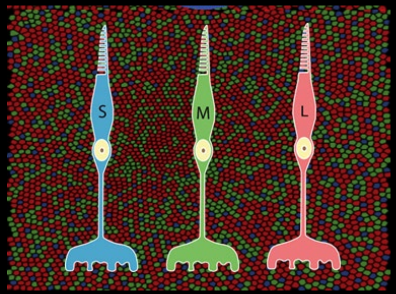
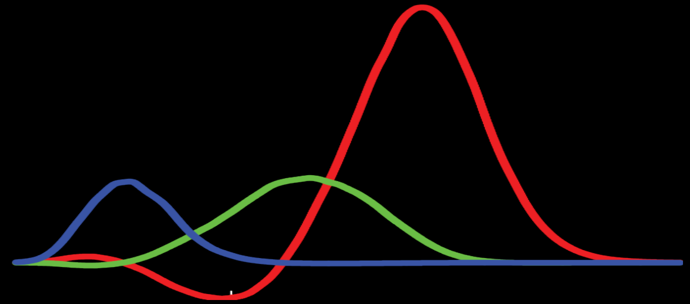
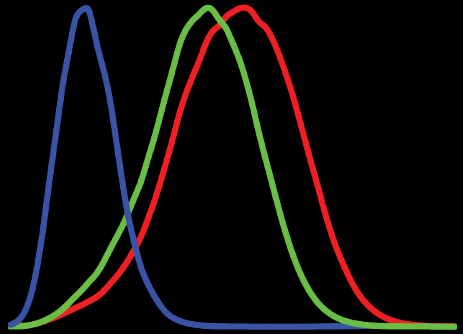
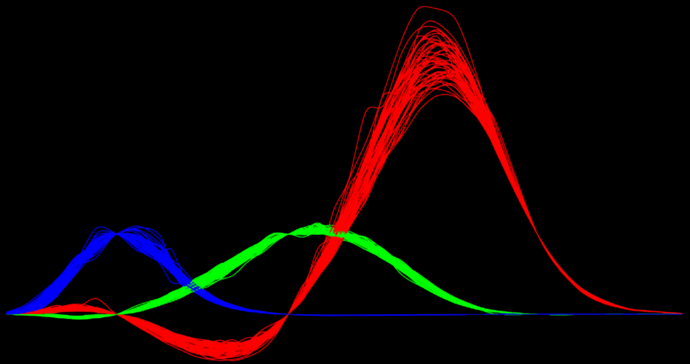


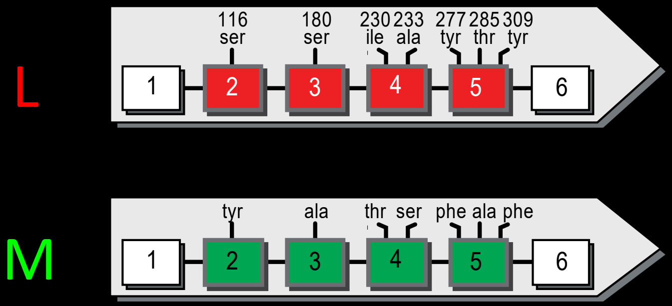
COLOUR MATCHING FUNCTIONS AND INDIVIDUAL DIFFERENCES





Andrew Stockman





International Color Consortium

CVRL IoO

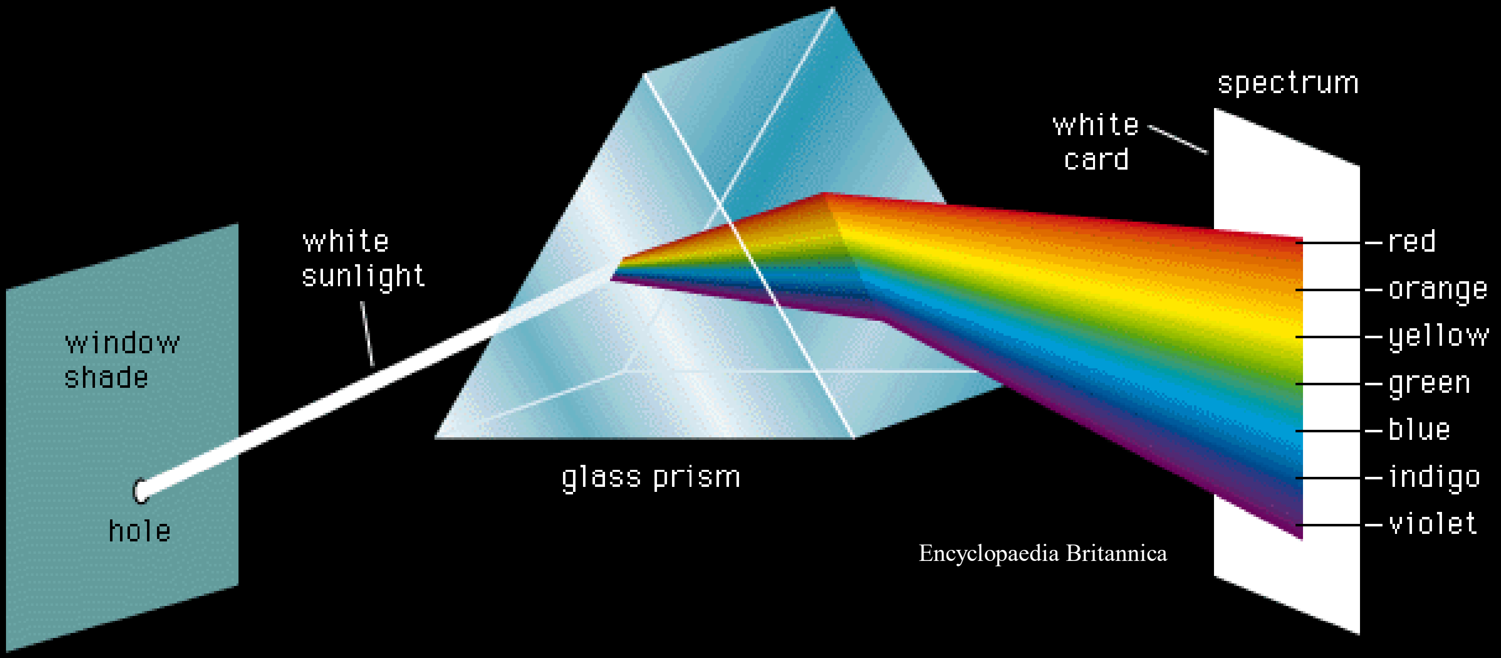
OUTLINE

1. Cone photoreceptors and colour vision
2. Trichromacy, univariance and the cone spectral sensitivities
3. Cone spectral sensitivities and colour matching functions
4. Individual differences

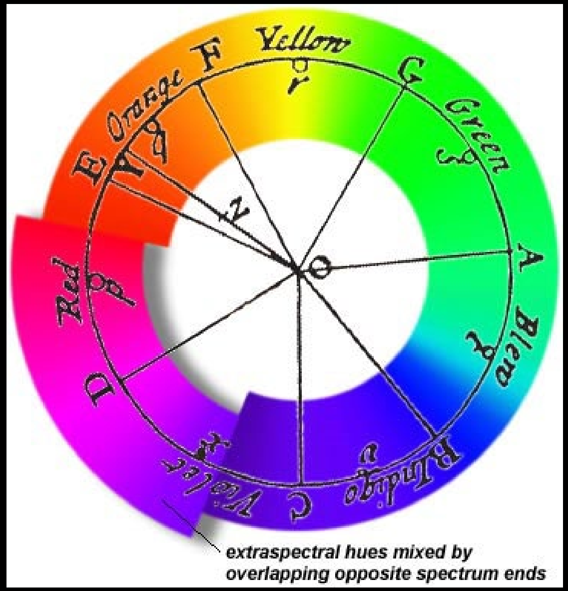
1. CONE PHOTORECEPTORS AND COLOUR VISION

Light

400 - 700 nm is important for vision

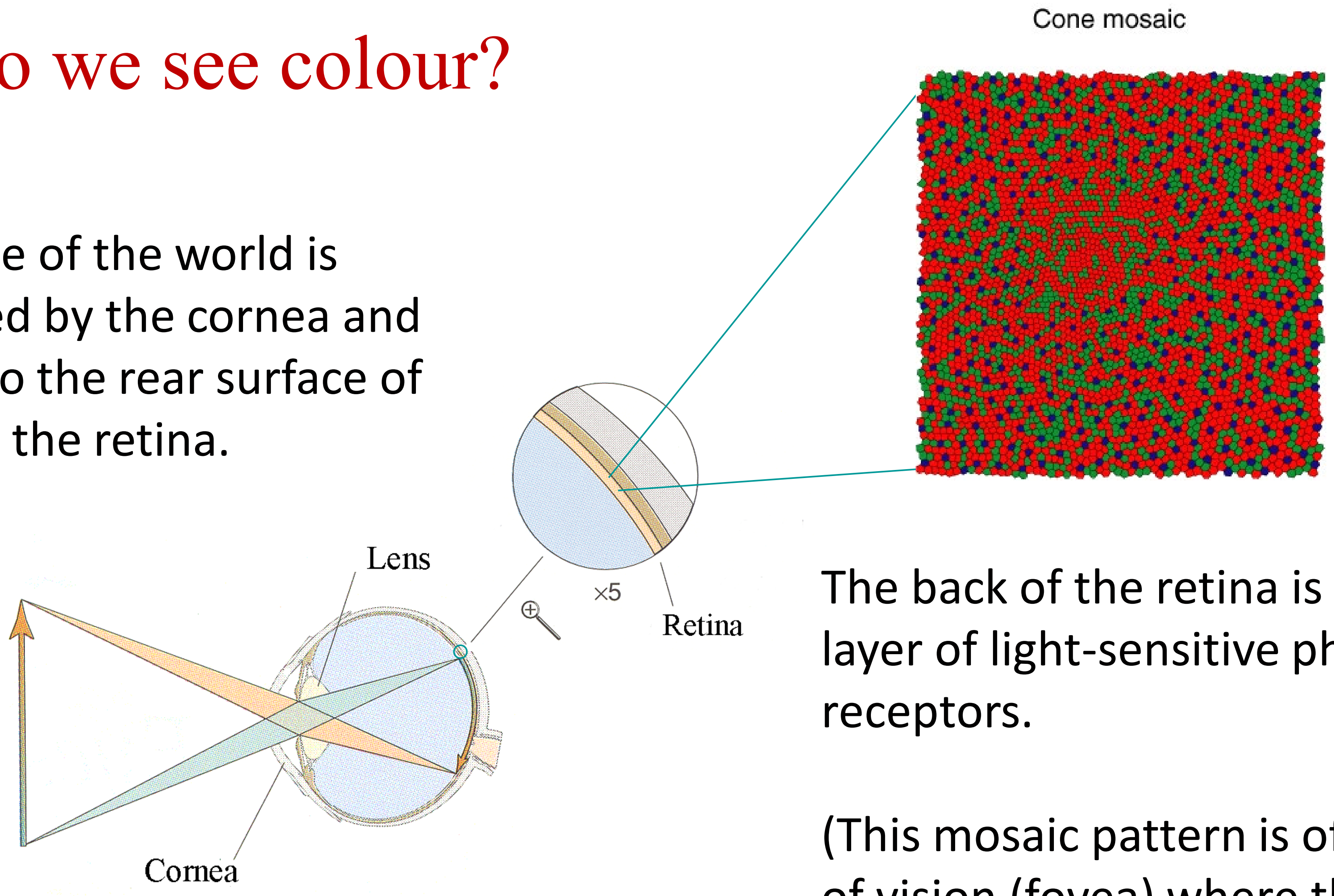


Encyclopaedia Britannica



How do we see colour?

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 photo-receptors.

(This mosaic pattern is of the centre of vision (fovea) where there are only cone (daytime) photoreceptors.)

Rods and cones

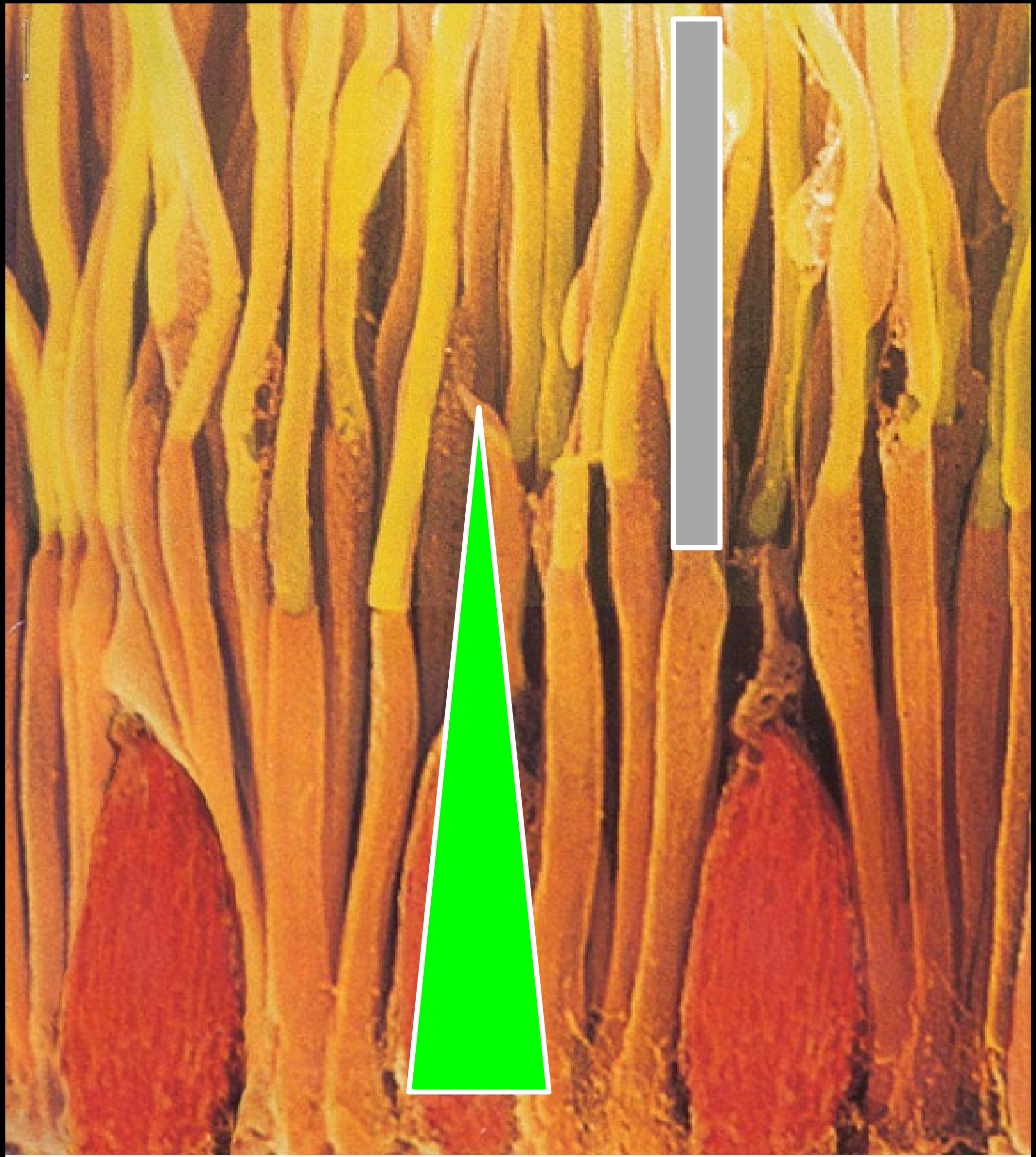
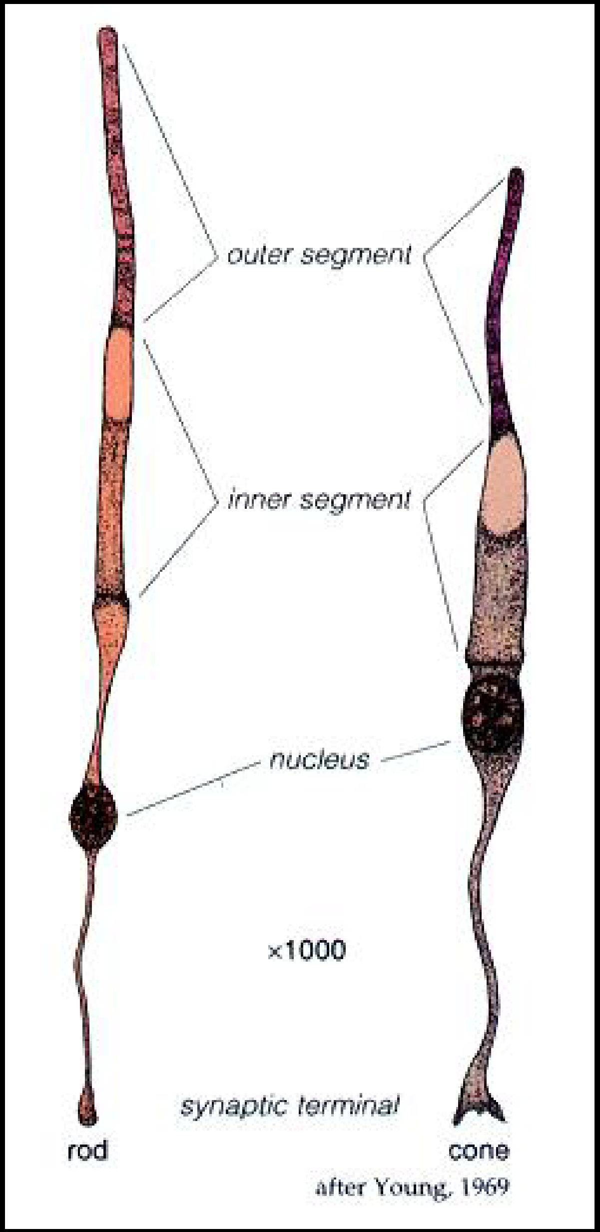


Fig1b. Scanning electron micrograph of the rods and cones of the primate retina. Image adapted from one by Ralph C. Eagle/Photo Researchers, Inc.

Webvision



Human photoreceptors

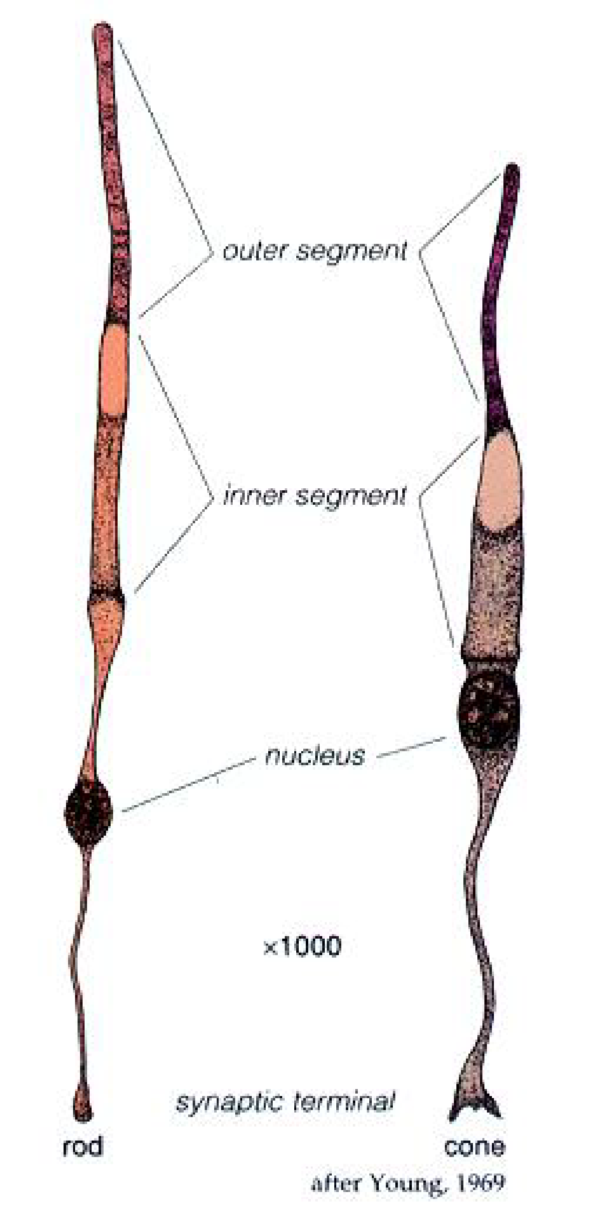
- Cones
  - Daytime, achromatic *and* chromatic vision
  - 3 types

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

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

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

Human photoreceptors



- Rods
  - Achromatic night vision
  - 1 type

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

Rod

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

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

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

How dependent are we on colour?

No colour…

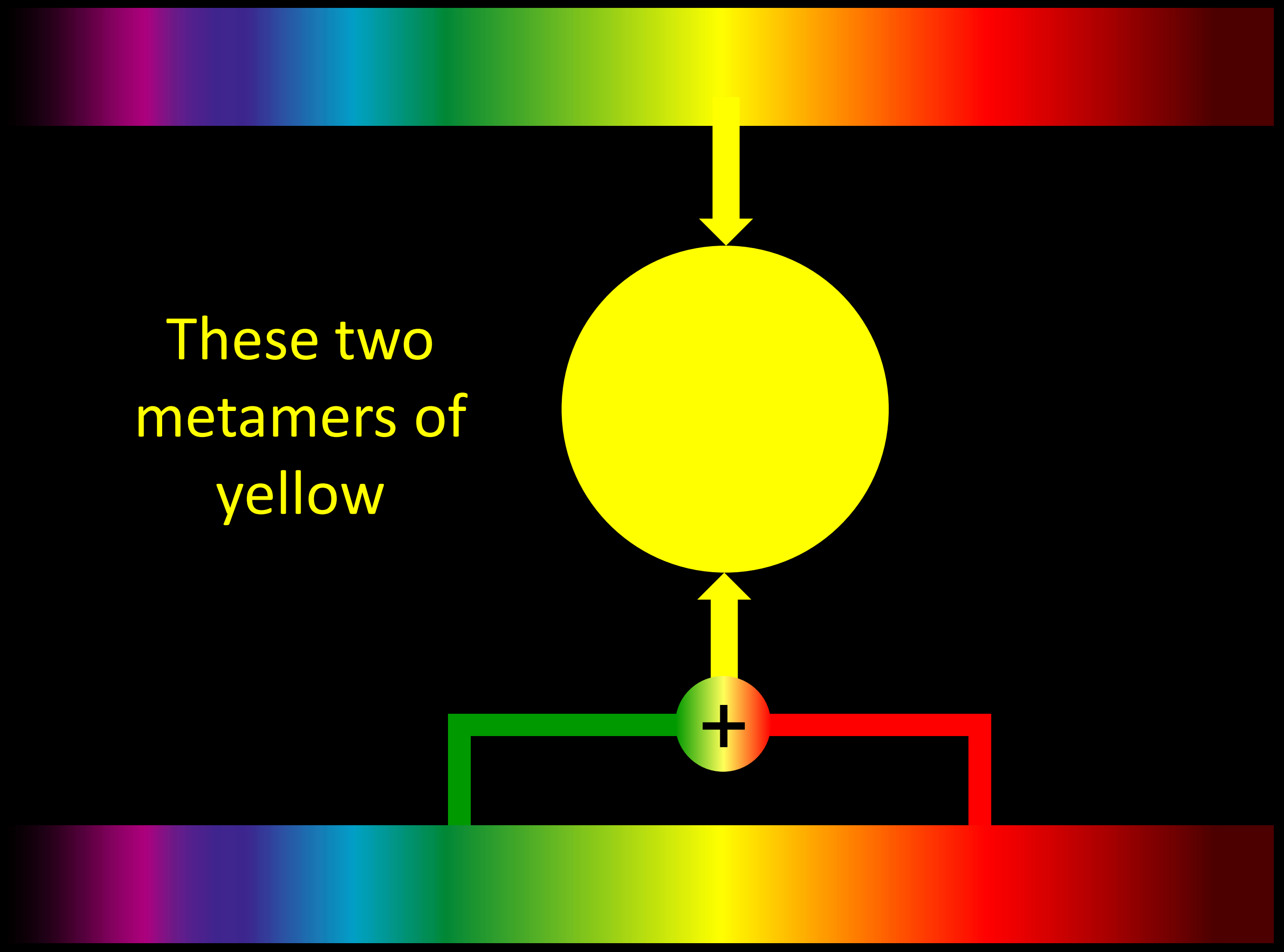
Colour…

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

Are the colours that we see…

a property mainly of physics or biology?

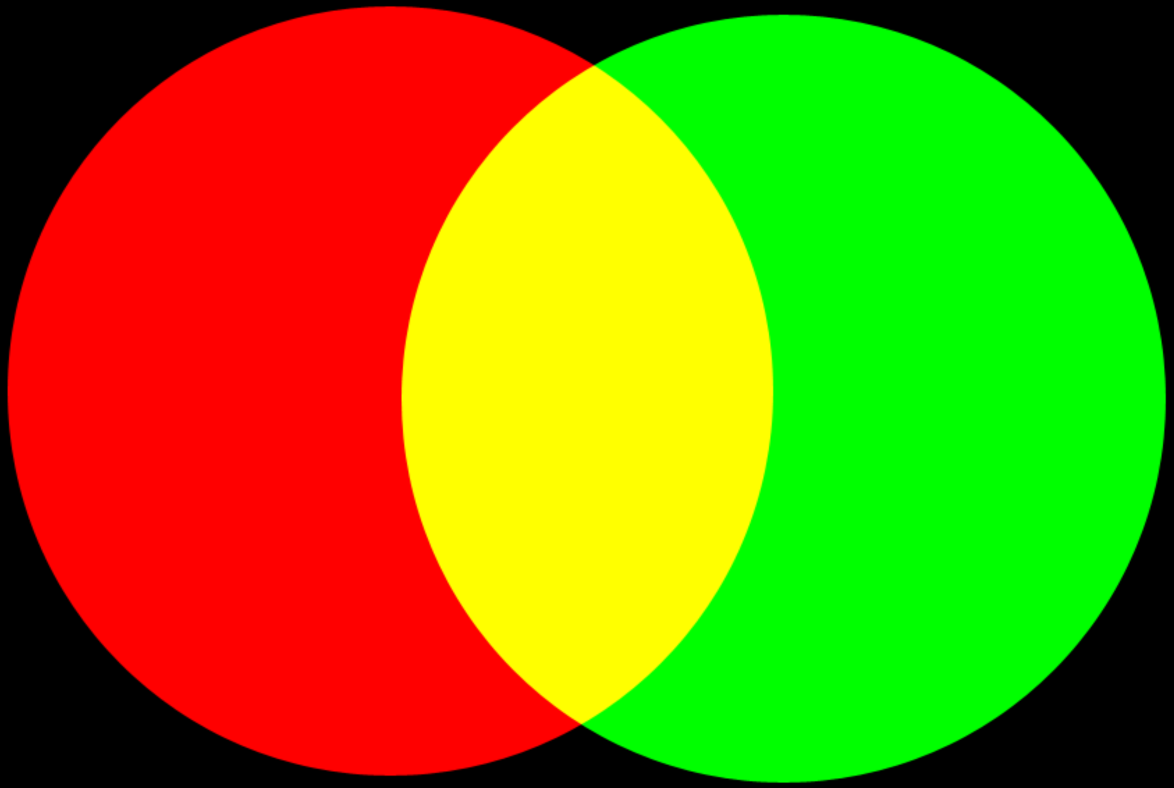
Colour isn't just about physics. For example:

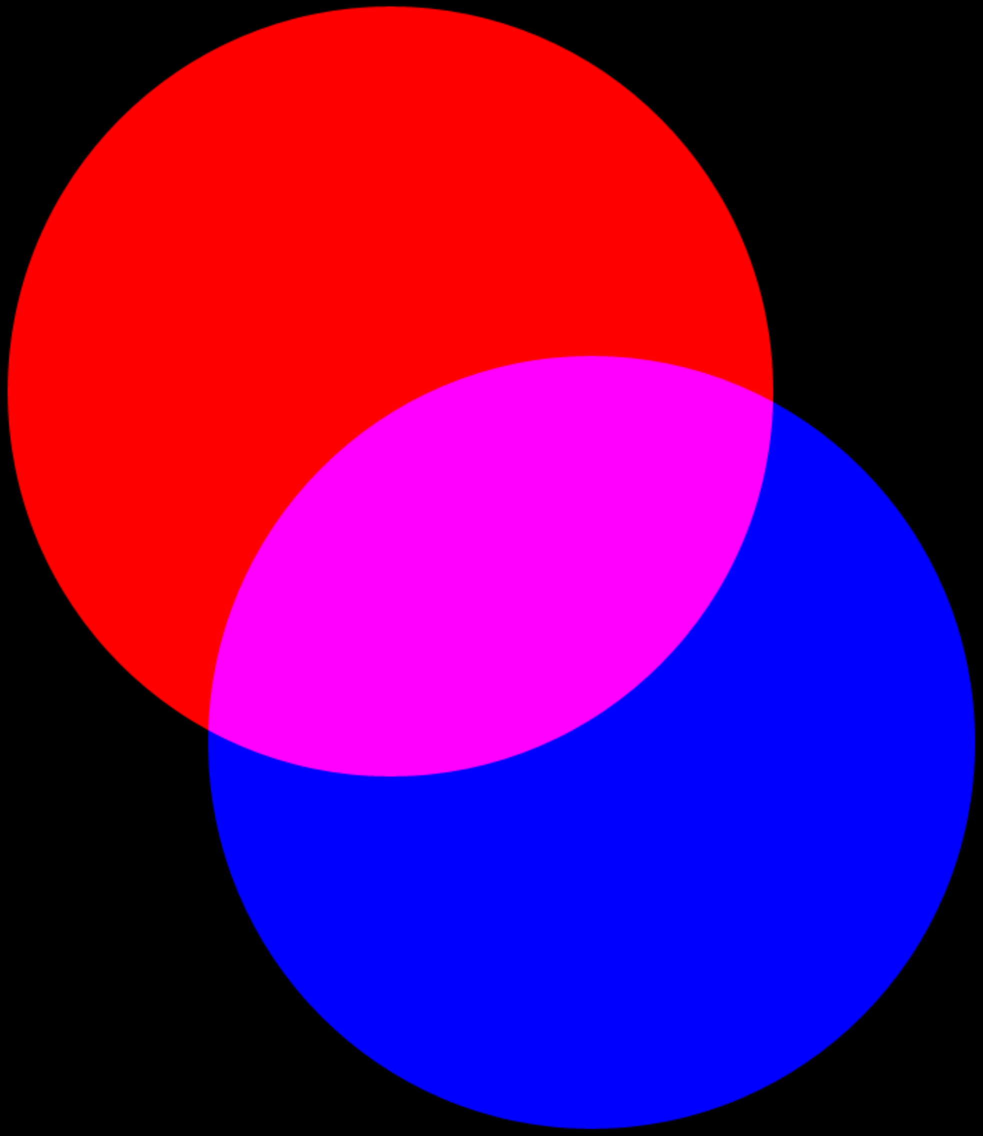


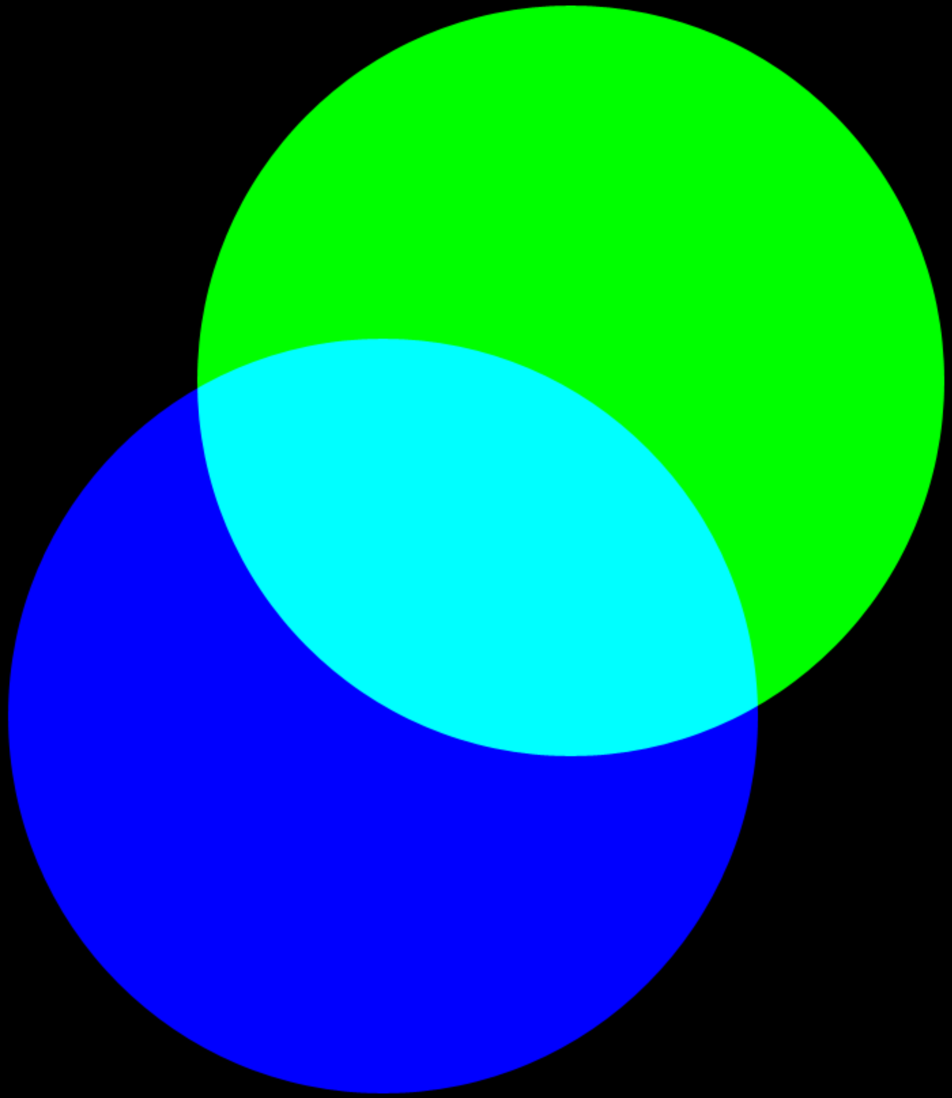
These two metamers of yellow

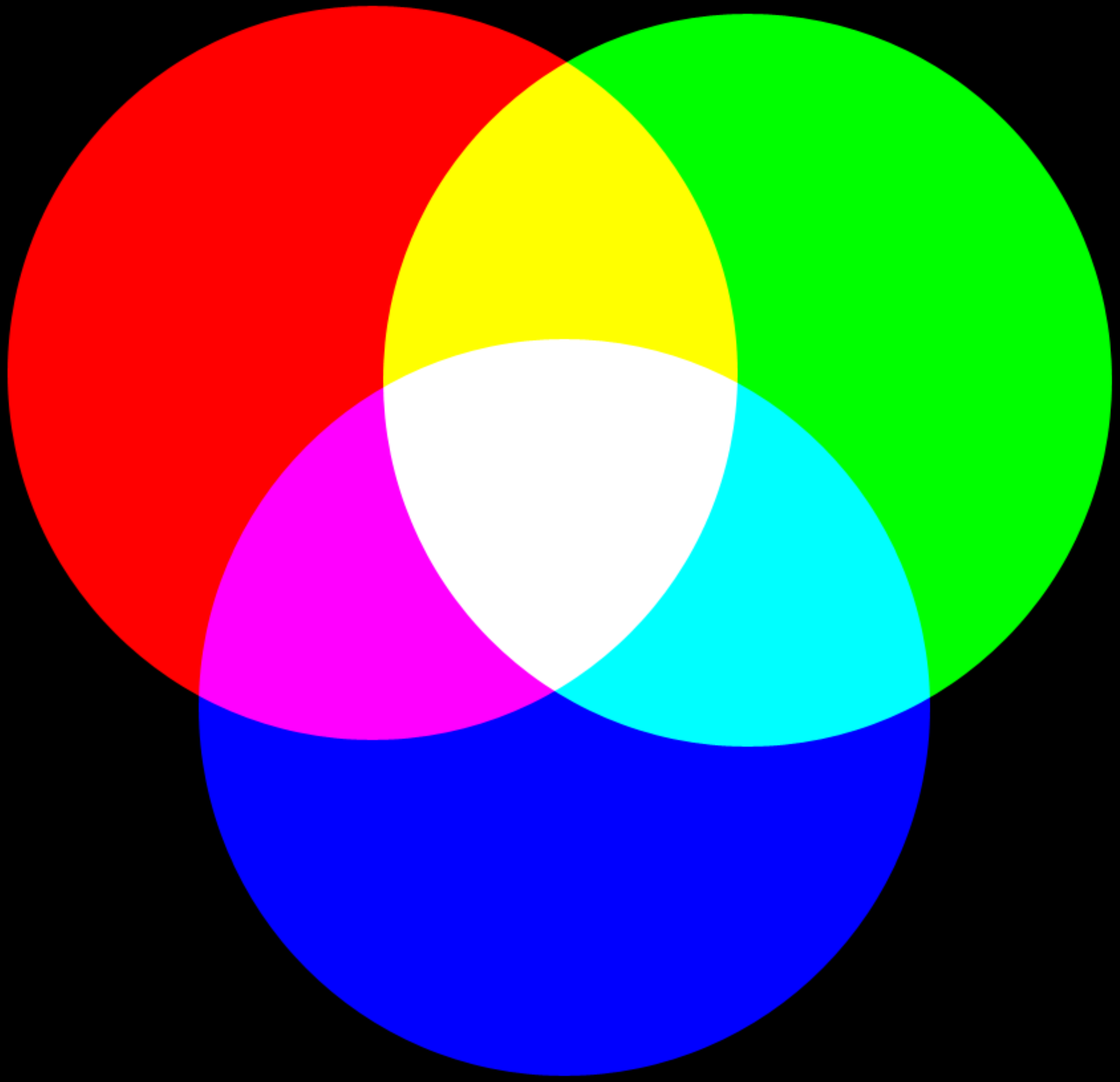
though physically very different, can appear identical.

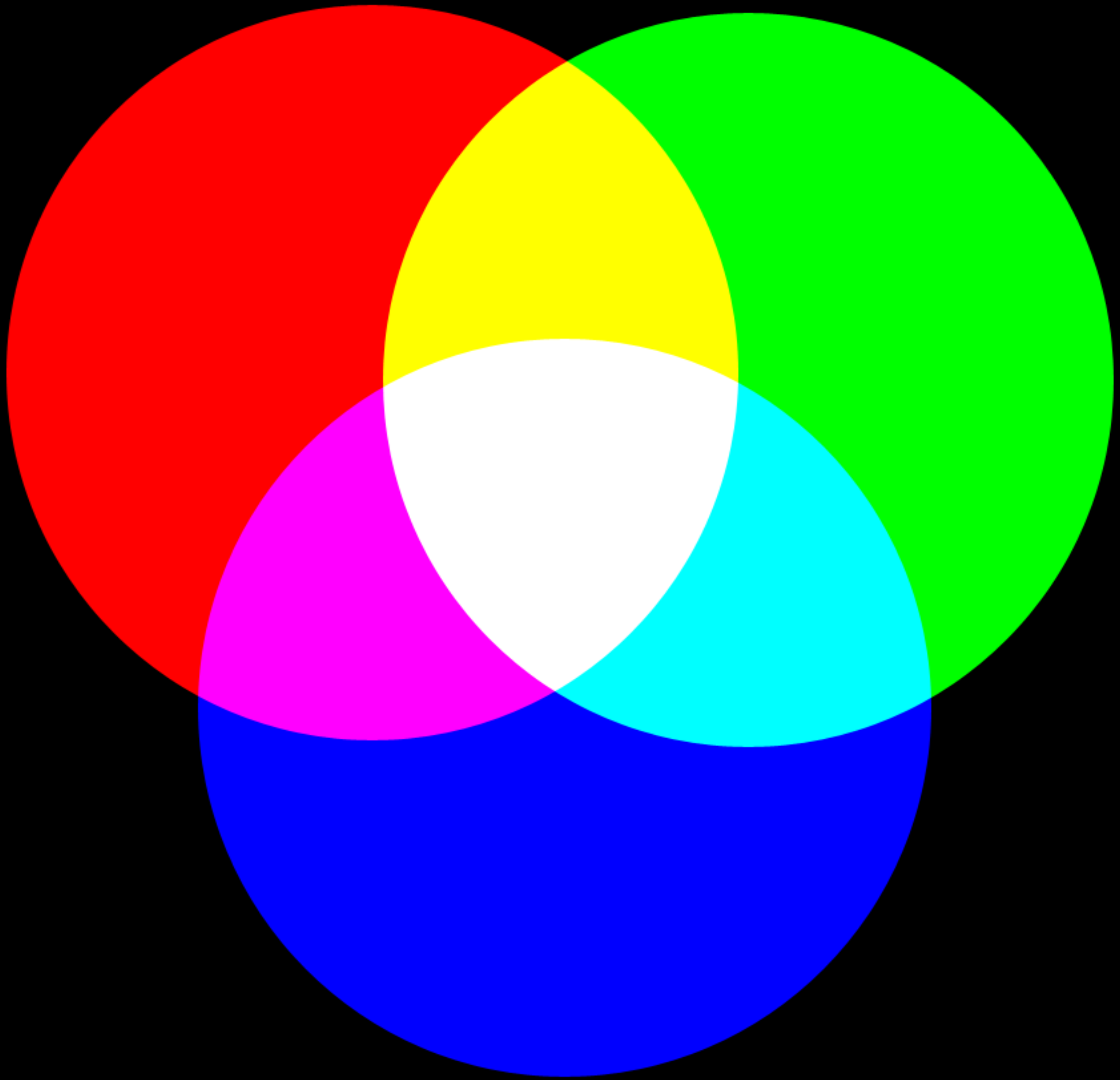
There are many other such metamers or matches…



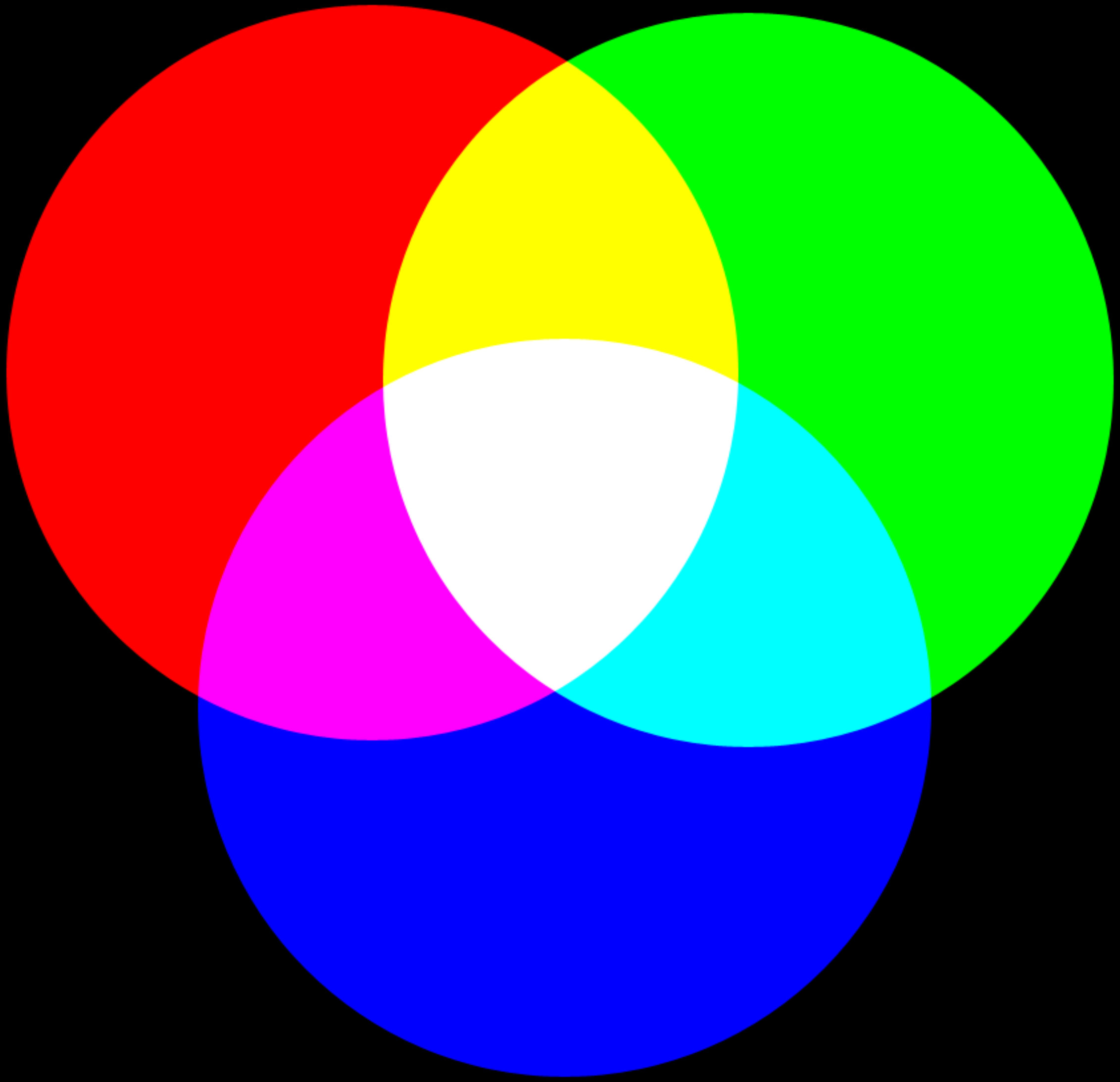






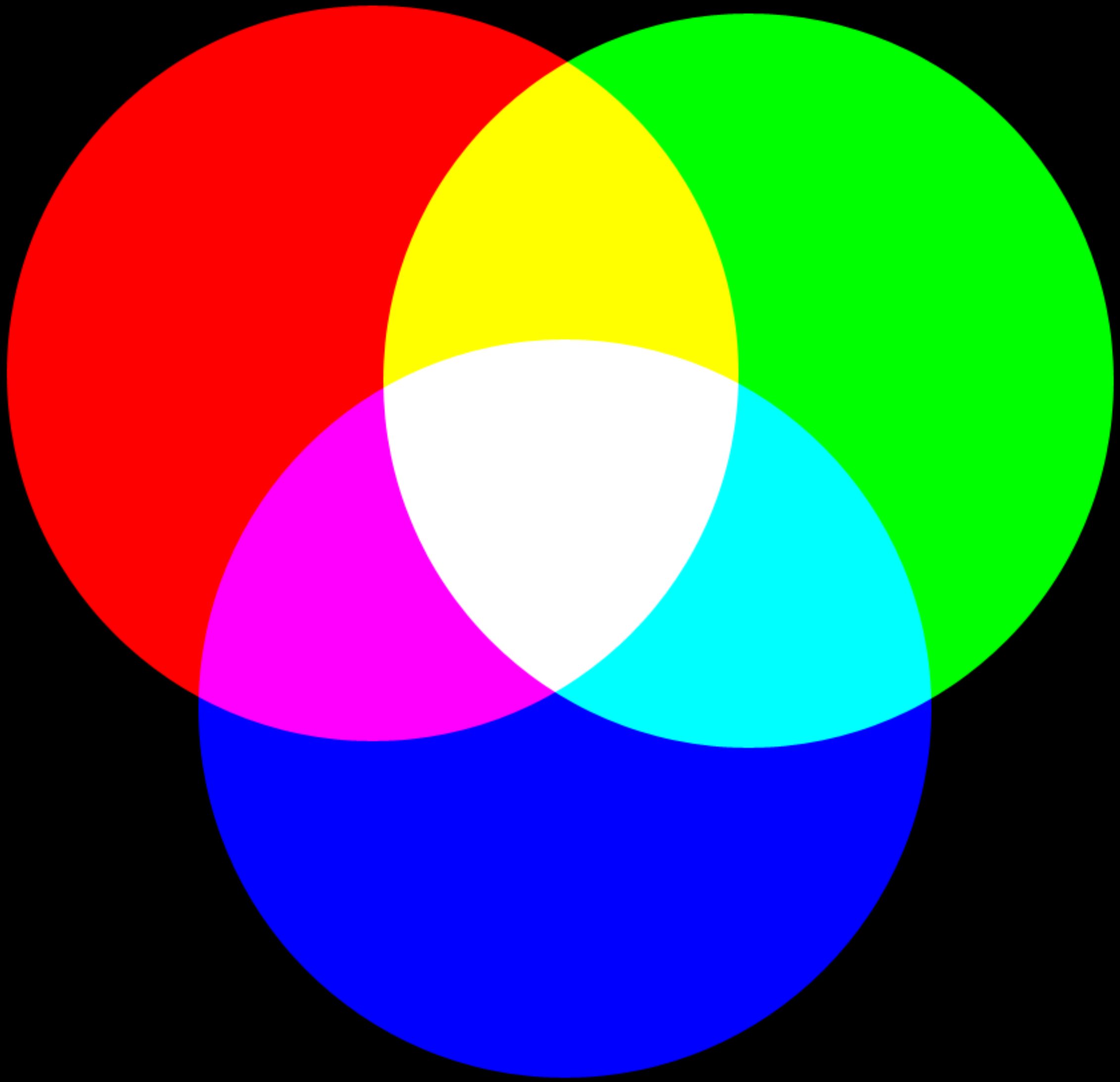


Before we knew about the underlying biology, additive colour mixing done in the 19th century revealed that colour vision was…



TRICHROMATIC

2. TRICHROMACY, UNIVARIANCE AND THE CONE SPECTRAL SENSITIVITIES



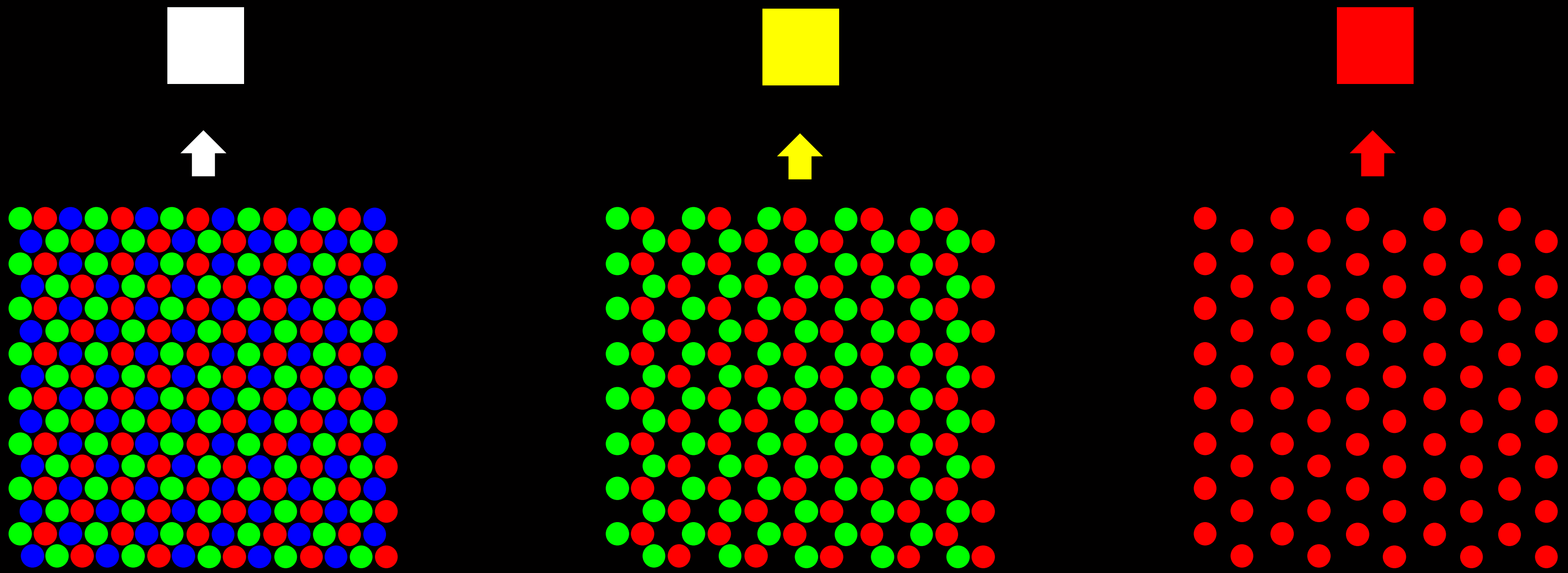
Trichromacy means that colour vision at the input to the visual system is relatively simple.

It is a 3-variable system…

Colour TV and video

Trichromacy is exploited in colour reproduction, since the myriad of colours that are 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 optics of the eye and thus appear as uniform patches of colour.



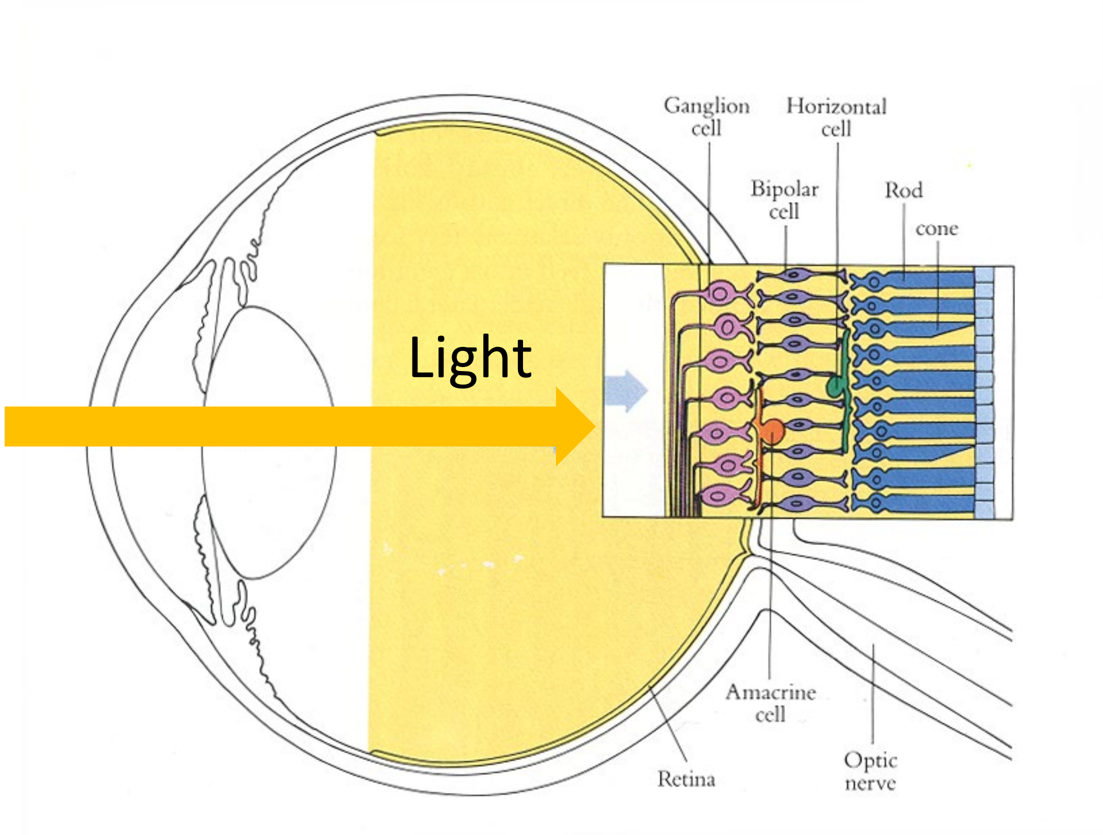
But why is human colour vision trichromatic?

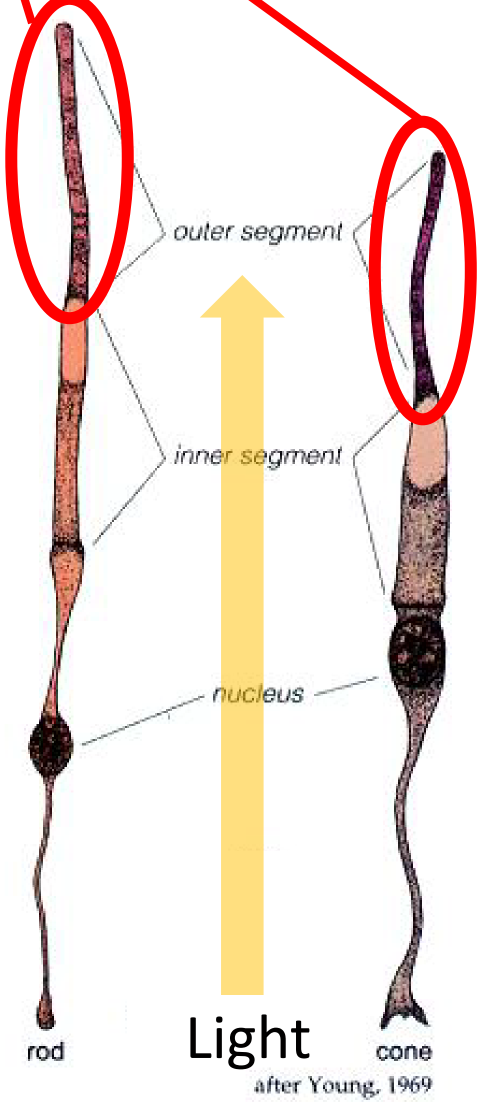
It is trichromatic because the output of each photoreceptor is:

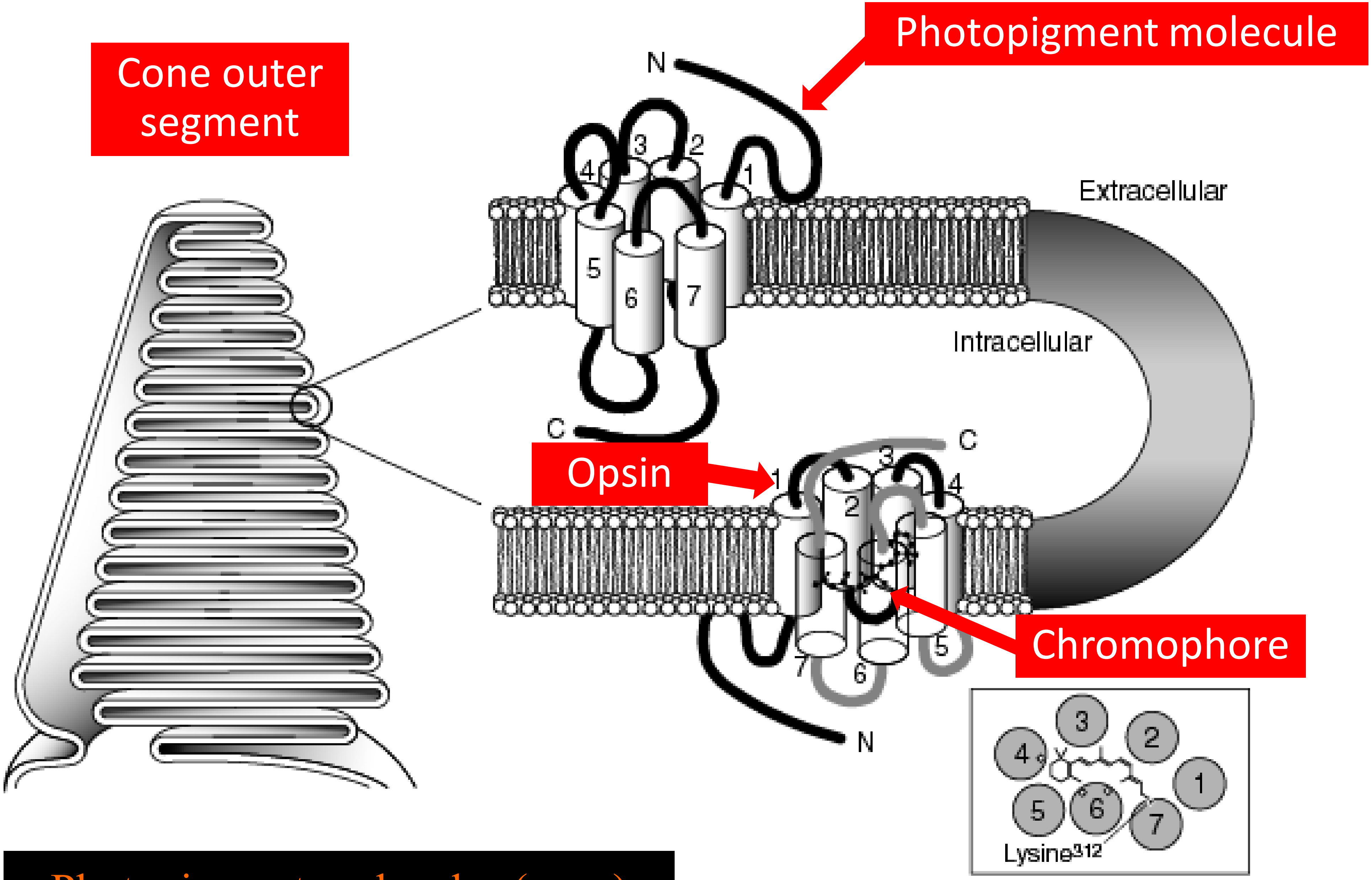
UNIVARIANT

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

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







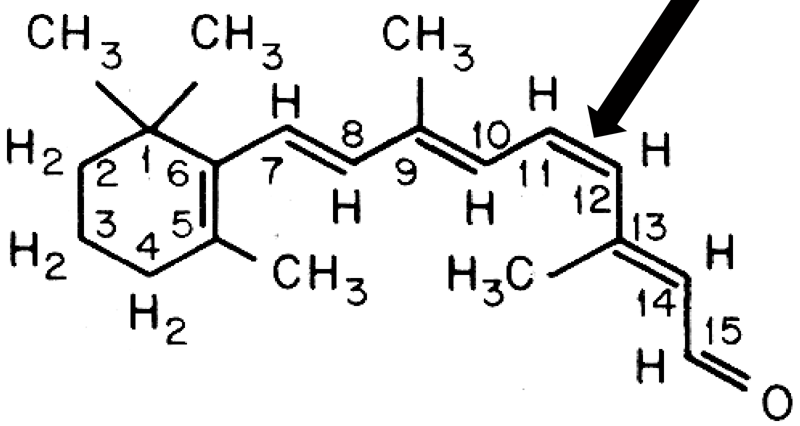
Photopigment molecules (cone)

From Sharpe, Stockman, Jägle & Nathans, 1999

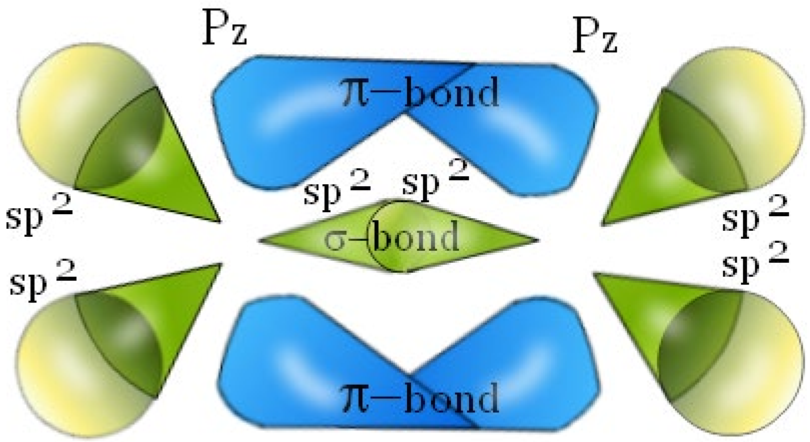
Chromophore

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

11-*cis* retinal

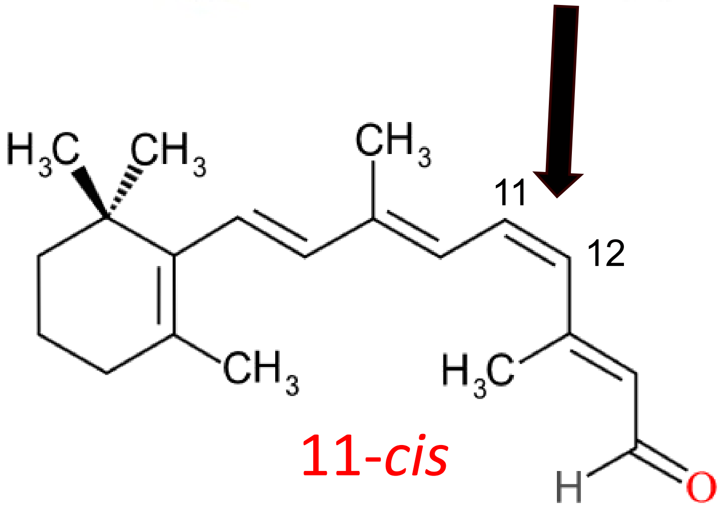


The molecule is twisted at the 11th carbon.

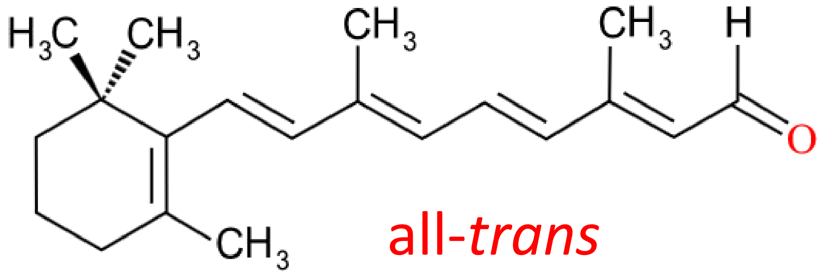


The double bond is made up of a σ and a π bond.

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



11-*cis*



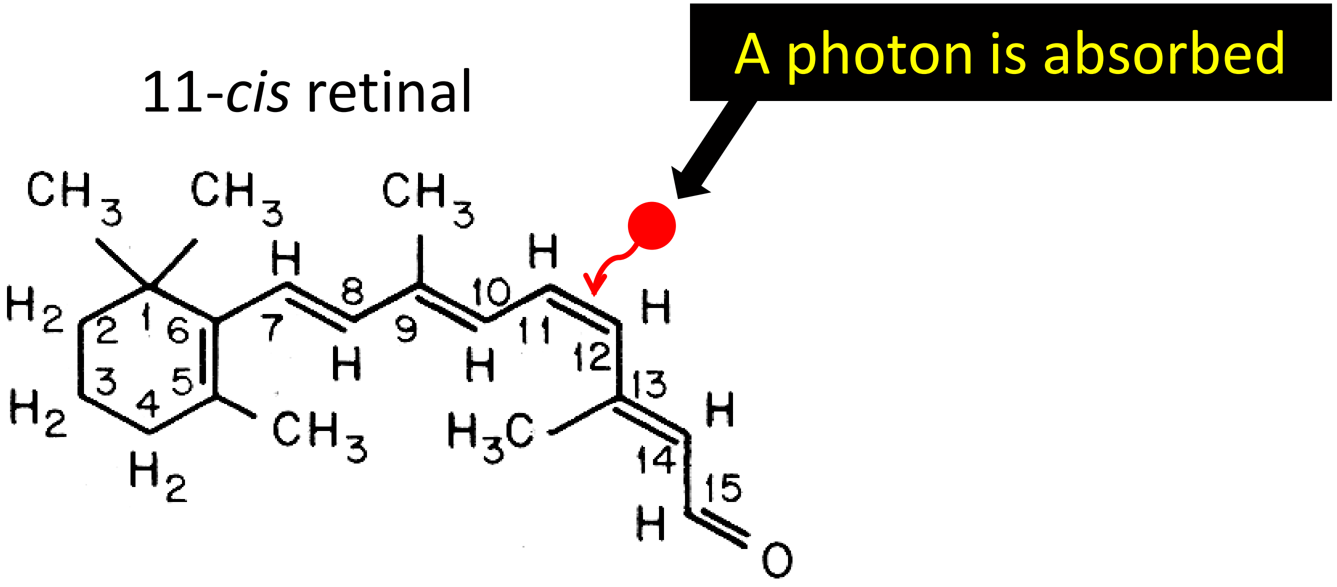
all-*trans*

There are therefore different “stereoisomers” of the molecule.

Chromophore

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

11-*cis* retinal

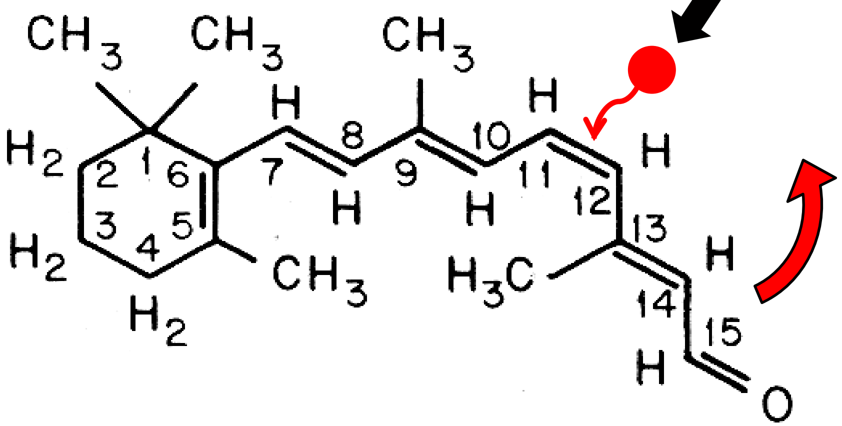


Chromophore

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

11-*cis* retinal

A photon is absorbed



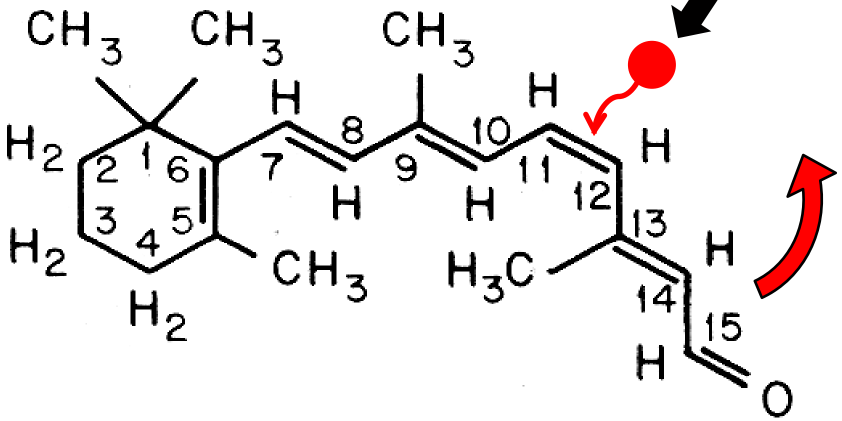
the energy of which initiates a conformational change to…

Chromophore

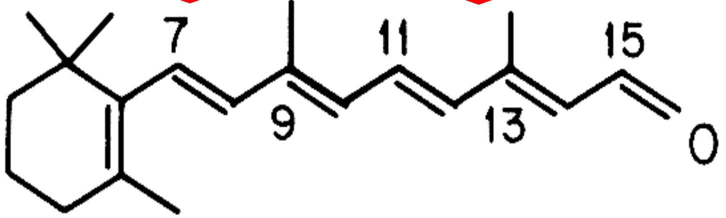
(*chromo*- colour, + -*phore*, producer)
Light-catching portion of any molecule

11-*cis* retinal

A photon is absorbed



the energy of which initiates a conformational change to…



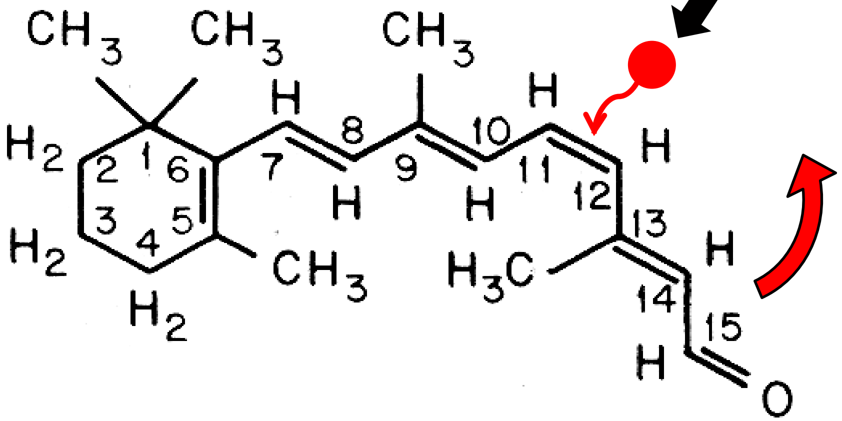
all-*trans* retinal

Chromophore

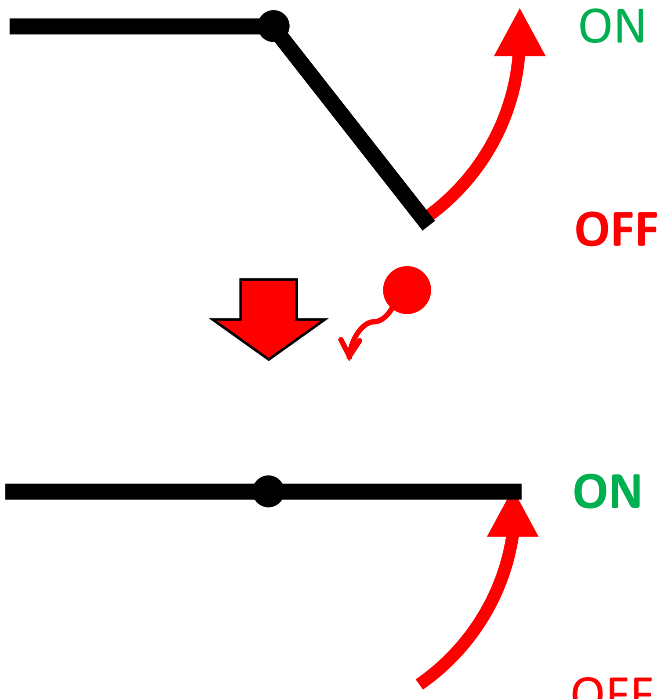
(*chromo*- colour, + -*phore,* producer)
Light-catching portion of any molecule

11-*cis* retinal

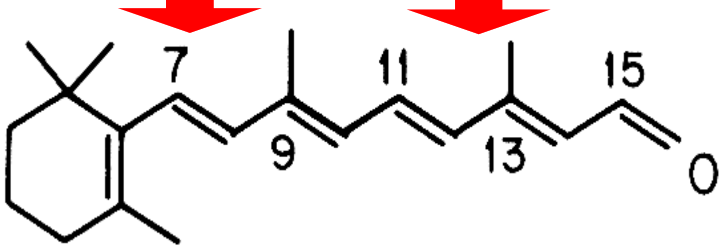
A photon is absorbed



Think of the molecule as a photo-sensitive switch!



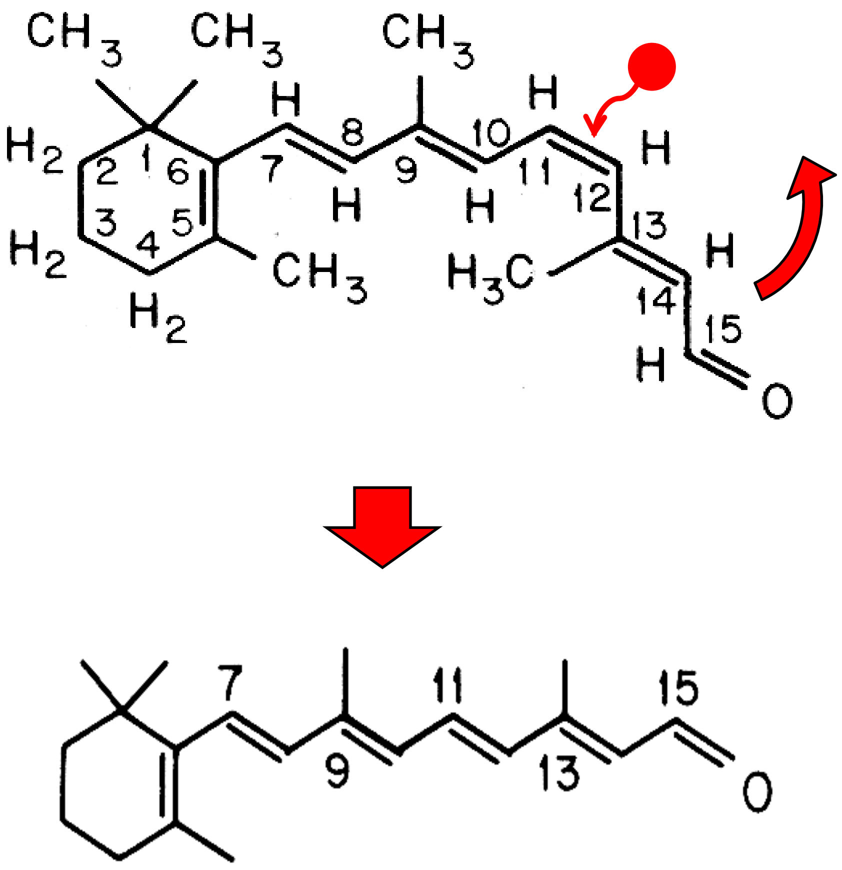
the energy of which initiates a conformational change to...



all-*trans* retinal

Chromophore

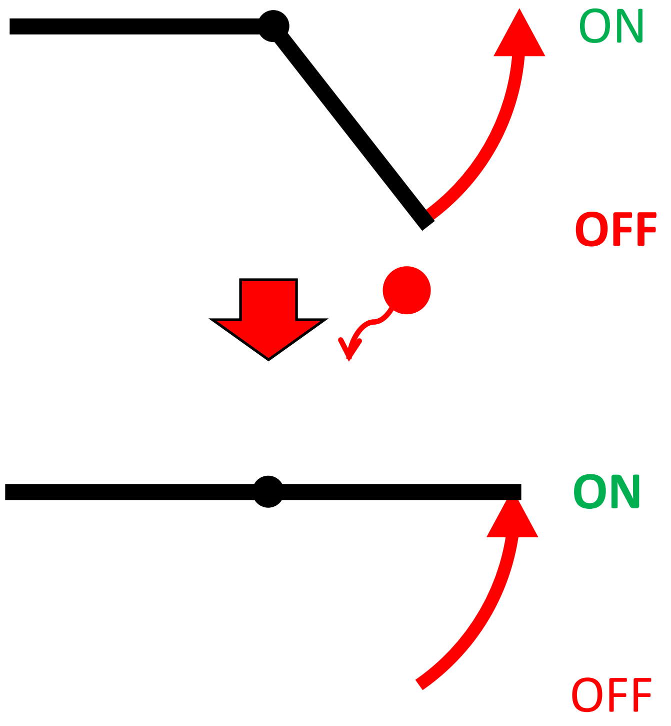
11-*cis* retinal



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.



Chromophore

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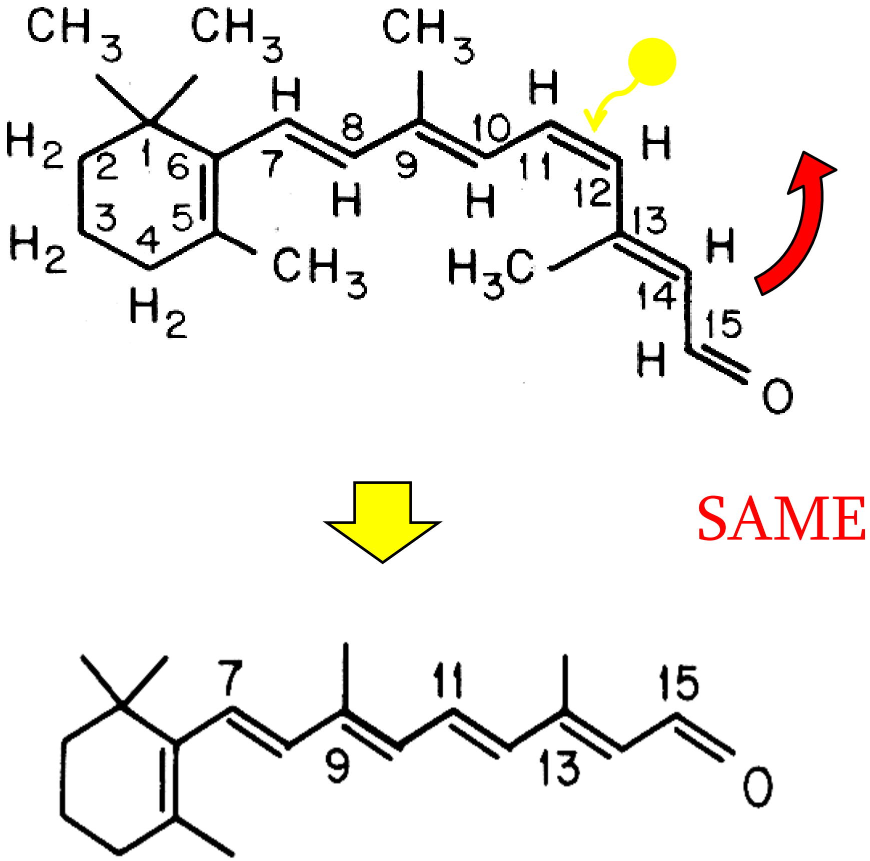
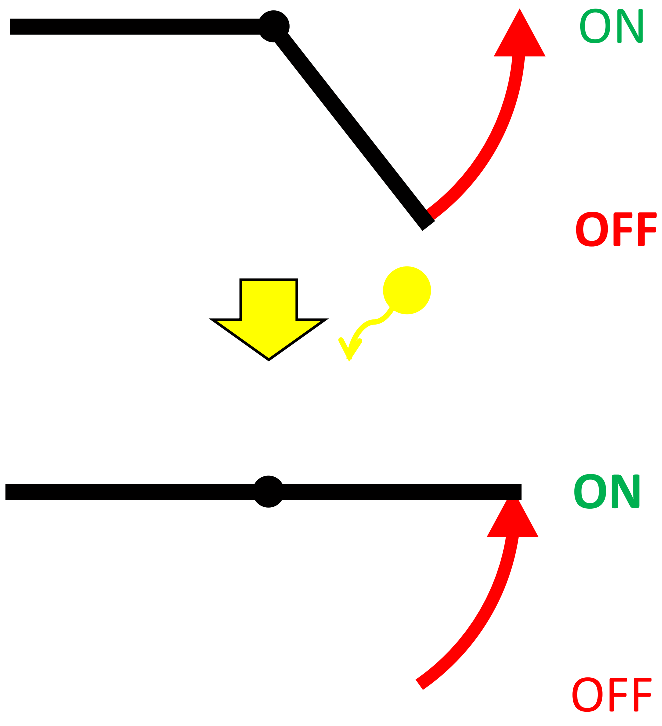
11-*cis* retinal



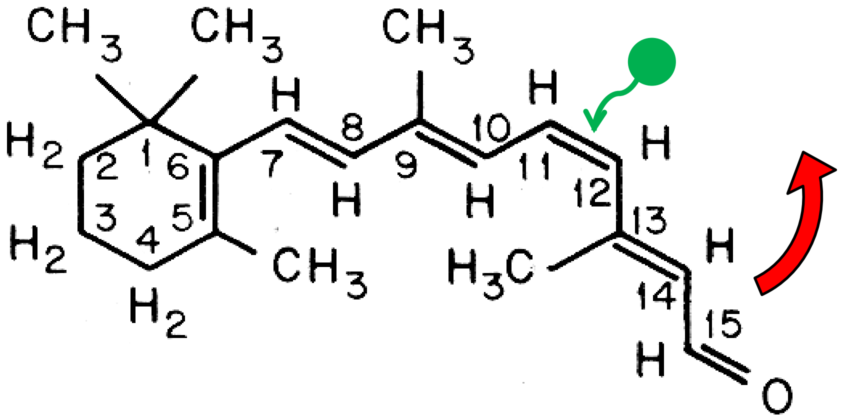
all-*trans* retinal

SAME EFFECT

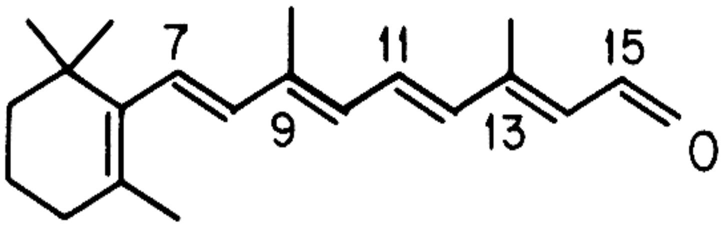


Chromophore

11-*cis* retinal



SAME EFFECT



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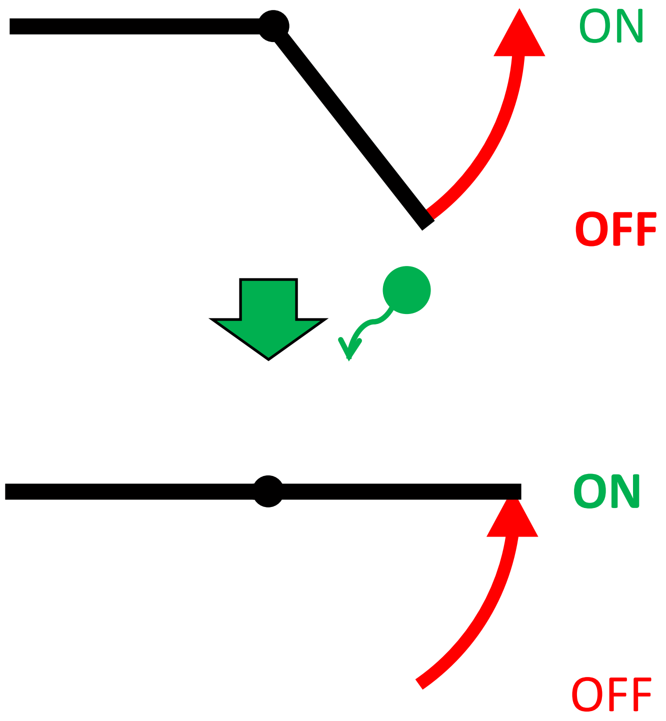
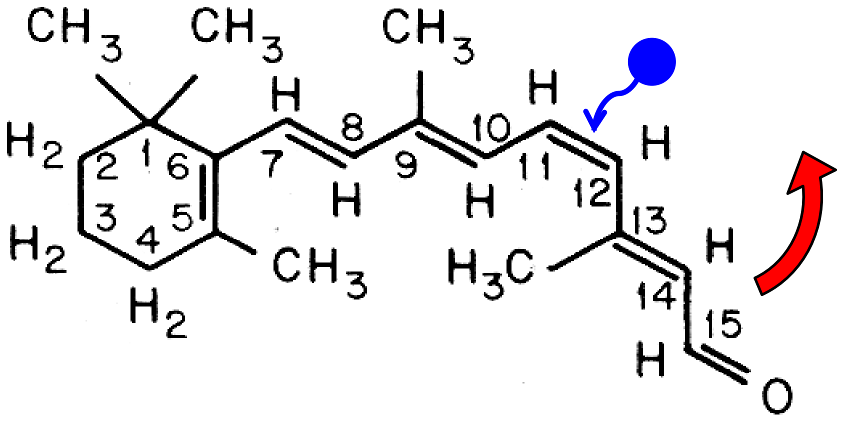
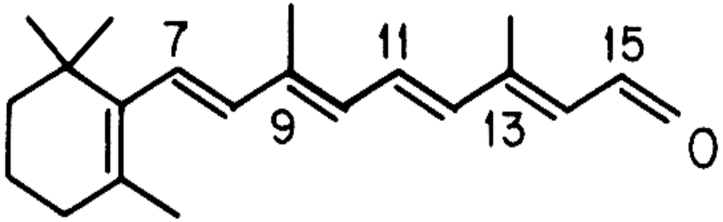


Chromophore

11-*cis* retinal



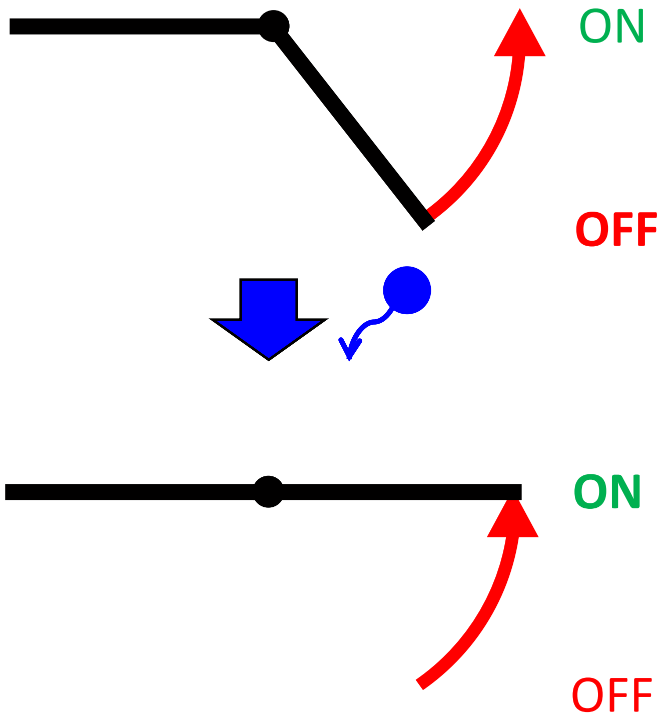
SAME EFFECT



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.

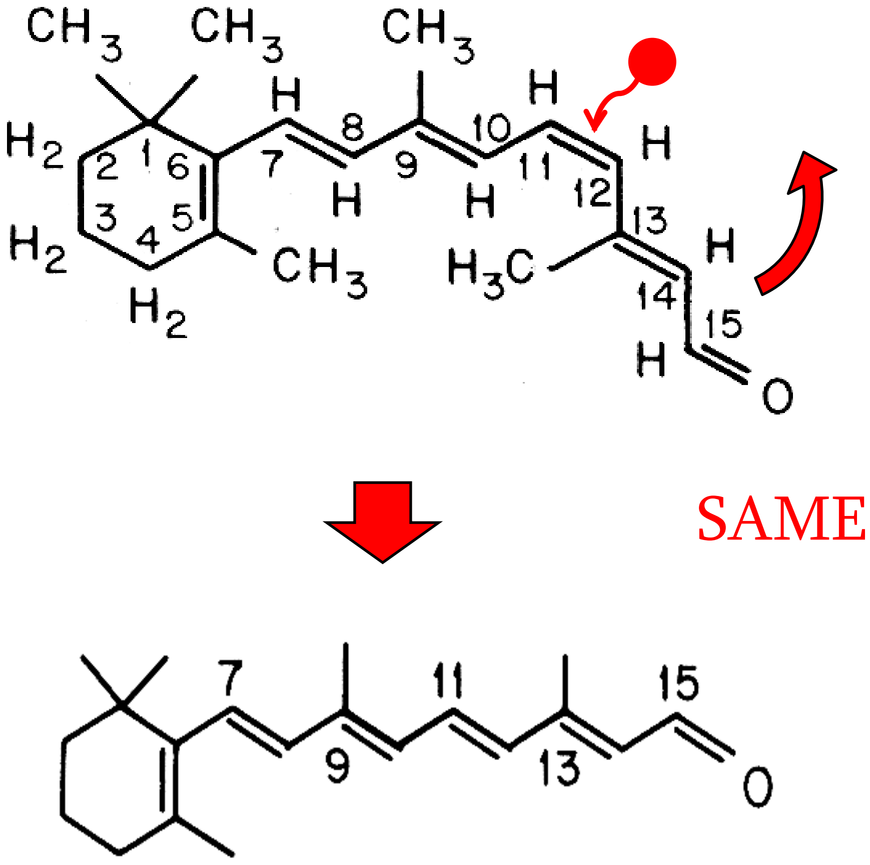


Chromophore

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

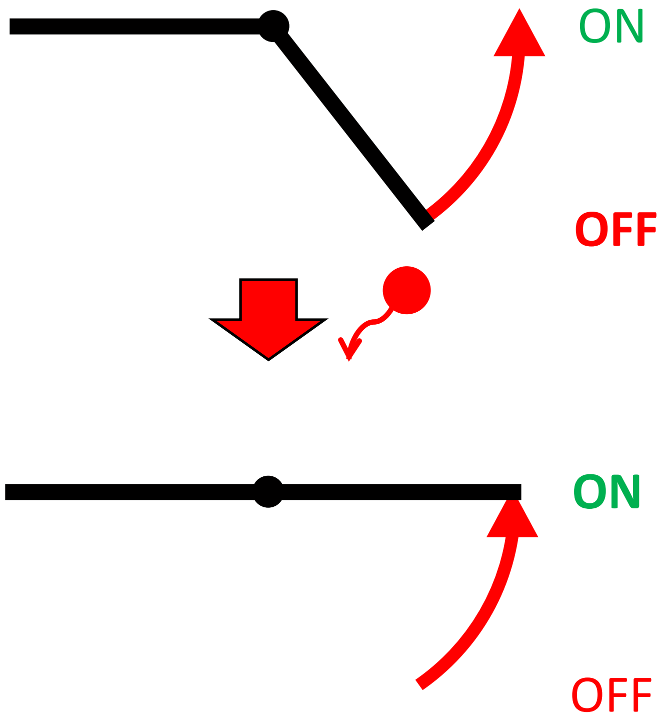
If a photon is absorbed it has the same effect as any other absorbed photon, whatever its wavelength.

11-*cis* retinal



all-*trans* retinal

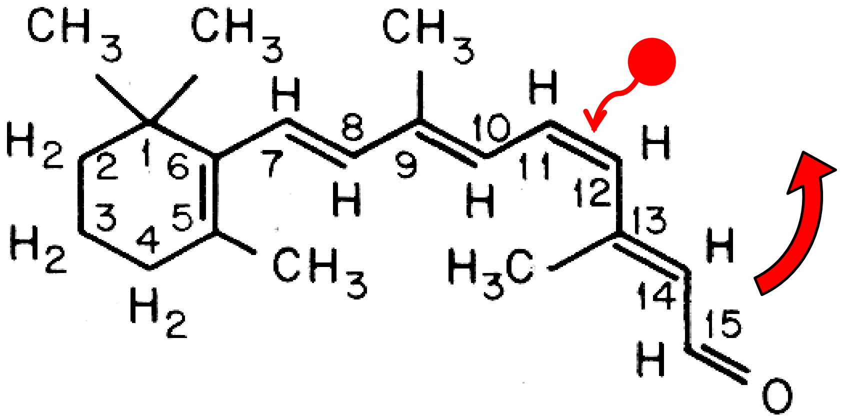
SAME EFFECT



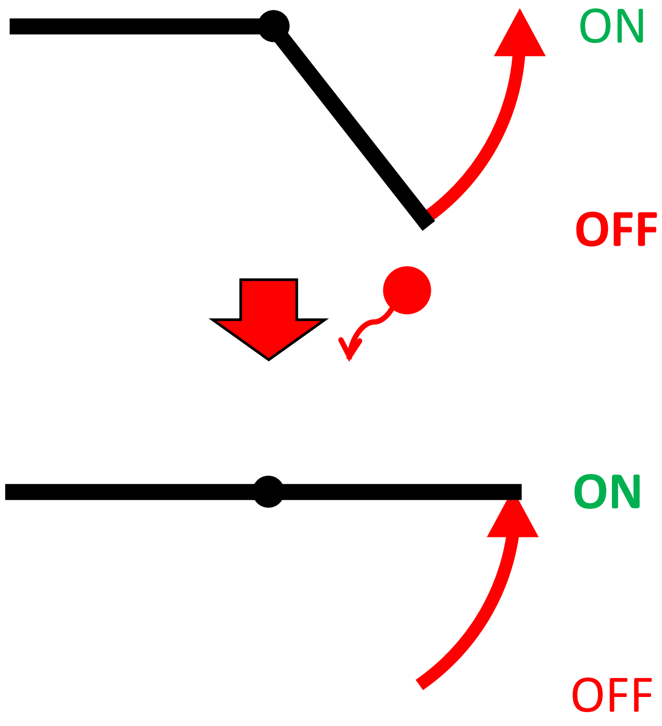
Chromophore

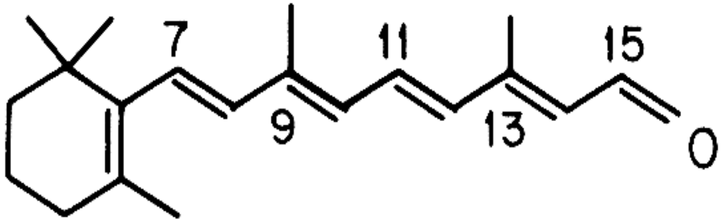
Can this process encode wavelength (colour)?

11-*cis* retinal



SAME EFFECT



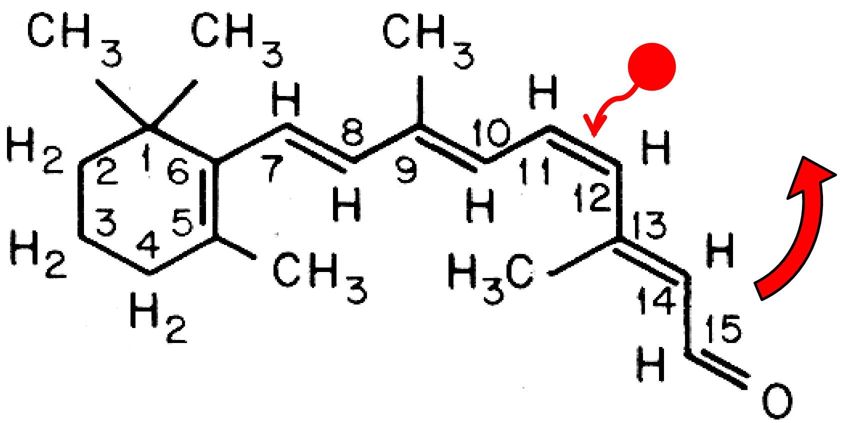


all-*trans* retinal

Chromophore

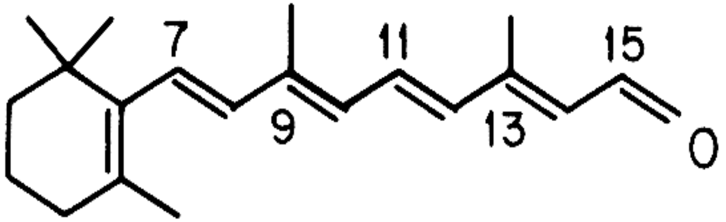
No, it cannot encode wavelength (colour)!

11-*cis* retinal

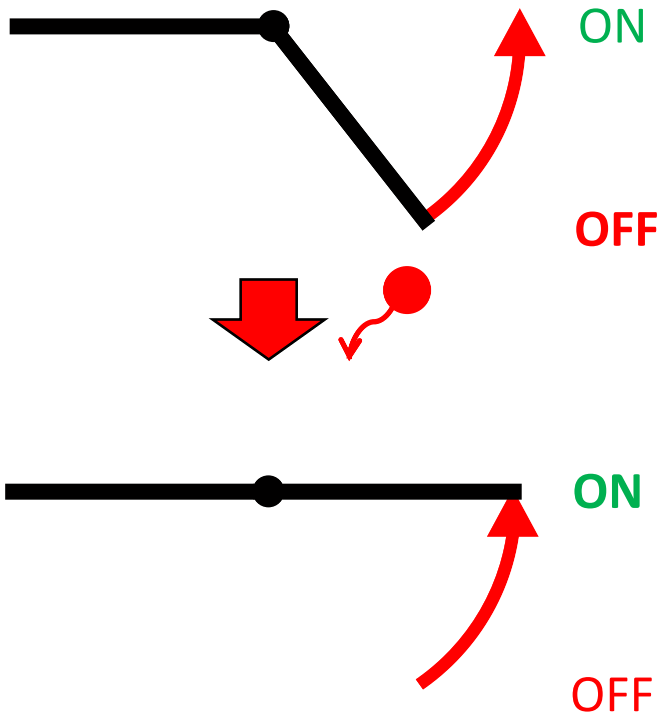


It is “UNIVARIANT”

SAME EFFECT

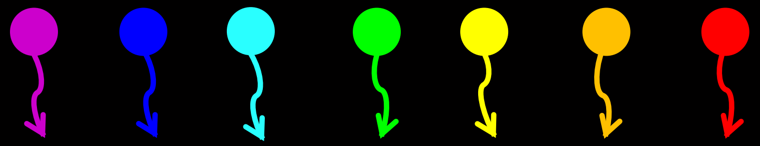


all-*trans* retinal



UNIVARIANCE

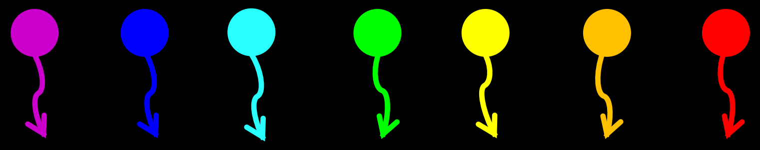
Once absorbed, all these photons…



have the same effect.

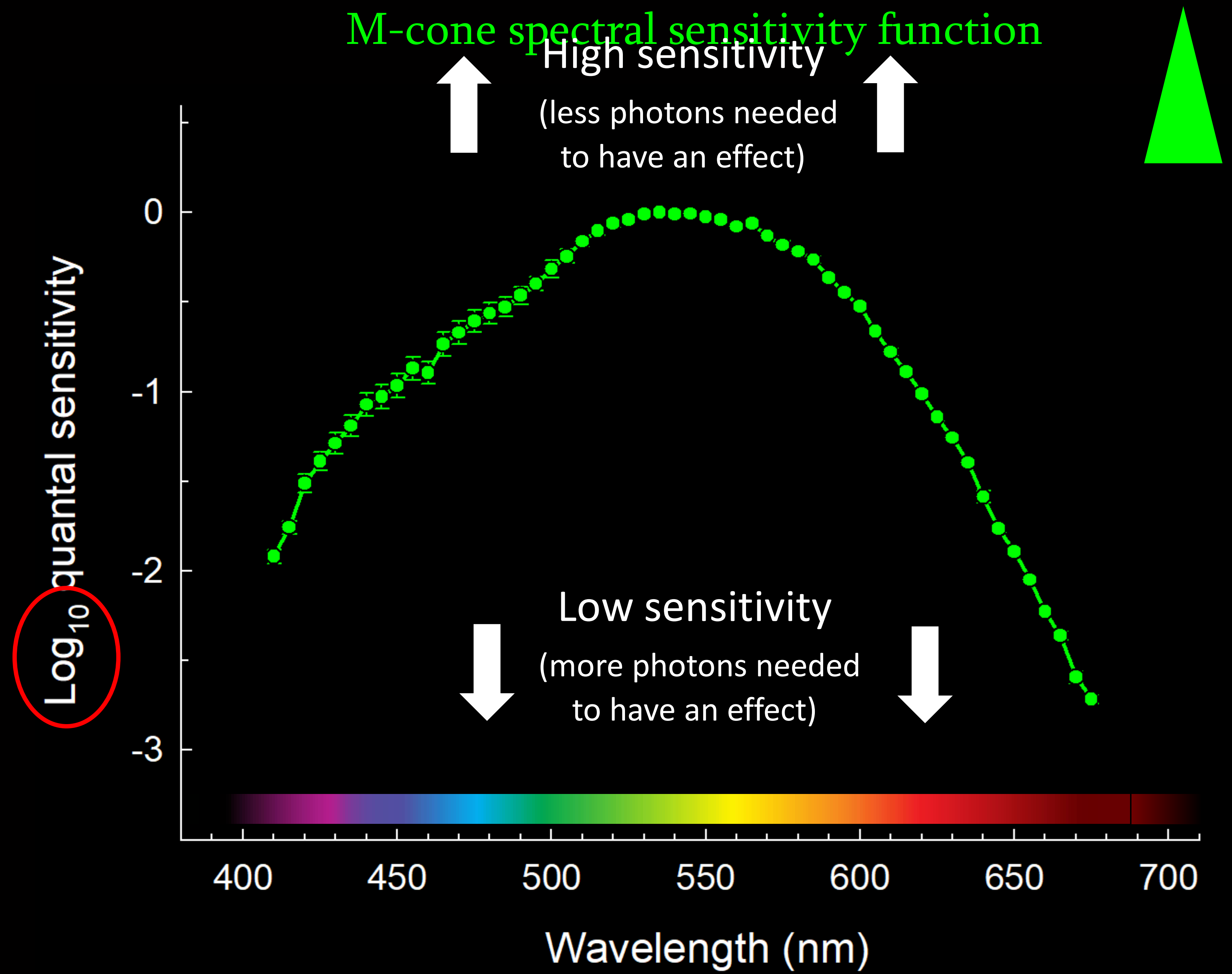
UNIVARIANCE

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

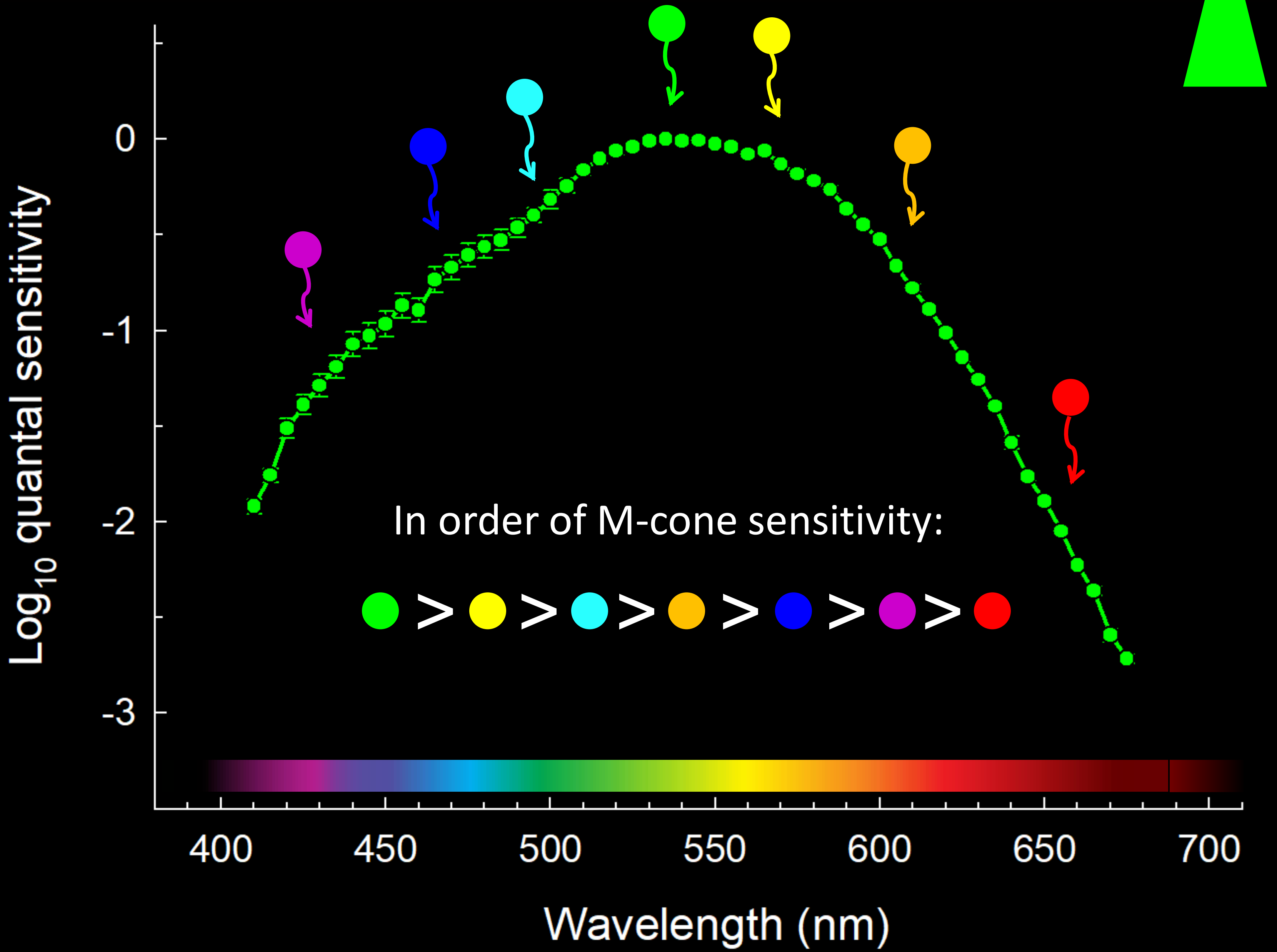


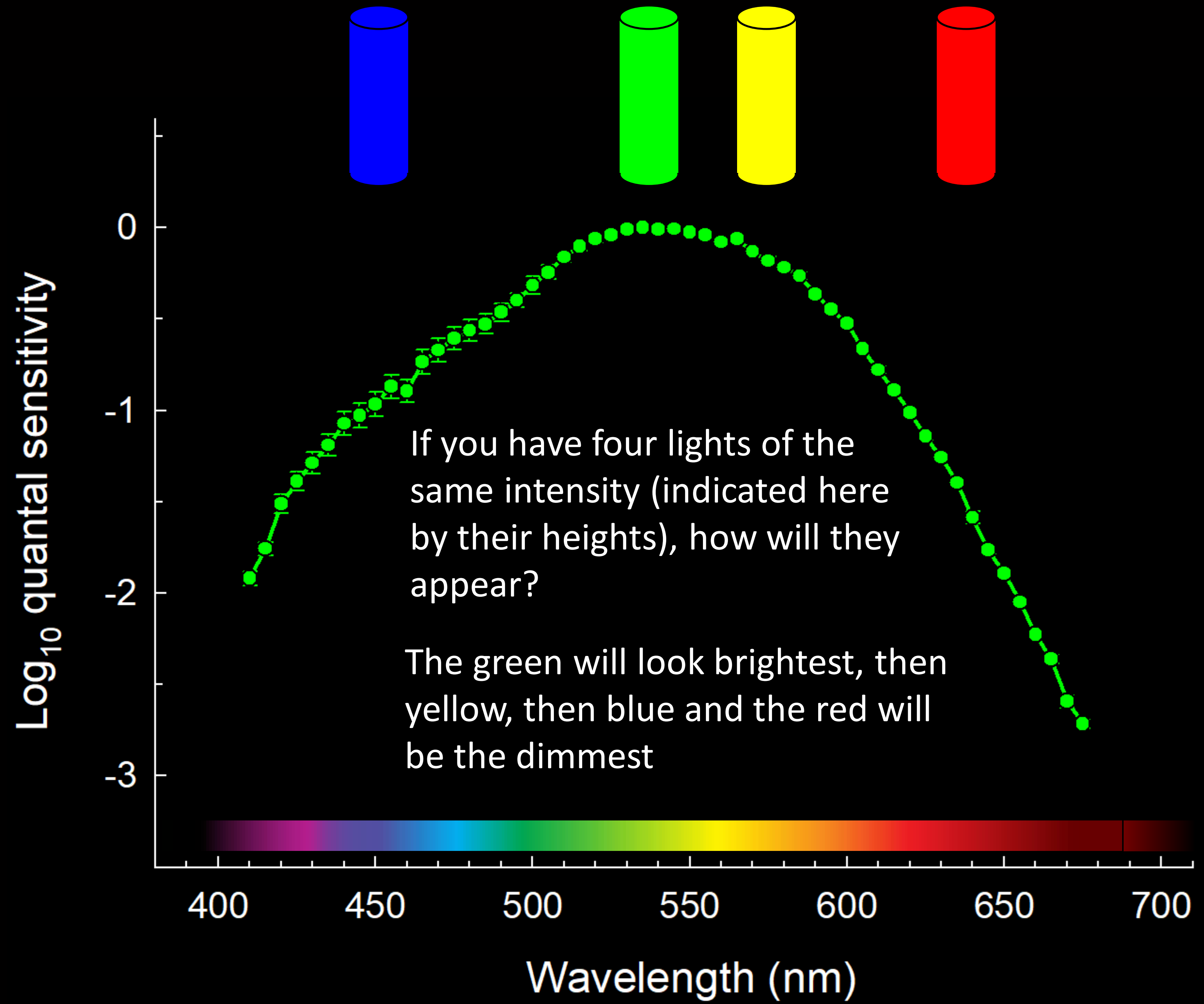
This is reflected in what is called the cone “spectral sensitivity function”, an example of which is the middle-wavelength-sensitive (M-) cone function…

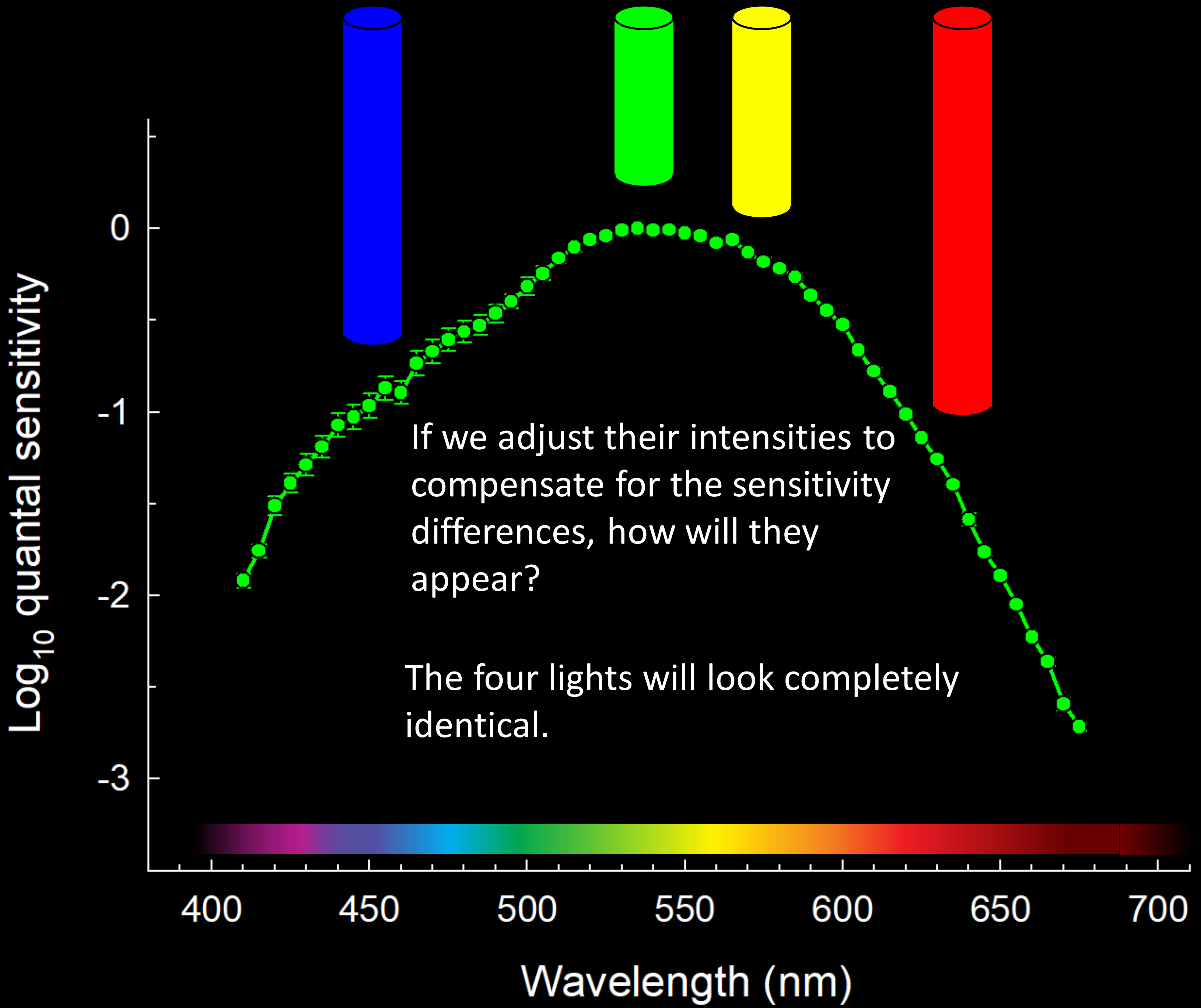
M-cone spectral sensitivity function



Imagine the sensitivity to these photons…

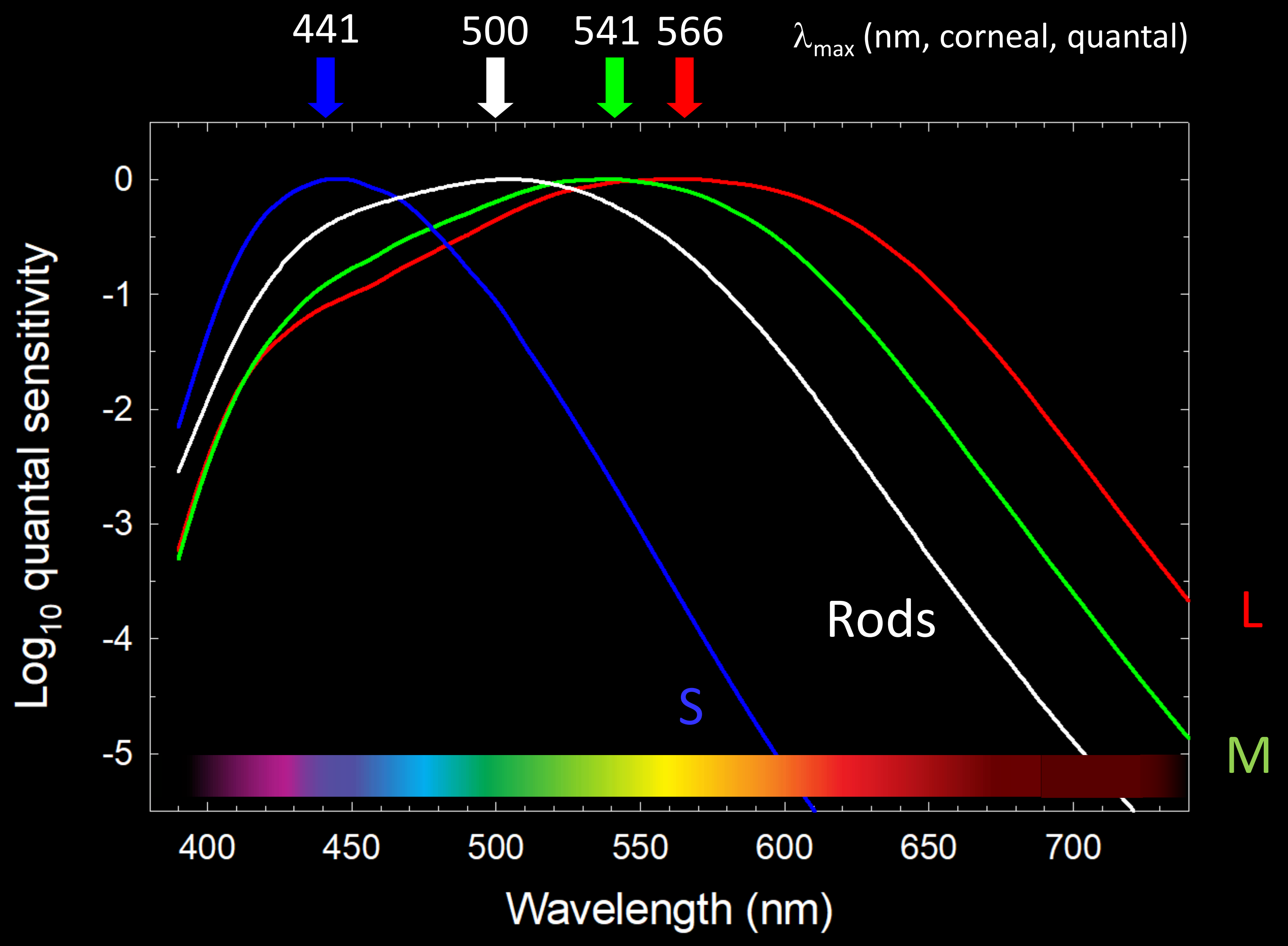



If you have four lights of the same intensity (indicated here by their heights), how will they appear?
The green will look brightest, then yellow, then blue and the red will be the dimmest
Log10 quantal sensitivity
0
-1
-2
-3
400
450
500
550
600
650
700
Wavelength (nm)



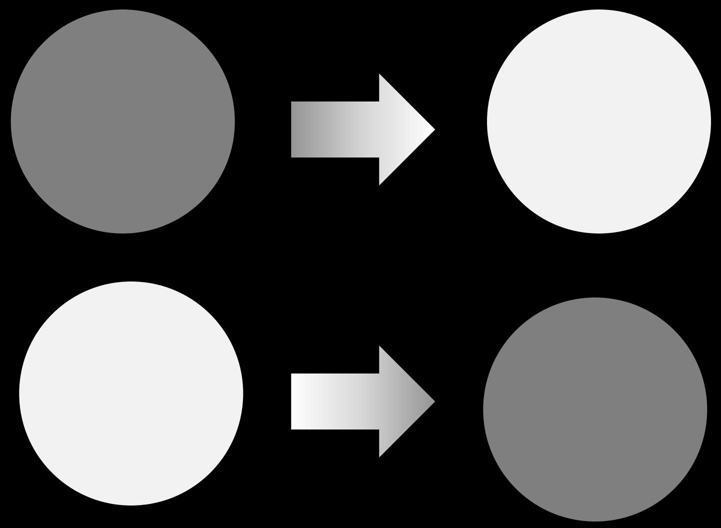
Log10 quantal sensitivity
0
-1
-2
-3
400
450
500
550
600
650
700
Wavelength (nm)
If we adjust their intensities to compensate for the sensitivity differences, how will they appear?
The four lights will look completely identical.

ROD AND CONE SPECTRAL SENSITIVITIES



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.

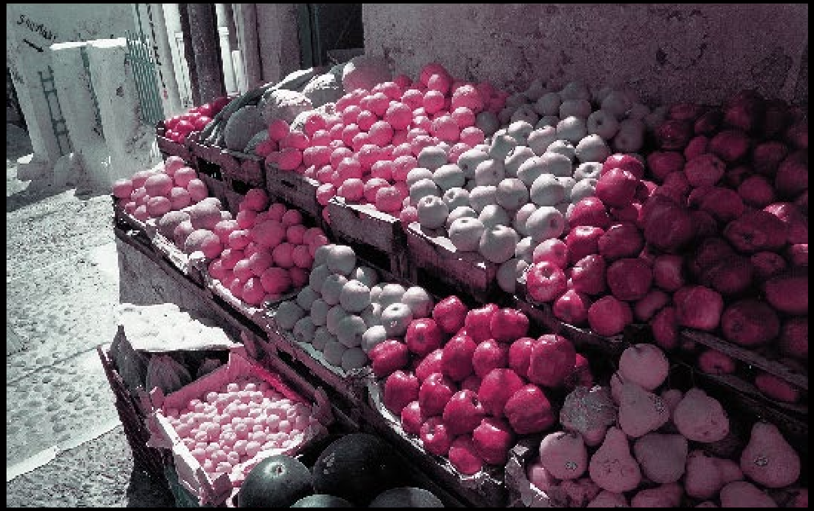
Because of univariance with only one photoreceptor, we would be colour-blind…

Examples: night vision, S-cone monochromats

With two, we are dichromatic:

Protanopia (missing L-cone)

Tritanopia (missing S-cone)



Deuteranopia (missing M-cone)

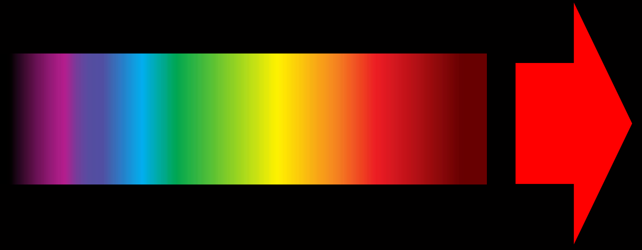
Simulations from Sharpe, Stockman, Jägle & Nathans, 1999

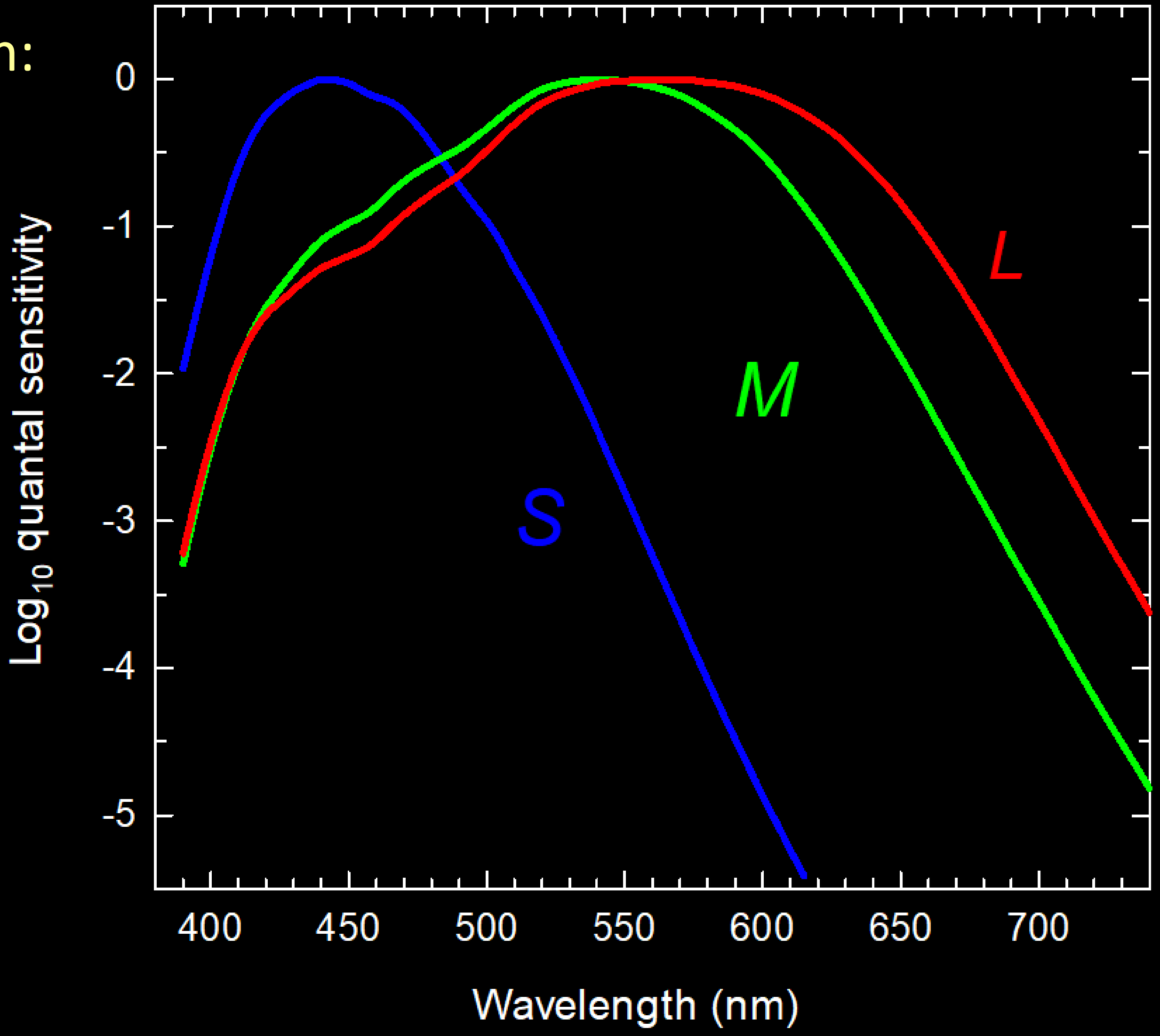
And with three, we enjoy trichromacy:

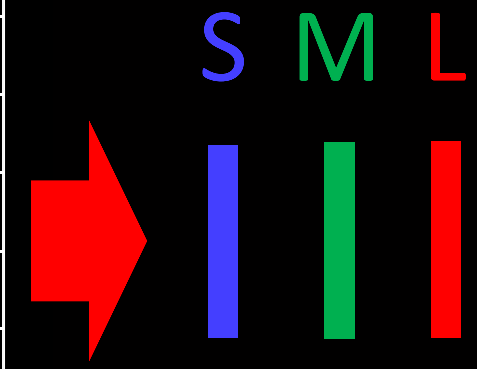
Information loss

At the first stage of vision:

λ

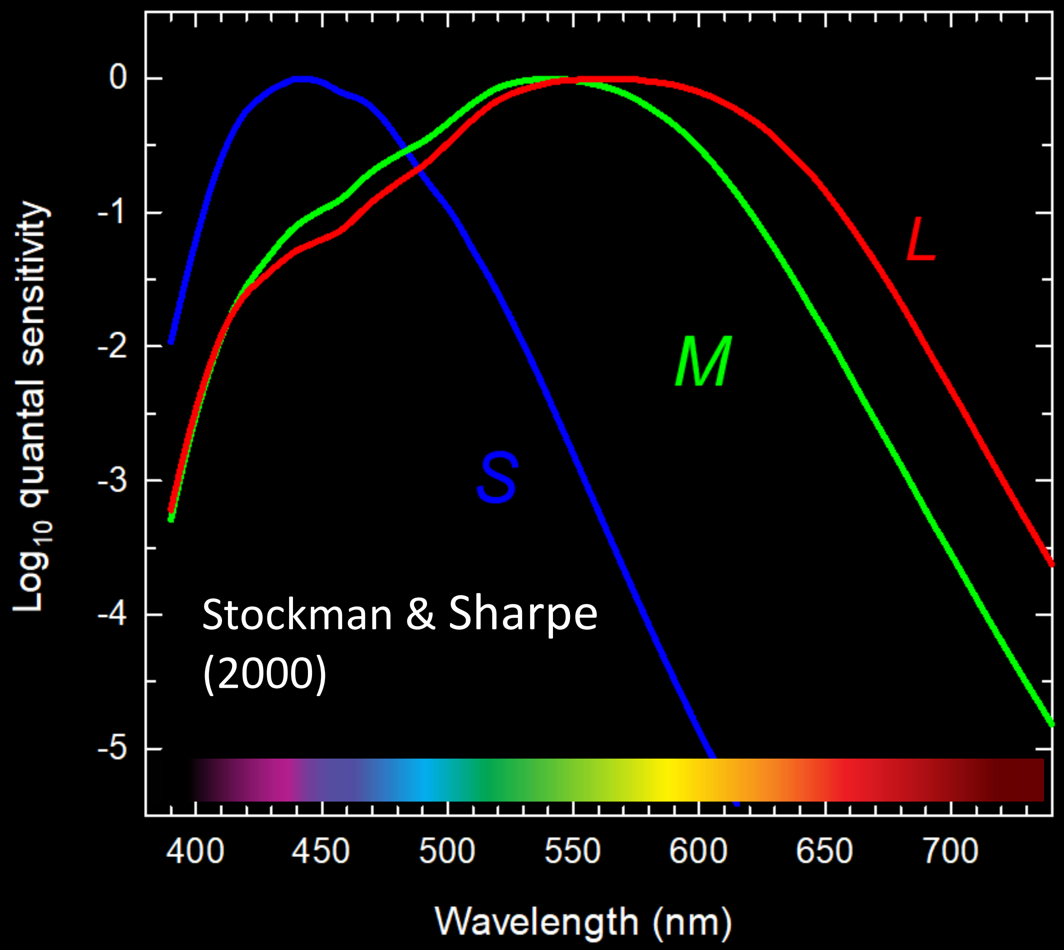






there is a massive loss
of spectral information!

The Stockman & Sharpe (2000) cone spectral sensitivities:



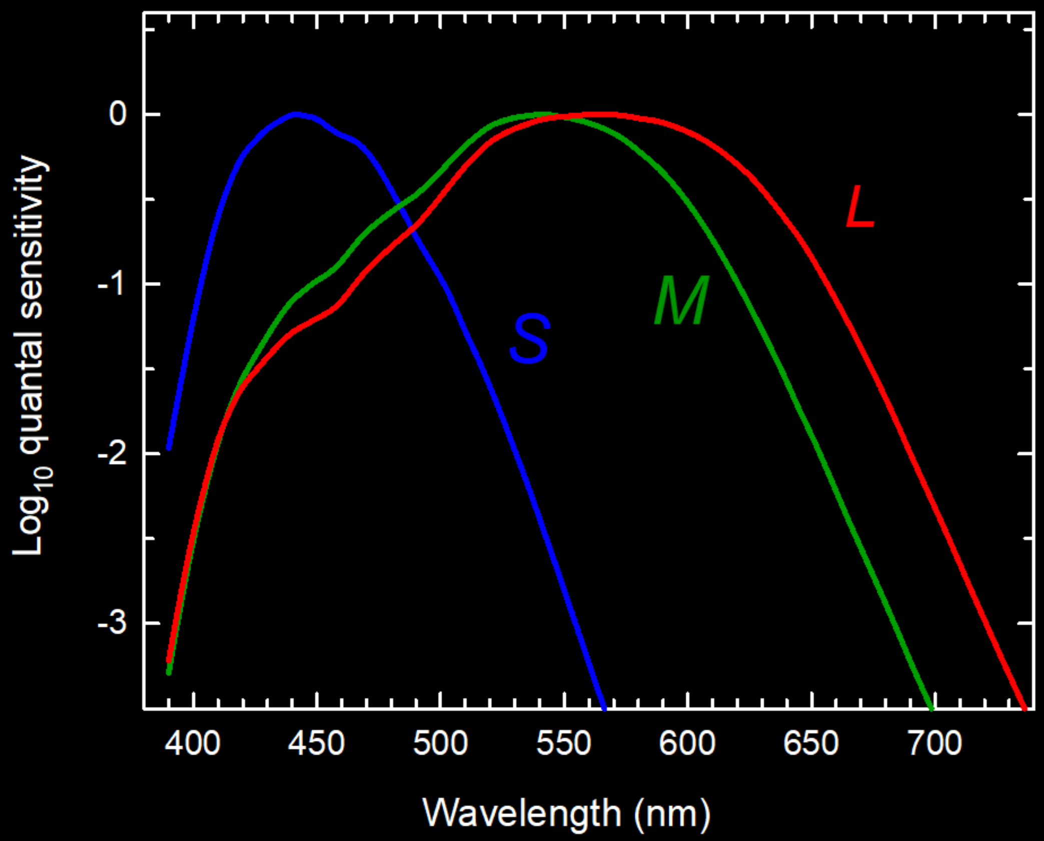
Now the "physiologically-relevant" LMS CIE (2006) colour matching functions.

Normal trichromacy depends on the spectral sensitivities of the three univariant cones (L, M and S)...

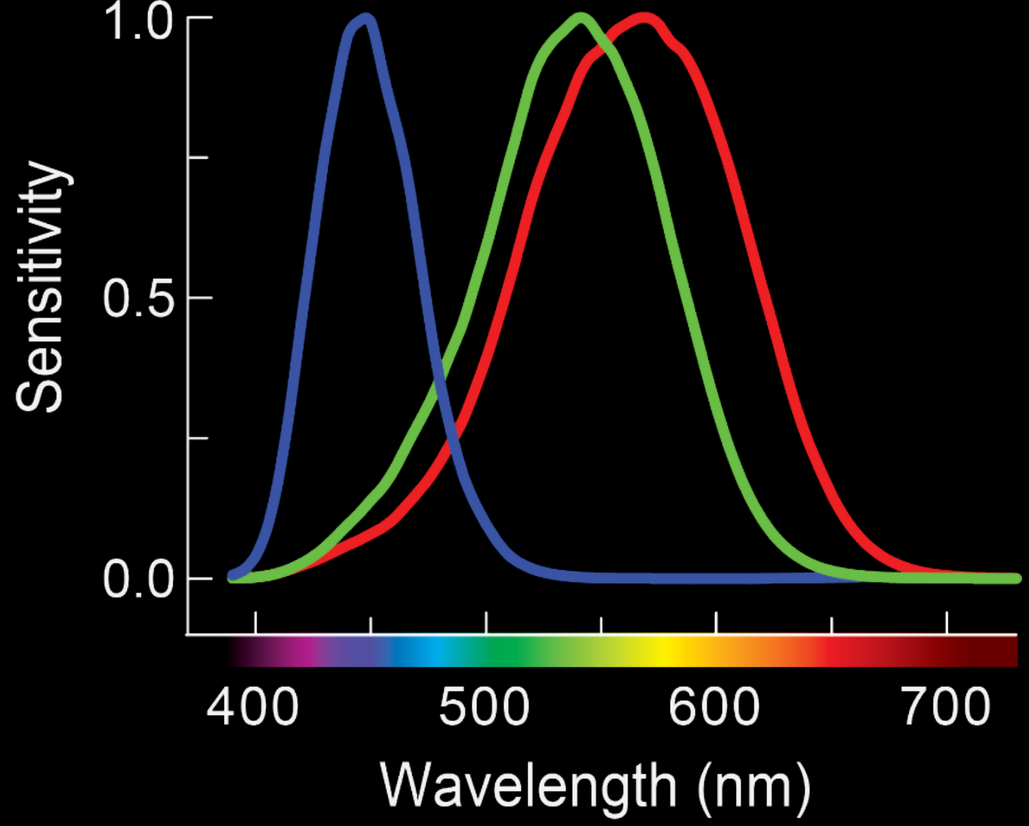
If we know these three spectral sensitivities, and thus the effects that lights have on the three cones, we can completely specify those lights.

Logarithmic and linear versions of the spectral sensitivities

Logarithmic

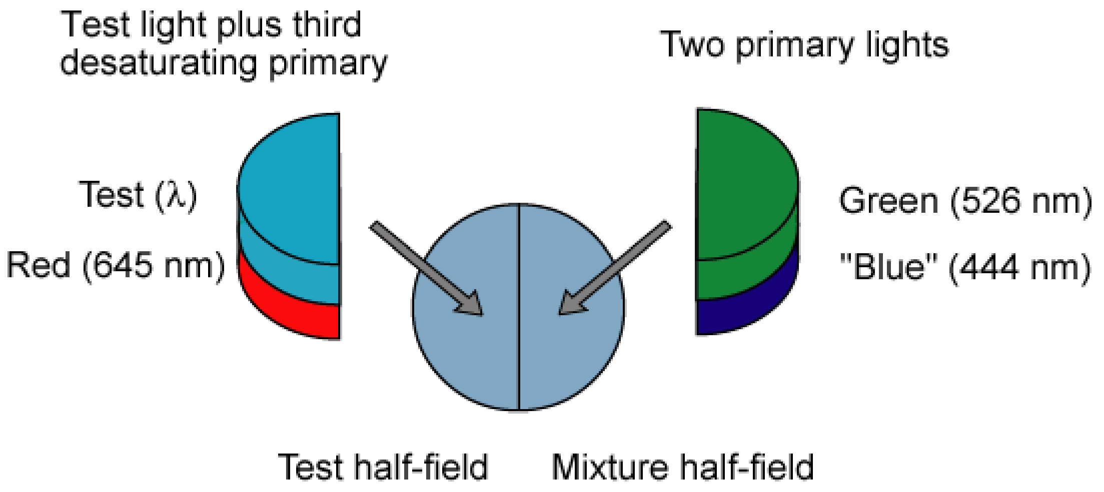


Linear

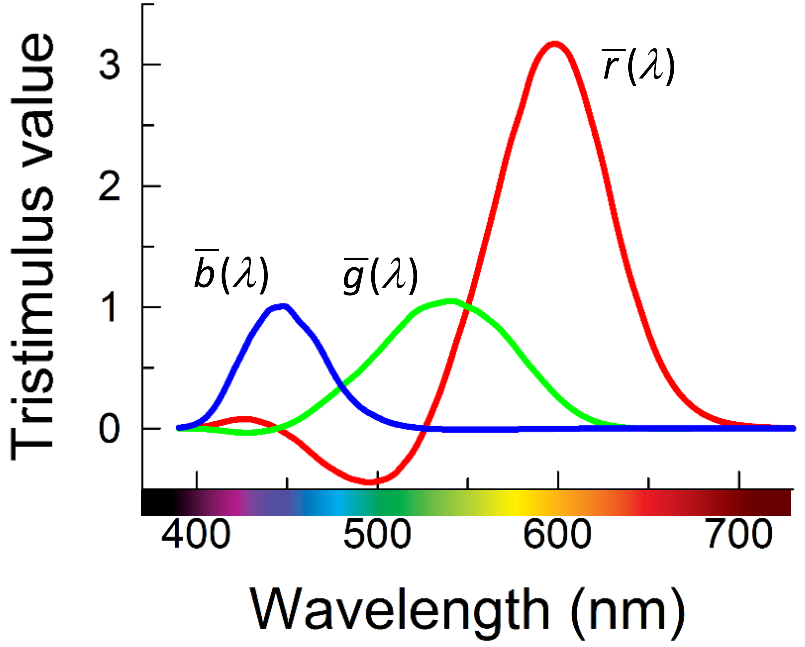


3. CONE SPECTRAL SENSITIVITIES AND COLOUR MATCHING FUNCTIONS

A classic way of specifying colours is by colour matching in a colour matching experiment:

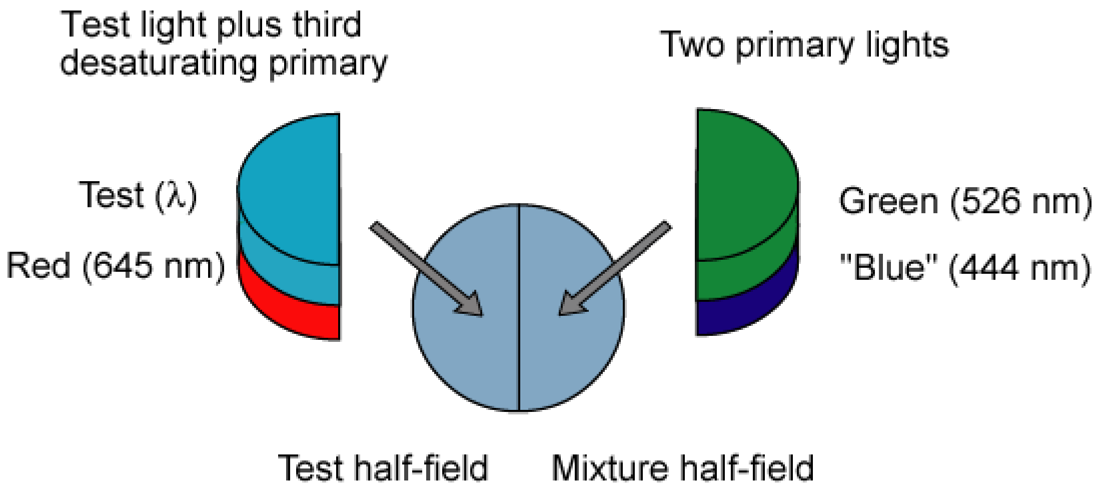


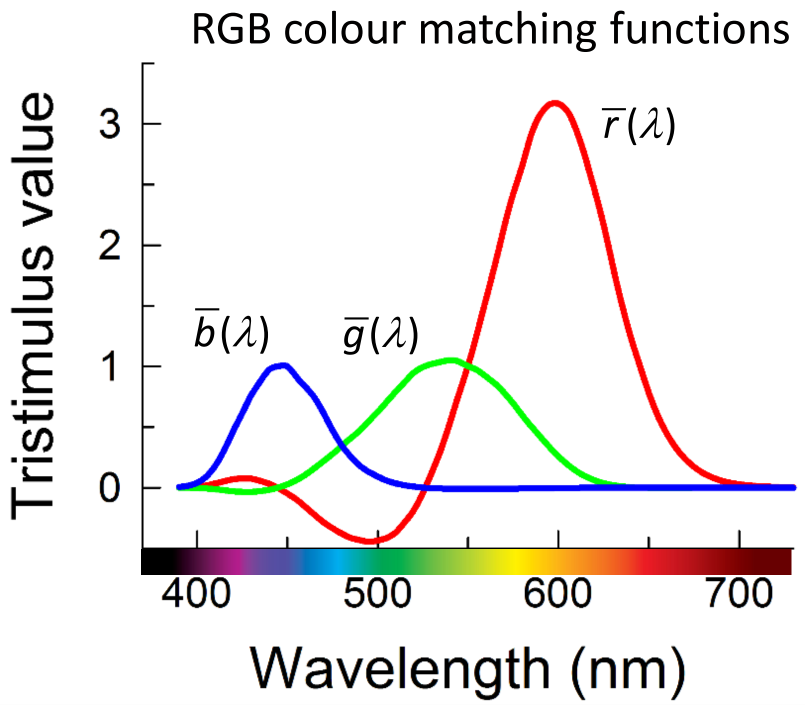
RGB colour matching functions



A classic way of specifying colours is by colour matching in a colour matching experiment:

Colour can be defined in terms of the three colour matching functions without knowing the spectral sensitivities of the underlying photoreceptors.

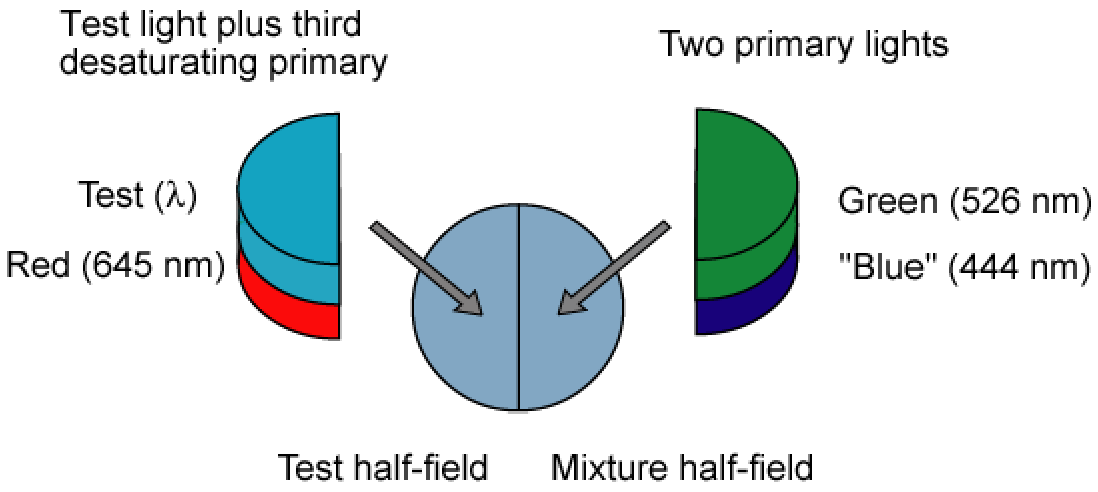




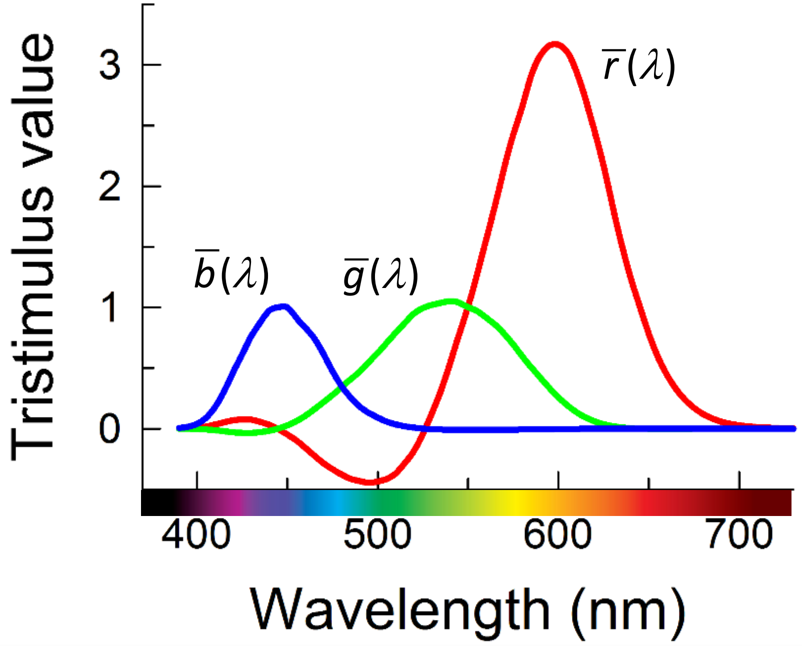
A classic way of specifying colours is by colour matching in a colour matching experiment:

Colour can be defined in terms of the three colour matching functions without knowing the spectral sensitivities of the underlying photoreceptors.

But what has this got to do with cone spectral sensitivities?



RGB colour matching functions



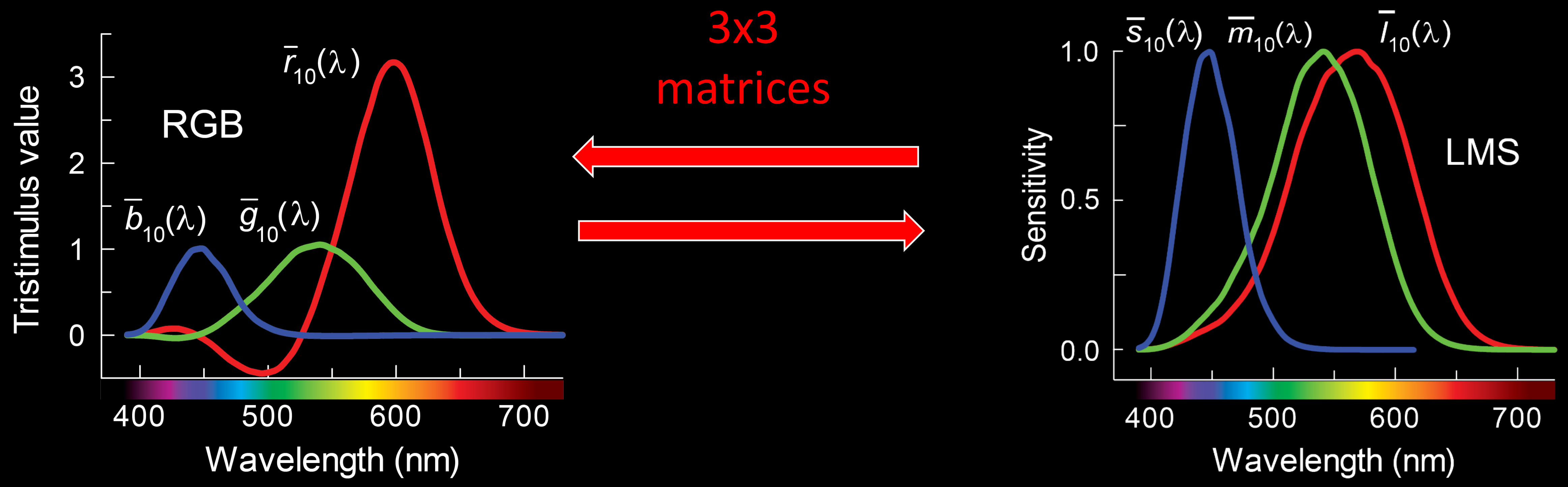
All colour matches are matches at the cone level and depend on the spectral sensitivities of the cones.

Consequently, the cone spectral sensitivities are the:

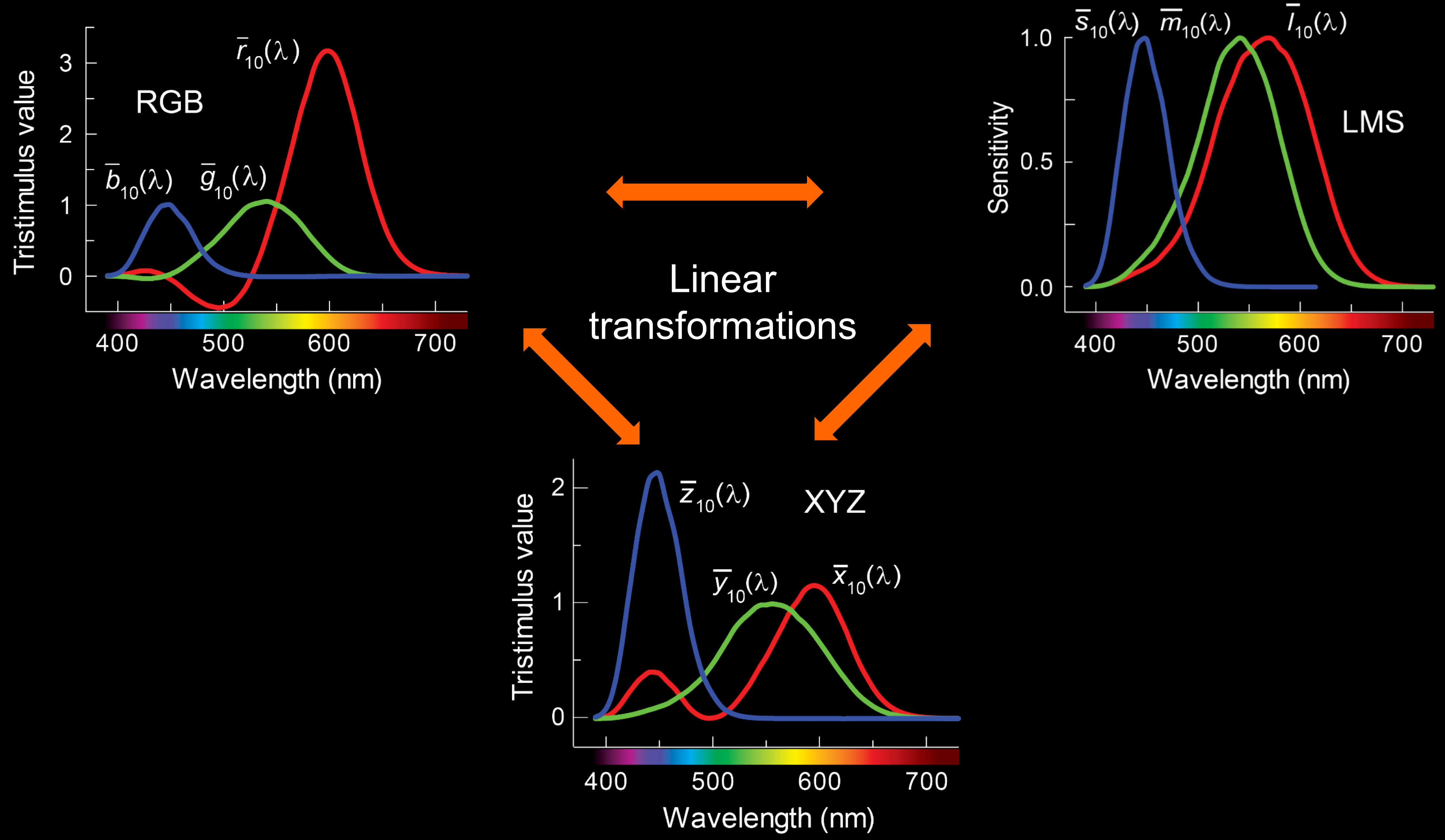
"Fundamental" colour matching functions

…upon which all other CMFs depend.

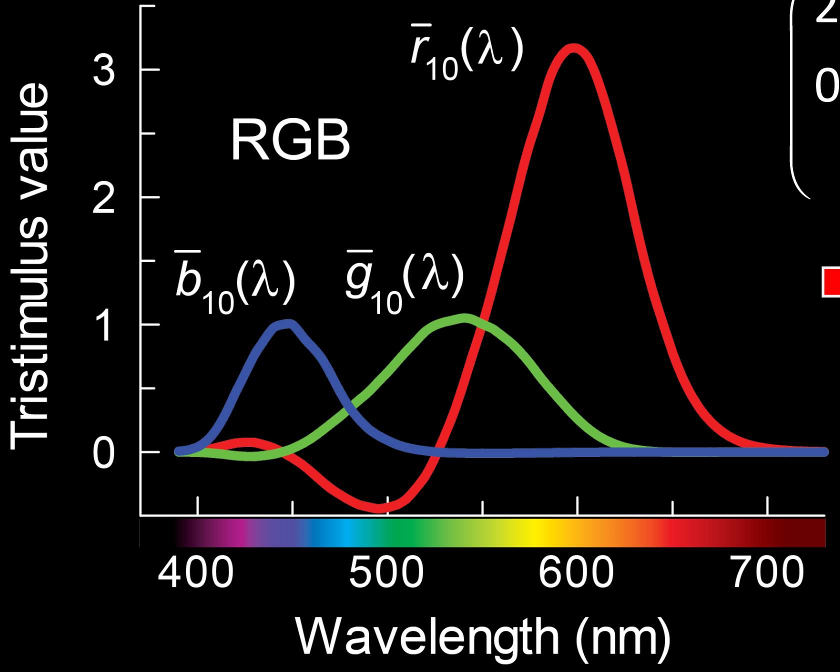
So there exists a simple linear transformations between RGB and LMS…



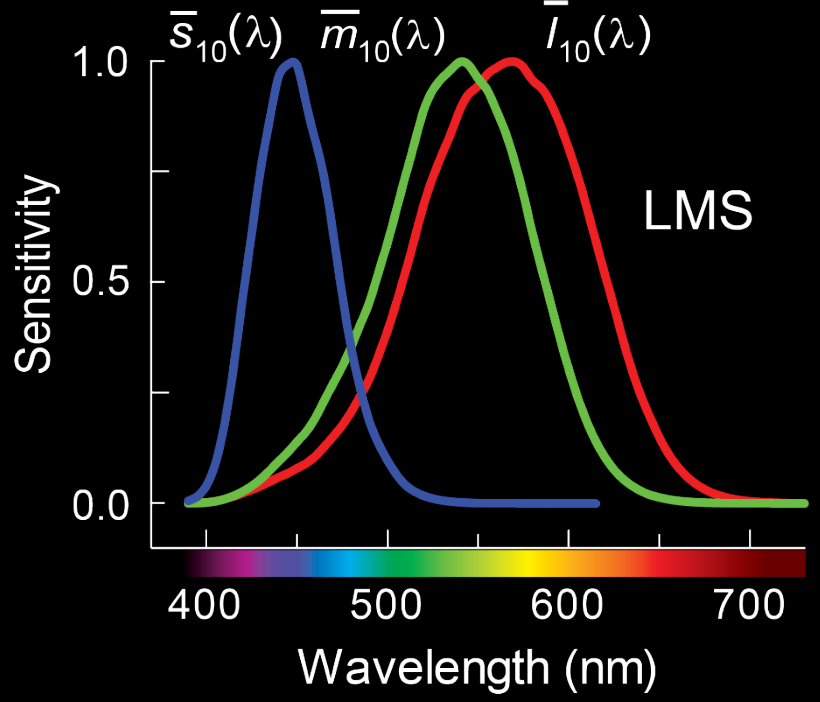
And also between RGB or LMS and XYZ.



The CIE 2006 LMS functions are defined as a linear transformation of Stiles & Burch (1959) RGB CMFs.



$$\begin{pmatrix} 2.846201 & 11.092490 & 1 \\ 0.168926 & 8.265895 & 1 \\ 0 & 0.010600 & 1 \end{pmatrix}$$



NEW DEFINITION OF LMS:

CIE Technical Report 170-1: 2006
Fundamental Chromaticity Diagram with Physiological Axes – Part 1

NEW DEFINITION OF XYZ:

CIE Technical Report 170-2: 2015
Fundamental Chromaticity Diagram with Physiological Axes – Part 2: Spectral Luminous Efficiency Functions and Chromaticity Diagrams

Together these represent a consistent set of "physiologically-relevant" (i.e., "correct") LMS, RGB and XYZ CMFs for 2-deg and 10-deg vision.

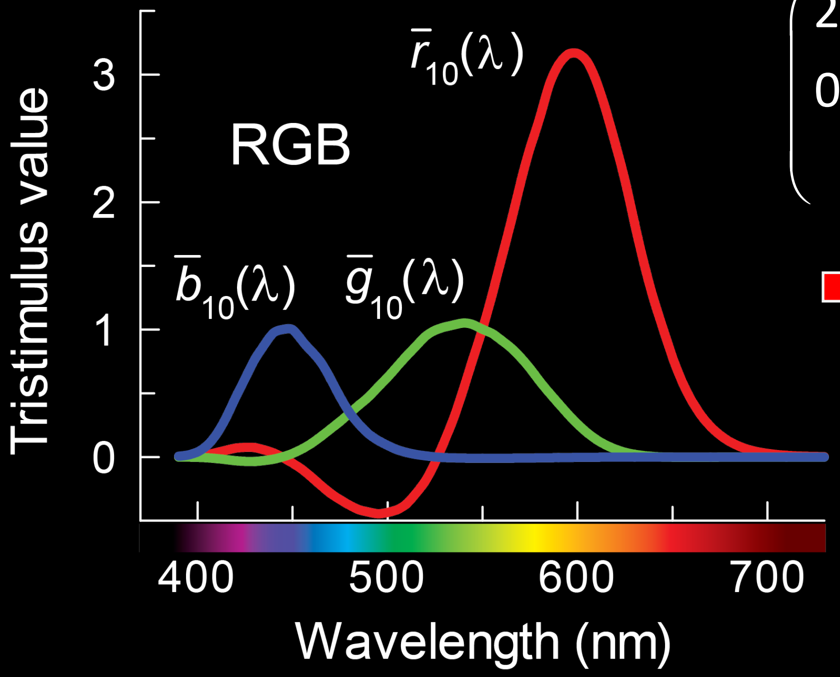
Most functions (ancient and modern) and the new CIE standards can be downloaded from:

CVRL database

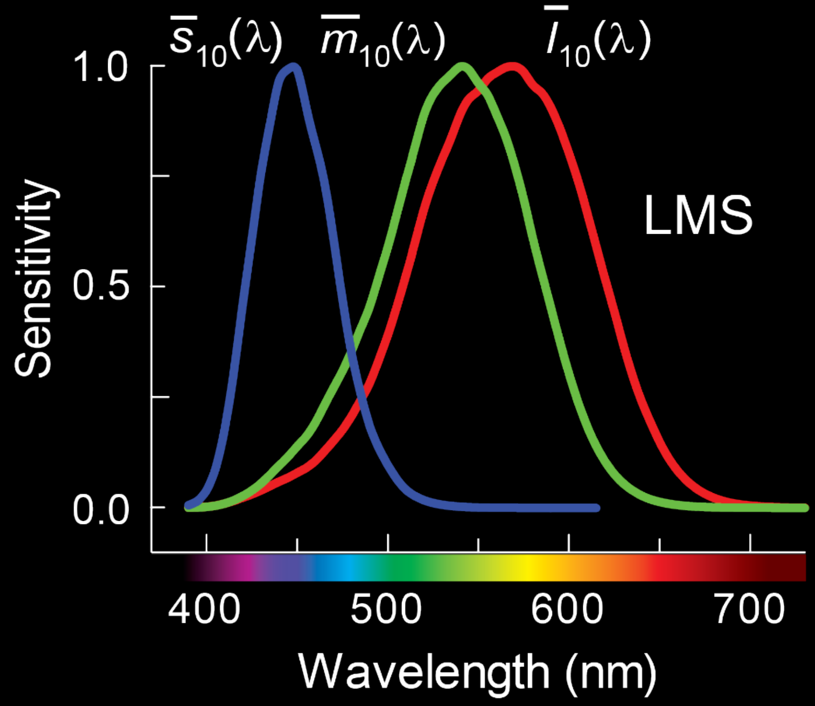
http://www.cvrl.org

4. INDIVIDUAL DIFFERENCES

As we just discussed, the CIE (2006) LMS standards represent the average normal spectral sensitivity or colour matching functions, based on linear transforms of the average Stiles & Burch (1959) CMFs.

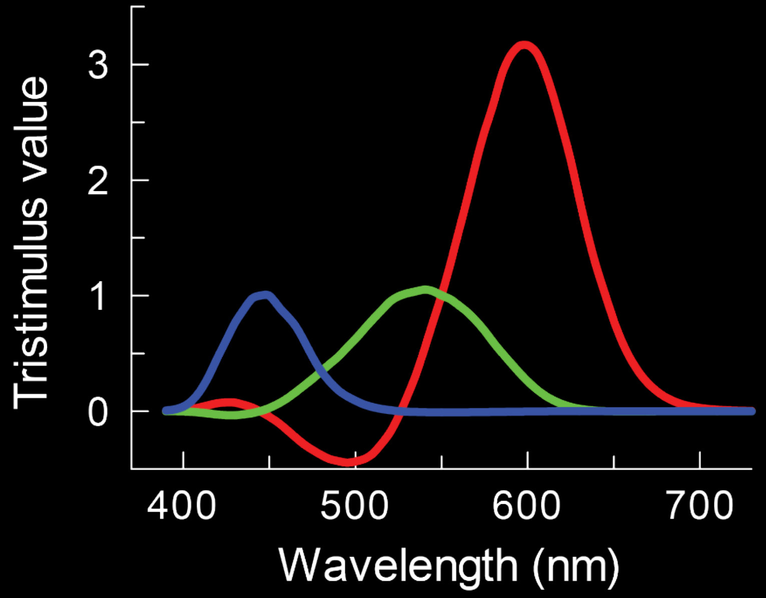


$$\begin{pmatrix} 2.846201 & 11.092490 & 1 \\ 0.168926 & 8.265895 & 1 \\ 0 & 0.010600 & 1 \end{pmatrix}$$



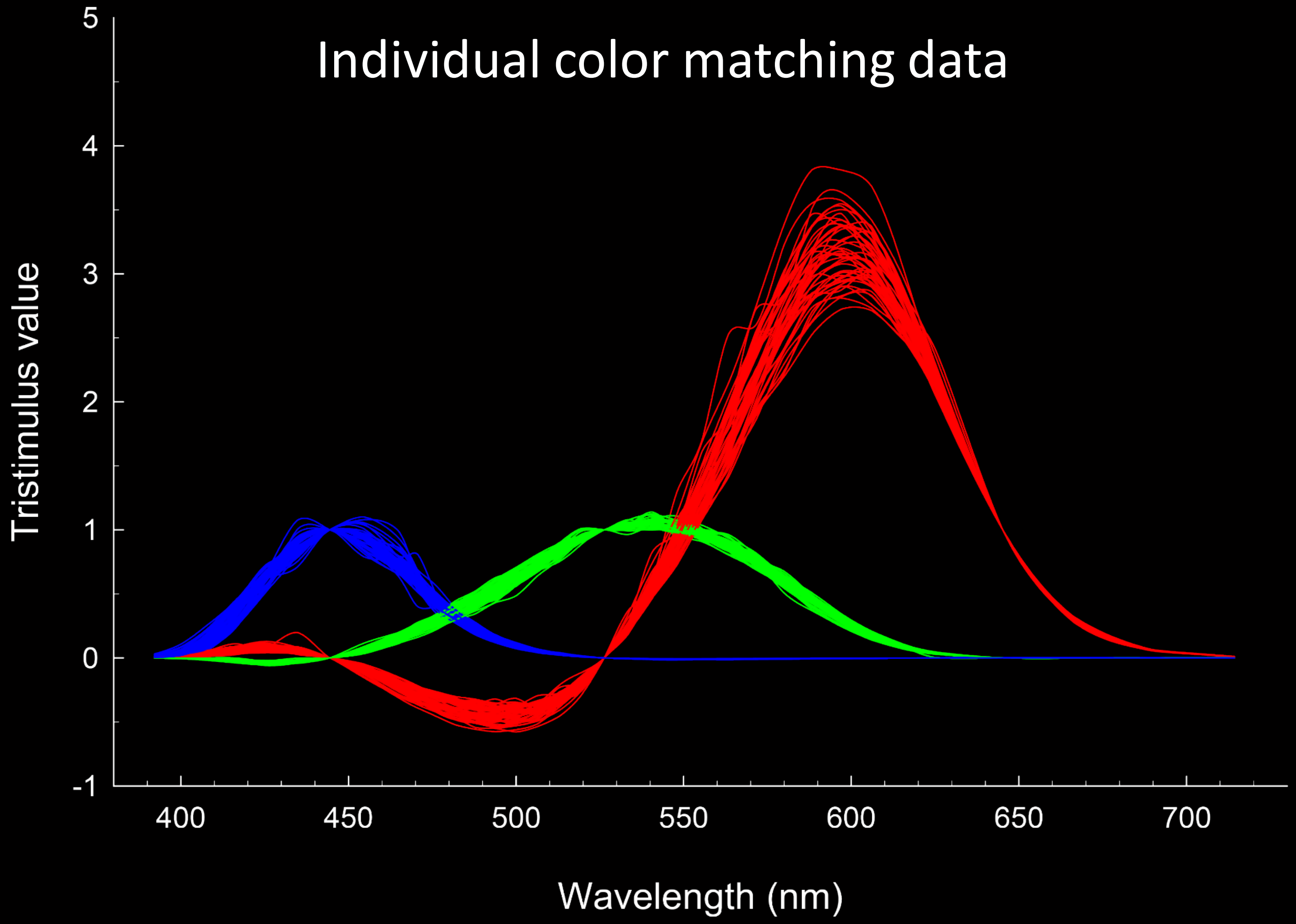
However, this underplays the sizeable individual differences found in the original Stiles & Burch colour matching data.

Mean color matching data

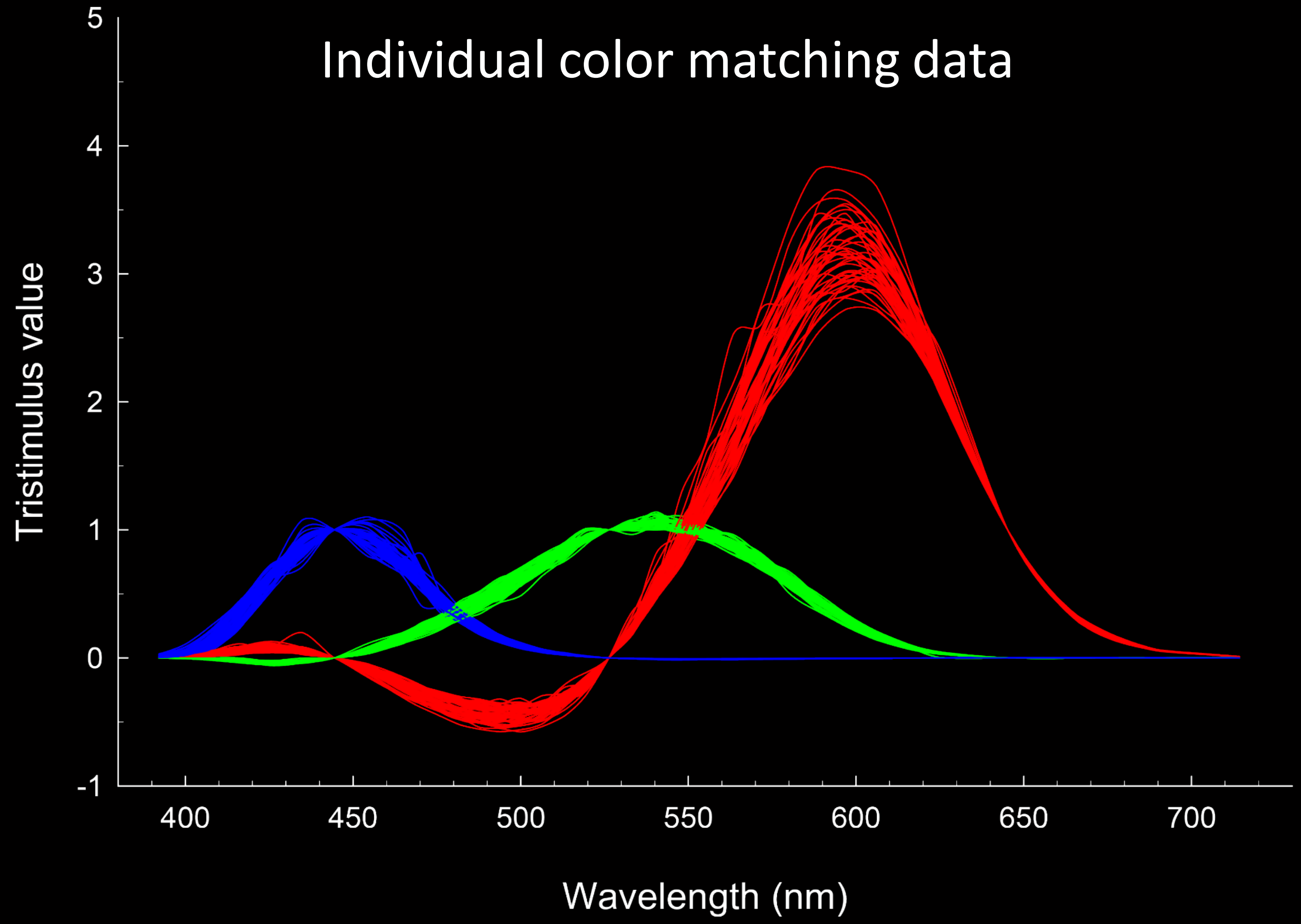


Stiles & Burch (1959) 10-deg CMFs

Individual color matching data



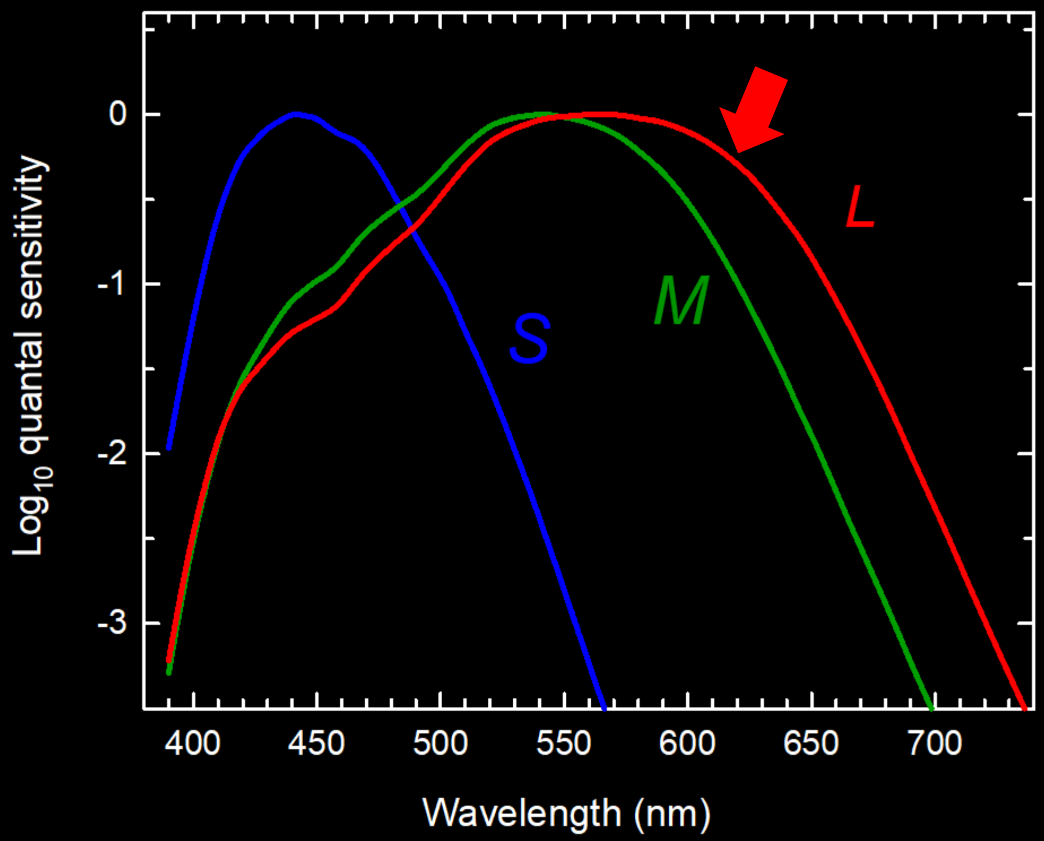
What causes these individual differences (and how can we model them)?



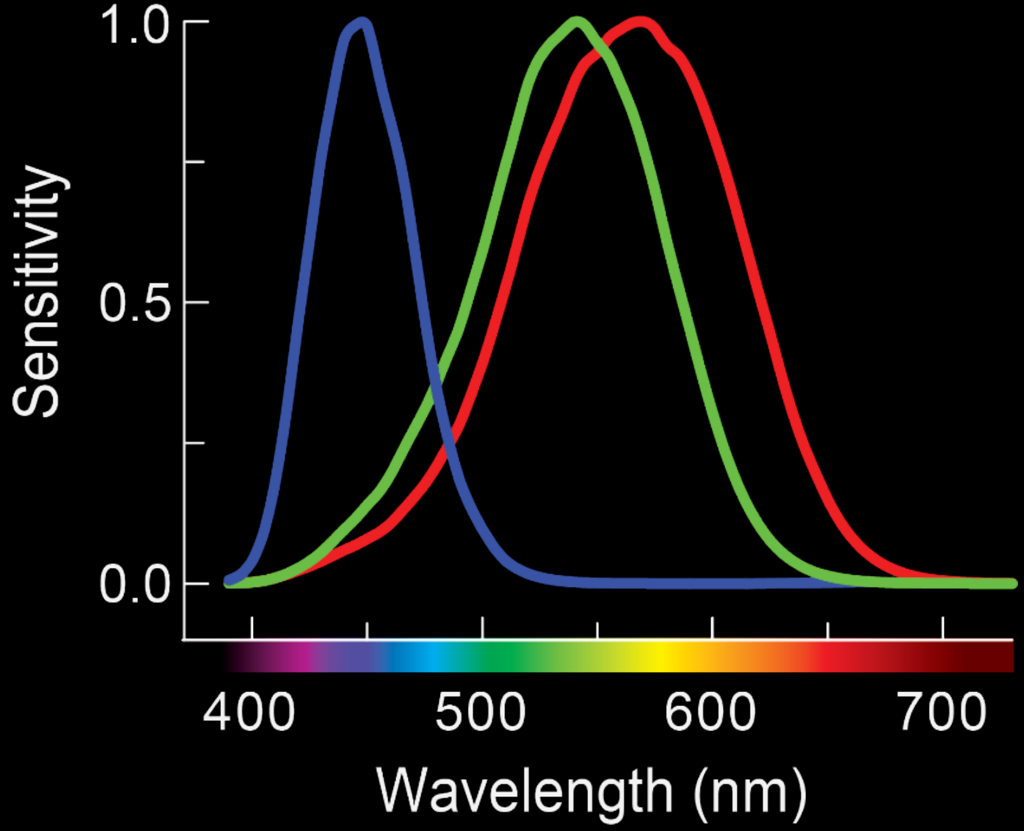
Stiles & Burch (1959) 10-deg CMFs

Individual differences are most easily visualized as effects on the cone spectral sensitivities or the “fundamental” LMS colour matching functions (rather than on XYZ or RGB CMFs)...

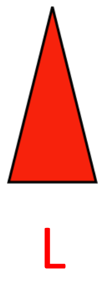
Logarithmic



Linear

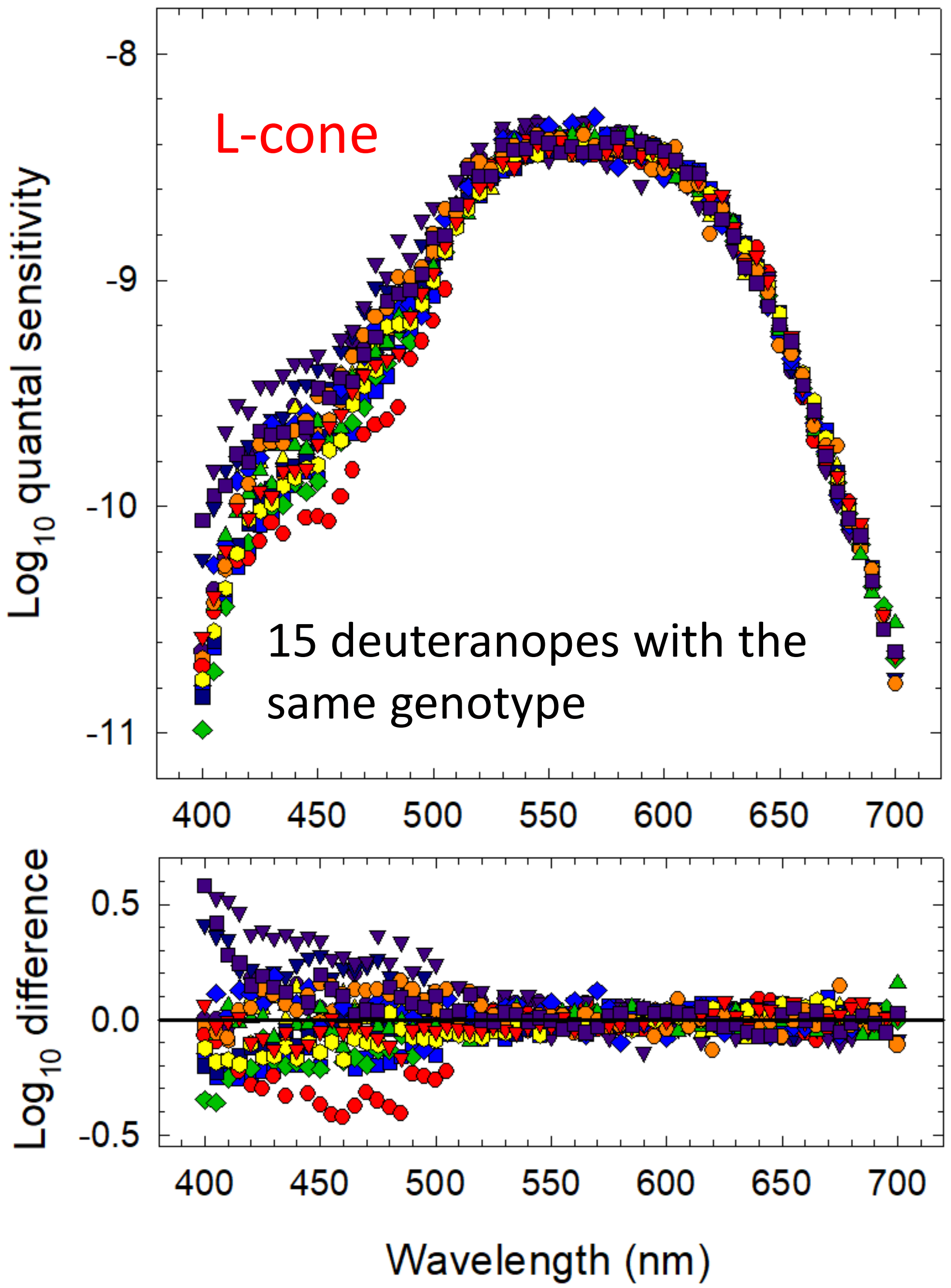


Individual data for deuteranopes with the same L-cone photopigment

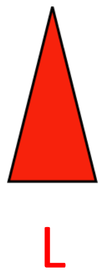


L-cone data from fifteen deuteranopes with the same genotype (and therefore with the same photopigment)

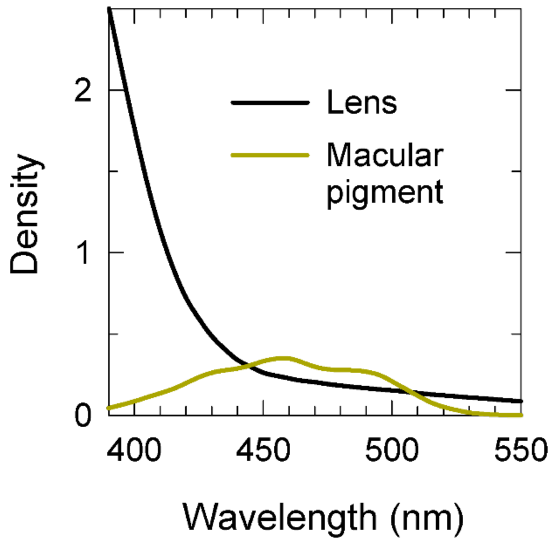
Why are the results so variable at short wavelengths?

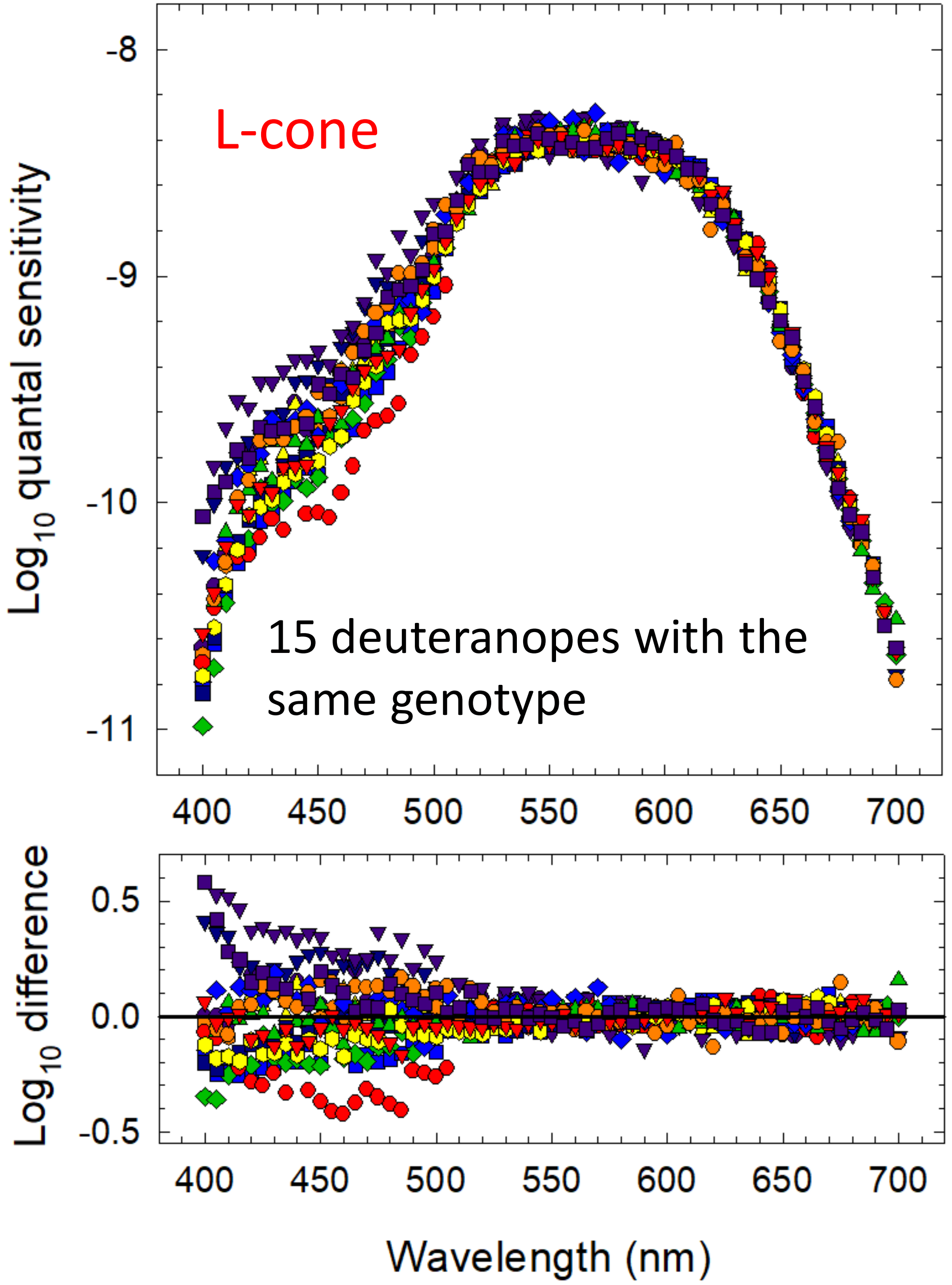


Individual data for deuteranopes with the same L-cone photopigment

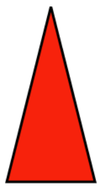


The variability is due to individual differences in macular and lens pigment optical densities.



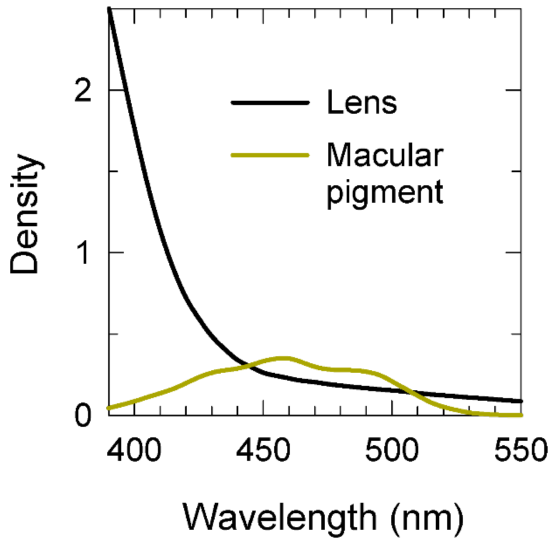


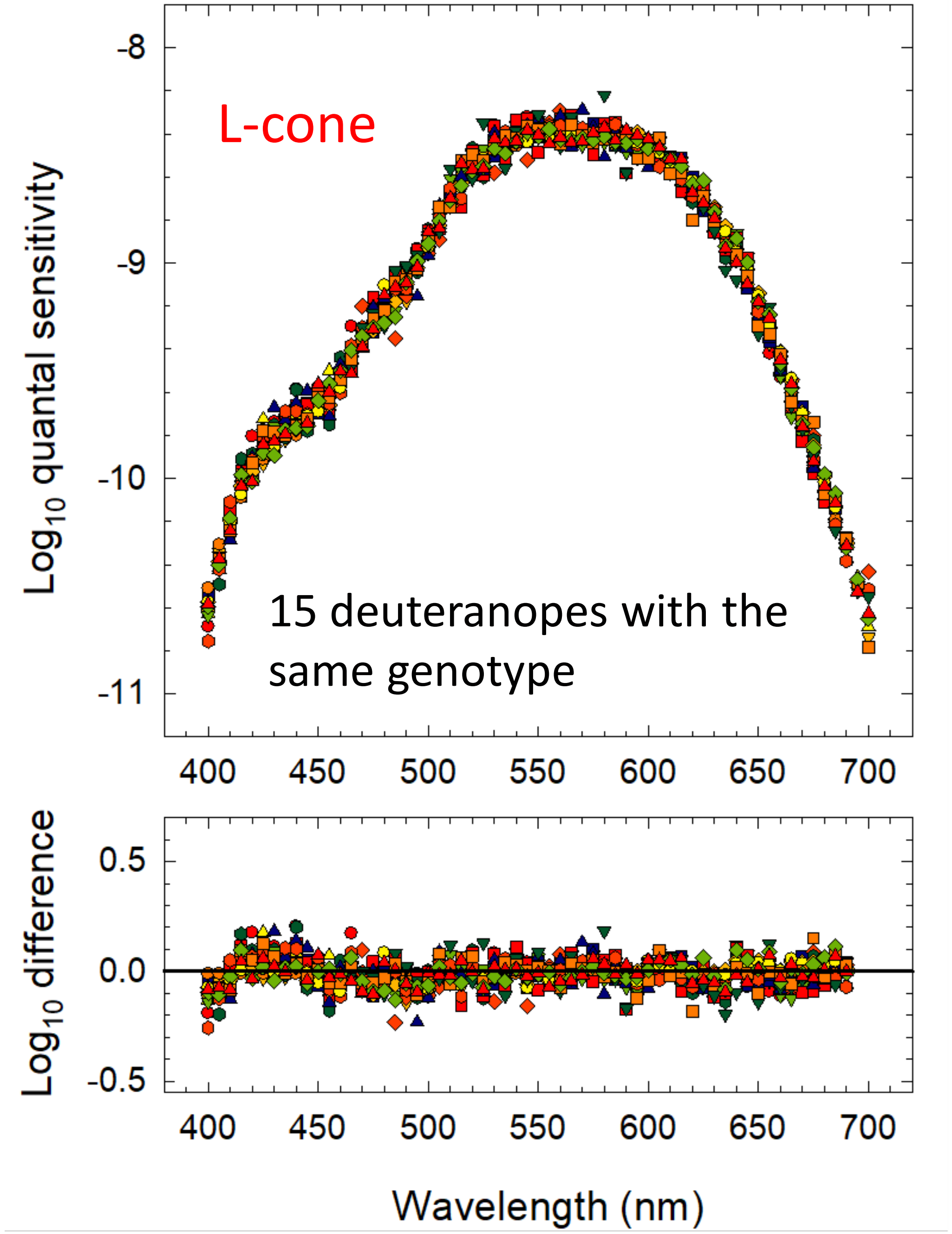
Individual data for deuteranopes with the same L-cone photopigment



L

L-cone data adjusted to the same mean macular and lens optical densities





What causes individual differences?

- Macular pigment optical density differences
- Lens pigment optical density differences
- Photopigment optical density differences
- Spectral shifts in photopigment sensitivity

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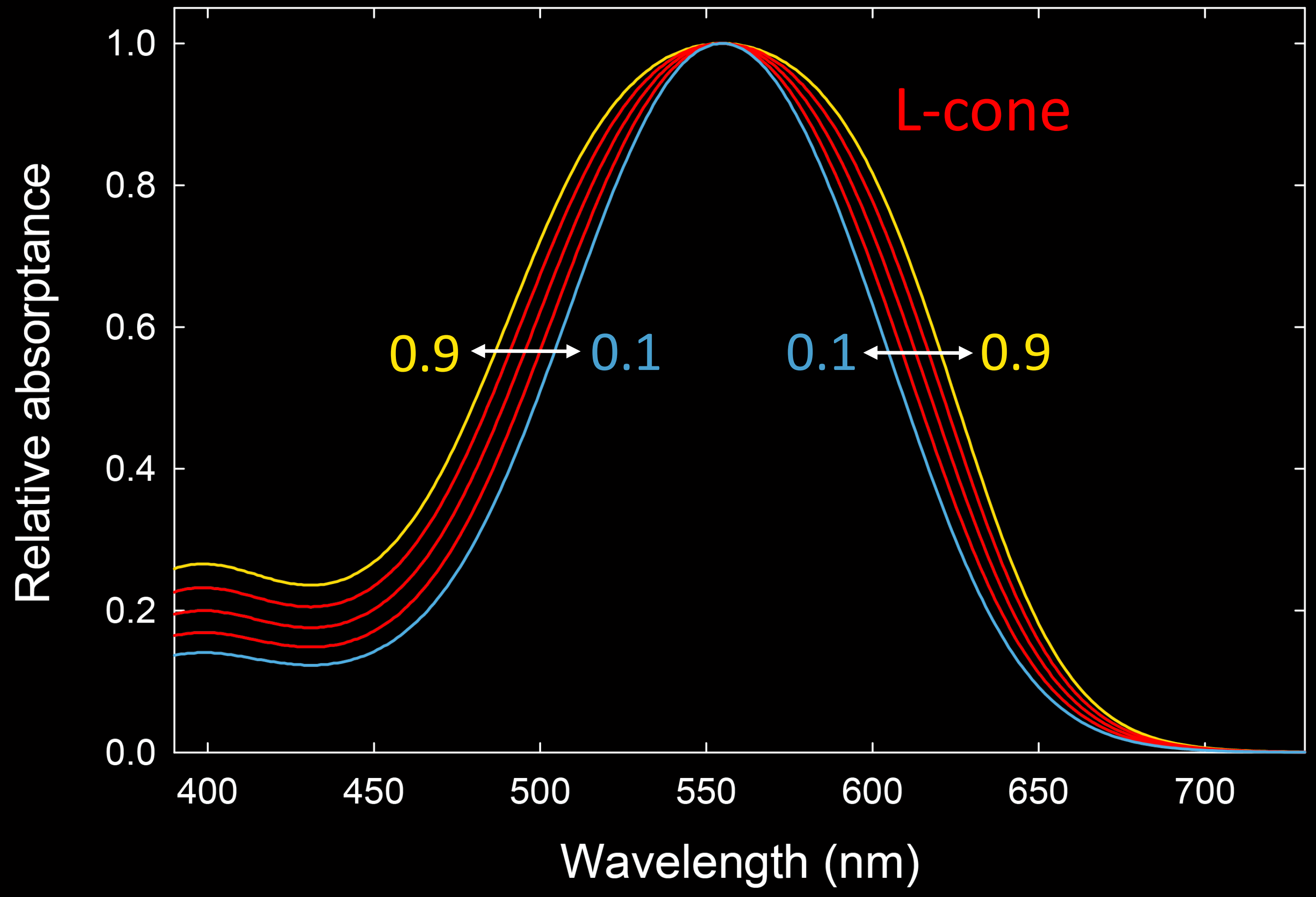
Individual differences in photopigment optical density

Increasing photopigment optical density broadens the spectral sensitivity around the λ_{max}.

Cone photopigments varying in optical density from 0.1 (narrow) to 0.9 (broad) in 0.2 steps

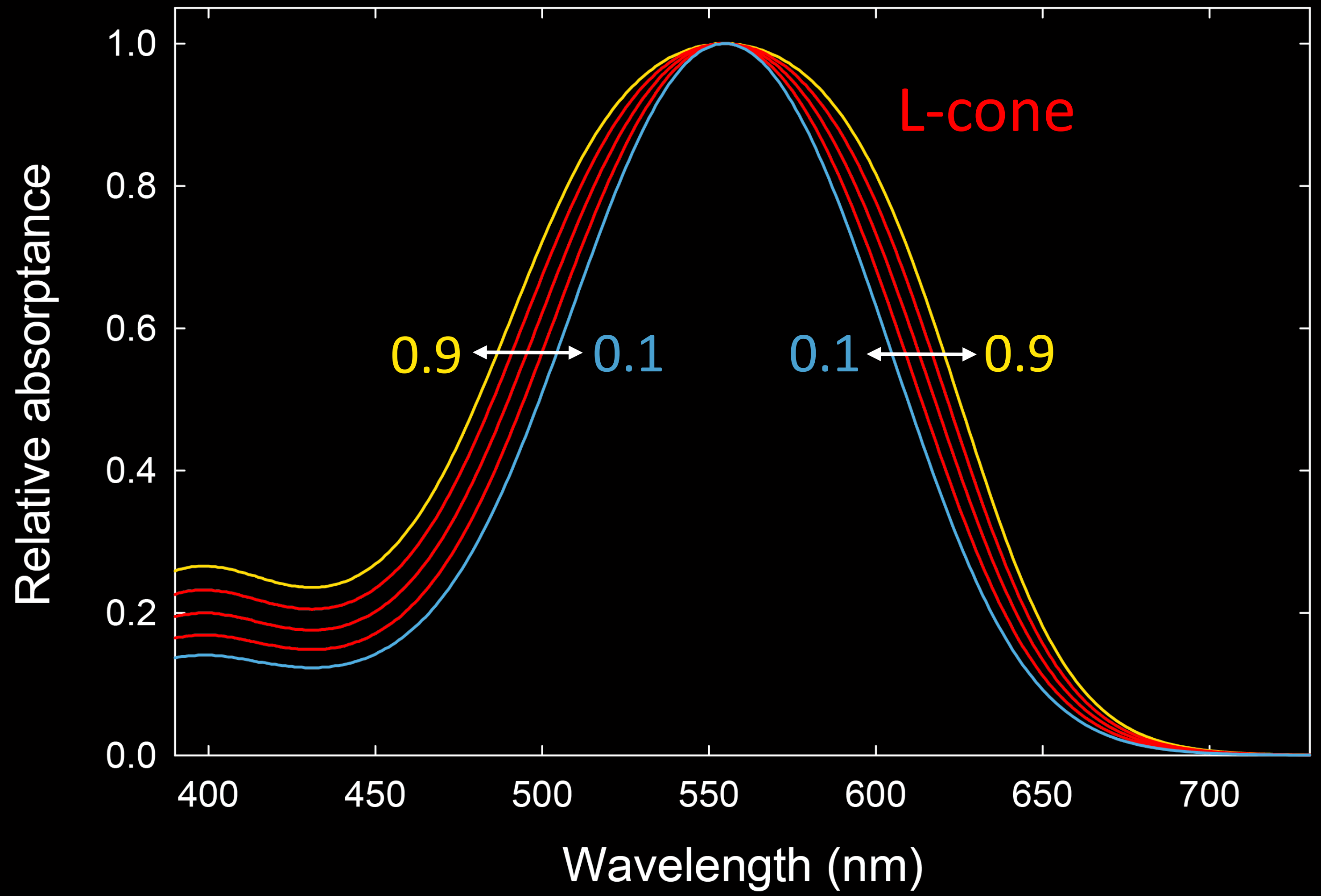


Individual differences in photopigment optical density

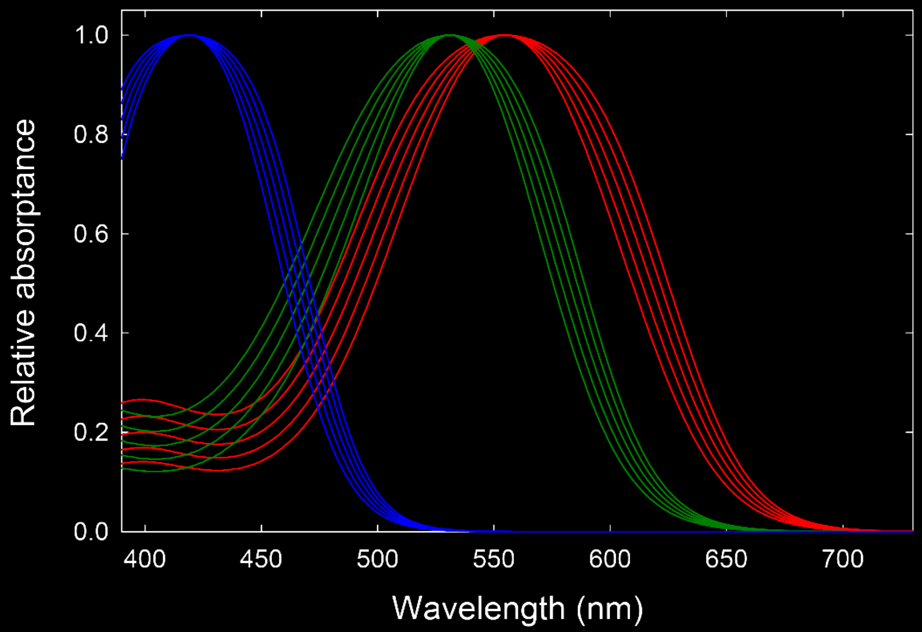
Increasing photopigment optical density broadens the spectral sensitivity around the λ_{max}.

Note that the photopigment in the longer cones in the fovea has an effectively higher optical density than photopigment in the shorter cones outside the fovea.

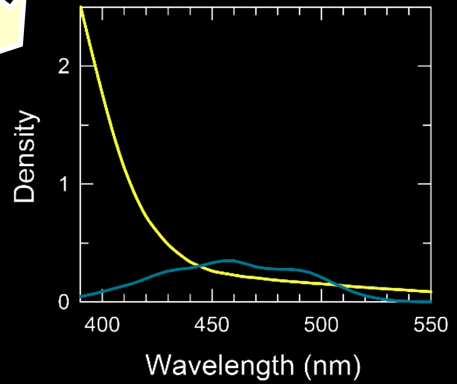
Cone photopigments varying in optical density from 0.1 (narrow) to 0.9 (broad) in 0.2 steps



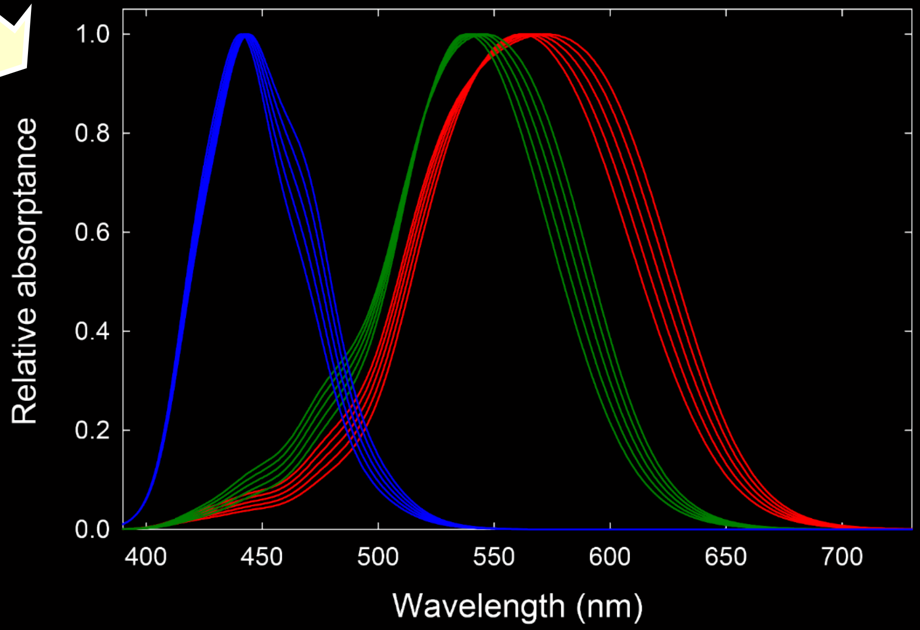
Photopigments



Add mean lens and macular filtering to produce the corneal spectral sensitivities.



Cone spectral sensitivities at the cornea

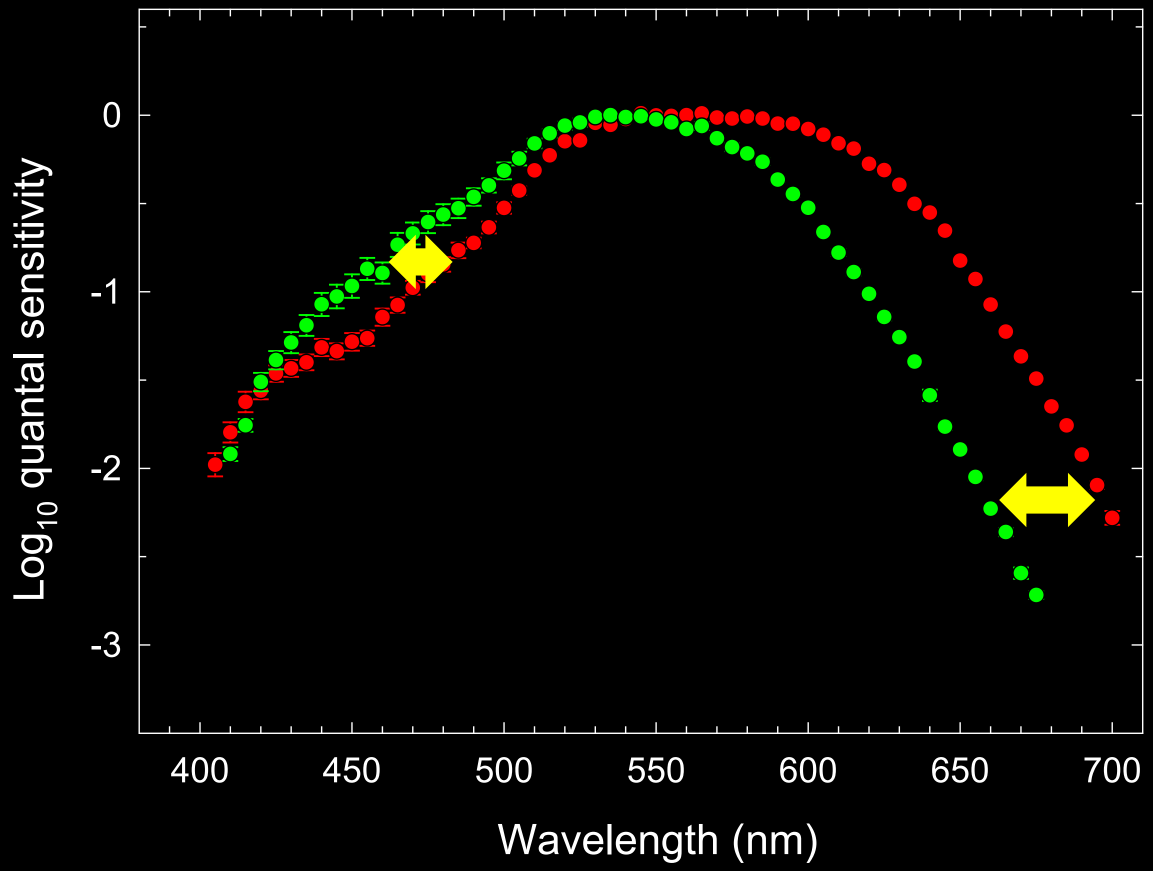


What causes individual differences?

- Macular pigment optical density differences
- Lens pigment optical density differences
- Photopigment optical density differences
- Spectral shifts in photopigment sensitivity

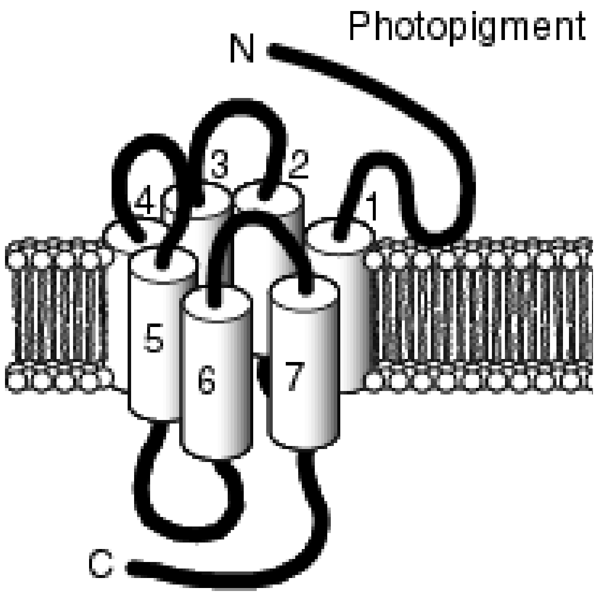
The variability is caused by shifts in the spectral positions of the M- and L-cone spectral sensitivity functions between the M- and L-cone extremes.

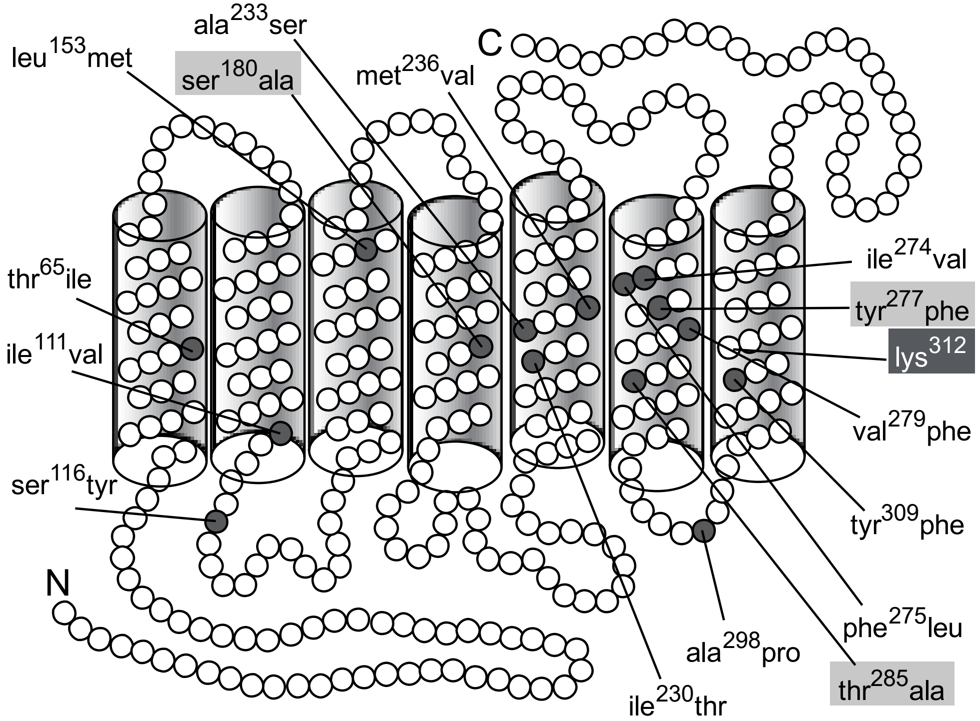
Why does this variability occur?



Amino acid differences between the L-and M-cone opsins

There are only fifteen amino acid differences between the L- and M-cone photopigment opsins. Only about seven of those cause wavelength shifts between their spectral sensitivities

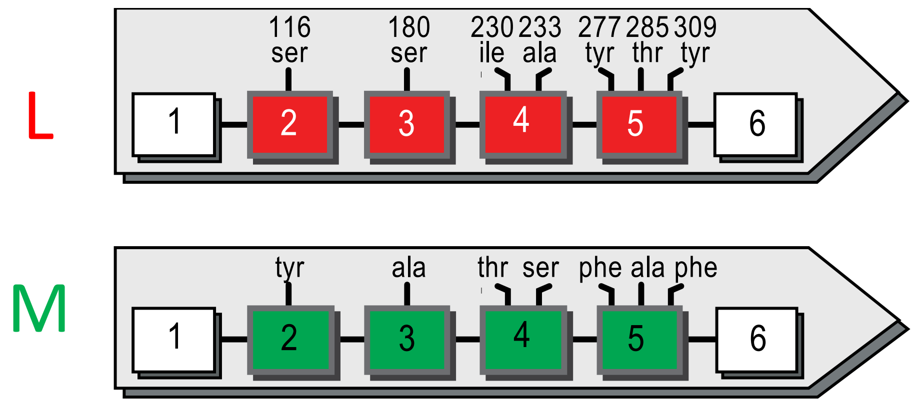


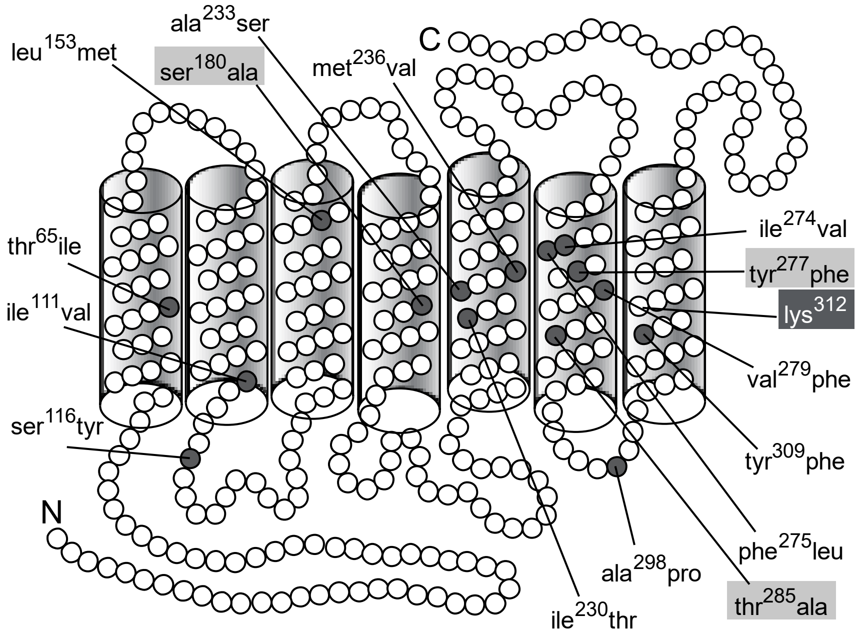


L vs M

From Sharpe, Stockman, Jägle & Nathans, 1999

Here are the SEVEN important amino acid differences between L and M that change spectral sensitivity in shorthand form…

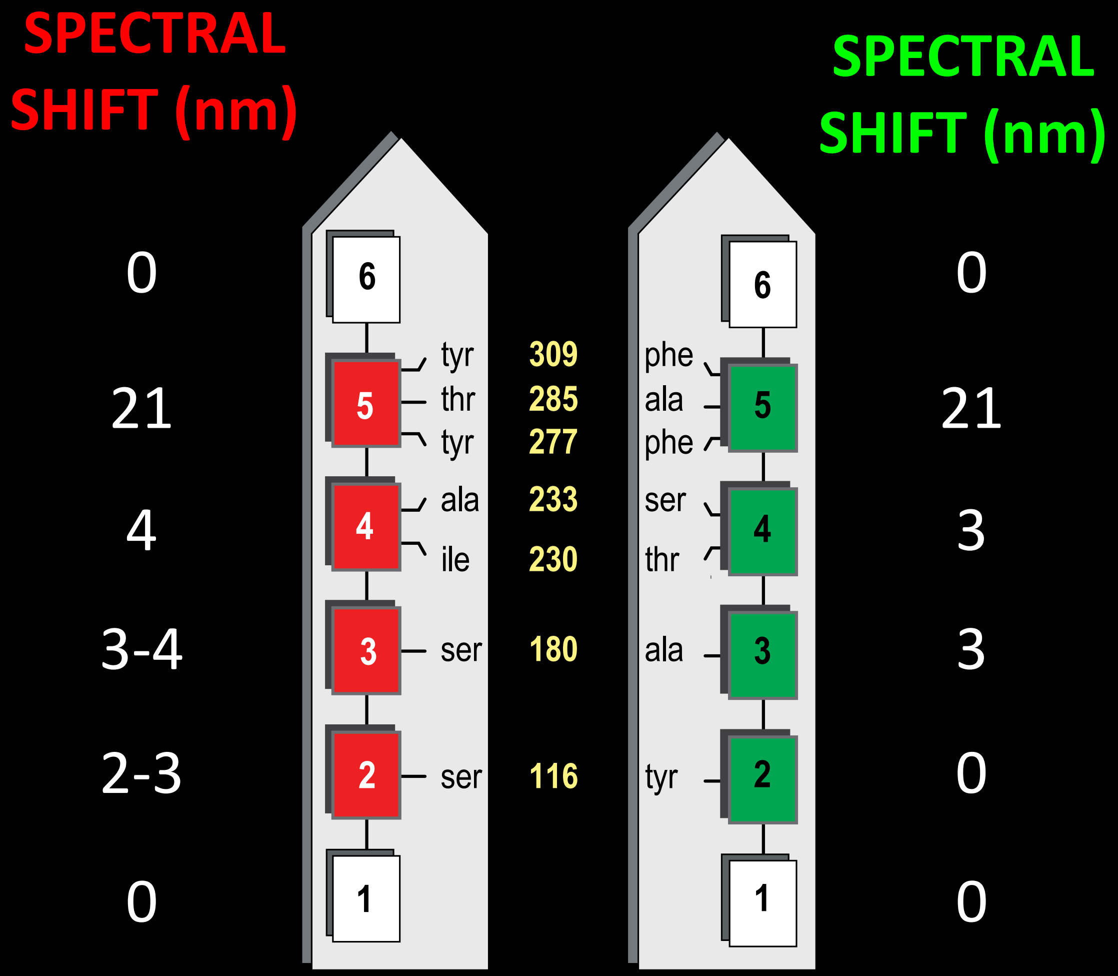




The L- and M-cone opsin genes on X-chromosome encode the sequence of amino acids that together build the opsin protein.

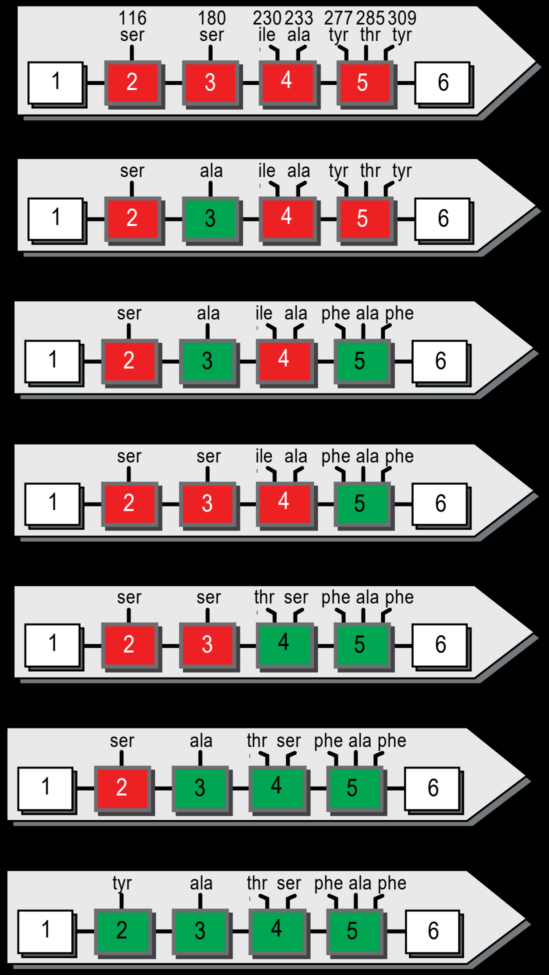
Because the L- and M-cones are next to each other their genetic information can get mixed up, so that you get hybrid (mixed) genes made up of some of the M sequence and some of the L sequence.

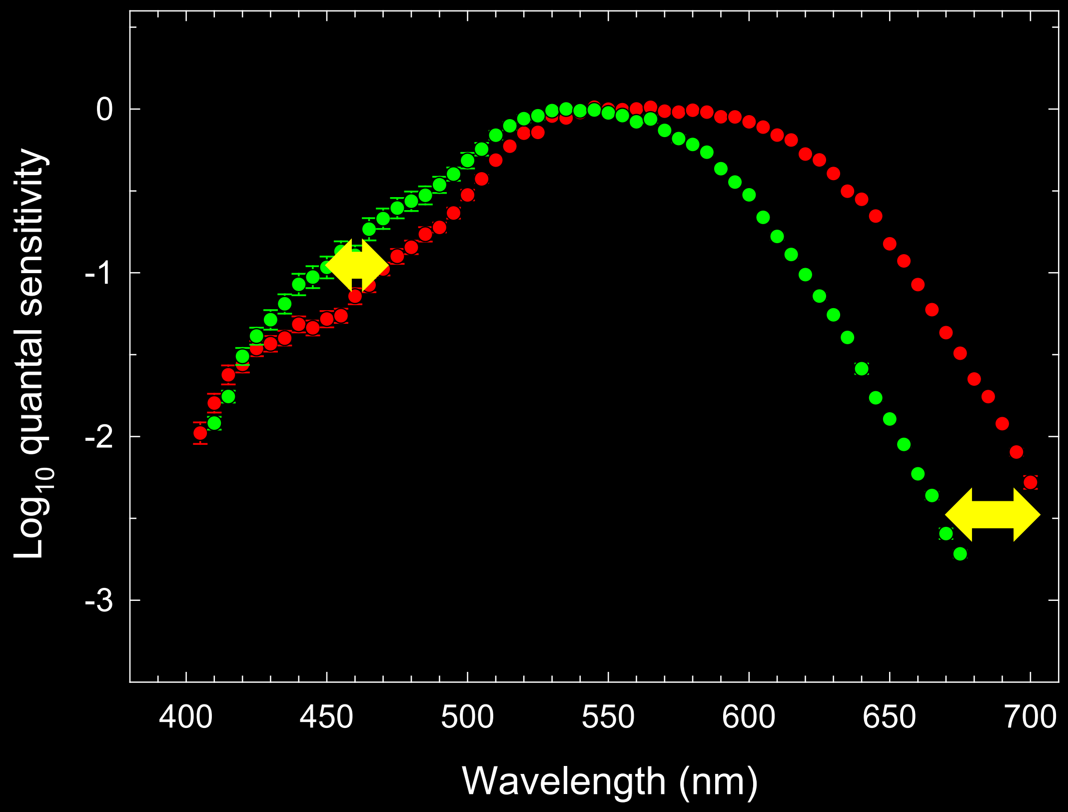
SUMMARY OF SPECTRAL SHIFTS



Values from Neitz and Neitz (2011)

Hybrid examples

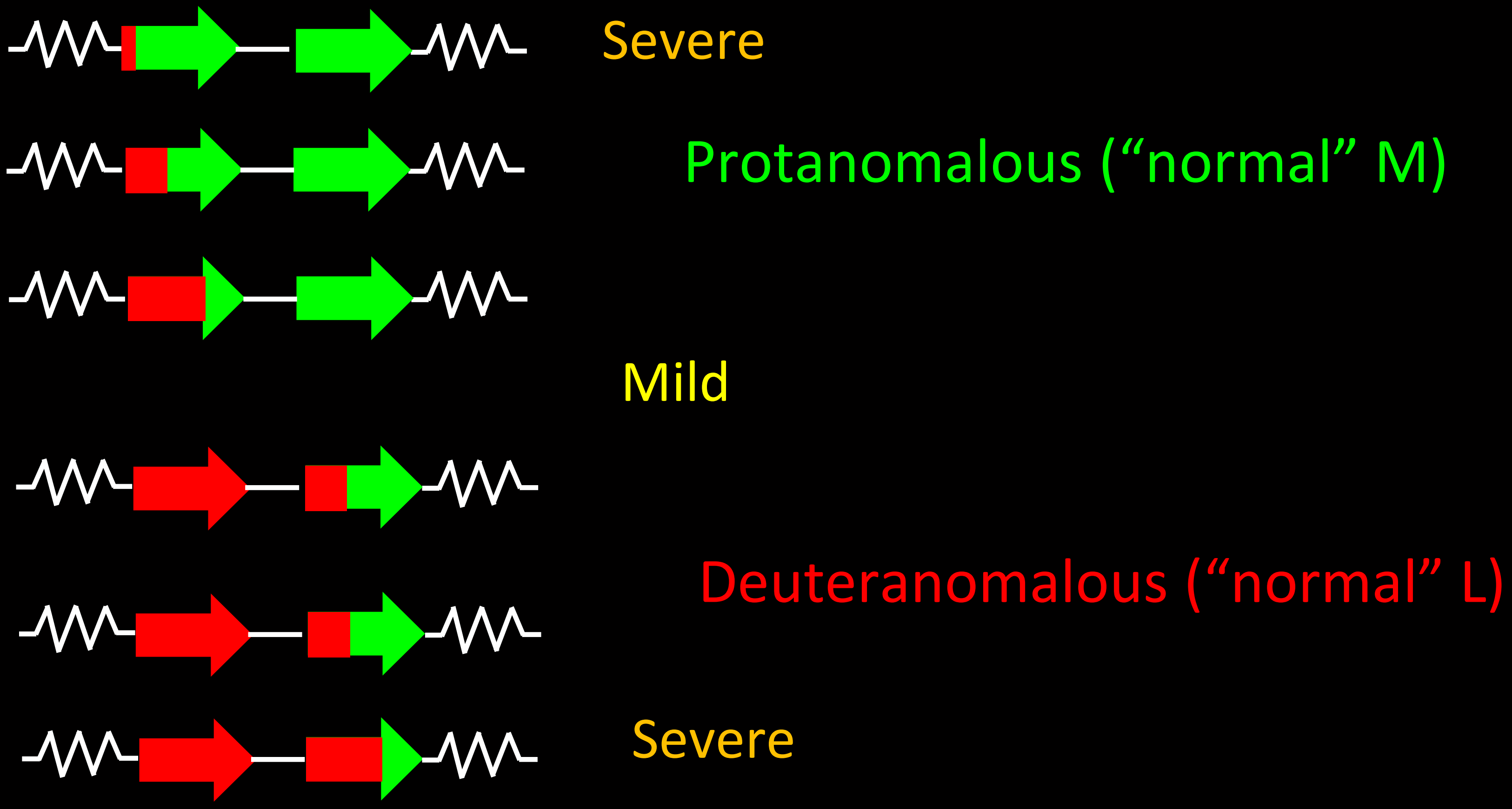




The spectral sensitivities of the hybrid photo-pigments vary between those of the M- and L-cones depending on where the crossover occurs.

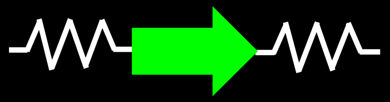
Anomalous trichromats

Male observers with two different genes one of which is hybrid are anomalous trichromats

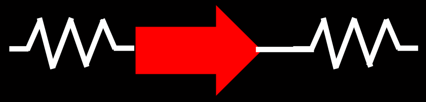


Red-green dichromats

Male observers with one gene (or two that are effectively the same) are dichromats



Protanope

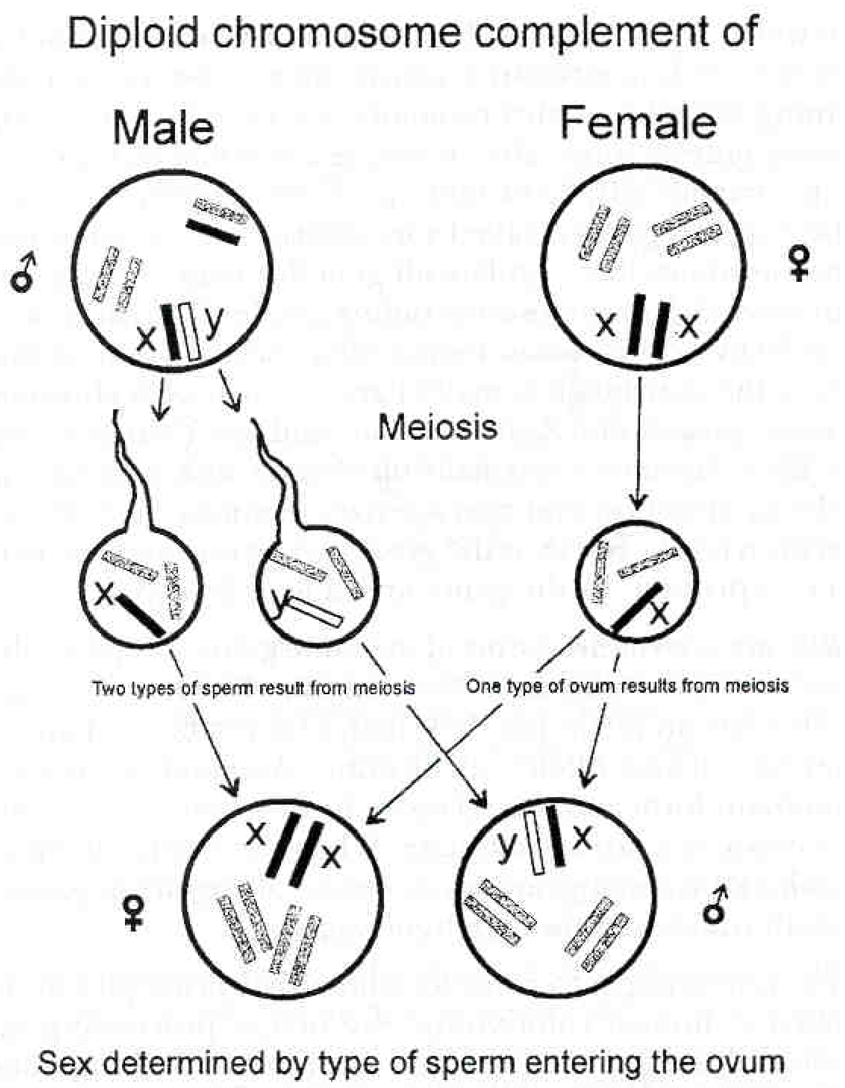


Deuteranope

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

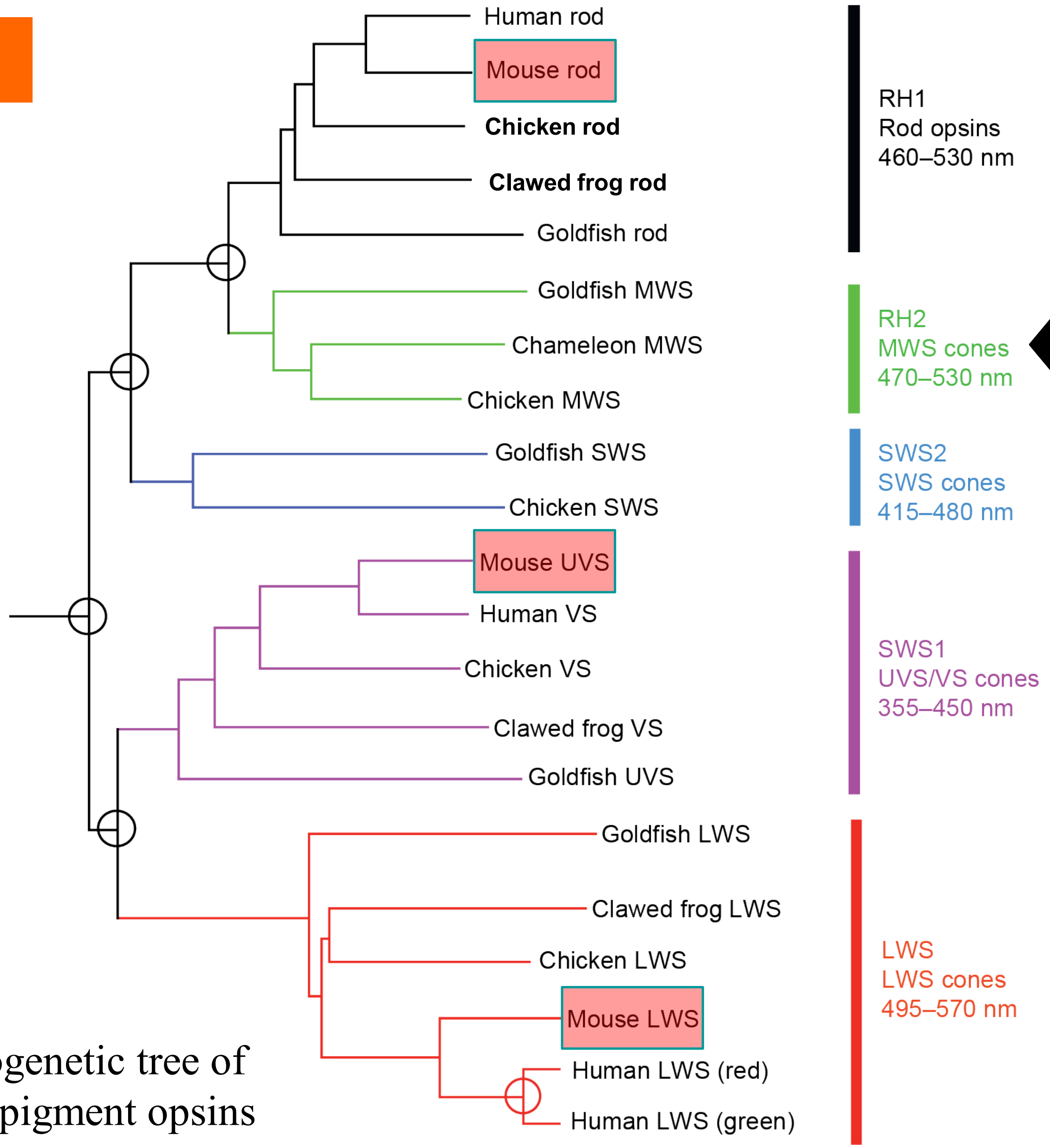
Condition		percent in UK Male	Female
Protanopia	no L cone	1.0	0.02
Protanomaly	milder form	1.0	0.03
Deuteranopia	no M cone	1.5	0.01
Deuteranomaly	milder form	5.0	0.4
Tritanopia	no SWS cone	0.008	0.008

XY inheritance



The emergence of two longer wavelength (M- and L-cones) occurred relatively recently in human evolution in old-world primates.

Mammals



Simplified phylogenetic tree of vertebrate visual pigment opsins

Most mammals (e.g., the mouse) have only L-cones and S-cones (and rods).

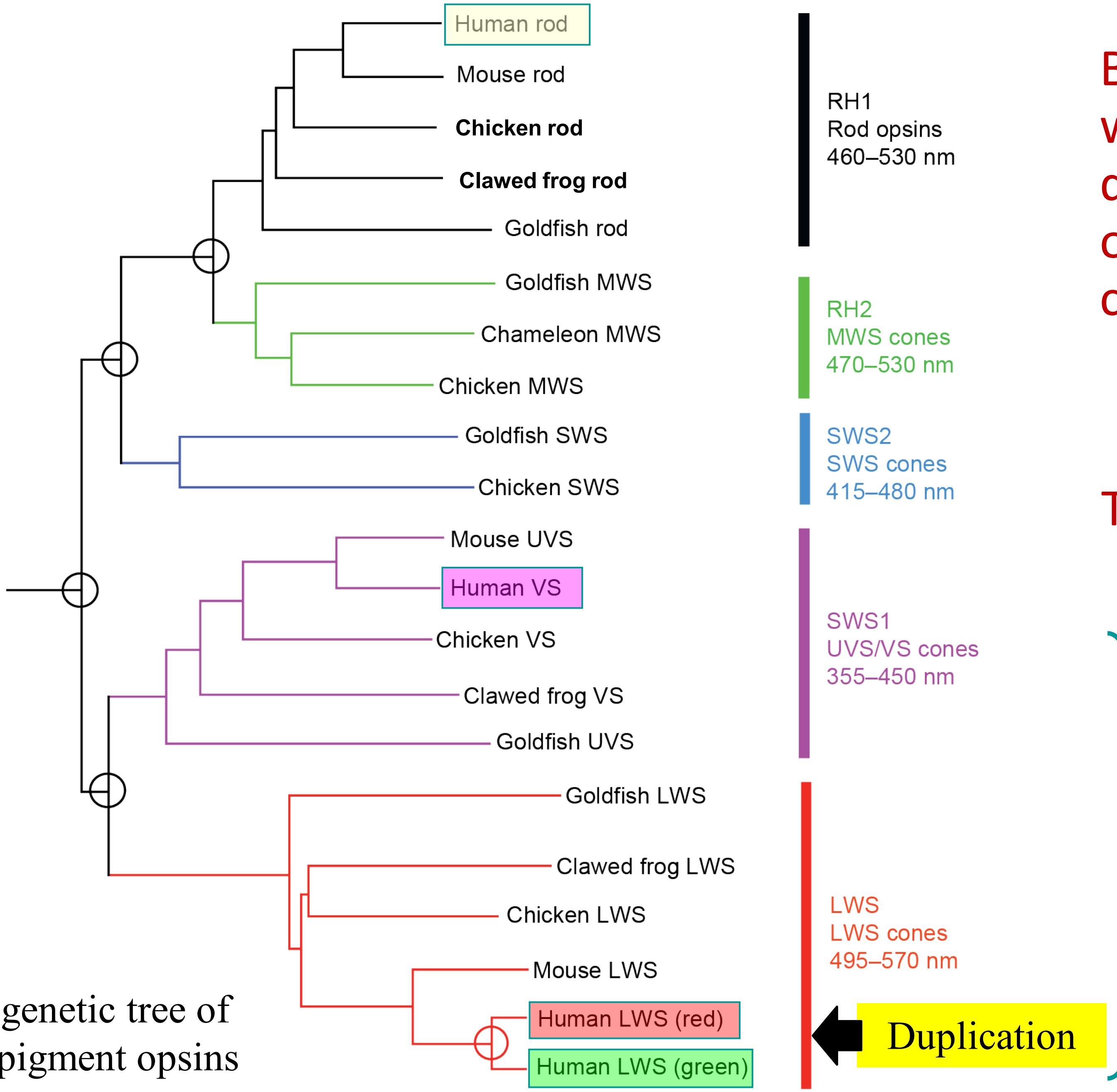
Lost M-cone opsin

They are therefore dichromatic.

Basis for dichromatic mammalian colour vision

Jim Bowmaker

Humans



Simplified phylogenetic tree of vertebrate visual pigment opsins

But about 35 mya ago in old world primates there was a duplication of the L-cone opsin gene on the X-chromosome that led to..

Trichromacy.

Basis for trichromatic colour vision

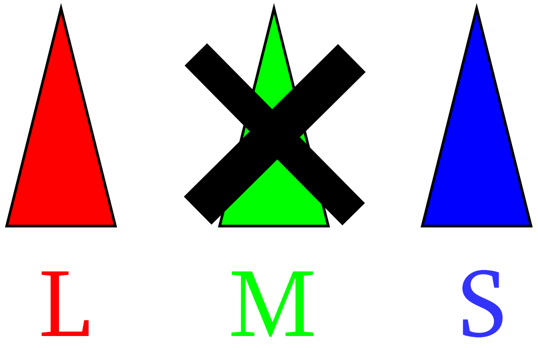
About 35 mya.

Jim Bowmaker

Credit: Euro Puppy Blog

Deuteranope

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



The emergence of two longer wavelength (M- and L-cones) occurred relatively recently in human evolution in old-world primates.

Why was it important?

No red-green discrimination

Source: Hans Irtel

Red-green discrimination

Source: Hans Irtel

What causes individual differences?

- Macular pigment optical density differences
- Lens pigment optical density differences
- Photopigment optical density differences
- Spectral shifts in photopigment sensitivity

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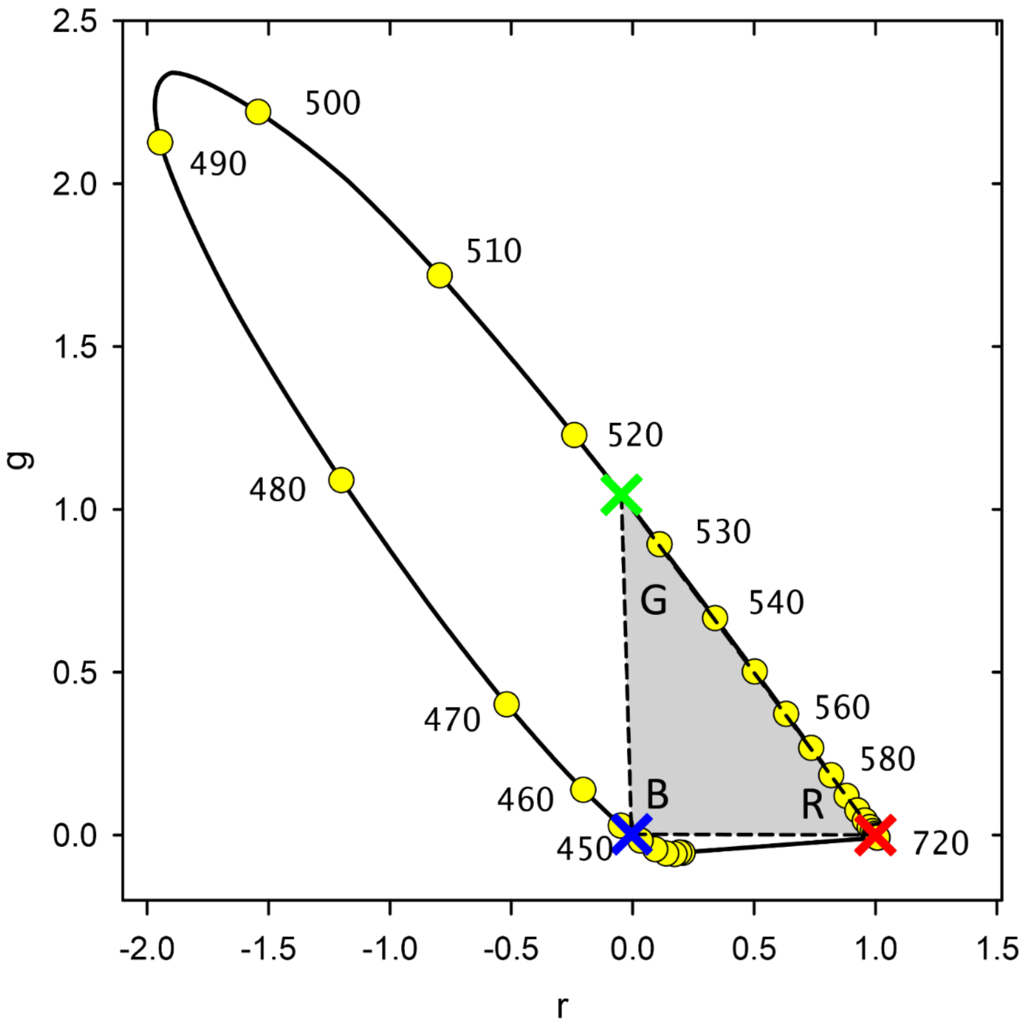
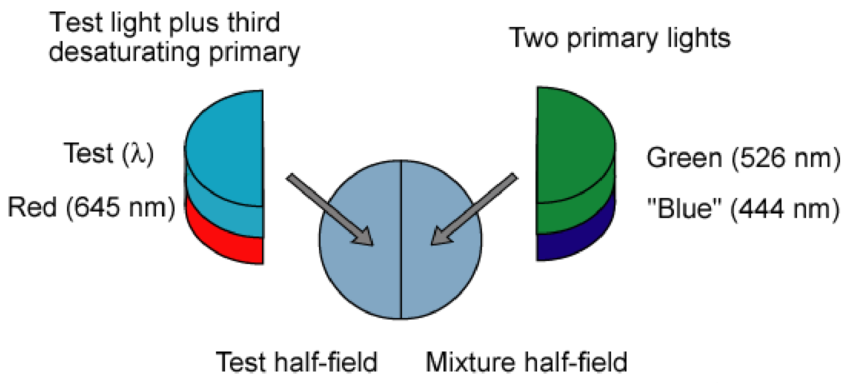
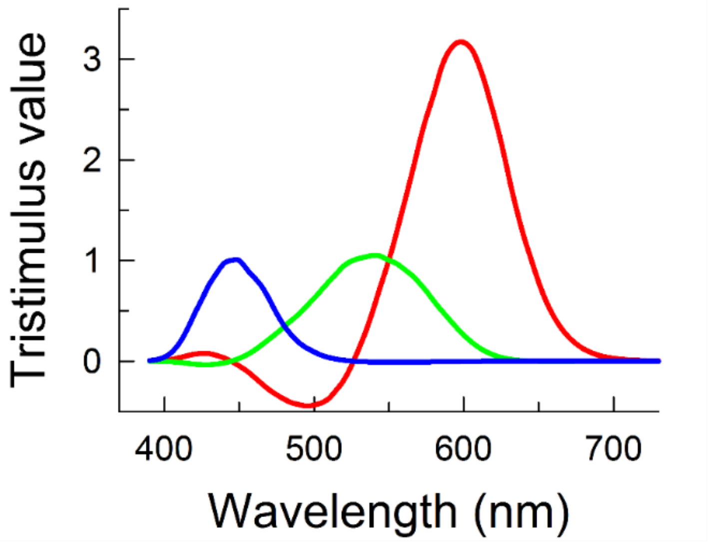
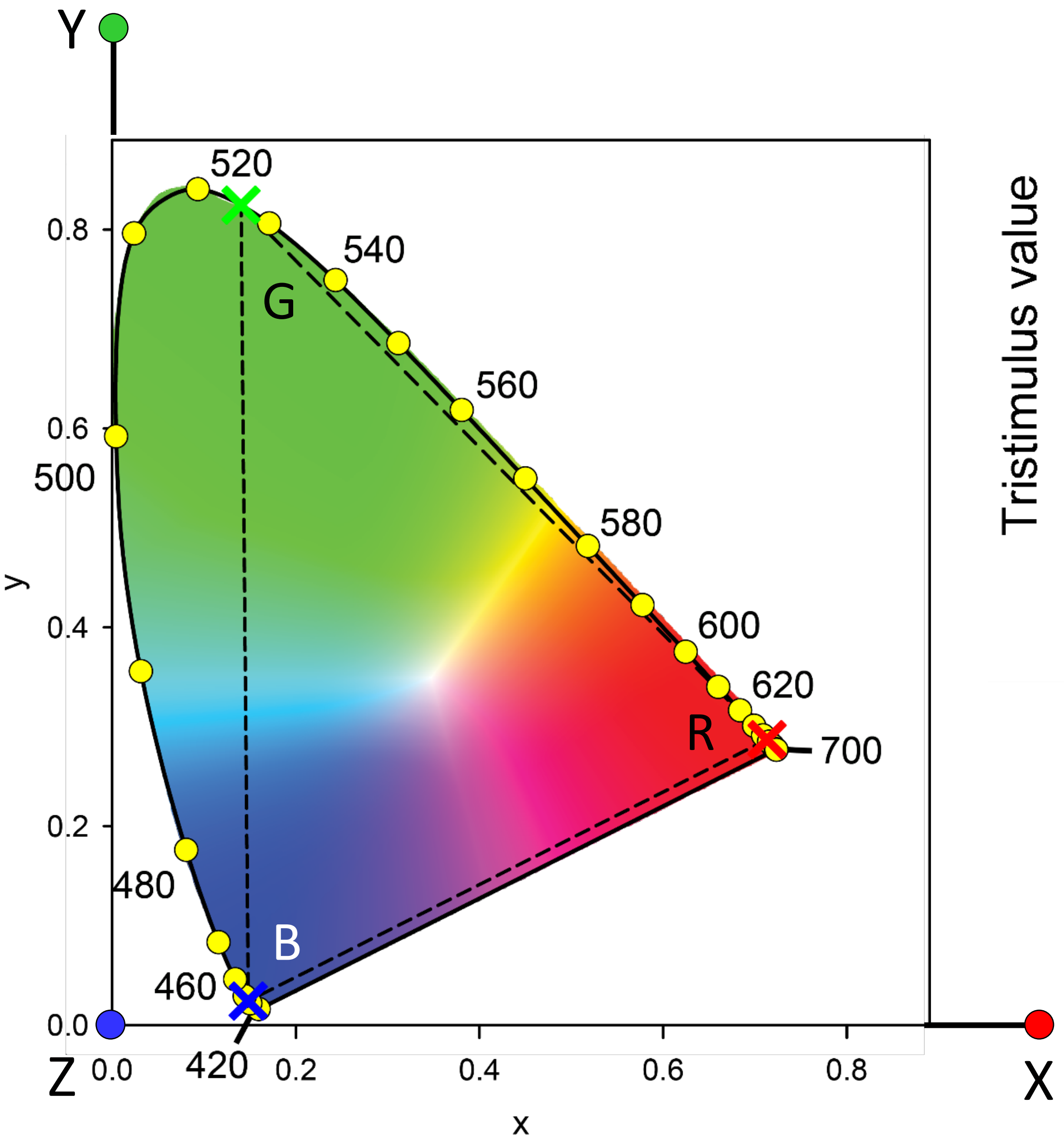
Stiles & Burch (1959) 10-deg *r,g* chromaticity coordinates



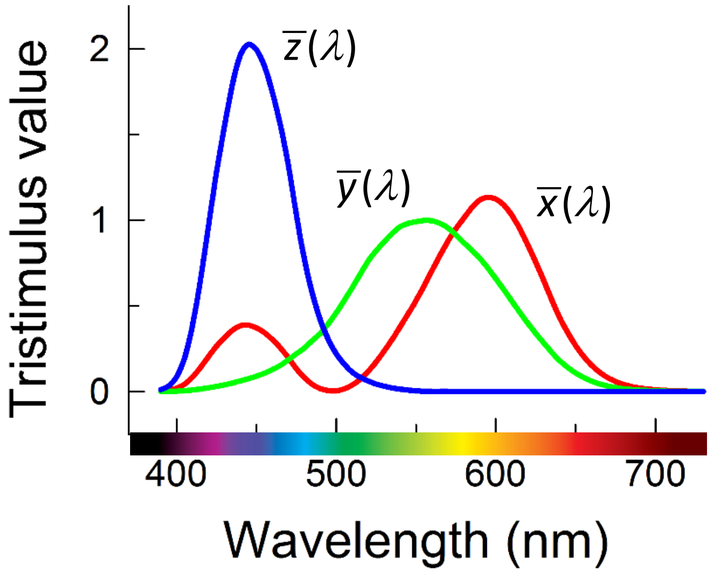
Why must there be negative primaries?







XYZ colour matching functions



All positive values

XYZ are imaginary (not physically-realizable) primaries