Neurobiology of Color Vision

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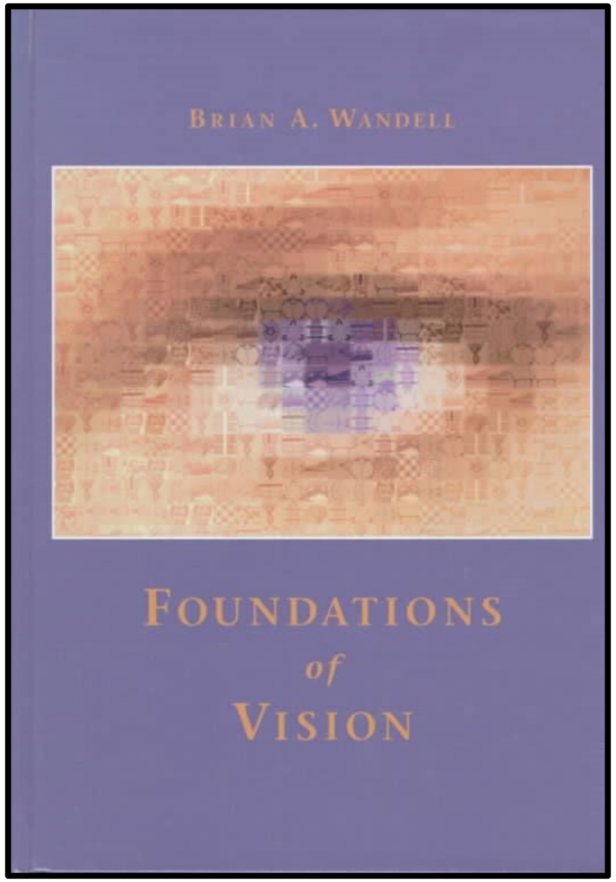
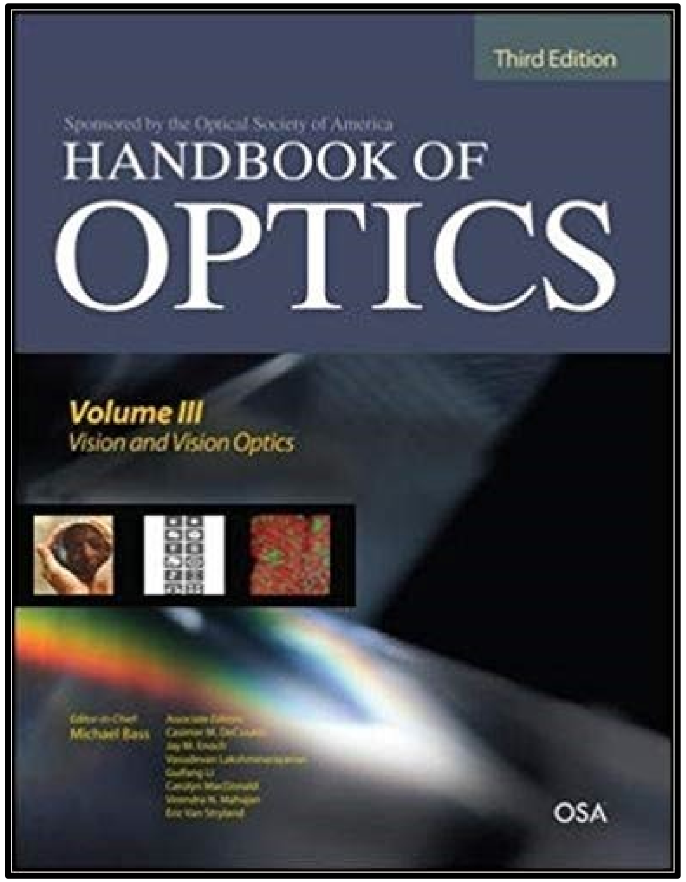
29 September 2020

1024 Farben, Gerhard Richter (1973)

Source material





10 COLORIMETRY

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11 COLOR VISION MECHANISMS

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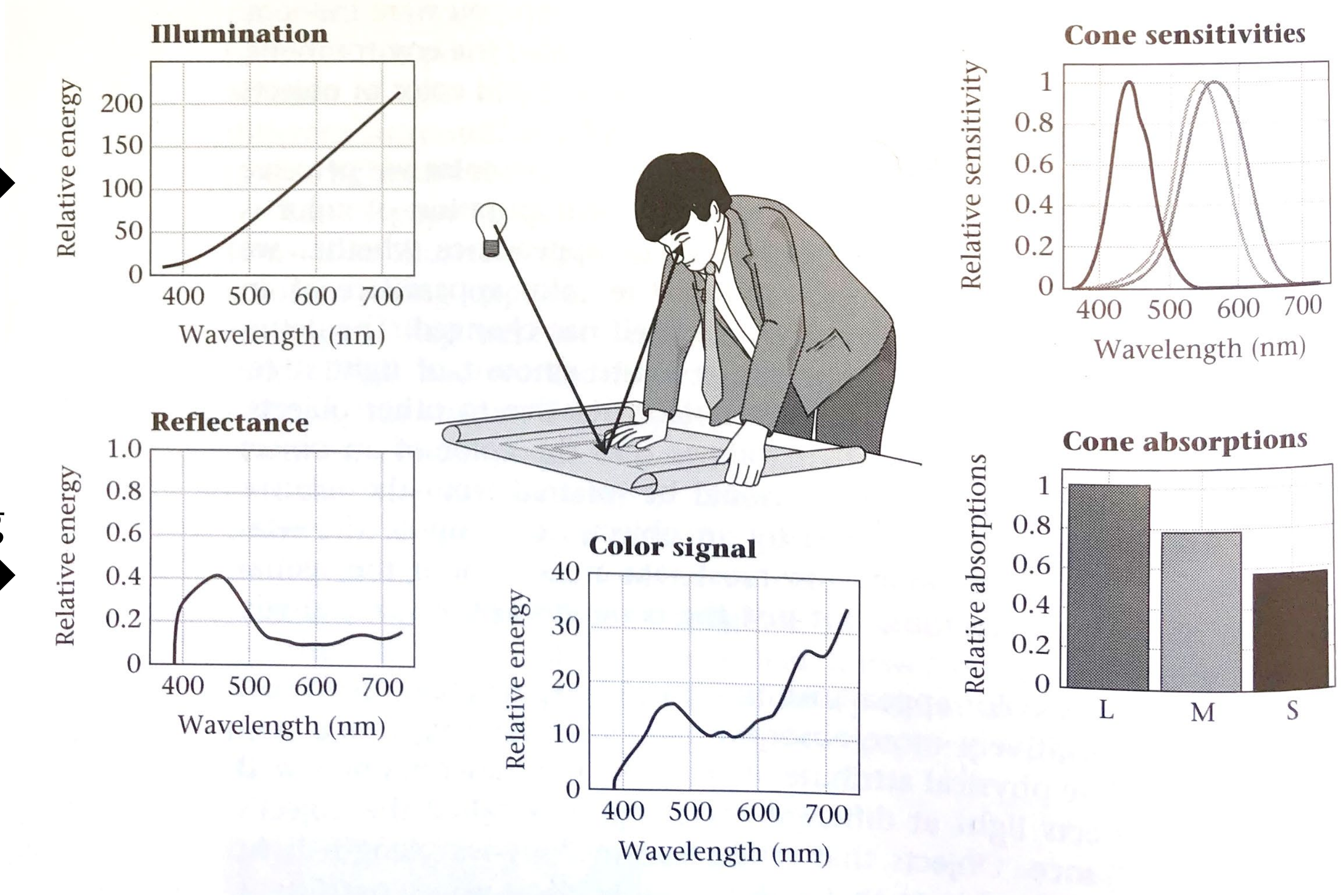
What is color vision?

but it doesn't know this ➔

the brain is trying
to estimate this ➔

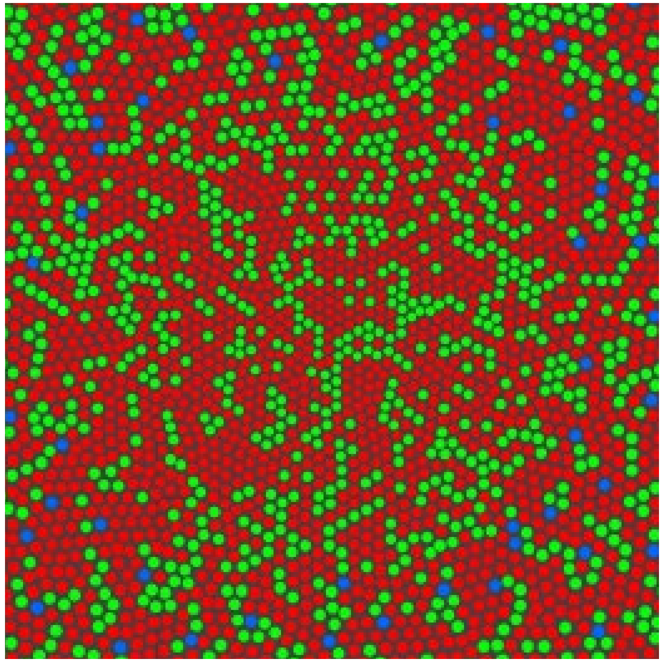


🡐 the brain knows this

Wandell (1995)

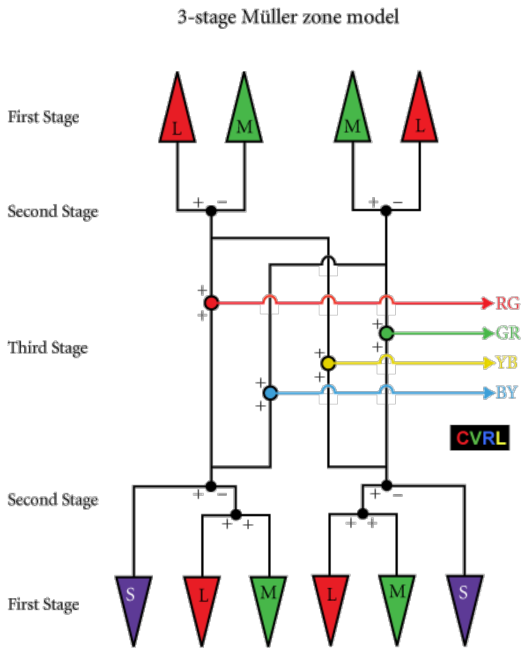
Overview

1. Encoding



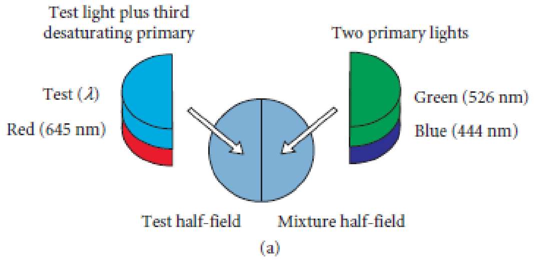
Cottaris et al. (2019)

2. Decoding

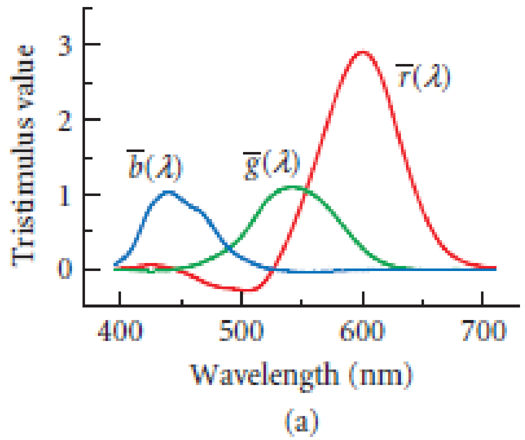


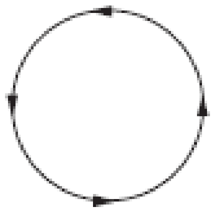
Stockman & Brainard (2010)

Color matching experiments: evidence for trichromacy

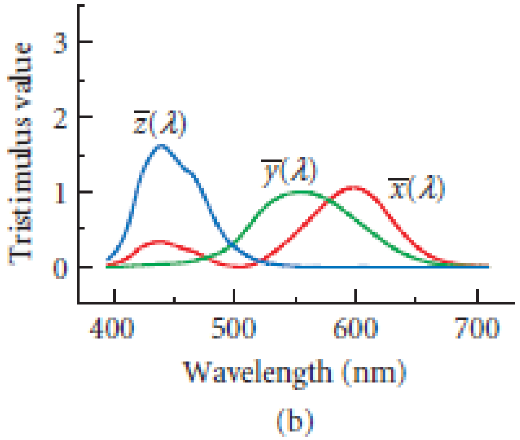


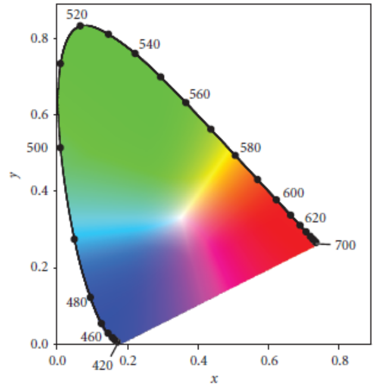
r, g, b primaries

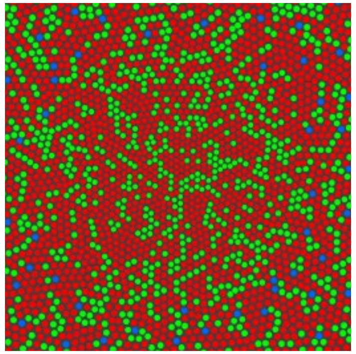


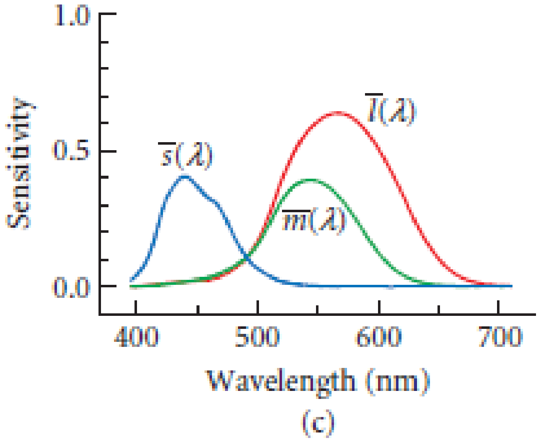


x, y, z primaries (CIE 1931)









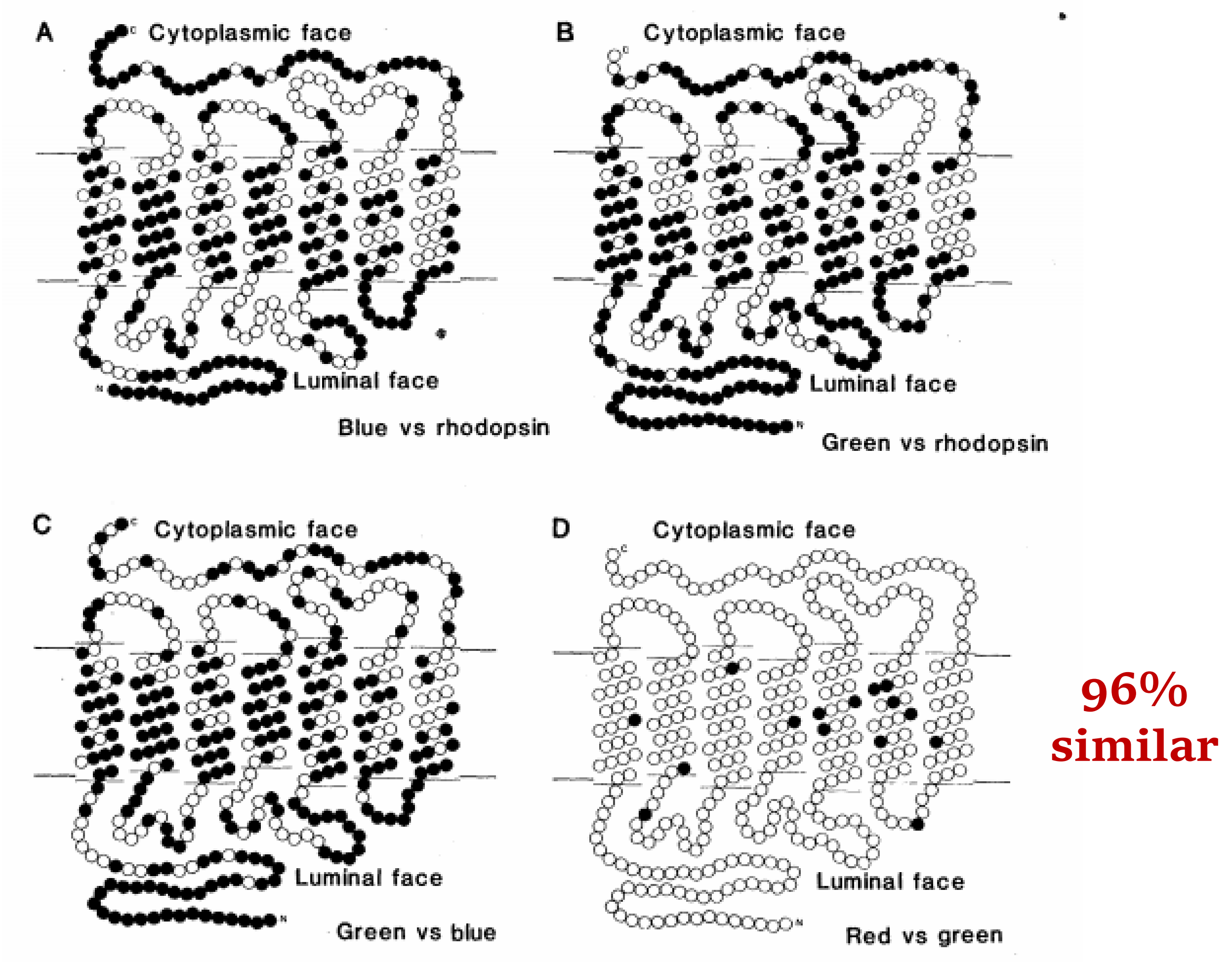
l, m, s primaries (Smith & Pokorny)

In primates, trichromacy emerged 30-40 million years ago

- Catarrhines (Old world monkeys and apes) are trichromats
  - L and M opsins encoded on adjacent opsin genes on X-chromosome

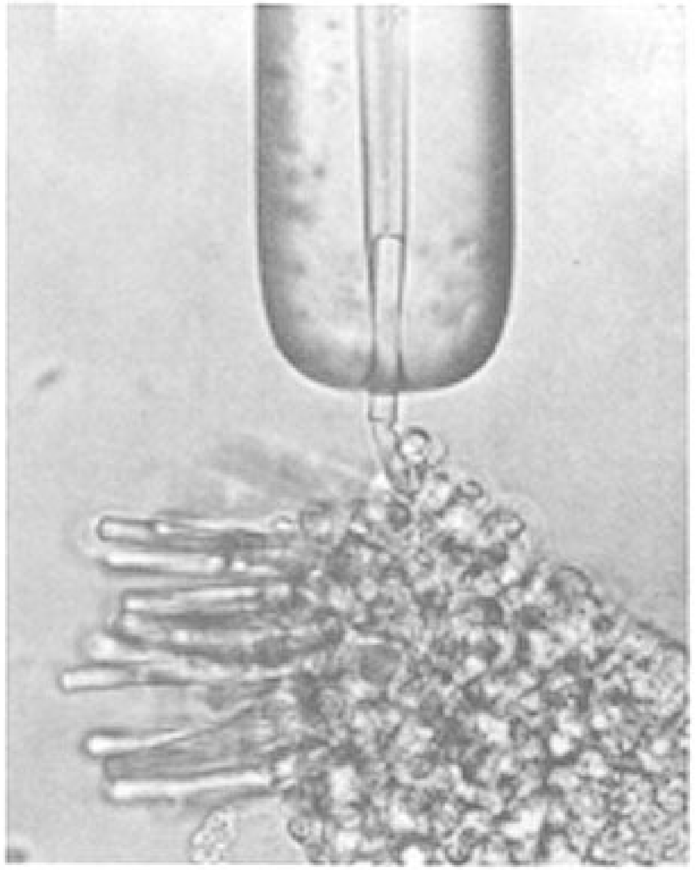
- Platyrrhines (New world monkeys) are more complicated:
  - M/L opsin encoded on a single, polymorphic X-chromosome gene locus
    - All males and homozygous females are dichromatic
    - Heterozygous females are trichromatic

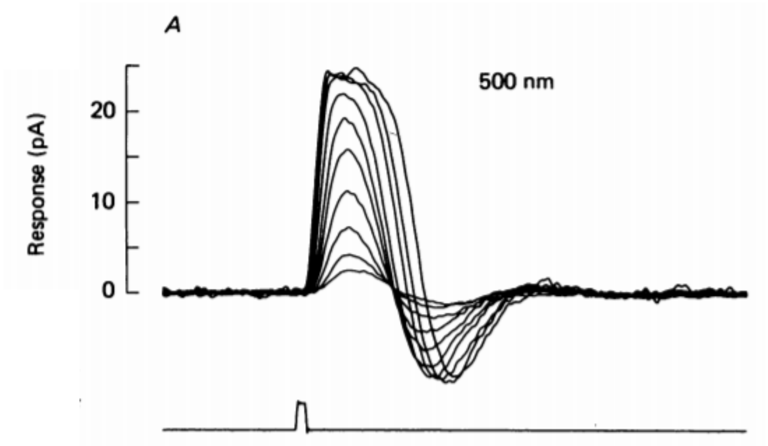
- S opsin is encoded by an autosomal gene on chromosome 7
  - Genetic locus is common to all primates

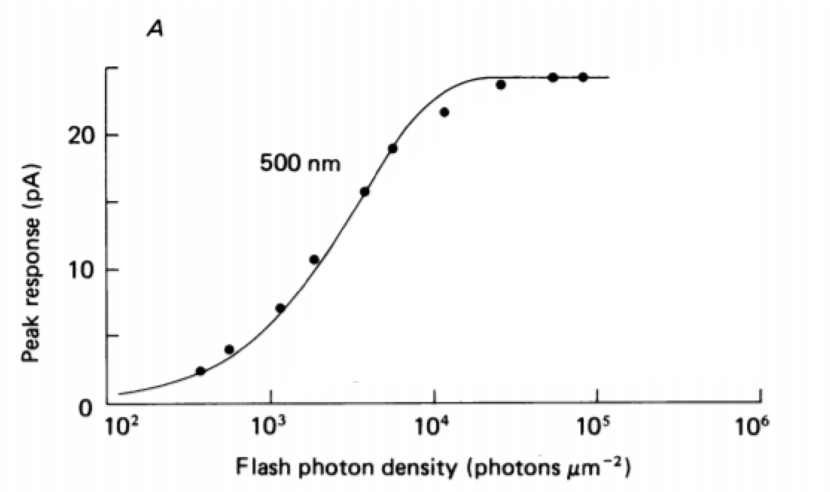


Nathans et al. (1986)

Cones transduce photons into neural signals

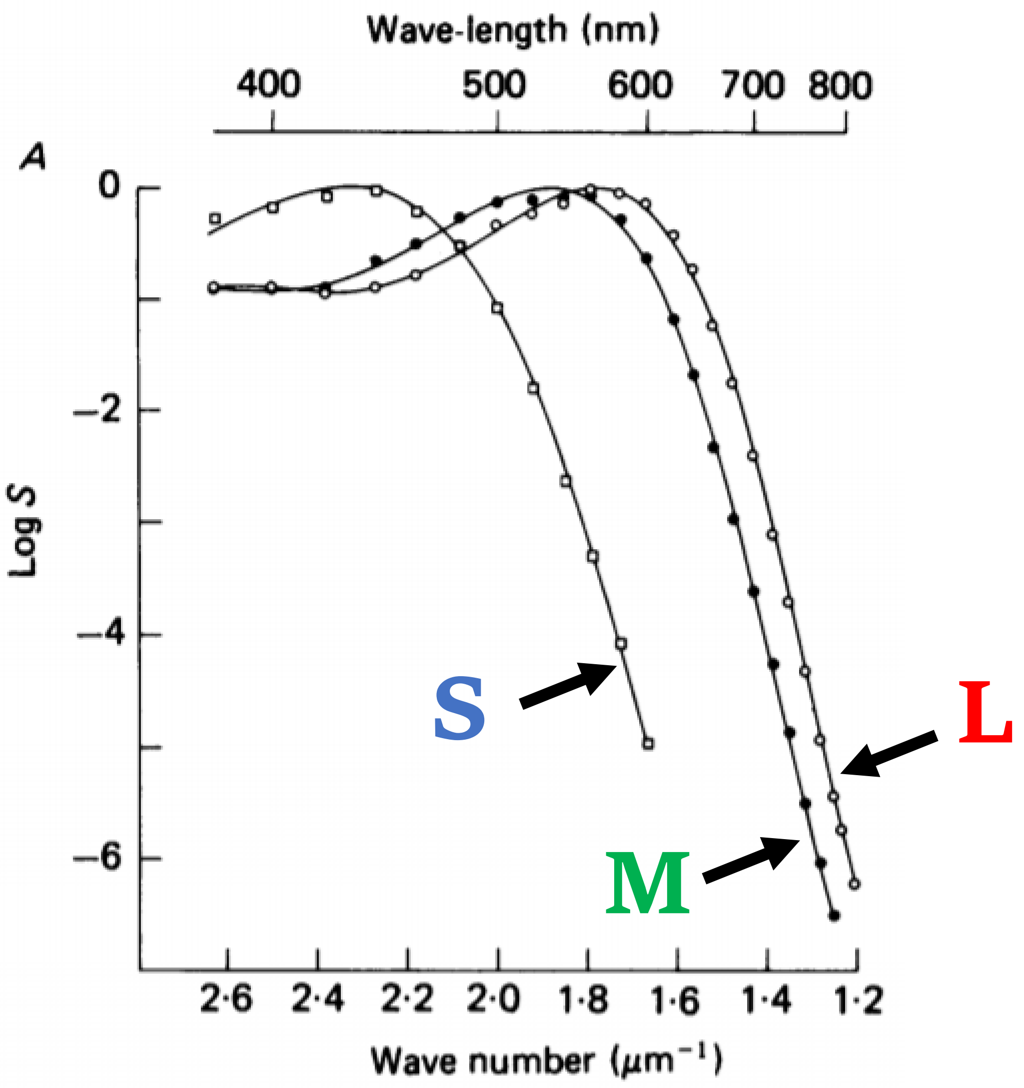






Baylor, Nunn, Schnapf (1987)

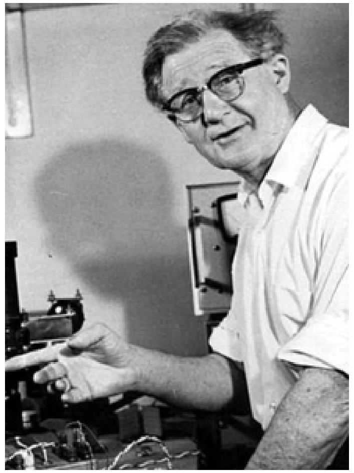
Spectral sensitivity of primate cones



Baylor, Nunn, Schnapf (1987)

The Principle of Univariance

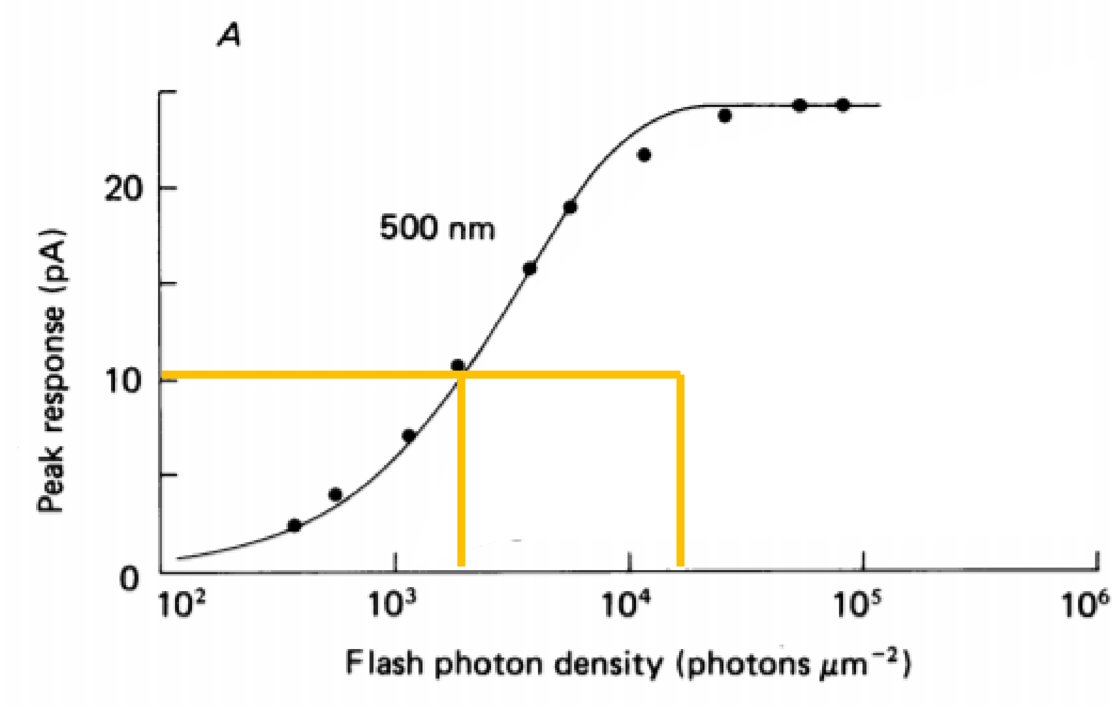
WAH Rushton, *J Physiol* (1972)



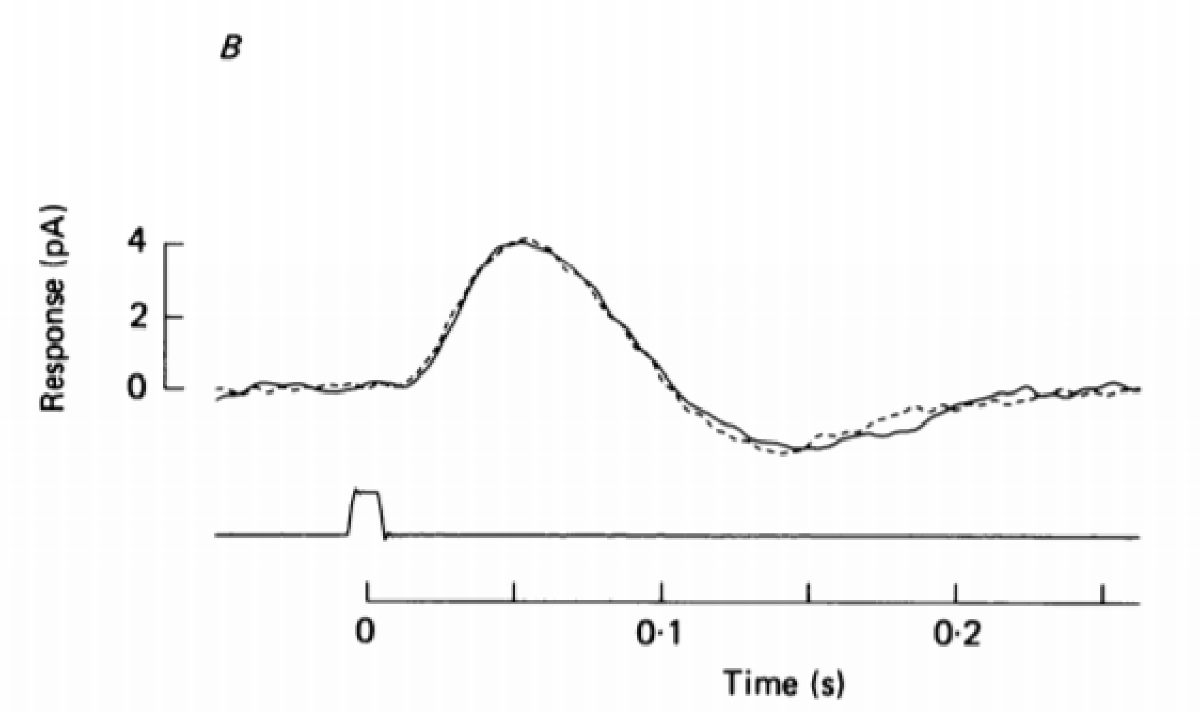
'brightness'. The effect of wave-length (as Koenig showed) is simply to modify the proportion of light that is absorbed, i.e. the proportion of incident quanta that are caught. Every quantum that *is* caught, however (whatever its wave-length), produces the same effect – its unit contribution to output. This very important property of rods, and indeed also of each kind of cone, this limitation of output to a single dimension of change, may be called the *Principle of Univariance* and stated thus: 'The output of a receptor depends upon its quantum catch, but not upon what quanta are caught.

Primate cones exhibit univariance

dose-response curves

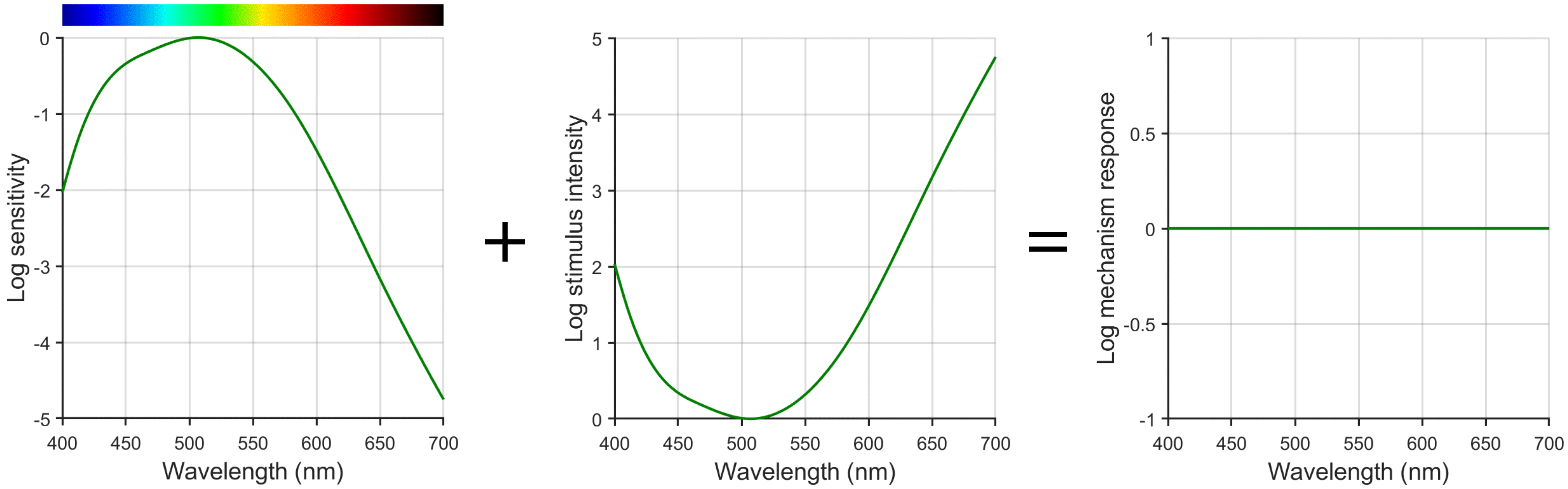


impulse-response curves (kinetics)



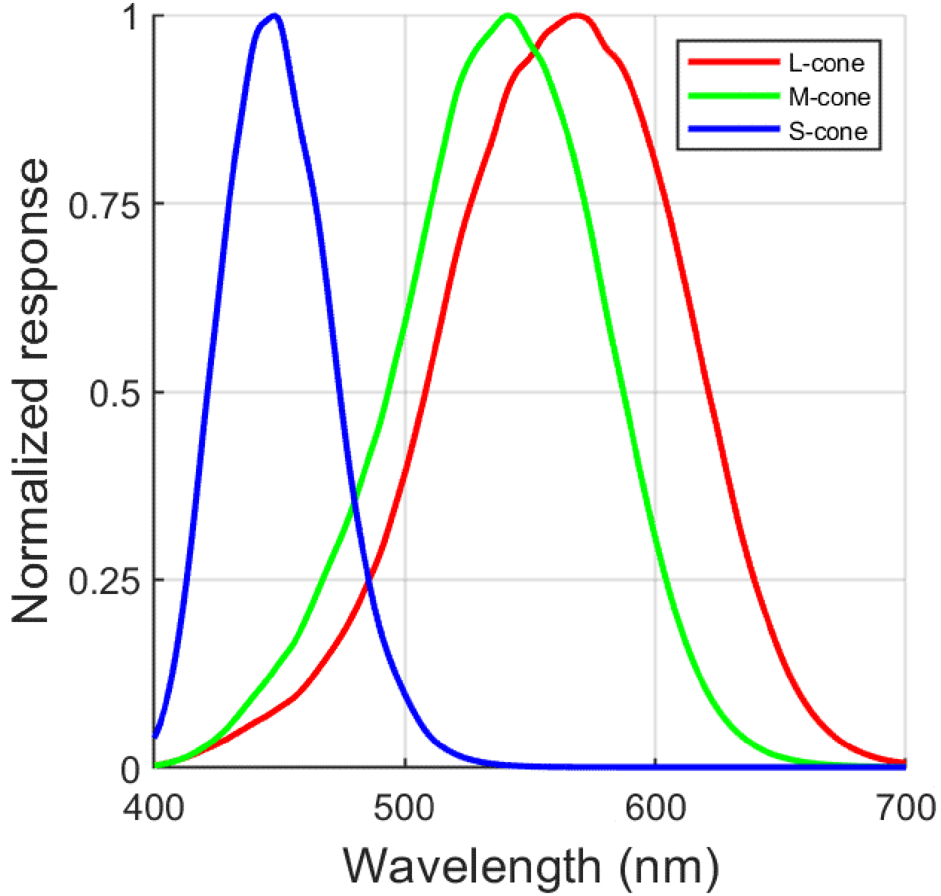
Baylor, Nunn, Schnapf (1987)

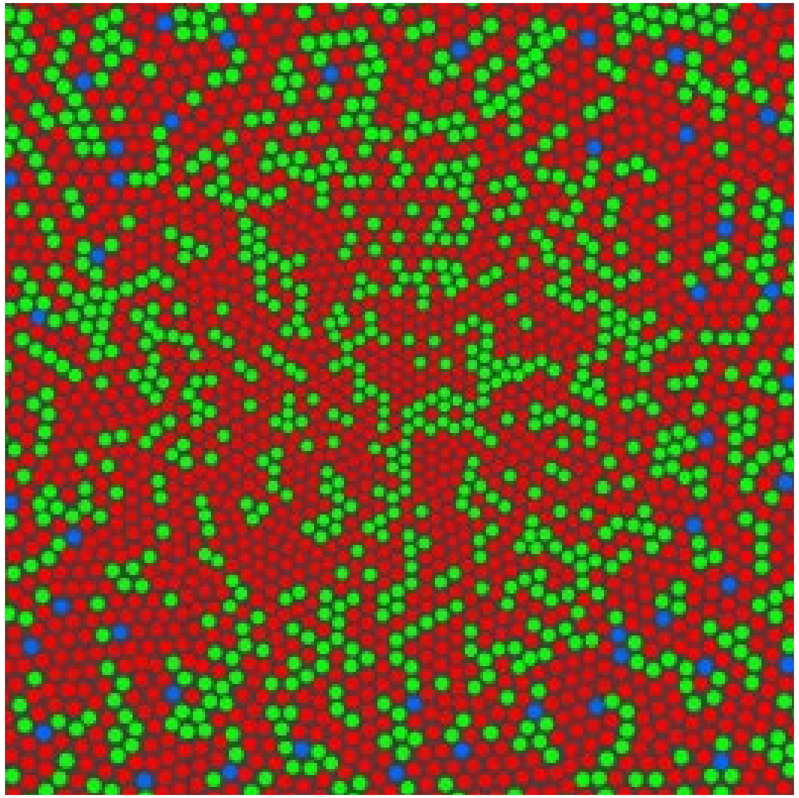
Univariant receptors conflate wavelength and intensity



With a single univariant mechanism, ***wavelength*** and ***intensity*** information are confounded in its output.

Color vision requires comparisons across cone classes!

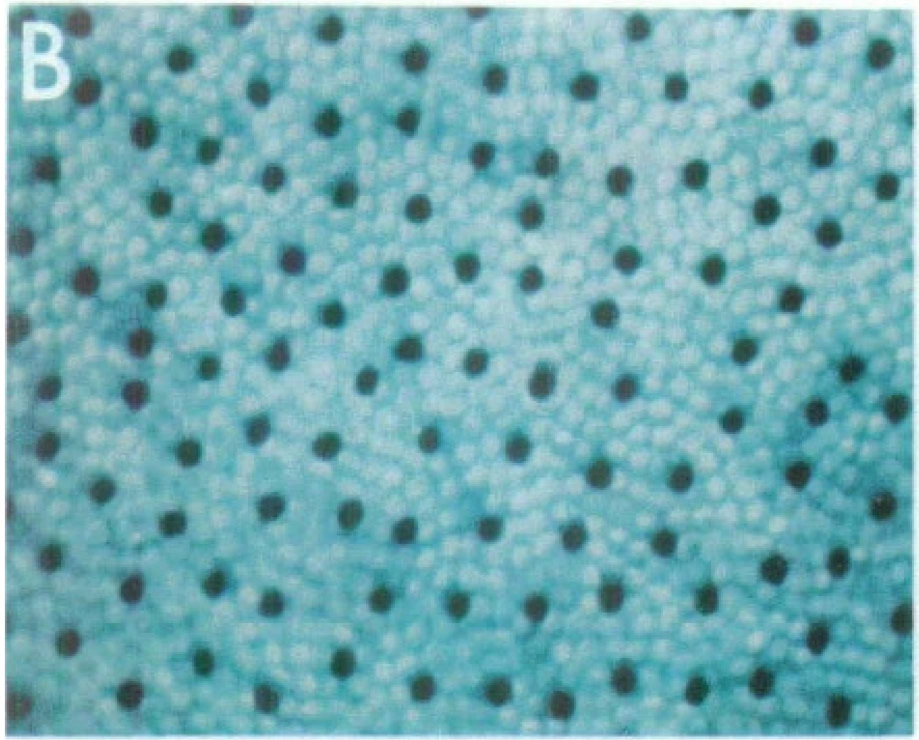




What is the spectral topography of the human cone mosaic?

S cones are sparse and absent from the central fovea

Macaque retina (dark spots = S cones)



de Monasterio et al (1985)

human

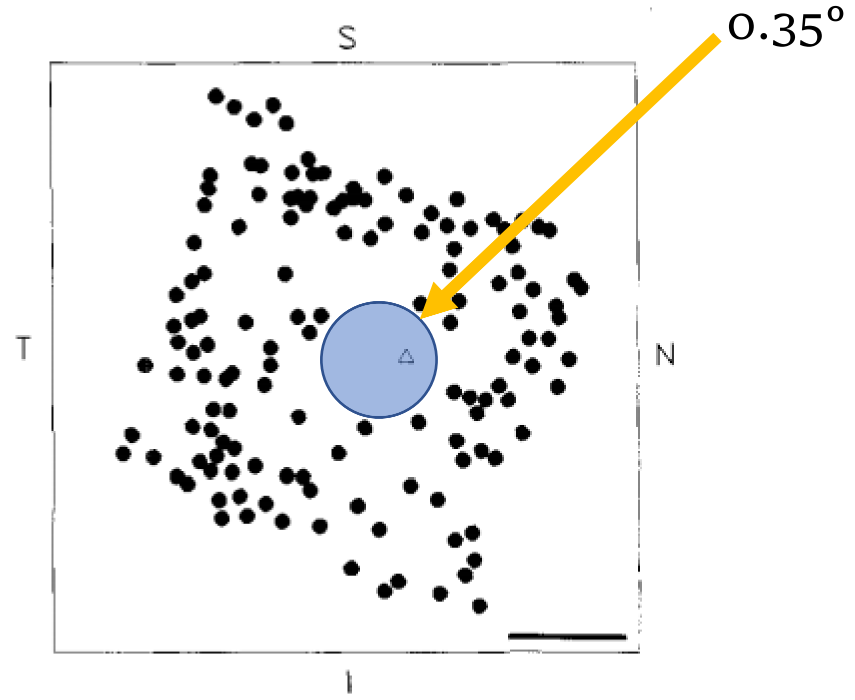
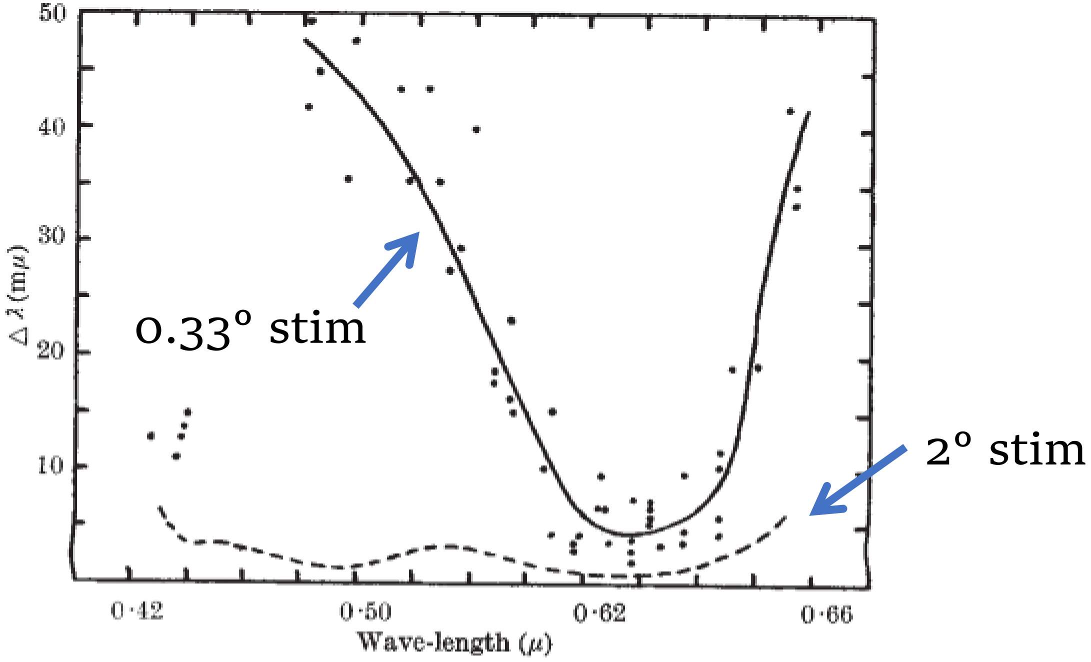


Fig. 5. Foveal blue-free zone. Blue cone inner segments are missing from the foveal center and are irregularly distributed around its edges. △ denotes highest overall cone density. A disk 100 μm (0.35°) in diameter could be placed in the foveal center without encroaching on any of these blue cones. S-superior; N-nasal; I-inferior; T-temporal. Bar = 100 μm.

Curcio et al (1991)

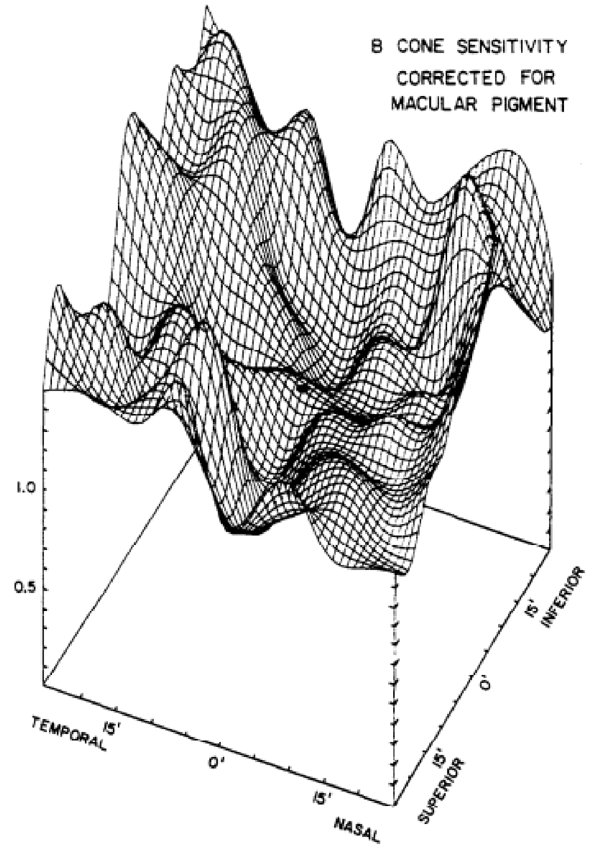
An S-cone-free fovea has visual consequences

Wavelength discrimination suffers in the blue region of the spectrum when stimuli are small



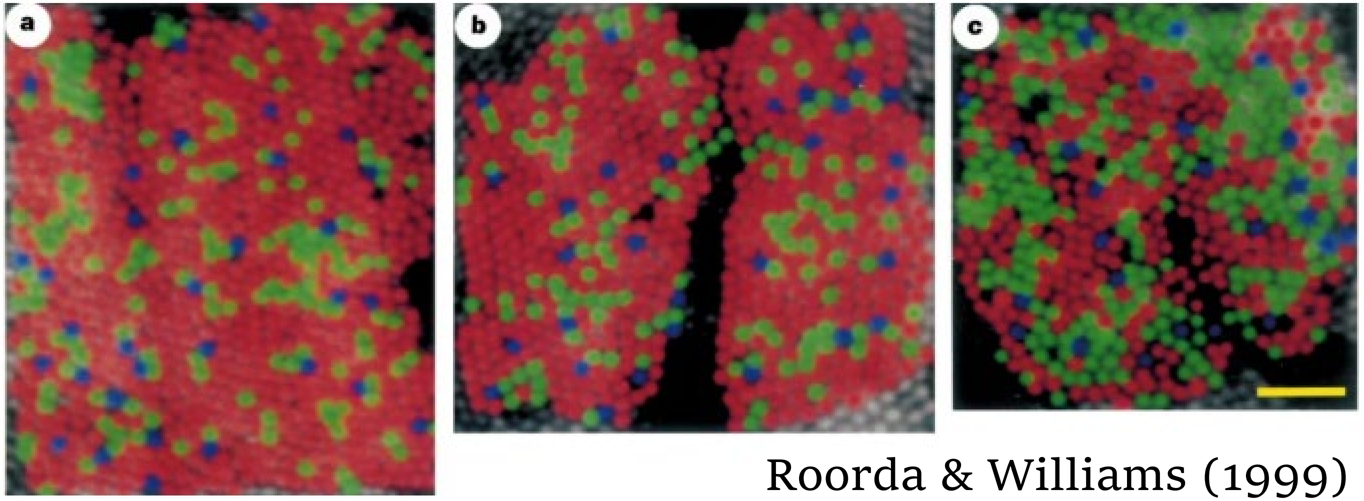
Willmer & Wright (1945)

Sensitivity to small, short-λ spots is low in the fovea and punctate elsewhere

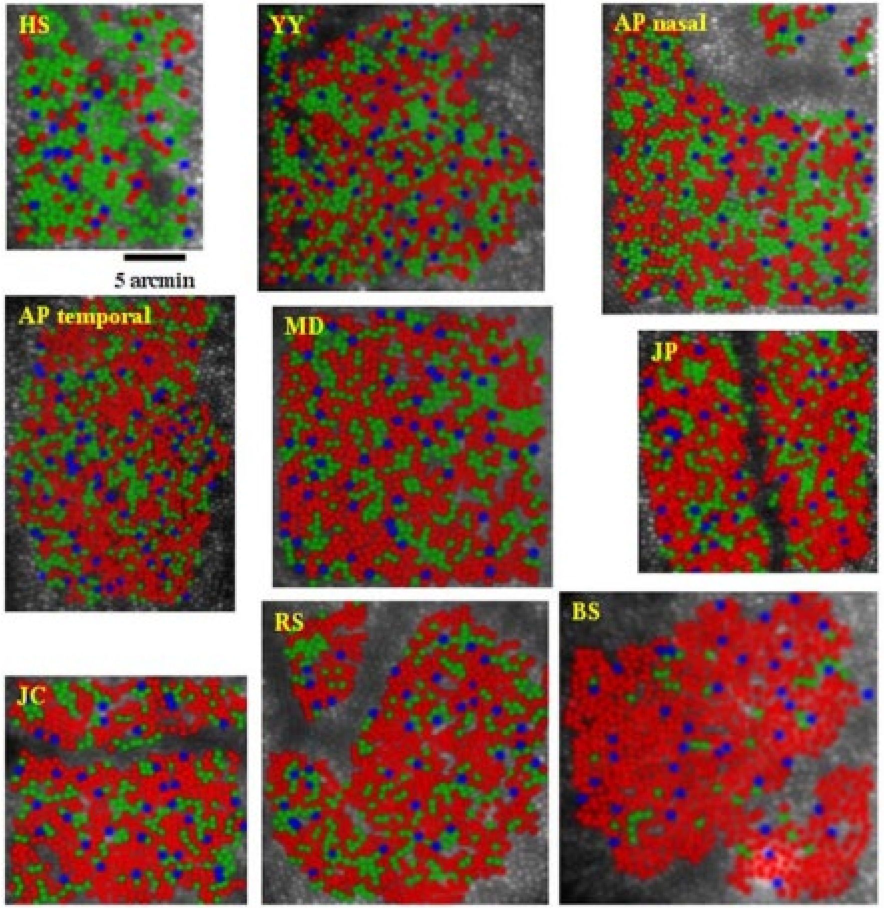


Williams et al. (1981)

Adaptive optics densitometry shows the L:M cone ratio varies across individuals with normal color vision



Roorda & Williams (1999)

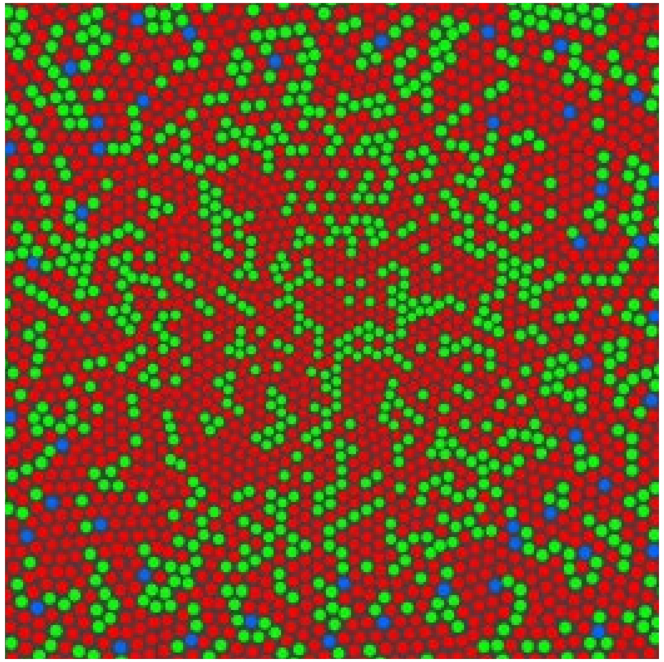


See also: Sabesan et al. (2015)

Hofer et al. (2005)

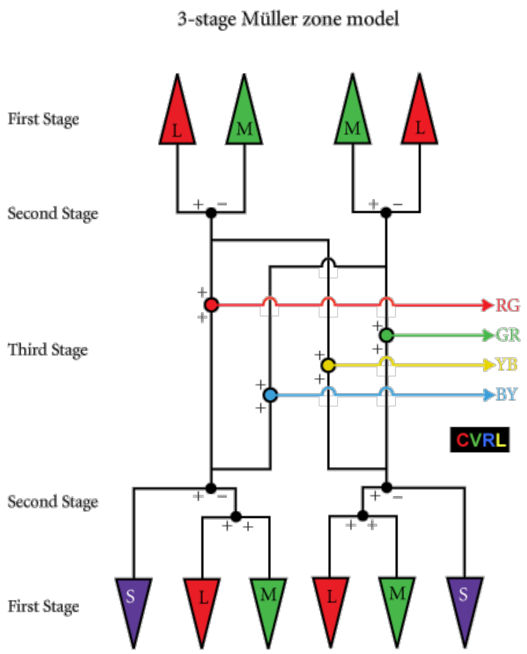
Overview

1. Encoding



Cottaris et al. (2019)

2. Decoding



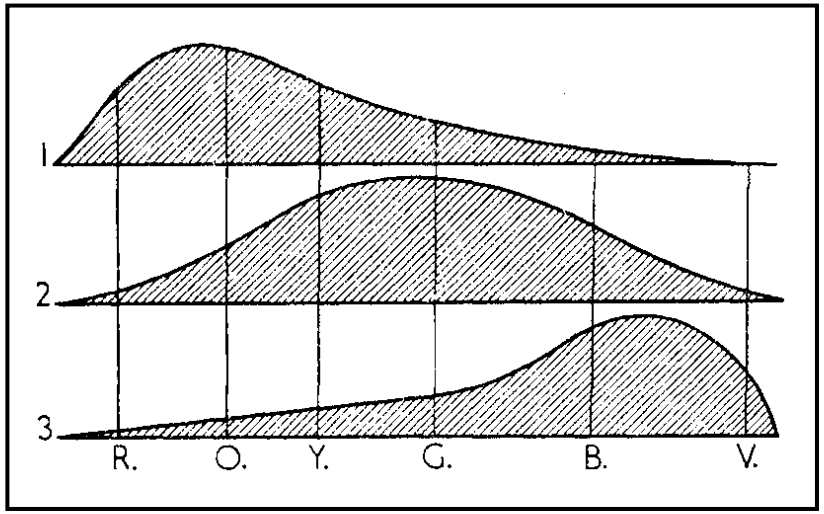
Stockman & Brainard (2010)

Young-Helmholtz's Trichromatic Color Vision Theory

1866 – Helmholtz presented a relatively complete description of color vision based on Thomas Young's original proposal (1802) of three fundamental retinal mechanisms.

A set of three sensory mechanisms can explain color vision:

- Each of the mechanisms is sensitive across the entire visible spectrum, but they differ in their spectral response properties.
- Also, around the same time: the first color matching experiments (Maxwell), Grassman's Laws, etc. supported a trichromatic theory of color vision.

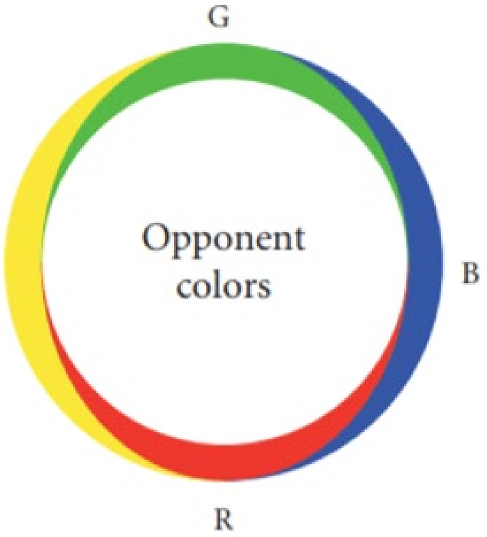


Slide courtesy of Dan Coates, Univ. of Houston

Hering's Color-Opponent Theory

Ewald Hering observed that unique hues come in opponent pairs:

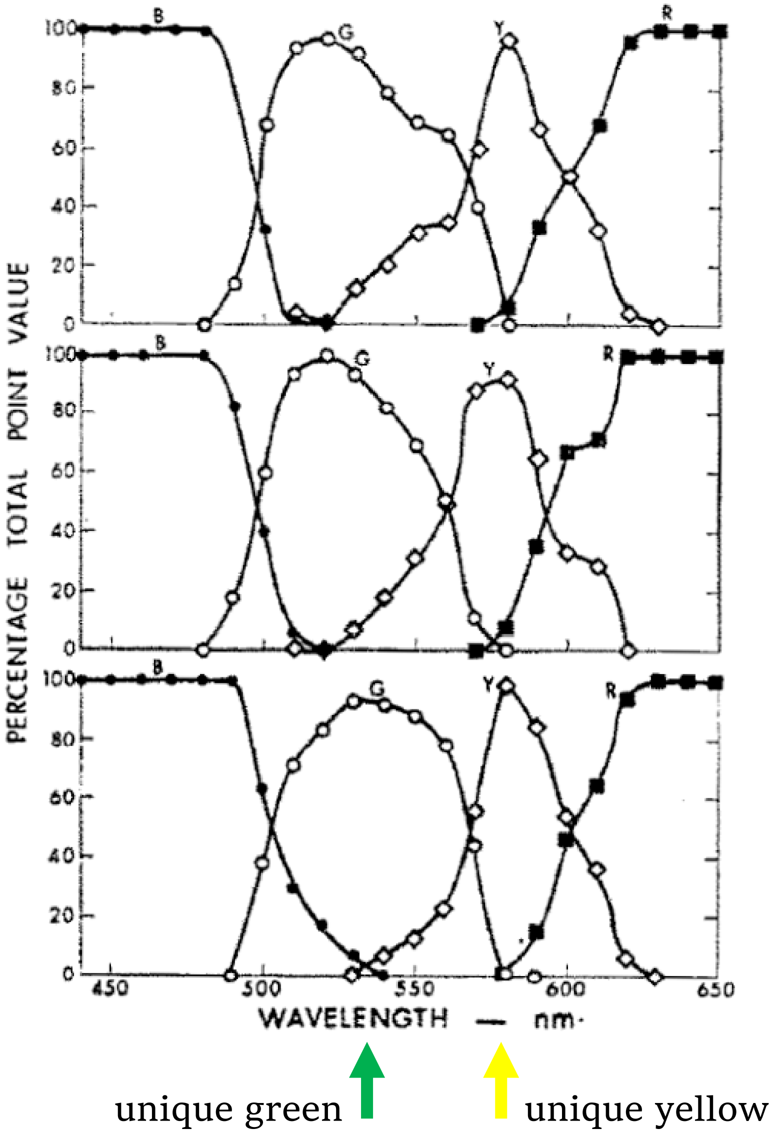
- opponent colors (e.g. R & G) cannot be seen in the same place at the same time
- thus no mixture contains R & G, or B & Y (there is no yellowish-blue)
  - the same rules don't seem to apply to achromatic dimension (we can see black and white at same time, i.e. gray)
- opponent colors are complements
- adaptation to one color will shift hue to its complement




keep staring at the black dot.


johnsadowski.com

Quantifying opponency: hue scaling experiments

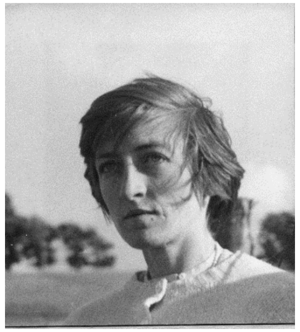


The color appearance of nearly all spectral lights can be described using just 1 or 2 unique hues.

Hue scaling functions reveal the wavelengths of the unique hues (except for unique red, which is non-spectral).

The sensation of “redness” seems to exclude the possibility of seeing “greenness” (and vice versa)
- the same holds for blue and yellow

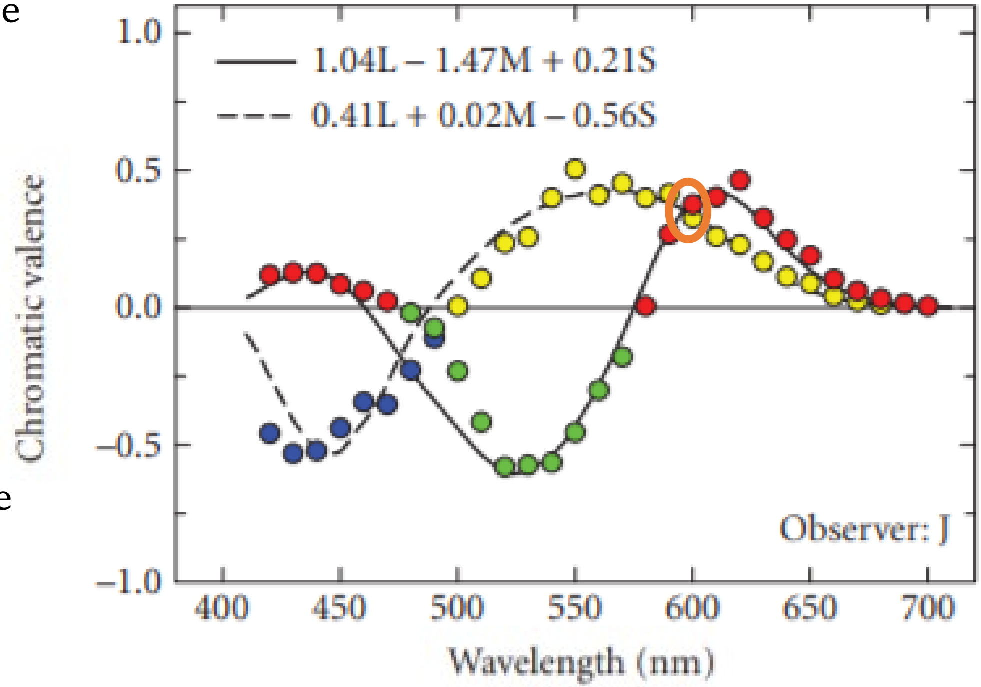
Quantifying opponency: hue cancellation experiments – Jameson & Hurvich (1955)



Dorothea Jameson

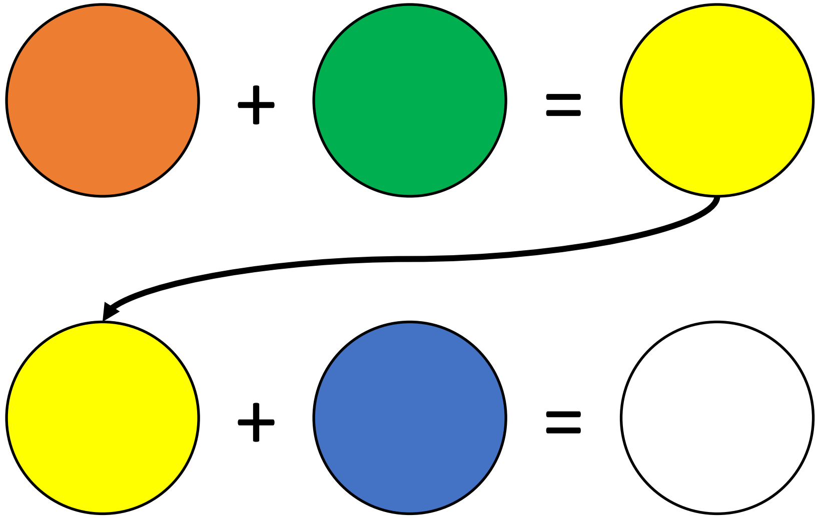
appears more reddish or yellowish

appears more greenish or bluish



600 nm test

0.4 units green



0.35 units blue

The 600 nm test must therefore contain 0.4 units of red (cancelled by green) and 0.35 units of yellow (cancelled by blue)

Do neurons in the visual system exhibit similar cone opponency?

Color-opponent neurons in the primate visual system?

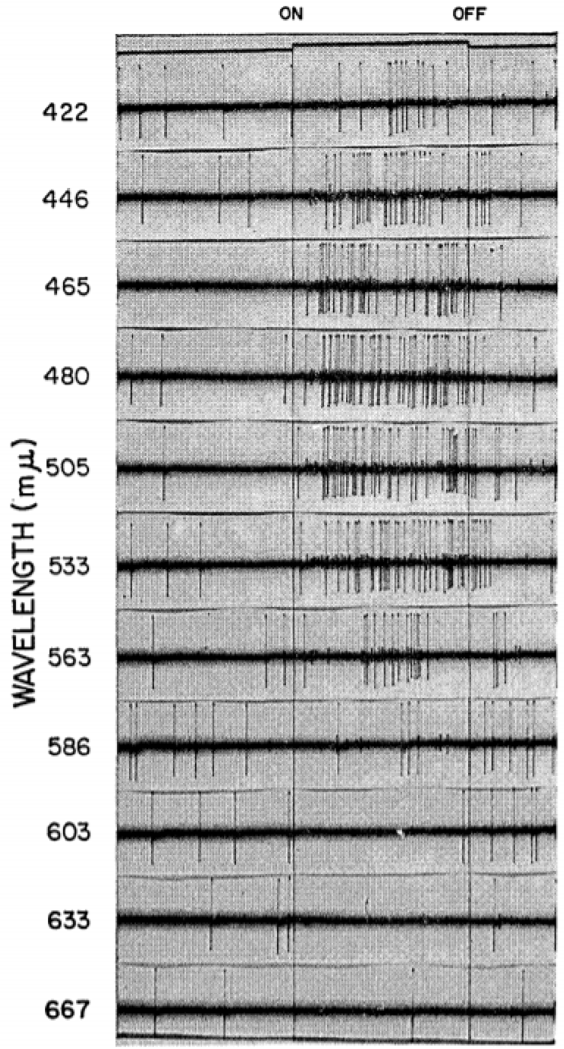
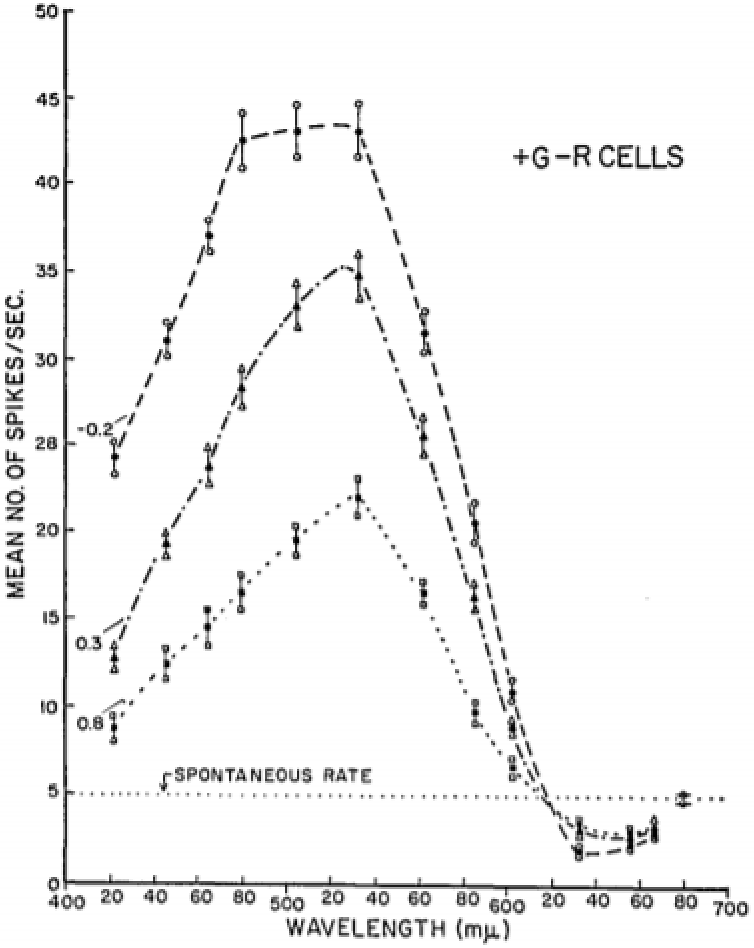
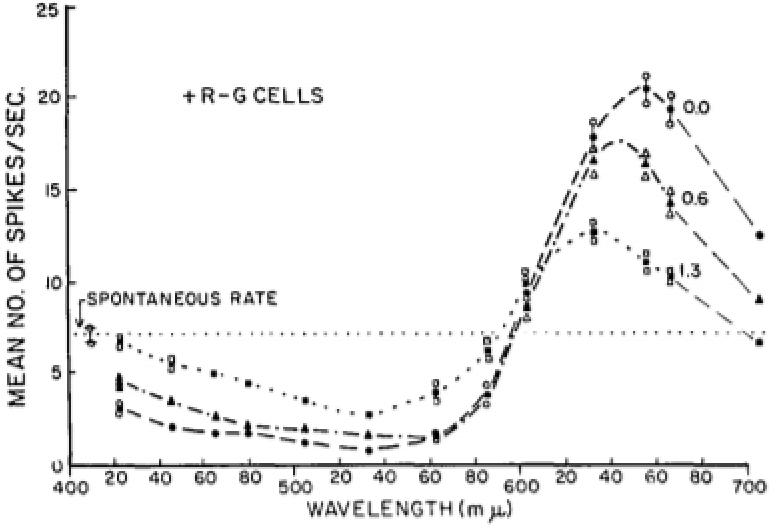


Fig. 7. Superimposed records from a +G−R cell. Details as for Fig. 5.





De Valois, Abramaov, Jacobs (1966)

Color-opponent neurons in the primate visual system?

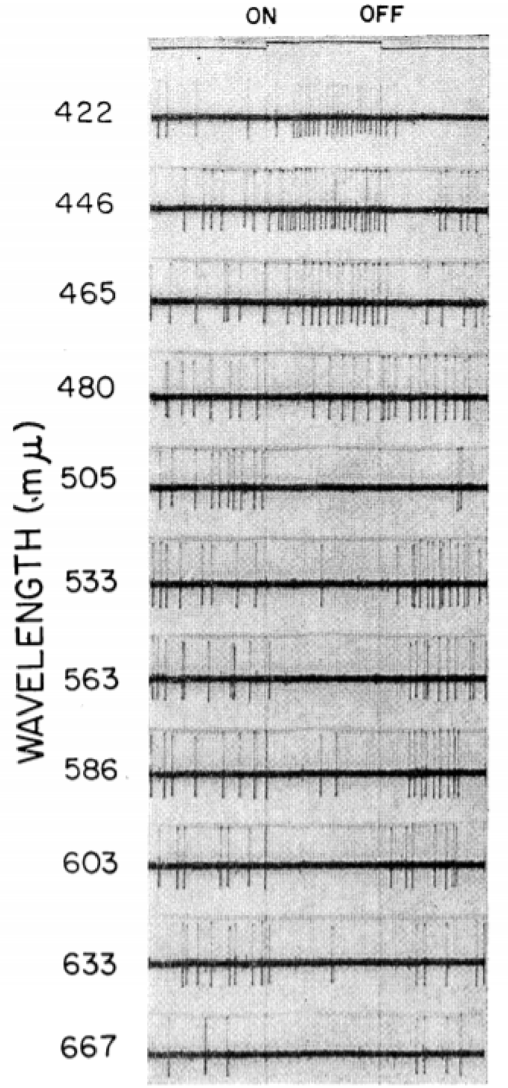
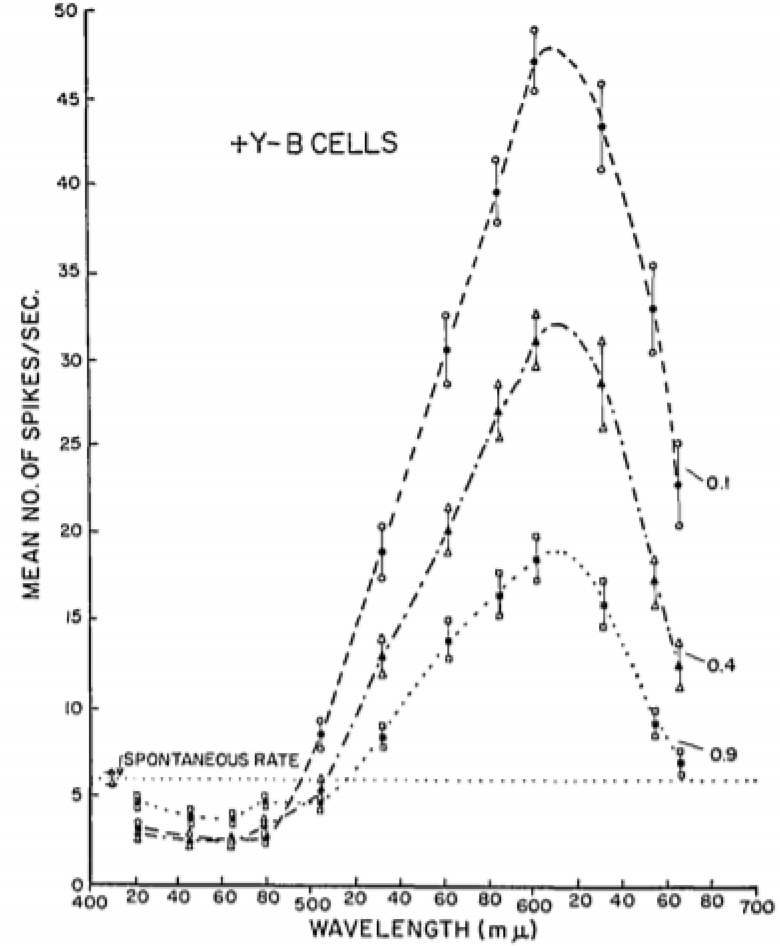
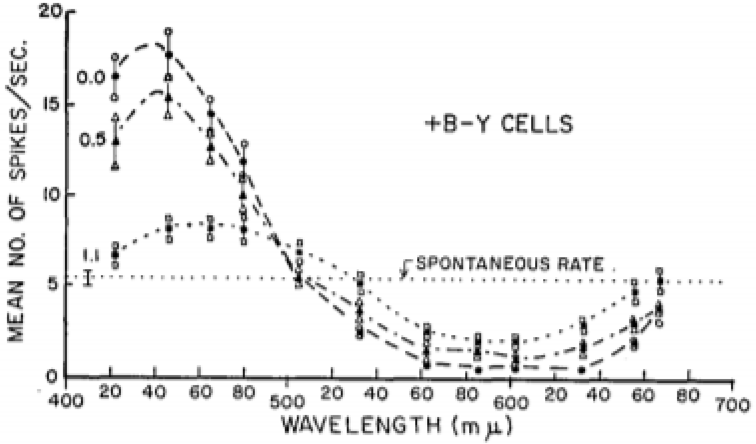


Fig. 8. Superimposed records from a +B−Y cell. Details as for Fig. 5.



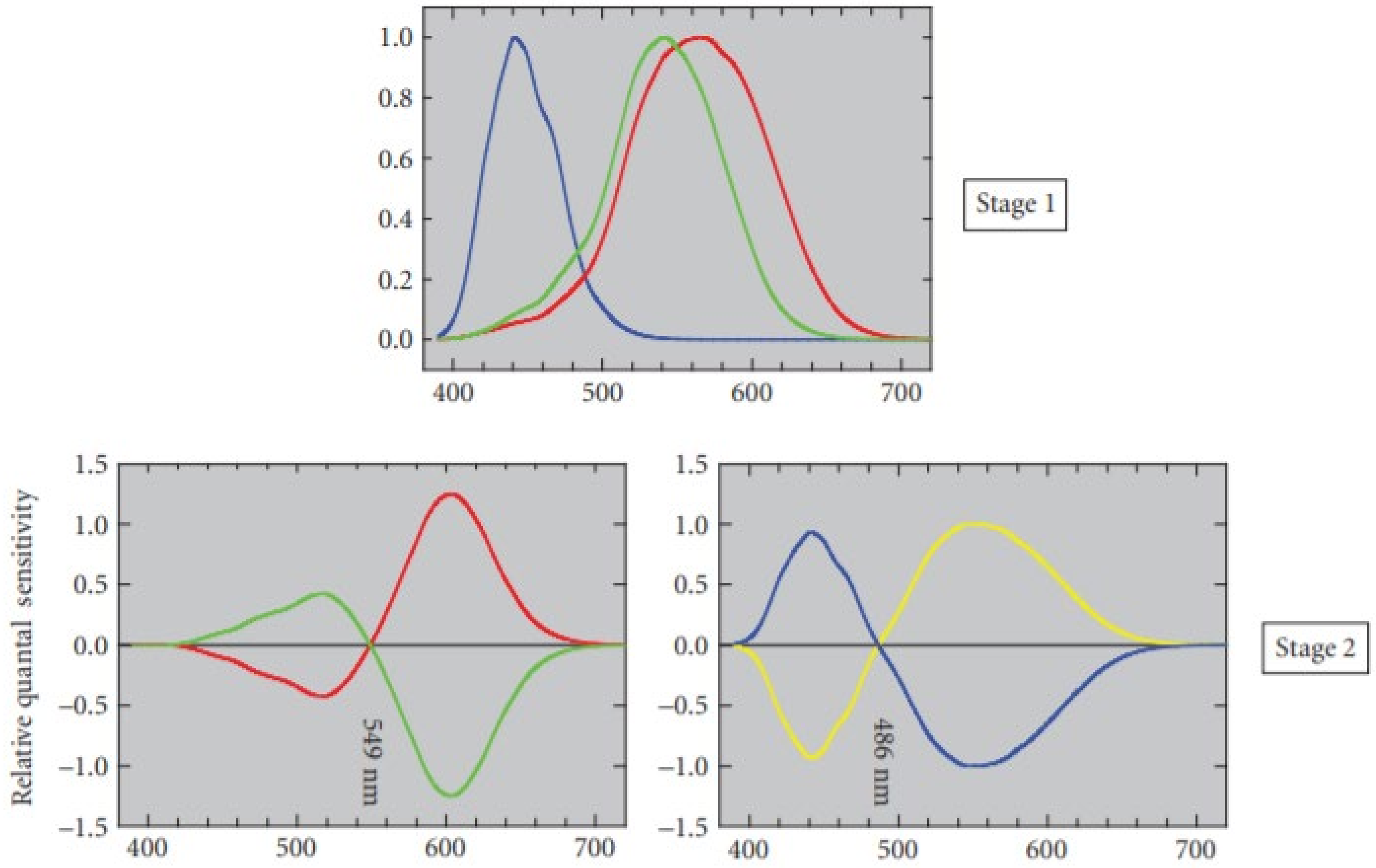


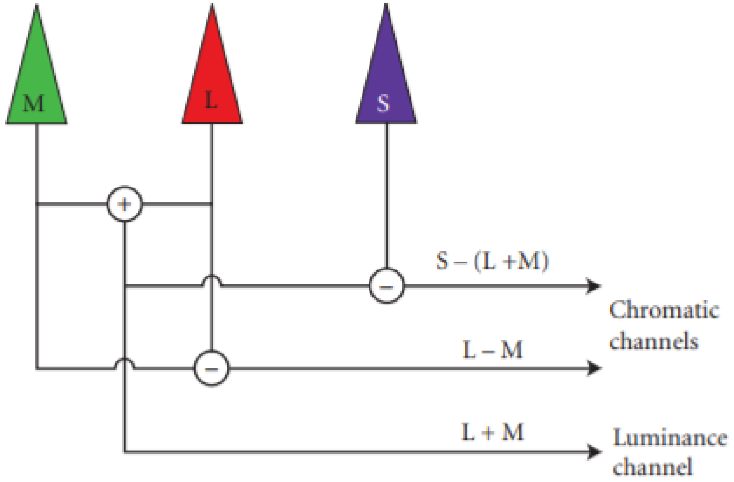
De Valois, Abramaov, Jacobs (1966)

Early color-opponent pathways

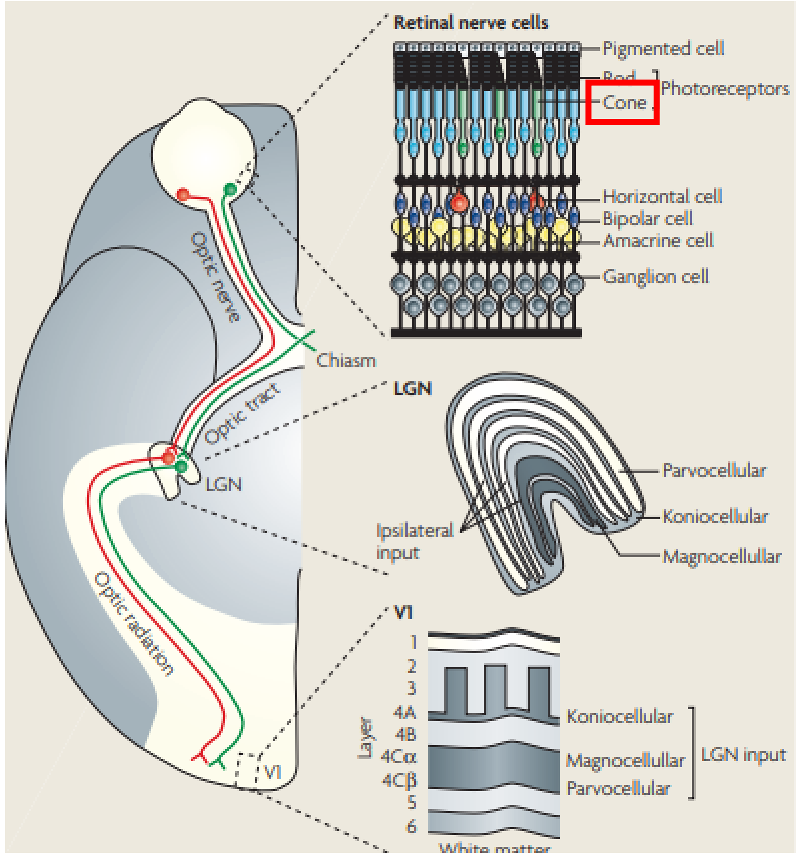
Cones

RGCs/LGN neurons

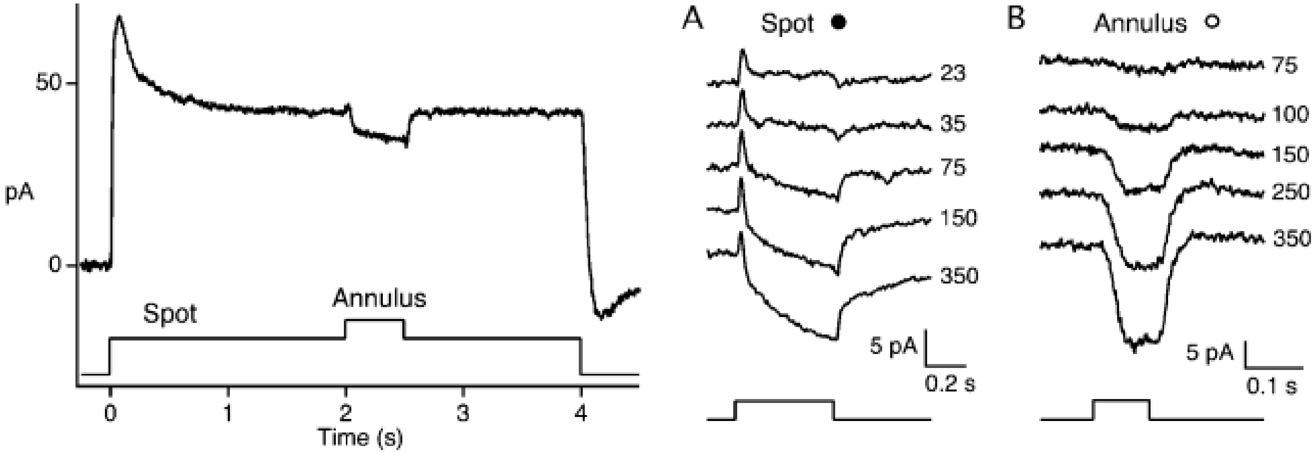




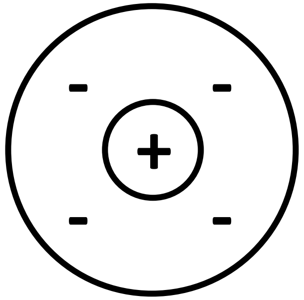
Where does color opponency arise?



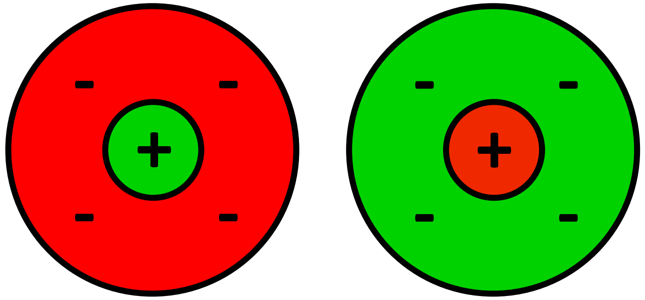
Solomon & Lennie (2007)



Verweij, Hornstein & Schnapf (2003)

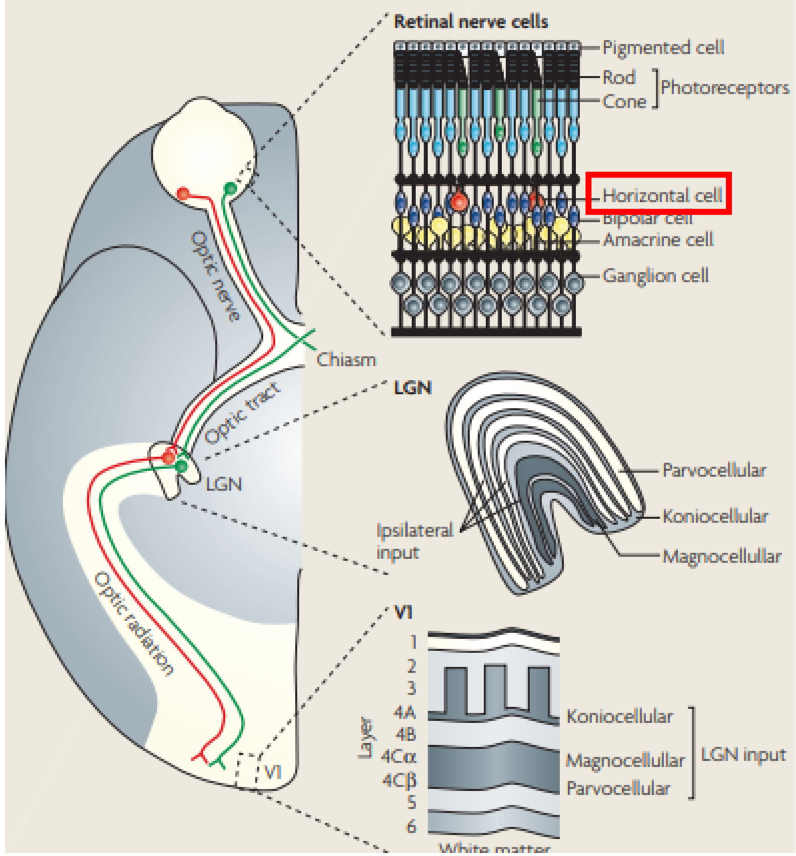


spatial opponency

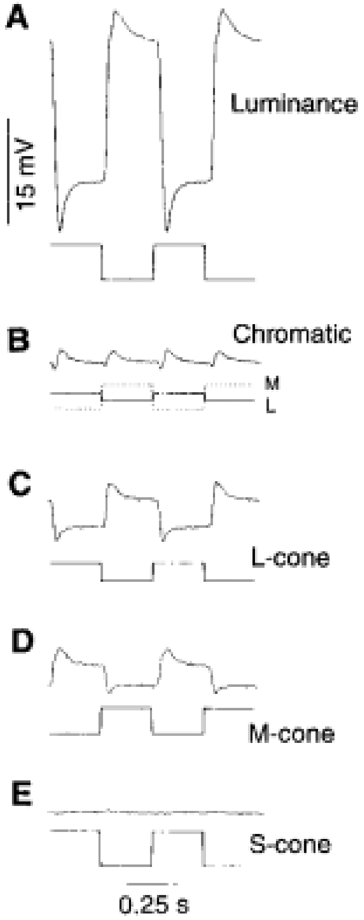


spectral opponency

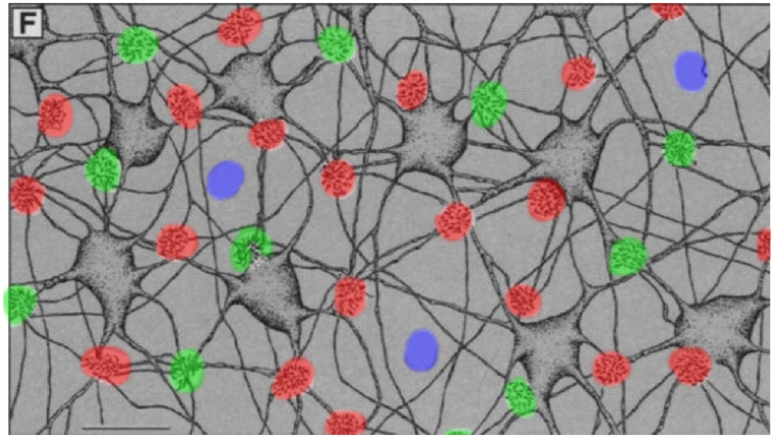
Lateral inhibition is mediated by horizontal cells



Solomon & Lennie (2007)

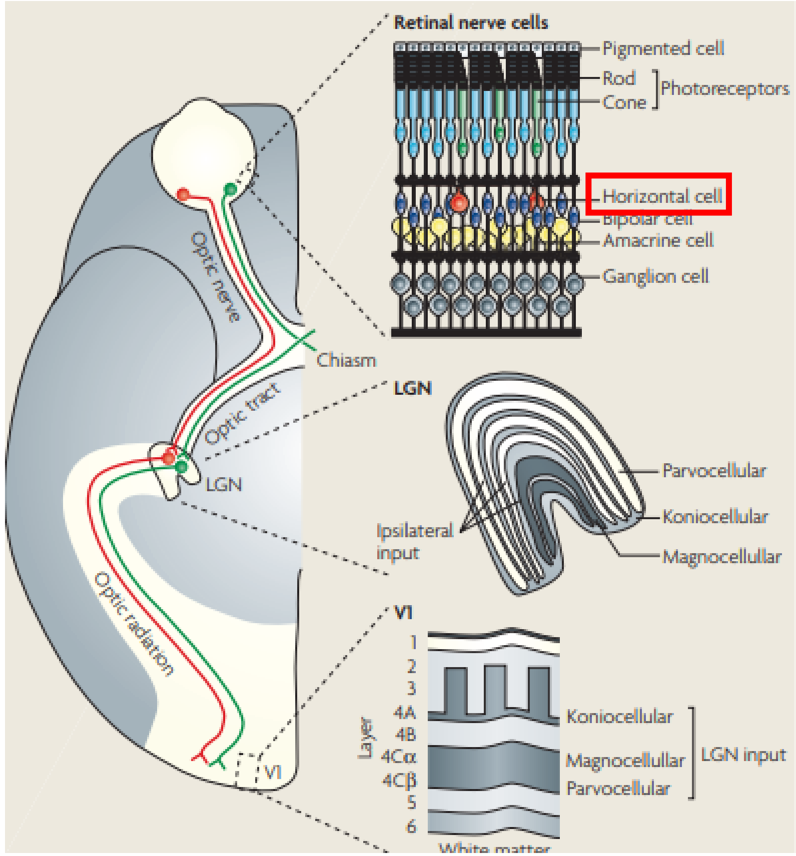


H1 horizontal cells

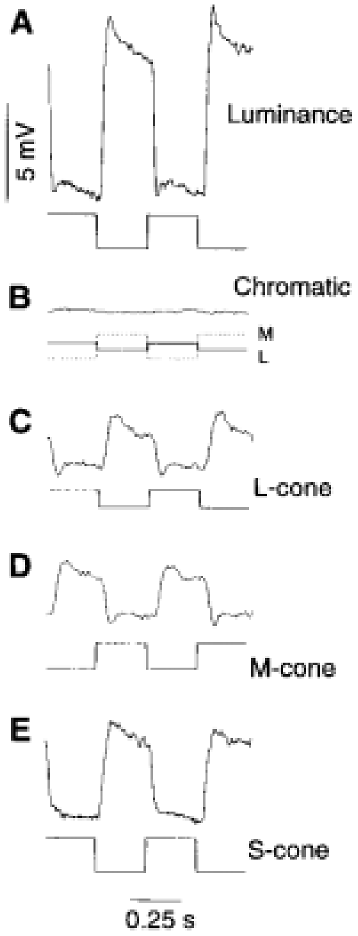


Dacey et al. (1996)

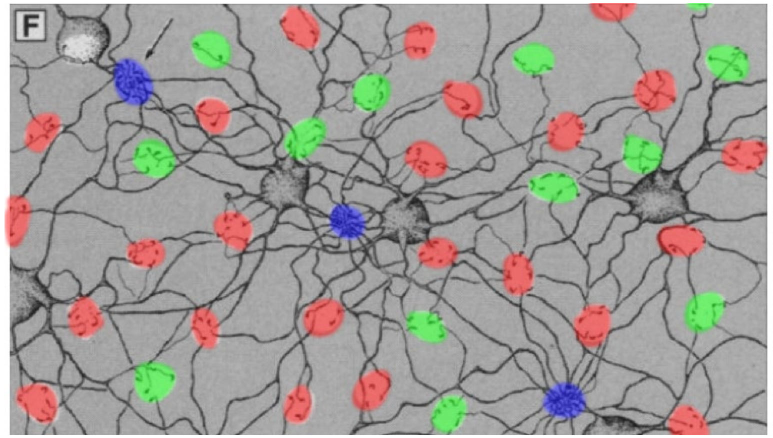
Lateral inhibition is mediated by horizontal cells



Solomon & Lennie (2007)

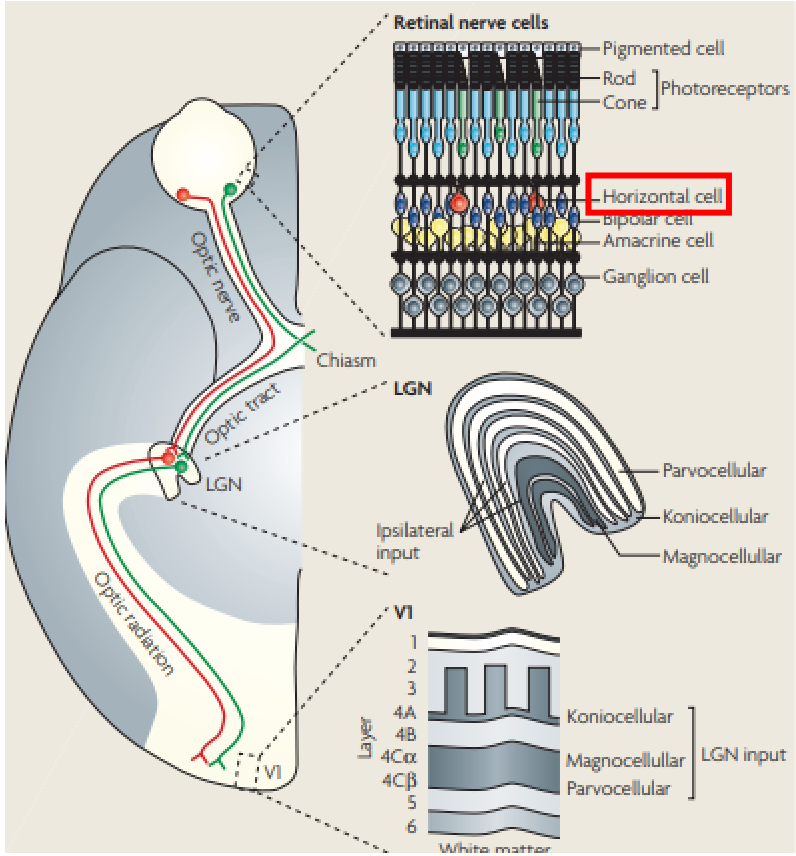


H2 horizontal cells

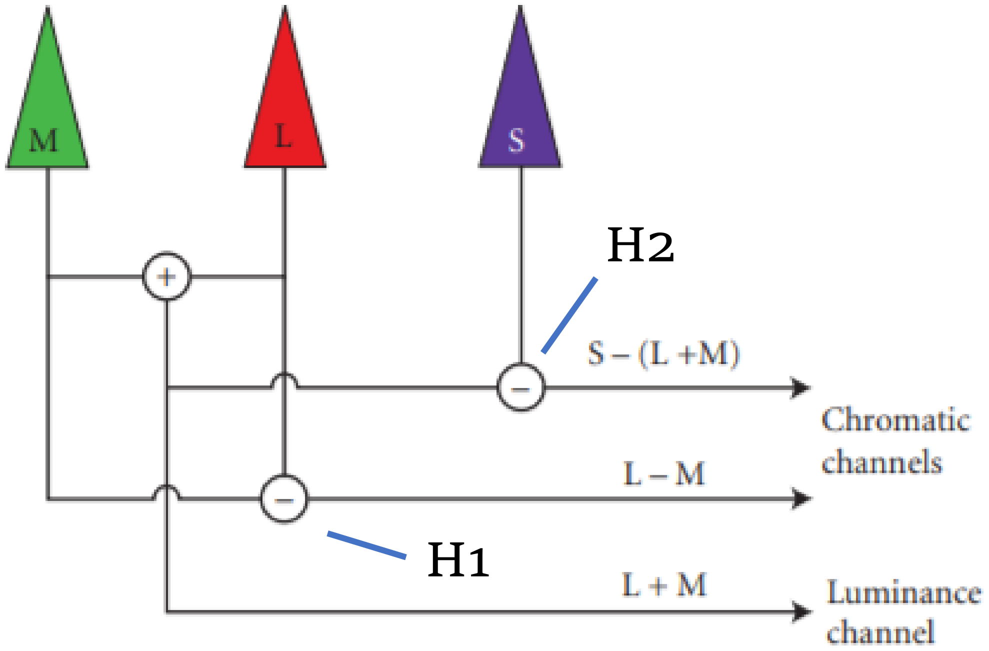


Dacey et al. (1996)

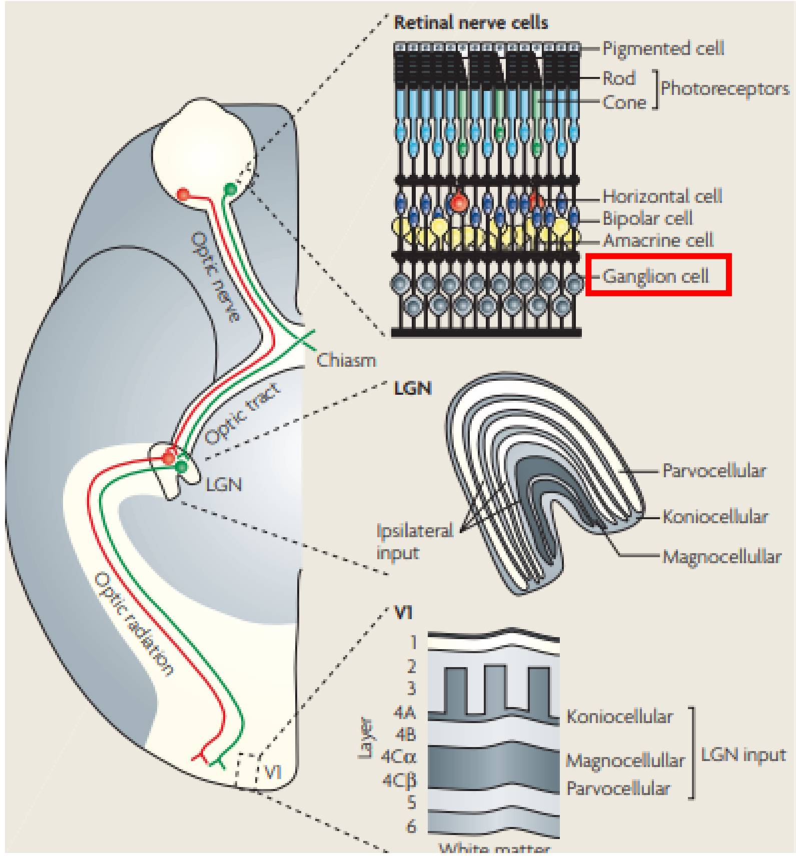
Lateral inhibition is mediated by horizontal cells



Solomon & Lennie (2007)

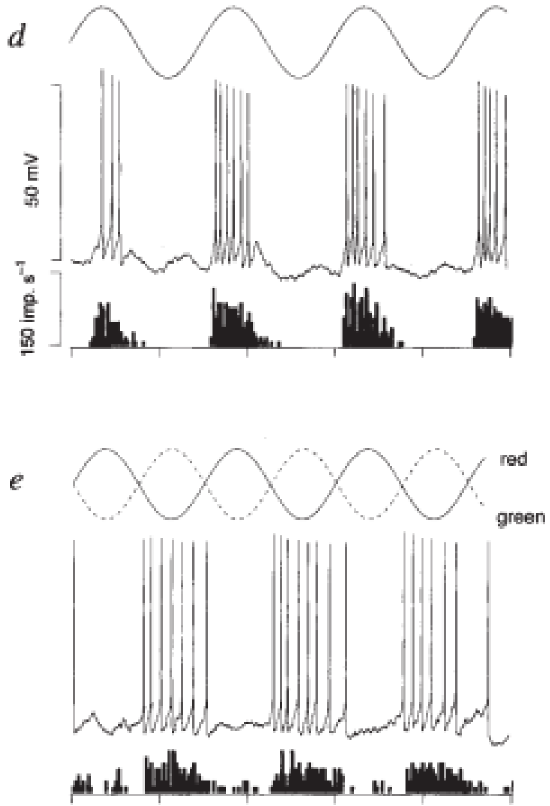


Receptive field organization in retinal ganglion cells



Solomon & Lennie (2007)

Midget RGC

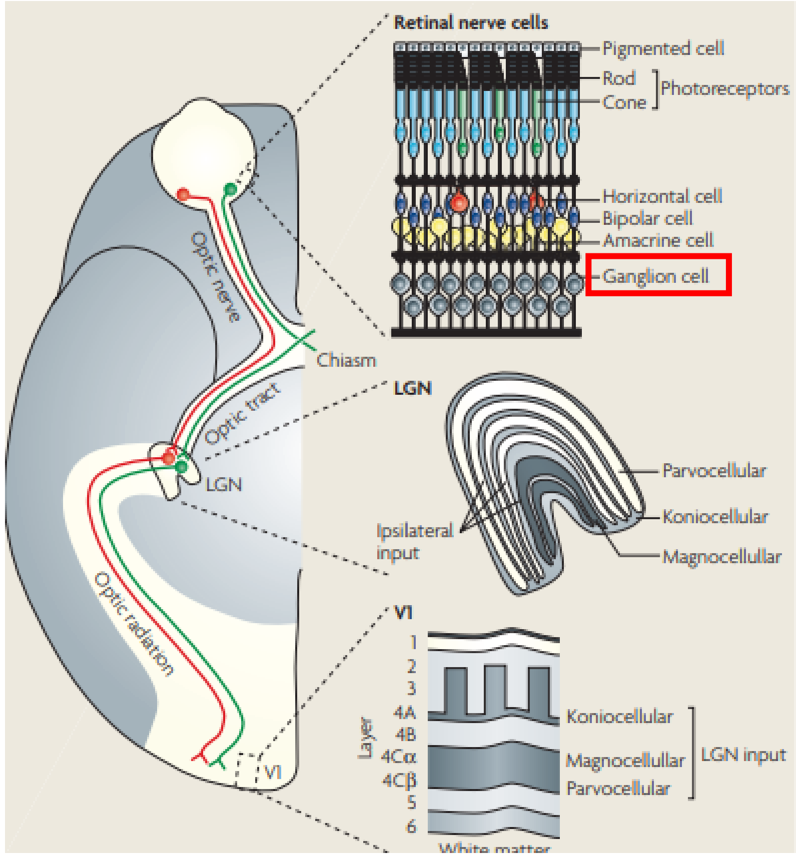


L+M (i.e. luminance)

L-M (i.e. chromatic)

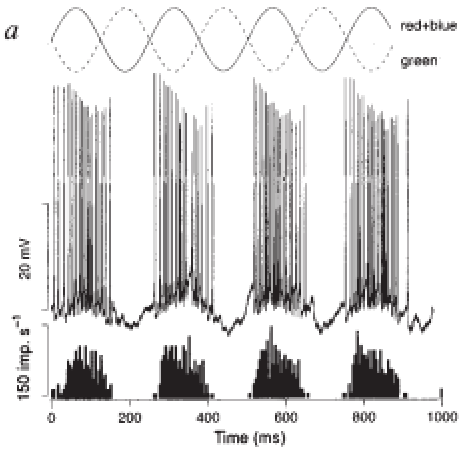
Dacey & Lee (1994)

Receptive field organization in retinal ganglion cells



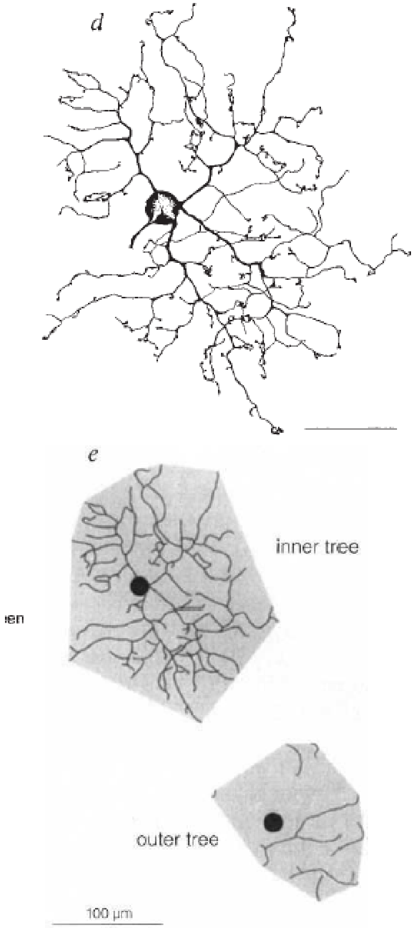
Solomon & Lennie (2007)

Small bistratified RGC

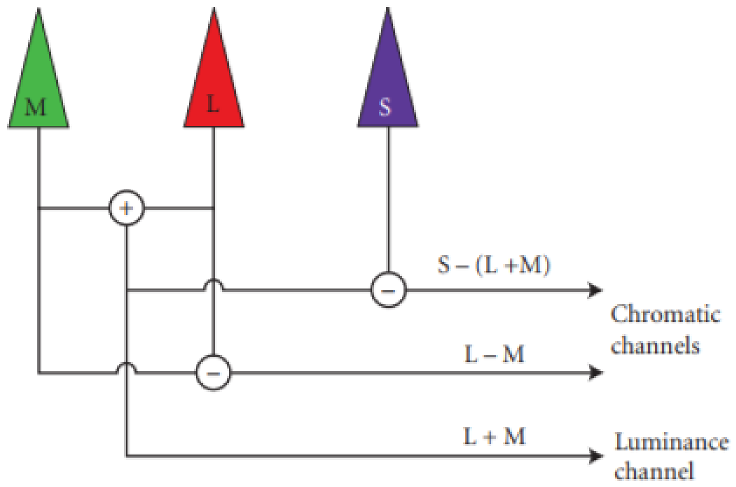


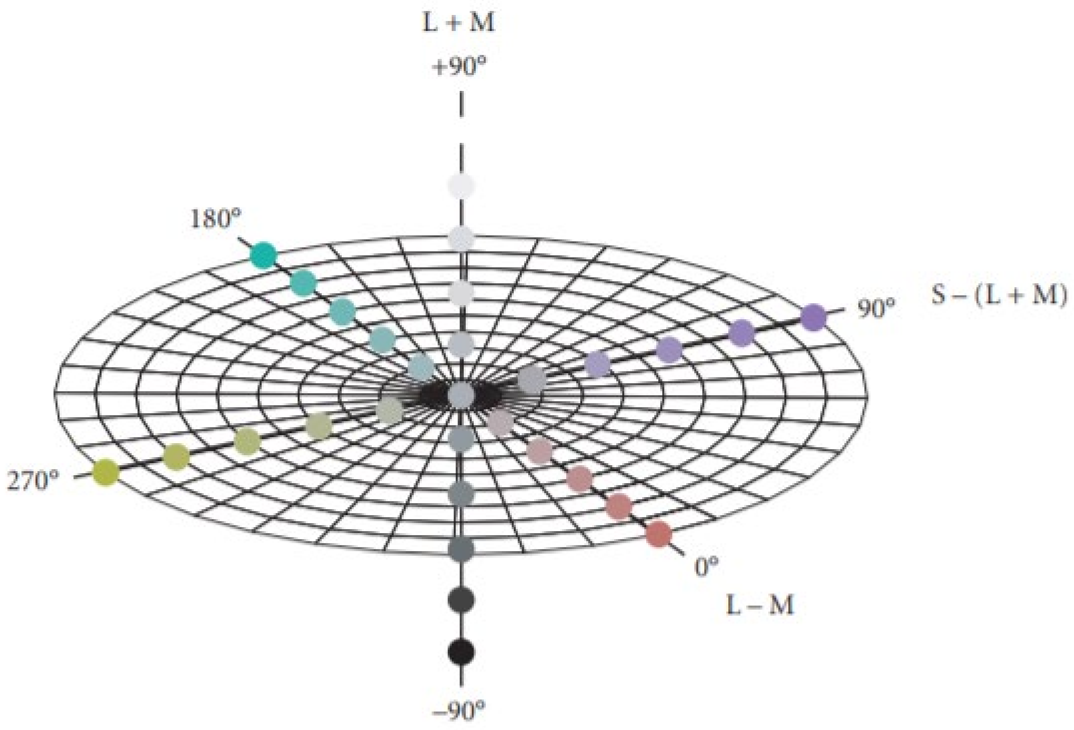
S-(L+M)

Dacey & Lee (1994)



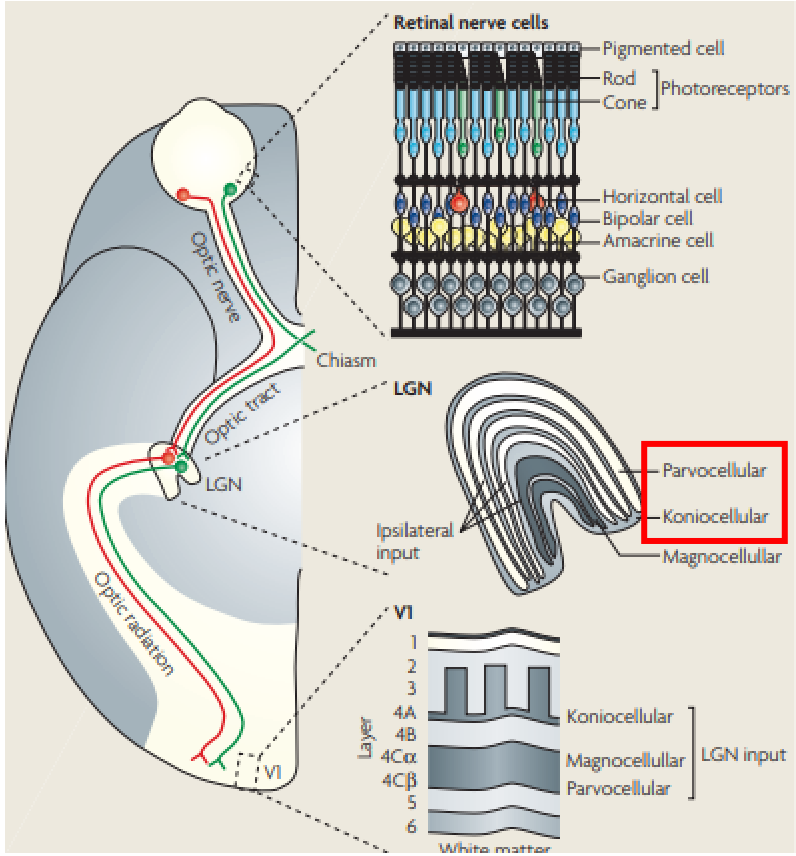
“Cardinal axes” of color space





Derrington, Krauskopf, Lennie (1984)

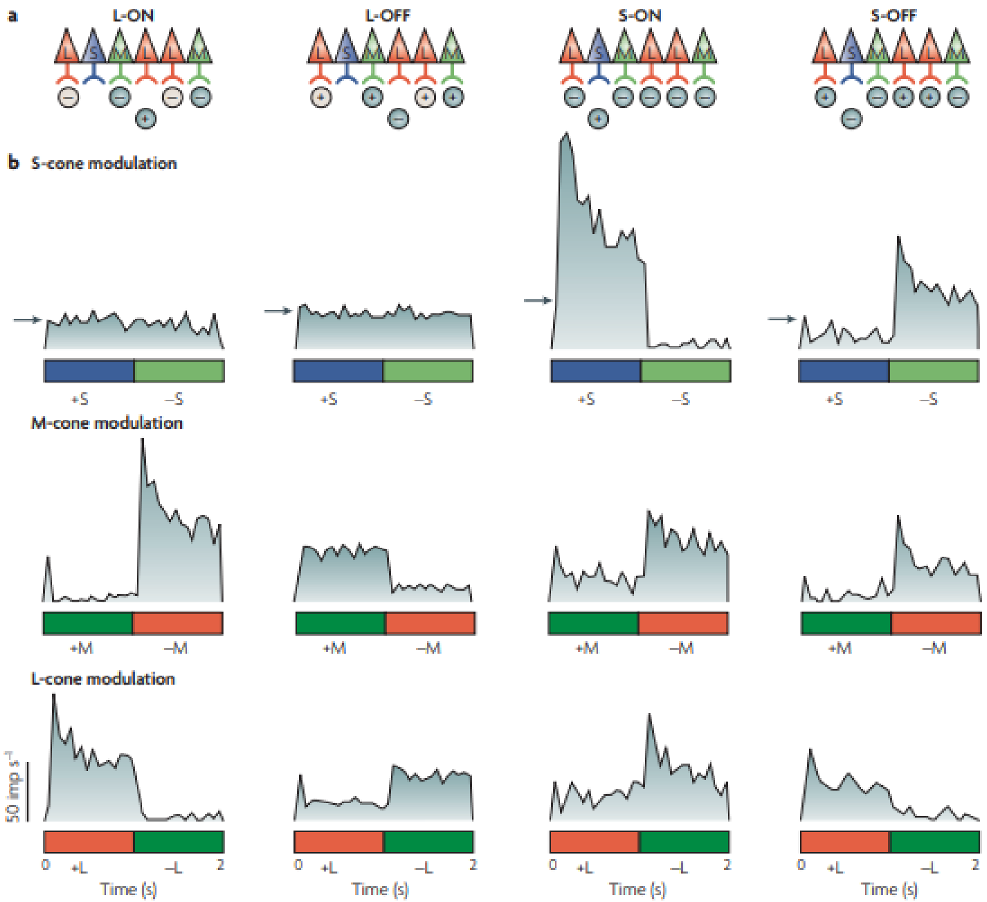
"Cardinal axes" of color space correspond to LGN physiology



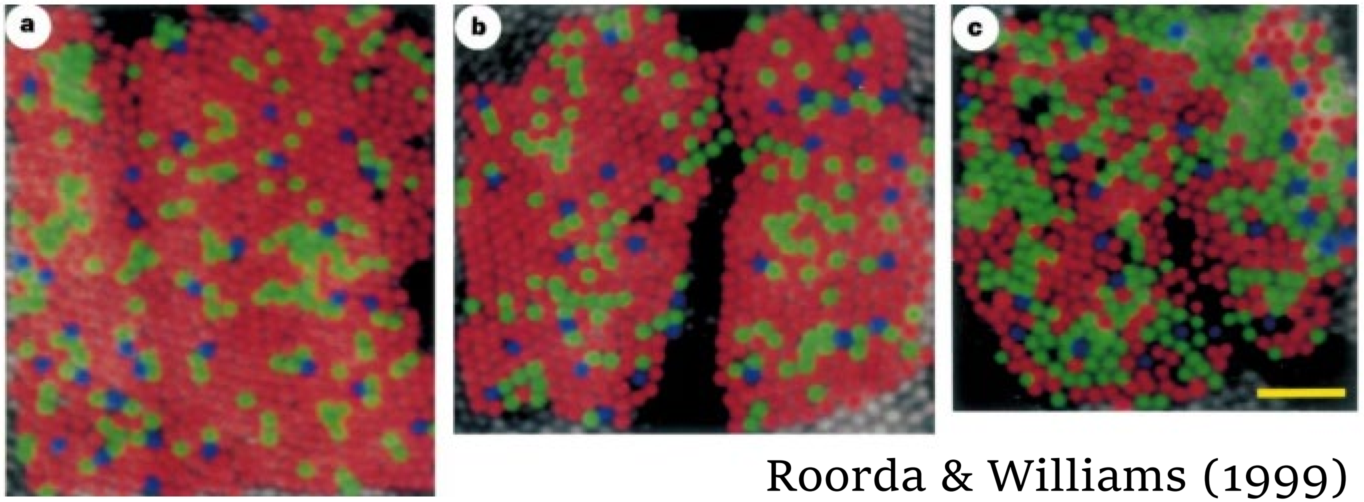
Solomon & Lennie (2007)

Parvo (midget)

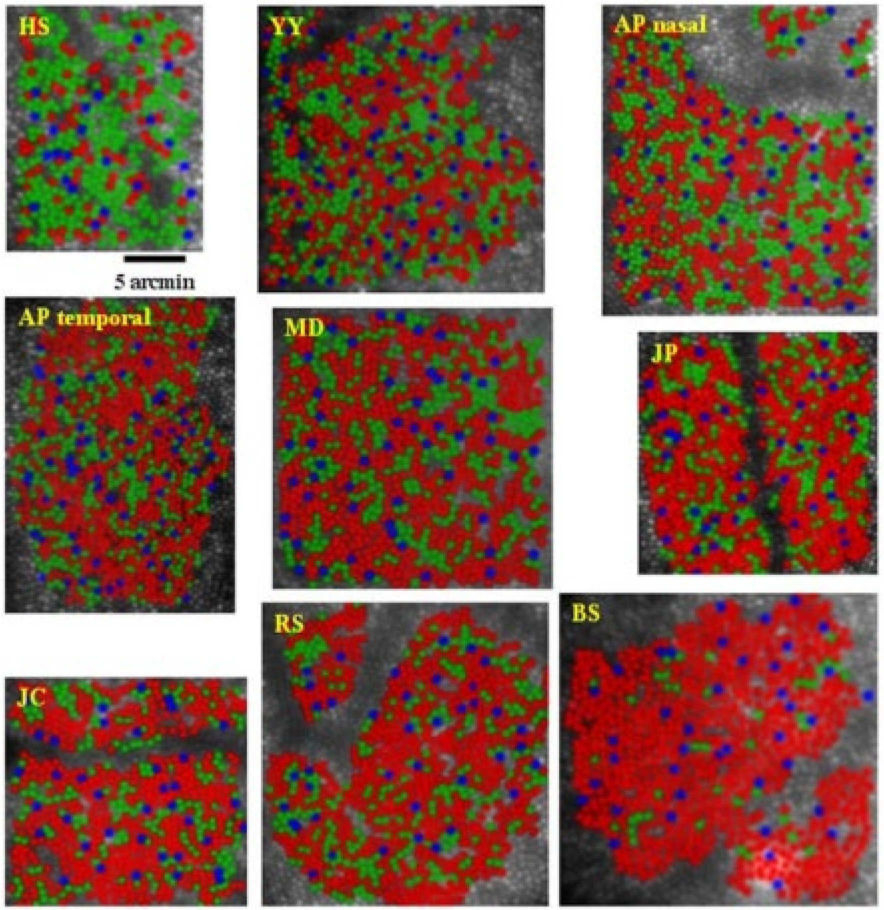
Konio (SBC)



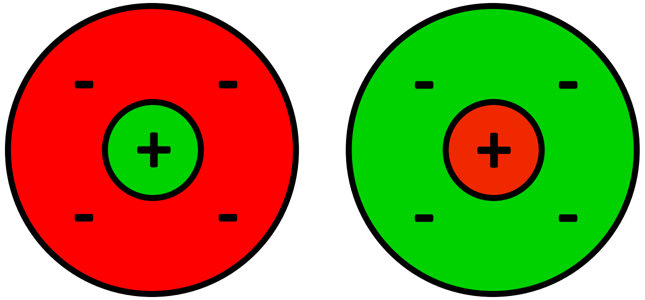
How does LMS topography influence midget RGC opponency?



Roorda & Williams (1999)

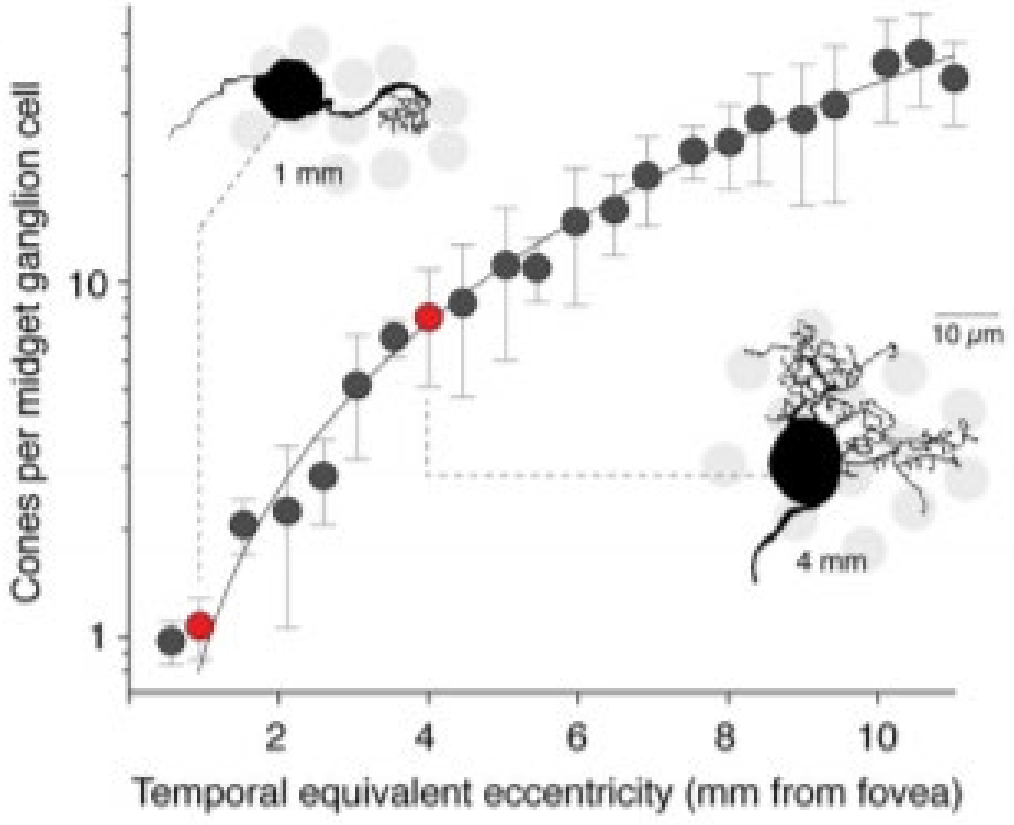


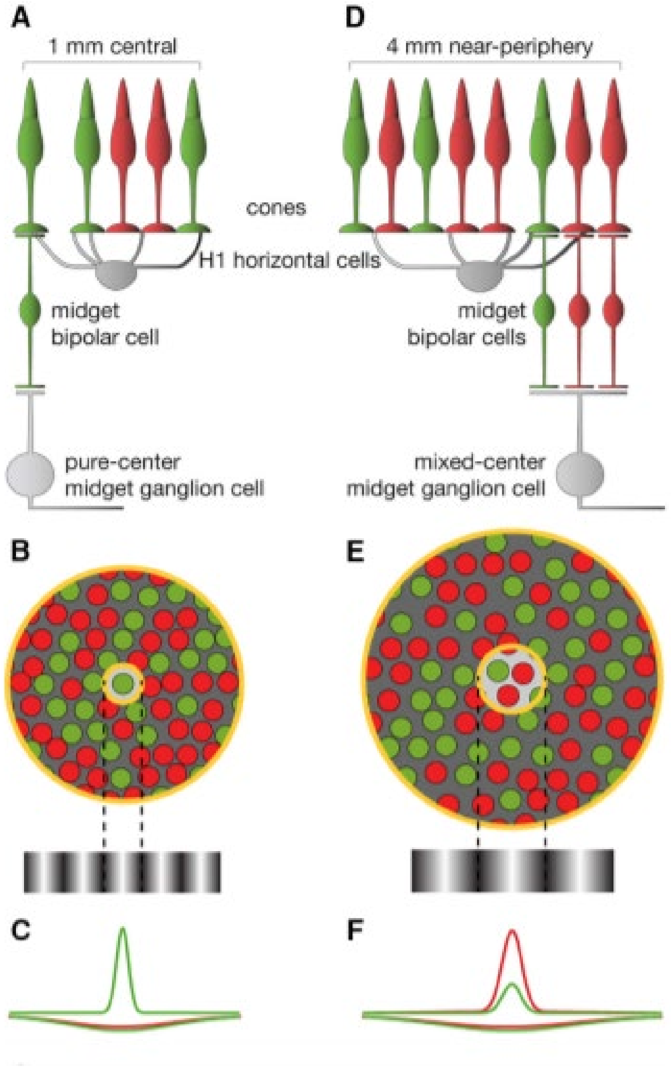
Hofer et al. (2005)



spectral opponency

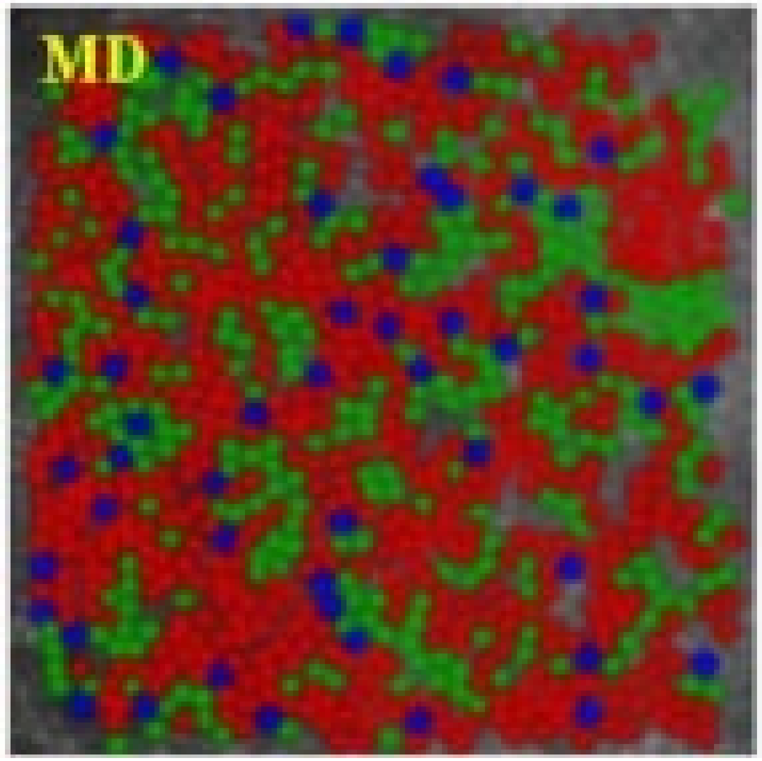
In the periphery, RGCs sample from multiple cones, reducing chromatic opponency on average





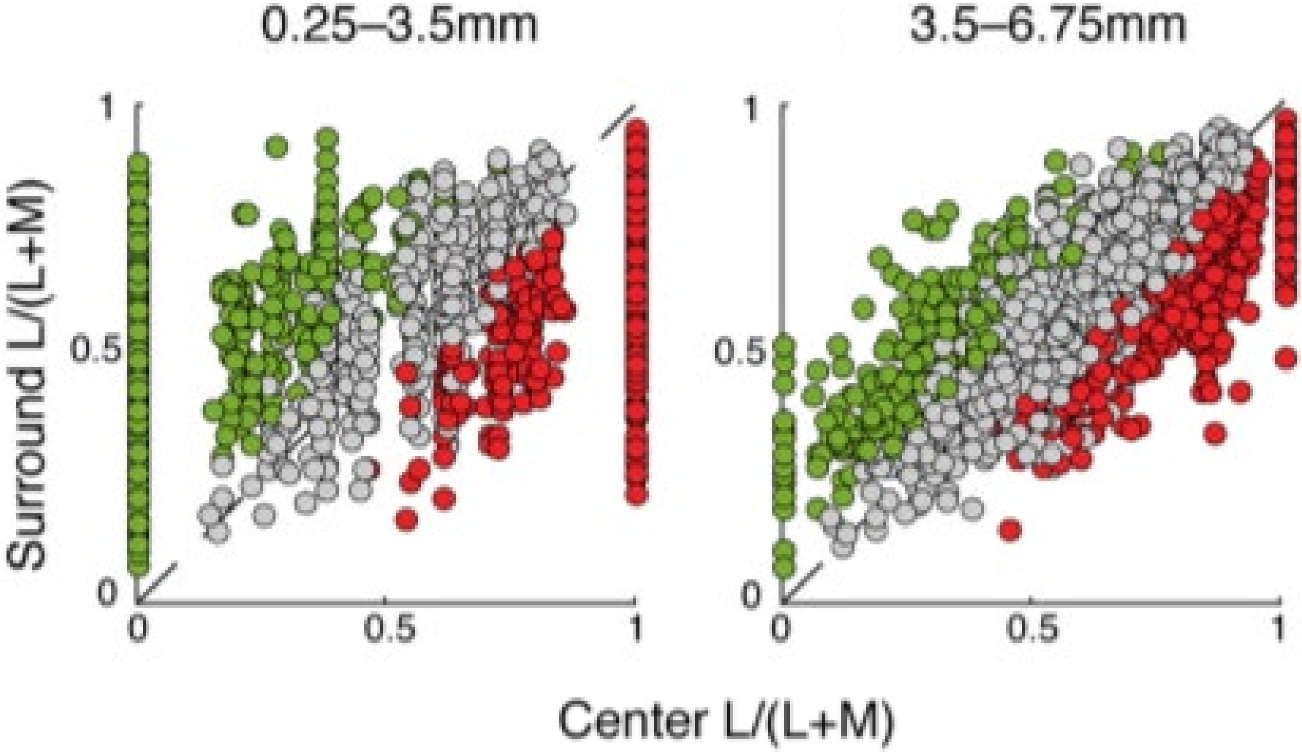
Wool et al (2018)

A random cone mosaic contains clusters of like-type cones, producing a subset of color-opponent midget RGCs, even with indiscriminate sampling



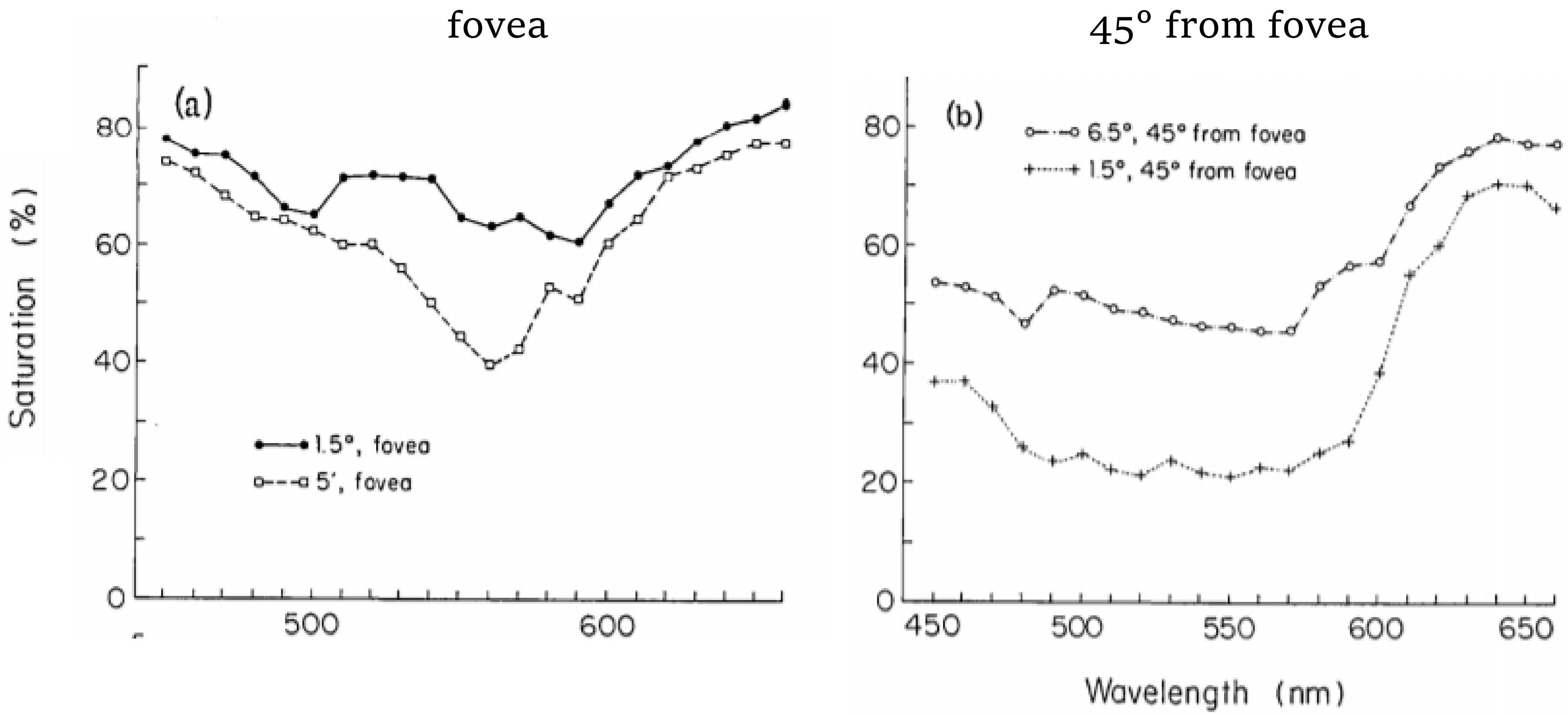
Hofer et al (2005)

Retinal eccentricity



Wool et al (2018)

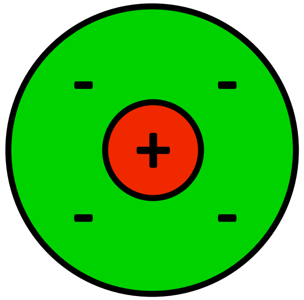
Color vision in the peripheral retina



Gordon & Abramov (1977)

Midget RGCs can signal both luminance and color information

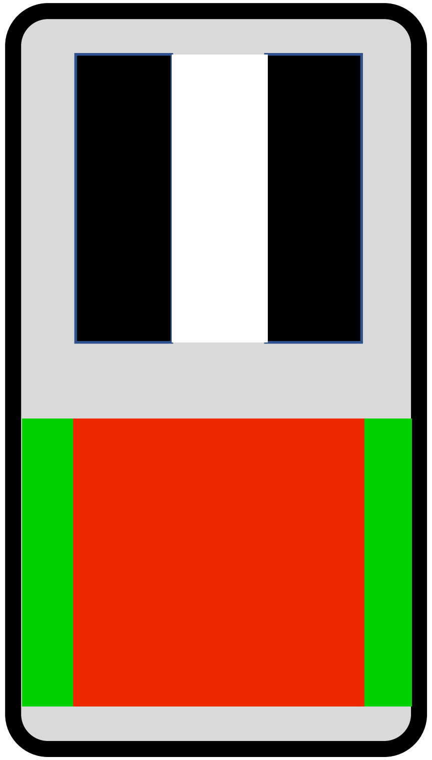
L – M receptive field

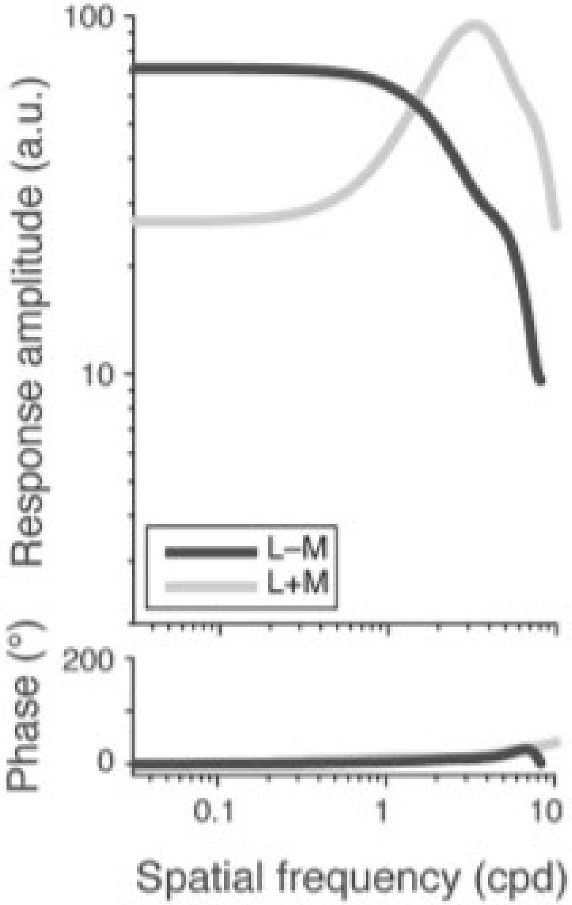


Preferred stimuli:

High-frequency luminance grating (L+M)

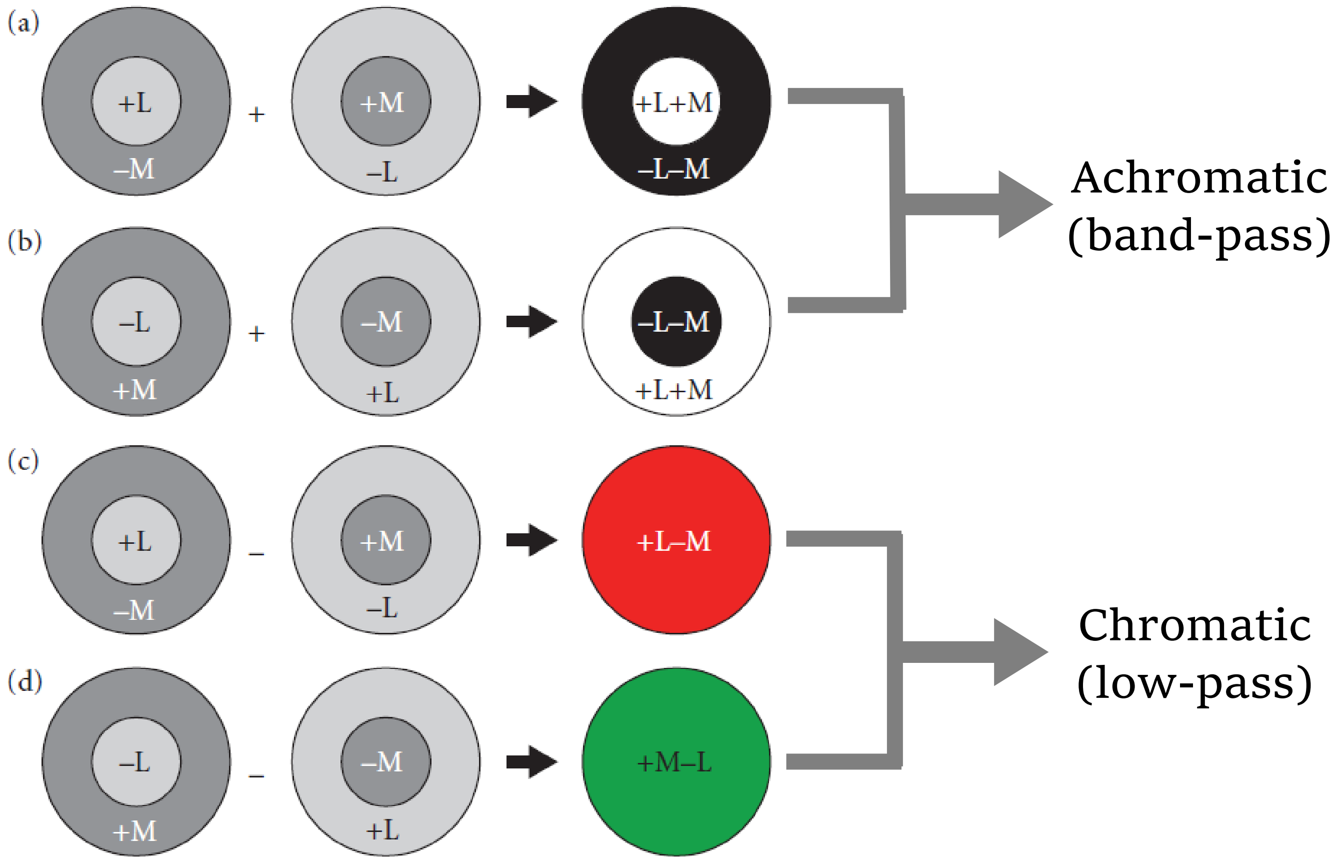
Low-frequency chromatic grating (L-M)





Wool et al (2018)

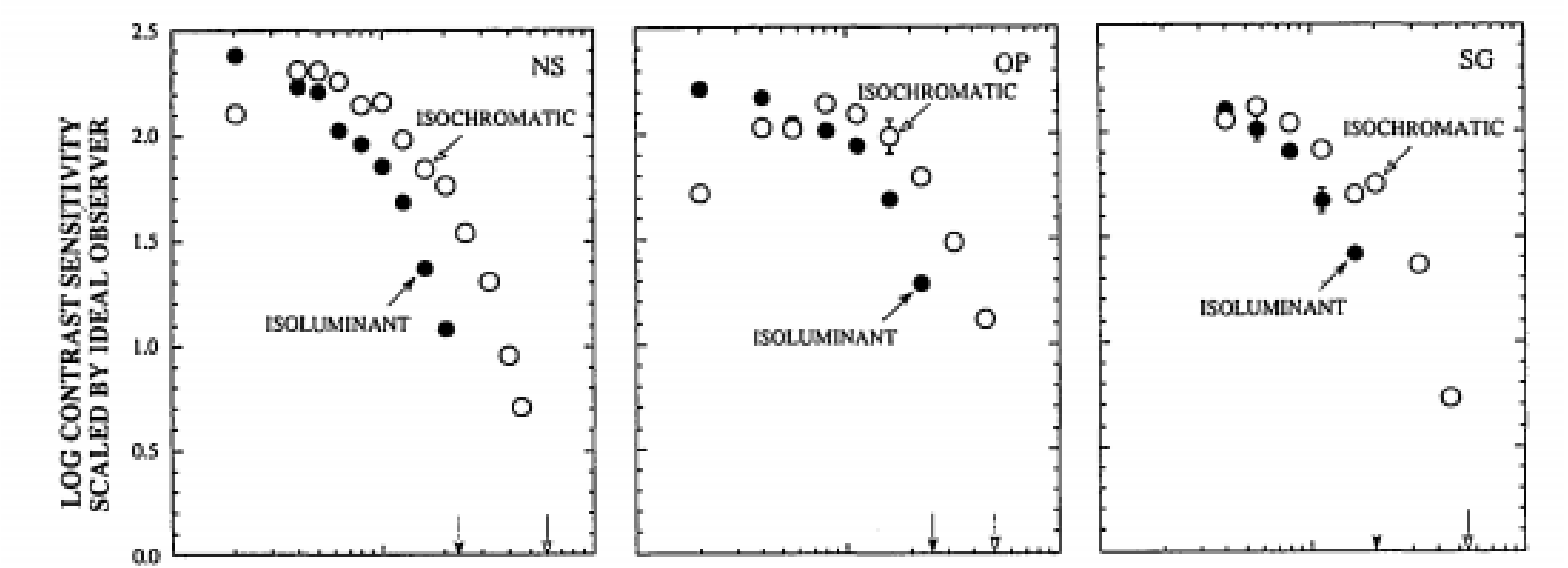
De-multiplexing luminance and color information



Stockman & Brainard (2010)

De-multiplexing luminance and color information

Visual resolution is higher – and more band-pass – for luminance (*isochromatic*) gratings than it is for red-green (*isoluminant*) gratings



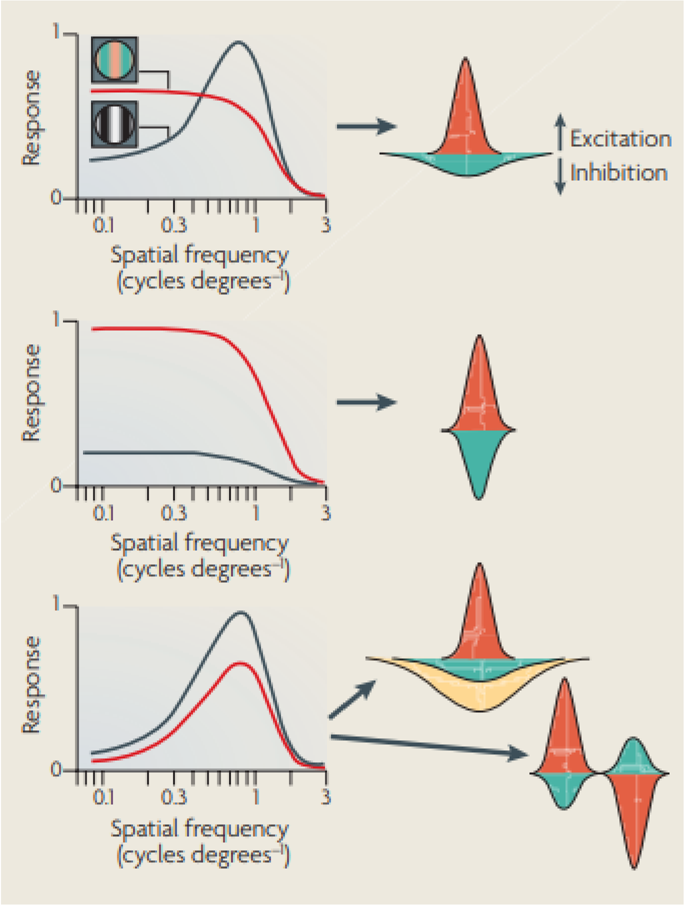
Sekiguchi, Williams, Brainard (1993)

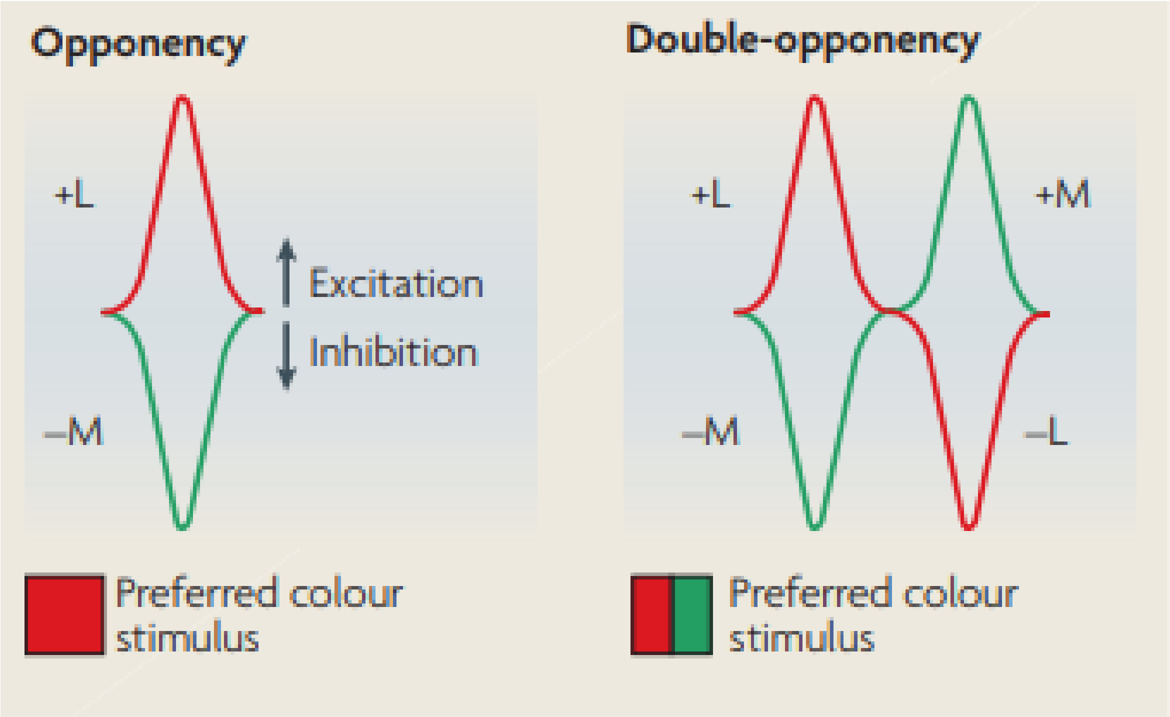
Diverse chromatic receptive field structure in the visual cortex has been observed with single-electrode recordings

excited by color & luminance

excited by color only

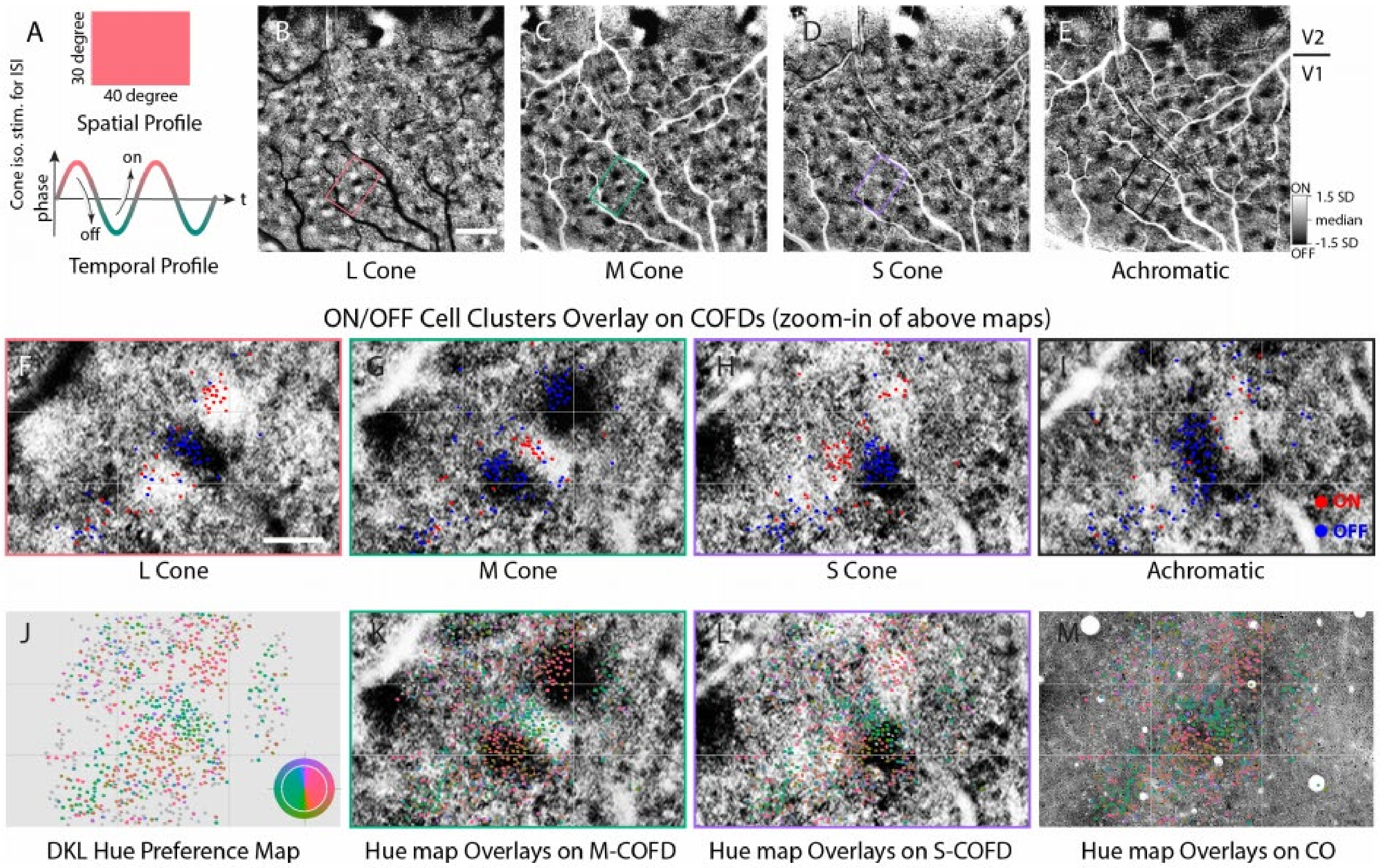
excited by chromatic & luminance edges



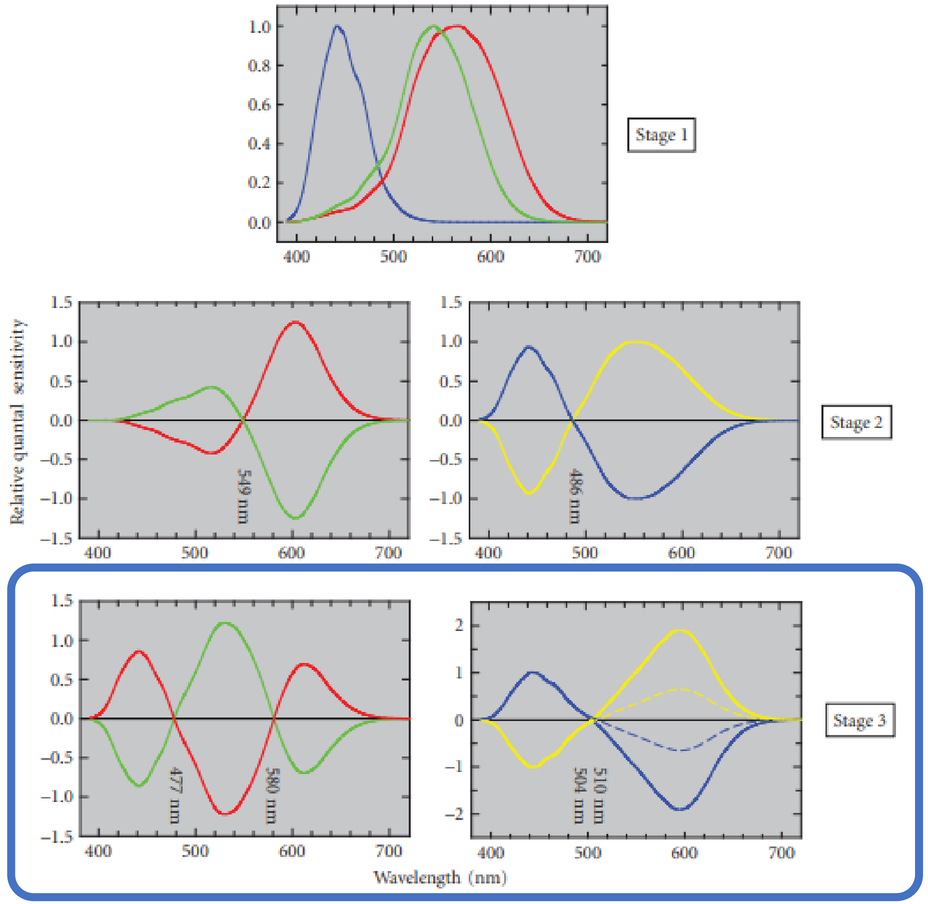


Solomon & Lennie (2007)

Two-photon imaging of population activity in V1 reveals how LGN opponency is transformed to align with color perception

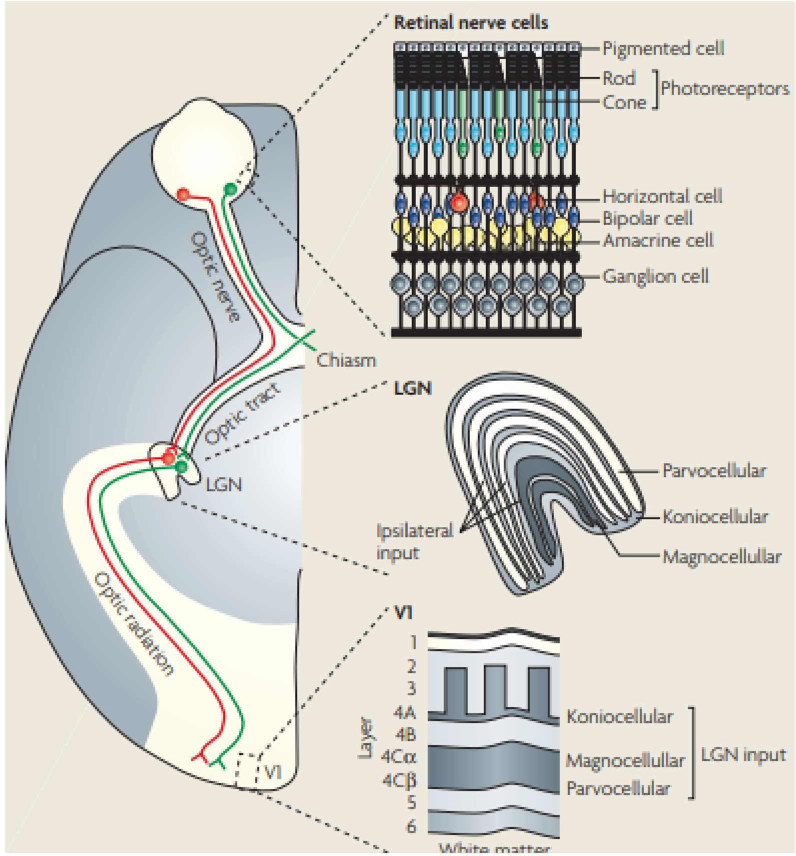


Li et al. (2020)

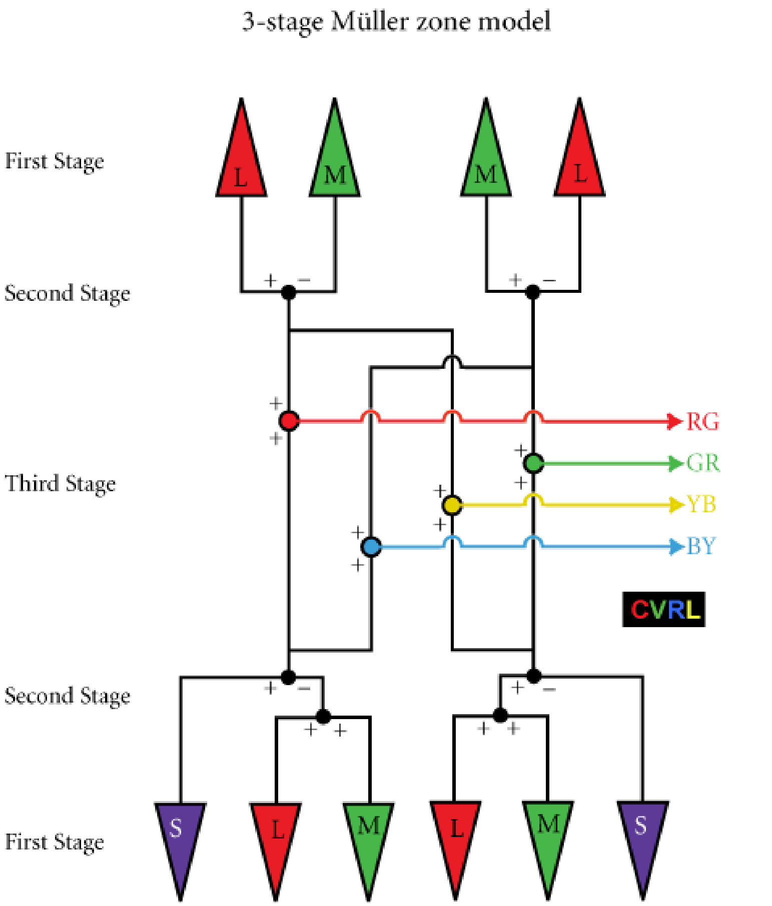


Stockman & Brainard (2010)

Summary

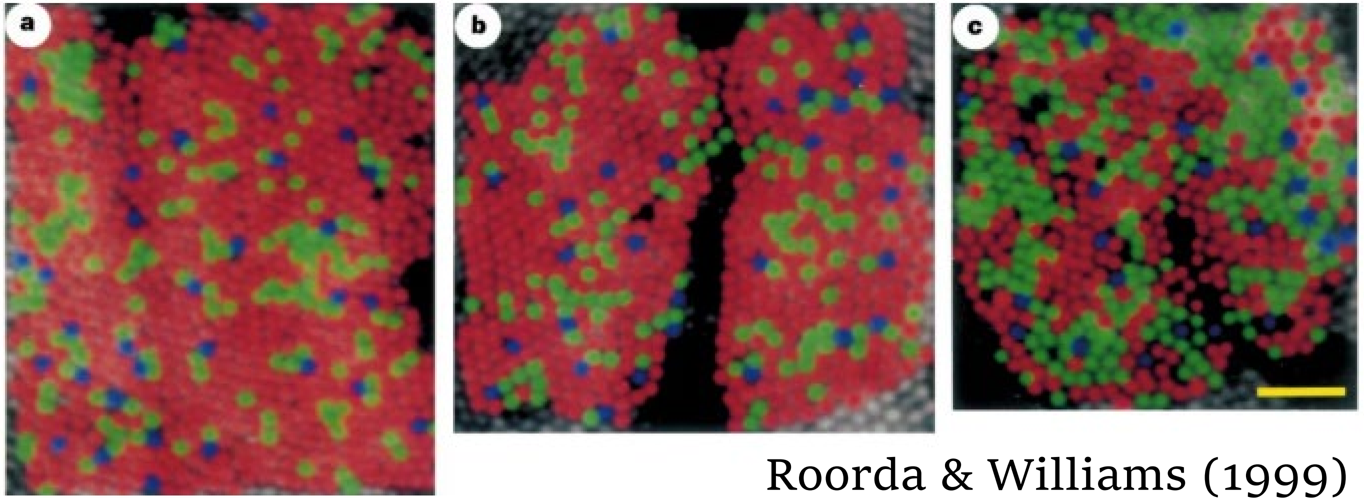


Solomon & Lennie (2007)



Stockman & Brainard (2010)

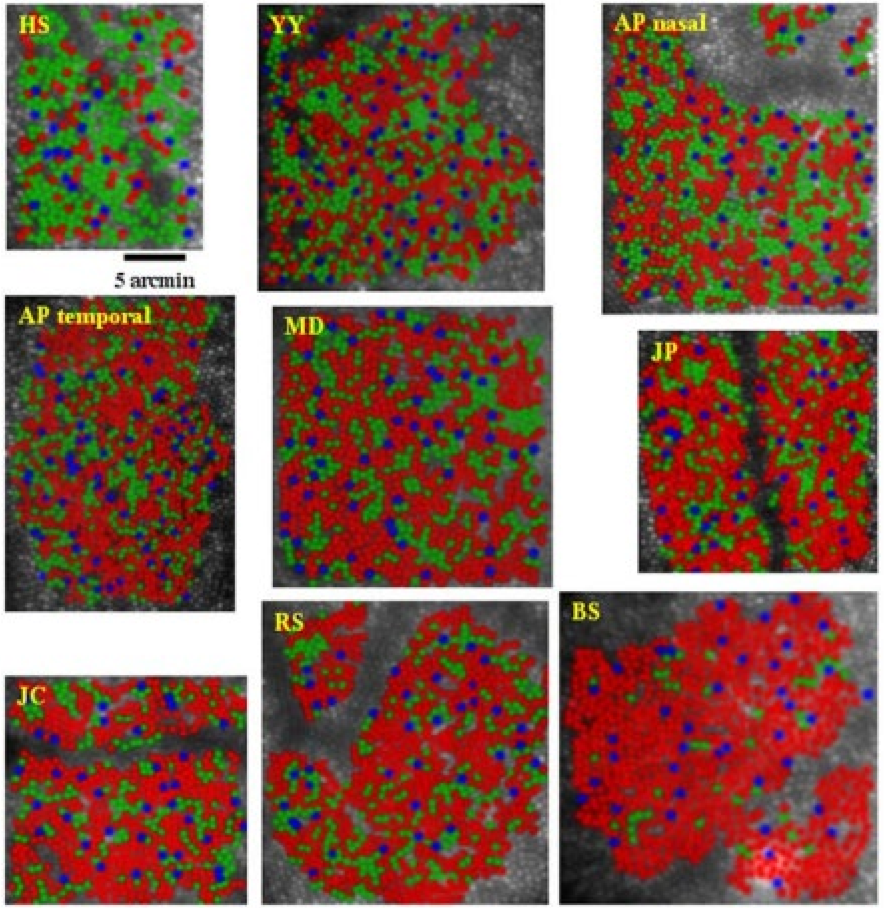
Spectral topography of cones in the human retina



Roorda & Williams (1999)

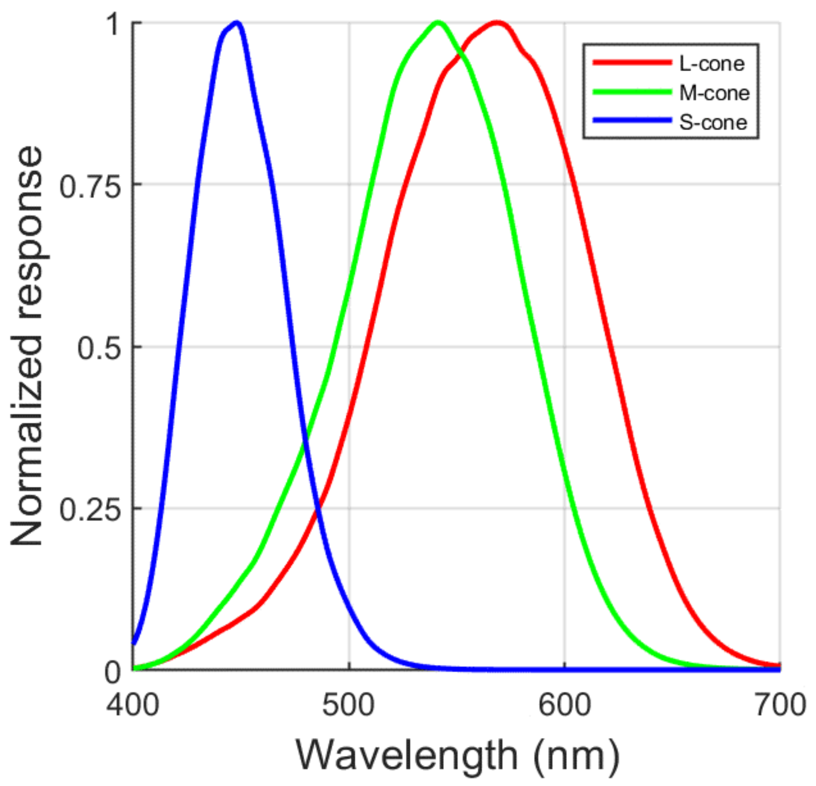
1. How does the topography of the cone mosaic govern the color appearance of cone-sized spots?

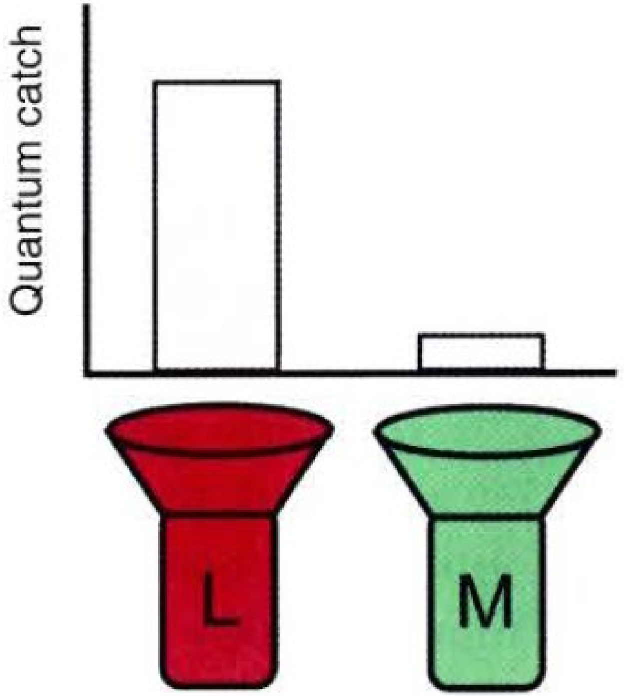
2. How can individuals with widely disparate L:M cone ratios have relatively normal red-green color perception?



Hofer et al. (2005)

At the cellular level, spatio-chromatic signals are ambiguous

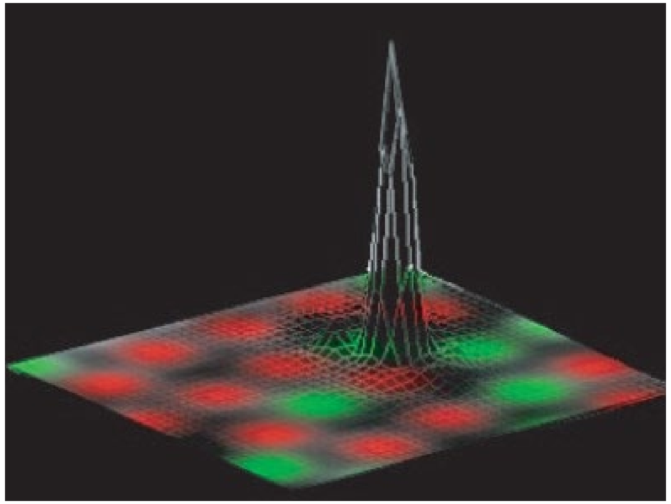


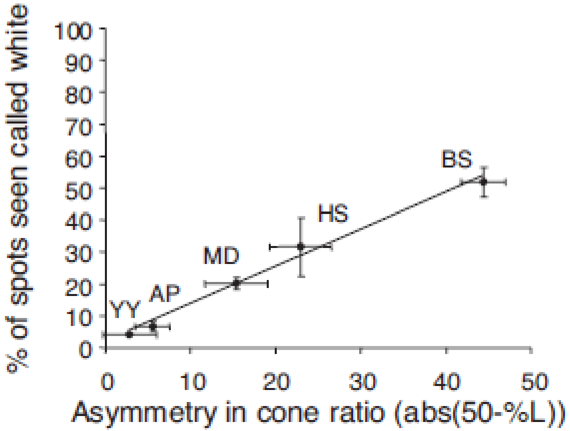


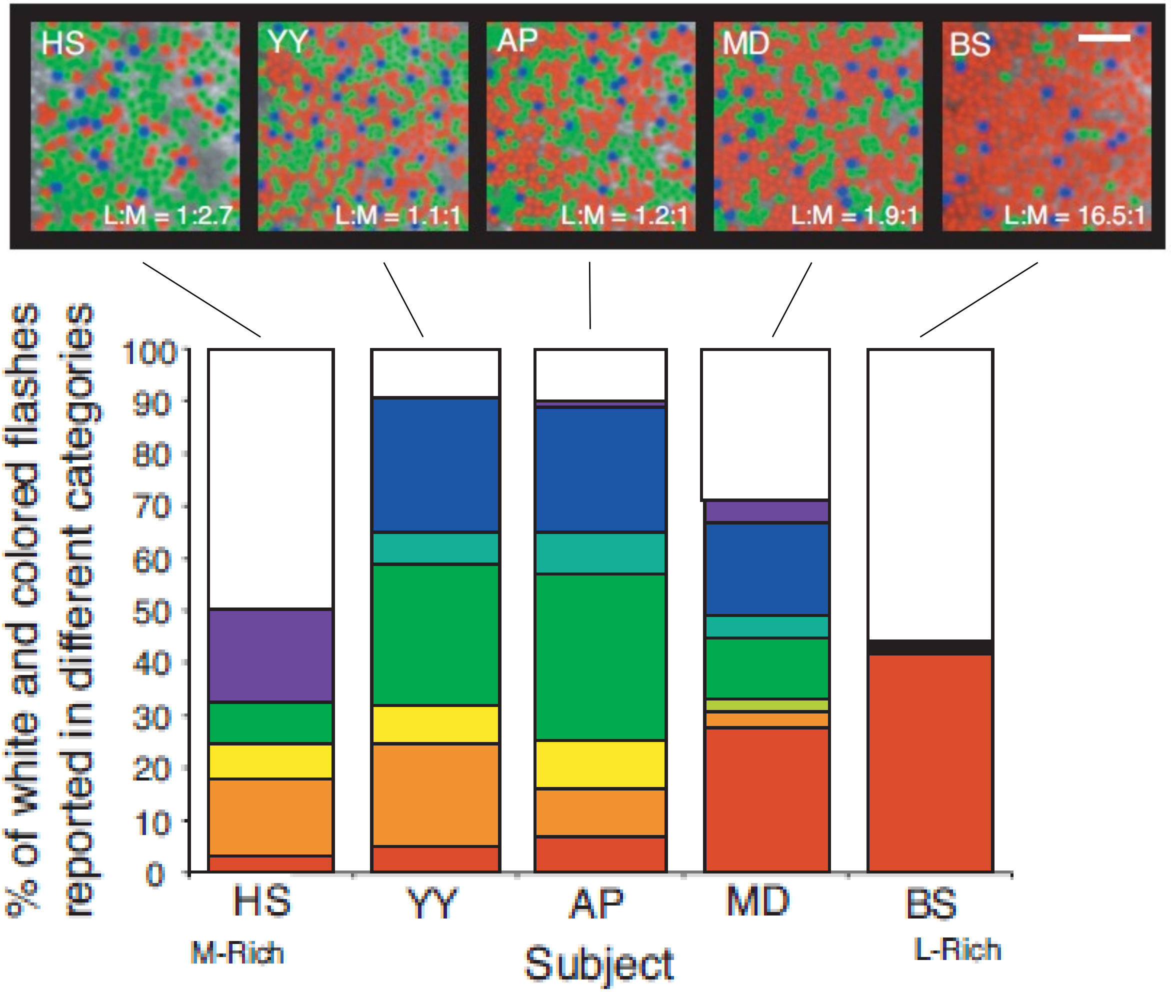
Hofer & Williams (2014)

Color appearance of cone-sized stimuli (Hofer et al, 2005)

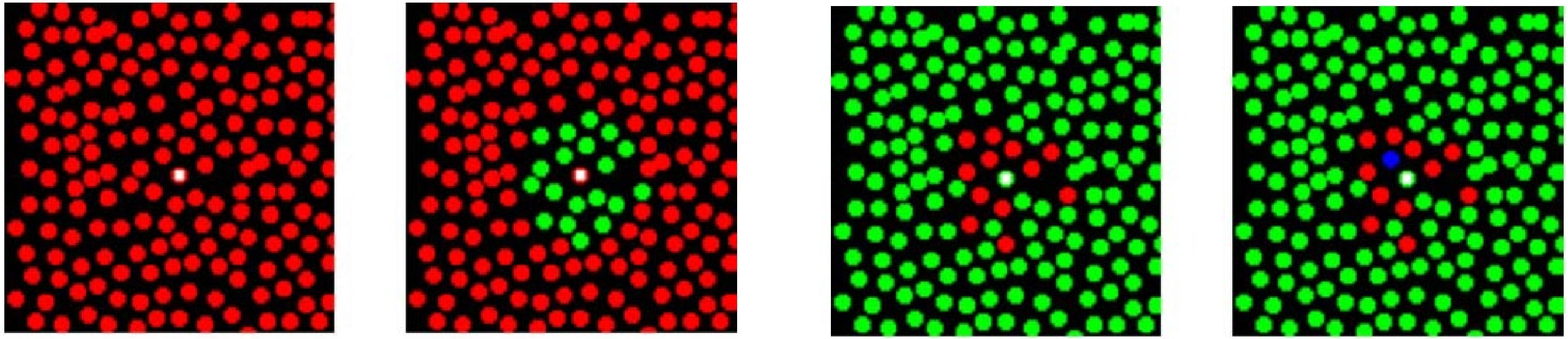
λ = 550 nm; black background





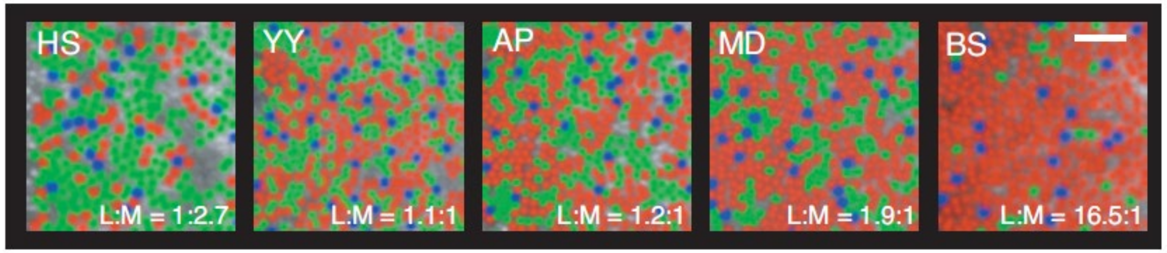


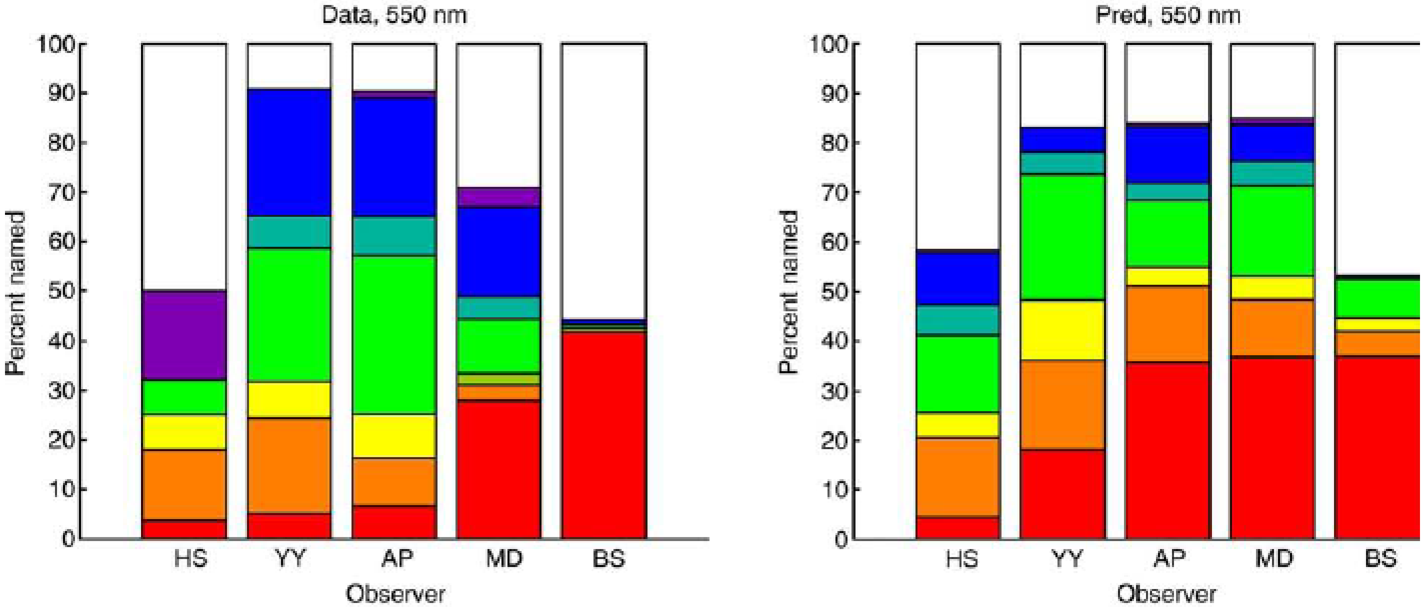
A Bayesian model of trichromatic reconstruction



Brainard, Williams, Hofer (2008)

A Bayesian model of trichromatic reconstruction

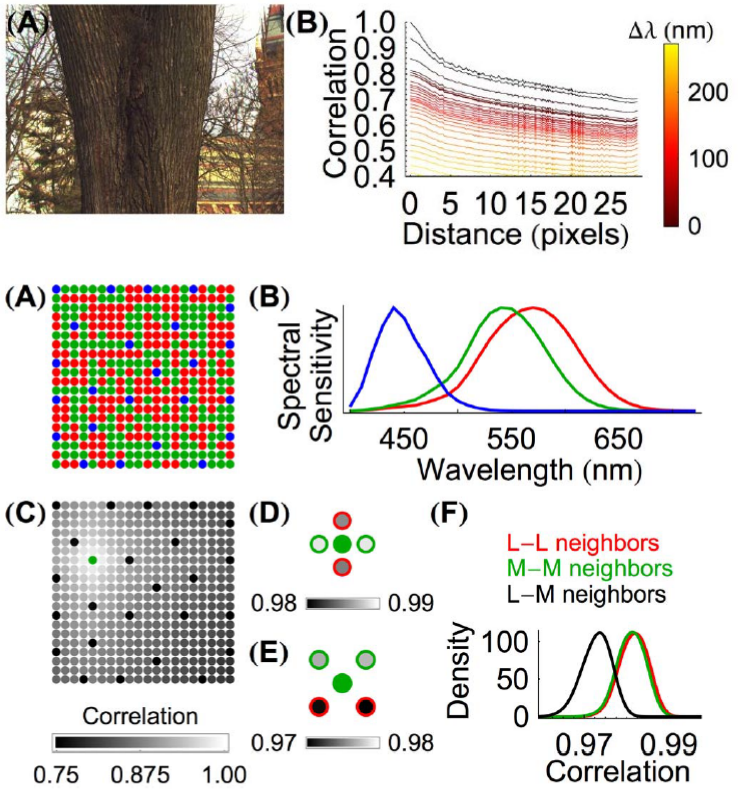




Brainard, Williams, Hofer (2008)

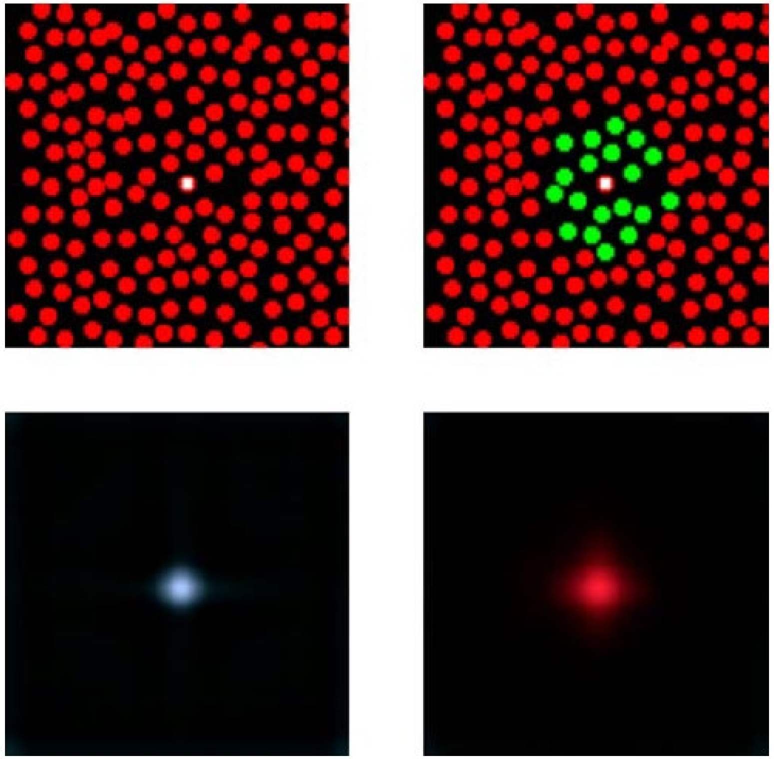
Predictions from Brainard et al. (2008)

1. Single-cone color responses should be consistent and cone-type-specific (i.e. the brain can learn the spectral topography of the cone mosaic)

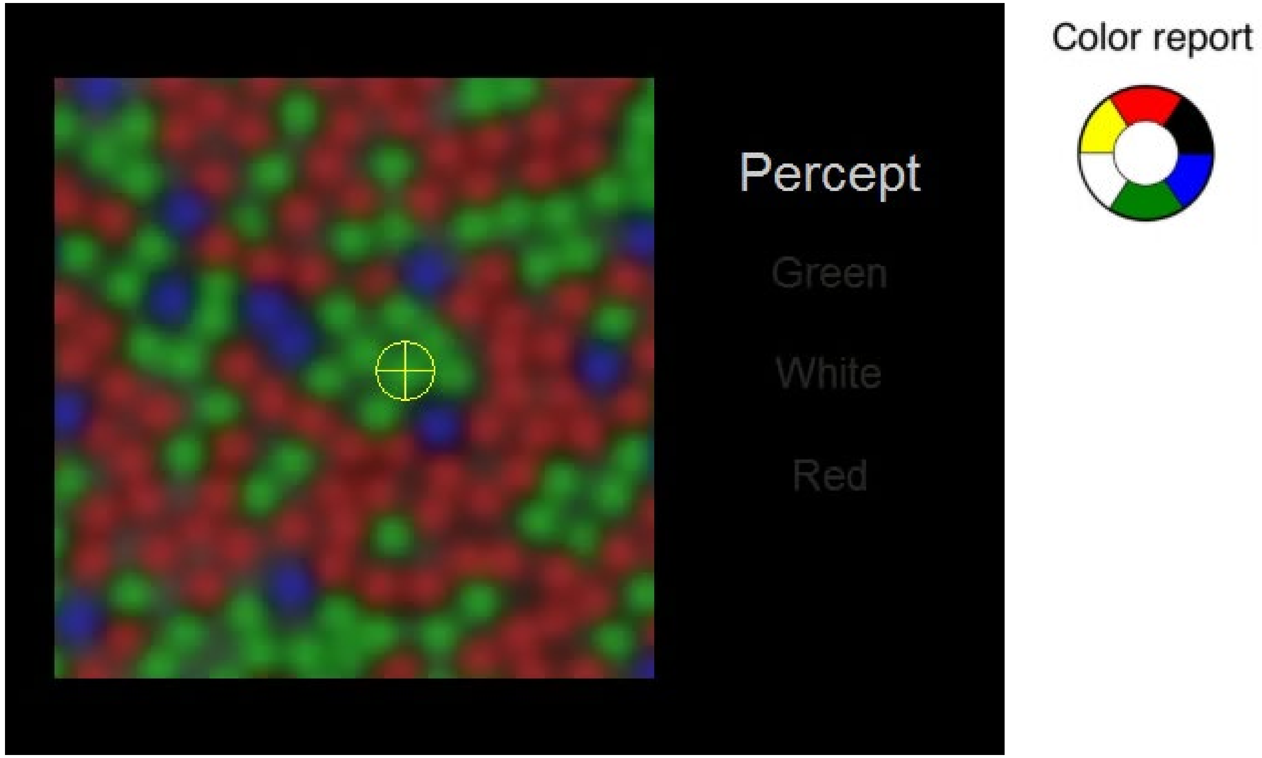


Benson et al. (2014)

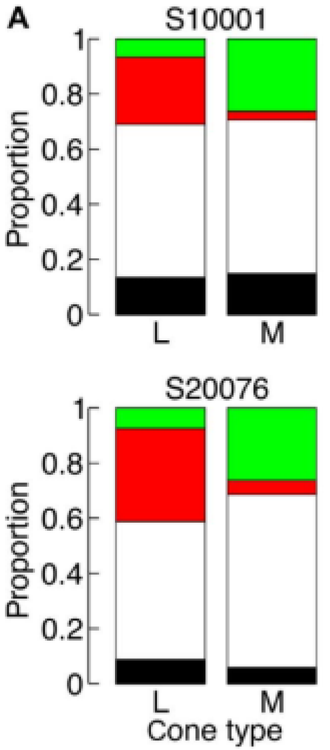
2. Chromatic sensations are more likely to arise from receptors in cone-opponent neighborhoods



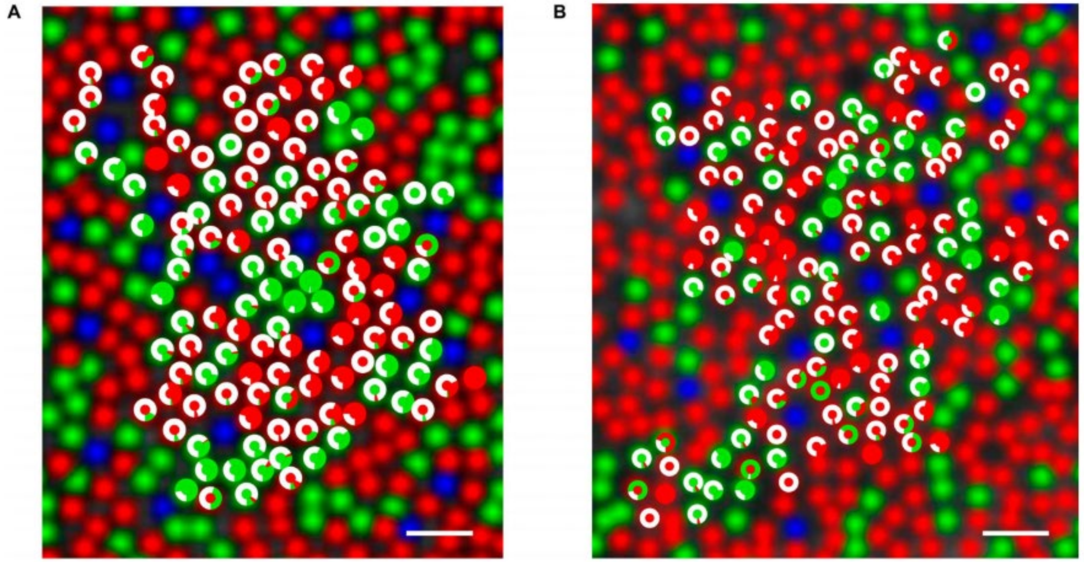
Sabesan et al. (2016)

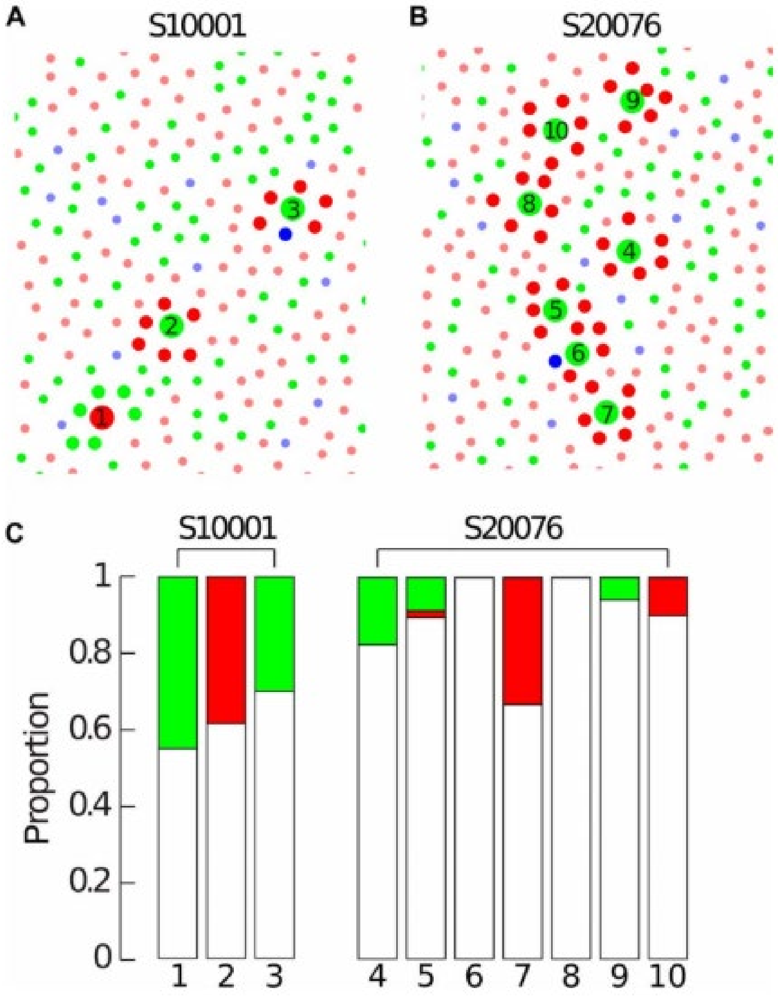


Sabesan et al. (2016)



S10001
S20076





Predictions from Brainard et al. (2008)

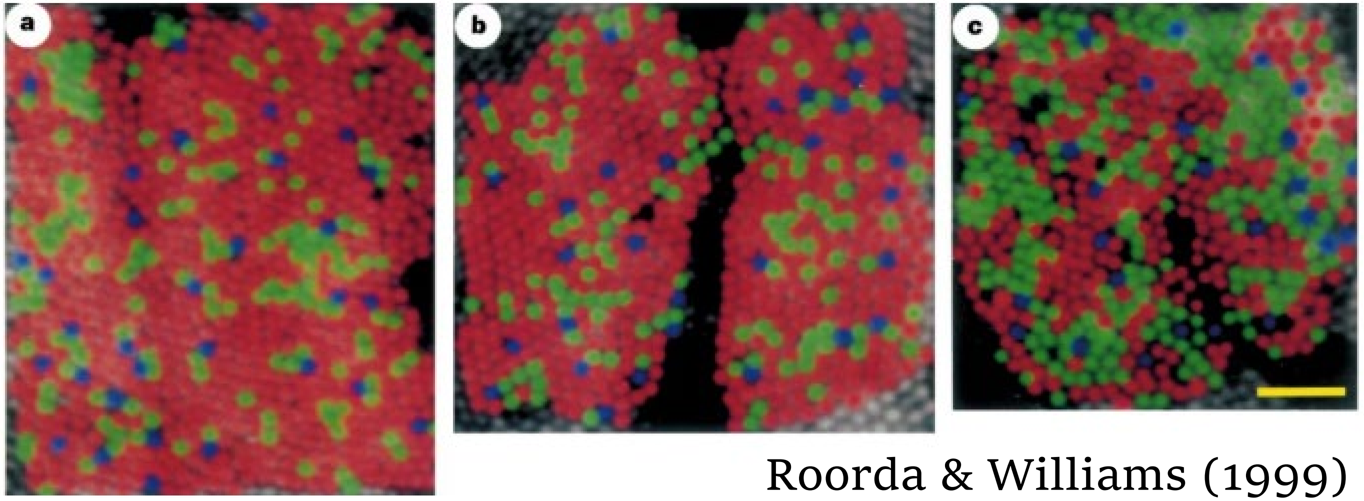
1. Single-cone color responses should be consistent and cone-type-specific (i.e. the brain can learn the spectral topography of the cone mosaic)

YES

2. Chromatic sensations are more likely to arise from receptors in cone-opponent neighborhoods

NO

Spectral topography of cones in the human retina



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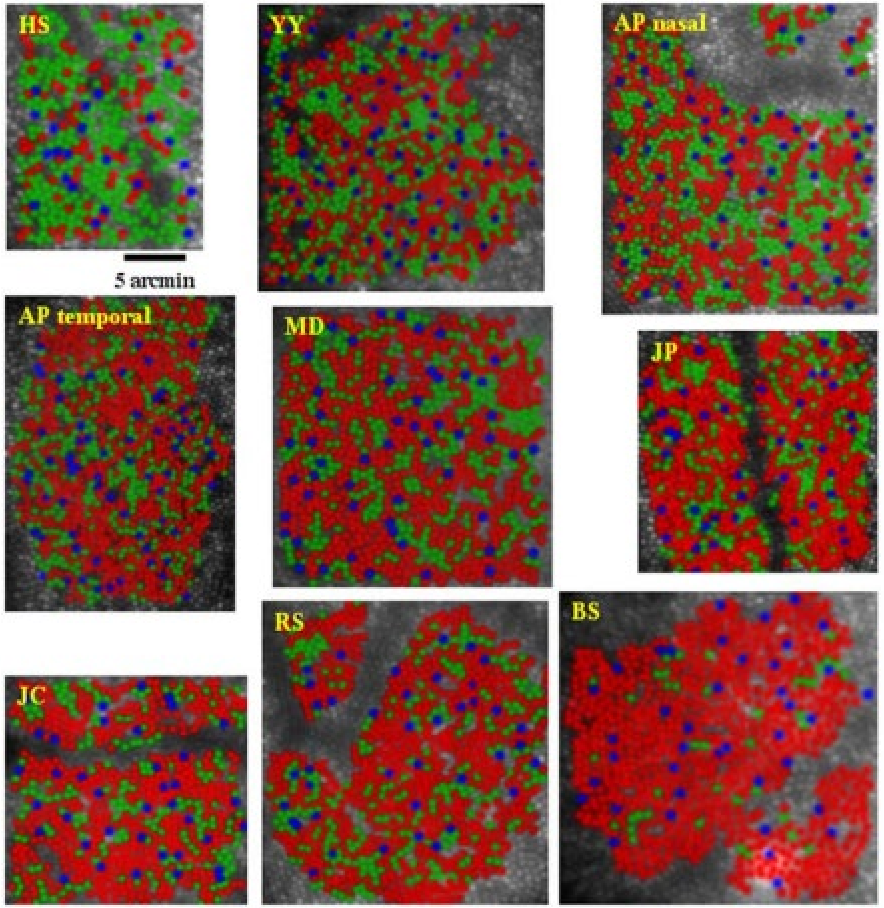
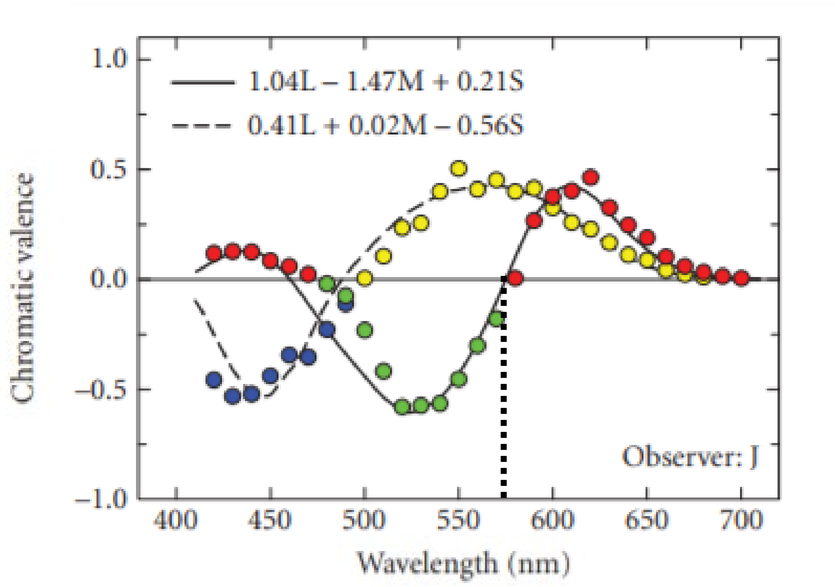
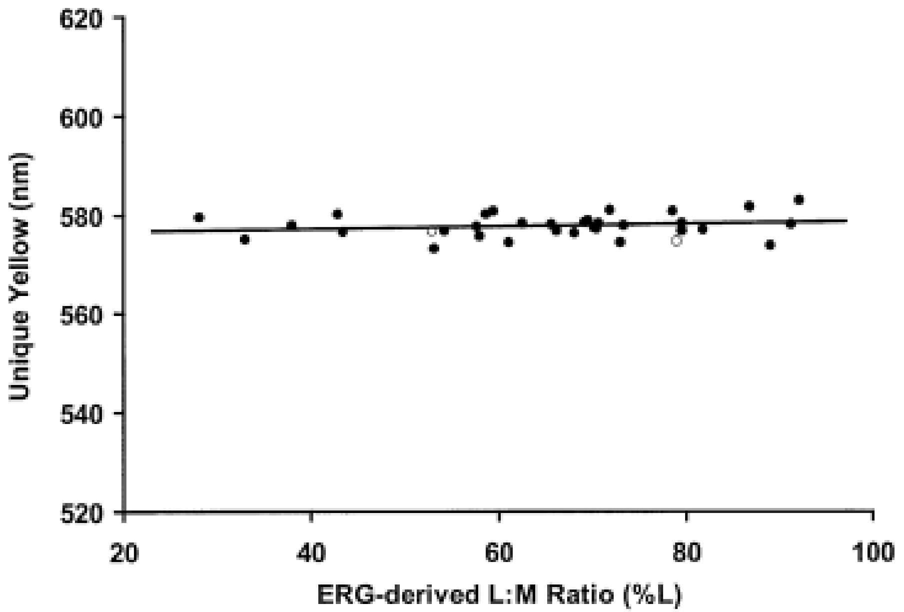


Hofer et al. (2005)

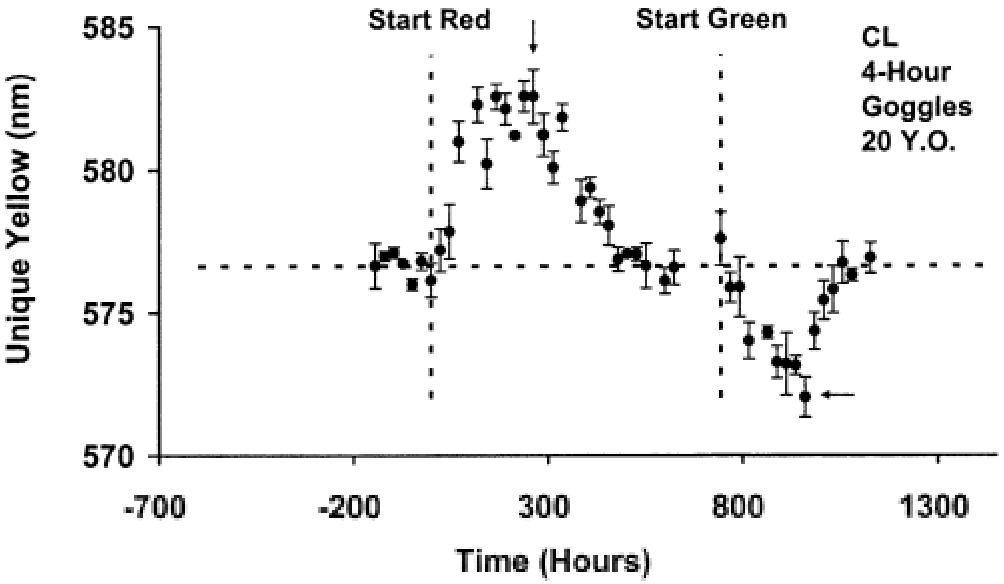
Unique yellow is the neutral point of the red-green opponent system



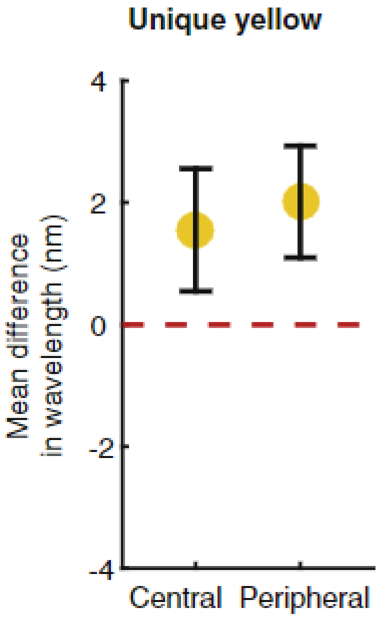


Neitz et al. (2002)

Unique yellow is shaped by the spectral characteristics of the environment

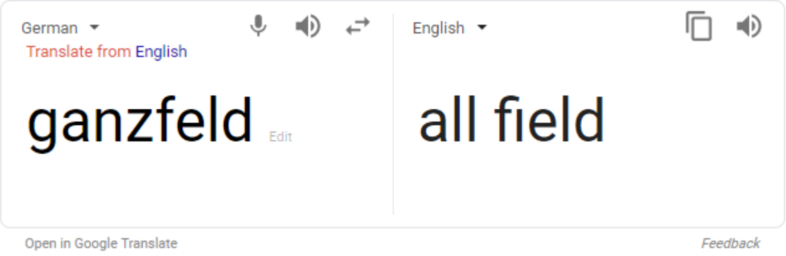


Neitz et al. (2002)



Welbourne et al. (2015)

Spatial factors in color appearance



ganzfeld.co.uk

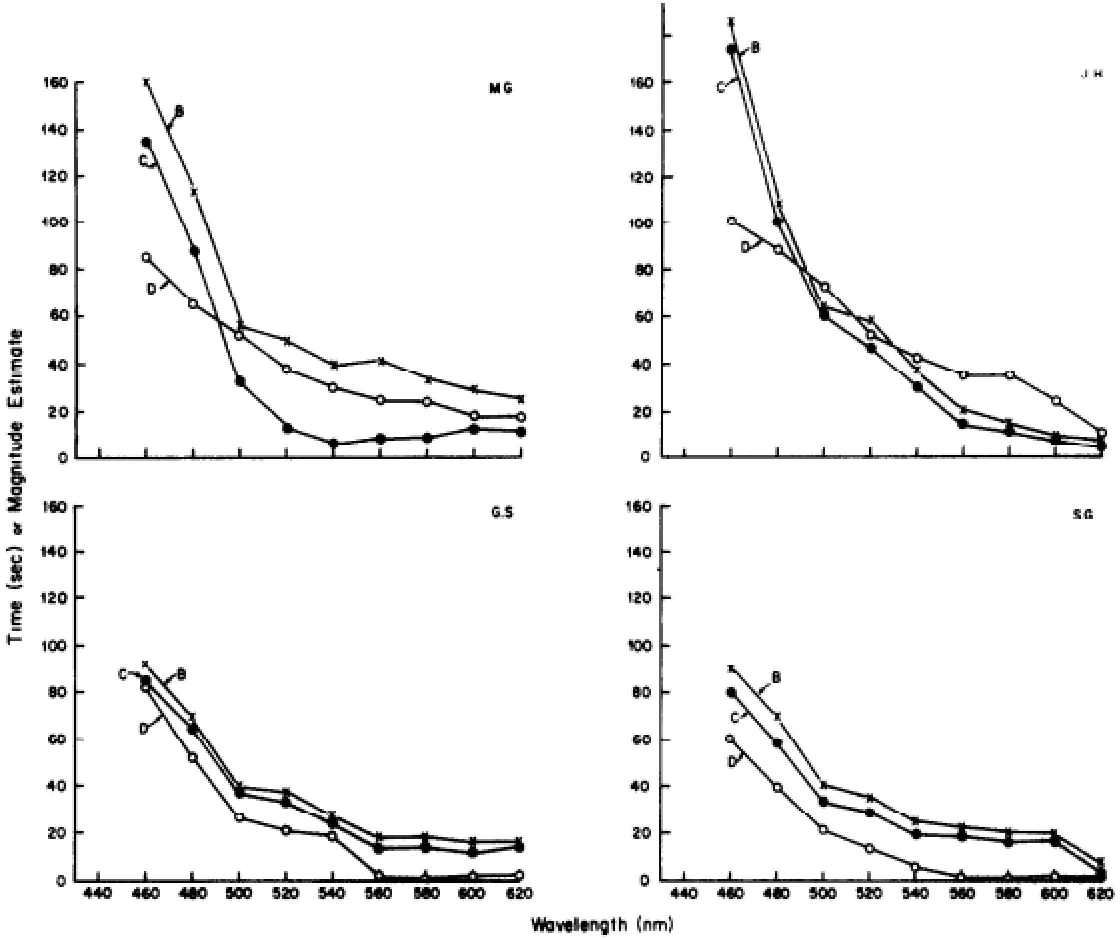


Fig. 2. Times to color desaturation (C) and brightness fade-out (B), and estimate of additional darkness (D) as a function of wavelength for equal luminance (26 cd/m²) stimuli, for 4 subjects.

Gur (1989)

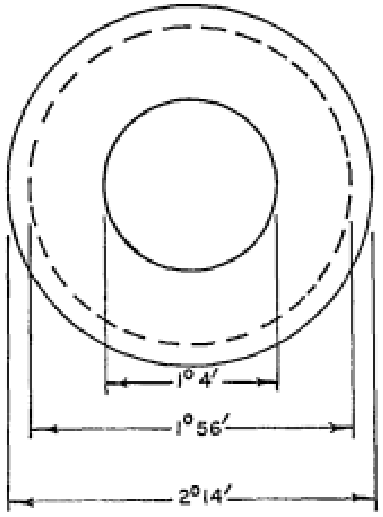
Spatial factors in color appearance – stabilized boundaries

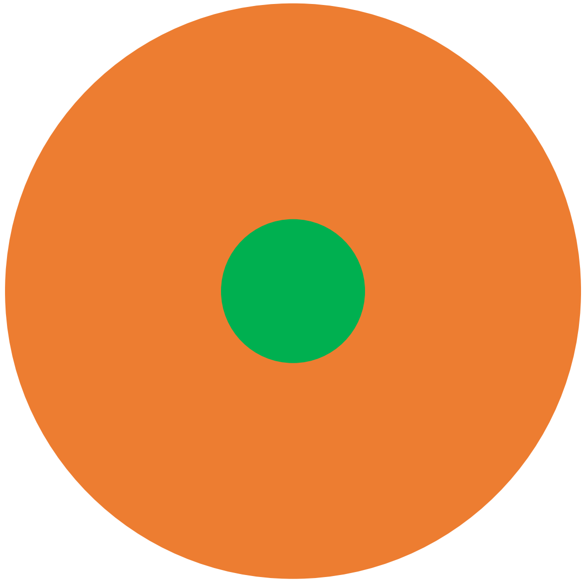
JOURNAL OF THE OPTICAL SOCIETY OF AMERICA VOLUME 53, NUMBER 6 JUNE 1963

Effect of Retinal Image Stabilization on the Appearance of Heterochromatic Targets*

JOHN KRAUSKOPF
Walter Reed Army Institute of Research,† Washington 12, D. C.
and
University of Maryland, College Park, Maryland

(Received 13 November 1962)



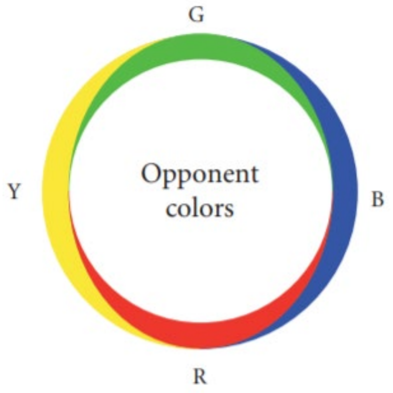


equality. It was found that the central disk disappeared intermittently. When this occurred, the whole target, disk and annulus, appeared homogeneous in color, the color being that of the annulus.

Spatial factors in color appearance – stabilized boundaries

On Seeing Reddish Green and Yellowish Blue

HEWITT D. CRANE
THOMAS P. PIANTANIDA
Visual Sciences Program,
SRI International, Menlo Park,
California 94025



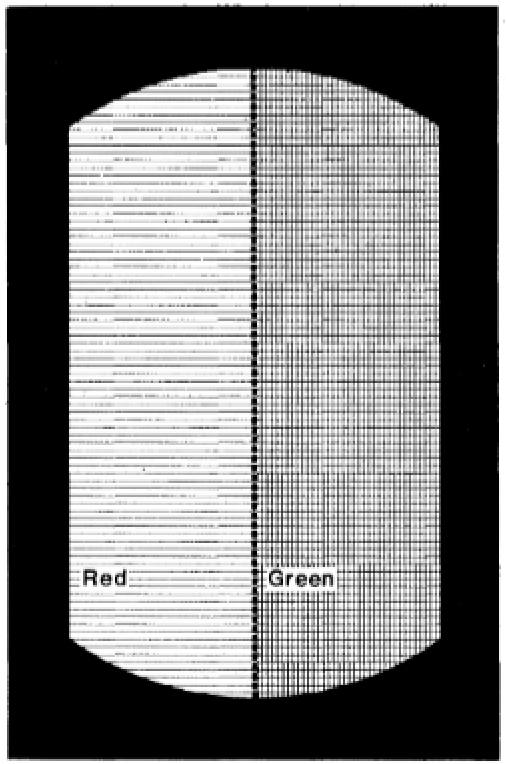


Fig. 1. A typical stimulus field. The dashed line indicates the stabilized boundary.