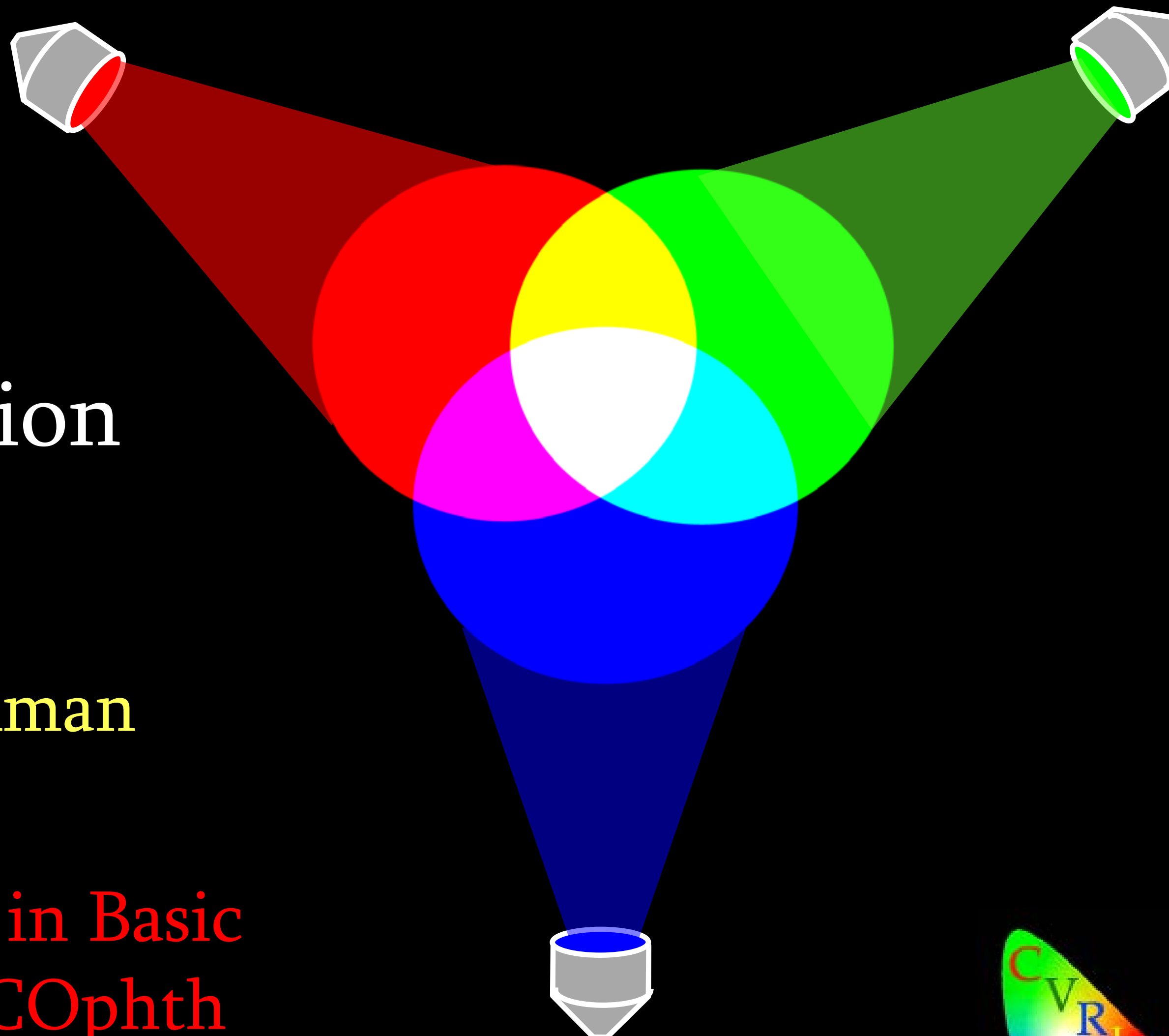
Colour Vision

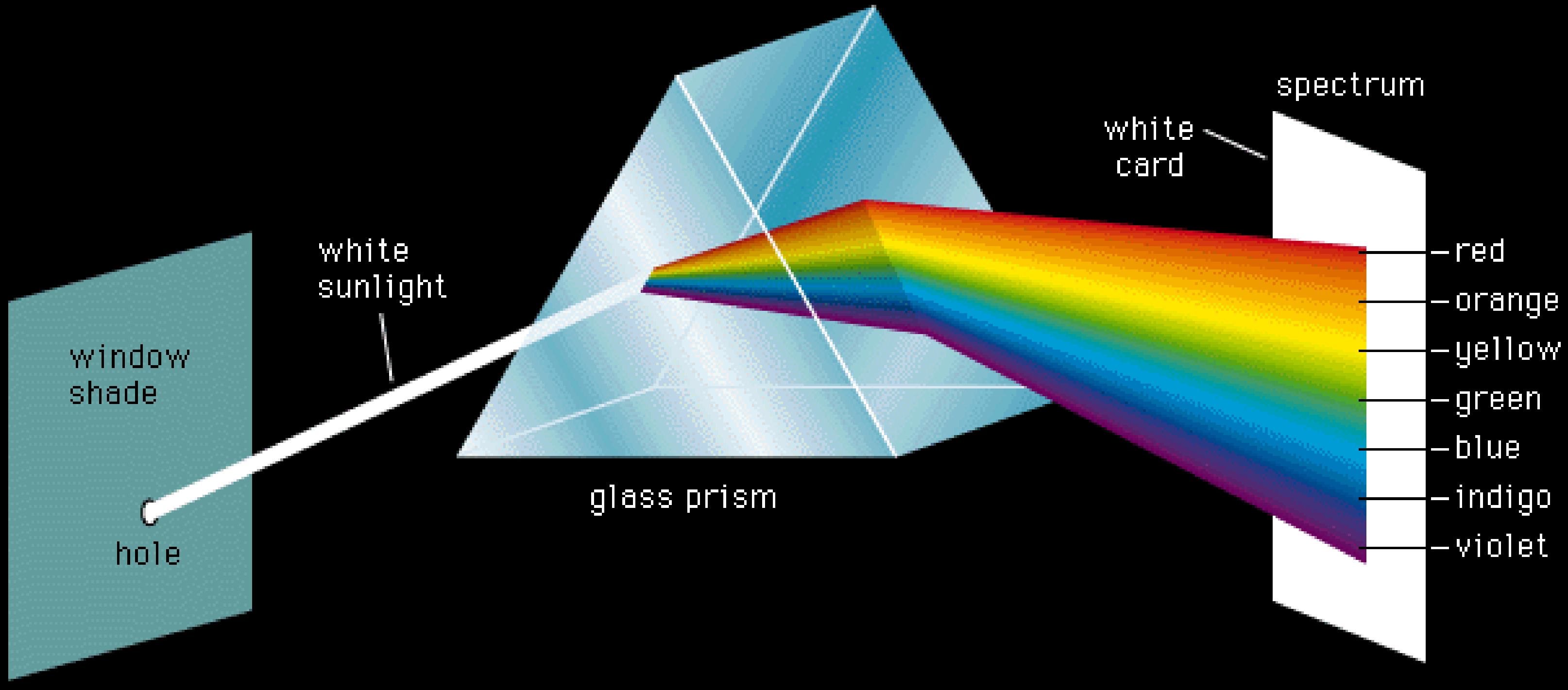
Andrew Stockman

Revision Course in Basic Sciences for FRCOphth



INTRODUCTION

Light 400 - 700 nm is most important for vision



How dependent are we on colour?

No colour…

Which are the apples, oranges, and grapefruits?

Colour…

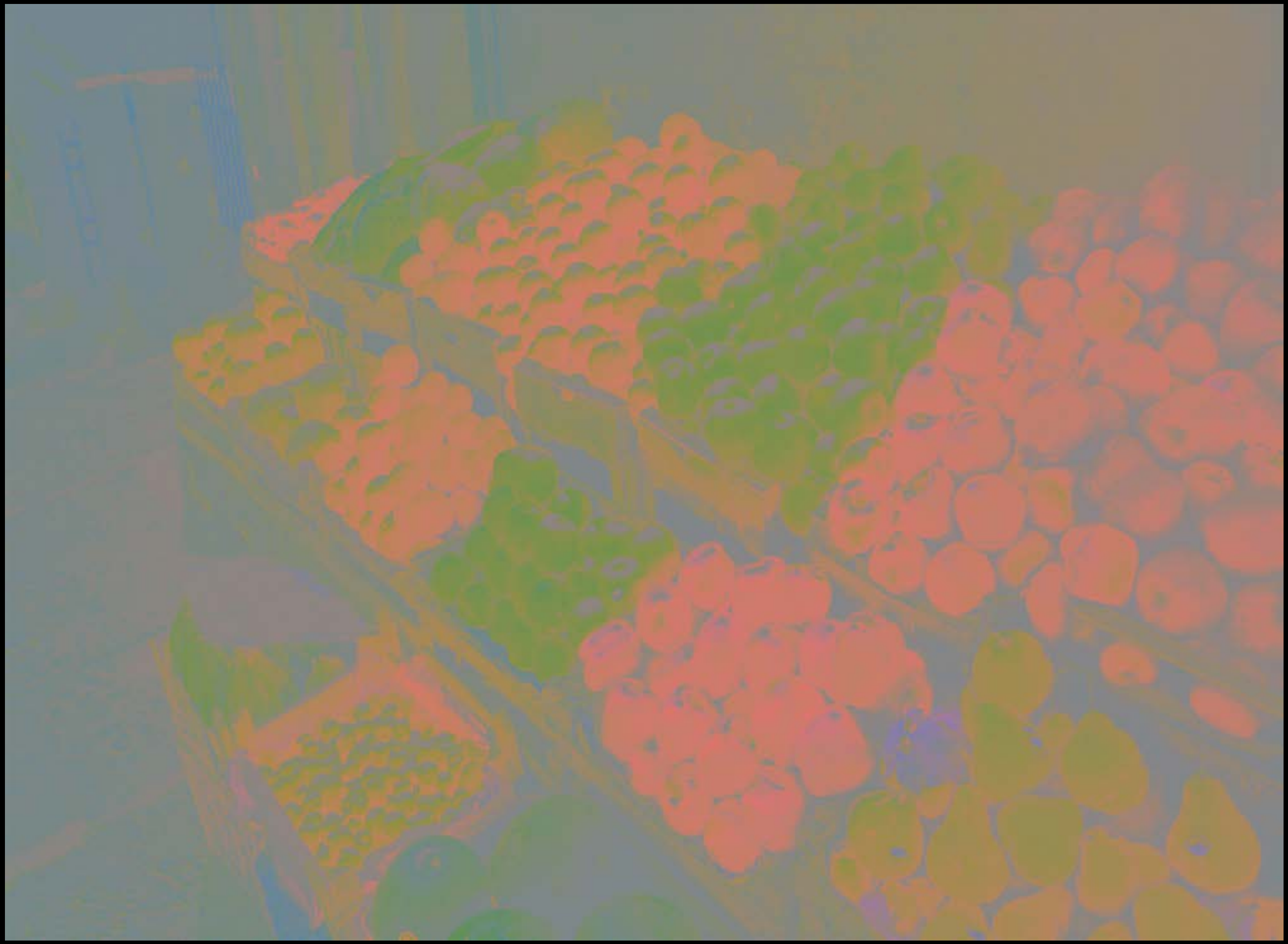
But how important is colour?

Split the image into...

ACHROMATIC COMPONENTS

CHROMATIC COMPONENTS

CHROMATIC COMPONENTS



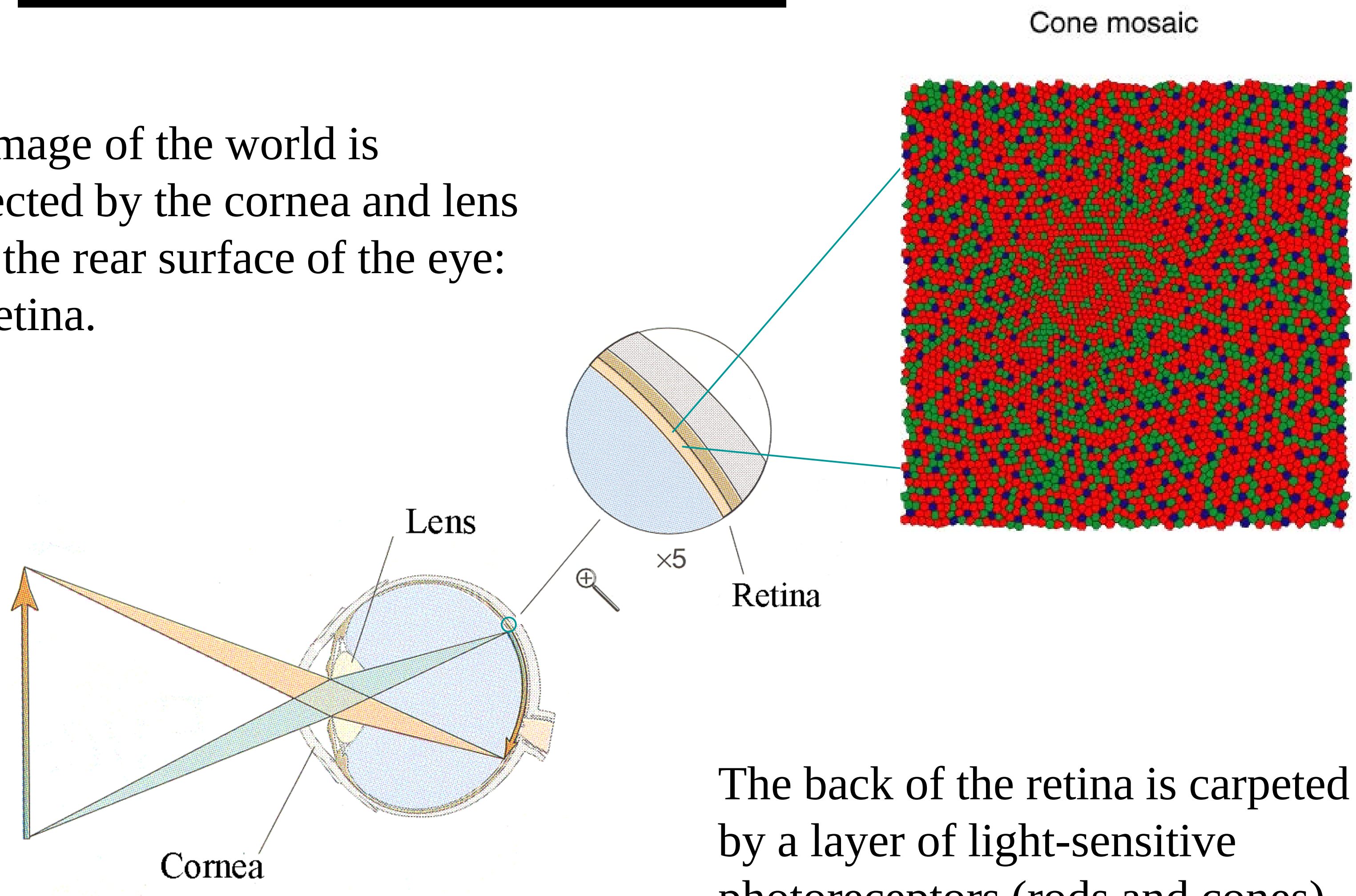
By itself chromatic information provides relatively limited information…

ACHROMATIC COMPONENTS

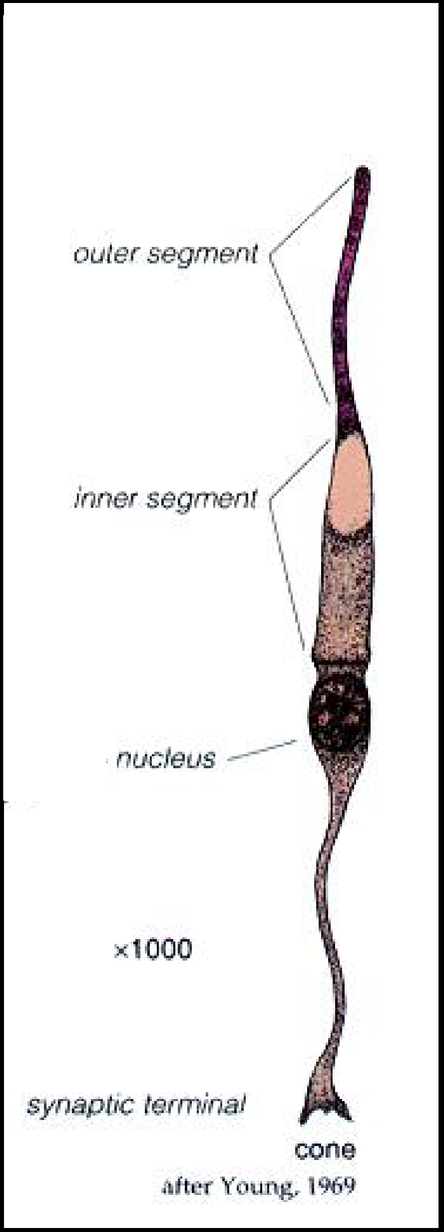
Achromatic information important for fine detail …

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).



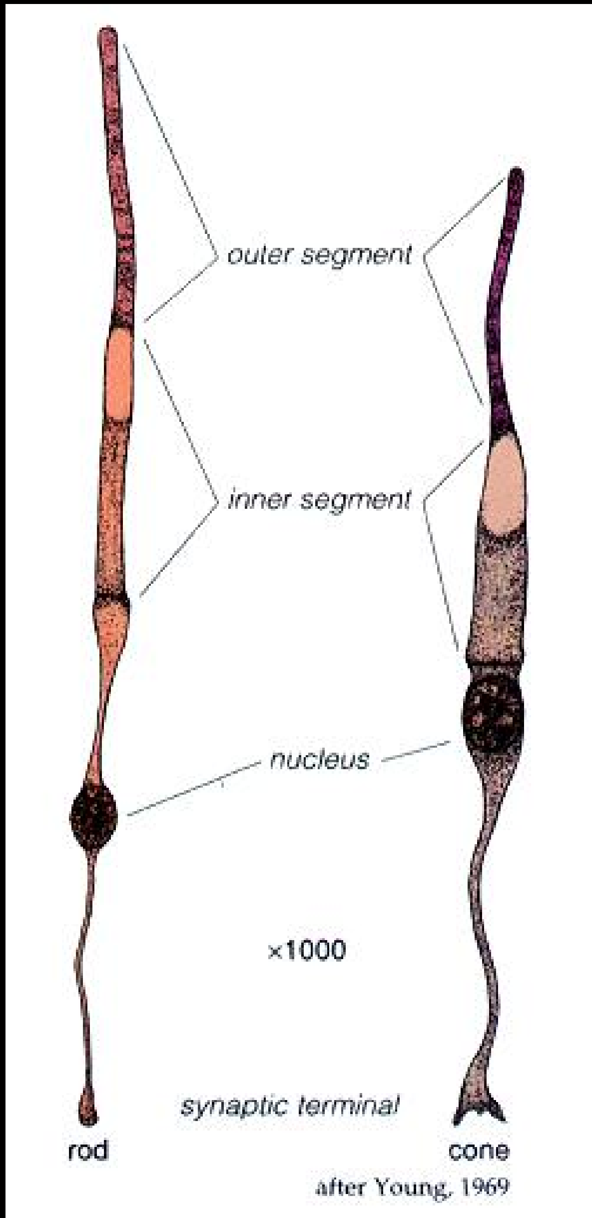
Human photoreceptors

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

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

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

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



Human photoreceptors

- **Rods**
  - Achromatic night vision
  - 1 type

Rod

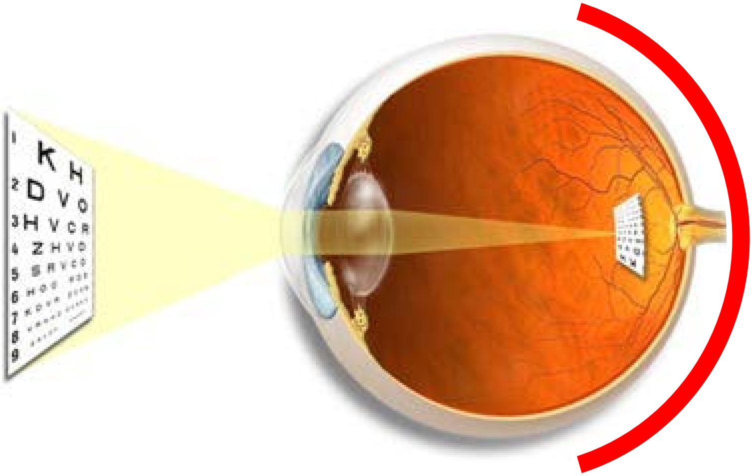
- **Cones**
  - Daytime, achromatic *and* chromatic vision
  - 3 types

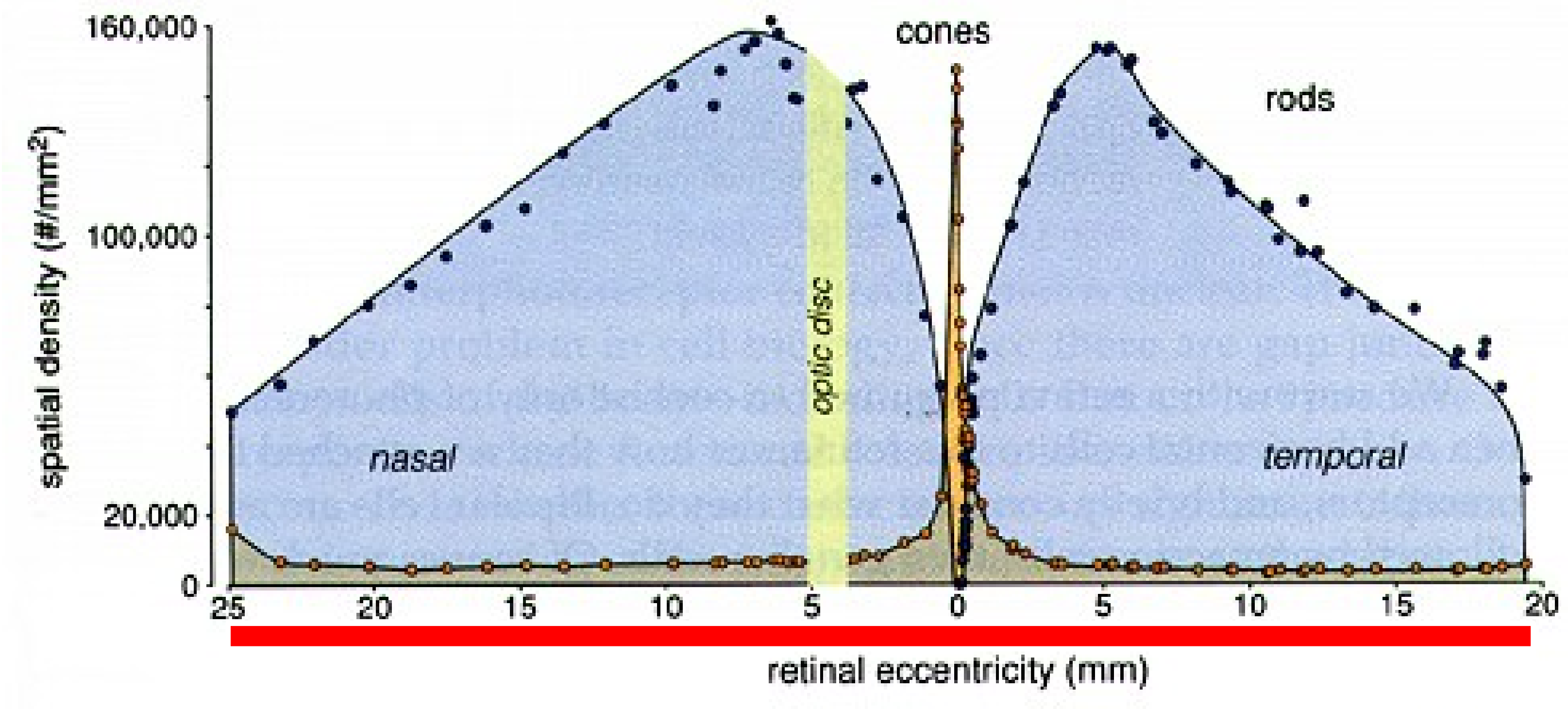
Long-wavelength-sensitive (L) or “red” cone

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

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

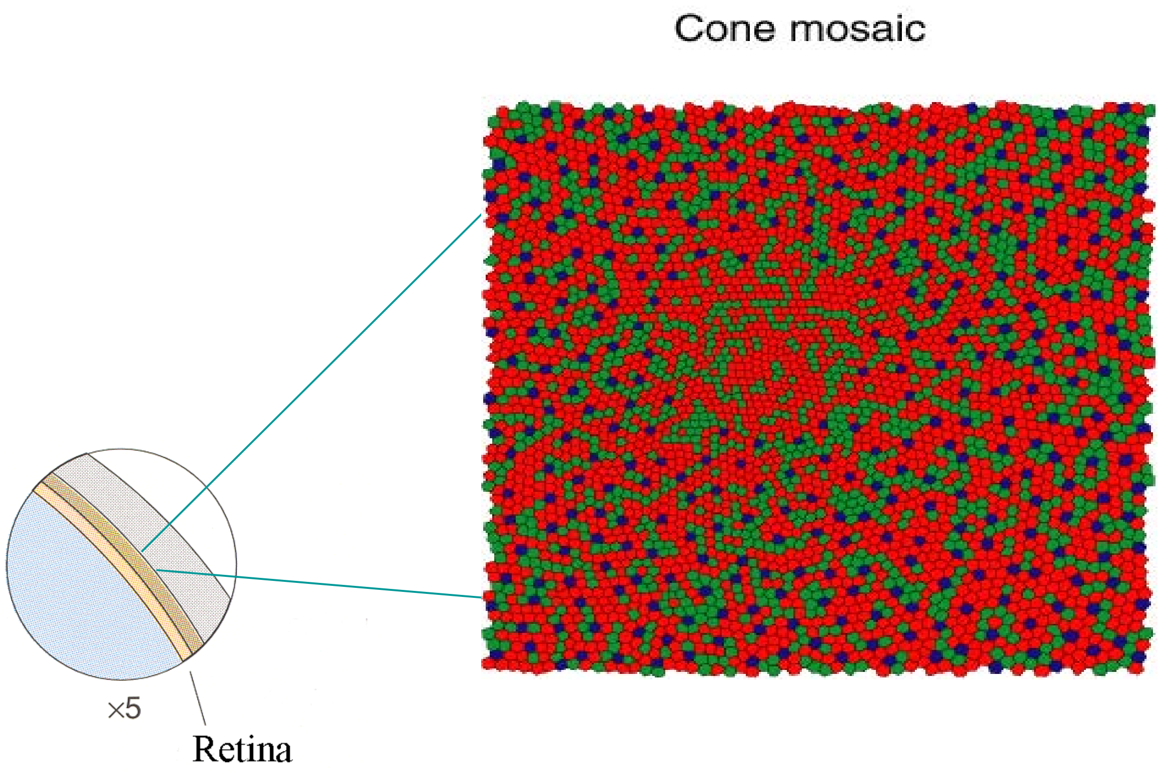
Rod and cone distribution





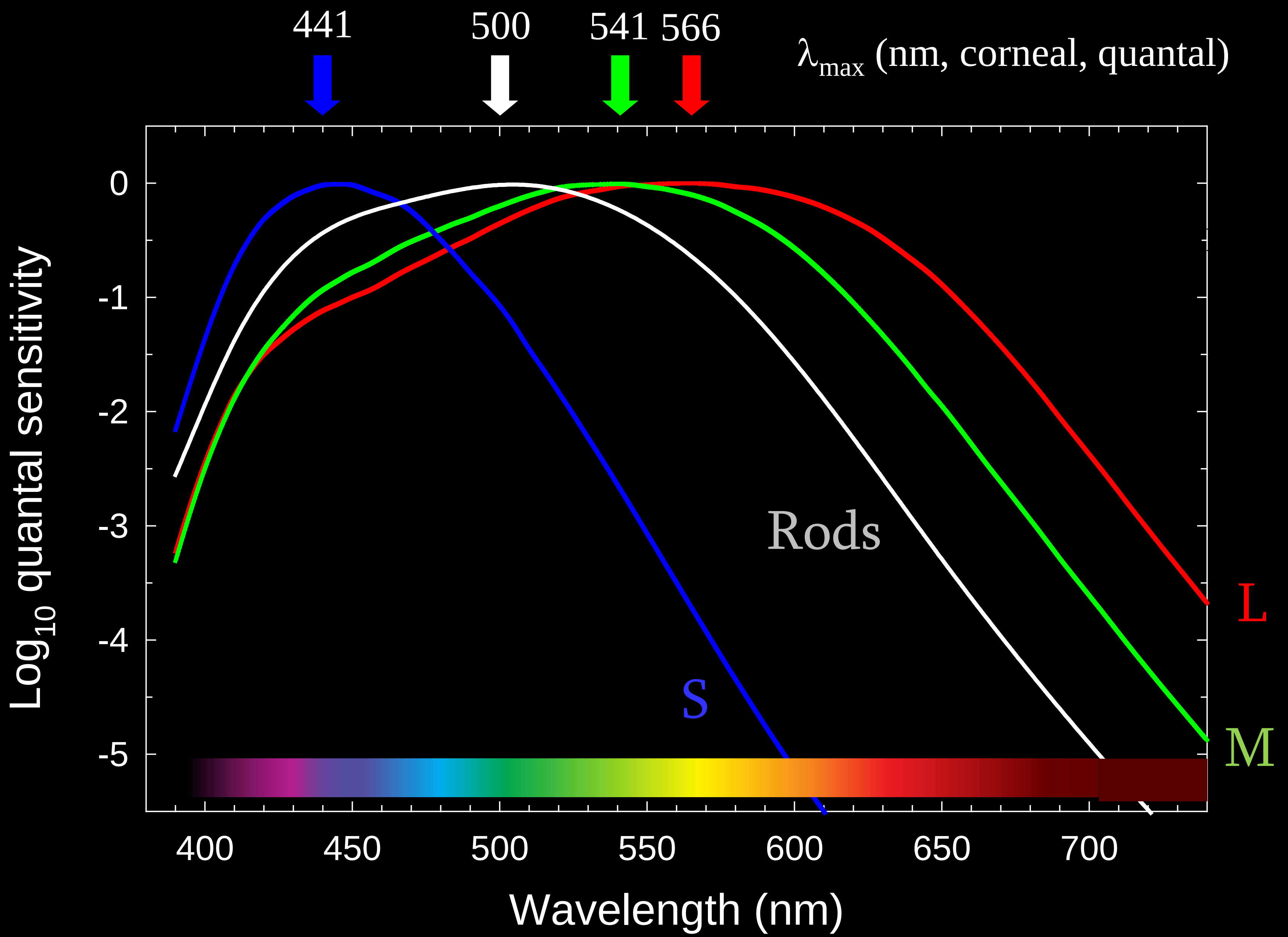
after Østerberg, 1935; as modified by Rodieck, 1988

0.3 mm of eccentricity is about 1 deg of visual angle



Central fovea is rod-free, and the very central foveola is rod- and S-cone free

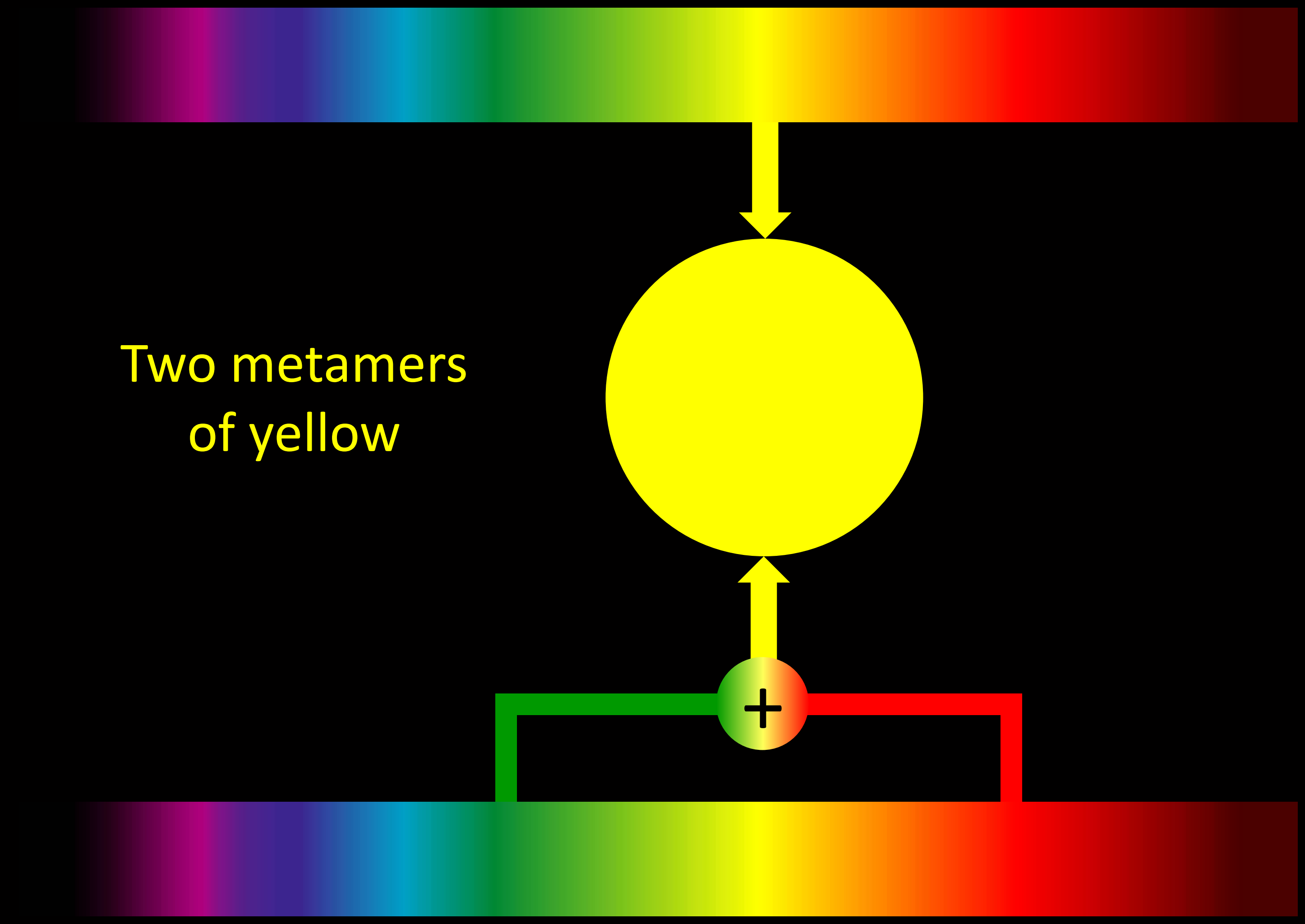
Four human photoreceptors have different spectral sensitivities



Colour…

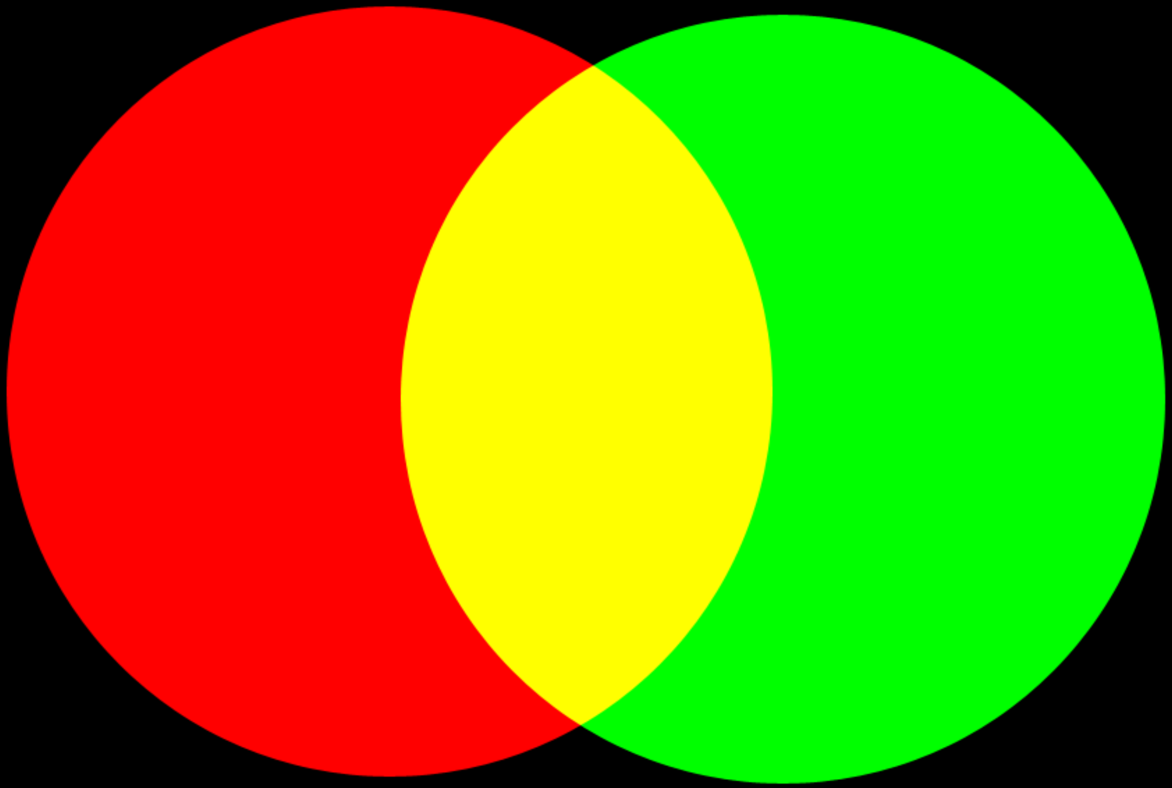
Is it mainly a property of physics or biology?

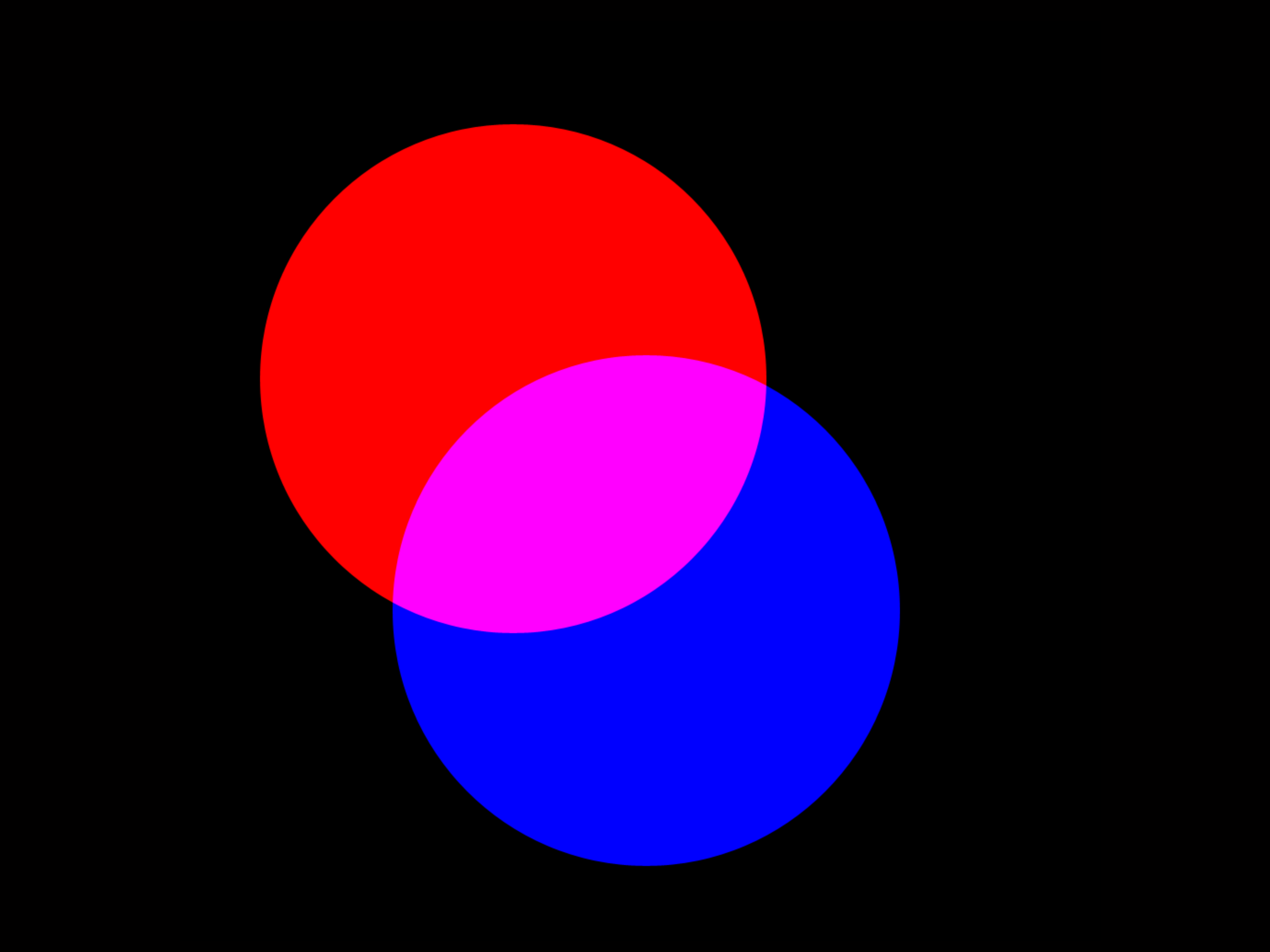
Colour isn't just about physics. For example:

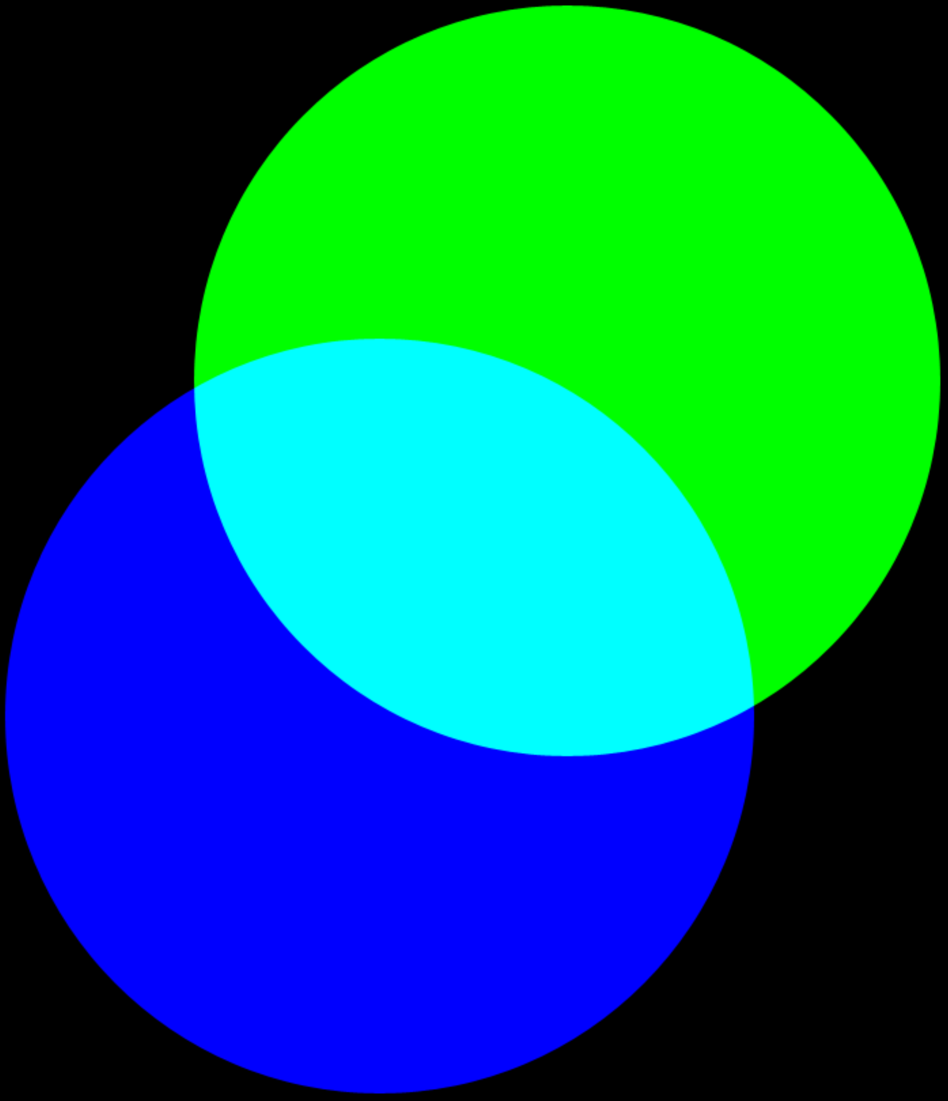


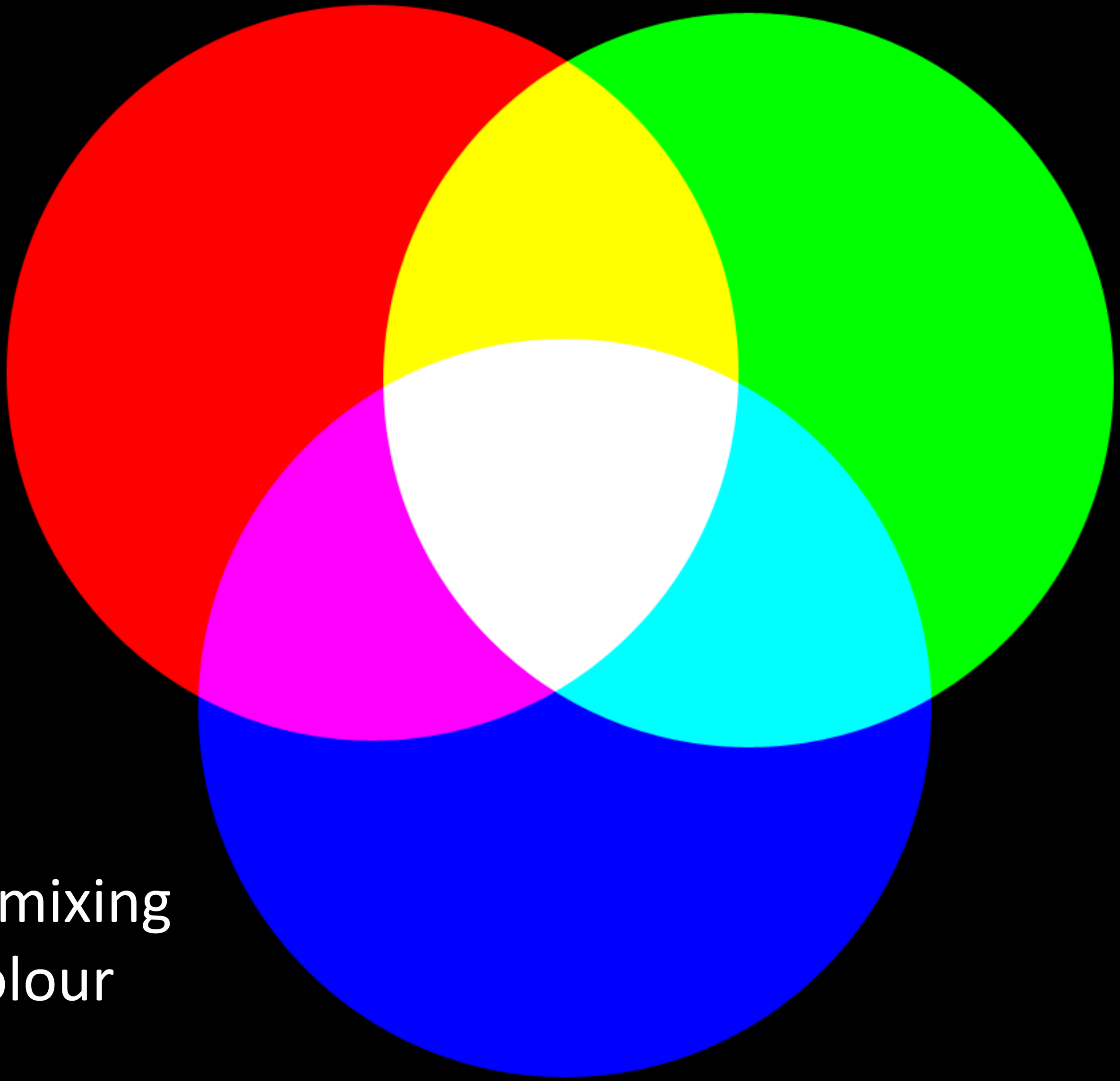
though physically very different, can appear identical.

There are many other such metamers or matches…

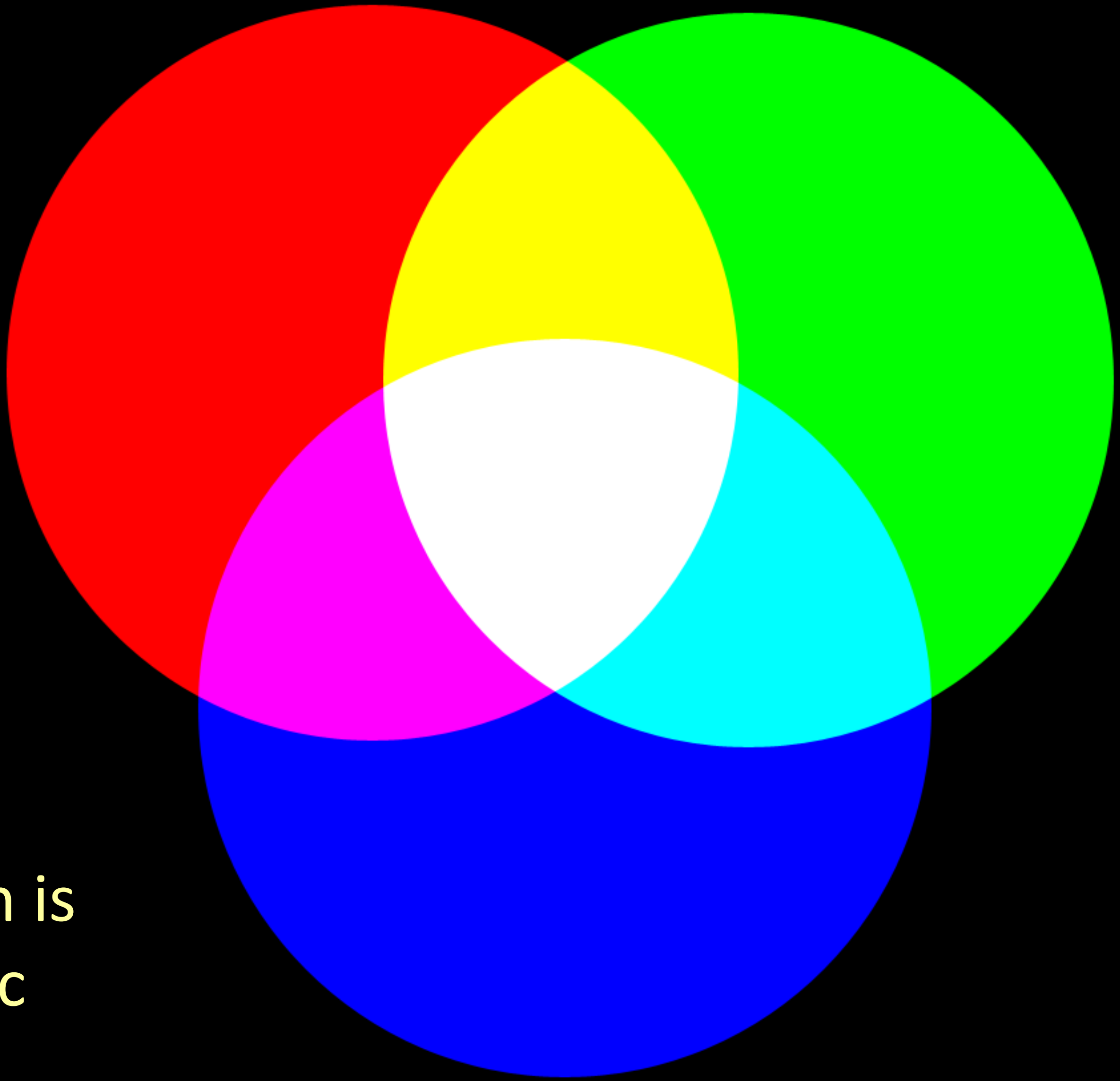




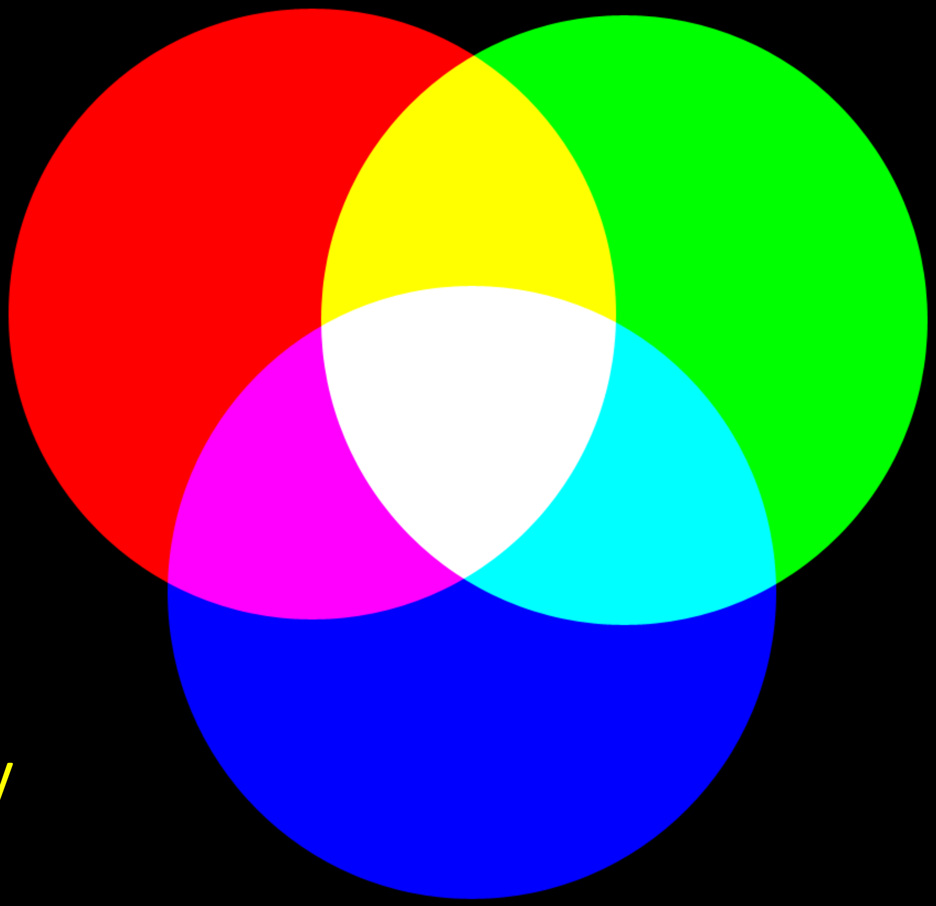




What can colour mixing tell us about colour vision?



Human vision is trichromatic



Trichromacy means that colour vision is relatively simple.

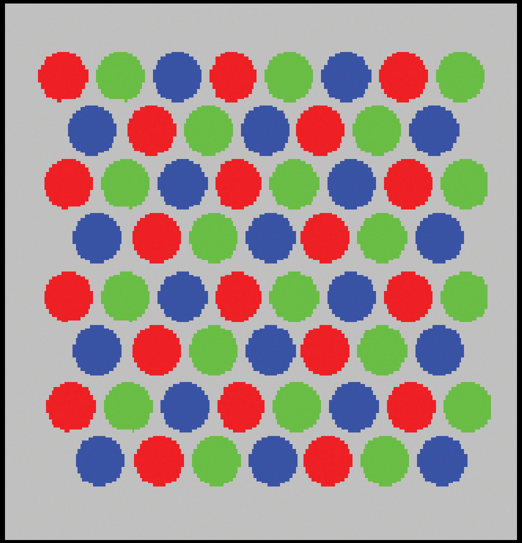
It is a 3 variable system…

Colour TV

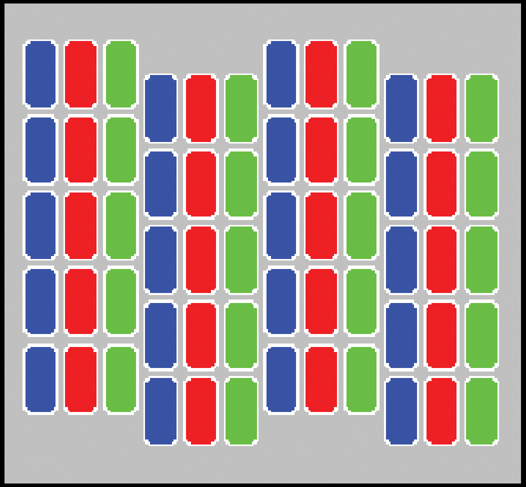
Trichromacy is exploited in colour reproduction, since the myriad of colours perceived can be produced by mixing together small dots of three colours.

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

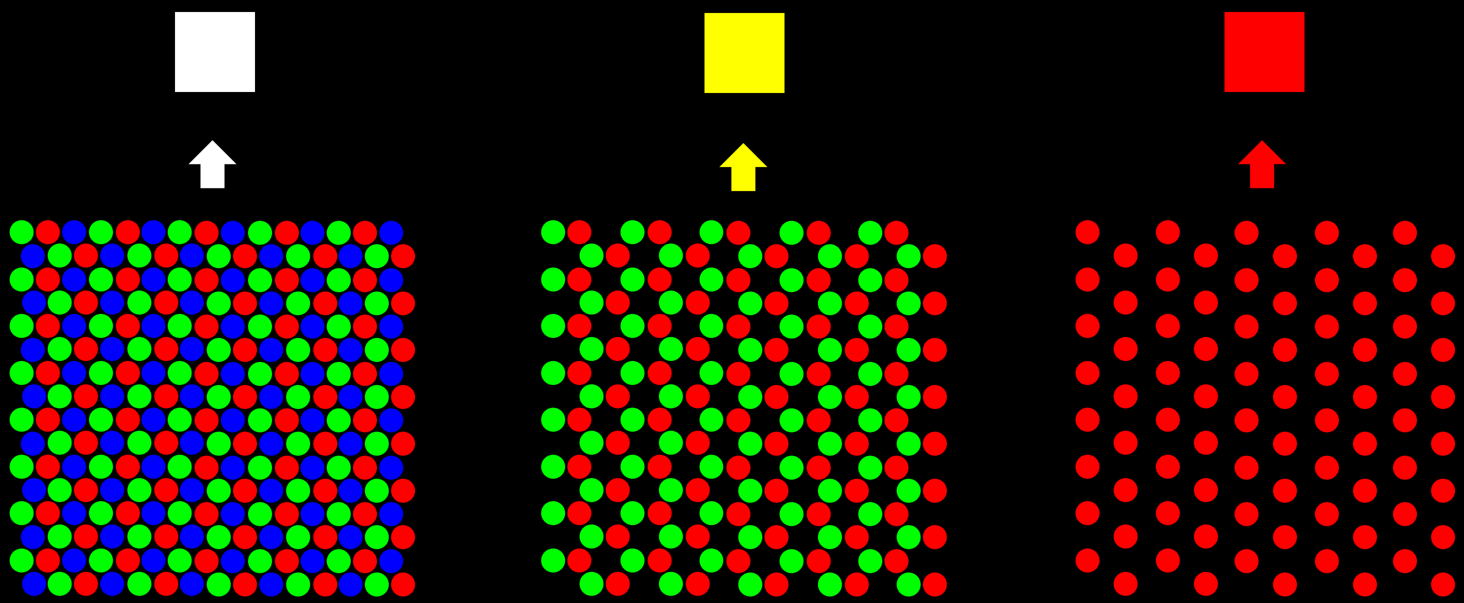
3-coloured dots



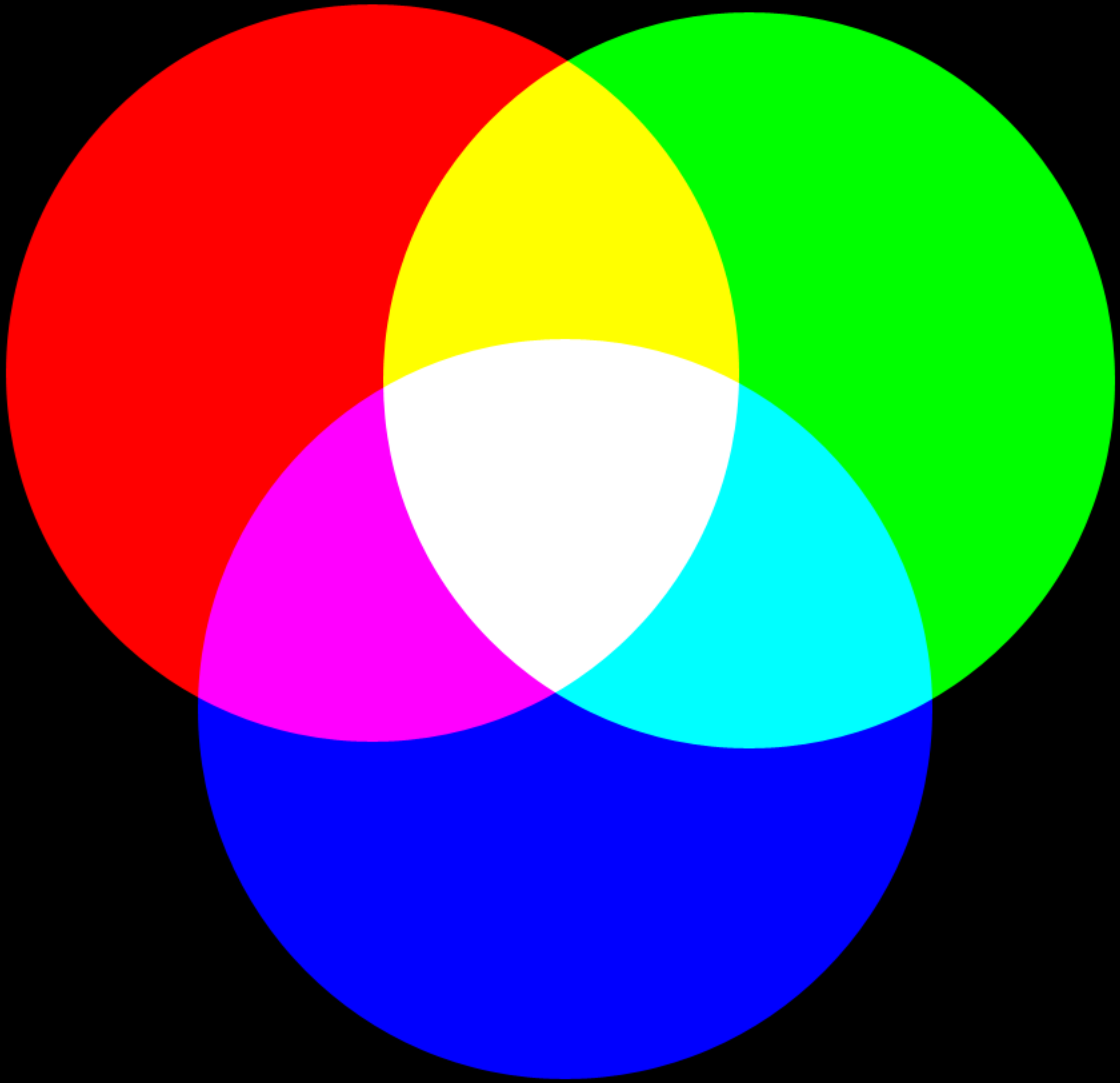
3-coloured bars



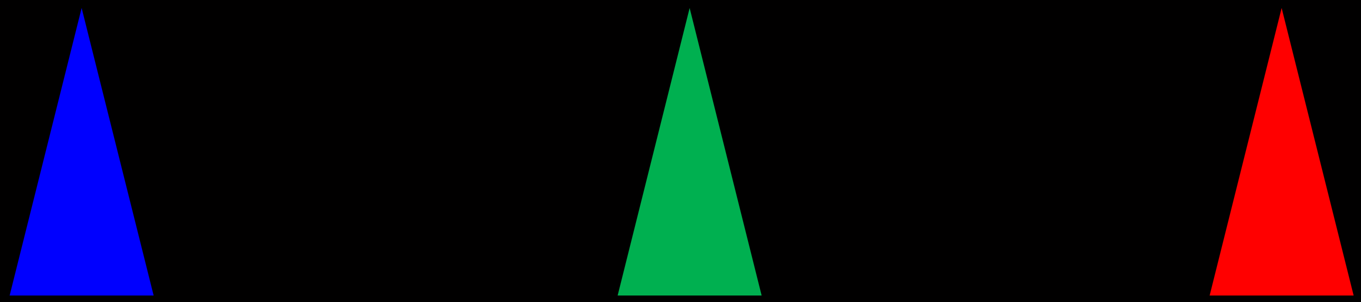
The dots produced by a TV or projector are so small that they are mixed together by the eye and thus appear as uniform patches of colour



Why is human vision trichromatic?



One reason is that just three cone photo-receptors underlie daytime colour vision. But what is it about each of them that makes colour vision trichromatic?



Short-wavelength-sensitive or “blue”

Middle-wavelength-sensitive or “green”

Long-wavelength-sensitive or “red”

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

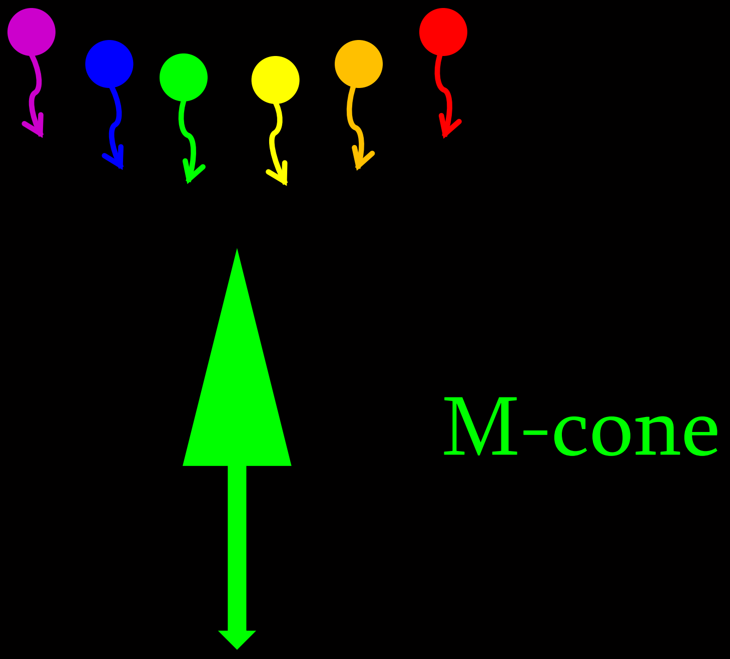
UNIVARIANT

What does univariant mean?

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

UNIVARIANCE

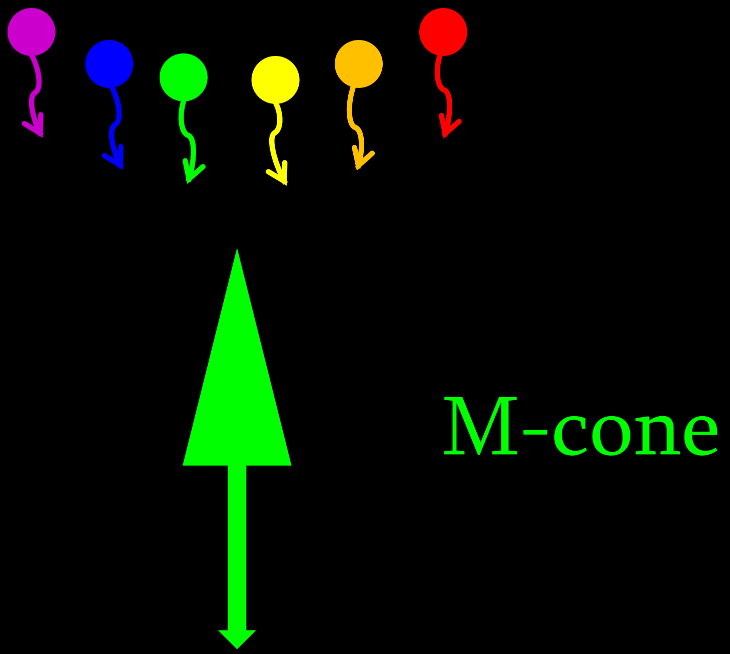
The effect of any absorbed photon is *independent* of its wavelength.



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

UNIVARIANCE

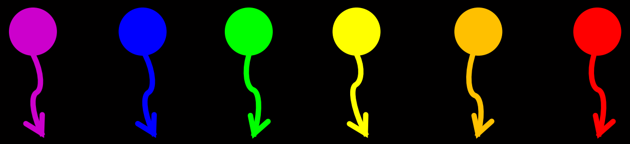
Crucially, the effect of any absorbed photon is *independent* of its wavelength.



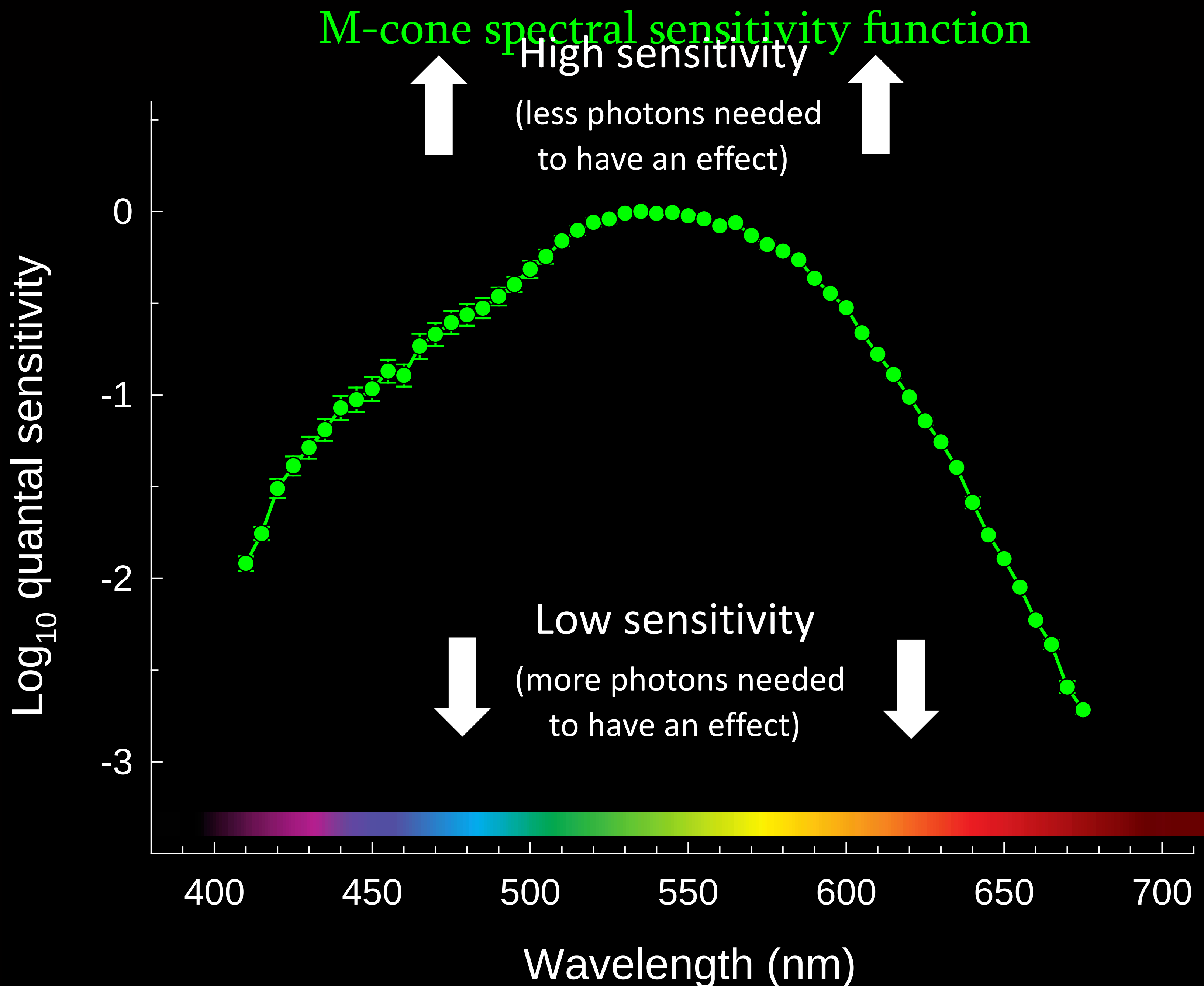
All the photoreceptor effectively does is to count photons.

UNIVARIANCE

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

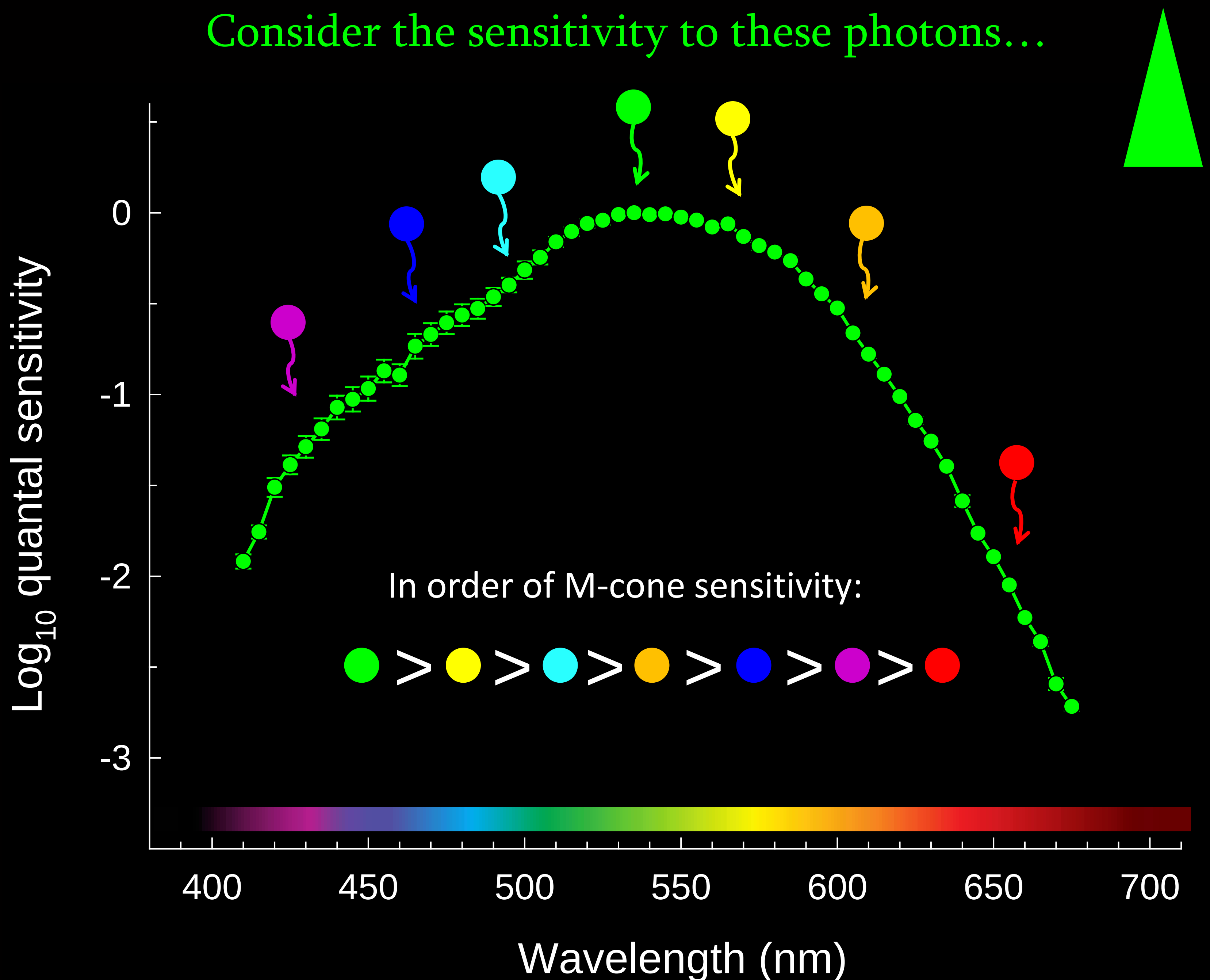


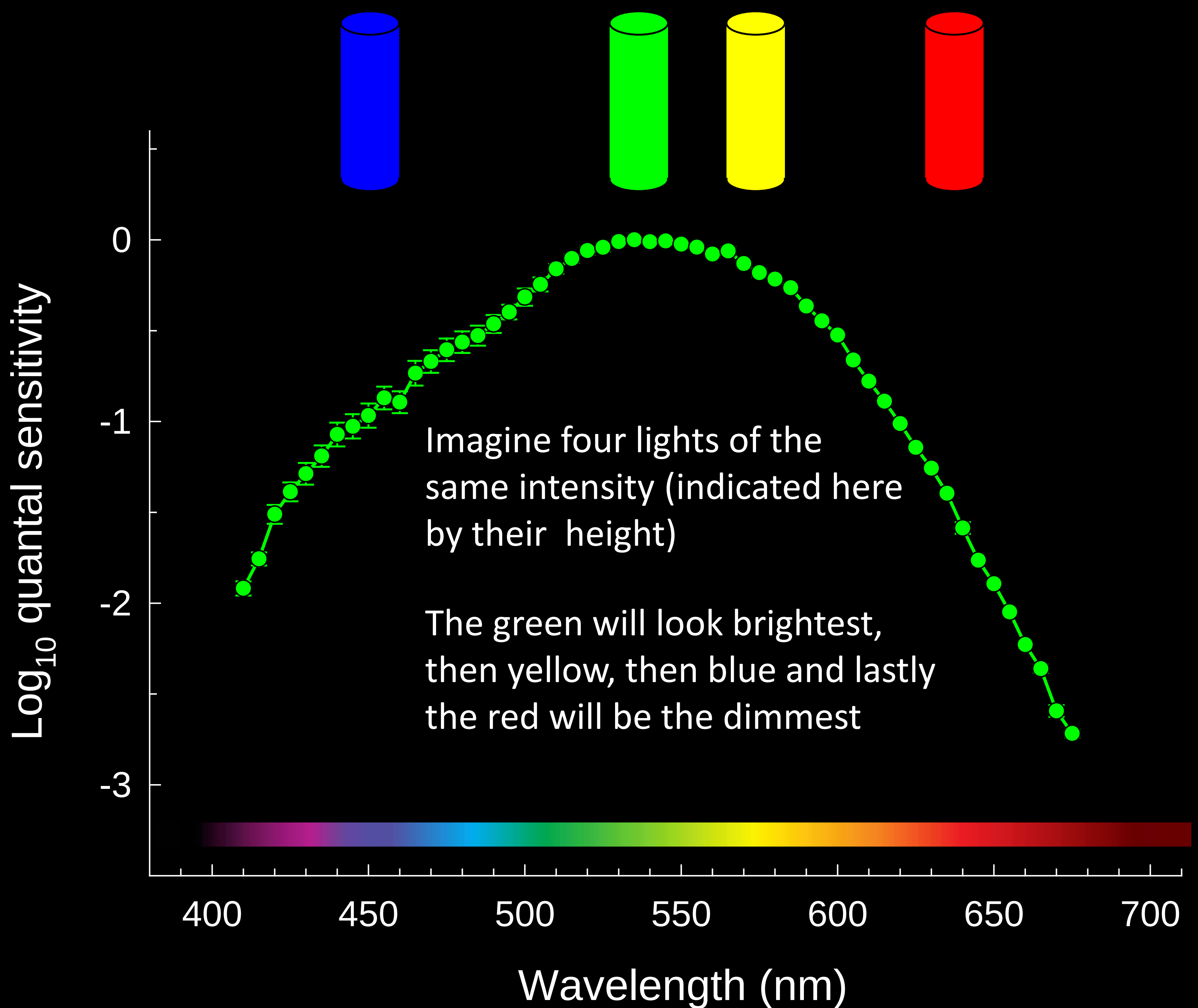
This is reflected in what is called a "spectral sensitivity function".



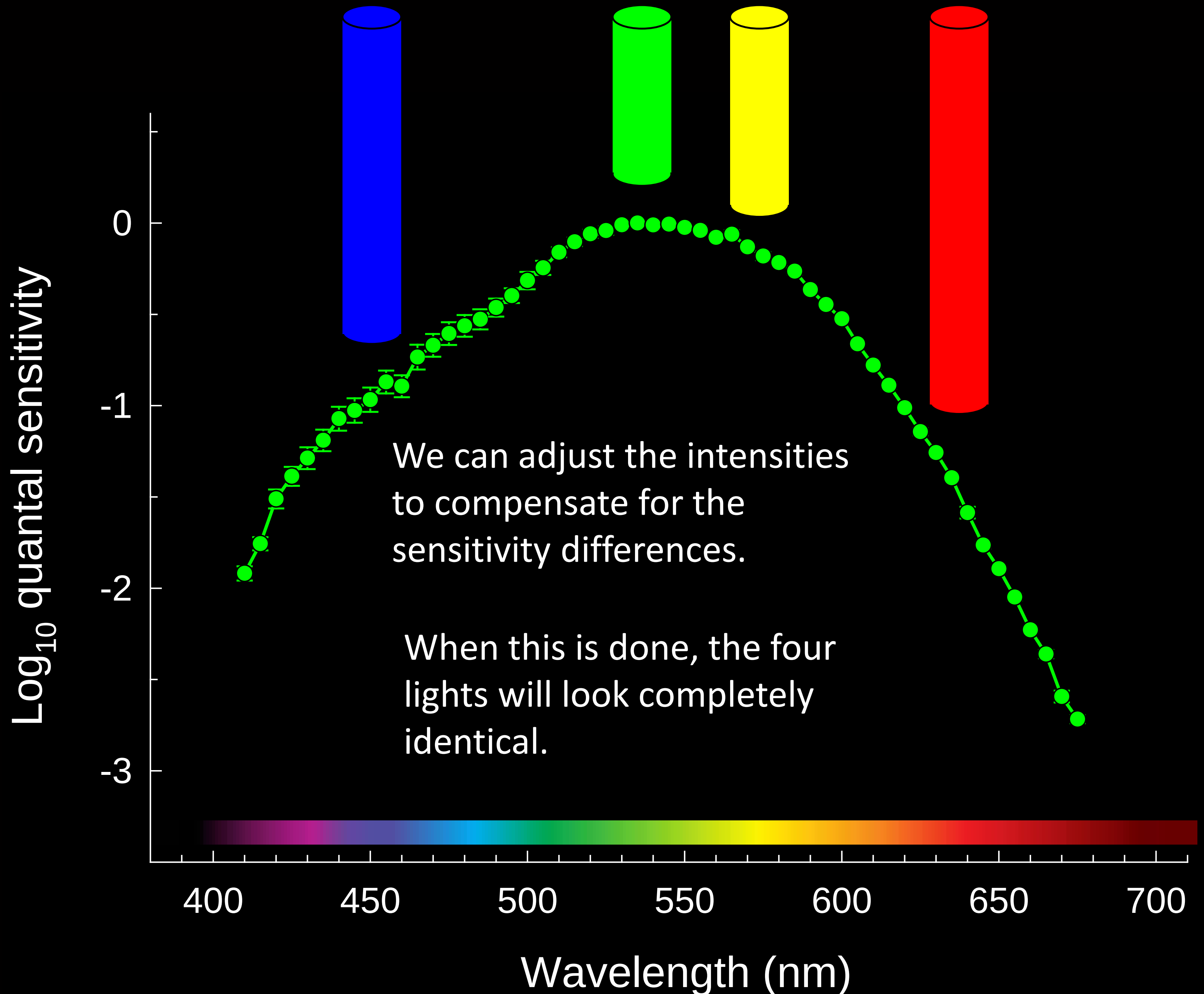
M-cone spectral sensitivity function
High sensitivity
(less photons needed
to have an effect)
Low sensitivity
(more photons needed
to have an effect)
Log10 quantal sensitivity
0
-1
-2
-3
400
450
500
550
600
650
700
Wavelength (nm)

Consider the sensitivity to these photons…

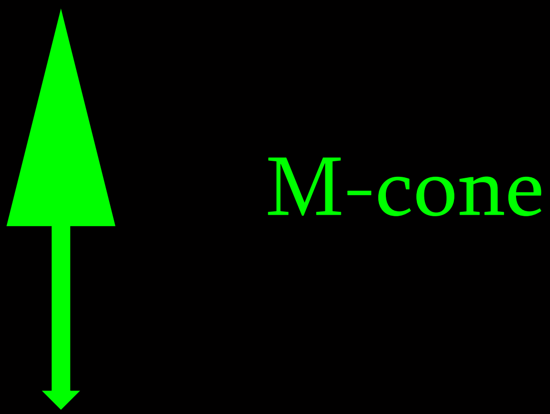




0
-1
-2
-3
Log10 quantal sensitivity
400
450
500
550
600
650
700
Wavelength (nm)
Imagine four lights of the same intensity (indicated here by their height)
The green will look brightest, then yellow, then blue and lastly the red will be the dimmest



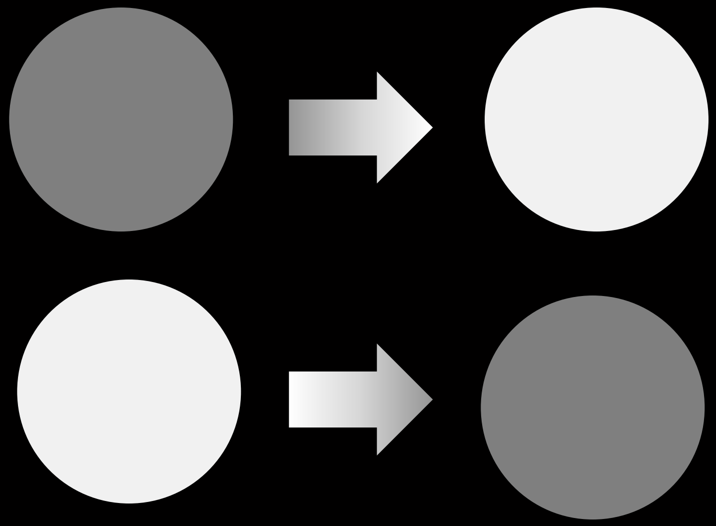
We can adjust the intensities to compensate for the sensitivity differences.
When this is done, the four lights will look completely identical.
0
-1
-2
-3
Log10 quantal sensitivity
400
450
500
550
600
650
700
Wavelength (nm)



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

UNIVARIANCE

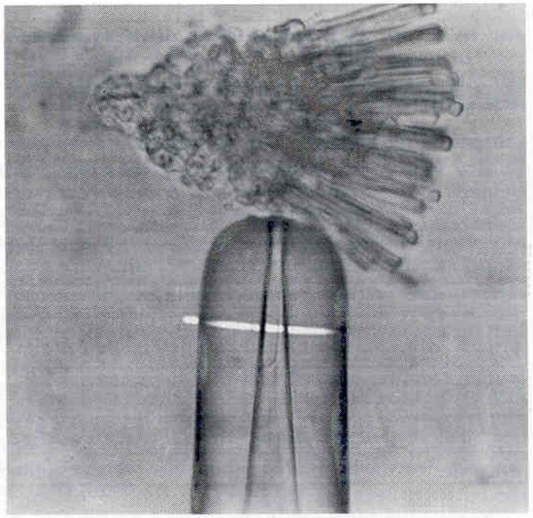
A change in photoreceptor output can be caused by a change in intensity or by a change in colour. There is no way of telling which.

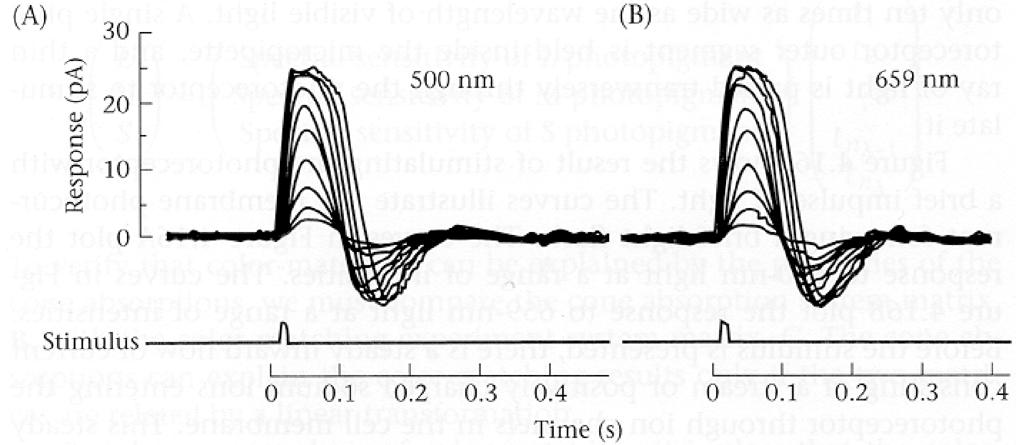


Colour or intensity change??

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

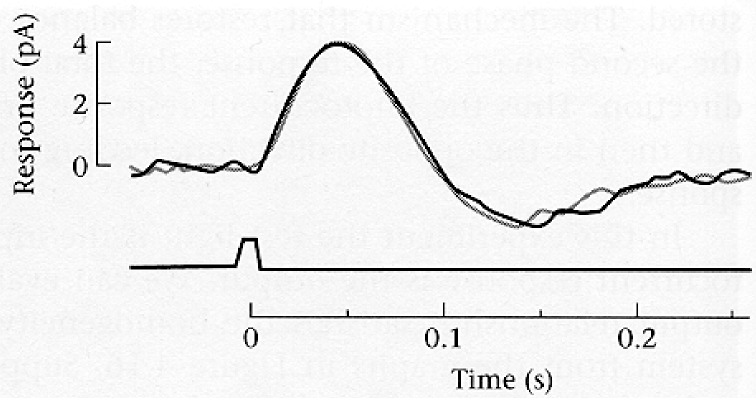
Univariance in suction electrode recordings





4.16 THE CONE PHOTOCURRENT in response to a brief test flash is biphasic. The amplitude of the photocurrent response increases with the stimulus intensity. The response functions are the same for different wavelengths of light: (A) stimulus wavelength = 500 nm; (B) stimulus intensity = 659 nm. The stimulus time course is shown below the photocurrent plots. Source: Baylor et al., 1987.

4.17 THE PRINCIPLE OF UNIVARIANCE states that absorption of a photon leads to the same neural response, no matter what the wavelength of the photon. The principle predicts that two stimuli at different wavelengths can be adjusted to equate the photocurrent response throughout its time course. This is shown here as the match between photocurrents in response to 550 nm (shaded line) and 659 nm (solid line) test lights set to a 9:1 intensity ratio. Source: Baylor et al., 1987.



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

Examples: night vision, blue cone monochromats

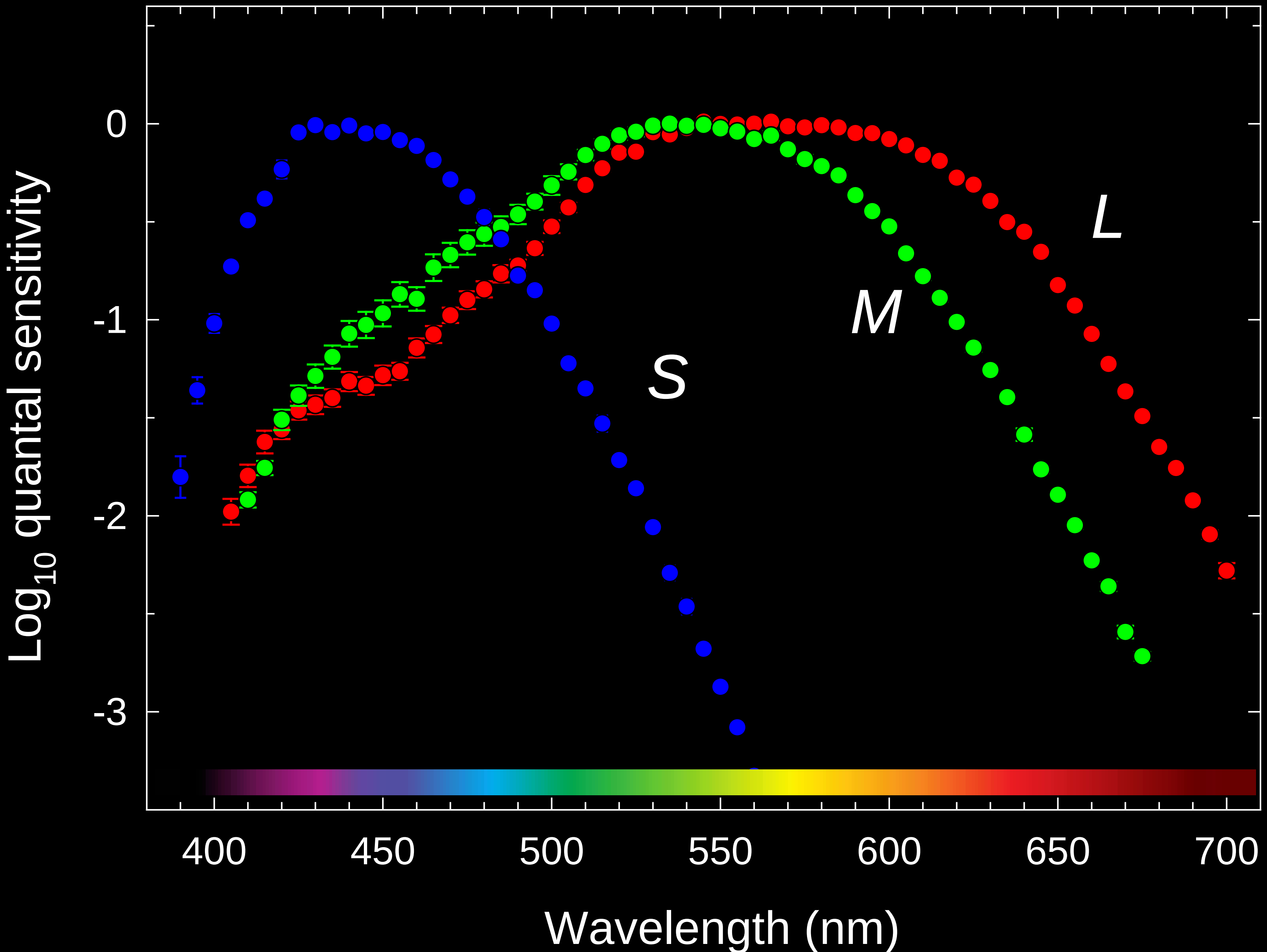
If we had only one photoreceptor, we would be colour-blind…

Examples: night vision, blue cone monochromats

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.

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



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

Their colour vision is therefore three dimensional or:

TRICHROMATIC

Trichromacy means our colour vision is actually limited

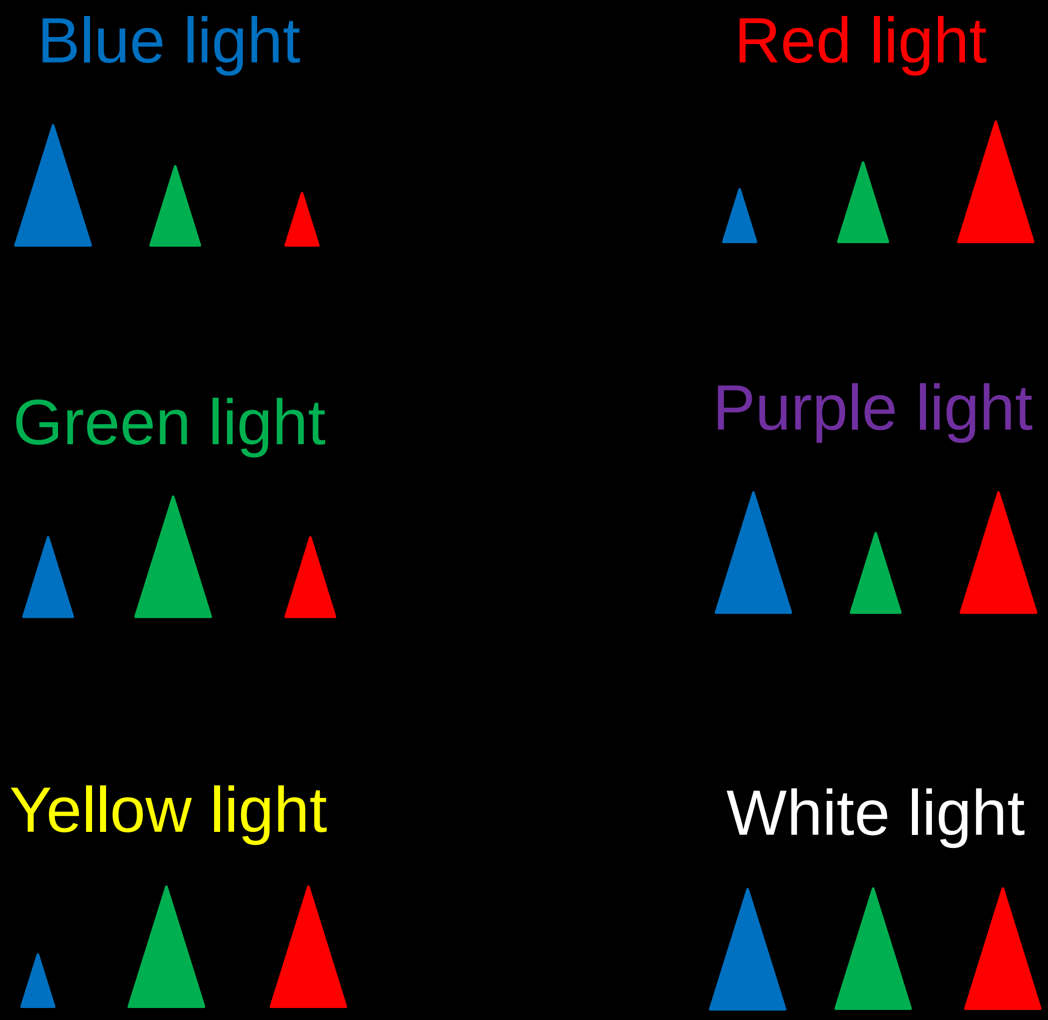
We confuse many pairs of colours that are spectrally very different. Such pairs are known as metameric pairs.

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.

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

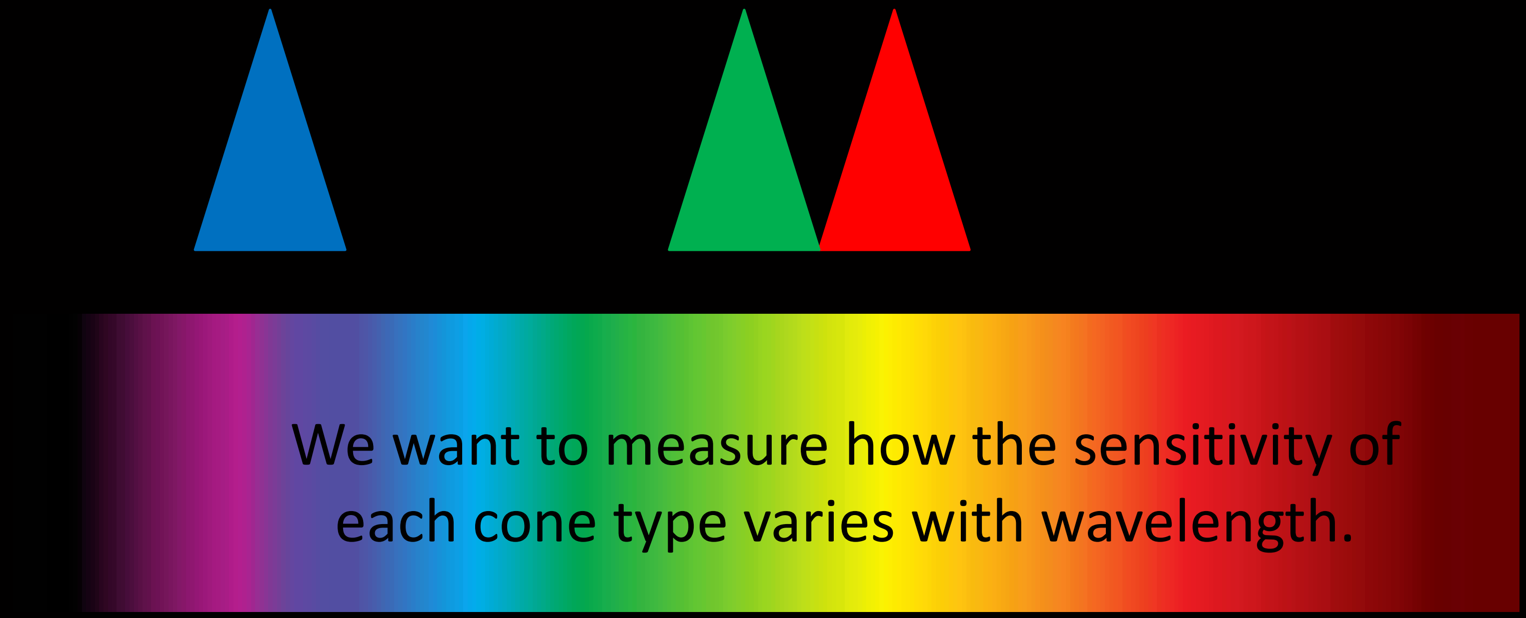
Or to put it another way: How is colour encoded at the input to the visual system?

Colour is encoded by the relative cone outputs



DETERMINING CONE SPECTRAL SENSITIVITIES

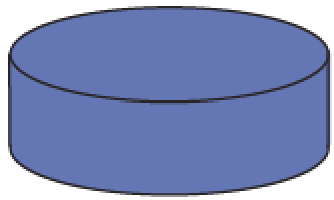
In other words:

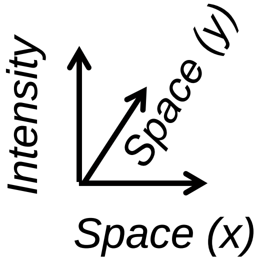


How might we do that?

Spectral sensitivity measurements

Flashing or flickering light

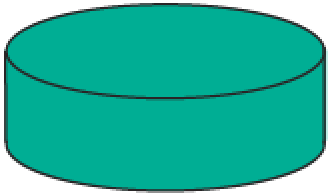


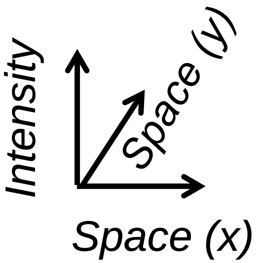


Observer sets the threshold for detecting the flash or flicker as a function of the wavelength of the light.

Spectral sensitivity measurements

Flashing or flickering light





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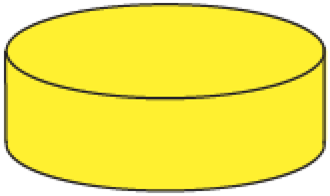
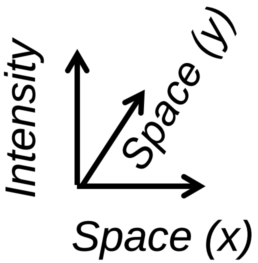
Spectral sensitivity measurements

Flashing or flickering light





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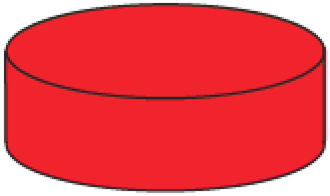
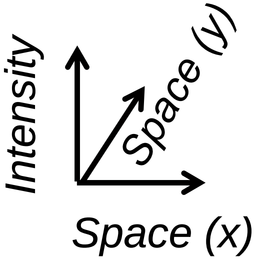
Spectral sensitivity measurements

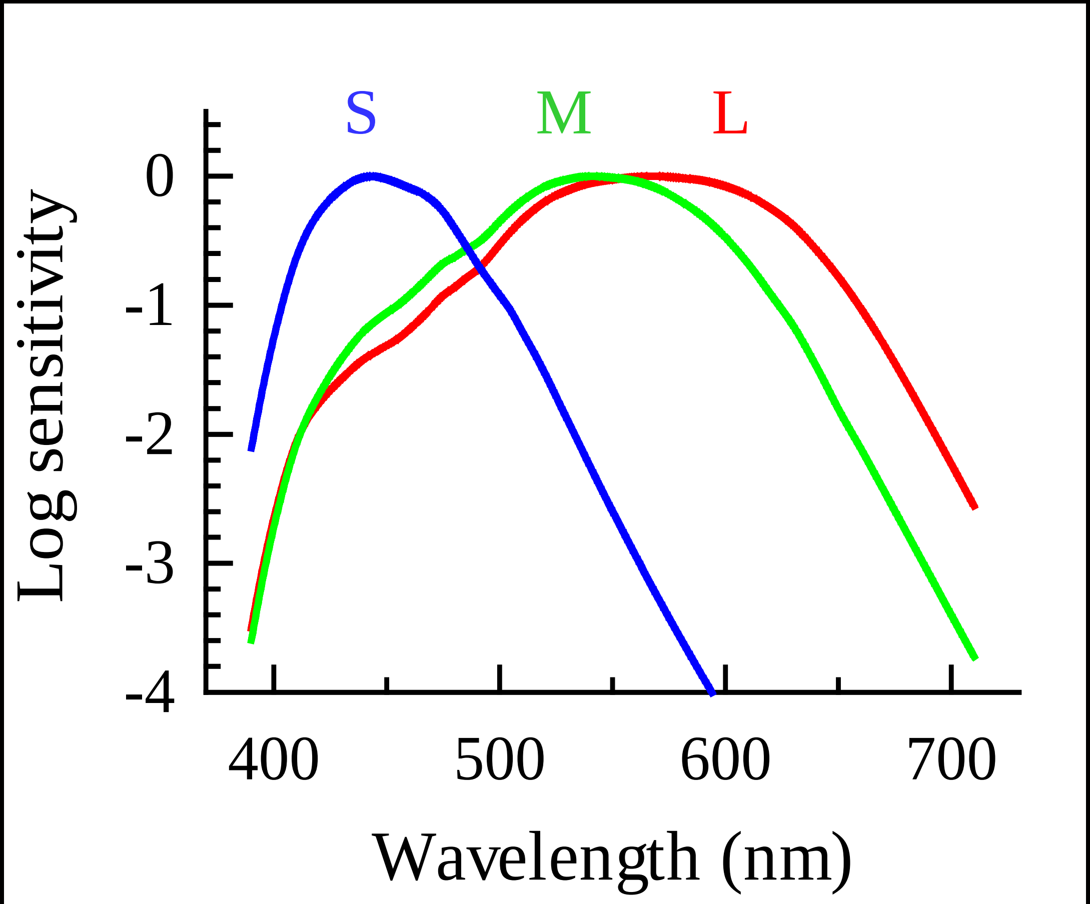
Flashing or flickering light





Observer sets the threshold for detecting the flash or flicker as a function of the wavelength of the light.

But the cone spectral sensitivities overlap throughout the spectrum.



Consequently, to measure them *separately* we have to use special subjects or special conditions.

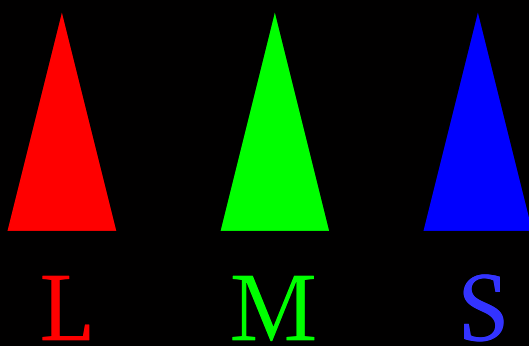
M- and L-cone measurements

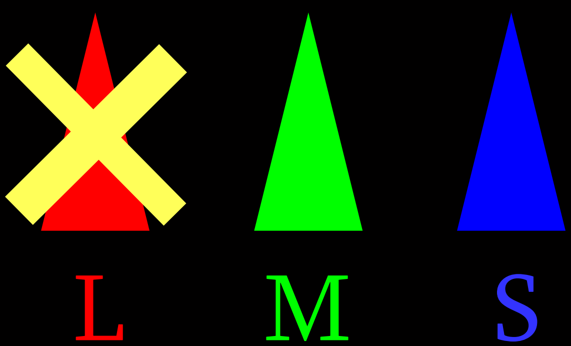
Use two special types of subjects:

- Deuteranopes
- Protanopes

Normal

Protanope

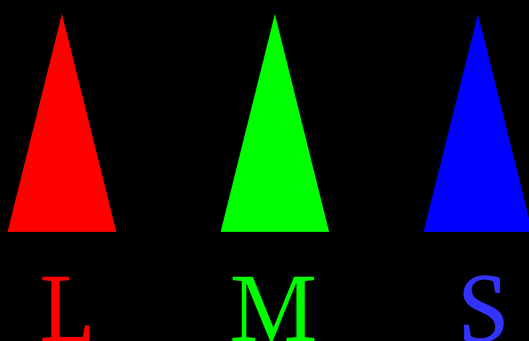


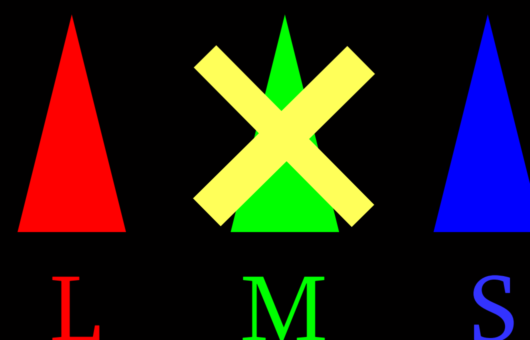


Protanopia

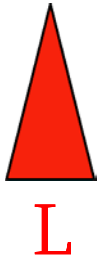
Normal

Deuteranope

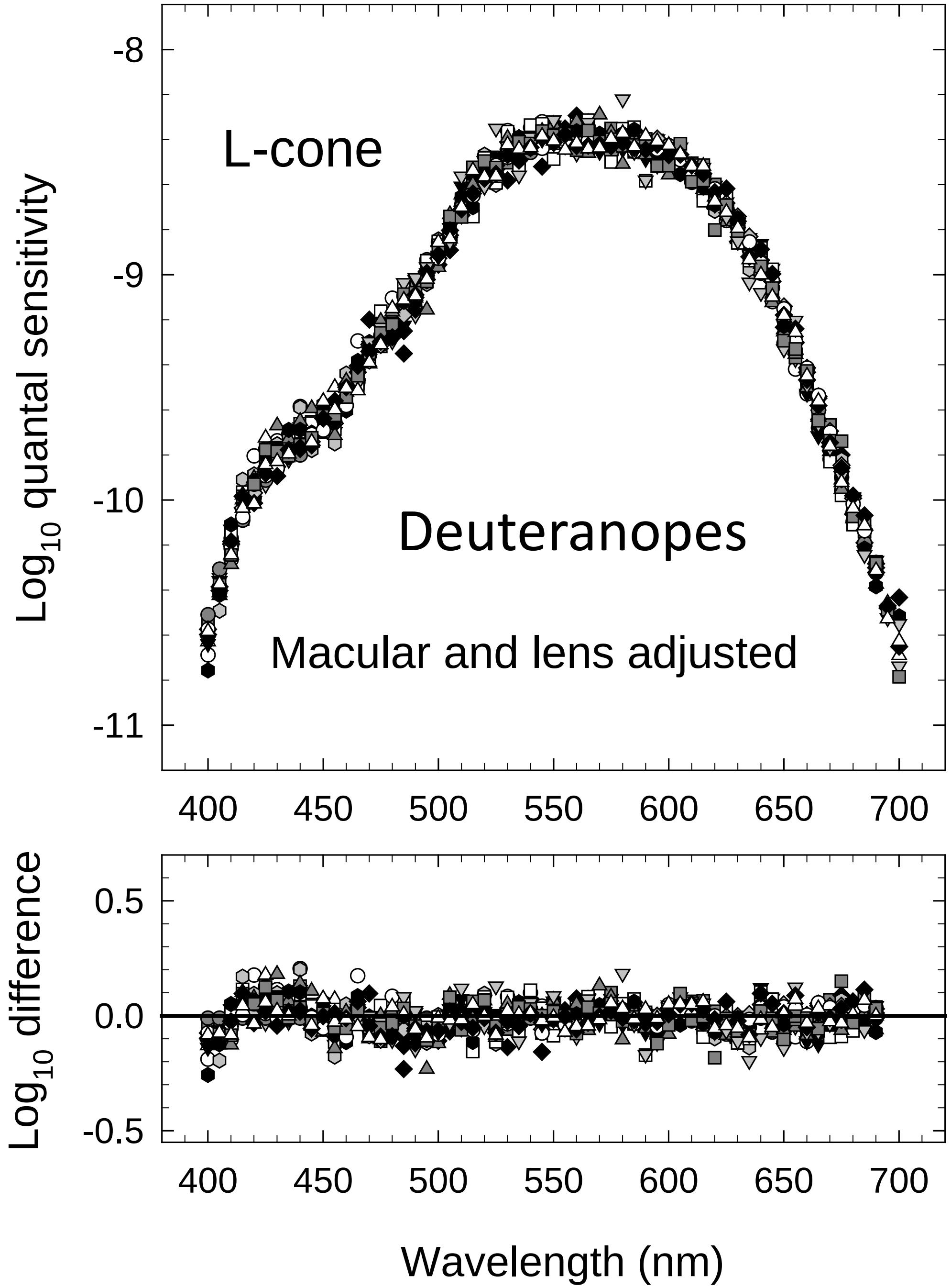


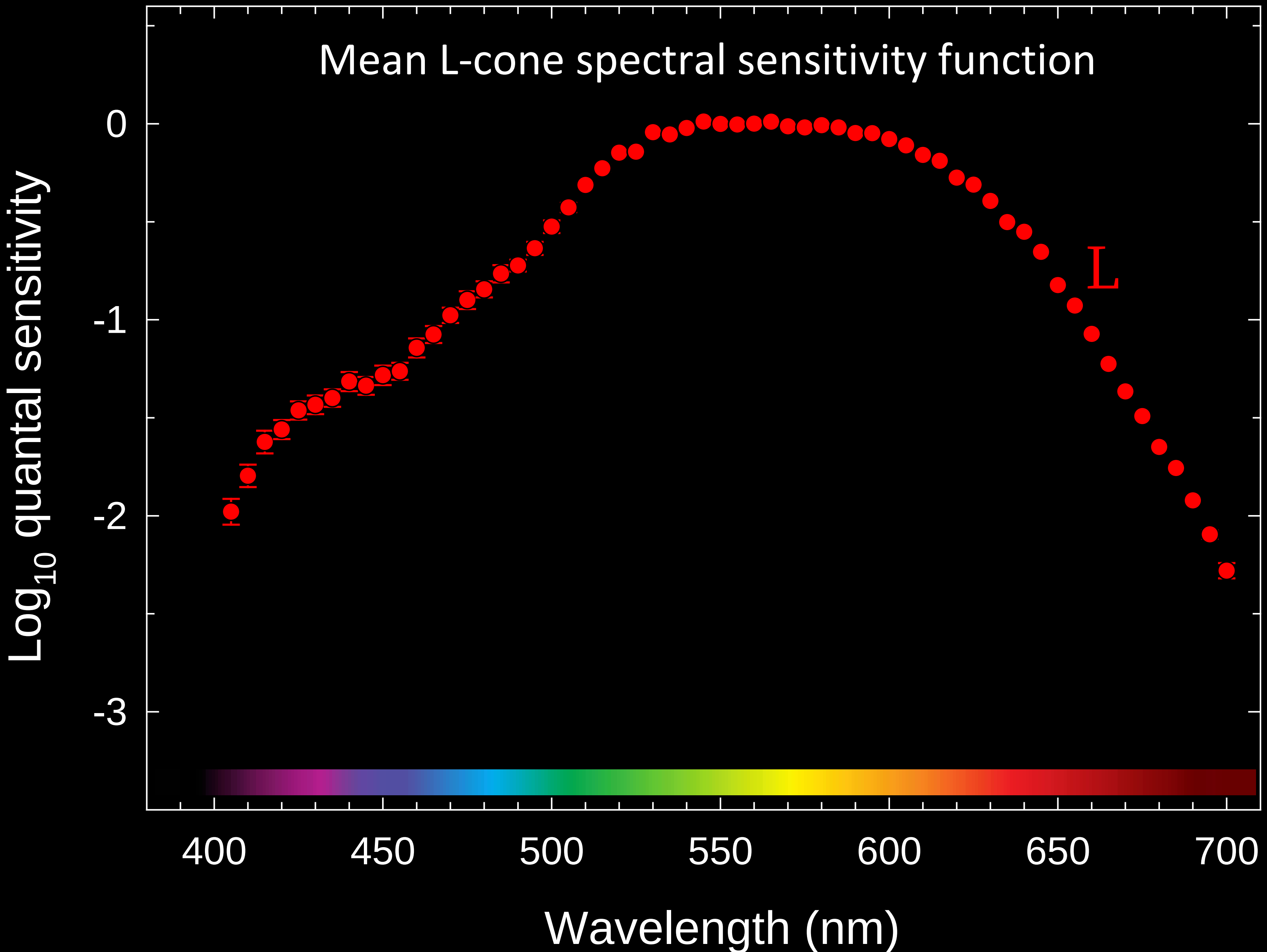


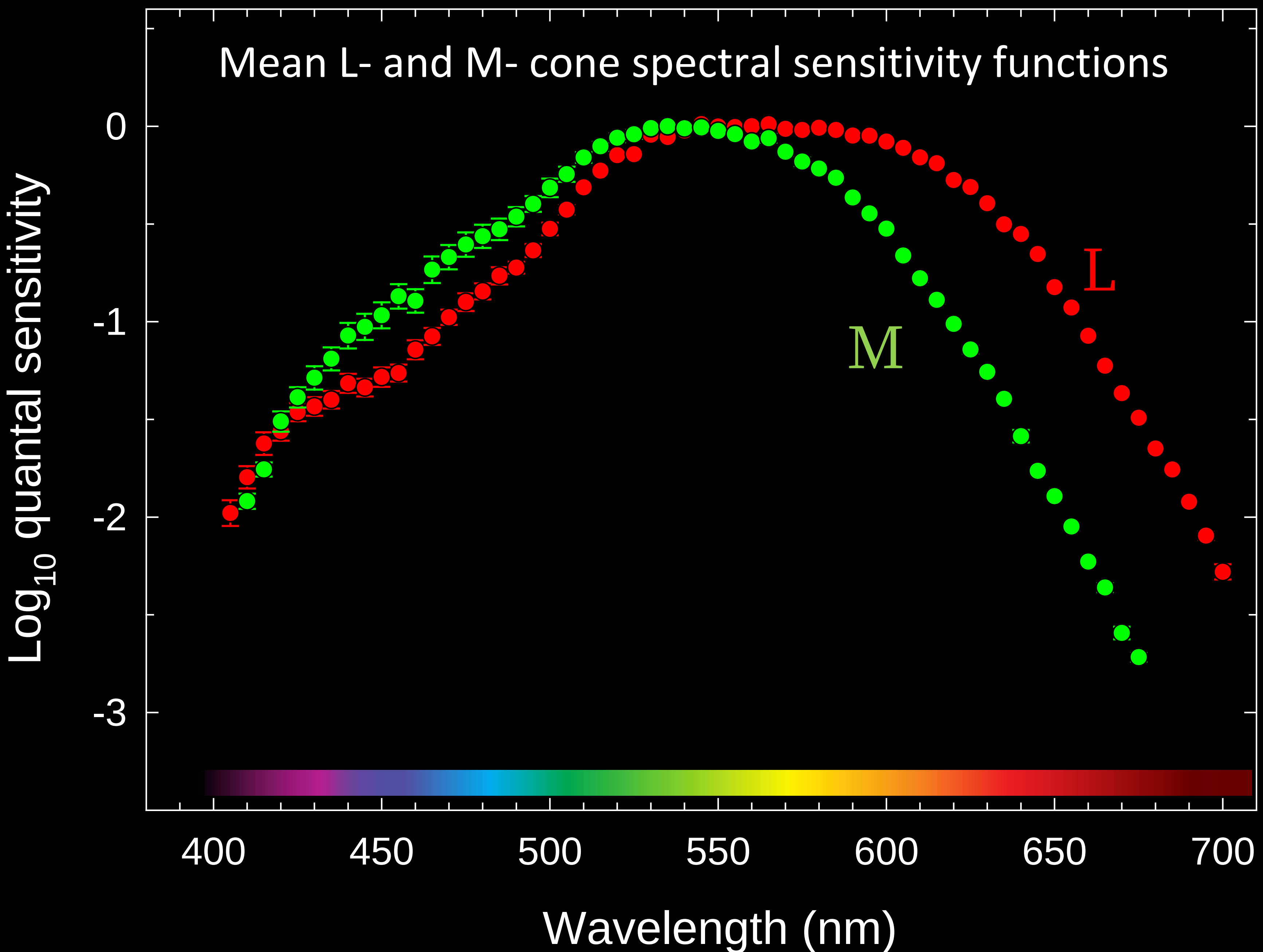
Deuteranopia



Adjusted L-cone data




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



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)

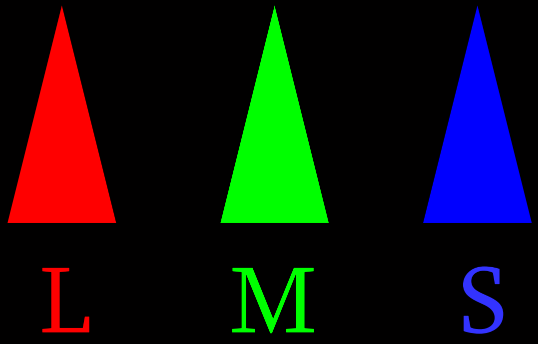
S-cone measurements

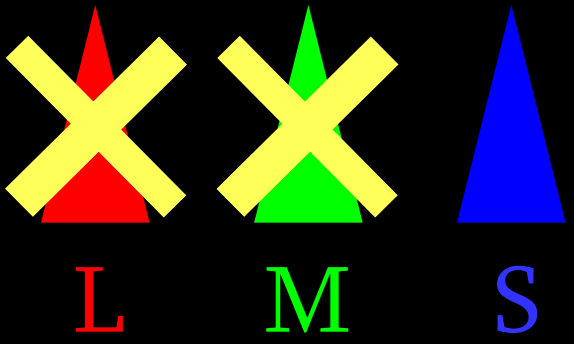
Two types of subjects:

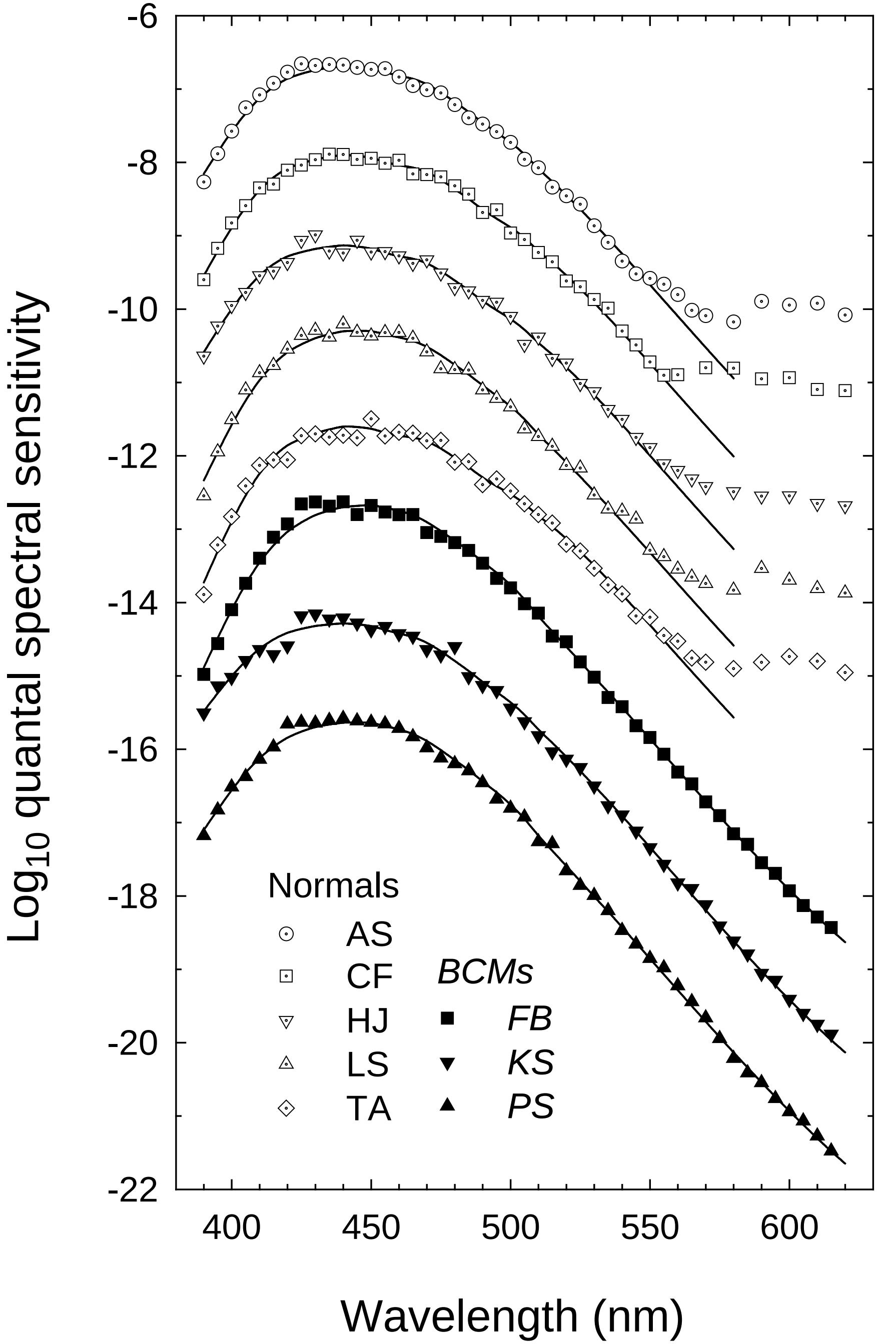
- S-cone (or blue cone) monochromats
- Colour normals

Normal

S-cone monochromat

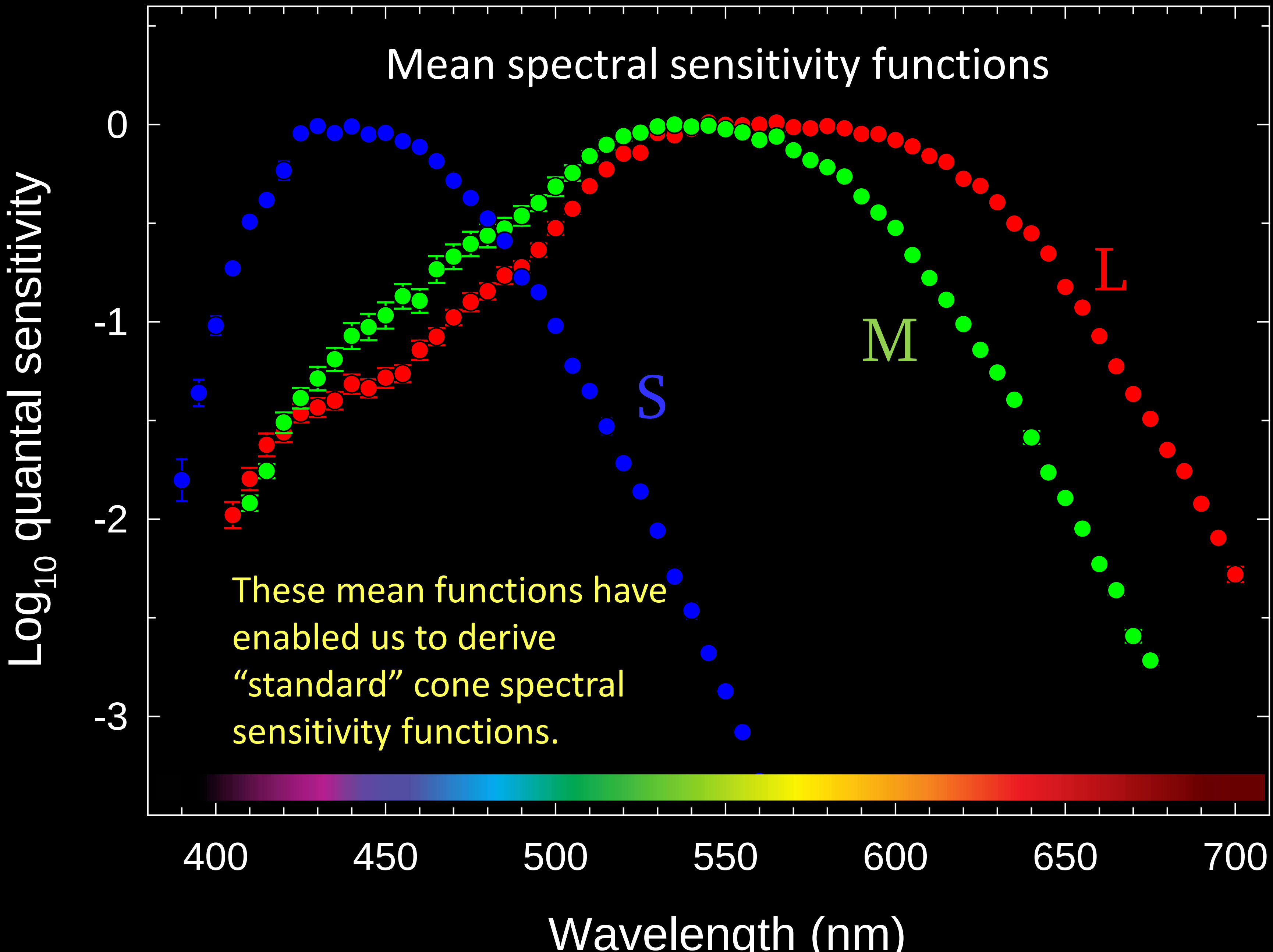






S-cone data

The Normal data were obtained on an intense orange adapting background that adapted (suppressed) the L- and M-cones.


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)

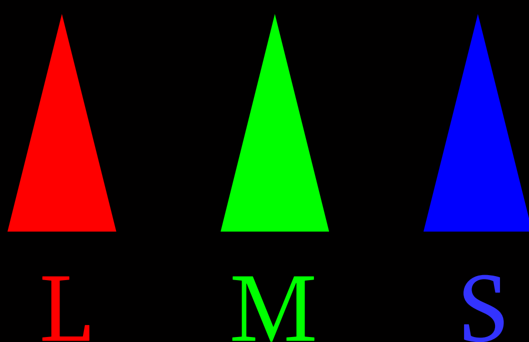
Why study spectral sensitivities?

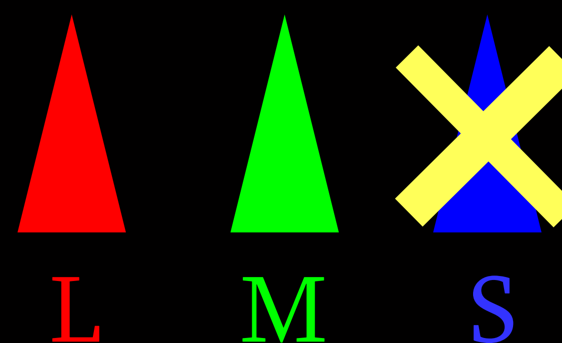
- A knowledge of the spectral sensitivities of the cones is important because it allows us to accurately and simply specify colours and to predict colour matches—for both colour normal and colour deficient people (and to understand the variability between individuals).

- Practical implications for colour printing, colour reproduction and colour technology.

Normal

Tritanope



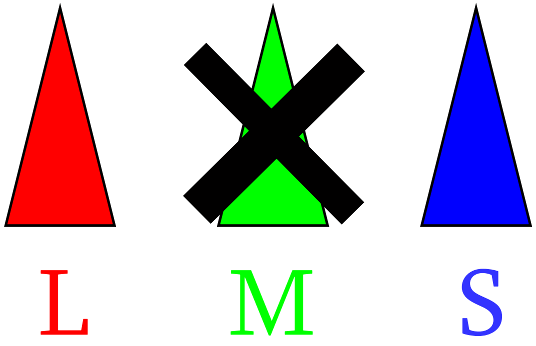


Tritanopia

Credit: Euro Puppy Blog

Deuteranope

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



COLOUR VISION AND MOLECULAR GENETICS

Normal

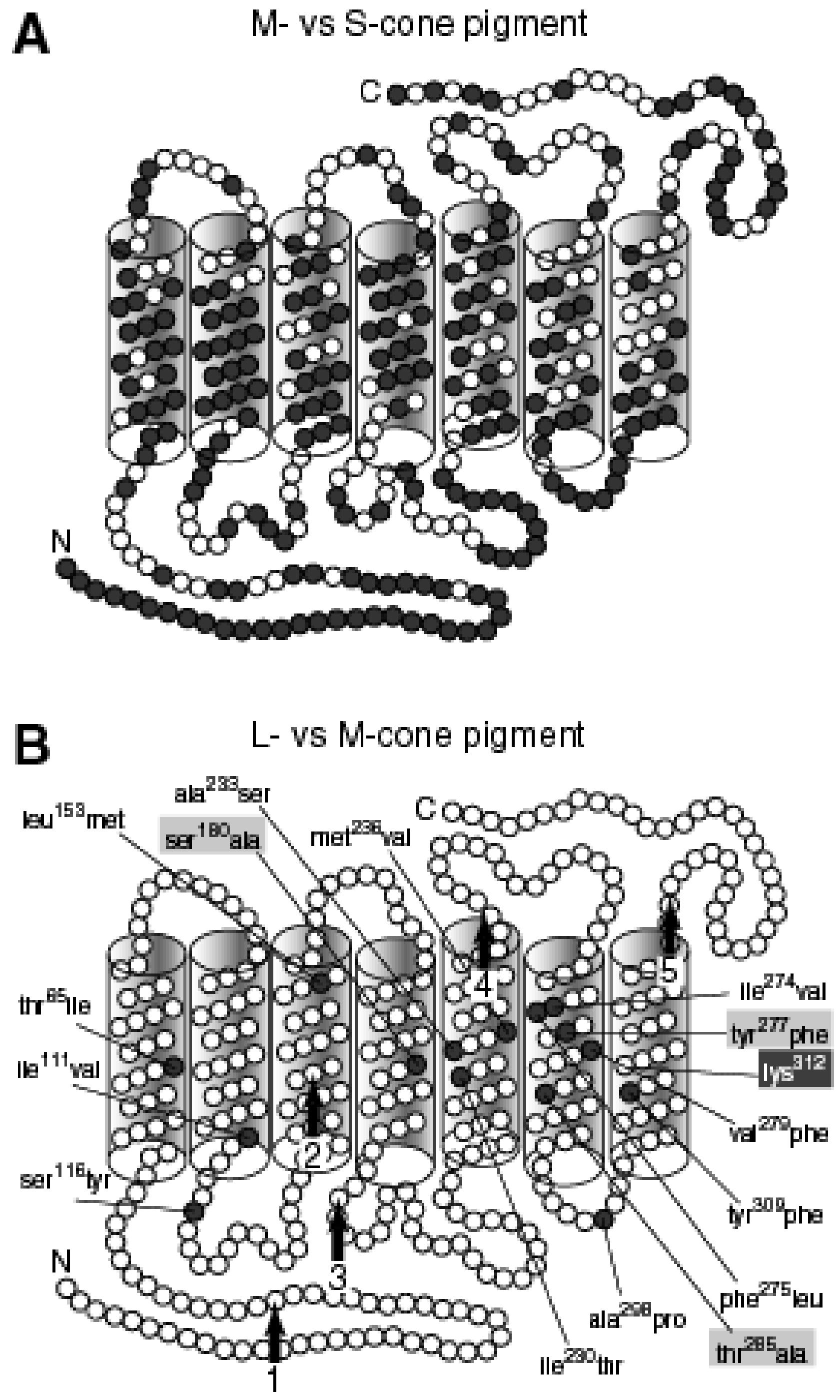
Deuteranope

Tritanope

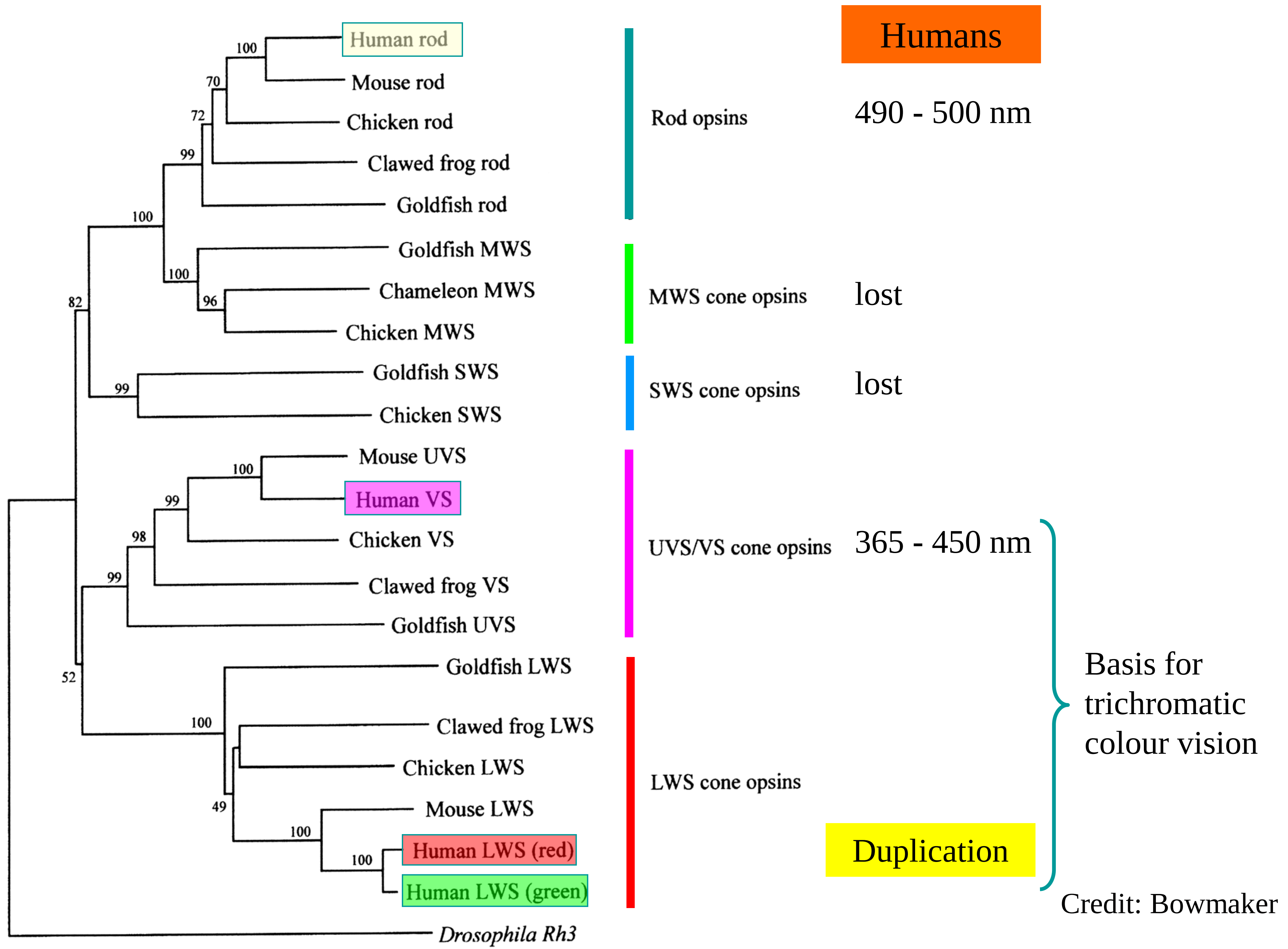
Protanope

From Sharpe, Stockman, Jägle & Nathans, 1999

Amino acid differences between photopigment opsins

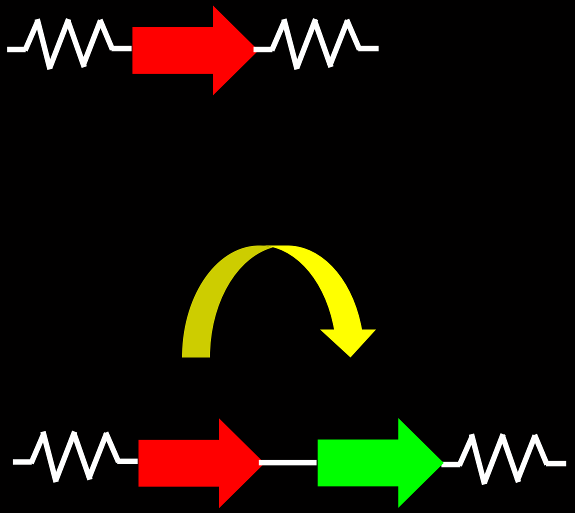


From Sharpe, Stockman, Jägle & Nathans, 1999



Credit: Bowmaker

Gene duplication on the X-chromosome



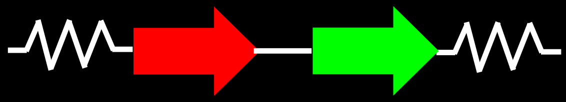
Mammal

Human/ Old world primate

L-cone photopigment opsin gene

M-cone photopigment opsin gene

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

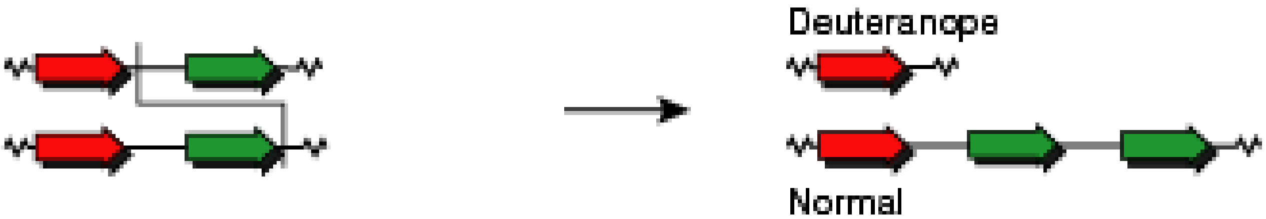


L-cone photopigment opsin gene

M-cone photopigment opsin gene

Crossovers during meiosis are common:

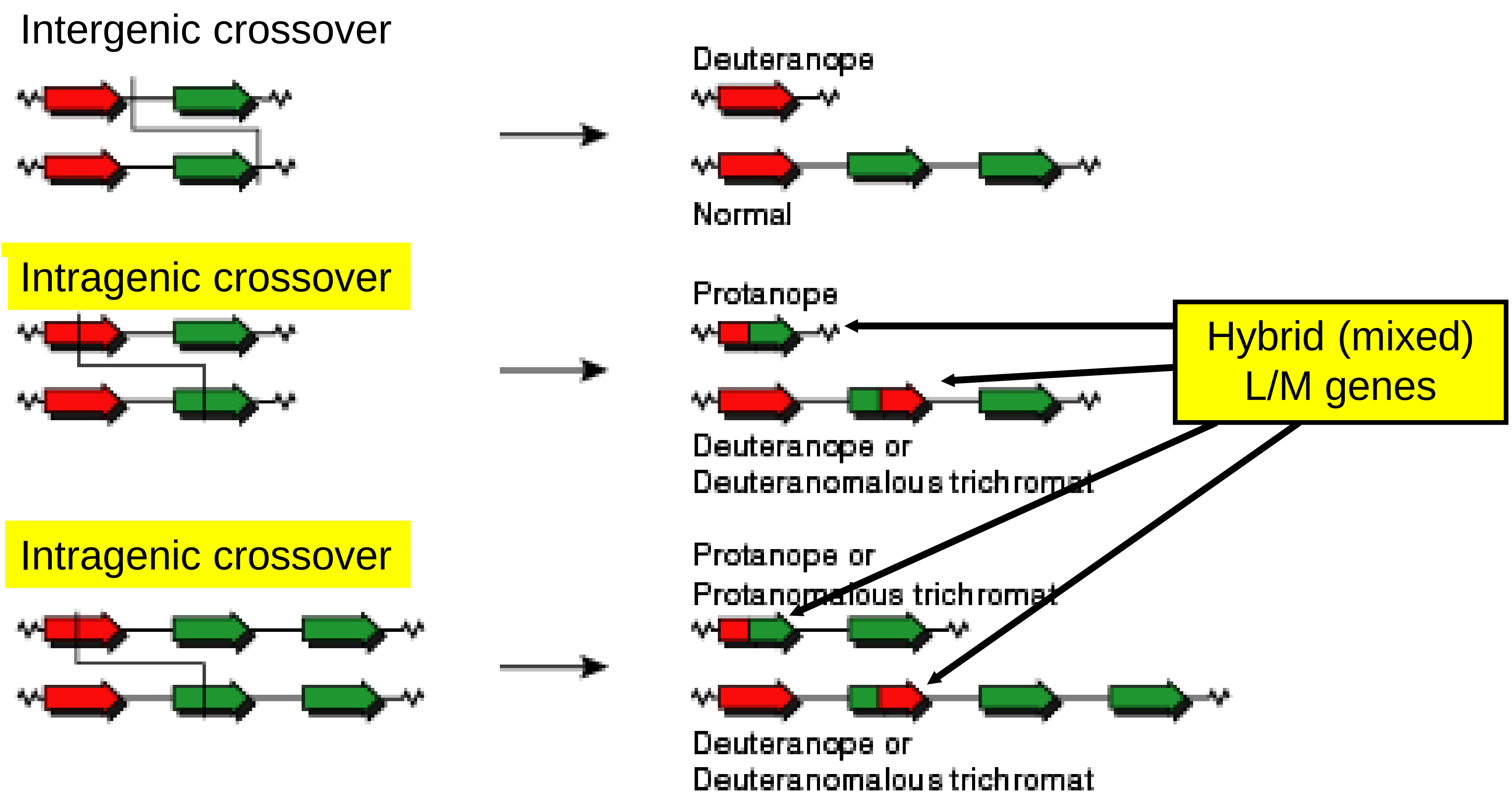
Intergenic crossover



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

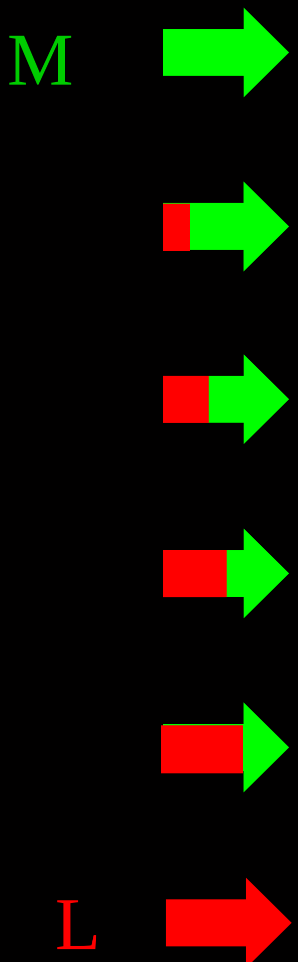
From Sharpe, Stockman, Jägle & Nathans, 1999

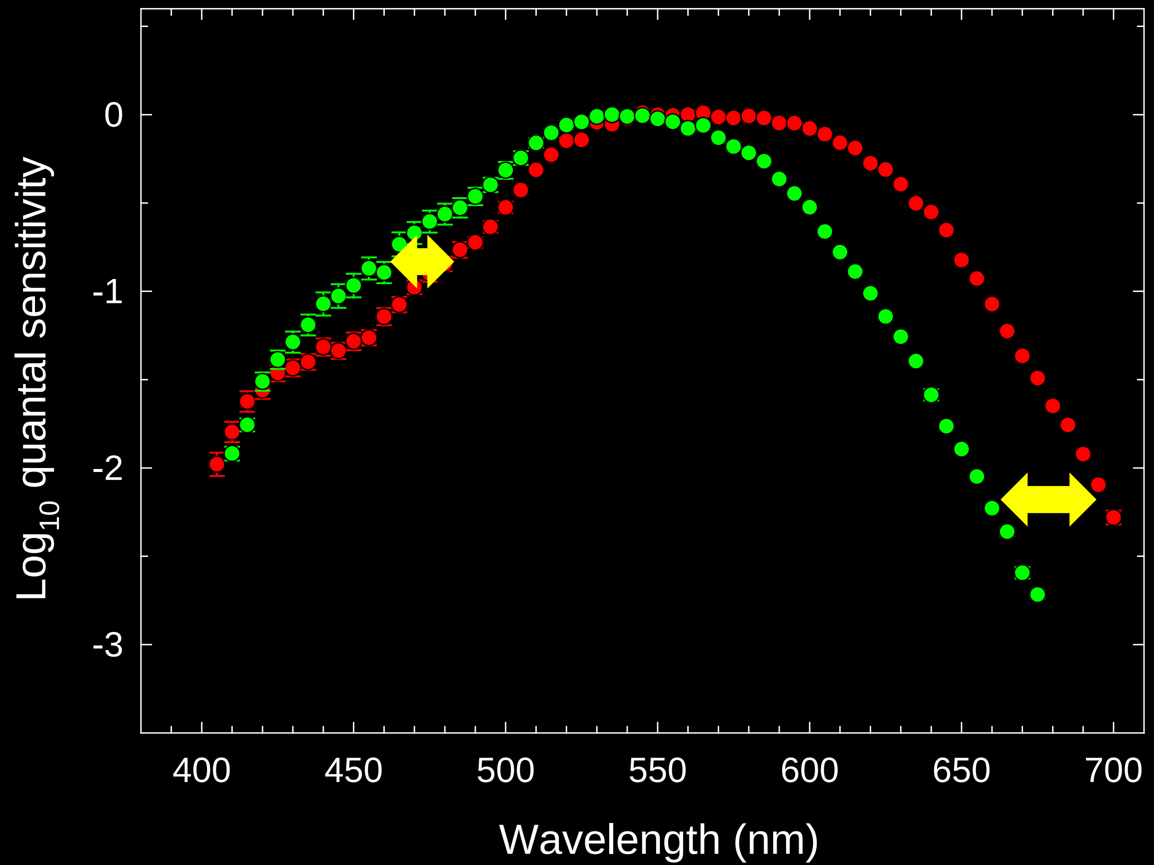
Intragenic crossovers produce hybrid or mixed L and M-cone genes



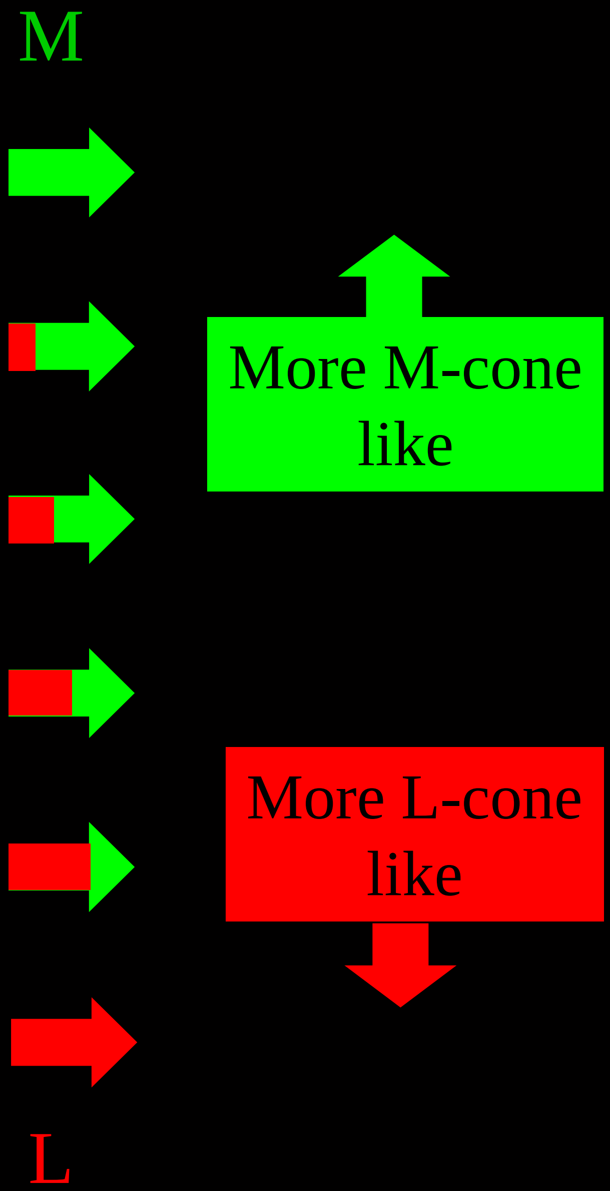
From Sharpe, Stockman, Jägle & Nathans, 1999

Intragenic crossovers

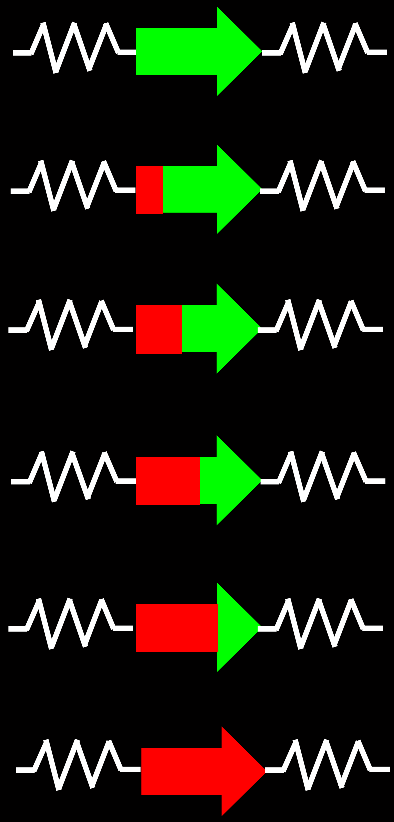




- The spectral sensitivities of the hybrid photopigments vary between those of the M- and L-cones depending on where the crossover occurs.


M
More M-cone like
More L-cone like
L

Single-gene dichromats

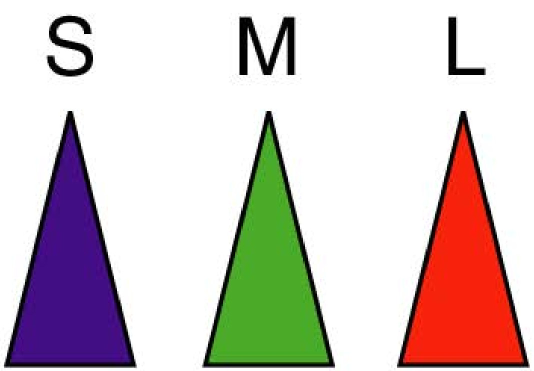


Protanope

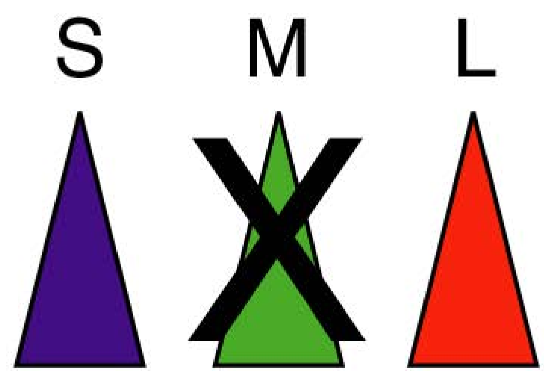
With just a single gene a male (with only one X-chromosome) must be a dichromat

Deuteranope

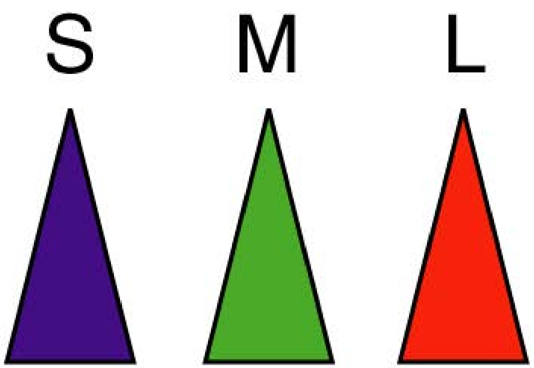
Normal



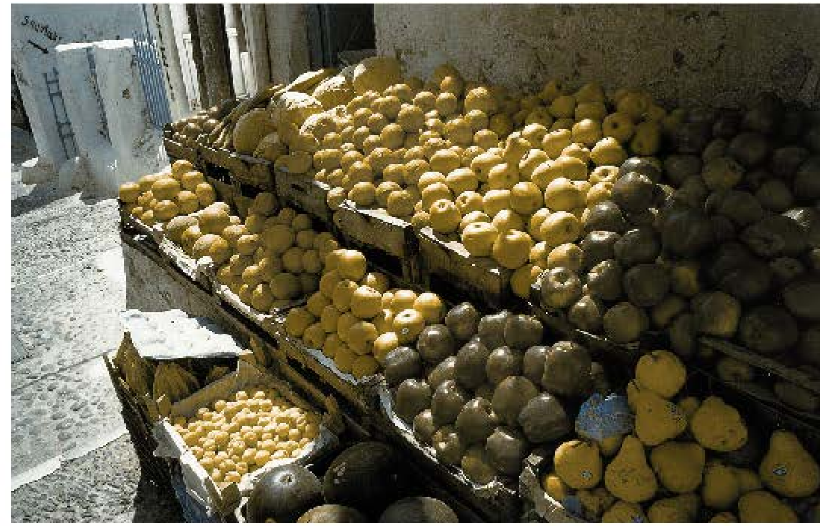
Deuteranope

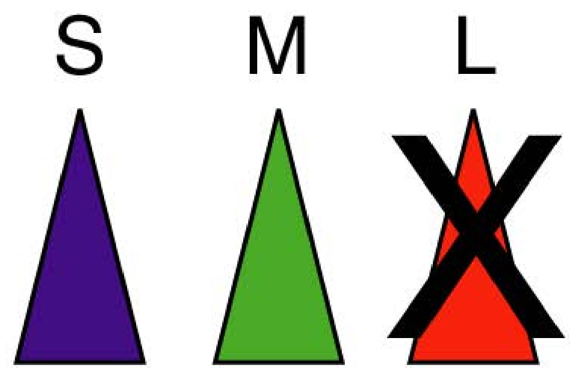


Normal

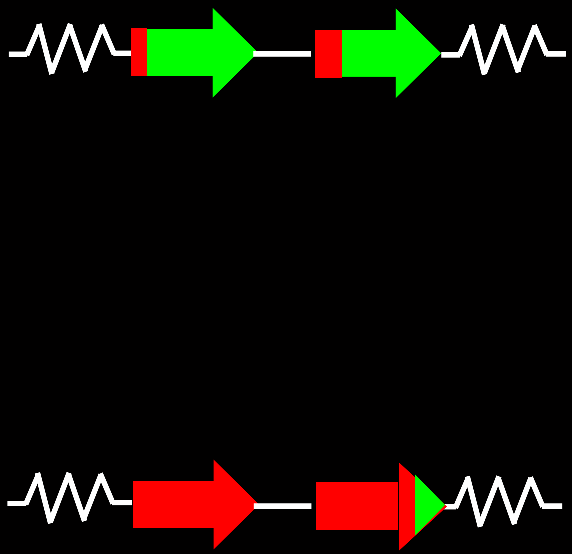


Protanope





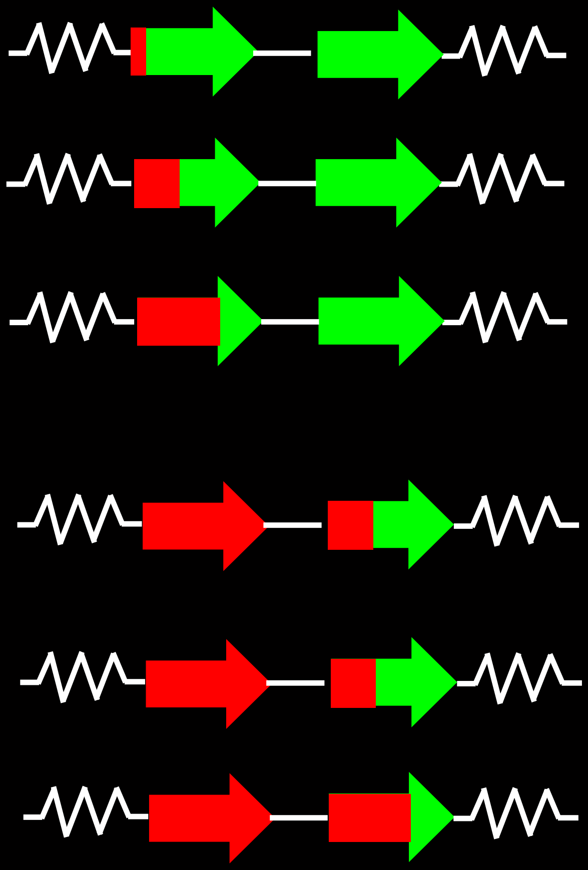
Multiple-gene dichromats



Males with two genes may also be effectively dichromats if the two genes produce very similar photopigments.

Anomalous trichromats

Males with two different genes are anomalous trichromats



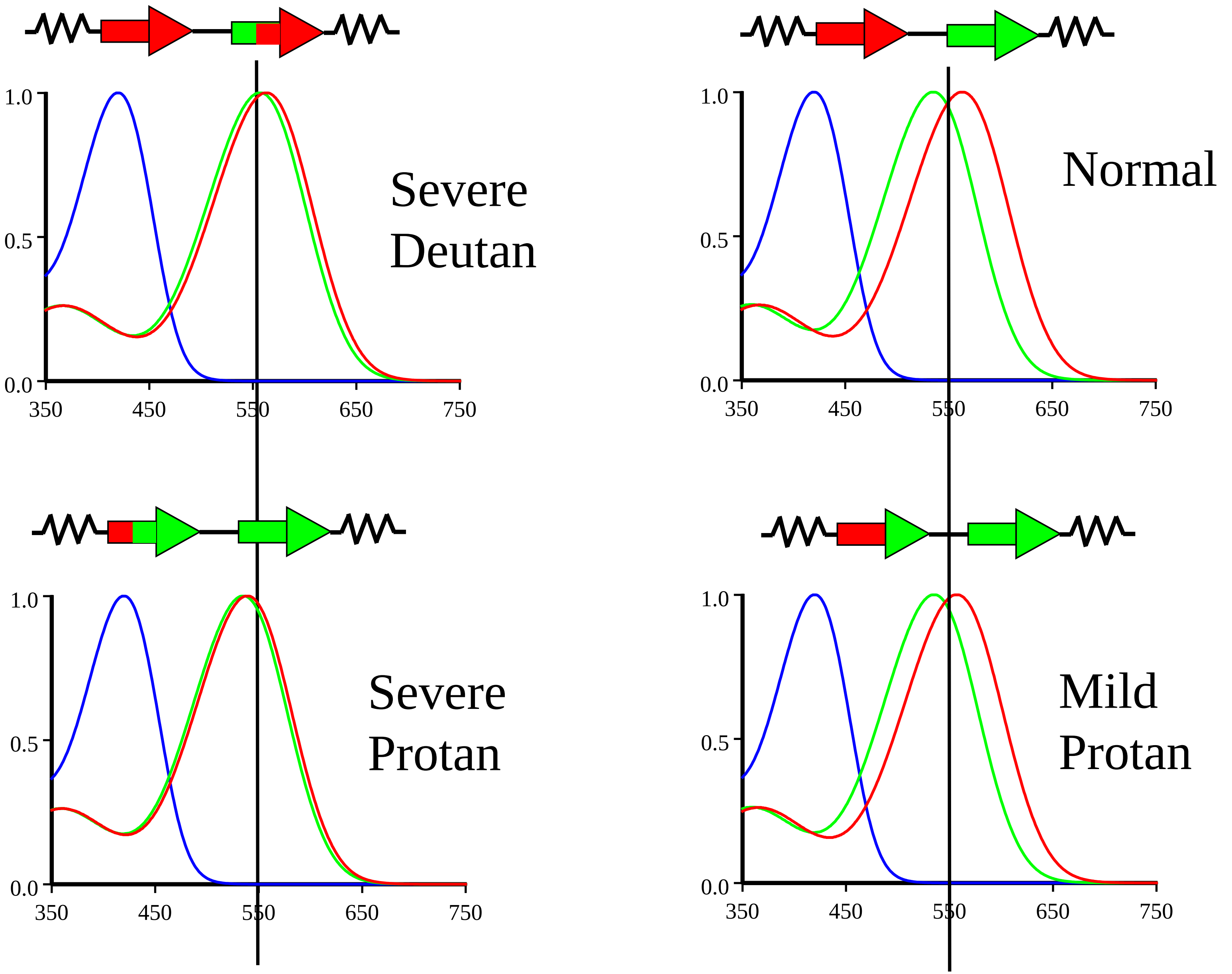
Severe

Protanomalous

Mild

Deuteranomalous

Severe



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

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

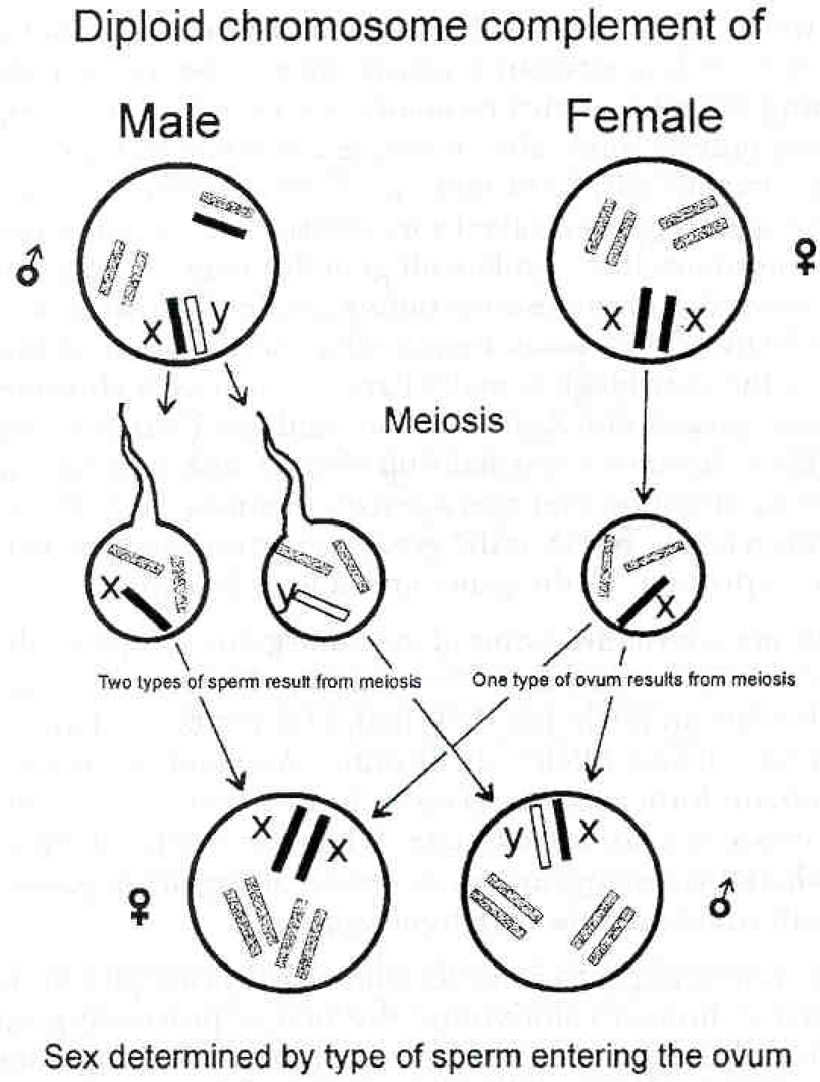
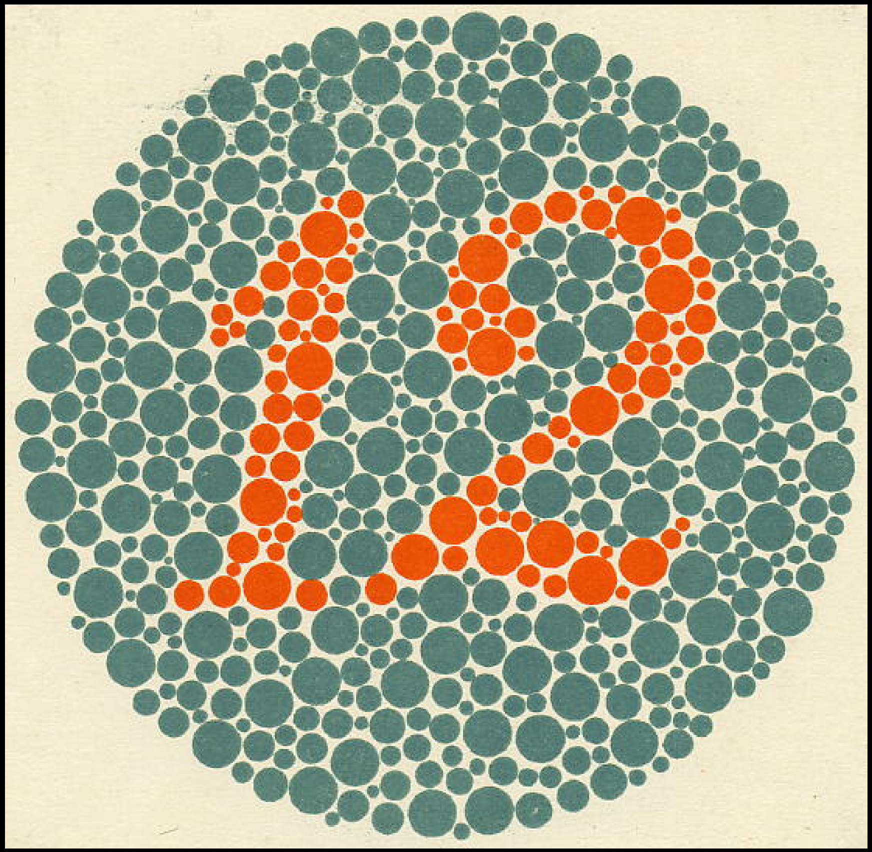


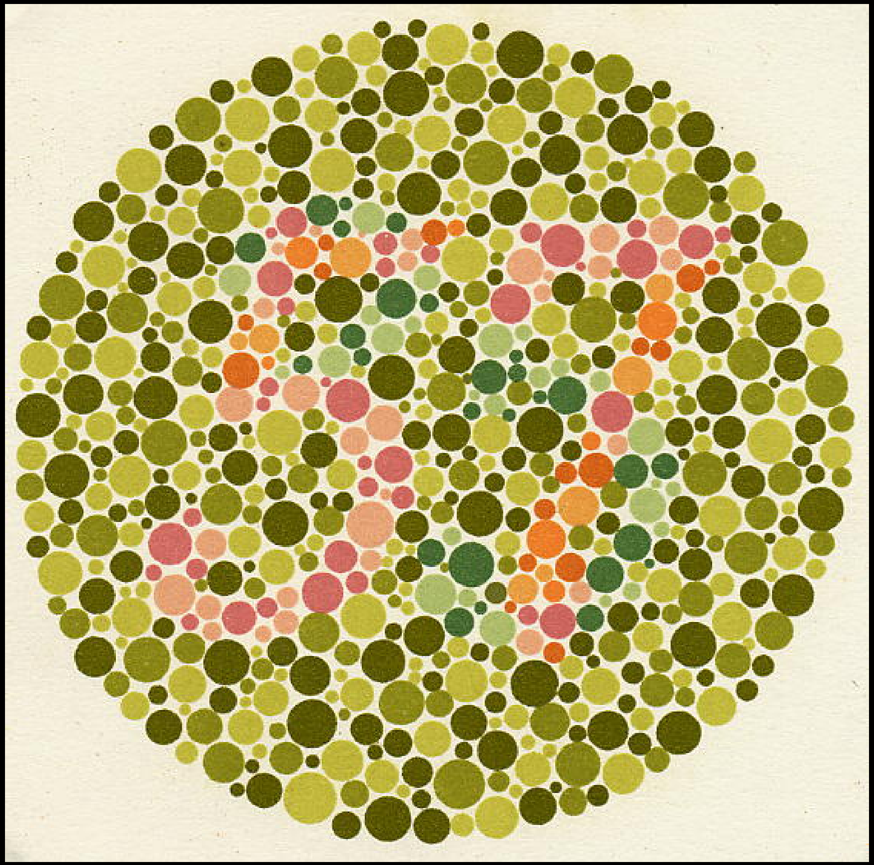
Figure 10.17 Prior to fertilization, meiotic division of germ cells results in two types of sperm, but only one type of ovum. Depending on which sperm is effective, the fertilized ovum will have two X cells and be female, or one X and one Y cell and be male. This diagram show why the X cell of the male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

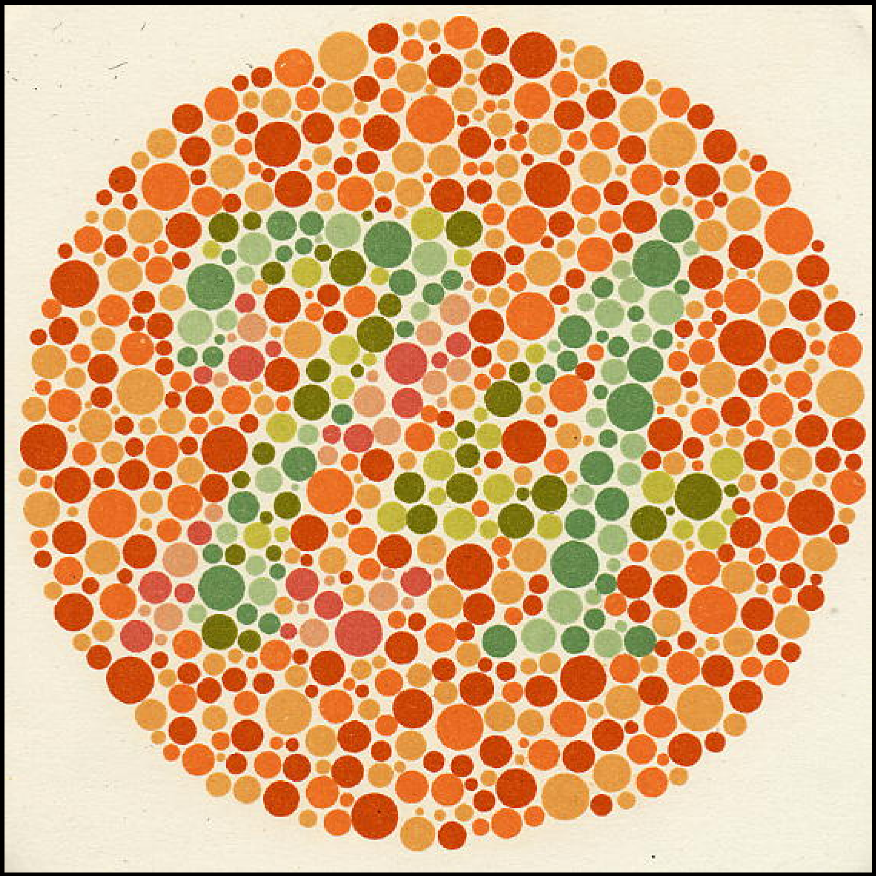
(S-cone opsin gene is on chromosome 7)

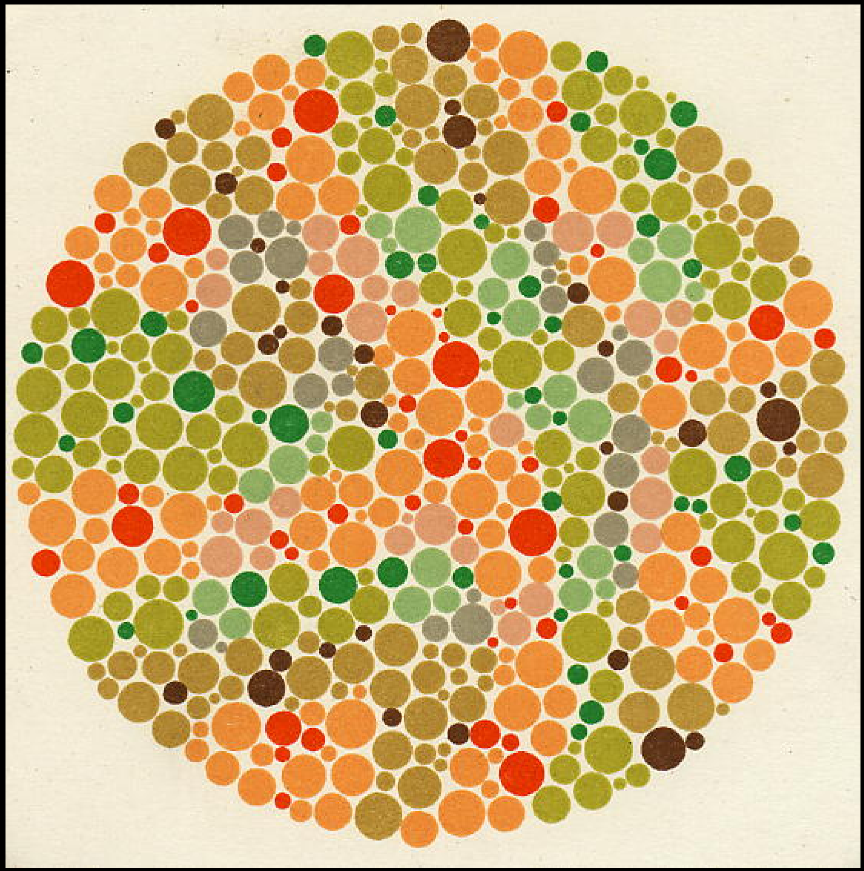
DIAGNOSING COLOUR VISION DEFICIENCIES

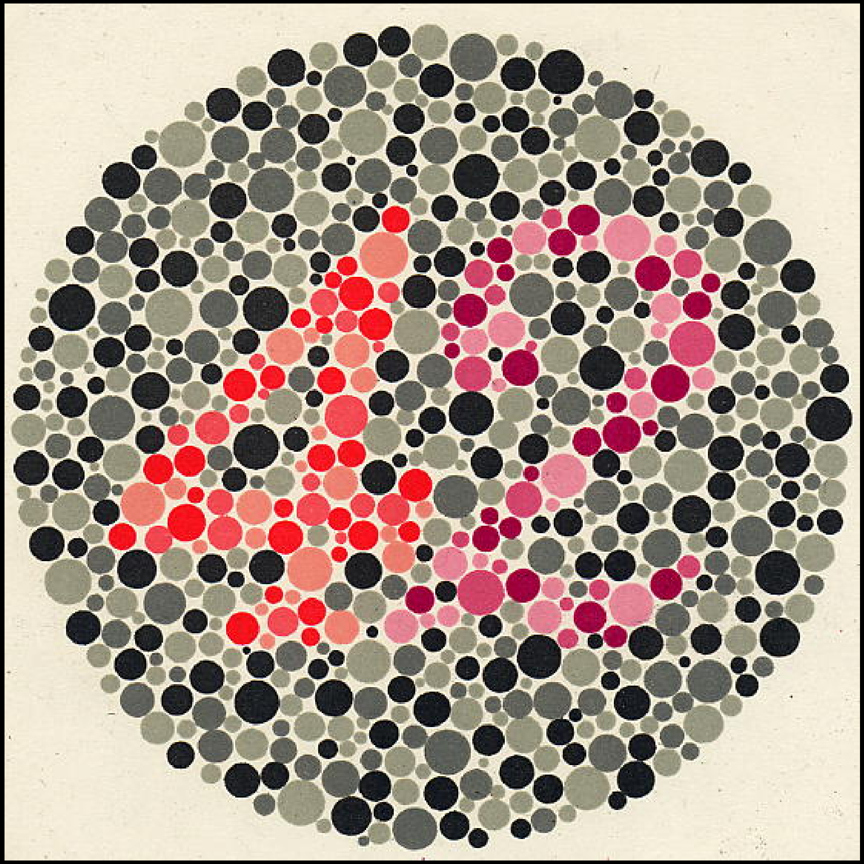
Ishihara plates







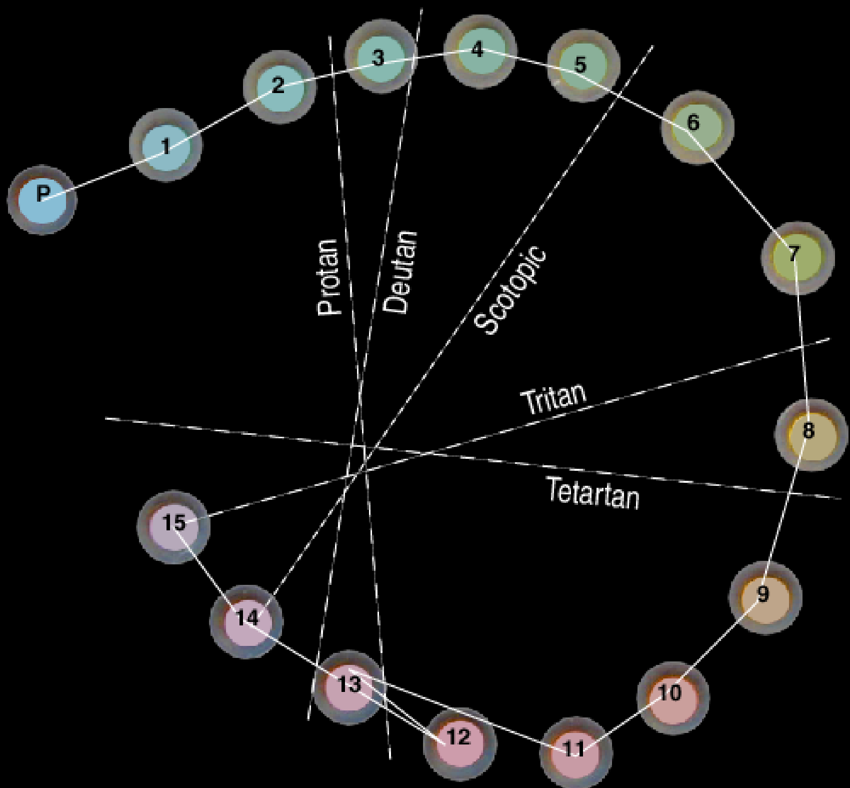




Tests measuring colour discrimination

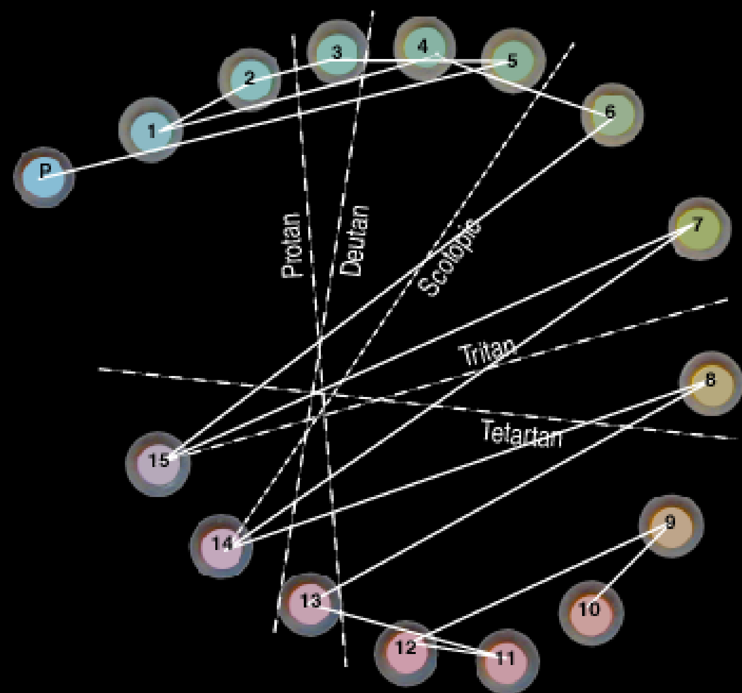
- Farnsworth-Munsell D-15 test
- Farnsworth-Munsell 100-hue test

Farnsworth-Munsell D-15



From: Ted Sharpe

Farnsworth-Munsell D-15



From: Ted Sharpe

D15 results

Mild | Severe

Protan

Deutan

Tritan

Rod monochromat

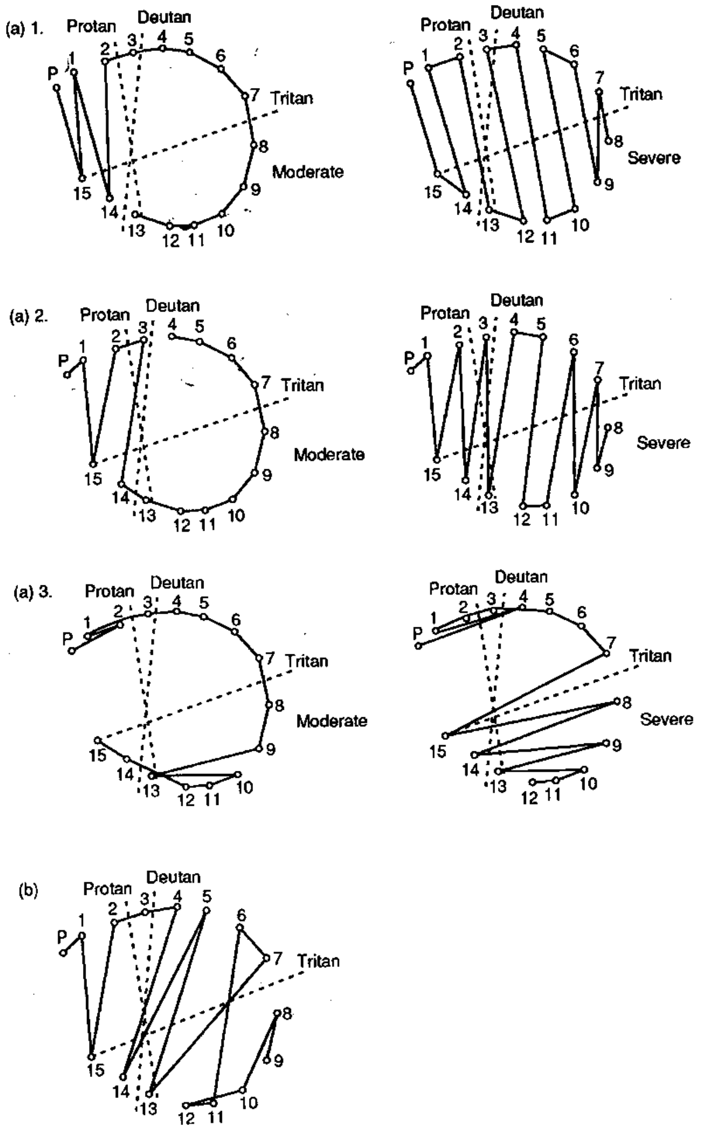
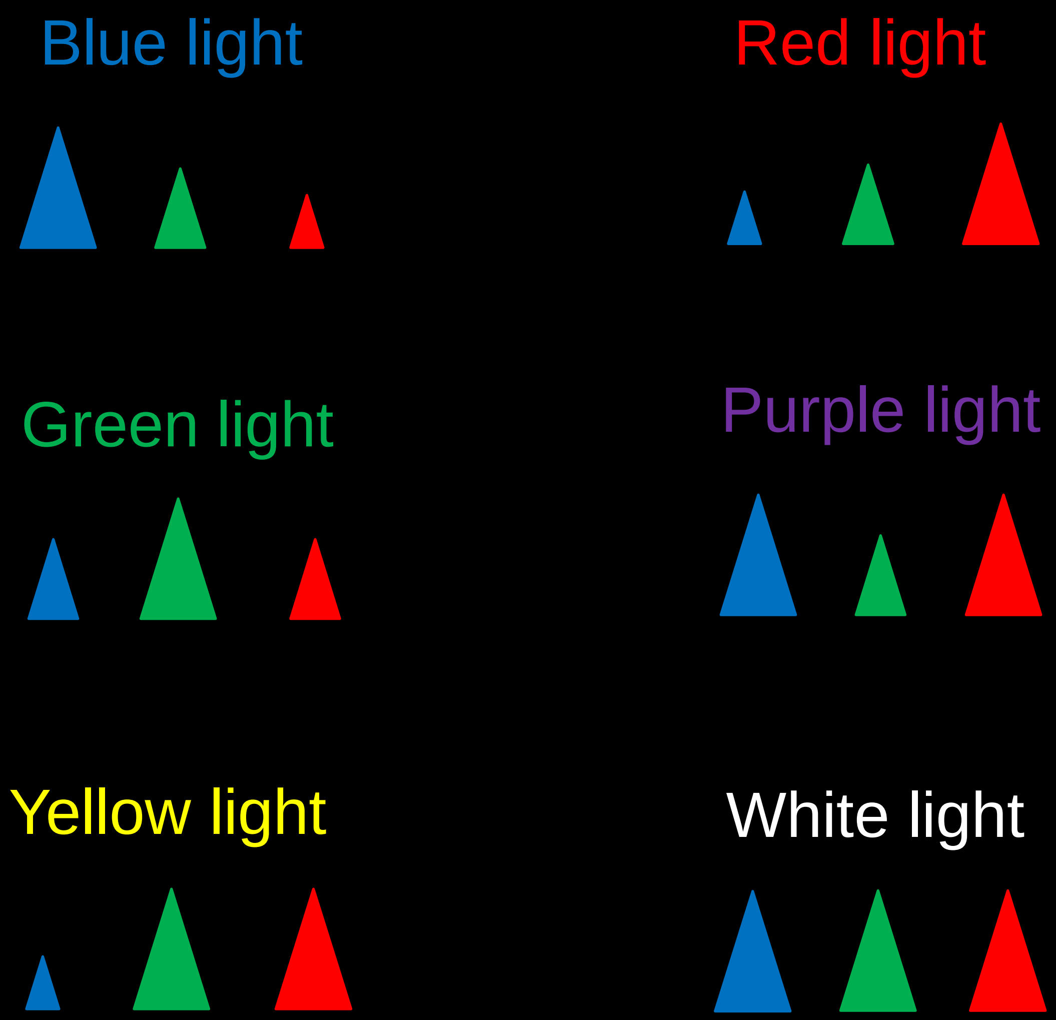


Fig. 7.1 Classification of the type of colour deficiency with the Farnsworth D15 test. (a) Protan, deutan, and tritan defects. 1. Moderate and severe protan defects. 2. Moderate and severe deutan defects. 3. Moderate and severe tritan defects. (b) Typical 'rod' monochromatism. The arrangement represents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

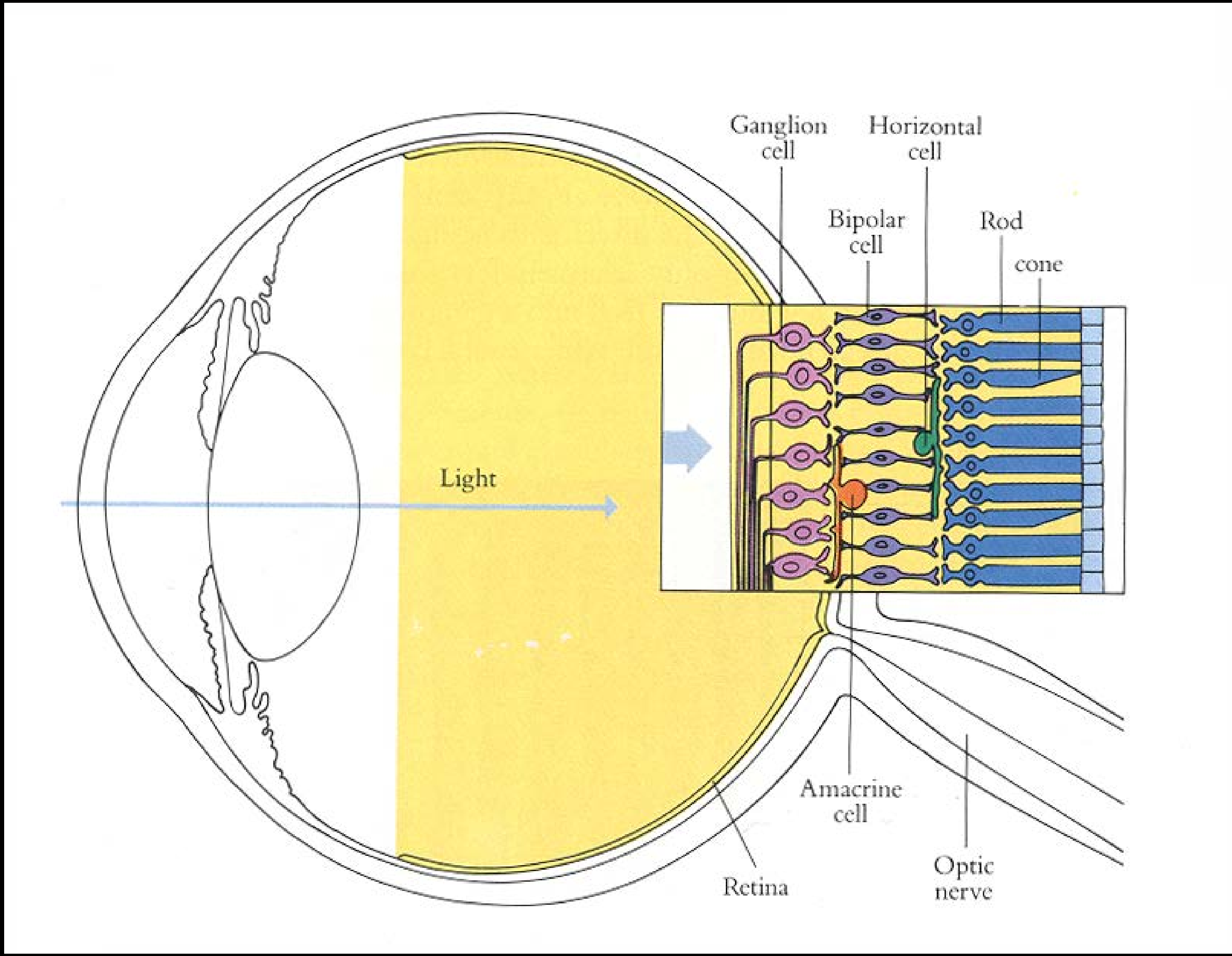
Credit: Jenny Birch

POSTRECEPTORAL COLOUR VISION

Colour is encoded initially by the relative outputs of the three different cone types.



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

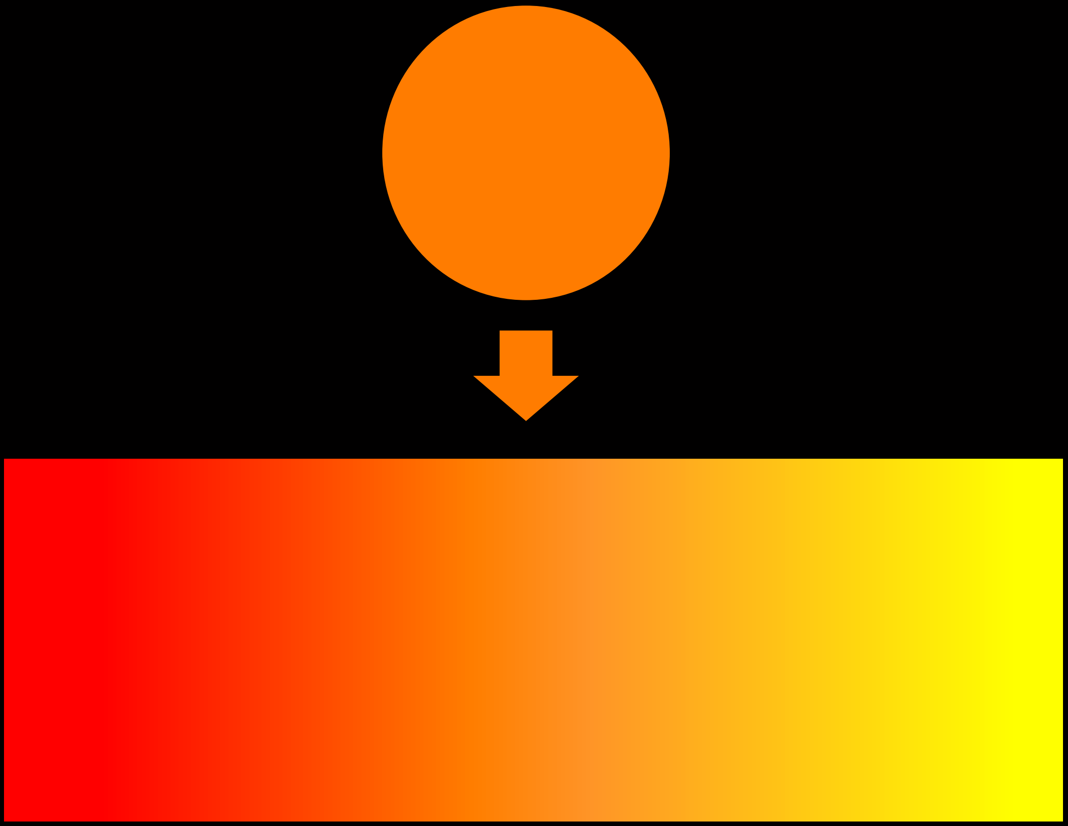


Colour phenomenology

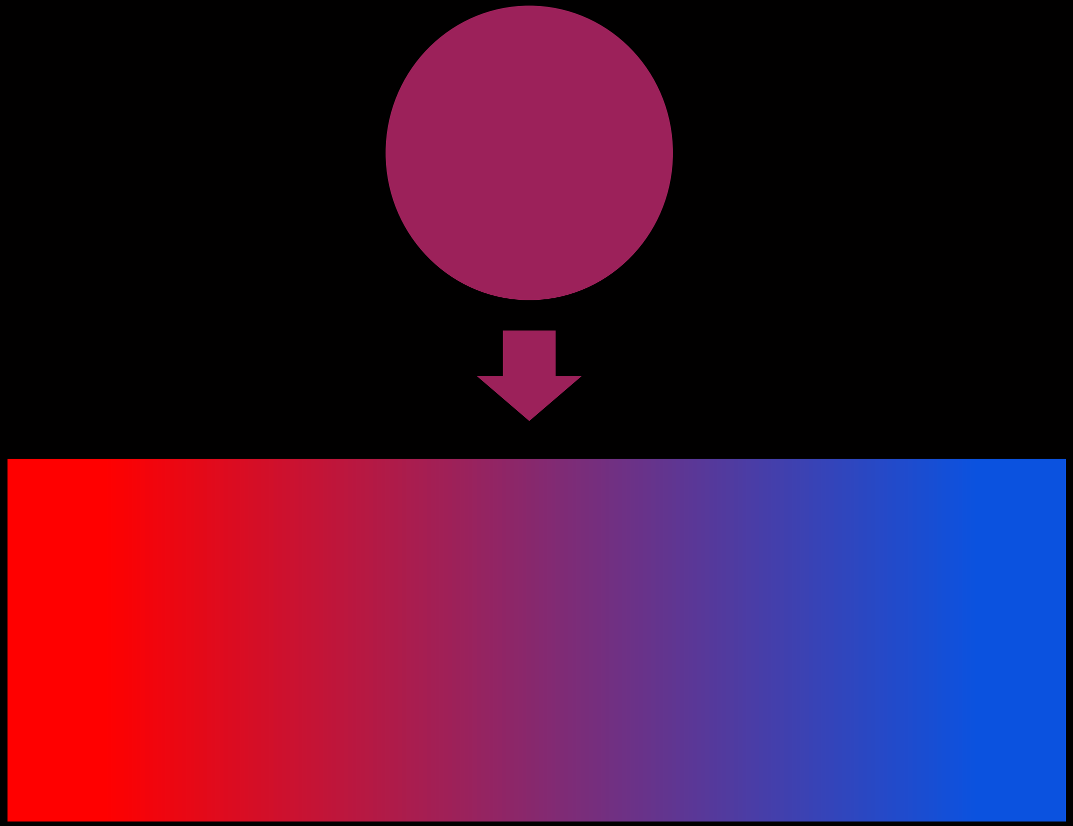
Can provide clues about how colours are processed after the photoreceptors…

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

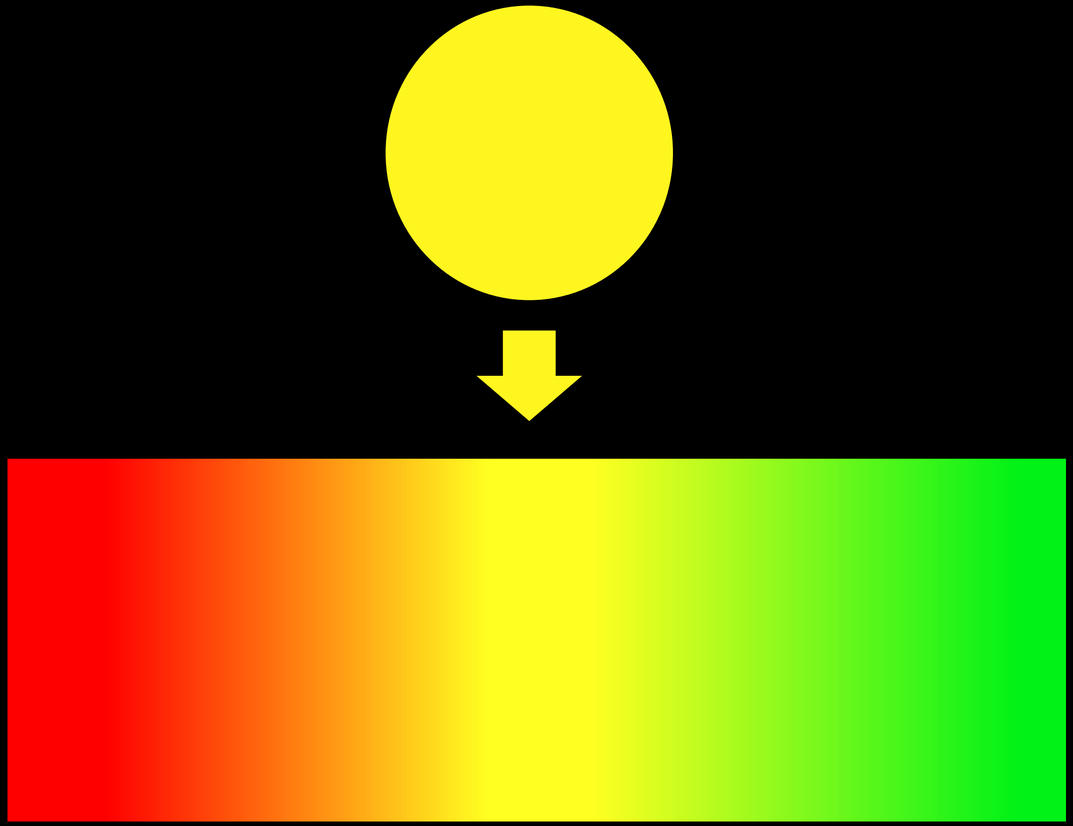
WHY?



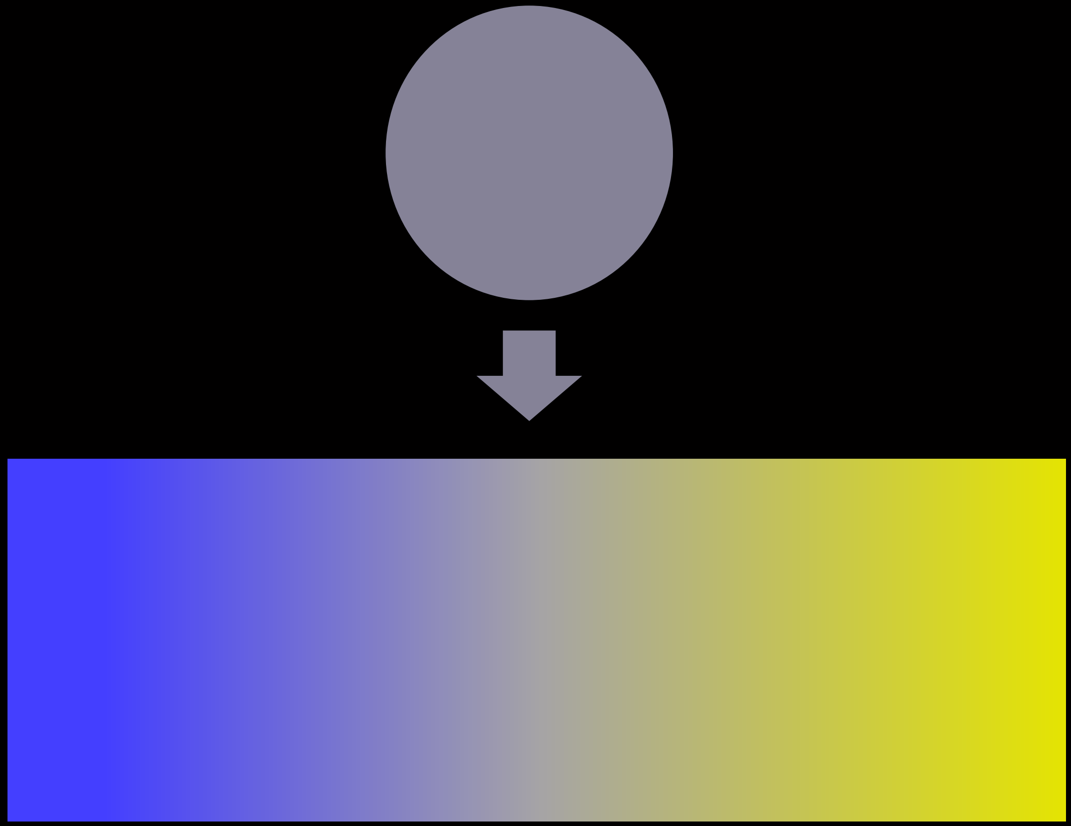
Reddish-yellows?



Reddish-blues?

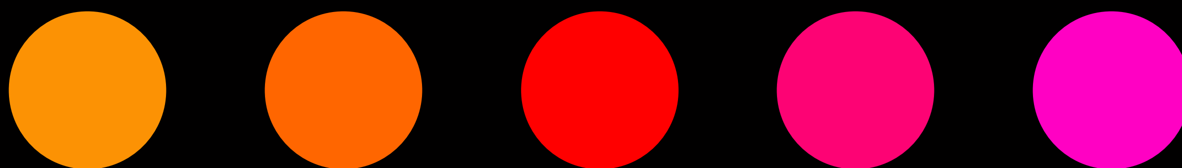


Reddish-greens?



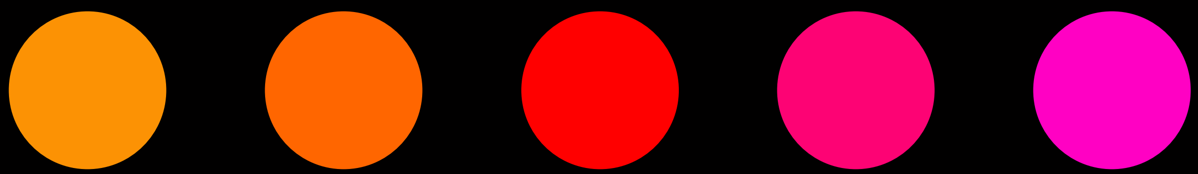
Bluish-yellow?

The colour opponent theory of Hering



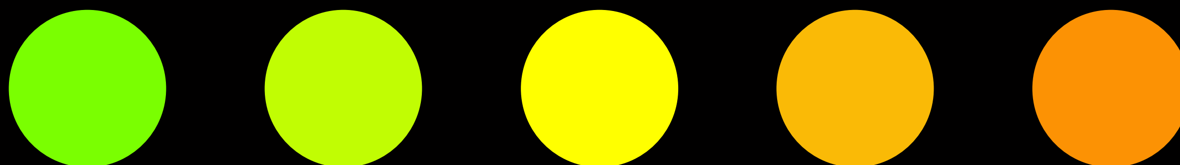
Reds can get bluer or yellower but not greener

The colour opponent theory of Hering



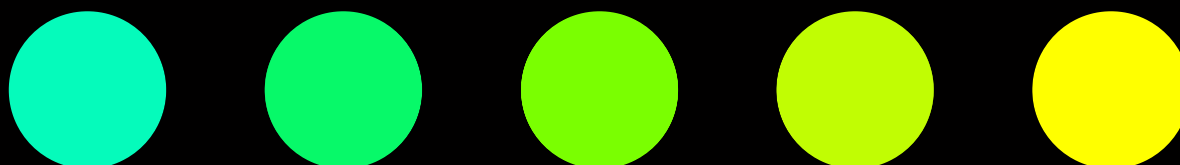
Reds can get bluer or yellower but not greener

The colour opponent theory of Hering



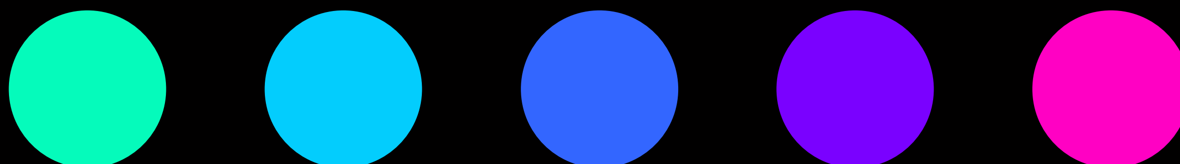
Yellows can get greener or redder but not bluer

The colour opponent theory of Hering



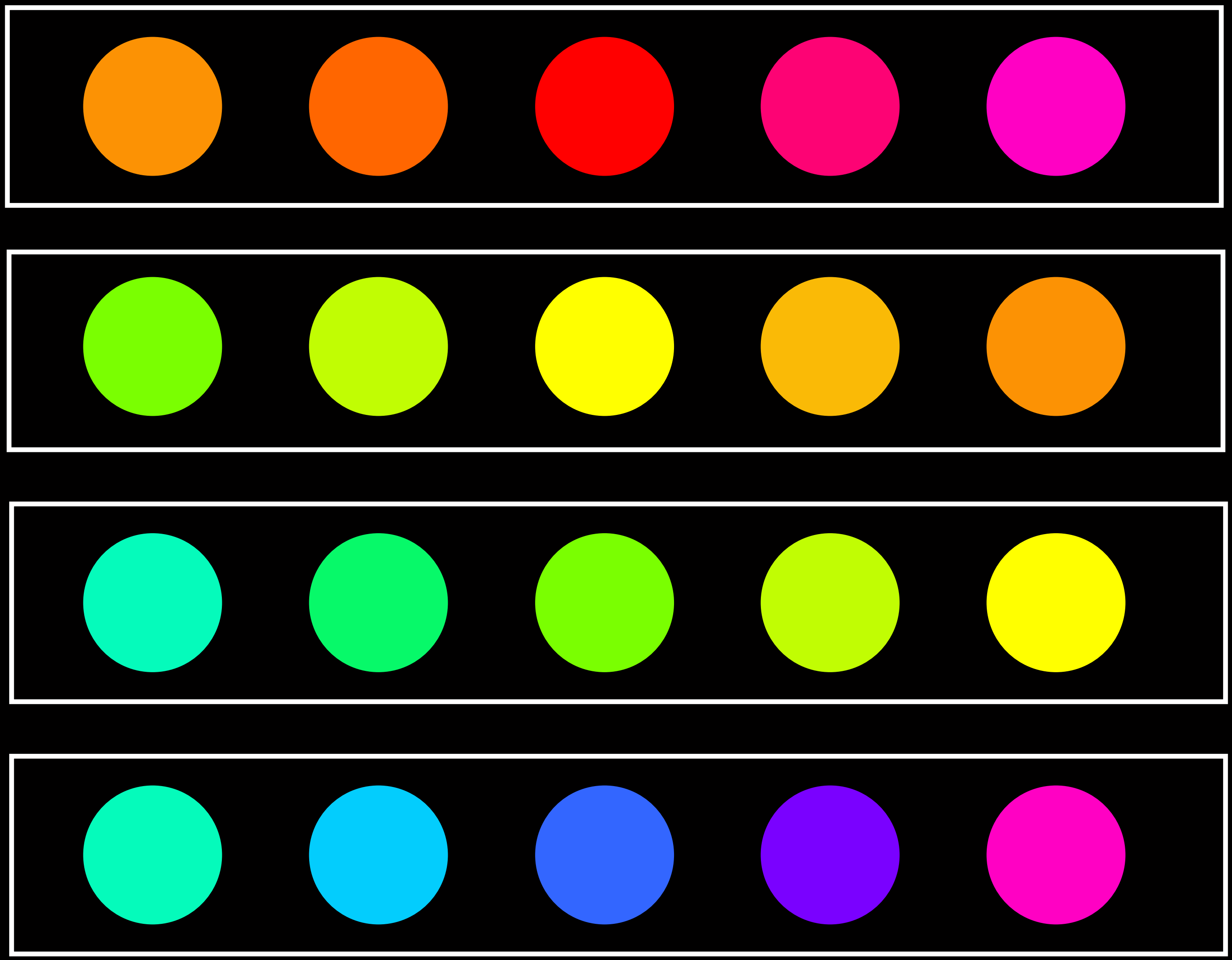
Greens can get bluer or yellower but not redder

The colour opponent theory of Hering

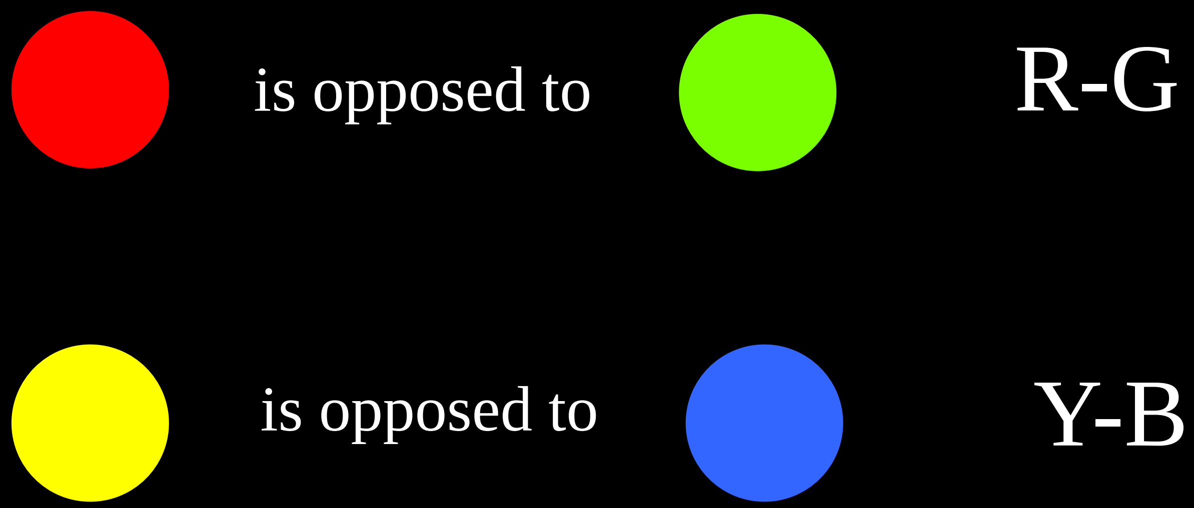


Blues can get greener or redder but not yellower

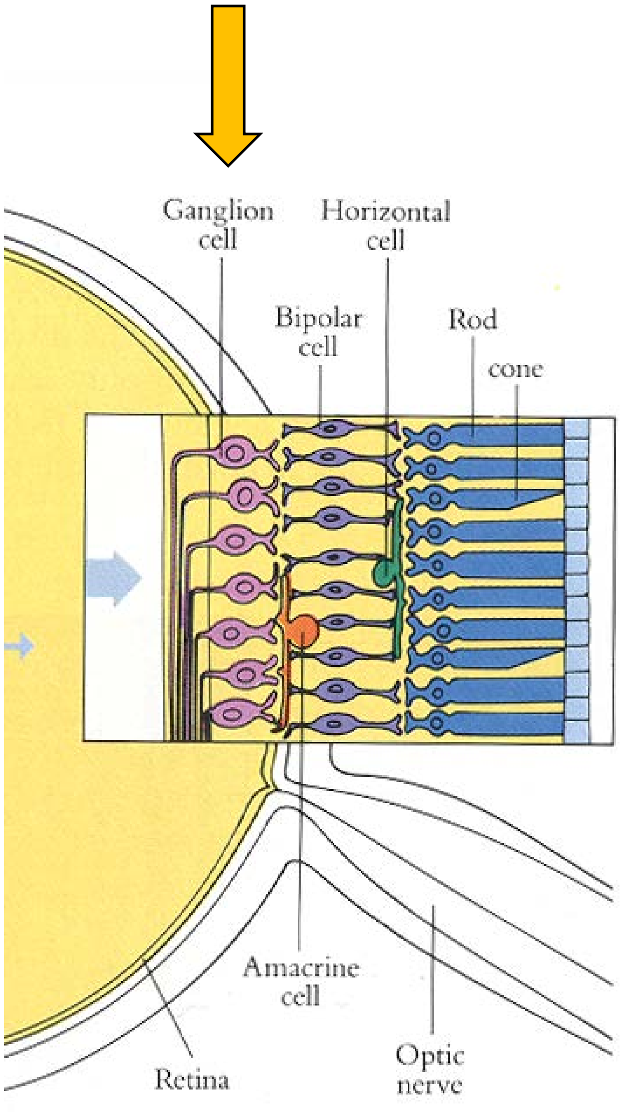
The colour opponent theory of Hering



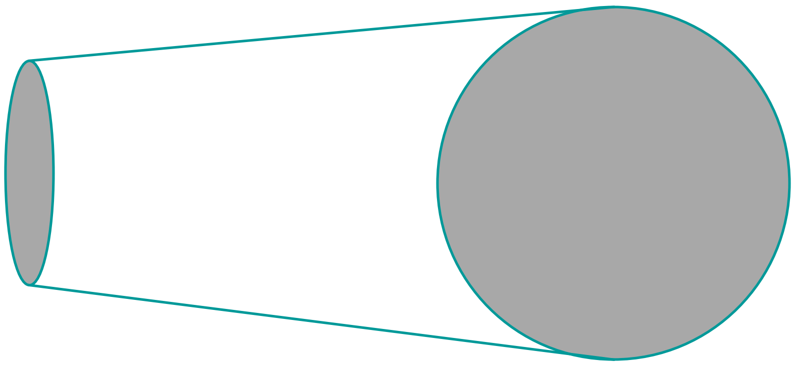
The colour opponent theory of Hering



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

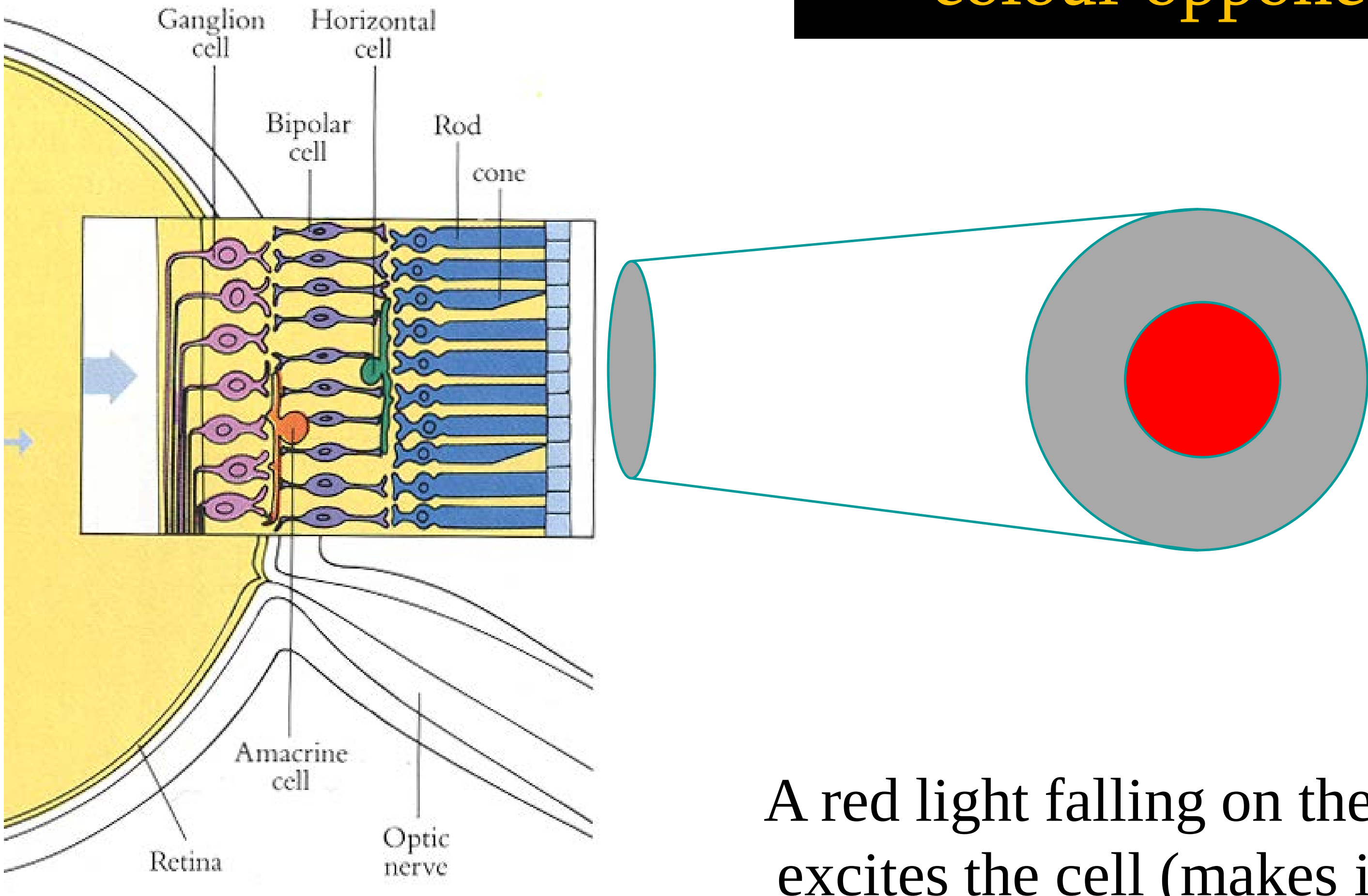


Some ganglion cells are colour opponent



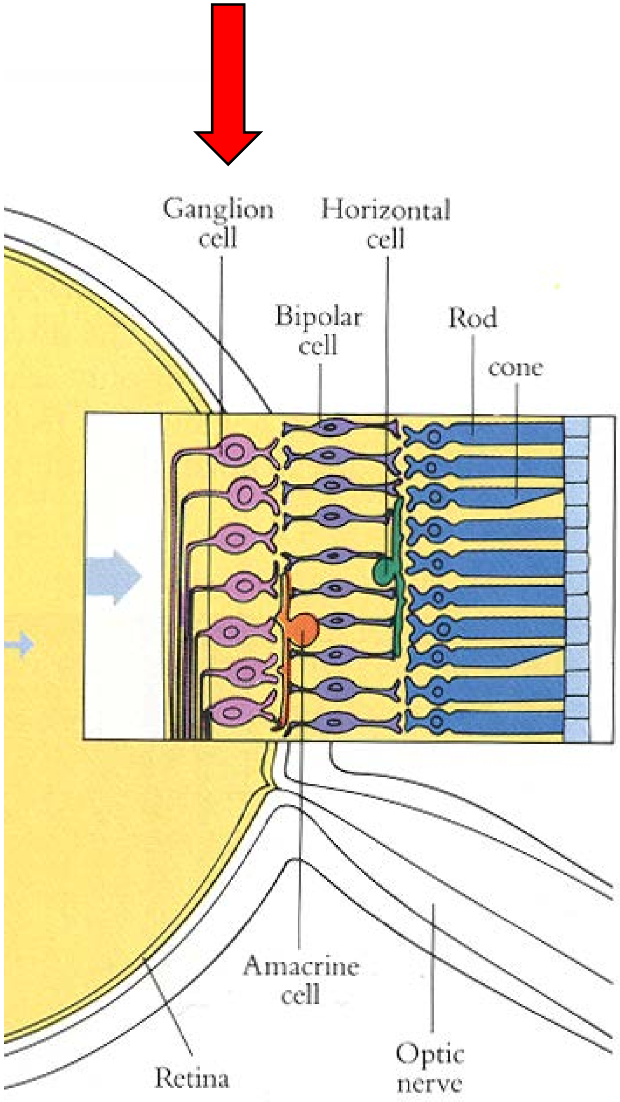
Imagine that this is the region of space that the cell "sees" in the external world

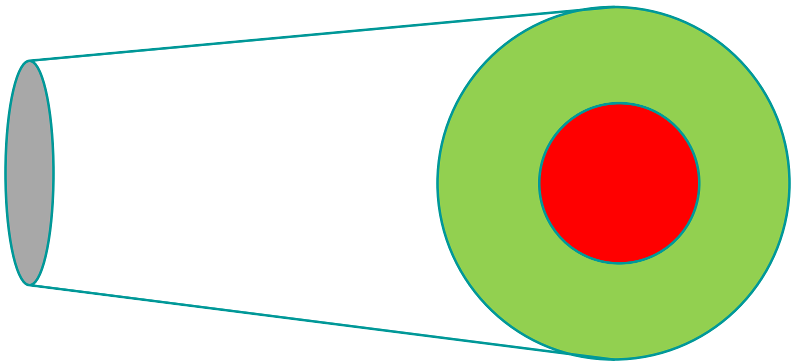
Some ganglion cells are colour opponent



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

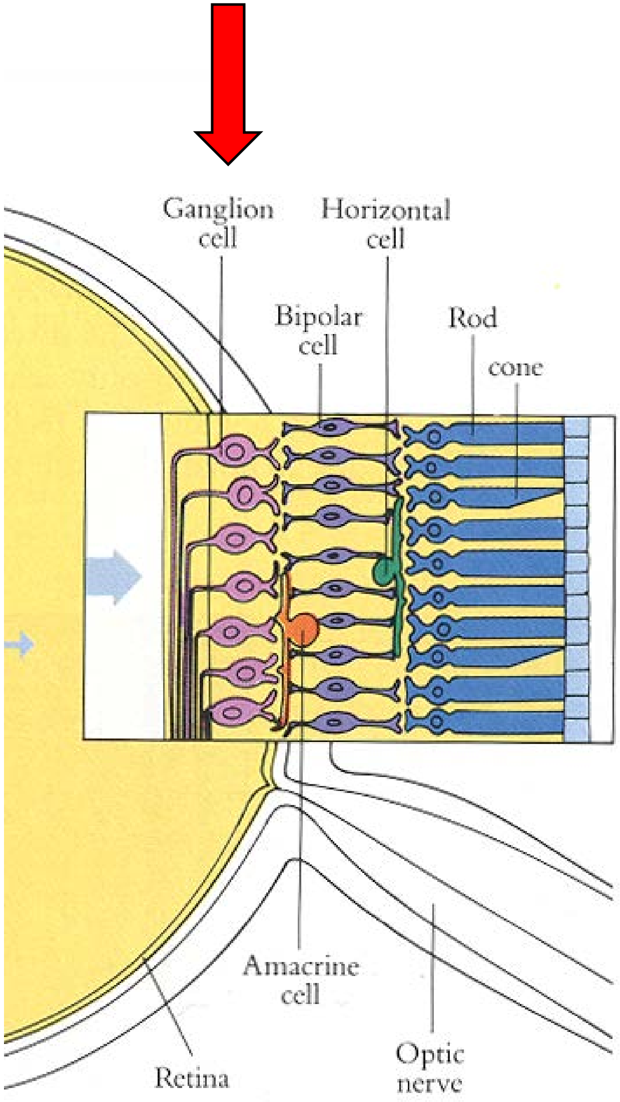
Some ganglion cells are colour opponent

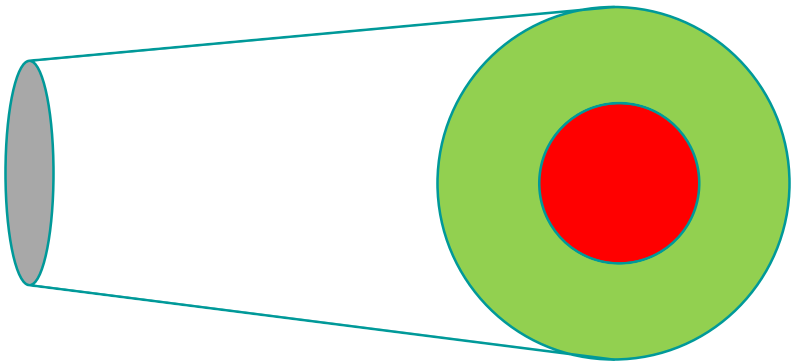




A green light falling on the surround area inhibits the cell (makes it fire slower)

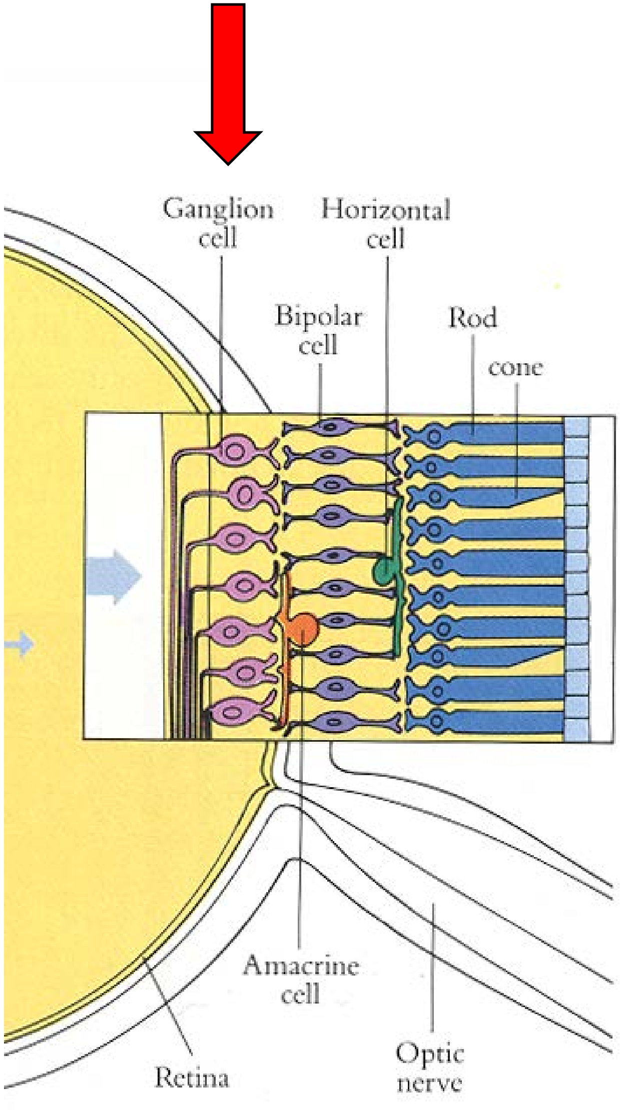
Some ganglion cells are colour opponent

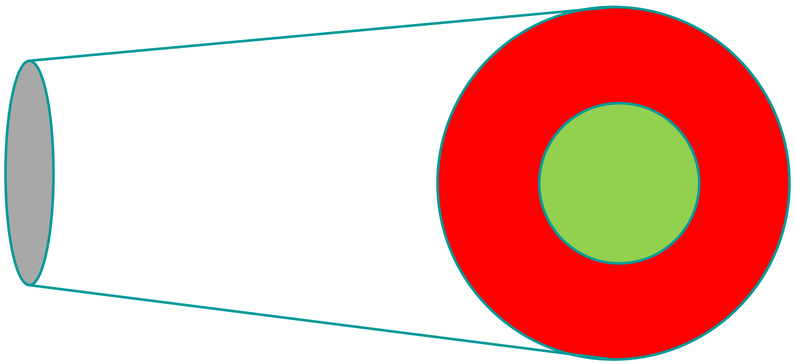




RED On-centre
GREEN Off-surround

Some ganglion cells are colour opponent

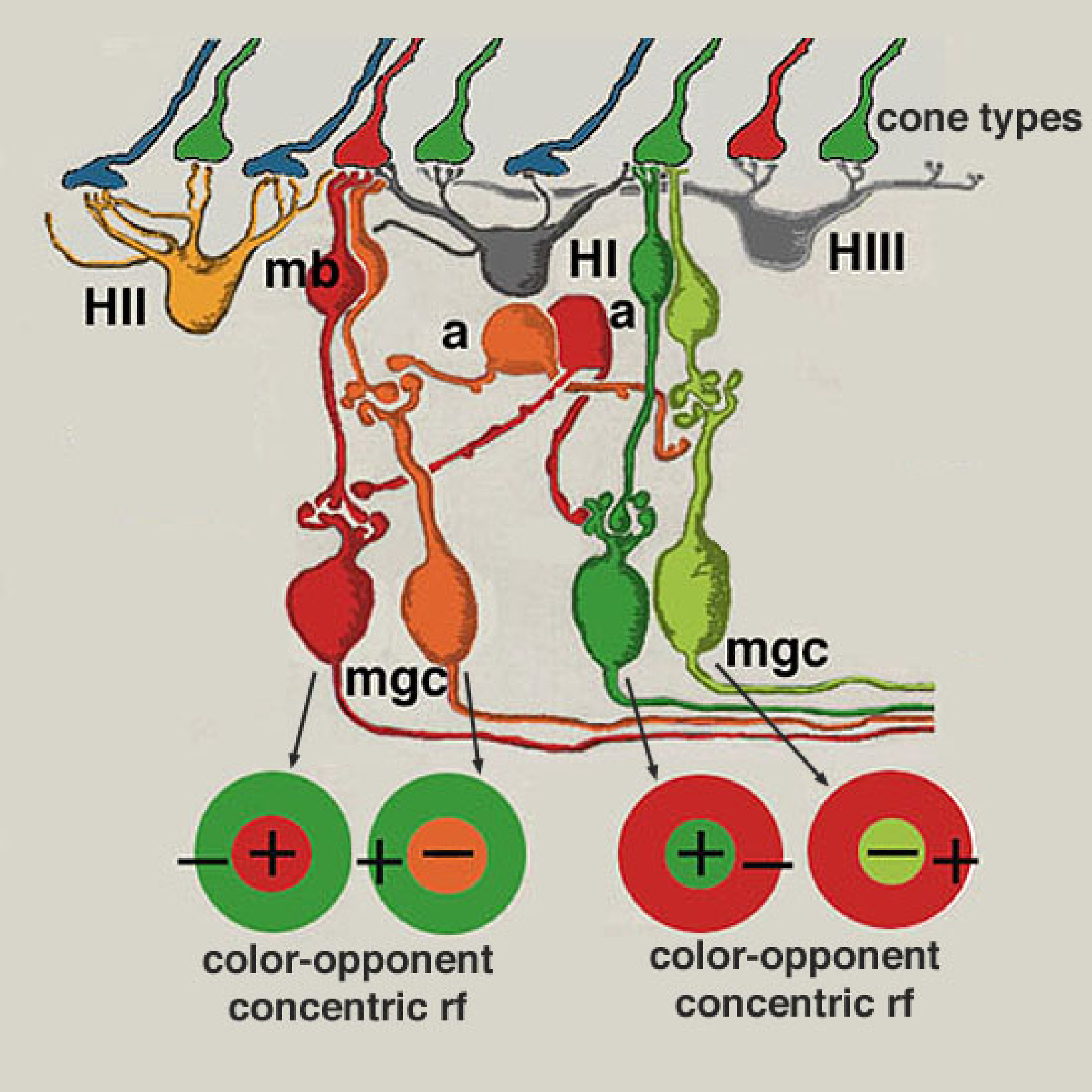




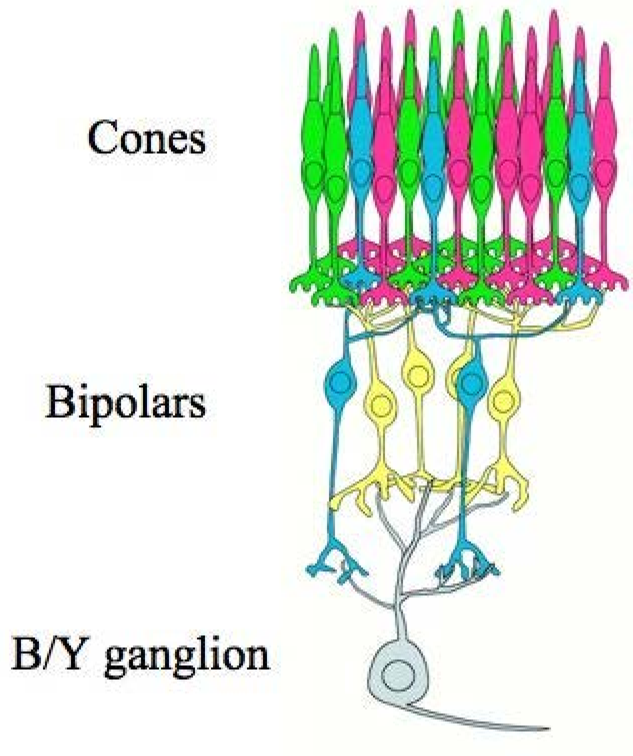
GREEN On-centre
RED Off-surround

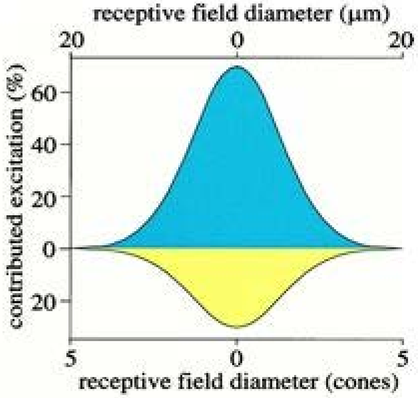
Red-green colour opponency

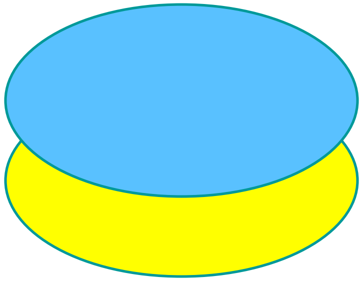
Four variants



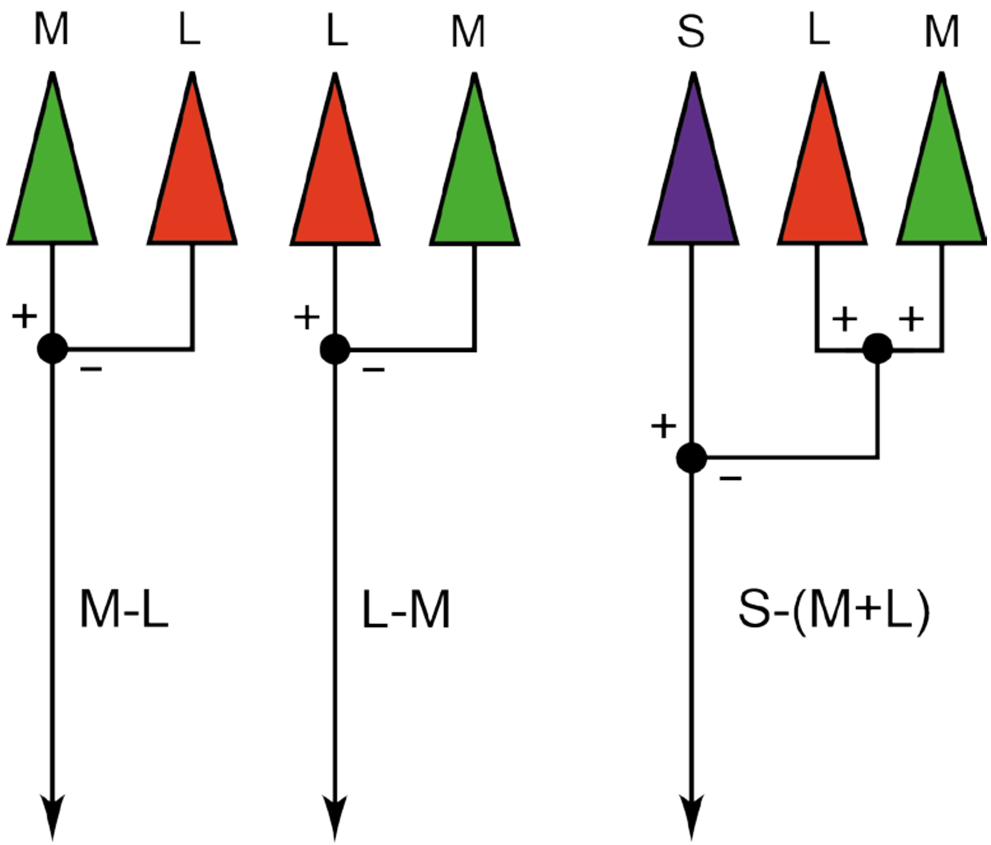
Blue/yellow pathway





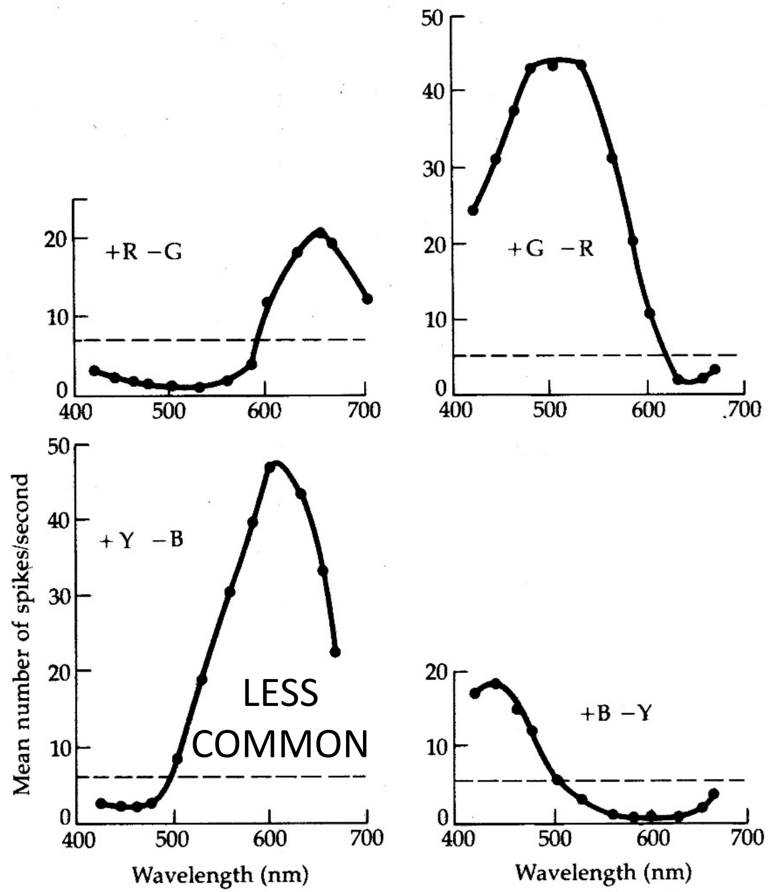


Source: David Heeger



Chromatic pathways

LGN cell responses



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

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)

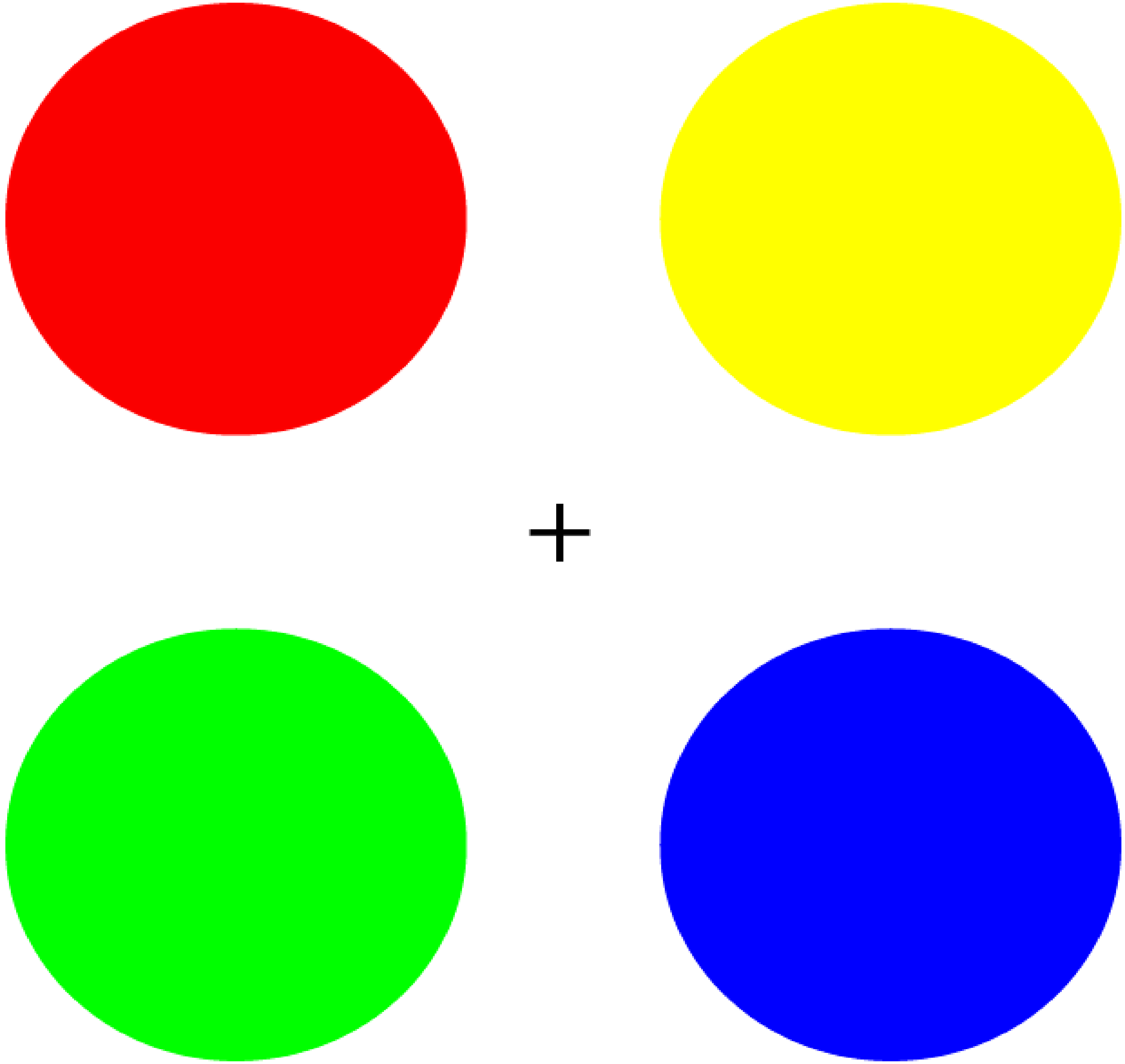
COLOUR CONTRAST

COLOUR ASSIMILATION

COLOUR AFTER-EFFECTS

(what precedes the patch)

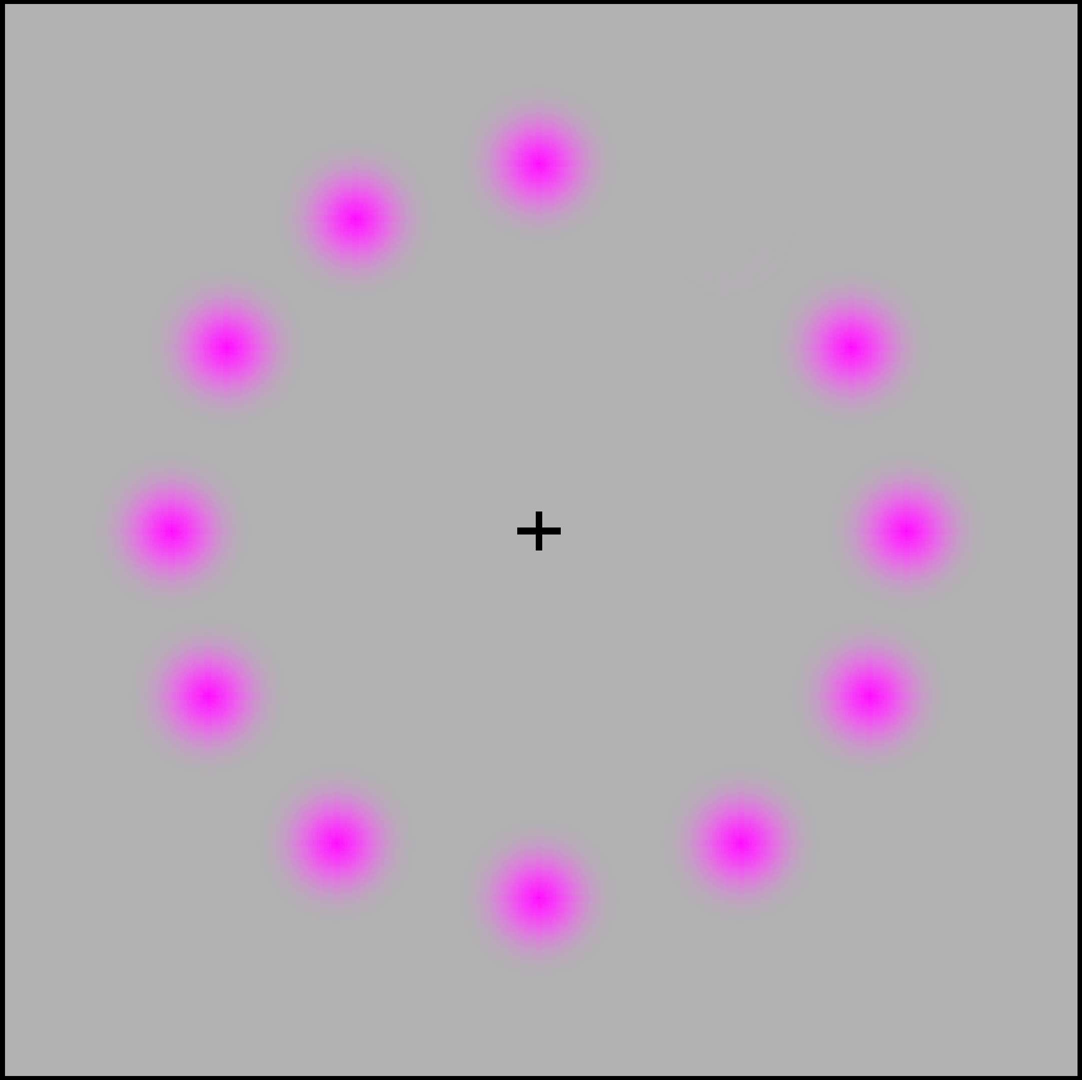
Colour
after-effects



+

Mediafire

Lilac chaser or Pac-Man illusion



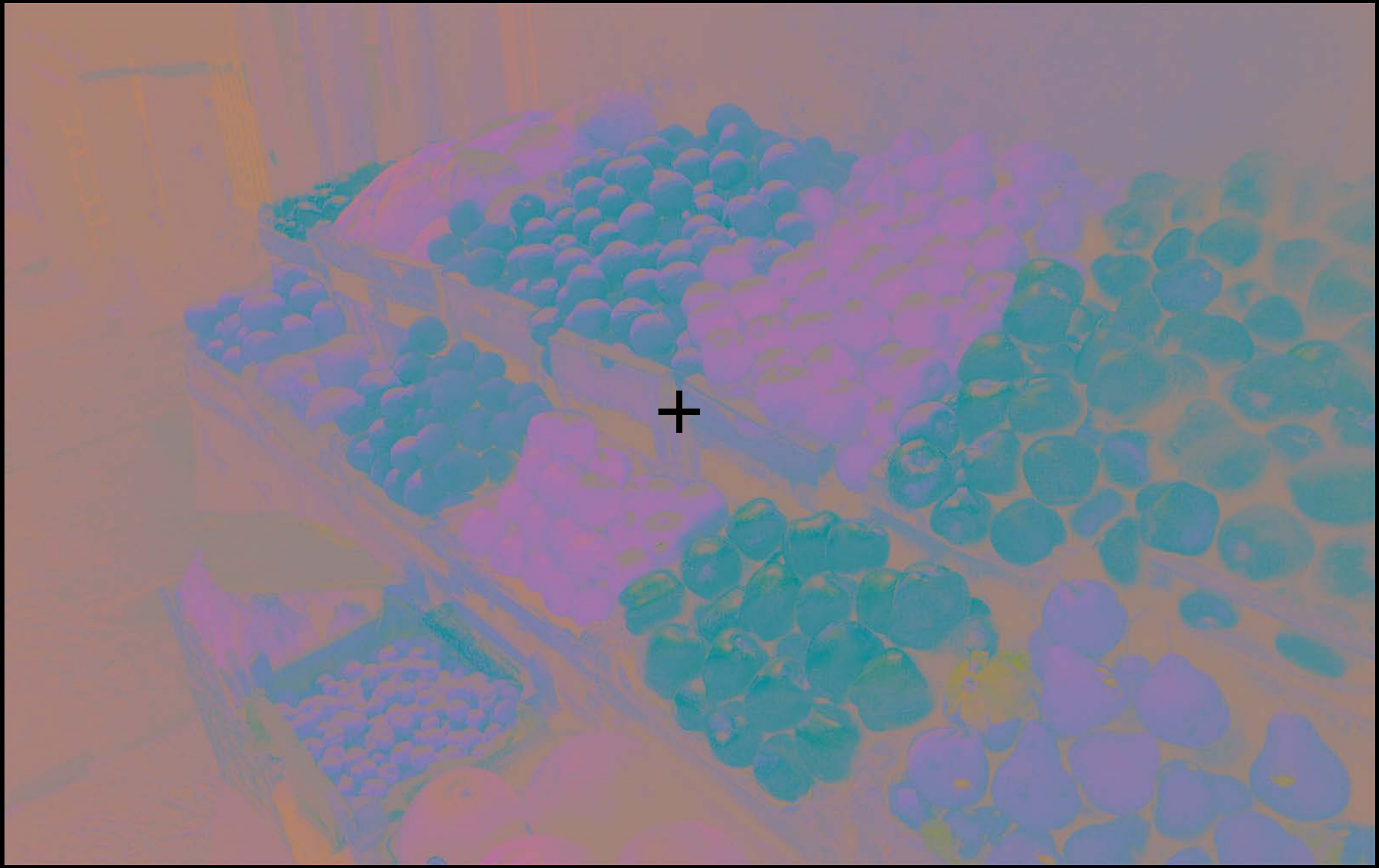
Jeremy Hinton

Lilac chaser or Pac-Man illusion

http://michaelbach.de/ot/index.html

Michael Bach and Jeremy Hinton


Souvlaki

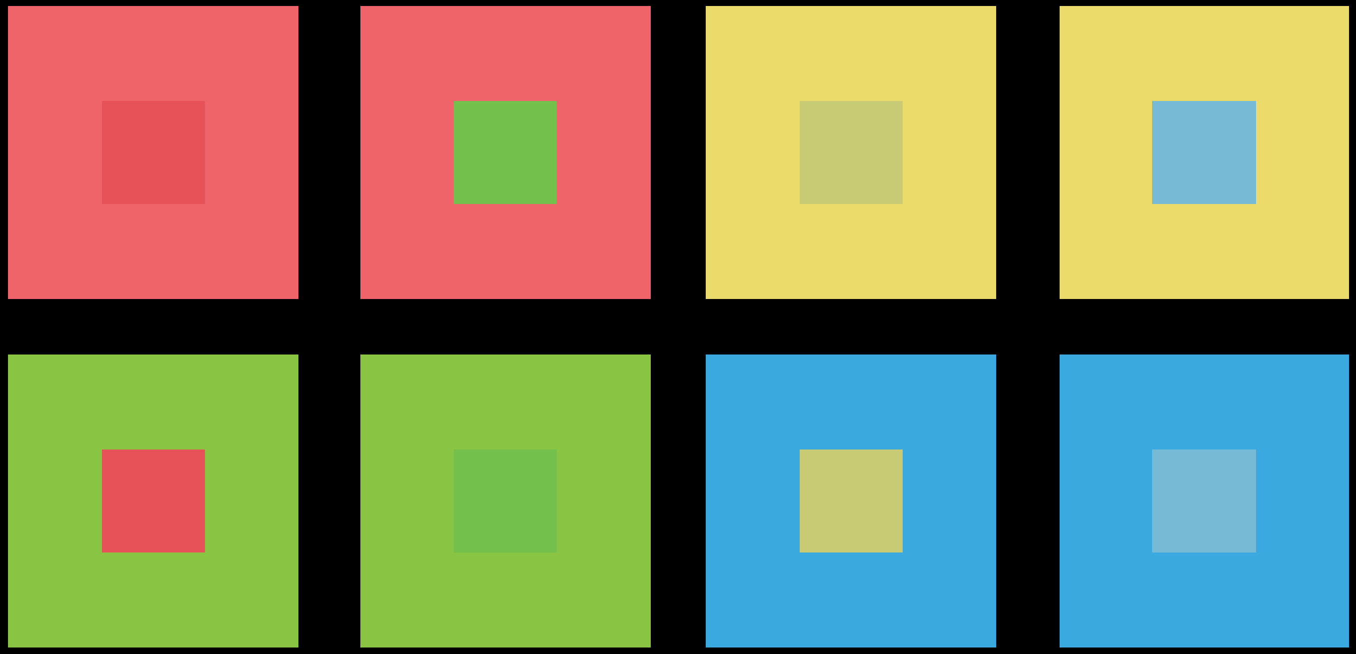


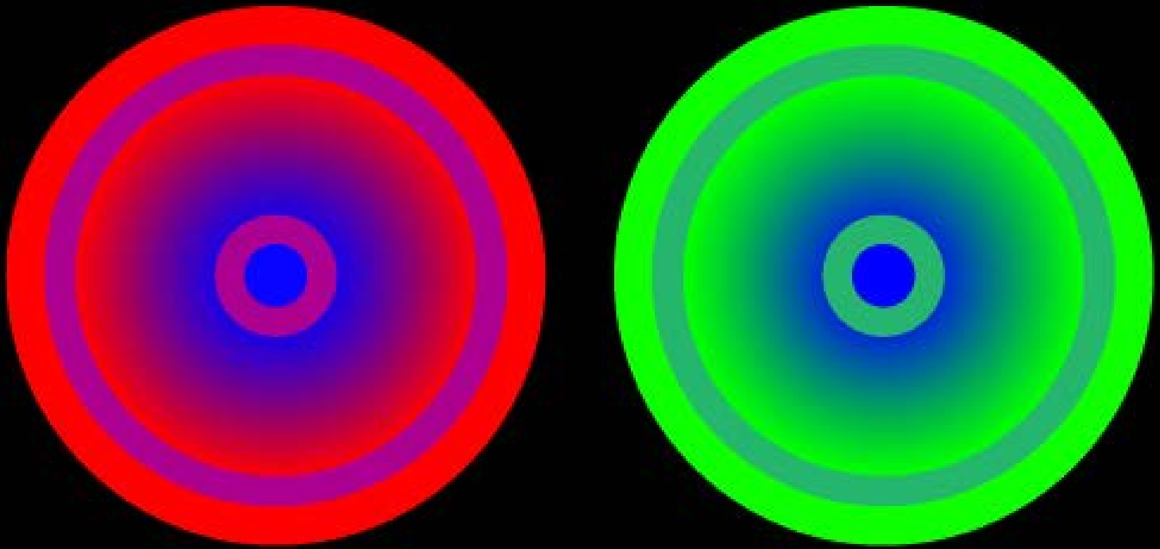

Souvlaki

COLOUR CONTRAST

(what surrounds the patch)

Color contrast

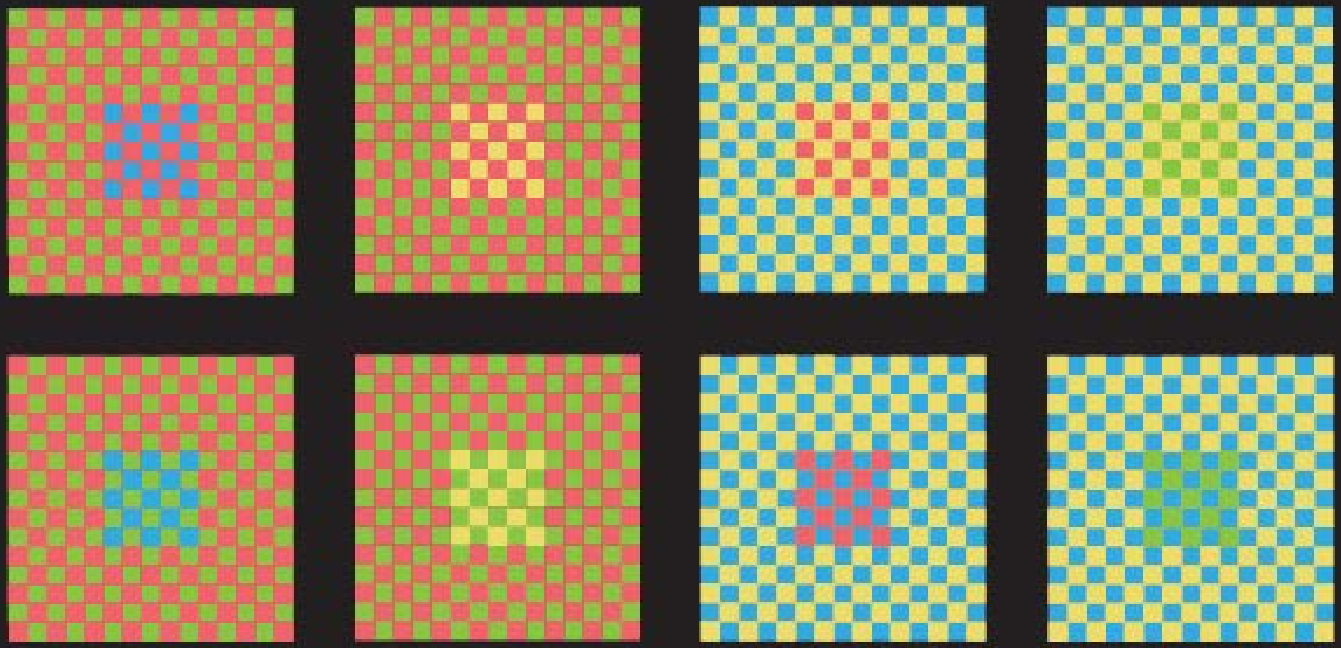




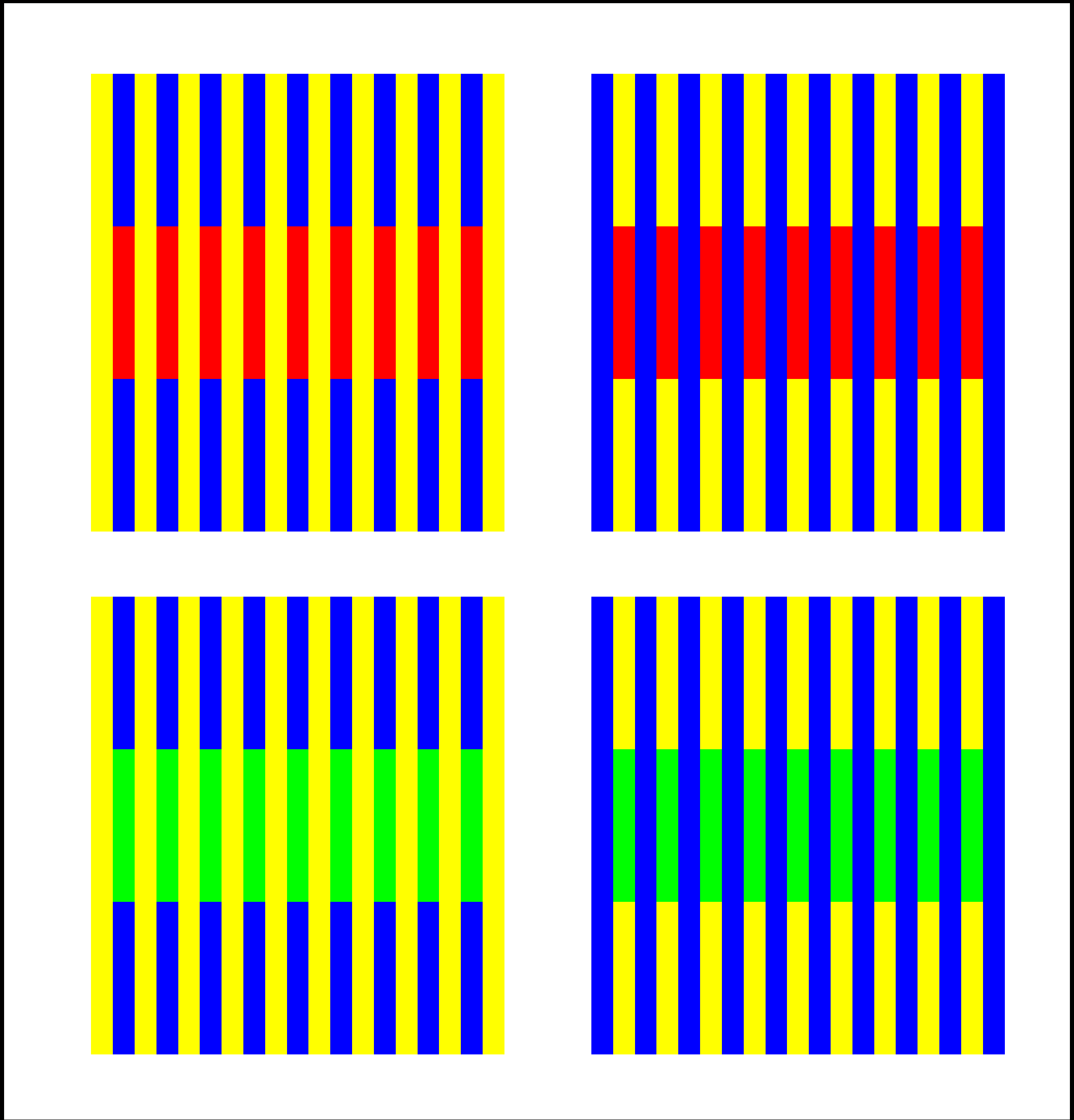
MacLeod

COLOUR ASSIMILATION

Color assimilation



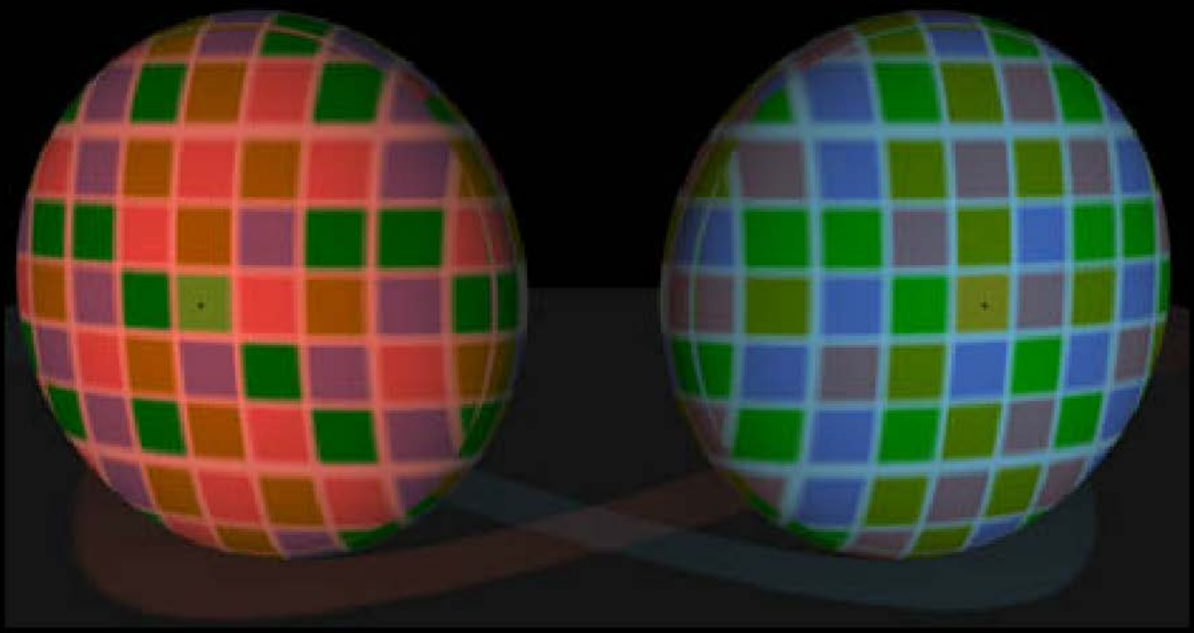
Munker illusion



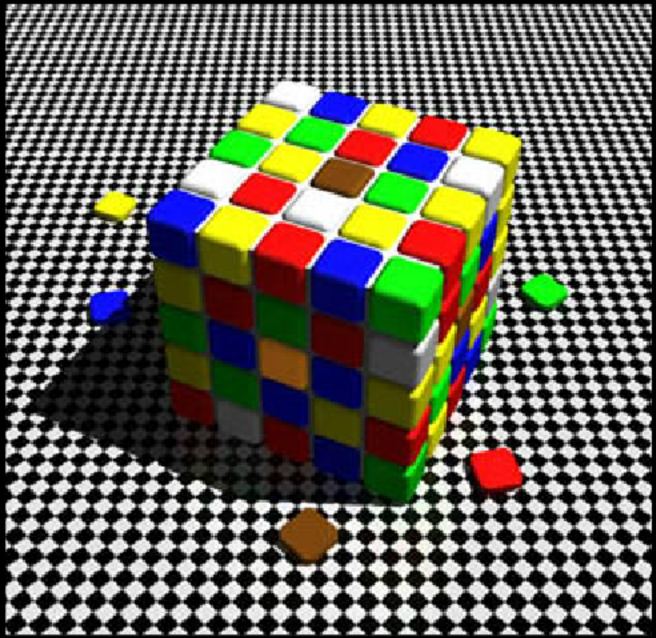
OTHER EFFECTS

Colour contrast and colour constancy

▶ Show mask



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)]

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?