

Lecture 9: Deficiencies and Evolution of Color Vision

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CSC 259/459, Fall 2024
Computer Imaging & Graphics

The Roadmap

Theoretical Preliminaries

Human Visual Systems

Color in Nature, Arts, & Tech

(a.k.a., the birth, life, and death of light)

Digital Camera Imaging

Modeling and Rendering

Applications



Introduction and Overview

Photoreceptors

Color Vision and Colorimetry

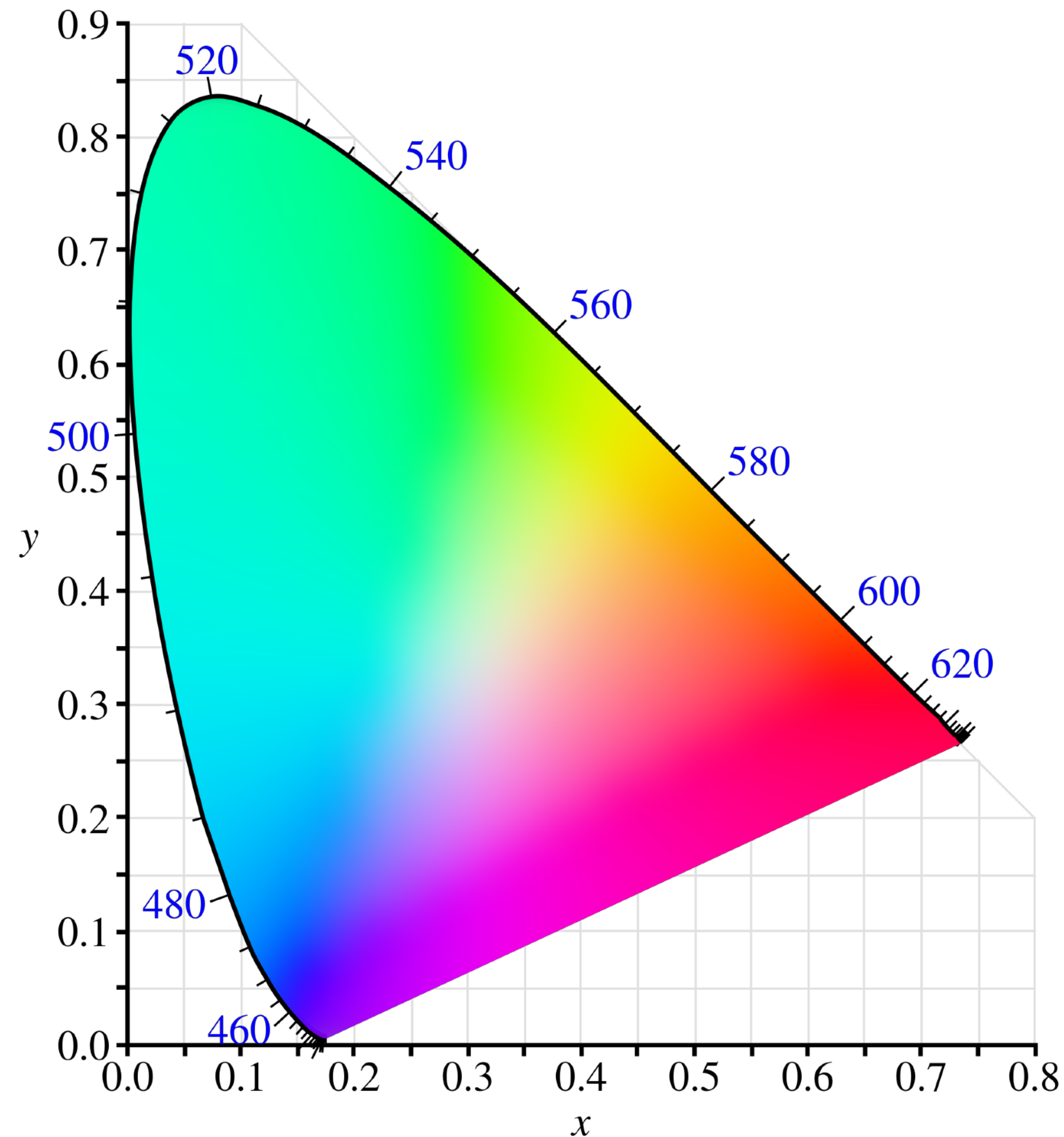
Color Vision Deficiency

Color Production

Visual Adaptations

xy-Chromaticity Space

<https://horizon-lab.org/colorvis/chromaticity.html>



Linear transformation

$$\begin{bmatrix} X \\ Y \\ Z \end{bmatrix} = T_{LMS2XYZ} \times \begin{bmatrix} L \\ M \\ S \end{bmatrix}$$

Perspective projection through $[0, 0, 0]$ to the $X+Y+Z=1$ plane

$$\begin{cases} x = \frac{X}{X+Y+Z} \\ y = \frac{Y}{X+Y+Z} \end{cases}$$

Color Vision Deficiency

- Dichromatic vision
- Anomalous trichromatic vision
- Other forms of CVD

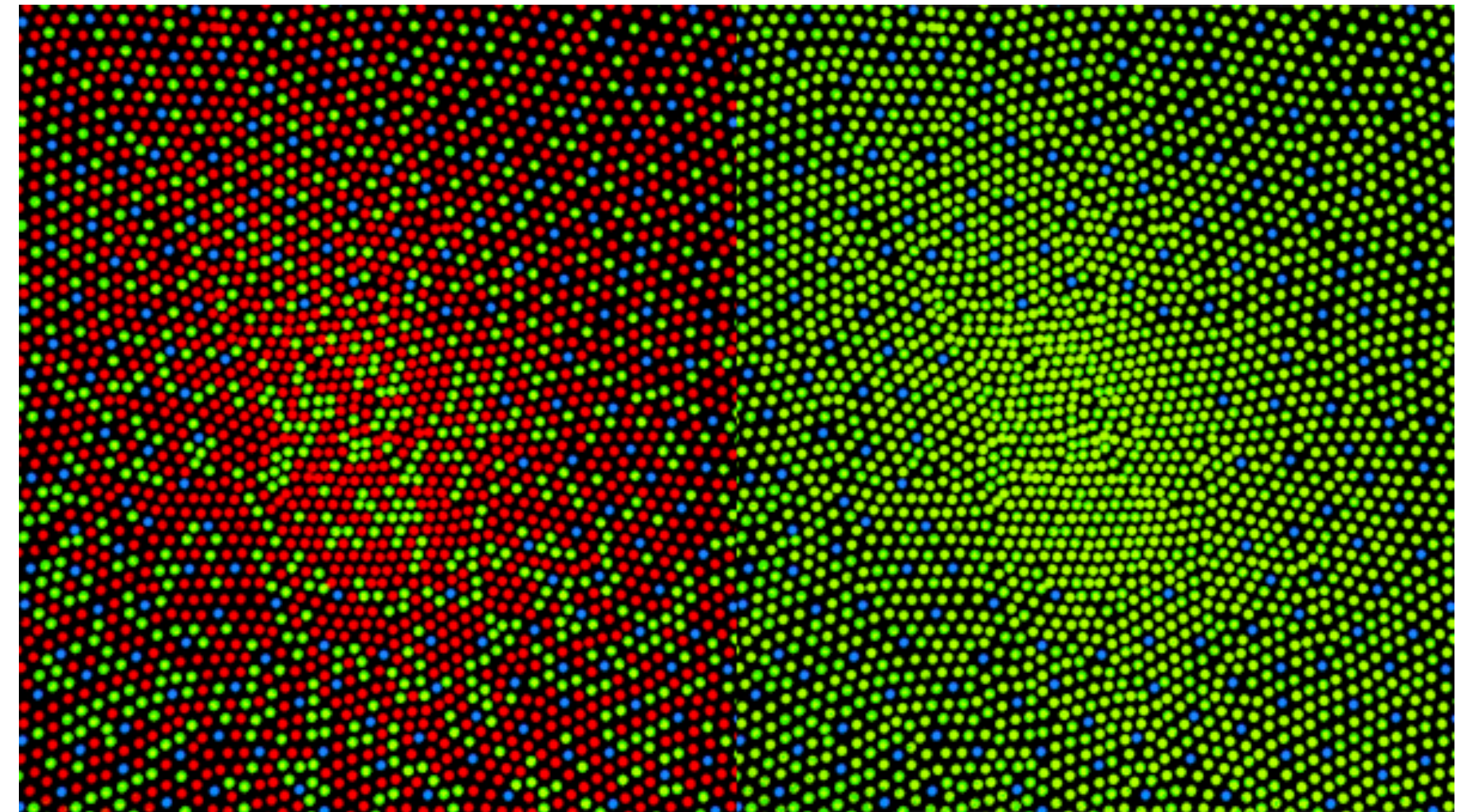
Math and visualization: <https://horizon-lab.org/colorvis/colorblind.html>

Dichromatic Vision

Normal vision is trichromatic; that is, there are three kinds of cone cells.

Dichromatic color vision: one class of cone cells are missing.

- **Protanopia**: missing **L** cones
- **Deuteranopia**: missing **M** cones
- **Tritanopia**: missing **S** cones.



Fovea cone cell distribution in a **trichromatic** vision.

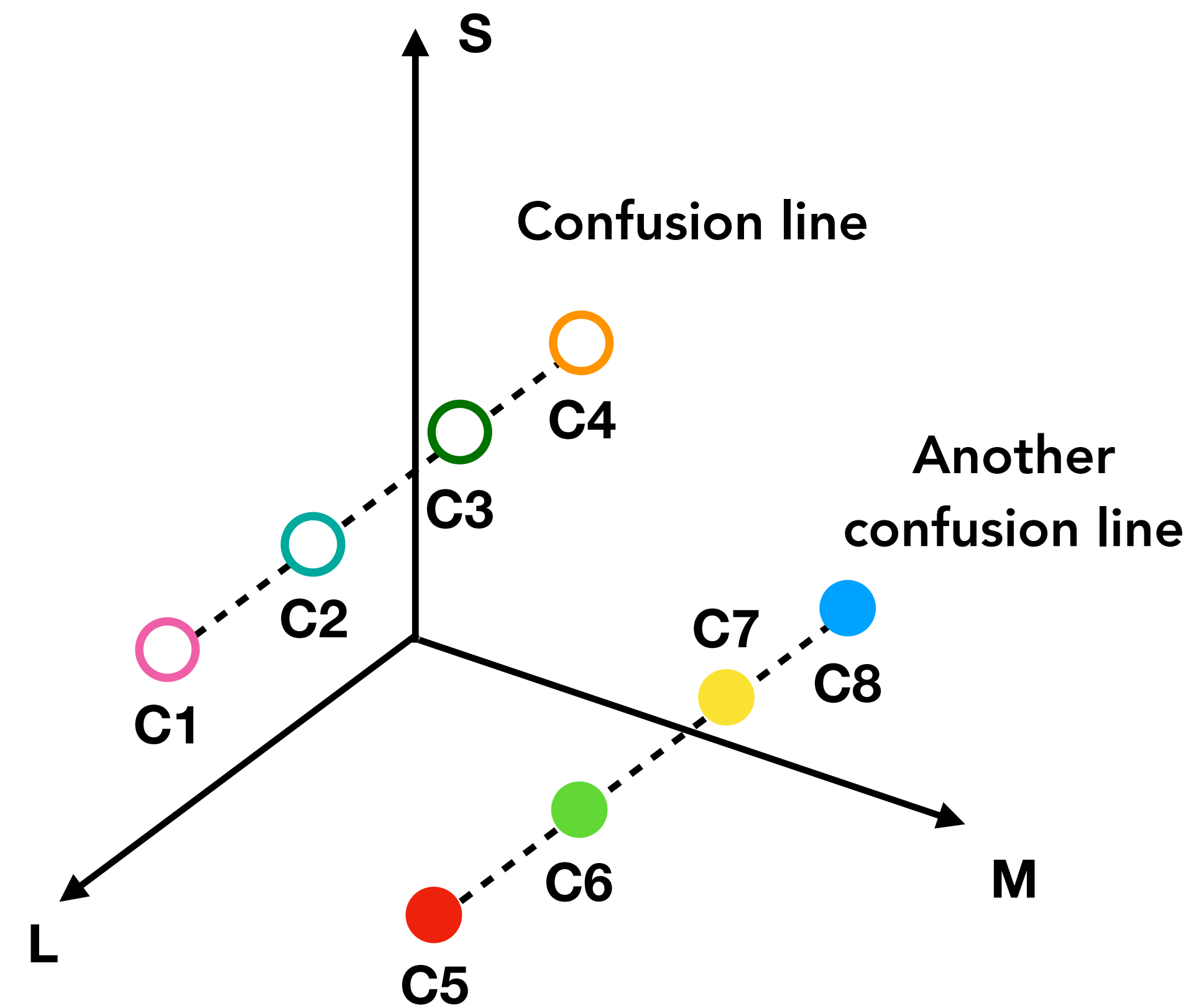
Fovea cone cell distribution of a **Protanopic** vision, where **L cones** are missing.

Lines of Confusion

For a protanope (which lacks L cones), all the colors that have the same M and S cone responses but **differ in L** would be perceived as the same color.

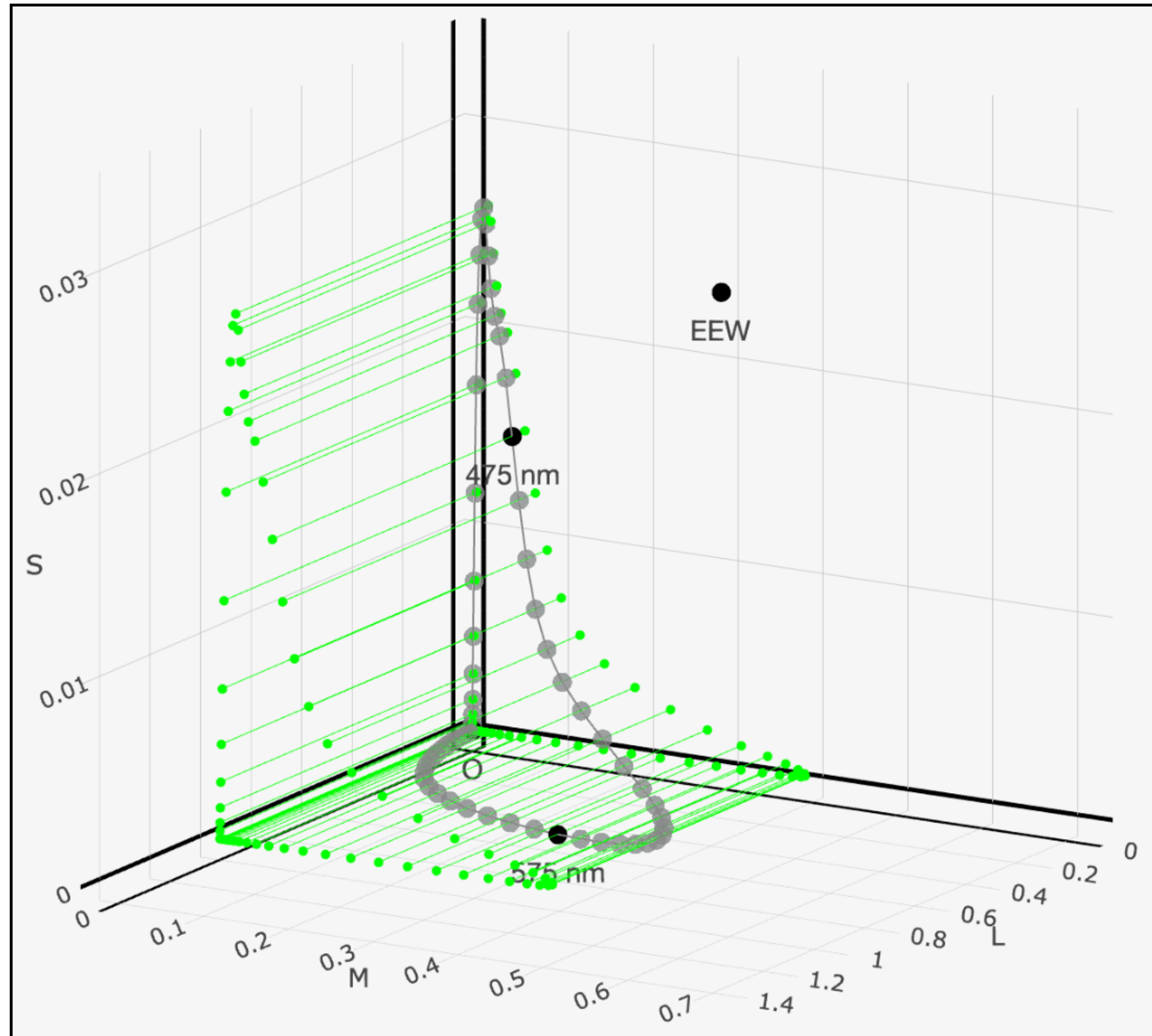
All the colors on a line parallel to the L-axis are seen as the same color by a protanope.

- C1~C4 are seen as the same color
- C5~C8 are seen as the same, but another color



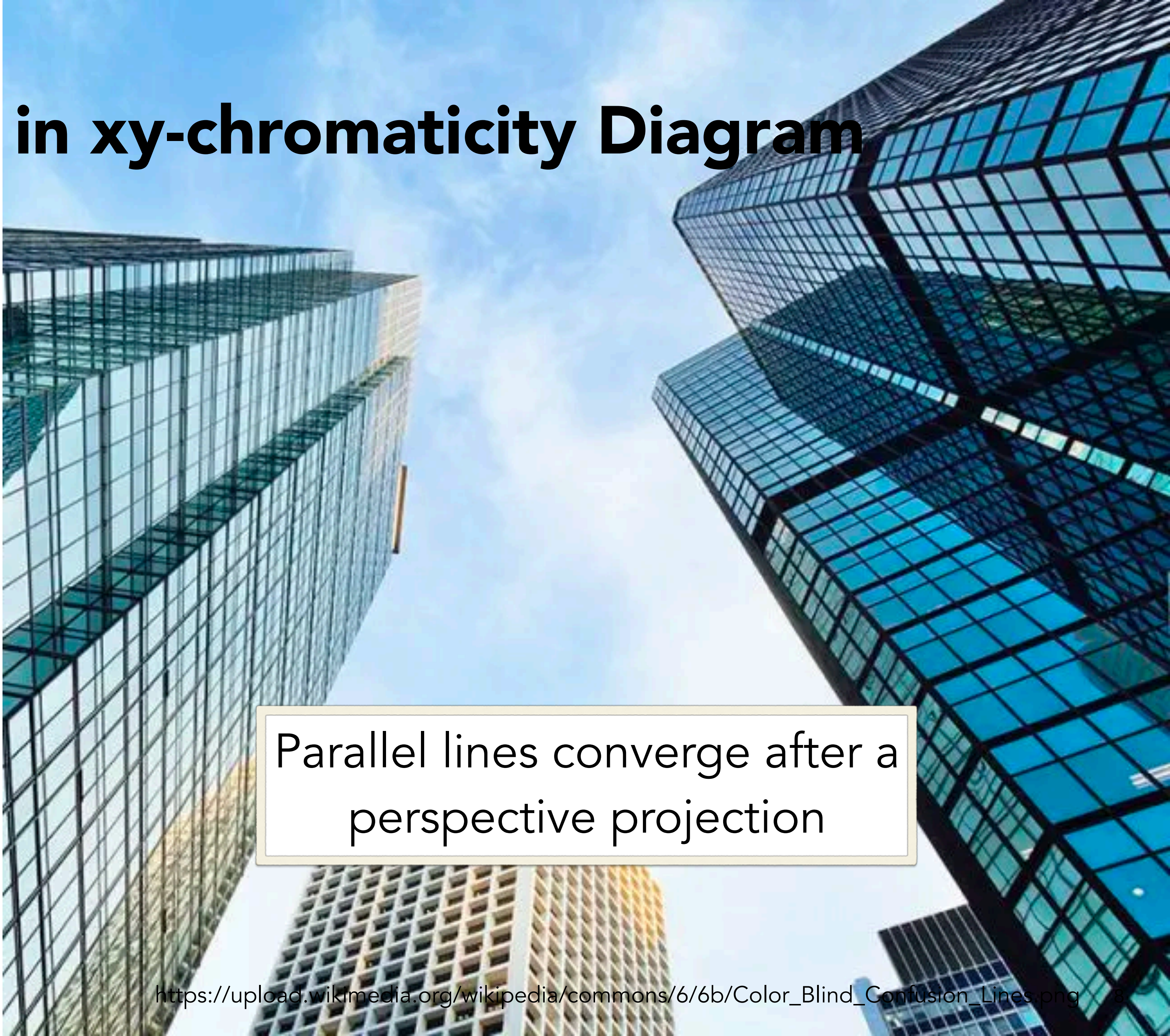
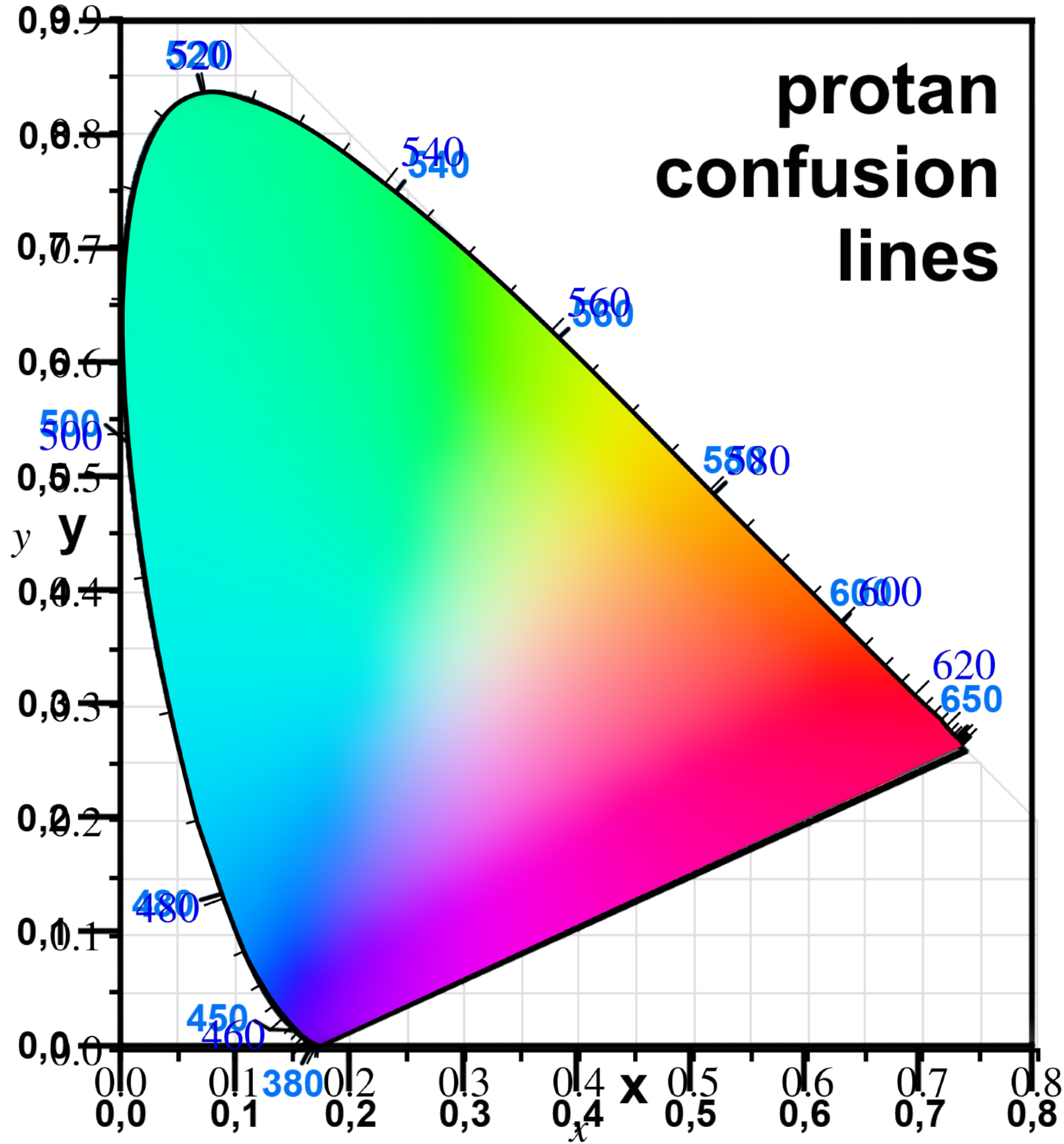
* This is an orthographic projection

Lines of Confusion Visualization in LMS Space



<https://horizon-lab.org/colorvis/colorblind.html>

Lines of Confusion in xy-chromaticity Diagram

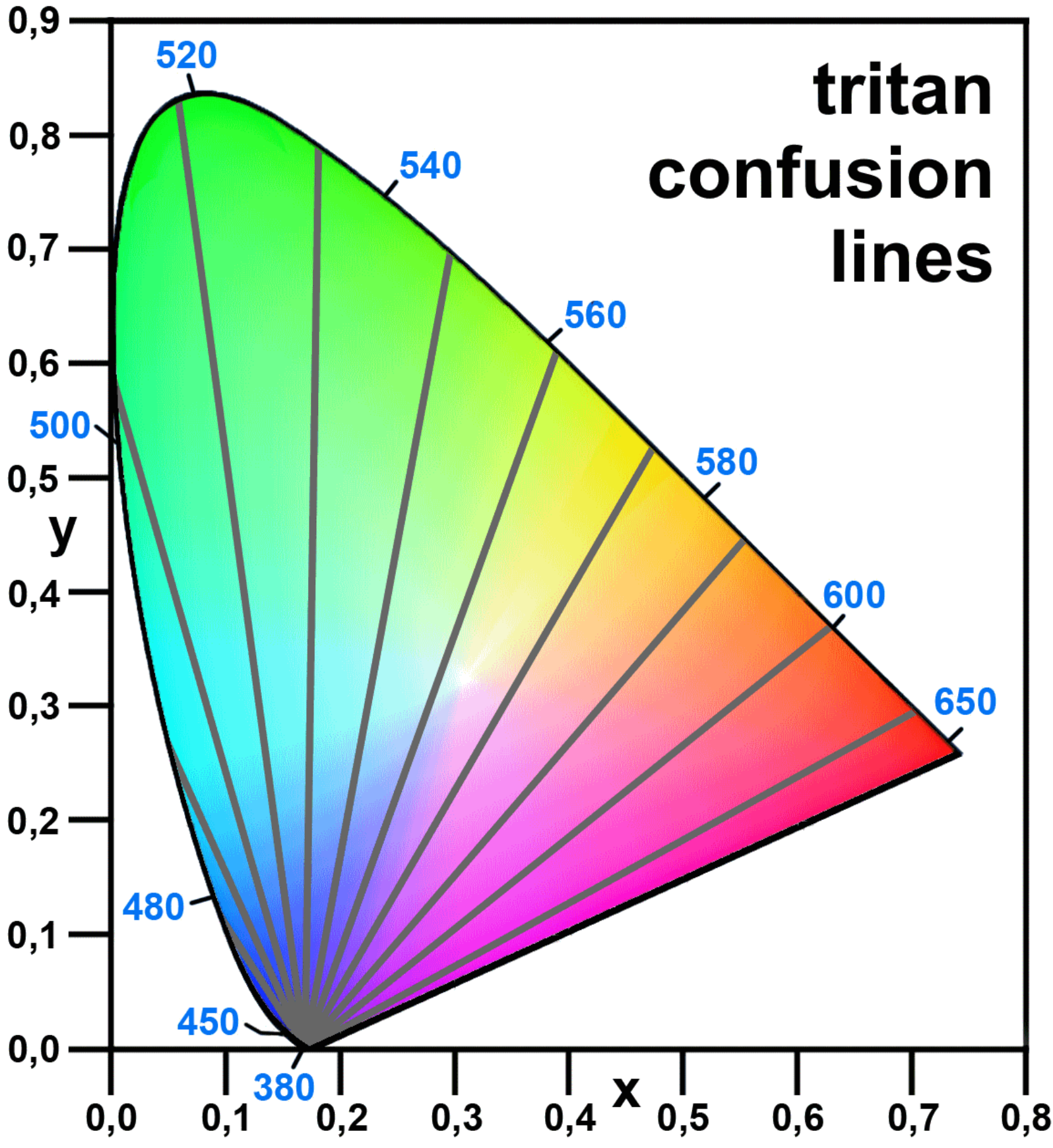
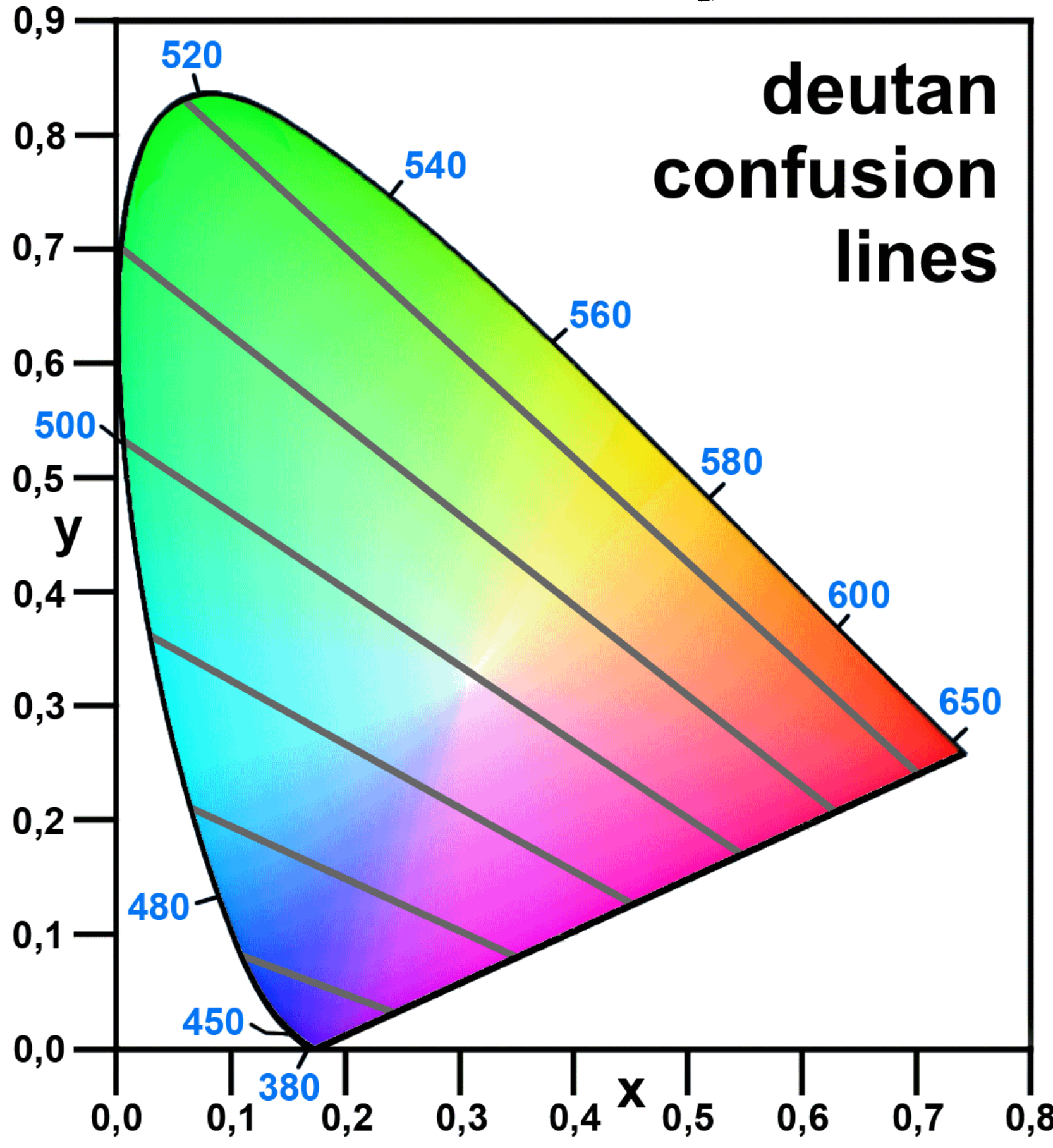
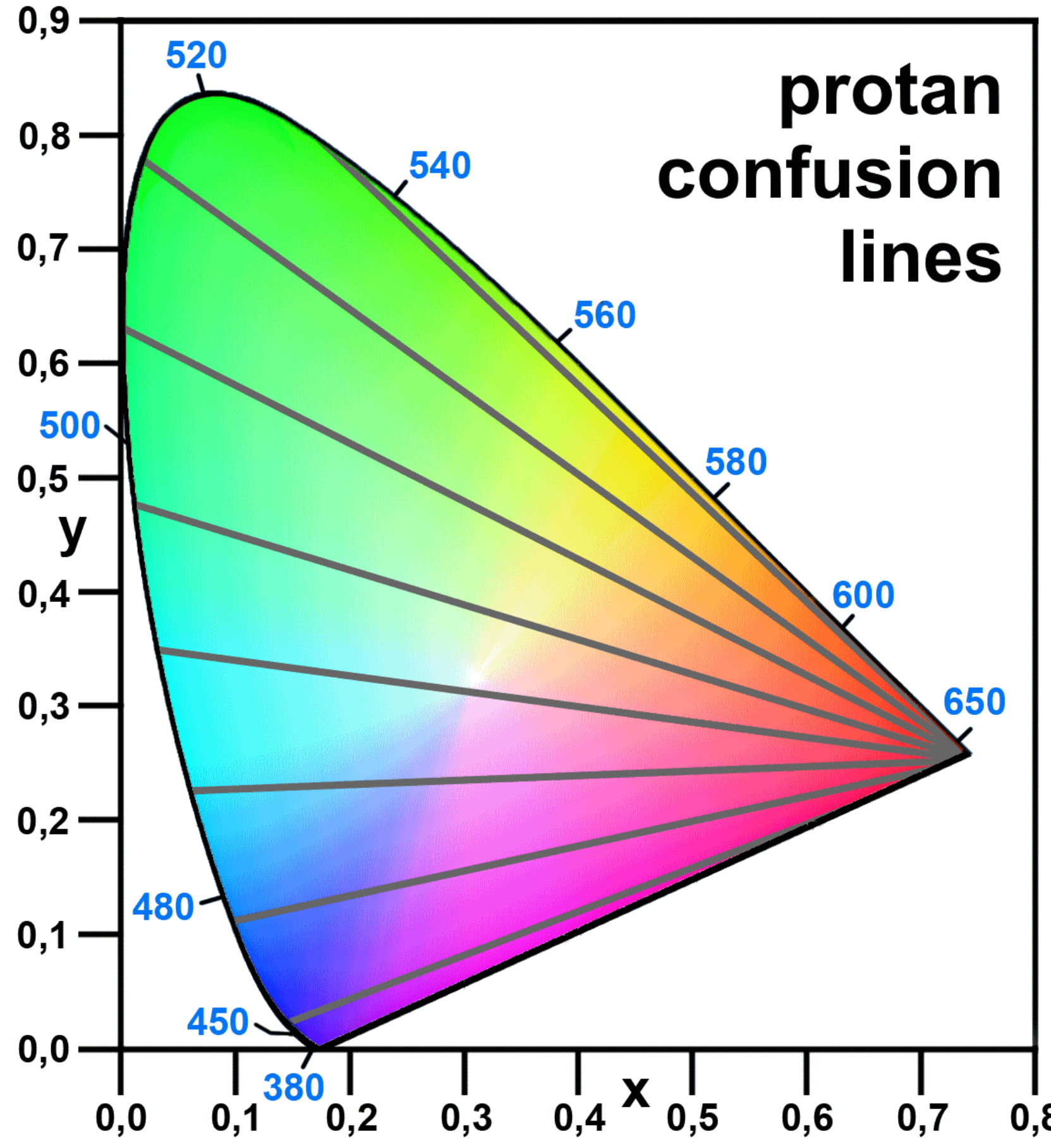


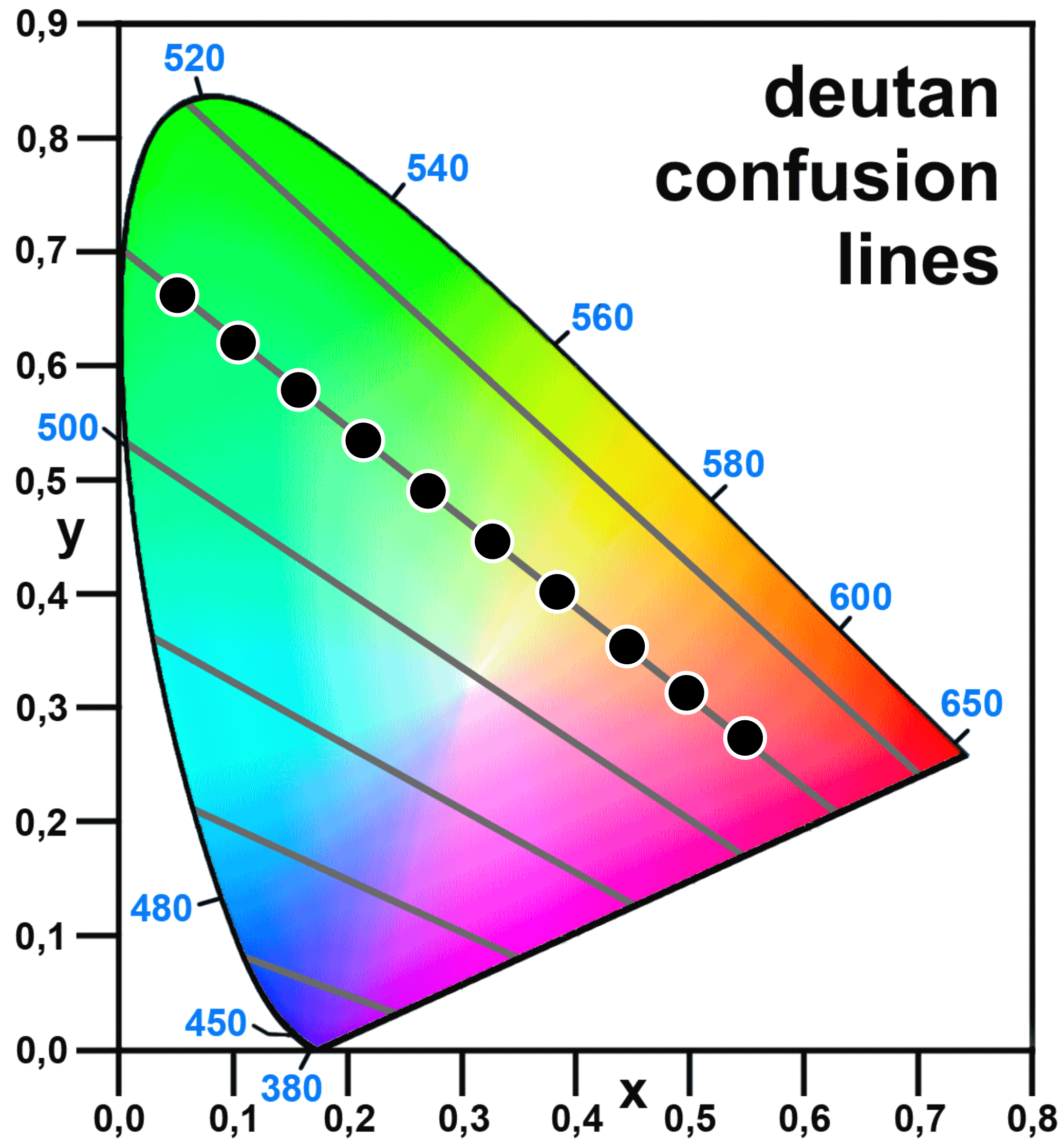
Parallel lines converge after a perspective projection

Lines of Confusion in xy-chromaticity Diagram

"Red-green blindness"

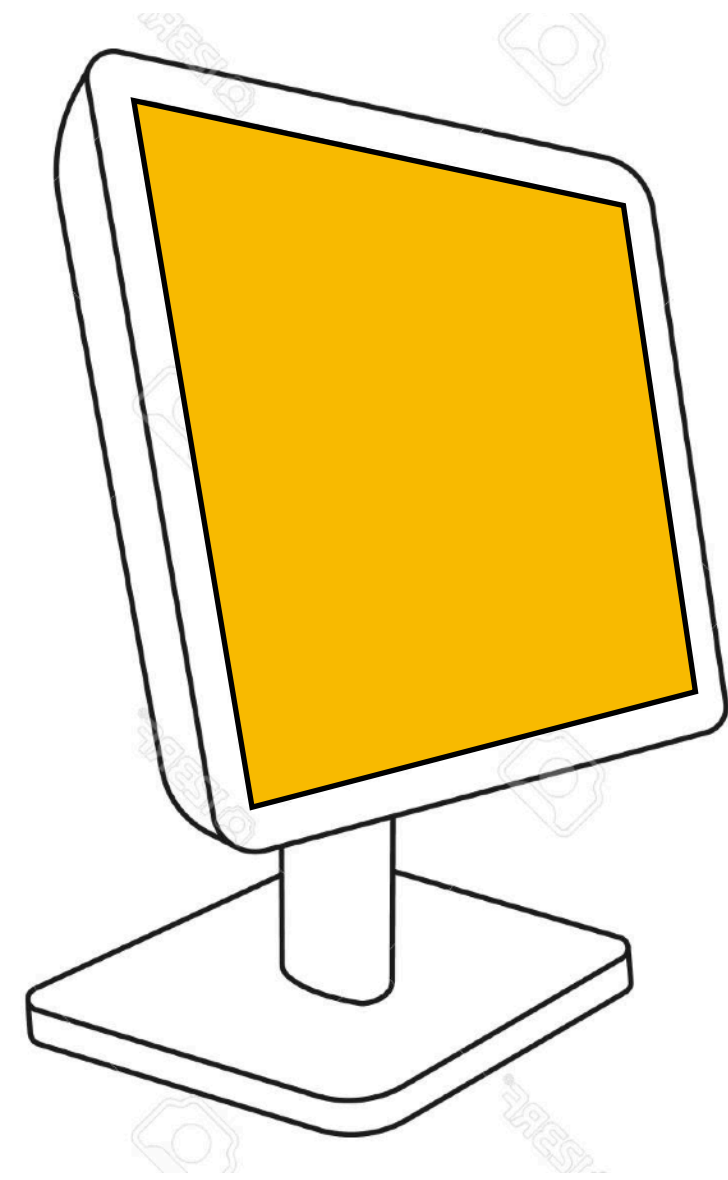
"Blue-yellow blindness"





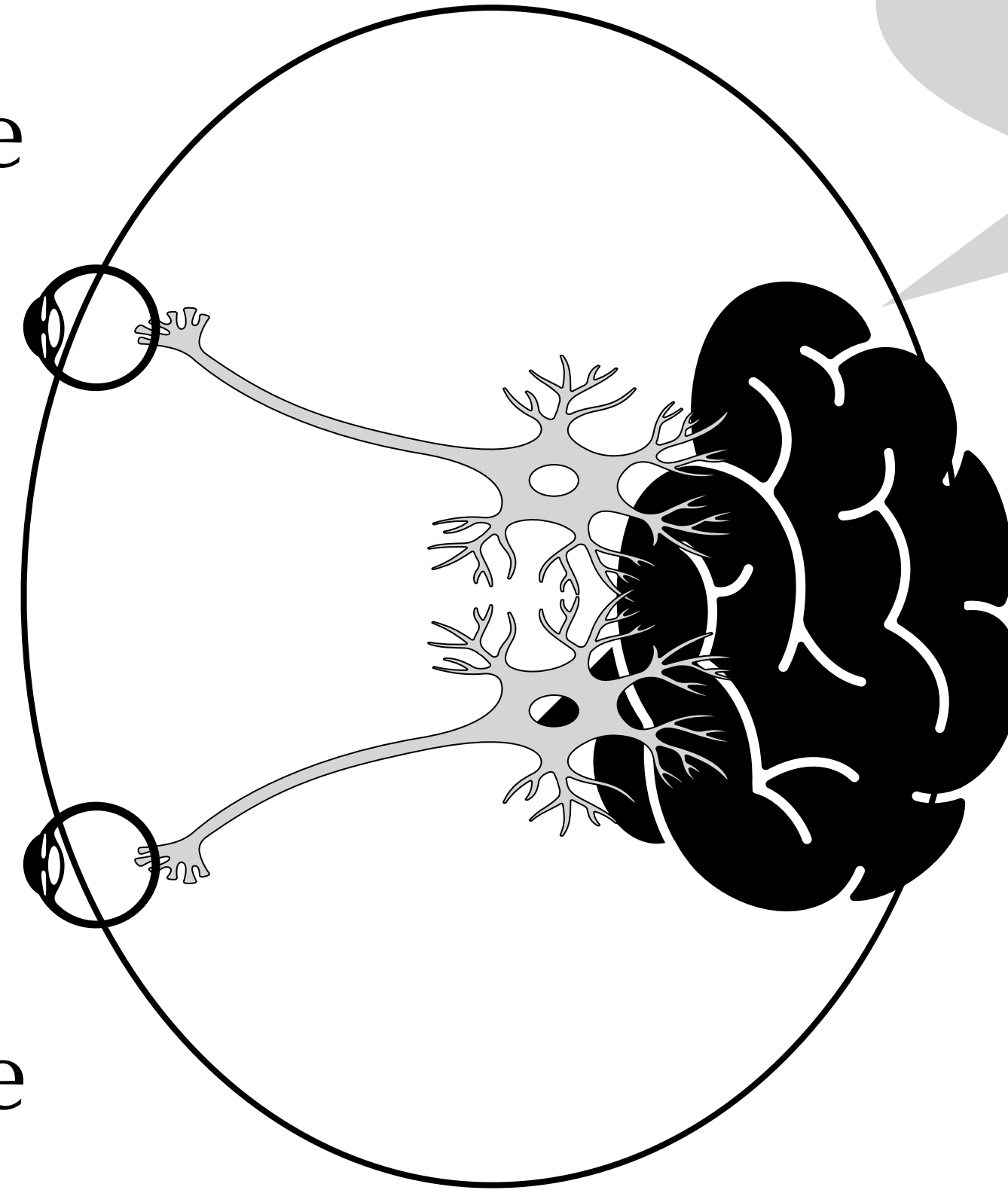
What are the colors that a deuteranope actually sees?

Unilateral Dichromats



Dichromatic eye

Trichromatic eye



Do both of my eyes see the same color?

Unilateral Dichromats

A Case of Unilateral Deuteranopia*

LOUISE L. SLOAN AND LORRAINE WOLLACH

Wilmer Ophthalmological Institute, Johns Hopkins

(Received N

Studies are reported of a subject with deuteranopia of the right eye and mild deuteranomaly of the left. On the Nagel anomaloscope this subject, using the right eye, matched both spectral red and spectral green to yellow. The left eye did not differ from normal with this test. Subject

Color Perceptions of Deuteranopic and Protanopic Observers

By Deane B. Judd

PERCEPTION OF COLOUR IN UNILATERAL TRITANOPIA

BY M. ALPERN*, K. KITAHARA*† AND D. H. KRANTZ‡

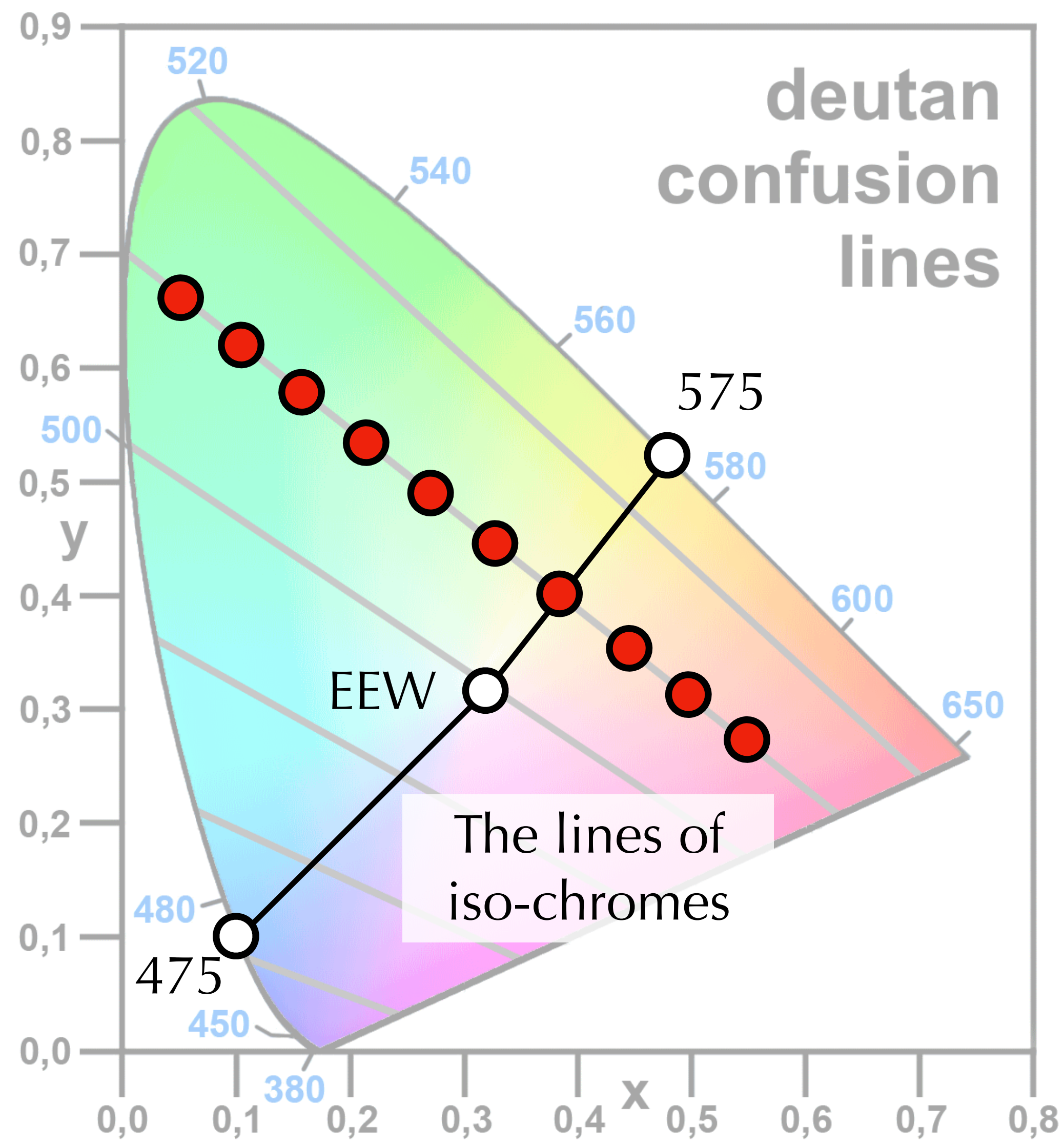
*From the *Vision Research Laboratory, University of Michigan, Ann Arbor, MI 48109, and †Bell Laboratories, Murray Hill, NJ 07974, U.S.A.*

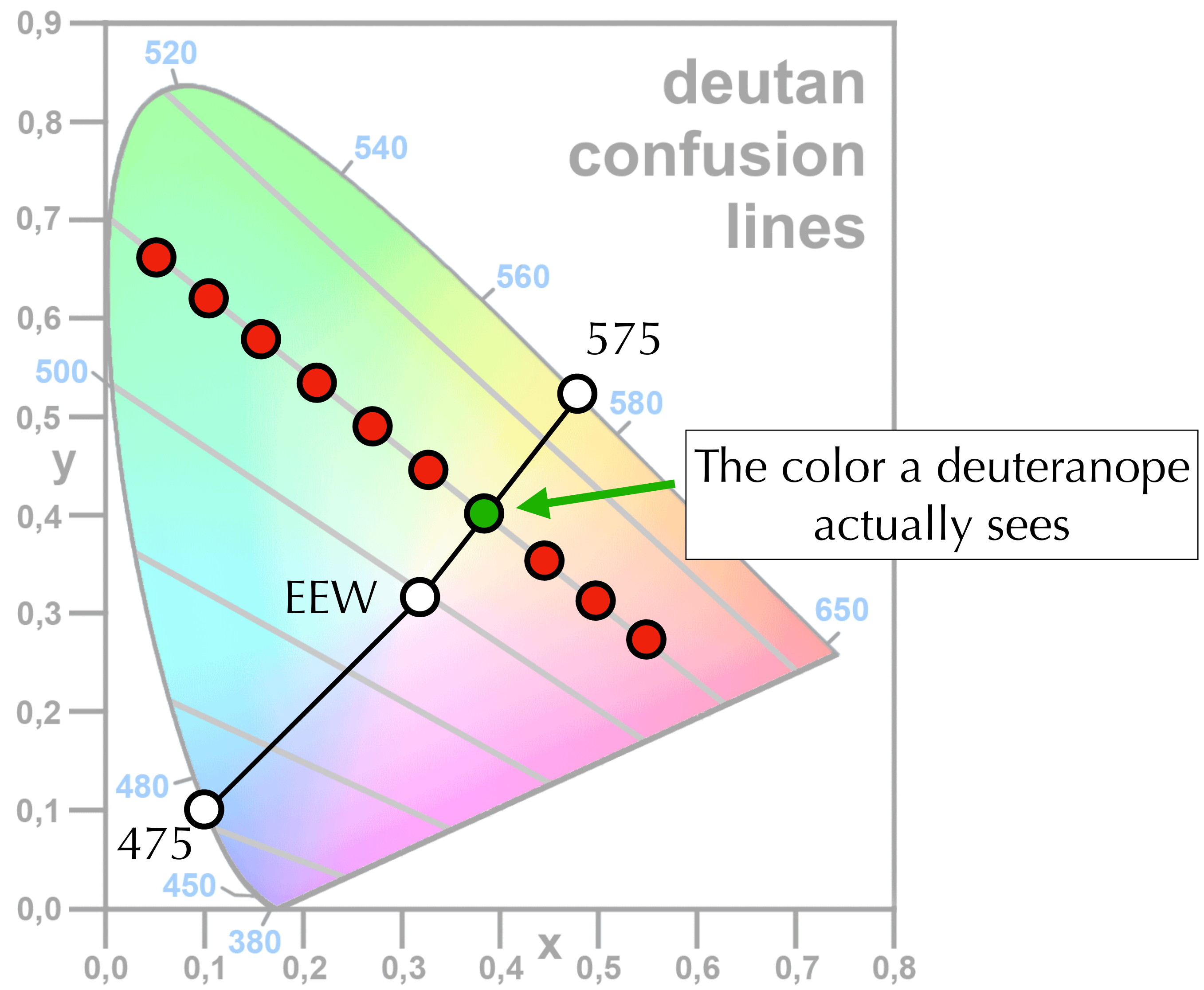
(Received 15 July 1981)

SUMMARY

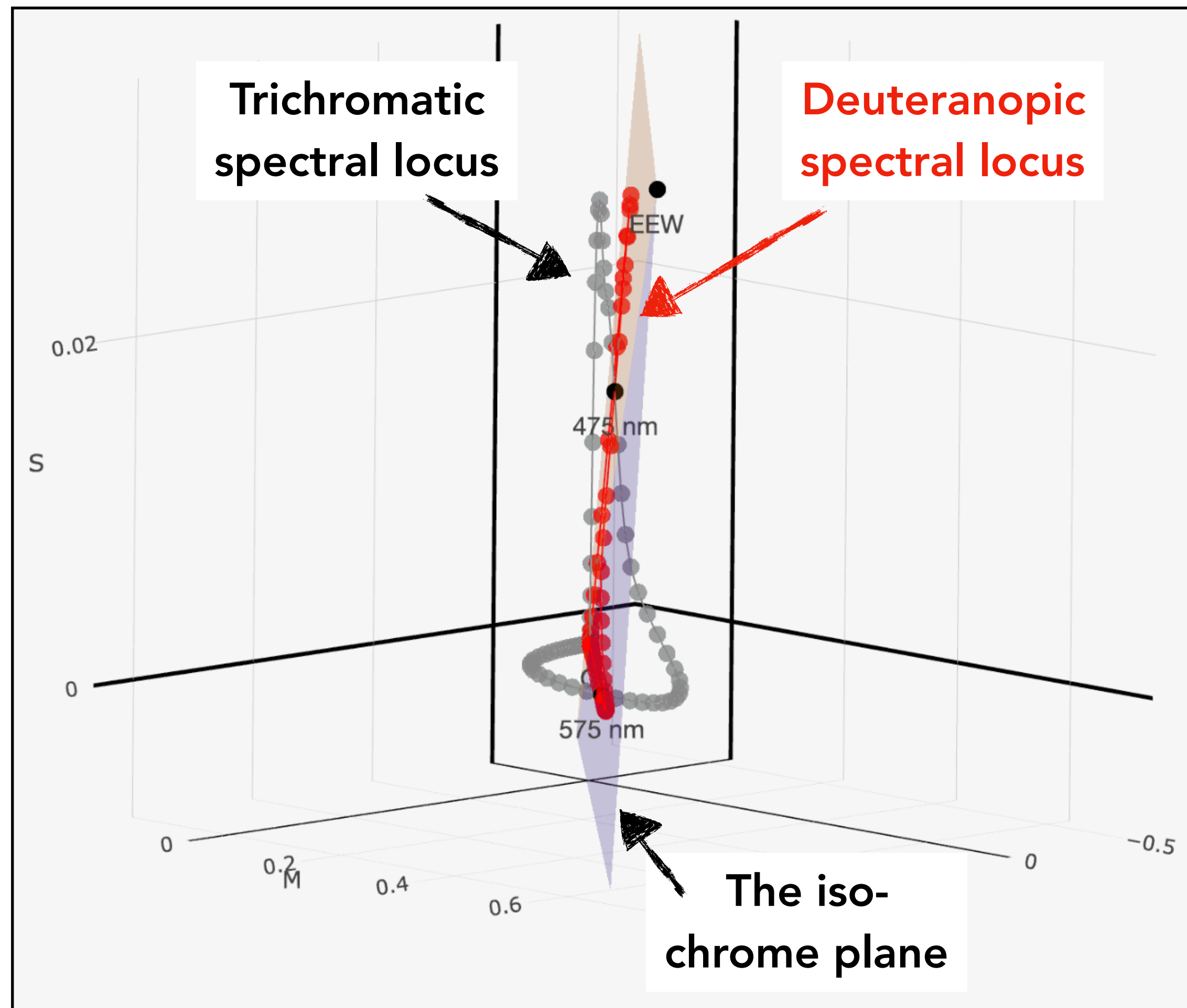
1. The unilateral tritanope described in the previous paper (Alpern, Kitahara & Krantz, 1983) was able to match every narrow-band light presented to his tritanopic eye with lights from a tristimulus colorimeter viewed in the adjacent field by the normal eye.

normal human males are concerned in the question: What do color perceptions corresponding to only understand better why to develop improved tests, but the nature of his color-confusions has trichromatic vision over a another portion, he may give a stic of the particular form of h observers are those born with rather considerable literature on pic and deuteranopic observers received under usual conditions observers. By combining this Bureau Research Paper RP1618) to give quantitative estimates of range of colors in the Munsell pic and deuteranopic Munsell ge the Munsell papers in ways romats, but also to get immediately perceived in these arrangements Munsell notations serve to





The Geometry of Dichromatic Vision in LMS Space



<https://horizon-lab.org/colorvis/colorblind.html>

And with three, we enjoy trichromacy:



With two, we
are dichromatic:

Protanopia (missing red sensor)



Tritanopia (missing blue sensor)



Deuteranopia (missing green sensor)



Color Vision Deficiency

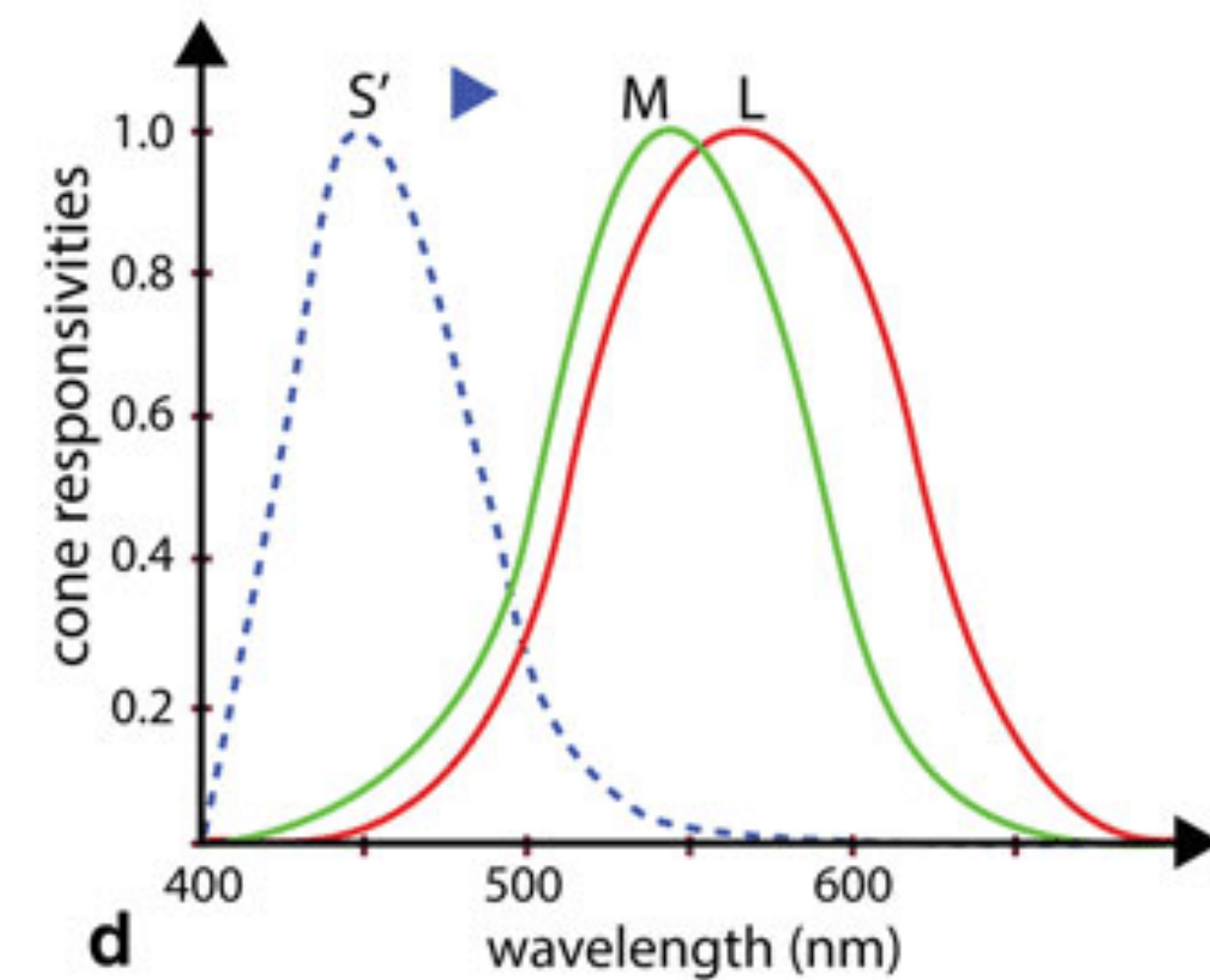
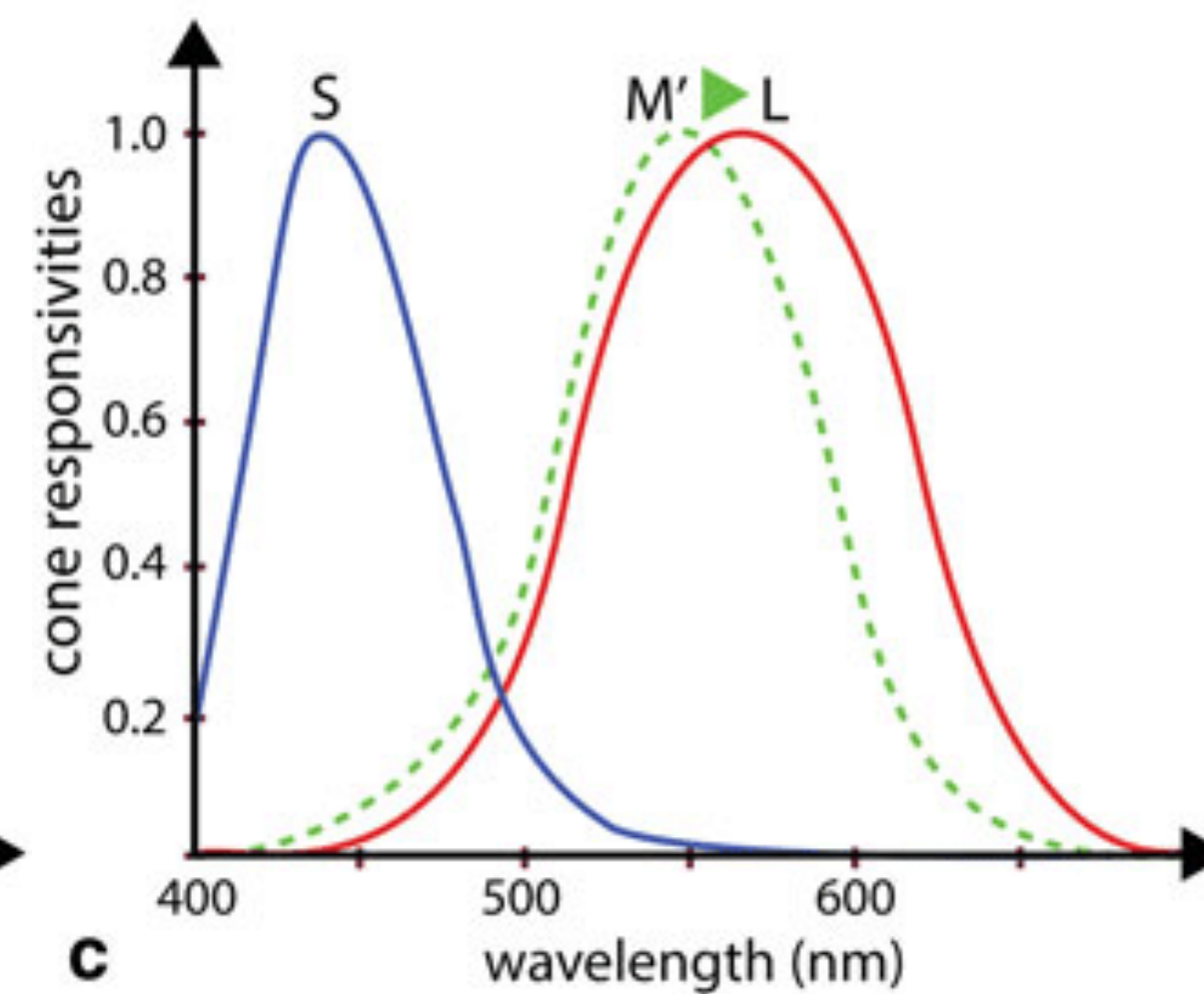
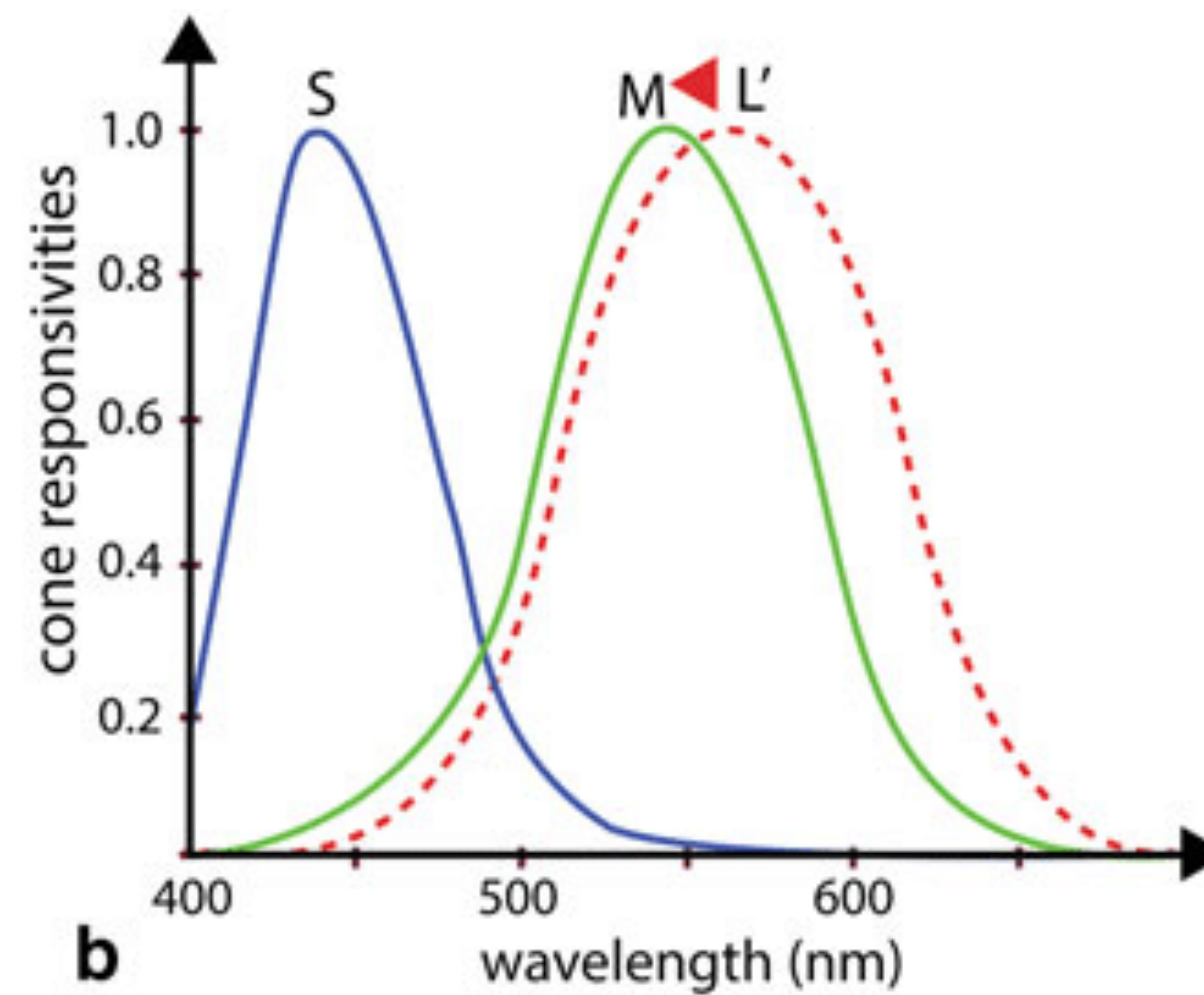
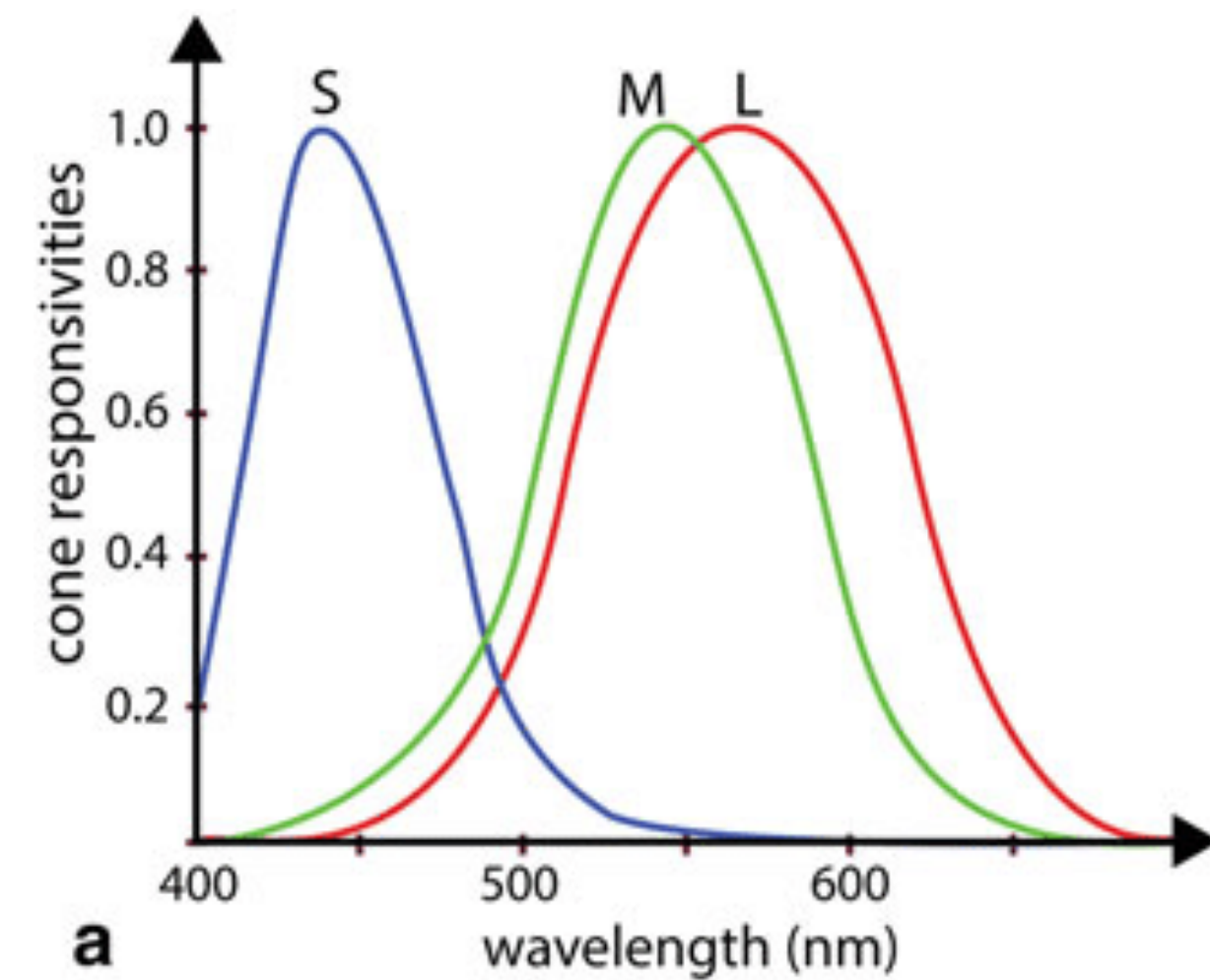
- Dichromatic vision
- Anomalous trichromatic vision
- Other forms of CVD

Anomalous Trichromacy

Protanomaly:
(~)553 nm ← 566 nm

Deuteranomaly:
543 nm → (~)560 nm

Tritanomaly

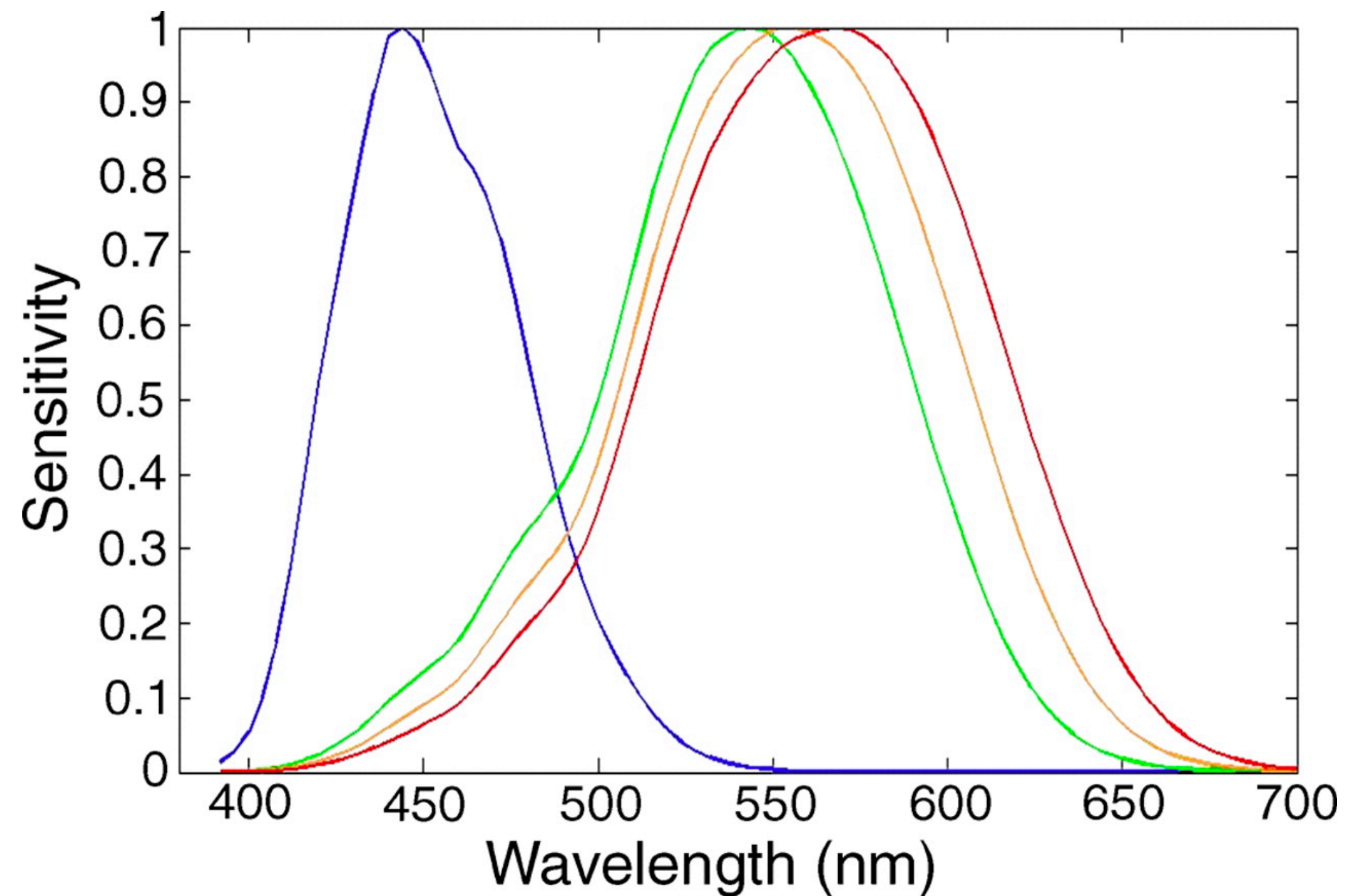


- Cone sensitivity peaks shift away from the normal peaks
 - Sensitivities of different cone types are more similar → weaker color discrimination
 - Each anomalous individual has a slightly different shift

General Statistics (caucasians; vary significantly across ethnic groups)

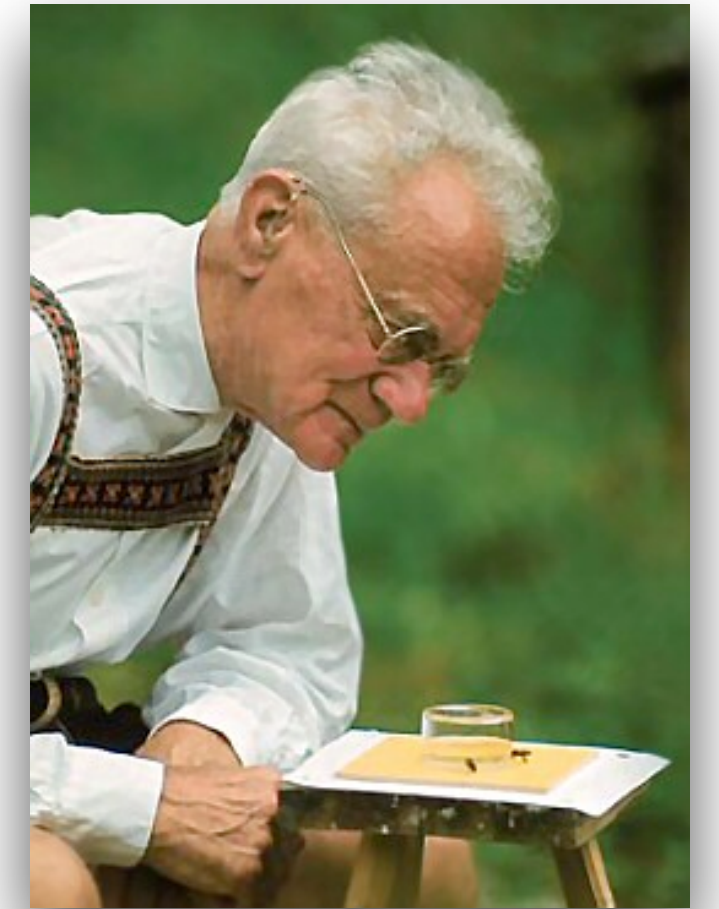
	Protanomaly	Protanopia	Deuteranomaly	Deuteranopia	Tritanomaly/ Tritanopia
Male %	1.0%	1.0%	4.9%	1.1%	<0.01%
Female %	0.02%	0.02%	0.38%	0.01%	<0.01%

Human Tetrachromacy

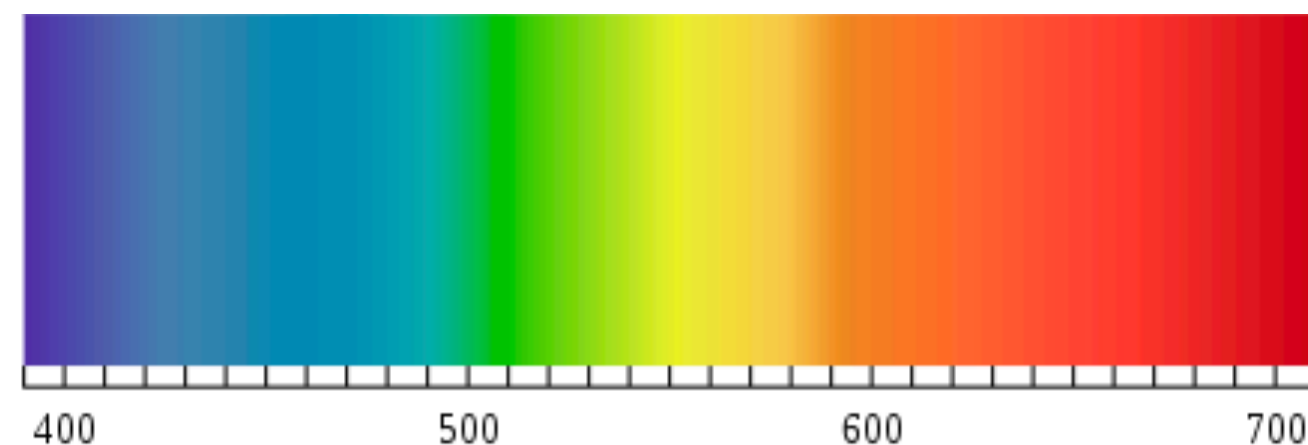
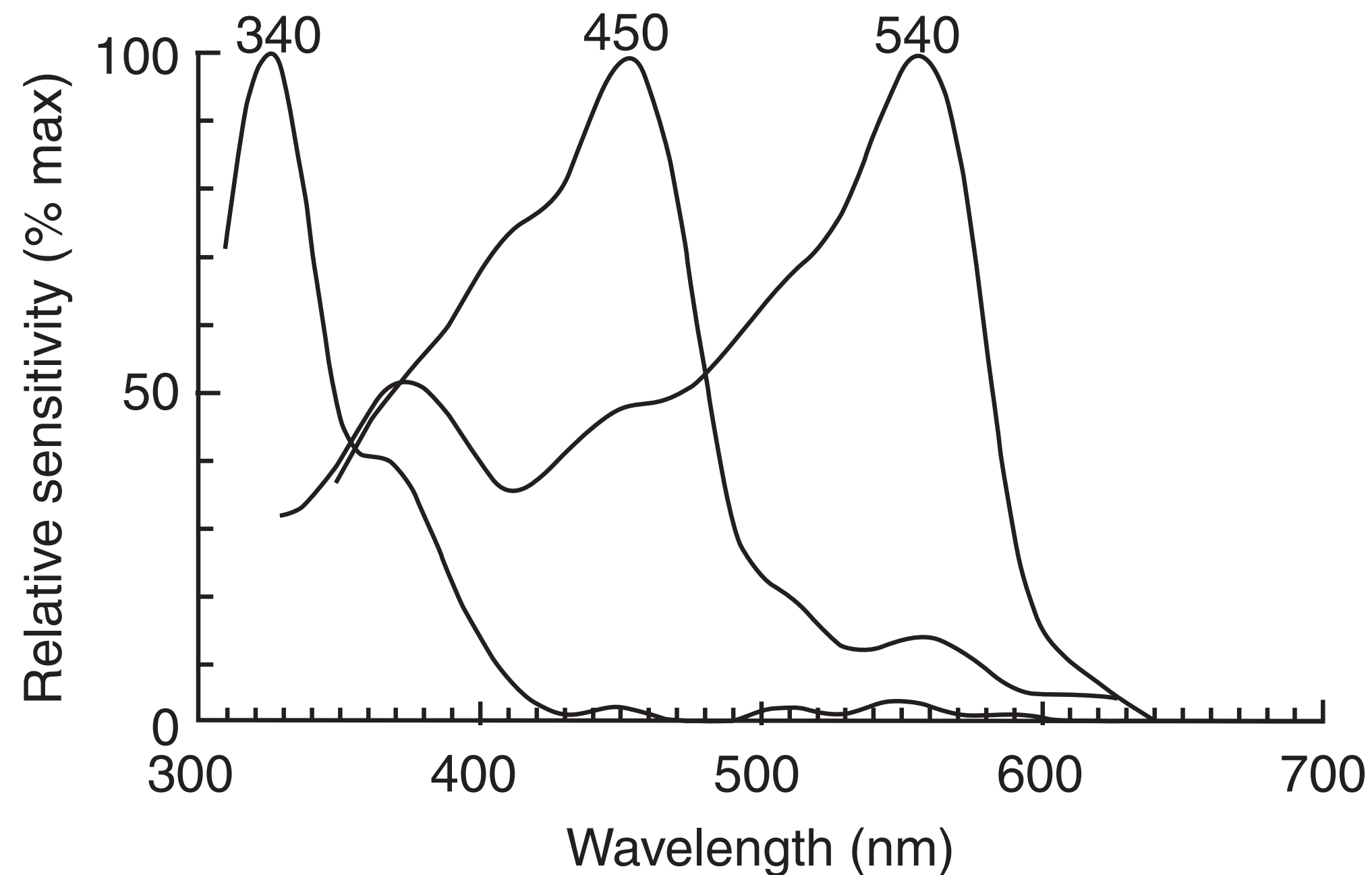


- Some people have four cone types, but they do not exhibit stronger color discrimination.
- Why? No neural circuits that can make use of the fourth cone type?
- Another view: neural circuits are plastic and can be trained to make use of the fourth cone type.

Bee Photoreceptor Sensitivities



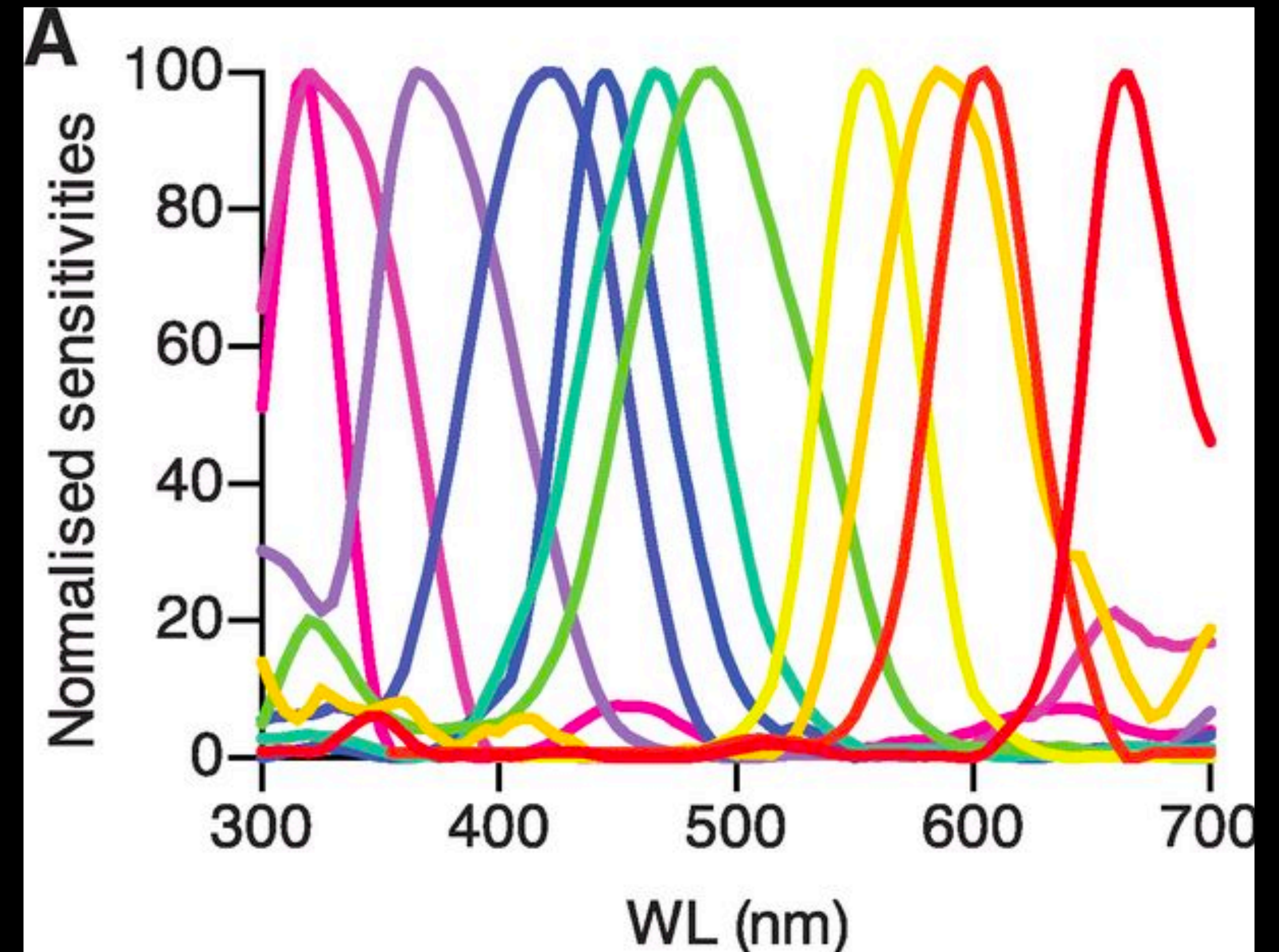
Karl von Frisch
(1973 Nobel prize)



- Bees have three photoreceptors, but their sensitivities are shifted toward lower wavelengths.
- So they can see UV lights but can't distinguish between red and black.
- Karl von Frisch, one of the first to experimentally show bees see color.

Mantis Shrimp

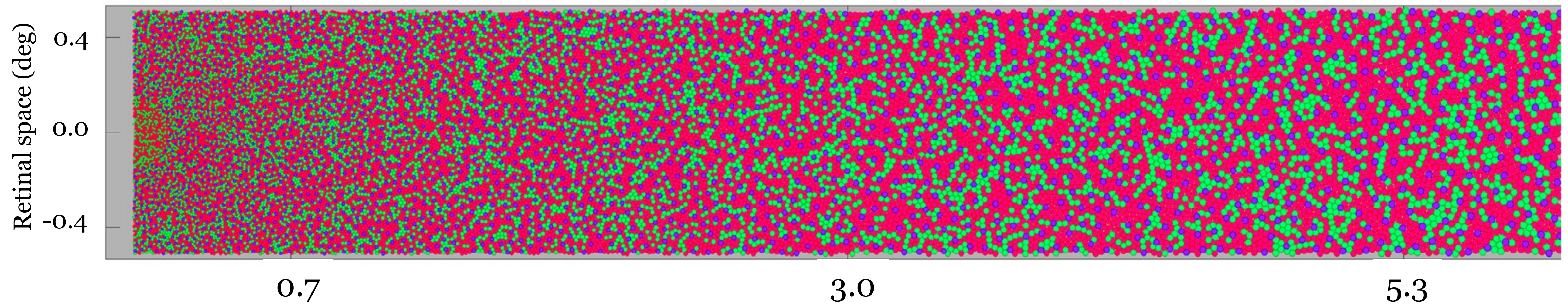
* Unclear if mantis shrimps can actually make use of all the photoreceptor classes to enhance their color vision



Color Vision Deficiency

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- Anomalous trichromatic vision
- Other forms of CVD

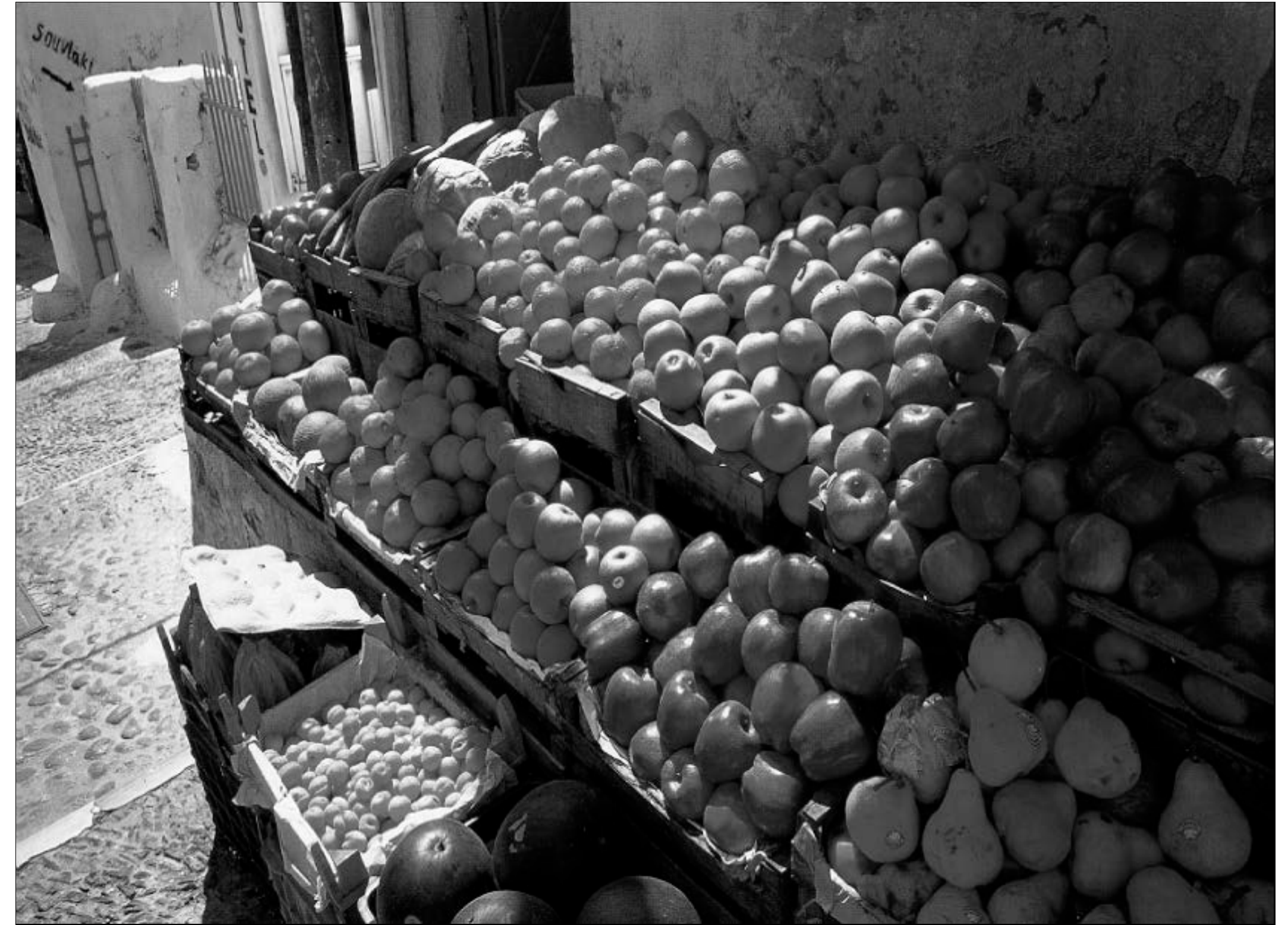
Small-Field Dichromacy



- At the central 20 arcmin of the fovea there are no S cones
- Human vision is effectively dichromatic there

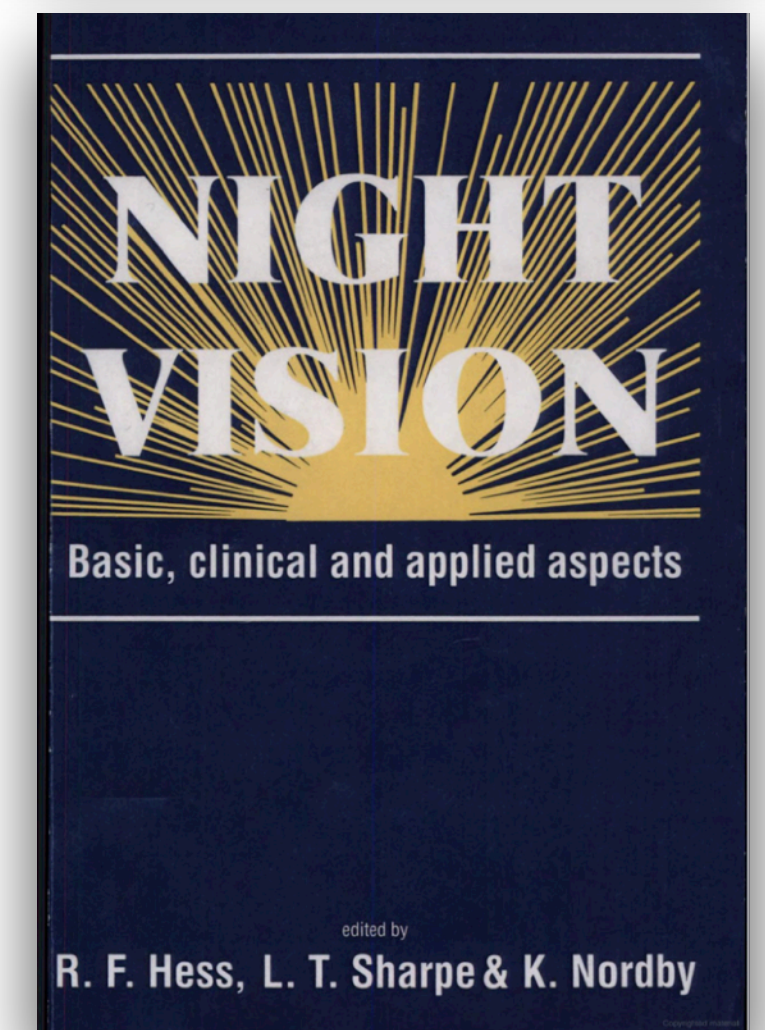
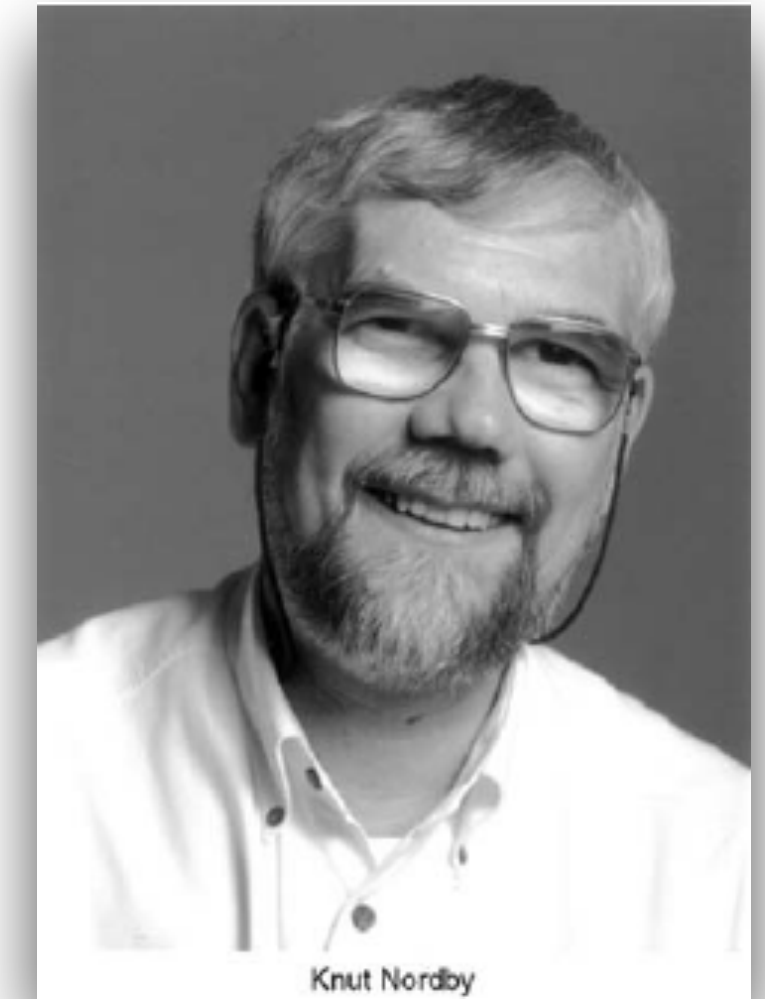
What If Only One Photoreceptor Type Exists?

Then you don't see color at all: you see only brightness differences



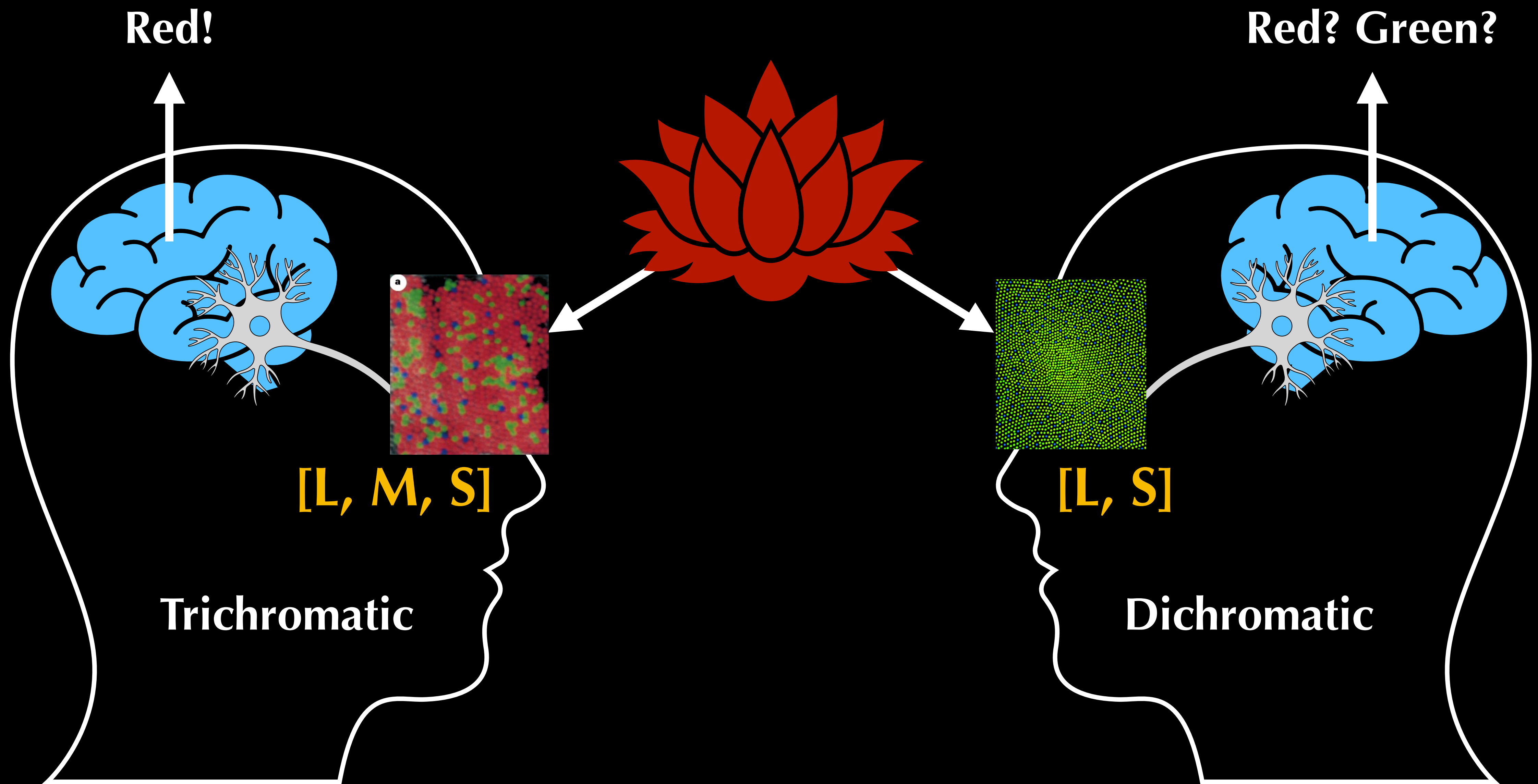
What If Only One Photoreceptor Type Exists?

- Rod monochromacy (20 per million people):
 - No cones, only rods
 - Rods are very sensitive to lights are usually activated at night so people with rod monochromacy have to wear very dark sunglasses
 - There are no rods in fovea, so people with rod monochromacy have low visual acuity
 - Knut Nordby (1942 — 2005)
- Cone monochromacy:
 - Most common is blue cone monochromacy: only S cones exist (why?)
 - At mesopic (twilight) vision they might have weak dichromacy

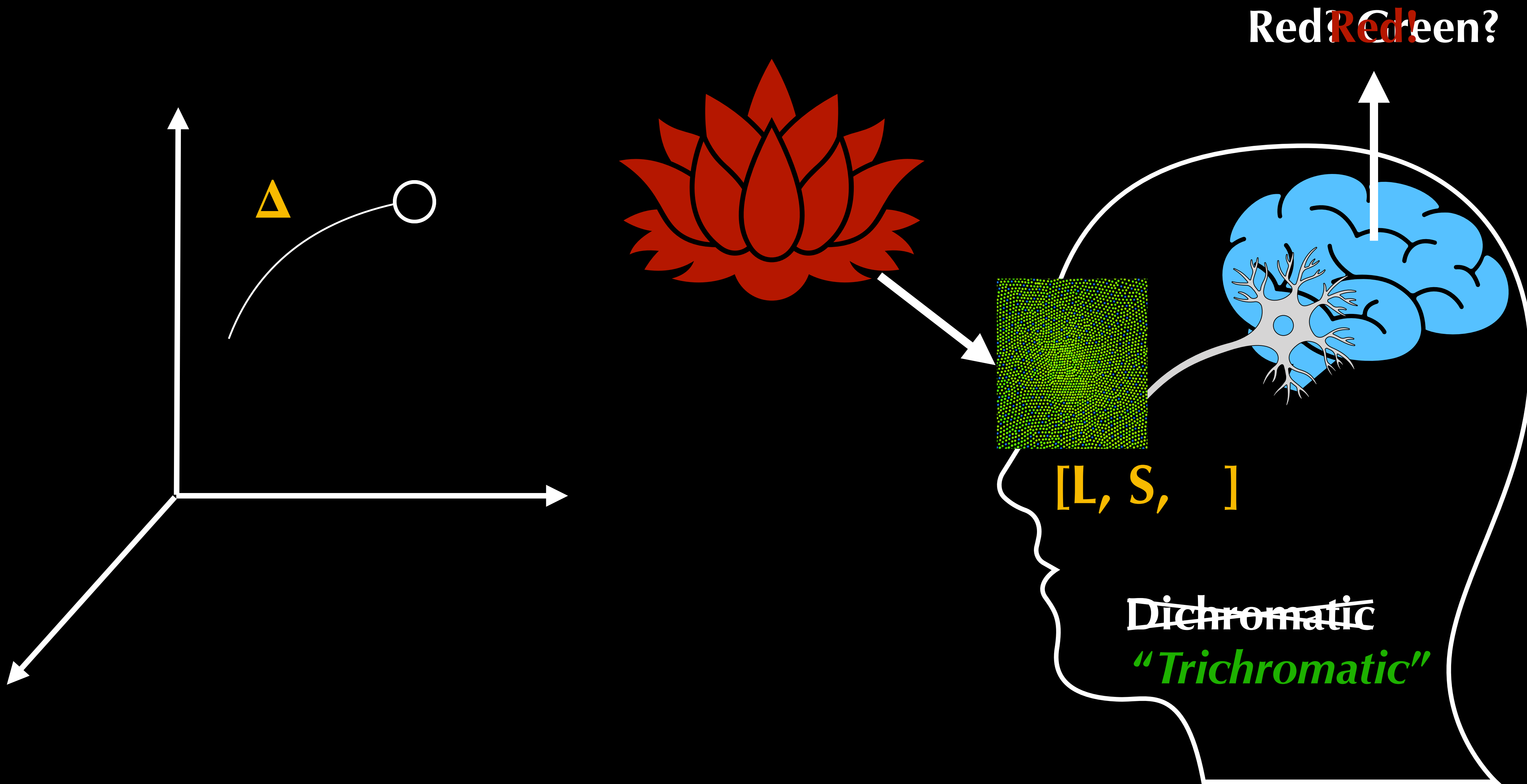


Computational Trichromacy Reconstruction

<https://colorvision.cs.rochester.edu/>



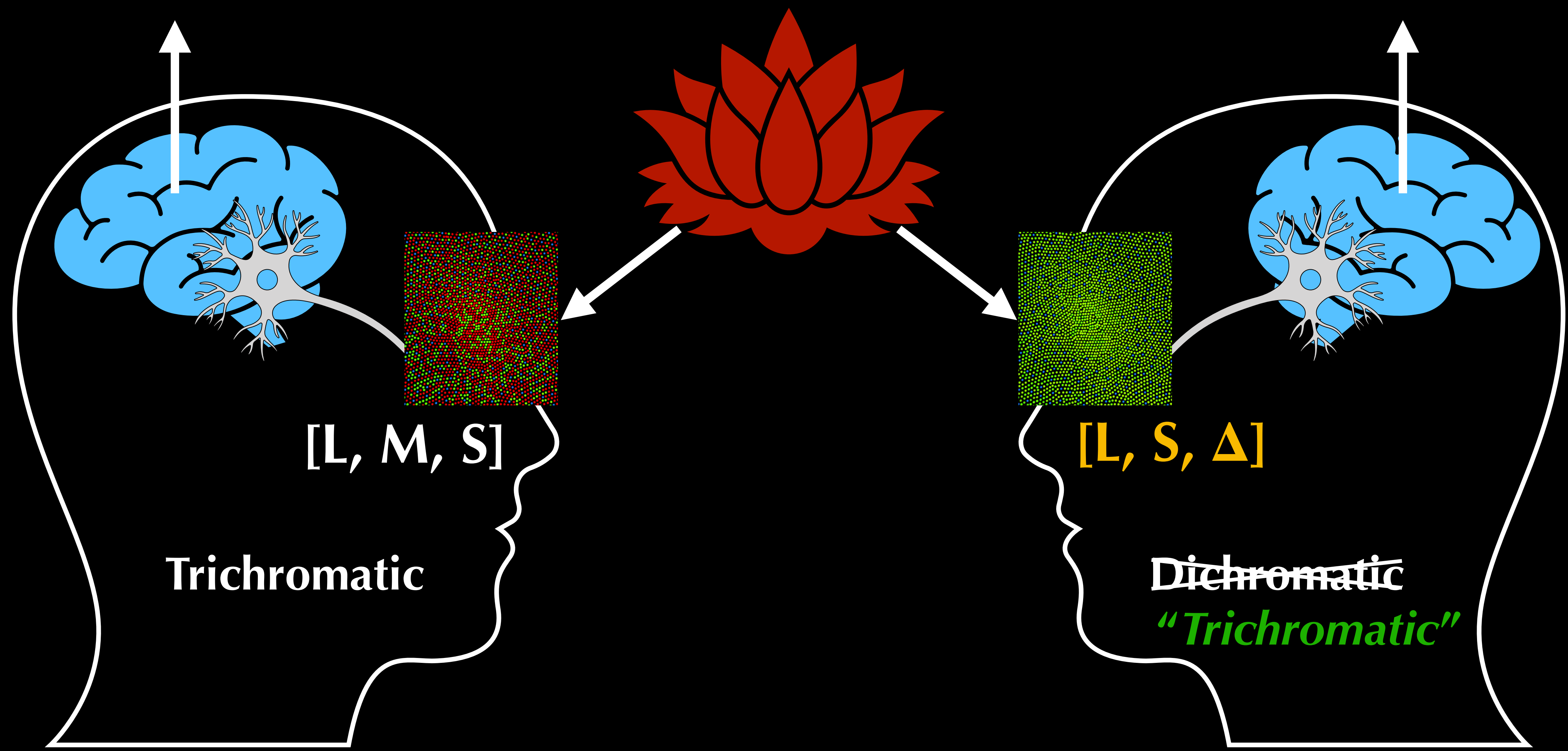
Can we restore the **missing dimension** to
rebuild trichromacy?



Still fundamentally different perceptions, but that's OK!

Red!

Red!



[L, M, S]

Trichromatic

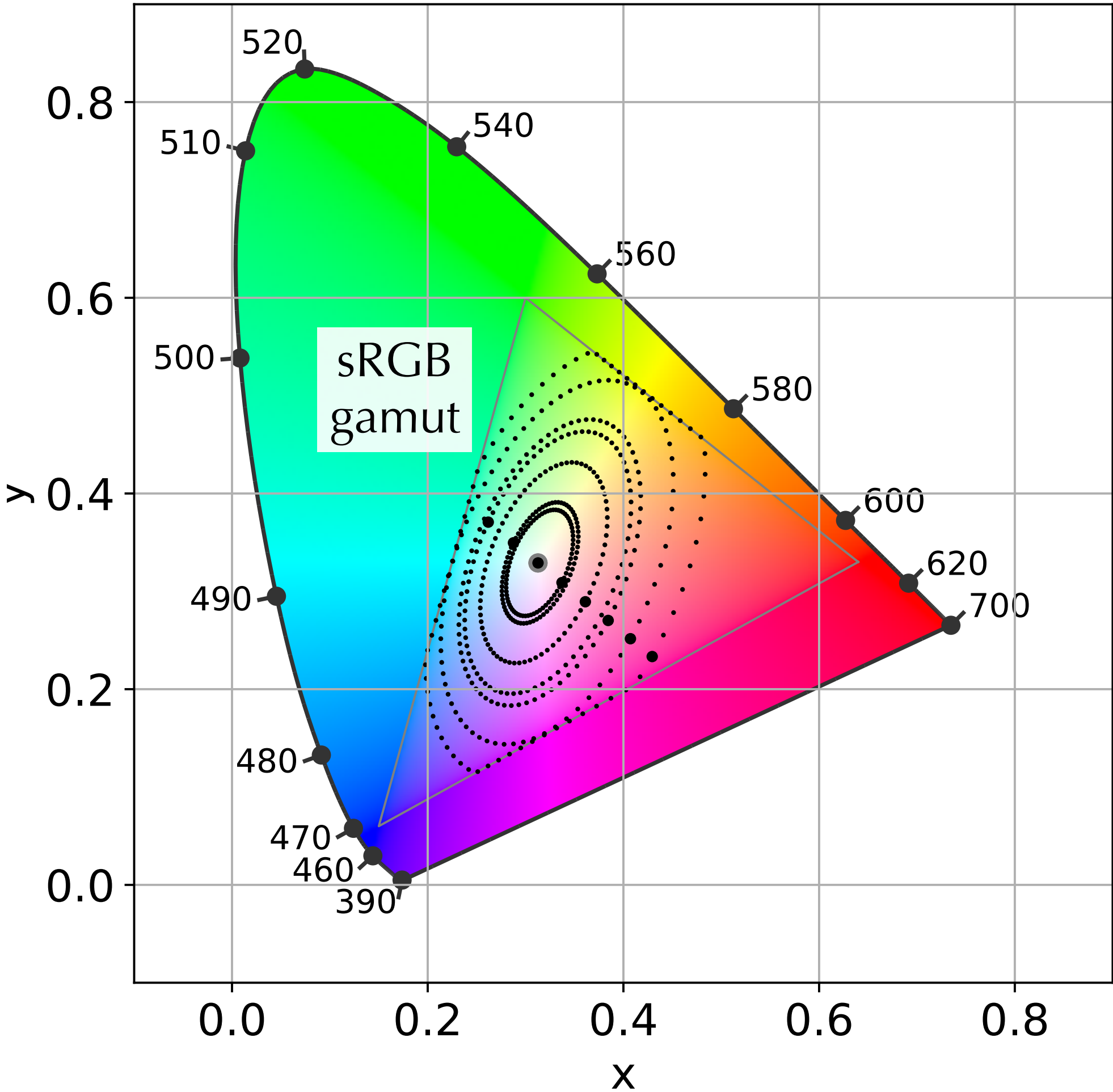
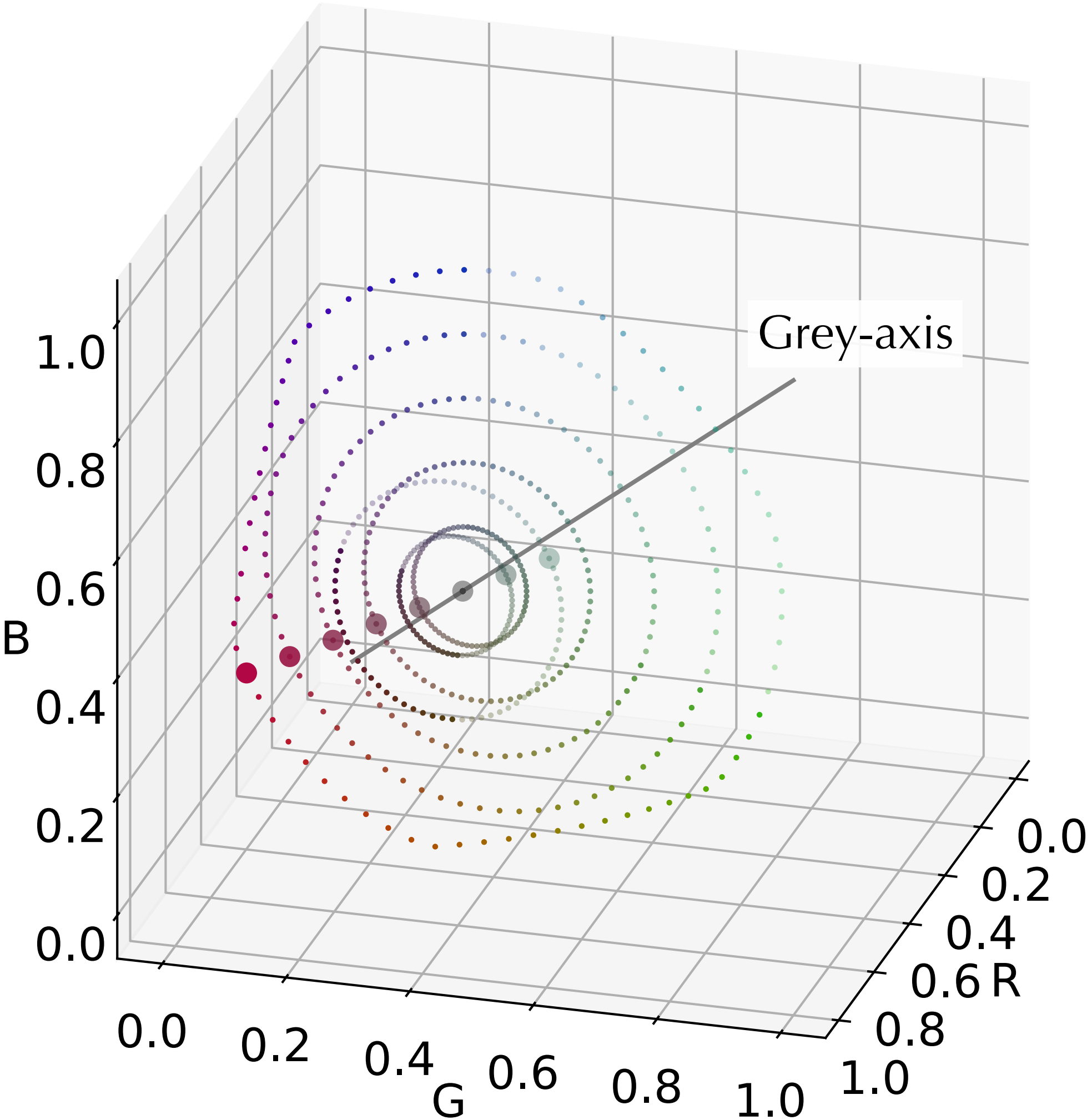
[L, S, Δ]

Dichromatic
"Trichromatic"

How to shift?

<https://colorvision.cs.rochester.edu/rotation-demo>

Intuition Behind Rotation



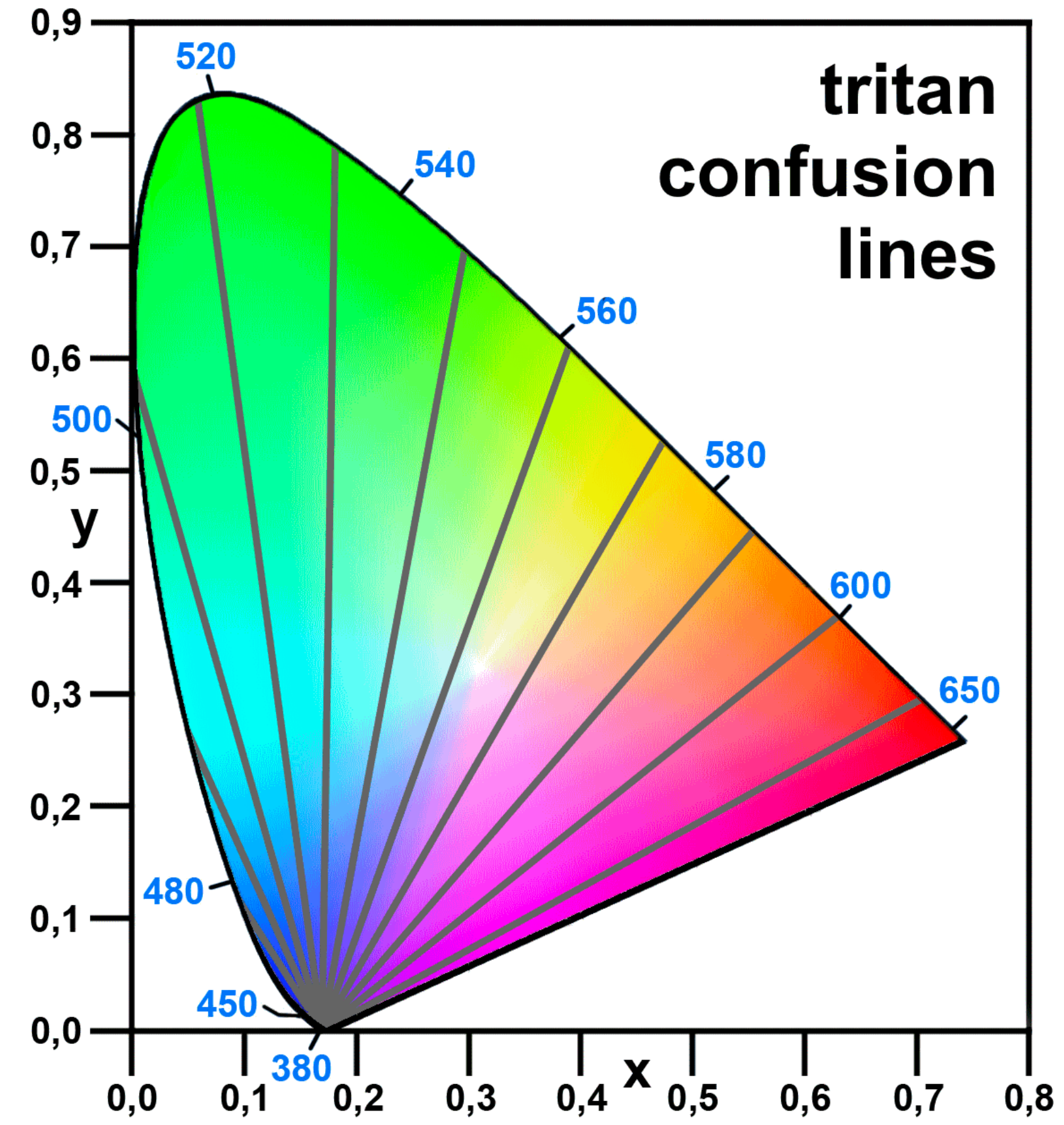
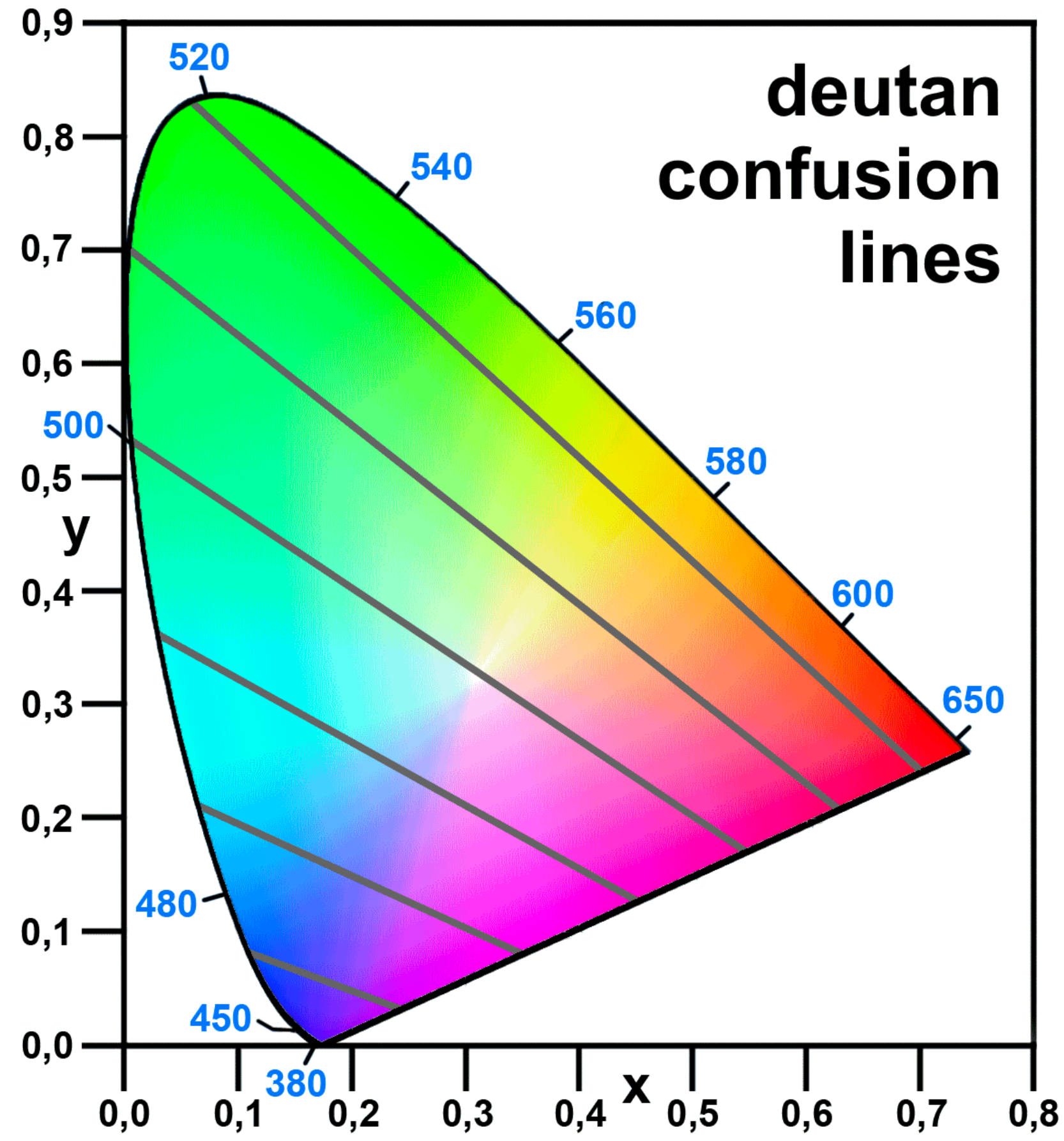
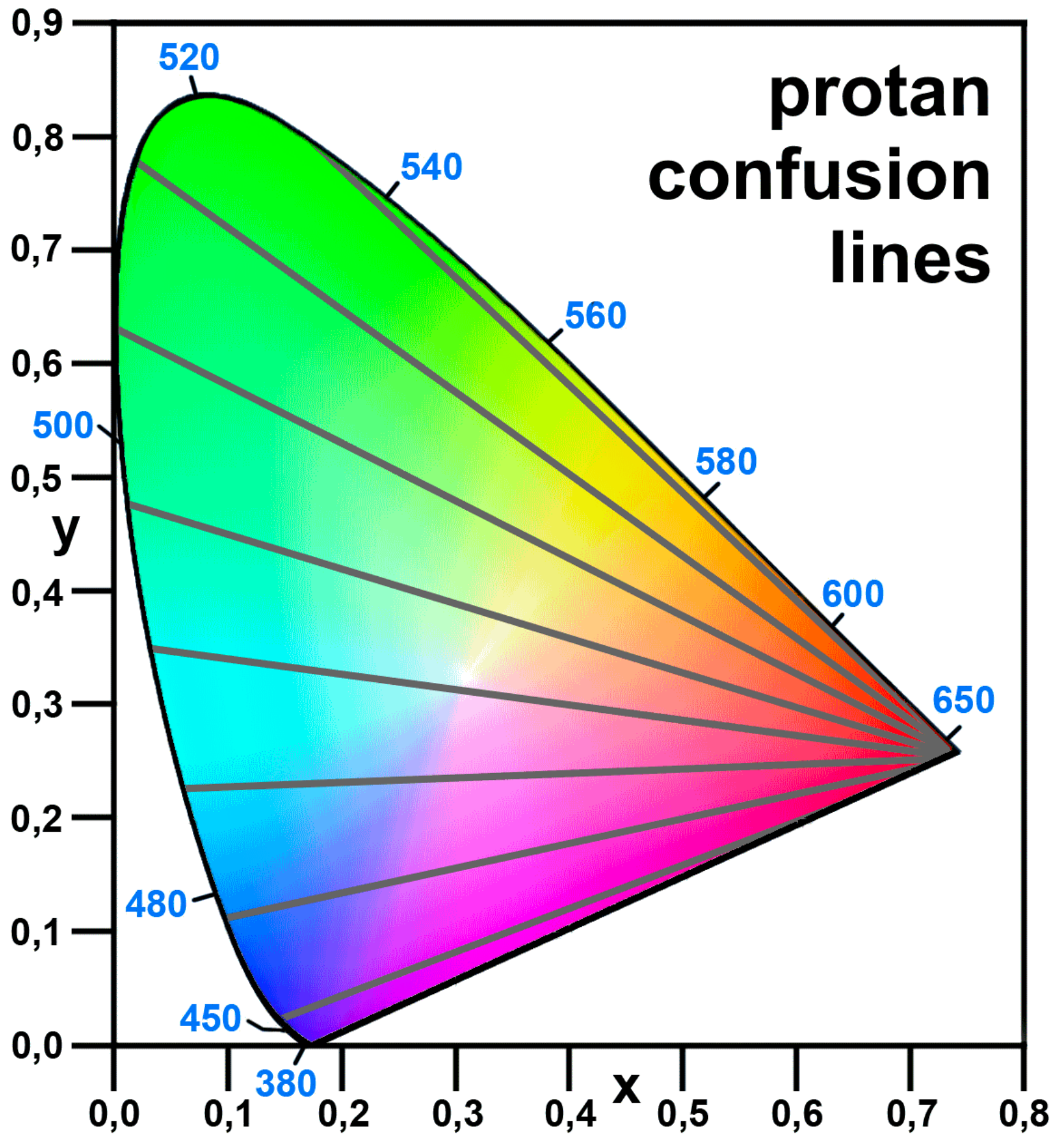
Could Rotational Shifts Be the Missing Dimension?

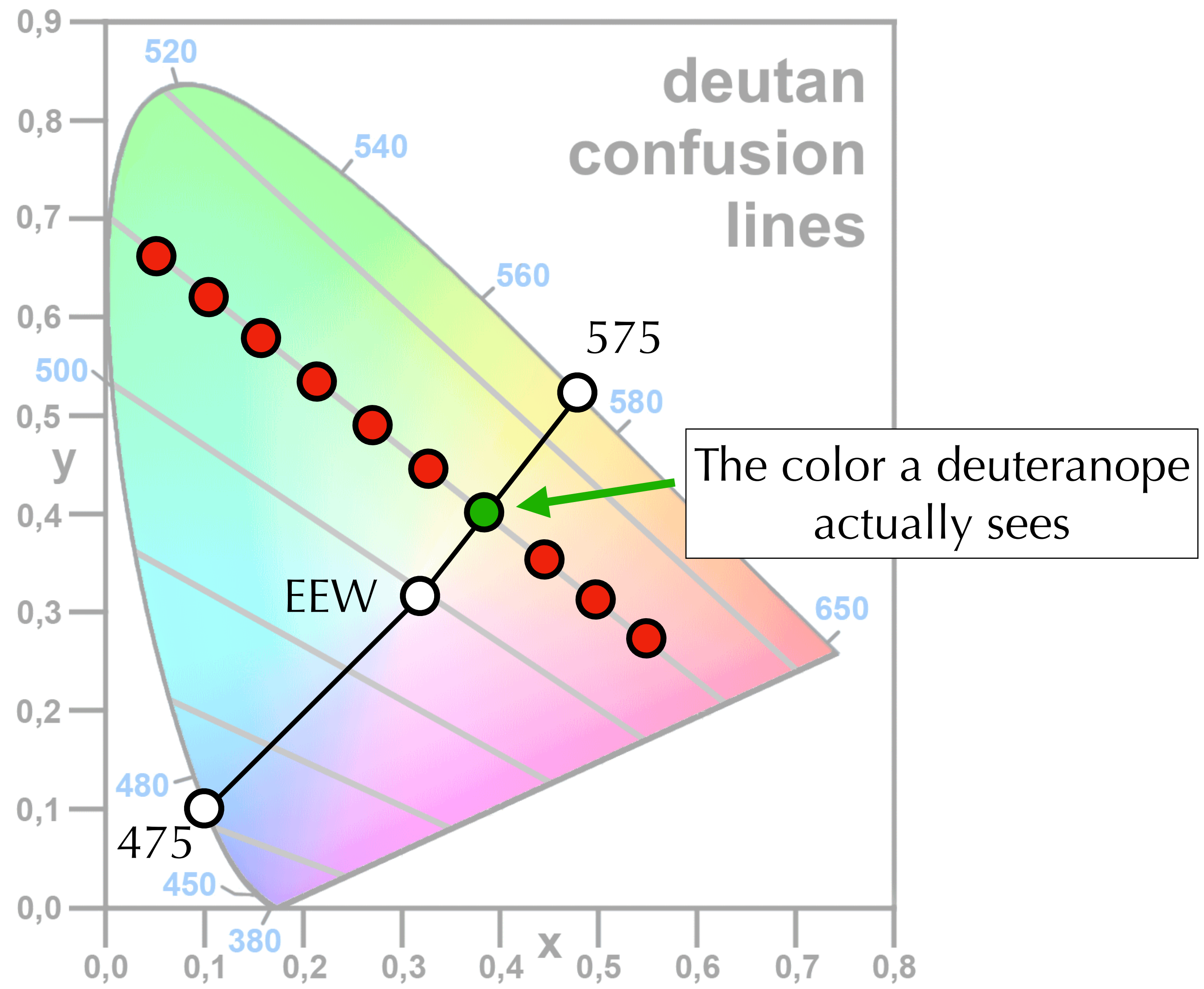
Requirement 1: rotational shifts must have discriminative power

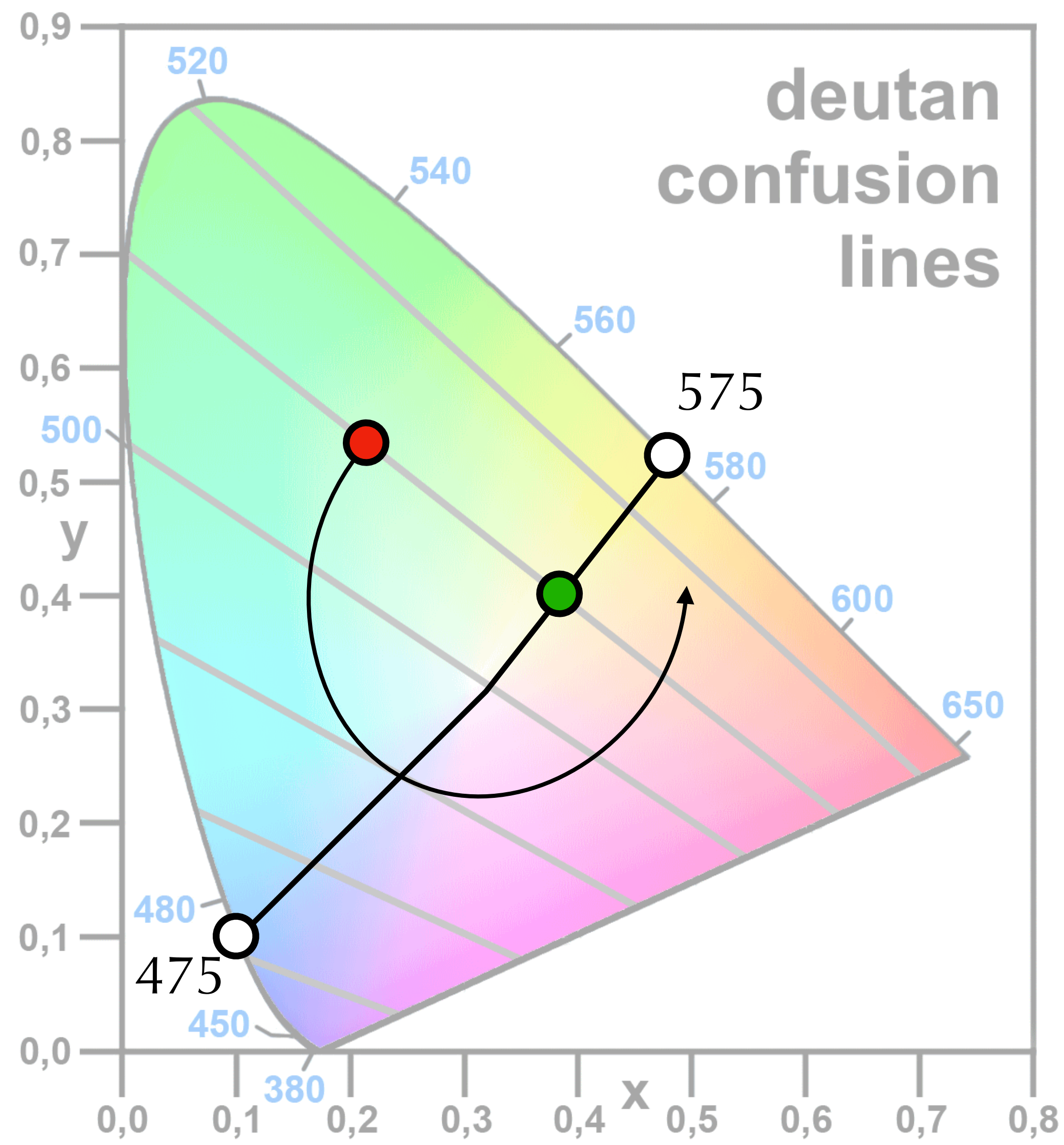
- That is, originally confusing colors will become distinct through rotation

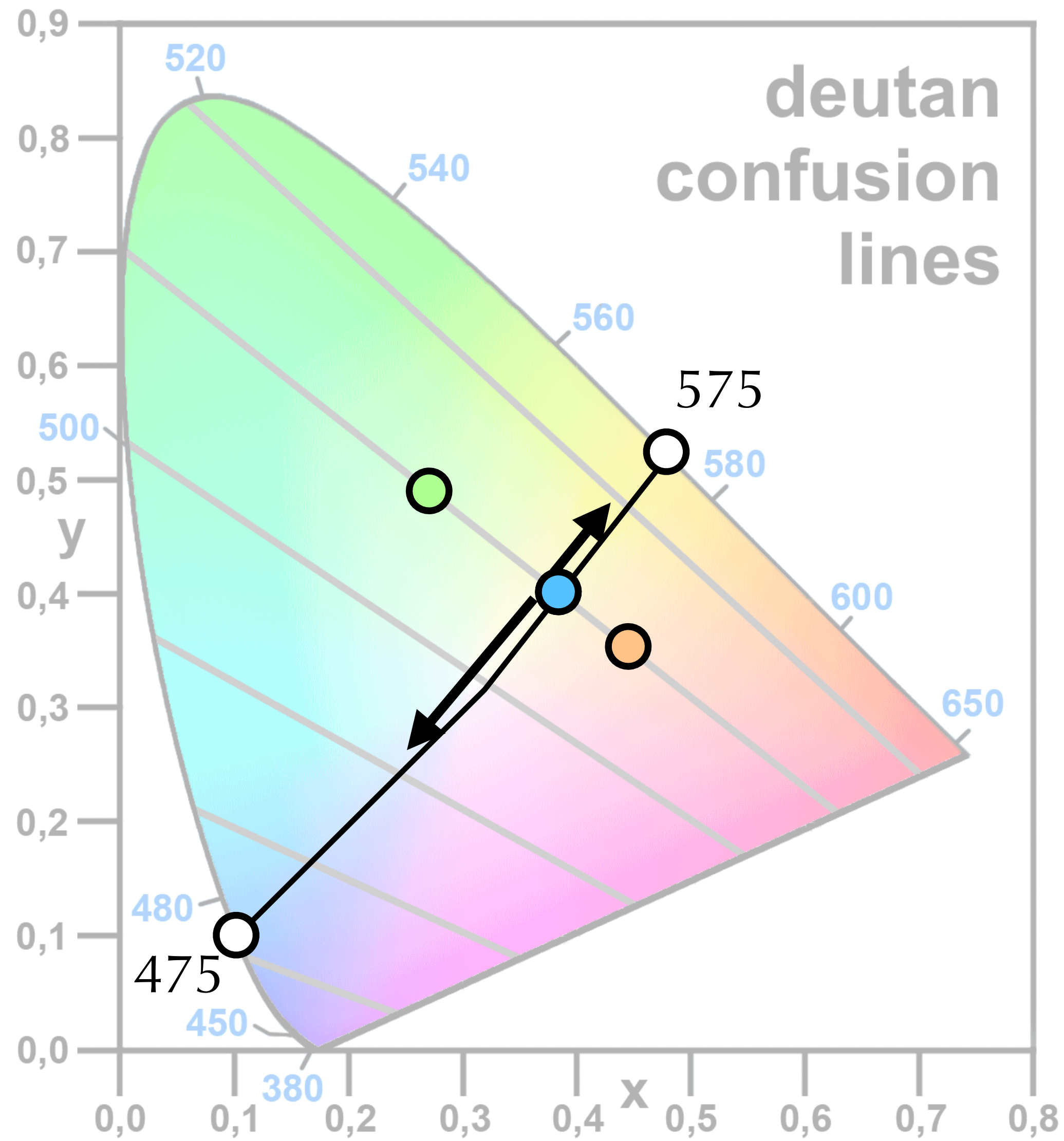
Requirement 2: rotational patterns must be easy to learn

- So that we can associate a pattern with a color name

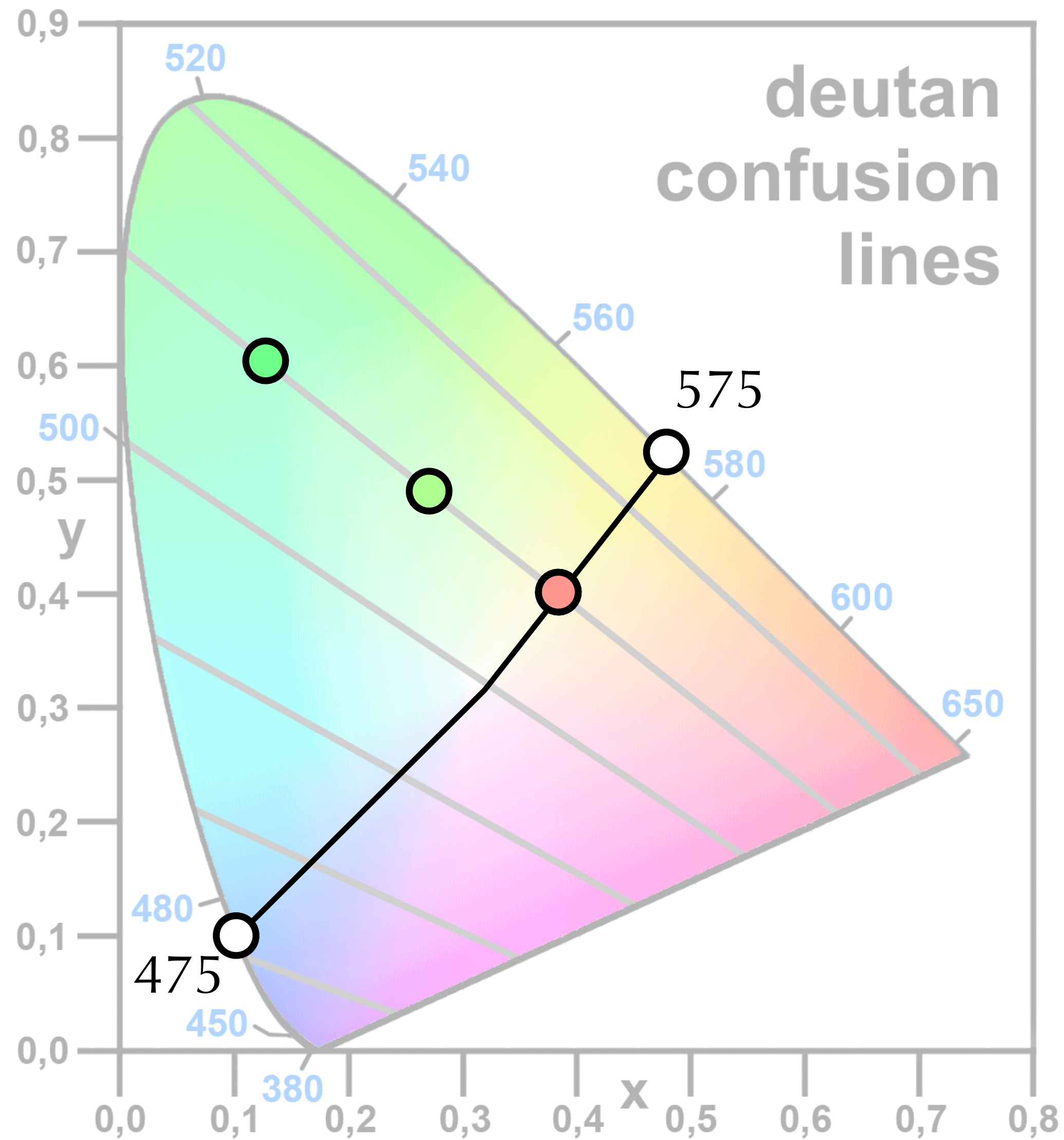




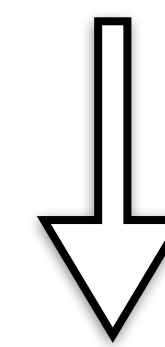




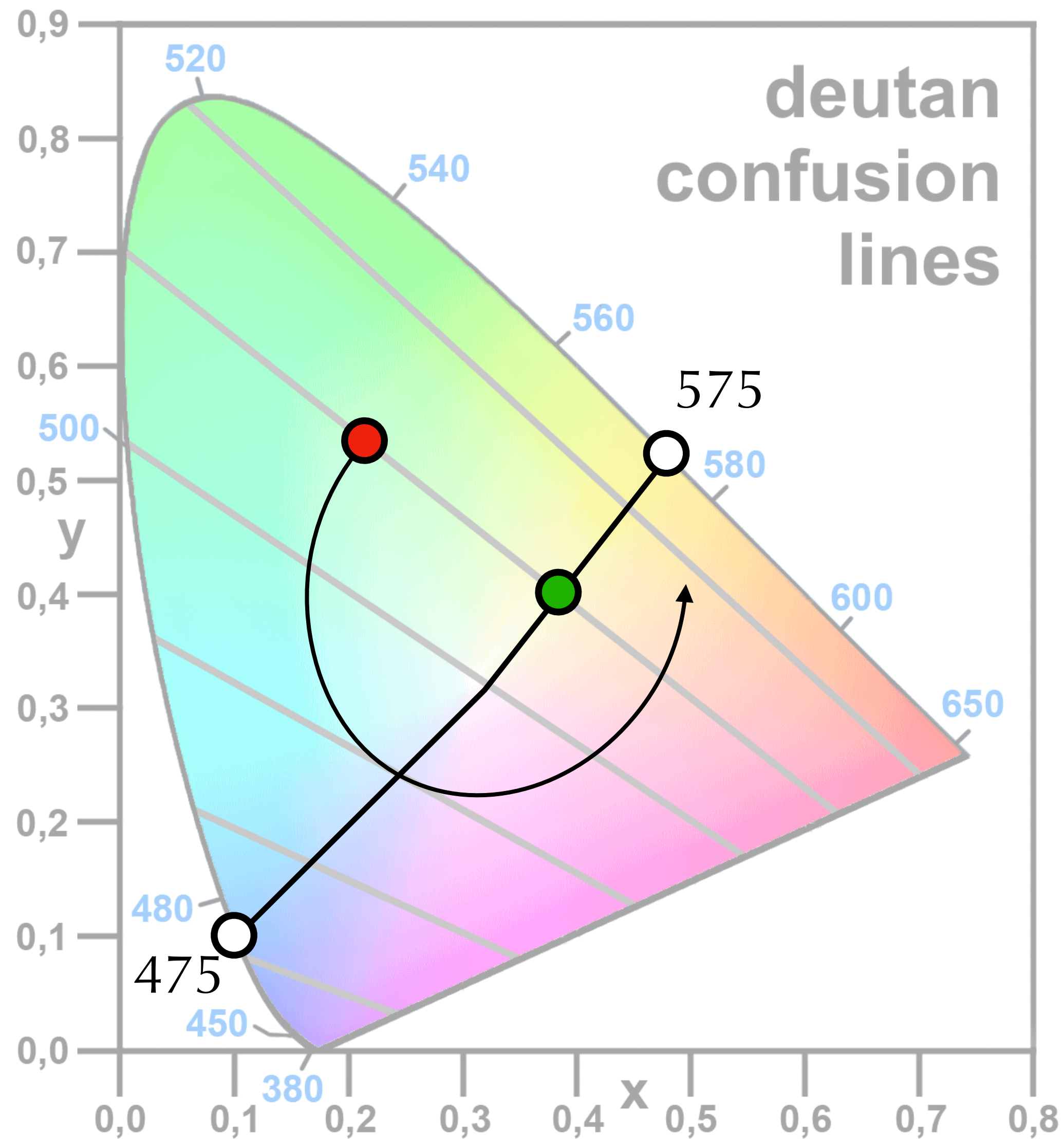
- **opposite** side of the iso-chrome lines
→ colors shift in opposite directions



- **opposite** side of the iso-chrome lines
→ colors shift in opposite directions
- **same** side of the iso-chrome lines
→ colors shift in different "speeds"



Confusing colors have unique color shift patterns — a third dimension that have **discriminative power**.



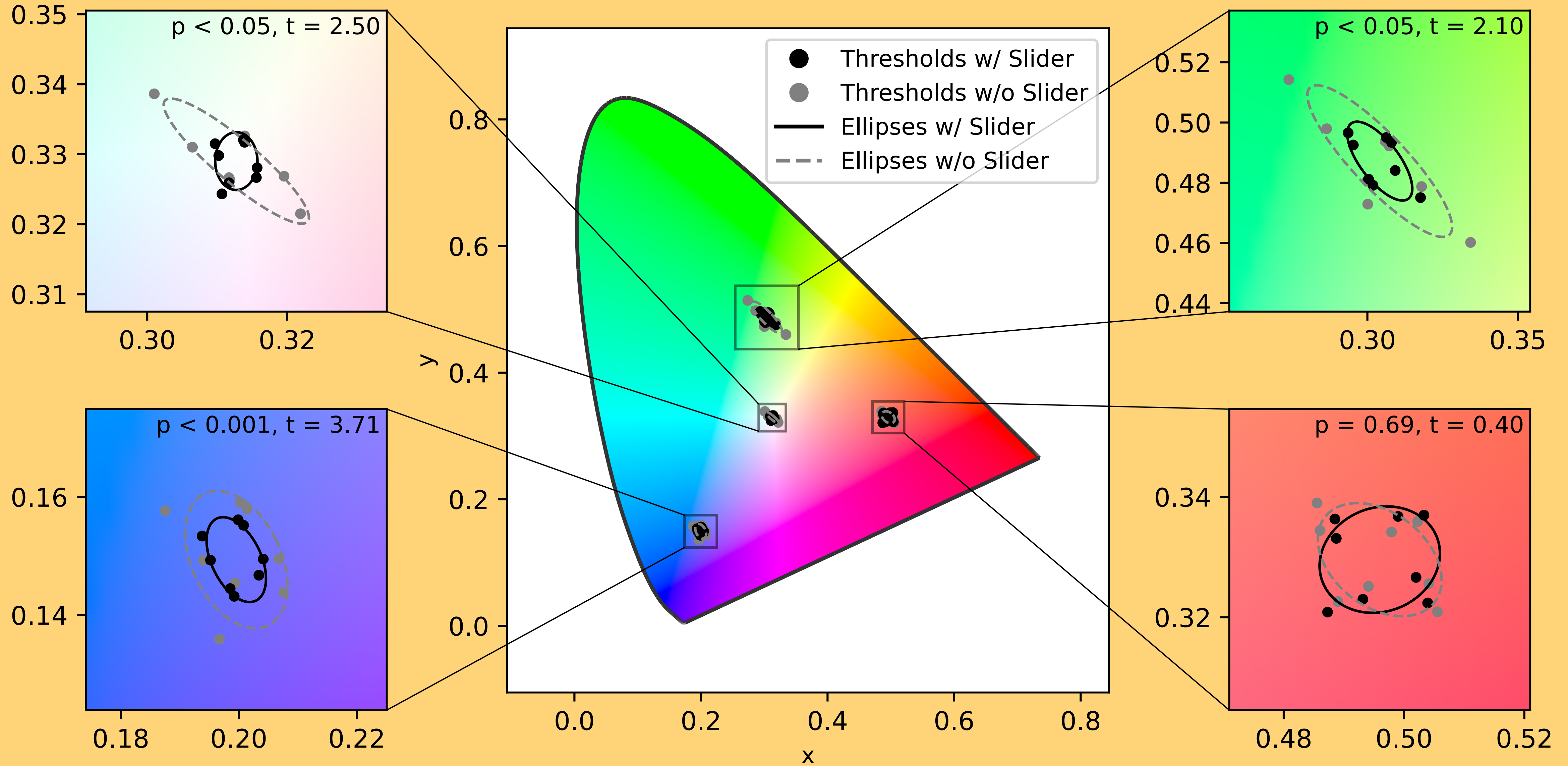
Rotation cycles through different hues, a regular pattern that's **easy to learn**.

Discrimination Task

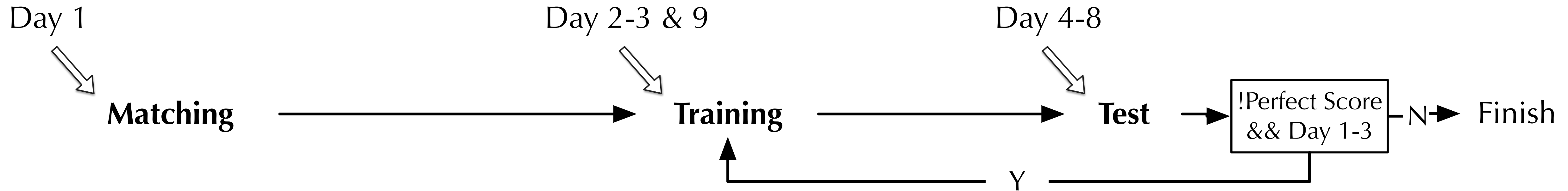
(N=16)



Deuteranomaly (N=7)



Longitudinal Naming Task (N=6; 9 days)



1

Next Pair >>

Saturation
Value
Hue

Light Green
Dark Red
Dark Green
Yellow
Light Pink
Dark Violet
Blue
Turquoise

1 Light Pink
2 Turquoise
3 Blue

1 Light Pink
2 Turquoise
3 Blue
4 Dark Violet
5 Yellow
6 Light Green
7 Dark Red
8 Dark Green

1 Light Pink
2 Turquoise
3 Blue

1 Light Pink
2 Turquoise
3 Blue
4 Dark Violet
5 Yellow
6 Light Green
7 Dark Red
8 Dark Green

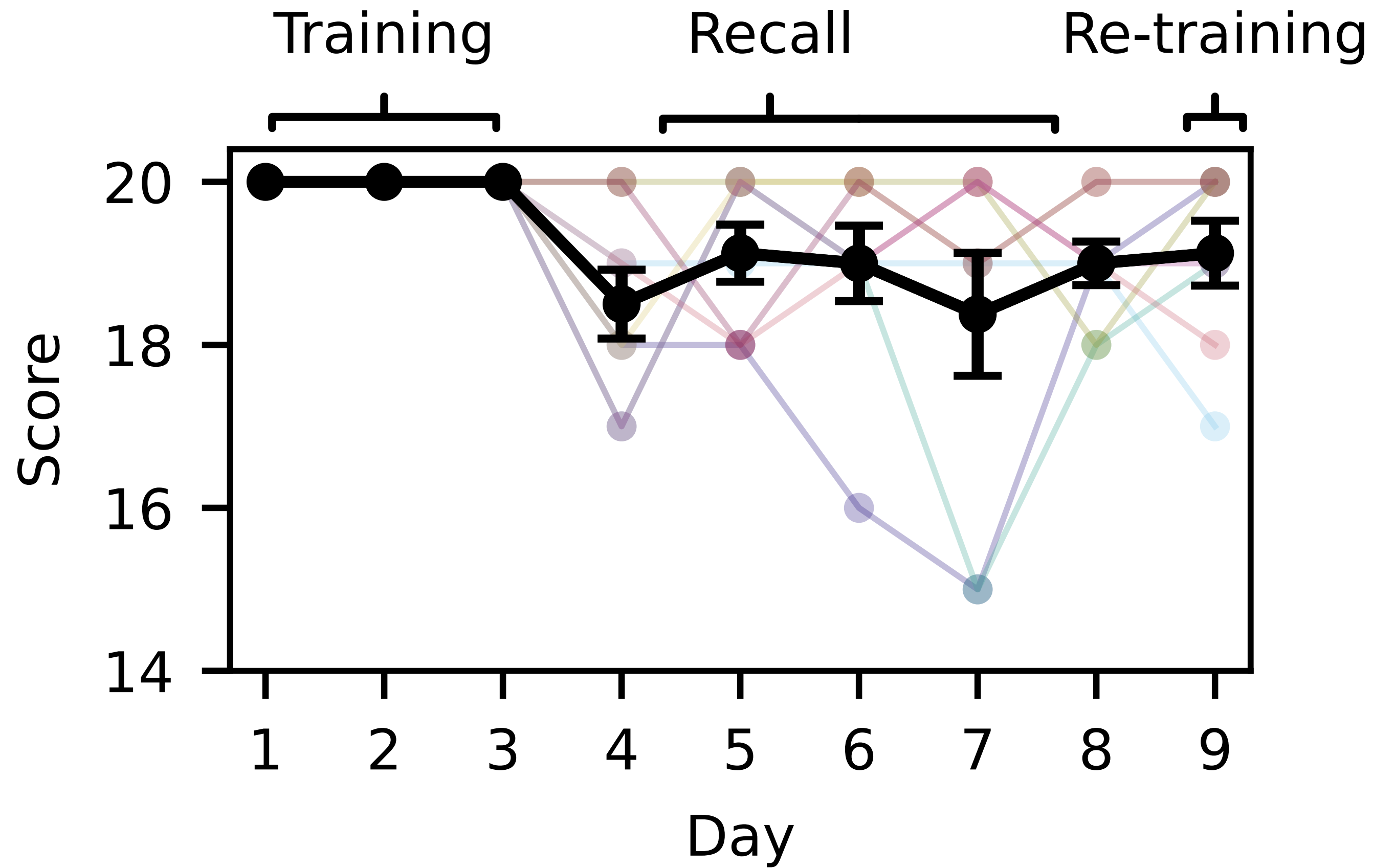
20 tests

4

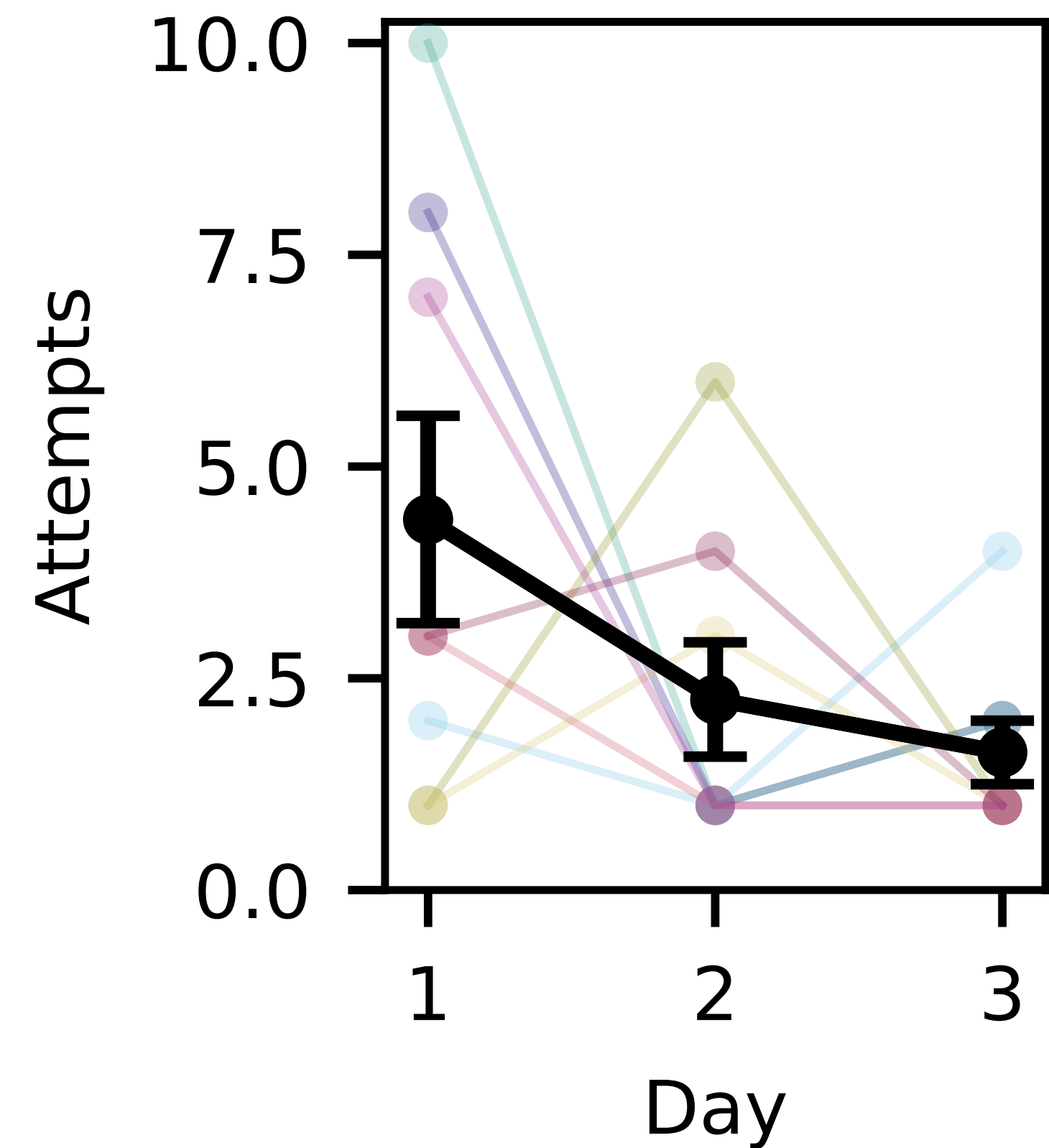
Finish

Saturation
Value
Hue

Recall performance is significantly above chance level (10/20)



Repeated training helps improve color naming performance

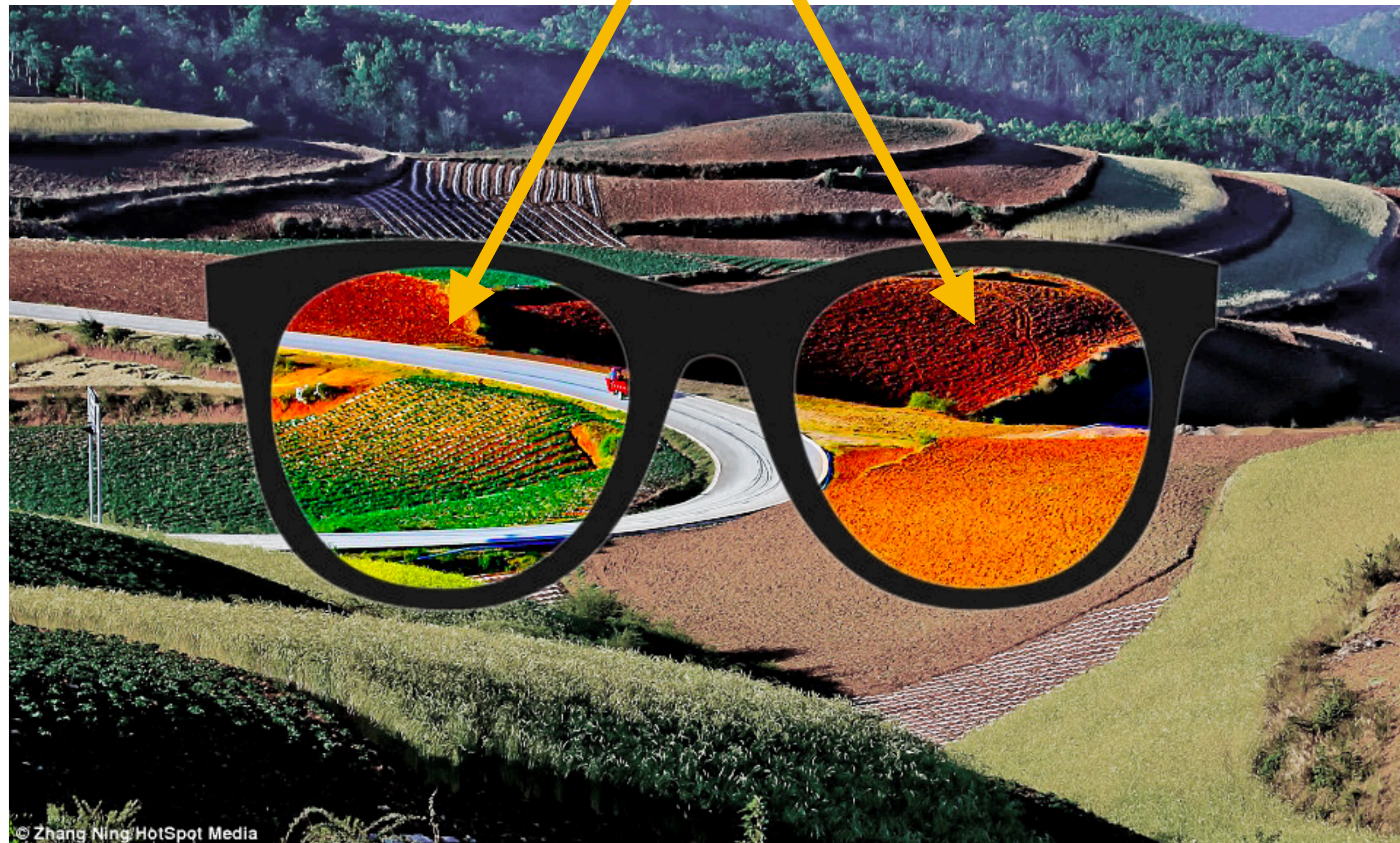


Corrective Glasses?



James. C. Maxwell

Different transmittance spectra



“I have since had a pair of spectacles constructed with **one eye-glass red and the other green**. These Mr X. intends to use for a length of time, and he hopes to acquire the habit of discriminating red from green tints **by their different effects** on his two eyes.”

Discrimination of binocular color mixtures in dichromacy: evaluation of the Maxwell–Cornsweet conjecture

Kenneth Knoblauch

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New York, New York 10022*

Matthew J. McMahon*

Center for Visual Science, University of Rochester, 274 Meliora Hall, Rochester, New York 14627

Received January 13, 1995; accepted April 10, 1995

We tested the Maxwell–Cornsweet conjecture that differential spectral filtering of the two eyes can increase the dimensionality of a dichromat’s color vision. Sex-linked dichromats wore filters that differentially passed long- and middle-wavelength regions of the spectrum to each eye. Monocularly, temporal modulation thresholds (1.5 Hz) for color mixtures from the Rayleigh region of the spectrum were accounted for by a single, univariant mechanism. Binocularly, univariance was rejected because, as in monocular viewing by trichromats, in no color direction could silent substitution of the color mixtures be obtained. Despite the filter-aided increase in dimension, estimated wavelength discrimination was quite poor in this spectral region, suggesting a limit to the effectiveness of this technique.

Color Vision Evolution

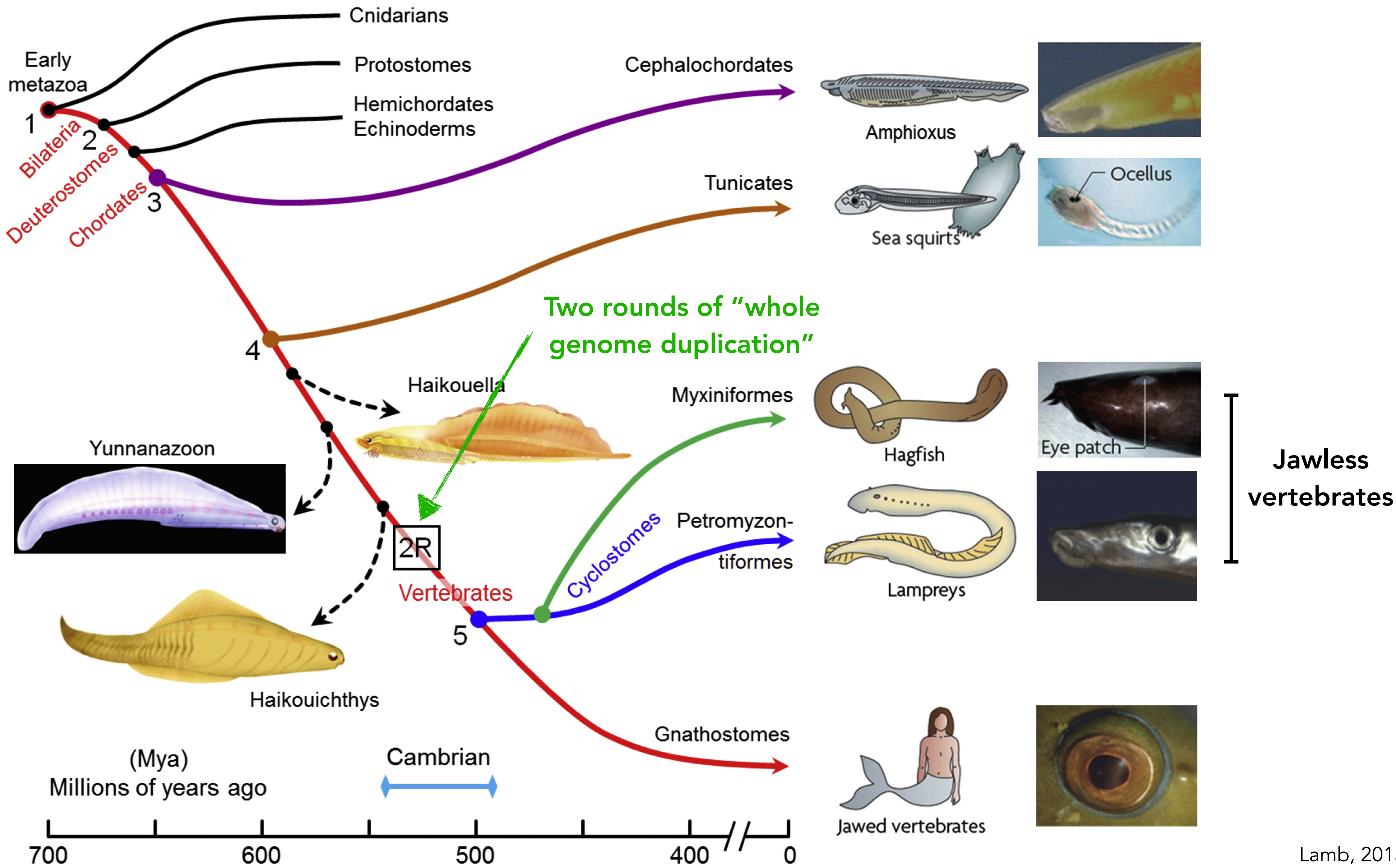
- Evolution of Trichromacy
- Genetic basis of CVDs



Nothing in biology makes sense
except in the light of evolution.

Theodosius Dobzhansky

“ quote fancy



Photoreceptor Evolution in Vertebrates

- Through many gene duplications, proto-vertebrates (ancestors to vertebrates) possessed 4 classes of genes, each coding a pigment class.
- Originally there was 1, which was duplicated to be three (one for melanopsin expressed in ipRGCs, another expressed in RPE, and another called C-opsin).
- C-opsin is duplicated to form pinopsin and a cone opsin, which is the LWS opsin.
- The LWS opsin is duplicated multiple times, first to form SWS, and then SWS is duplicated to SWS1 and SWS2, and then SWS2 is duplicated to form RHL, so in the end proto-vertebrates have LWS, SWS1, SWS2, RHL. Of course these are ancestral genes, and their extant variants are different.
- RHL means “rod like”; it was given the name because its duplicate later evolved to be expressed in rhodopsin.

Photoreceptor Evolution in Vertebrates

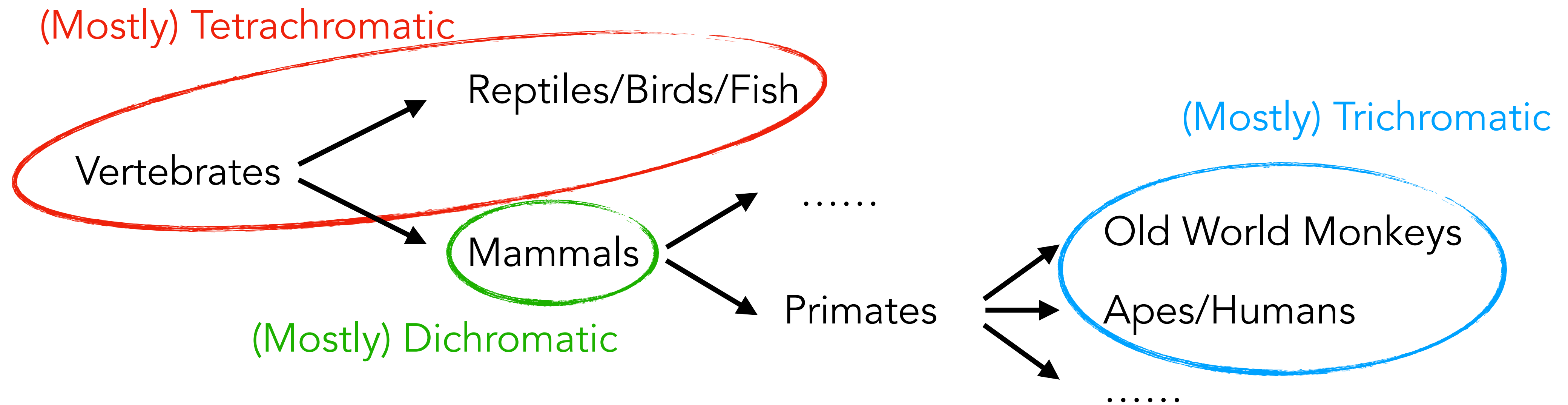
- Then there were two rounds of Whole Genome Duplication (WGD)
 - Happened ~530–500 Mya toward the end of the Cambrian epoch.
 - The two rounds of WGD quadrupled the number of genes, but each duplication was followed by extensive loss of genes (so not all 4 copies of a gene remained).
 - WGD led to an explosion of new species (more genes available to be mutated, etc.).
- **Vertebrates appeared after 1R. After 1R, ancestral vertebrates possessed five opsin genes**
 - SWS1, SWS2, RH1, RH2, and 1 LWS (not all 4 copies of each gene were retained; 2 copies of RHL were retained: RH1 and RH2)
 - 1R also duplicated other non-opsin genes important for phototransduction (e.g., G proteins, PDEs, cGMPs, etc.)

Photoreceptor Evolution in Vertebrates

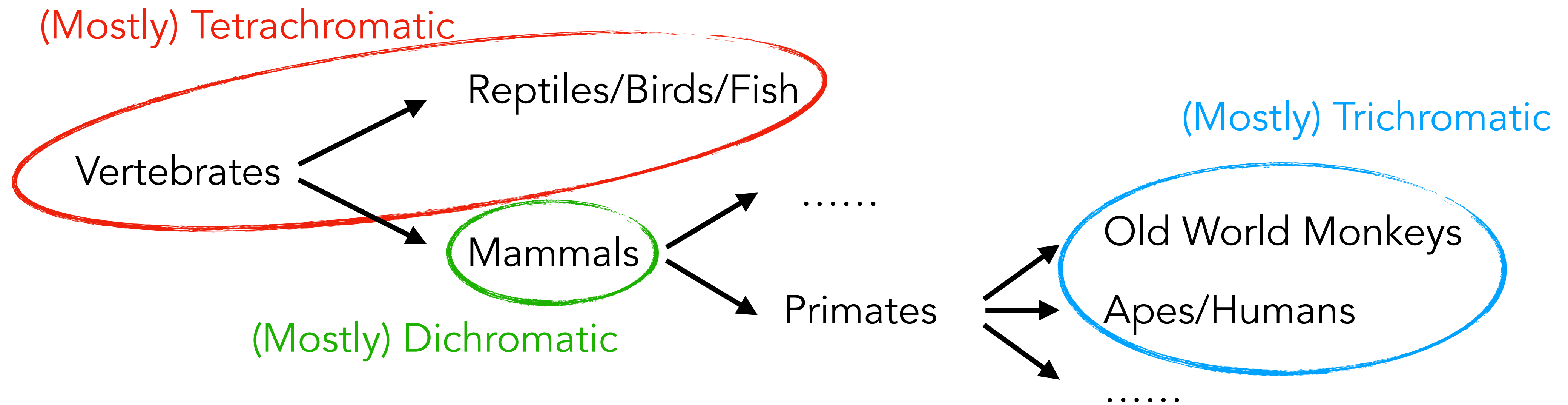
- 1R is important for the rod-cone duplex vision in today's vertebrates:
 - RH1 evolved to become ancestral rhodopsin (pigment for rods).
 - And other non-opsin, phototransduction genes duplicated from 1R also evolved to express different isoforms in cone and rod photoreceptors today.
- Then jawless and jawed vertebrates split.
 - Both jawless and jawed vertebrates possess scotopic and photopic vision (see above).
 - In fact proto-vertebrates had scotopic vision too, but that was mediated by pinopsins.

Photoreceptor Evolution in Vertebrates

- 2R happened to only jawed vertebrates.
 - 2R introduces a few new genes that allow jawed vertebrates to possess true, modern rod photoreceptors.
 - For instance, in jawless vertebrates rods and cones look very similar, but 2R changed the morphology of rods in jawed vertebrates so that they look differently than cones.
 - But morphology apparently isn't important for scotopic vision: northern hemisphere lampreys have rods that look like cones but physiologically behave like rods [[Morshedian and Fain 2015](#)]. Whether you call that a rod or a cone is largely a matter of opinion.



- Some proto-vertebrate already had four classes of genes (through local gene duplications) that code four different pigments/opsins
- A descent of this creature went through two rounds of WGD
 - Whole Genome Duplication; ~530–500 Mya (Cambrian epoch)
 - Each followed by extensive loss of genes (so not all 4 copies of a gene remain)
 - Now five classes of opsins (SWS1, SWS2, RH1, RH2, and LWS)



- **RH1 gene evolved (~500-430 Mya?) to express rod pigment**
 - For life at night & in deep ocean; rod pathway piggybacks on existing cone pathway
- **Early mammals (~age of dinosaurs) are nocturnal so they lost two genes**
 - Only LWS and SWS1 genes retained and expressed in cone pigments
- **Trichromacy emerged in Catarrhini (common ancestors of old world monkeys, apes, and humans) through gene duplication**

*** Numbers in parentheses denote the approximate number of known living species.**

Order

Suborder

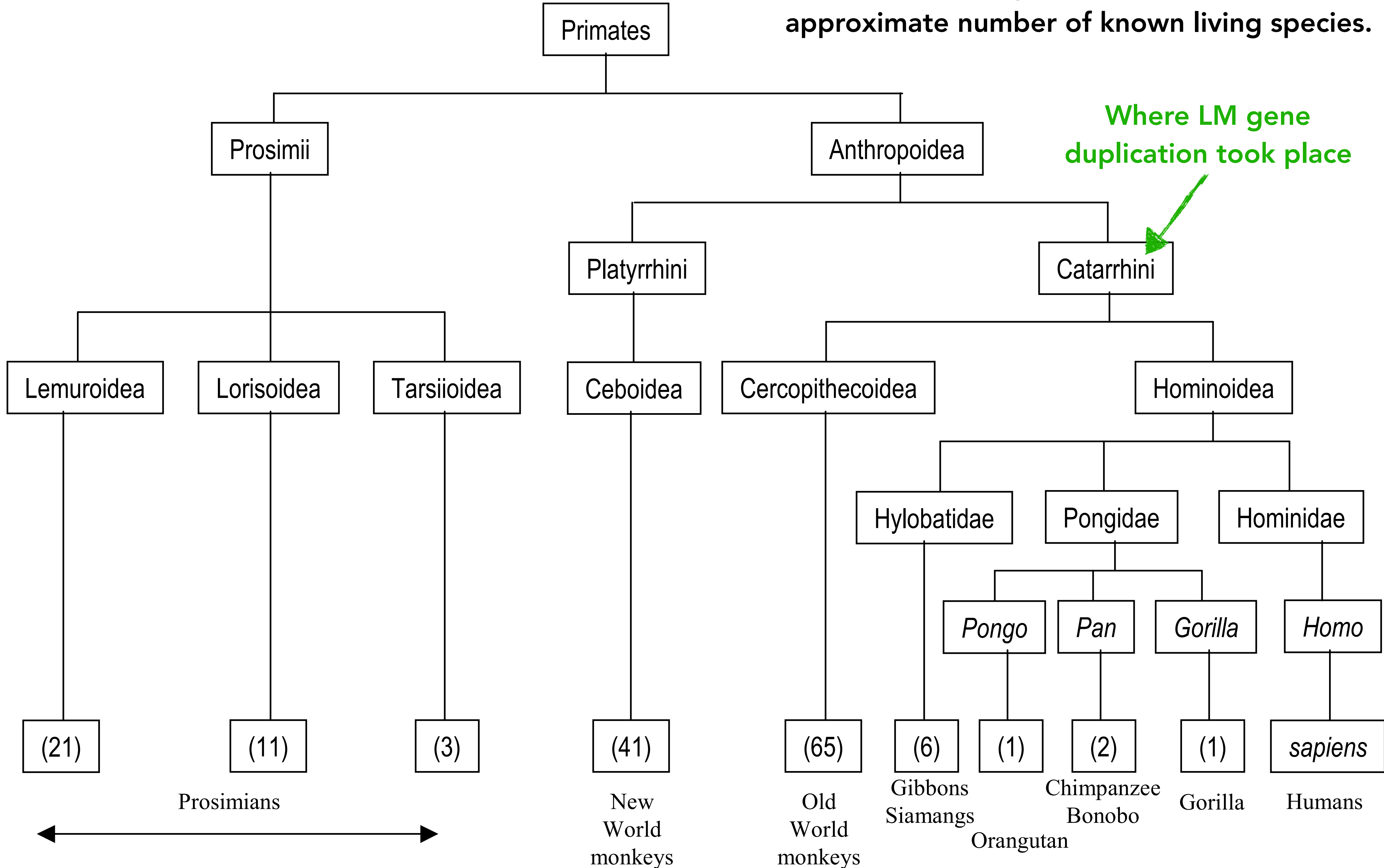
Infraorder

Superfamily

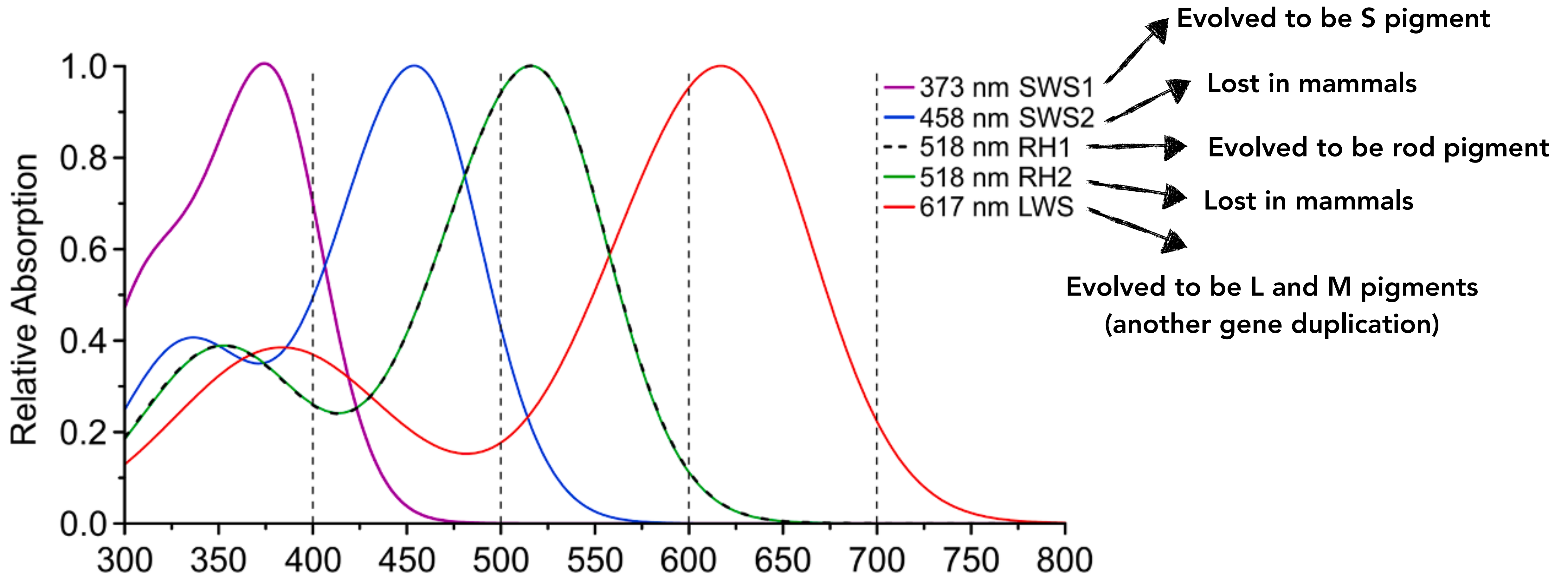
Family

Genus

Species



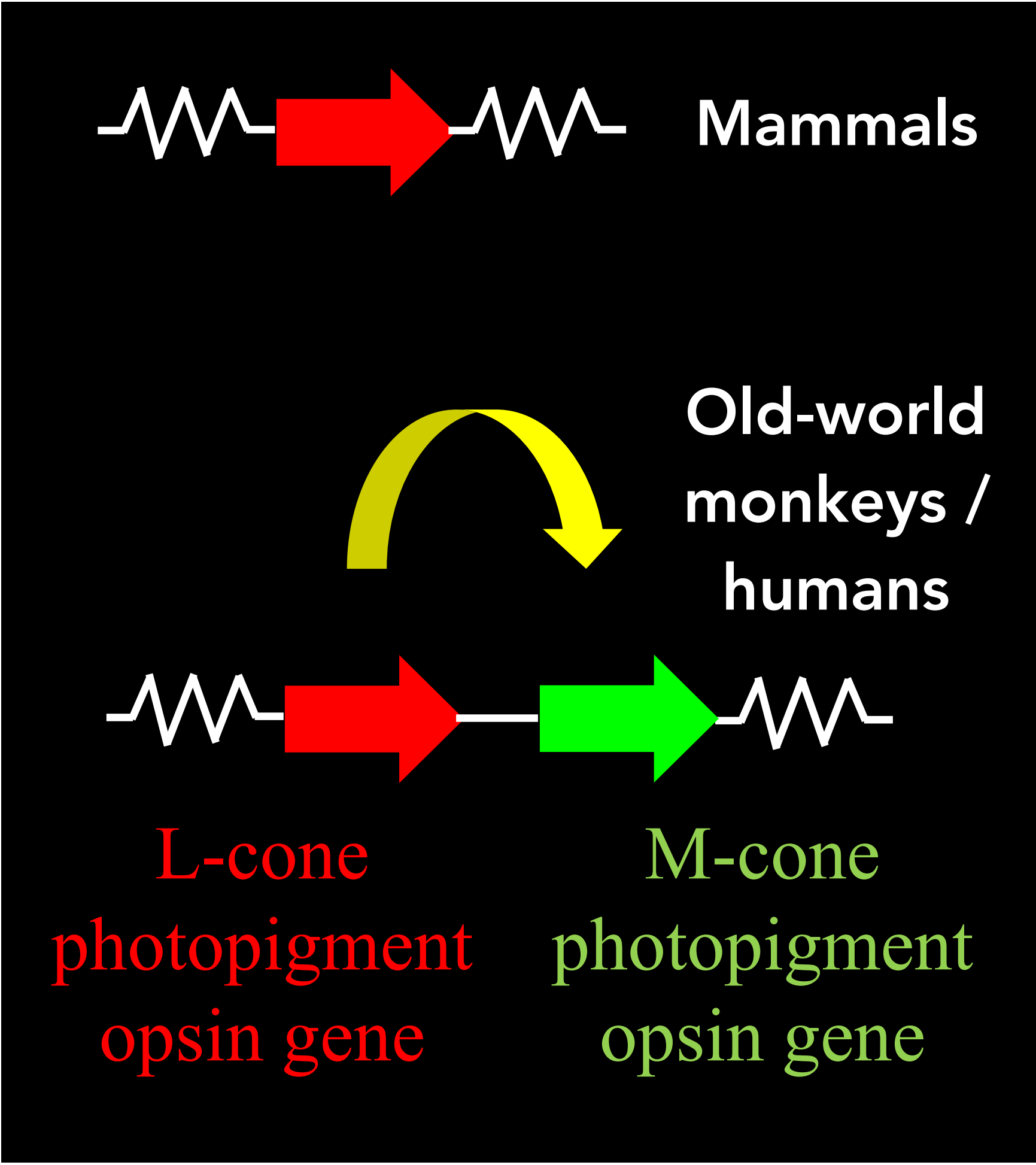
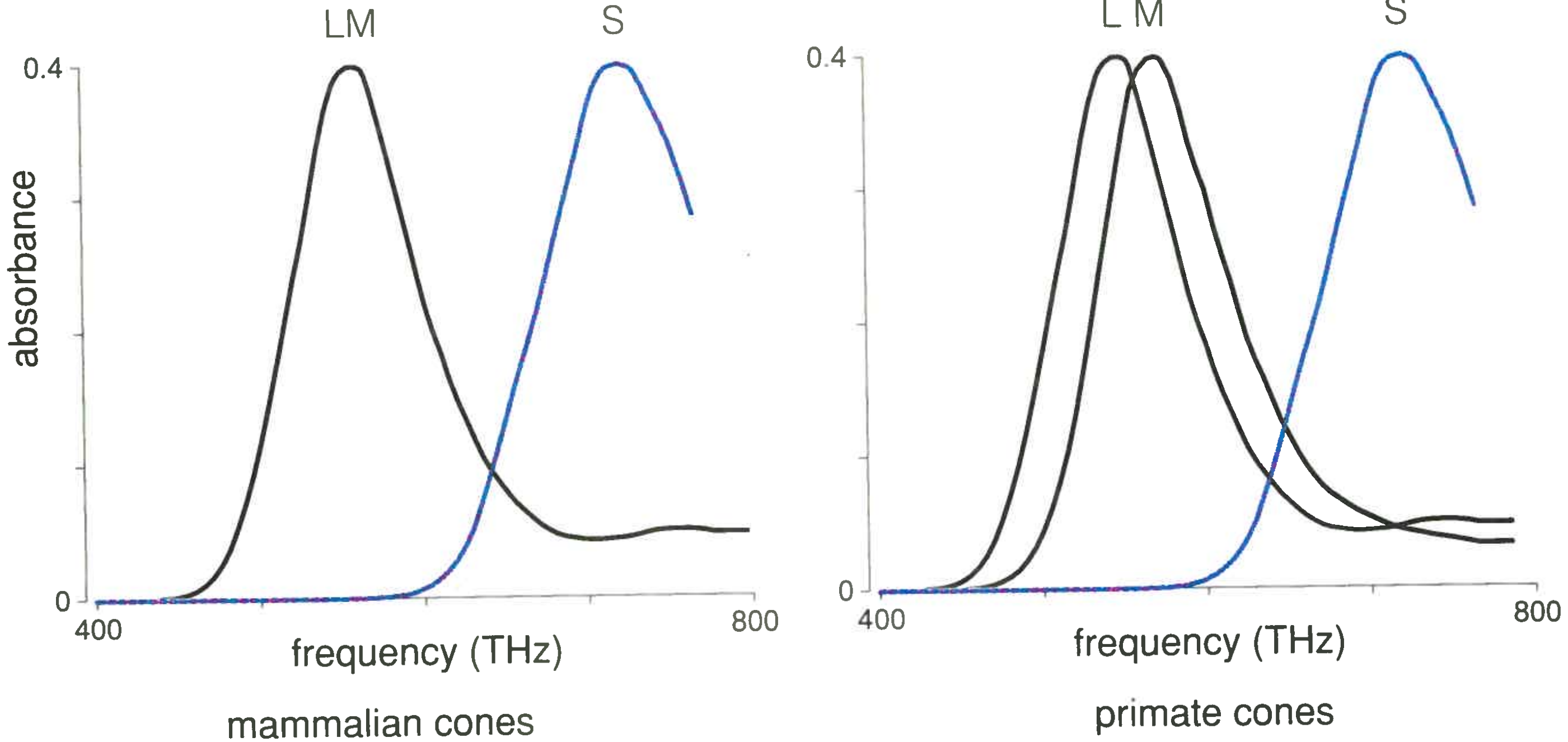
Five Classes of Cone Pigments in Jawed Vertebrates



* Predicted normalized pigment absorbance (~absorption using MSP)

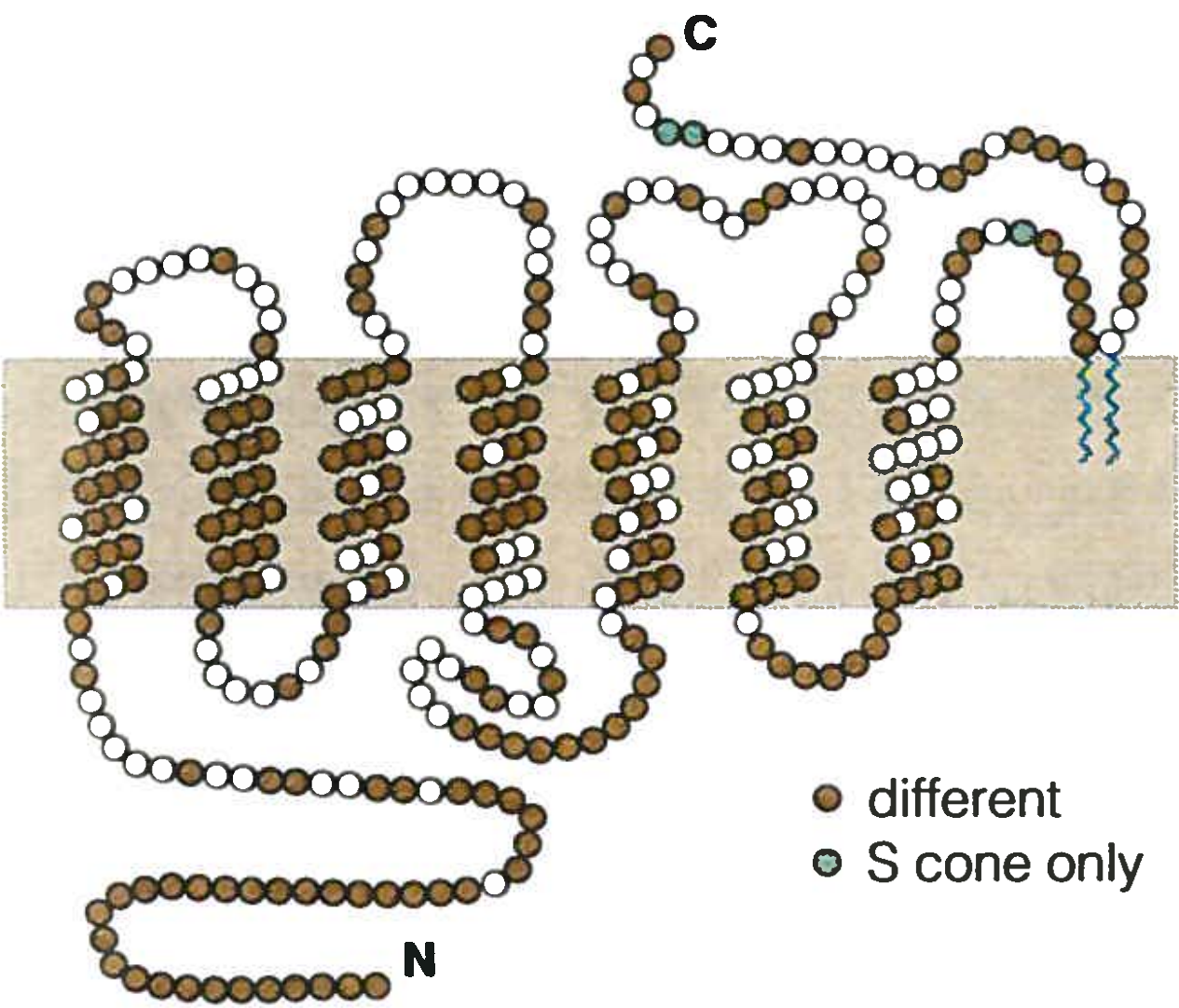
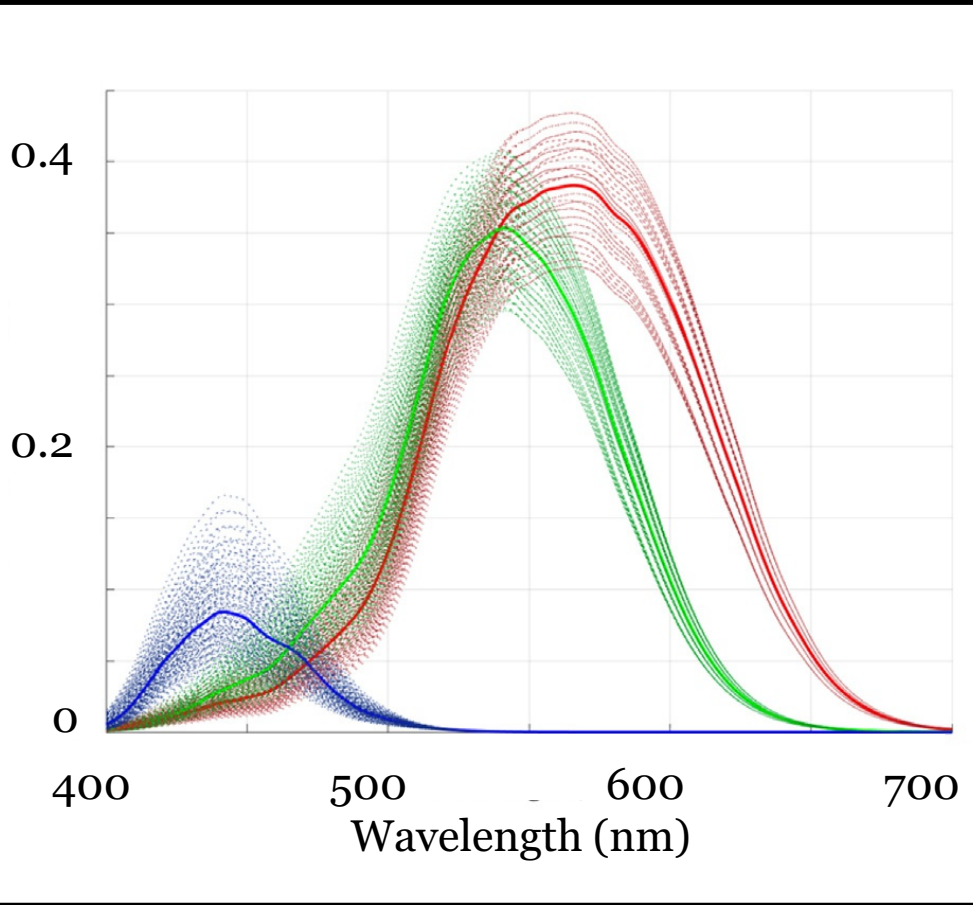
* From extant species; ancestral pigments likely differ

Gene Duplication on the X Chromosome

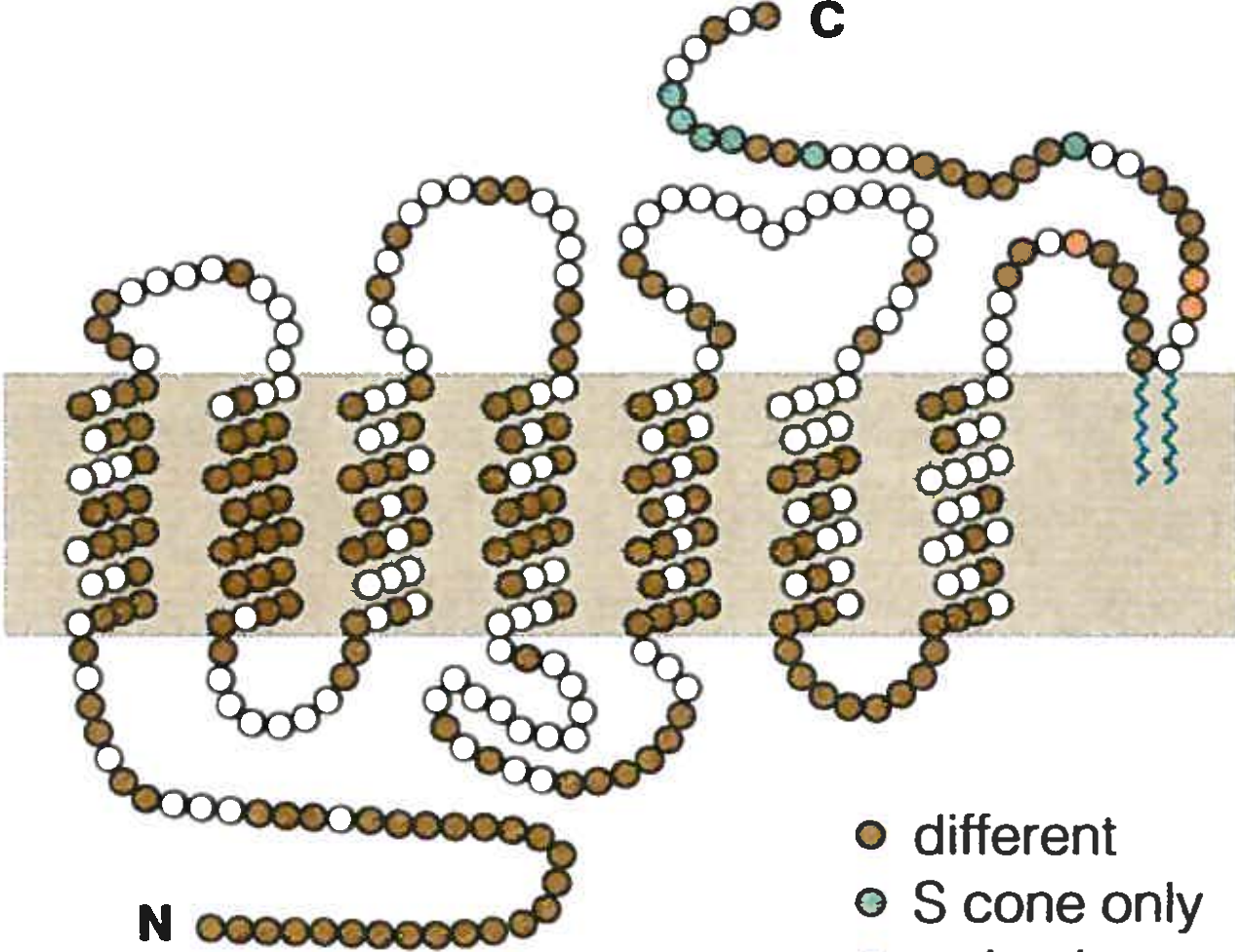


L and M Cone Pigments are Very Similar

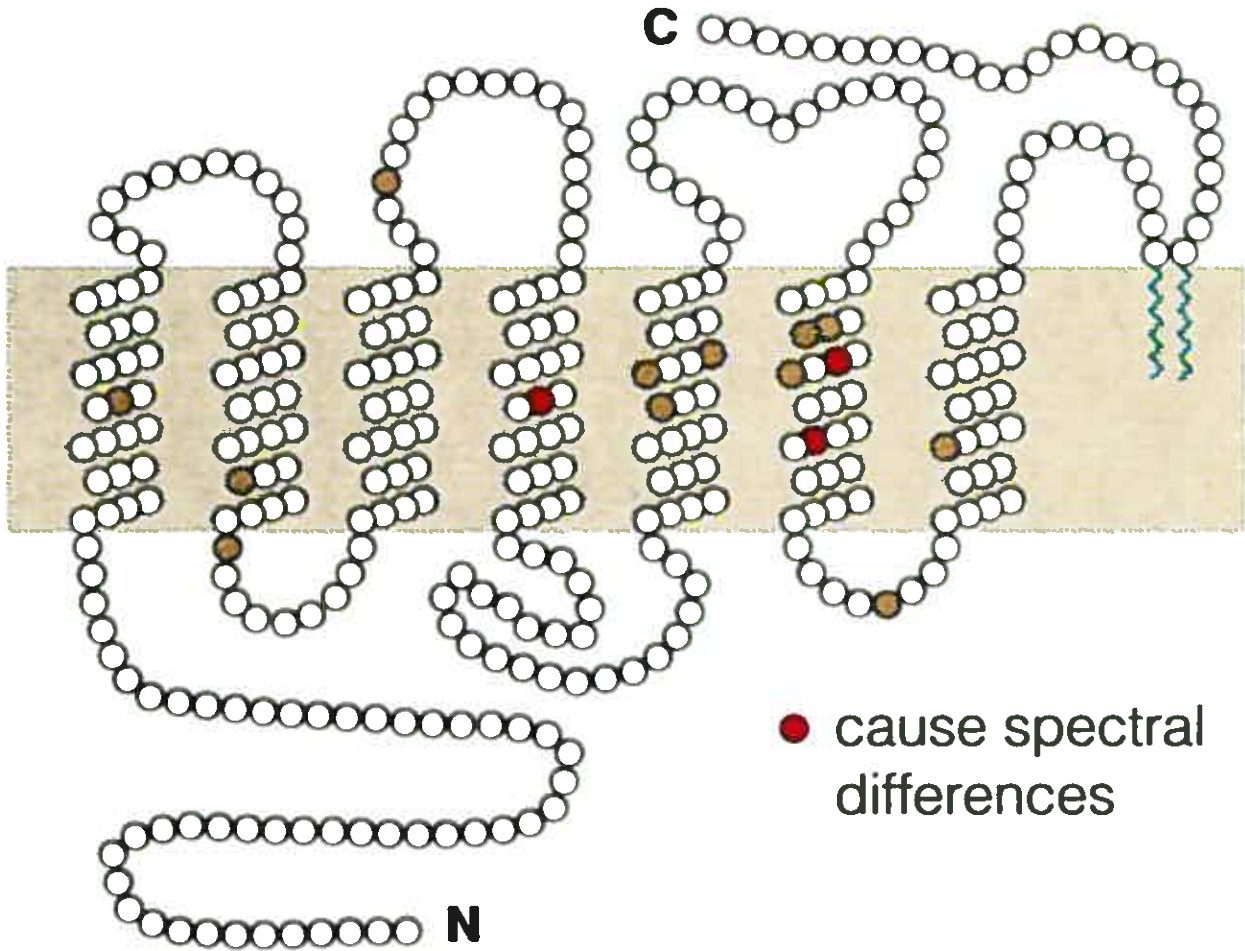
because the duplication is recent (~30 Mya)



M and S cone differences

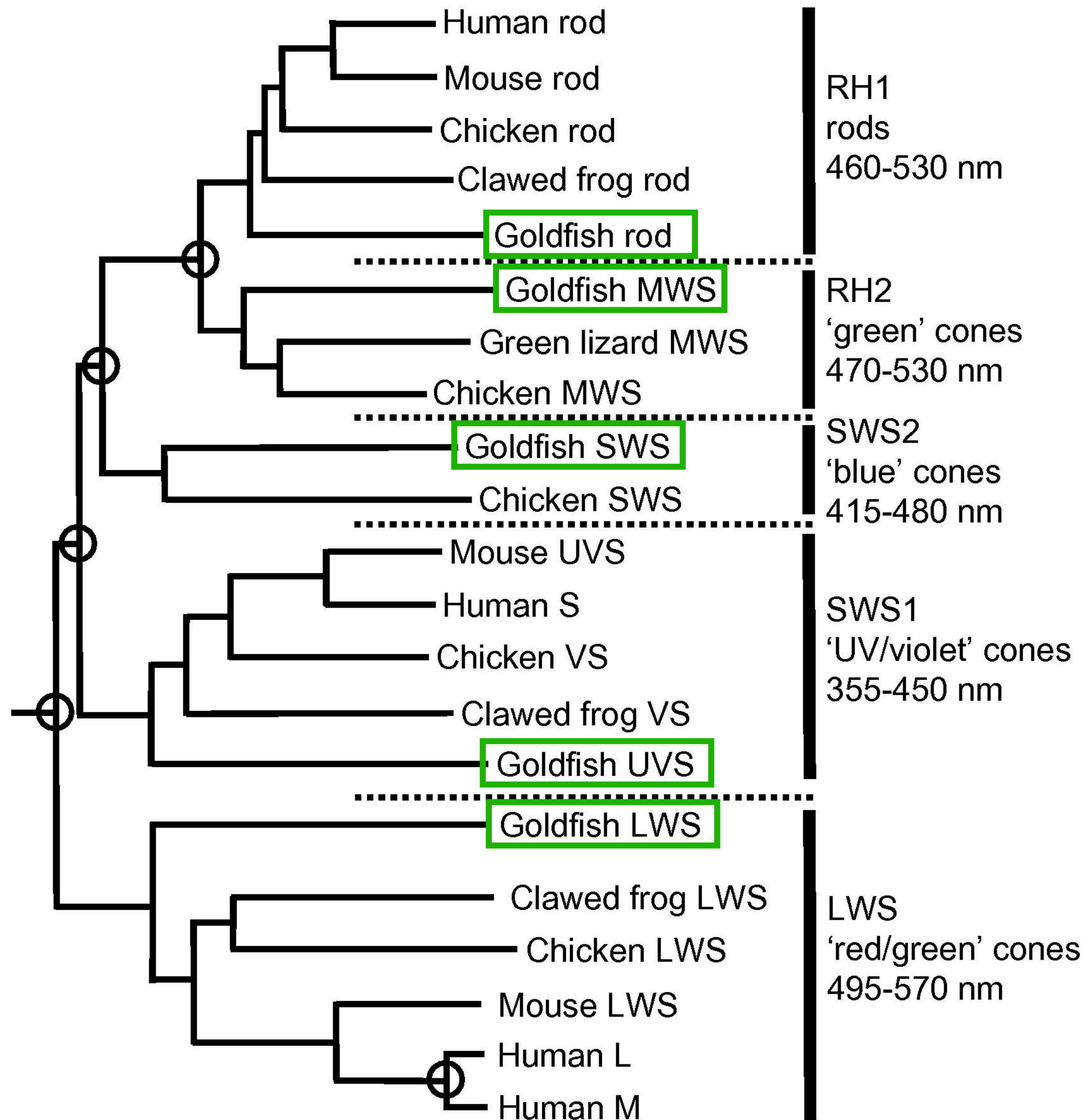


S cone and rod differences
source: Nathans, Thomas, and Hogness, 1986



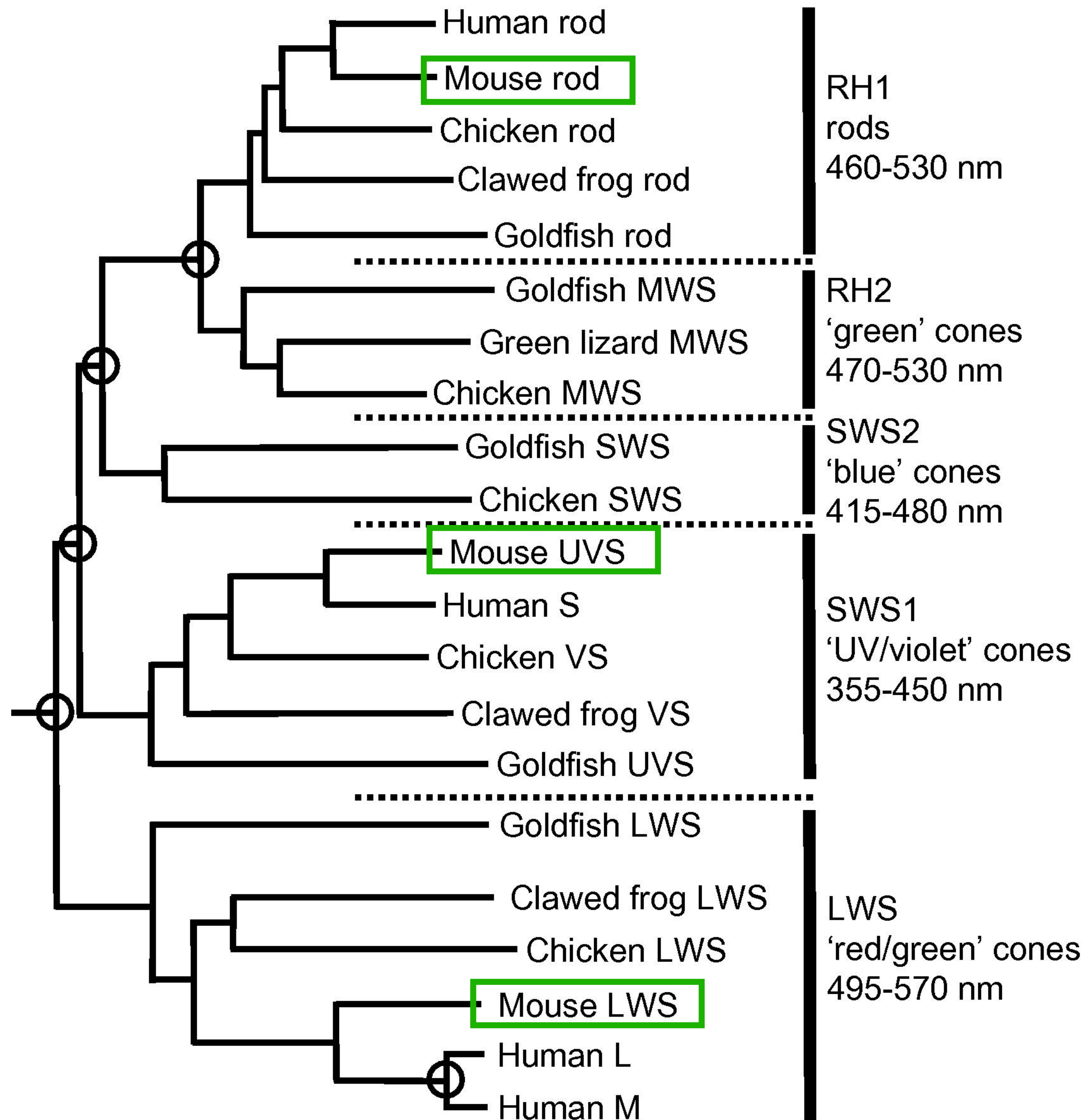
M and L cone differences
source: Nathans et al., 1986

96% of the amino acids are the same

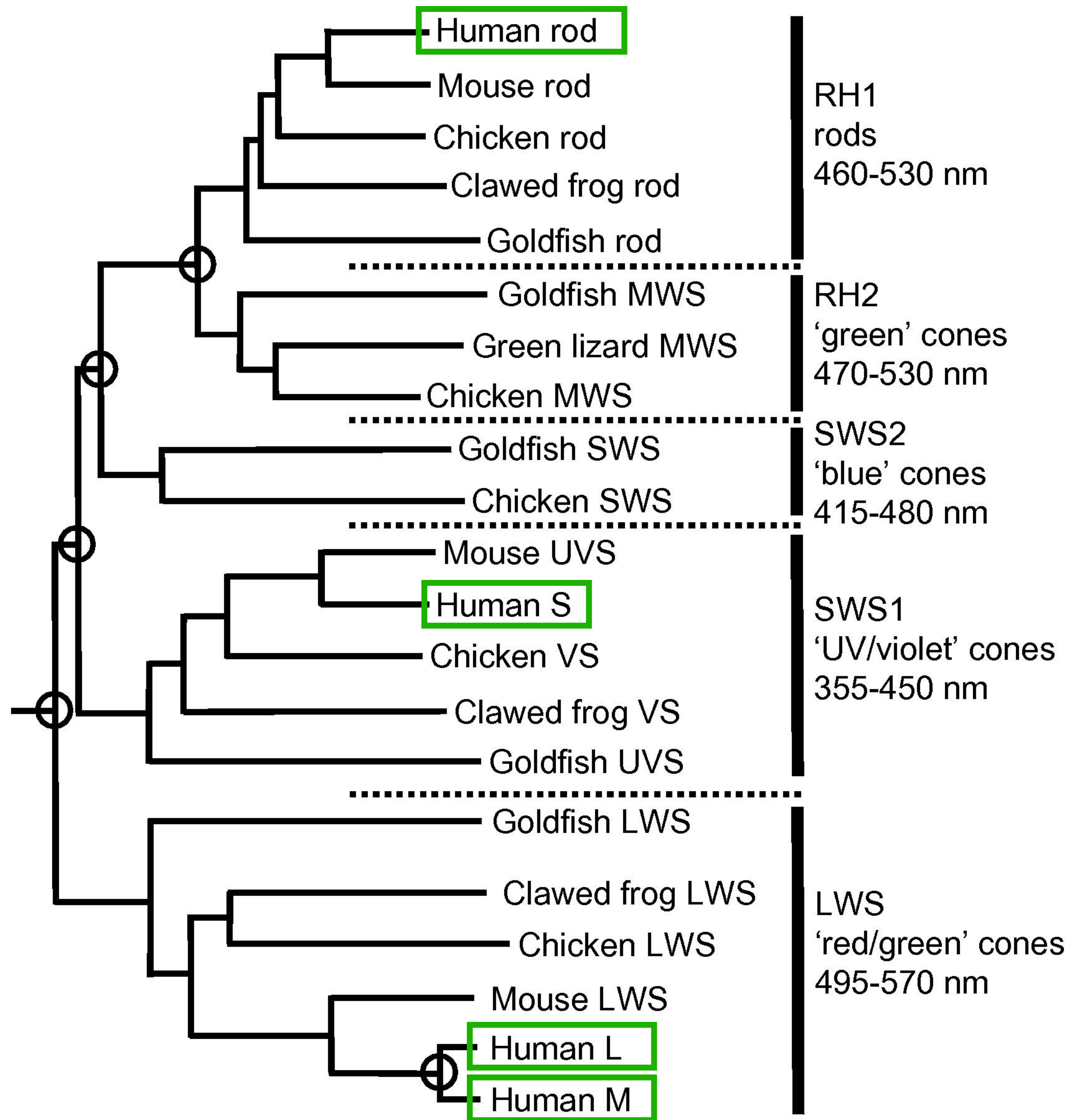


Goldfish (Tetrachromatic)

*Also see Figure 8B, Lamb 2022 for 2R WGD



Mouse (Dichromatic)

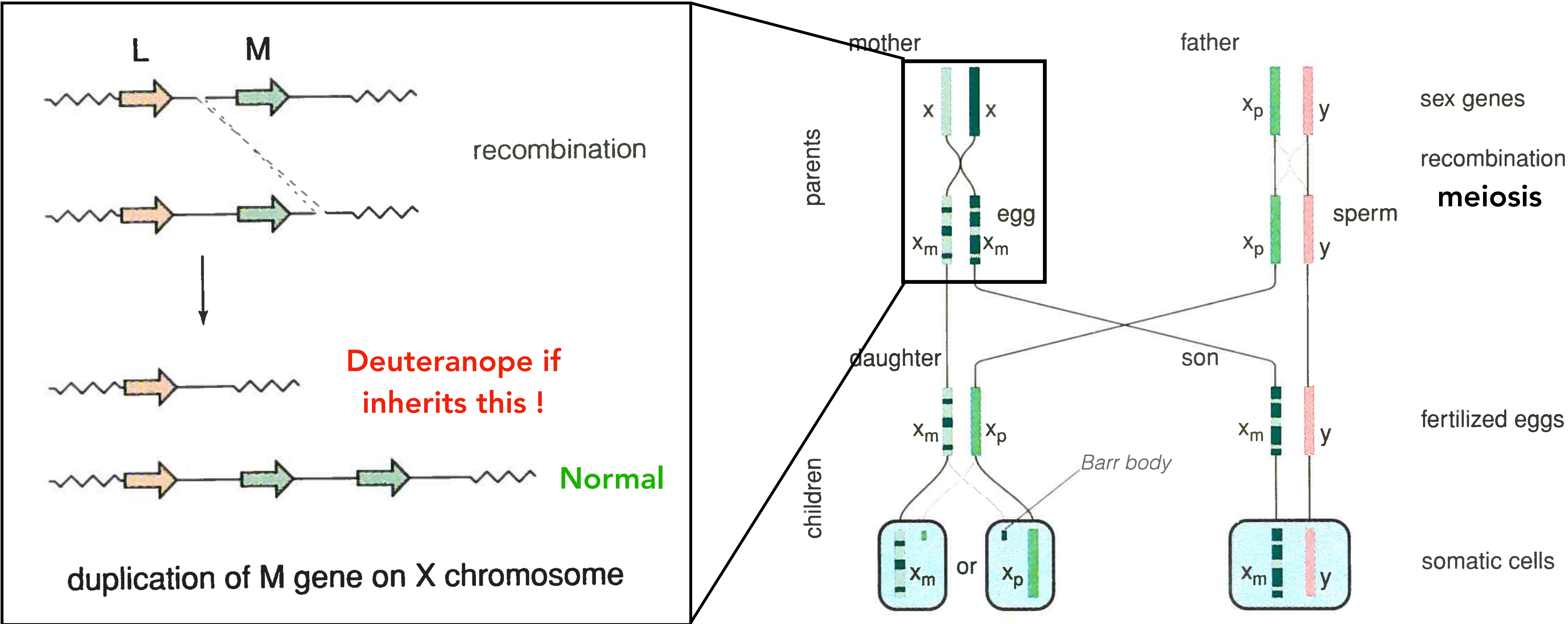


Human (Trichromatic)

Color Vision Evolution

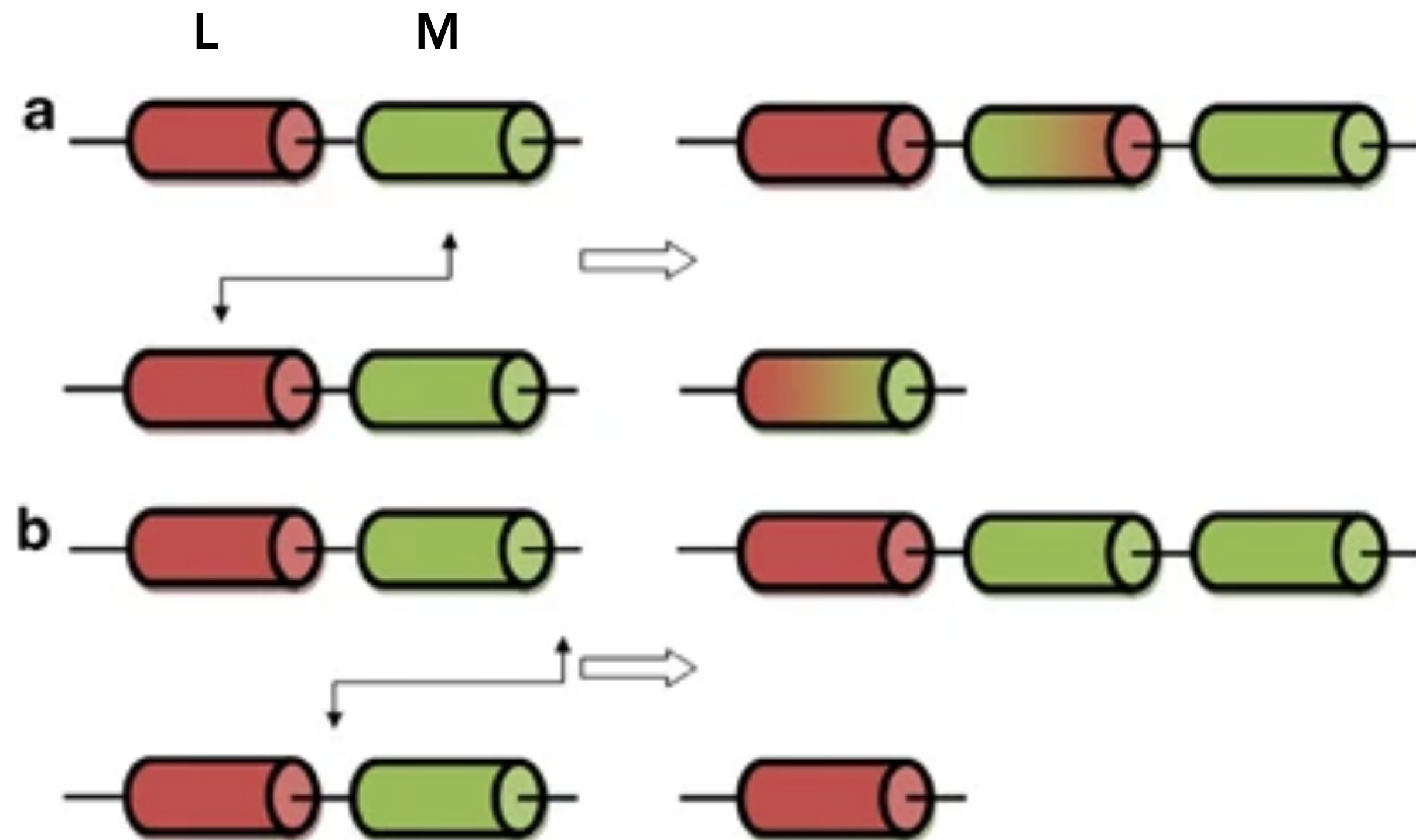
- Evolution of Trichromacy
- Genetic basis of CVDs

Genetic Basis of Color Vision Deficiency

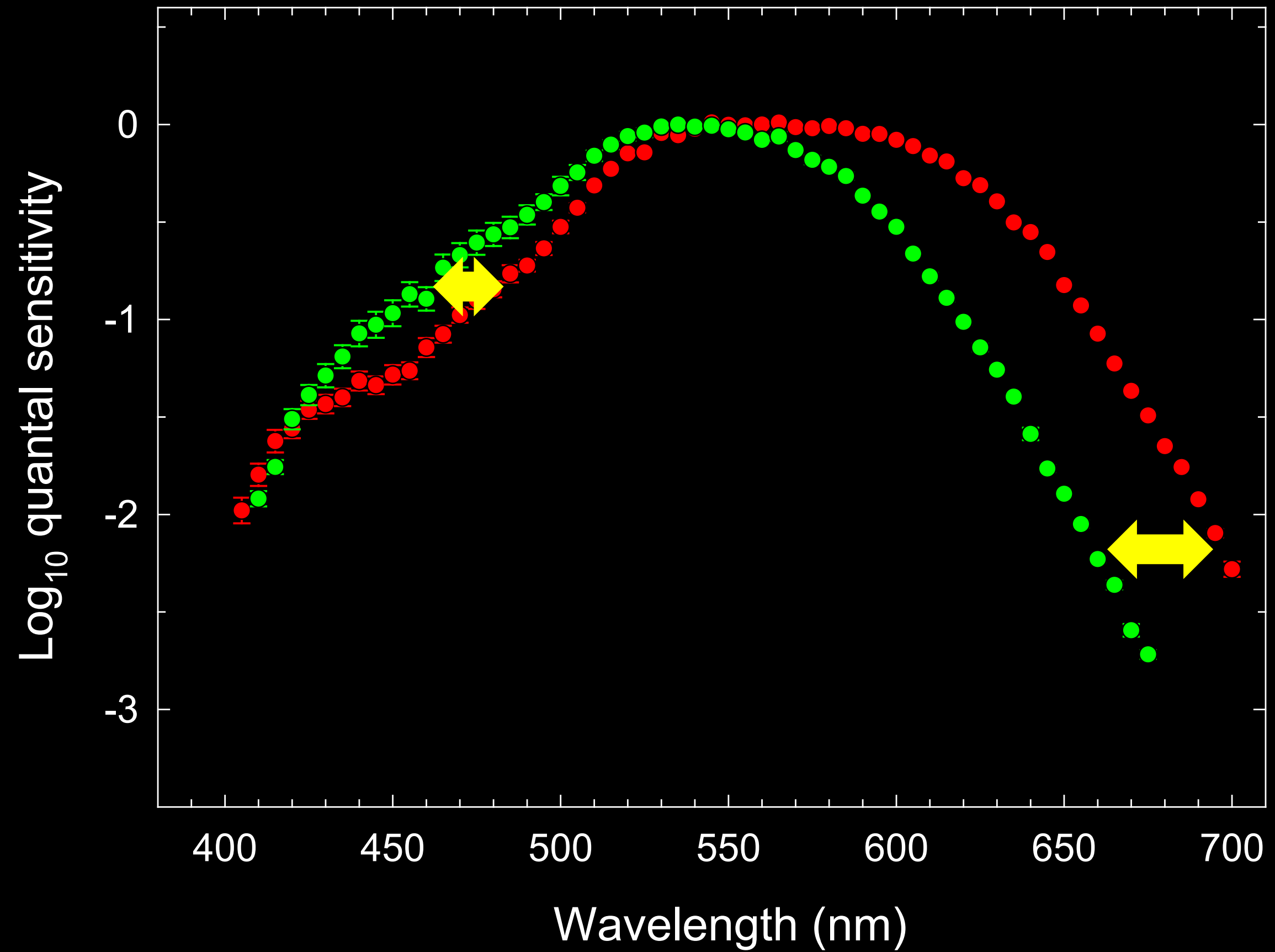
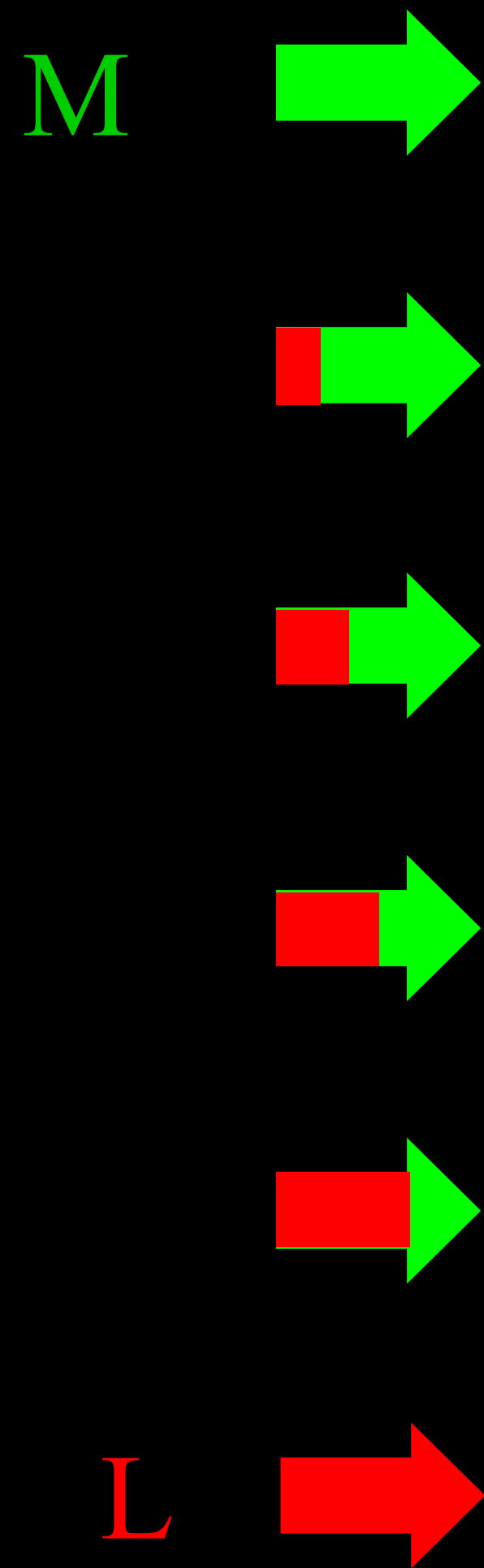



* Only the first two genes are sufficiently expressed to affect pigments [Simunovic 2009]

Genetic Basis of Color Vision Deficiency

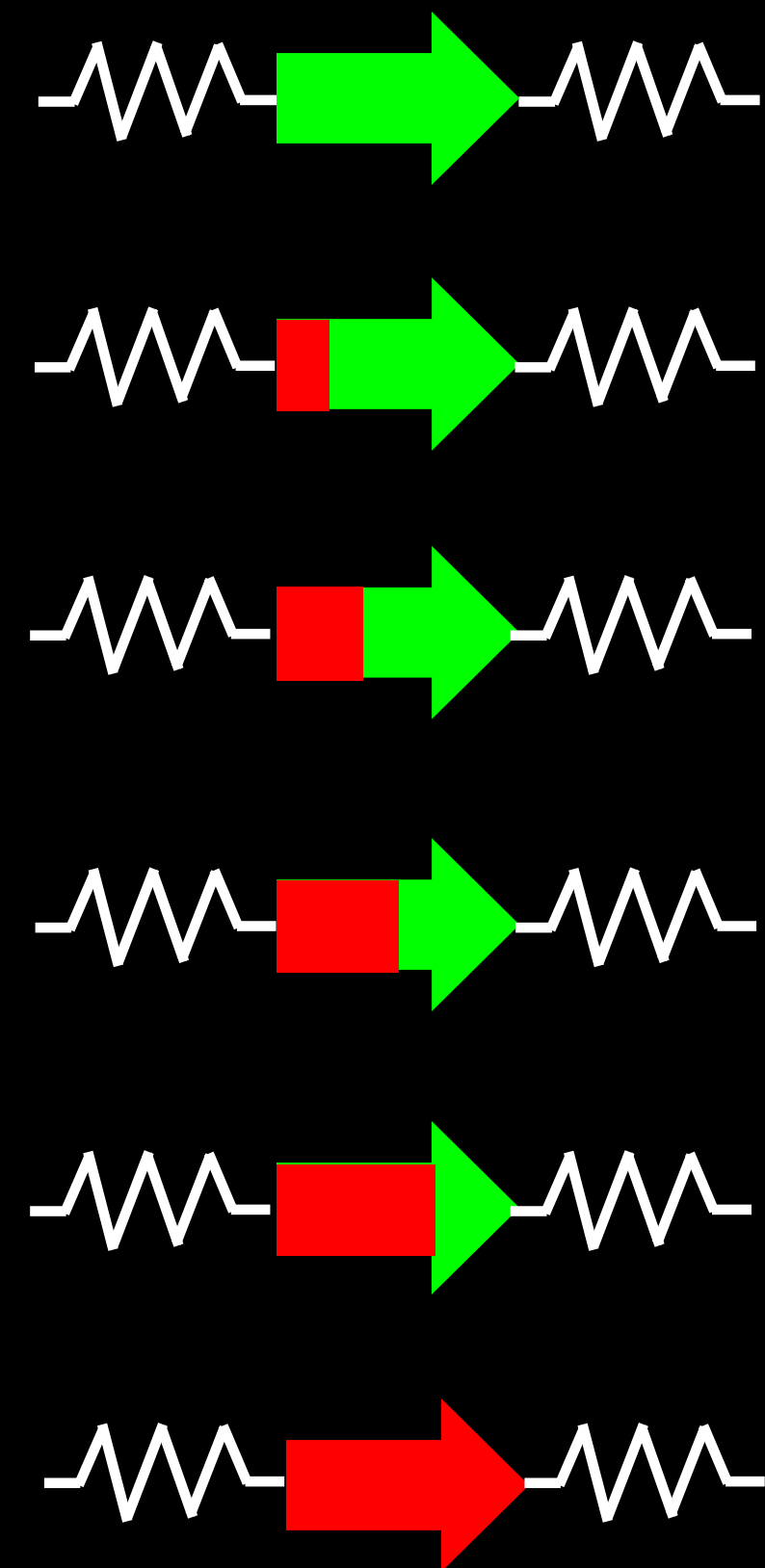


- L and M genes are tandemly arrayed and are subject to crossovers during recombination, which might lead to deletion of a whole gene or hybrid genes in a X chromosome.
- Inheriting such an X chromosome causes CVD.




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

Single-gene dichromats



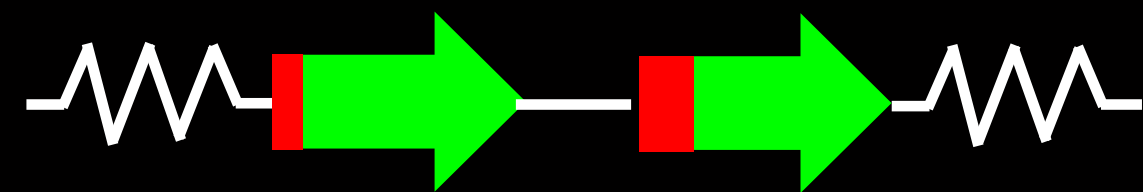
Protanope

Abnormal
"L" (or "M")
cones

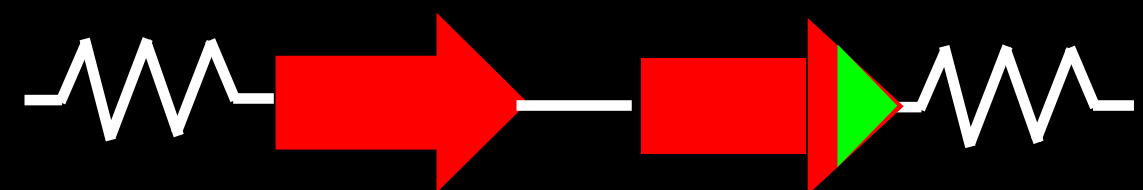
Deuteranope

With a single gene male
observers must be dichromats

Multiple-gene dichromats

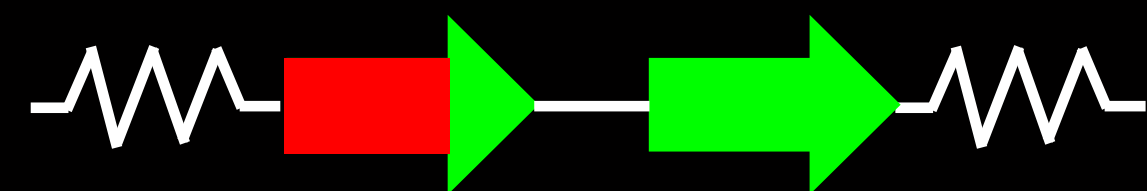
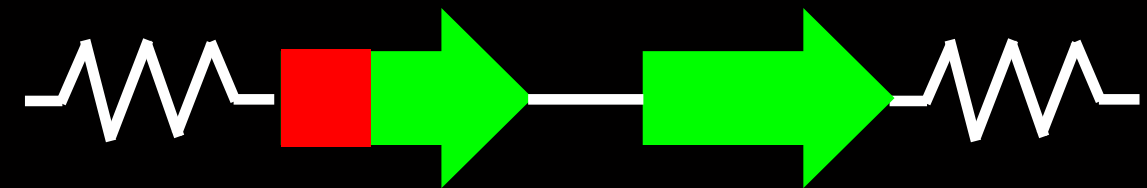
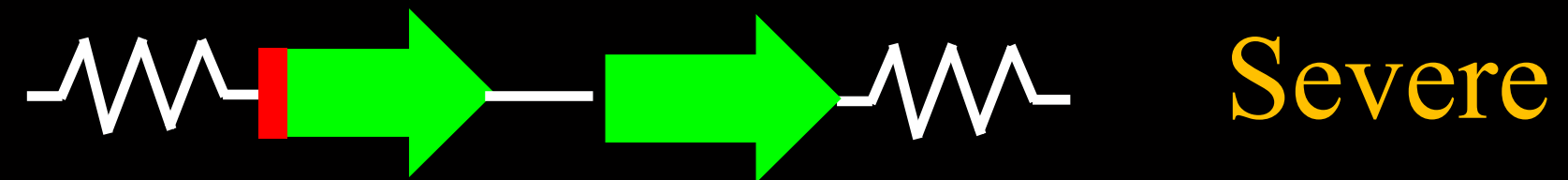


Male observers with two similar genes may also be effectively dichromats

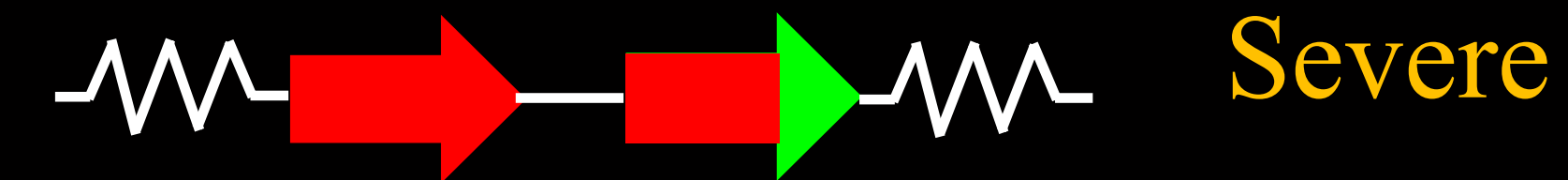
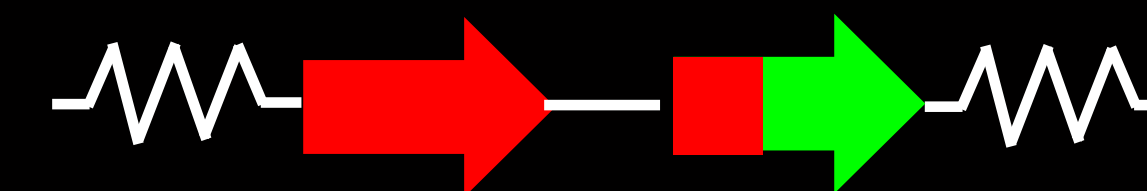
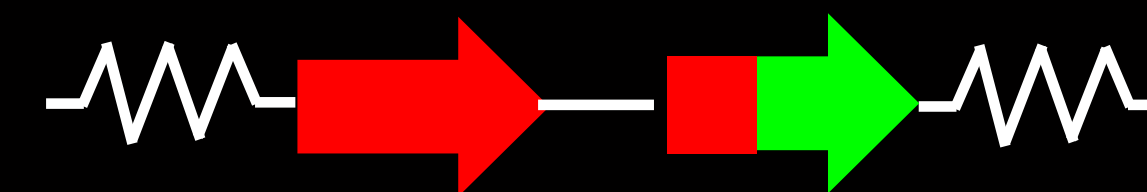


Anomalous trichromats

Male observers with two different genes are anomalous trichromats

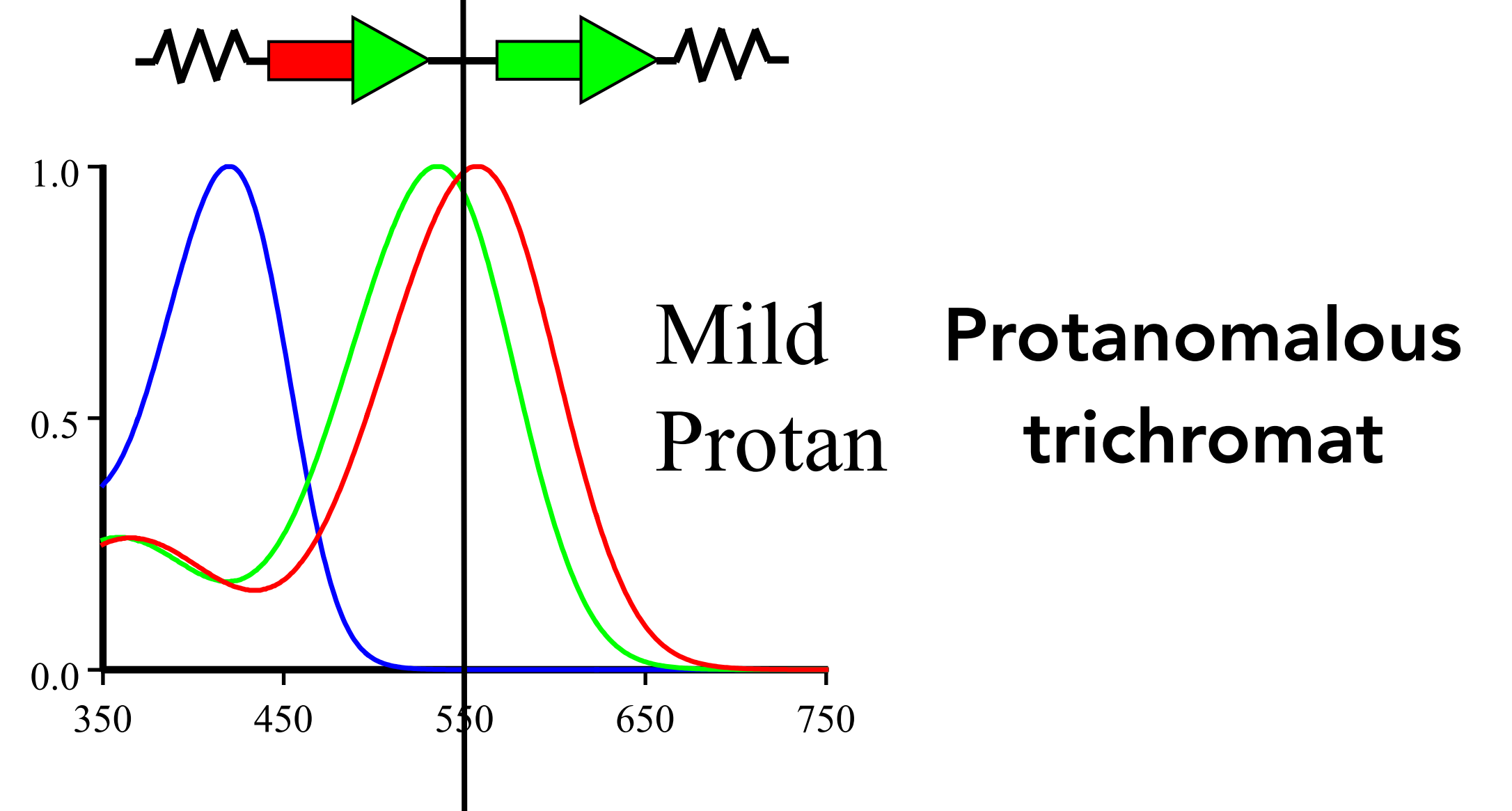
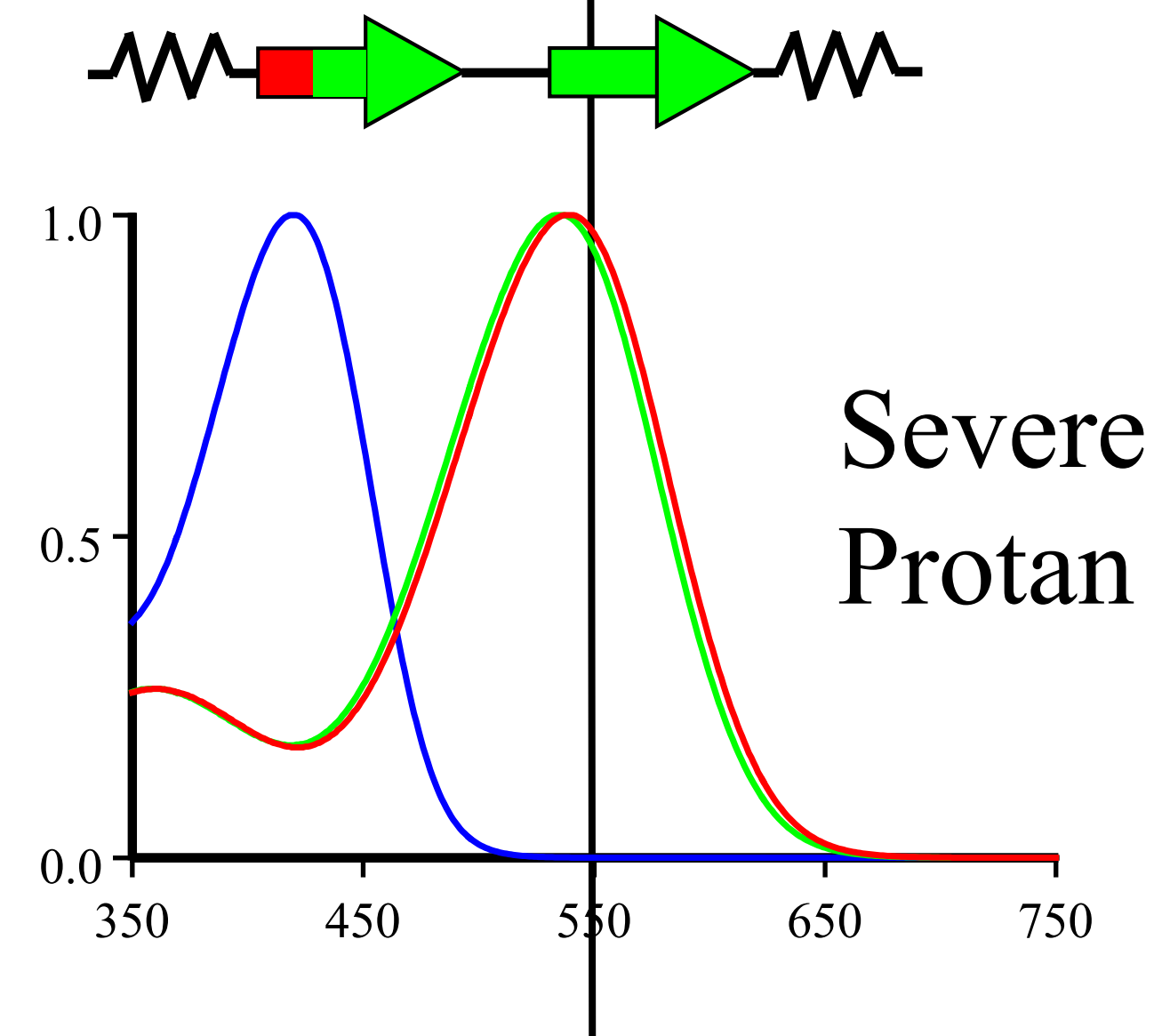
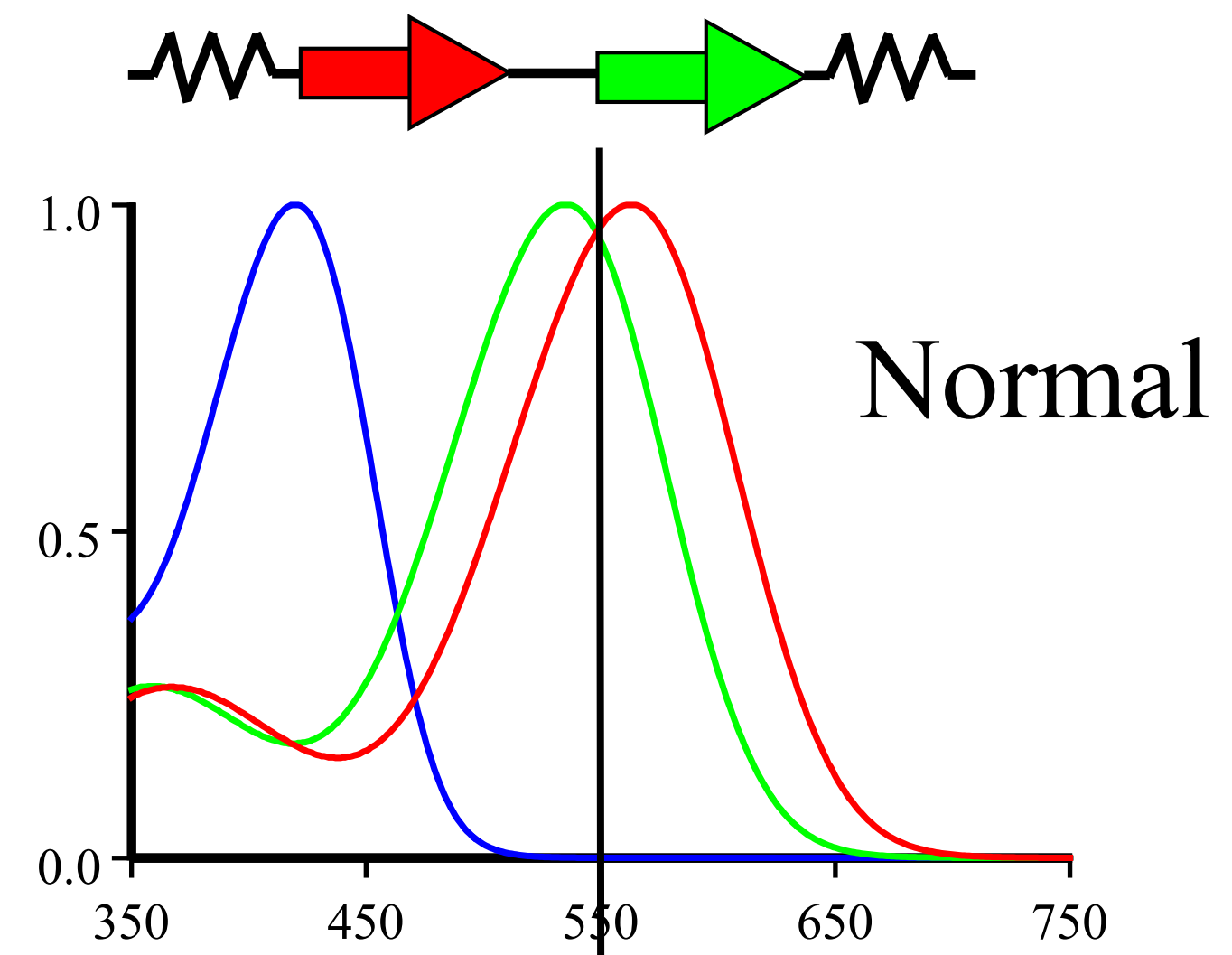
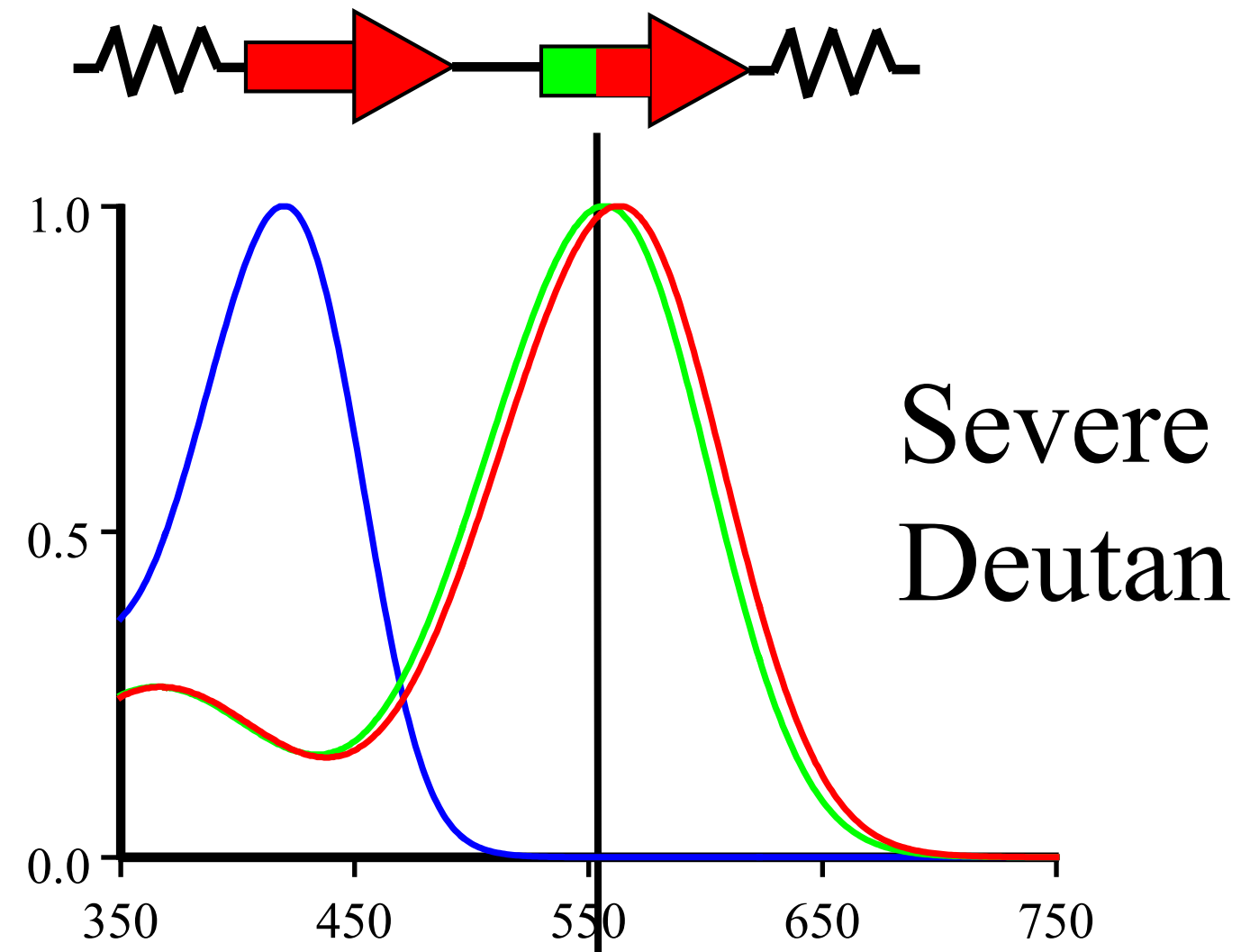


Mild



Protanomalous

Deuteranomalous



Why is CVD More Prevalent in Males?

	Protanomaly	Protanopia	Deuteranomaly	Deuteranopia	Tritanomaly/ Tritanopia
Male %	1.0%	1.0%	4.9%	1.1%	<0.01%
Female %	0.02%	0.02%	0.38%	0.01%	<0.01%

- Most CVDs are due to L/M genes cross-overs on X chromosomes
 - Genes for L and M cone pigments lie together on the X chromosome and are thus subject to unequal recombination/crossovers
 - Females have two X chromosomes

Why are S-Cone CVDs Rate?

	Protanomaly	Protanopia	Deuteranomaly	Deuteranopia	Tritanomaly/ Tritanopia
Male %	1.0%	1.0%	4.9%	1.1%	<0.01%
Female %	0.02%	0.02%	0.38%	0.01%	<0.01%

- Gene for S cone pigment is in a nonsex chromosome (chromosome 7)
 - They are not subject to L/M gene cross-overs
 - Gene mutations causing changes in S-cone pigment are much more rare

Things to Take Away

- Dichromats miss one class of cone photoreceptors (functionally)
- Each dichromatic vision has a set of parallel confusion lines
 - Colors on the confusion lines are perceptually the same for a dichromat
 - Confusion lines converge in the xy-chromaticity plot
 - Color matching experiments on unilateral dichromates allow us to estimate what colors are correctly perceived by dichromats
- Computational trichromacy reconstruction
- Color vision deficiencies in humans are due to erroneous LM gene duplication that happened at the basis of old-world primates