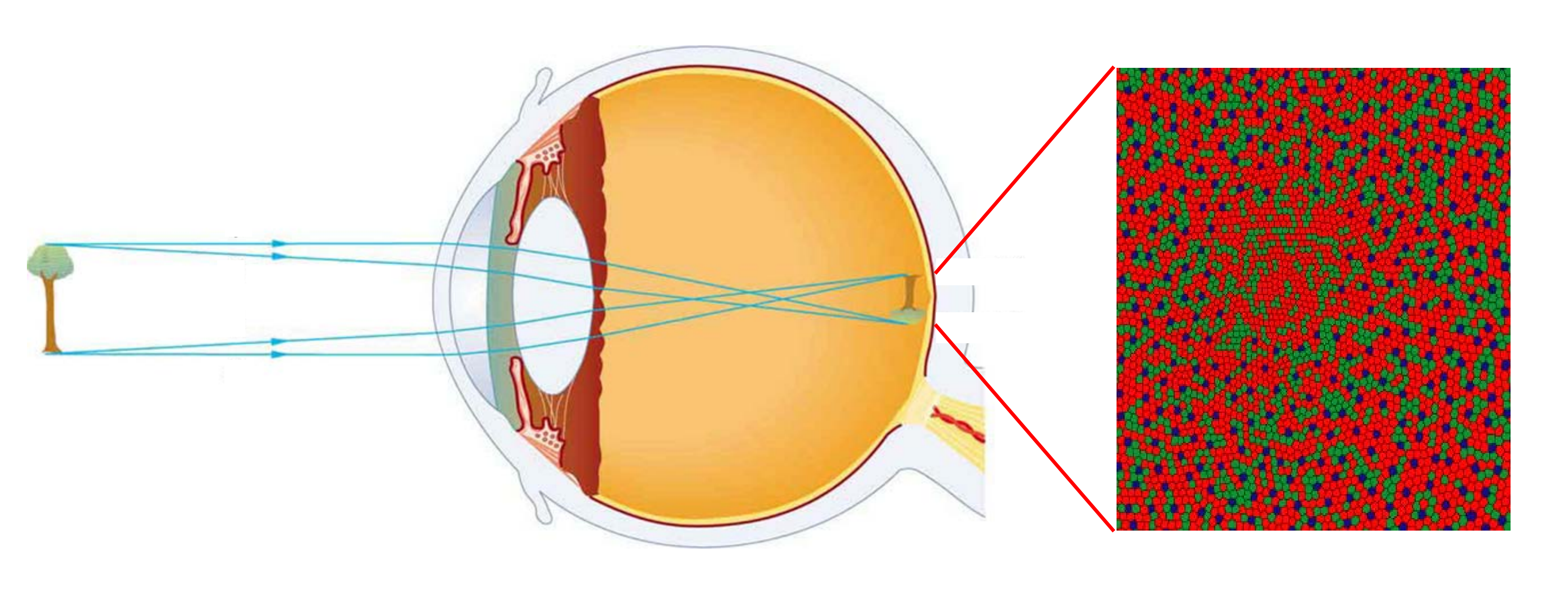
Visual optics, rods and cones and retinal processing

Andrew Stockman



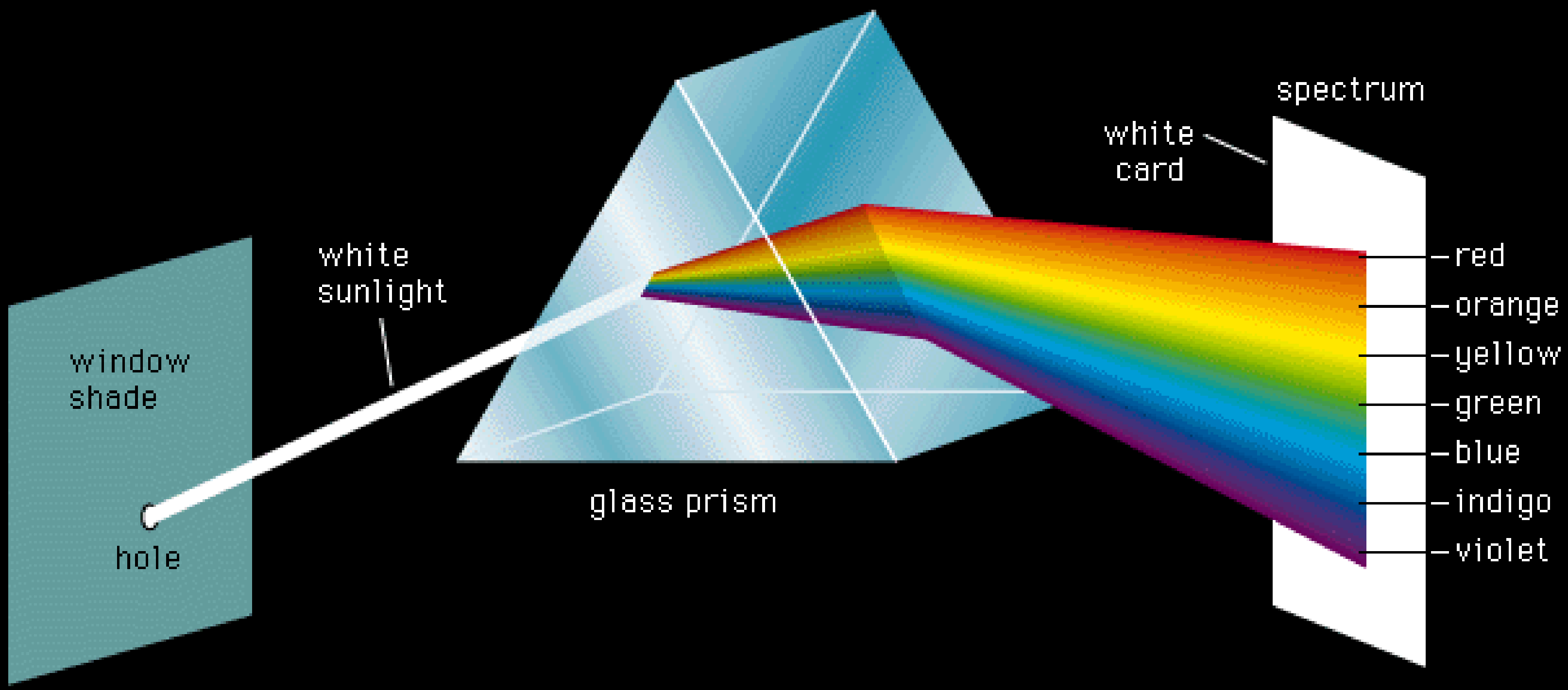
MSc Neuroscience course

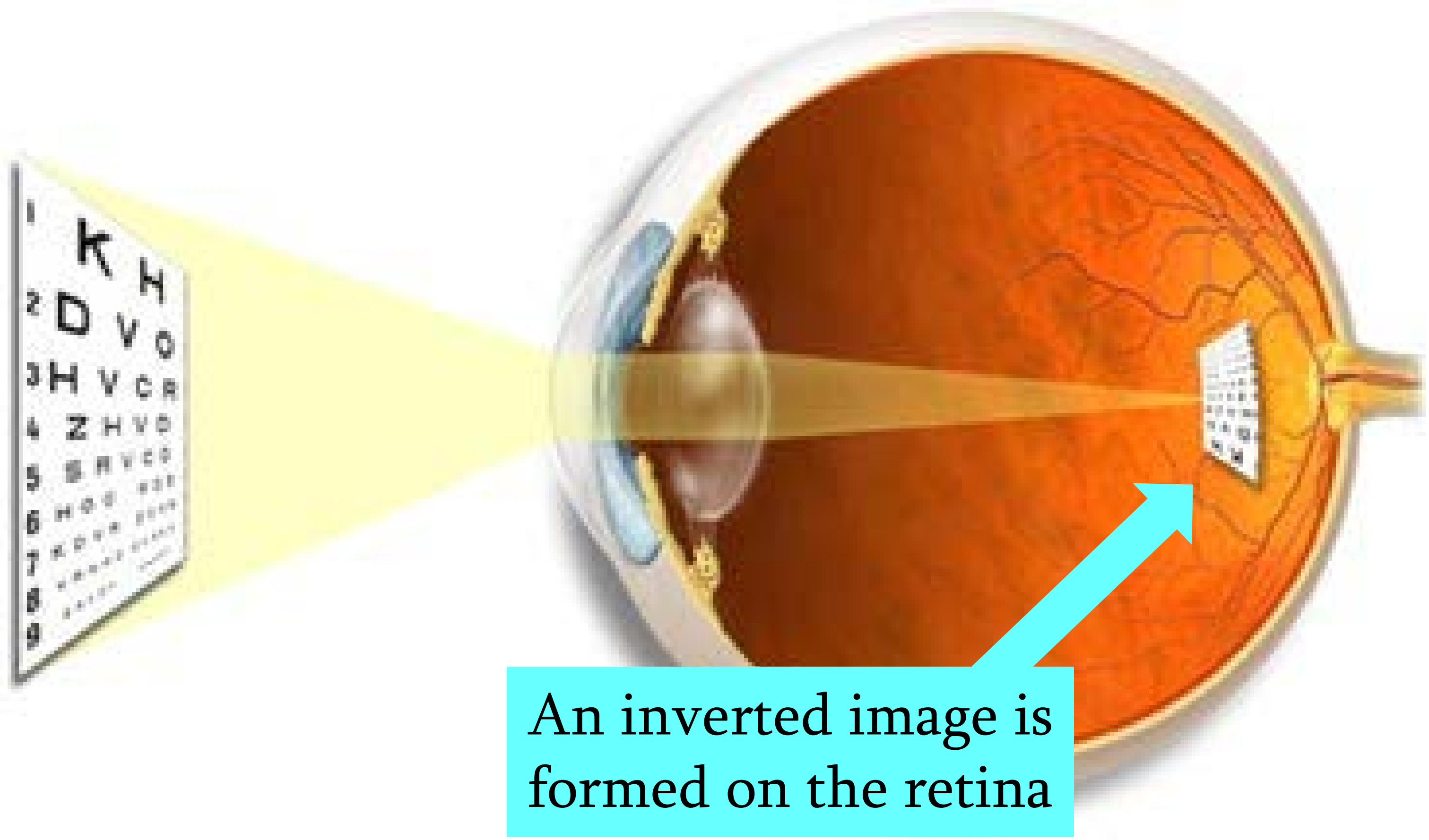
Outline

- The eye
- Visual optics
- Image quality
- Measuring image quality
- Rods and cones
- Univariance
- Trichromacy
- Chromatic processing
- Retina and retinal processing

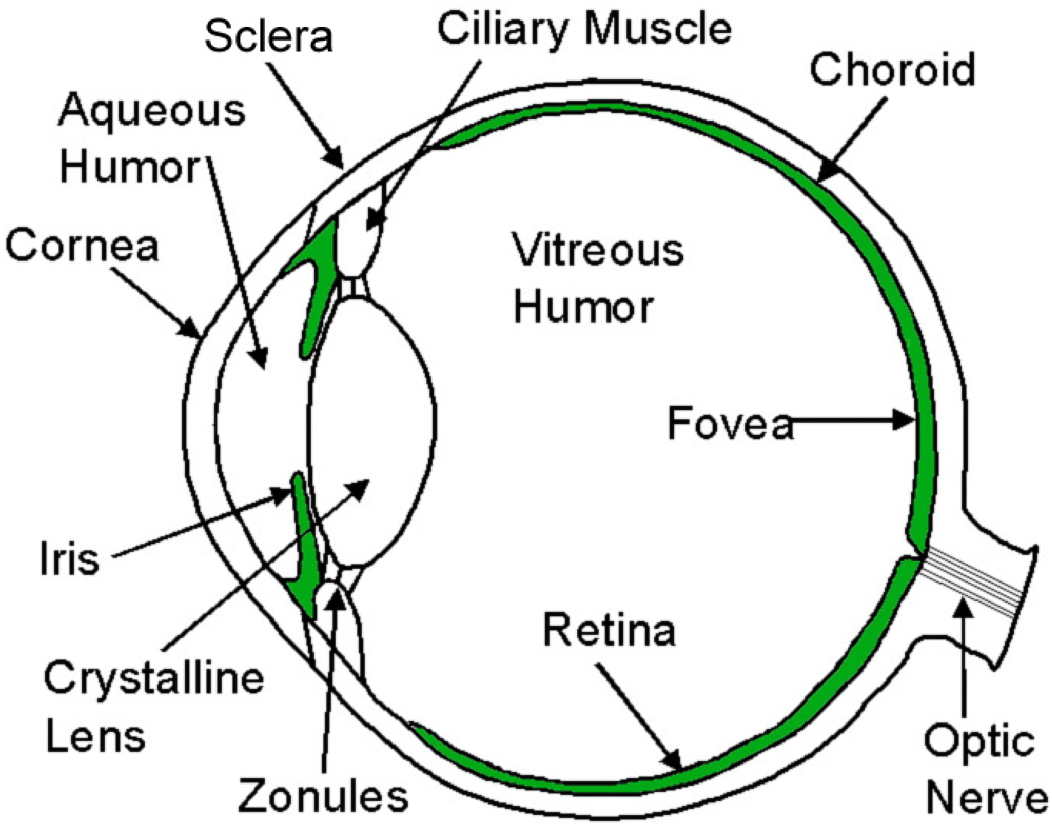
Light

400 - 700 nm is important for vision




An inverted image is formed on the retina

Retinal cross-section



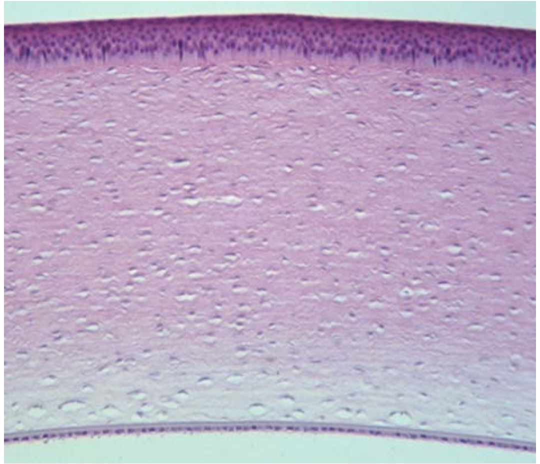
Cornea – Clear membrane on the front of the eye.
Crystalline Lens – Lens that
can change shape to alter focus.
Retina – Photosensitive inner lining of eye
Fovea – central region of retina with sharpest vision.
Optic Nerve – bundle of nerve fibers that carry information to the brain.

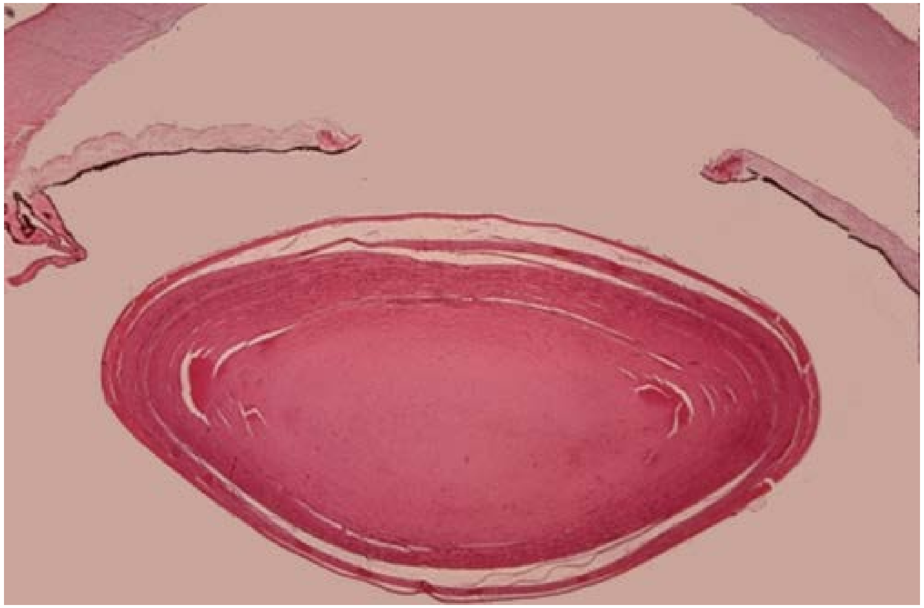
Jim Schwiegerling

Visual optics

Cornea

Crystalline lens



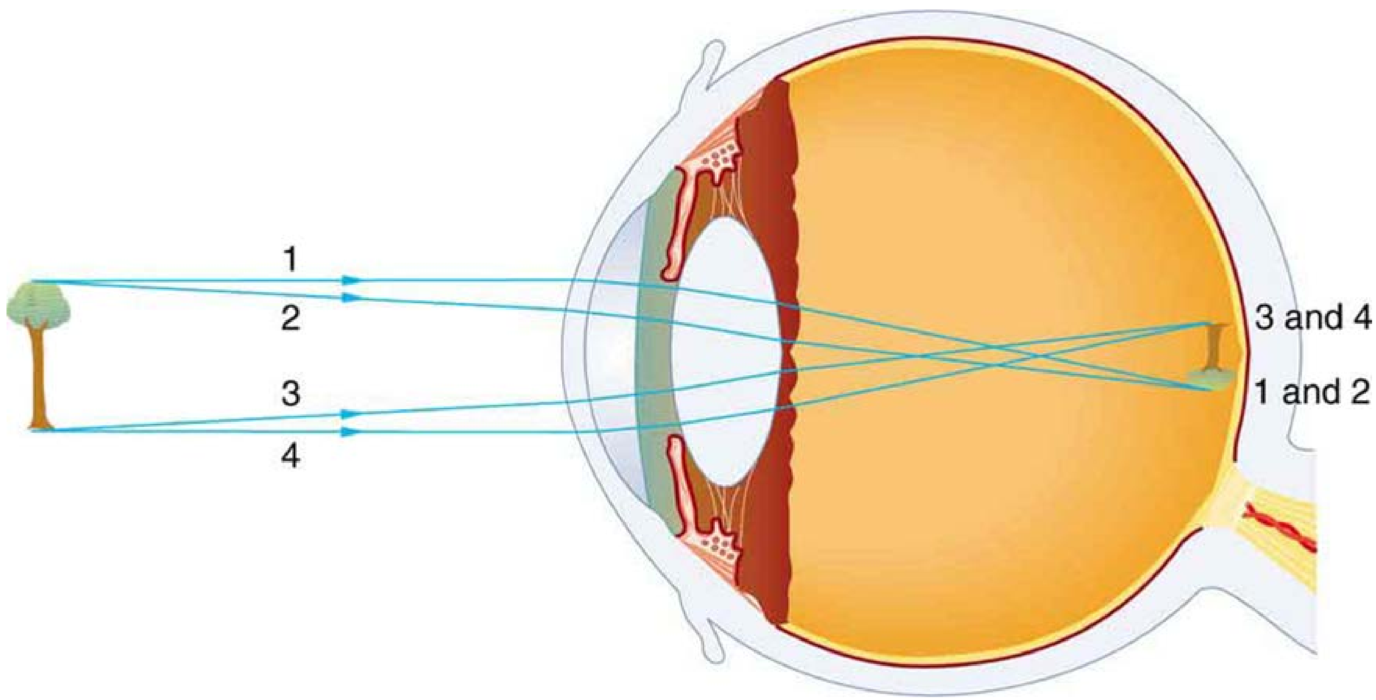


Jim Schwiegerling

Jim Bowmaker dissecting an eye…

BBC Horizon: Light Fantastic (2006)

Image formation

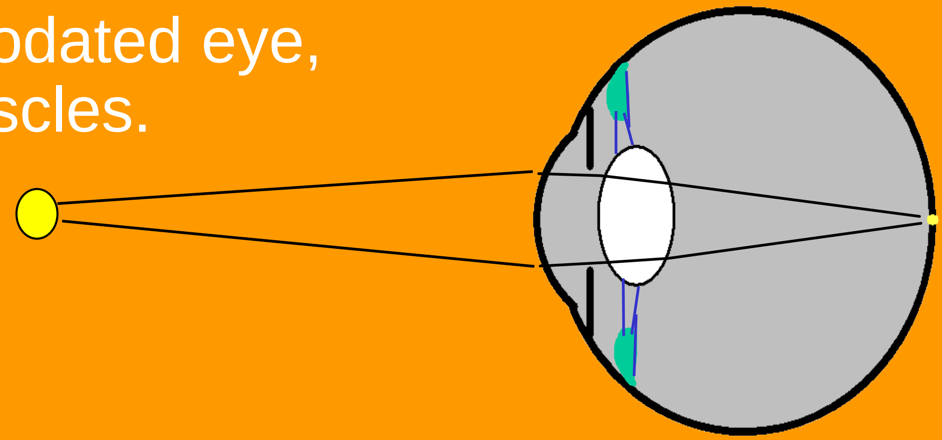


Openstax College Physics

Accommodation to Target Distance

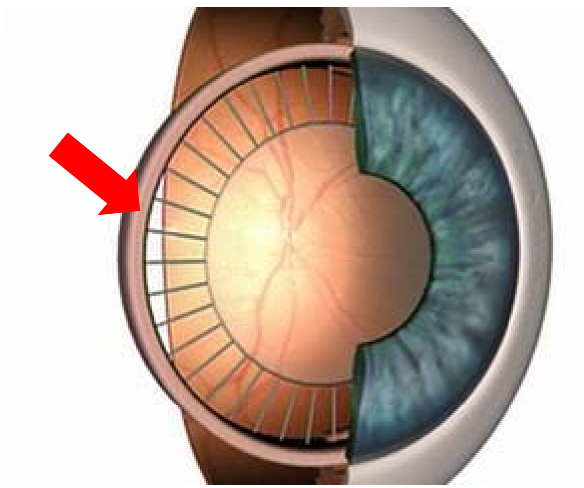
Distant target, relaxed ciliary muscles

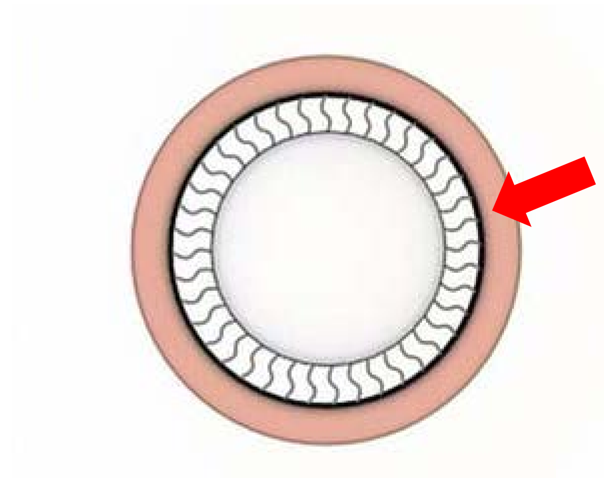
Near target, accommodated eye, constricted ciliary muscles.



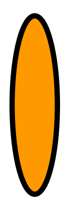
Larry Thibos

Accommodation

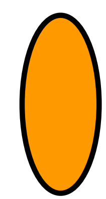




Relaxed ciliary muscle pulls zonules taut an flattens crystalline lens.



Constricted ciliary muscle releases tension on zonules and crystalline lens bulges.



Jim Schwiegerling

Image quality

Point spread function

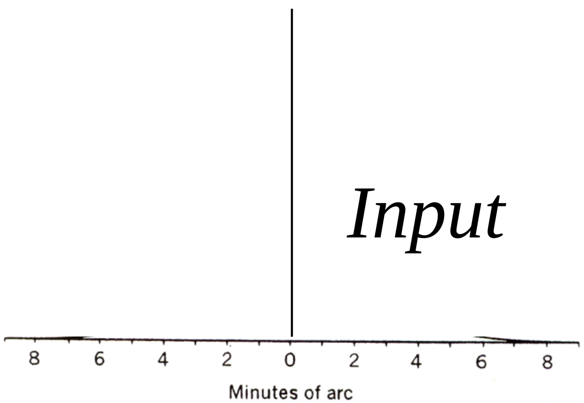
Optical systems are rarely ideal.

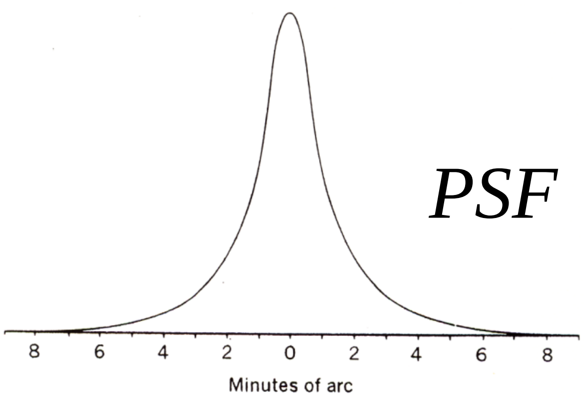
scene $\longrightarrow$ **Optical System** $\longrightarrow$ image

Point spread function of Human Eyes

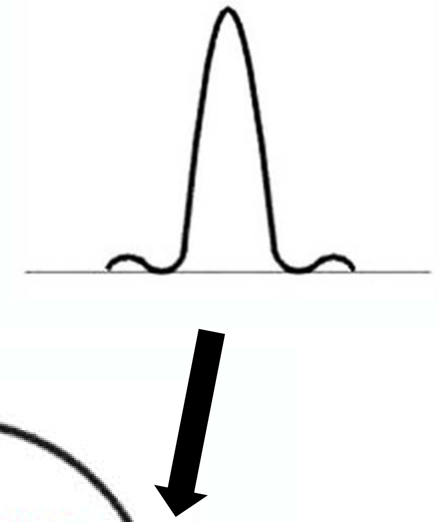
$\delta(x) \longrightarrow$ **Optical System** $\longrightarrow PSF(x)$

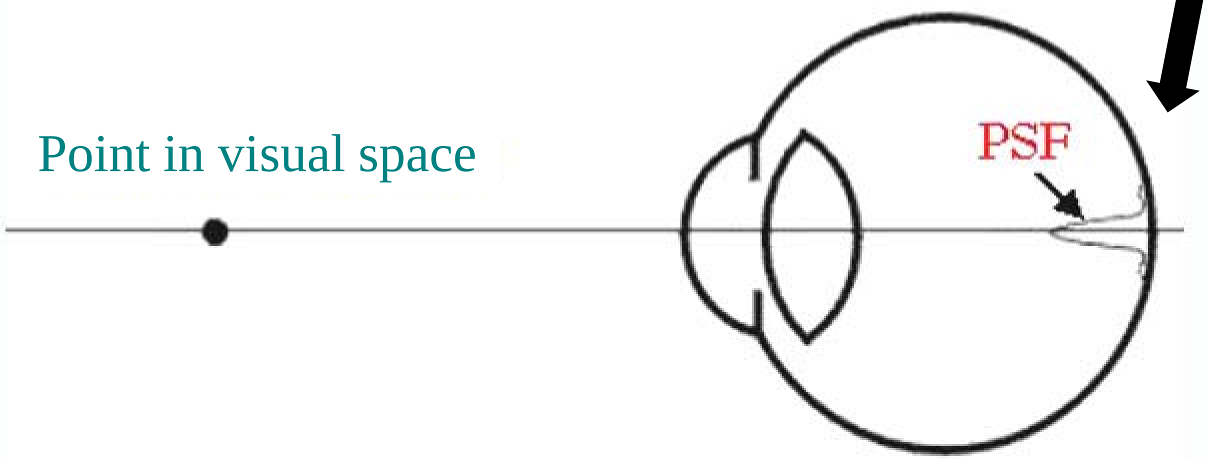
point source — point spread function





Point spread function (PSF)



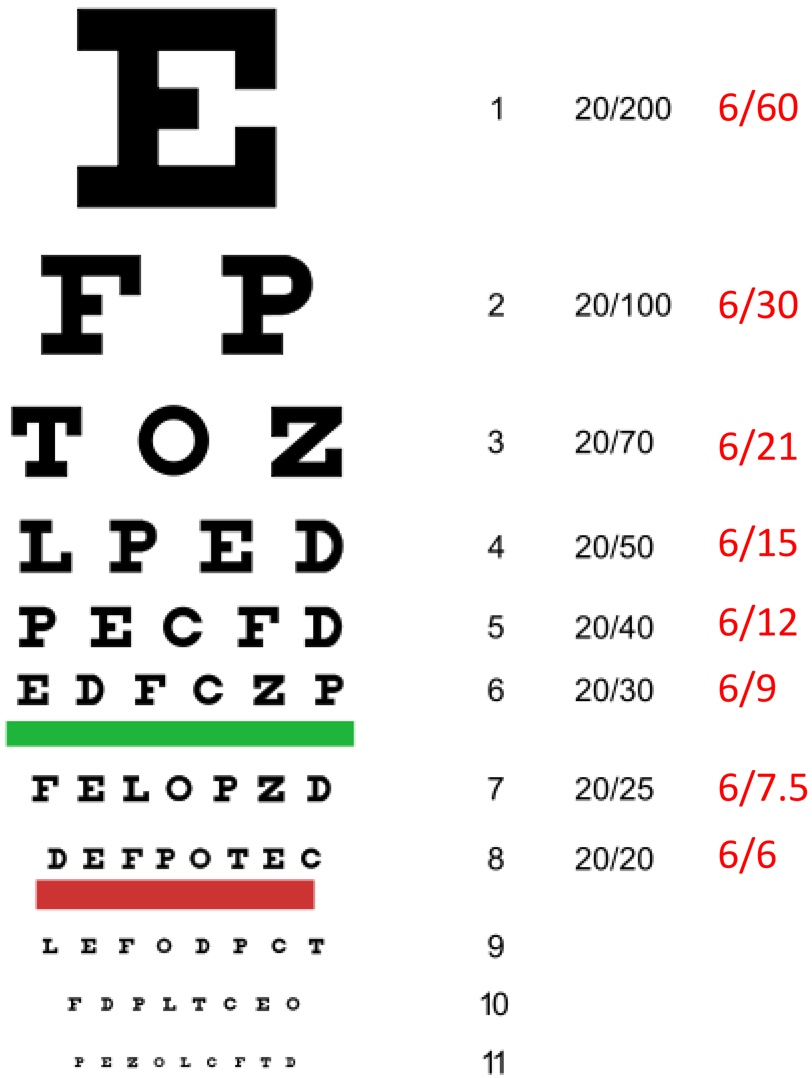


From Webvision, Michael Kalloniatis

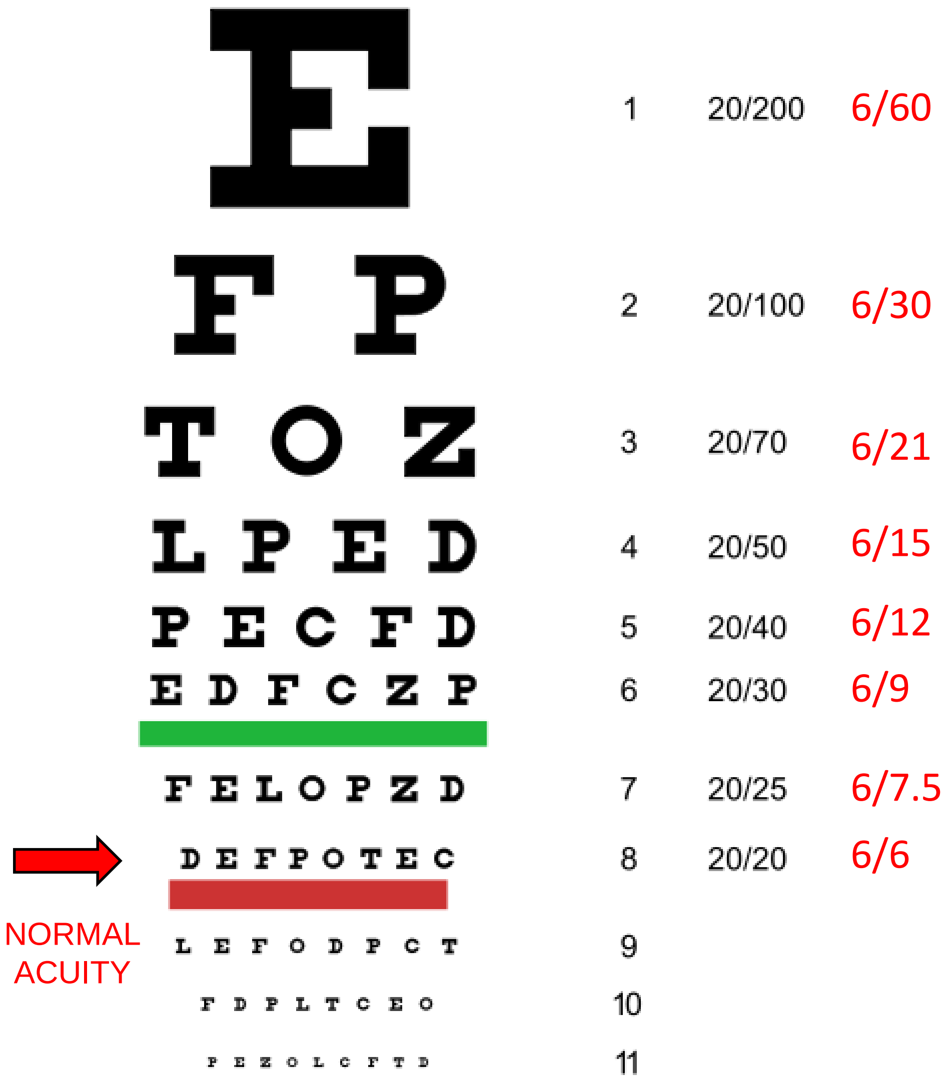
The Point Spread Function (PSF) characterizes the optical performance of the eye.

Measuring image quality perceptually or “psychophysically”

1. Visual acuity measures



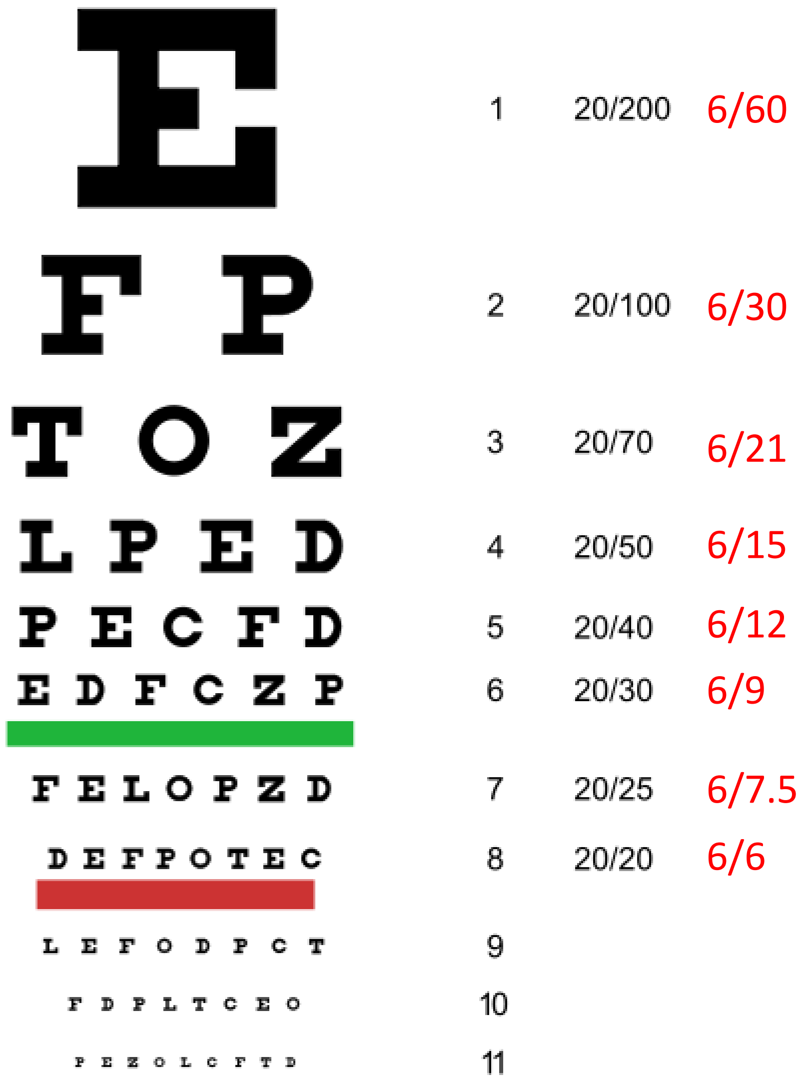
Smallest resolvable black and white target. Many different types of tests are available , but the letter chart introduced by Snellen in 1862 is the most common.

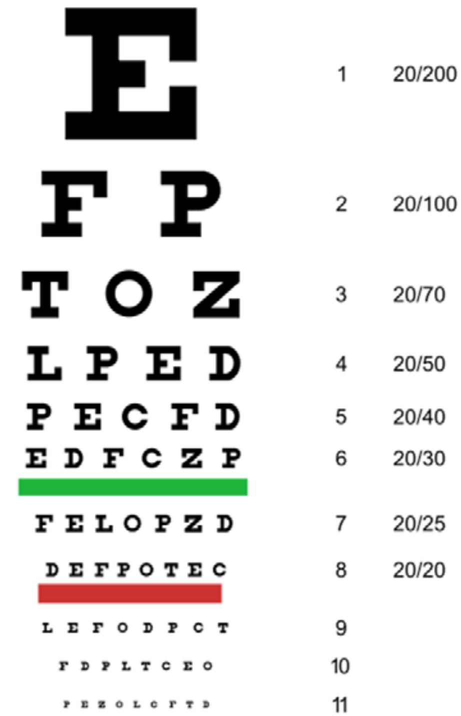


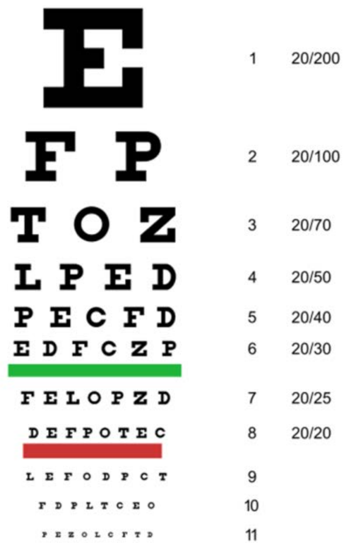
Snellen defined "standard vision" as the ability to recognize one of his optotypes when it subtended 5 minutes of arc. Thus, the optotype can only be recognized if the person viewing it can discriminate a spatial patterns separated by visual angles of 1 minute of arc.

A Snellen chart is placed at a standard distance, twenty feet in the US (6 metres in Europe). At this distance, the symbols on the line representing "normal" acuity subtend an angle of five minutes of arc, and the thickness of the lines and of the spaces between the lines subtends one minute of arc. This line, designated 20/20, is the smallest line that a person with normal acuity can read at a distance of twenty feet.

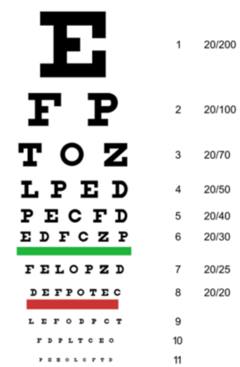
The letters on the 20/40 line are twice as large. A person with normal acuity could be expected to read these letters at a distance of forty feet. This line is designated by the ratio 20/40. If this is the smallest line a person can read, the person's acuity is "20/40."


E
F P
T O Z
L P E D
P E C F D
E D F C Z P
F E L O P Z D
D E F P O T E C
L E F O D P C T
F D P L T C E O
P E Z O L C F T D
1 20/200 6/60
2 20/100 6/30
3 20/70 6/21
4 20/50 6/15
5 20/40 6/12
6 20/30 6/9
7 20/25 6/7.5
8 20/20 6/6
9
10
11


E
F P
T O Z
L P E D
P E C F D
E D F C Z P
F E L O P Z D
D E F P O T E C
1 20/200
2 20/100
3 20/70
4 20/50
5 20/40
6 20/30
7 20/25
8 20/20
9
10
11



E 1 20/200
F P 2 20/100
T O Z 3 20/70
L P E D 4 20/50
P E C F D 5 20/40
E D F C Z P 6 20/30
F E L O P Z D 7 20/25
D E F P O T E C 8 20/20
L E F O D P C T 9
F D P L T C E O 10
P E Z O L C F T D 11



E 1 20/200
F P 2 20/100
T O Z 3 20/70
L P E D 4 20/50
P E C F D 5 20/40
E D F C Z P 6 20/30
F E L O P Z D 7 20/25
D E F P O T E C 8 20/20
L E F O D P C T 9
F D P L T C E O 10
P E Z O L C F T D 11

Visual Acuity: four standard methods

Letter acuity (Snellen)

Can the subject correctly identify the letter or the letter orientation?

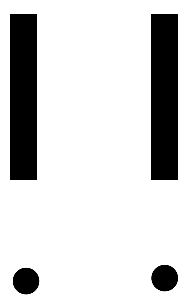
Grating acuity

Orientation resolution acuity

Detection acuity

2-line resolution

2-point resolution



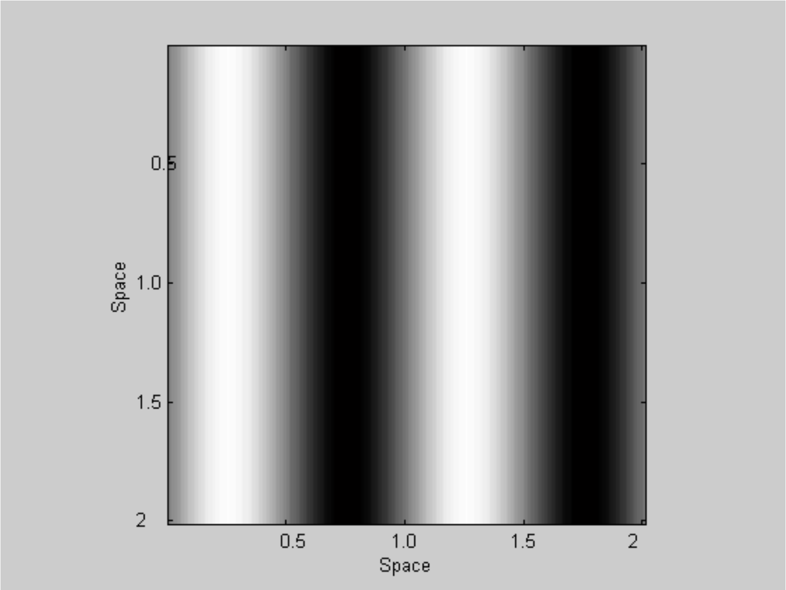
Can the subject see two lines or points rather than one?

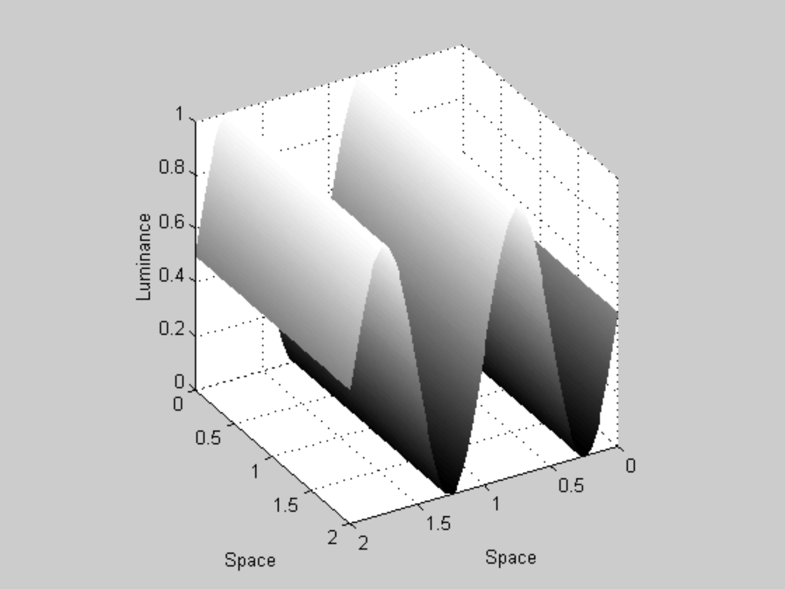
Arthur Bradley

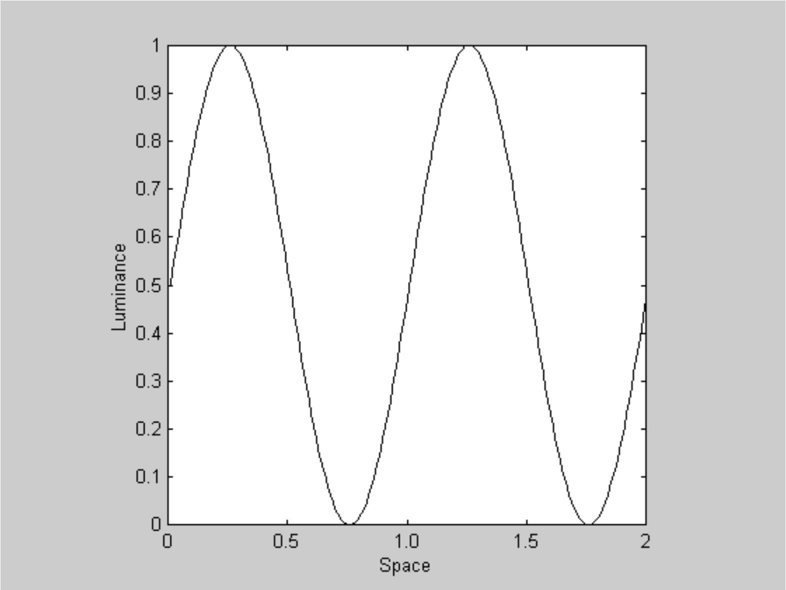
Measuring image quality perceptually or psychophysically

2. Spatial contrast sensitivity measures

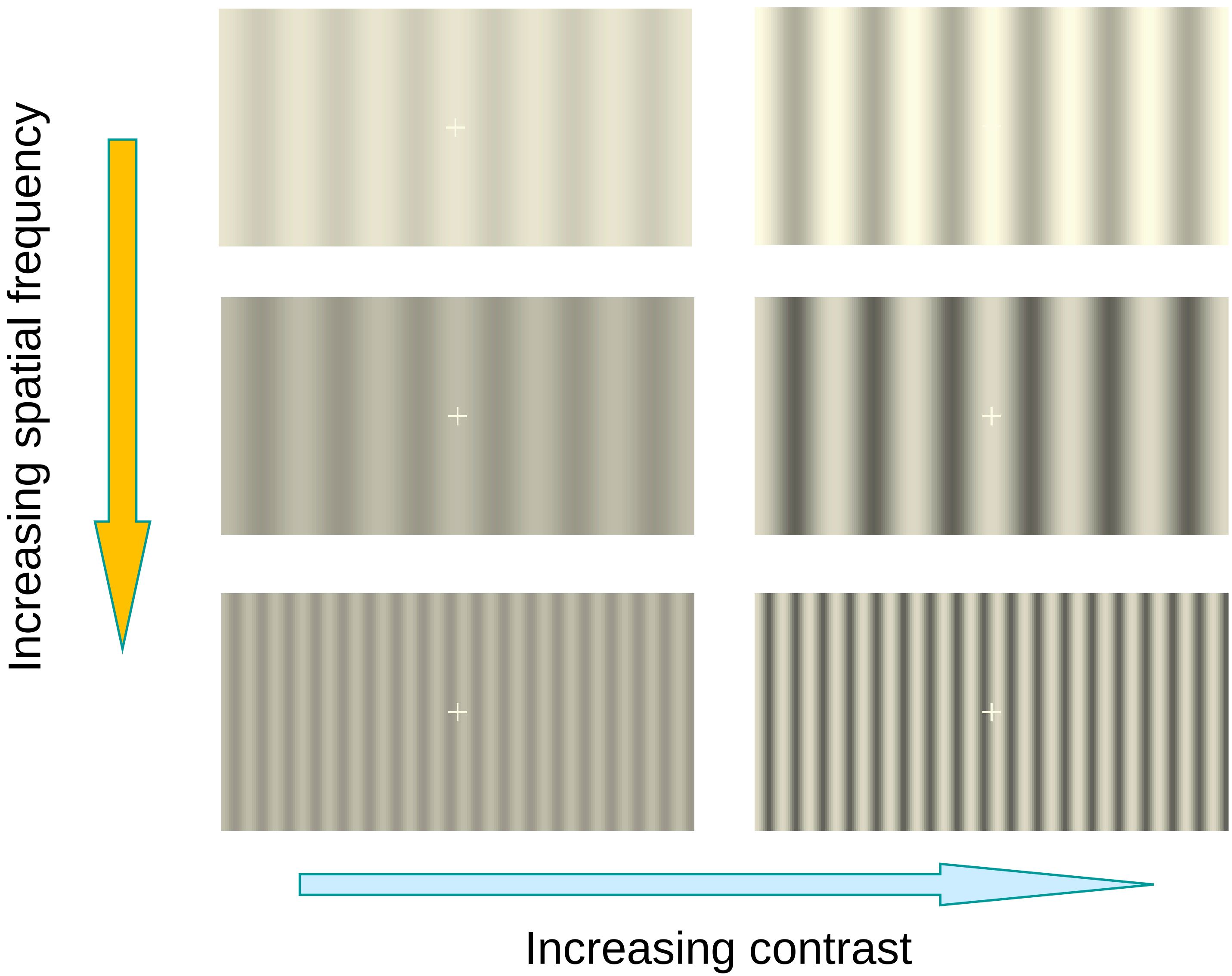
Spatial frequency





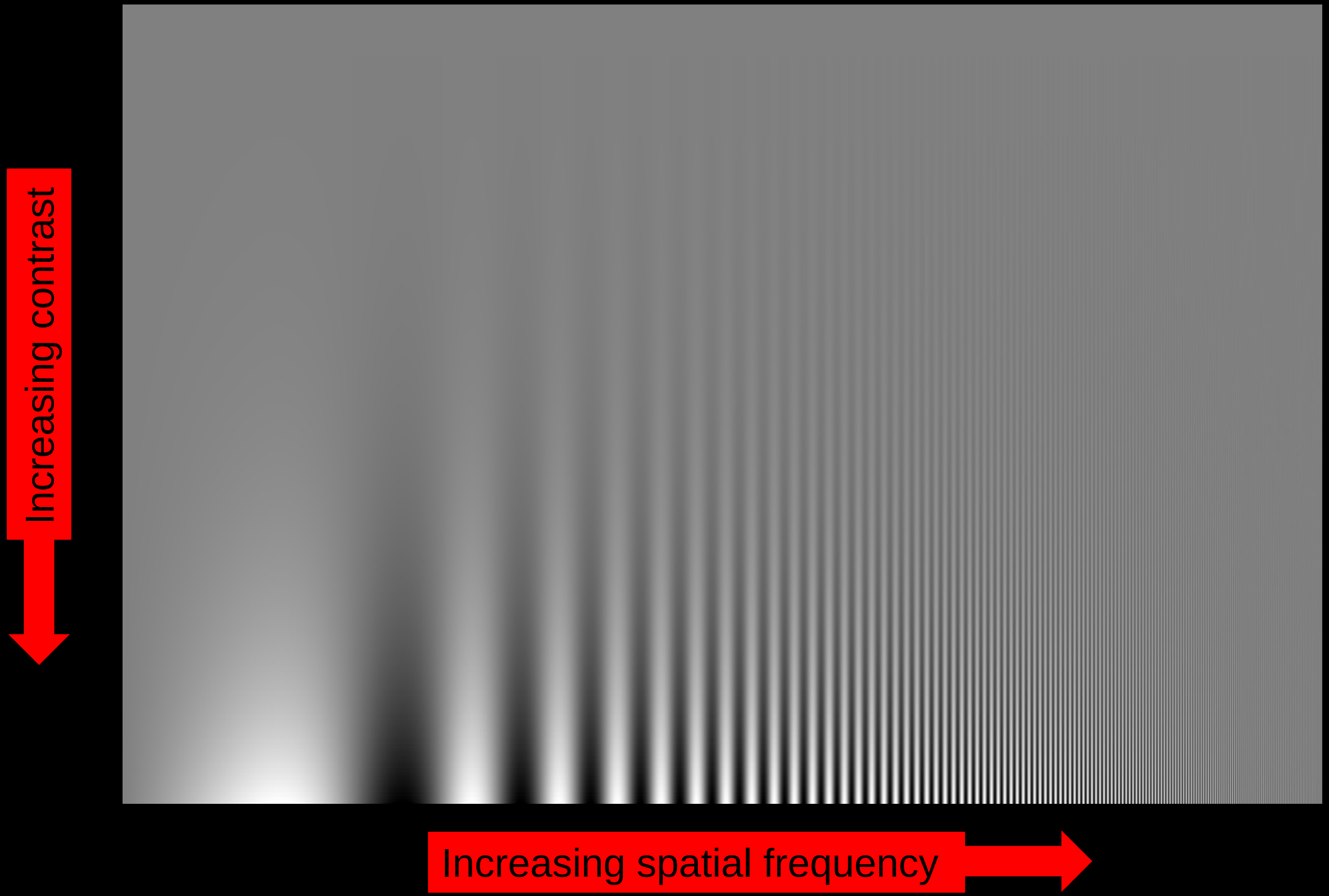


Spatial frequency gratings



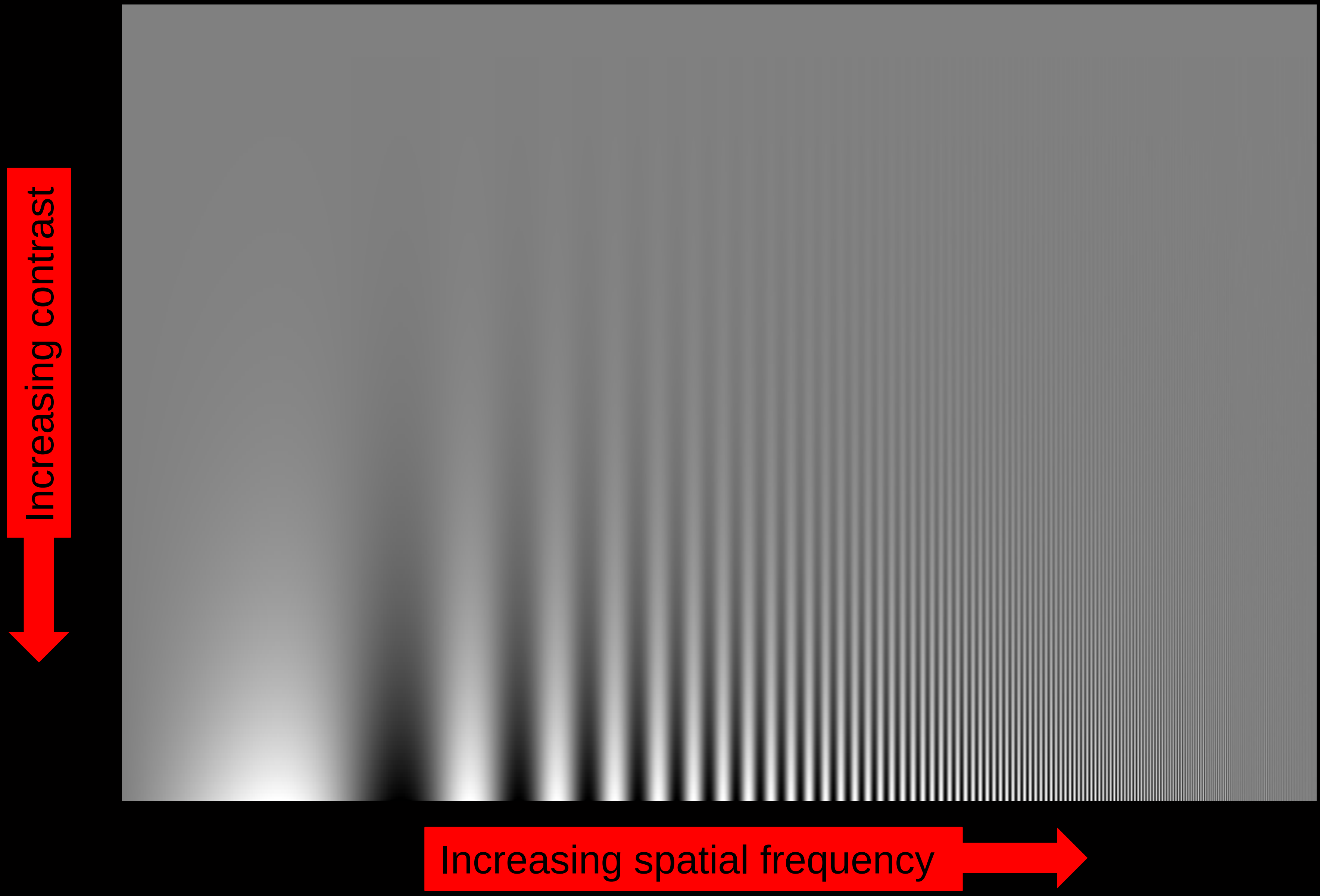
Spatial MTF

Spatial frequency in this image increases in the horizontal direction and modulation depth decreases in the vertical direction.



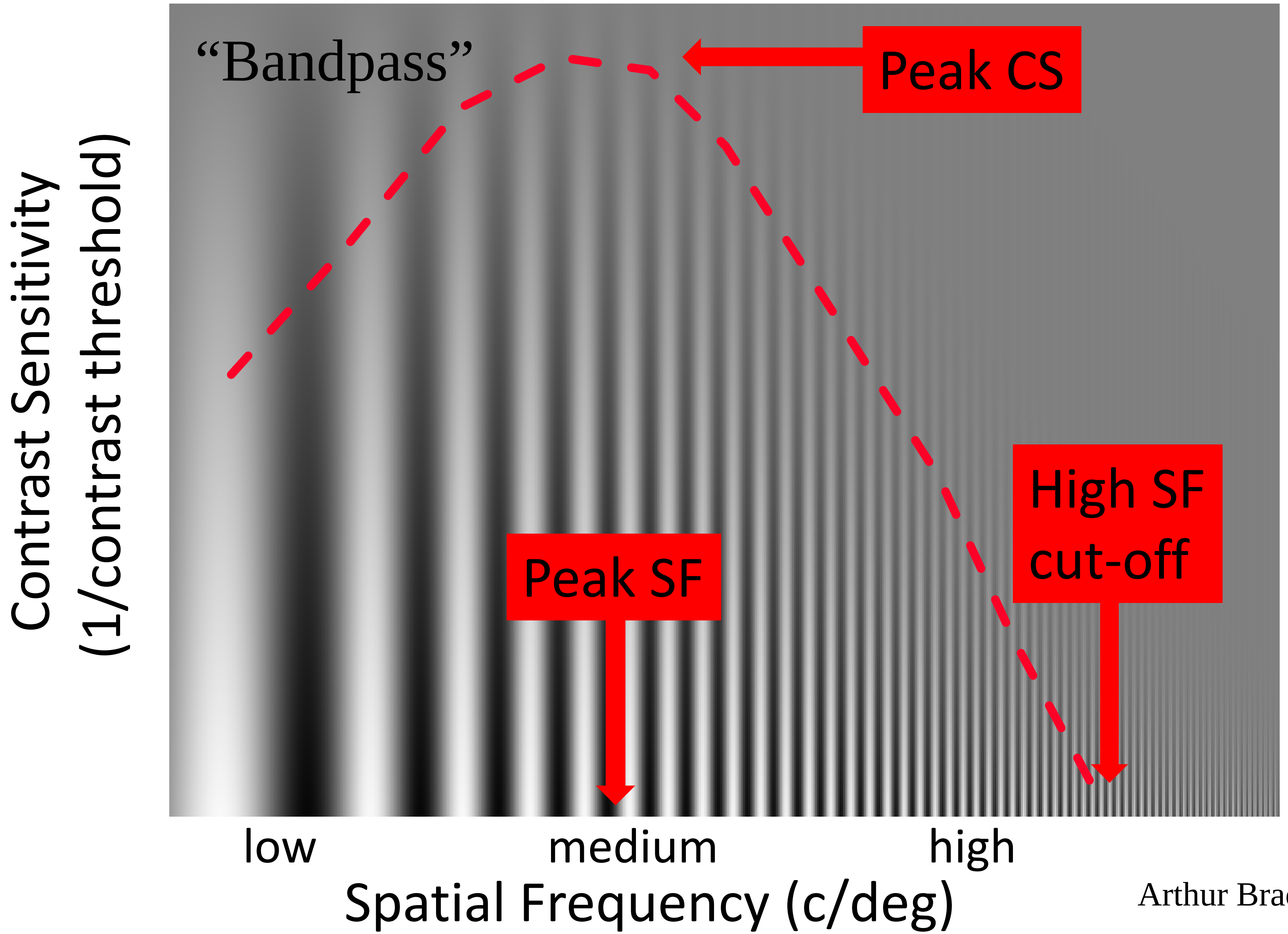
Spatial MTF

The apparent border between visible and invisible modulation corresponds to your own visual modulation transfer function.



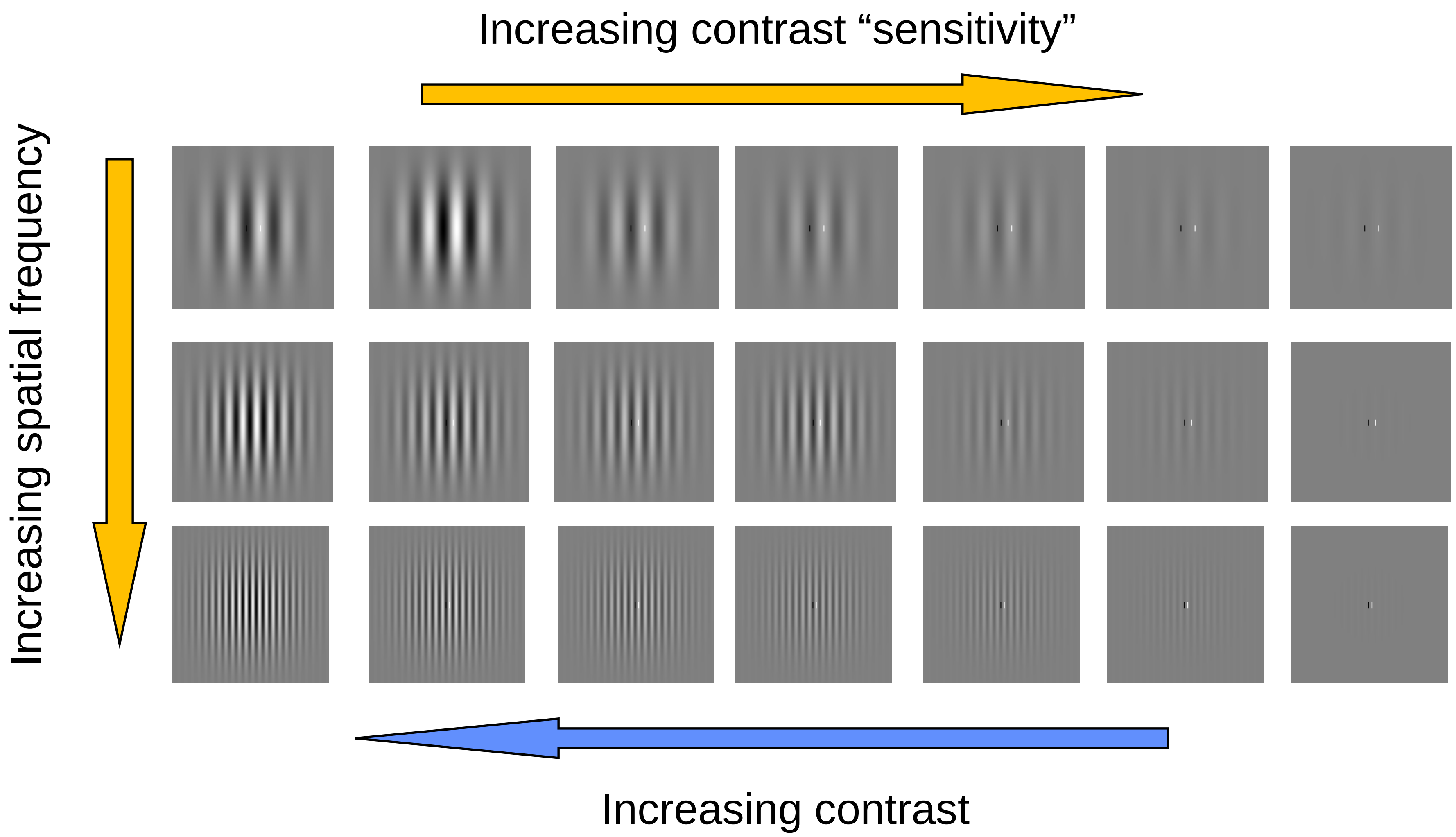
2. Grating Contrast Sensitivity

Contrast Sensitivity Function (CSF)



Arthur Bradley

Example of grating contrast sensitivity test using printed gratings



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Spatial CSFs

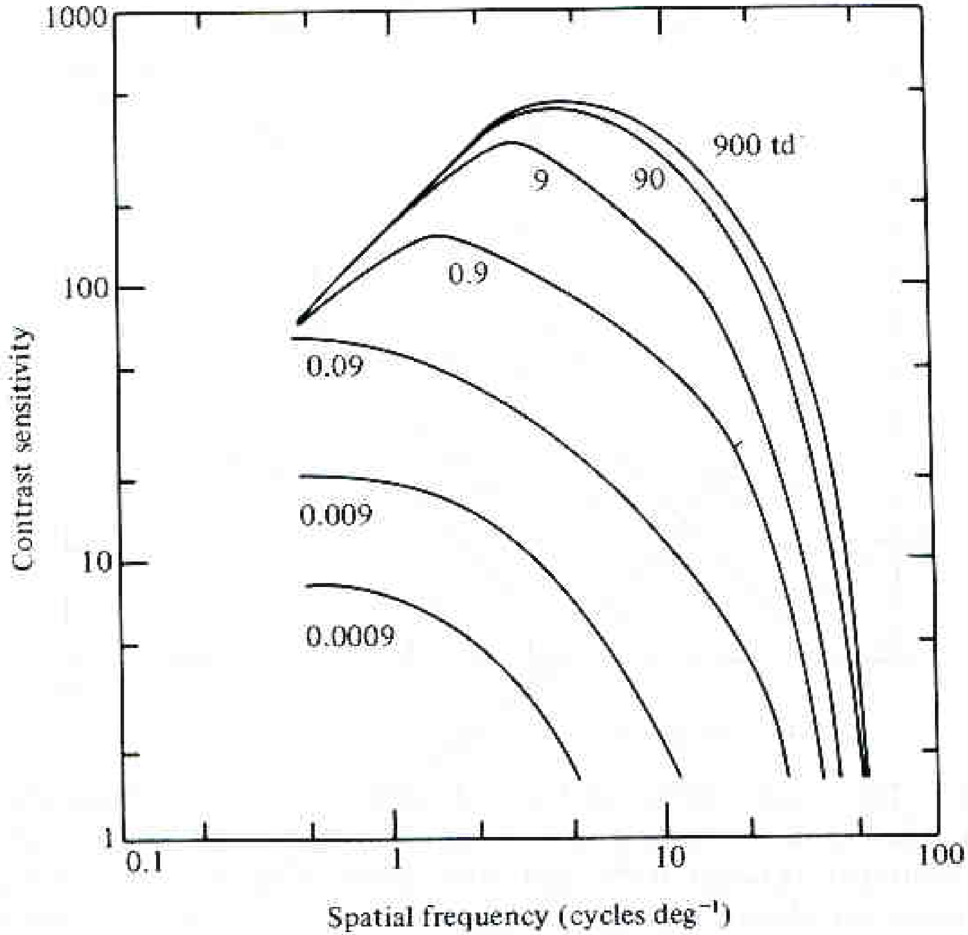
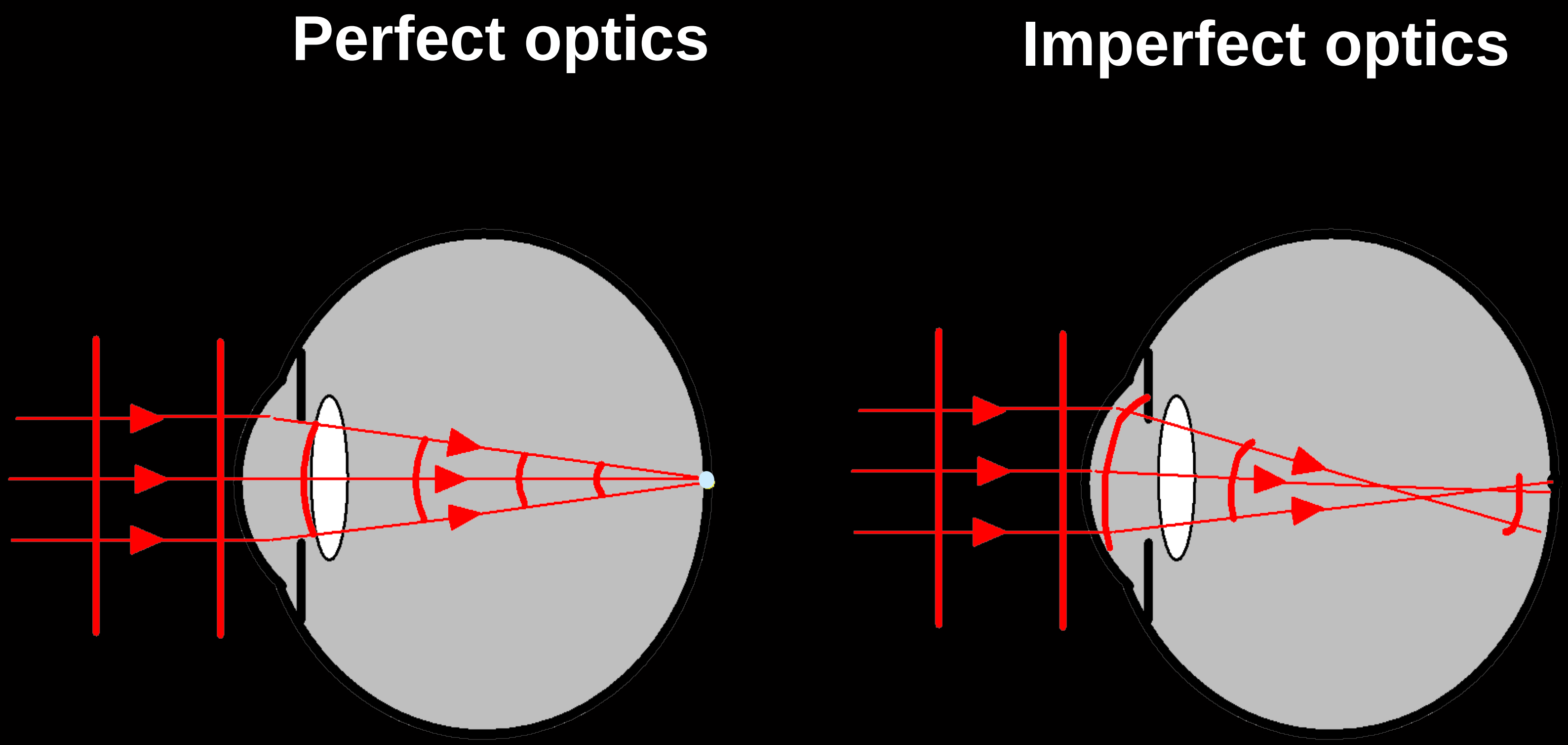


Fig. 8.4. Spatial contrast sensitivity curves at seven different retinal illuminance levels between 0.0009 and 900 trolands. The subject viewed the gratings through a 2 mm diameter artificial pupil. The wavelength of the light was 525 nm. Notice the loss of sensitivity for medium and high frequencies as the retinal illumination is decreased. (Adapted from Van Nes & Bouman, 1967.)

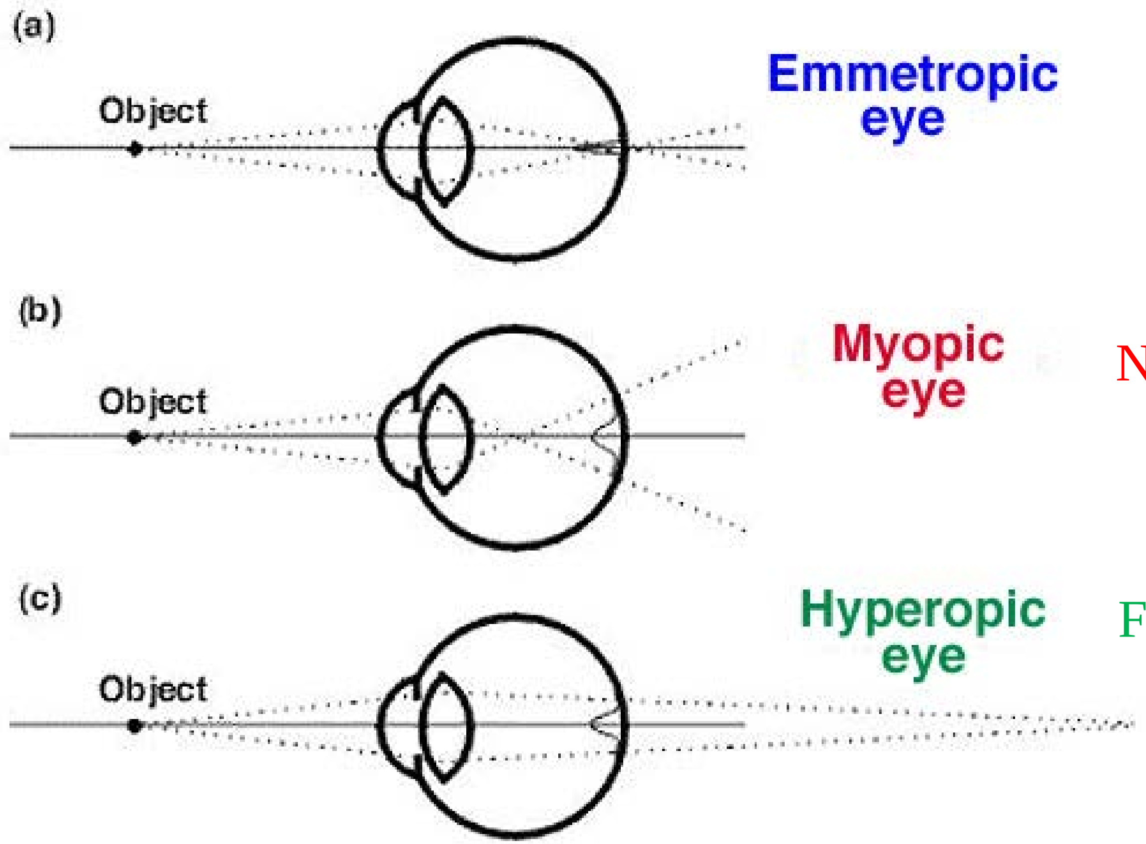
Refractive errors

Aberrations of the Eye



Larry Thibos

PSFs for different refractive errors



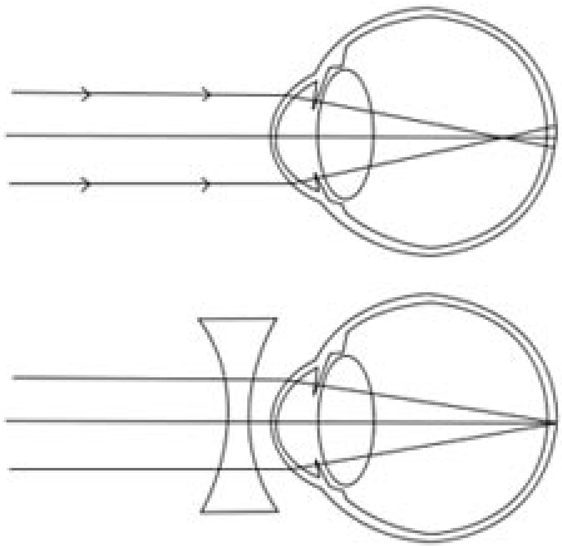
Nearsighted

Far-sighted

From Webvision, Michael Kalloniatis

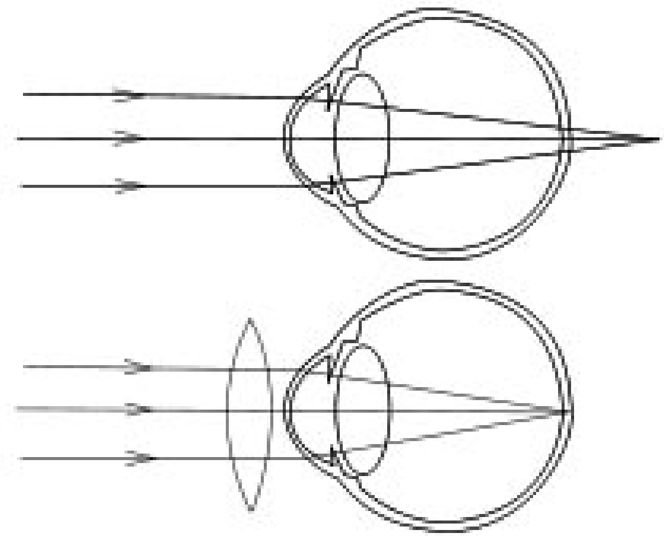
Corrective lenses

Myopia

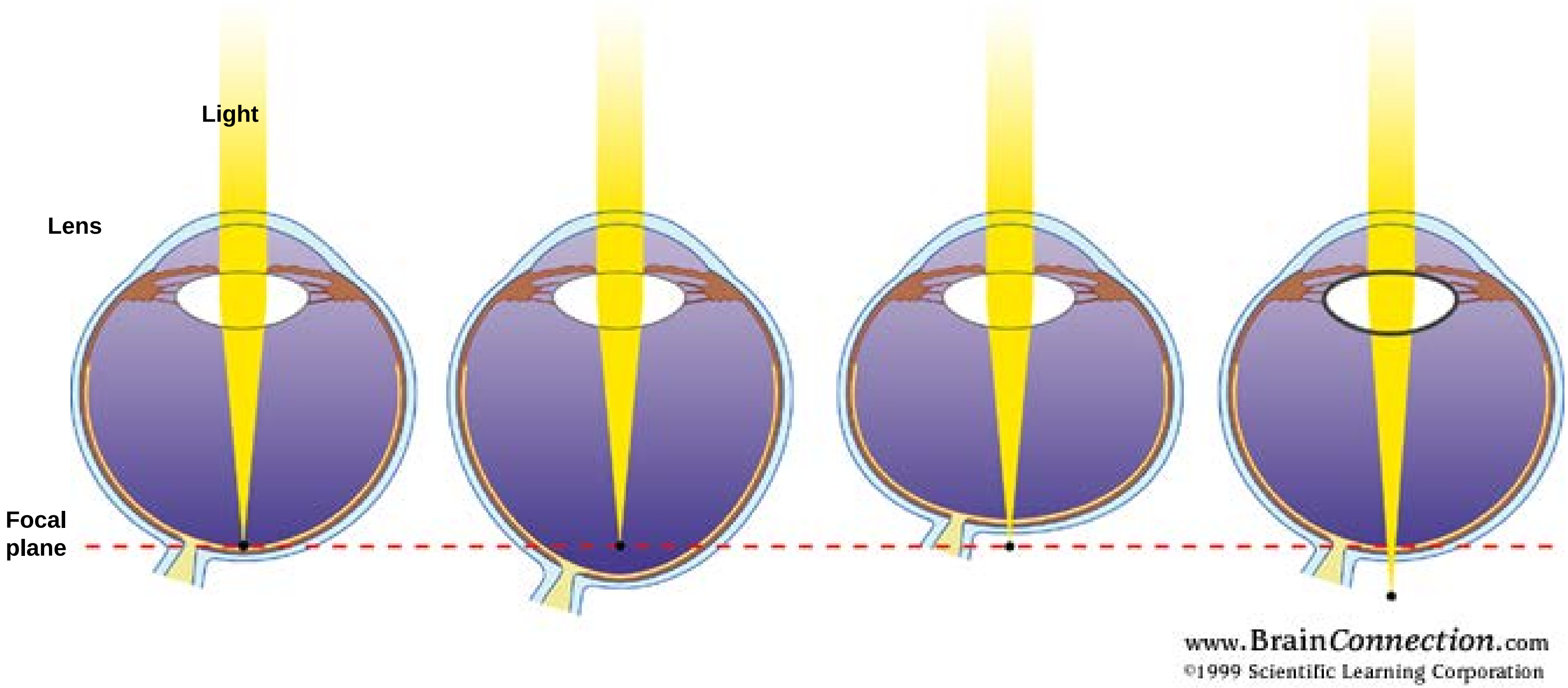


Near-sighted

Hyperopia



Far-sighted



Emmetropia (normal)

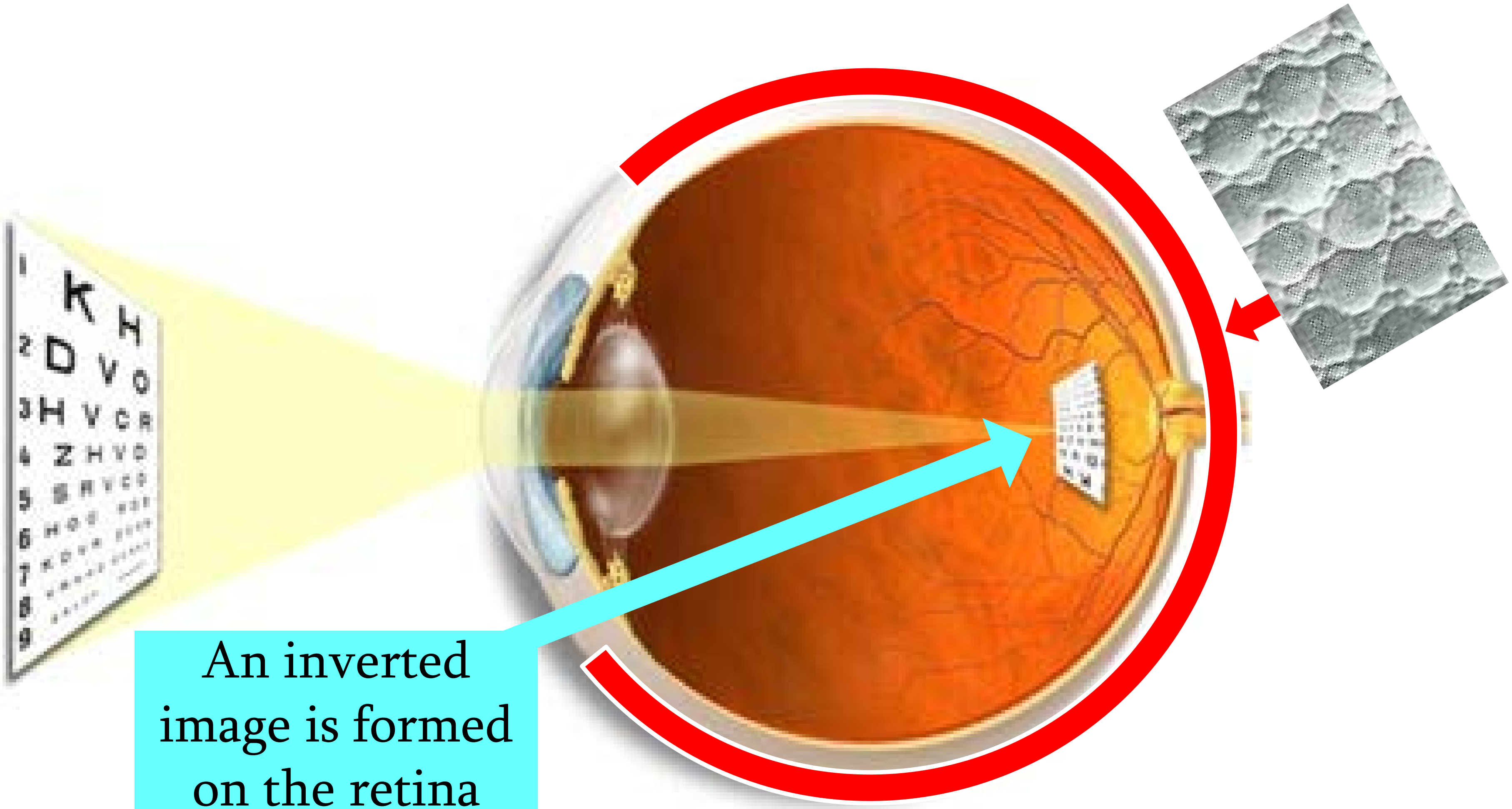
Myopia (nearsightedness)

Hyperopia (farsightedness)

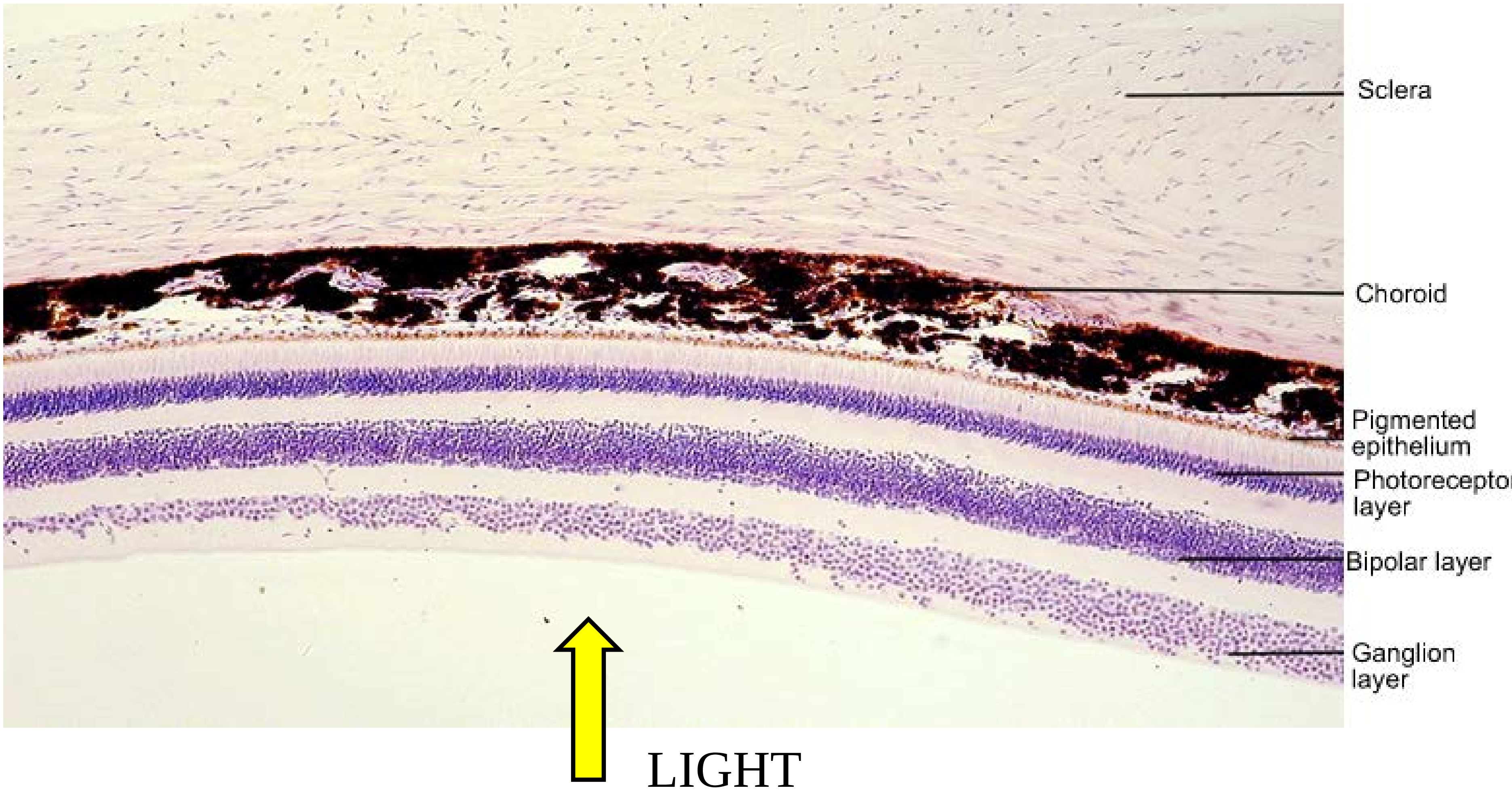
Presbyopia (aged)

ROD AND CONE VISION

The retina is carpeted with light-sensitive rods and cones



Retinal cross-section



Retina 200 ×

Rods and cones

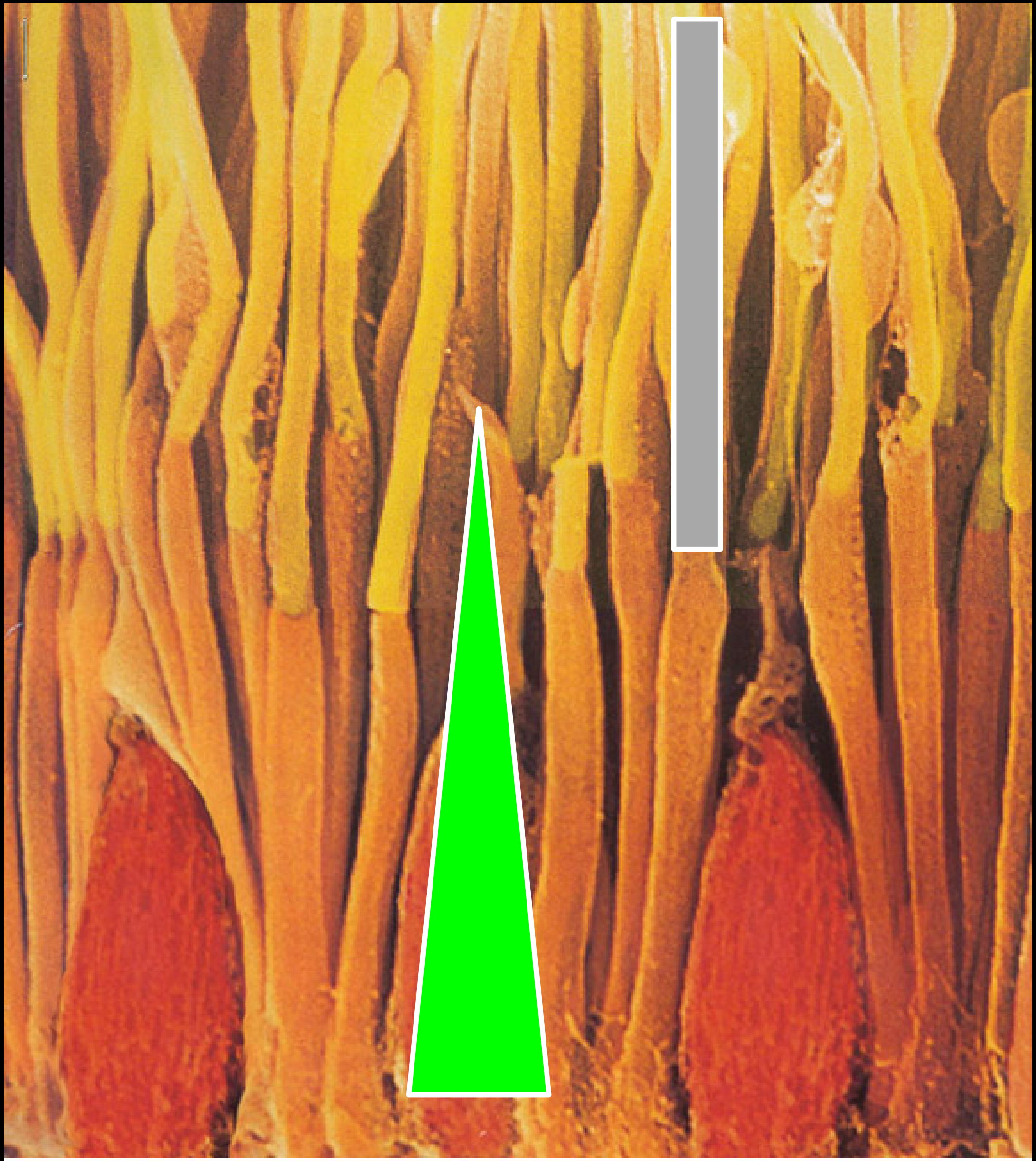
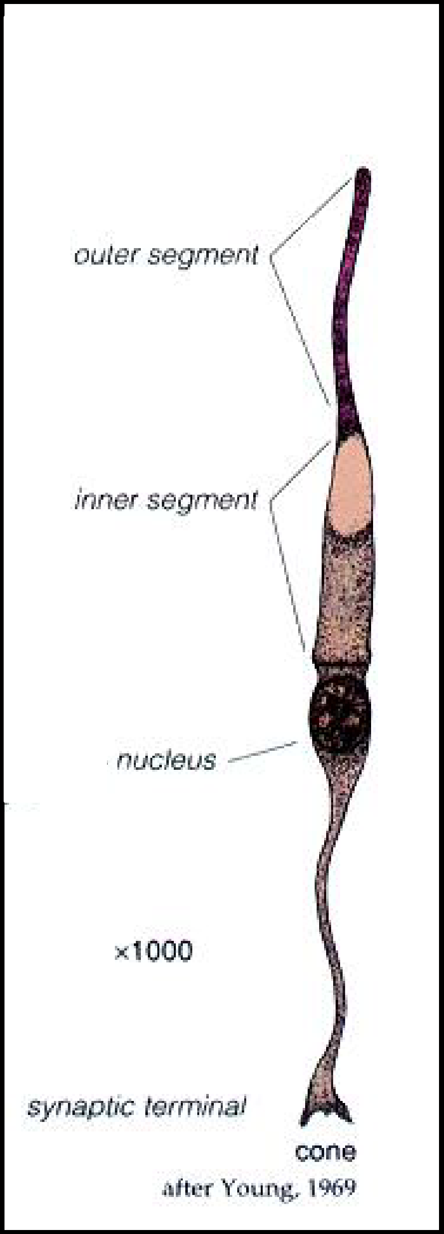


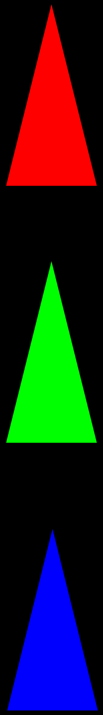
Fig1b. Scanning electron micrograph of the rods and cones of the primate retina. Image adapted from one by Ralph C. Eagle/Photo Researchers, Inc.

Webvision



Human photoreceptors

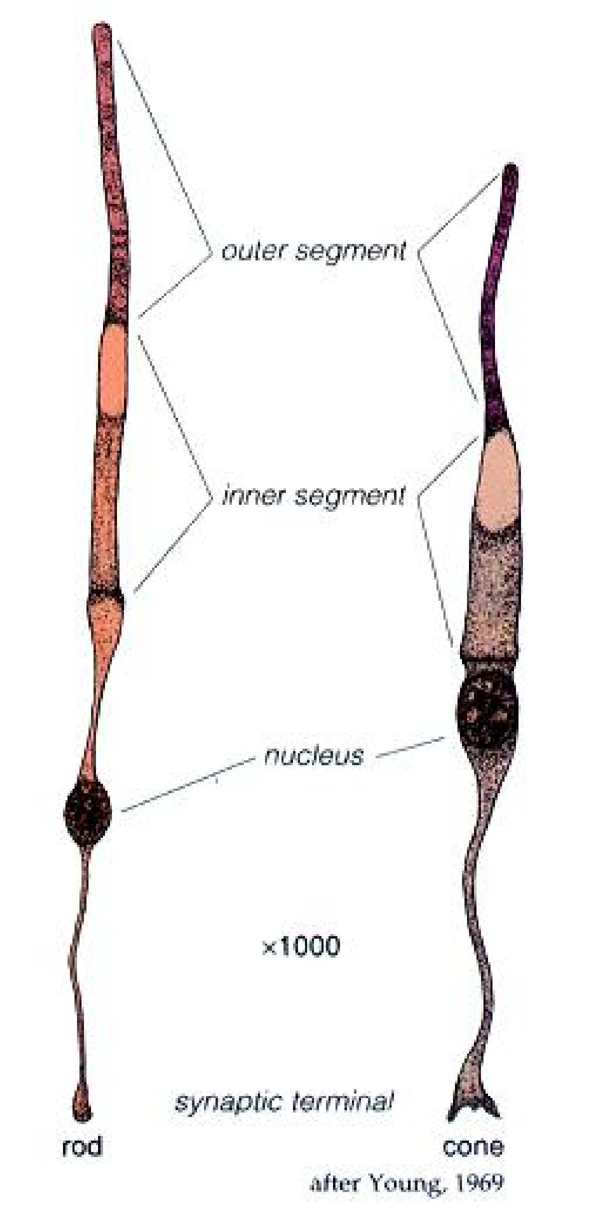
- <u>Cones</u>
  - Daytime, achromatic *and* chromatic vision
  - 3 types



Long-wavelength-sensitive (L) or "red" cone

Middle-wavelength-sensitive (M) or "green" cone

Short-wavelength-sensitive (S) or "blue" cone



Human photoreceptors

- Rods
  - Achromatic night vision
  - 1 type

Rod

- Cones
  - Daytime, achromatic *and* chromatic vision
  - 3 types

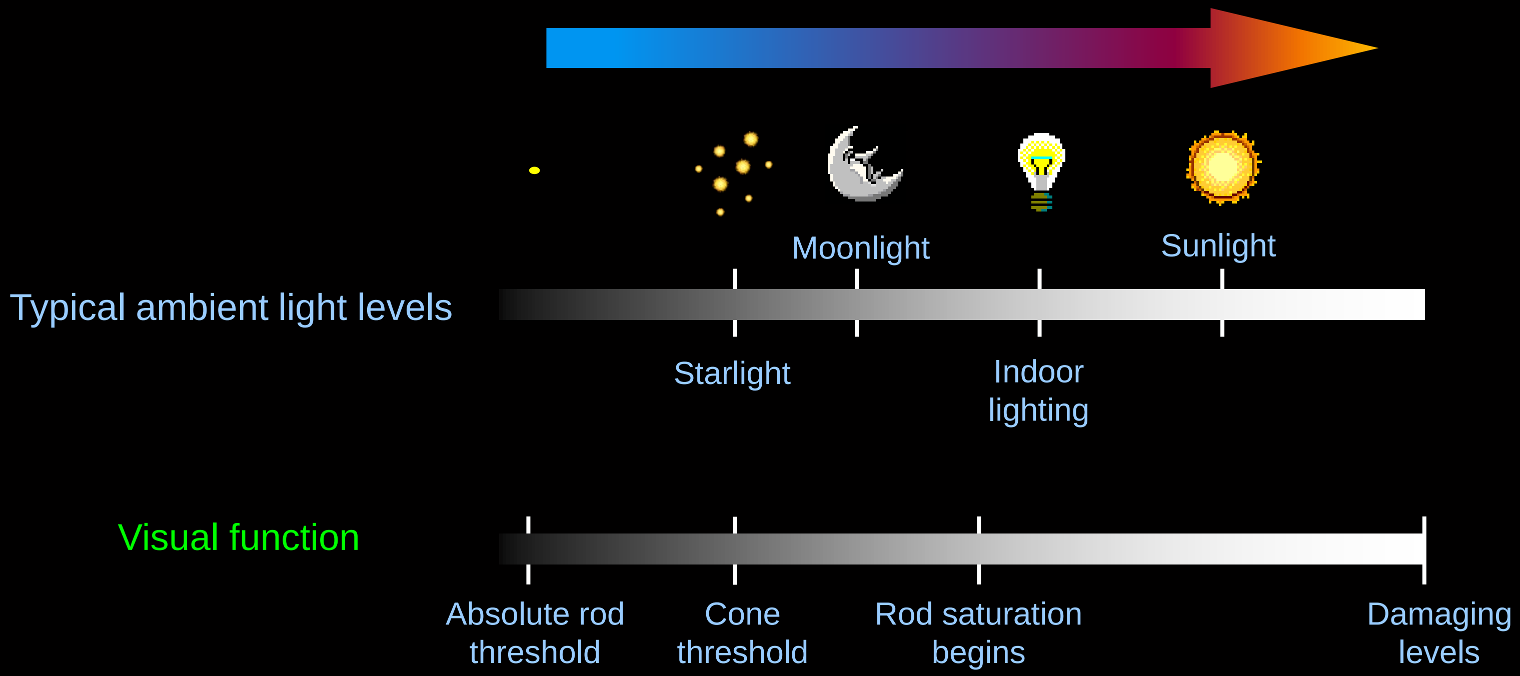
Long-wavelength-sensitive (L) or “red” cone

Middle-wavelength-sensitive (M) or “green” cone

Short-wavelength-sensitive (S) or “blue” cone

Why do we have rods and cones?

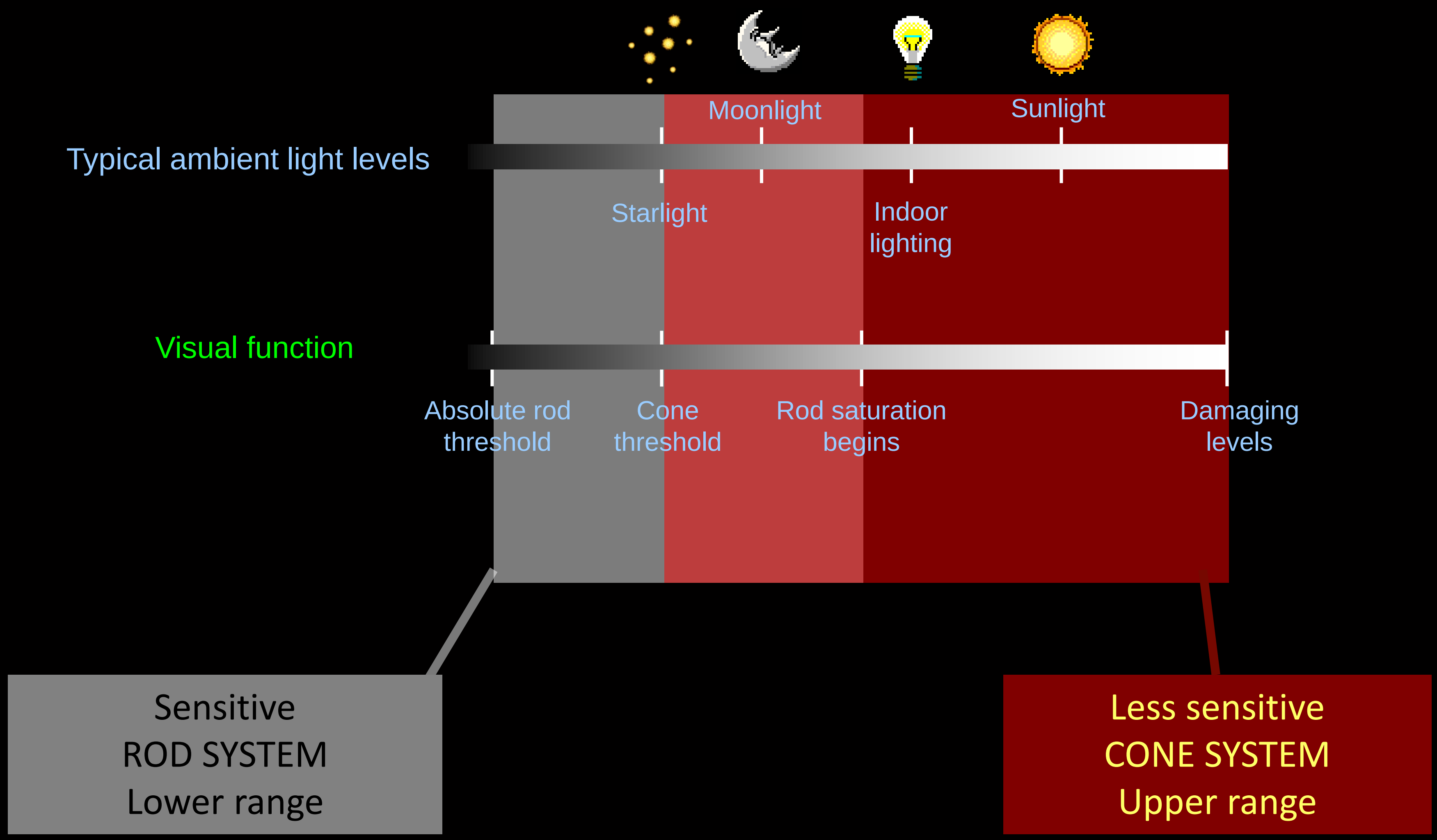
Our vision has to operate over an enormous range of 10^{12} (1,000,000,000,000) levels



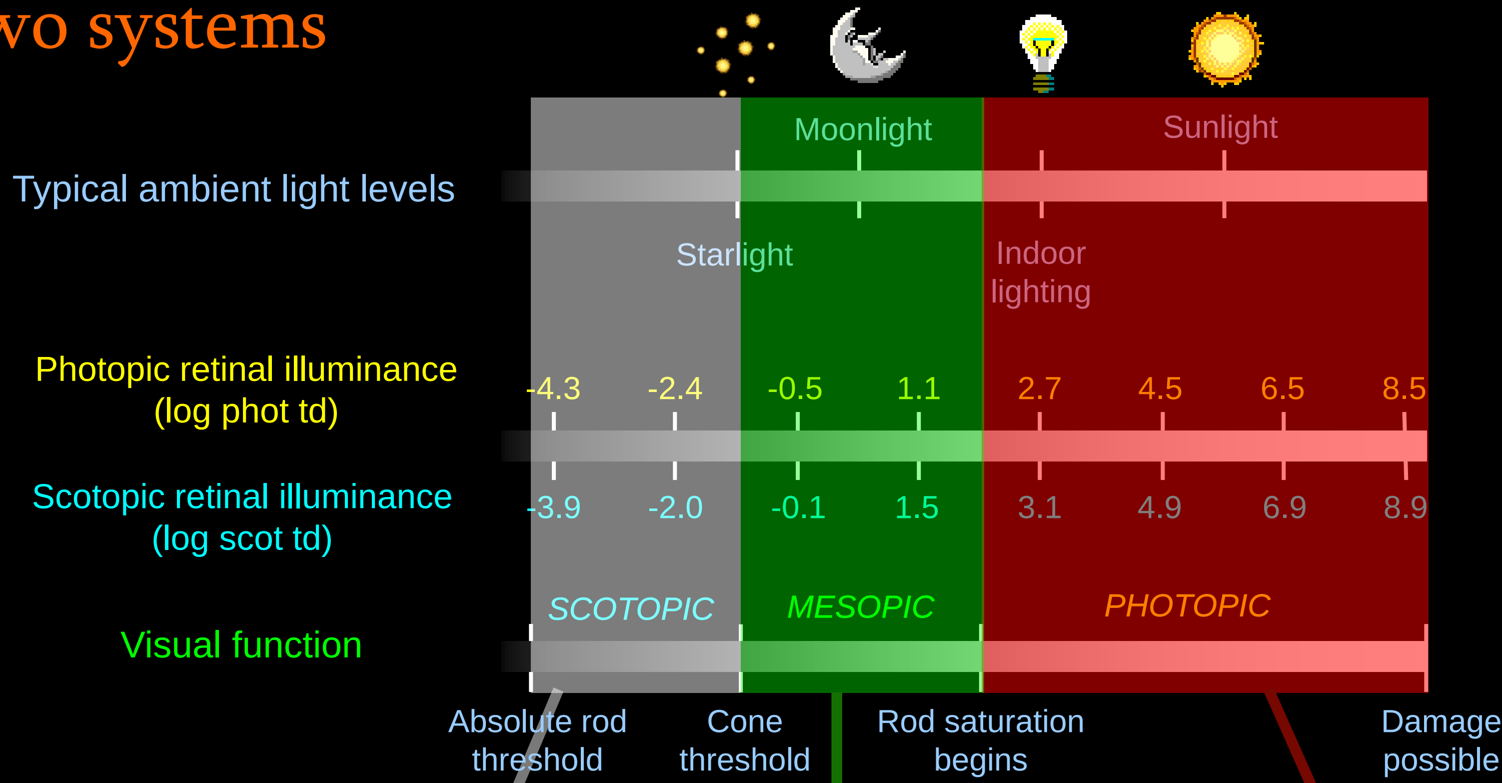
To cover that range we have two different types of photoreceptor...

Rods that are optimized for low light levels

Cones that are optimized for higher light levels



Two systems



Scotopic levels
(below cone threshold)
where rod vision
functions alone.
A range of c. $10^{3.5}$

Mesopic levels
where rod and cone
vision function
together.
A range of c. 10^3

Photopic levels
(above rod saturation)
where cone vision
functions alone.
A range of > 10^6

Rod vision

- Achromatic
- High sensitivity
- Poor detail and no colour

Cone vision

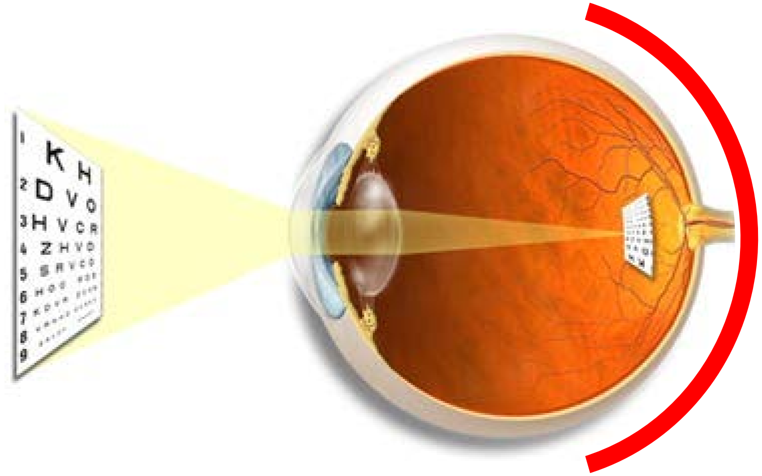
- Achromatic and chromatic
- Lower sensitivity
- Detail and good colour

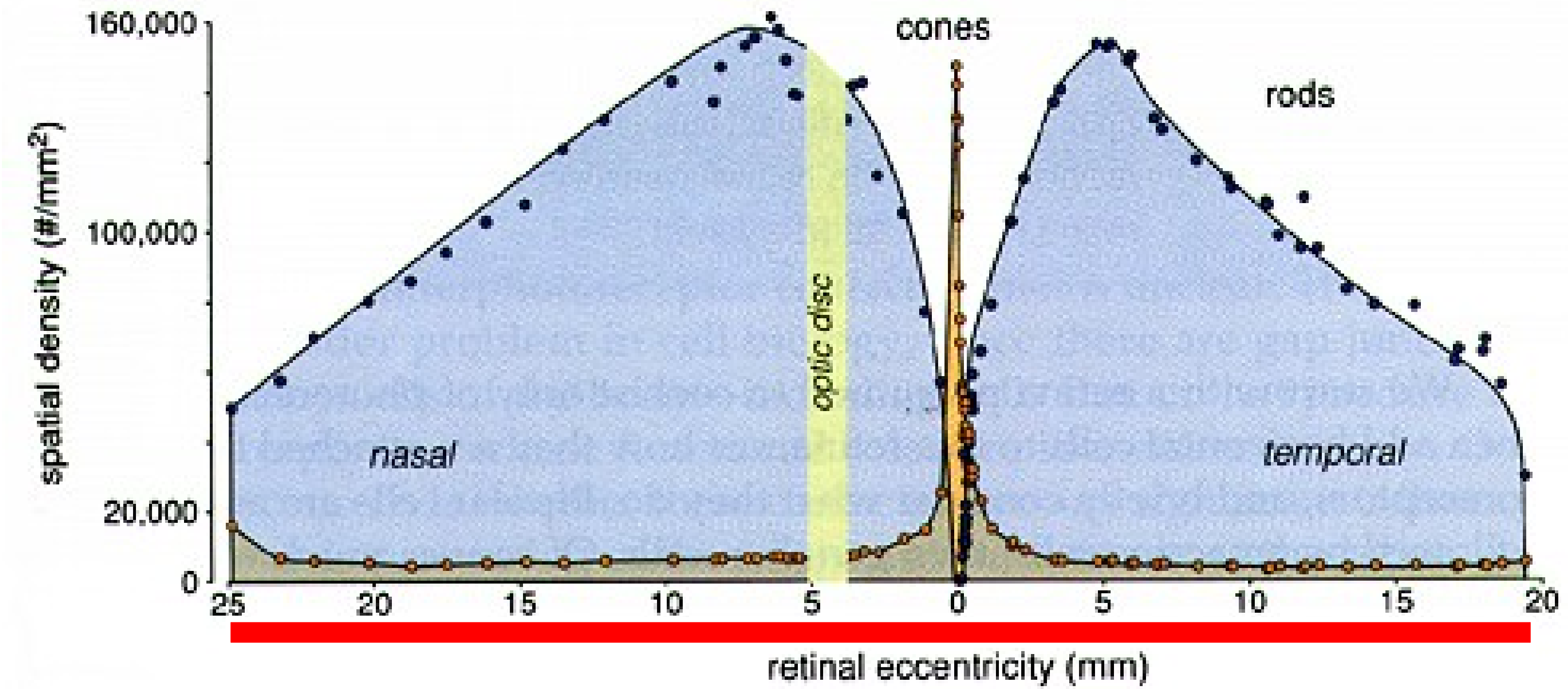
Facts and figures

There are about 120 million rods. They are absent in the central 0.3 mm diameter area of the fovea, known as the *fovea centralis*.

There are only about 6 to 7 million cones. They are much more concentrated in the fovea.

Rod and cone distribution

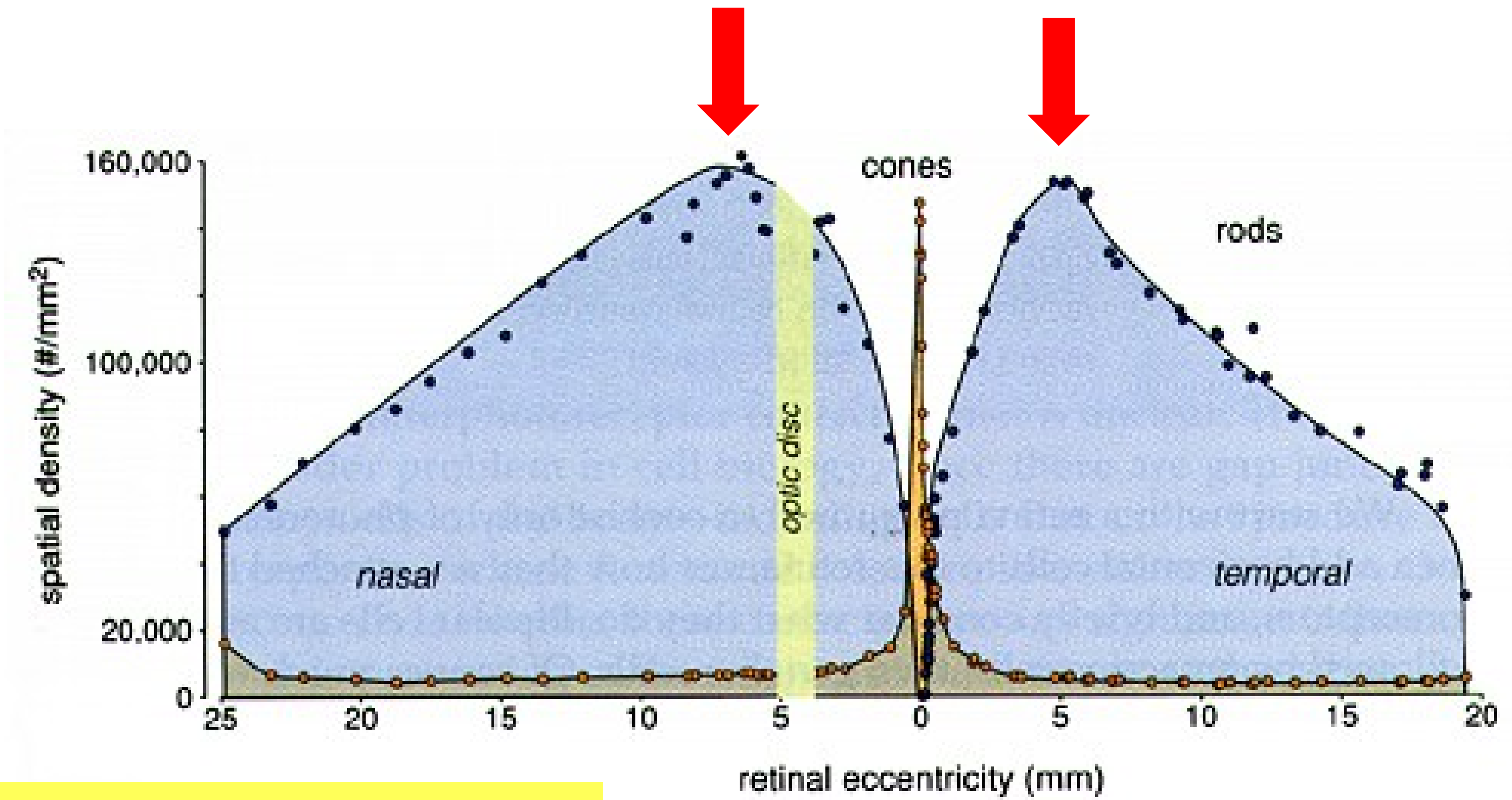




after Østerberg, 1935; as modified by Rodieck, 1988

0.3 mm of eccentricity is about 1 deg of visual angle

Rod density peaks at about
20 deg eccentricity

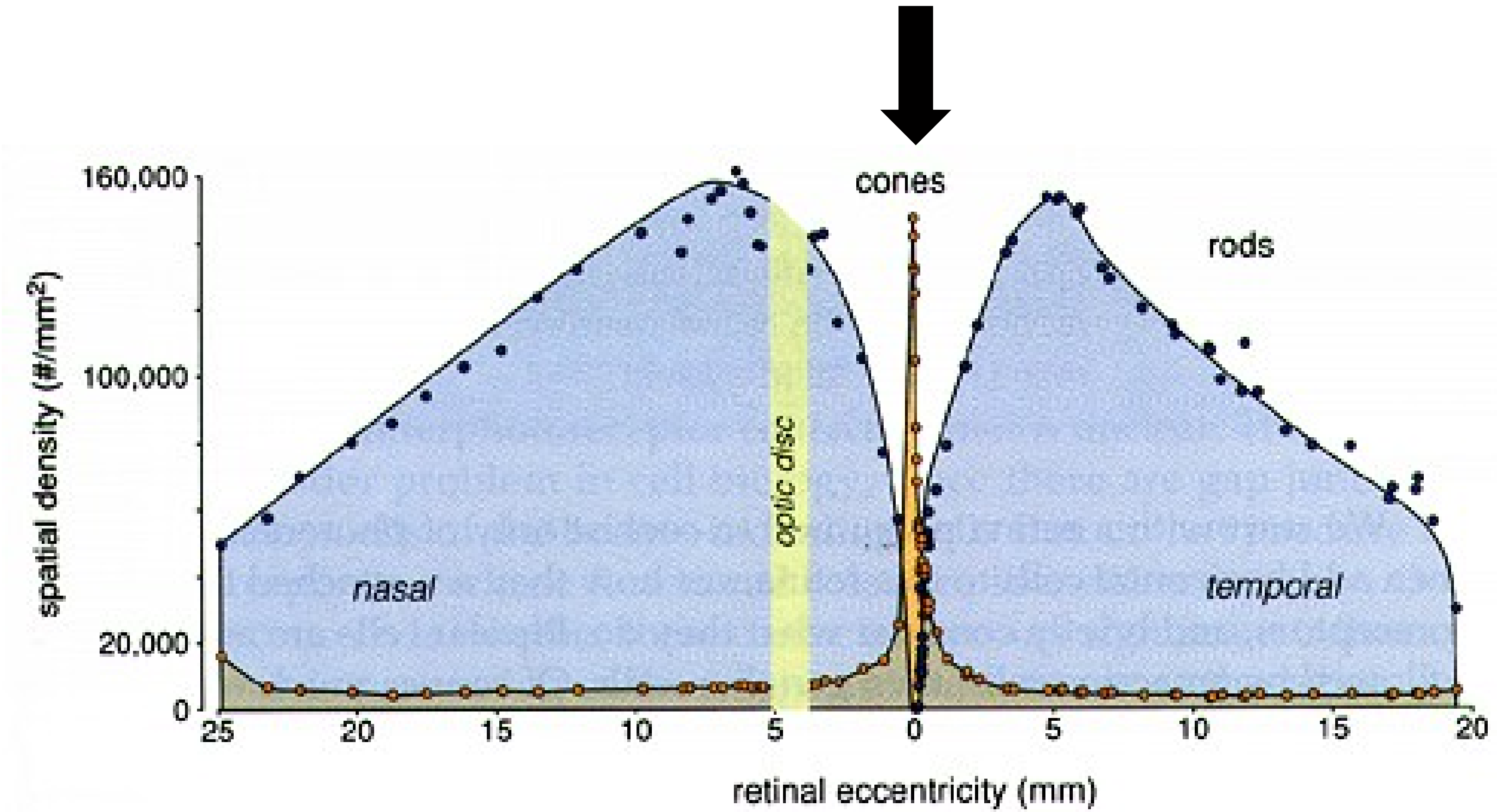


after Østerberg, 1935; as modified by Rodieck, 1988

At night, you have to look away from things to see them in more detail

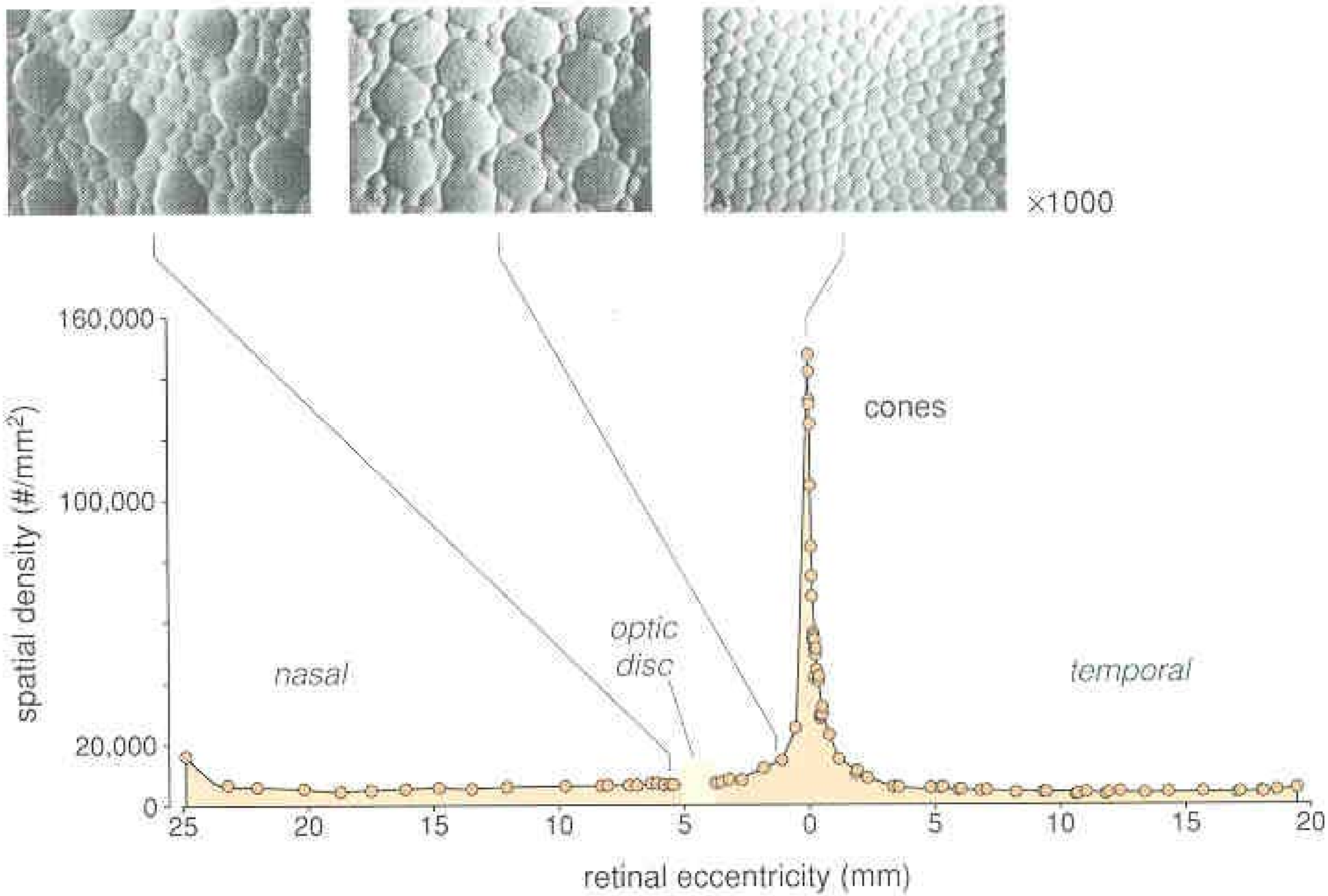
During the day, you have to look at things directly to see them in detail

Cones peak at the centre of vision at 0 deg



after Østerberg, 1935; as modified by Rodieck, 1988

Cone distribution and photoreceptor mosaics

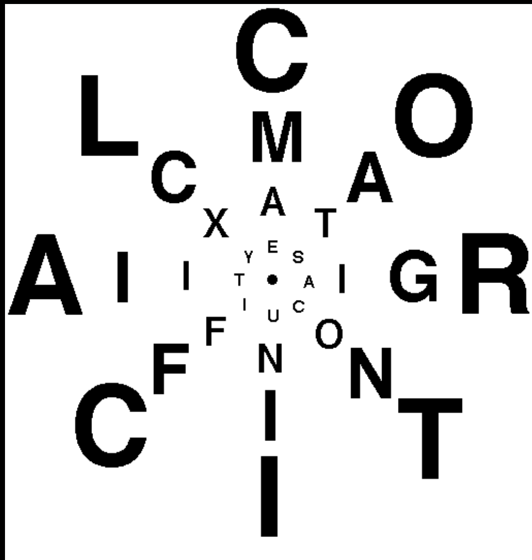


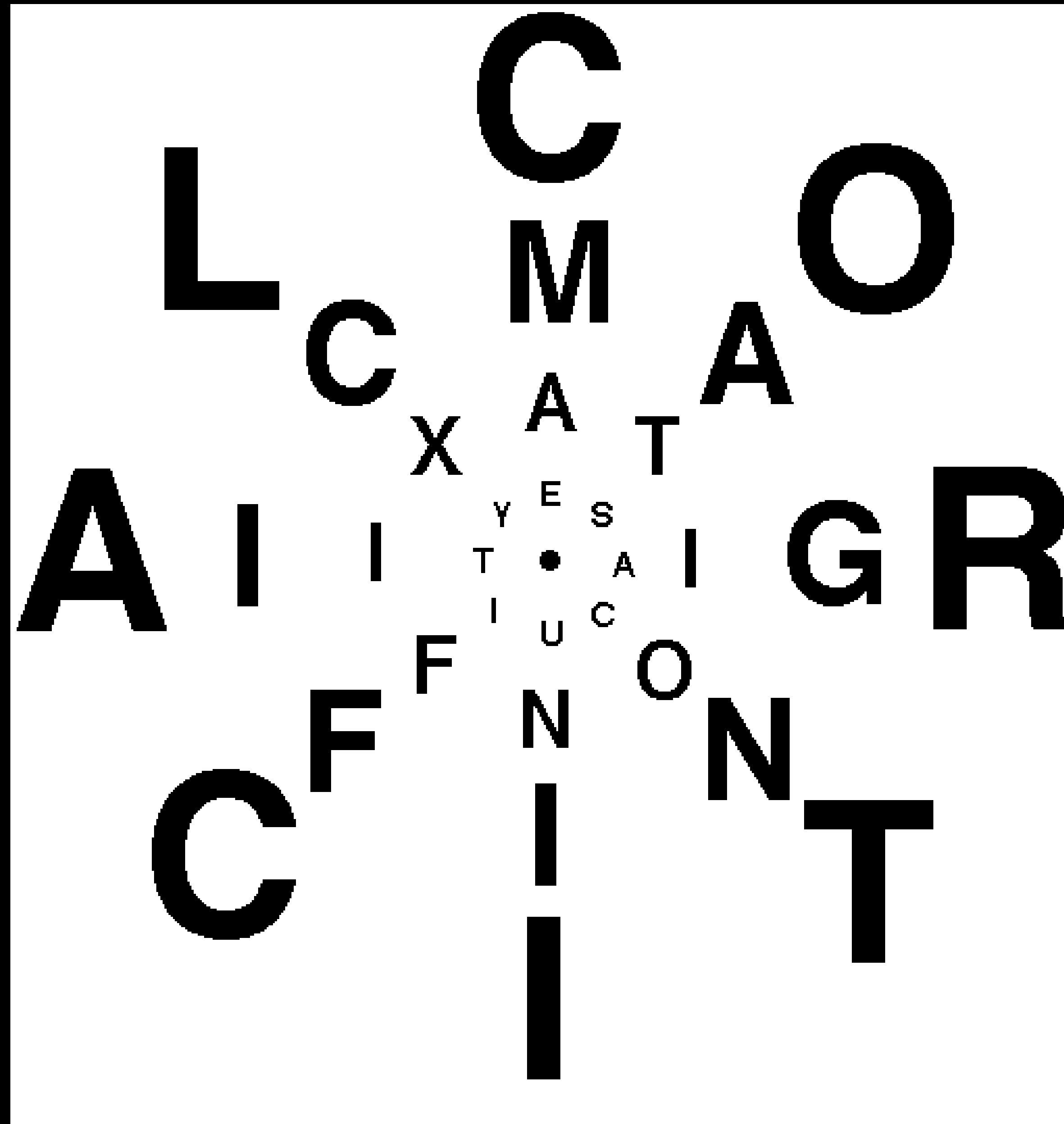
after Østerberg, 1935; as modified by Rodieck 1988;
micrographs from Curcio et al., 1990

The human visual system is a foveating system

Simulation of what we see when we fixate with cone vision…

Credit: Stuart Anstis, UCSD

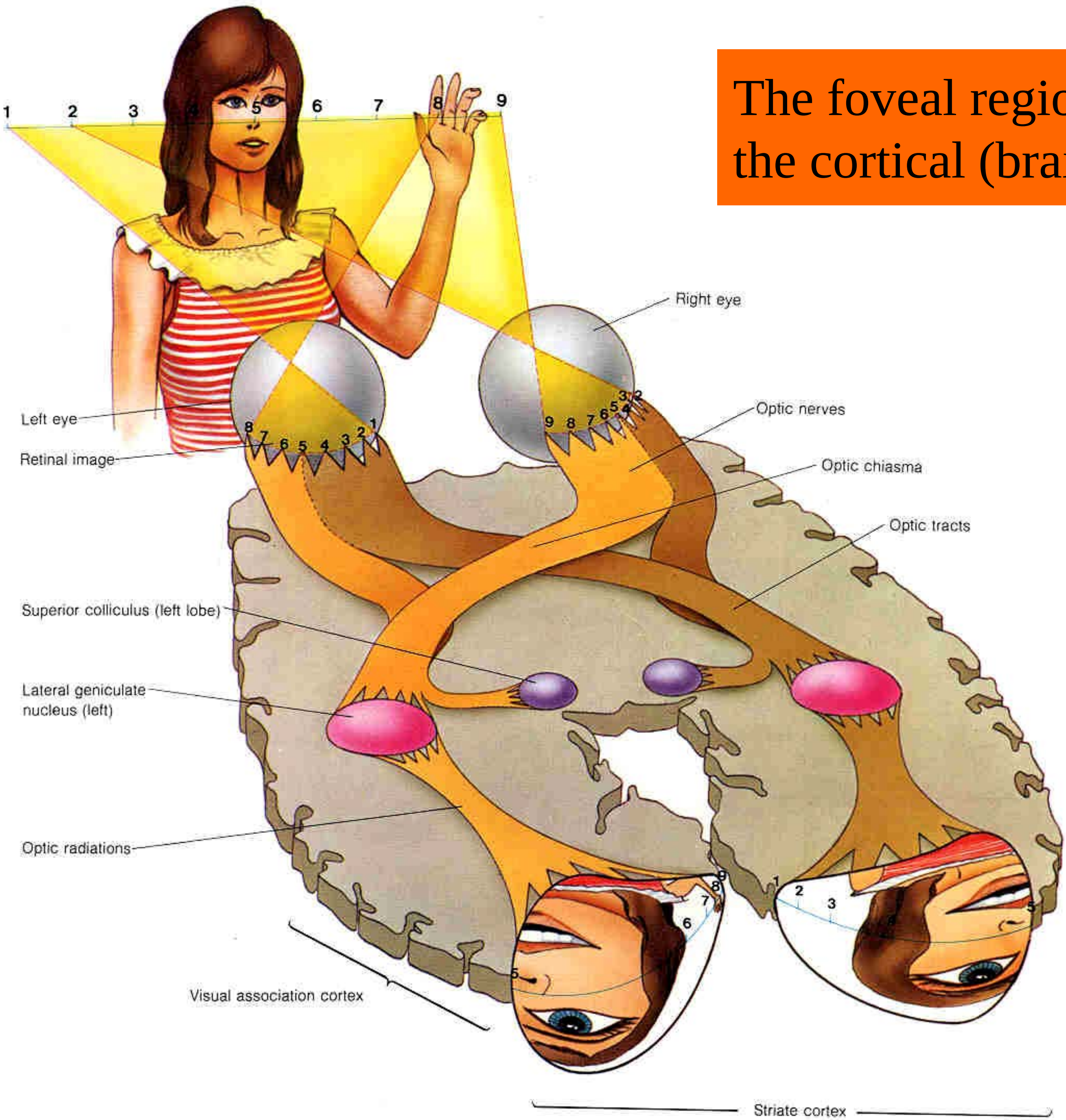




Visual acuity gets much poorer with eccentricity

Credit: Stuart Anstis, UCSD

The foveal region is magnified in the cortical (brain) representation



ROD AND CONE DIFFERENCES

Rod and cone differences can be demonstrated using several techniques, including perceptual measurements.

Rod-cone threshold sensitivity differences

How might we measure them?

Rod and cone threshold versus intensity curves

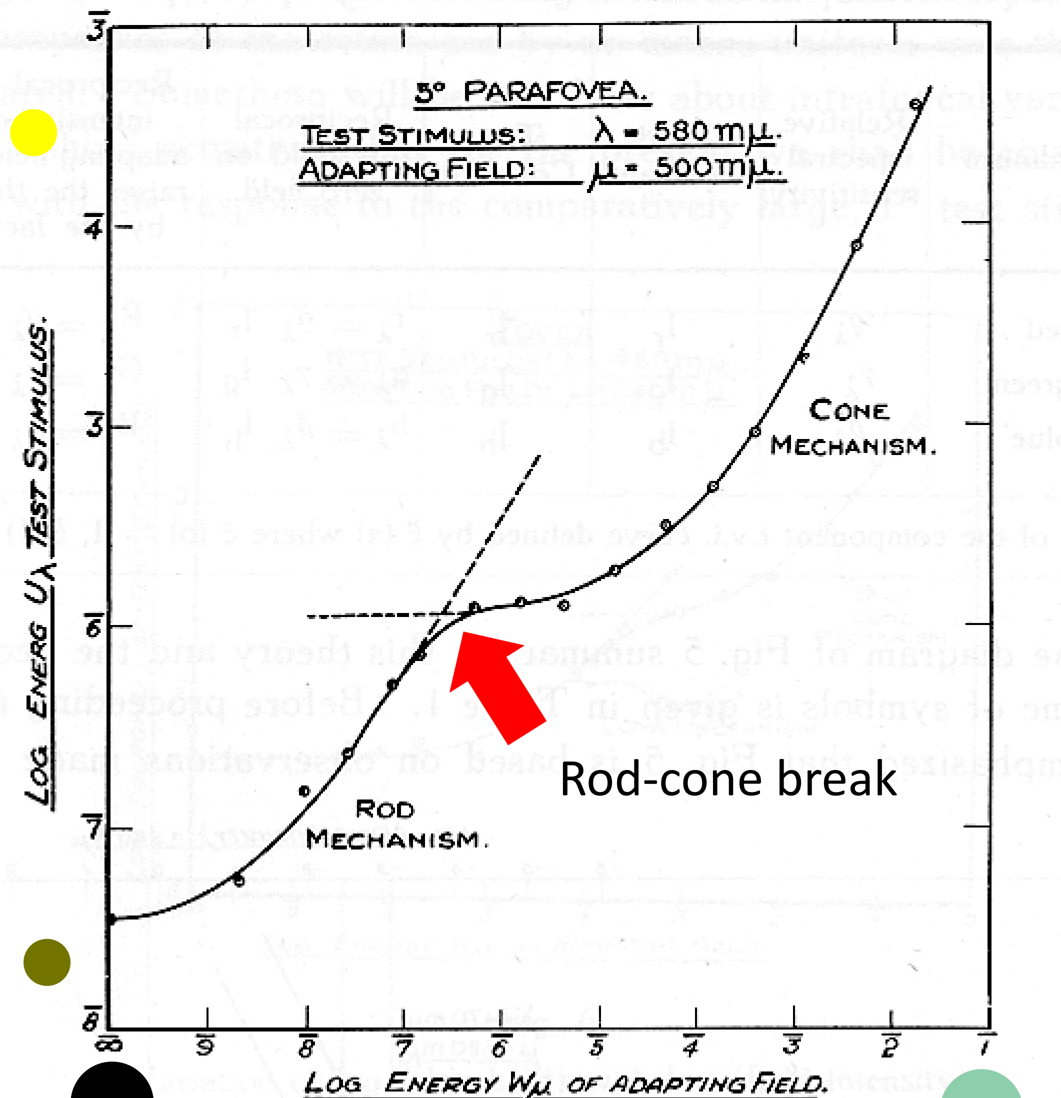


Fig. 4.

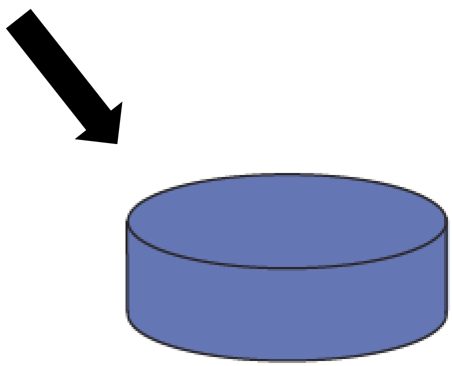
Variation of log (threshold) with log (field intensity) for a 1° flashing test stimulus of yellow light (exposure time 0.063 sec.) on a blue-green field: 5°- parafoveal vision. (Stiles, 1939)

Rods are about one thousand times more sensitive than cones. They can be triggered by individual photons.

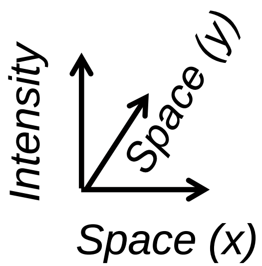
Spectral sensitivity differences

Threshold versus target wavelength measurements

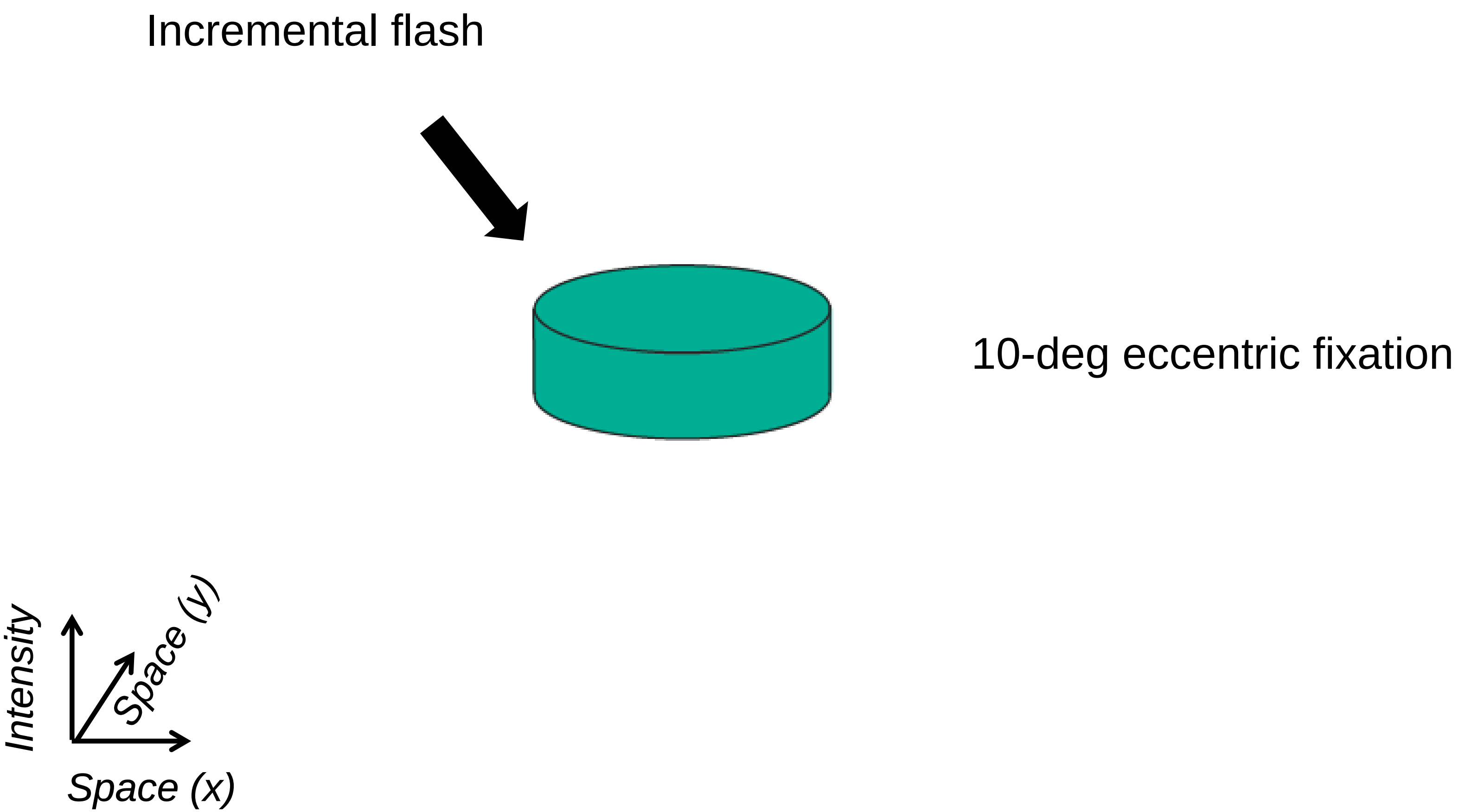
Incremental flash



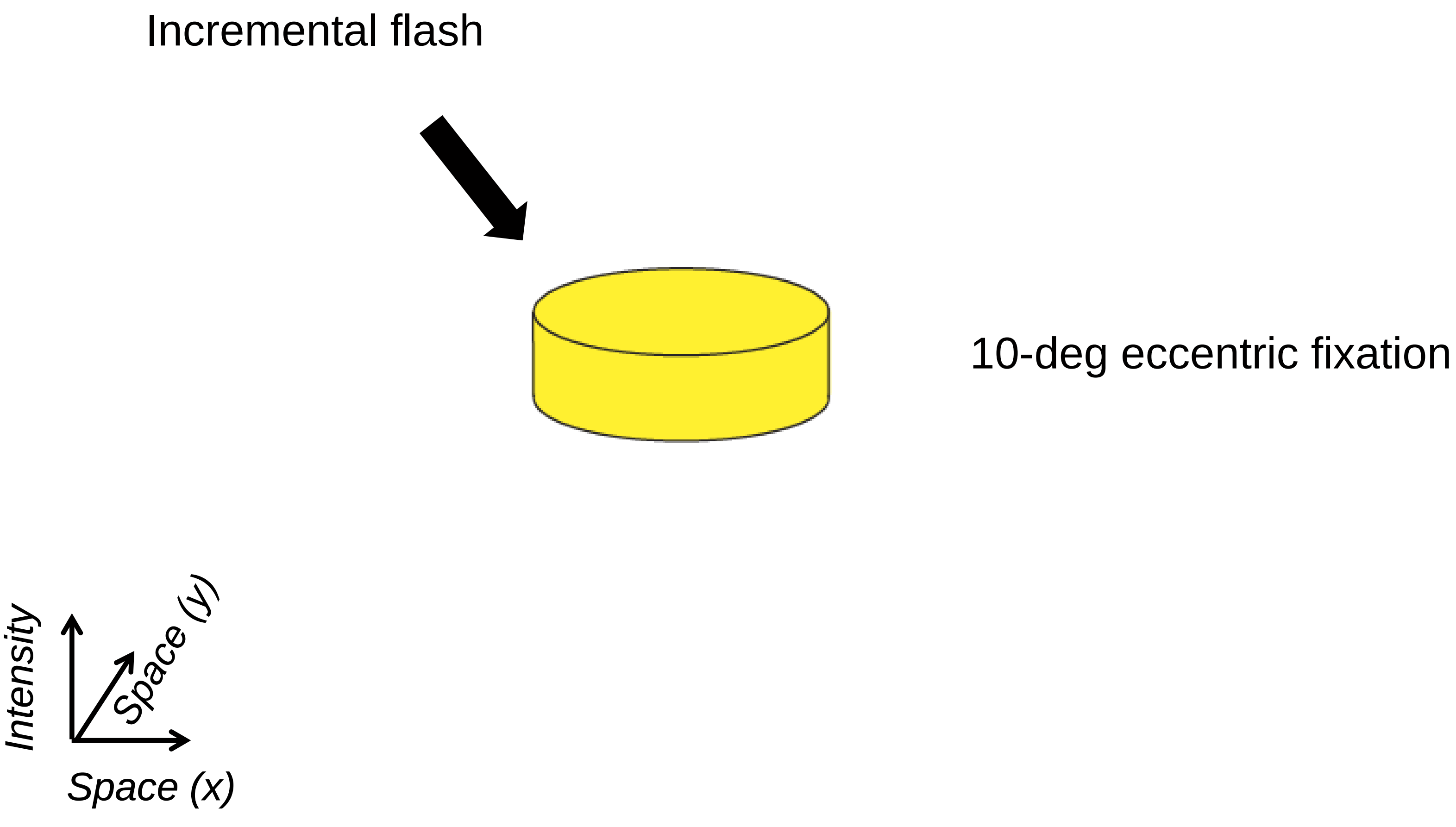
10-deg eccentric fixation



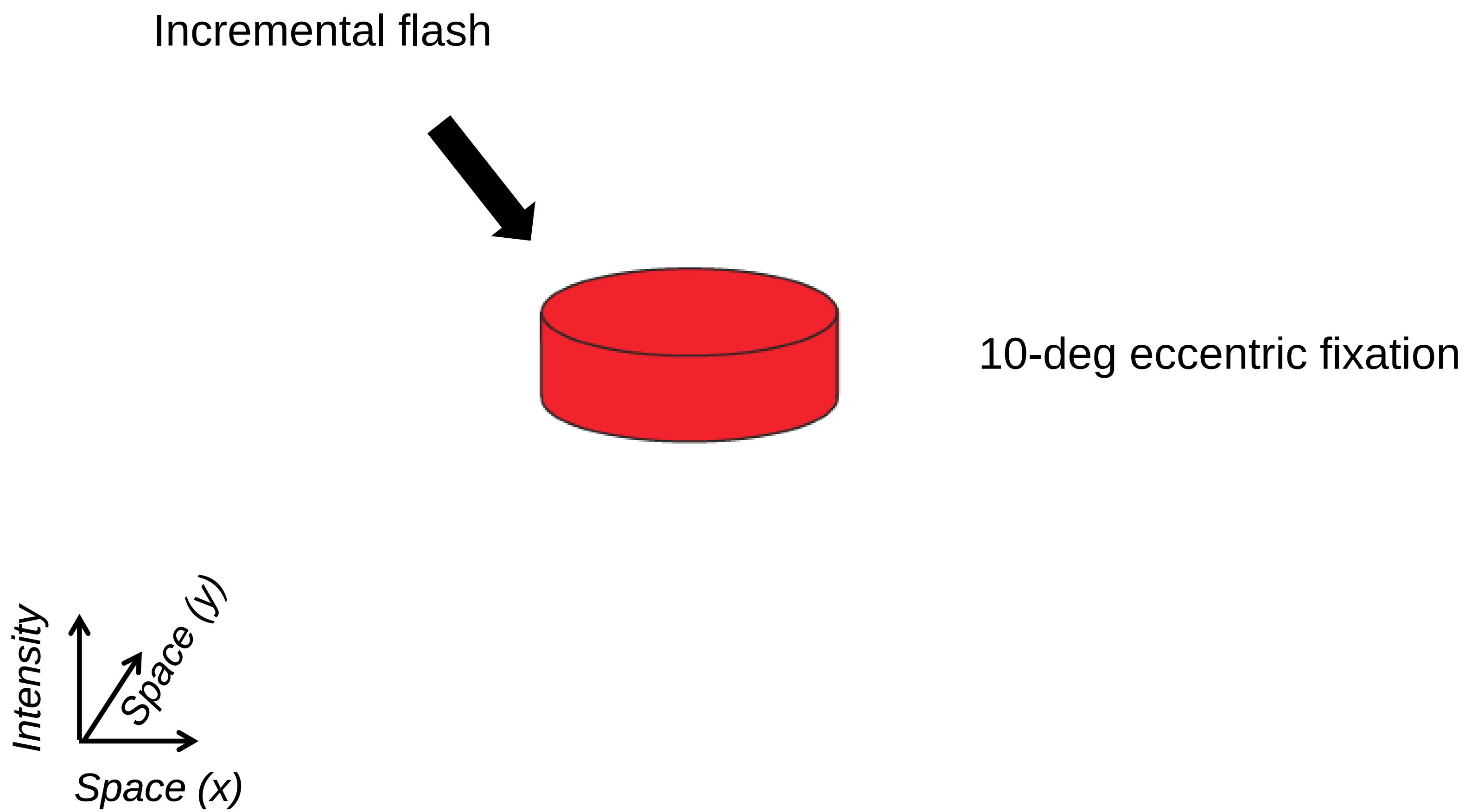
Threshold versus target wavelength measurements



Threshold versus target wavelength measurements



Threshold versus target wavelength measurements



Rod and cone spectral sensitivity curves

Plotted as “thresholds” versus wavelength curves

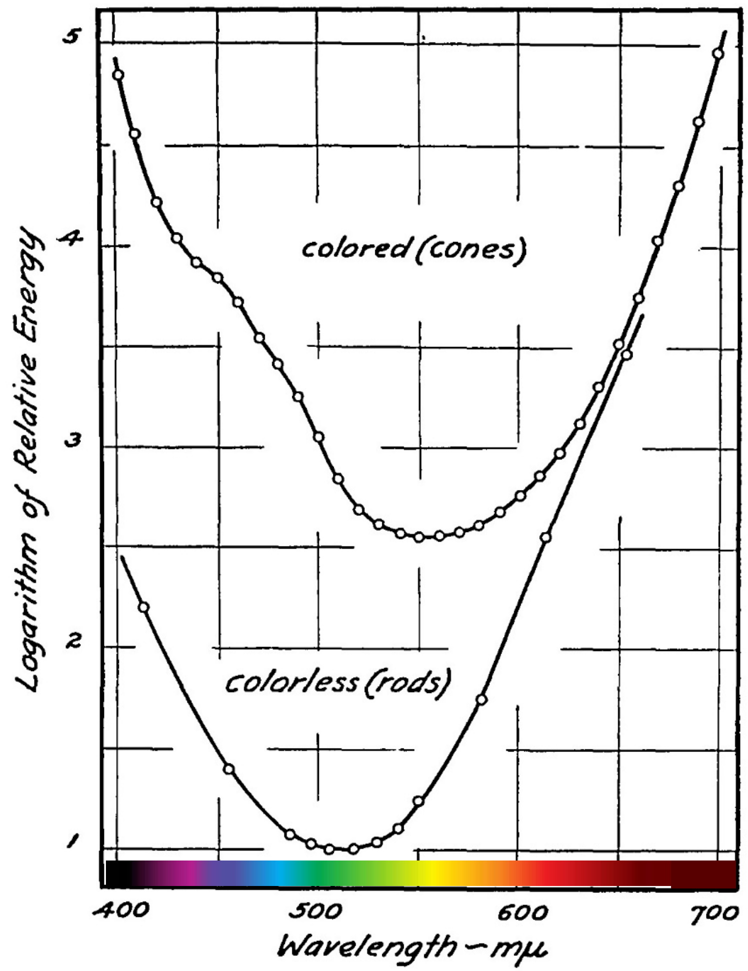
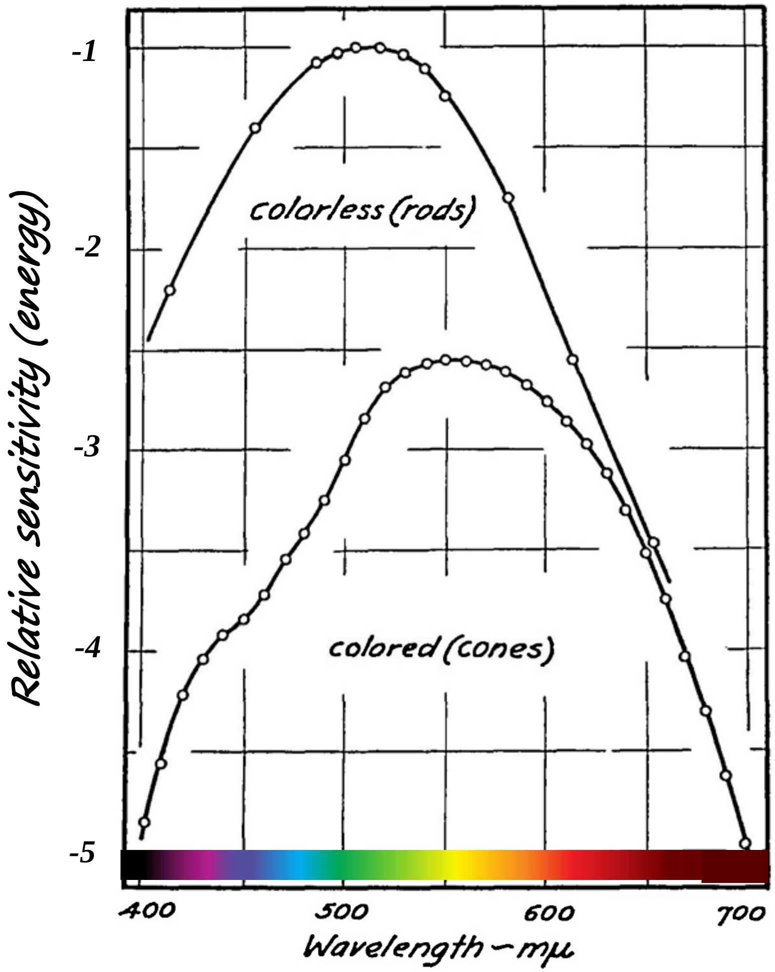


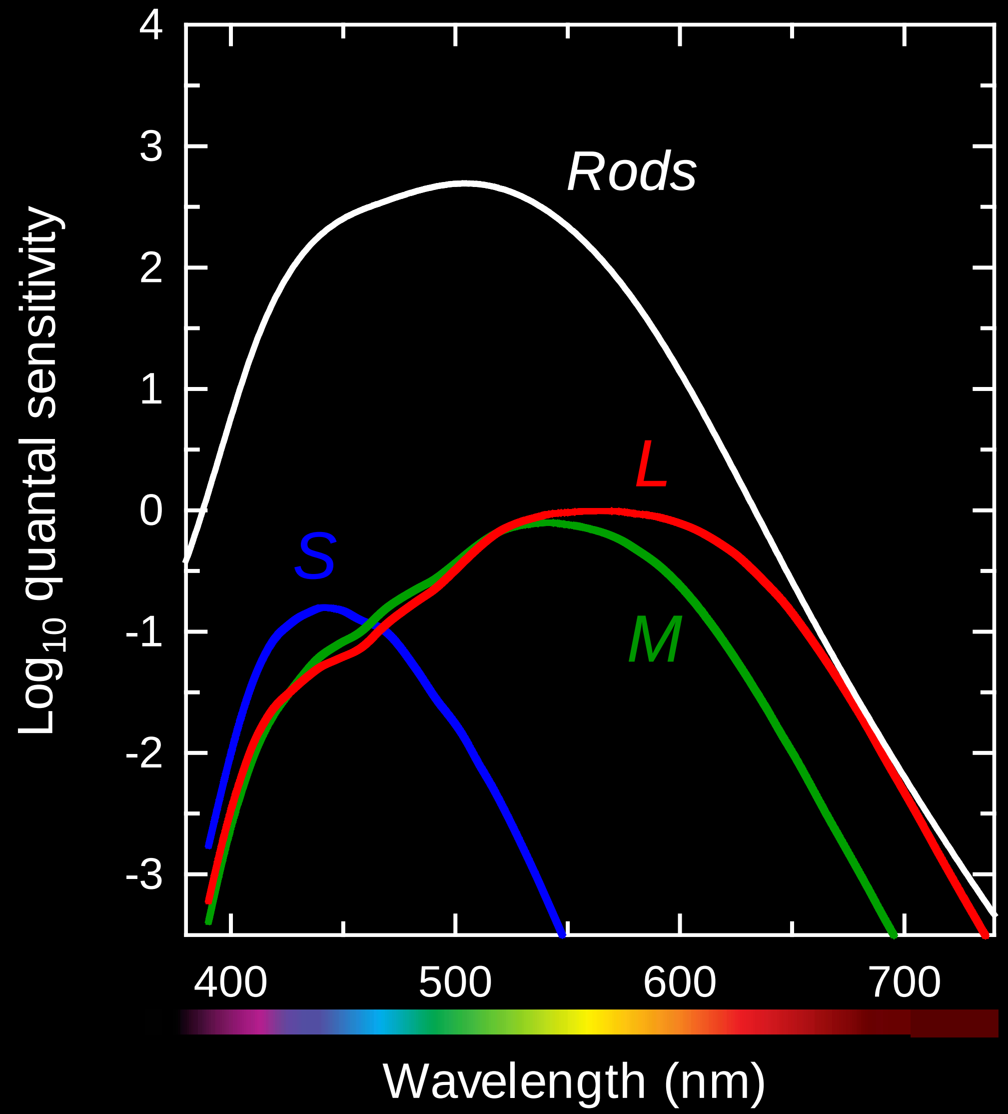
FIG. 2. Spectrum sensibility curves for rod and cone vision on a real energy basis. The data for the separate curves are from the same sources as in Fig. 1. The position of the two curves on the ordinates corresponds to the fact that after complete dark adaptation, any region of the retina outside the fovea sees red light of 650 mμ as colorless at the threshold, and as colored only above the threshold. The precise energy increment above the threshold for the appearance of color (cone function) varies for different parts of the retina; in the parafovea it lies between 0.1 and 1.0 log unit.

Plotted as the more conventional spectral "sensitivity" curve



Sensitivity = 1/threshold
or
log (sensitivity) = -log(threshold)

Approximate dark-adapted photoreceptor sensitivities.

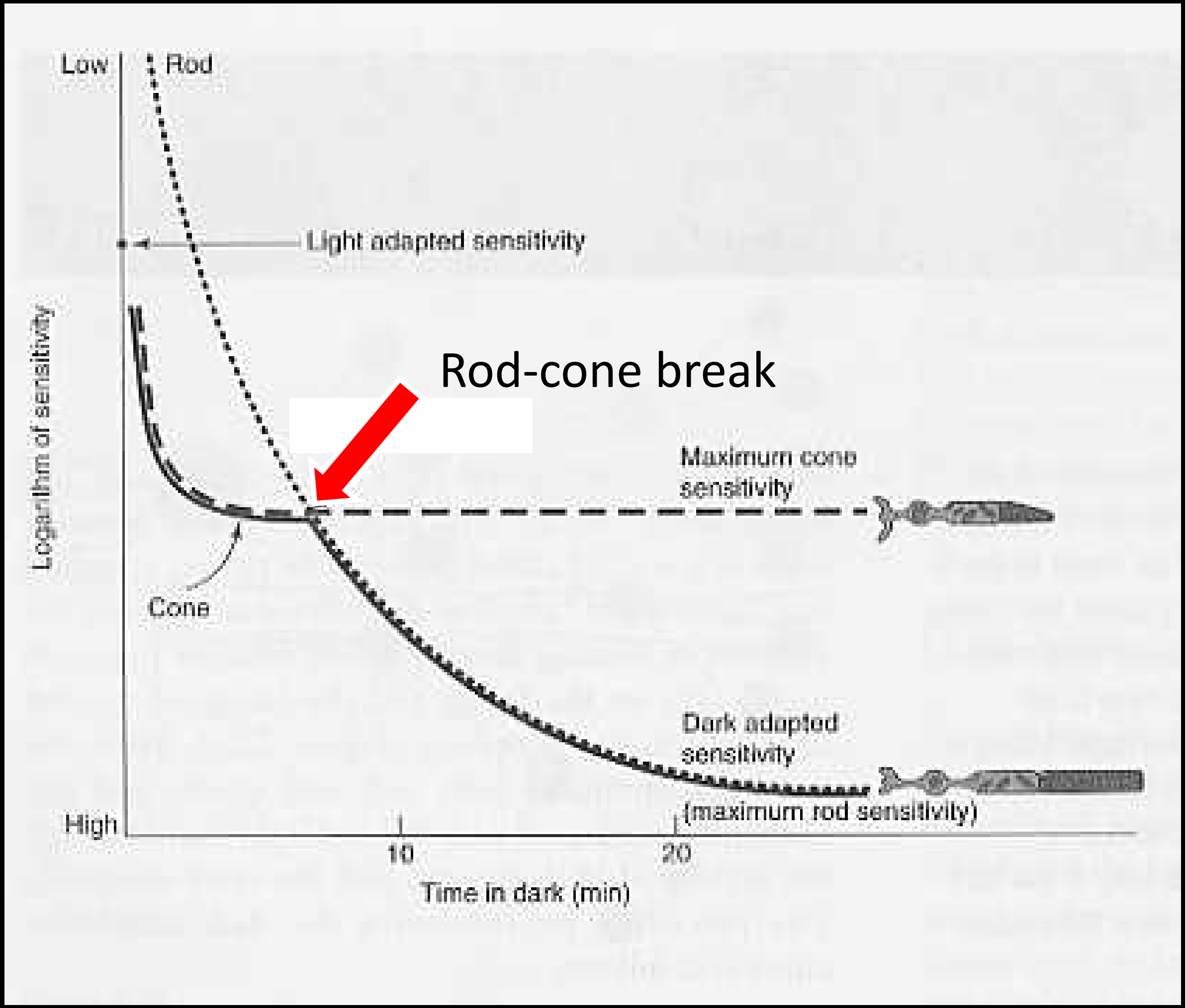


The Purkinje Shift

A change in the relative brightness of colours as the light level changes because of the difference in spectral sensitivity between rod and cone vision (*e.g.,* reds and oranges become darker as rods take over)

Simulated: Dick Lyon & Lewis Collard at Wikimedia

Rod-cone dark adaptation curves



Rod-cone dark adaptation curves

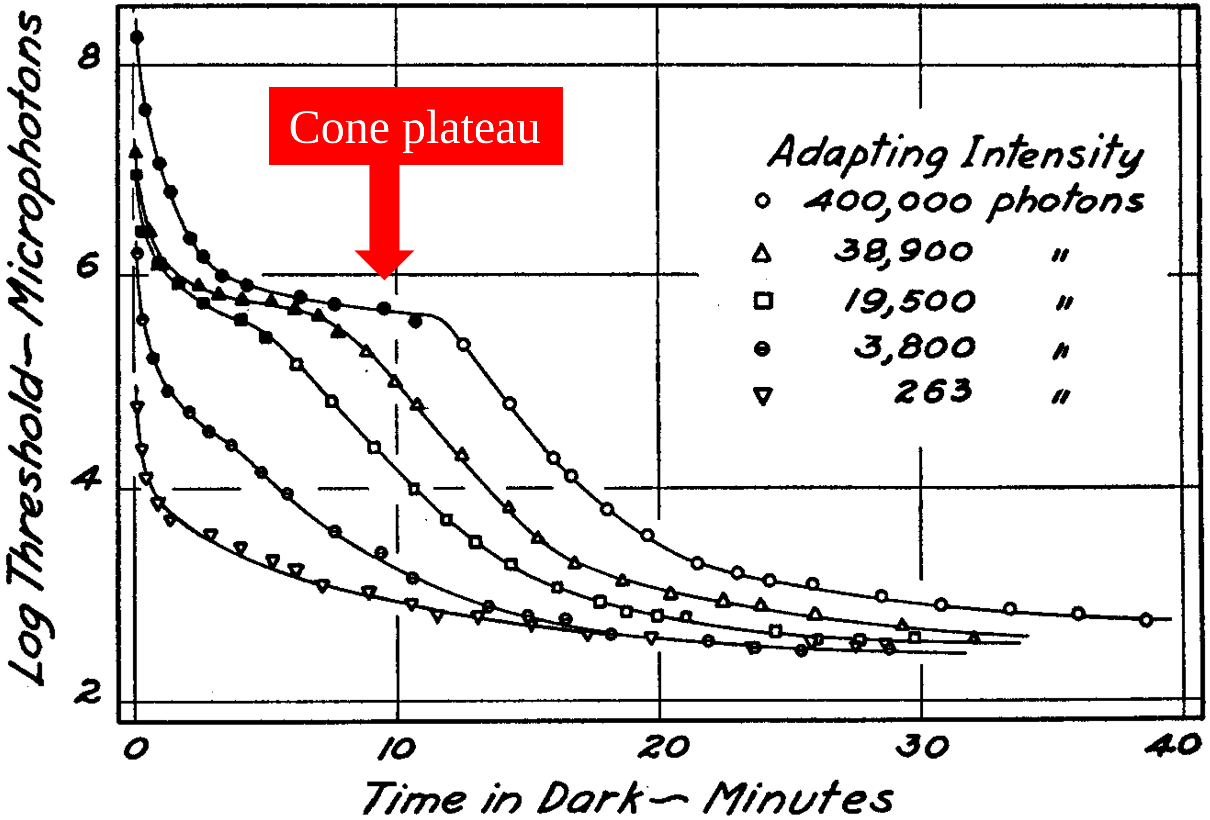


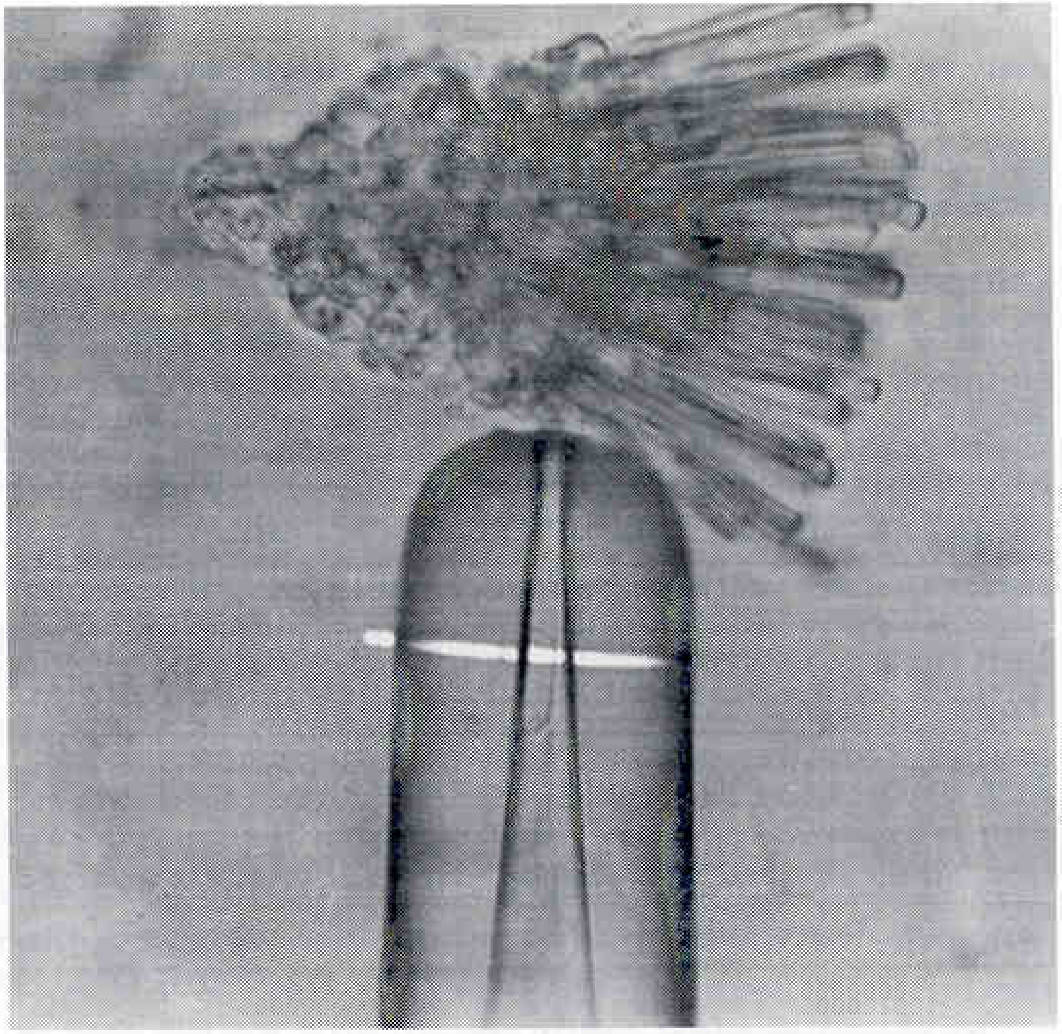
FIG. 2. The course of dark adaptation as measured with violet light following different degrees of light adaptation. The filled-in symbols indicate that a violet color was apparent at the threshold, while the empty symbols indicate that the threshold was colorless.

Rods take much longer to recover after a bleach than cones

From Hecht, Haig & Chase (1937)

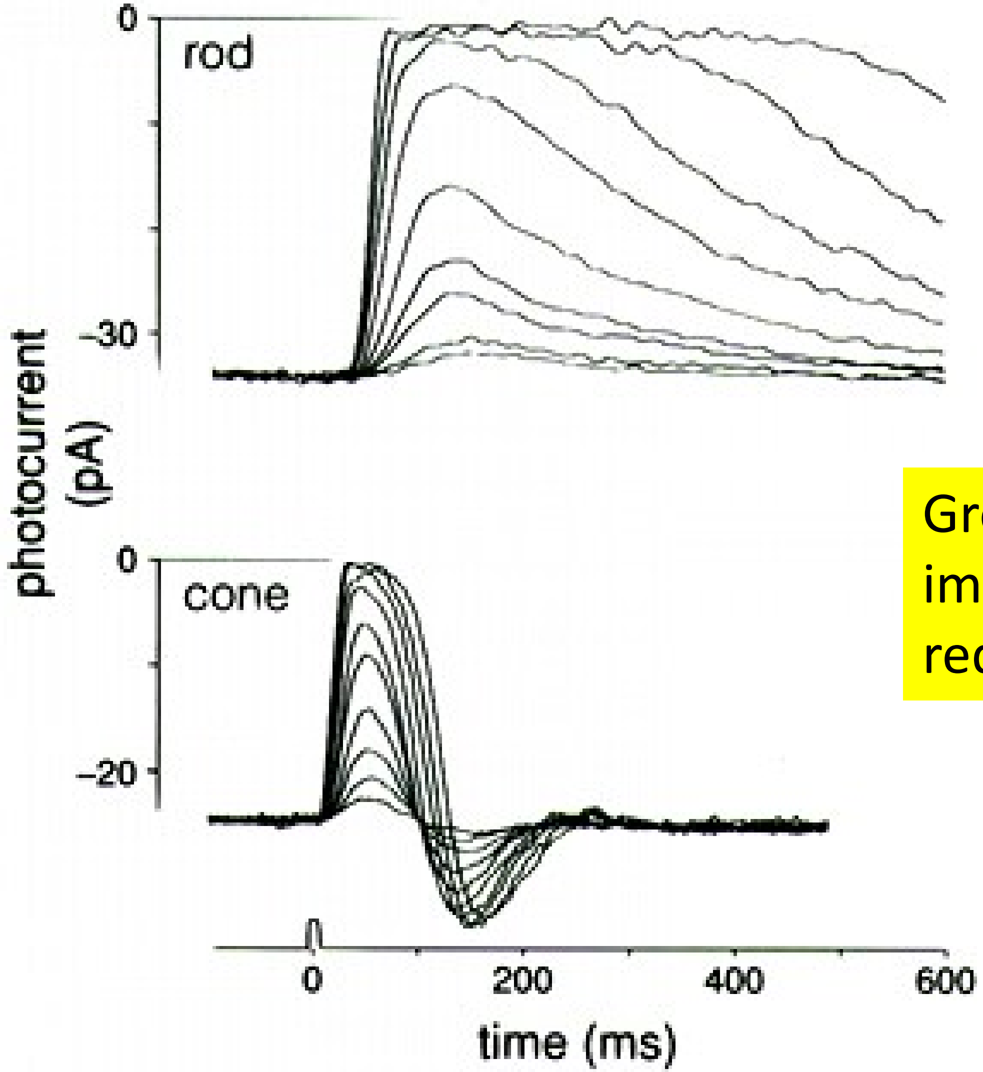
Temporal differences

Suction electrode recording



4.15 MEASURING CONE PHOTOCURRENTS. The image shows a portion of macaque retina suspended in solution. A single photoreceptor from this retinal section has been drawn into a micropipette and is being stimulated by a beam of light passing transversely through the photoreceptor and micropipette. Courtesy of Denis Baylor.

Photocurrent responses



Greater temporal integration improves rod sensitivity (but reduces temporal acuity)

source: Baylor, 1987

Highest flicker rates that can just be seen (c.f.f.)

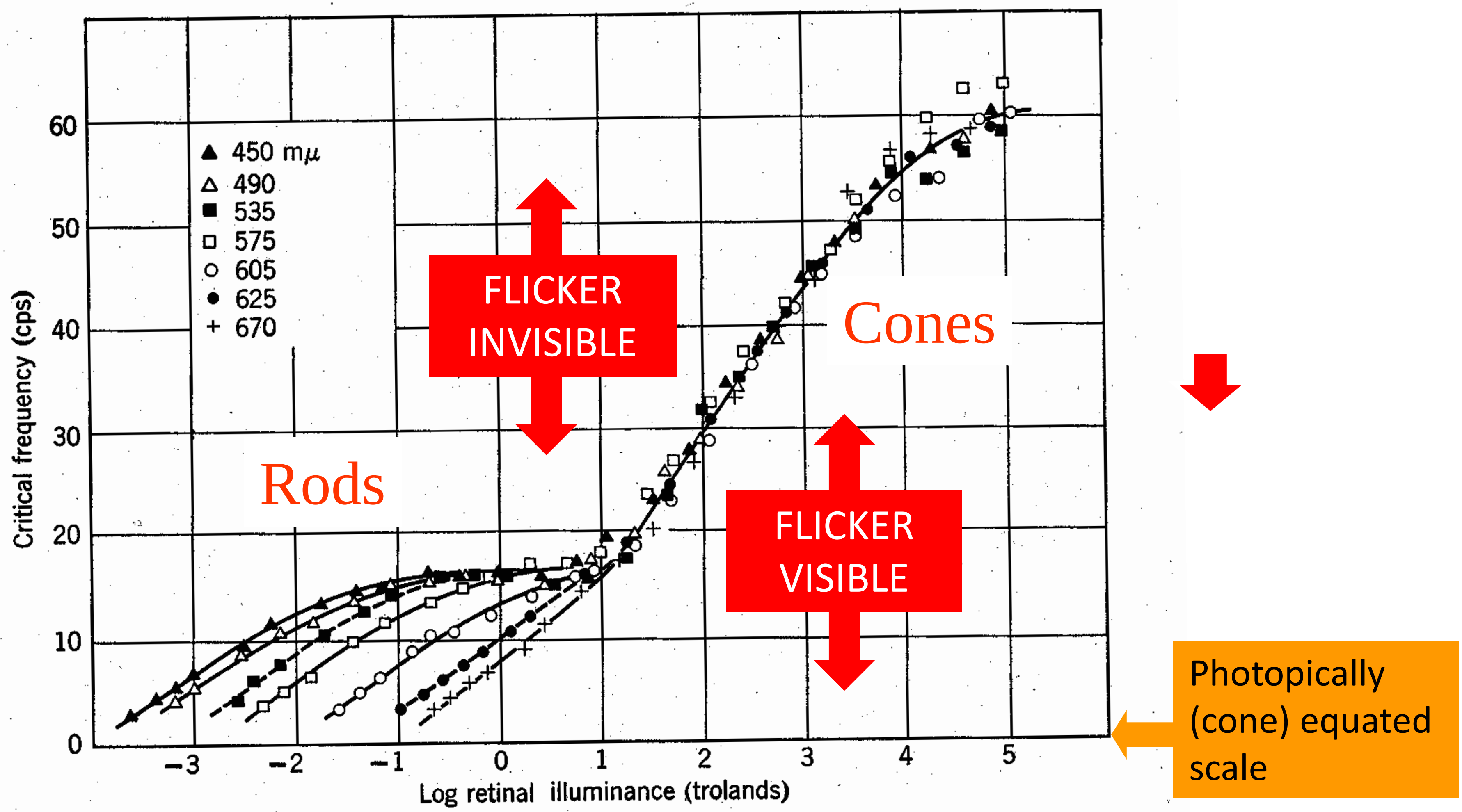
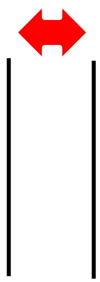


FIG. 10.6 Relation of CFF to log retinal illuminance for seven spectral regions. (Hecht and Shlaer, 1936. Reprinted by permission of The Rockefeller Institute Press from *The Journal of General Physiology*, 1936, **19**, 956–979; Fig. 3.)

Spatial differences
(visual acuity)

Rod and cone visual acuities



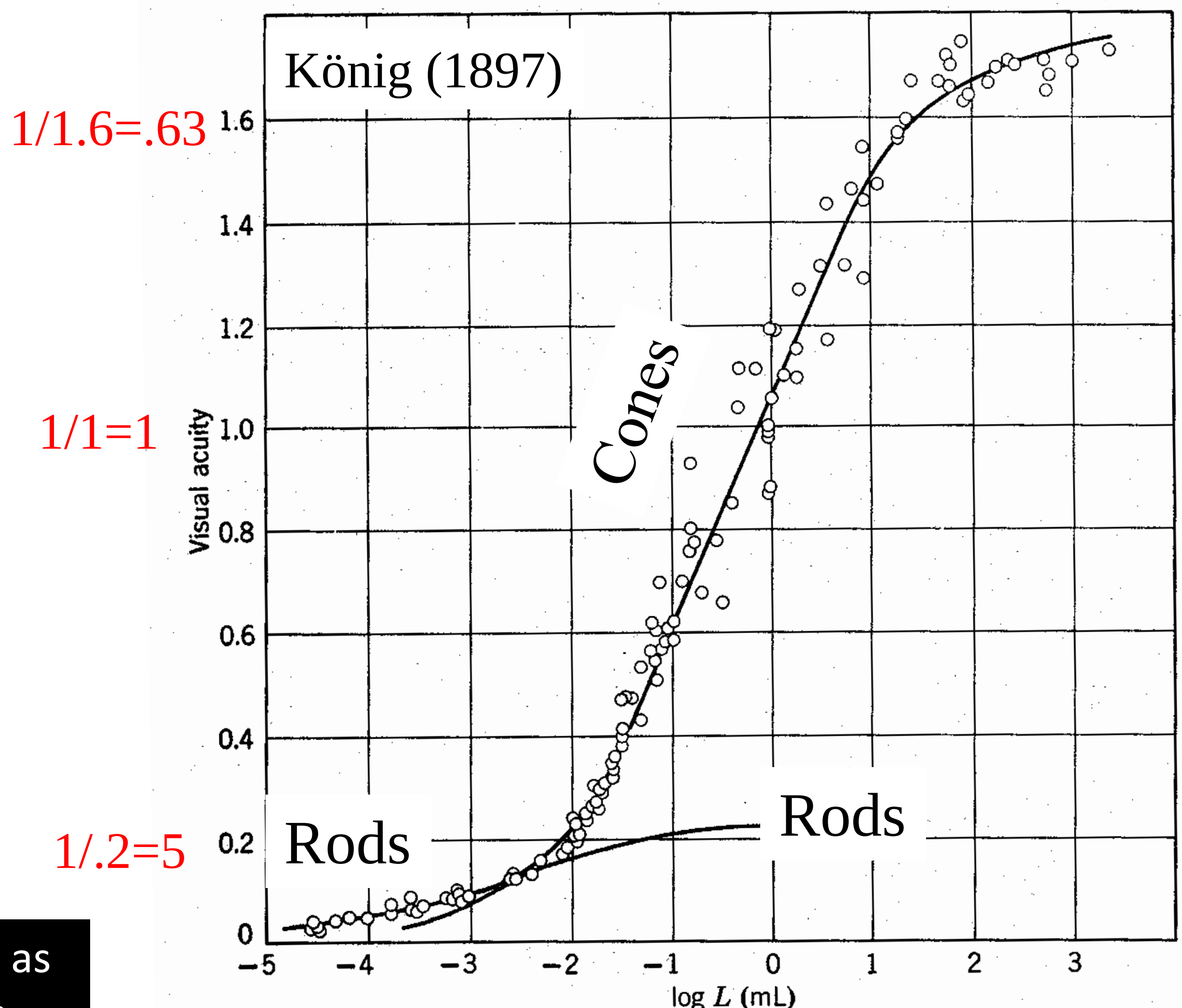


FIG. 11.14 König's data for the relation between visual acuity and illumination, as replotted by Hecht (1934). The shallow curve for the lower limb of the data is an equation for rods, whereas the upper curve is for cones. The task is one of recognizing the orientation of a hook form of test object.

The acuity here is defined as the reciprocal value of the size of the gap (measured in arc minutes) that can be reliably identified.

Rod and cone visual acuities

Greater spatial integration improves rod sensitivity but reduces acuity

The loss must be postreceptoral because the rods are smaller than cones in the periphery)

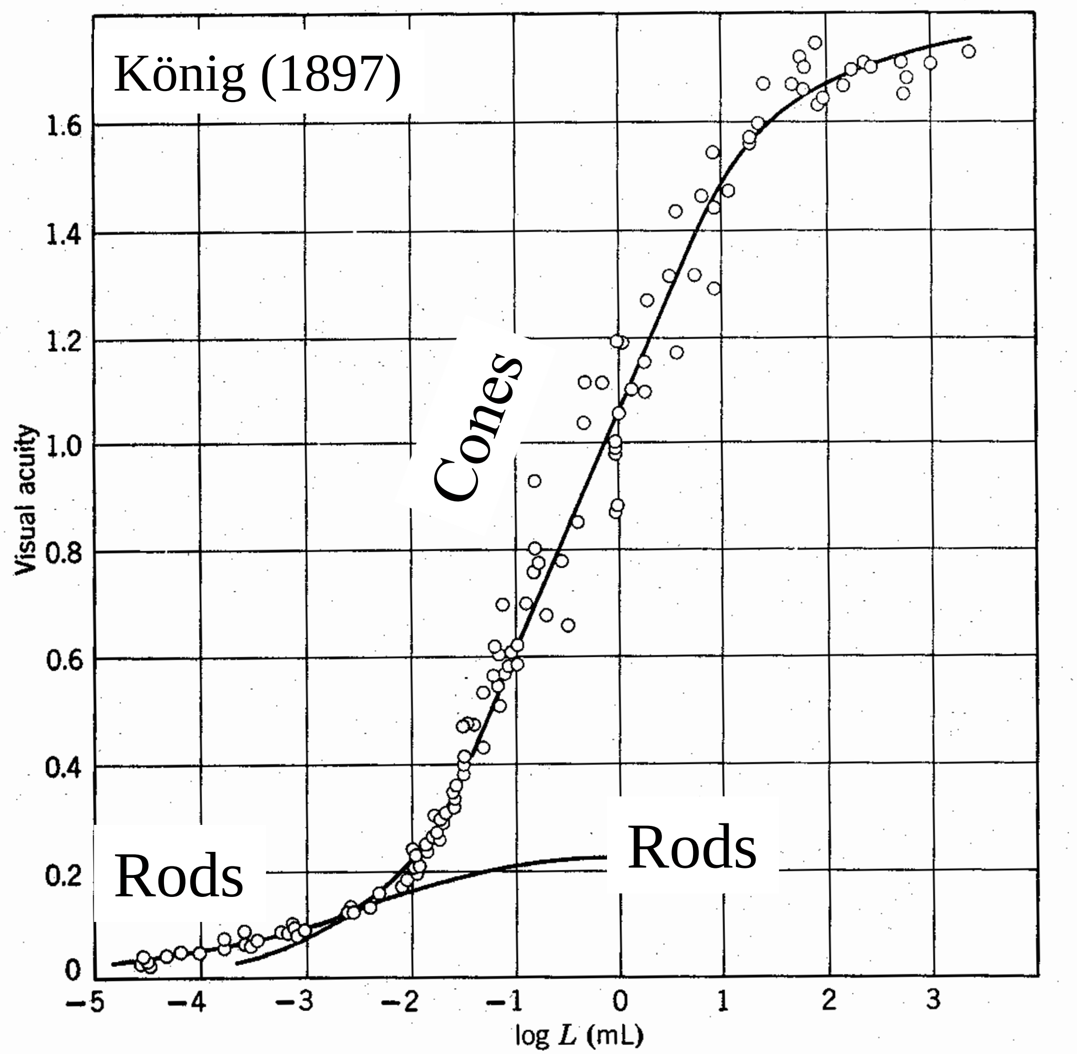


FIG. 11.14 König's data for the relation between visual acuity and illumination, as replotted by Hecht (1934). The shallow curve for the lower limb of the data is an equation for rods, whereas the upper curve is for cones. The task is one of recognizing the orientation of a hook form of test object.

Rod vision is achromatic

Why?

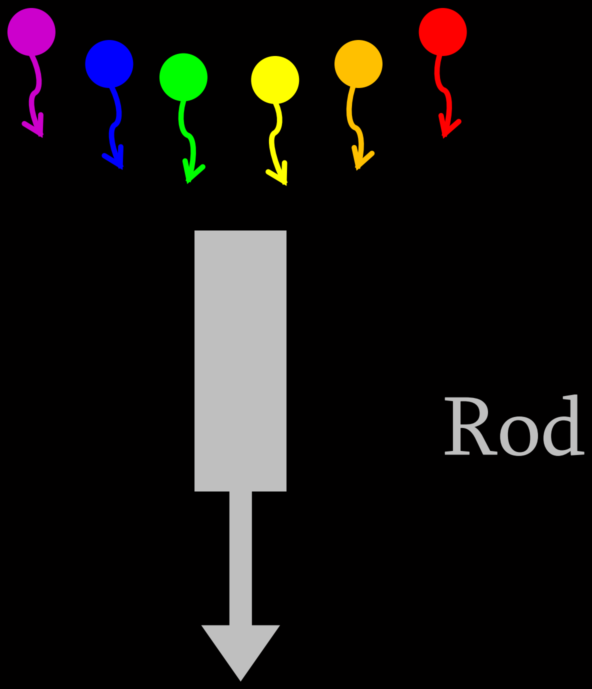
Vision at the photoreceptor stage is relatively simple because the output of each photoreceptor is:

UNIVARIANT

What does univariant mean?

UNIVARIANCE

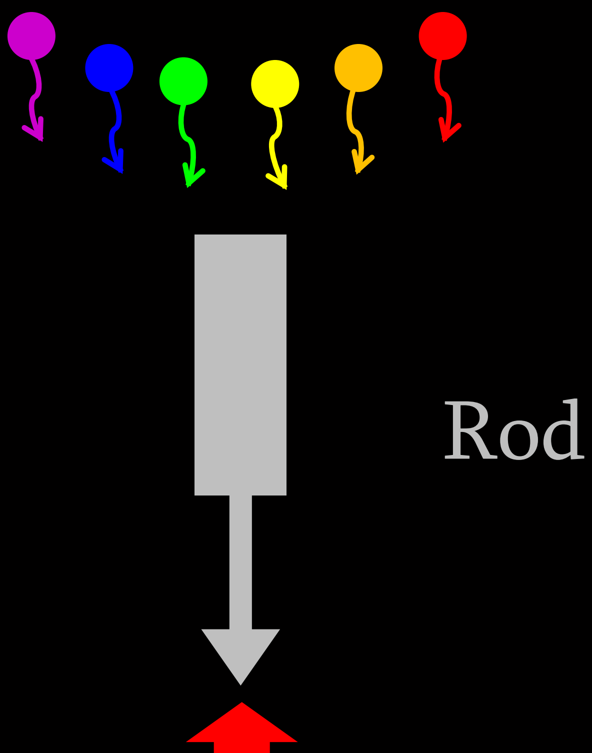
Crucially, the effect of any absorbed photon is *independent* of its wavelength.



Once absorbed a photon produces the *same* change in photoreceptor output whatever its wavelength.

UNIVARIANCE

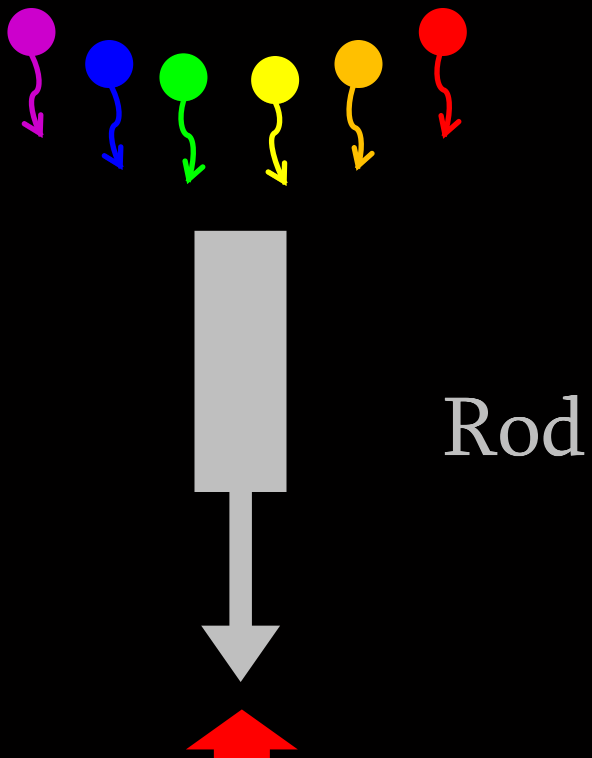
Crucially, the effect of any absorbed photon is *independent* of its wavelength.



So, if you monitor the rod output, you can't tell which "colour" of photon has been absorbed.

UNIVARIANCE

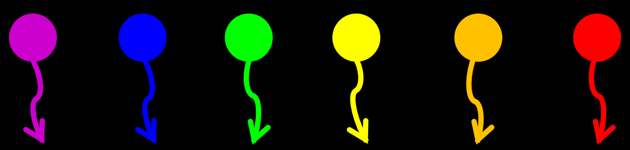
Crucially, the effect of any absorbed photon is *independent* of its wavelength.



All the photoreceptor effectively does is to count photons.

UNIVARIANCE

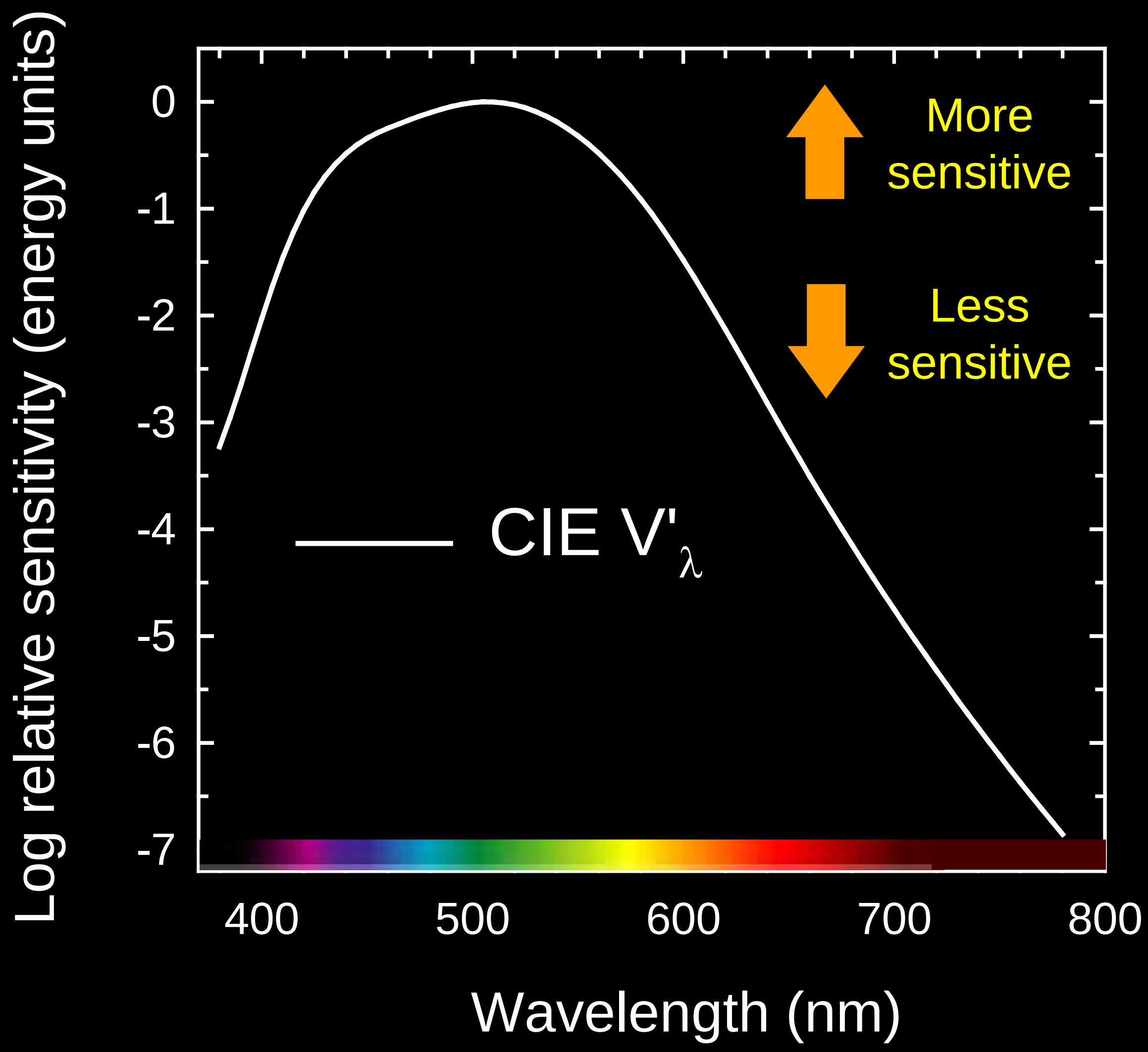
What does vary with wavelength is the probability that a photon will be absorbed.



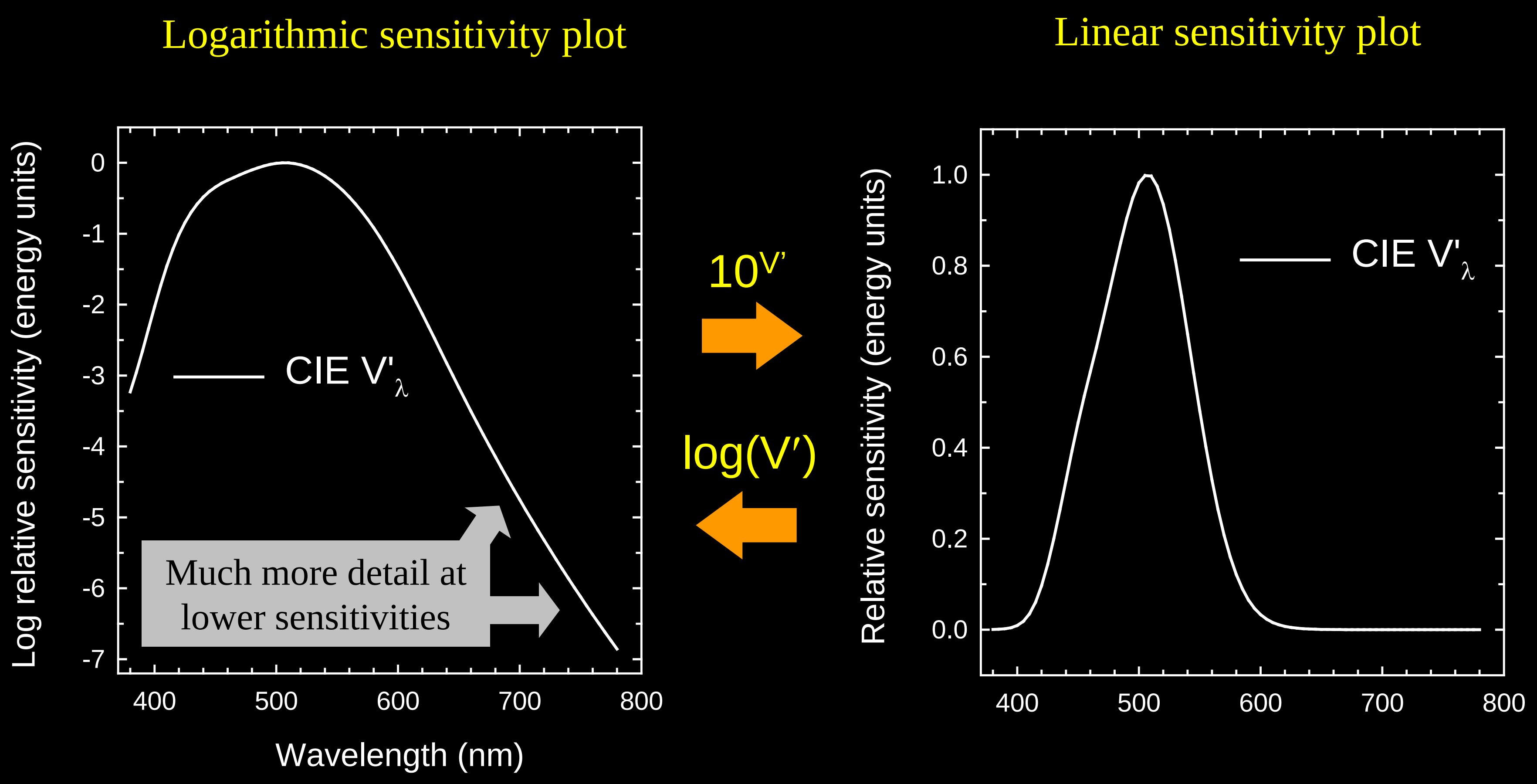
This is reflected in what is called a "spectral sensitivity function".

Rod spectral sensitivity function

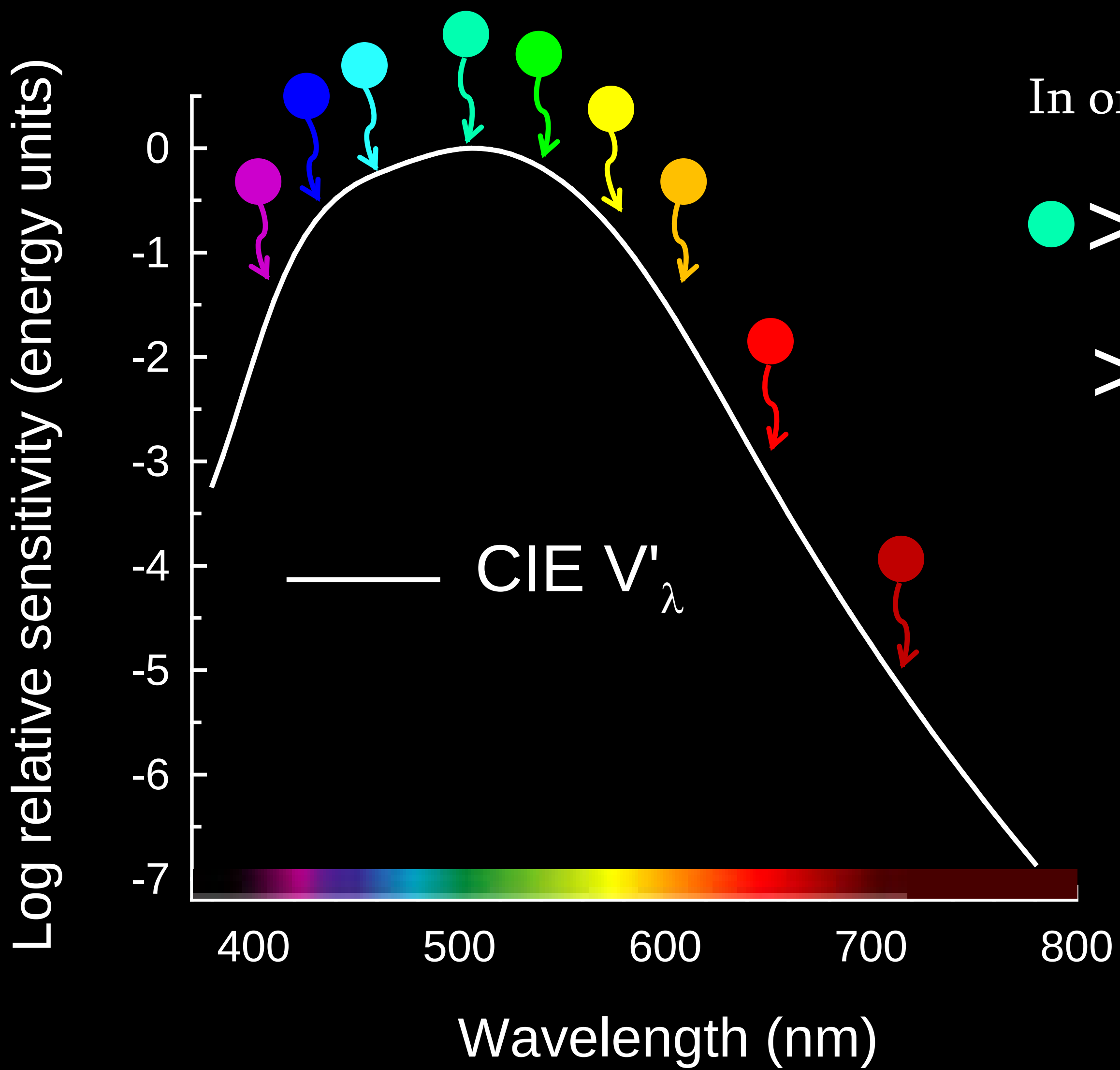
(also known as the scotopic luminosity curve, CIE V'_λ)



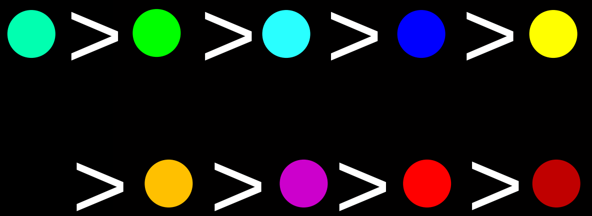
Rod spectral sensitivity function (V'_λ)

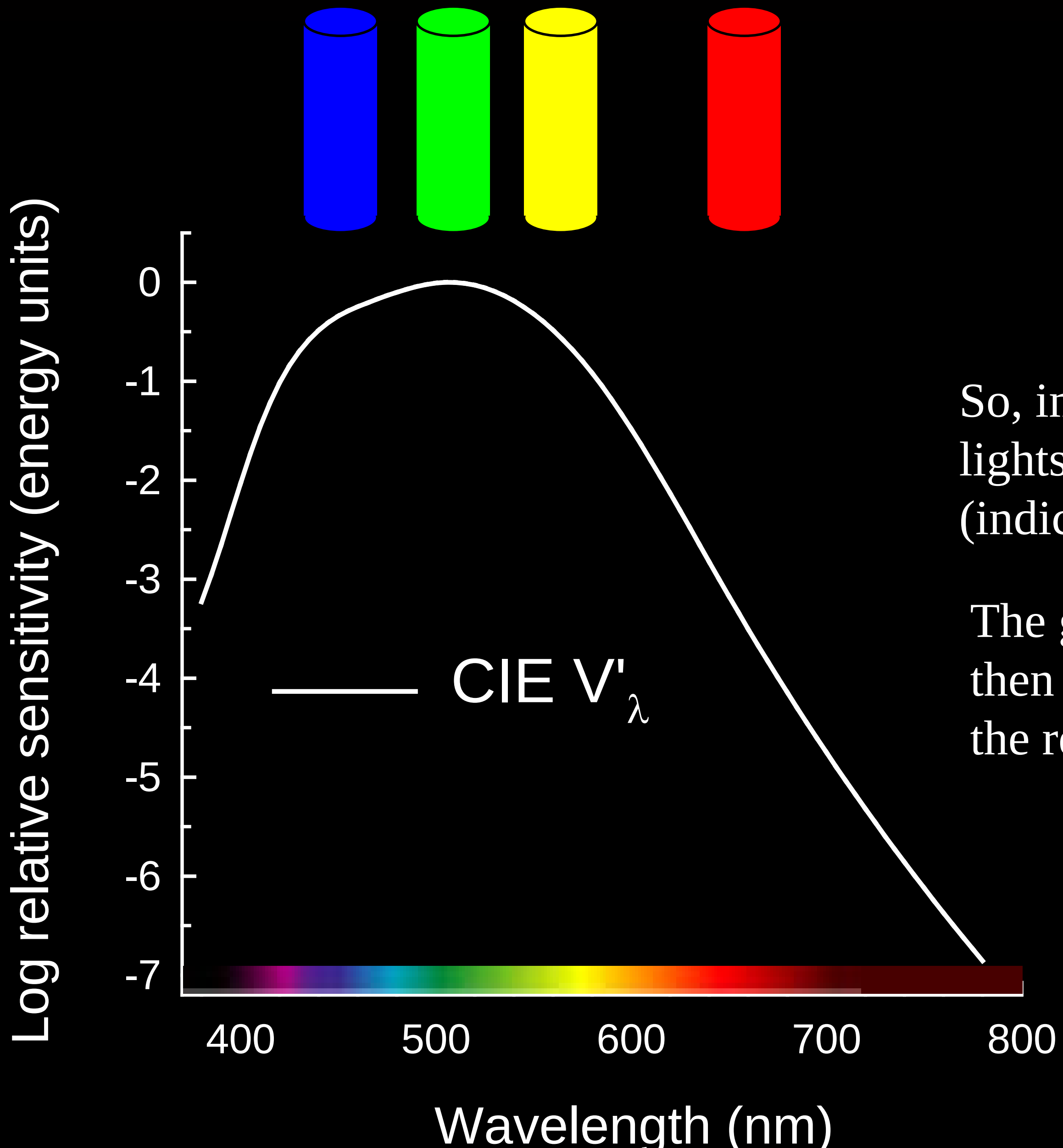


Rod spectral sensitivity function (V'_λ)



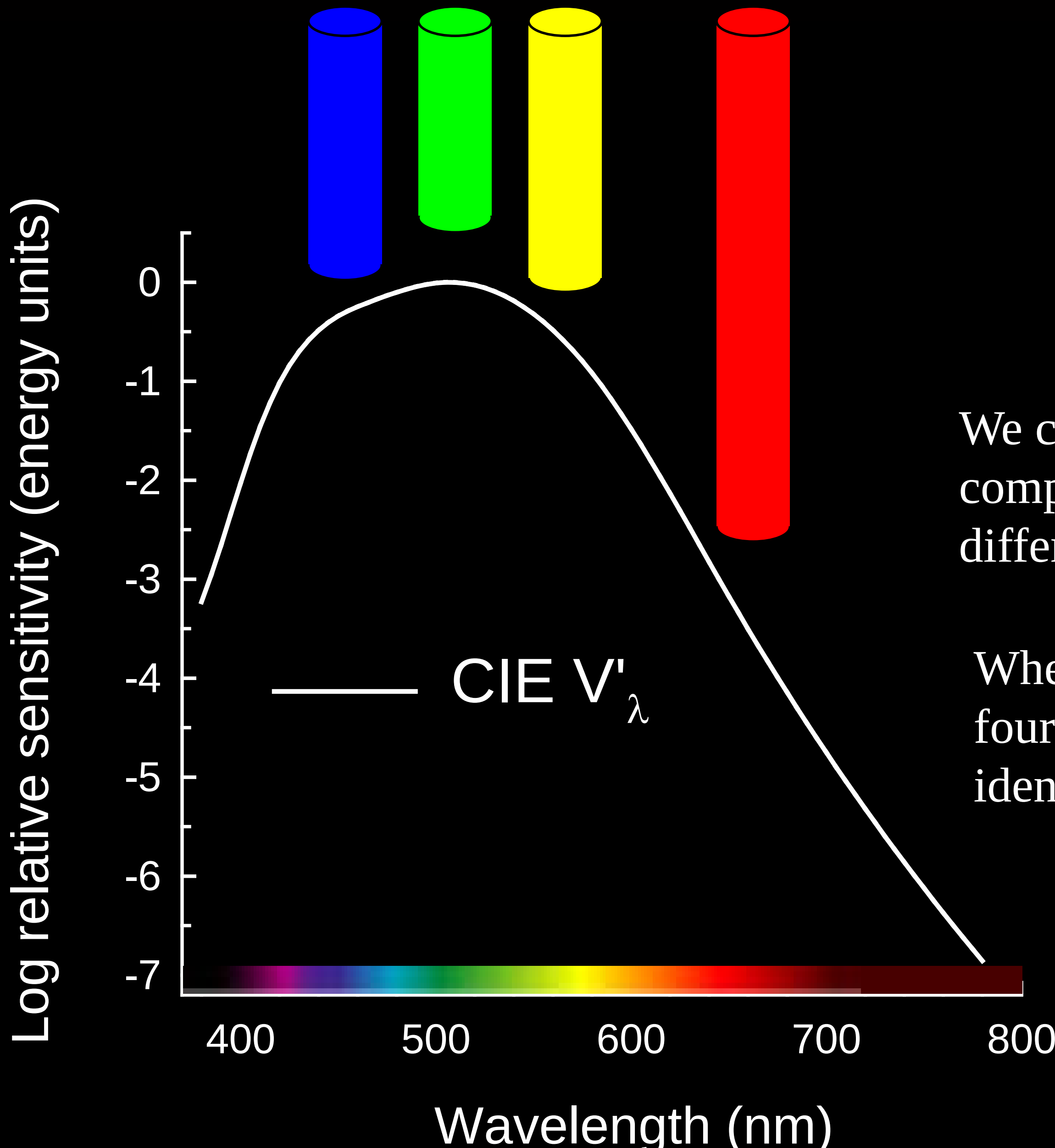
In order of rod sensitivity:





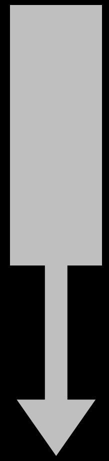
So, imagine you have four lights of the same intensity (indicated here by the height)

The green will look brightest, then blue, then yellow and lastly the red will be the dimmest



We can adjust the intensities to compensate for the sensitivity differences.

When this has been done, the four lights will look completely identical.

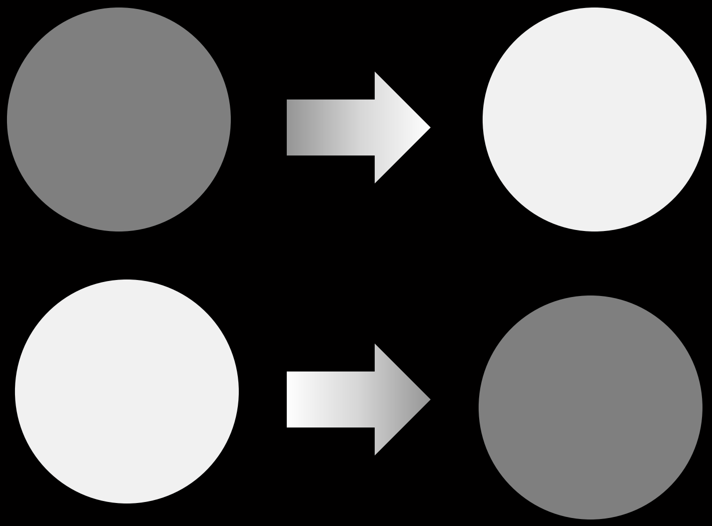


Rod

Changes in light intensity are confounded with changes in colour (wavelength)

UNIVARIANCE

A change in photoreceptor output can be caused by a change in intensity or by a change in colour. There is no way of telling which.



Colour or intensity change??

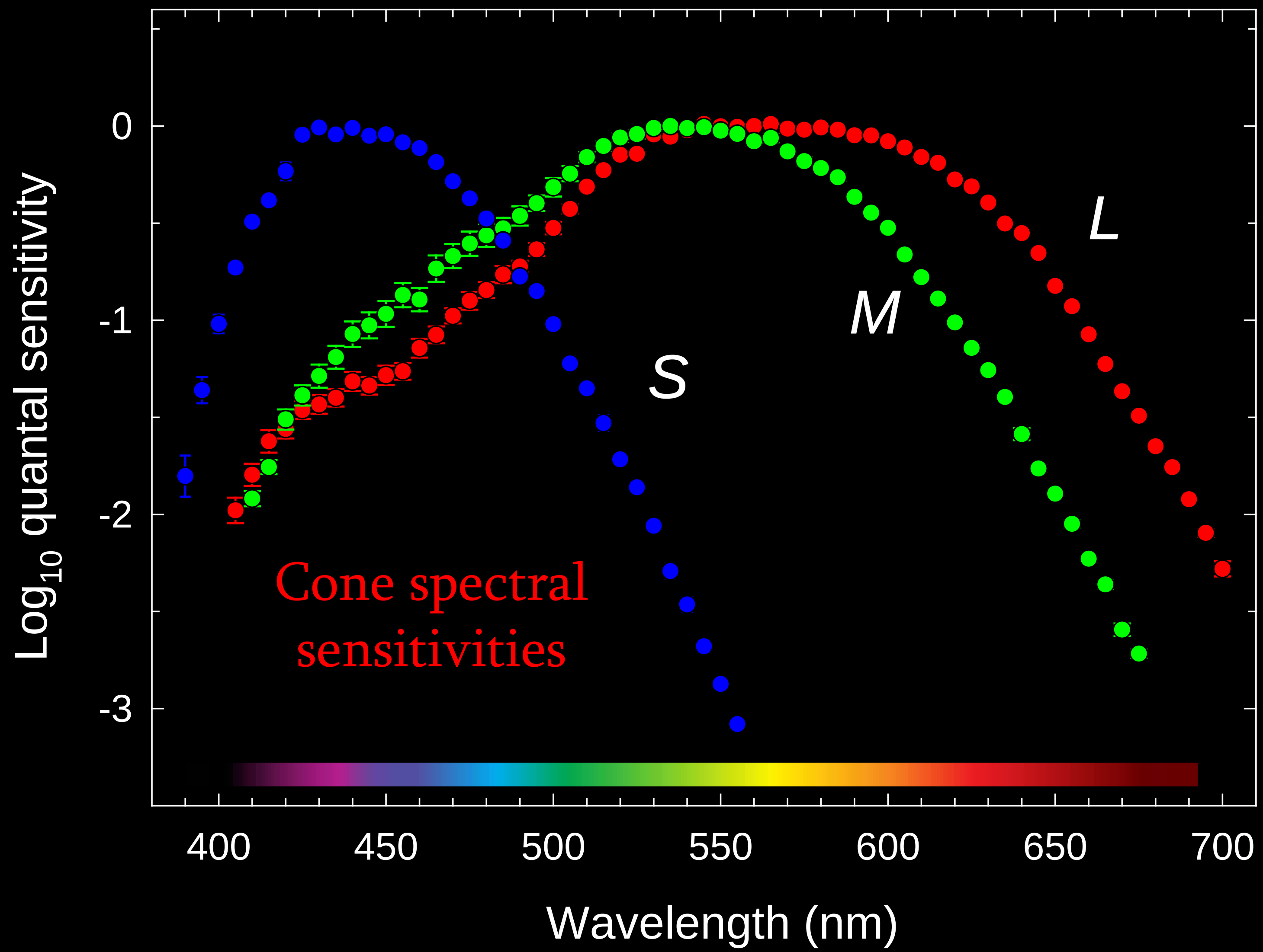
Each photoreceptor is therefore 'colour blind', and is unable to distinguish between changes in colour and changes in intensity.

A consequence of univariance is that we are colour-blind when only one photoreceptor operates…

Examples: SCOTOPIC VISION, cone monochromacy

With three cone photoreceptors, our colour vision is trichromatic…

The probability of photon absorption varies differently with wavelength for the three cone types so that the cones have different spectral sensitivities…

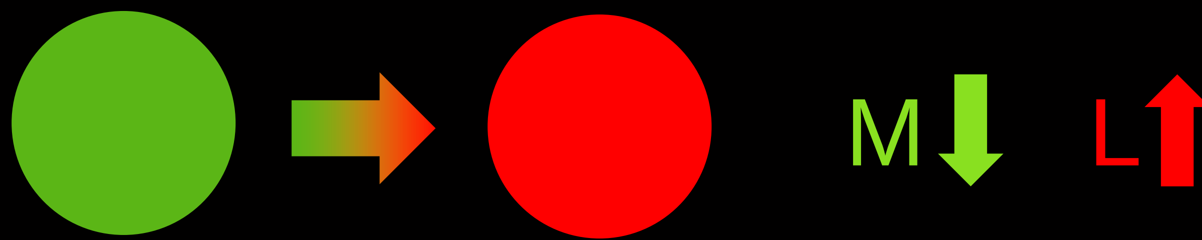


So, if each photoreceptor is colour-blind, how do we see colour?

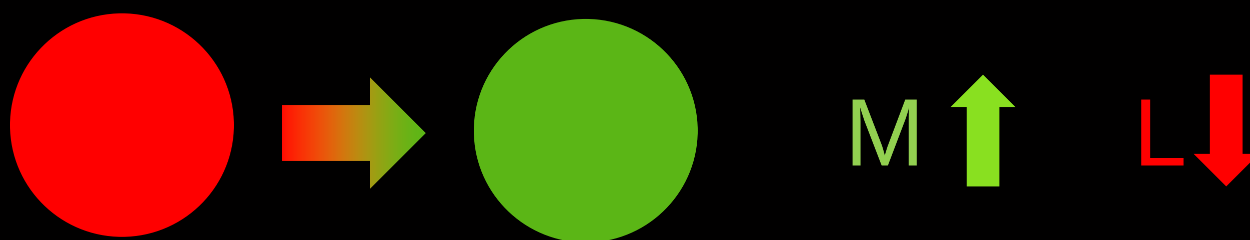
Or to put it another way:
How is colour encoded?

TRICHROMACY

A change in colour from green to red causes a relative increase in the L-cone output but causes a decrease in the M-cone output.

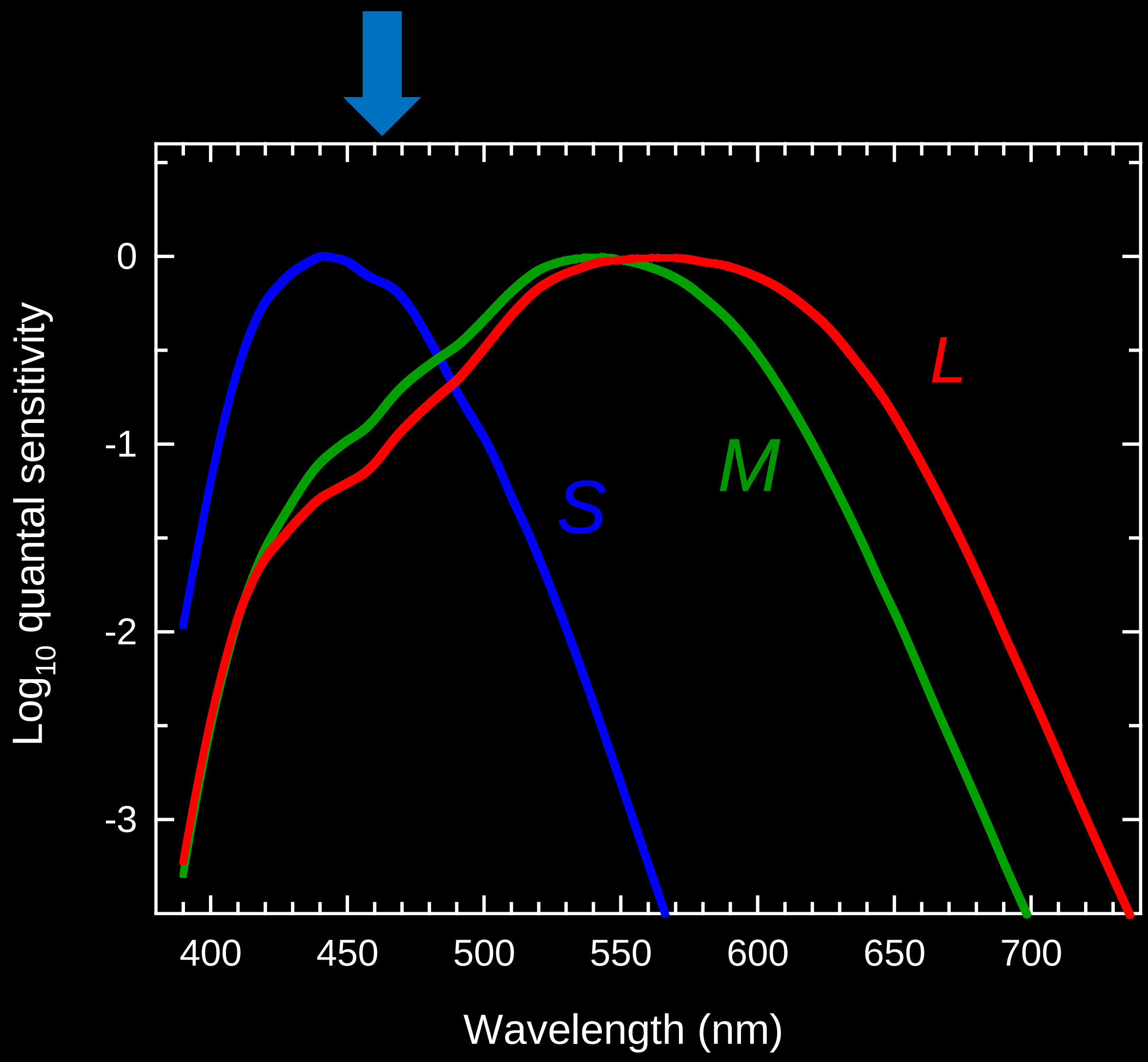


A change in colour from red to green causes a relative increase in the M-cone output but causes a decrease in the L-cone output.

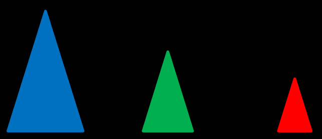


Thus, colour can be encoded by *comparing* the outputs of different cone types…

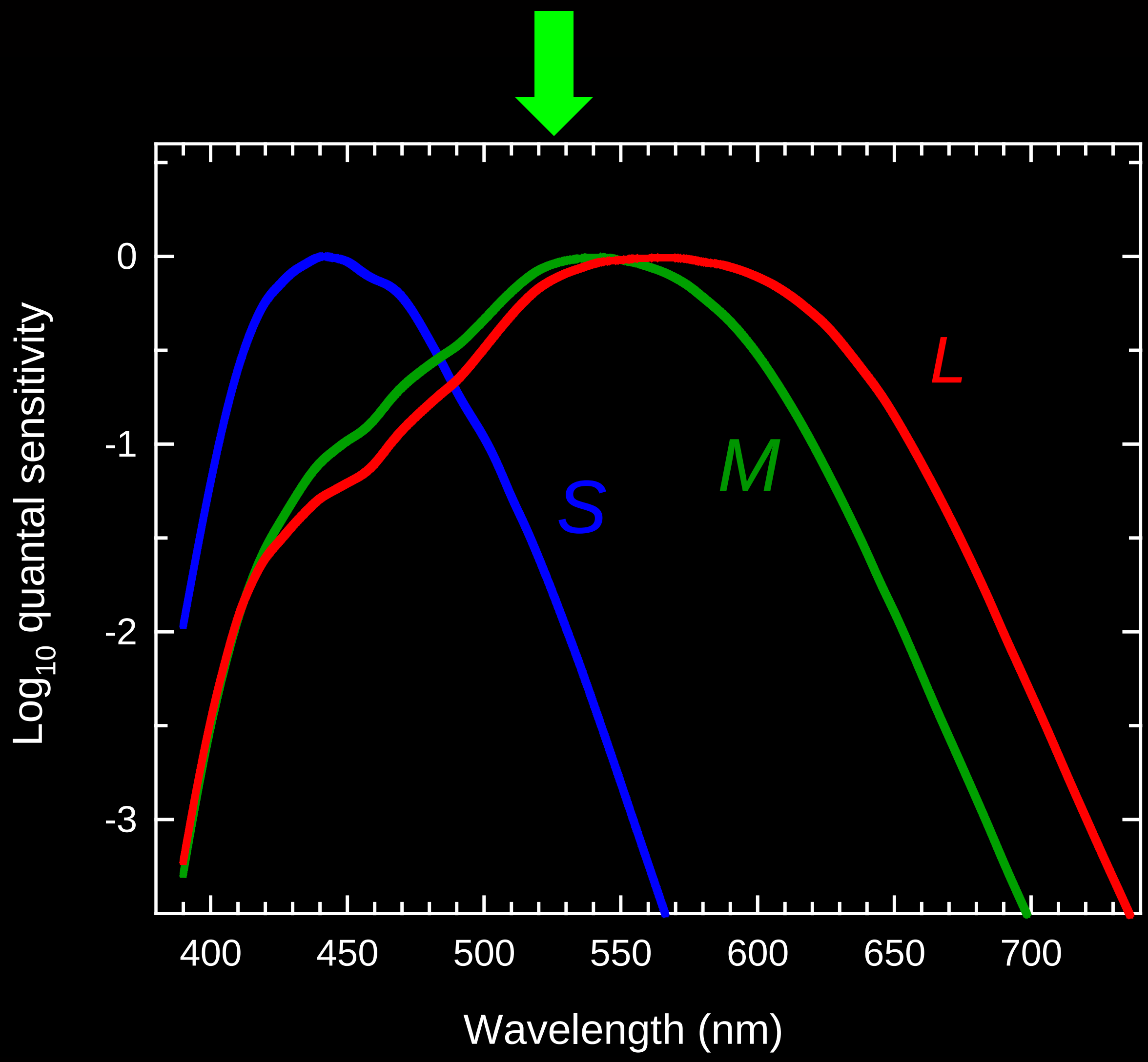
At the photoreceptors, colour is encoded by the relative cone outputs



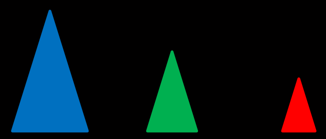
Blue light



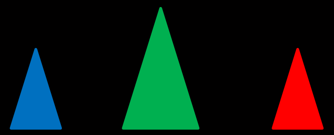
Colour is encoded by the relative cone outputs



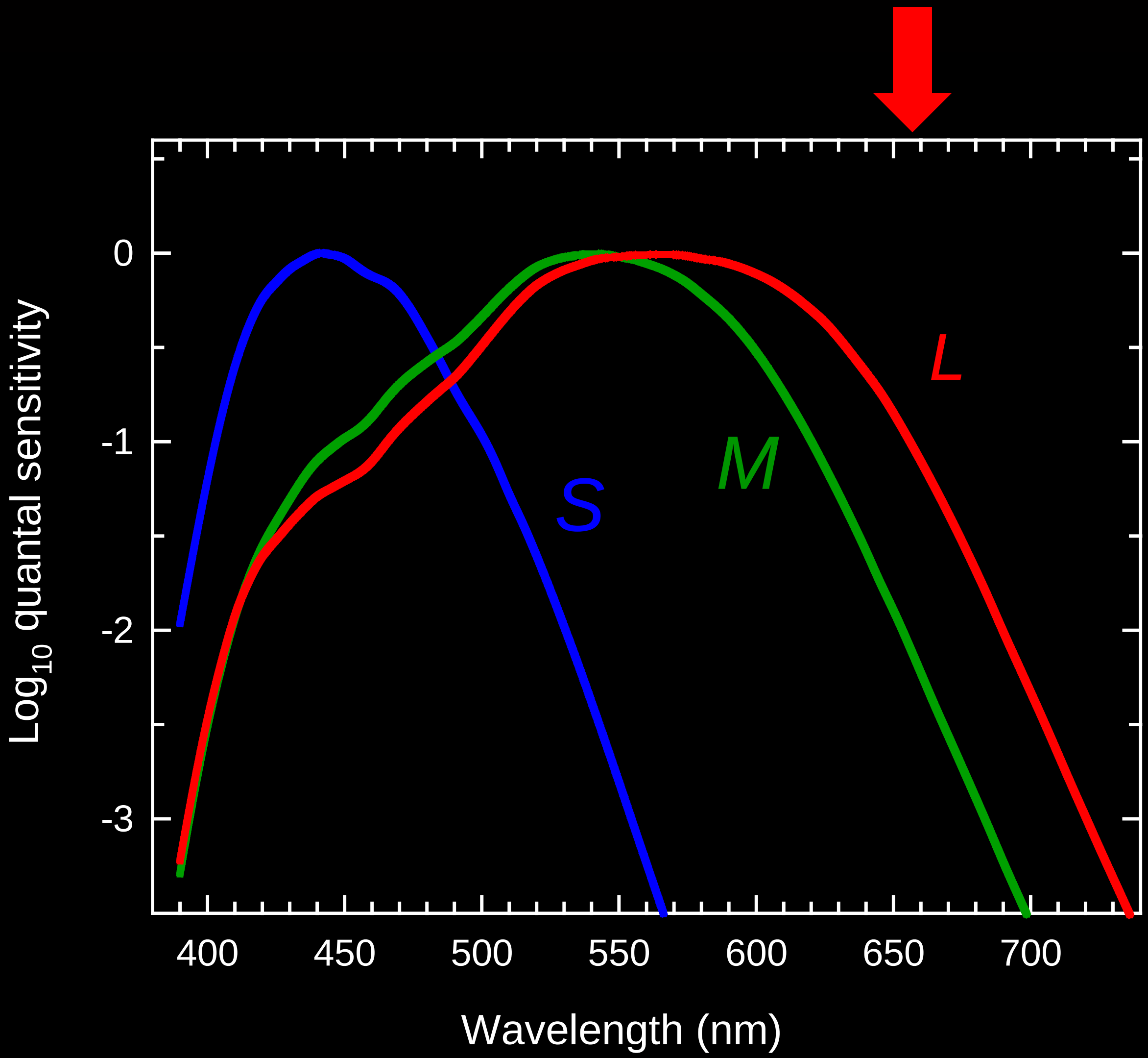
Blue light



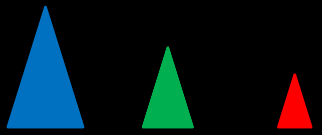
Green light



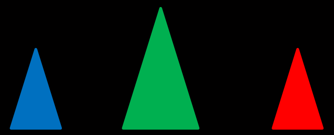
Colour is encoded by the relative cone outputs



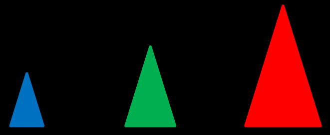
Blue light



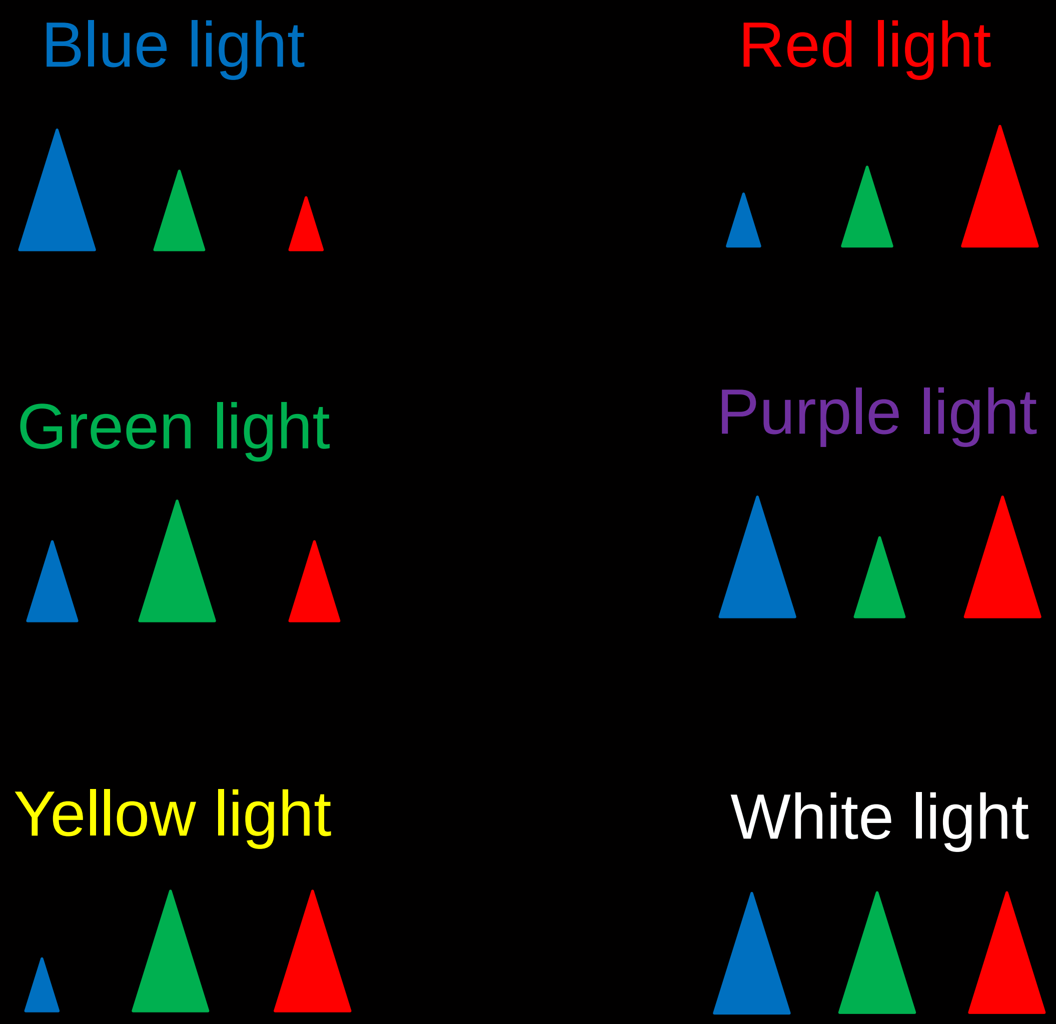
Green light



Red light

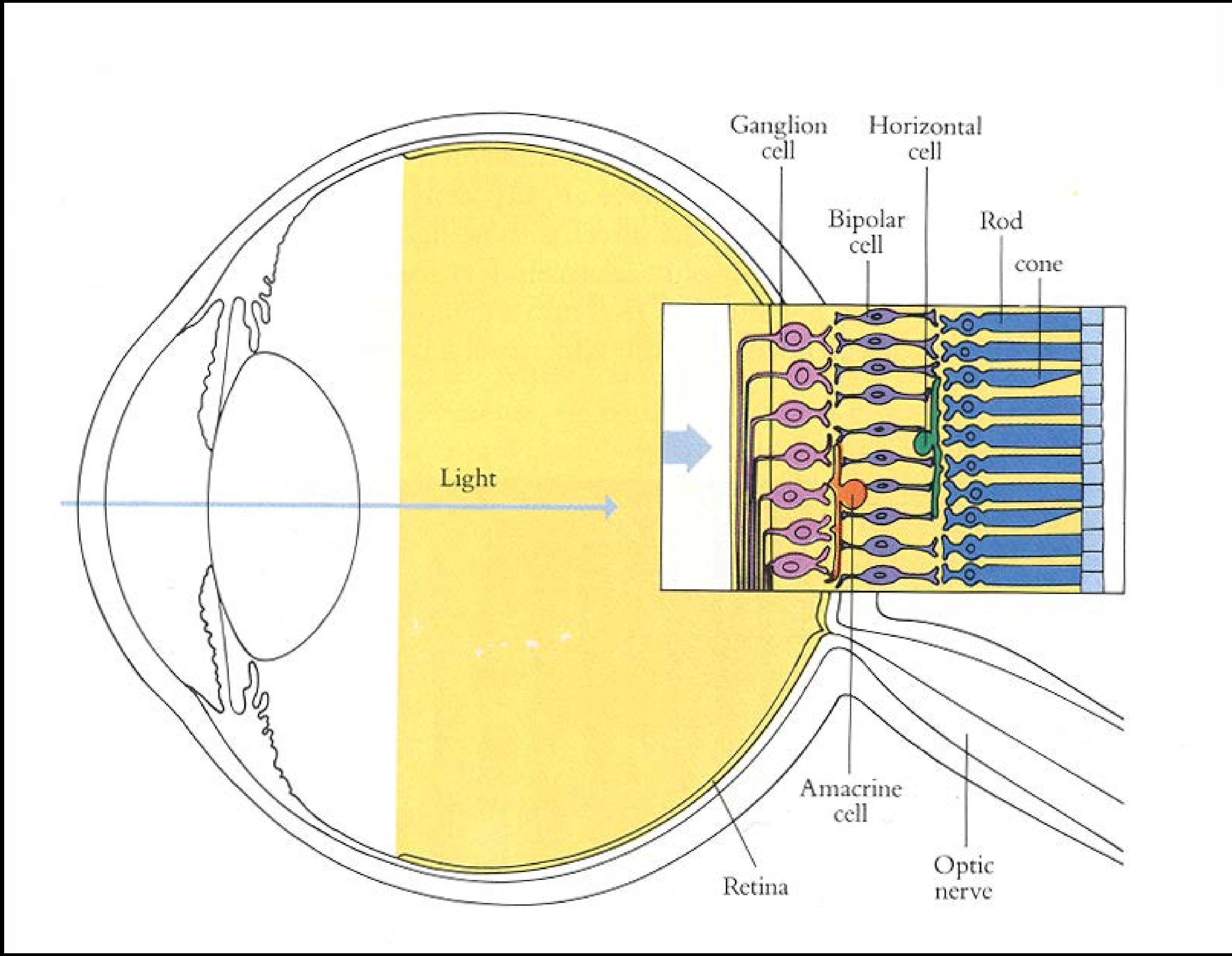


Colour is encoded by the relative cone outputs



POSTRECEPTORAL COLOUR VISION

But what happens next (i.e., how is colour encoded after the photoreceptors)?

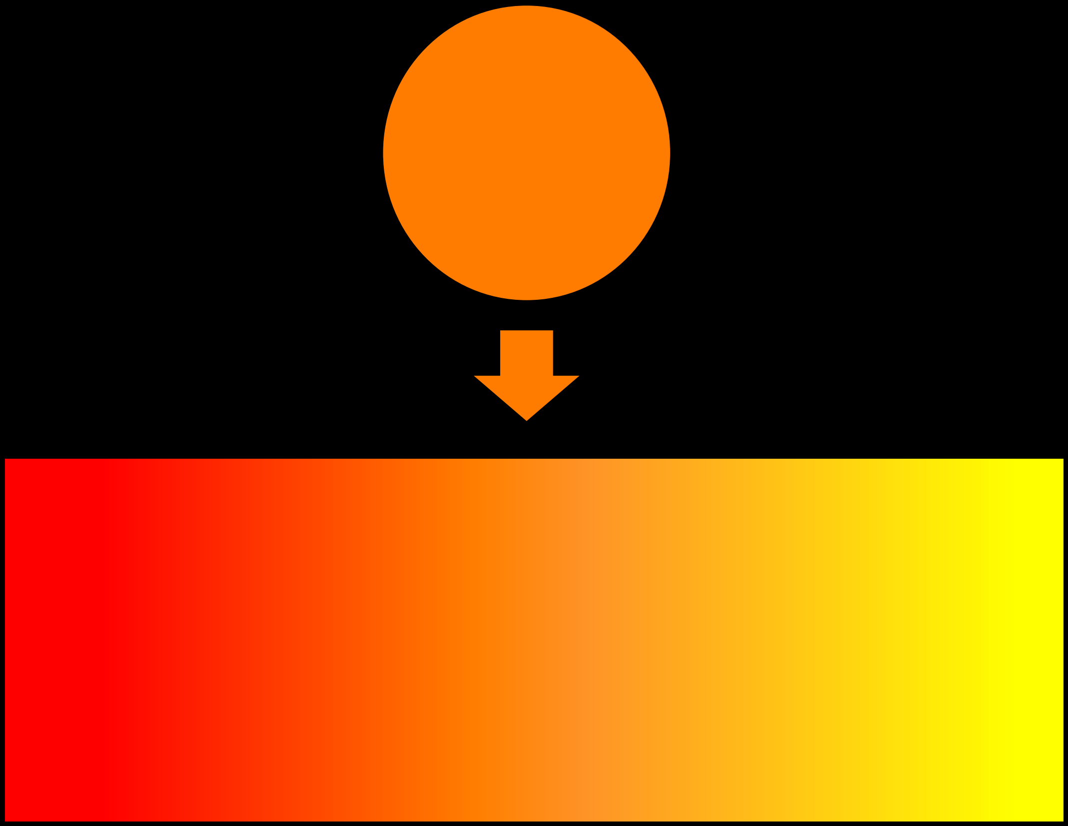


Colour phenomenology

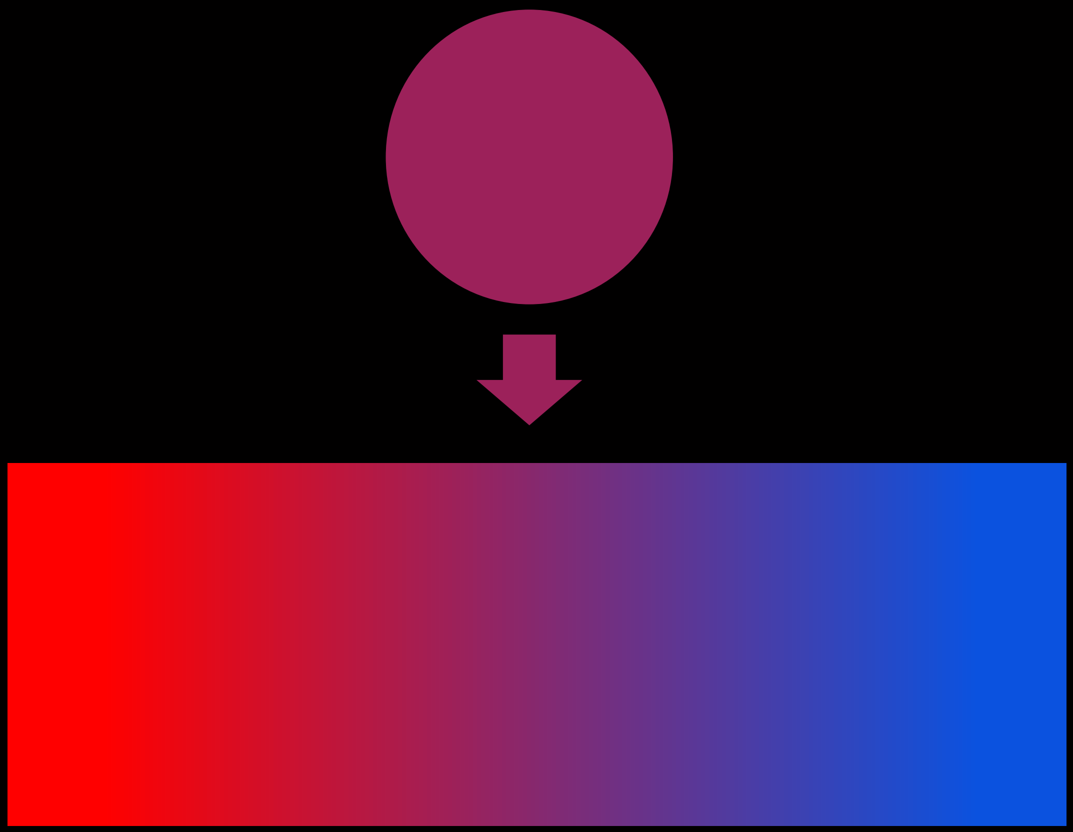
Can provide clues about how colours are processed after the photoreceptors…

- Which pairs of colours coexist in a single, uniform patch of colour?
- Which pairs never coexist?

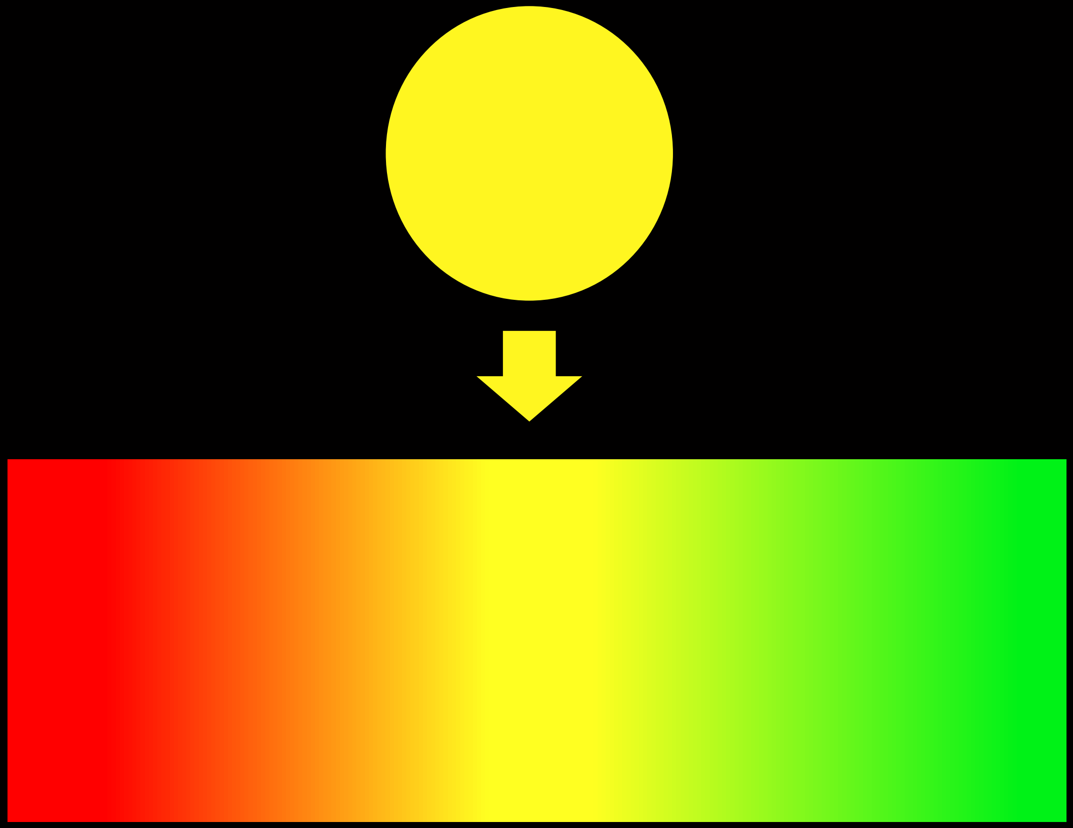
WHY?



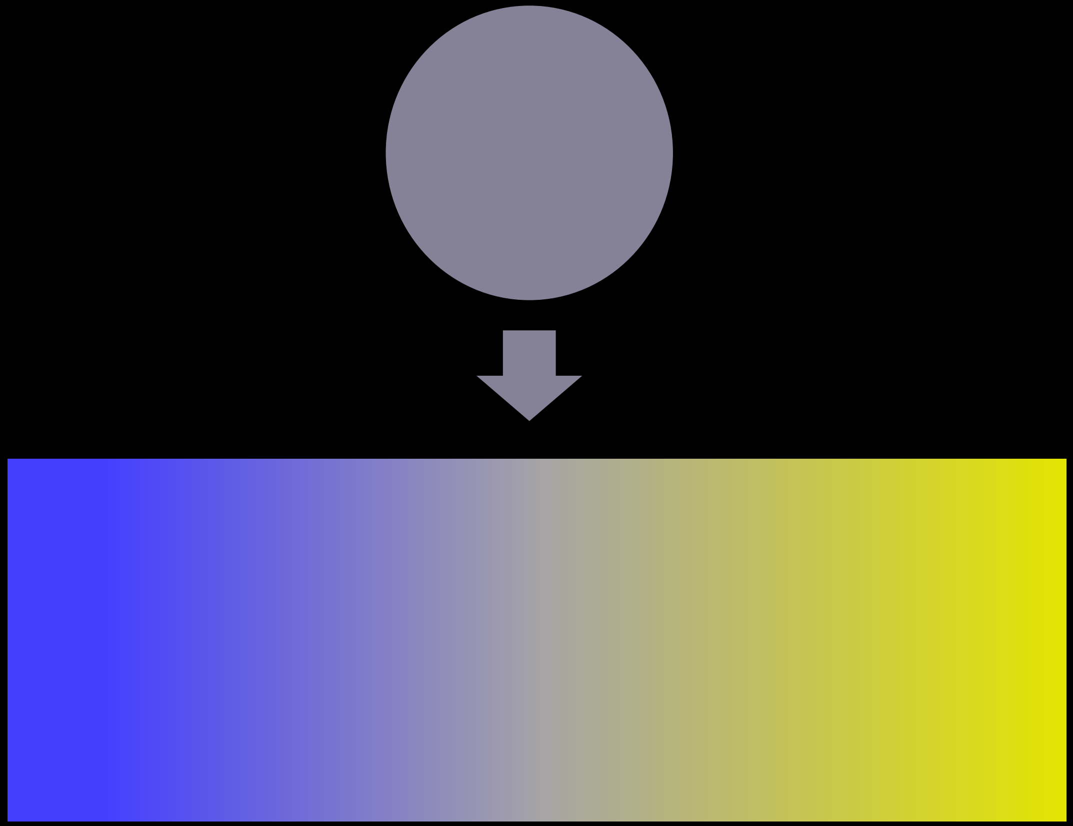
Reddish-yellows?



Reddish-blues?

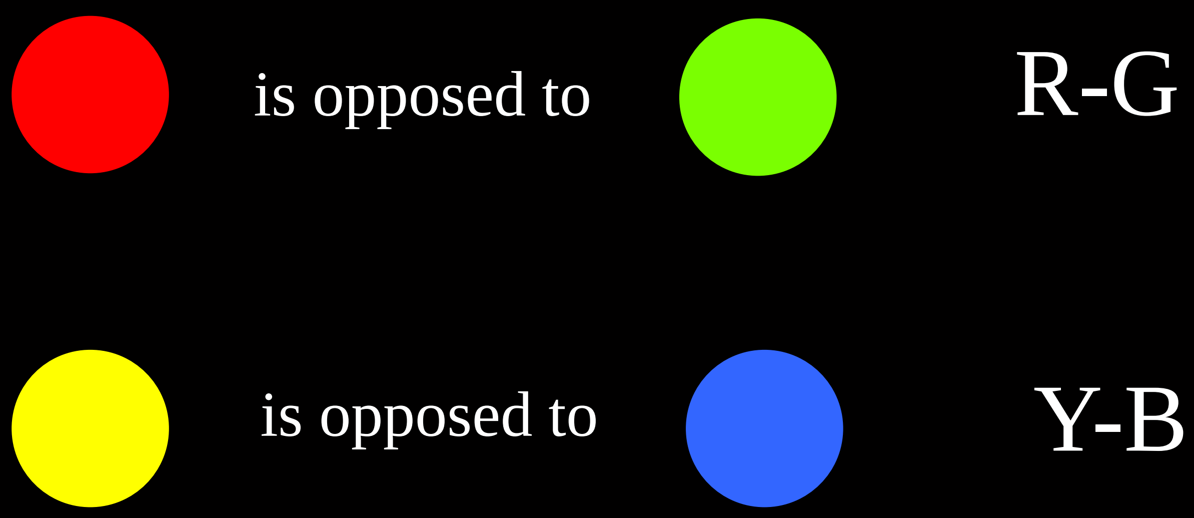


Reddish-greens?



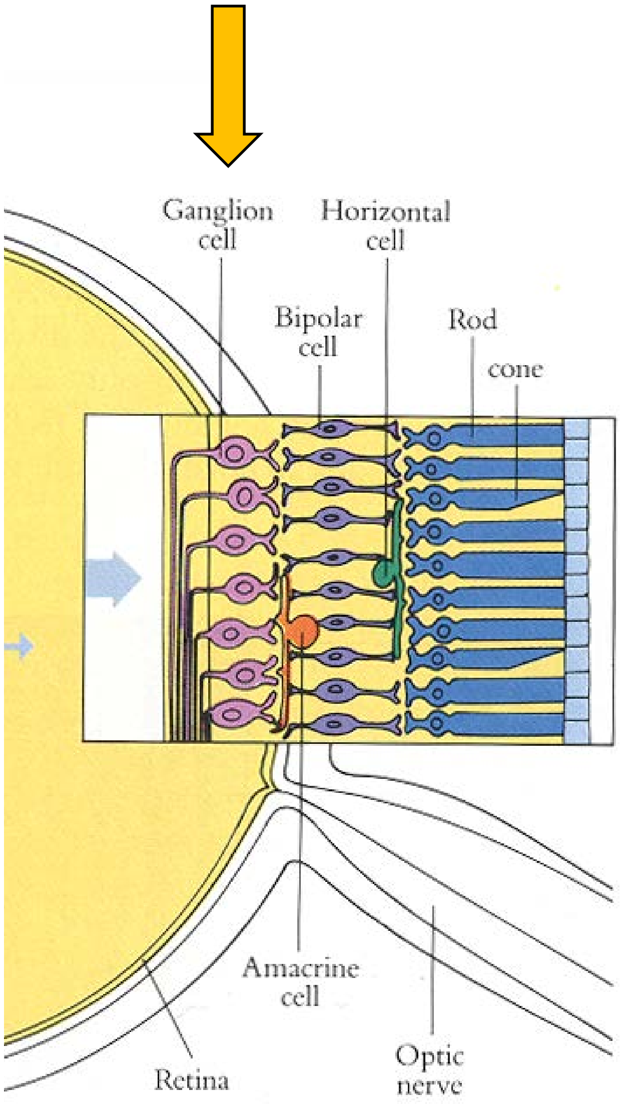
Bluish-yellow?

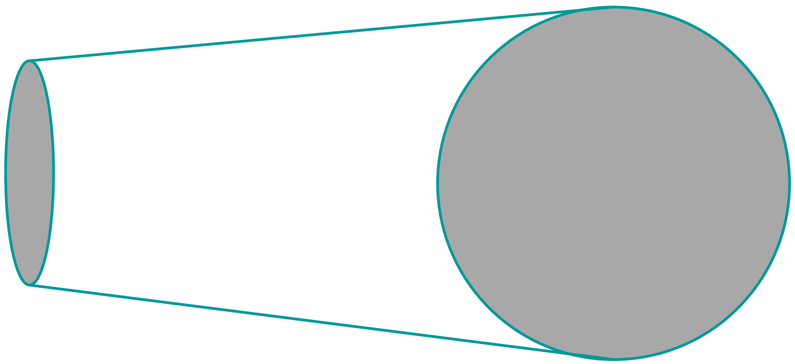
The colour opponent theory of Hering



How might this be related to visual processing after the cones?

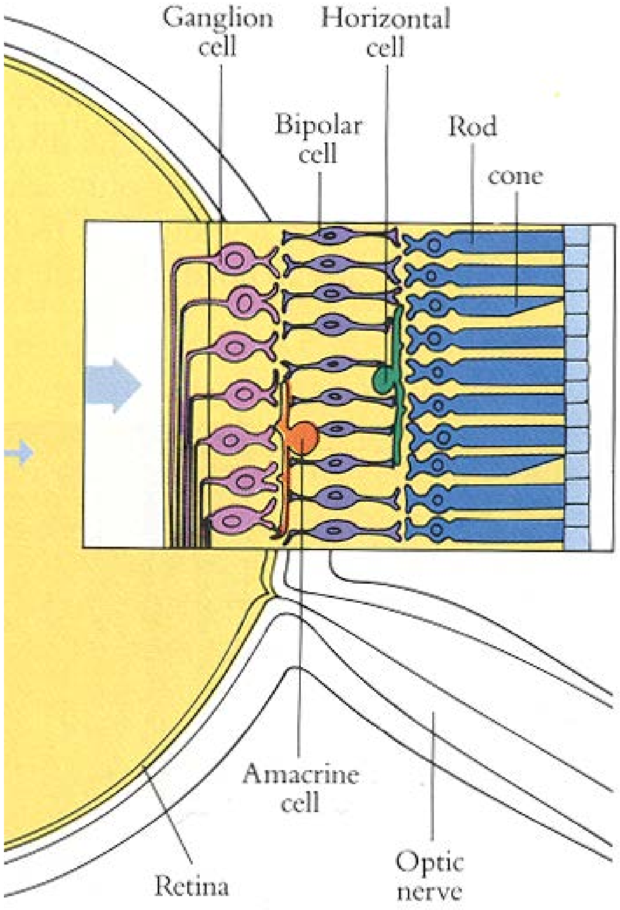
Some ganglion cells are colour opponent

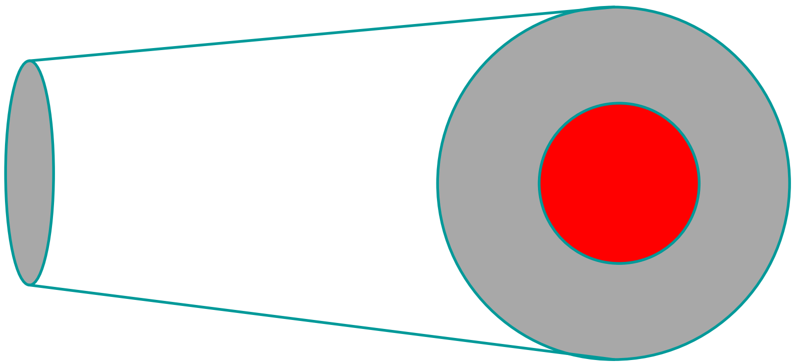




Imagine that this is the region of space that the cell “sees” in the external world

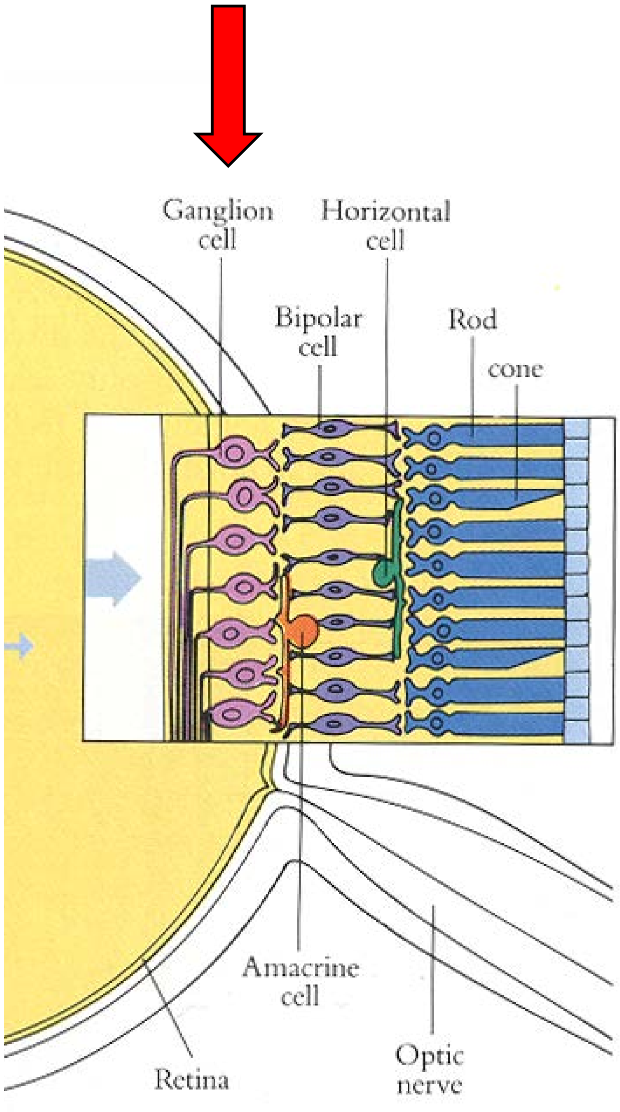
Some ganglion cells are colour opponent

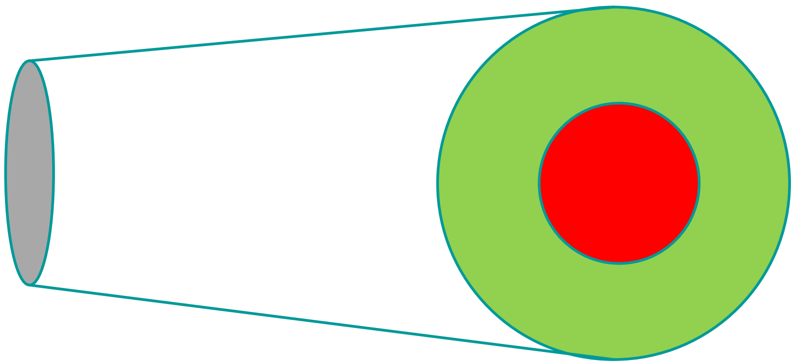




A red light falling on the central area excites the cell (makes it fire faster)

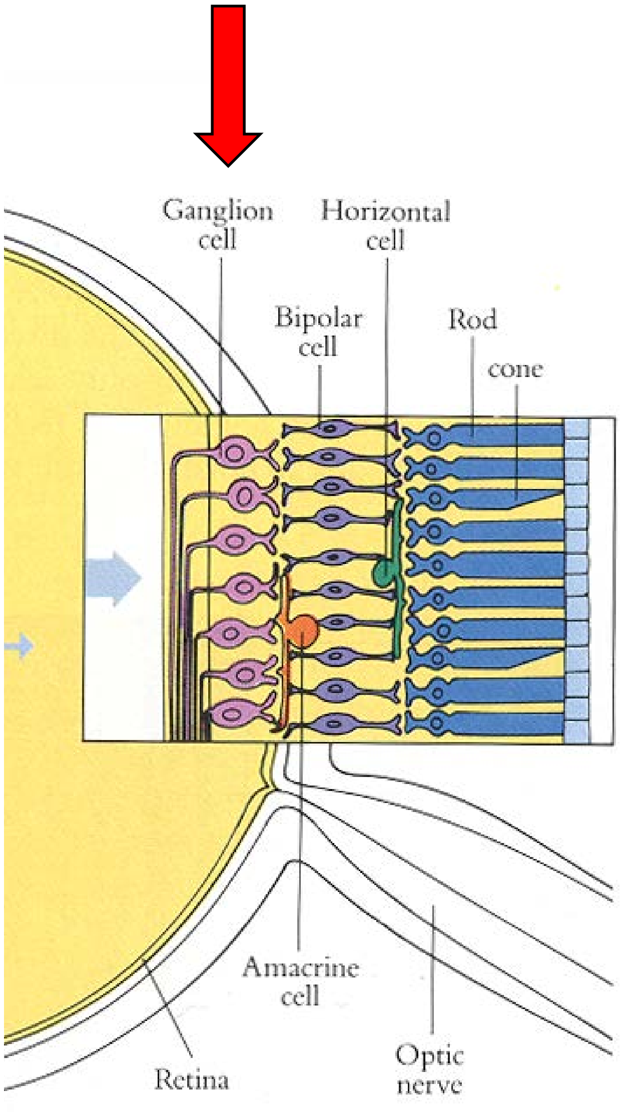
Some ganglion cells are colour opponent

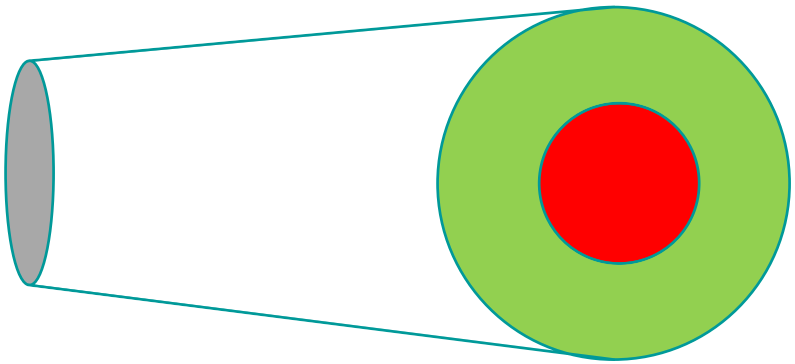




A green light falling on the surround area inhibits the cell (makes it fire slower)

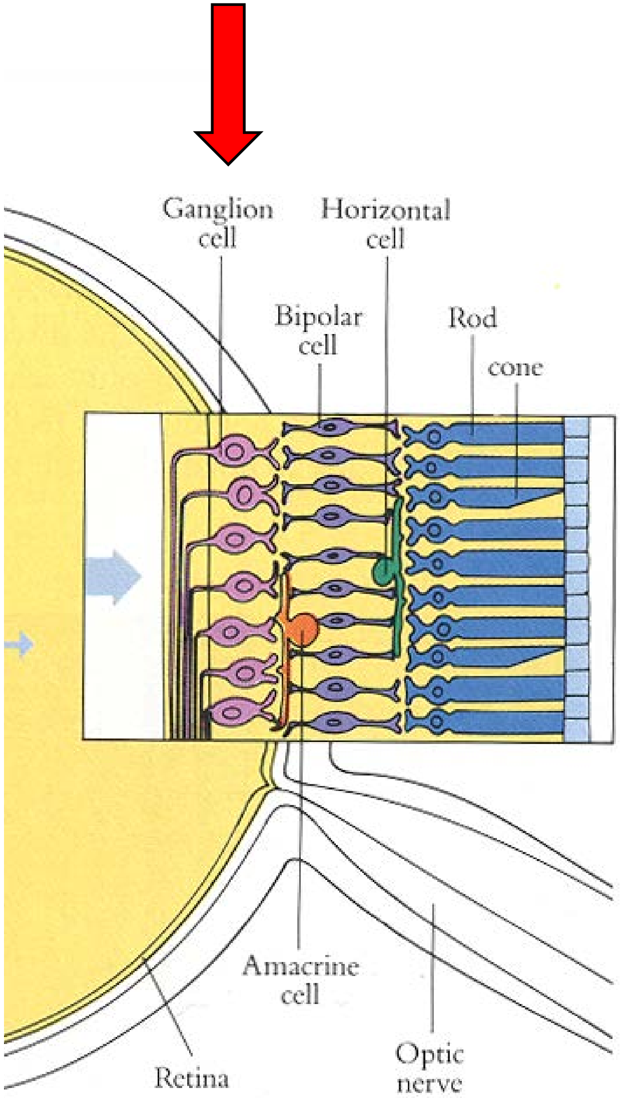
Some ganglion cells are colour opponent

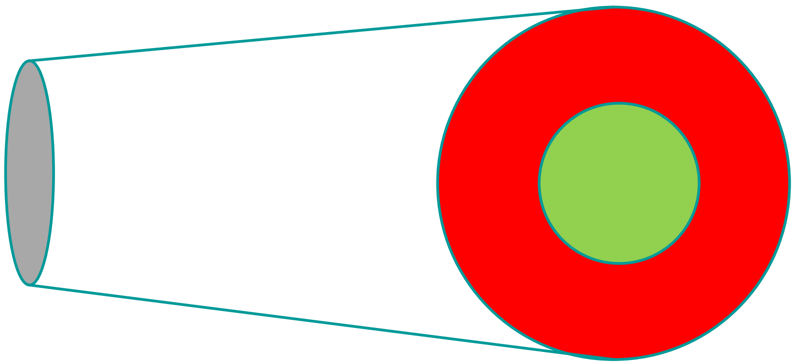




RED On-centre
GREEN Off-surround

Some ganglion cells are colour opponent

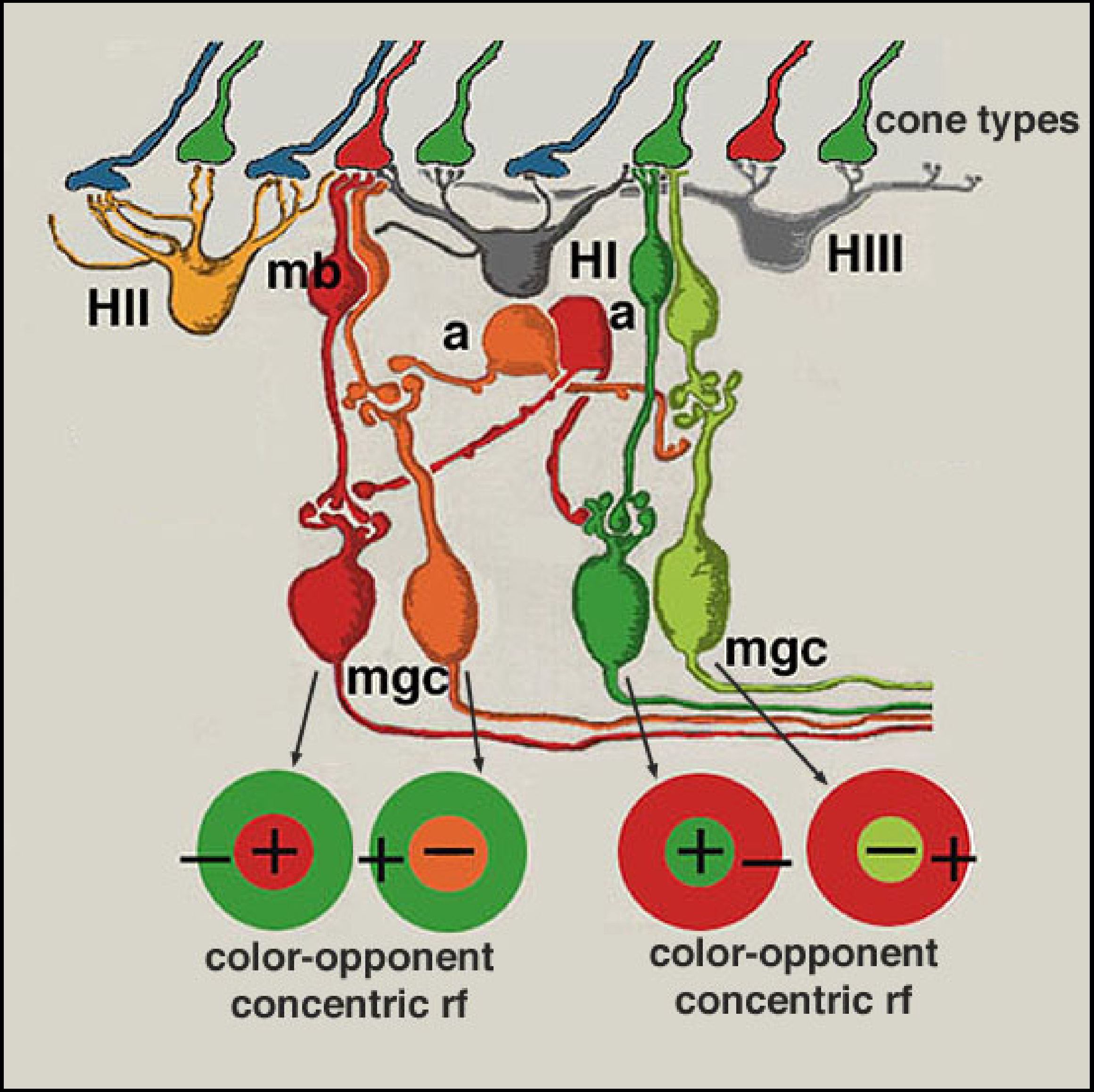




GREEN On-centre
RED Off-surround

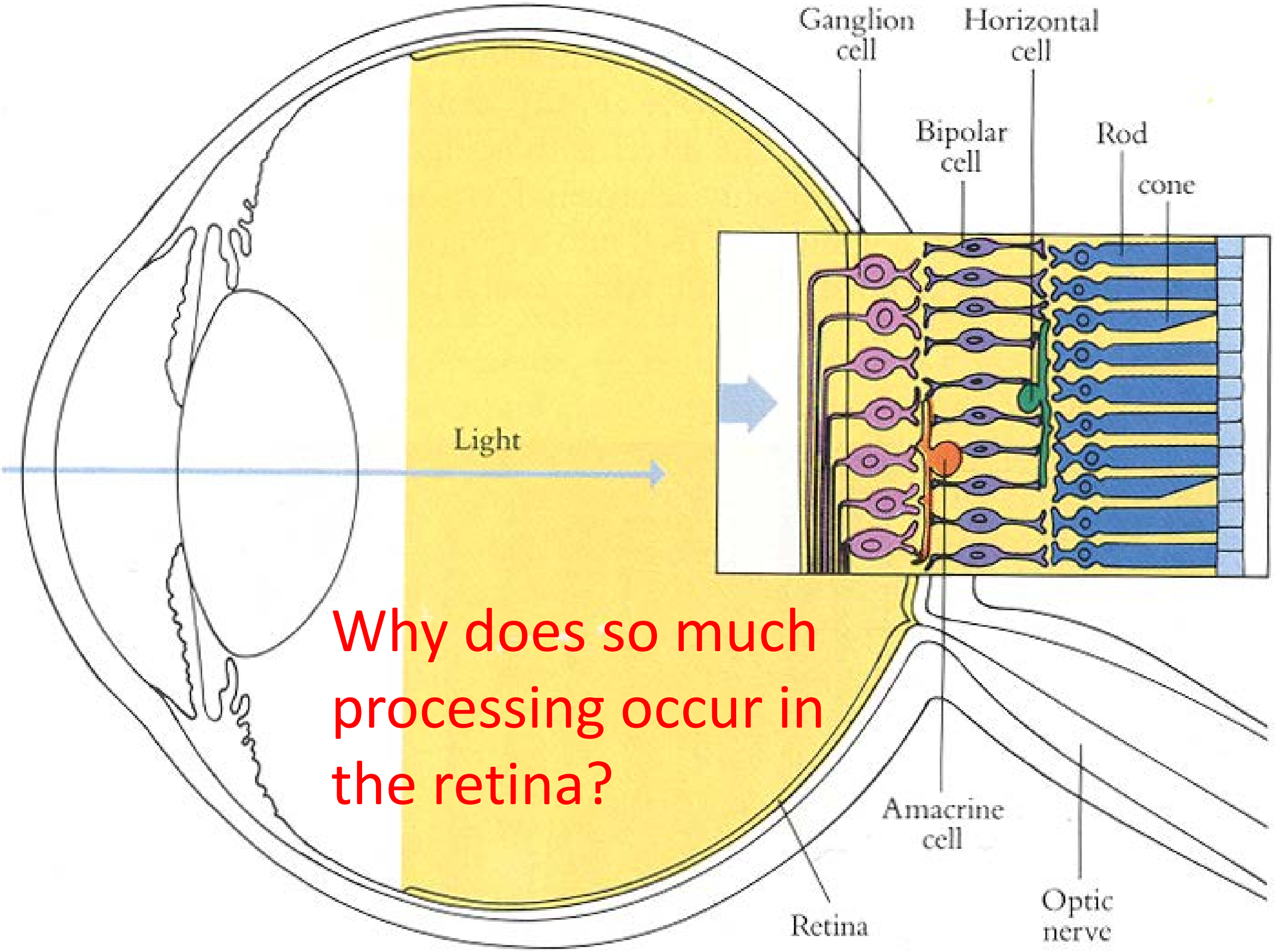
Red-green colour opponency

Four variants



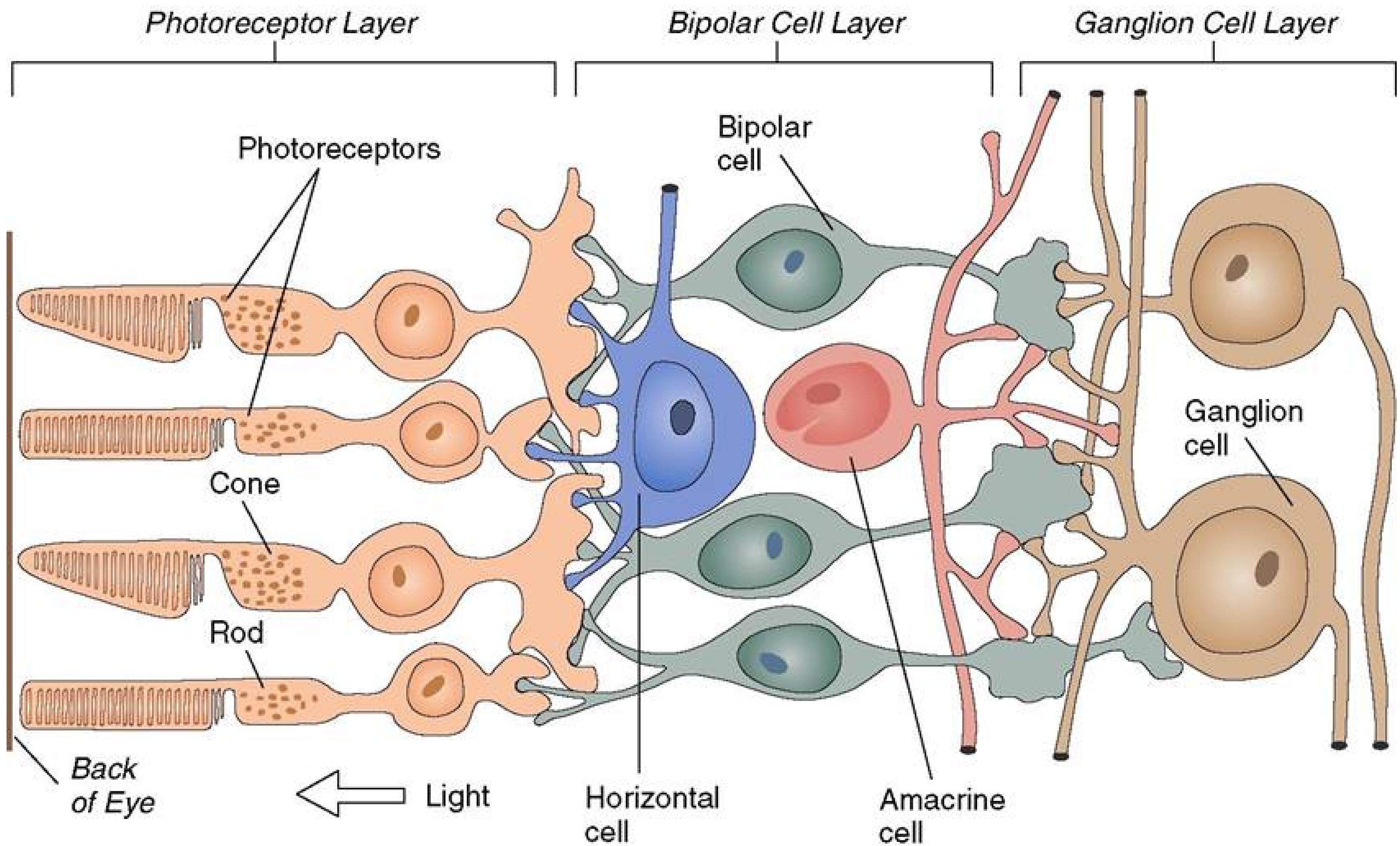
RETINAL PROCESSING

Signal processing in the retina



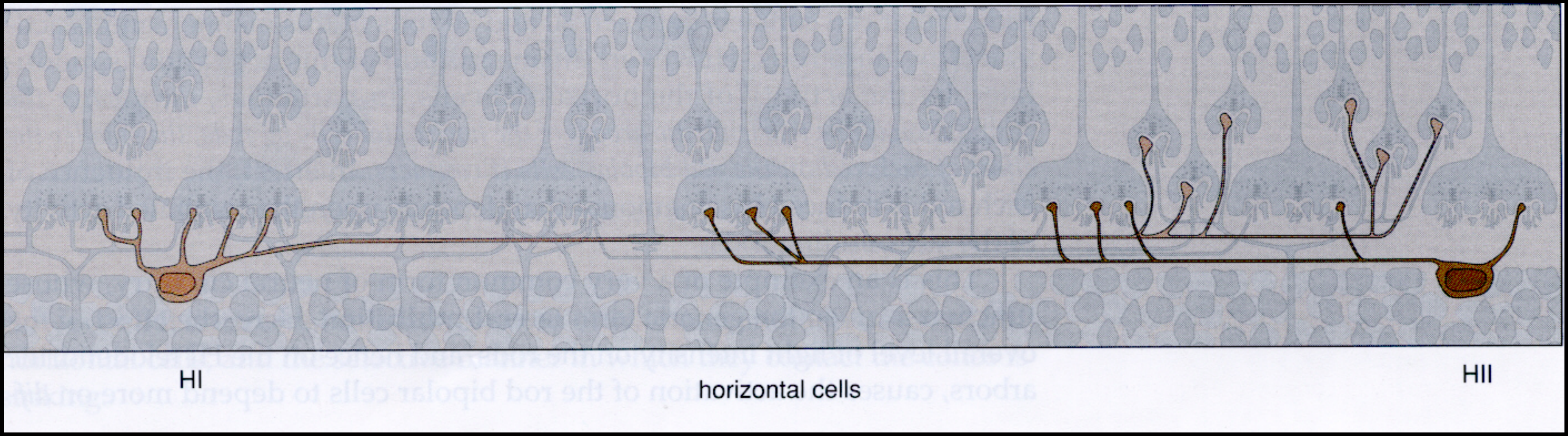
Why does so much processing occur in the retina?

Main cell types in retina



Horizontal cells

Lateral interactions

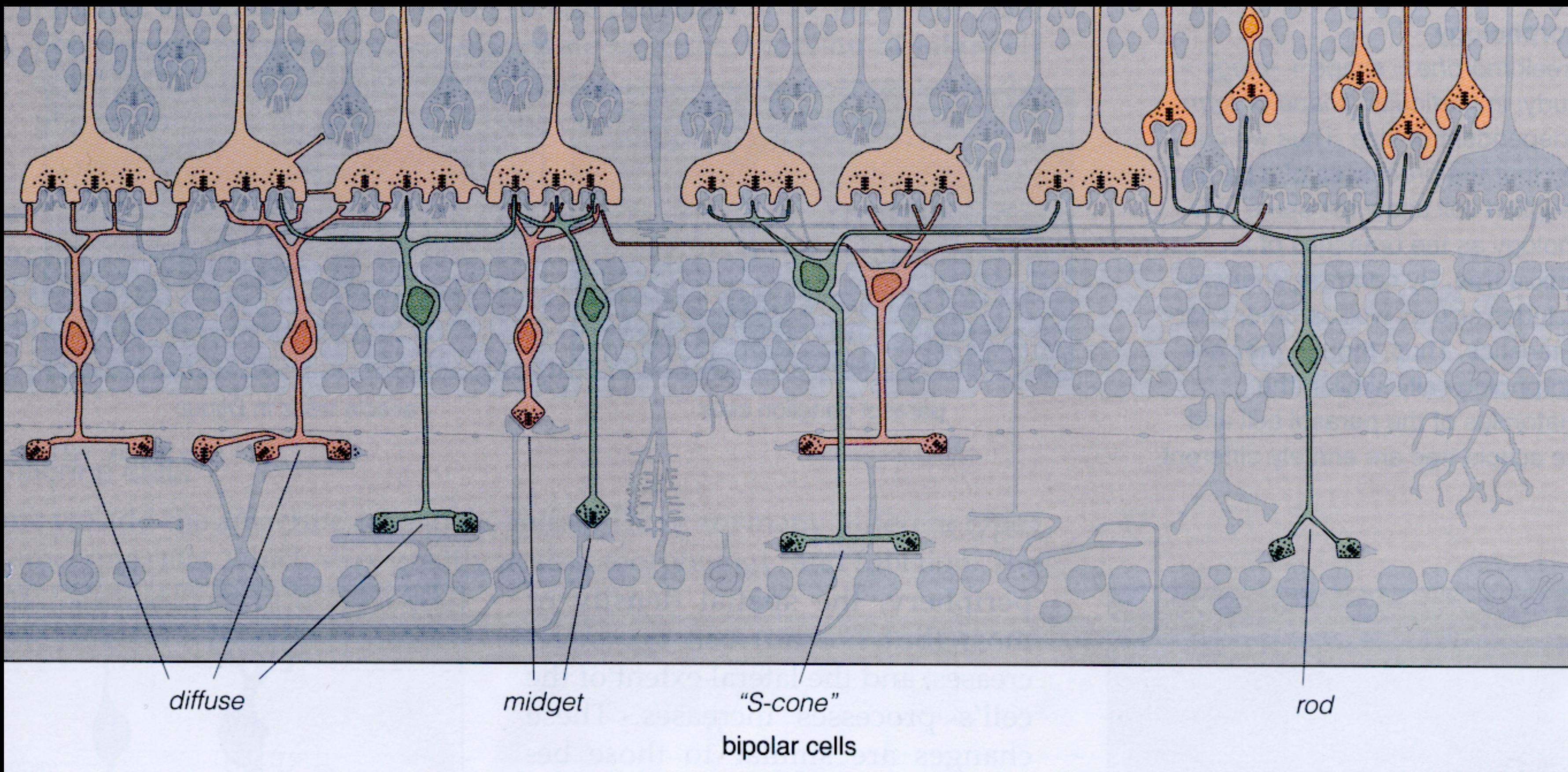


From Rodieck (1998)

What sort of processing can be achieved by lateral interactions?

Bipolar cells

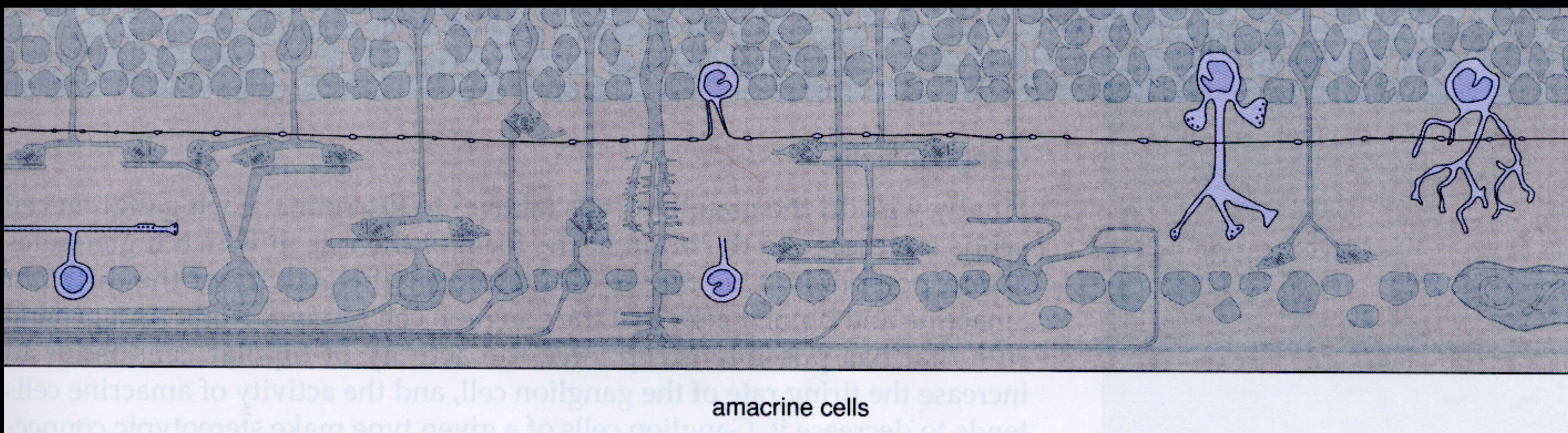
ON (greener) and
OFF (redder) varieties



Parallel processing?

From Rodieck (1998)

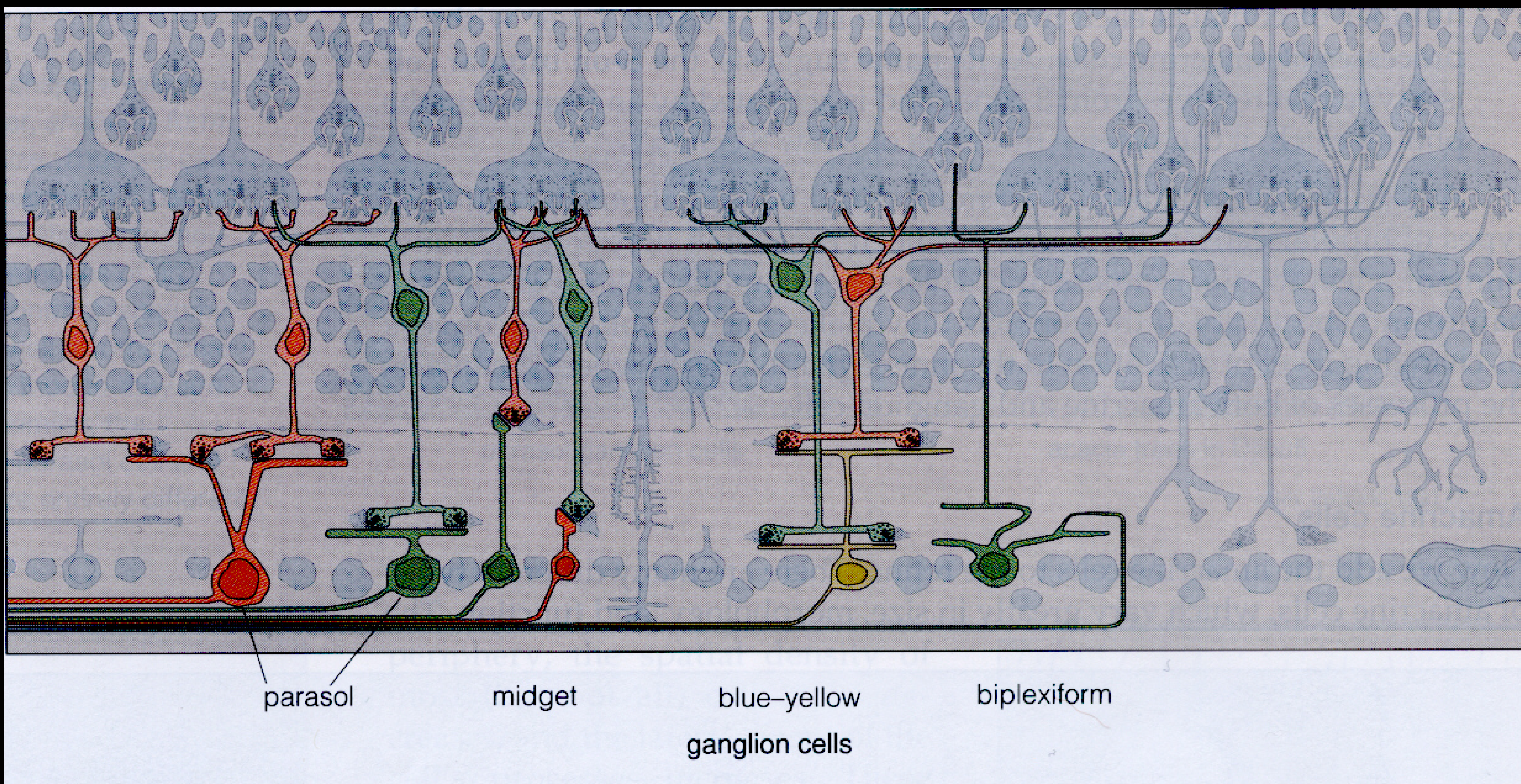
Amacrine cells



From Rodieck (1998)

Ganglion cells

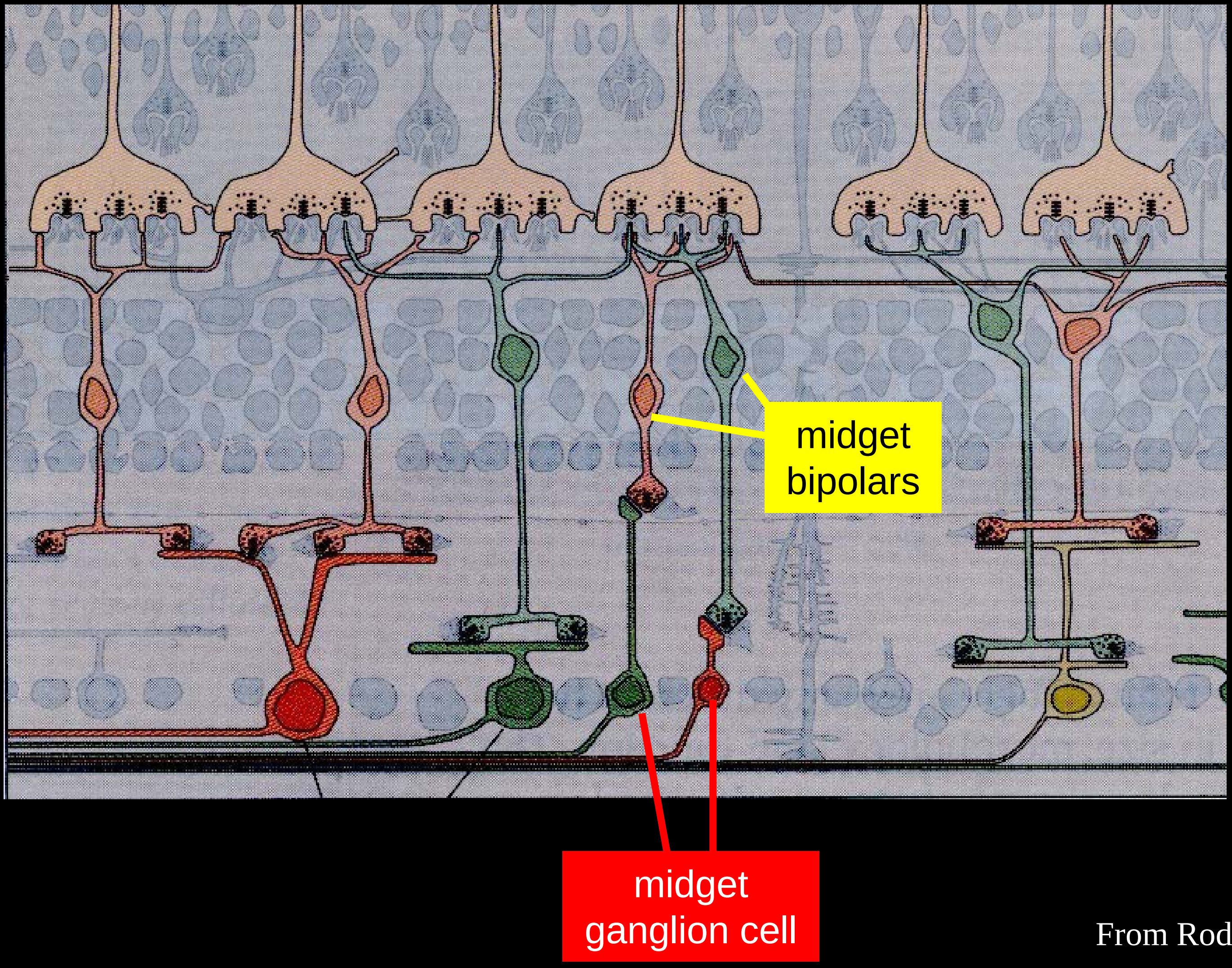
ON and OFF varieties



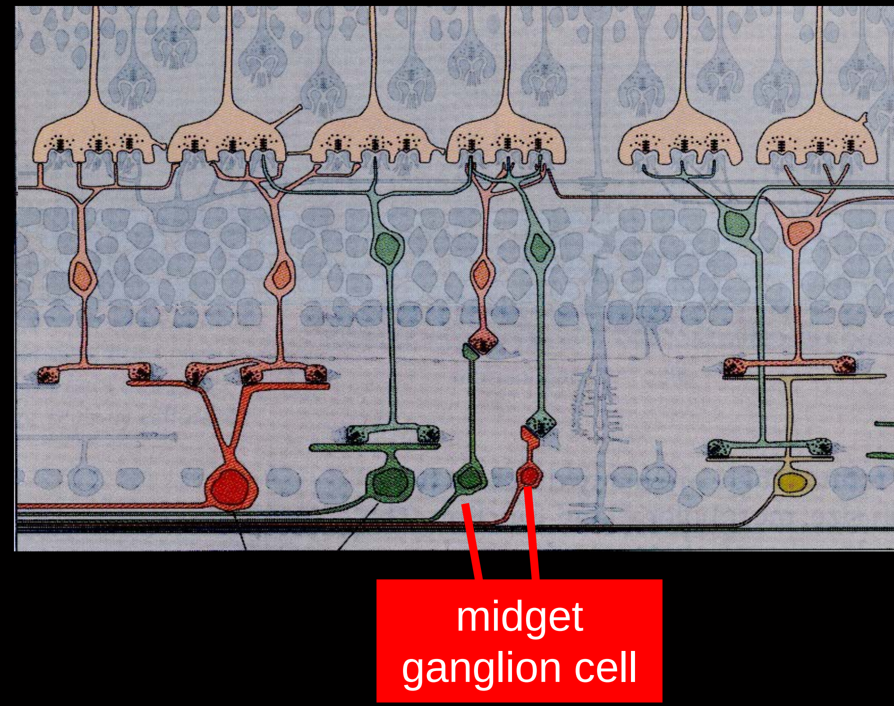
Parallel processing?

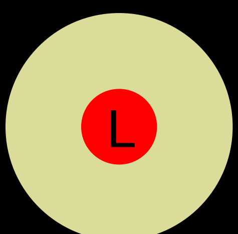
From Rodieck (1998)

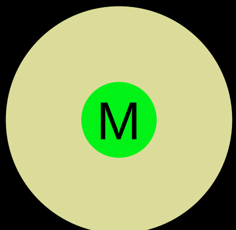
Parvocellular



From Rodieck (1998)



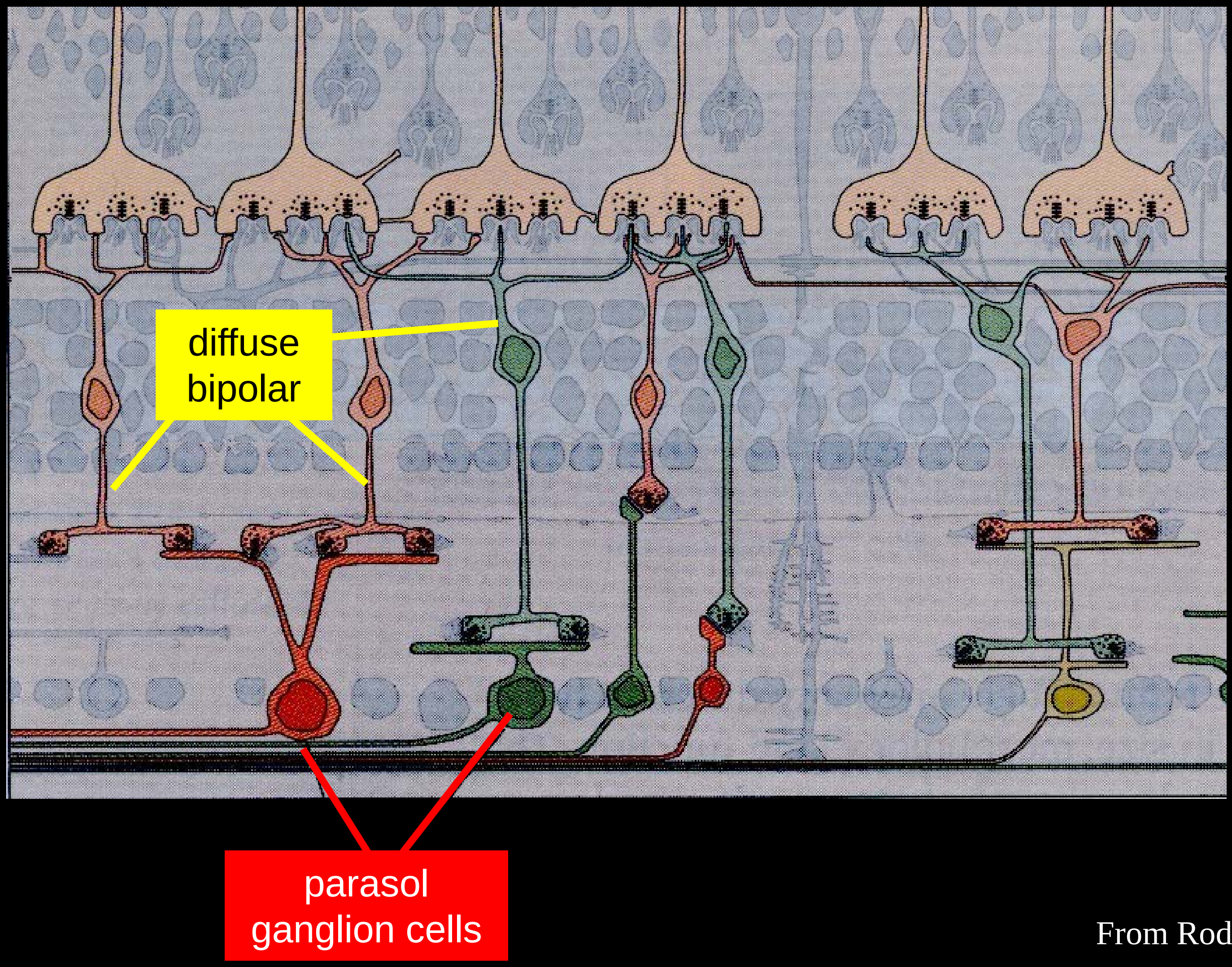




These cells are chromatically opponent simply by virtue of the fact that they have single cone inputs to the centre of their receptive fields!

Luminance pathways, which produce achromatic percepts, have been linked to the magnocellular stream.

Magnocellular



From Rodieck (1998)

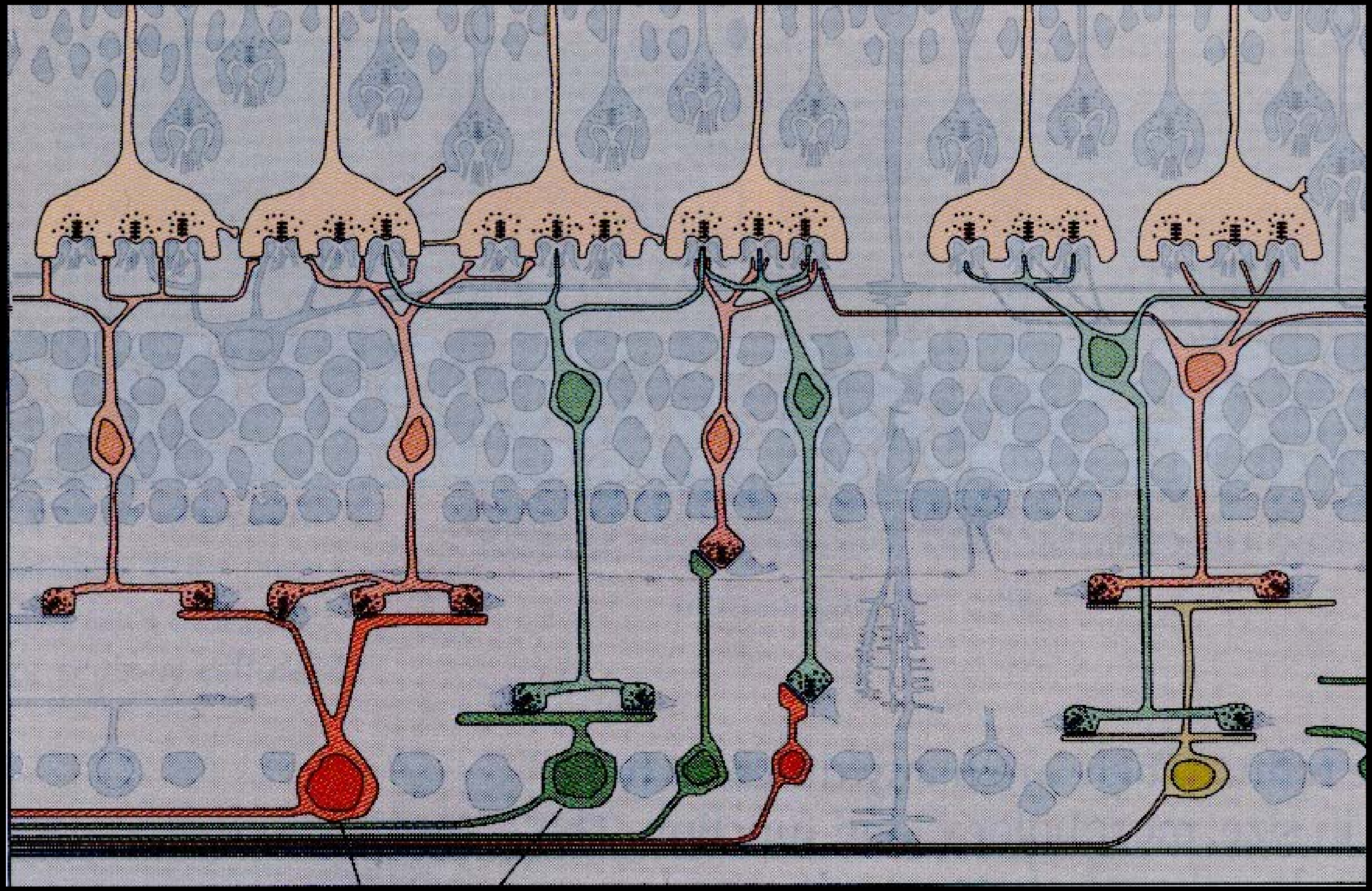
- Chromatic pathways, which produce chromatic percepts, have been linked to the parvocellular and koniocellular retinal streams.
- Luminance pathways, which produce achromatic percepts, have been linked to the magnocellular stream, but *also* depend on the parvocellular stream.

Parvocellular pathway:

- High spatial frequencies (spatial detail)
- Low temporal frequencies
- Chromatic
- Lower contrast sensitivity

Magnocellular pathway:

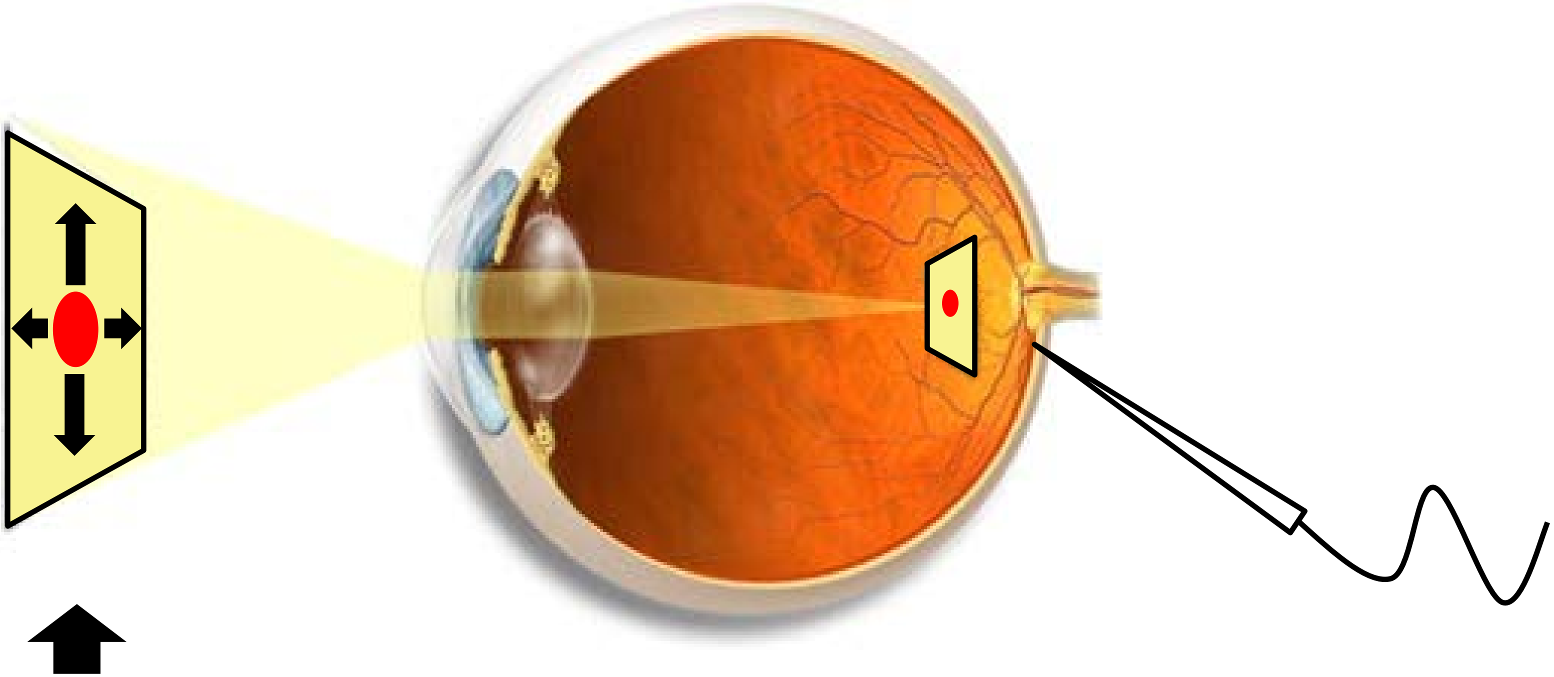
- High temporal frequencies (motion/flicker)
- Low spatial frequencies
- Achromatic
- Higher contrast sensitivity



From Rodieck (1998)

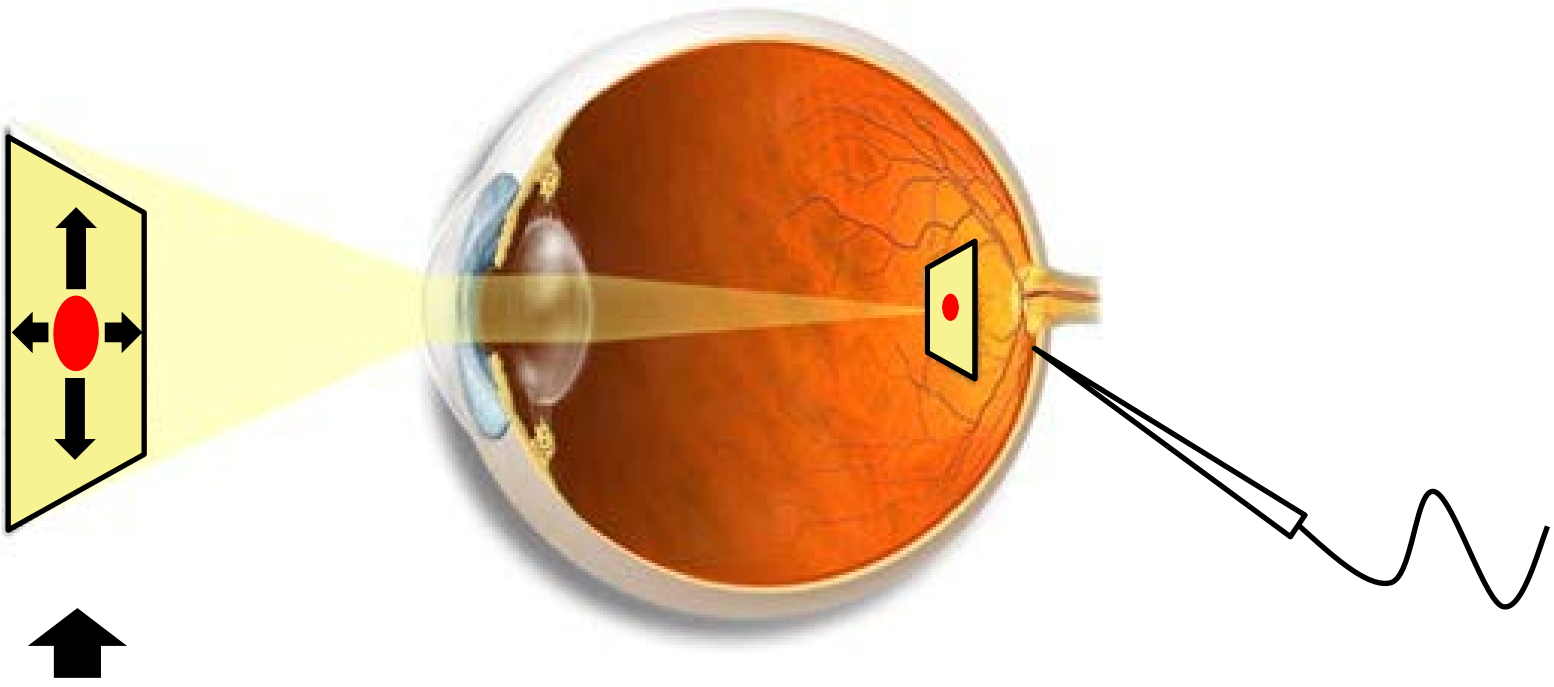
Physiological recordings

We can investigate what a cell encodes by recording its response to visual stimulation and so “map” its receptive field



Find the area in visual space to which the cell responds.

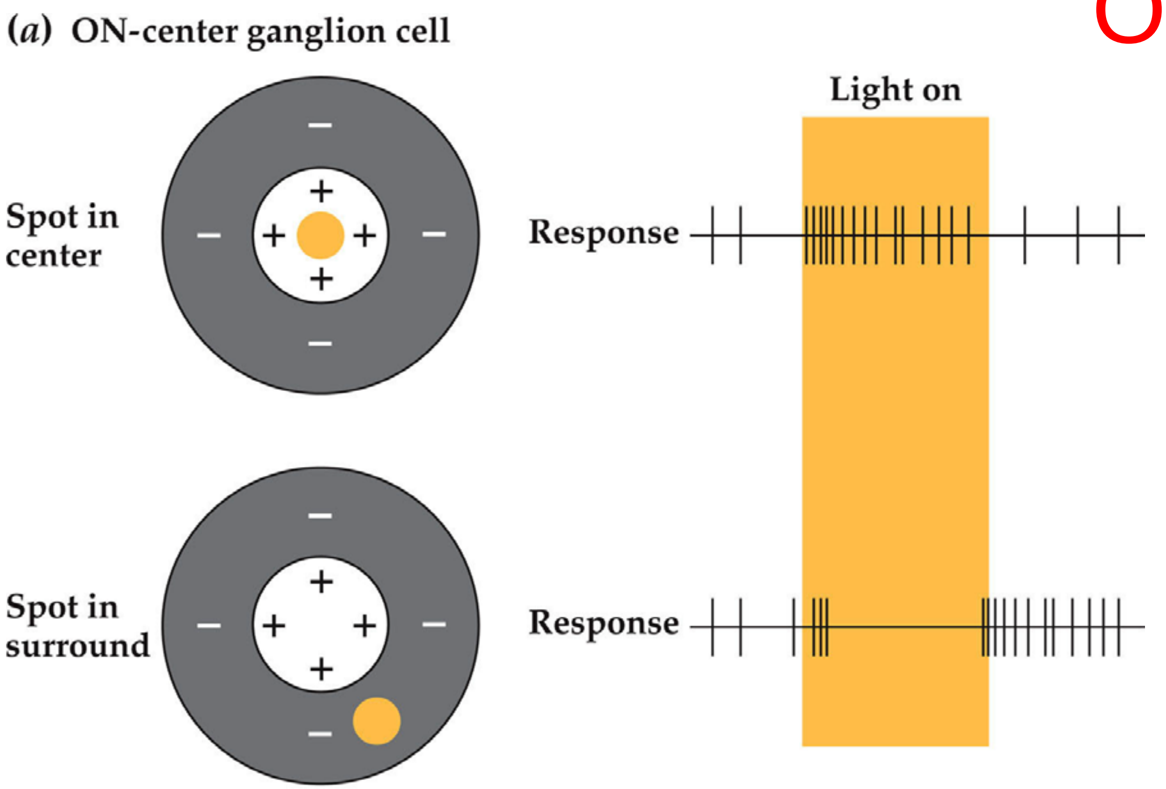
We can investigate what a cell encodes by recording its response to visual stimulation and so “map” its receptive field



And find out which types of stimuli optimally stimulate the cell.

Neural codes and signal processing (centre-surround)

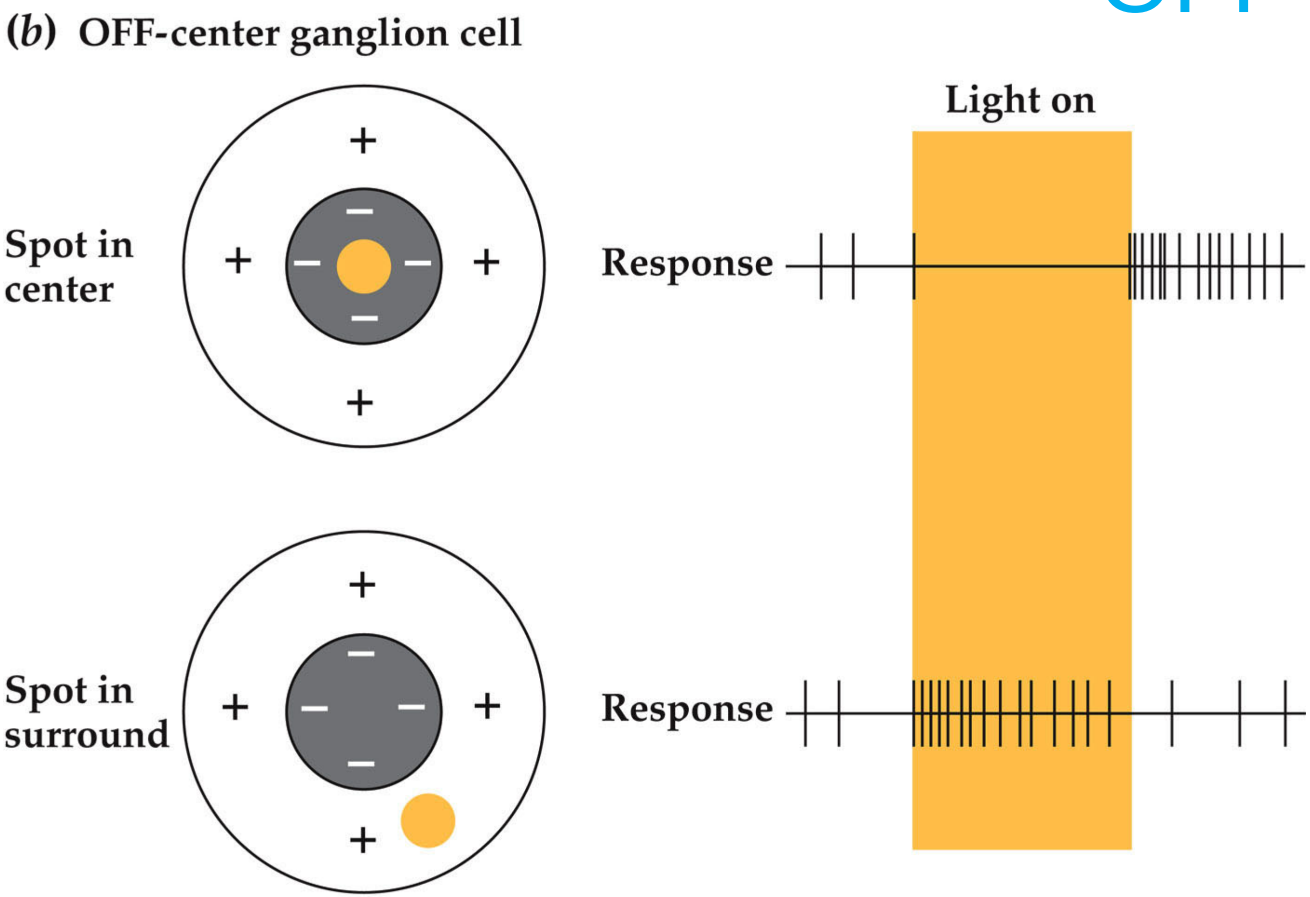
ON cell



SENSATION & PERCEPTION 3e, Figure 2.14 (Part 1)

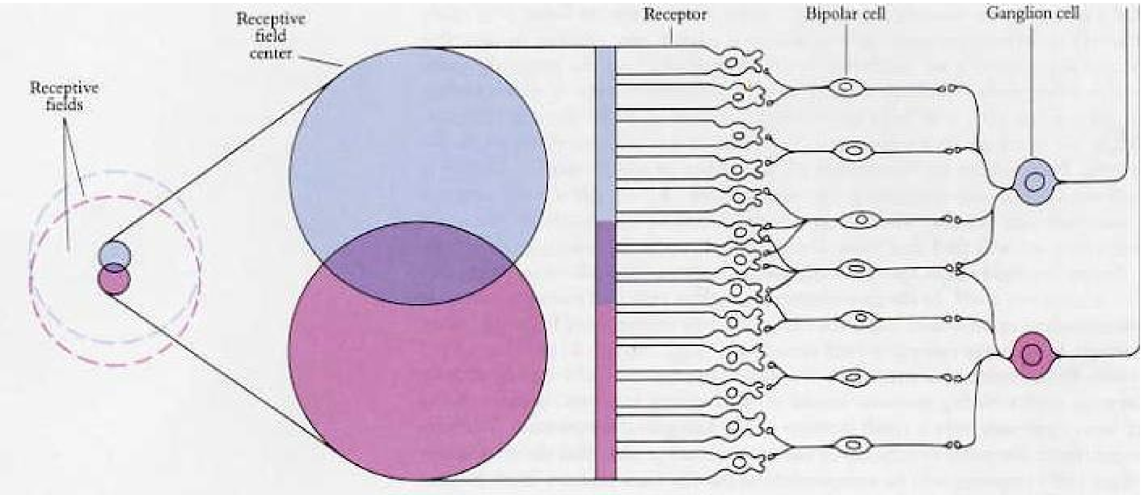
Neural codes and signal processing (centre-surround)

OFF cell



SENSATION & PERCEPTION 3e, Figure 2.14 (Part 2)

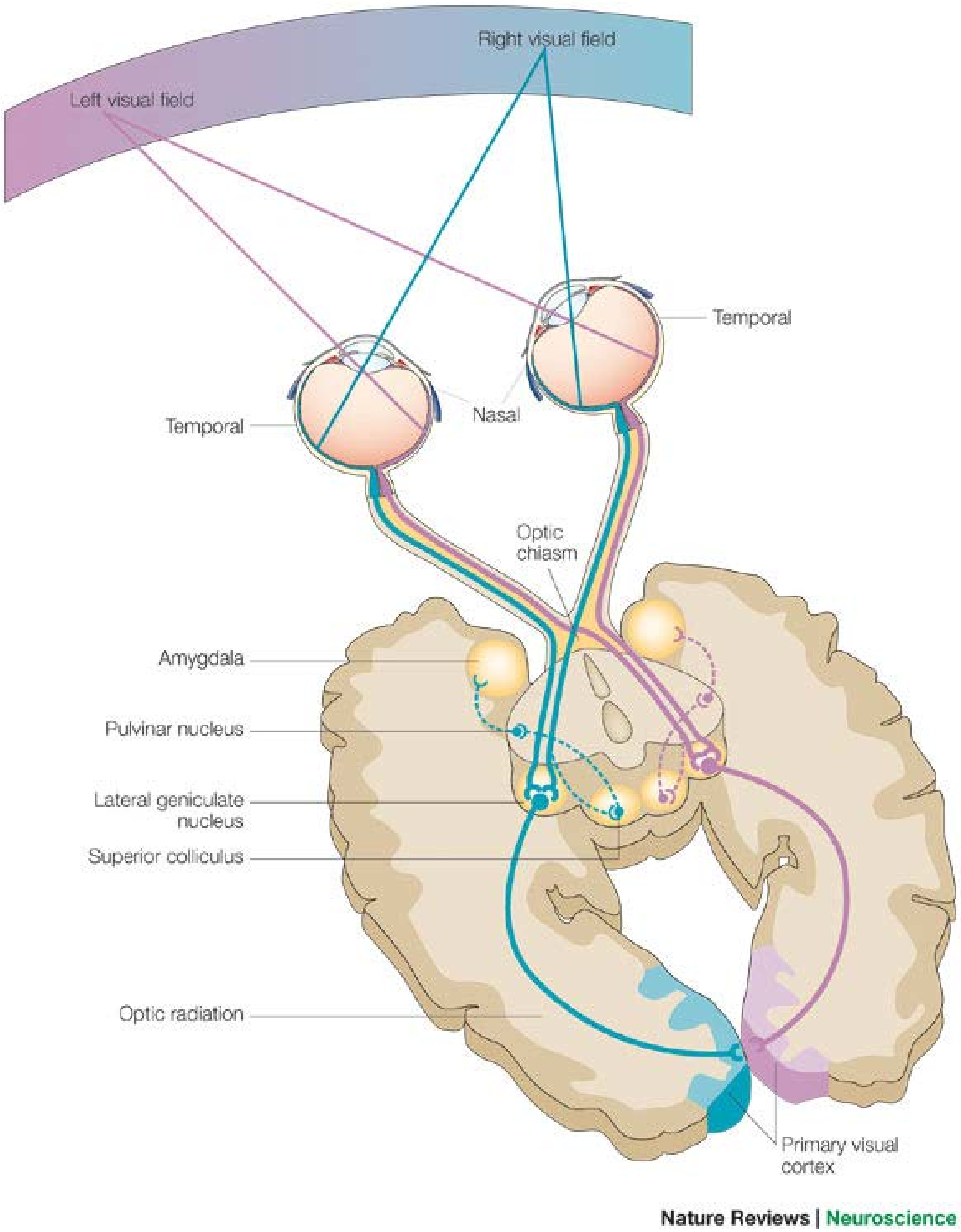
Retinotopic maps



David Hubel

From retina to brain…

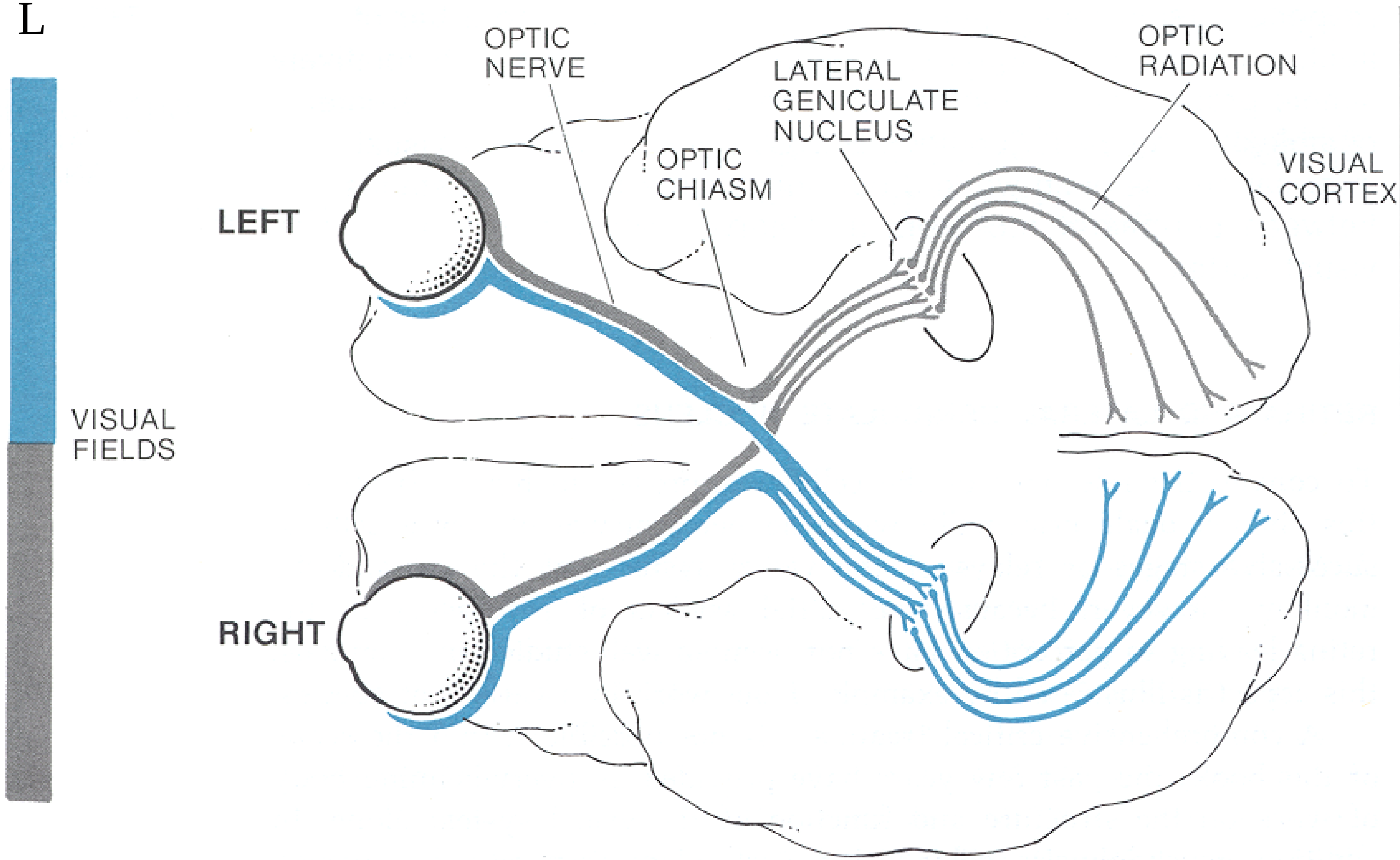
Geniculo-striate pathway



Hannula, Simons & Cohen, 2005

Visual pathways

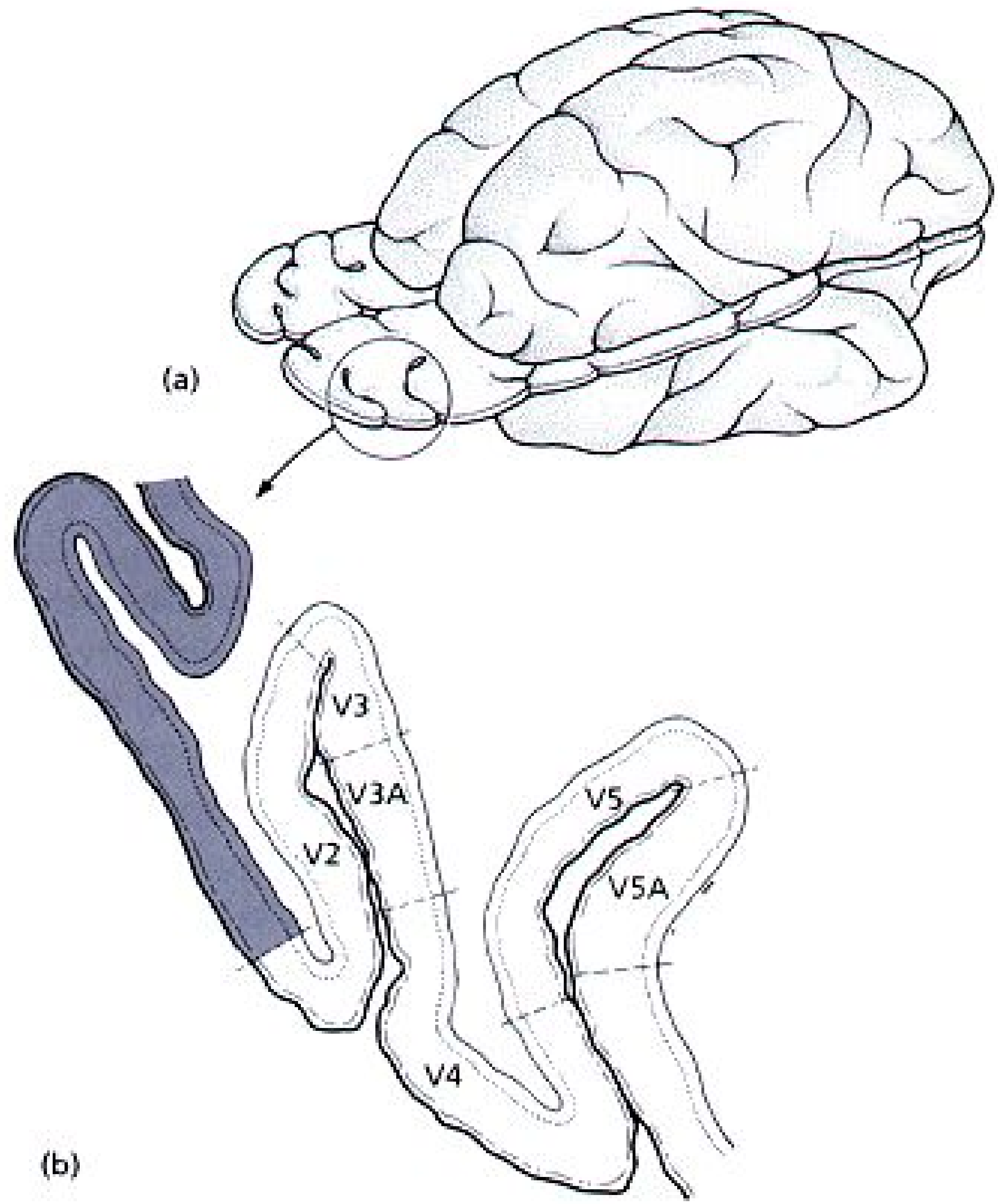
L



R

From below

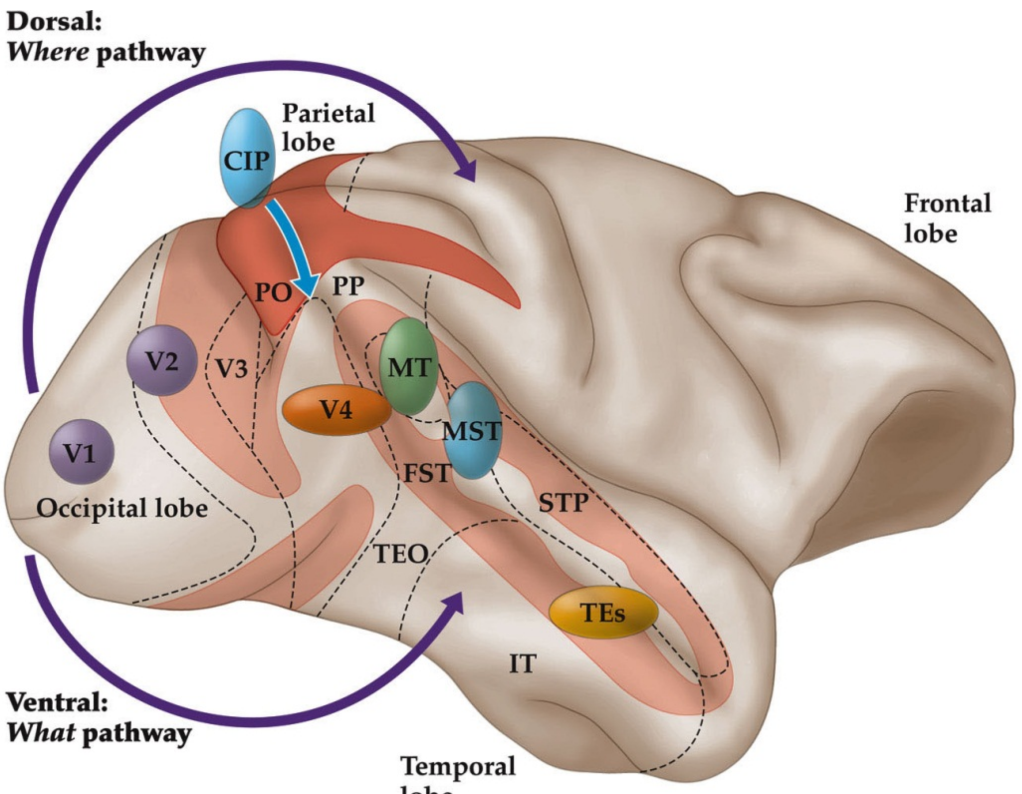
V1-V5



Streams of processing…

Dorsal stream – 'Where' pathway specialized for spatial location.

Ventral stream – 'What' pathway specialized for object identification and recognition.



SENSATION & PERCEPTION 3e, Figure 4.2