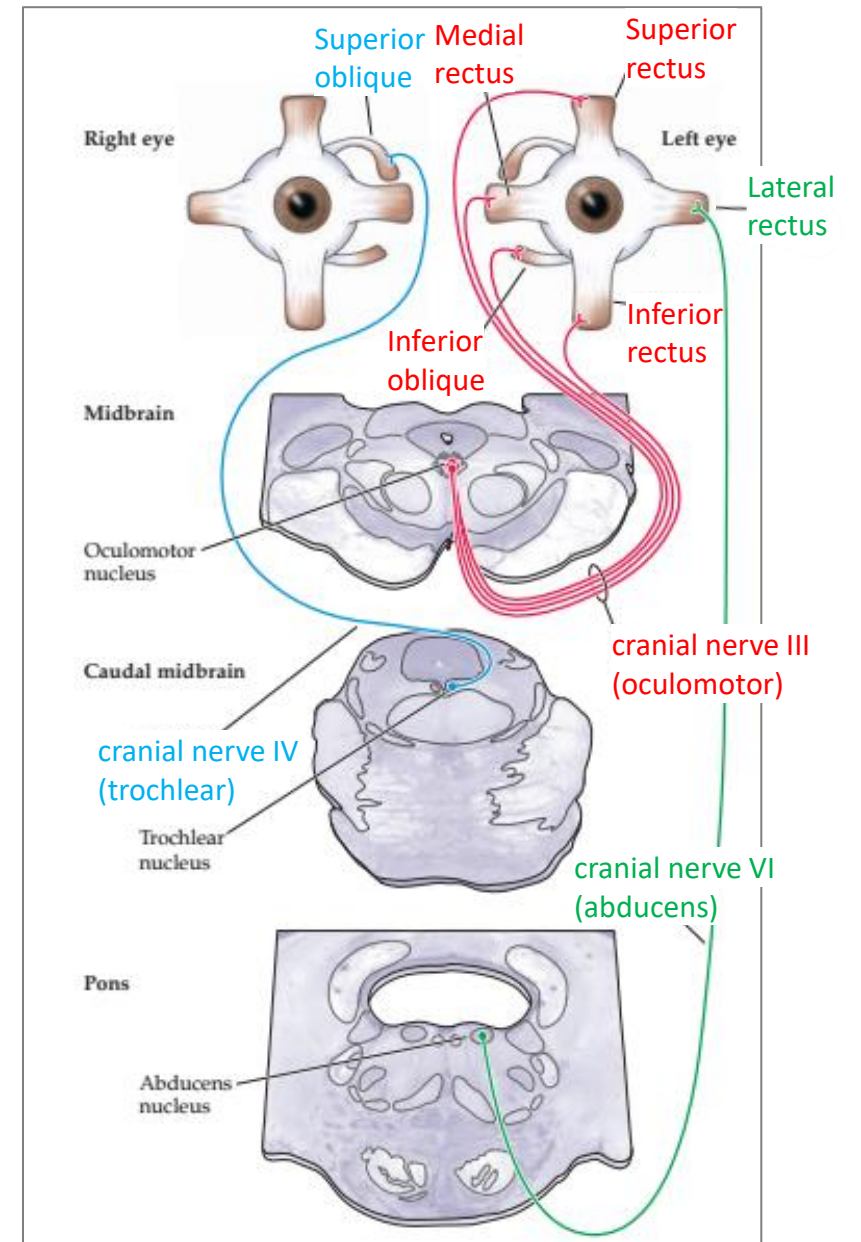
adapted from Purves et al. (2018), p. 449

There are 6 extra-ocular muscles which enable the eyeballs to move:

- the **superior and inferior oblique**
 - the **superior and inferior rectus**
 - the **medial and lateral rectus**
- } **vertical** movements
- => **horizontal** movements

The extra-ocular muscles are innervated by 3 cranial nerves:

- the **superior, inferior, and medial rectus**, and the **inferior oblique** => cranial nerve III (**oculomotor**)
- the **superior oblique** => cranial nerve IV (**trochlear**)
- the **lateral rectus** => cranial nerve VI (**abducens**)



adapted from Purves et al. (2018), p. 450

Structure of the eye

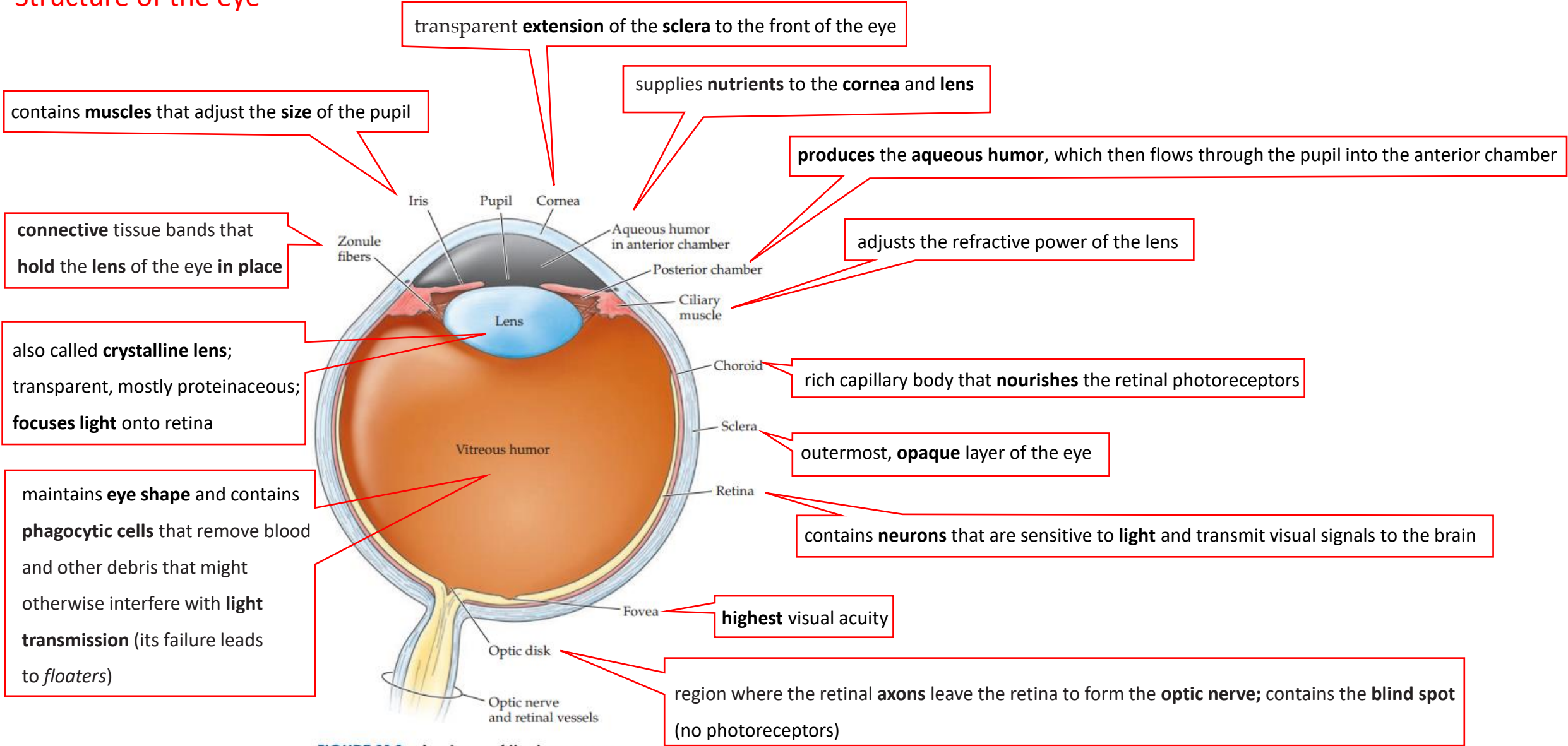
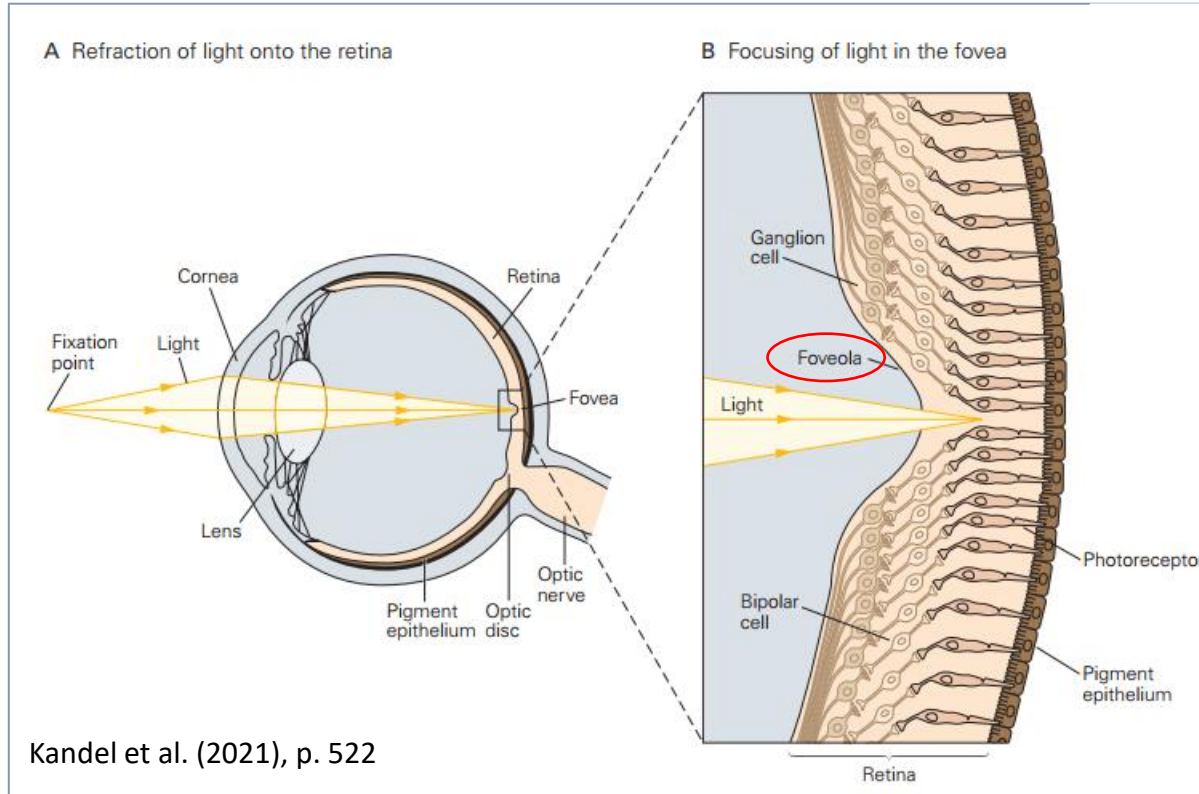


FIGURE 11.1 Anatomy of the human eye.

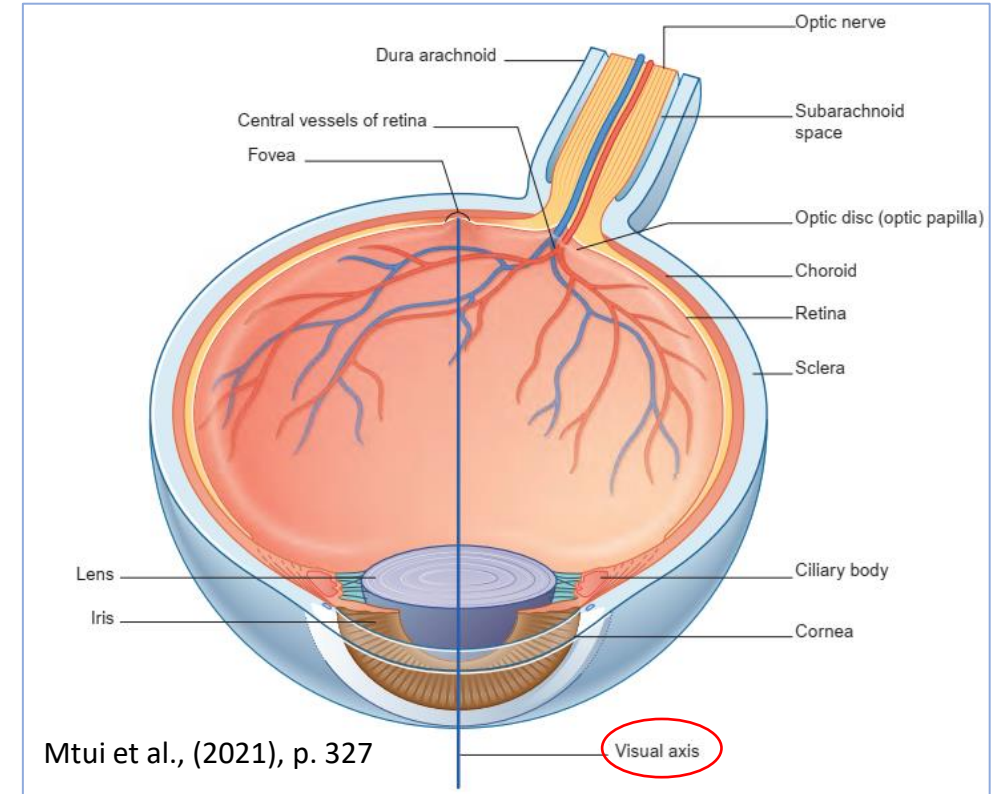
Purves et al. (2018), p. 234

The retina

The retina



Kandel et al. (2021), p. 522



Mtui et al., (2021), p. 327

Figure 22-1 The eye projects the visual scene onto the retina's photoreceptors.

A. Light from an object in the visual field is **refracted by the cornea and lens** and **focused onto the retina**.

B. In the **foveola**, corresponding to **the very center of gaze**, the **proximal neurons of the retina are shifted aside** so light has **direct access to the photoreceptors**.

foveola = the **center** of the fovea; contains **only cone cells**, more **densely packed** than anywhere else on the retina => **maximal acuity**

visual axis = a line passing from the **centre of the visual field** of the eye, through the **centre of the lens**, to the **fovea**.

Note that the **optic nerve** is protected by **meninges**.

If you need a refresher on **refraction** and **reflection**, please see: <https://www.britannica.com/science/light/Reflection-and-refraction>

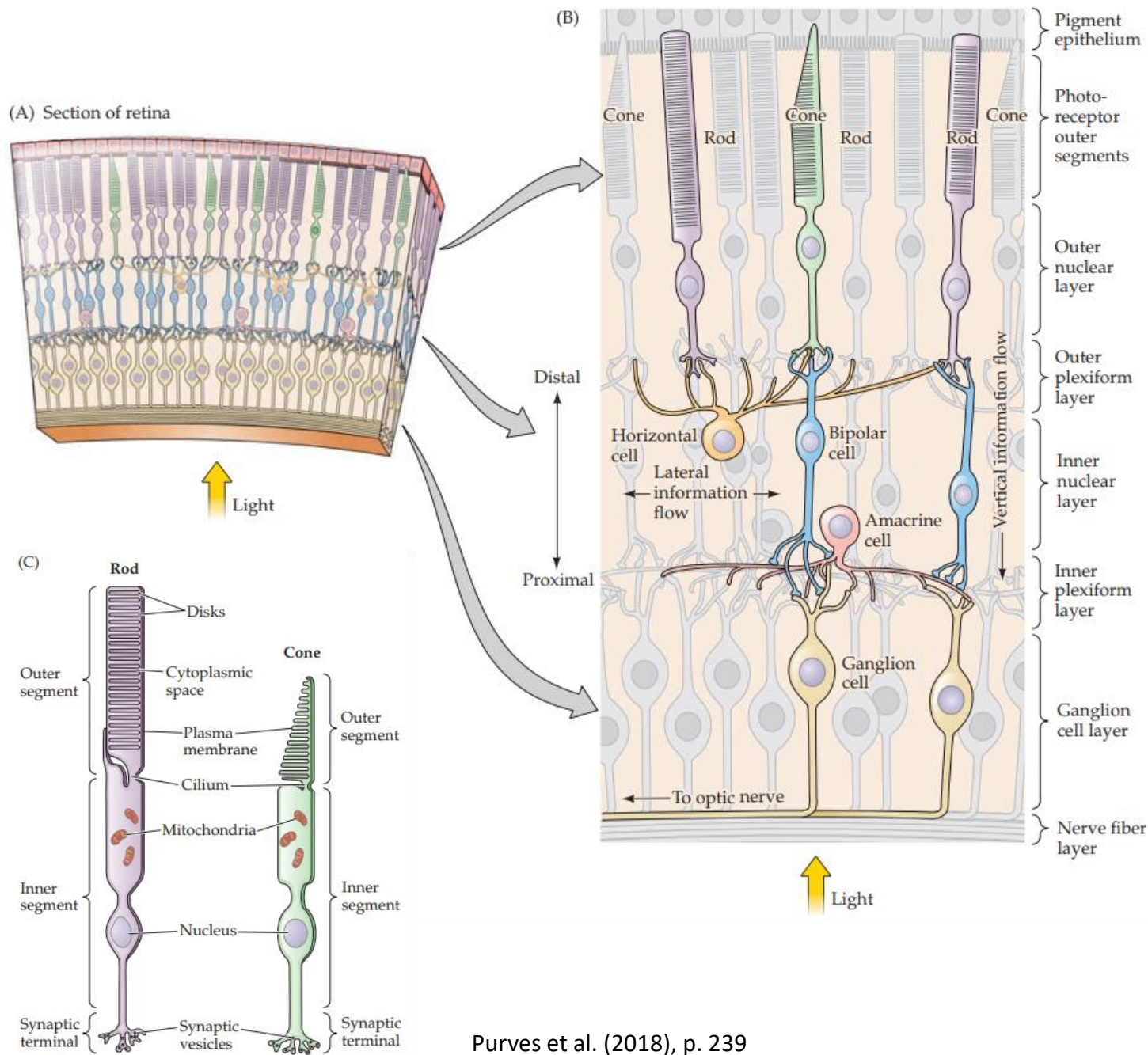
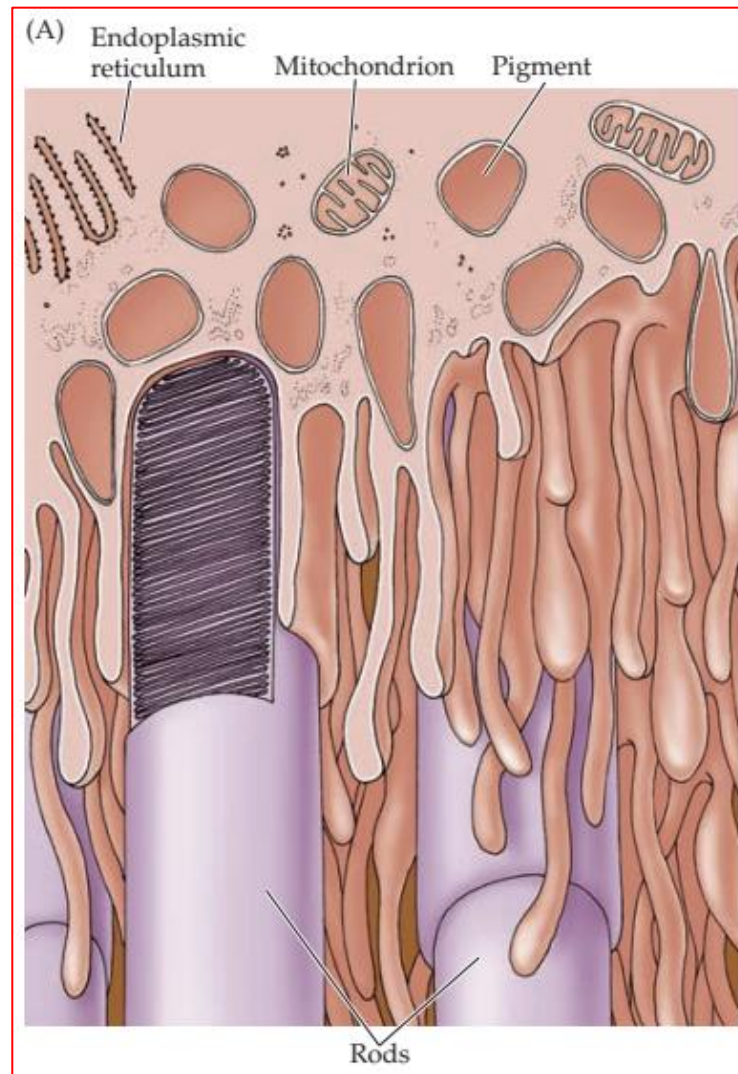
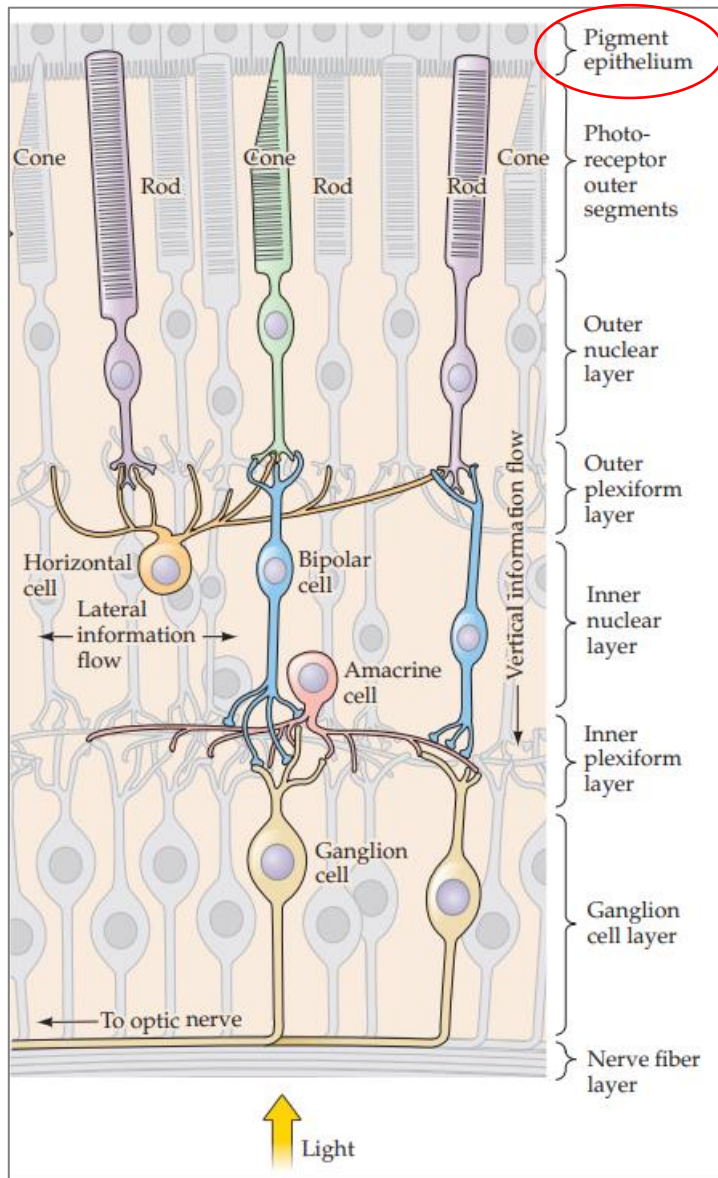


FIGURE 11.5 Structure of the retina. (A) Section of the retina showing overall arrangement of **retinal layers**. (B) Diagram of the basic circuitry of the retina. A **three-neuron chain—photoreceptor, bipolar cell, and ganglion cell**—provides the most direct route for transmitting visual information to the brain. **Horizontal cells and amacrine cells mediate lateral interactions in the outer and inner plexiform layers, respectively.** The terms **inner and outer** designate relative distances from the center of the eye (inner, near the center of the eye; outer, away from the center, or toward the pigment epithelium). (C) Structural differences between **rods and cones**. Although generally similar in structure, rods and cones differ in their size and shape, as well as in the arrangement of the membranous disks in their outer segments.

There are five basic classes of neurons in the retina: **photoreceptors** (i.e., **rods** and **cones**), **bipolar** cells, **ganglion** cells, **horizontal** cells, and **amacrine** cells. The cell bodies and processes of these neurons are stacked in alternating layers, with the **cell bodies** located in the **inner nuclear, outer nuclear, and ganglion cell layers**, and the **processes and synaptic contacts** located in the **inner plexiform and outer plexiform layers**.



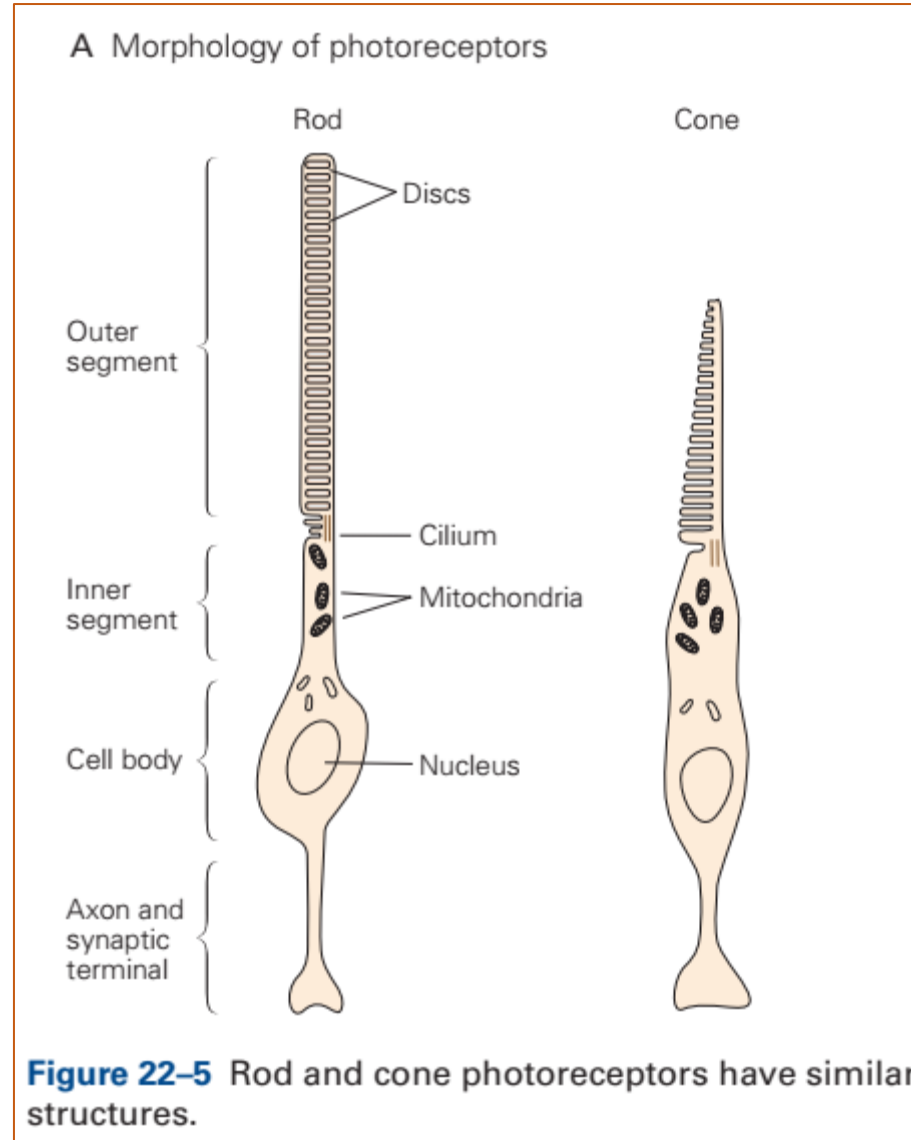
Purves et al. (2018), p. 240

Light rays must pass through various **non-light-sensitive** elements of the retina as well as the retinal vasculature **before** reaching the outer segments of the **photoreceptors** where **photons are absorbed**.

The reason for this curious feature is that the cells that make up the retinal **pigment epithelium** have long processes that extend into the photoreceptor layer, surrounding the tips of the outer segments of each **photoreceptor**.

Rods and cones

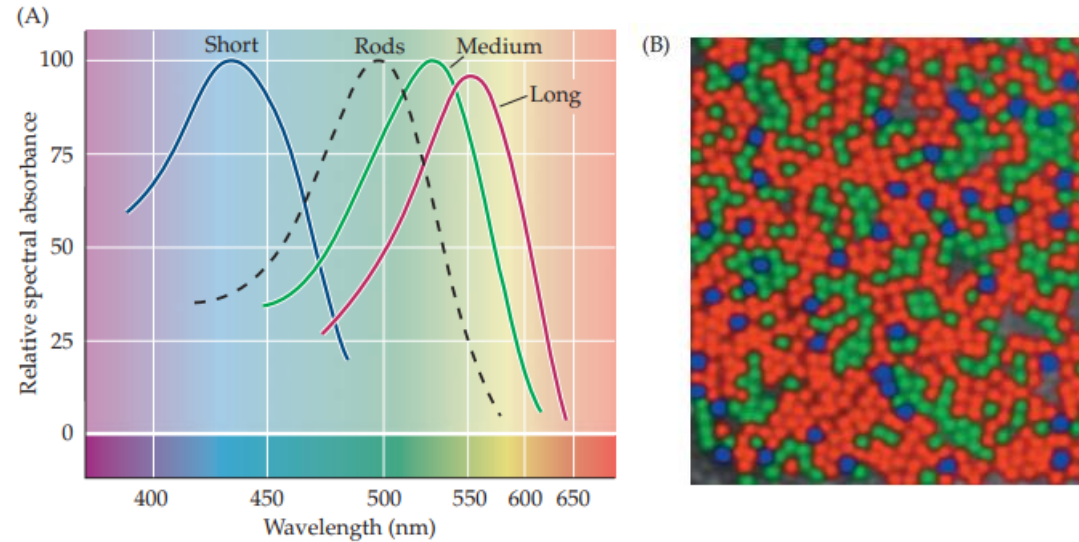
Rods can signal the absorption of a **single photon** and are responsible for **vision under dim illumination** such as moonlight. But as the light level increases toward dawn, the electrical response of rods becomes **saturated** and the cells **cease to respond** to variations in intensity.



Cones are much **less sensitive to light**; they make no contribution to night vision but are solely responsible for **vision in daylight**. Their response is considerably **faster** than that of rods.

Color vision

FIGURE 11.14 Absorption spectra and distribution of cone opsins.



(A) Light absorption spectra of the four photopigments in normal human retina. Solid curves represent the three cone opsins; the dashed curve shows rod rhodopsin for comparison.

(B) Mapping the distribution of different cone types within the living retina.

Purves et al. (2018), p. 248

light

electromagnetic radiation having wavelengths between ~ 400 and 700 nm

photon

a single unit of light

opsins

G-protein-coupled receptors present in the photoreceptor cells of the retina

rhodopsin

G-protein-coupled receptors present in the rod photoreceptors

Cones can be classified according to their **spectral**

sensitivities: **blue**: short (**S**) **green**: medium (**M**) **red**: long (**L**)

Phototransduction

Action potentials are not required to transmit information over the relatively **short** distances => in the retina, photoreceptors (i.e., rods and cones) do not exhibit action potentials, but a **graded change** in membrane potential (**graded potentials**).

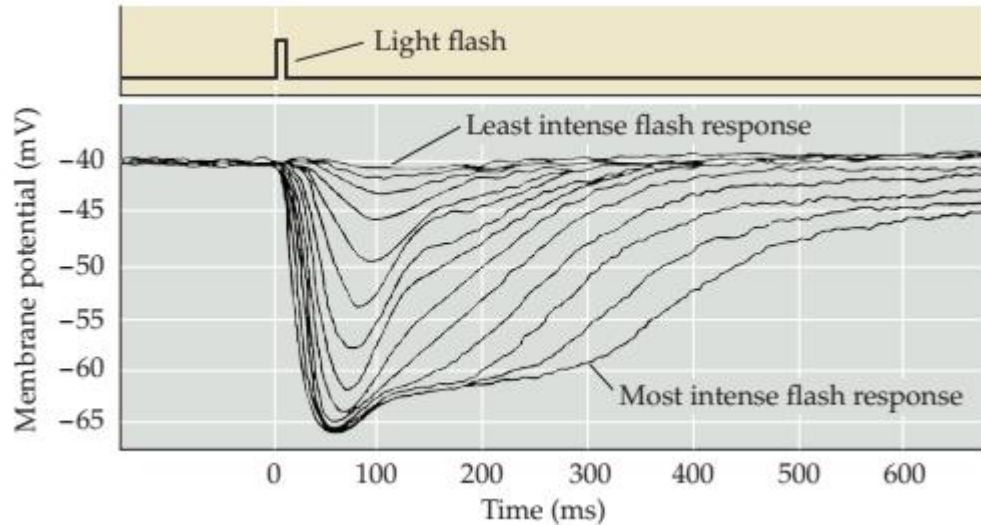


FIGURE 11.7 Hyperpolarization of a photoreceptor. This **intra-cellular recording** is from **a single cone** stimulated with **different amounts of light** (the cone has been taken from a turtle retina, which accounts for the relatively long time course of the response). **Each trace represents the response to a brief flash that was varied in intensity**. At the highest light levels, the response amplitude saturates (at about -65 mV). The hyperpolarizing response is characteristic of vertebrate photoreceptors. (After Baylor, 1987.)

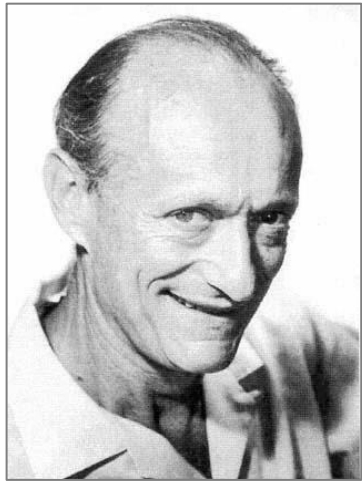
Purves et al. (2018), p. 242

Stimulating a photoreceptor => membrane **hyperpolarization** rather than depolarization.

As in other nerve cells, transmitter release is dependent on voltage-sensitive Ca²⁺ channels in the terminal membrane: (a) in the **dark**, photoreceptors are relatively **depolarized** => **many** open **Ca²⁺ channels** => **high** rate of **transmitter** release; (b) in the **light**, photoreceptors are **hyperpolarized** => **fewer** open **Ca²⁺ channels** => **reduced** rate of **transmitter** release.

The **reason** for this unusual arrangement compared with that in other sensory receptor cells is not known, but it may have to do with the challenge of responding to both increases and decreases of luminance.

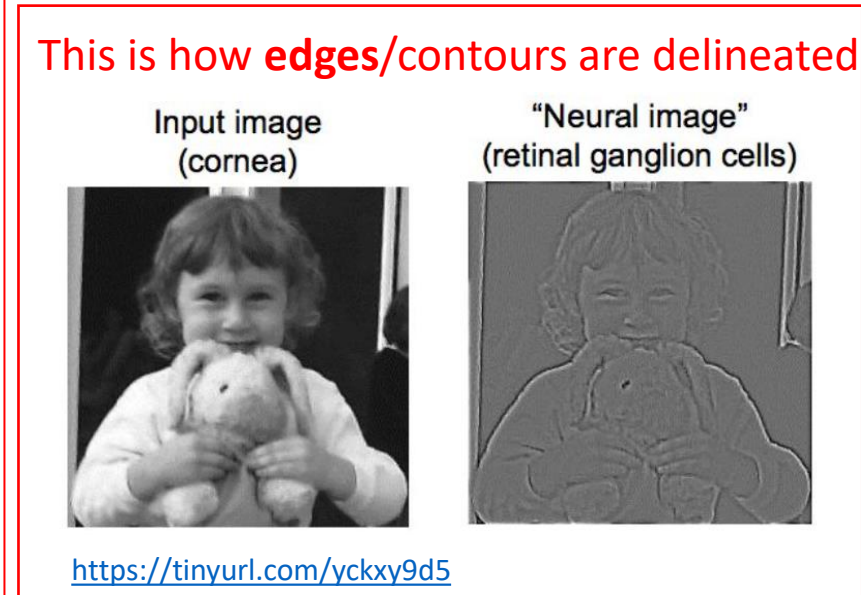
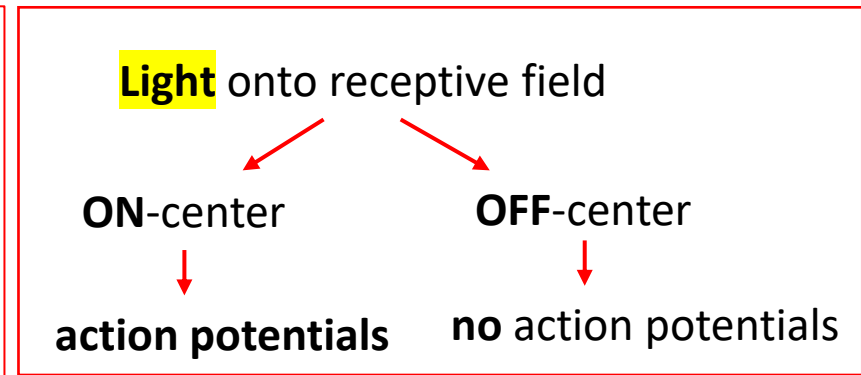
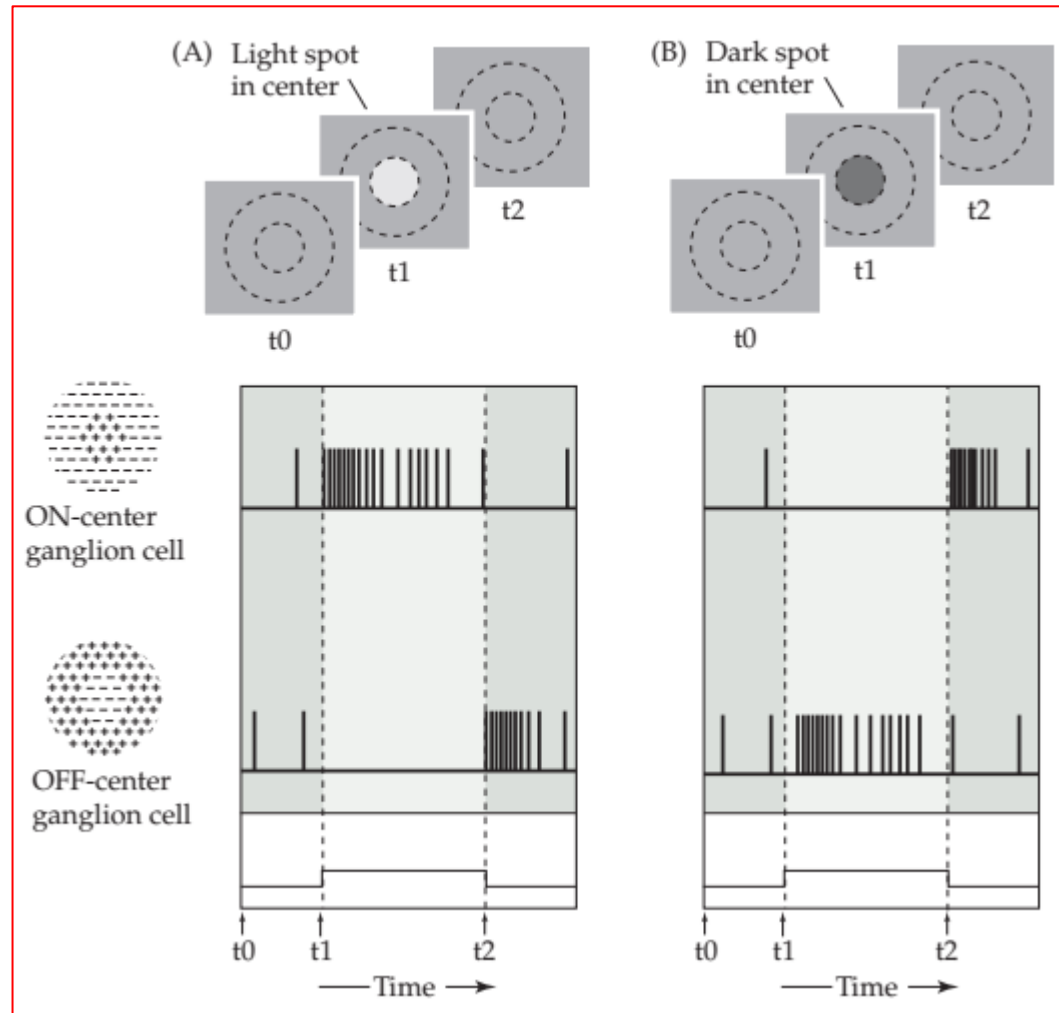
Retinal ganglion cells



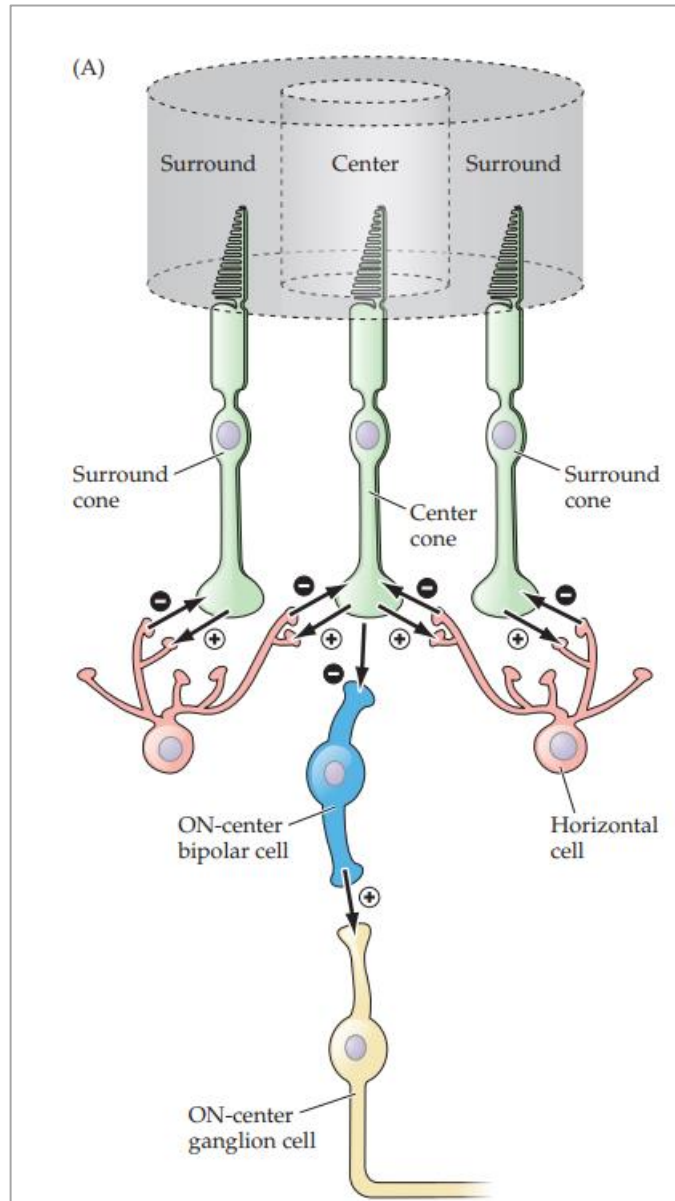
Stephen Kuffler
(1913 — 1980)

Two classes of
ganglion cells

Stephen Kuffler discovered that retinal **ganglion** cells had a **central** region that **excited** the neuron and a **surrounding** region that **antagonized** the center. Each ganglion cell responds to stimulation of a small circular patch of the retina, which defines the cell's **receptive field**.



Lateral inhibition

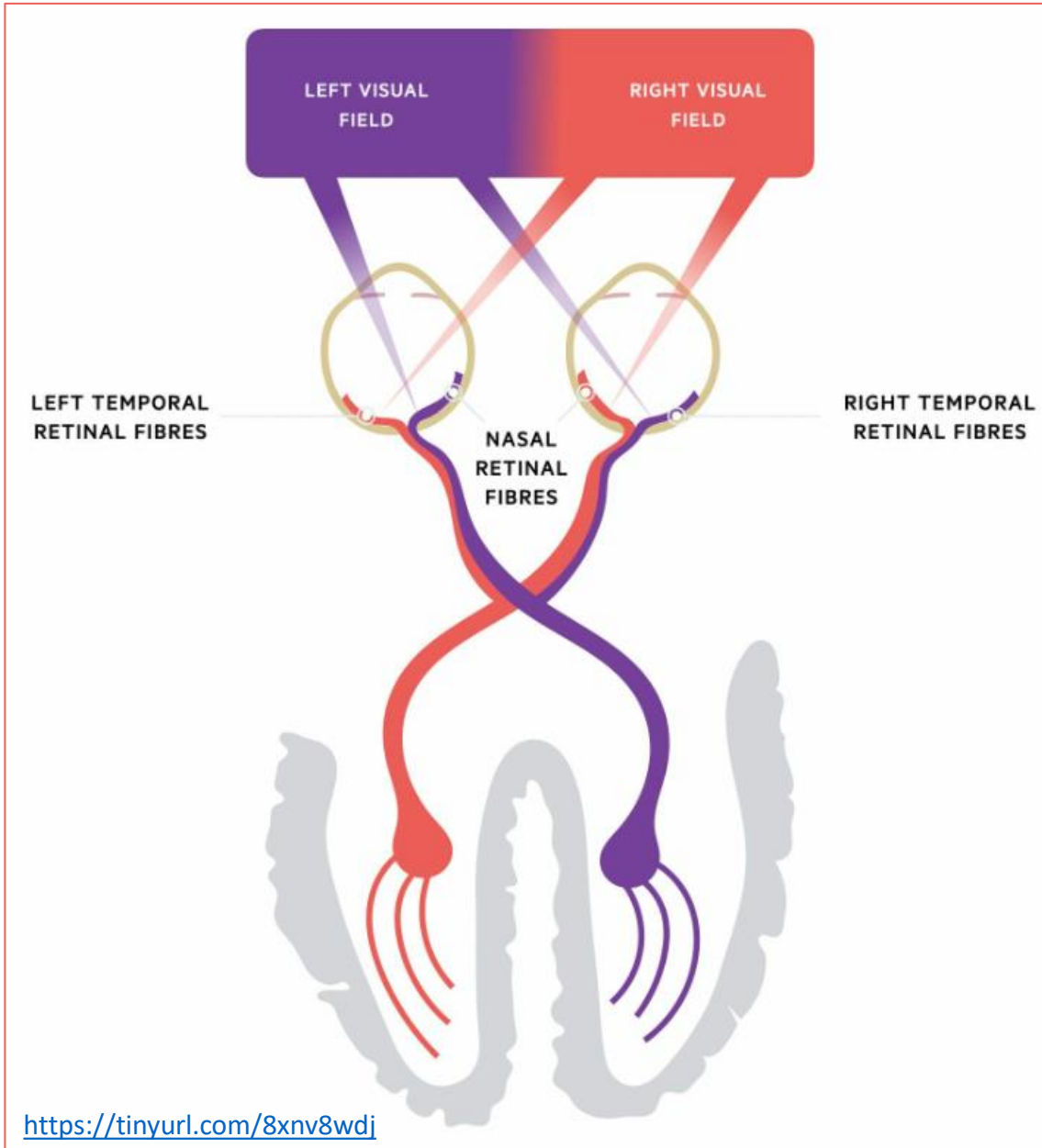


Lateral inhibition is produced in the retina by **interneurons** (**horizontal** and **amacrine** cells) that pool signals over a neighborhood of presynaptic **feedforward** cells (**photoreceptors** and **bipolar** cells) and send inhibitory signals back to them.

The typical center-surround receptive field structure of a ganglion cell is the **combination** of the **excitatory center** created by the **feedforward** cells and the **inhibitory surround** formed by the **interneurons**.

FIGURE 11.21 Circuitry responsible for the receptive field surround of an ON-center retinal ganglion cell. (A) Functional anatomy of horizontal cell inputs responsible for generating surround antagonism. A plus indicates a sign-conserving synapse; a minus represents a sign-inverting synapse.

Visual field



visual field

area that can be seen when the eyes are fixed on a single point (135° vertically and 180° horizontally)

The visual field => two components:

- (1) **Left** visual field: detected by the **right temporal retinal fibres** (outer) and **left nasal retinal fibres** (inner);
- (2) **Right** visual field: detected by the **left temporal retinal fibres** (outer) and **right nasal retinal fibres** (inner).

Note that the **nasal fields of vision from each eye overlap** in forward gaze => when assessing visual fields, it is important to assess **each eye individually**.

Locate the blind spot on your own retina



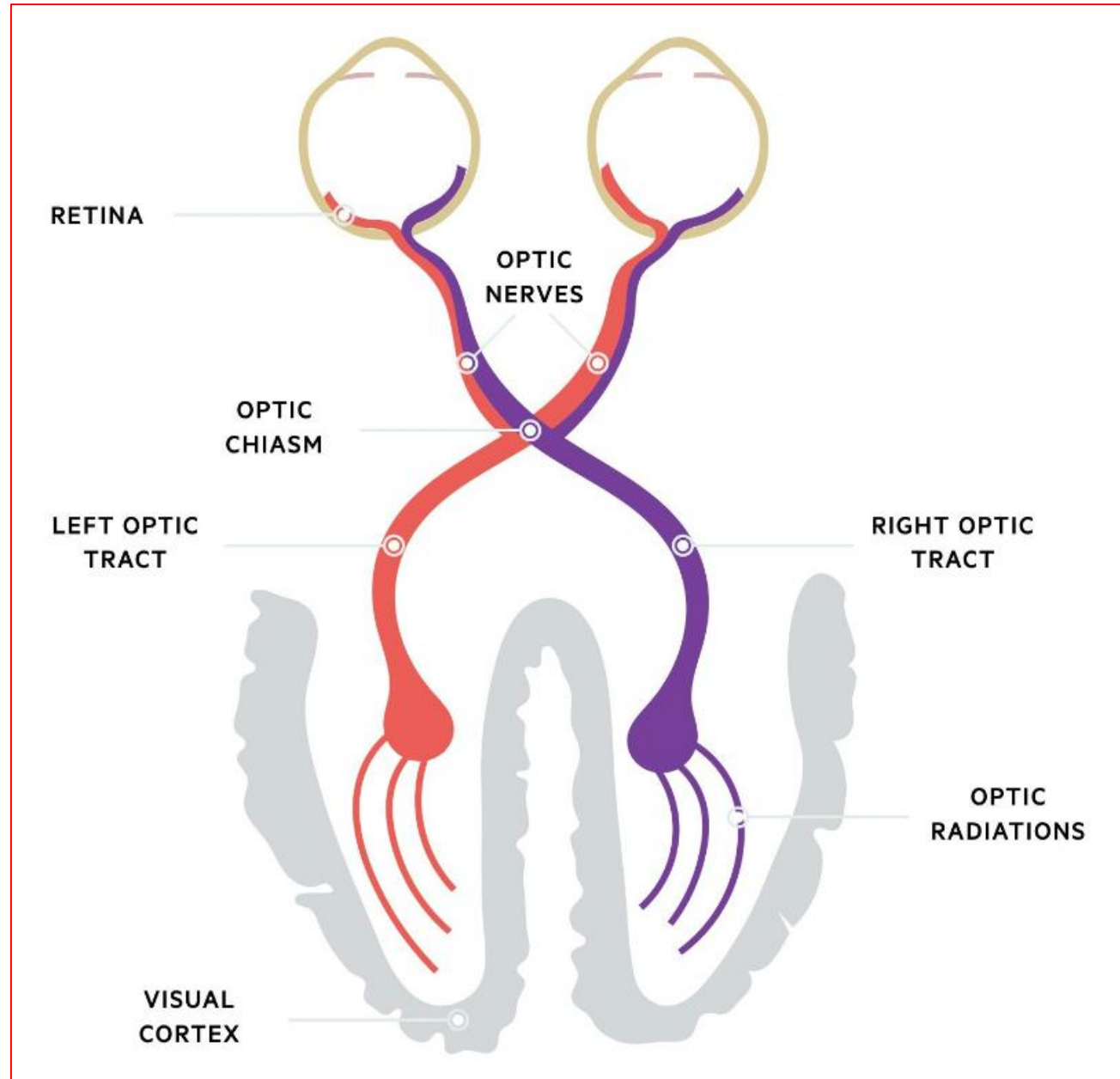
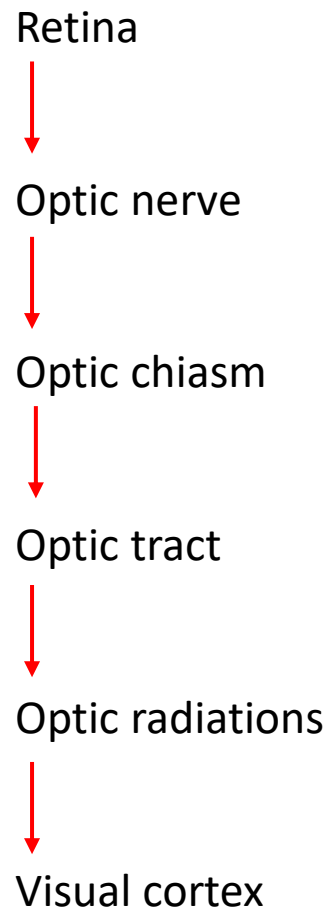
Figure 22-4 The blind spot of the human retina. Locate the blind spot in your left eye by shutting the right eye and fixating the cross with the left eye. Hold the book about 12 inches from your eye and move it slightly nearer or farther until the circle on the left disappears. Now place a pencil vertically on the page

and sweep it sideways over the circle. Note the pencil appears unbroken, even though no light can reach your retina from the region of the circle. Next, move the pencil lengthwise and observe what happens when its tip enters the circle. (Adapted, with permission, from Hurvich 1981.)

Kandel et al. (2021), p. 525

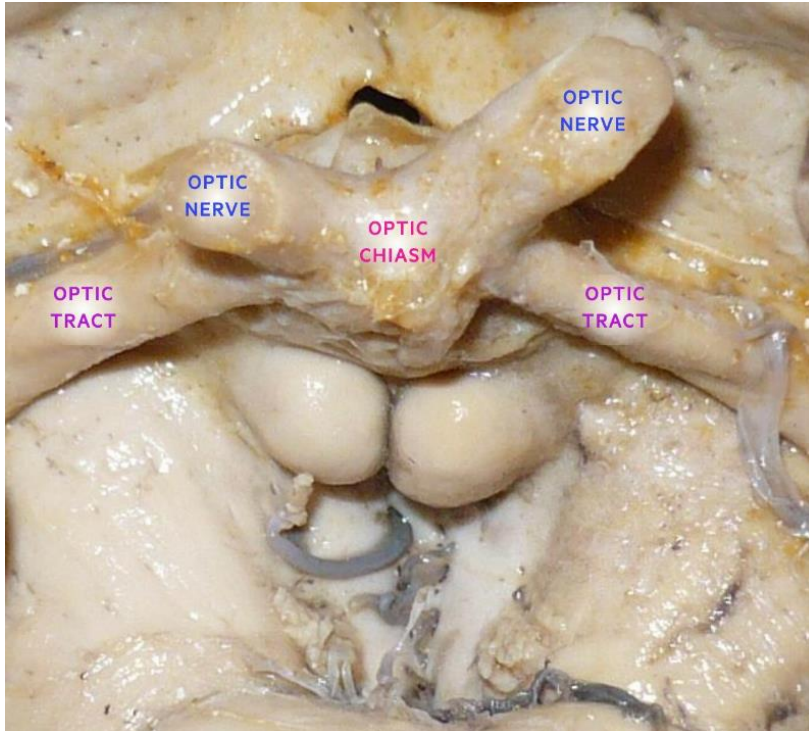
The visual pathway

Components of the visual pathway



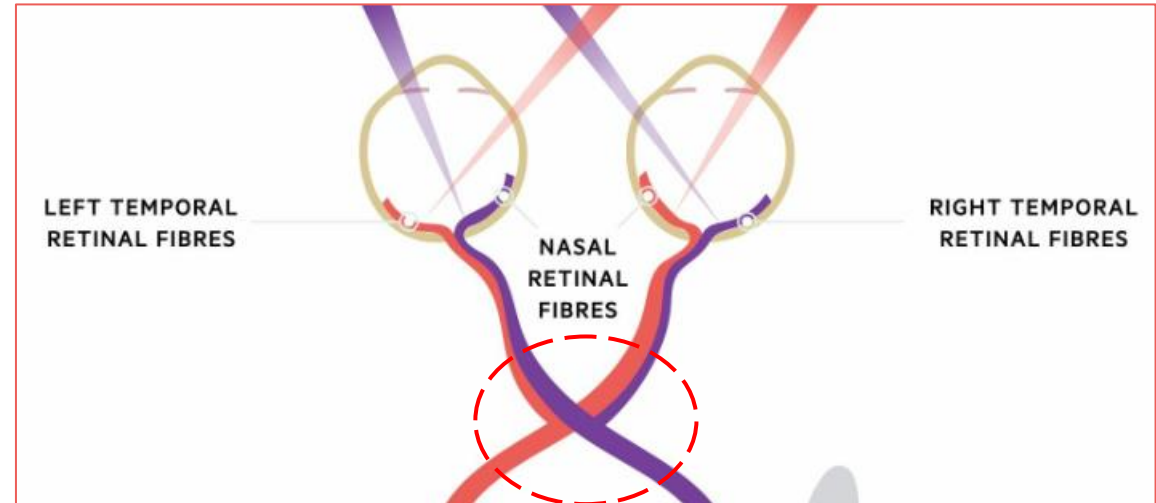
<https://tinyurl.com/8xnv8wdj>

The optic nerve and the optic chiasm



<https://tinyurl.com/8xnv8wdj>

Optic nerve: **cranial nerve II**; made up of >1 million **myelinated axons** of the retinal **ganglion cells**; transmits visual information from the ganglion cells in the **retina** to the **visual cortex** (occipital lobe).

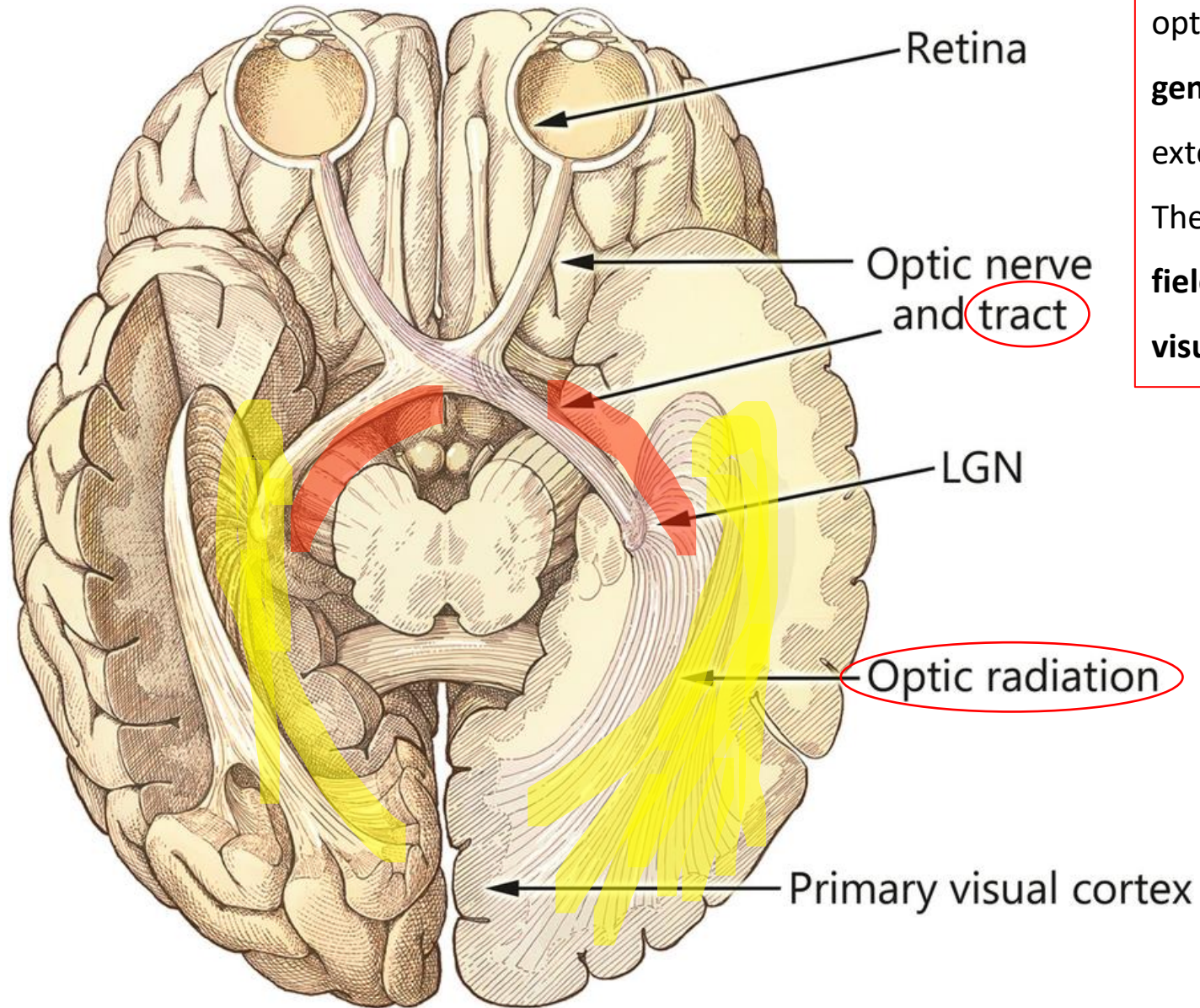


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Optic chiasm: the location where **retinal fibres** of the optic nerve **cross over** (i.e., **decussate**).

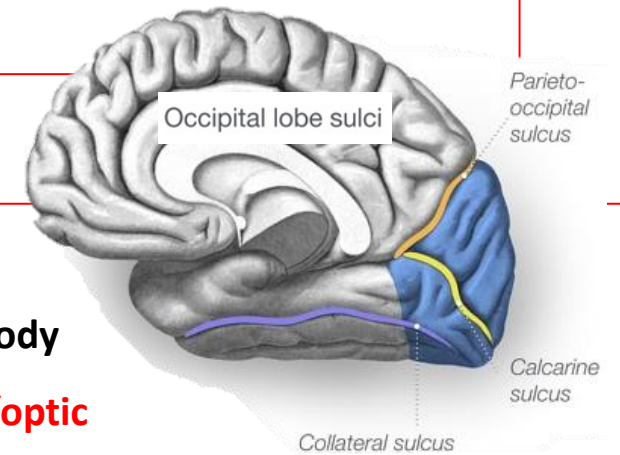
Note that not all retinal fibers cross over: **nasal** retinal fibres **cross** at the optic chiasm to join the temporal fibres on the other side, but **temporal** retinal fibres **do not cross** at the optic chiasm and are joined by the nasal fibres from the other side.

The optic tract and the optic radiation



The **left** and **right optic tract** are continuations of the optic nerves. These tracts synapse with the **lateral geniculate body** within the midbrain (considered an extension of the **thalamus**).

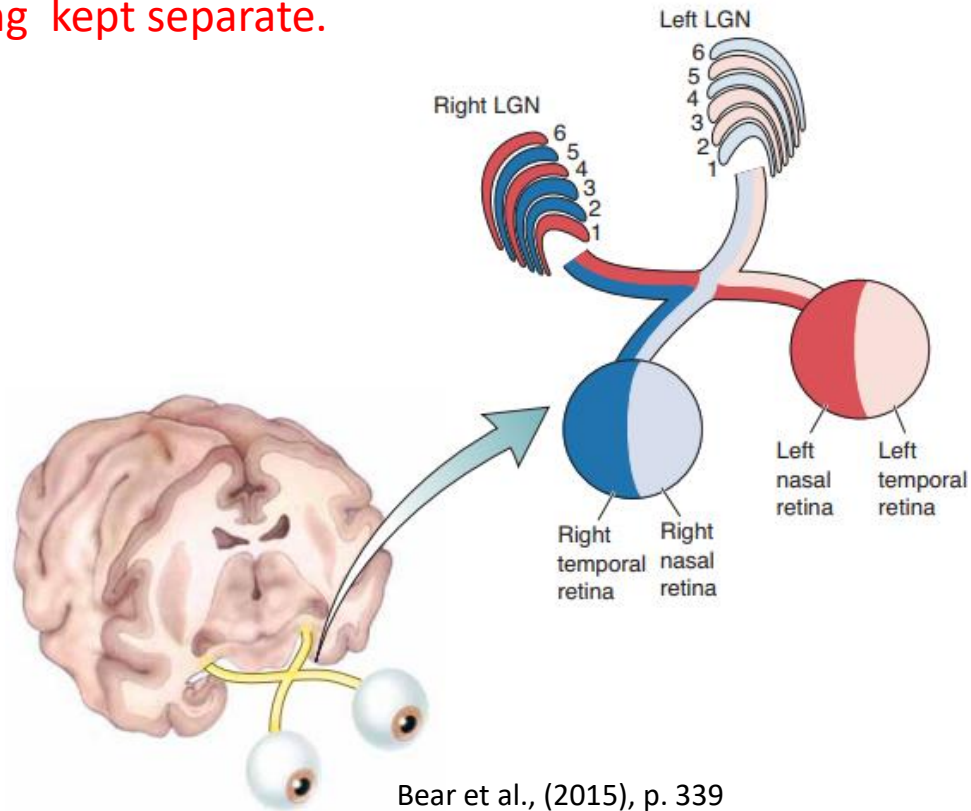
The **right optic tract** corresponds to the **left visual field** and the **left optic tract** corresponds to the **right visual field**.



Neurons from the **lateral geniculate body** (collectively called "**optic radiation**") pass dorsally towards <https://tinyurl.com/45t6zmn> the **calcarine sulcus**. They form **two loops**: (1) **upper** (through **parietal lobe**) => **inferior** visual field, and (2) **lower** (through **temporal lobe**) => **superior** visual field.

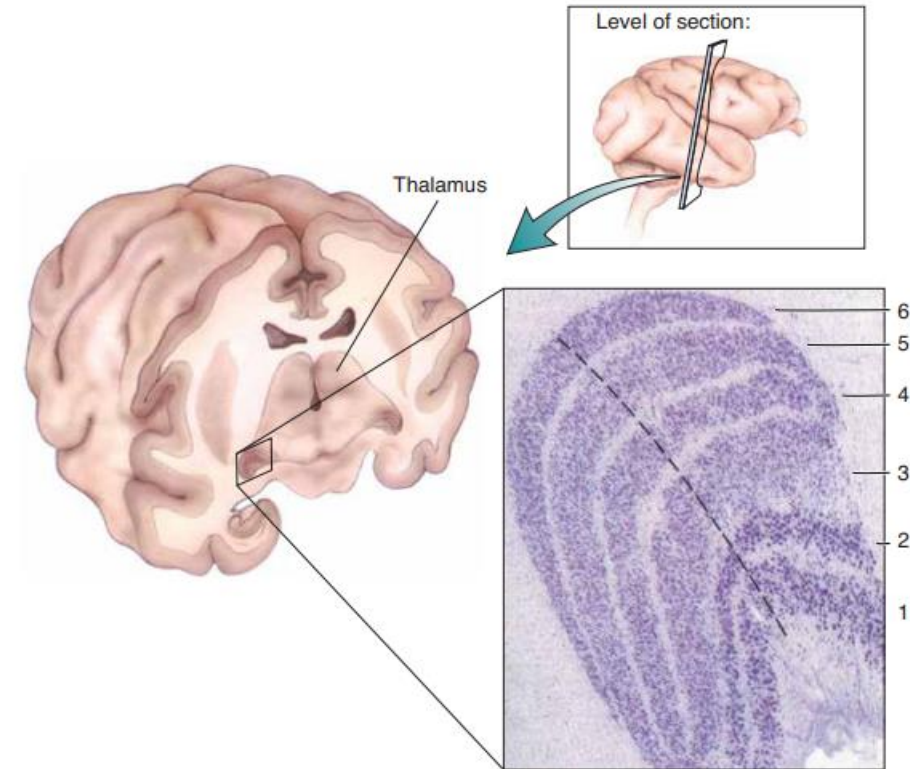
The lateral geniculate nucleus

The lateral geniculate nucleus (LGN) is composed of six layers => different types of retinal information are being kept separate.



At the LGN, **input** from the two eyes is kept **separate**.

In the **right LGN**, the right eye (**ipsilateral**) axons synapse on LGN cells in **layers 2, 3, and 5**. The left eye (**contralateral**) axons synapse on cells in layers **1, 4, and 6**.



▲ **FIGURE 10.7**
The LGN of the macaque monkey. The tissue has been stained to show cell bodies, which appear as purple dots. Notice particularly the six principal layers and the larger size of the cells in the two ventral layers (layers 1 and 2).
(Source: Adapted from Hubel, 1988, p. 65.)

Bear et al., (2015), p. 338

In addition

> [Handb Clin Neurol. 2021;178:31-50. doi: 10.1016/B978-0-12-821377-3.00018-0.](#)

Retinal ganglion cells and the magnocellular, parvocellular, and koniocellular subcortical visual pathways from the eye to the brain

Samuel G Solomon ¹

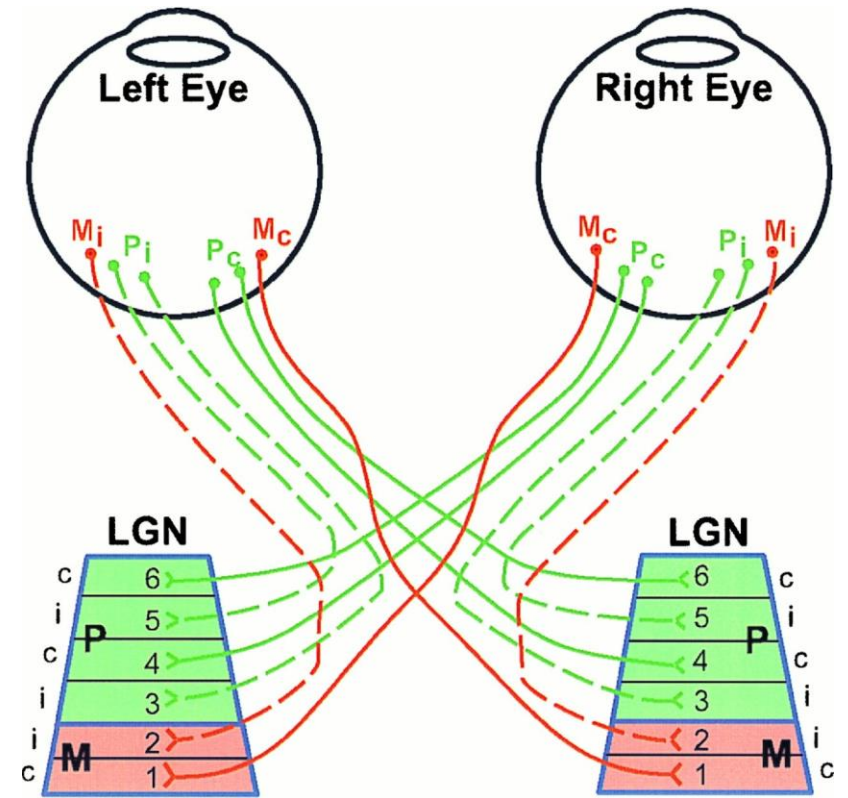
<https://pubmed.ncbi.nlm.nih.gov/33832683/>

Affiliations + expand

PMID: 33832683 DOI: [10.1016/B978-0-12-821377-3.00018-0](https://doi.org/10.1016/B978-0-12-821377-3.00018-0)

Abstract

In primates including humans, most retinal ganglion cells send signals to the lateral geniculate nucleus (LGN) of the thalamus. The anatomical and functional properties of the two major pathways through the LGN, the parvocellular (P) and magnocellular (M) pathways, are now well understood. Neurones in these pathways appear to convey a filtered version of the retinal image to primary visual cortex for further analysis. The properties of the P-pathway suggest it is important for high spatial acuity and red-green color vision, while those of the M-pathway suggest it is important for achromatic visual sensitivity and motion vision. Recent work has sharpened our understanding of how these properties are built in the retina, and described subtle but important nonlinearities that shape the signals that cortex receives. In addition to the P- and M-pathways, other retinal ganglion cells also project to the LGN. These ganglion cells are larger than those in the P- and M-pathways, have different retinal connectivity, and project to distinct regions of the LGN, together forming heterogeneous koniocellular (K) pathways. Recent work has started to reveal the properties of these K-pathways, in the retina and in the LGN. The functional properties of K-pathways are more complex than those in the P- and M-pathways, and the K-pathways are likely to have a distinct contribution to vision. They provide a complementary pathway to the primary visual cortex, but can also send signals directly to extrastriate visual cortex. At the level of the LGN, many neurones in the K-pathways seem to integrate retinal with non-retinal inputs, and some may provide an early site of binocular convergence.

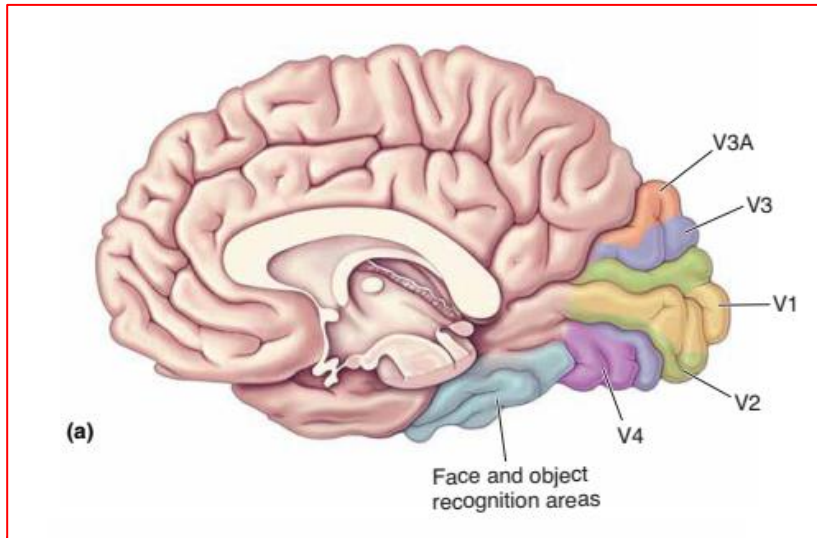


Schematic illustration of neuronal connections between the eyes and the LGN in the macaque monkey. The connections subserving the left and right eyes might be either parvocellular (P, about 80%), magnocellular (M, about 10%) or others (K, I, or S about 10%, not shown). The different types of ganglion cells in the retina are intermixed, although the percentage of P cells is higher in the central retina than at the periphery. In the LGN, layers 1 and 2 are magnocellular (red), and layers 3–6 parvocellular (green). The set of M ganglion cells in a given eye that project to the contralateral LGN terminate in layer 1, whereas those that project ipsilaterally terminate in layer 2. The P ganglion cells project to layers 3 and 5 to the LGN on the same side, and 4 and 6 on the opposite side.

<https://www.pnas.org/doi/10.1073/pnas.94.11.5900>

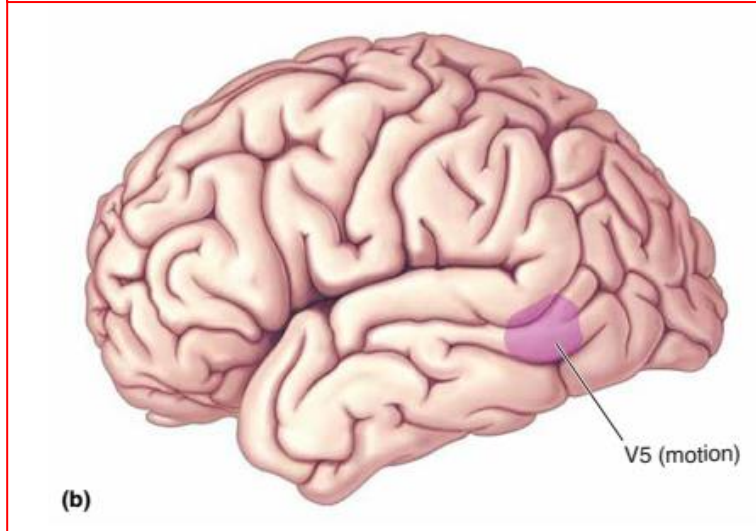
The visual cortex

Subdivisions of the visual cortex



retinotopy

mapping of the visual input from the retinas to neurons within the visual stream



◀ FIGURE 10.28

Visual areas in the human brain. (a) Compared to monkeys, human visual areas are shifted more to the medial wall of the occipital lobe, and many are buried in sulci. **Early visual areas including V1, V2, V3, V3A, and V4 are retinotopically organized.** Higher temporal lobe areas involved in face and object recognition are not retinotopic. (b) A variety of areas responsive to visual motion are found on the lateral aspect of the brain. The most studied of these is area V5, also known as MT. (Source: Zeki, 2003, Fig. 2.)

Bear et al., (2015), p. 357



Retinotopic Maps

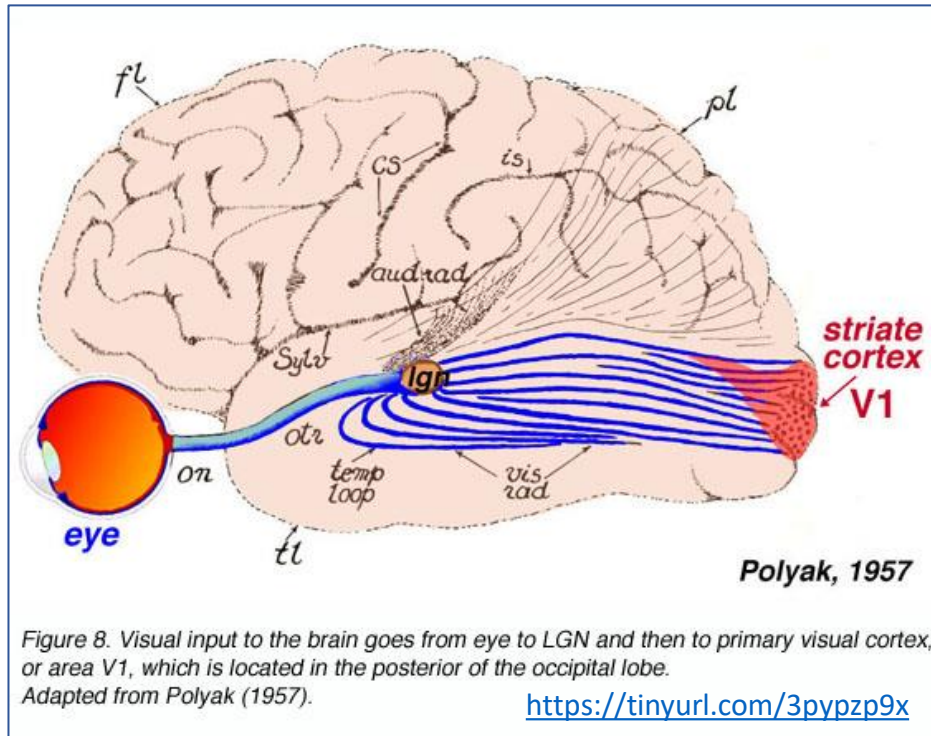
Nancy Kanwisher

Massachusetts Institute of Technology

<https://www.youtube.com/watch?app=desktop&v=MhFJIgeY-ZY>

V1 is also called “**striate cortex**”, while **V1 – V5** are “**extrastriate areas**”.

Primary visual cortex (V1, or striate cortex)



V1 is organized in **six layers**, the **fourth** one receiving **input** from the **LGN**. It contains **simple** and **complex** cells. The **simple** cells respond to **preferred orientations/edges**, while the **complex** ones respond to **moving** oriented bars.

Cells in V1 are **selective** for **orientation**



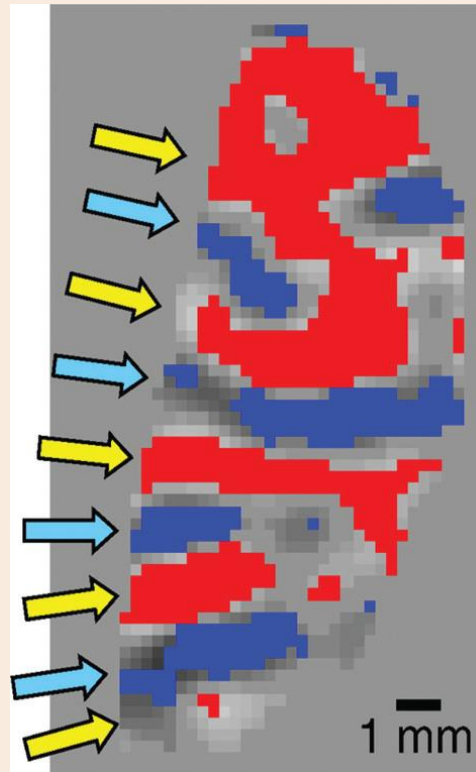
<https://www.youtube.com/watch?v=ePP0G7FJGPI>

V1 and ocular dominance columns

The presence of **ocular dominance columns** was also discovered by **David Hubel** and **Torsten Wiesel**. They noted that cells with different **ocular preference** did not appear to be “scattered at random through the cortex.”

Human **ocular dominance columns** (fMRI at 7 tesla). The image depicts a 3 mm thick slice through a flat portion of the cortex on the lower bank of the calcarine sulcus. Differential increases in activity following left eye stimulation (blue) and right eye stimulation (red) with a flickering checkerboard; arrows indicate the locations of left (cyan) and right (yellow) ocular dominance columns.

Adams & Horton, (2009)

A photograph of Nancy Kanwisher, a neuroscientist at MIT, standing behind a laptop and presenting. To her right is a projection screen displaying a slide. The slide has a logo at the top and text that includes "Yacoub et al (2008), humi" and a bulleted list with "orientation selectivity" and "ocular dominance co". Below the photograph, the text "Ocular Dominance Columns" is centered, followed by a horizontal line, then "Nancy Kanwisher" in a larger font, and "Massachusetts Institute of Technology" below that.

Ocular Dominance Columns

Nancy Kanwisher
Massachusetts Institute of Technology

<https://www.youtube.com/watch?v=1EMf2YOYCX8>

The Nobel Prize in Physiology or Medicine 1981

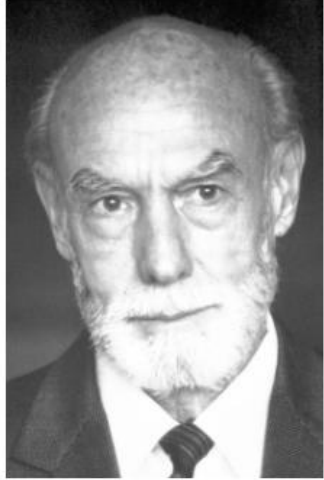


Photo from the Nobel Foundation archive.
Roger W. Sperry
Prize share: 1/2



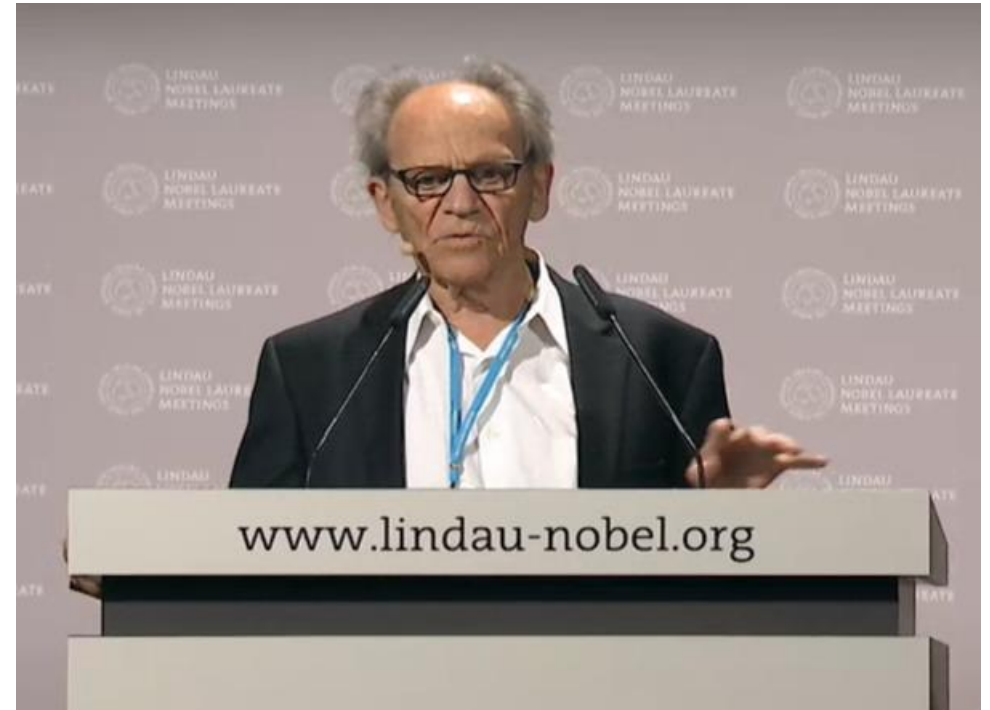
Photo from the Nobel Foundation archive.
David H. Hubel
Prize share: 1/4



Photo from the Nobel Foundation archive.
Torsten N. Wiesel
Prize share: 1/4

The Nobel Prize in Physiology or Medicine 1981 was divided, one half awarded to Roger W. Sperry "for his discoveries concerning the functional specialization of the cerebral hemispheres", the other half jointly to David H. Hubel and Torsten N. Wiesel "for their discoveries concerning information processing in the visual system"

<https://www.nobelprize.org/prizes/medicine/1981/summary/>



<https://mediatheque.lindau-nobel.org/recordings/37943>



The experiments of David Hubel and Torsten Wiesel

A serendipitous moment



Listening to the V1 neurons firing

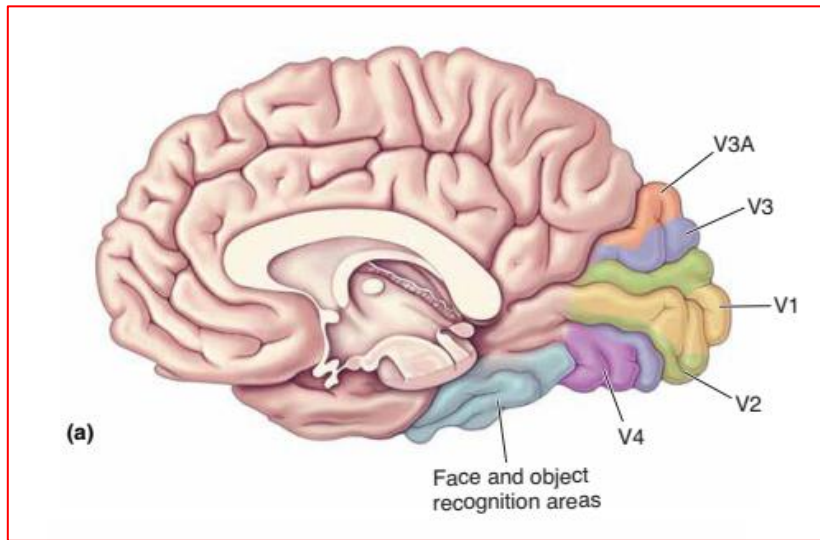


The whole story, as told by Torsten Wiesel



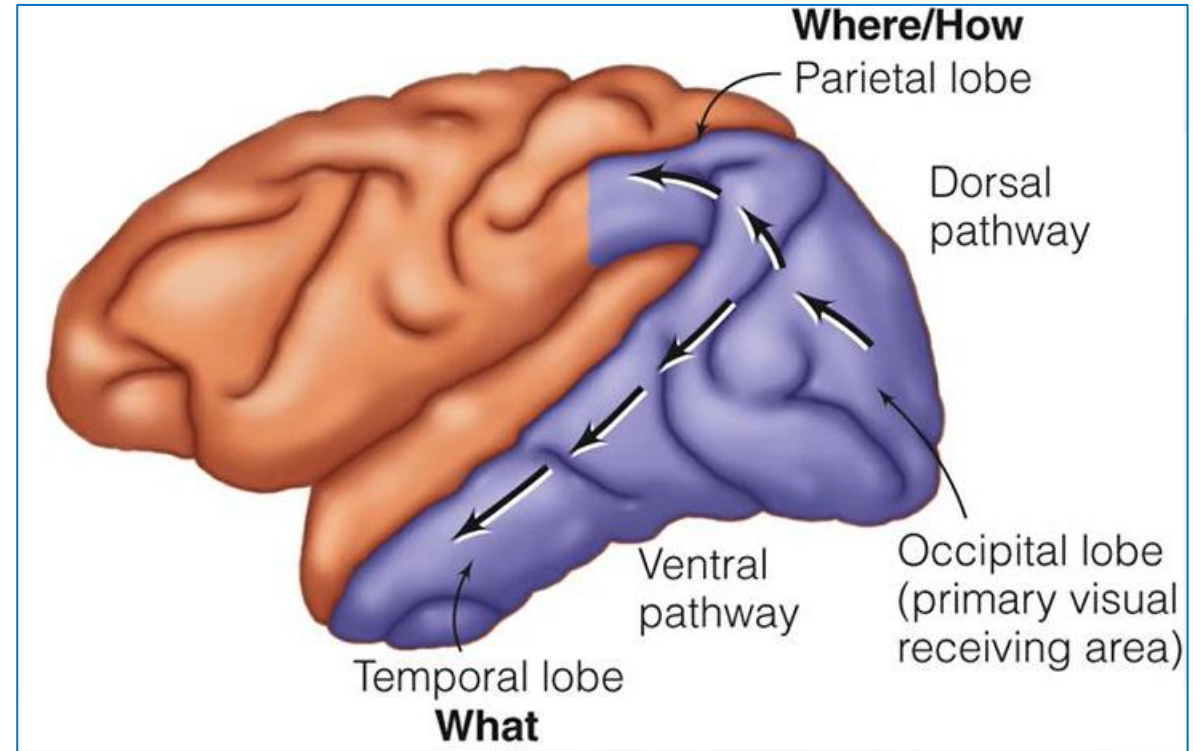
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V2 and the what v. where pathways



Bear et al., (2015), p. 357

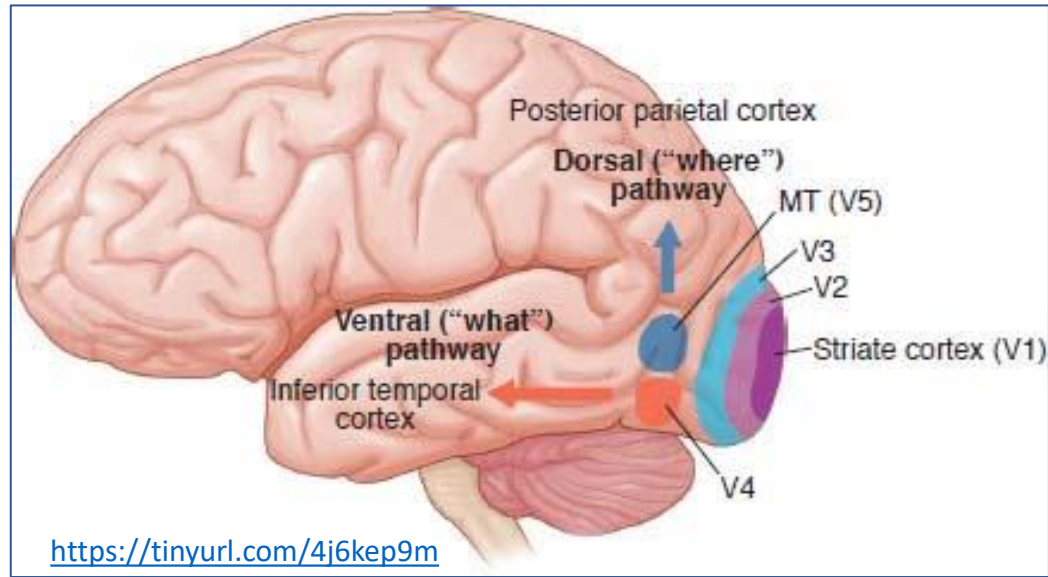
V2 receives **input** from V1 and performs more **complex** information processing, e.g., responding to **differences in color, spatial frequency, moderately complex patterns**, and object **orientation**. V2 sends **feedback** connections to V1 and has **feedforward** connections with V3-V5.



Mishkin, Ungerleider, & Macko, (1983)

Information leaving V2 splits into the **dorsal** and **ventral** streams, specialized in processing **different aspects** of visual information. The **dorsal (“what”)** stream => **object recognition**, while the **ventral (“where”)** => **spatial** tasks and visual-motor skills.

V3, V4, and V5



- **V3** is much less characterized compared to the other areas, and has **no clear histologic delineation** from V2. It is though to contribute to the perception of **color** and **motion**.
- **V4** is part of the **ventral visual stream**, and is specialized in perceiving **colors**. Lesions in this area => cerebral achromatopsia.
- **V5** is part of the **dorsal visual stream**, and is sensitive to **motion** and **direction**.

[Vis Neurosci](#). Author manuscript; available in PMC 2016 Jun 9.

Published in final edited form as:

[Vis Neurosci](#). 2015 Jan; 32: E014.

doi: [10.1017/S0952523815000115](https://doi.org/10.1017/S0952523815000115)

PMCID: PMC4900470

NIHMSID: NIHMS790972

PMID: [26241035](https://pubmed.ncbi.nlm.nih.gov/26241035/)

Topographic organization of areas V3 and V4 and its relation to supra-areal organization of the primate visual system

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Abstract

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Areas V3 and V4 are commonly thought of as individual entities in the primate visual system, based on definition criteria such as their representation of visual space, connectivity, functional response properties, and relative anatomical location in cortex. Yet, large-scale functional and anatomical organization patterns not only emphasize distinctions within each area, but also links across visual cortex. Specifically, the visuotopic organization of V3 and V4 appears to be part of a larger, supra-areal organization, clustering these areas with early visual areas V1 and V2. In addition, connectivity patterns across visual cortex appear to vary within these areas as a function of their supra-areal eccentricity organization. This complicates the traditional view of these regions as individual functional "areas." Here, we will review the criteria for defining areas V3 and V4 and will discuss functional and anatomical studies in humans and monkeys that emphasize the integration of individual visual areas into broad, supra-areal clusters that work in concert for a common computational goal. Specifically, we propose that the visuotopic organization of V3 and V4, which provides the criteria for differentiating these areas, also unifies these areas into the supra-areal organization of early visual cortex. We propose that V3 and V4 play a critical role in this supra-areal organization by filtering information about the visual environment along parallel pathways across higher-order cortex.

Further reading

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An Annotated Journey through Modern Visual Neuroscience

Stuart Trenholm and Arjun Krishnaswamy

Journal of Neuroscience 2 January 2020, 40 (1) 44-53; DOI: <https://doi.org/10.1523/JNEUROSCI.1061-19.2019>

Abstract

Recent advances in microscopy, genetics, physiology, and data processing have expanded the scope and accelerated the pace of discovery in visual neuroscience. However, the pace of discovery and the ever increasing number of published articles can present a serious issue for both trainees and senior scientists alike: with each passing year the fog of progress thickens, making it easy to lose sight of important earlier advances. As part of this special issue of the Journal of Neuroscience commemorating the 50th anniversary of SfN, here, we provide a variation on Stephen Kuffler's *Oldies but Goodies* classic reading list, with the hope that by looking back at highlights in the field of visual neuroscience we can better define remaining gaps in our knowledge and thus guide future work. We also hope that this article can serve as a resource that will aid those new to the field to find their bearings.

<https://www.jneurosci.org/content/40/1/44.abstract>

More on the LGN and the complex V1 cells

Review > Prog Neurobiol. 2017 Sep;156:214-255. doi: 10.1016/j.pneurobio.2017.06.002.

Epub 2017 Jun 19.

Towards building a more complex view of the lateral geniculate nucleus: Recent advances in understanding its role

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PMID: 28634086 DOI: 10.1016/j.pneurobio.2017.06.002

Abstract

The lateral geniculate nucleus (LGN) has often been treated in the past as a linear filter that adds little to retinal processing of visual inputs. Here we review anatomical, neurophysiological, brain imaging, and modeling studies that have in recent years built up a much more complex view of LGN. These include effects related to nonlinear dendritic processing, cortical feedback, synchrony and oscillations across LGN populations, as well as involvement of LGN in higher level cognitive processing. Although recent studies have provided valuable insights into early visual processing including the role of LGN, a unified model of LGN responses to real-world objects has not yet been developed. In the light of recent data, we suggest that the role of LGN deserves more careful consideration in developing models of high-level visual processing.

<https://pubmed.ncbi.nlm.nih.gov/28634086/>

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RESEARCH ARTICLE

Learning receptive field properties of complex cells in V1

Yanbo Lian , Ali Almasi, David B. Grayden, Tatiana Kameneva, Anthony N. Burkitt , Hamish Meffin 

Abstract

There are two distinct classes of cells in the primary visual cortex (V1): simple cells and complex cells. One defining feature of complex cells is their spatial phase invariance; they respond strongly to oriented grating stimuli with a preferred orientation but with a wide range of spatial phases. A classical model of complete spatial phase invariance in complex cells is the energy model, in which the responses are the sum of the squared outputs of two linear spatially phase-shifted filters. However, recent experimental studies have shown that complex cells have a diverse range of spatial phase invariance and only a subset can be characterized by the energy model. While several models have been proposed to explain how complex cells could learn to be selective to orientation but invariant to spatial phase, most existing models overlook many biologically important details. We propose a biologically plausible model for complex cells that learns to pool inputs from simple cells based on the presentation of natural scene stimuli. The model is a three-layer network with rate-based neurons that describes the activities of LGN cells (layer 1), V1 simple cells (layer 2), and V1 complex cells (layer 3). The first two layers implement a recently proposed simple cell model that is biologically plausible and accounts for many experimental phenomena. The neural dynamics of the complex cells is modeled as the integration of simple cells inputs along with response normalization. Connections between LGN and simple cells are learned using Hebbian and anti-Hebbian plasticity. Connections between simple and complex cells are learned using a modified version of the Bienenstock, Cooper, and Munro (BCM) rule. Our results demonstrate that the learning rule can describe a diversity of complex cells, similar to those observed experimentally.

<https://journals.plos.org/ploscompbiol/article?id=10.1371/journal.pcbi.1007957>

Review > Neuroscientist. 2009 Feb;15(1):62-77. doi: 10.1177/1073858408327806.

Ocular dominance columns: enigmas and challenges

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PMID: 19218231 PMCID: PMC6913877 DOI: 10.1177/1073858408327806

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Abstract

In some mammalian species, geniculocortical afferents serving each eye are segregated in layer 4C of striate cortex into stripes called ocular dominance columns. Having described the complete pattern of ocular dominance columns in the human brain, the authors enumerate here the principal enigmas that confront future investigators. Probably the overarching challenge is to explain the function, if any, of ocular dominance columns and why they are present in some species and not others. A satisfactory solution must account for the enormous natural variation, even within the same species, among individuals in column expression, pattern, periodicity, and alignment with other components of the functional architecture. Another major priority is to explain the development of ocular dominance columns. It has been established clearly that they form without visual experience, but the innate signals that guide their segregation and maturation are unknown. Experiments addressing the role of spontaneous retinal activity have yielded contradictory data. These studies must be reconciled, to pave the way for new insights into how columnar structure is generated in the cerebral cortex.

<https://pubmed.ncbi.nlm.nih.gov/19218231/>