

UCL

Advanced Colour

NEUR 3001/G001/M001
Advanced Visual
Neuroscience

Andrew
Stockman

INTRODUCTION

Light

400 - 700 nm is important for vision

white sunlight

hole

window shade

glass prism

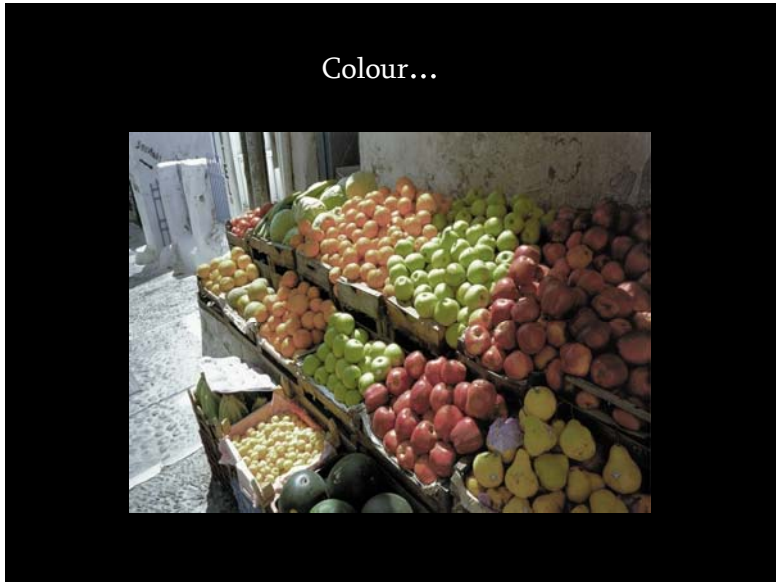
white card

spectrum

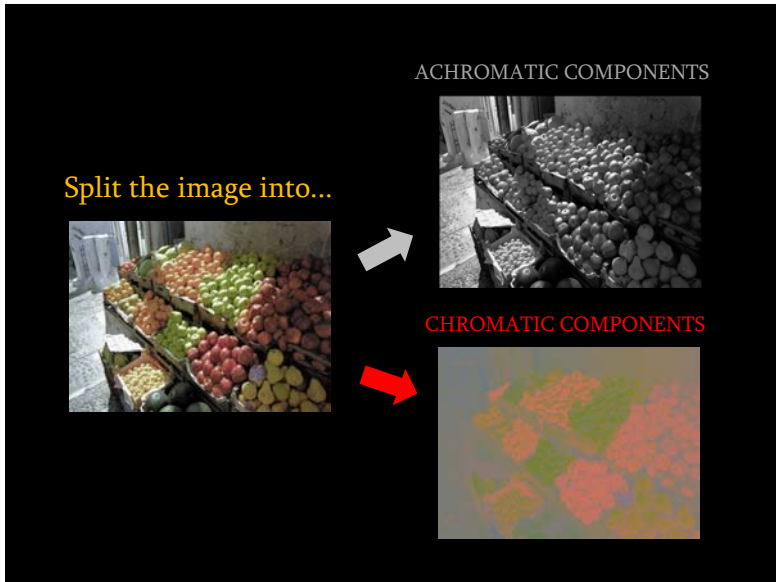
- red
- orange
- yellow
- green
- blue
- indigo
- violet

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How dependent are we on colour?



But just how important is colour?




CHROMATIC COMPONENTS



Chromatic information *by itself* provides relatively limited information...

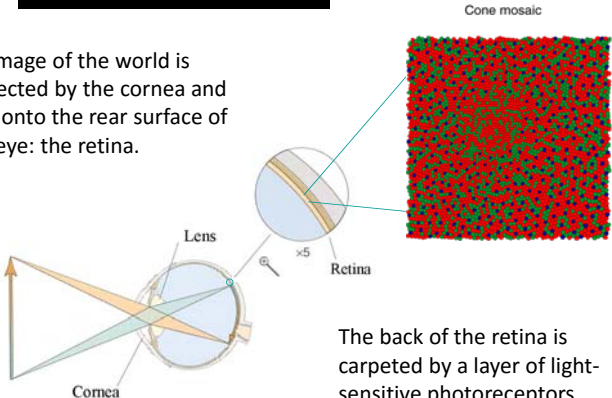
ACHROMATIC COMPONENTS



Achromatic information is 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.

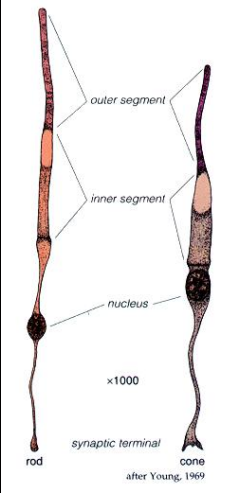


The back of the retina is carpeted by a layer of light-sensitive photoreceptors (rods and cones).

Human photoreceptors

Rods


- Achromatic night vision
- 1 type




Rod

Cones


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



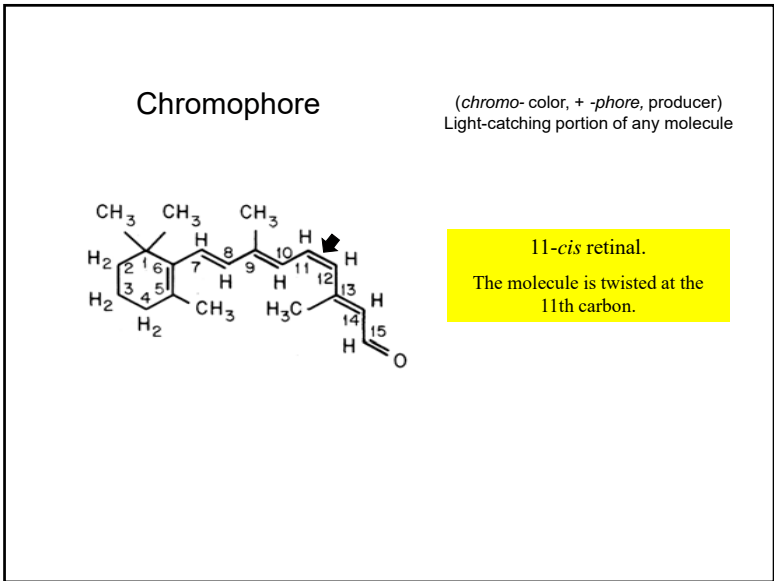
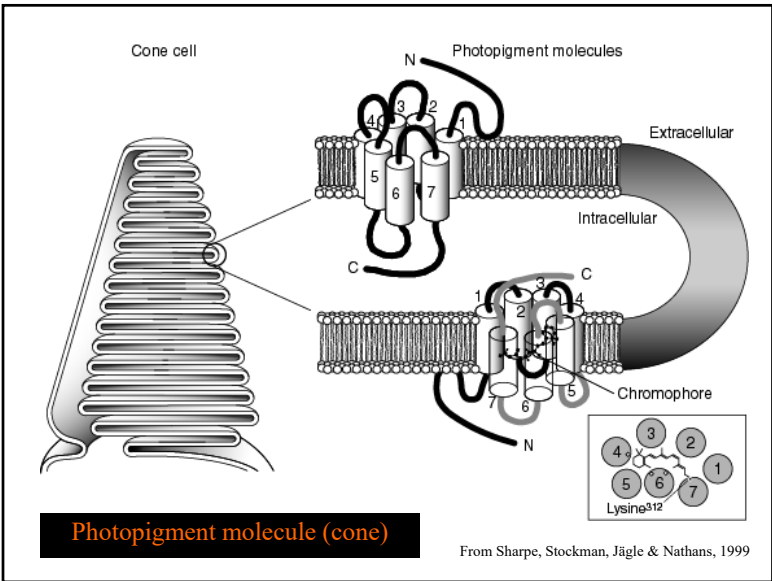
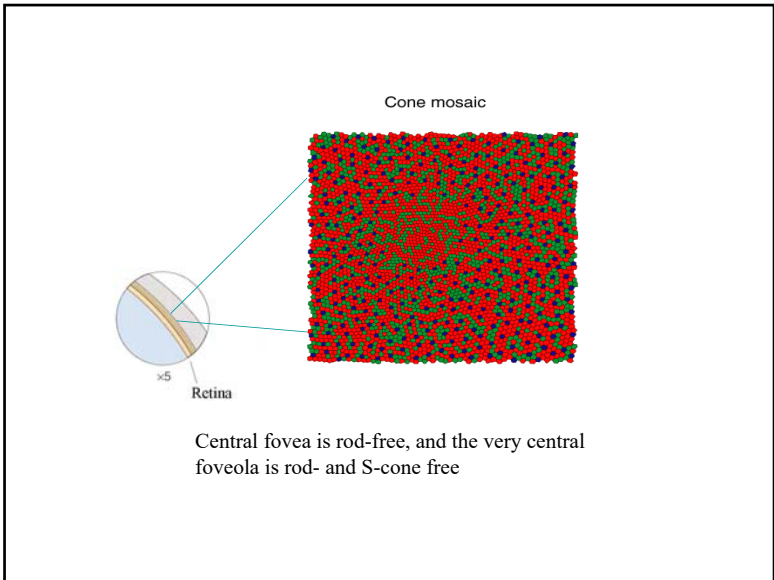
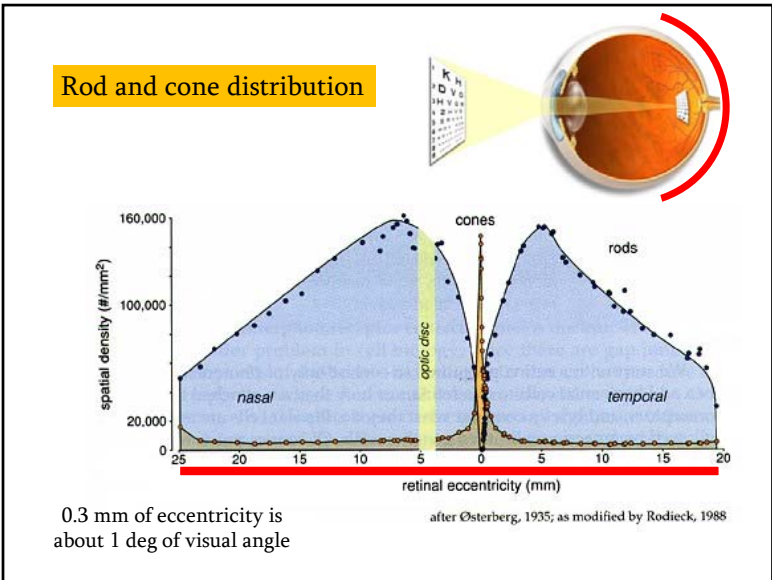
Long-wavelength-sensitive (L) or "red" cone



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



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



Chromophore

A photon is absorbed

The diagram shows the chemical structure of 11-cis-retinal, a polyene chain with a cyclohexene ring at one end and an aldehyde group at the other. The carbon atoms in the chain are numbered from 1 to 15. A red dot representing a photon is shown hitting the C11-C12 double bond, which is in a cis configuration.

Chromophore

A photon is absorbed

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

The diagram shows the chemical structure of 11-cis-retinal, similar to the previous one. A red dot representing a photon is shown hitting the C11-C12 double bond. A red arrow points from the photon towards the C11-C12 bond, indicating the initiation of a conformational change.

Chromophore

A photon is absorbed

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

all-trans retinal
(side chains omitted for simplicity).

The diagram shows the chemical structure of all-trans-retinal, which is the result of the conformational change from 11-cis-retinal. The polyene chain is now in a straight, all-trans configuration. A red arrow points from the 11-cis-retinal structure down to the all-trans-retinal structure.

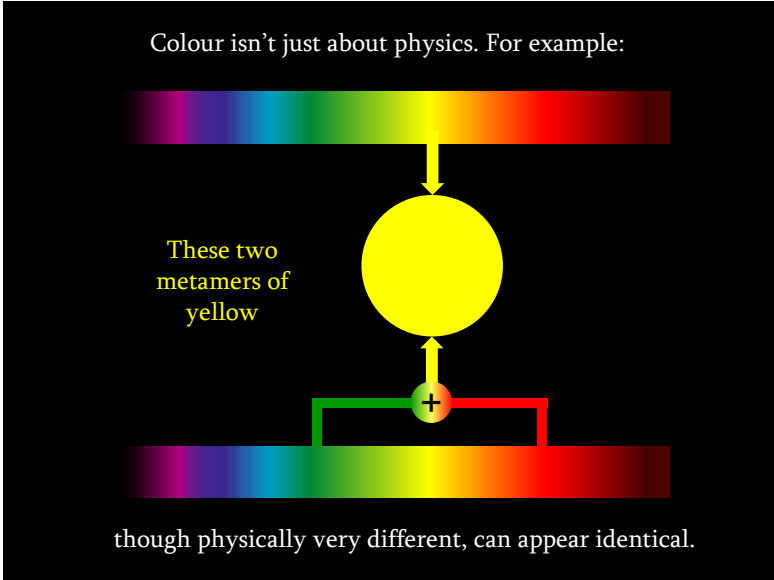
Chromophore

This process is binary:
all (1) or nothing (0).

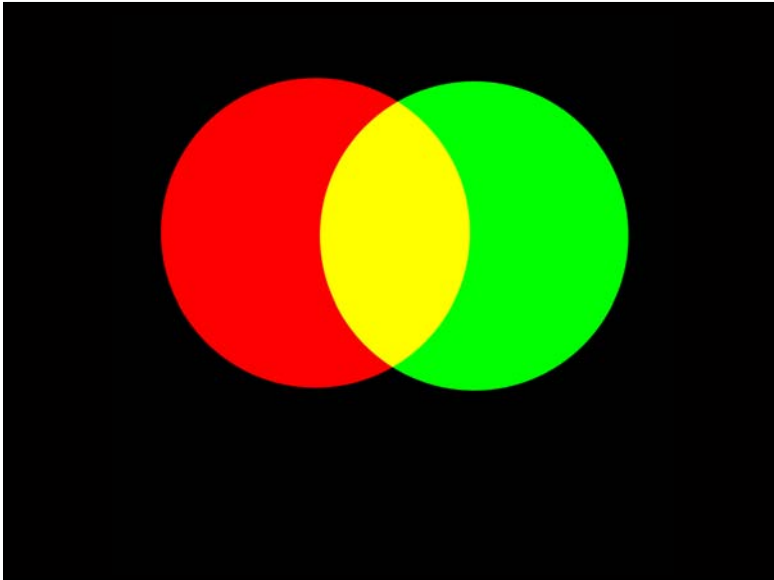
What does that tell us
about how wavelength
be encoded?

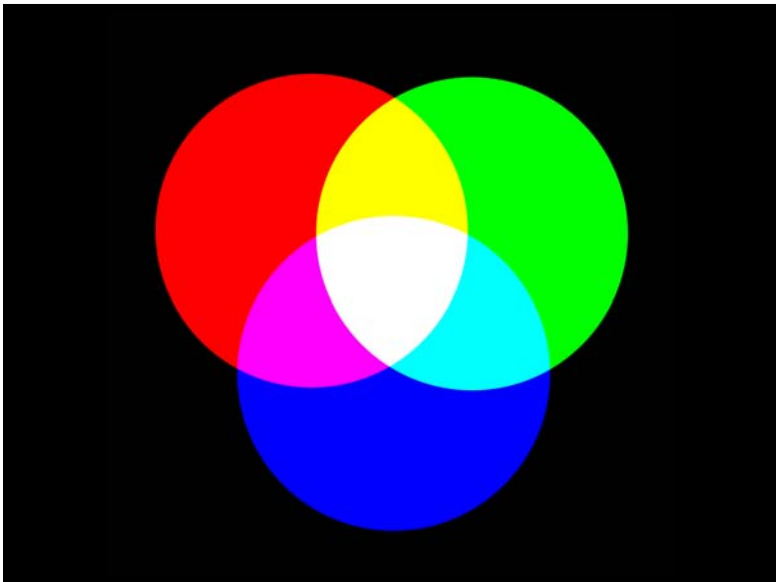
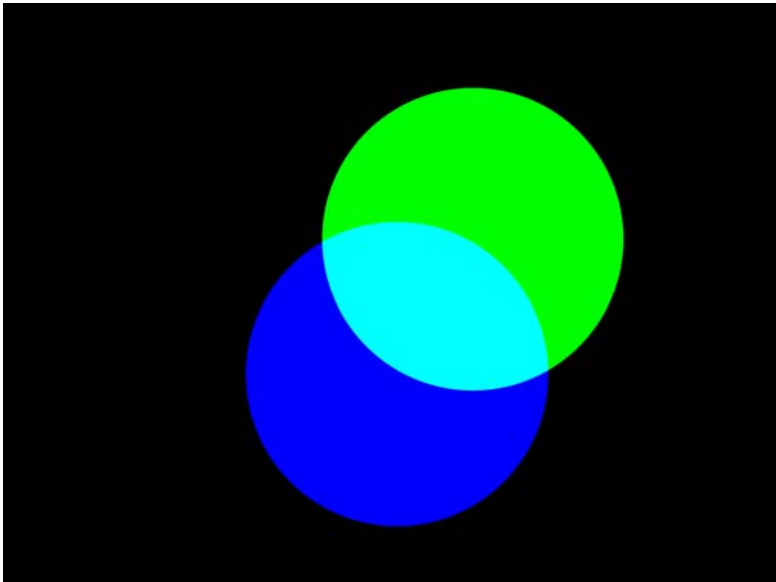
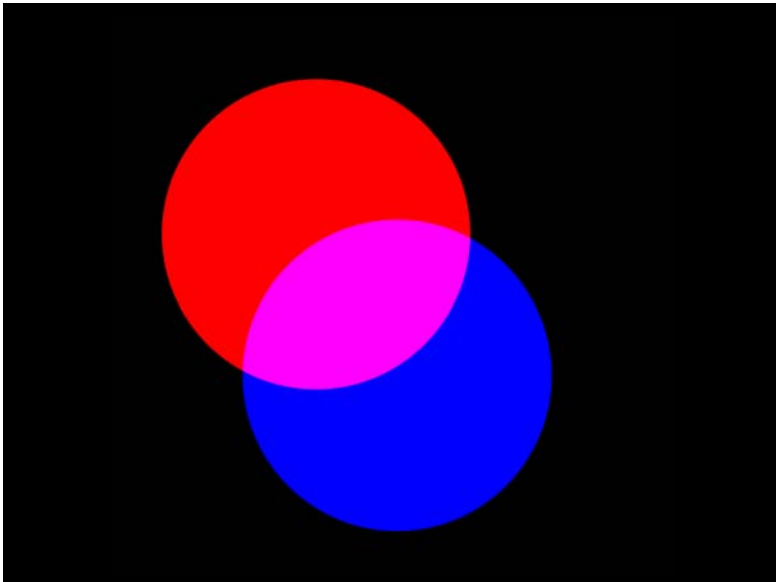
The diagram shows the chemical structure of all-trans-retinal, similar to the previous one. A red arrow points from the 11-cis-retinal structure down to the all-trans-retinal structure. The text to the right of the structure discusses the binary nature of the process and its relationship to wavelength encoding.

Is colour, as we perceive it, mainly a property of physics or biology?



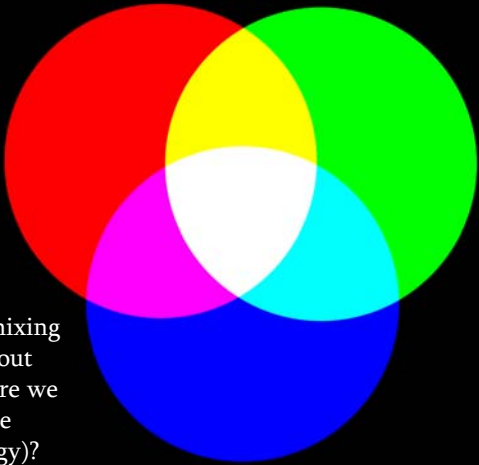
There are many other such metamers or matches...



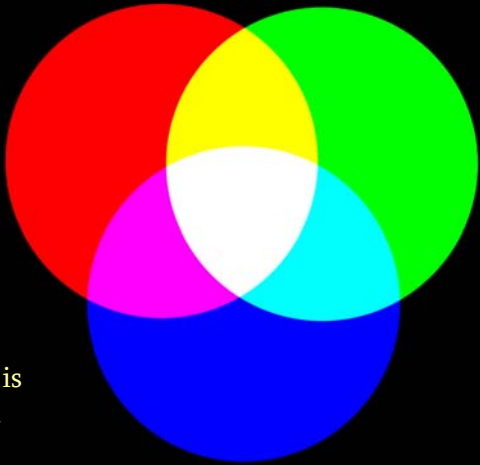


COLOUR MIXING

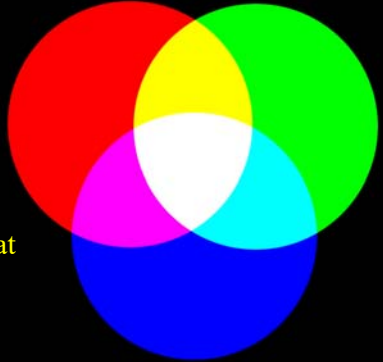
A screenshot of a software interface titled "COLOUR MIXING" on a black background. It features three horizontal sliders, each labeled "Brightness" and "255". The top slider is positioned at the right end. In the top right corner, there is a small red circular icon. At the bottom right, there is a small white rectangular box containing text: "© Thomas of Boston University 2010" and "http://www.thomasofboston.com".



What was colour mixing able to tell us about colour vision (before we knew about the underlying biology)?



Human vision is trichromatic.



Trichromacy means that colour vision is relatively simple.

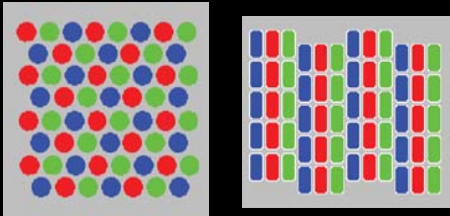
It is a 3 variable system...

Colour TV

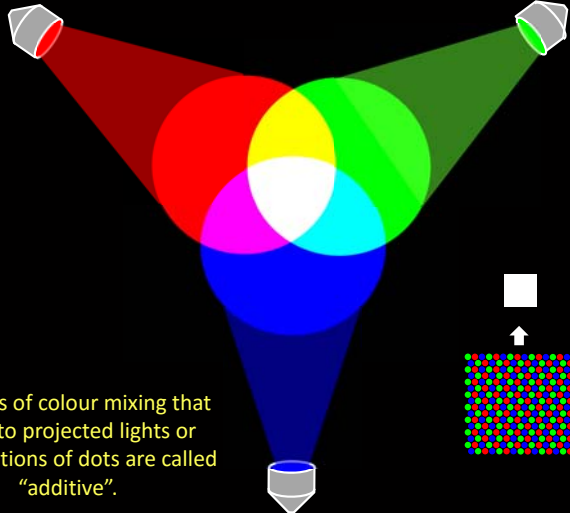
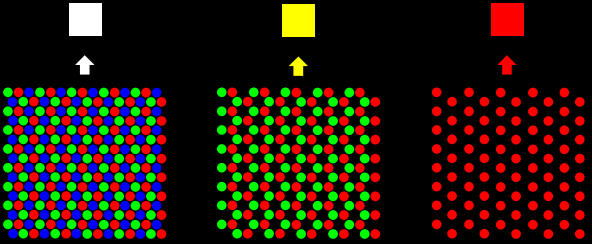
Trichromacy is exploited in colour reproduction, since the myriad of colours perceived can be produced by mixing together small dots of three colours.

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



The laws of colour mixing that apply to projected lights or combinations of dots are called "additive".

But what about mixing paints?


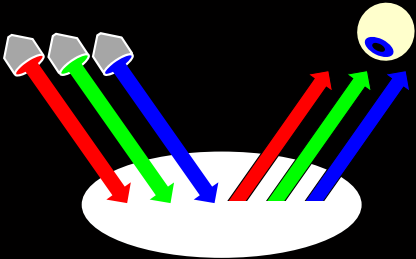
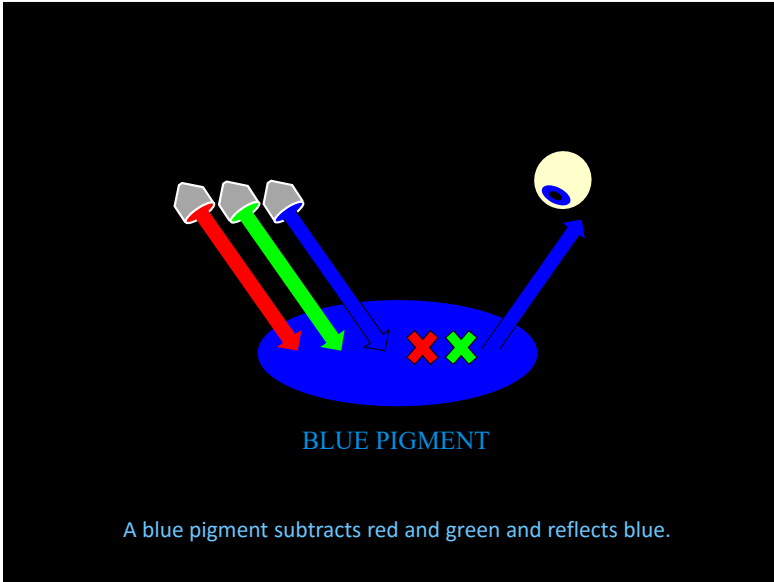
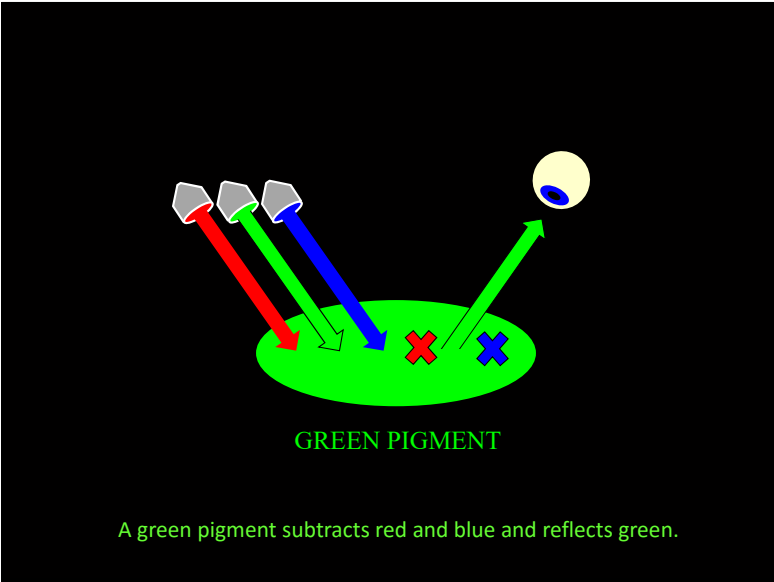
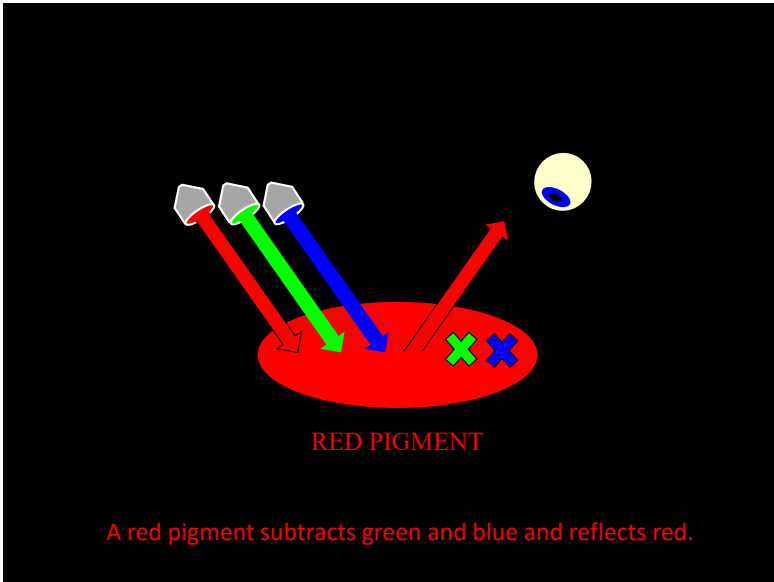
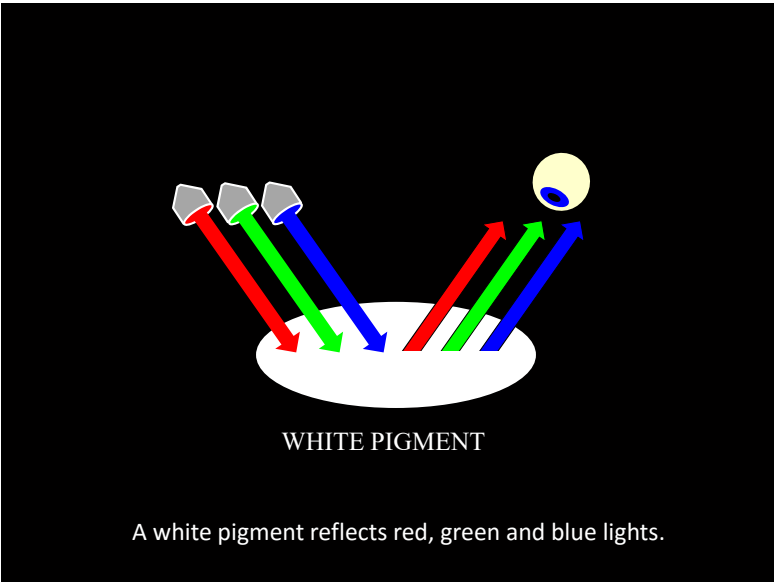


Photo: Jozsef Szasz-Fabian

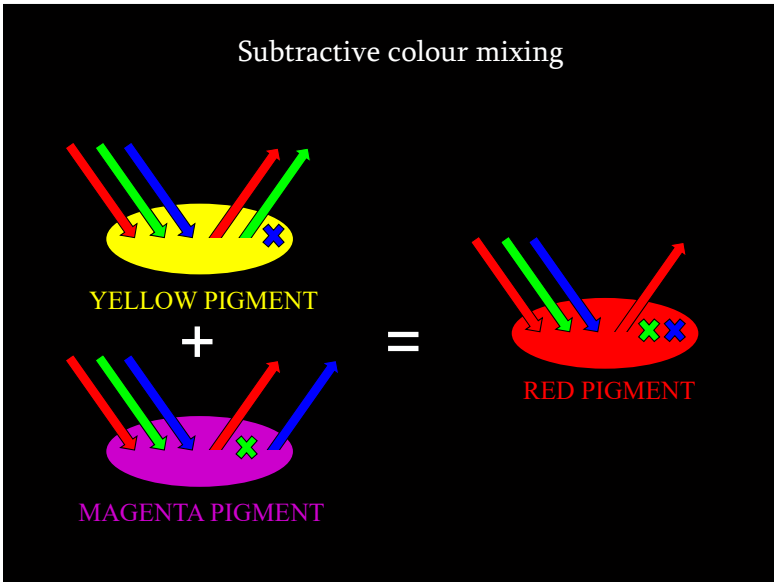
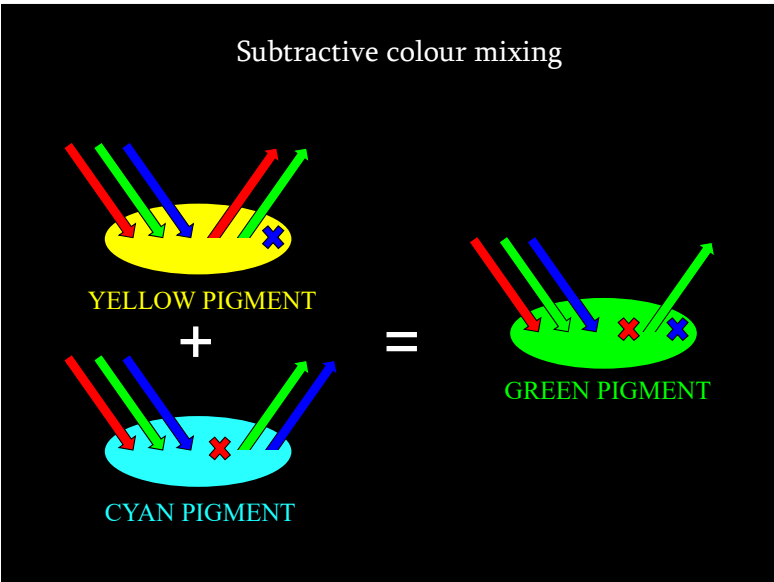
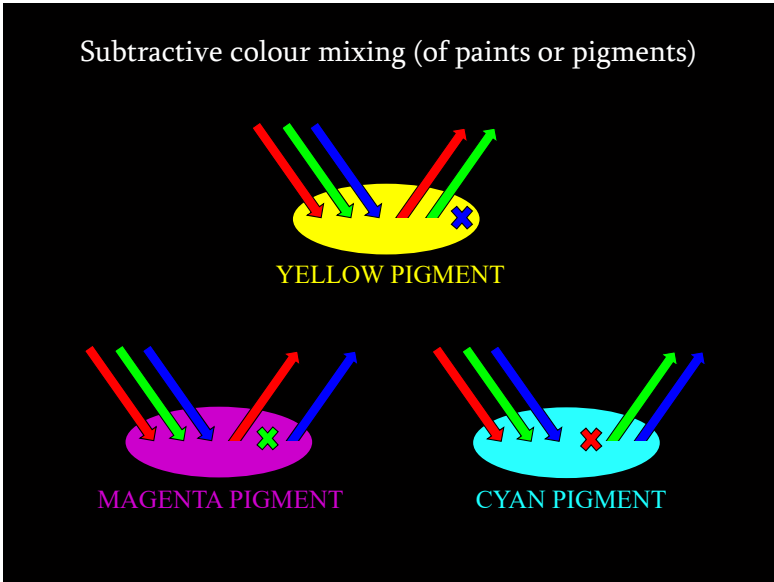
The laws of colour mixing that apply to pigments or paints are different because they depend on what is absorbed or "subtracted" from the reflected light by the pigment.

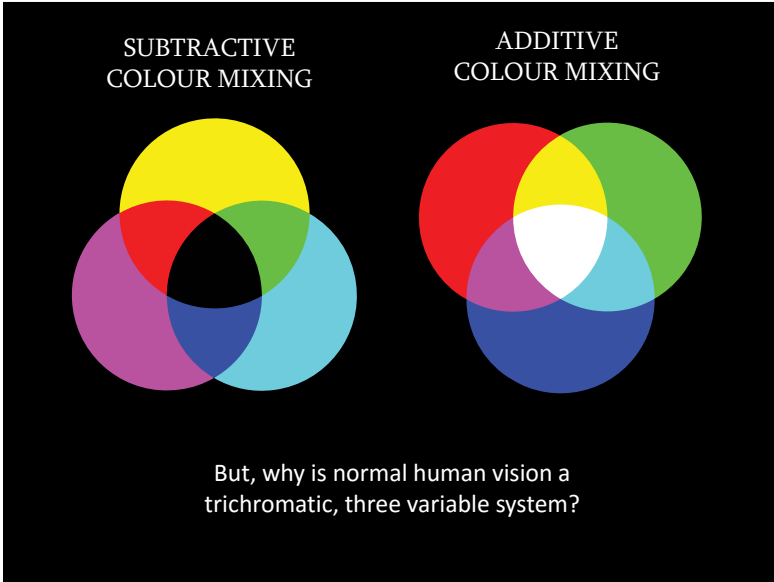
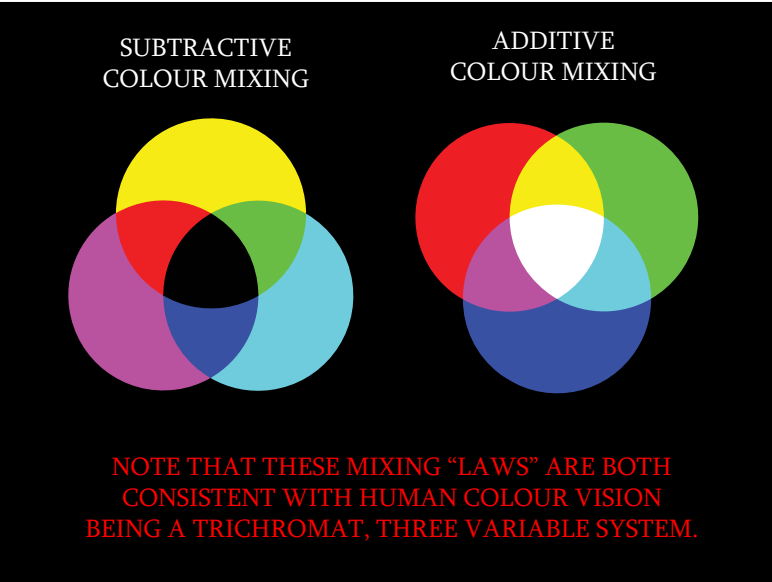
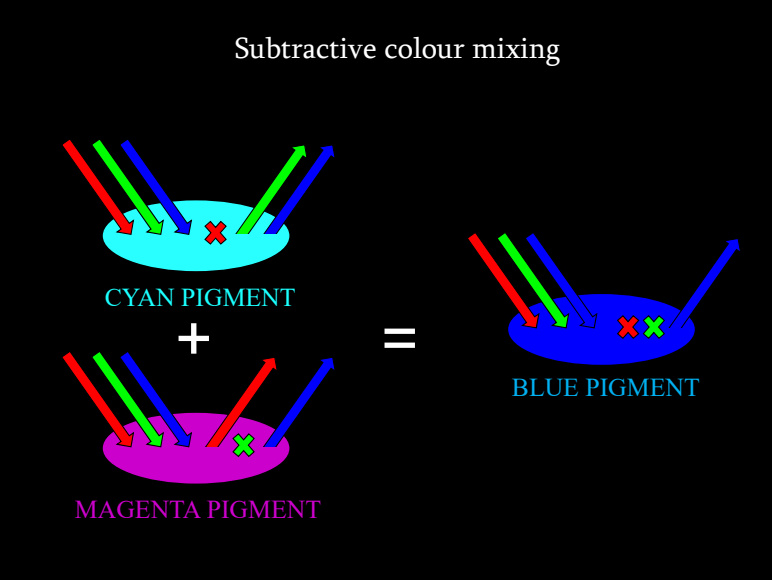


WHITE PIGMENT




Laws of subtractive colour mixing
(of paints or pigments)





One reason, of course, is because just three cone photo-receptors underlie daytime colour vision.



Short-wavelength-sensitive or "blue" Middle-wavelength-sensitive or "green" Long-wavelength-sensitive or "red"

But trichromacy also depends on the fact that the output of each photoreceptor is:

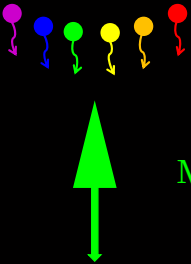
"UNIVARIANT"

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.

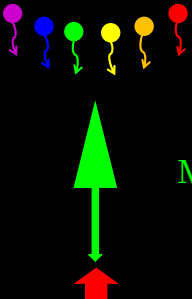


M-cone

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.

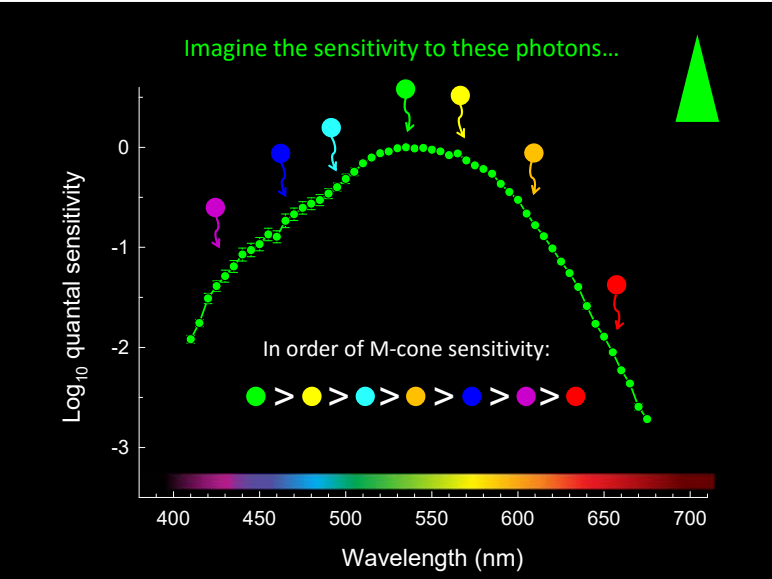
M-cone

All the photoreceptor effectively does is 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".

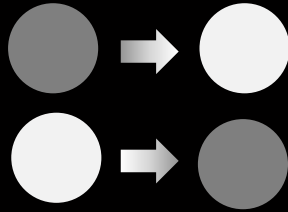


M-cone

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.



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

Univariance

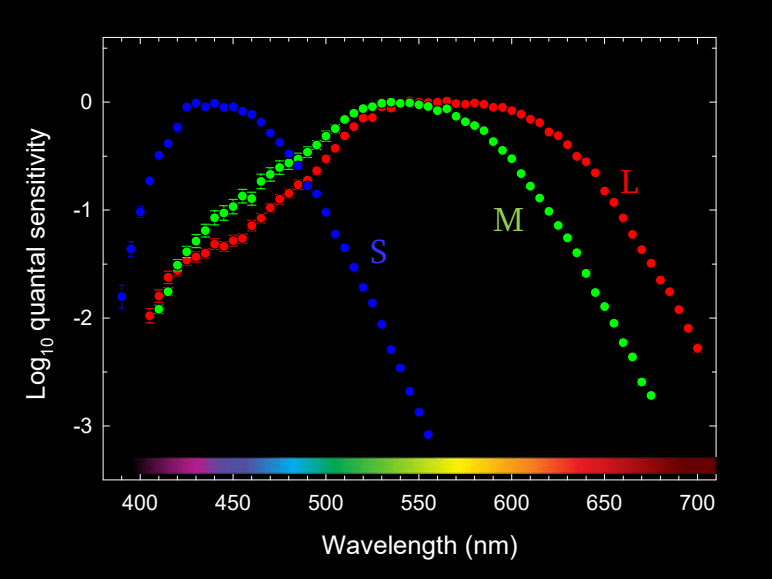
If a cone is n times less sensitive to light A than to light B, then if A is set to be n times brighter than B, the two lights will appear identical whatever their wavelengths.

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



Examples: night vision, blue cone monochromats

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



Their colour vision is therefore three dimensional or:

TRICHROMATIC

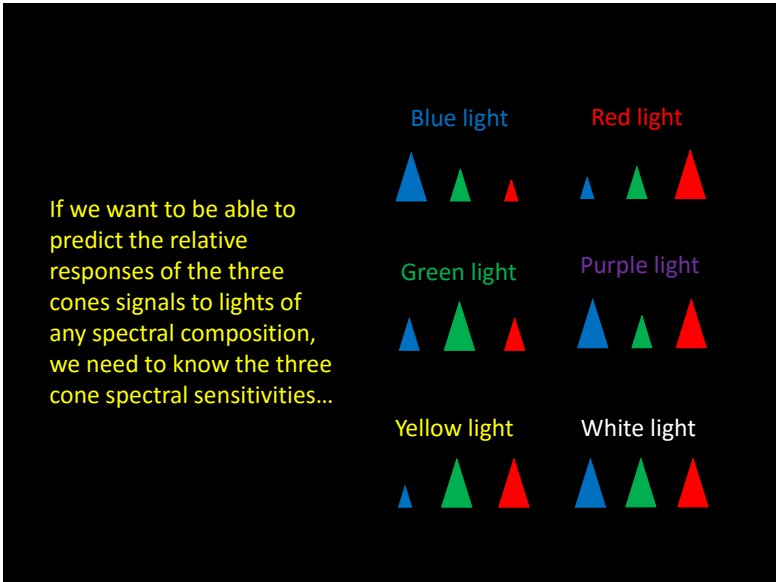
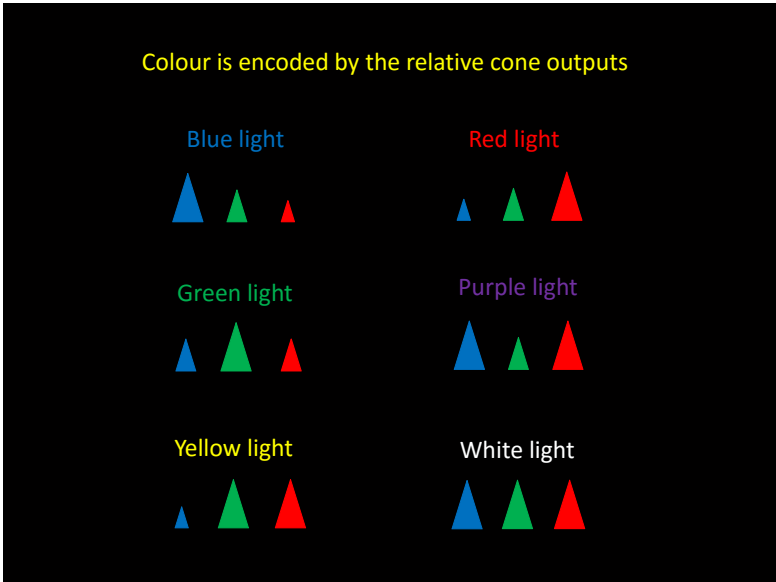
Trichromacy means our colour vision is actually limited

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

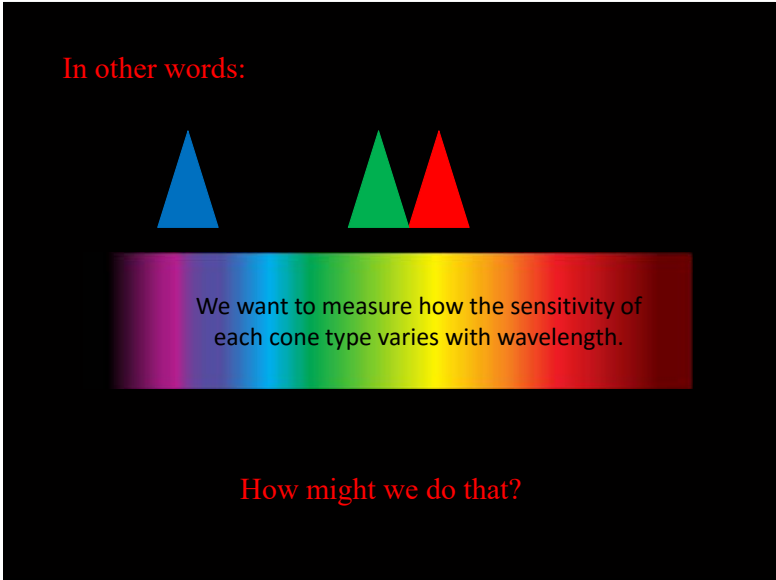
Many of these confusions would be obvious to a being with 4 cone photoreceptors—just as the confusions of colour deficient people are obvious to us.

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?




DETERMINING CONE SPECTRAL SENSITIVITIES

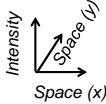


Spectral sensitivity measurements

Flashing or flickering light




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

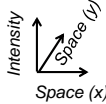


Spectral sensitivity measurements

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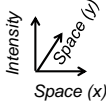


Spectral sensitivity measurements

Flashing or flickering light




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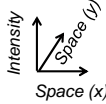


Spectral sensitivity measurements

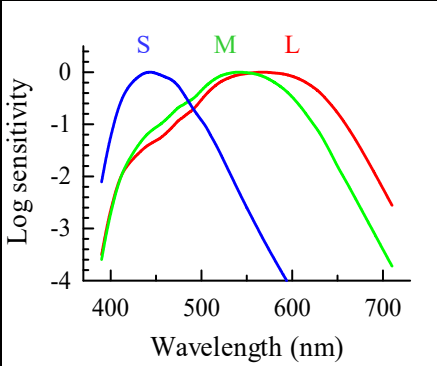
Flashing or flickering light



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

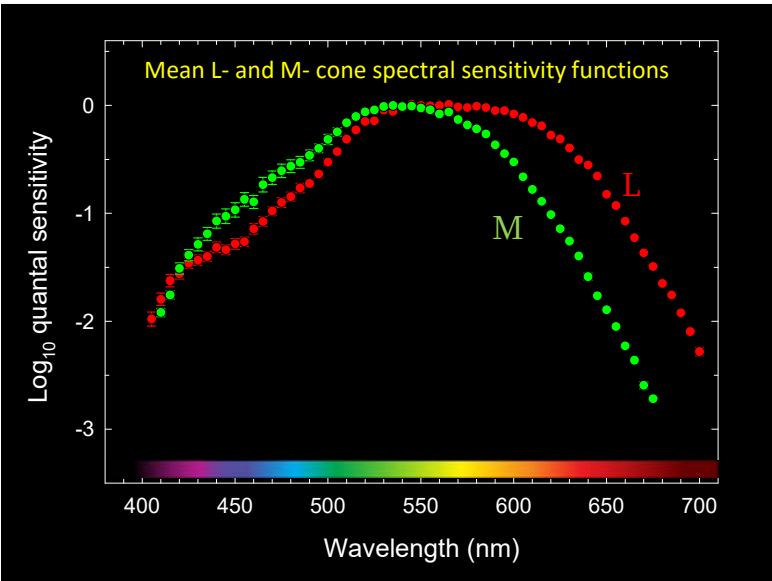
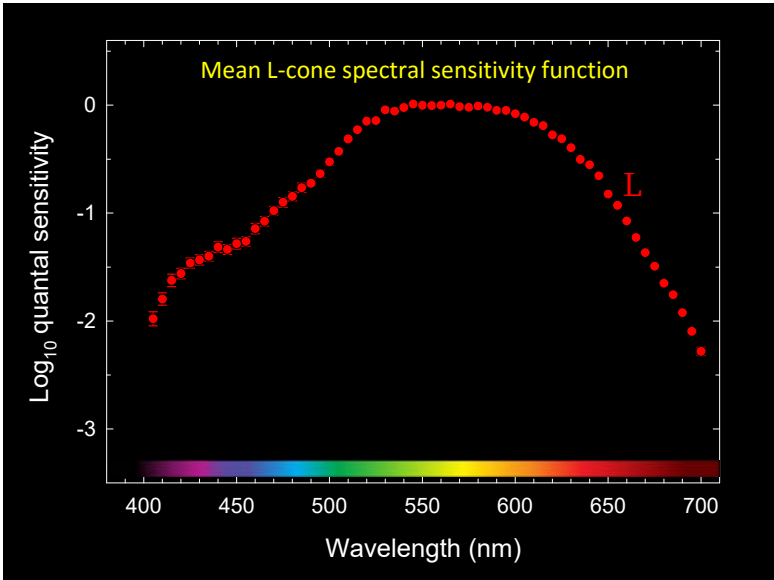
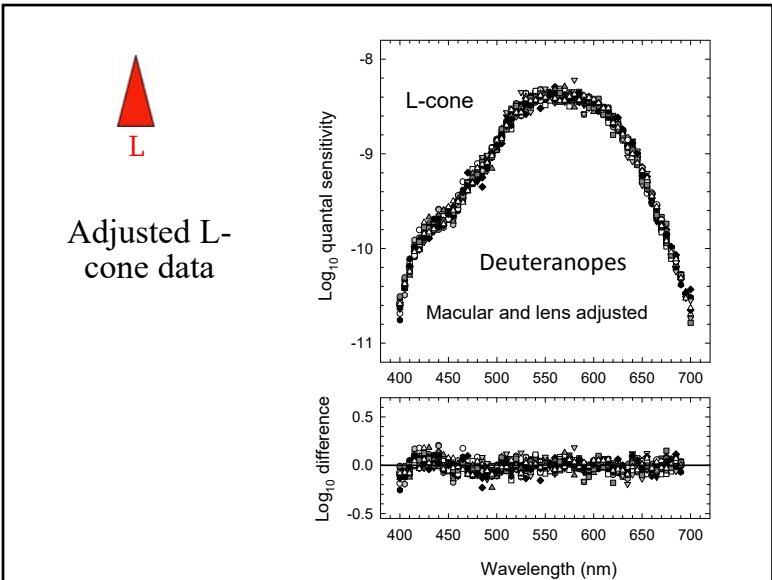
L M S ~~L~~ M S

Protanopia

Normal Deuteranope

L M S ~~L~~ M S

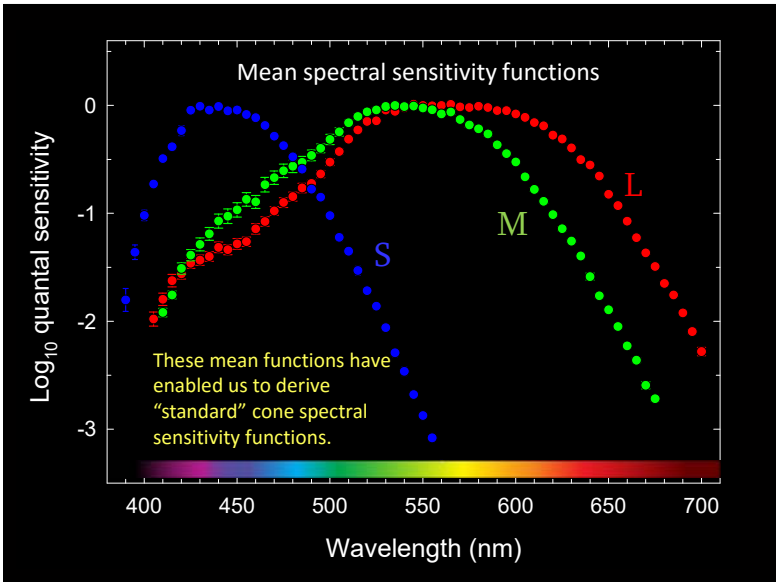
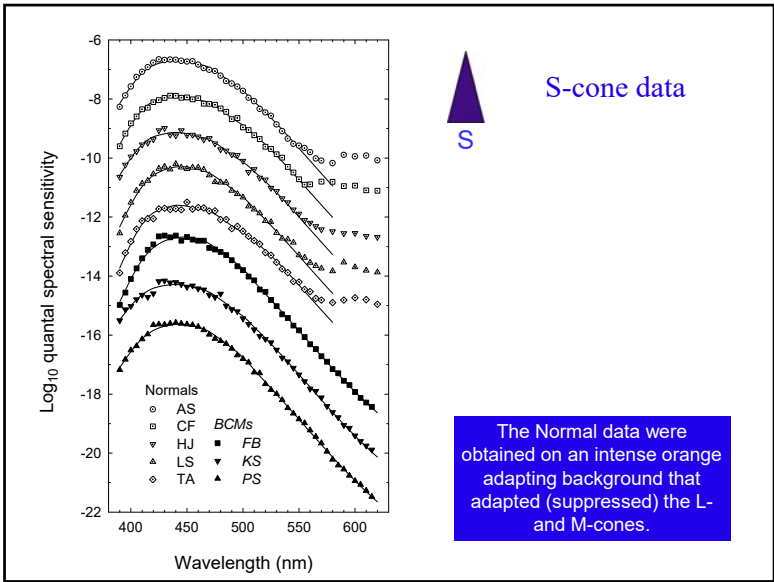
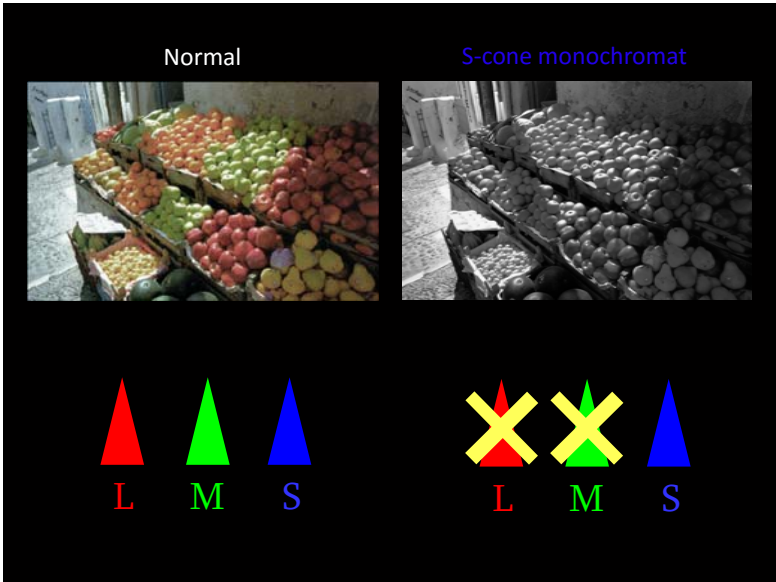
Deuteranopia



S-cone measurements

Two types of subjects:


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

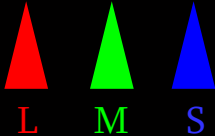



Why study spectral sensitivities?

- ▶ 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.

Normal Tritanope




L M S L M S

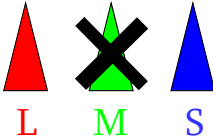
Tritanopia

Deuteranope



Credit: Euro Puppy Blog

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




L M S

COLOUR VISION AND MOLECULAR GENETICS

Normal Deuteranope

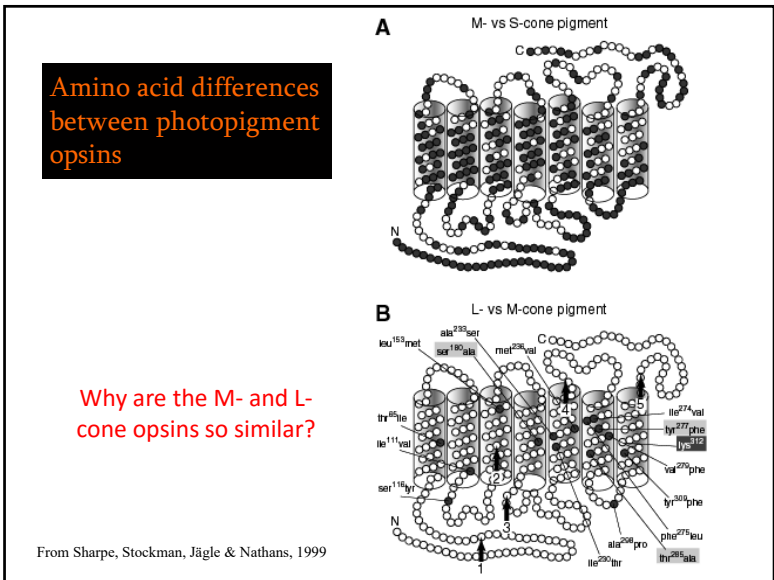
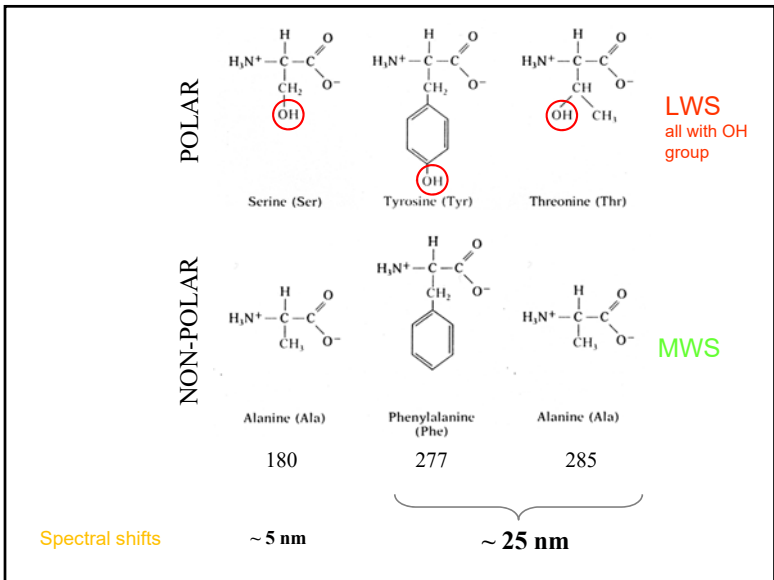
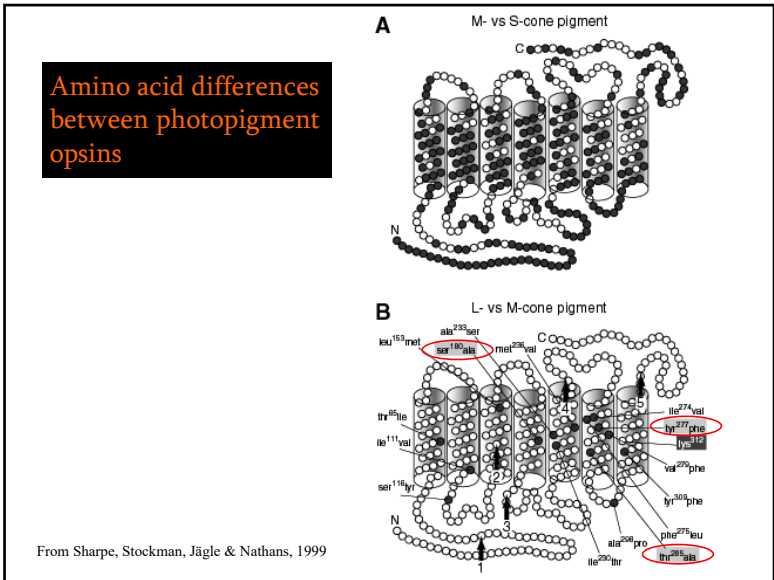
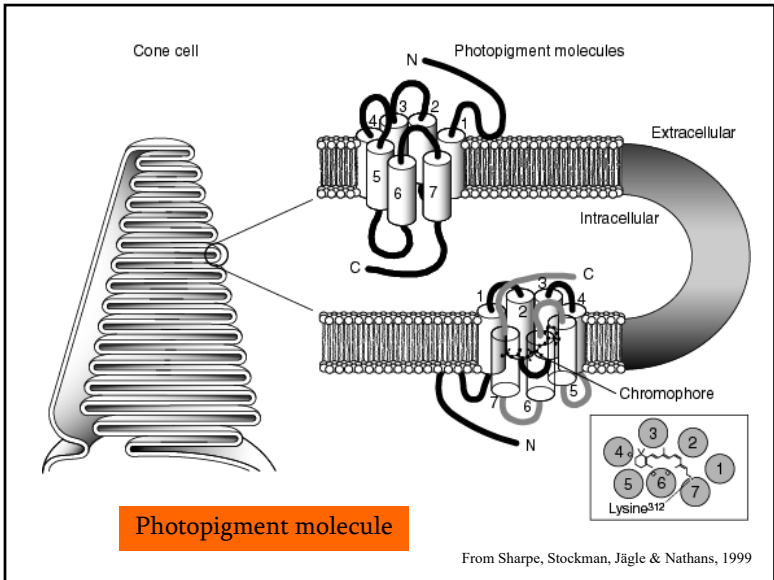


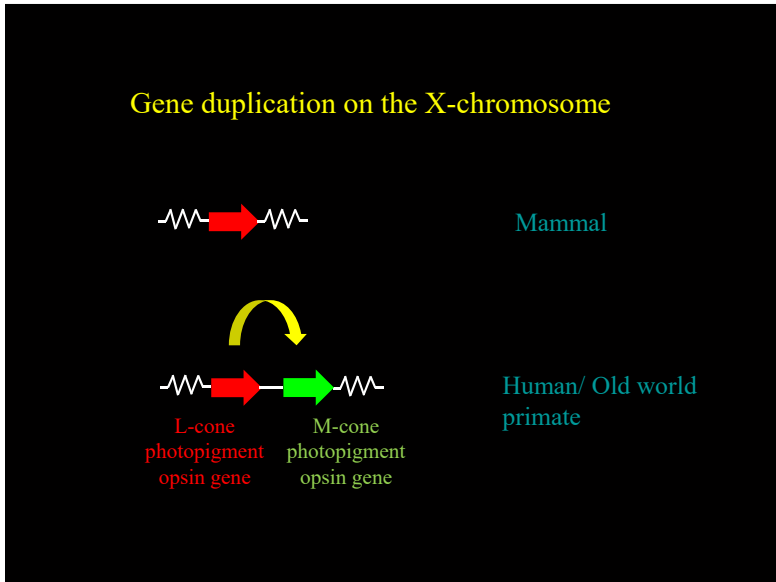
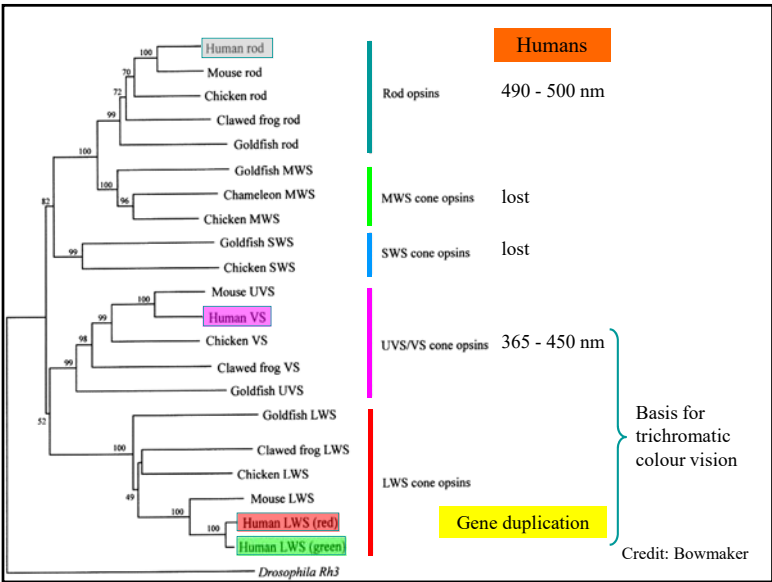
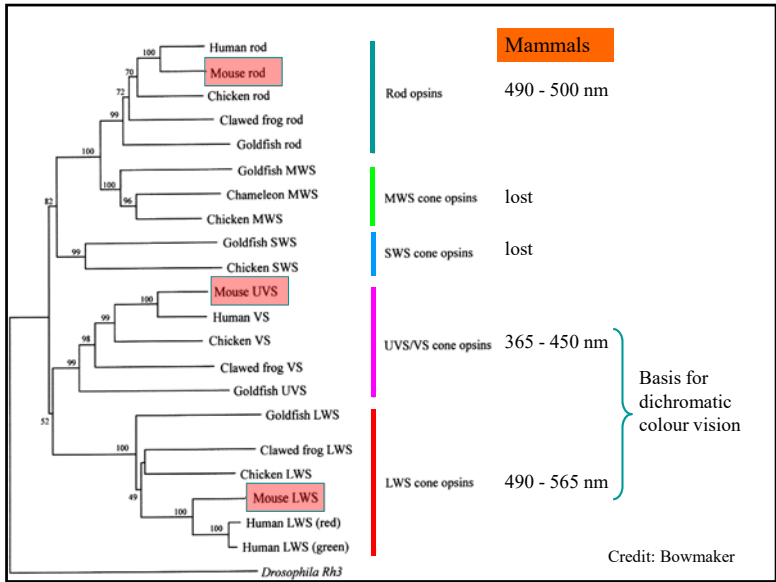
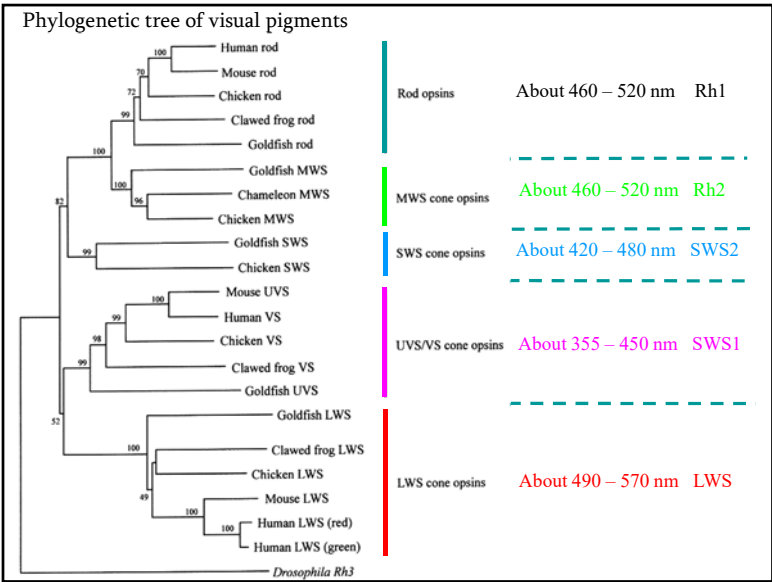
Protanope



How do red-green colour vision deficiencies arise?

From Sharpe, Stockman, Jägle & Nathans, 1999





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 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

Deuteranope

Normal

Protanope

Hybrid (mixed) L/M genes

Deuteranope or Deuteranomalous trichromat

Protanope or Protanomerous trichromat

Deuteranope or Deuteranomalous trichromat

From Sharpe, Stockman, Jägle & Nathans, 1999

Log₁₀ quantal sensitivity

Wavelength (nm)

M

More M-cone like

More L-cone like

L

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

Single-gene dichromats

Protanope

Deuteranope

With a single gene male observers must be dichromats

Multiple-gene dichromats

Male observers with two similar genes may also be effectively dichromats if the two genes produce similar photopigments.

Anomalous trichromats

Severe

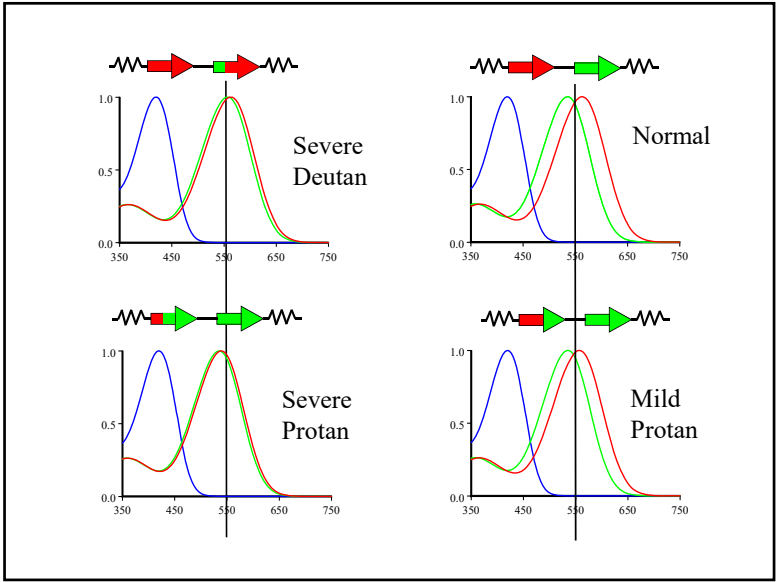
Protanomalous

Mild

Deuteranomalous

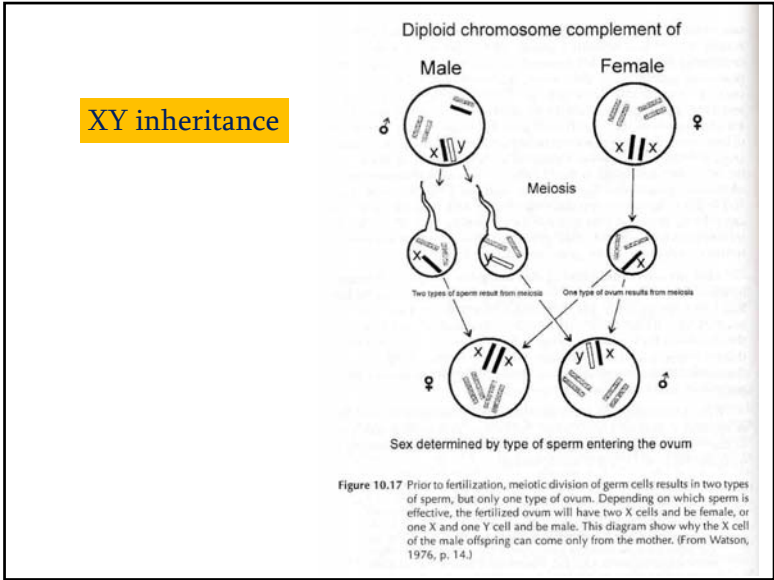
Severe

Male observers with two different genes are "anomalous" trichromats



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



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

Why is it important?



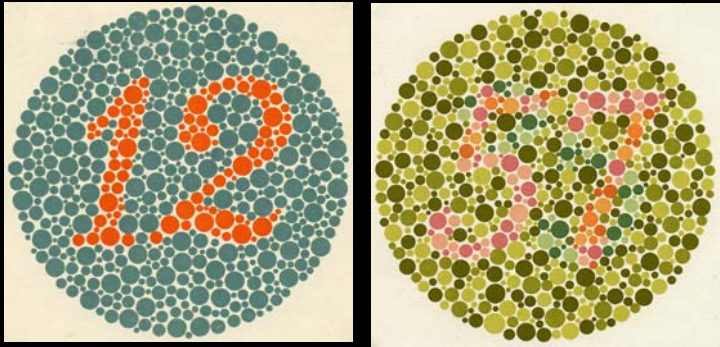
Red-green discrimination

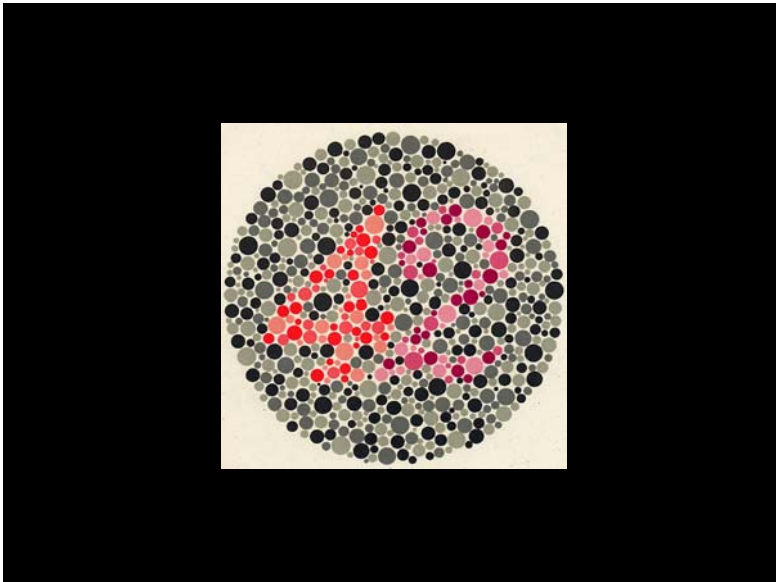


Source: Hans Jretel

DIAGNOSING COLOUR VISION DEFICIENCIES

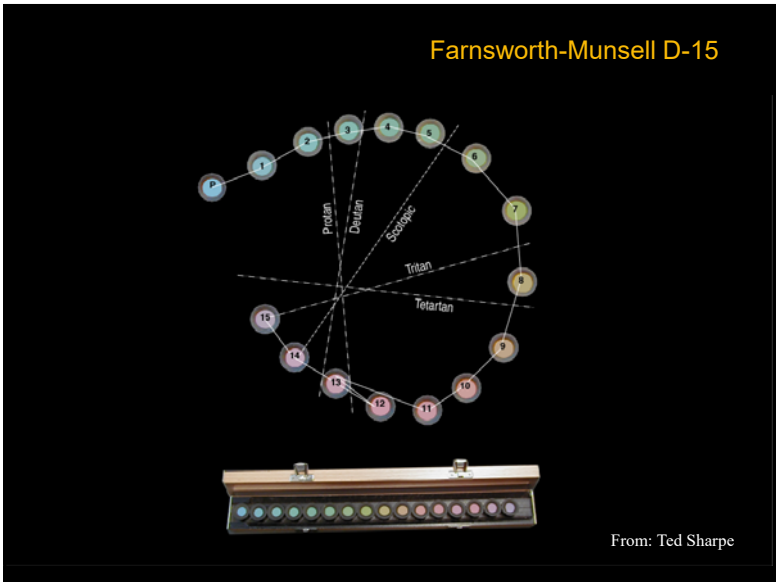
Ishihara plates

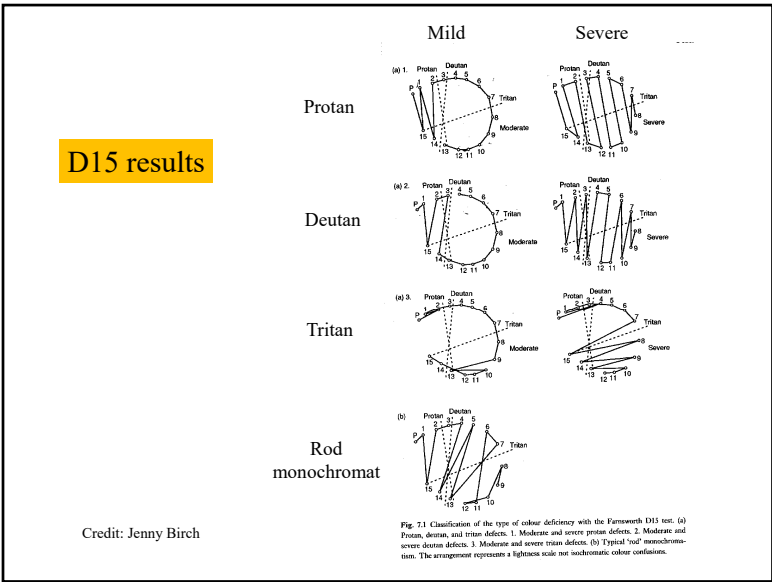




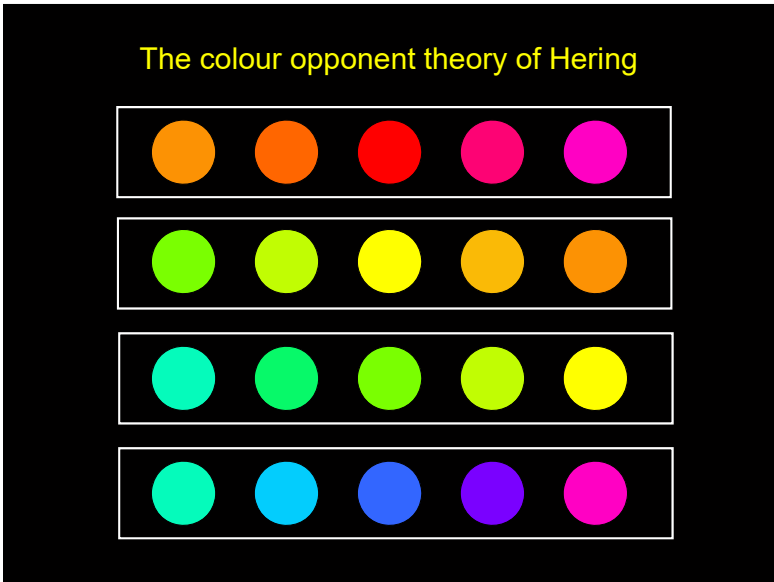
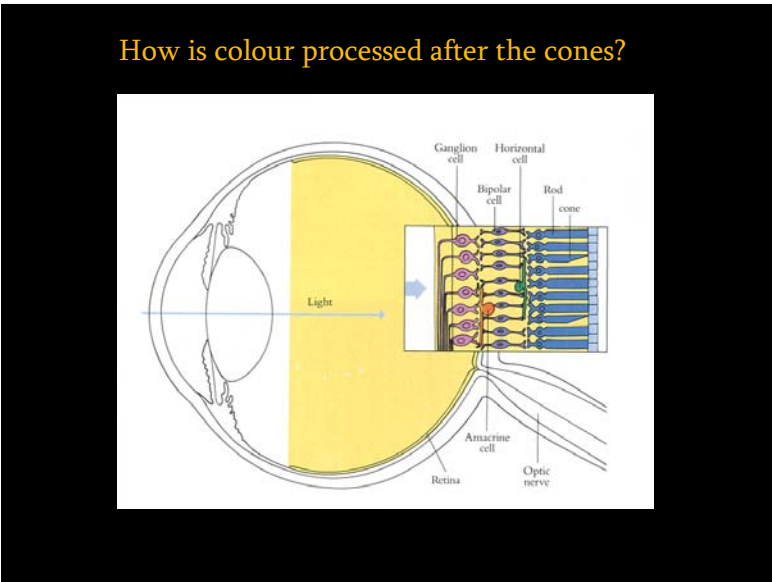
Tests measuring colour discrimination

- Farnsworth-Munsell D-15 test





POSTRECEPTORAL COLOUR VISION



The colour opponent theory of Hering

Red is opposed to Green R-G

Yellow is opposed to Blue Y-B

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

Some ganglion cells are colour opponent

RED On-centre
GREEN Off-surround

Some ganglion cells are colour opponent

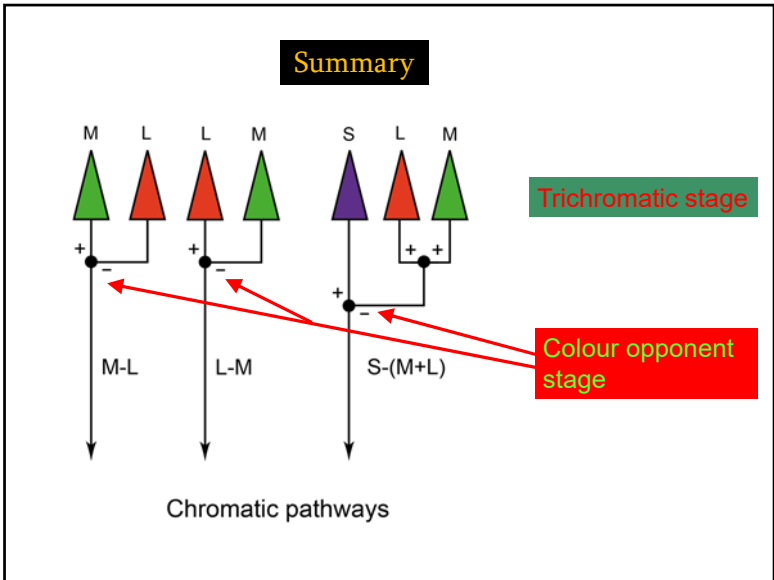
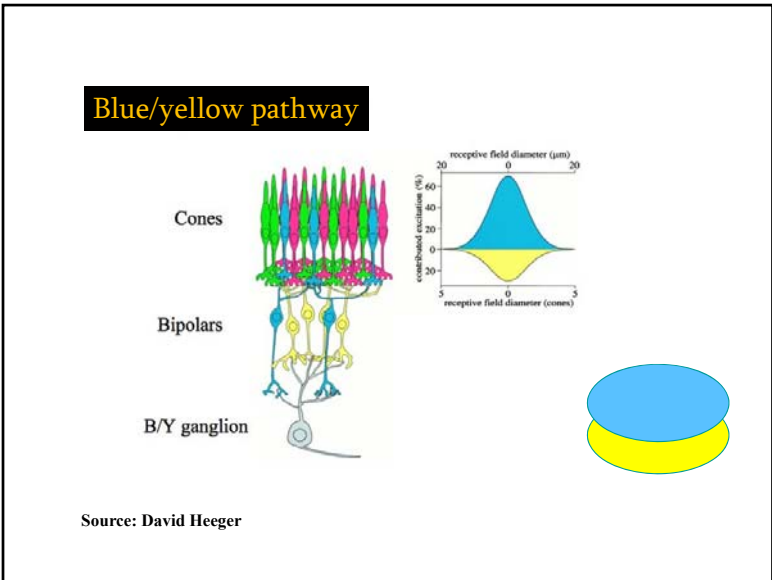
GREEN On-centre
RED Off-surround

Red-green colour opponency

Four variants

color-opponent concentric rf

color-opponent concentric rf



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

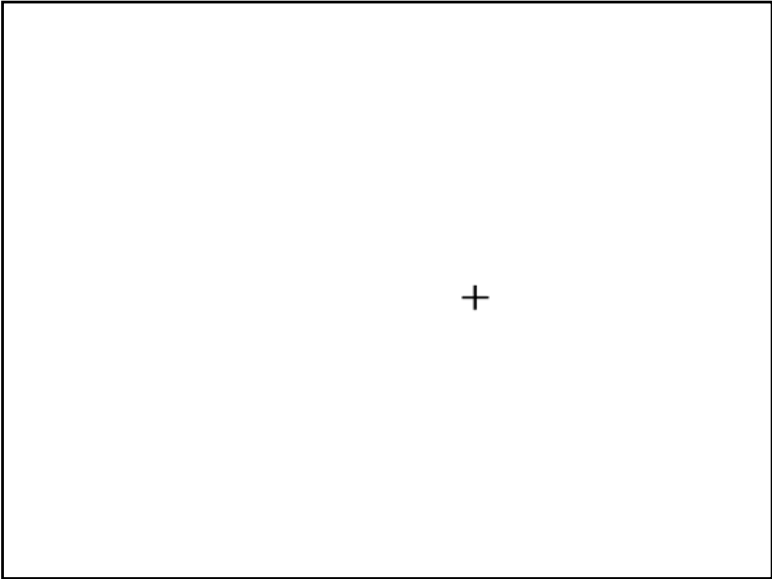
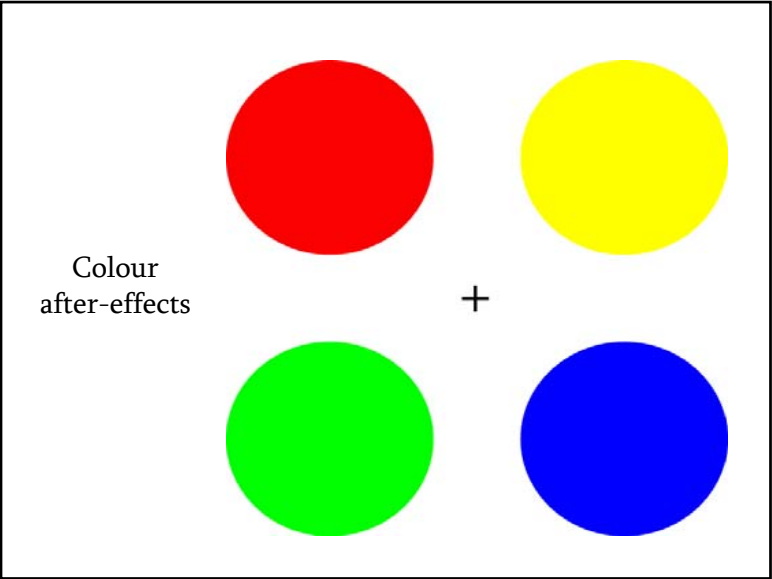
- (ii) What surrounds it (in space)

COLOUR CONTRAST

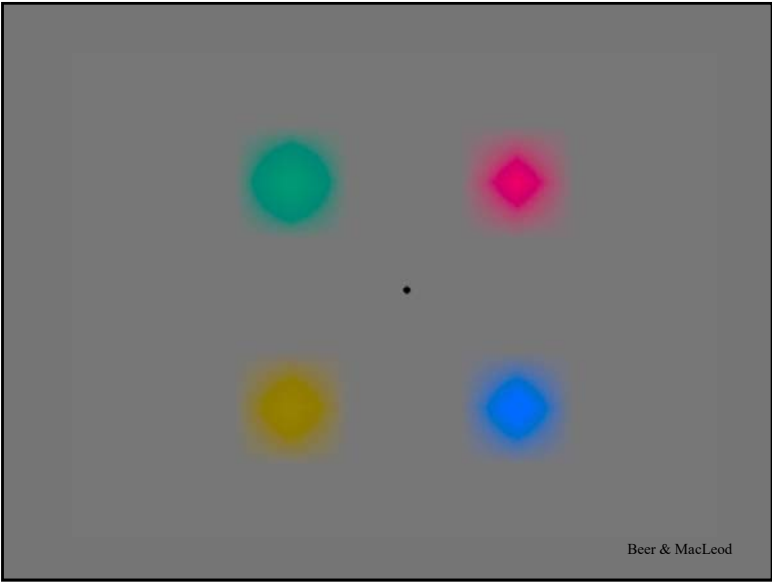
COLOUR ASSIMILATION

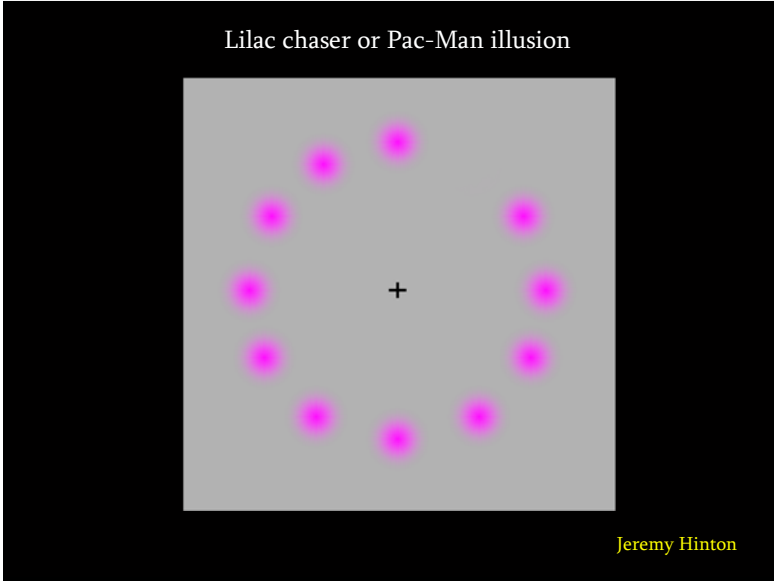
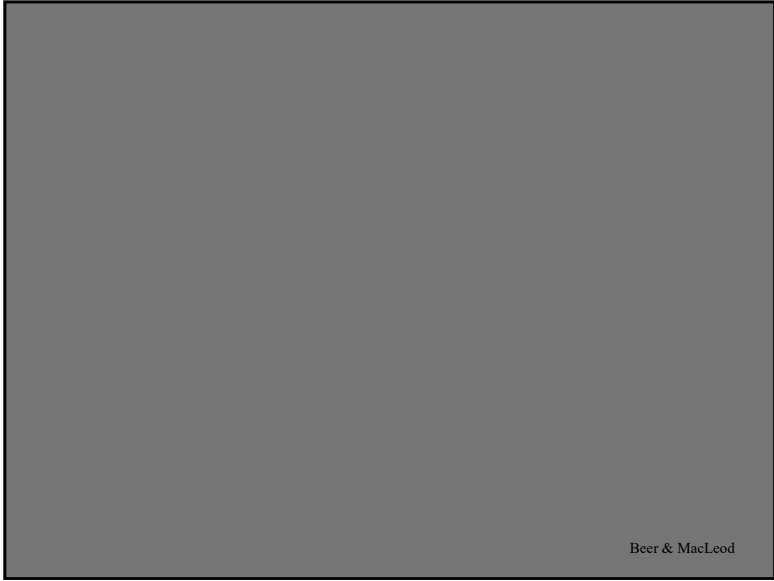
COLOUR AFTER-EFFECTS

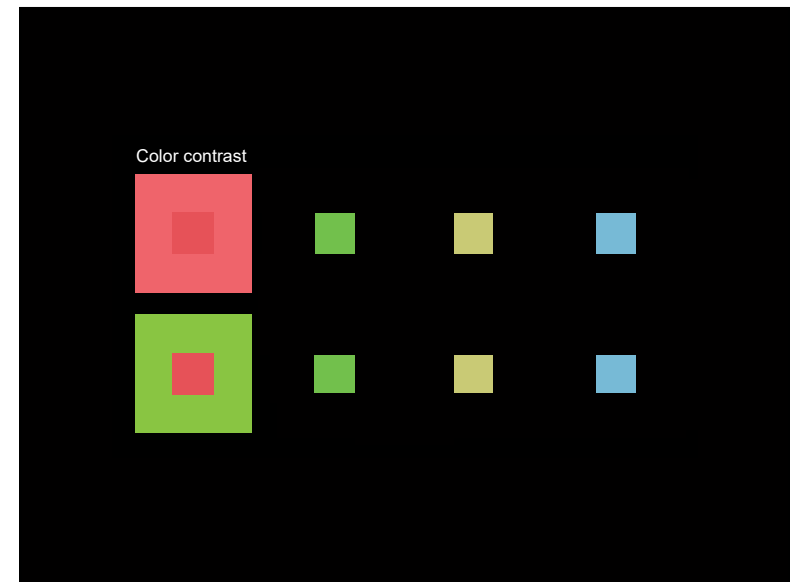
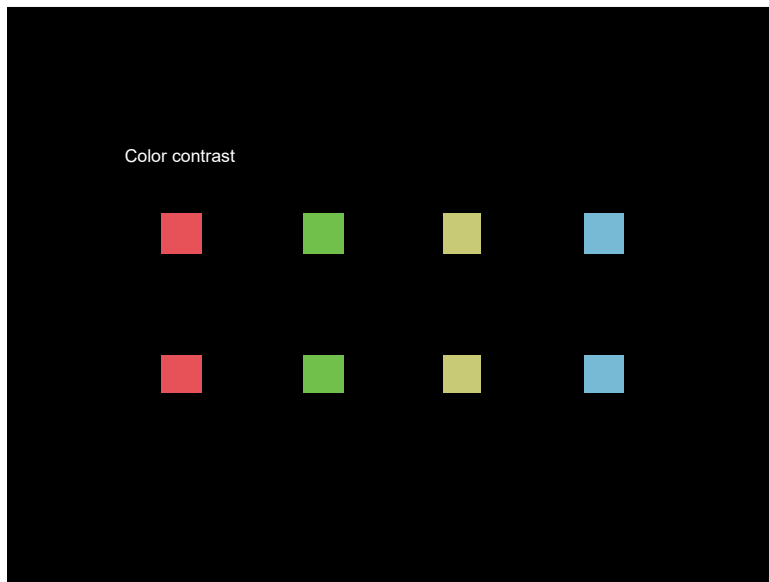
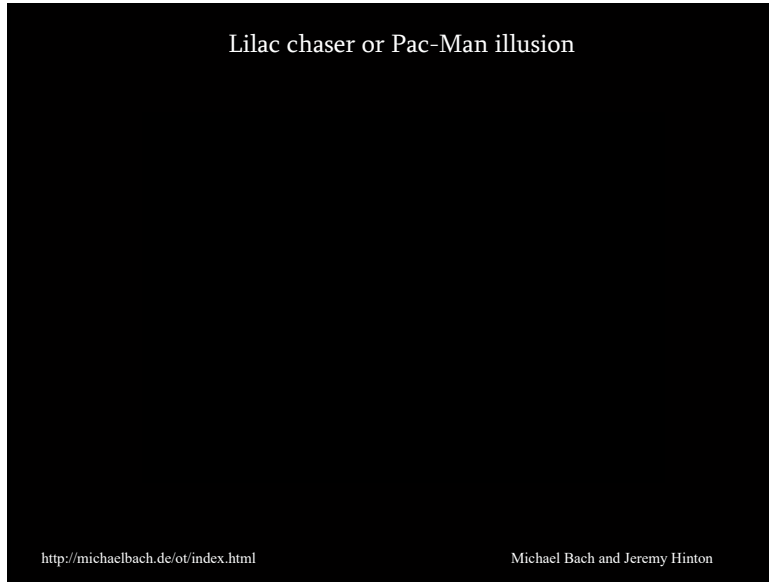
(what precedes the patch)

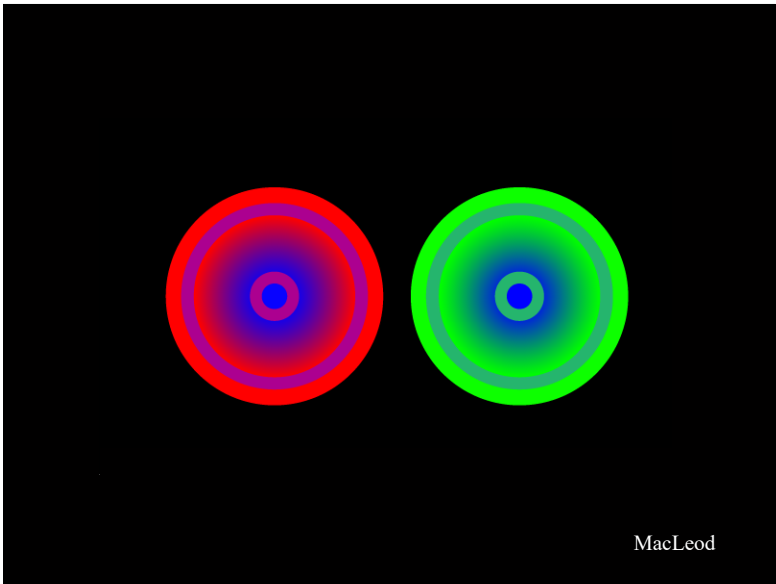
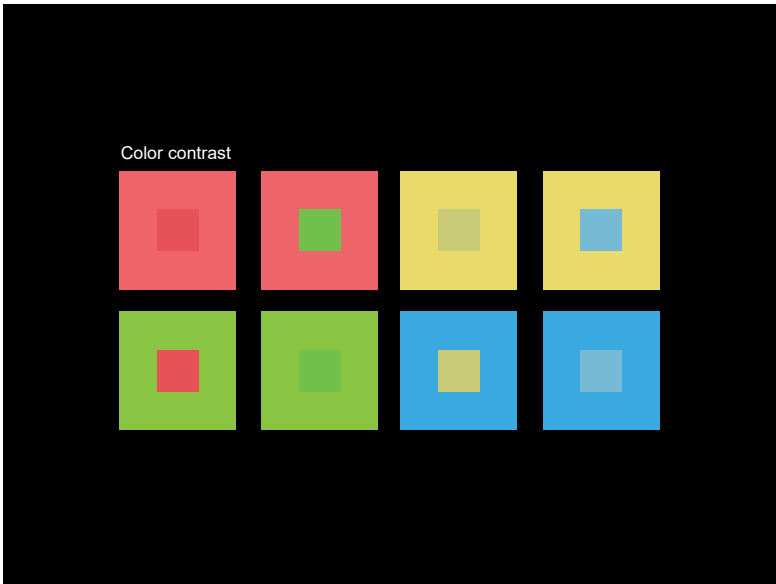
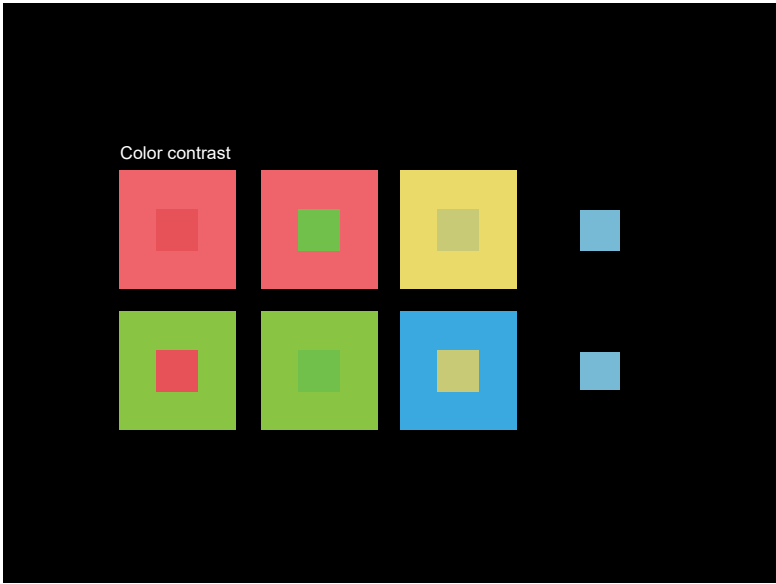
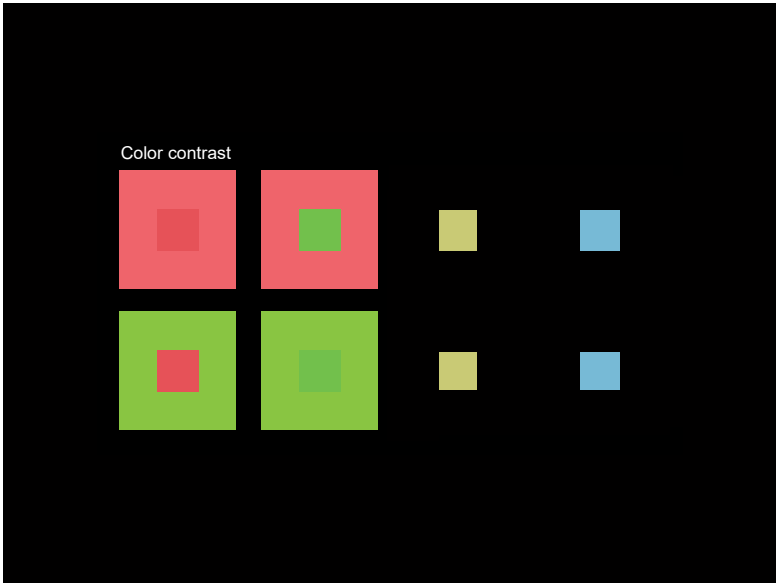


You don't have to see things for them to produce an after-effect...

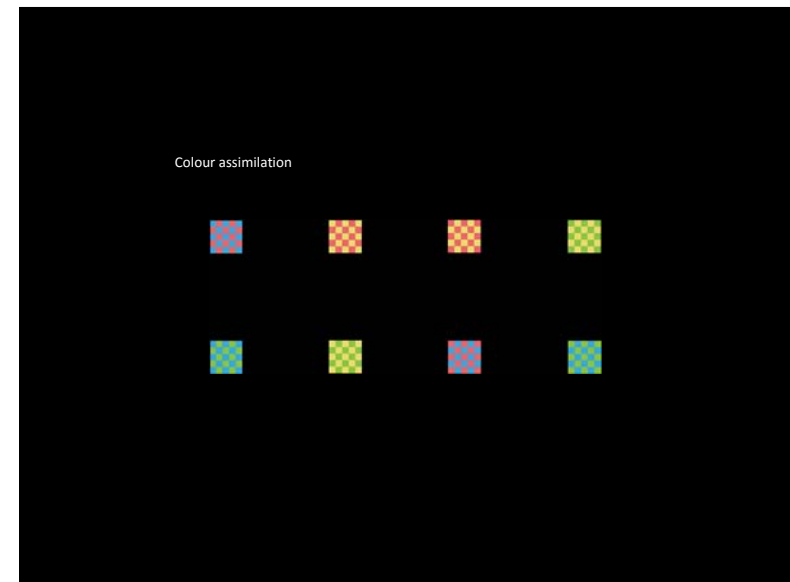
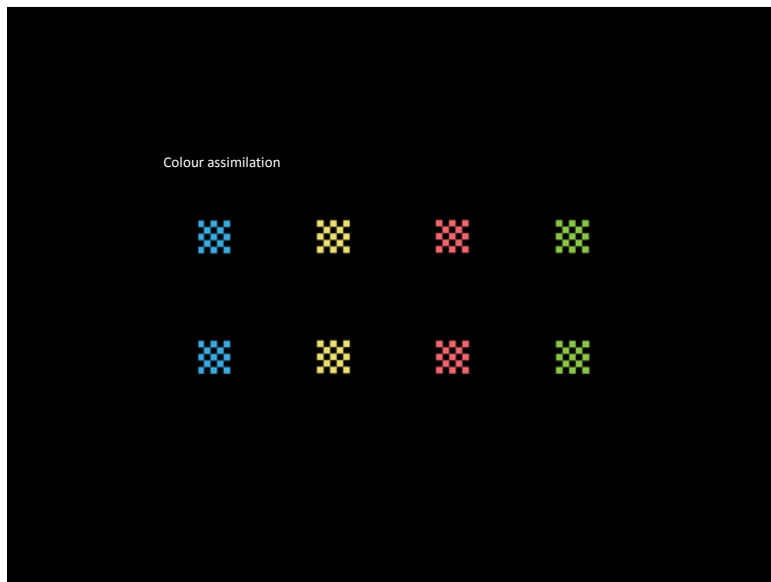
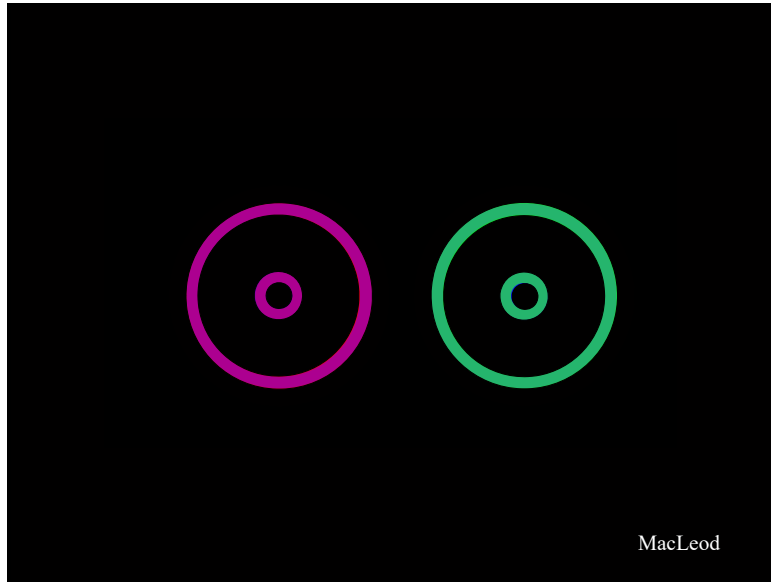


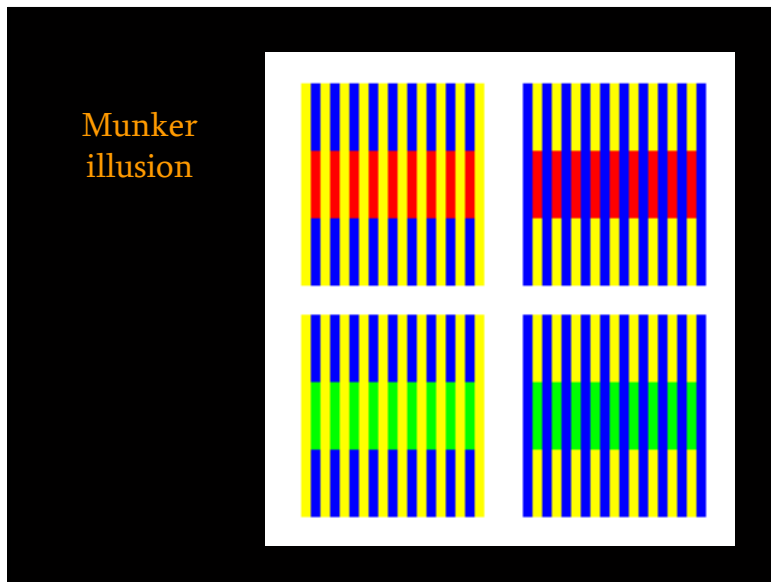
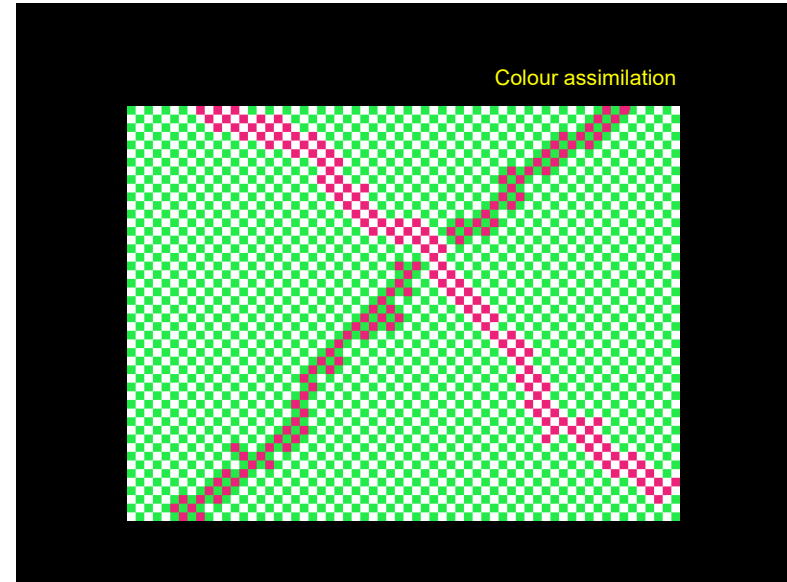
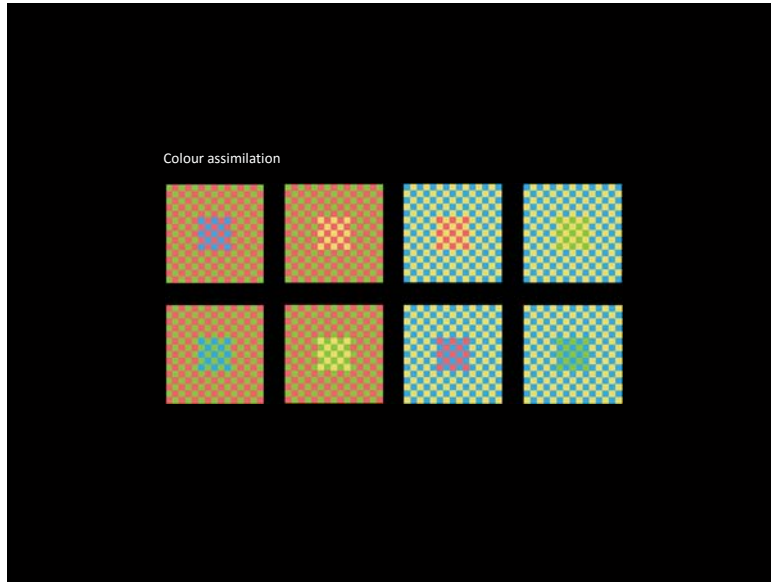




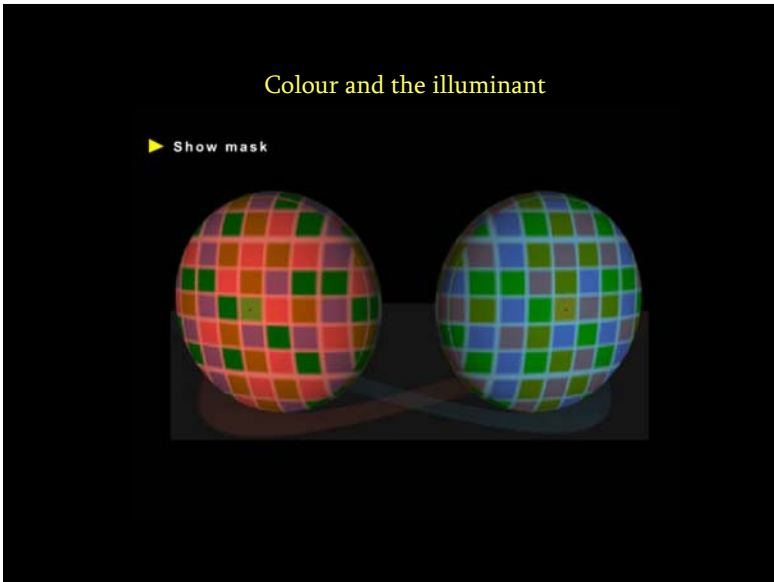
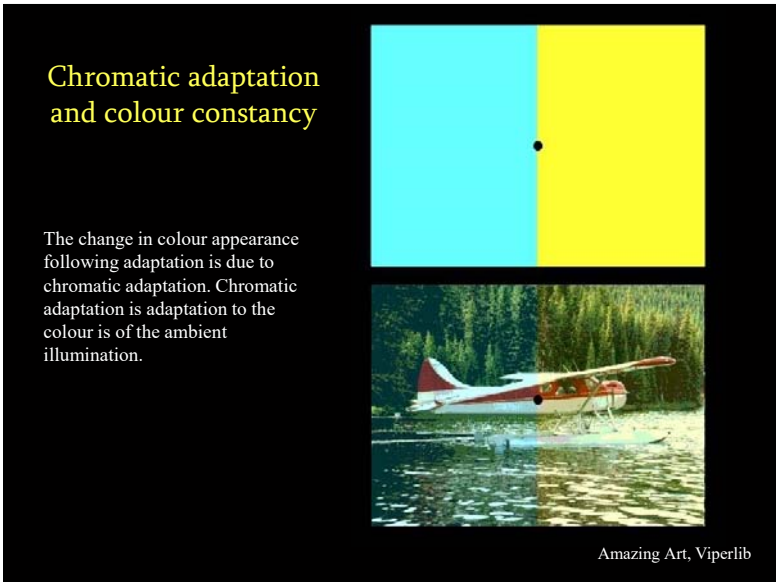
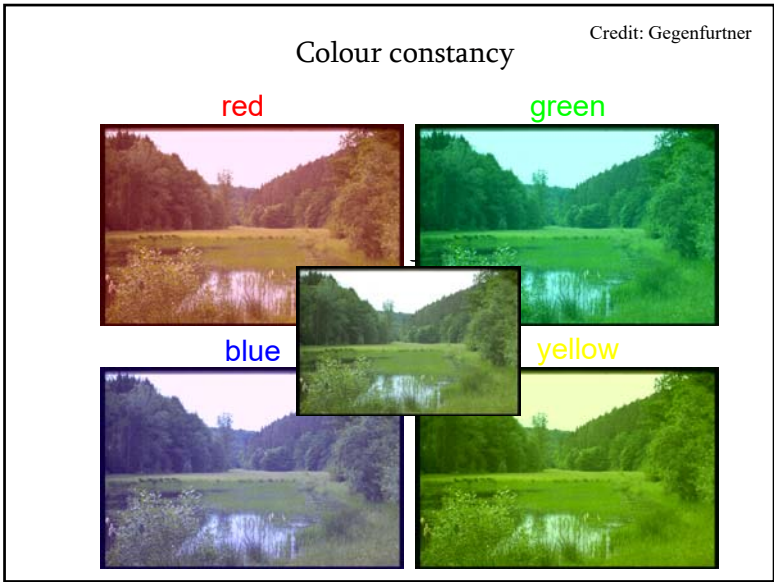


MacLeod






COLOUR CONSTANCY



Colour and brightness

THE EFFECT OF COLOR ON BRIGHTNESS PERCEPTION



The color of the "brown" Chitka-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)]
© Copyright Dale Purves 2000 All rights reserved.

This image combines illusions of form and colour. The central element of the two 'X' objects appear very different in colour (dark blue on the left and light yellow on the right). What's more, the angles of each 'X' appear either smaller or larger than 90 degrees.

MASK

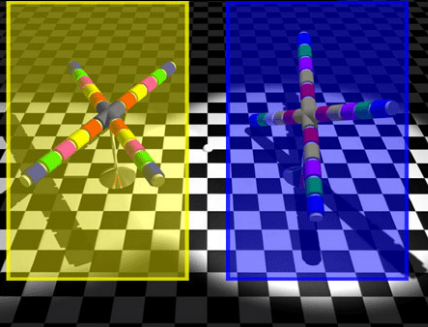


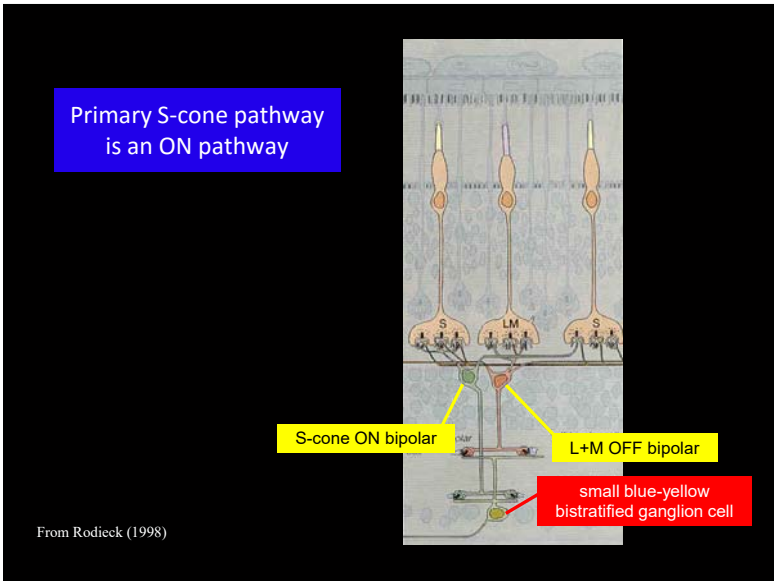
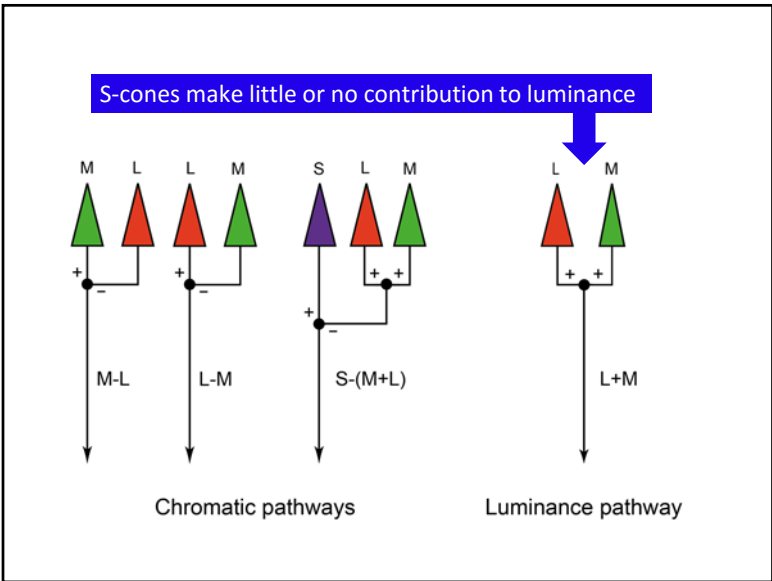
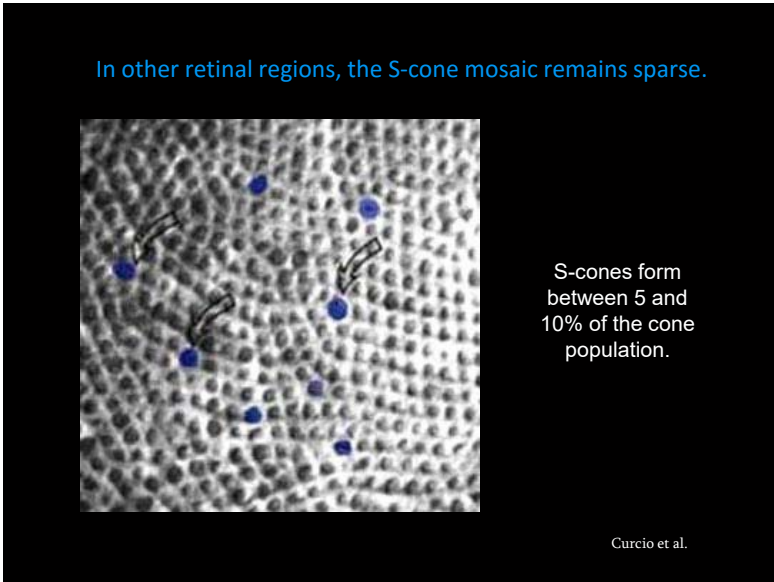
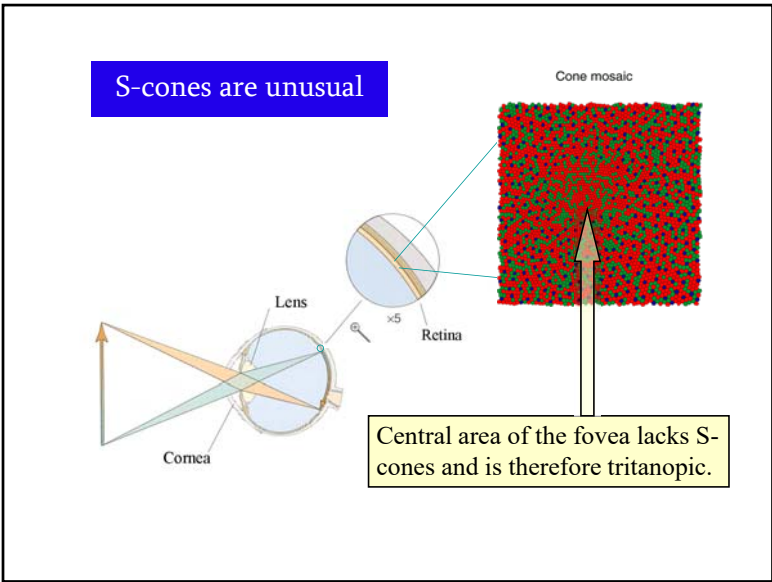
Image by R. Beau Lotto

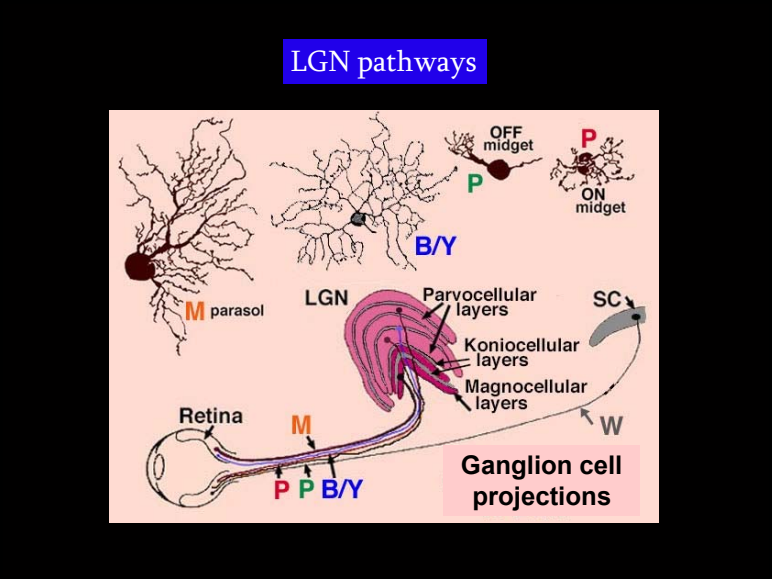
IMAGE



Image by R. Beau Lotto

S-CONE MEDIATED VISION IS UNUSUAL

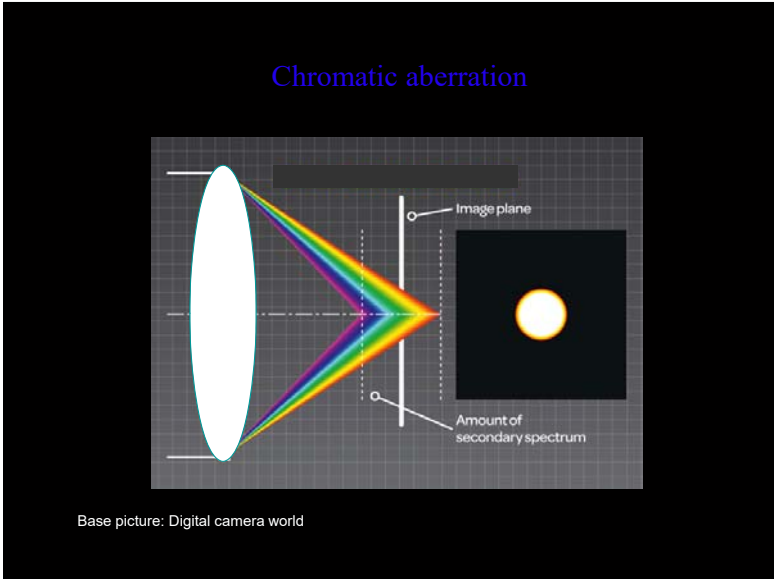


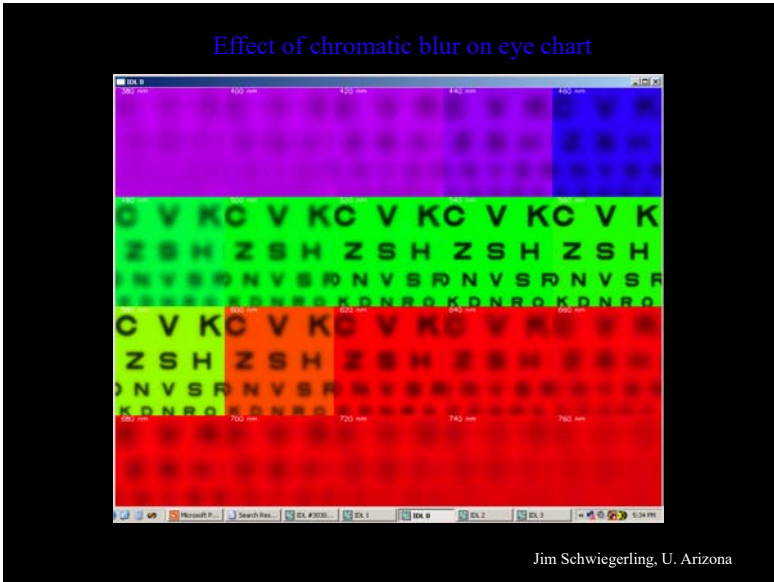


S-cone vision is slow

A red circular logo is located in the top right corner. Below it is a small rectangular box containing text that is mostly illegible but appears to include copyright information: "© Trustees of British University, 2003".

Why is S-cone vision sparse?





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 **GREEN**, 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?