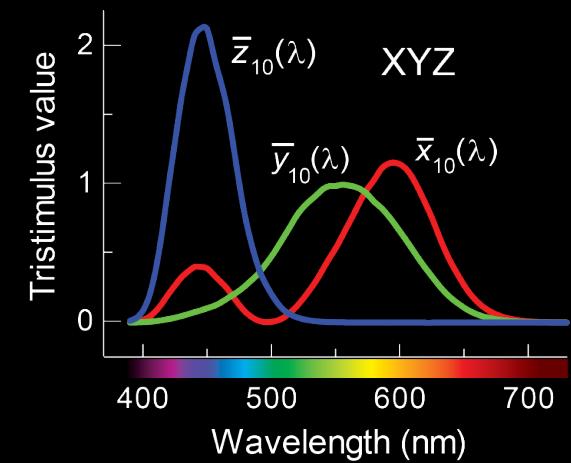
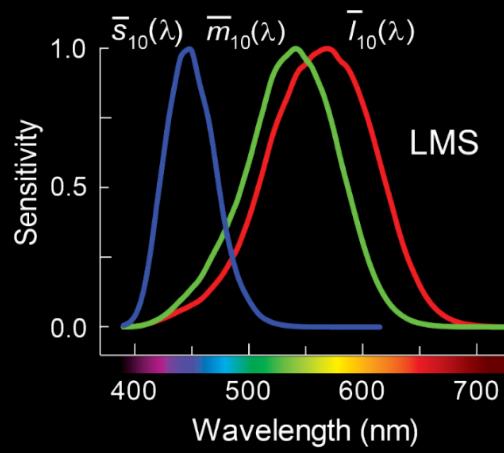


Cone spectral sensitivities, colour matching functions and individual differences

Andrew Stockman

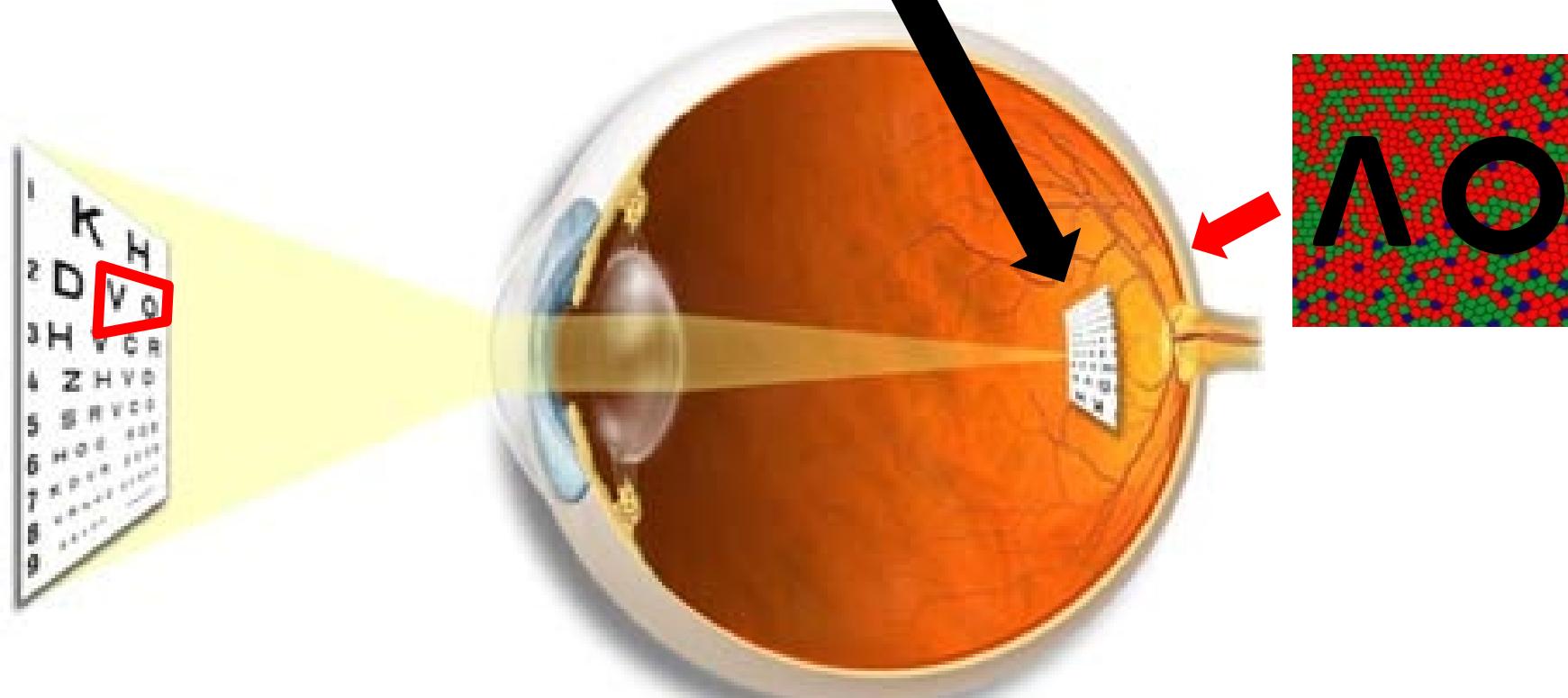


1. CONES AND TRICHROMACY



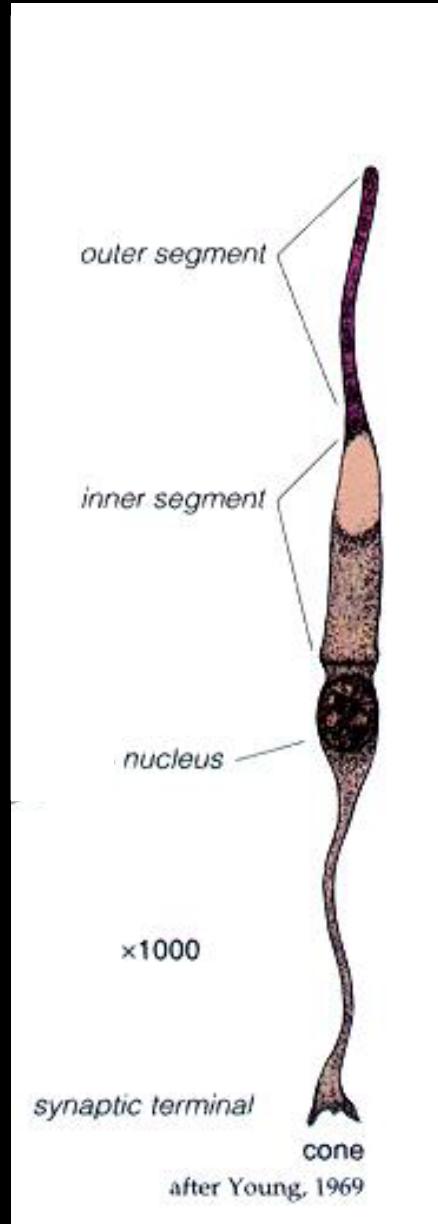
Human colour vision

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

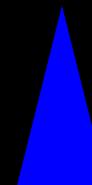
- Daytime, achromatic *and* chromatic vision
- 3 types



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

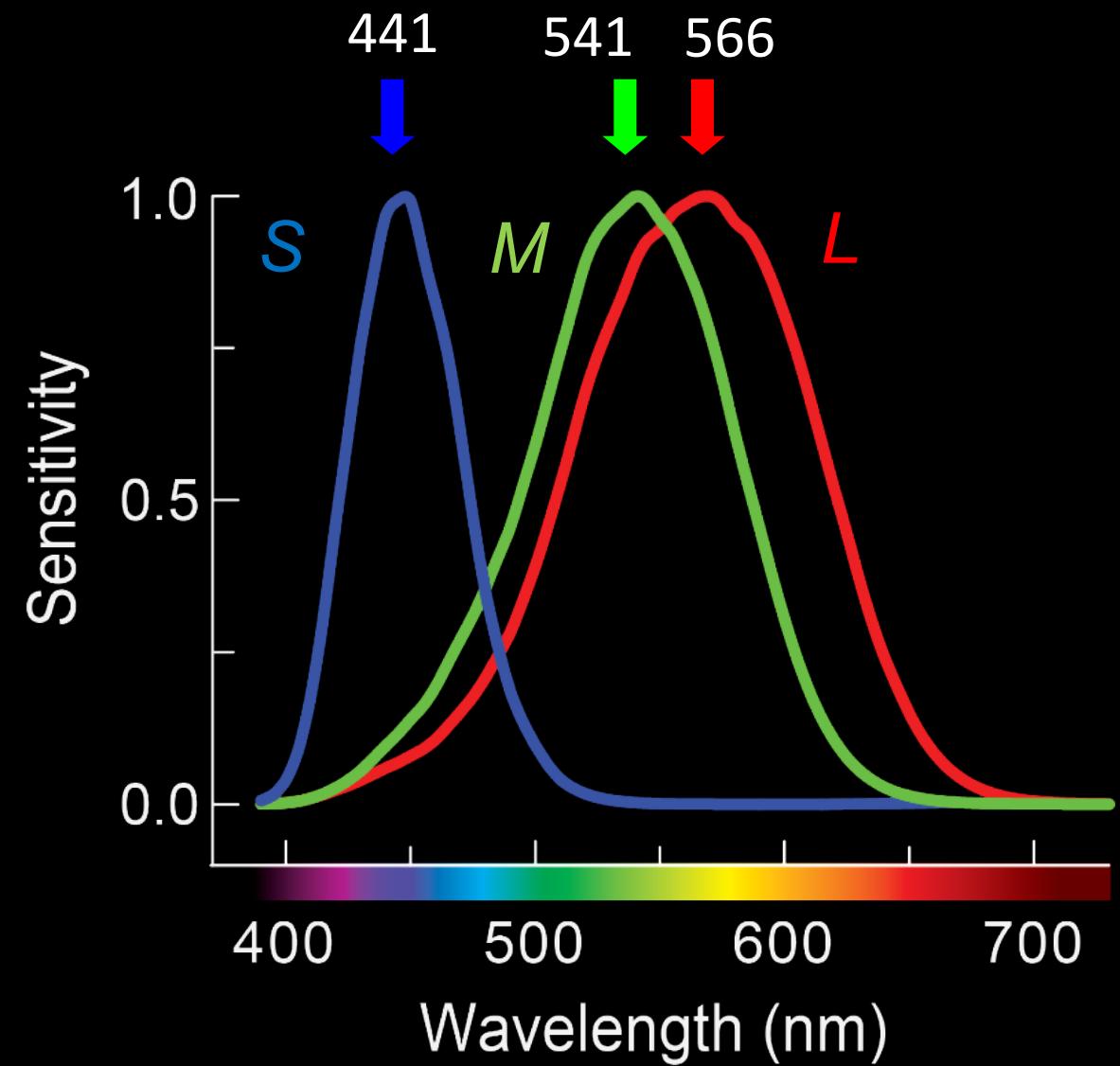
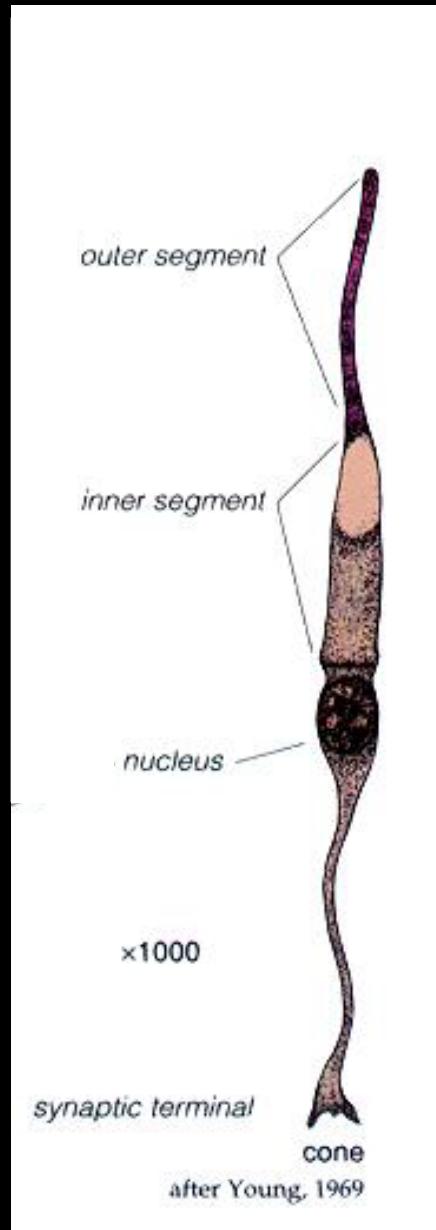


Middle-wavelength-sensitive (M) or
“green” cone



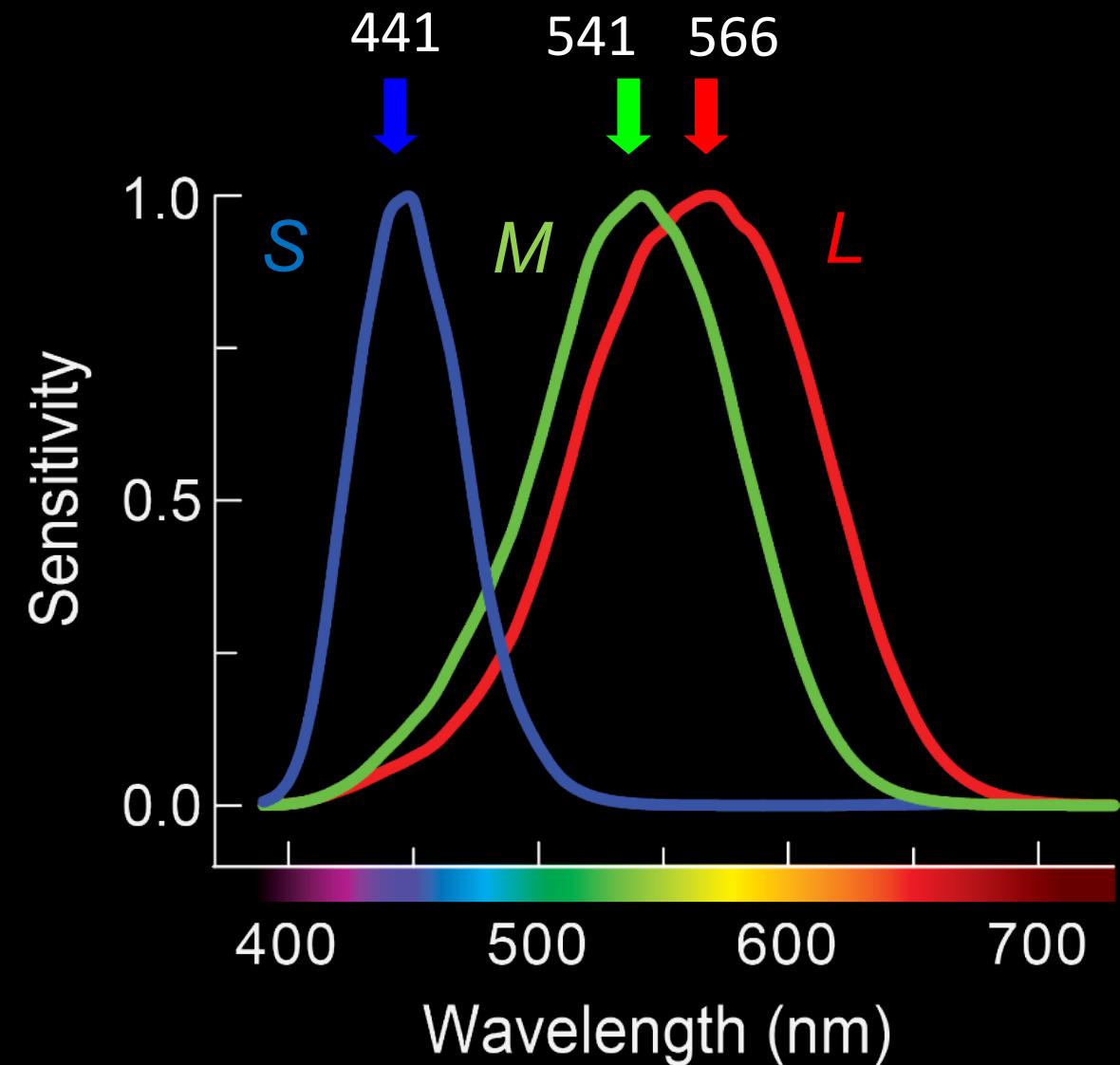
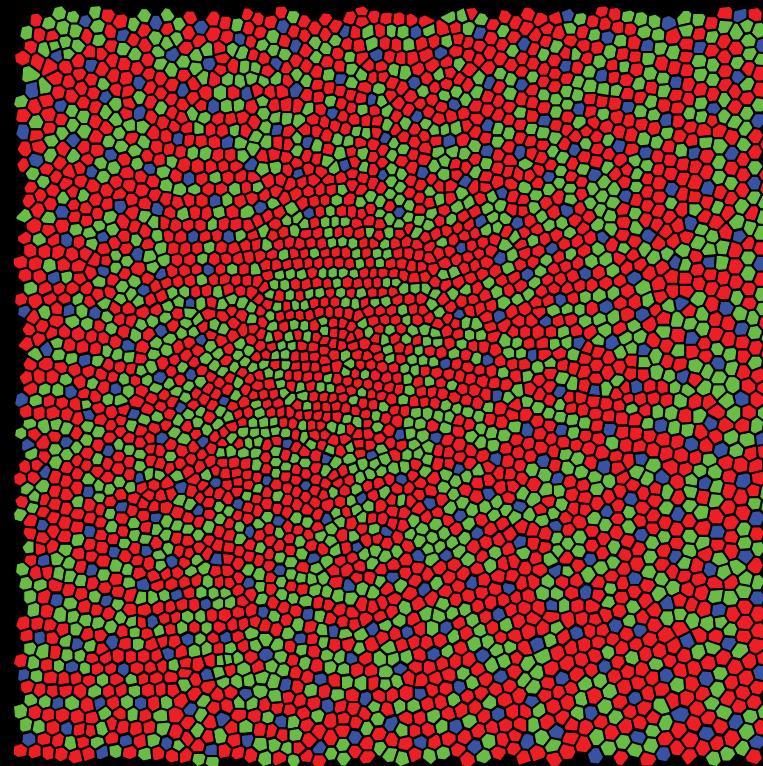
Short-wavelength-sensitive (S) or
“blue” cone

Human cone (sensor) spectral sensitivities



Human cone (sensor) spectral sensitivities

Human foveal sensor array

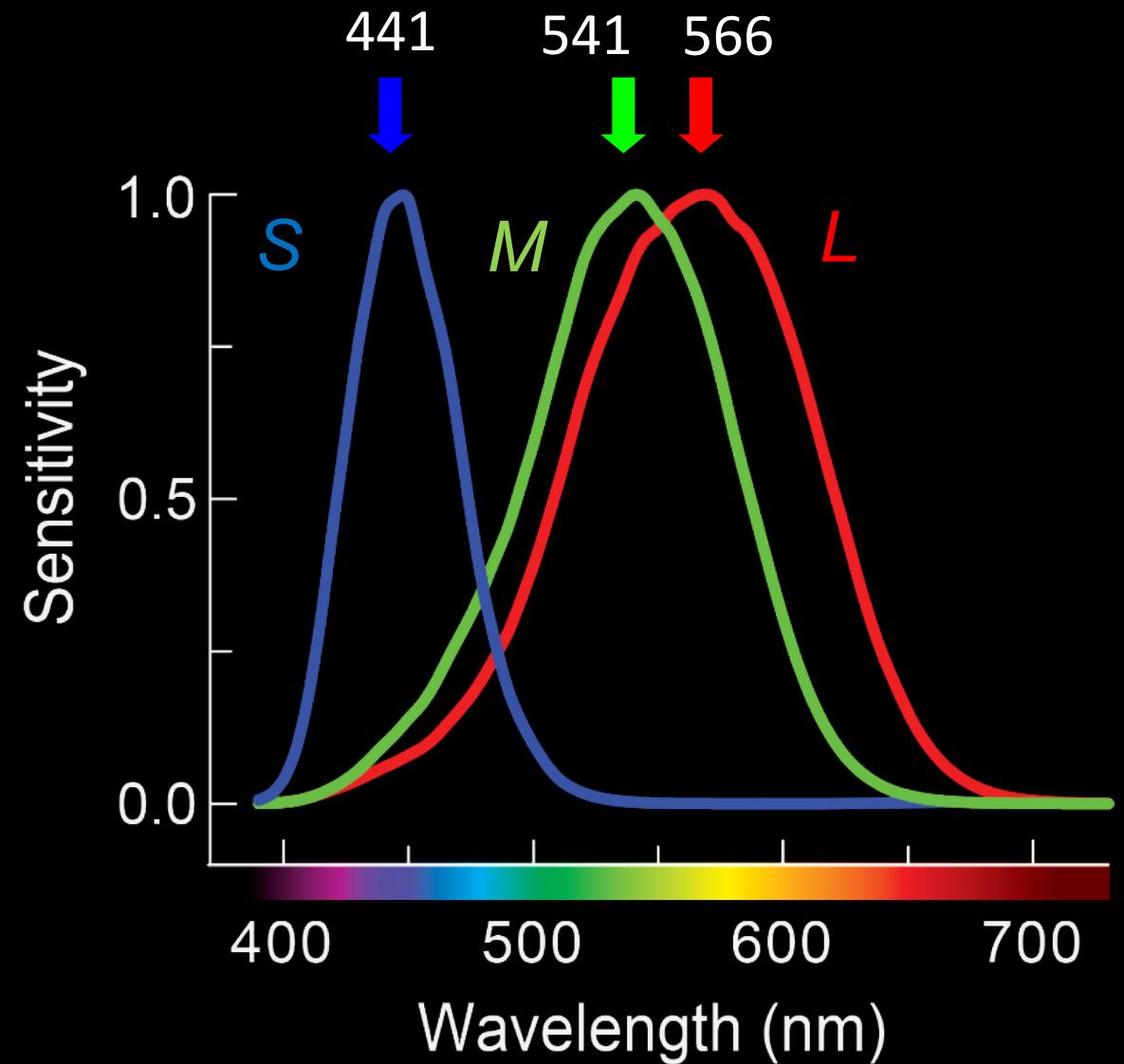


Trichromacy

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.

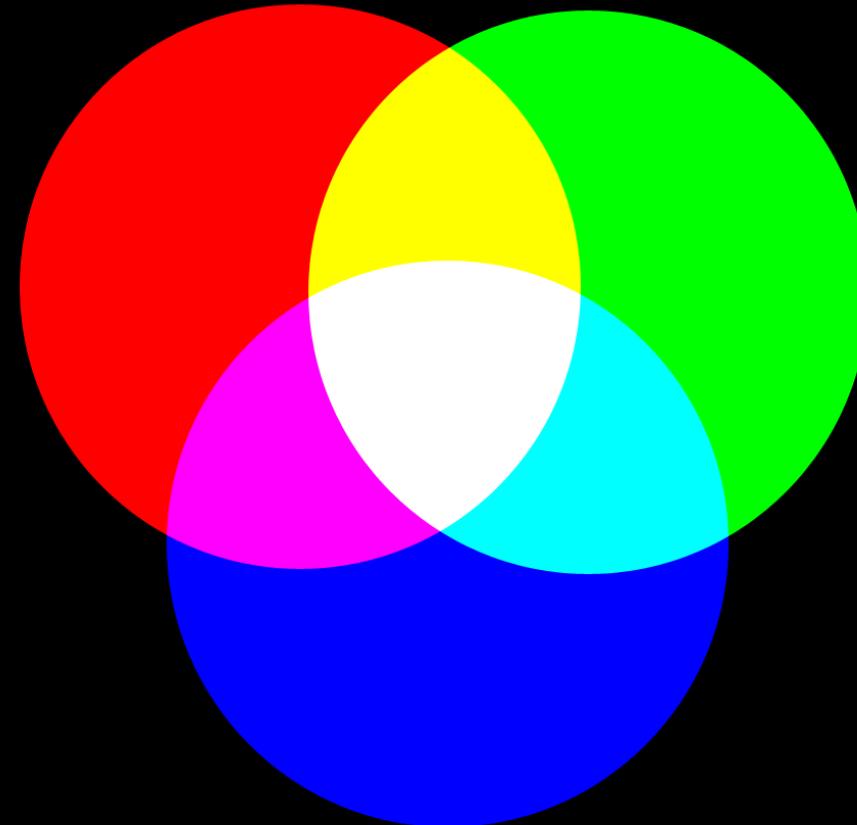
Human colour vision is trichromatic



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).

Human colour vision is trichromatic



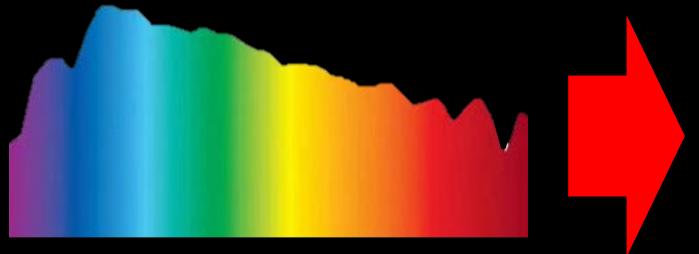
Trichromacy means that colour vision at the input to the visual system is simple, since you can match any colour in terms of just 3 primary colours (e.g., RGB).

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

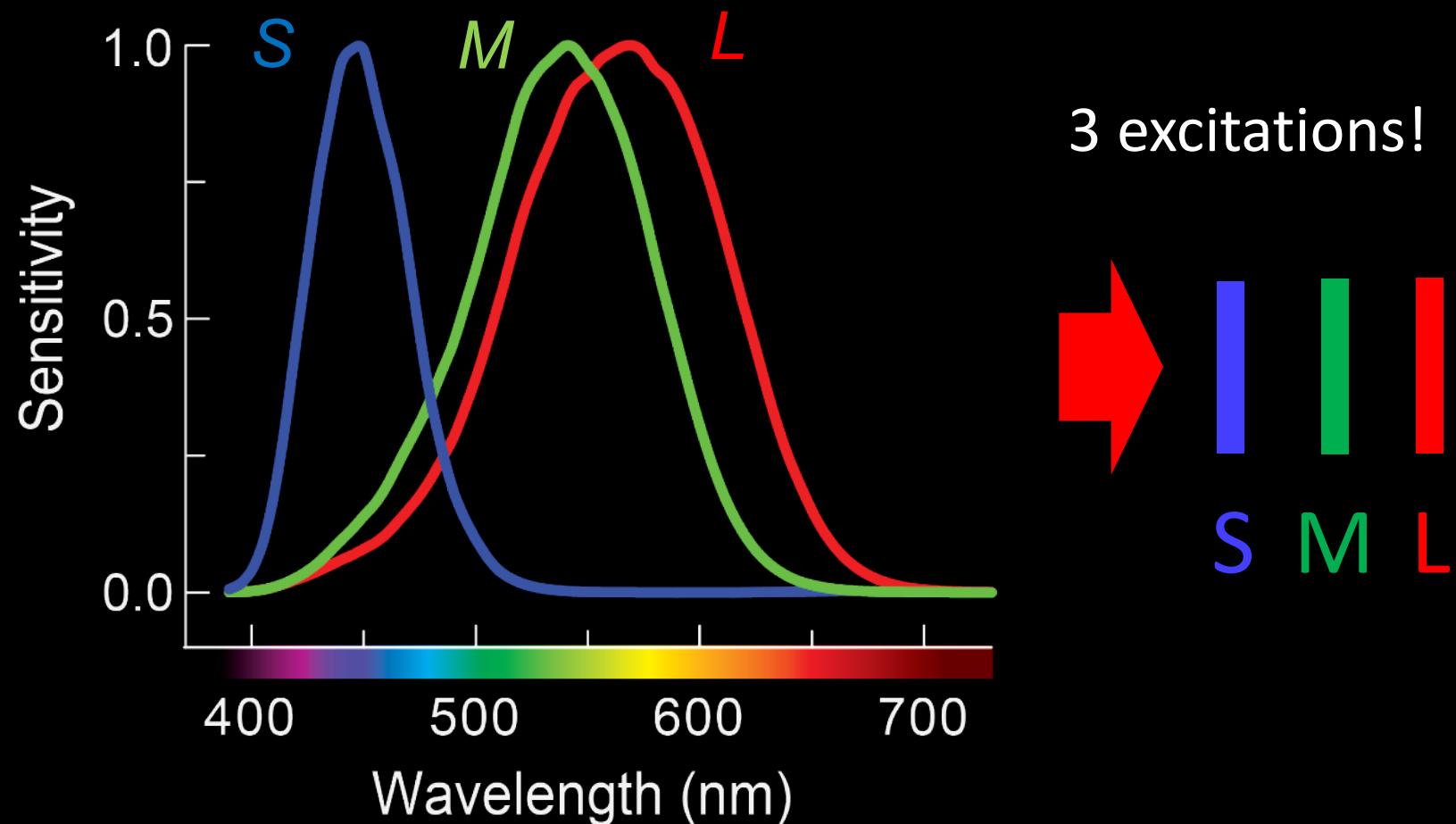
Trichromacy

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

Continuous Spectral Power Distribution

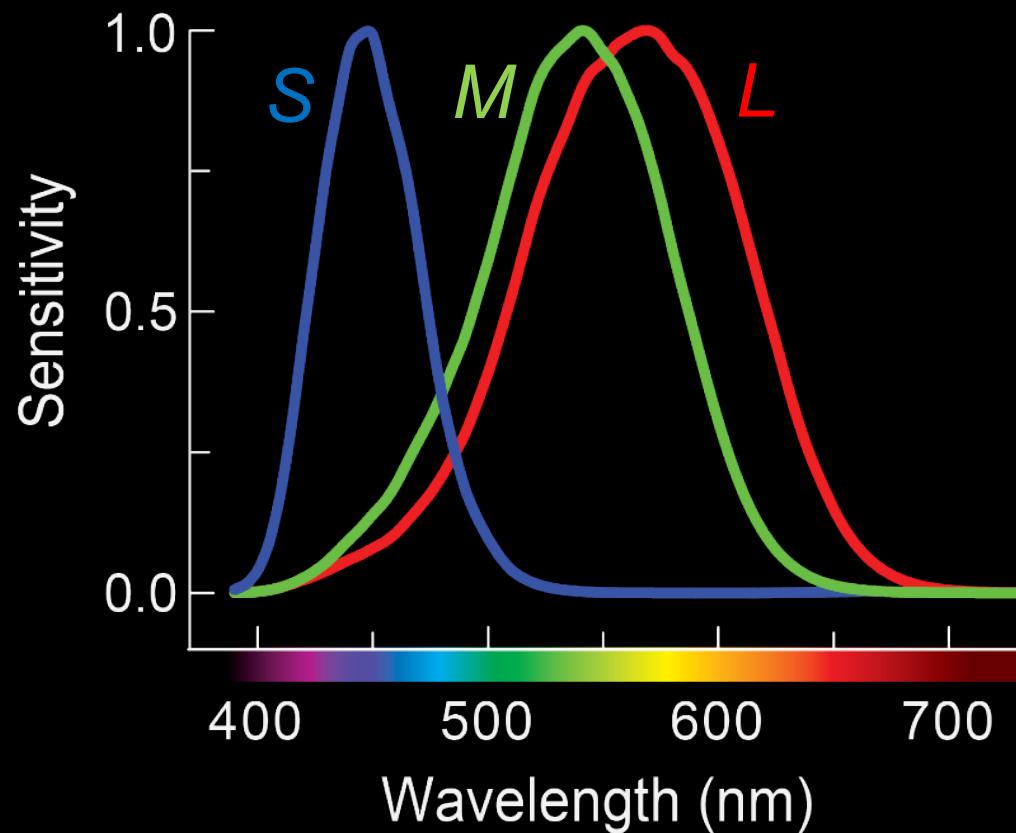


Wavelength

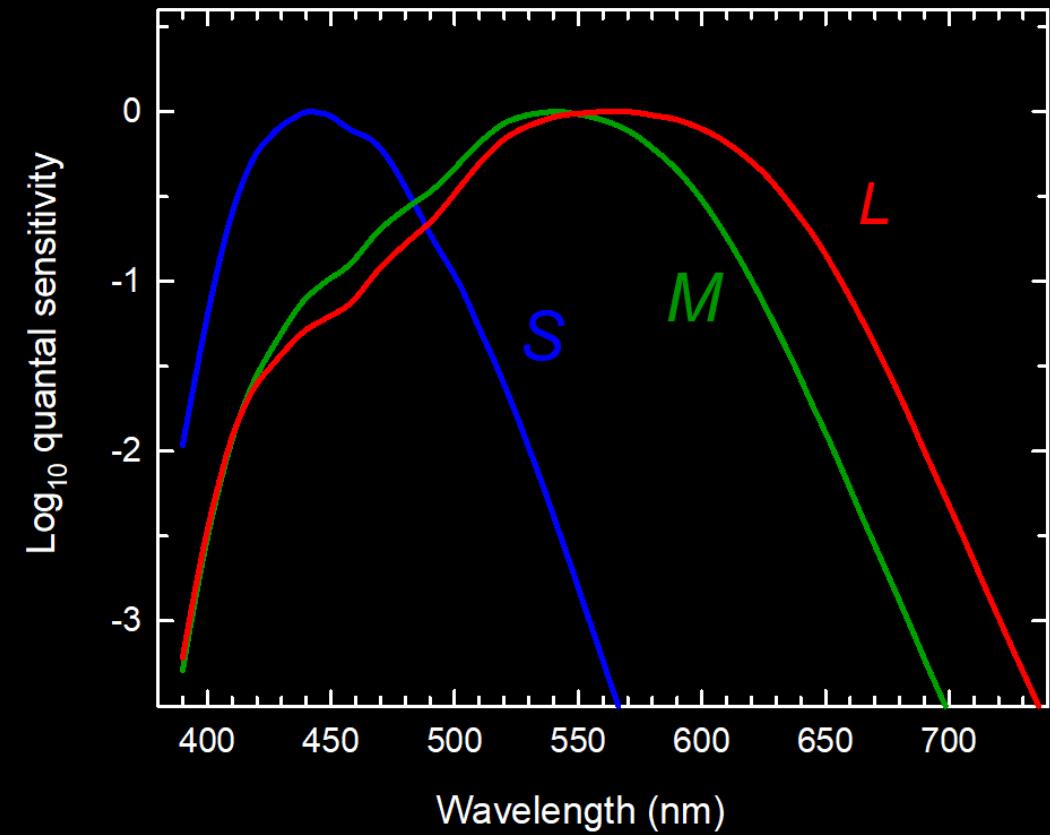


I'll be showing linear and logarithmic versions of the cone spectral sensitivities:

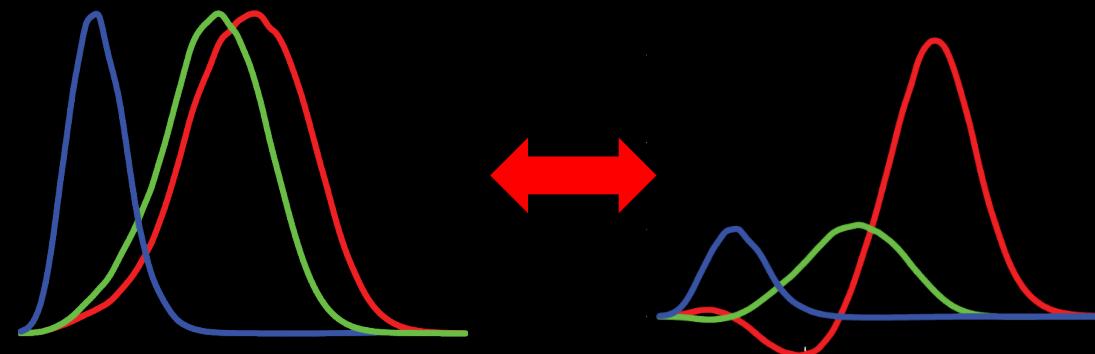
Linear



Logarithmic

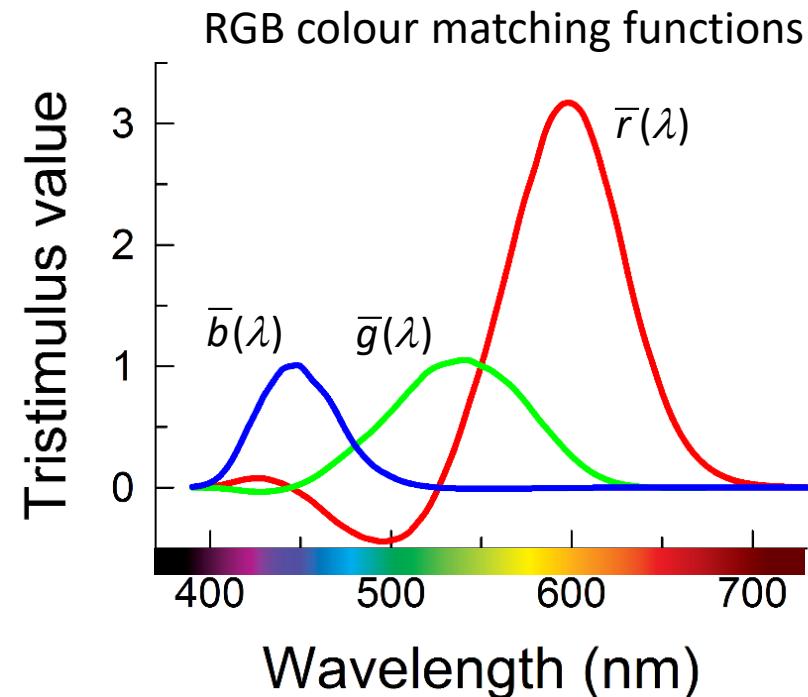
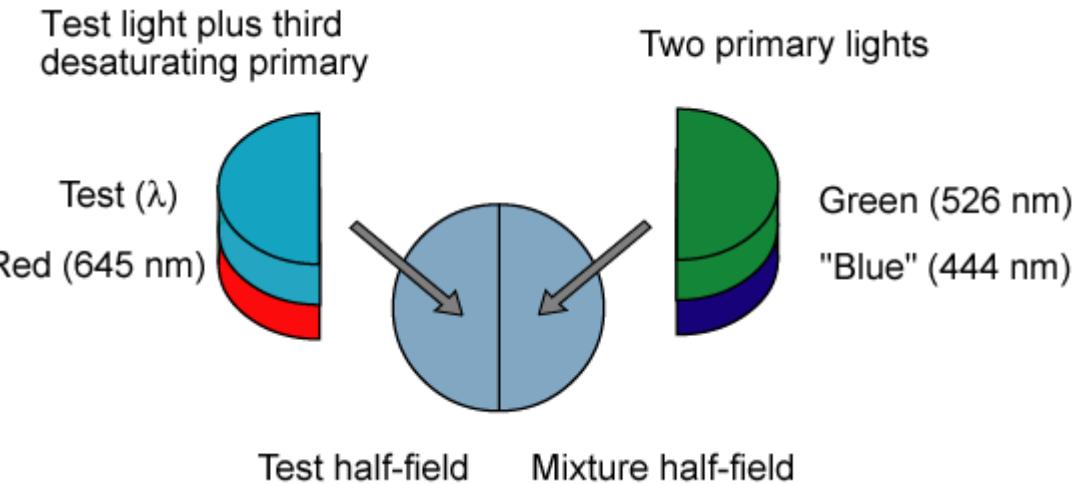


2. CONE SPECTRAL SENSITIVITIES AND COLOUR MATCHES



Colour matching

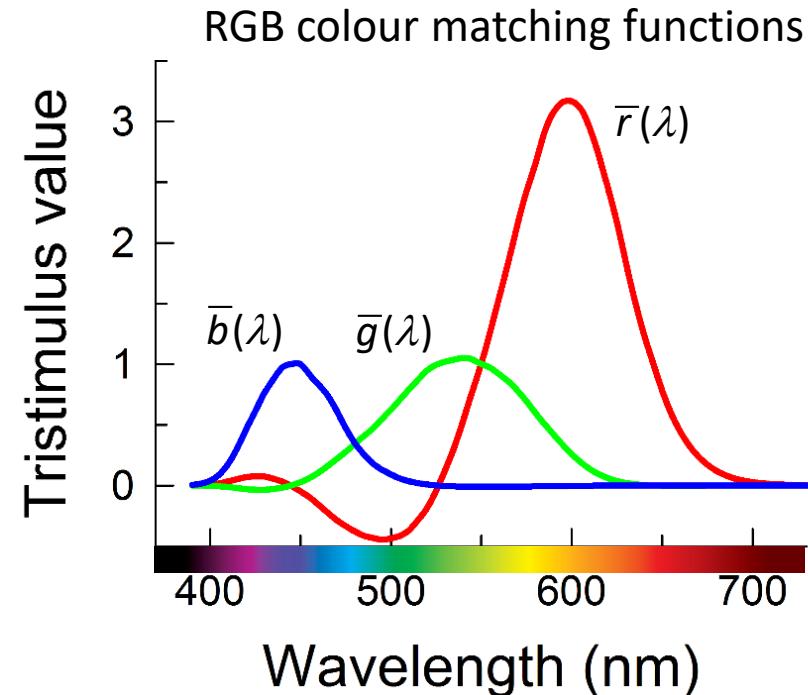
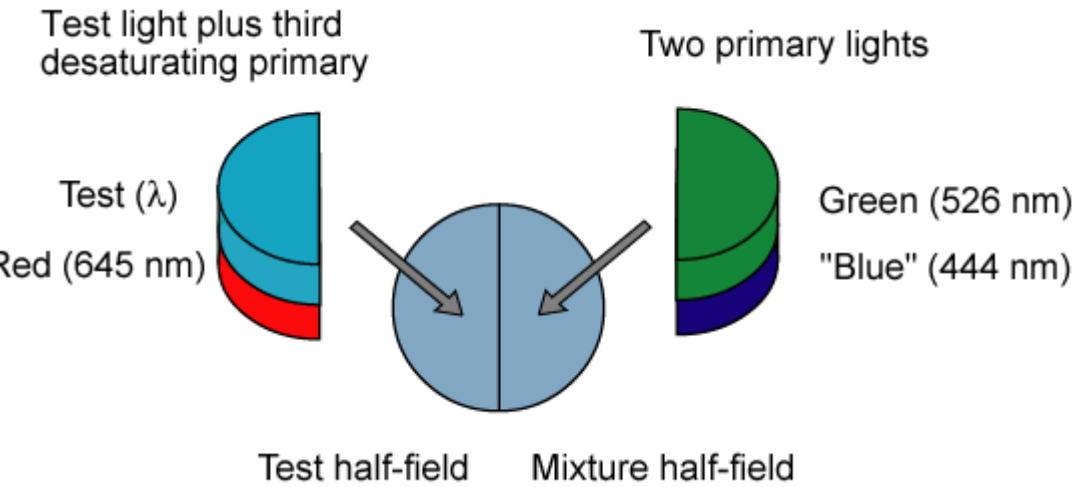
Another way of specifying colours is by making colour matches in a colour matching experiment:



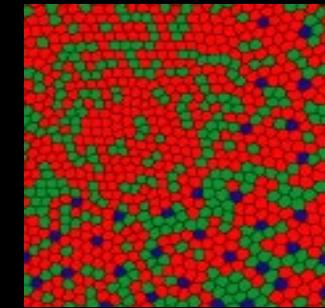
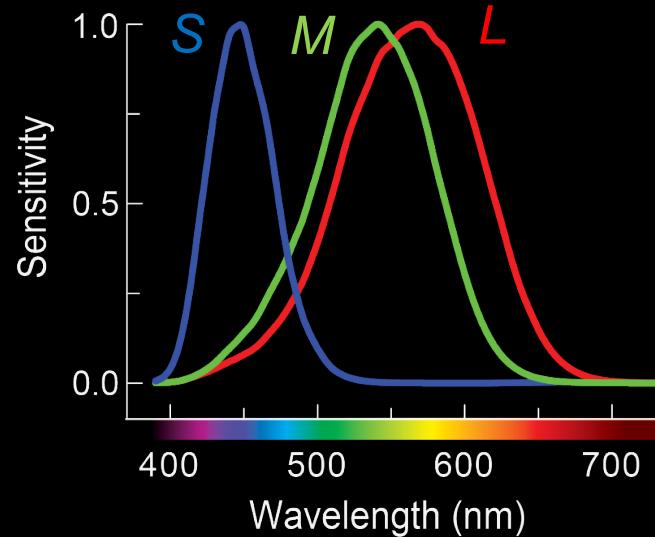
Colour matching

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.



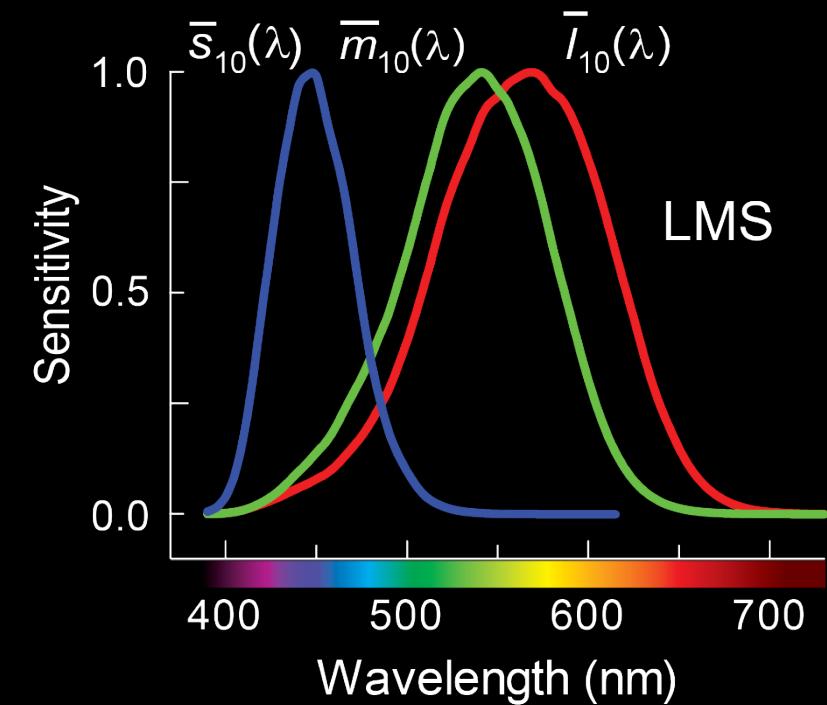
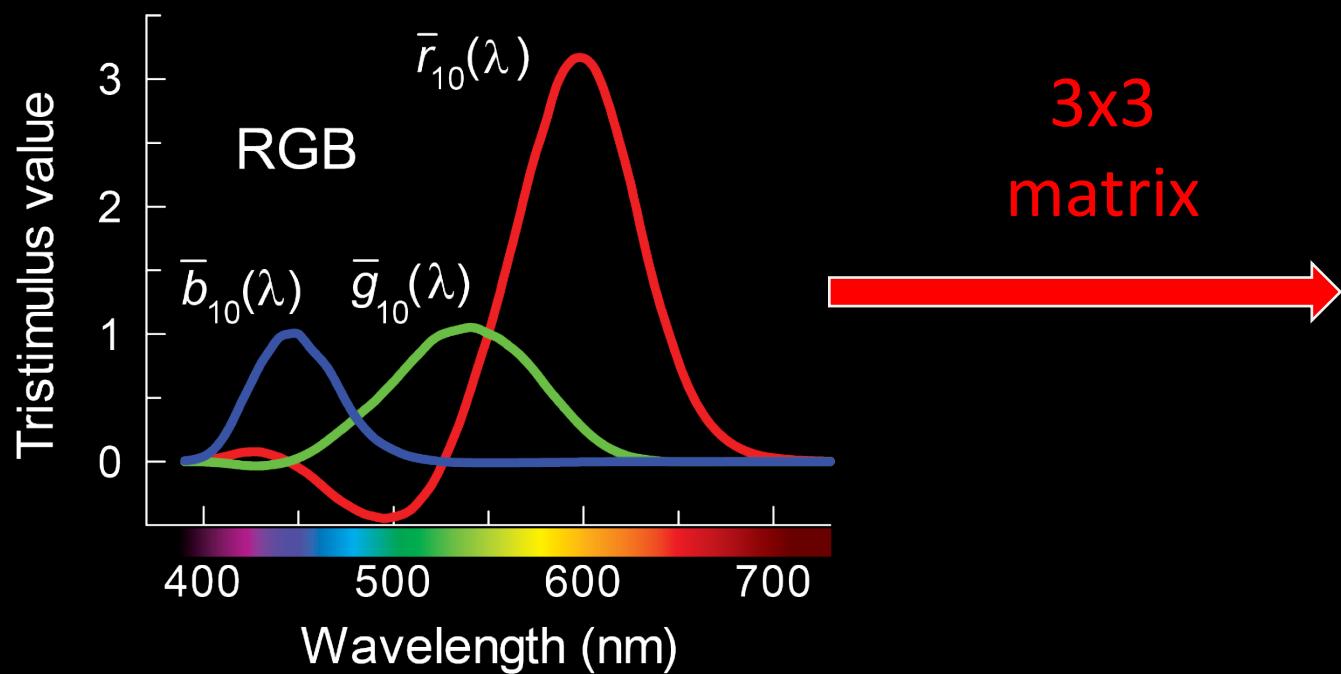
Consequently, the cone spectral sensitivities are the:

“Fundamental” colour matching functions

...upon which all other CMFs depend.

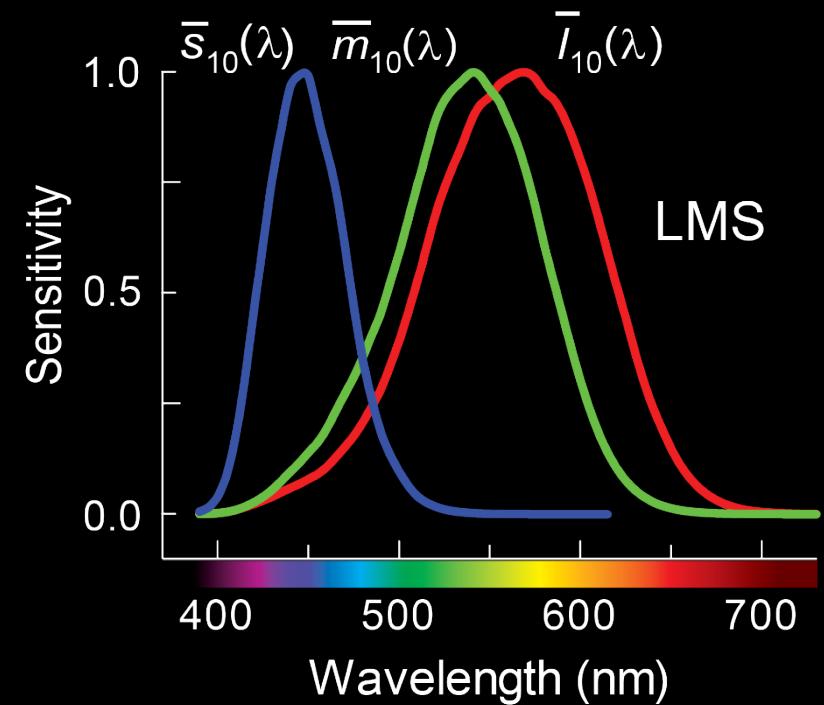
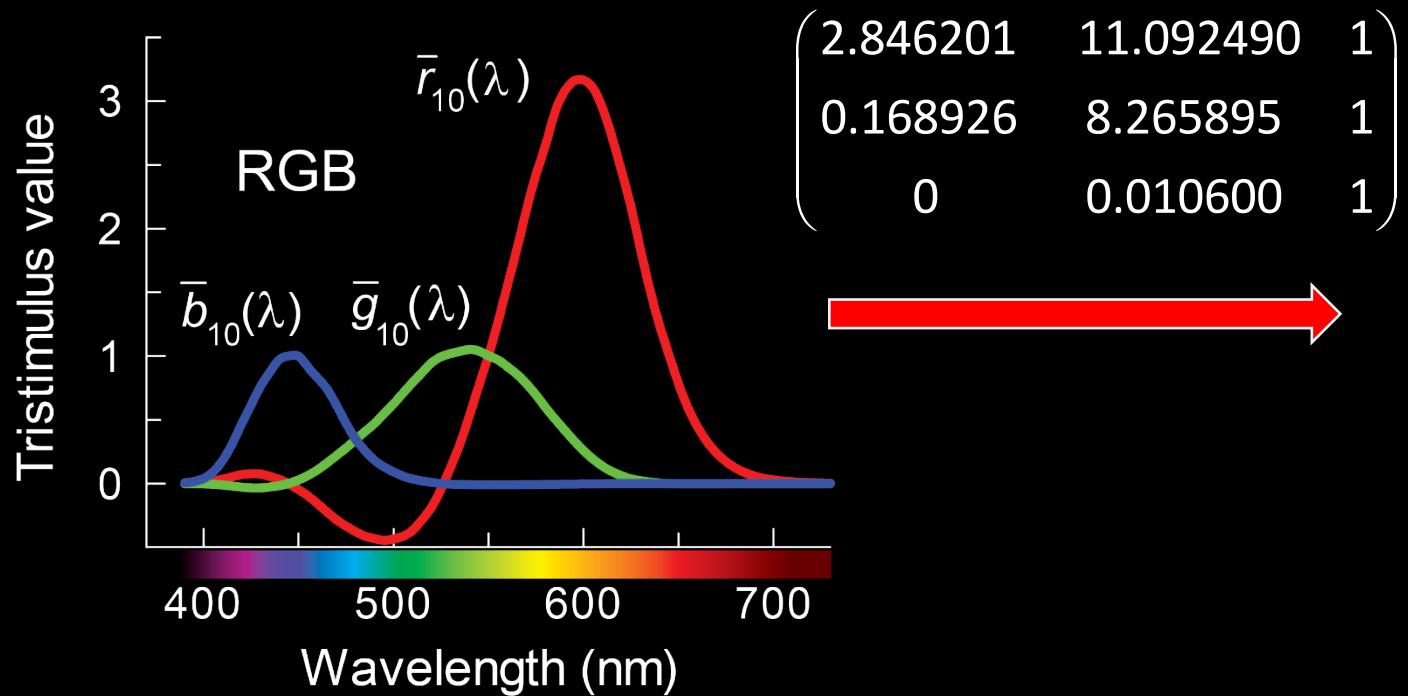
CMFs

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

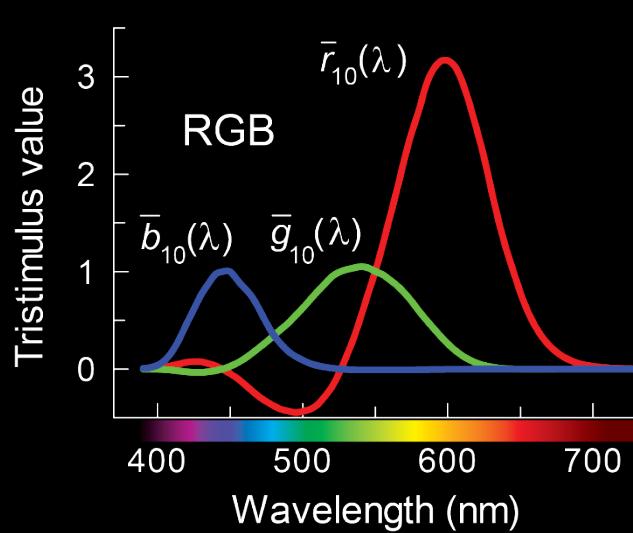


CMFs

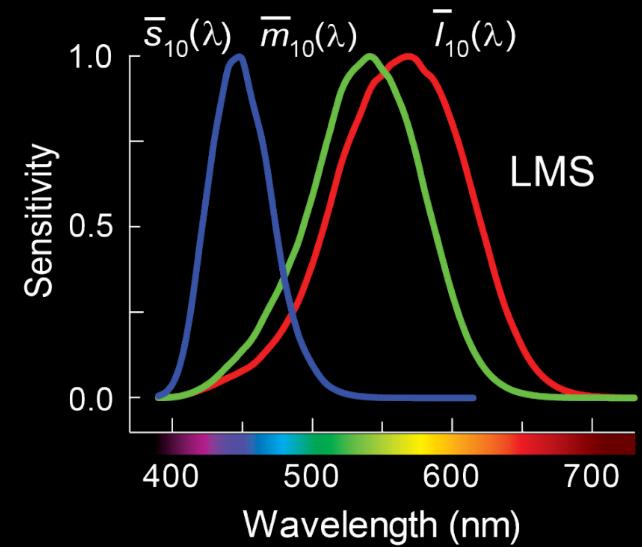
In 2006, the CIE defined the new standard LMS functions as a linear transformation of Stiles & Burch (1959) 10° RGB CMFs based on the work of Stockman & Sharpe (2000):



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

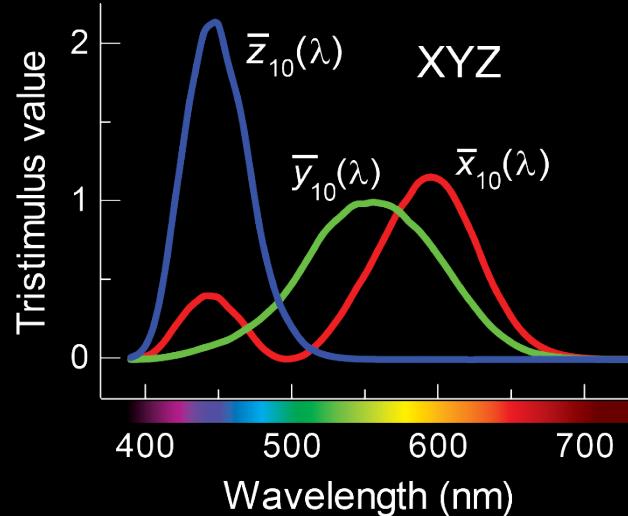
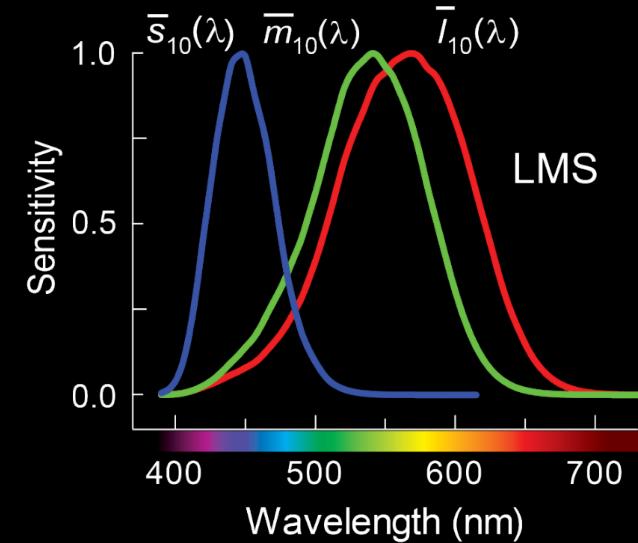
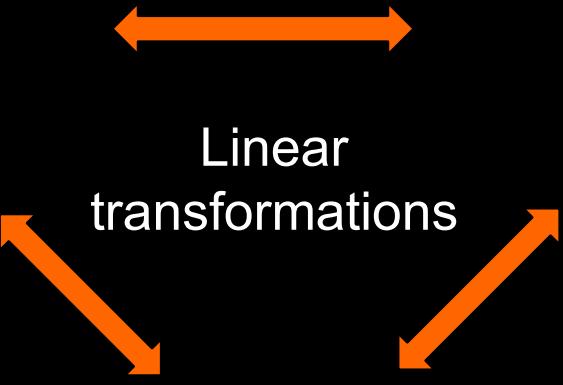
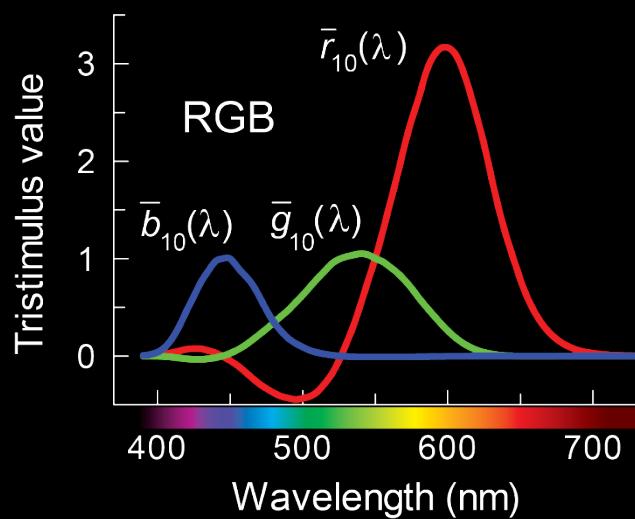


↔
Linear
transformation



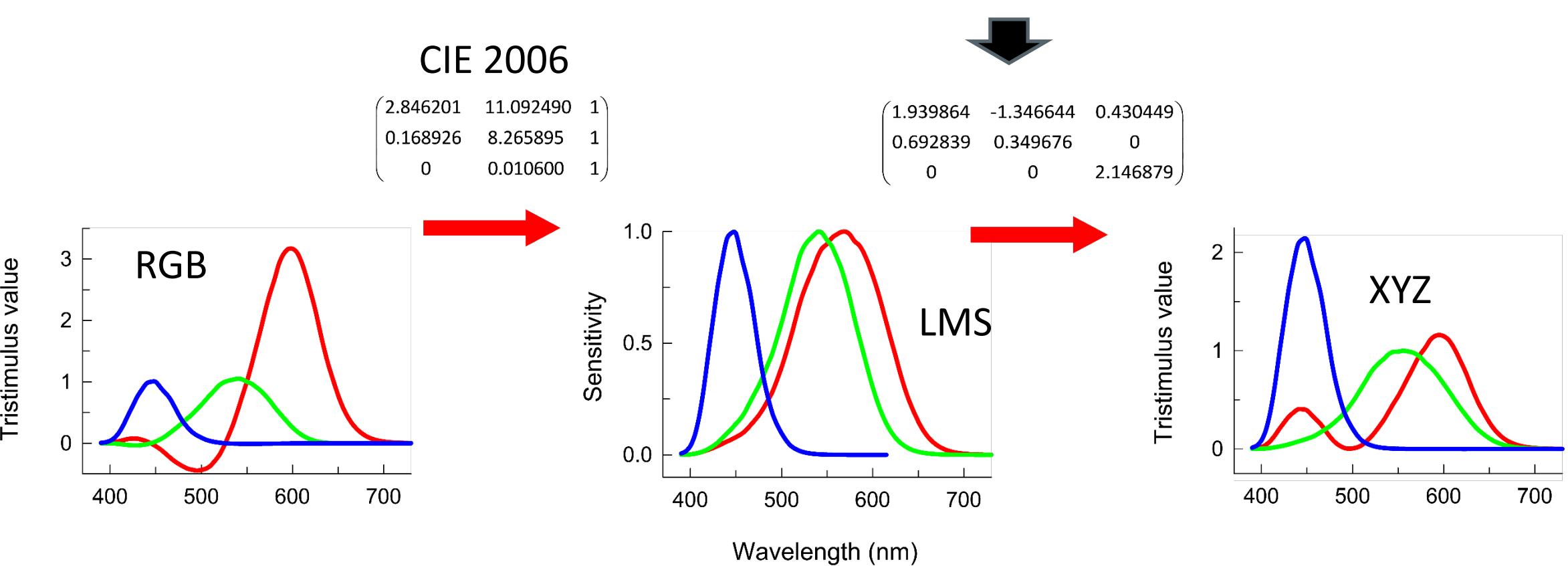
As well as the linear transformation from RGB to LMS...

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

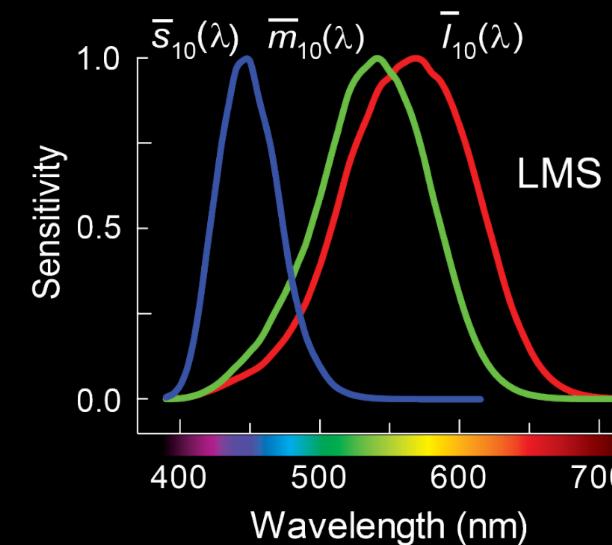
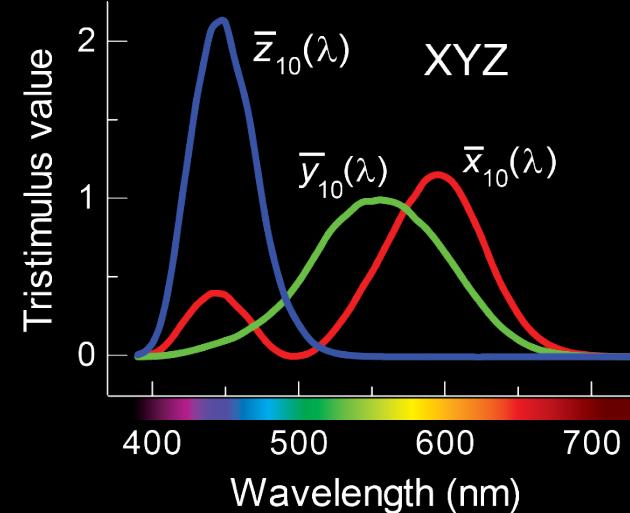
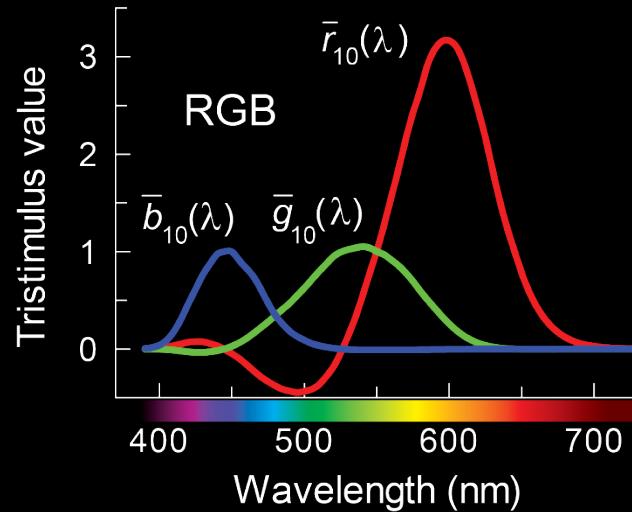


There is also a simple linear transformation between RGB and LMS and XYZ, which was defined by the CIE in 2015.

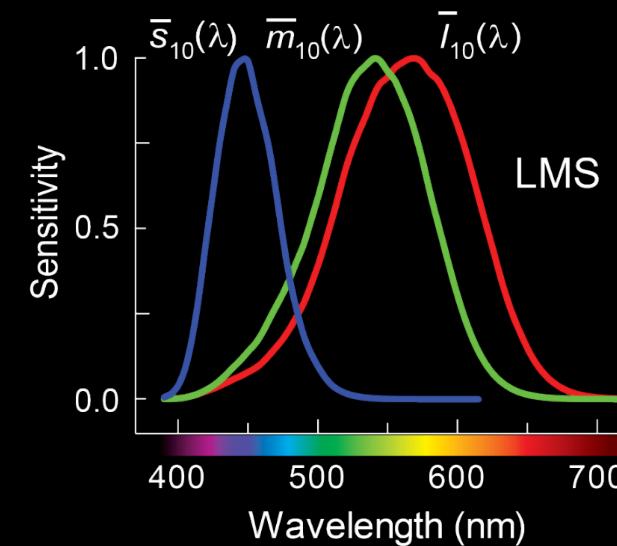
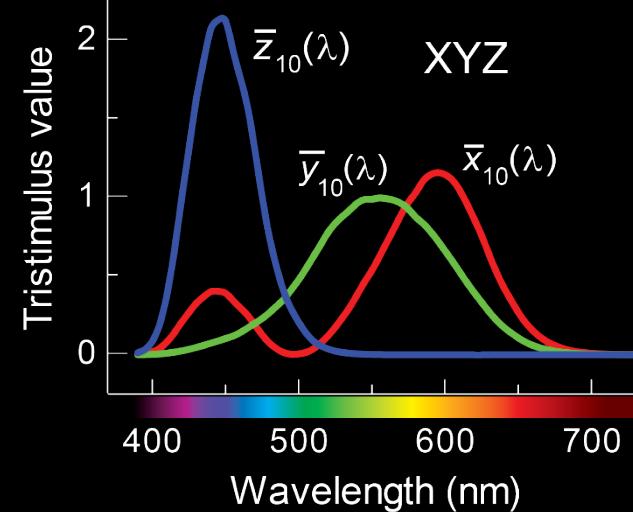
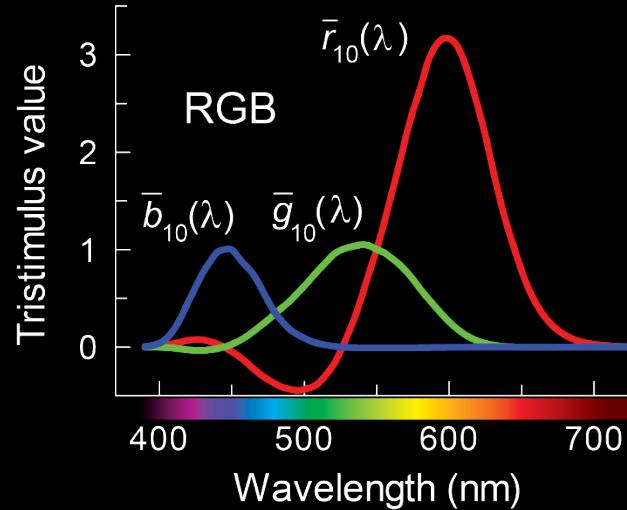
In 2015, the CIE defined the linear transformation
from the 2006 LMS cone fundamentals to a new XYZ:



Why do we need colour matching functions?

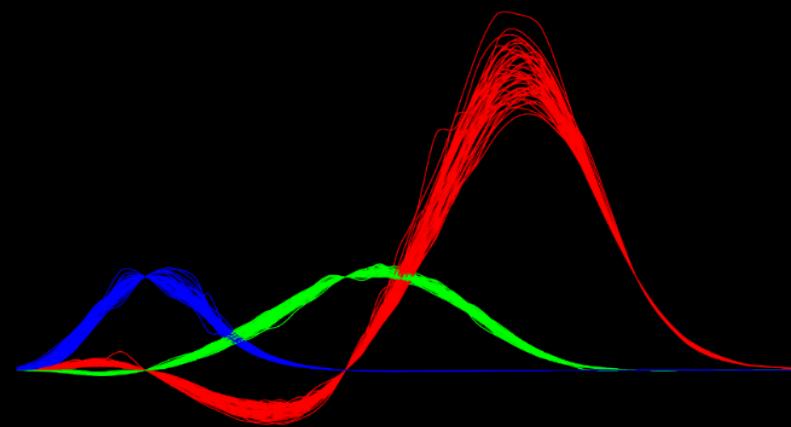


Why do we need colour matching functions?



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...

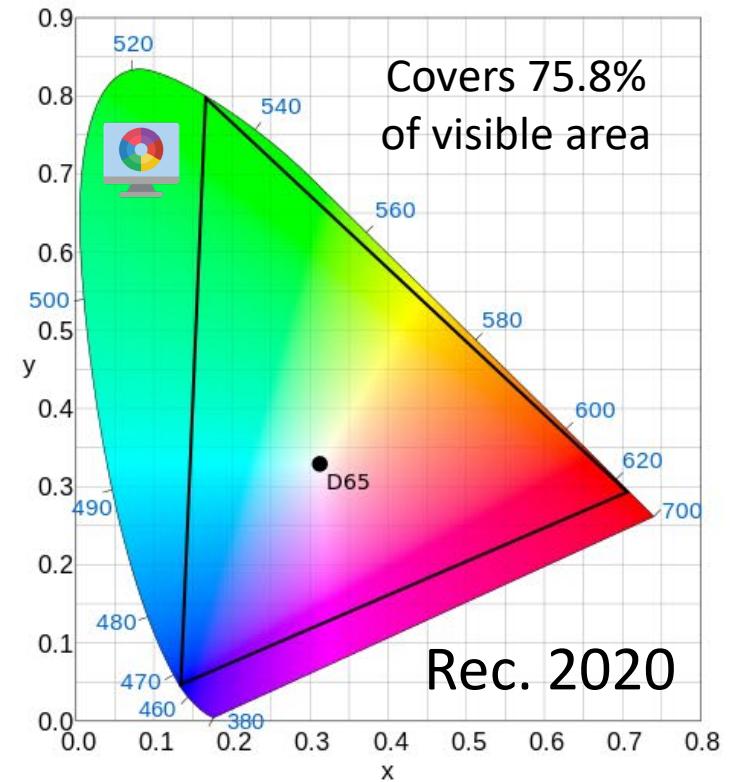
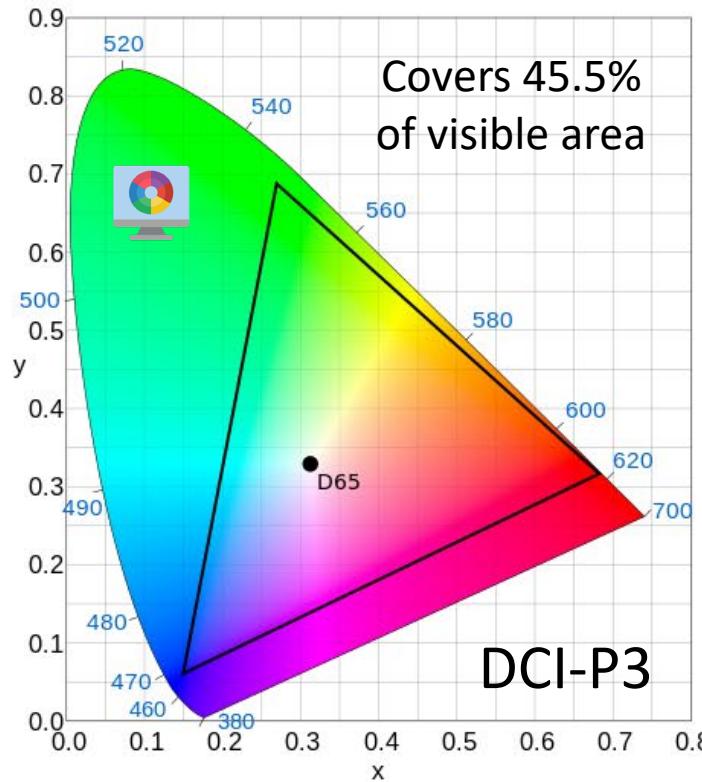
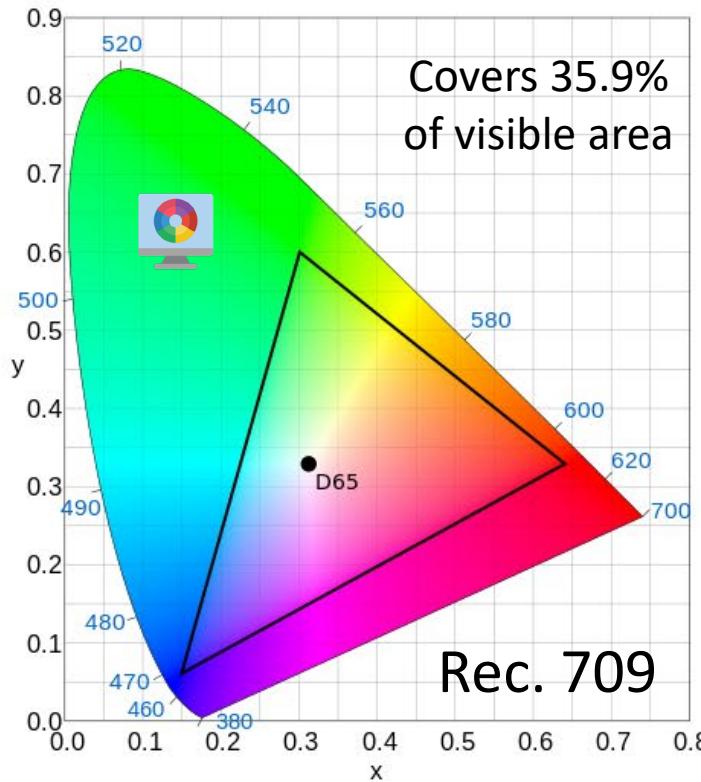
3. INDIVIDUAL DIFFERENCES



Display standards



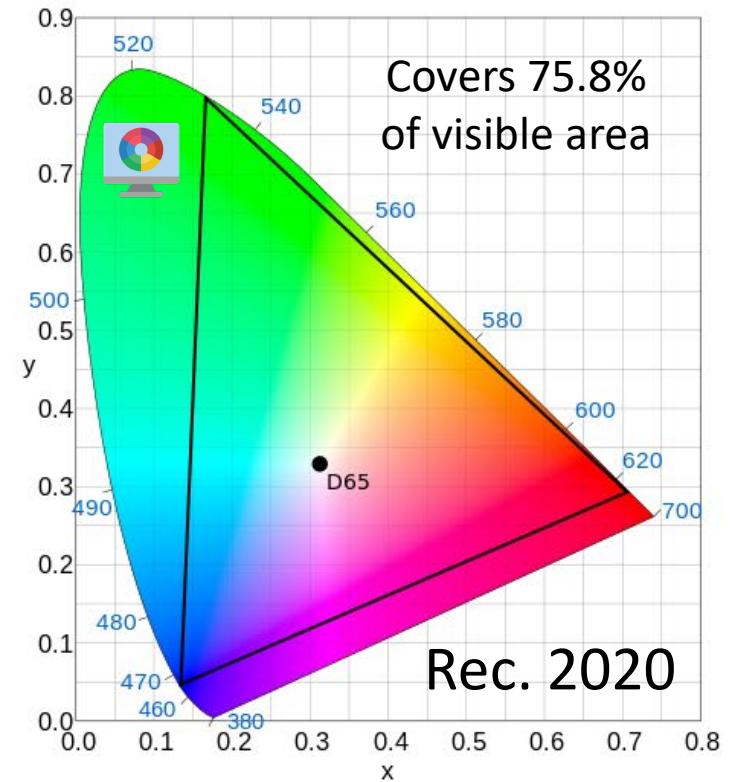
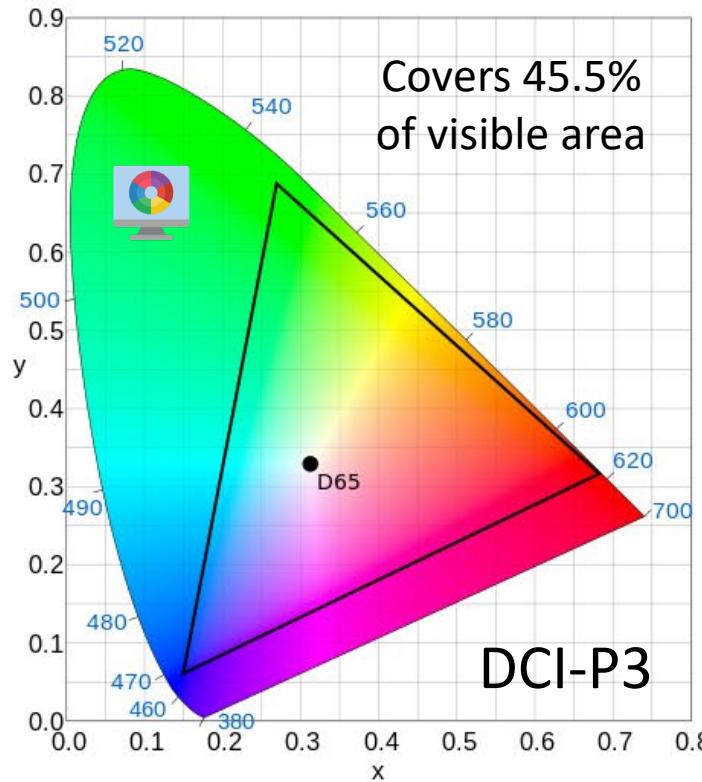
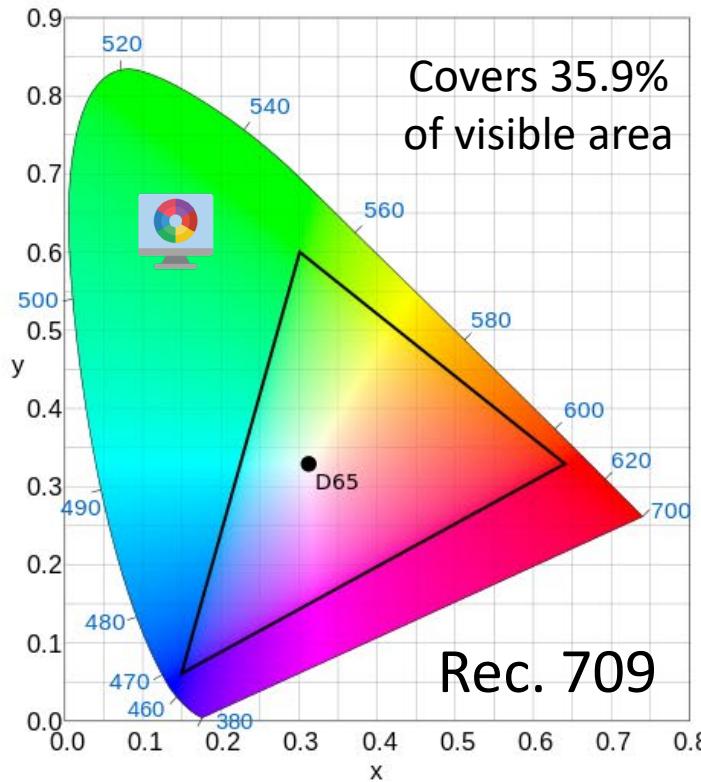
In principle, then, if we know the chromaticities of a colour (in terms of XYZ, LMS or RGB), we should be able reproduce it on any display, and it should look similar for all observers across all displays...



Display standards

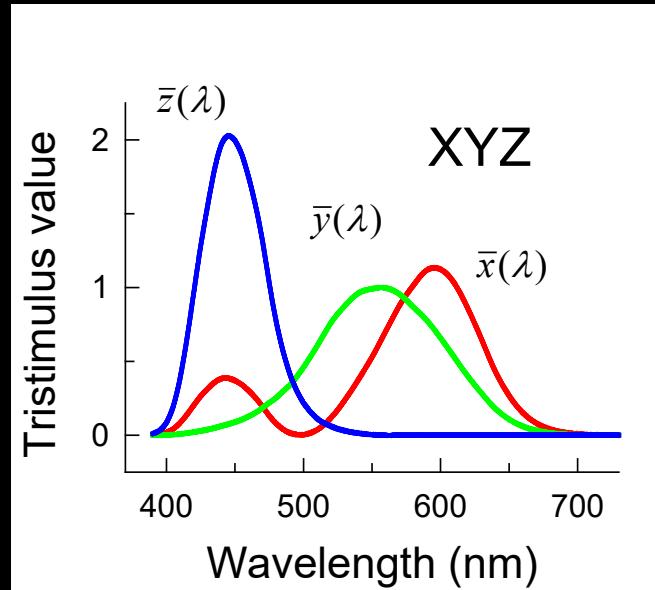


But there are problems...!

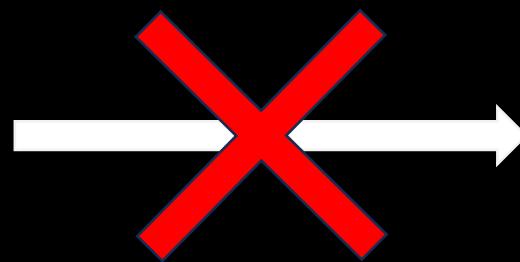
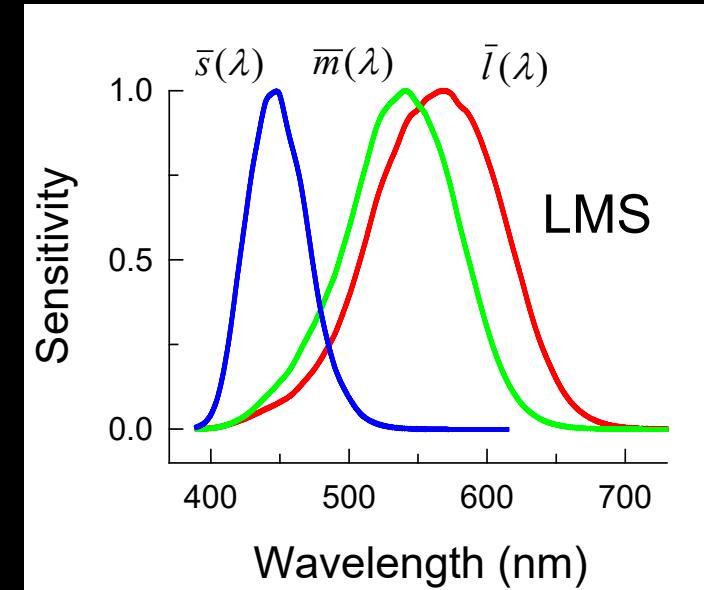


The first problem is that the CIE 1931 XYZ CMFs used extensively to define display colours are **substantially** incorrect, as a result of which there is no valid transformation from 1931 XYZ to **any** LMS...

CIE 1931 2-deg XYZ (or RGB) CMFs



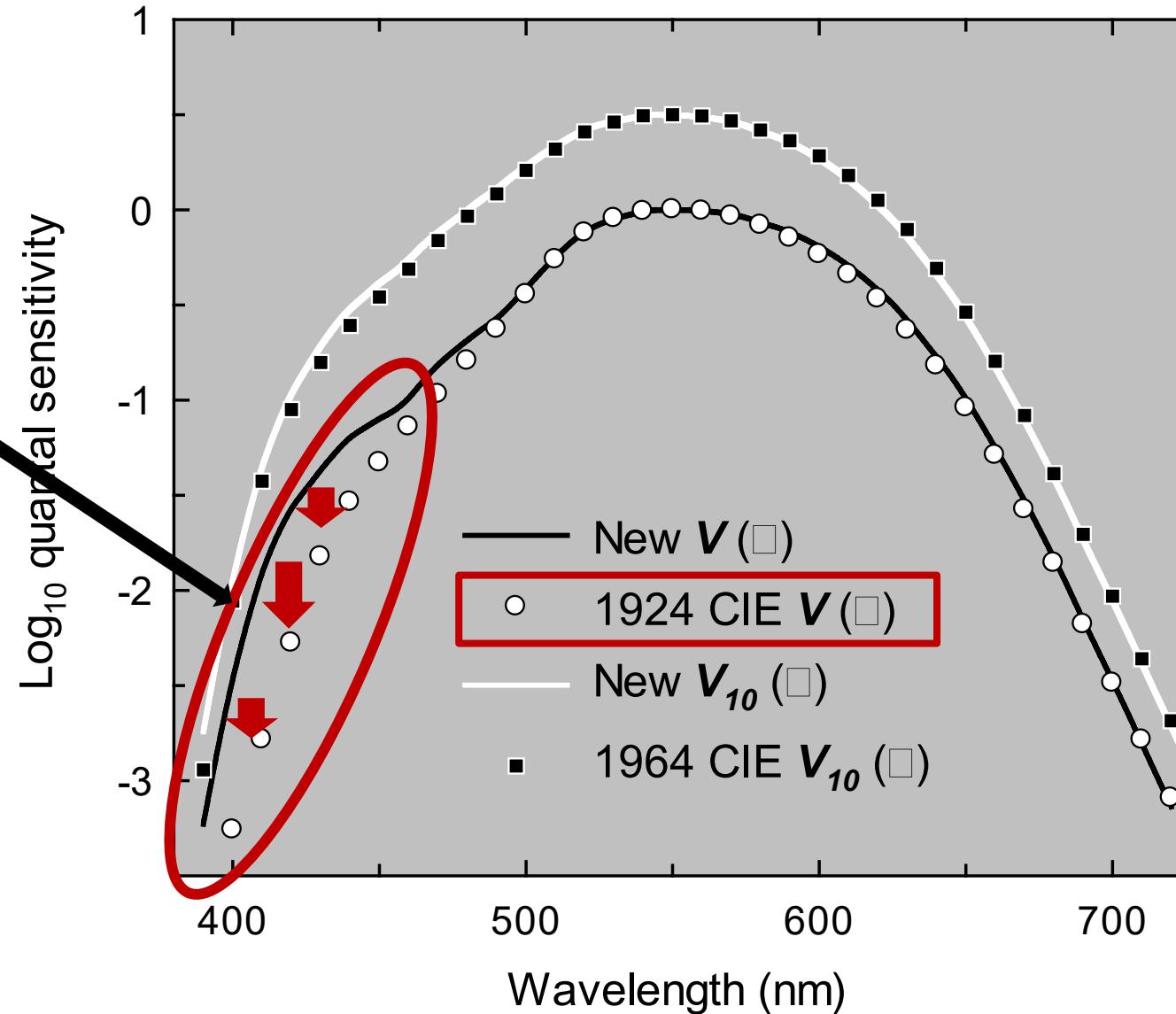
2-deg LMS cone fundamentals



Why?

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!

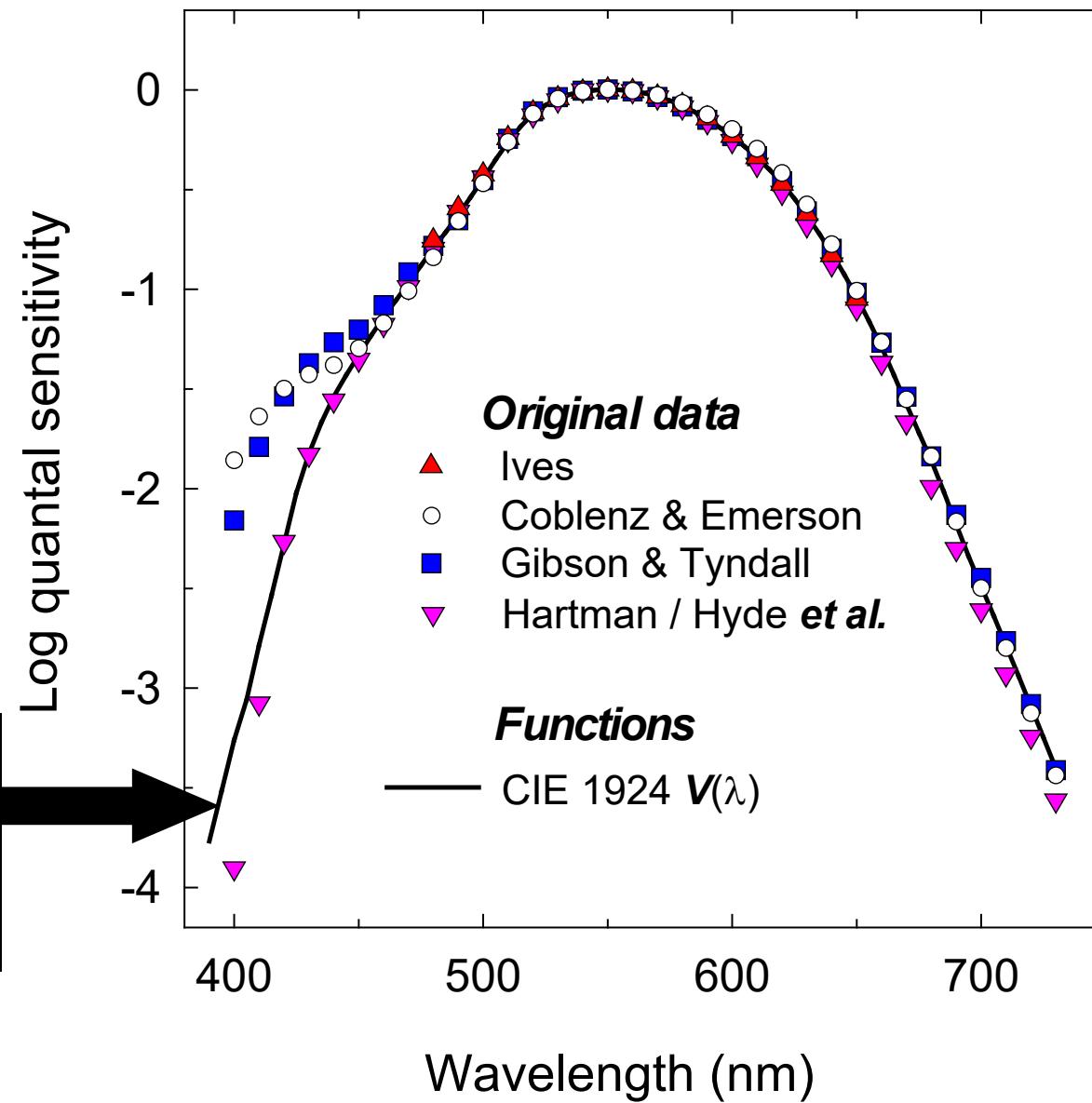


The mistake is related to the choice of $V(\lambda)$ back in 1924...

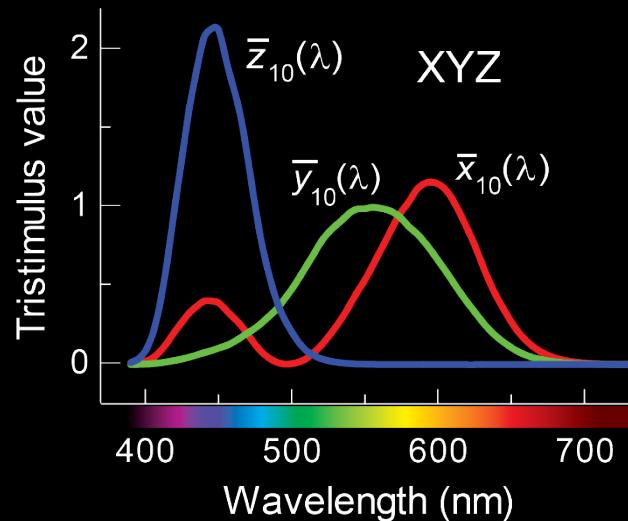
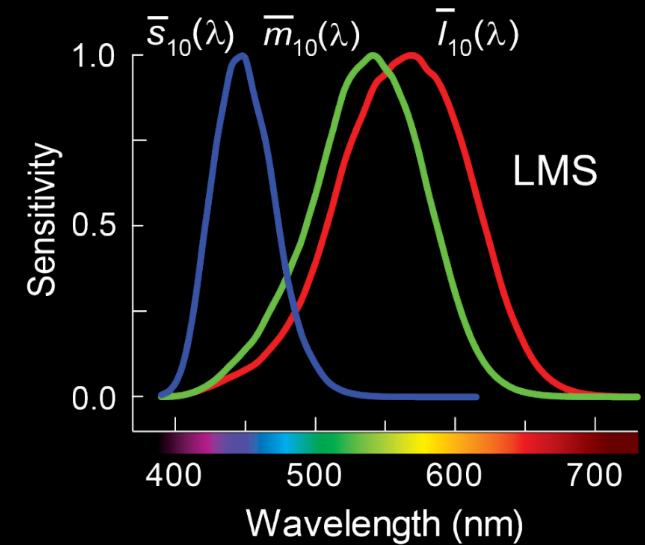
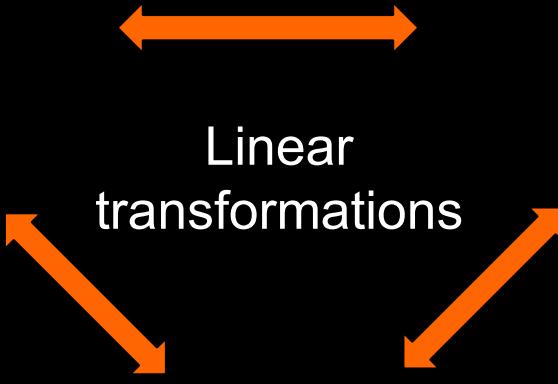
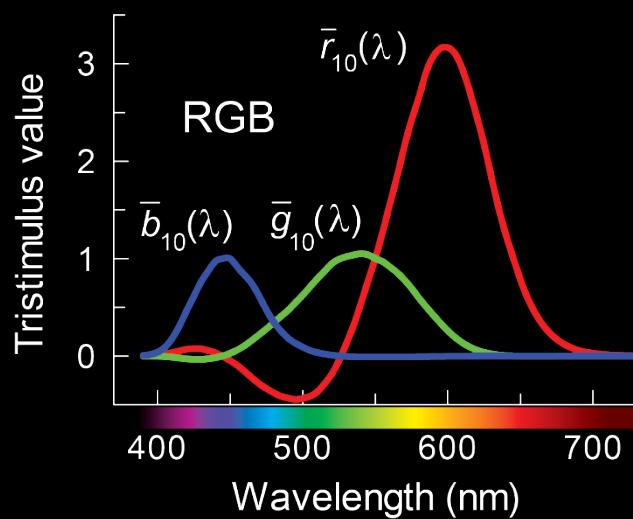
Original data used to derive CIE $V(\lambda)$
(which is also CIE 1931 Y)

And here is what the CIE chose in 1924!

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

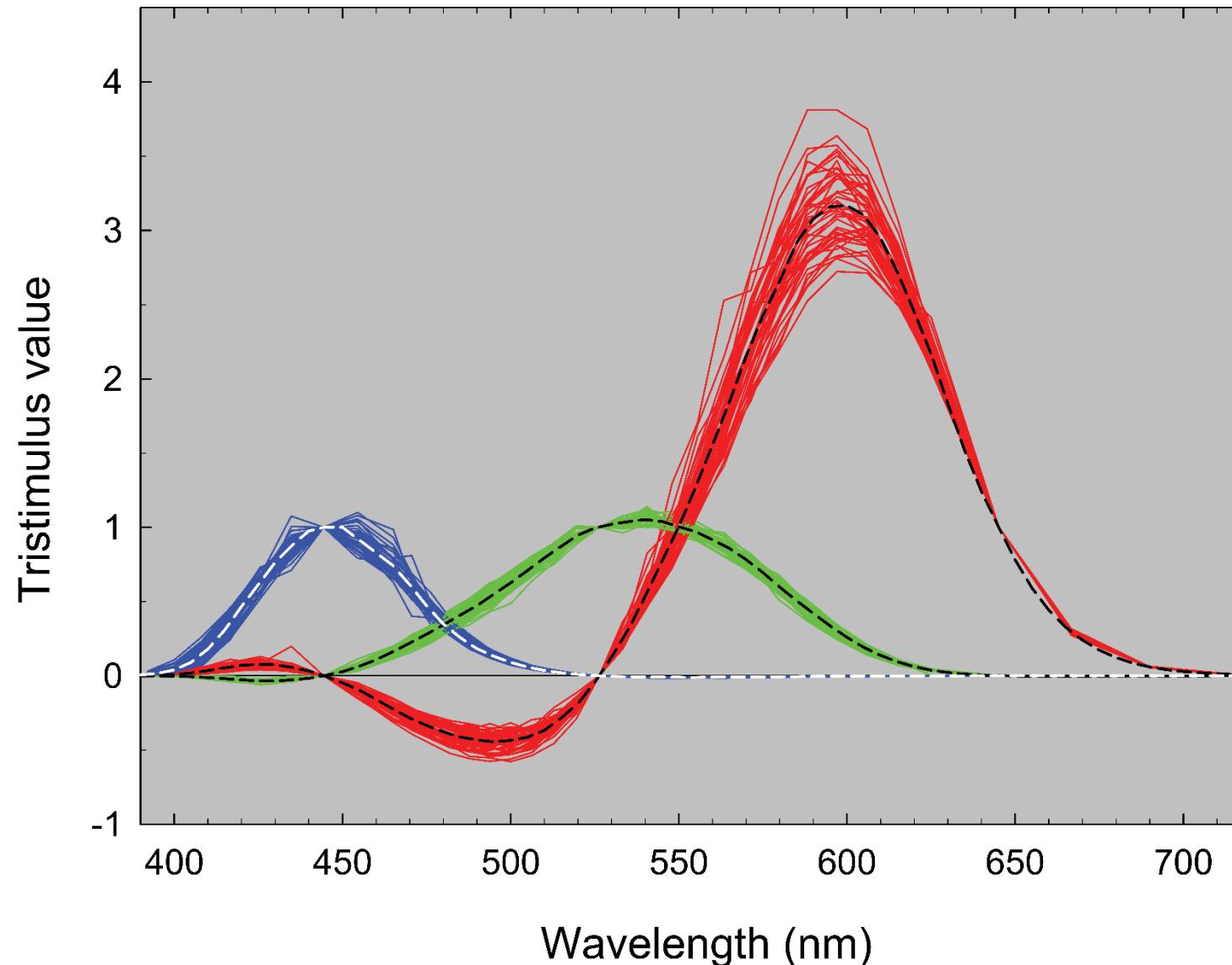


CIE (2006) LMS AND CIE (2015) XYZ CMFs



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.

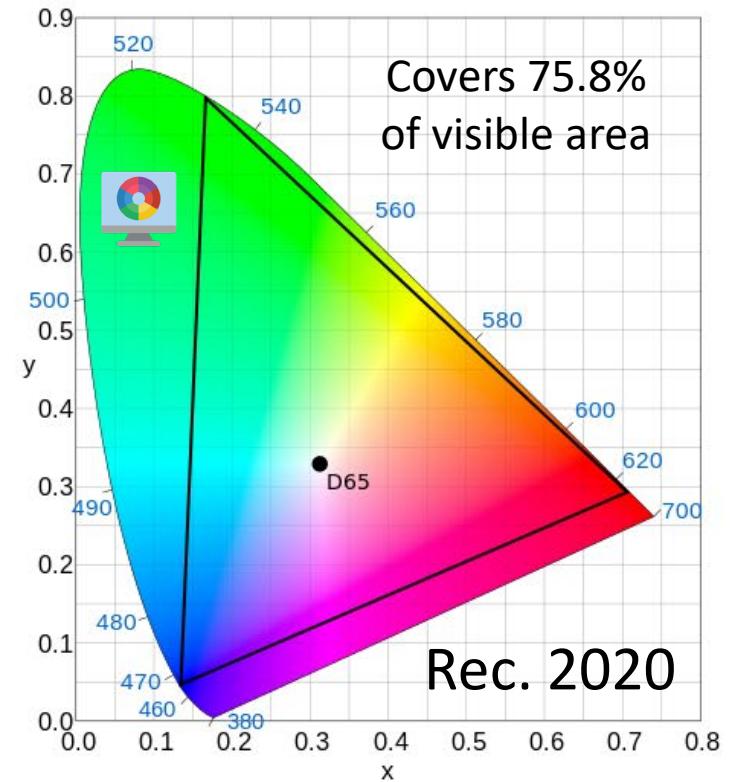
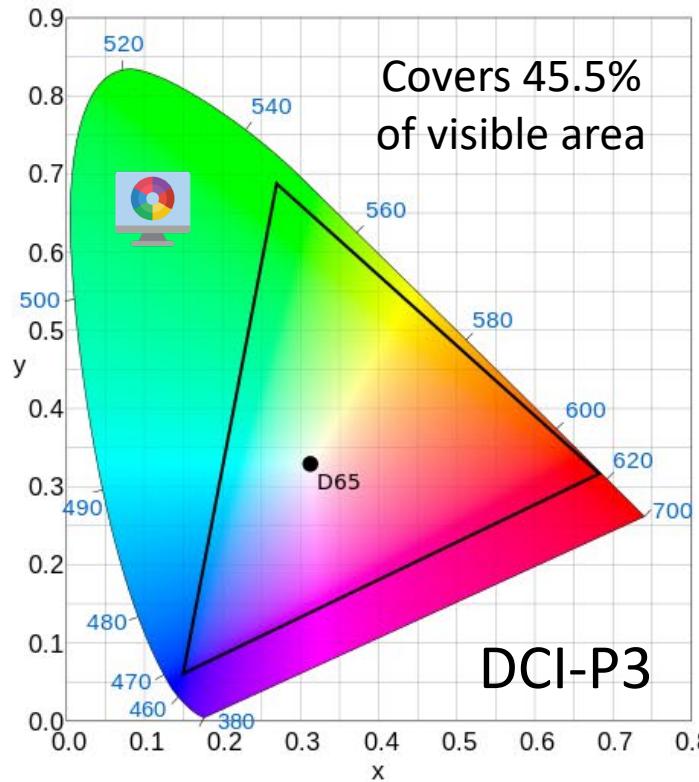
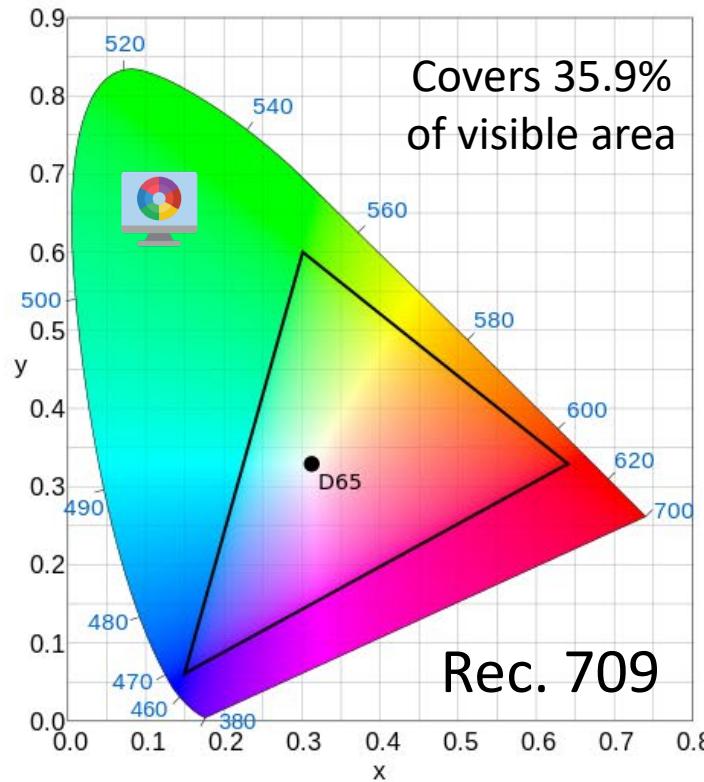


Stiles & Burch (1959)
10-deg CMFs

Display standards



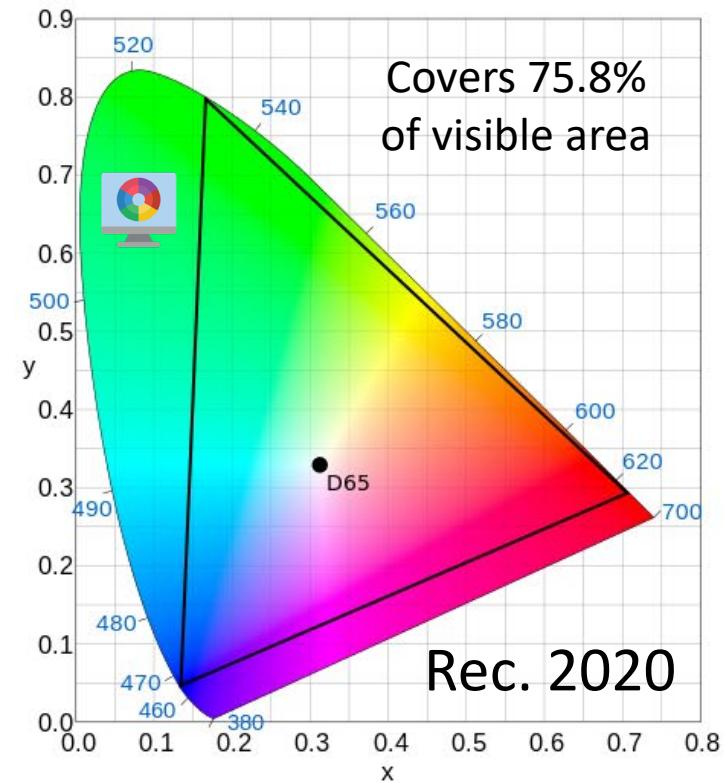
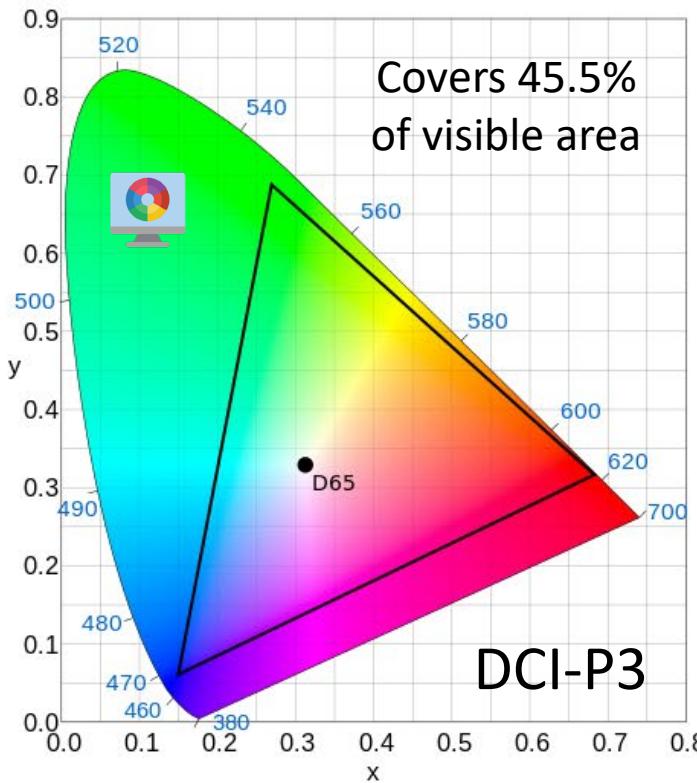
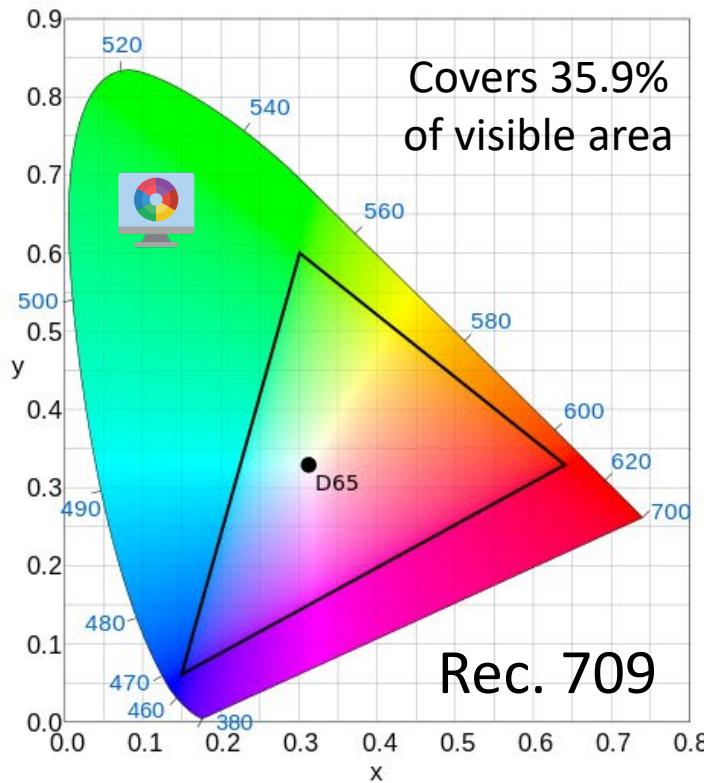
Because of these individual differences the colours produced on displays by using the same x,y values may look different for different observers on the same display and across different displays.



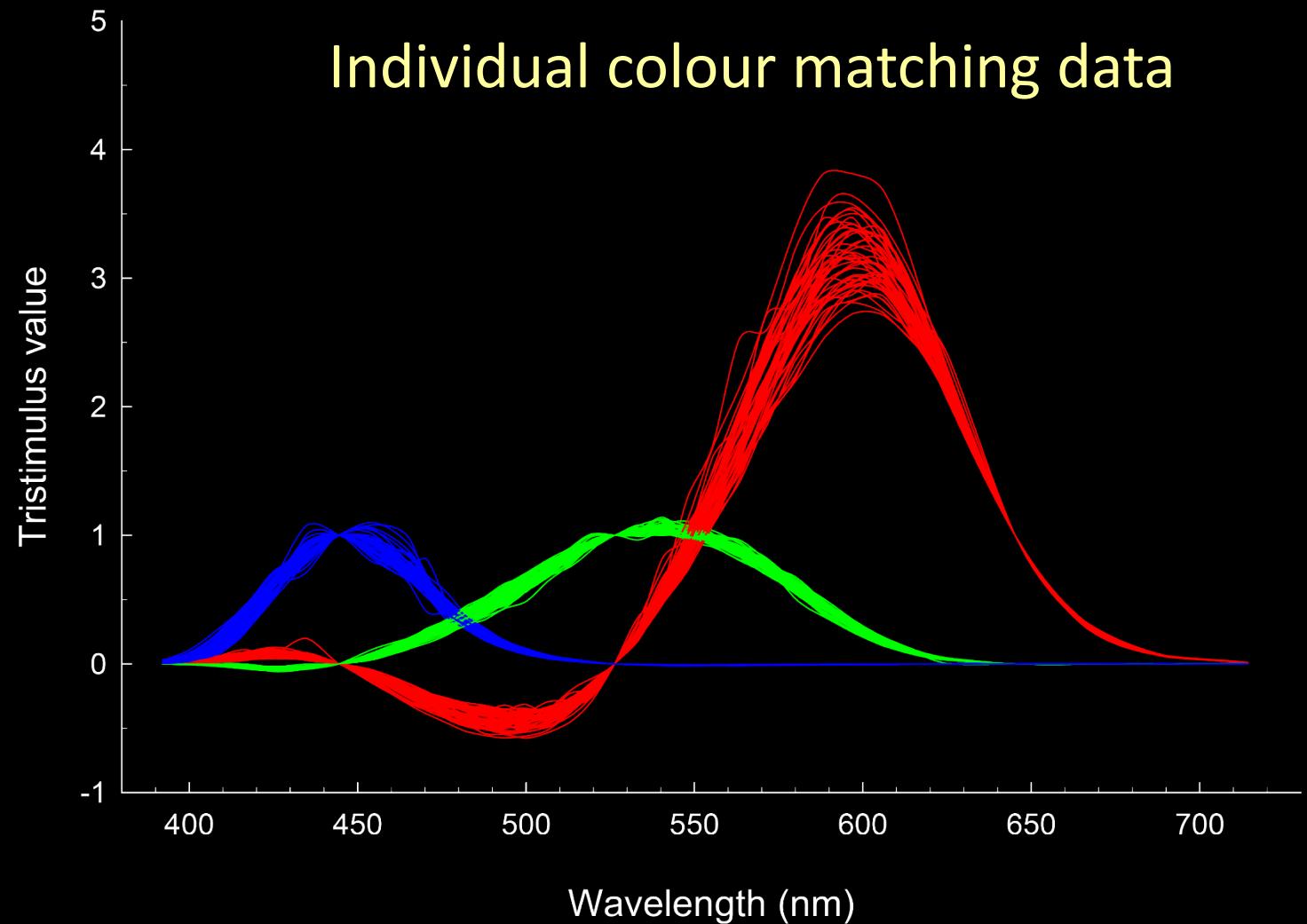
Display standards



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 ...



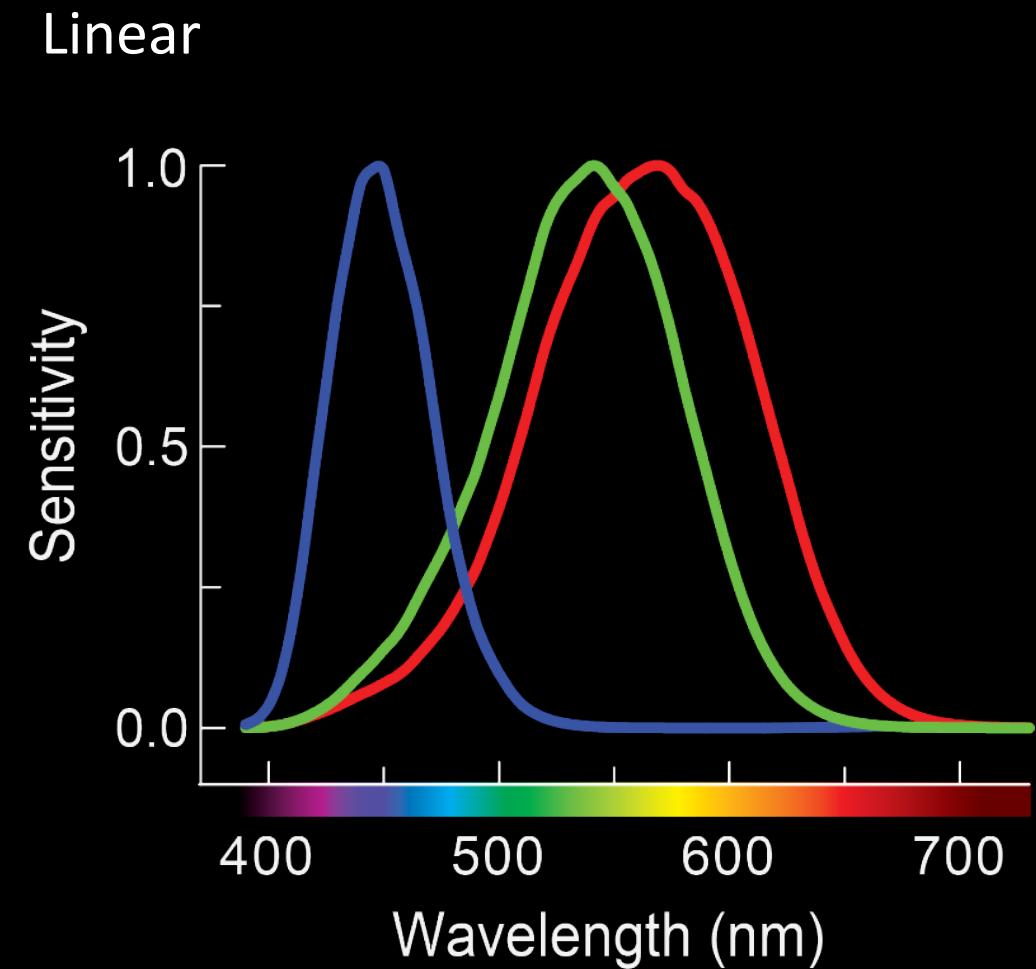
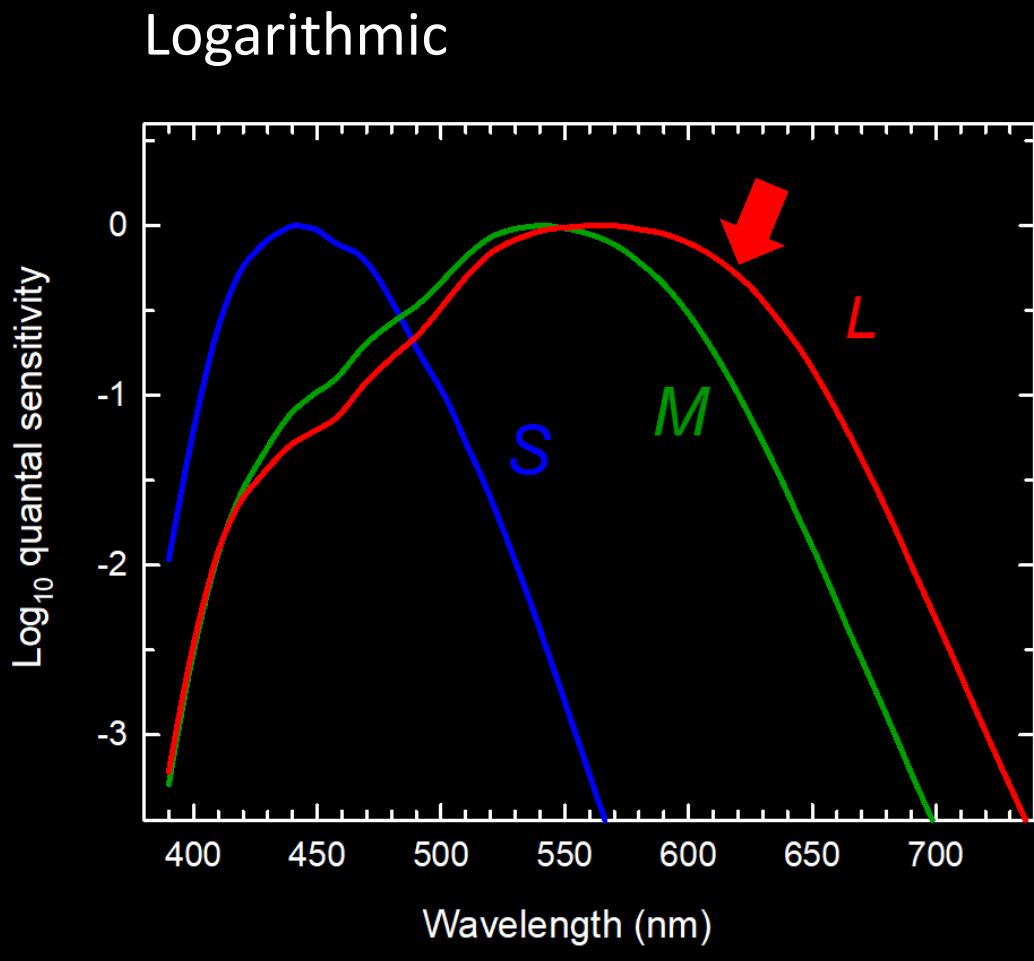
What causes these
individual differences?



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)...

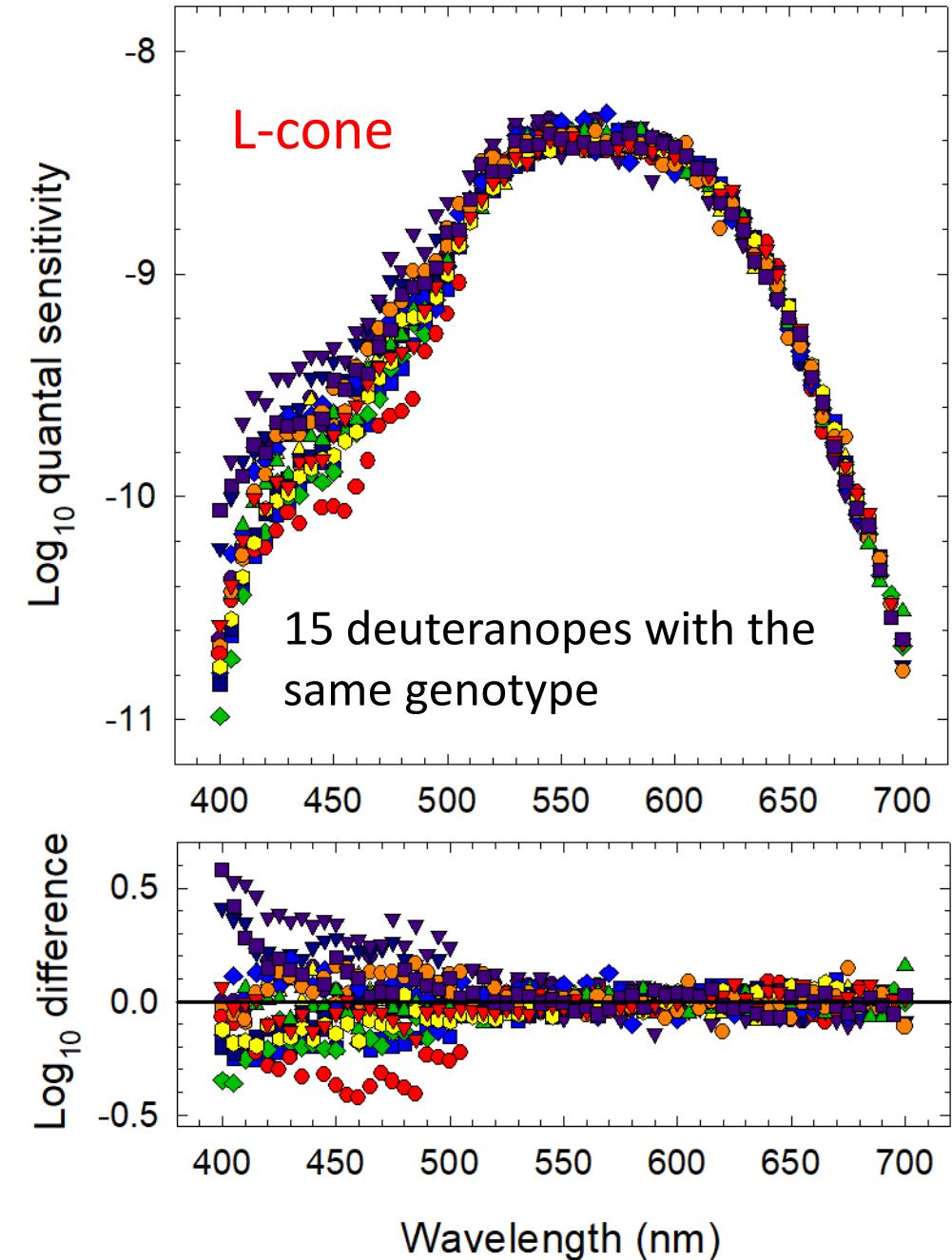


Individual data for deutanopes with the same L-cone photopigment



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

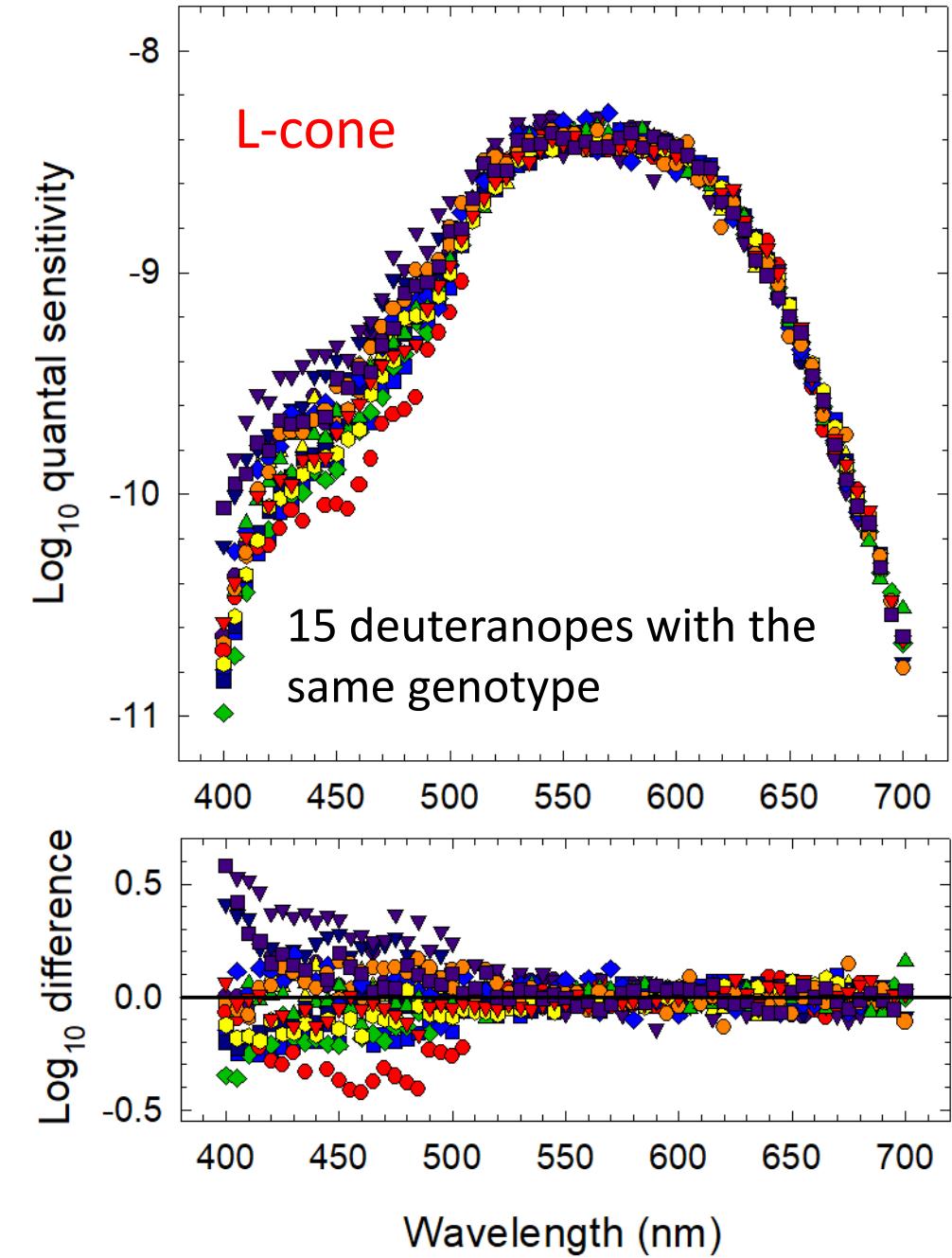
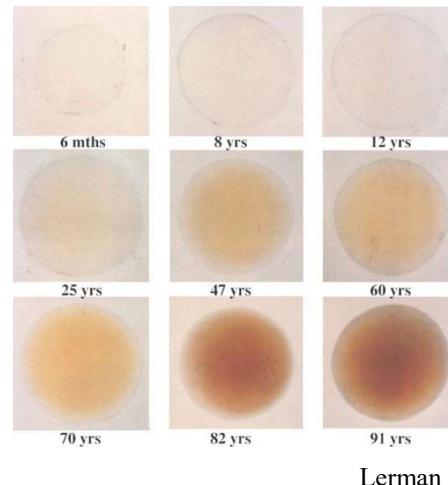
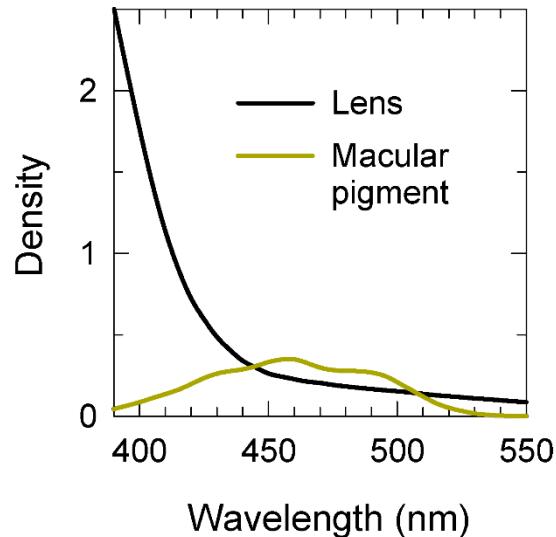
Why are the results so variable at short wavelengths?



Individual data for deuteranopes with the same L-cone photopigment



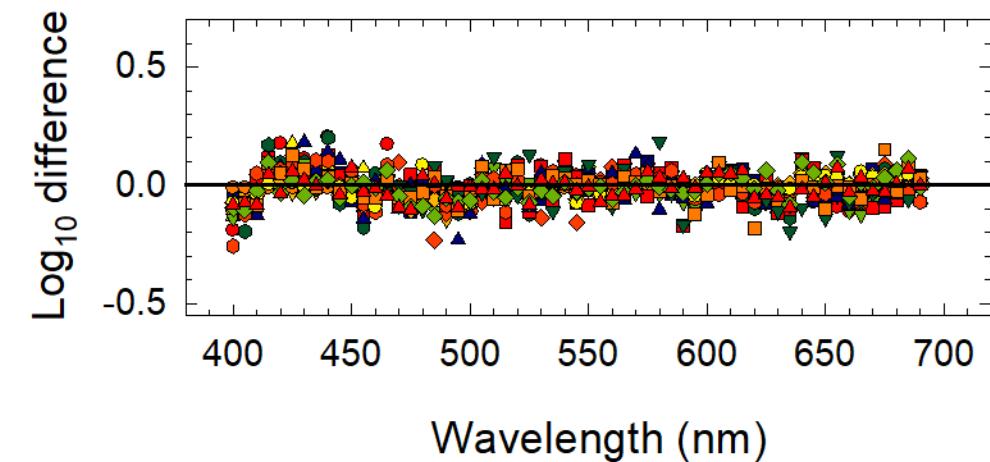
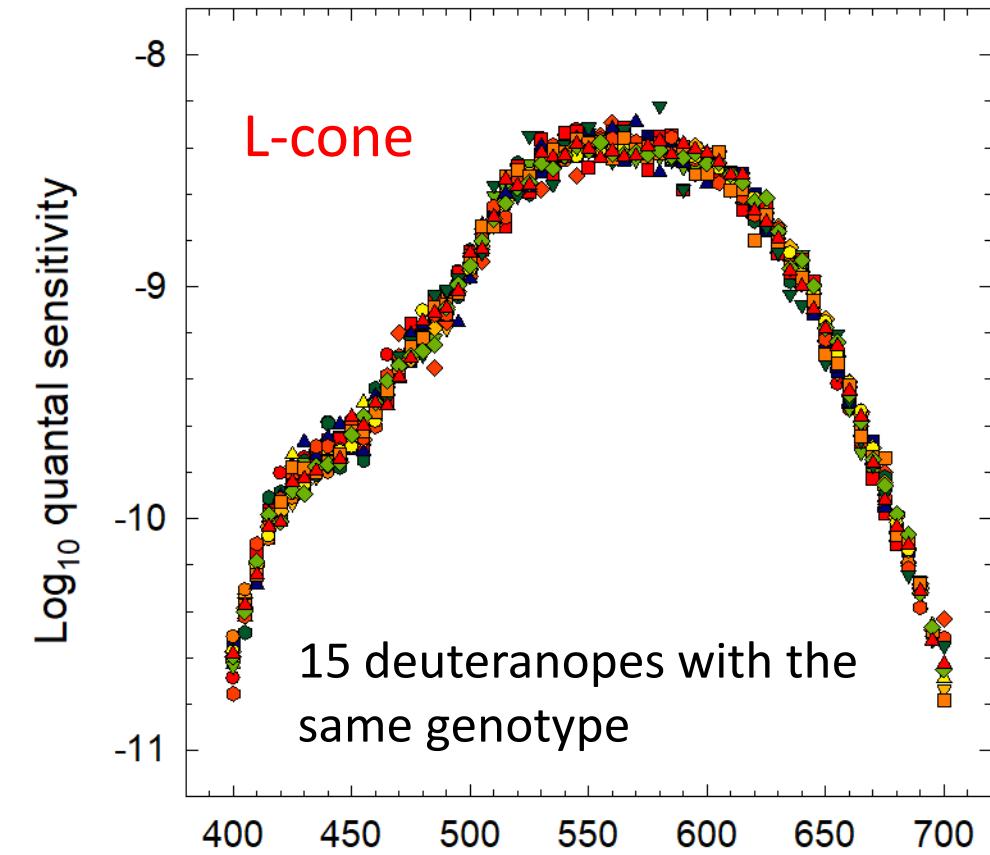
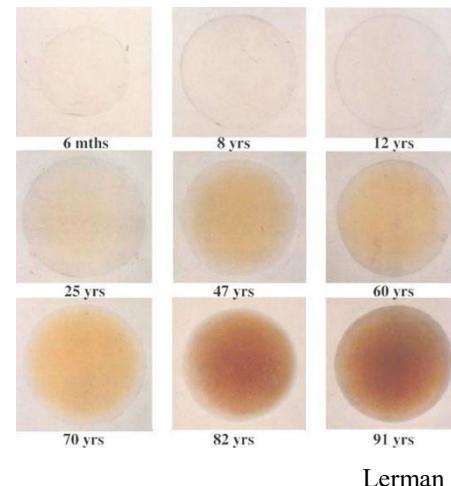
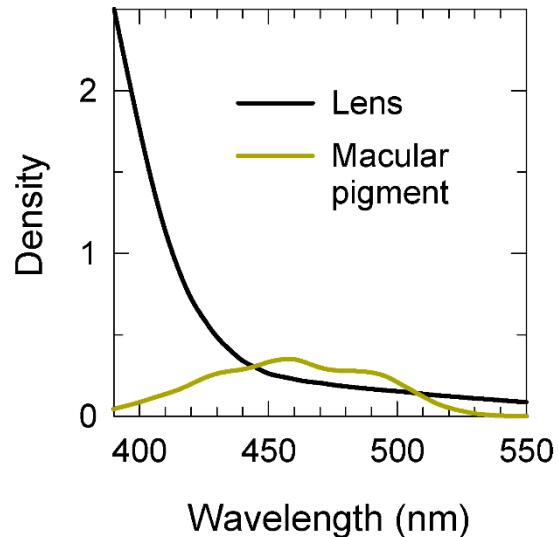
The variability is due to individual differences in macular and lens pigment optical densities.



Individual data for deuteranopes with the same L-cone photopigment



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



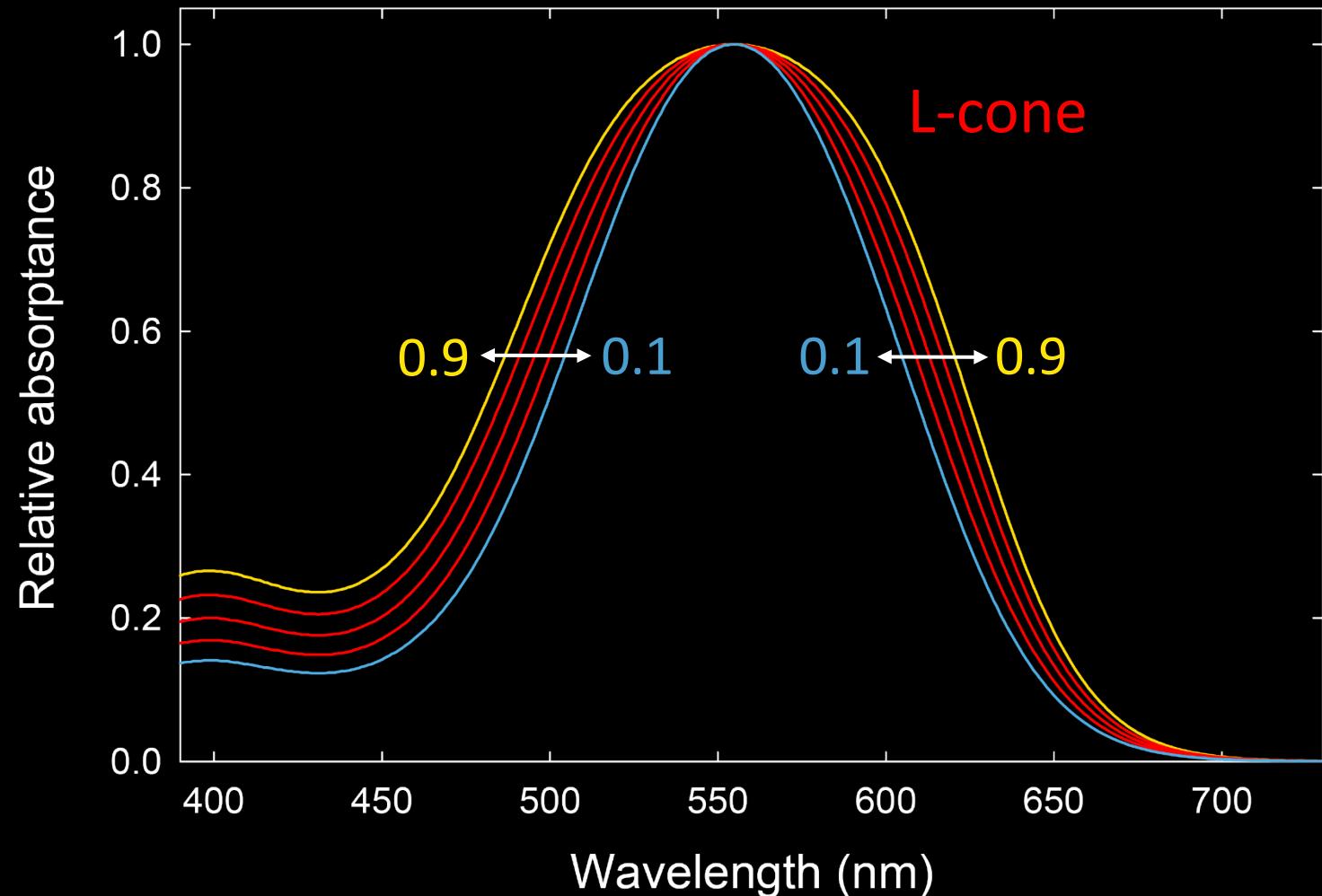
What causes individual differences?

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

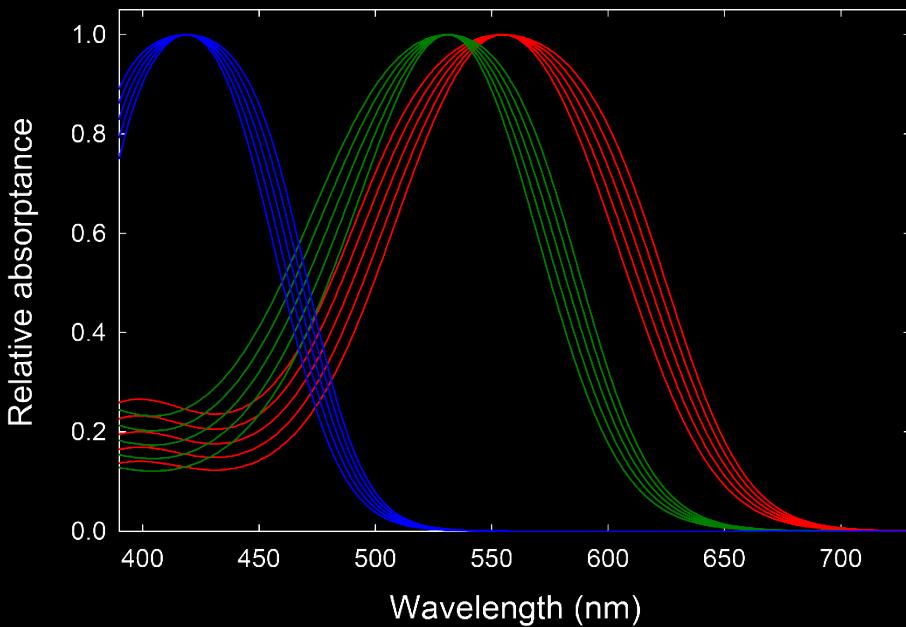
Individual differences in photopigment optical density

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

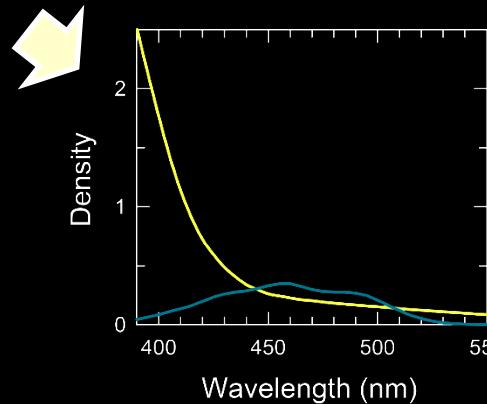
Cone photopigments varying in optical density from 0.1 (narrow) to 0.9 (broad) in 0.2 steps



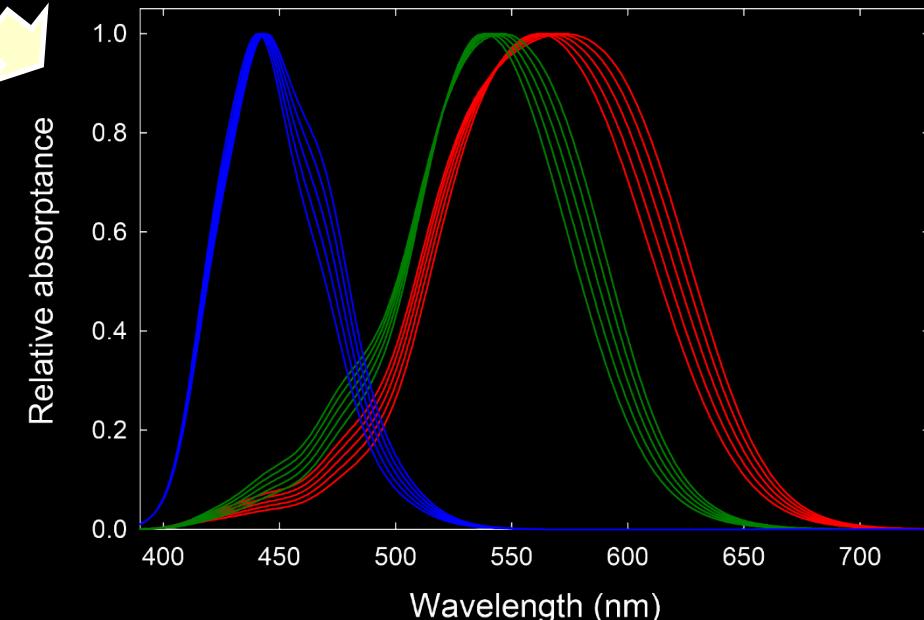
Photopigments



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



Cone spectral sensitivities
at the cornea



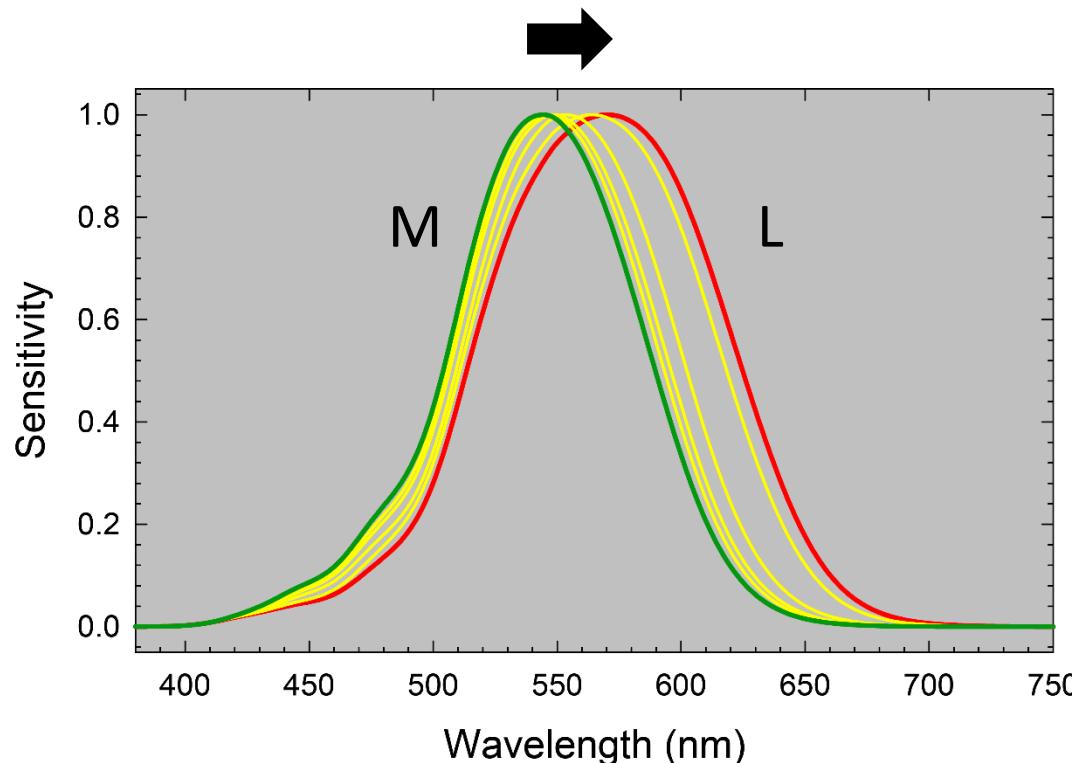
What causes individual differences?

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

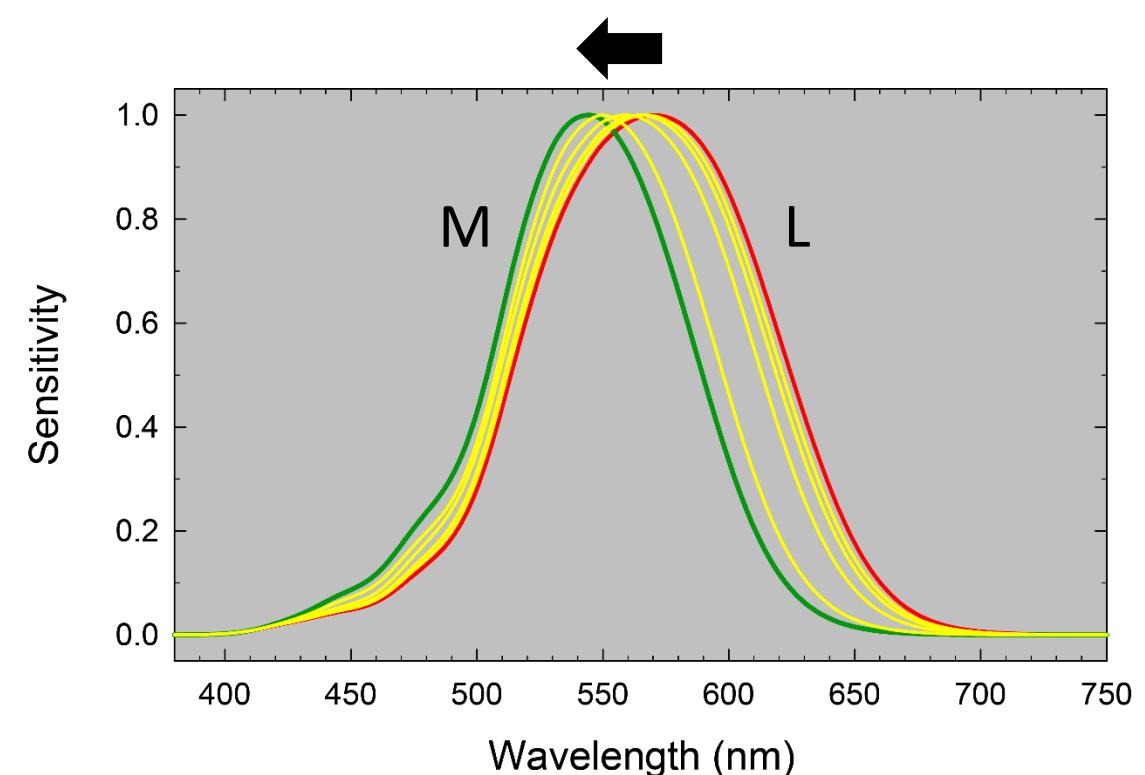
Why are there spectral shifts?

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.

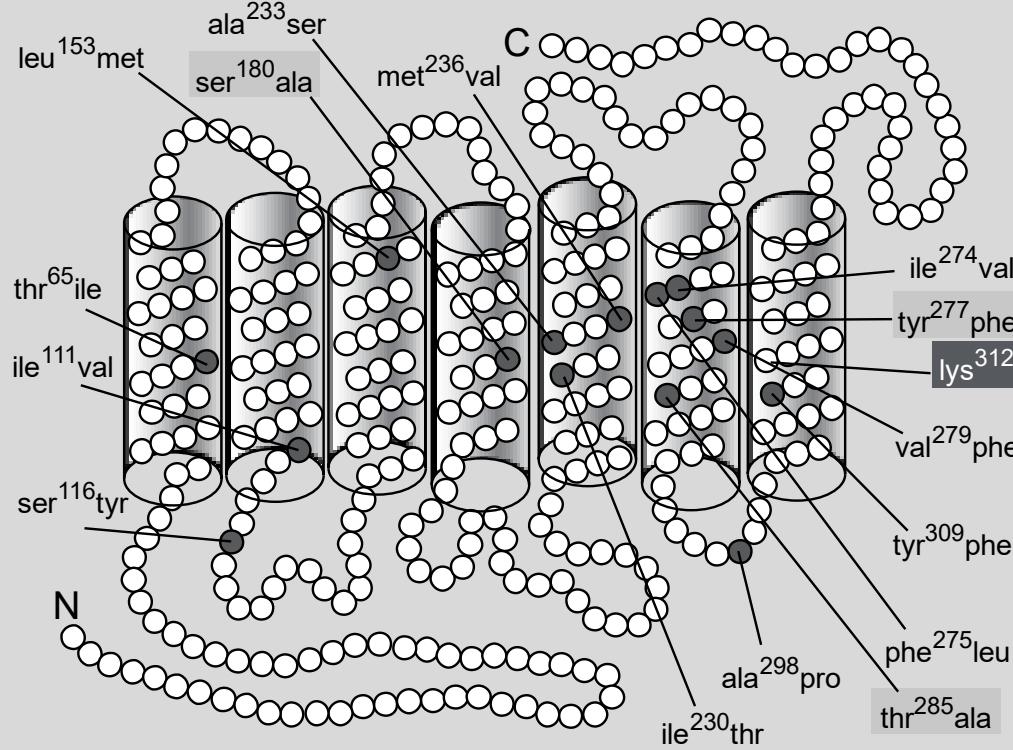


L-cone functions can shift towards M.



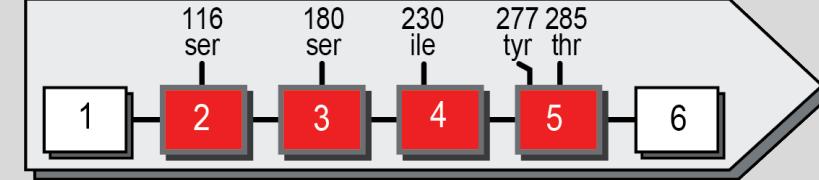
Amino acid differences between the L-and M-cone photopigment opsins

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.

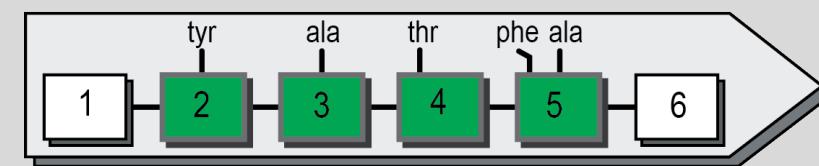


Simplified representation of gene (amino acid) sequences for L and M

L(S180)



M



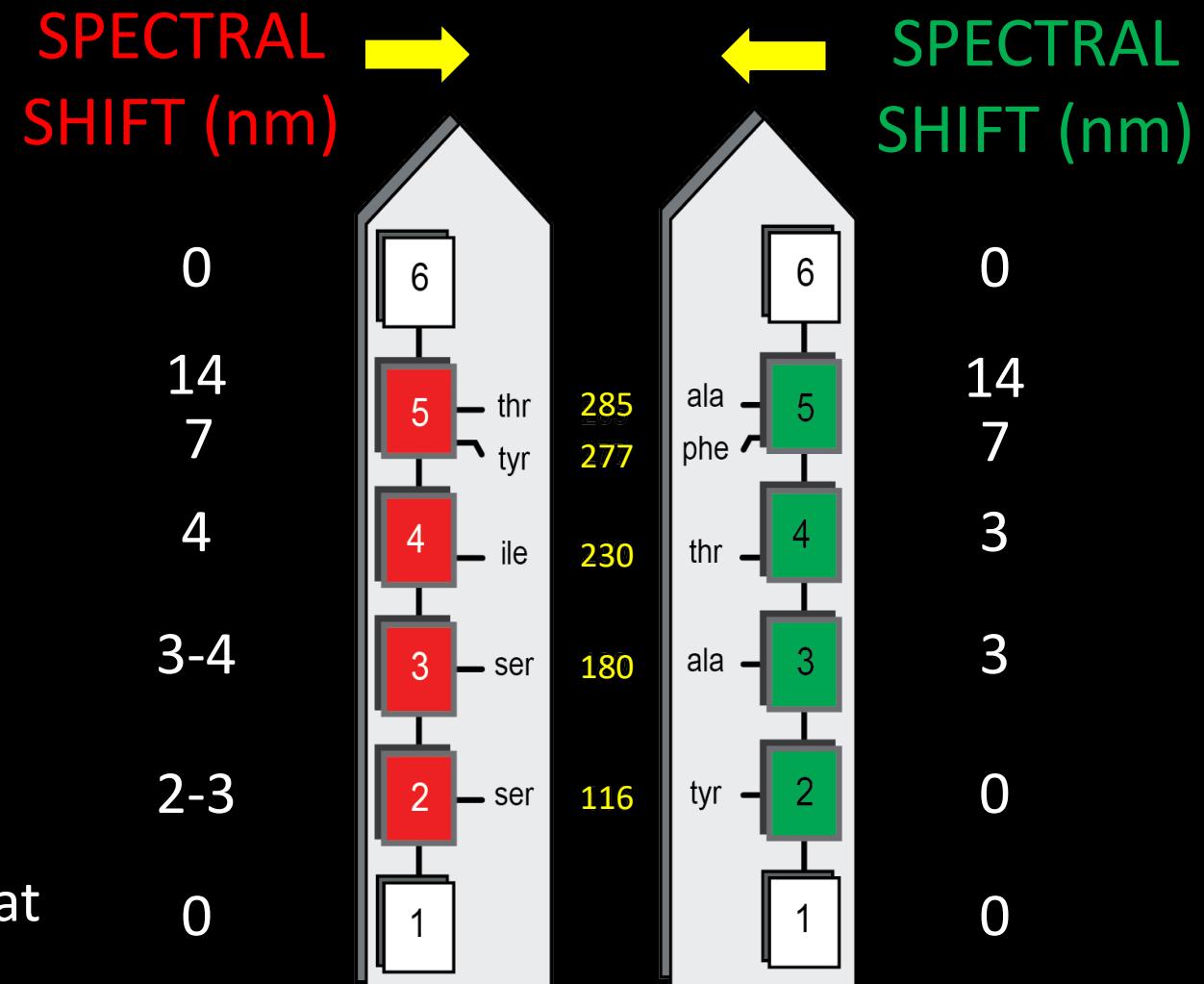
N end

C end

SPECTRAL SHIFTS

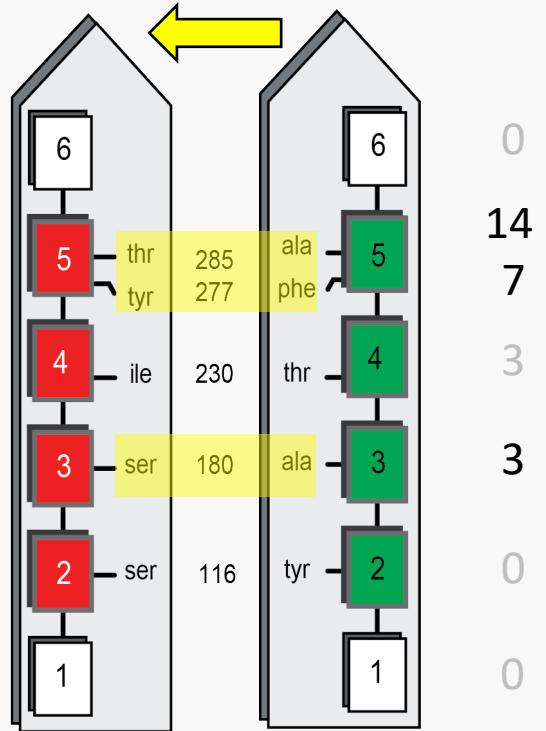
Estimates of the spectral shifts caused by changing the five important amino acid from the L-cone to M-cone versions or *vice versa*.

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



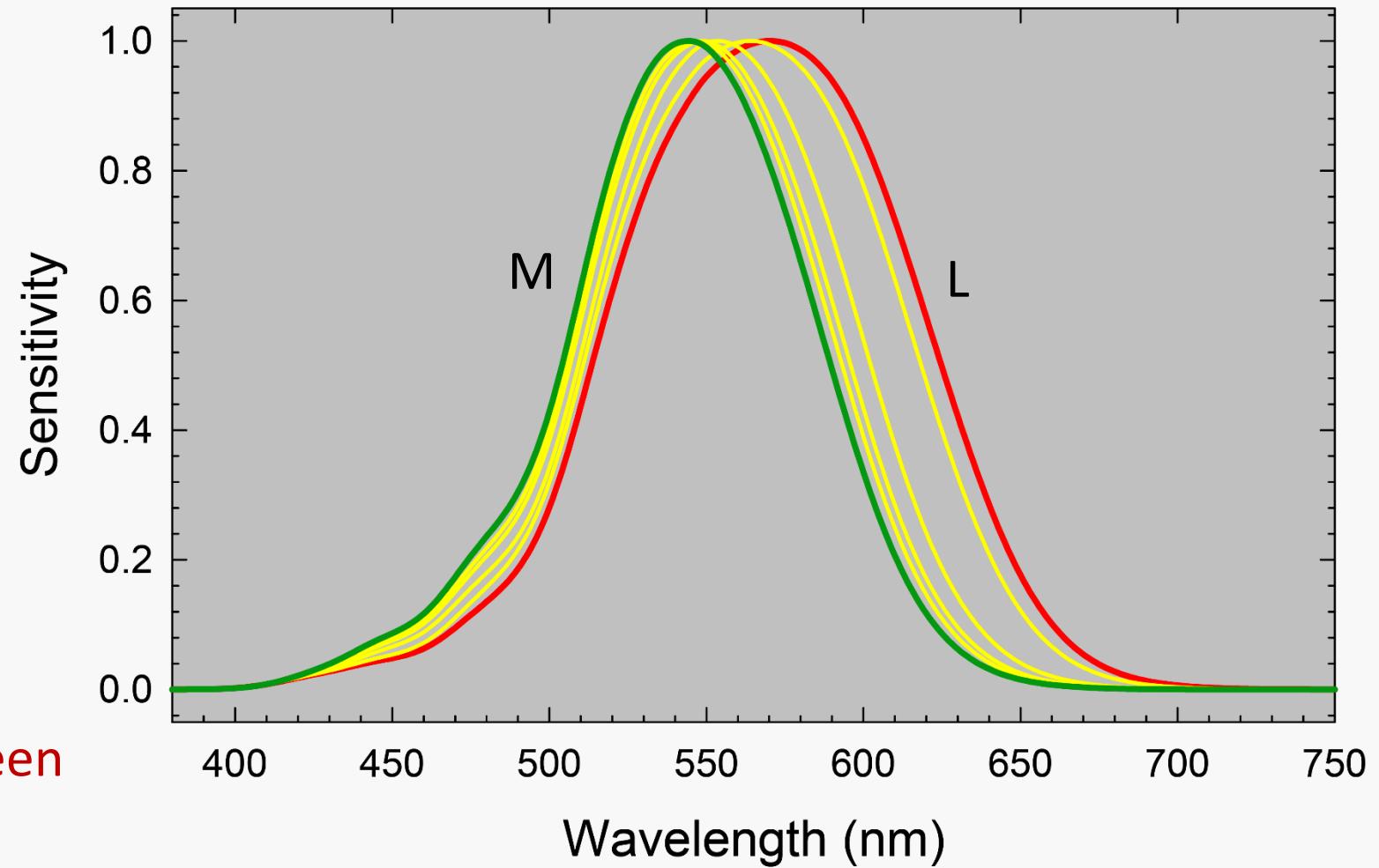
Values from Neitz and Neitz (2011)

M-cone shifts (hybrids)

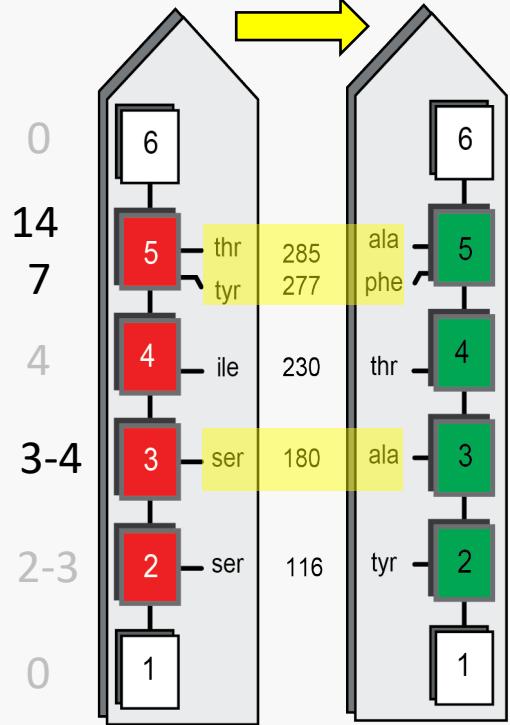


M-cone shifts can cause a red-green colour vision deficiency called deutanomaly or deutanopia.

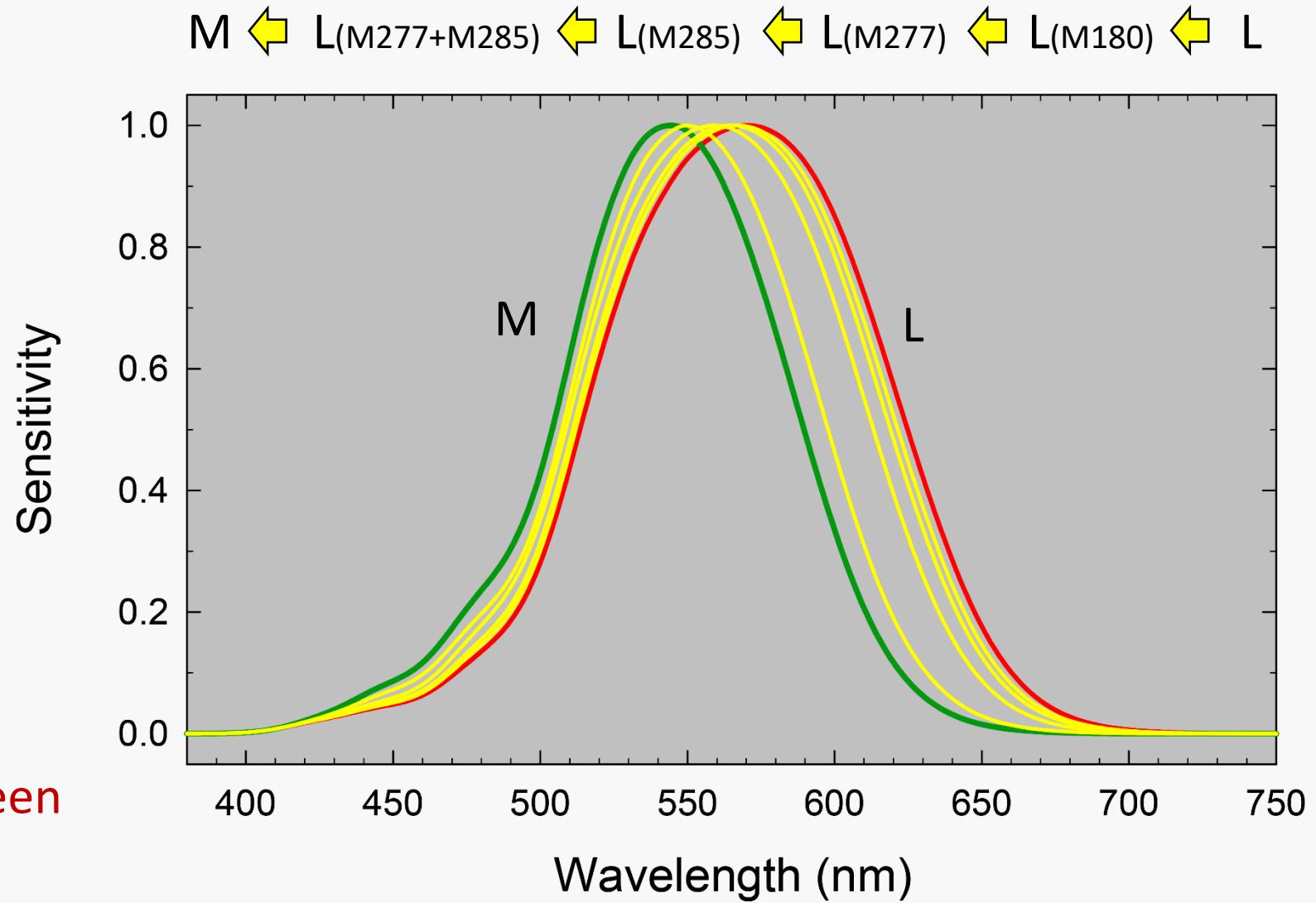
$M \rightarrow M_{(L180)} \rightarrow M_{(L277)} \rightarrow M_{(L285)} \rightarrow M_{(L277+L285)} \rightarrow L$



L-cone shifts (hybrids)



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



CVD prevalence

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

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

Condition	percent in UK	
	Male	Female
Protanopia	no L cone	1.0 0.02
Protanomaly	milder form	1.0 0.03
Deutanopia	no M cone	1.5 0.01
Deutanomaly	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.

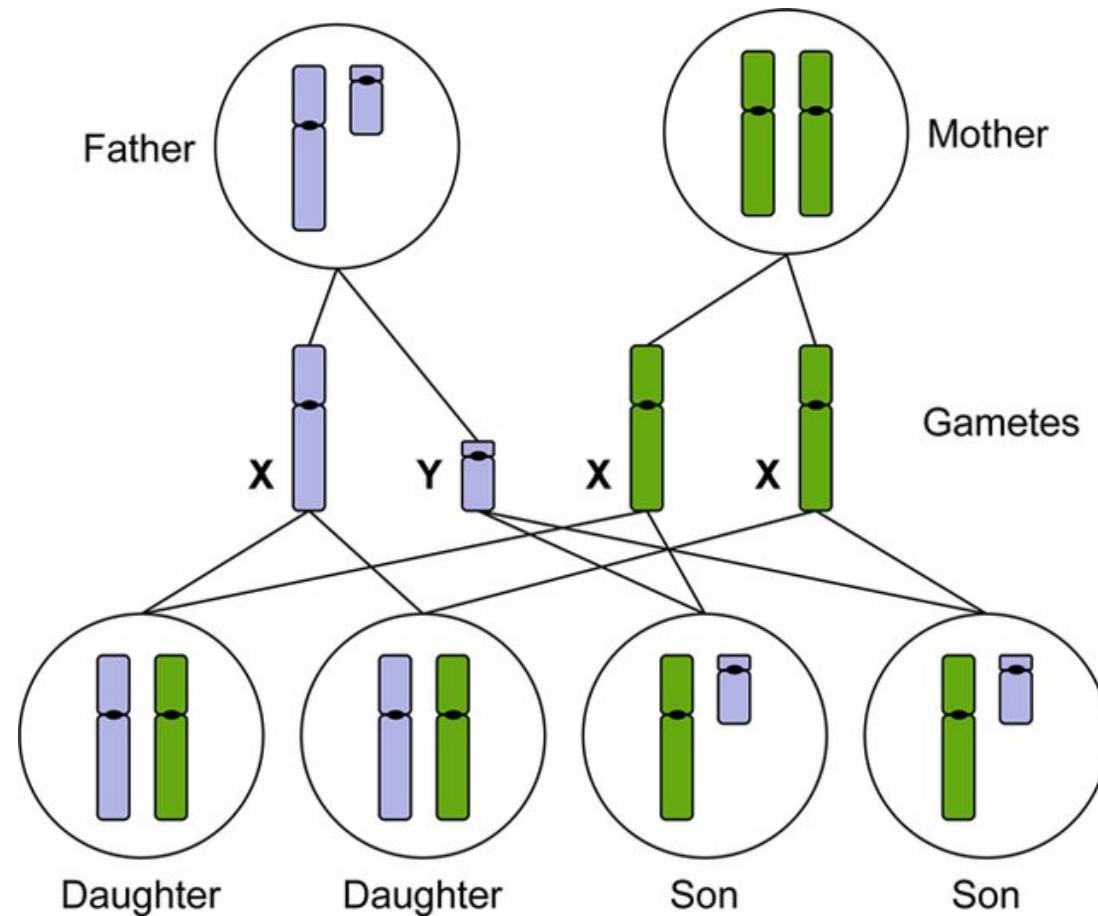


Figure 7 from Jackson, Marks, May & Wilson (2018) *Essays in Biochemistry* 62, 643-723

What causes individual differences?

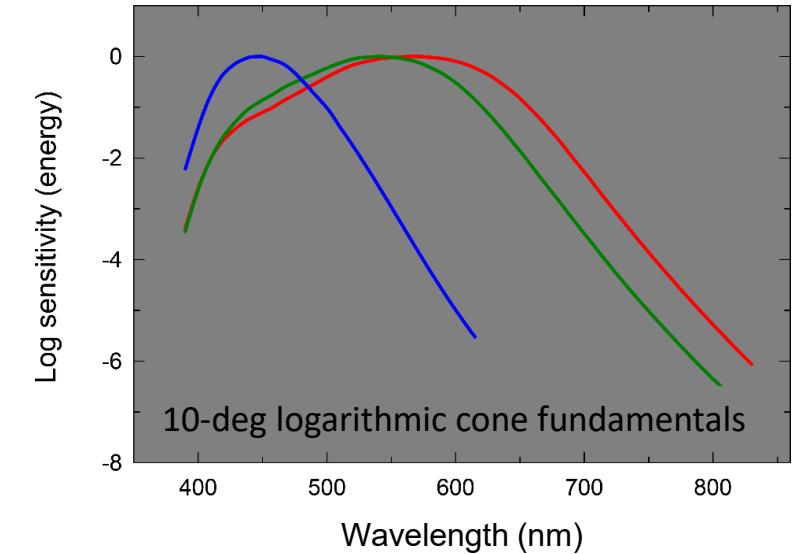
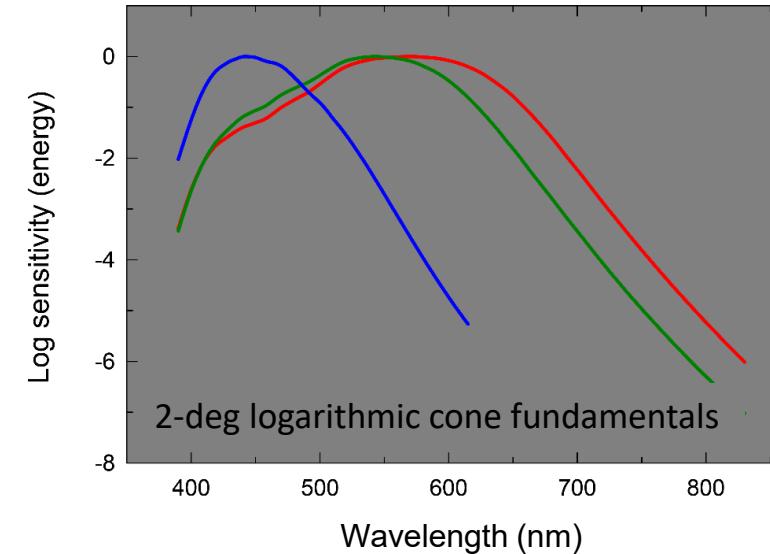
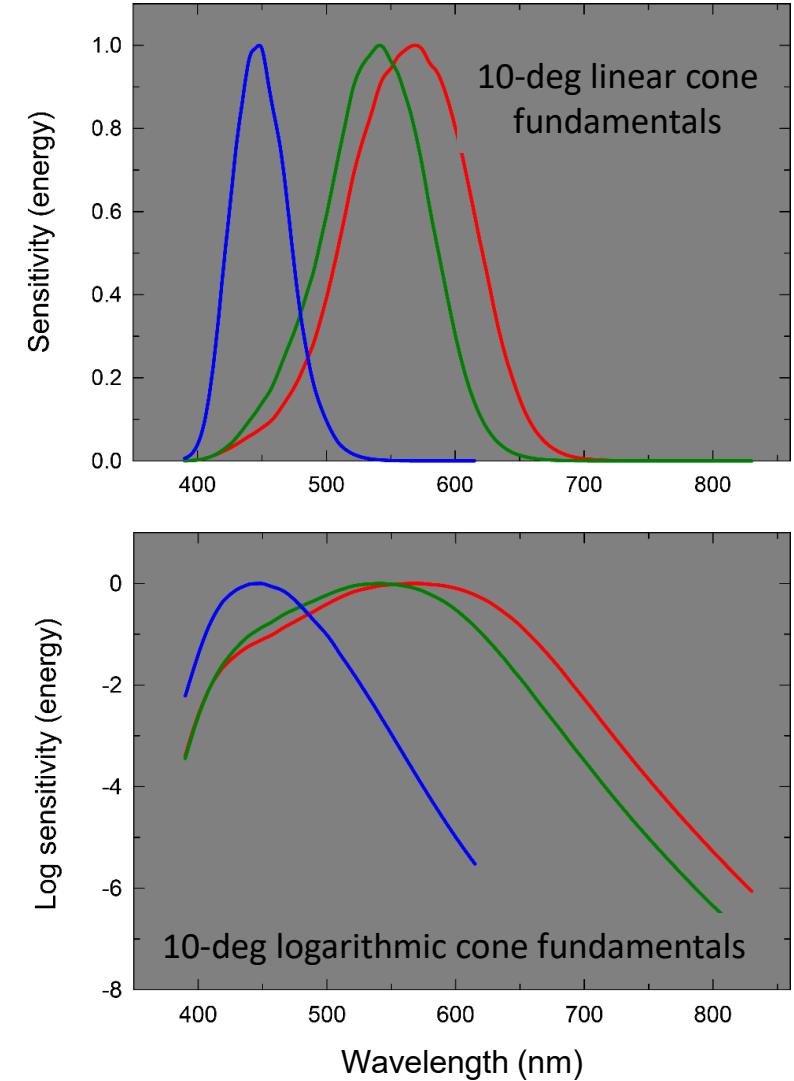
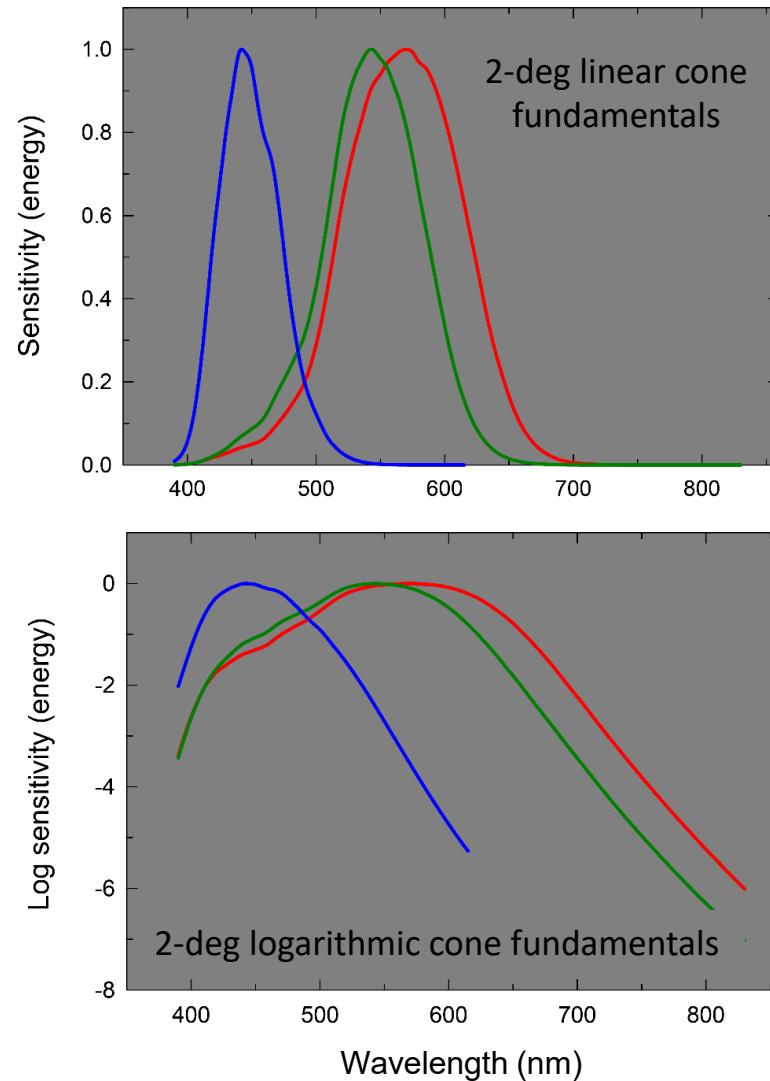
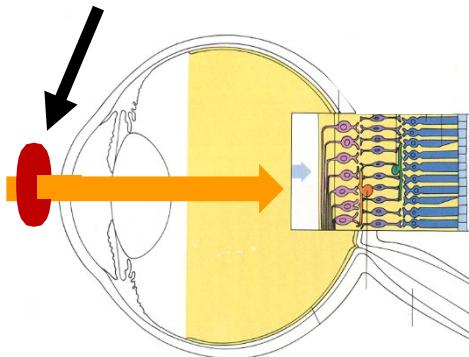
- ▶ Macular pigment optical density differences
- ▶ Lens pigment optical density differences
- ▶ Photopigment optical density differences
- ▶ Spectral shifts in photopigment sensitivity

4. MODELLING INDIVIDUAL DIFFERENCES



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

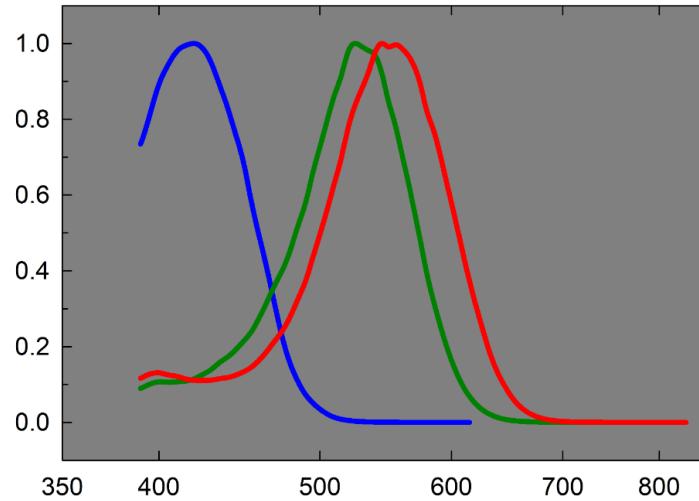
Measured with respect to
light entering the cornea



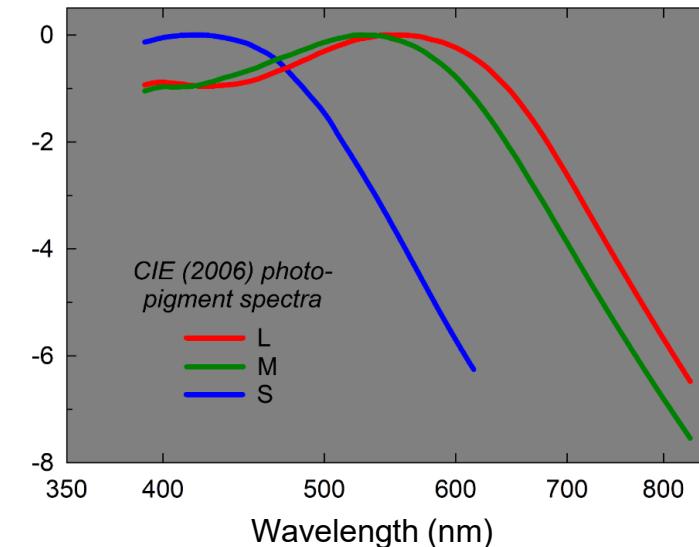
The new CIE standards also define the macular and lens pigment optical density spectra, the photopigment optical densities and the photopigment spectra.

Photopigment absorbance curves

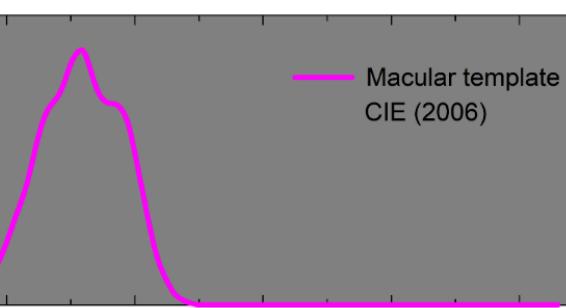
Absorbance



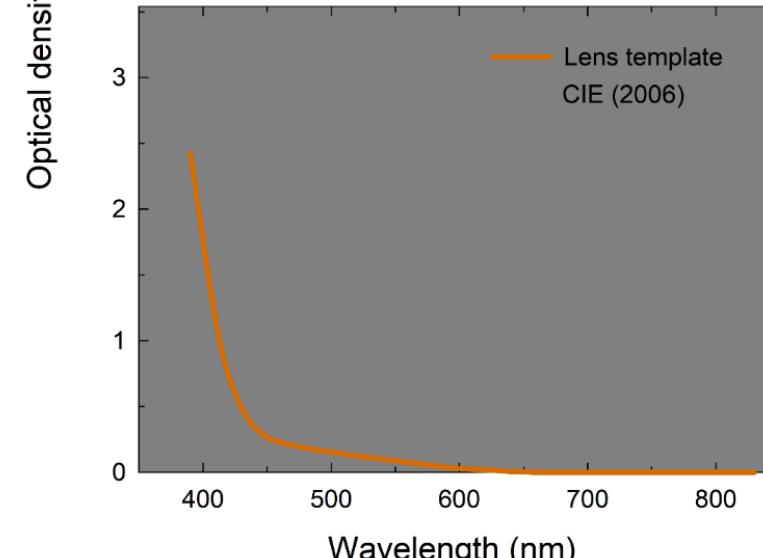
Log absorbance



Macular and lens pigment optical density spectra

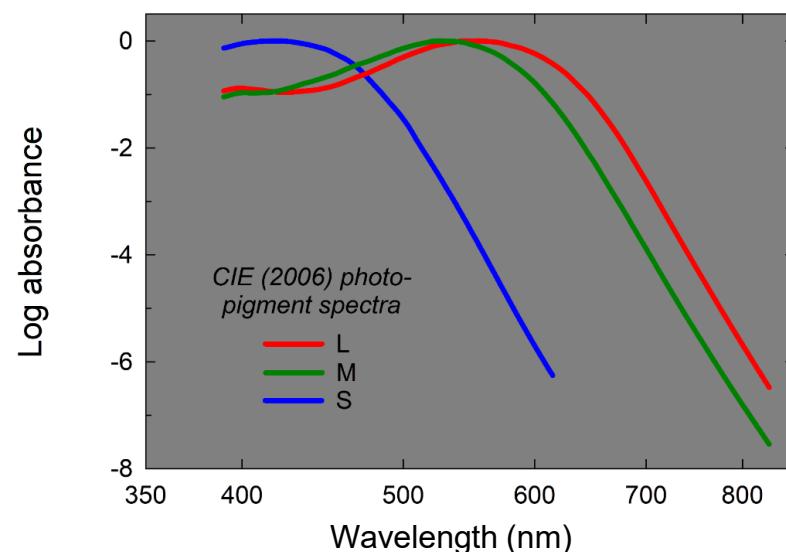
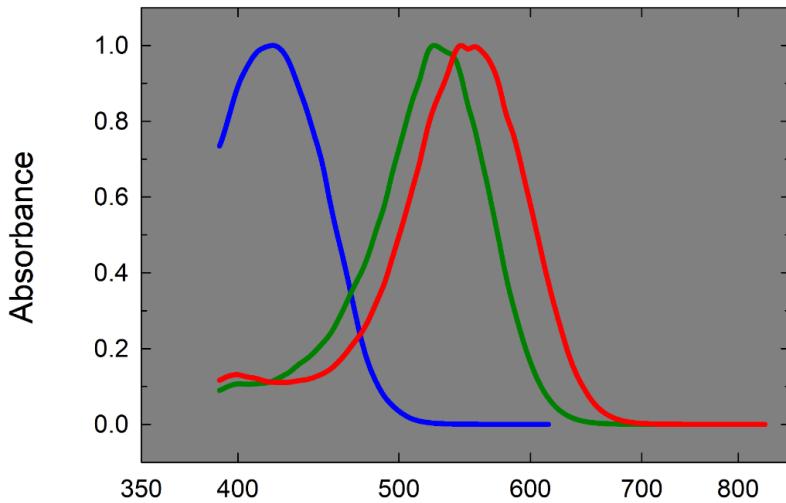


Optical density

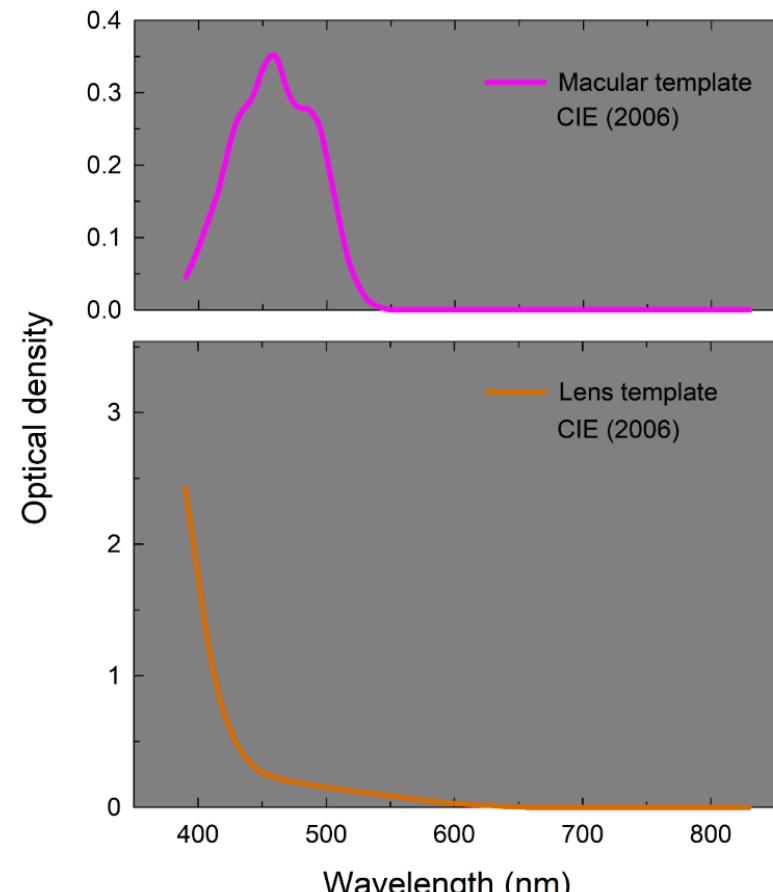


We model individual differences by adjusting the photopigment absorbance curves and varying the macular and lens optical densities

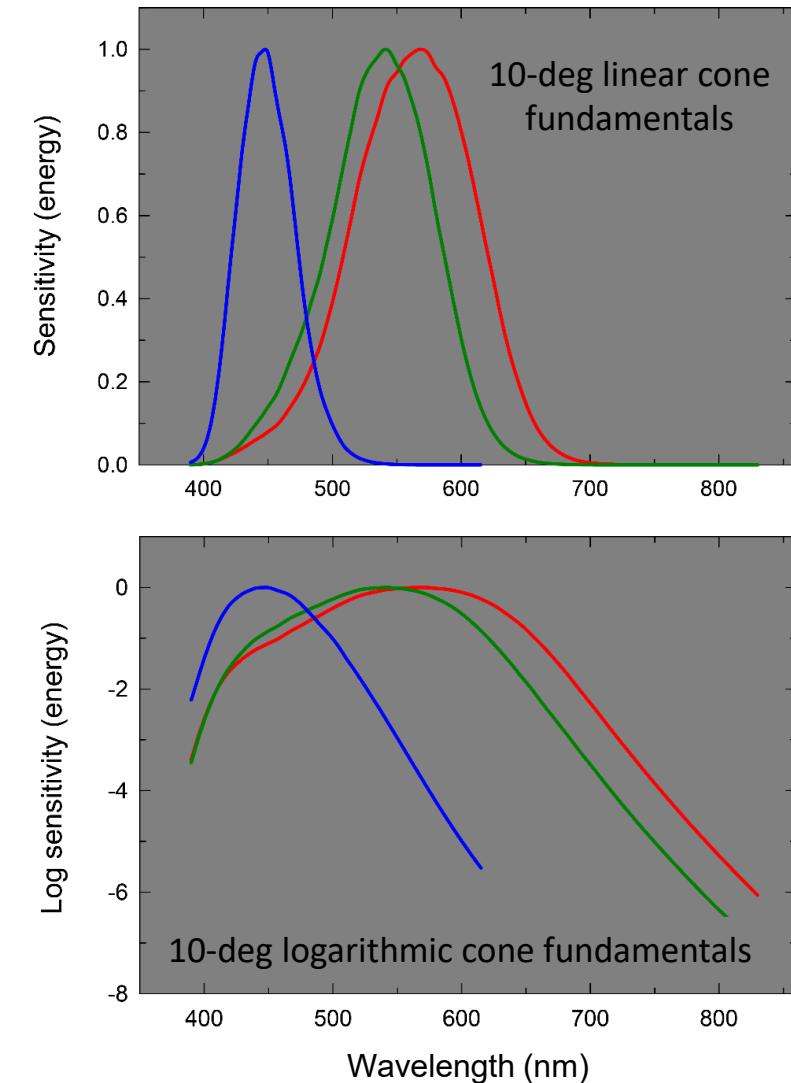
Photopigment absorbance curves

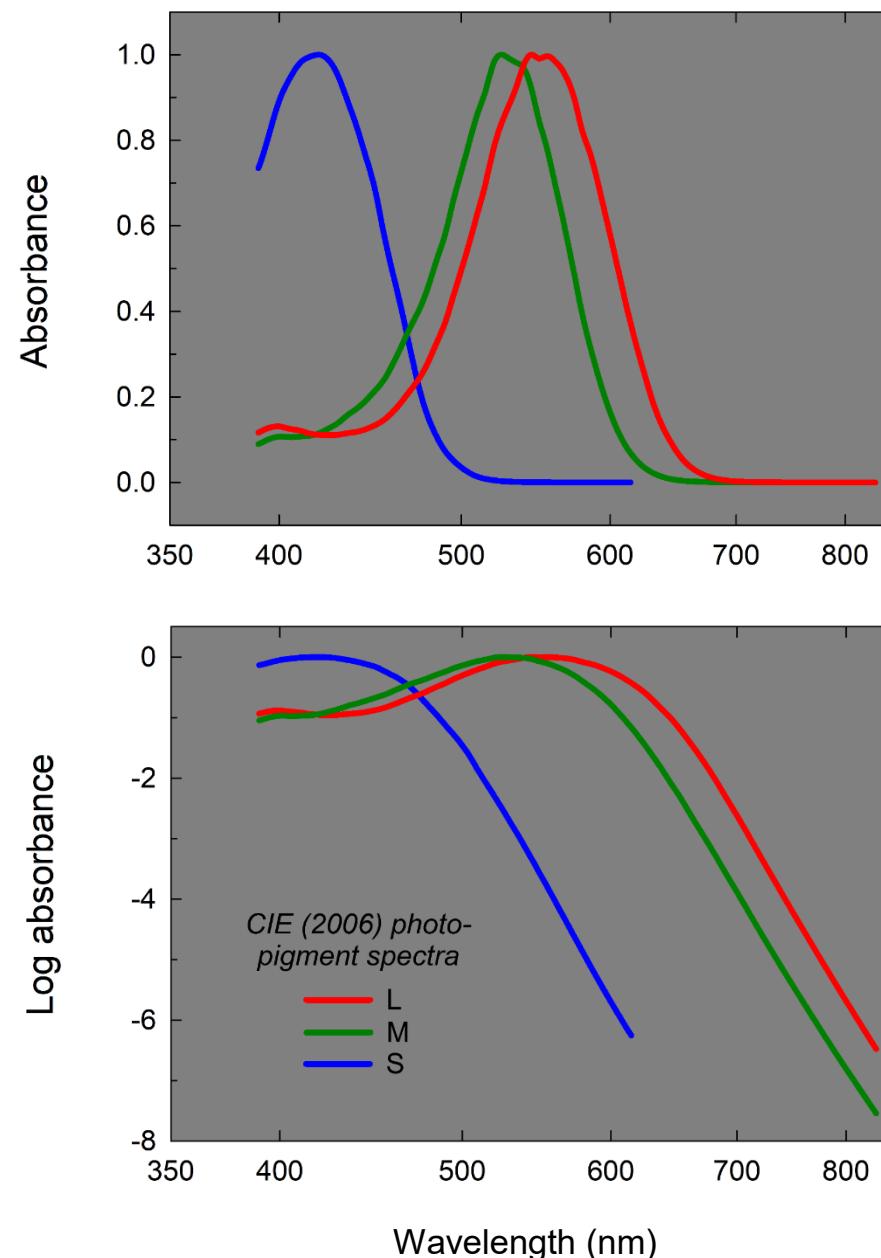


Macular and lens pigment optical density spectra

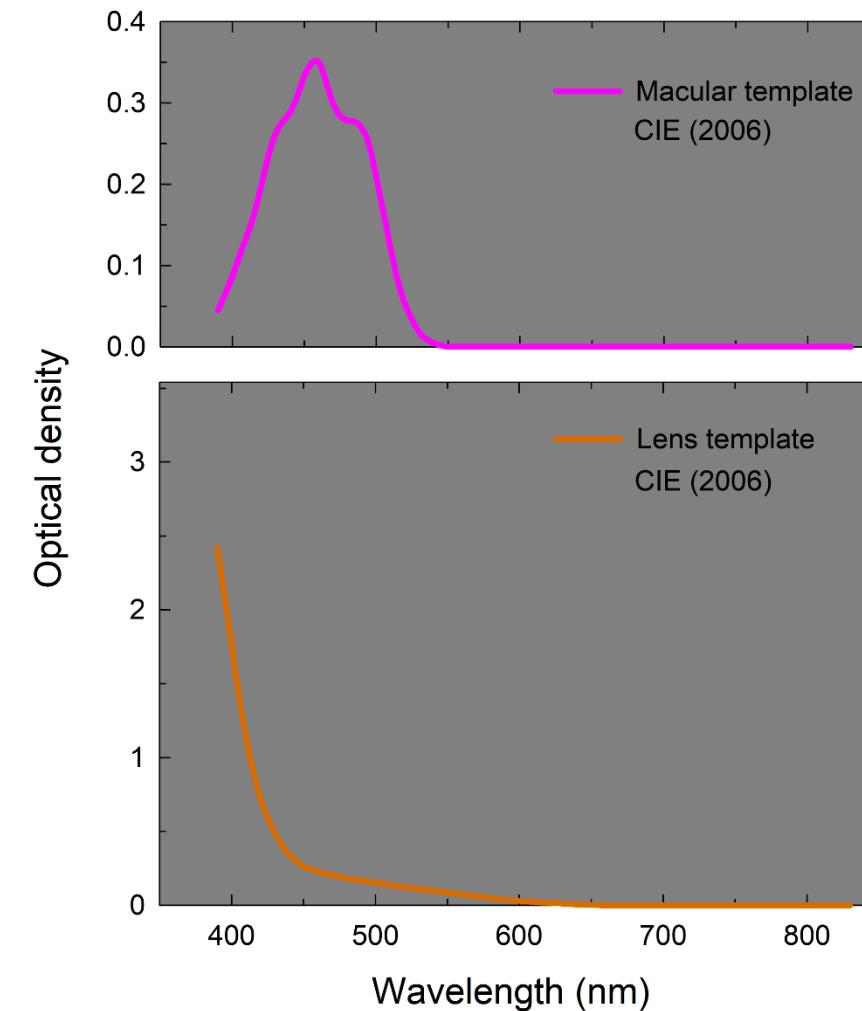


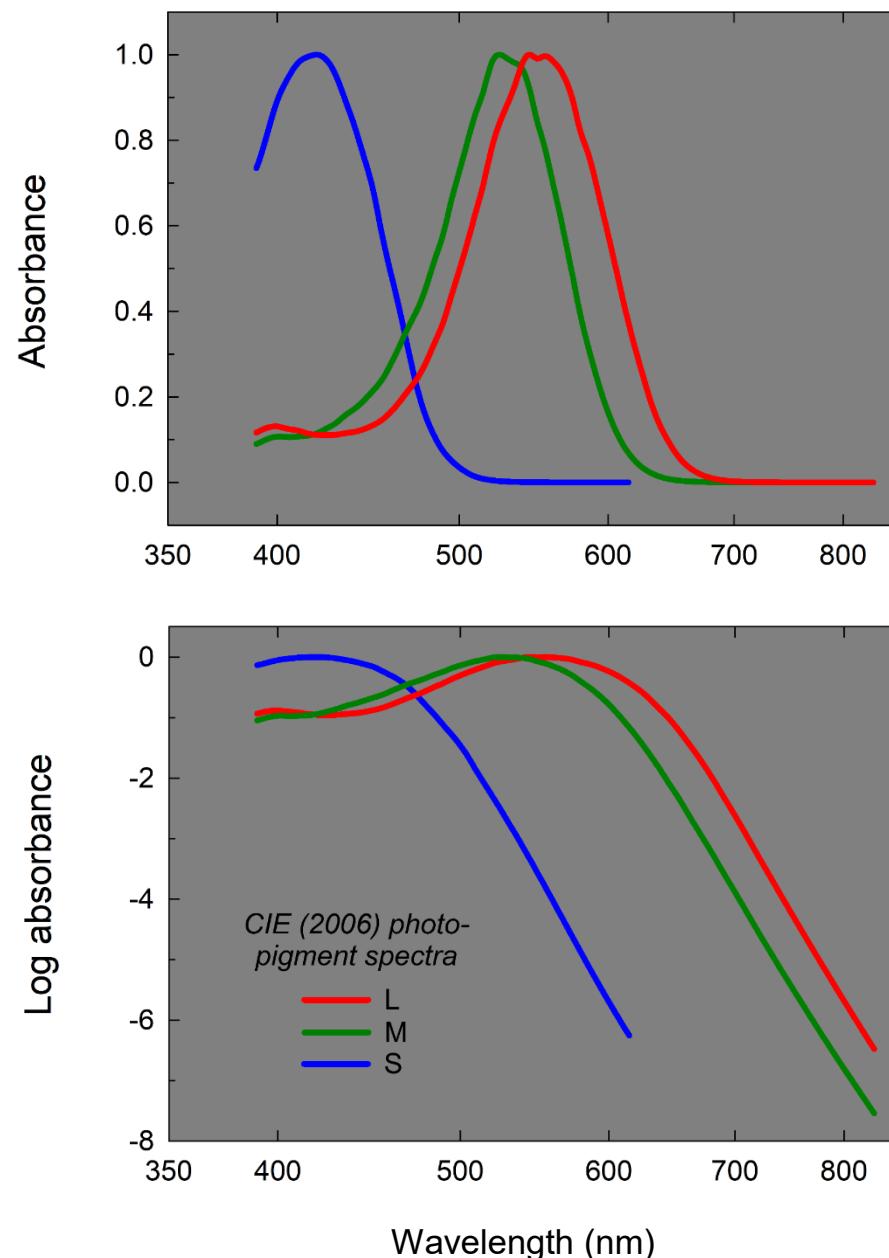
Corneal spectral sensitivities



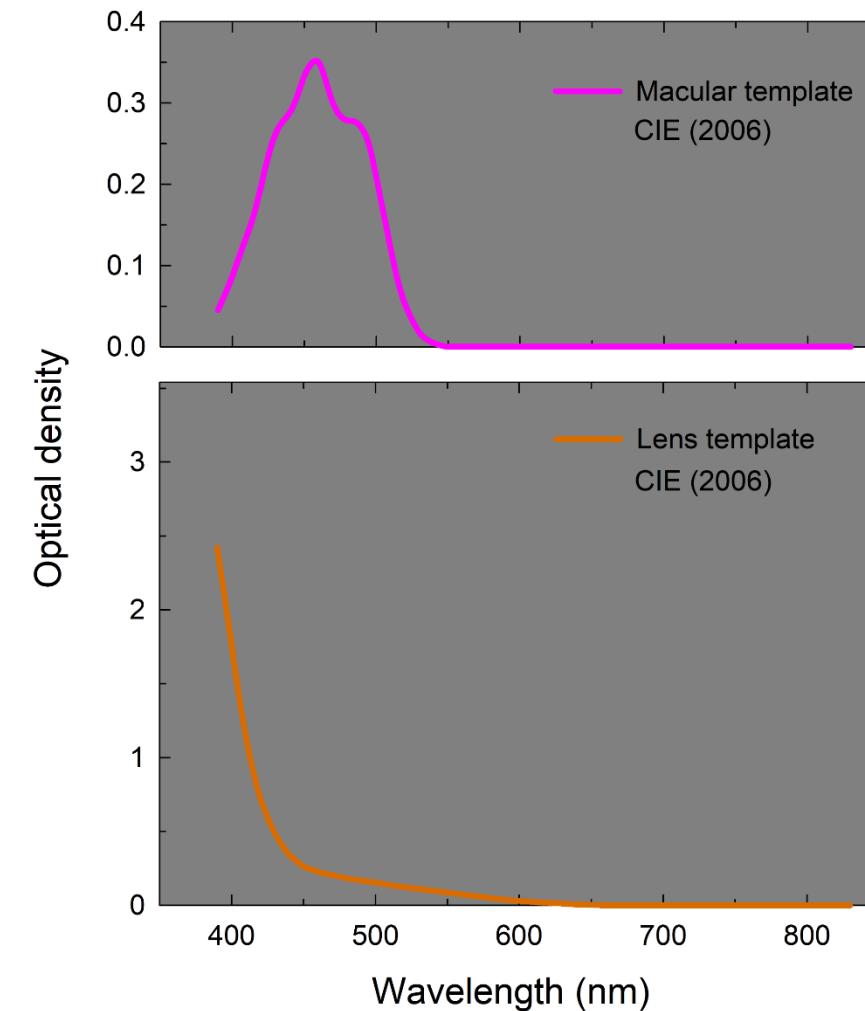


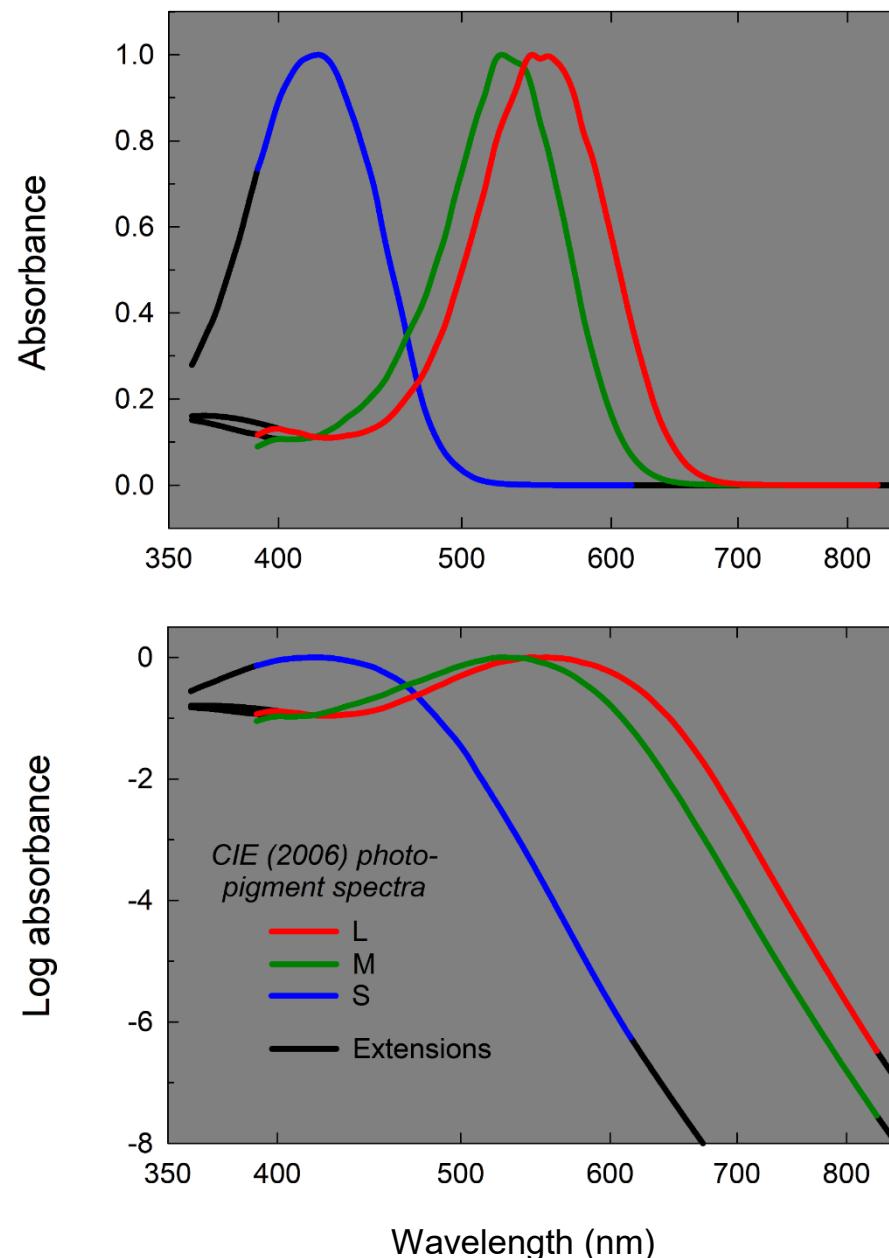
Unfortunately, the CIE (2006) LMS standards are defined as discrete values at 5 or 1 nm steps rather than as continuous functions of wavelength.



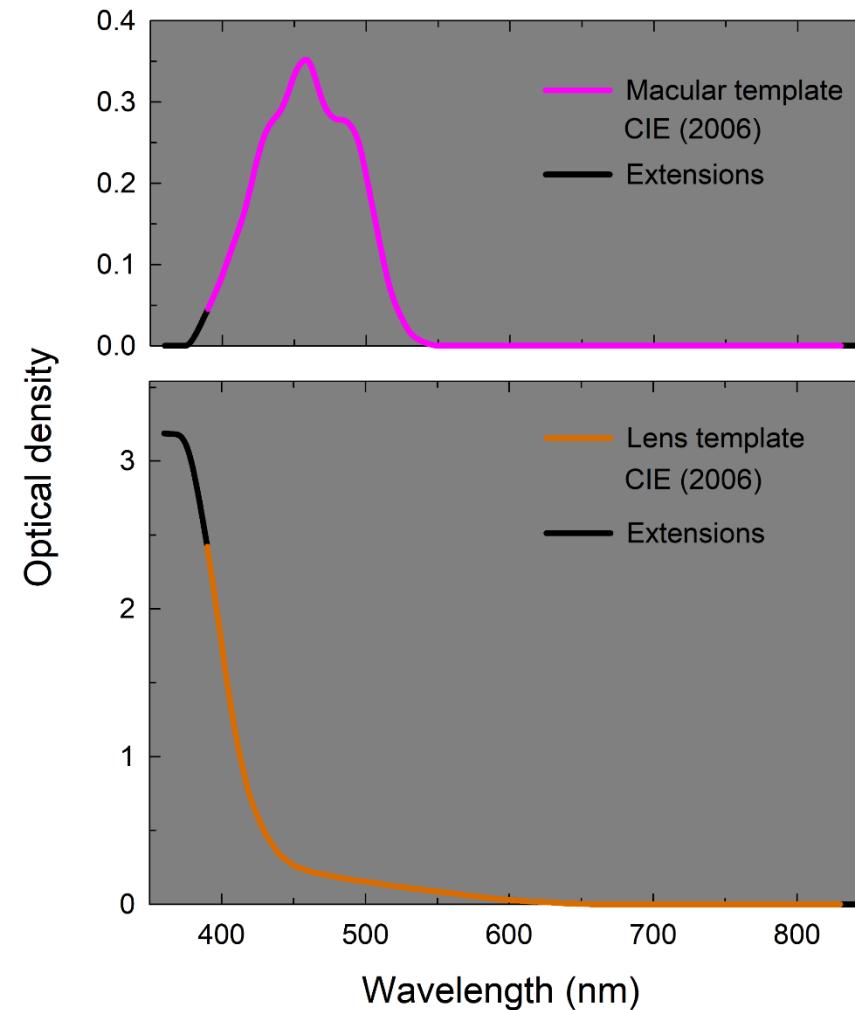


For computational convenience, we want to define these as continuous functions of wavelength...





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



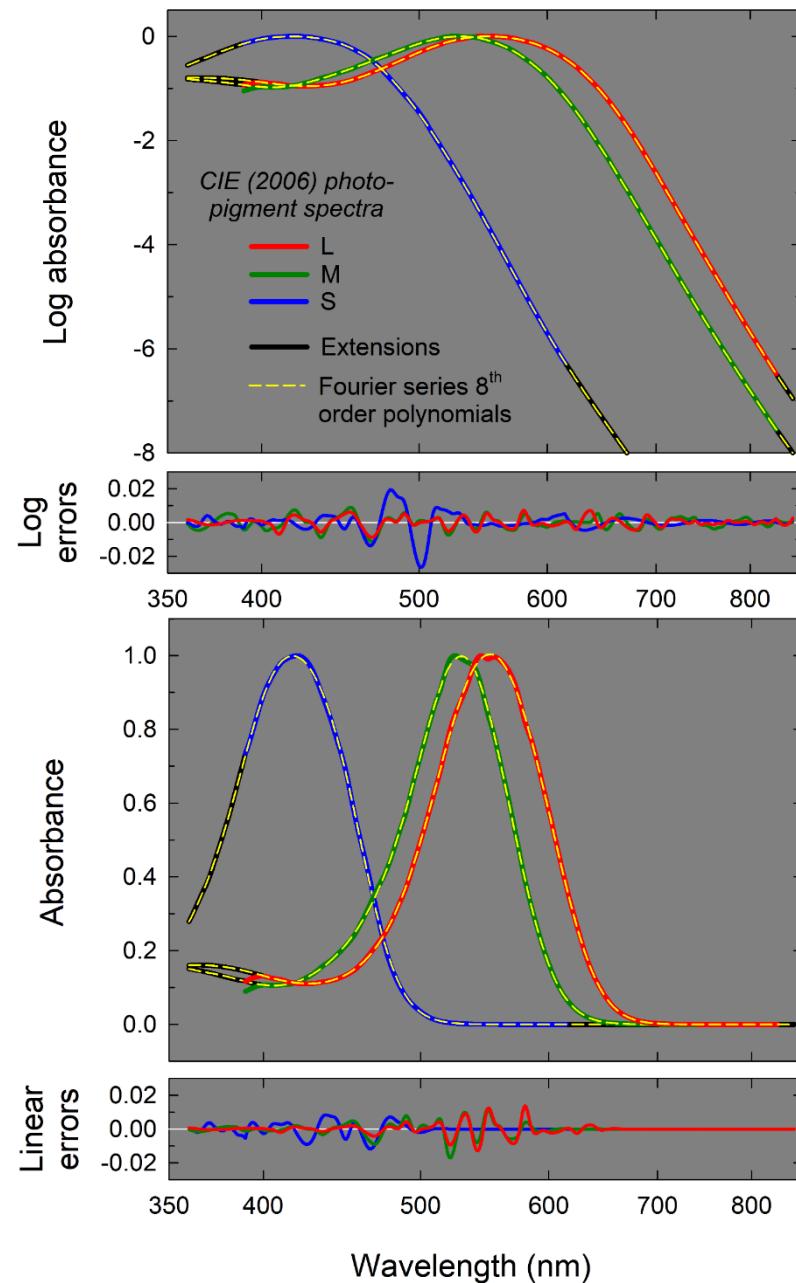
Fourier polynomials were then fitted to the discrete functions and then used to define the template shapes

The templates are of the general form:

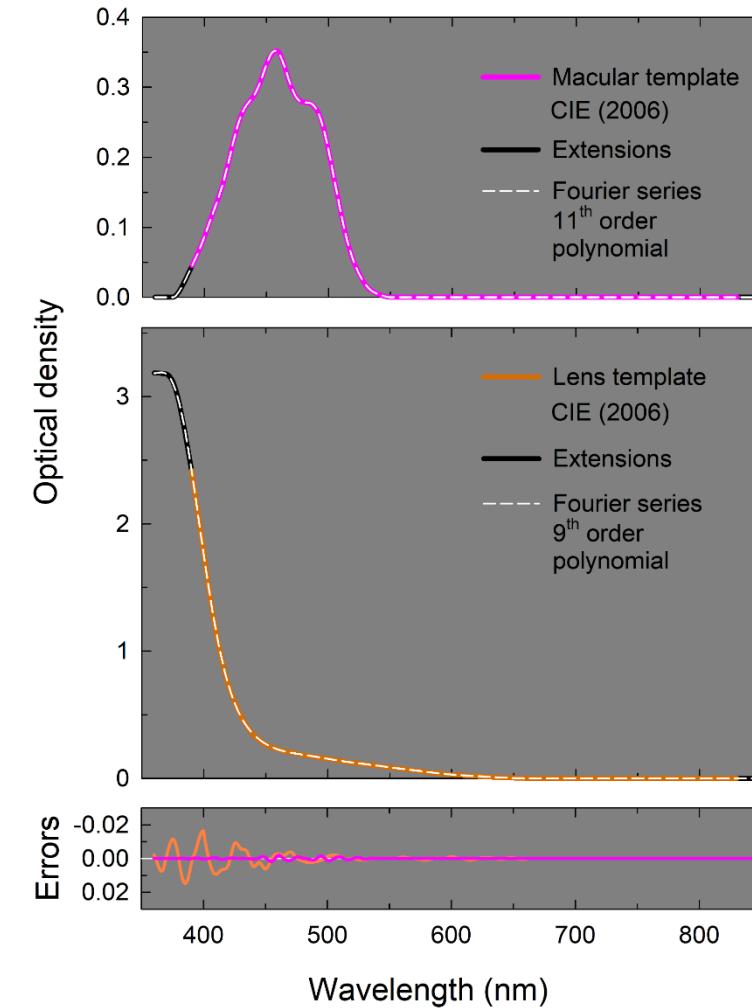
$$F(\theta) = a_0 + \sum_{k=1}^n [a_k \cos(k\theta) + b_k \sin(k\theta)]$$

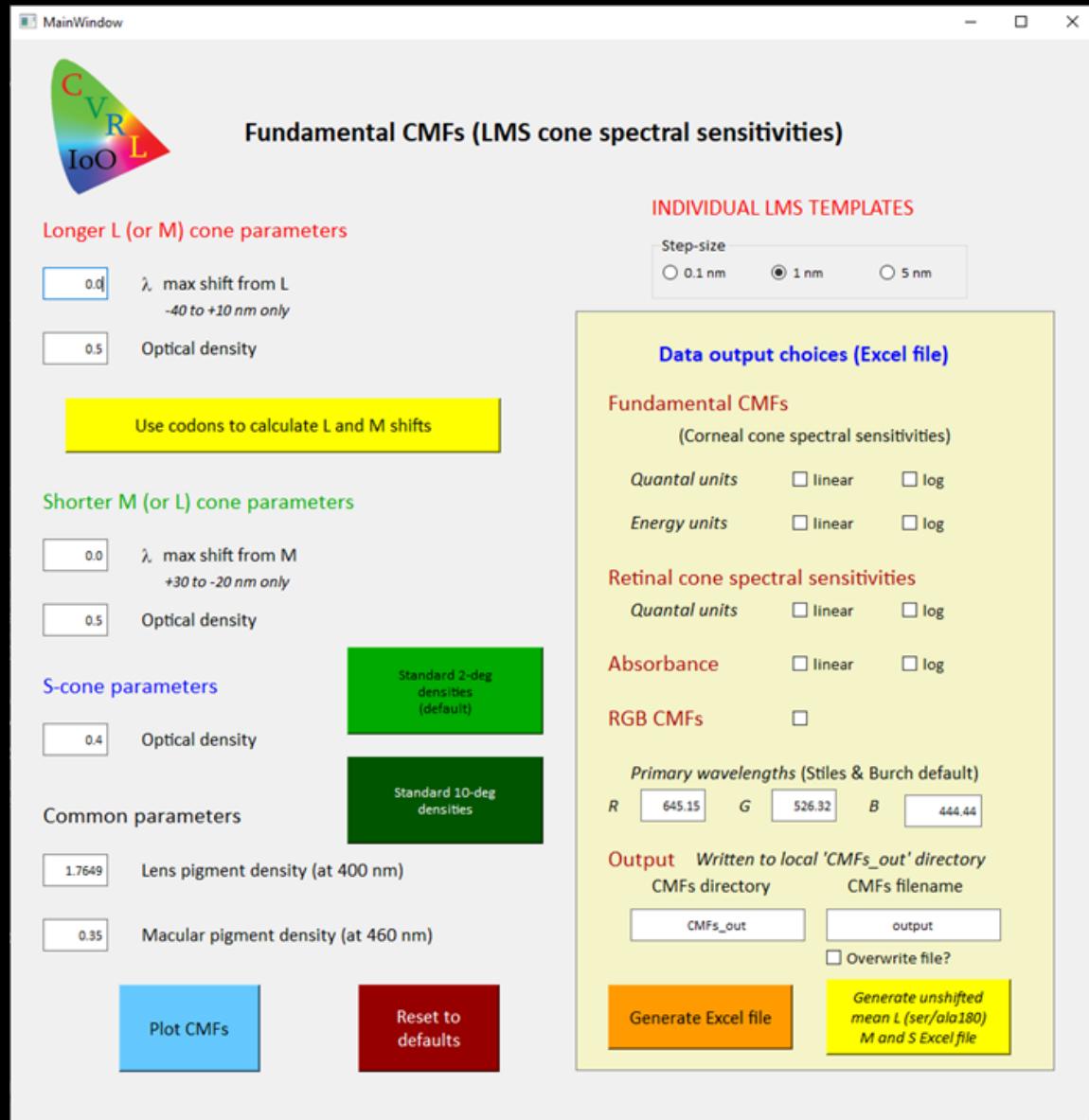
n is the number of harmonics.

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



Important that they describe both log and linear absorbances!





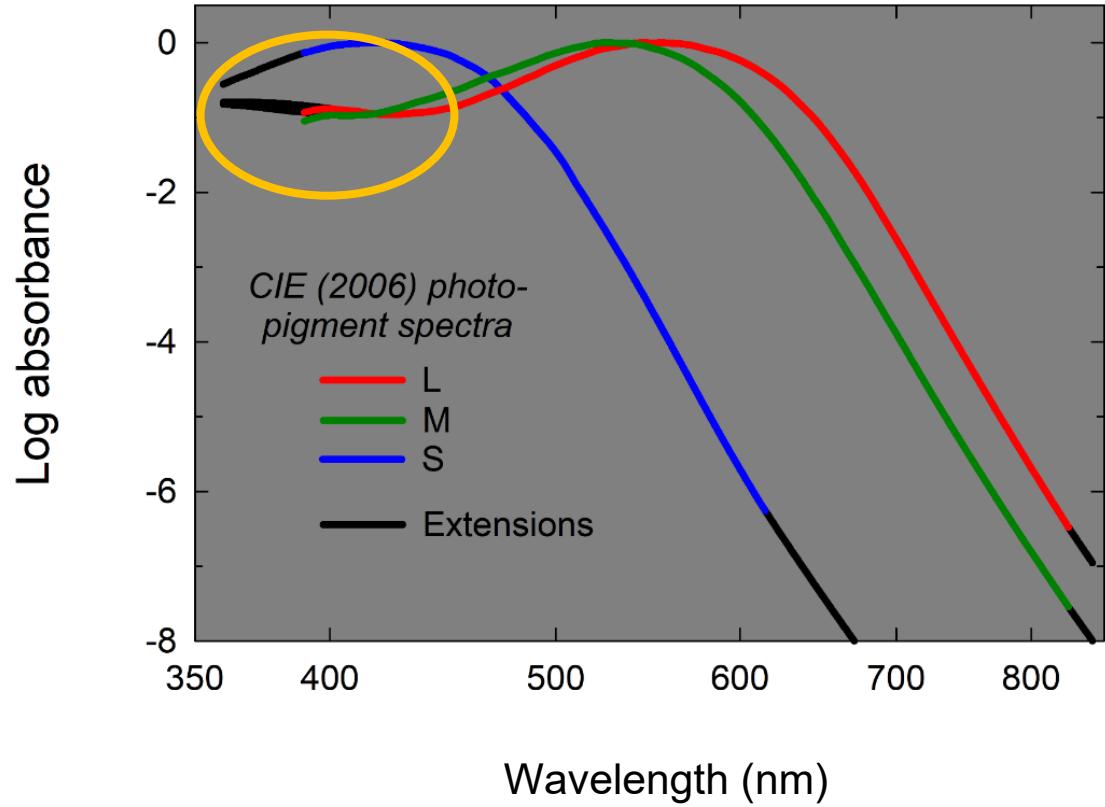
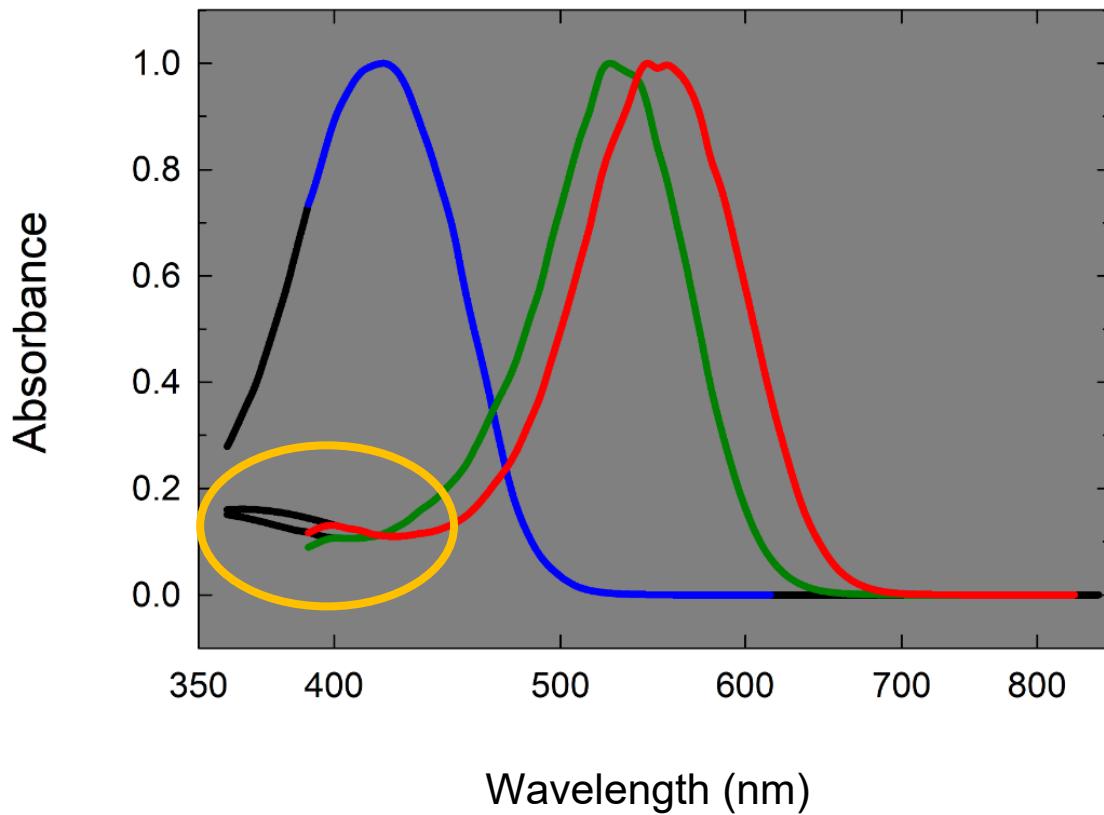
Shorter ML-cone				Longer LM-cone		
Codon	M	L	Exon	M	L	Codon
116	<input checked="" type="radio"/> Tyr	<input type="radio"/> Ser	2	<input type="radio"/> Tyr	<input checked="" type="radio"/> Ser	116
180	<input checked="" type="radio"/> Ala	<input type="radio"/> Ser	3	<input type="radio"/> Ala	<input checked="" 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) **0** LM shift (nm) **0** **Done**

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):

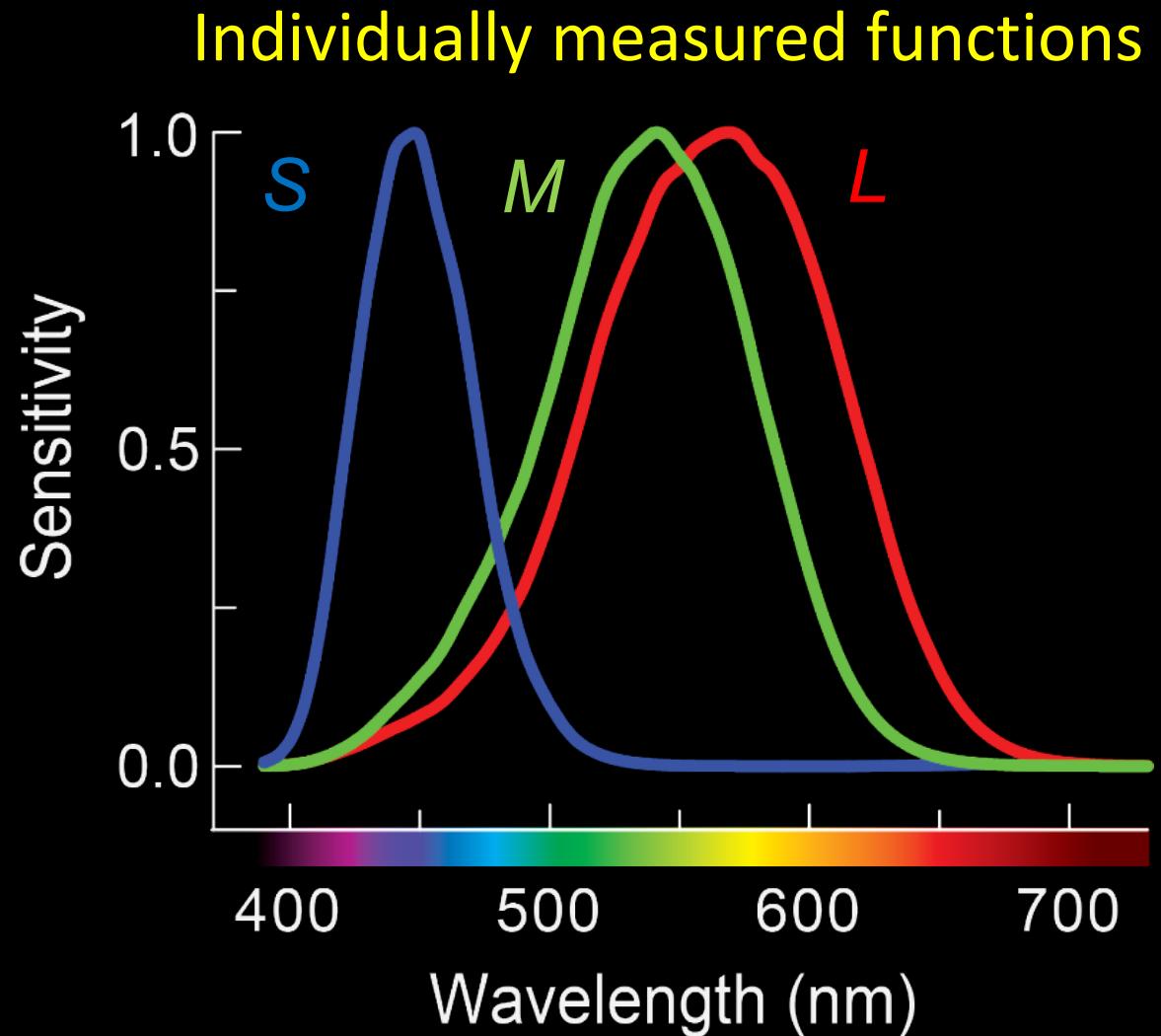


5. MEASURING INDIVIDUAL DIFFERENCES

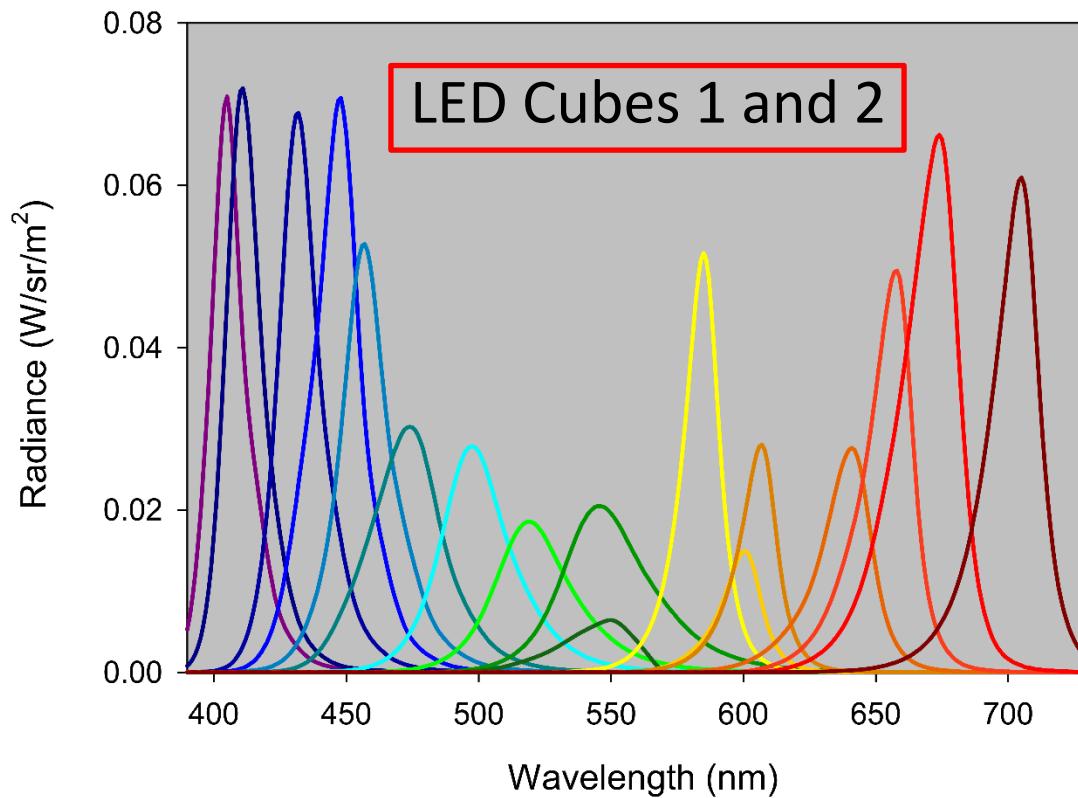


Individual cone spectral sensitivities (colour matching functions)

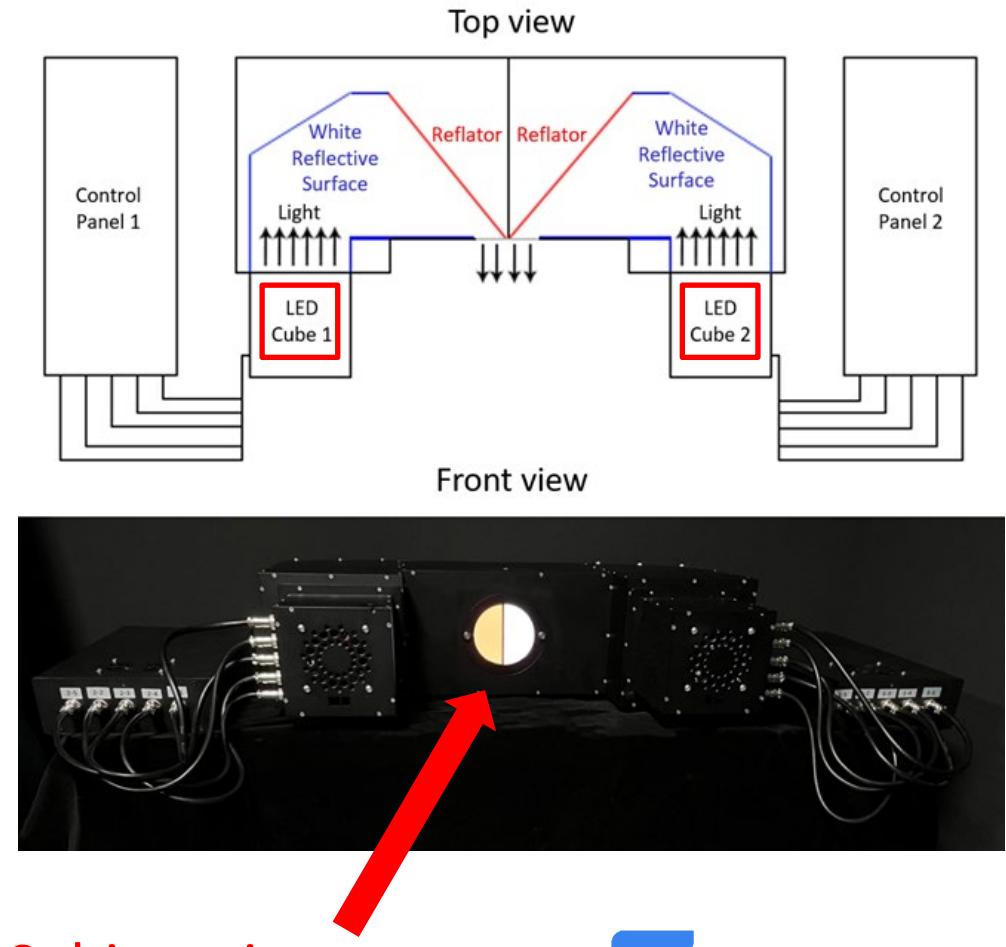
We can overcome the problems of individual differences by measuring an individual's own cone spectral sensitivities.



Trichromator (LEDMax) (developed in collaboration with Thouslite)



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

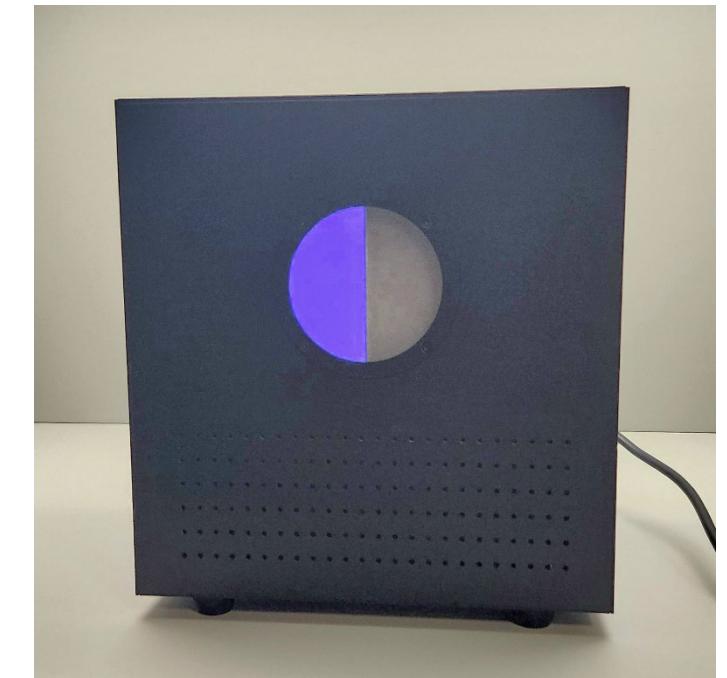
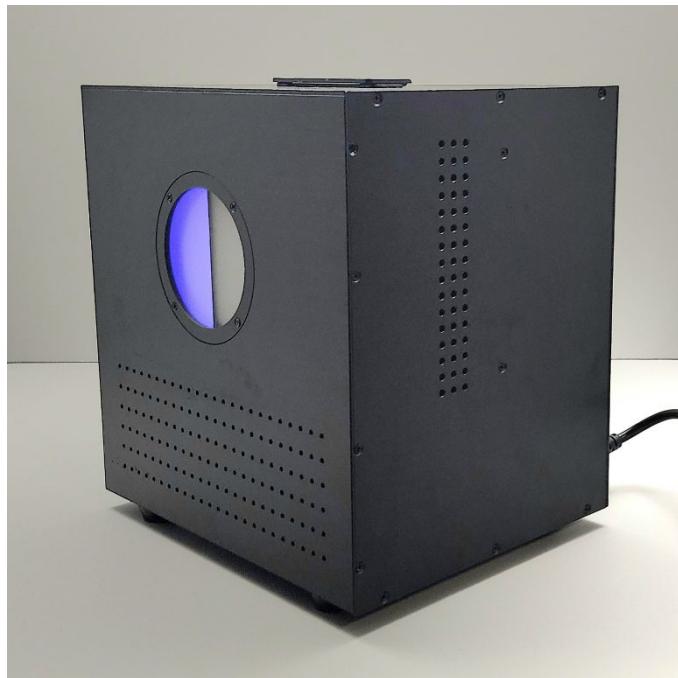


Subject view

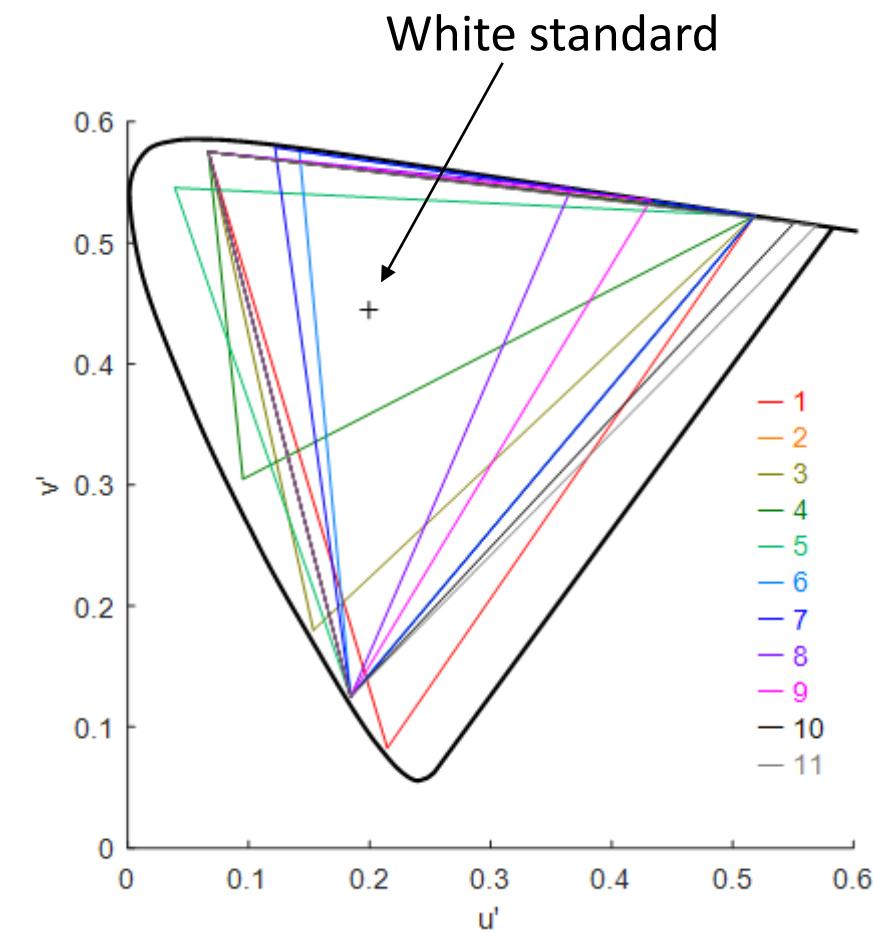
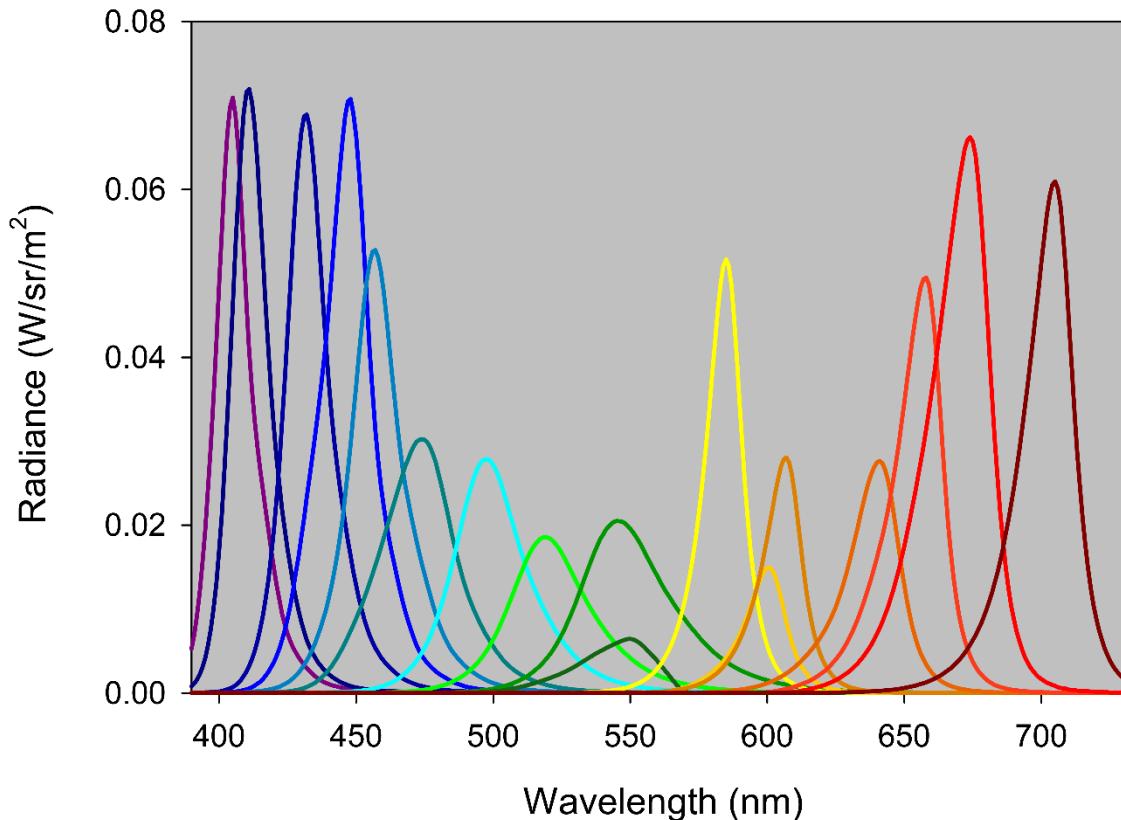
THOUSLITE

Trichromator (LEDMax) updated version

A newer compact version
has been developed...

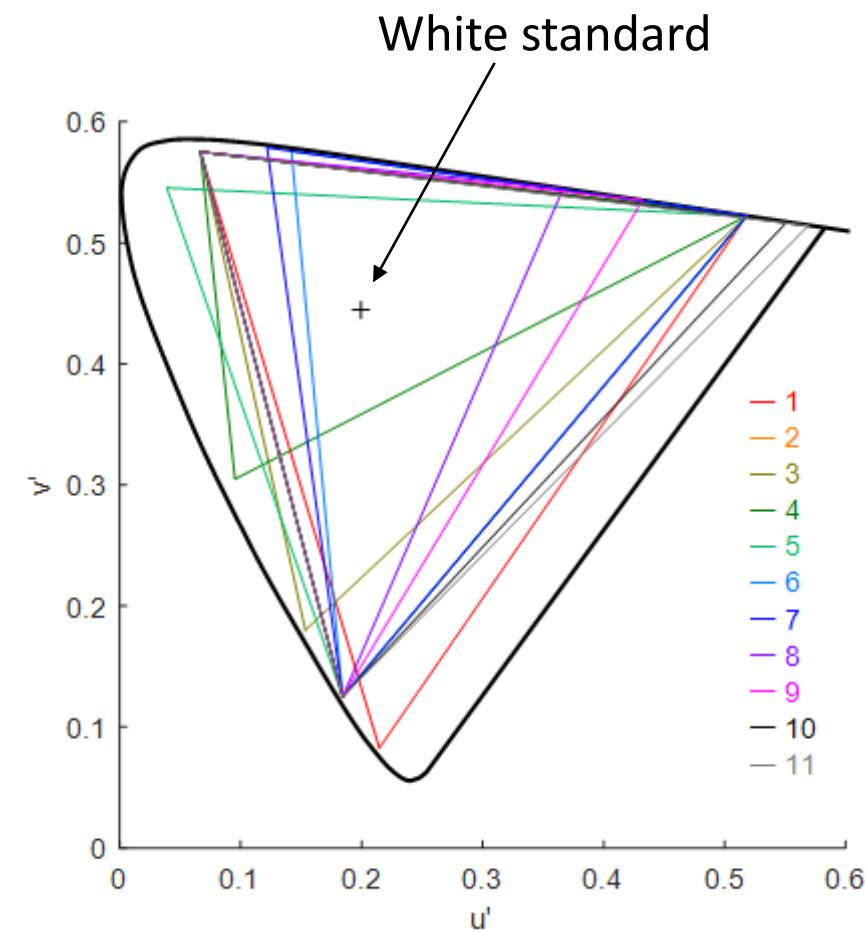
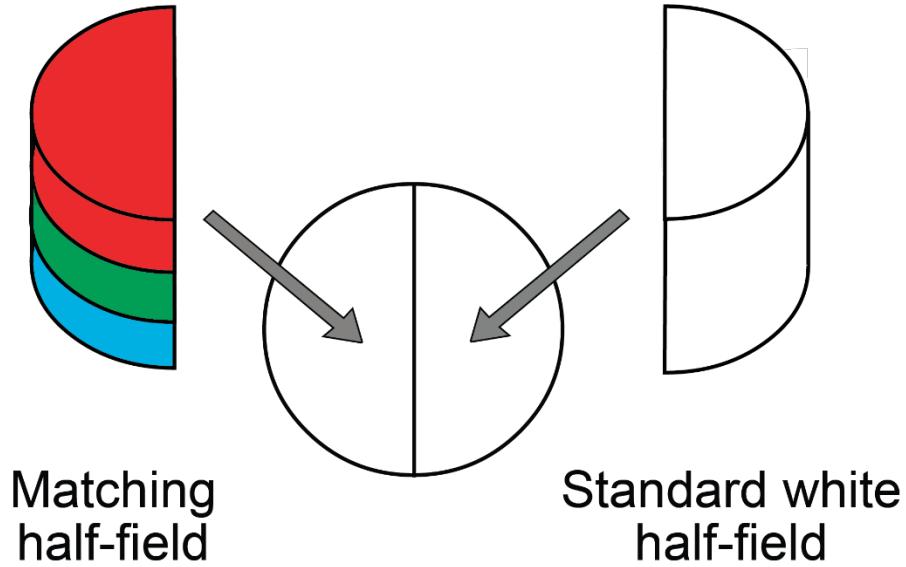


Colour matching measurements



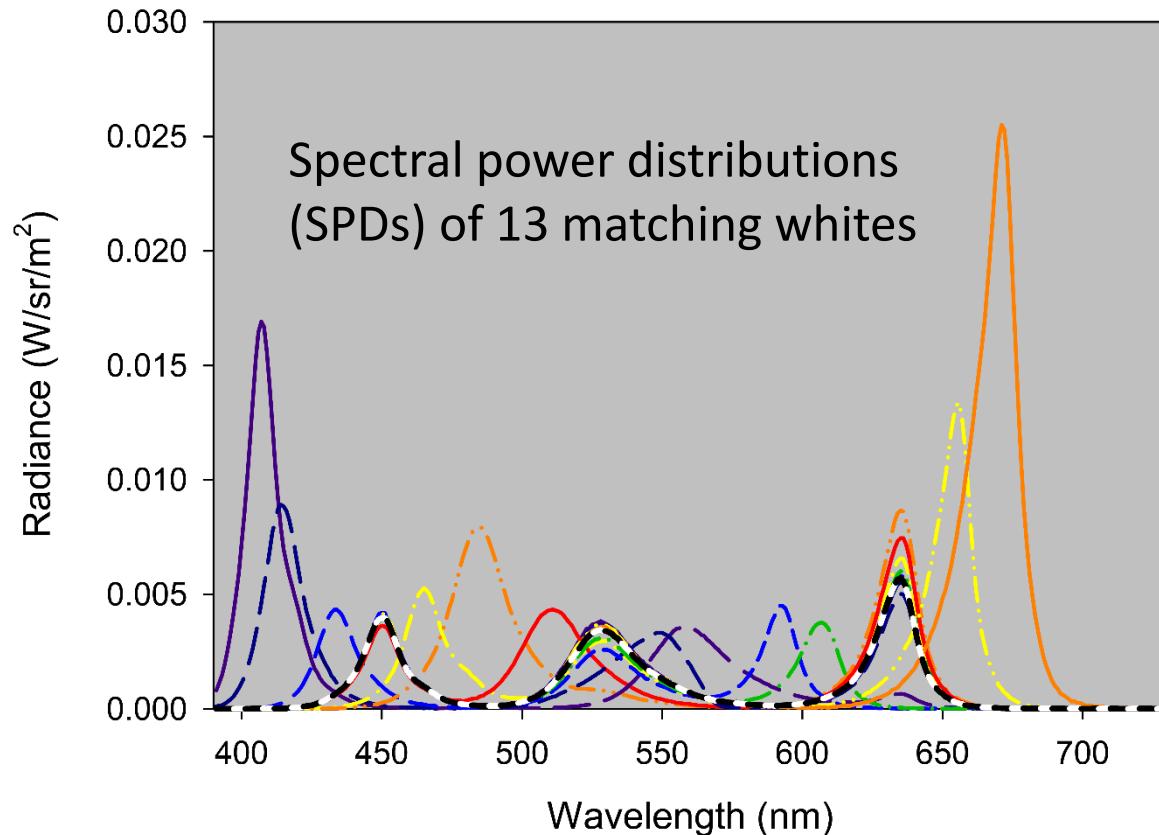
We chose 11 triplets of LEDs (primaries lights) that can be optically mixed to match a white standard (+)...

Colour matching measurements

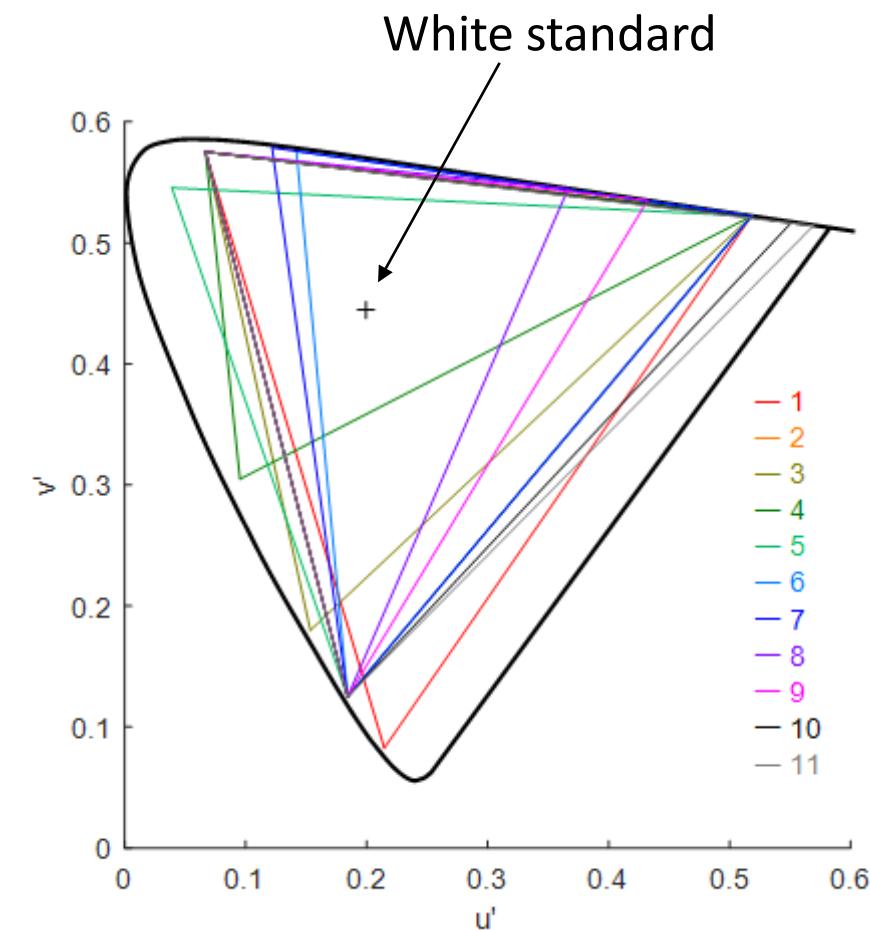


We then asked observers to adjust the intensities of each of the 11 triplets of primaries to match the white standard...

Colour matching results

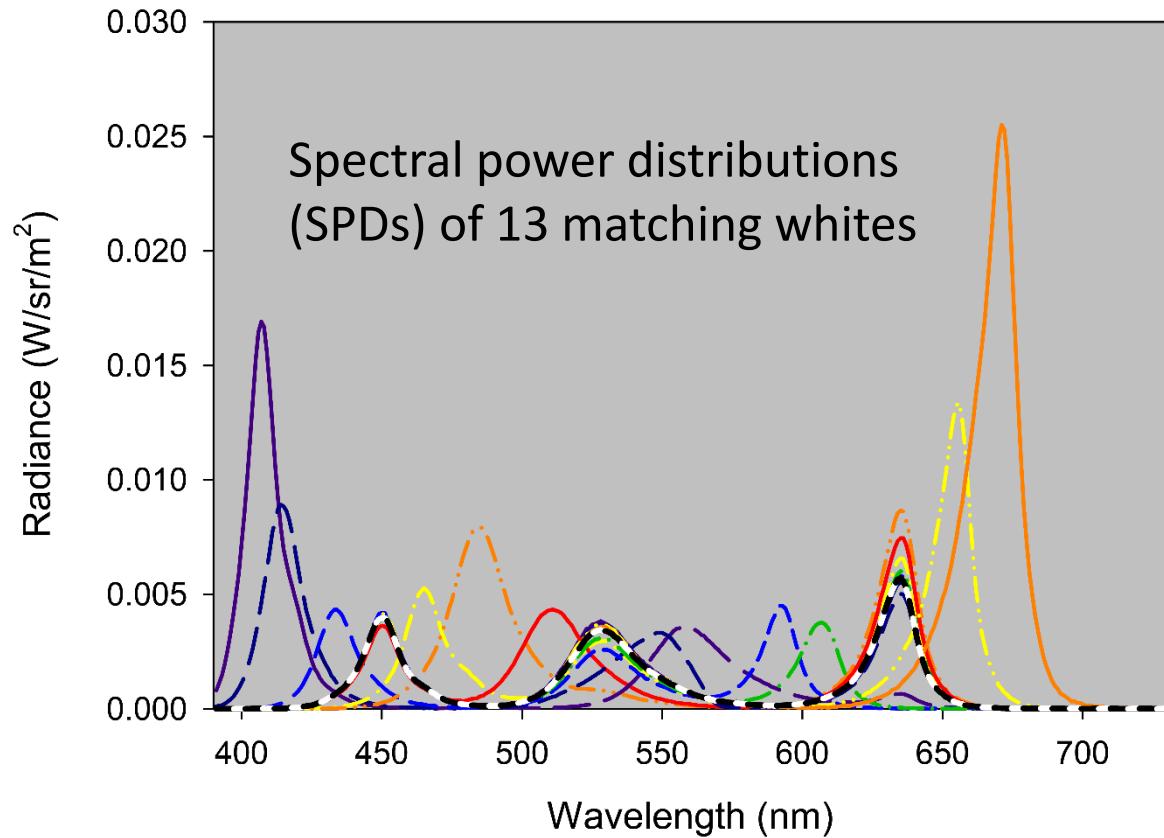


Here are the SPDs for the 13 matching whites (each SPD is made up of all three primaries) set by one of our subjects.



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

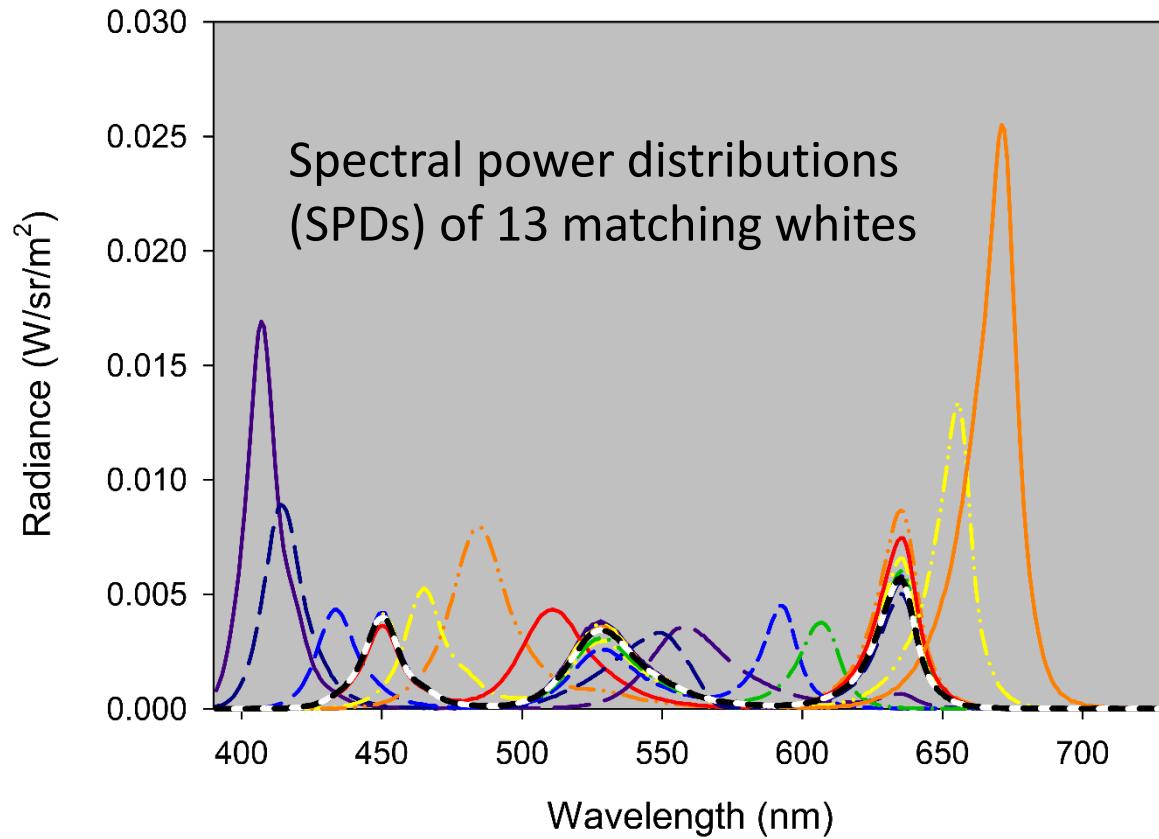
Colour matching analysis



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

So...

Colour matching analysis

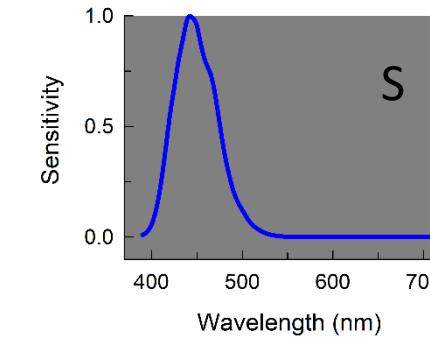


Cross-multiply
and integrate

X

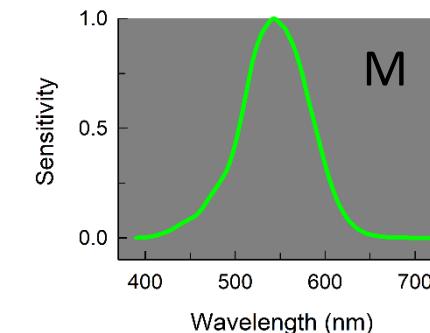
X

X



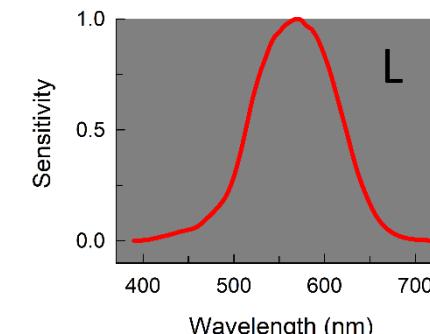
==

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



==

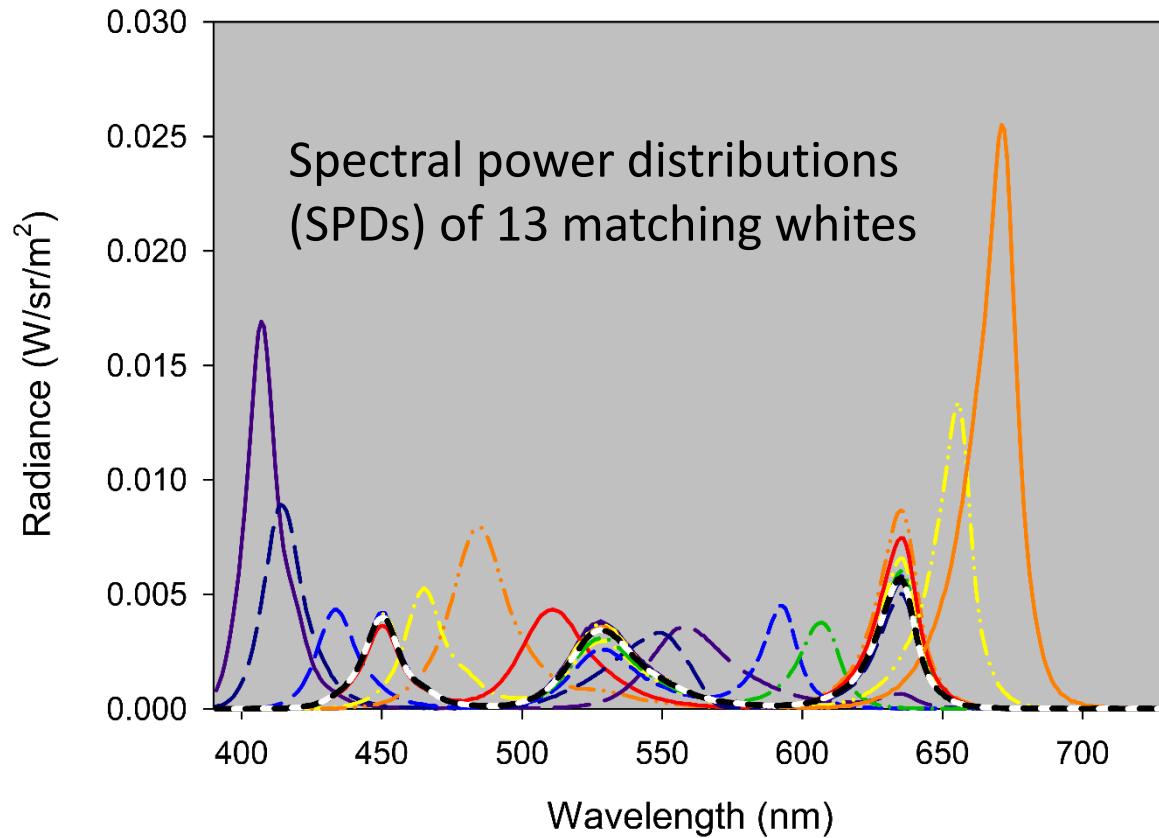
All 13 should
produce the *same*
M-cone excitation



==

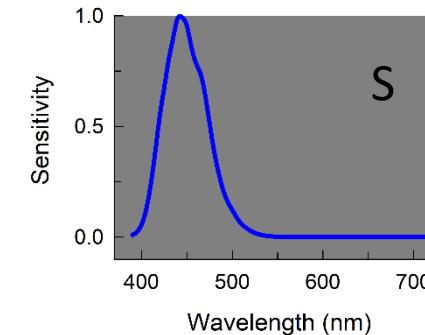
All 13 should
produce the *same*
L-cone excitation

Colour matching analysis



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

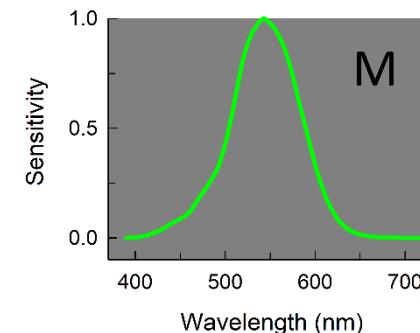
X



==

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

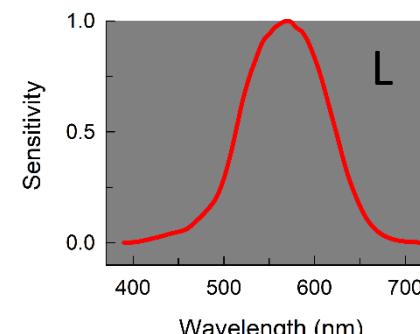
X



==

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

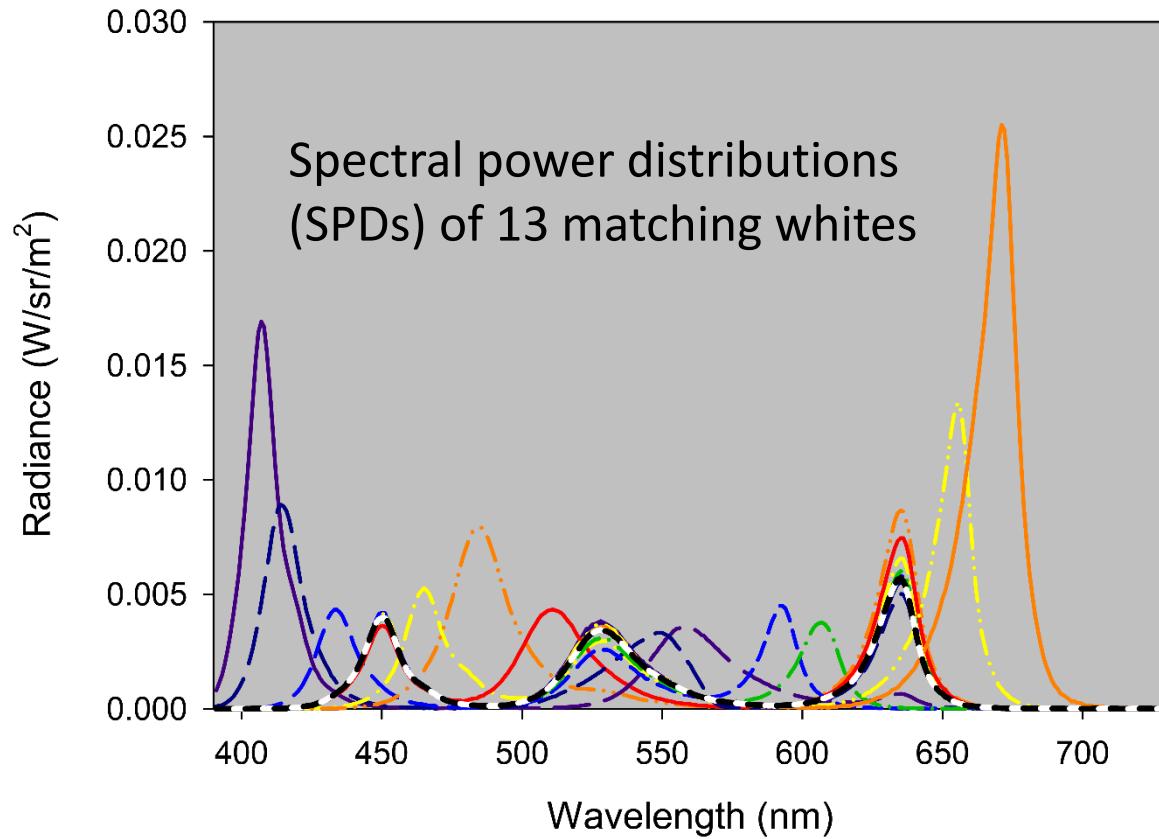
X



==

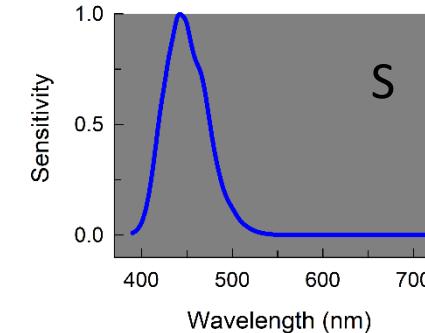
All 13 should produce the *same* L-cone excitation

Colour matching analysis



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

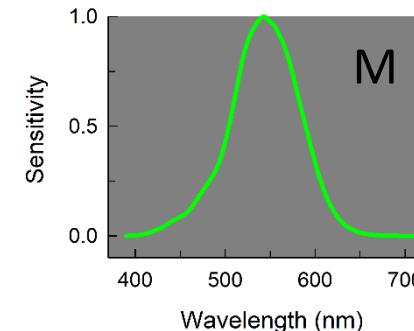
X



==

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

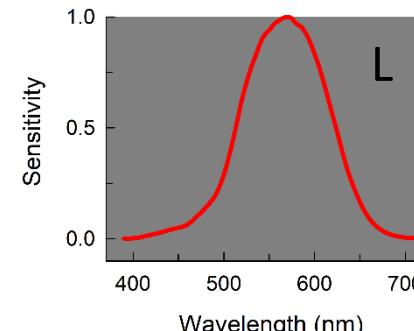
X



==

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

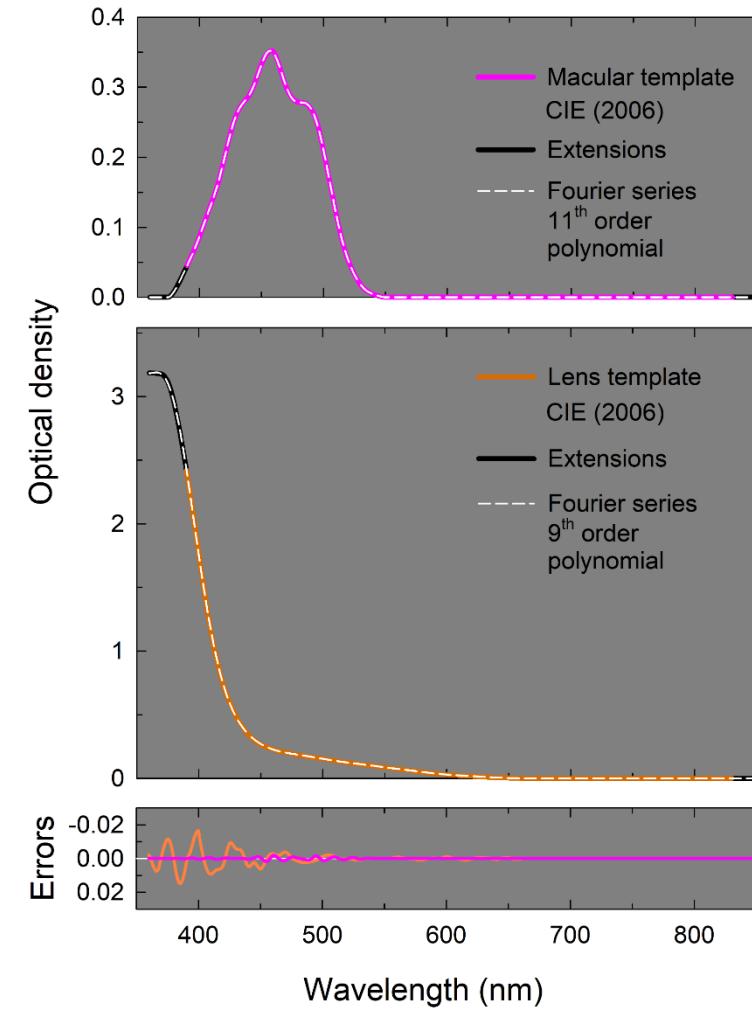
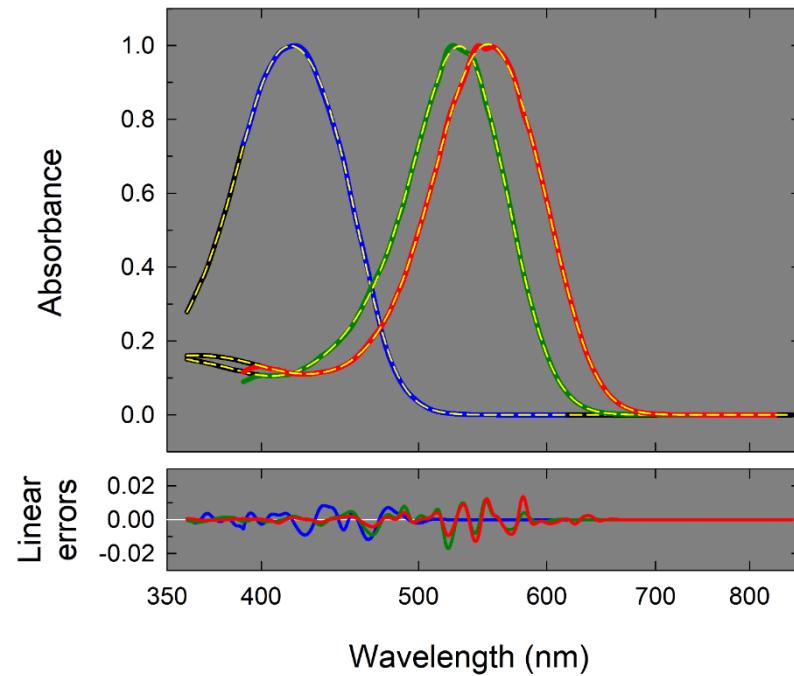
X



==

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

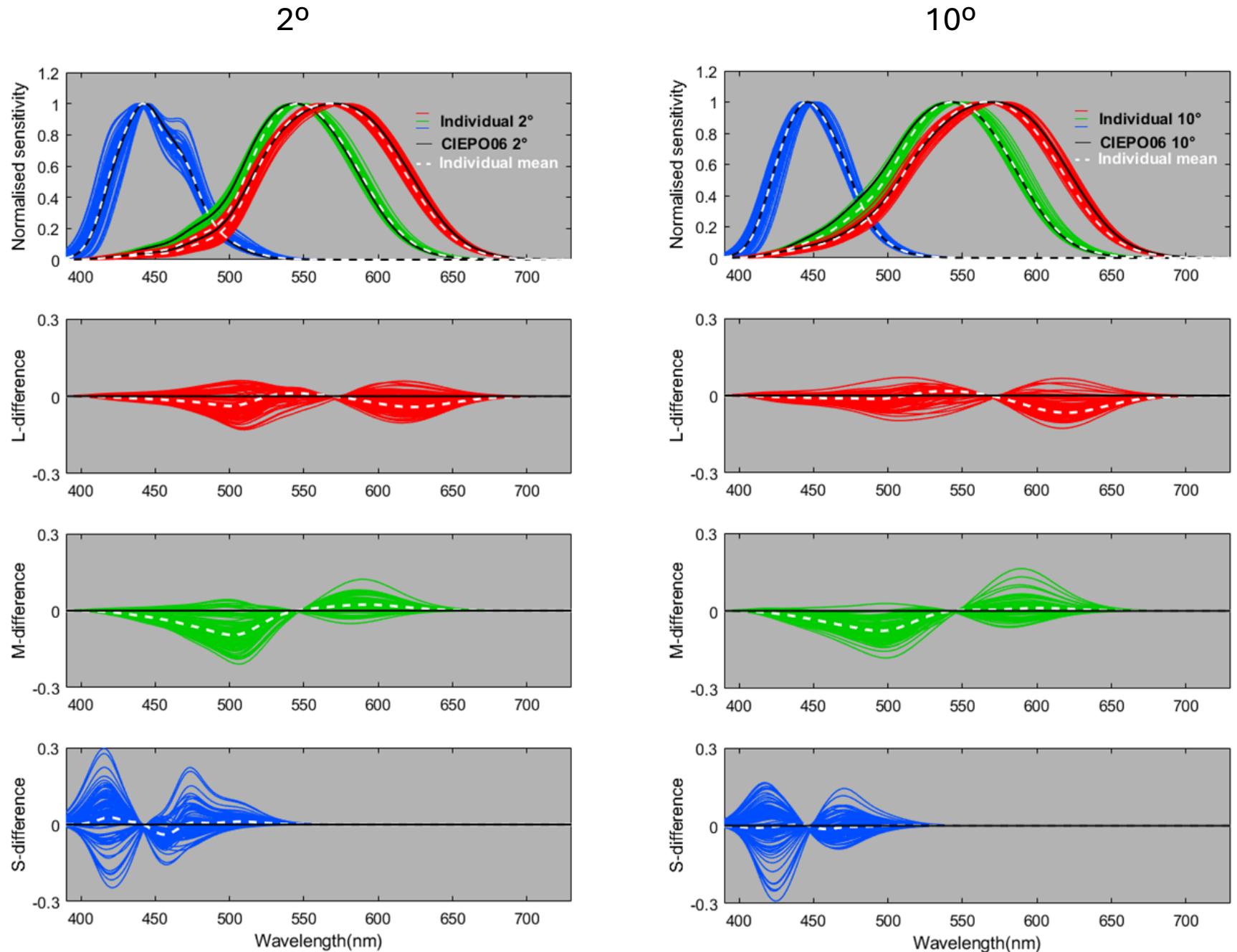
We use the continuous template functions for the model fitting...

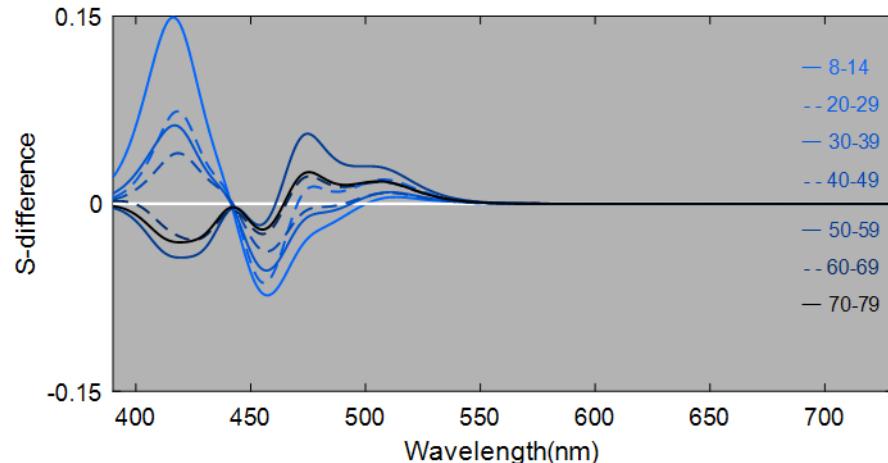
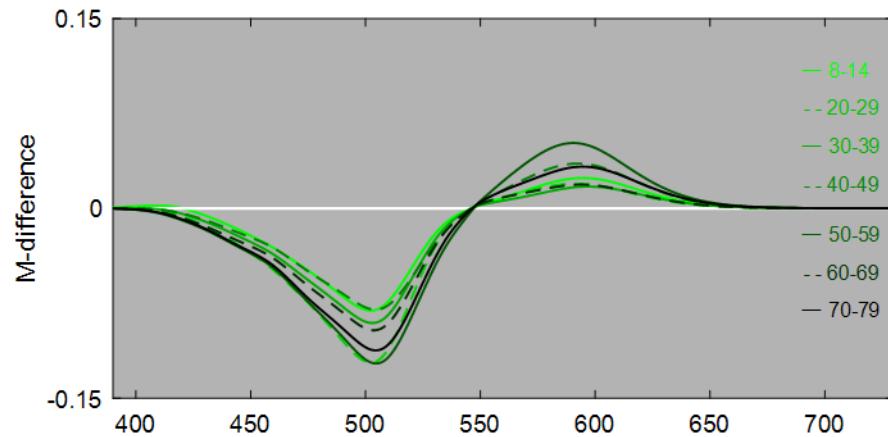
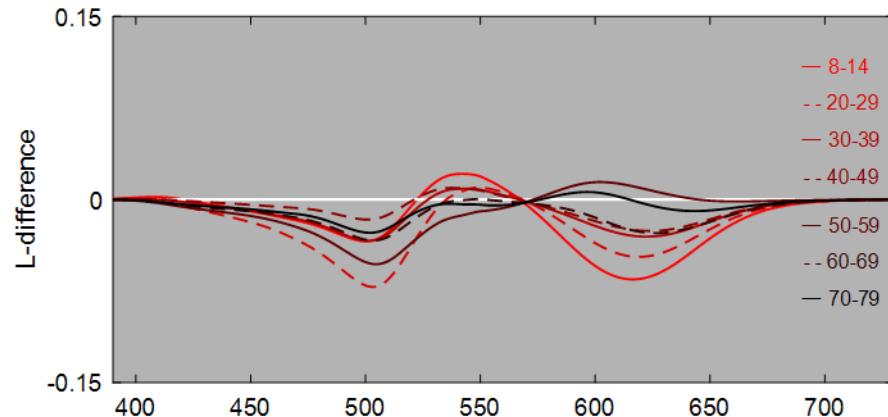


Base results

100 observers from
8 to 79 years old.

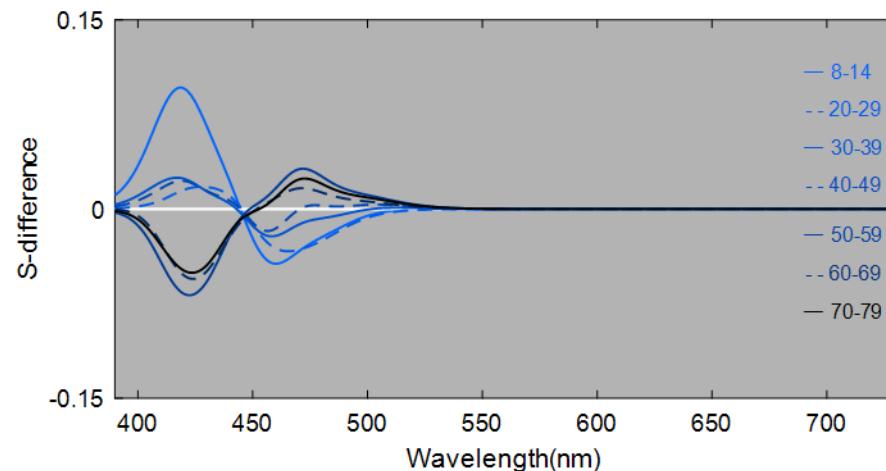
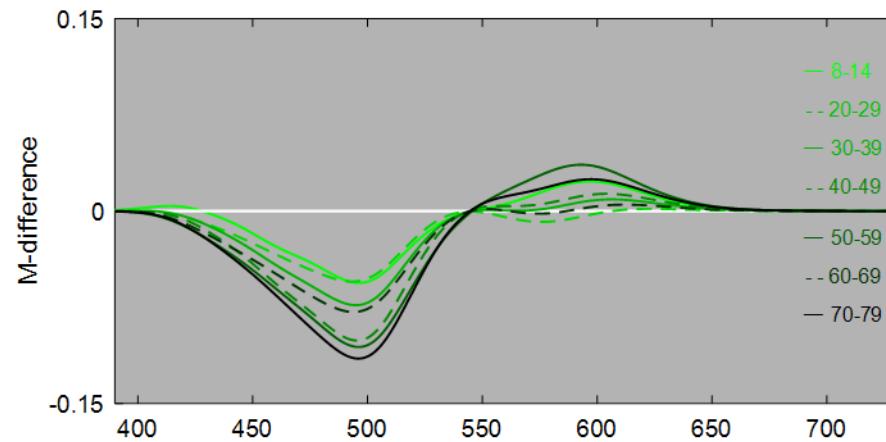
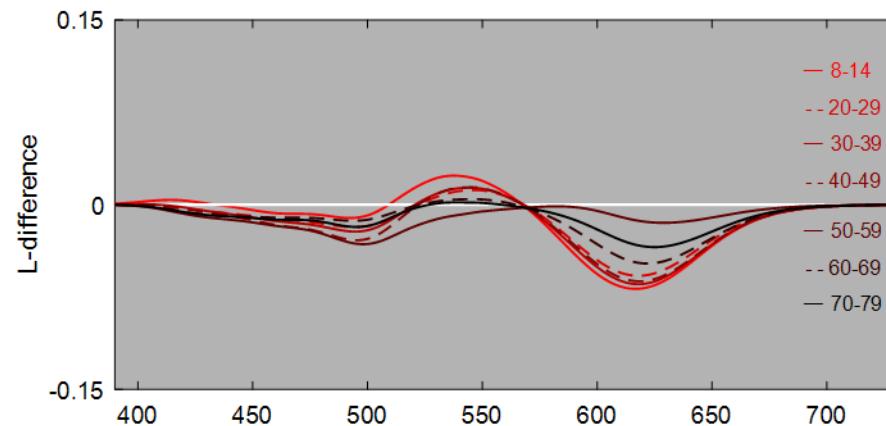
Colour normal
(CIE 2006)





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.

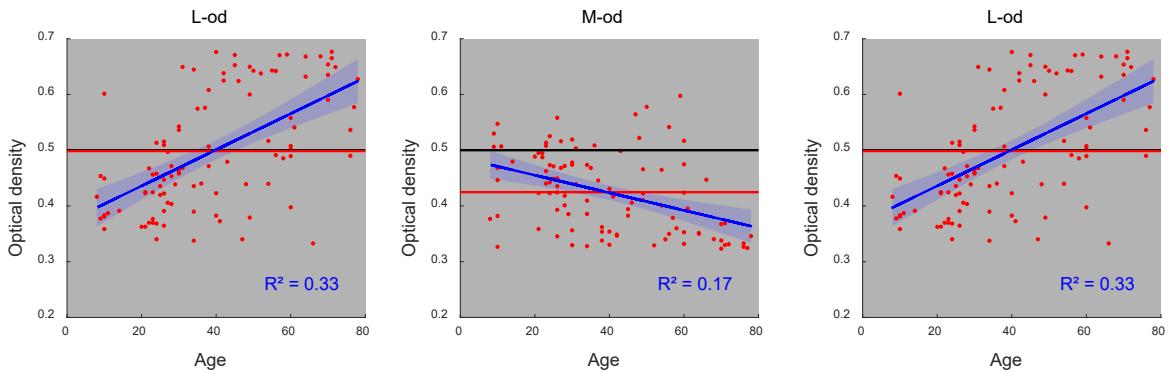


10° cone spectral sensitivity differences by age

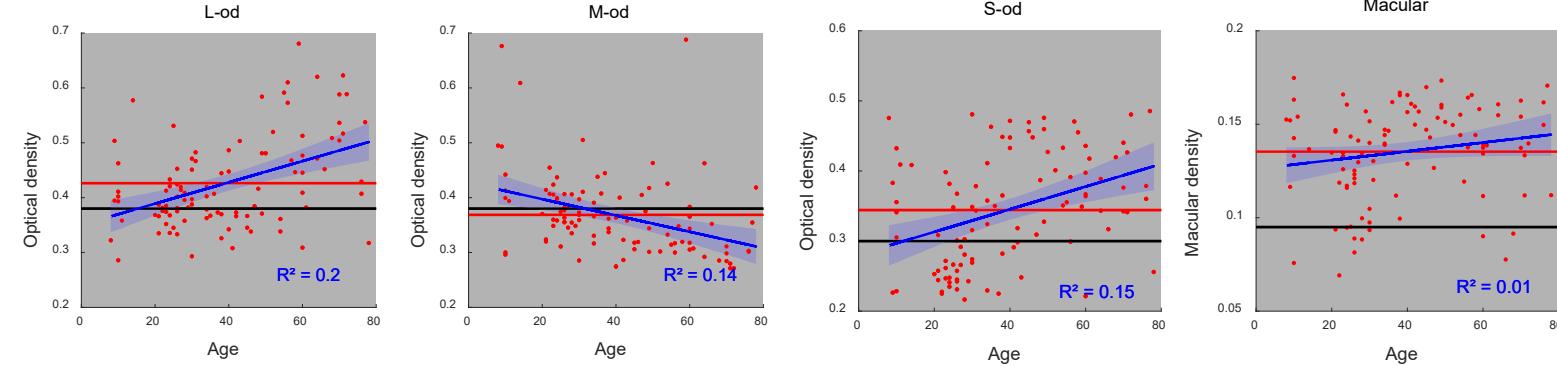
Differences between the observers' 10° mean cone spectral sensitivities and the standard CIEPO06 10° cone spectral sensitivities (solid white line) by age.

Best-fitting parameters

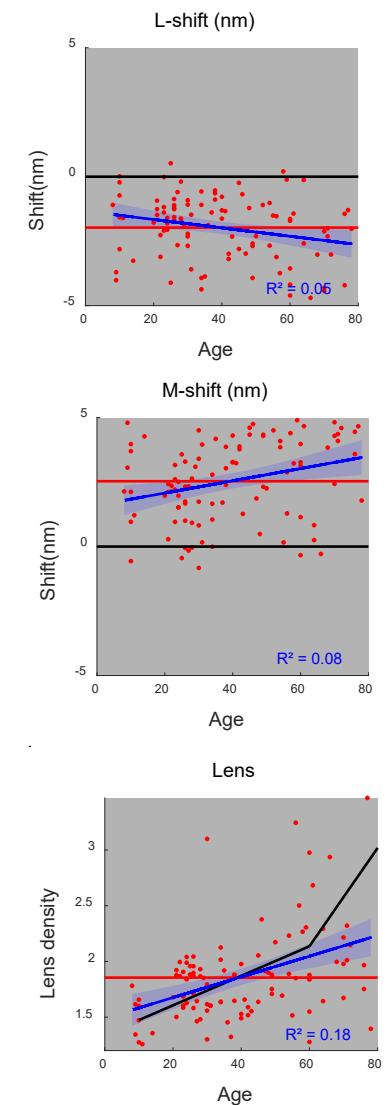
2° match parameters



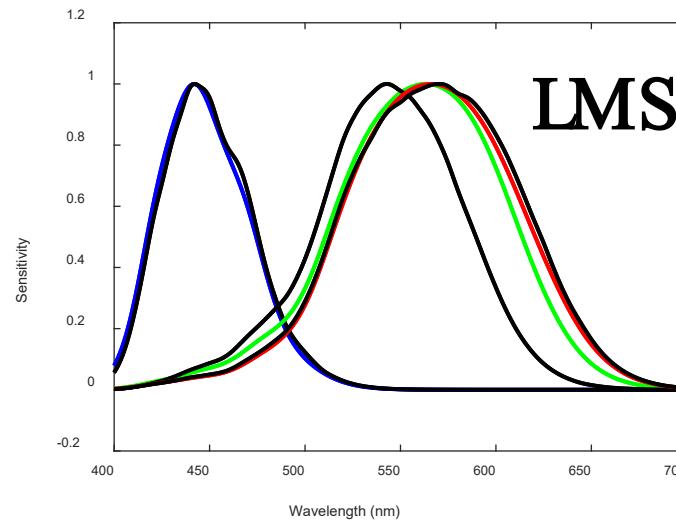
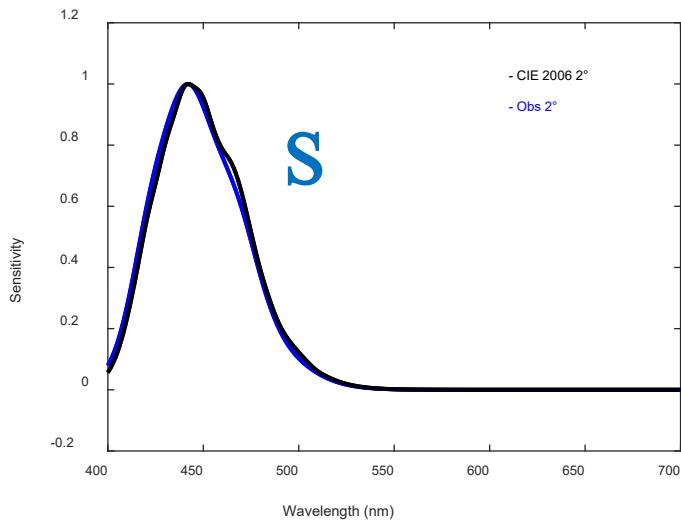
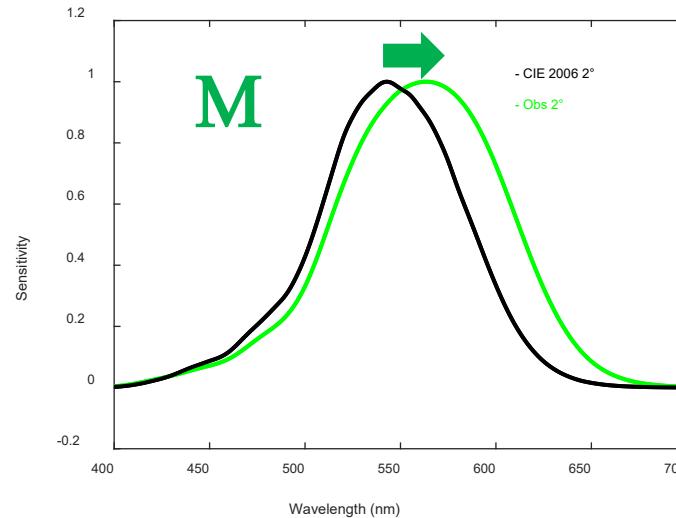
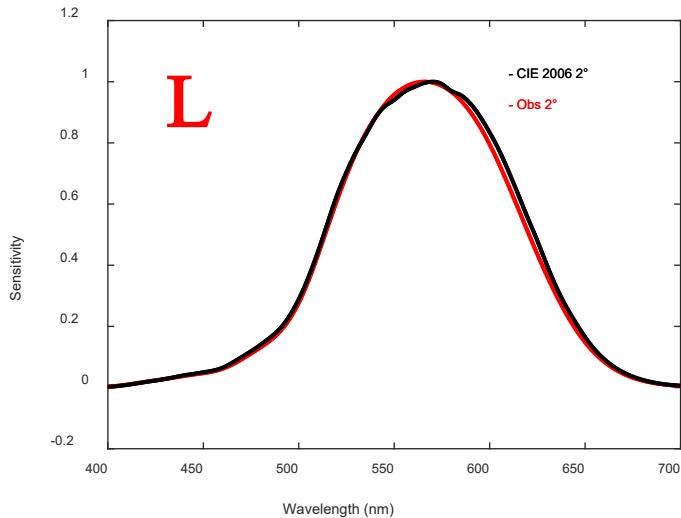
10° match parameters



2 and 10° match parameters



Deuteranomalous observer

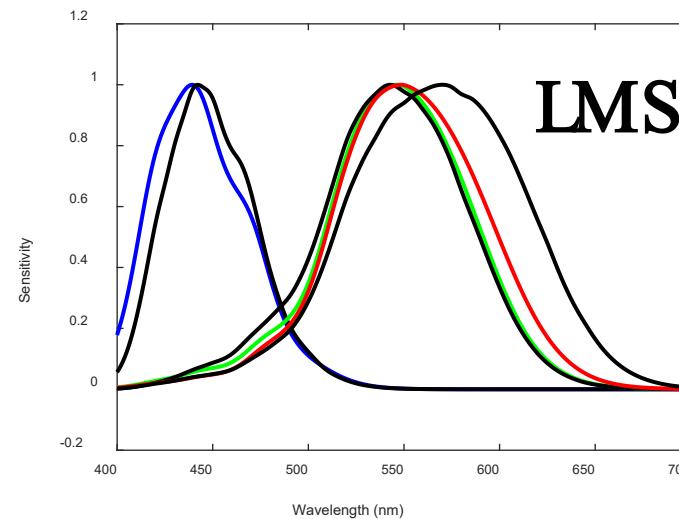
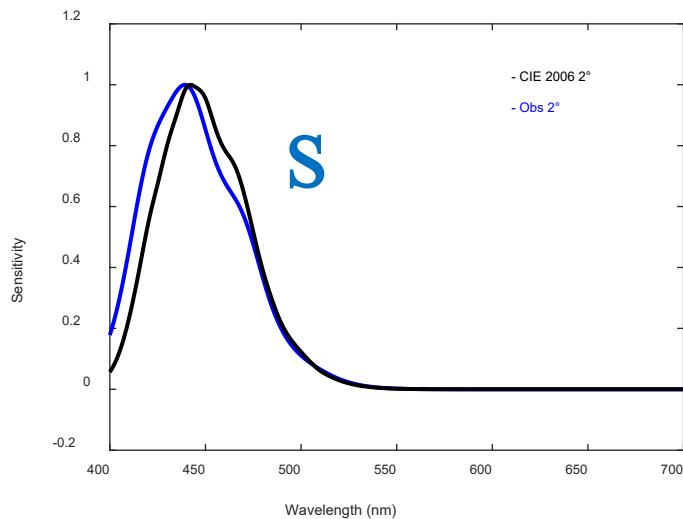
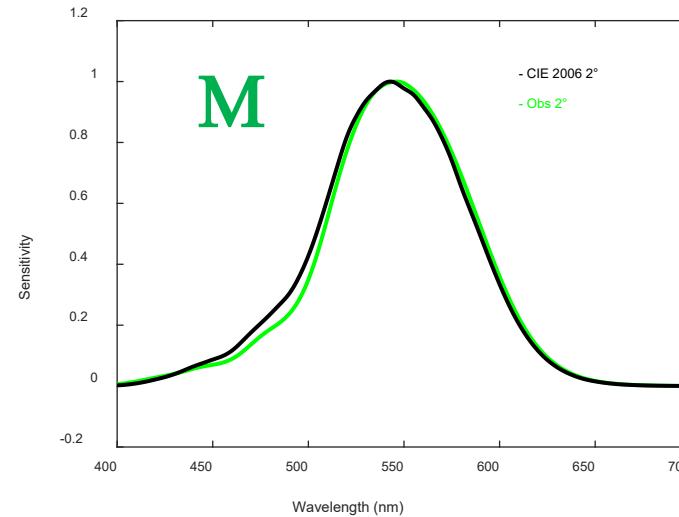
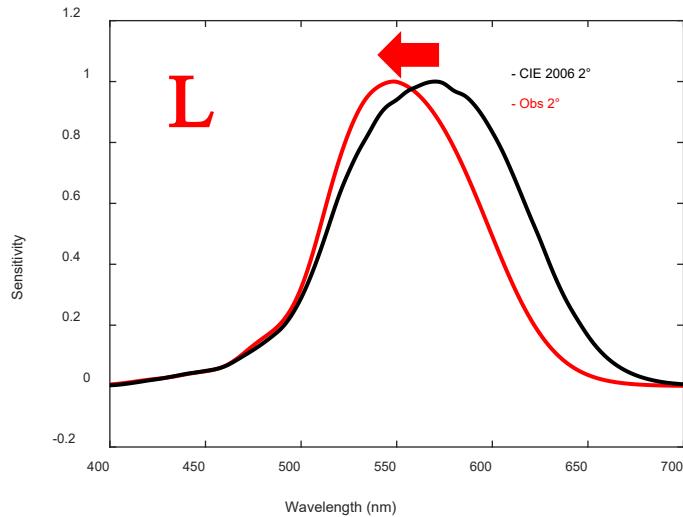


Red-green colour vision deficiency

— 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

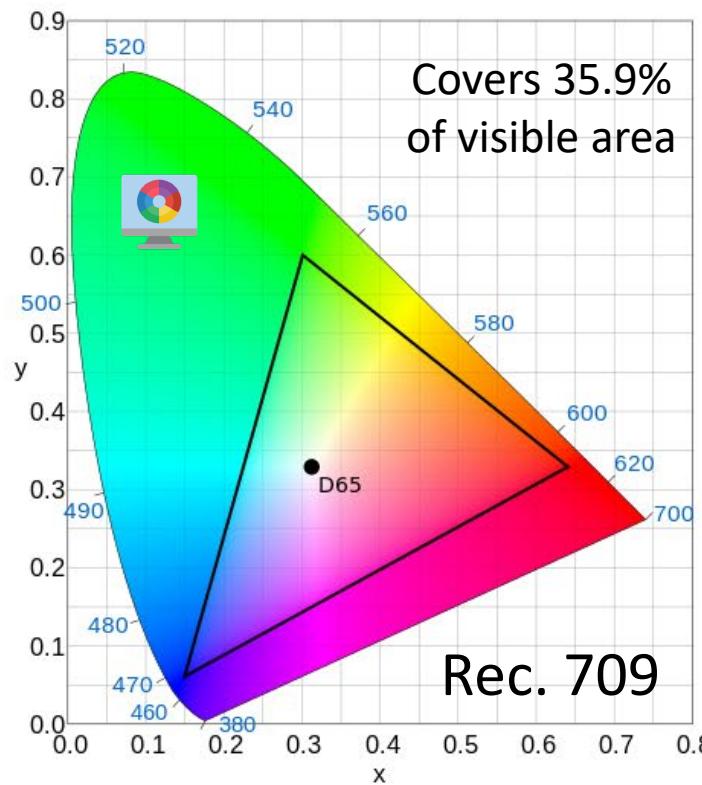


Red-green colour vision deficiency

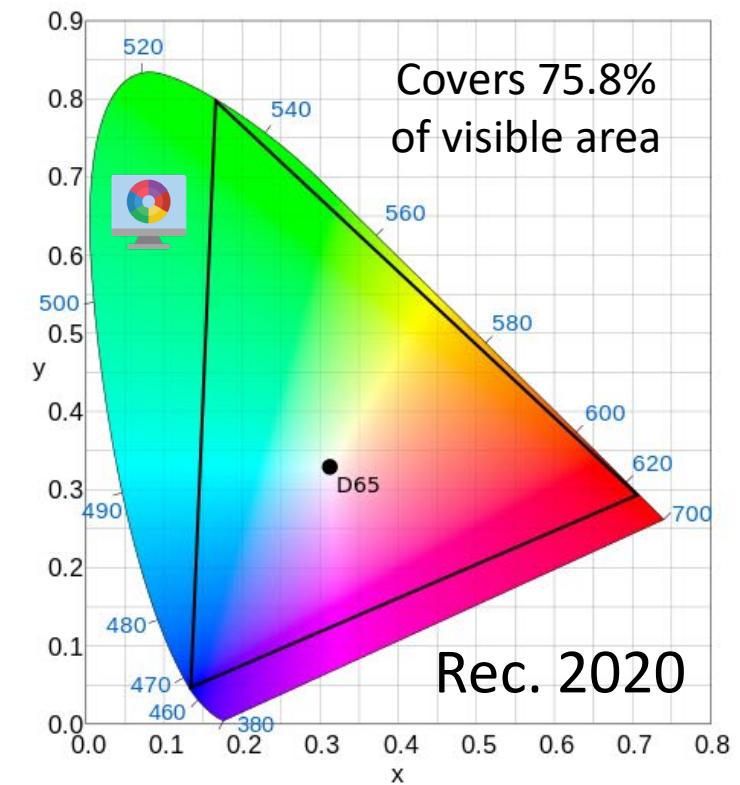
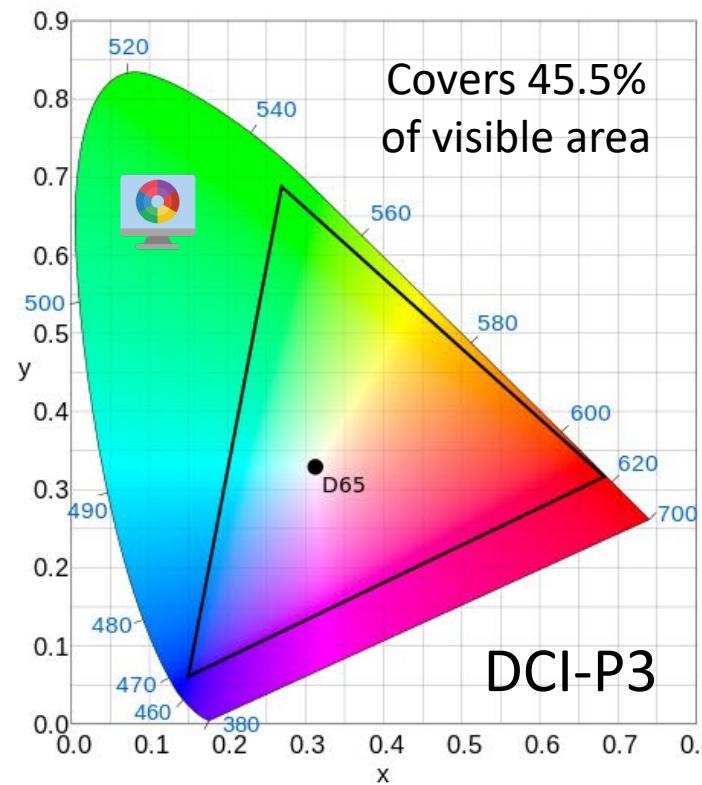
— Colour normal (CIE 2006)

	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

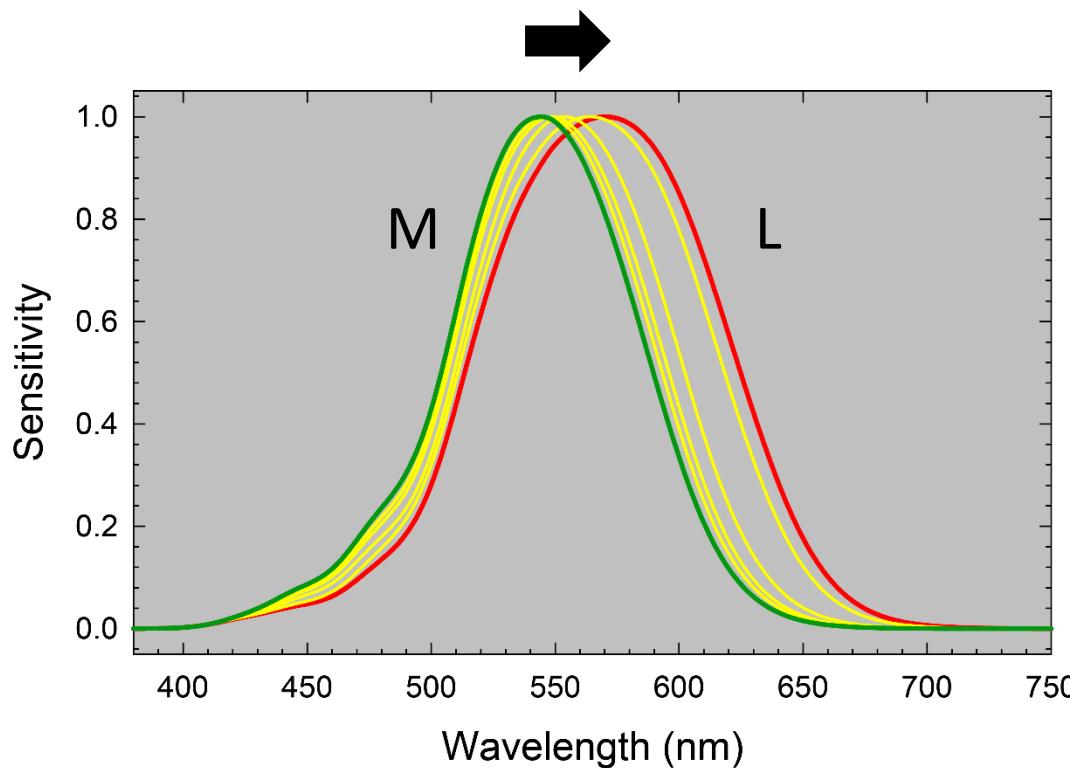


Using this method, we can produce individualized colour matching functions and thus produce consistent colours with different displays.

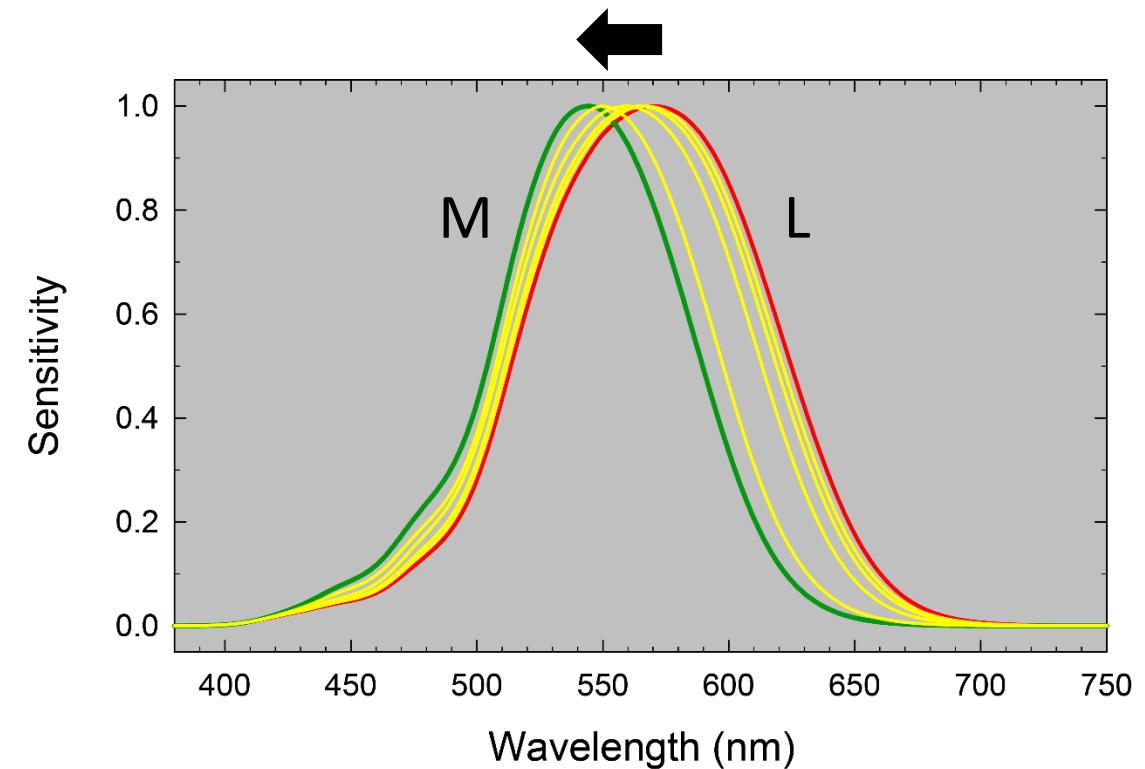


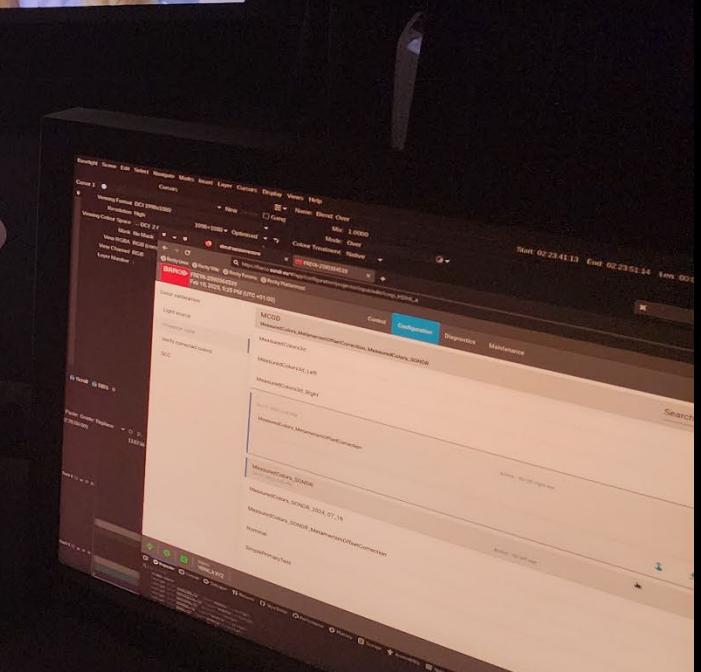
If you don't have correct for individual differences, spectral shifts of the M or L-cones can substantially change the appearance of display devices with narrow band primaries and large colour gamuts.

M-cone functions can shift towards L.



L-cone functions can shift towards M.





Deuteranomaly prediction: Xenon to RGB laser projector

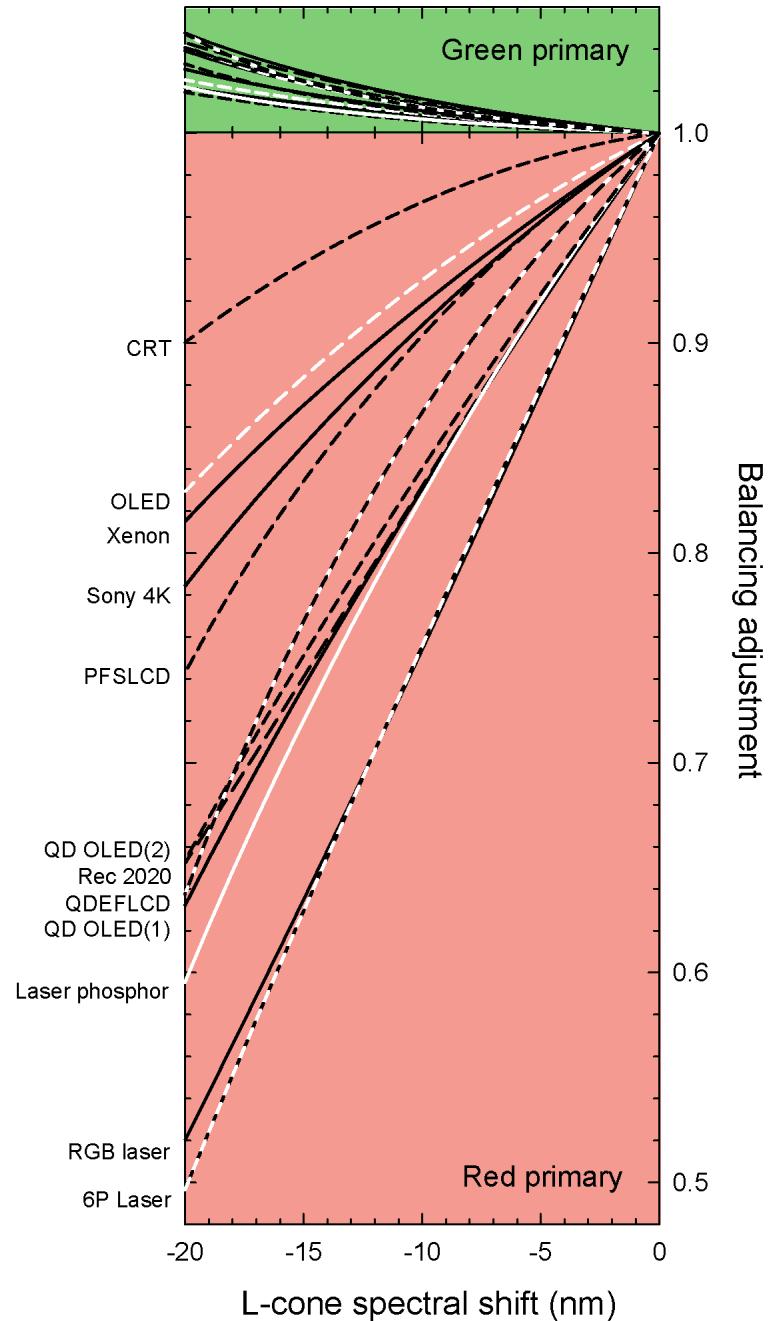


Andy Rider

R +42%
G -14%

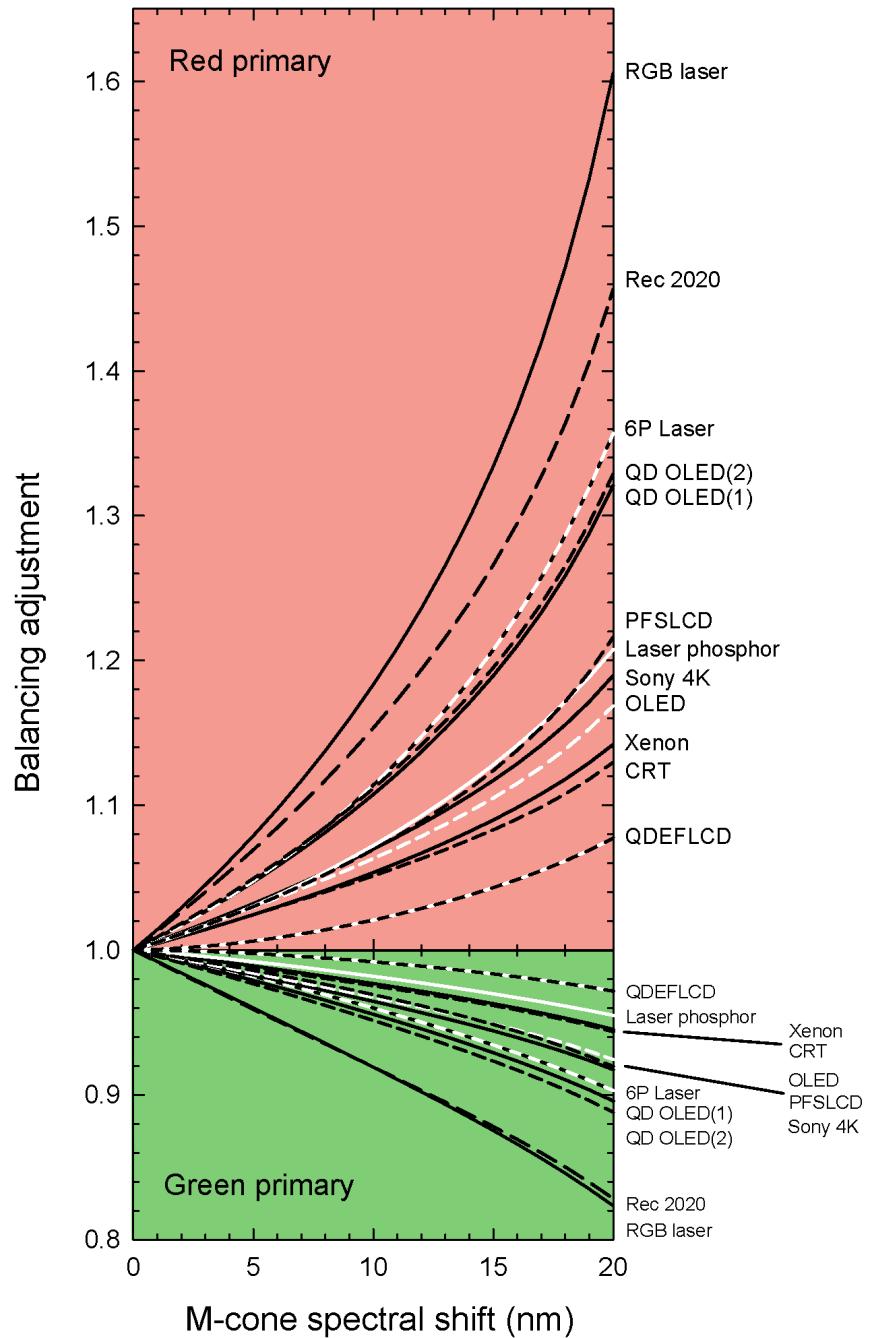


Bigger colour gamut

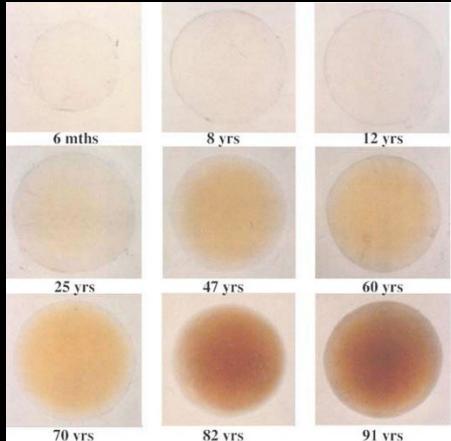


All displays show some level of discrepancy for anomalous observers, but some are worse than others

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>