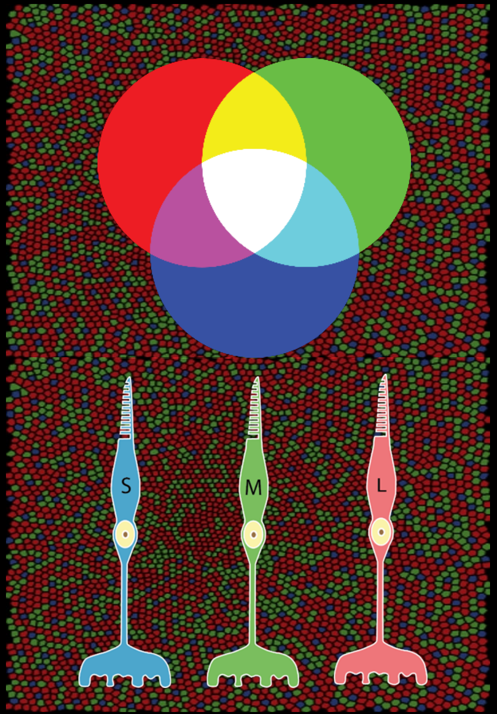
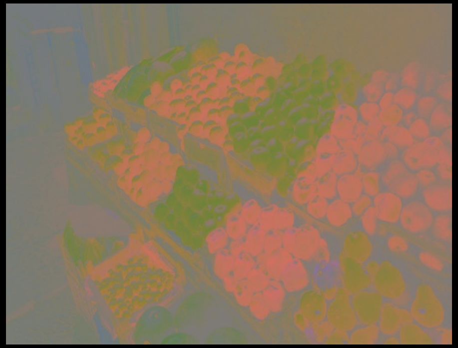


Human colour vision processing from eye to brain

Andrew Stockman

Image Processing Laboratory
VIPLab Seminar



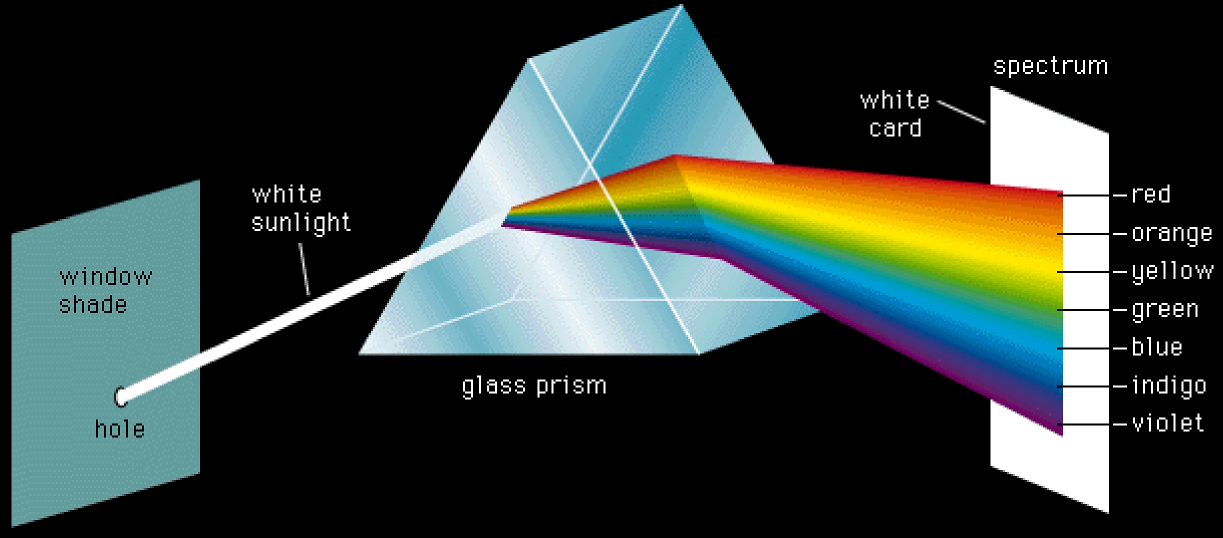
OUTLINE

- Basics of colour vision
- Trichromacy and Univariance
- Encoding colour
- Cone spectral sensitivities
- Postreceptoral chromatic and achromatic vision
- Colour after-effects
- Colour constancy
- Colour contrast and assimilation
- Colour and cognition
- Colour vision deficiencies

BASICS OF COLOUR VISION

Light

400 - 700 nm is important for vision



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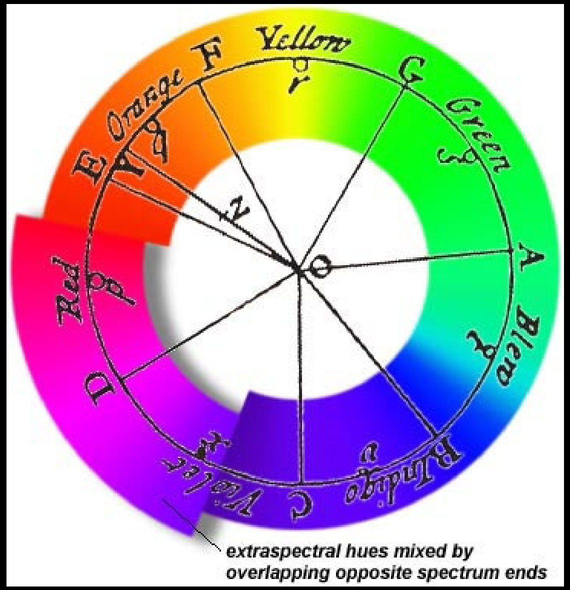


How dependent are we
on colour?

No colour…

Colour…

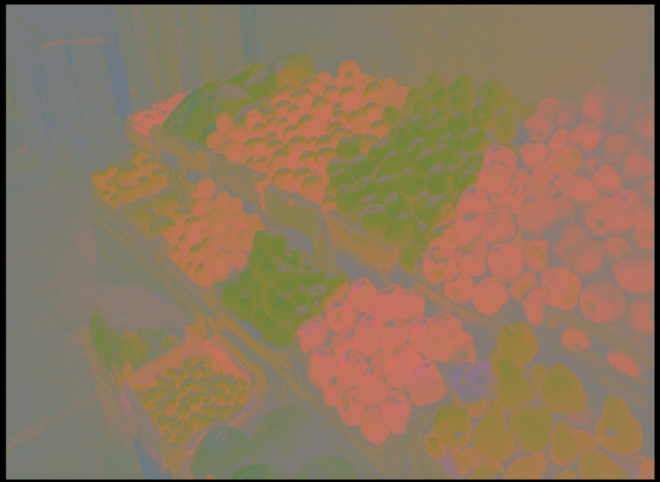
Colour is important because it helps us to discriminate objects from their surroundings.

But just how important
is colour?

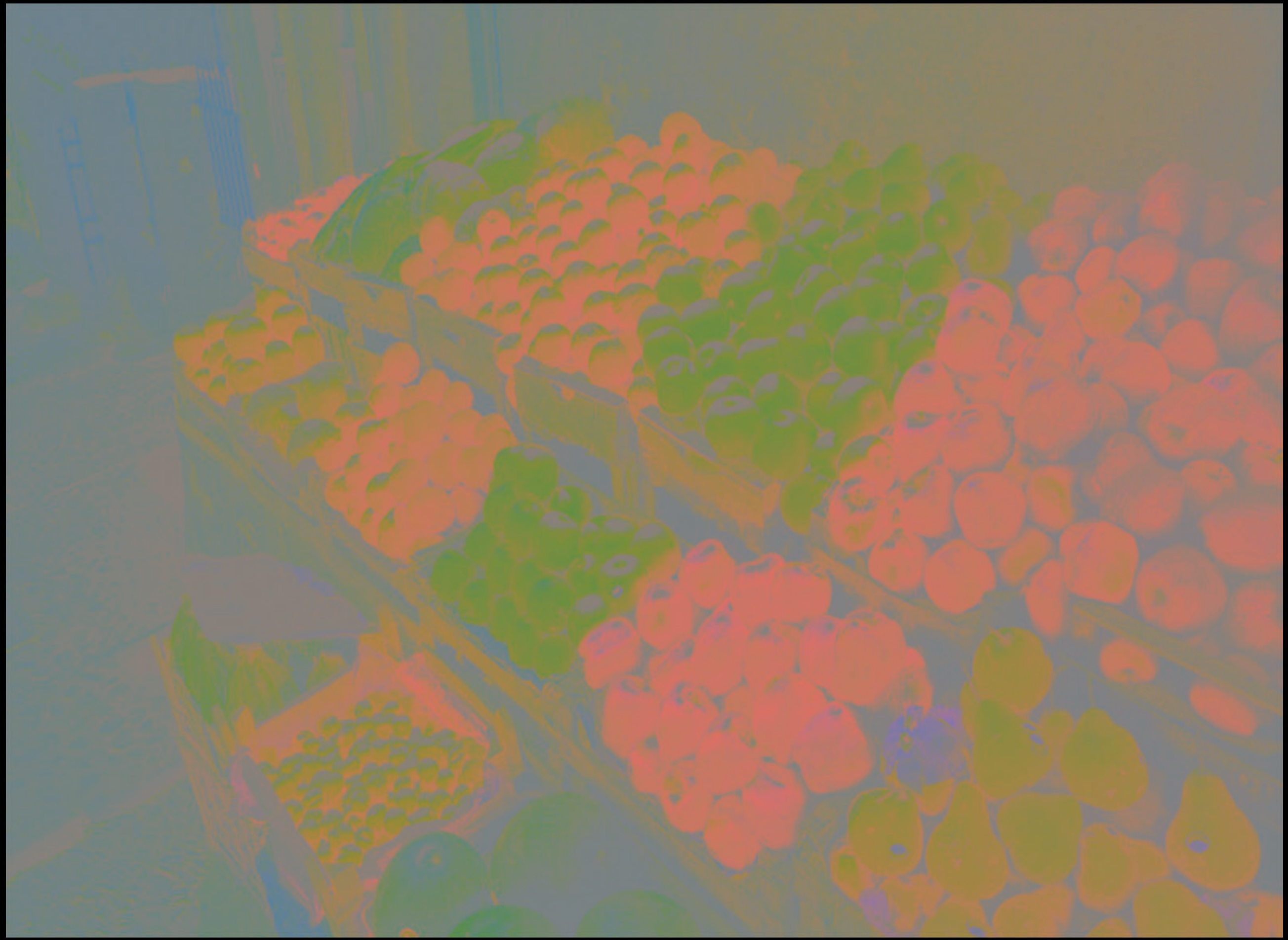
Split the image into...

ACHROMATIC COMPONENTS

CHROMATIC COMPONENTS



CHROMATIC COMPONENTS



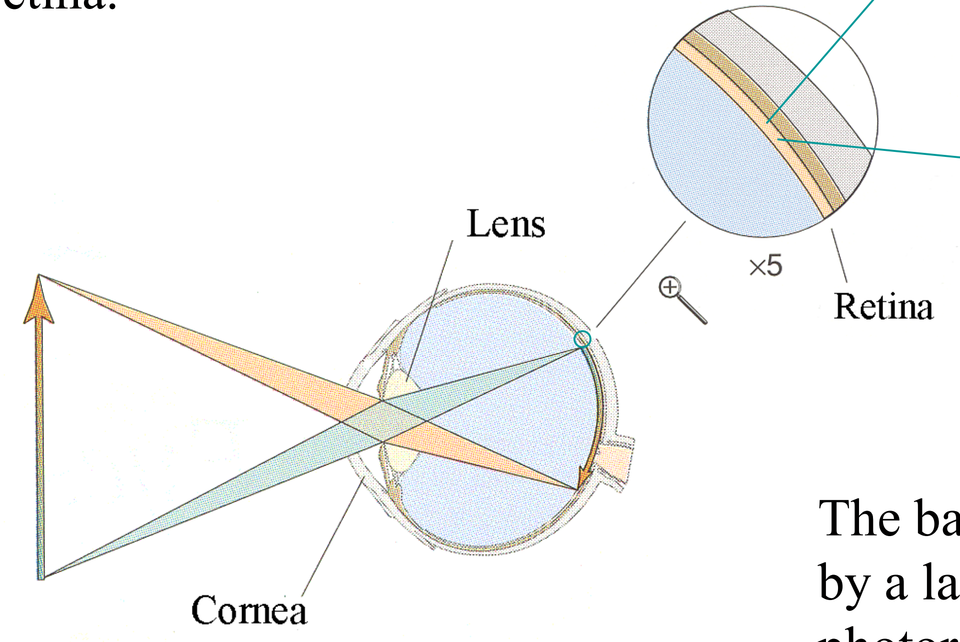
By itself chromatic information provides relatively limited information…

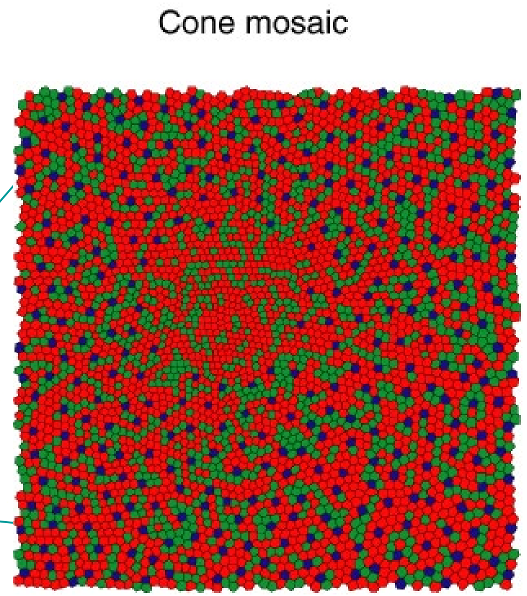
ACHROMATIC COMPONENTS

Achromatic information important for fine detail …

How do we see colours?

An image of the world is projected by the cornea and lens onto the rear surface of the eye: the retina.





The back of the retina is carpeted by a layer of light-sensitive photoreceptors (rods and cones).

Rods and cones

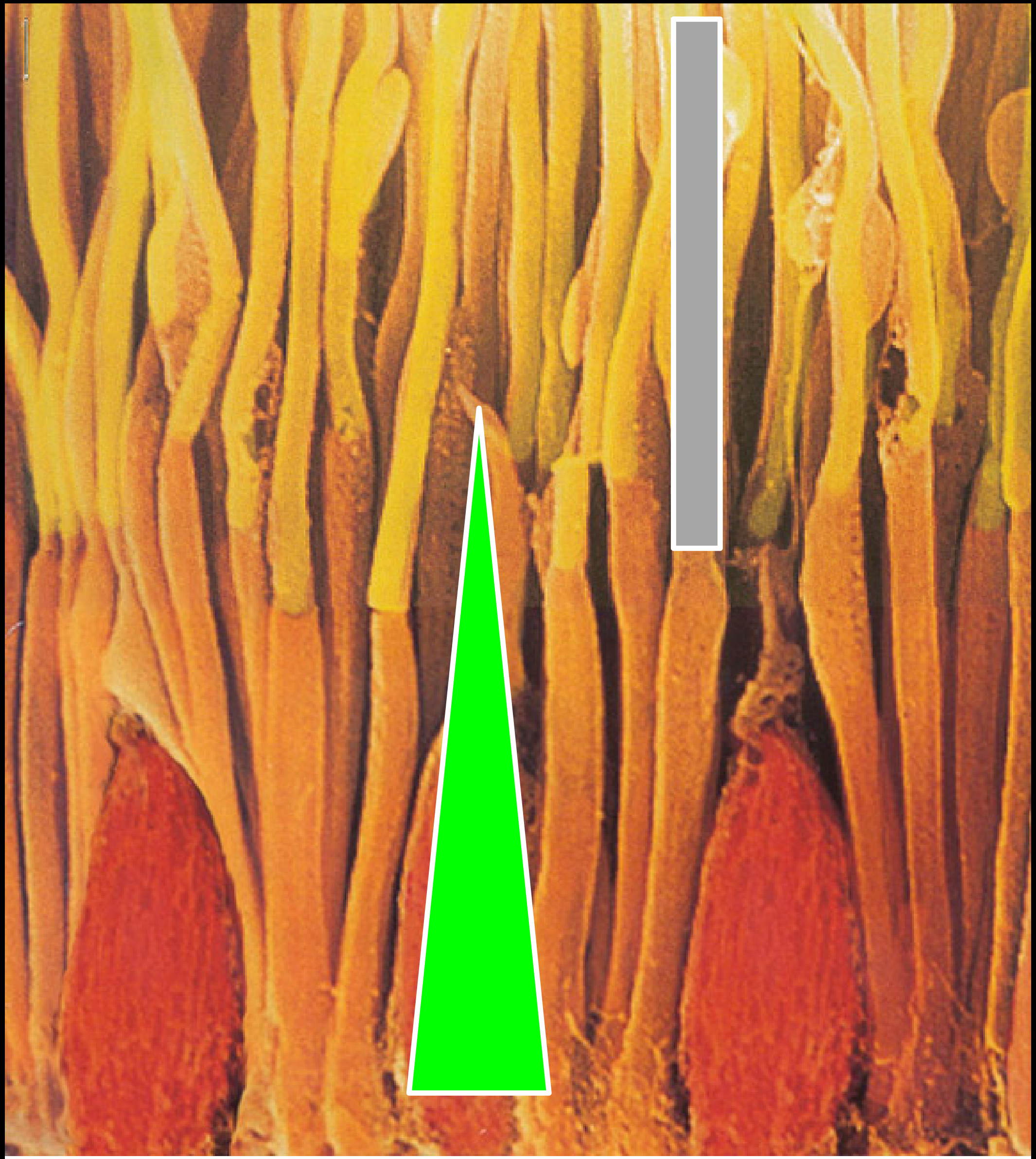
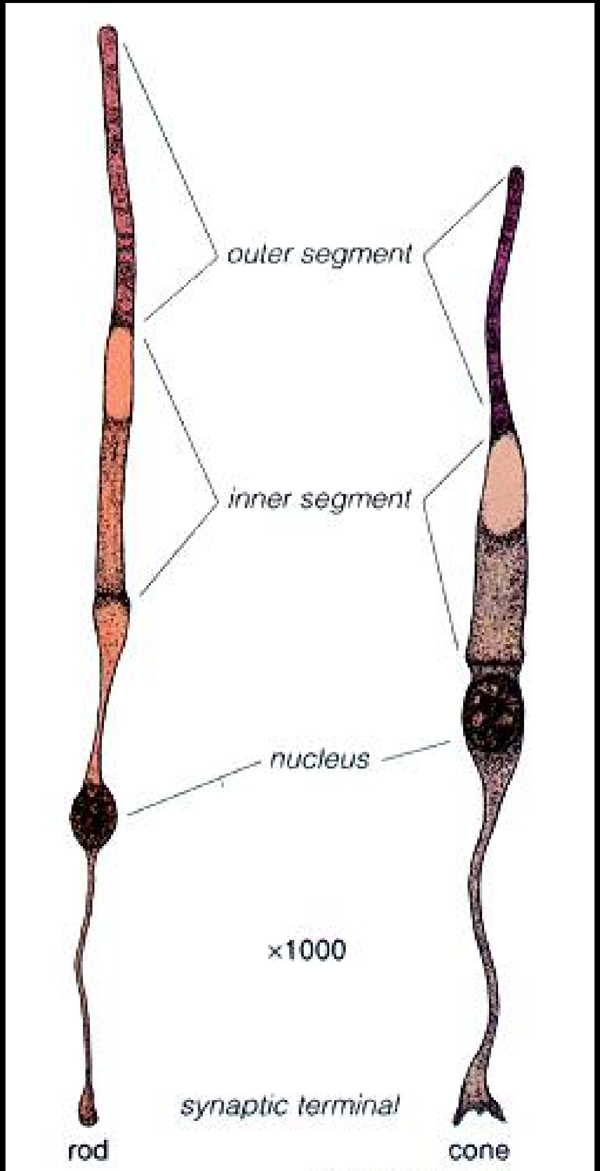


Fig1b. Scanning electron micrograph of the rods and cones of the primate retina. Image adapted from one by Ralph C. Eagle/Photo Researchers, Inc.

Webvision



after Young, 1969

Human photoreceptors

- <u>Rods</u>
  - Achromatic night vision
  - 1 type

Rod

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

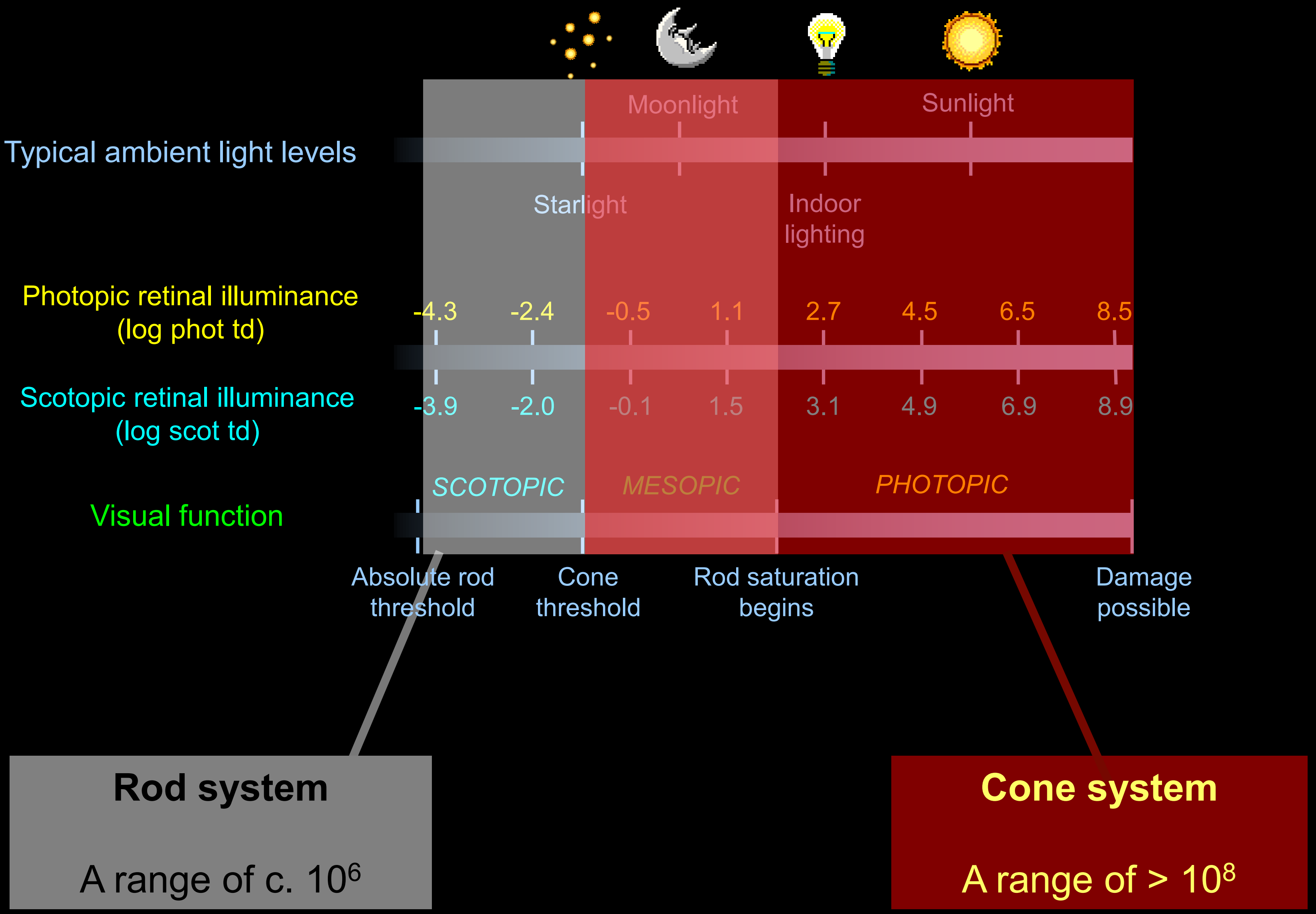
Long-wavelength-sensitive (L) or "red" cone

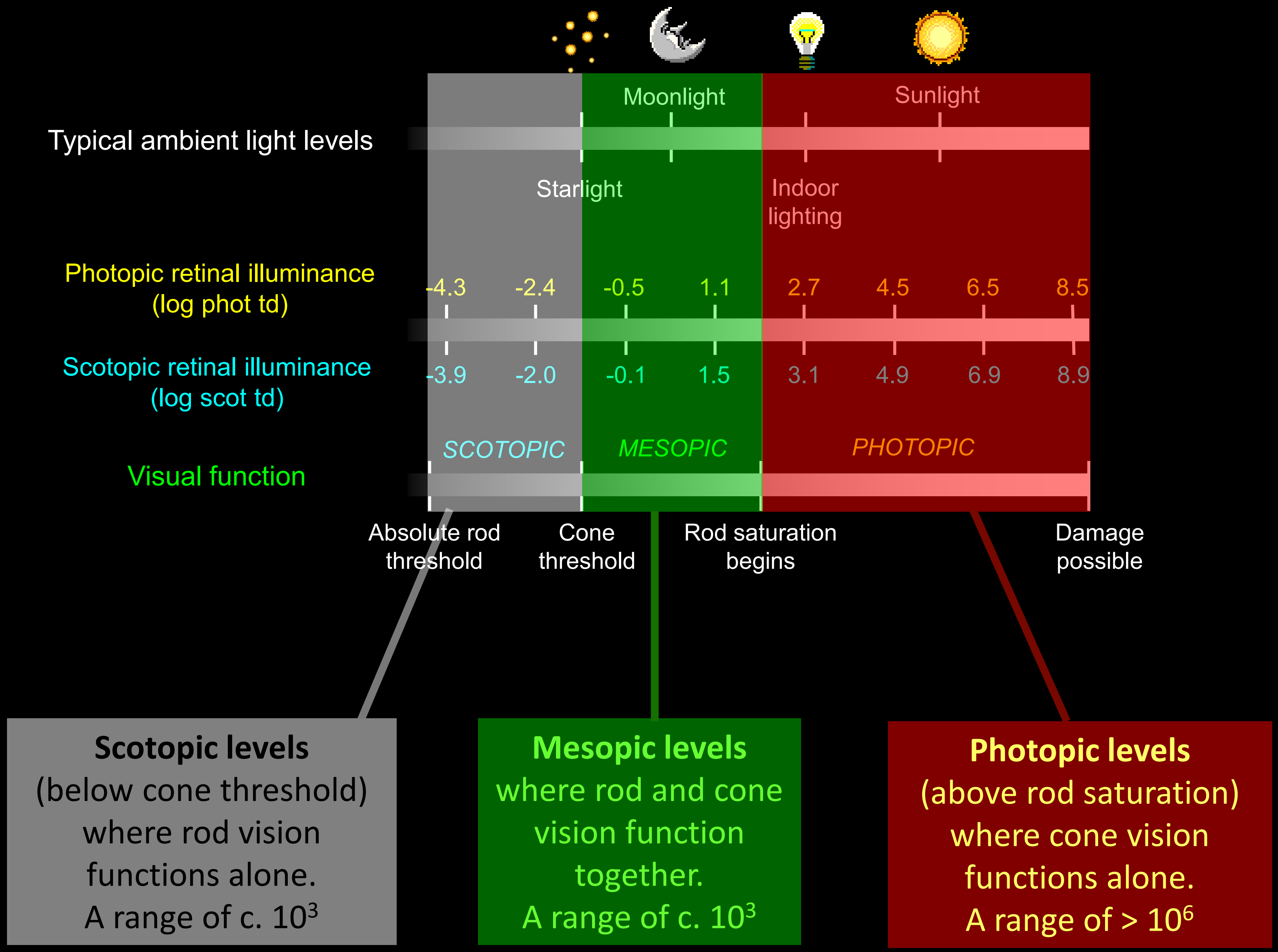
Middle-wavelength-sensitive (M) or "green" cone

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

Why do we have rods and cones?

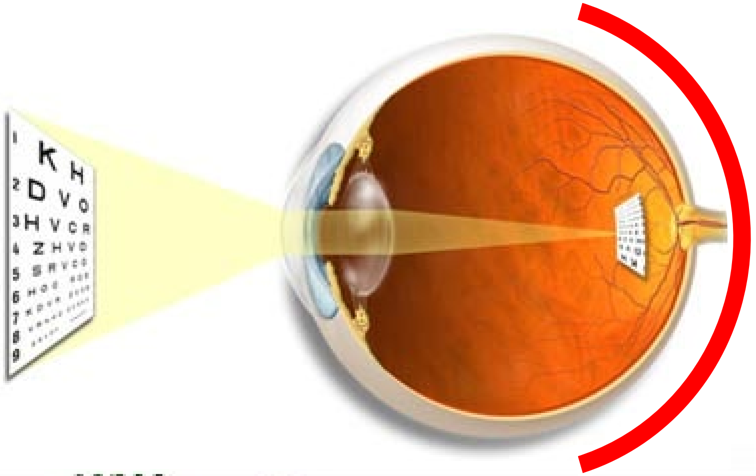
Rod and cone systems are optimized for different light levels

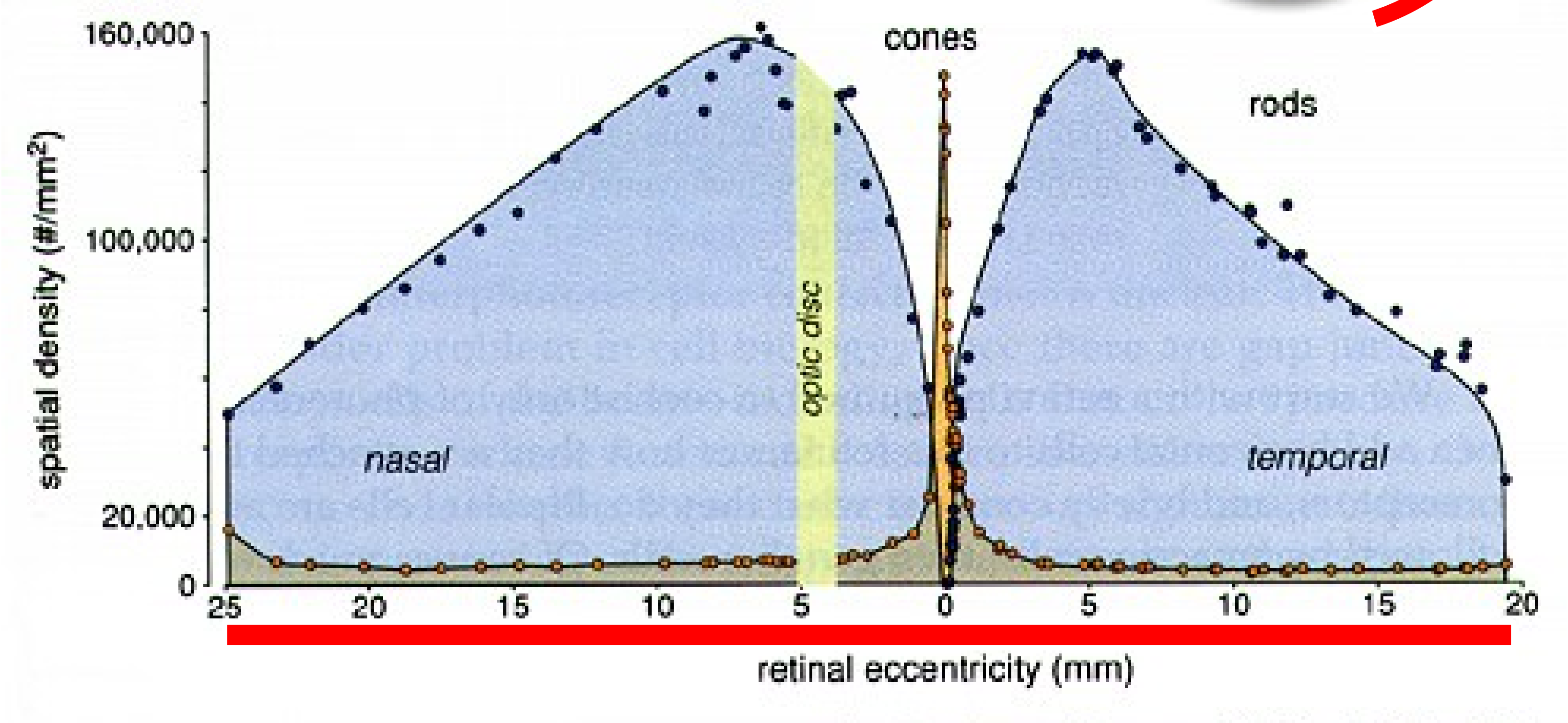




Moonlight
Sunlight
Typical ambient light levels
Starlight
Indoor lighting
Photopic retinal illuminance (log phot td)
-4.3
-2.4
-0.5
1.1
2.7
4.5
6.5
8.5
Scotopic retinal illuminance (log scot td)
-3.9
-2.0
-0.1
1.5
3.1
4.9
6.9
8.9
SCOTOPIC
MESOPIC
PHOTOPIC
Visual function
Absolute rod threshold
Cone threshold
Rod saturation begins
Damage possible
Scotopic levels
(below cone threshold) where rod vision functions alone.
A range of c. 10³
Mesopic levels
where rod and cone vision function together.
A range of c. 10³
Photopic levels
(above rod saturation) where cone vision functions alone.
A range of > 10⁶

Rod and cone distribution

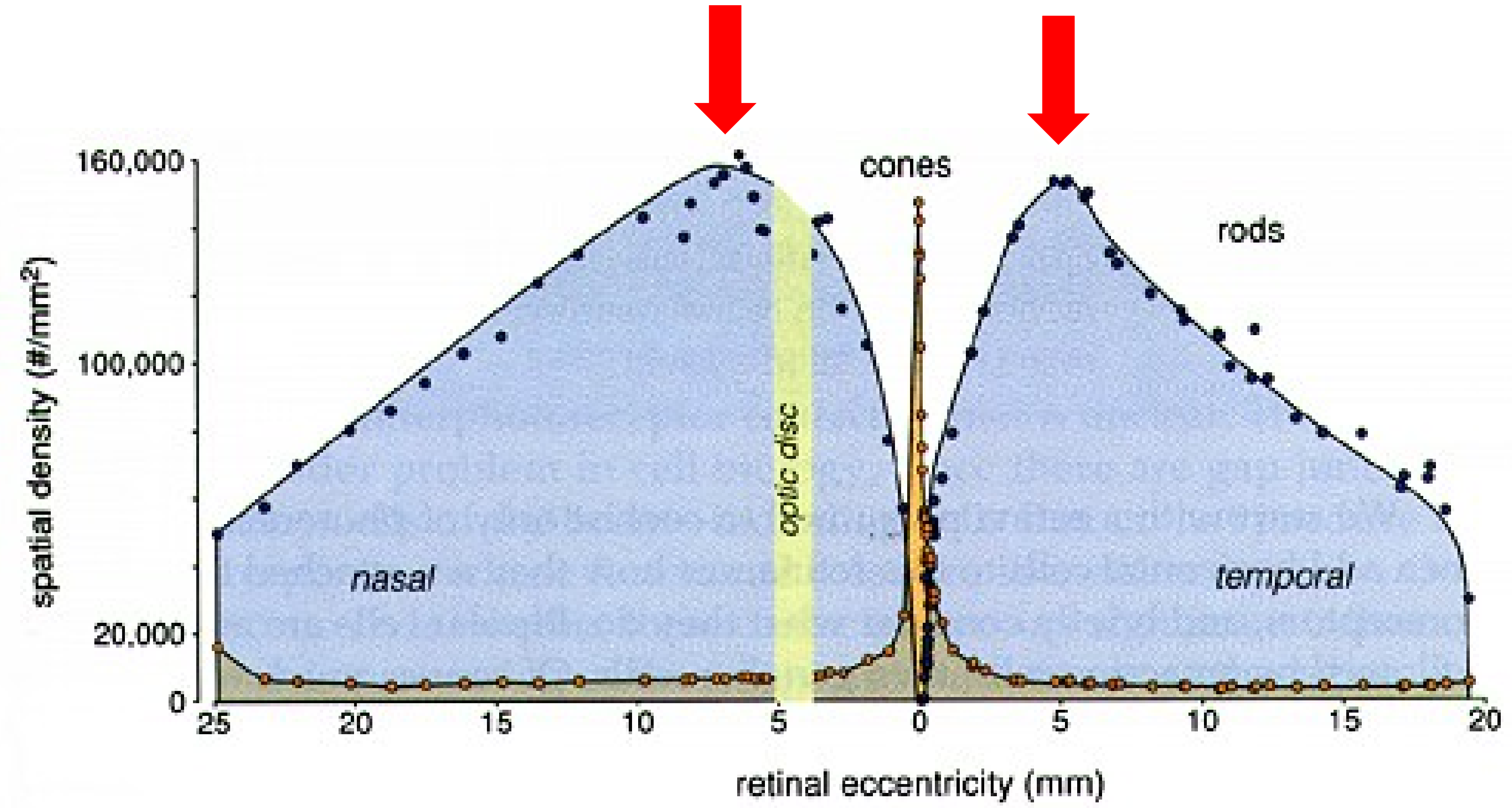




after Østerberg, 1935; as modified by Rodieck, 1988

0.3 mm of eccentricity is about 1 deg of visual angle

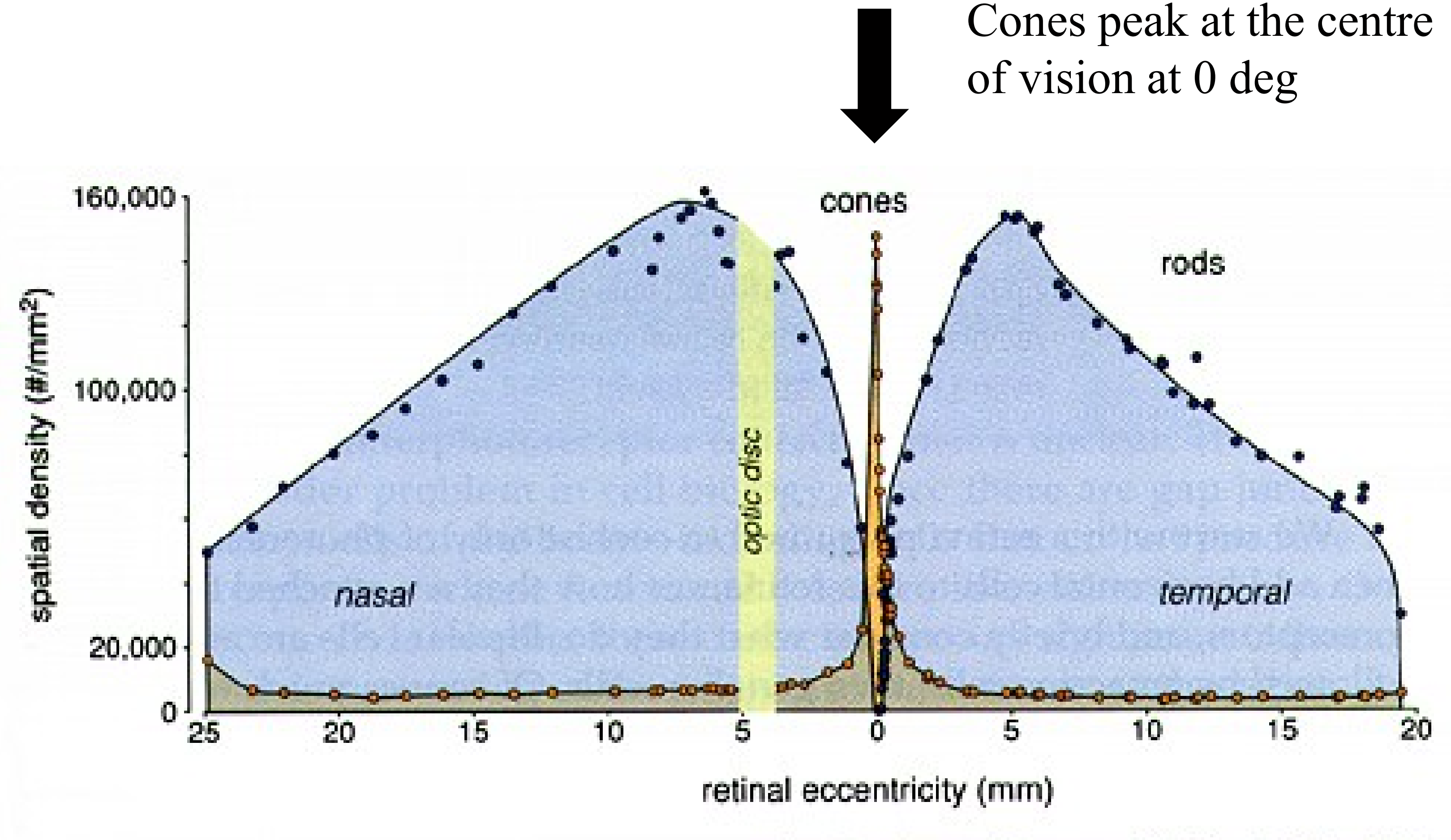
Rod density peaks at about
20 deg eccentricity



after Østerberg, 1935; as modified by Rodieck, 1988

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

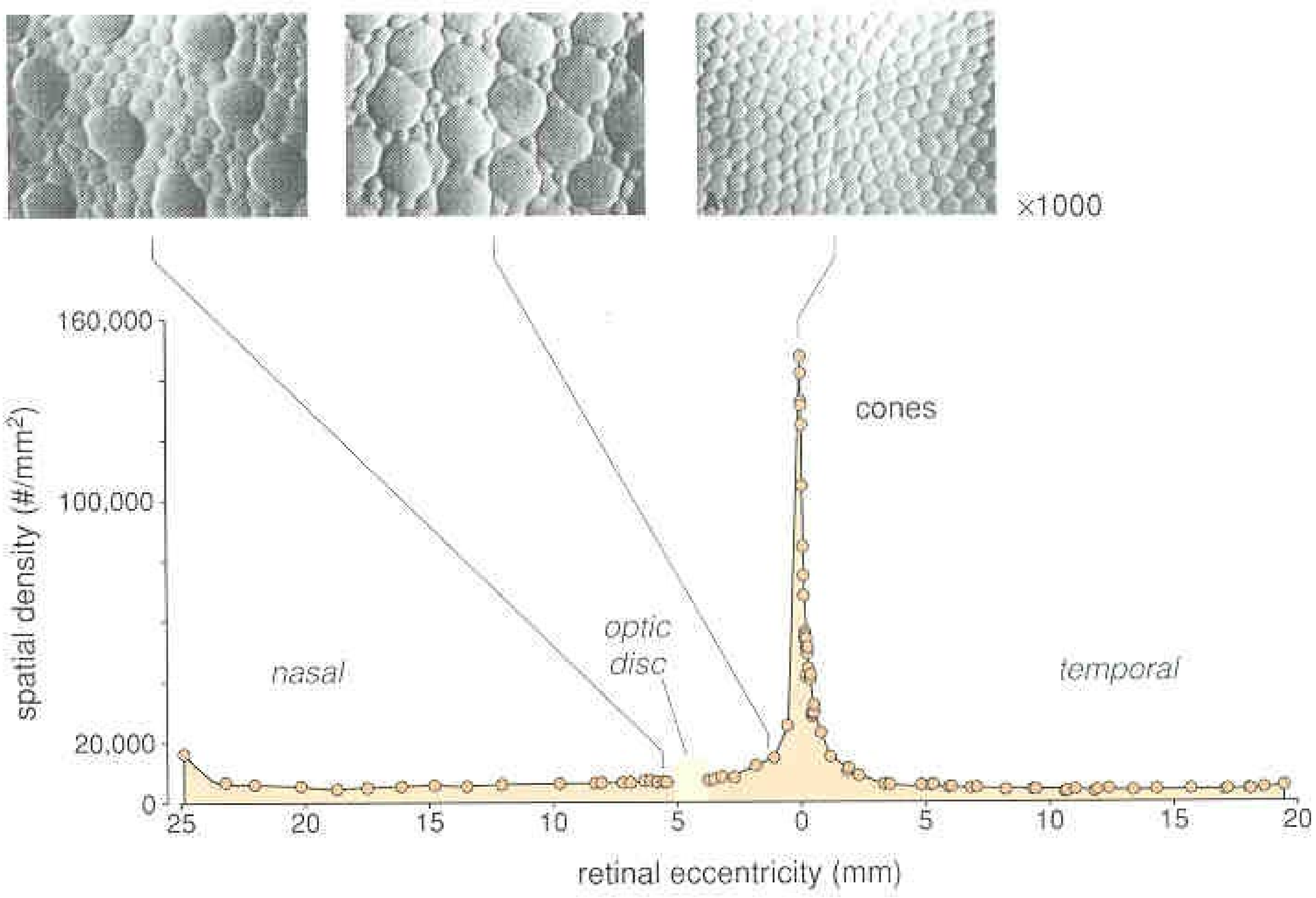
Cones peak at the centre of vision at 0 deg



after Østerberg, 1935; as modified by Rodieck, 1988

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

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.

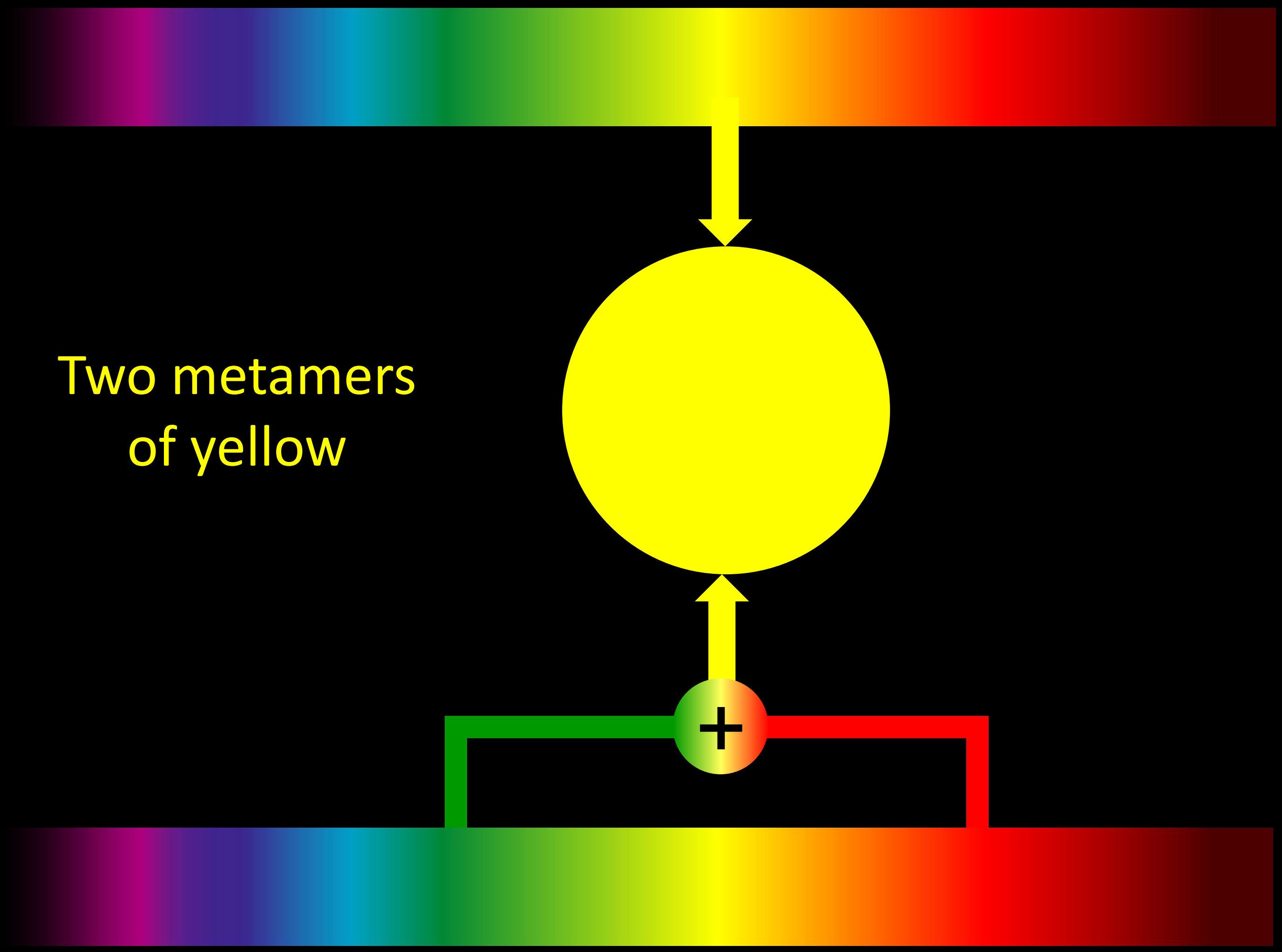
Credit: Stuart Anstis, UCSD

Are the colours that we see…

a property mainly of physics or biology?

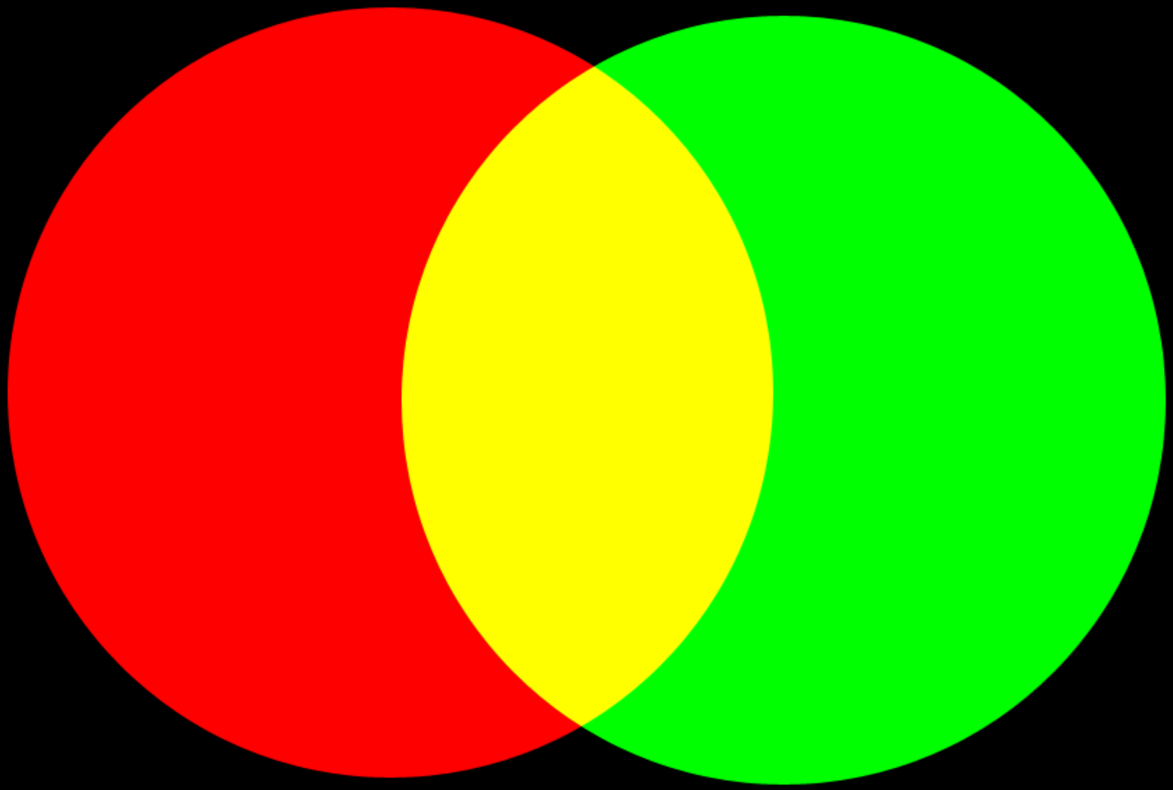
Colour isn't just about physics

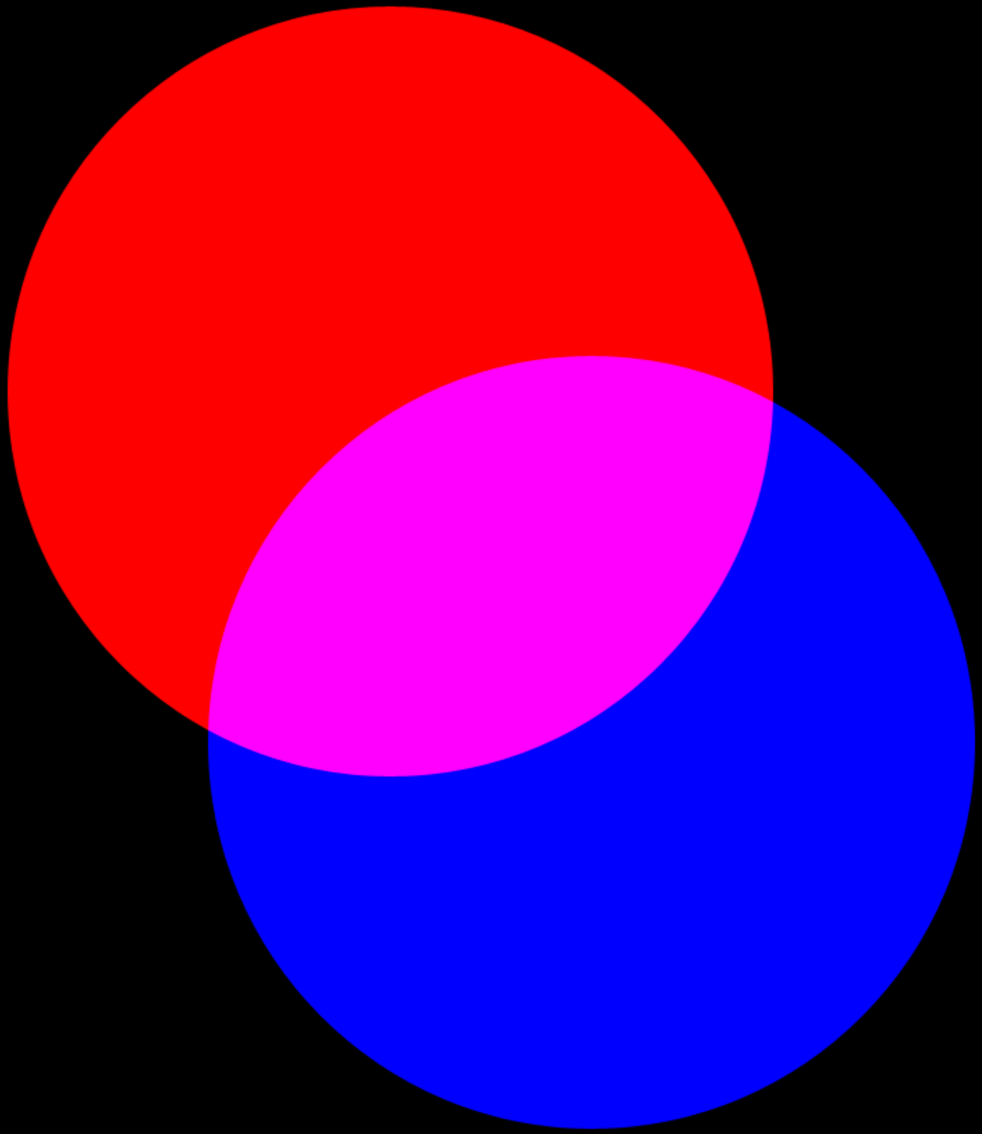
For example:

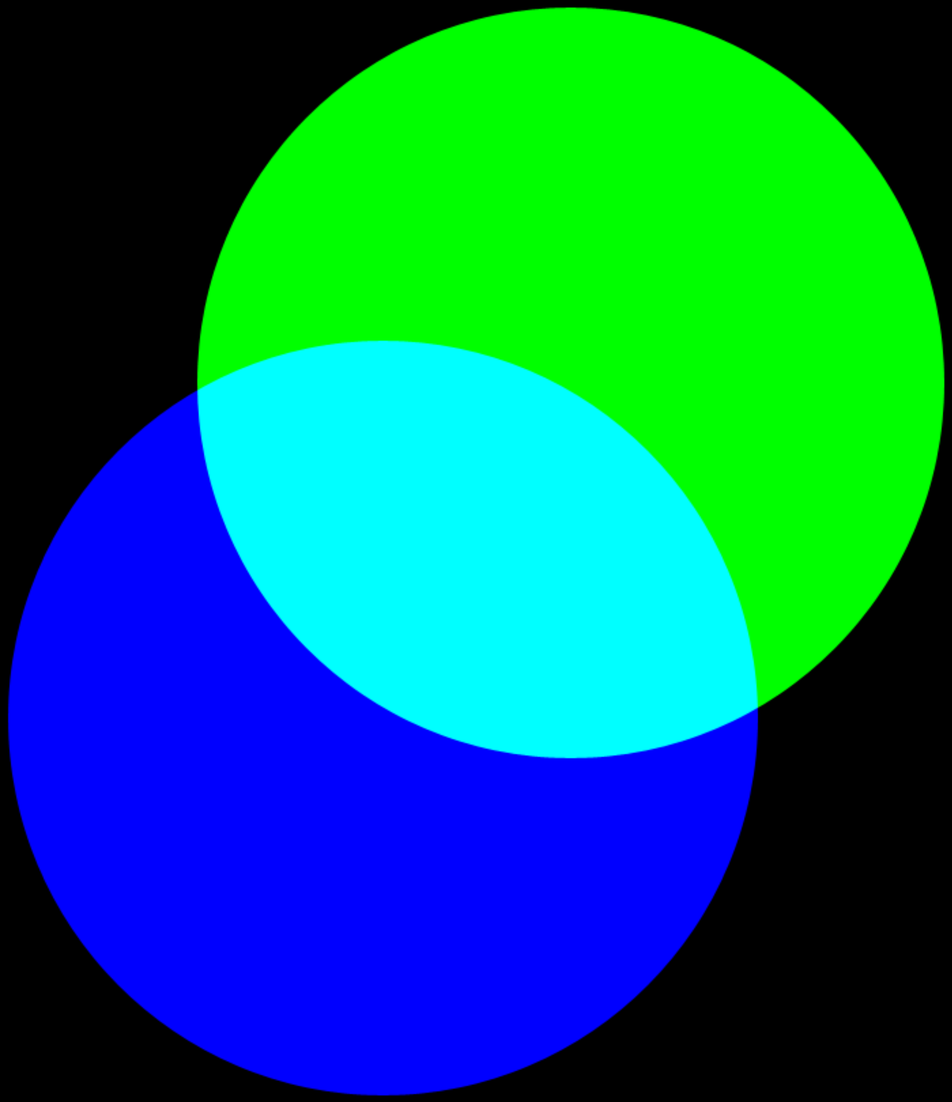


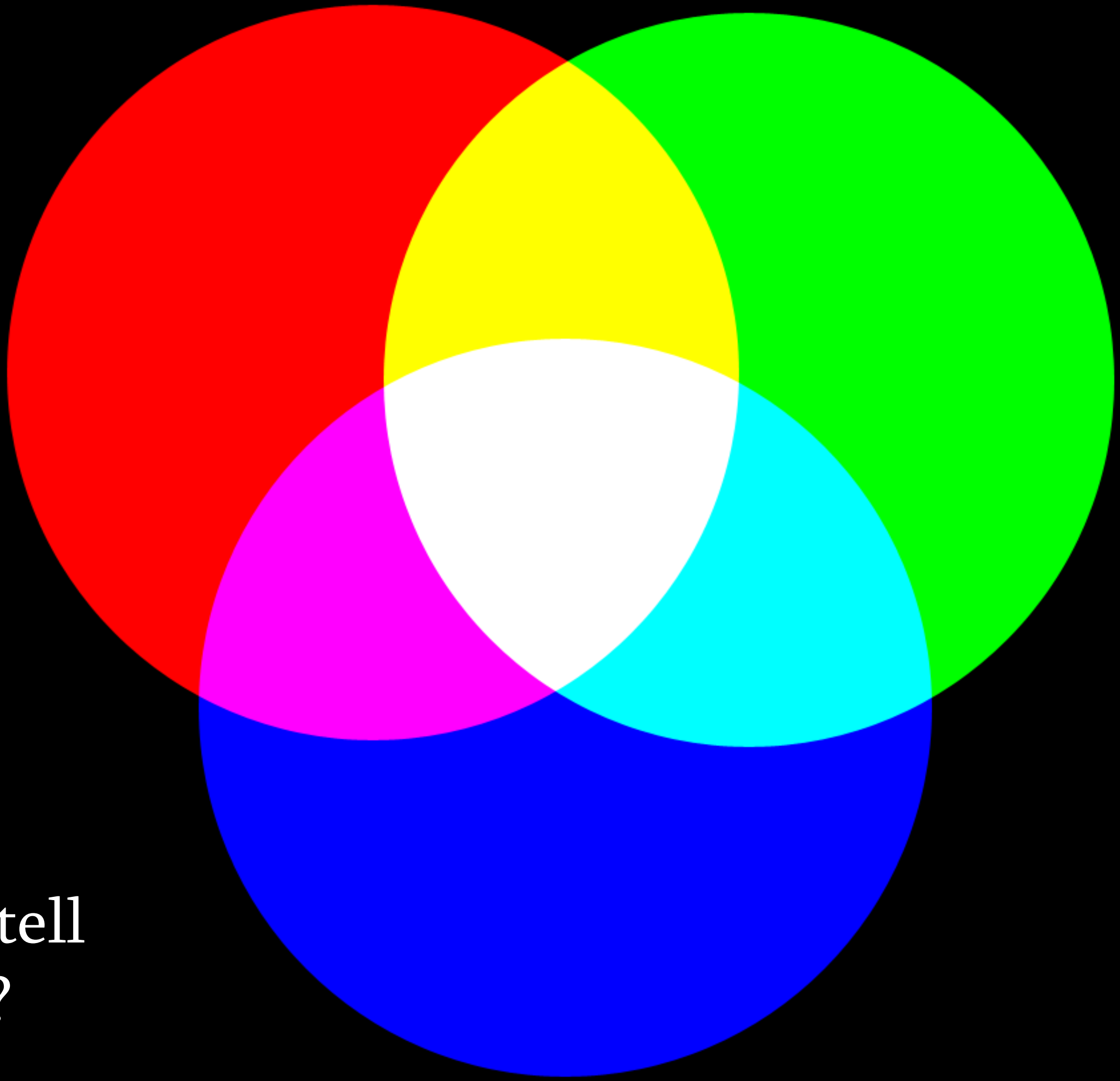
though physically very different, can appear identical.

There are many other such metamers or matches…

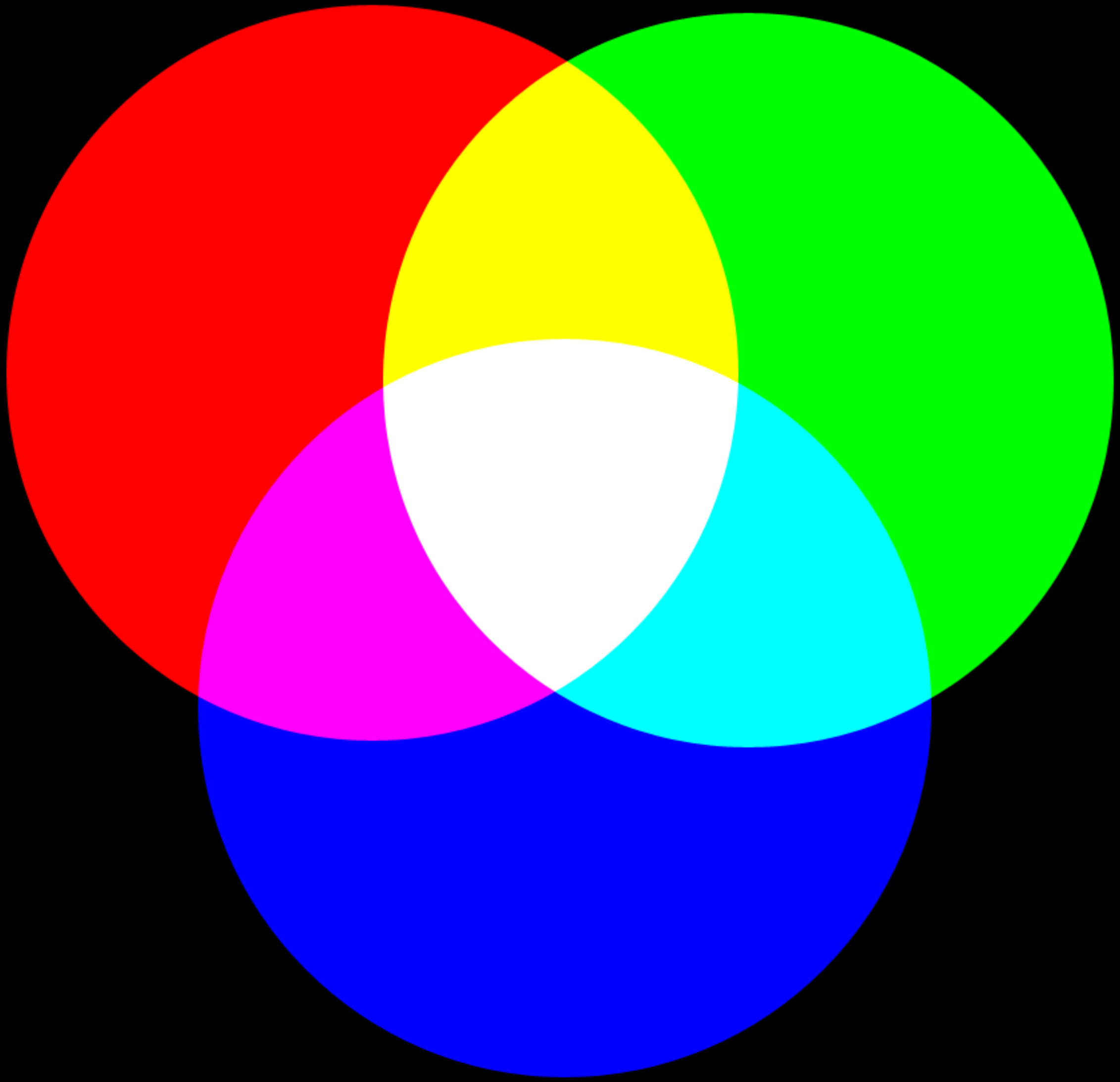




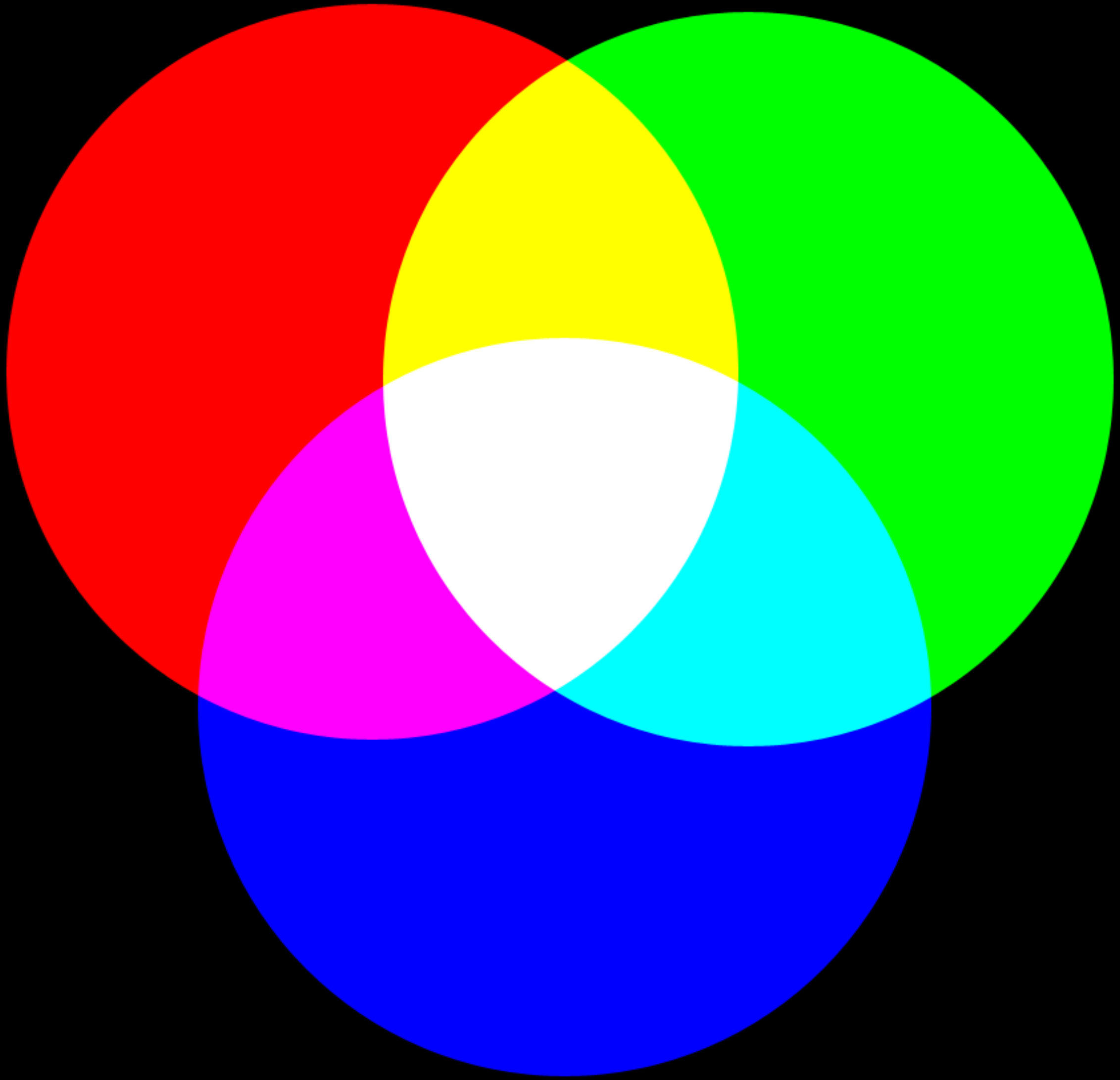




What can colour mixing tell us about colour vision?

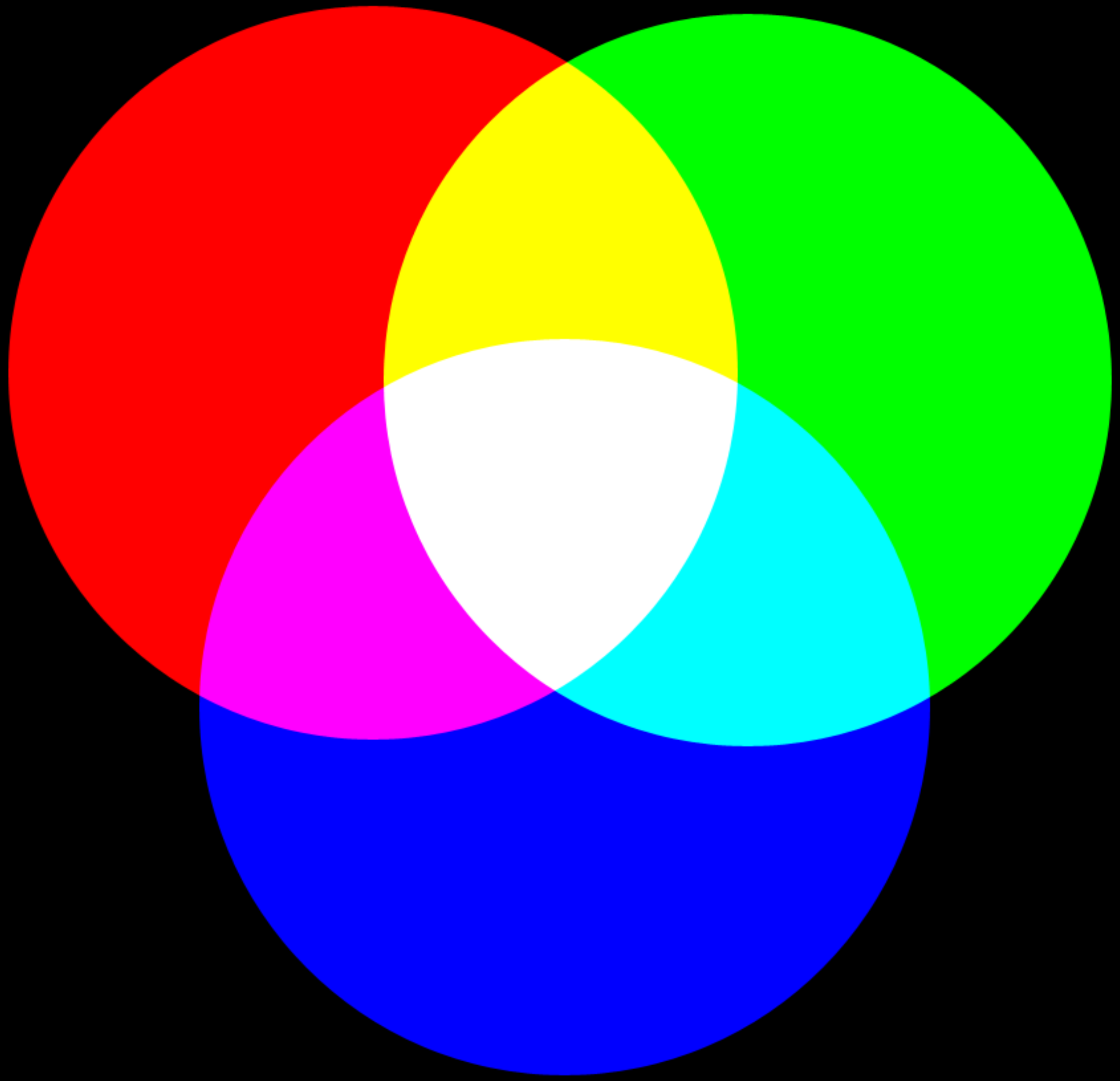


Before we knew about the underlying biology, additive colour mixing done in the 19th century revealed that colour vision was…



TRICHROMATIC

TRICHROMACY AND UNIVARIANCE



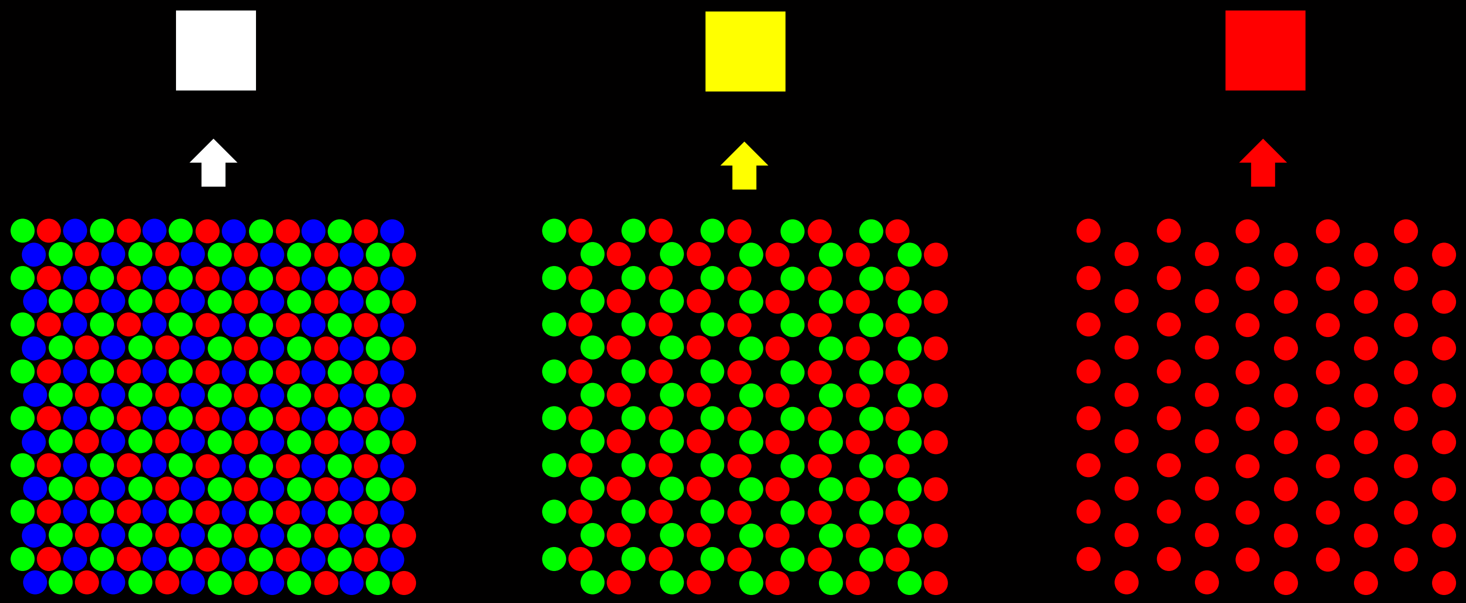
Trichromacy means that colour vision at the input to the visual system is relatively simple.

It is a 3 variable system...

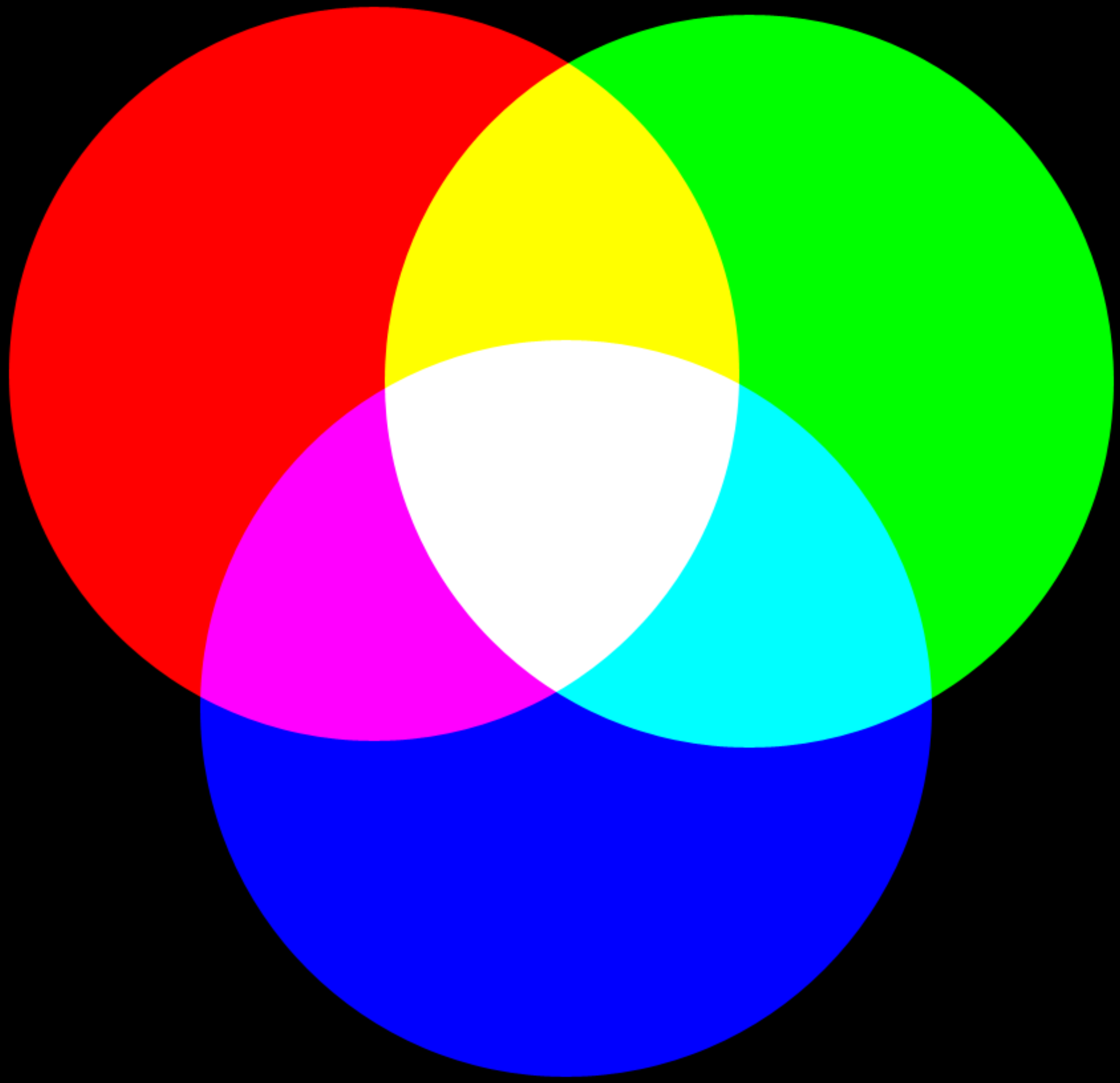
Colour TV

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

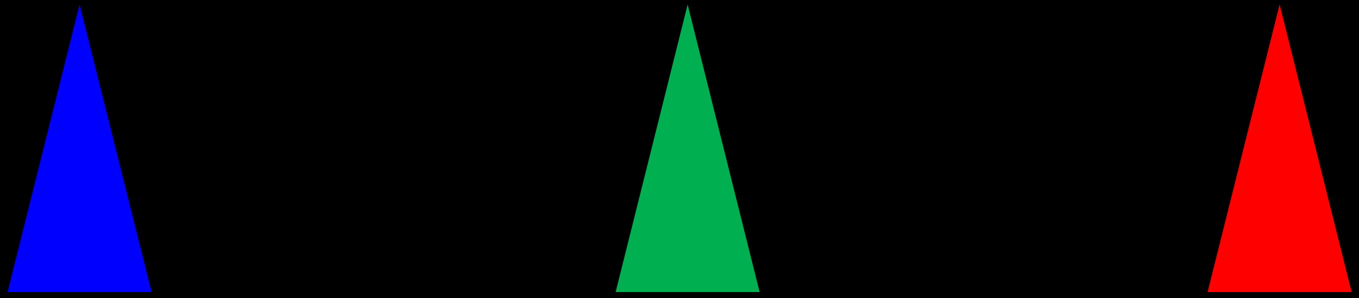
The dots produced by a TV or projector are so small that they are mixed together by the eye and thus appear as uniform patches of colour.



Why is human
vision trichromatic?



The main reason is because just three cone photoreceptors are responsible for daytime colour vision.



Short-wavelength-sensitive or “blue”

Middle-wavelength-sensitive or “green”

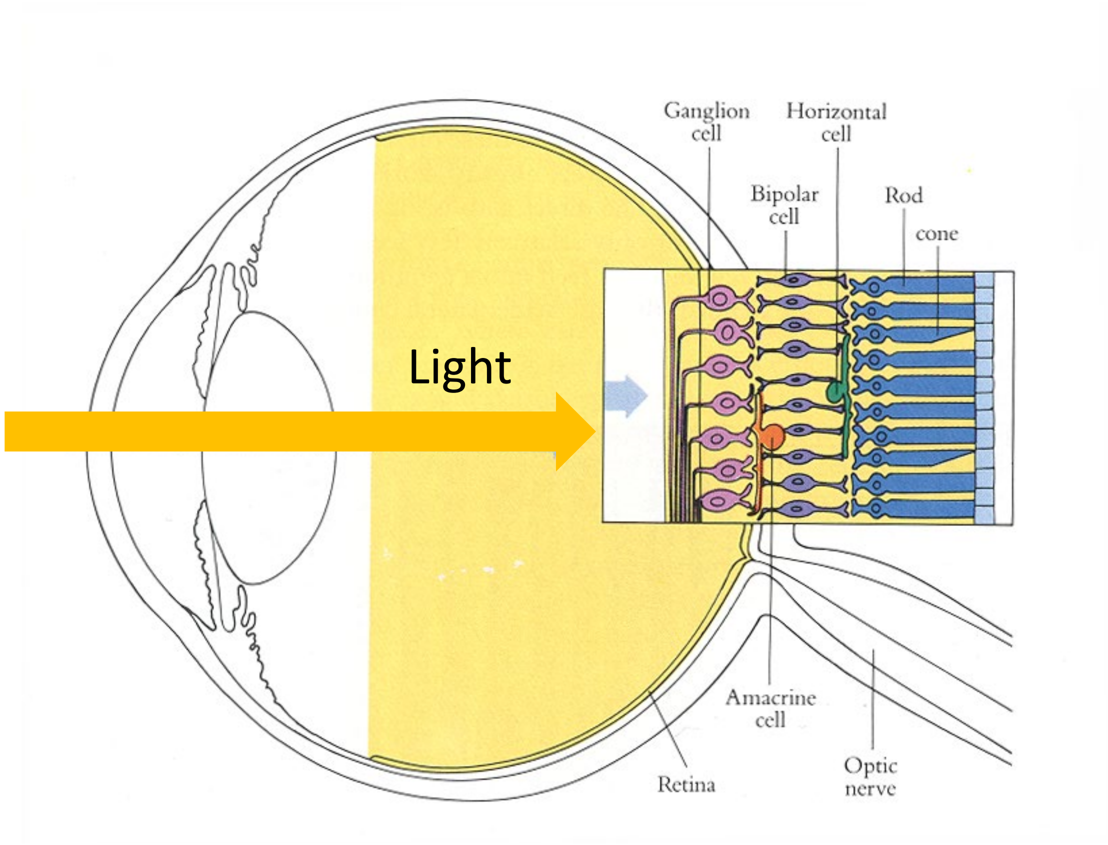
Long-wavelength-sensitive or “red”

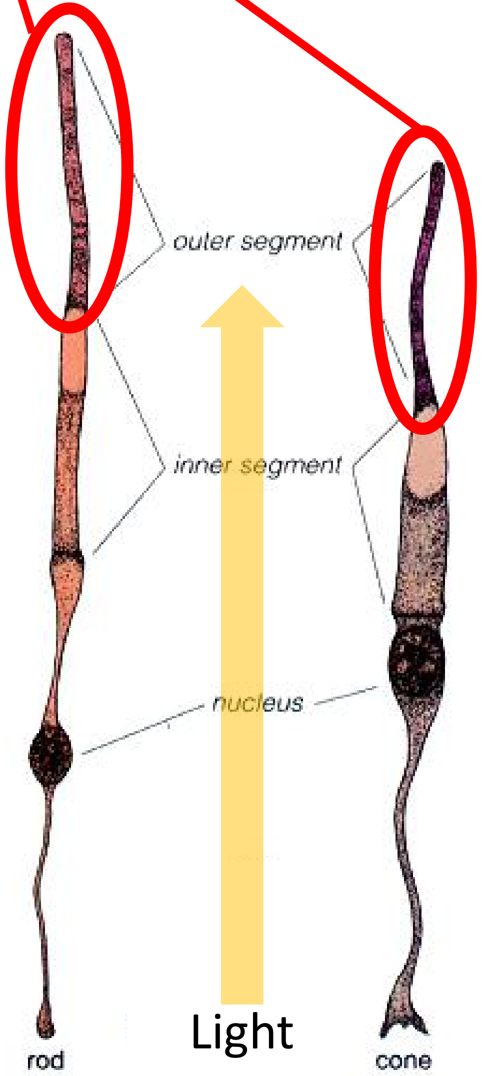
And because each one produces a UNIVARIANT output.

UNIVARIANCE

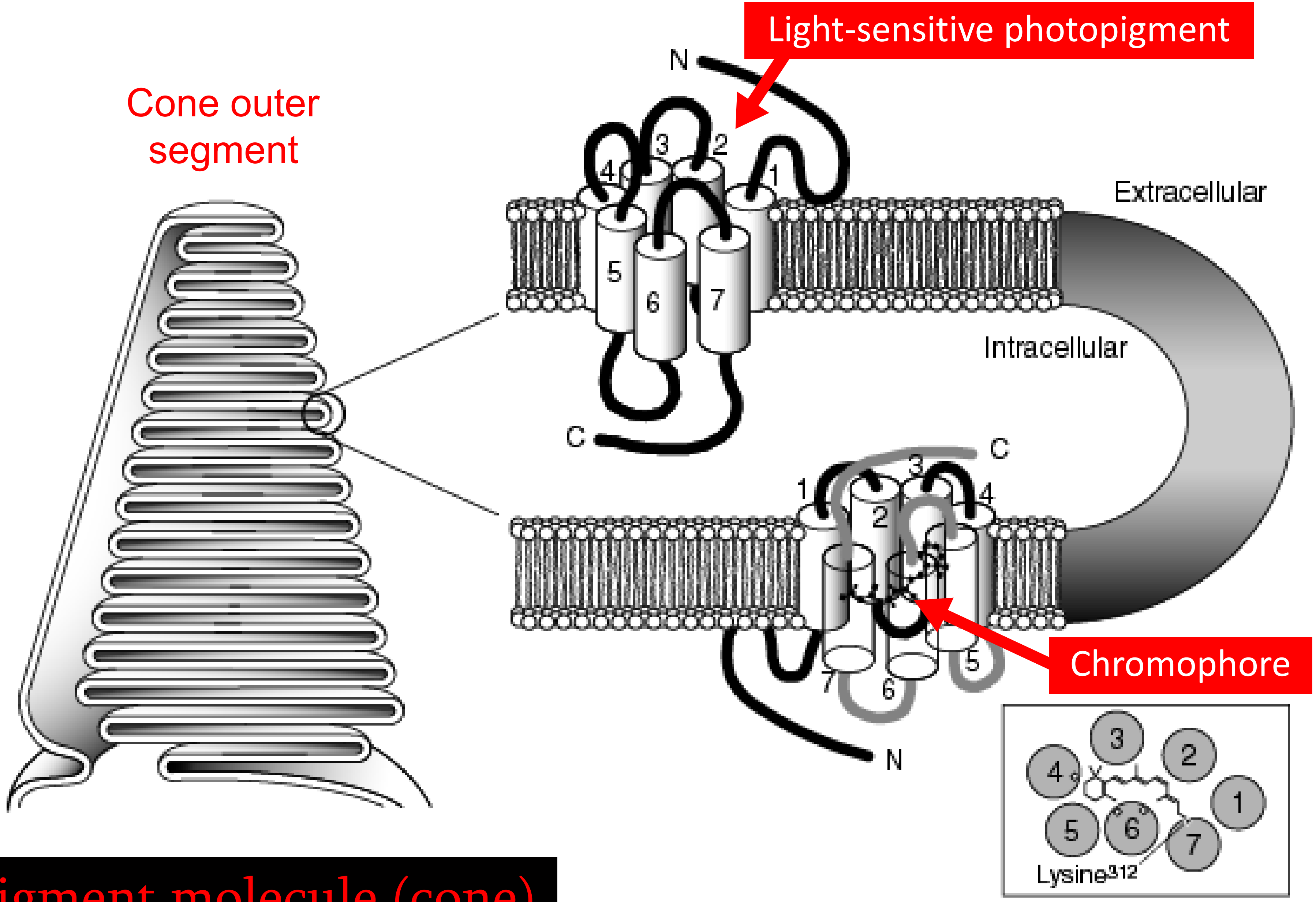
Univariance can be explained simply at the molecular level by the interaction of photons with the photopigment molecules in each photoreceptor…

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





after Young, 1969



Photopigment molecule (cone)

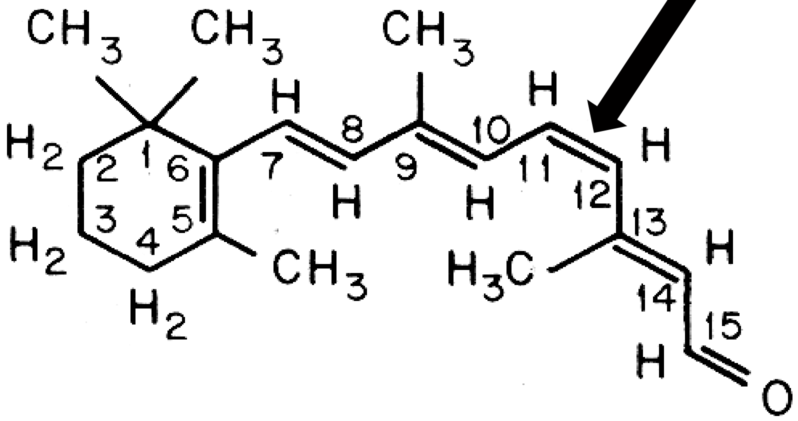
From Sharpe, Stockman, Jägle & Nathans, 1999

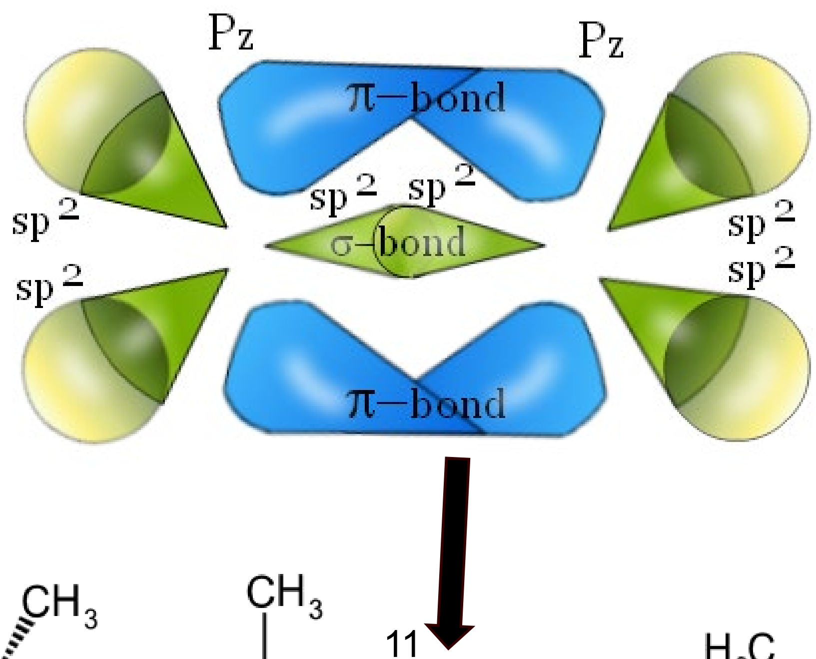
Chromophore

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

11-*cis* retinal

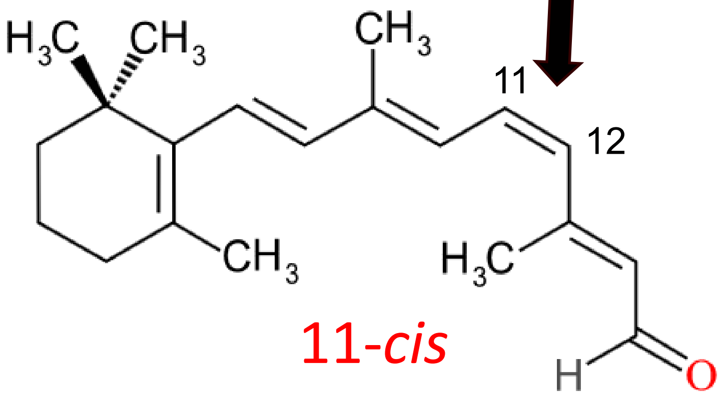
The molecule is twisted at the 11th carbon.



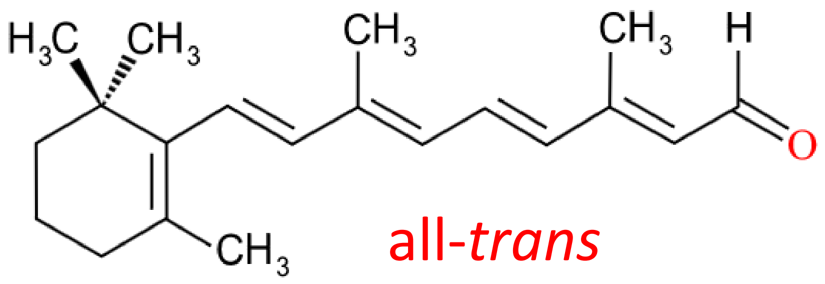


The double bond is made up of a σ and a π bond.

Together, they prevent rotation around the double-bond axis.



11-*cis*



all-*trans*

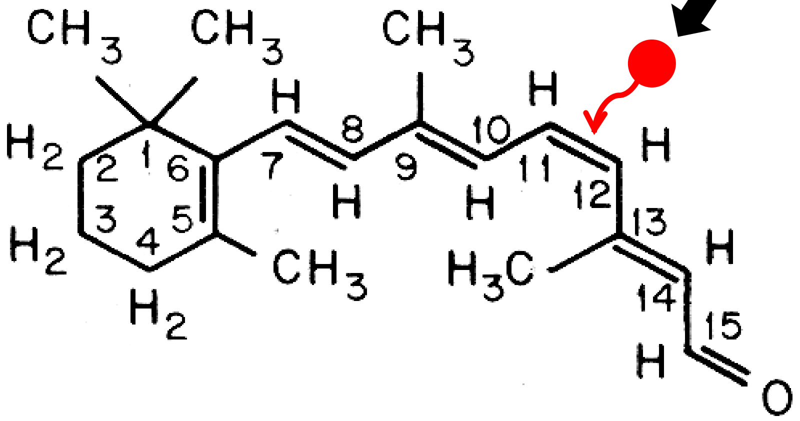
Therefore there are different “stereoisomers”.

Chromophore

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

A photon is absorbed

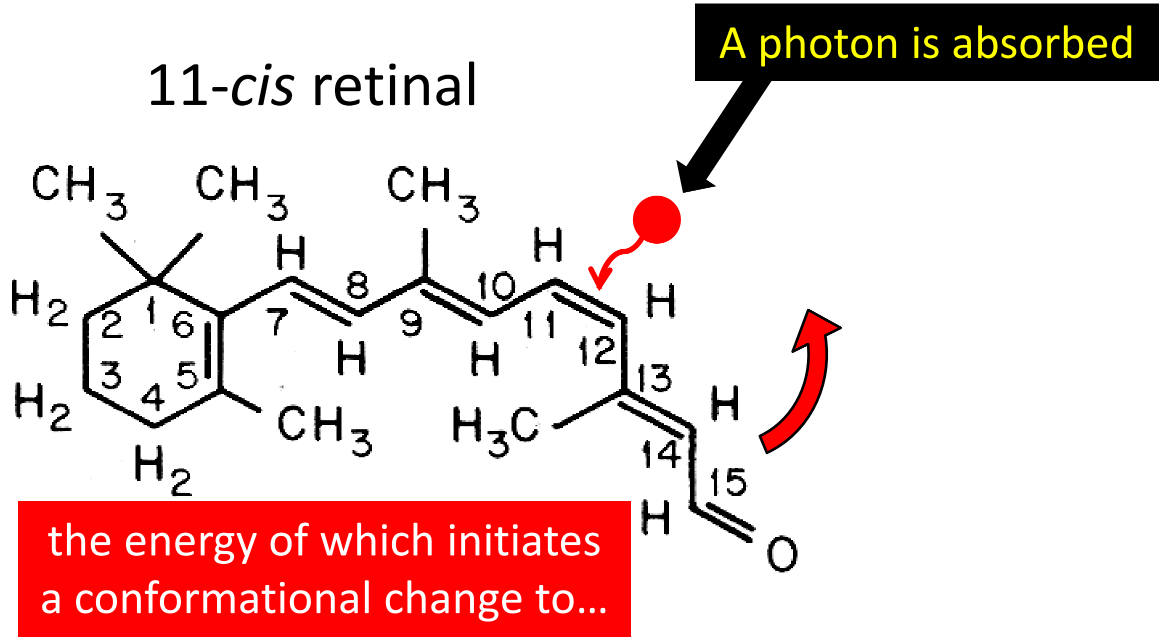
11-*cis* retinal



Chromophore

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

11-*cis* retinal



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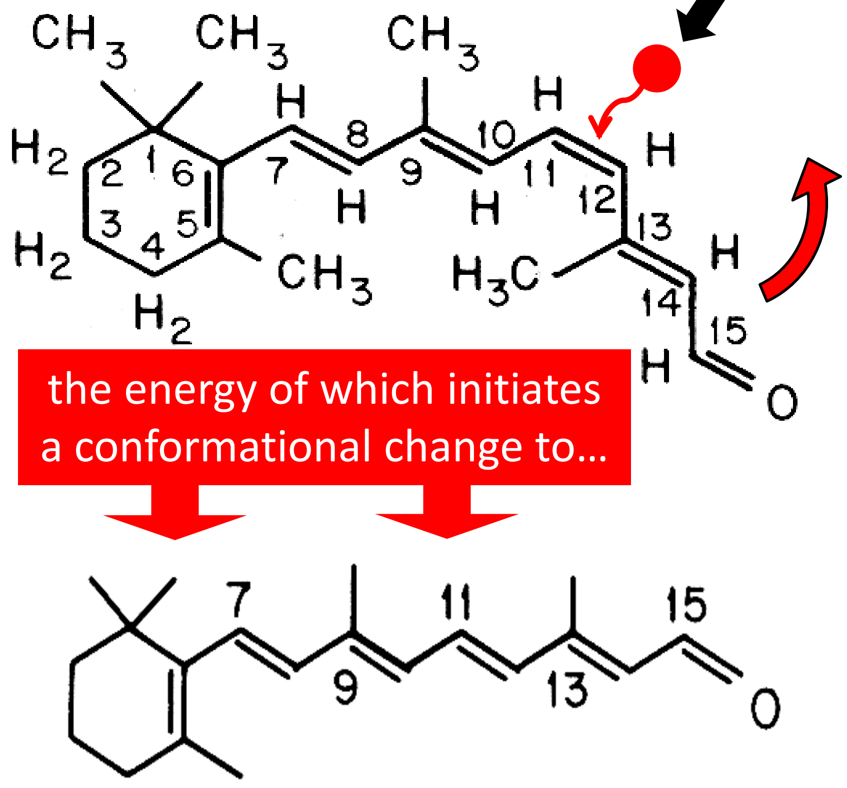
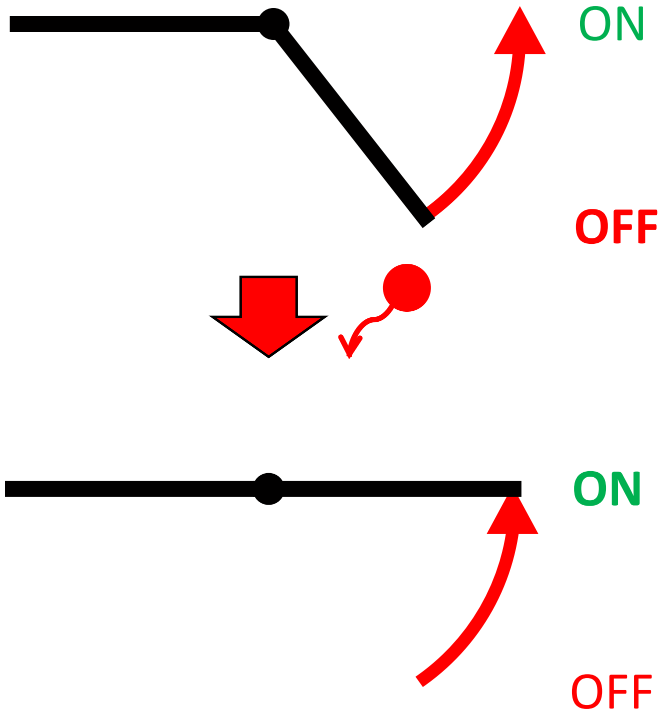


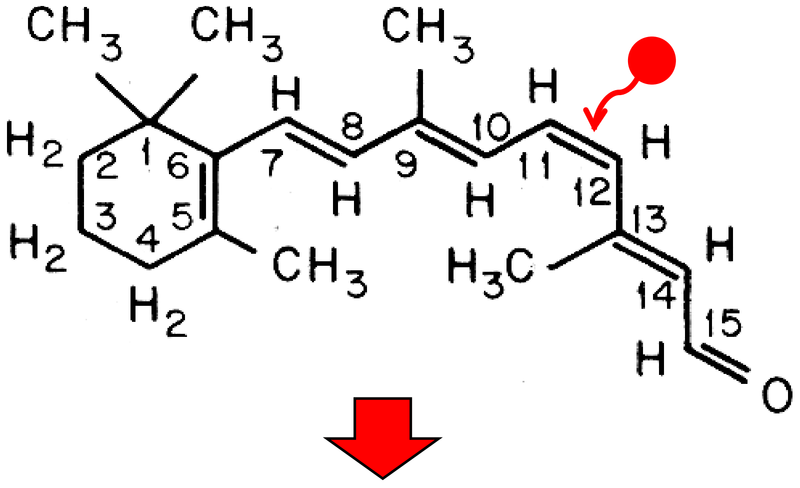
all-*trans* retinal

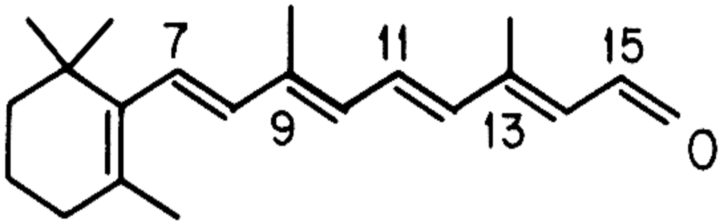
Think of the molecule as a photo-sensitive switch!



Chromophore

11-*cis* retinal

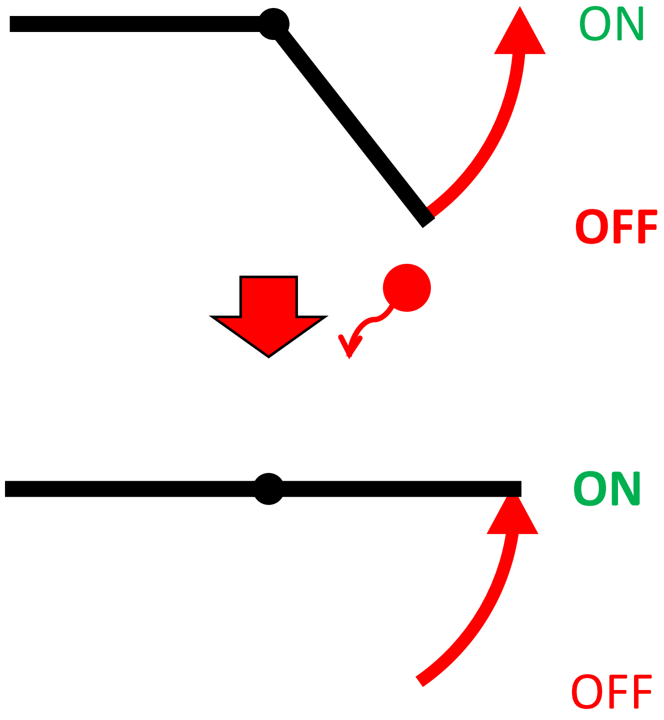




all-*trans* retinal

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.



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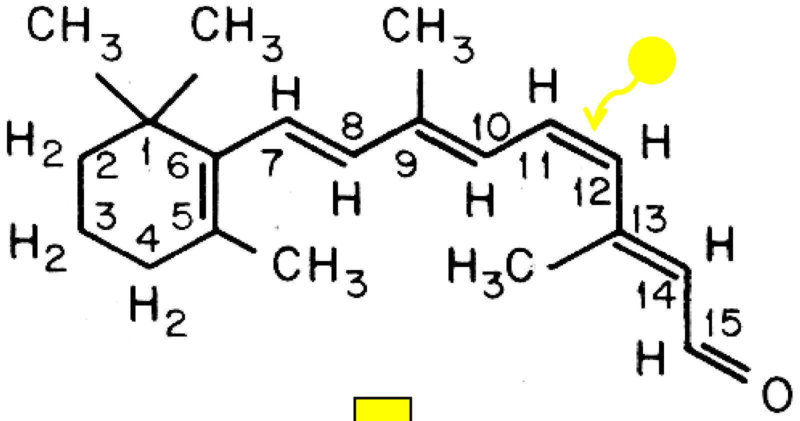
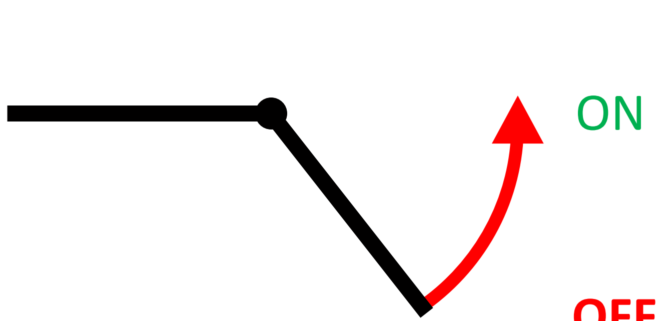
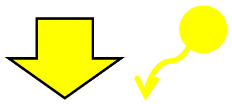
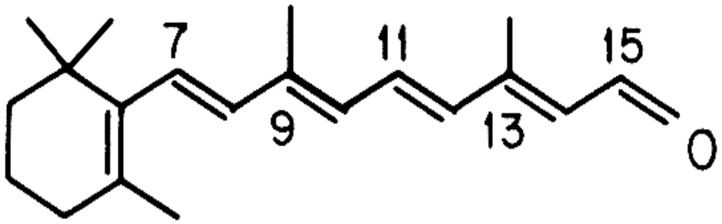


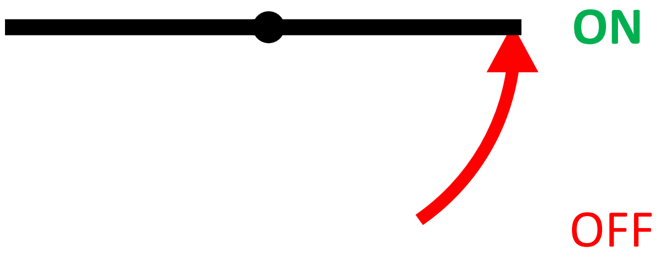


SAME EFFECT





all-*trans* retinal



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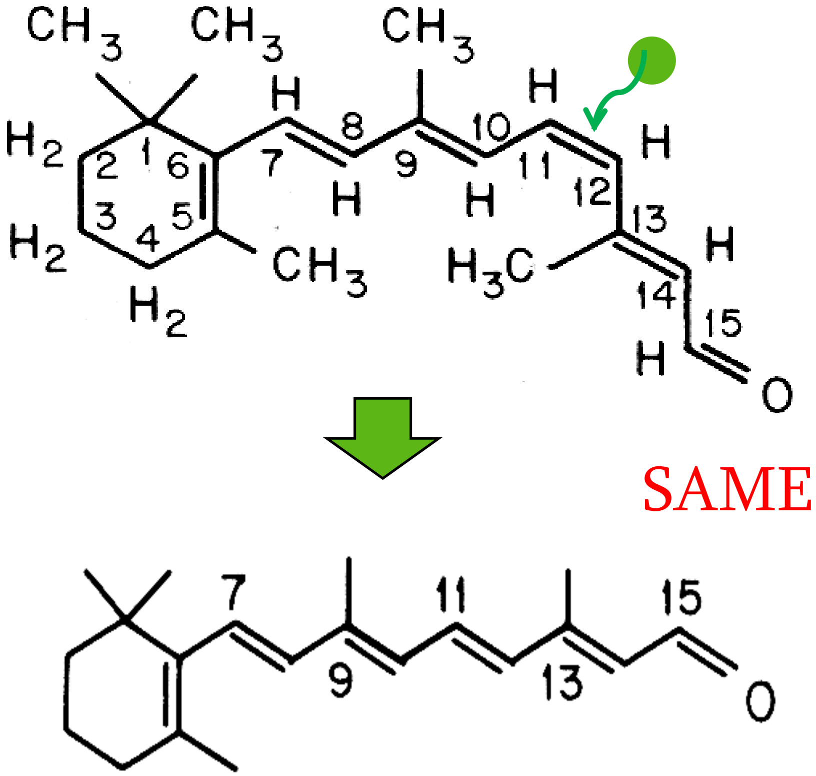

all-*trans* retinal

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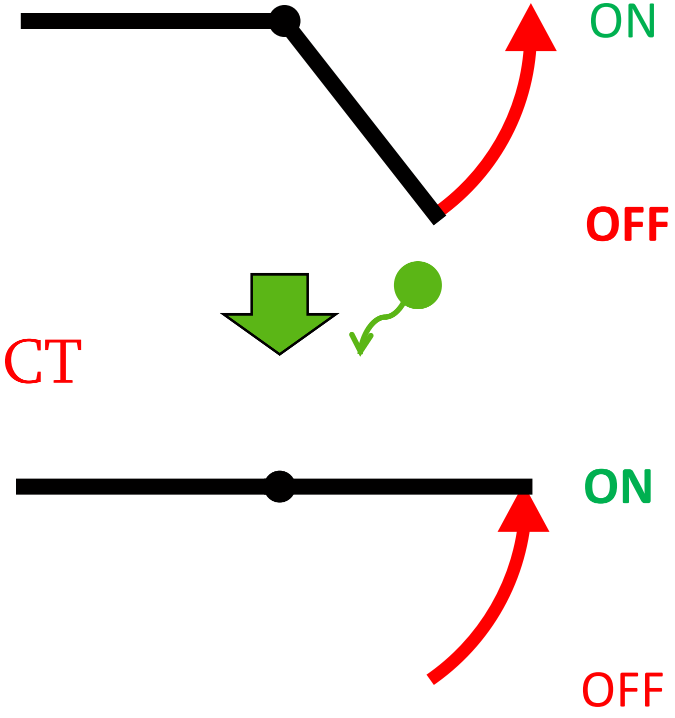

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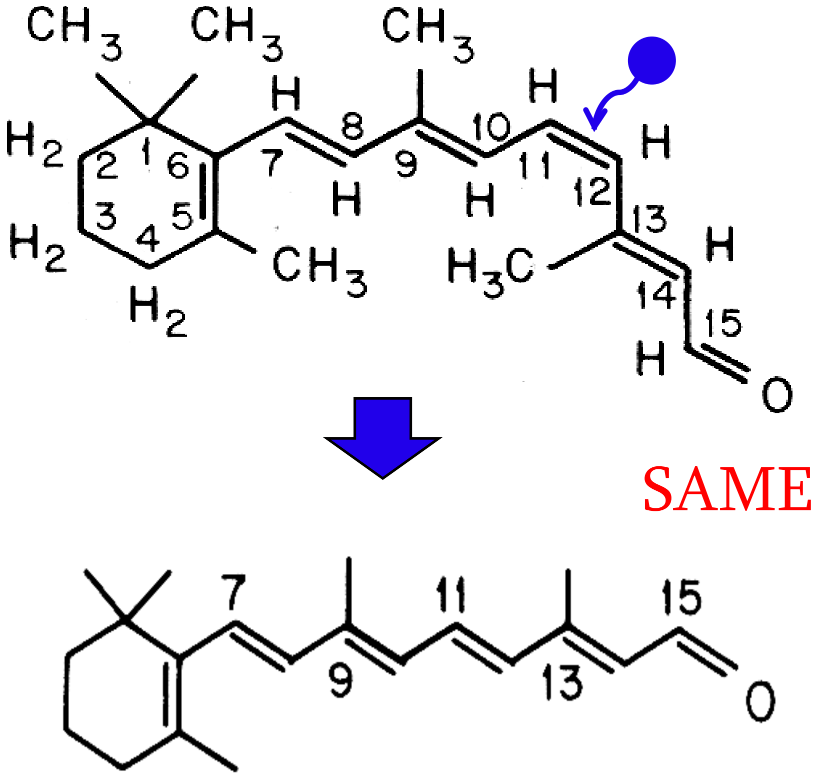
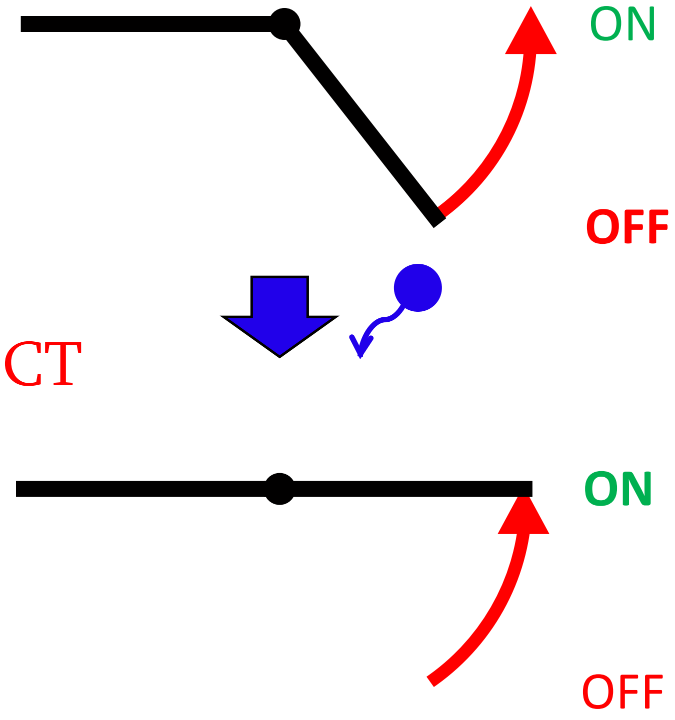


all-*trans* retinal

SAME EFFECT



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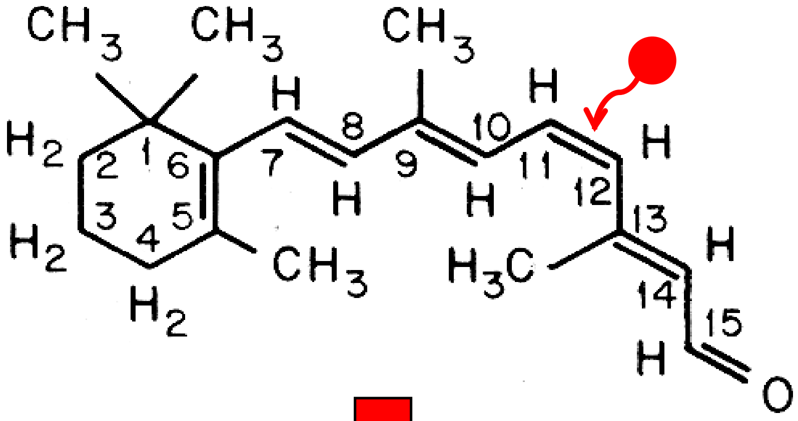
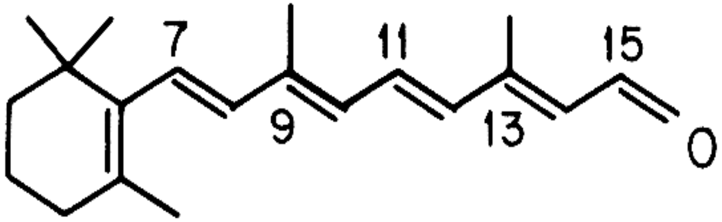
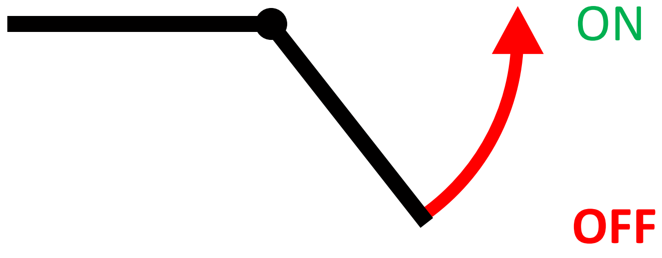
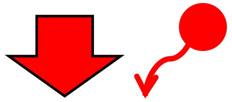


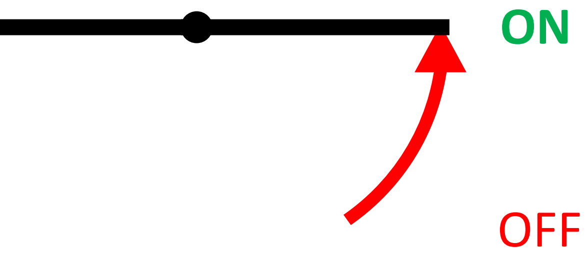
SAME EFFECT



all-*trans* retinal



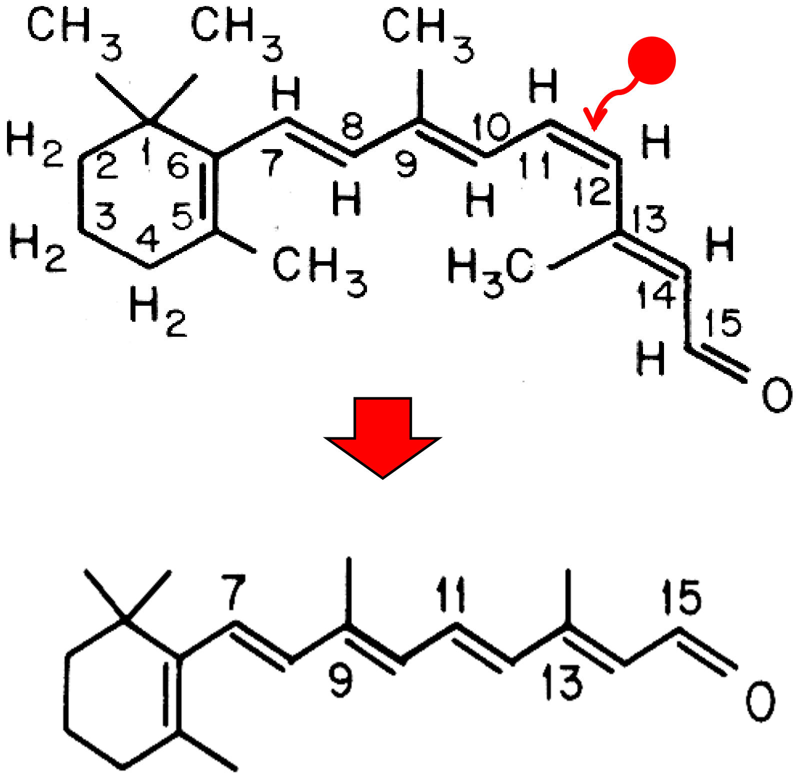




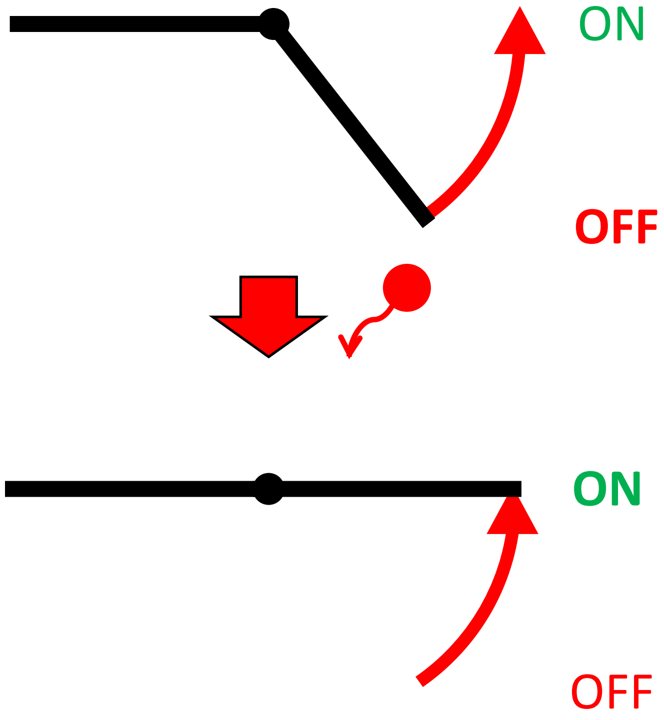
Chromophore

Can this process encode wavelength (colour)?

11-*cis* retinal



all-*trans* retinal

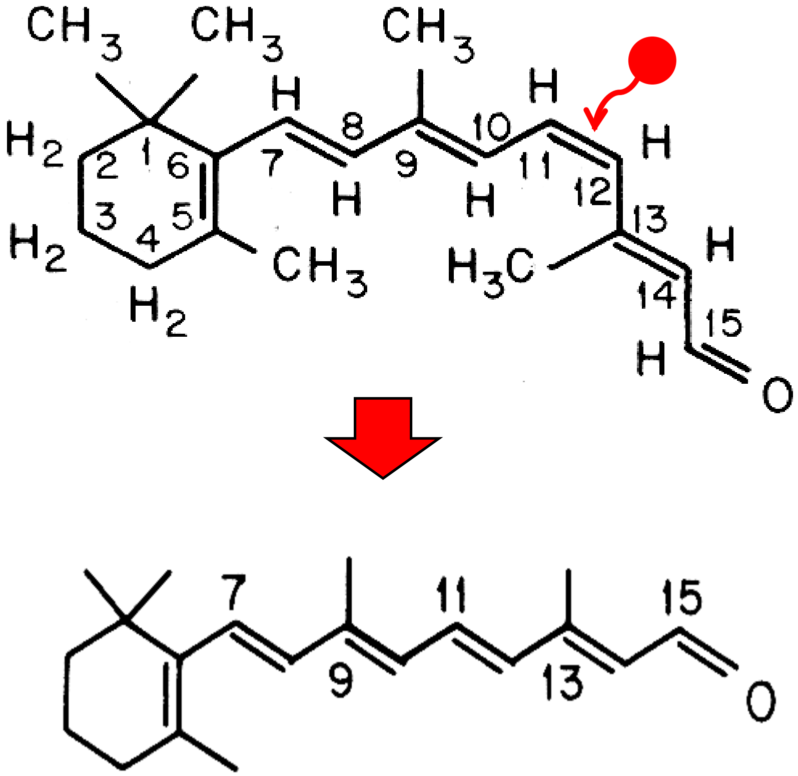


Chromophore

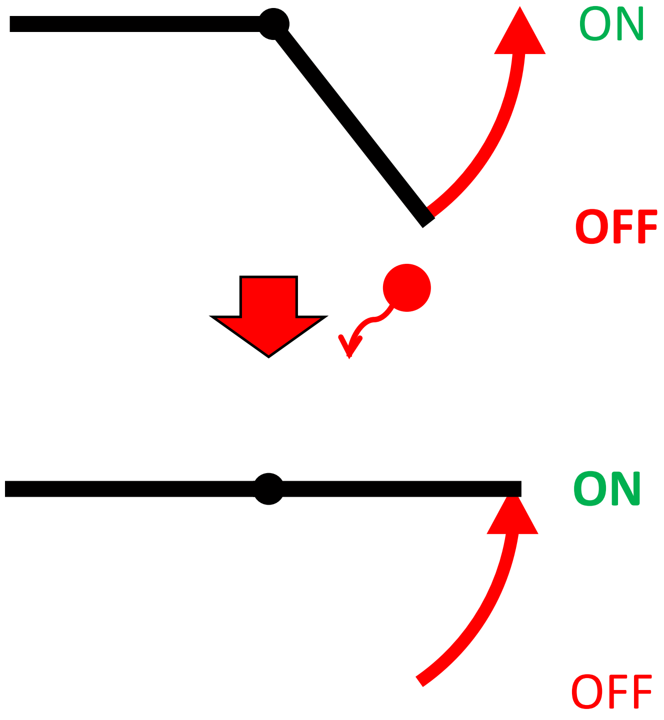
No, it cannot encode wavelength (colour)!

It is “UNIVARIANT”

11-*cis* retinal



all-*trans* retinal



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

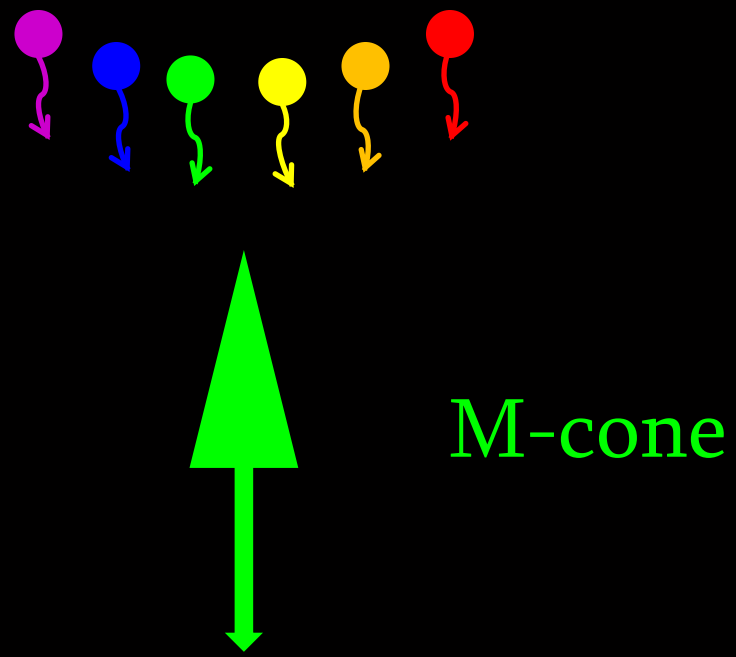
“UNIVARIANT”

What does univariance mean in practice?

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

UNIVARIANCE

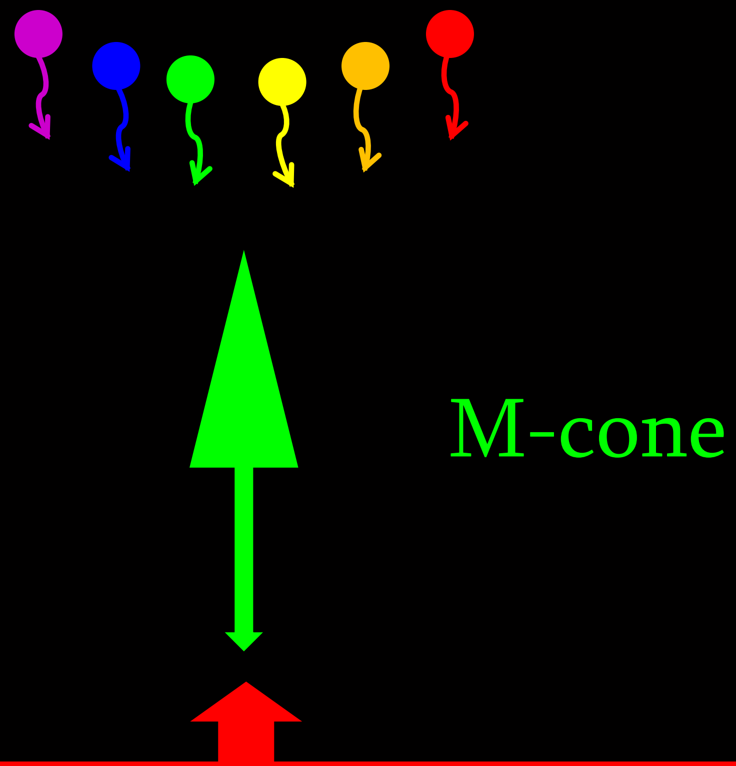
Crucially, the effect of any absorbed photon is *independent* of its wavelength.



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

UNIVARIANCE

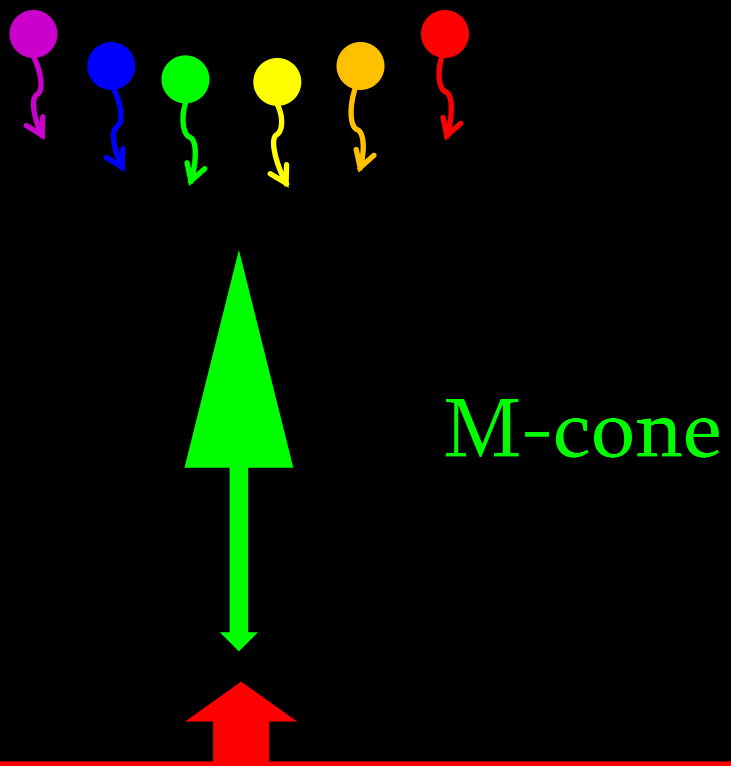
Crucially, the effect of any absorbed photon is *independent* of its wavelength.



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

UNIVARIANCE

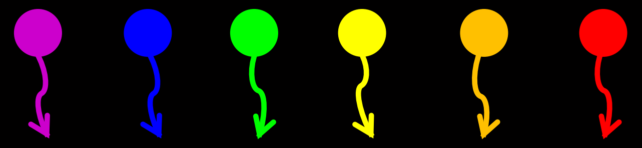
Crucially, the effect of any absorbed photon is *independent* of its wavelength.



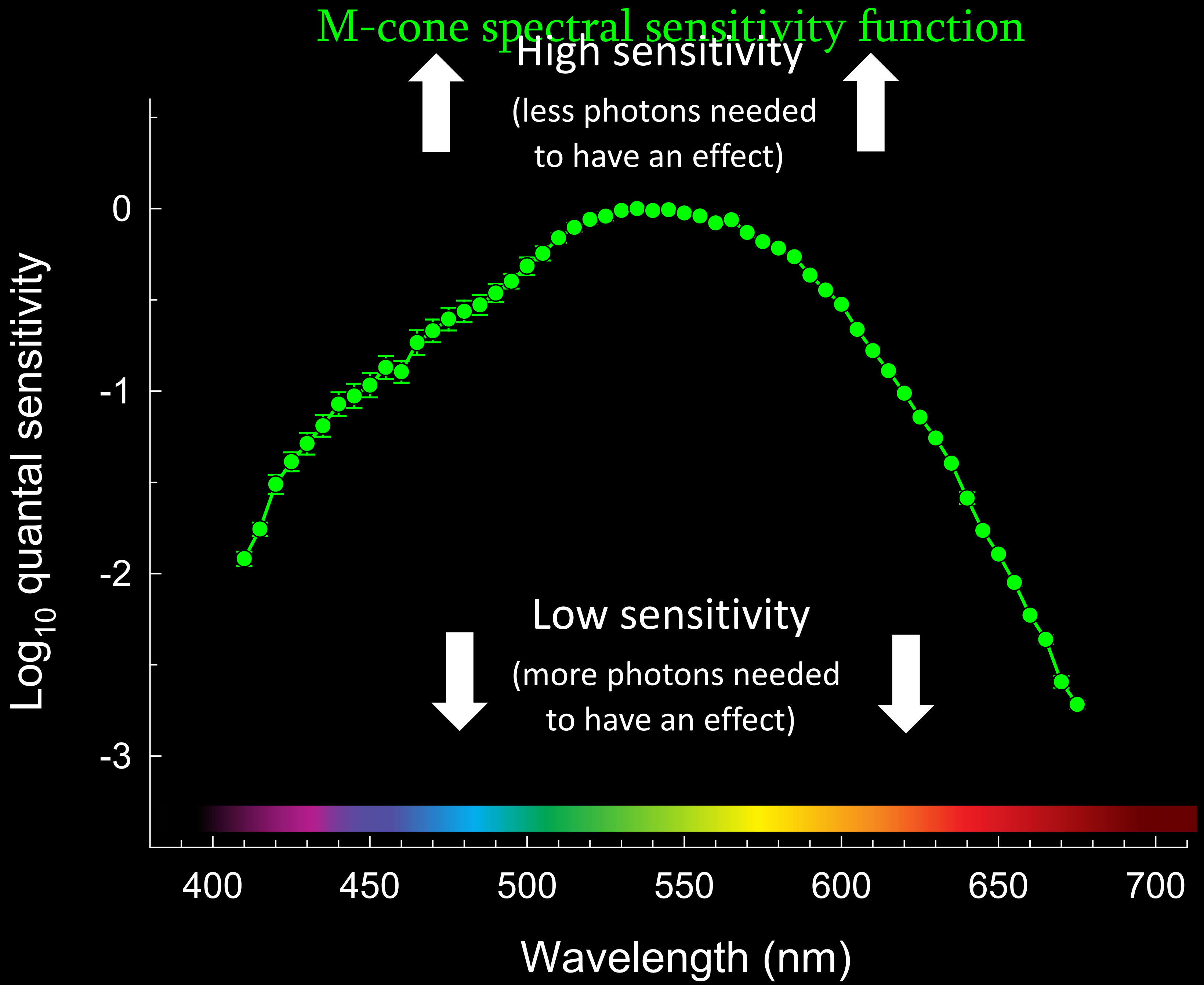
All the photoreceptor effectively does is to count photons.

UNIVARIANCE

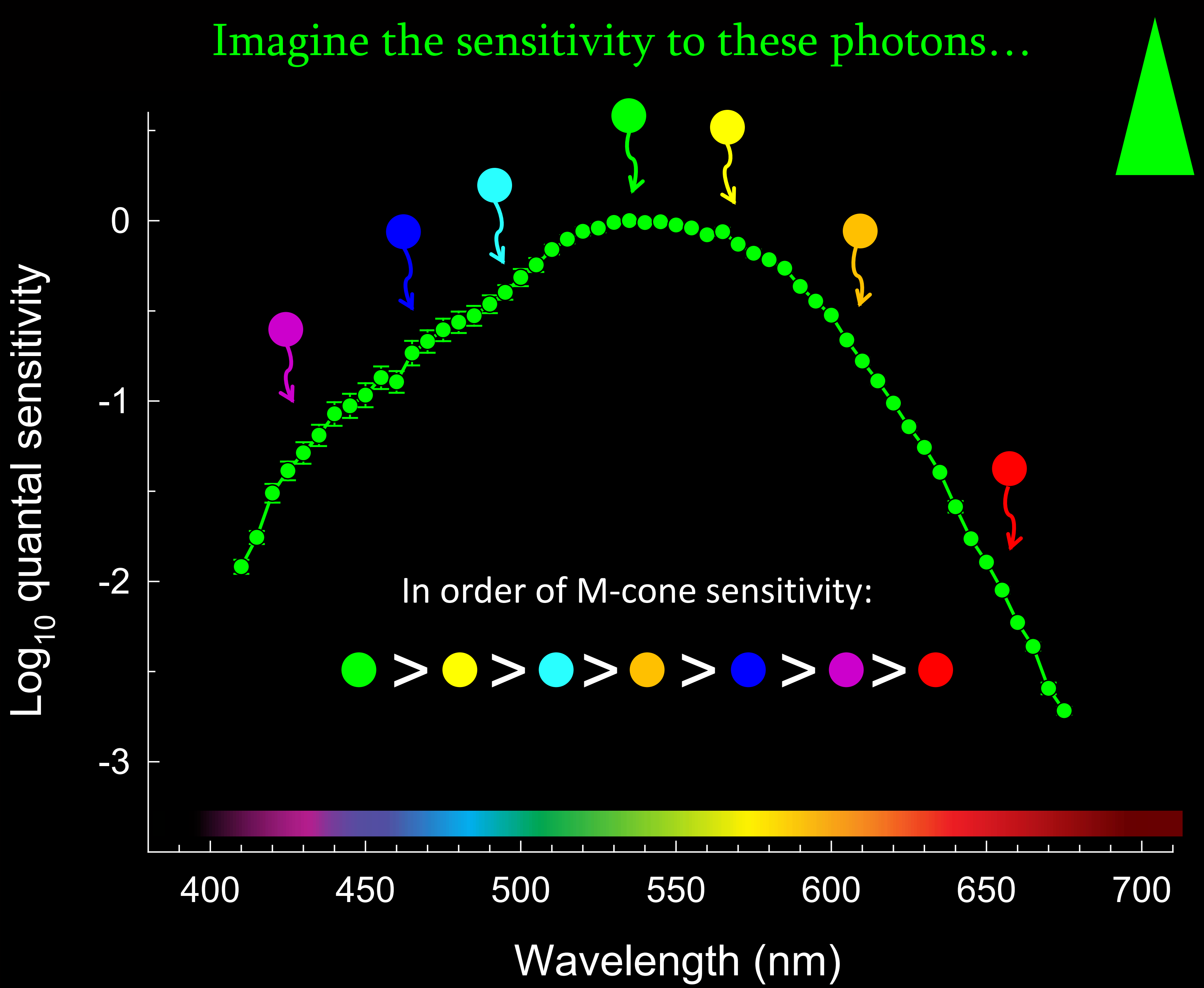
What does vary with wavelength is the probability that a photon will be absorbed.

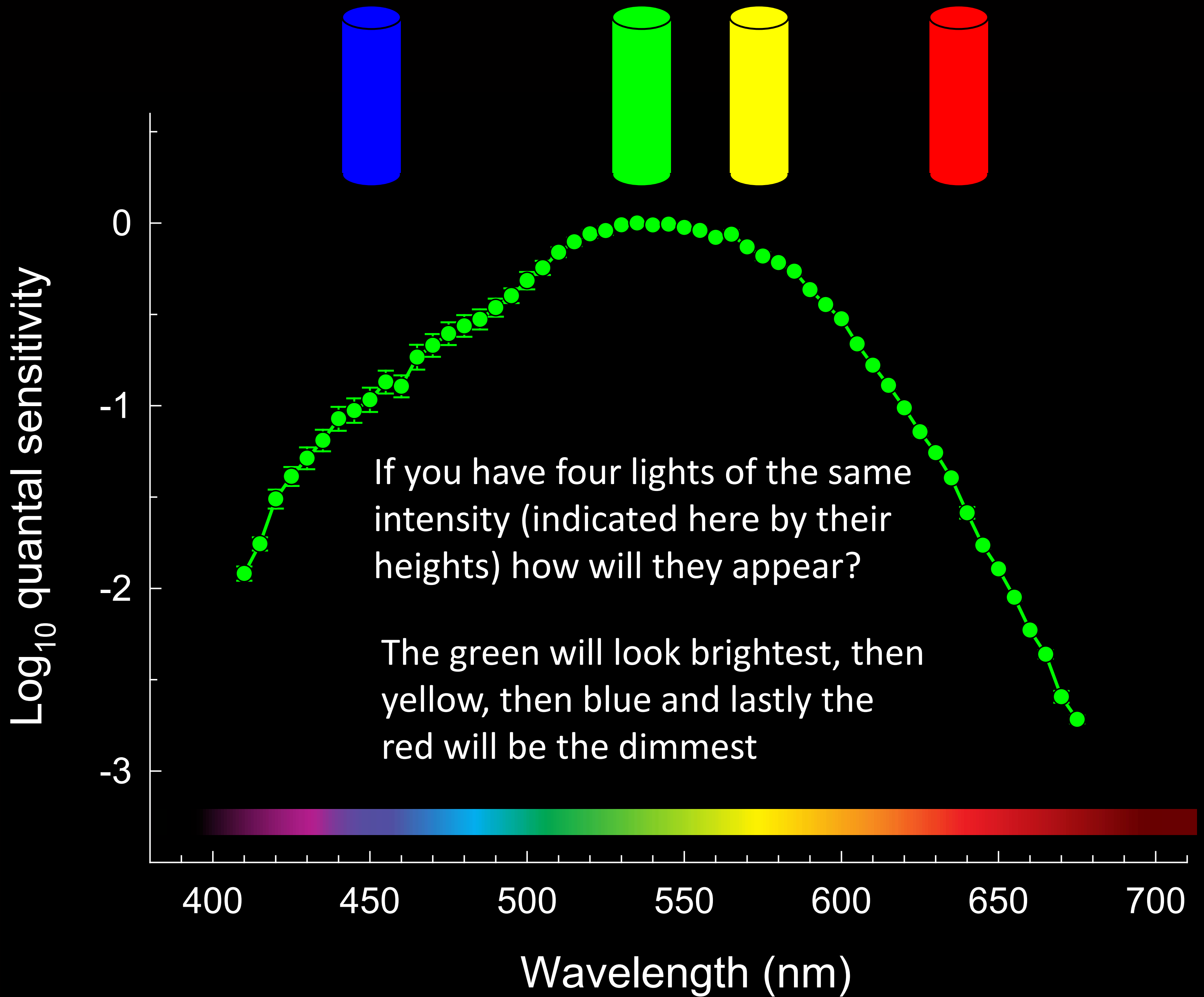


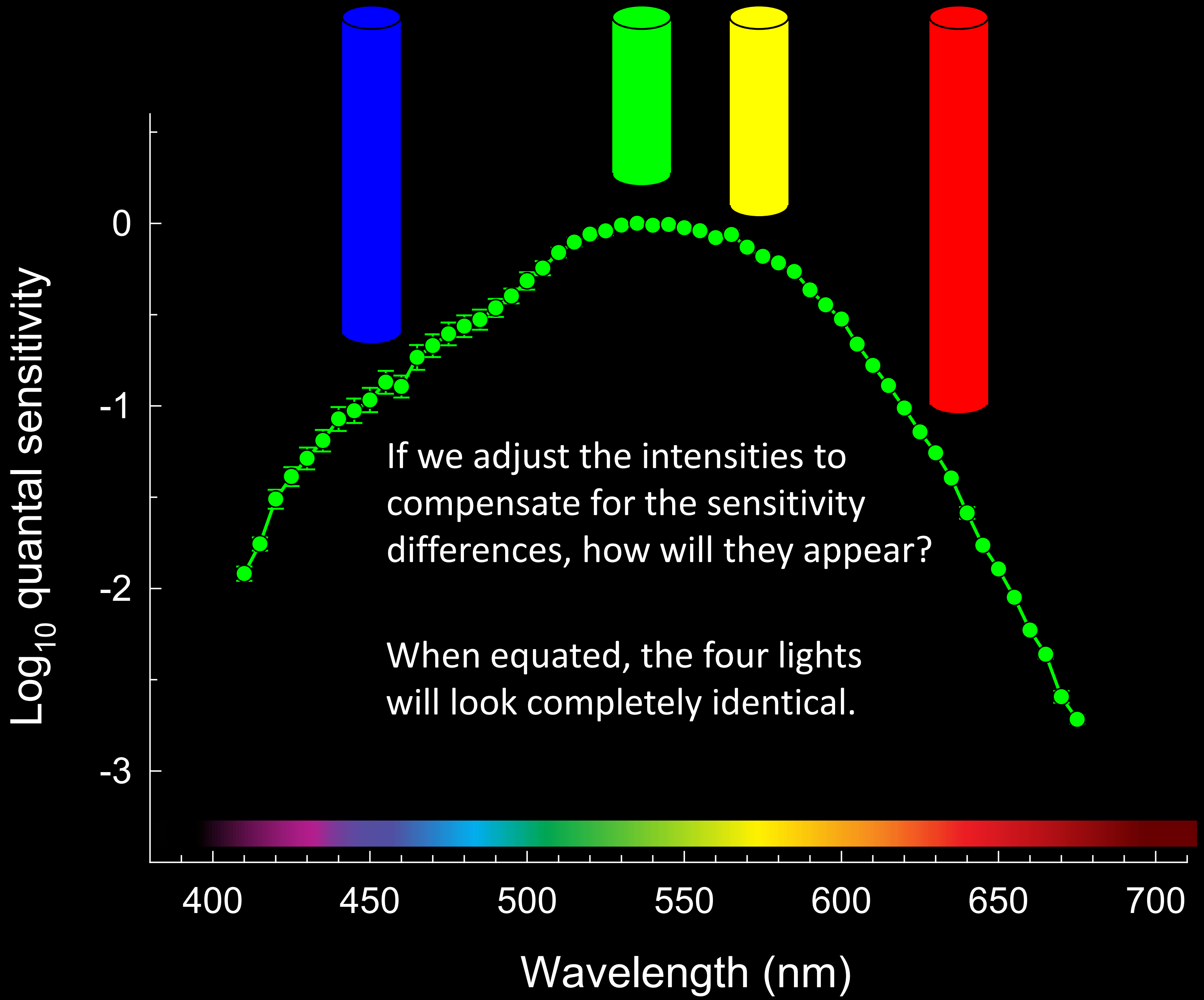
This is reflected in what is called a "spectral sensitivity function".

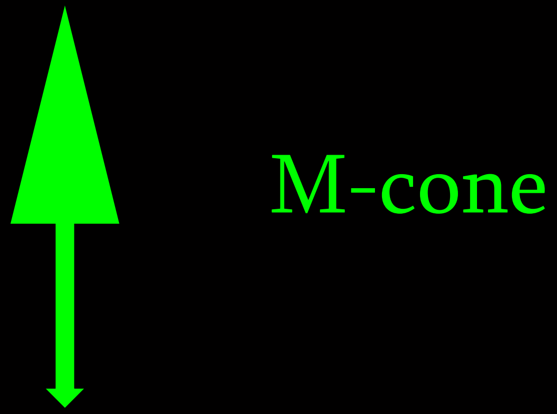


M-cone spectral sensitivity function
High sensitivity
(less photons needed
to have an effect)
Low sensitivity
(more photons needed
to have an effect)
Log10 quantal sensitivity
0
-1
-2
-3
400
450
500
550
600
650
700
Wavelength (nm)


Imagine the sensitivity to these photons…
Log10 quantal sensitivity
0
-1
-2
-3
In order of M-cone sensitivity:
> > > > > >
400
450
500
550
600
650
700
Wavelength (nm)


Log$_{10}$ quantal sensitivity
0
-1
-2
-3
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 appear?
The green will look brightest, then yellow, then blue and lastly the red will be the dimmest

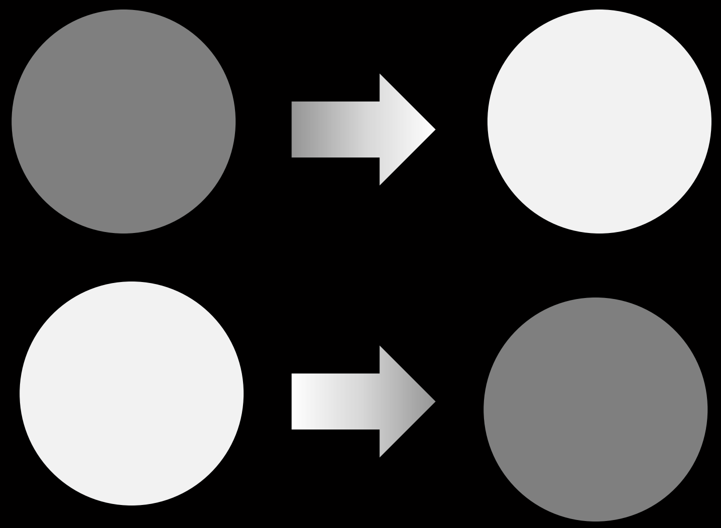

0
-1
-2
-3
Log10 quantal sensitivity
If we adjust the intensities to compensate for the sensitivity differences, how will they appear?
When equated, the four lights will look completely identical.
400
450
500
550
600
650
700
Wavelength (nm)



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.

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, we would be colour-blind…

Examples: night vision, blue cone monochromats

With two, we are dichromatic:

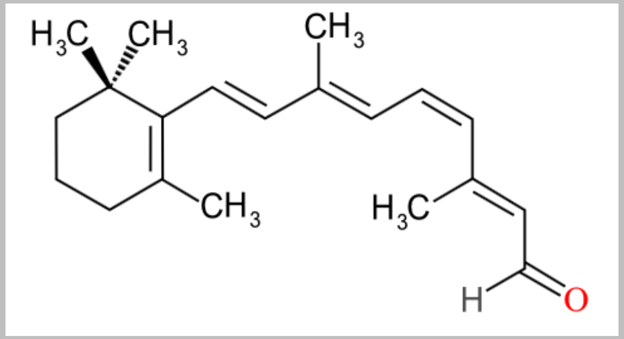
Protanopia (missing L-cone)

Tritanopia (missing S-cone)

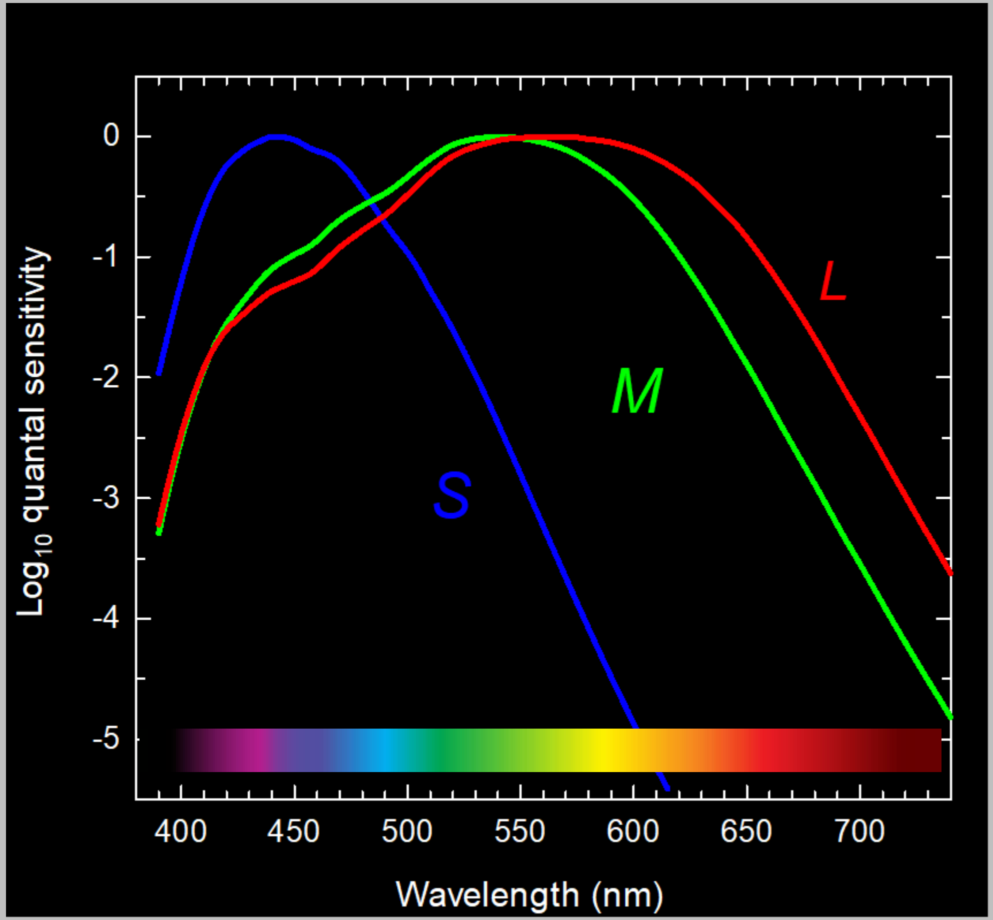
Deuteranopia (missing M-cone)

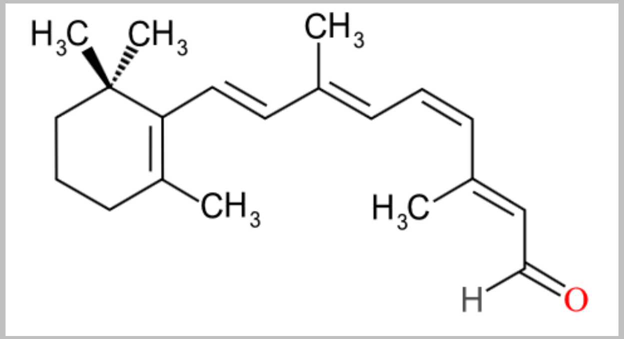
Simulations from Sharpe, Stockman, Jägle & Nathans, 1999

With three cone photoreceptors, our colour vision is trichromatic…

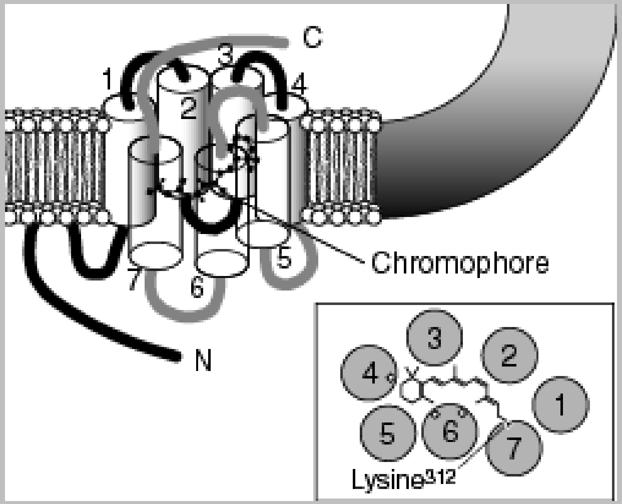


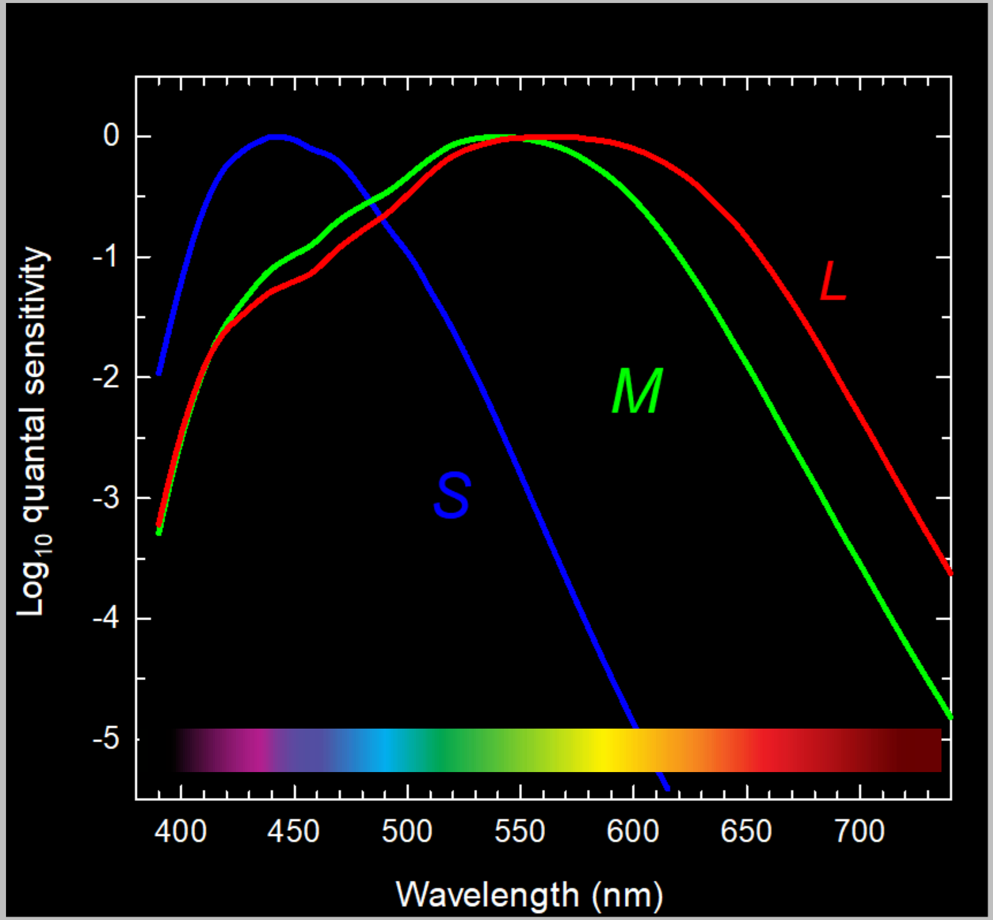
The three cones (and rods) have different spectral sensitivities, but they have the same chromophore (11-*cis*-retinal), so why are the spectral sensitivities different?





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



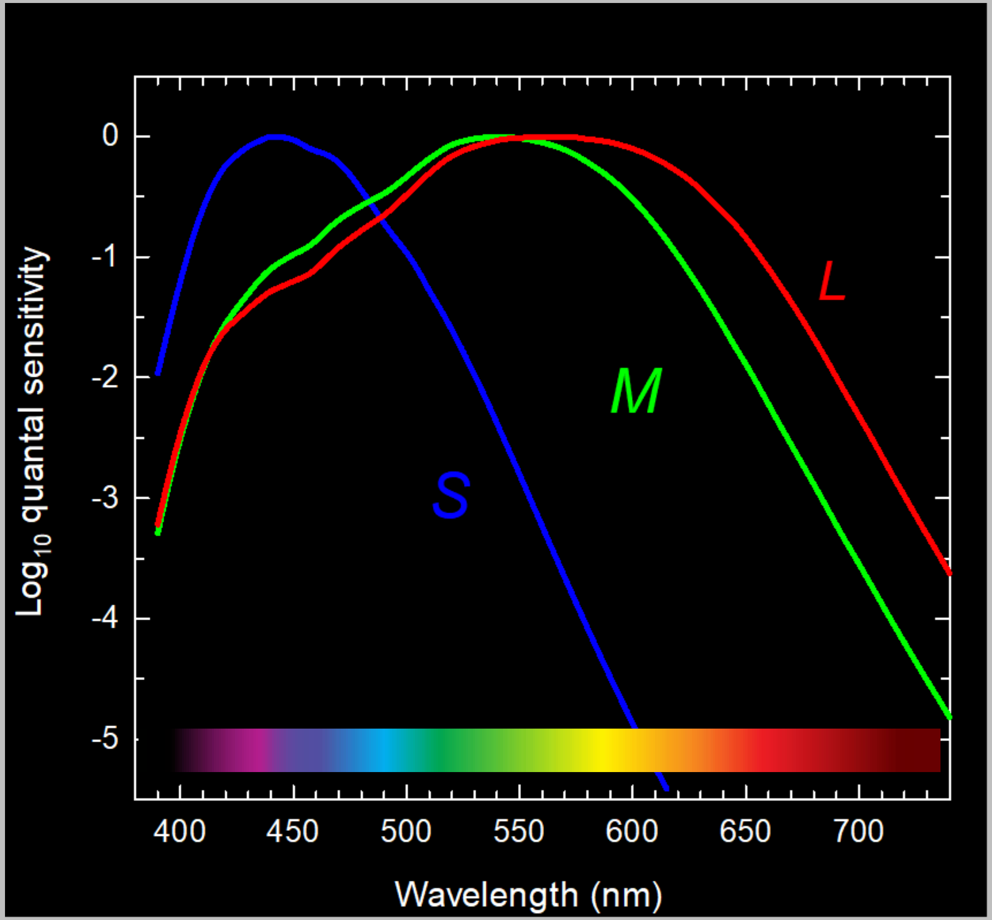


$$E = hc/\lambda$$

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

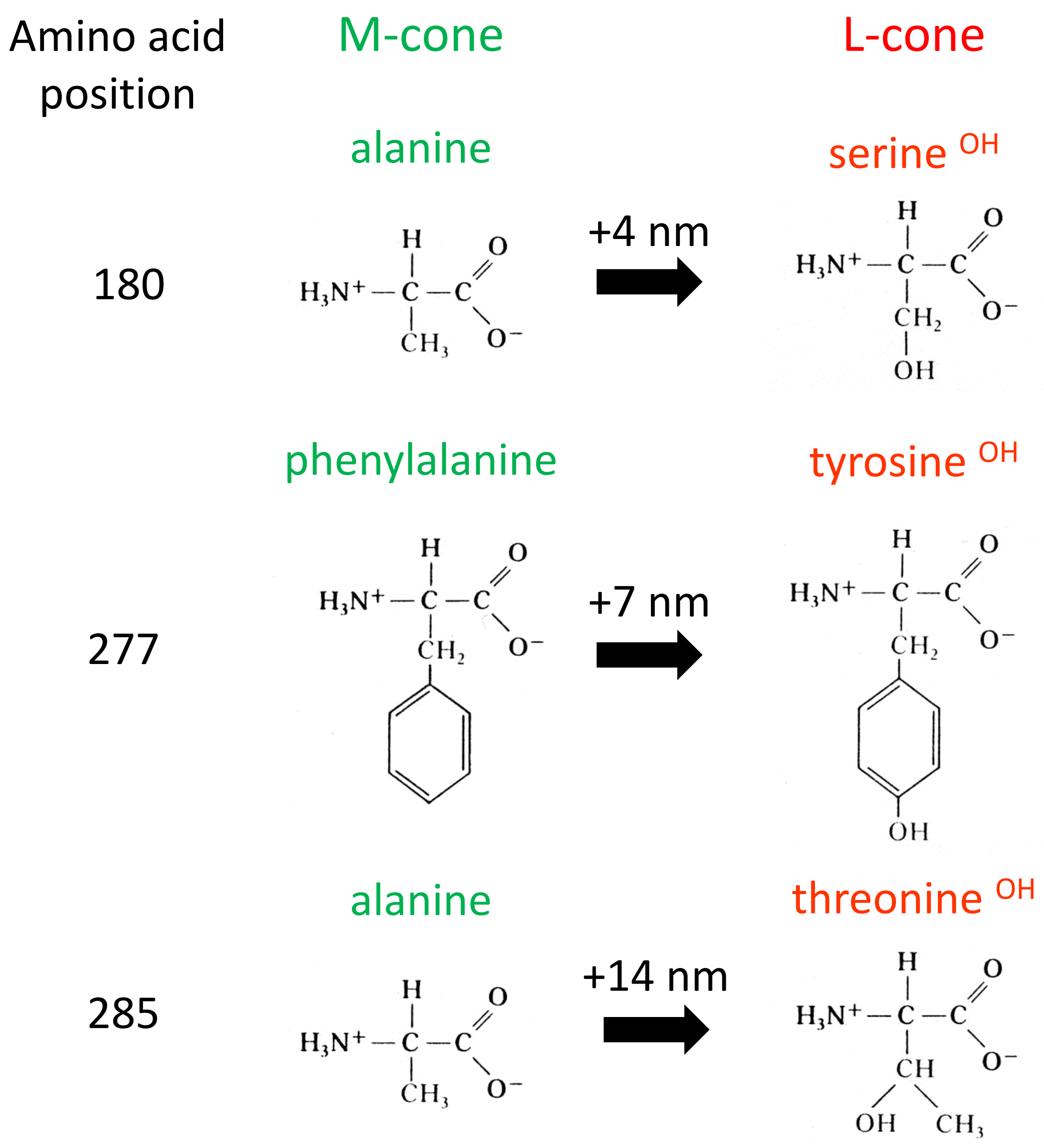
$h = 6.62606957 \times 10^{-34}$ J.s

$c = 2.99792458 \times 10^{8}$ 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

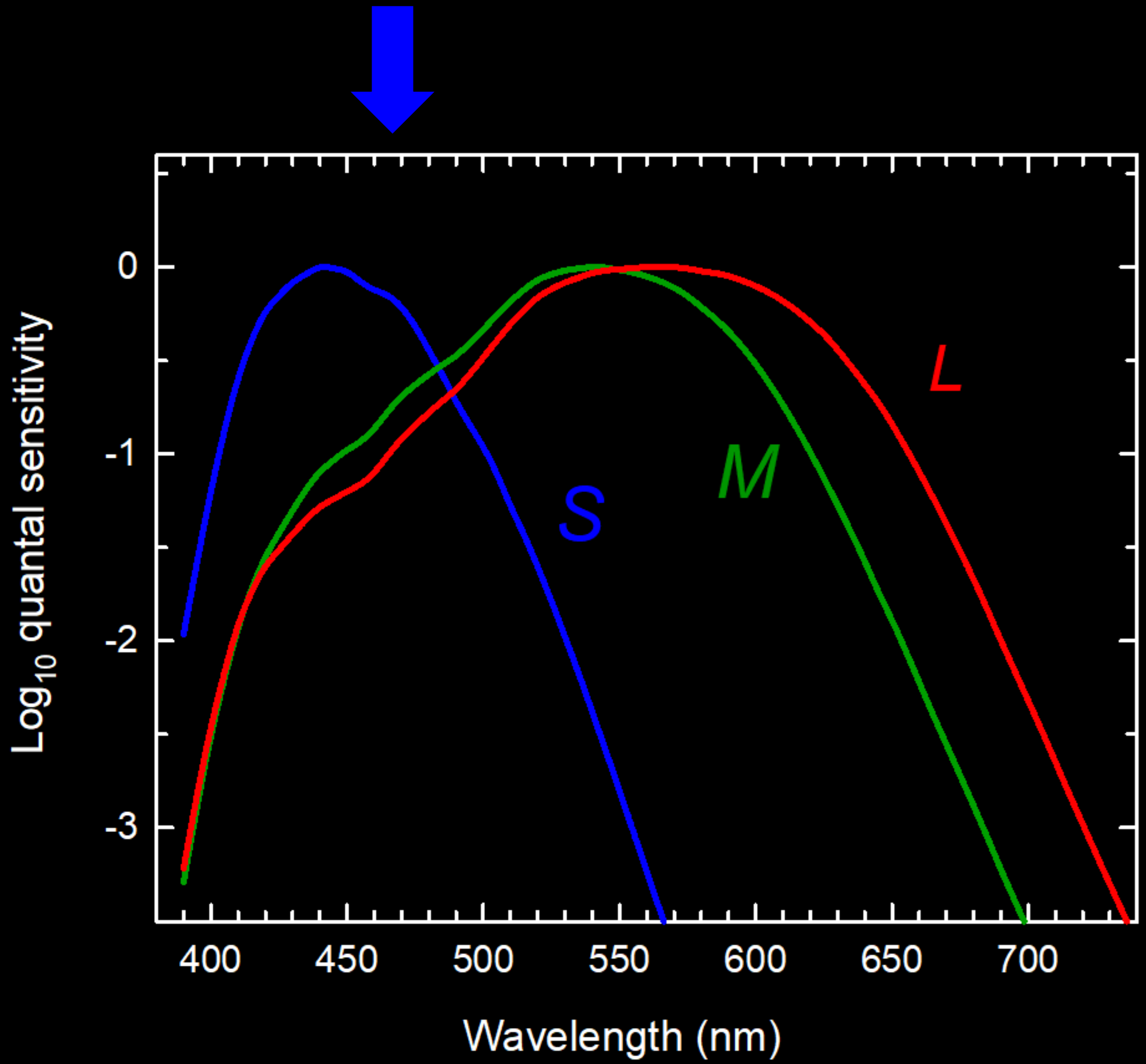
The spectral sensitivity differences between the M- and L-cone, for example, are due to three amino acid substitutions.



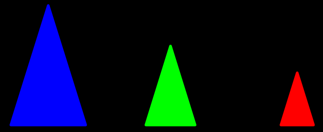
So, if each photoreceptor is colour-blind (univariant), how do we see colour?

Or to put it another way: How is colour encoded at the input to the visual system?

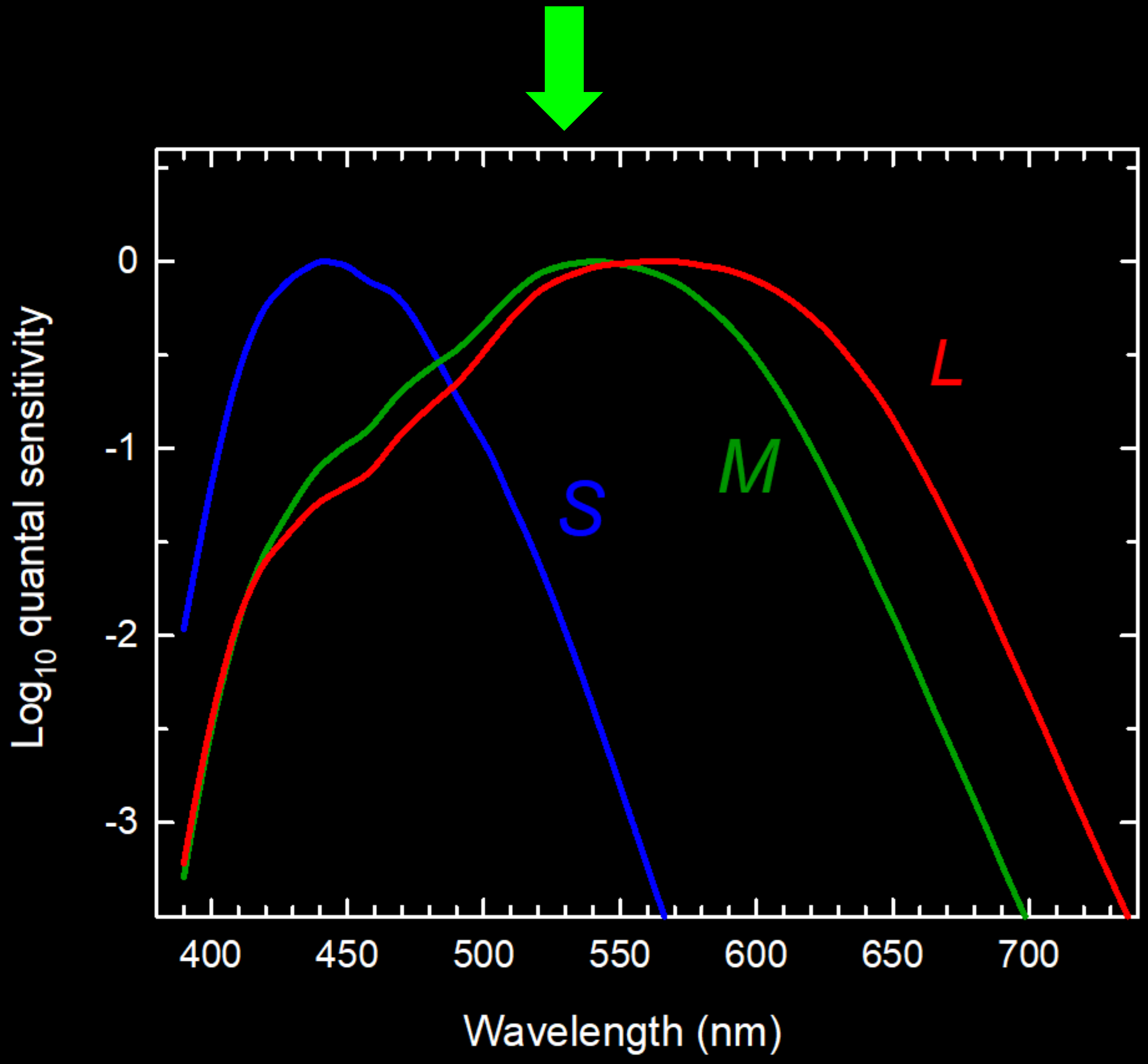
Colour is encoded by the relative cone outputs



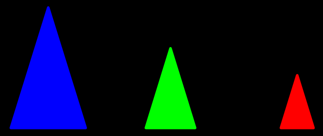
Blue light



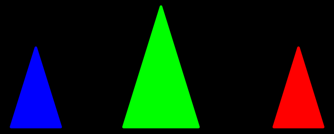
Colour is encoded by the relative cone outputs



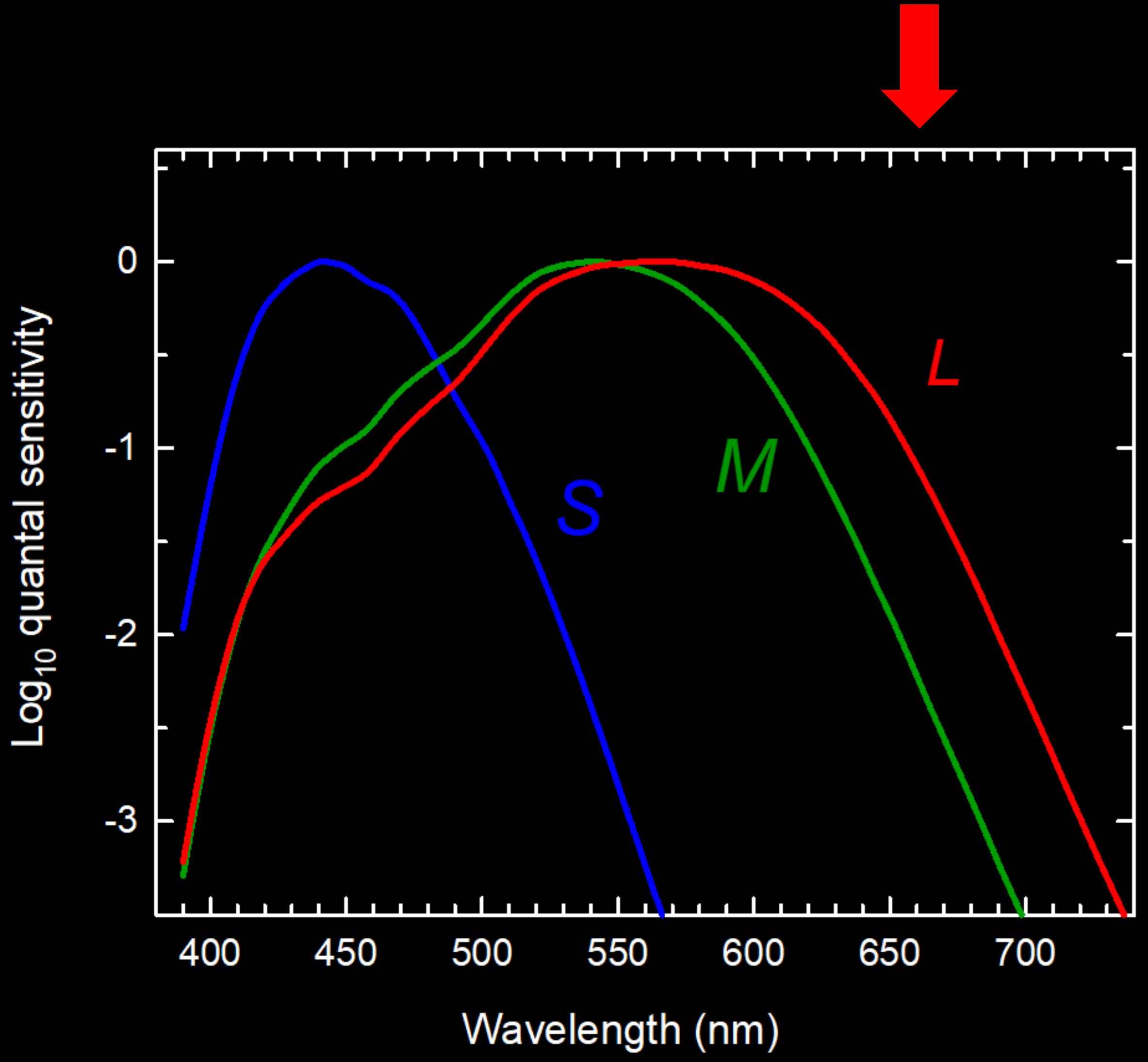
Blue light

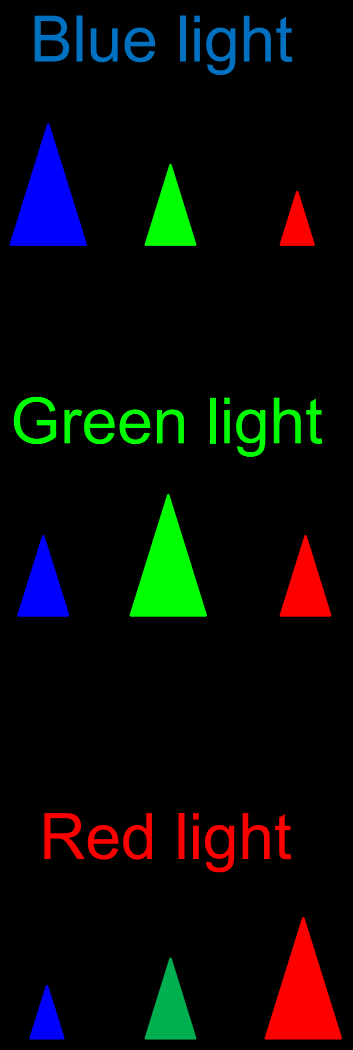


Green light

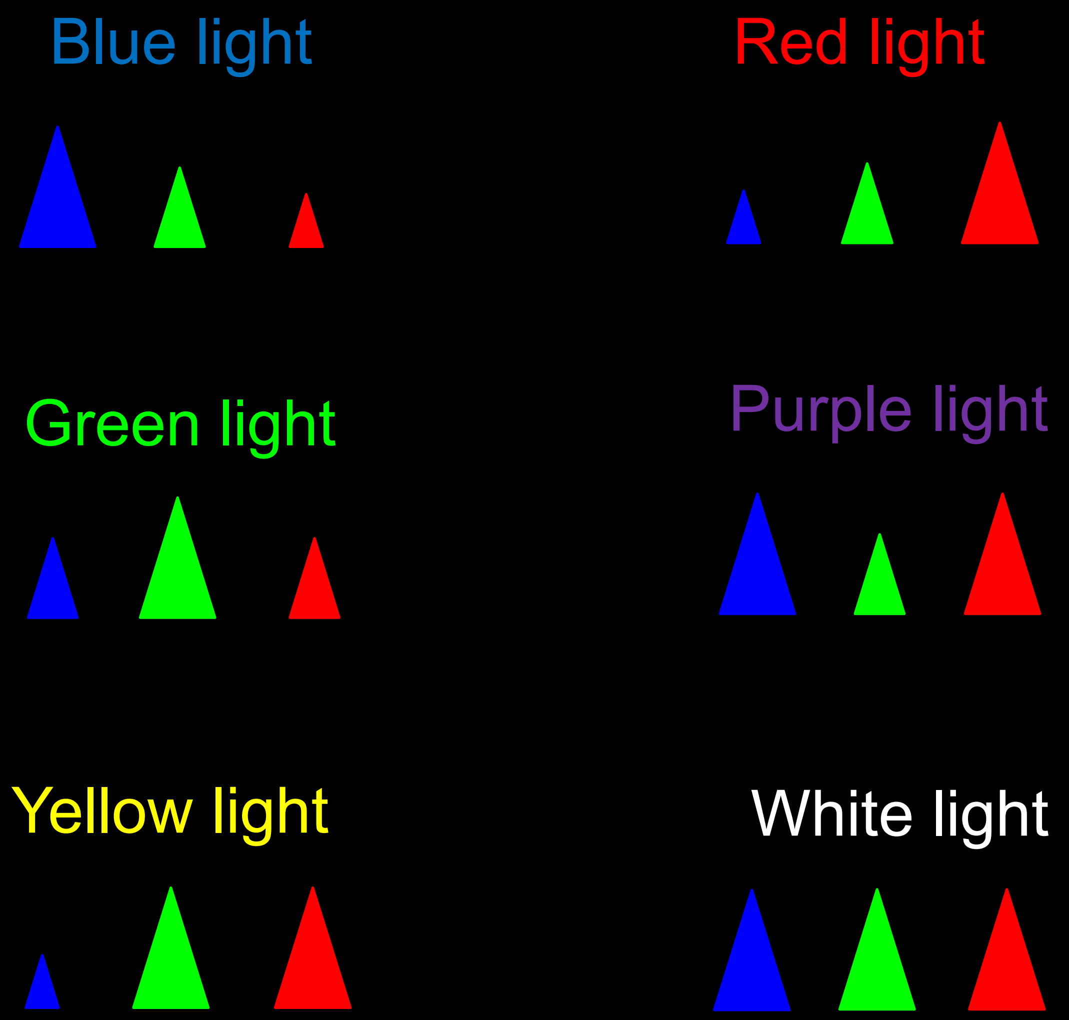


Colour is encoded by the relative cone outputs



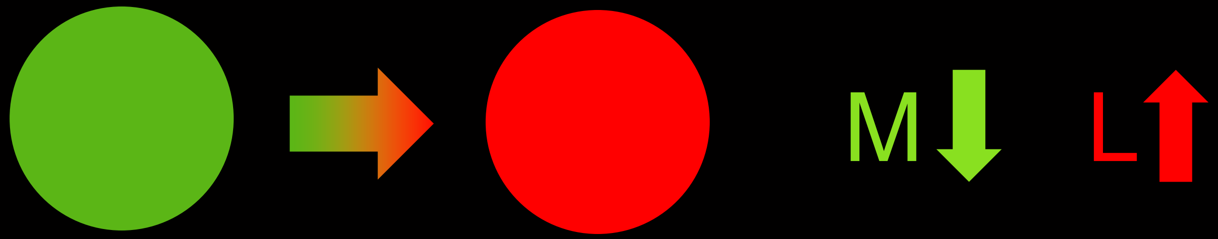


Colour is encoded by the relative cone outputs

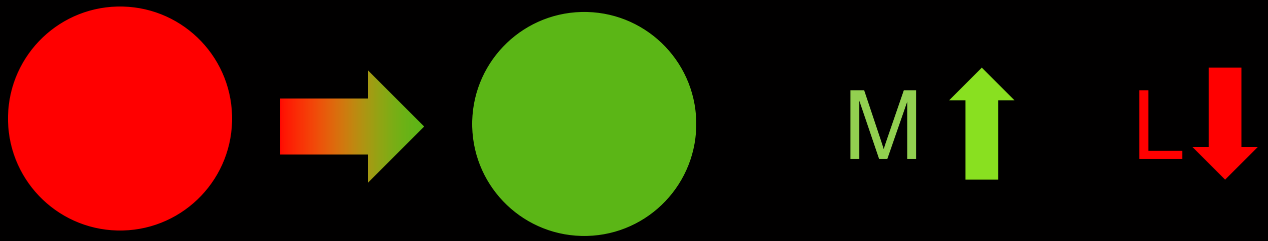


TRICHROMACY

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…

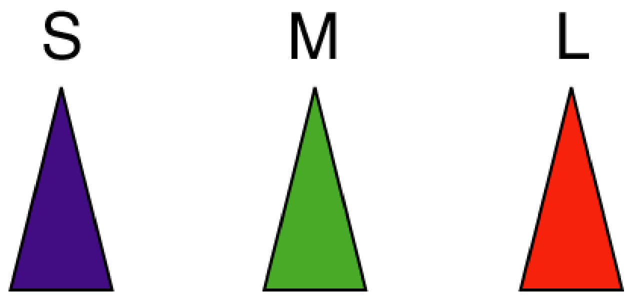
Trichromacy actually means our colour vision is limited

- We confuse many pairs of colours that are spectrally very different. Such pairs are known as metameric pairs.

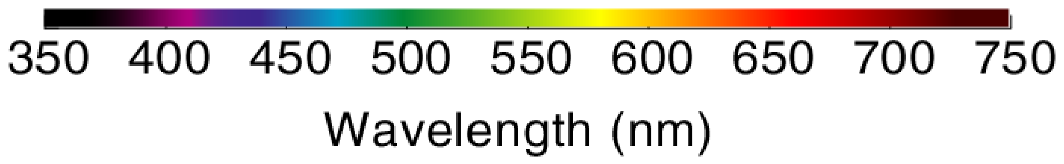
- Many of these confusions would be obvious to a being with 4 cone photoreceptors—just as the confusions of colour deficient people are obvious to us.

DETERMINING CONE SPECTRAL SENSITIVITIES

In other words…

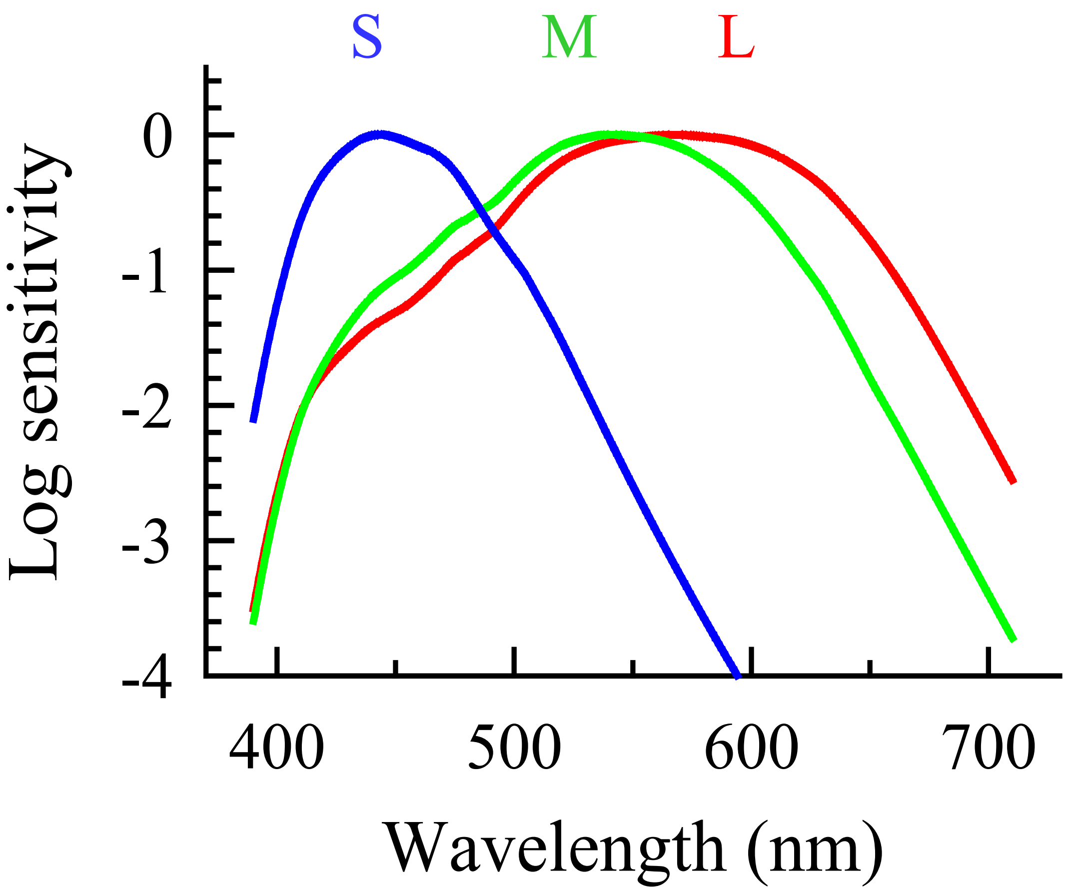


How can we measure how the sensitivity of each cone type varies with wavelength (or spectral colour)?



The cone spectral sensitivities overlap extensively throughout the spectrum.

Consequently, we have to use special subjects or special conditions to be able isolate the the response of a single cone type.



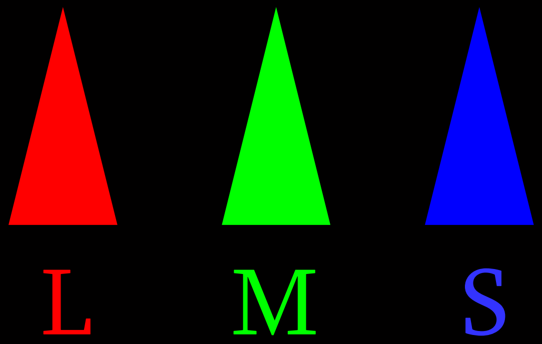
M- and L-cone measurements

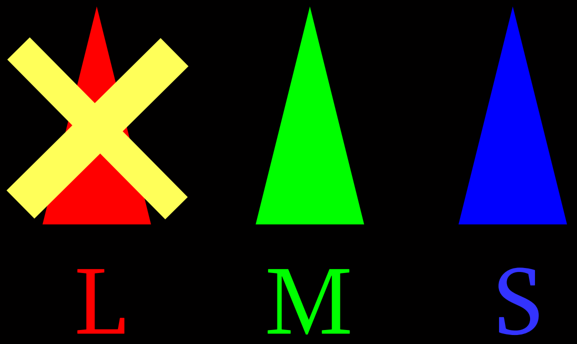
Use two special types of subjects:

- Deuteranopes
- Protanopes

Normal

Protanope

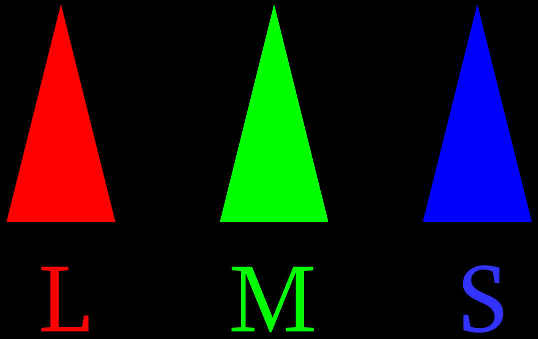


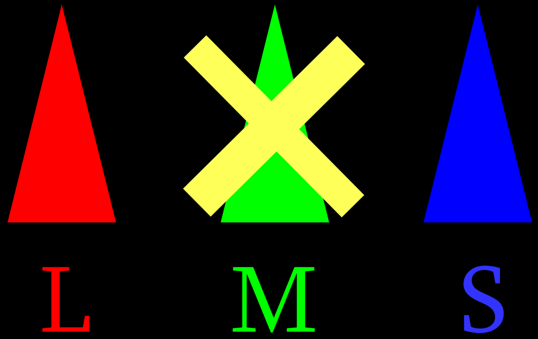


Protanopia

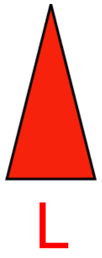
Normal

Deuteranope

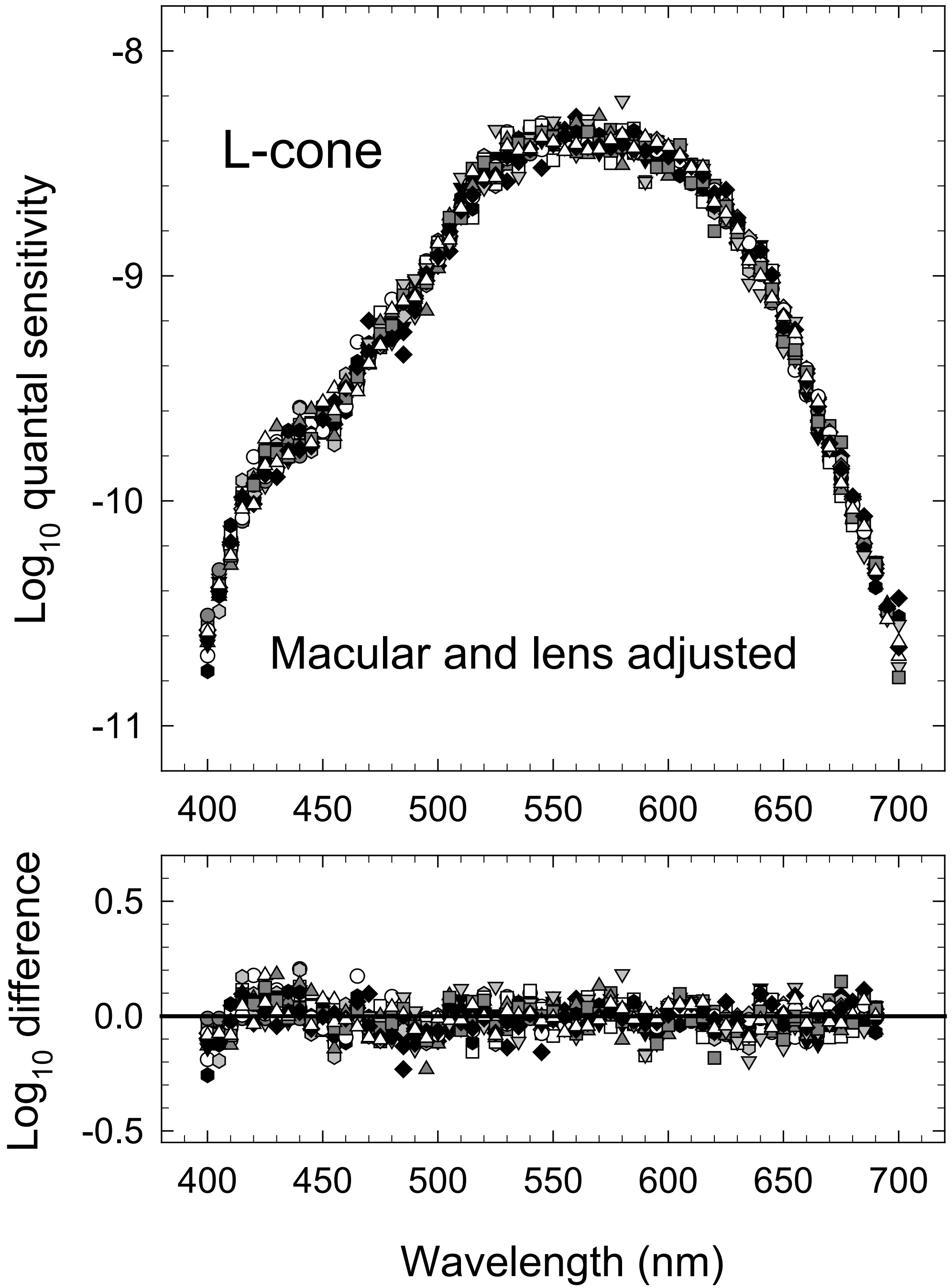


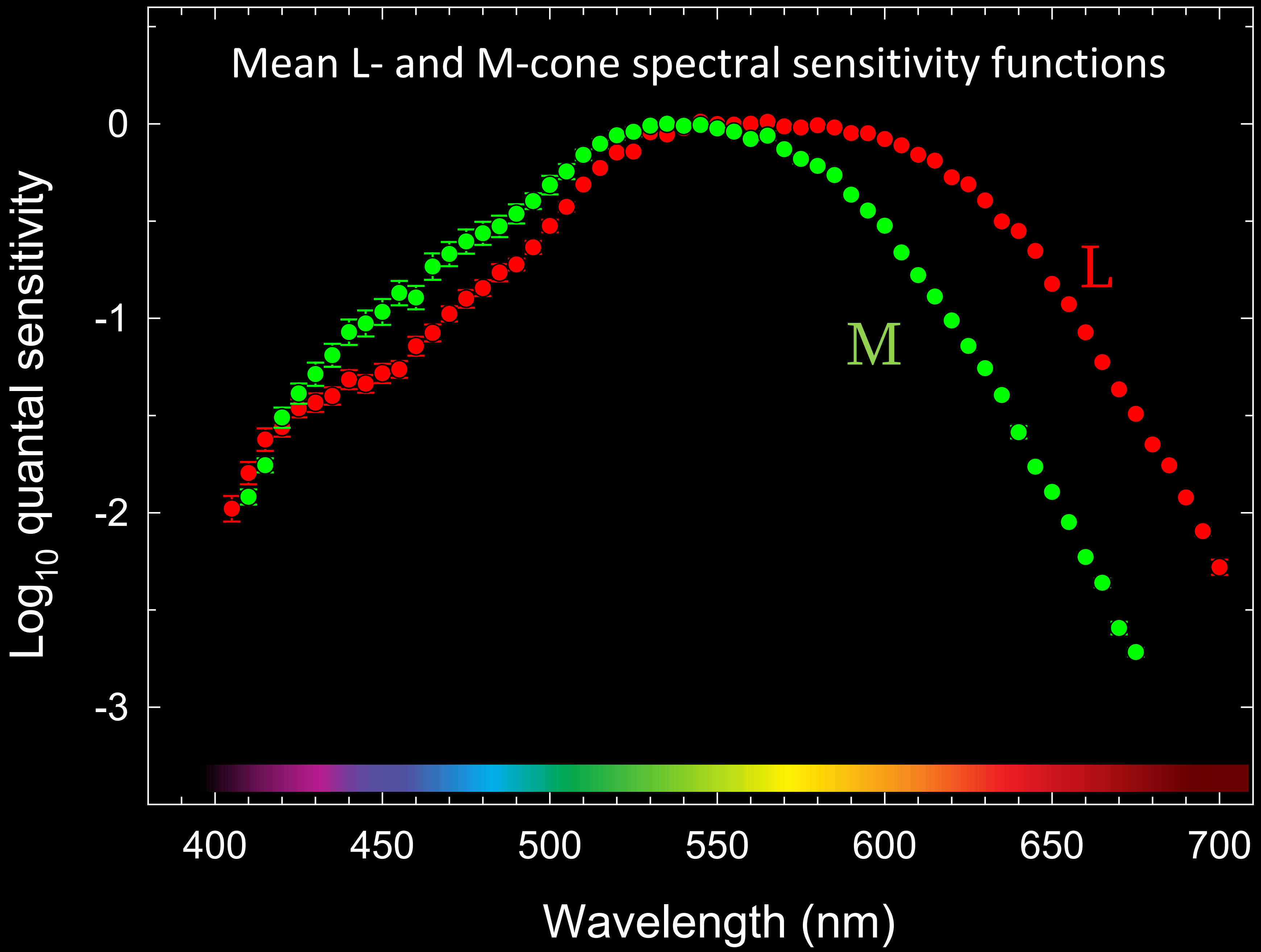


Deuteranopia



(Adjusted) L-cone data





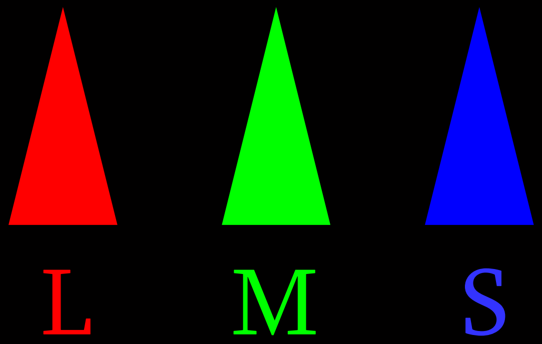
Mean L- and M-cone spectral sensitivity functions
0
-1
-2
-3
Log10 quantal sensitivity
L
M
400
450
500
550
600
650
700
Wavelength (nm)

S-cone measurements

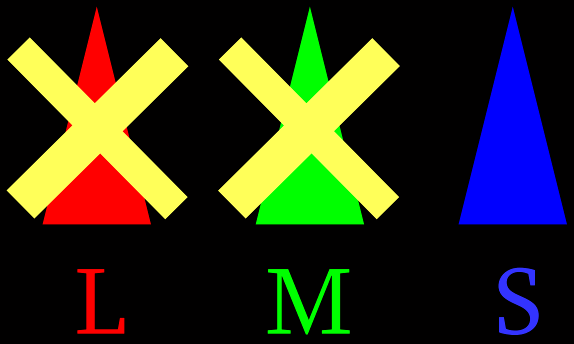
Two types of subjects:

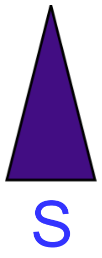
- S-cone (or blue cone) monochromats
- Colour normals

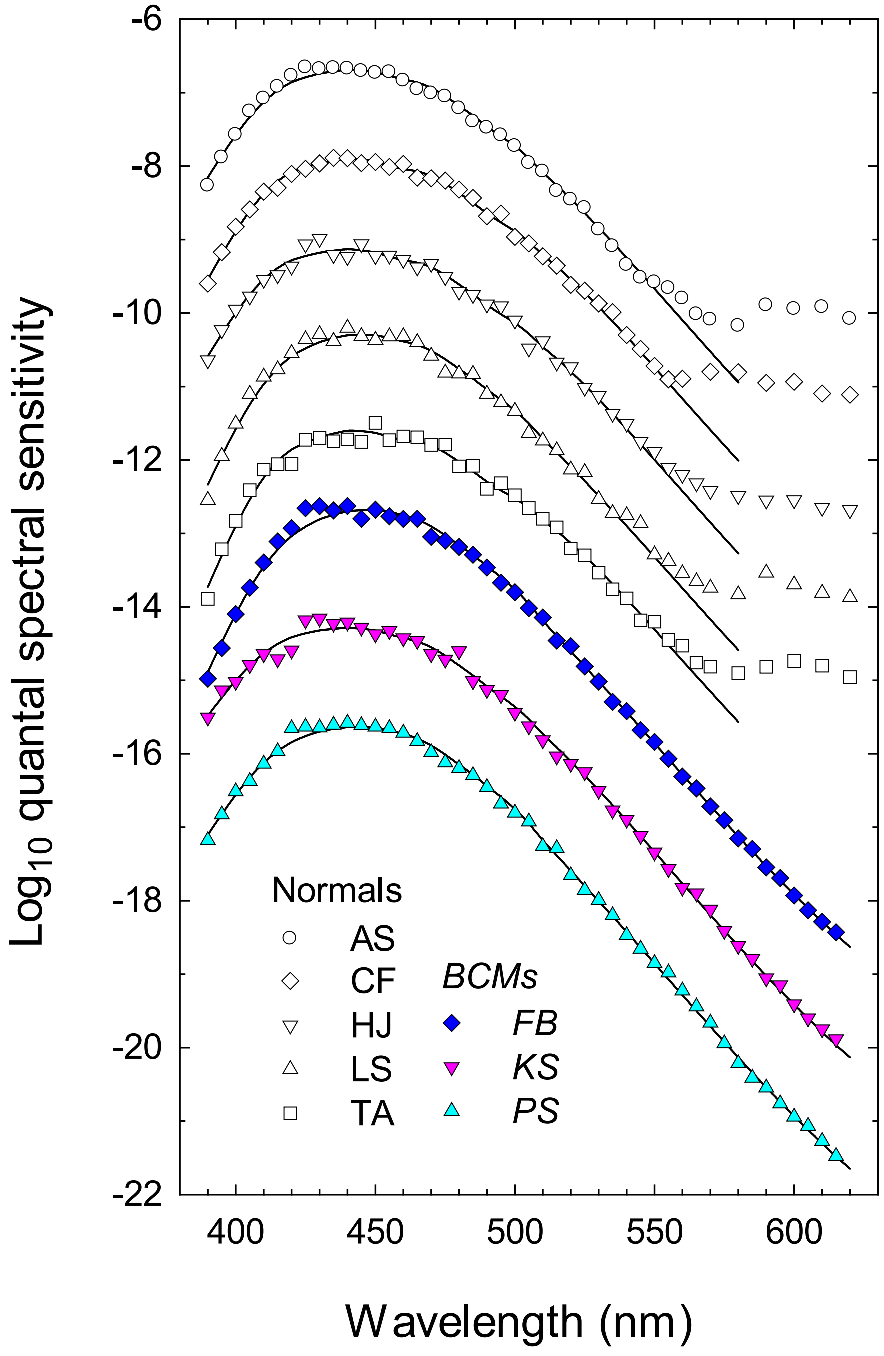
Normal



S-cone monochromat

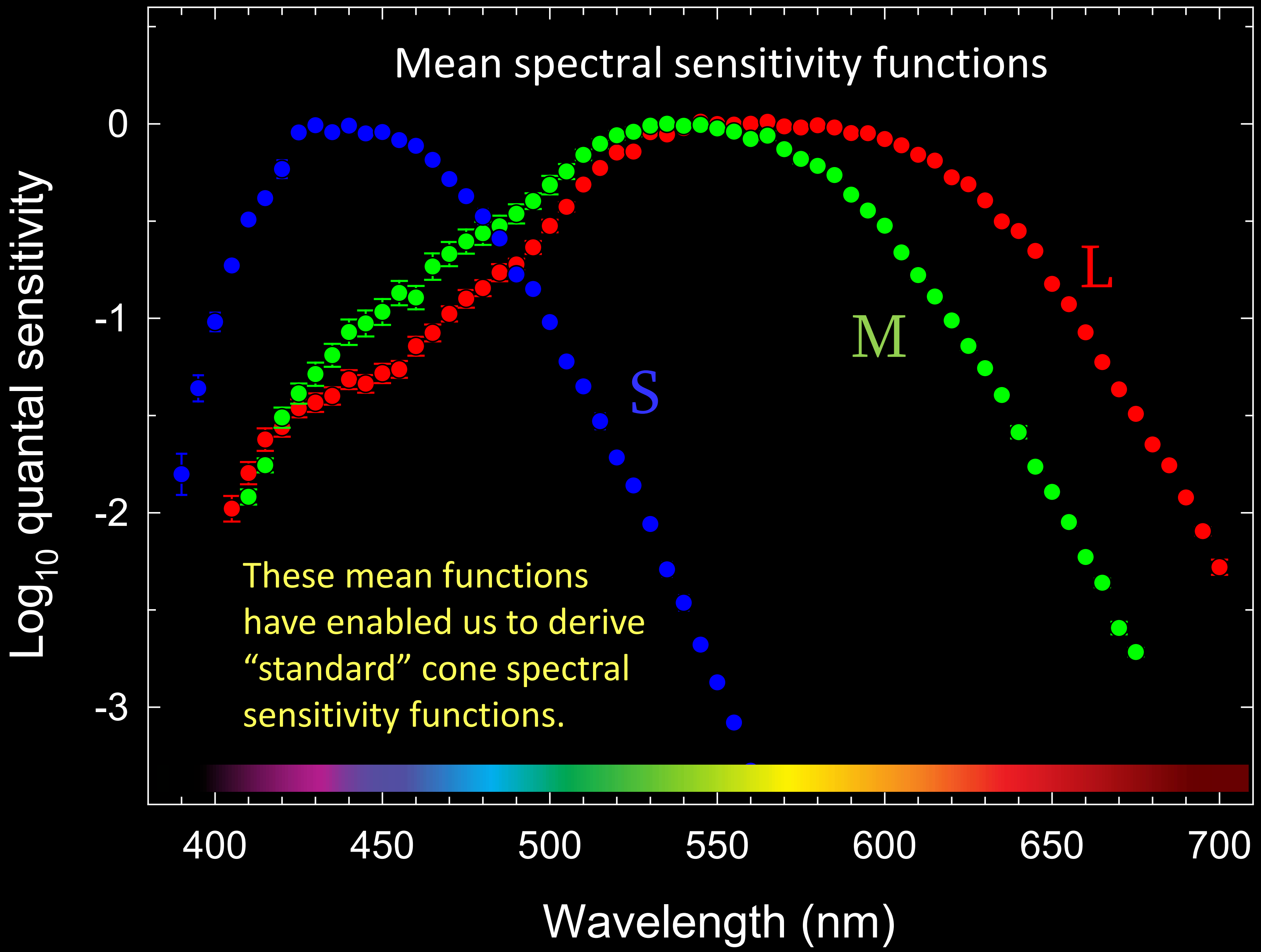






S-cone data

The Normal data were obtained on an intense orange adapting background that was there to suppress the L- and M-cone sensitivities.



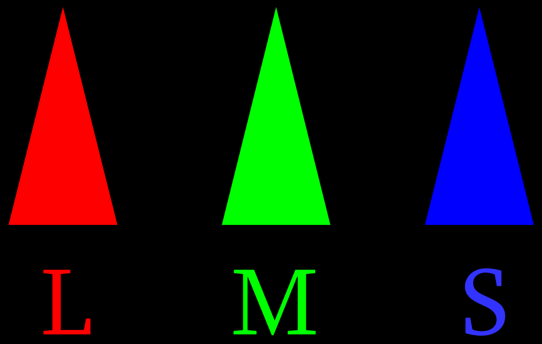
Mean spectral sensitivity functions
0
-1
-2
-3
Log10 quantal sensitivity
S
M
L
These mean functions
have enabled us to derive
"standard" cone spectral
sensitivity functions.
400
450
500
550
600
650
700
Wavelength (nm)

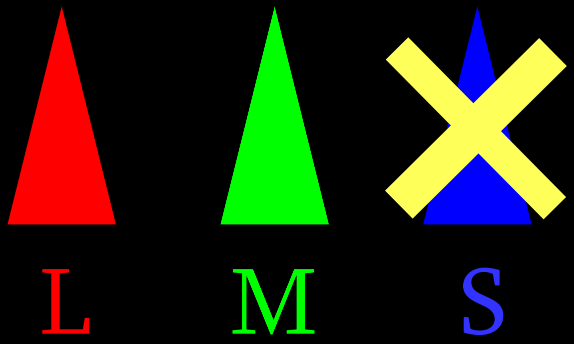
Why study spectral sensitivities?

- A knowledge of the spectral sensitivities of the cones is important because it allows us to accurately and simply specify colours and to predict colour matches—for both colour normal and colour deficient people (and to understand the variability between individuals).
- Practical implications for colour printing, colour reproduction and colour technology.

Normal

Tritanope

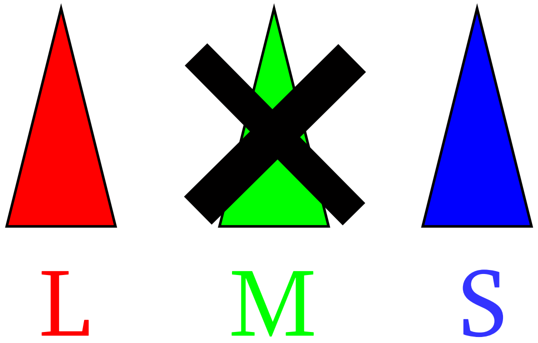




Tritanopia

Credit: Euro Puppy Blog

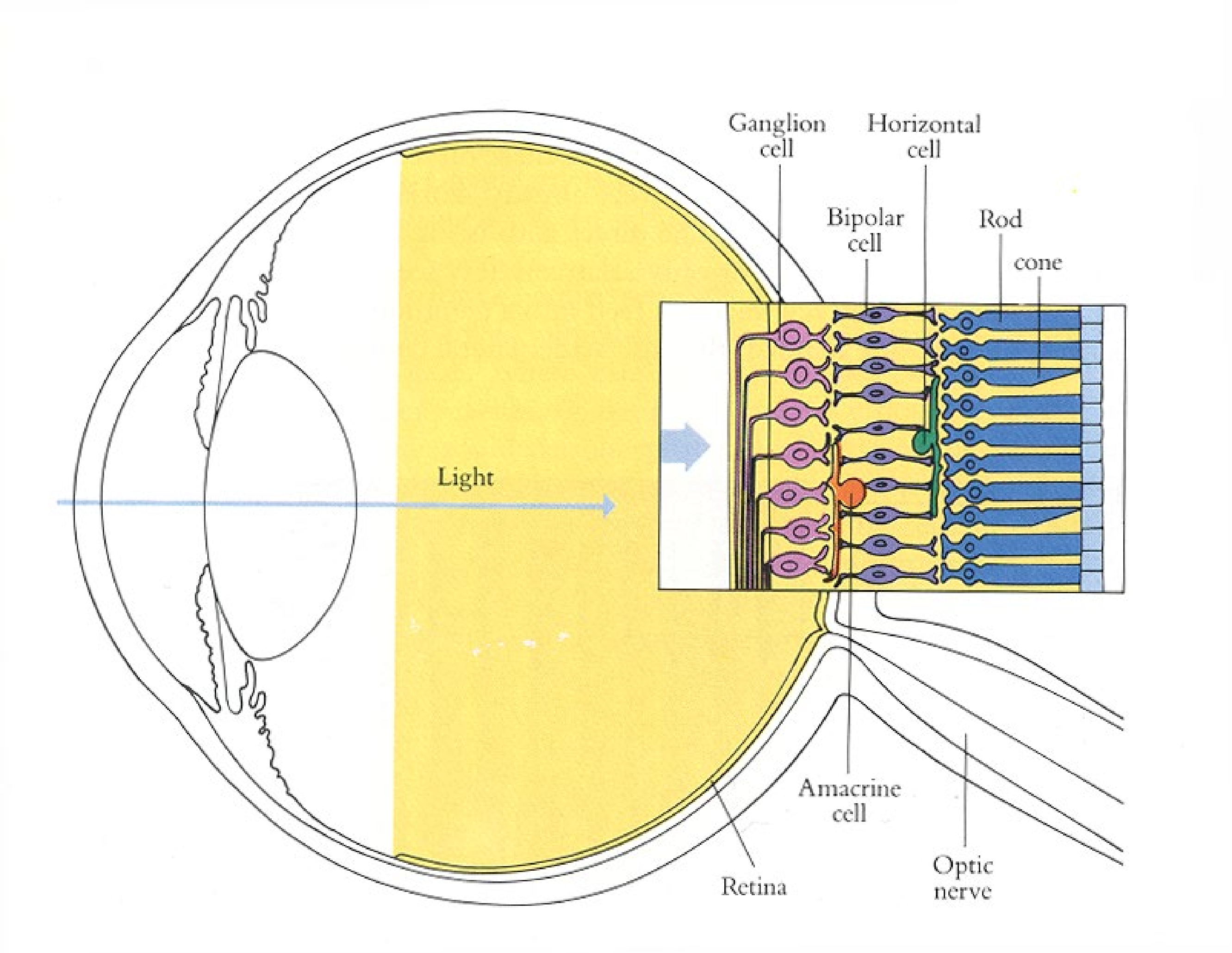
Deuteranope



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

POSTRECEPTORAL COLOUR VISION

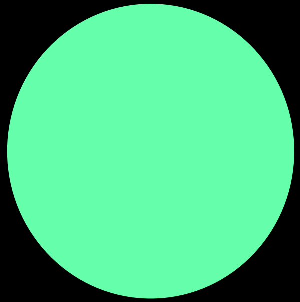
But what happens next (i.e., how is colour encoded after the photoreceptors)?



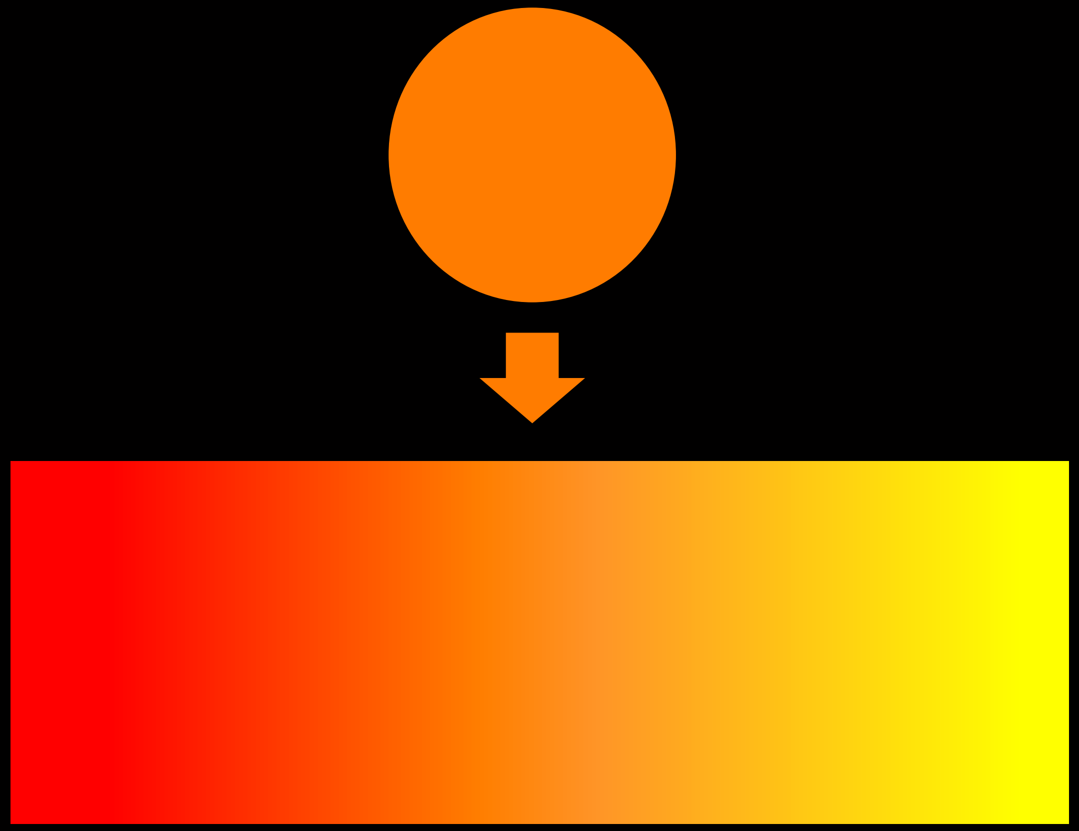
Colour phenomenology

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

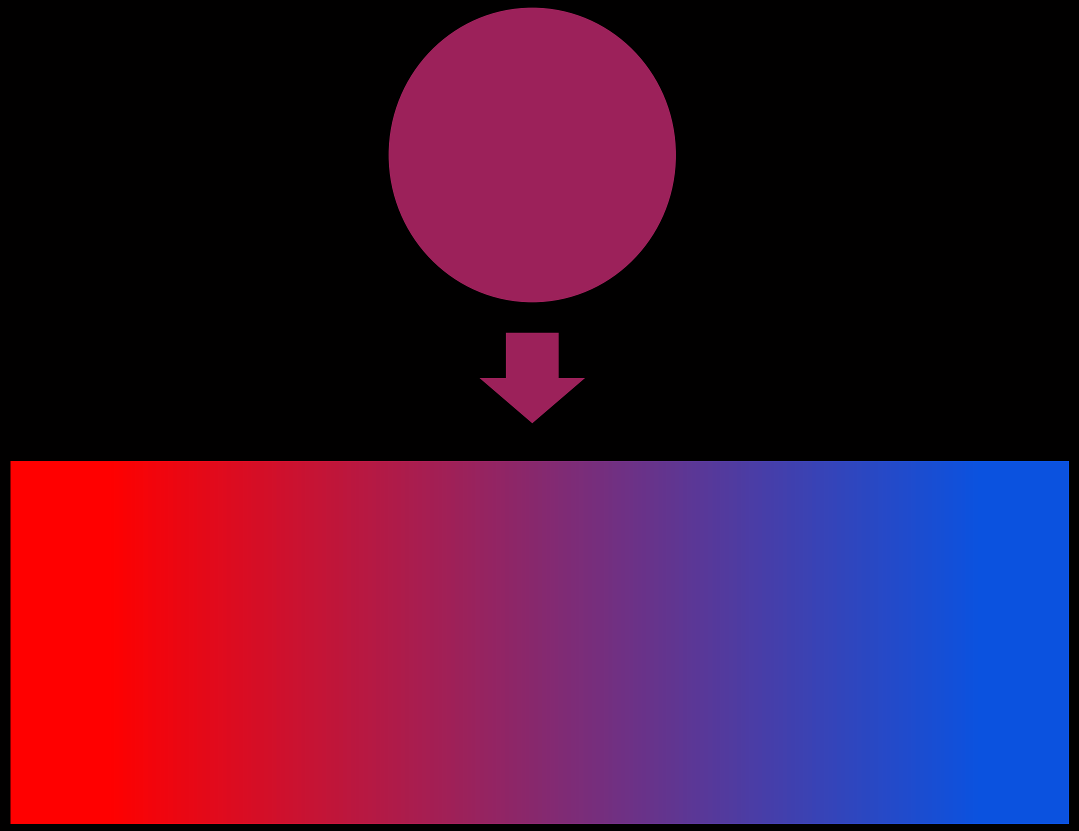
Imagine a single patch of colour inside a dark surround



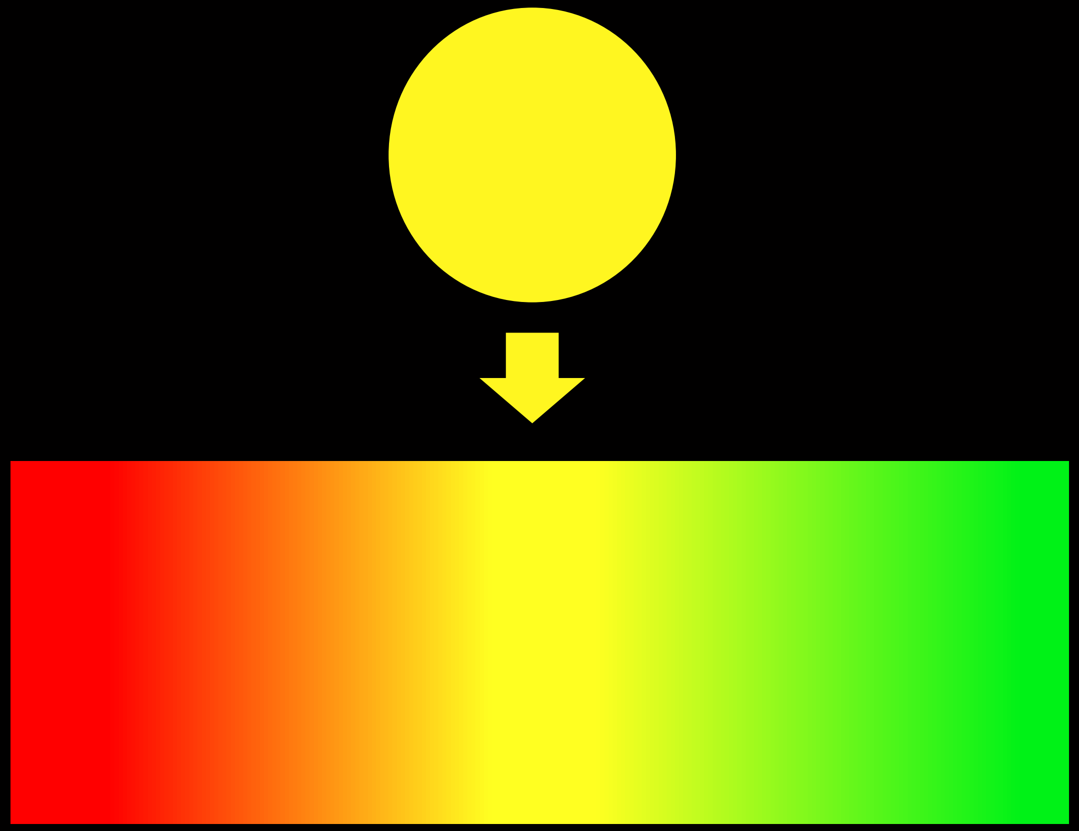
- Which pairs of colours can coexist in a single, uniform patch of colour?
- Which pairs can never coexist?



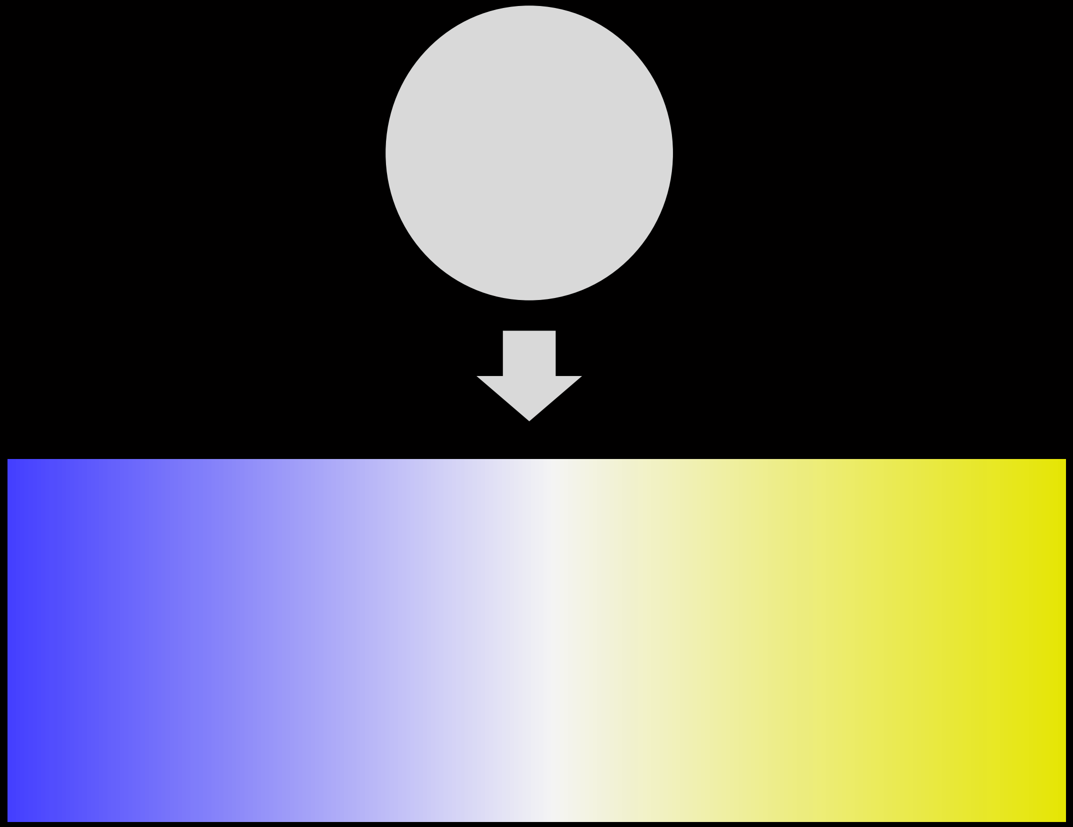
Can a single patch be reddish-yellow? ✓



Can it be reddish-blue? ✓

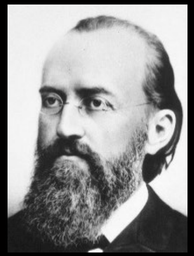


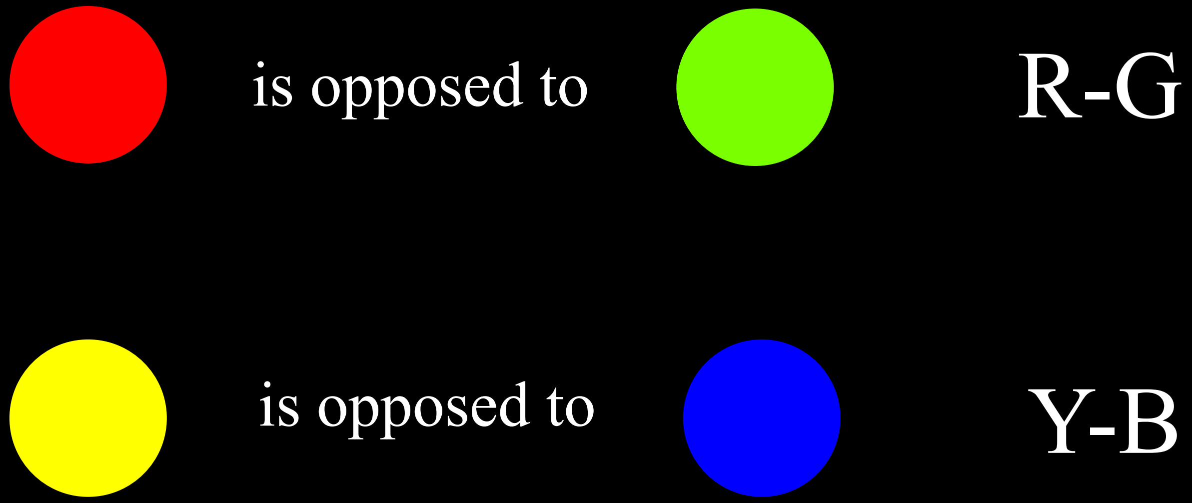
Can it be reddish-green?



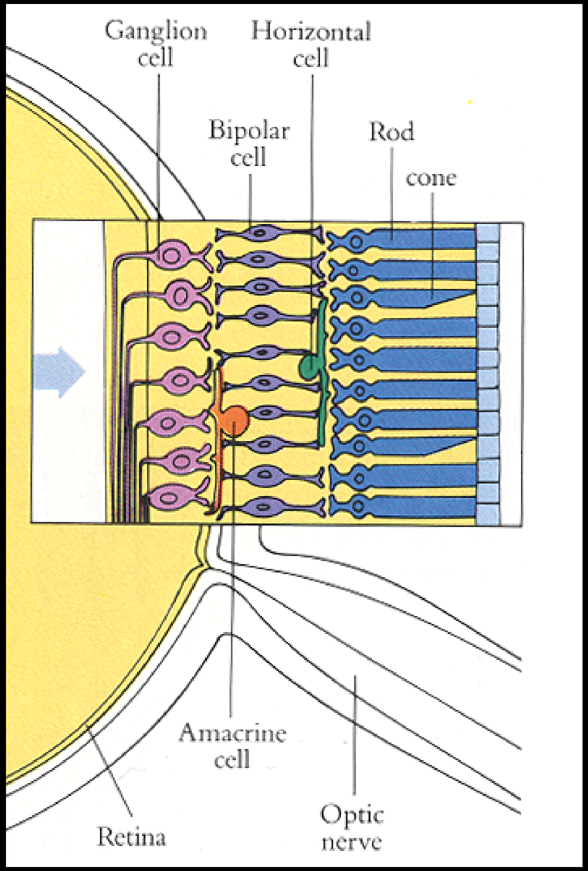
Can it be bluish-yellow? ✗

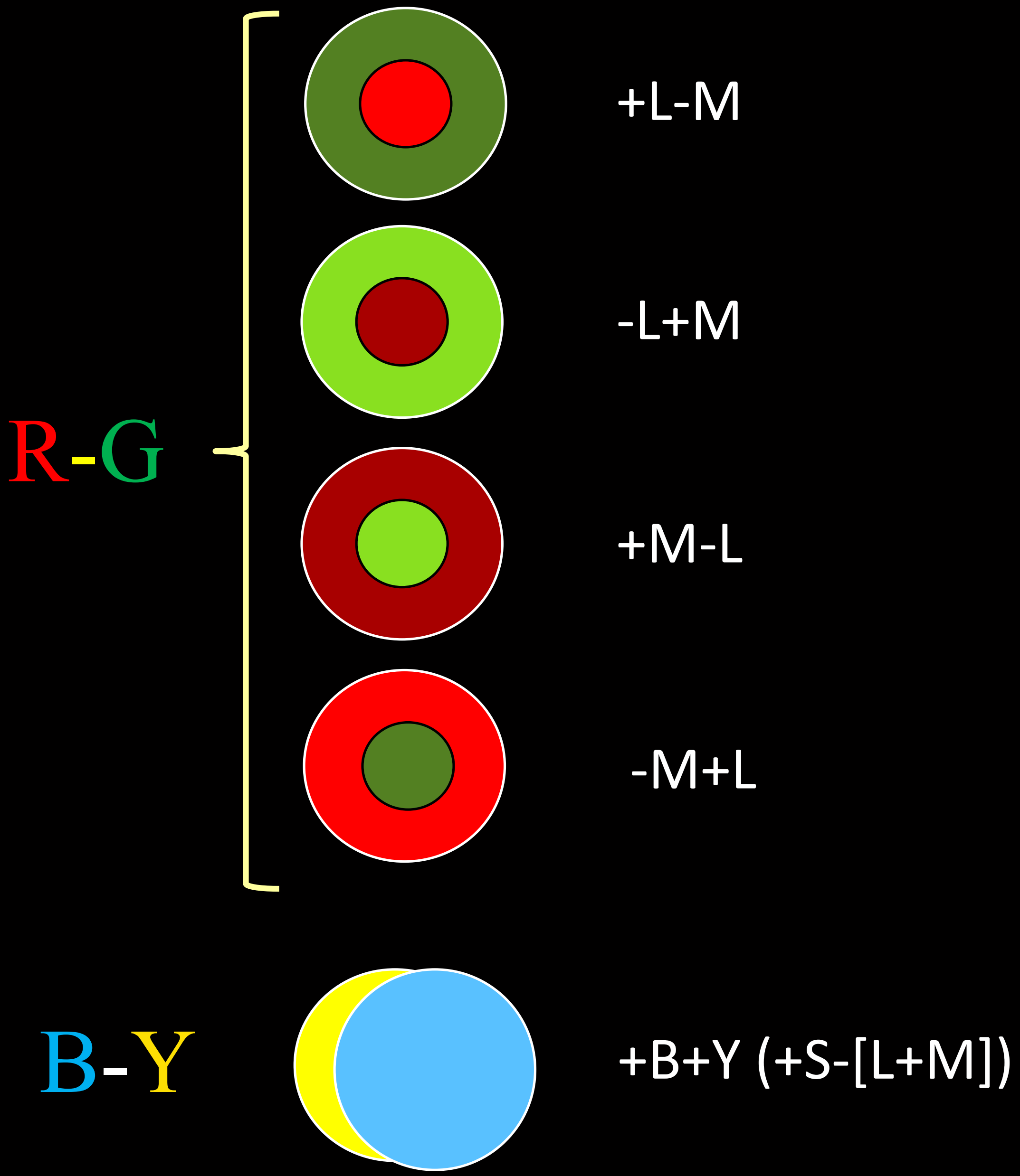
The colour opponent theory of Hering



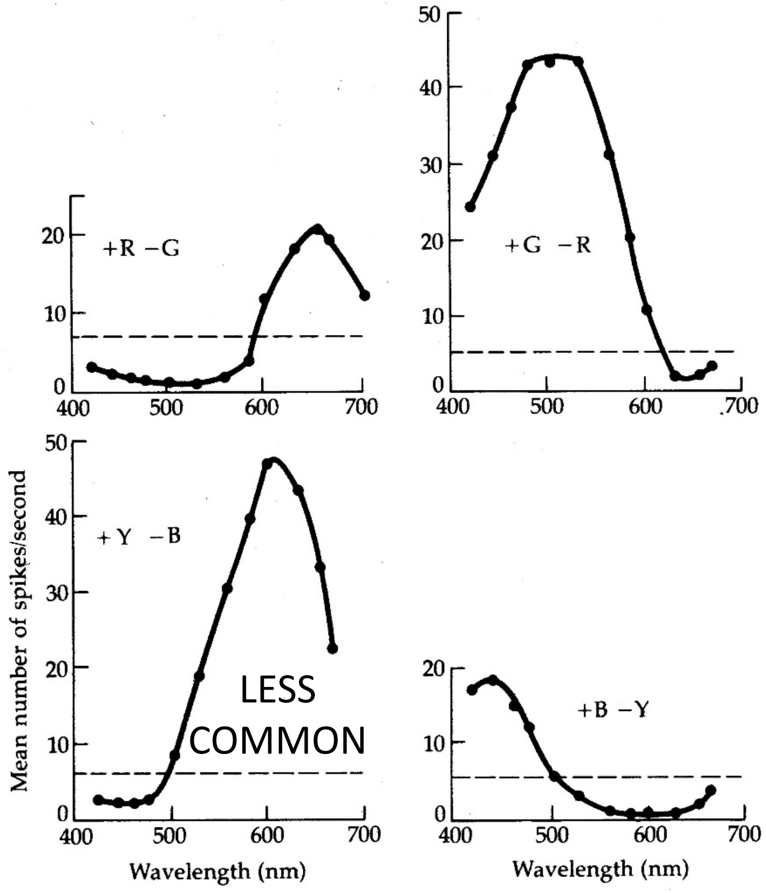


Cells in the early visual pathway oppose the signals from different cone classes and can be loosely classified as "red-green" or "blue-yellow" opponent:





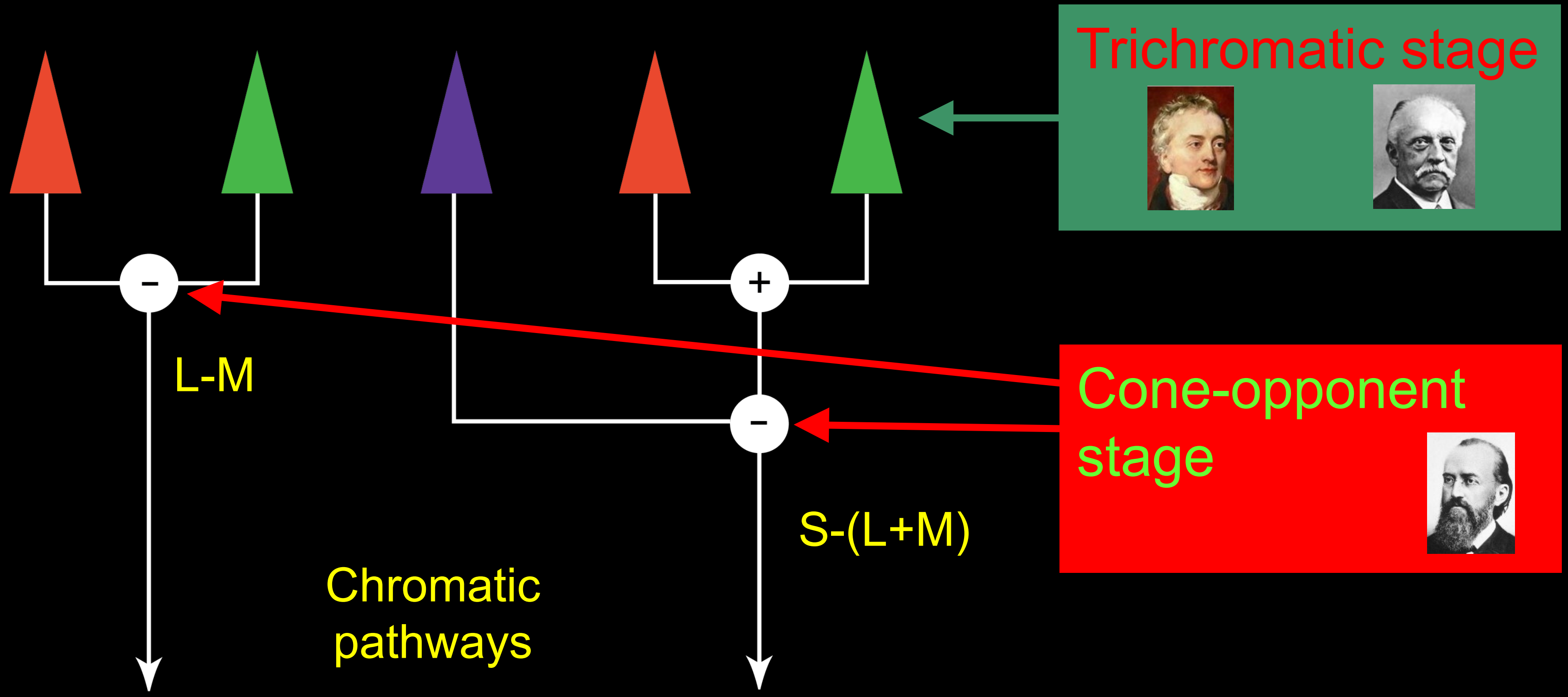
LGN cell responses



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.

Standard (basic) psychophysical model

[Based on Boynton (1979)]

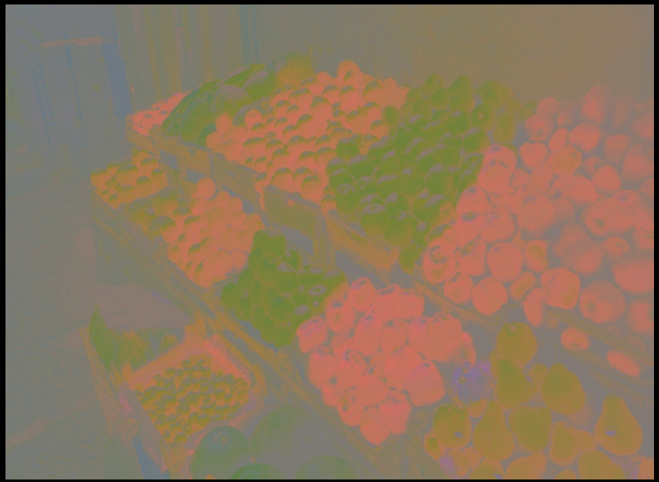


Chromatic pathways [L-M and S-(L+M)] that produce a chromatic percept.

So that’s colour (chromatic) encoding, but what about “luminance” (achromatic) encoding?

ACHROMATIC COMPONENTS

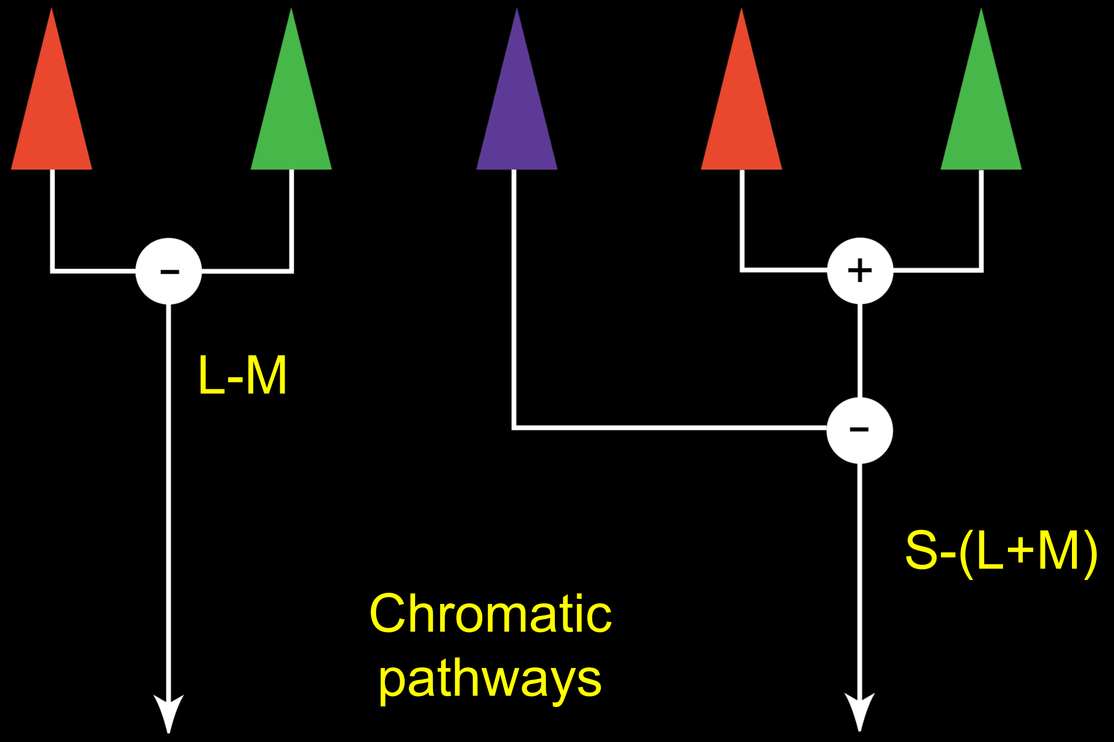
CHROMATIC COMPONENTS



Chromatic and achromatic pathways

Standard (basic) psychophysical model

[Based on Boynton (1979)]

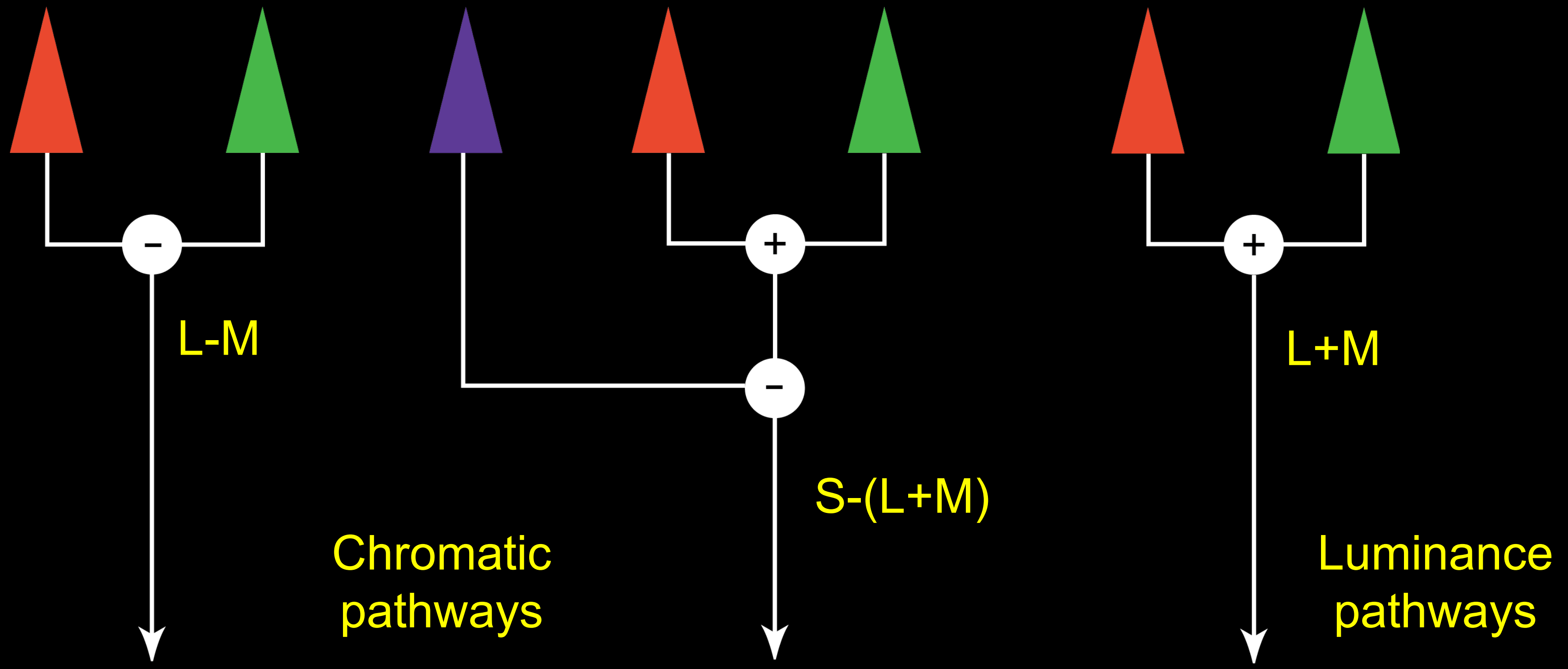


Chromatic pathways [L-M and S-(L+M)] that produce a chromatic percept.

In addition to the chromatic pathways there are also luminance pathways…

Standard (basic) psychophysical model

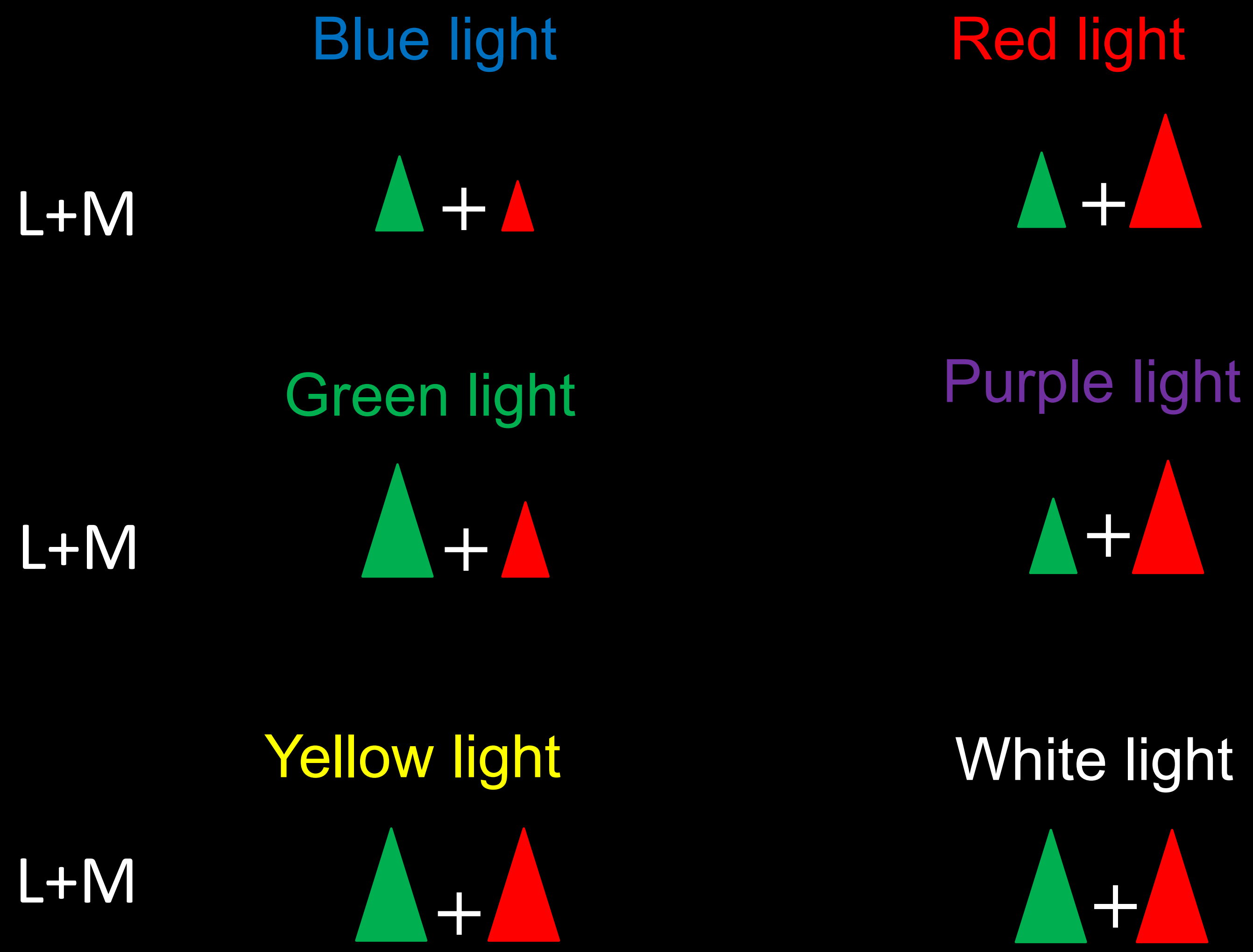
[Based on Boynton (1979)]

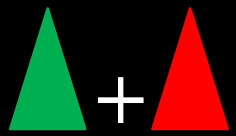


Chromatic pathways [L-M and S-(L+M)] that produce a chromatic percept.

Luminance pathways (L+M) that produce an achromatic percept.

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





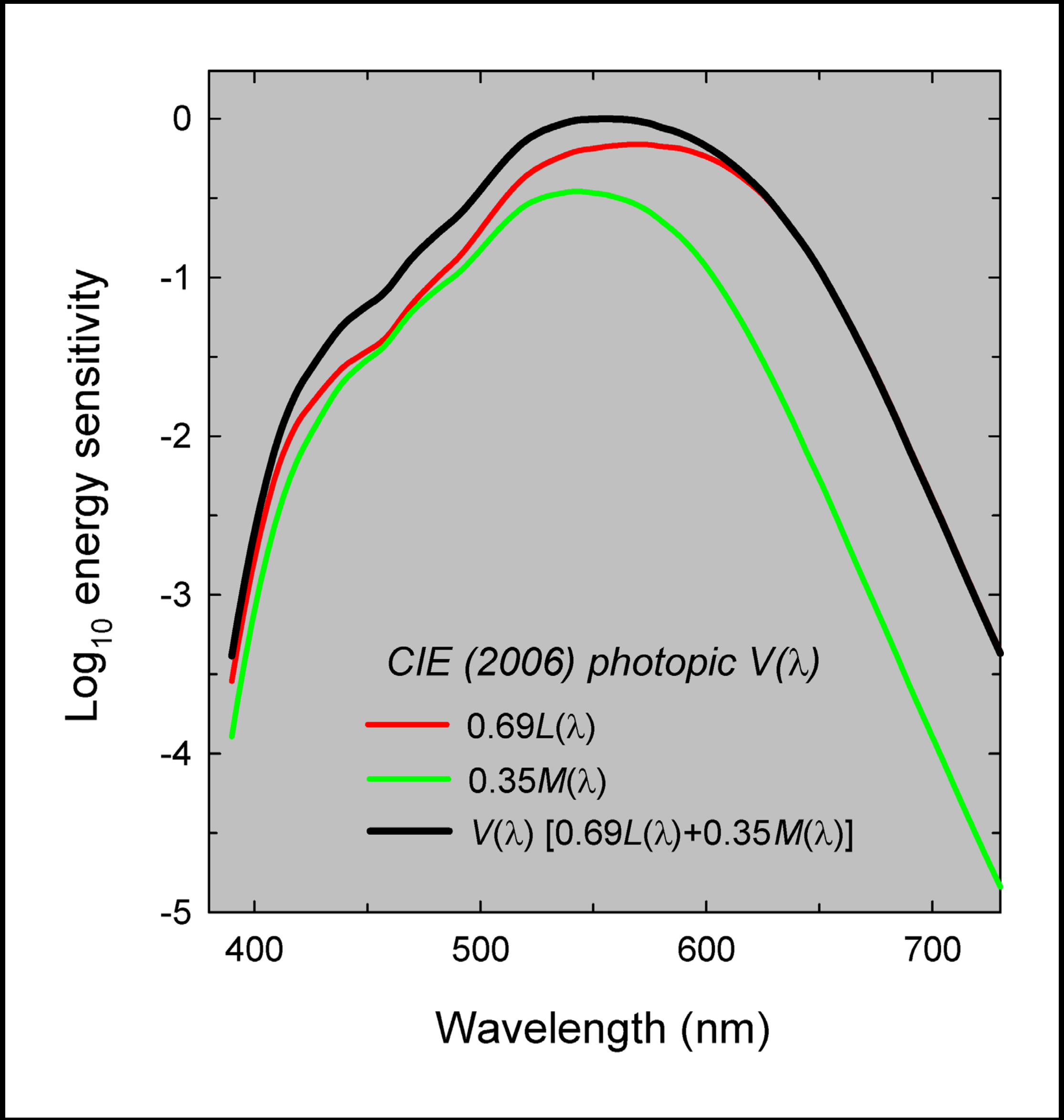
Assumed characteristics of the luminance pathway

Little or no S-cone input! (Just L+M)

Typically L-cone > M-cone input (2:1)

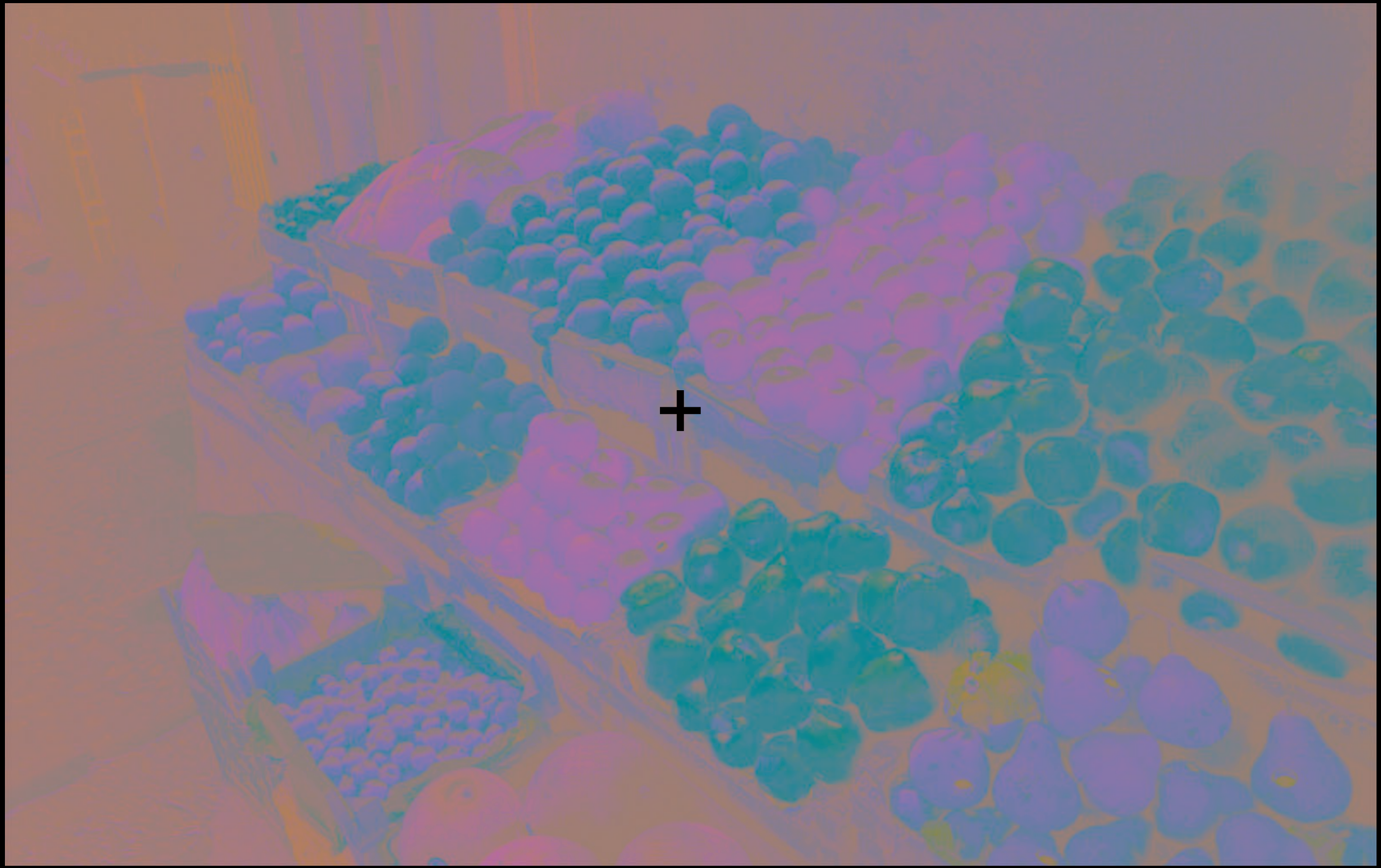
Ratio of L-cone to M-cone inputs highly variable across individuals.

Spectral sensitivity is known as V(λ) or the photopic luminous efficiency function and defines lux, cd/m^2 and trolands.

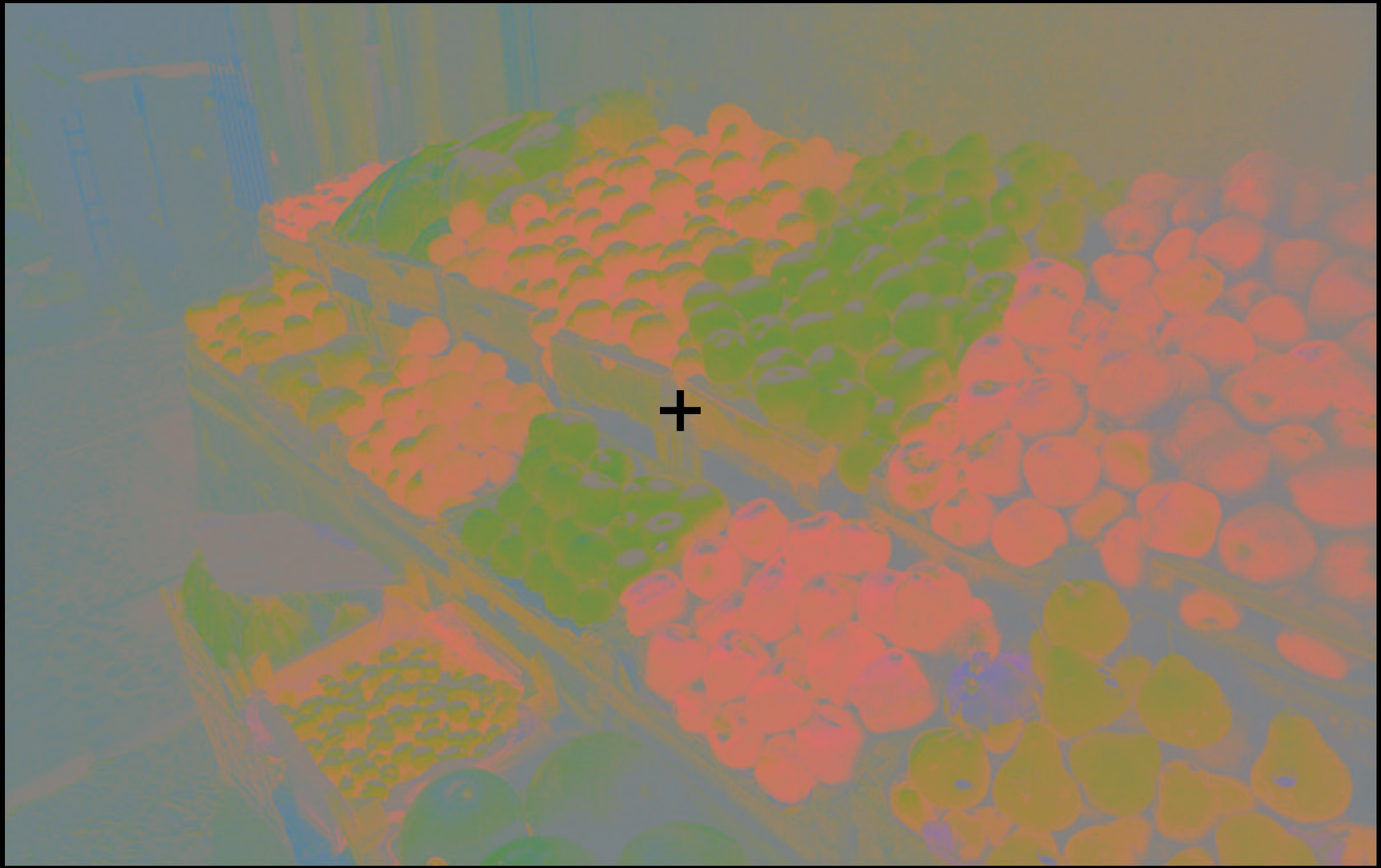


Colour is in many ways secondary
to luminance


Souvlaki




Souvlaki

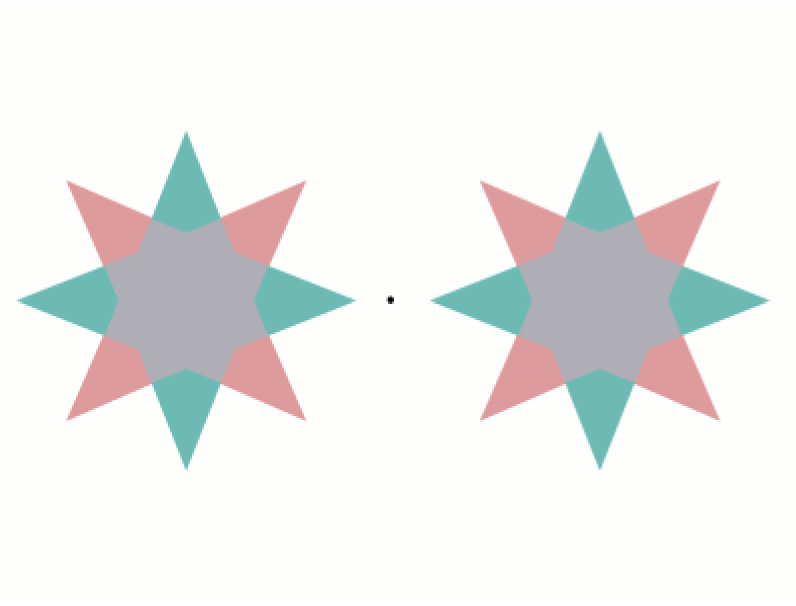



Souvlaki

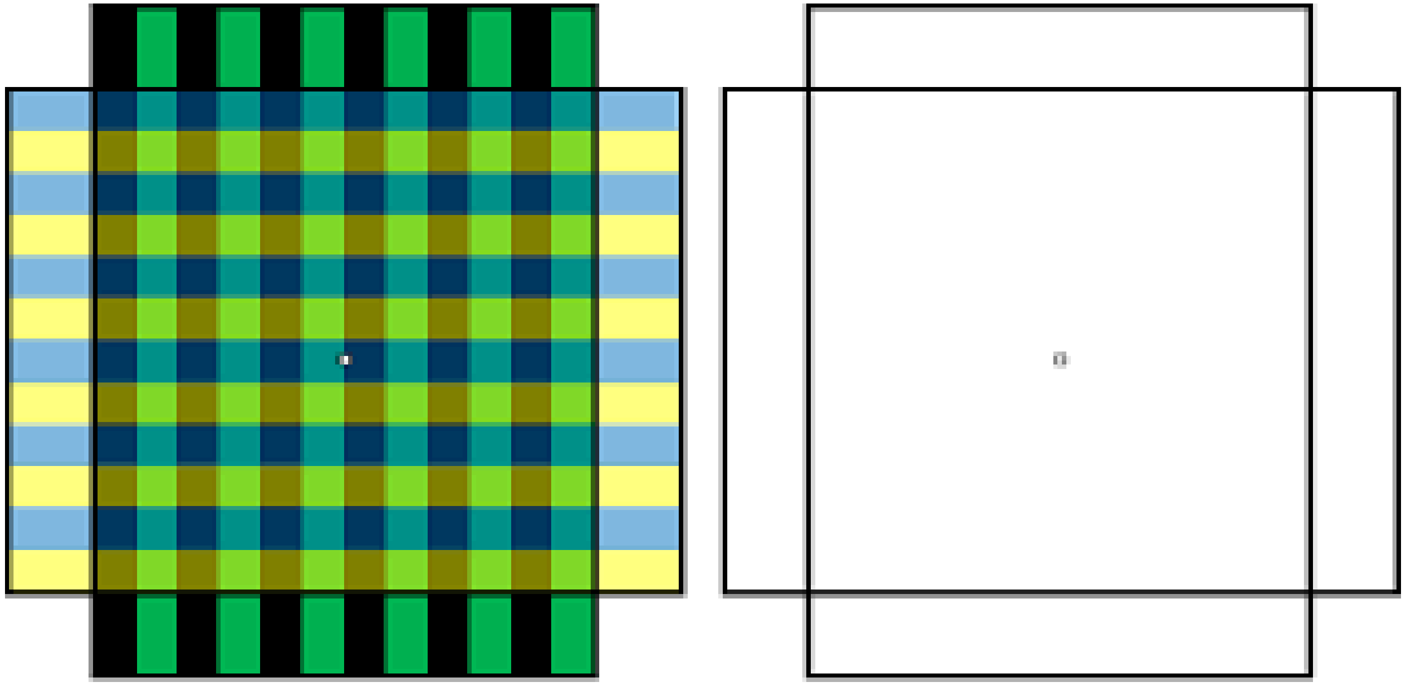

Souvlaki

G. Seurat (*c.* 1889-90)
Le Chahut
[The High-Kick, Can-Can]

Courtesy: Jack Werner

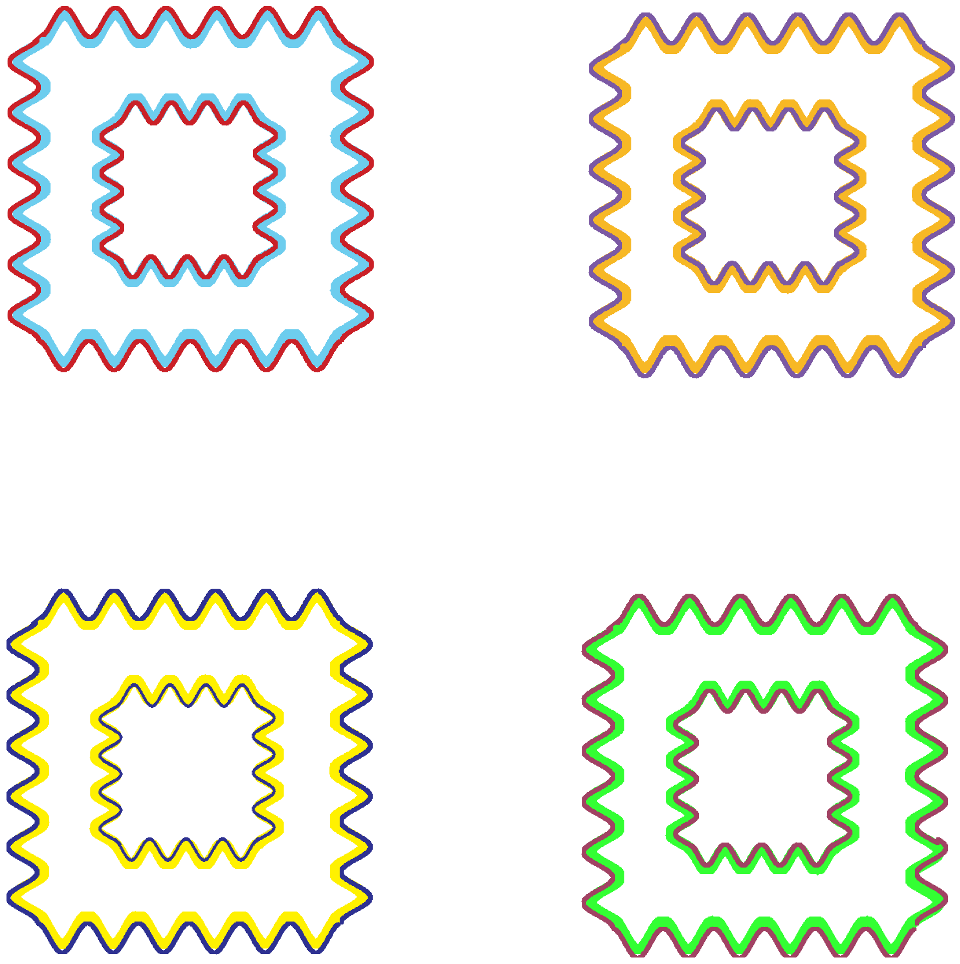


Rob van Lier, Mark Vergeer & Stuart Anstis



Peter Tse

Watercolour effect



So far, we've mainly been talking about the colours of isolated patches of light. But the colour of a patch depends also upon:

(i) What precedes it (in time)

COLOUR AFTER-EFFECTS

(ii) What surrounds it (in space)

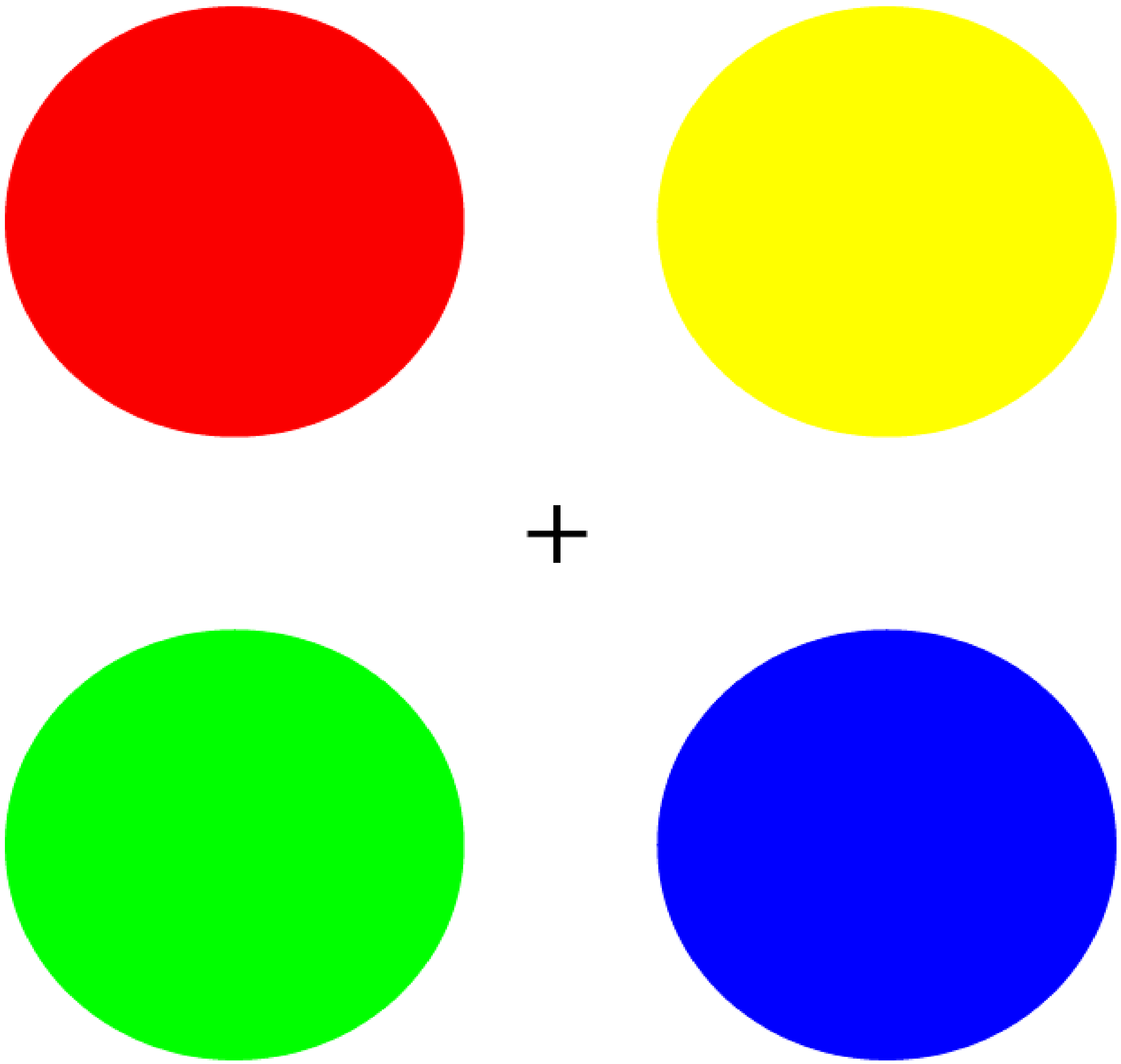
COLOUR CONTRAST

COLOUR ASSIMILATION

COLOUR AFTER-EFFECTS

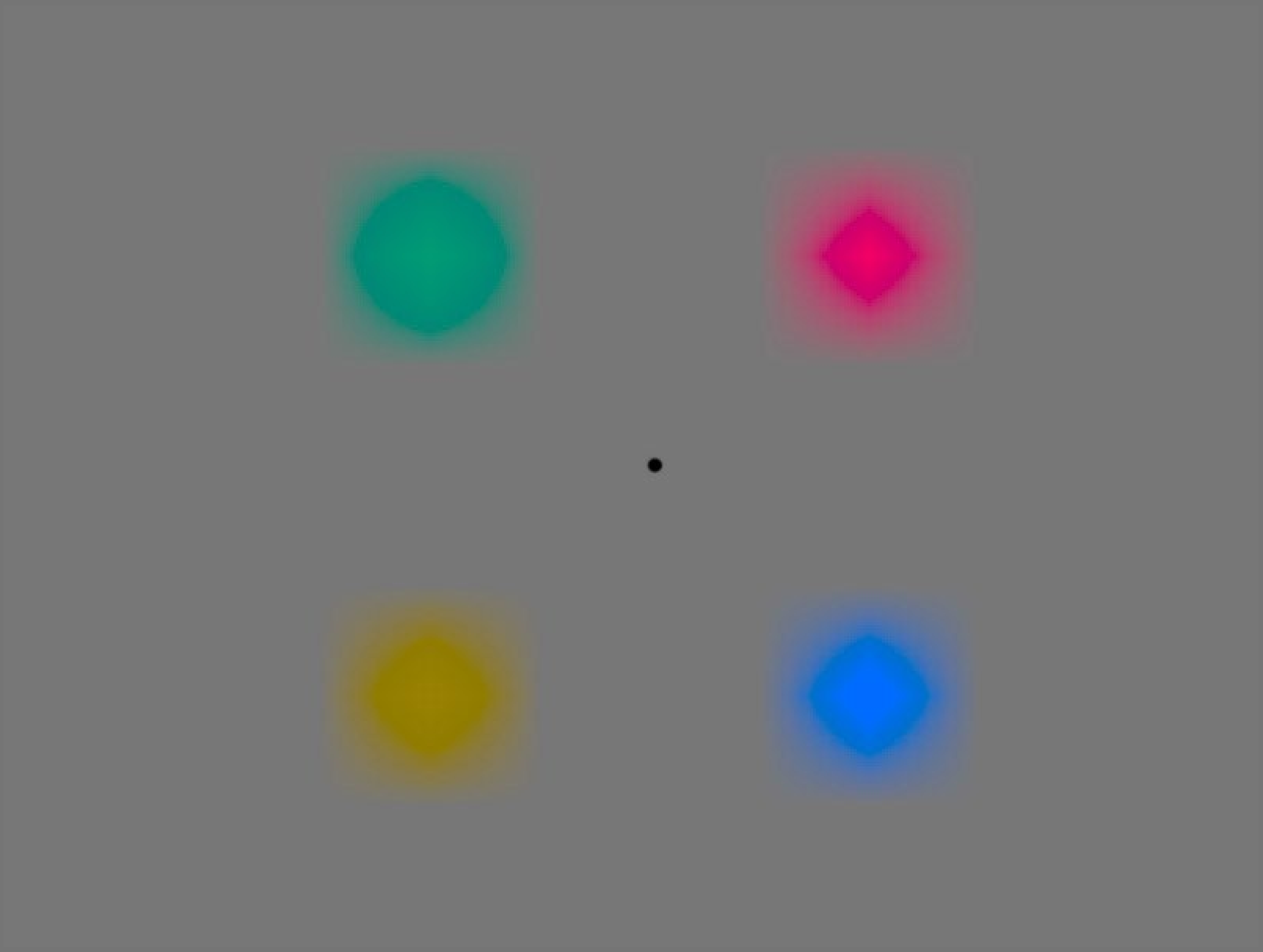
(what precedes the patch)

Colour after-effects



+

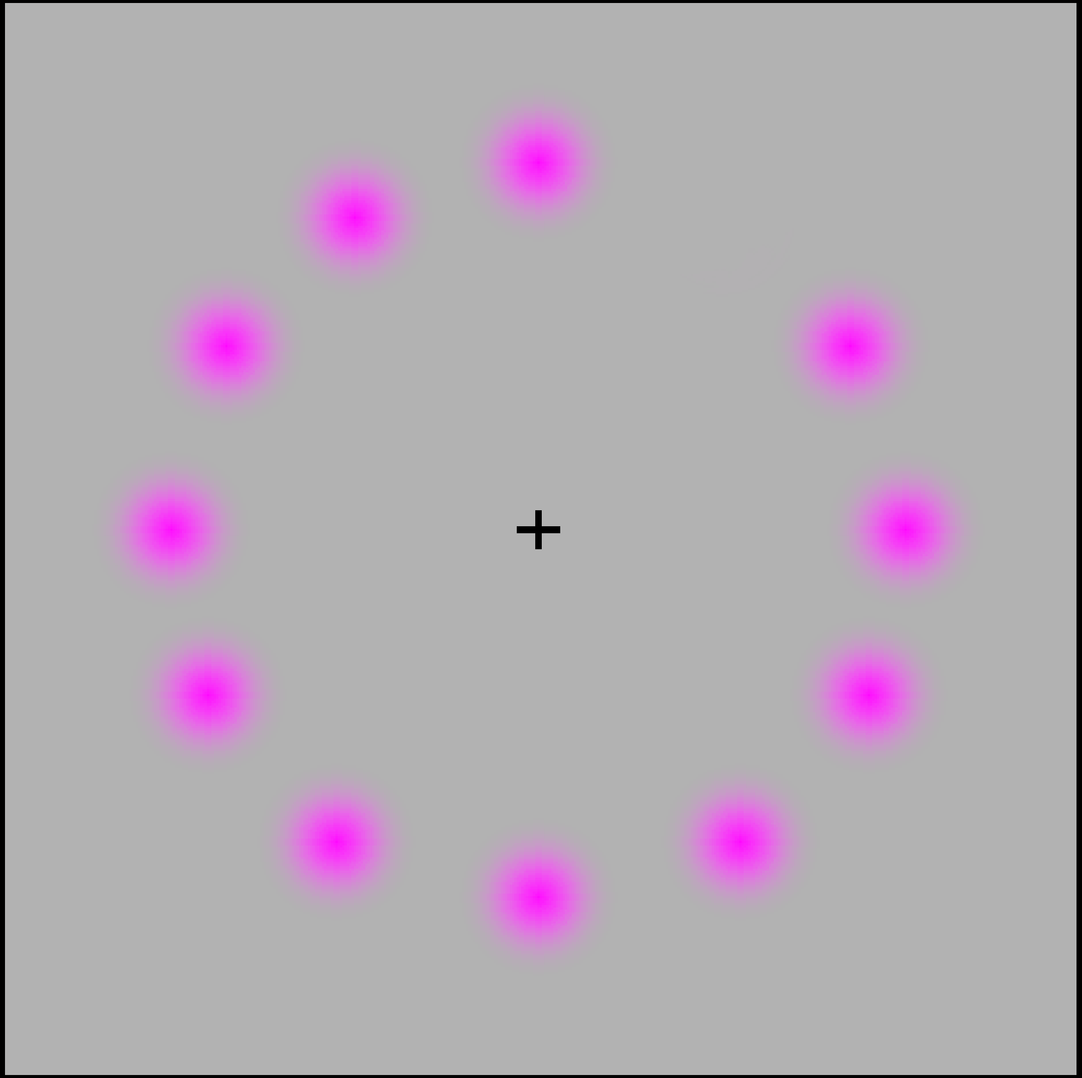
You don’t have to see things for them to produce an after-effect...



Beer & MacLeod

Mediafire

Lilac chaser or Pac-Man illusion



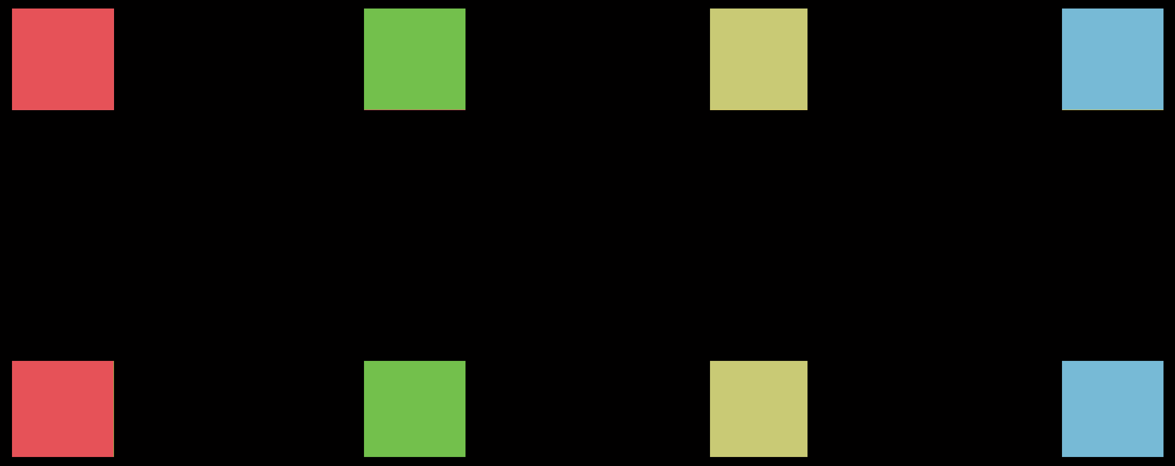
Jeremy Hinton

Michael Bach

COLOUR CONTRAST

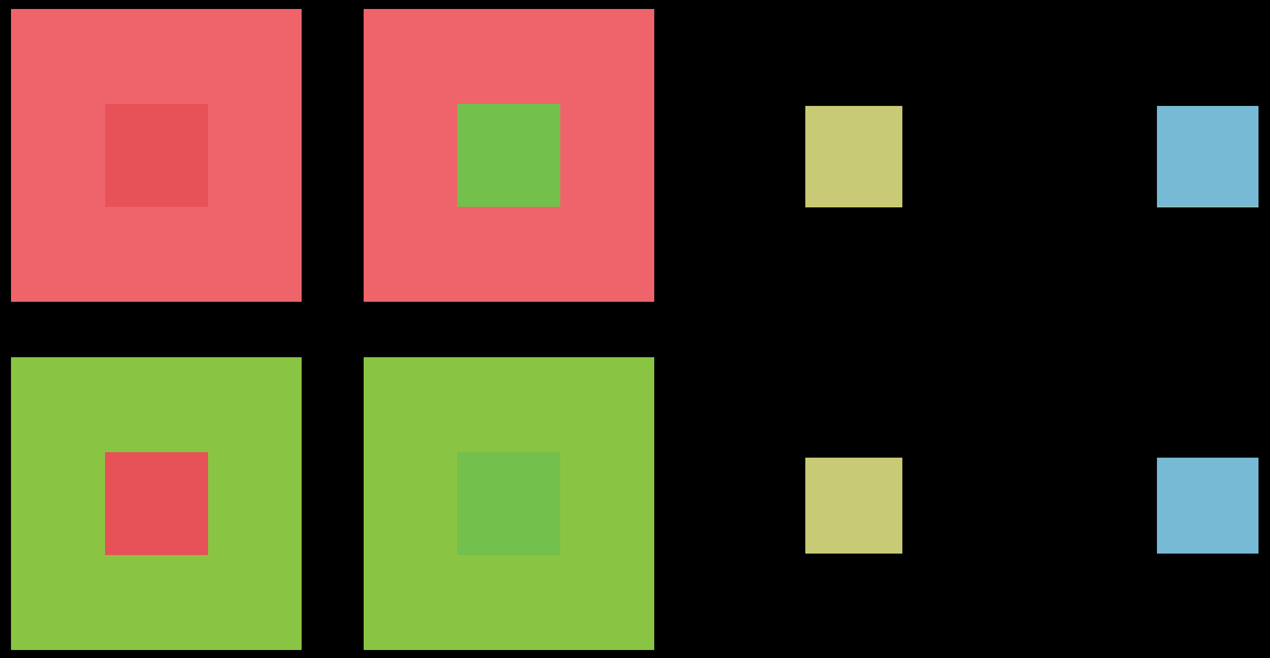
(what surrounds the patch)

Colour contrast

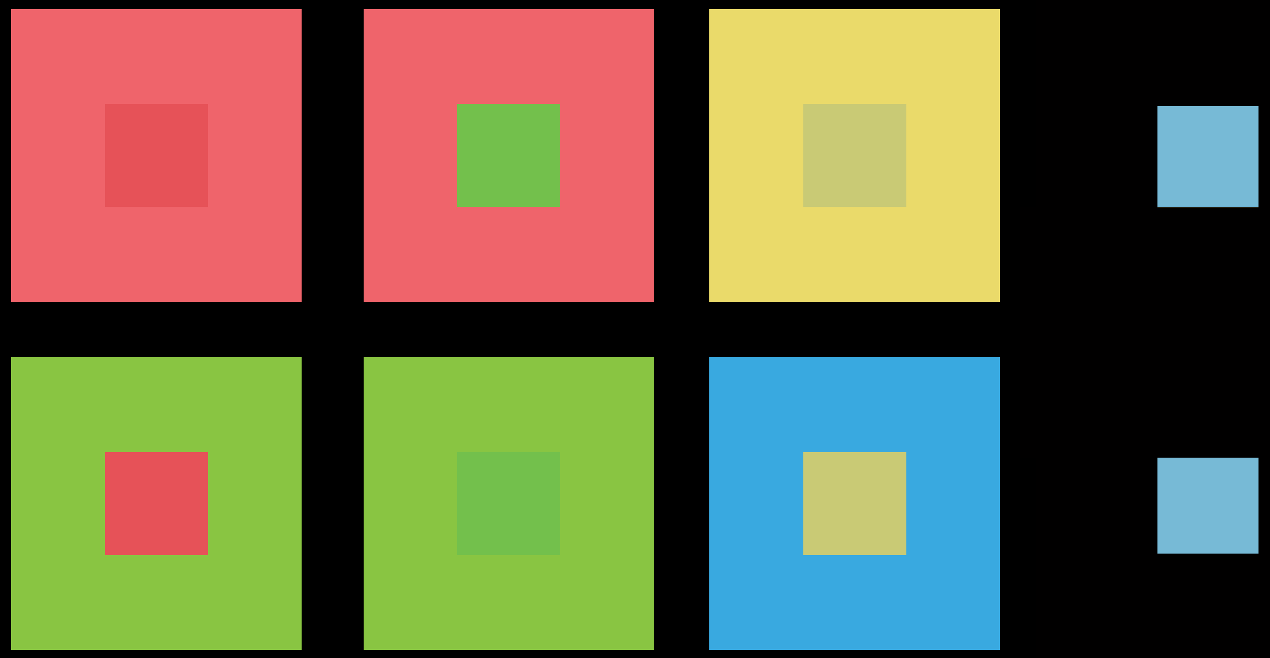


Colour contrast

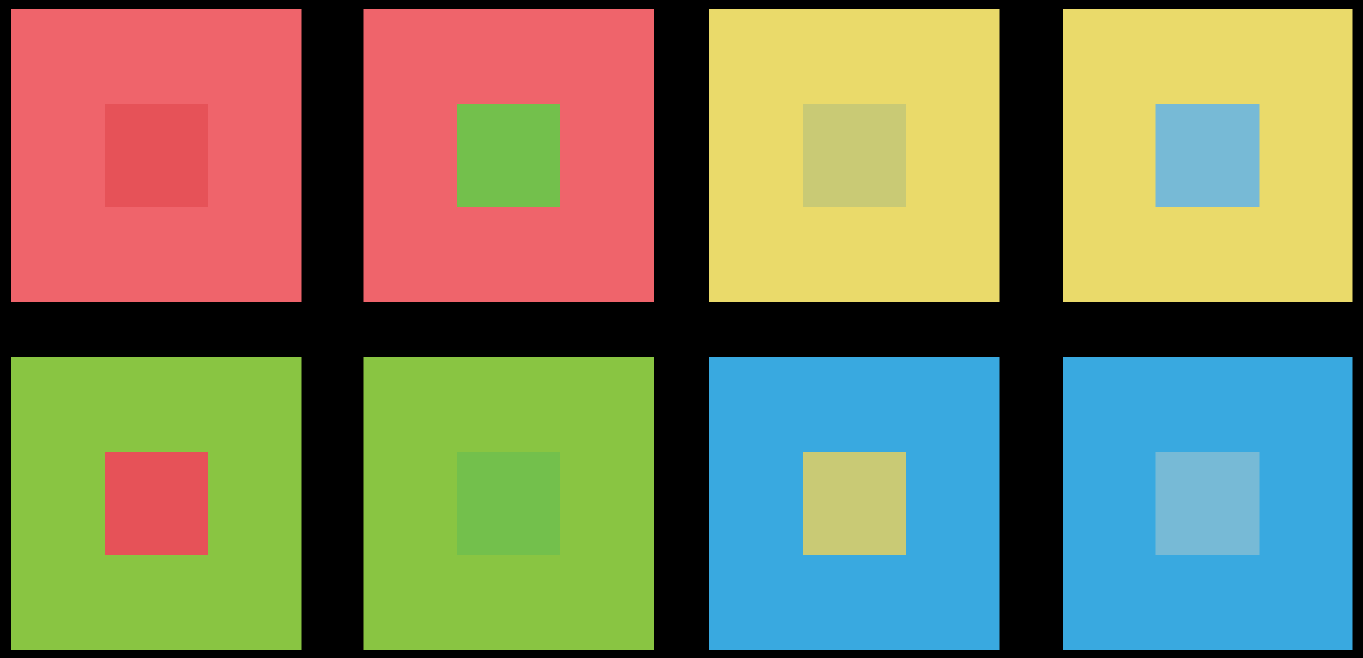
Colour contrast



Colour contrast



Colour contrast



The Night Cafe in Arles, *by Vincent Van Gogh* Watercolour, 1888.

Claude Monet, The Regatta at Argenteuil, c. 1872
Musee d'Orsay, Paris

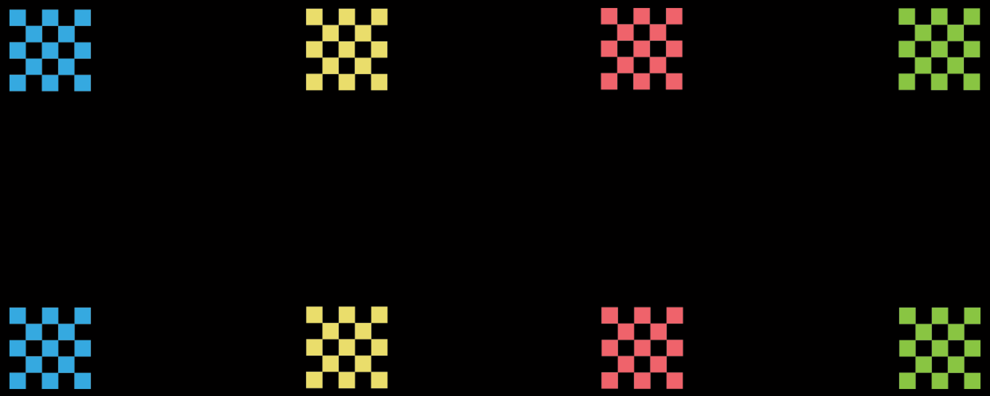
Colour contrast can enhance colour appearance

Chevreul circles

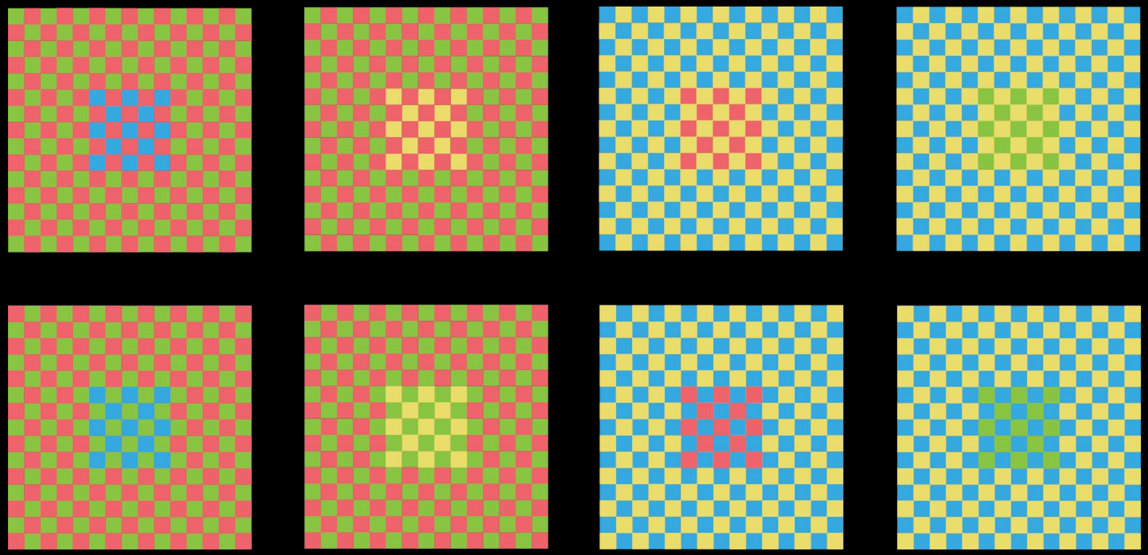
Webexhibits.org

COLOUR ASSIMILATION

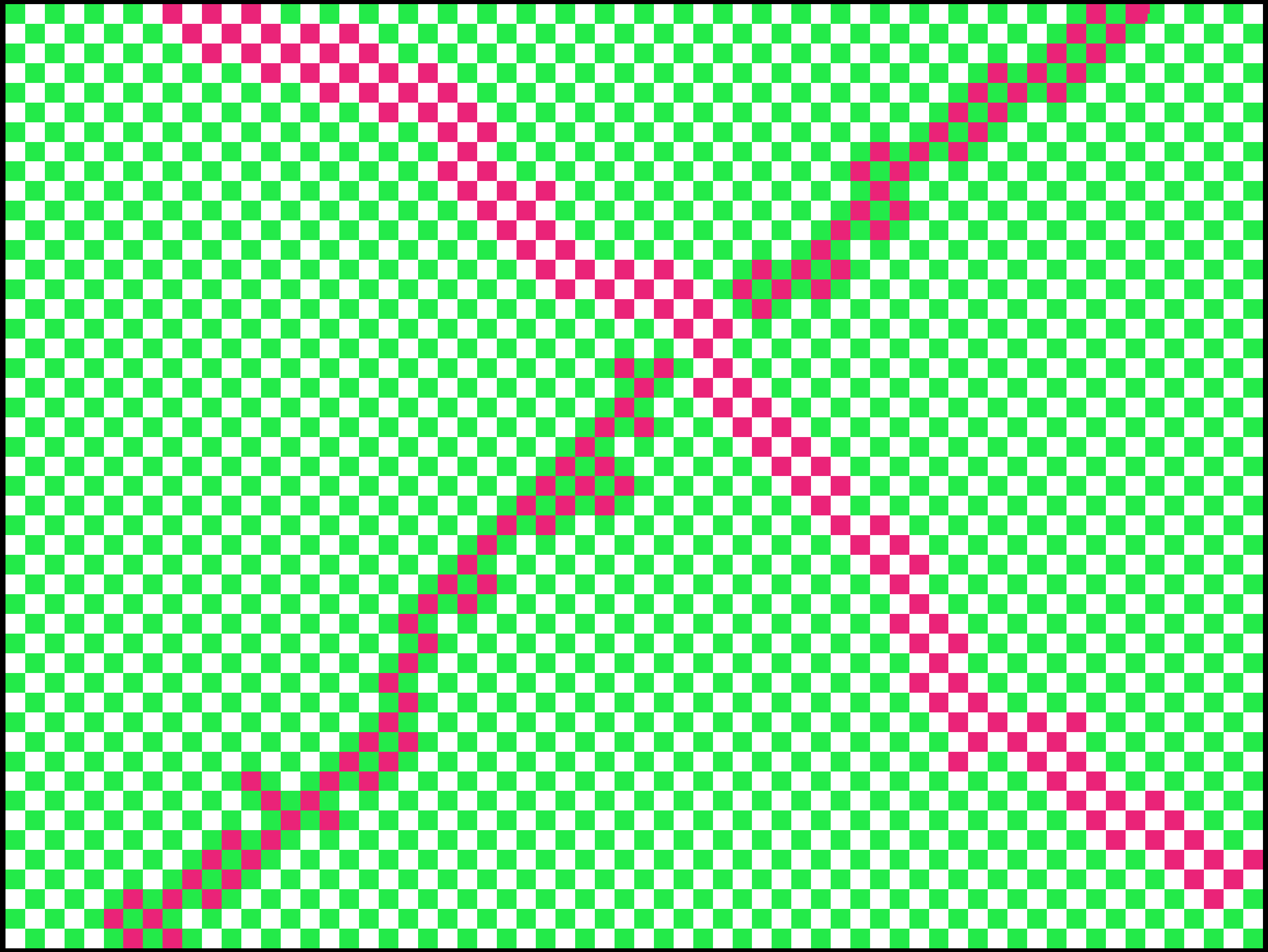
Colour assimilation



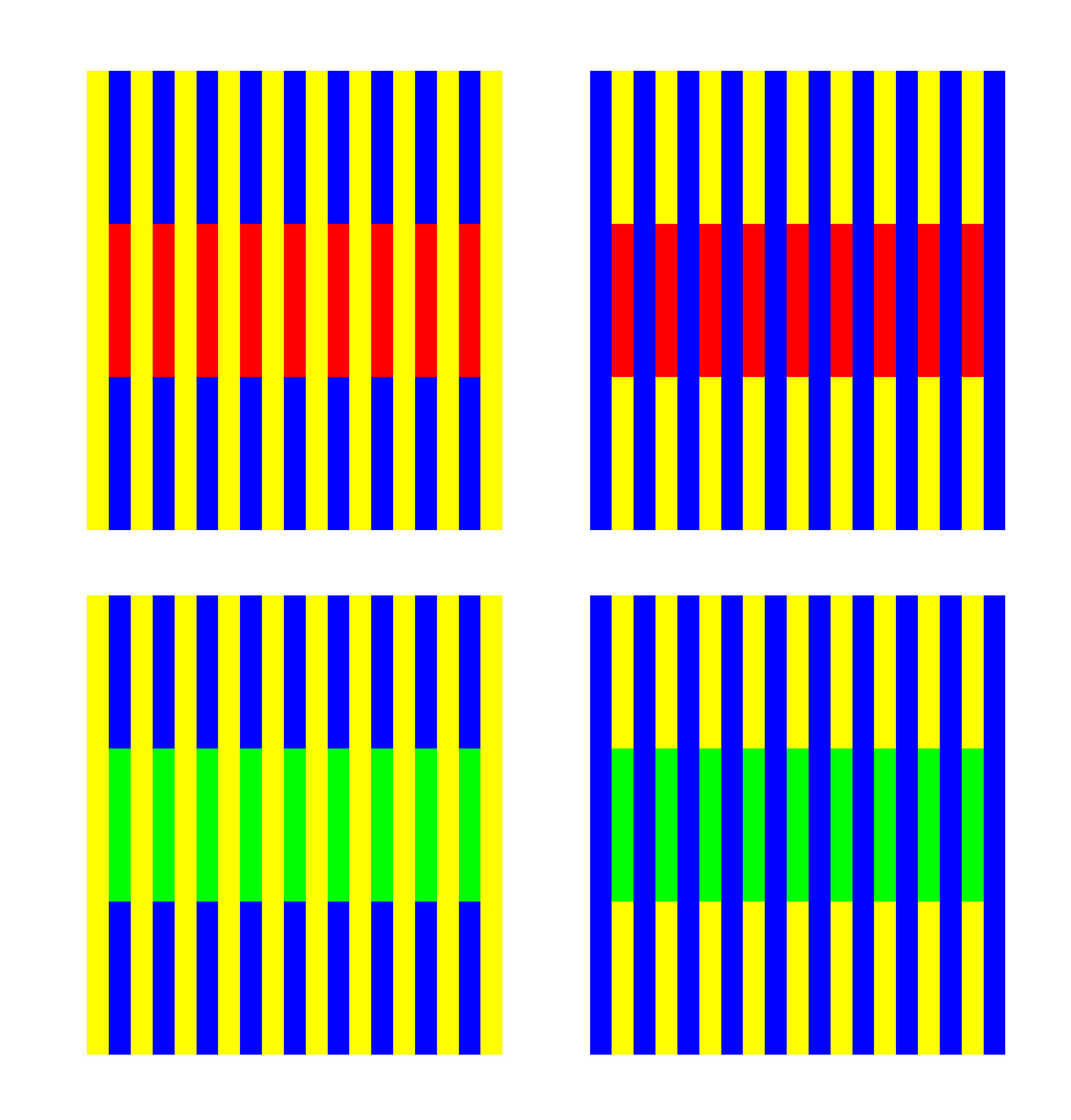
Colour assimilation



Colour assimilation



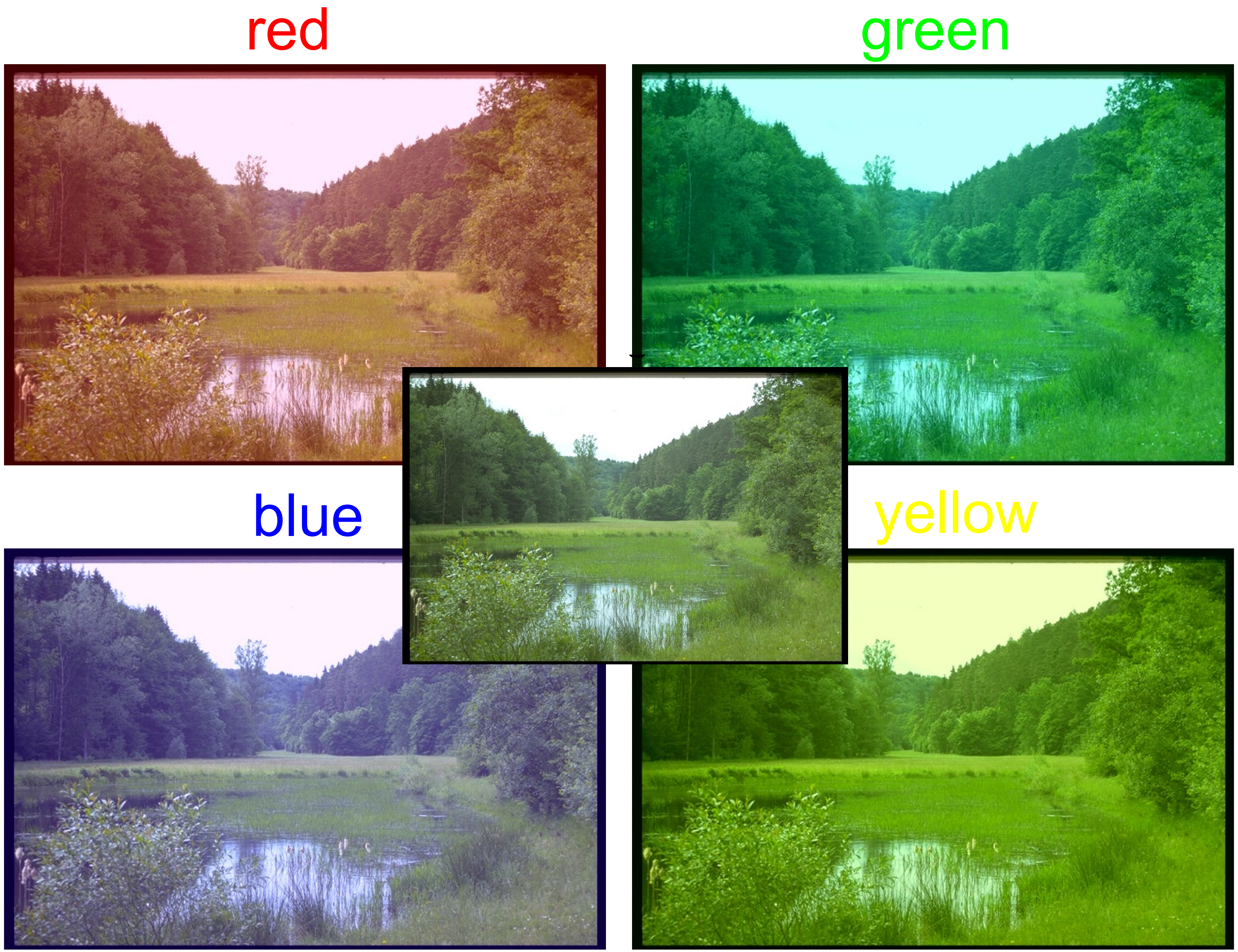
Munker illusion



COLOUR CONSTANCY

Colour constancy

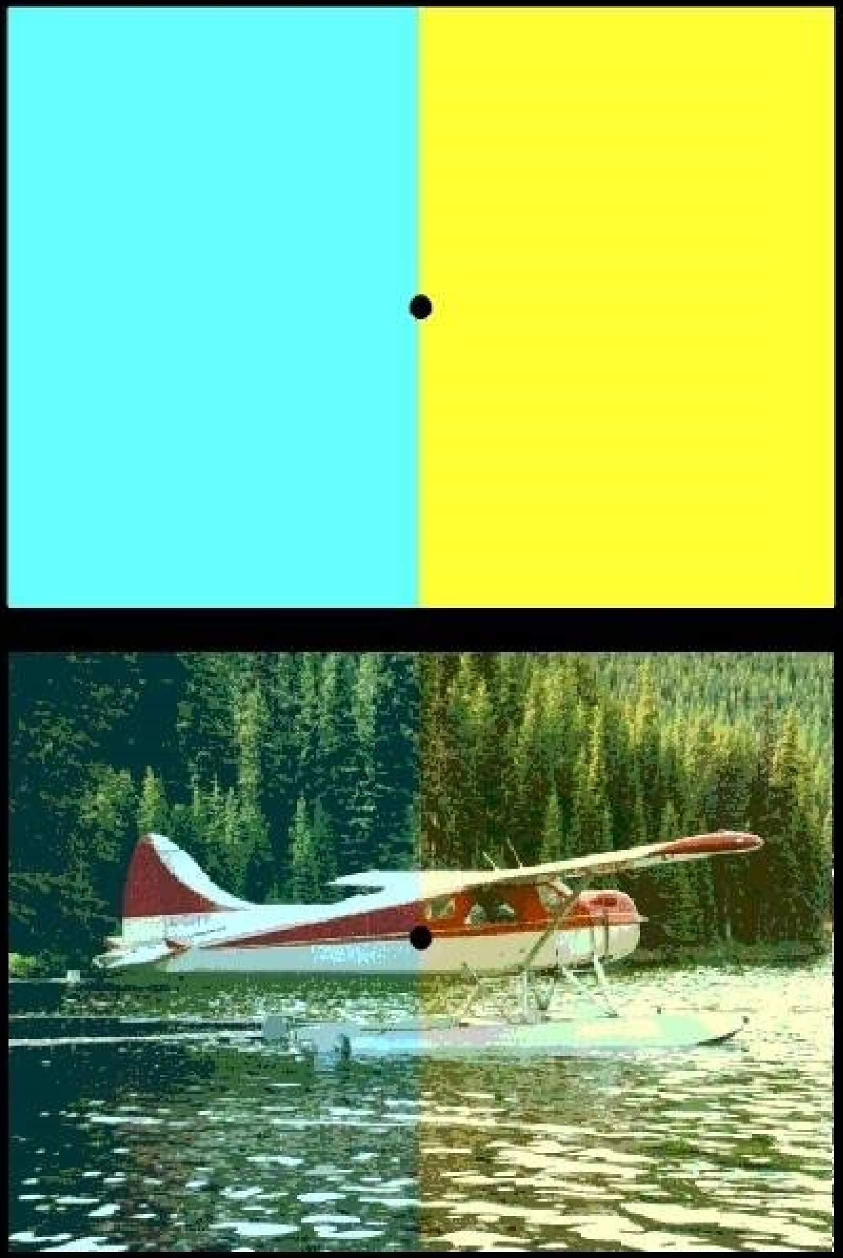
Colour constancy



Credit: Gegenfurtner

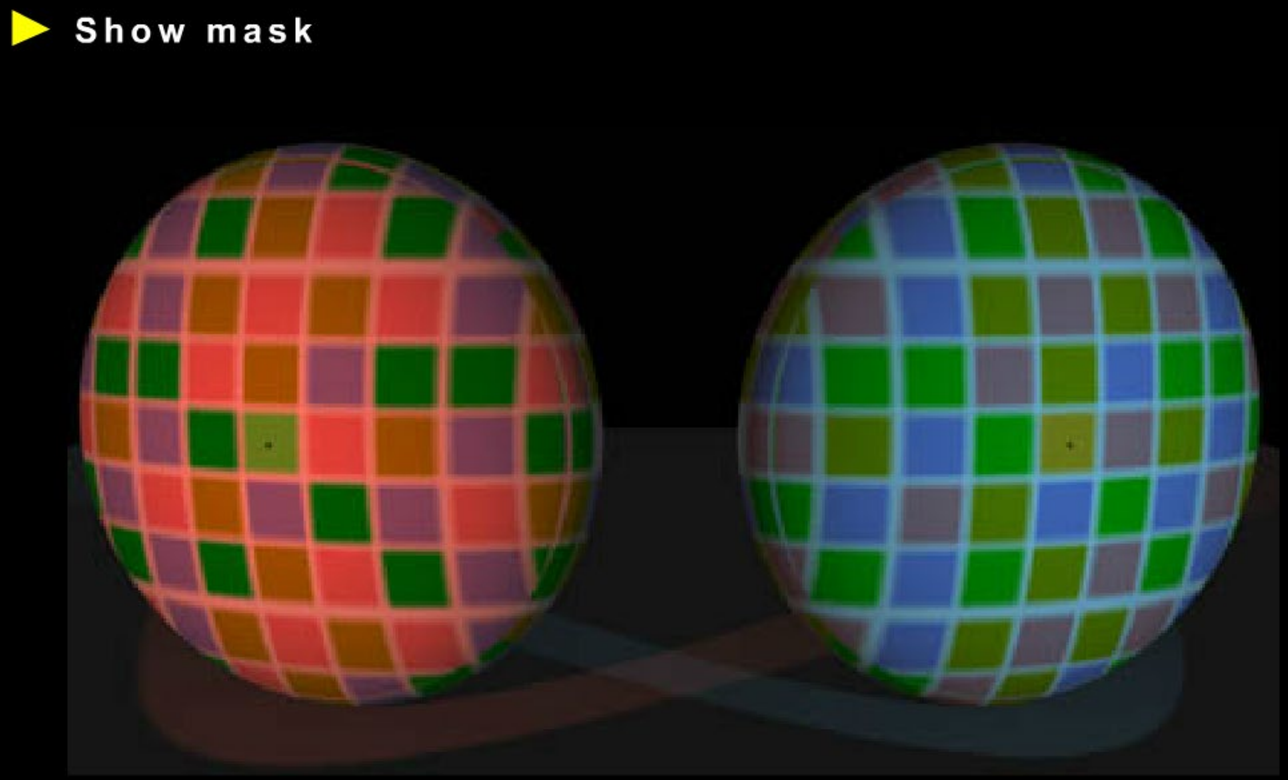
Chromatic adaptation and colour constancy

The change in colour appearance following adaptation is due to chromatic adaptation. Chromatic adaptation is adaptation to the colour is of the ambient illumination.



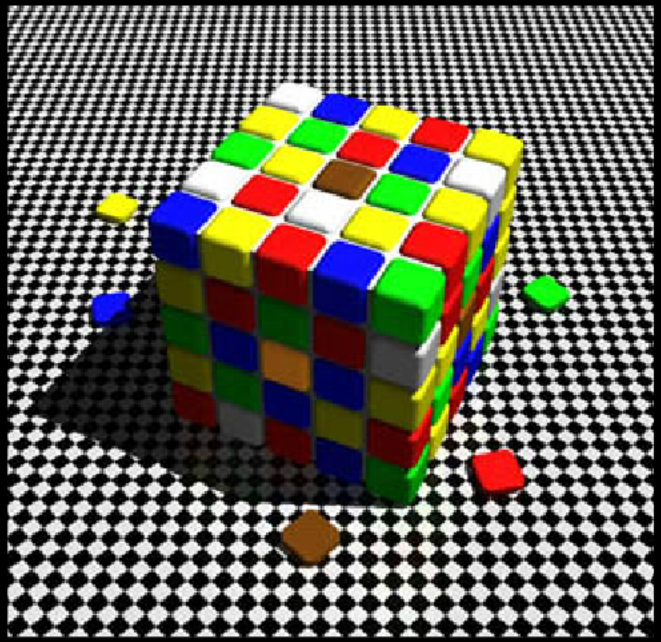
Amazing Art, Viperlib

Colour and the illuminant



Colour and brightness

THE EFFECT OF COLOR ON BRIGHTNESS PERCEPTION



The color of the "brown" Chiclet-like square in the middle of the upper face of the cube is identical to the "orange" square in the middle of the shaded face. To prove this, click on the "Play" button (top) to view an animation in which all but the center two squares are covered by a mask, or click on the "Move mask" button (bottom) to manually position the mask over the center squares.

[From Lotto, R. B. & Purves, D. The Effects of Color on Brightness. *Nature Neuroscience* 2, 1010-1014 (1999)]

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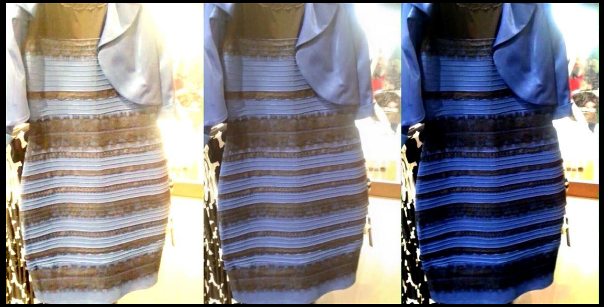
The dress…

The dress…



www.wired.com

COLOUR AND COGNITION

Stroop effect

Say to yourself the colours of the **ink** in which the following words are written -- as fast as you can.

So, for **RED**, say “red”.

But for **RED**, say “green”

Ready, steady…

TEST 1

RED	GREEN	BLUE	YELLOW	PINK
ORANGE	BLUE	GREEN	BROWN	WHITE
GREEN	YELLOW	PINK	RED	ORANGE
BROWN	RED	WHITE	BLUE	YELLOW
WHITE	ORANGE	GREEN	BROWN	RED

How long?

TEST 2

BLUE	PINK	WHITE	RED	BROWN
BROWN	RED	BLUE	GREEN	ORANGE
YELLOW	BLUE	RED	ORANGE	WHITE
BROWN	RED	GREEN	WHITE	RED
RED	PINK	BLUE	GREEN	WHITE

How long?

COLOUR VISION DEFICIENCIES

Normal

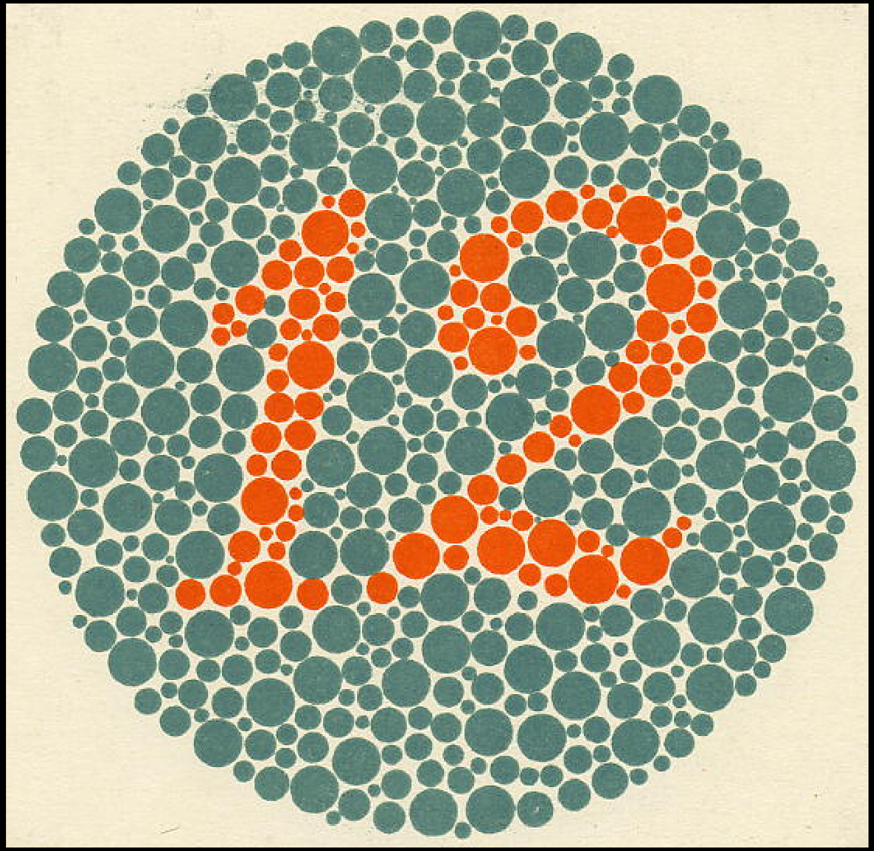
Deuteranope

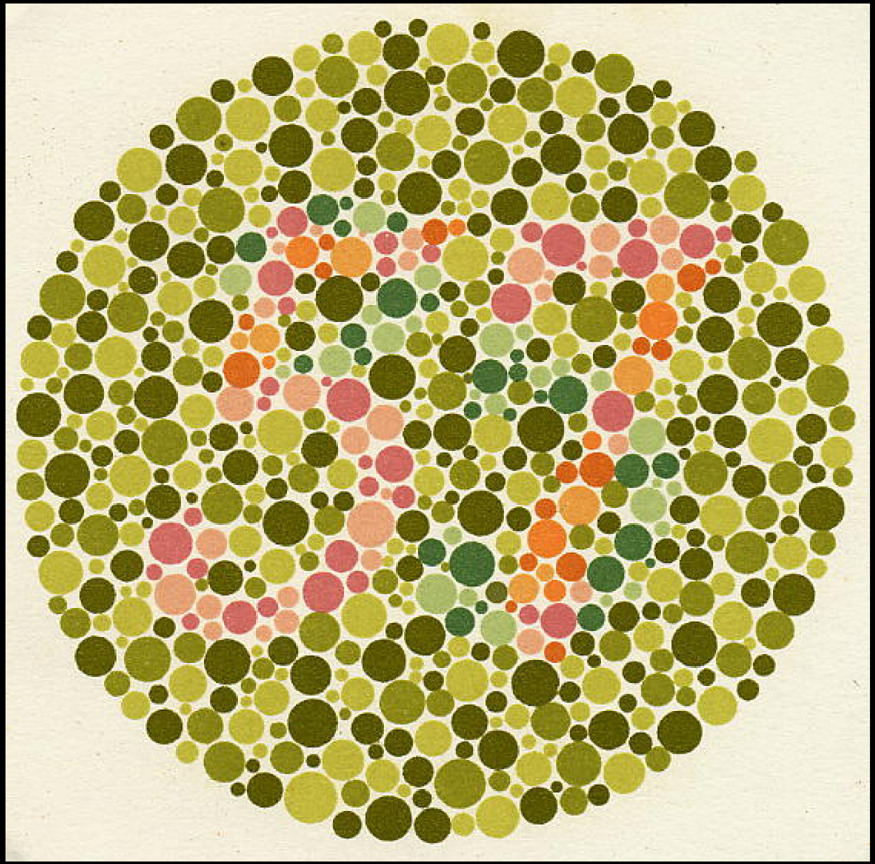
Tritanope

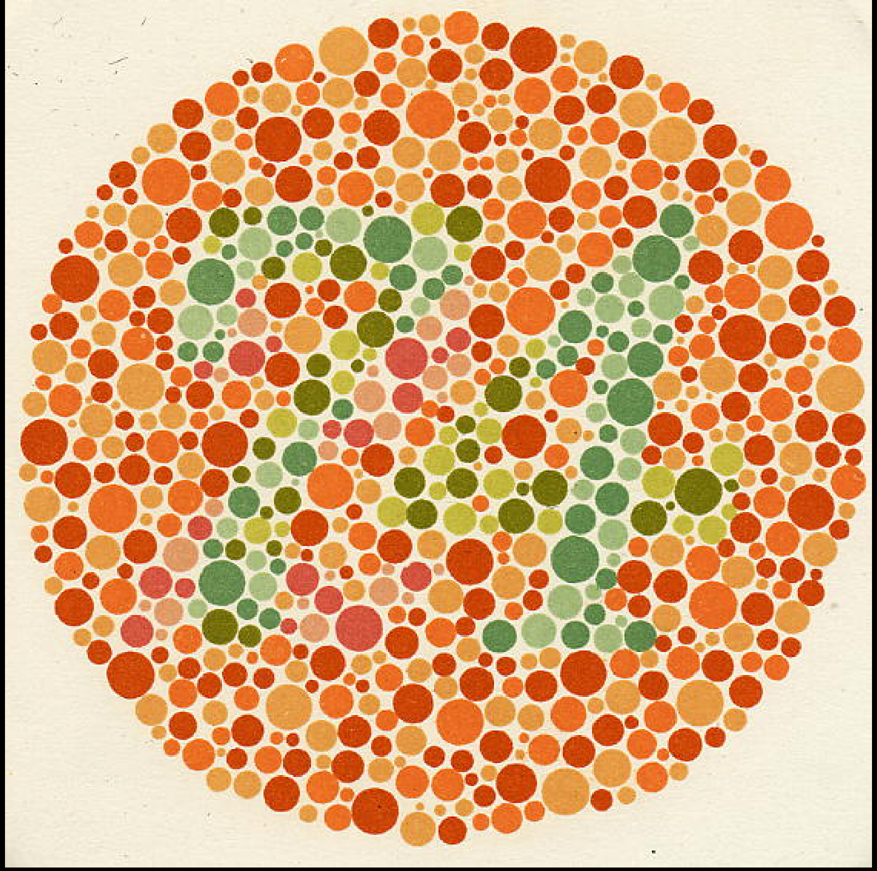
Protanope

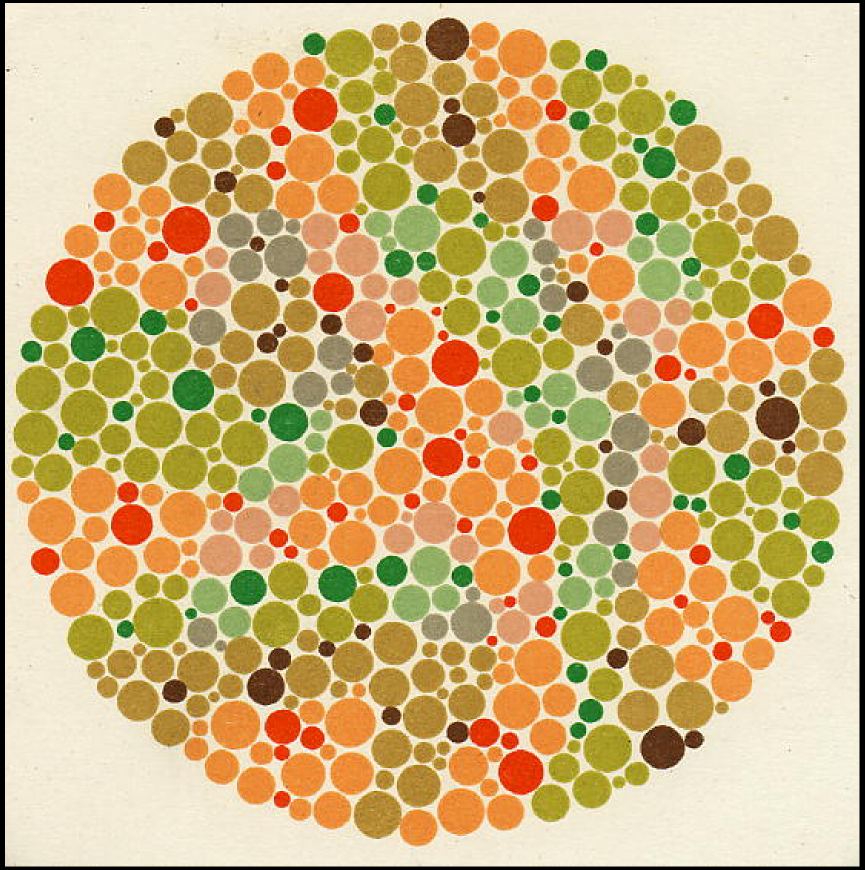
From Sharpe, Stockman, Jägle & Nathans, 1999

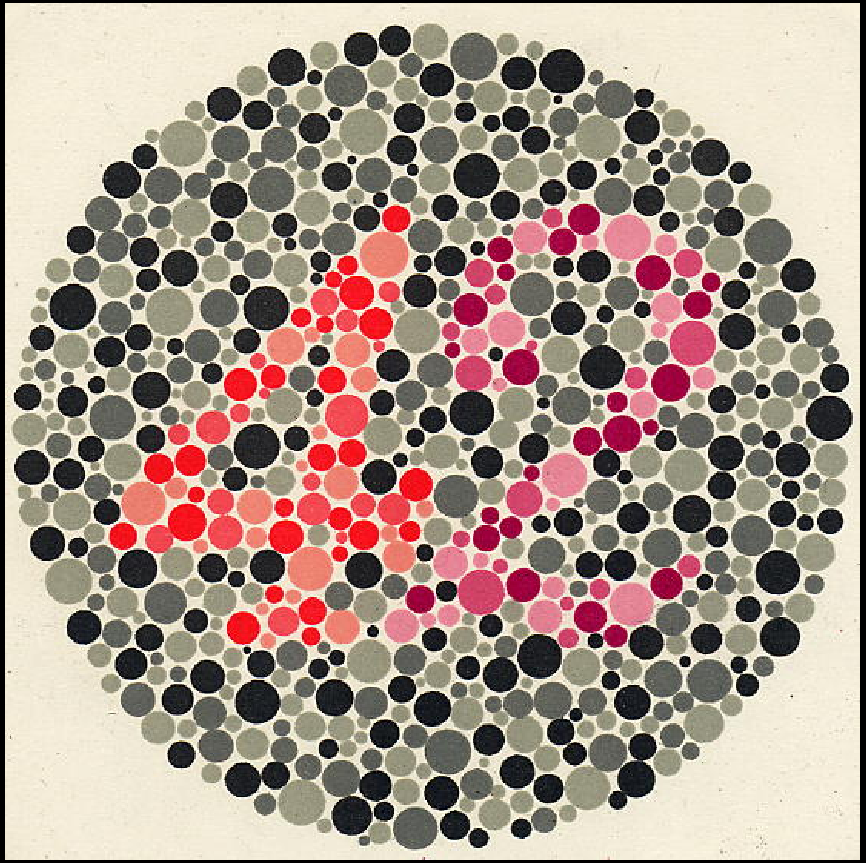
Ishihara plates











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

Condition		percent in UK Male	percent in UK 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

XY inheritance

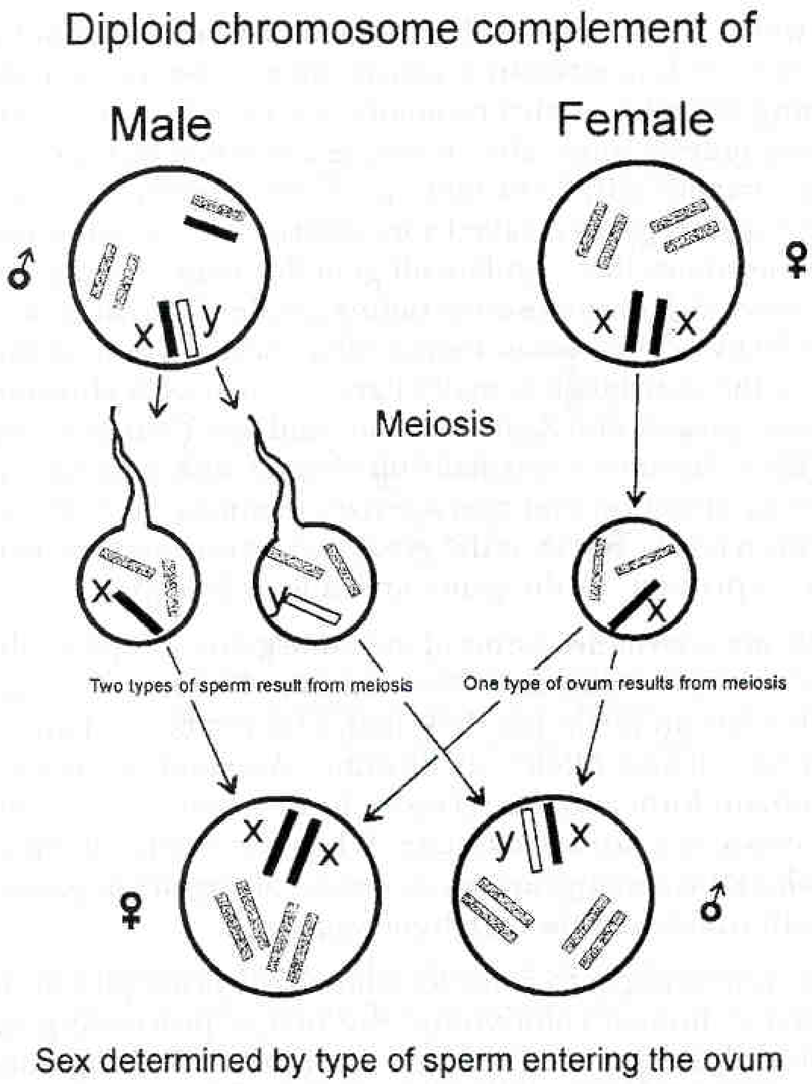


Figure 10.17 Prior to fertilization, meiotic division of germ cells results in two types of sperm, but only one type of ovum. Depending on which sperm is effective, the fertilized ovum will have two X cells and be female, or one X and one Y cell and be male. This diagram show why the X cell of the male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

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

Why might it have been important?

No red-green discrimination

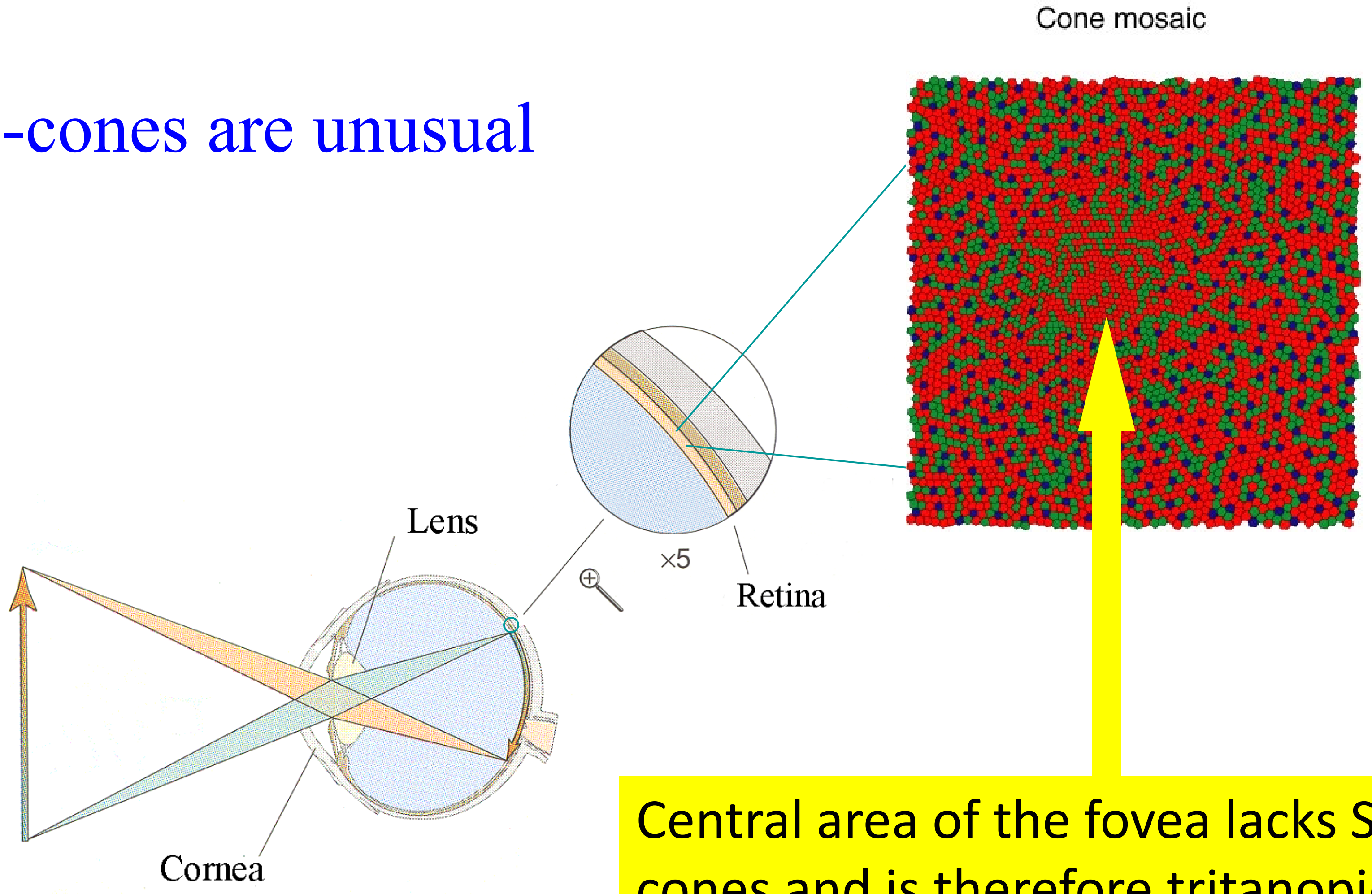
Source: Hans Irtel

Red-green discrimination

Source: Hans Irtel

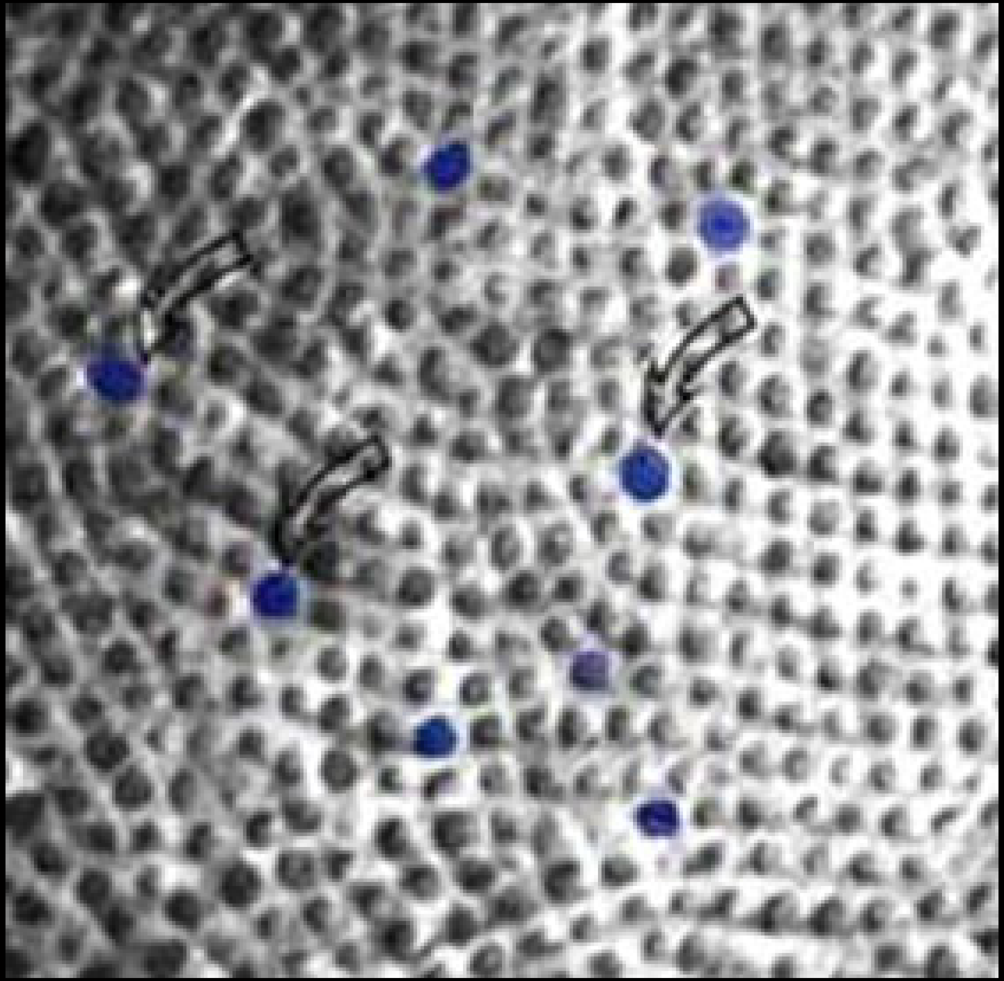
S-CONE MEDIATED VISION
IS UNUSUAL

S-cones are unusual



Central area of the fovea lacks S-cones and is therefore tritanopic.

In other retinal regions, the S-cone mosaic remains sparse.

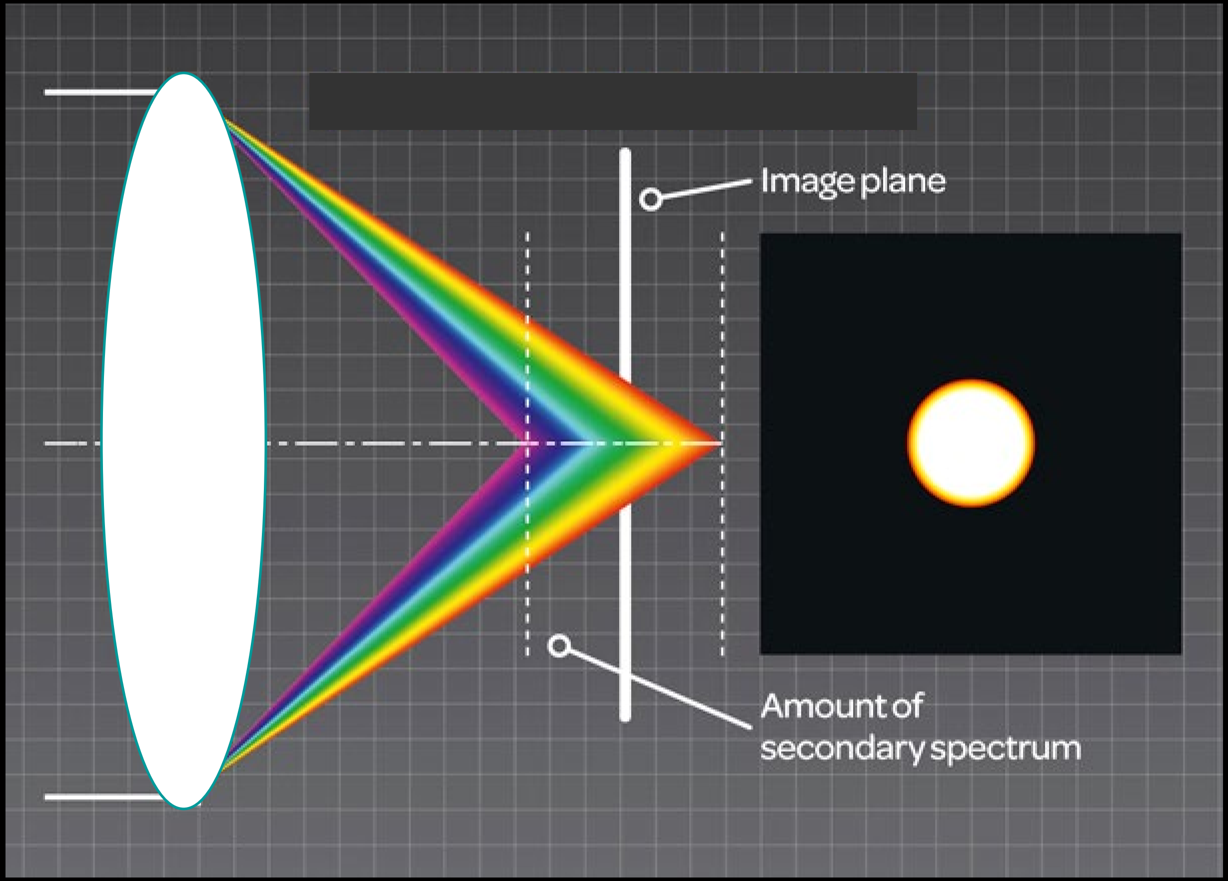


S-cones form between 5 and 10% of the cone population.

Curcio et al.

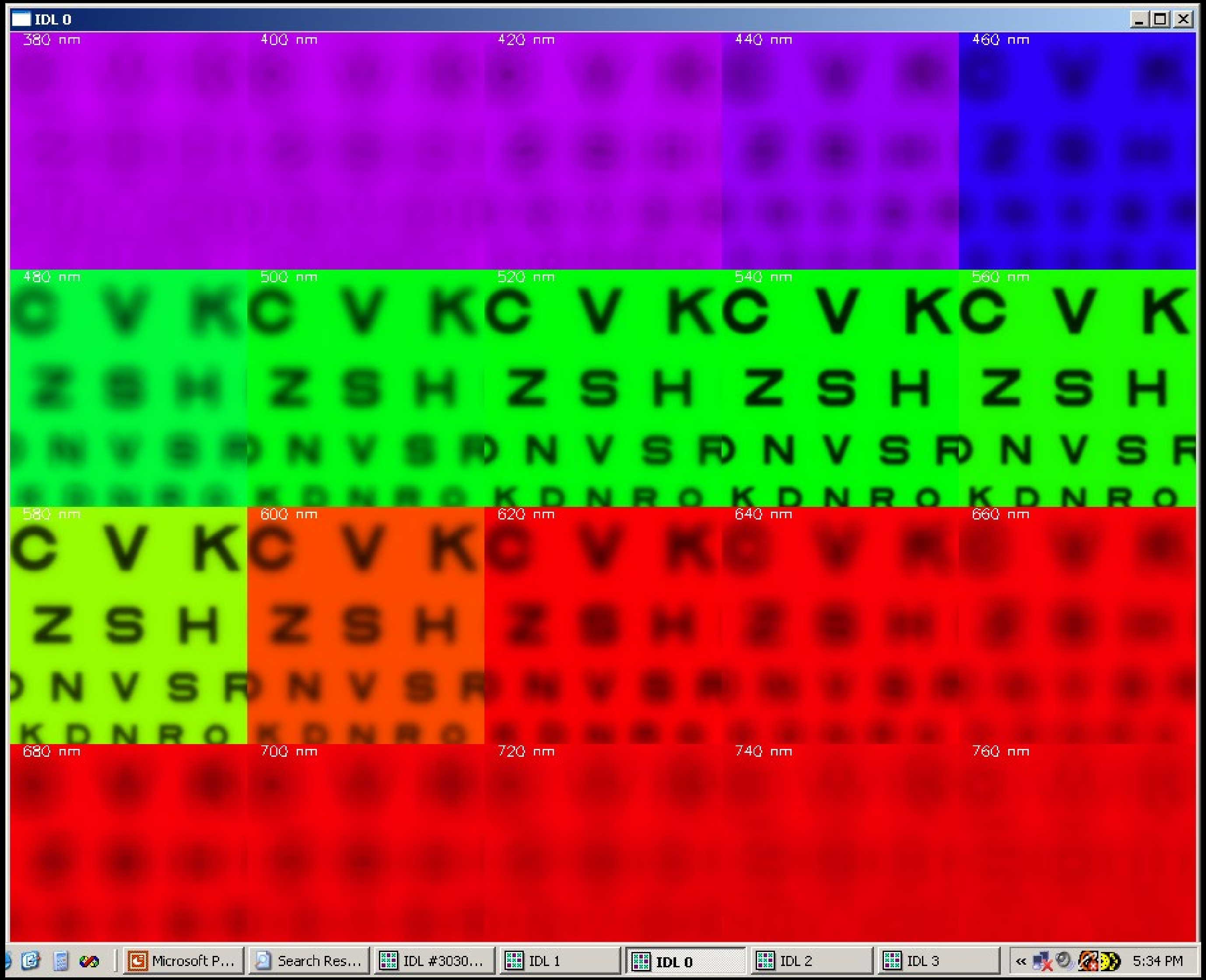
Why is S-cone vision sparse?

Chromatic aberration



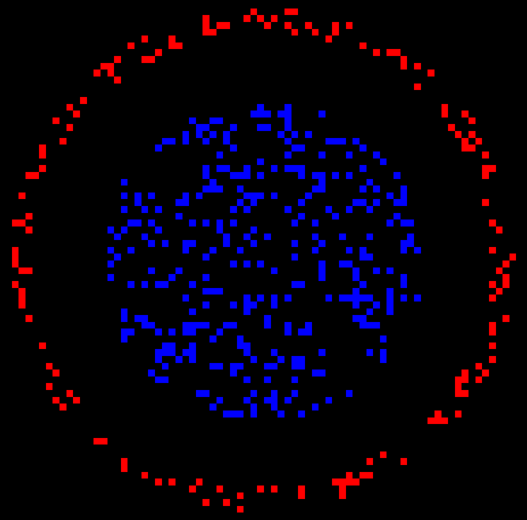
Base picture: Digital camera world

Effect of chromatic blur on eye chart



Jim Schwiegerling, U. Arizona

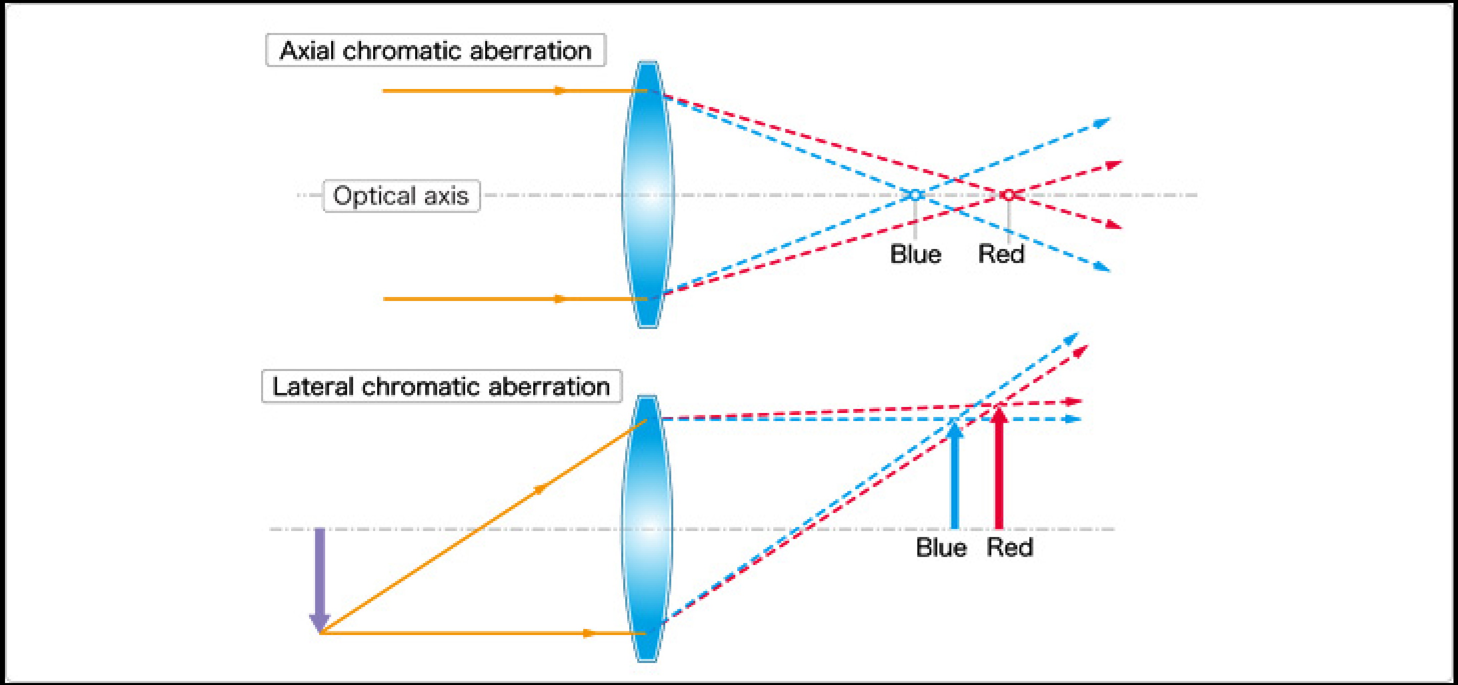
Chromostereopsis



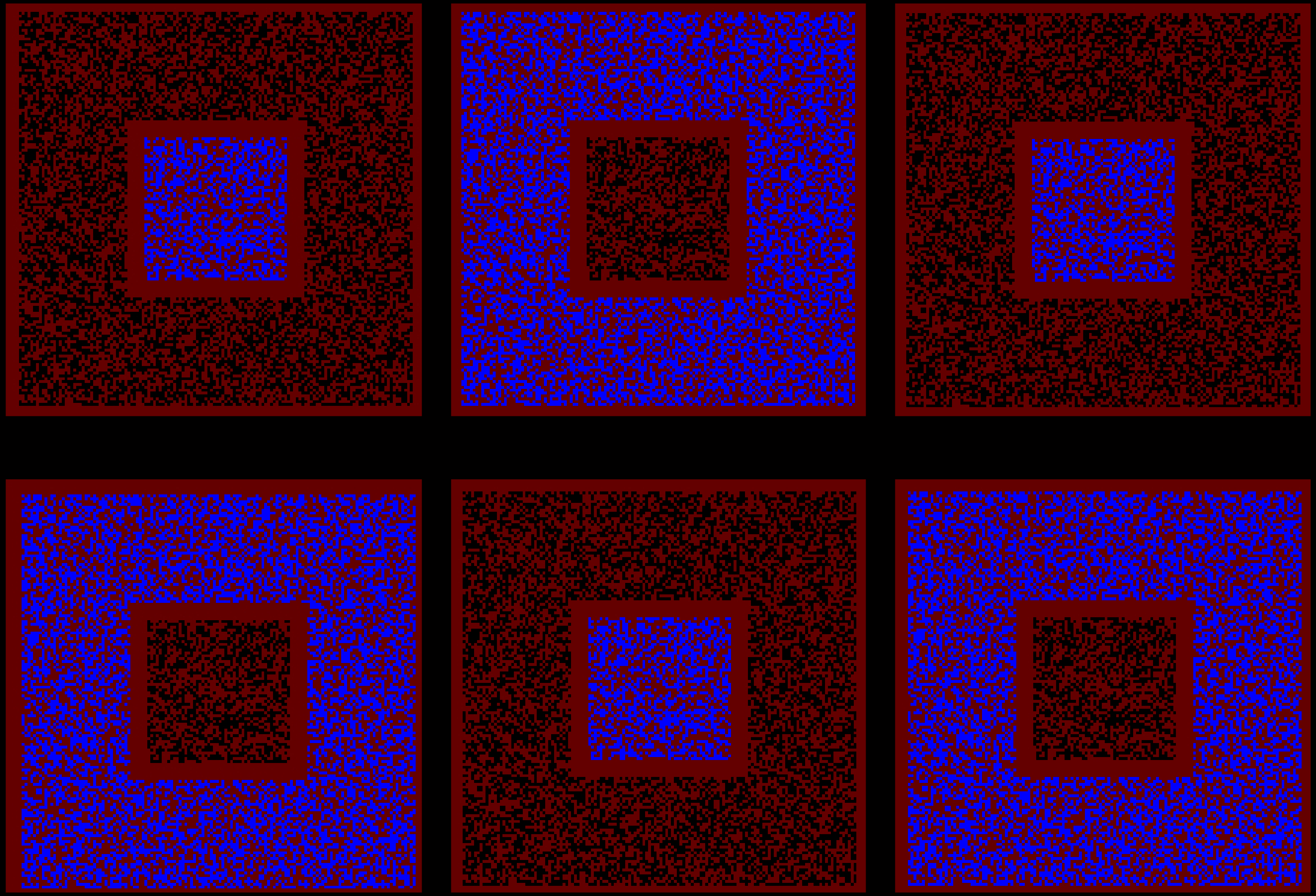
Different colours are perceived
at different depths...

Akitaoka Kitaoka

Linked to lateral chromatic aberrations…



Chromostereoscopic windows



Akitaoka Kitaoka