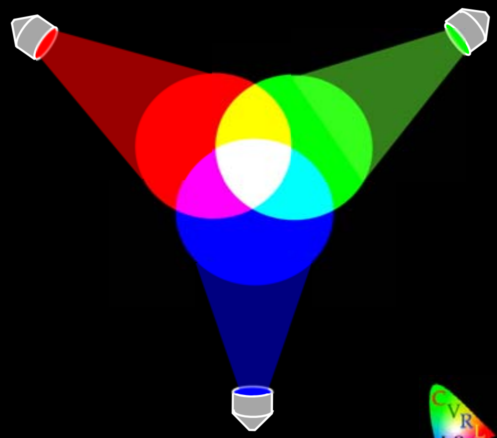
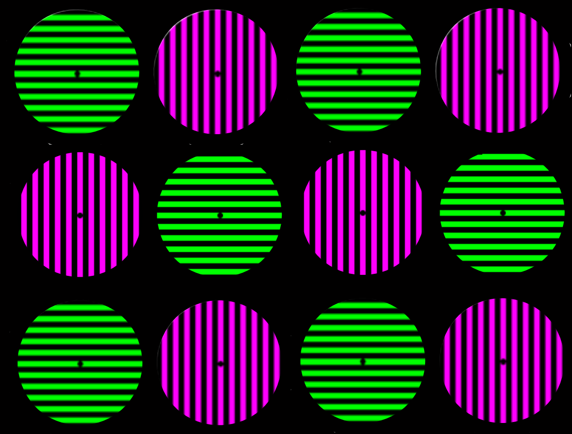
Colour Vision



MSc Neuroscience course

Andrew Stockman

McCollough effect adapting pattern



LONG-TERM "CONTINGENT" ADAPTATION

Akiyoshi Kitaoka

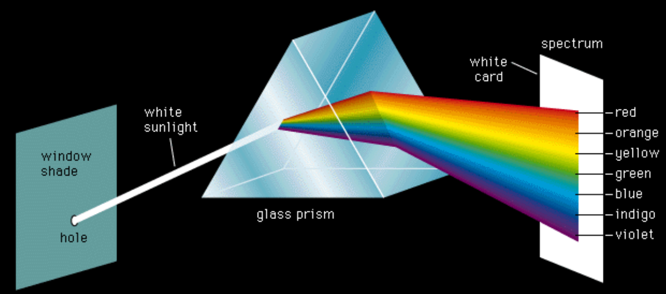
INTRODUCTION

Lecture notes at http://www.cvrl.org

Click on "MSc Neuroscience" in left menu.

Light

400 - 700 nm is important for vision



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How dependent are we on colour?

No colour…

Colour…

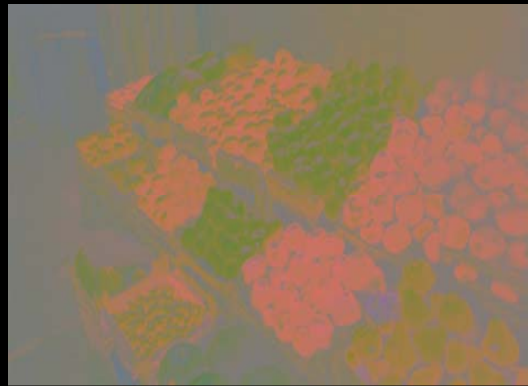
But just how important is colour?

Split the image into...

ACHROMATIC COMPONENTS

CHROMATIC COMPONENTS

CHROMATIC COMPONENTS



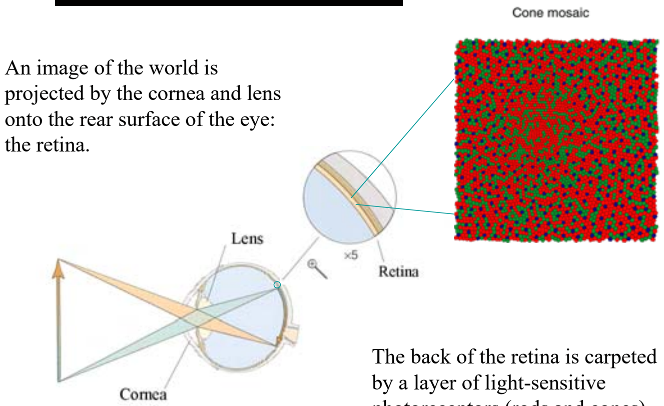
By itself chromatic information provides relatively limited information…

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

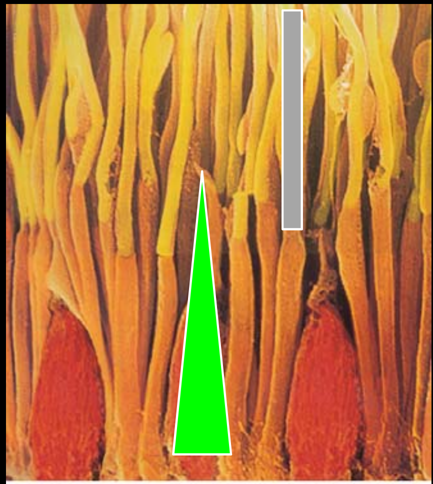
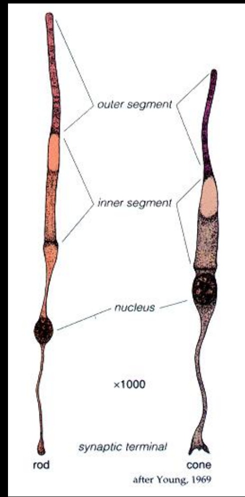


Fig1b. Scanning electron micrograph of the rods and cones of the primate retina. Image adapted from one by Ralph C. Eagle/Photo Researchers, Inc.

Webvision

Human photoreceptors



- Rods
  - Achromatic night vision
  - 1 type

Rod

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

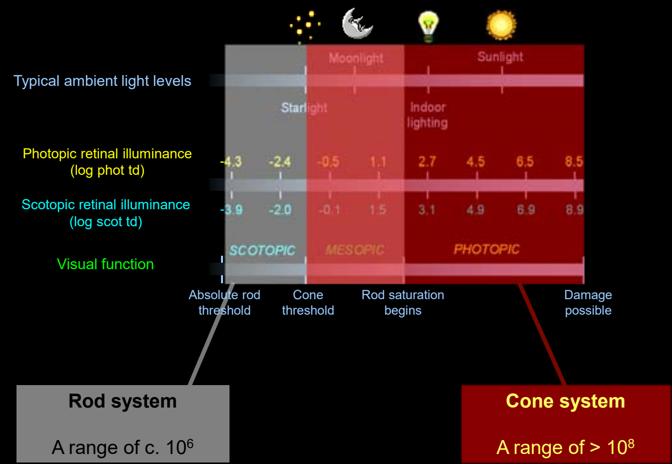
Long-wavelength-sensitive (L) or "red" cone

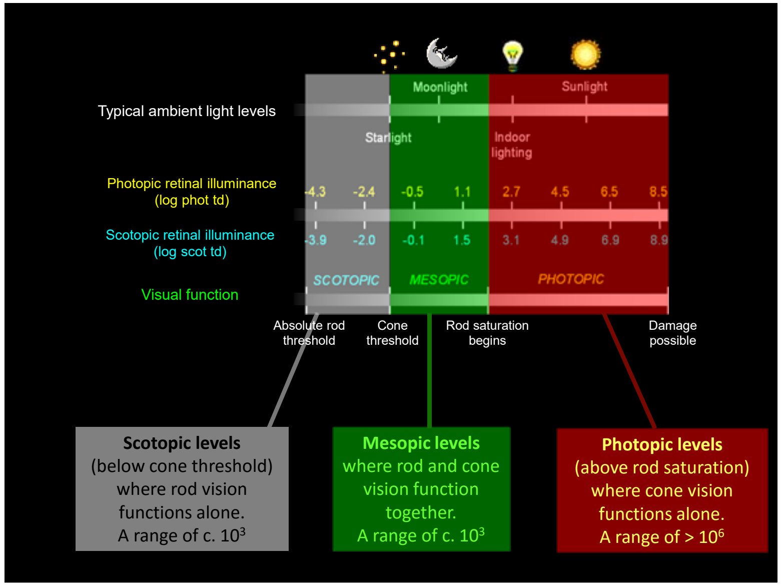
Middle-wavelength-sensitive (M) or "green" cone

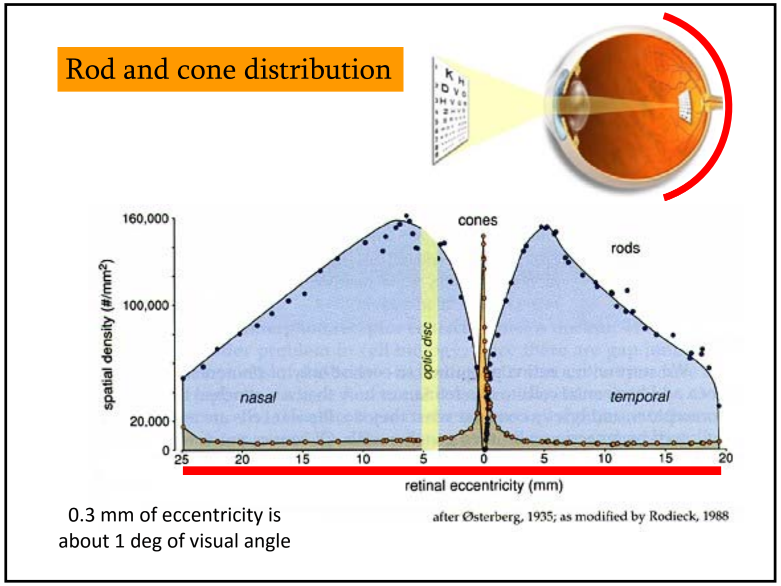
Short-wavelength-sensitive (S) or "blue" cone

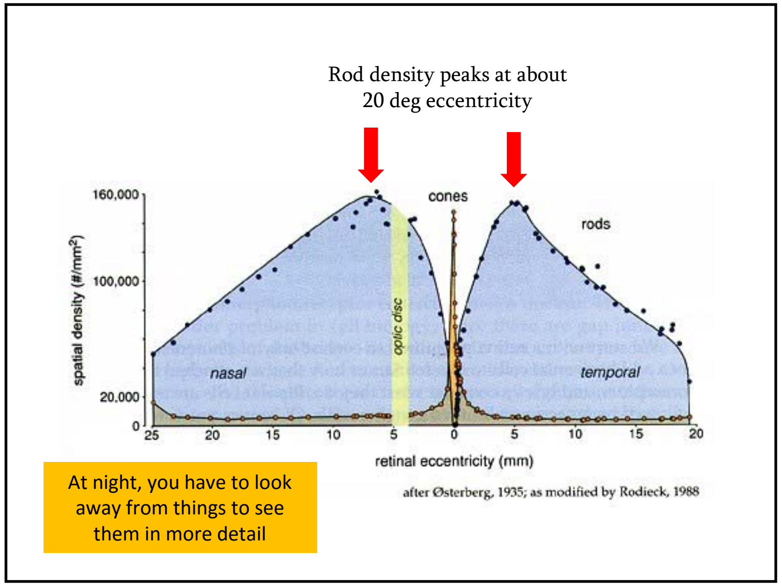
Why do we have rods and cones?

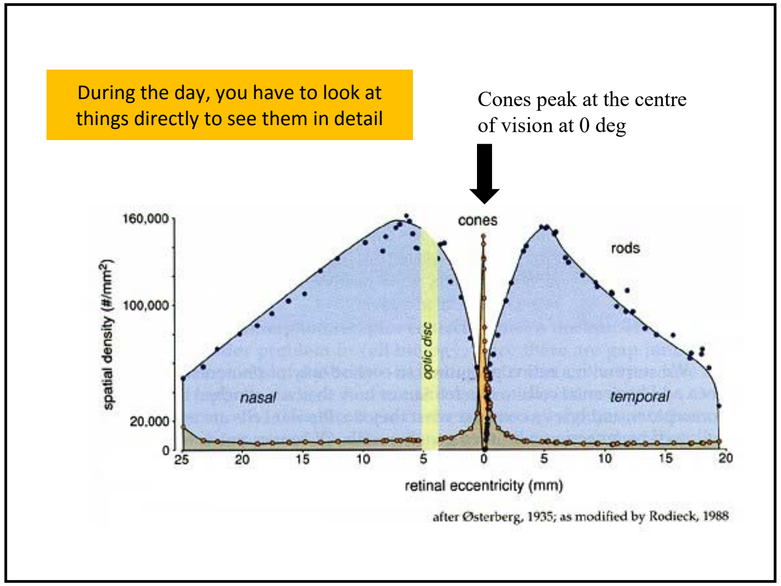
Rod and cone systems are optimized for different light levels




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
Visual function
SCOTOPIC
MESOPIC
PHOTOPIC
Absolute rod threshold
Cone threshold
Rod saturation begins
Damage possible
Scotopic levels (below cone threshold) where rod vision functions alone. A range of c. 10^3
Mesopic levels where rod and cone vision function together. A range of c. 10^3
Photopic levels (above rod saturation) where cone vision functions alone. A range of > 10^6


Rod and cone distribution
160,000
100,000
20,000
0
spatial density (#/mm²)
cones
rods
nasal
temporal
optic disc
25 20 15 10 5 0 5 10 15 20
retinal eccentricity (mm)
0.3 mm of eccentricity is about 1 deg of visual angle
after Østerberg, 1935; as modified by Rodieck, 1988

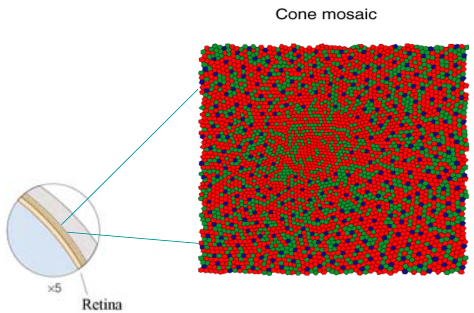

Rod density peaks at about 20 deg eccentricity
160,000
100,000
20,000
0
spatial density (#/mm²)
cones
rods
nasal
temporal
optic disc
25 20 15 10 5 0 5 10 15 20
retinal eccentricity (mm)
At night, you have to look away from things to see them in more detail
after Østerberg, 1935; as modified by Rodieck, 1988


During the day, you have to look at things directly to see them in detail
Cones peak at the centre of vision at 0 deg
160,000
100,000
20,000
0
spatial density (#/mm²)
cones
rods
nasal
temporal
optic disc
25 20 15 10 5 0 5 10 15 20
retinal eccentricity (mm)
after Østerberg, 1935; as modified by Rodieck, 1988

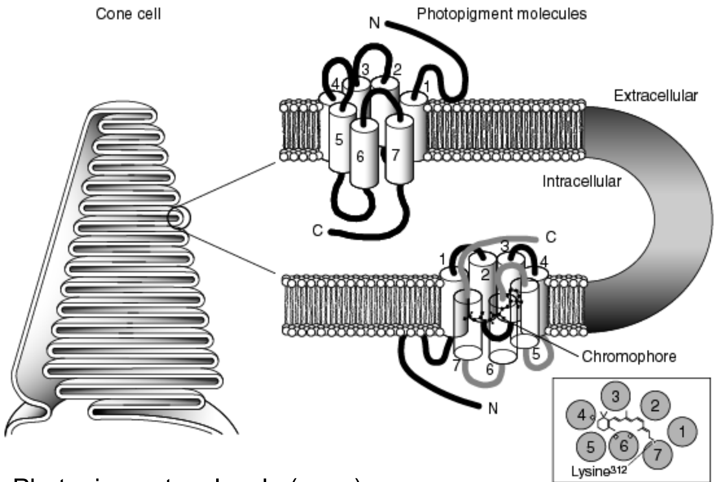
The human visual system
is a foveating system

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

Credit: Stuart Anstis, UCSD



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

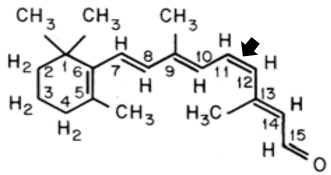


Photopigment molecule (cone)

From Sharpe, Stockman, Jägle & Nathans, 1999

Chromophore

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

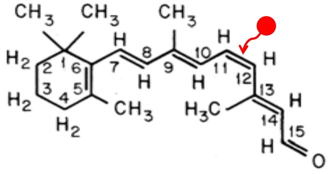


11-*cis* retinal.

The molecule is twisted at the 11th carbon.

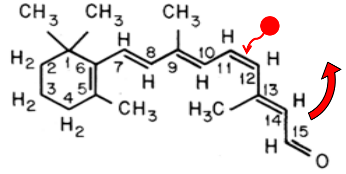
Chromophore

A photon is absorbed



Chromophore

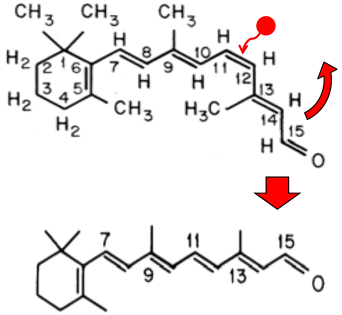
A photon is absorbed



the energy of which initiates a conformational change to…

Chromophore

A photon is absorbed



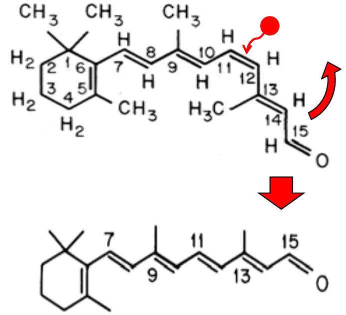
the energy of which initiates a conformational change to…

all-*trans* retinal

(side chains omitted for simplicity).

Chromophore

How can this process encode wavelength?

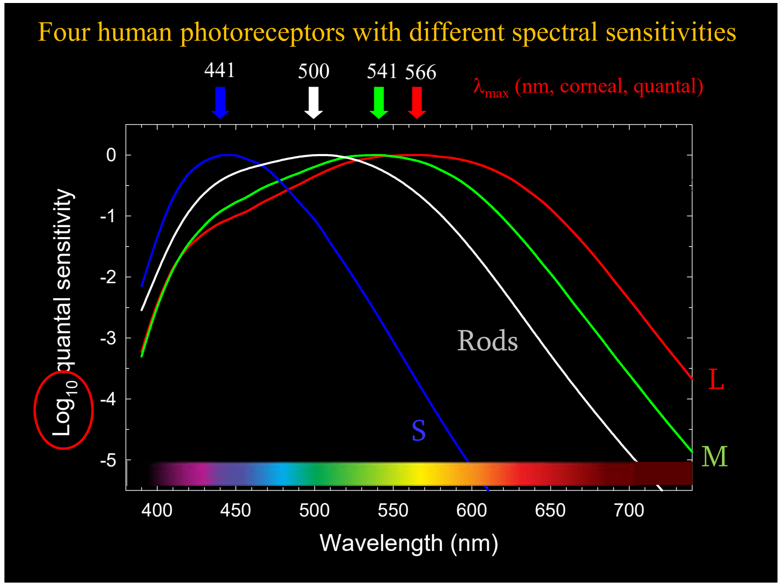


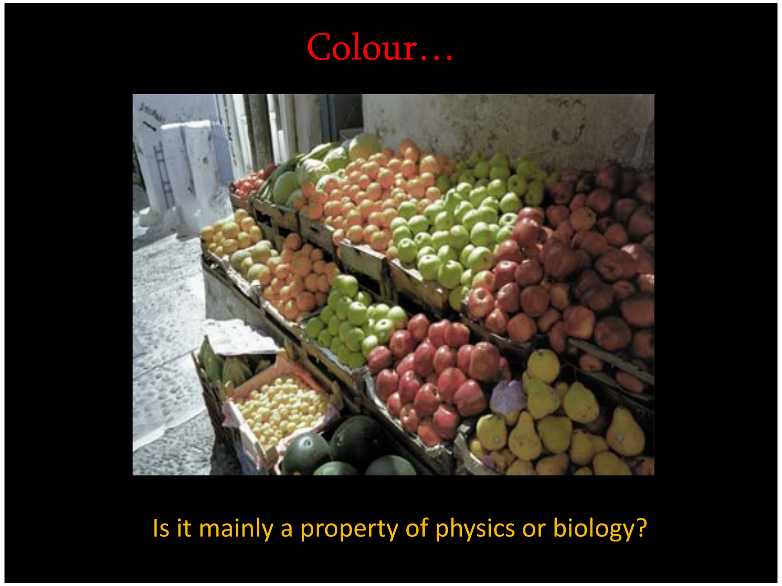
11-*cis* retinal.

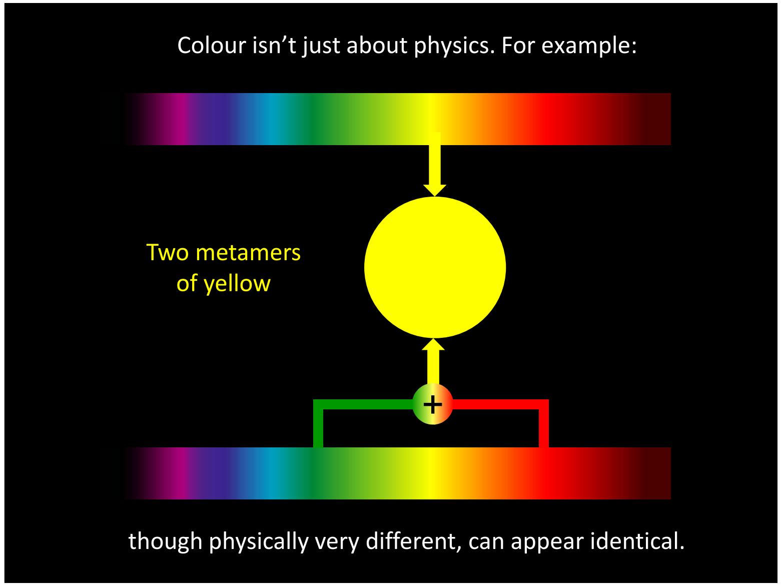
all-*trans* retinal.

Can it?

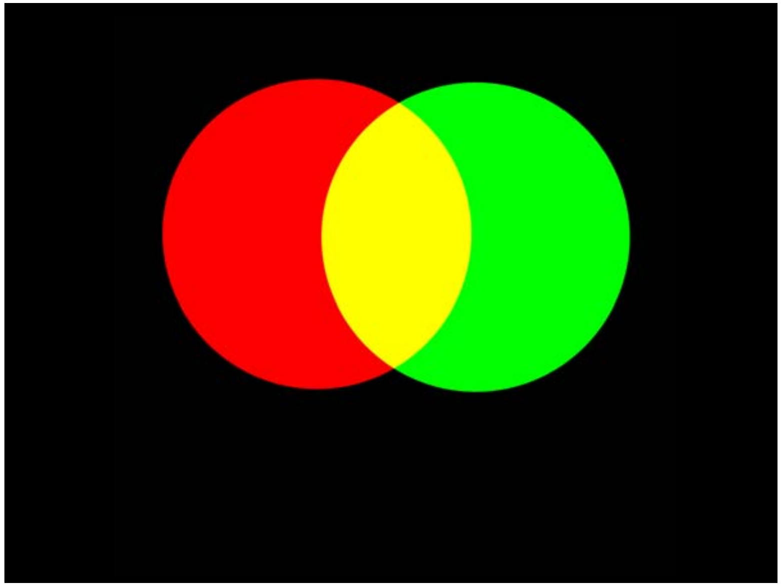

Vision at the photoreceptor stage is relatively simple because the output of each photoreceptor is:
UNIVARIANT
We'll come back to this…

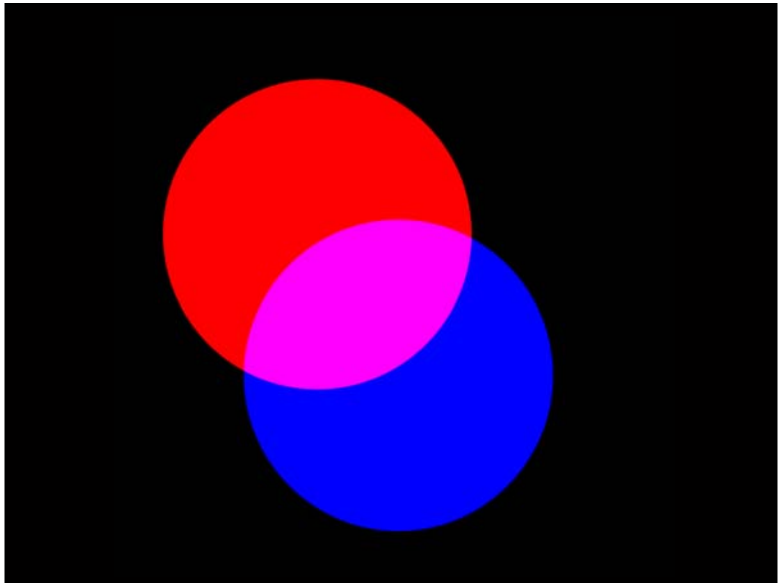

Four human photoreceptors with different spectral sensitivities
441
500
541
566
λmax (nm, corneal, quantal)
Log10 quantal sensitivity
0
-1
-2
-3
-4
-5
Rods
S
L
M
400
450
500
550
600
650
700
Wavelength (nm)

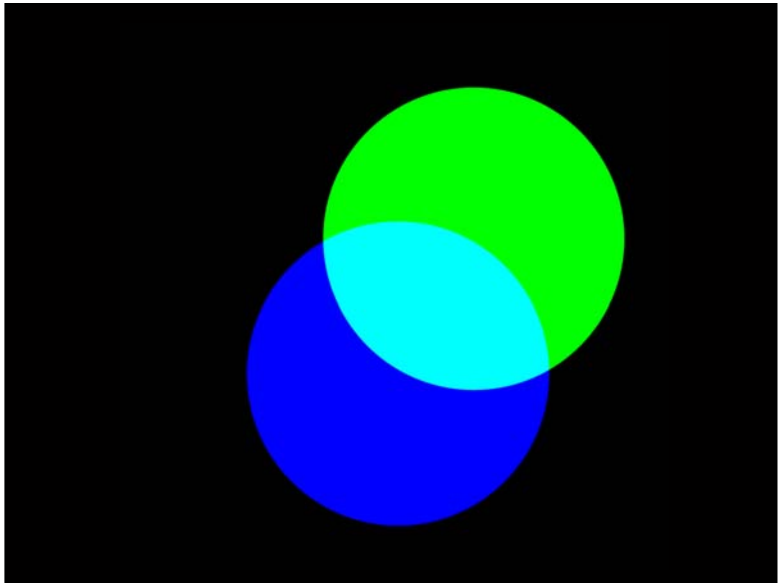

Colour…
Is it mainly a property of physics or biology?


Colour isn't just about physics. For example:
Two metamers of yellow
+
though physically very different, can appear identical.

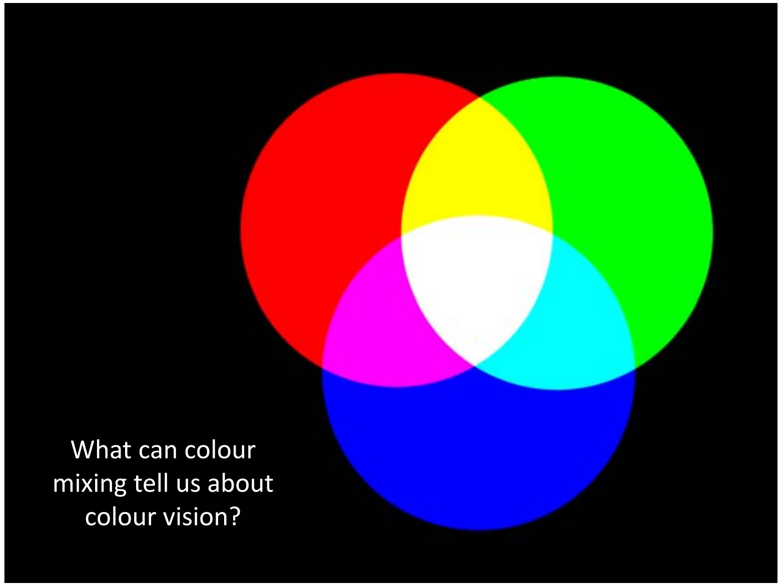
There are many other such
metamers or matches…

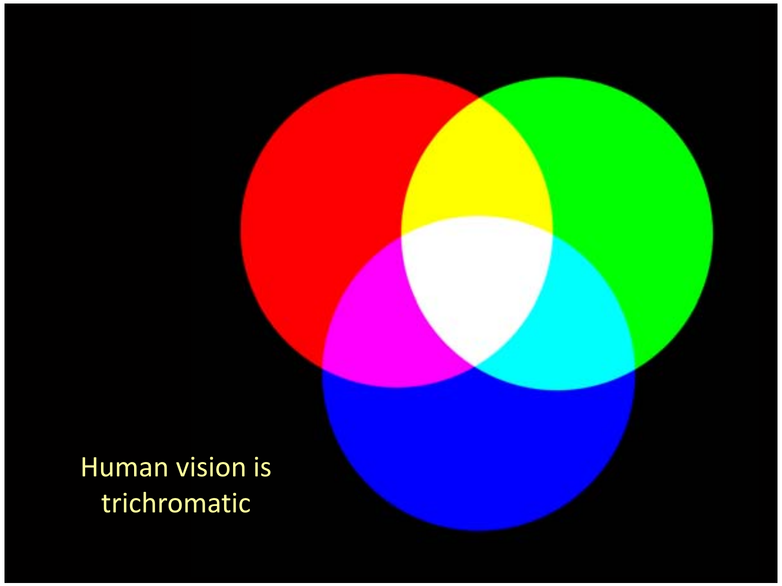


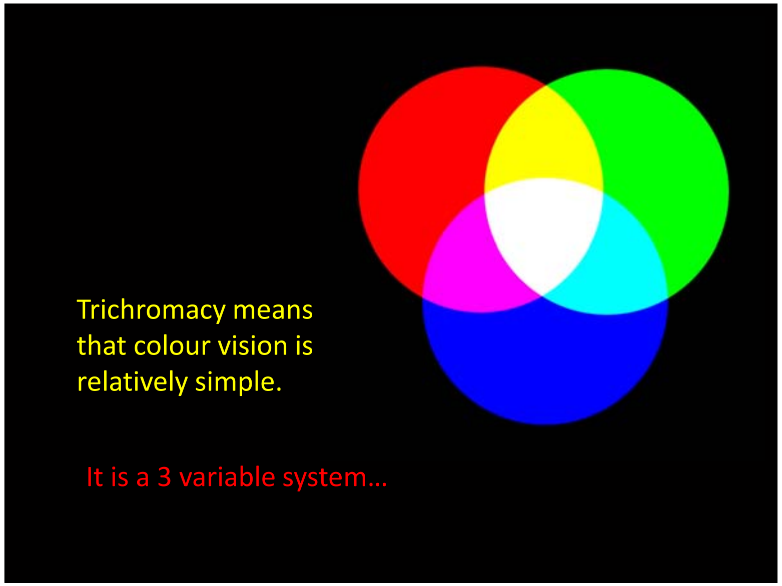


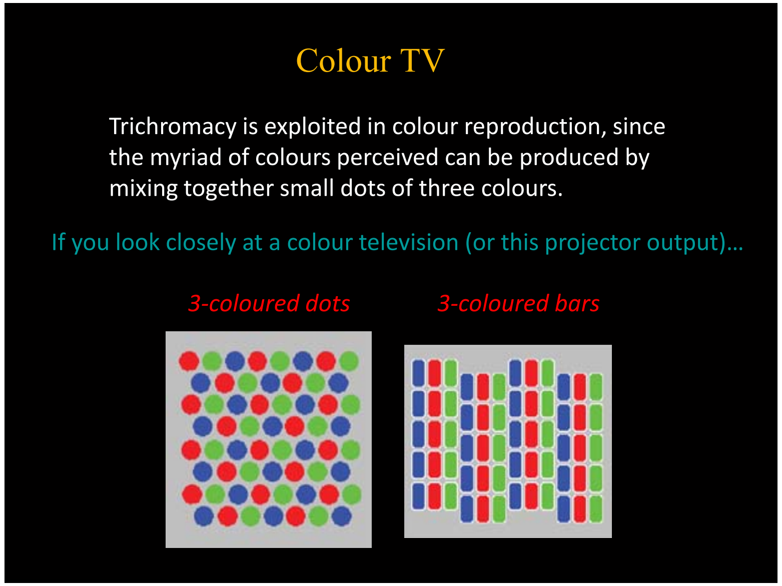


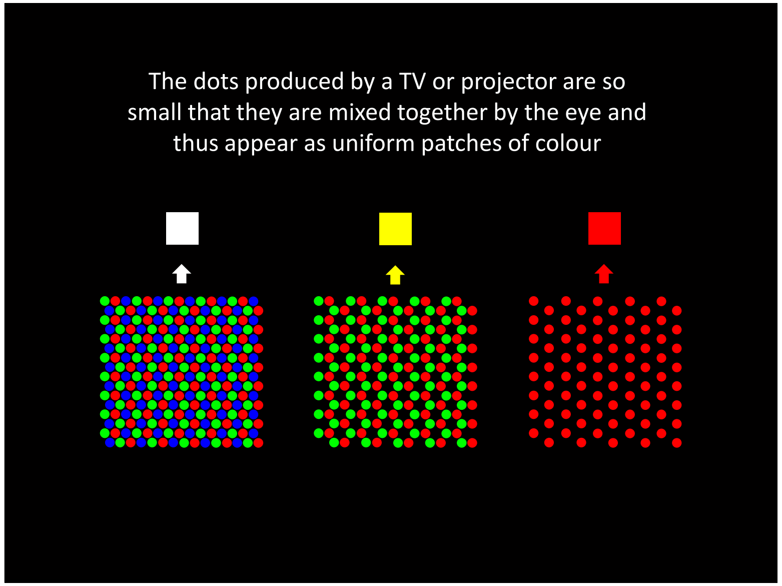

Colour mixing
Brightness
255
Brightness
255
Brightness
255

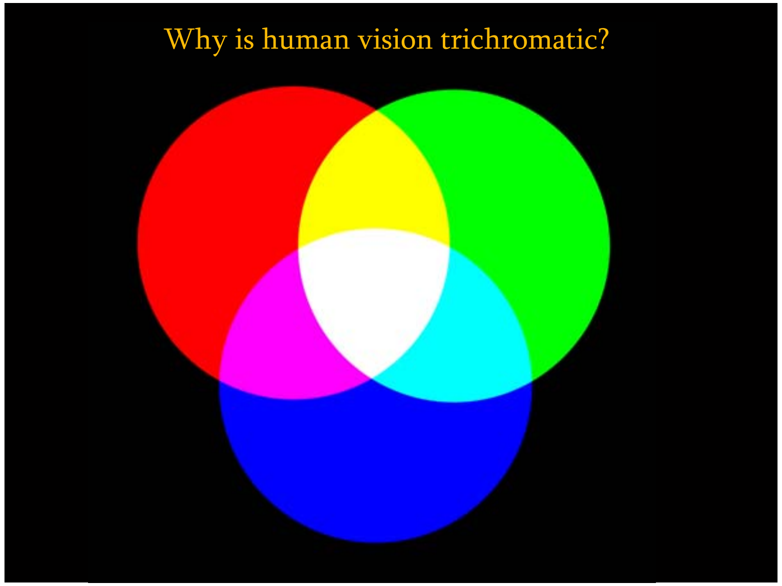

What can colour
mixing tell us about
colour vision?

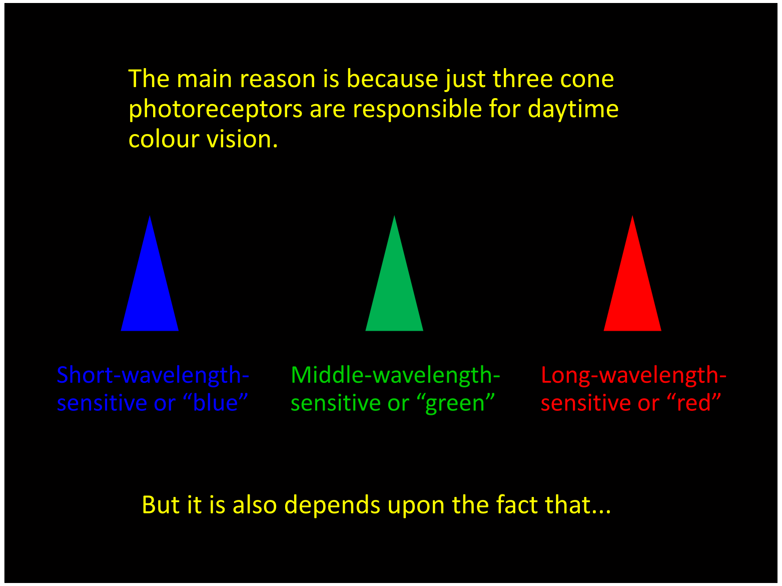

Human vision is
trichromatic

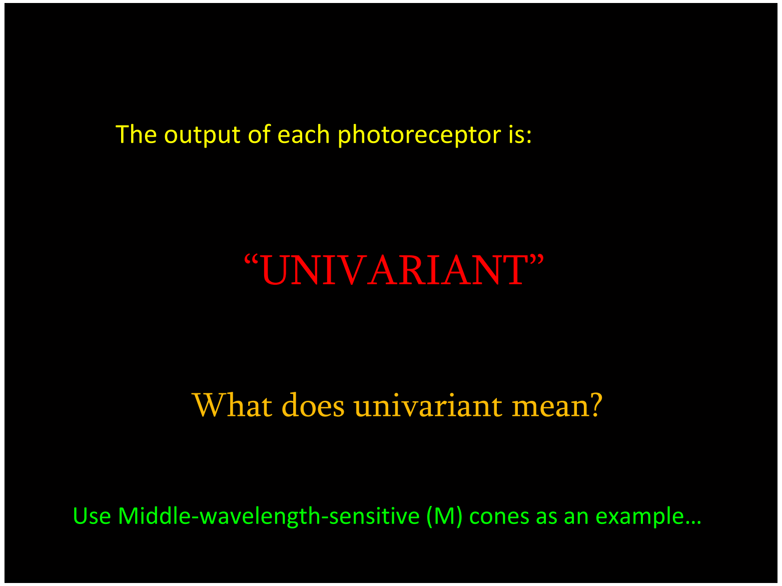

Trichromacy means
that colour vision is
relatively simple.
It is a 3 variable system…

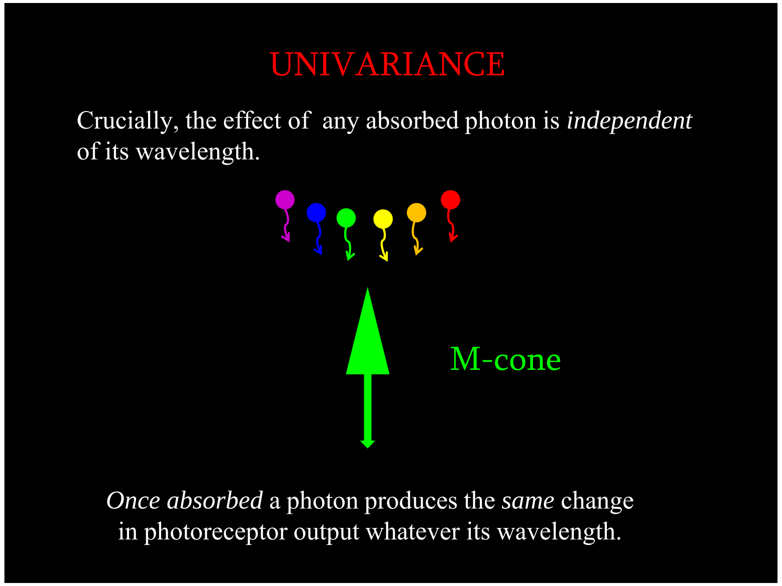

Colour TV
Trichromacy is exploited in colour reproduction, since the myriad of colours perceived can be produced by mixing together small dots of three colours.
If you look closely at a colour television (or this projector output)...
3-coloured dots
3-coloured bars

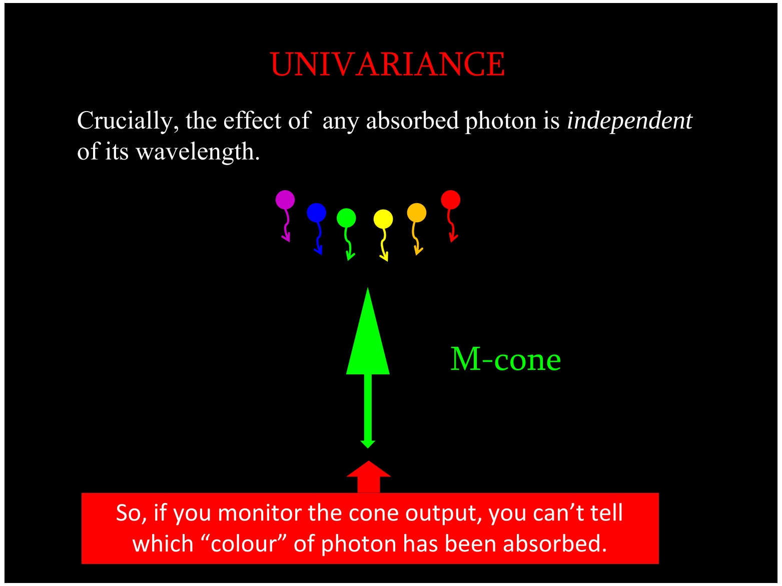

The dots produced by a TV or projector are so small that they are mixed together by the eye and thus appear as uniform patches of colour

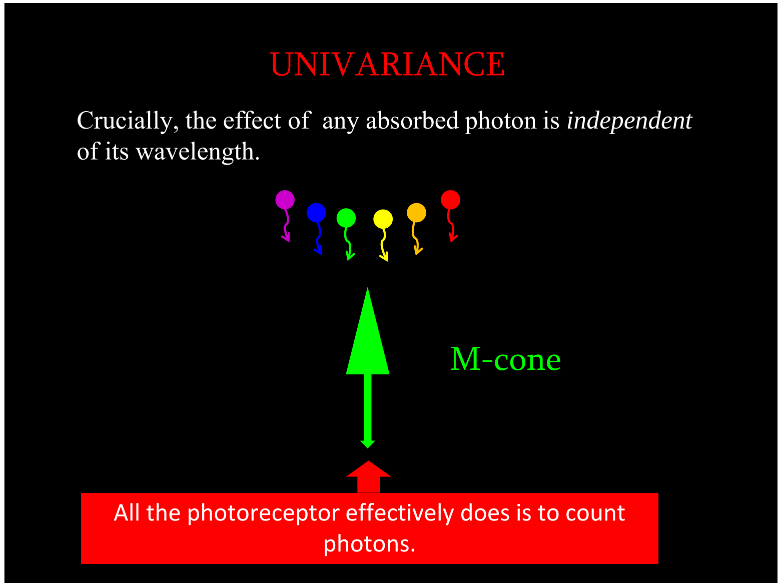

Why is human vision trichromatic?

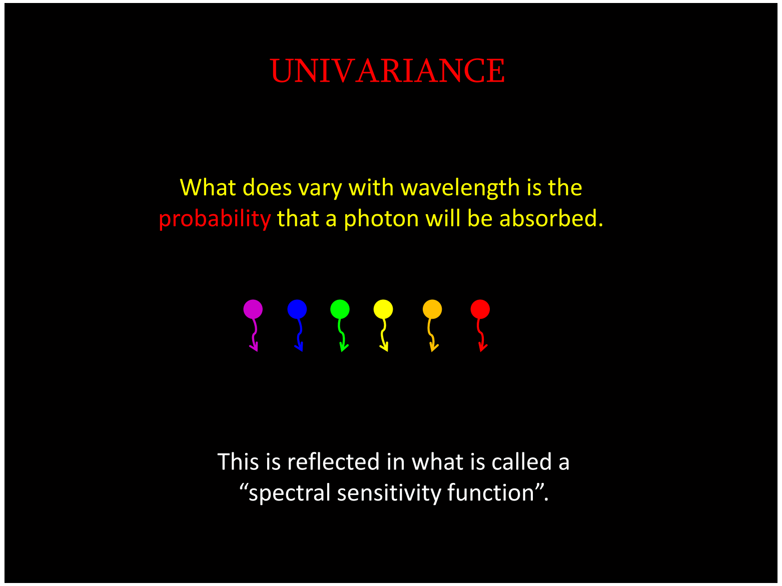

The main reason is because just three cone photoreceptors are responsible for daytime colour vision.
Short-wavelength-sensitive or "blue"
Middle-wavelength-sensitive or "green"
Long-wavelength-sensitive or "red"
But it is also depends upon the fact that...

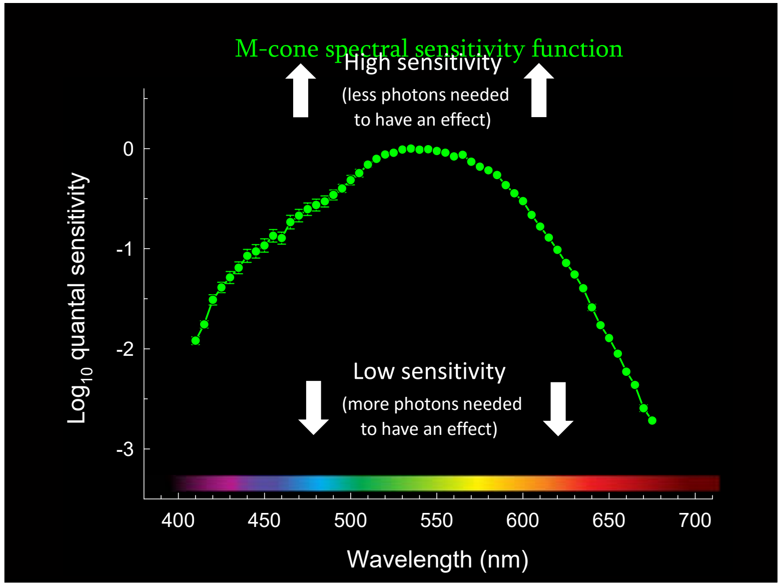

The output of each photoreceptor is:
"UNIVARIANT"
What does univariant mean?
Use Middle-wavelength-sensitive (M) cones as an example...

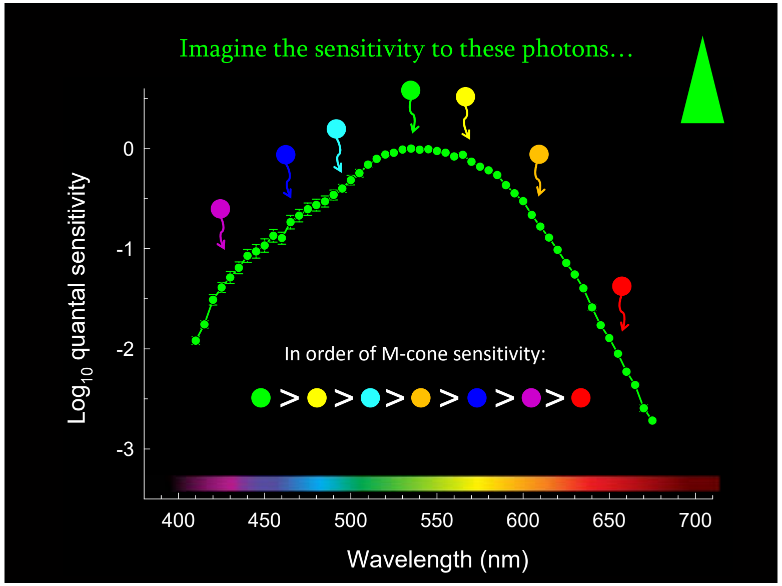

UNIVARIANCE
Crucially, the effect of any absorbed photon is *independent* of its wavelength.
M-cone
Once absorbed a photon produces the *same* change in photoreceptor output whatever its wavelength.

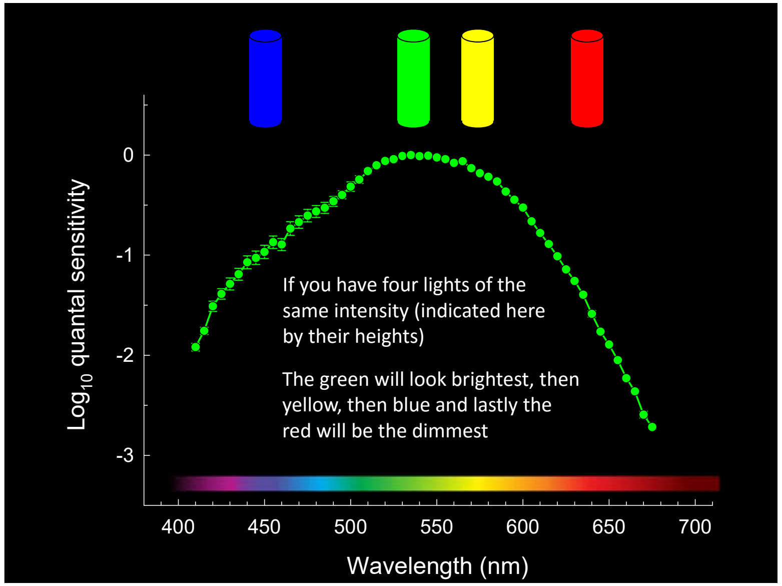

UNIVARIANCE
Crucially, the effect of any absorbed photon is *independent* of its wavelength.
M-cone
So, if you monitor the cone output, you can't tell which "colour" of photon has been absorbed.

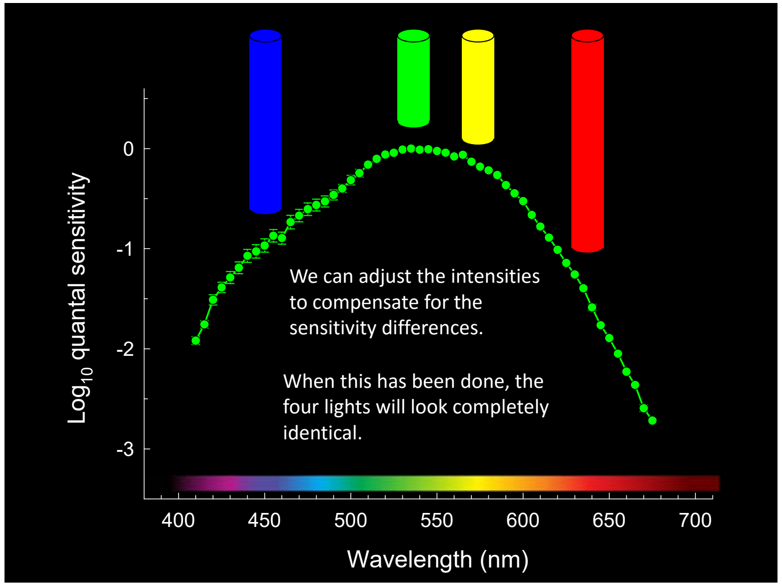

UNIVARIANCE
Crucially, the effect of any absorbed photon is *independent* of its wavelength.
M-cone
All the photoreceptor effectively does is to count photons.

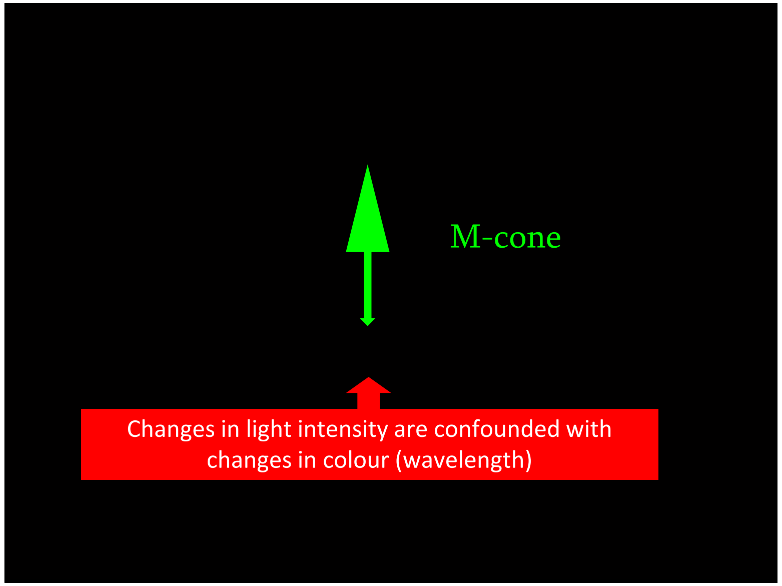

UNIVARIANCE
What does vary with wavelength is the
probability that a photon will be absorbed.
This is reflected in what is called a
"spectral sensitivity function".

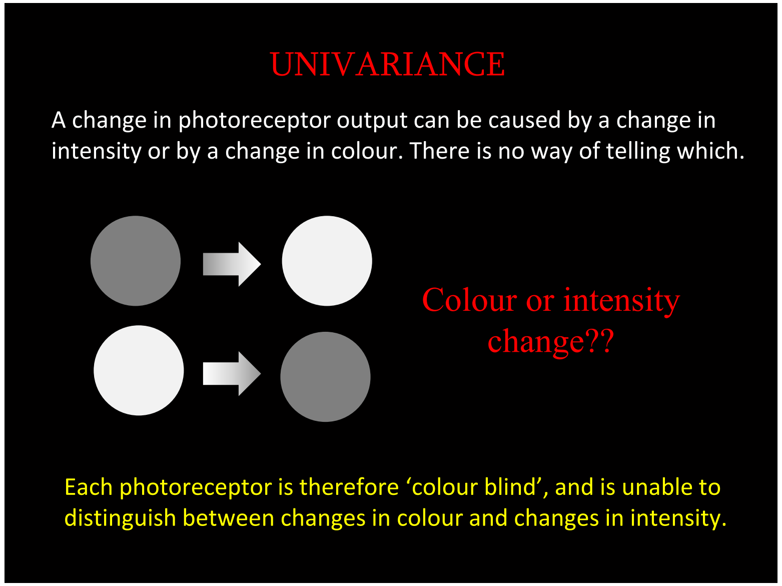

M-cone spectral sensitivity function
High sensitivity
(less photons needed
to have an effect)
Low sensitivity
(more photons needed
to have an effect)
Log10 quantal sensitivity
0
-1
-2
-3
400
450
500
550
600
650
700
Wavelength (nm)

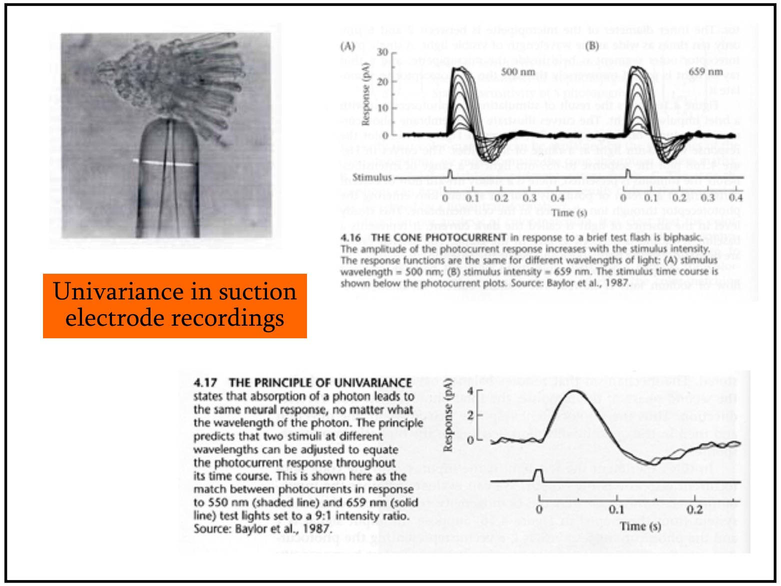

Imagine the sensitivity to these photons…
In order of M-cone sensitivity:
> > > > > >
Log10 quantal sensitivity
0
-1
-2
-3
400
450
500
550
600
650
700
Wavelength (nm)


If you have four lights of the
same intensity (indicated here
by their heights)
The green will look brightest, then
yellow, then blue and lastly 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)
We can adjust the intensities to compensate for the sensitivity differences.
When this has been done, the four lights will look completely identical.


M-cone
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
(A)
(B)
Response (pA)
500 nm
659 nm
Stimulus
Time (s)
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.
Response (pA)
Time (s)

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 three cone photoreceptors, our colour vision is trichromatic…

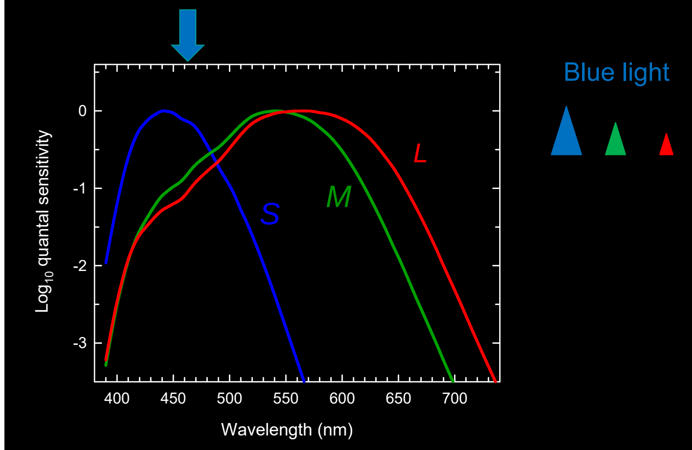
So, if each photoreceptor is colour-blind, how do we see colour?

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

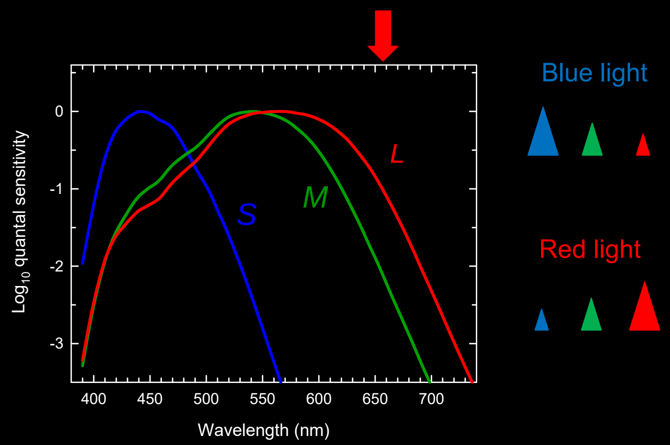
Trichromacy actually means our colour vision is limited

- 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.

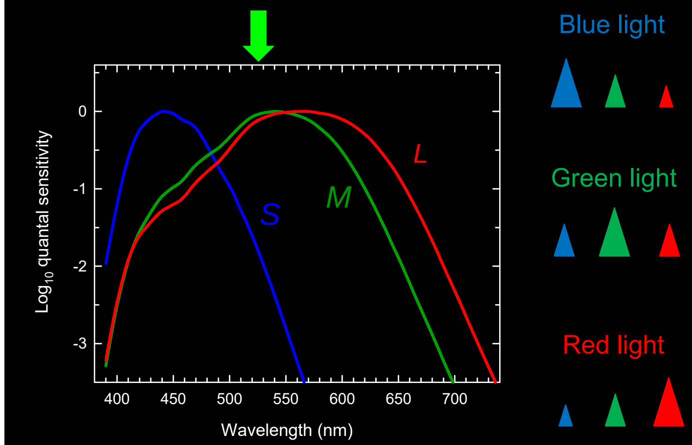
Colour is encoded by the relative cone outputs



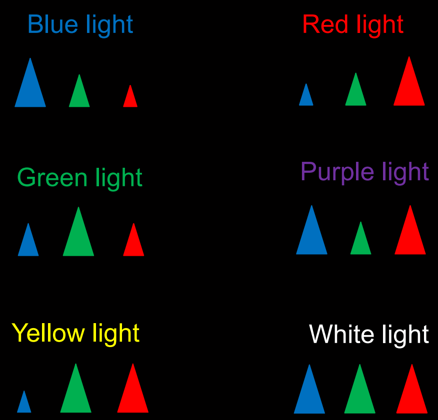
Colour is encoded by the relative cone outputs



Colour is encoded by the relative cone outputs

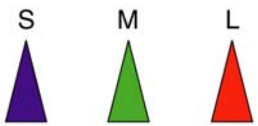


Colour is encoded by the relative cone outputs

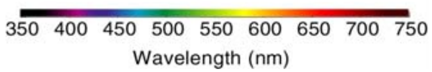


DETERMINING CONE SPECTRAL SENSITIVITIES

In other words…

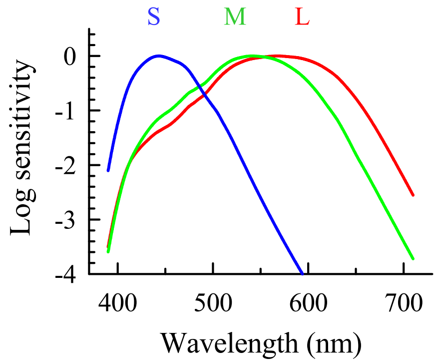


How can we measure how the sensitivity of each cone type varies with wavelength (or spectral colour)?



The cone spectral sensitivities overlap extensively throughout the spectrum.

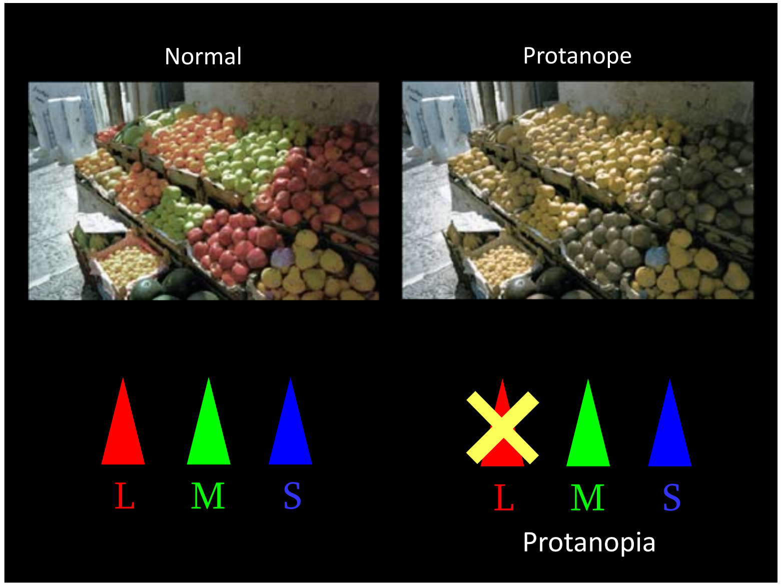
Consequently, we have to use special subjects or special conditions to be able isolate the the response of a single cone type.

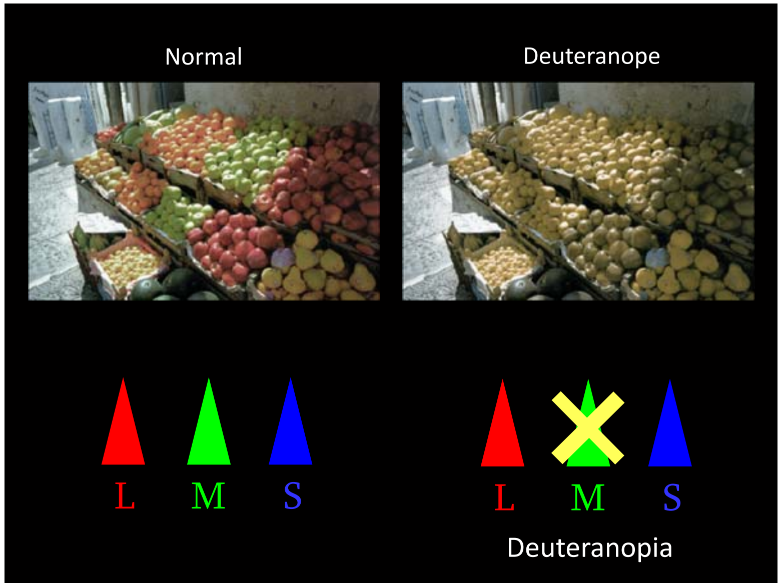


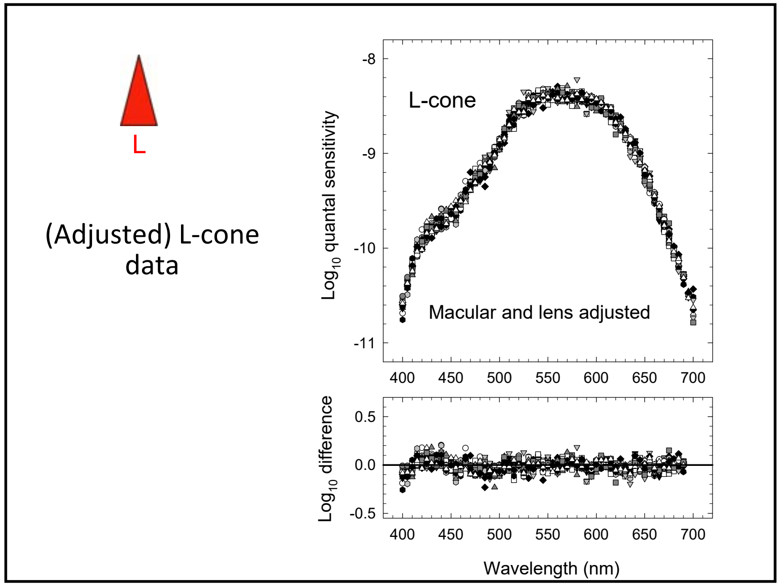
M- and L-cone measurements

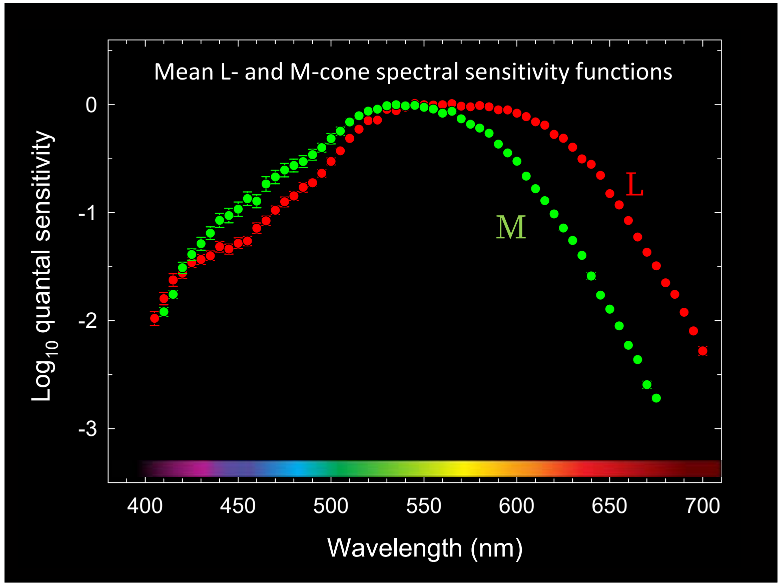
Use two special types of subjects:

- Deuteranopes
- Protanopes





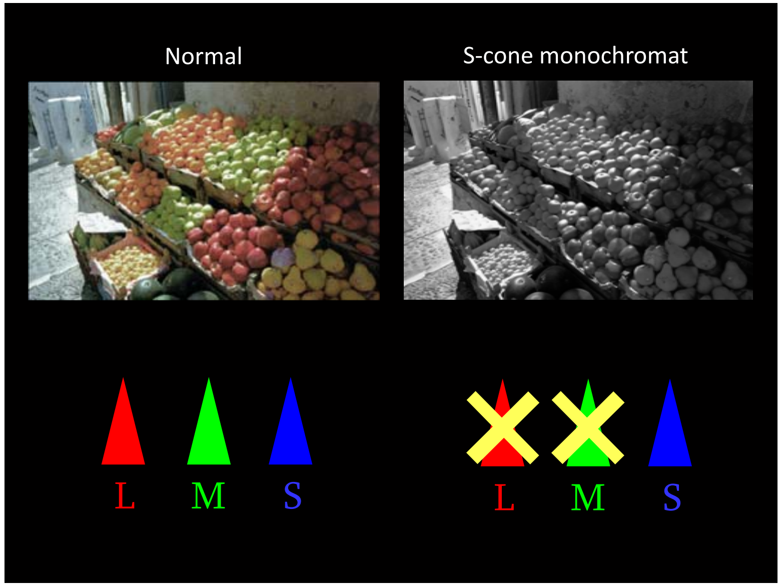


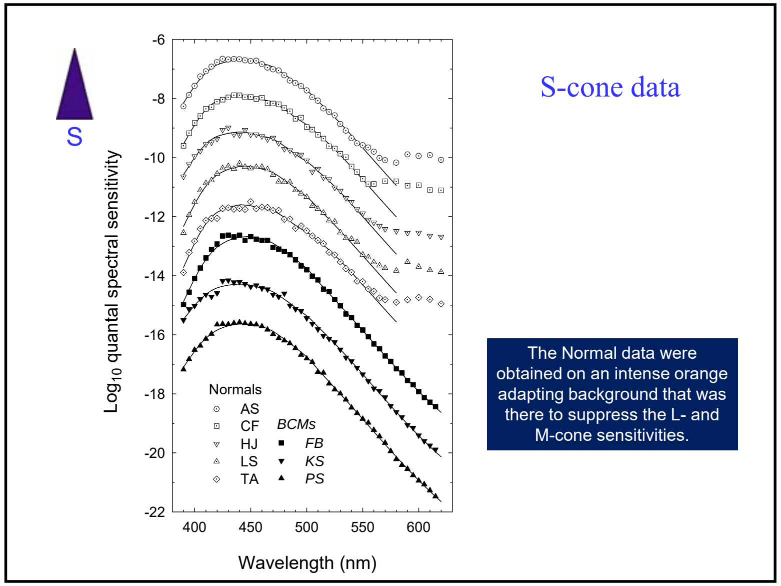


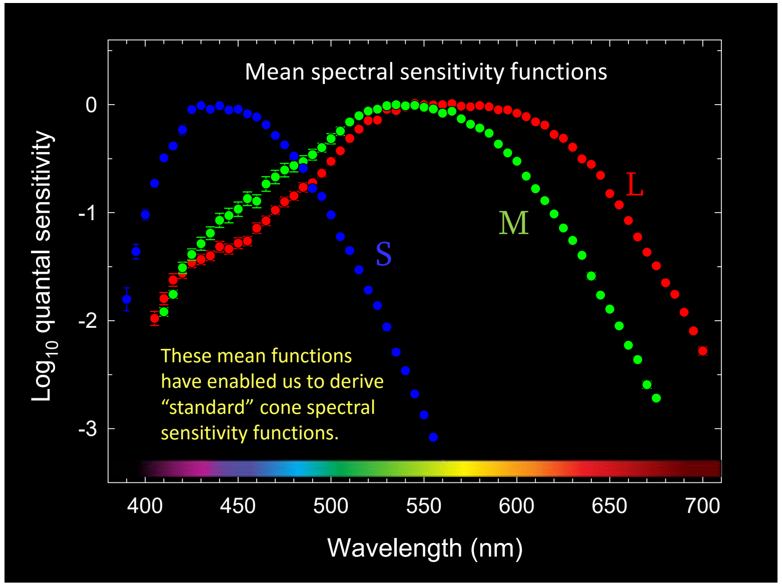
S-cone measurements

Two types of subjects:

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

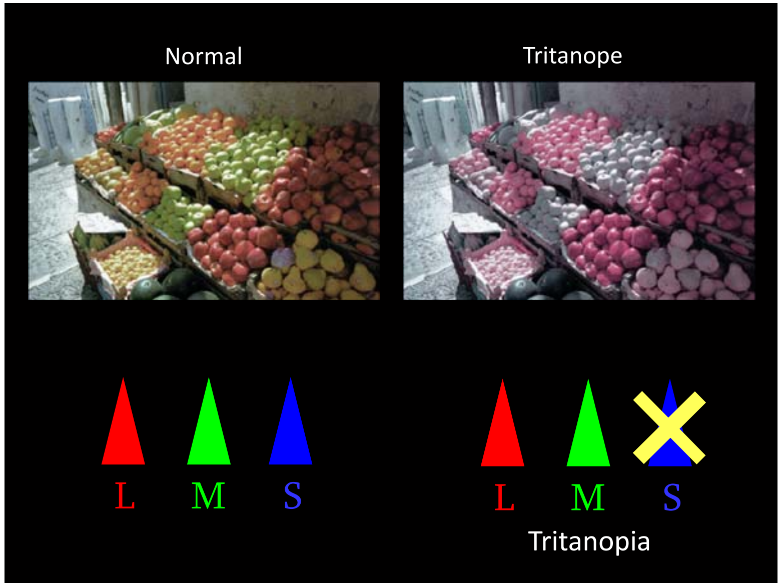


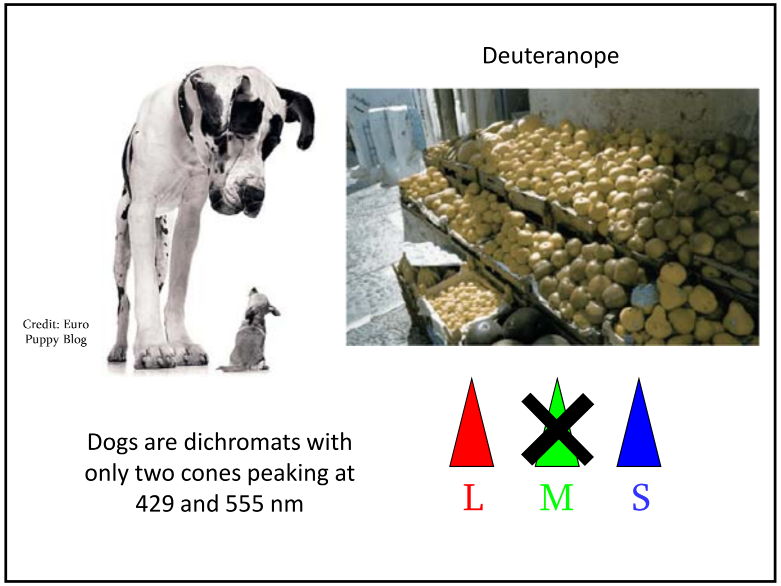




Why study spectral sensitivities?

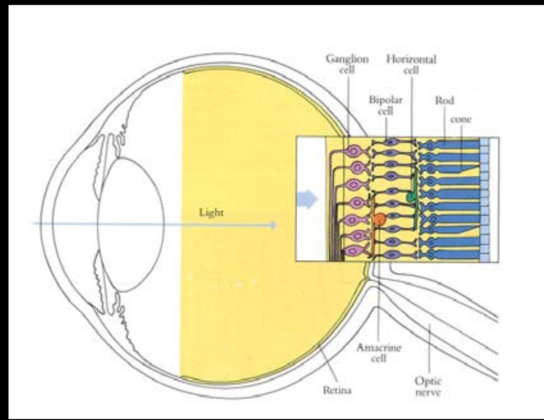
- A knowledge of the spectral sensitivities of the cones is important because it allows us to accurately and simply specify colours and to predict colour matches—for both colour normal and colour deficient people (and to understand the variability between individuals).
- Practical implications for colour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





POSTRECEPTORAL COLOUR VISION

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



Colour phenomenology

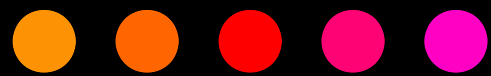
Can provide clues about how colours are processed after the photoreceptors…

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

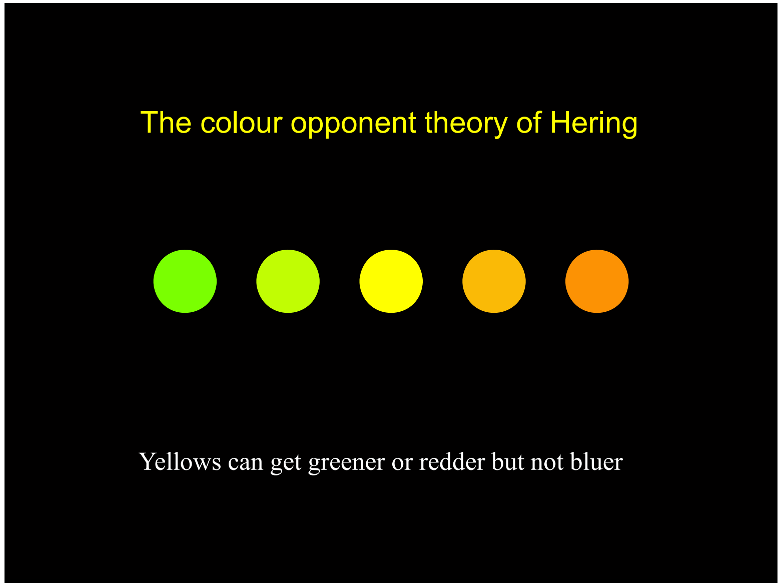
Reddish-greens? Reddish-yellows? Bluish-reds? Bluish-yellow? ??

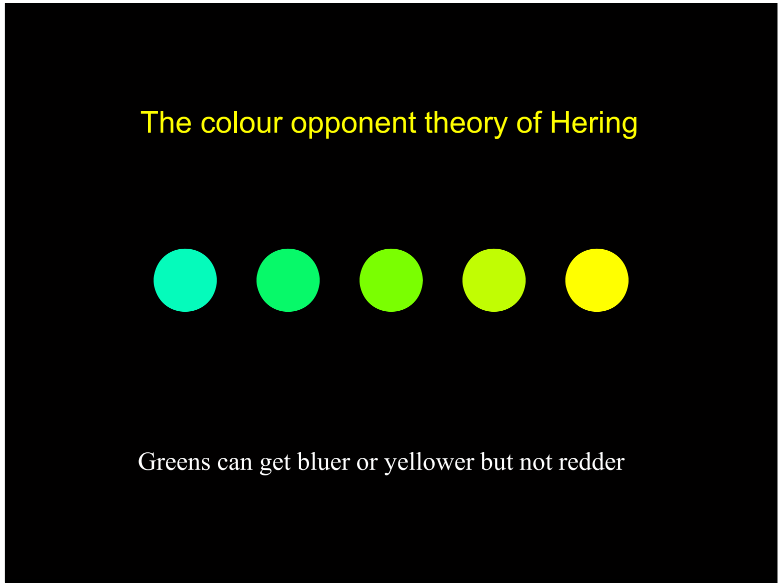
WHY?

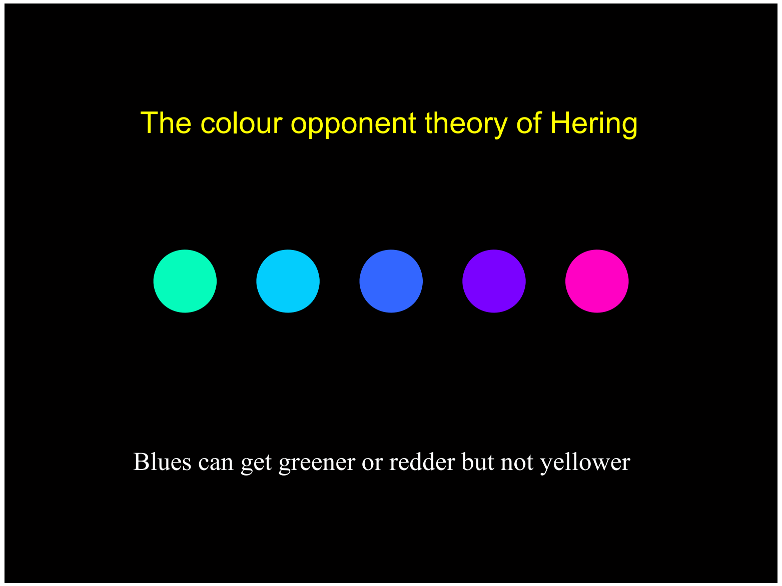
The colour opponent theory of Hering

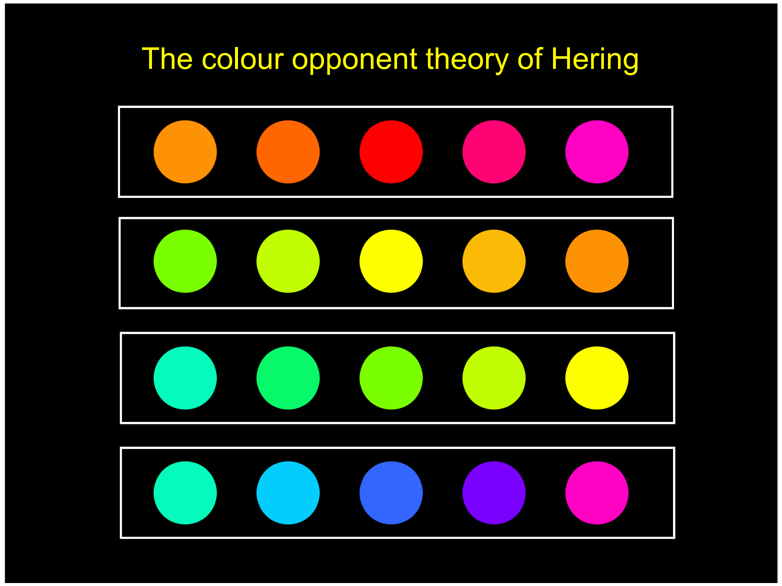


Reds can get bluer or yellower but not greener


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

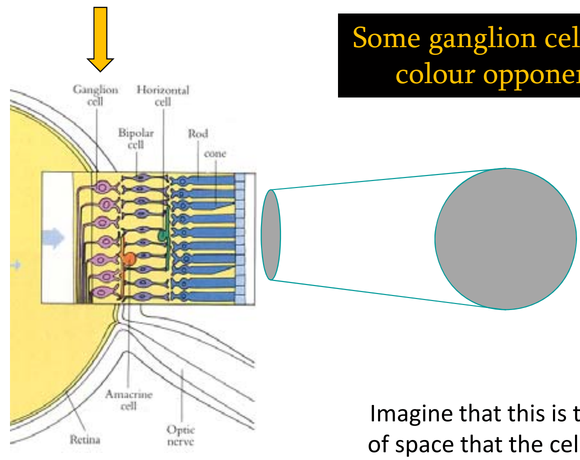
The colour opponent theory of Hering

is opposed to R-G

is opposed to Y-B

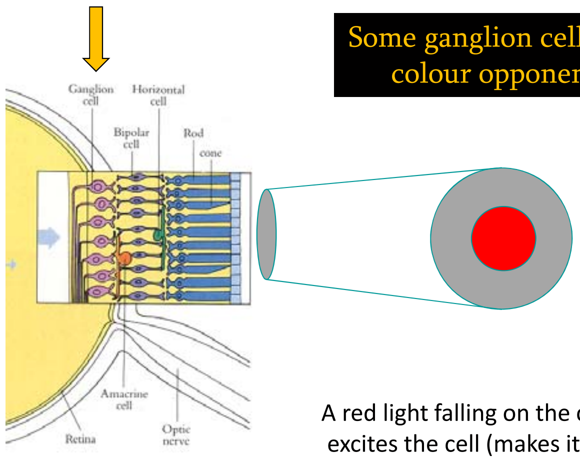
How might this be related to visual processing after the cones?

Some ganglion cells are colour opponent



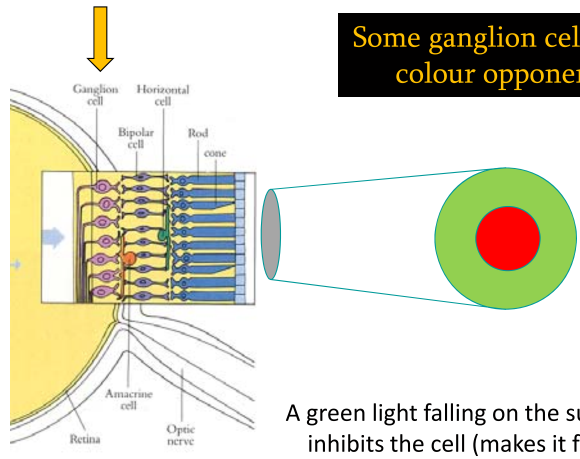
Imagine that this is the region of space that the cell “sees” in the external world

Some ganglion cells are colour opponent



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

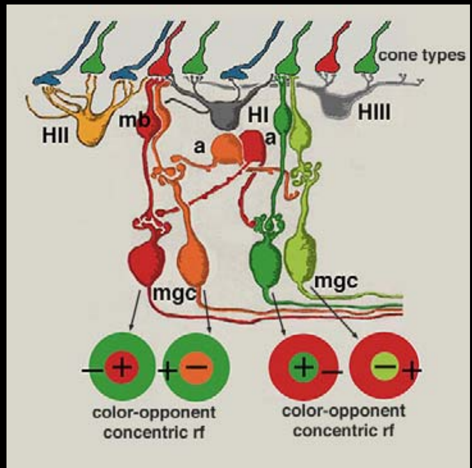
Some ganglion cells are colour opponent



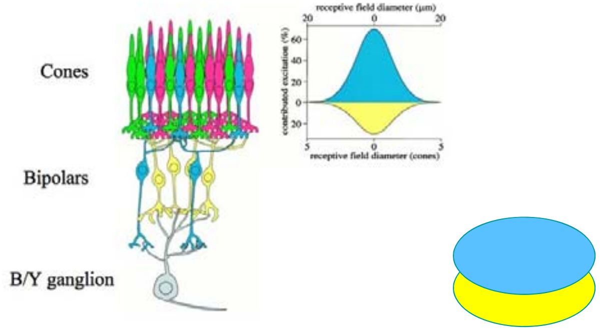
A green light falling on the surround area inhibits the cell (makes it fire slower)

Red-green colour opponency

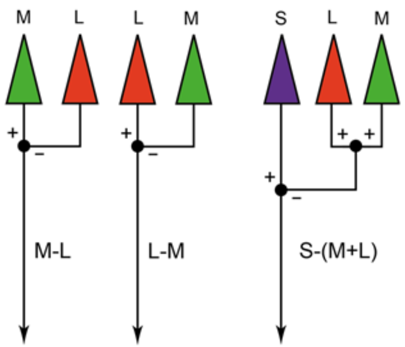
Four variants



Blue/yellow pathway

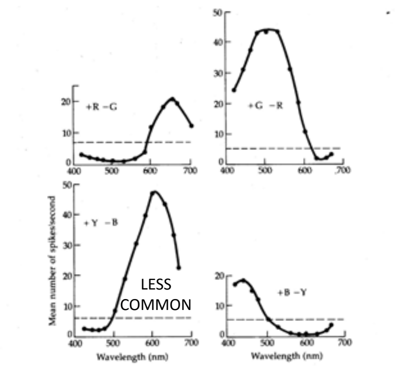


Source: David Heeger

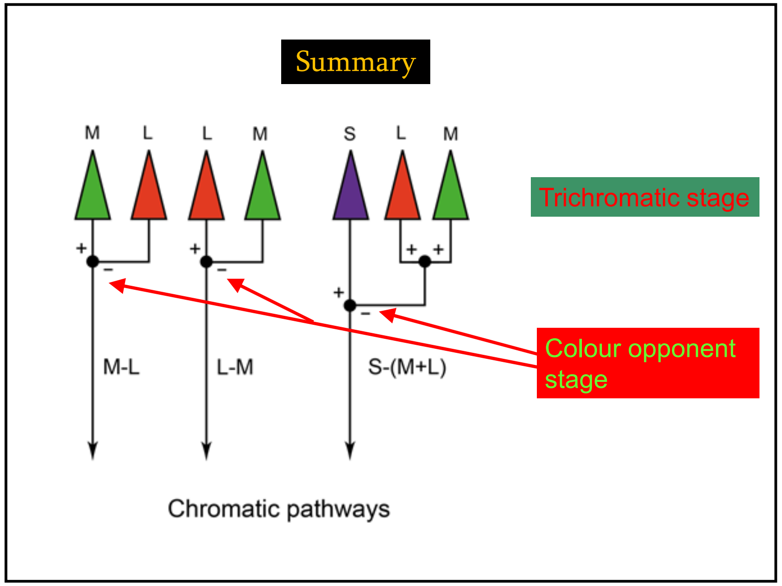


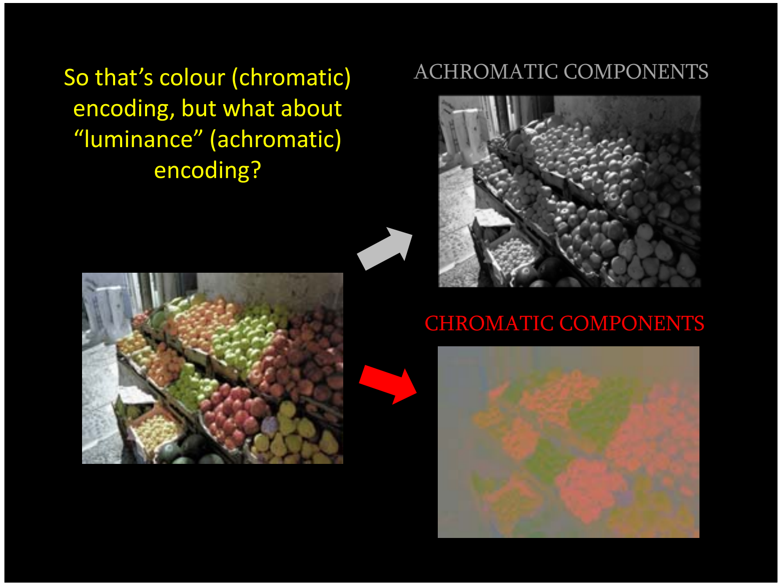
Chromatic pathways

LGN cell responses



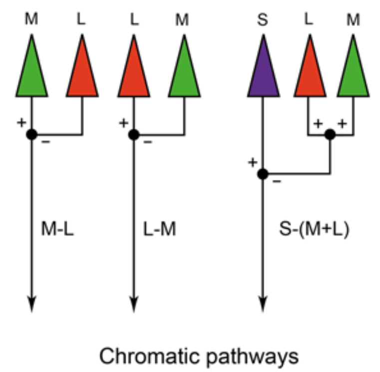
8 AVERAGE FIRING RATES of large sample of cells of each of six LGN cell types as a function of wavelength. Top four cells are spectrally opponent ones and bottom two are spectrally nonopponent cells. The cells on the left are, in principle, "mirror images" of those on the right.

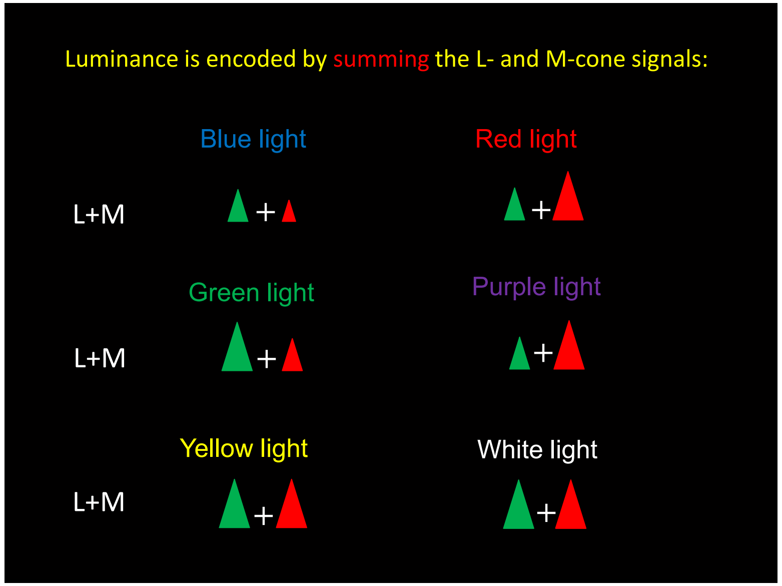




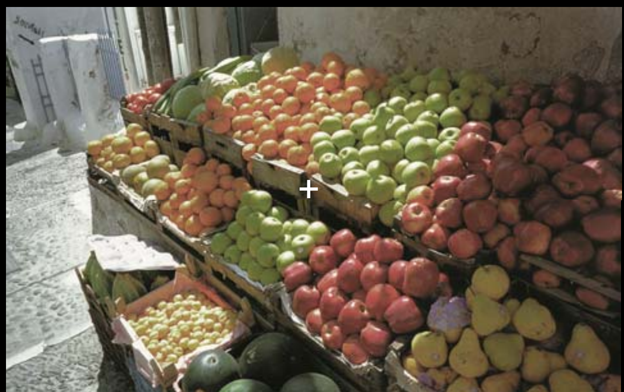
Chromatic and achromatic pathways

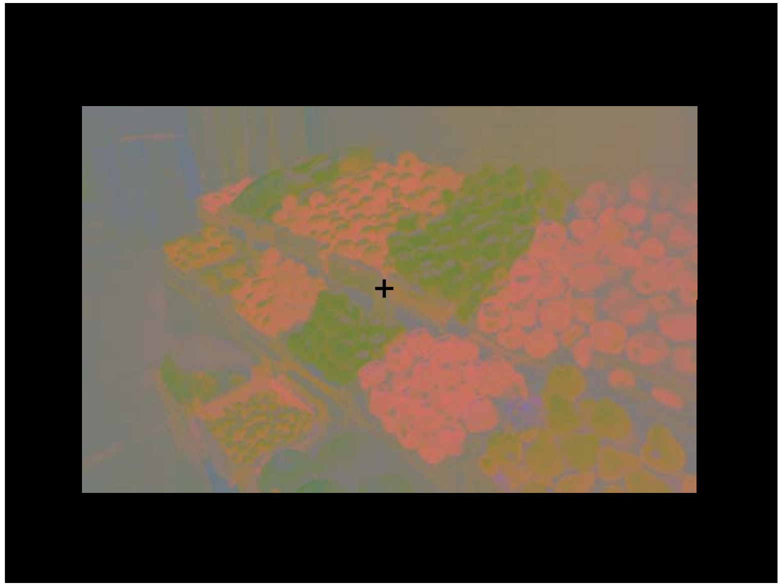
In addition to neural pathways that signal colour there are also pathways that signal intensity or luminance:

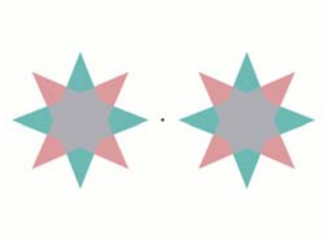




Colour is in many ways secondary to luminance

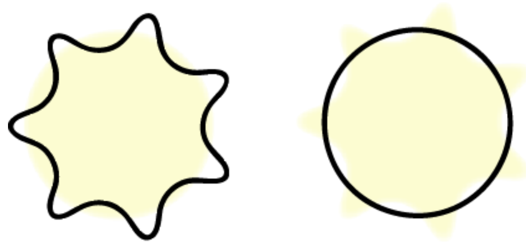




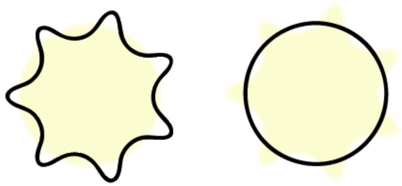


Rob van Lier, Mark Vergeer & Stuart Anstis

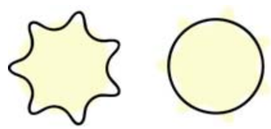
Boynton illusion



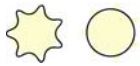
Boynton illusion



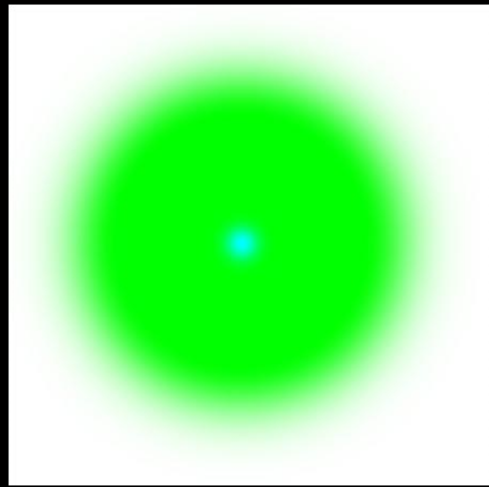
Boynton illusion



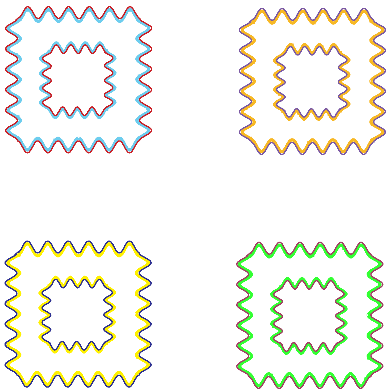
Boynton illusion



Fading dot



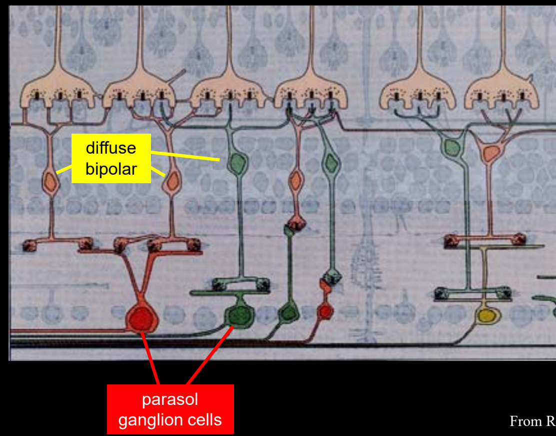
Watercolour effect



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

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

Magnocellular

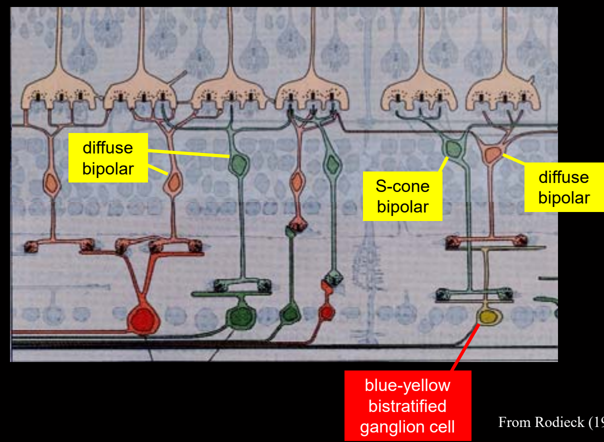


Diffuse bipolar cells sum across M- and L-cones

From Rodieck (1998)

Chromatic pathways, which produce chromatic percepts, have been linked to the koniocellular stream for S-(L+M)…

Koniocellular

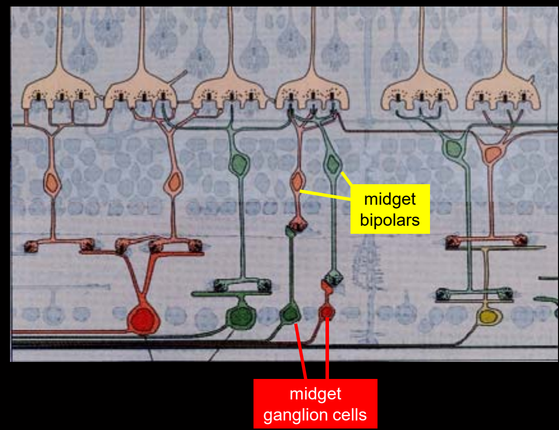


From Rodieck (1998)

Chromatic pathways, which produce chromatic percepts, have been linked to the koniocellular stream for S-(L+M)...

And also to the parvocellular retinal stream for L-M.

Parvocellular

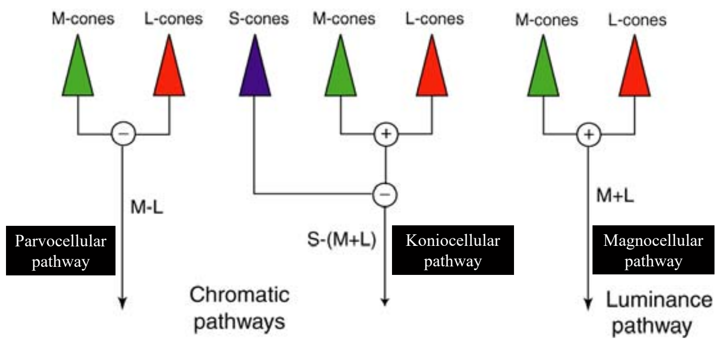


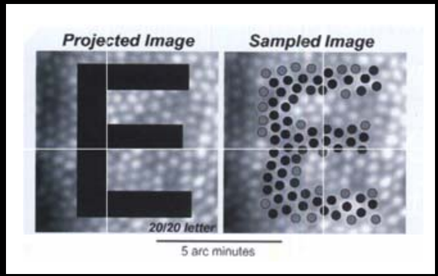
In the fovea, midget bipolar cells have single M- and L-cone inputs.

From Rodieck (1998)

Although luminance pathways have been linked to the magnocellular stream, they must *also* depend on the parvocellular stream.

[Based on Boynton (1979)]





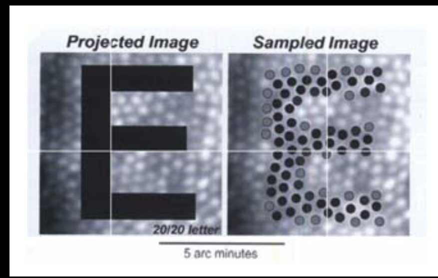
Austin Roorda, 2004

To be able to resolve this E at the resolution limit, there must be enough samples.

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

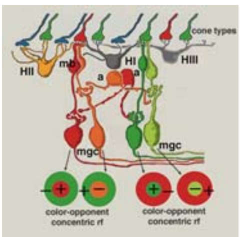
The magnocellular pathway, with diffuse bipolar cells, does not.

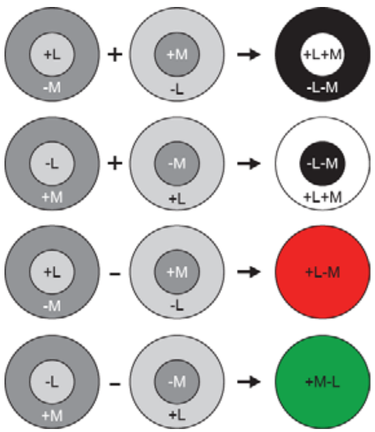
The parvocellular pathway must be double-duty supporting finely detailed luminance vision as well as much more coarse colour vision.



Austin Roorda, 2004

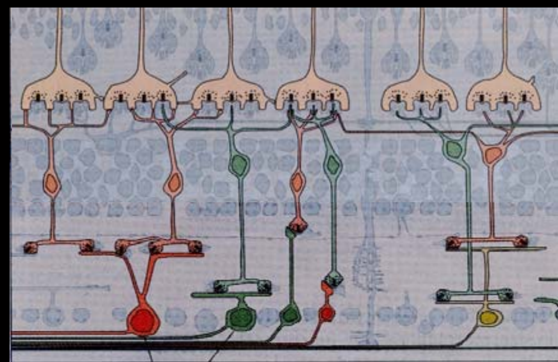
Multiplexing colour and luminance information





Magnocellular pathway:
- High temporal frequencies (motion)
- Low spatial frequencies
- Achromatic
- Higher contrast sensitivity

Parvocellular pathway:
- High spatial frequencies (detail)
- Low temporal frequencies
- Chromatic
- Lower contrast sensitivity



From Rodieck (1998)

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)

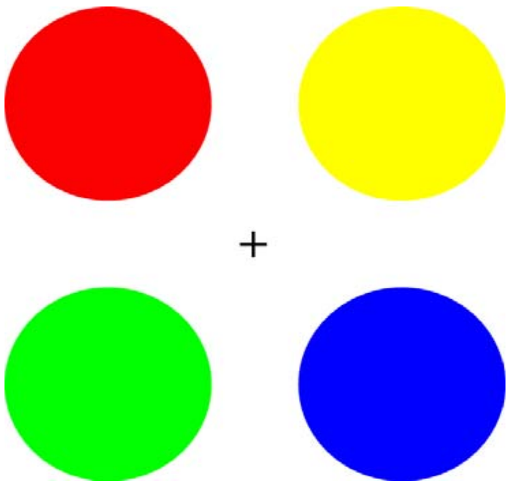
COLOUR CONTRAST

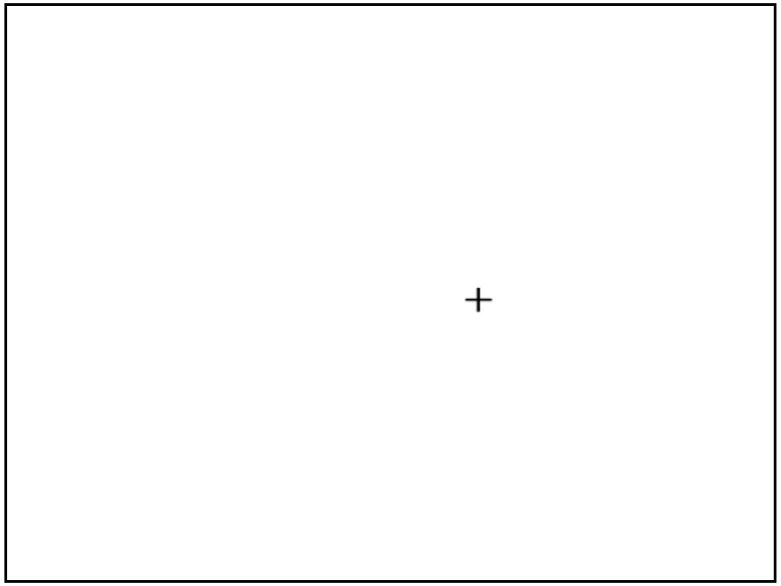
COLOUR ASSIMILATION

COLOUR AFTER-EFFECTS

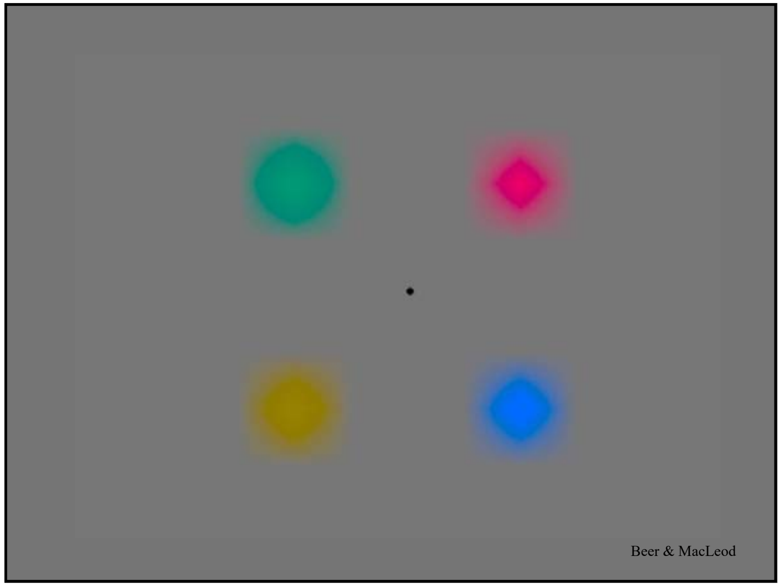
(what precedes the patch)

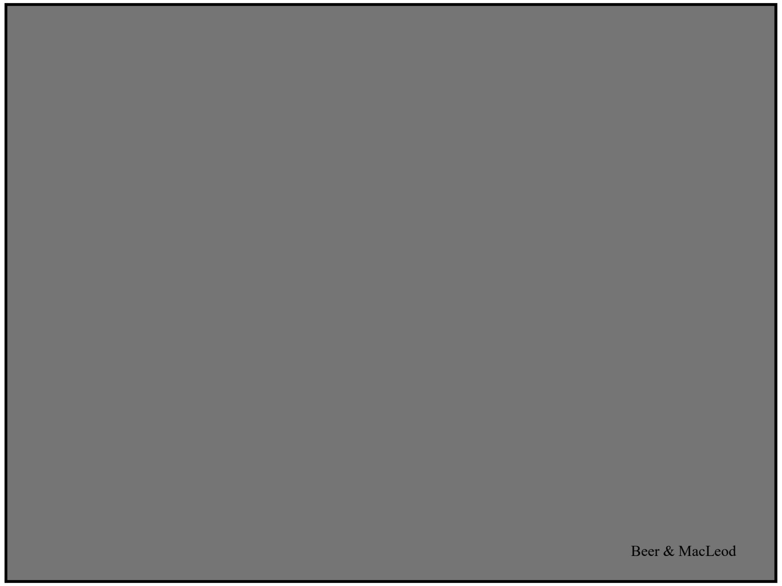
Colour after-effects

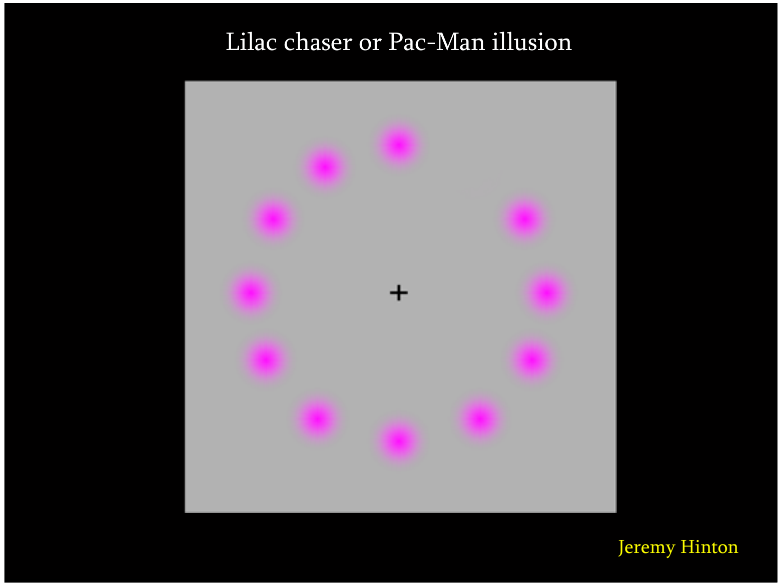




You don't have to see things for
them to produce an after-effect...

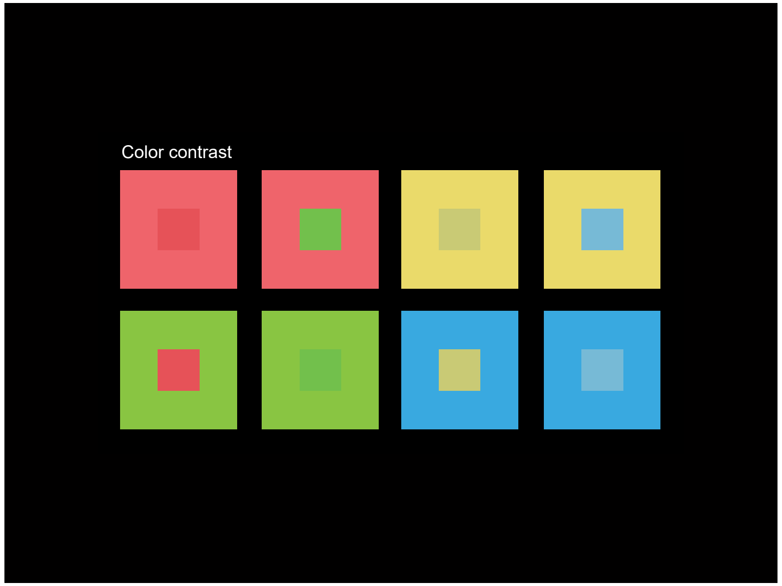


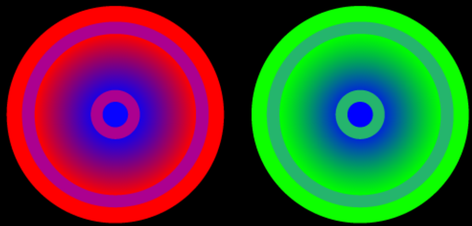




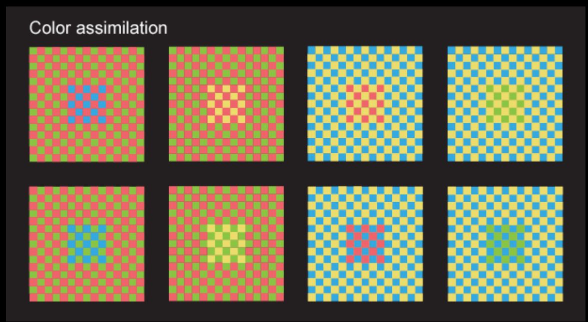
COLOUR CONTRAST

(what surrounds the patch)

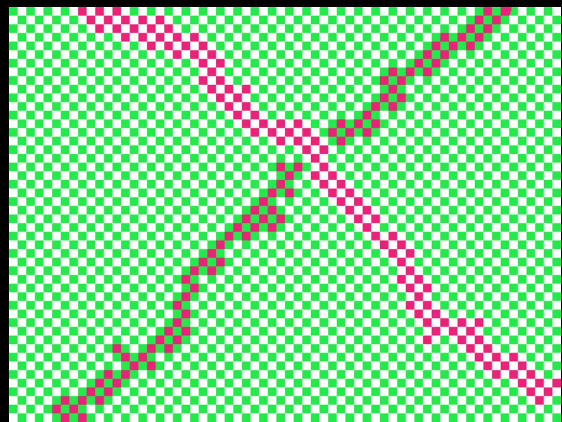




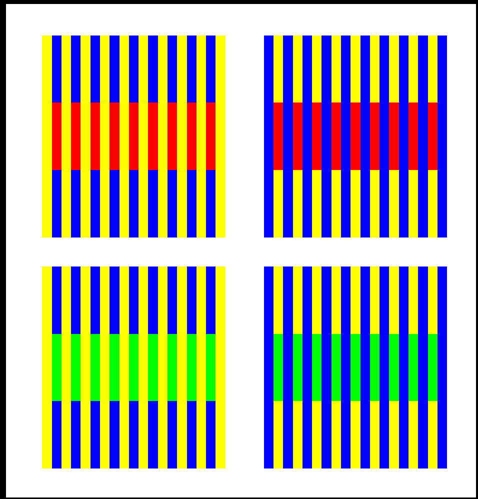
COLOUR ASSIMILATION



Colour assimilation



Munker illusion

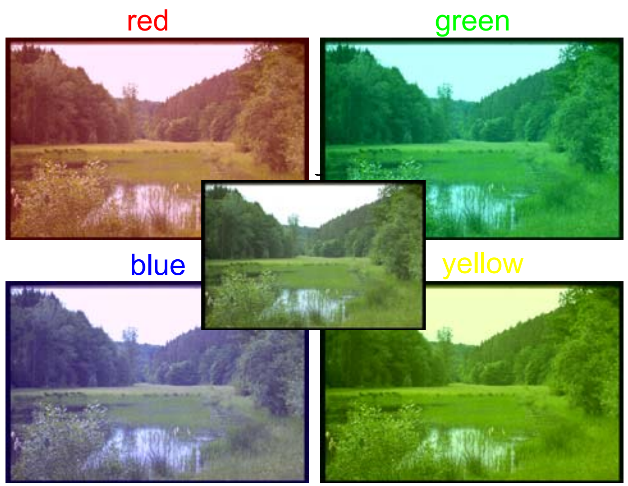


COLOUR CONSTANCY

Colour constancy

Colour constancy

Credit: Gegenfurtner

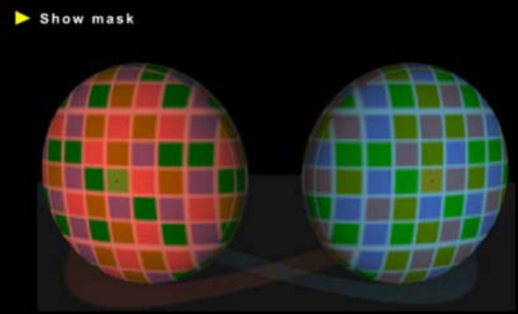


Chromatic adaptation and colour constancy

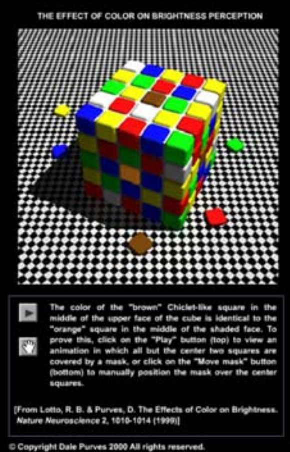
The change in colour appearance following adaptation is due to chromatic adaptation. Chromatic adaptation is adaptation to the colour is of the ambient illumination.

Amazing Art, Viperlib

Colour and the illuminant



Colour and brightness



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

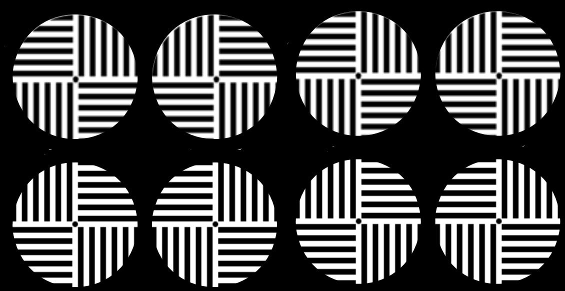
How long?

TEST 2

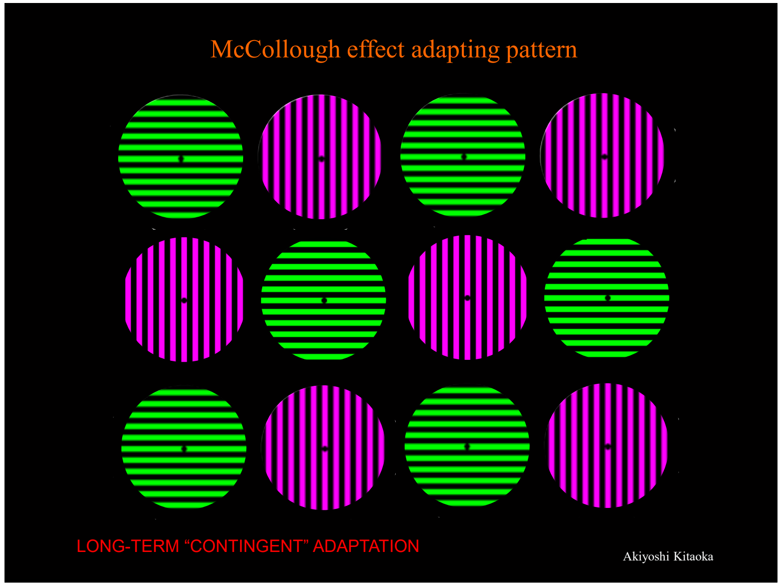
BLUE	PINK	WHITE	RED	BROWN
BROWN	RED	BLUE	GREEN	ORANGE
YELLOW	BLUE	RED	ORANGE	WHITE
BROWN	RED	GREEN	WHITE	RED
RED	PINK	BLUE	GREEN	WHITE

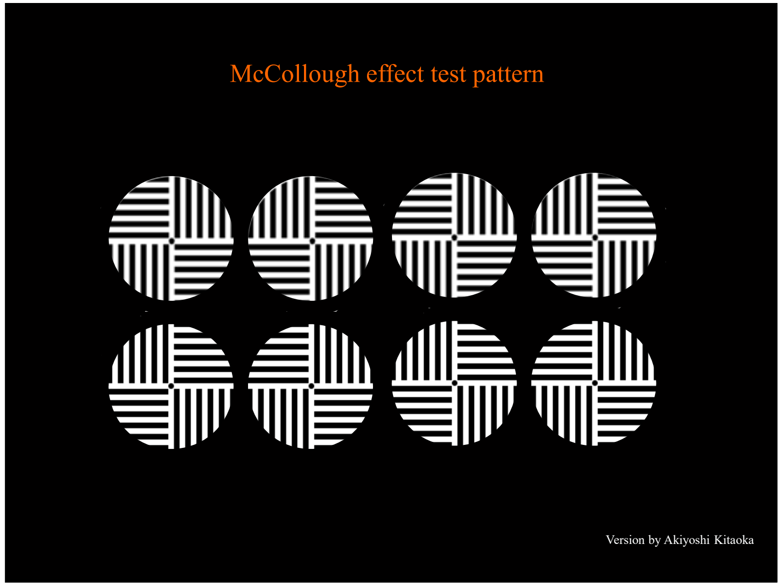
How long?

McCollough effect test pattern

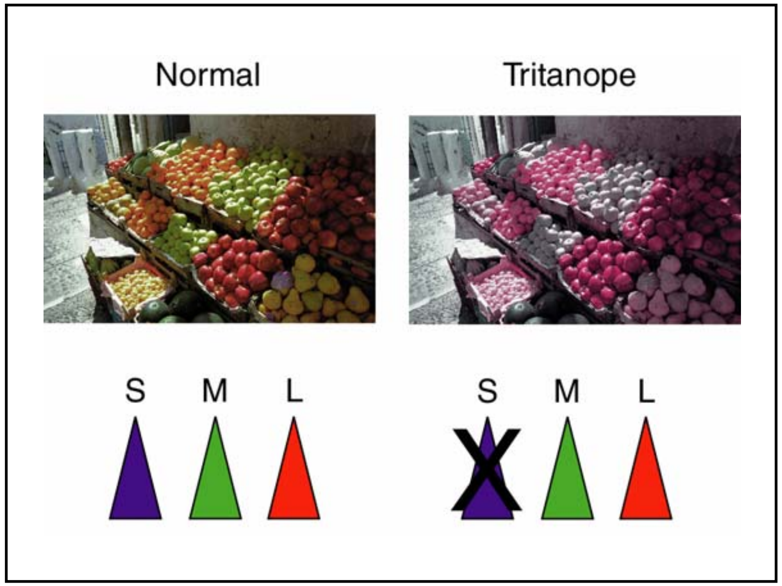


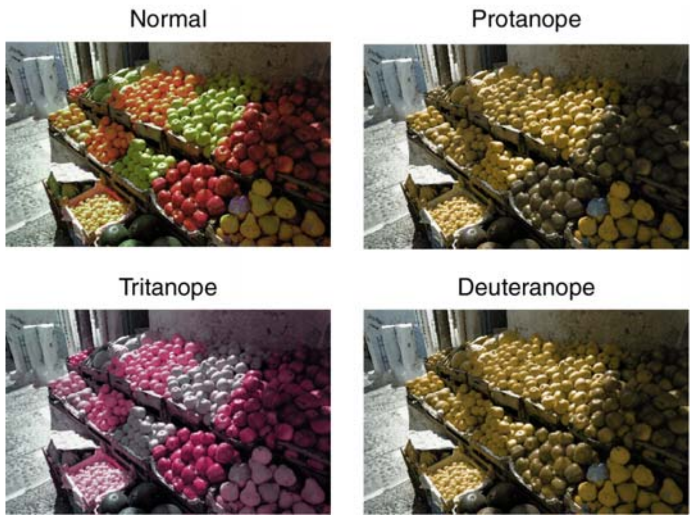
Version by Akiyoshi Kitaoka





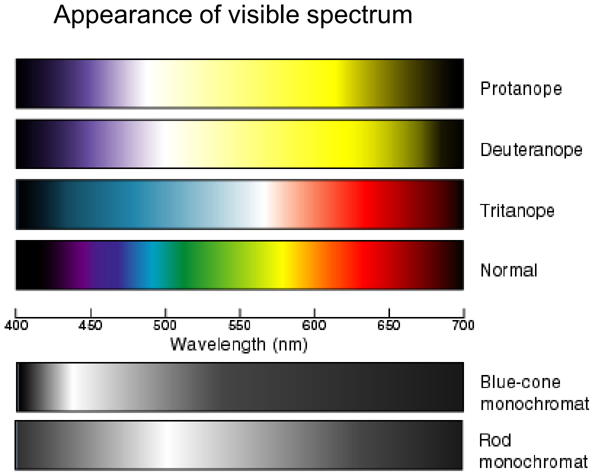
COLOUR VISION, COLOUR DEFICIENCIES AND MOLECULAR GENETICS



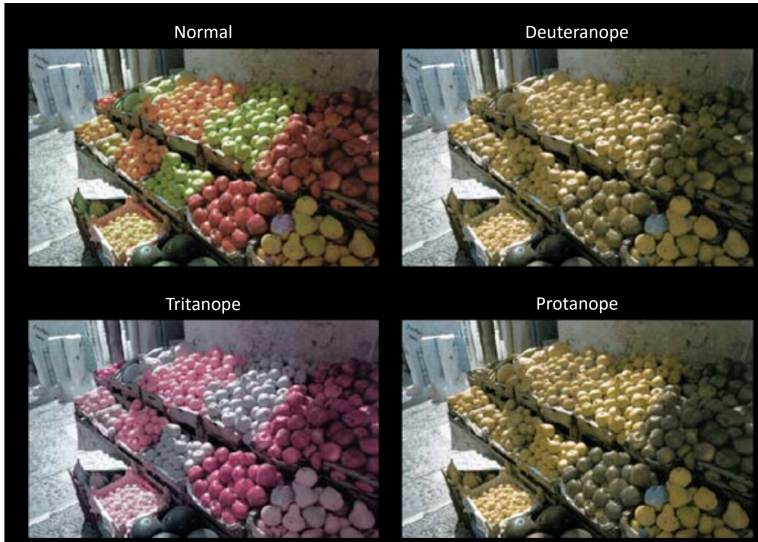


Colour deficiency simulations

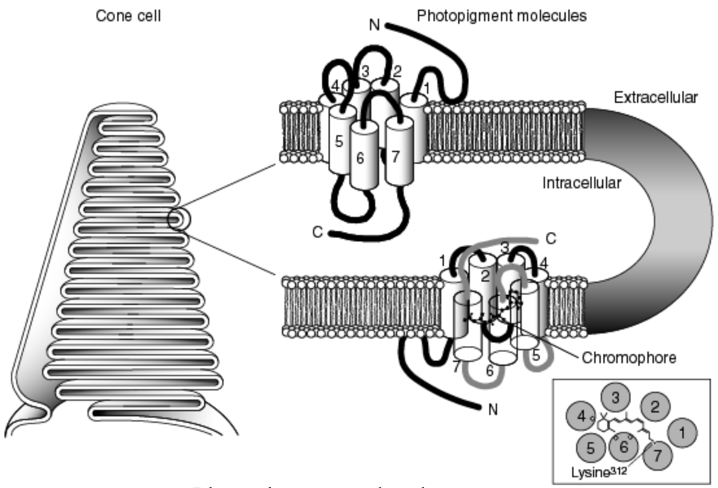
From Sharpe, Stockman, Jägle & Nathans, 1999



COLOUR VISION AND MOLECULAR GENETICS



From Sharpe, Stockman, Jägle & Nathans, 1999



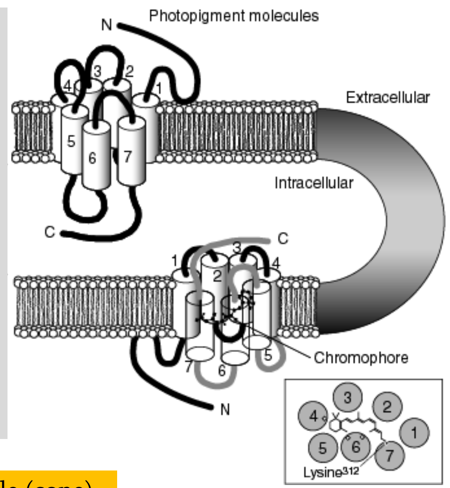
Photopigment molecule

From Sharpe, Stockman, Jägle & Nathans, 1999

The spectral sensitivity of the photopigment depends on the energy required to flip the chromophore from it *11-cis* form to its all-*trans* form.

But the same chromophore is used in all four human photo-pigments.

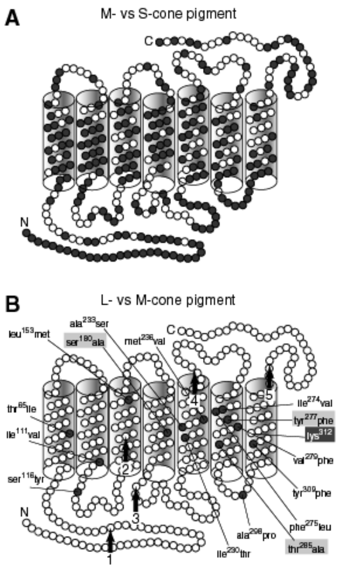
The energy is modified by changes in the amino acids in the surrounding opsin molecule.



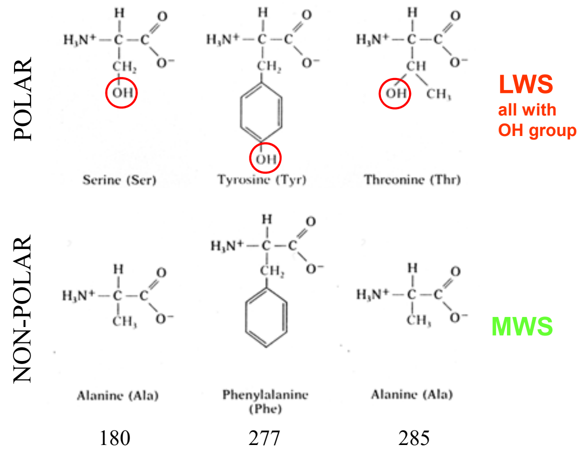
Photopigment molecule (cone)

From Sharpe, Stockman, Jägle & Nathans, 1999

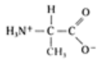
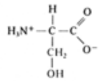
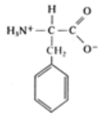
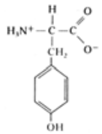
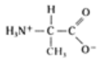
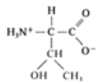
Amino acid differences between photopigment opsins



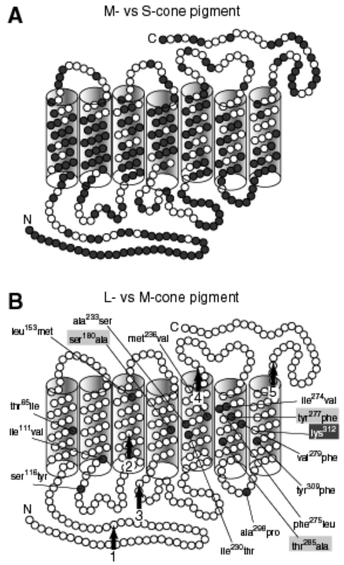
From Sharpe, Stockman, Jägle & Nathans, 1999



Tuning Site	MWS	LWS	
180	alanine	serine OH-	~ 5 nm
277	phenylalanine	tyrosine OH-	~ 25 nm
285	alanine	threonine OH-	

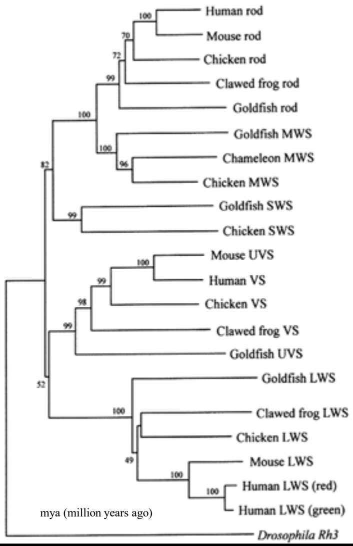
Amino acid differences between photopigment opsins



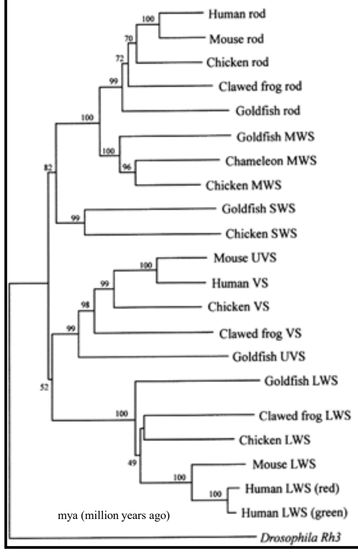
Why are the M- and L-cone opsins so similar?

From Sharpe, Stockman, Jägle & Nathans, 1999

Phylogenetic tree of visual pigments



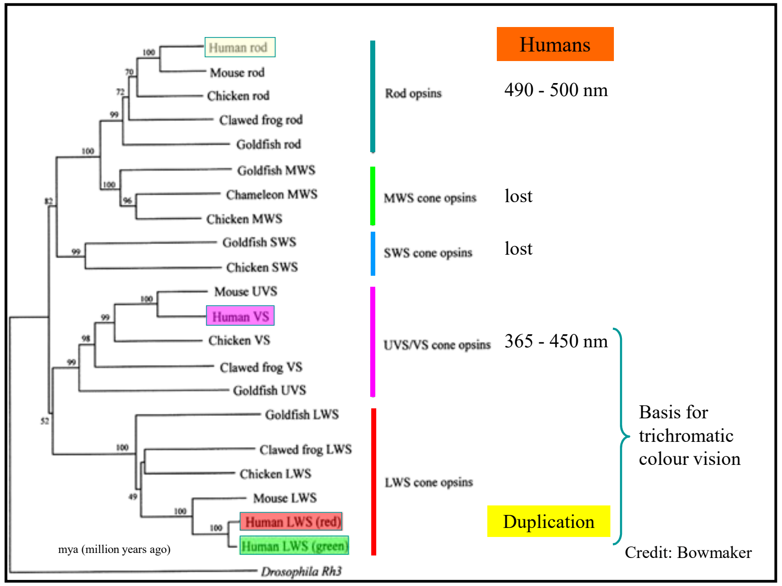
Rod opsins	About 460 – 520 nm	Rh1
MWS cone opsins	About 460 – 520 nm	Rh2
SWS cone opsins	About 420 – 480 nm	SWS2
UVS/VS cone opsins	About 355 – 450 nm	SWS1
LWS cone opsins	About 490 – 570 nm	LWS

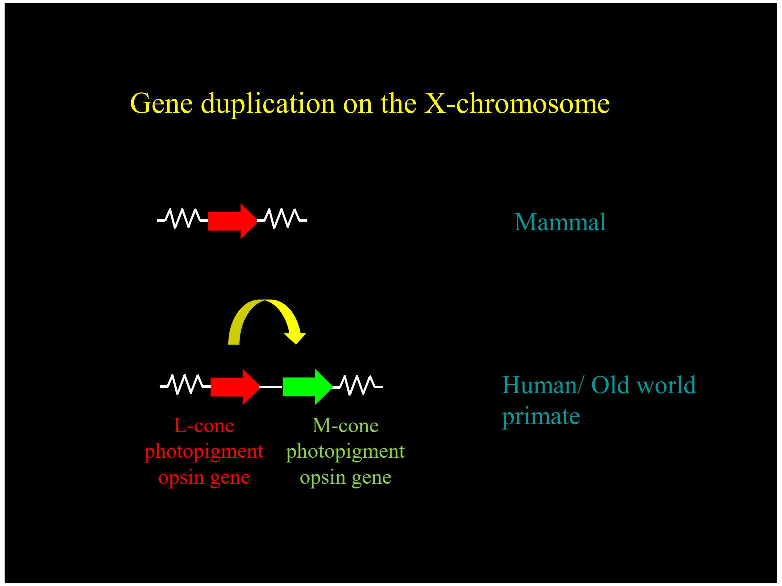


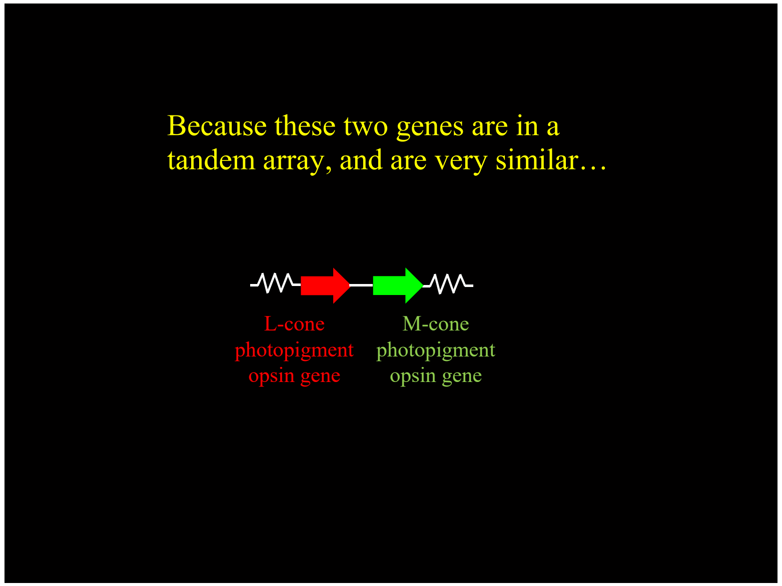
	Mammals
Rod opsins	490 - 500 nm
MWS cone opsins	lost
SWS cone opsins	lost
UVS/VS cone opsins	365 - 450 nm
LWS cone opsins	490 - 565 nm

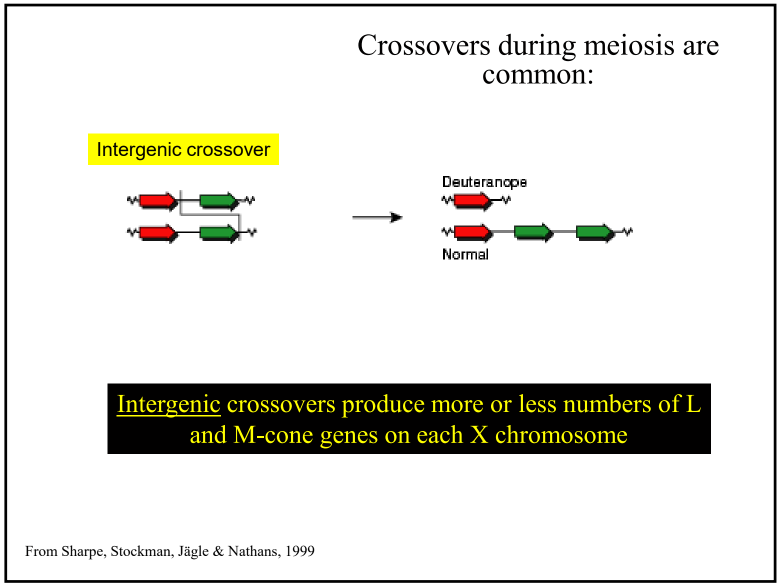
Basis for dichromatic colour vision

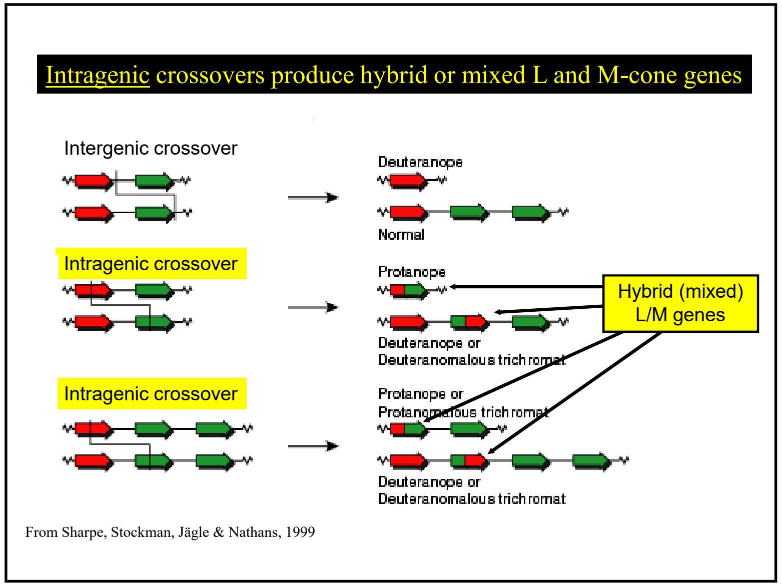
Credit: Bowmaker

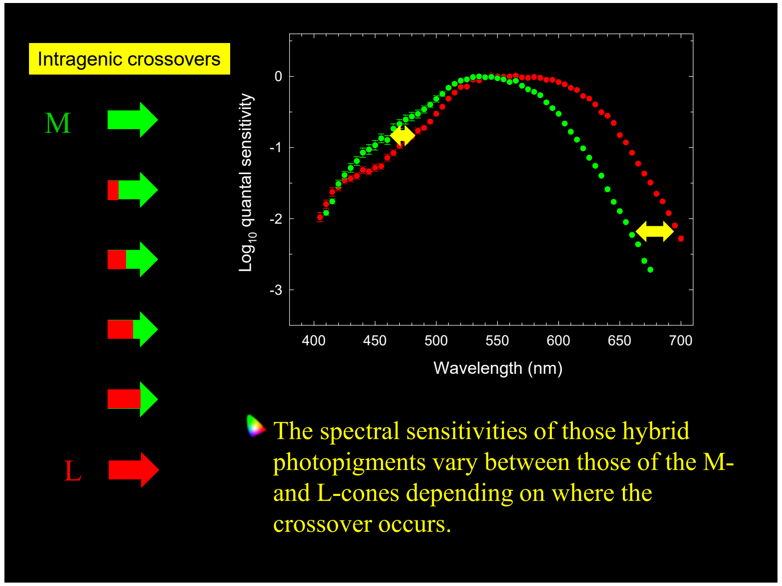

Human rod
Mouse rod
Chicken rod
Clawed frog rod
Goldfish rod
Goldfish MWS
Chameleon MWS
Chicken MWS
Goldfish SWS
Chicken SWS
Mouse UVS
Human VS
Chicken VS
Clawed frog VS
Goldfish UVS
Goldfish LWS
Clawed frog LWS
Chicken LWS
Mouse LWS
Human LWS (red)
Human LWS (green)
mya (million years ago)
Drosophila Rh3
Rod opsins
MWS cone opsins
SWS cone opsins
UVS/VS cone opsins
LWS cone opsins
Humans
490 - 500 nm
lost
lost
365 - 450 nm
Basis for trichromatic colour vision
Duplication
Credit: Bowmaker

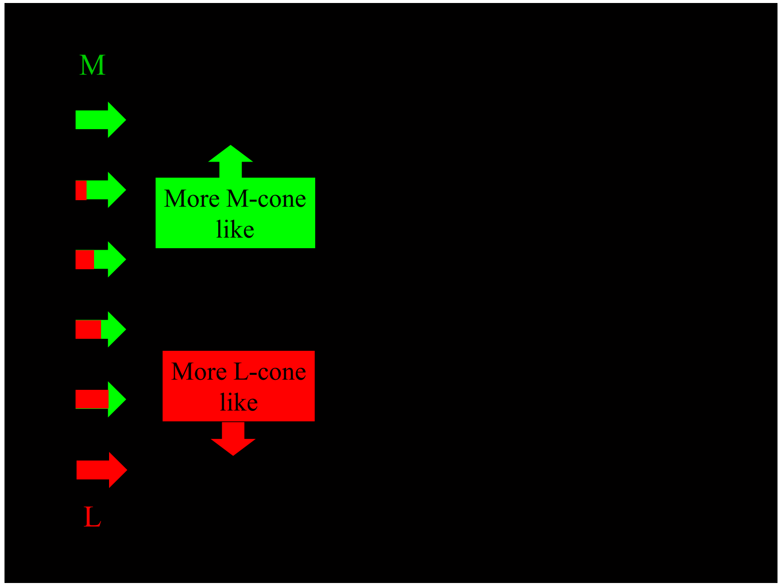

Gene duplication on the X-chromosome
Mammal
Human/ Old world primate
L-cone photopigment opsin gene
M-cone photopigment opsin gene

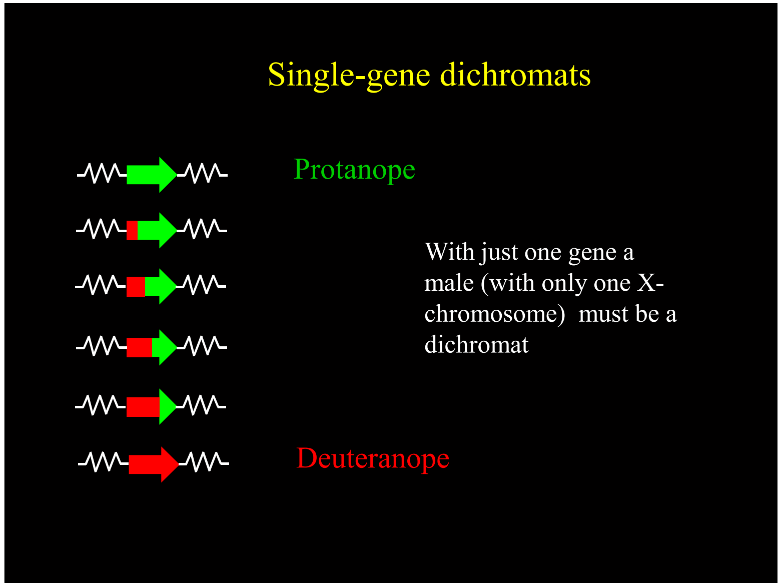

Because these two genes are in a tandem array, and are very similar…
L-cone photopigment opsin gene
M-cone photopigment opsin gene

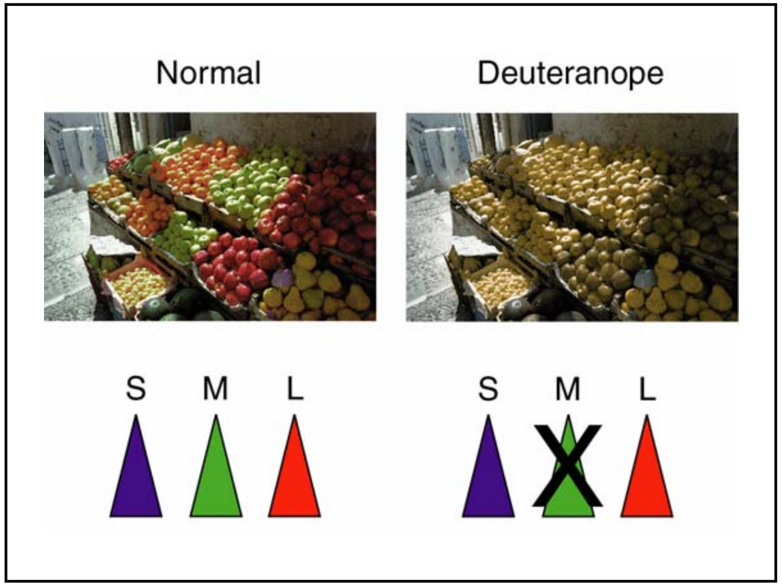

Crossovers during meiosis are common:
Intergenic crossover
Deuteranope
Normal
Intergenic crossovers produce more or less numbers of L and M-cone genes on each X chromosome
From Sharpe, Stockman, Jägle & Nathans, 1999

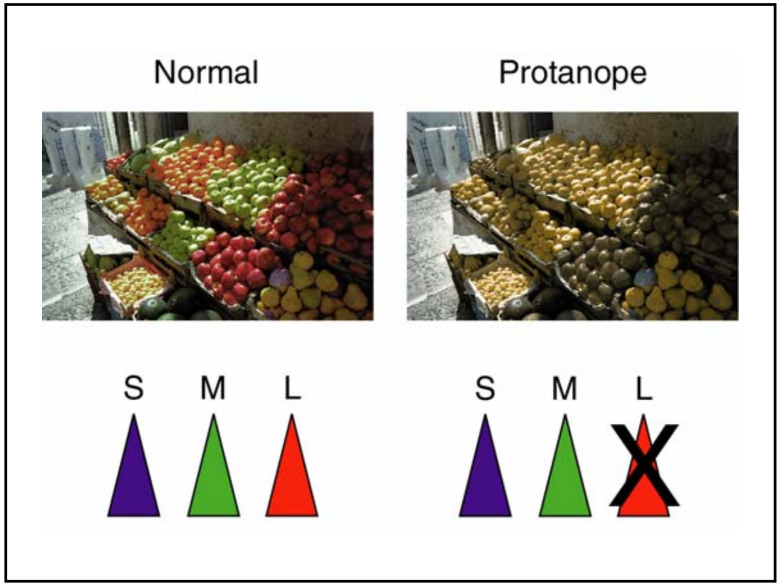

Intragenic crossovers produce hybrid or mixed L and M-cone genes
Intergenic crossover
Deuteranope
Normal
Intragenic crossover
Protanope
Hybrid (mixed) L/M genes
Deuteranope or
Deuteranomalous trichromat
Intragenic crossover
Protanope or
Protanomalous trichromat
Deuteranope or
Deuteranomalous trichromat
From Sharpe, Stockman, Jägle & Nathans, 1999

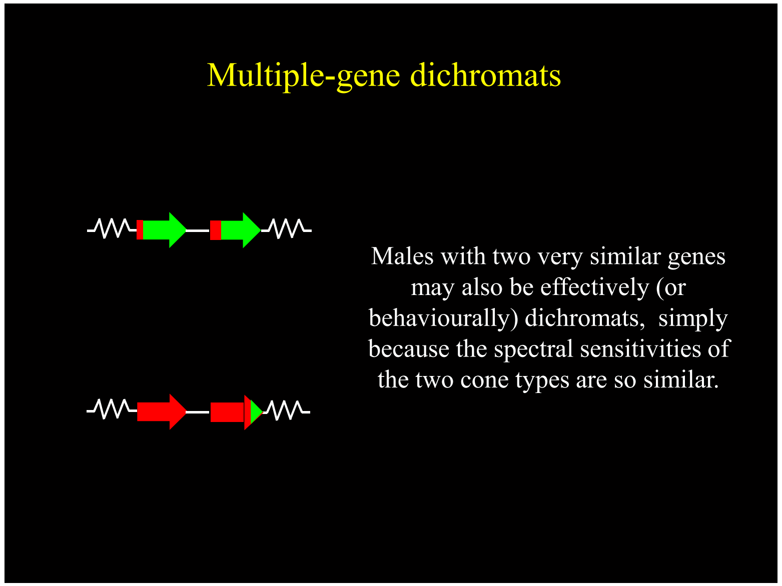

Intragenic crossovers
M
L
Log10 quantal sensitivity
0
-1
-2
-3
400
450
500
550
600
650
700
Wavelength (nm)
The spectral sensitivities of those hybrid photopigments vary between those of the M- and L-cones depending on where the crossover occurs.

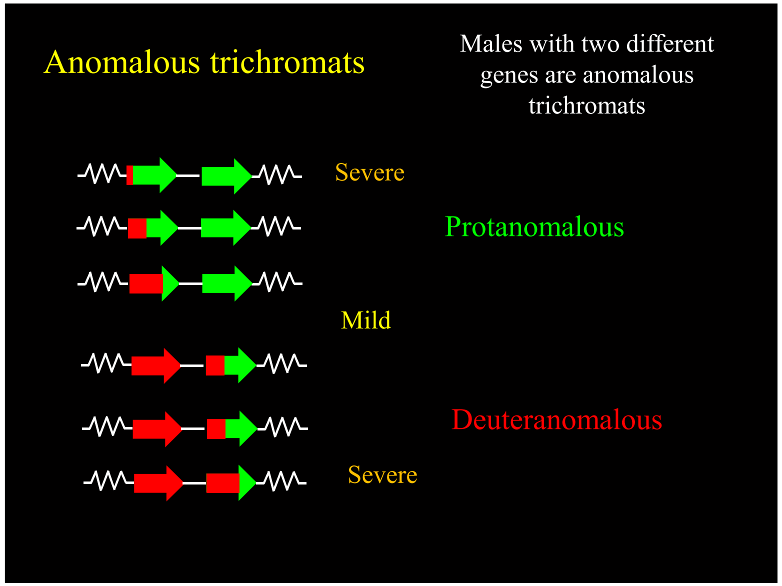

M
More M-cone like
More L-cone like
L

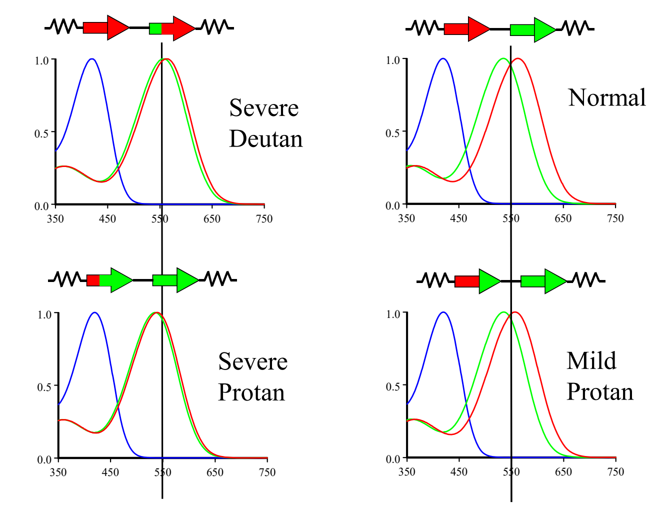

Single-gene dichromats
Protanope
With just one gene a male (with only one X-chromosome) must be a dichromat
Deuteranope


Normal
Deuteranope
S
M
L
S
M
L


Normal
Protanope
S
M
L
S
M
L


Multiple-gene dichromats
Males with two very similar genes may also be effectively (or behaviourally) dichromats, simply because the spectral sensitivities of the two cone types are so similar.


Anomalous trichromats
Males with two different genes are anomalous trichromats
Severe
Protanomalous
Mild
Deuteranomalous
Severe



Main types of colour vision defects with approximate proportions of appearance 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

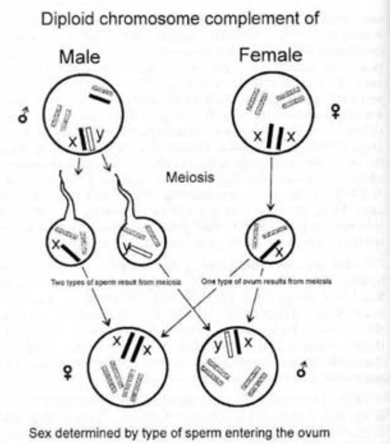


Figure 10.17 Prior to fertilization, meiotic division of germ cells results in two types of sperm, but only one type of ovum. Depending on which sperm is effective, the fertilized ovum will have two X cells and be female, or one X and one Y cell and be male. This diagram show why the X cell of the male 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 is it important?

No red-green discrimination

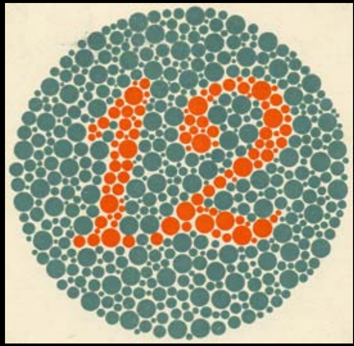
Source: Hans Irtel

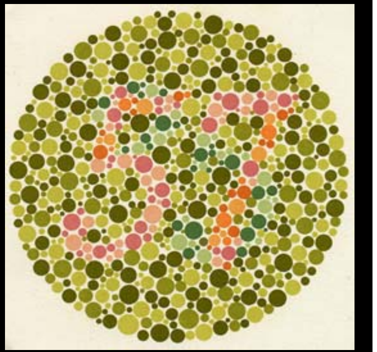
Red-green discrimination

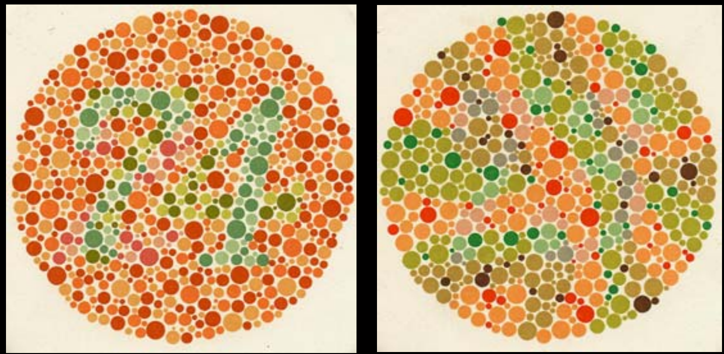
Source: Hans Irtel

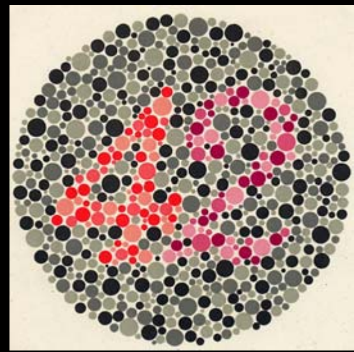
DIAGNOSING COLOUR VISION DEFICIENCIES

Ishihara plates



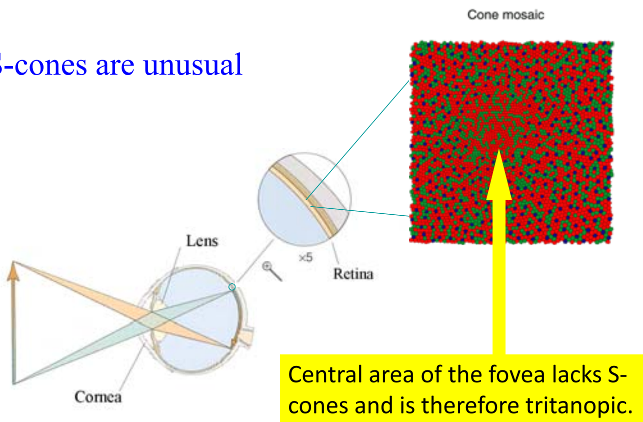




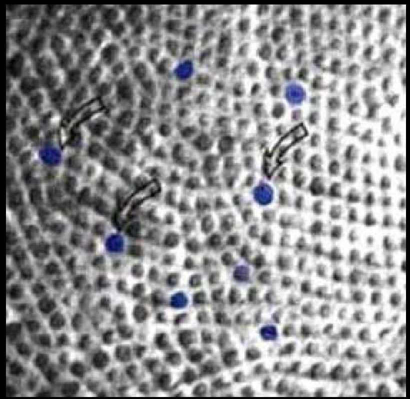


S-CONE MEDIATED VISION
IS UNUSUAL

S-cones are unusual



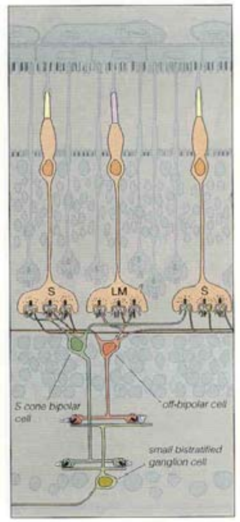
In other retinal regions, the S-cone mosaic remains sparse.



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

Curcio et al.

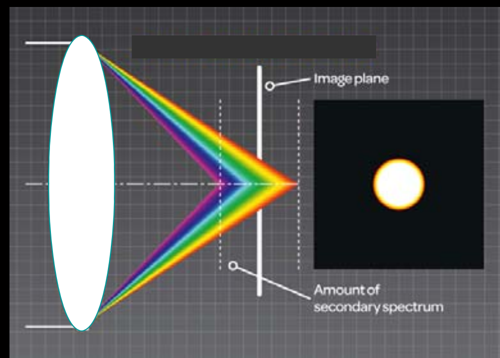
S-cone pathway
ON pathway



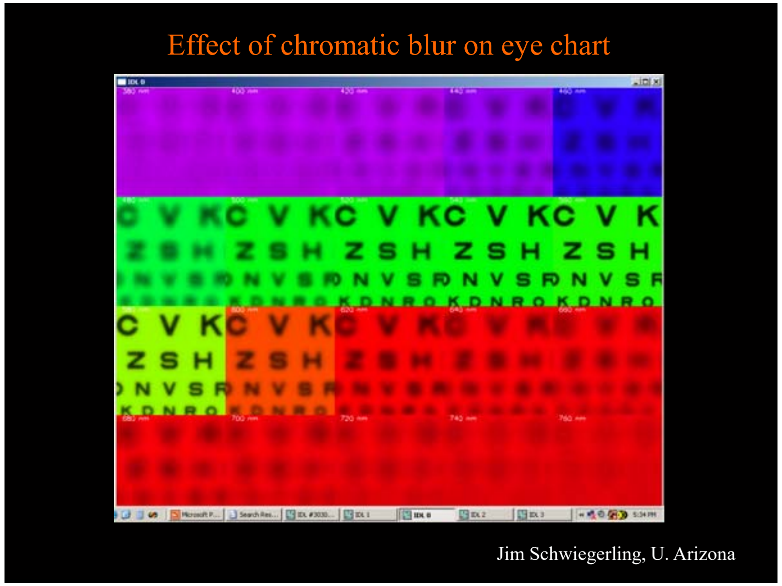
S cone on pathway

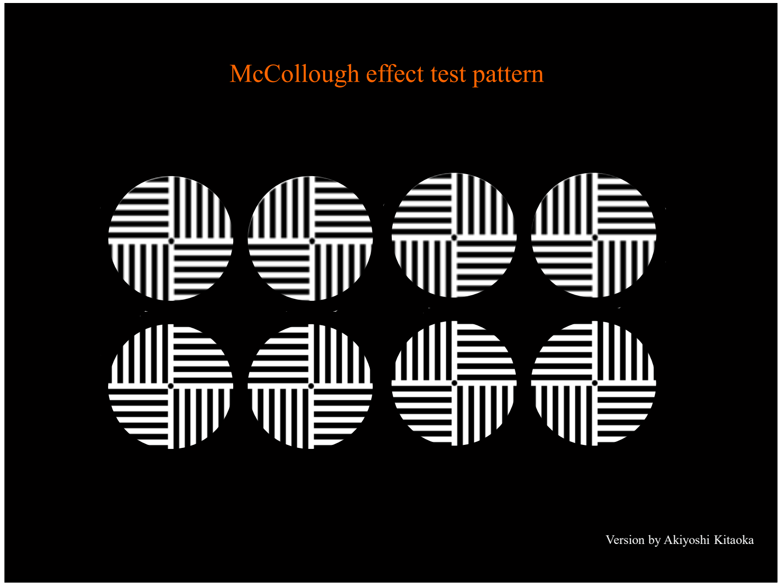
Why is S-cone vision sparse?

Chromatic aberration



Base picture: Digital camera world


Effect of chromatic blur on eye chart
Jim Schwiegerling, U. Arizona


McCollough effect test pattern
Version by Akiyoshi Kitaoka