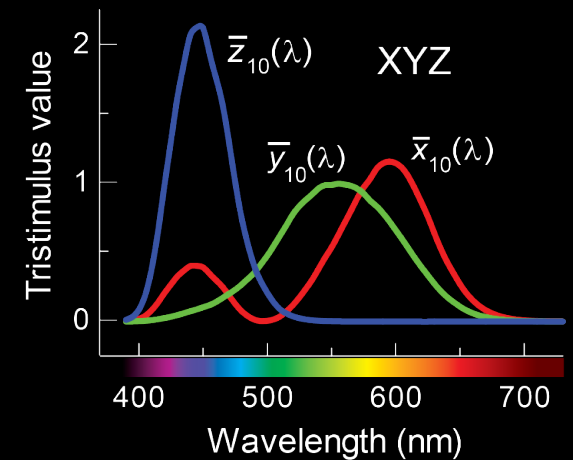
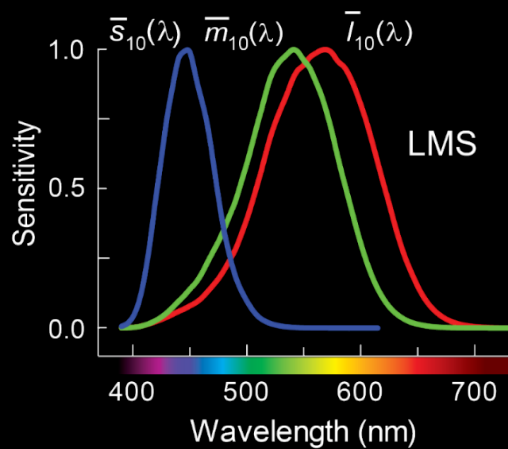


# Cone spectral sensitivities, colour matching functions and individual differences

Andrew Stockman



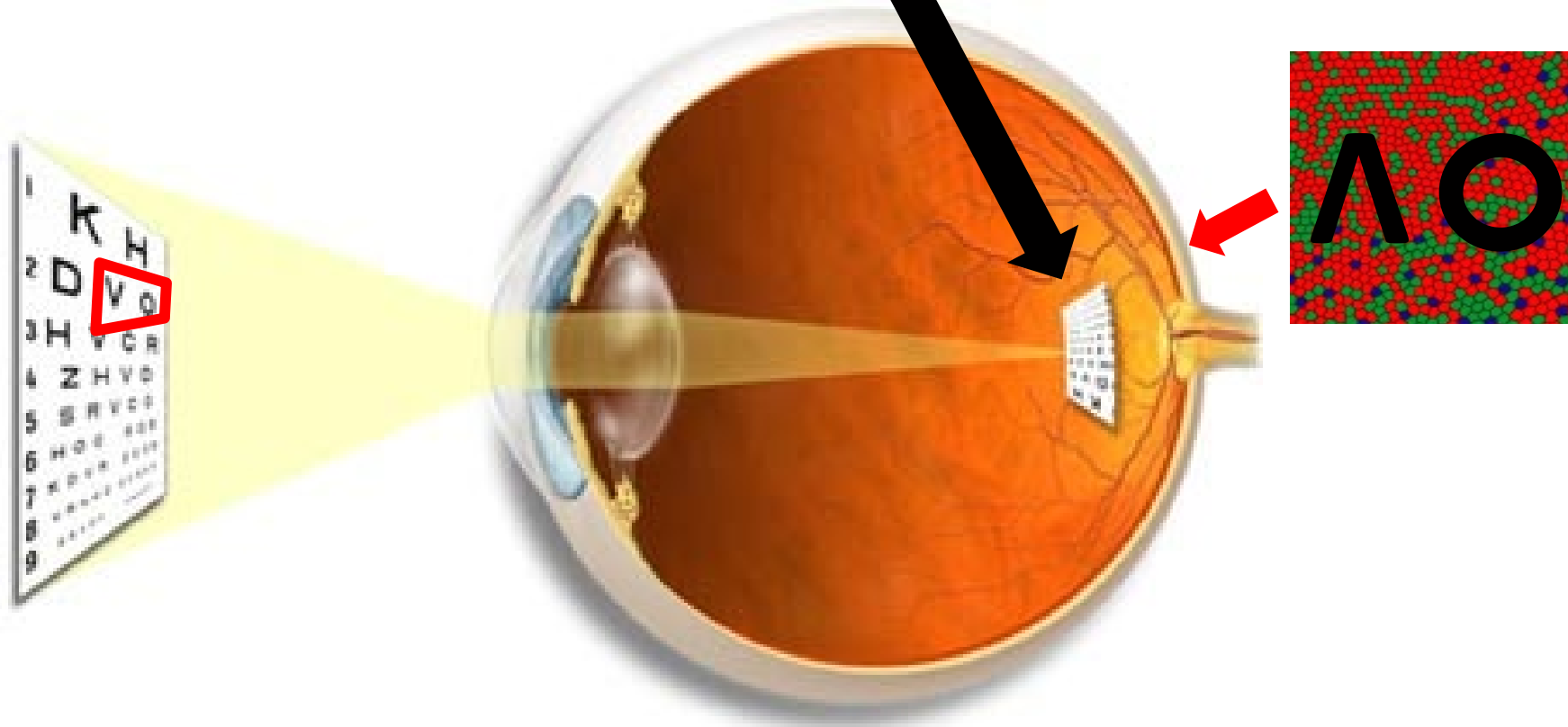
# 1. CONES AND TRICHRMACY



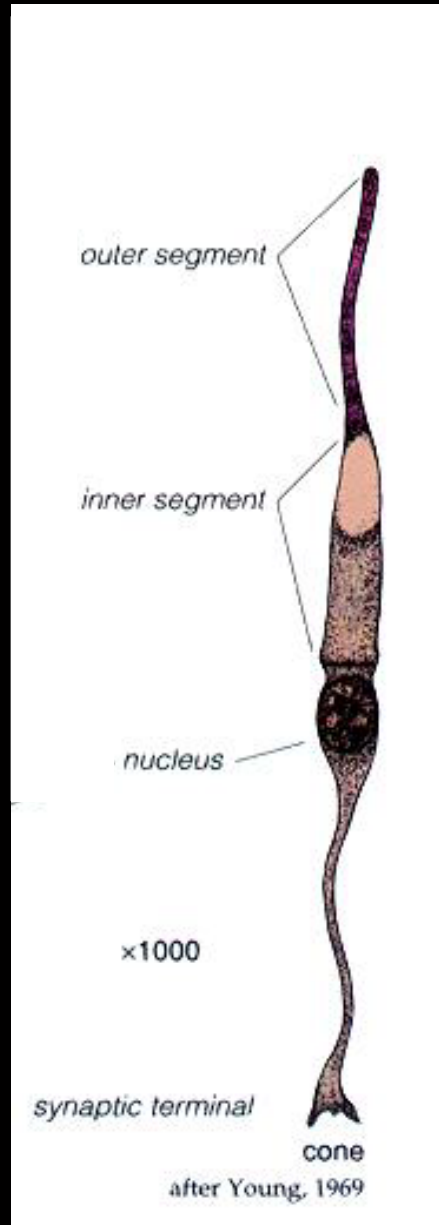
# Human colour vision

An inverted image of the outside world is formed on the retina by the cornea and lens

The retina is carpeted with light-sensitive cones (and rods)



# Human cone photoreceptors (sensors)



## Cones

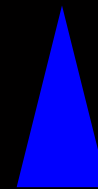
- Daytime, achromatic *and* chromatic vision
- 3 types



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

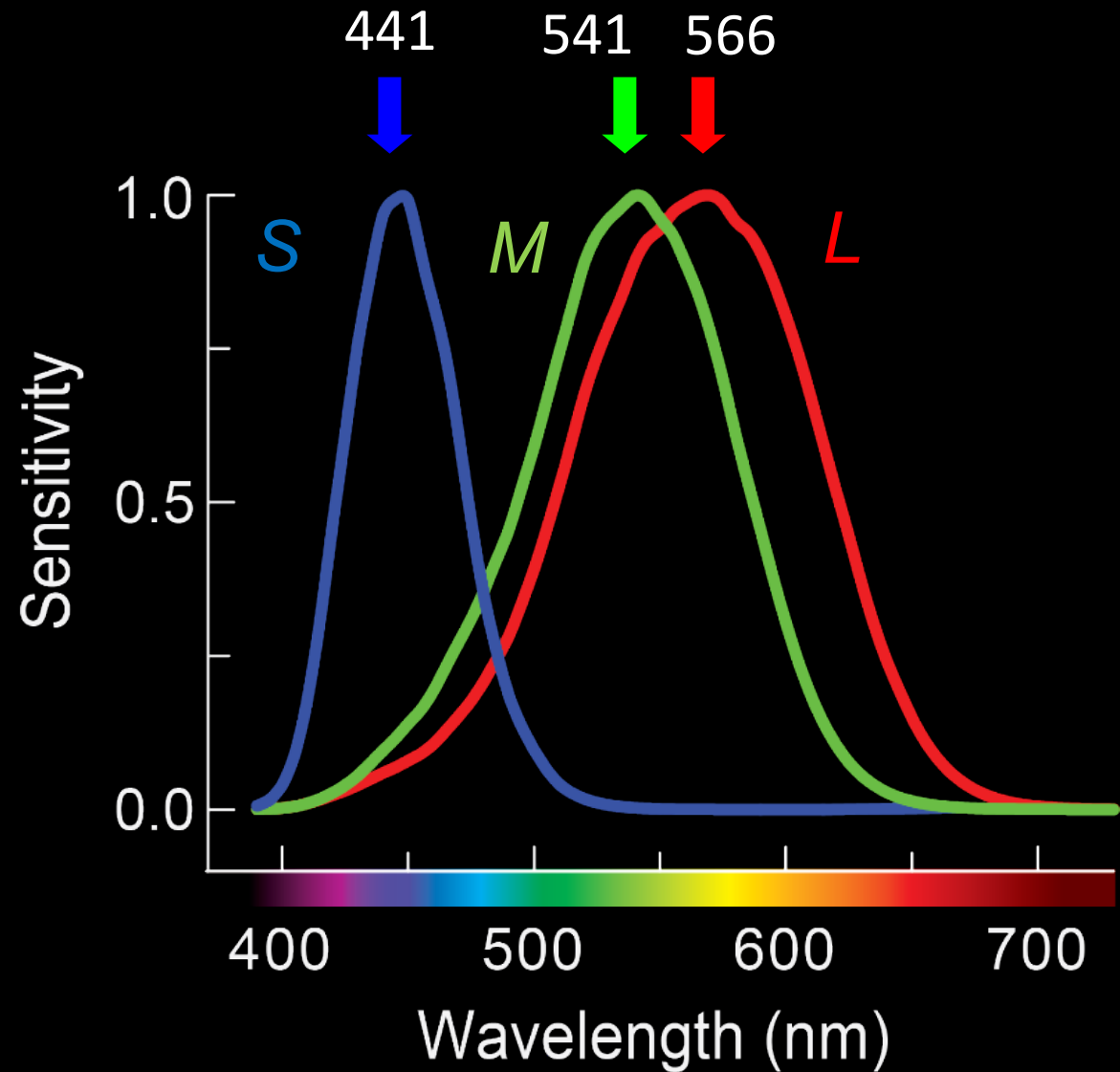
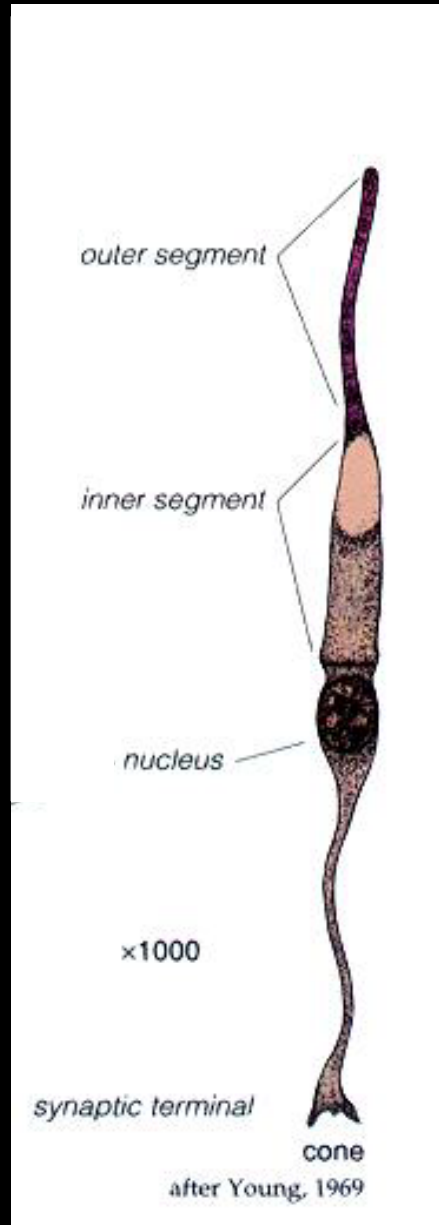


Middle-wavelength-sensitive (M) or "green" cone



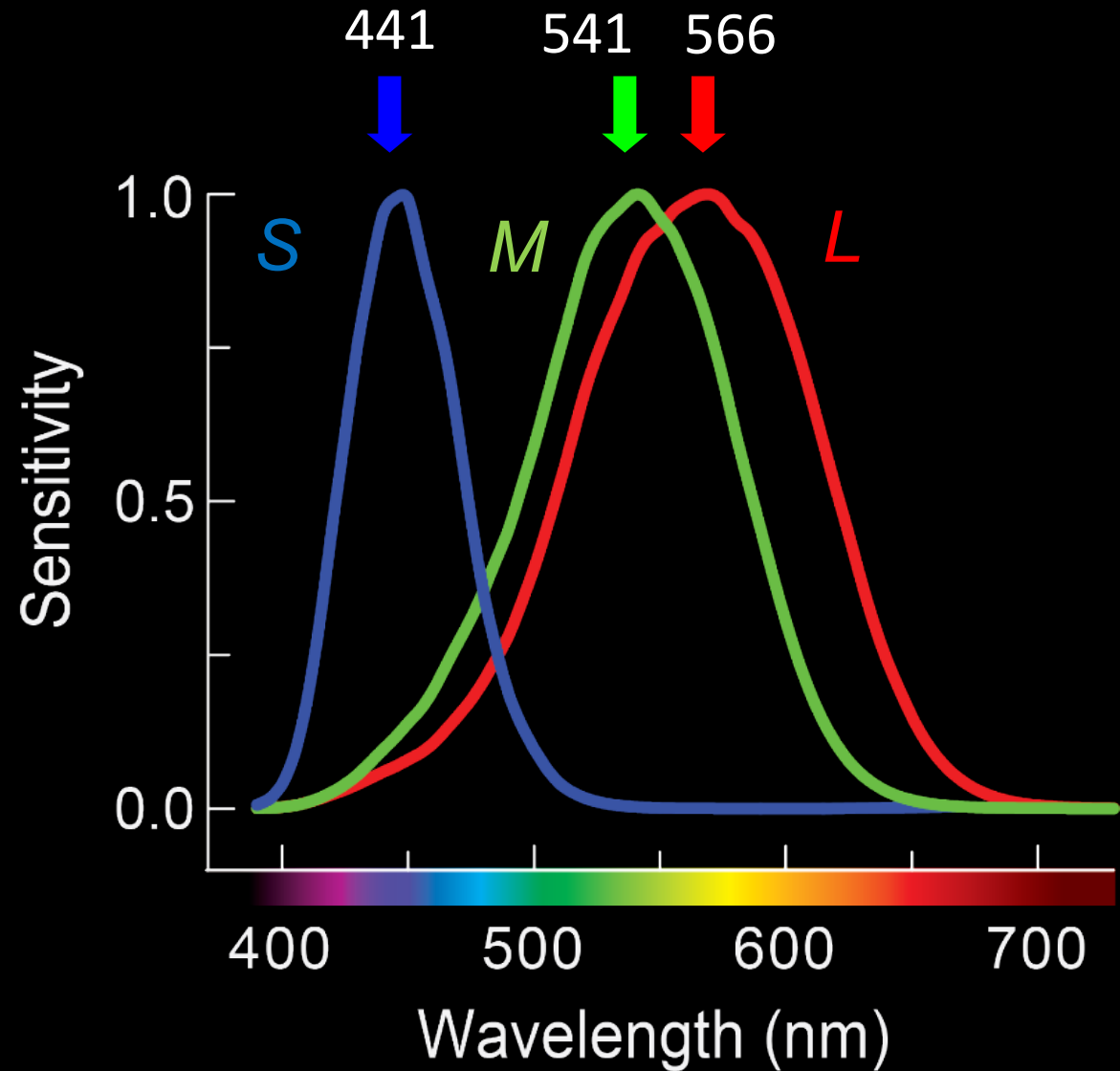
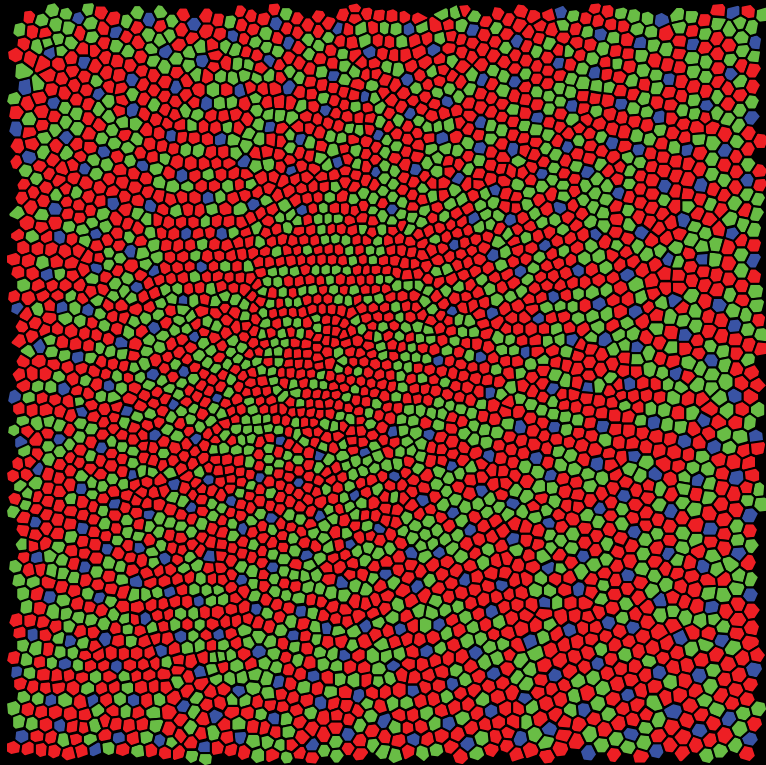
Short-wavelength-sensitive (S) or "blue" cone

# Human cone (sensor) spectral sensitivities



# Human cone (sensor) spectral sensitivities

Human foveal sensor array

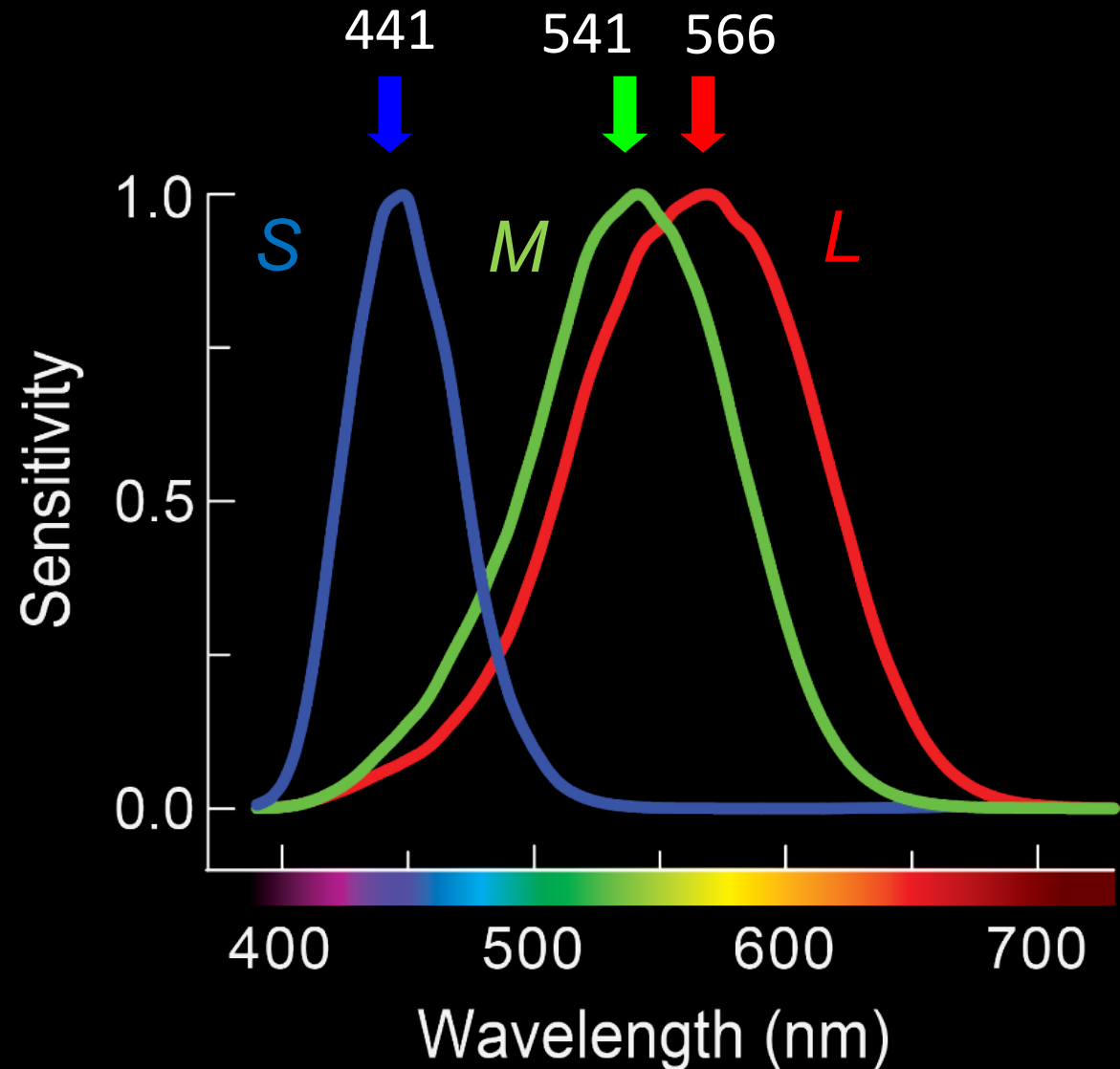


# Trichromacy

Trichromacy arises because there are just three cone types (L, M & S) with different spectral sensitivities. Each responds only according to the *number* of photons it absorbs (independent of their wavelengths).

If we know the three cone spectral sensitivities, and thus the effects that a light has on each of them, we can completely specify that light.

Human colour vision is trichromatic

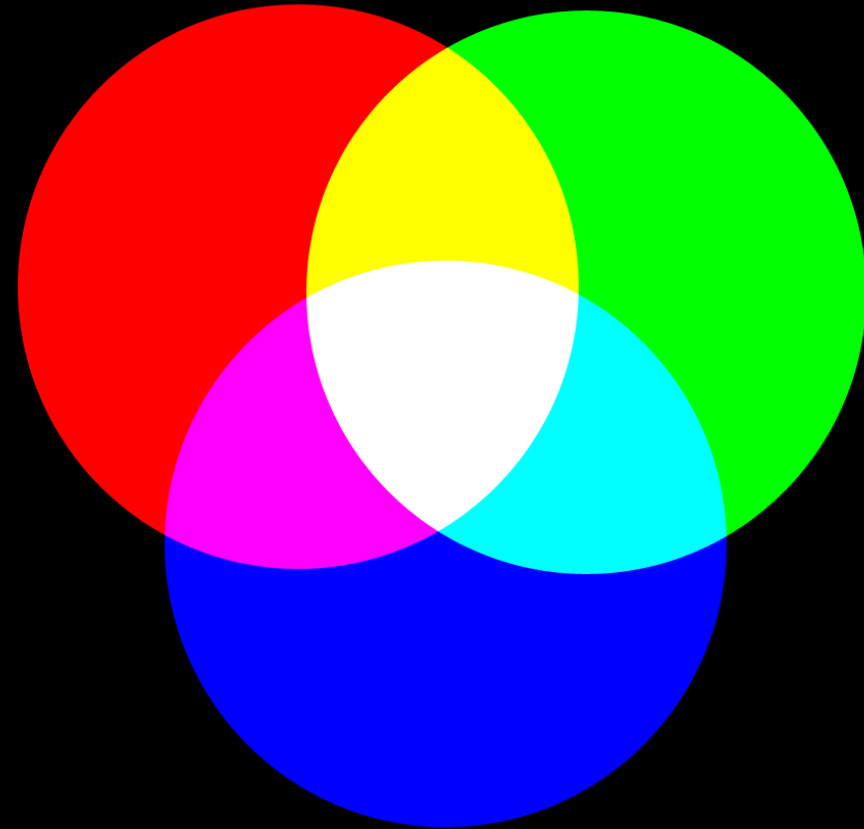


# Trichromacy

Trichromacy arises because there are just three cone types (L, M & S) with different spectral sensitivities. Each responds only according to the *number* of photons it absorbs (independent of their wavelengths).

Trichromacy means that colour vision at the input to the visual system is simple, since you can match any colour in terms of just 3 primary colours (e.g., RGB).

Human colour vision is trichromatic



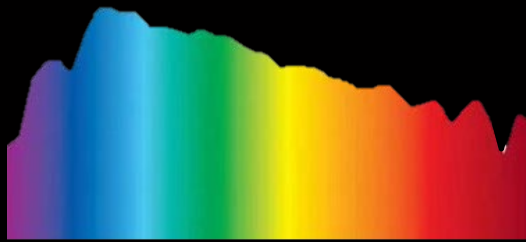
It is a 3-variable system defined by LMS, RGB or XYZ...



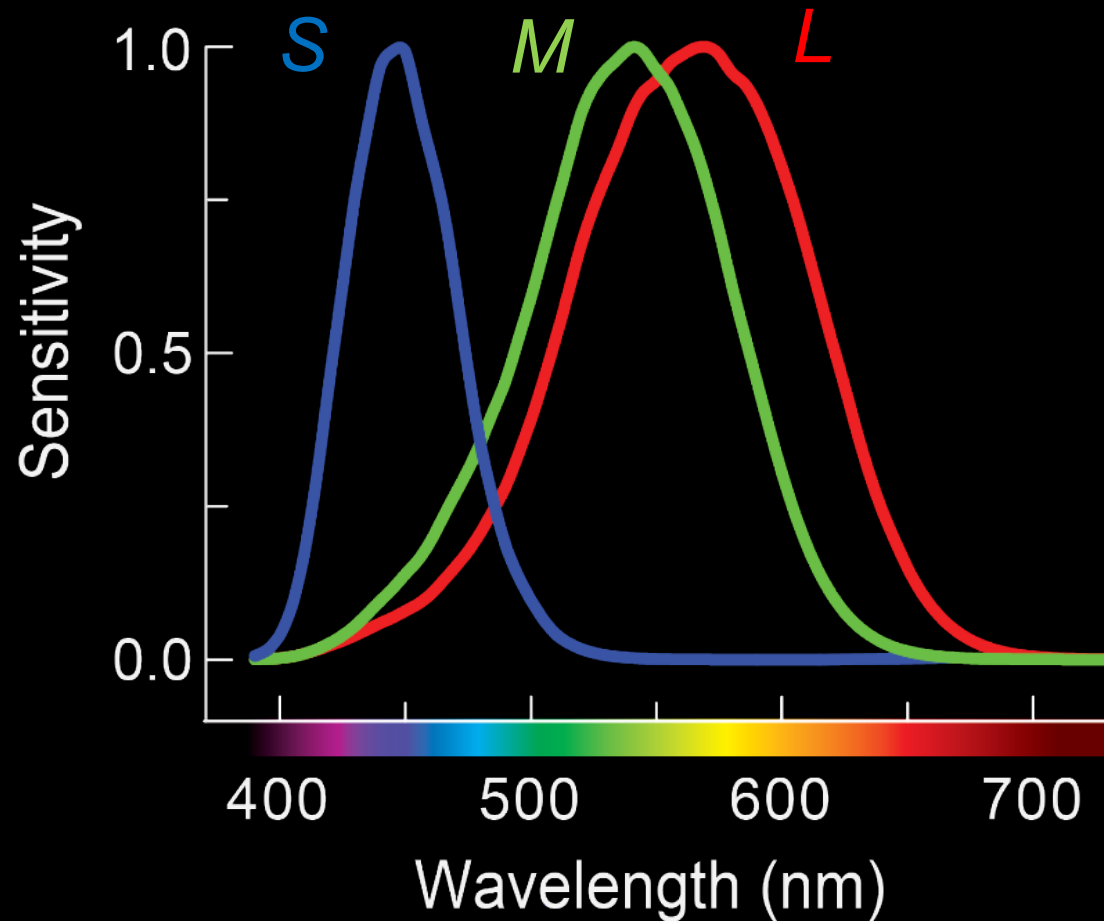
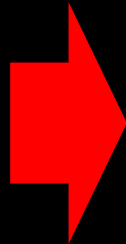
# Trichromacy

Means that at the first stage of vision there is a massive loss of spectral information!

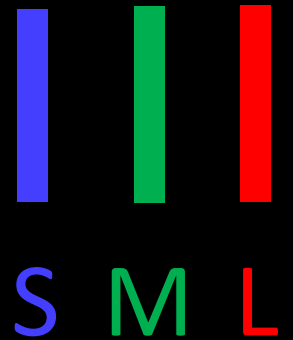
Continuous Spectral Power Distribution



Wavelength

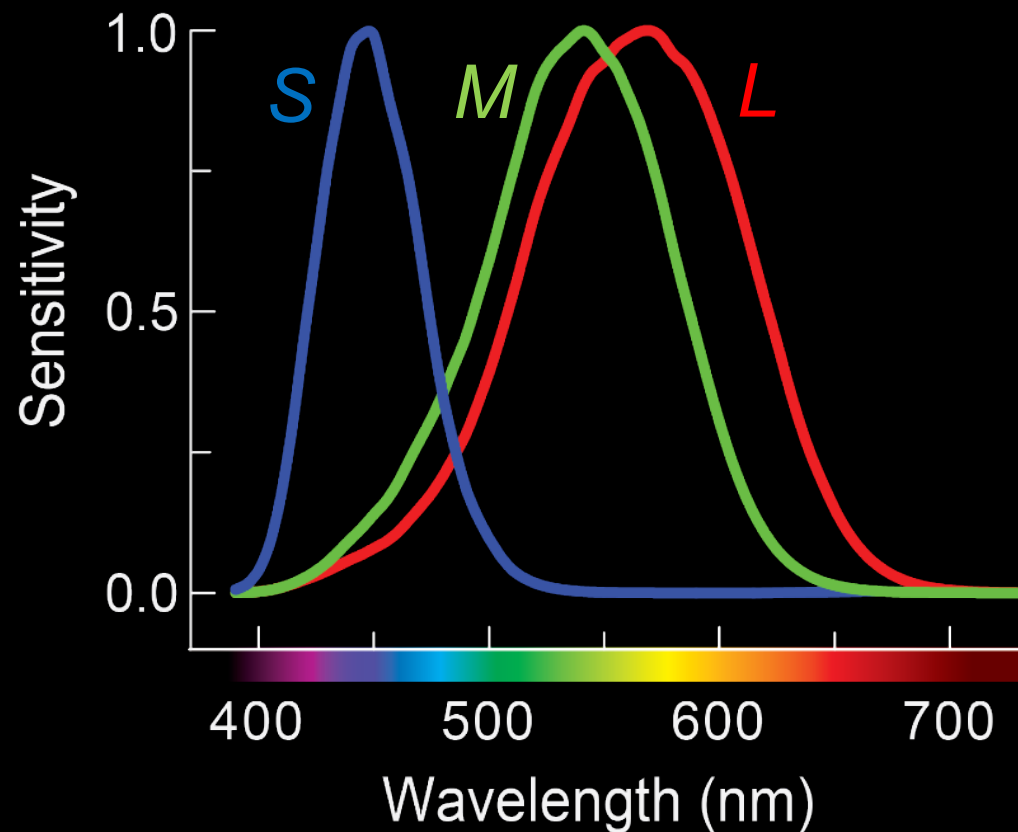


3 excitations!

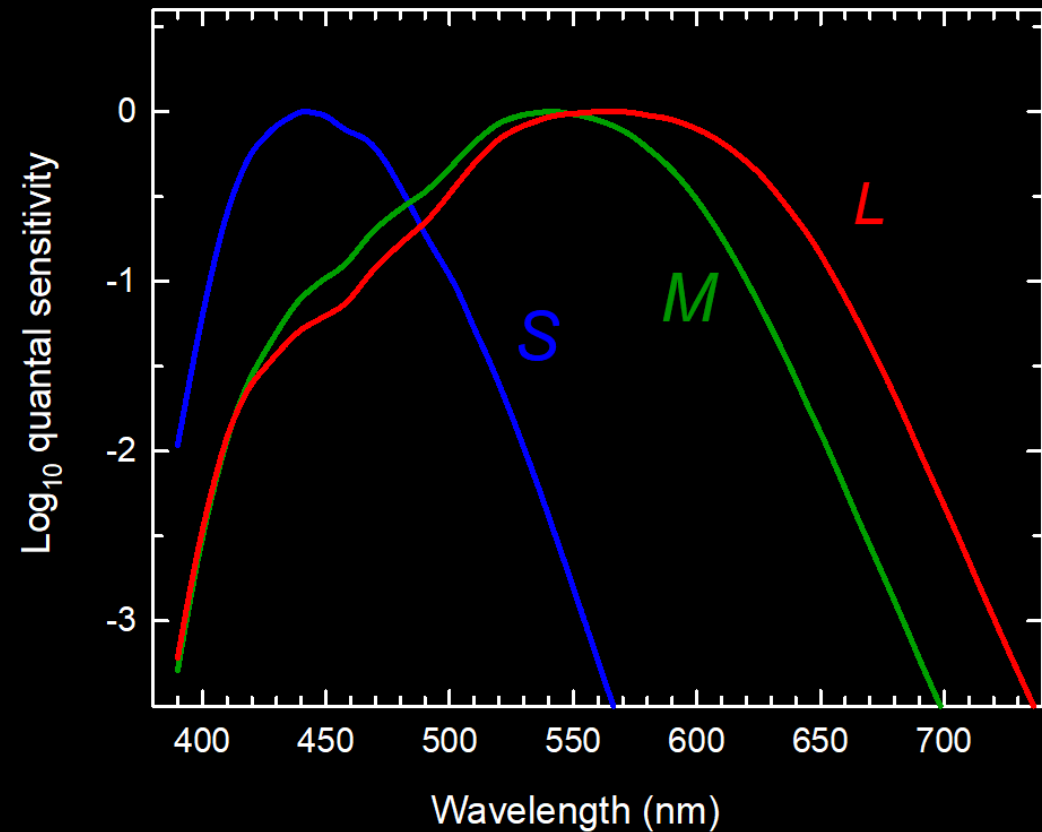


I'll be showing linear and logarithmic versions of the cone spectral sensitivities:

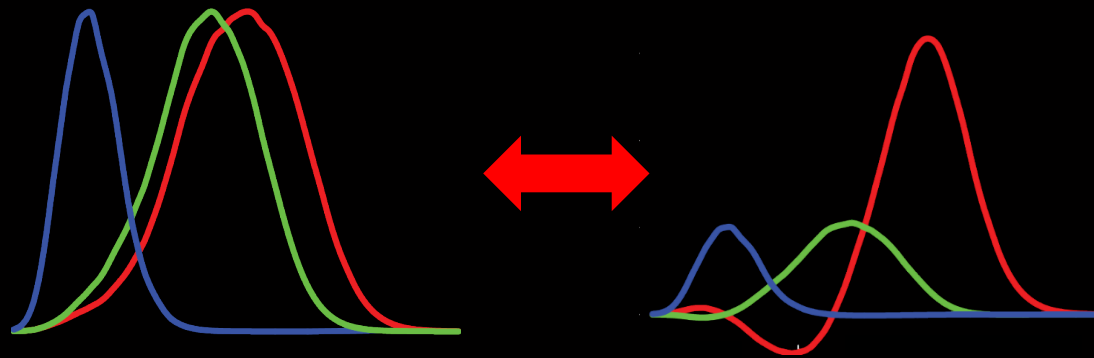
Linear



Logarithmic

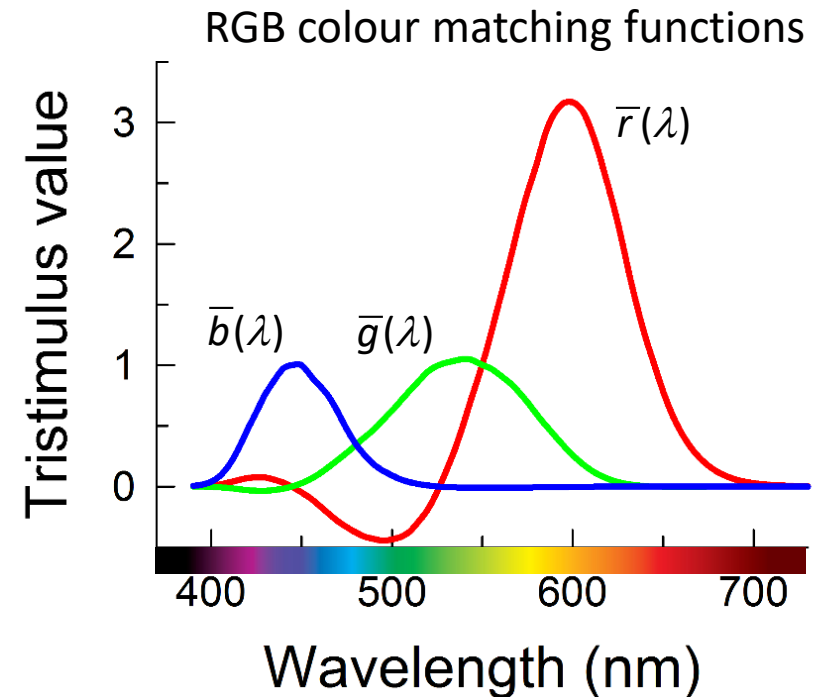
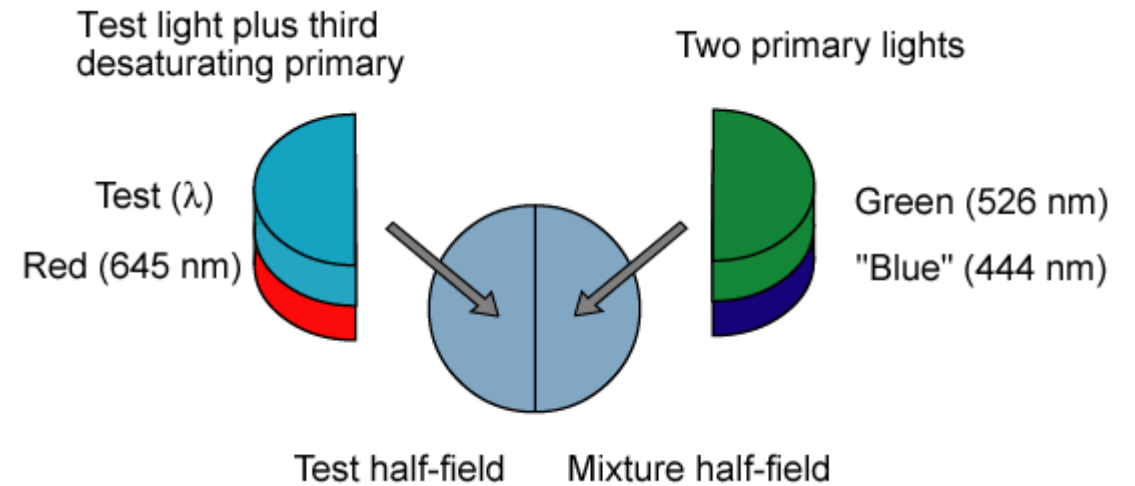


## 2. CONE SPECTRAL SENSITIVITIES AND COLOUR MATCHES



# Colour matching

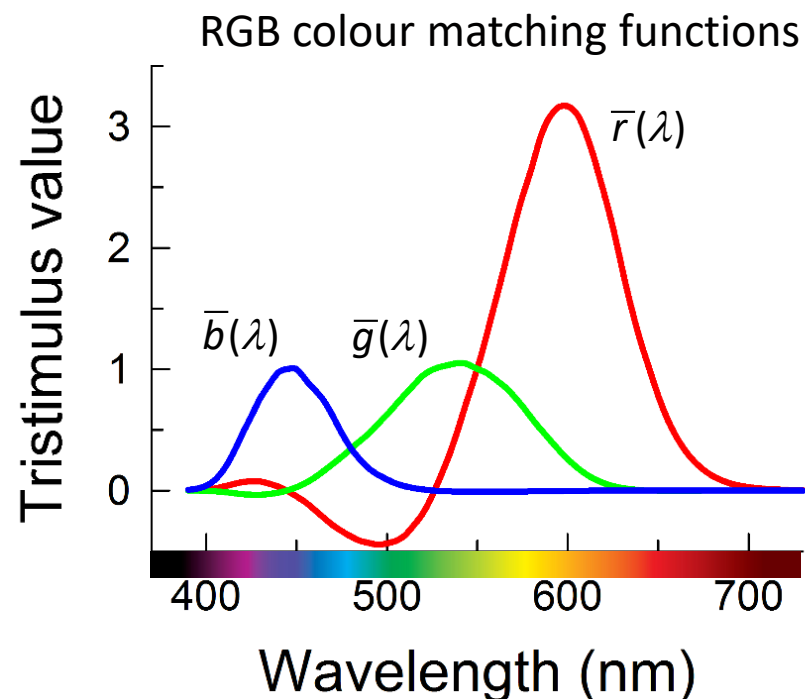
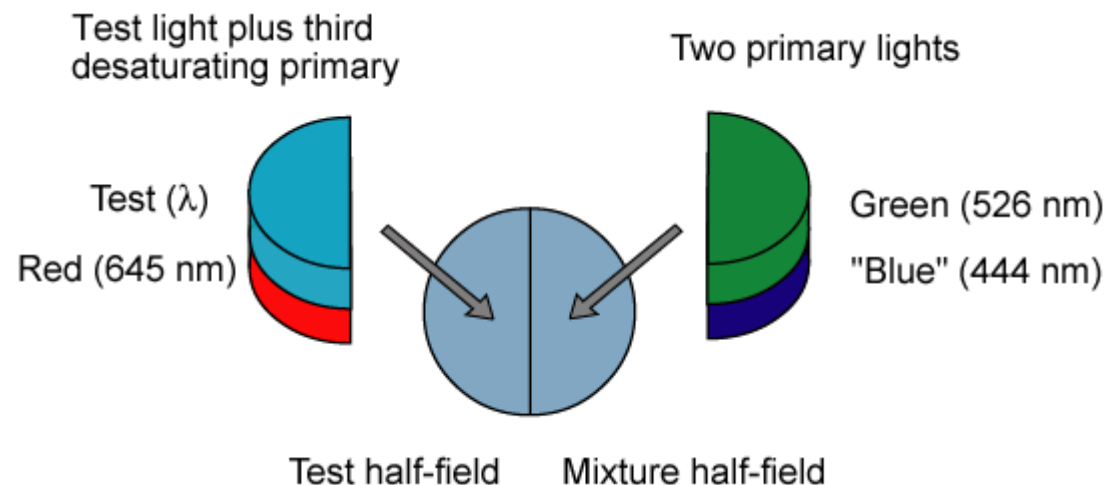
Another way of specifying colours is by making colour matches in a colour matching experiment:



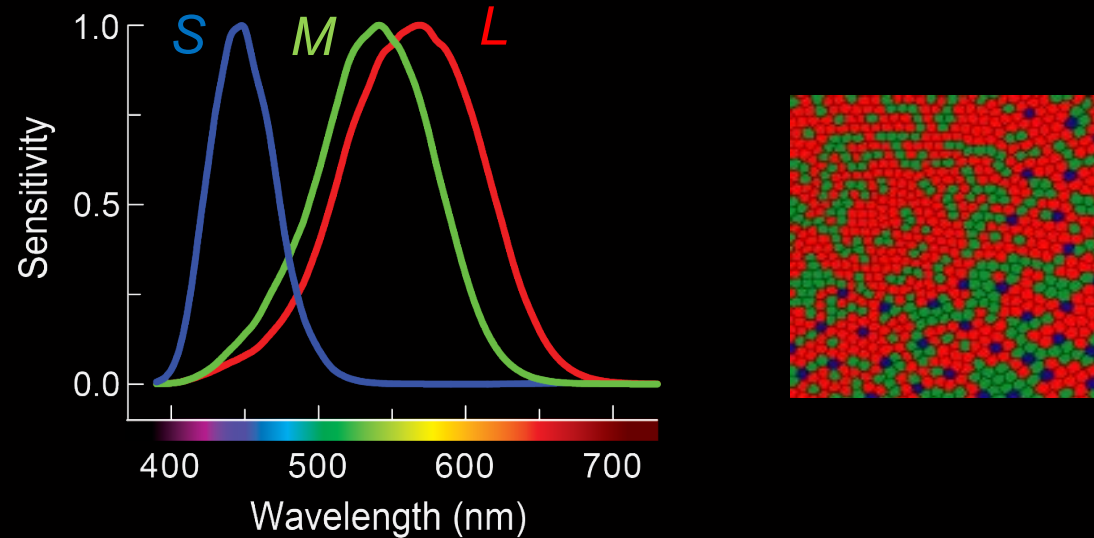
# Colour matching

Another way of specifying colours is by making colour matches in a colour matching experiment:

But what has colour matching got to do with cone spectral sensitivities?



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



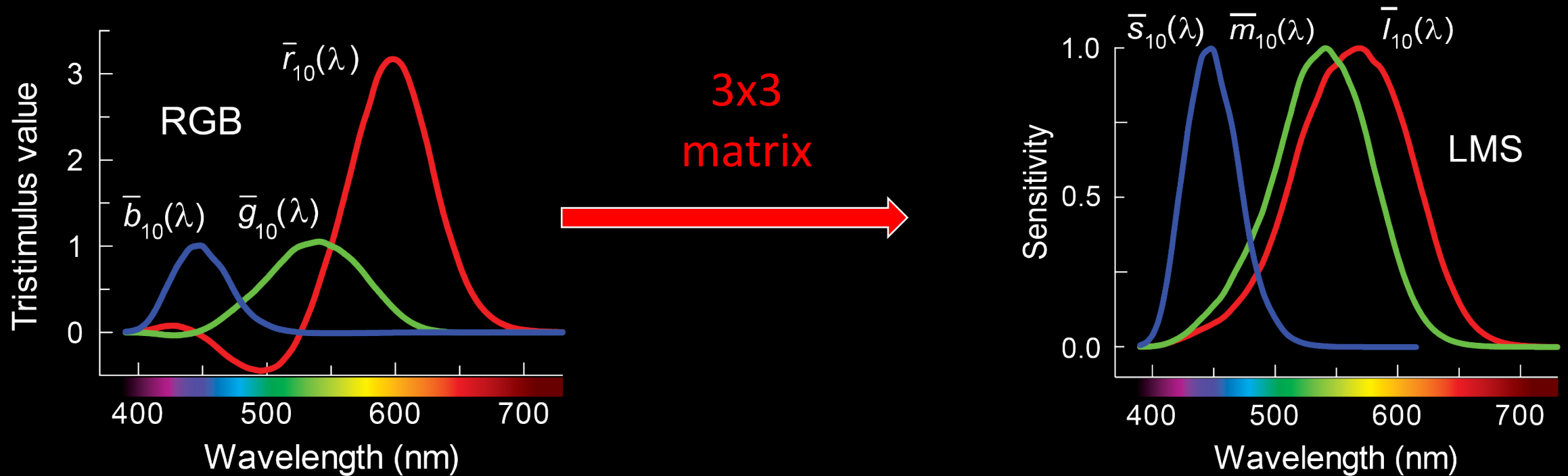
Consequently, the cone spectral sensitivities are the:

**“Fundamental” colour matching functions**

...upon which all other CMFs depend.

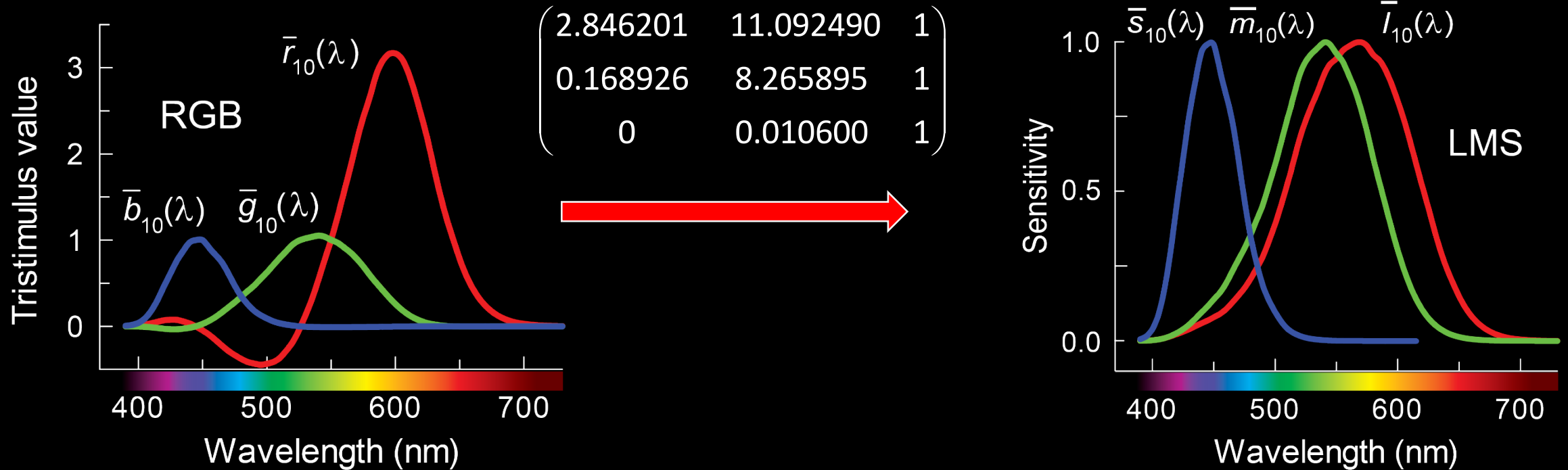
# CMFs

As a result, there should be a simple linear transformations between RGB and LMS...



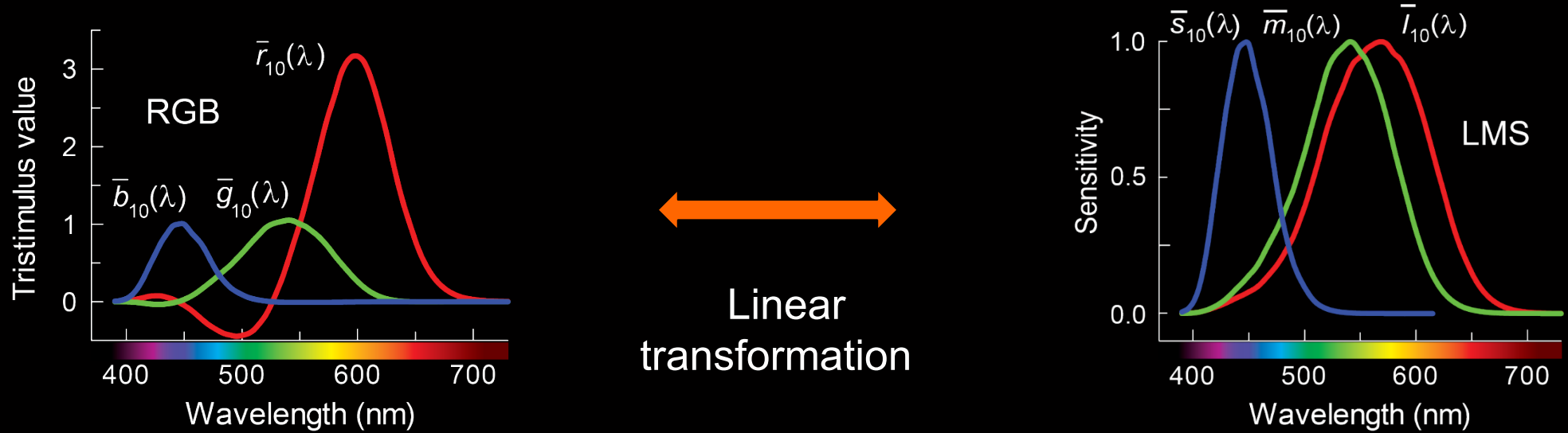
# CMFs

In 2006, the CIE defined the new standard LMS functions as a linear transformation of Stiles & Burch (1959) 10° RGB CMFs based on the work of Stockman & Sharpe (2000):



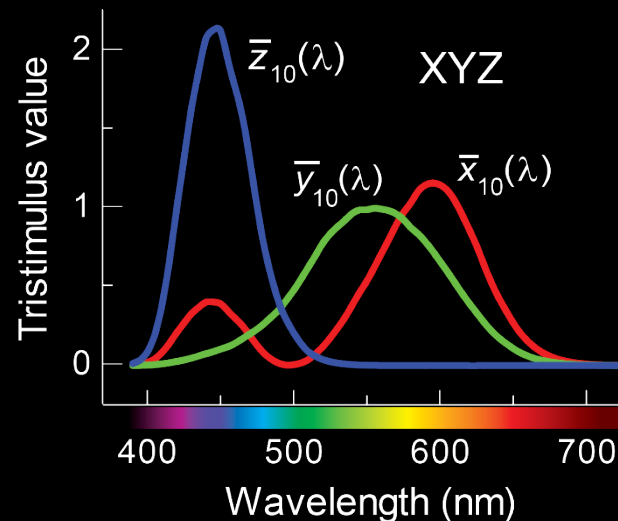
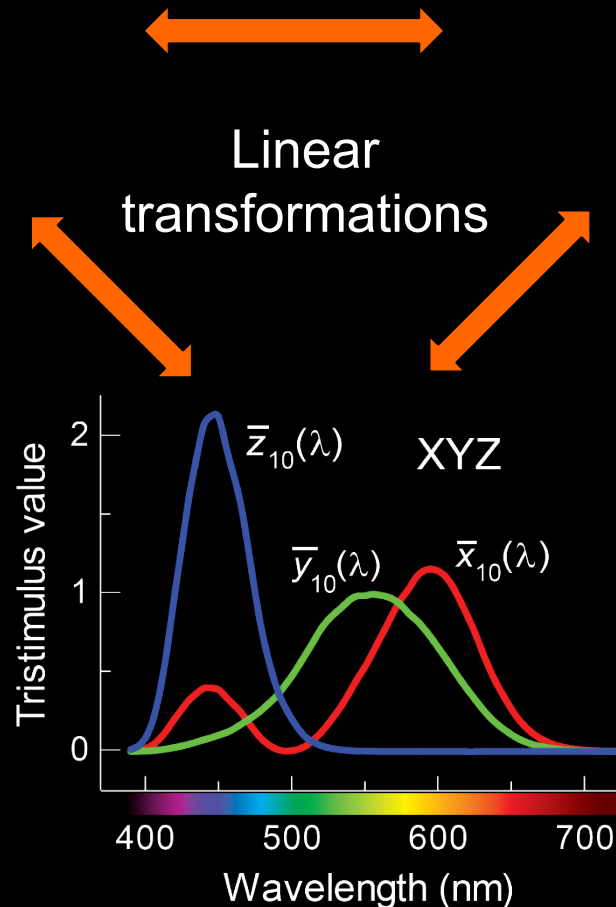
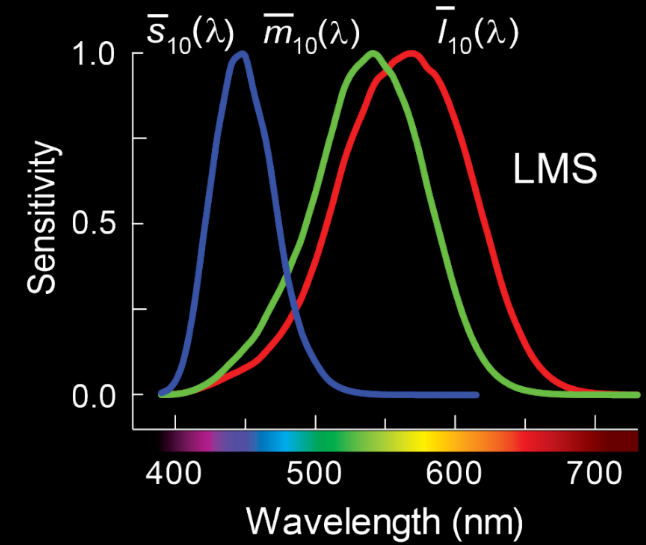
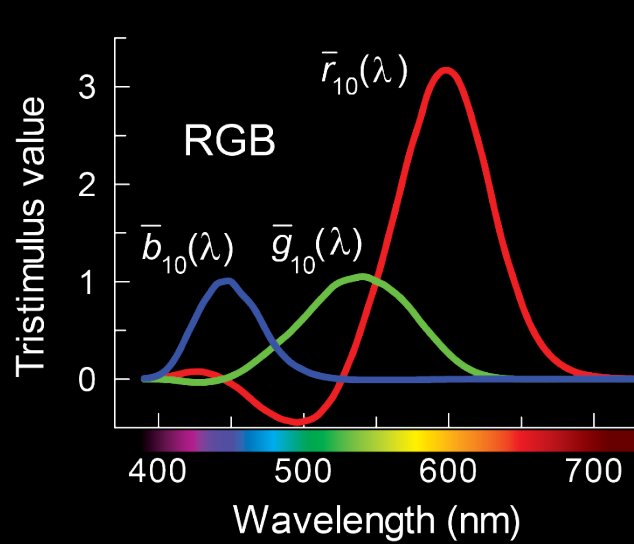


# Stiles & Burch (1959) RGB AND CIE (2006) LMS



As well as the linear transformation from RGB to LMS...

# Stiles & Burch (1959) RGB AND CIE (2006) LMS AND CIE (2015) XYZ CMFs



There is also a simple linear transformation between RGB and LMS and XYZ, which was defined by the CIE in 2015.

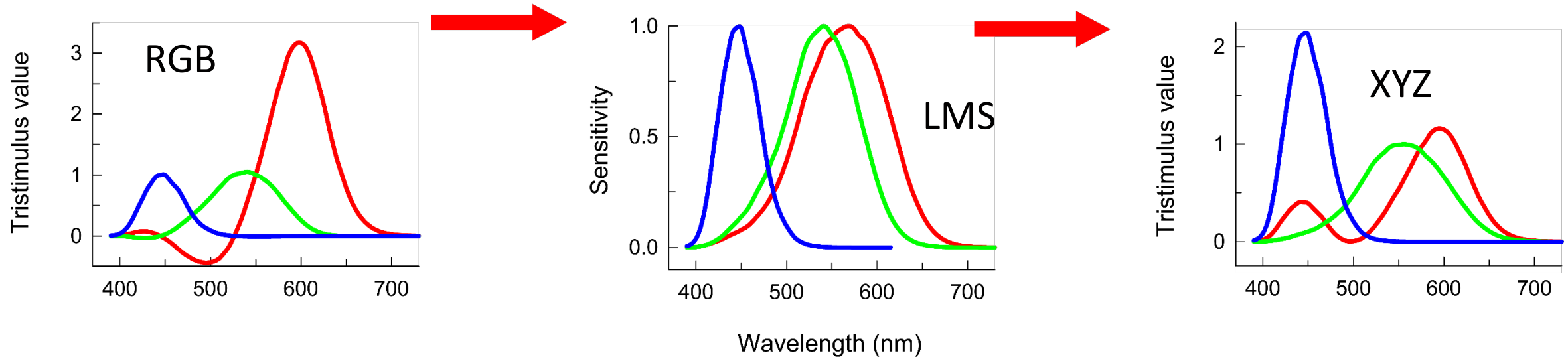
In 2015, the CIE defined the linear transformation  
from the 2006 LMS cone fundamentals to a new XYZ:



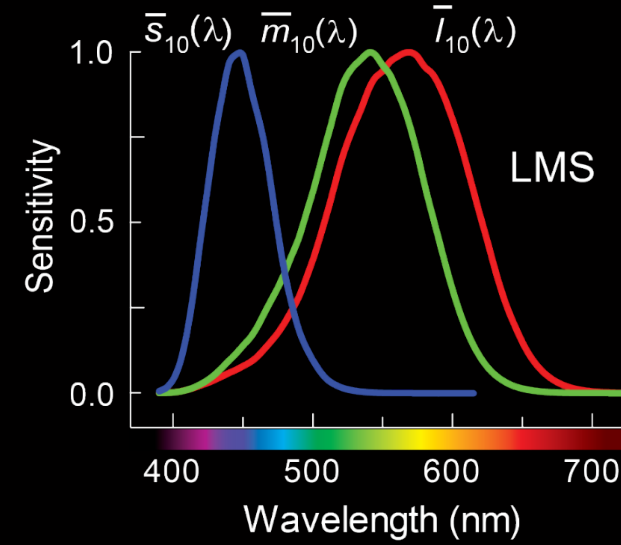
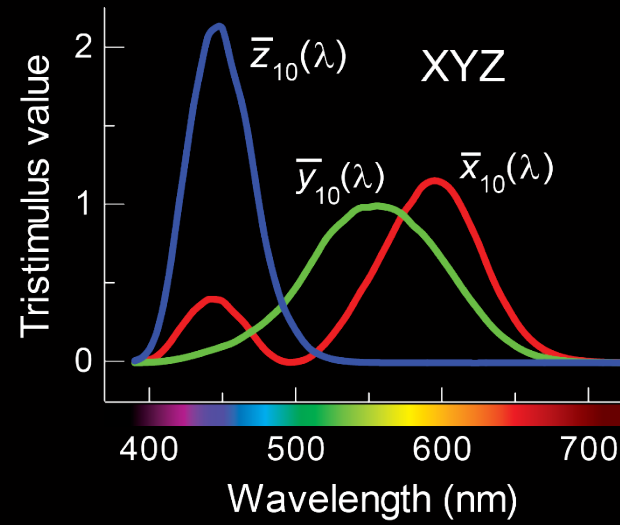
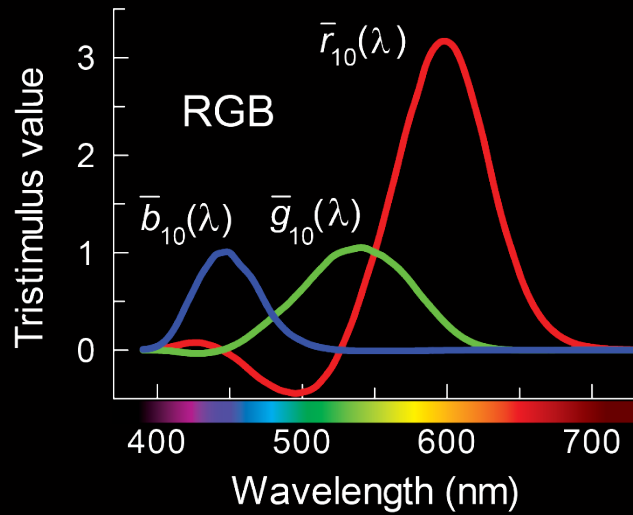
CIE 2006

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

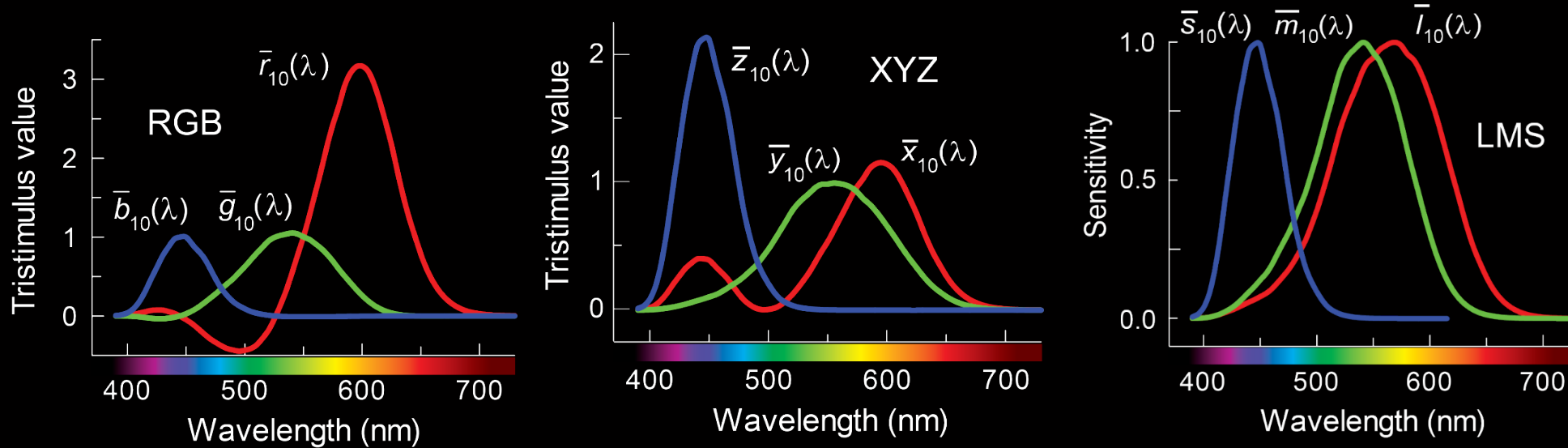
$$\begin{pmatrix} 1.939864 & -1.346644 & 0.430449 \\ 0.692839 & 0.349676 & 0 \\ 0 & 0 & 2.146879 \end{pmatrix}$$



# Why do we need colour matching functions?



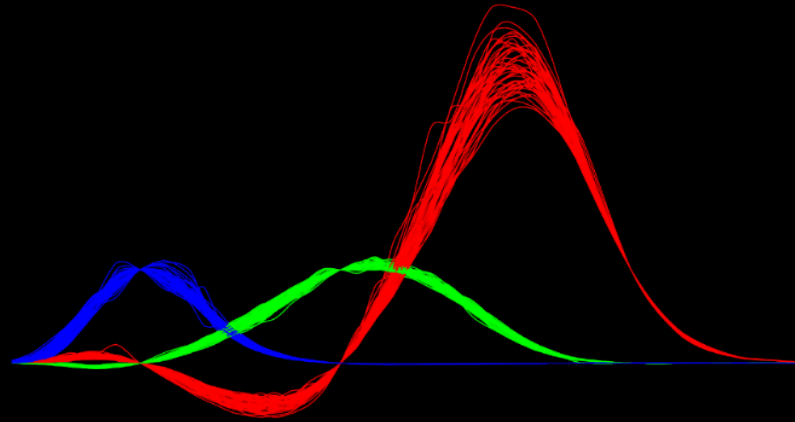
# Why do we need colour matching functions?



Because colours can be defined in terms of any of these three standard (mean) colour matching functions (Stiles & Burch (1959) RGB, CIE (2006) LMS AND CIE (2015) XYZ CMFs). And if they are linear combinations of one another, it shouldn't matter which one we use...



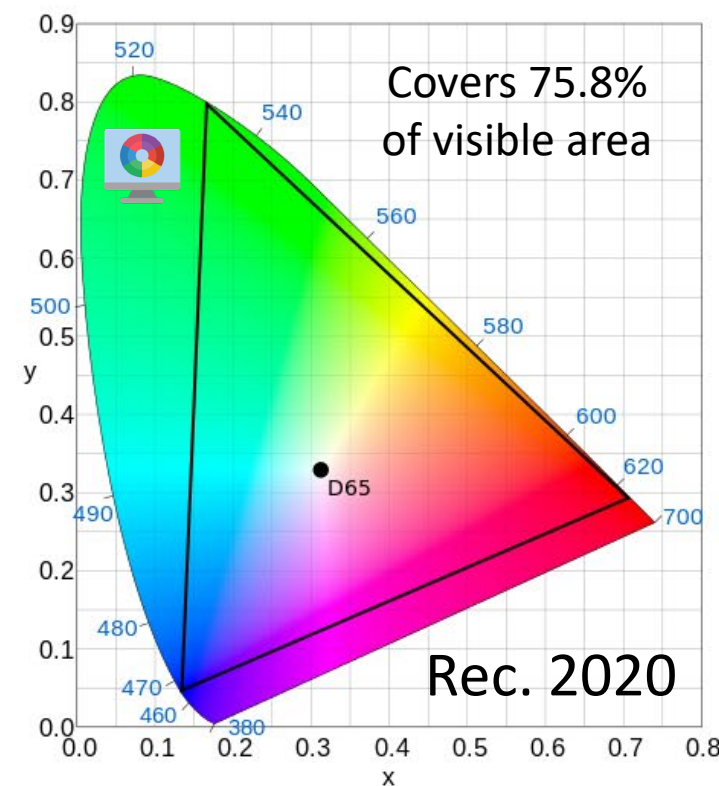
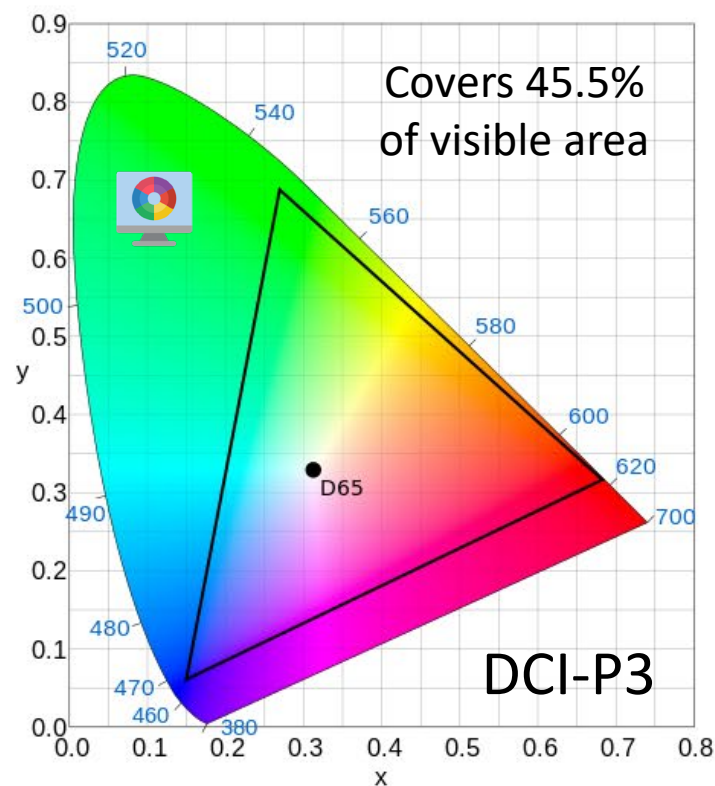
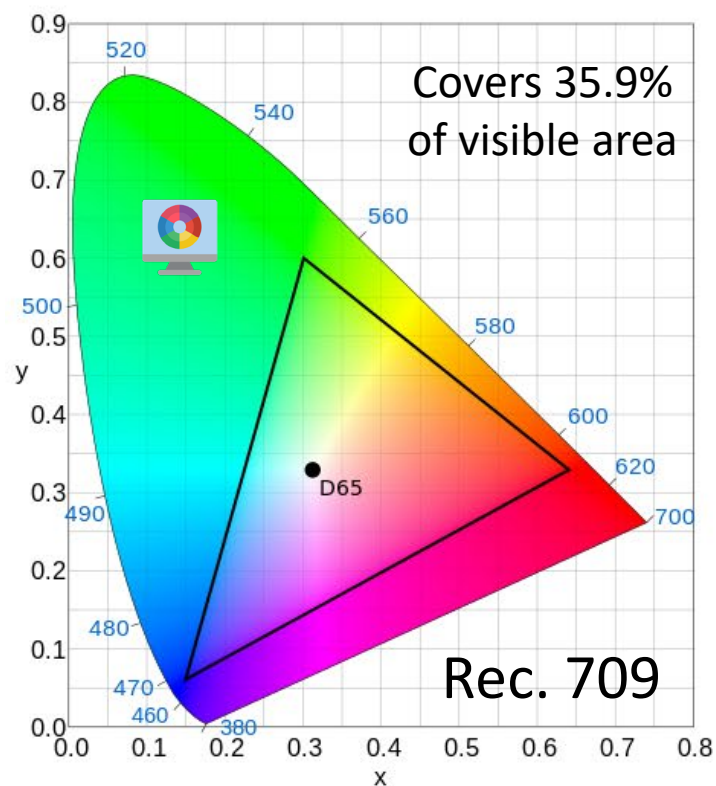
### 3. INDIVIDUAL DIFFERENCES



# Display standards



In principle, then, if we know the chromaticities of a colour (in terms of XYZ, LMS or RGB), we should be able reproduce it on any display, and it should look similar for all observers across all displays...

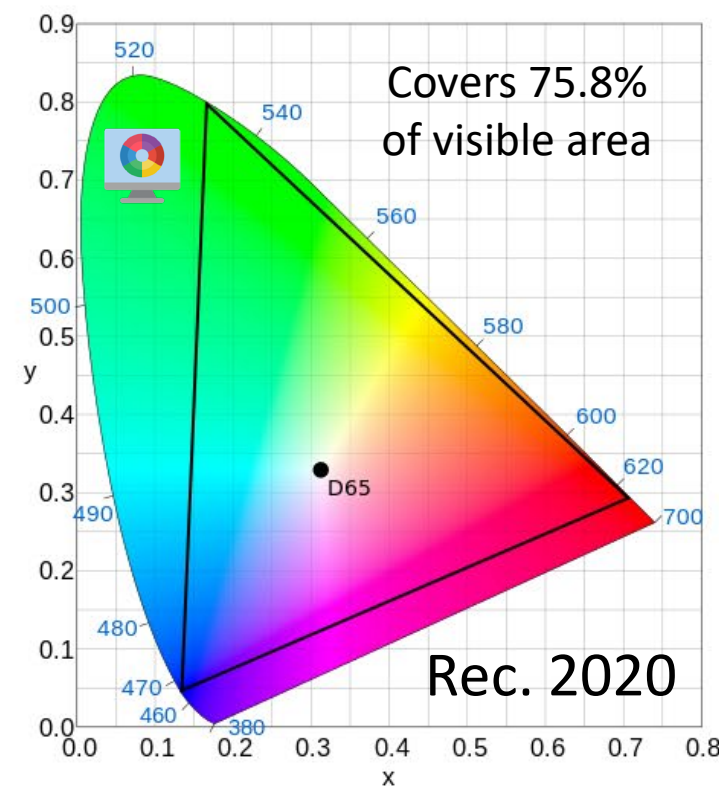
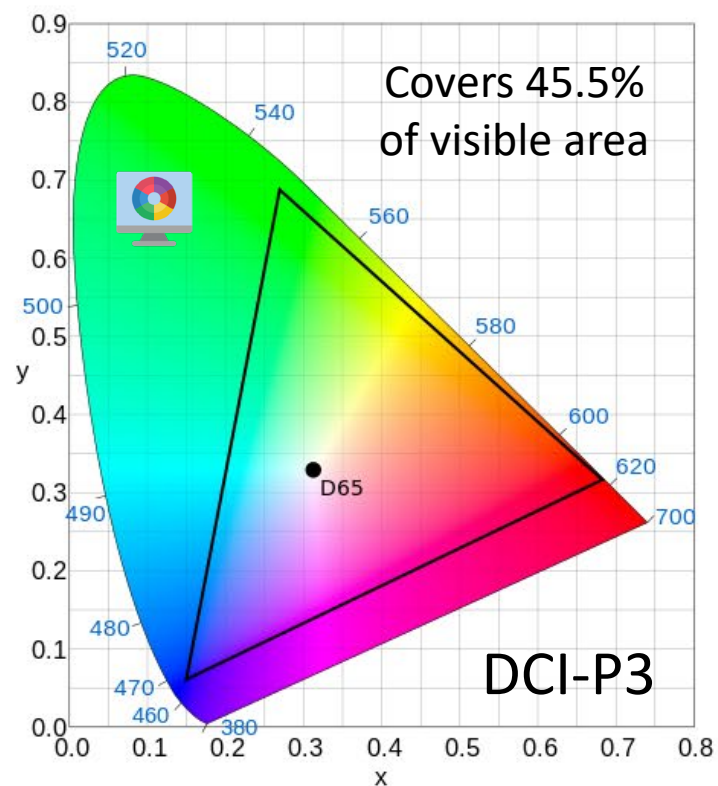
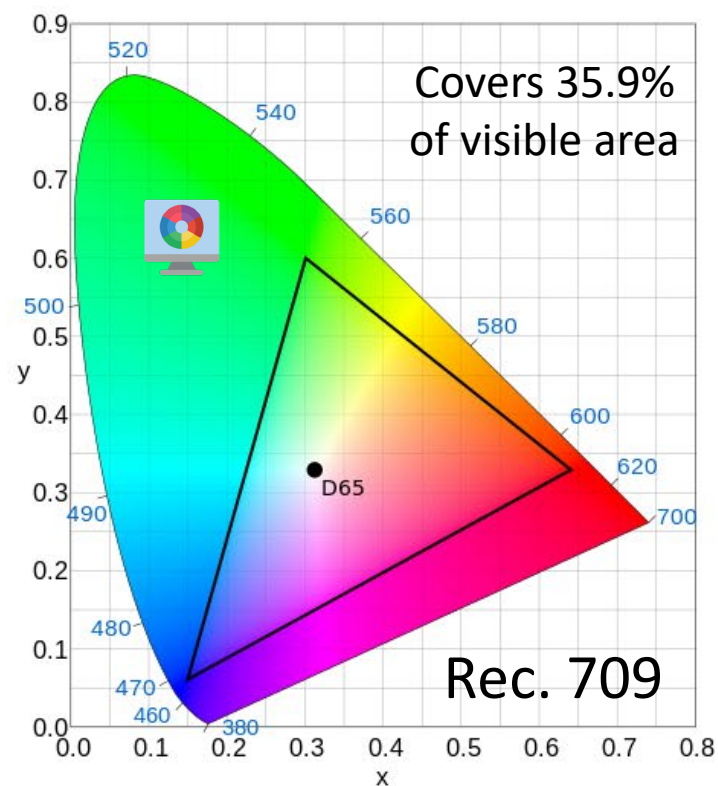




# Display standards



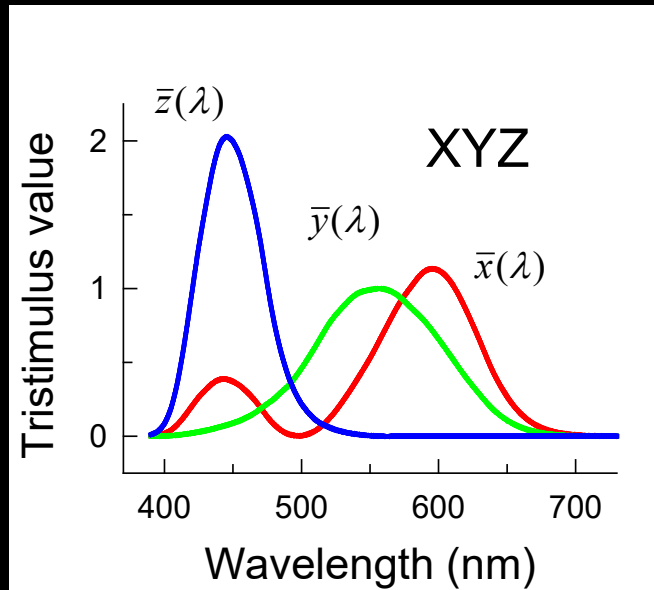
But there are problems...!





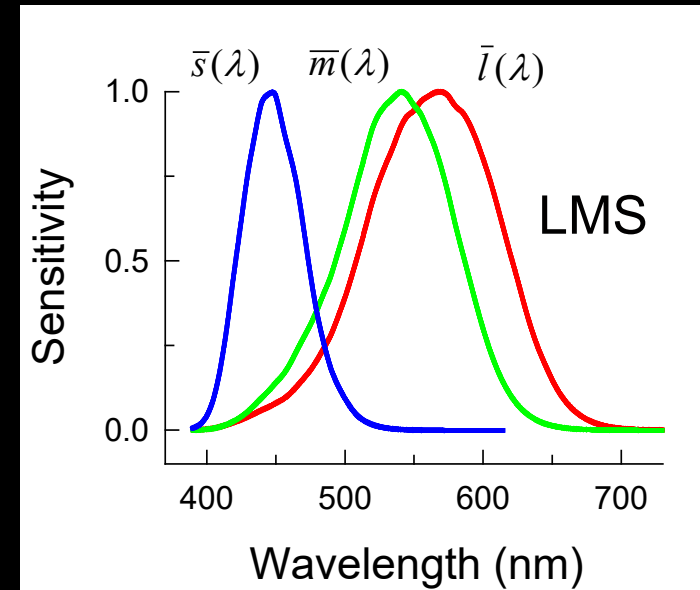
The first problem is that the CIE 1931 XYZ CMFs used extensively to define display colours are **substantially** incorrect, as a result of which there is no valid transformation from 1931 XYZ to **any** LMS...

CIE 1931 2-deg XYZ (or RGB) CMFs



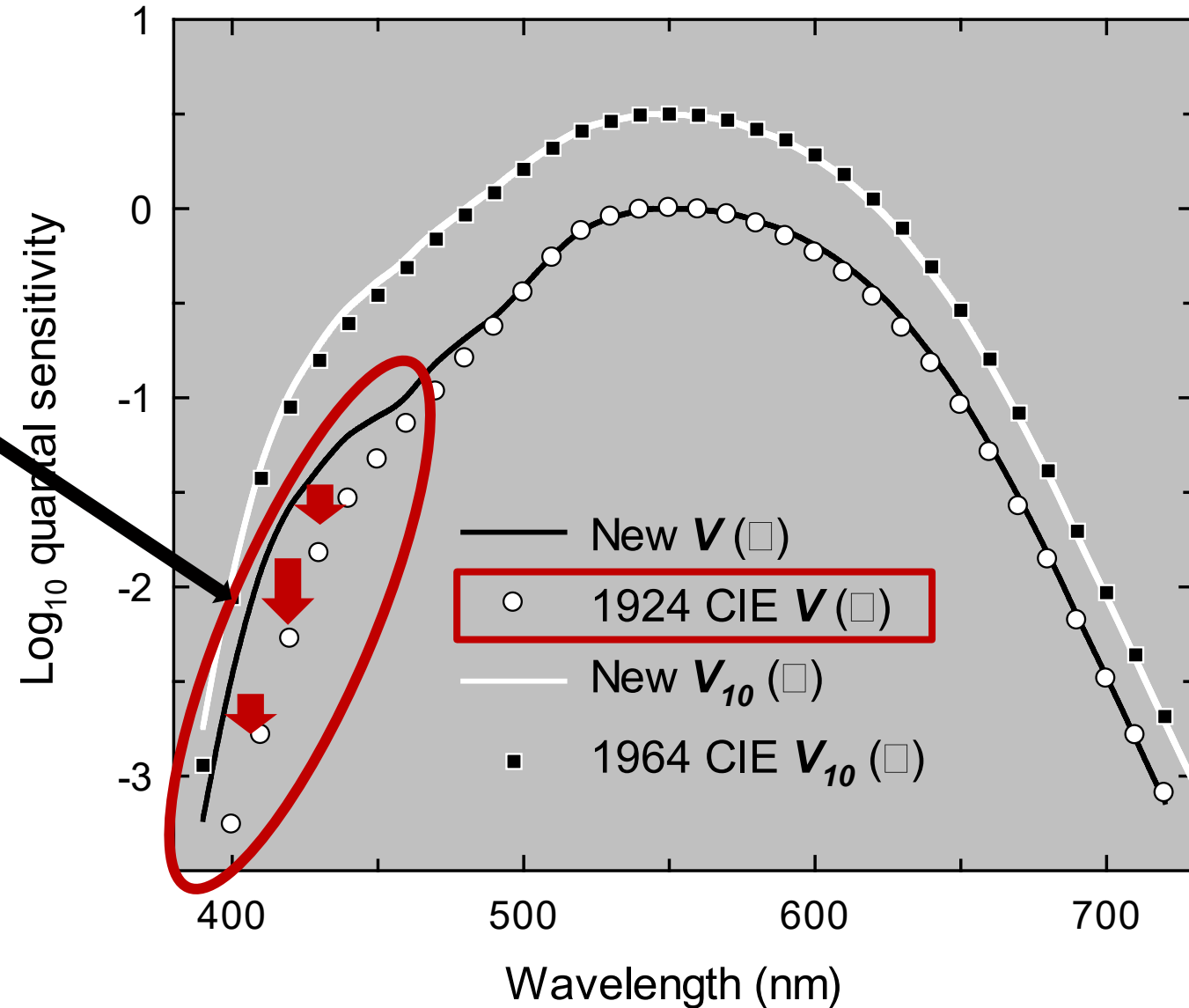
Why?

2-deg LMS cone fundamentals



The problem arises because of a serious error in the 1924  $V(\lambda)$  function  
(which is also the Y function of 1931 XYZ CMFs)...

This error propagates into  
the 1931 X, Y and Z colour  
matching functions!

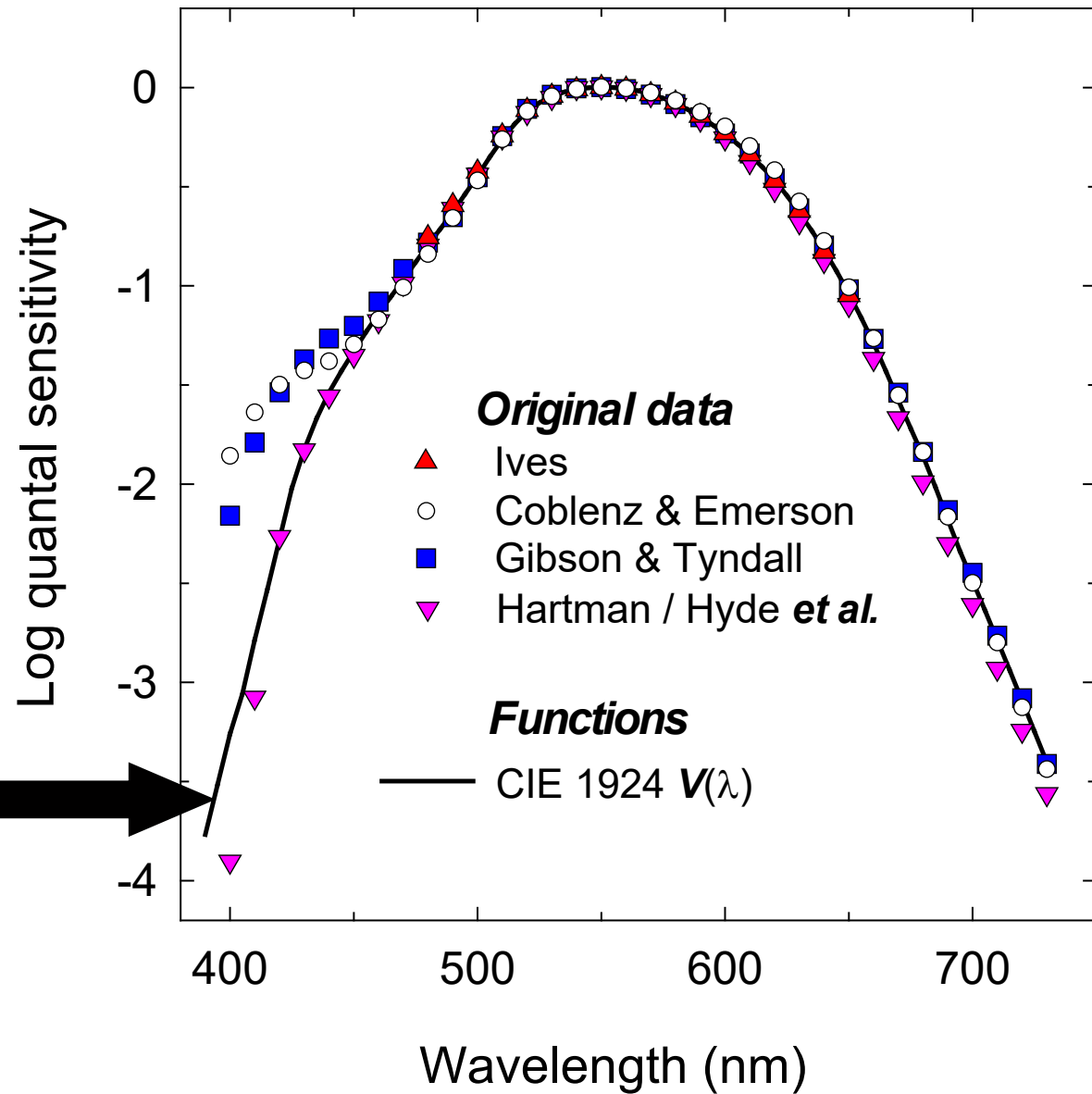


The mistake is related to the choice of  $V(\lambda)$  back in 1924...

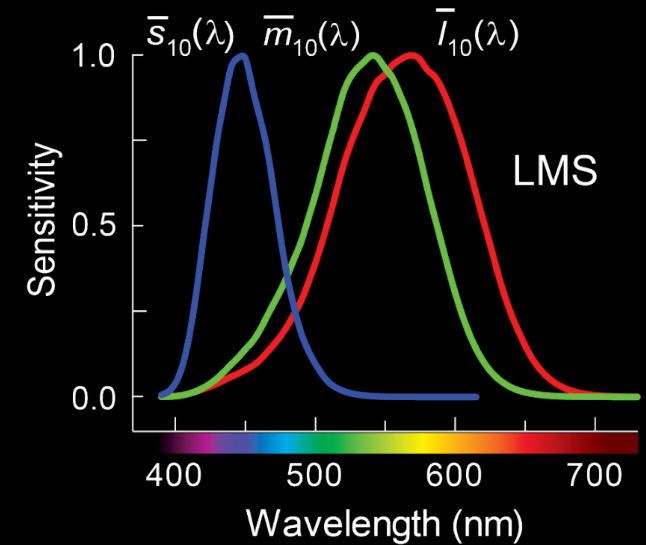
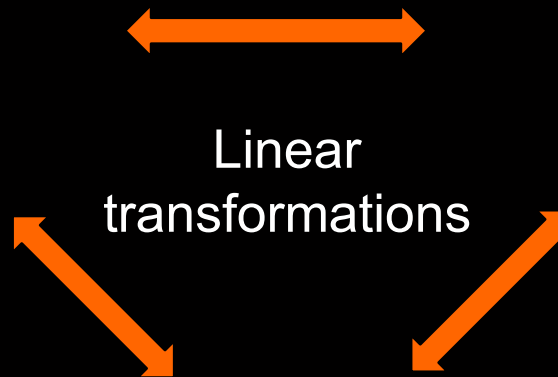
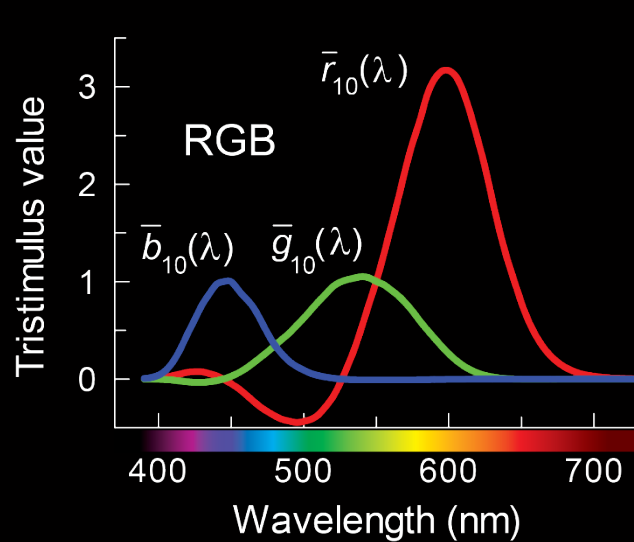
Original data used to derive CIE  $V(\lambda)$   
(which is also CIE 1931  $Y$ )

And here is what the CIE chose in  
1924!

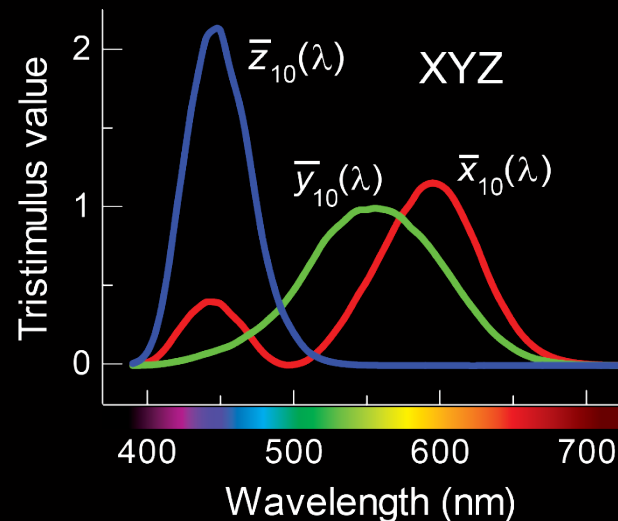
This unfortunate choice continues to  
plague colorimetry and photometry  
100 years later



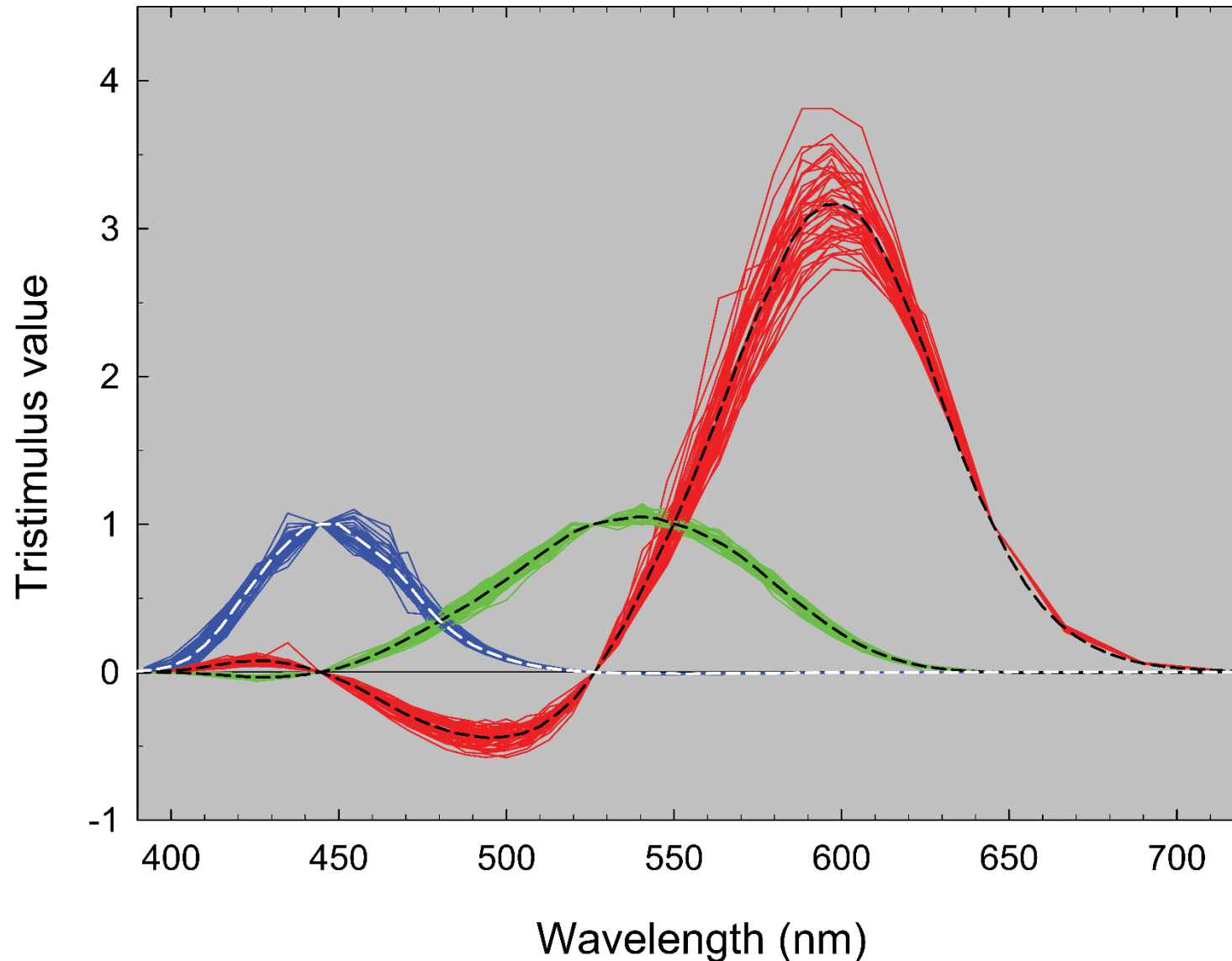
# CIE (2006) LMS AND CIE (2015) XYZ CMFs



We can overcome the defects in the CIE 1931 standard functions by using instead the CIE 2006 LMS or CIE 2015 XYZ CMFs.



However, the use of standard or mean colour matching functions hides the sizeable individual differences found in all colour matching and cone spectral sensitivity data.

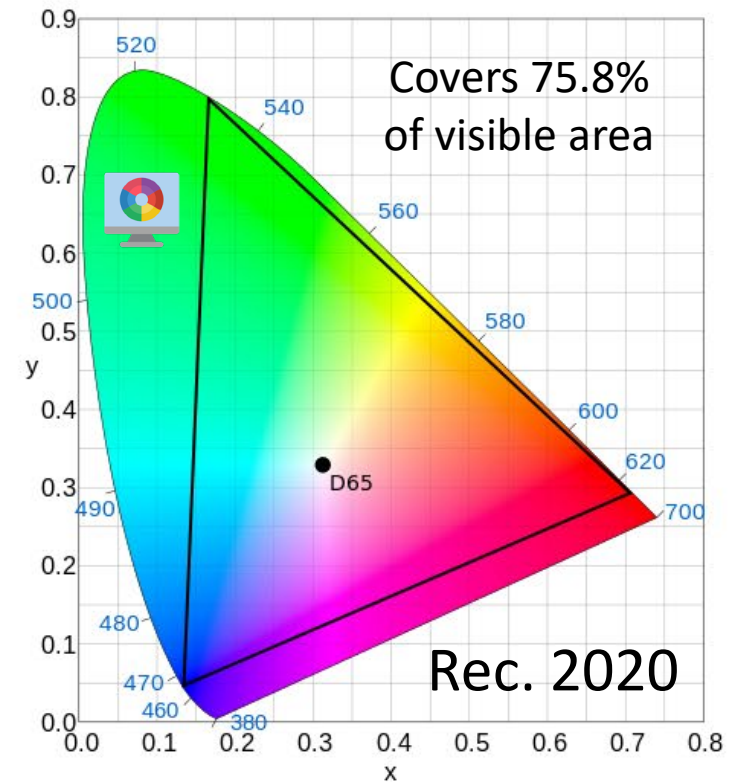
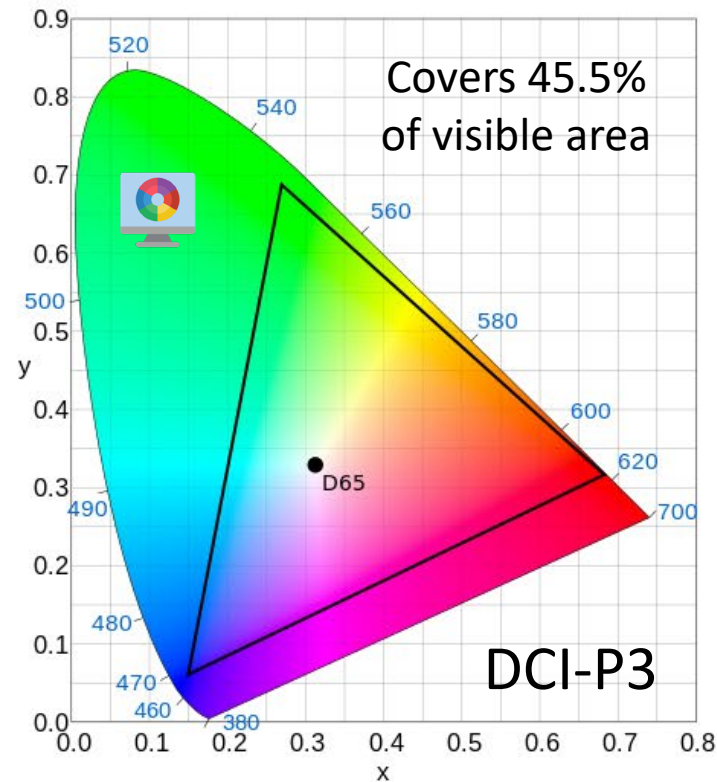
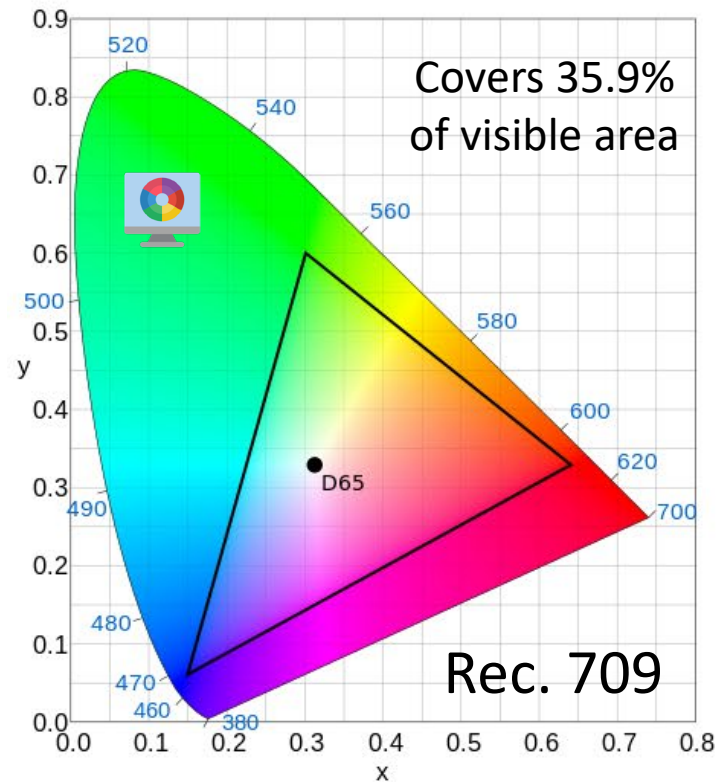


Stiles & Burch (1959)  
10-deg CMFs

# Display standards

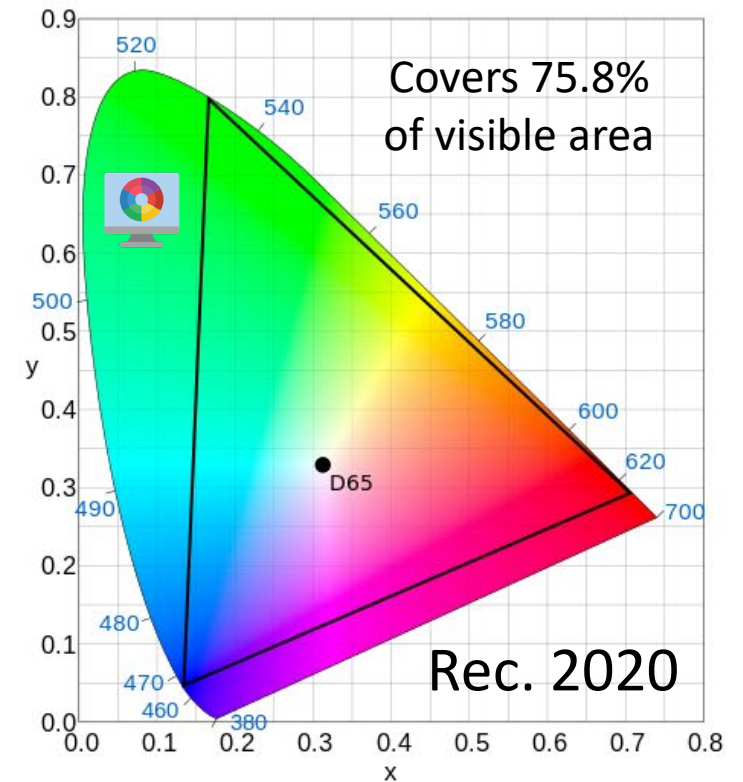
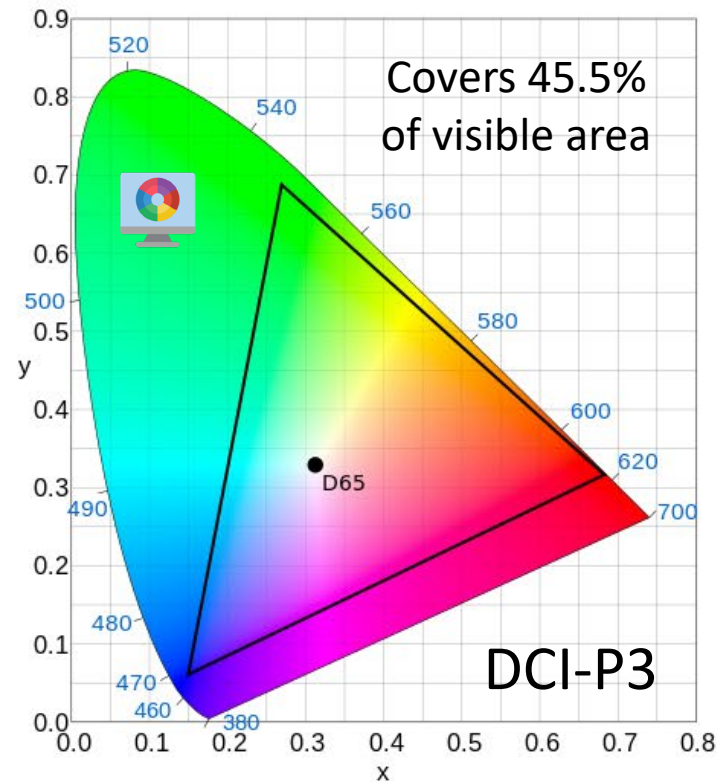
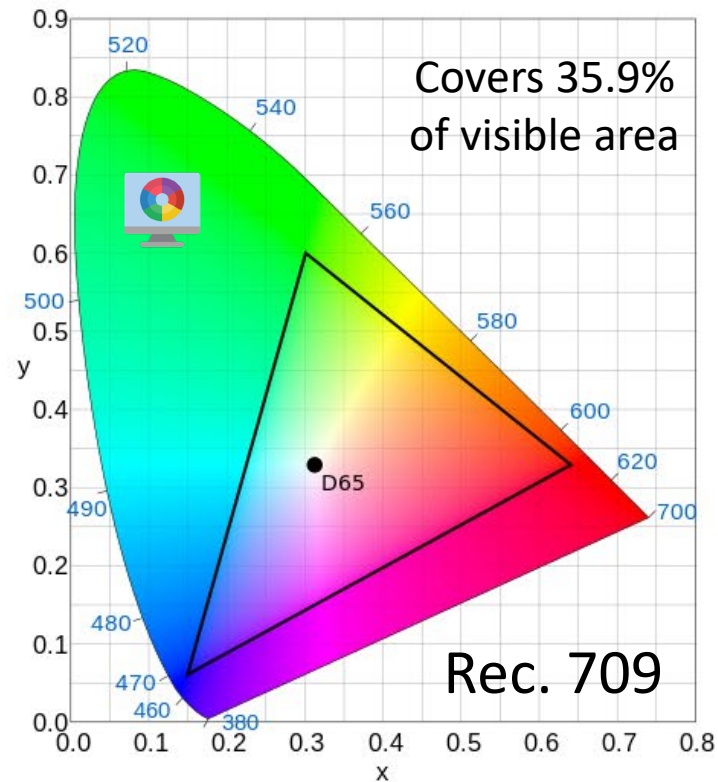


Because of these individual differences the colours produced on displays by using the same x,y values may look different for different observers on the same display and across different displays.



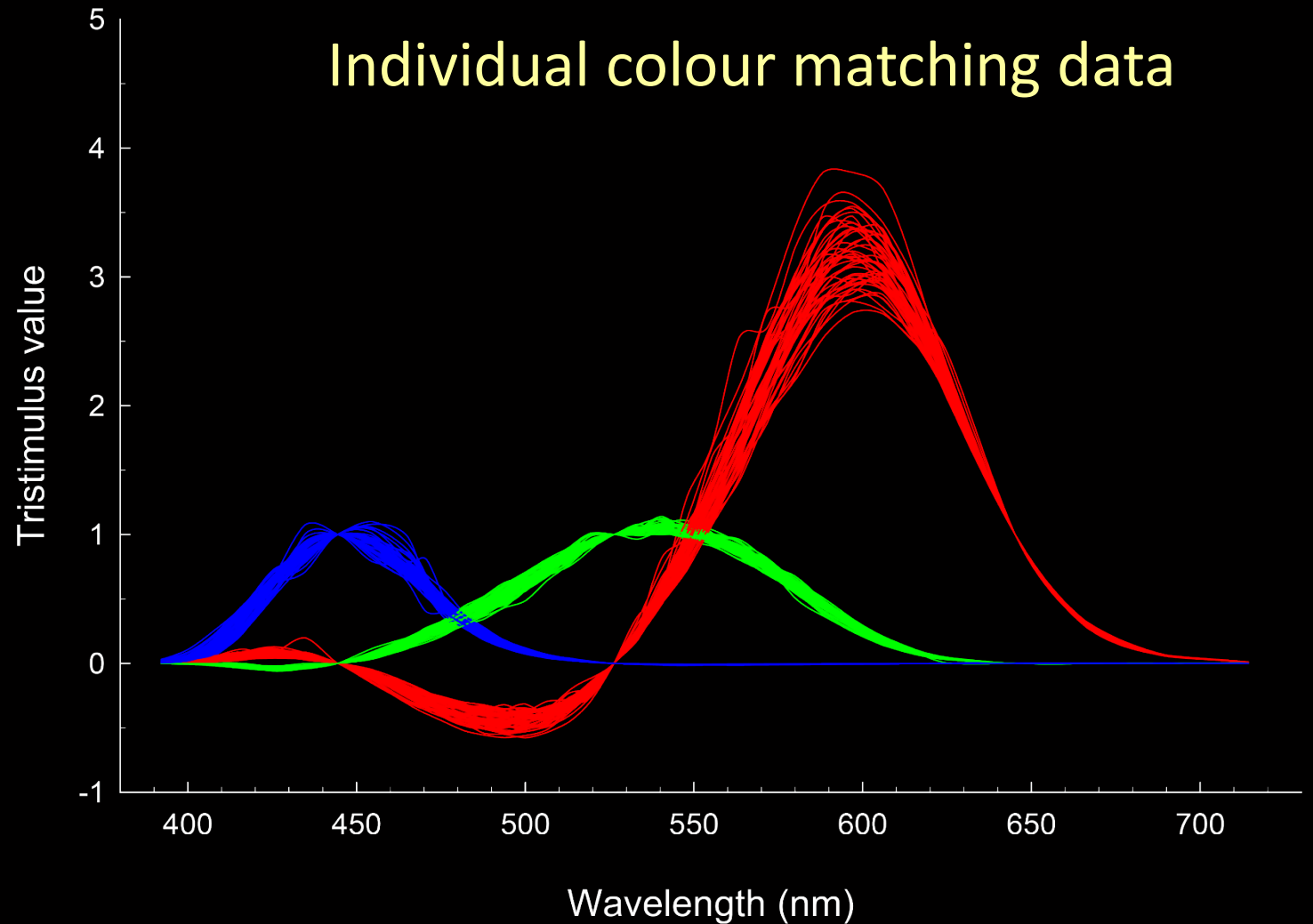
# Display standards

If we want to accurately reproduce colours on a display that will look the same for different observers, we must also take **individual differences** into account ...





What causes these individual differences?



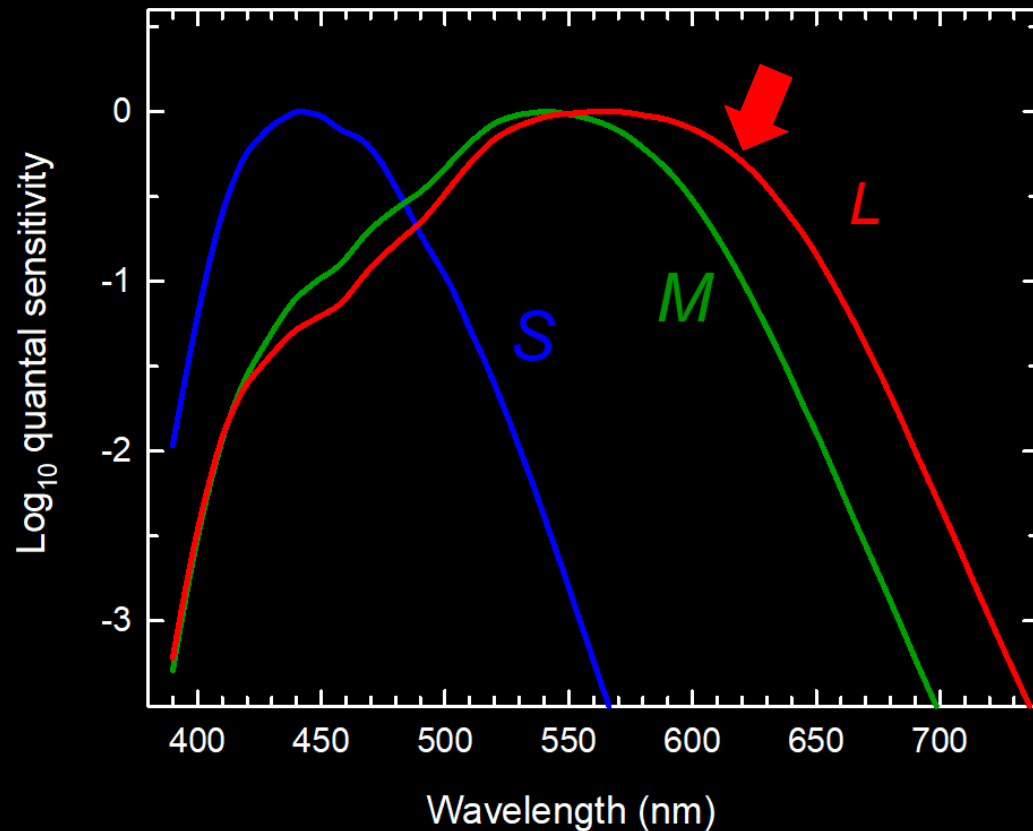


# What causes individual differences?

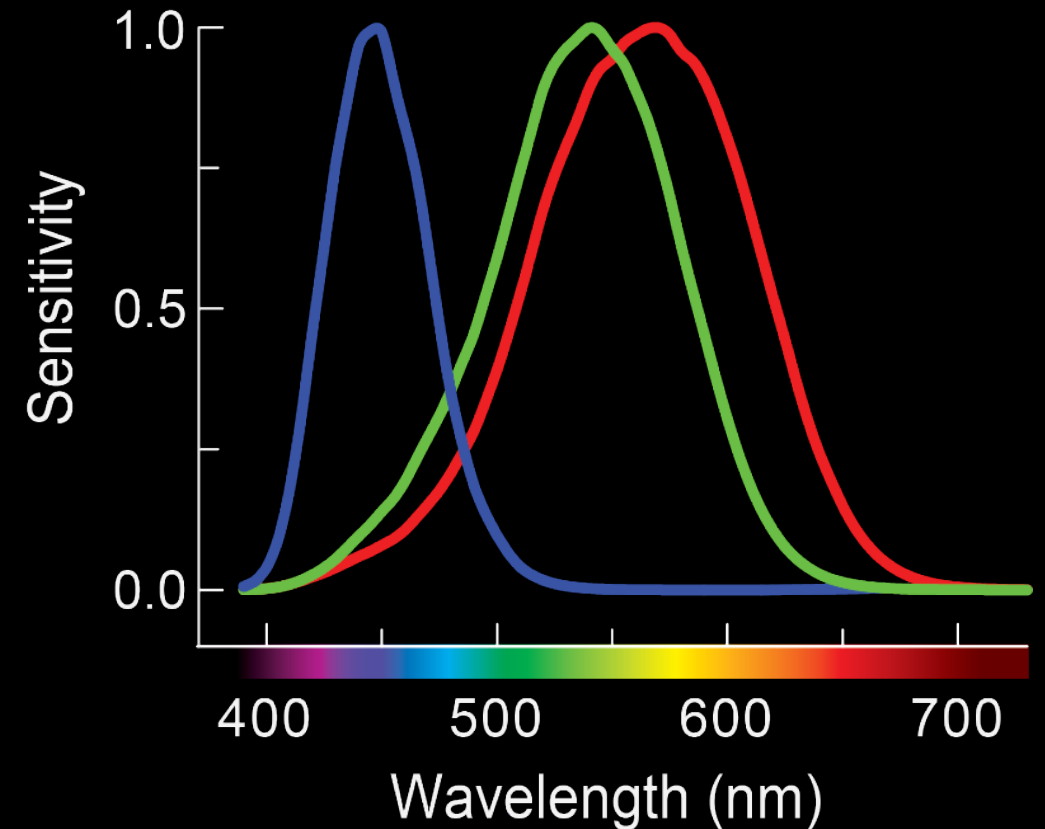
- ▶ Macular pigment optical density differences
- ▶ Lens pigment optical density differences
- ▶ Photopigment optical density differences
- ▶ Spectral shifts in photopigment sensitivity

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

Logarithmic



Linear

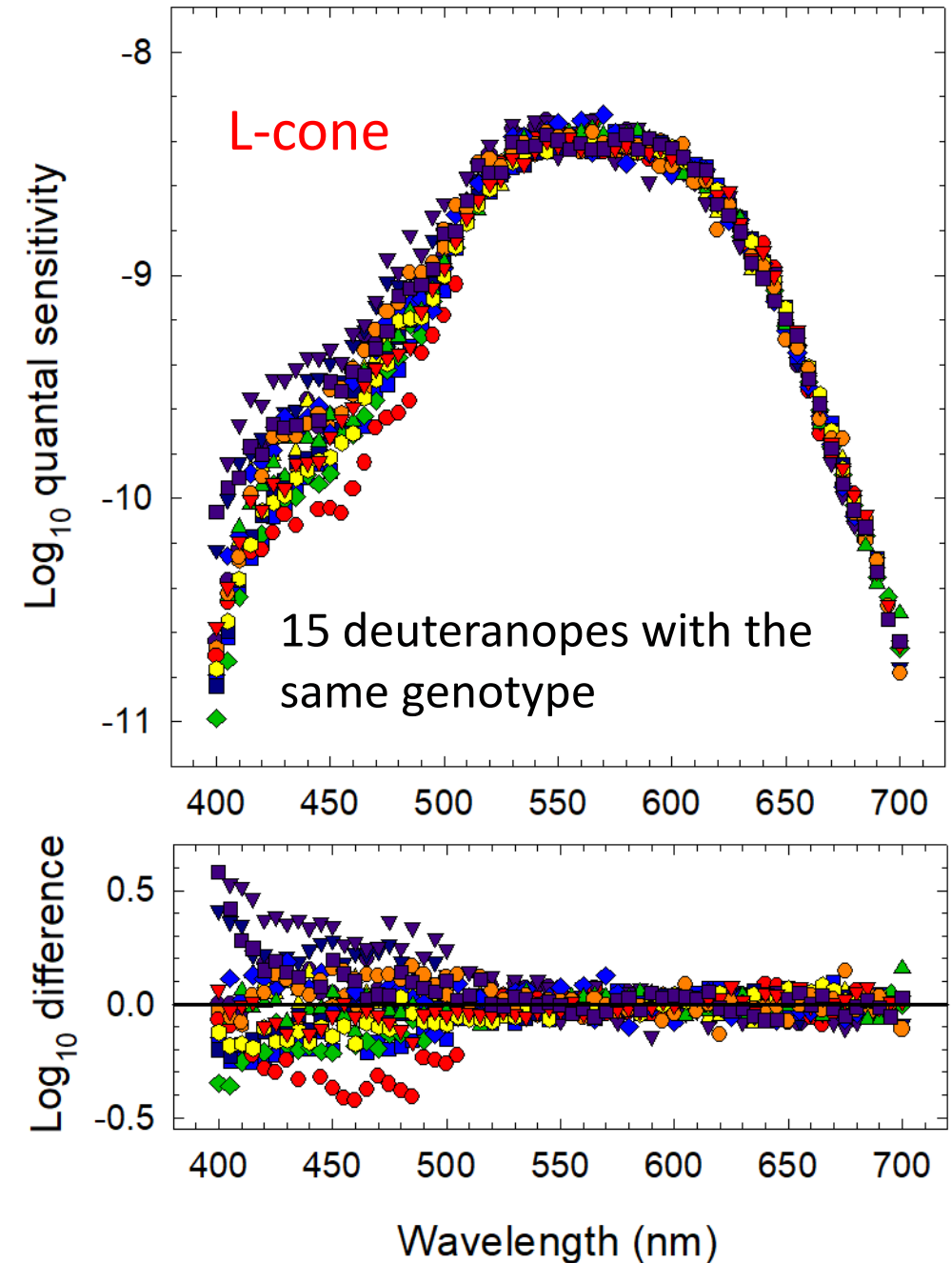


## Individual data for deuteranopes with the same L-cone photopigment



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

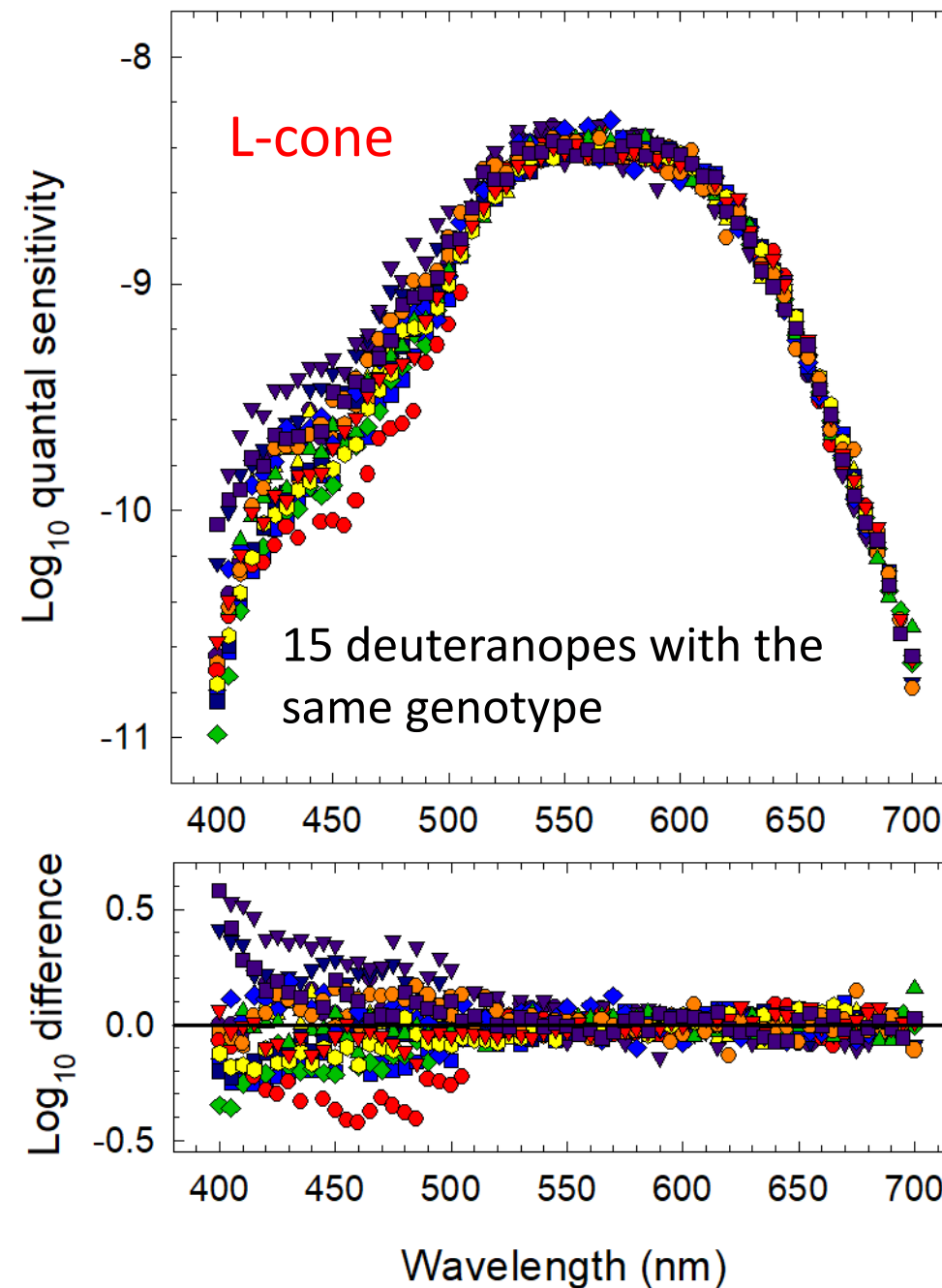
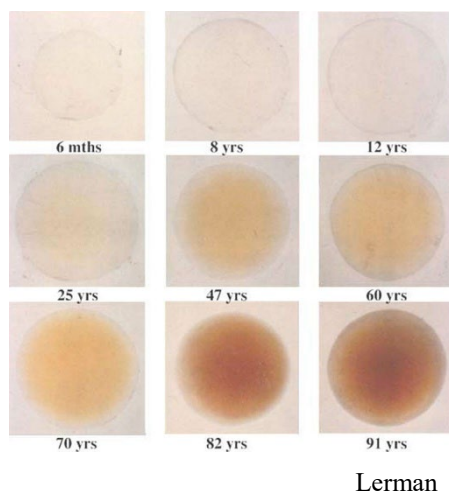
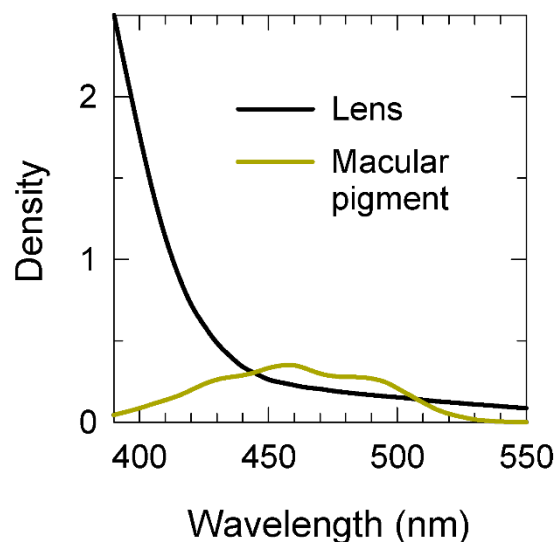
Why are the results so variable at short wavelengths?



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



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

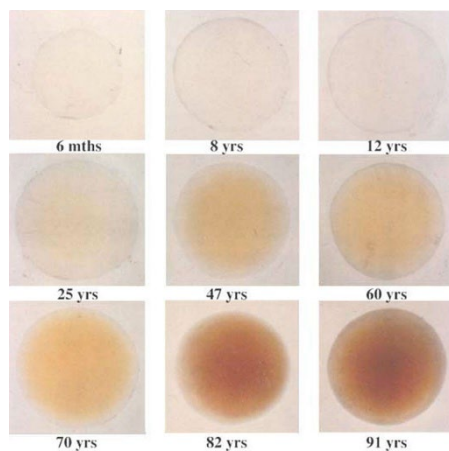
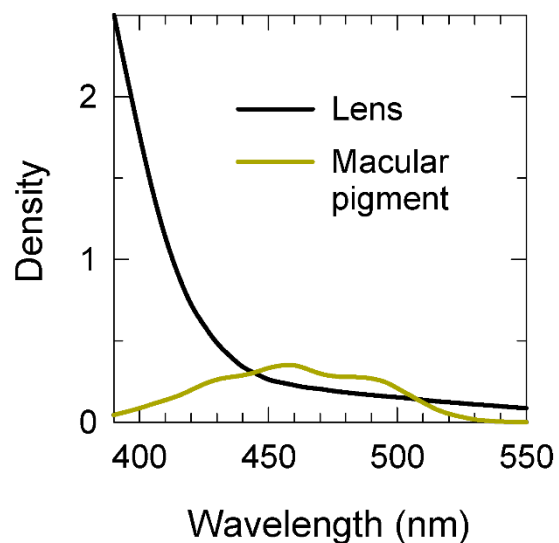


# Individual data for deuteranopes with the same L-cone photopigment

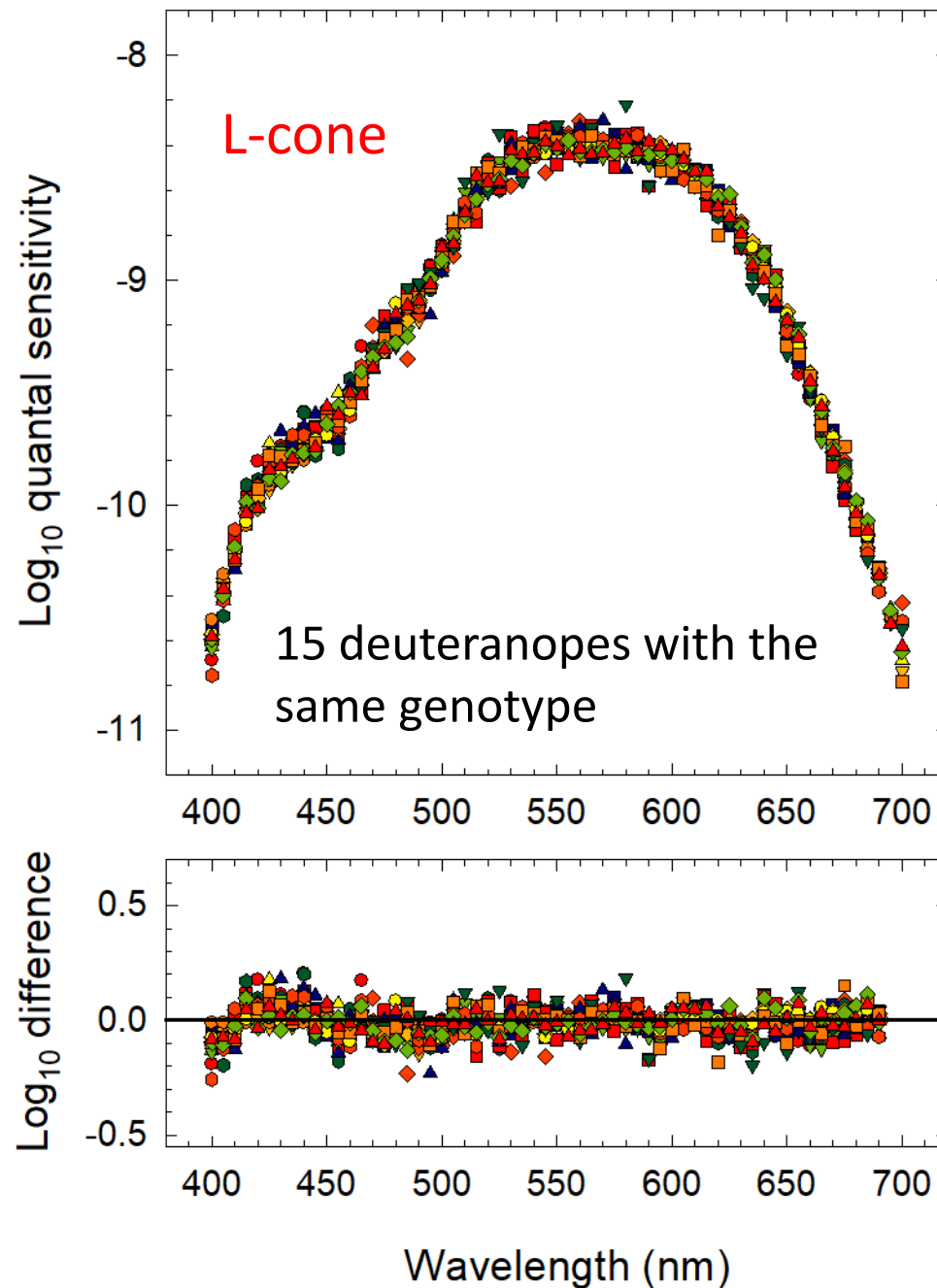


L

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



Lerman



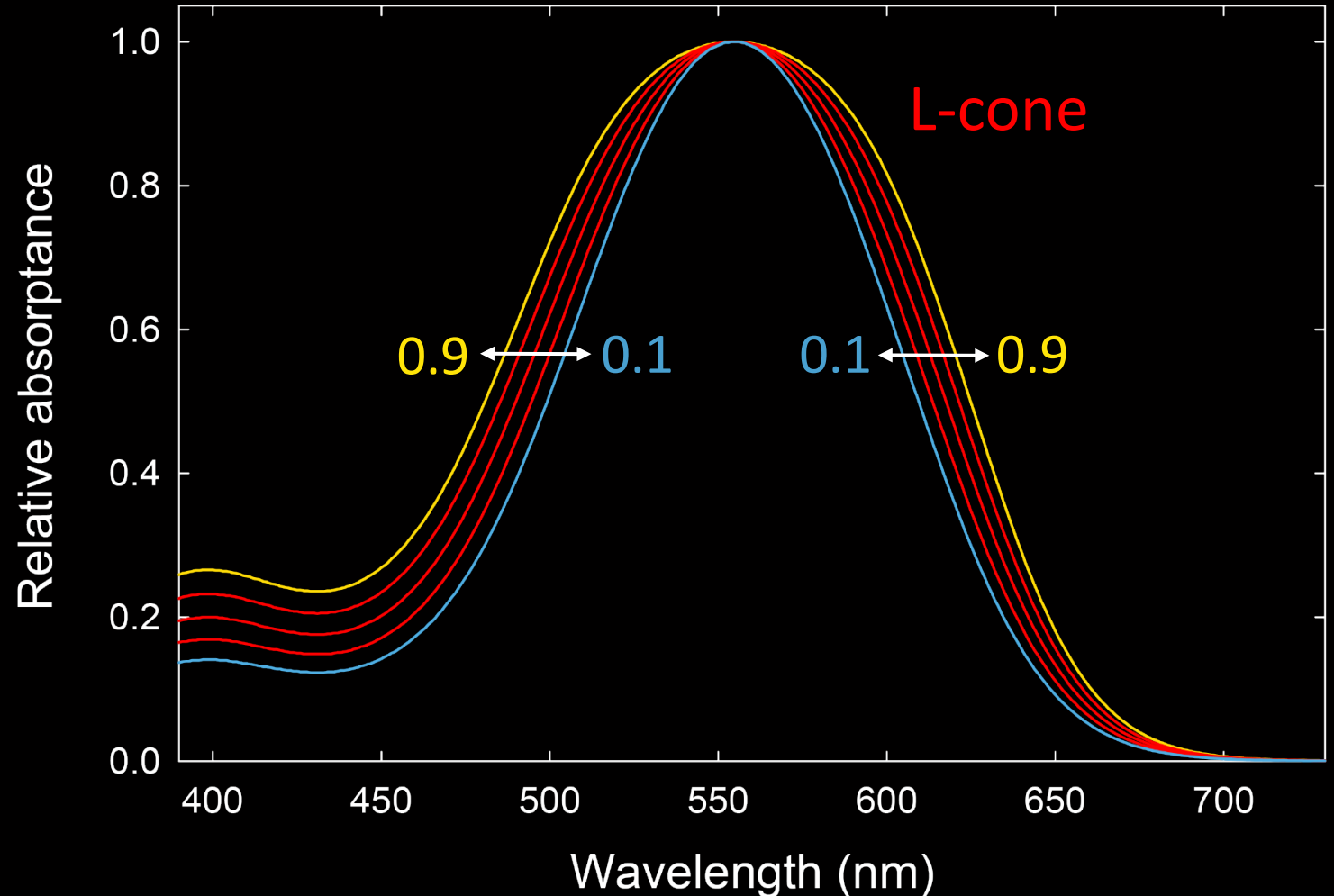
# What causes individual differences?

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

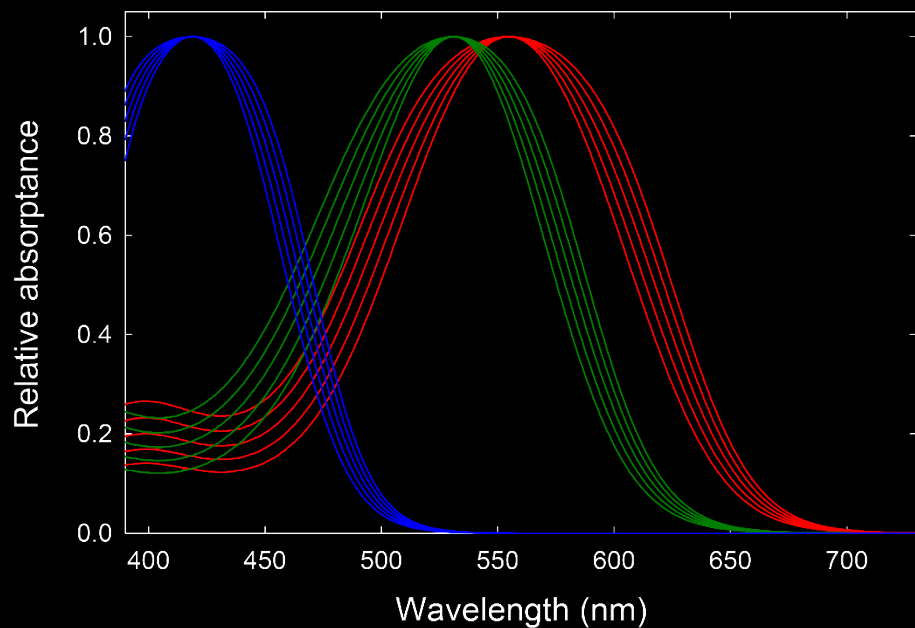
# Individual differences in photopigment optical density

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

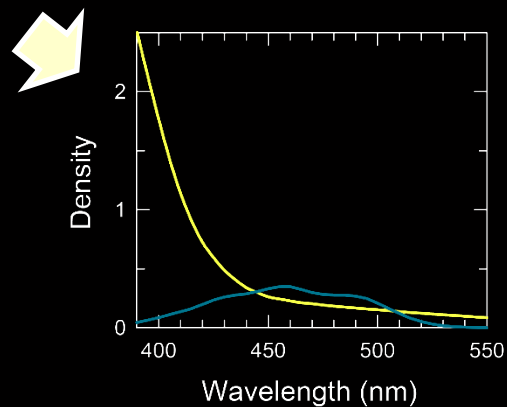
Cone photopigments varying in optical density  
from 0.1 (narrow) to 0.9 (broad) in 0.2 steps



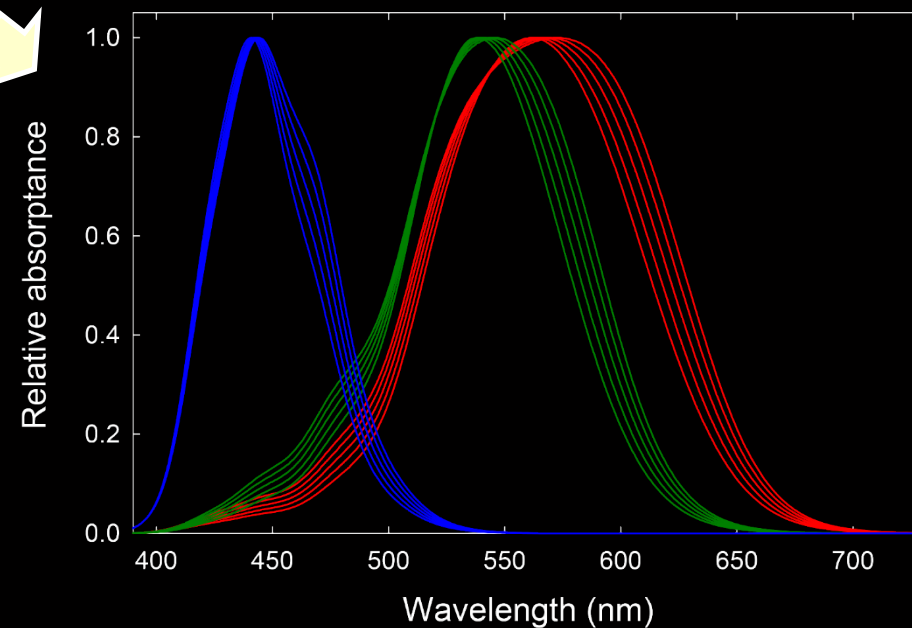
# Photopigments



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



## Cone spectral sensitivities at the cornea





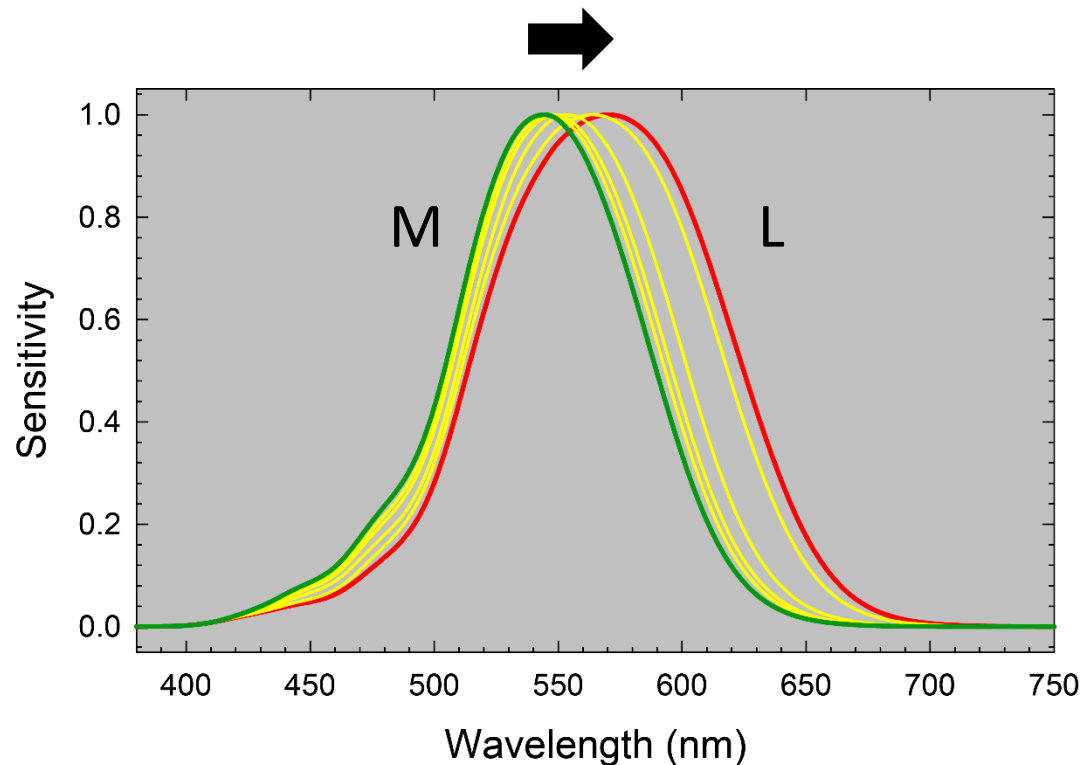
# What causes individual differences?

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

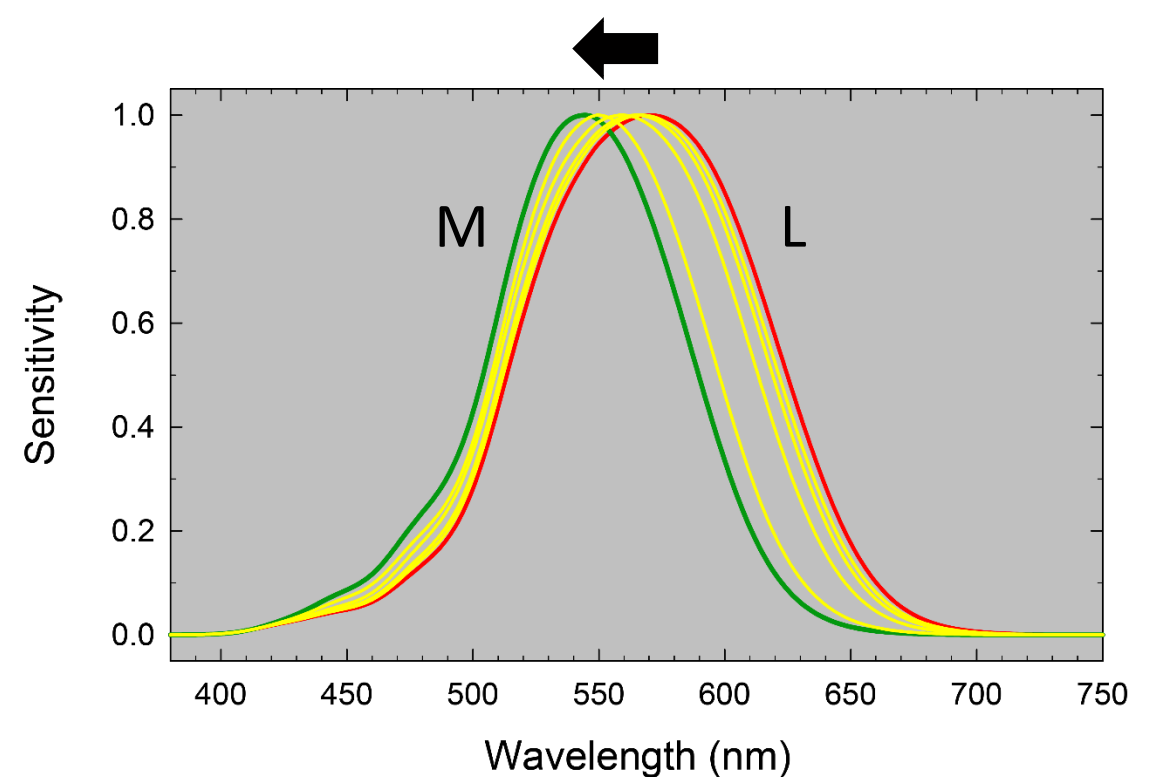
# Why are there spectral shifts?

Spectral shifts in the positions of the M- and L-cone spectral sensitivity functions are caused by changes (substitutions) in the genes that encode the M- and L-cone photopigments.

M-cone functions can shift towards L.

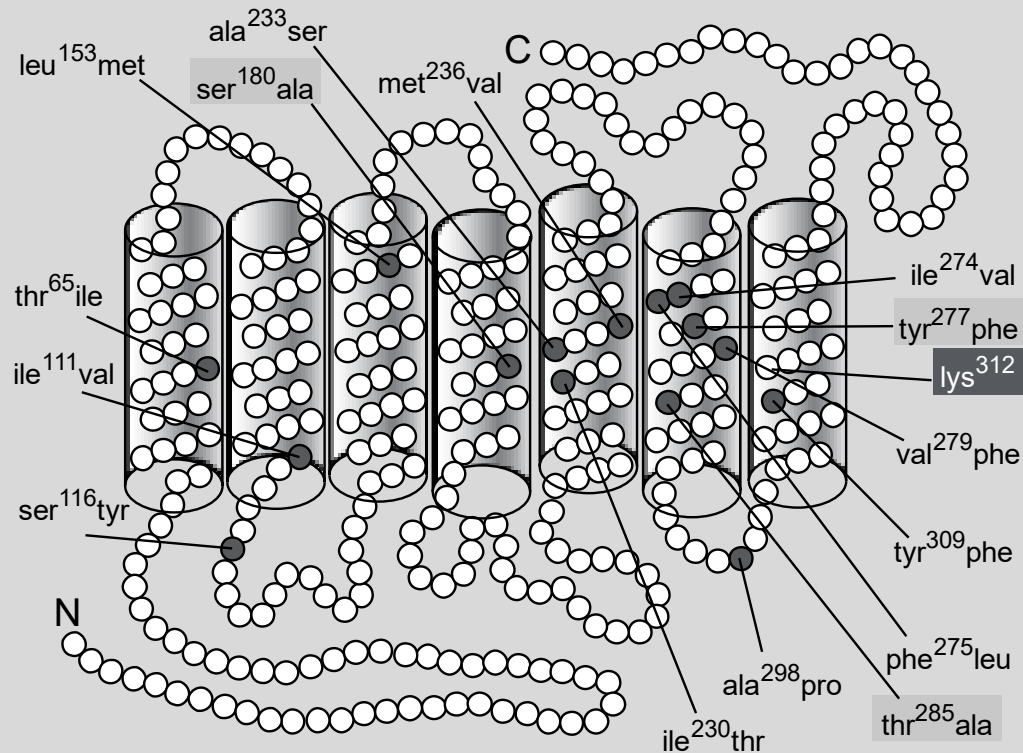


L-cone functions can shift towards M.



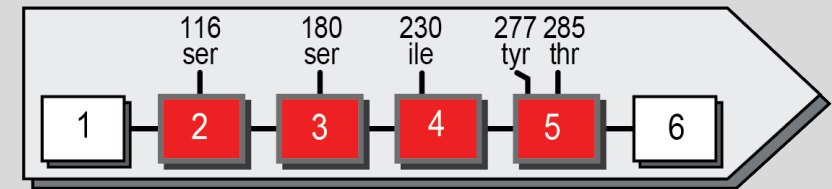
# Amino acid differences between the L-and M-cone photopigment opsins

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

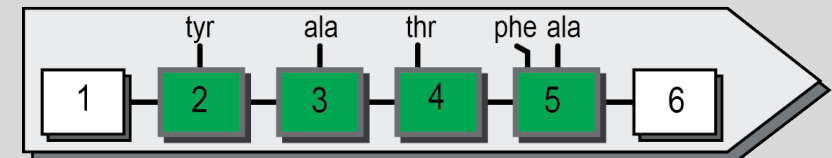


Simplified representation of gene  
(amino acid) sequences for L and M

L(S180)



M



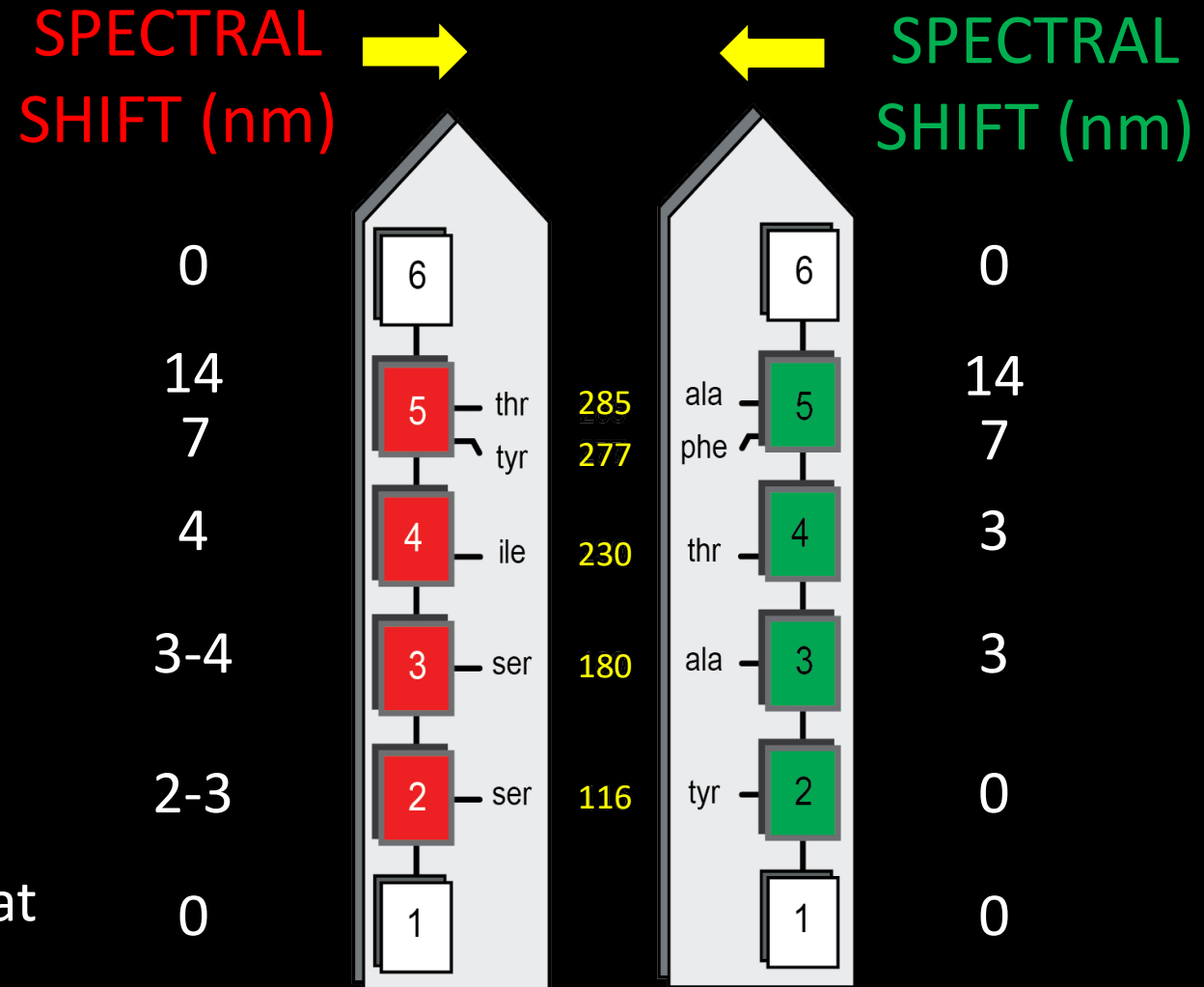
N end

C end

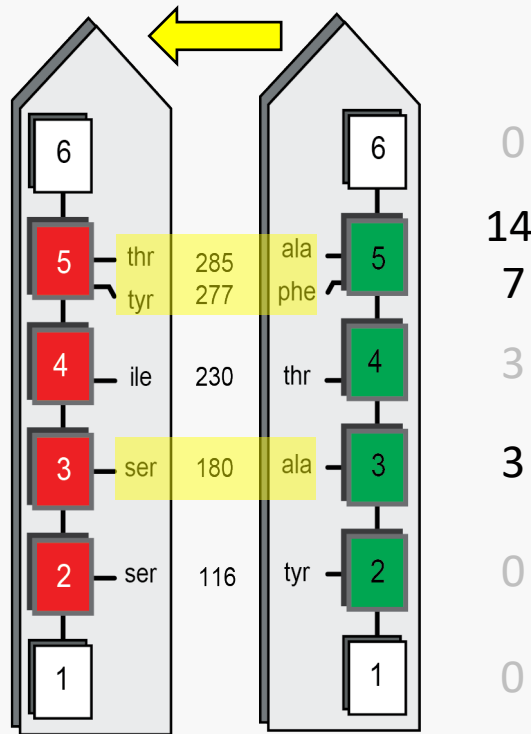
# SPECTRAL SHIFTS

Estimates of the spectral shifts caused by changing the five important amino acid from the L-cone to M-cone versions or *vice versa*.

These amino acids surround the visual chromophore in the photopigment. Changing them changes the energy and thus the photon that triggers its conformational change...

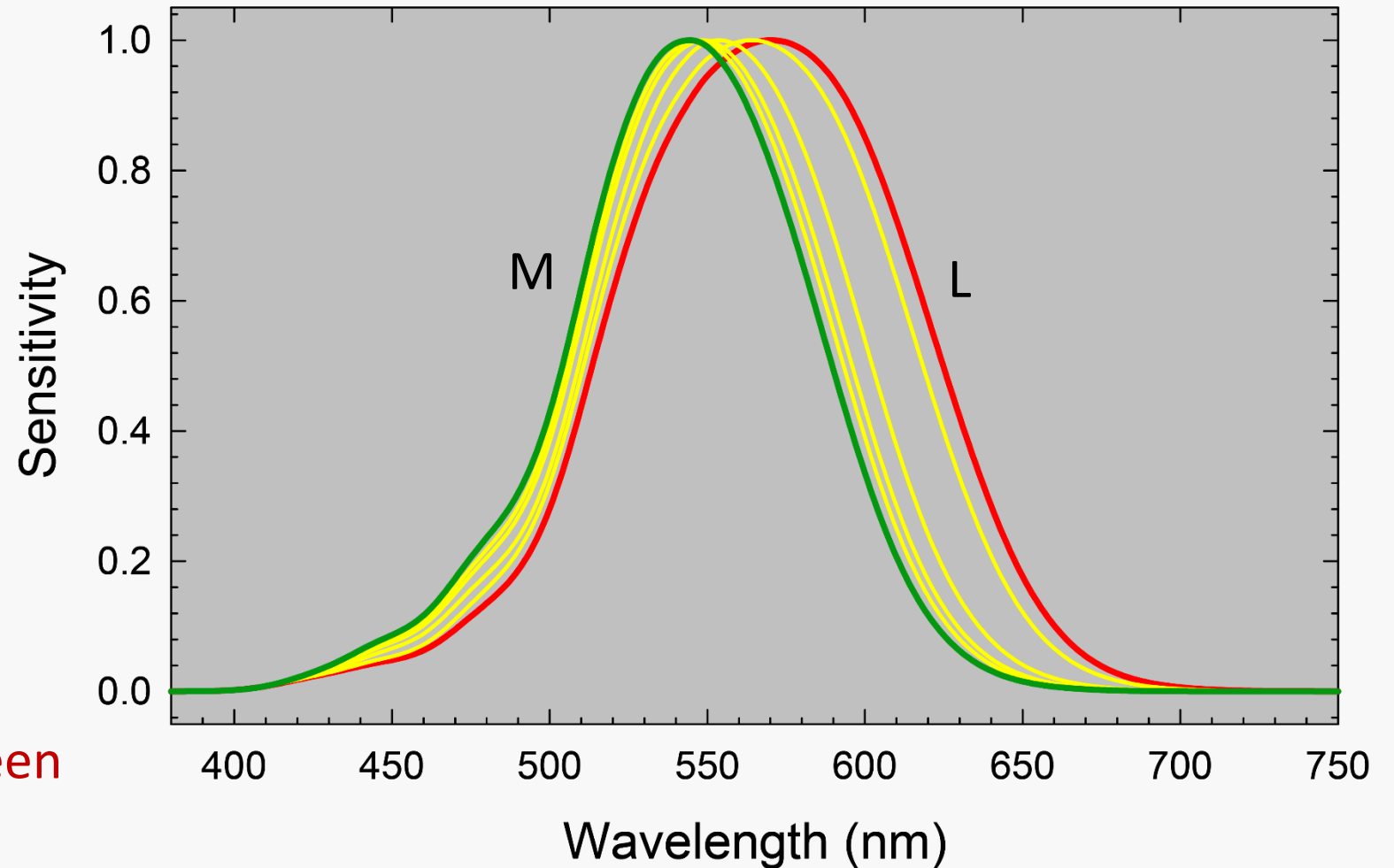


# M-cone shifts (hybrids)

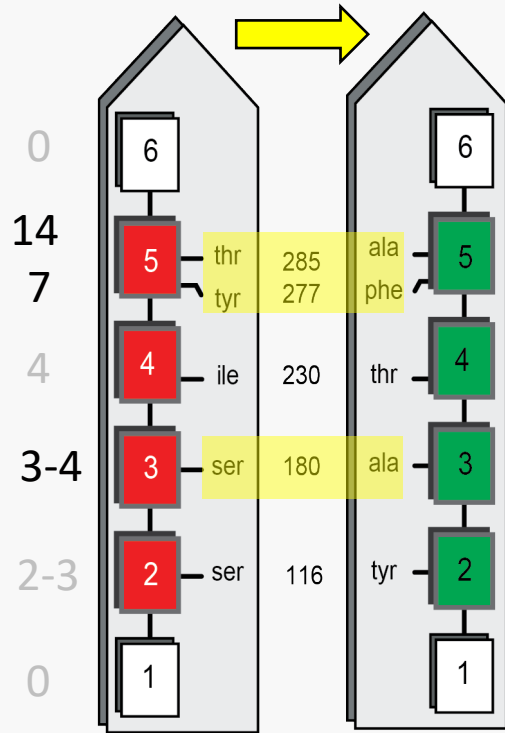


M-cone shifts can cause a red-green colour vision deficiency called deuteranomaly or deuteranopia.

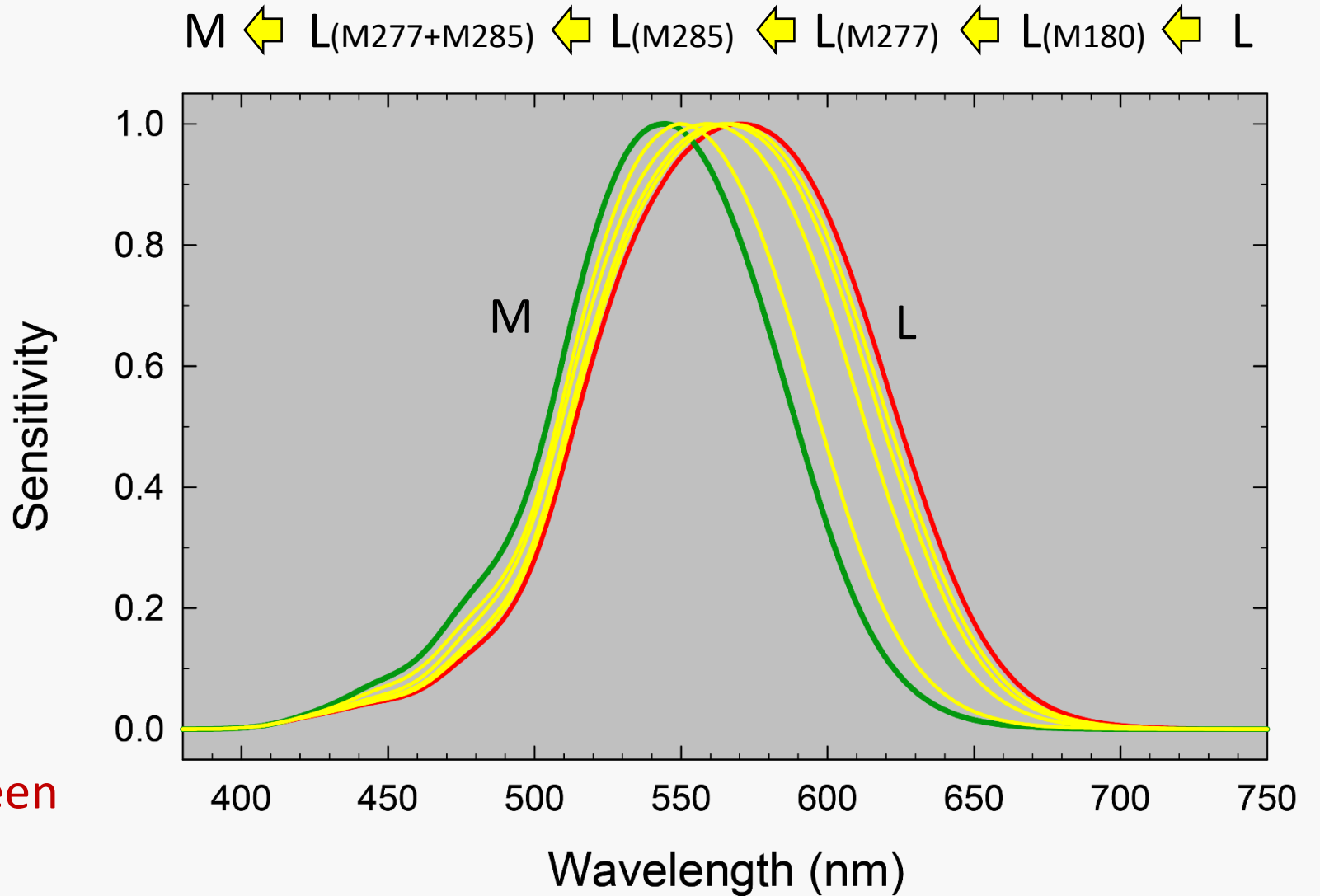
M → M<sub>(L180)</sub> → M<sub>(L277)</sub> → M<sub>(L285)</sub> → M<sub>(L277+L285)</sub> → L



# L-cone shifts (hybrids)



L-cone shifts can cause a red-green colour vision deficiency called protanomaly or protanopia.



# CVD prevalence

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

So more than 5% of males will see colours differently from colour normals.

		percent in UK	
Condition		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
TOTALS		8.50%	0.46%

# XY inheritance

The L-cone and M-cone opsin genes are on the X-chromosome, so women have two copies but men only one.

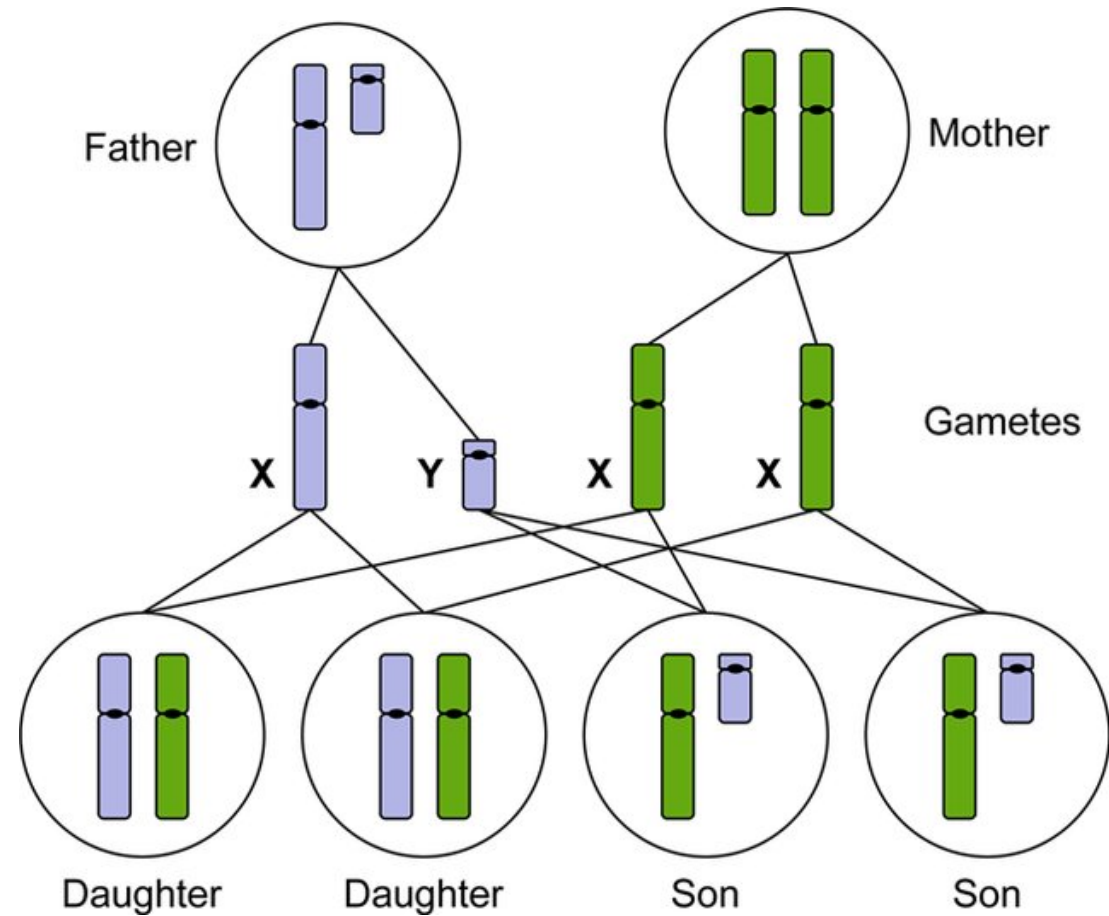


Figure 7 from Jackson, Marks, May & Wilson  
(2018) *Essays in Biochemistry* 62, 643-723



# What causes individual differences?

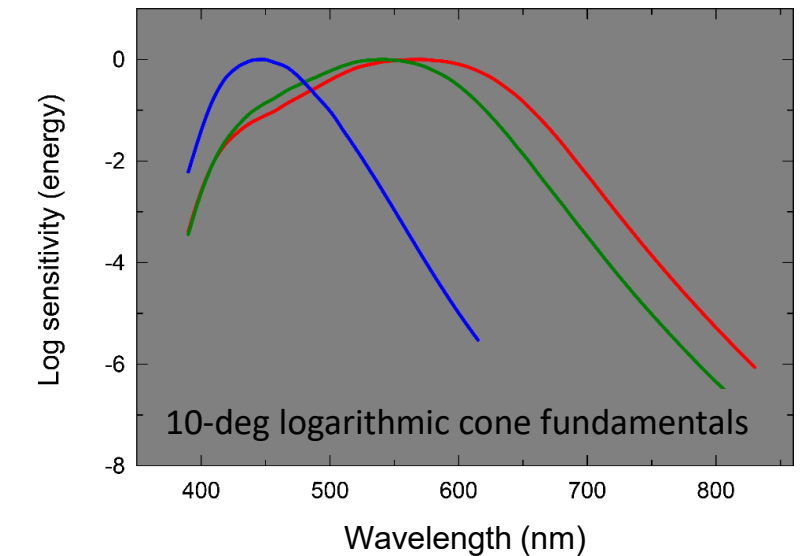
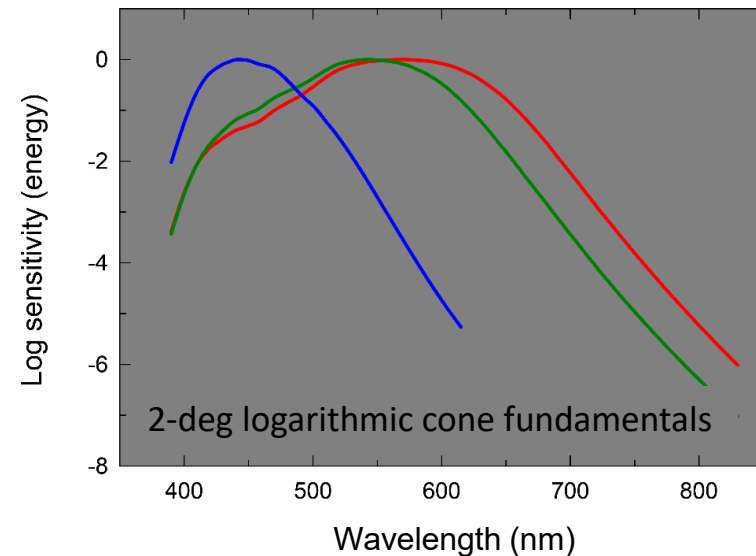
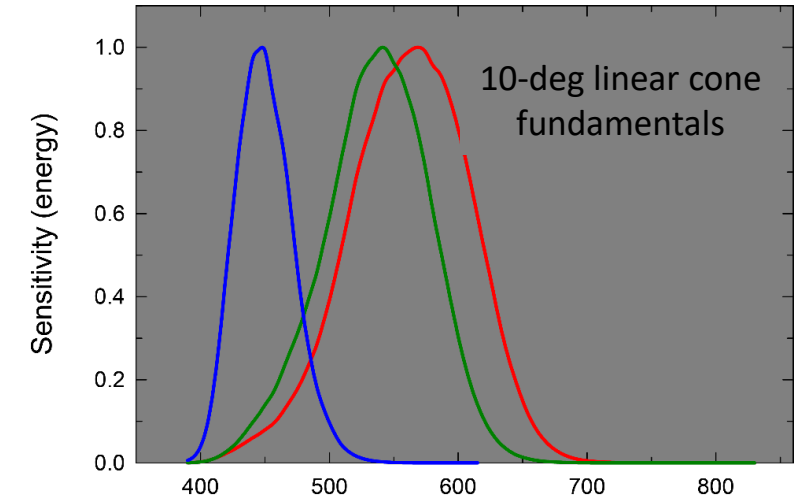
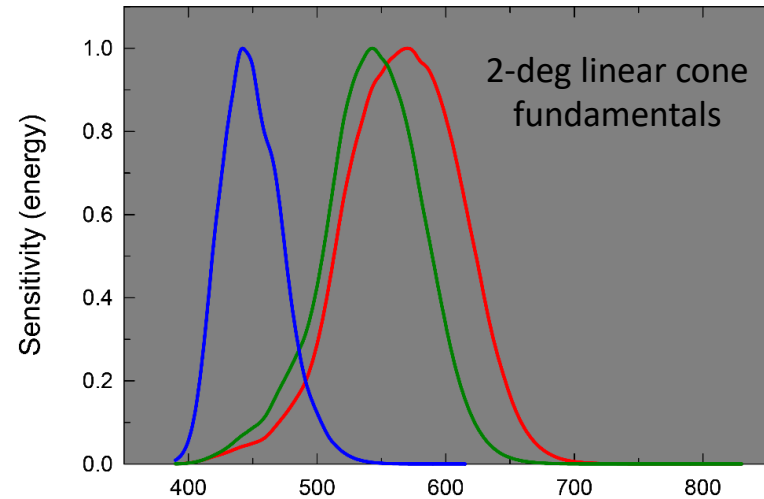
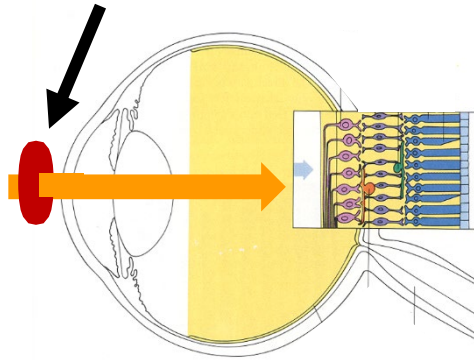
- ▶ Macular pigment optical density differences
- ▶ Lens pigment optical density differences
- ▶ Photopigment optical density differences
- ▶ Spectral shifts in photopigment sensitivity

## 4. MODELLING INDIVIDUAL DIFFERENCES



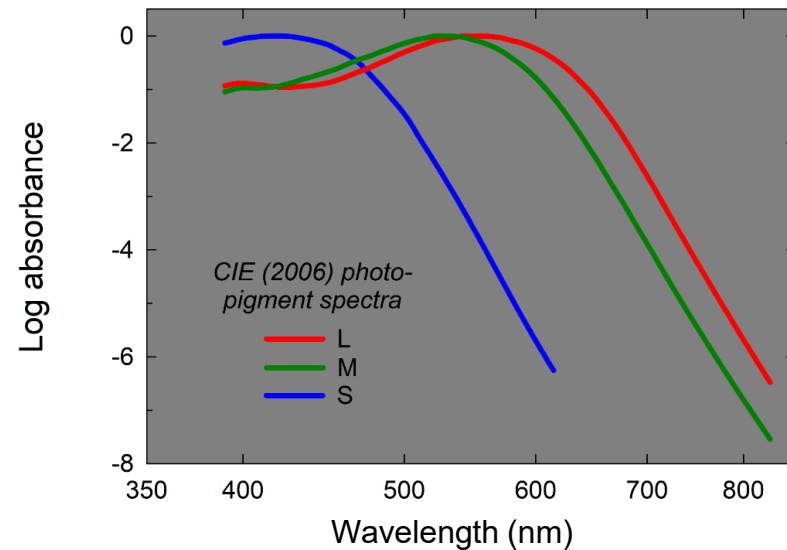
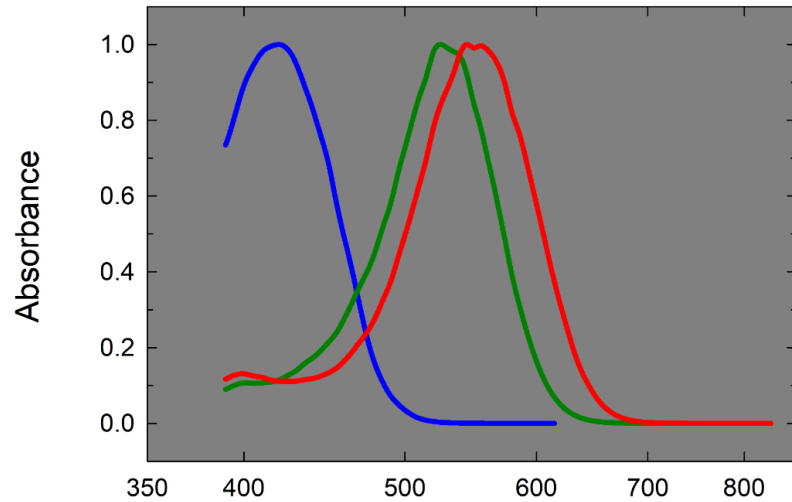
# Stockman & Sharpe (2000) and CIE (2006) standard LMS observers for 2-deg and 10-deg vision.

Measured with respect to  
light entering the cornea

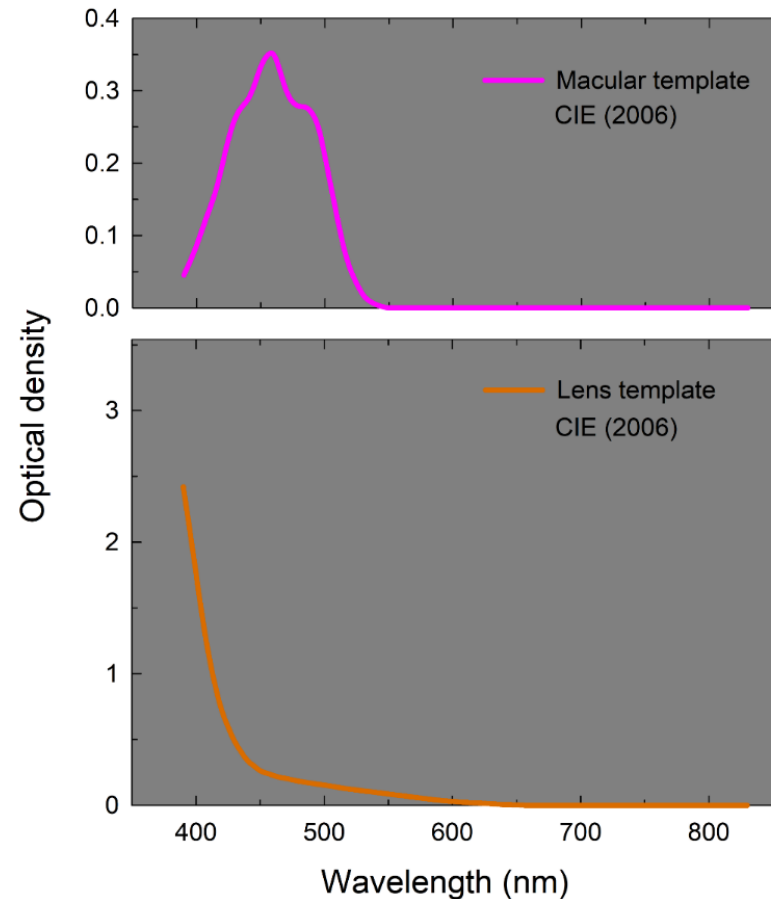


The new CIE standards also define the macular and lens pigment optical density spectra, the photopigment optical densities and the photopigment spectra.

Photopigment absorbance curves

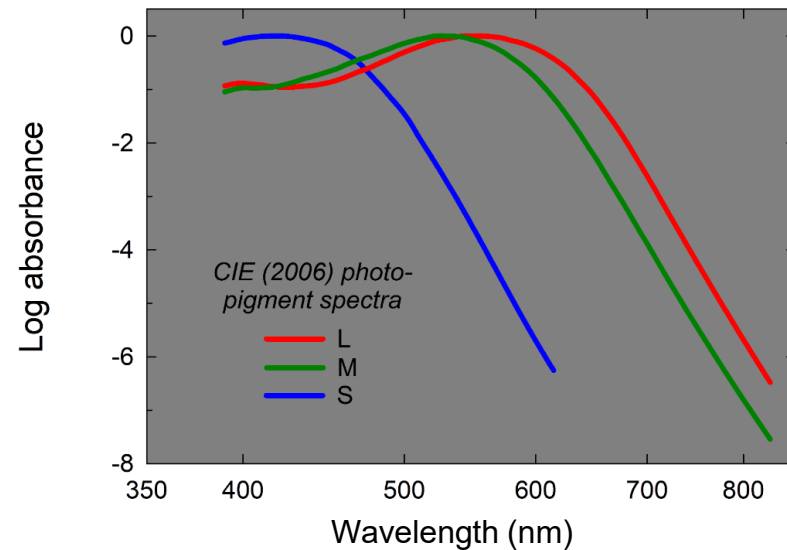
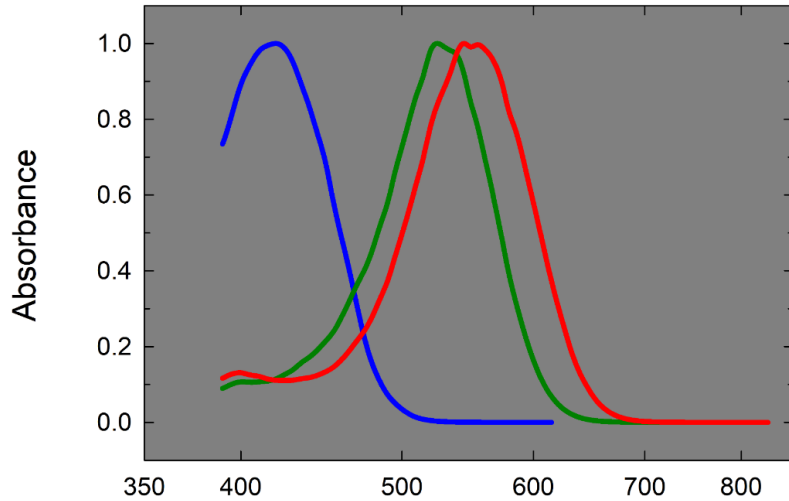


Macular and lens pigment optical density spectra

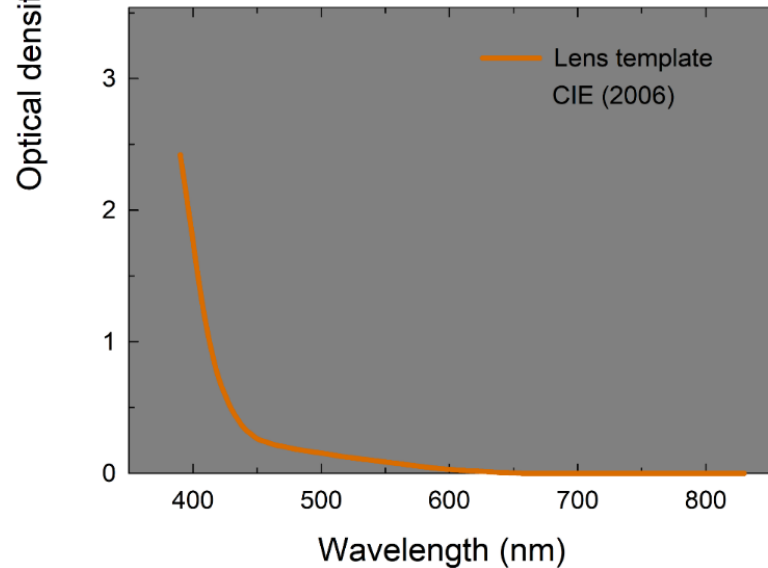
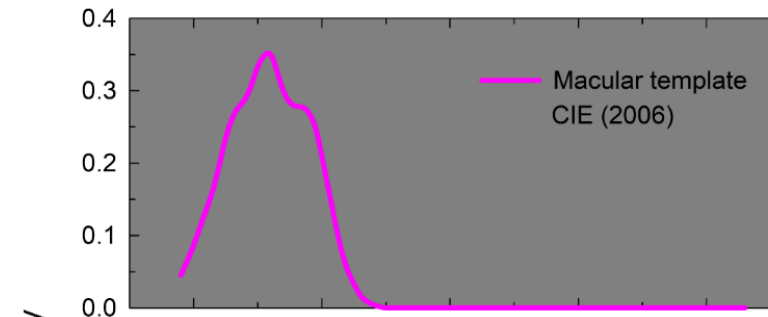


We model individual differences by adjusting the photopigment absorbance curves and varying the macular and lens optical densities

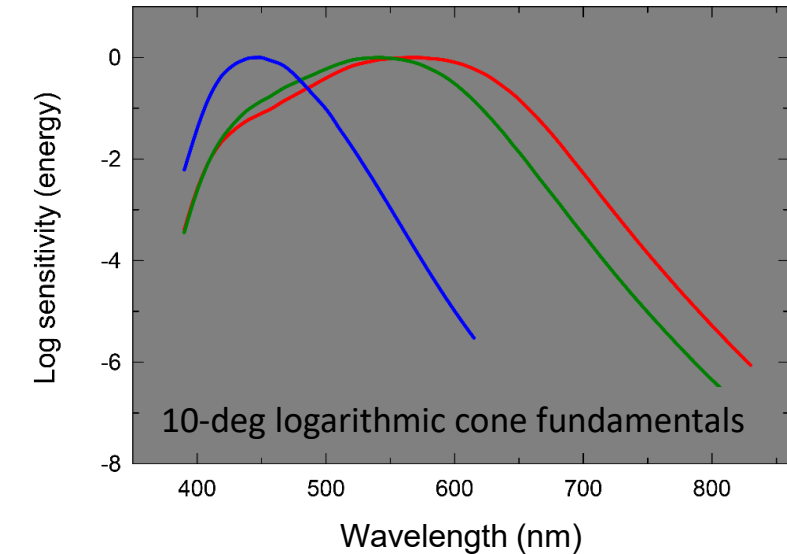
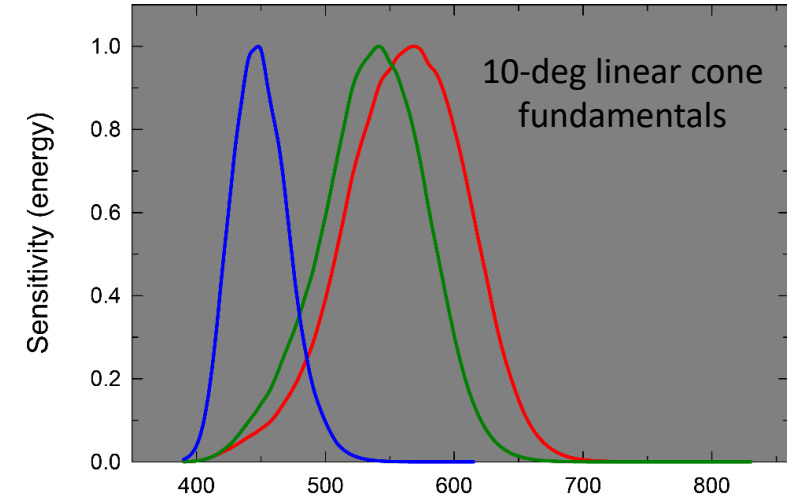
Photopigment absorbance curves



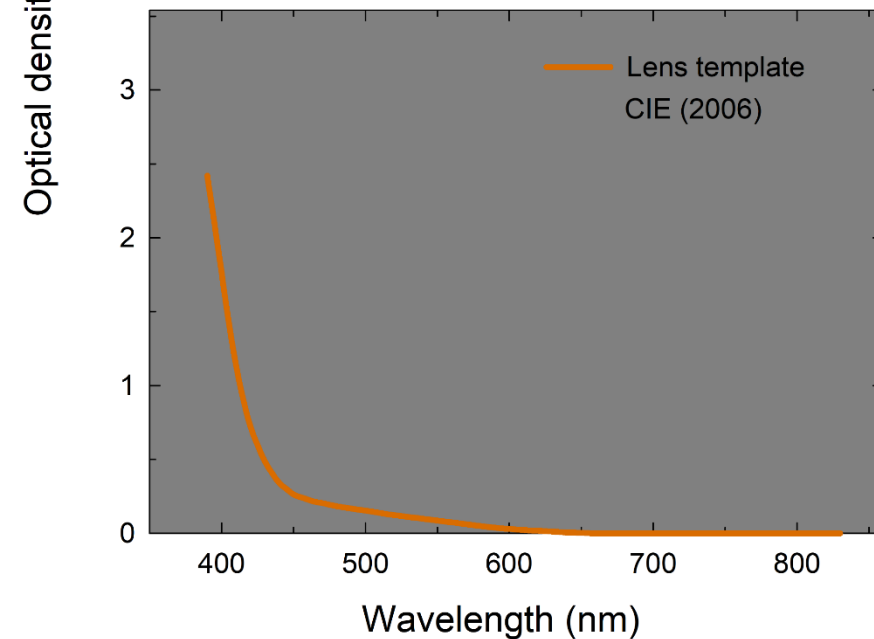
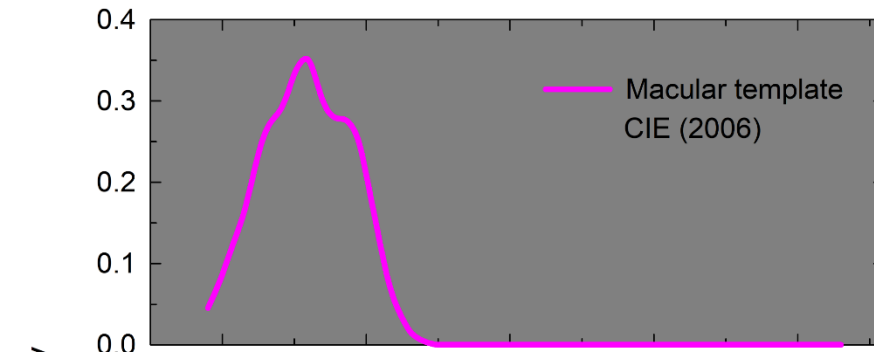
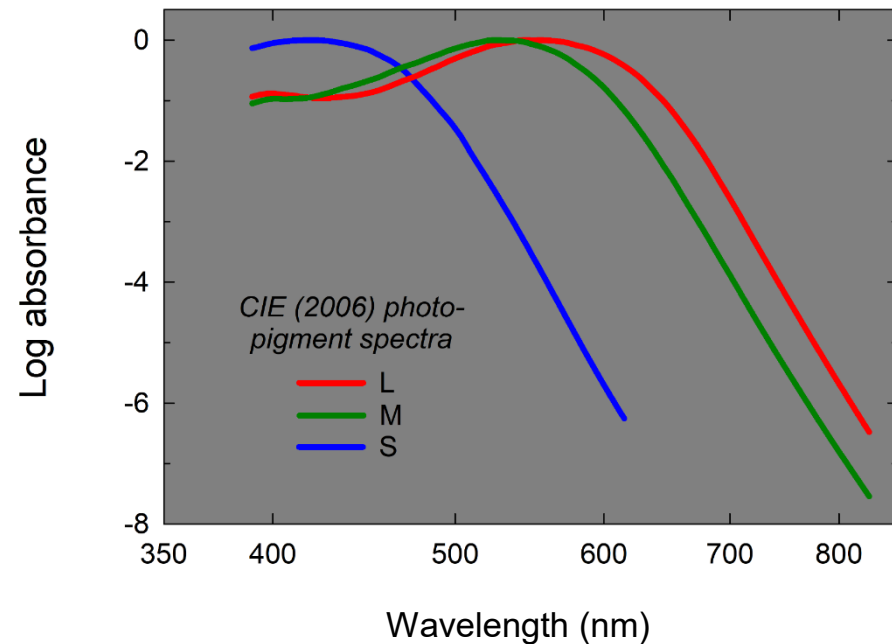
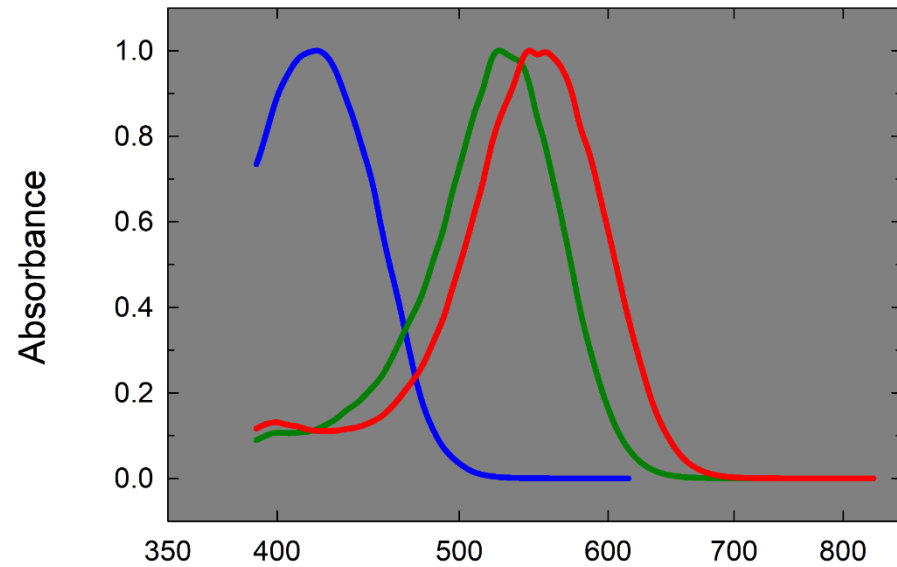
Macular and lens pigment optical density spectra



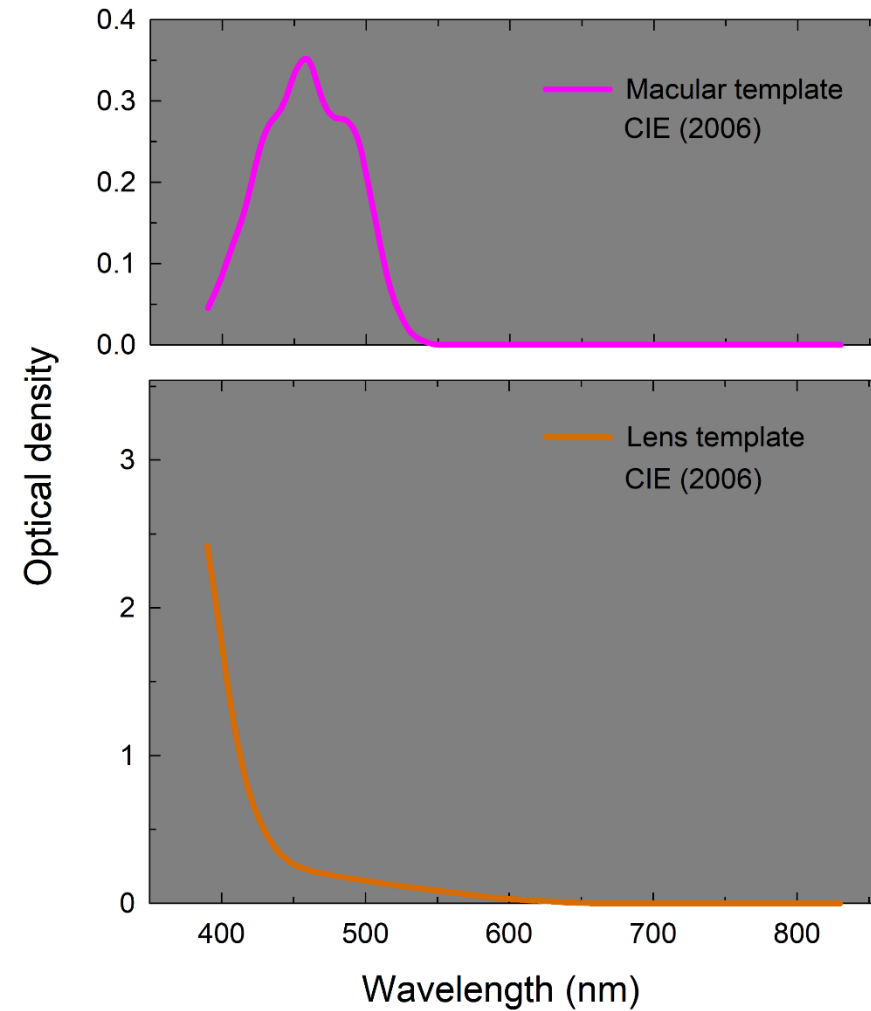
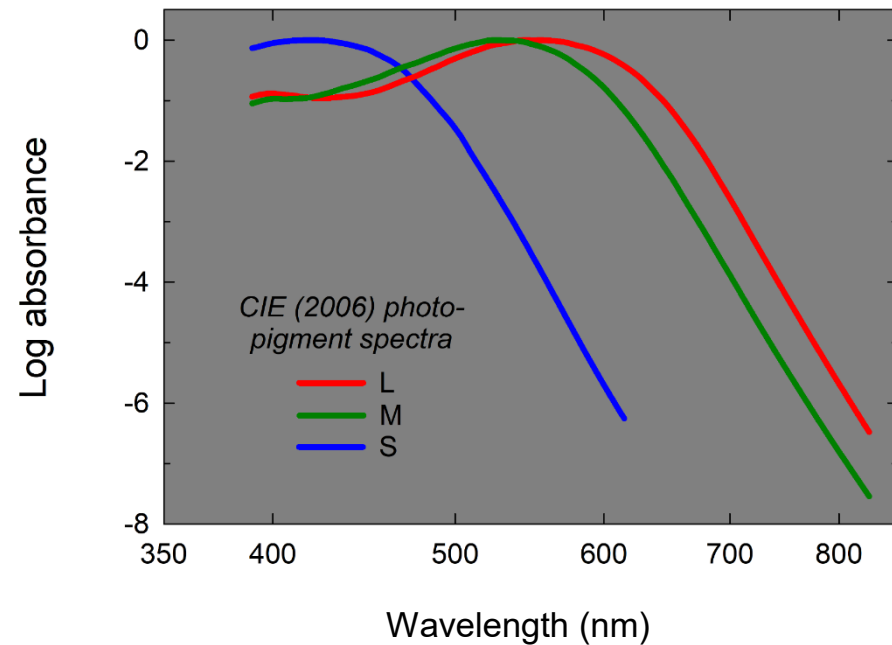
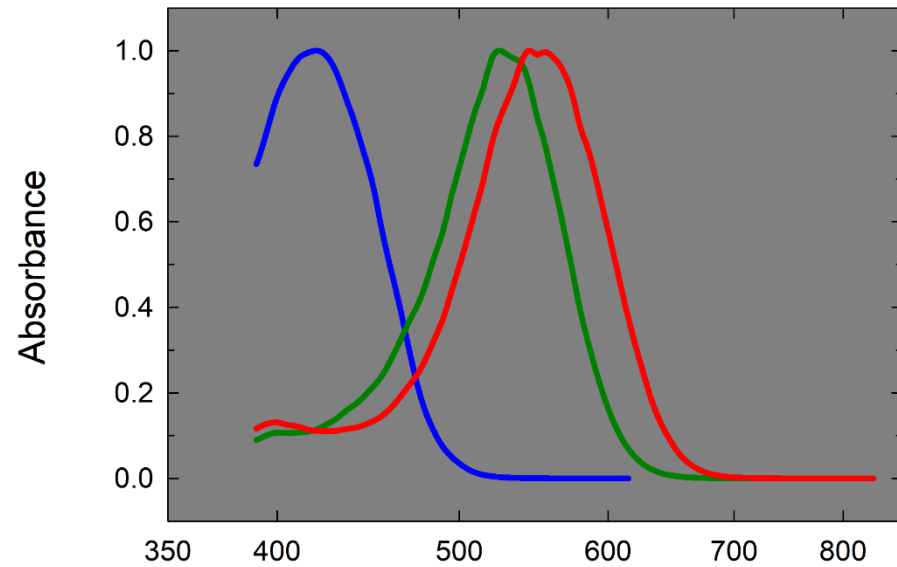
Corneal spectral sensitivities

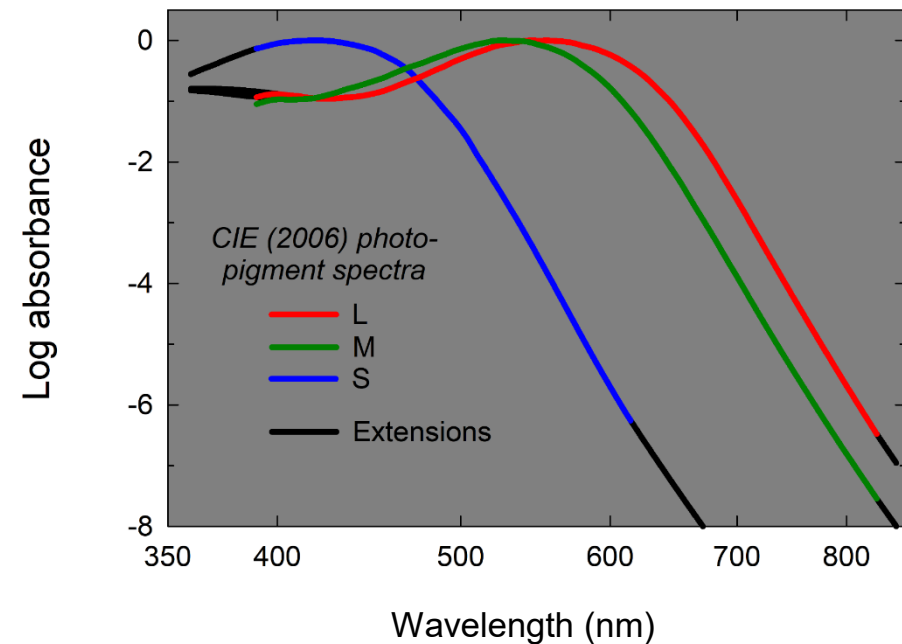
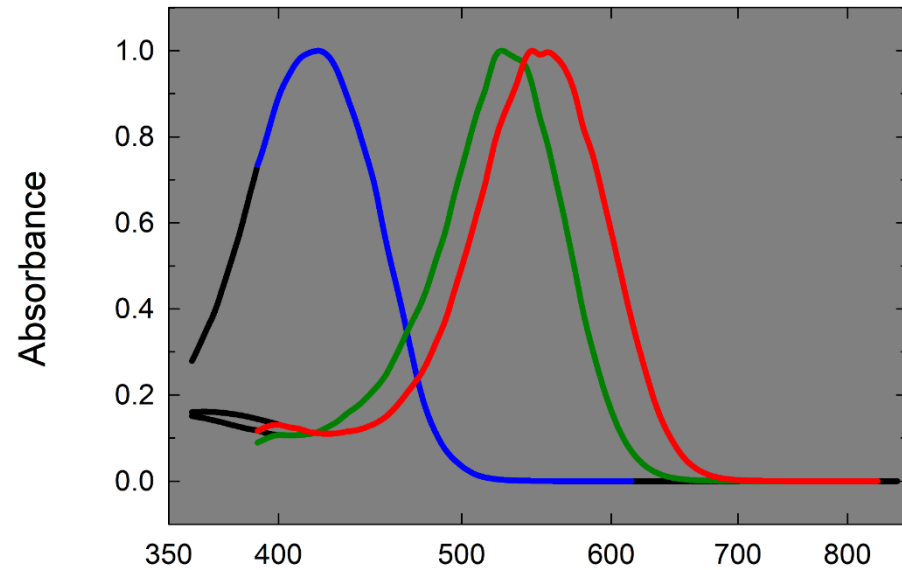


Unfortunately, the CIE (2006) LMS standards are defined as discrete values at 5 or 1 nm steps rather than as continuous functions of wavelength.

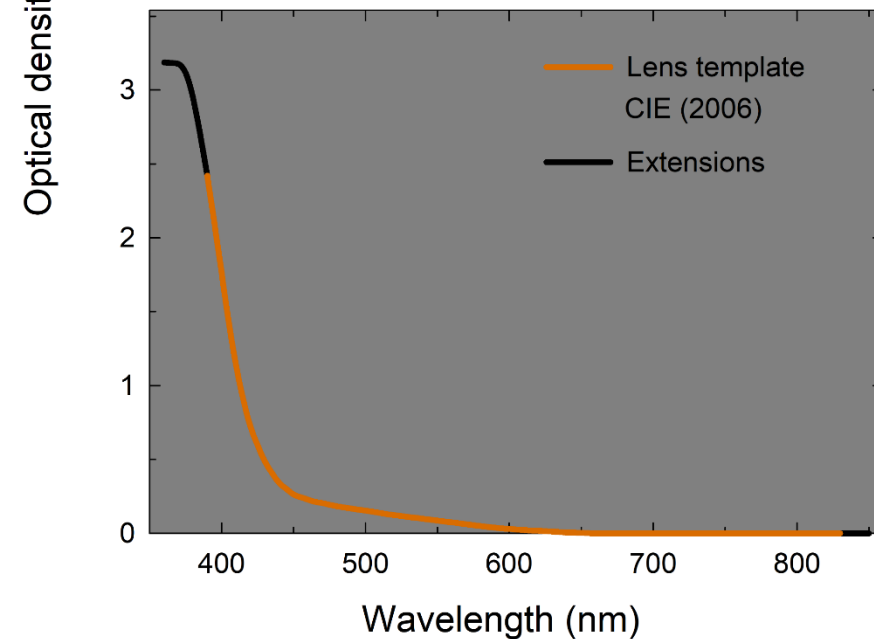
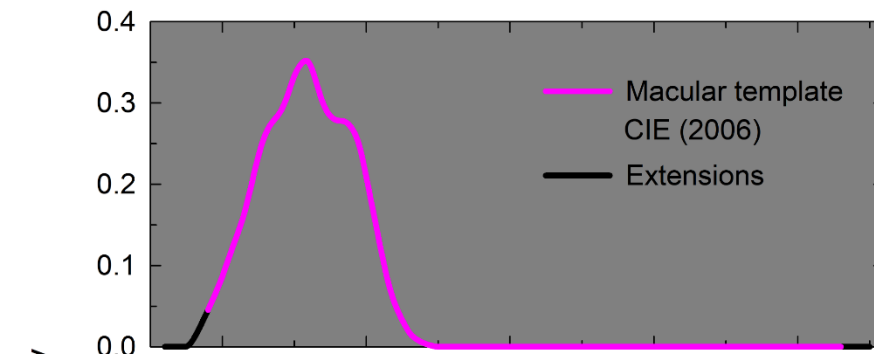


For computational convenience, we want to define these as continuous functions of wavelength...





First, we extended the discrete functions to 360 nm at short wavelengths and 850 nm at long (partly to allow spectral shifts).





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

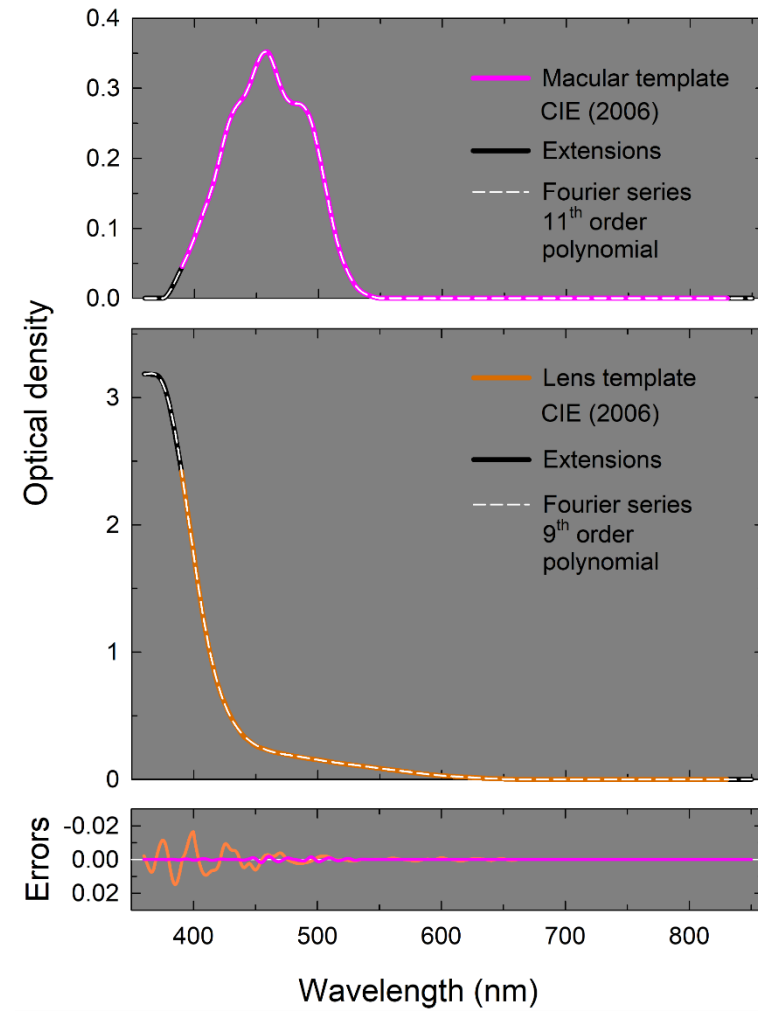
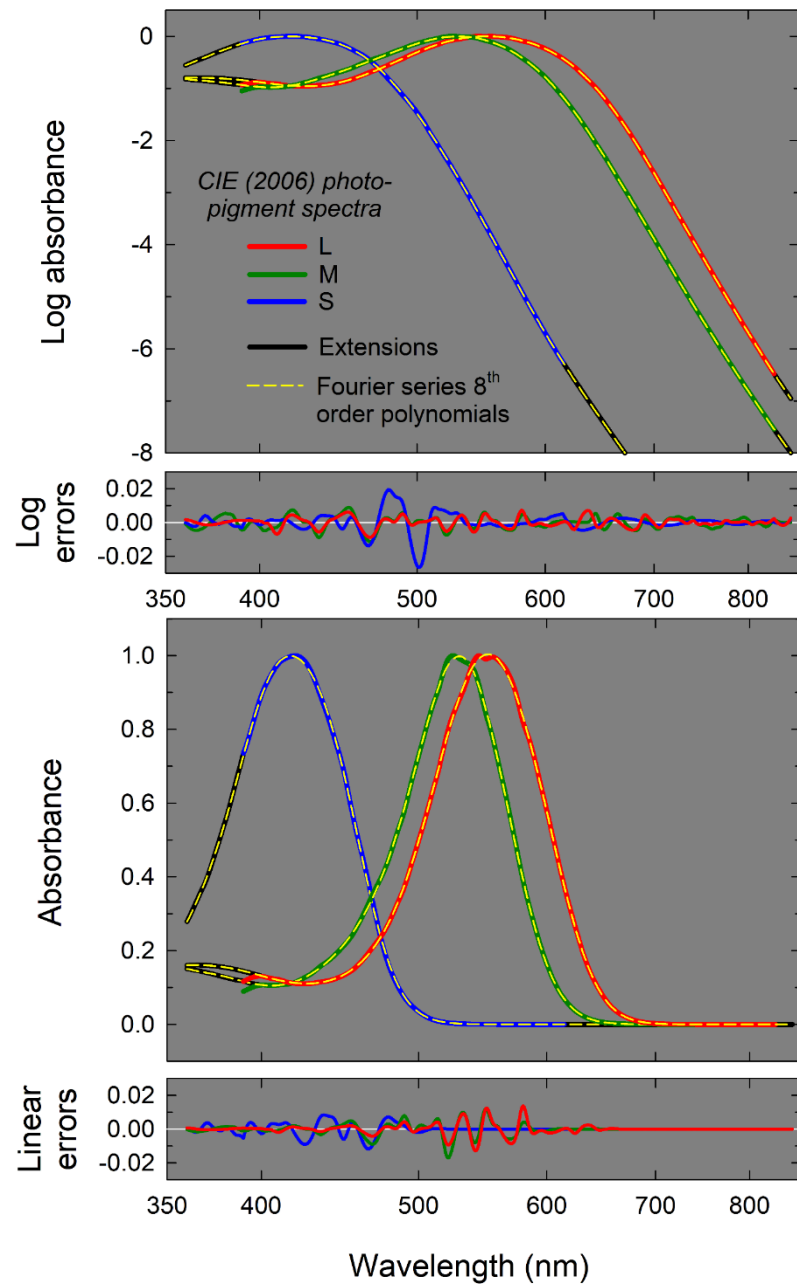
The templates are of the general form:

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


$n$  is the number of harmonics.

*Continuous functions of wavelength with little error when used to reconstruct fundamentals.*

Important that they describe both log and linear absorbances!



MainWindow



## Fundamental CMFs (LMS cone spectral sensitivities)

**Longer L (or M) cone parameters**

$\lambda$  max shift from L  
-40 to +10 nm only

Optical density

**Shorter M (or L) cone parameters**

$\lambda$  max shift from M  
+30 to -20 nm only

Optical density

**S-cone parameters**

Optical density

**Common parameters**

Lens pigment density (at 400 nm)

Macular pigment density (at 460 nm)

**Individual LMS Templates**

Step-size  
☐ 0.1 nm ☒ 1 nm ☐ 5 nm

**Data output choices (Excel file)**

**Fundamental CMFs**  
(Corneal cone spectral sensitivities)

Quantal units ☐ linear ☐ log

Energy units ☐ linear ☐ log

**Retinal cone spectral sensitivities**

Quantal units ☐ linear ☐ log

**Absorbance** ☐ linear ☐ log

**RGB CMFs** ☐

Primary wavelengths (Stiles & Burch default)  
R  G  B

**Output** Written to local 'CMFs\_out' directory

CMFs directory  CMFs filename

☐ Overwrite file?

**Buttons:** Plot CMFs, Reset to defaults, Generate Excel file, Generate unshifted mean L (ser/ala180) M and S Excel file

MainWindow

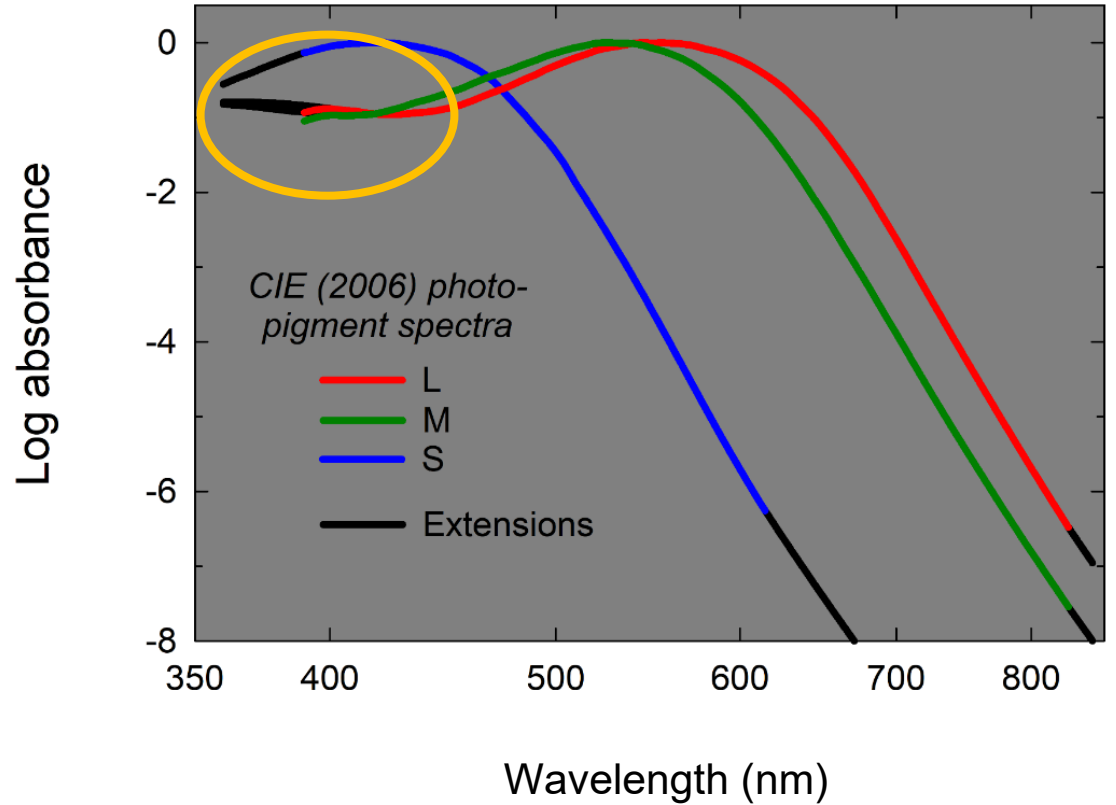
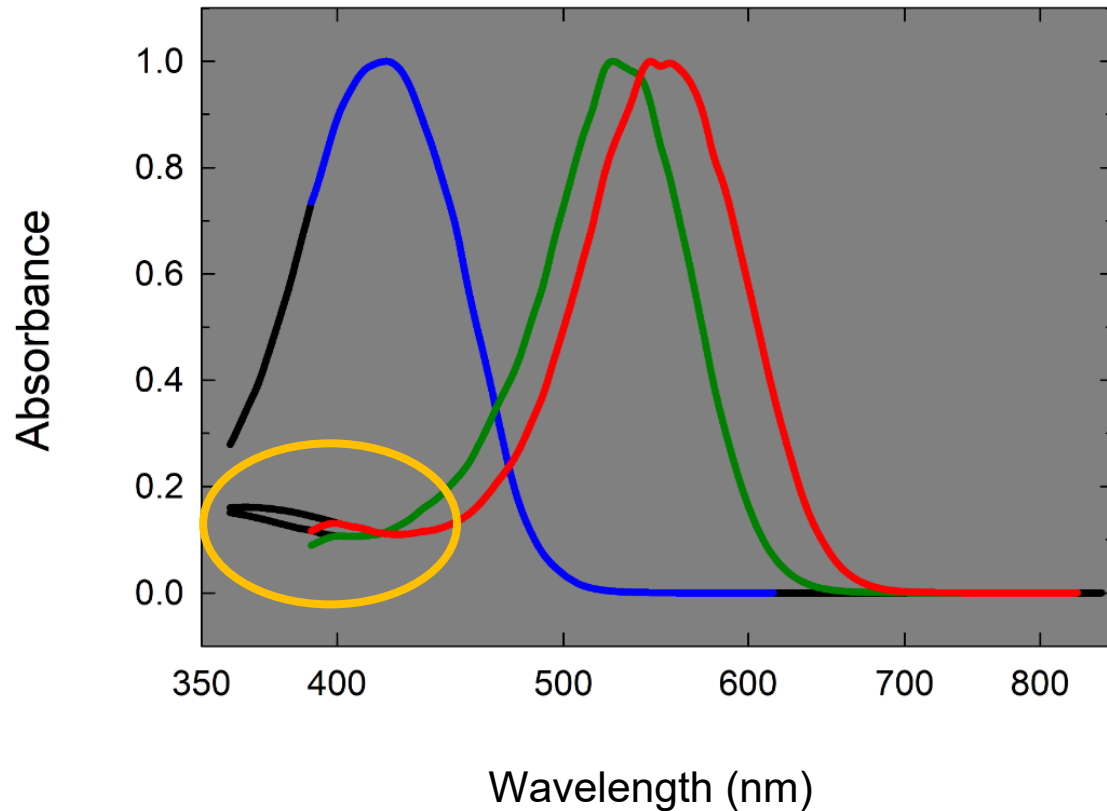
Shorter ML-cone			Longer LM-cone			
Codon	M	L	Exon	M	L	Codon
116	<input checked="" type="radio"/> Tyr <input type="radio"/> Ser		2	<input type="radio"/> Tyr <input checked="" type="radio"/> Ser		116
180	<input checked="" type="radio"/> Ala <input type="radio"/> Ser		3	<input type="radio"/> Ala <input checked="" type="radio"/> Ser		180
230	<input checked="" type="radio"/> Thr <input type="radio"/> Ile		4	<input type="radio"/> Thr <input checked="" type="radio"/> Ile		230
233	<input checked="" type="radio"/> Ser <input type="radio"/> Ala			<input type="radio"/> Ser <input checked="" type="radio"/> Ala		233
277	<input checked="" type="radio"/> Phe <input type="radio"/> Tyr			<input type="radio"/> Phe <input checked="" type="radio"/> Tyr		277
285	<input checked="" type="radio"/> Ala <input type="radio"/> Thr		5	<input type="radio"/> Ala <input checked="" type="radio"/> Thr		285
309	<input checked="" type="radio"/> Phe <input type="radio"/> Tyr			<input type="radio"/> Phe <input checked="" type="radio"/> Tyr		309

ML shift (nm)  **Done** LM shift (nm)

Stockman, A., & Rider, A. T. (2023). Formulae for generating standard and individual human cone spectral sensitivities. *Color Research & Application*, 48(6), 818-840.  
doi: <https://doi.org/10.1002/col.22879>

Python program is available on Github at: <https://github.com/CVRL-IoO/Individual-CMFs.git>

Involved one correction of the CIE 2006 functions (to which we'll come back):

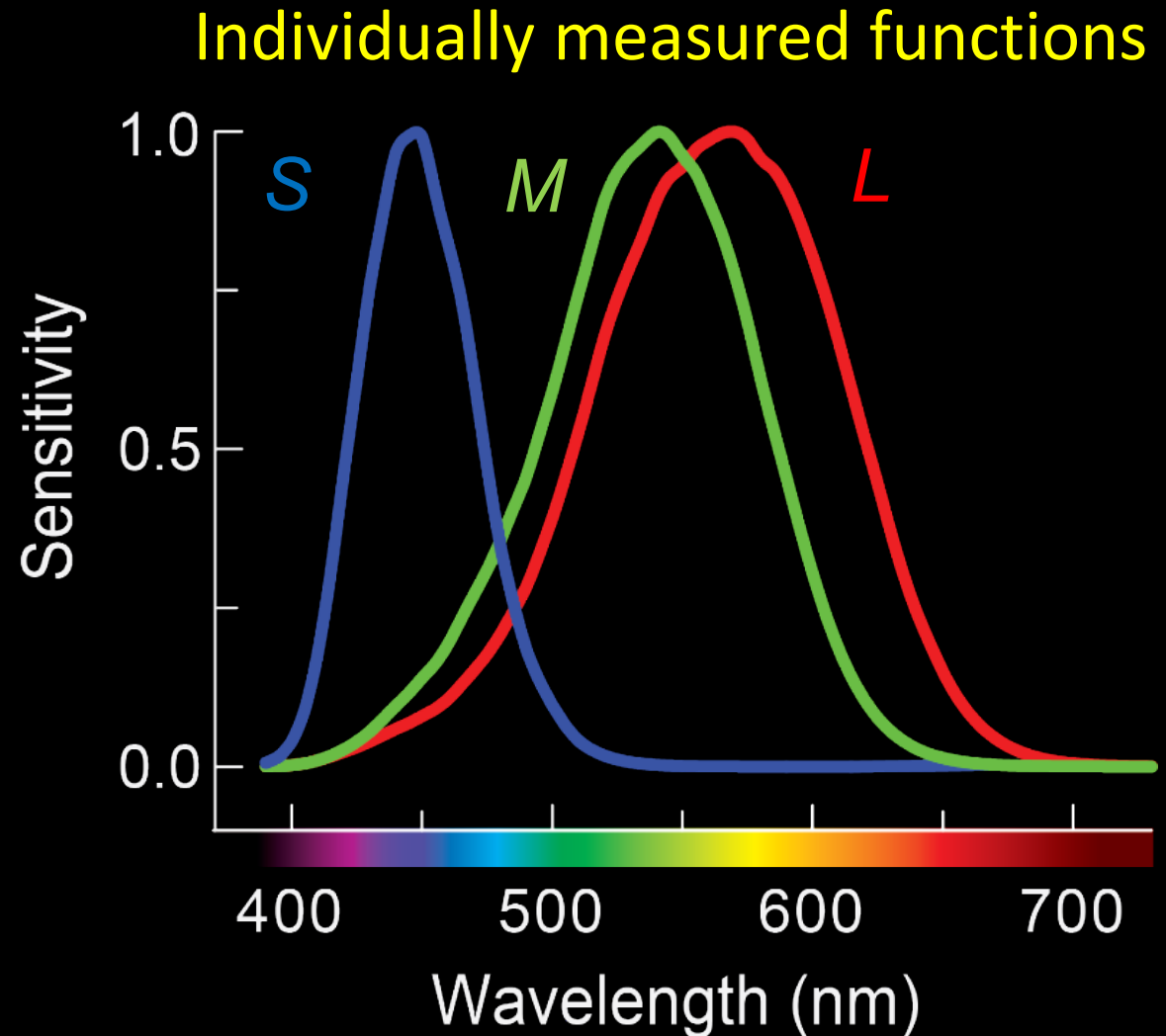


## 5. MEASURING INDIVIDUAL DIFFERENCES

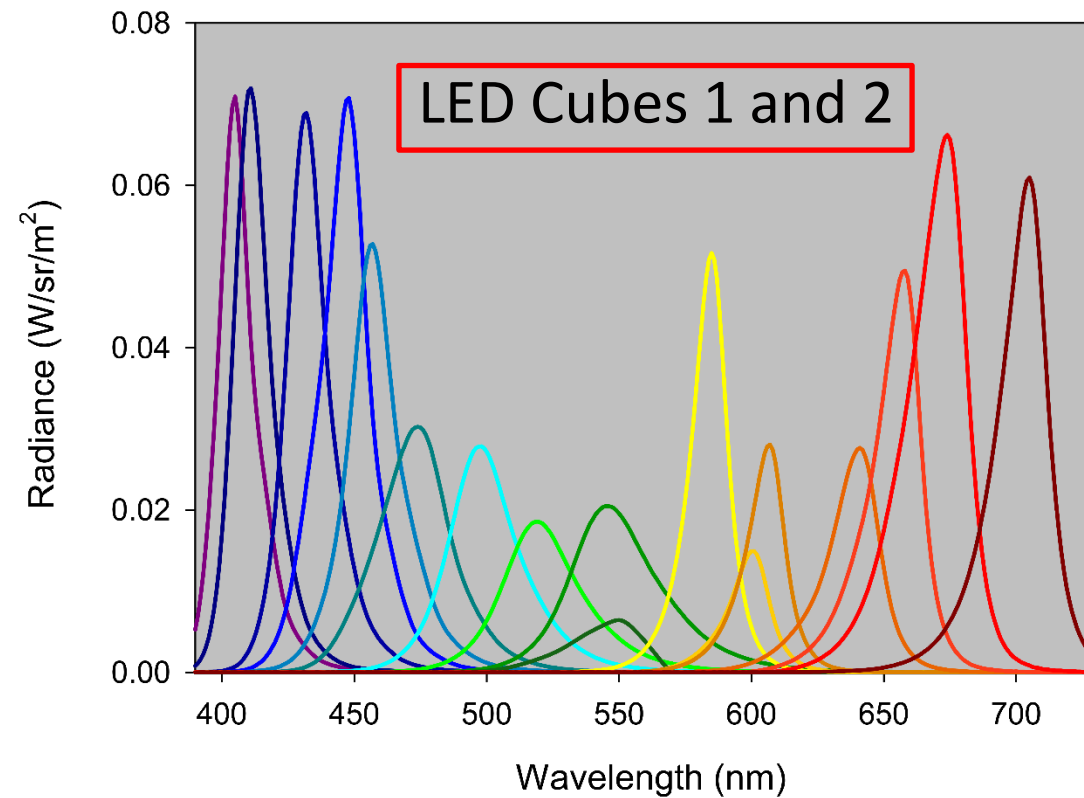


# Individual cone spectral sensitivities (colour matching functions)

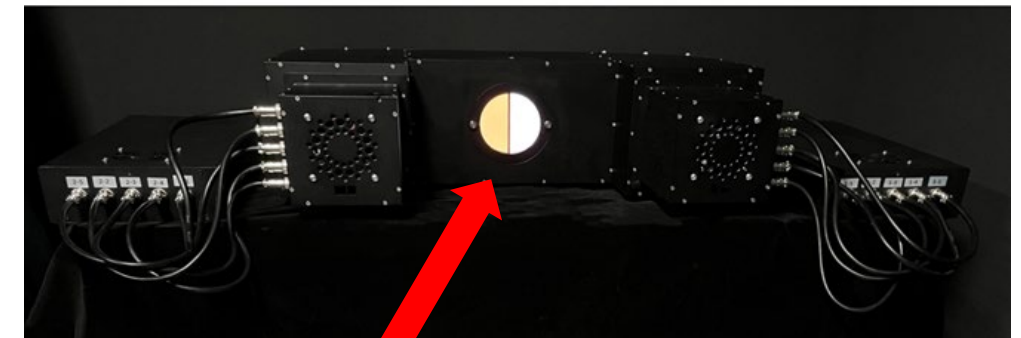
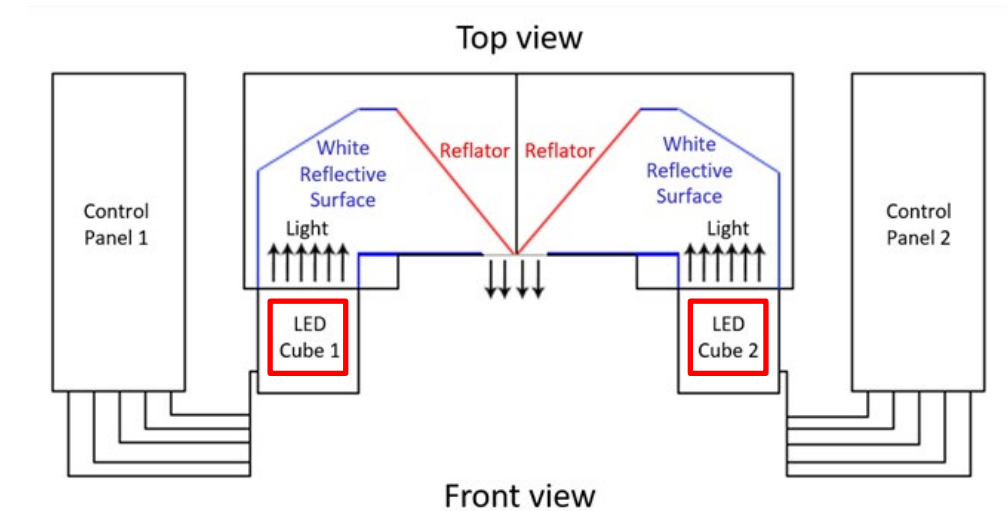
We can overcome the problems of individual differences by measuring an individual's own cone spectral sensitivities.



# Trichromator (LEDMax) (developed in collaboration with Thouslite)



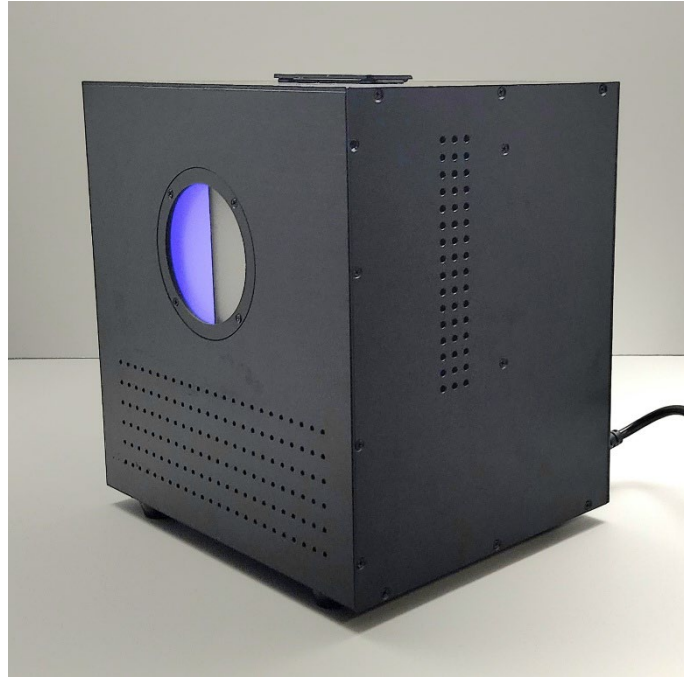
Collaborative work with Ronnier Luo's lab  
with Lucas Shi and Alan Song and Andy Rider



Subject view

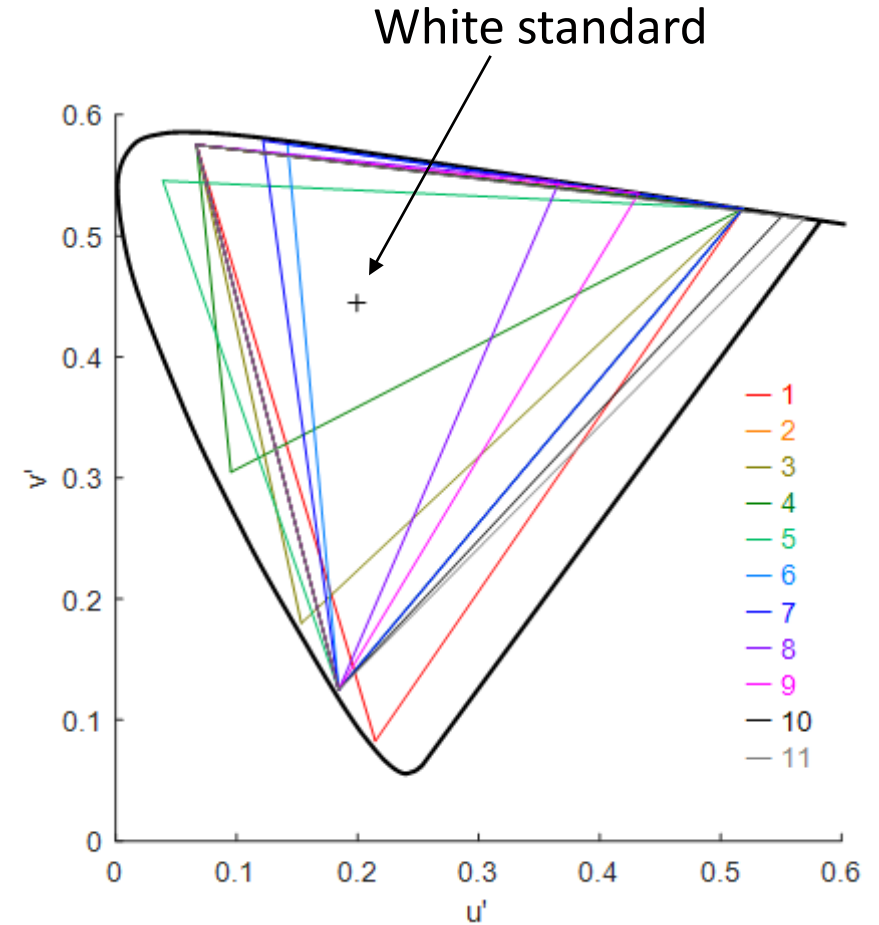
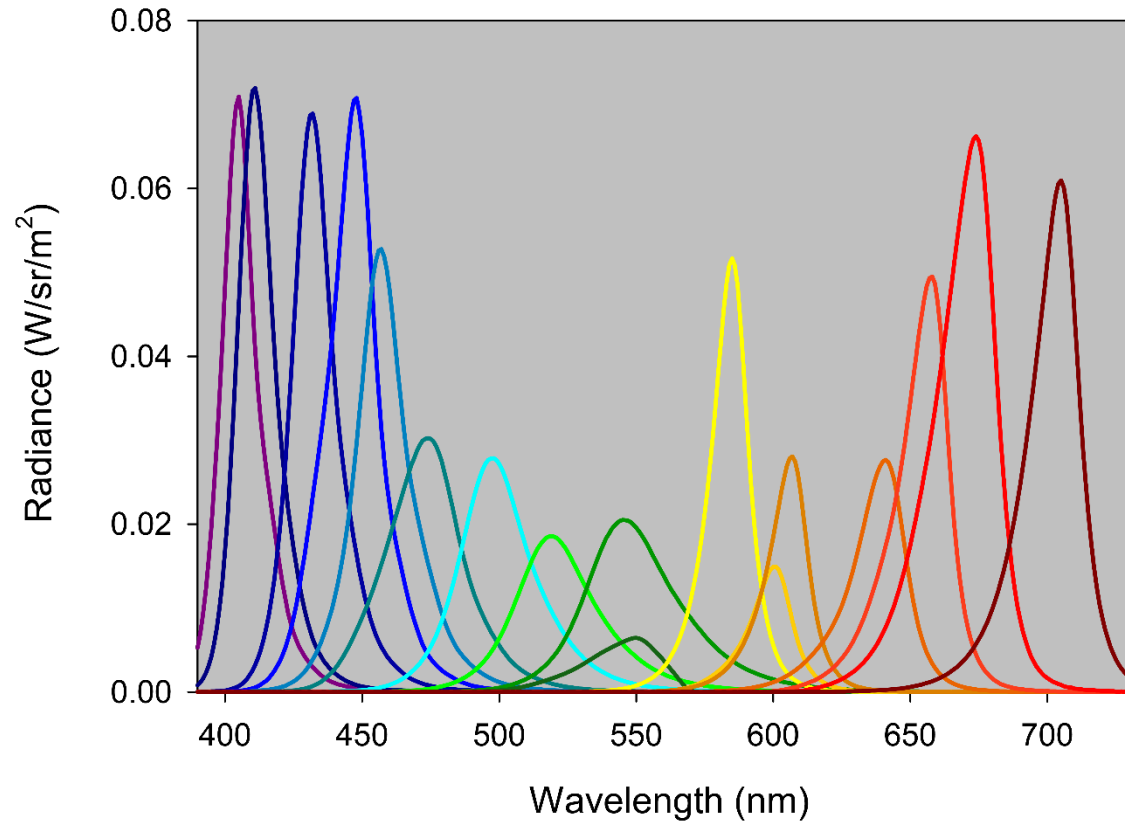
# Trichromator (LEDMax) updated version

A newer compact version  
has been developed...



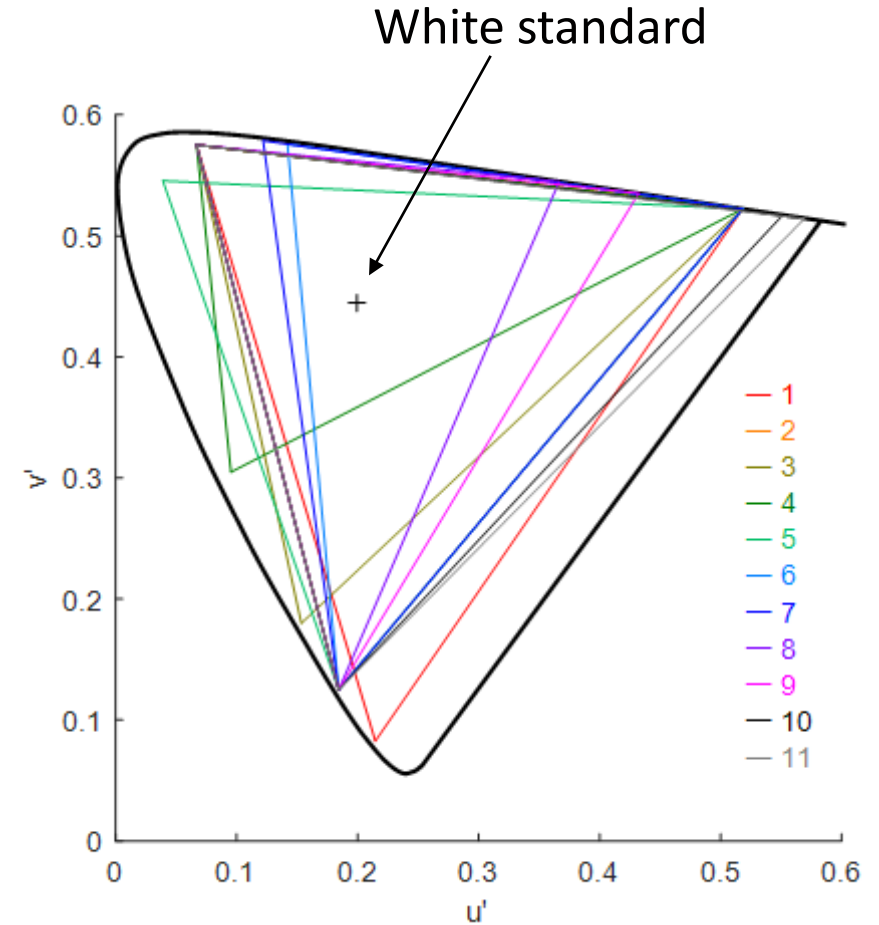
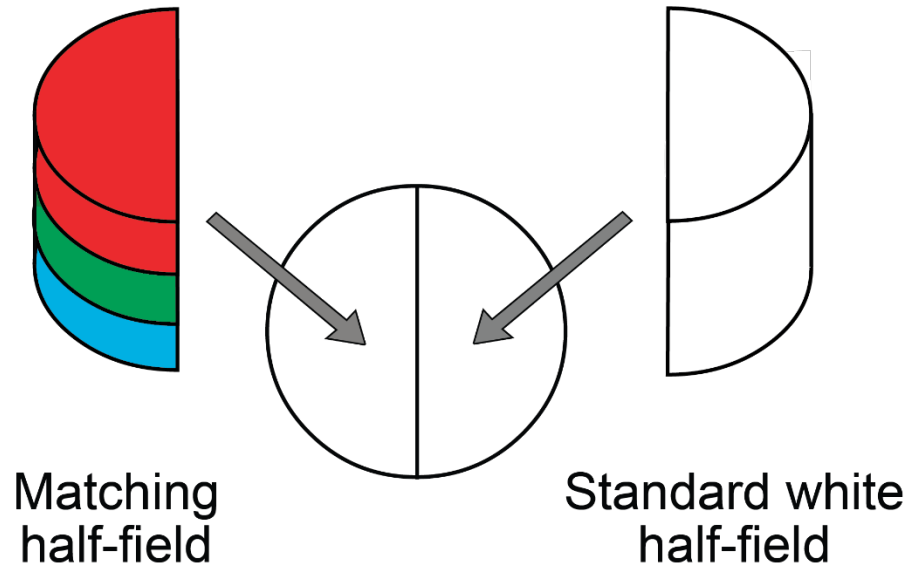


# Colour matching measurements



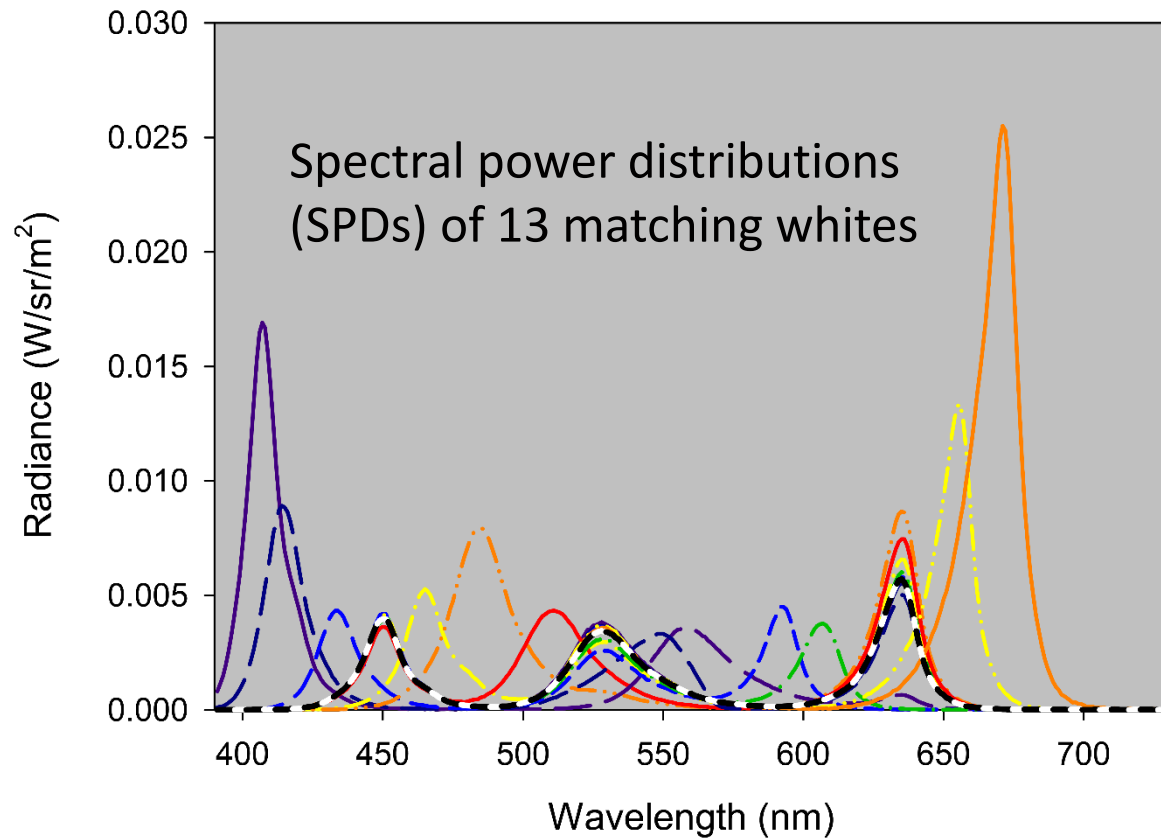
We chose 11 triplets of LEDs (primaries lights) that can be optically mixed to match a white standard (+)...

# Colour matching measurements

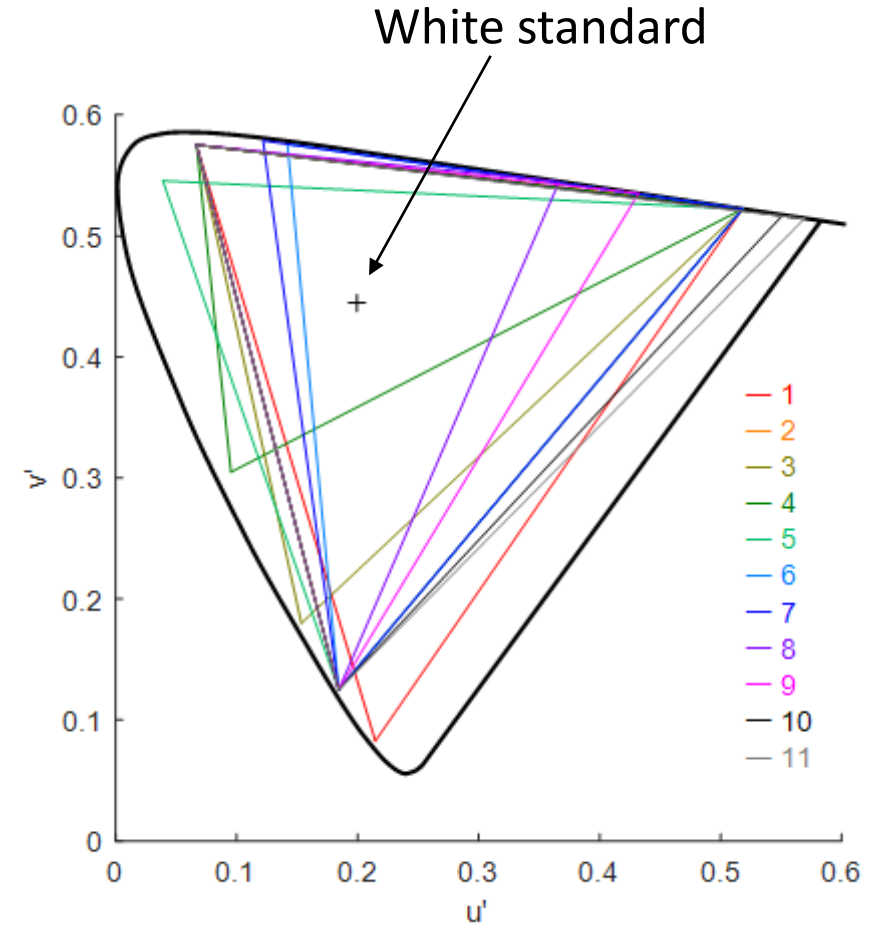


We then asked observers to adjust the intensities of each of the 11 triplets of primaries to match the white standard...

# Colour matching results

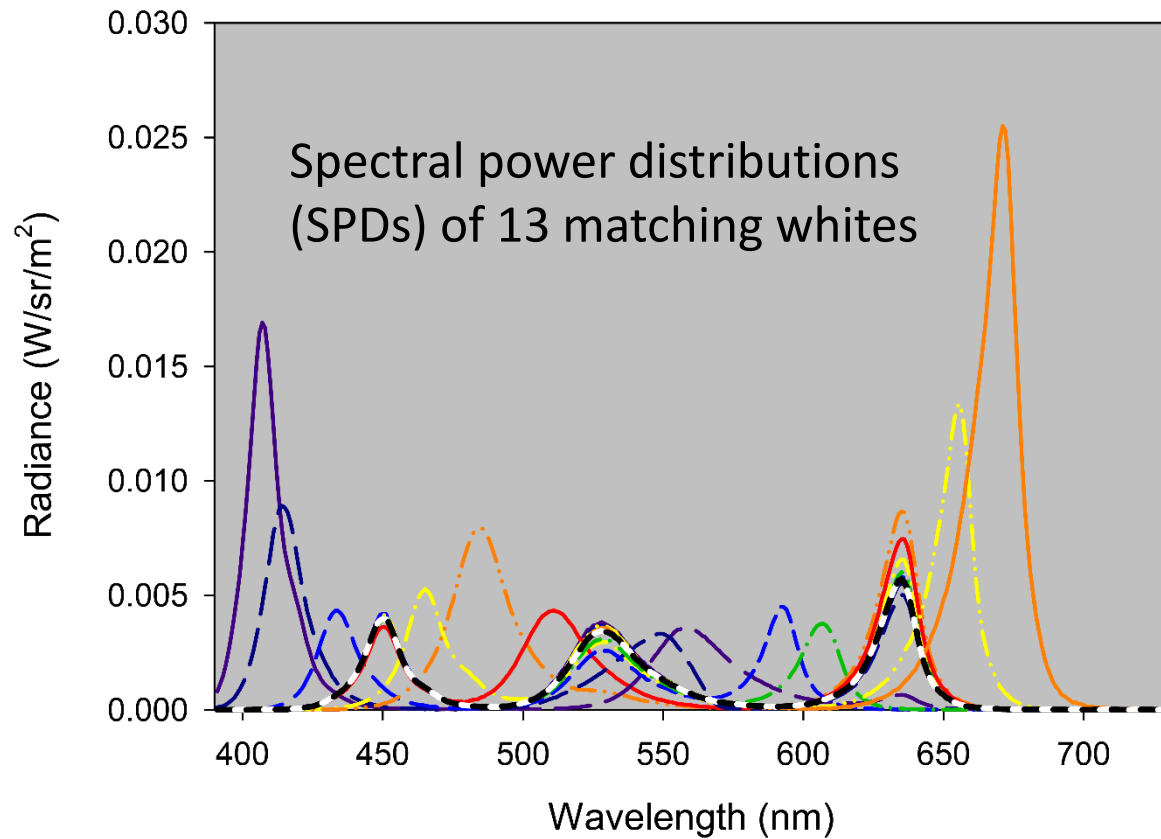


Here are the SPDs for the 13 matching whites (each SPD is made up of all three primaries) set by one of our subjects.



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

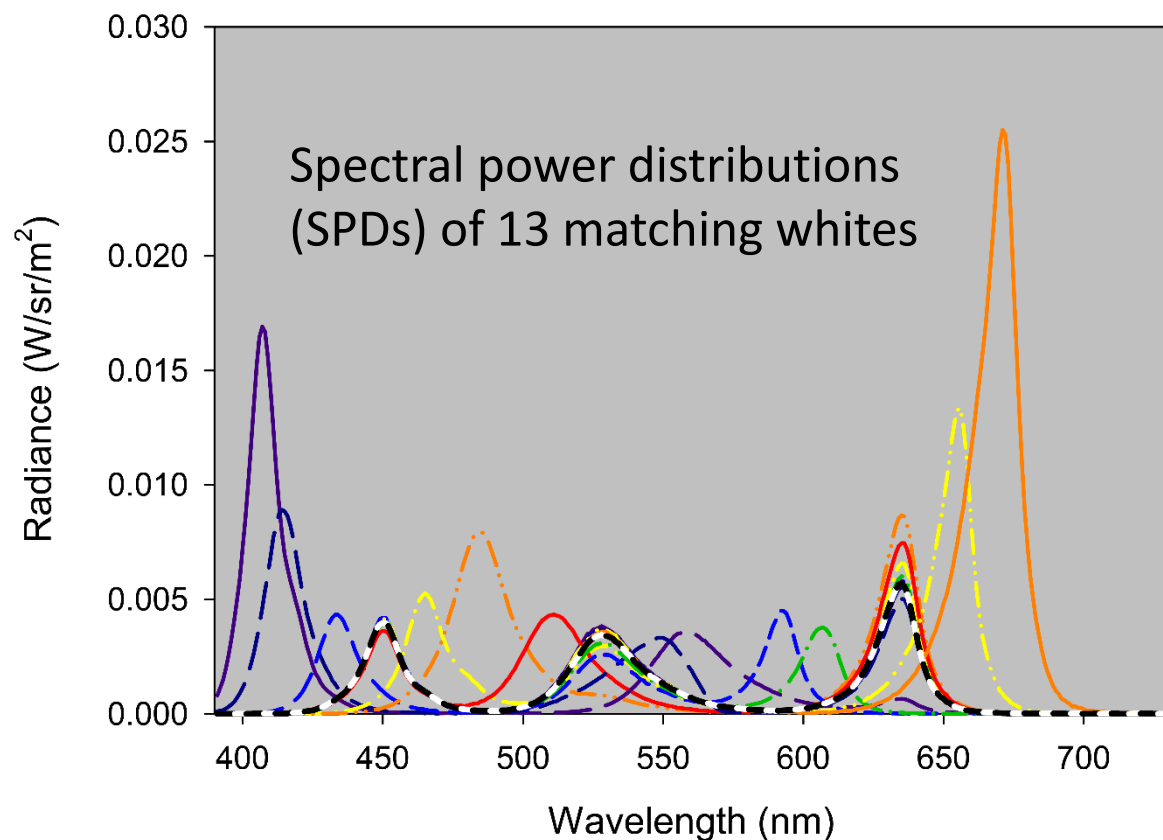
# Colour matching analysis



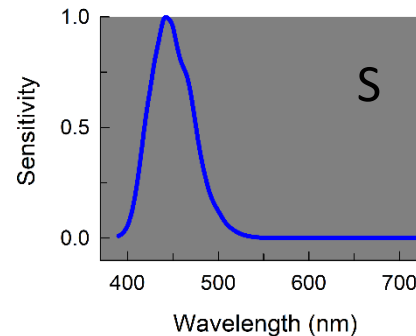
These 13 matching whites should all produce identical L-, M- and S-cone excitations.

So...

# Colour matching analysis



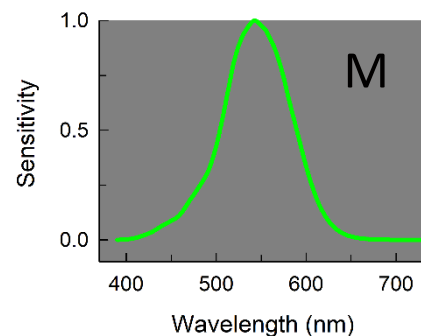
X



=

All 13 should produce the *same* S-cone excitation

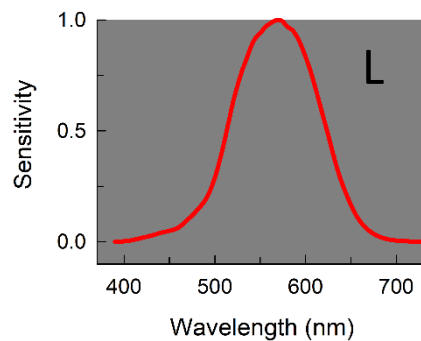
X



=

All 13 should produce the *same* M-cone excitation

X

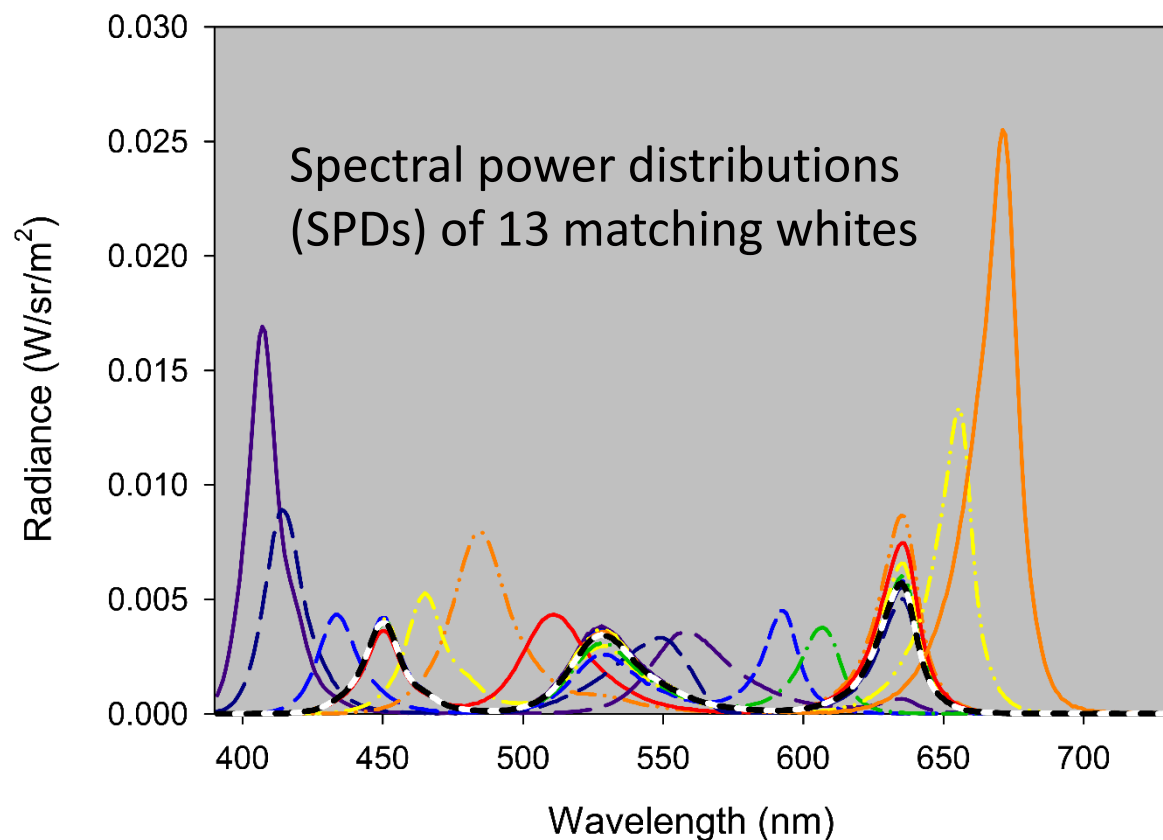


=

All 13 should produce the *same* L-cone excitation

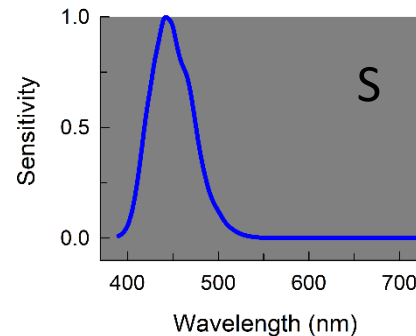
Cross-multiply  
and integrate

# Colour matching analysis



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

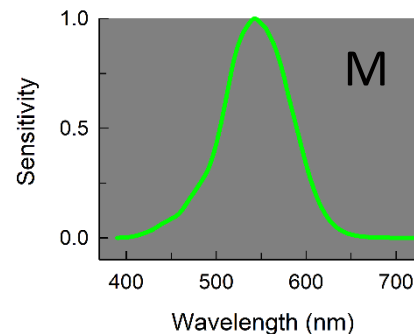
X



=

All 13 should produce the *same* S-cone excitation

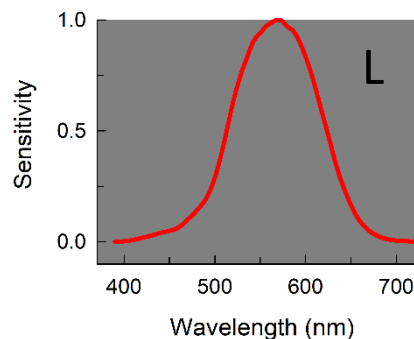
X



=

All 13 should produce the *same* M-cone excitation

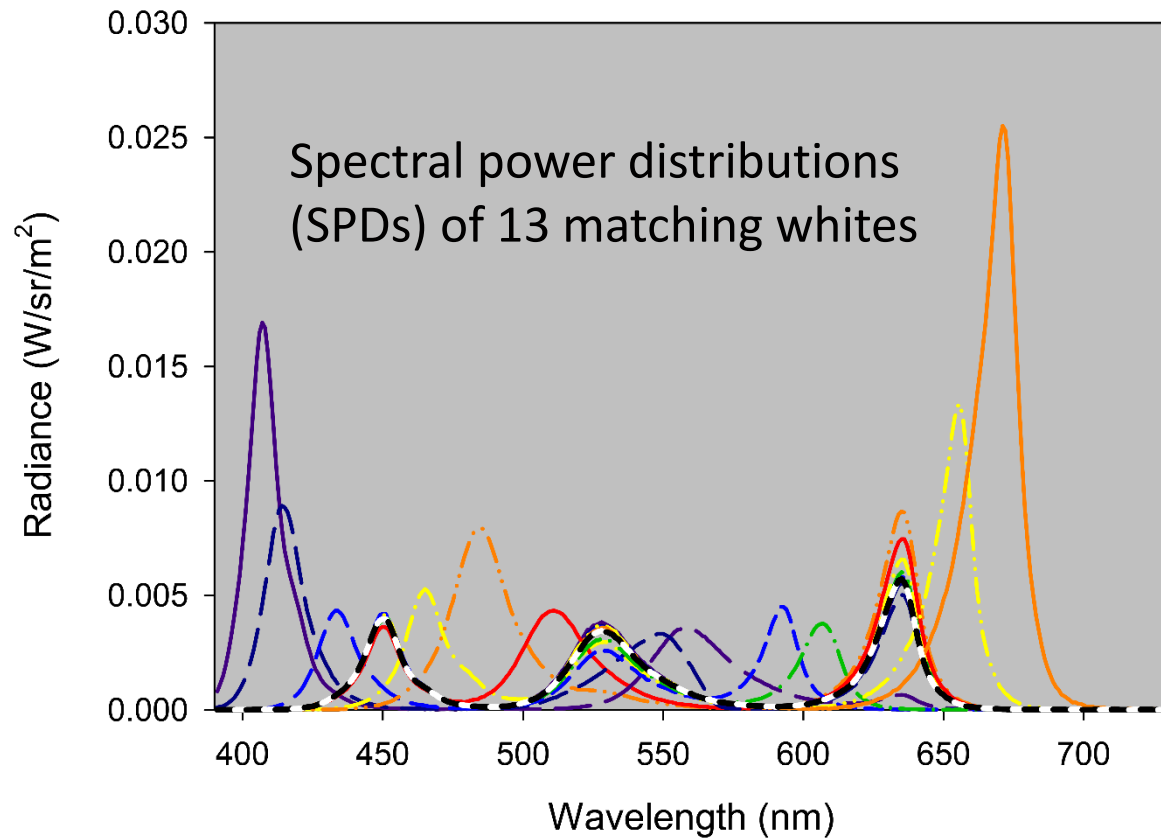
X



=

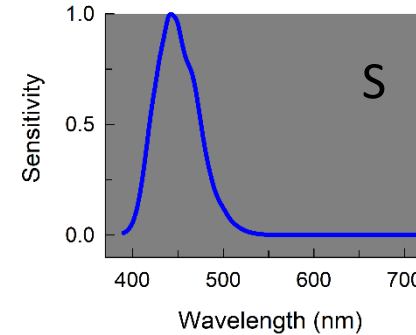
All 13 should produce the *same* L-cone excitation

# Colour matching analysis



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

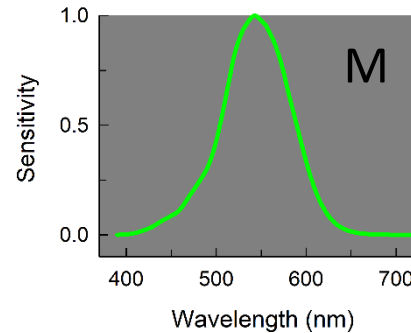
X



=

All 13 should produce the *same* S-cone excitation

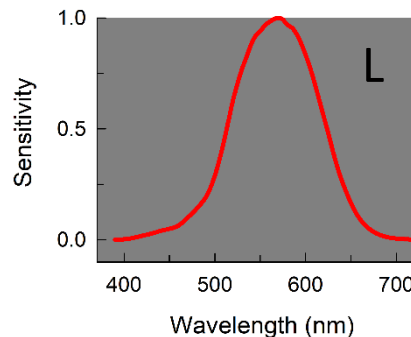
X



=

All 13 should produce the *same* M-cone excitation

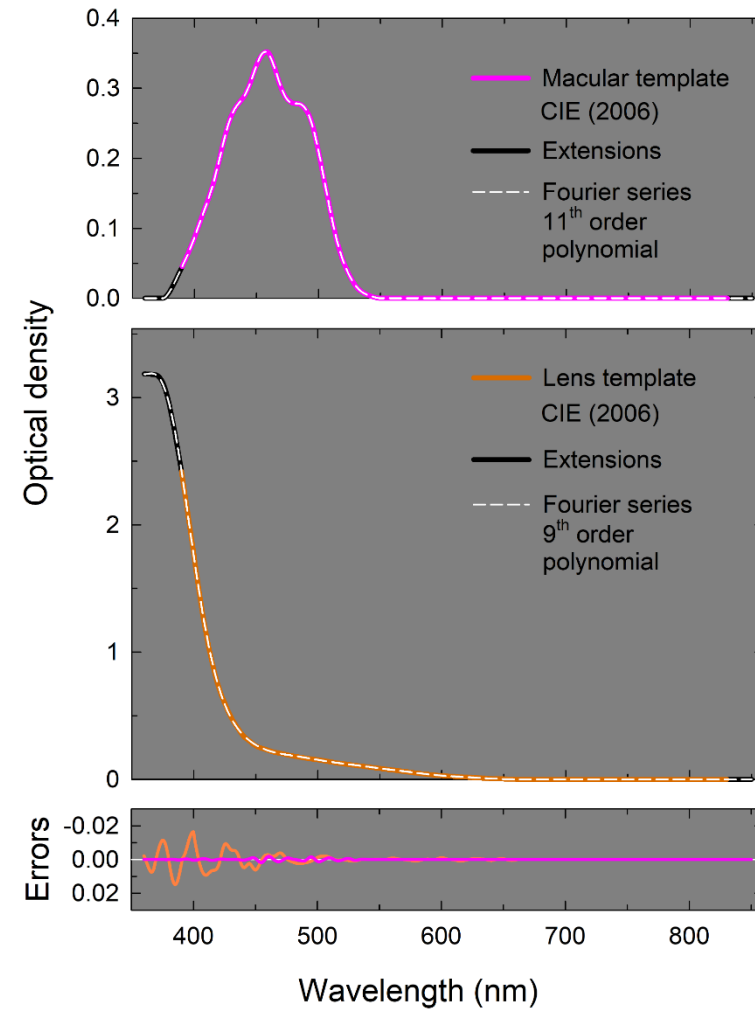
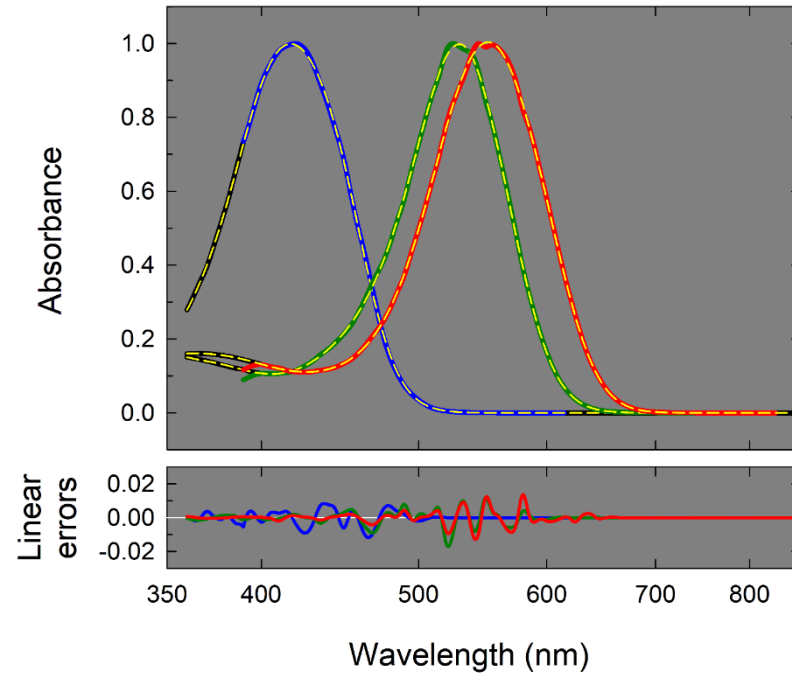
X



=

All 13 should produce the *same* L-cone excitation

We use the continuous template functions for the model fitting...

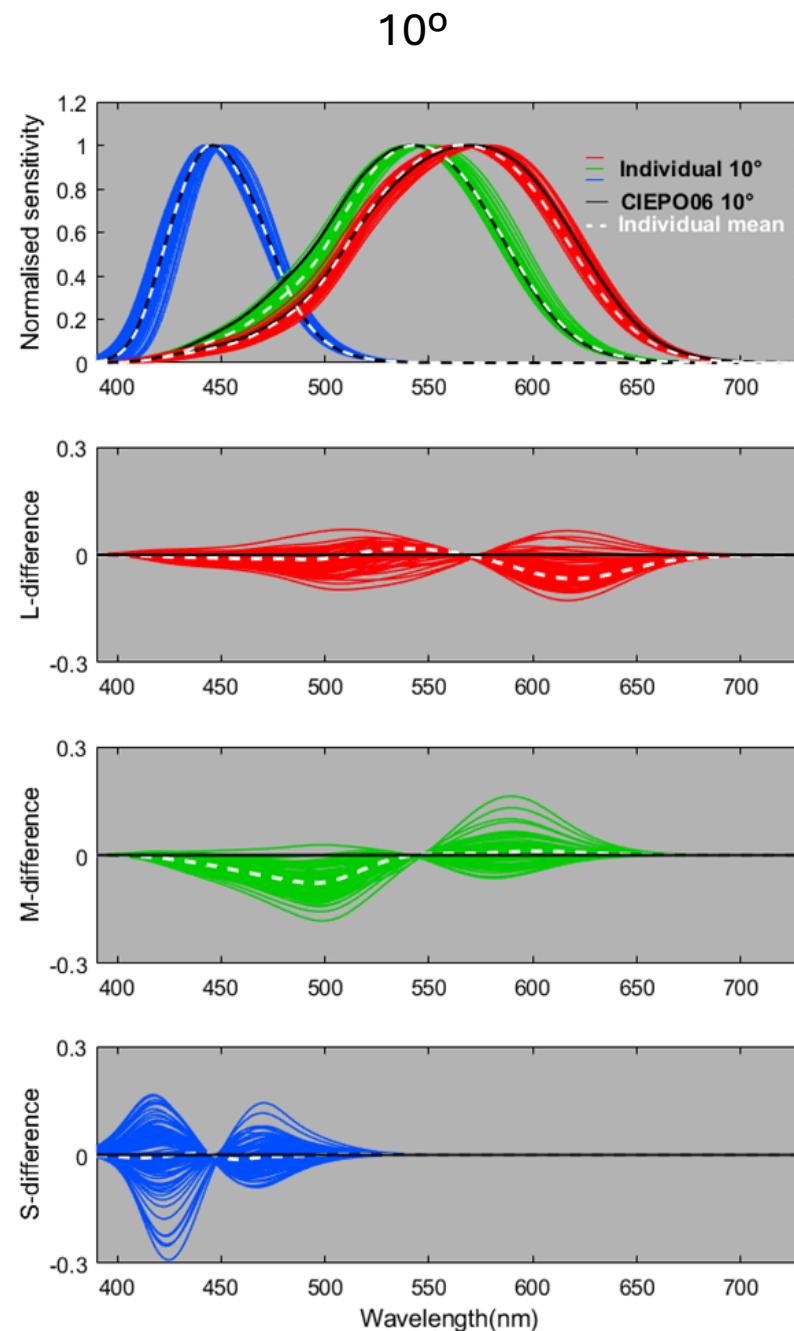
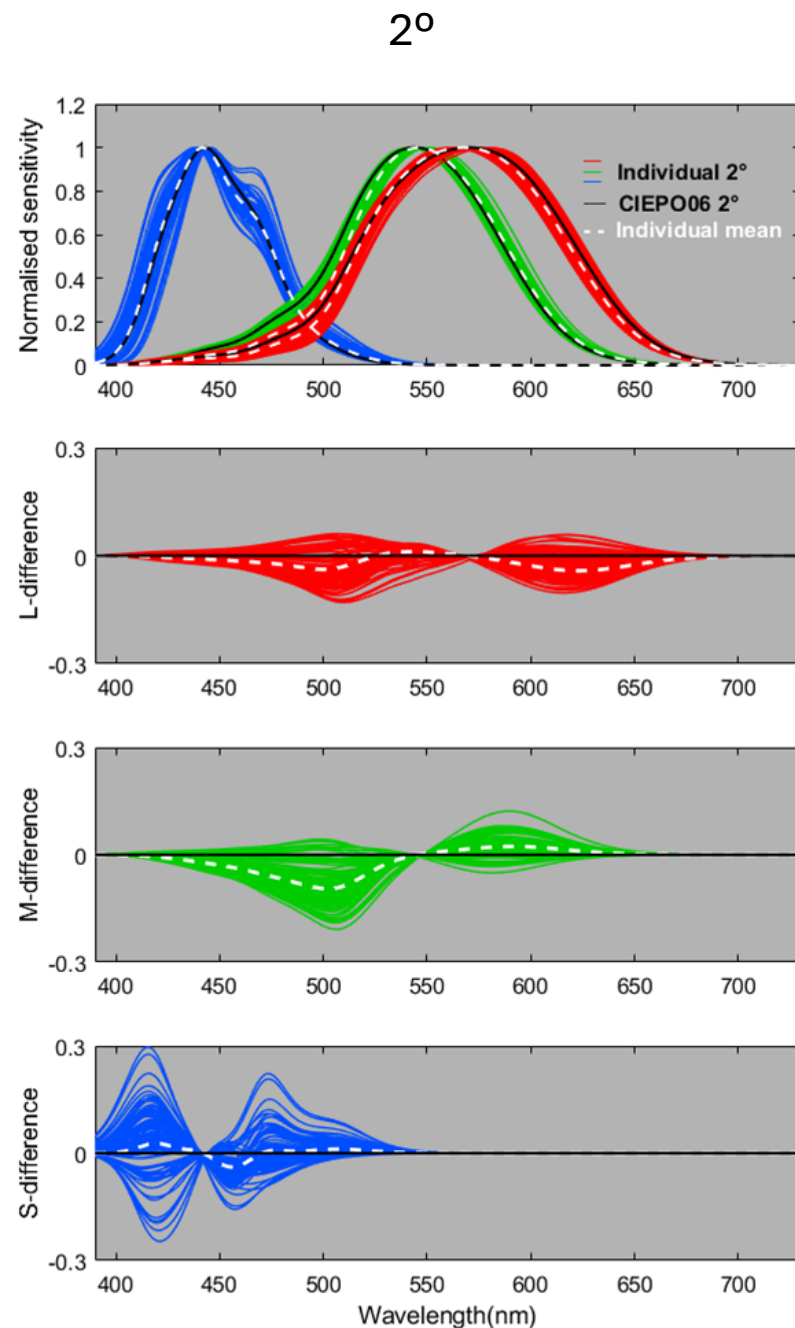


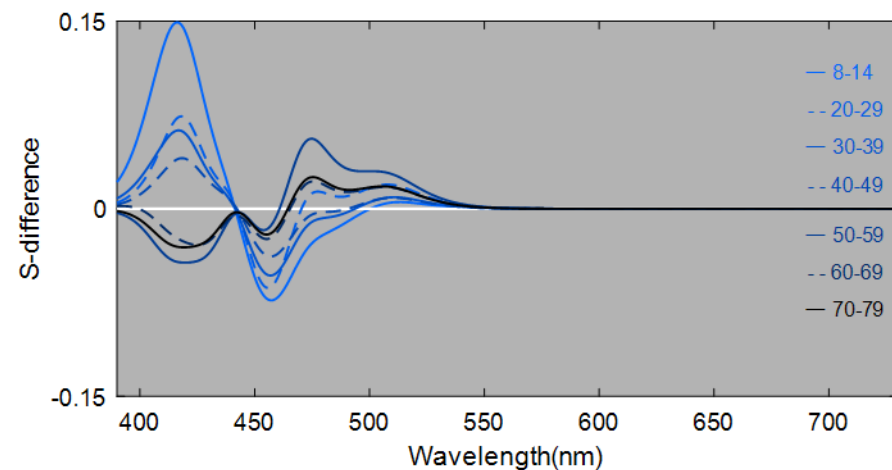
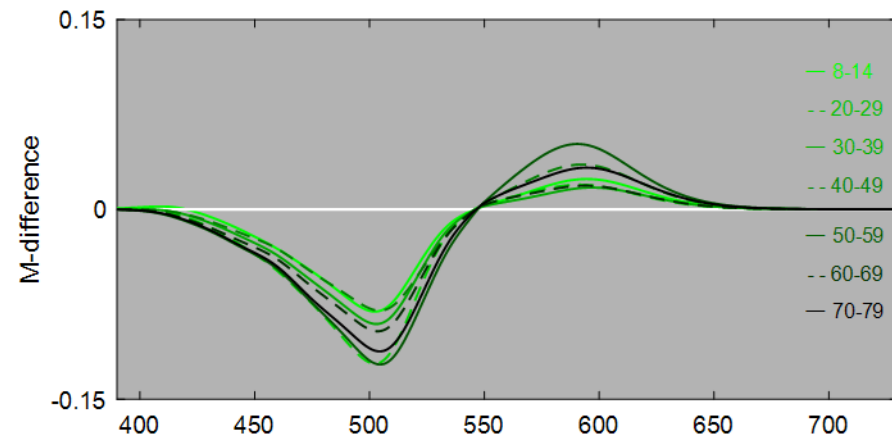
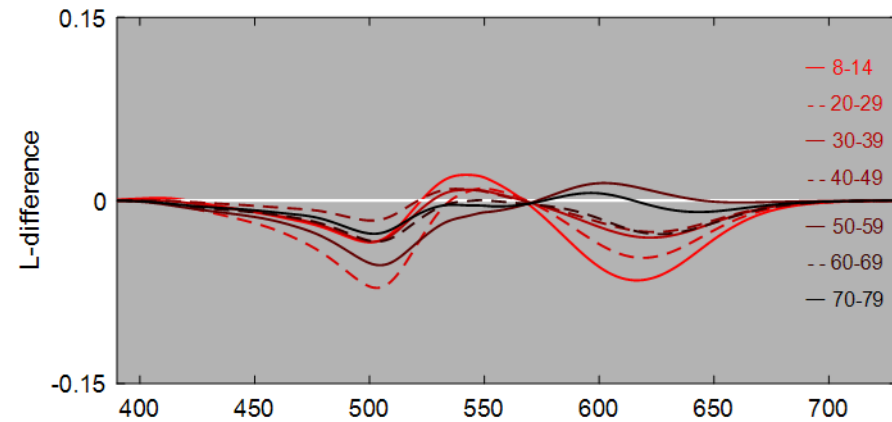


# Base results

100 observers from  
8 to 79 years old.

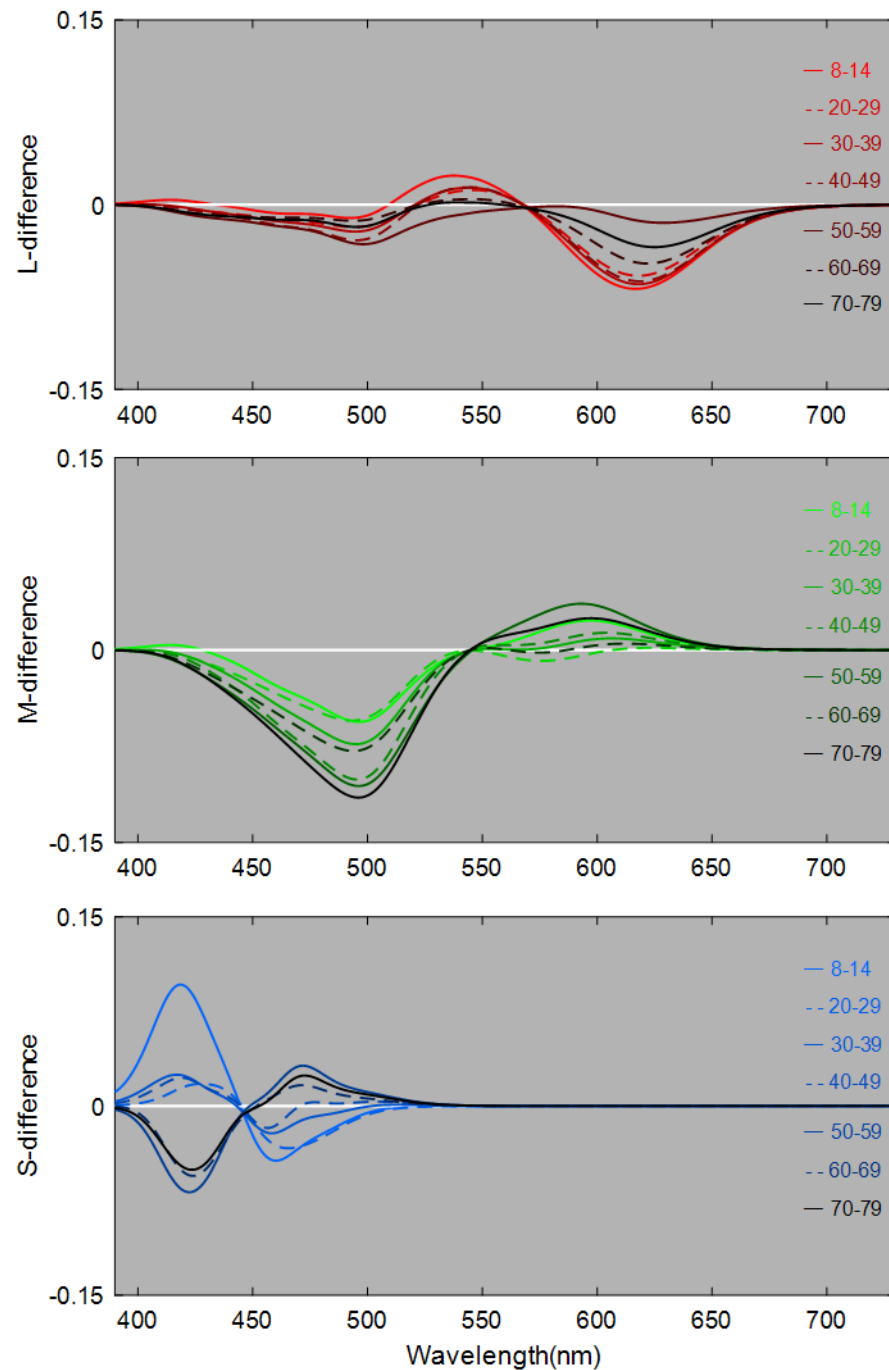
— Colour normal  
(CIE 2006)





## 2° cone spectral sensitivity differences by age

Differences between the observers' 2° mean cone spectral sensitivities and the standard CIEPO06 2° cone spectral sensitivities (solid white line) by age.



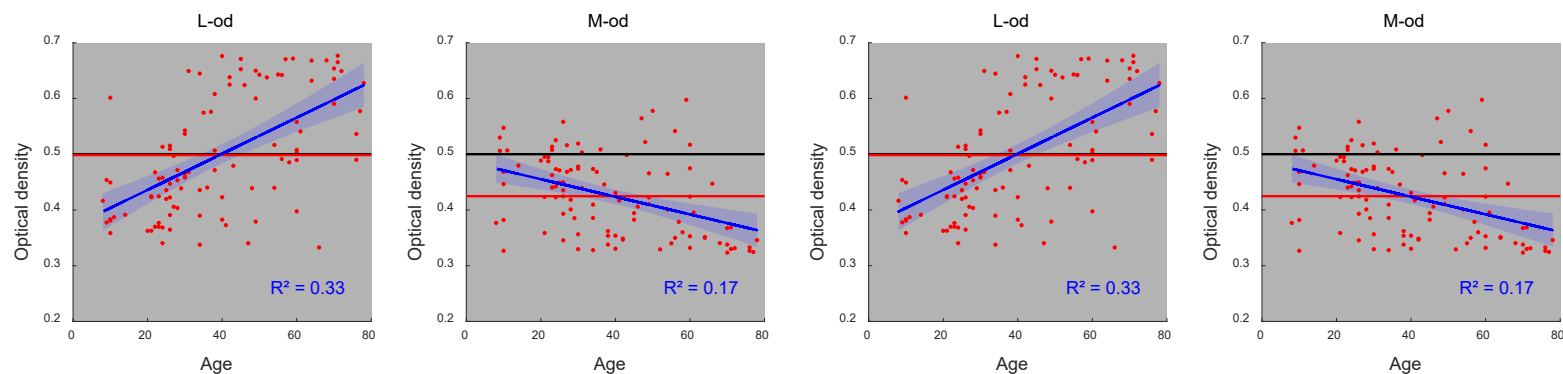
## 10° cone spectral sensitivity differences by age

Differences between the observers' 10° mean cone spectral sensitivities and the standard CIEPO06 10° cone spectral sensitivities (solid white line) by age.

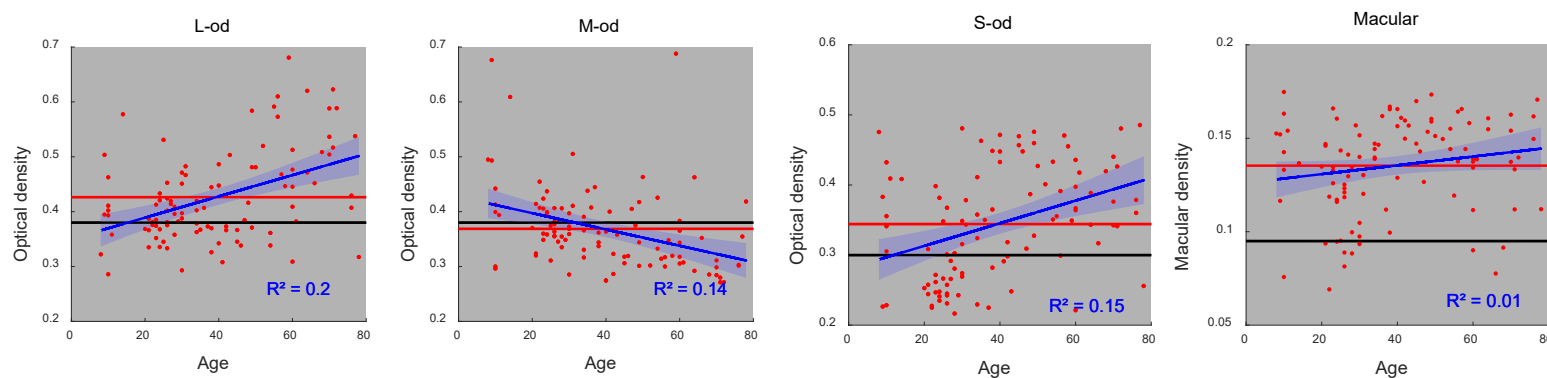
# Best-fitting parameters

2 and 10° match parameters

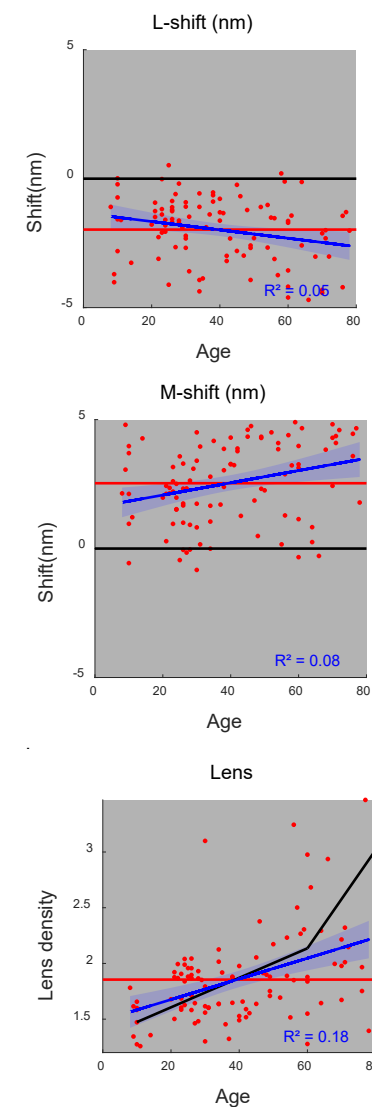
## 2° match parameters



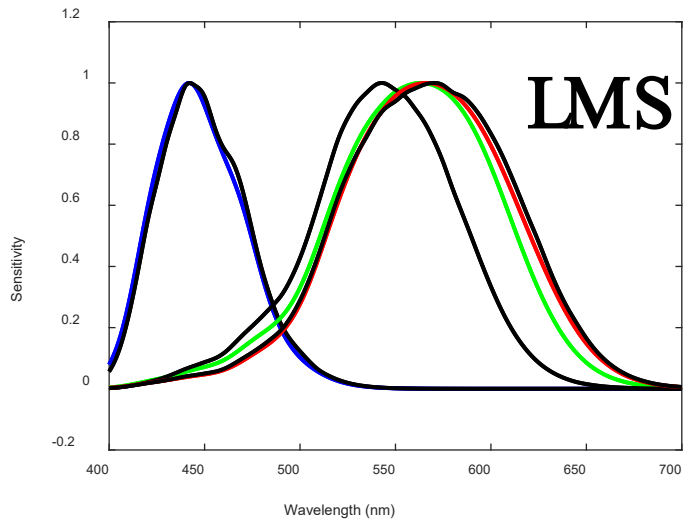
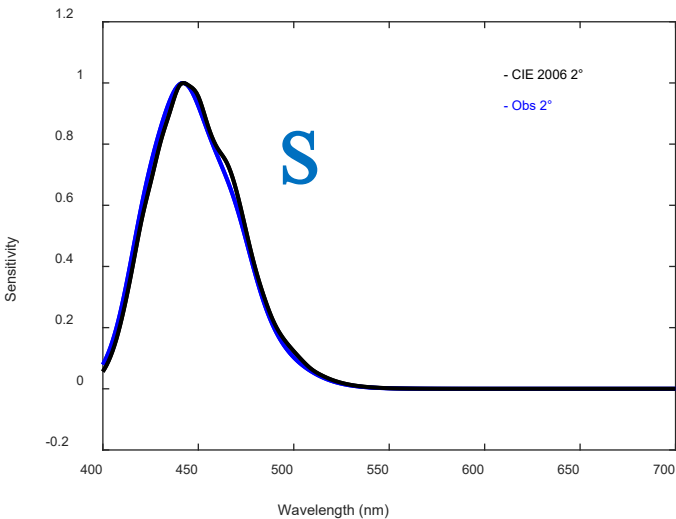
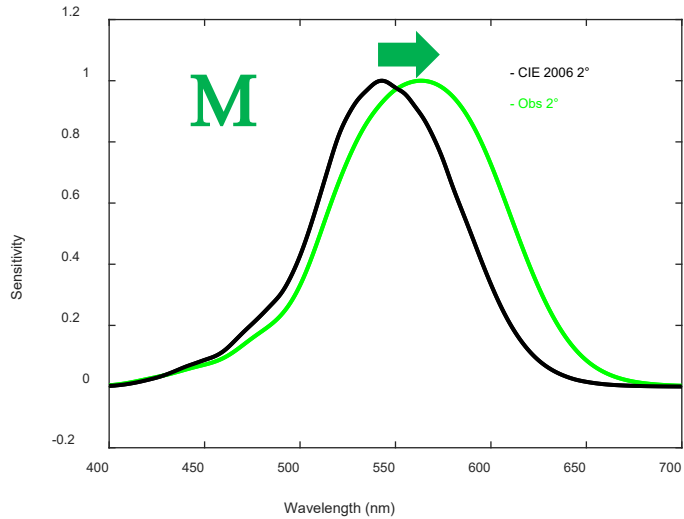
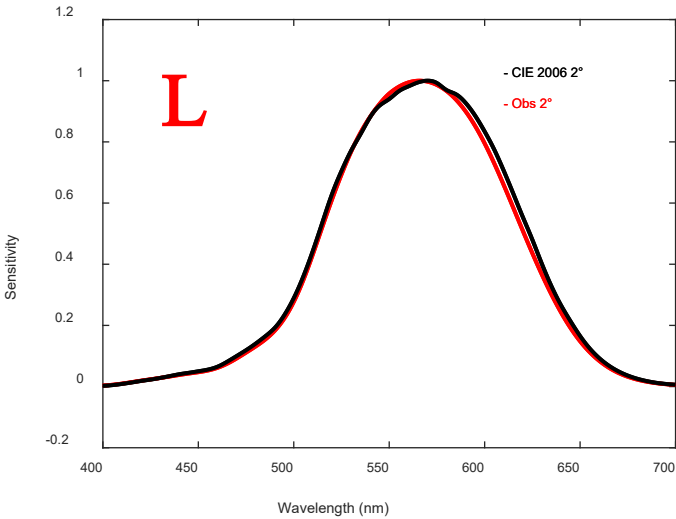
## 10° match parameters



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# Deuteranomalous observer

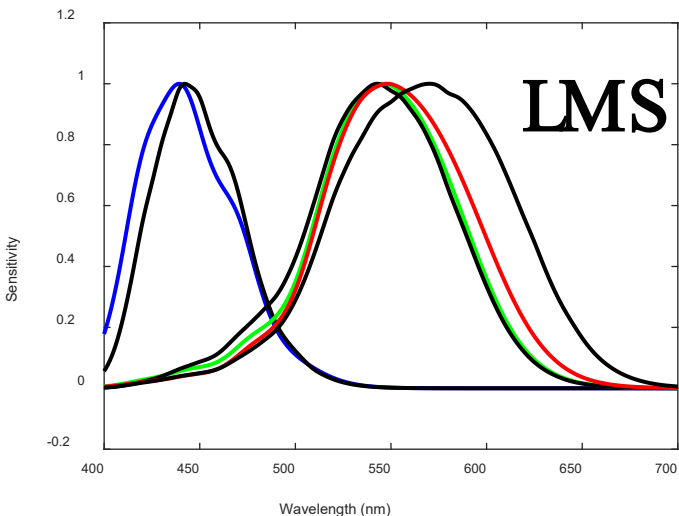
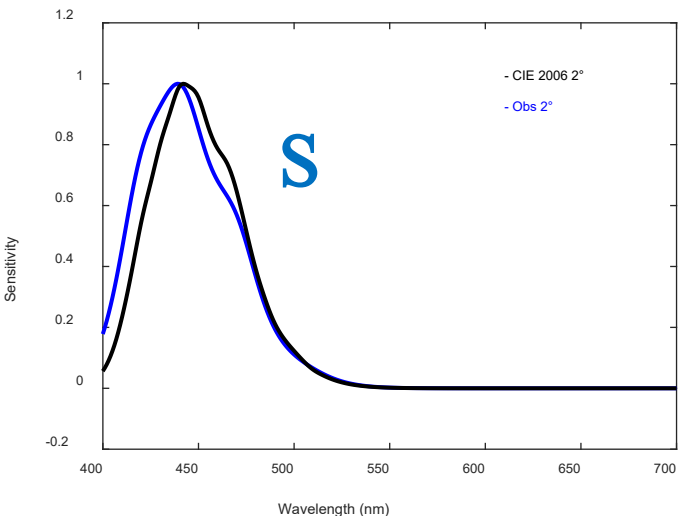
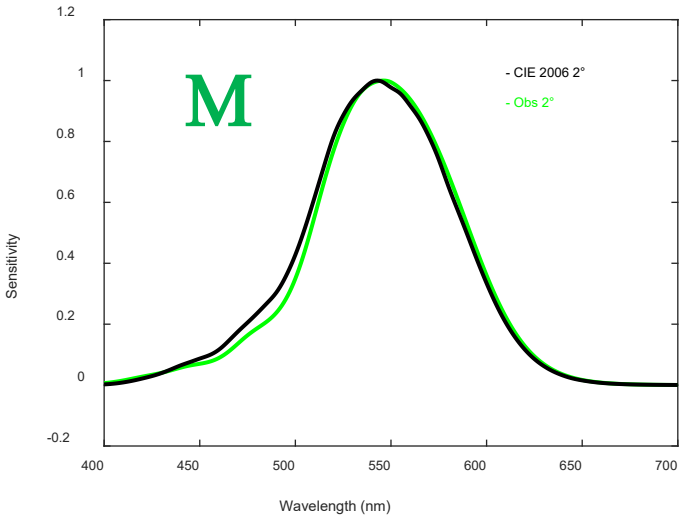
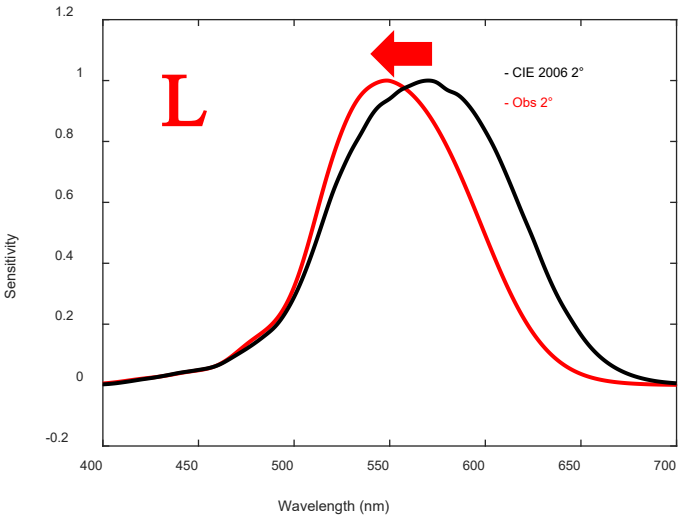


Red-green colour  
vision deficiency

— Colour normal  
(CIE 2006)

	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

# Protanomalous observer



Red-green colour vision deficiency

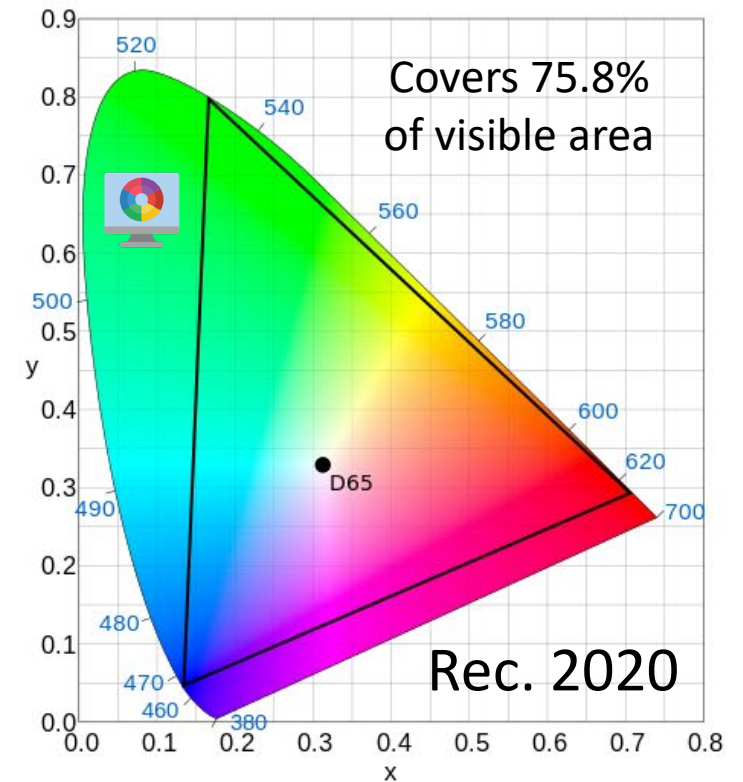
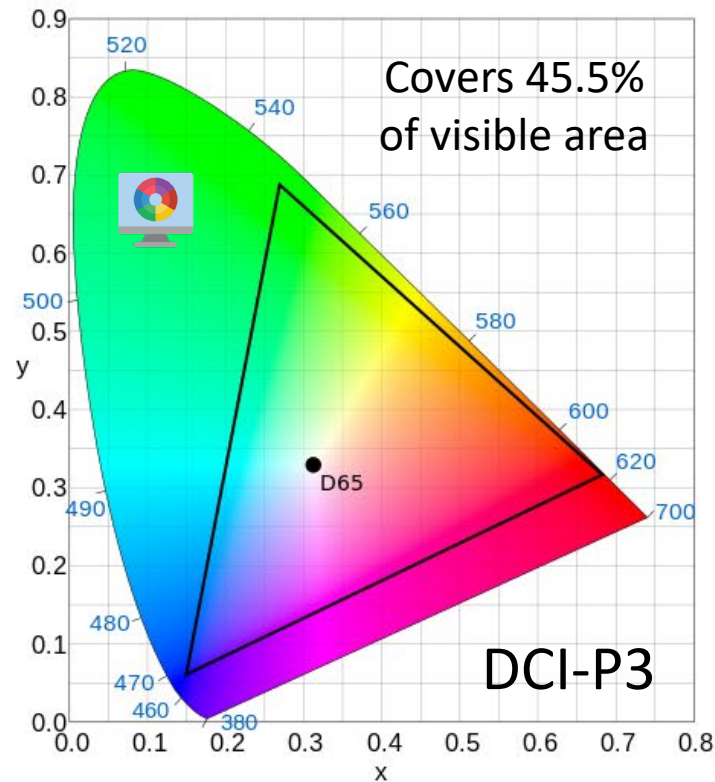
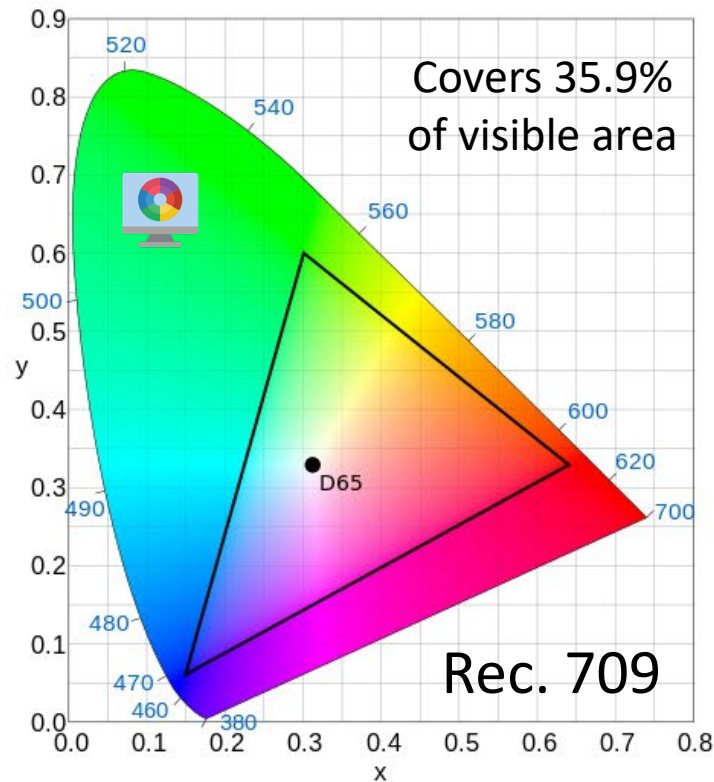
— Colour normal (CIE 2006)

	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

# Displays

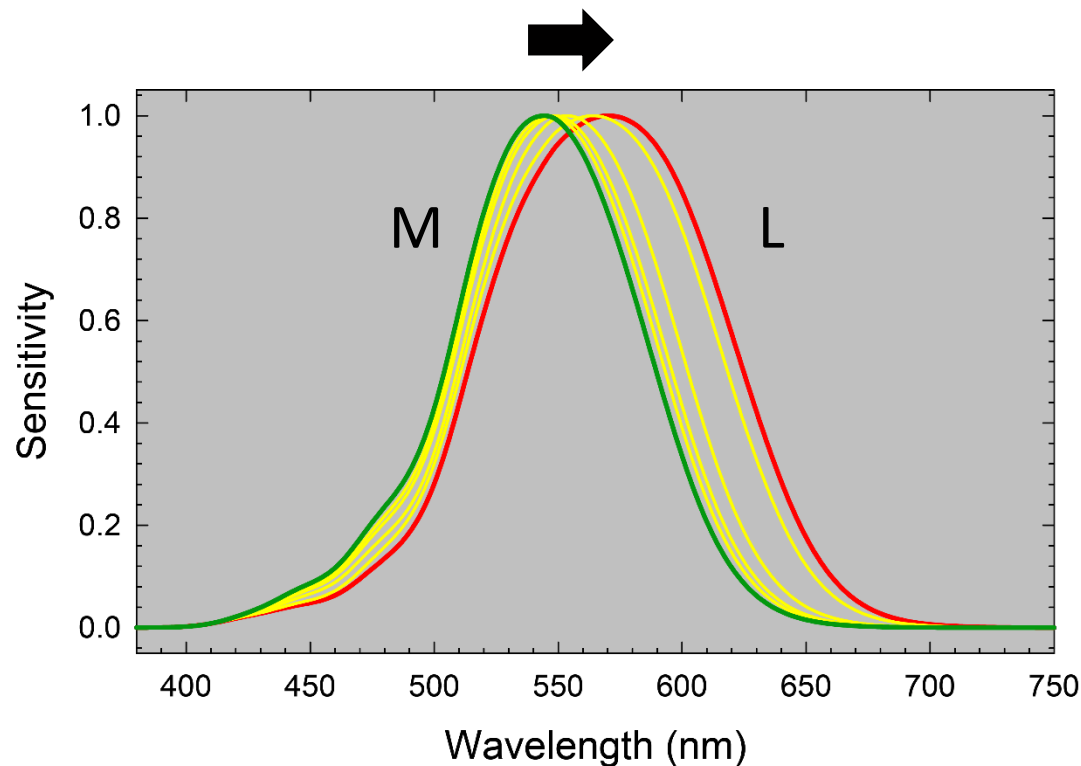


Using this method, we can produce individualized colour matching functions and thus produce consistent colours with different displays.

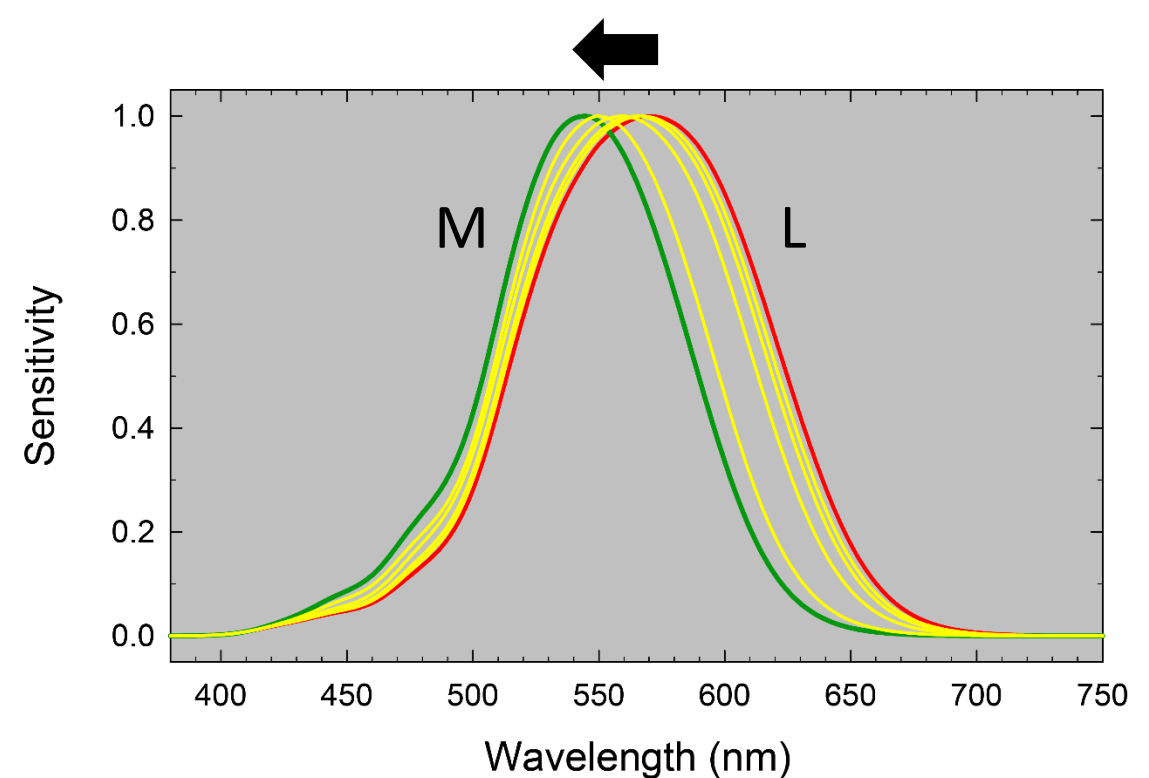


If you don't have correct for individual differences, spectral shifts of the M or L-cones can substantially change the appearance of display devices with narrow band primaries and large colour gamuts.

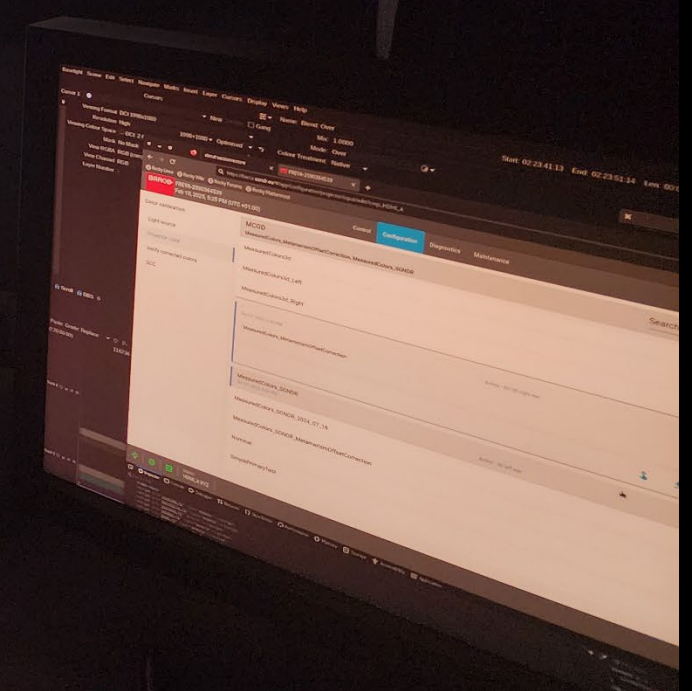
M-cone functions can shift towards L.



L-cone functions can shift towards M.







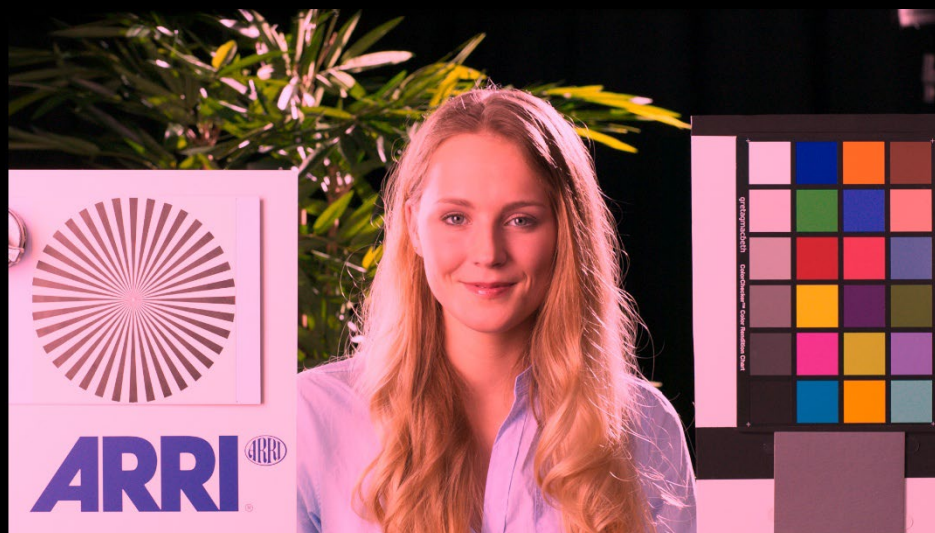
# Deuteranomaly prediction: Xenon to RGB laser projector



Andy Rider

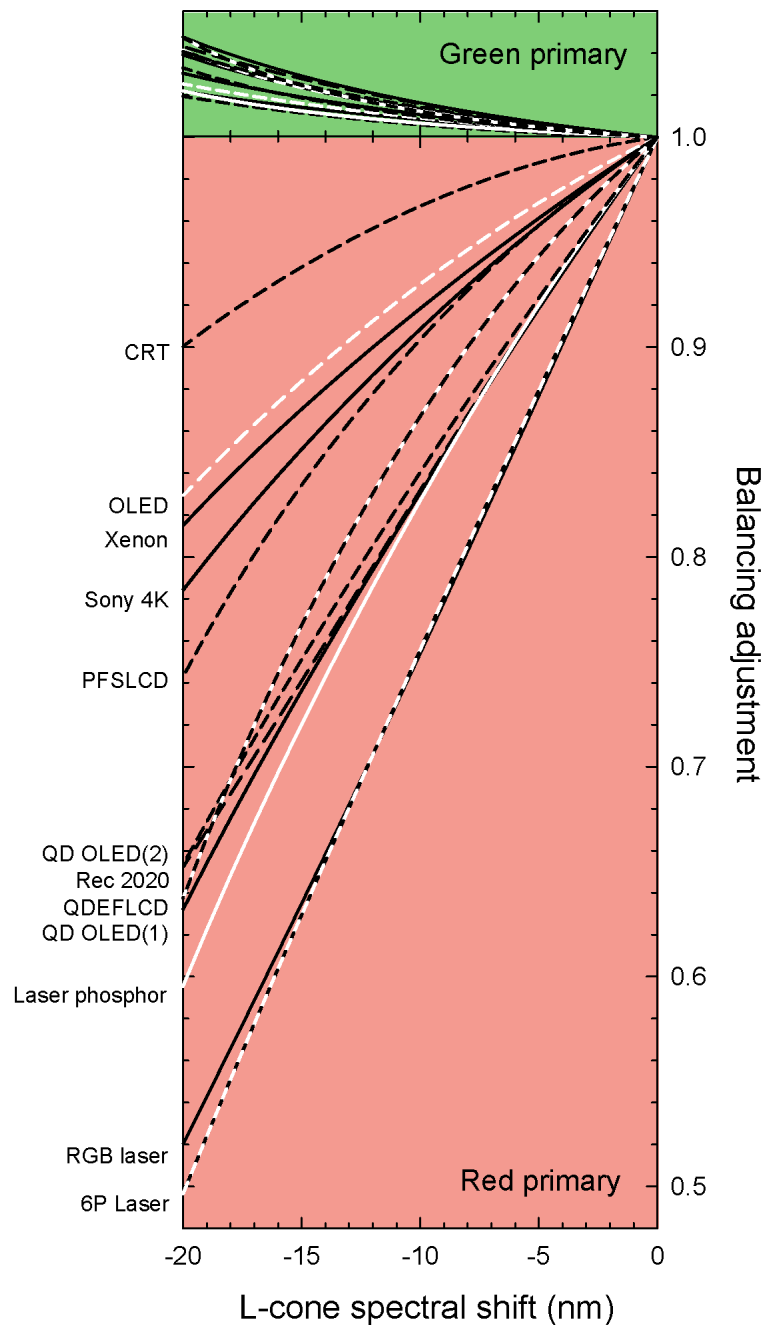


R +42%  
G -14%



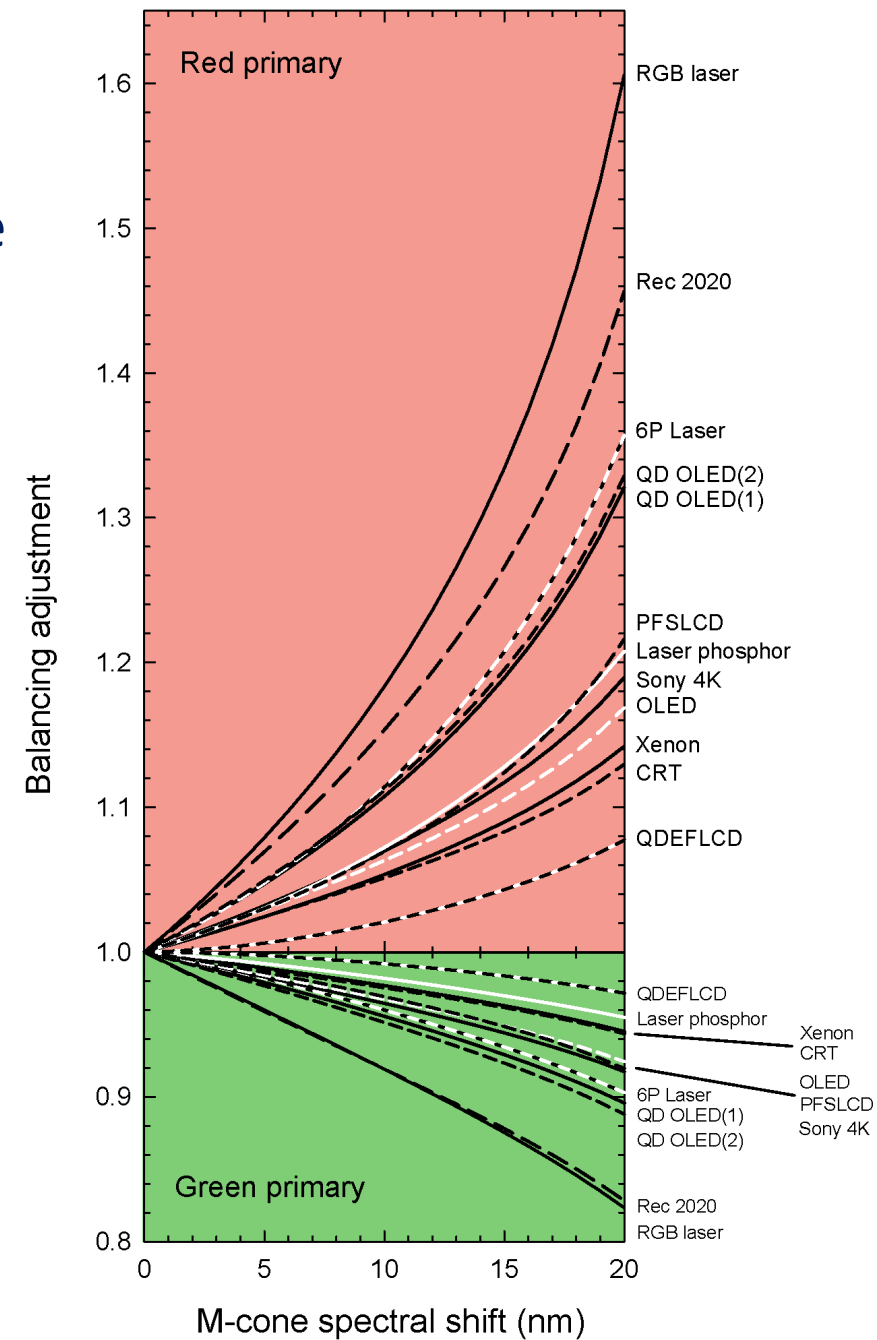
Bigger colour gamut



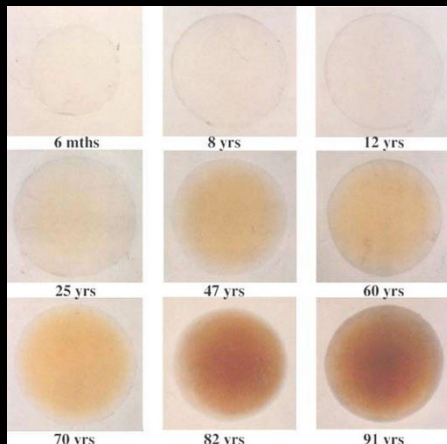


All displays show some level of discrepancy for anomalous observers, but some are worse than others

In general, wider colour gamut displays have worse the discrepancy, but not perfect correlation

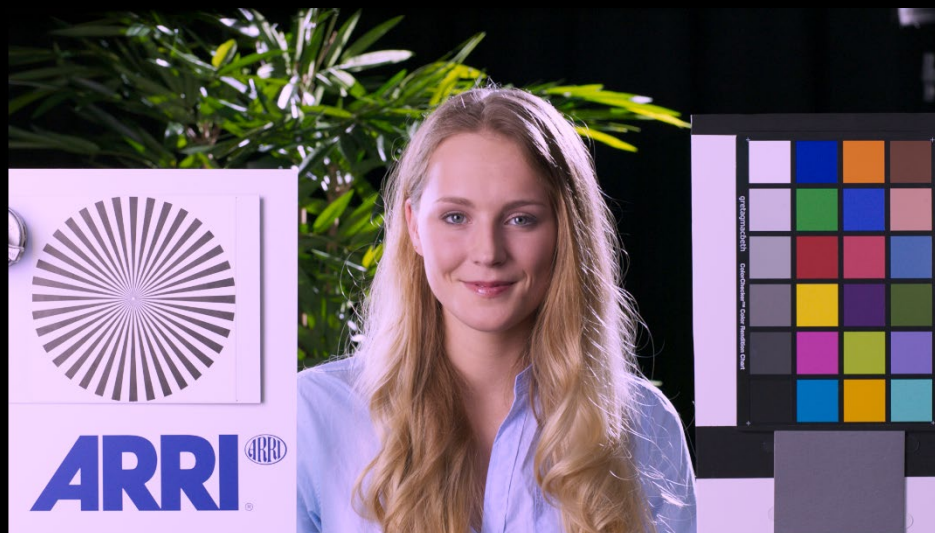


# Young to old prediction: Xenon to Rec. 2020



Lerman

R +6%  
G -6%  
B +18%



Bigger colour gamut

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



CVRL database

<http://www.cvrl.org>