Photopigments and phototransduction

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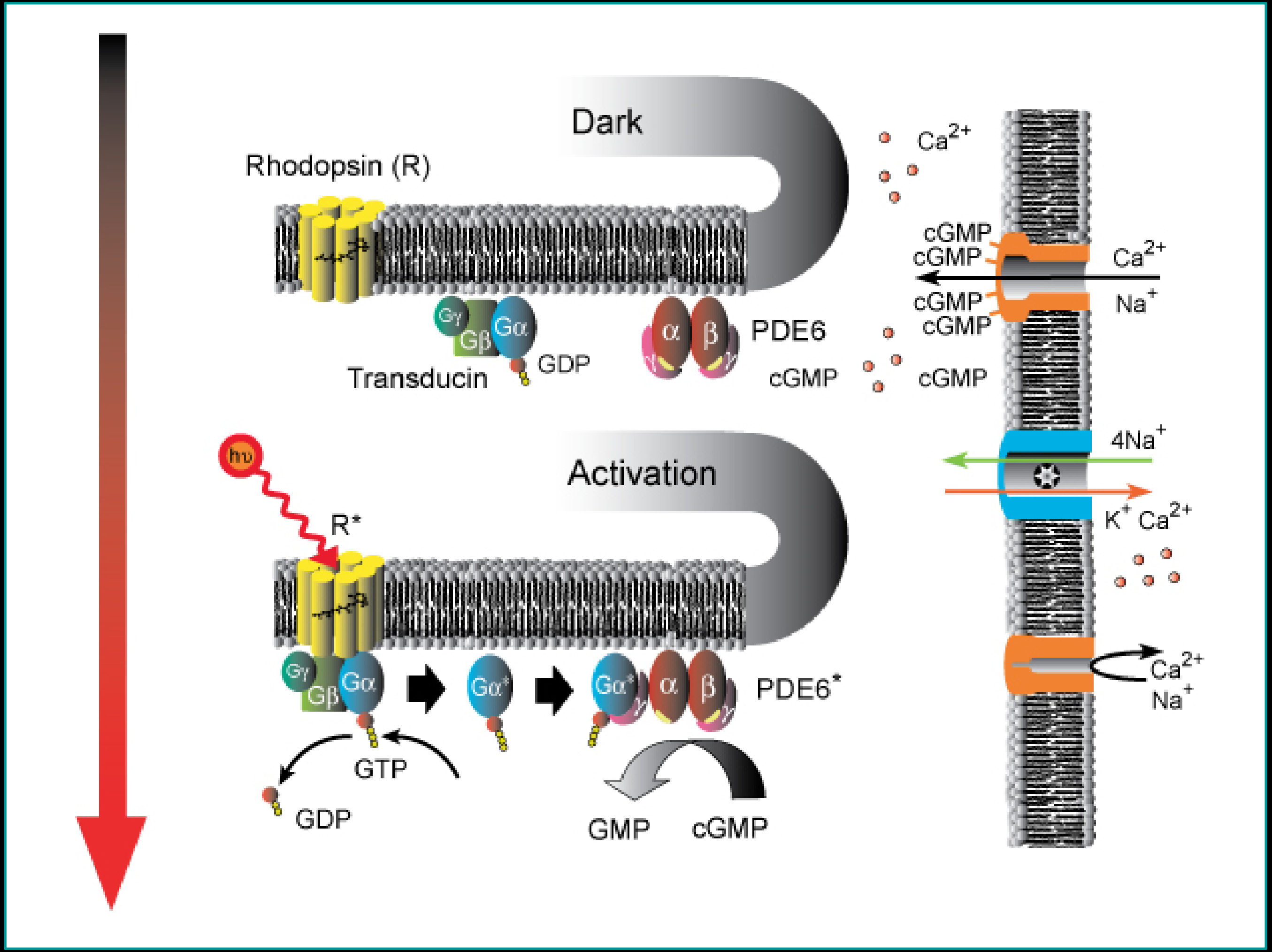
Ophthalmology MSc

Retina – Uveitis – Oncology module

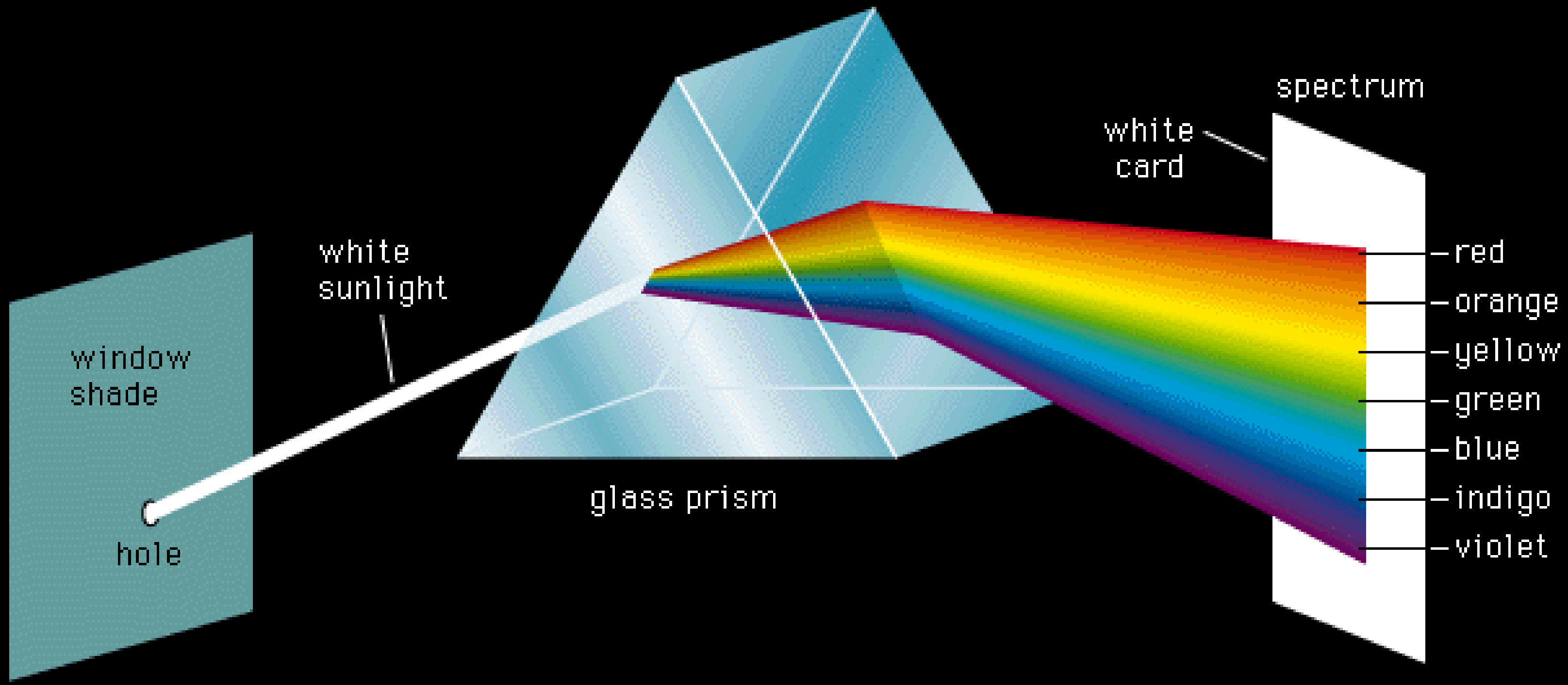


BACKGROUND

Notes online at http://www.cvrl.org

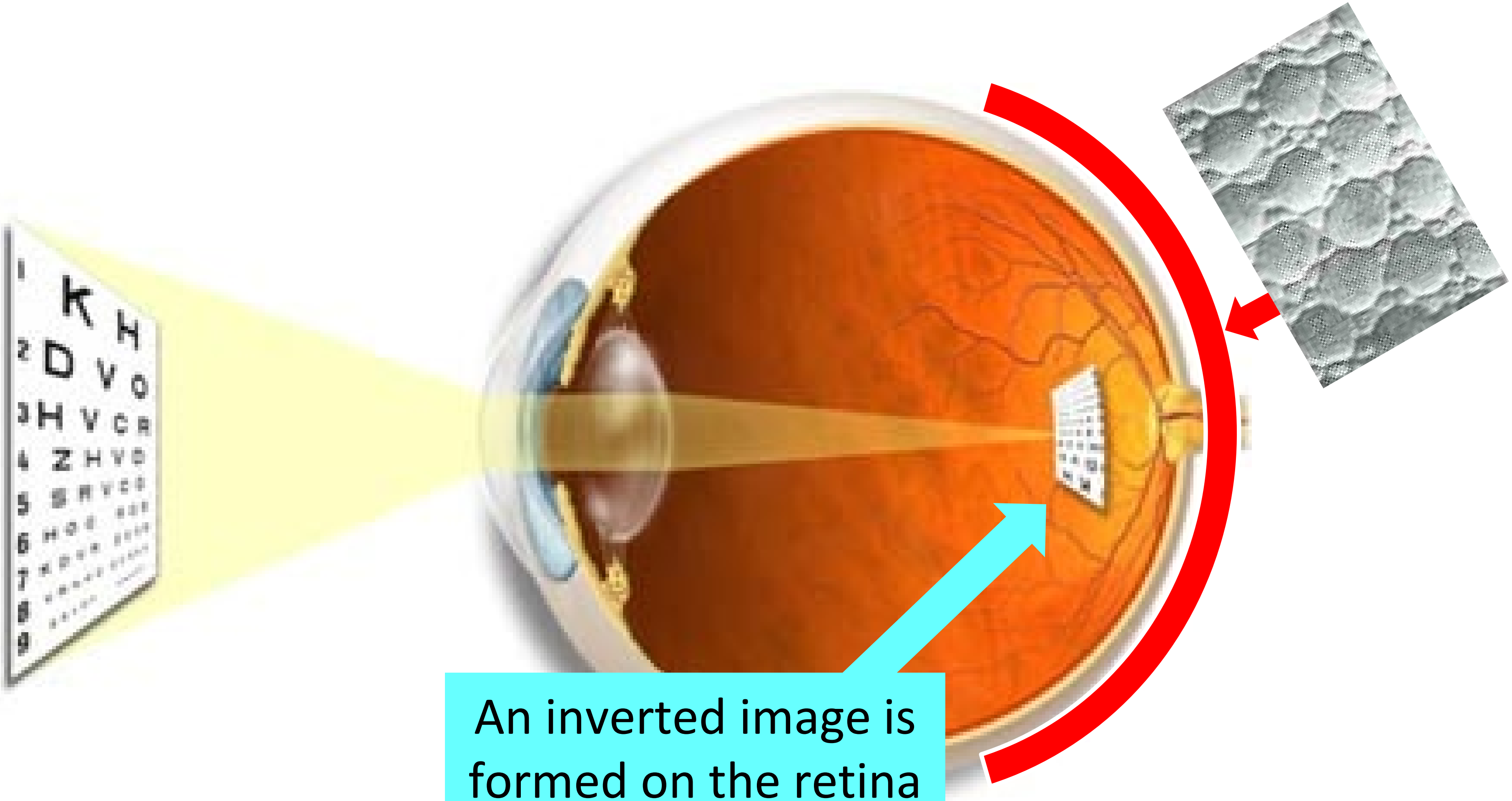
Light

400 - 700 nm is important for vision



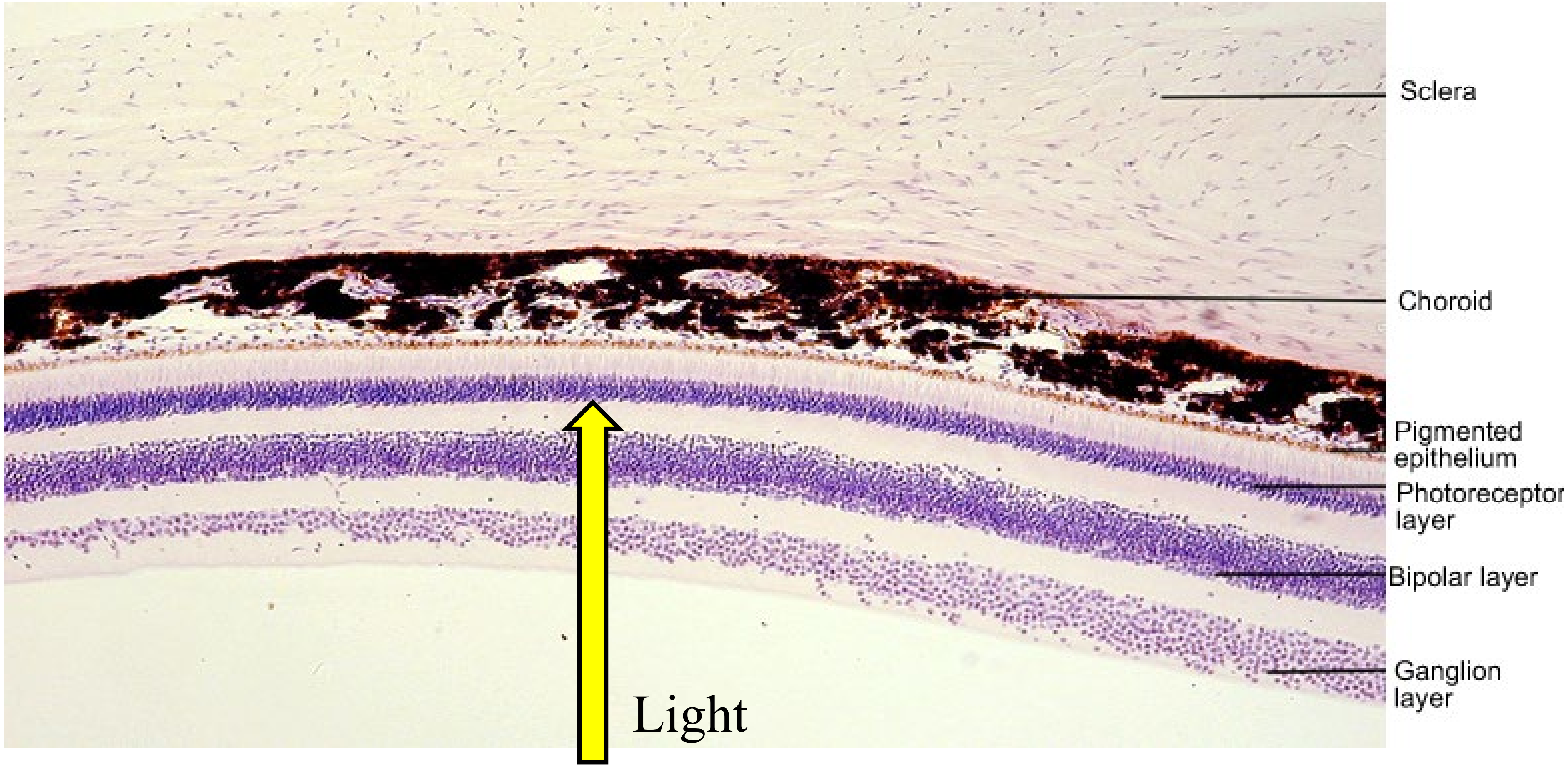
The eye

The retina is carpeted with light-sensitive rods and cones



An inverted image is formed on the retina

Retinal Cross-Section



Retina 200 ×

Rods and cones

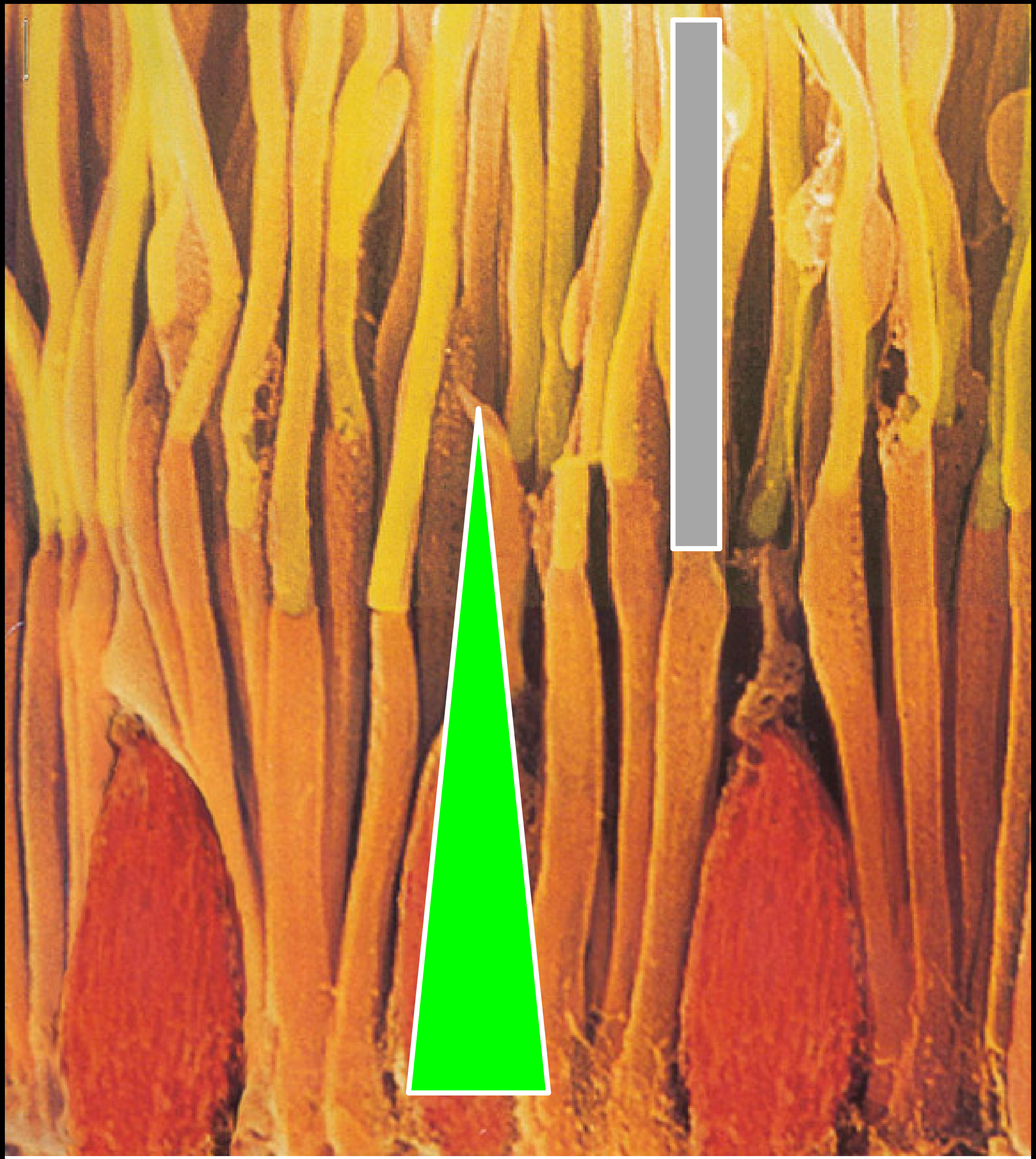
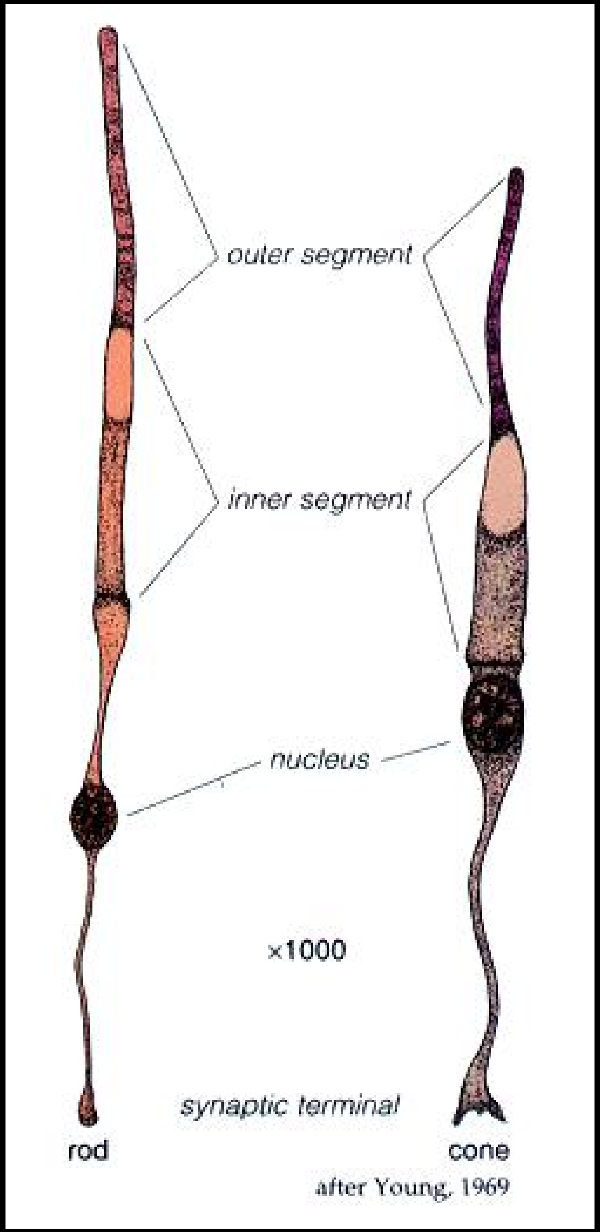


Fig1b. Scanning electron micrograph of the rods and cones of the primate retina. Image adapted from one by Ralph C. Eagle/Photo Researchers, Inc.

Webvision



Human photoreceptors

- Rods
  - Achromatic night vision
  - 1 type

Rod

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

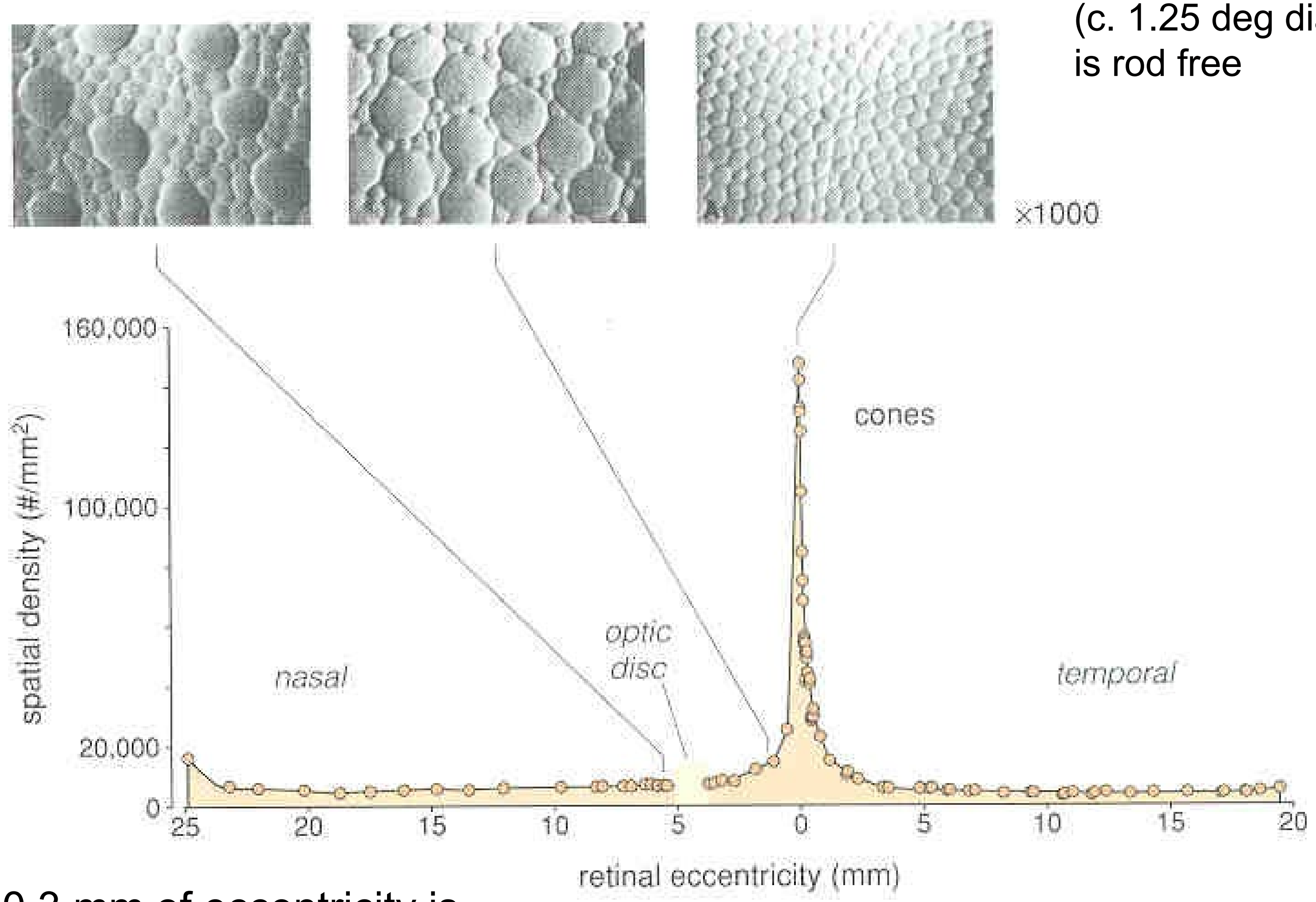
Long-wavelength-sensitive (L) or "red" cone

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

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

Human photoreceptor mosaics

The central foveola (c. 1.25 deg diam.) is rod free

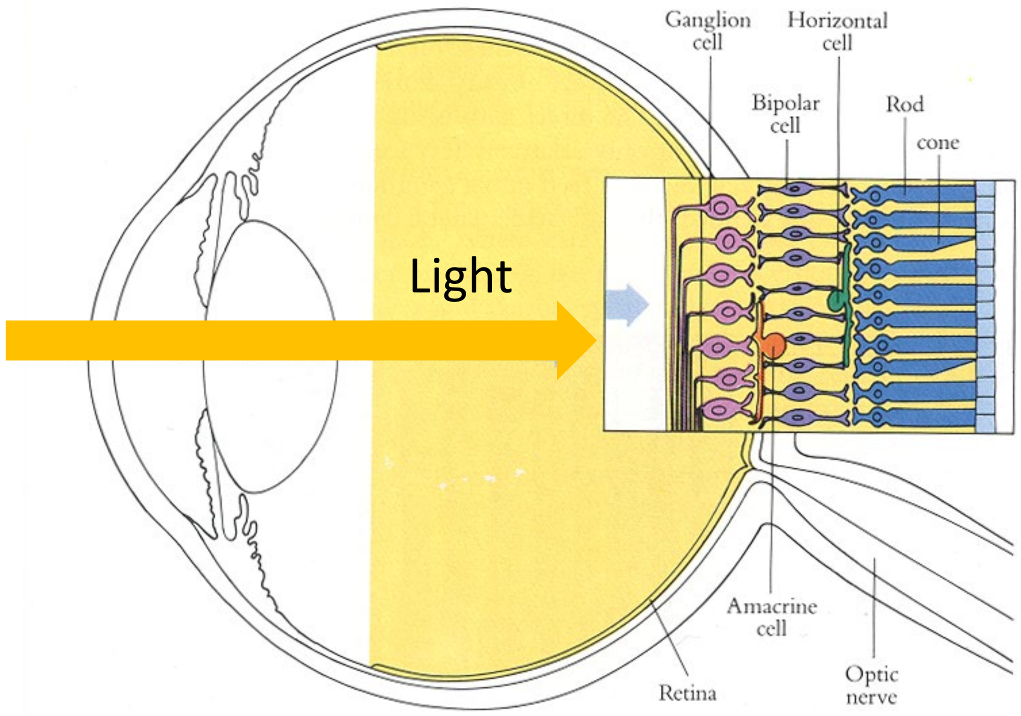


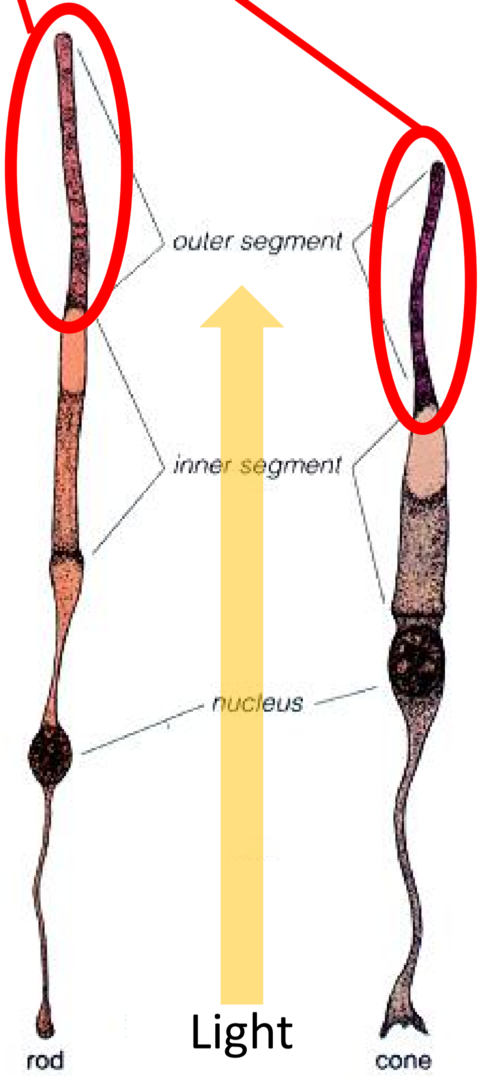
0.3 mm of eccentricity is about 1 deg of visual angle

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

Light and the eye

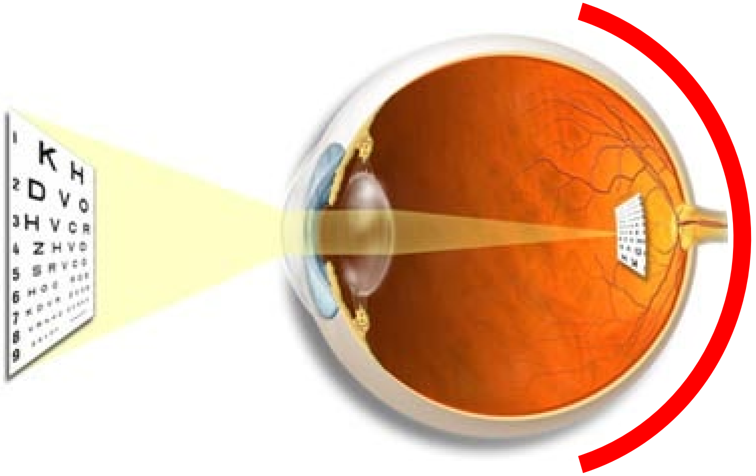
The light-sensitive photopigment lies inside the rod and cone outer segments.

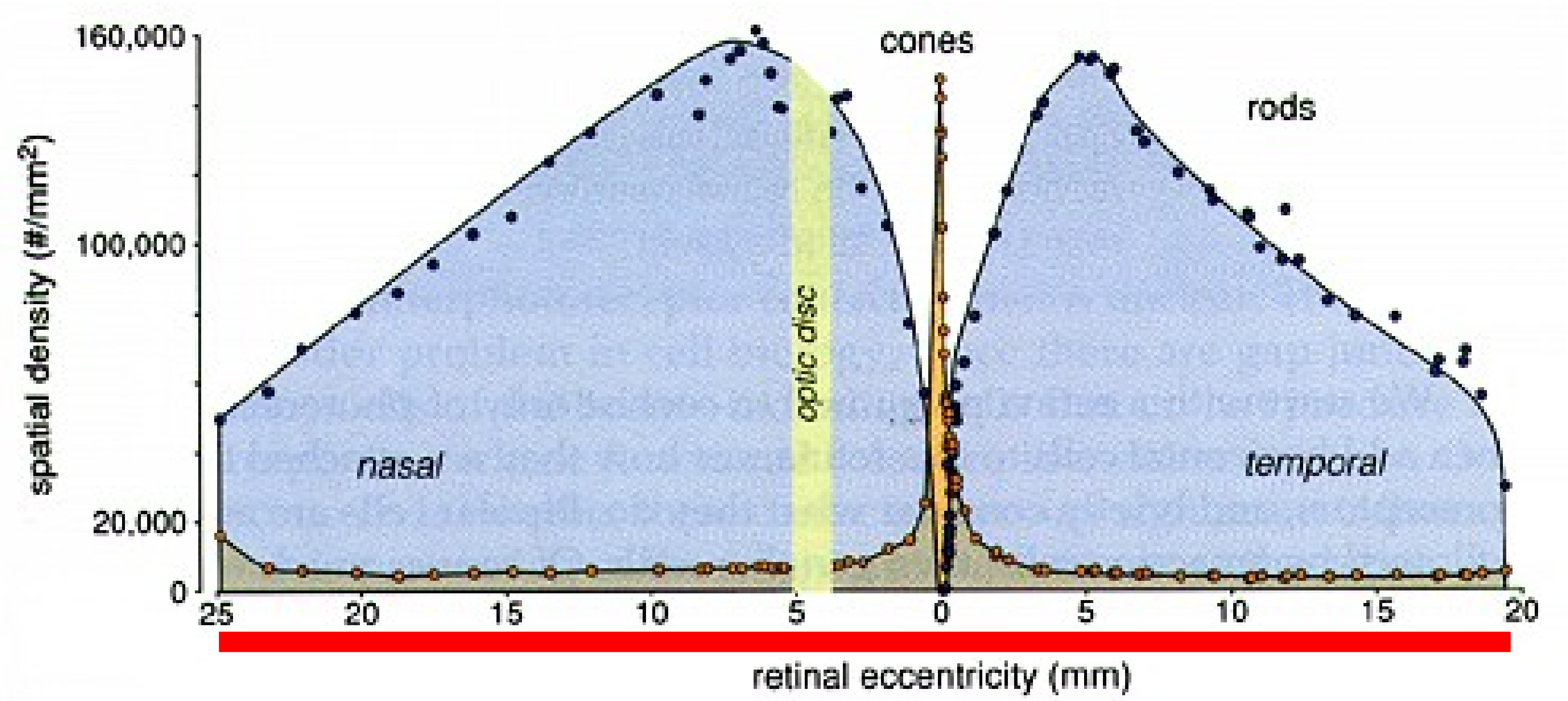




after Young, 1969

Rod and cone distribution

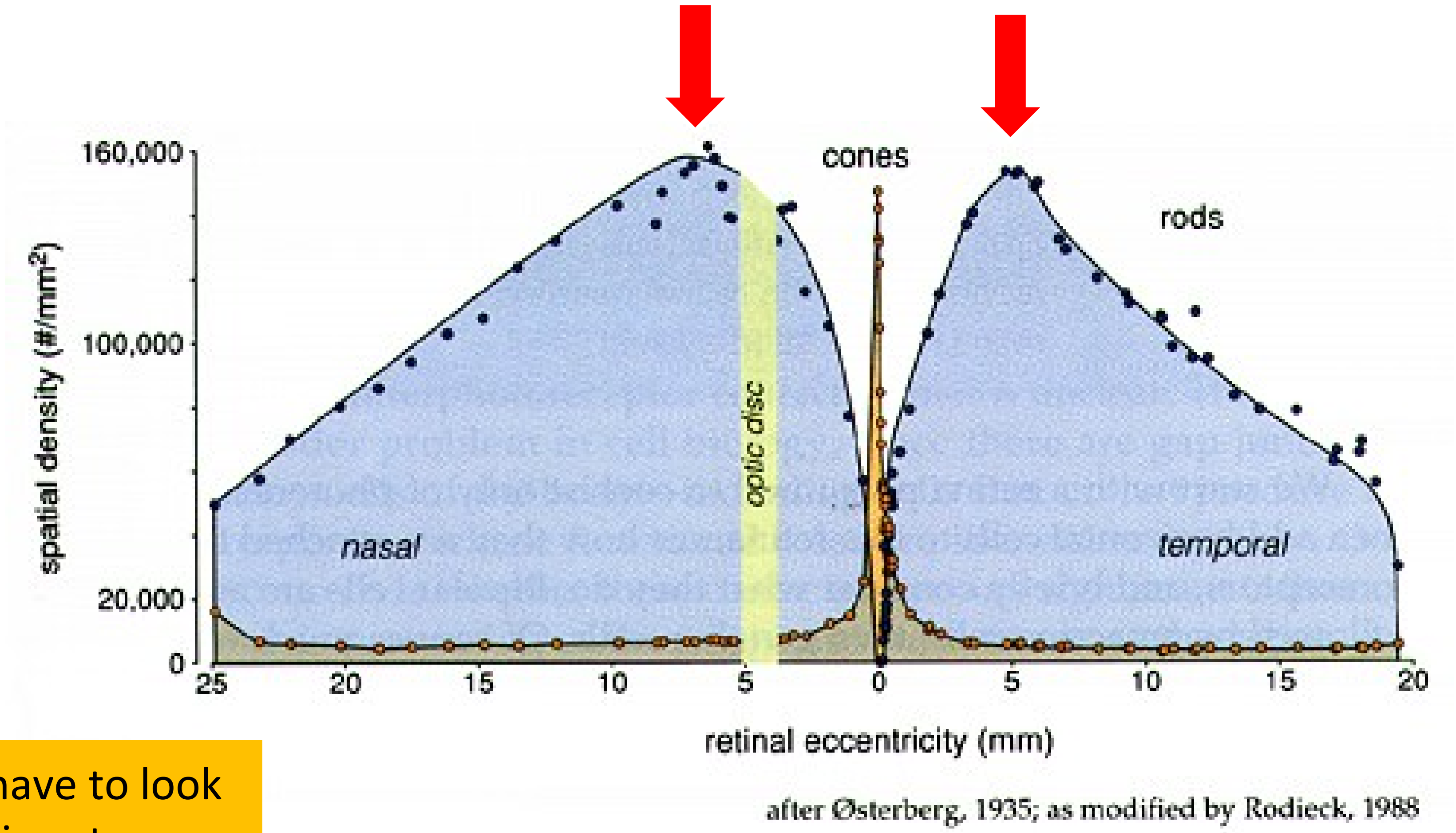




after Østerberg, 1935; as modified by Rodieck, 1988

0.3 mm of eccentricity is about 1 deg of visual angle

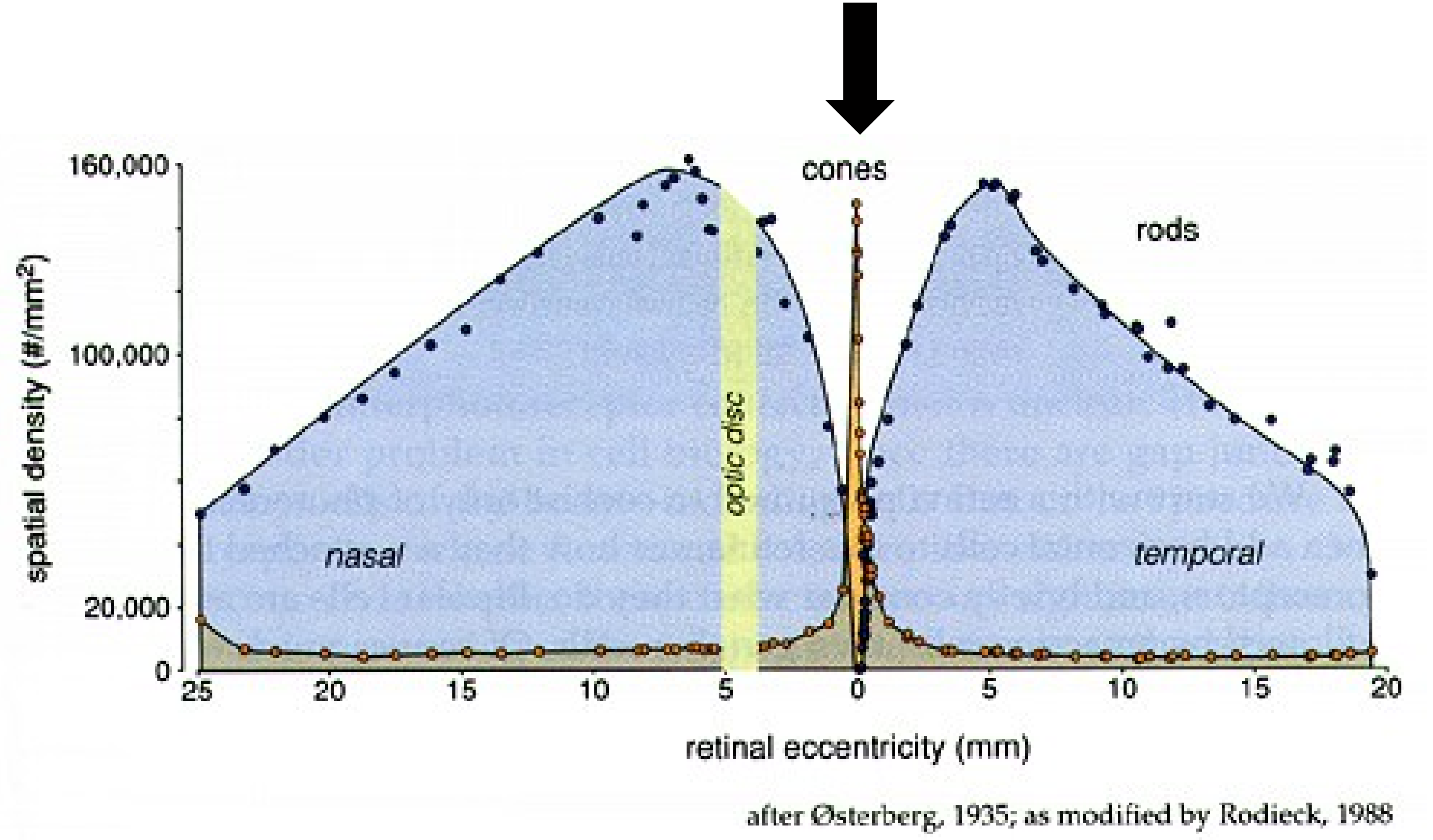
Rod density peaks at about
20 deg eccentricity



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



The Human visual system is a foveating system

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

Credit: Stuart Anstis, UCSD

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.

Rods and cones

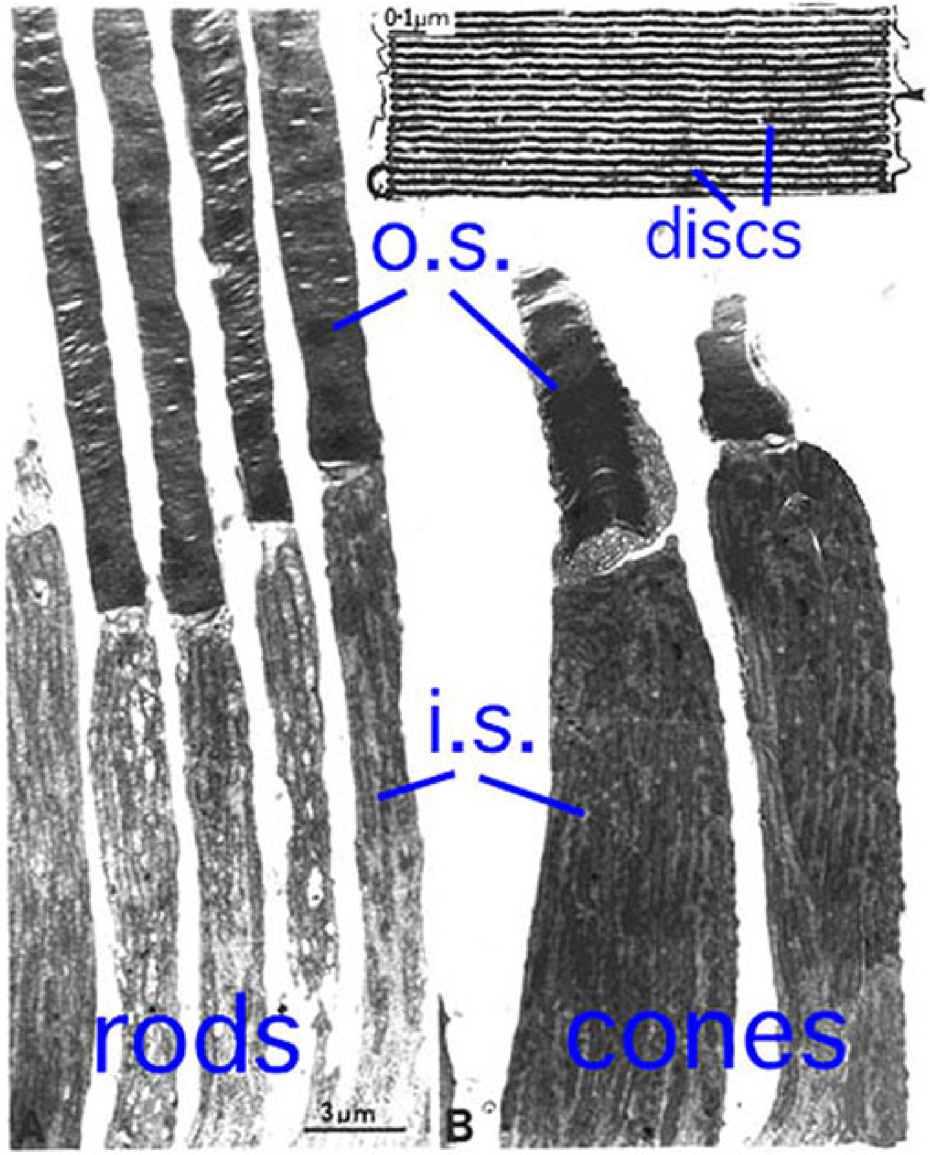


Fig 2. Low magnification EM image of monkey rods and cones with an enlargement of the outer segment discs.

Webvision

Rod vision

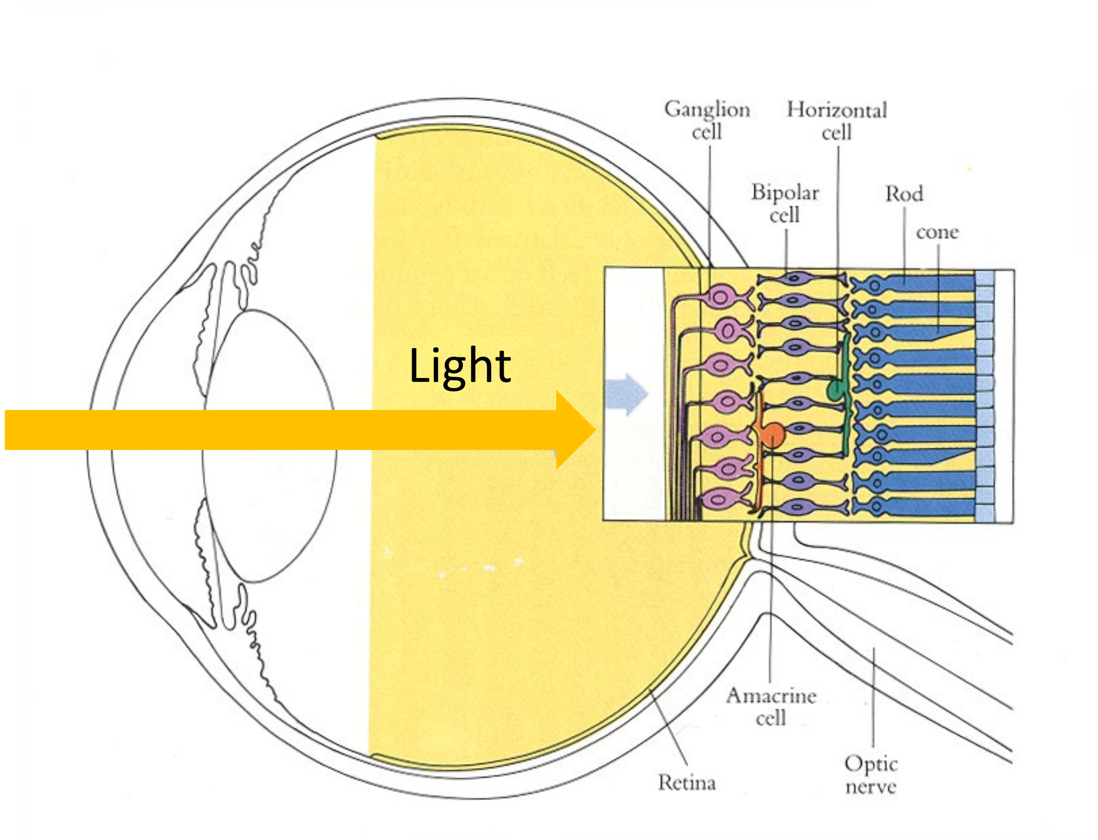
- Achromatic
- High sensitivity
- Poor detail and no colour

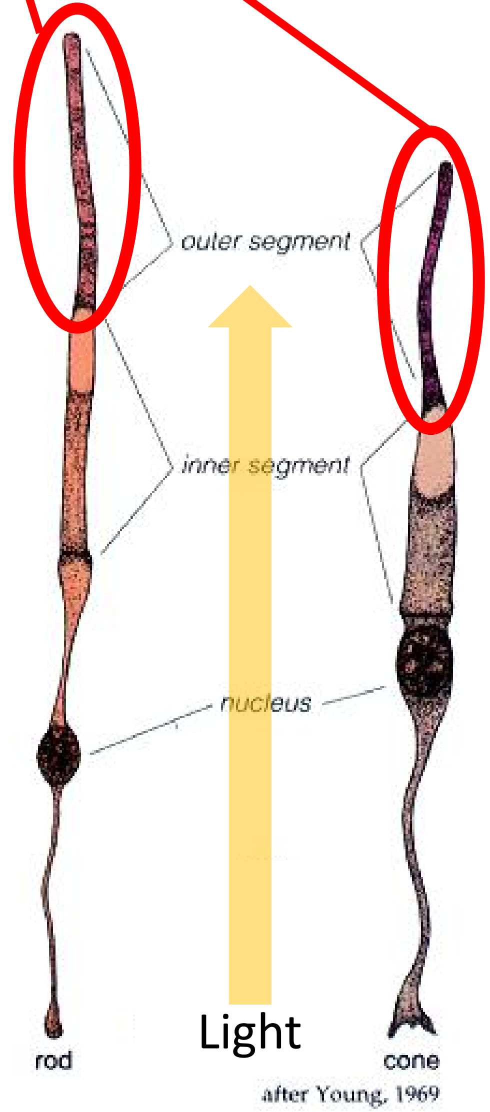
Cone vision

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

Light and the eye

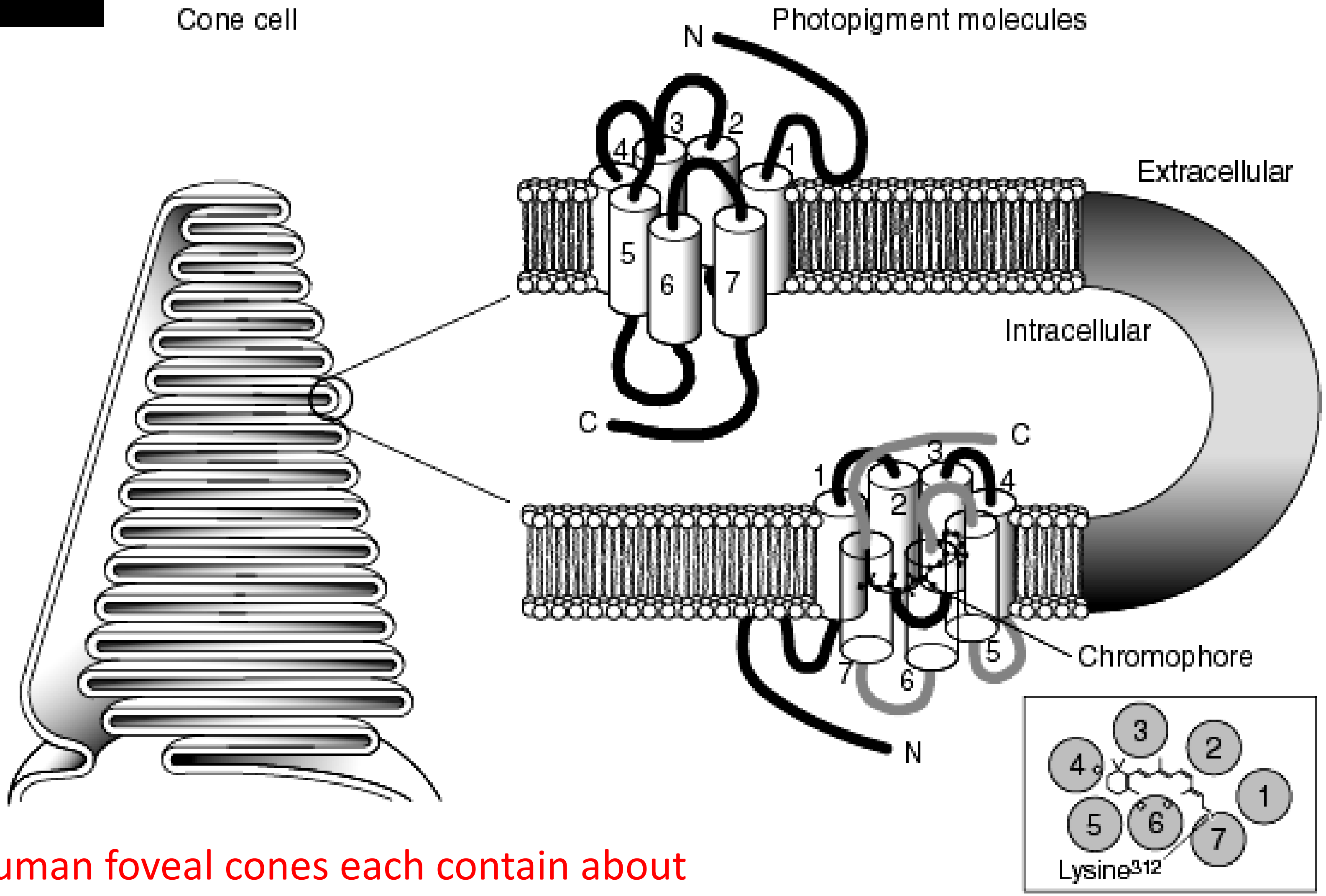
The light-sensitive photopigment lies inside the rod and cone outer segments.





Arrangement of visual pigment molecules

The molecule consists of protein, opsin, forming 7 transmembrane α-helices, surrounding the chromophore, retinal, the aldehyde of Vitamin A



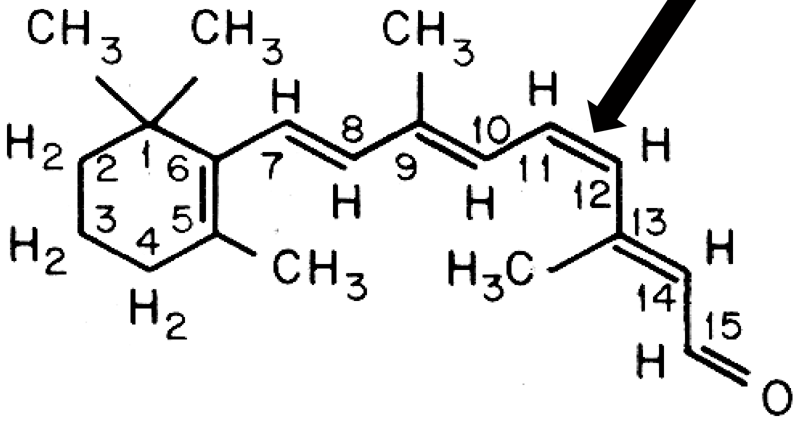
Human foveal cones each contain about 10^{10} visual pigment molecules

Chromophore

(*chromo*- colour, + -*phore,* producer)
Light-catching portion of any molecule

11-*cis* retinal

The molecule is twisted at the 11th carbon.



Chromophore

(*chromo*- colour, + -*phore,* producer)
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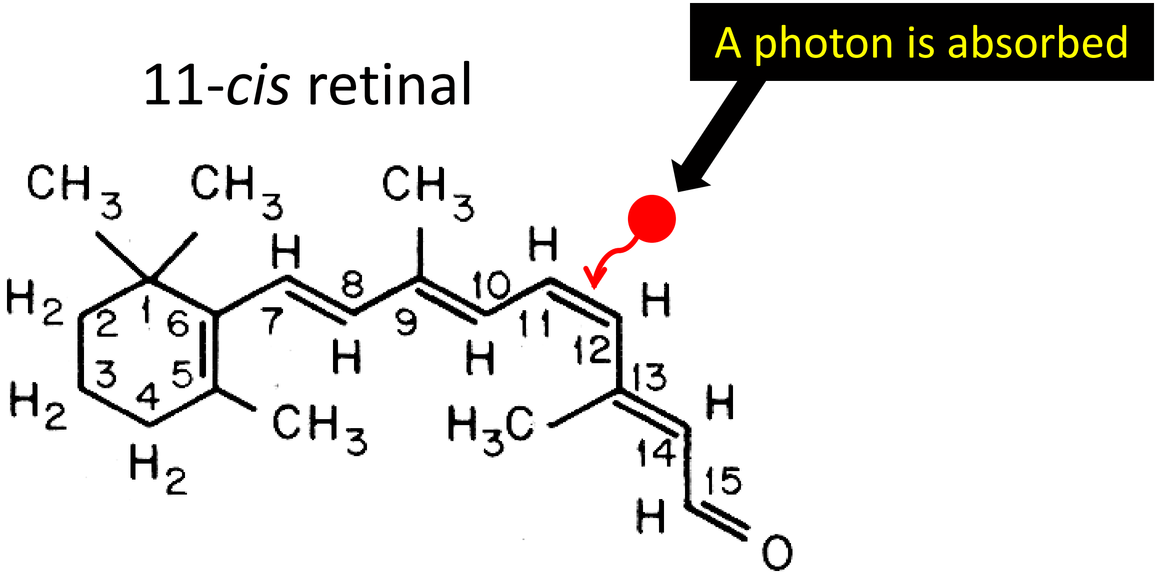
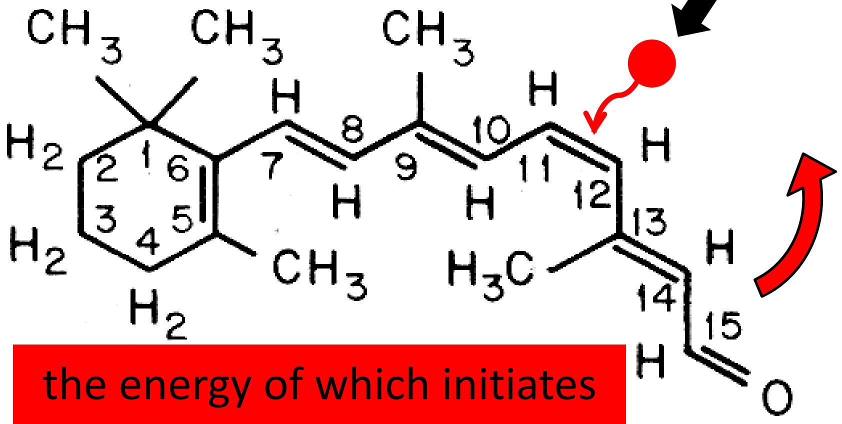


Chromophore

(*chromo-* colour, + *-phore,* producer)
Light-catching portion of any molecule

11-*cis* retinal

A photon is absorbed



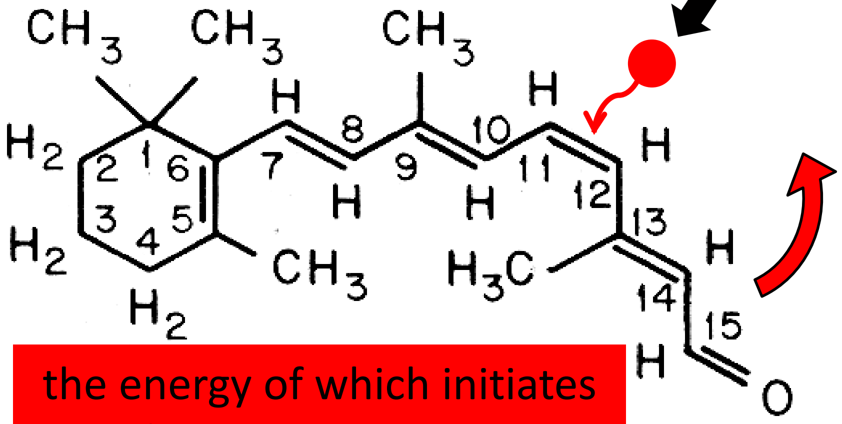
the energy of which initiates
a conformational change to…

Chromophore

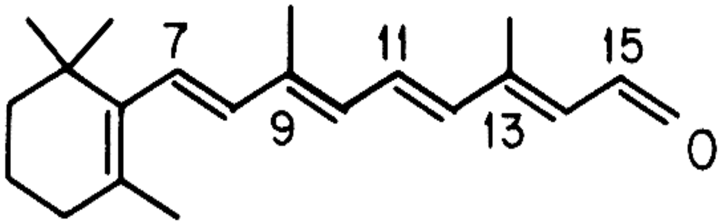
(*chromo*- colour, + -*phore*, producer)
Light-catching portion of any molecule

A photon is absorbed

11-*cis* retinal

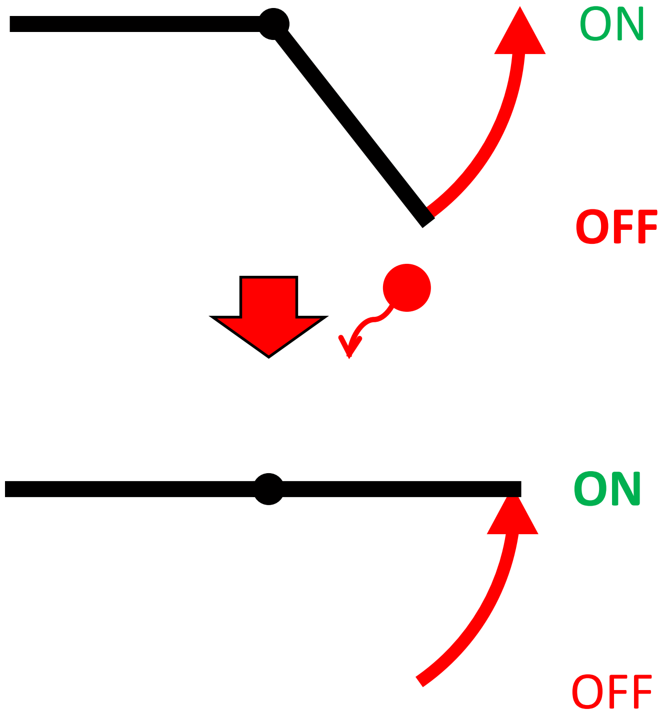


the energy of which initiates a conformational change to…



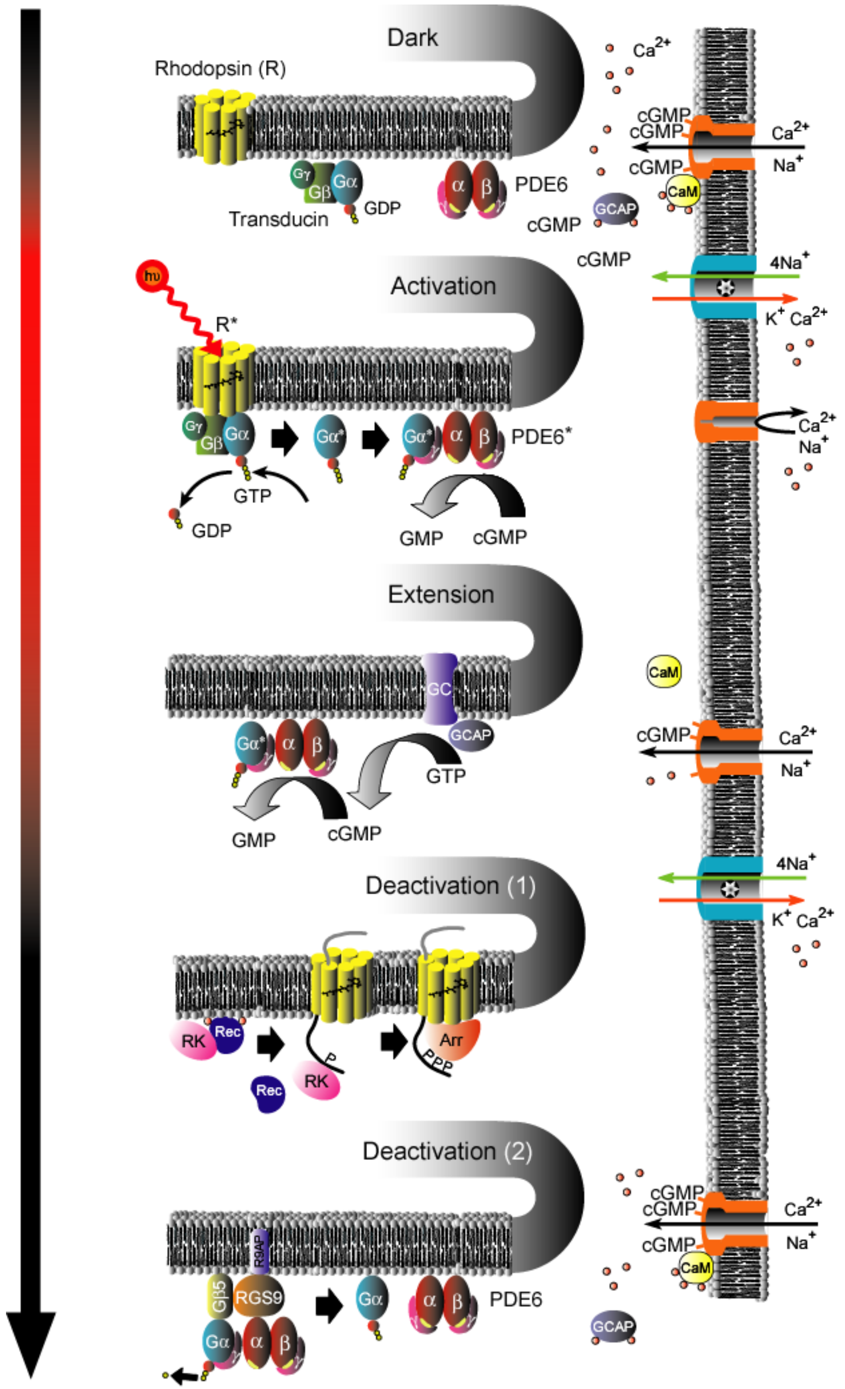
all-*trans* retinal

Think of the molecule as a photo-sensitive switch!



PHOTOTRANSDUCTION

Energy of absorbed photon is converted (transduced) to an electrical neural signal, the receptor potential.

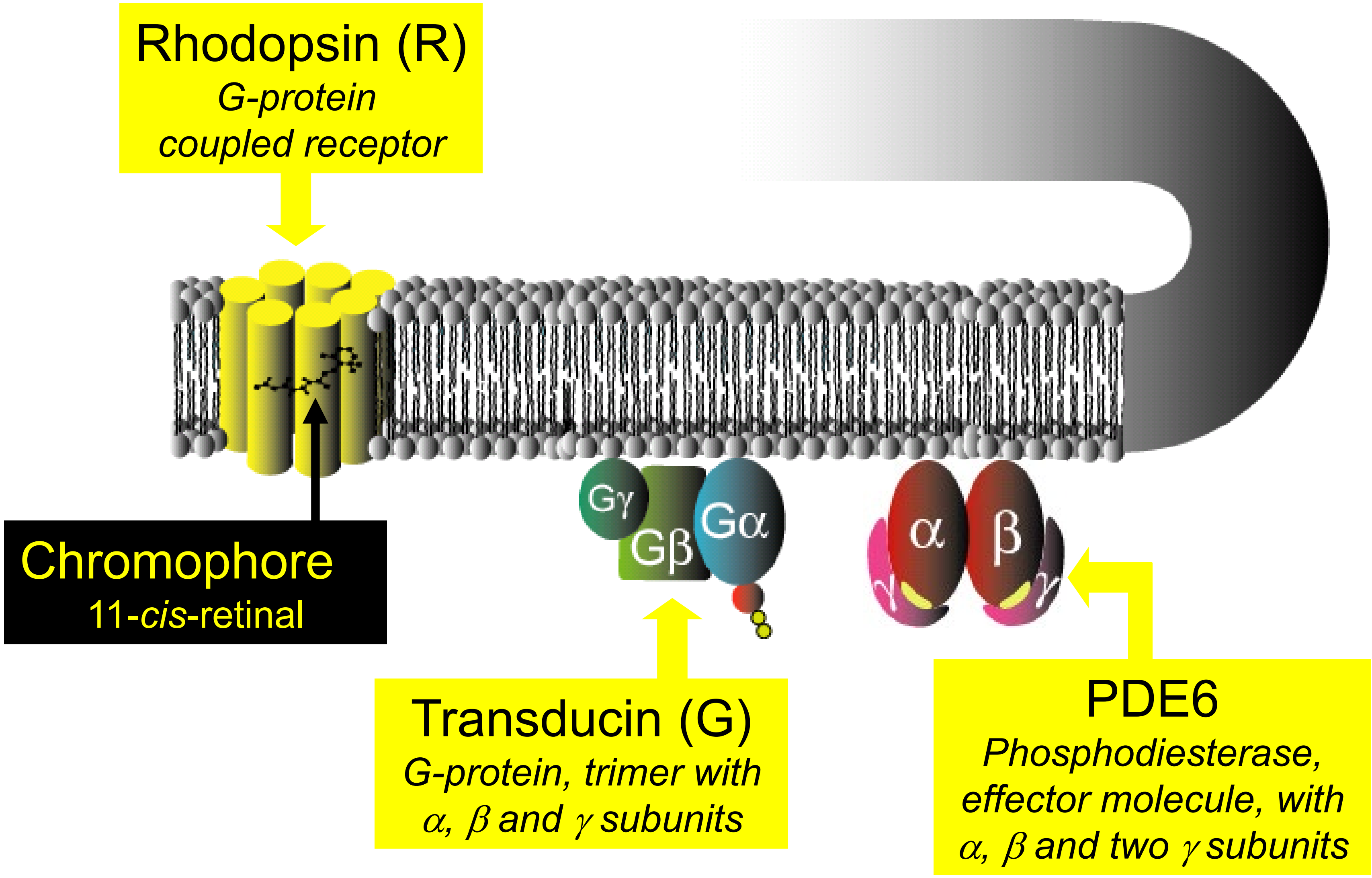


Phototransduction

- Activation
- Range extension
- Deactivation

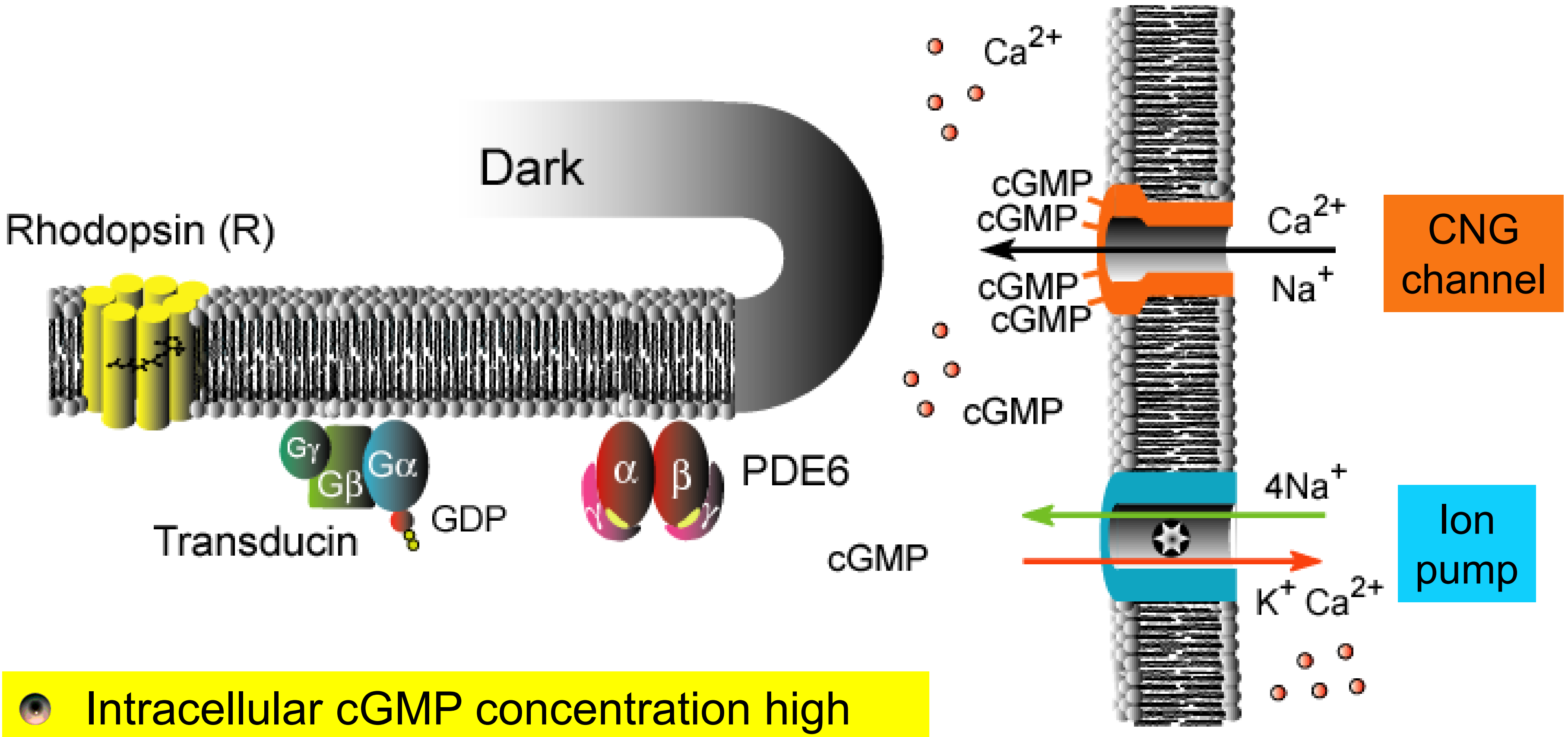
Inspired by:
Pugh, Nikonov, & Lamb (1999). *Current Opinion on Neurobiology, 9*, 410-418.
Burns & Arshavsky (2005). *Neuron, 48*, 387-401.

Main molecular players in the cascade



In the Dark…

In the Dark

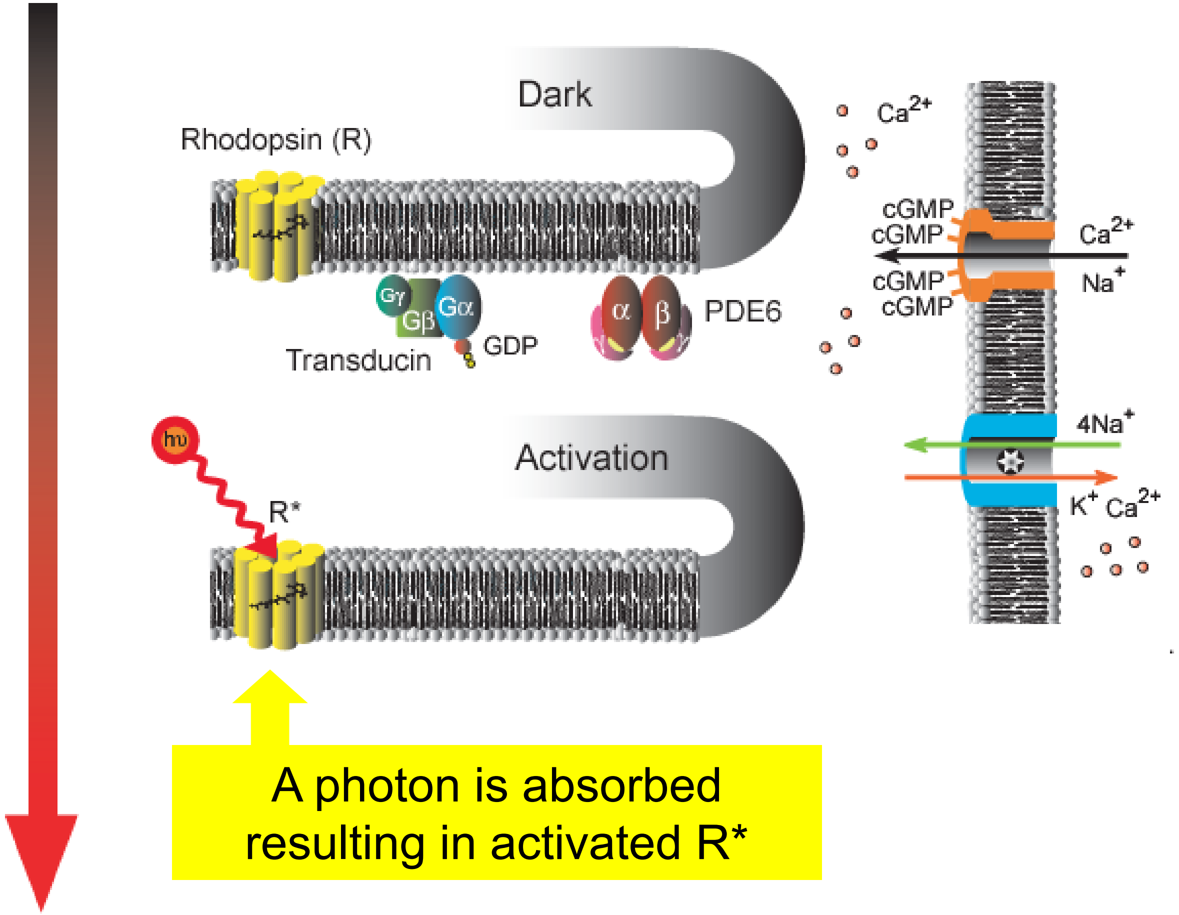


- Intracellular cGMP concentration high
- CNG channels open

CNG = Cyclic Nucleotide Gated channel

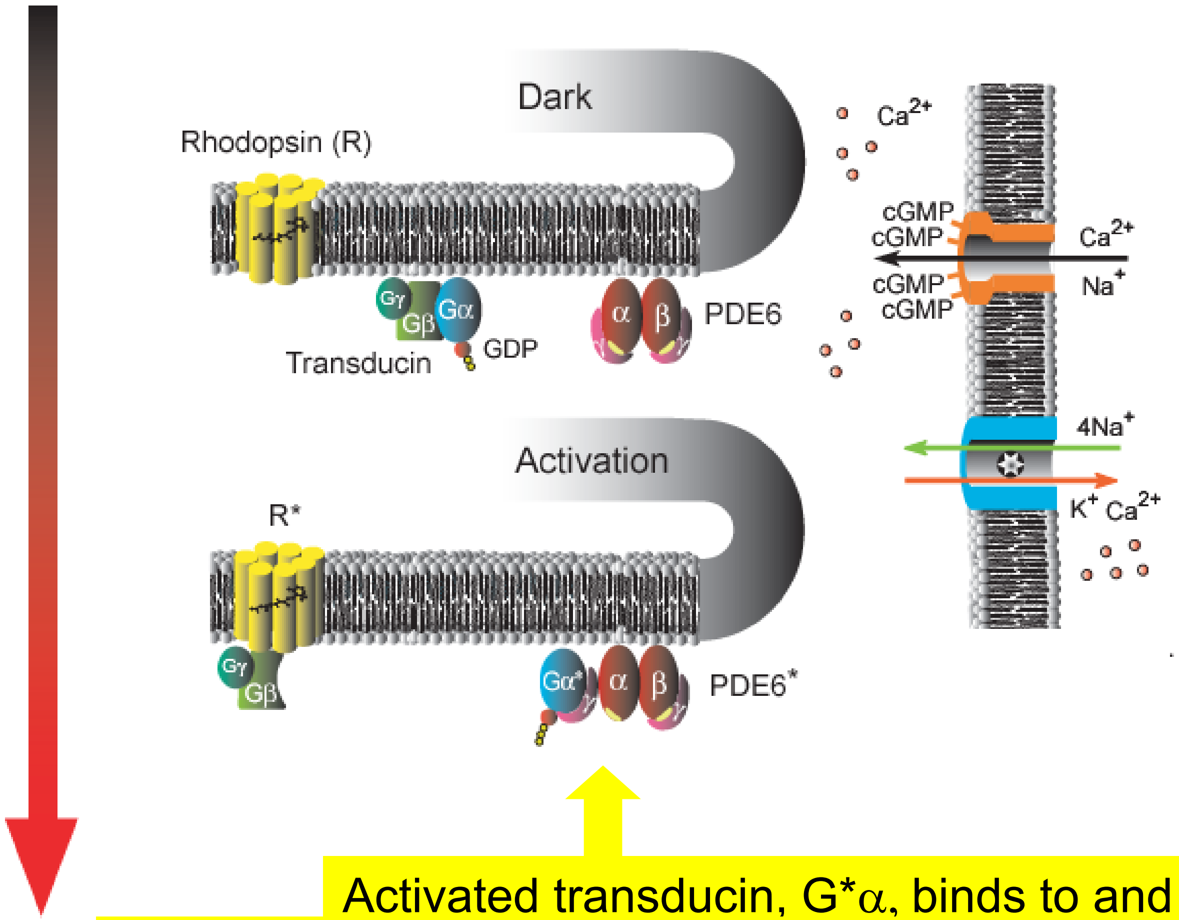
Activation steps

Activation steps



A photon is absorbed resulting in activated R*

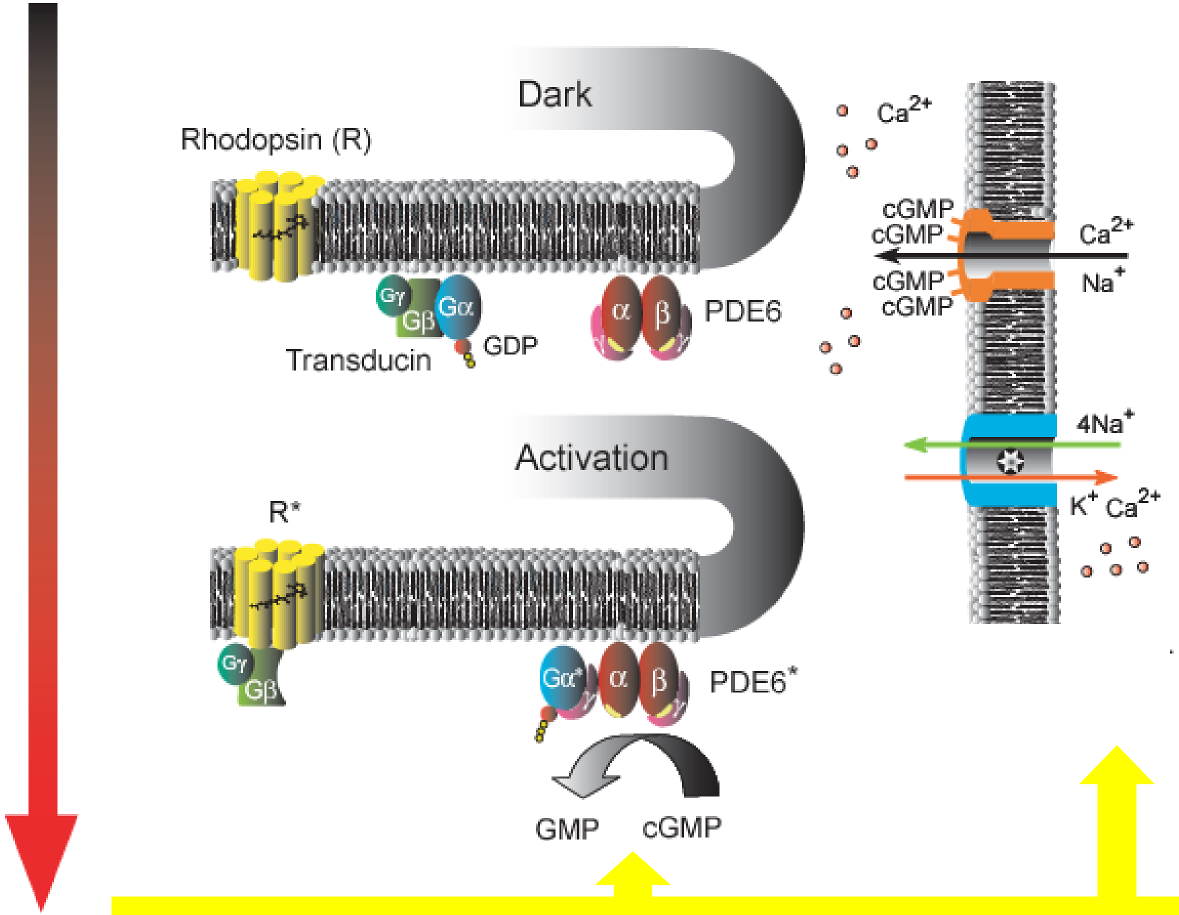
Activation steps



Activated transducin, G*α, binds to and activates

R* catalyses the exchange of GDP for GTP on the G-protein, producing the activated subunit G*α, which dissociates

Activation steps



The drop in cGMP leads to closure of the CNG channels, which blocks the entry of Na^{+} and Ca^{2+} ions into the outer segment, causing the outer segment to hyperpolarize.

How many photons are needed for us to detect light (when fully dark-adapted)?

When fully dark-adapted, we can detect as few as 7-10 photons.

How is this possible?

Amplification

The absorption of a single photon is sufficient to change the membrane conductance. How?

A single R* catalyses the activation of c. 500 transducin molecules. Each G*α can stimulate one PDE6*, which in turn can break down 10^3 molecules of cGMP per second. Thus, a single R* can cause the hydrolysis of $>10^5$ molecules of cGMP per second!

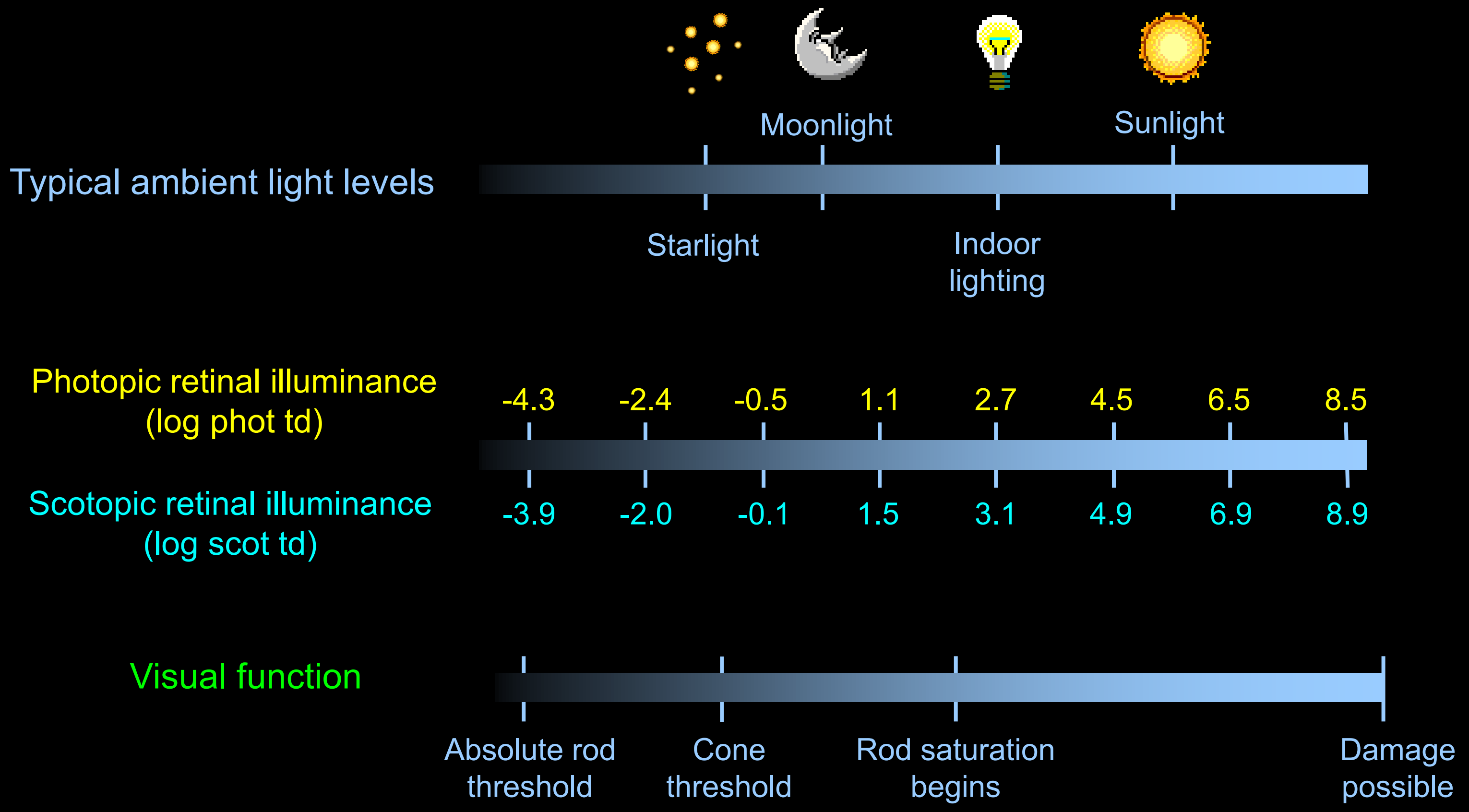
Amplification is beneficial at low light levels, but what negative effects might amplification have at high light levels?

An important function of the photoreceptor and the transduction cascade is:

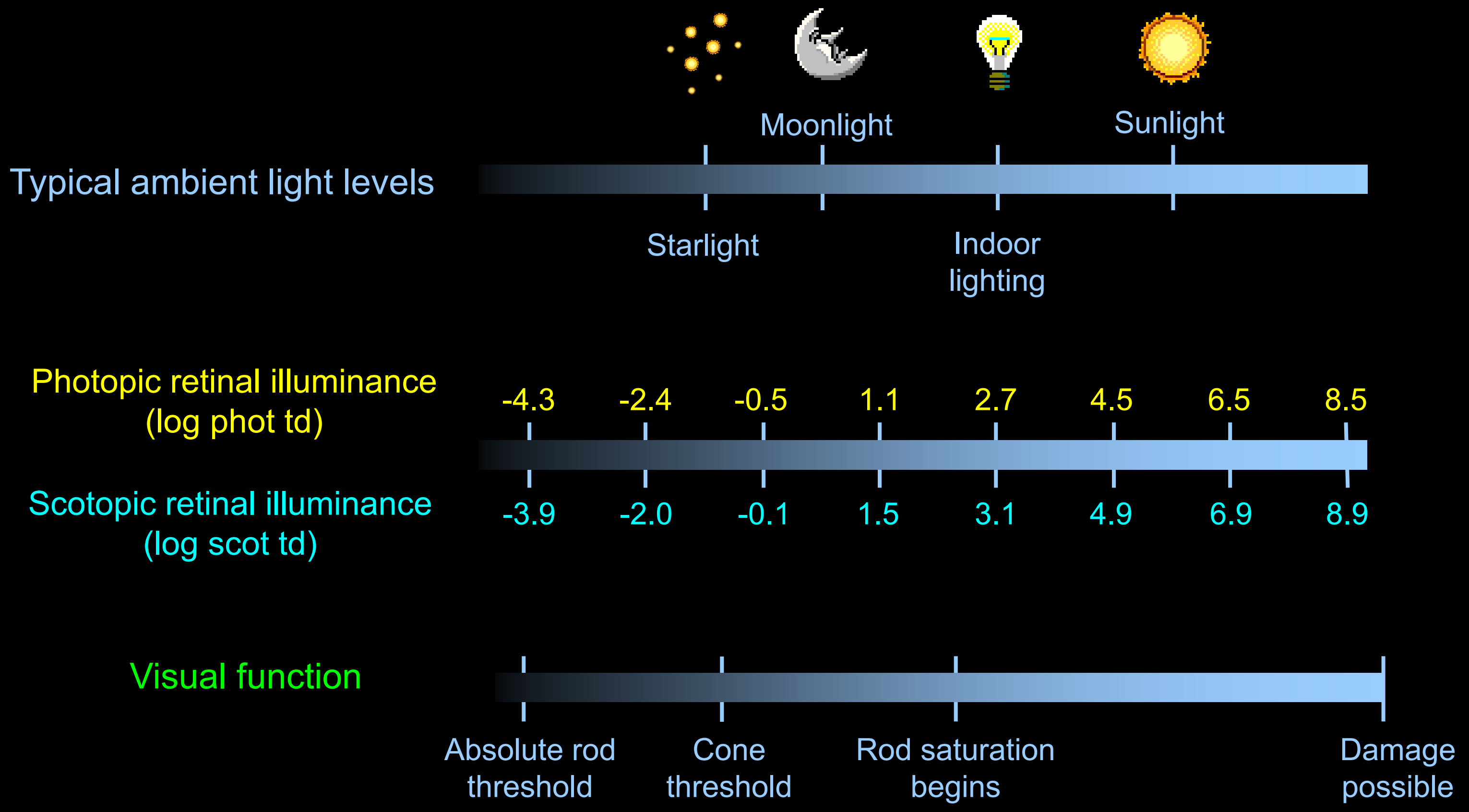
Range extension and light adaptation

Why is light adaptation or sensitivity regulation important?

Because the visual system must maintain itself within a useful operating range over the roughly 10^{12} change in illumination: from absolute rod threshold to levels at which photoreceptor damage can occur.



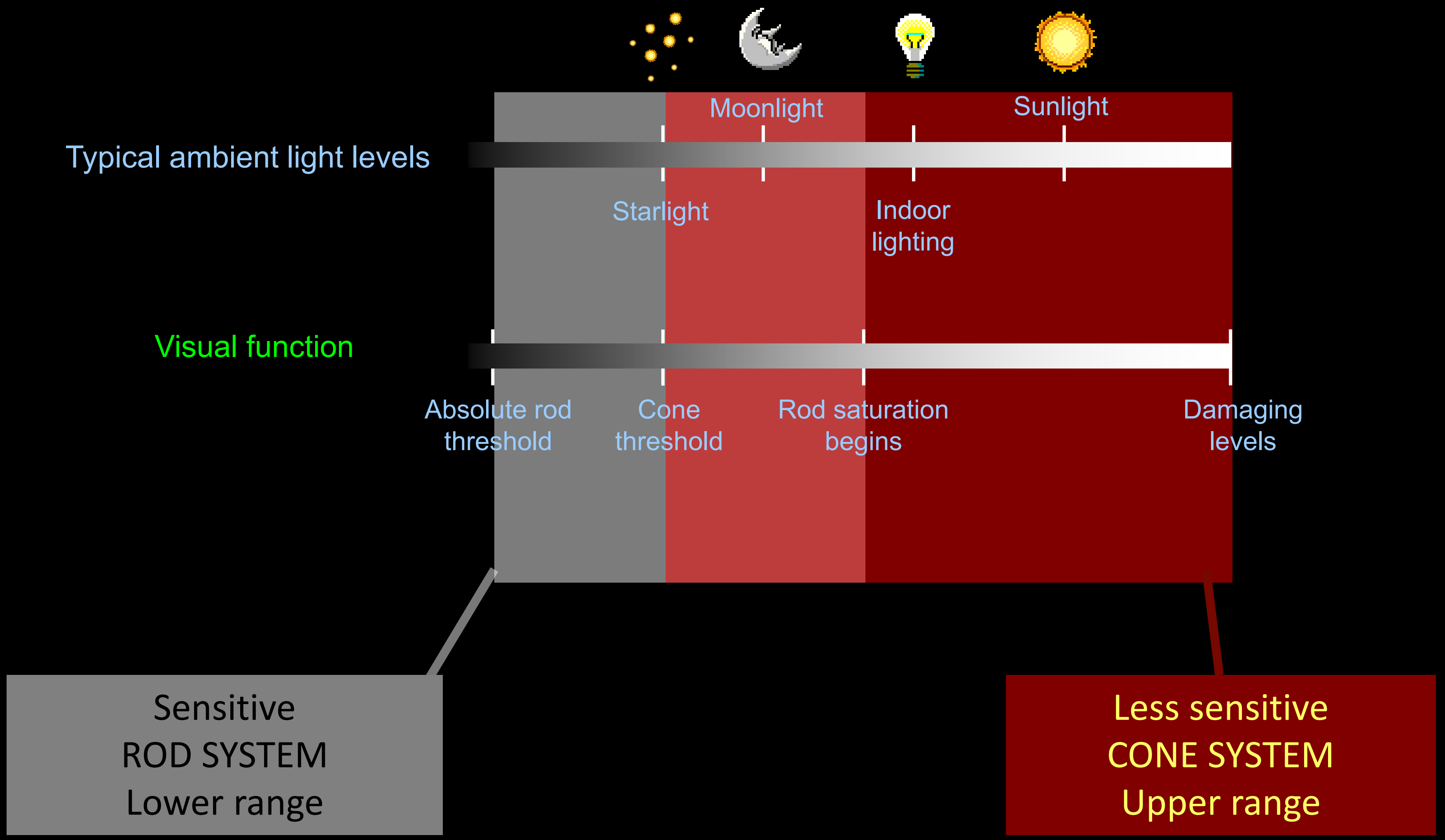
It must do so despite the fact that that a typical postreceptoral neuron can operate over a range of only c. 10^3.



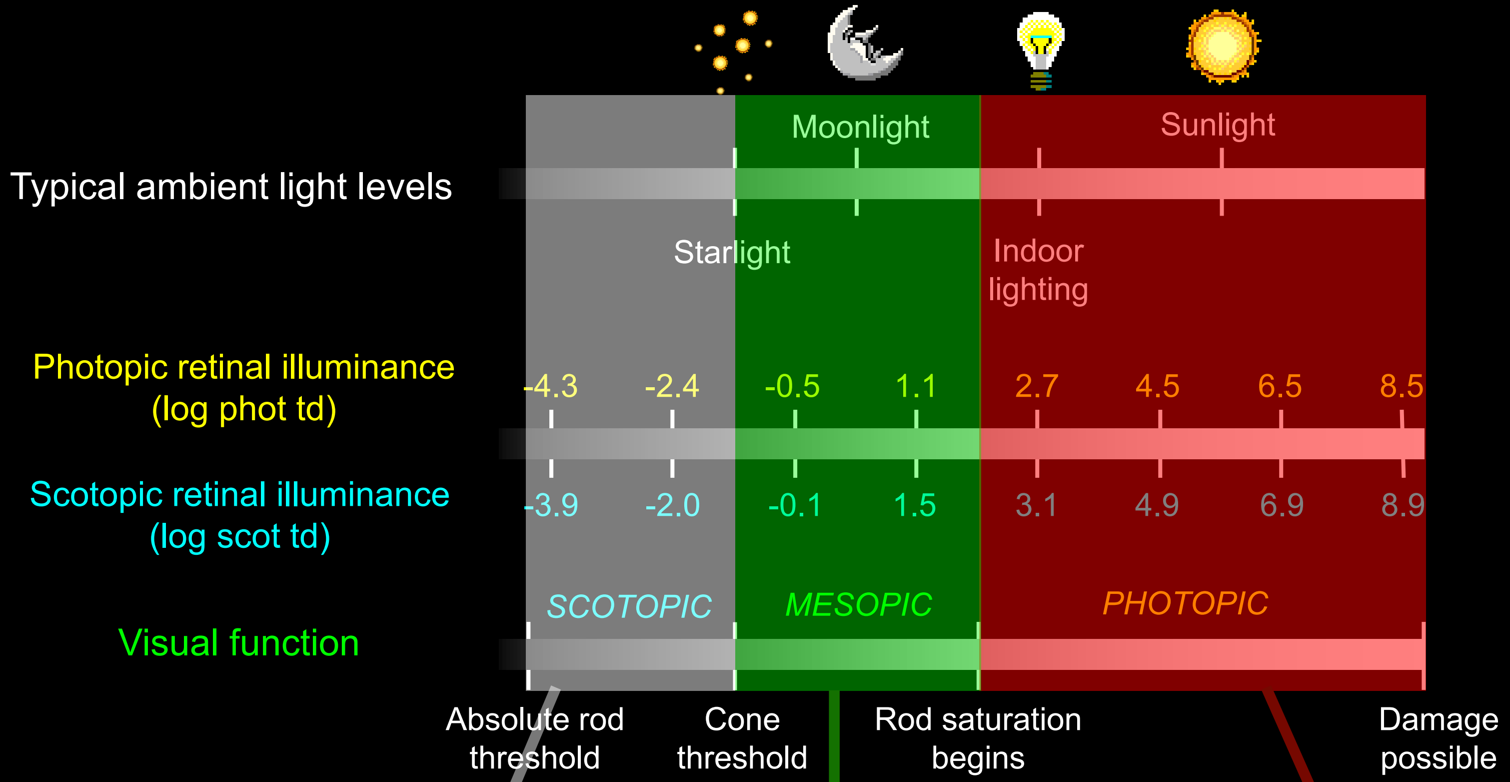
Rods and cones

Rods that are optimized for low light levels

Cones that are optimized for higher light levels



Rods and cones



Scotopic levels
(below cone threshold) where rod vision functions alone.
A range of c. 10^3

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

Adaptation and sensitivity…

System must ADAPT to changes in light level

Ideally, the system should be very sensitive at low light levels, so that it can detect a few photons, but then much, much less sensitive at high light levels.

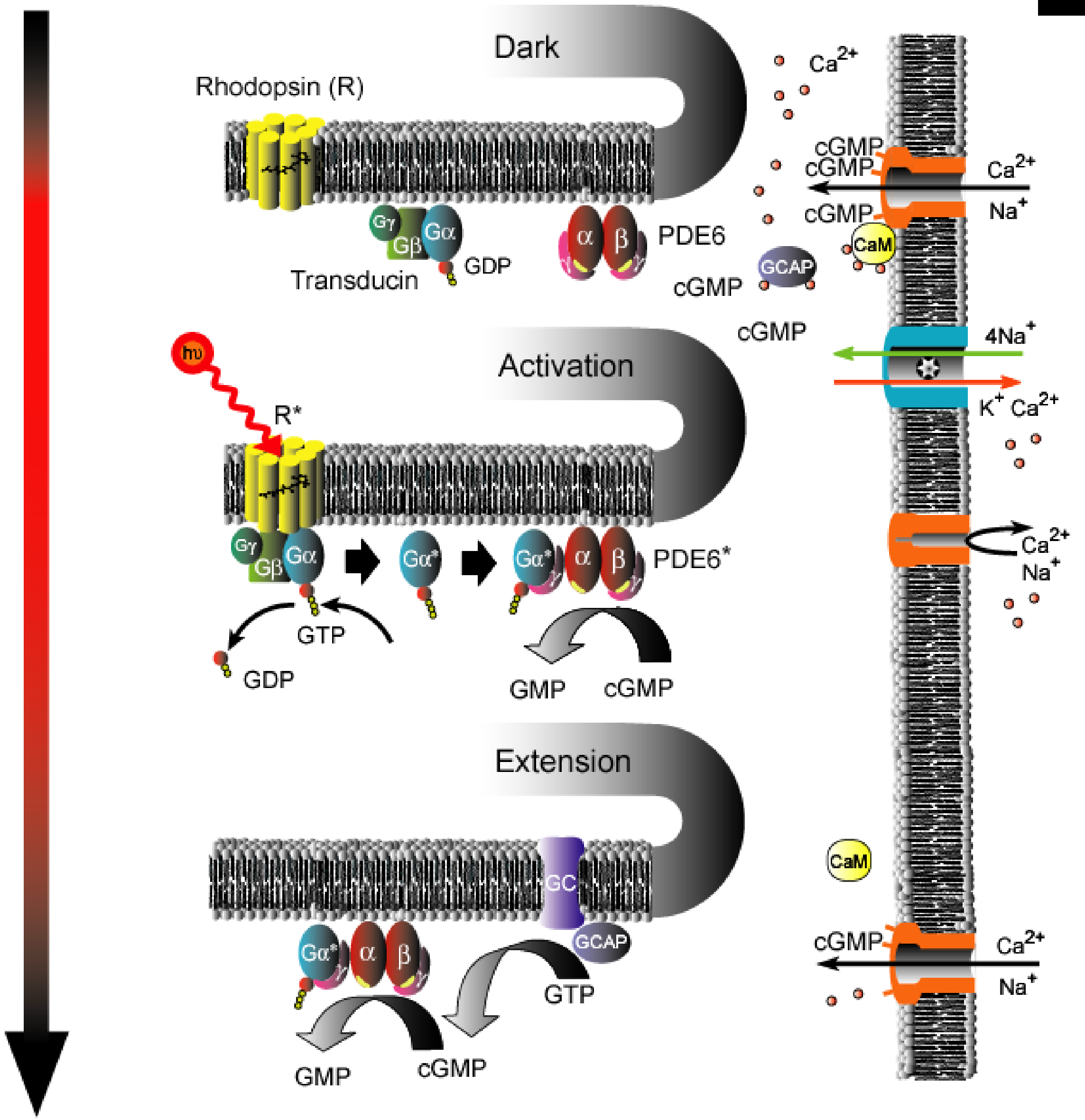
How can this achieved within the transduction cascade?

Adaptation and sensitivity…

At low light levels the sensitivity is very high: A single R* can cause the hydrolysis of $>10^5$ molecules of cGMP per second!

But as the light level increases, the system will saturate (as you run out of "stuff").

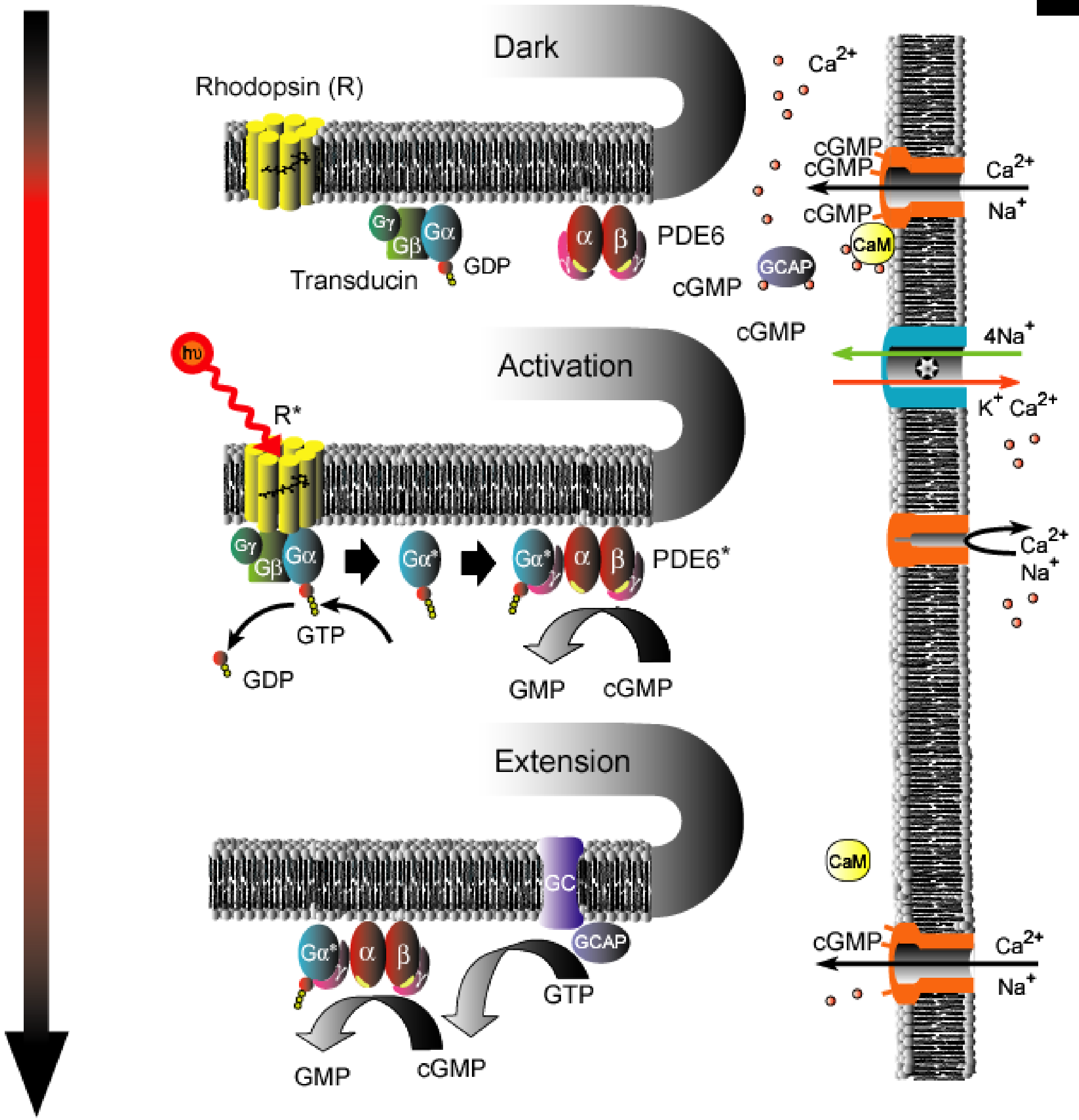
Range extension (1)



Reduction in $[Ca^{2+}]$ causes Calmodulin (CaM) to dissociate from the CNG channels raising the affinity of the channels for cGMP

Ca^{2+} feedback

Range extension (2)



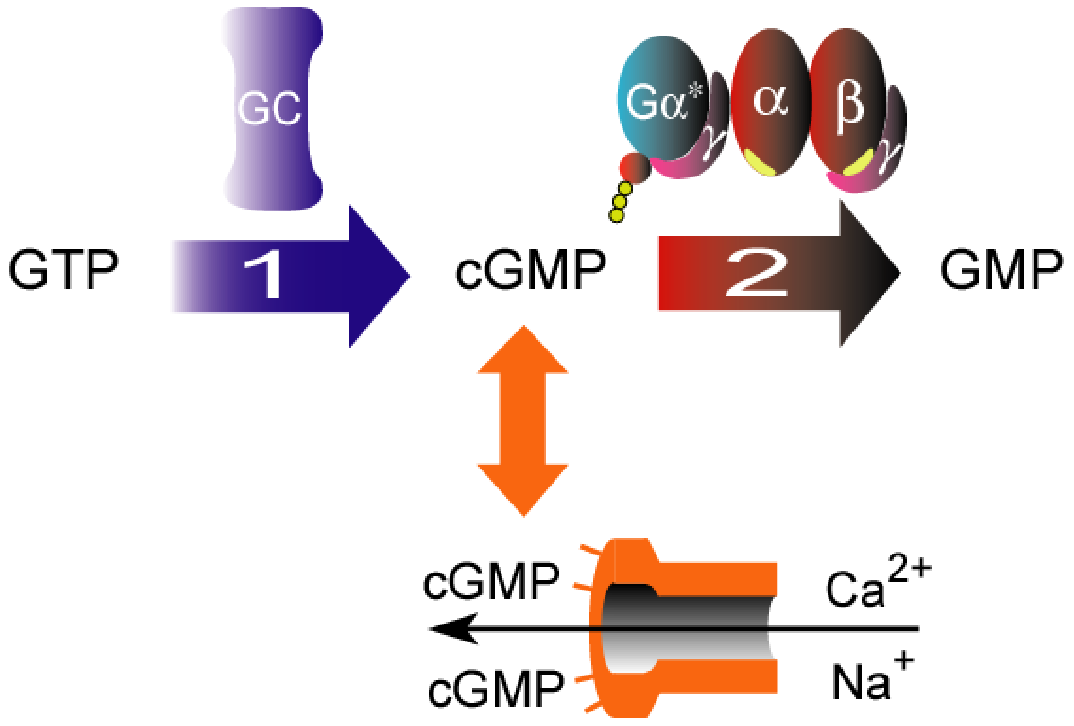
Reduction in $[Ca^{2+}]$ causes Calmodulin (CaM) to dissociate from the CNG channels raising the affinity of the channels for cGMP

Reduction in $[Ca^{2+}]$ causes dissociation of Ca^{2+} from GCAP, allowing it to bind to GC increasing the rate of resynthesis of cGMP

Ca^{2+} feedback

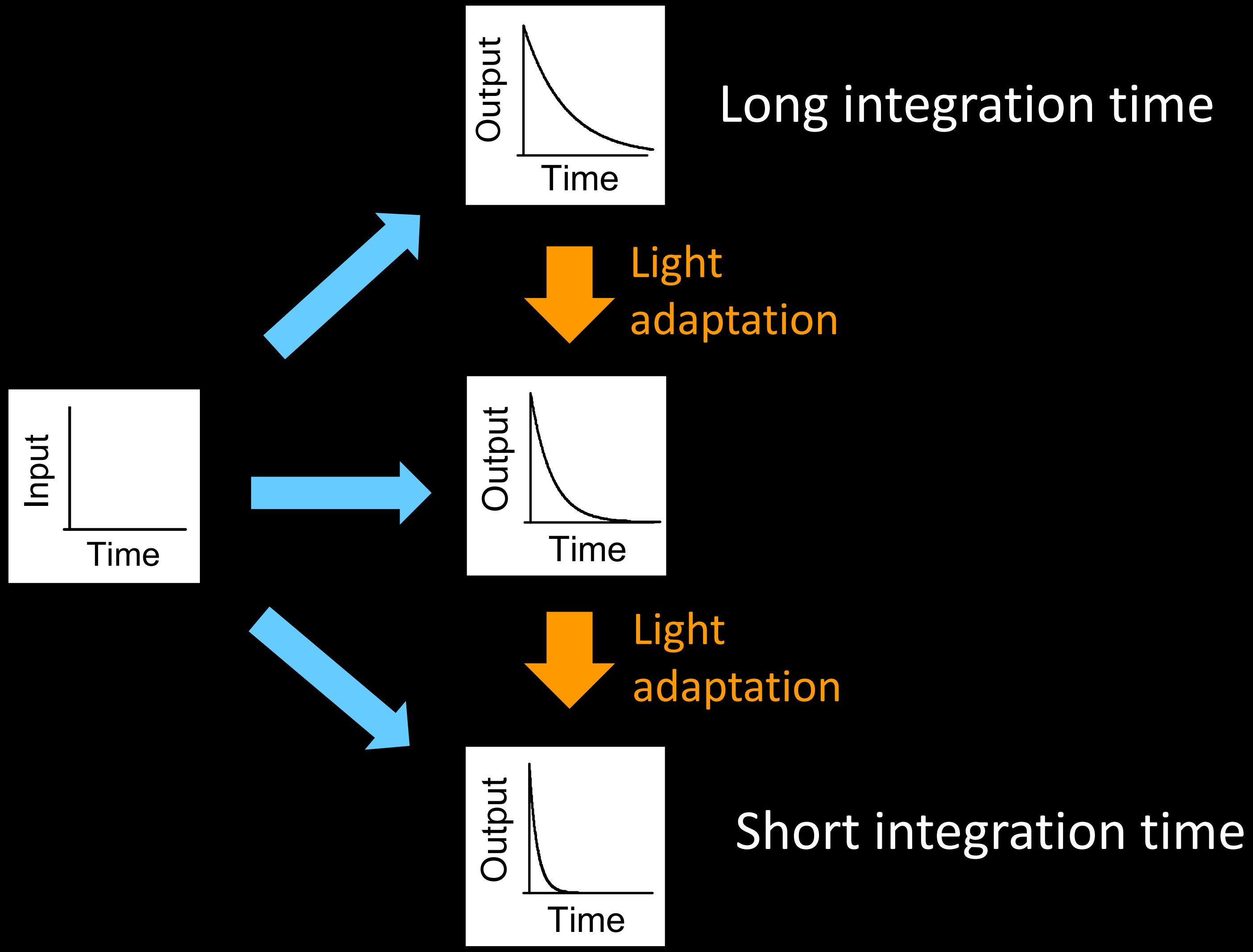
Adaptation: Speeding up the visual response

Increase in concentration of G*α-PDE6* in light speeds up rate of reaction 2 and speeds up the visual response

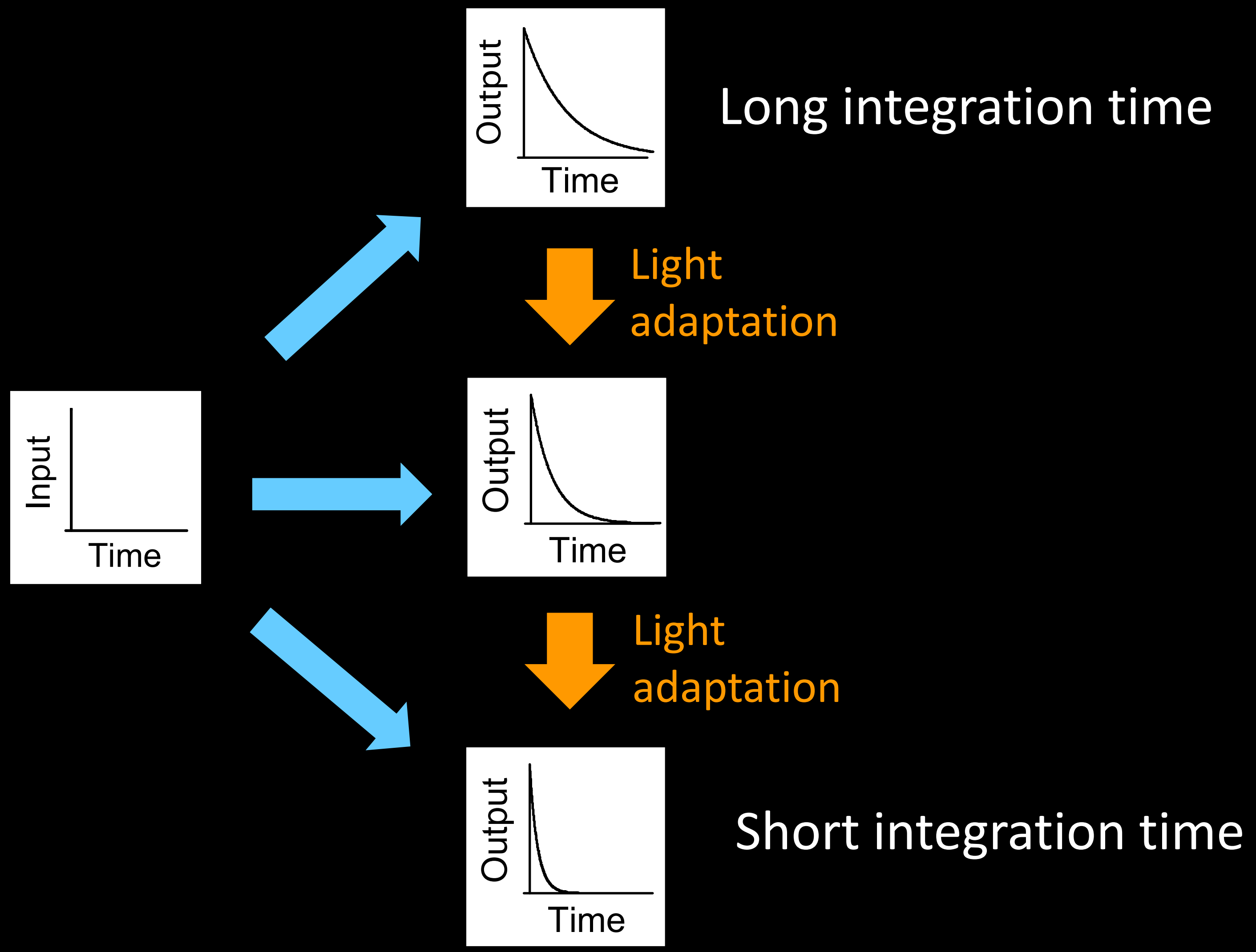


How does speeding up the visual response help light adaptation?

It reduces the integration time of the system...



What are the benefits of this type of adaptation?

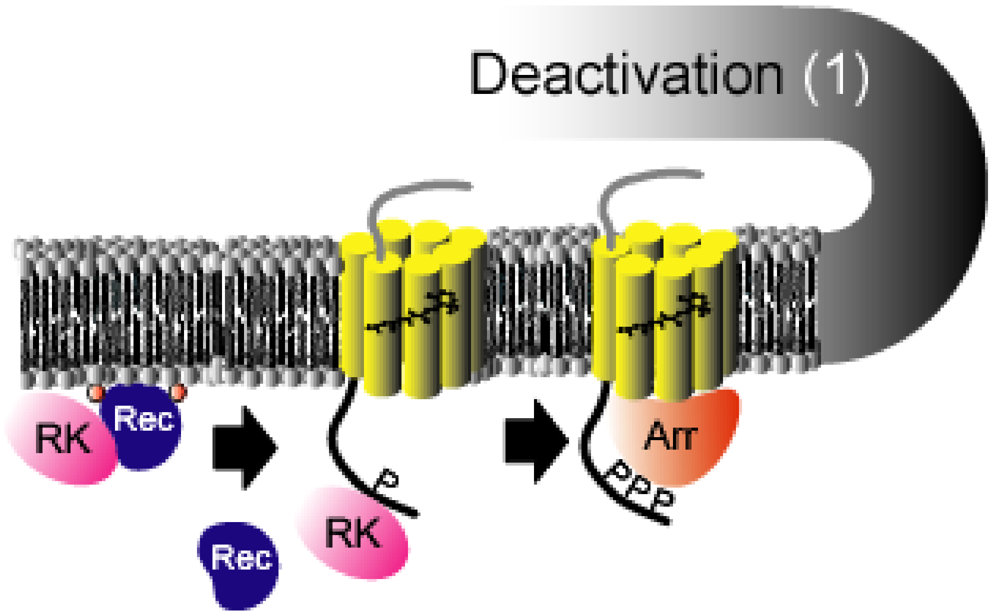


Deactivation

Speeding up deactivation also decreases temporal integration.

Deactivation steps

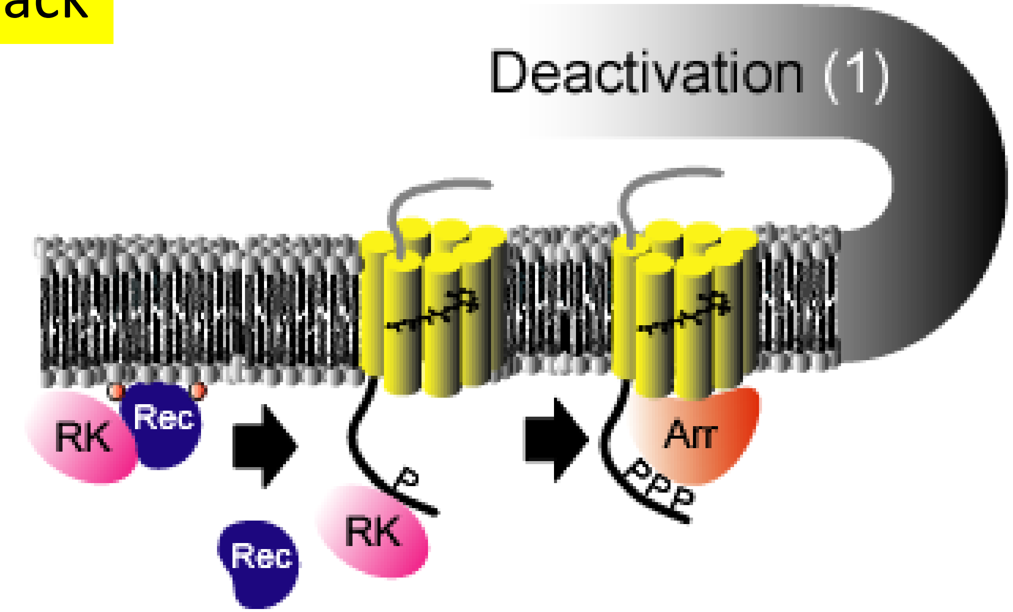
Ca^{2+} feedback



Rec-2Ca^{2+} forms a complex with RK, blocking its activity. When [Ca^{2+}] drops, Ca^{2+} dissociates and Rec goes into solution.

Deactivation steps

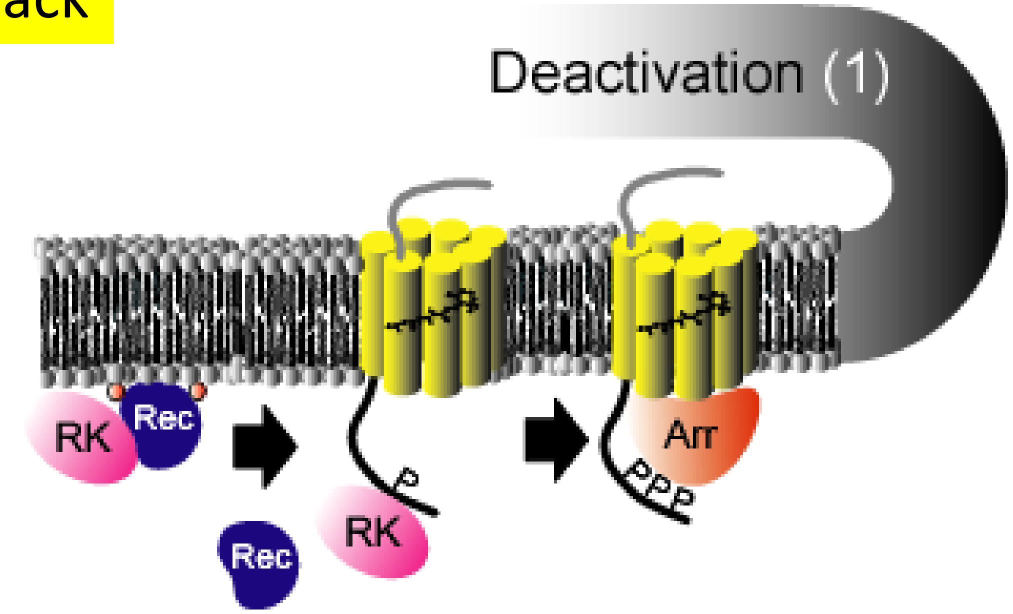
Ca^{2+} feedback



Free RK multiply phosphorylates R*

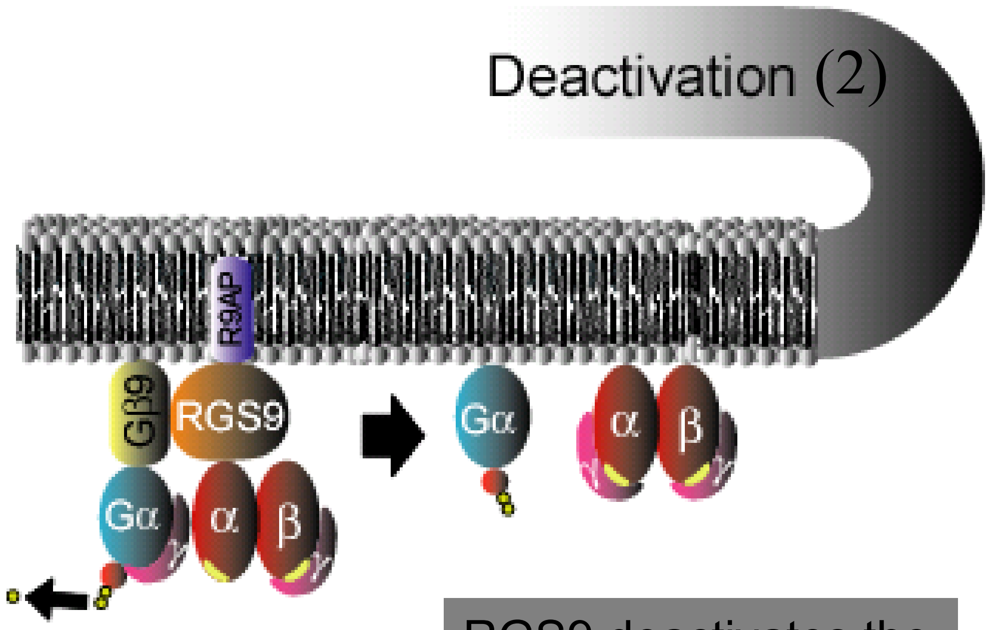
Deactivation steps

Ca^{2+} feedback



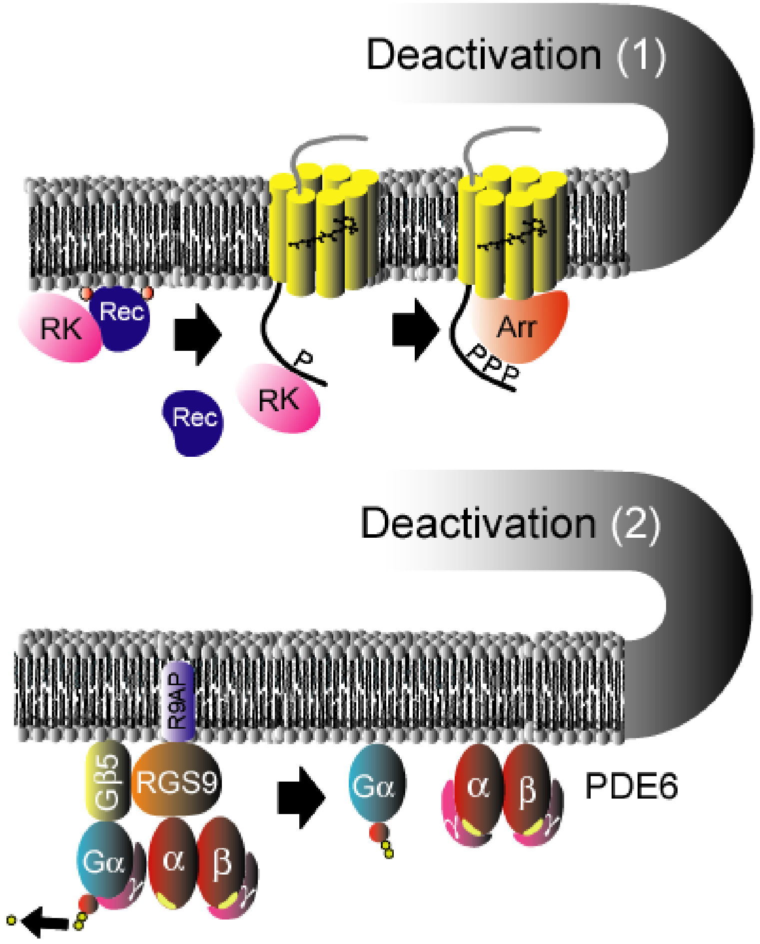
Arrestin (Arr) quenches the phosphorylated R*

Deactivation steps



RGS9 deactivates the activated G*α-PDE6* complex.

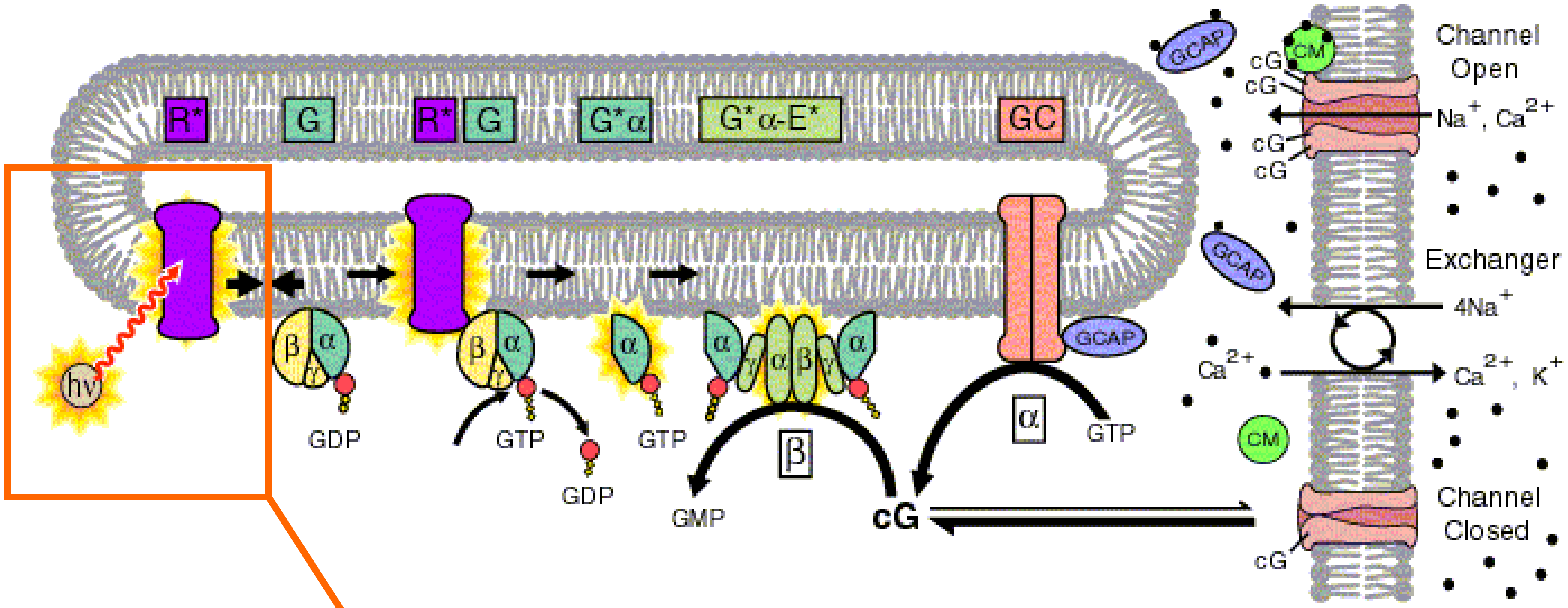
Deactivation steps



Second run through…

Phototransduction cascade activation stages

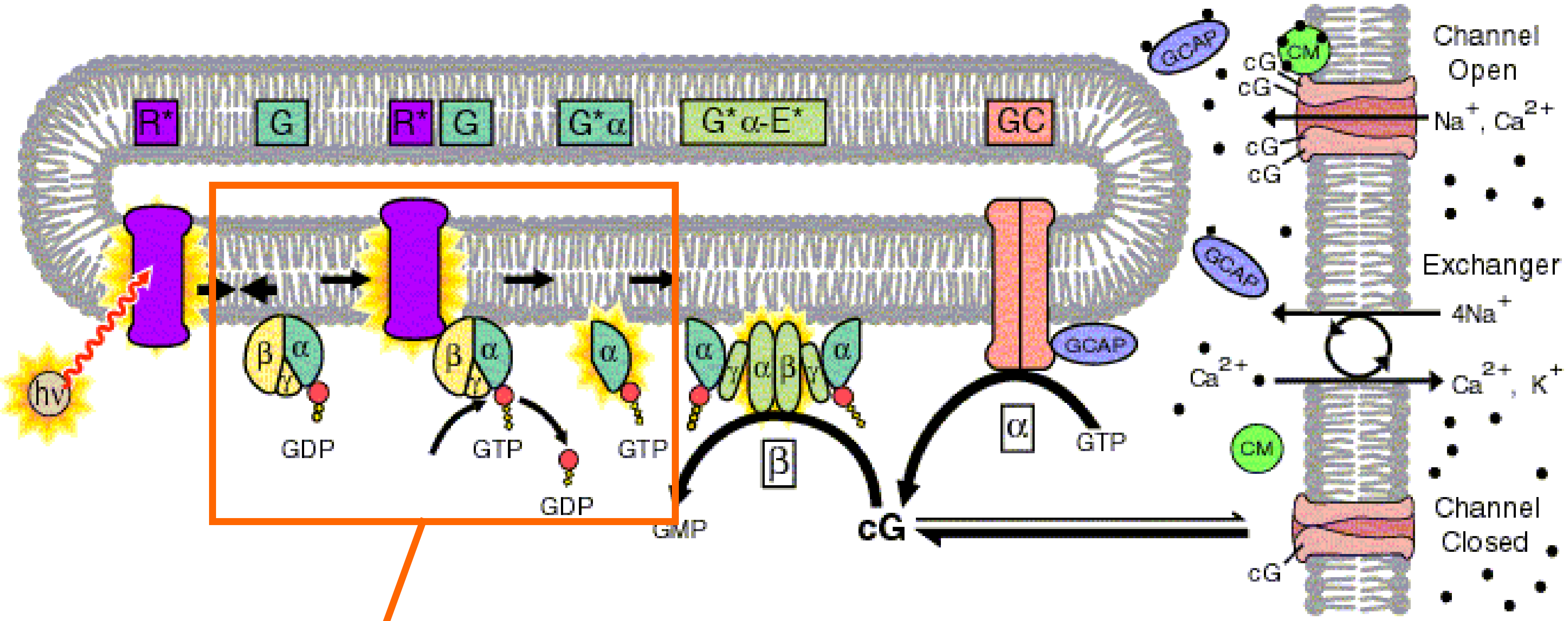
Activation steps of the phototransduction cascade



A photon is absorbed resulting in activated R*

Credit: Pugh, Nikonov & Lamb

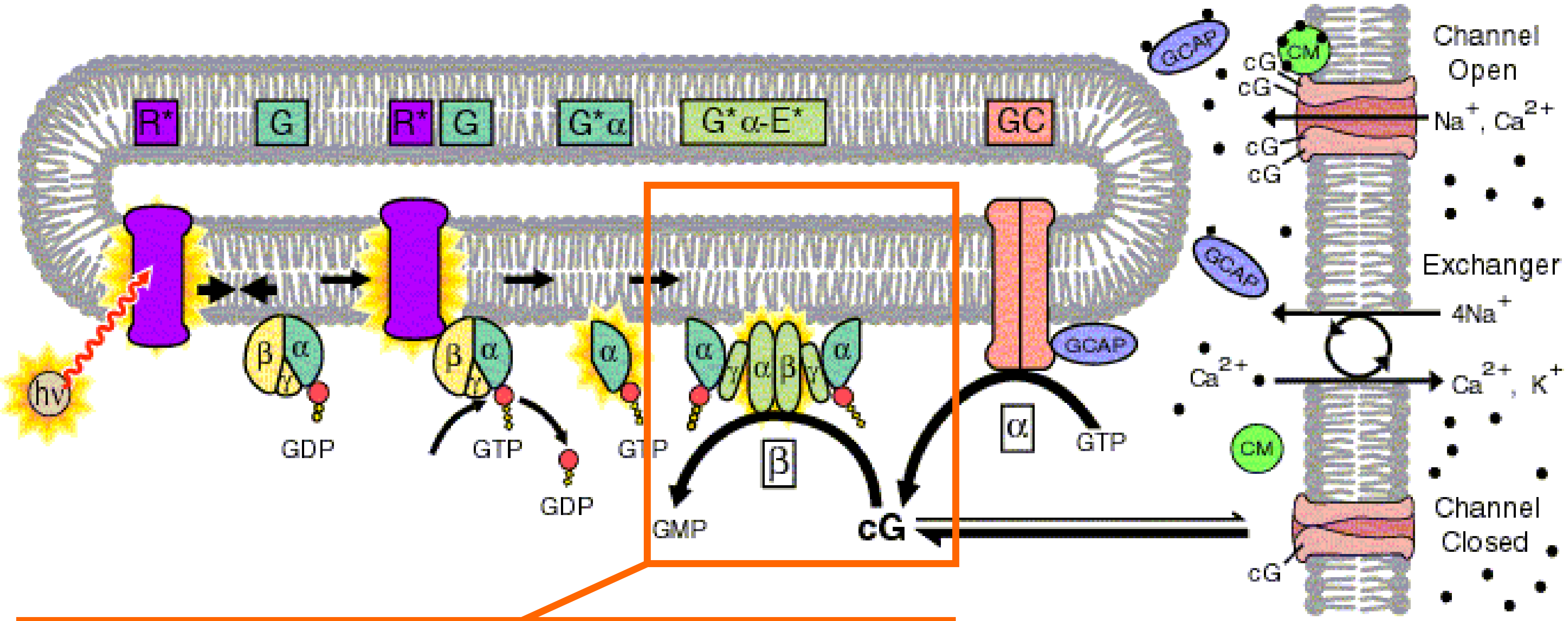
Activation steps of the phototransduction cascade



R* catalyses the exchange of GDP for GTP on the G-protein, producing the activated transducin, subunit G*α (Gα-GTP).

Credit: Pugh, Nikonov & Lamb

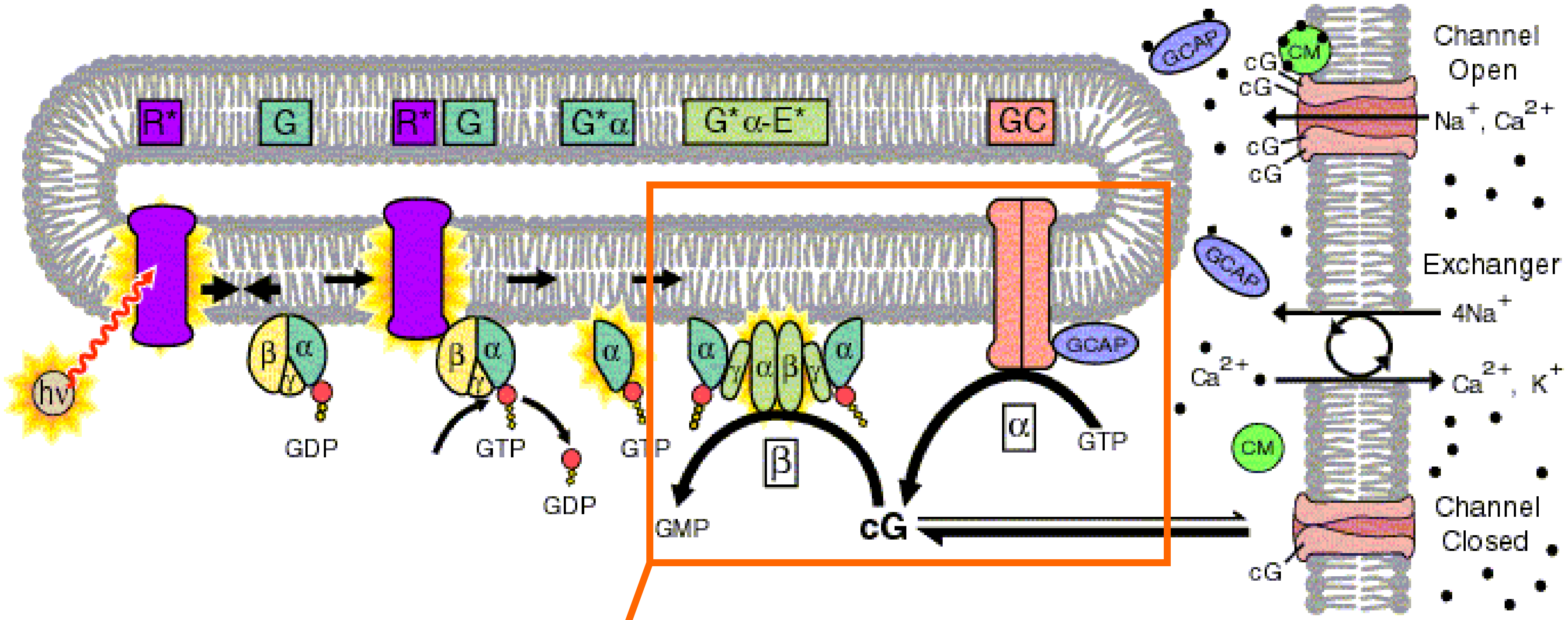
Activation steps of the phototransduction cascade



Activated transducin, G*α, in turn, binds to and activates phospho-diesterase (PDE6) by displacing γ inhibitory subunits to produce PDE6*.

Credit: Pugh, Nikonov & Lamb

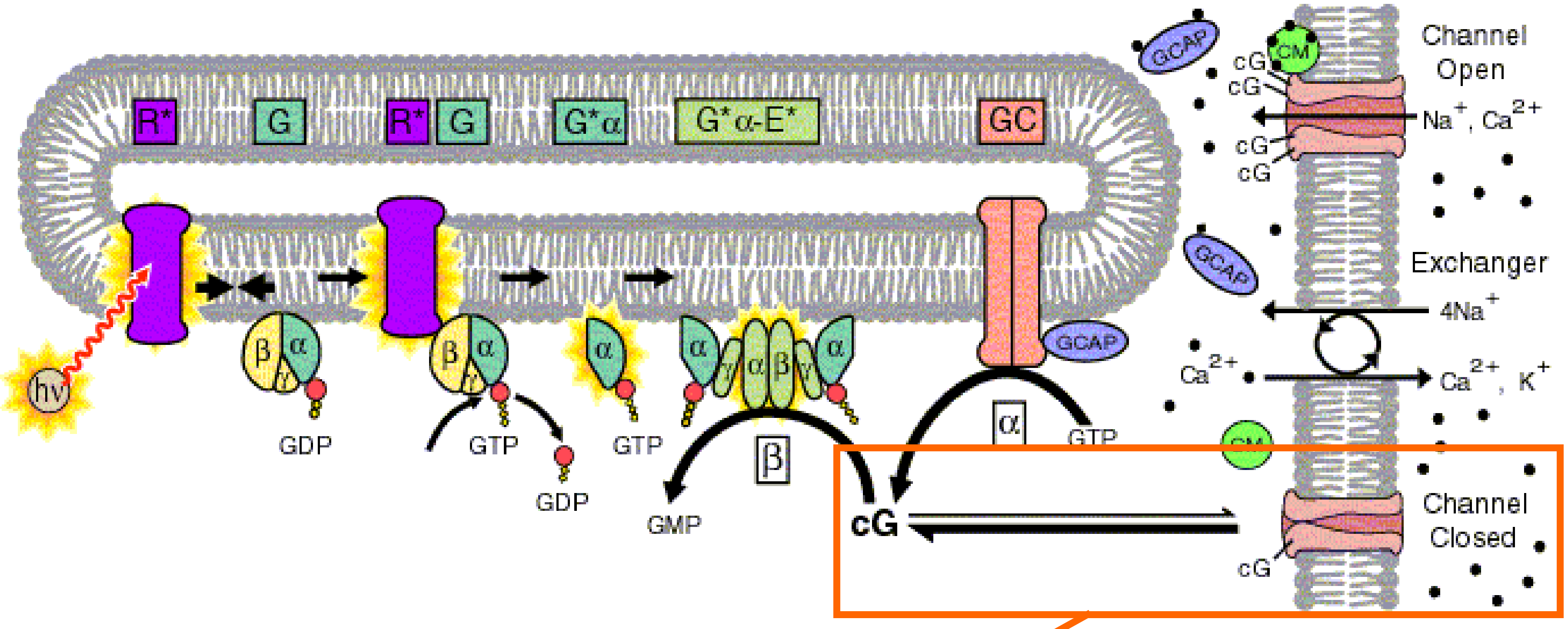
Activation steps of the phototransduction cascade



PDE6* (G*α-E*) activity produces a local drop in cytoplasmic cG (cGMP)

Credit: Pugh, Nikonov & Lamb

Activation steps of the phototransduction cascade

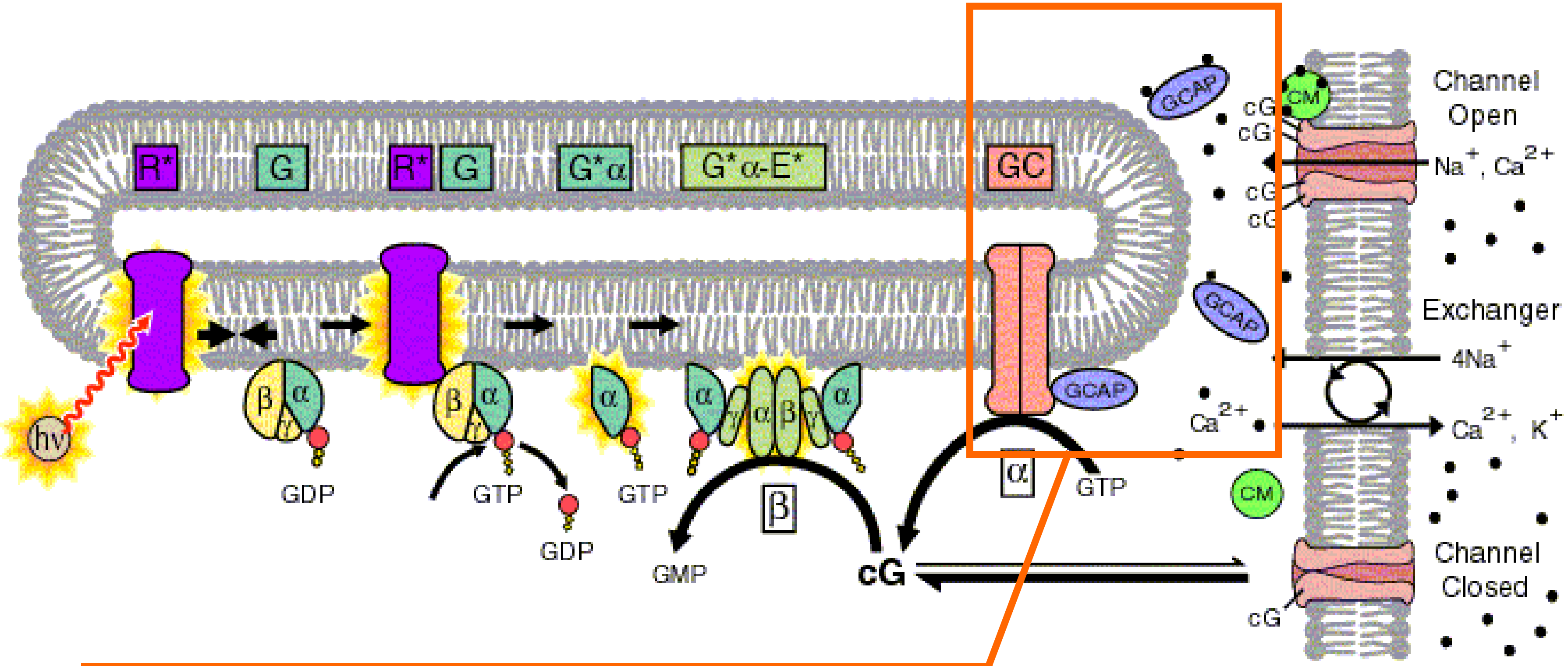


A drop in cGMP leads to closure of cGMP gated channels, blocking the entry of Na^+ and Ca^{2+} into the outer segment. The ion exchanger continues to function lowering $[Ca^{2+}]$ in the outersegment.

Credit: Pugh, Nikonov & Lamb

Phototransduction cascade inactivation steps

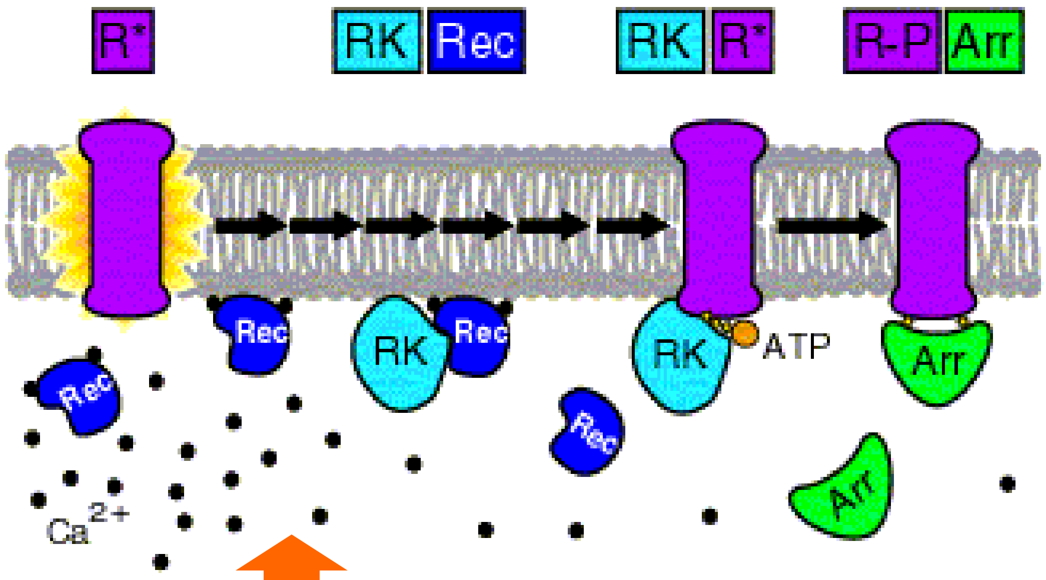
Inactivation steps of the phototransduction cascade



Removal of Ca^{2+} activates guanylate cyclase activating protein, GCAP. Activated GCAP binds to guanylate cyclase, stimulating production of cG.

Ca^{2+} feedback

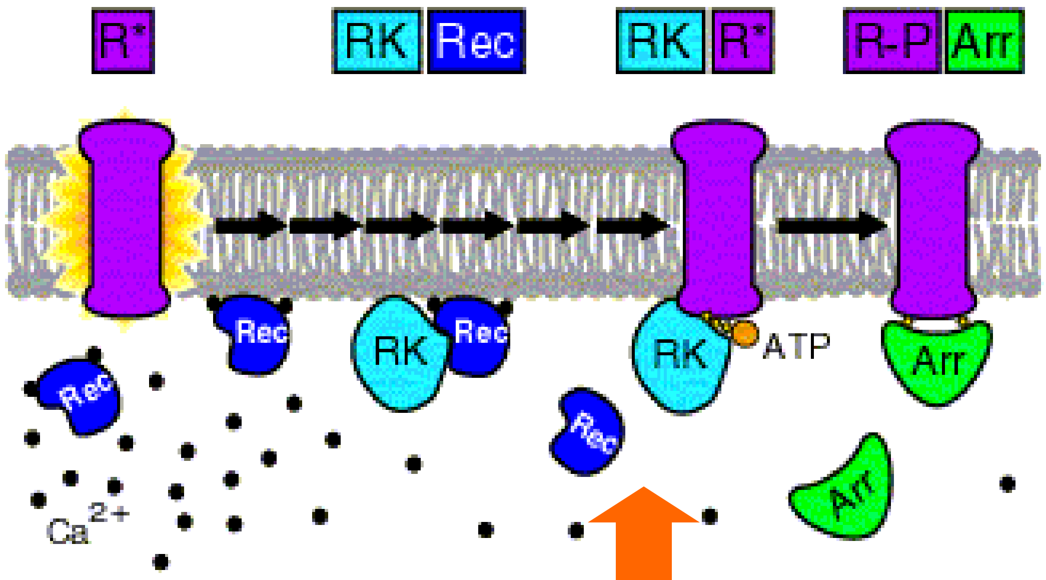
Credit: Pugh, Nikonov & Lamb



In the dark, when [Ca^{2+}] is high, most of recoverin (Rec) is in the calcium bound form at the membrane; Rec-2Ca^{2+} forms a complex bond with rhodopsin kinase (RK) blocking its activity.

Ca^{2+} feedback

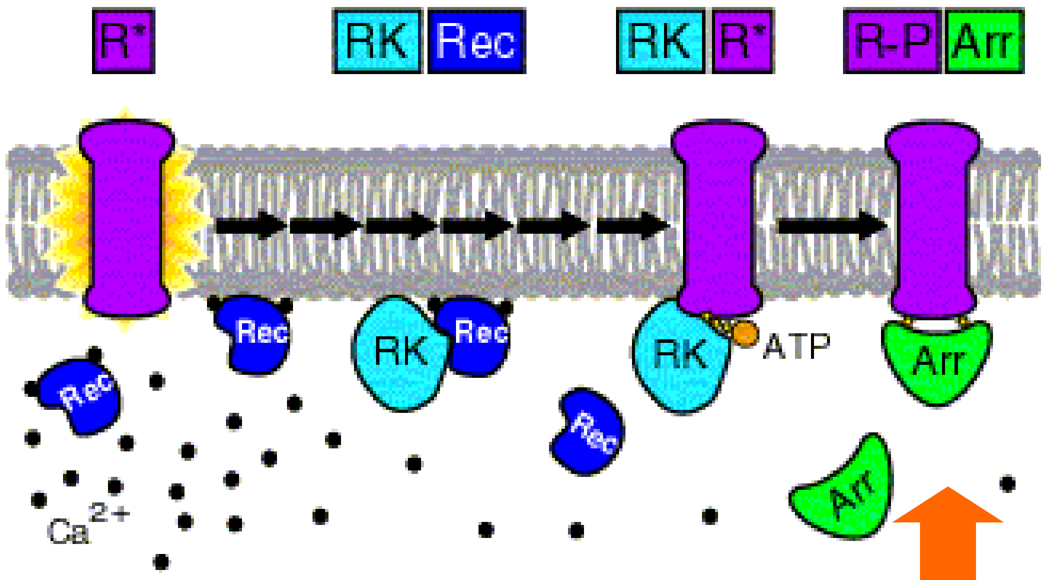
Credit: Pugh, Nikonov & Lamb



When [Ca^{2+}] drops, Ca^{2+} dissociates from Rec, which moves into solution. Free RK rapidly increases, increasing its interaction with R*, and leading to its rapid phosphorylation.

Ca^{2+} feedback

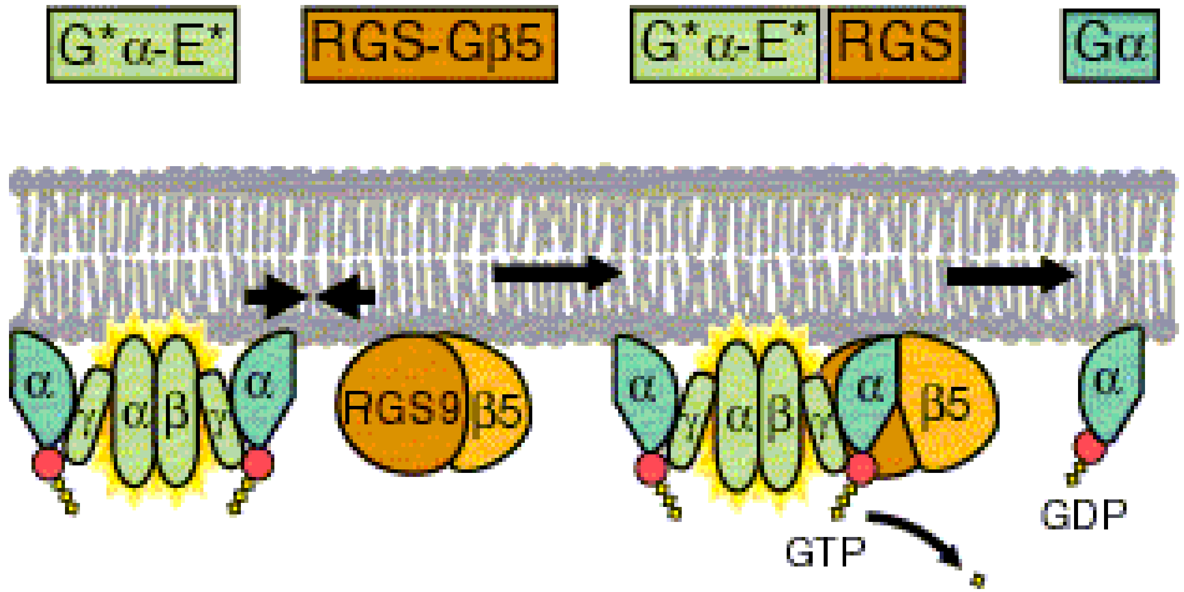
Credit: Pugh, Nikonov & Lamb



Arrestin (Arr) then binds quenching the activity of R*.

Ca^{2+} feedback

Credit: Pugh, Nikonov & Lamb

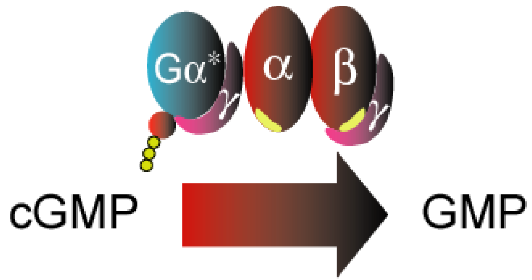


G*α-E* is inactivated when the terminal phosphate of its bound GTP is hydrolyzed, which occurs when the RGS9-Gβ5 protein binds to the complex.

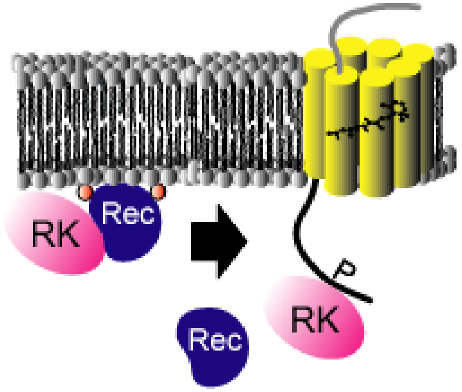
Credit: Pugh, Nikonov & Lamb

Summary of molecular adaptation mechanisms

Mechanisms that shorten the visual integration time

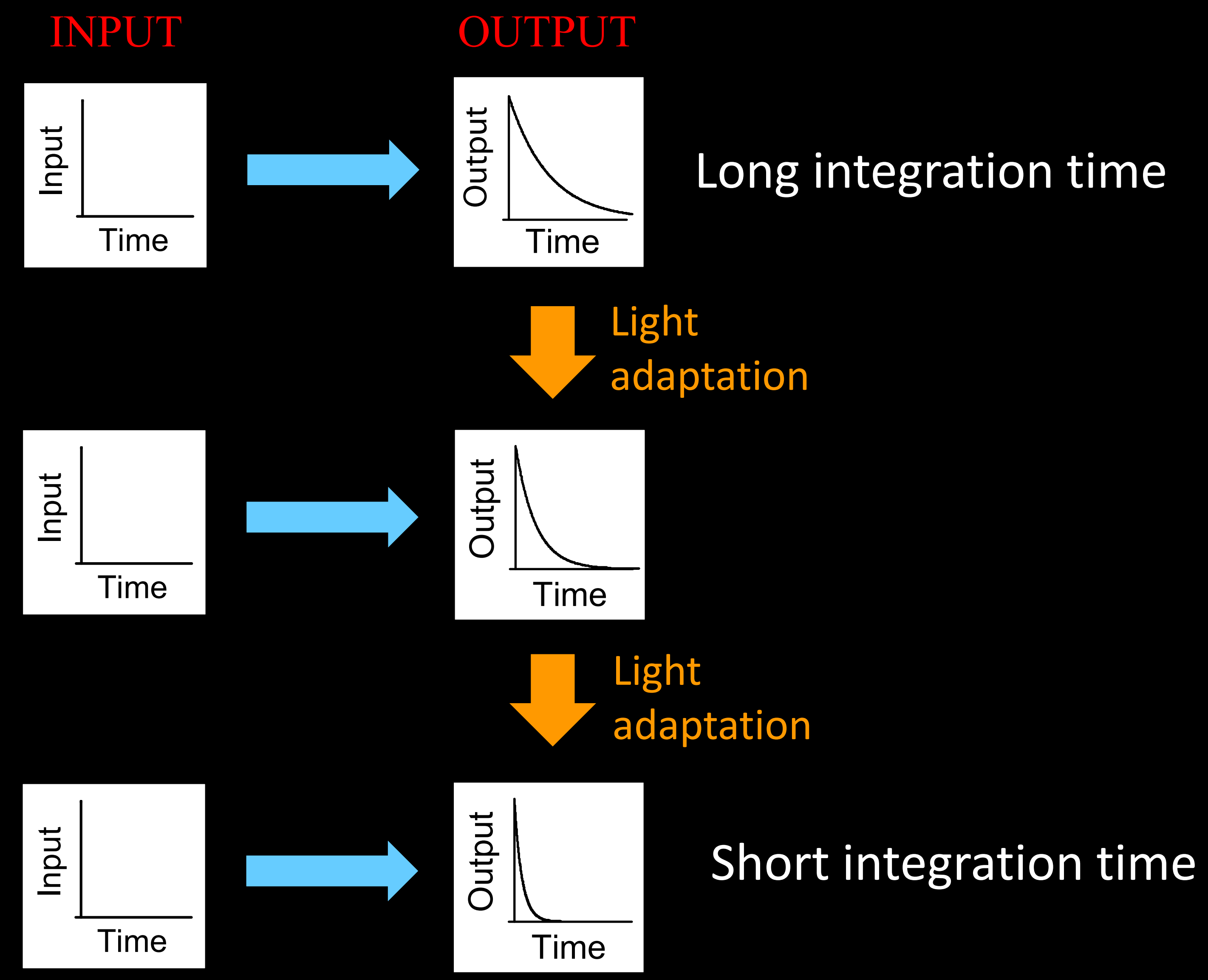


[G*α-PDE6*] dependent Increased rate of hydrolysis of cGMP to GMP

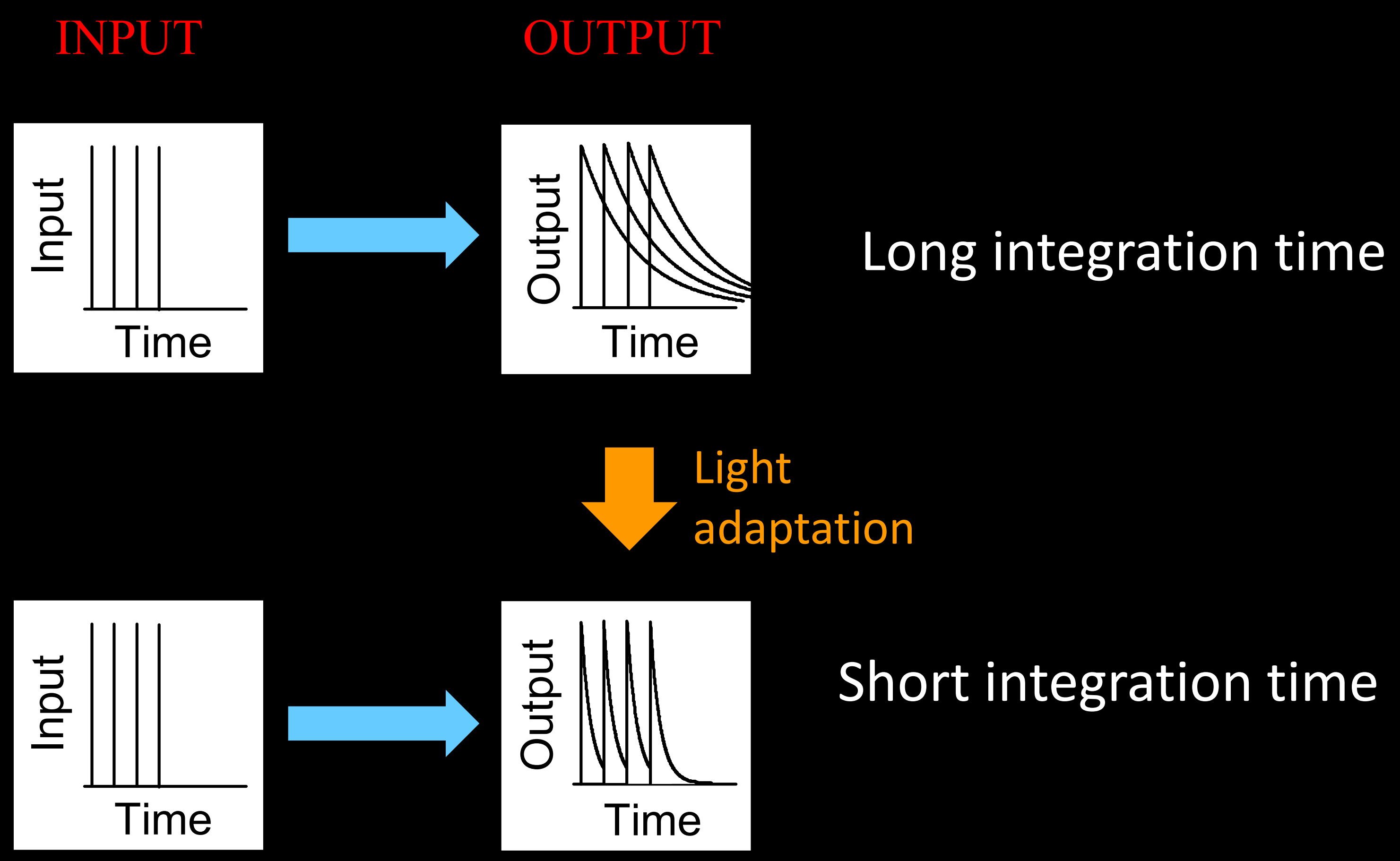


[Ca^{2+}] dependent activity of Rec

Changing the integration time of the system…



Shortening the integration time of the system increases sensitivity to higher flicker rates…

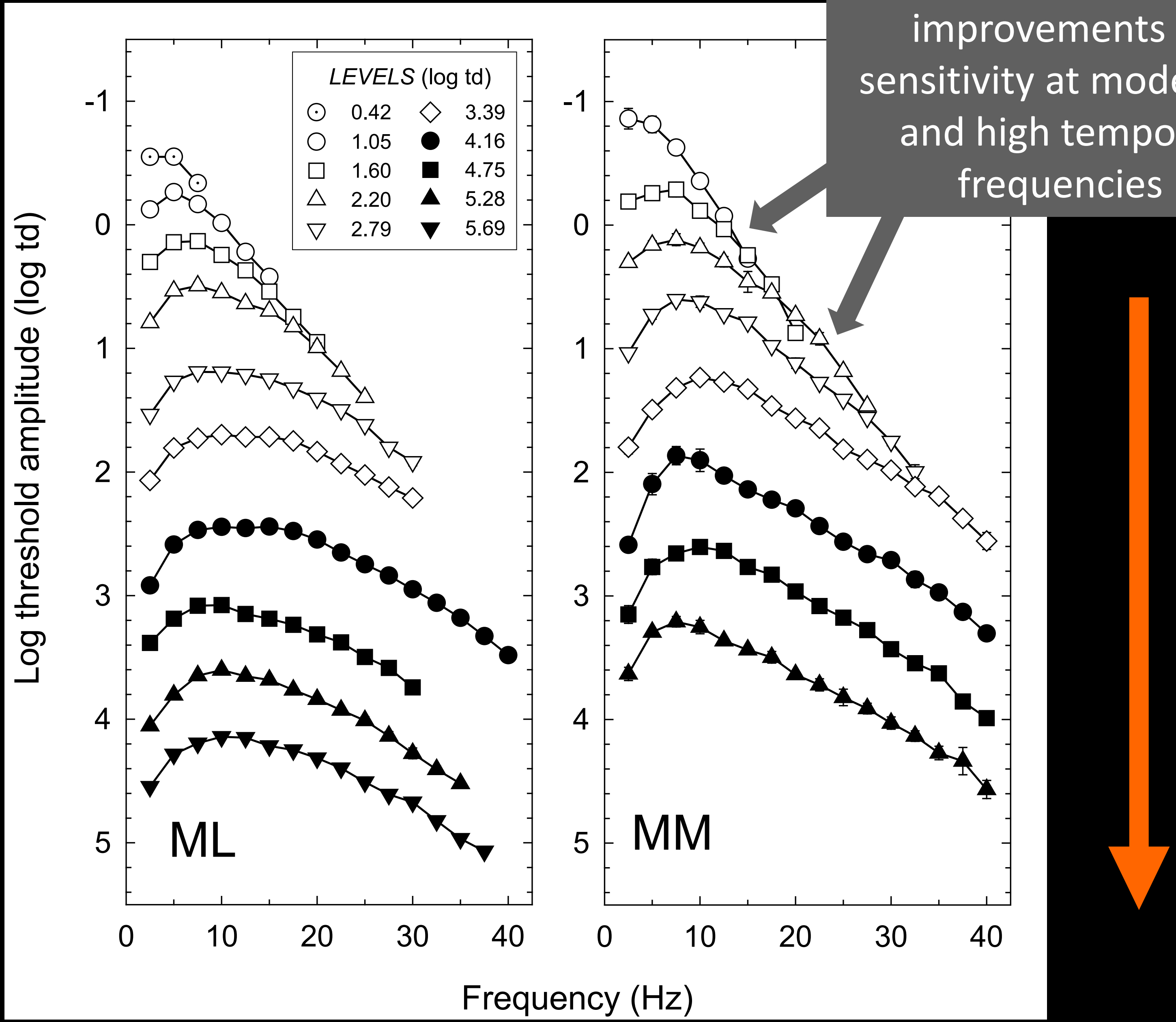


Human temporal response

- An excellent way of characterizing the effects of light adaptation psychophysically is to measure changes in the temporal response.

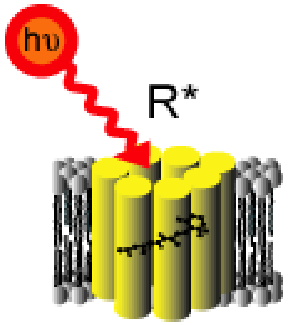
- Focus on changes in temporal sensitivity.

Changes in temporal sensitivity

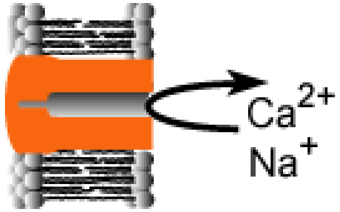


Substantial relative improvements in sensitivity at moderate and high temporal frequencies

Mechanisms that simply decrease sensitivity

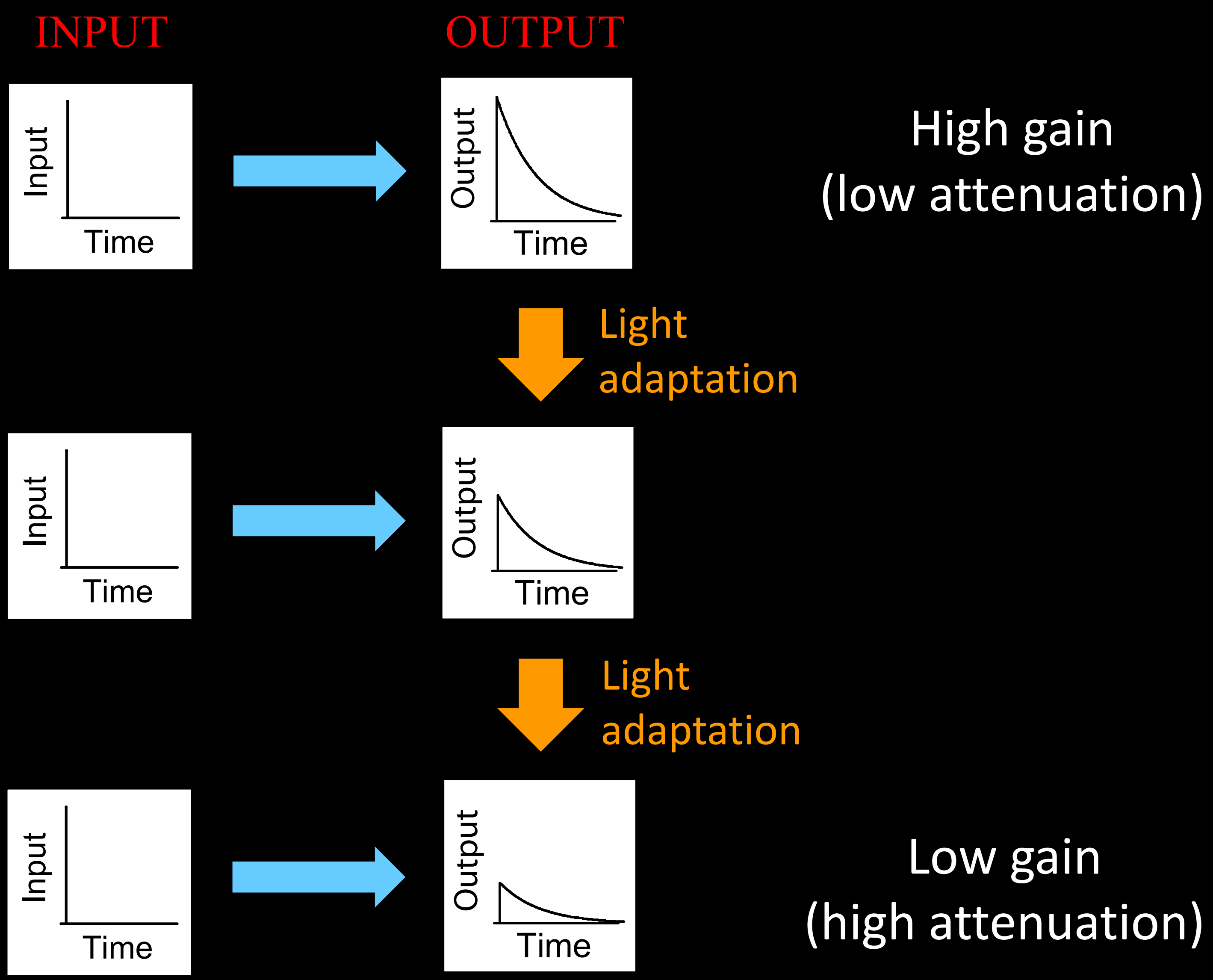


Photopigment bleaching (less photopigment available at high light levels)



Reduction in the number of open CNG-gated channels

Changing the gain (attenuation) of the system…



PHOTOTRANSDUCTION – CONES VERSUS RODS

Cones versus rods

Cones have different isoforms of:

Visual pigment, transducin, arrestin
PDE6, cGMP channel, and recoverin.

Quantitative differences. In cones:

(i) R* forms 4 times faster than for rods - faster onset of light response.

(ii) R* decays 10-50 times faster (lower amplification factor).

(iii) GTPase activating protein (RGS-Gβ5) expressed at much higher levels - shorter $G^*\alpha$ (activated transducin) lifetime - faster recovery.

(iv) Clearance of Ca^{2+} from cone outer segments is several times faster than for rods.

(v) cGMP channels in cones are twice as permeable to Ca^{2+} than in rods.

Cones versus rods

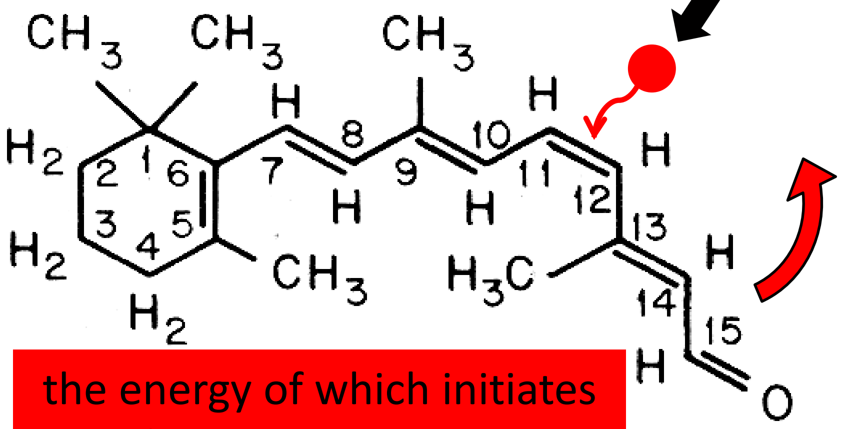
- Cones are 25 - 100 times less sensitive to single photons.
- They catch fewer photons (less visual pigment).
- They respond with faster kinetics (isoforms of transduction cascade).
- They have a much greater ability to adapt to background light.
- They do not saturate at normal environmental light levels.

TRANSDUCTION AND UNIVARIANCE

Chromophore

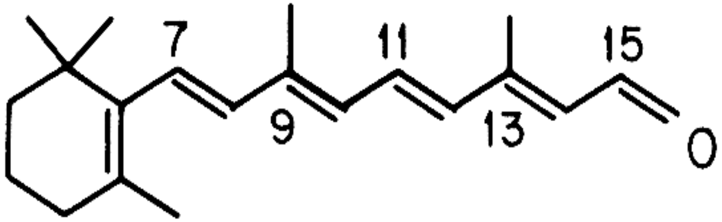
(*chromo*- colour, + -*phore*, producer)
Light-catching portion of any molecule

11-*cis* retinal



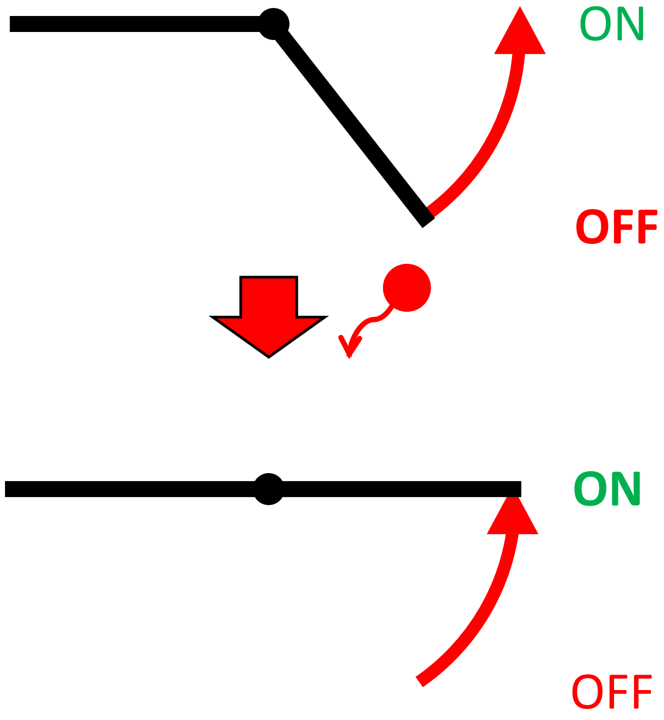
A photon is absorbed

the energy of which initiates a conformational change to…



all-*trans* retinal

Think of the molecule as a photo-sensitive switch!

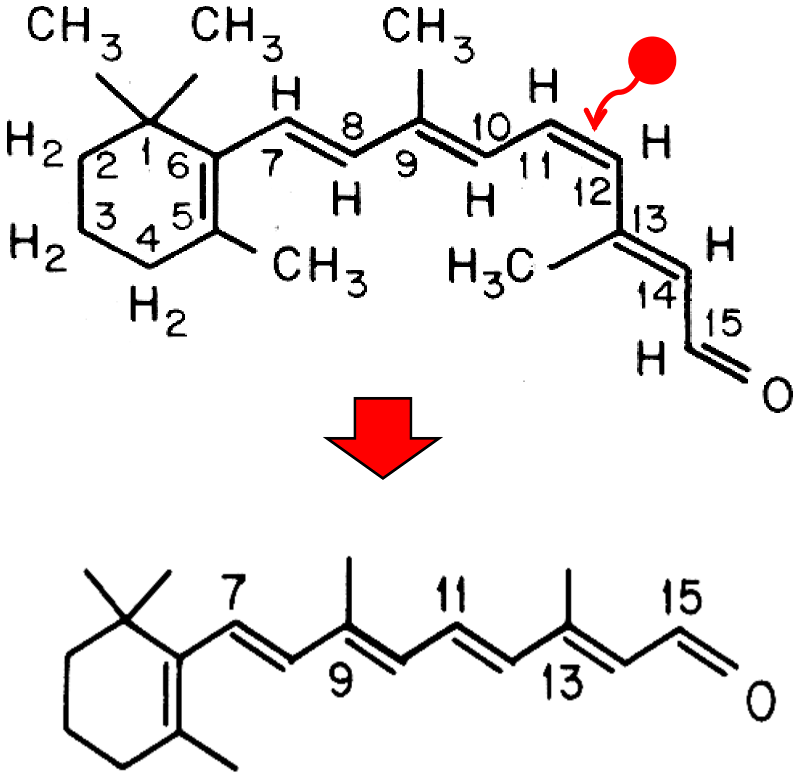


Chromophore

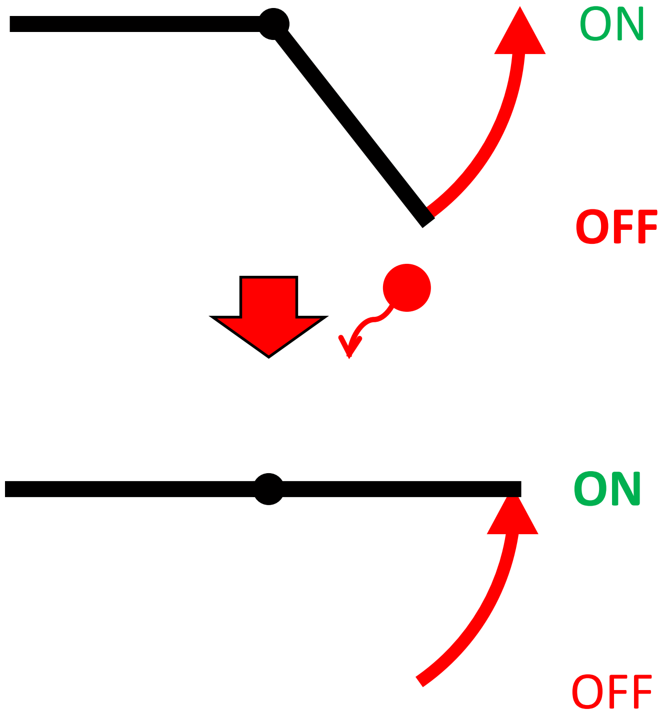
Crucially, the event is binary or “all or nothing”.

If a photon is absorbed it has the same effect as any other absorbed photon, whatever its wavelength.

11-*cis* retinal



all-*trans* retinal



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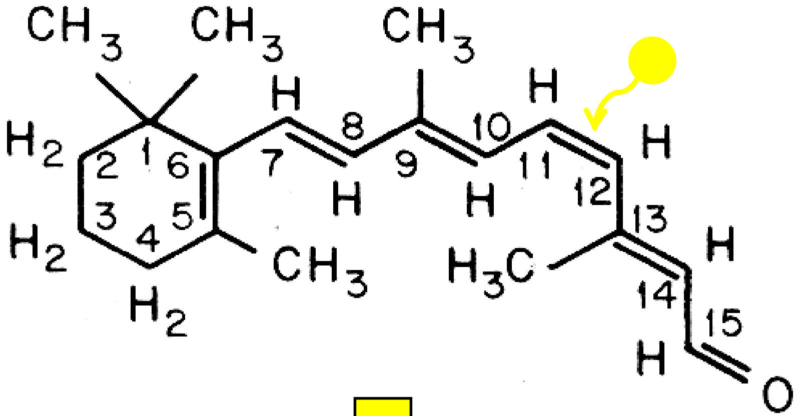
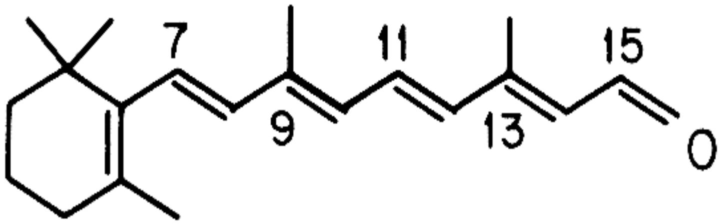
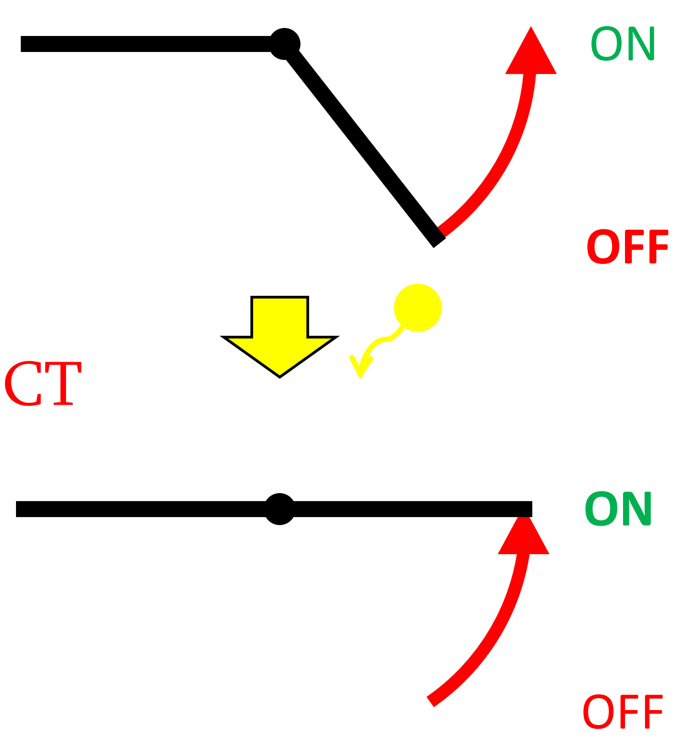


SAME EFFECT



all-*trans* retinal



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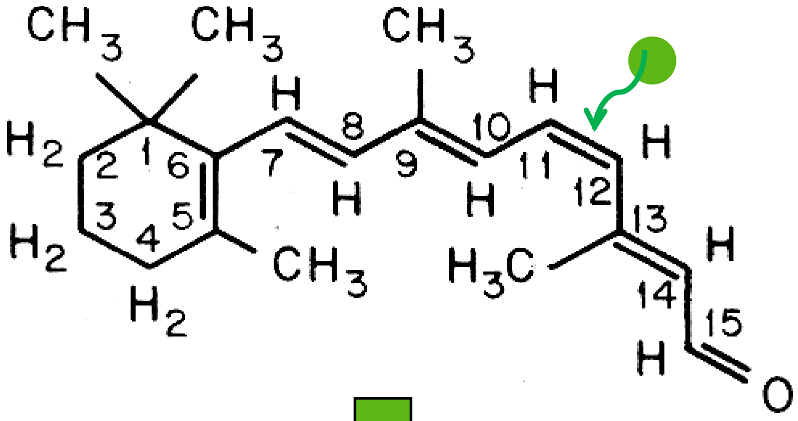
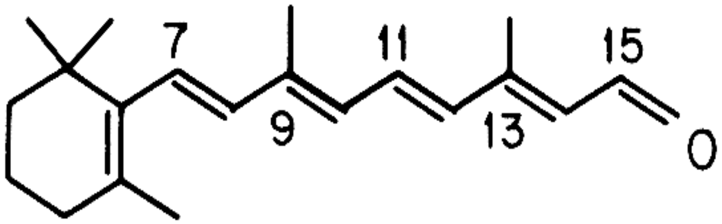
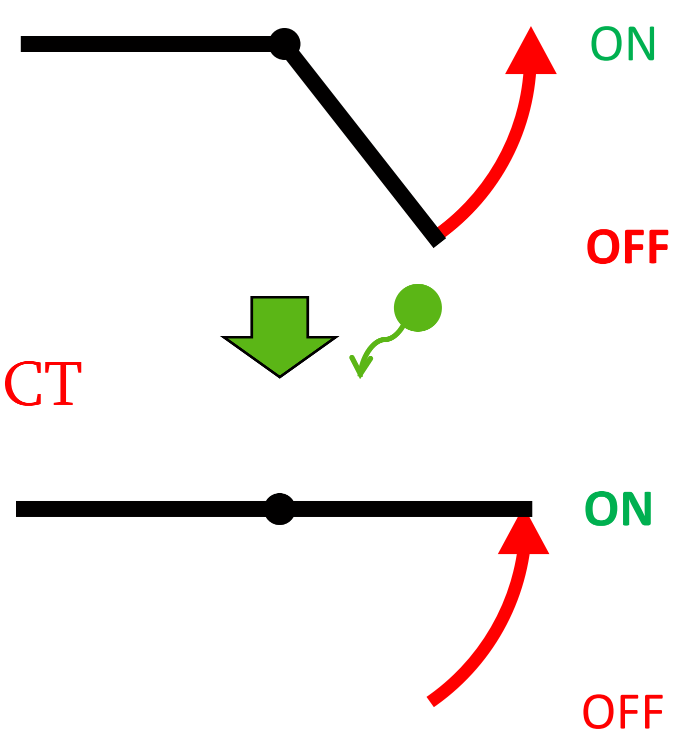


SAME EFFECT



all-*trans* retinal



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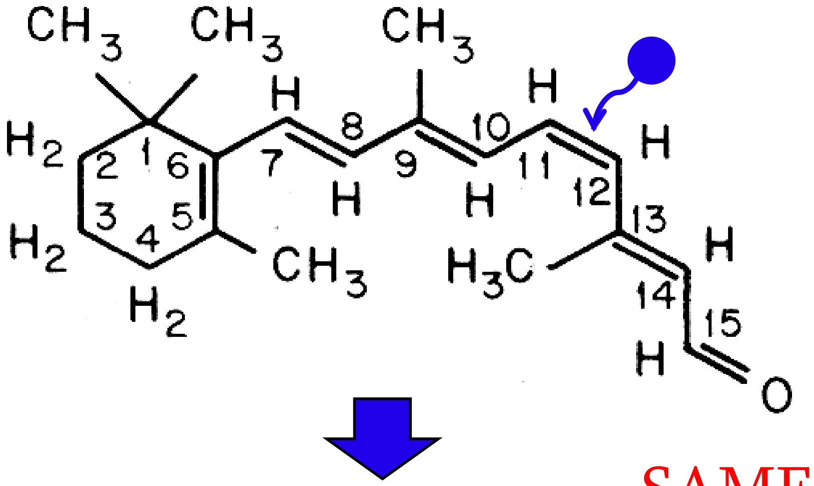
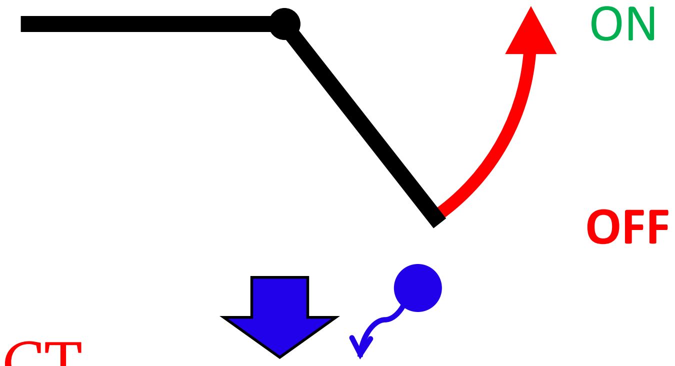
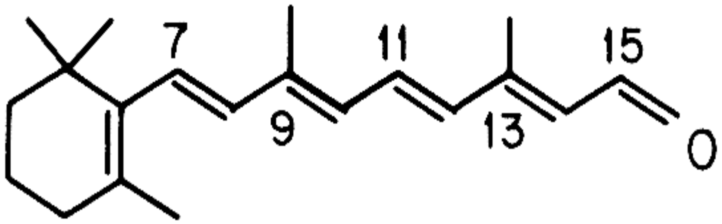
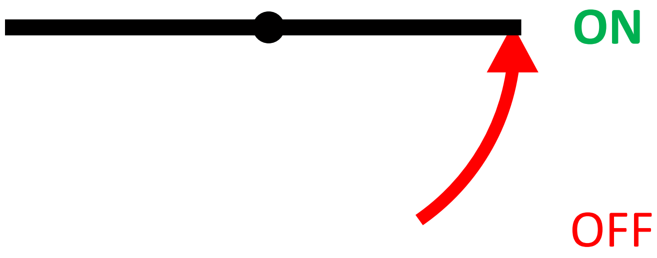




SAME EFFECT



all-*trans* retinal



Chromophore

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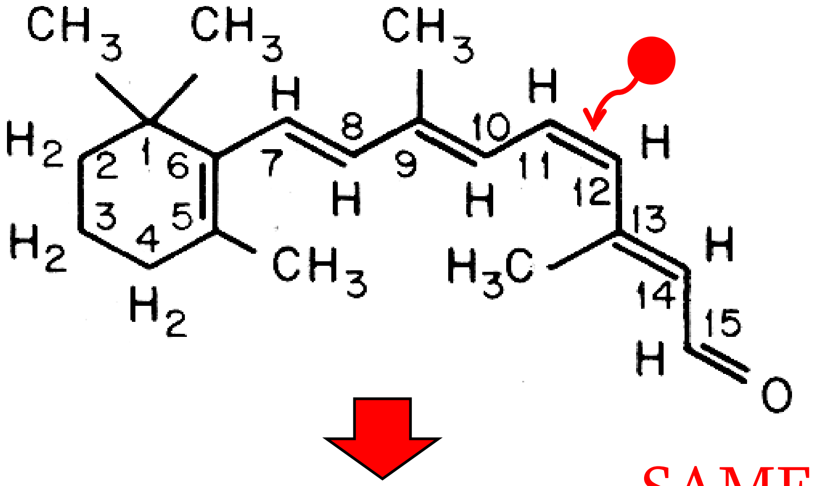
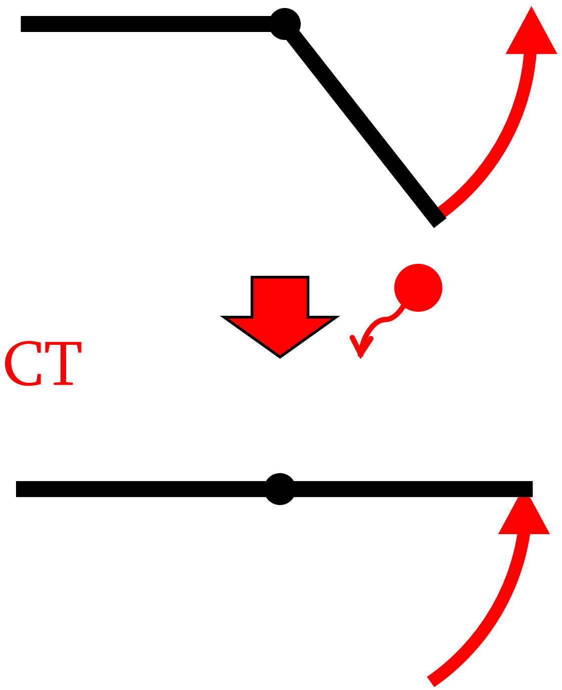
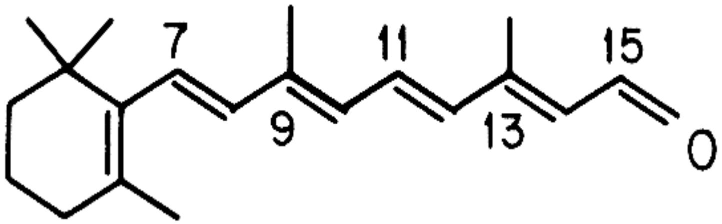


SAME EFFECT



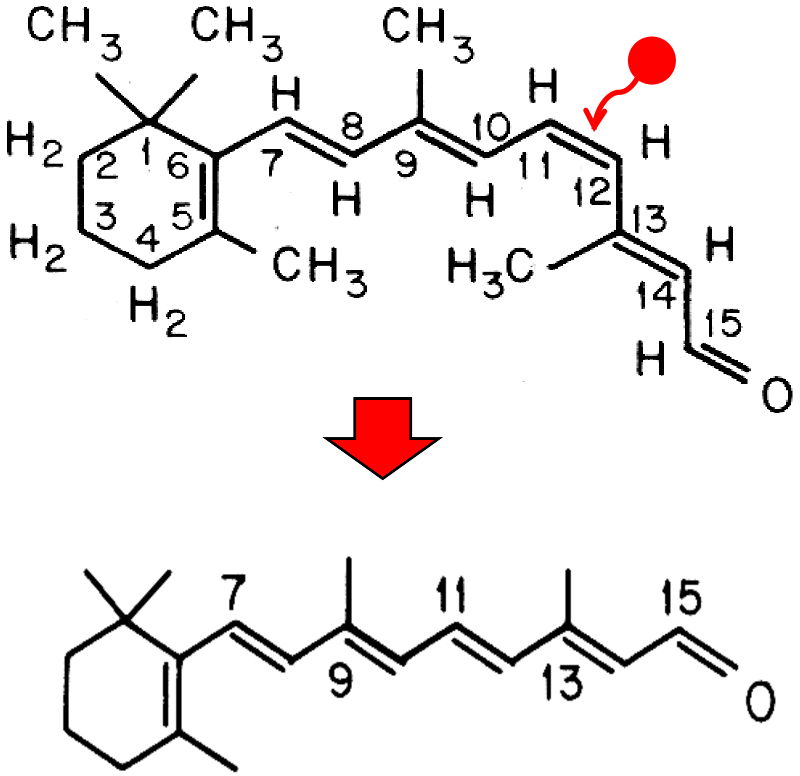


all-*trans* retinal

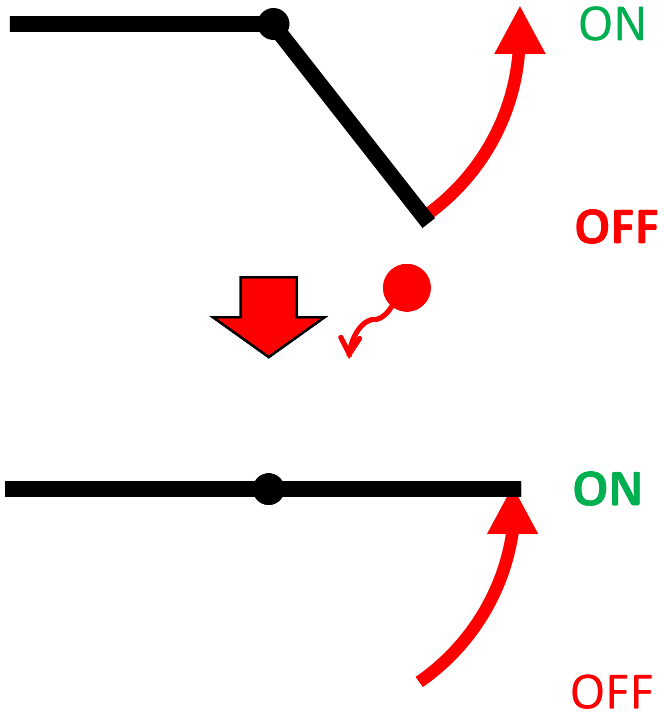
Chromophore

Can this process encode wavelength (colour)?

11-*cis* retinal



all-*trans* retinal

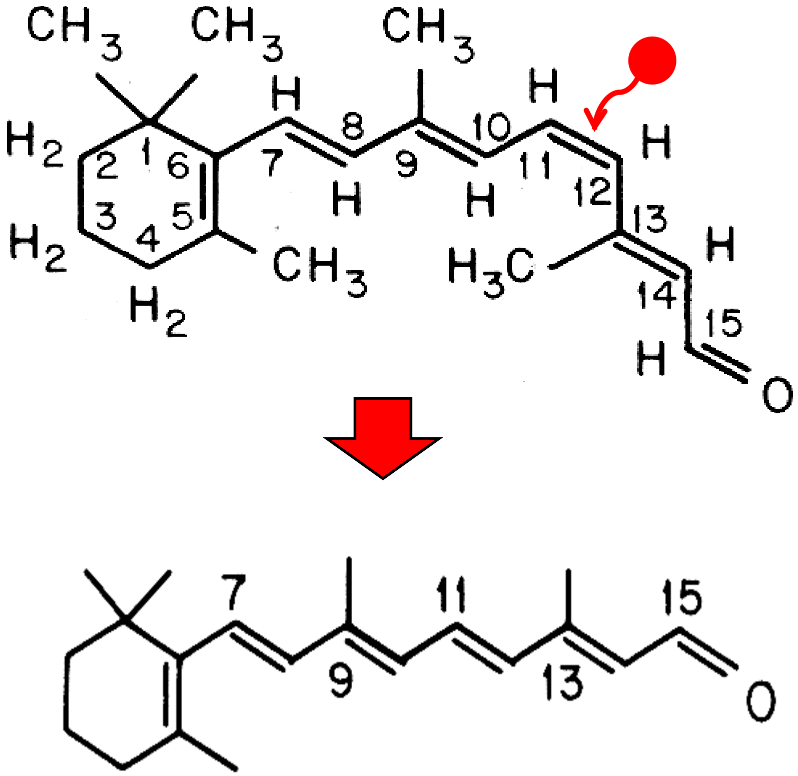


Chromophore

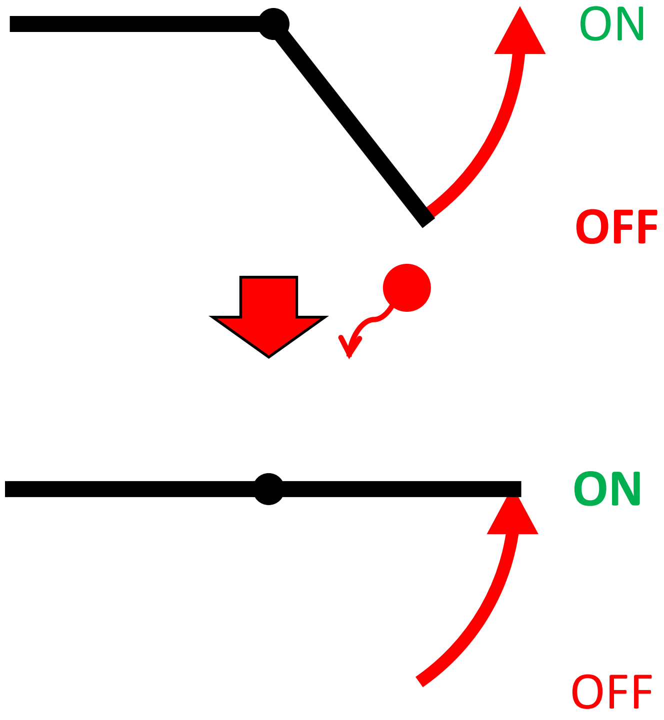
No, it cannot encode wavelength (colour)!

It is "UNIVARIANT"

11-*cis* retinal



all-*trans* retinal



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

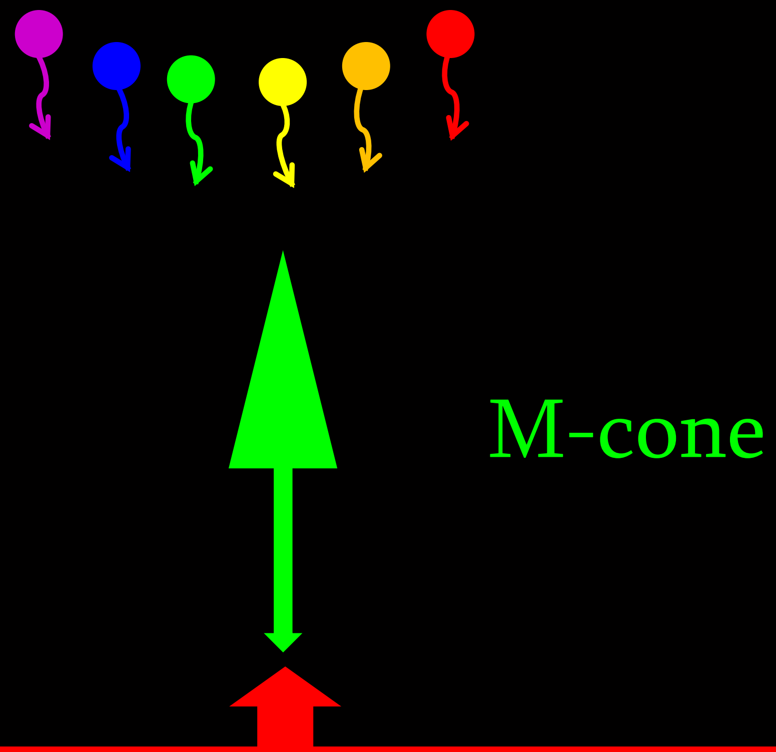
“UNIVARIANT”

What does univariance mean in practice?

Use Middle-wavelength-sensitive (M) cones as an example…

UNIVARIANCE

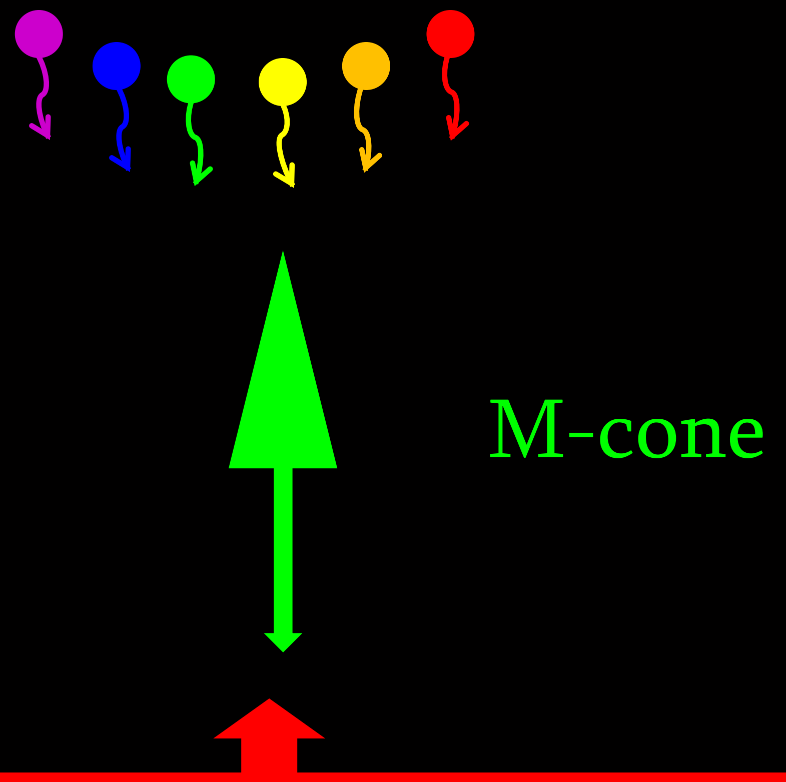
Crucially, the effect of any absorbed photon is *independent* of its wavelength.



So, if you monitor the cone output, you can’t tell which wavelength (energy) of photon has been absorbed.

UNIVARIANCE

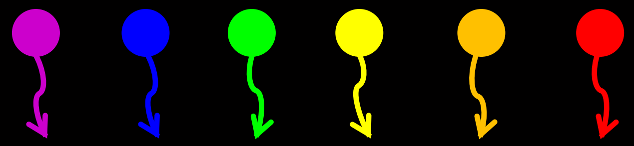
Crucially, the effect of any absorbed photon is *independent* of its wavelength.



All the photoreceptor effectively does is to count photons.

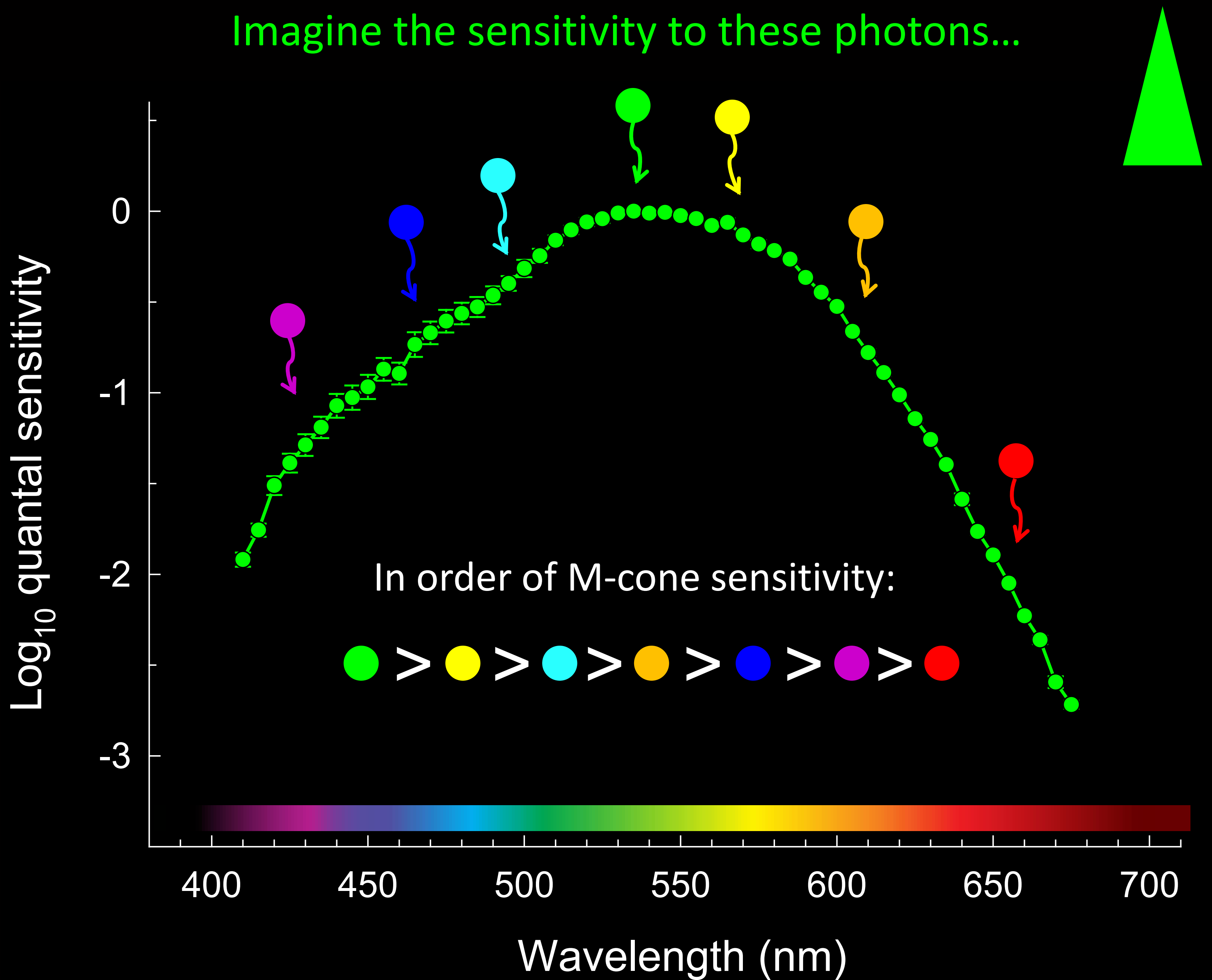
UNIVARIANCE

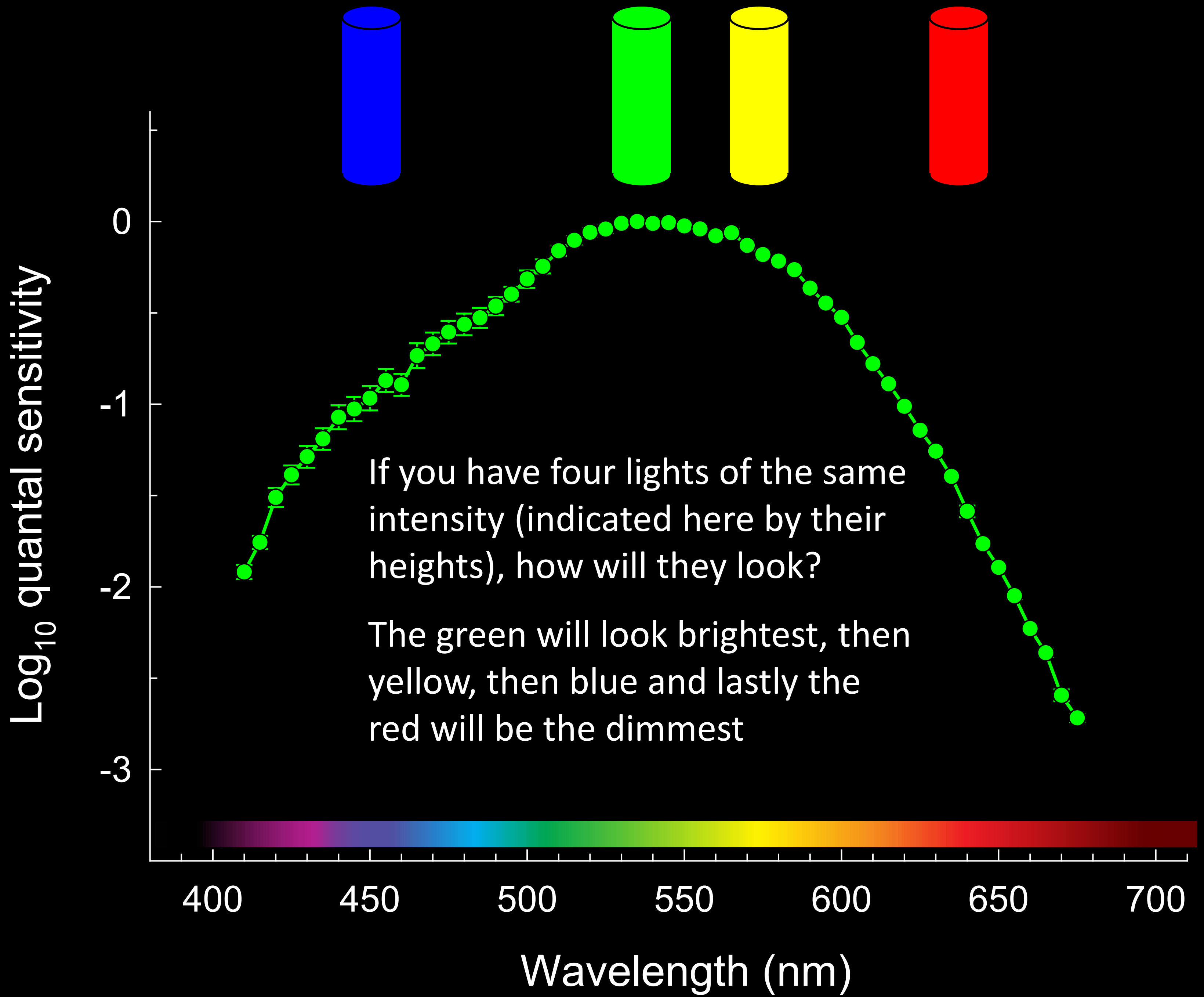
What does vary with wavelength is the probability that a photon will be absorbed.



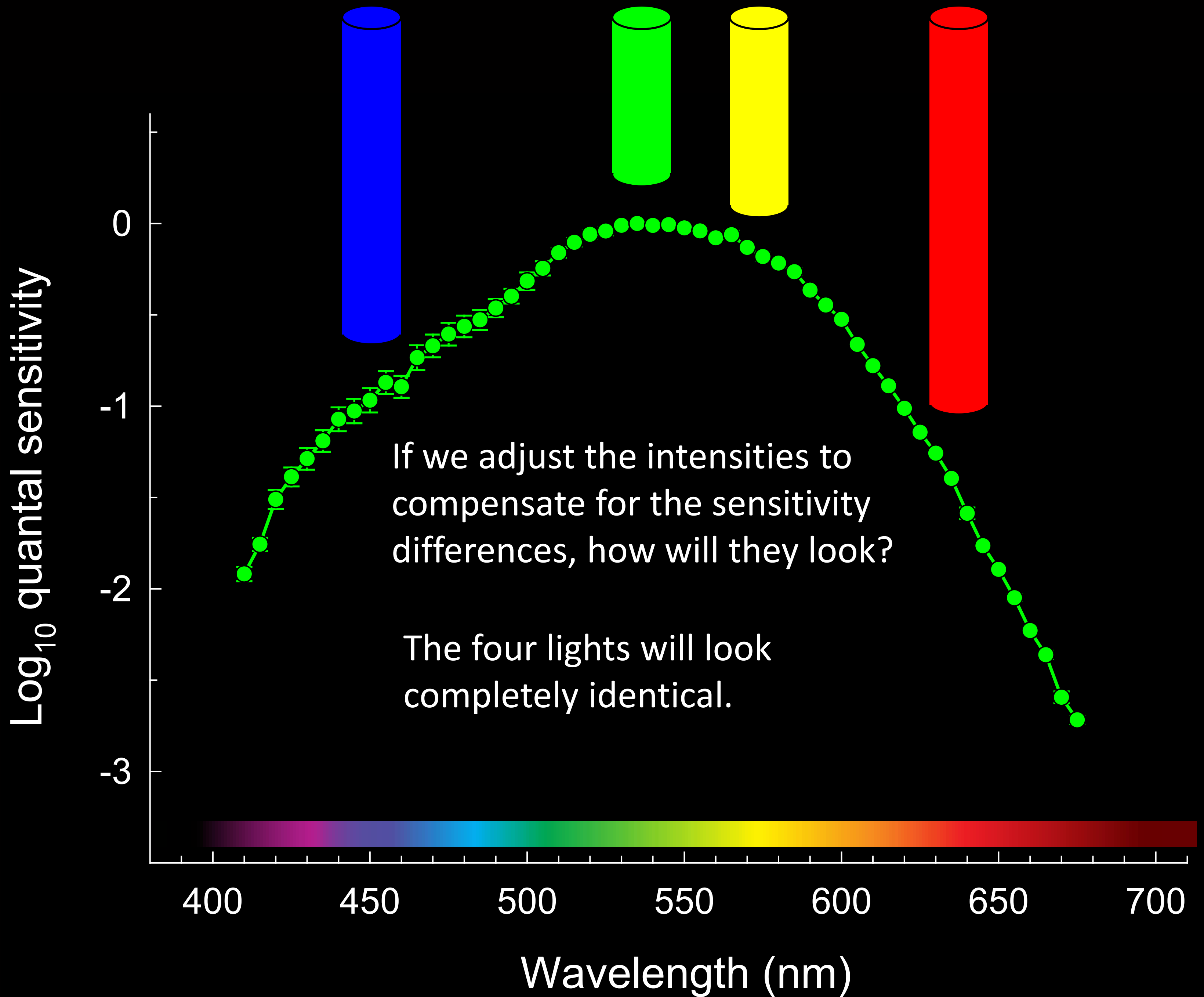
This is reflected in what is called a "spectral sensitivity function".

Imagine the sensitivity to these photons...



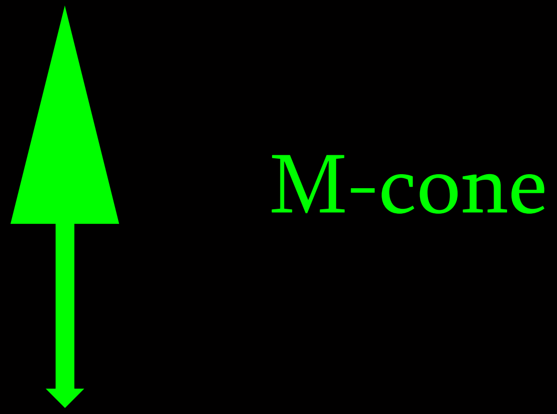


0
-1
-2
-3
Log10 quantal sensitivity
400
450
500
550
600
650
700
Wavelength (nm)
If you have four lights of the same intensity (indicated here by their heights), how will they look?
The green will look brightest, then yellow, then blue and lastly the red will be the dimmest



If we adjust the intensities to compensate for the sensitivity differences, how will they look?

The four lights will look completely identical.



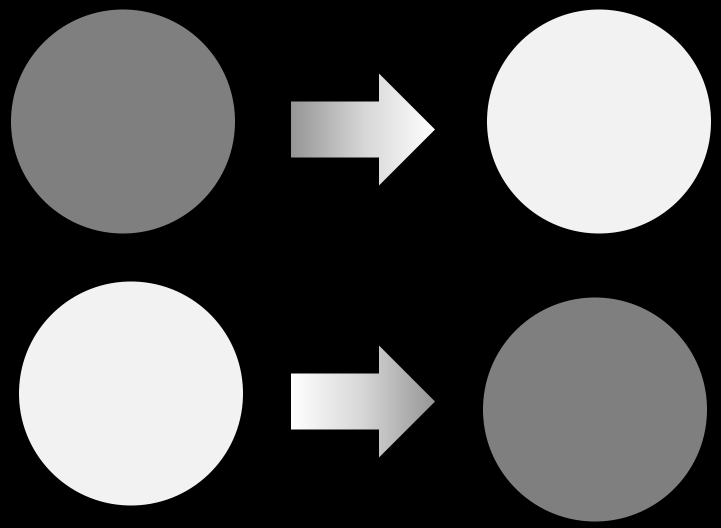
Changes in light intensity are confounded with changes in colour (wavelength)

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

UNIVARIANT

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.



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

Univariance

If a cone is *n* times less sensitive to light A than to light B, then if A is set to be *n* times brighter than B, the two lights will appear identical whatever their wavelengths.

If we had only one photoreceptor type
in our eyes, what colours would we see?

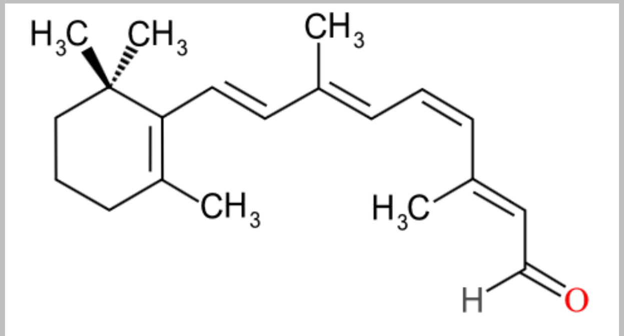
If we had only one photoreceptor, we would be colour-blind…

Examples: night vision, blue cone monochromats

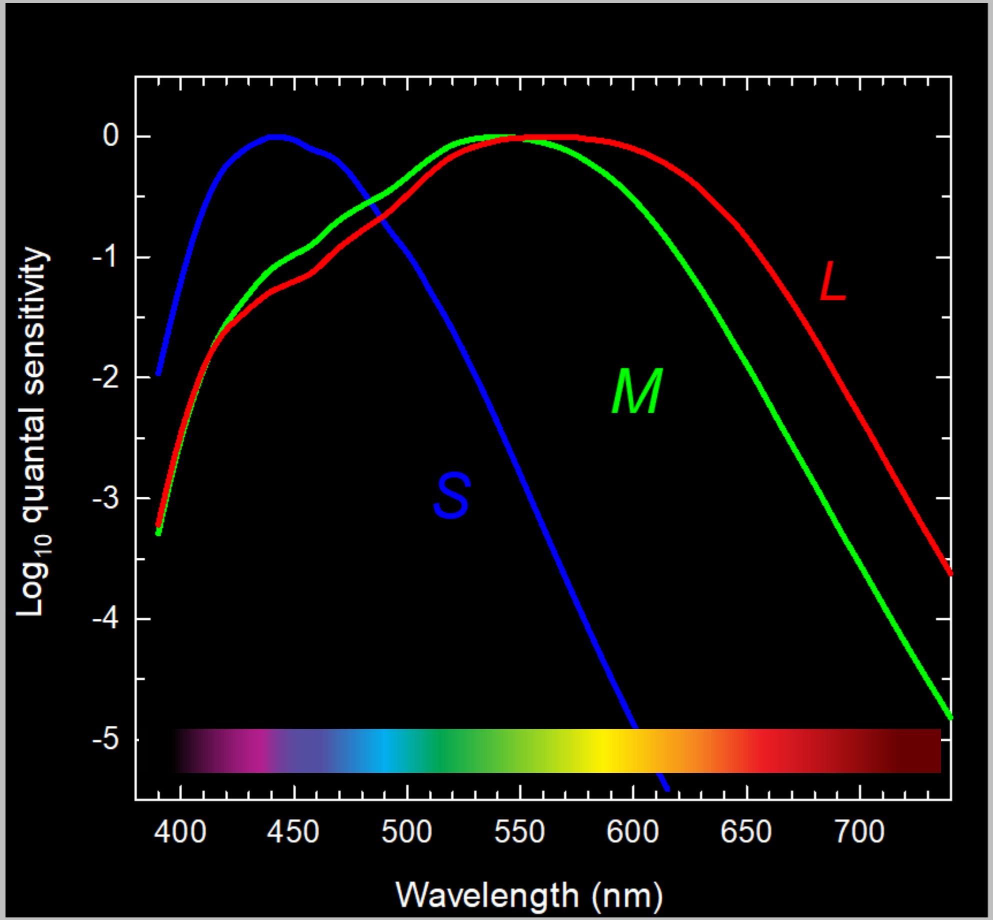
So, how do we see colours?

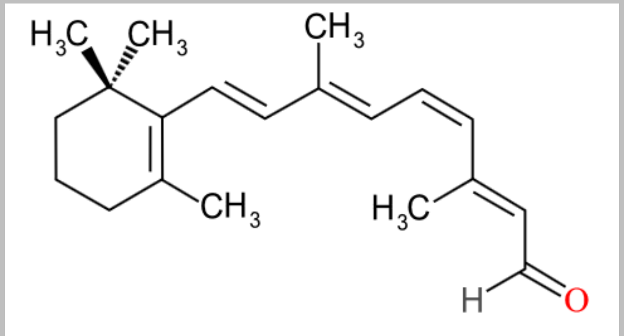
People with normal colour vision
have three univariant cones with
different spectral sensitivities…

CONE SPECTRAL SENSITIVITY DIFFERENCES

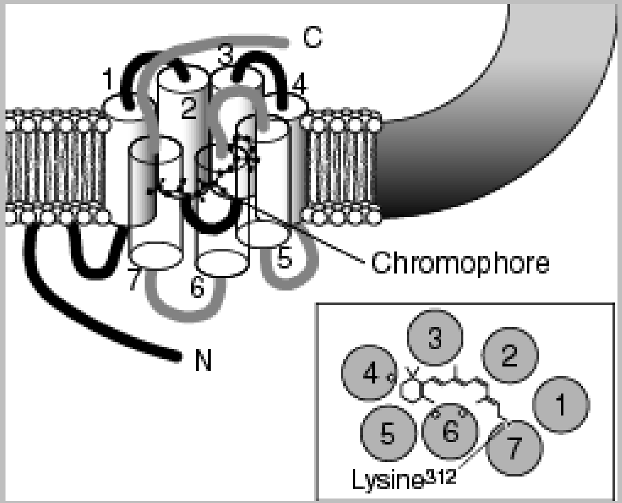


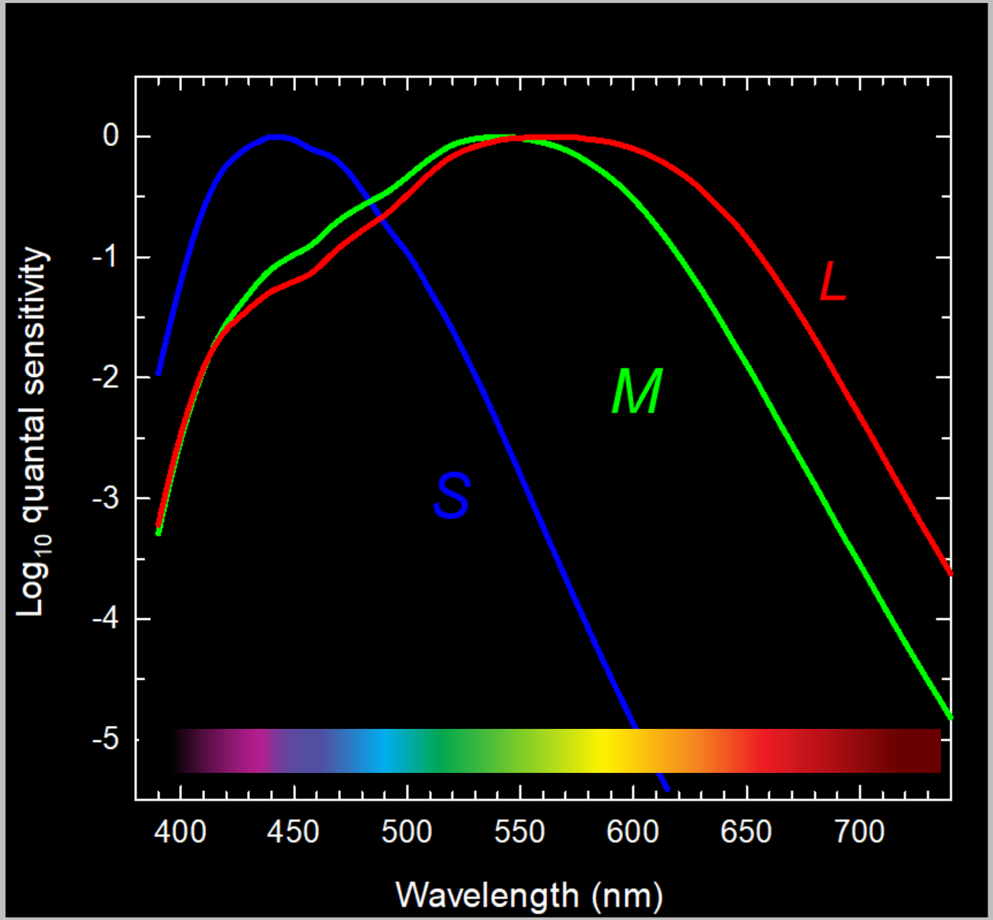
The three cones (and rods) have different spectral sensitivities, but they have the same chromophore (11-*cis*-retinal), so why are the spectral sensitivities different?





They are different because the amino acids in the opsin molecule surrounding the chromophore are different and change the initiation energy.





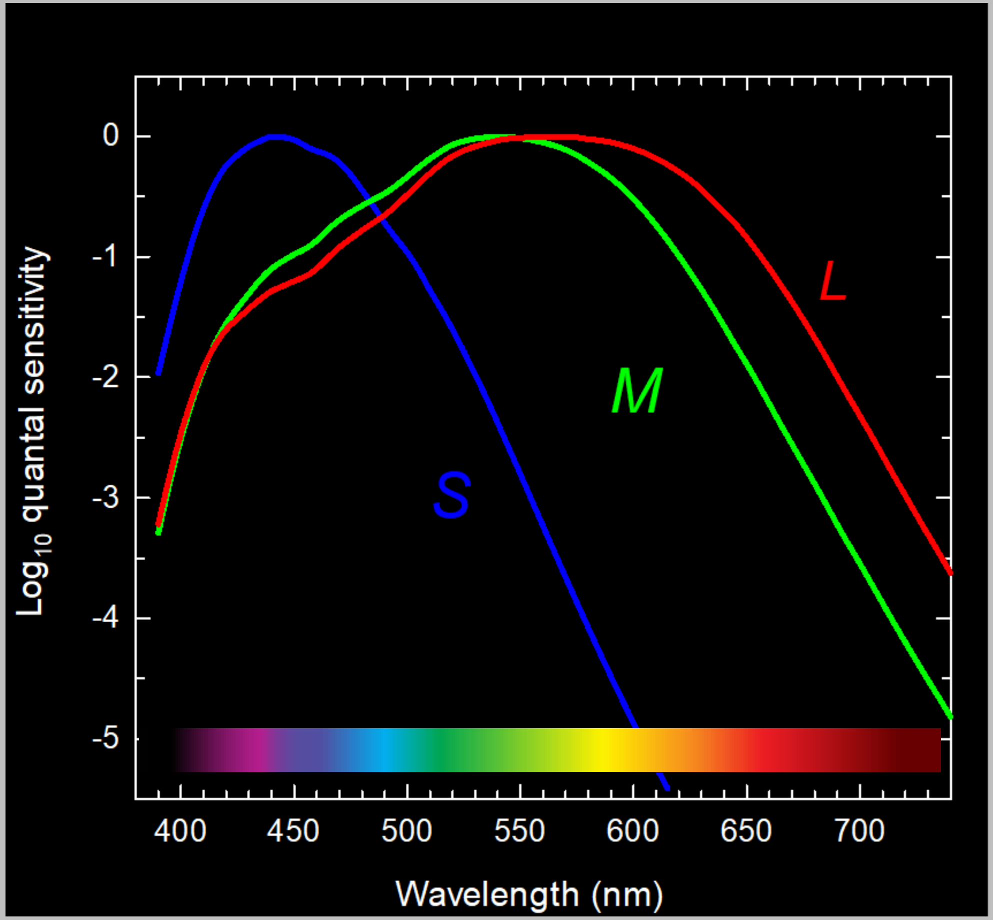
$$E = hc/\lambda$$

We can calculate the initiation energy from the peaks of the spectral sensitivity functions (at the retina).

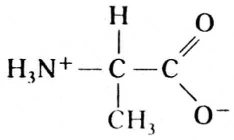
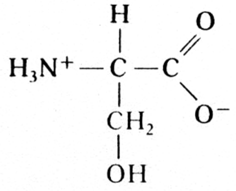
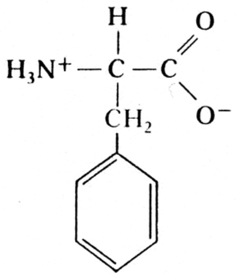
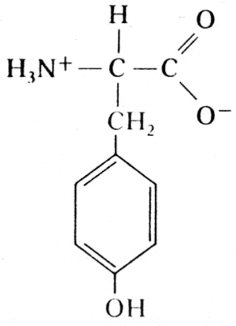
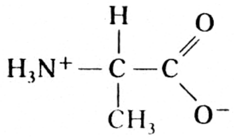
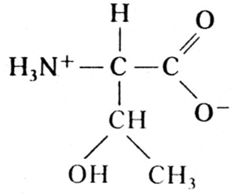
$h = 6.62606957 \times 10^{-34}$ J.s

$c = 2.99792458 \times 10^{8}$ m.s^{-1}

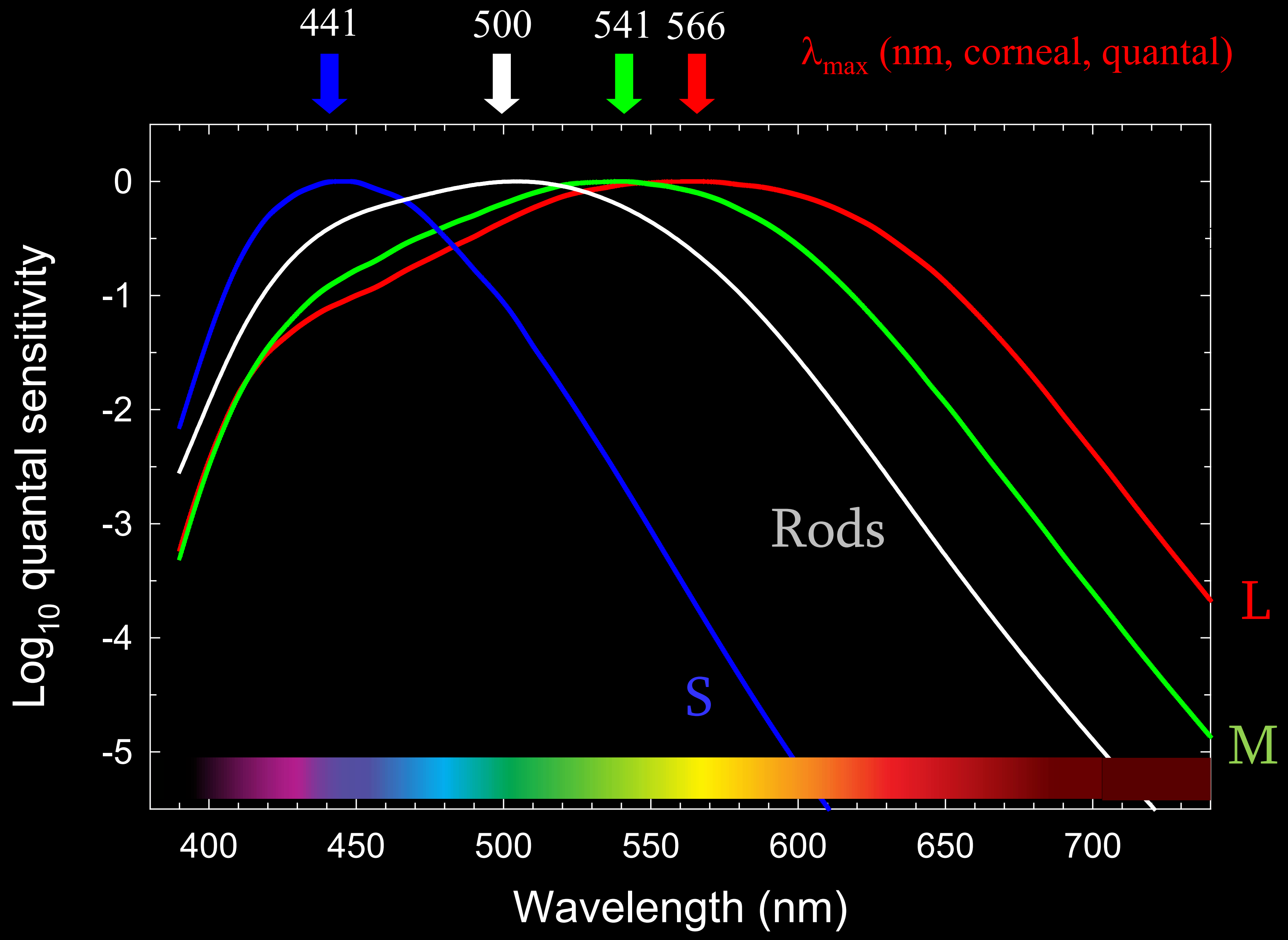
S	421 nm	4.72×10^{-19} J
M	530 nm	3.75×10^{-19} J
L	559 nm	3.55×10^{-19} J



The spectral sensitivity differences between the M- and L-cone, for example, are due to three amino acid substitutions.

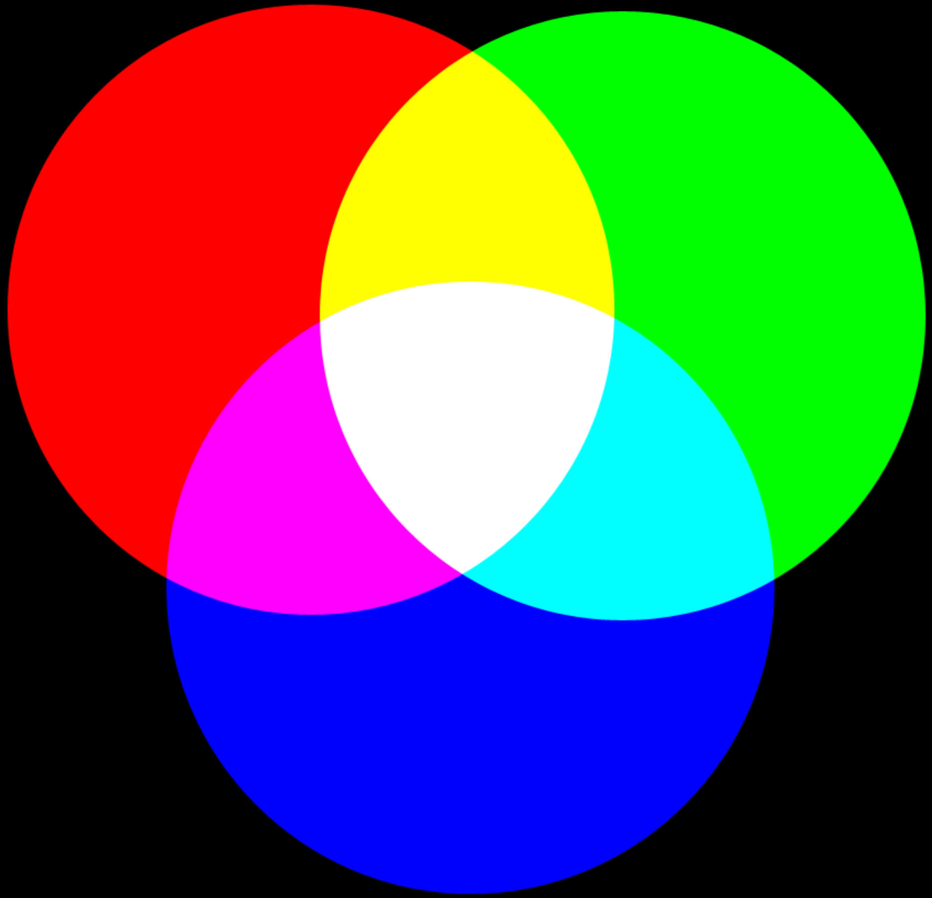
Amino acid position	M-cone		L-cone
180	alanine 	+4 nm	serine OH 
277	phenylalanine 	+7 nm	tyrosine OH 
285	alanine 	+14 nm	threonine OH 

Four human photoreceptors have different spectral sensitivities



With three cone types with different spectral sensitivities colour vision is three dimensional or:

TRICHROMATIC



Trichromacy means that colour vision is relatively simple.

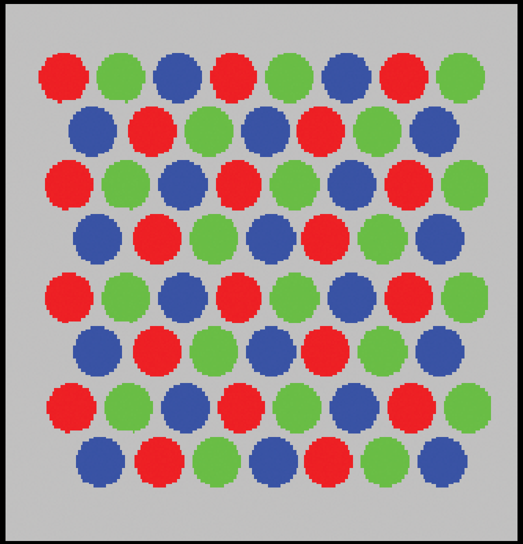
It is a 3 variable system…

Colour TV

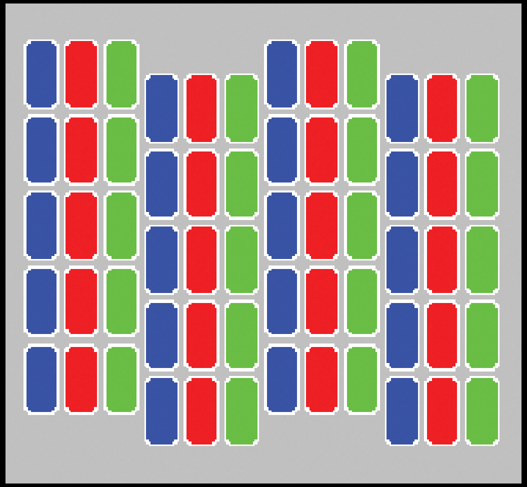
Trichromacy is exploited in colour reproduction, since the myriad of colours perceived can be produced by mixing together small dots of three colours.

If you look closely at a colour television (or this projector output)…

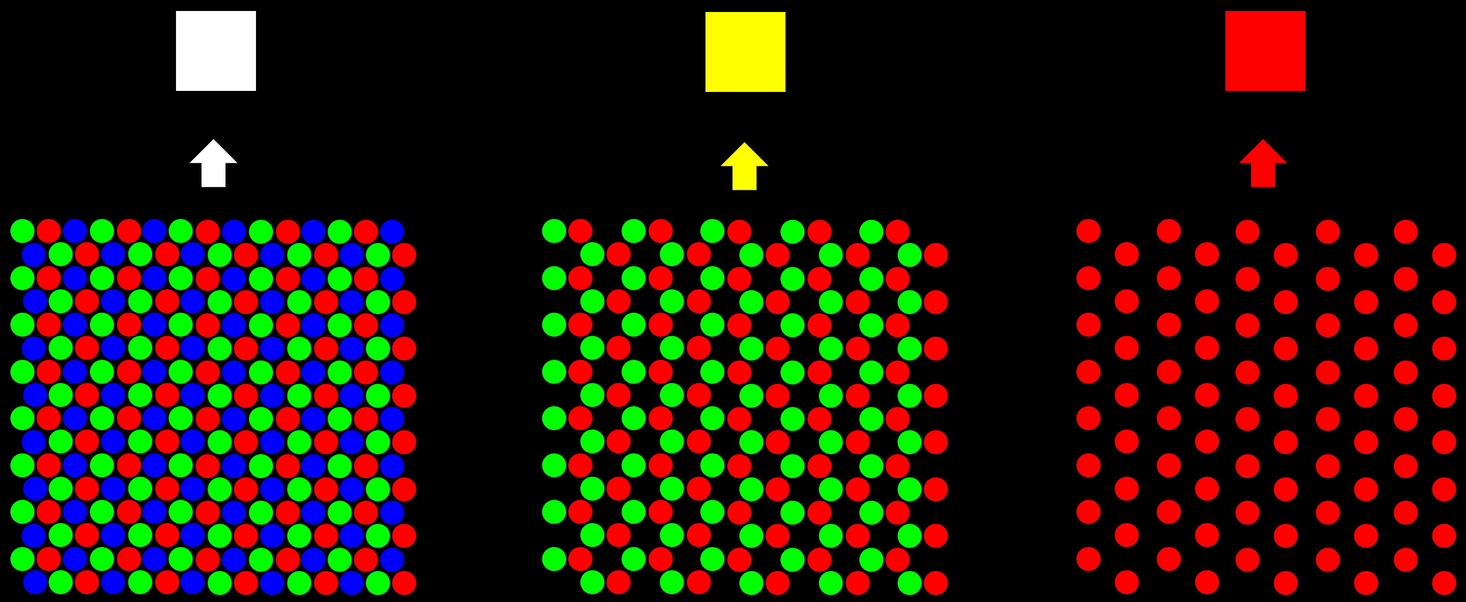
3-coloured dots



3-coloured bars



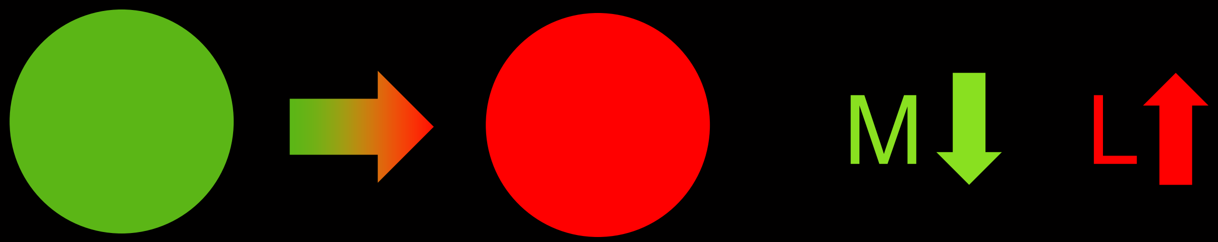
The dots produced by a TV or projector are so small that they are mixed together by the eye and thus appear as uniform patches of colour



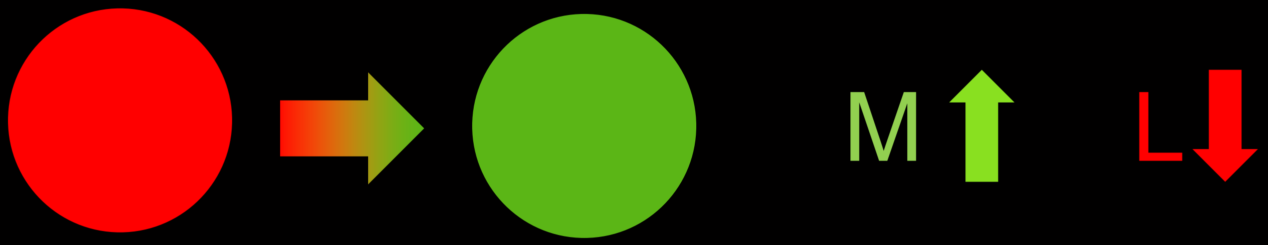
How is colour encoded?

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.

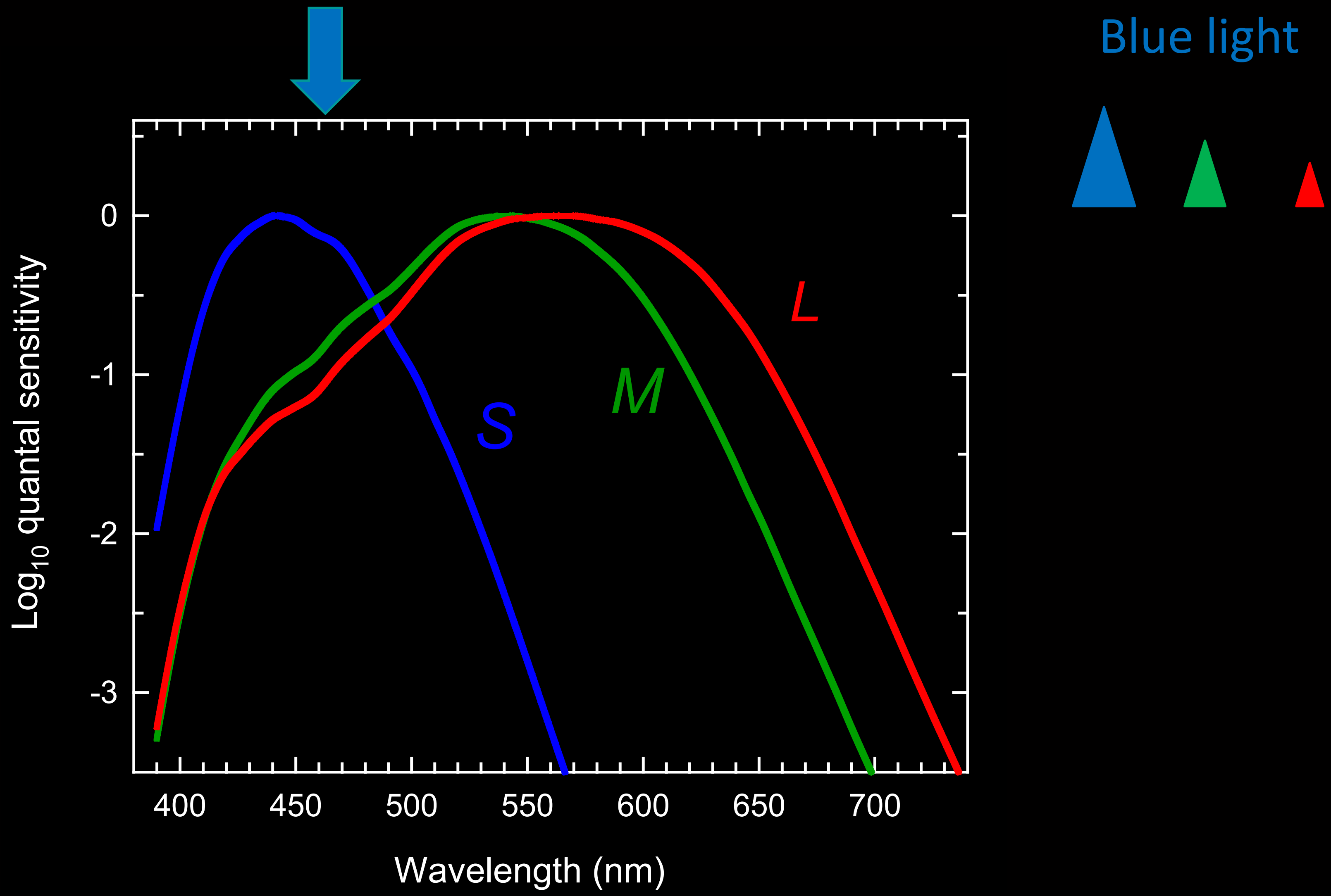


A change in colour from red to green causes a relative increase in the M-cone output but causes a decrease in the L-cone output.

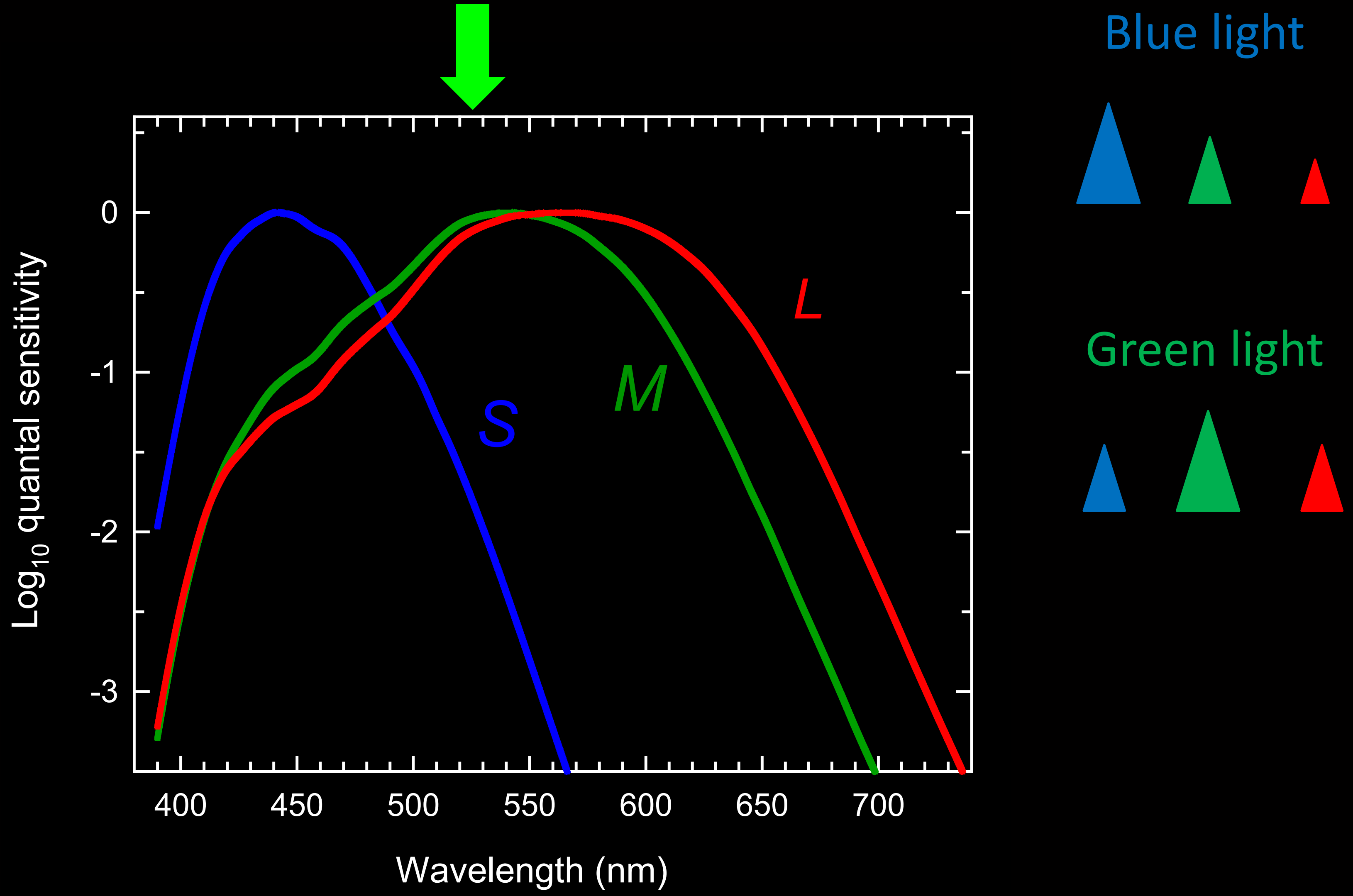


Thus, colour can be encoded by *comparing* the outputs of different cone types…

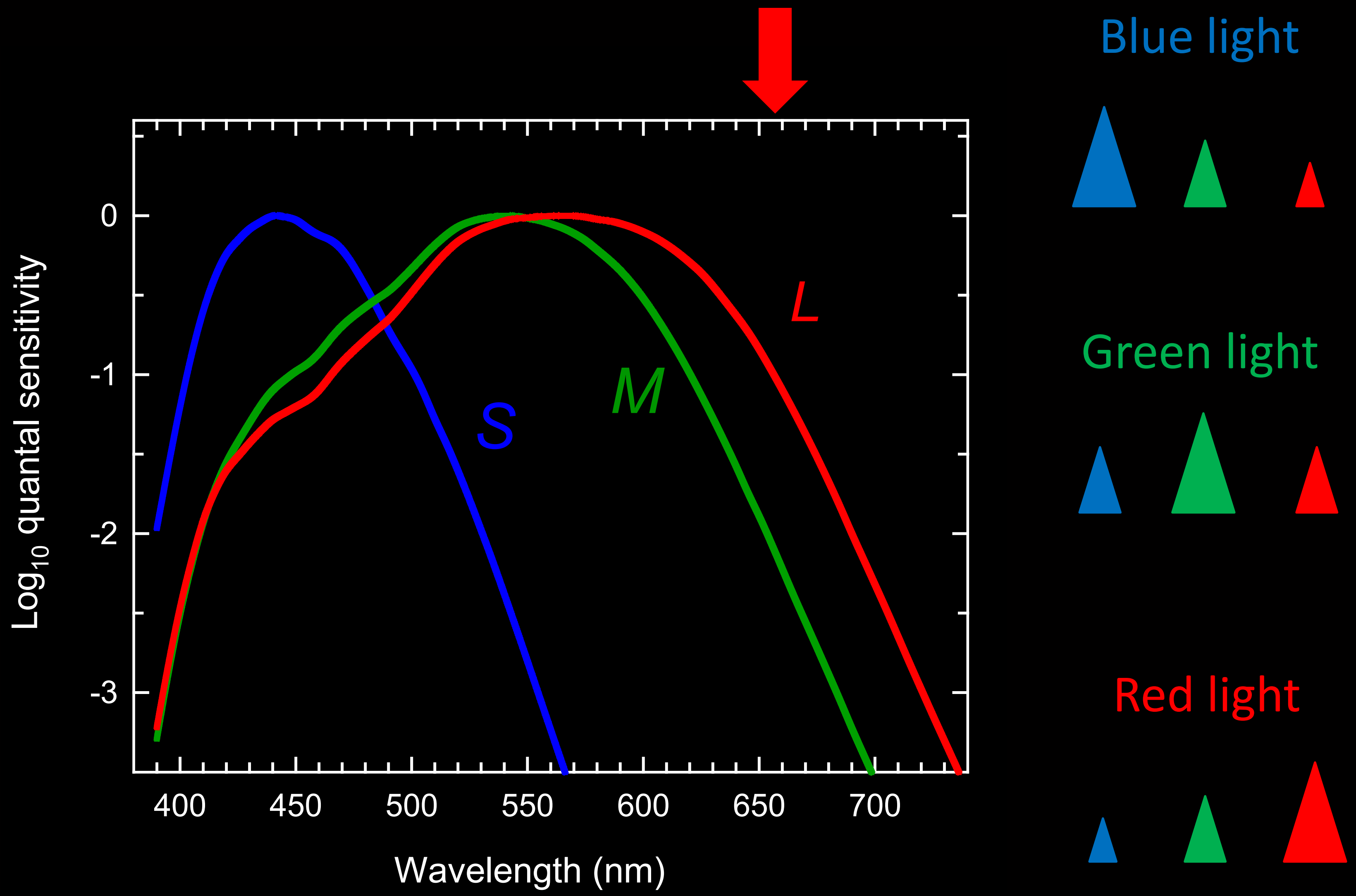
Colour is encoded by the relative cone outputs



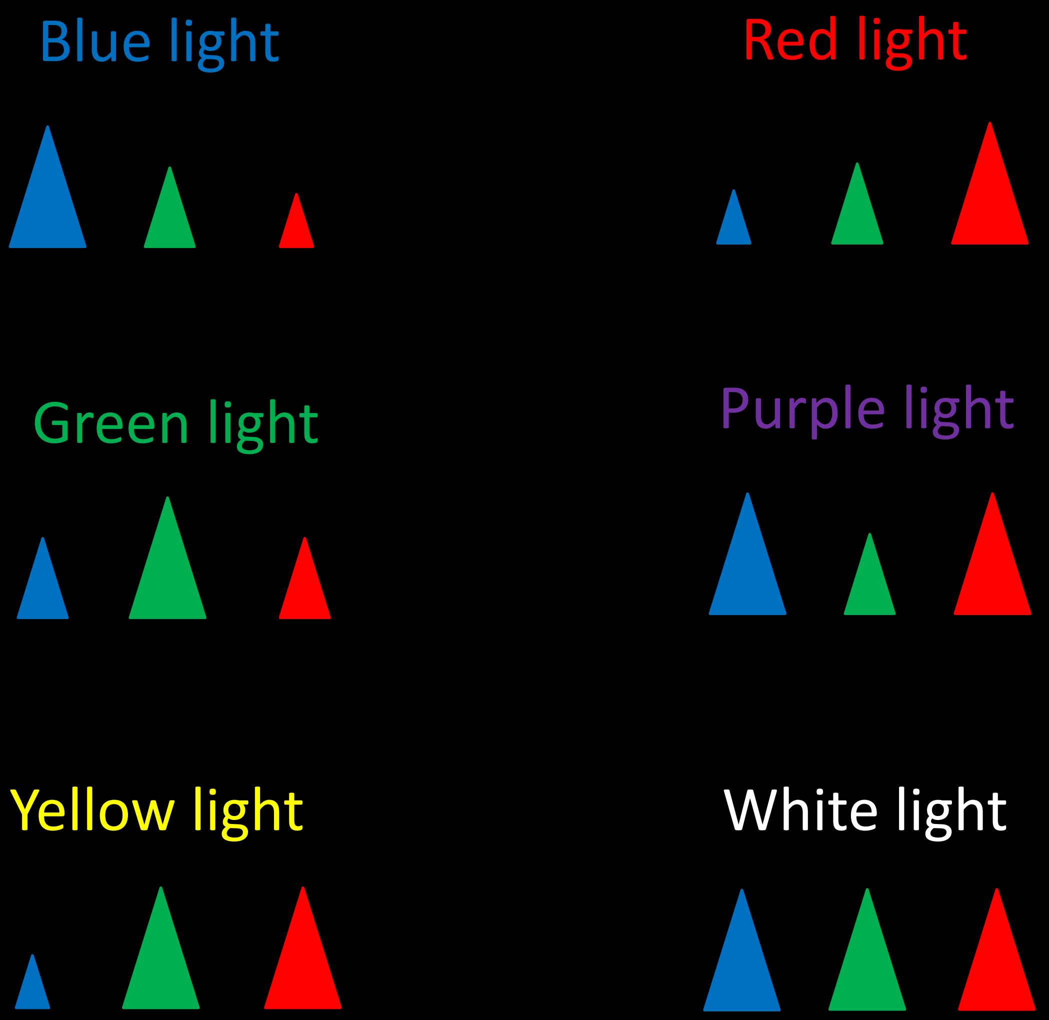
Colour is encoded by the relative cone outputs



Colour is encoded by the relative cone outputs



Colour is encoded by the relative cone outputs



COLOUR VISION DEFICIENCIES

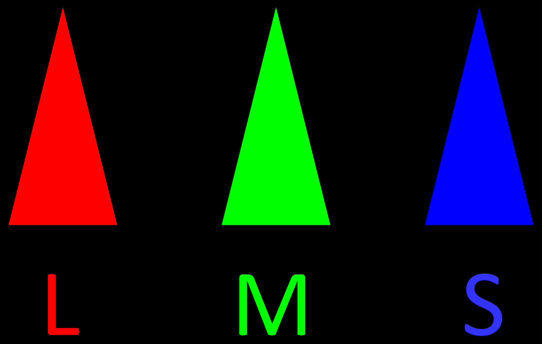
Not everybody has the same colour vision…

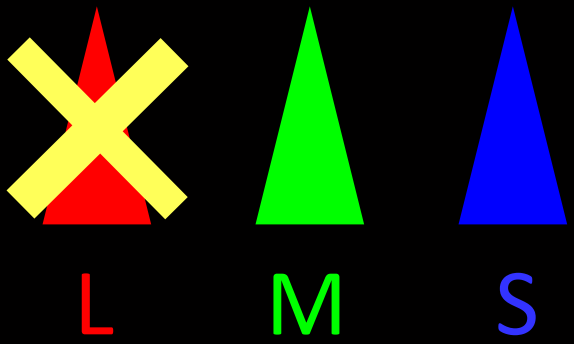
A common form of colour deficiency is red-green colour deficiency.

Two examples are:

Normal

Protanope

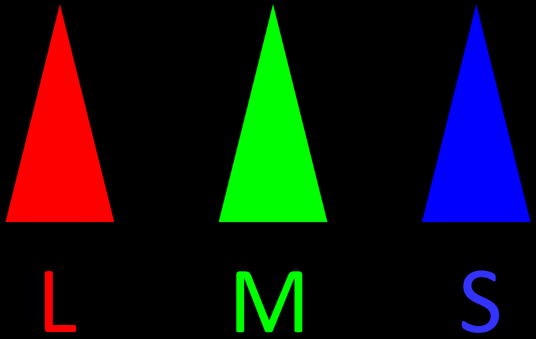


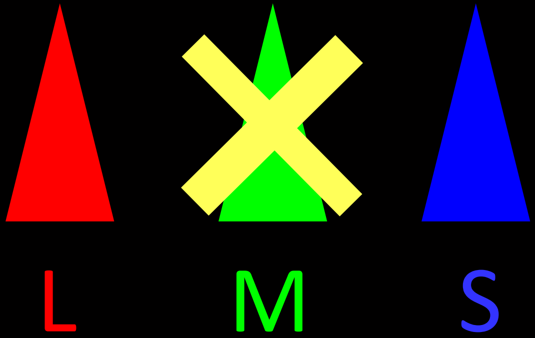


Protanopia

Normal

Deuteranope



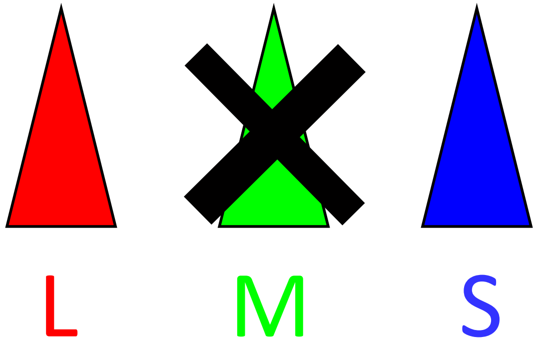


Deuteranopia

Credit: Euro Puppy Blog

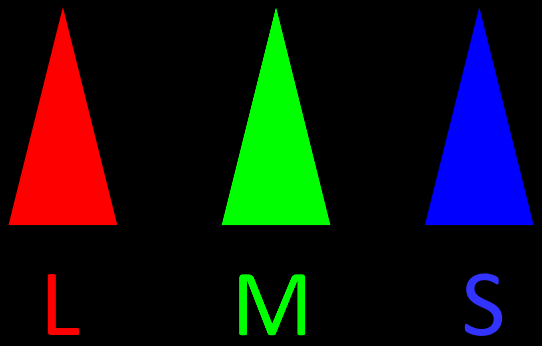
Deuteranope

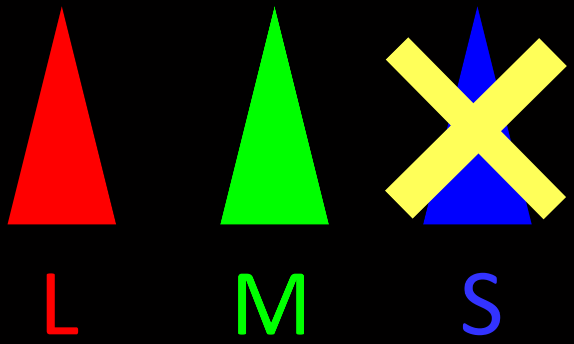
Dogs are dichromats with only two cones peaking at 429 and 555 nm



Normal

Tritanope





Tritanopia

Main types of colour vision defects with approximate proportions of appearance in the population.

		percent in UK	
Condition		Male	Female
Protanopia	no L cone	1.0	0.02
Protanomaly	milder form	1.0	0.03
Deuteranopia	no M cone	1.5	0.01
Deuteranomaly	milder form	5.0	0.4
Tritanopia	no SWS cone	0.008	0.008

Why is there this pattern of inheritance?

XY inheritance

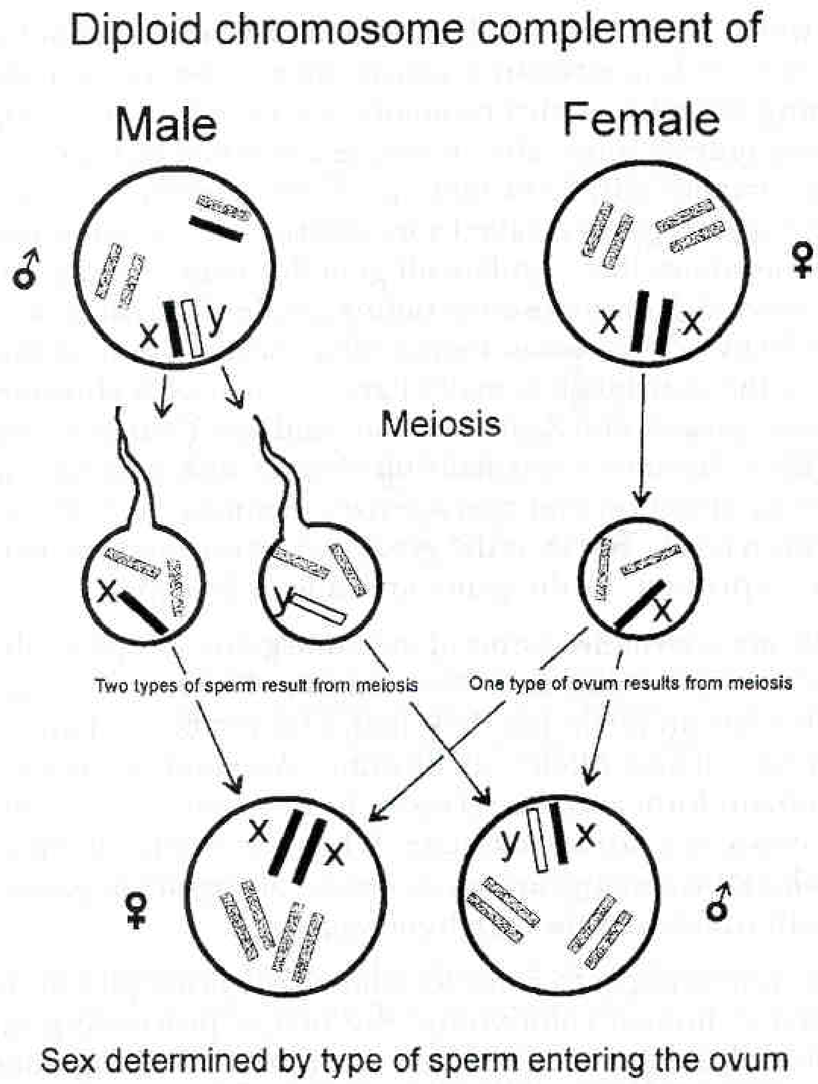
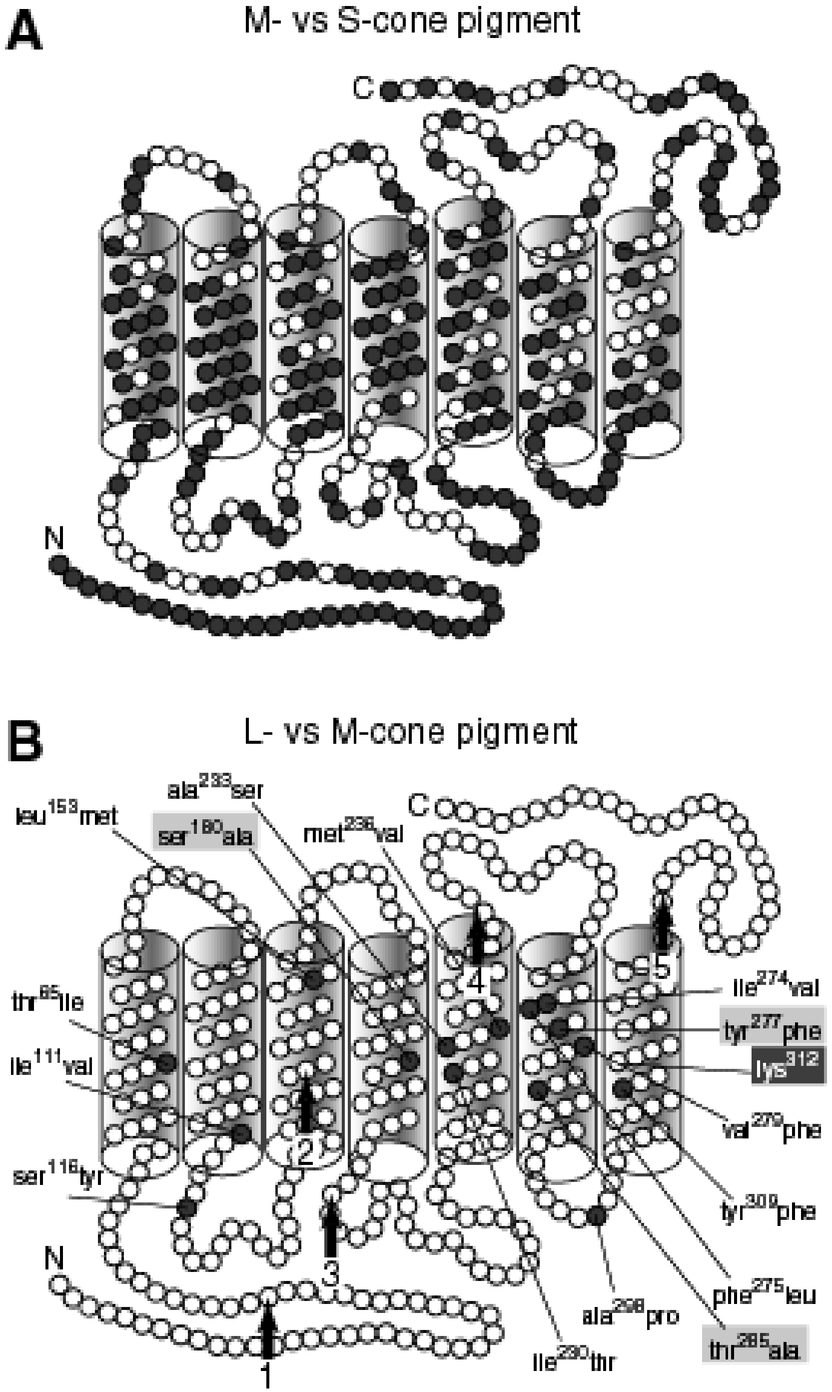


Figure 10.17 Prior to fertilization, meiotic division of germ cells results in two types of sperm, but only one type of ovum. Depending on which sperm is effective, the fertilized ovum will have two X cells and be female, or one X and one Y cell and be male. This diagram show why the X cell of the male offspring can come only from the mother. (From Watson, 1976, p. 14.)

COLOUR VISION AND MOLECULAR GENETICS

(Origins of red-green colour deficiencies)

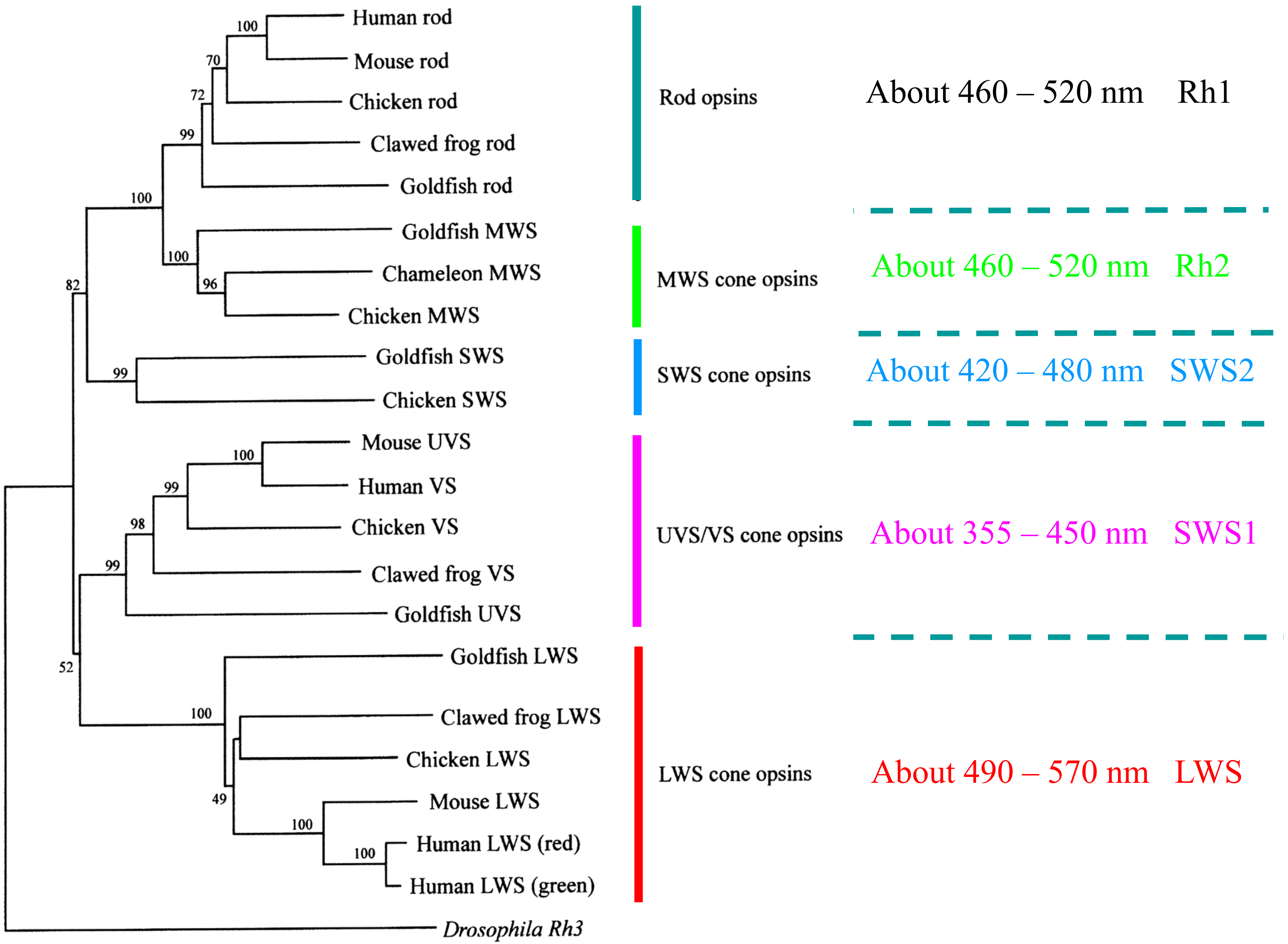
Amino acid differences between photopigment opsins

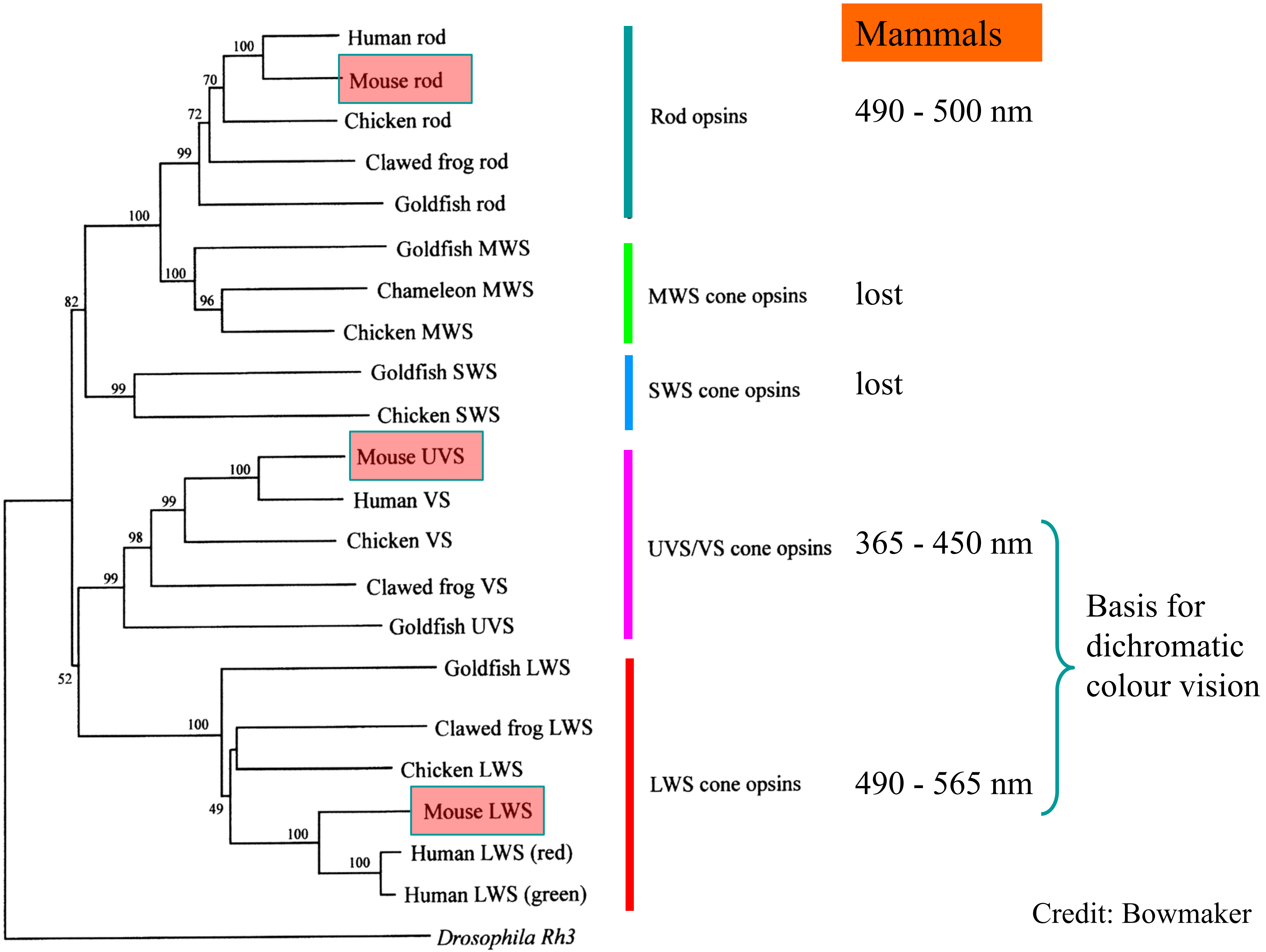


Why are the M- and L-cone opsins so similar?

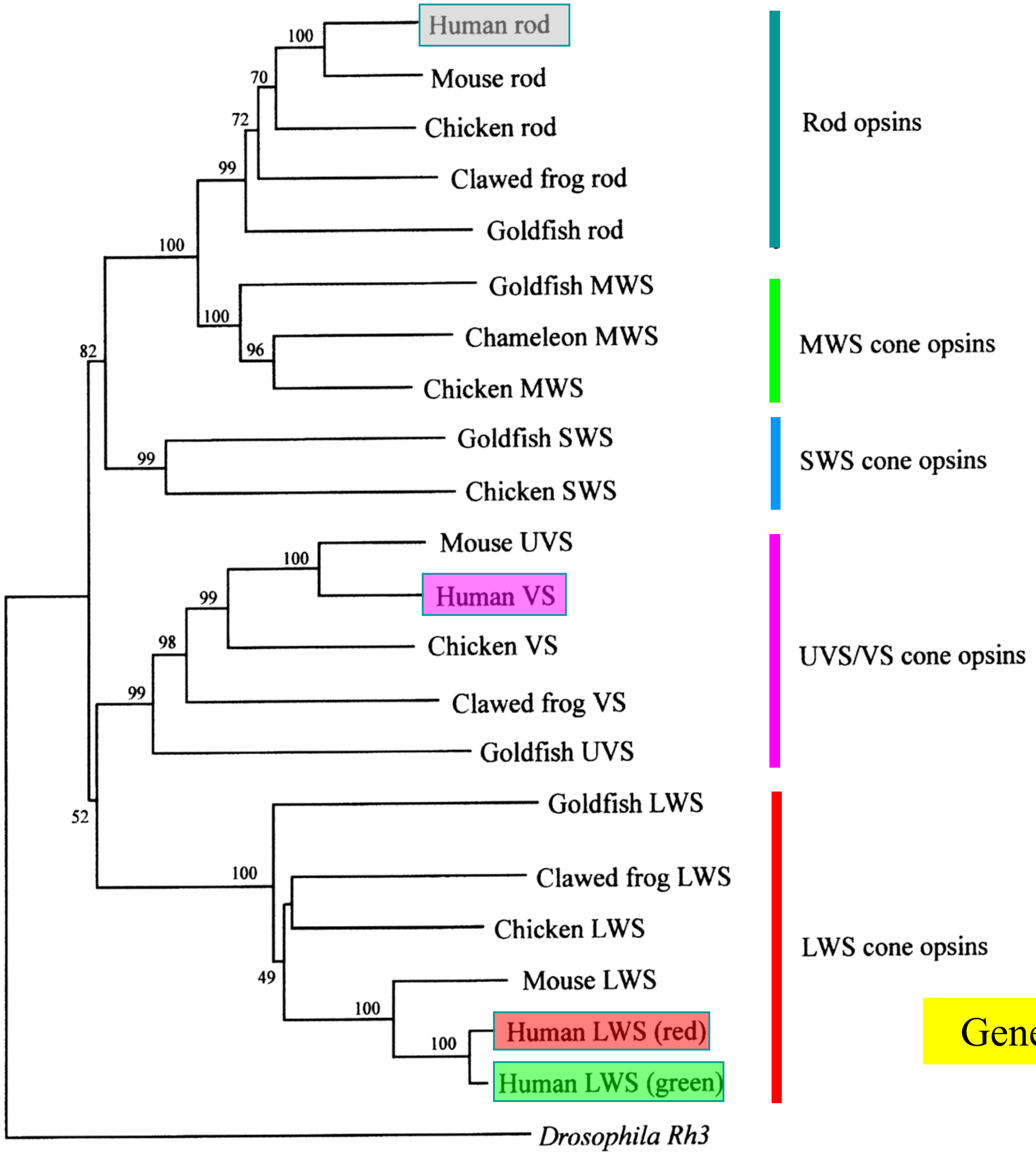
From Sharpe, Stockman, Jägle & Nathans, 1999

Phylogenetic tree of visual pigments





Credit: Bowmaker



Humans

490 - 500 nm

lost

lost

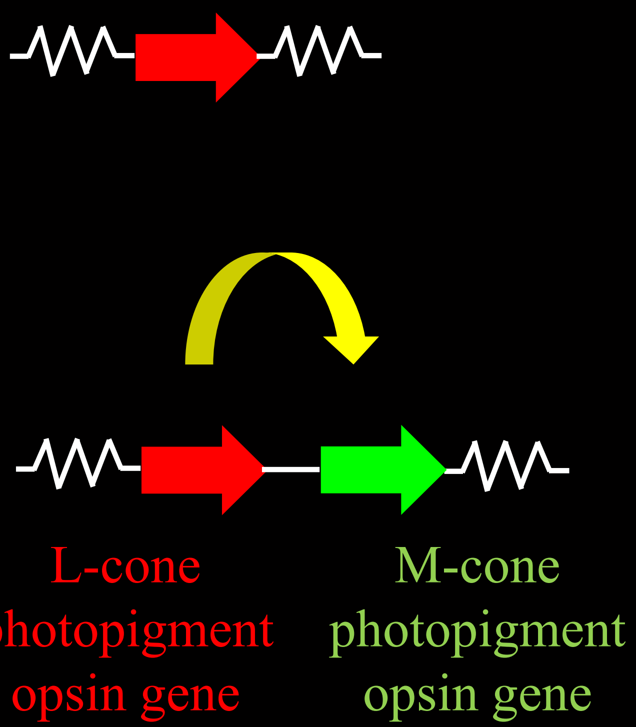
365 - 450 nm

Basis for trichromatic colour vision

Gene duplication

Credit: Bowmaker

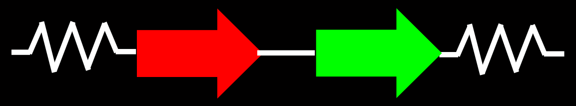
Gene duplication on the X-chromosome



Mammal

Human/ Old world primate

Because these two genes are in a tandem array, and are very similar…

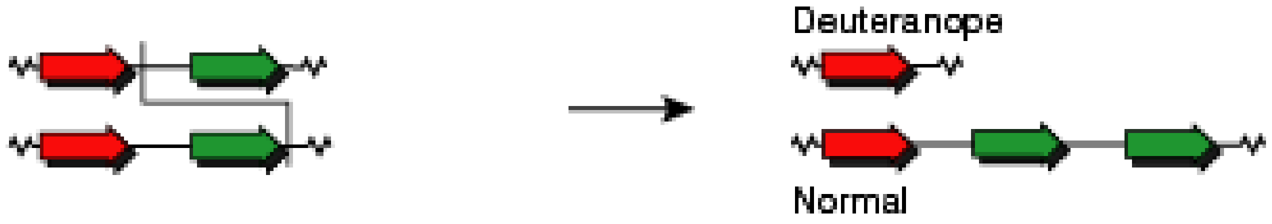


L-cone
photopigment
opsin gene

M-cone
photopigment
opsin gene

Crossovers during meiosis are common:

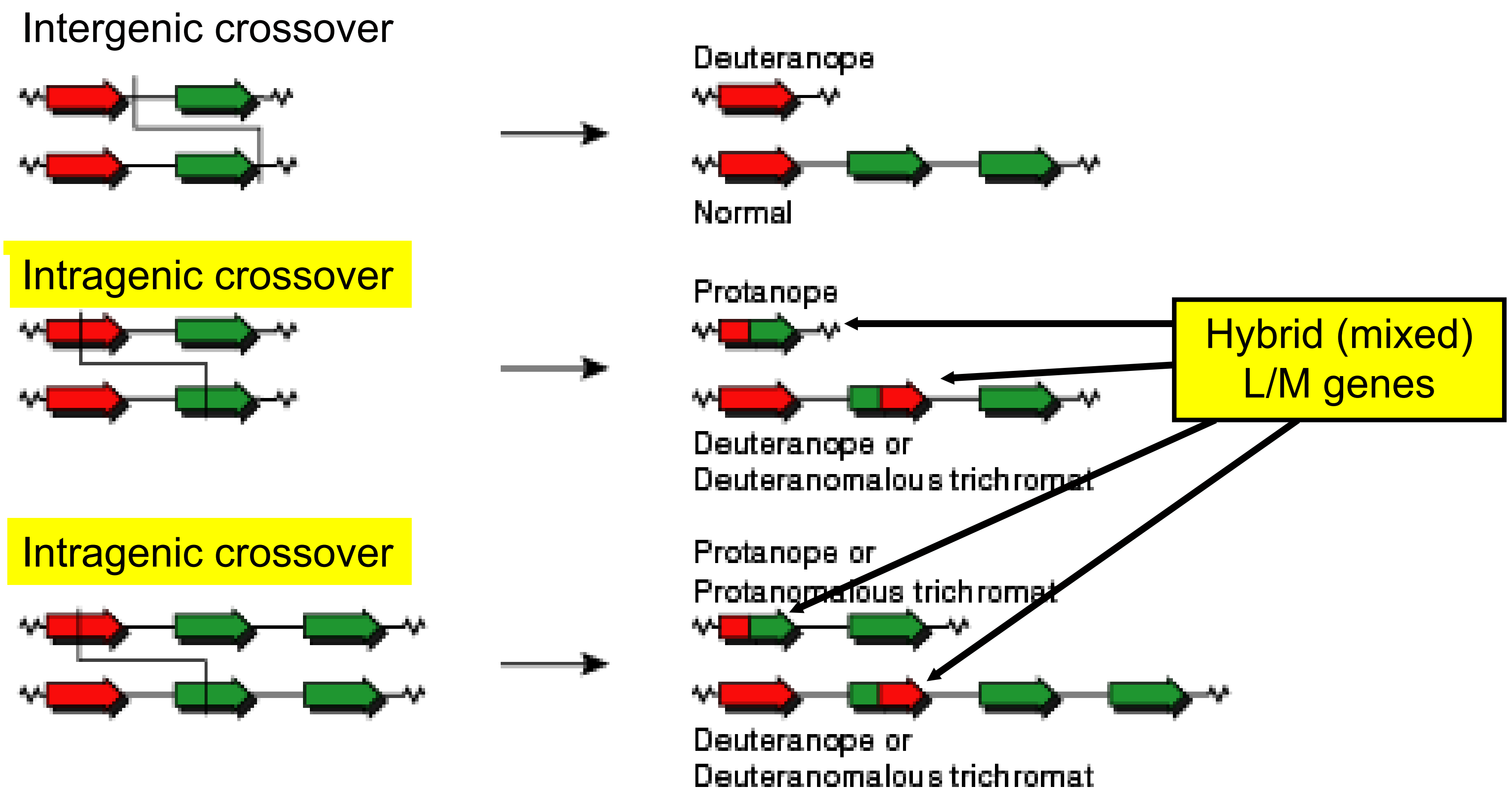
Intergenic crossover



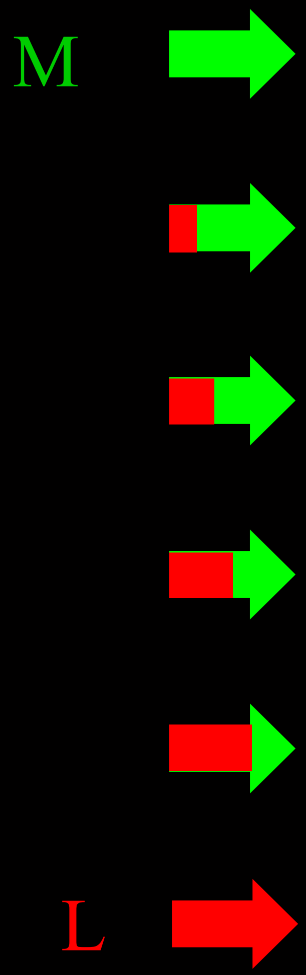
Intergenic crossovers produce more or less L and M-cone genes on each X chromosome

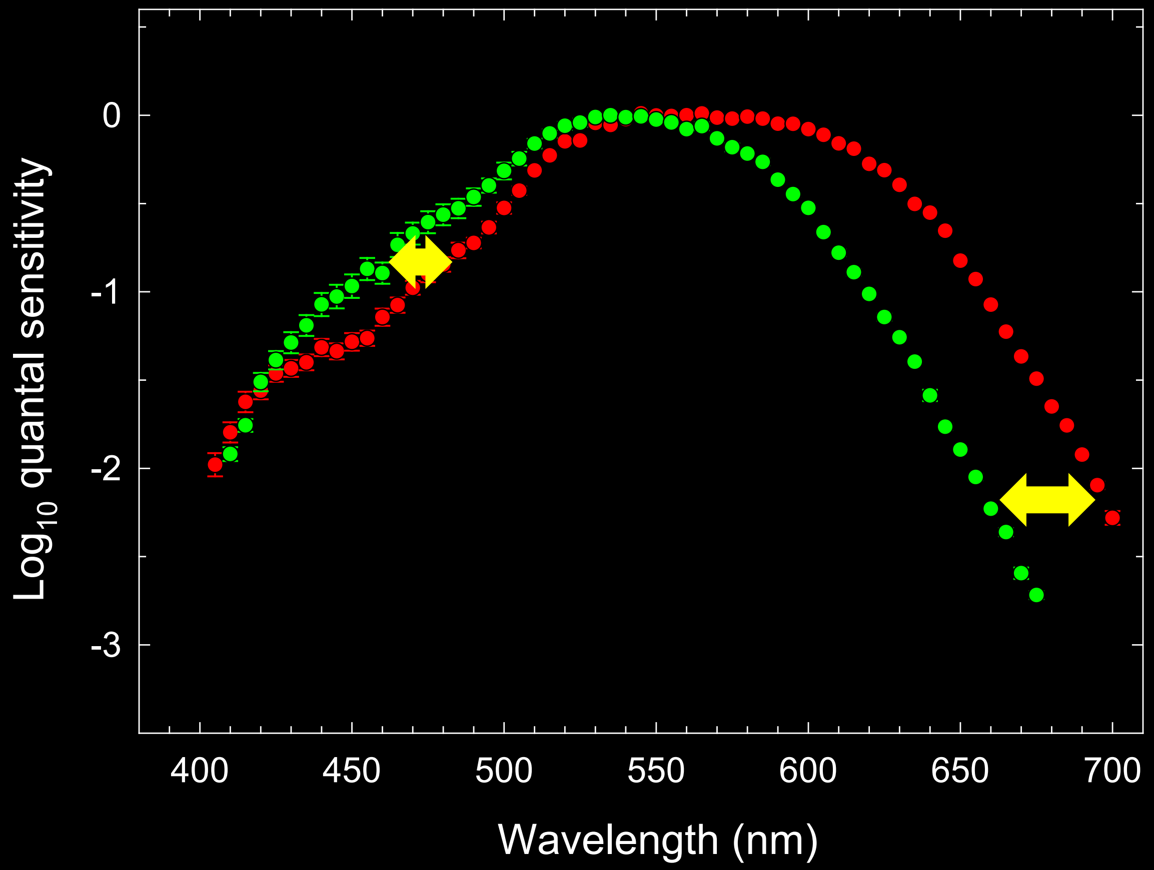
From Sharpe, Stockman, Jägle & Nathans, 1999

Intragenic crossovers produce hybrid or mixed L and M-cone genes



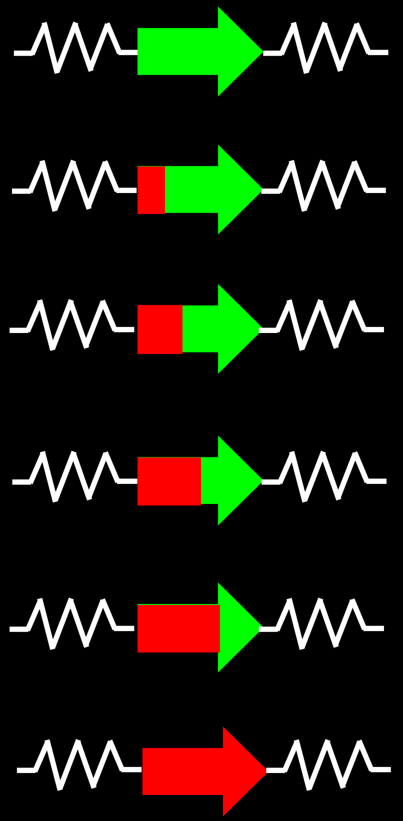
From Sharpe, Stockman, Jägle & Nathans, 1999





The spectral sensitivities of the hybrid photopigments vary between those of the M- and L-cones depending on where the crossover occurs.

Single-gene dichromats

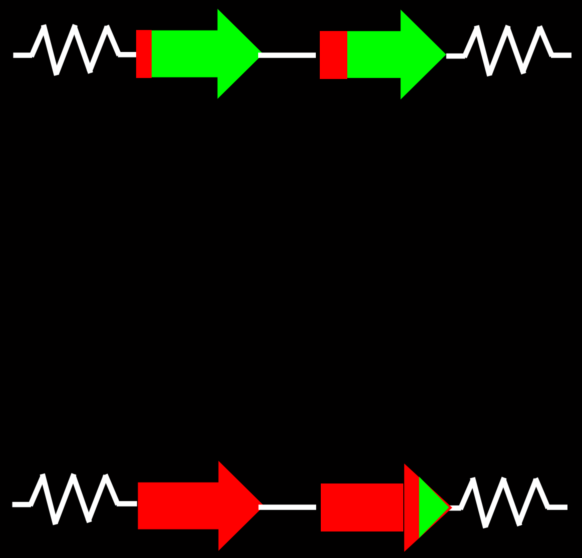


Protanope

Deuteranope

With a single gene male
observers must be dichromats

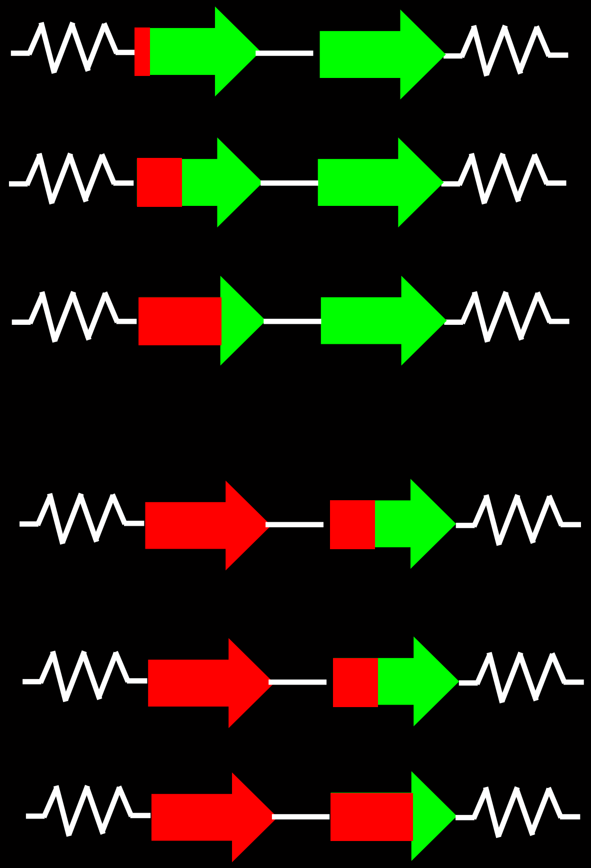
Multiple-gene dichromats



Male observers with two similar genes may also be effectively dichromats

Anomalous trichromats

Male observers with two different genes are anomalous trichromats



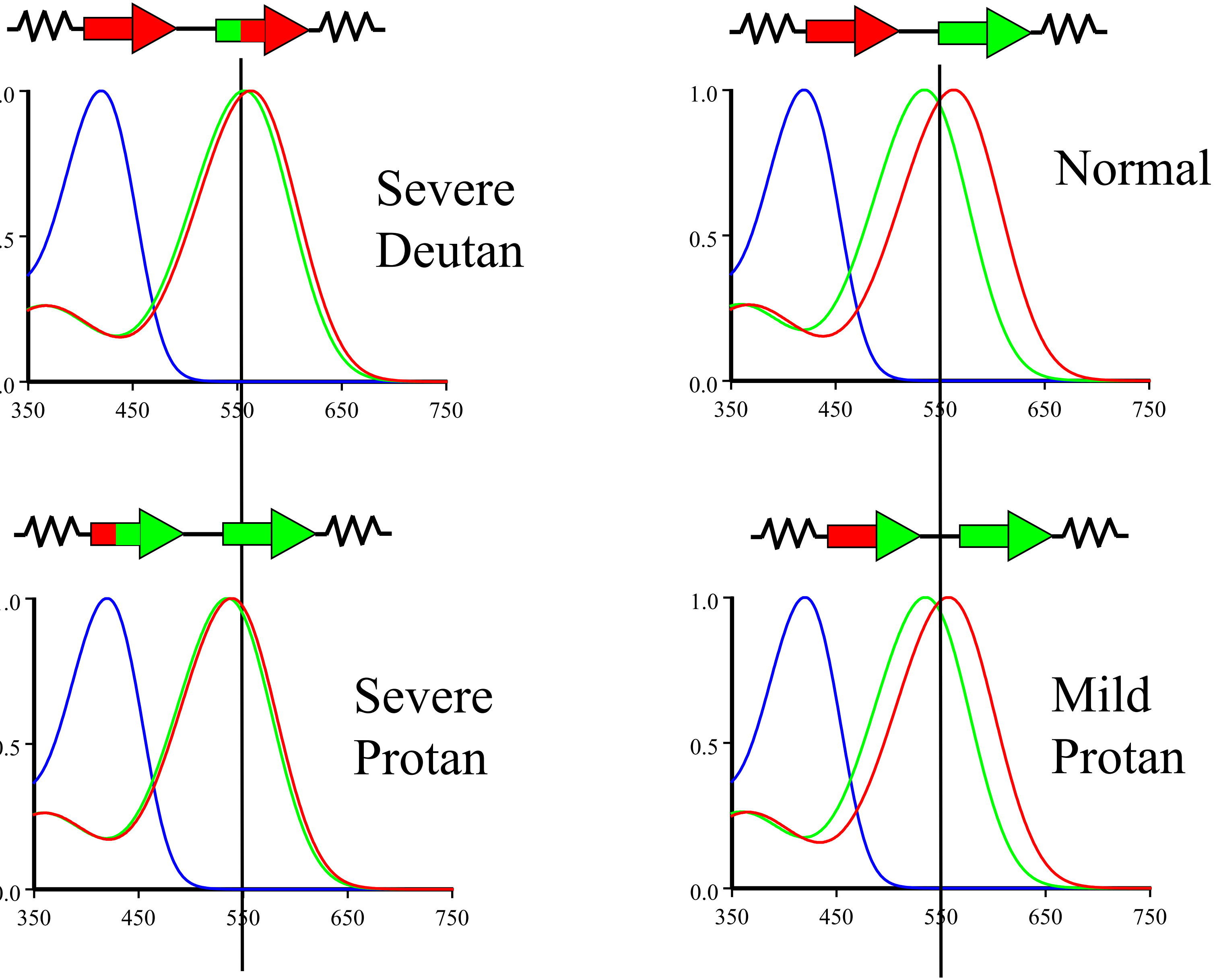
Severe

Protanomalous

Mild

Deuteranomalous

Severe



Severe Deutan
Normal
Severe Protan
Mild Protan
1.0
0.5
0.0
350
450
550
650
750

The emergence of two longer wavelength (M- and L-cones) is thought to have occurred relatively recently in primate evolution.

Why is it important?

No red-green discrimination

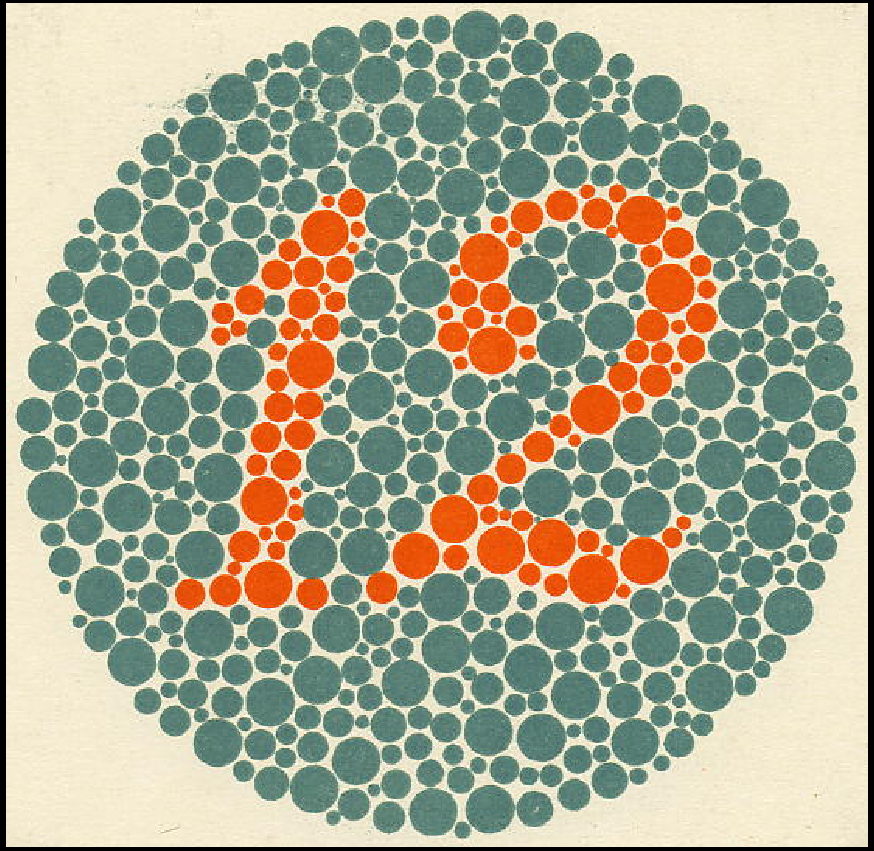
Source: Hans Irtel

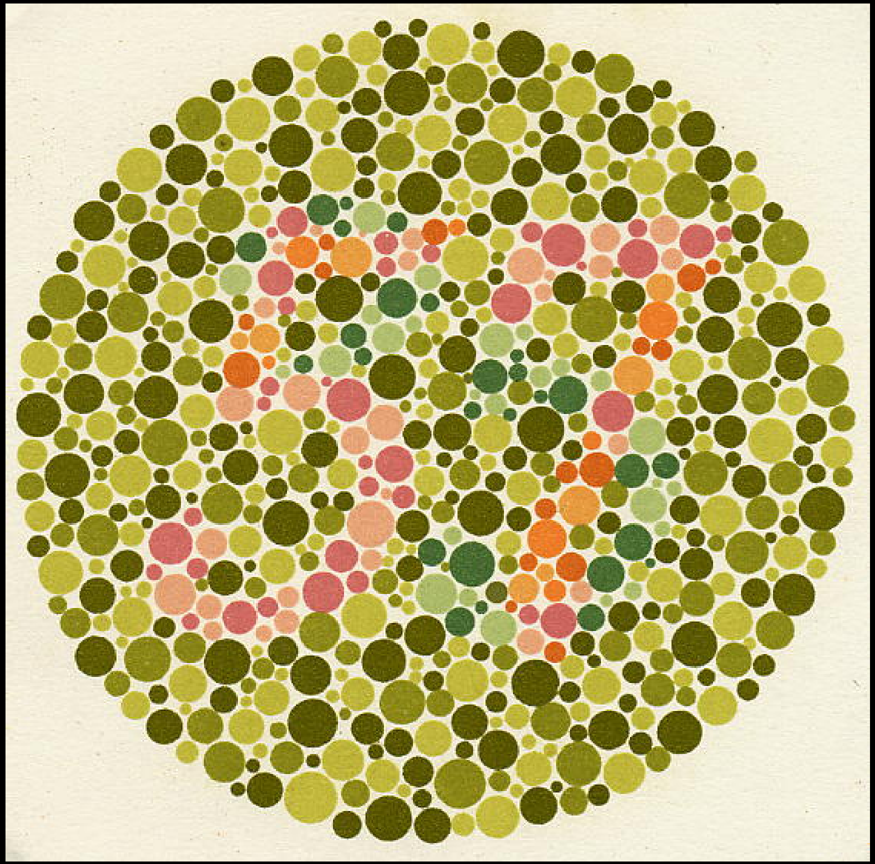
Red-green discrimination

Source: Hans Irtel

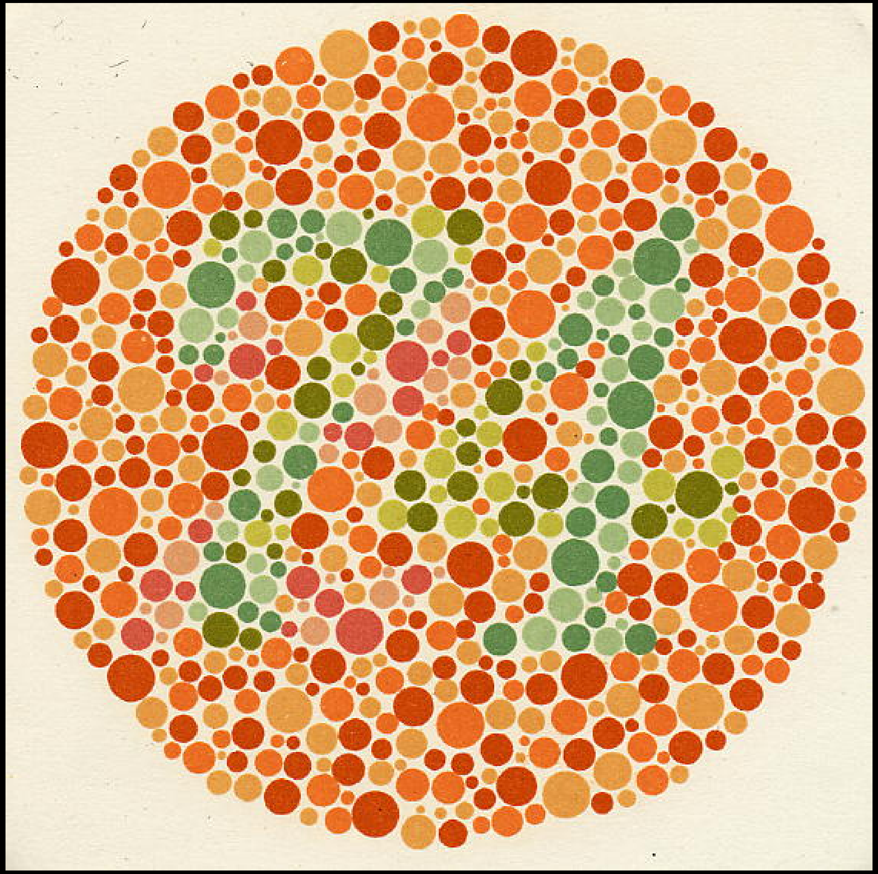
DIAGNOSING COLOUR VISION DEFICIENCIES

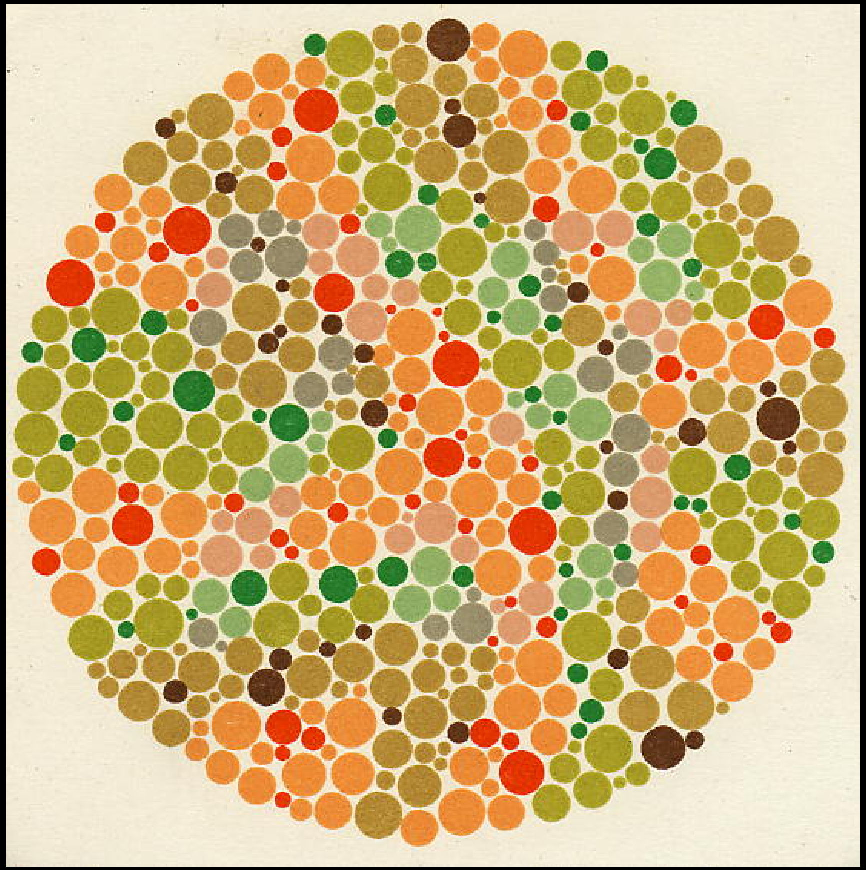
Ishihara plates



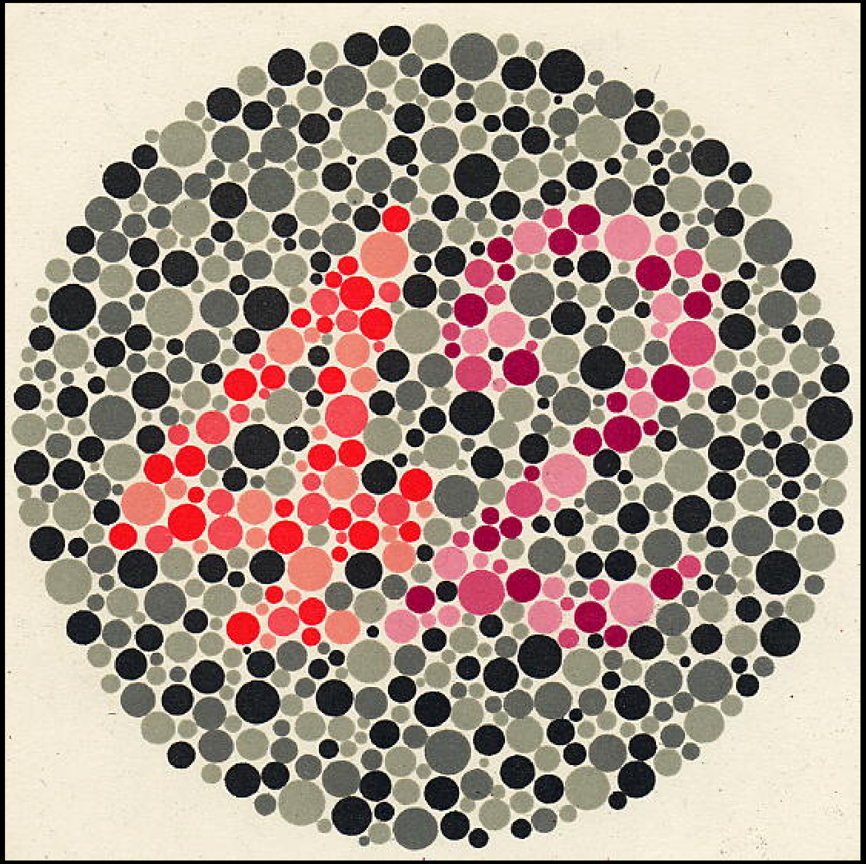


Ishihara plates





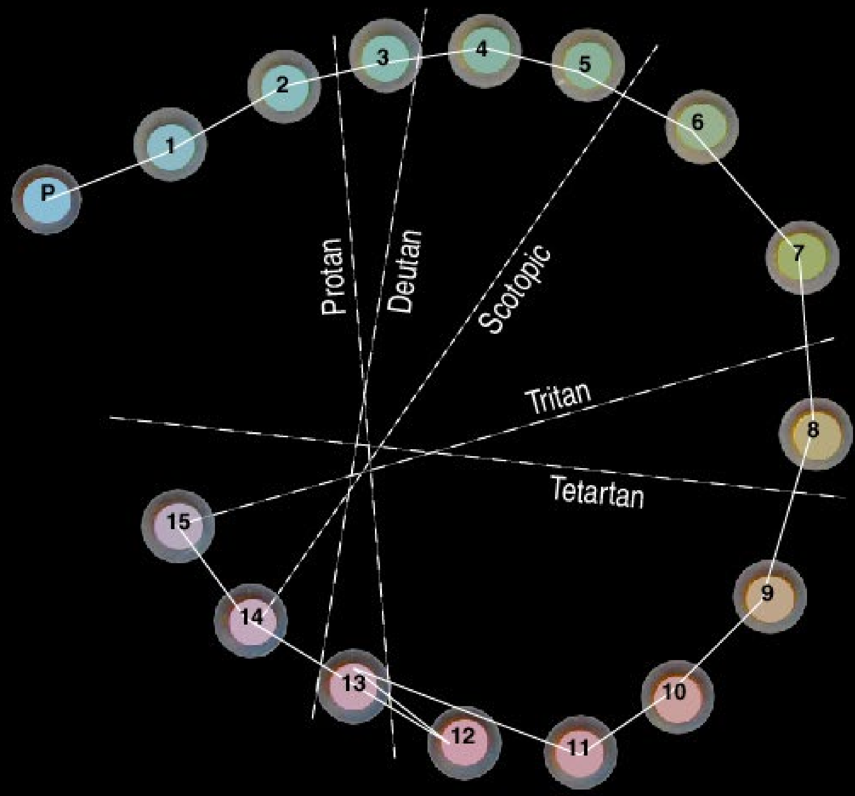
Ishihara plates



Tests measuring colour discrimination

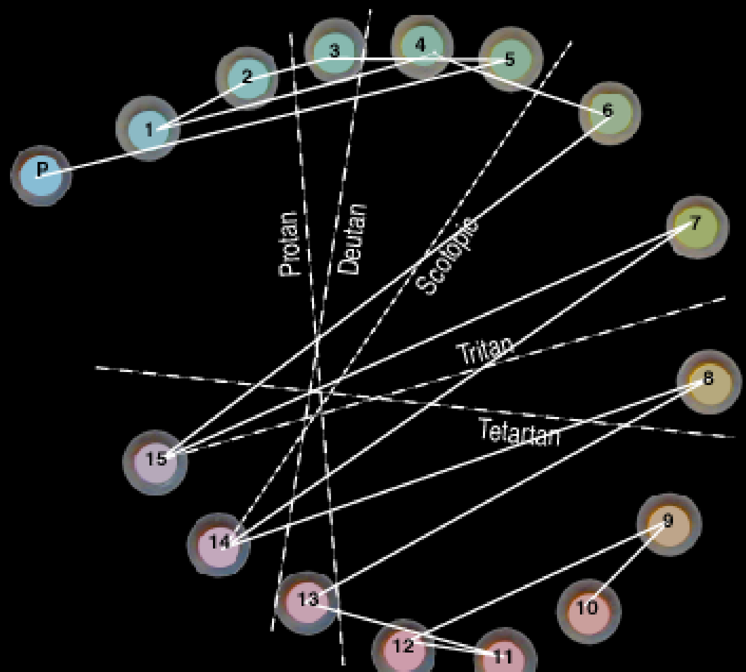
- Farnsworth-Munsell D-15 test
- Farnsworth-Munsell 100-hue test

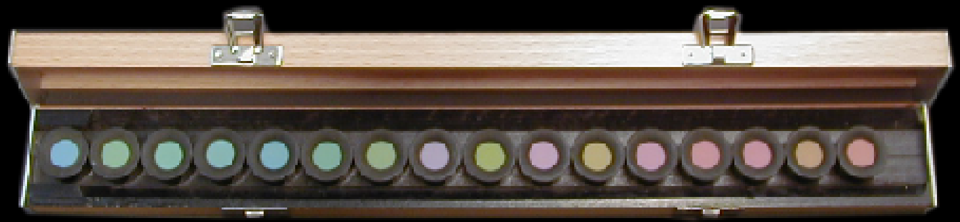
Farnsworth-Munsell D-15



From: Ted Sharpe

Farnsworth-Munsell D-15





From: Ted Sharpe

D15 results

Mild

Severe

Protan

Deutan

Tritan

Rod monochromat

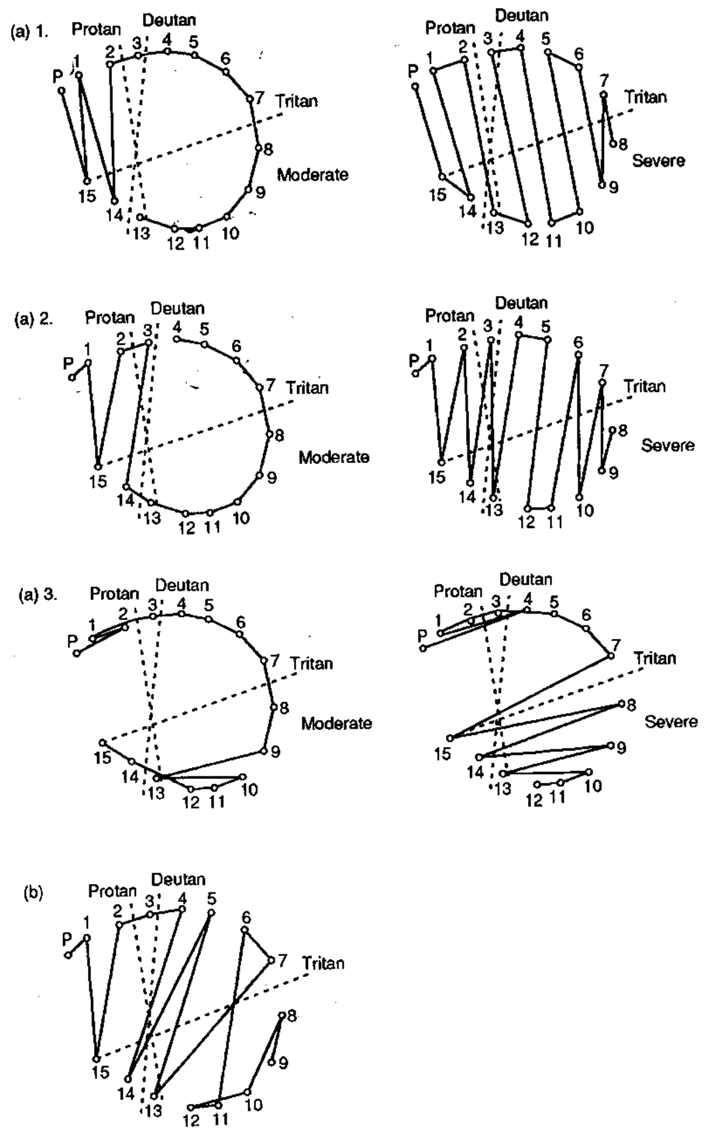


Fig. 7.1 Classification of the type of colour deficiency with the Farnsworth D15 test. (a) Protan, deutan, and tritan defects. 1. Moderate and severe protan defects. 2. Moderate and severe deutan defects. 3. Moderate and severe tritan defects. (b) Typical 'rod' monochromatism. The arrangement represents a lightness scale not isochromatic colour confusions.

Credit: Jenny Birch