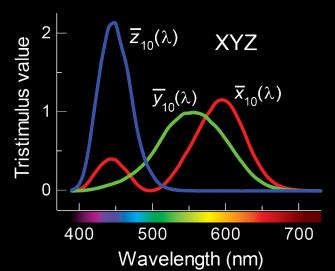


## Modelling and estimating individual cone spectral sensitivities



Andy Rider

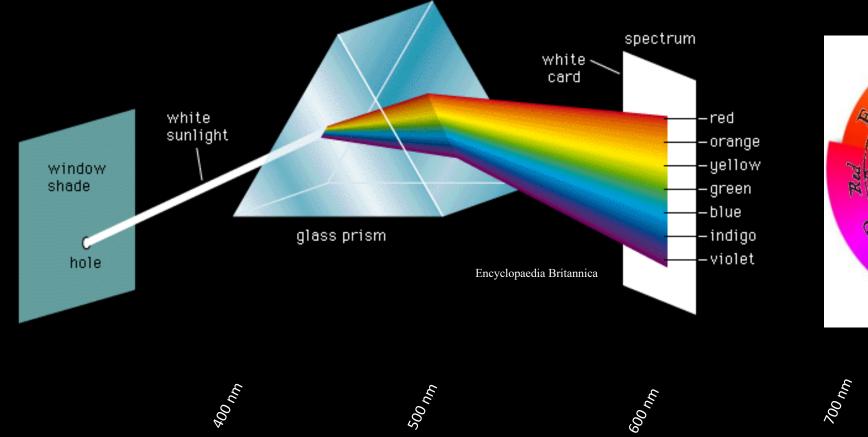


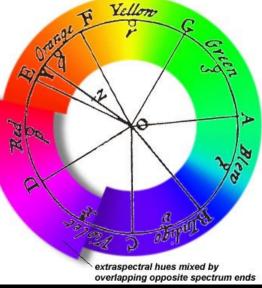
# Outline

- Introduction to vision, cone spectral sensitivities, and colour matching functions (CMFs)
- Individual differences in cone fundamentals and CMFs
- Modelling cone fundamentals
- Estimating individual differences



### 390 - 700 nm is important for vision

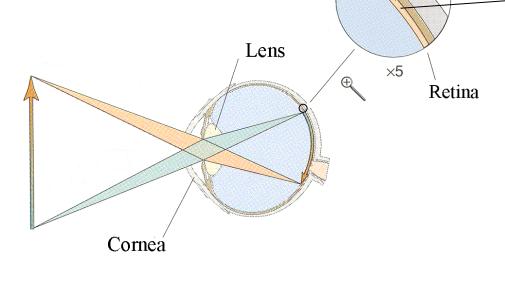




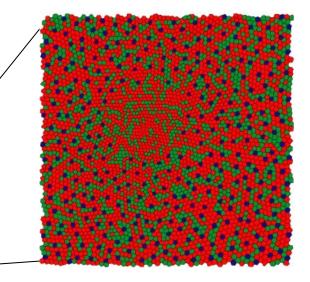


## How do we see colour?

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

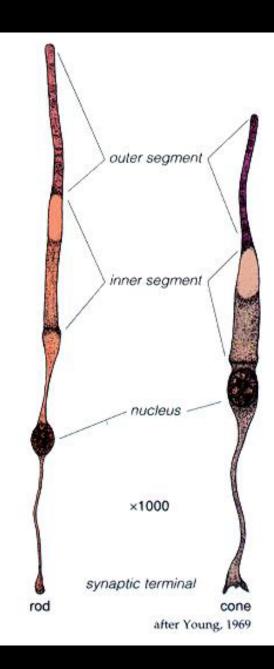


Cone mosaic



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.)



# Human photoreceptors

Rods

 Achromatic night vision

1 type

Rod

<u>Cones</u>

 Daytime, achromatic and chromatic vision

3 types

Long-wavelengthsensitive (L) cone or "red" cone

Middle-wavelengthsensitive (M) cone or "green" cone

Short-wavelengthsensitive (S) cone or "blue" cone

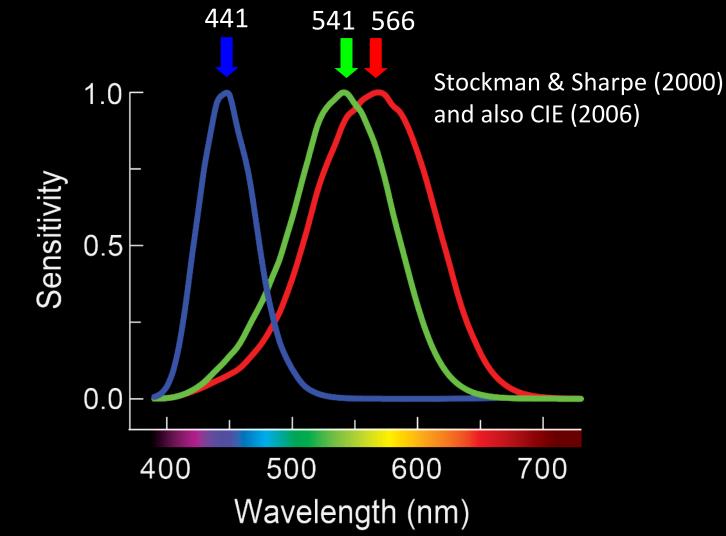
## Trichromacy



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

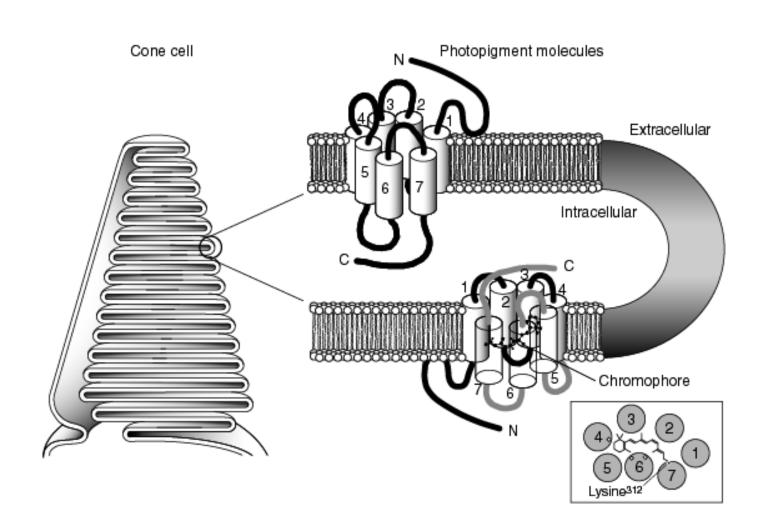
It is a 3-variable system

Trichromacy arises because there are just three cone types each of which is "univariant" and each cone type which has a different spectral sensitivity.



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

## Cone outer segment

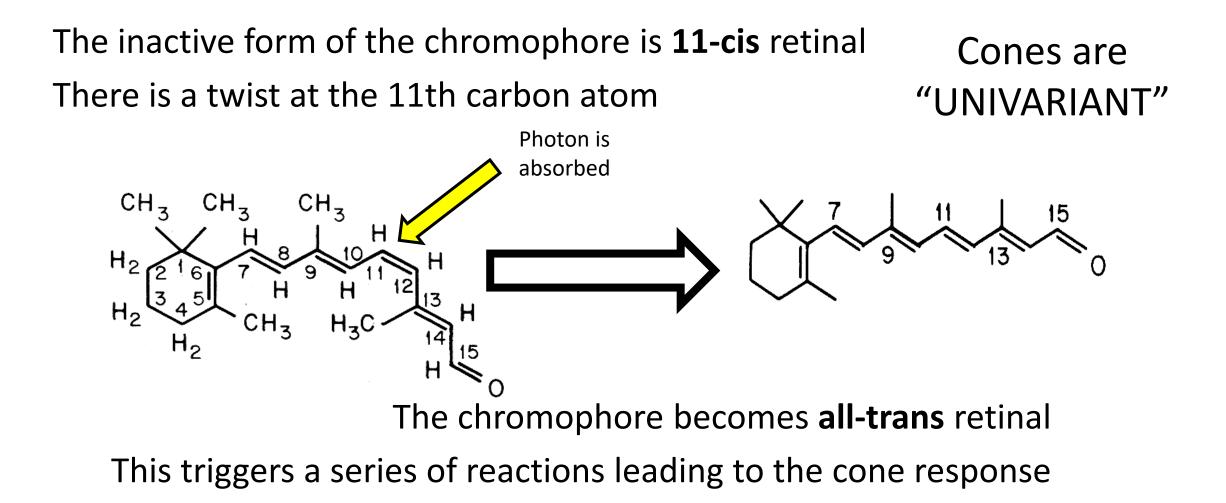


The photopigment, **opsin**, has 7 transmembrane helices

The chromophore, **retinal** (the aldehyde of vitamin A), sits in the middle



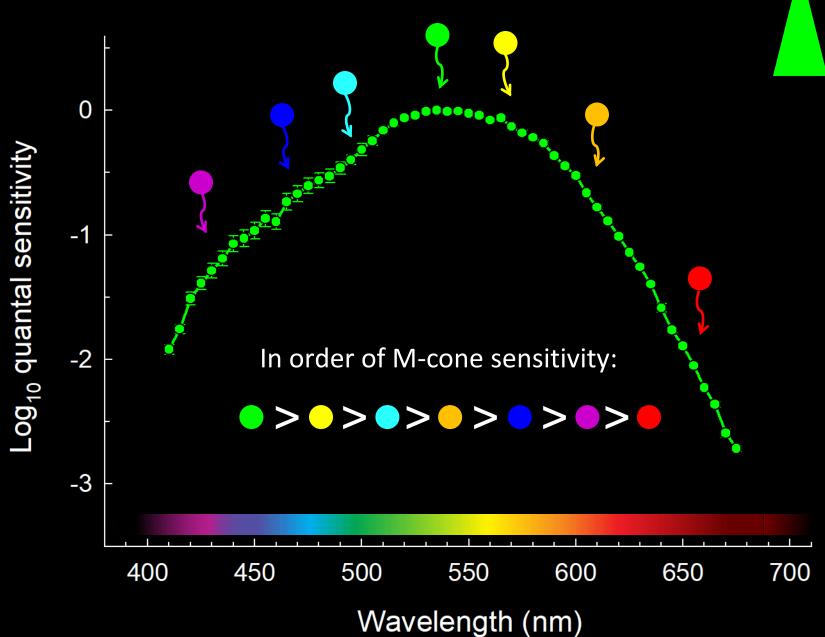
Doesn't matter what wavelength!



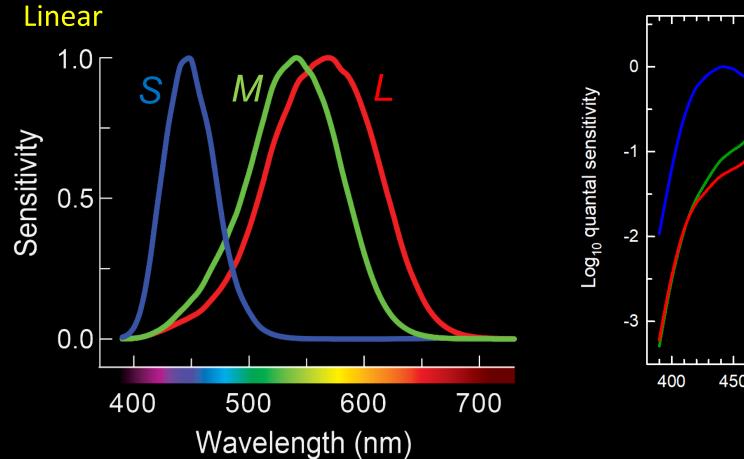
## Univariance

- Cones are "photon counters"
- Wavelength information is lost at the first step in vision, how do we get it back?
- Wavelength changes the *probability* of a photon being absorbed
- This dependency varies between cone types

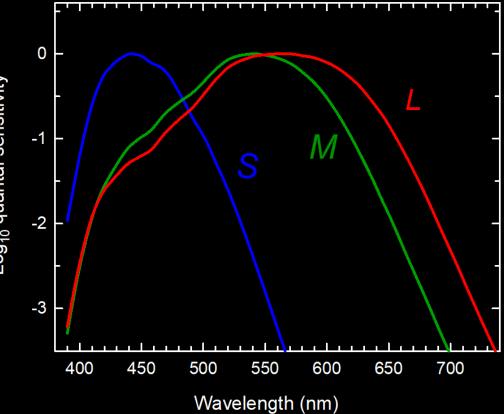
#### Imagine the sensitivity to these photons...



I'll be showing linear and logarithmic versions of the cone spectral sensitivities:

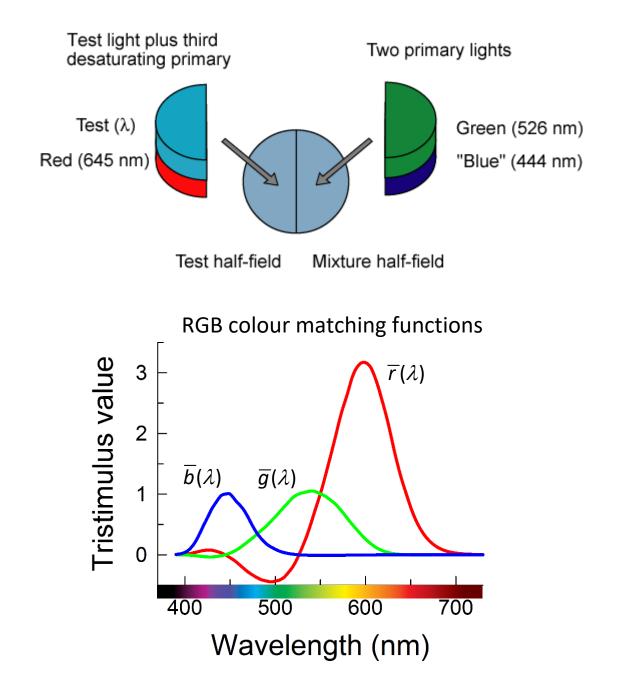


#### Logarithmic



- Measuring cone sensitivities in isolation is difficult/impossible as they overlap throughout the visible region
- Monochromats are rare
  - S-cone monochromacy < 1 in 100,000
  - L or M cone monochromacy < 1 in 1,000,000
- Dichromatic vision is more prevalent and can provide useful corroboration, see Stockman and Sharpe, 2000
- Before molecular genetics, it wasn't clear that monochromatic and dichromatic vision are due to a simple deletion – do they lack some cone type(s) with the remaining cones being exactly the same as in normal trichromats?
- Can we extract the same information another way?

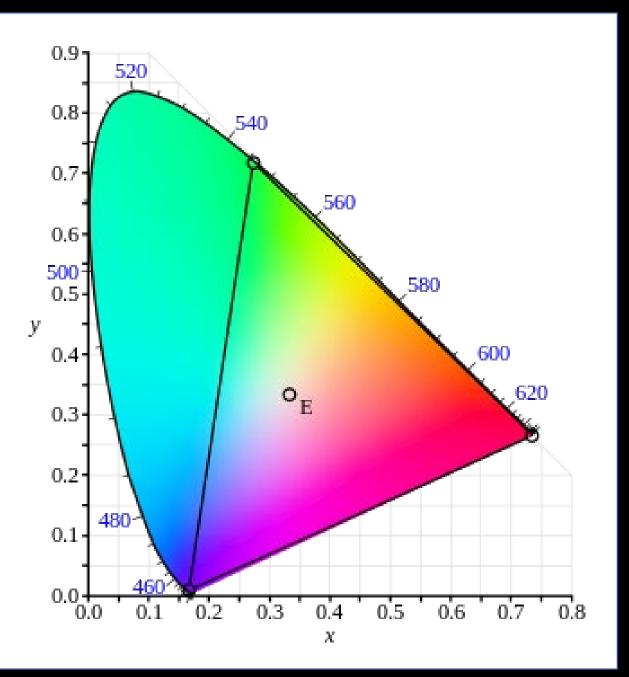
Another way of specifying colours that does not depend on knowing the cone spectral sensitivities is by making colour matches in a colour matching experiment:



Why are RGB functions negative for some wavelengths?

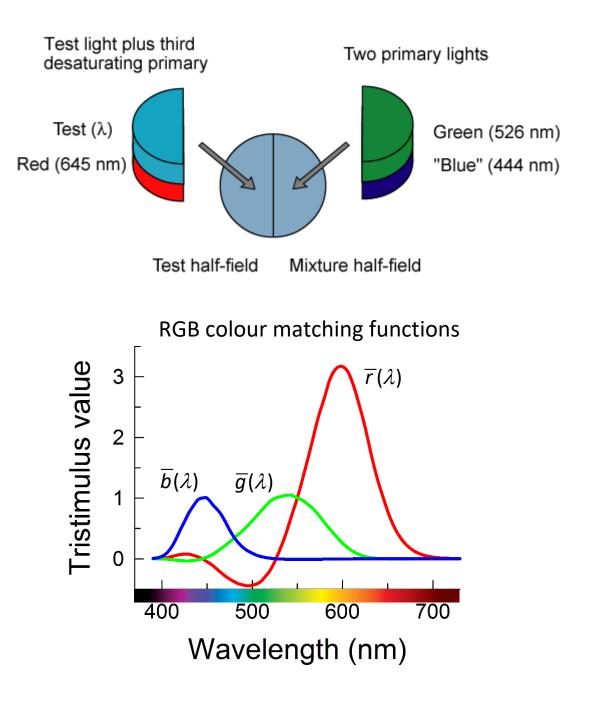
or

### Why do we need to "desaturate" the test field?



Another way of specifying colours that does not depend on knowing the cone spectral sensitivities is by making colour matches in a colour matching experiment:

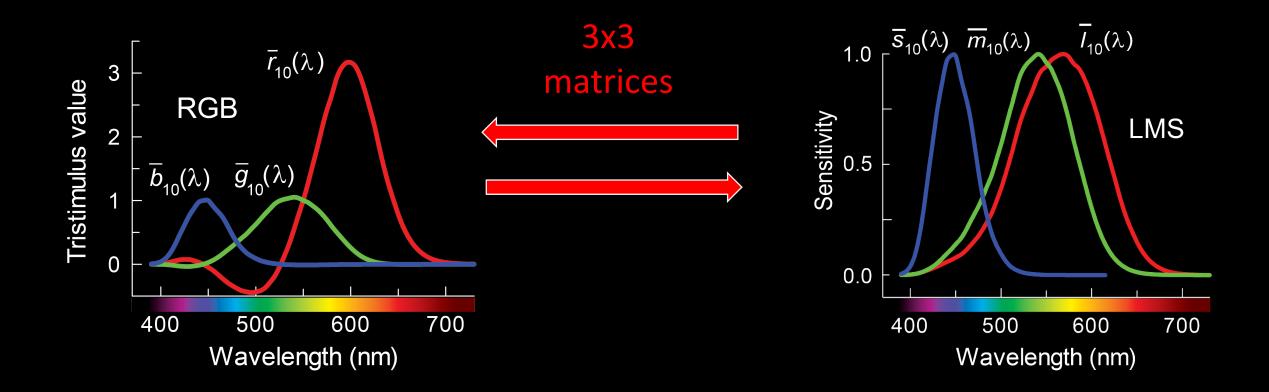
But what has this got to do with cone spectral sensitivities?

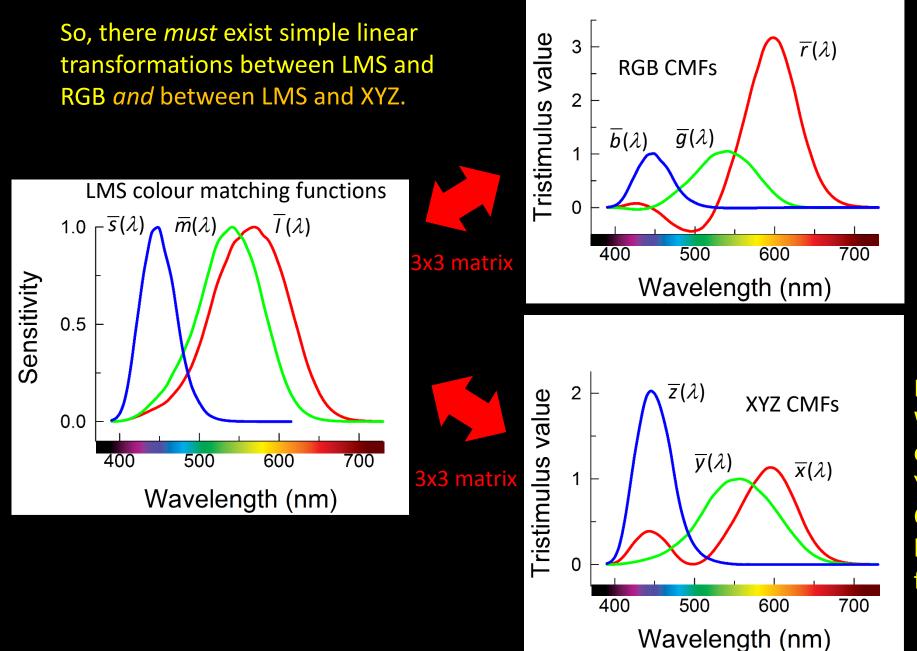


All colour matches are matches at the cone level and depend on the spectral sensitivities of the cones.

Consequently, the cone spectral sensitivities are the: **"Fundamental" colour matching functions** ...upon which all other CMFs depend.

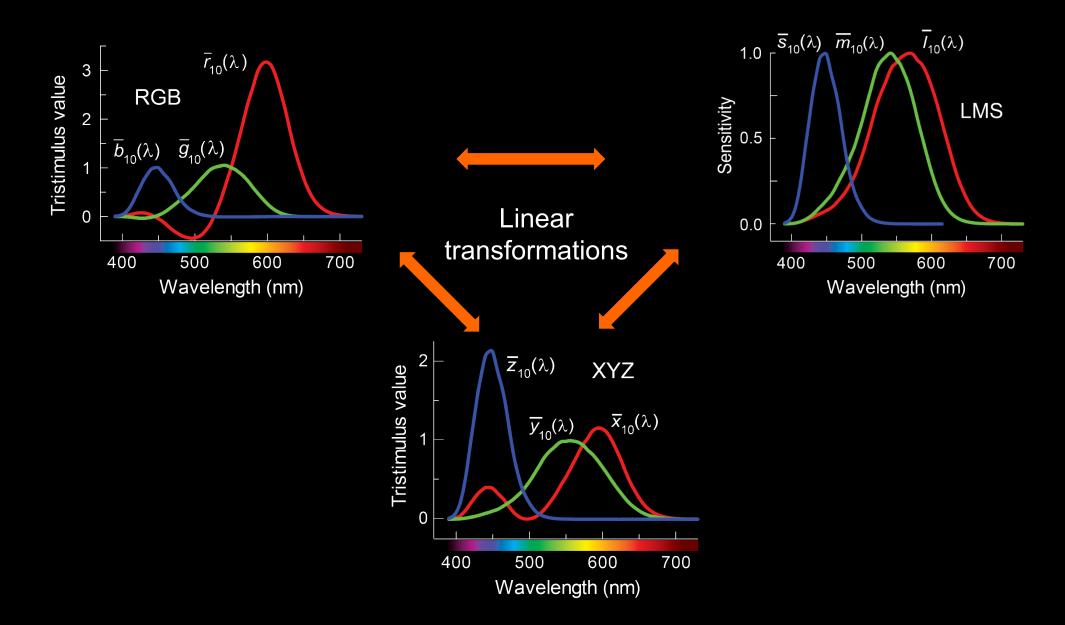
#### Accordingly, there exist simple linear transformations between RGB and LMS...

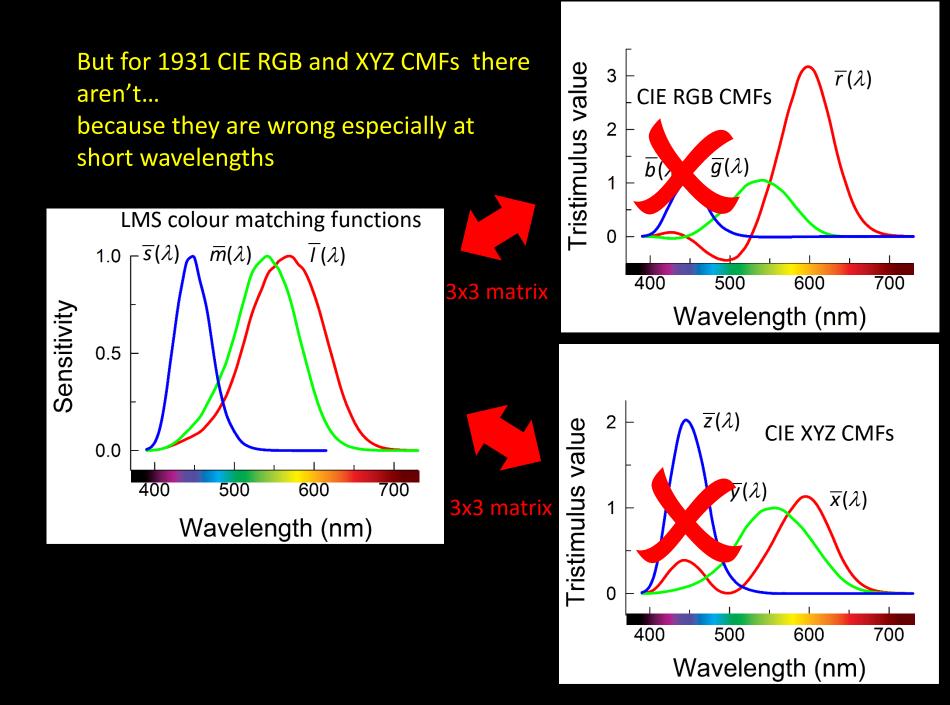




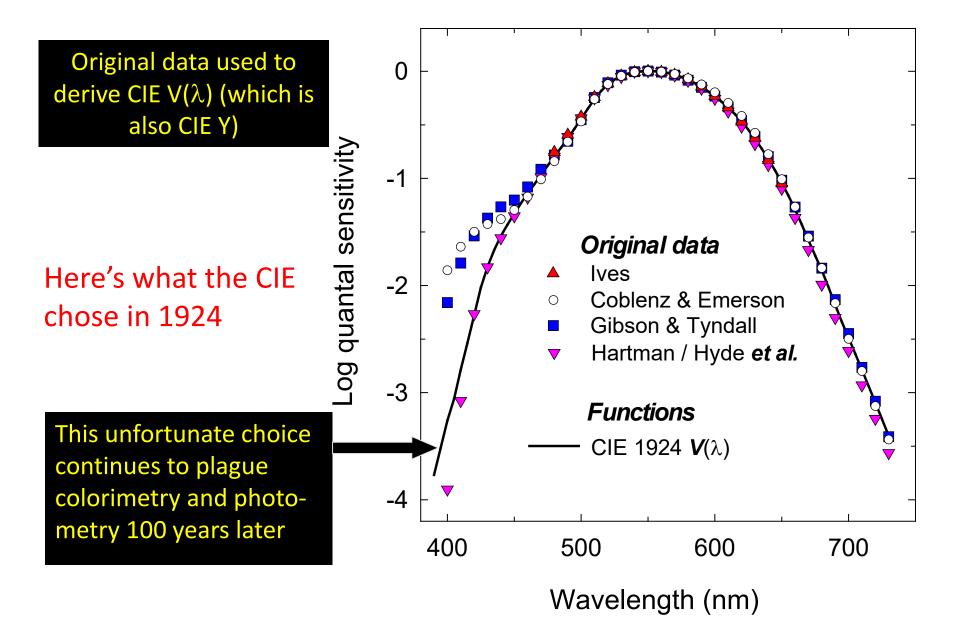
Based on Guild and Wright relative color matches with Y defined by the CIE 1924 Iuminosity function, V(λ)

#### And also between RGB and LMS and XYZ.

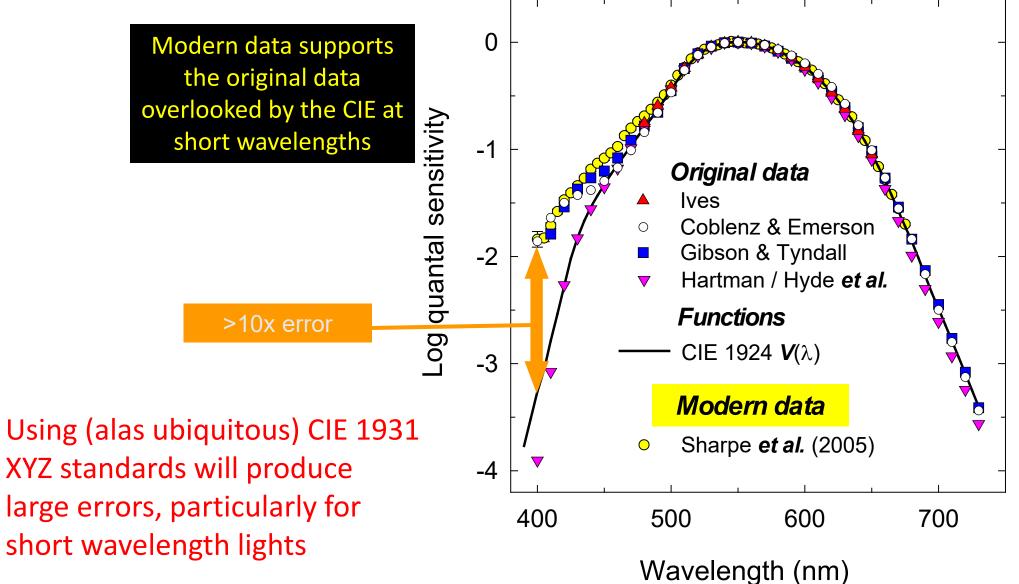




The reason is related to the choice of V( $\lambda$ ) back in 1924...



The reason is related to the choice of V( $\lambda$ ) back in 1924...



In 1991, CIE technical committee TC1-36 was established that led to:

## 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

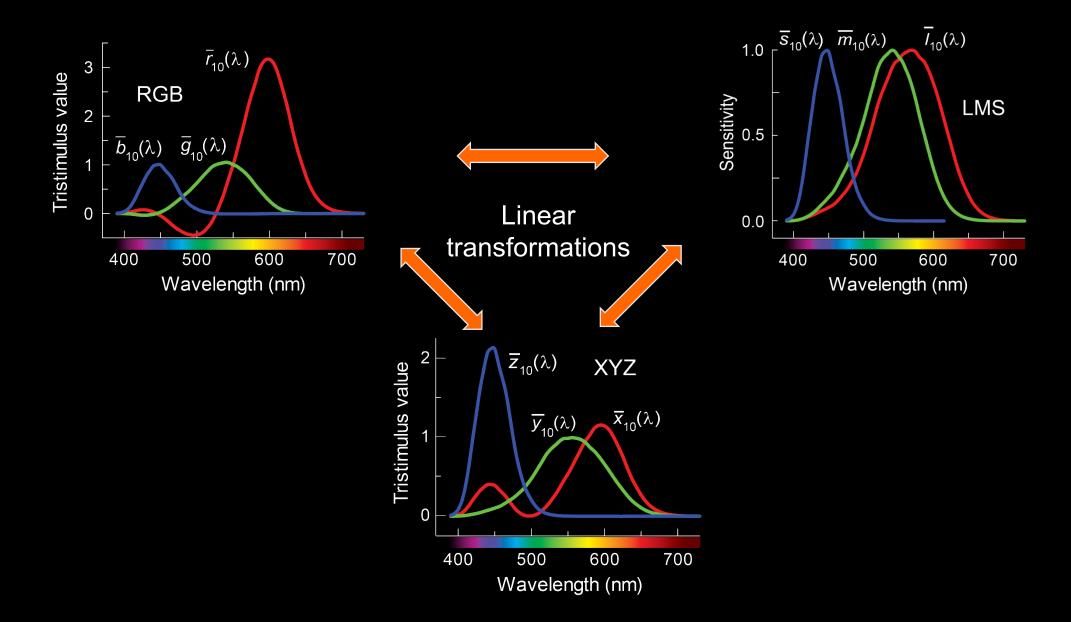
Together these represent a consistent set of "physiologically-relevant" LMS, RGB and XYZ CMFs for 2-deg and 10-deg vision

#### CIE 2006 LMS functions are defined as a linear transformation of Stiles & Burch (1959) RGB CMFs The Stockman & Sharpe (2

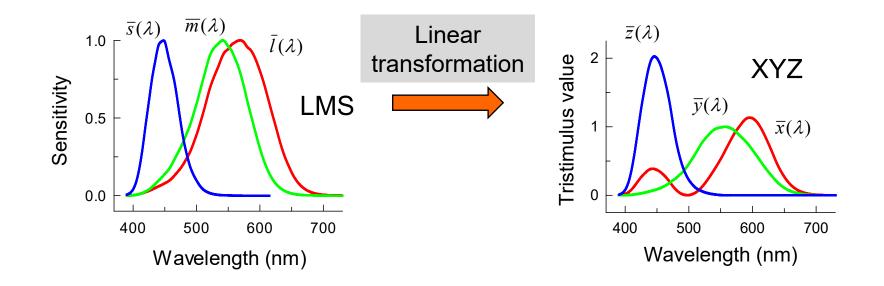
The Stockman & Sharpe (2000) cone fundamentals and other flicker photometry measurements have been used to generate new CIE XYZ CMFs...



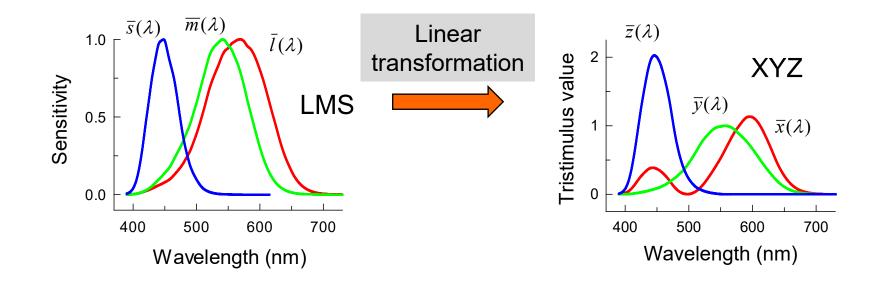
#### Linear transformations between RGB and LMS and XYZ (CIE 2015).



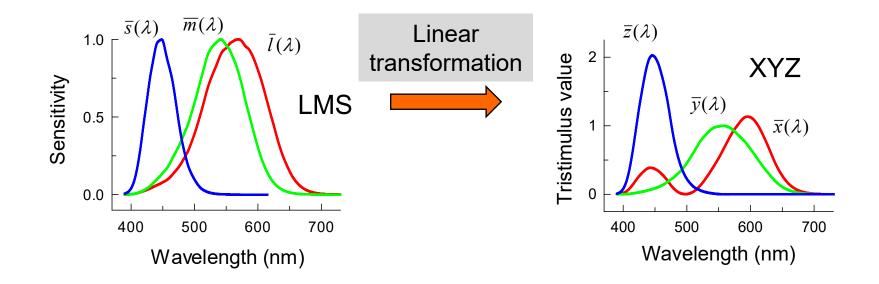
### Linear transformation from the CIE (2006) LMS CMFs to the new XYZ CMFs

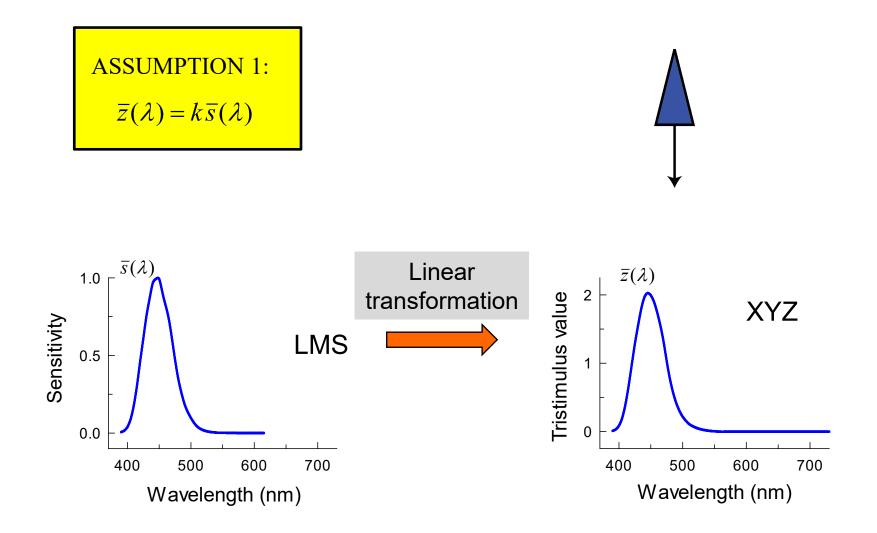


### Requires a series of simple assumptions...

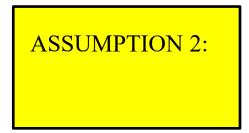


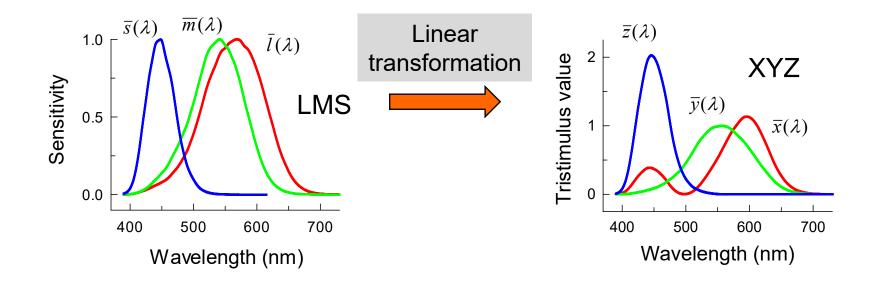


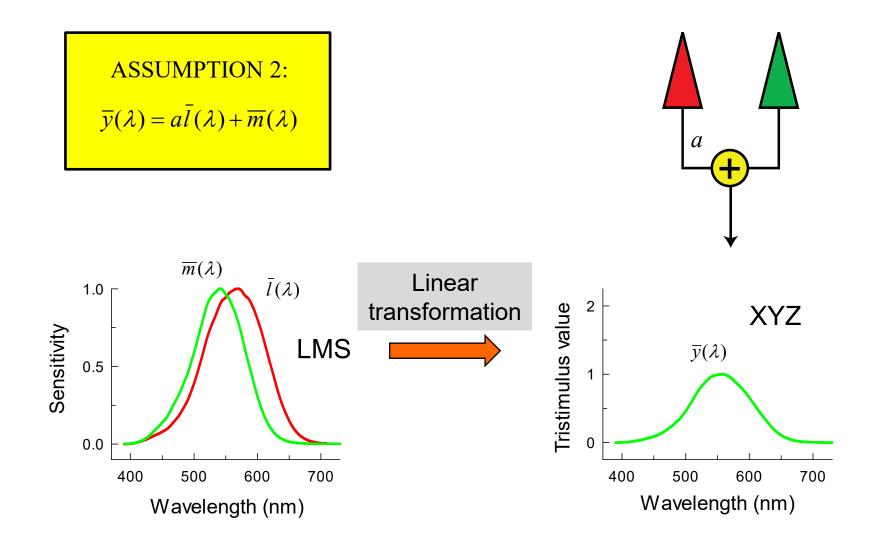




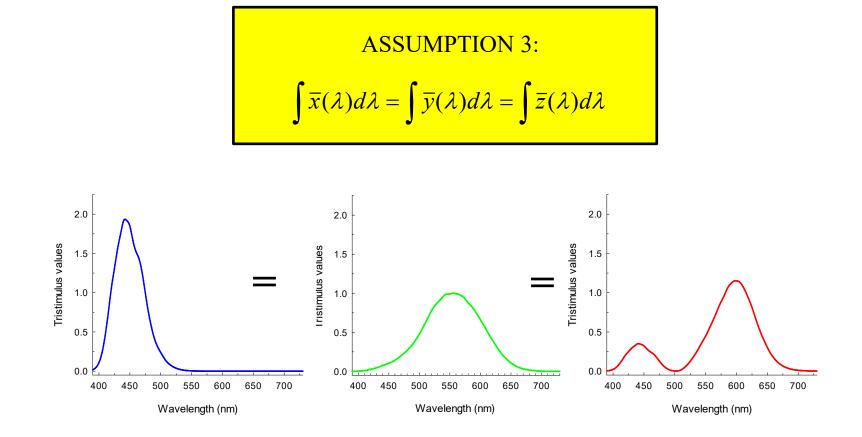
The  $\bar{s}(\lambda)$  and  $\bar{z}(\lambda)$  CMFs are the same (except for a scaling factor).





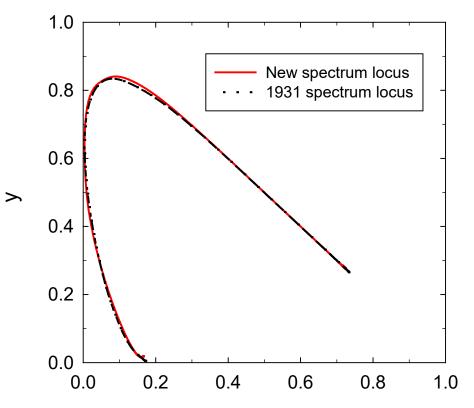


The  $\bar{y}(\lambda)$  CMF (or V( $\lambda$ ), the luminous efficiency function) is a linear combination of the  $\bar{l}(\lambda)$  and  $\bar{m}(\lambda)$  CMFs.



Equal areas for an equal energy spectrum

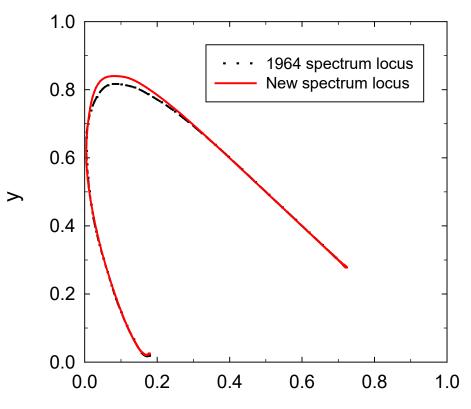
ASSUMPTION 4: Choice of  $a\overline{l}(\lambda) + b\overline{m}(\lambda) + c\overline{s}(\lambda) = \overline{x}(\lambda)$ Should minimize the Euclidian differences between the new chromaticity coordinates and the old ones (1931 or 1964).



#### 2-deg x,y chromaticity coordinates

Fits by Jan Henrik Wold

ASSUMPTION 4: Choice of  $a\overline{l}_{10}(\lambda) + b\overline{m}_{10}(\lambda) + c\overline{s}_{10}(\lambda) = \overline{x}_{10}(\lambda)$ Should minimize the Euclidian differences between the new chromaticity coordinates and the old ones.



#### 10-deg x, y chromaticity coordinates

Fits by Jan Henrik Wold

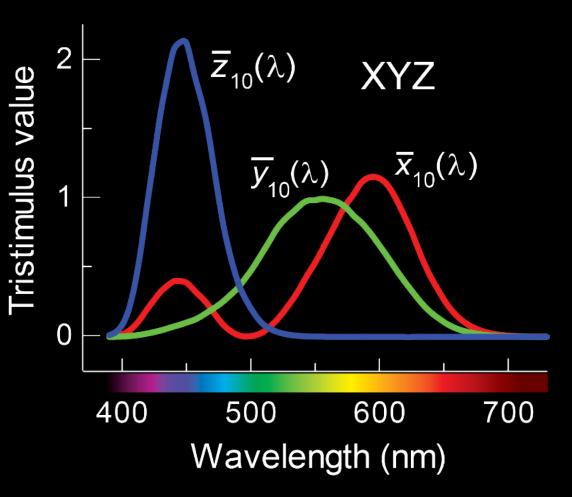
## What are the XYZ CMFs recommended by the CIE?

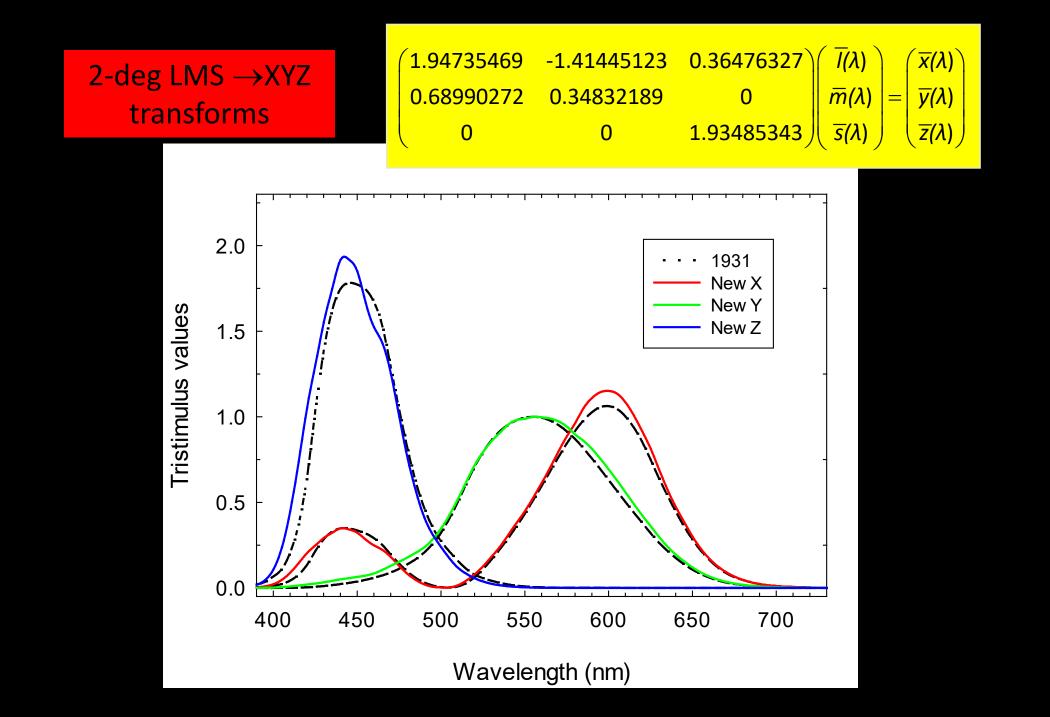
They are a linear combination of the CIE 2006 LMS cone fundamentals.

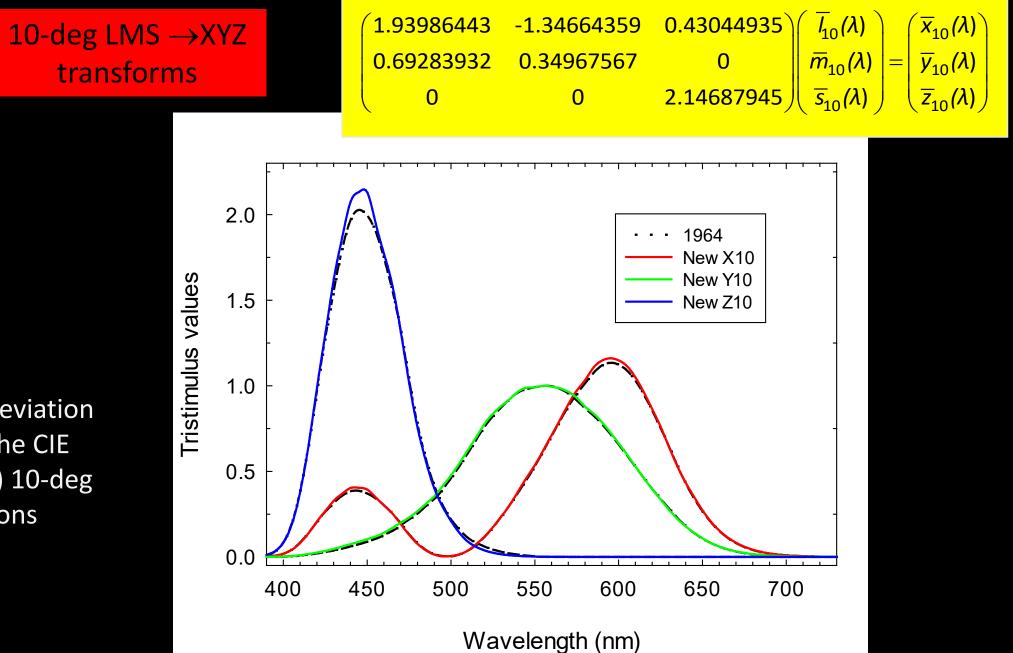
Z is S.

The derivation of Y is based on the work of: Sharpe, Stockman, Jagla & Jägle (2005). *Journal of Vision*, 5, 948-968. Sharpe, Stockman, Jagla & Jägle (2011). *Color Research & Application*, 36, 42-46.

X was chosen by Jan Henrik Wold.

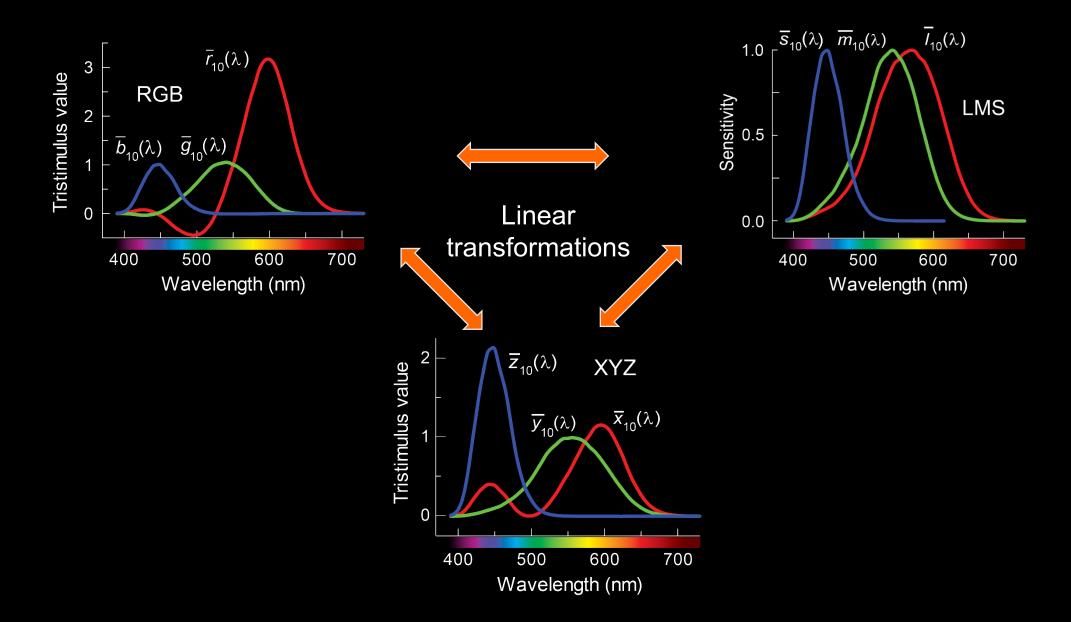




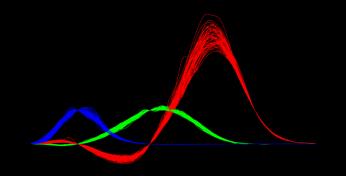


Less deviation with the CIE (1964) 10-deg functions

#### Linear transformations between RGB and LMS and XYZ (CIE 2015).



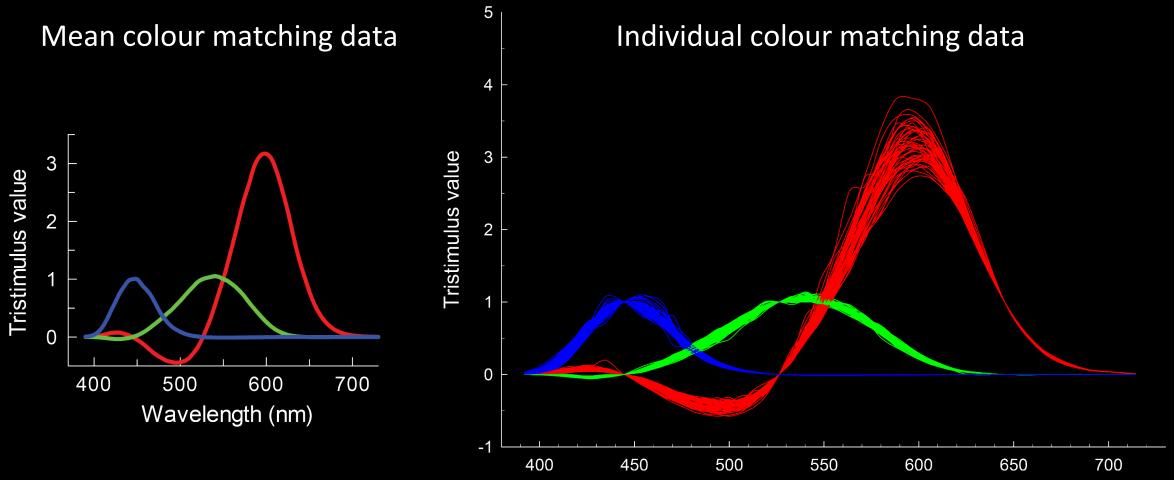
### INDIVIDUAL DIFFERENCES



As just discussed, the CIE (2006) LMS standards represent the average normal spectral sensitivity or colour matching functions and are defined as a linear transformation of the average Stiles & Burch (1959) CMFs.



However, this underplays the sizeable individual differences between the colour matches made by colour-normal observers that can be seen in the original individual Stiles & Burch colour matching data.

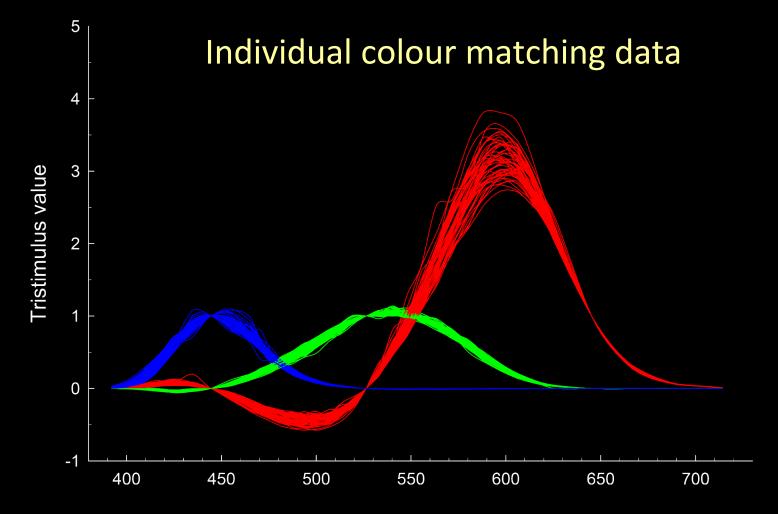


Stiles & Burch (1959) 10-deg CMFs

Wavelength (nm)

## What causes these individual differences?

### How can we model them?



Wavelength (nm)

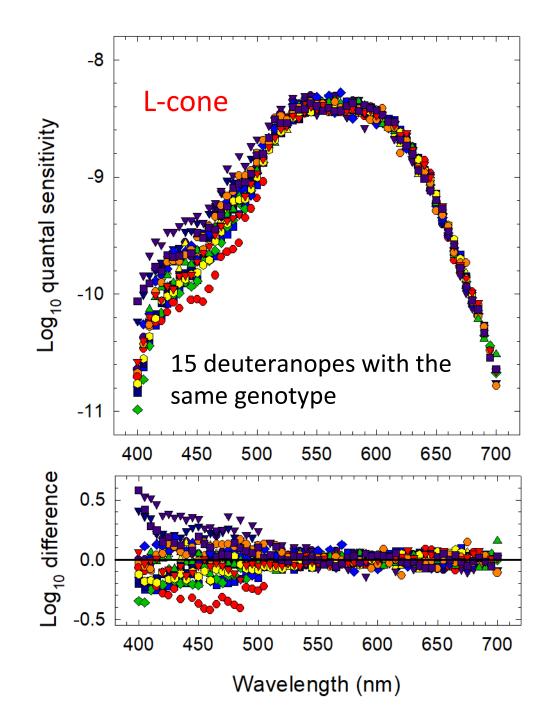
# What causes individual differences?

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

### Individual data for deuteranopes with the same L-cone photopigment

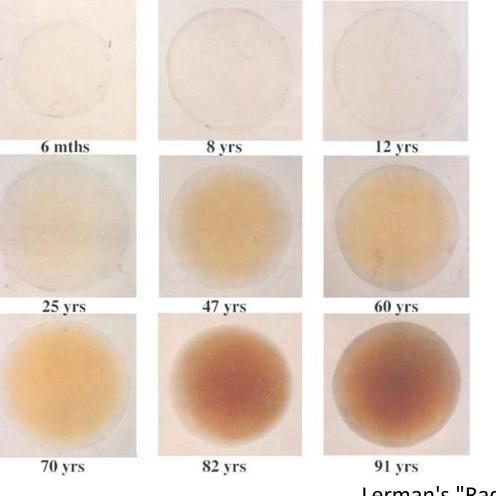
L-cone data from fifteen deuteranopes with the same genotype (and therefore with the same photopigment) (*Stockman and Sharpe, 1999*)

Why are the results so variable at short wavelengths?



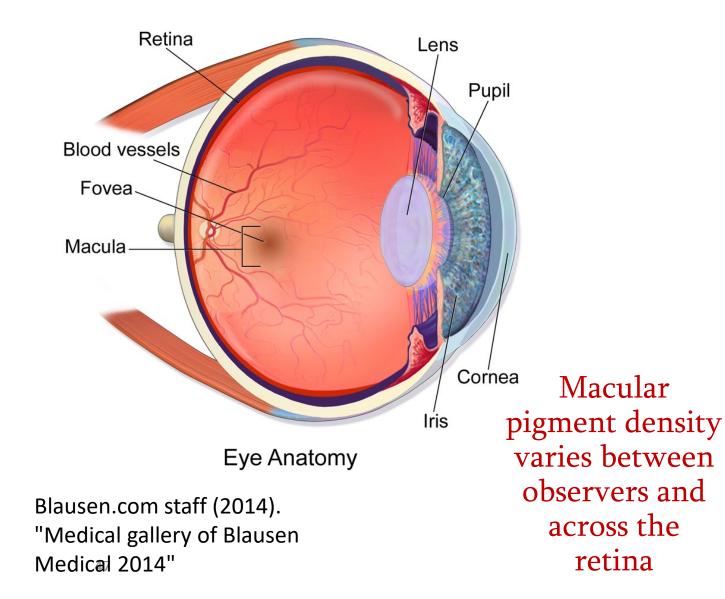
## Lens pigment

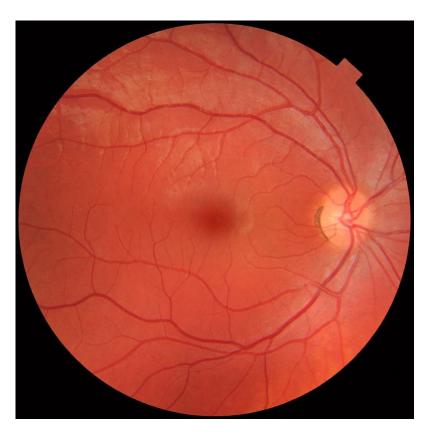
Lens pigment density varies between observers and across the lifespan



Lerman's "Radiant Energy and the Eye"

## Macular pigment

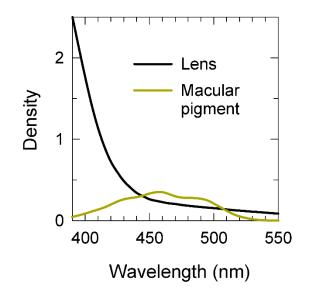


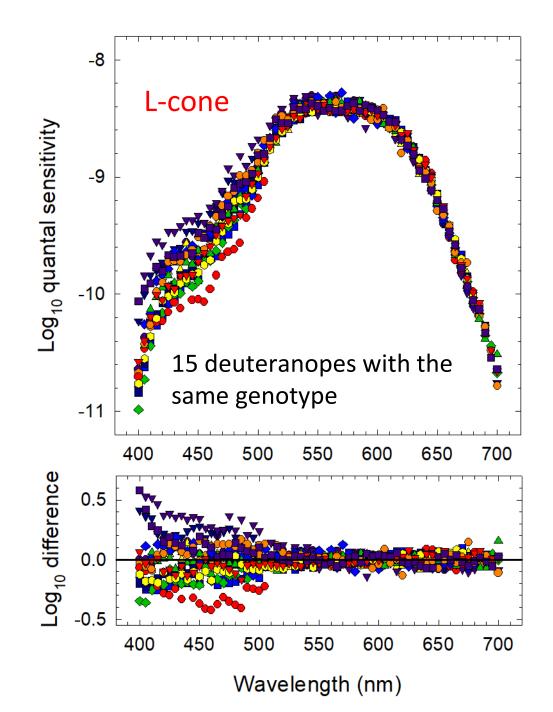


Häggström, M. (2014). "Medical gallery of Mikael Häggström 2014"

### Individual data for deuteranopes with the same L-cone photopigment

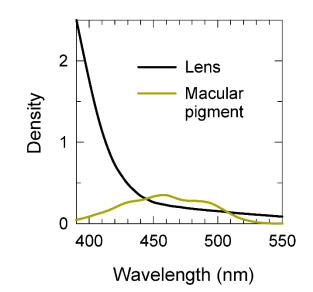
The variability is due to individual differences in macular and lens pigment optical densities.

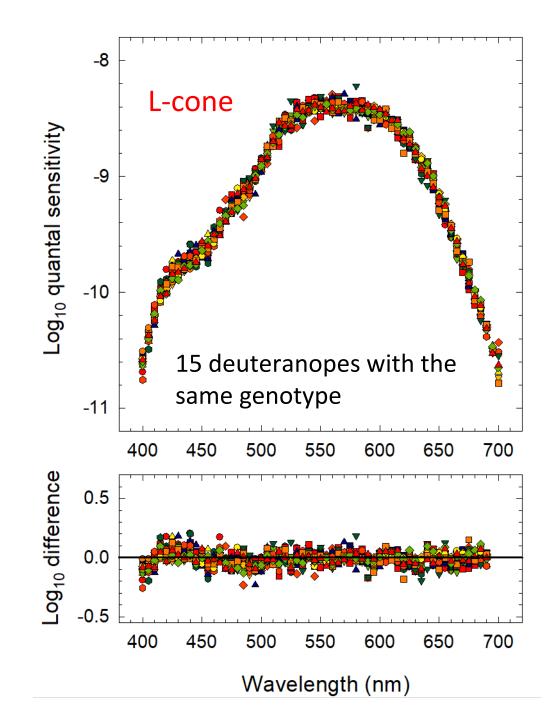




### Individual data for deuteranopes with the same L-cone photopigment

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

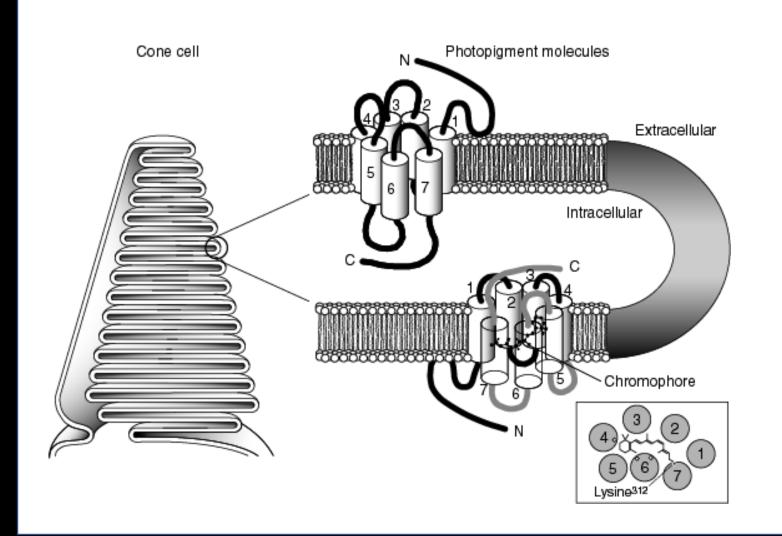




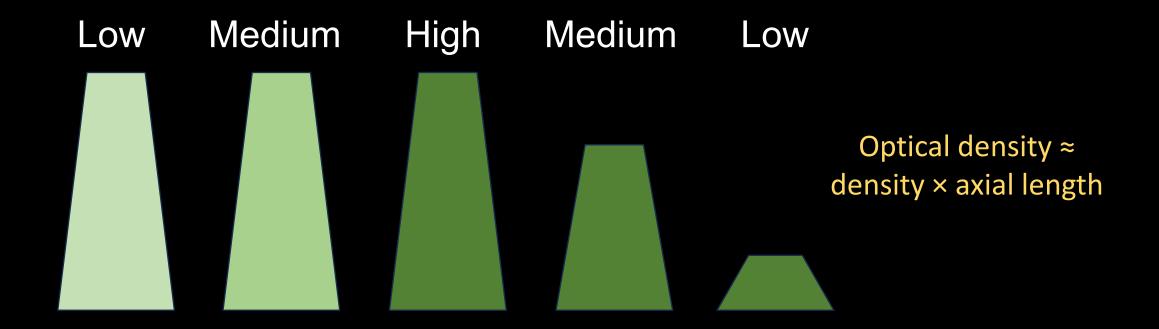
### What causes individual differences?

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

## Photopigments in the cones



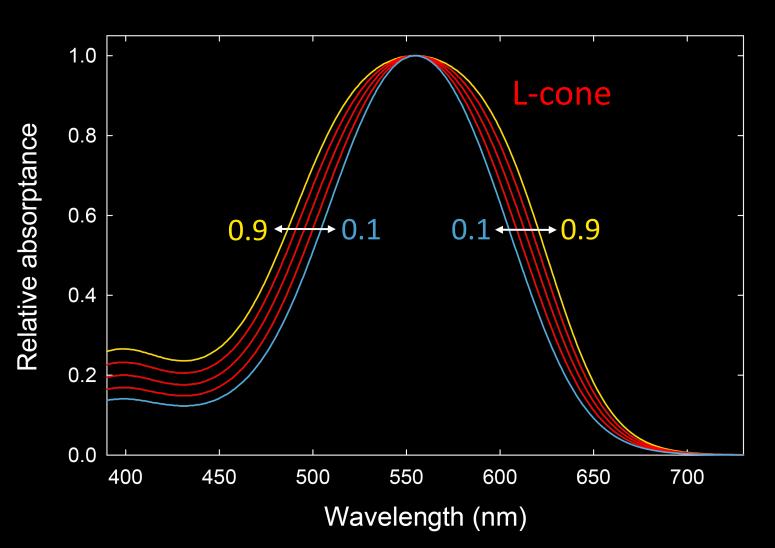
Photopigment optical density



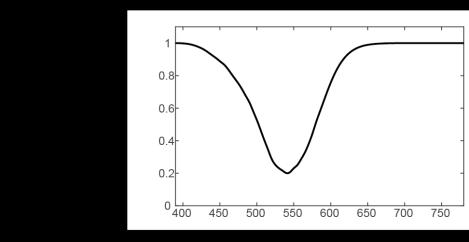
### Individual differences in photopigment optical density

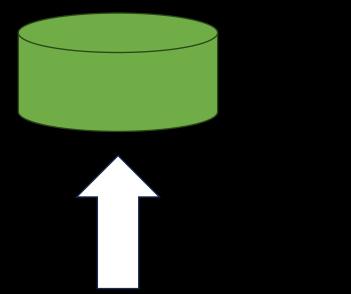
Increasing photopigment optical density broadens the spectral sensitivity around the  $\lambda_{max}$ 

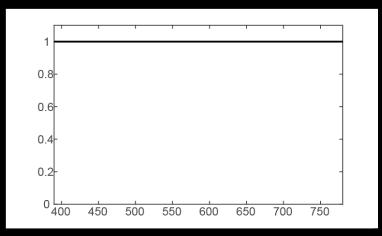
Cone photopigments varying in optical density from 0.1 (narrow) to 0.9 (broad) in 0.2 steps



## Self-screening

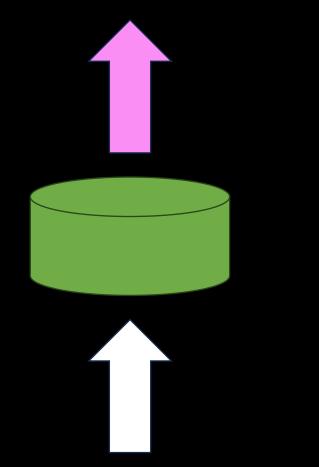




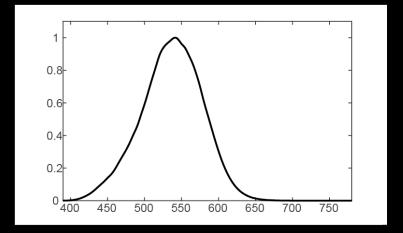


### Self-screening

## Difference between light entering and light exiting gives the light absorbed

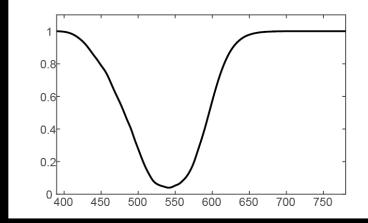


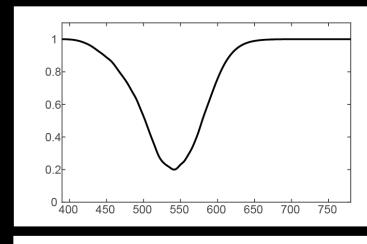
#### Absorbance spectrum

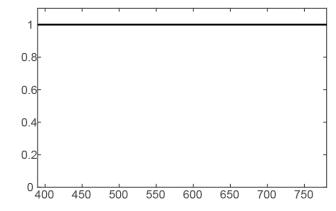


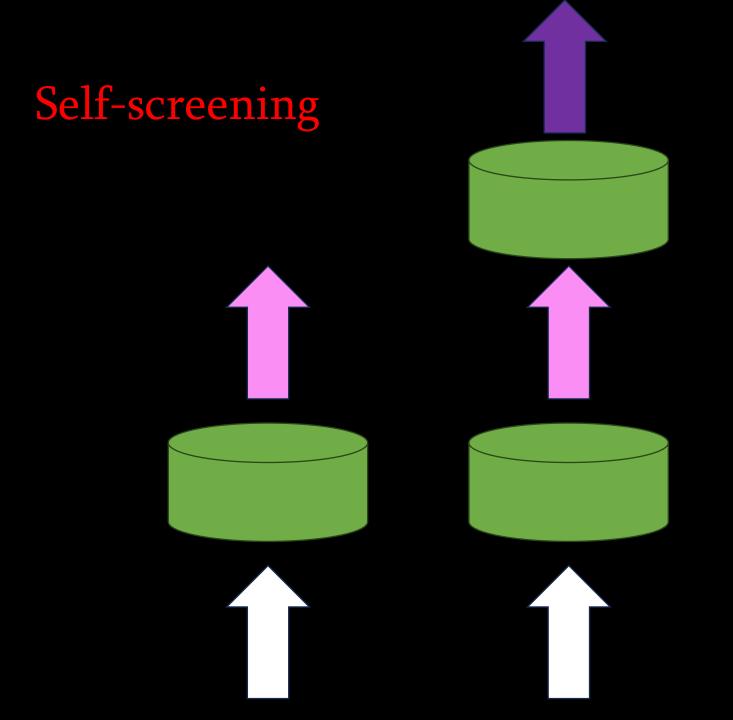
## Self-screening

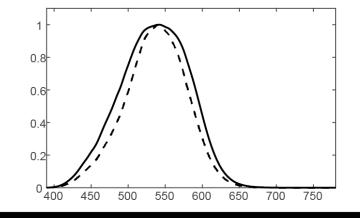








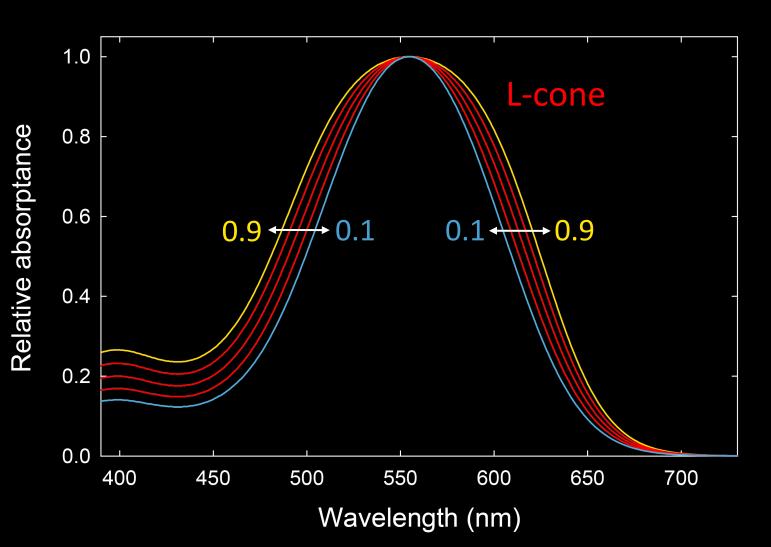




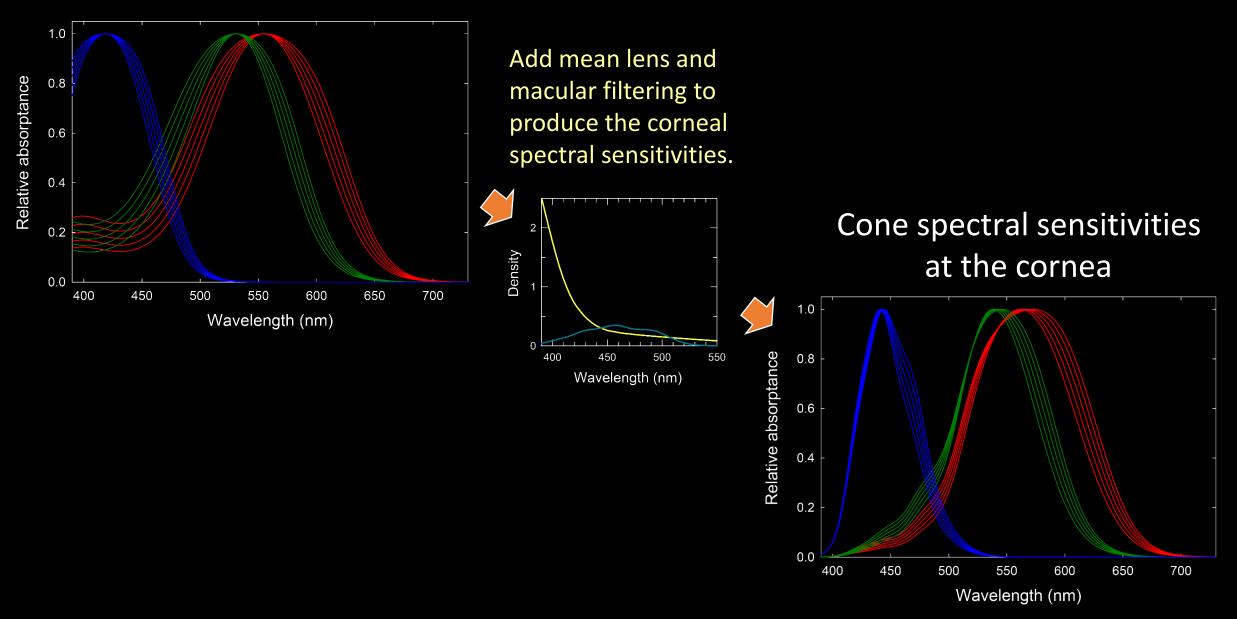
### Individual differences in photopigment optical density

Increasing photopigment optical density broadens the spectral sensitivity around the  $\lambda_{max}$ 

Note that the photopigment optical density also varies with eccentricity because the cones in the fovea are longer and thus have a higher photopigment optical density than cones outside the fovea Cone photopigments varying in optical density from 0.1 (narrow) to 0.9 (broad) in 0.2 steps



#### Photopigments



# What causes individual differences?

Macular pigment optical density differences

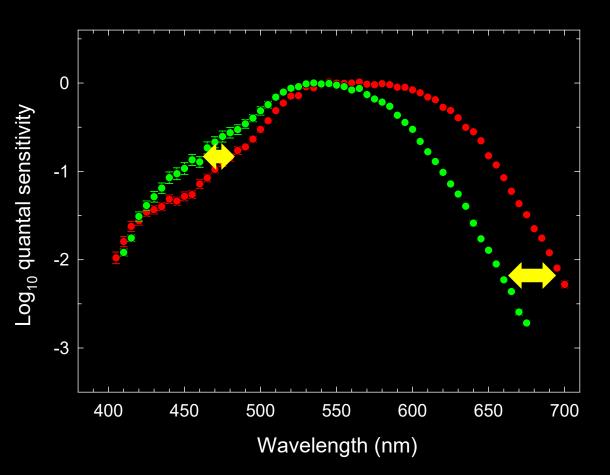
Lens pigment optical density differences

Photopigment optical density differences

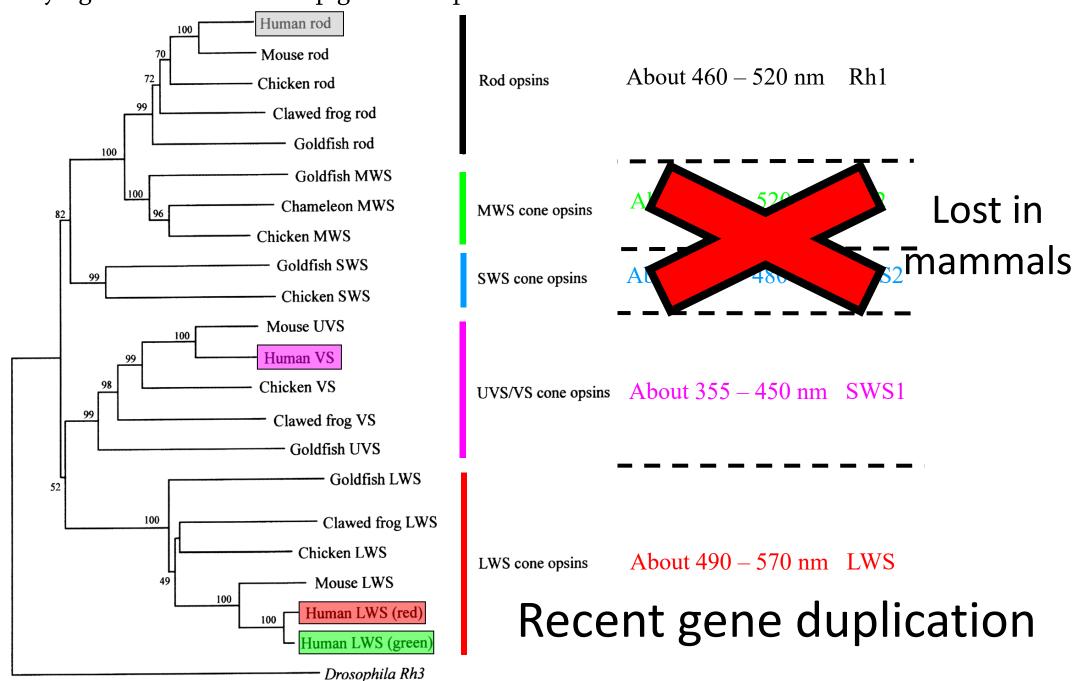
Spectral shifts in photopigment sensitivity

### Why does this variability occur?

The shifts are the result of variability in the genetic codes for the M- and L-cone photopigments



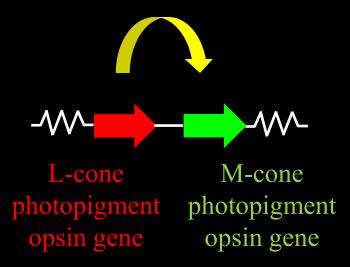
Phylogenetic tree of visual pigments / opsins



### Gene duplication on the X-chromosome

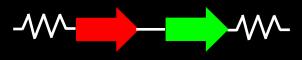


Mammal



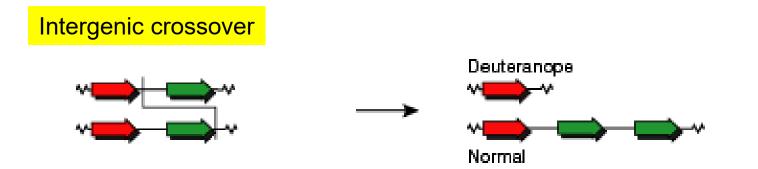
Human/ Old world primate

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



L-coneM-conephotopigmentphotopigmentopsin geneopsin gene

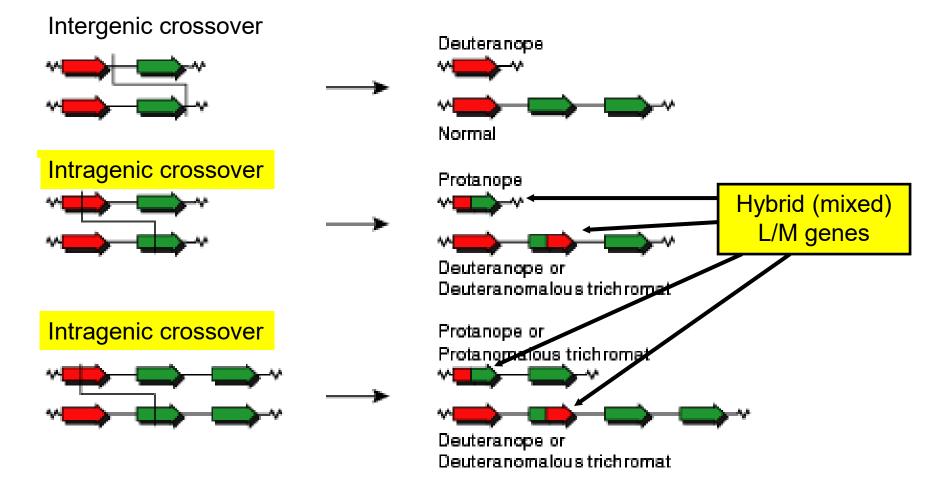
## Crossovers during meiosis are common:



Intergenic crossovers produce more or fewer L and Mcone genes on each X chromosome

From Sharpe, Stockman, Jägle & Nathans, 1999

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



From Sharpe, Stockman, Jägle & Nathans, 1999

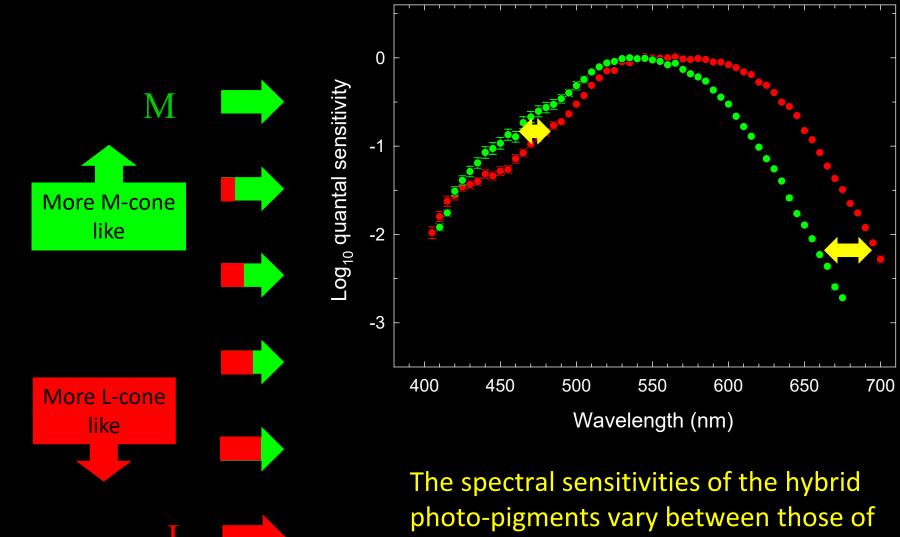
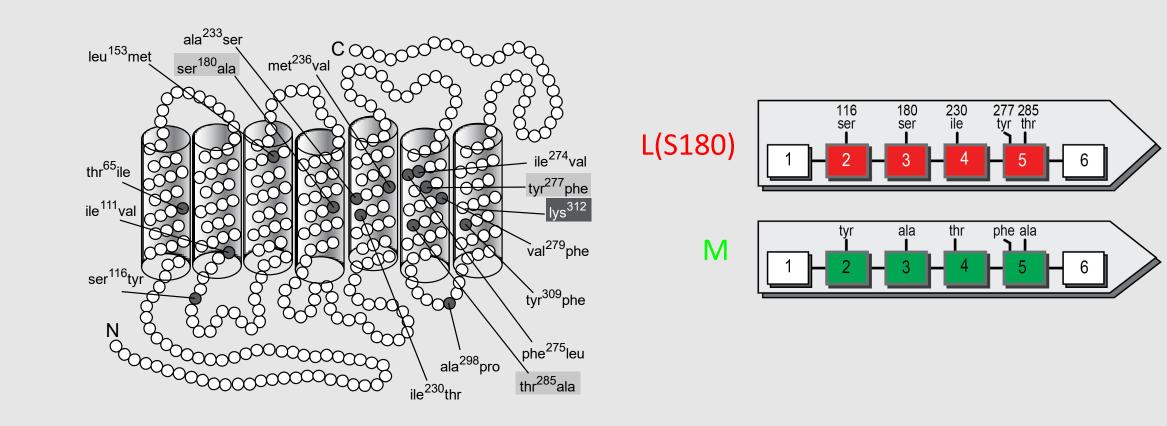


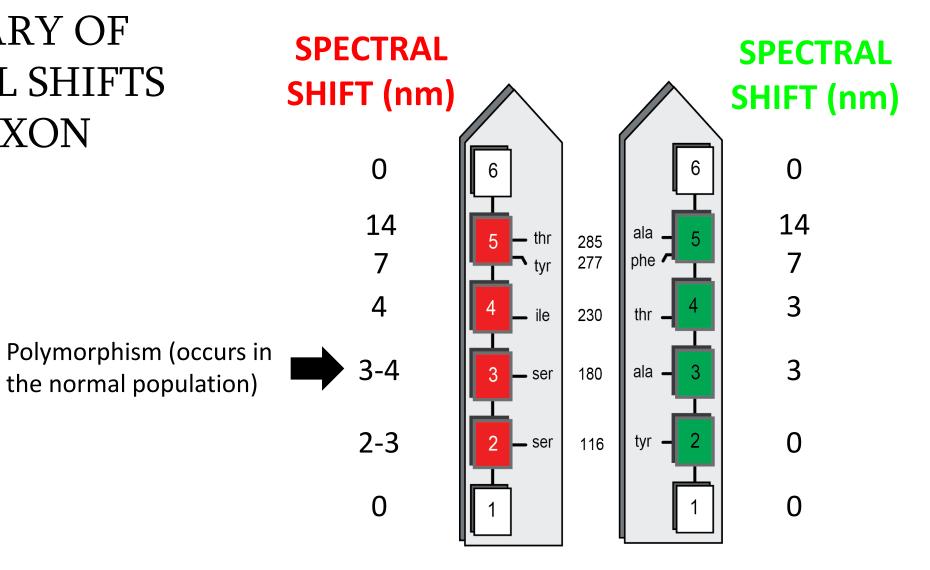
photo-pigments vary between those of the M- and L-cones depending on where the crossover occurs.

### 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 five of those cause wavelength shifts between their spectral sensitivities.



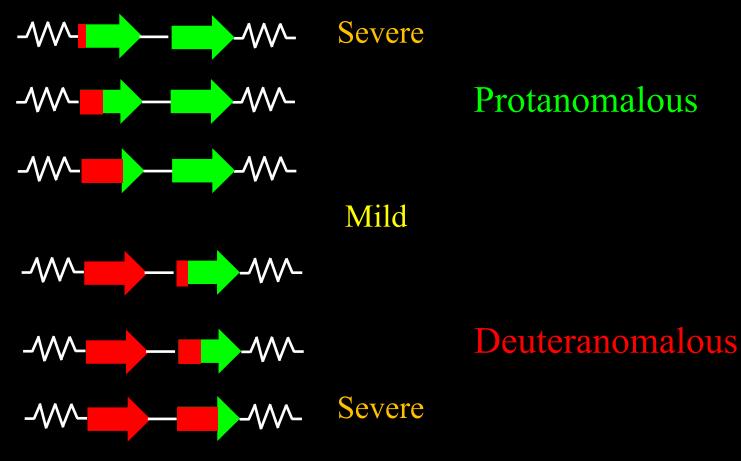
### SUMMARY OF SPECTRAL SHIFTS PER EXON

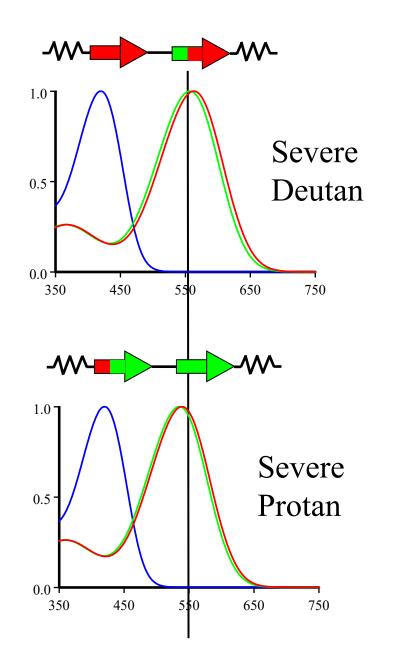


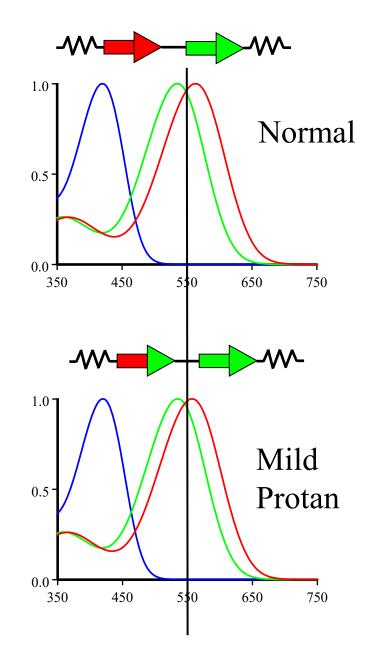
Values from Neitz and Neitz (2011)

### Anomalous trichromats

Male observers with two different genes are "anomalous" trichromats







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

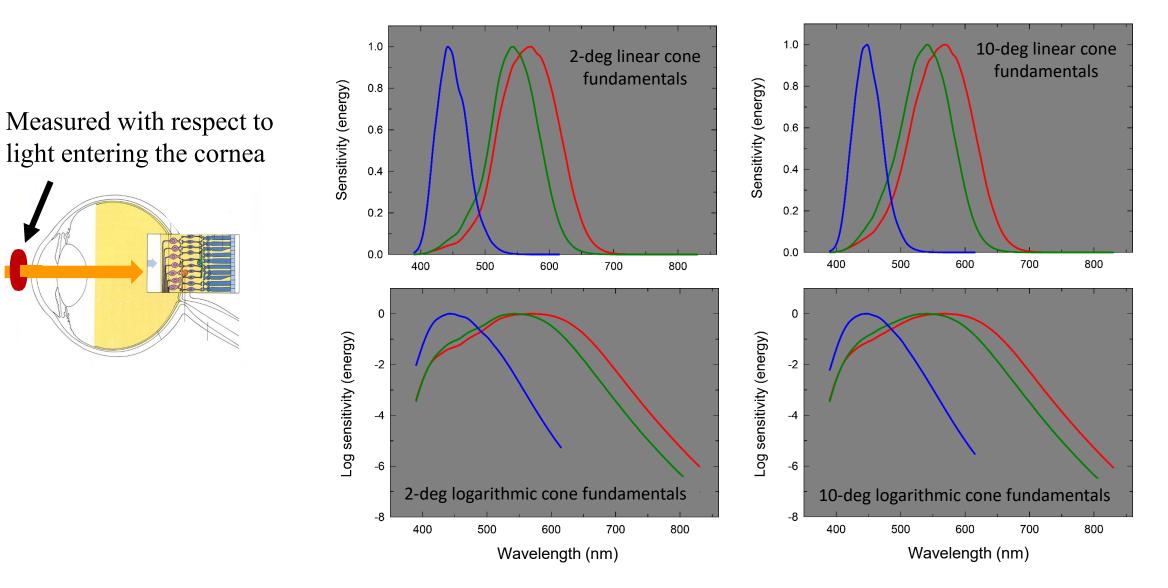
		percen	percent in UK	
Condition		Male	Female	
Protanopia Protanomaly	no L cones milder form	1.0 1.0	0.02 0.03	
Deuteranopia Deuteranomaly	no M cones milder form	1.5 5.0	0.01 0.4	
Tritanopia	no S cones	0.008	0.008	

# What causes individual differences?

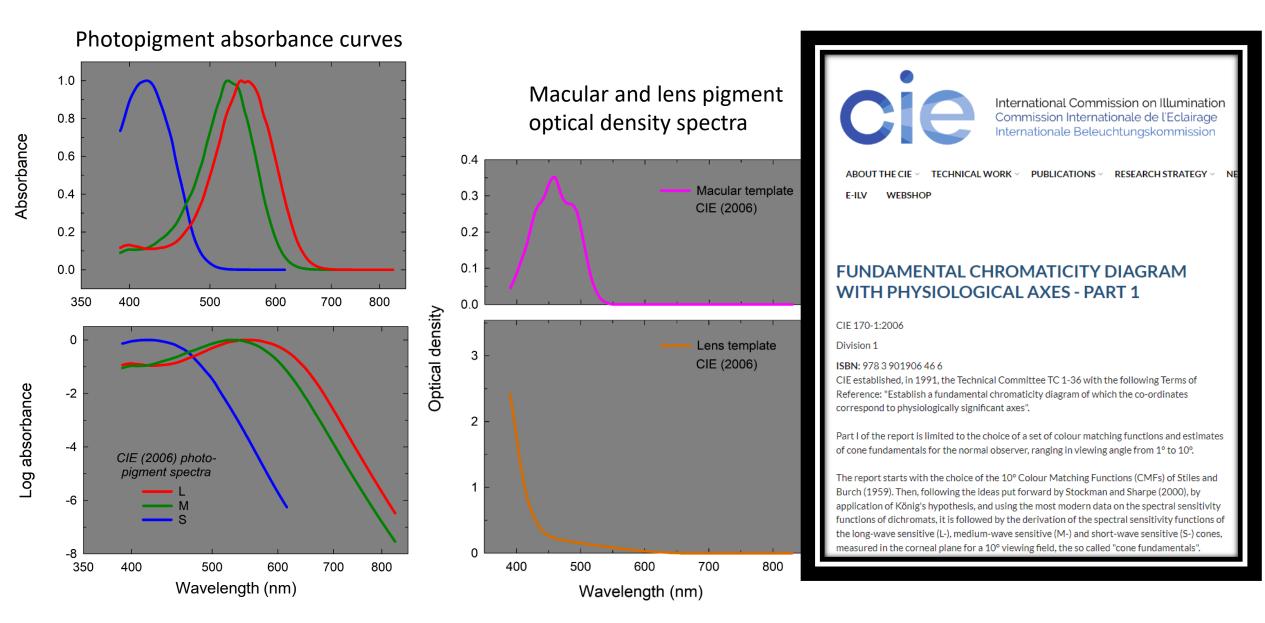
Macular pigment optical density differences
Lens pigment optical density differences
Photopigment optical density differences
Spectral shifts in photopigment sensitivity

MODELLING INDIVIDUAL DIFFERENCES

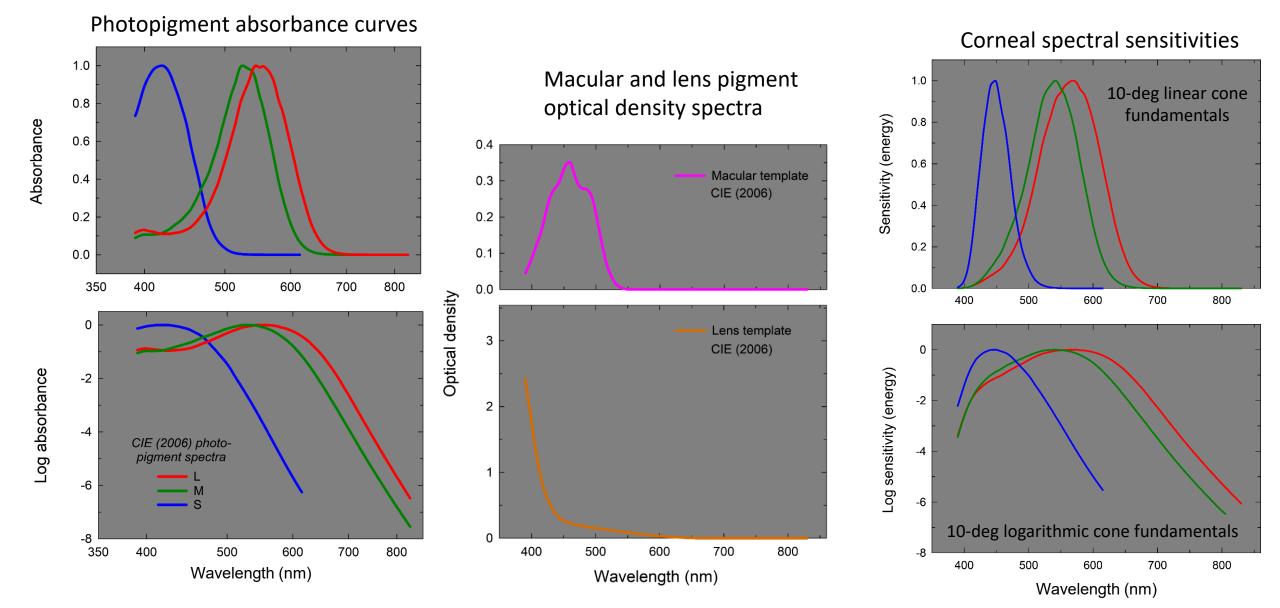
#### Stockman & Sharpe (2000) and CIE (2006) standard LMS observers for 2-deg and 10-deg vision.

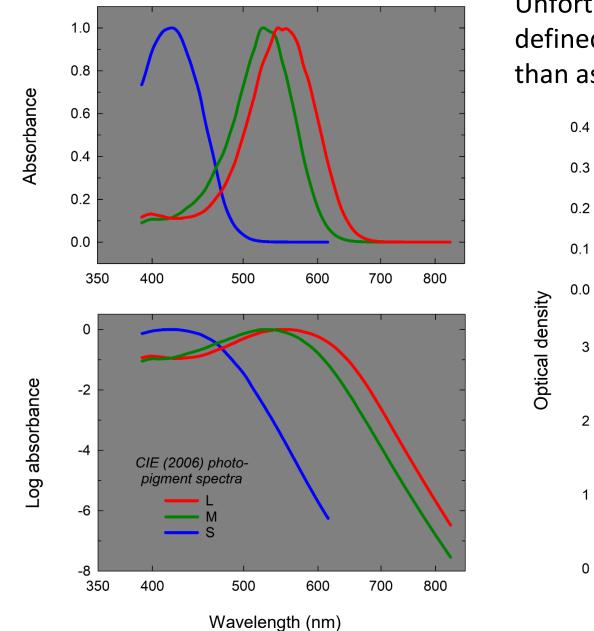


The new CIE standards also define the macular and lens pigment optical density spectra, the photopigment optical densities and the photopigment spectra.

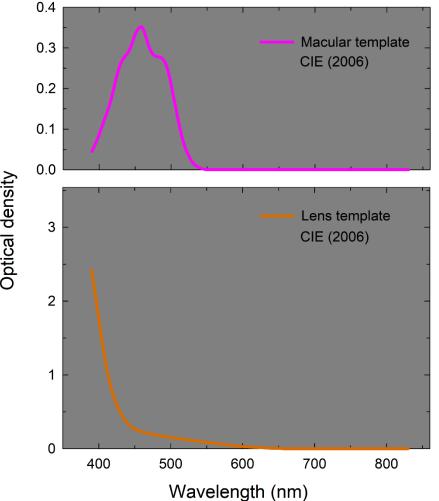


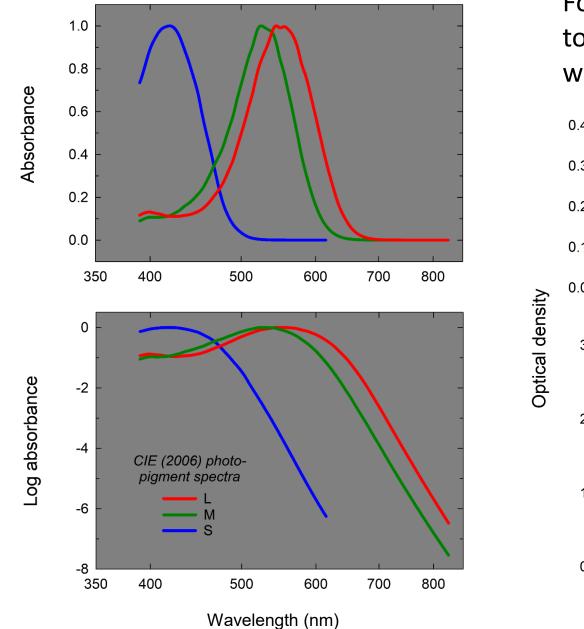
### We model individual differences by adjusting the photopigment absorbance curves and varying the macular and lens optical densities



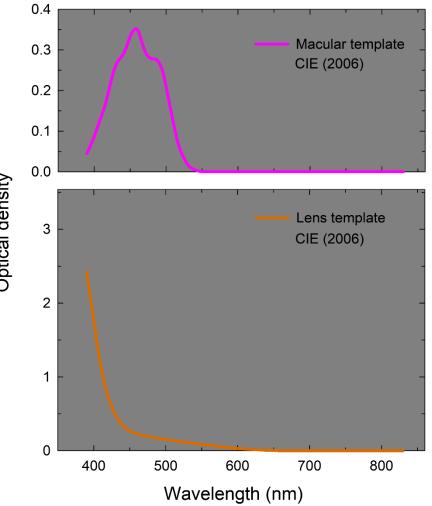


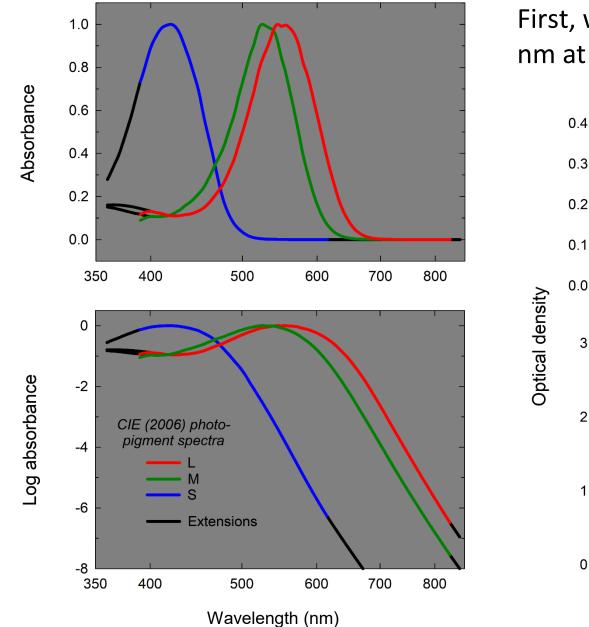
Unfortunately, the CIE (2006) LMS standards are defined as discrete values at 5 or 1 nm steps rather than as continuous functions of wavelength.



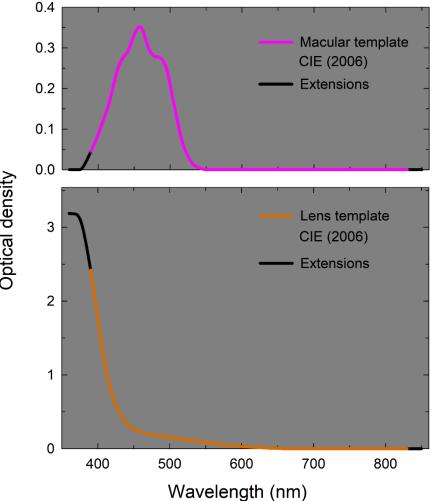


For computational convenience, we want to define these as continuous functions of wavelength...





### First, we extended the discrete functions to 360 nm at short wavelengths and 850 nm at long.



Fourier polynomials were then fitted to the discrete functions and then used to define the template shapes

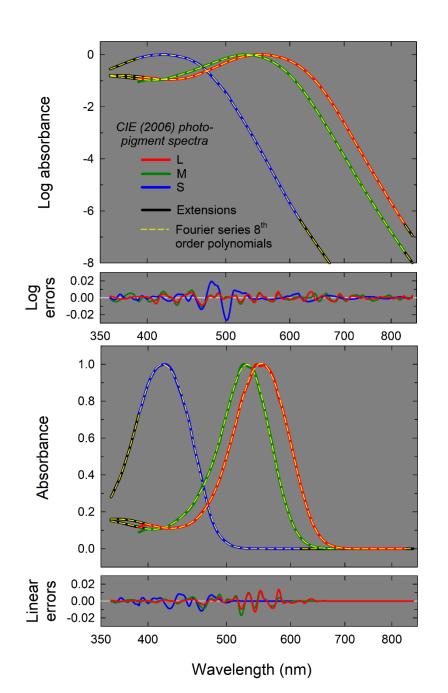
The templates are of the general form:

$$F(\theta) = a_0 + \sum_{k=1}^n \left[ a_k \cos(k\theta) + b_k \sin(k\theta) \right]$$

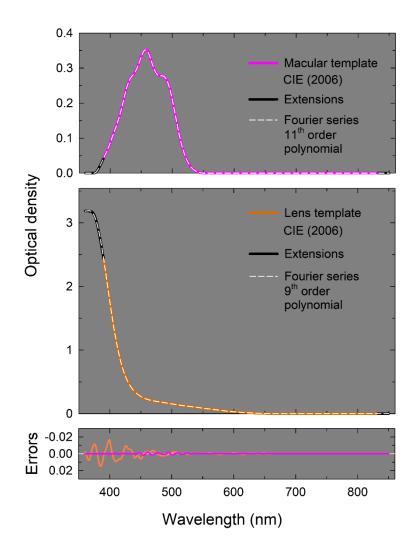
 $\theta = \pi \frac{\log_{10}(\lambda/360)}{\log_{10}(850/360)}$ 

*n* is the number of harmonics.

Continuous functions of wavelength with little error when used to reconstruct fundamentals. No theoretical basis or significance to any individual parameter, just a template.



Important that they describe both log and linear absorbances



### For (even) more details...



RESEARCH ARTICLE 🔂 Open Access 💿 🛈

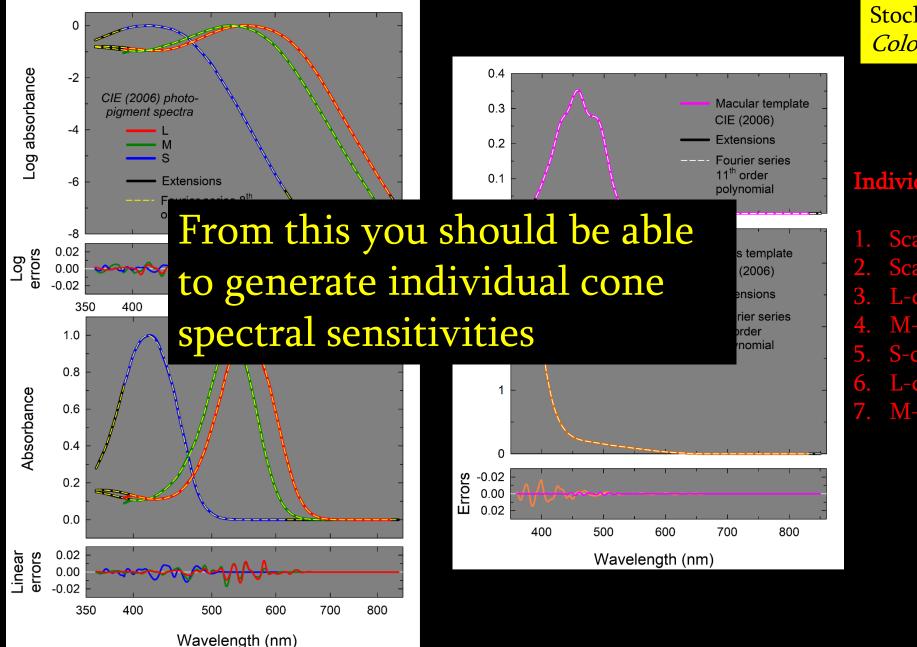
## Formulae for generating standard and individual human cone spectral sensitivities

Andrew Stockman 🔀, Andrew T. Rider

First published: 19 July 2023 | https://doi.org/10.1002/col.22879 | Citations: 1

First published: 19 July 2023 | https://doi.org/10.1002/col.22879 | Citations: 1

Andrew Stockman 🔀, Andrew T. Ride

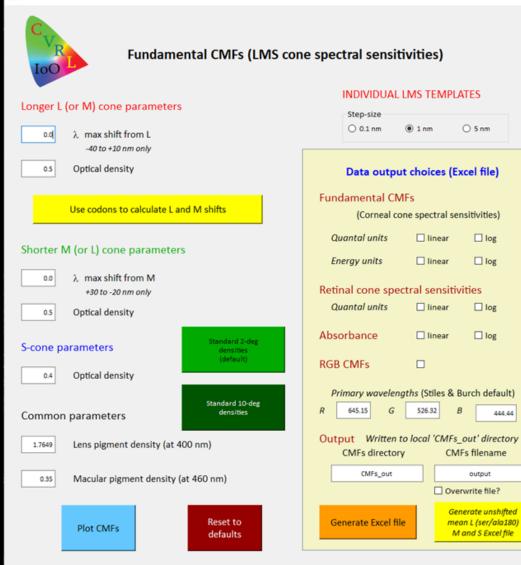


#### Stockman and Rider, 2023. *Color Research and Application*

#### **Individual difference parameters**

- 1. Scalar for lens density
- 2. Scalar for macular density
- B. L-cone optical density
- 4. M-cone optical density
- 5. S-cone optical density
- 6. L-cone spectral shift
- 7. M-cone spectral shift

#### MainWindow



■ MainWindow – □ ×							
Shorter ML-cone Codon M L Exon							
116	● Tyr (	Ser	2	⊖ Tyr	● Ser	116	
180	● Ala (	Ser	3	🔾 Ala	● Ser	180	
230	● Thr (	🔵 Ile		◯ Thr	Ile	230	
233	● Ser (	🔿 Ala	4	🔾 Ser	● Ala	233	
277	● Phe(	🔾 Tyr		🔿 Phe	Tyr	277	
285	● Ala (	🔾 Thr	5	🔿 Ala	Thr	285	
309	● Phe(	🔾 Tyr		🔘 Phe	● Tyr	309	
ML shift (nm) <b>0</b> Done LM shift (nm) <b>0</b>							

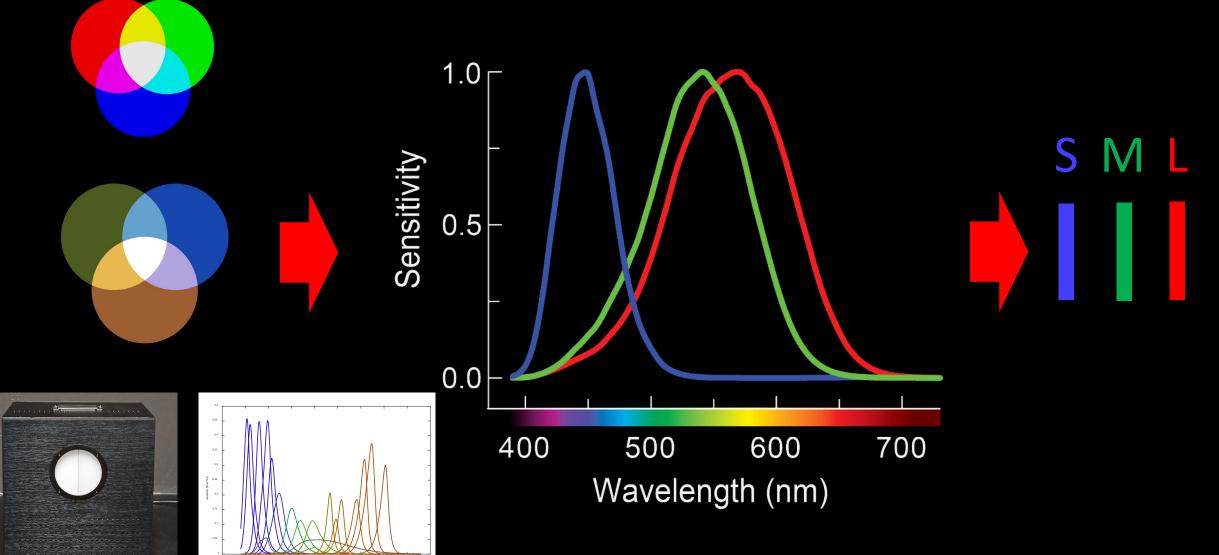
Stockman & Rider (2023) Color Research and Application.

Python program is available on Github at:

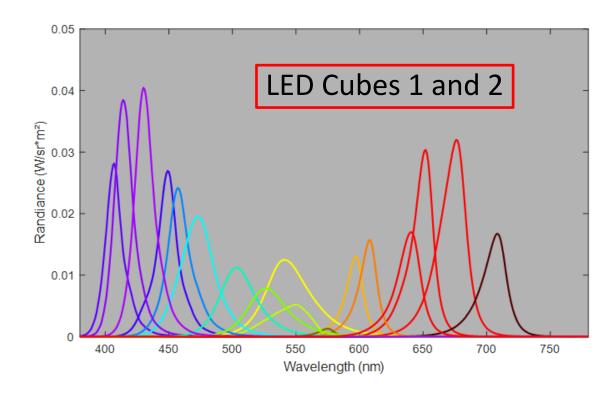
https://github.com/CVRL-IoO/Individual-CMFs.git

### ESTIMATING INDIVIDUAL DIFFERENCES

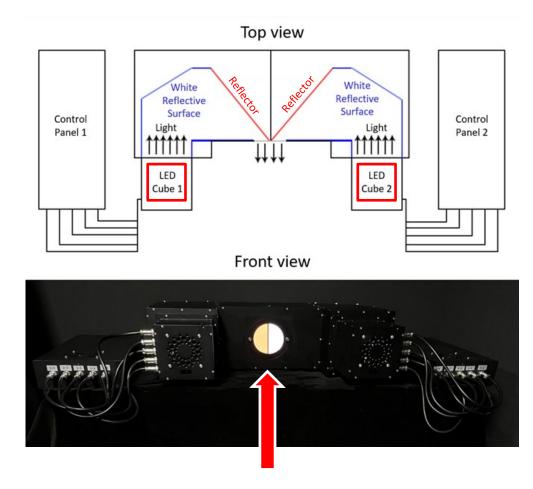
### With individual cone fundamentals we can predict colour matches: Or vice versa...



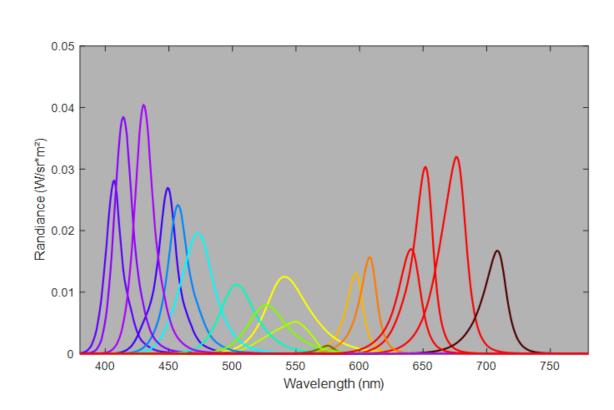
#### Trichromator (LEDMax) developed by Thouslite

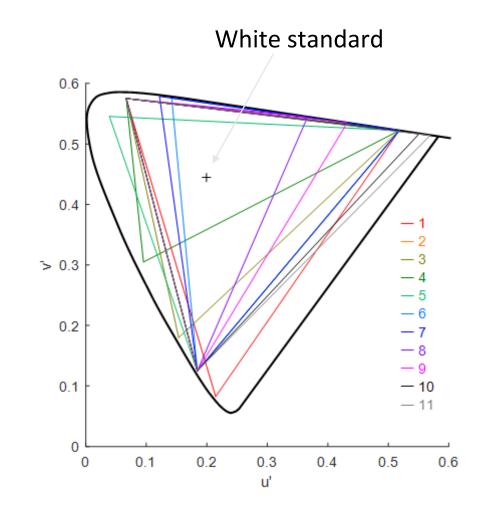


Collaborative work with Ronnier Luo's lab with Lucas Shi and Alan Song and Andrew Stockman

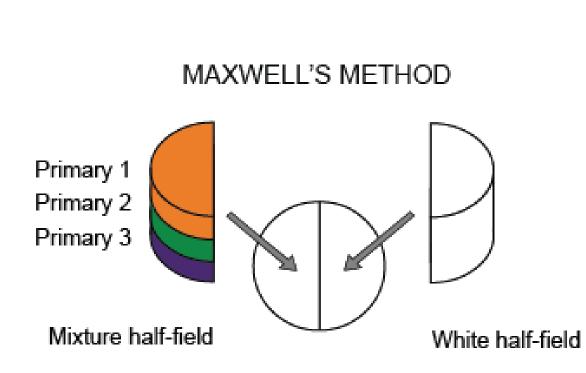


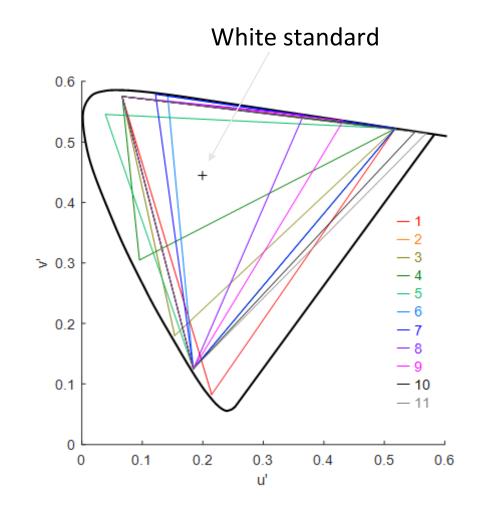
Subject view





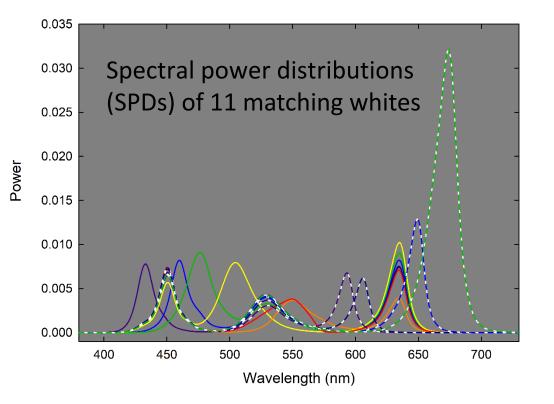
We chose 11 triplets of LEDs (primaries lights) that can be optically mixed to match a white standard (+)...

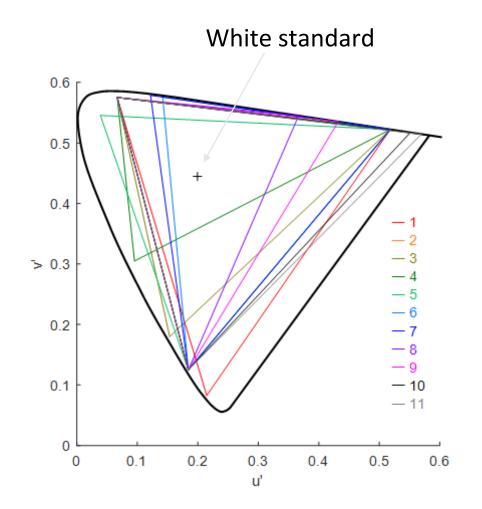




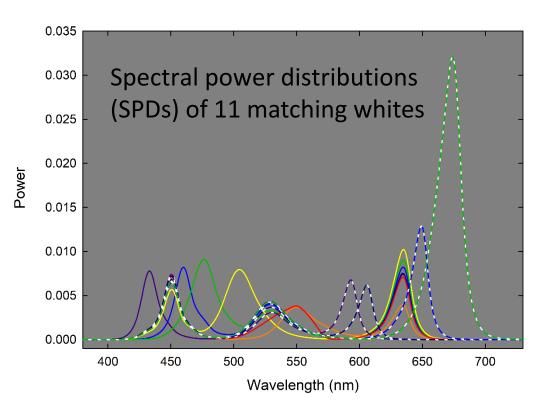
We then asked observers to adjust the intensities of each of the 11 triplets of primaries to match the white standard...

Here are the SPDs for the 11 matching whites (each SPD is made up of all three primaries) set by one of our subjects.



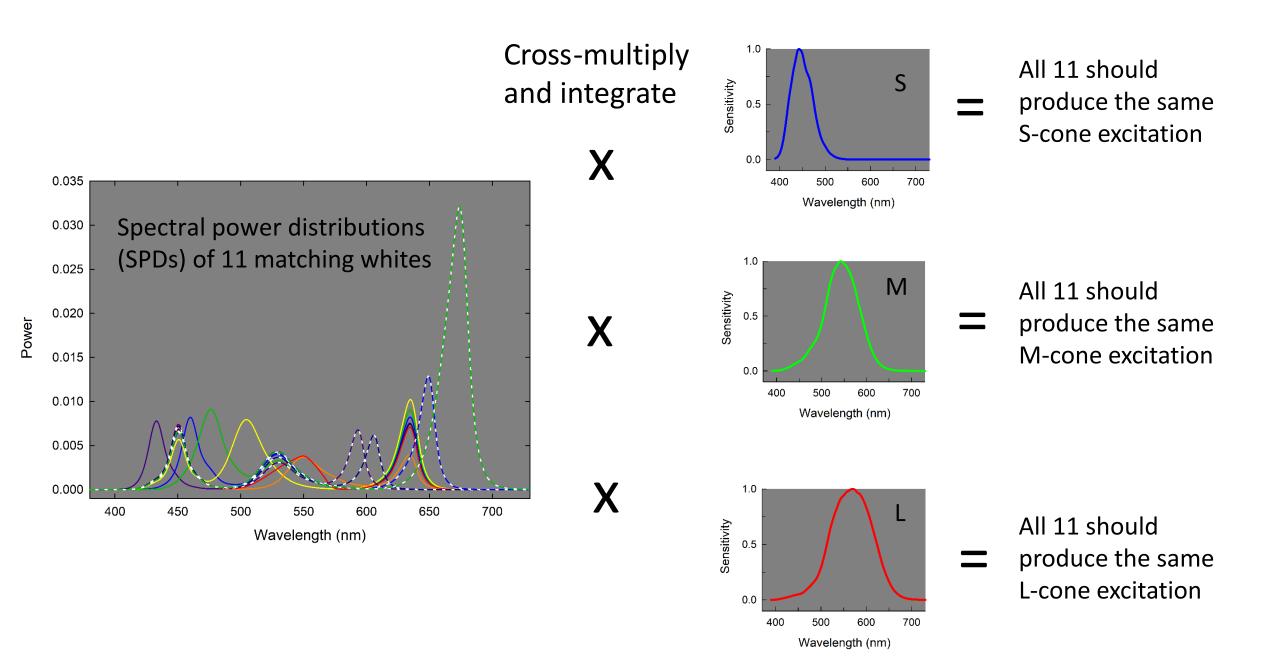


We then asked observers to adjust the intensities of each of the 11 triplets of primaries to match the white standard...

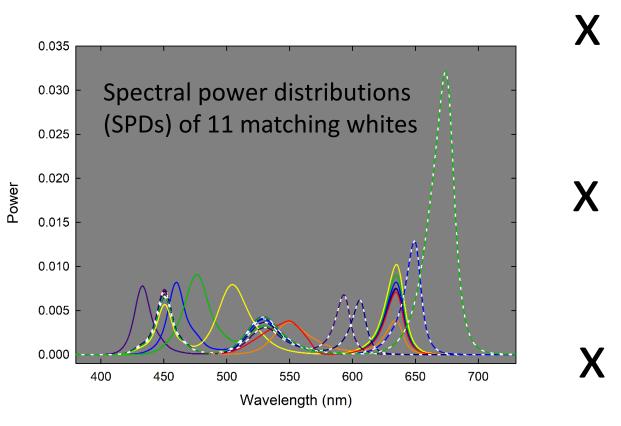


These 11 matching whites should all produce identical L-, M- and Scone excitations.

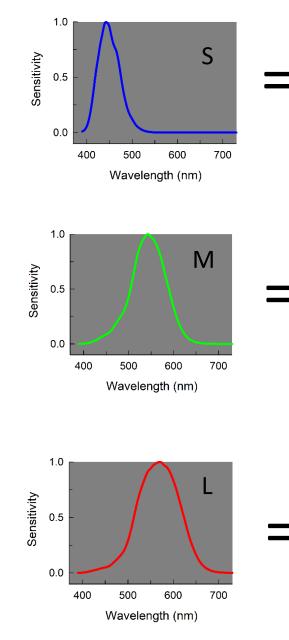
So...



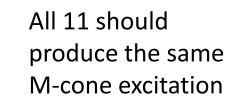
Goal is to find the versions of S, M and L that are closest to producing equal excitations.



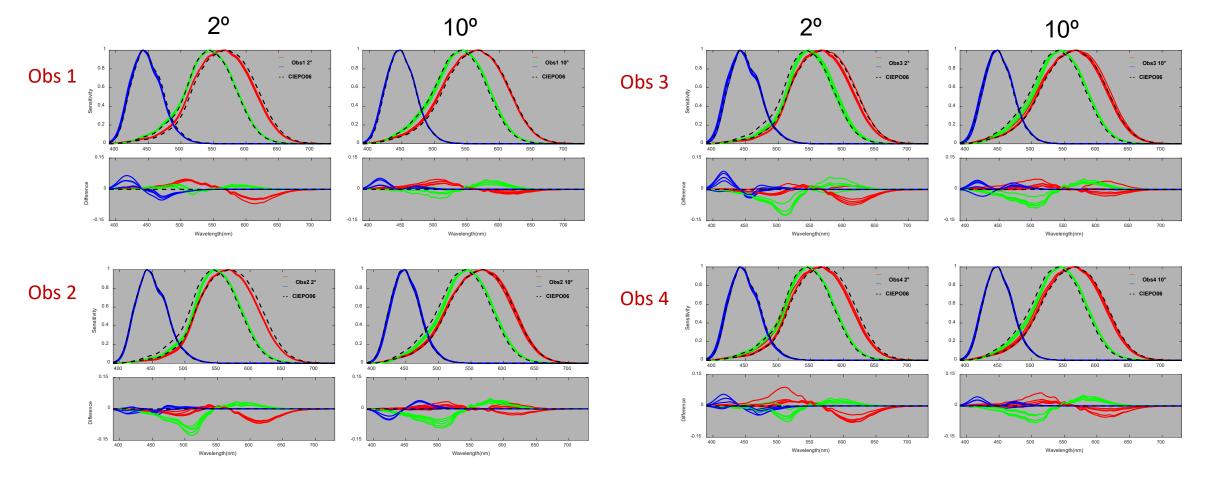
By varying individual differences in lens, macular, and photopigment optical densities and allowing spectral shifts in M and L.



All 11 should produce the same S-cone excitation

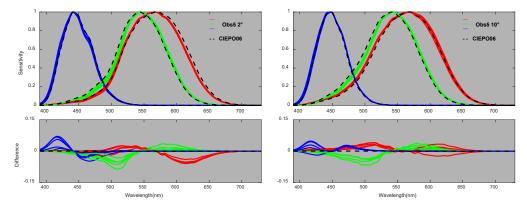


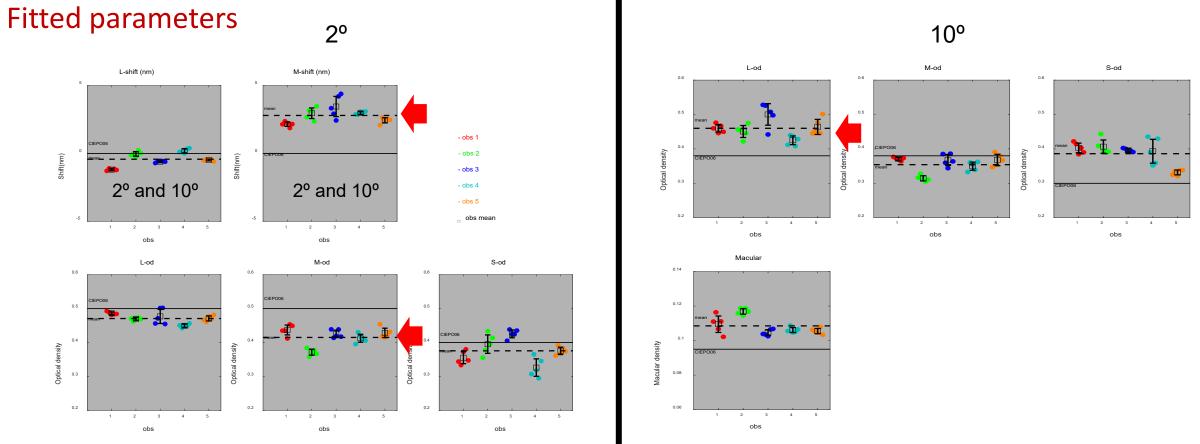
All 11 should produce the same L-cone excitation

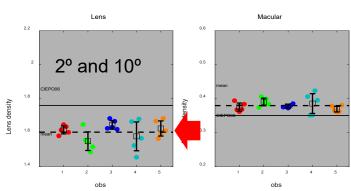


Here are the cone fundamentals that best predict Obs 5 the colour matches measured and estimated five times in five subjects.

### The CIEPO06 curves are the CIE standard LMS functions







We simultaneously fit 22 colour matches: 11 at 2° and 11 at 10° and assumed the same L- and M-shifts and lens densities for 2° and 10°.

### For more details...



#### RESEARCH ARTICLE 🔂 Open Access 🛛 💿 🕥 🗐 🏵

### A multi-primary trichromator to derive individual color matching functions and cone spectral sensitivities

Keyu Shi, Ming Ronnier Luo 🔀 Andrew T. Rider, Tingwei Huang, Lihao Xu, Andrew Stockman

First published: 29 March 2024 | https://doi.org/10.1002/col.22928

First published: 29 March 2024 | https://doi.org/10.1002/col.22928

Keyu Shi, Ming Ronnier Luo 📉 Andrew T. Rider, Tingwei Huang, Lihao Xu, Andrew Stockman

#### Now measured in a total of 51 young observers.

### **RGB** method

).15

400

450

500

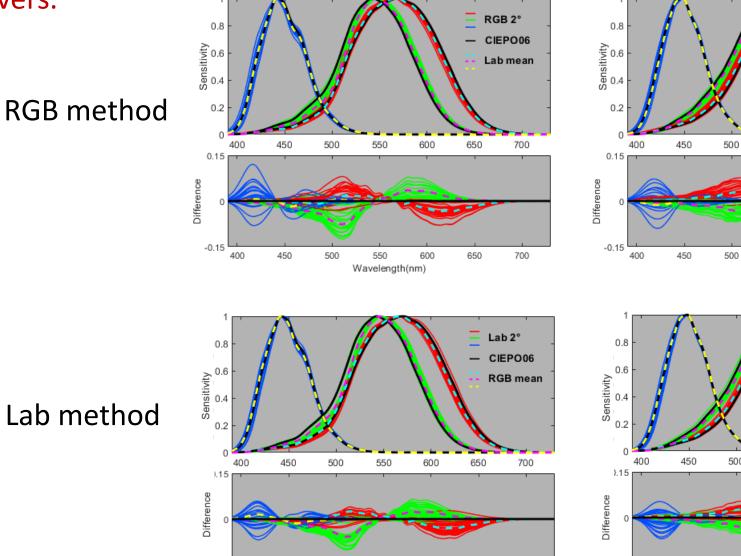
550

Wavelength(nm)

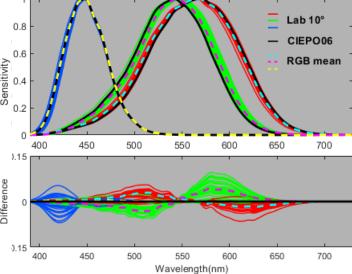
600

650

700



2°



10°

550

550

Wavelength(nm)

600

600

650

650

RGB 10°

CIEPO06

Lab mean

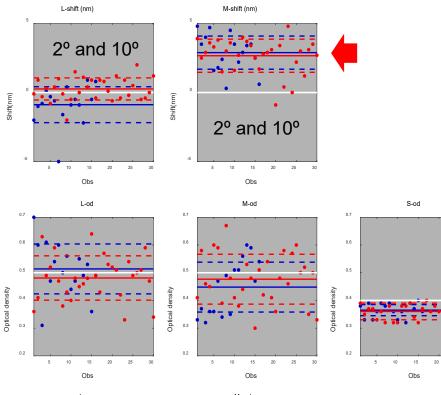
700

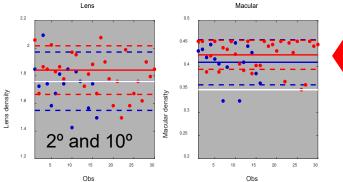
700

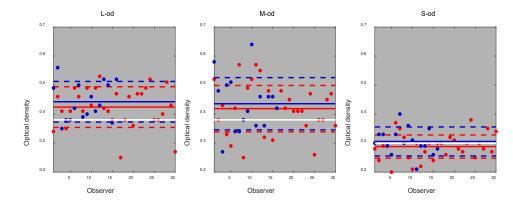
#### Fitted parameters

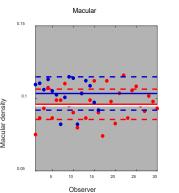
2°

10°





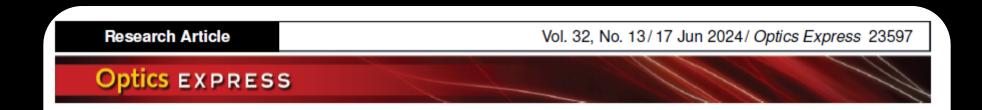




#### 51 young observers.

Shi, K., Luo, M. R., Rider, A. T., Song, S., Huang, T., & Stockman, A. (2024). Individual differences in color matches and cone spectral sensitivities in 51 young adults. Optics Express, 32(13), 23597-23616.

### For more details...



### Individual differences in color matches and cone spectral sensitivities in 51 young adults

KEYU SHI,<sup>1</sup> Ming Ronnier Luo,<sup>1,\*</sup> Andrew T. Rider,<sup>2</sup> Siyuan Song,<sup>1</sup> Tingwei Huang,<sup>3</sup> and Andrew Stockman<sup>1,2</sup>

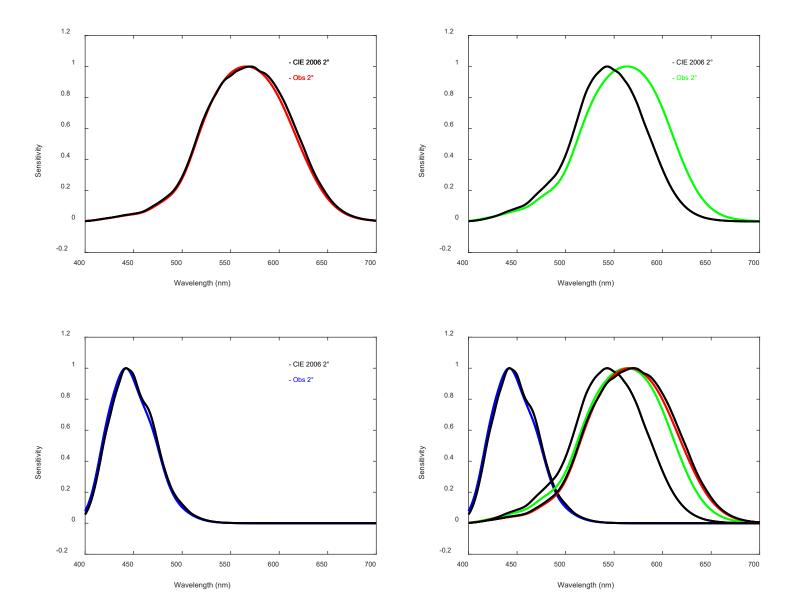
<sup>1</sup>State Key Laboratory of Extreme Photonics and Instrumentation, Zhejiang University, Hangzhou, China <sup>2</sup>Institute of Ophthalmology, University College London, EC1 V 9EL London, United Kingdom <sup>3</sup>Thousand Lights Lighting (Changzhou) Limited, Changzhou, China \*m.r.luo@zju.edu.cn

<sup>3</sup>Thousand Lights Lighting (Changzhou) Limited, Changzhou, China \*m.r.luo@zju.edu.cn We are now working on different age groups and have measured 100 observers from 8 to 80 years old.

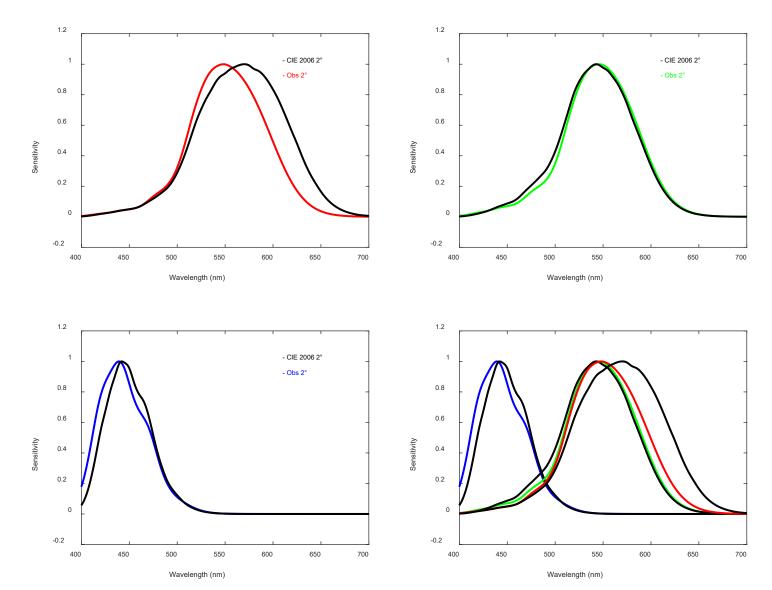
And also for, so far, 22 colour deficient observers, for whom, remarkably, the methods seem also to work. Here are two examples...

**CVDs** 

#### Typical severe deuteranomalous/ deuteranopic observer



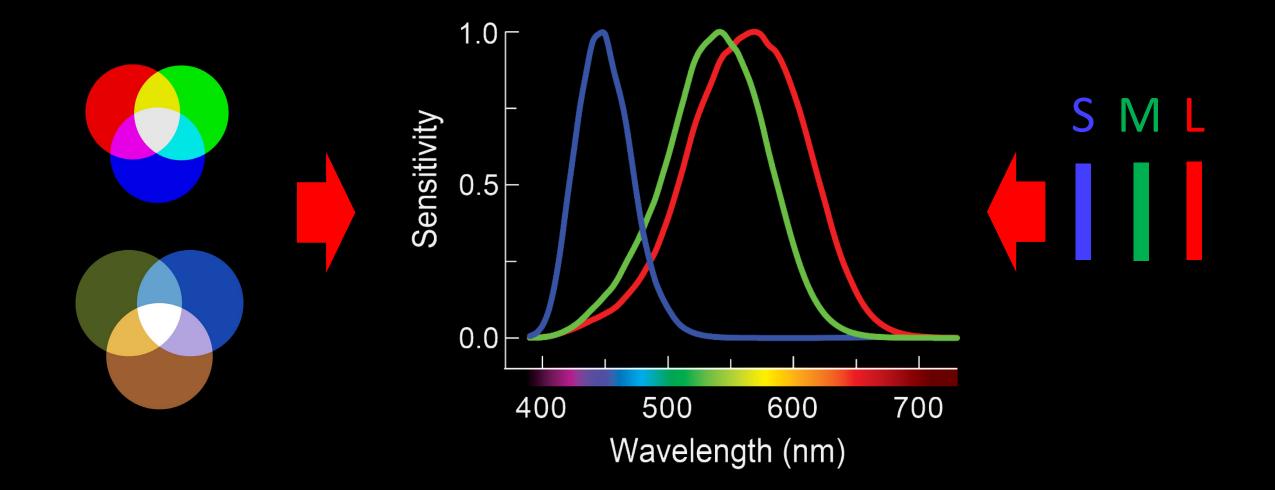
	Obs	CIE 2006 2°
L- shift	-0.1	0
M- shift	19.8	0
Density of L-	0.31	0.5
Density of M-	0.69	0.5
Density of S-	0.31	0.4
Lens density	1.57	1.76
Macular density	0.321	0.350



#### Typical severe protanomalous/ protanopic observer

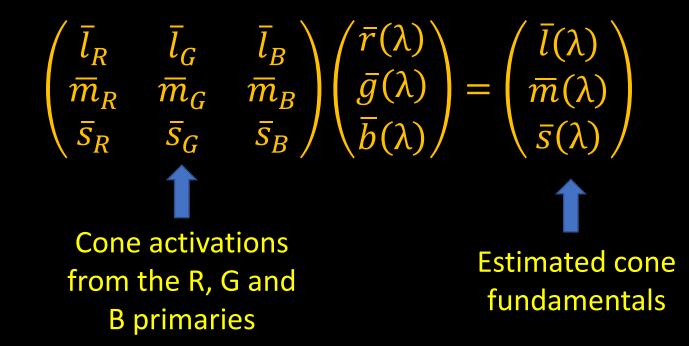
	Obs	CIE 2006 2°
L- shift	-19.5	0
M- shift	0.3	0
Density of L-	0.34	0.5
Density of M-	0.64	0.5
Density of S-	0.35	0.4
Lens density	1.29	1.76
Macular density	0.536	0.350

We have used a model of cone fundamentals and predicted individual cone fundamentals from a series of colour matches



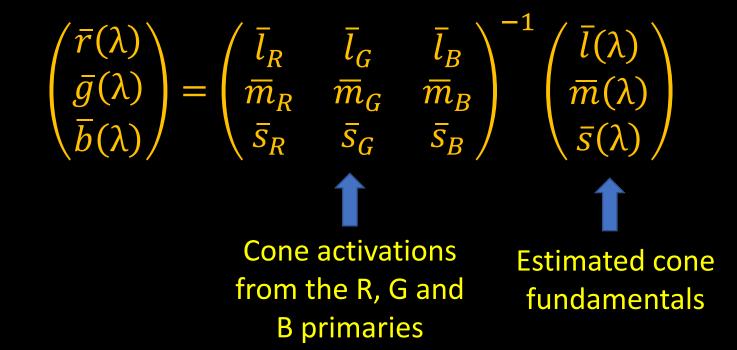
### Converting to other CMFs

• LMS to RGB is simple



### Converting to other CMFs

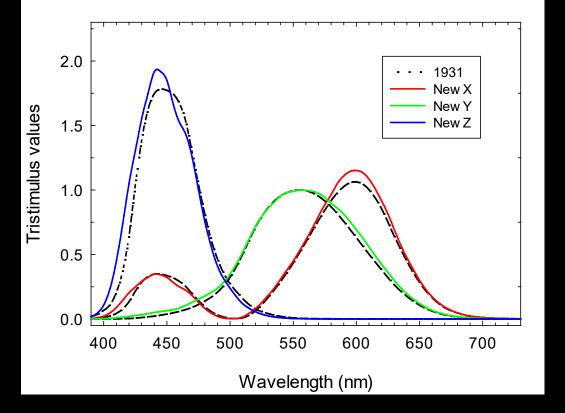
• LMS to RGB is simple



### Converting to other CMFs

### • LMS to XYZ is not so simple

2-deg LMS →XYZ transforms



(1.94735469	-1.41445123	0.36476327	$\left( \overline{l}(\lambda) \right)$		$\left(\overline{x}(\lambda)\right)$
0.68990272	0.34832189	0	$\overline{m}(\lambda)$	=	$\overline{y}(\lambda)$
0	0	1.93485343			

Z is a scaled version of S

- Y is a weighted sum of L and M  $\{= V(\lambda)\}$
- X is not physiologically relevant

### Summary

- Standard or 'mean' cone spectral sensitivities (fundamental CMFs) are helpful for describing colours for the average observer
- But the underlying functions can vary between observers for several physical, physiological and genetic factors
- We can parametrically model these variations to generate individualised cone fundamentals and colour matching functions
- We can perform colour matching experiments to estimate an individual's cone fundamentals and examine variability due to:
  - Age
  - Ethnicity
  - Colour vision deficiency

### Applications

- Display technologies
  - TVs, monitors, phones, laptops, tablets, projectors
- Colour reproduction and lighting
- Silent substitution
  - "Cone isolating" stimuli may not be, for different observers
  - Intrinsically photosensitive retinal ganglion cells (melanopsin containing)
  - Rods

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



### https://github.com/CVRL-IoO/Individual-CMFs.git

### Thank you

Andrew Stockman, UCL Ronnier Luo, Zhejiang University Lucas Shi, Zhejiang University Alan Song, Zhejiang University Tingwei Huang, Thouslite Ltd





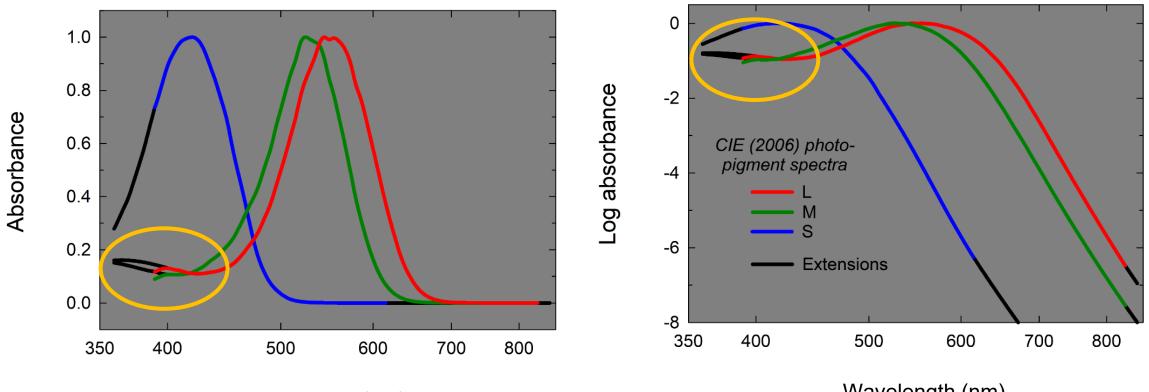
Biotechnology and Biological Sciences Research Council Biological Sciences

**D**C

### Uncertainty at very short wavelengths

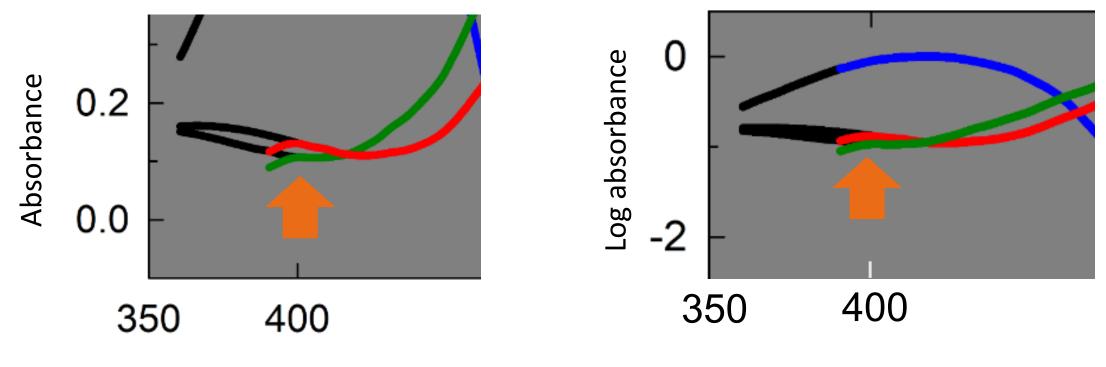
- General lack of colour matching data in this region
- Lens and macular pigment densities <390 nm are uncertain</li>
- Fluorescence of the lens and cornea affect colour matches

#### One correction of the CIE 2006 functions:

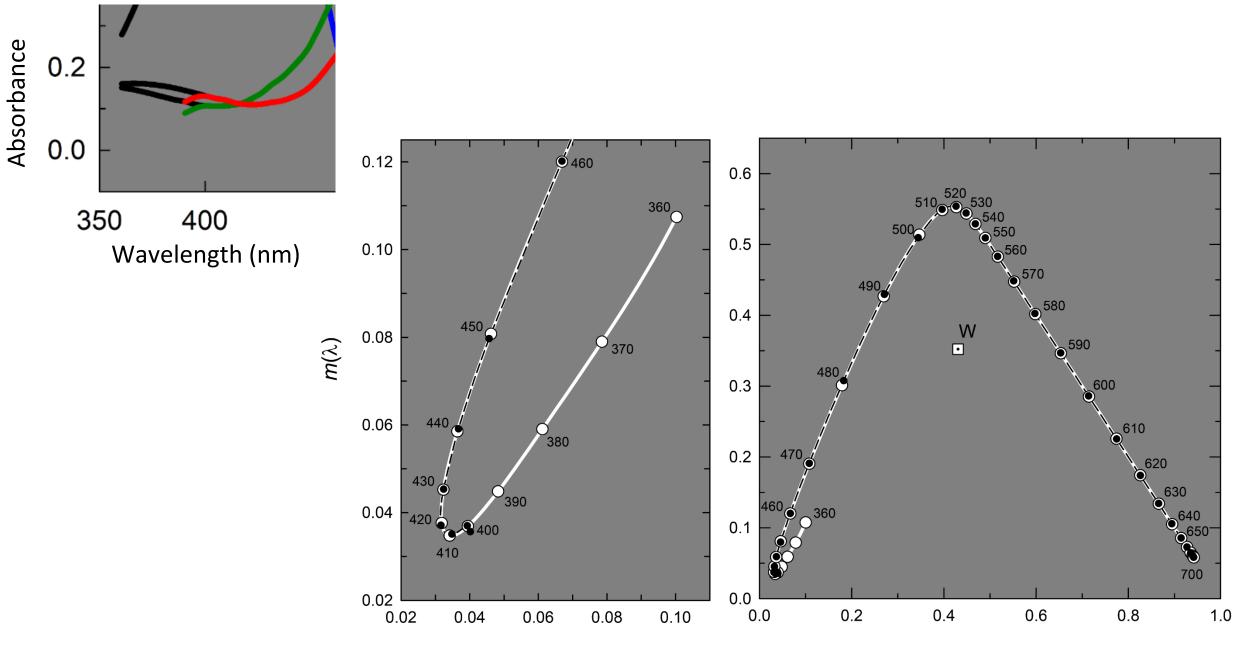


Wavelength (nm)

Wavelength (nm)



Wavelength (nm)



*Ι*(λ)

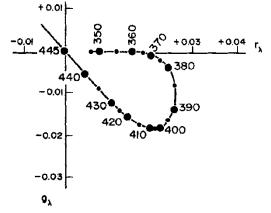


Figure 8. Chromaticity diagram averaged from two aphakic observers in the UV. Subjects matched a split field with primaries at 445 and 625 nm on the left and UV with 525 nm on the right. The color matching functions  $r_{\lambda}$ ,  $g_{\lambda}$ and  $b_{\lambda}$  were equated by means of W. D. Wright's (1946) convention with normalizing wavelengths 494 and 582.5 nm. From these the  $(r_{\lambda}, g_{\lambda})$  chromaticity diagram for UV stimuli, representing the lower left corner of the color triangle, is drawn here. Redrawn from Tan (1971).

#### Aphakics

#### Originally from Tan (1971) thesis

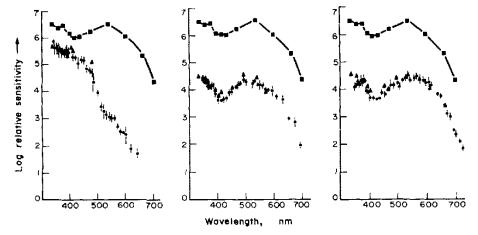


Figure 7. Photopic and cone spectral sensitivities of aphakic observers. (**II**), Fovcal spectral sensitivity which is a composite spectrum of the 3 phototopic (cone) spectra. Left: blue cone spectra; (**O**), give the foveal spectrum obtained against a bright orange background (Wratten 23 A filter, 5.13 log Trolands) averaged for two subjects; (**A**), show the spectral sensitivity of the  $\pi$ 3 mechanism determined for one subject. Middle: green cone spectra; (**O**), foveal spectrum obtained against a bright purple background (Wratten 34 filter, 4.78 log Trolands) averaged for two subjects; (**A**), spectral sensitivity of the  $\pi$ 4 mechanism determined for one subject. Right: yellow (red) cone spectra; (**O**), spectral sensitivity of the  $\pi$ 4 mechanism determined for one subject. Right: yellow (red) cone spectra; (**O**), spectral spectrum obtained against a bright blue background (Wratten 47 filter, 5.22 log Trolands) averaged for two subjects; (**A**), show the spectral sensitivity of the  $\pi$ 5 mechanism determined for one subject. Redrawn from Tan (1971).