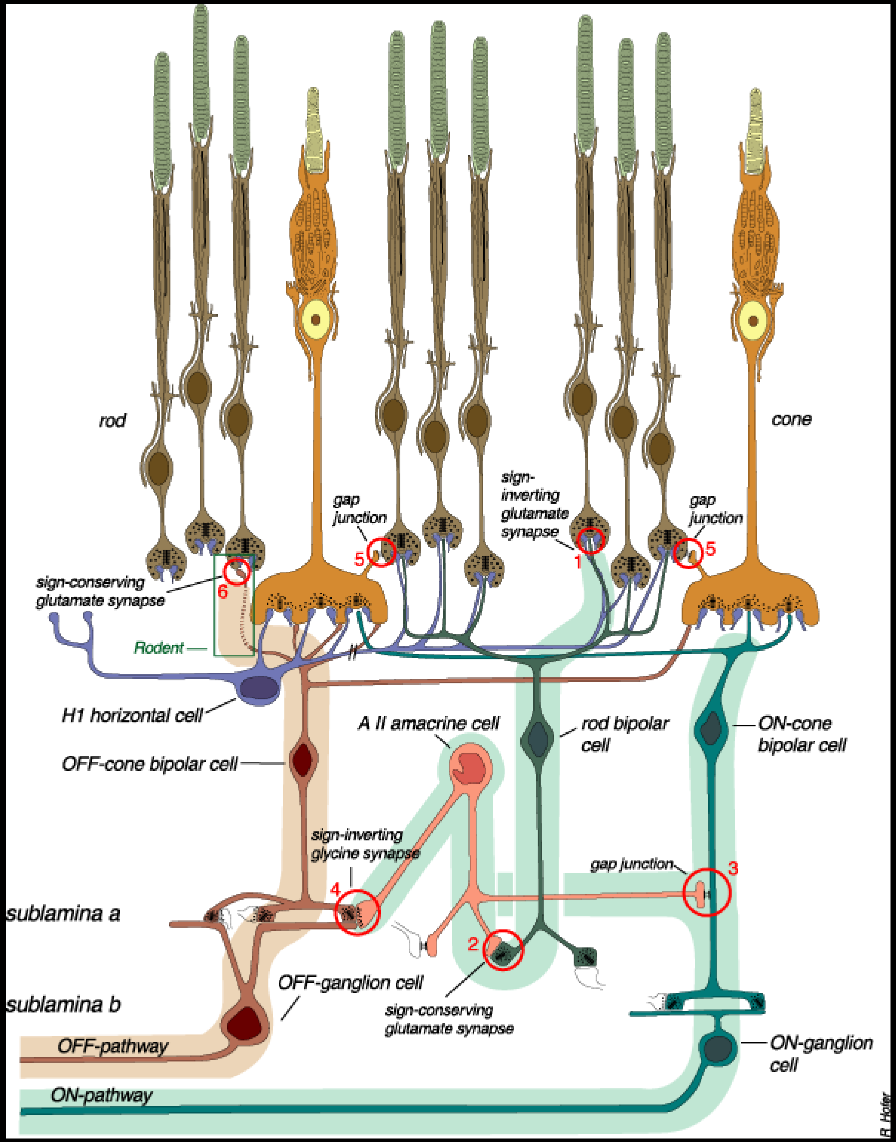
Achromatic and chromatic vision, rods and cones.

Andrew Stockman

NEUR 0017
Visual Neuroscience

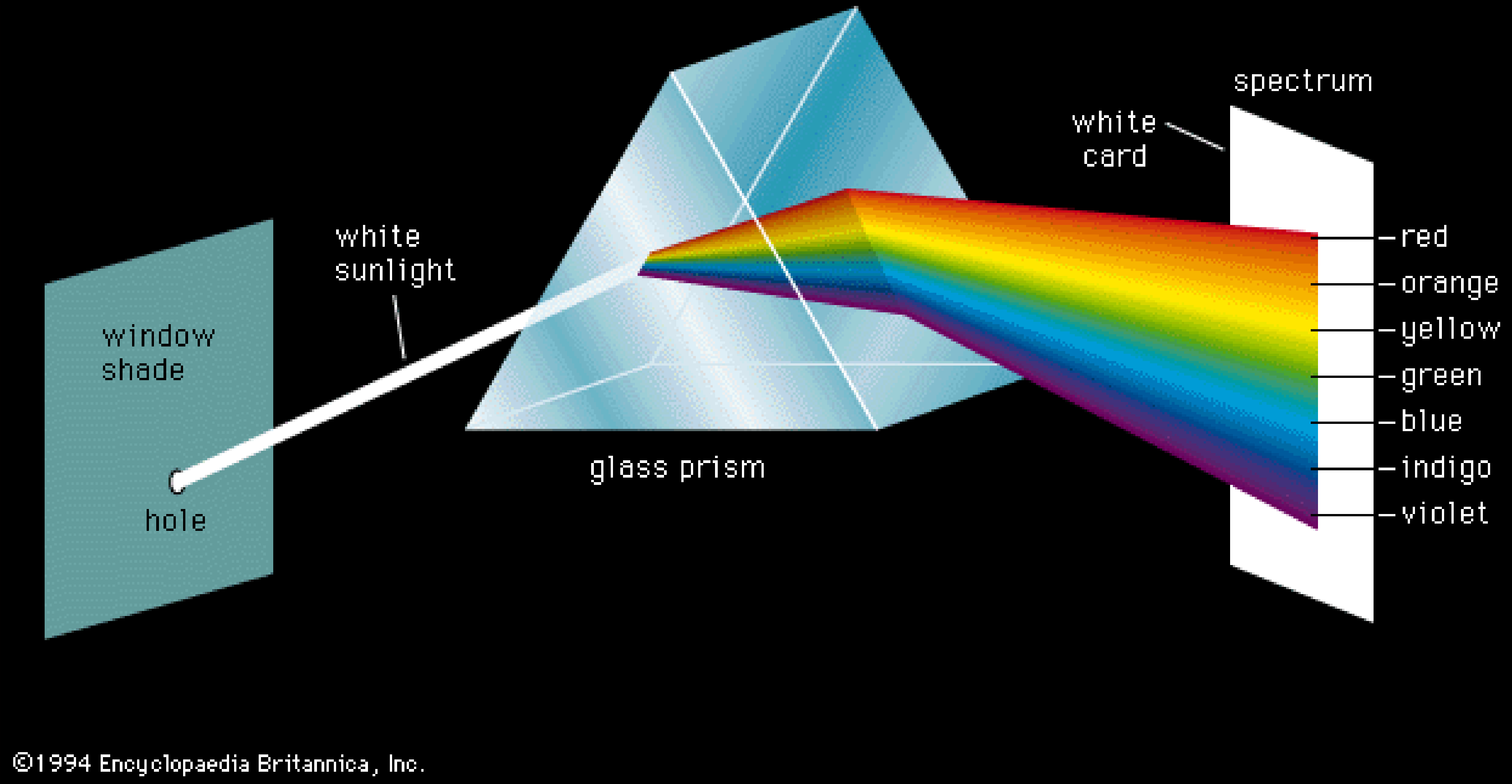


Outline

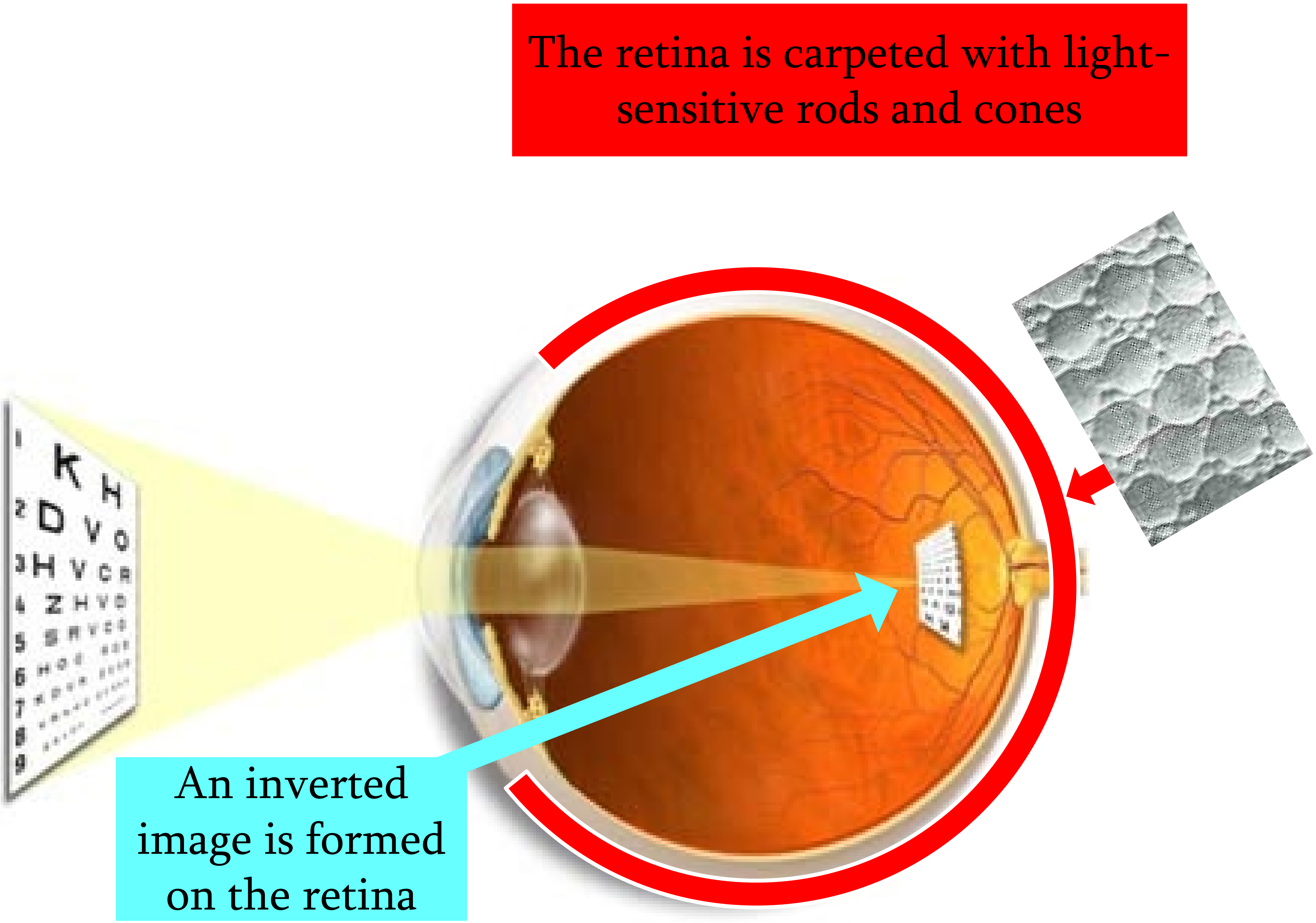
- Introduction
- Rod and cone vision
- Rod vision is achromatic
- How do we see colour with cone vision?
- Vision and visual pathways
- Achromatic and chromatic cone vision (colour and luminance)

Light

400 - 700 nm is important for vision



ROD AND CONE VISION


The retina is carpeted with light-sensitive rods and cones
An inverted image is formed on the retina

Rods and cones

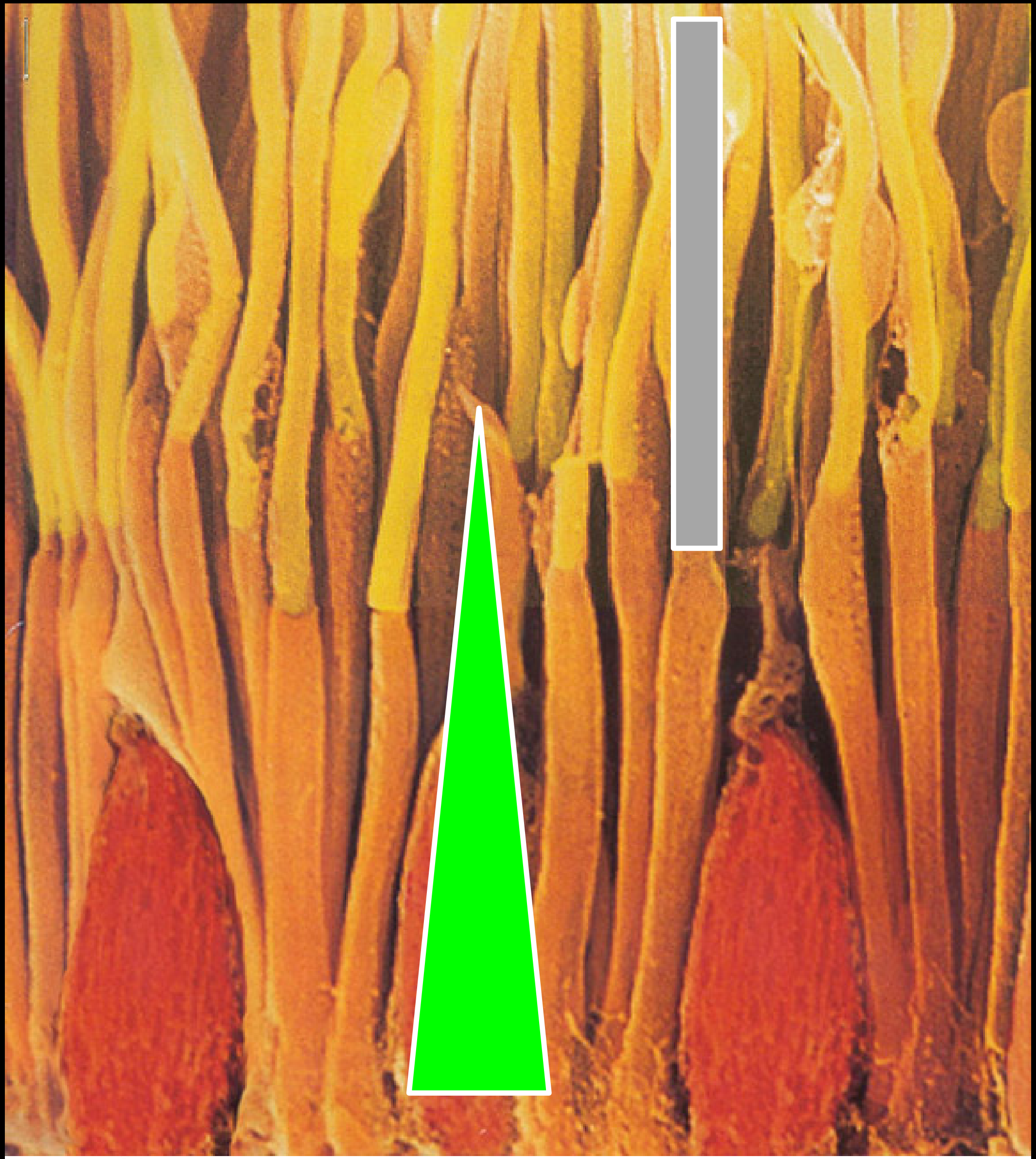
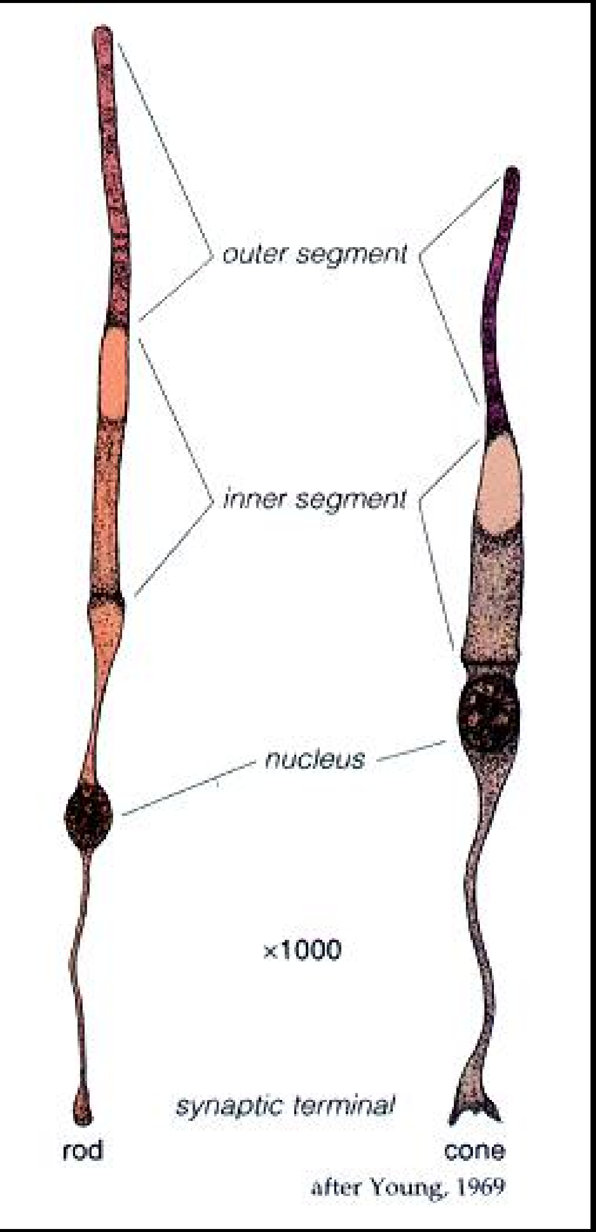


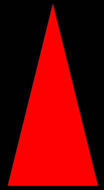
Fig1b. Scanning electron micrograph of the rods and cones of the primate retina. Image adapted from one by Ralph C. Eagle/Photo Researchers, Inc.

Webvision

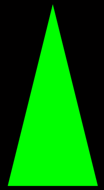


Human photoreceptors

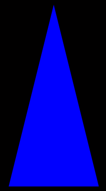
- <u>Cones</u>
  - Daytime, achromatic *and* chromatic vision
  - 3 types



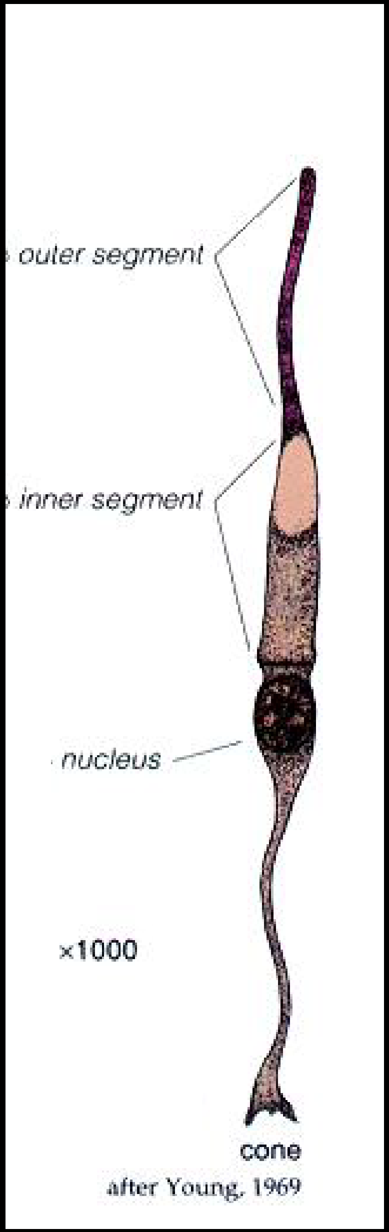
Long-wavelength-sensitive (L) or "red" cone



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

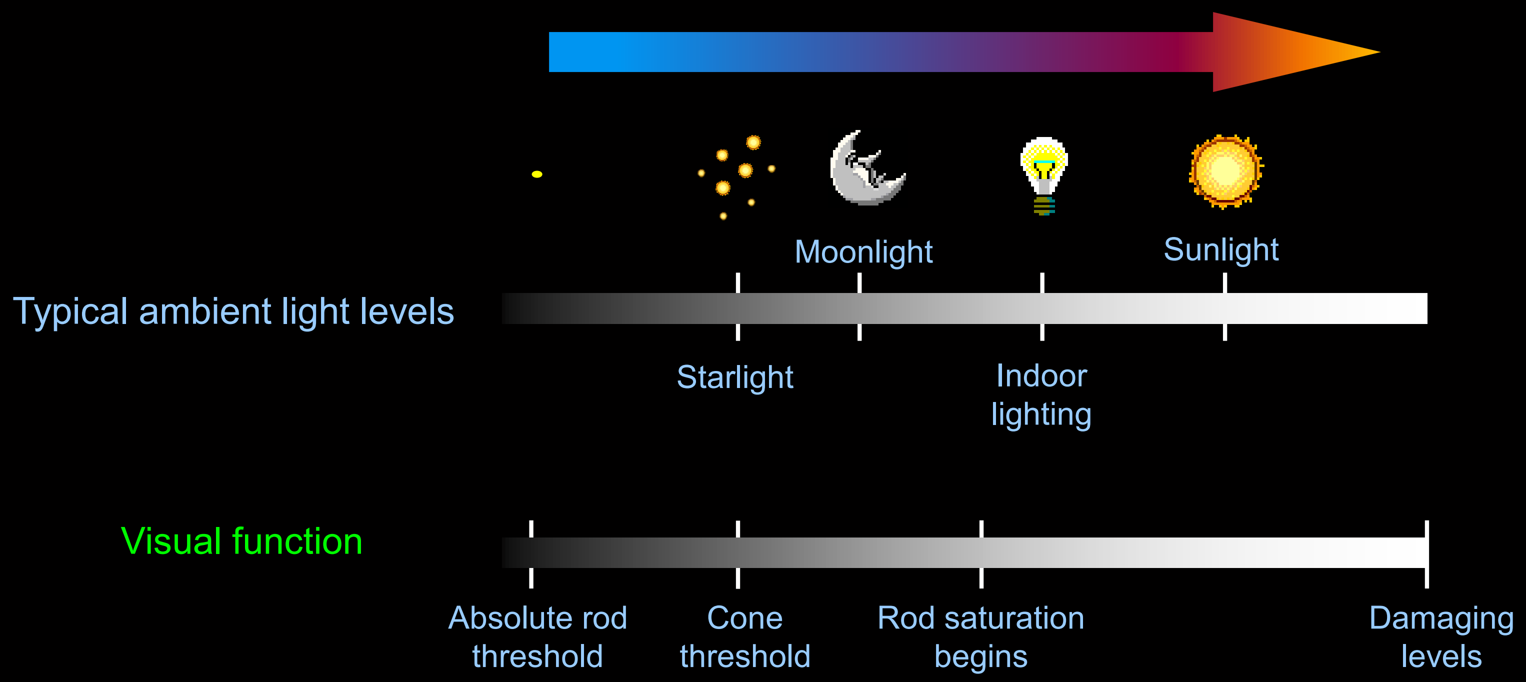
Long-wavelength-sensitive (L) or "red" cone

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

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

Why do we have rods and cones?

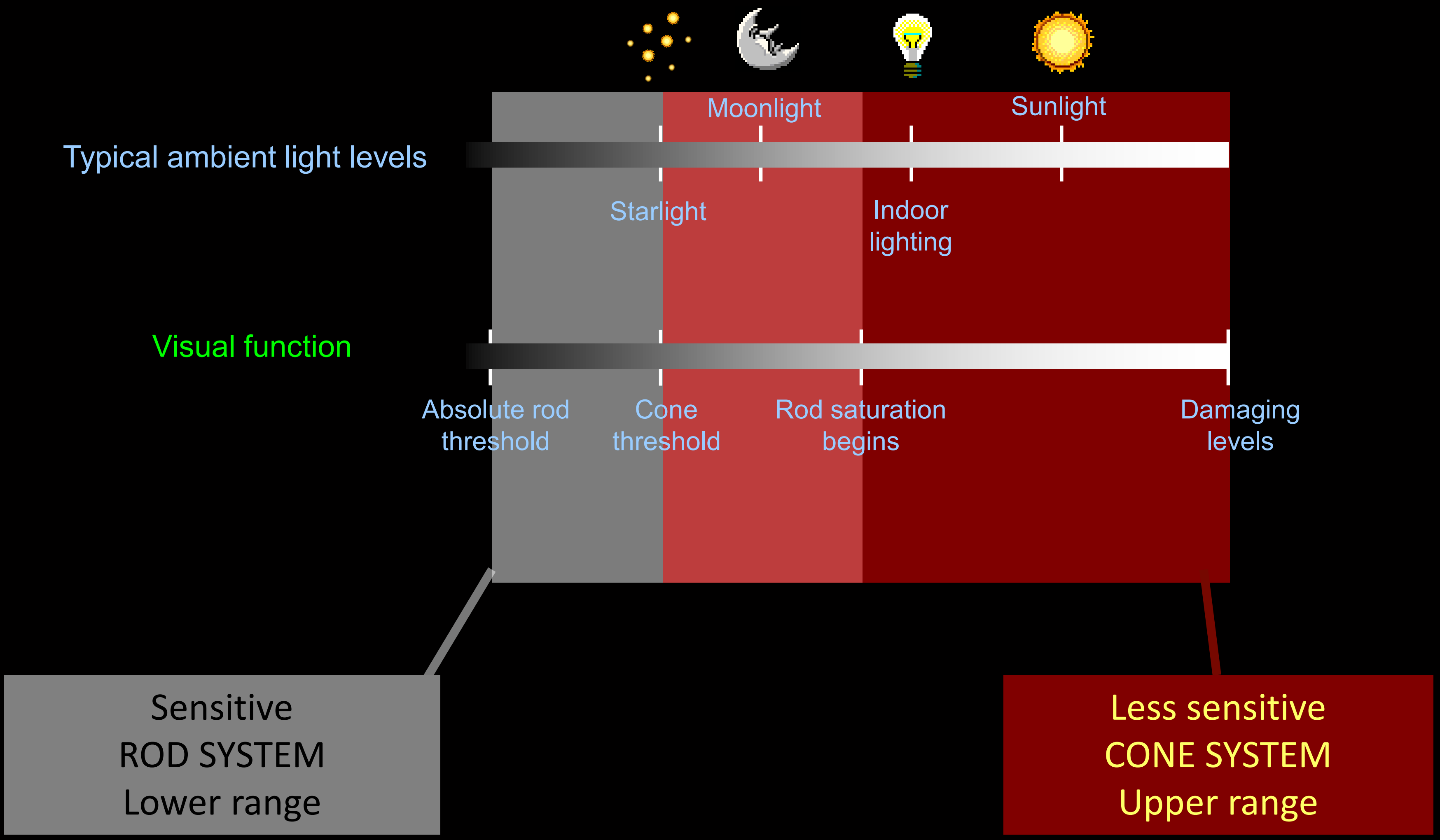
Our vision has to operate over an enormous range of 10^{12} (1,000,000,000,000) levels



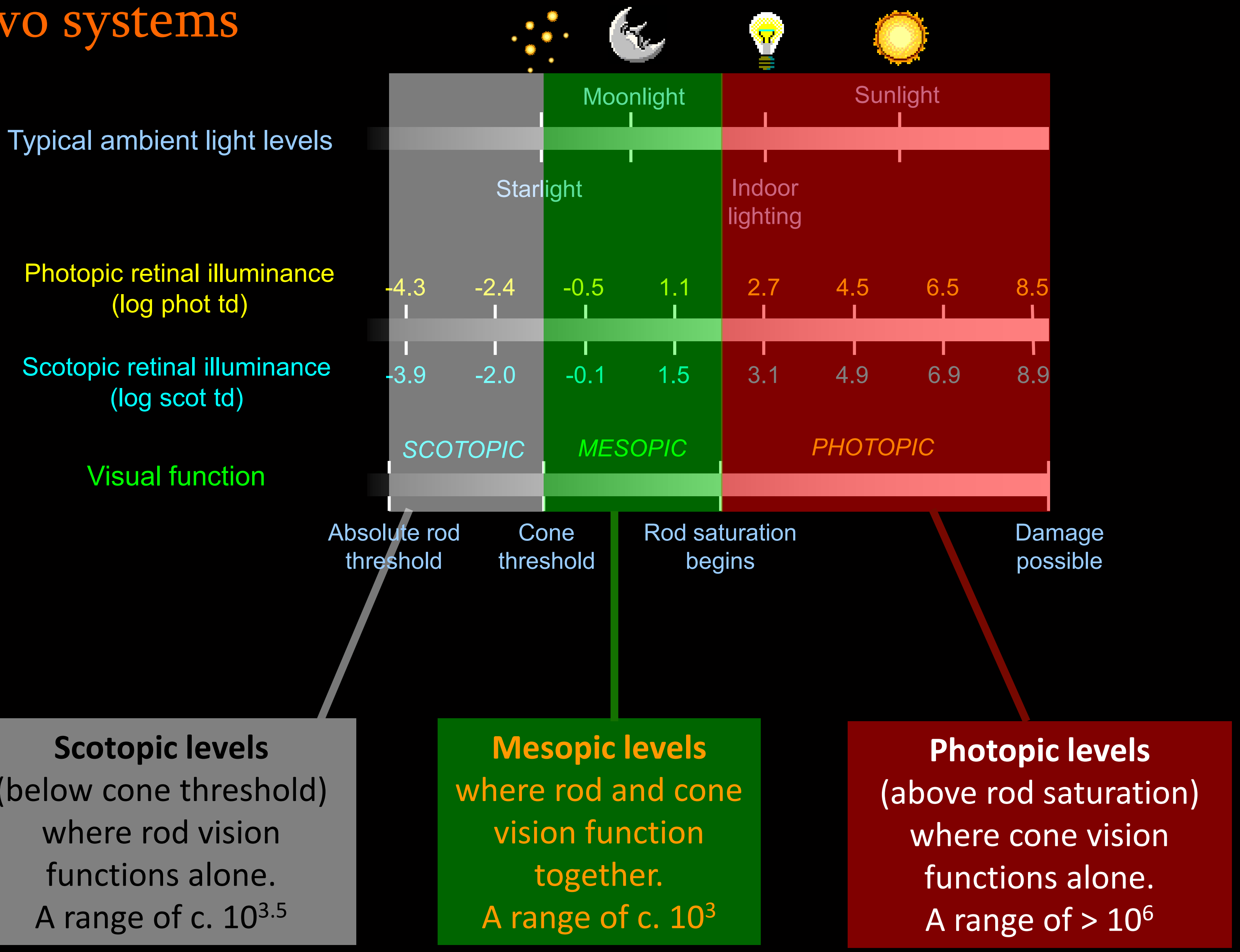
To cover that range we have two different types of photoreceptor...

Rods that are optimized for low light levels

Cones that are optimized for higher light levels



Two systems



Moonlight
Sunlight
Typical ambient light levels
Starlight
Indoor lighting
Photopic retinal illuminance (log phot td)
-4.3 -2.4 -0.5 1.1 2.7 4.5 6.5 8.5
Scotopic retinal illuminance (log scot td)
-3.9 -2.0 -0.1 1.5 3.1 4.9 6.9 8.9
SCOTOPIC
MESOPIC
PHOTOPIC
Visual function
Absolute rod threshold
Cone threshold
Rod saturation begins
Damage possible
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

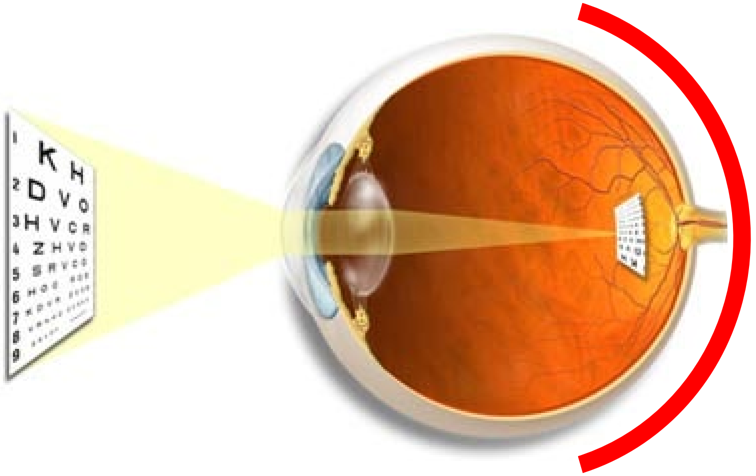
- Achromatic and chromatic
- Lower sensitivity
- Detail and good colour

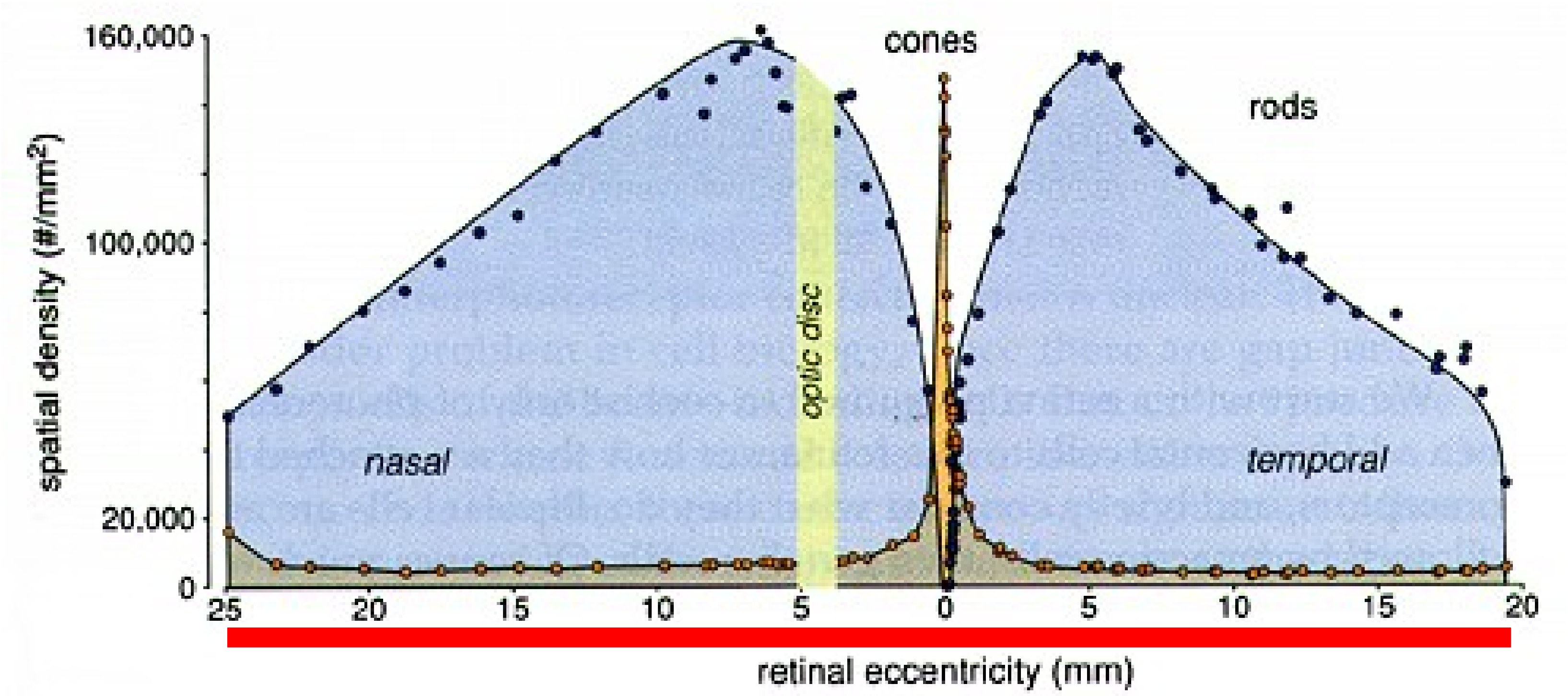
Facts and figures

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

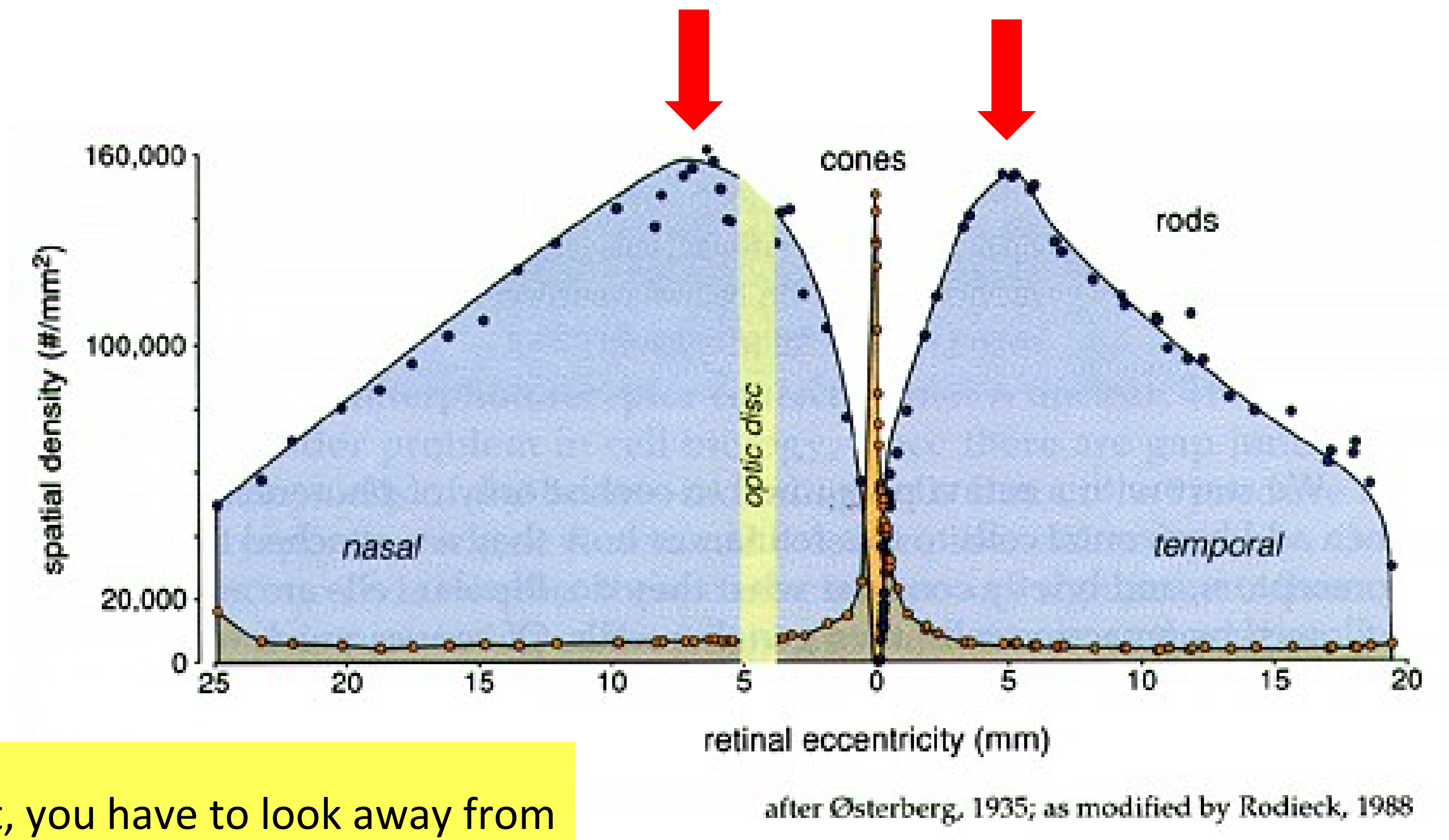




after Østerberg, 1935; as modified by Rodieck, 1988

0.3 mm of eccentricity is
about 1 deg of visual angle

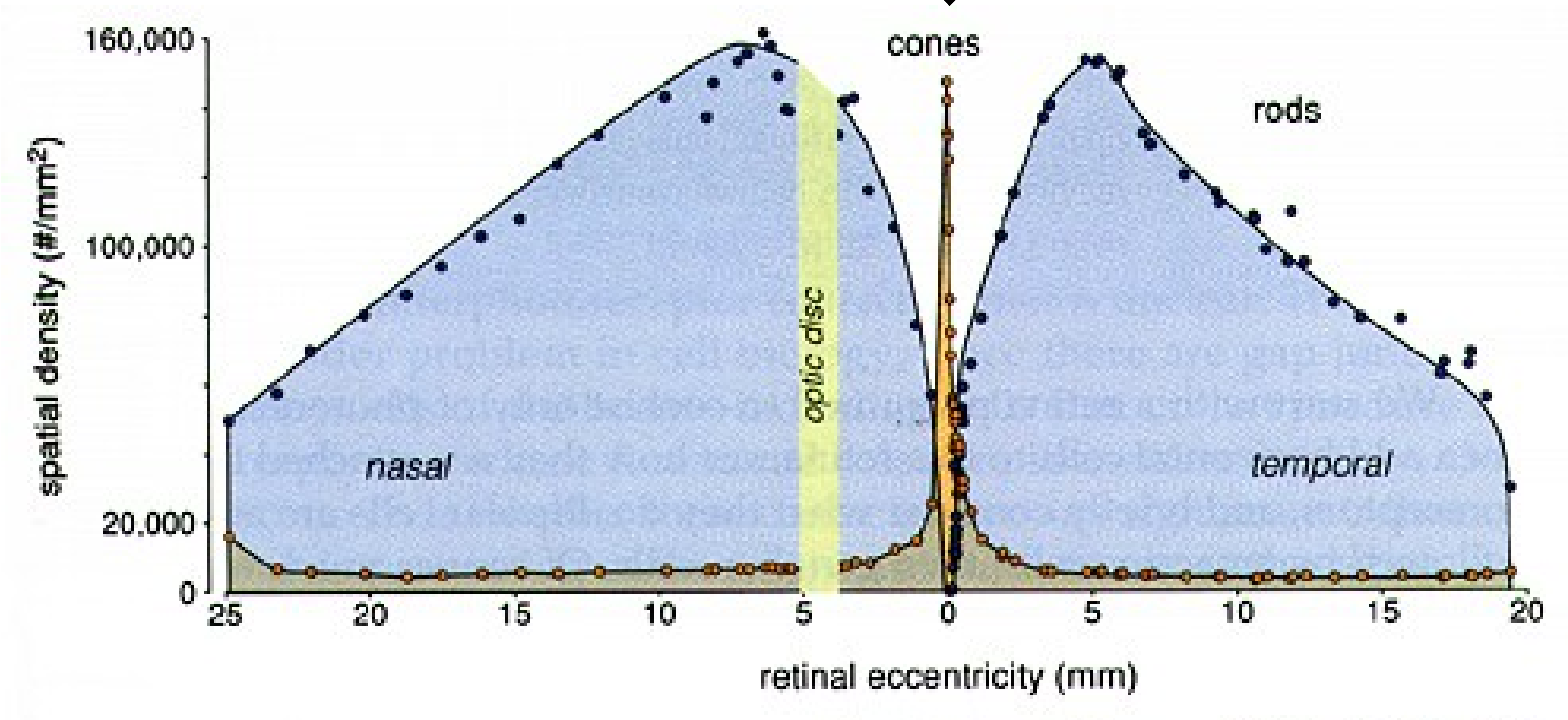
Rod density peaks at about
20 deg eccentricity



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

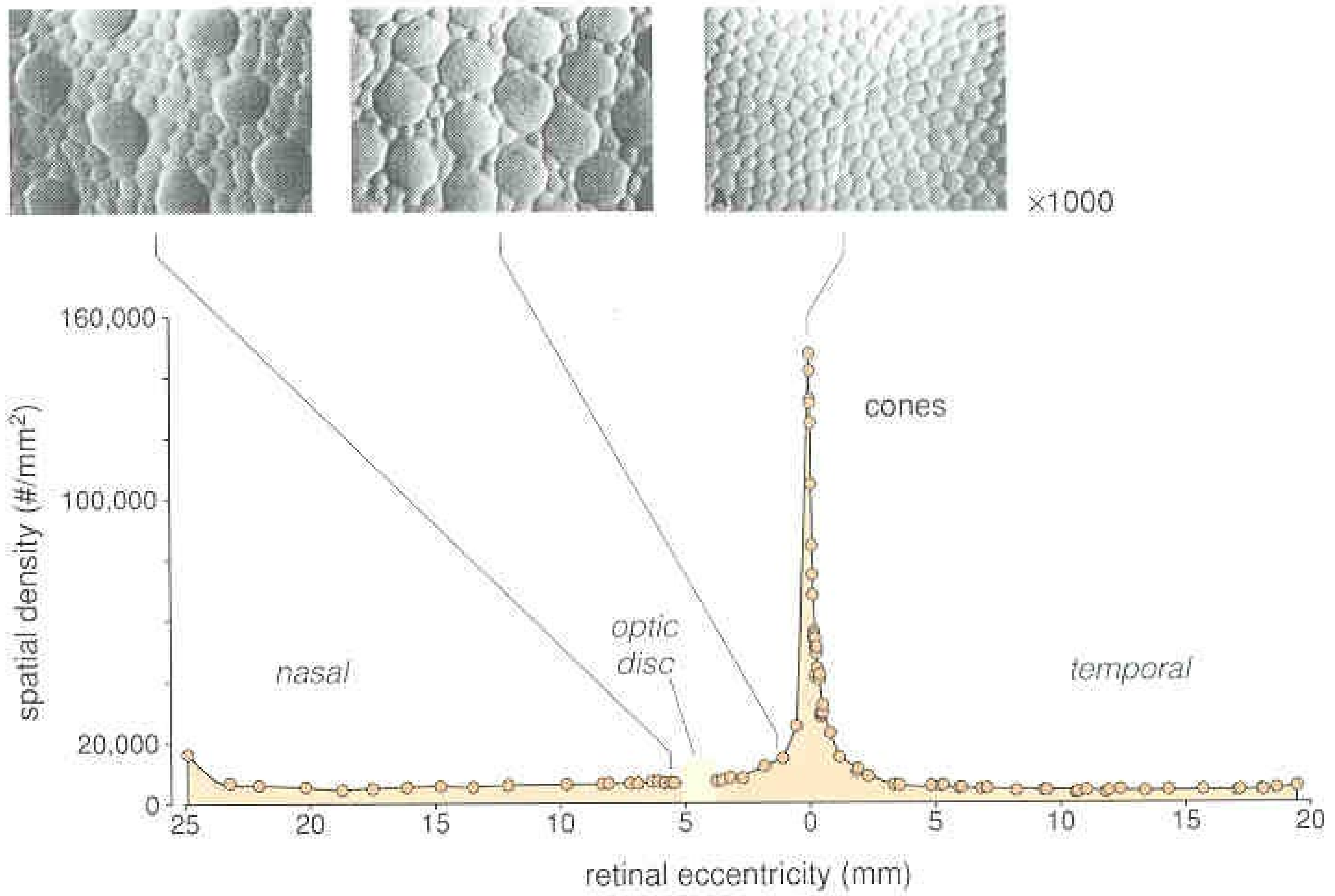
During the day, you have to look at things directly to see them in detail

Cones peak at the centre of vision at 0 deg



after Østerberg, 1935; as modified by Rodieck, 1988

Cone distribution and photoreceptor mosaics

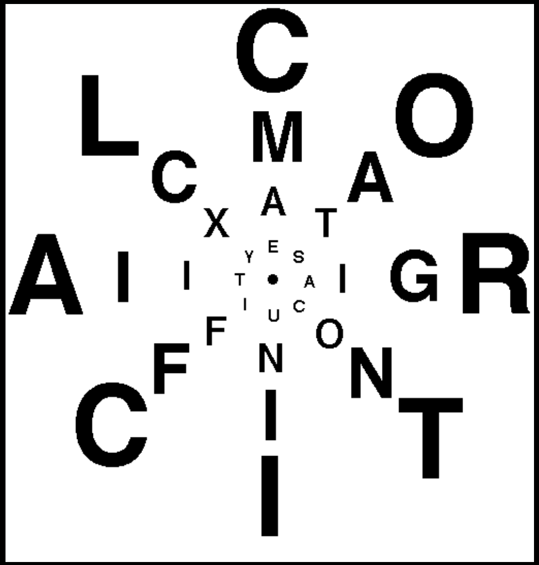


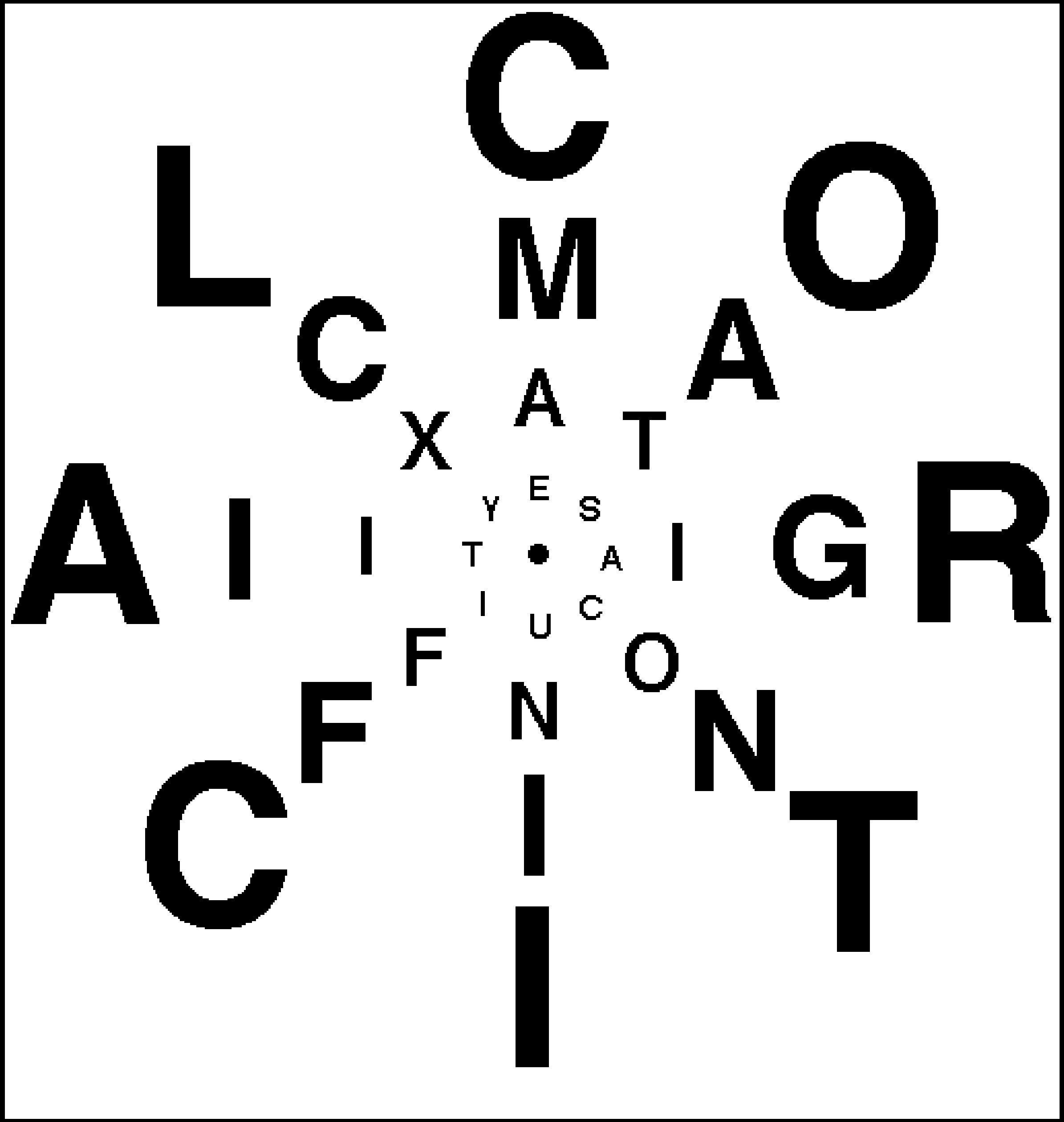
after Østerberg, 1935; as modified by Rodieck 1988;
micrographs from Curcio et al., 1990

The human visual system is a “foveating” system

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

Credit: Stuart Anstis, UCSD

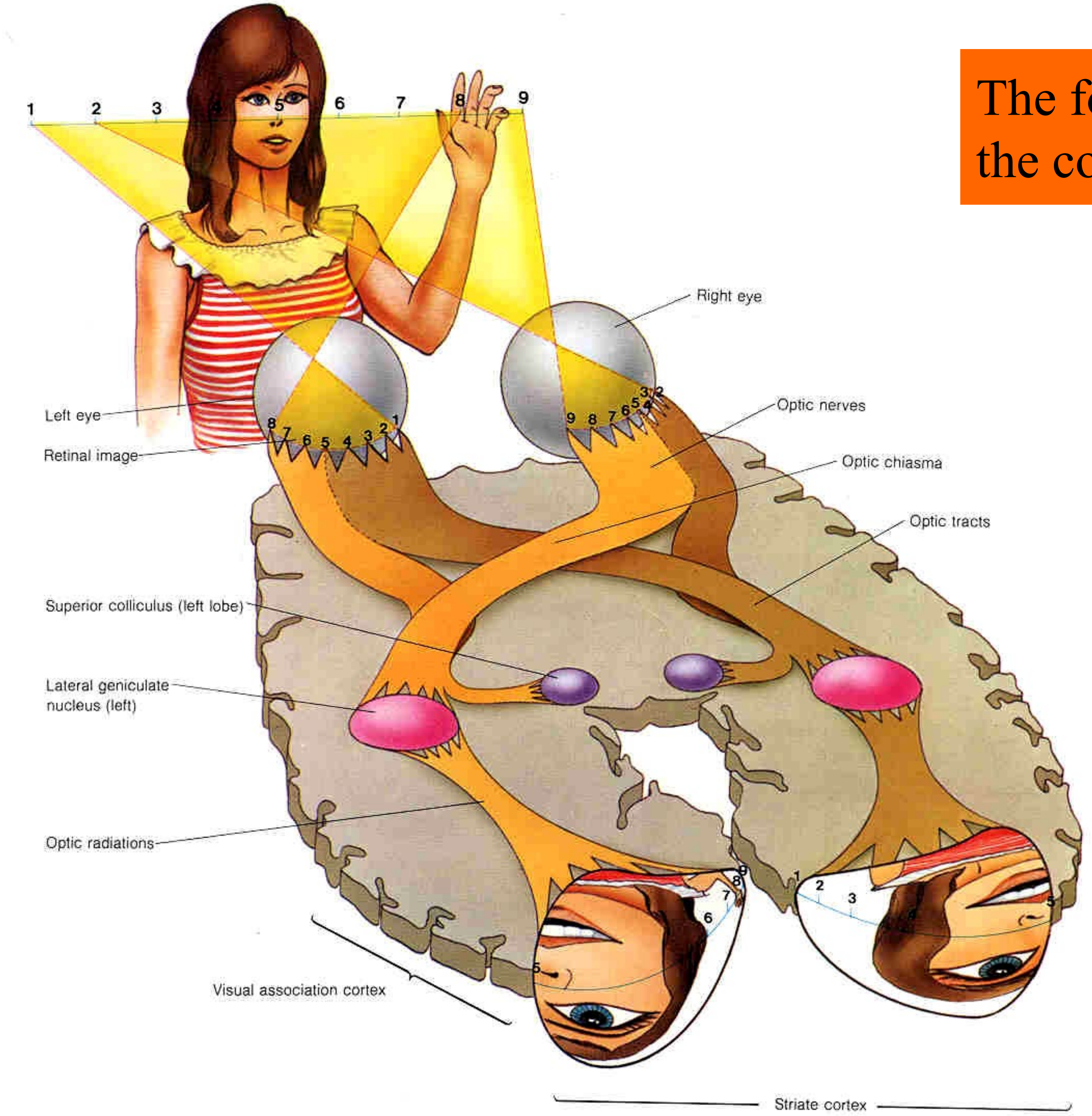




Visual acuity gets much poorer with eccentricity

Credit: Stuart Anstis, UCSD

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

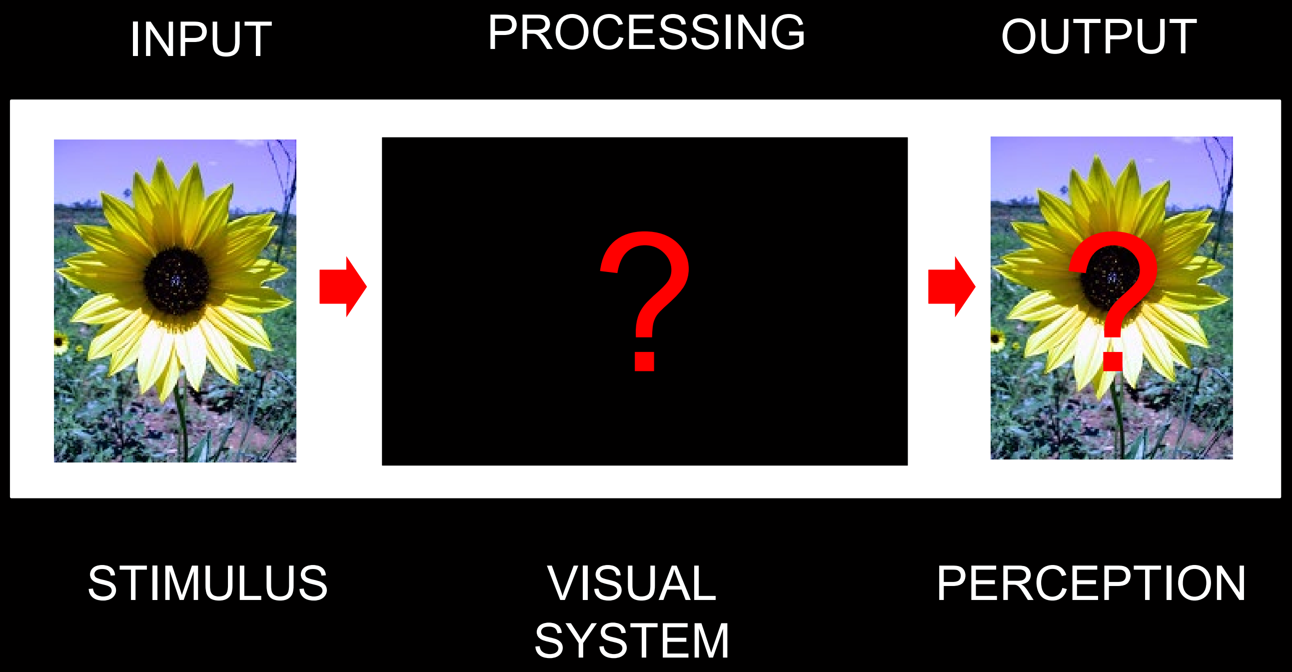


ROD AND CONE DIFFERENCES

Rod and cone differences can be demonstrated using several techniques, including visual psychophysics.

What is visual psychophysics?

Psychophysicists study human vision by measuring an observer's performance on carefully chosen perceptual tasks.



The idea is to work out what is going on inside the visual system from the relationship between the stimulus at the input and the response of the observer.

Rod-cone threshold sensitivity differences

How might we measure them?

Rod and cone threshold versus intensity curves

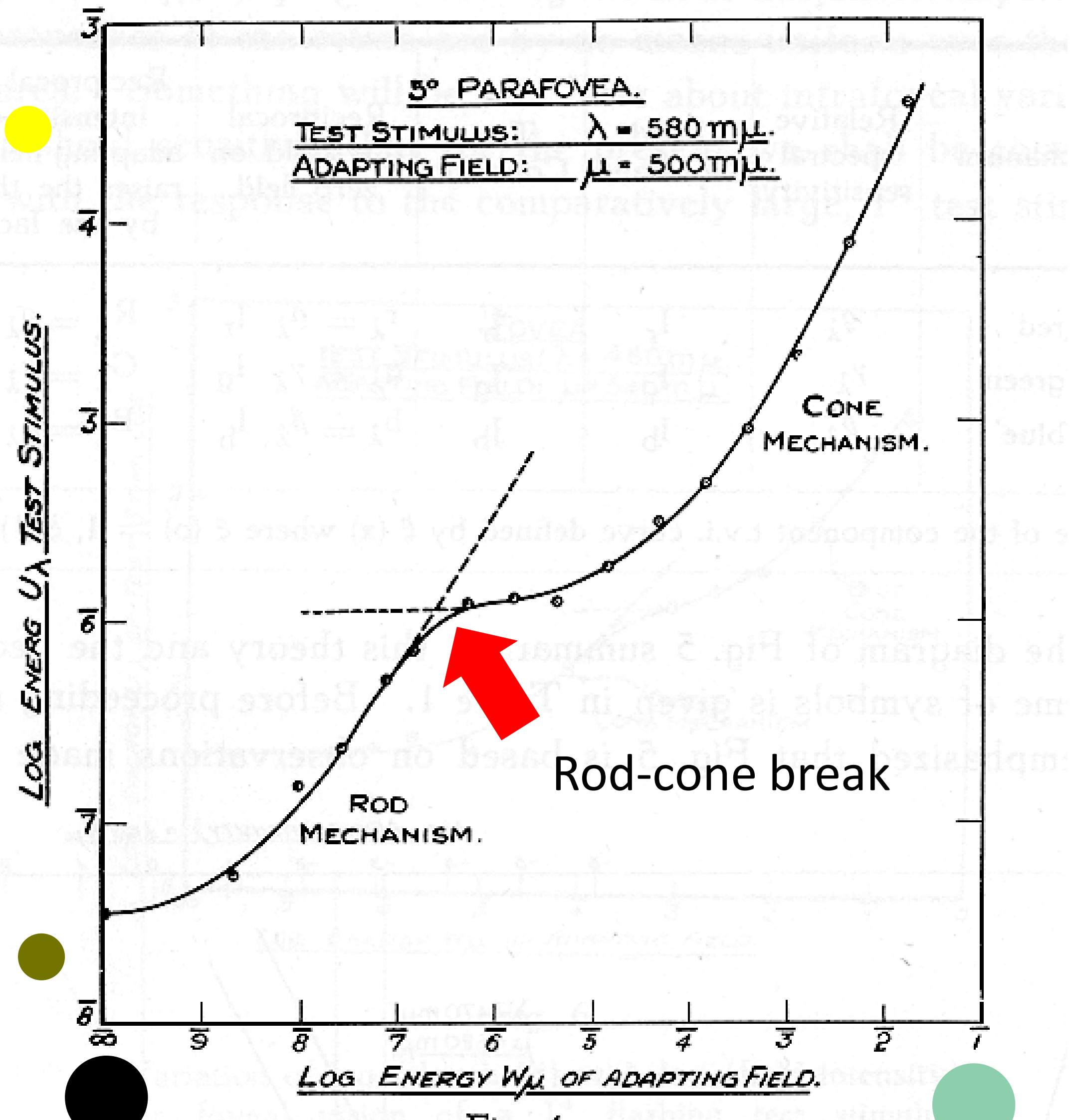


Fig. 4.

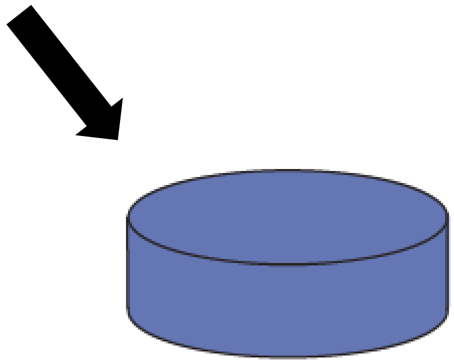
Variation of log (threshold) with log (field intensity) for a 1° flashing test stimulus of yellow light (exposure time 0.063 sec.) on a blue-green field: 5°- parafoveal vision. (Stiles, 1939)

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

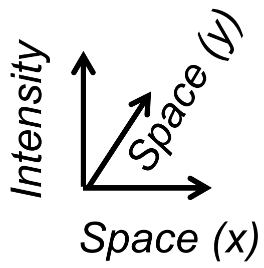
Spectral sensitivity differences

Threshold versus target wavelength measurements

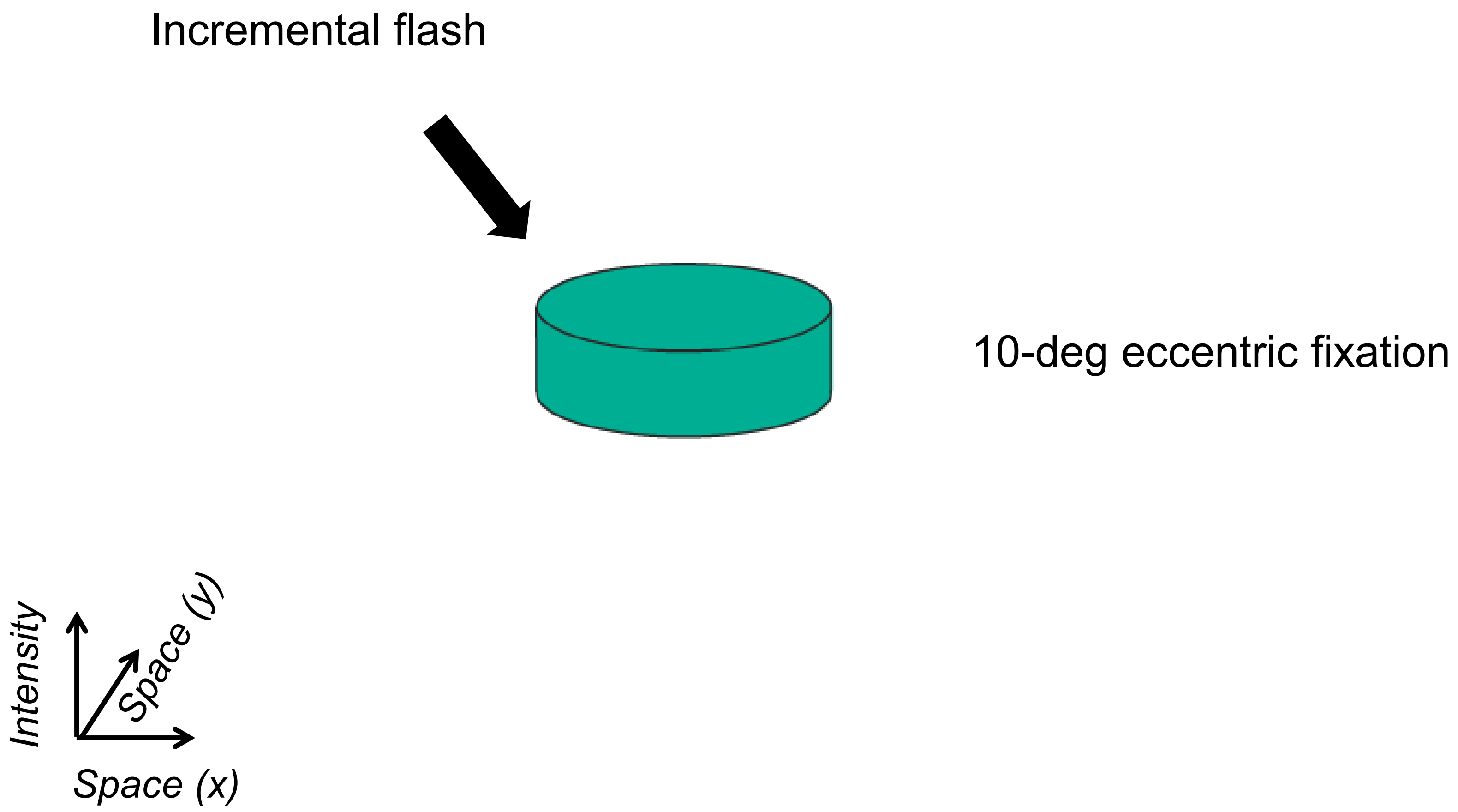
Incremental flash



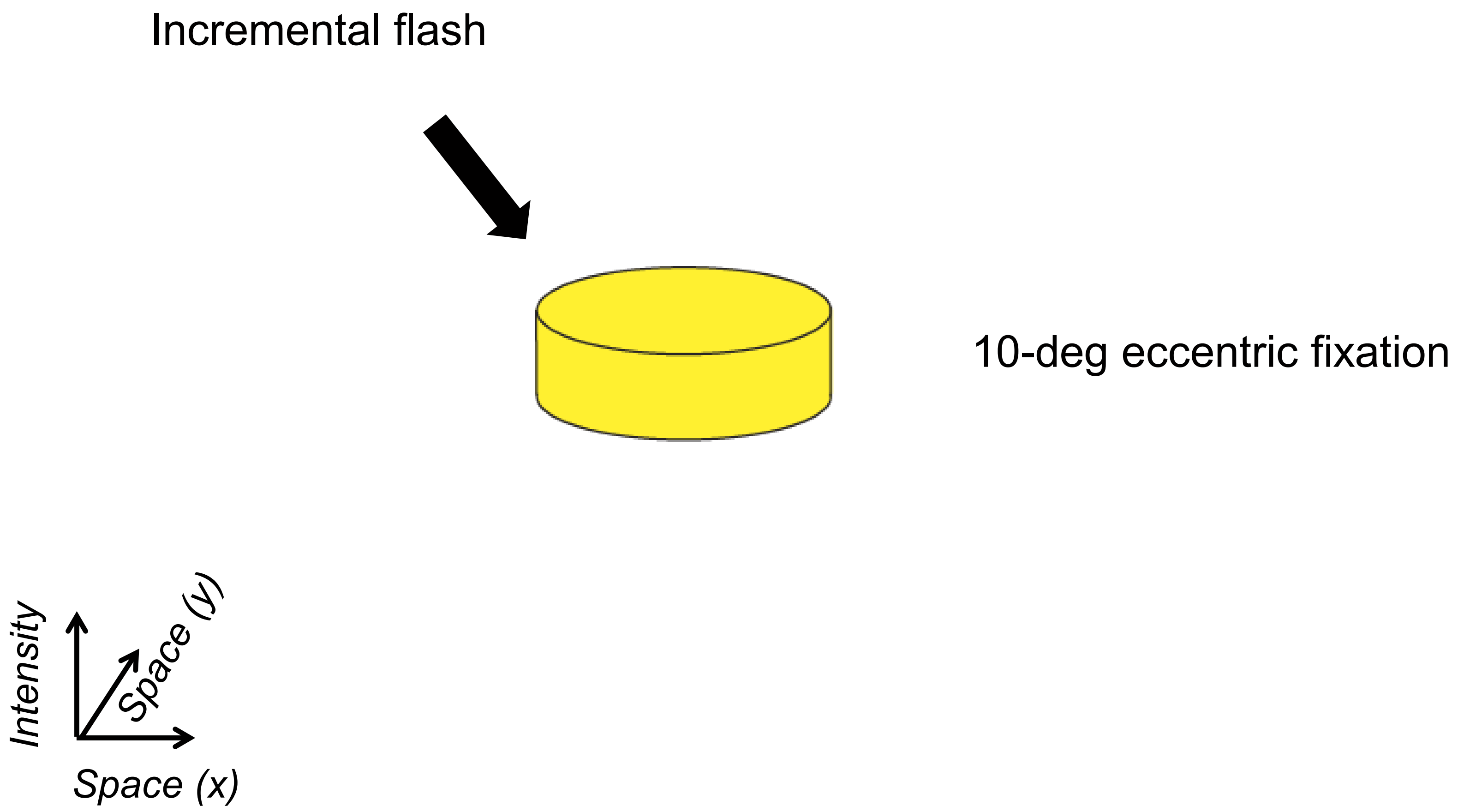
10-deg eccentric fixation



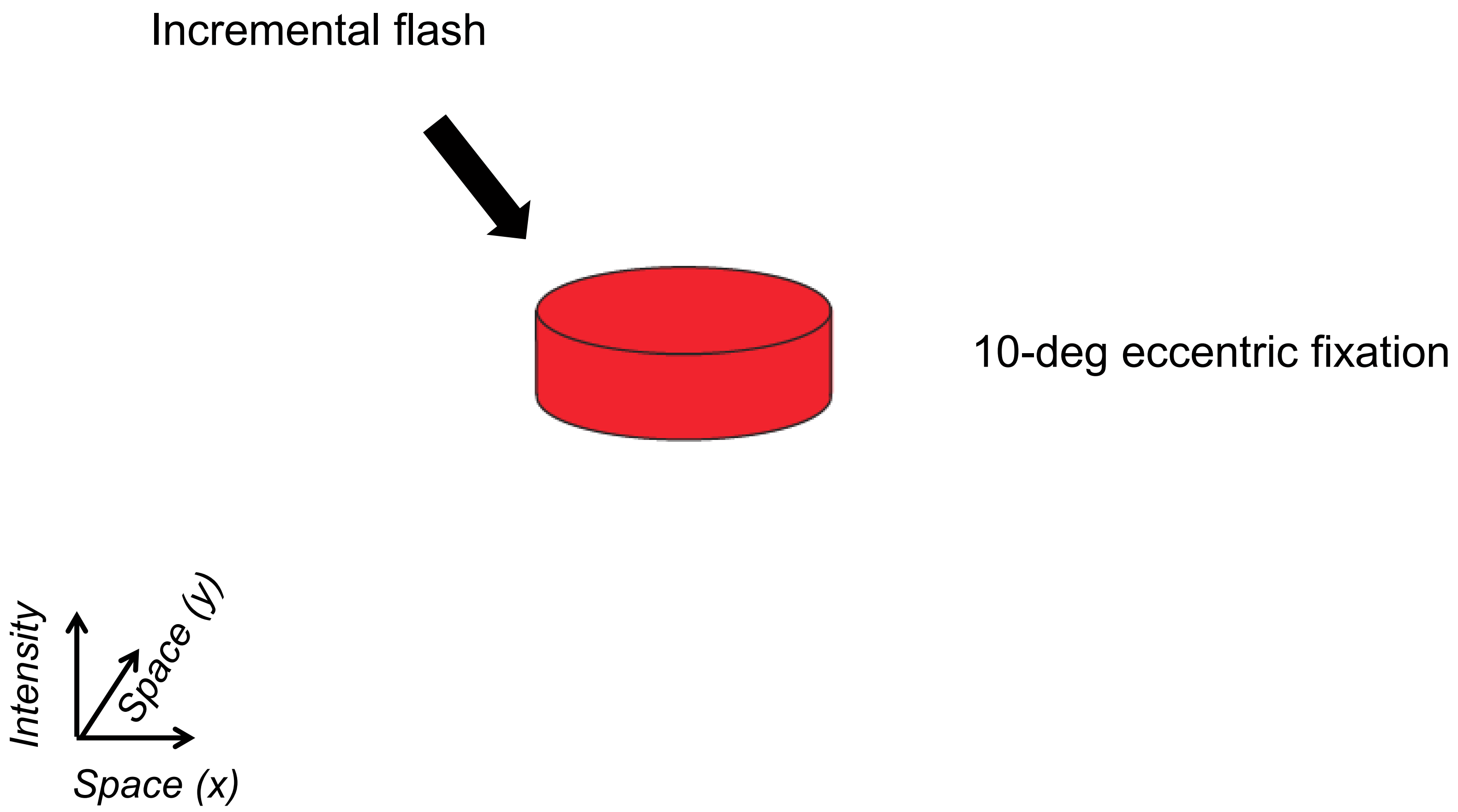
Threshold versus target wavelength measurements



Threshold versus target wavelength measurements



Threshold versus target wavelength measurements



Rod and cone spectral sensitivity curves

Plotted as "thresholds" versus wavelength curves

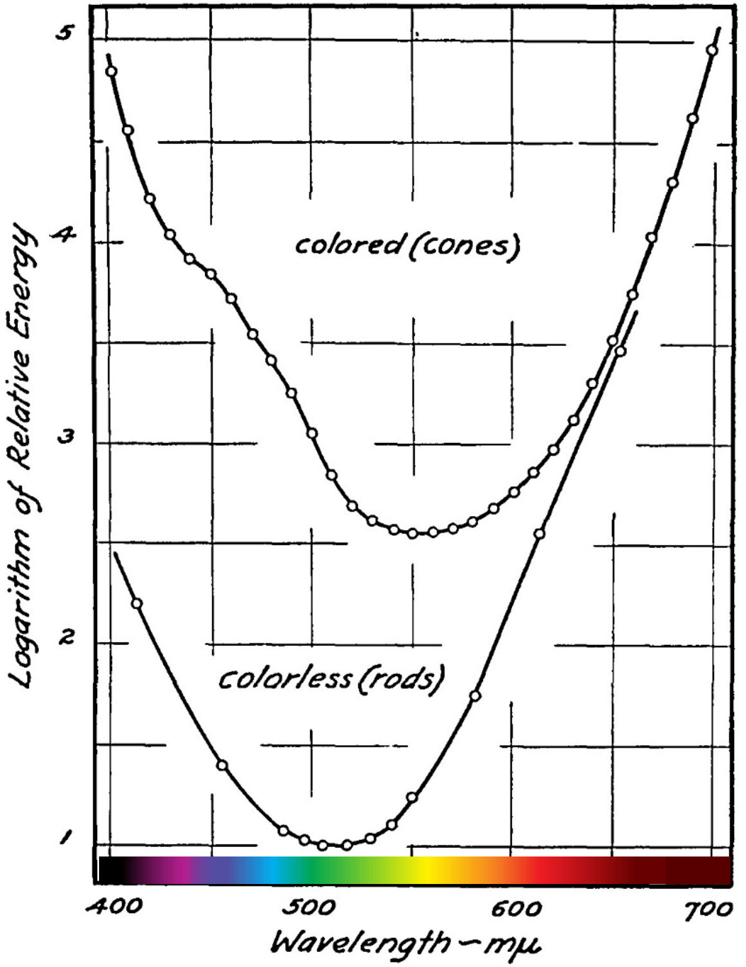
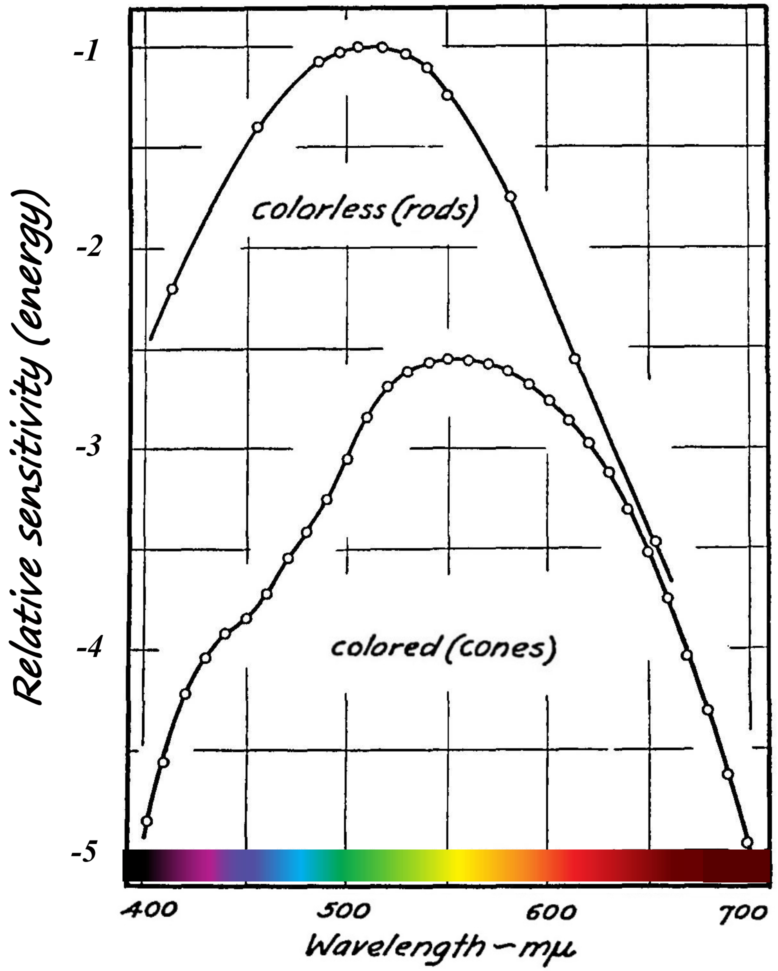


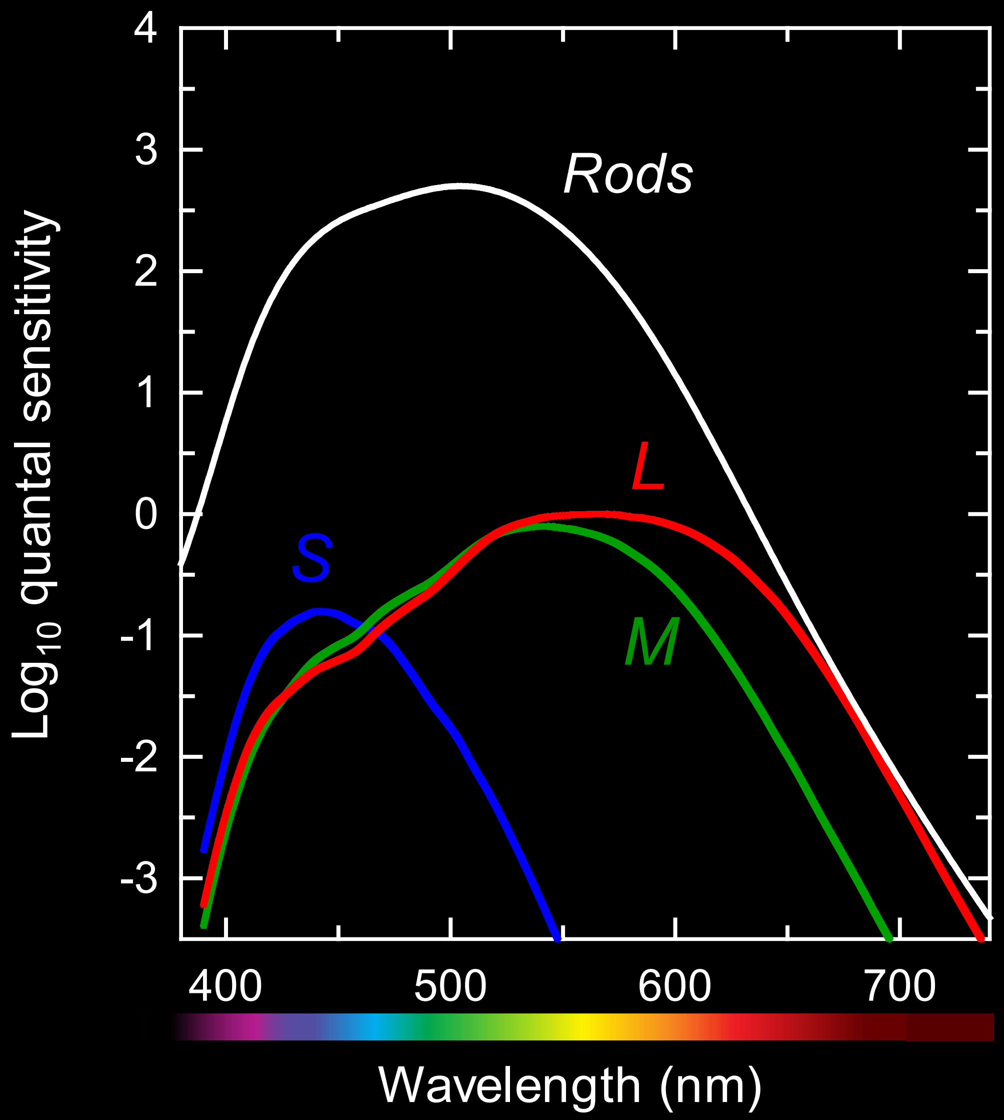
FIG. 2. Spectrum sensibility curves for rod and cone vision on a real energy basis. The data for the separate curves are from the same sources as in Fig. 1. The position of the two curves on the ordinates corresponds to the fact that after complete dark adaptation, any region of the retina outside the 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.

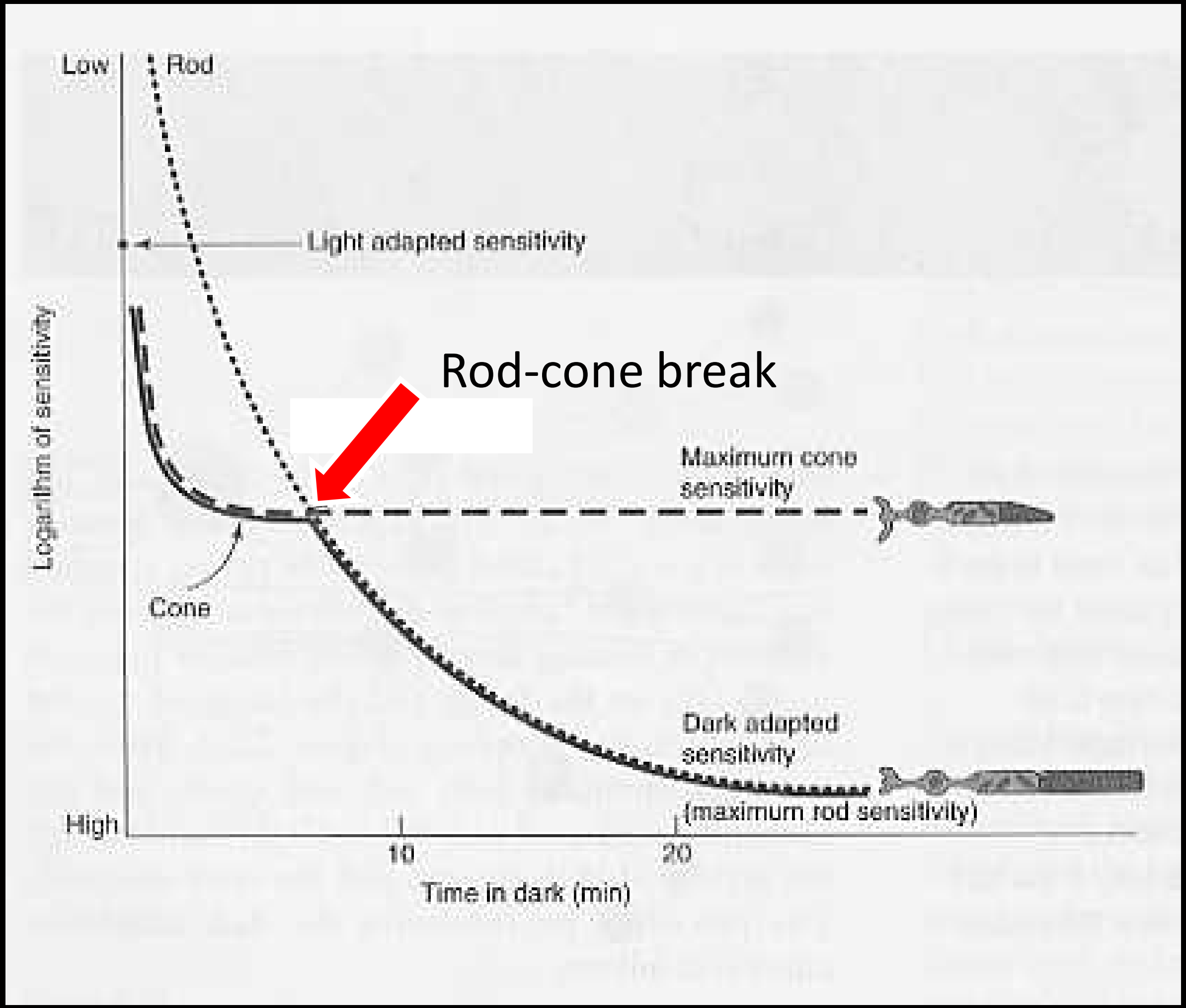


The Purkinje Shift

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

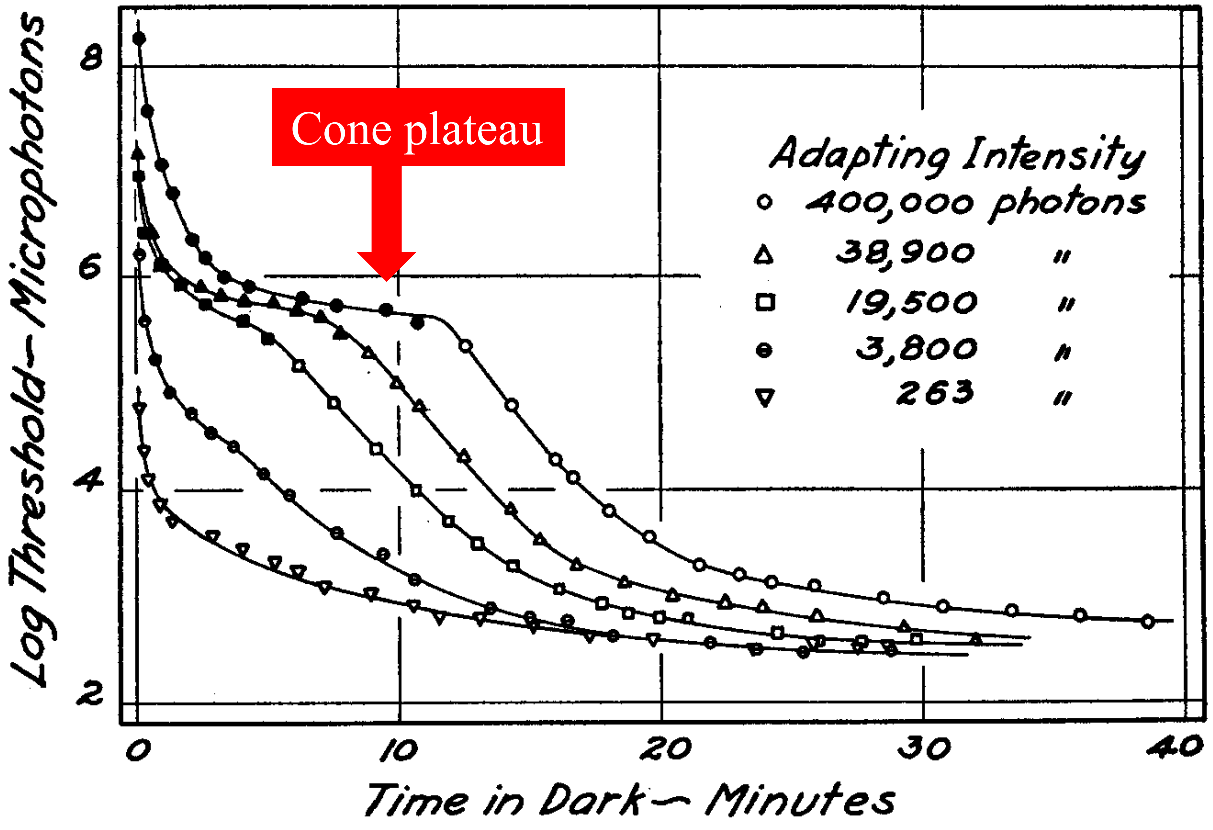


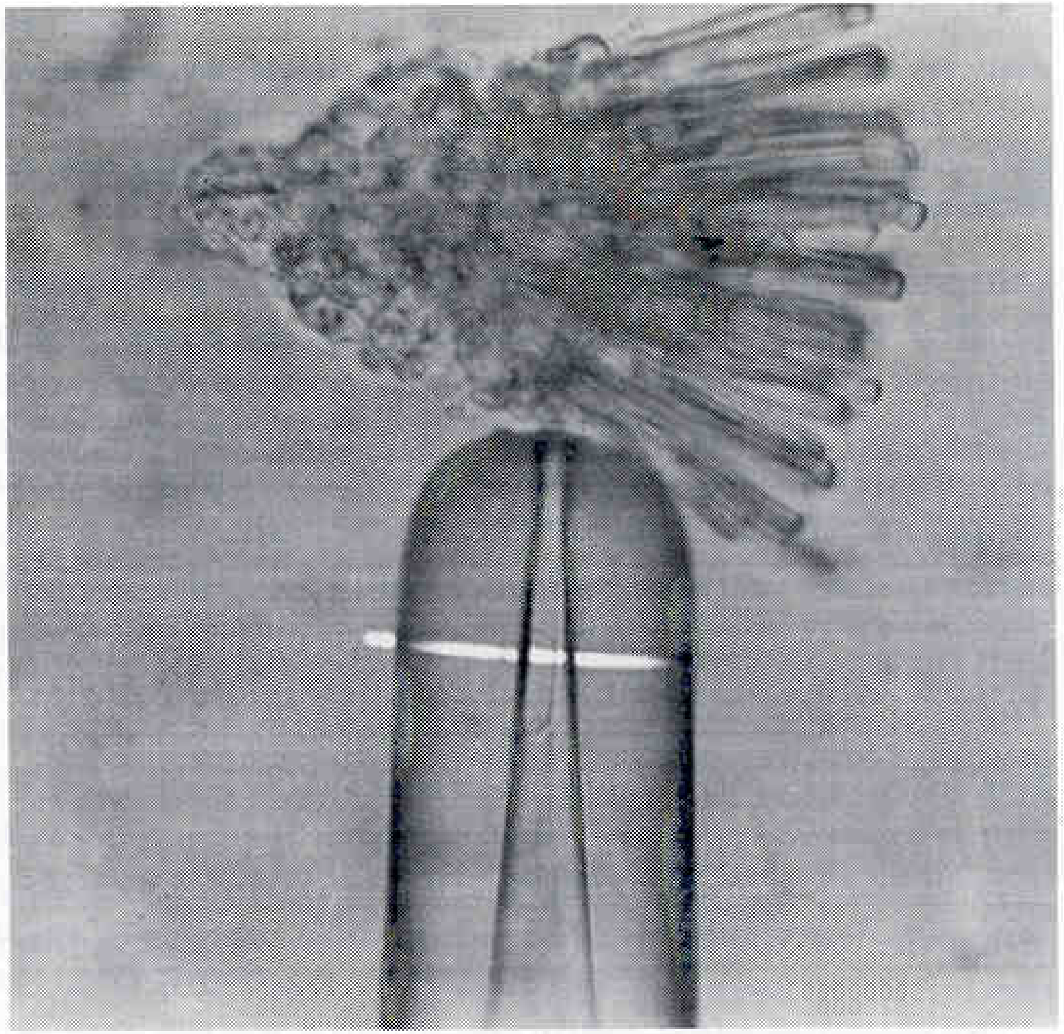
FIG. 2. The course of dark adaptation as measured with violet light following different degrees of light adaptation. The filled-in symbols indicate that a violet color was apparent at the threshold, while the empty symbols indicate that the threshold was colorless.

Rods take much longer to recover after a bleach than cones

From Hecht, Haig & Chase (1937)

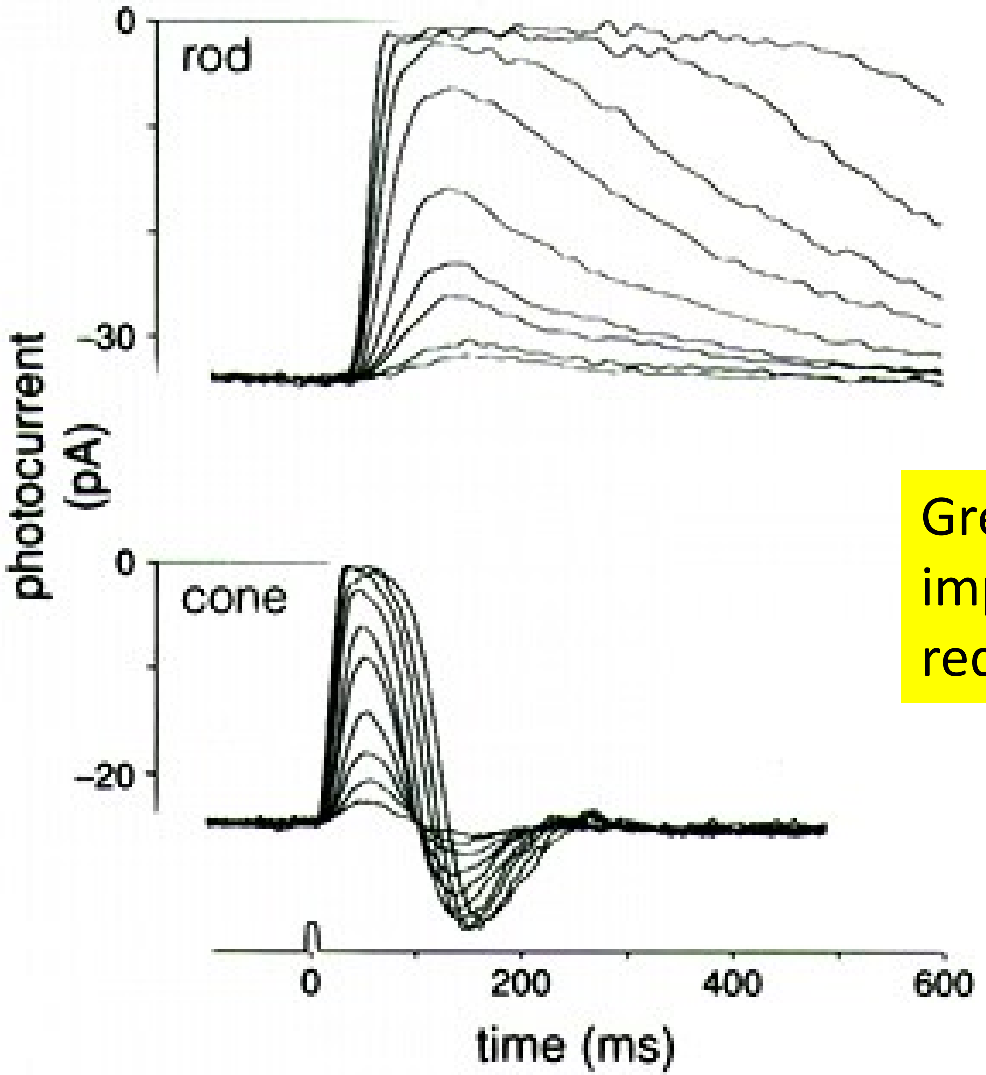
Temporal differences

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.)…

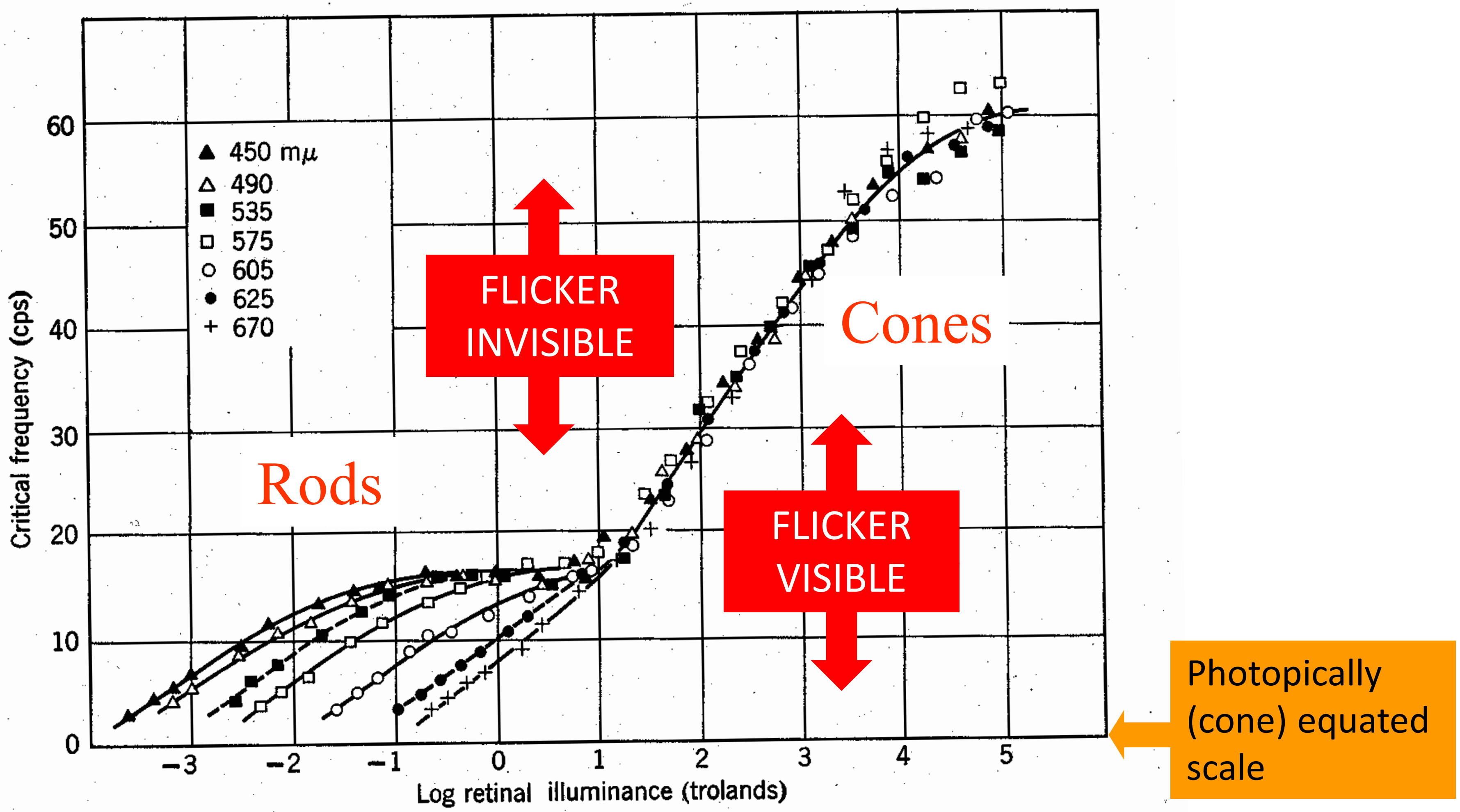
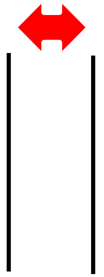


FIG. 10.6 Relation of CFF to log retinal illuminance for seven spectral regions. (Hecht and Shlaer, 1936. Reprinted by permission of The Rockefeller Institute Press from *The Journal of General Physiology*, 1936, **19**, 956–979; Fig. 3.)

Spatial differences
(visual acuity)

Rod and cone visual acuities

Visual acuity



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

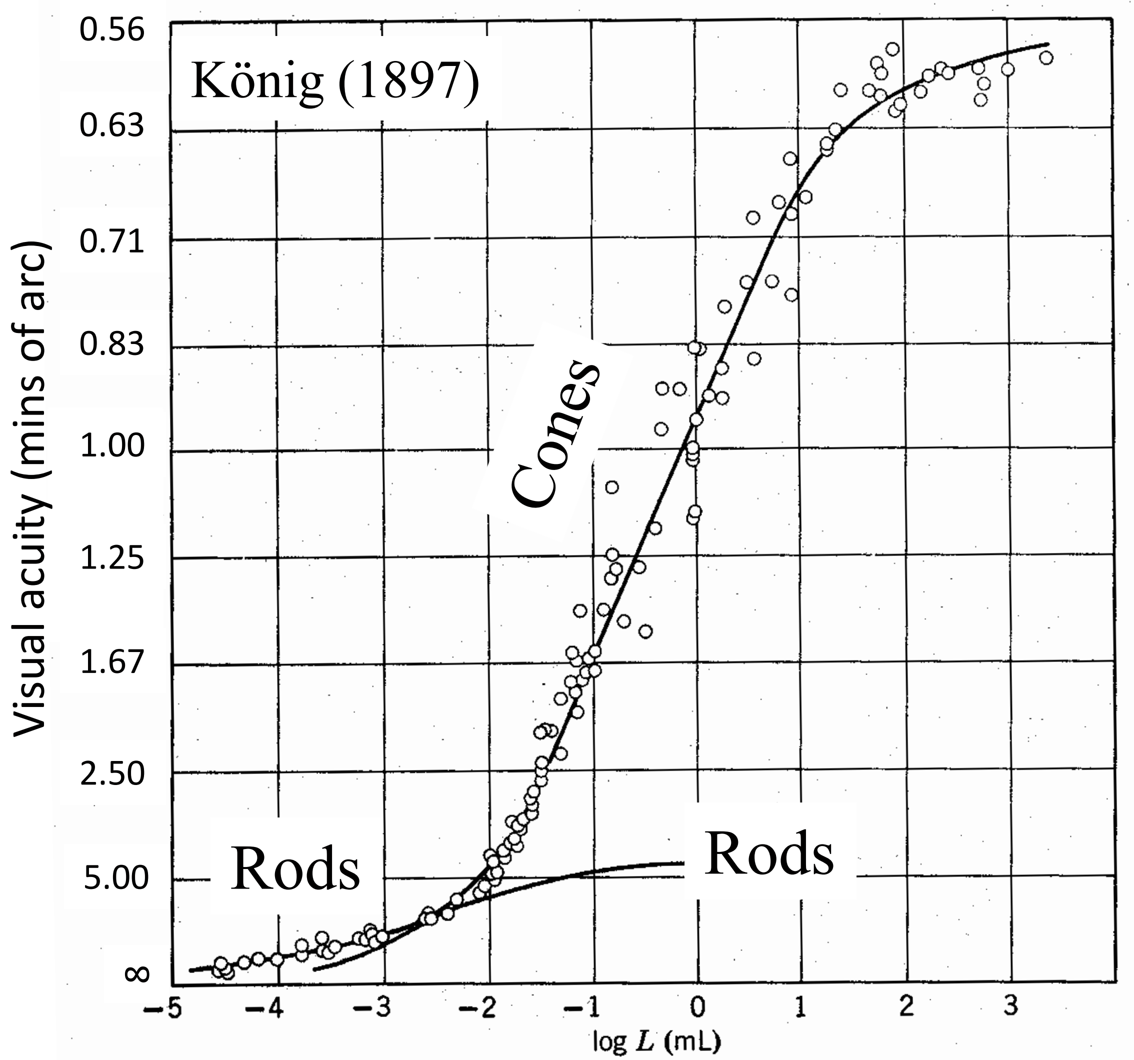
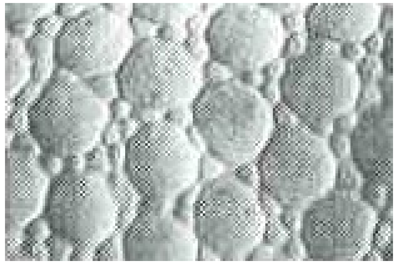


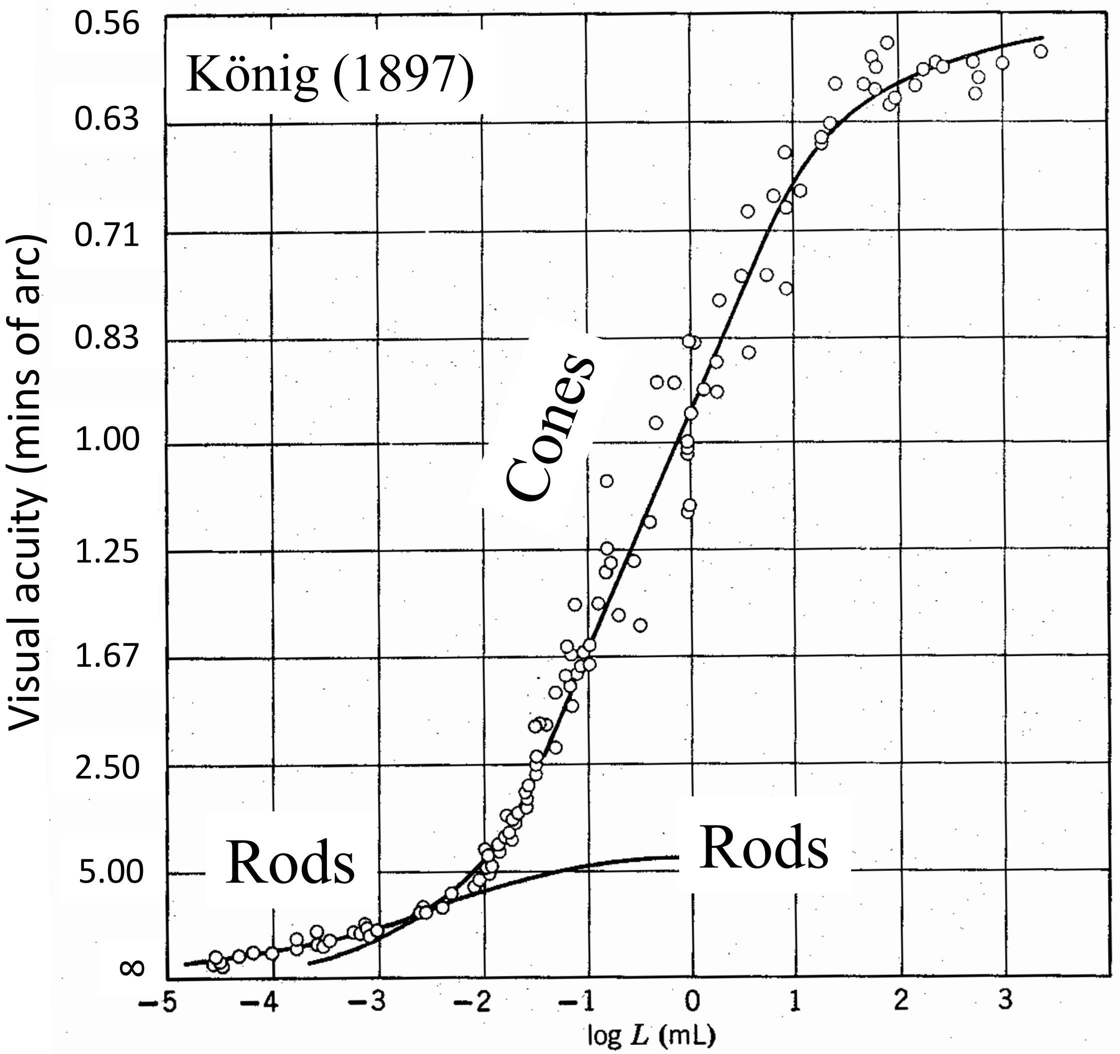
FIG. 11.14 König's data for the relation between visual acuity and illumination, as replotted by Hecht (1934). The shallow curve for the lower limb of the data is an equation for rods, whereas the upper curve is for cones. The task is one of recognizing the orientation of a hook form of test object.

Rod 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)





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Rod vision is achromatic

Why?

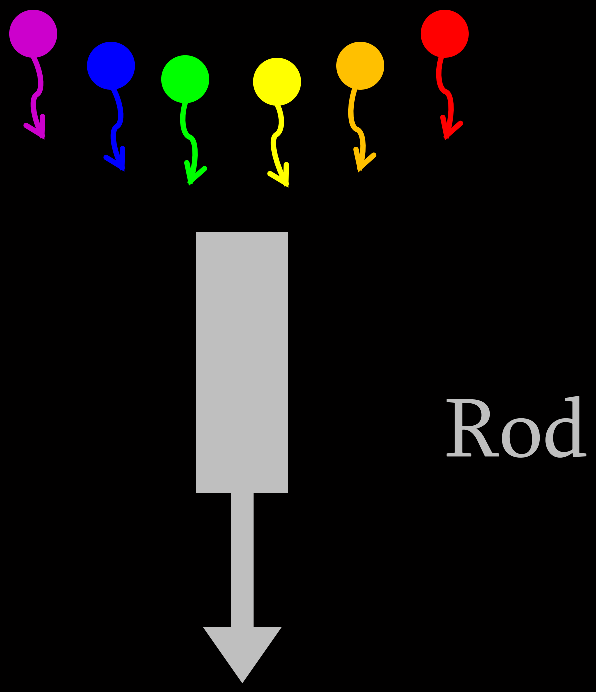
Vision at the photoreceptor stage is relatively simple because the output of each photoreceptor is:

UNIVARIANT

What does univariant mean?

UNIVARIANCE

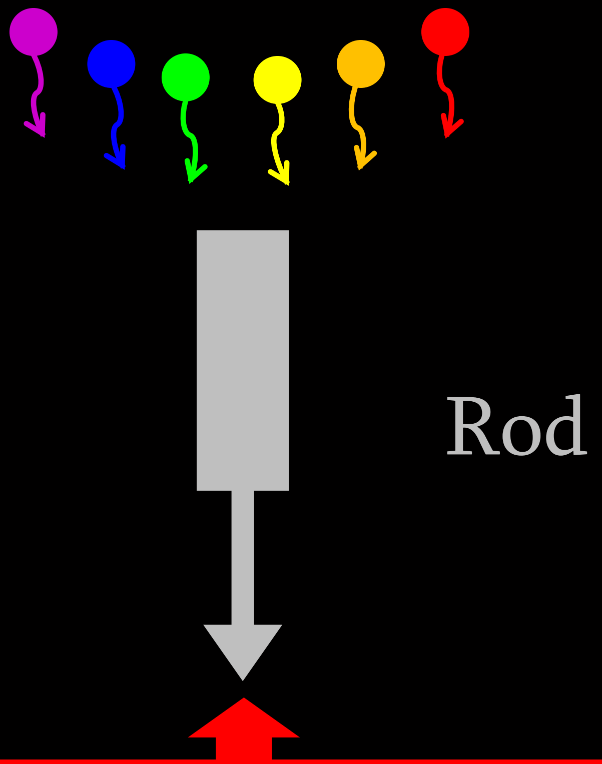
Crucially, the effect of any absorbed photon is *independent* of its wavelength.



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

UNIVARIANCE

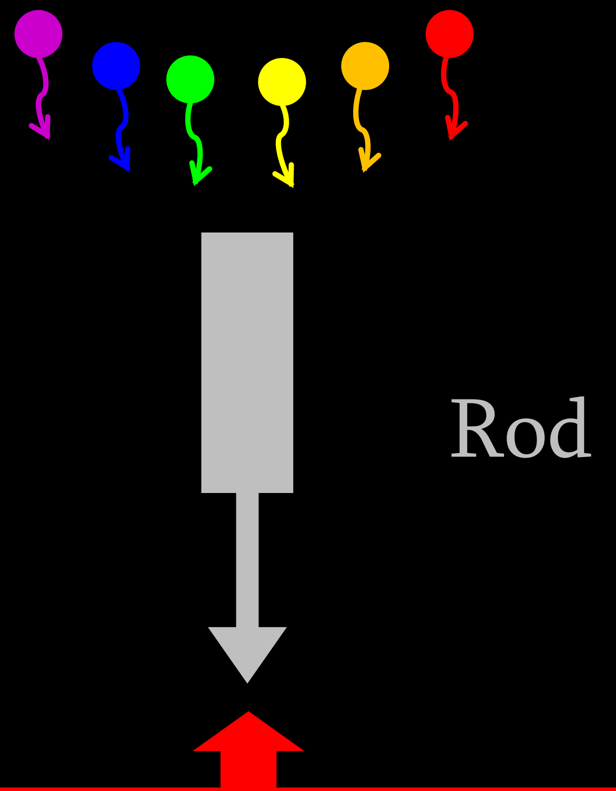
Crucially, the effect of any absorbed photon is *independent* of its wavelength.



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

UNIVARIANCE

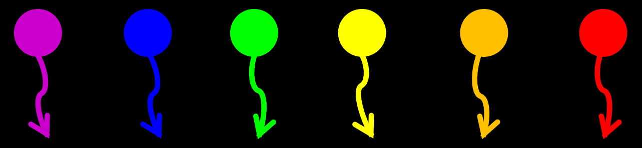
Crucially, the effect of any absorbed photon is *independent* of its wavelength.



All the photoreceptor effectively does is to count photons.

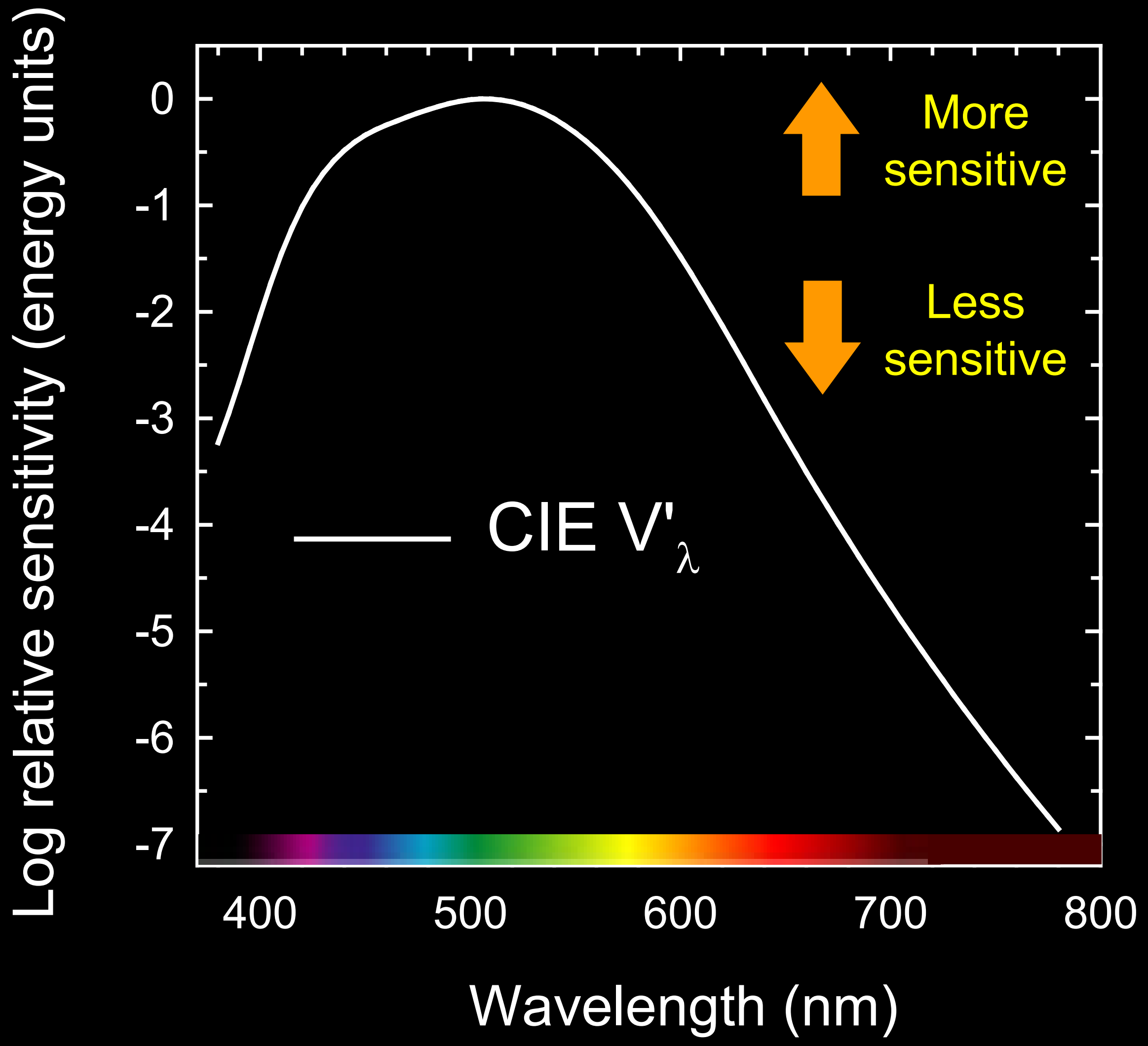
UNIVARIANCE

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



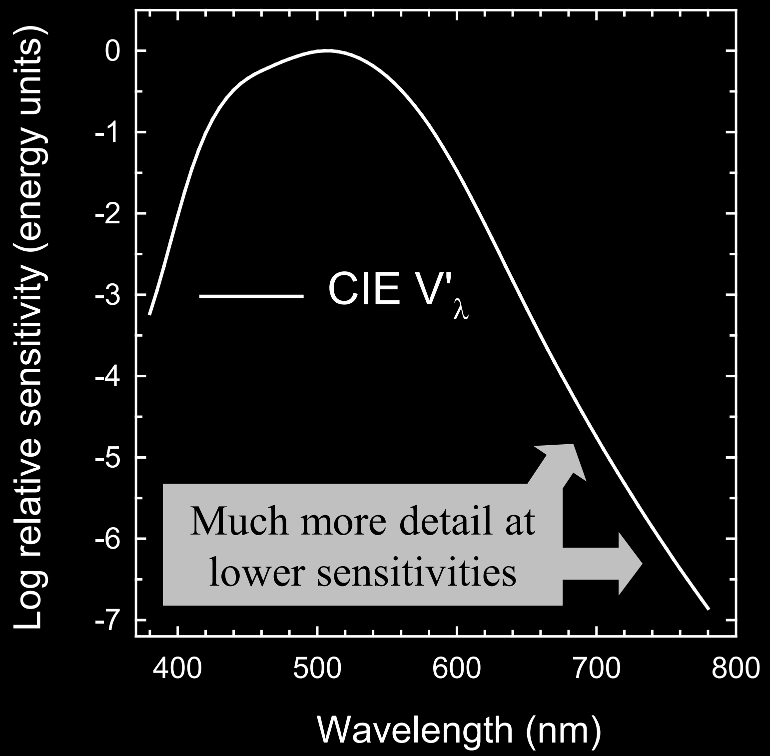
This is reflected in what is called a "spectral sensitivity function".

Rod spectral sensitivity function
(also known as the scotopic luminosity curve, CIE V'_λ)



Rod spectral sensitivity function (V'_λ)

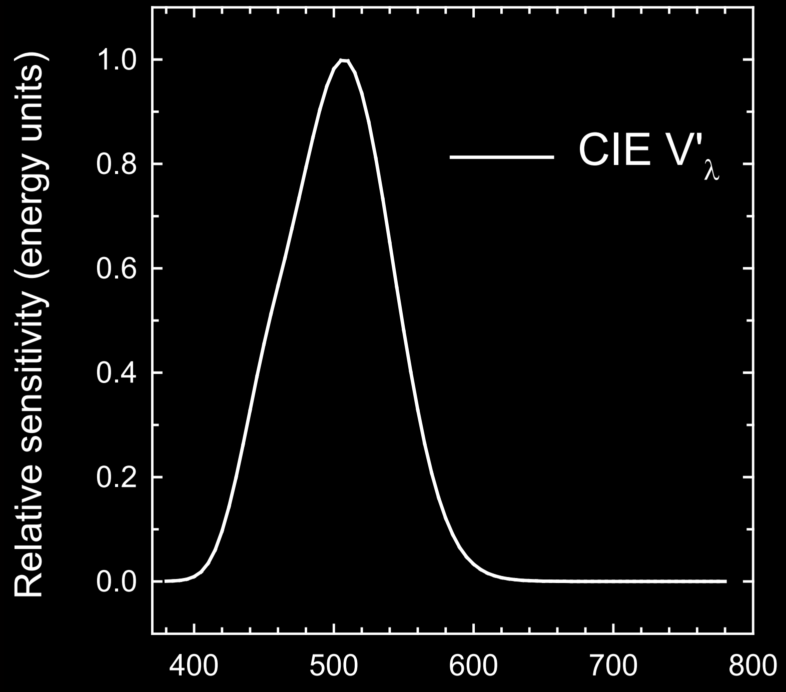
Logarithmic sensitivity plot



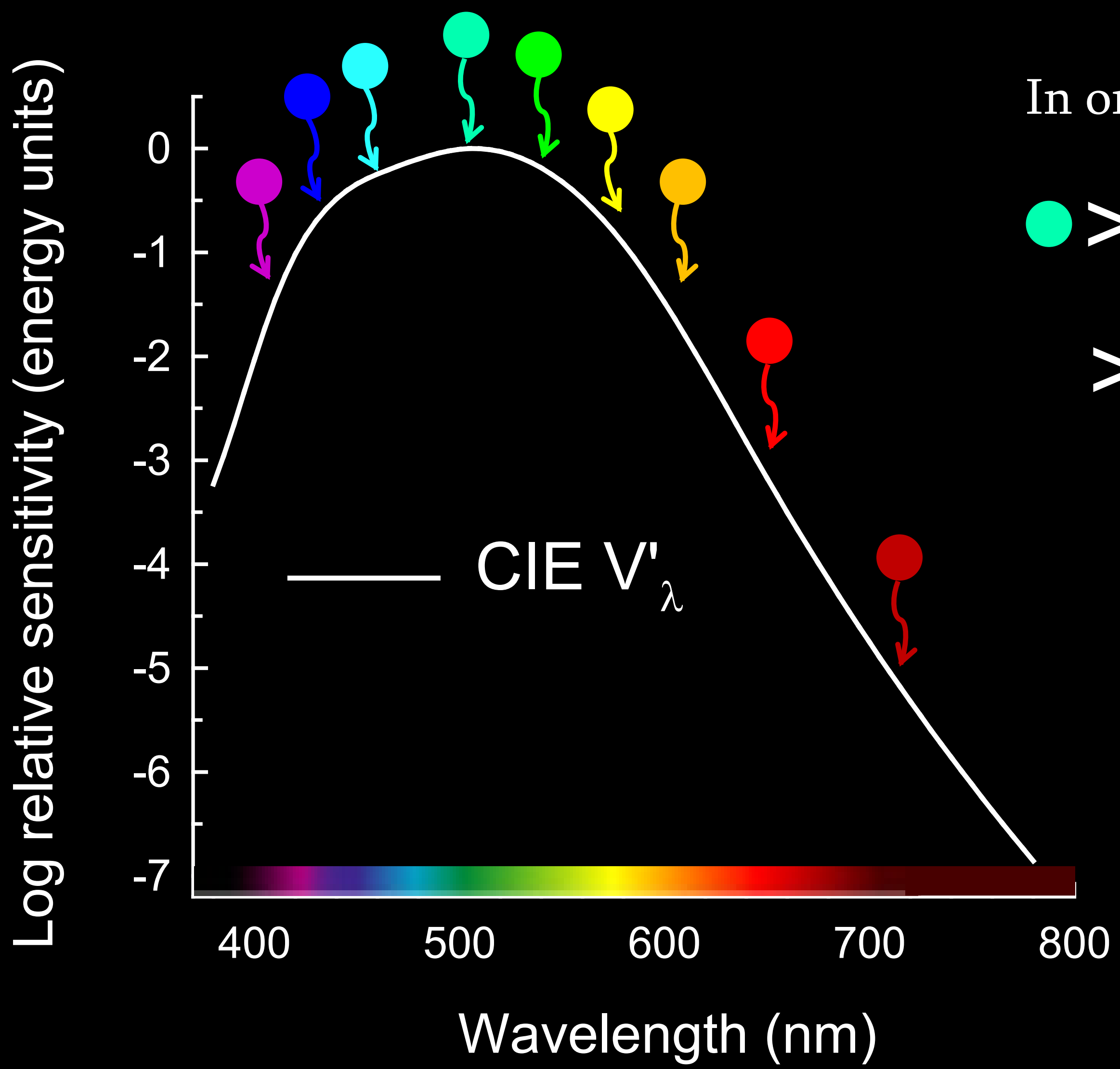
$10^{V'}$

$\log(V')$

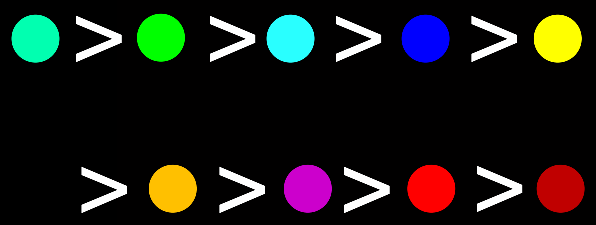
Linear sensitivity plot

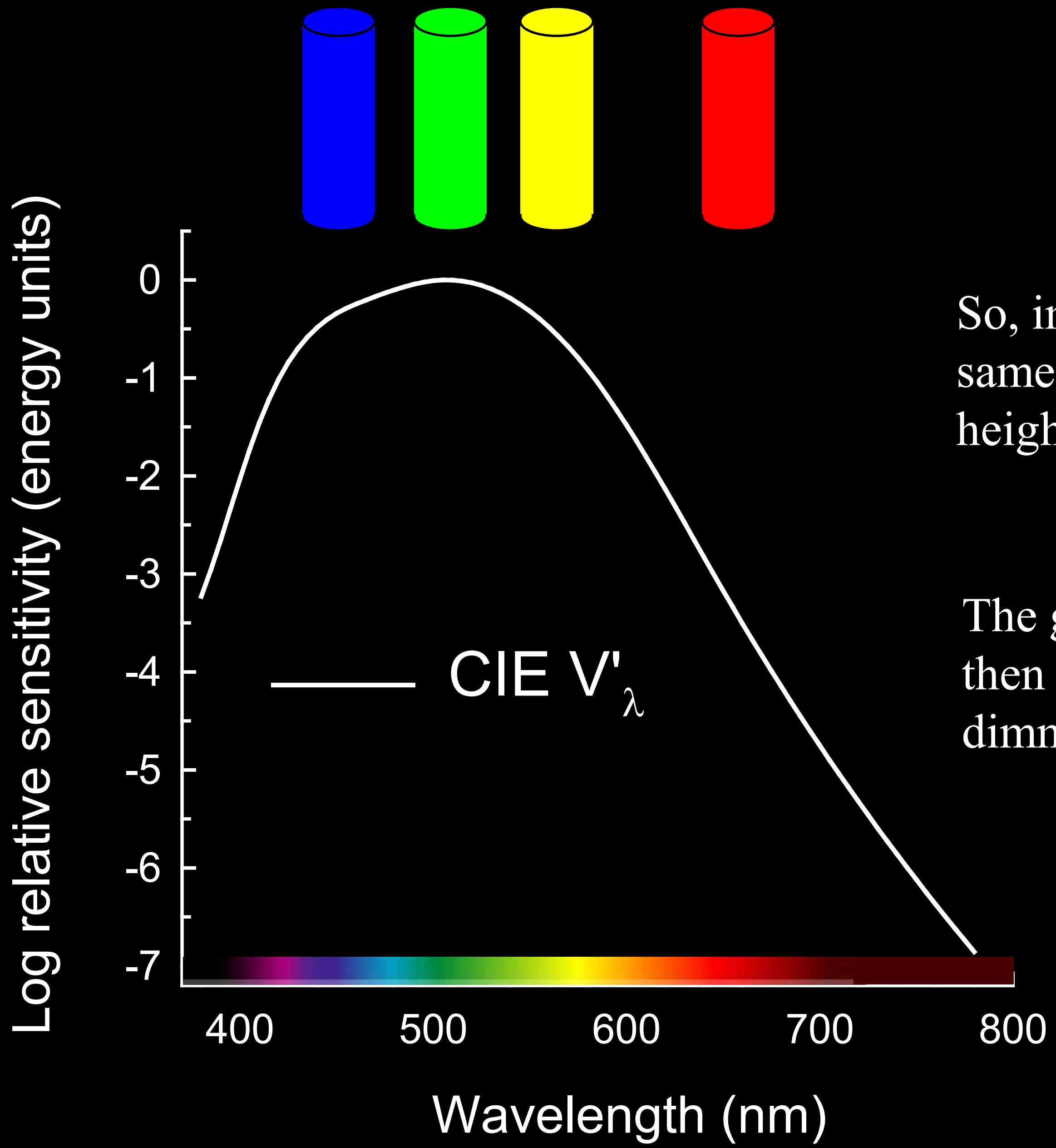


Rod spectral sensitivity function (V'_λ)



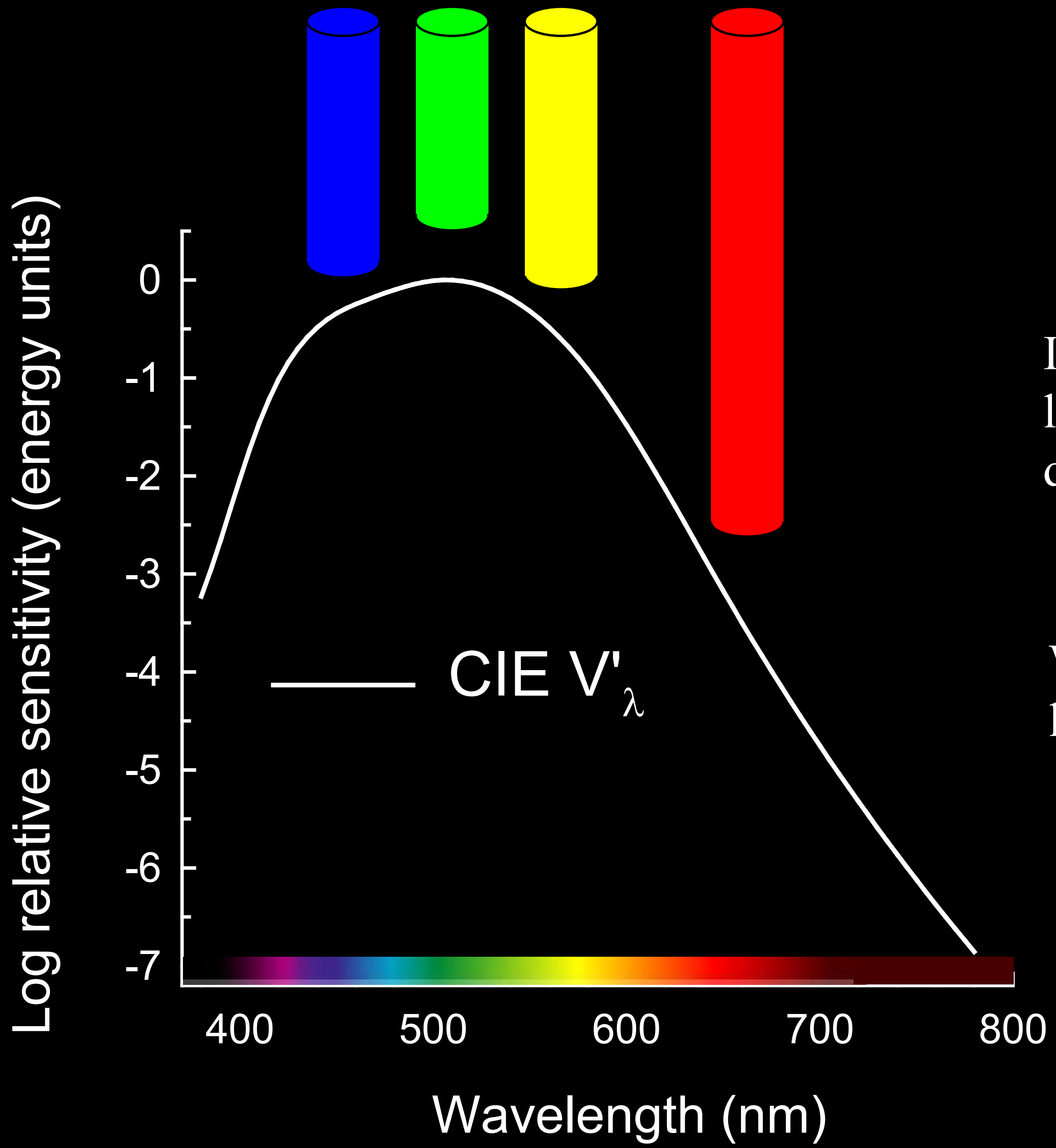
In order of rod sensitivity:





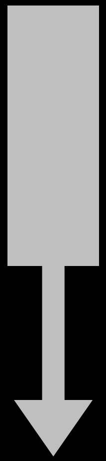
So, imagine you have four lights of the same intensity (indicated here by their height). How will they appear?

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



If instead we adjust the intensities of the light to compensate for the sensitivity differences, how will they appear?

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

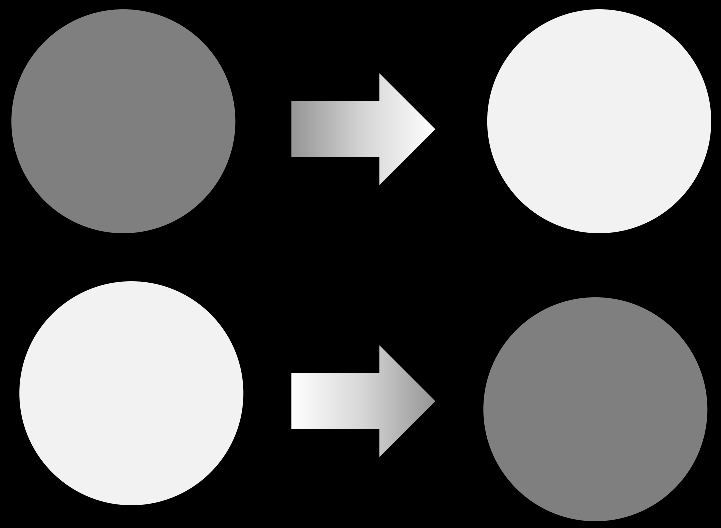


Rod

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.



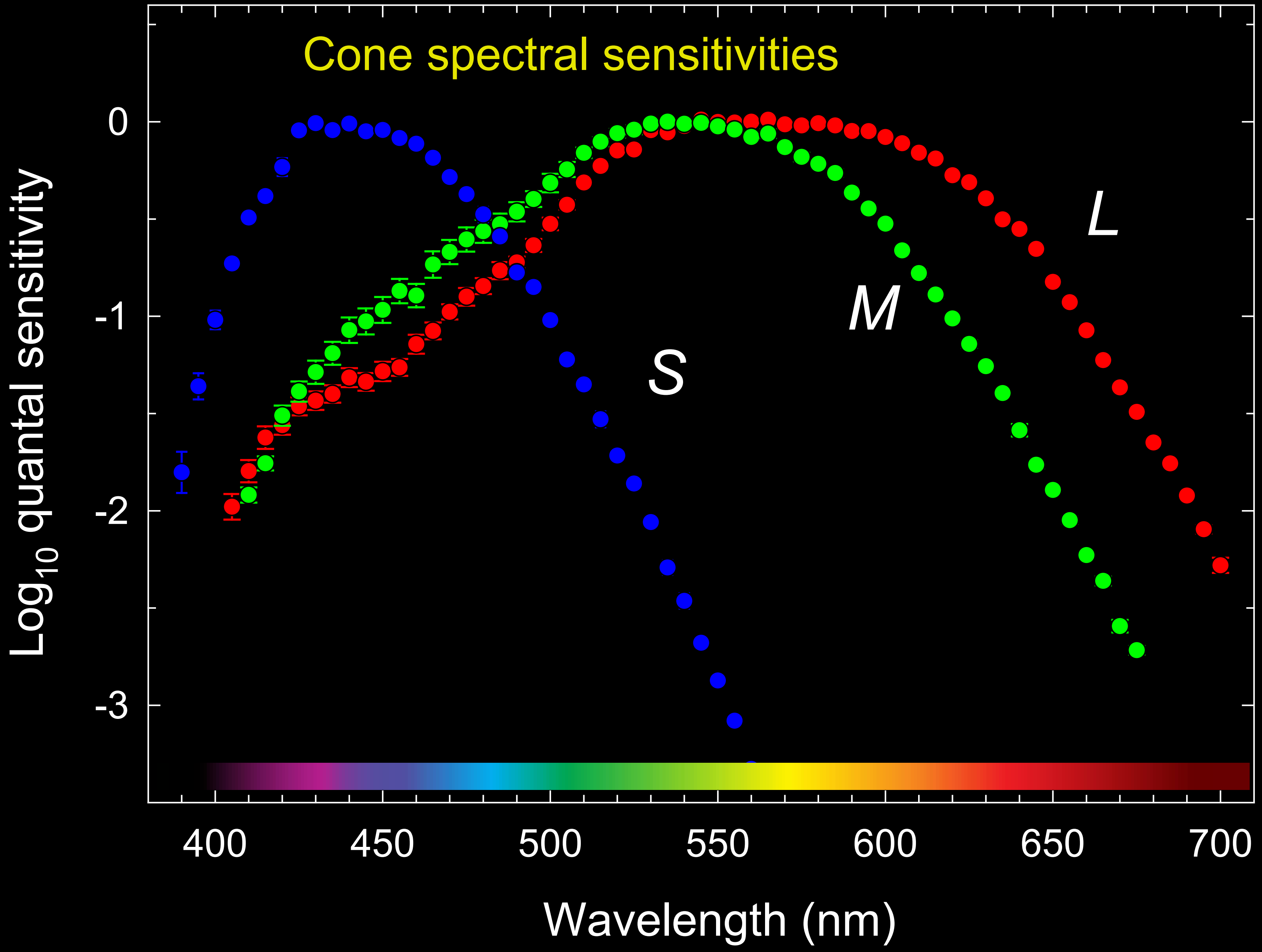
Colour or intensity change??

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…

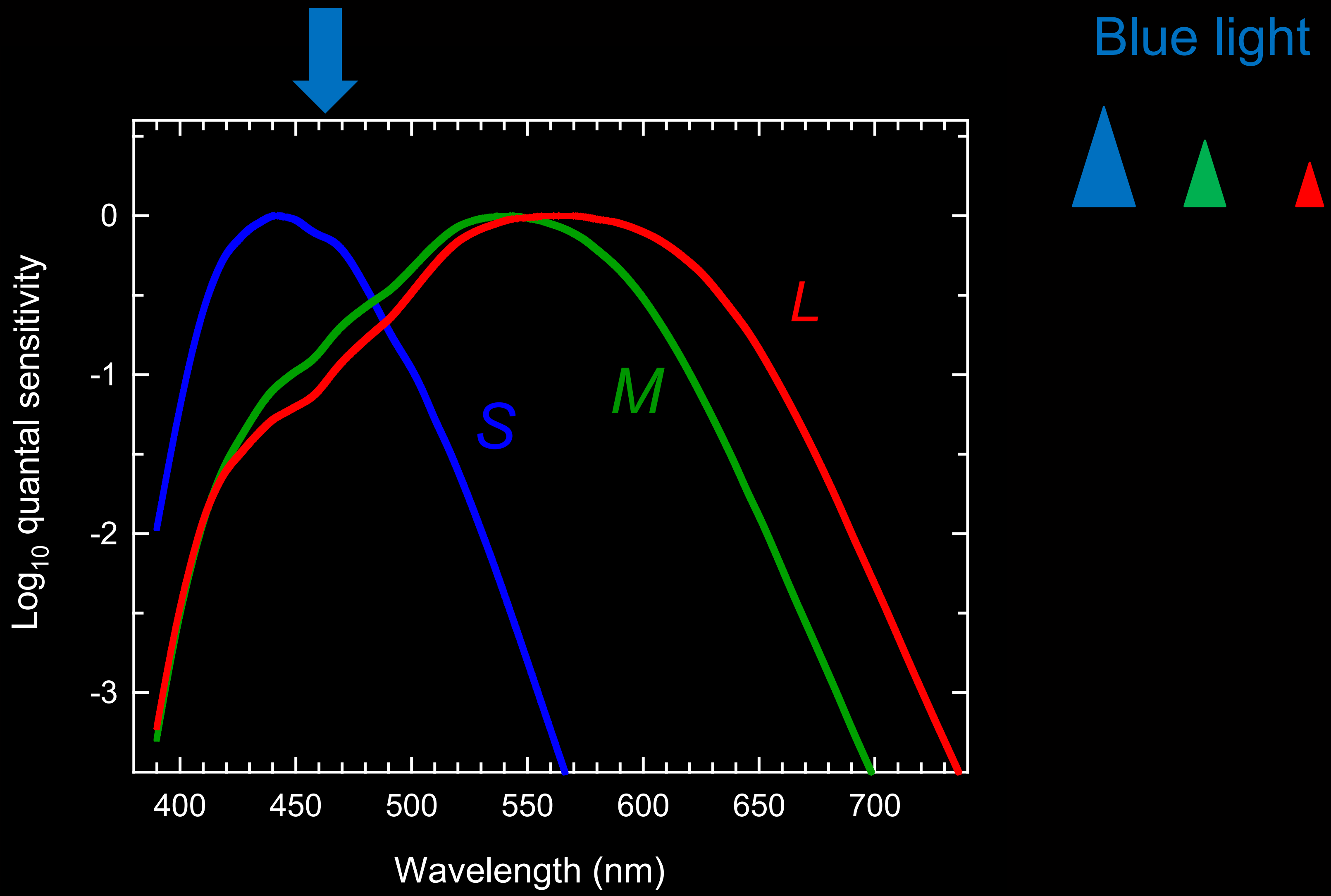


Cone spectral sensitivities
0
-1
-2
-3
Log10 quantal sensitivity
S
M
L
400
450
500
550
600
650
700
Wavelength (nm)

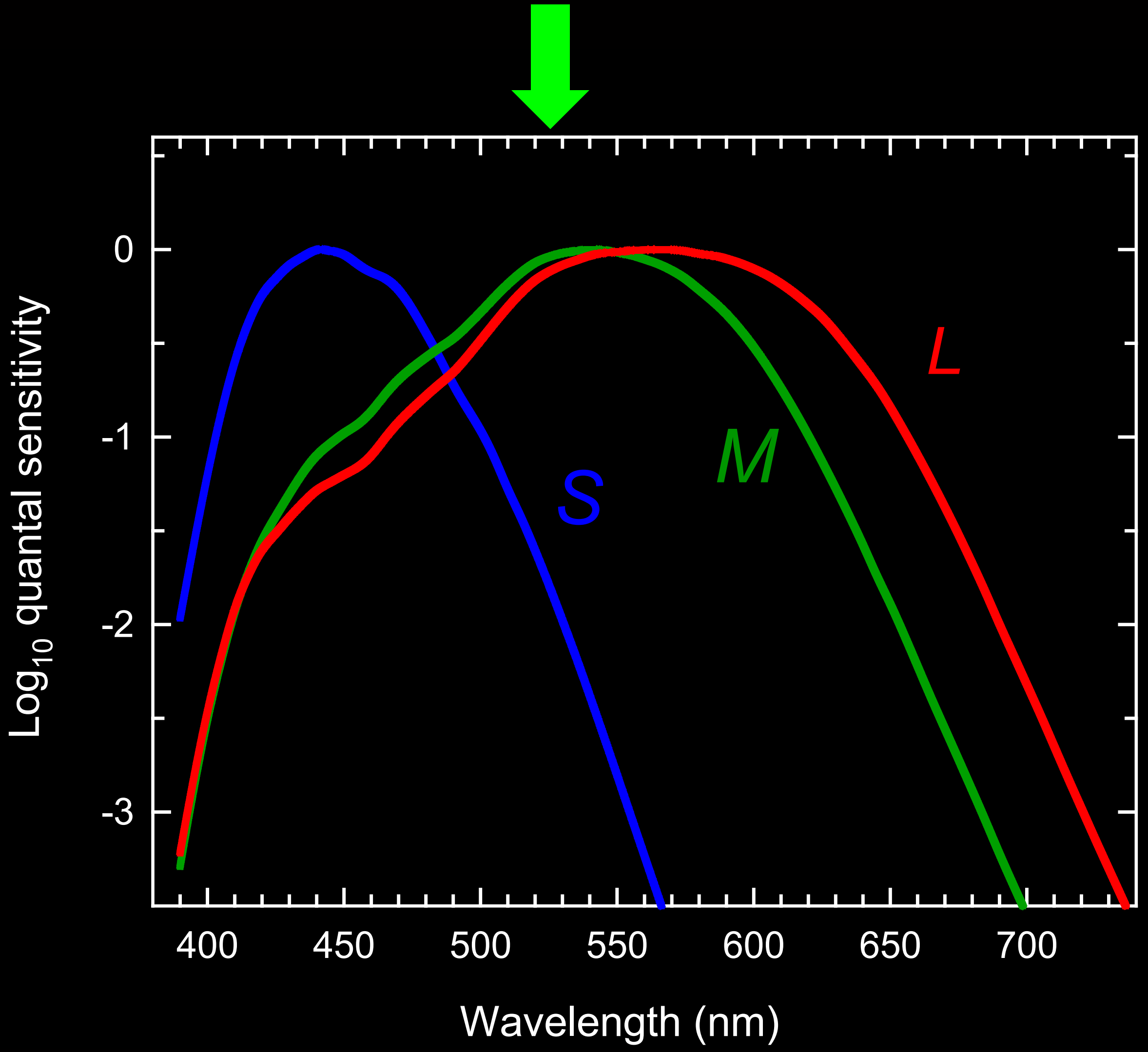
So, if each photoreceptor is colour-blind, how do we see colour?

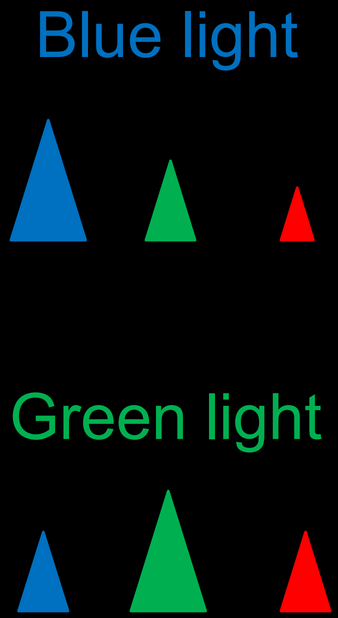
Or to put it another way: How is colour encoded?

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

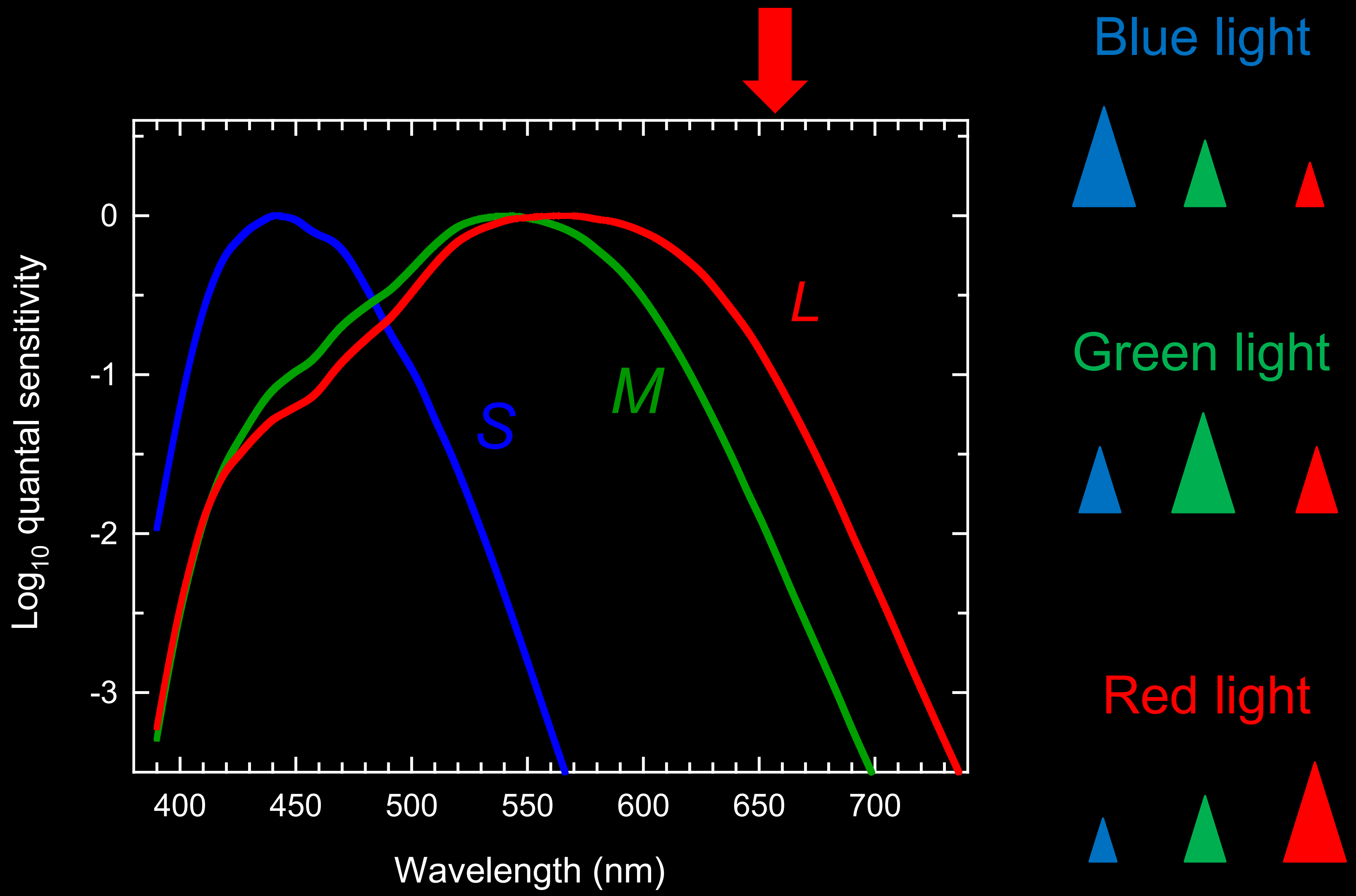


Colour is encoded by the relative cone outputs

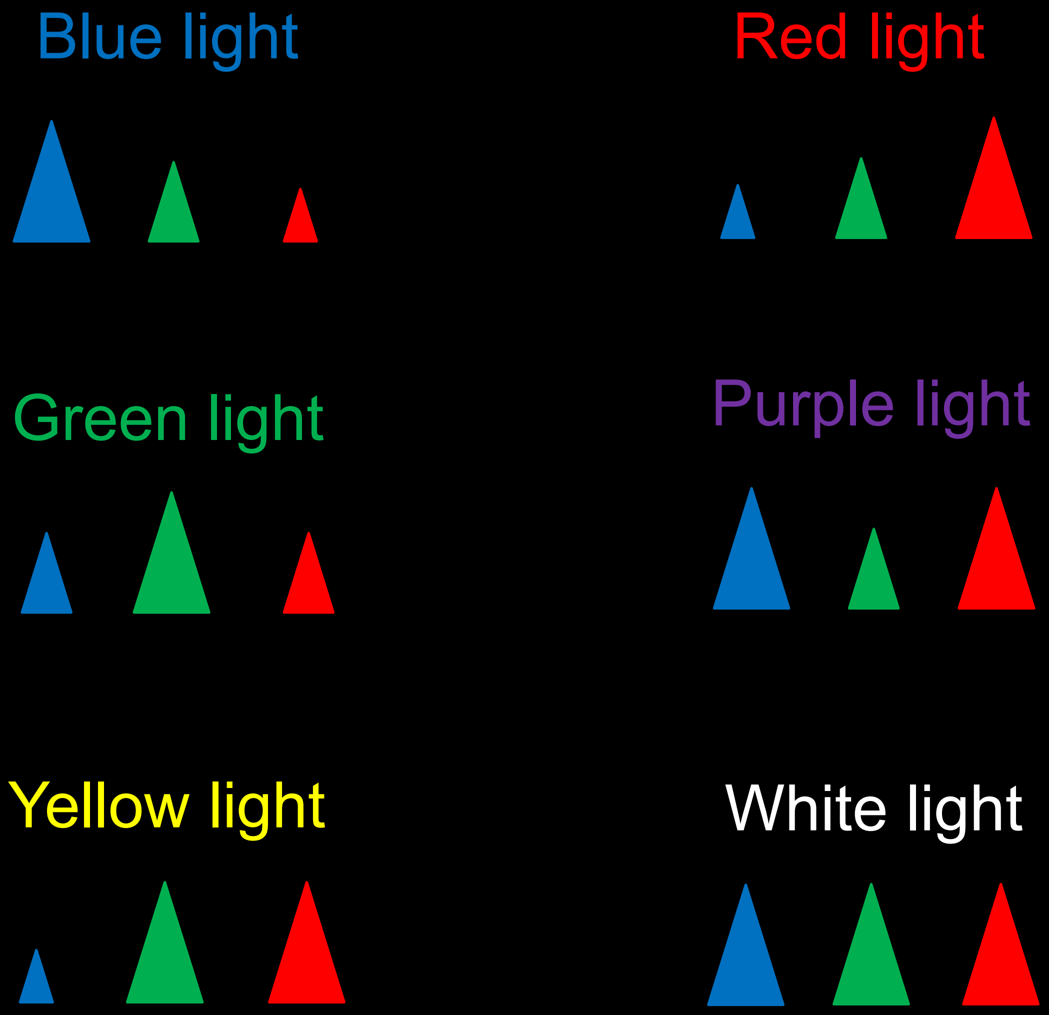




Colour is encoded by the relative cone outputs



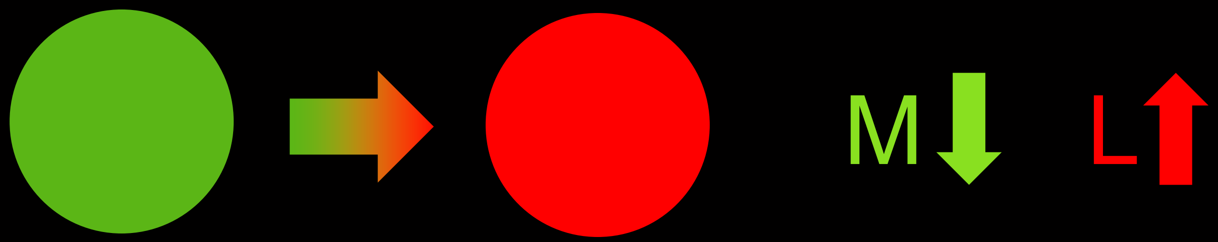
Colour is encoded by the relative cone outputs



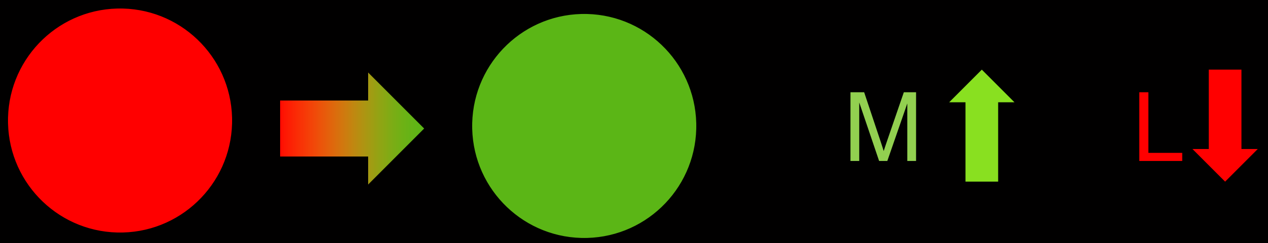
Because there are three univariant cones in the eye, human colour vision is a three-variable “trichromatic” system that depends on the relative outputs of the three cones.

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…

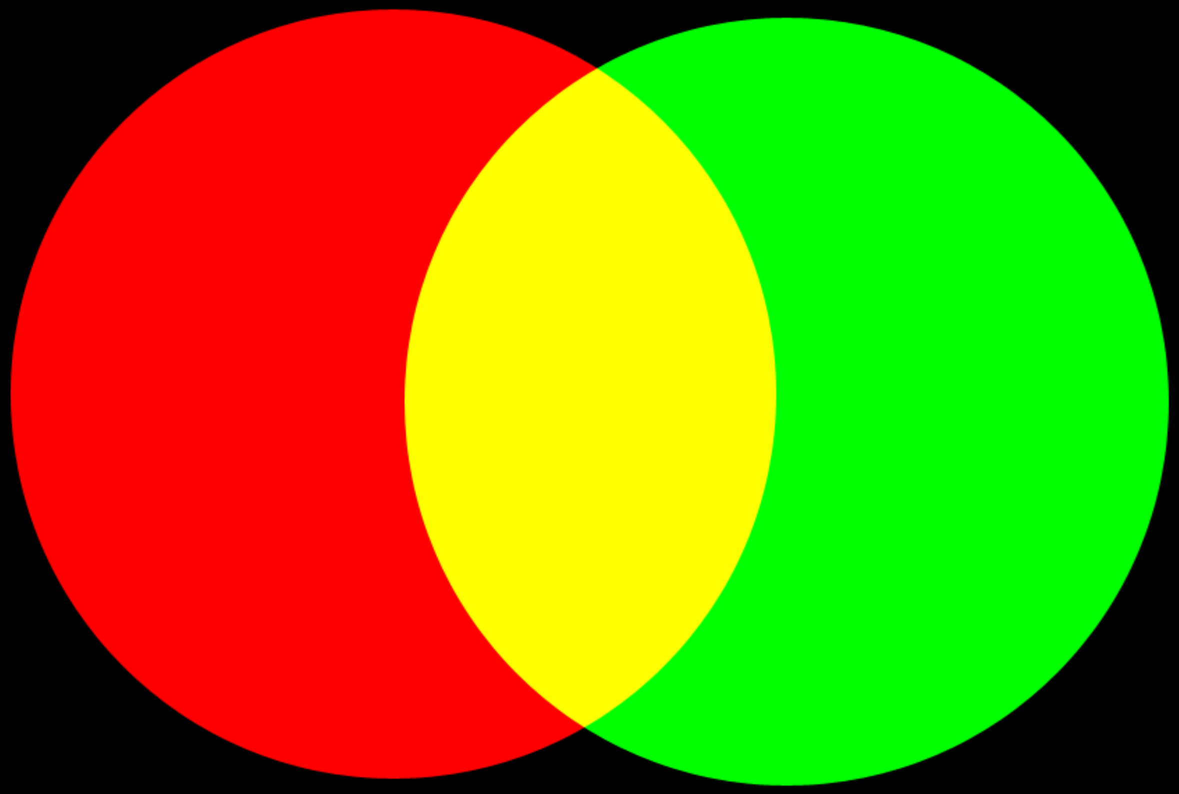
TRICHROMACY

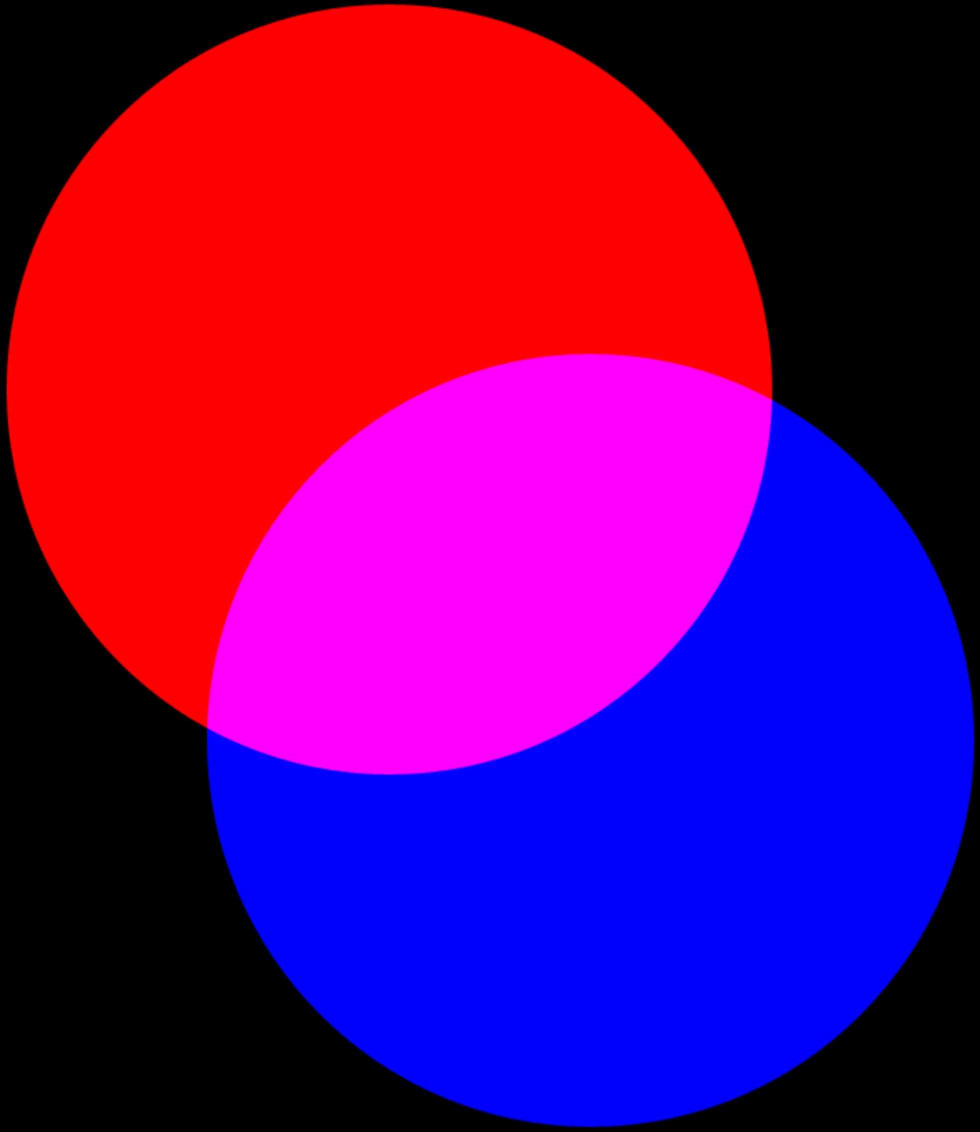
Because we have just three univariant cones, coloured lights are entirely defined by the three cone excitations they produce.

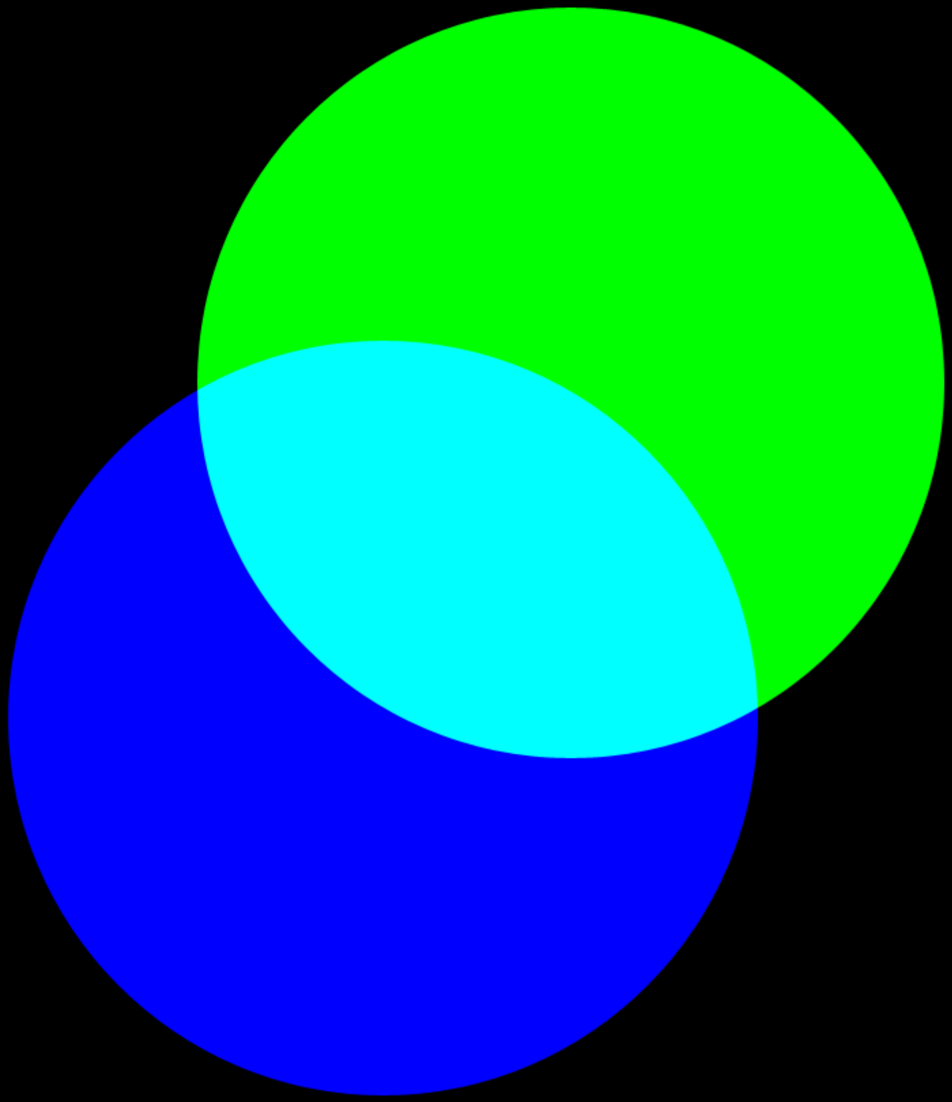
Any pairs of lights that produce the *same* triplet of excitations must be indistinguishable.

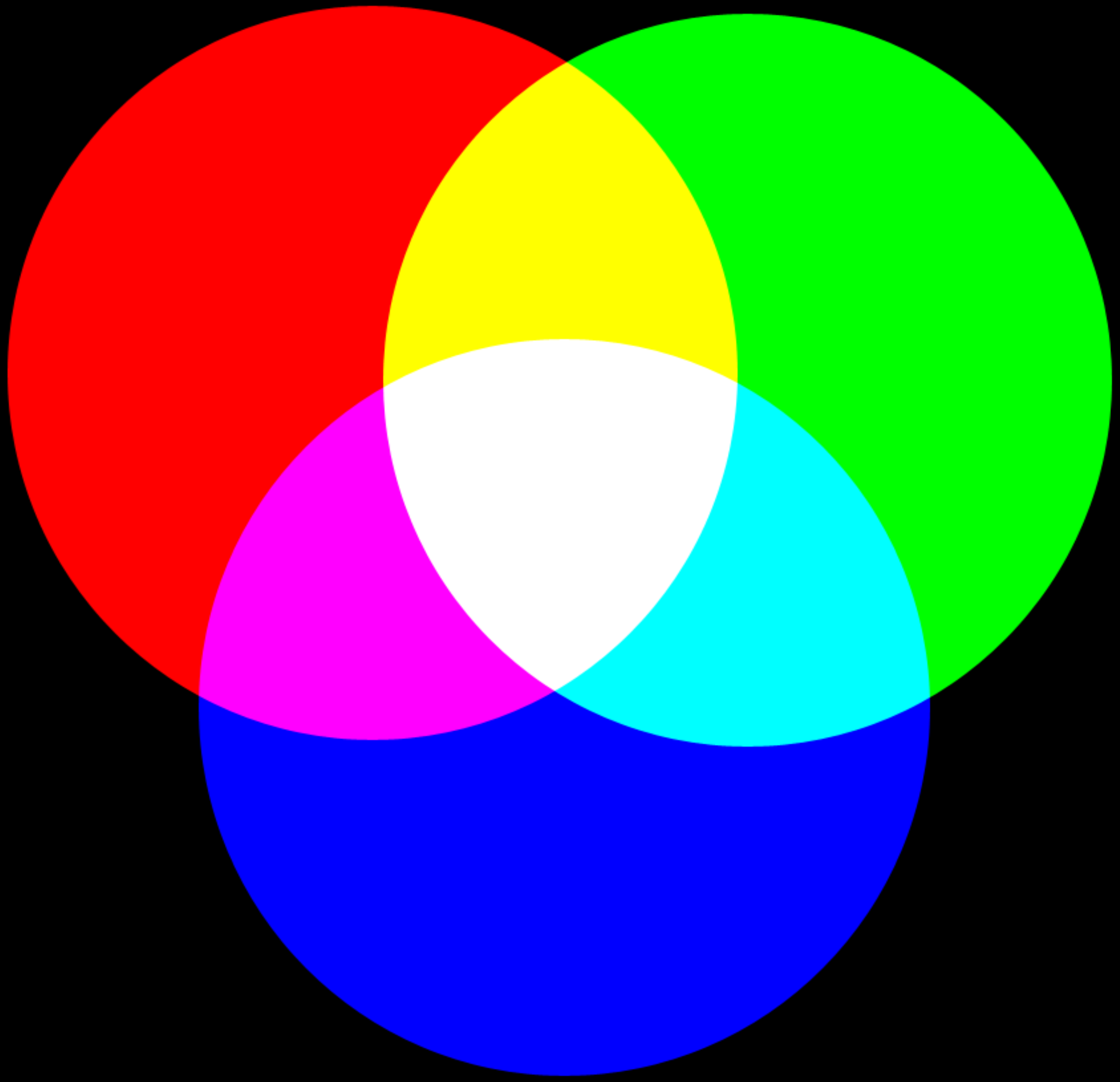
Pairs of lights that are physically different but indistinguishable are known as “metamers”.

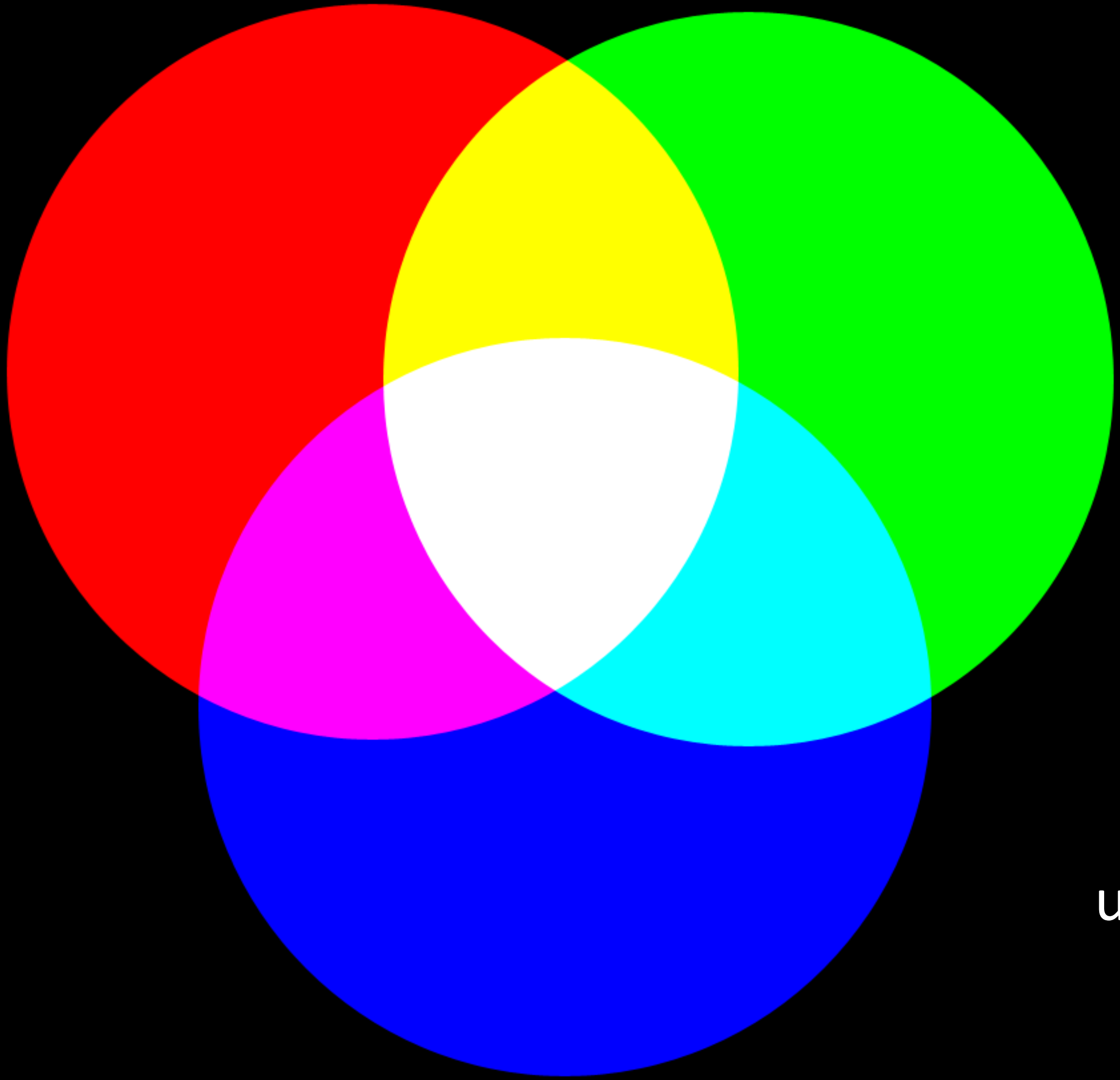
There are many metamers…



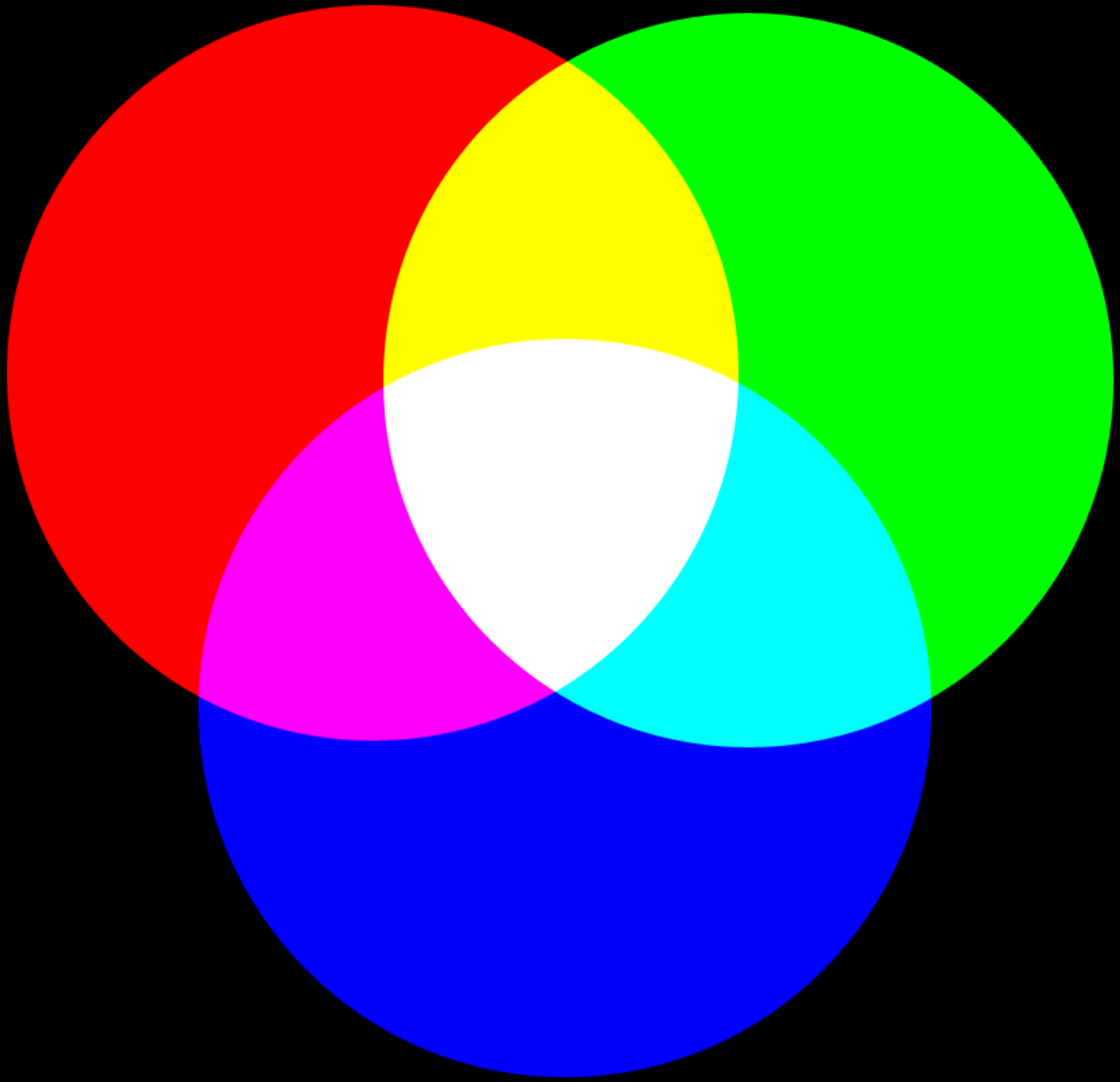




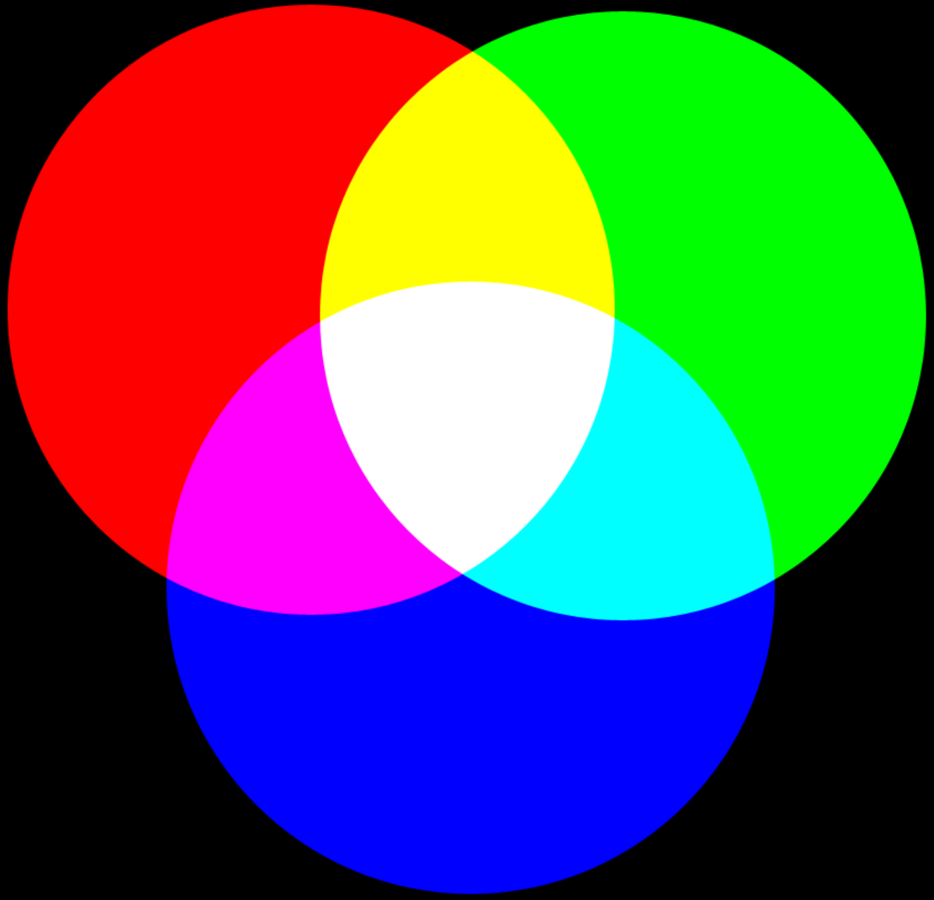




Before we knew about the underlying biology, additive colour mixing done in the 19th century revealed that colour vision was…



TRICHROMATIC



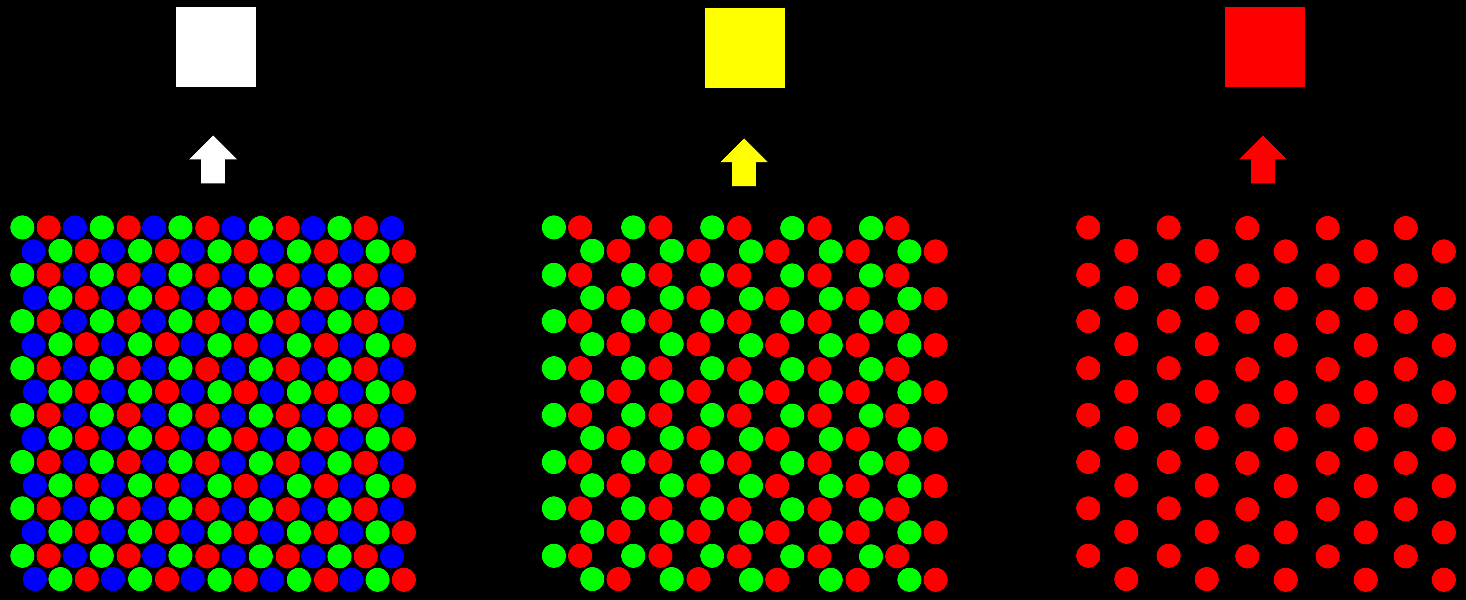
Trichromacy means that colour vision at the input to the visual system is relatively simple.

It is a 3 variable system…

Colour TV

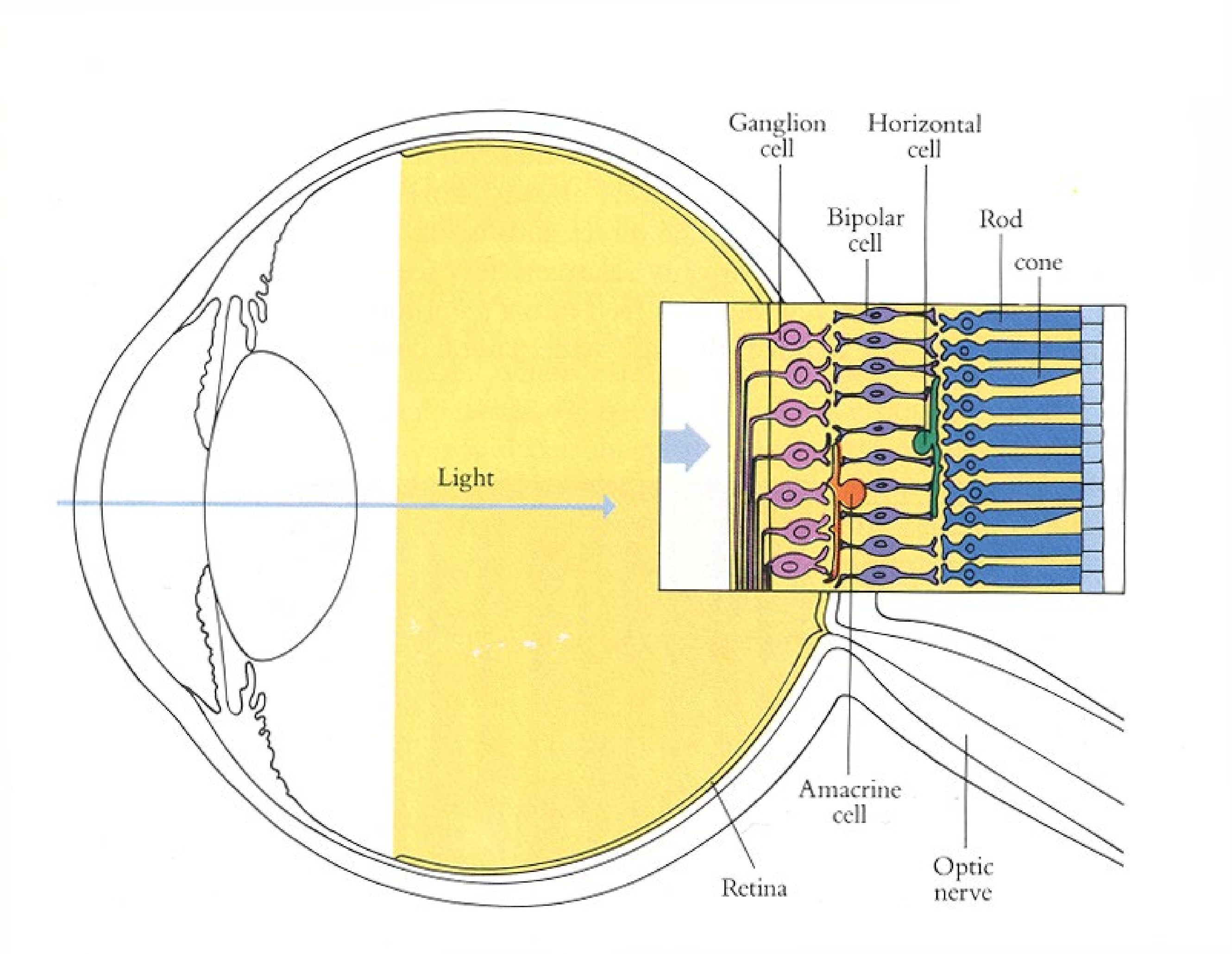
Trichromacy is exploited in colour reproduction, since the myriad of colours perceived can be produced by mixing together small dots of three colours.

The dots produced by a TV or projector are so small that they are mixed together by the eye and thus appear as uniform patches of colour.



POSTRECEPTORAL COLOUR VISION

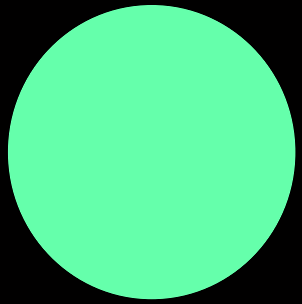
But what happens next (i.e., how is colour encoded after the photoreceptors)?



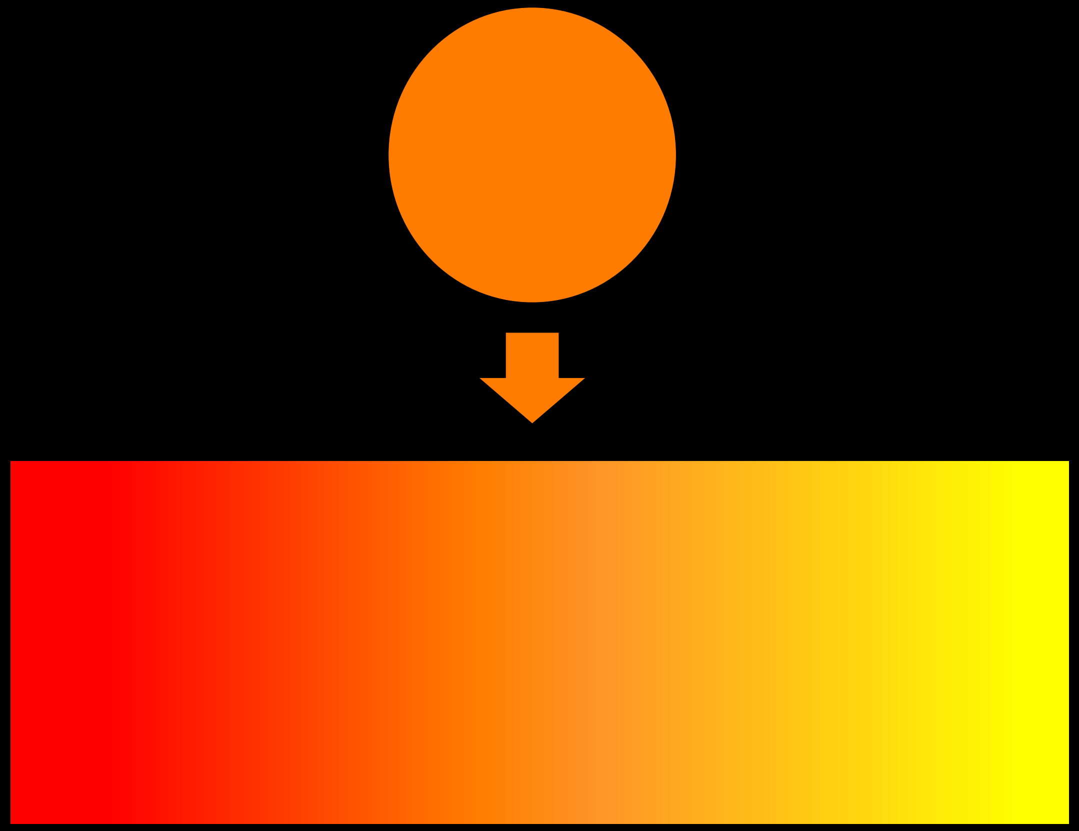
Colour phenomenology

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

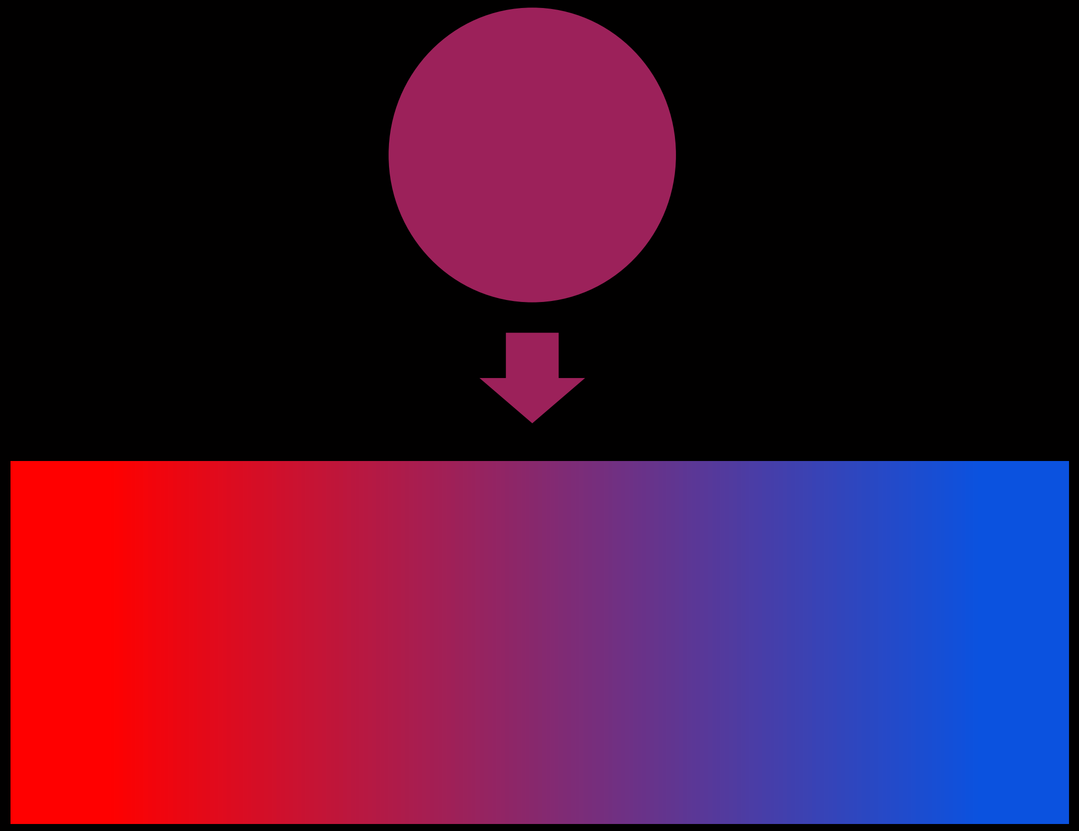
Imagine a single patch of colour inside a dark surround



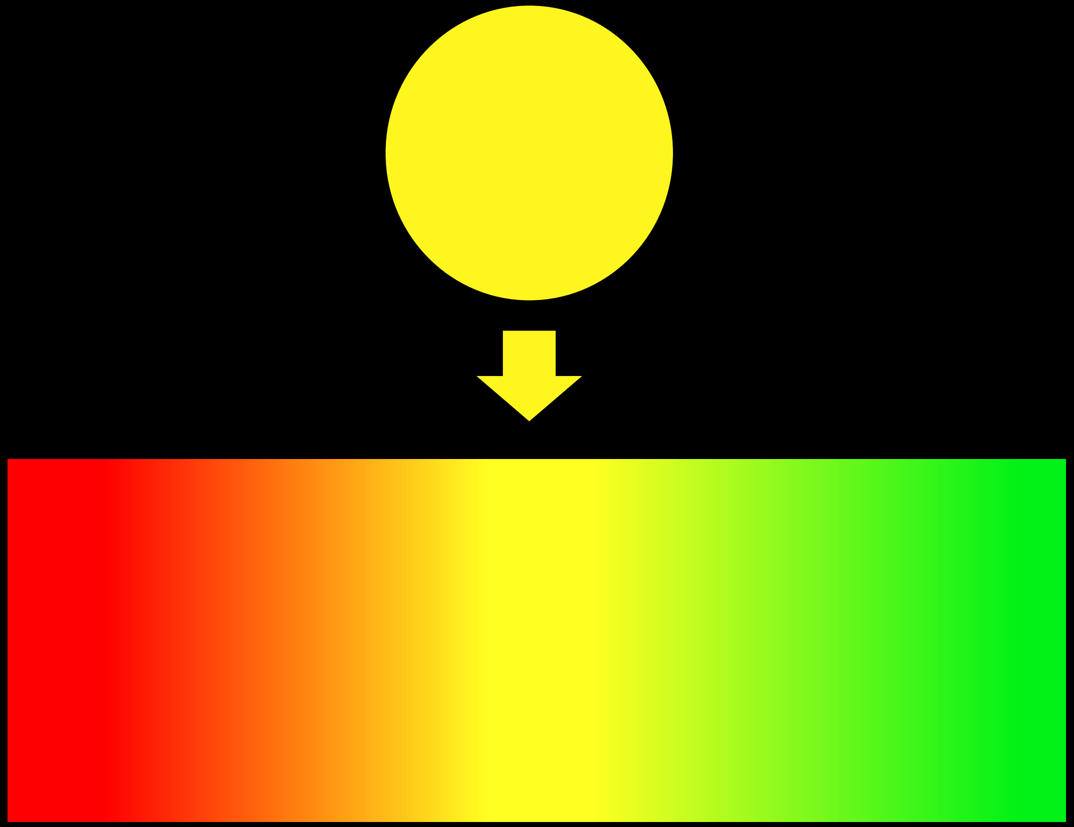
- Which pairs of colours can coexist in a single, uniform patch of colour?
- Which pairs can never coexist?



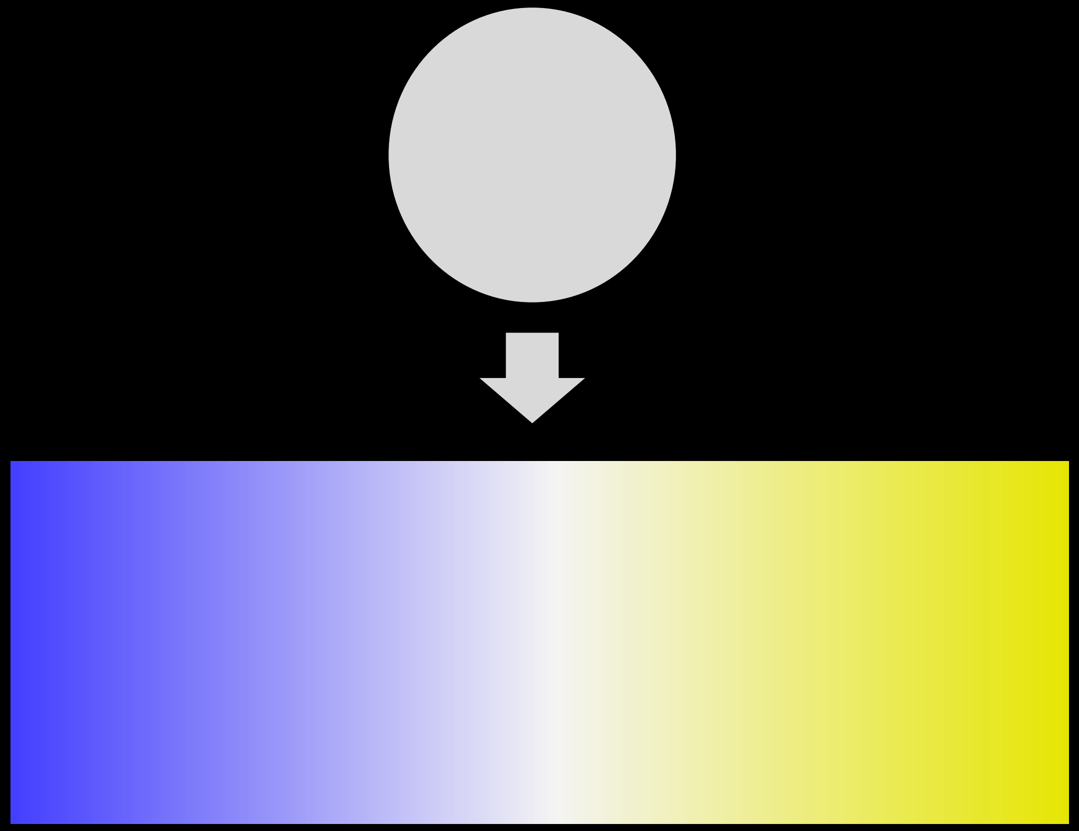
Can a single patch be reddish-yellow? ✓



Can it be reddish-blue? ✓



Can it be reddish-green?



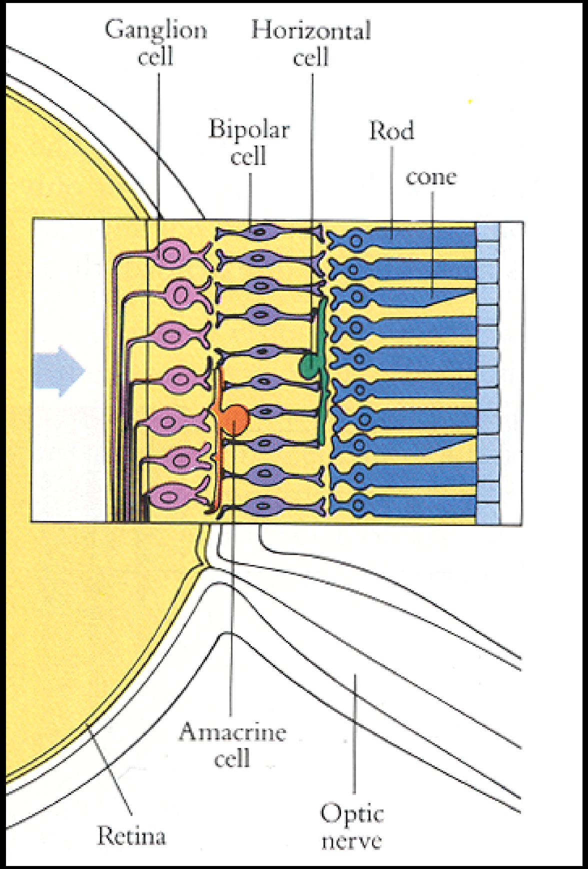
Can it be bluish-yellow? ✗

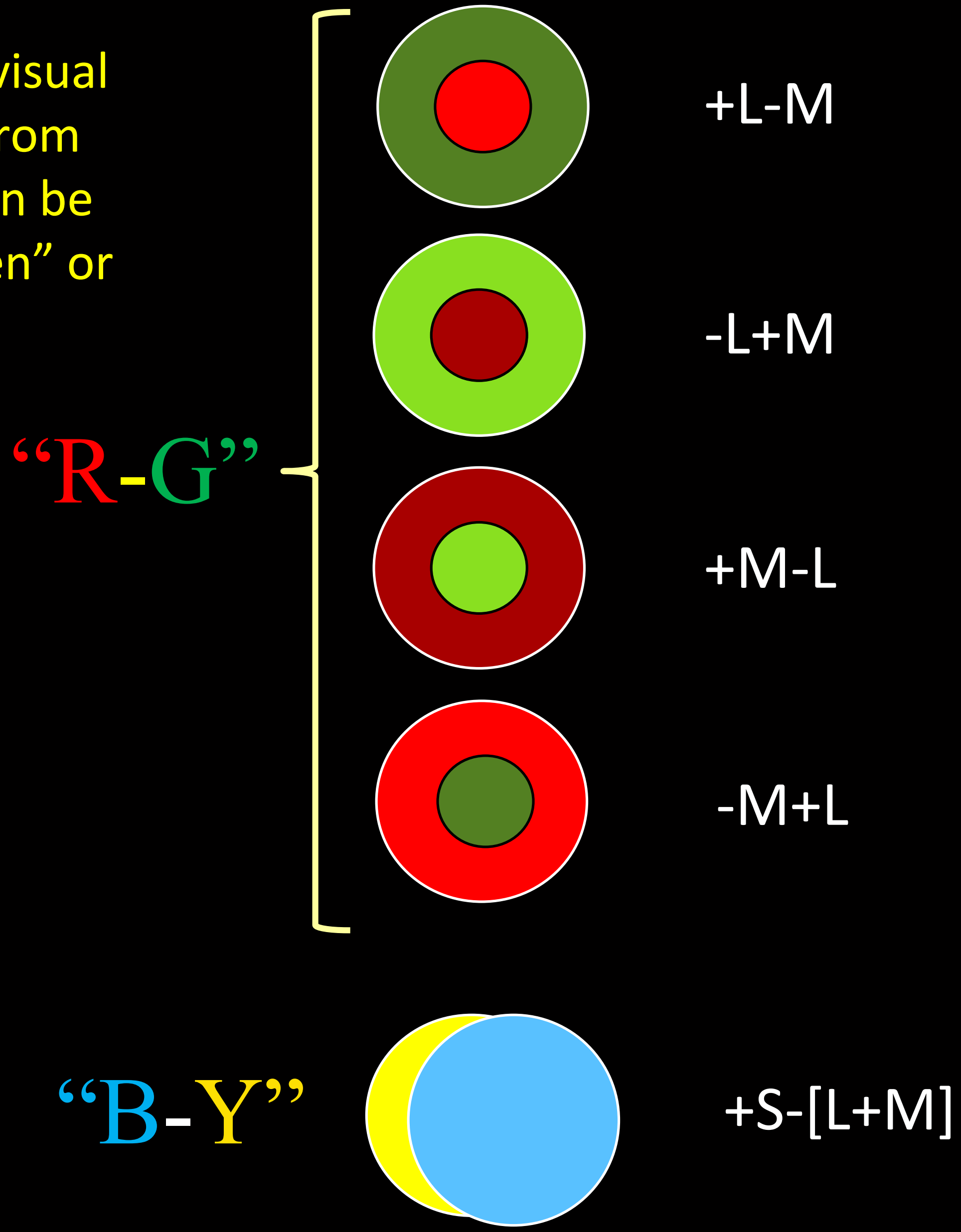
The colour opponent theory of Hering

is opposed to R-G

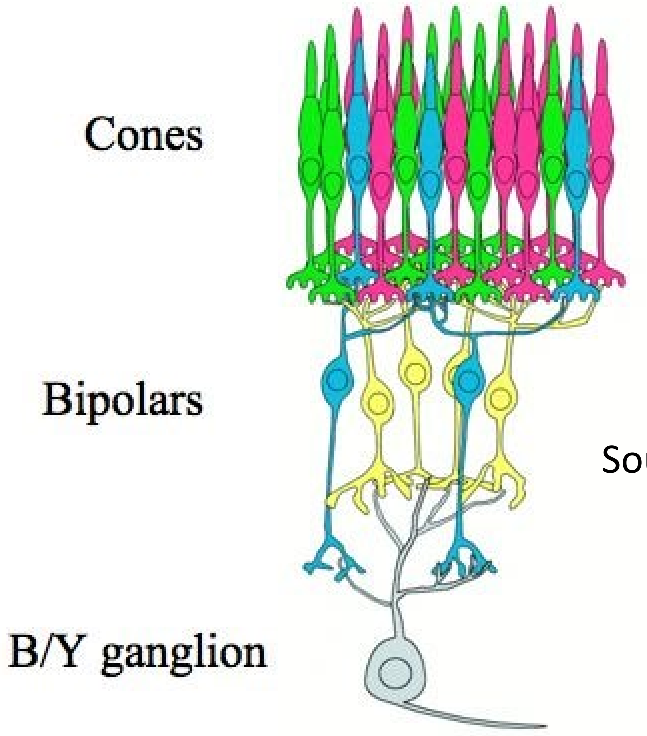
is opposed to Y-B

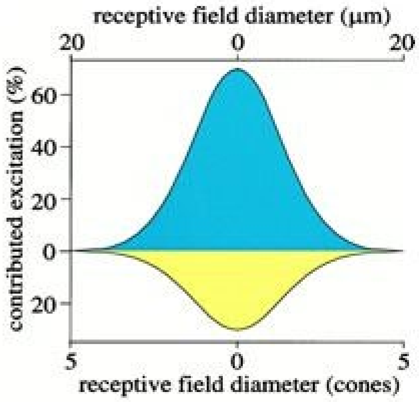
And indeed cells in the early visual pathway oppose the signals from different cone classes and can be loosely classified as “red-green” or “blue-yellow” opponent.



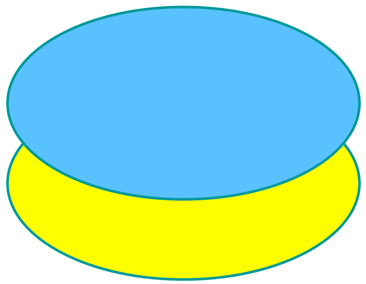


Blue/yellow pathway

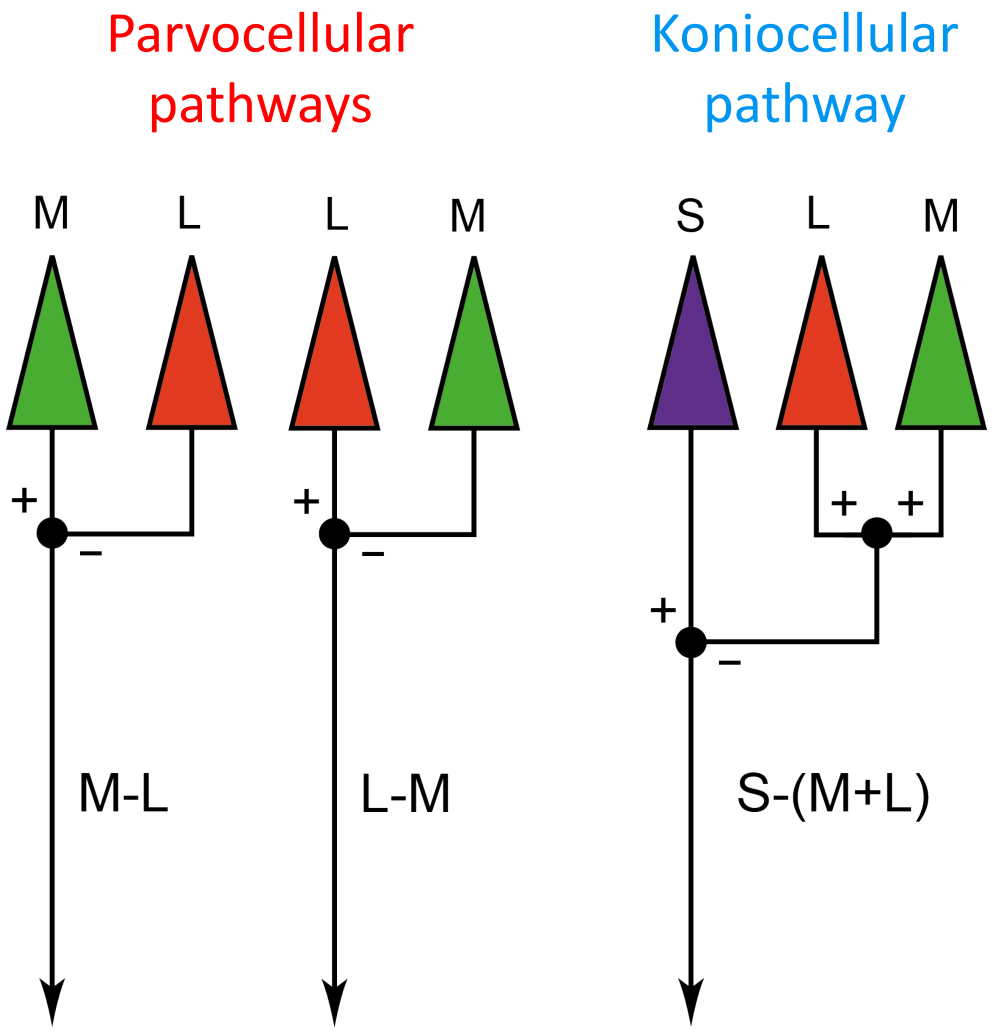




Source: David Heeger

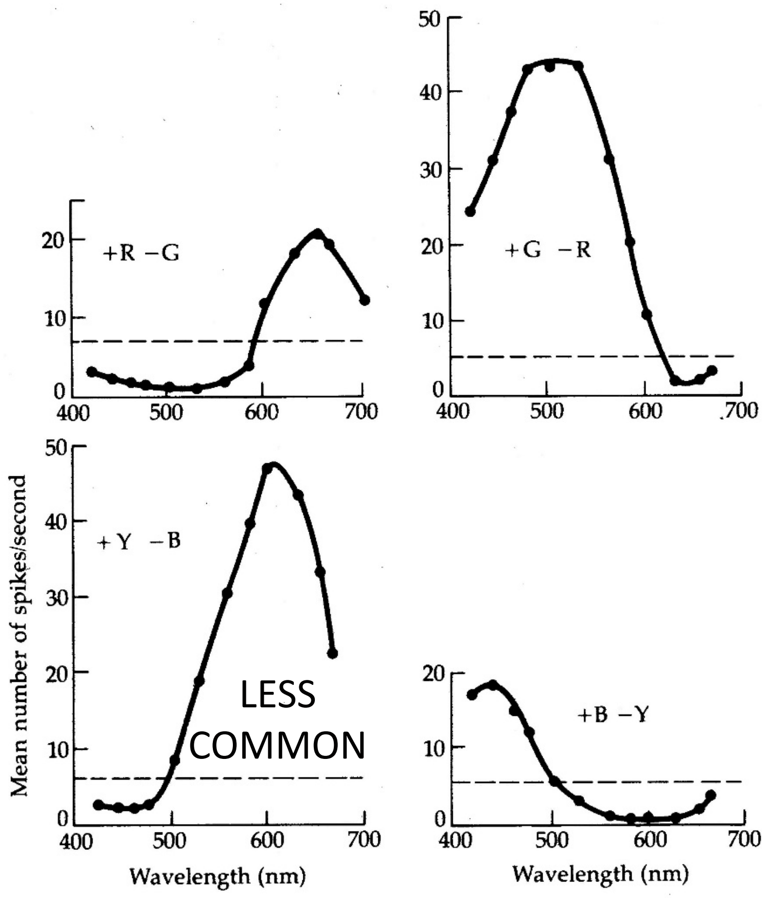


“Koniocellular” pathway



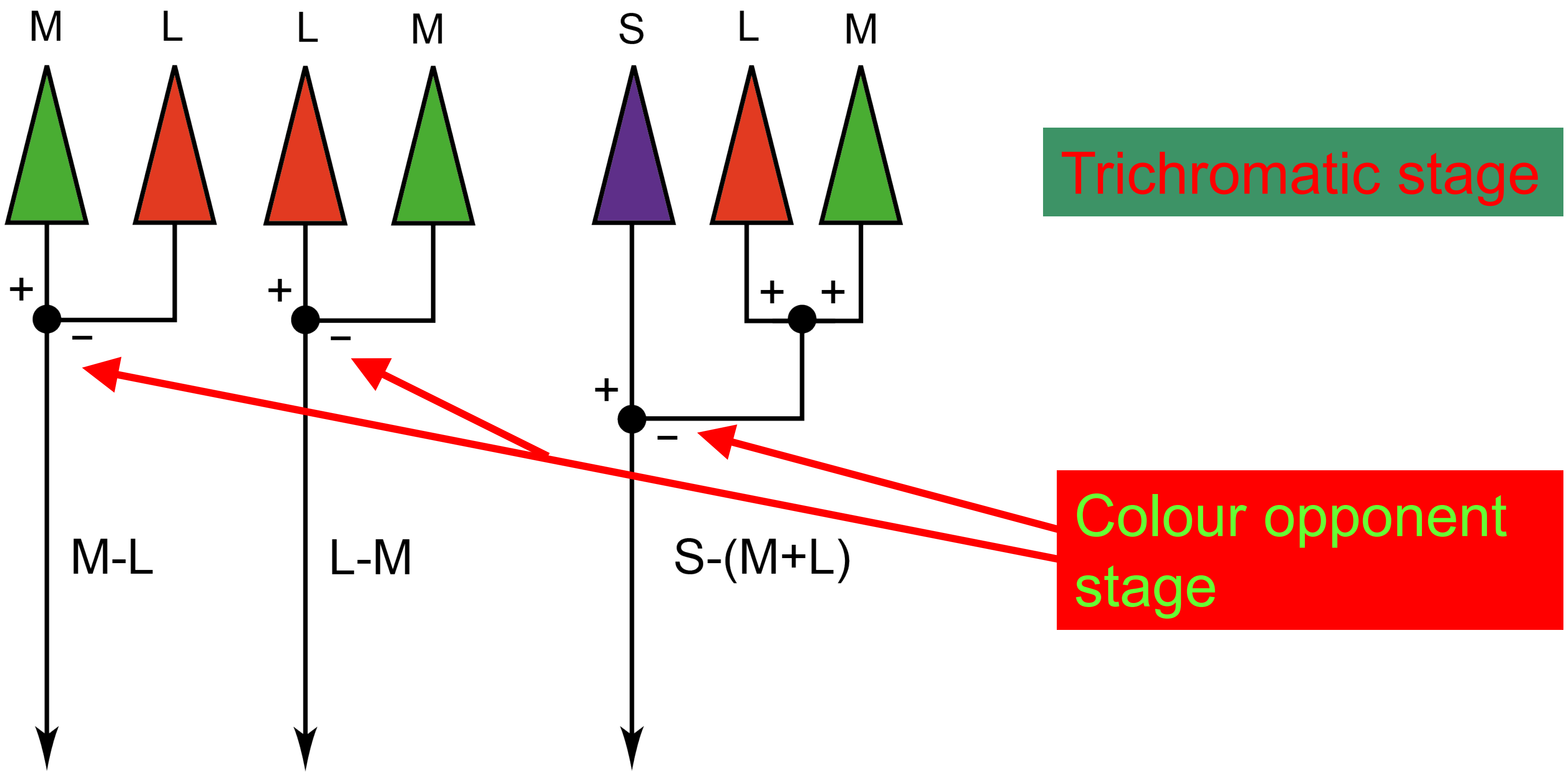
Chromatic pathways

LGN cell responses



8 AVERAGE FIRING RATES of large sample of cells of each of six LGN cell types as a function of wavelength. Top four cells are spectrally opponent ones and bottom two are spectrally nonopponent cells. The cells on the left are, in principle, "mirror images" of those on the right.

Summary



Chromatic pathways

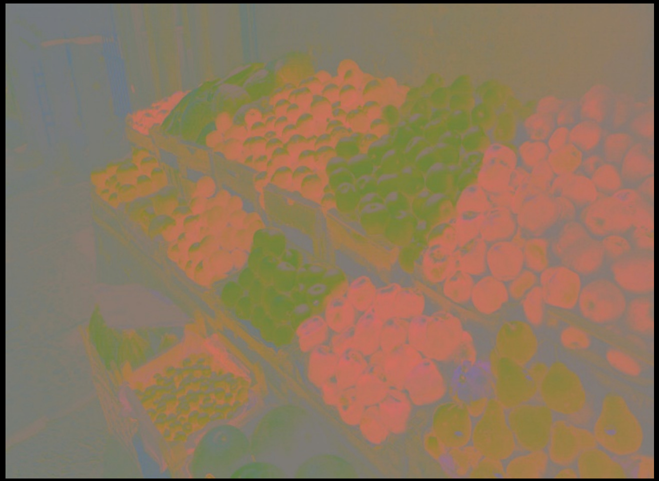
So we’ve talked about colour (chromatic) vision, but what about “luminance” (achromatic) vision?

Colour…

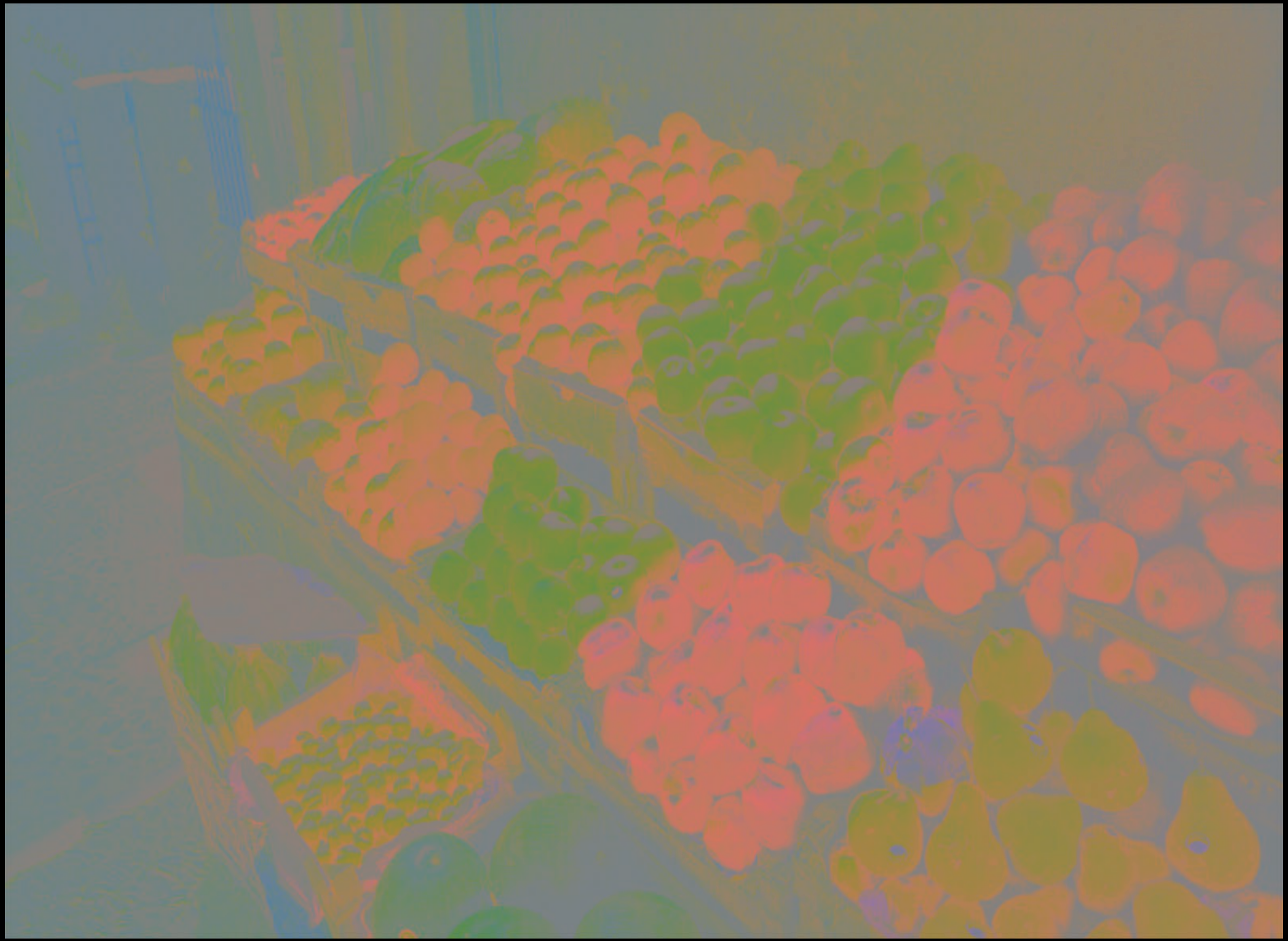
Split the image into...

ACHROMATIC COMPONENTS

CHROMATIC COMPONENTS



CHROMATIC COMPONENTS



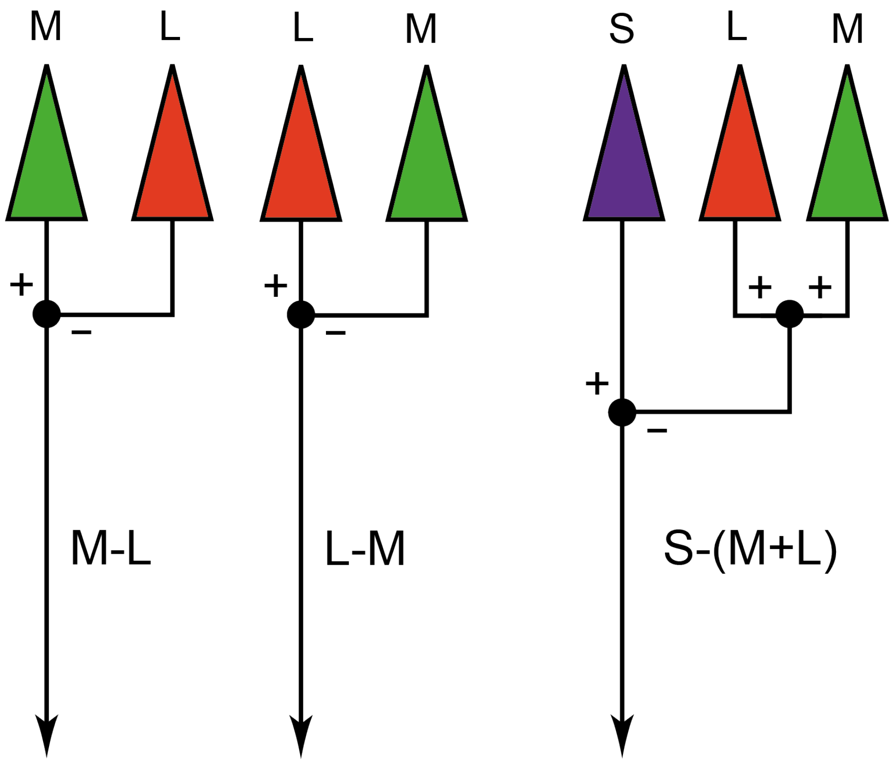
By itself chromatic information provides relatively limited information…

ACHROMATIC COMPONENTS

Achromatic information important for fine detail …

Achromatic and chromatic cone vision (colour and luminance)

In addition to neural pathways that signal colour there are also pathways that signal intensity or luminance:



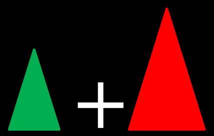
Chromatic pathways

Luminance is encoded by summing the L- and M-cone signals:

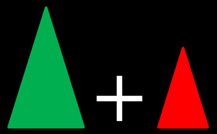
Blue light

L+M 

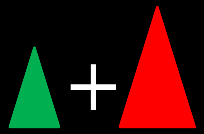
Red light



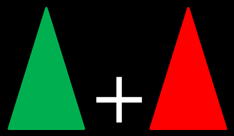
Green light

L+M 

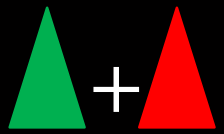
Purple light



Yellow light

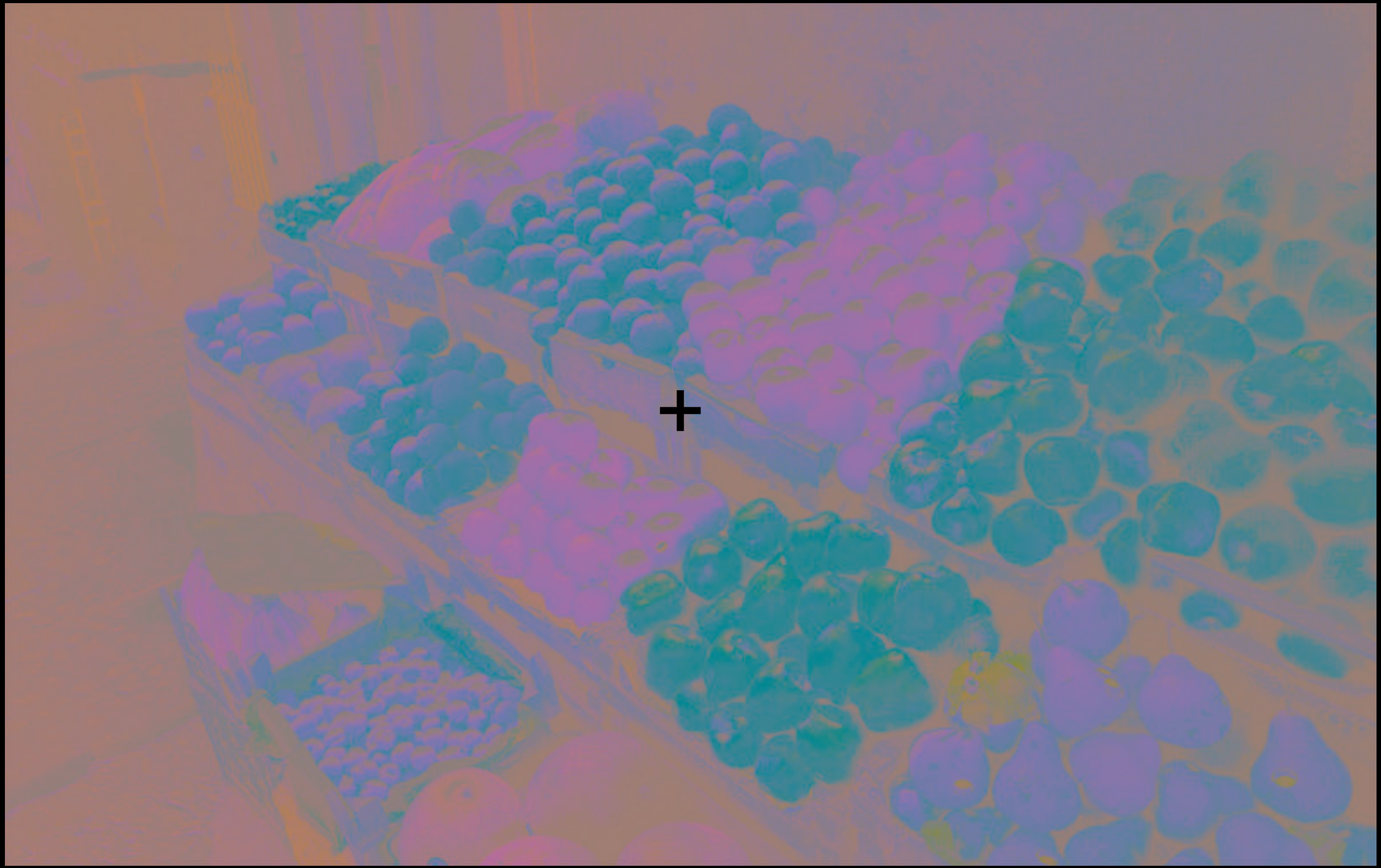
L+M 

White light

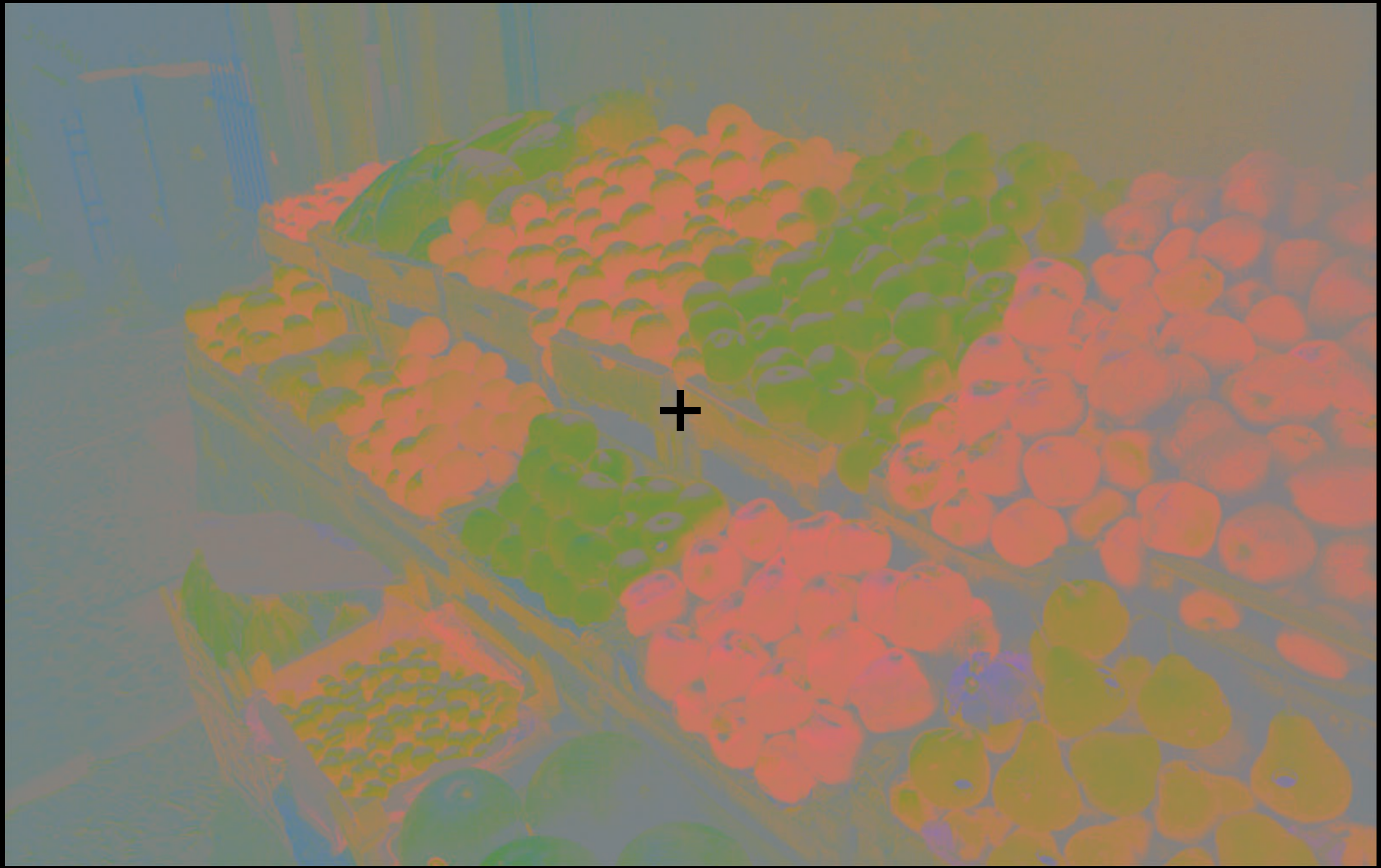


Colour is in many ways secondary to luminance


Souvlaki

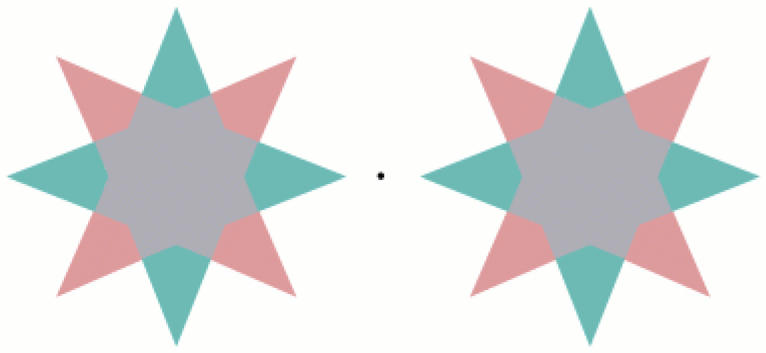



Souvlaki



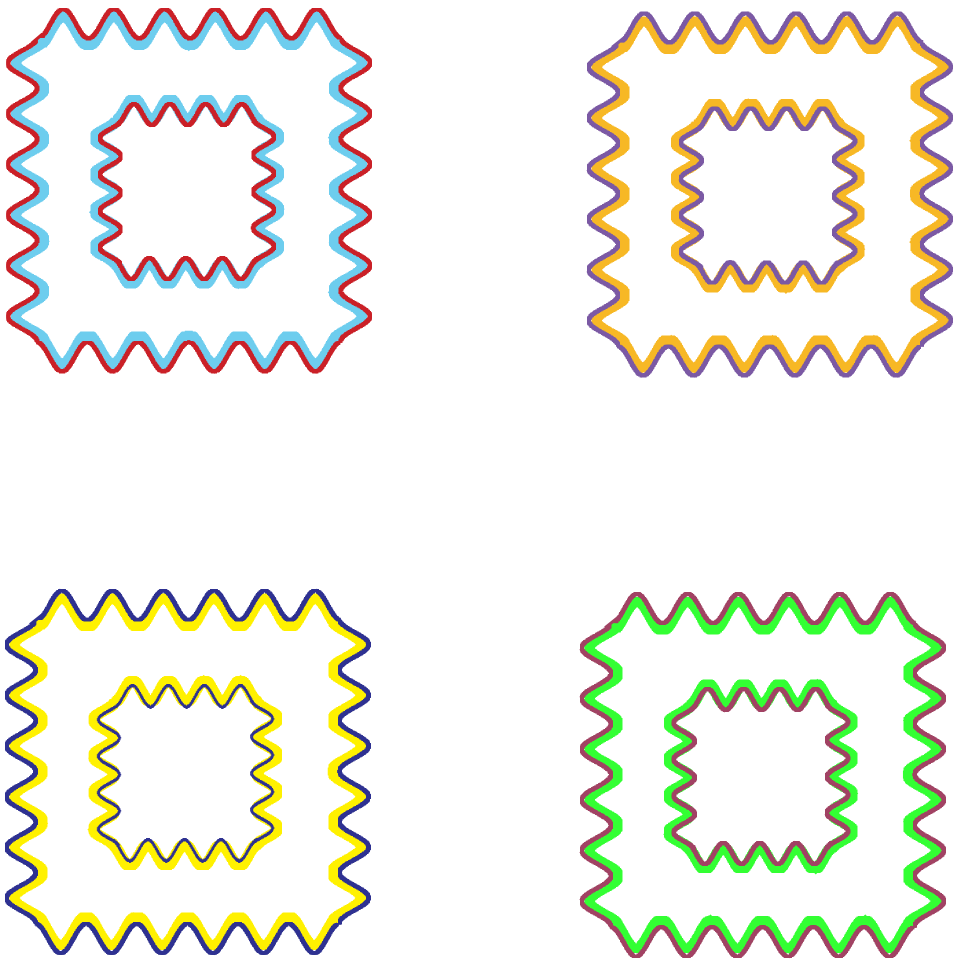

Souvlaki


Souvlaki

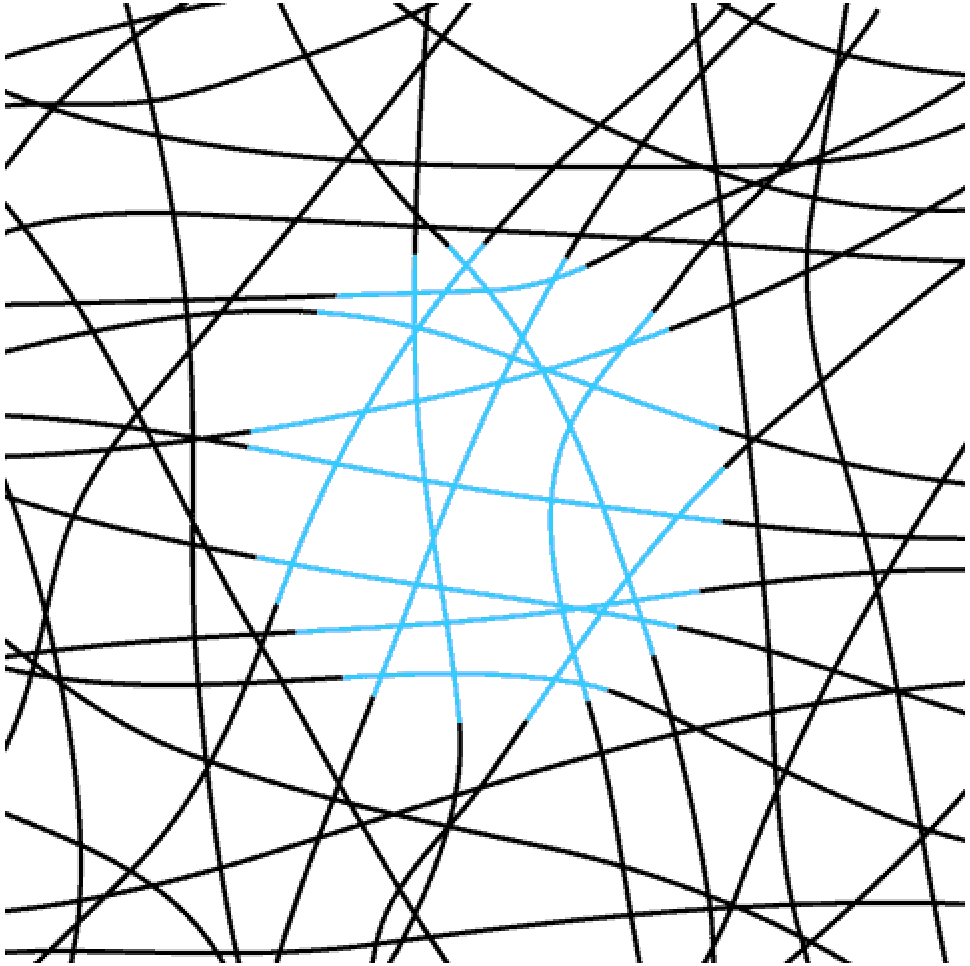


Rob van Lier, Mark Vergeer & Stuart Anstis

Watercolour effect

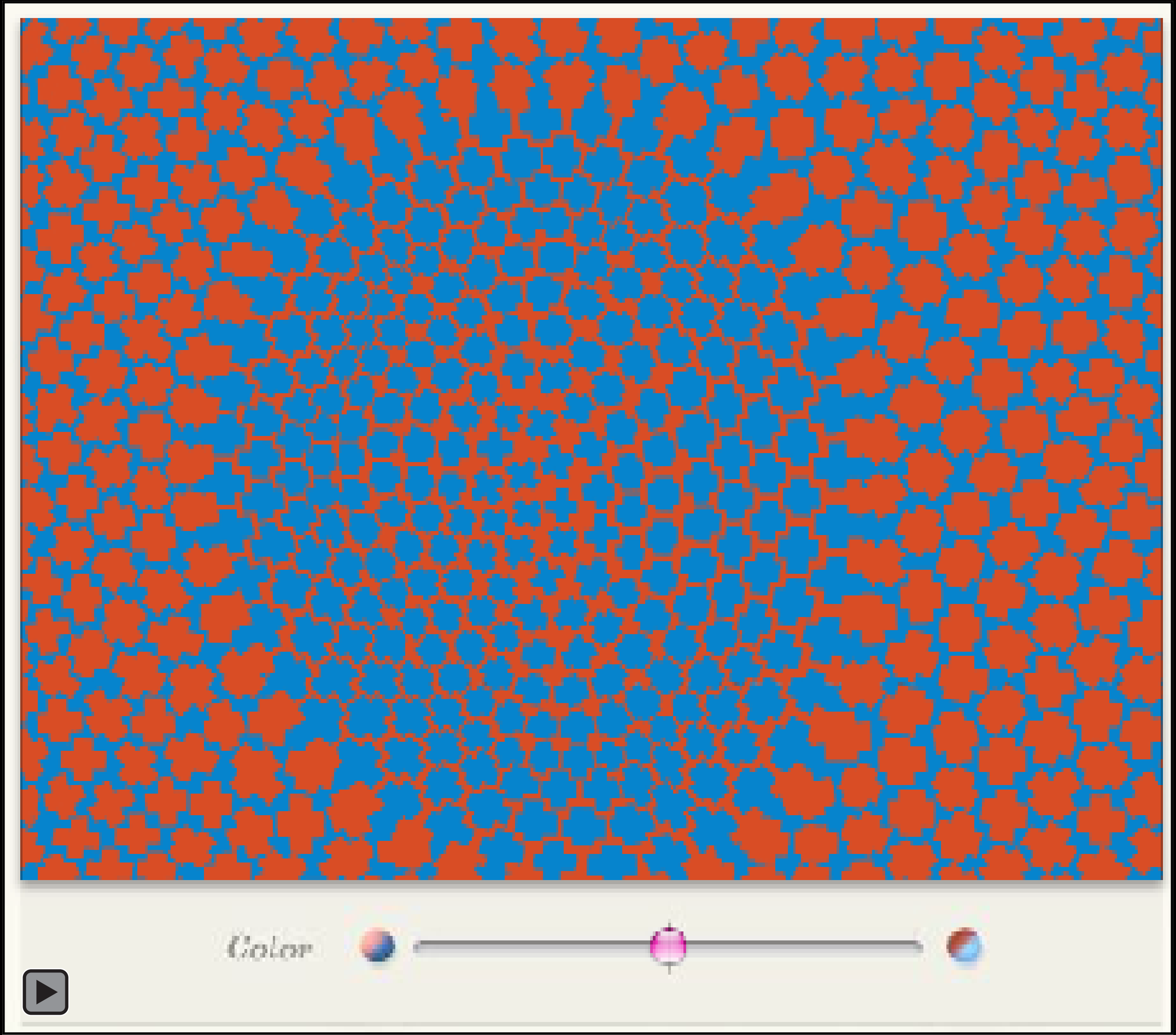


Neon Spreading



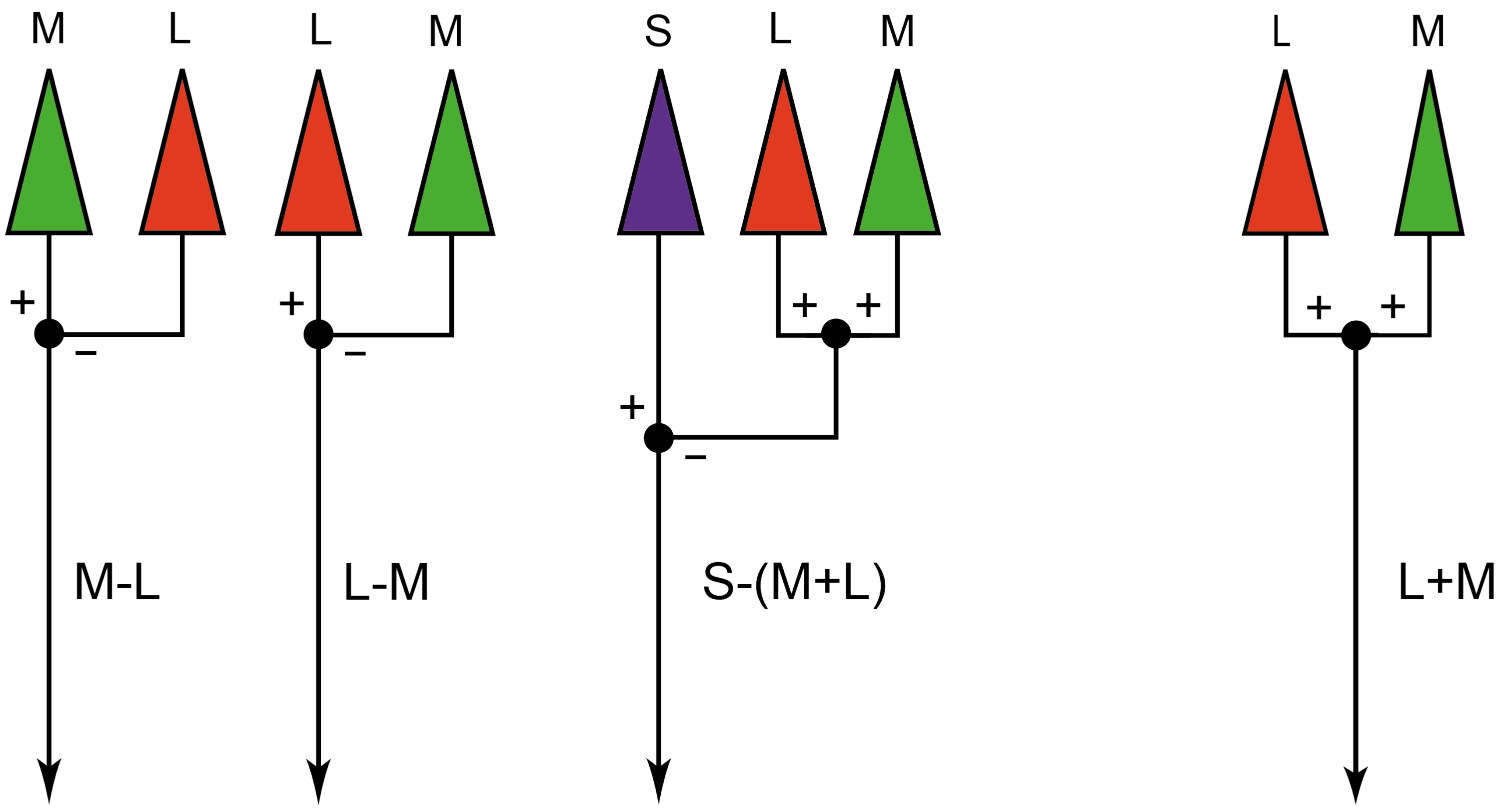
www.blelb.com

Interesting artistic effects occur when vision depends only on colour (and not on luminance)



'Plus Reversed', Richard Anuszkiewicz, 1960

What are the postreceptoral neural substrates of the chromatic and luminance pathways?

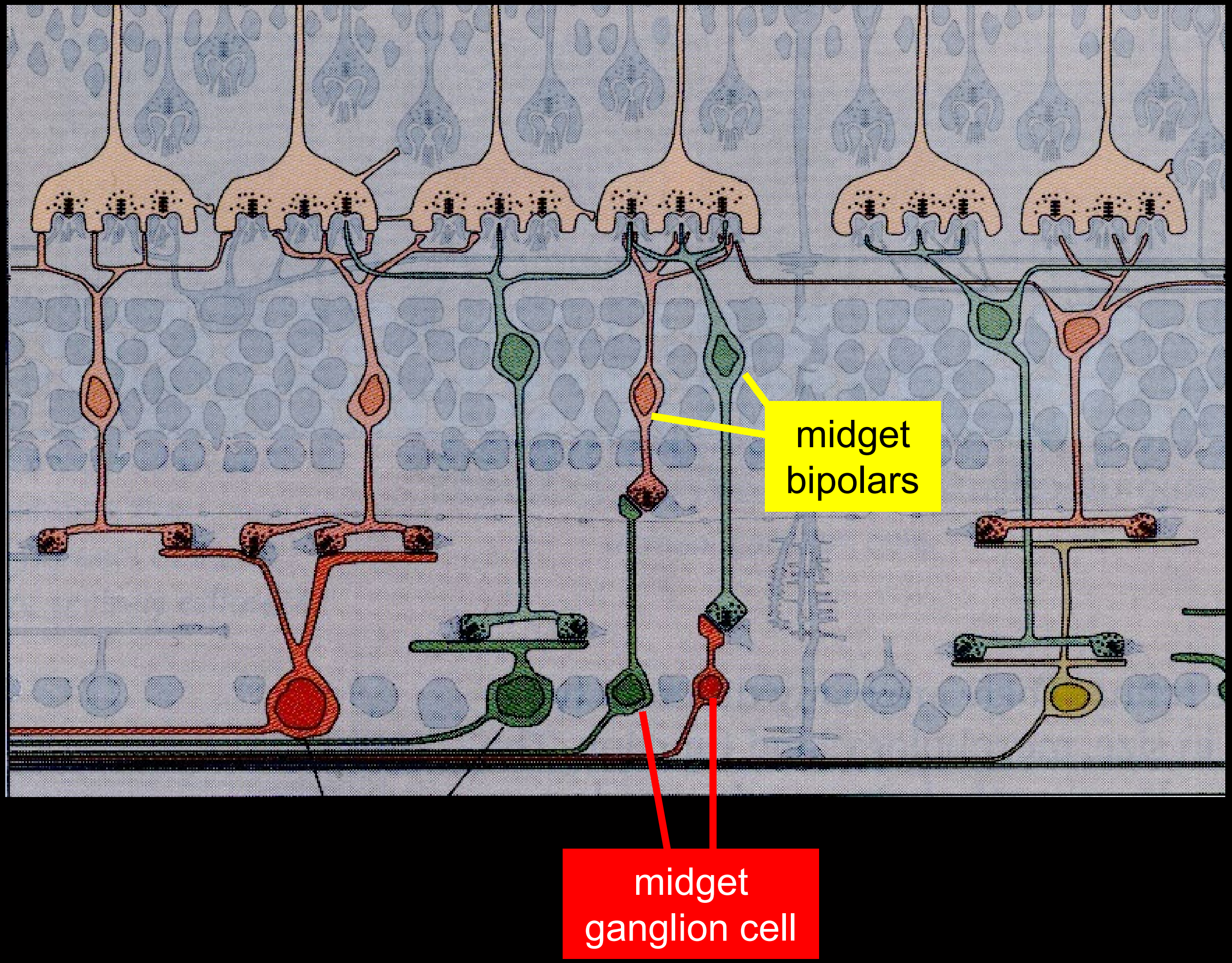


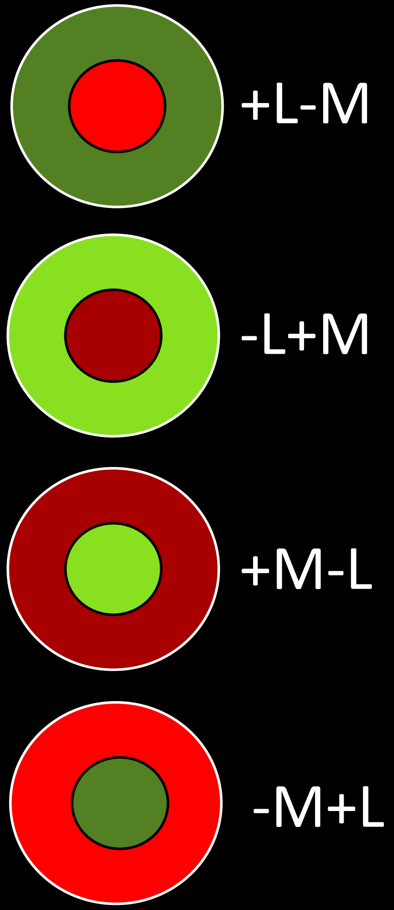
Chromatic pathways

Luminance pathway

Red-green chromatic pathways have been linked to the parvocellular retinal stream for L-M.

Parvocellular

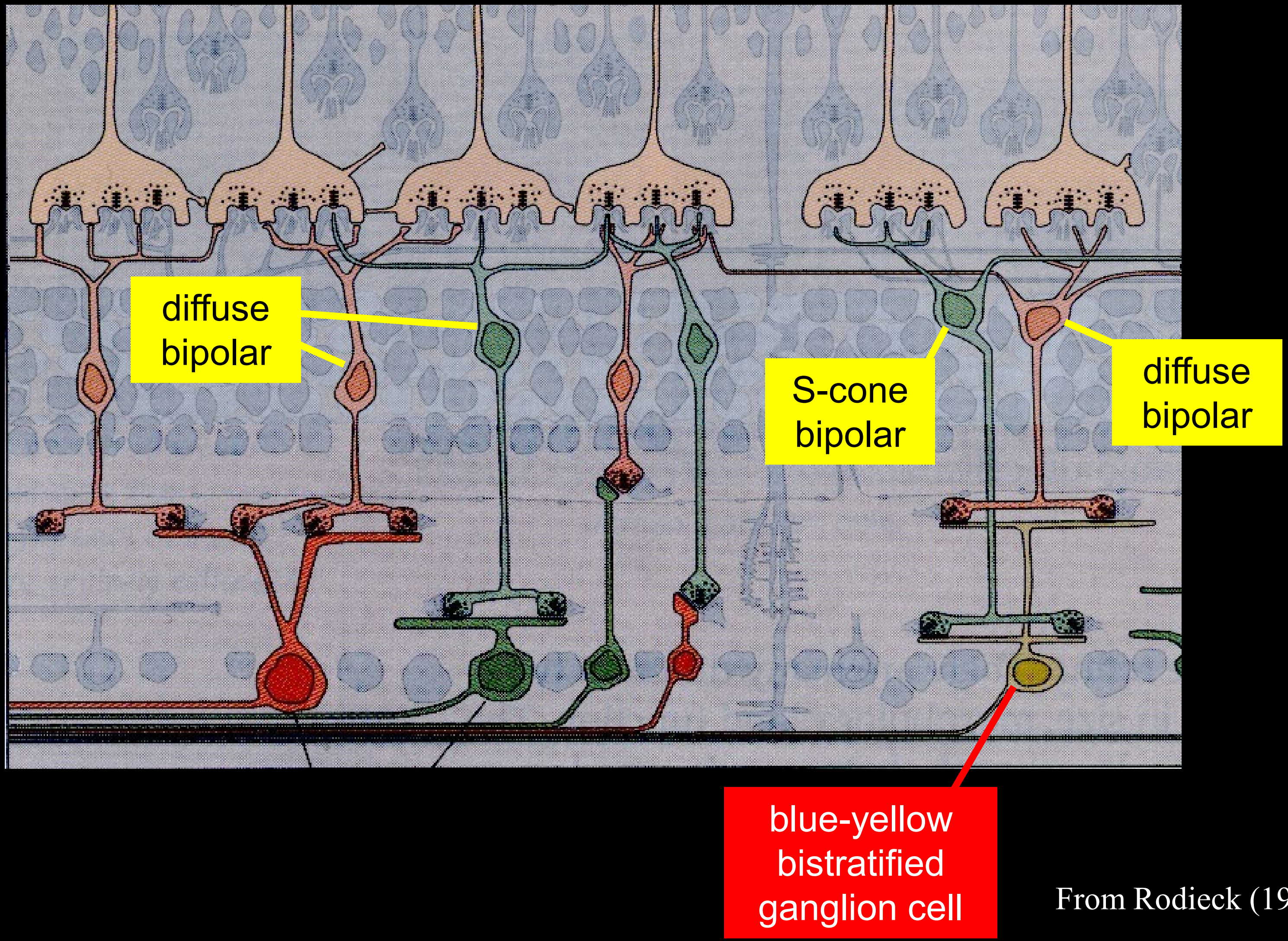




From Rodieck (1998)

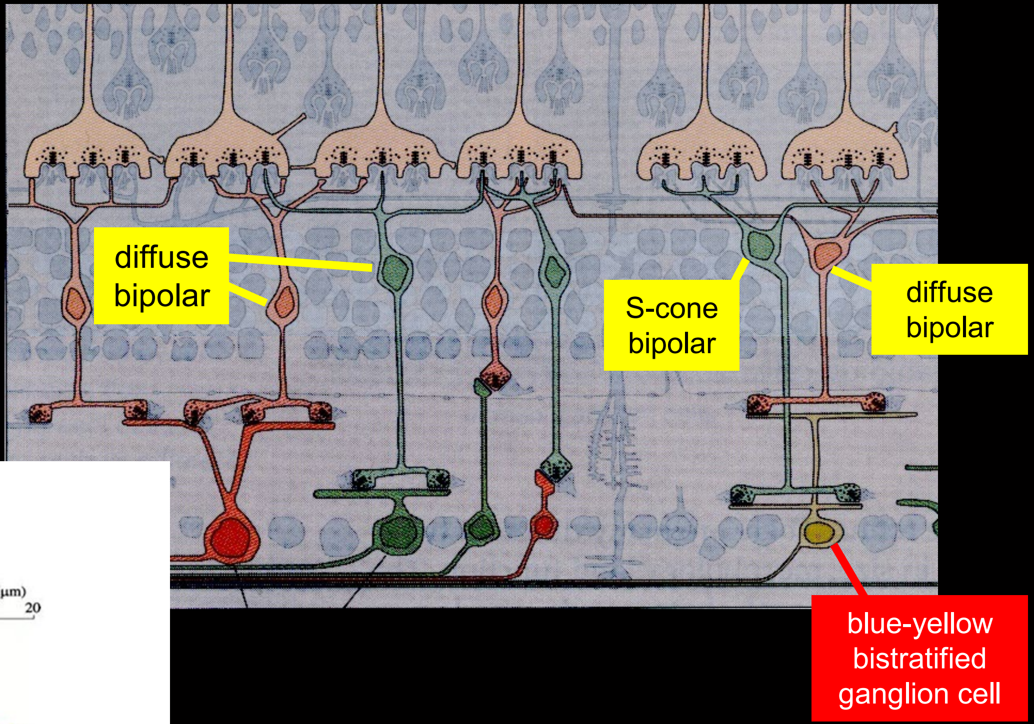
Blue-yellow chromatic pathways have been linked to the koniocellular stream…

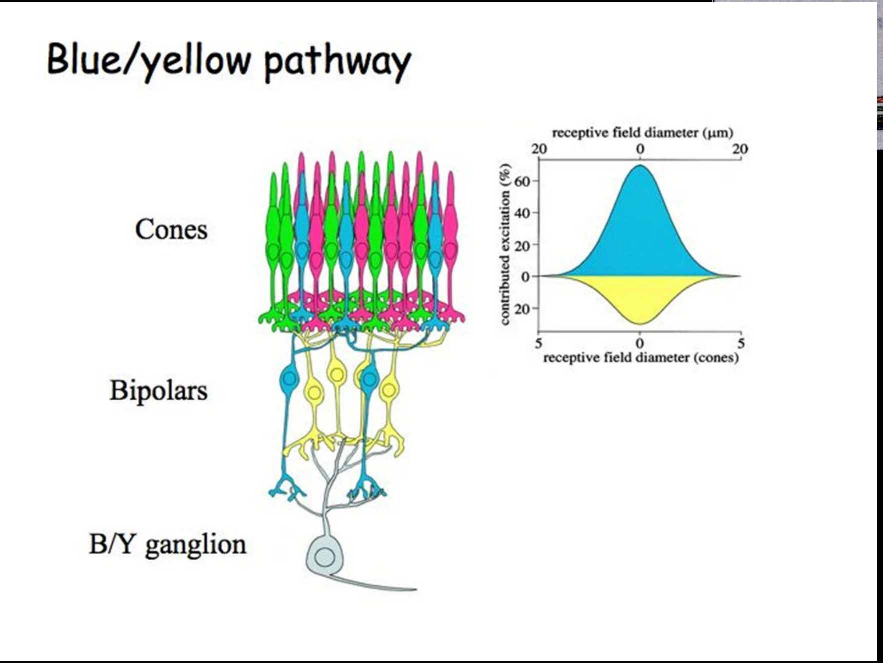
Koniocellular



From Rodieck (1998)

Koniocellular

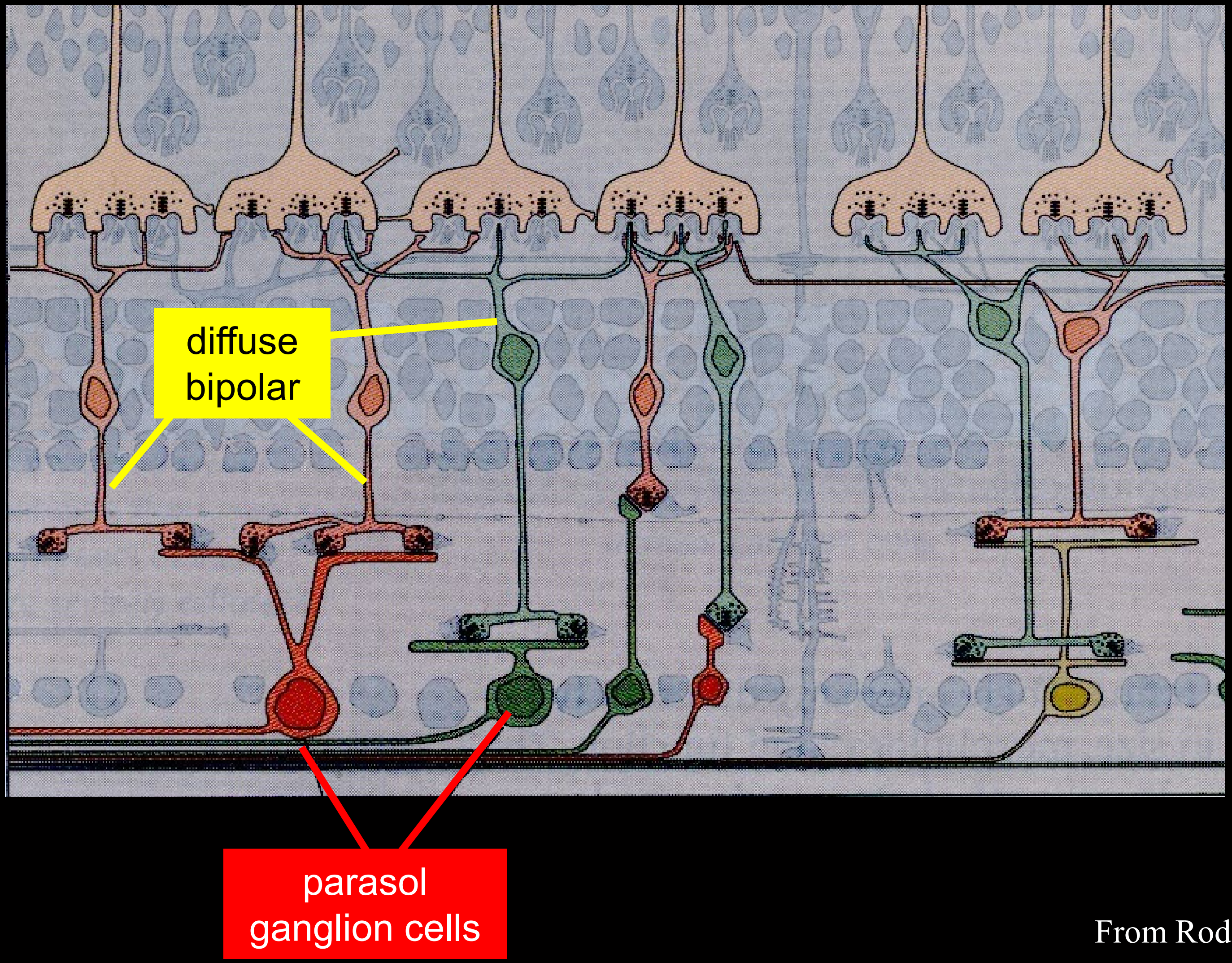




From Rodieck (1998)

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

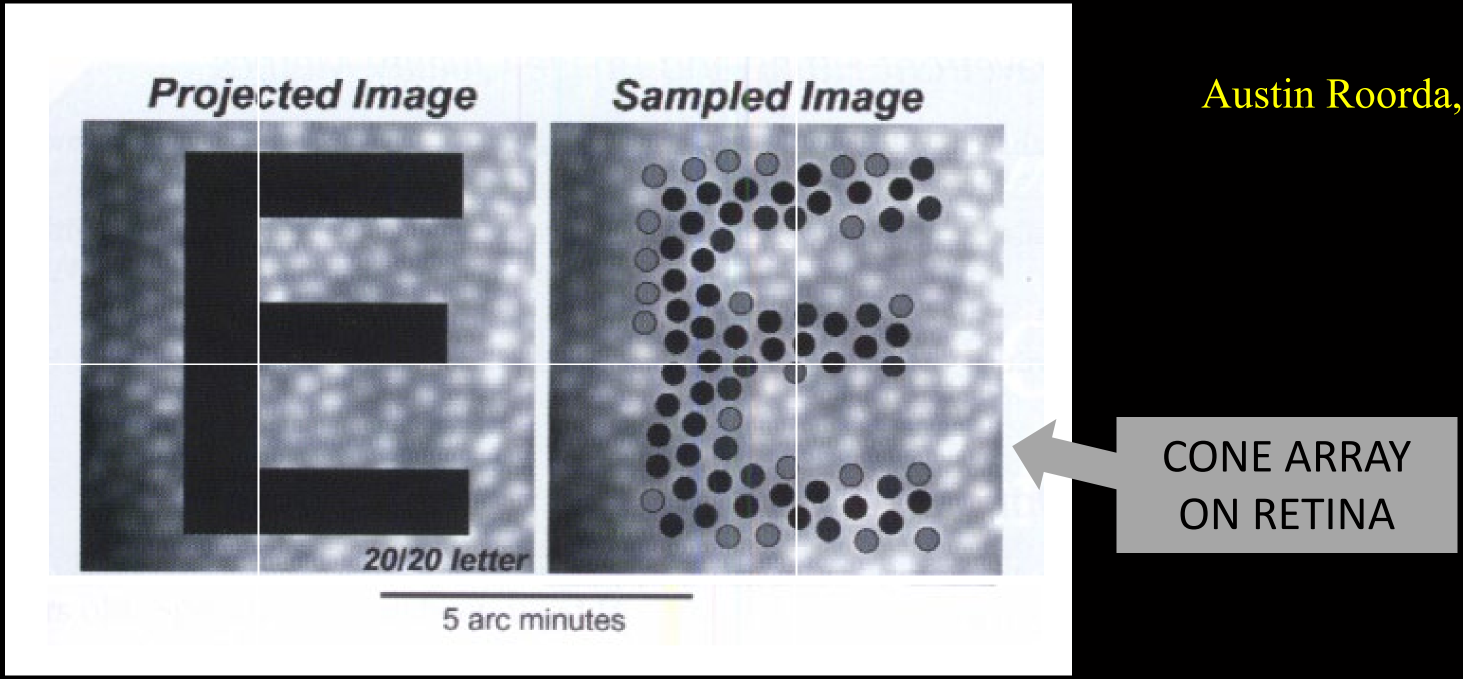
Magnocellular



From Rodieck (1998)

But the luminance pathways must be made of more than just the magnocellular stream.

Why? Consider spatial acuity…



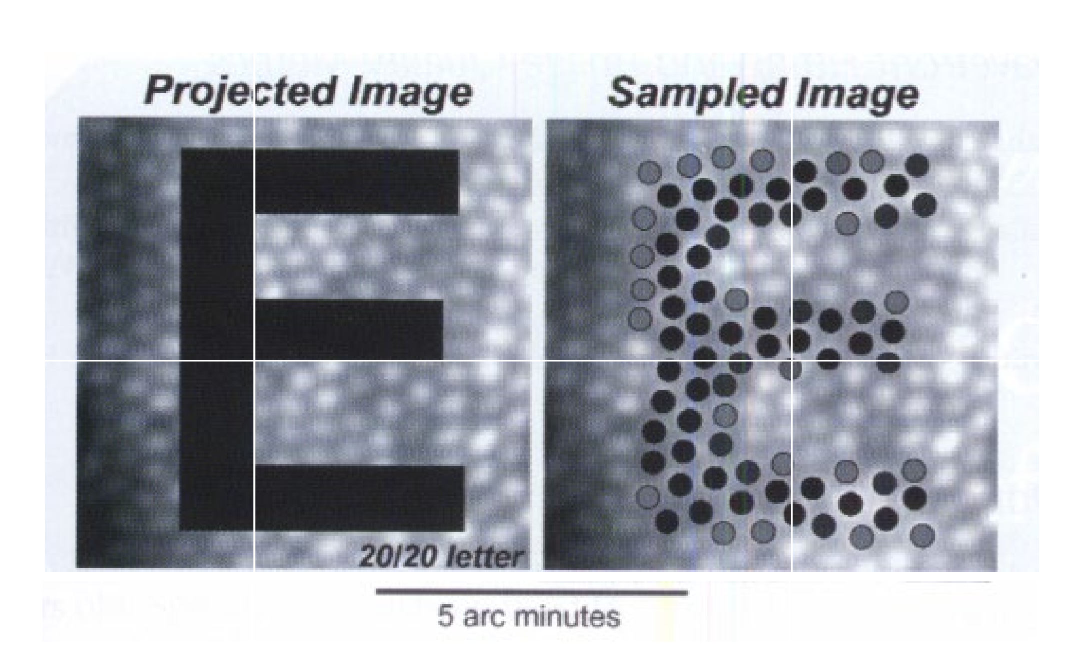
Austin Roorda, 2004

To be able to resolve this E, the image must be sampled at enough points.

The parvocellular pathway, with its one-to-one cone to bipolar connections, provides enough samples.

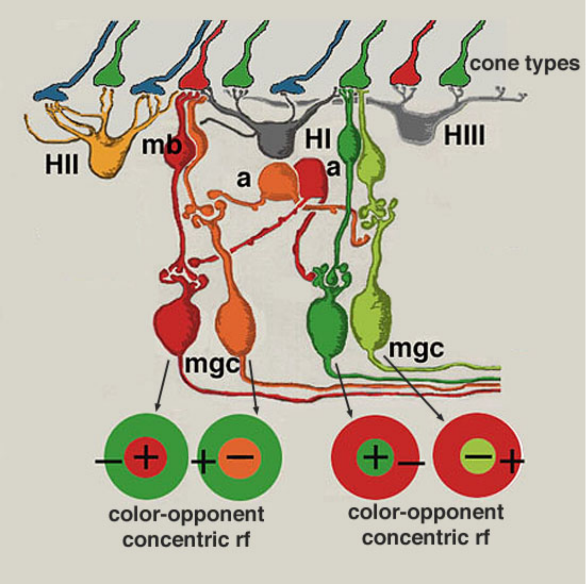
The magnocellular pathway, with diffuse bipolar cells and many-to-one cone to bipolar connections, does not.

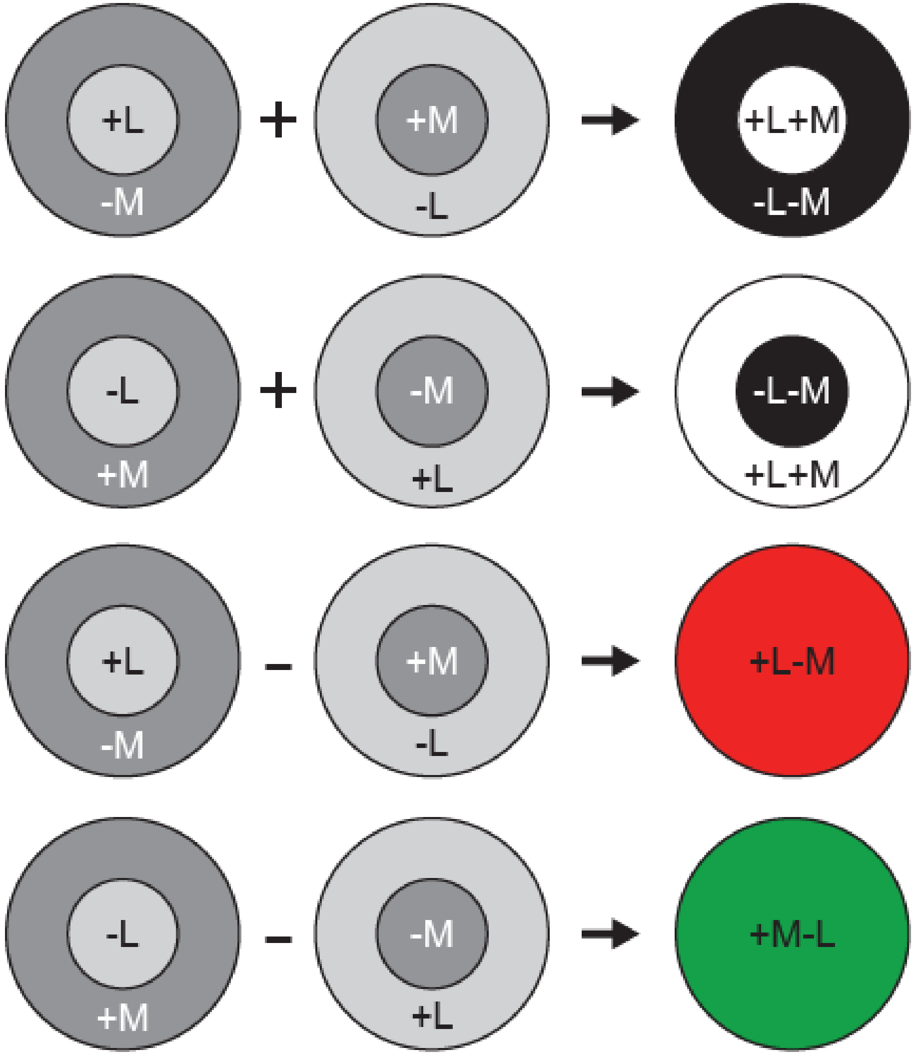
The parvocellular pathway must be double-duty supporting finely detailed luminance vision as well as more coarsely colour vision.



Austin Roorda, 2004

Colour and luminance information are “multiplexed” in the parvocellular pathway





- Chromatic pathways, which produce chromatic percepts, have been linked to the parvocellular retinal stream.

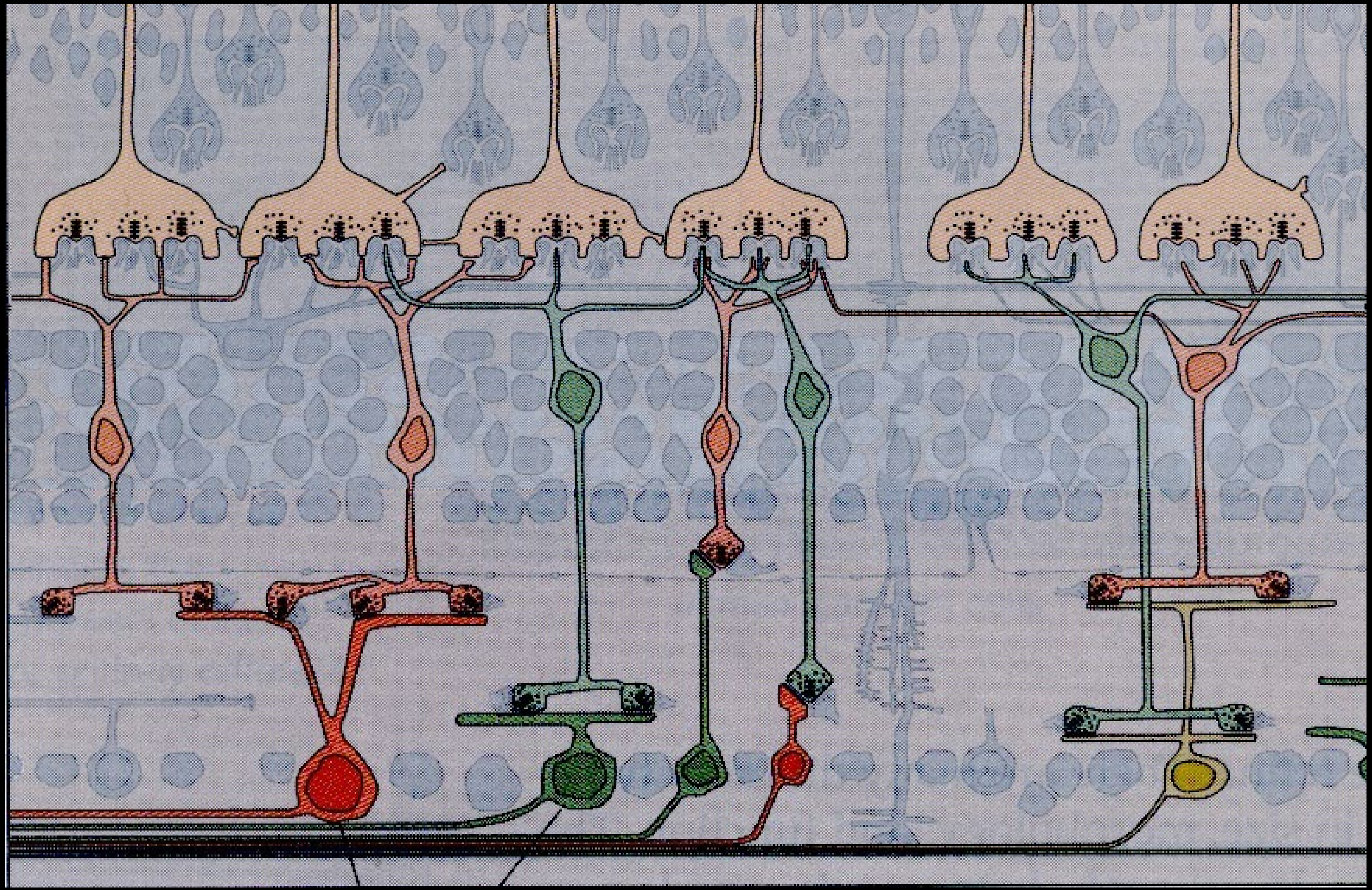
- Luminance pathways, which produce achromatic percepts, have been linked to the magnocellular stream, but *also* depend on the parvocellular stream.

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)