Seeing color through different eyes – Individual differences in human color perception

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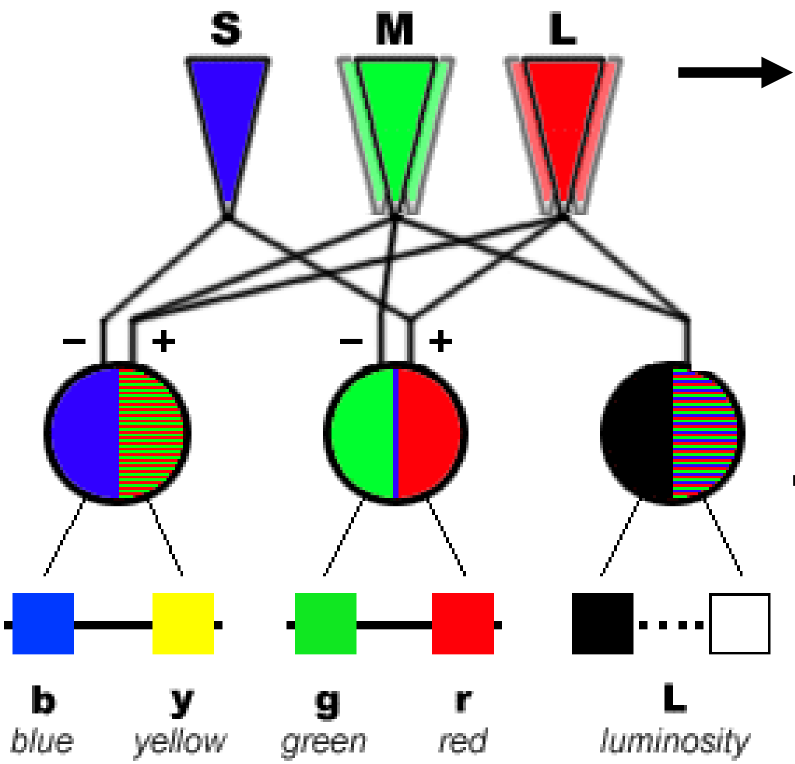
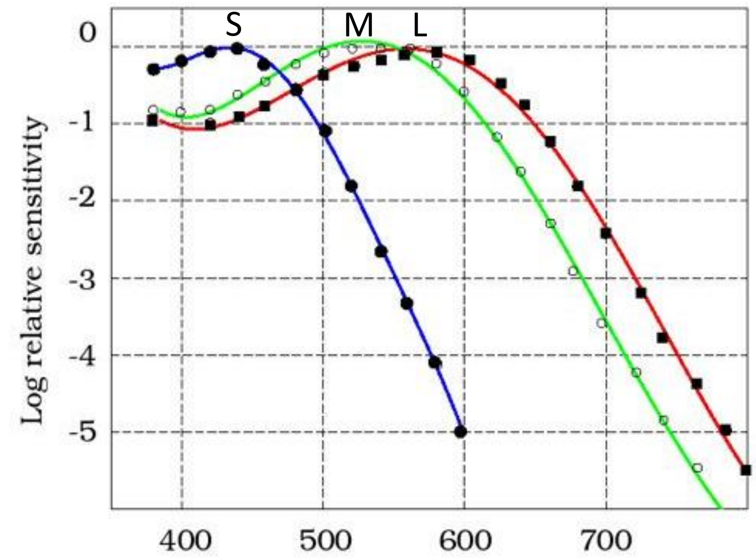
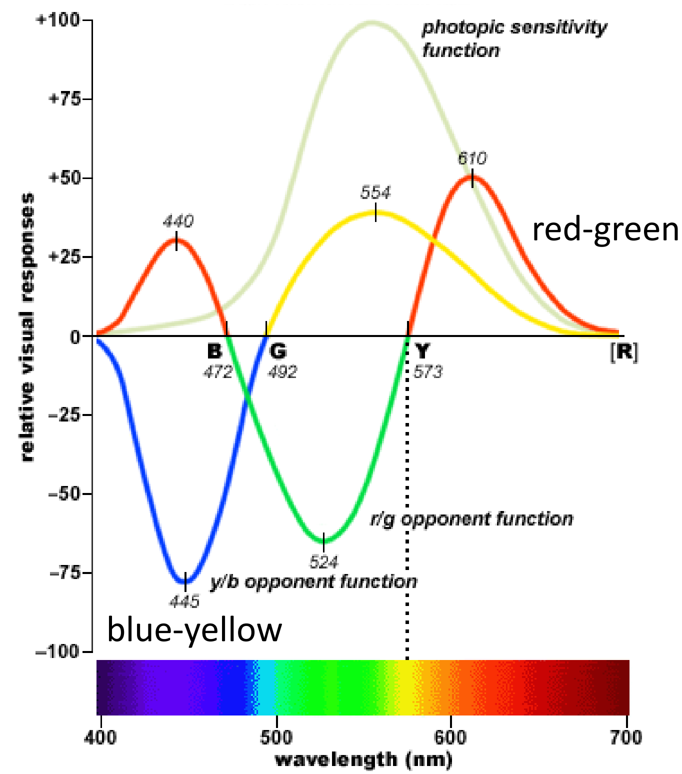
The textbook model of color vision





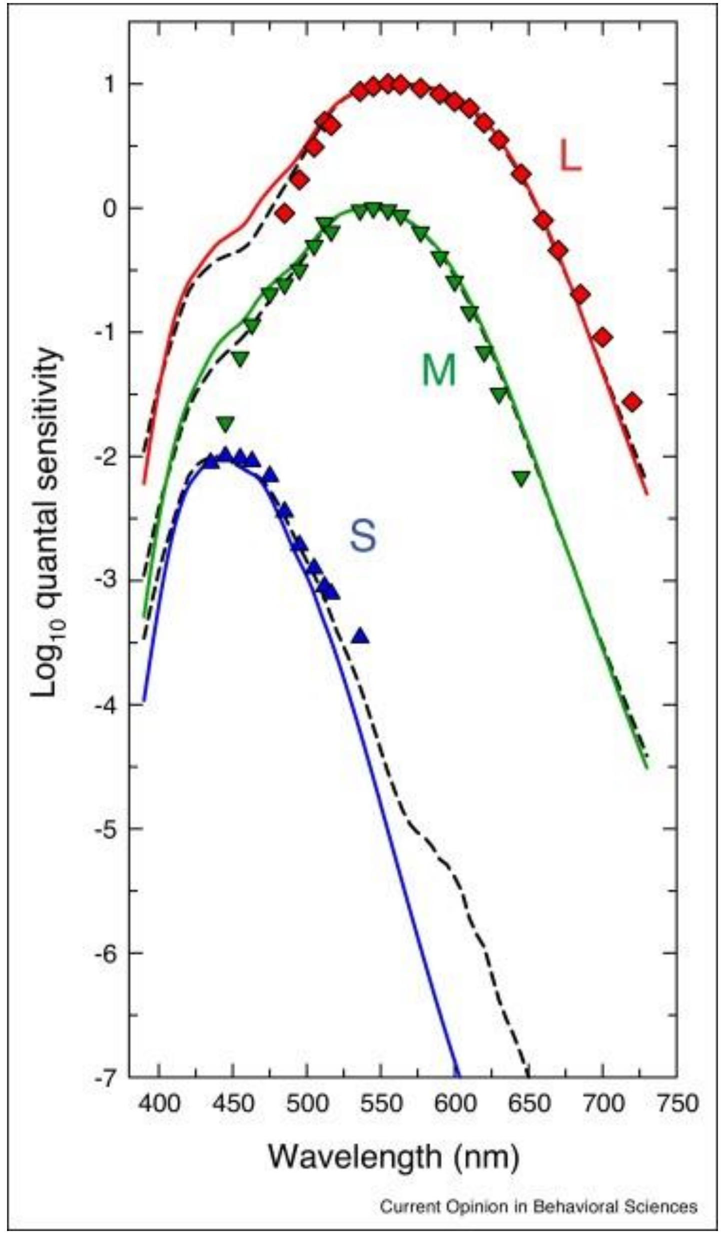


Normal variations in color vision

1. Variations in spectral sensitivity
    a. Sources of variation
    b. Implications
    c. Measuring sensitivity differences

2. Variations in color appearance
    a. Adaptation and compensation
    b. Color inferences
    c. Color categories

The Standard Observer

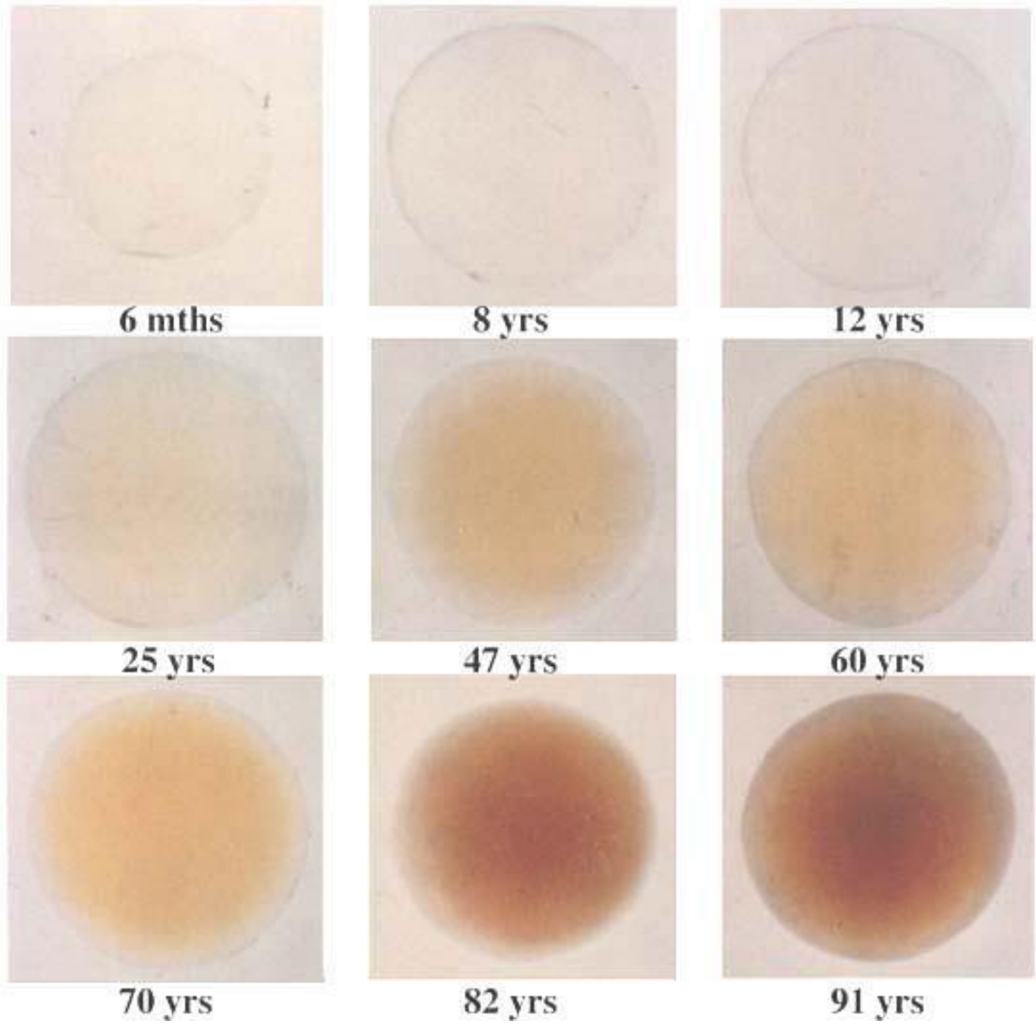


Stockman, Cur Op Beh Sci 2019; cvrl.org

Sources of variation in spectral sensitivity

1. Lens pigment
2. Macular pigment
3. Photopigment peak (λ_{max})
4. Photopigment optical density
5. Relative numbers of cones

Variations in lens pigment density with aging



Lerman *Radiant energy and the eye* 1980

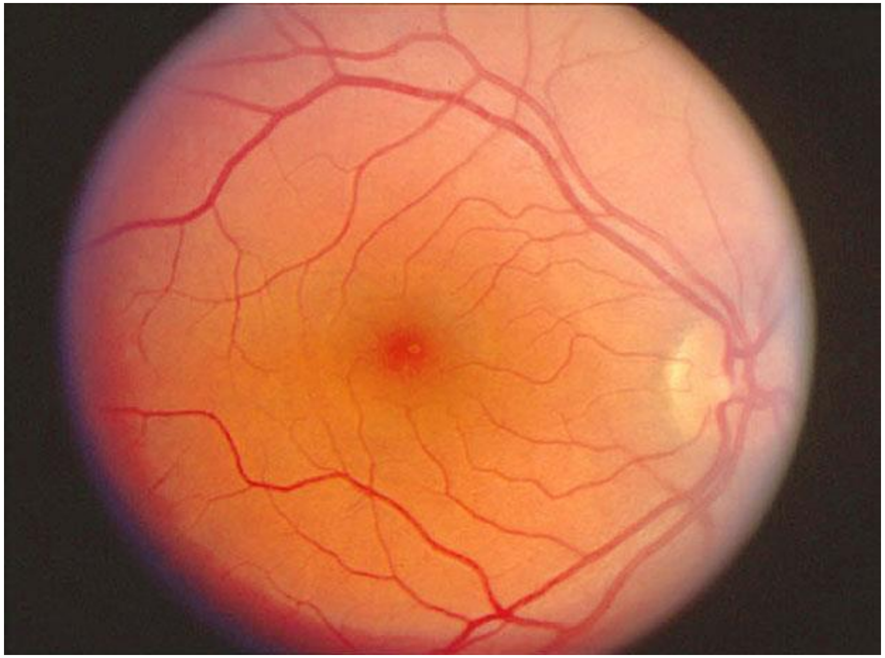
Color changes predicted by lens density changes

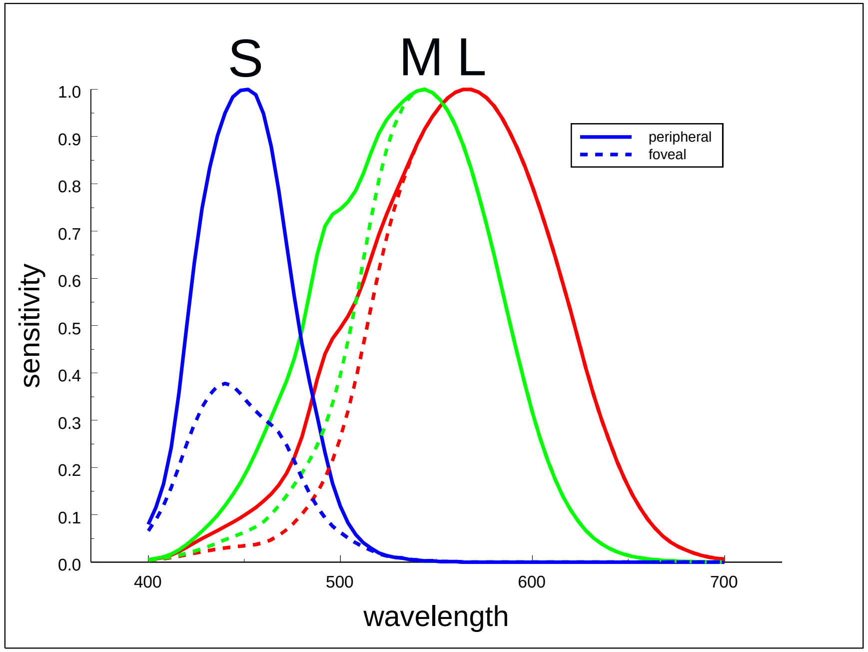
as seen by
young observer

image filtered through
lens of older eye

Compensation for variations over space

e.g. macular pigment screens the foveal receptors, so that they receive less shortwave light





This is a primary factor prompting different standard observers for 2° and 10° fields

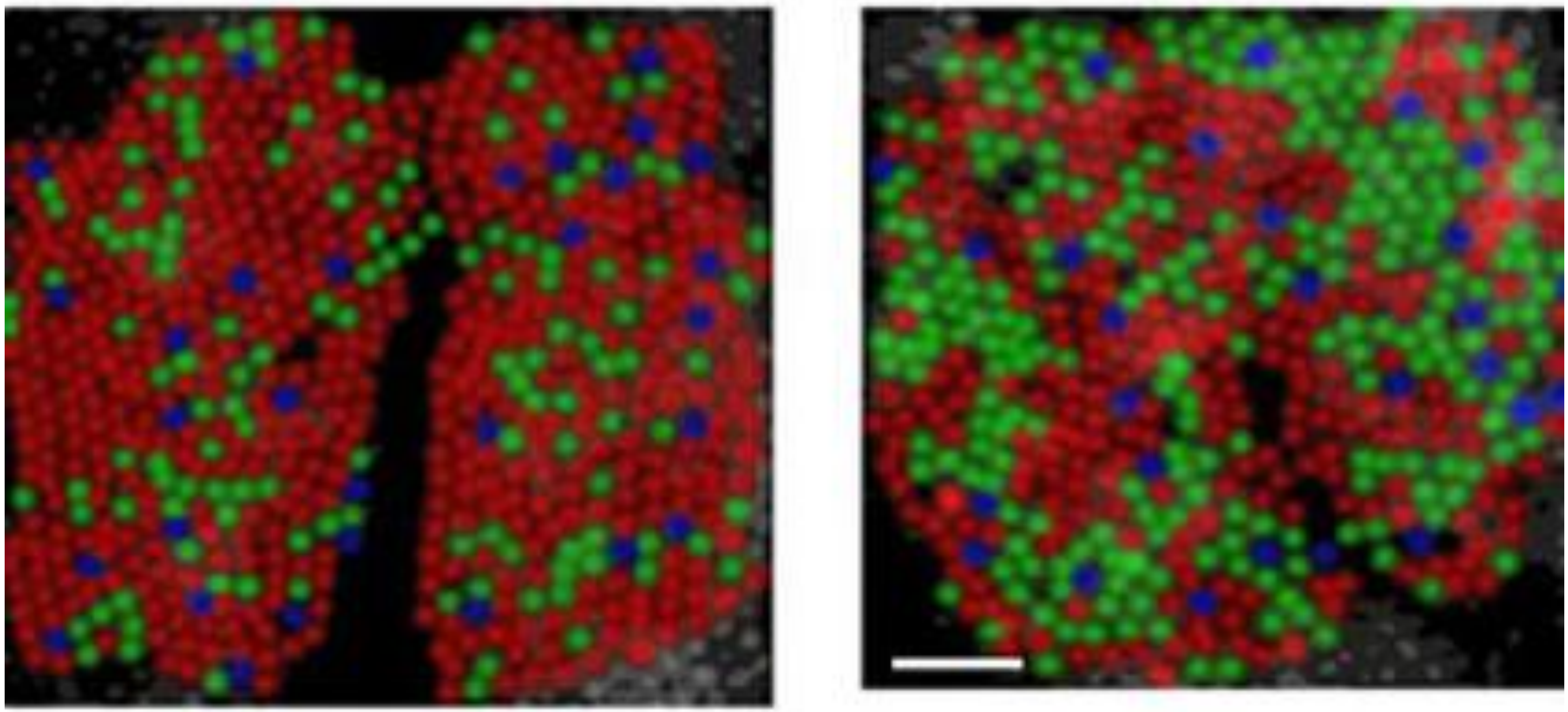
Color changes predicted by macular density changes

As seen by the fovea

As filtered by the periphery

Variation in cone ratios

L:M cone ratios can vary over a ~20-fold range



Roorda and Williams Nature 1999; Hofer et al. J Neurosci 2005

Why do these variations matter?

1. The standard observer is an average that does not describe any individual

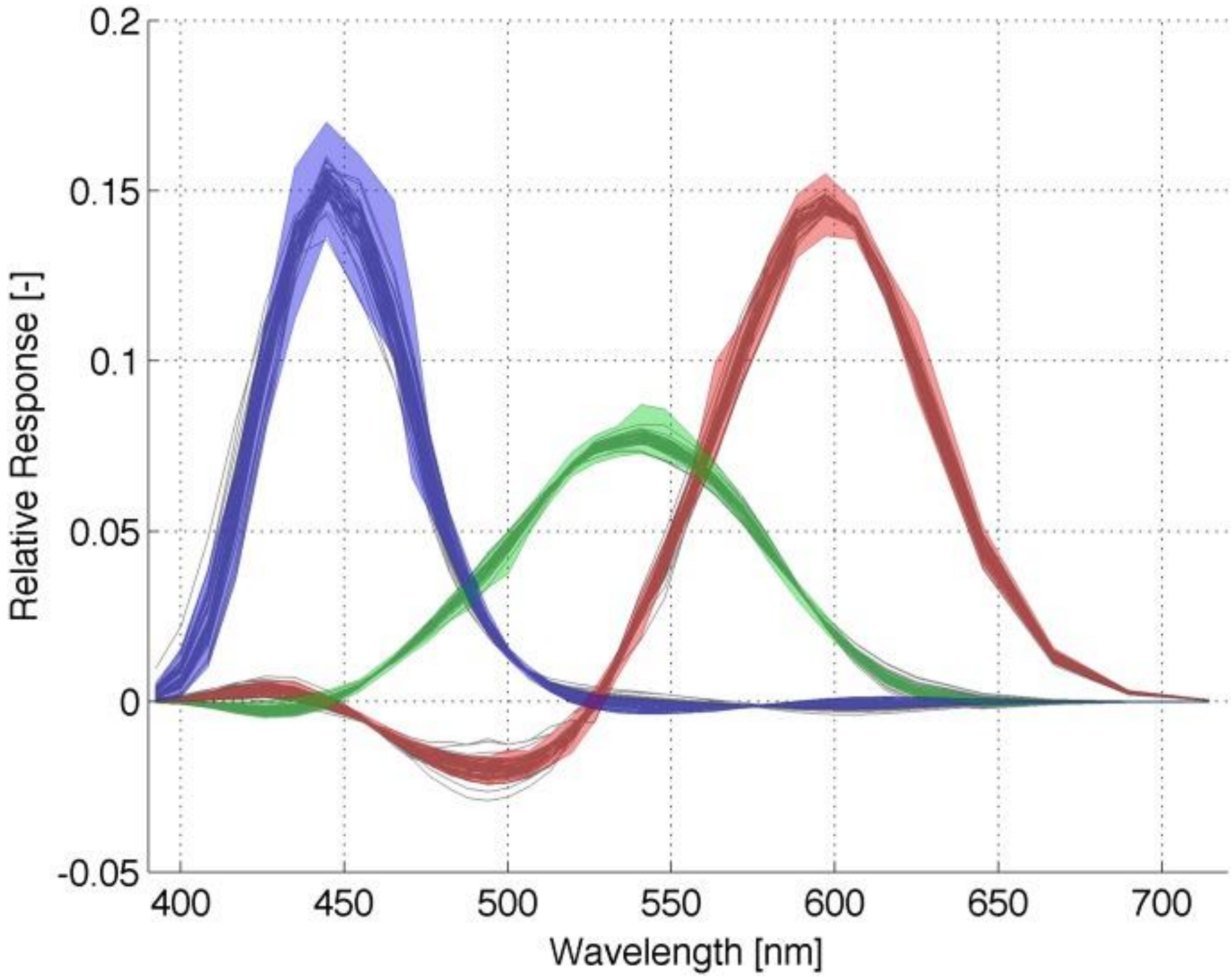
2. Specifying the individual observer is important for:

***Applications*: to render colors and information**
e.g. understanding the effects of displays and illuminants

***Research*: to study the visual system**
e.g. isolating and characterizing mechanisms
e.g. using individual differences to reveal mechanisms

Applications: e.g. colorimetry and observer metamerism

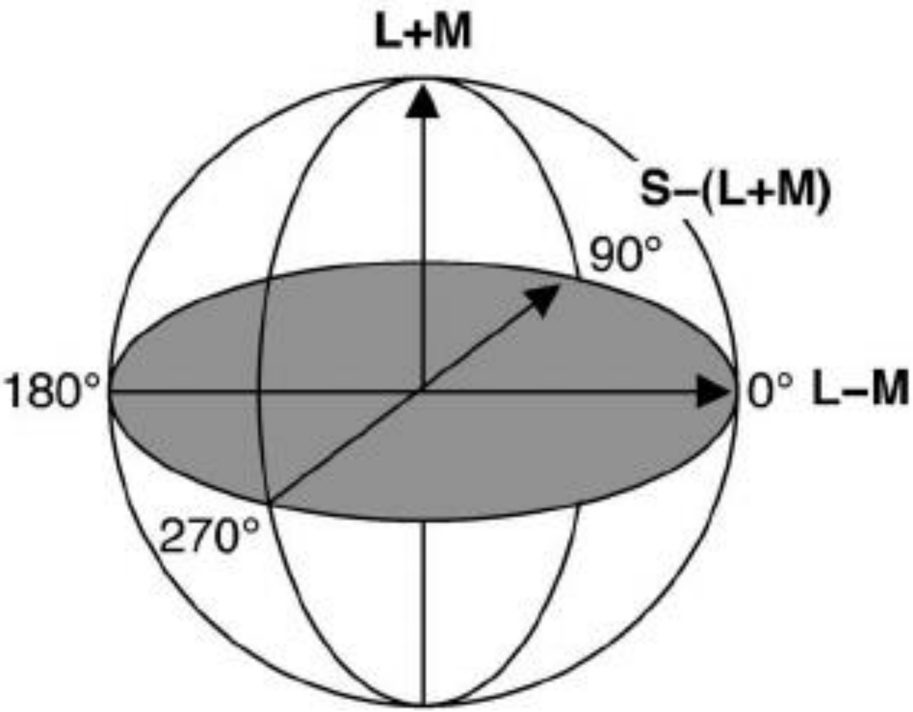
Lights that look different to one observer will be indistinguishable to another
Thus colorimetry should incorporate both the mean and the variance

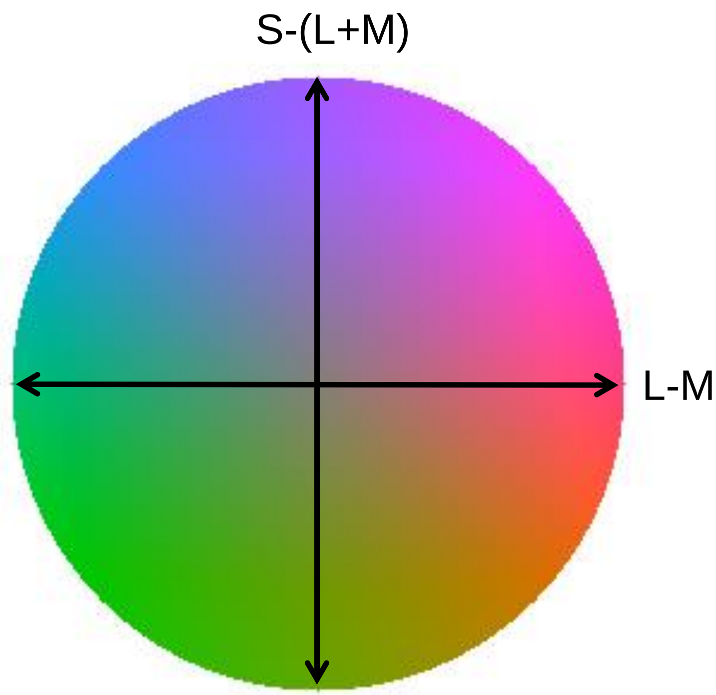


Asano et al. PLoS One 2016; Murdoch and Fairchild Lighting Res Tech 2017

Research: e.g. cardinal directions

The stimuli that isolate cones or post-receptoral pathways differ for each individual



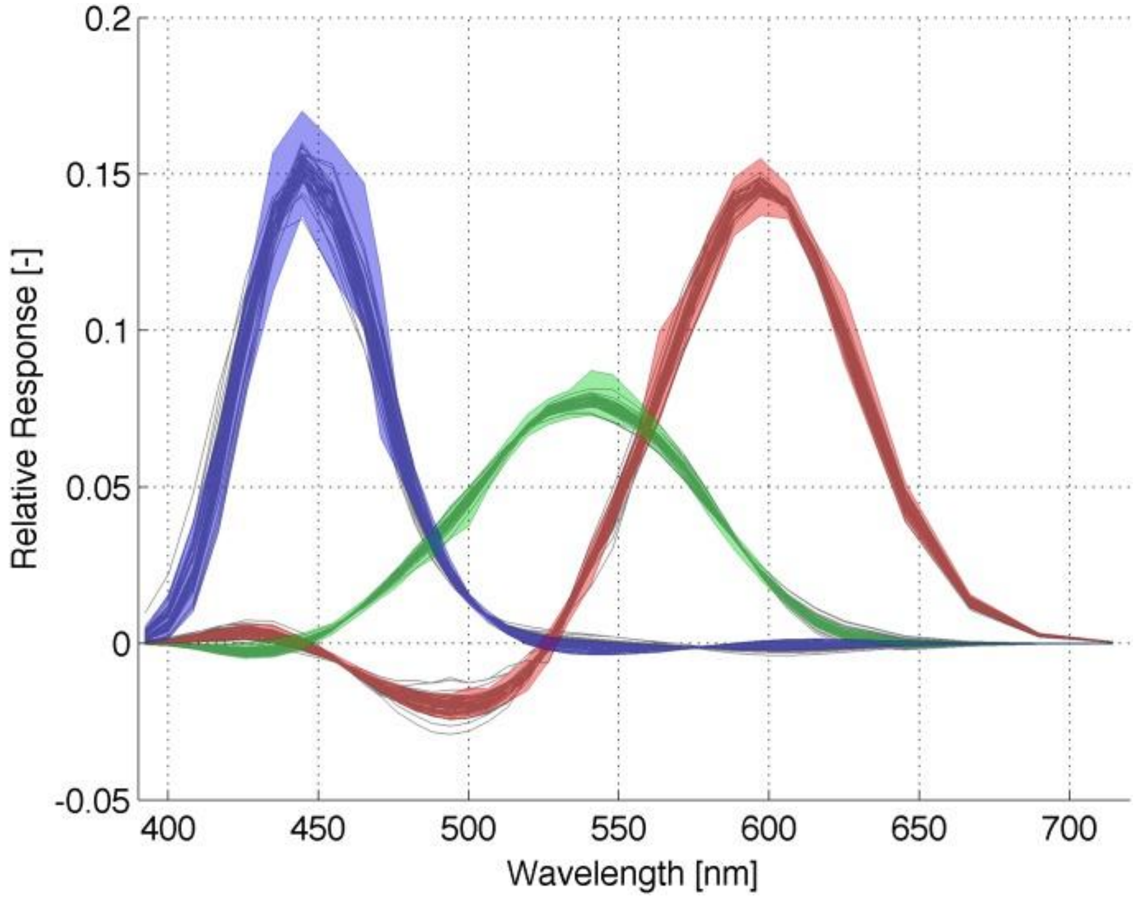


Krauskopf, Williams, and Heeley Vision Res, 1982

2 approaches for measuring and correcting for individual differences

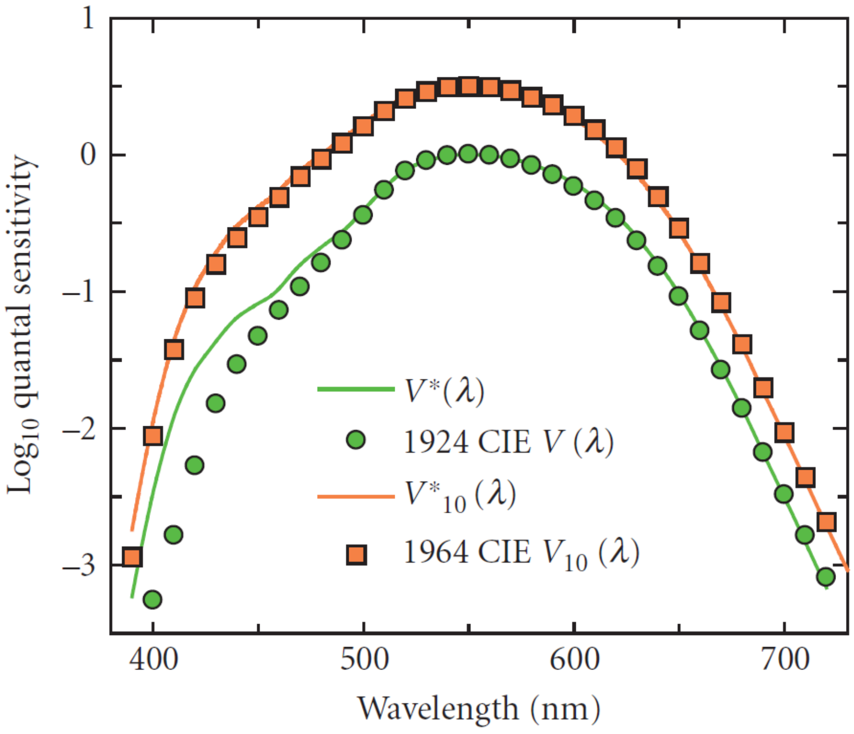
1. **Direct** – measure the individual's sensitivity or matches
   e.g. directly measure an observer's color matches

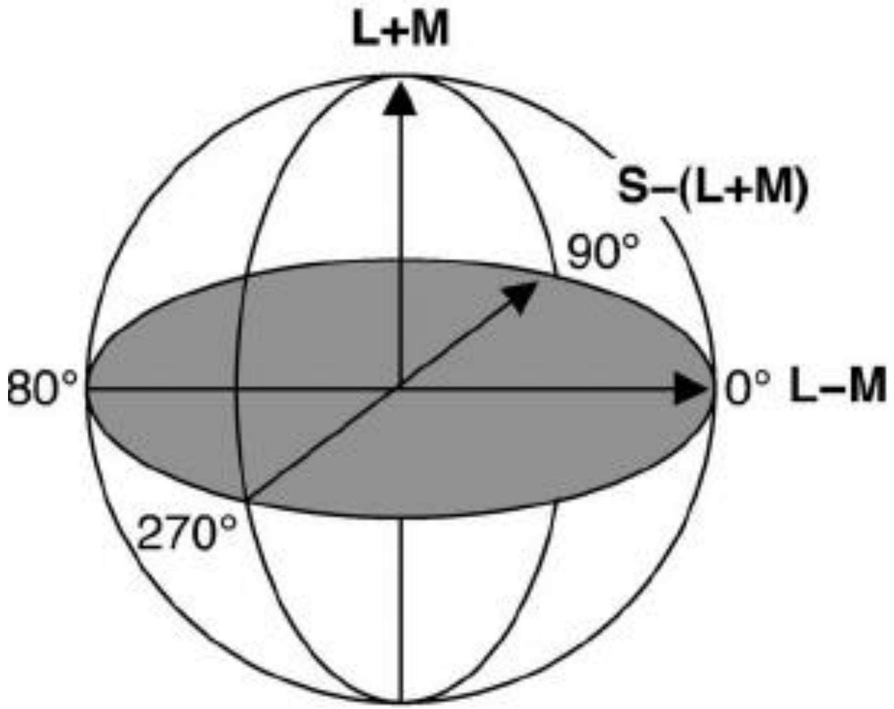
2. **Indirect** – measures sources of variation to predict sensitivity
   e.g. correct sensitivity based on measurement of macular pigment density



Individual differences in luminance sensitivity

Luminance = sum of L+M cone responses
and thus varies with L and M sensitivities and ratios





Stockman and Brainard OSA Handbook of Optics 2010

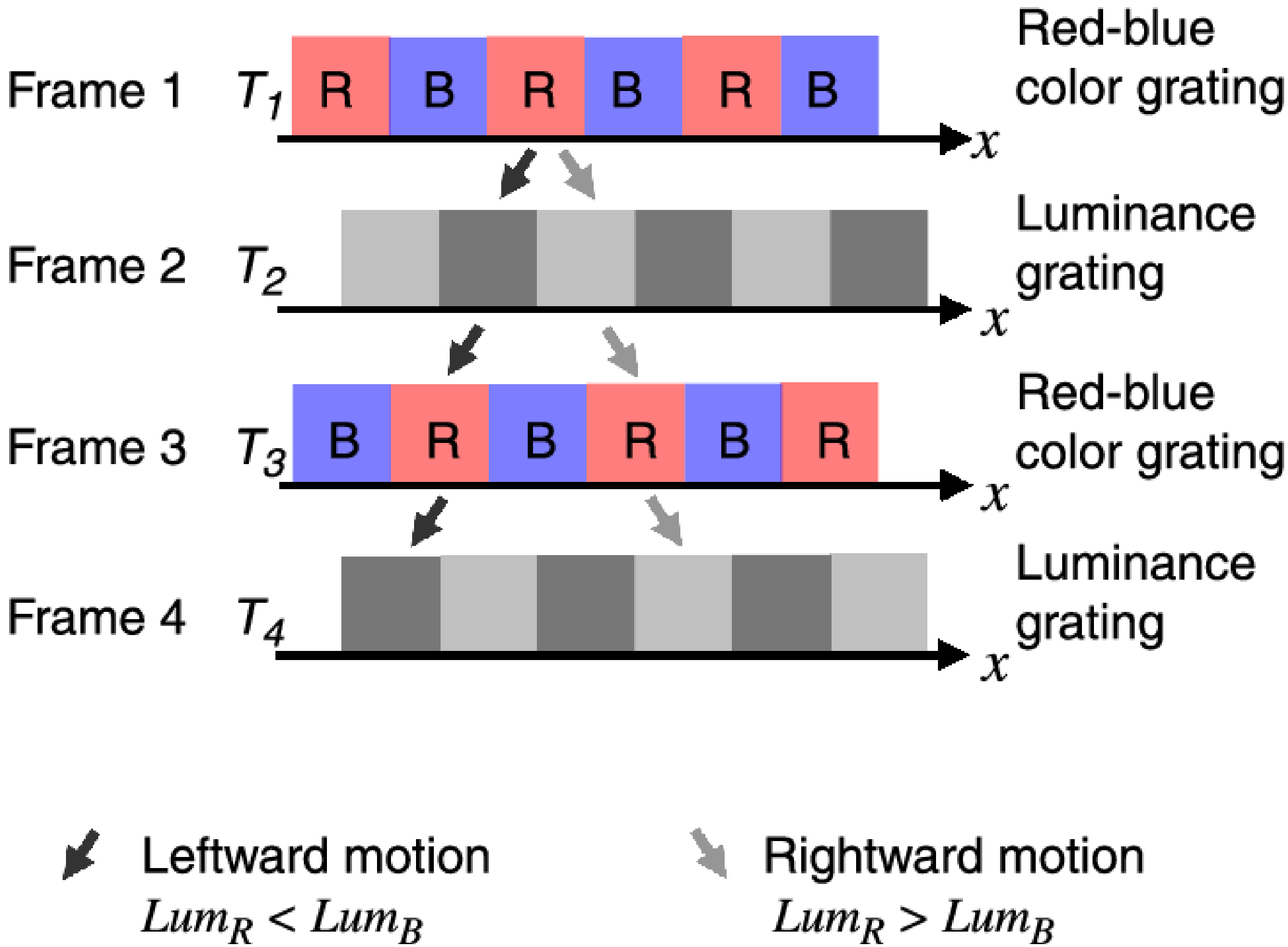
Common methods for measuring luminance:

1. Flicker photometry
   - based on poor temporal resolution for color

2. Minimally distinct border
   - based on poor spatial resolution for color

3. Minimum motion
   - based on nulling luminance signal for motion

Minimum Motion Technique



Cavanagh, Anstis, and MacLeod JOSA A 1987

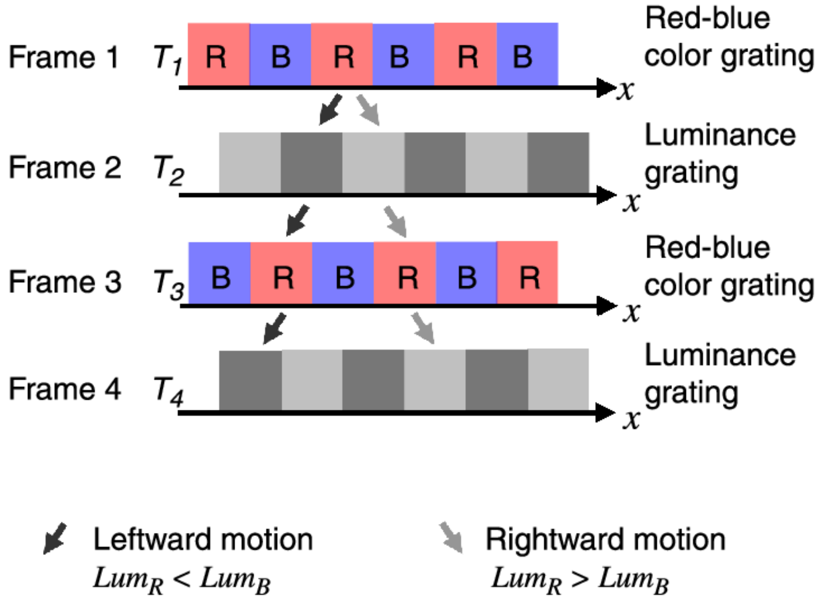
A possible shortcut for approximating an individual's sensitivity:

Predicting color matches from luminance matches

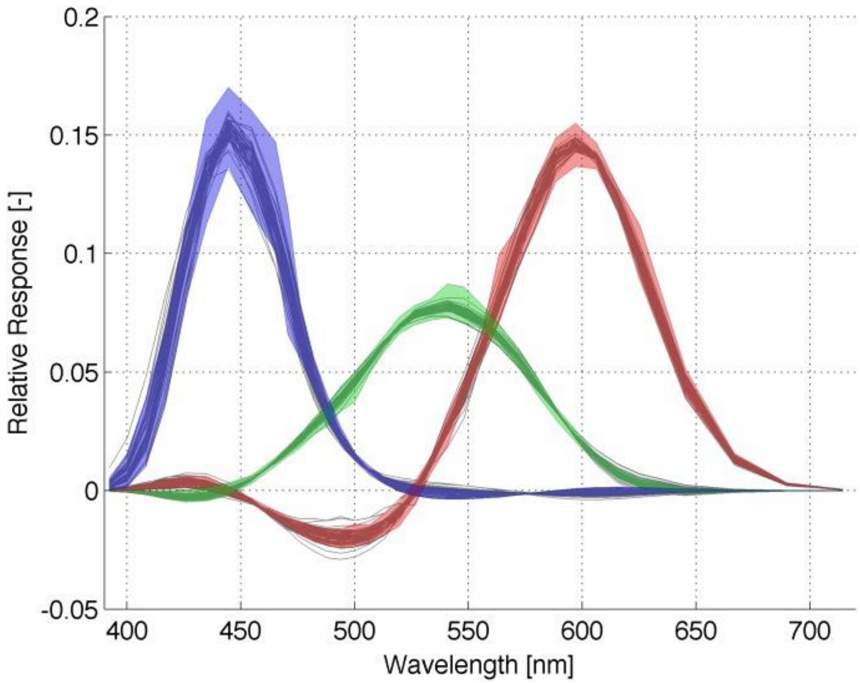
Luminance matches and color matches are affected by common factors

Thus if we could estimate these factors from an individual's luminance settings we could approximate the observer's spectral sensitivity

Using this



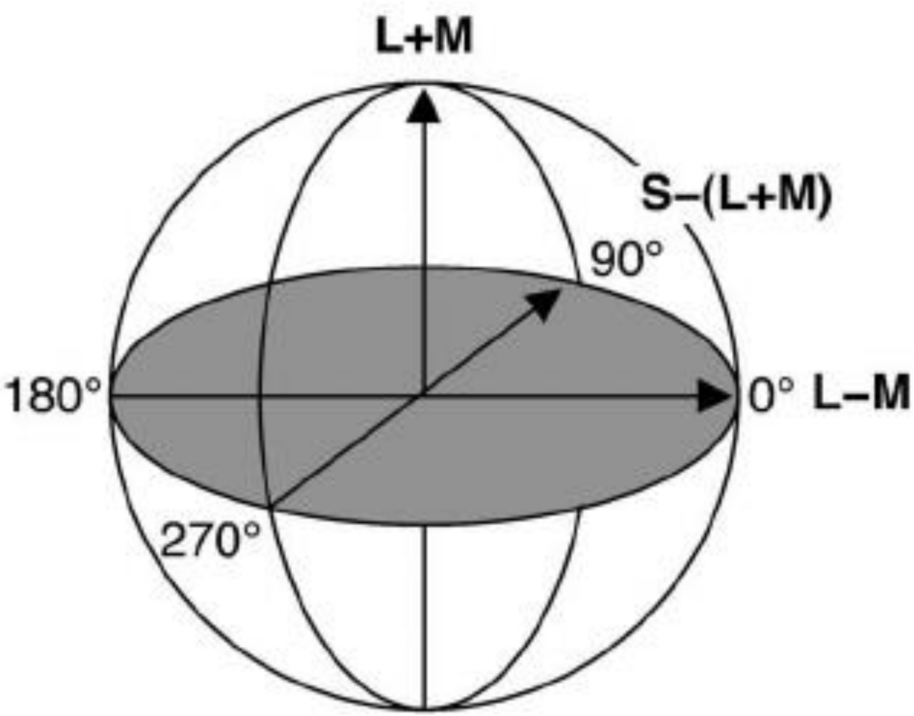
to predict this

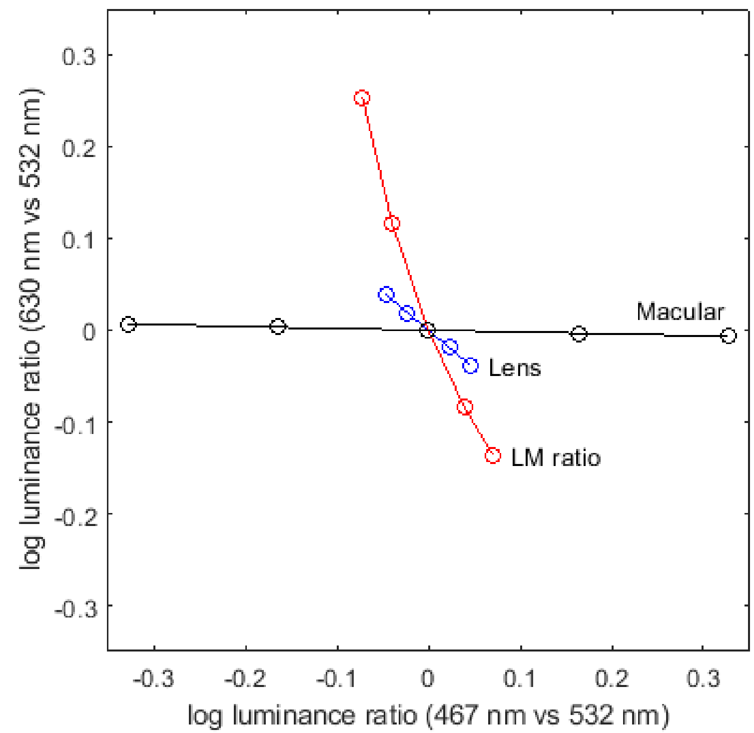


Lee et al JOSA A 2020

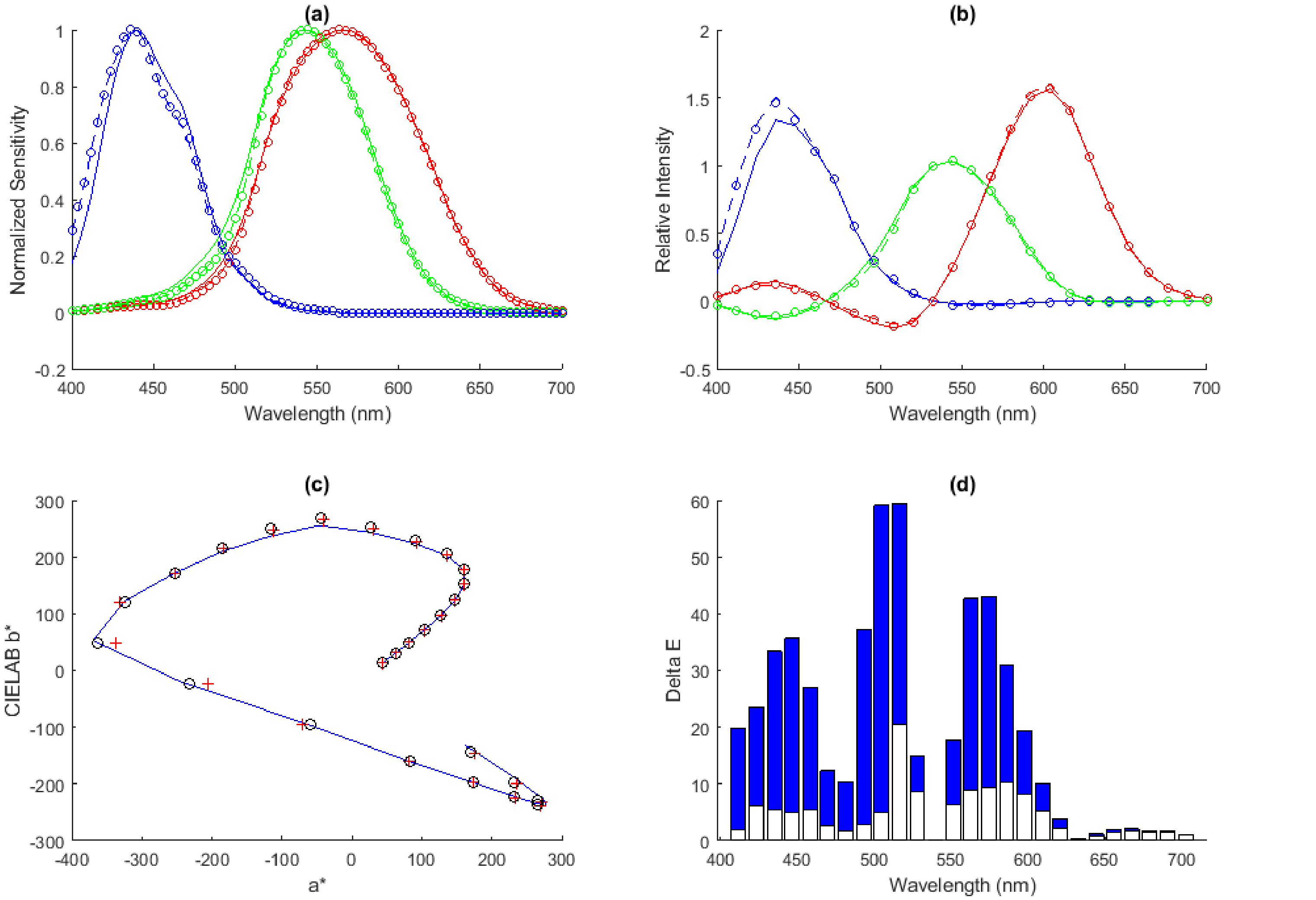
Variations in lens and macular density and cone ratios tilt the equiluminant plane in different ways

Thus values for these factors can be estimated from the luminance matches

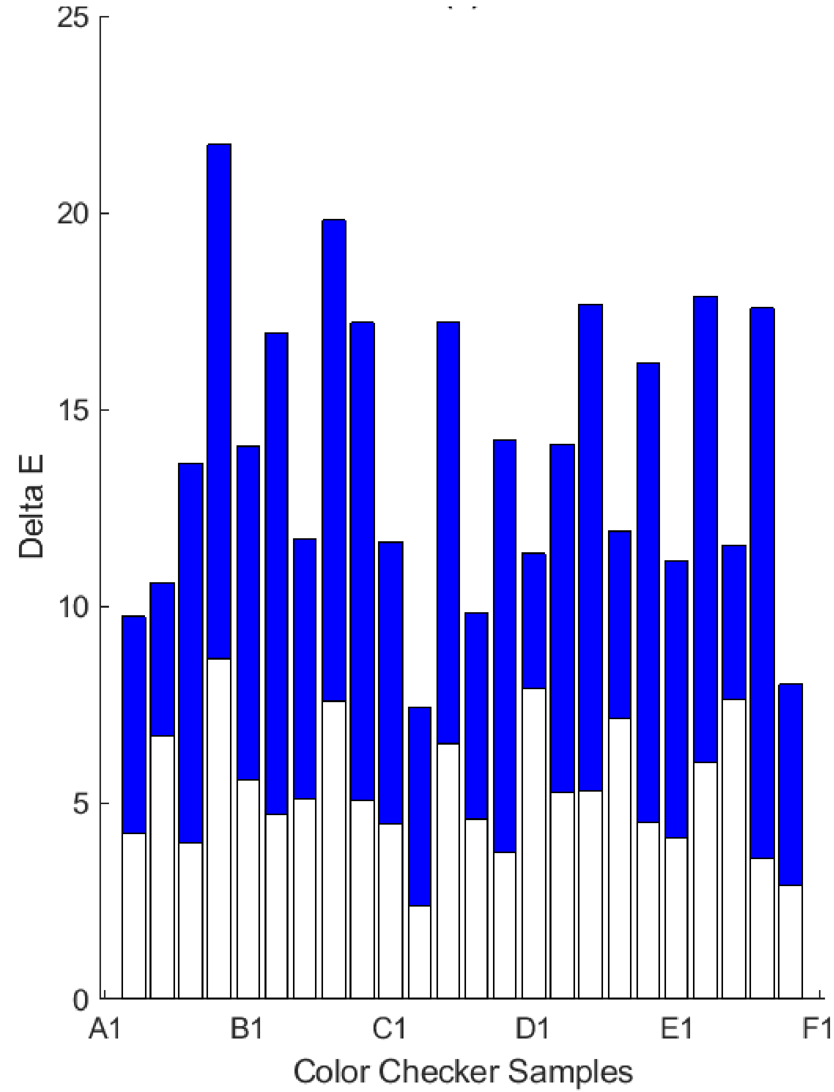




If you know the lens and macular values yo can then approximate the color matches



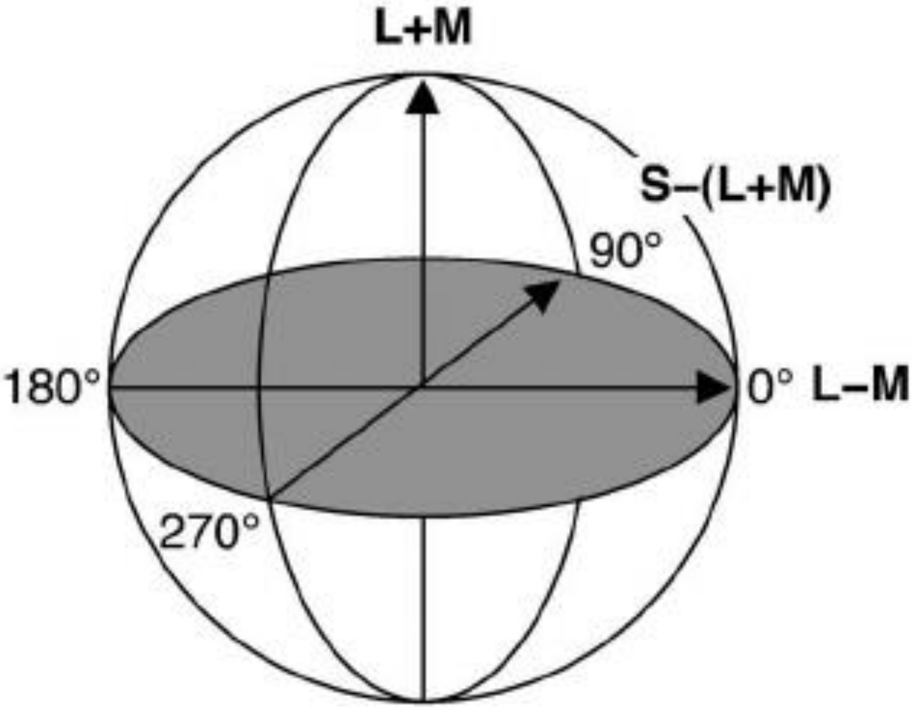
Knowing only the lens and macular densities is enough to correct for much (but not all) of the error from assuming a standard observer

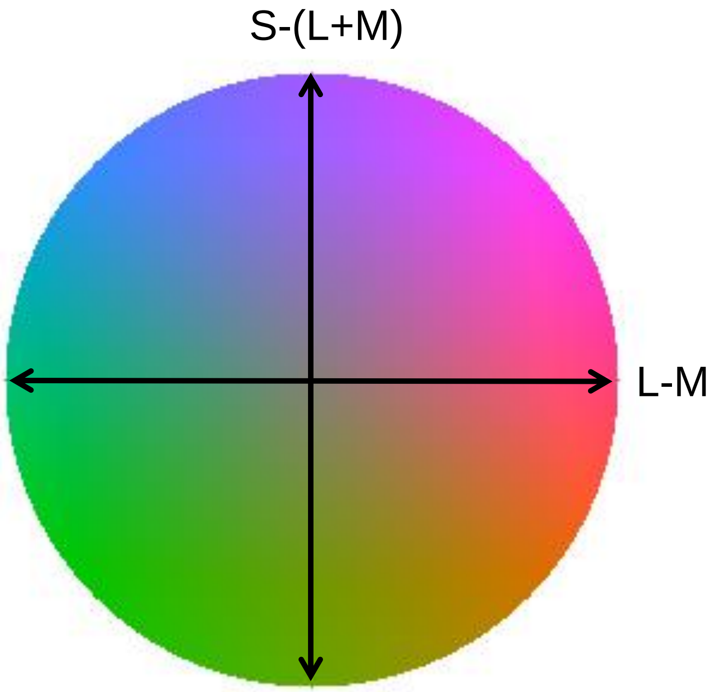


Lee et al JOSA A 2020

Research: e.g. cardinal directions

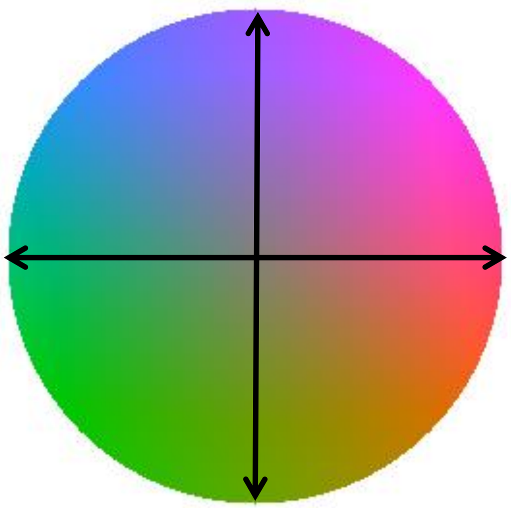
Isolating the individual's chromatic axes

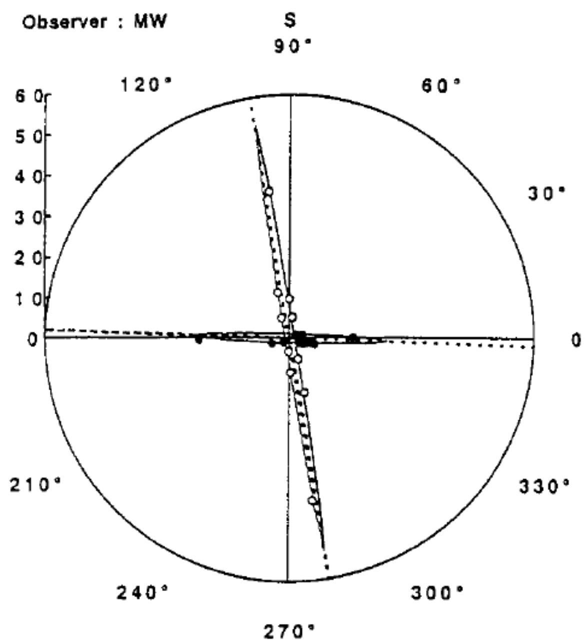


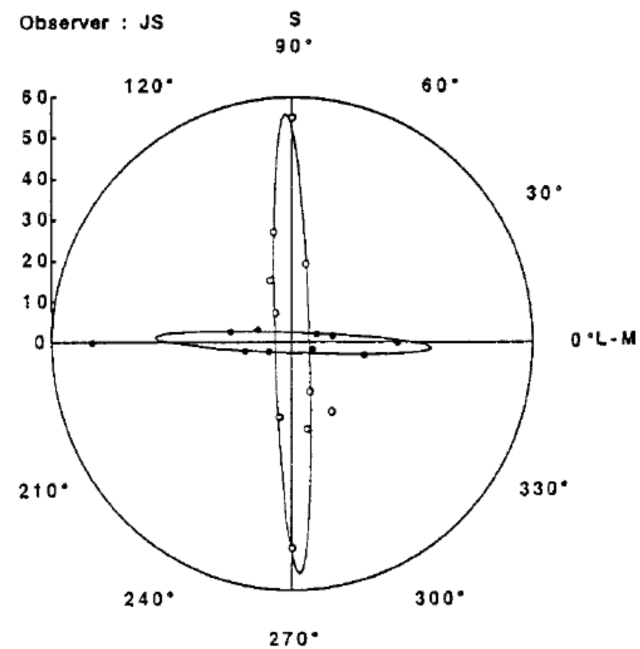


Techniques for identifying the cardinal axes:

1. Chromatic adaptation: to desensitize cones
2. Transient tritanopia: to desensitize post-receptoral channel
3. Minimally distinct border: based on poor spatial resolution of S cones



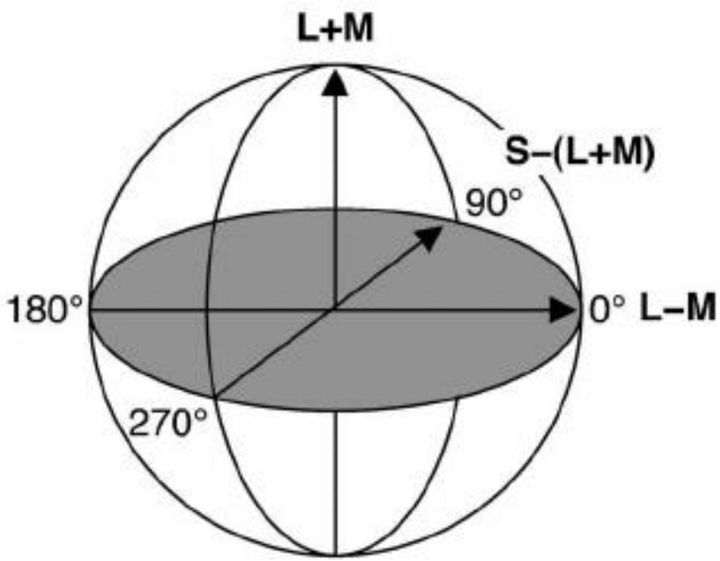


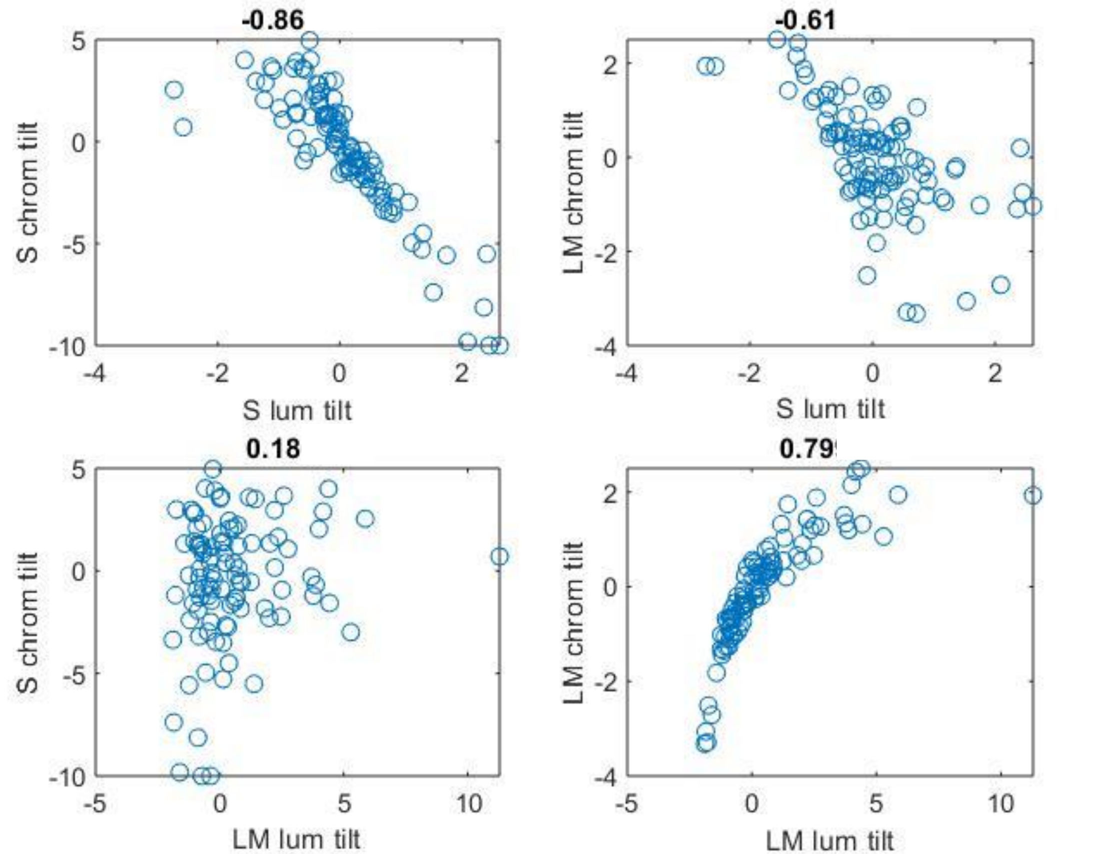


Webster et al. JOSA A 2000; Smithson et al. Norm Def Color Vison 2003

Predicting chromatic axes from luminance matches

There are strong correlations between tilt of the luminance plane and rotation of the chromatic axes





Richardson et al. VSS 2020

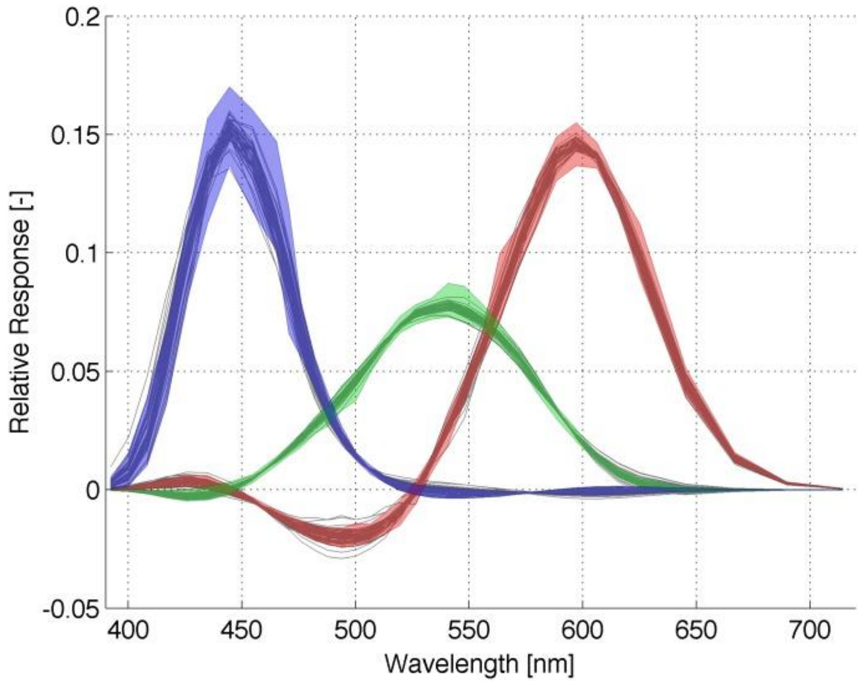
For more details attend the virtual Vision Sciences Society Conference June 20-24!

Research: Using individual differences to reveal mechanisms of color vision

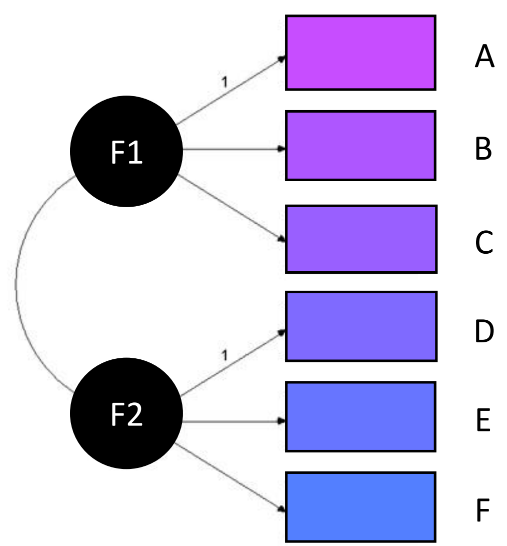
e.g. differences in color matching are correlated for some wavelengths but not others

The pattern of correlations can reveal the factors responsible for the variations

using this



to predict this



Webster and MacLeod JOSA 1988

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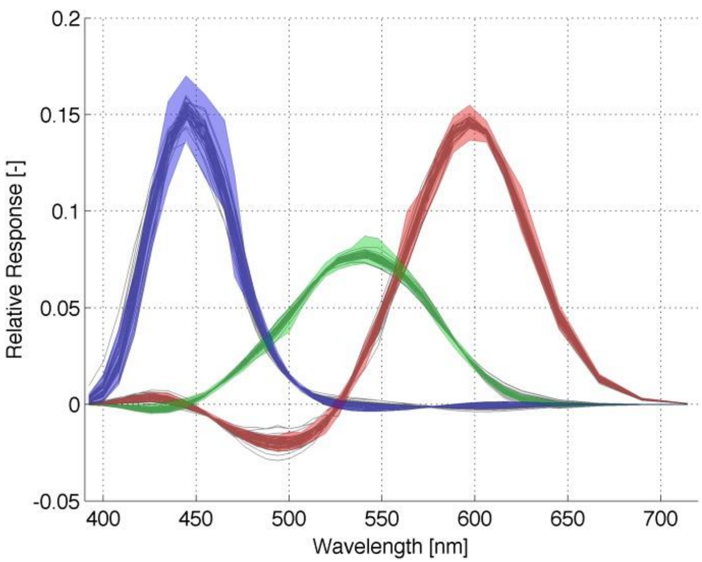

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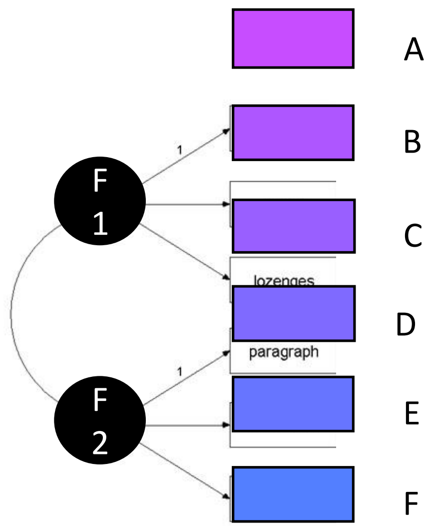
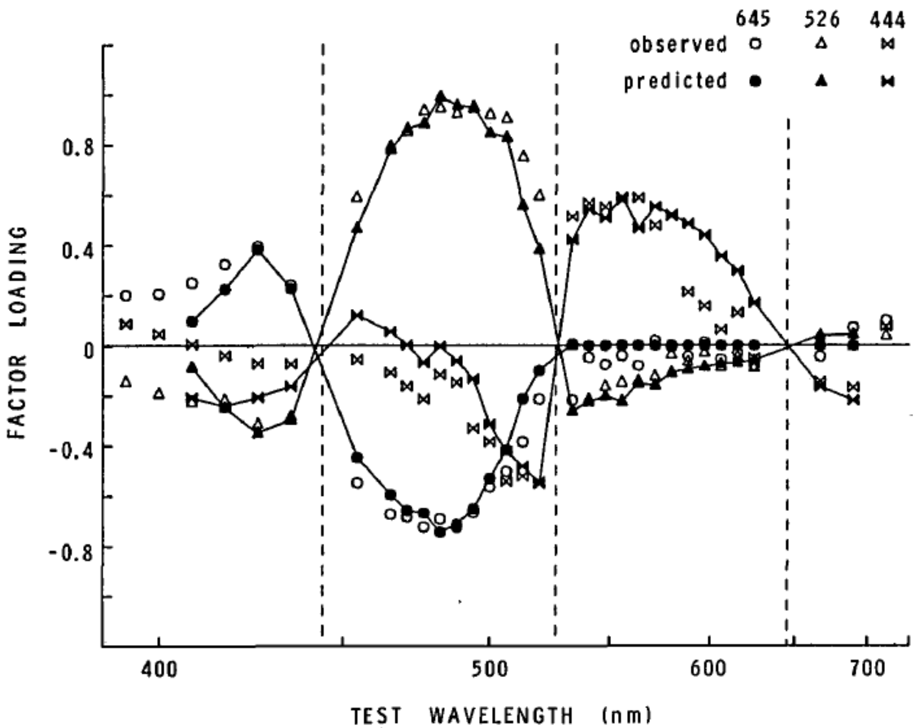


from this!

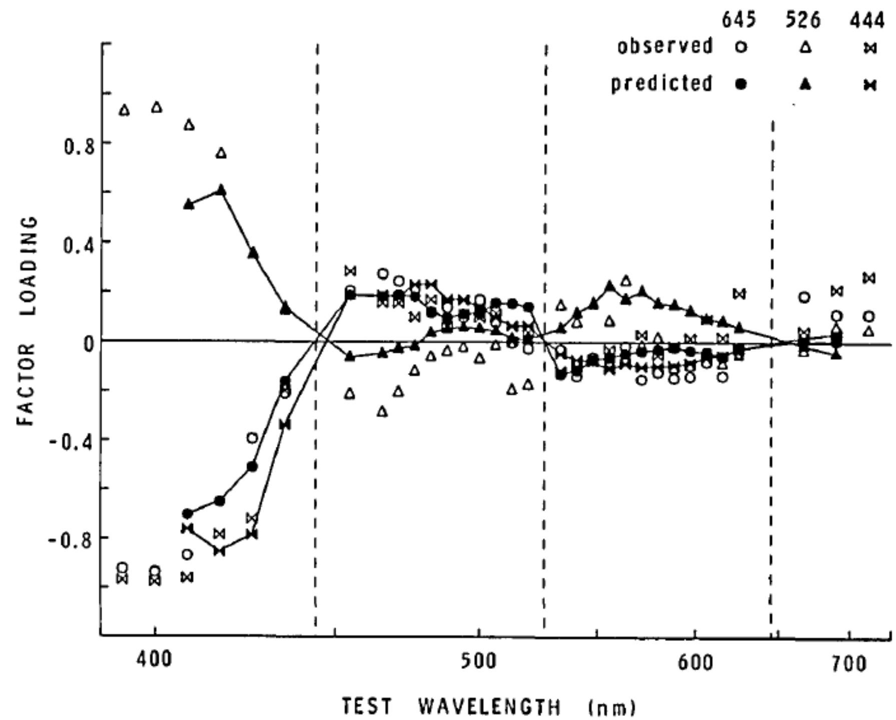
Webster and MacLeod JOSA 1988

Factor analyses of the correlations reveal latent variables closely conforming to independent variations in macular and lens pigment density

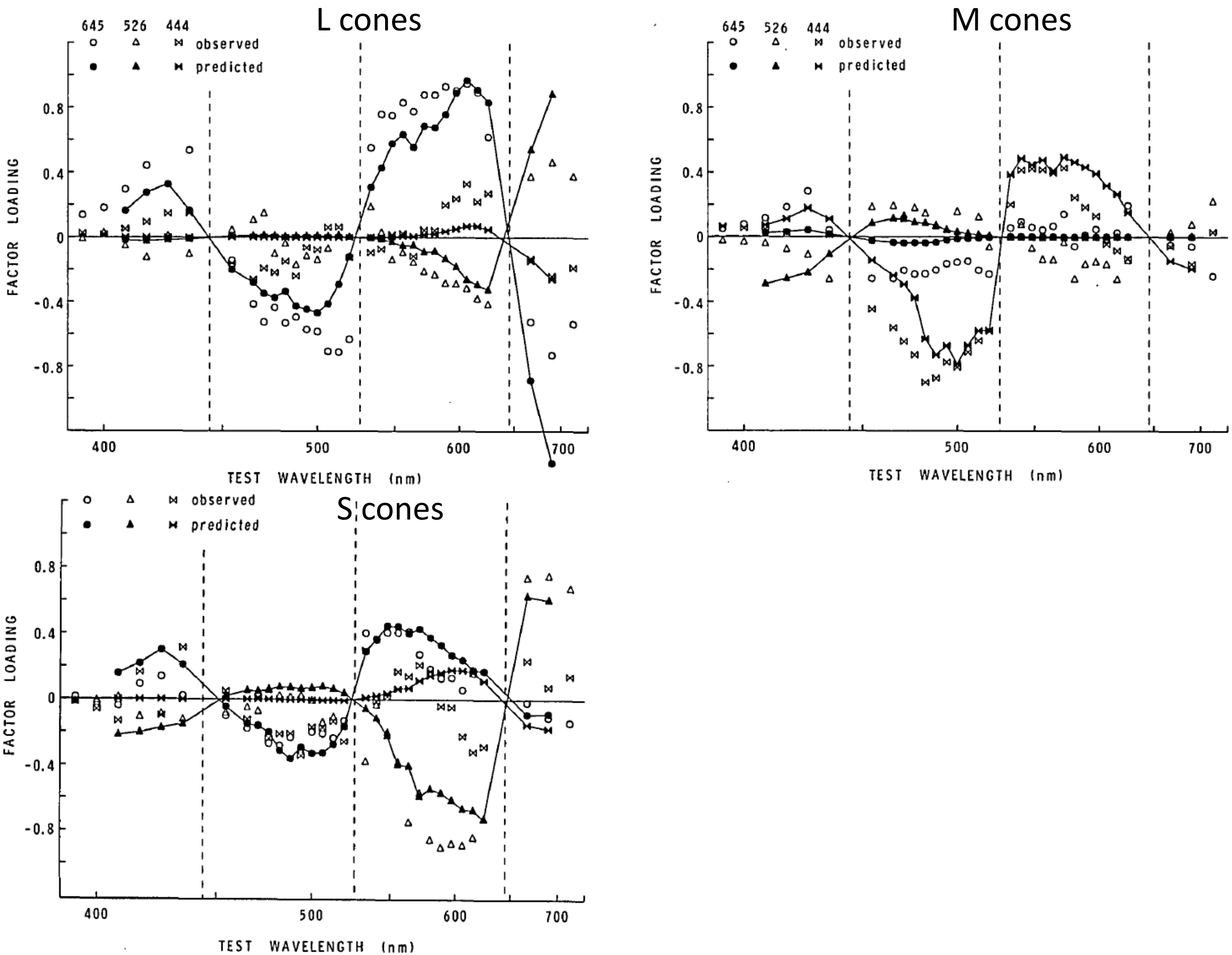
macular pigment density



lens pigment density



Variations were also consistent with independent λ_{max} variations in the cones



Interim Summary

1. There are large normal variations in spectral sensitivity
2. These are important to account for in both applications and basic research
3. They can also be harnessed to reveal visual processes

using individual differences to infer visual and cognitive functions:
Wilmer Spatial Vision 2008; Peterzell Elec Imaging 2016; Mollon et al. Vision Res 2017; Hedge et al. Beh Res Meths 2018

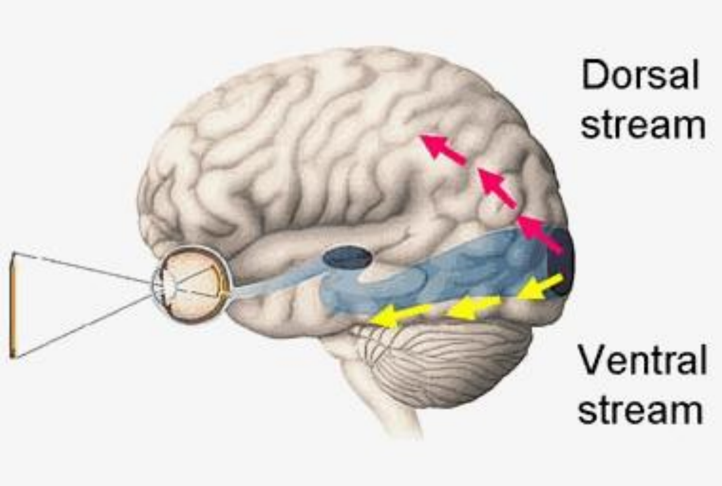
Normal variations in color vision

1. Variations in spectral sensitivity
    a. Sources of variation
    b. Implications
    c. Measuring sensitivity differences

2. Variations in color appearance
    a. Adaptation and compensation
    b. Color inferences
    c. Color categories

What shapes individual differences in color appearance?

Our brain?



Our world?

Our experience?

Differences in sensitivity show little relationship to differences in color appearance

Examples:

1. Color percepts are relatively unaffected by the cone ratios
   (Miyahara et al. Vision Res 1998; Brainard et al. JOSA A 2000)

2. Color perception remains stable despite sensitivity changes with aging
   (Werner and Schefrin JOSA A 1990, 1993; Wuerger PLoS One 2013)

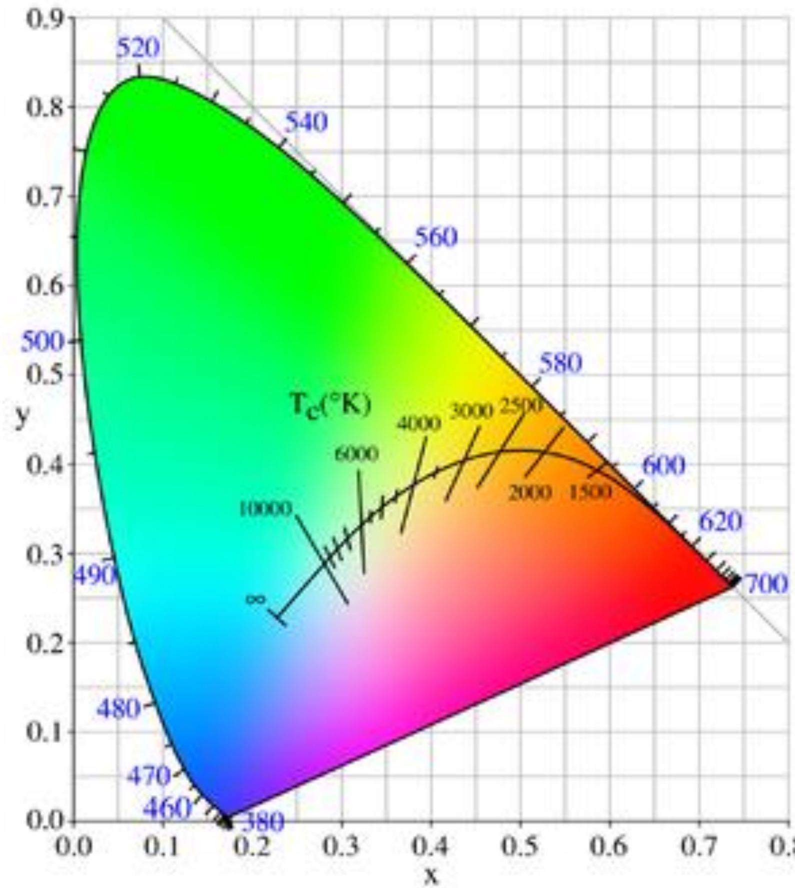
3. Color perception remain stable despite sensitivity changes with eccentricity
   (Webster and Leonard JOSA A 2008; Webster et al. Proc Roy Soc B 2010; Bompas et al. JOV 2013)

Emery and Webster Cur Op Beh Sci 2019; Billock Comp Brain Beh 2020; Webster JOSA A 2020

Color appearance and the environment

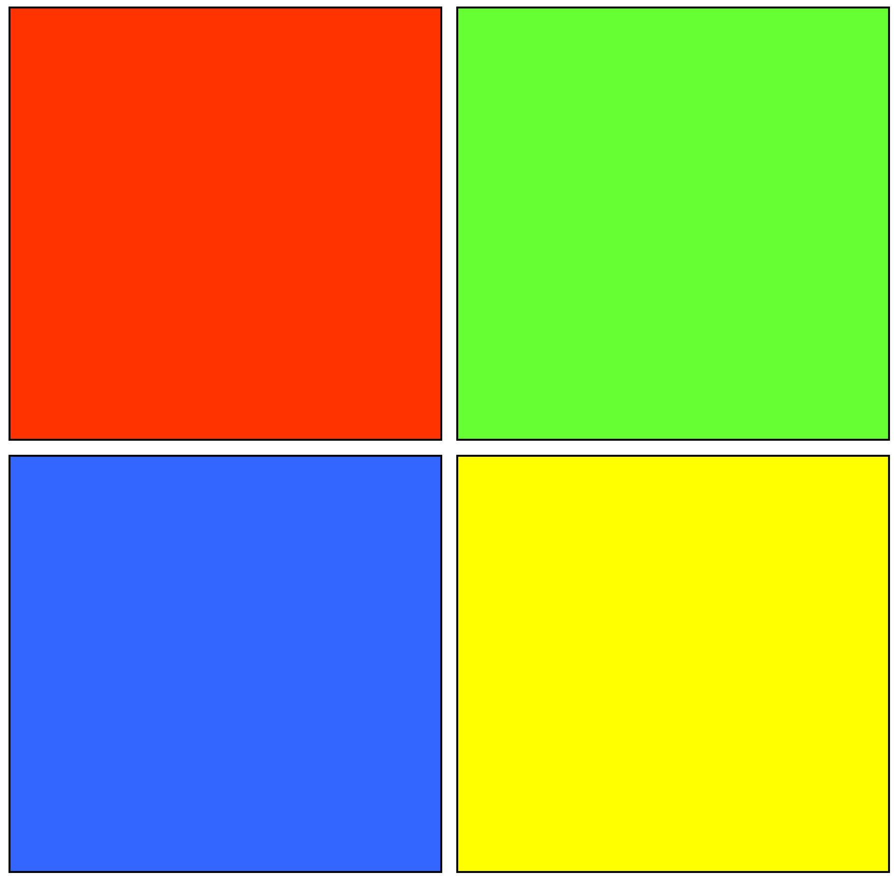
Many aspects of color perception may be tied to properties of the environment

e.g. salient colors (e.g. blue and yellow) may look special
because they are salient properties of the world (e.g. sun and sky)



Mollon Visual Neuroscience, 2006

The visual system is highly adaptable,
and thus color appearance is calibrated by
the specific environment we are exposed to



Adaptation and Compensation

Because adaptation adjusts the observer to their environment, these adjustments tend to compensate or discount for the observer's sensitivity

Webster JOV 2011; Webster Ann Rev Vis Sci 2015

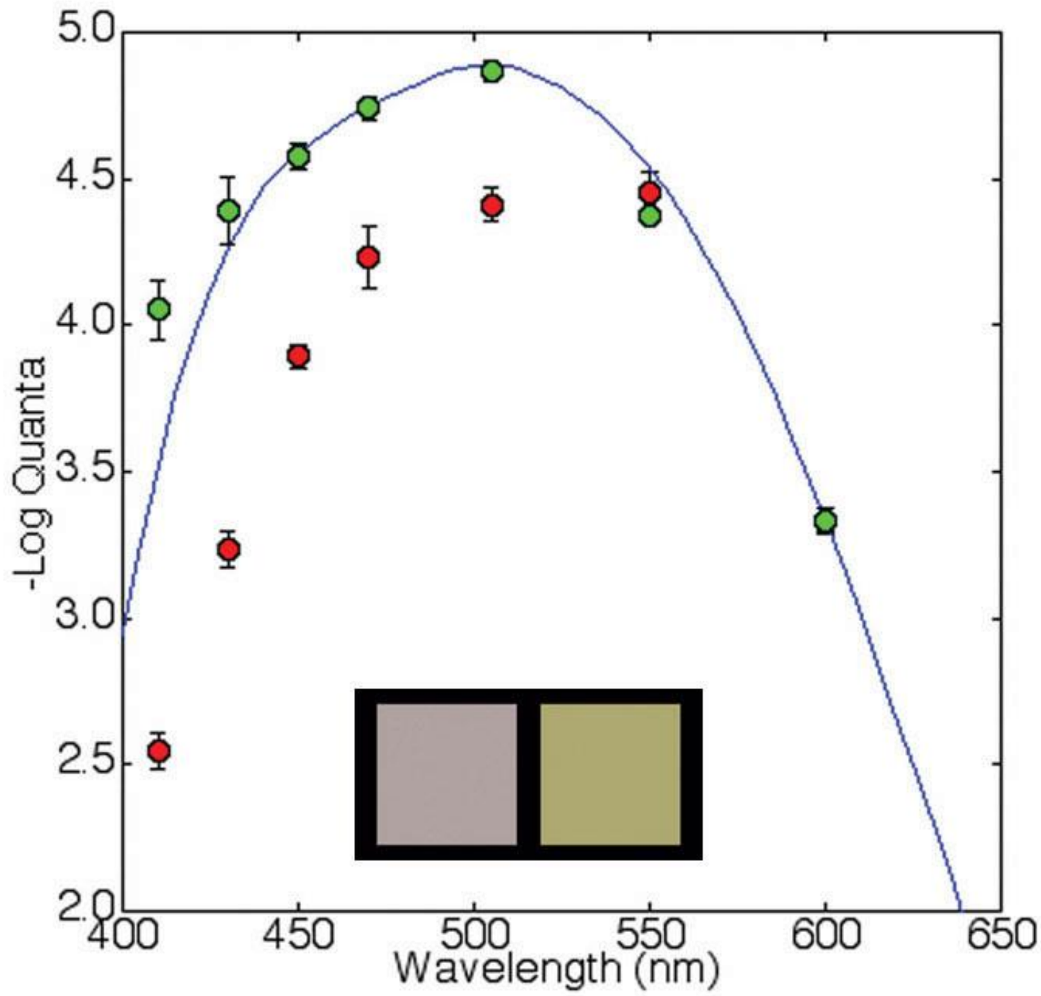
Discounting the mean: e.g. compensating for lens pigment

as seen by
young observer

image filtered through
lens of older eye

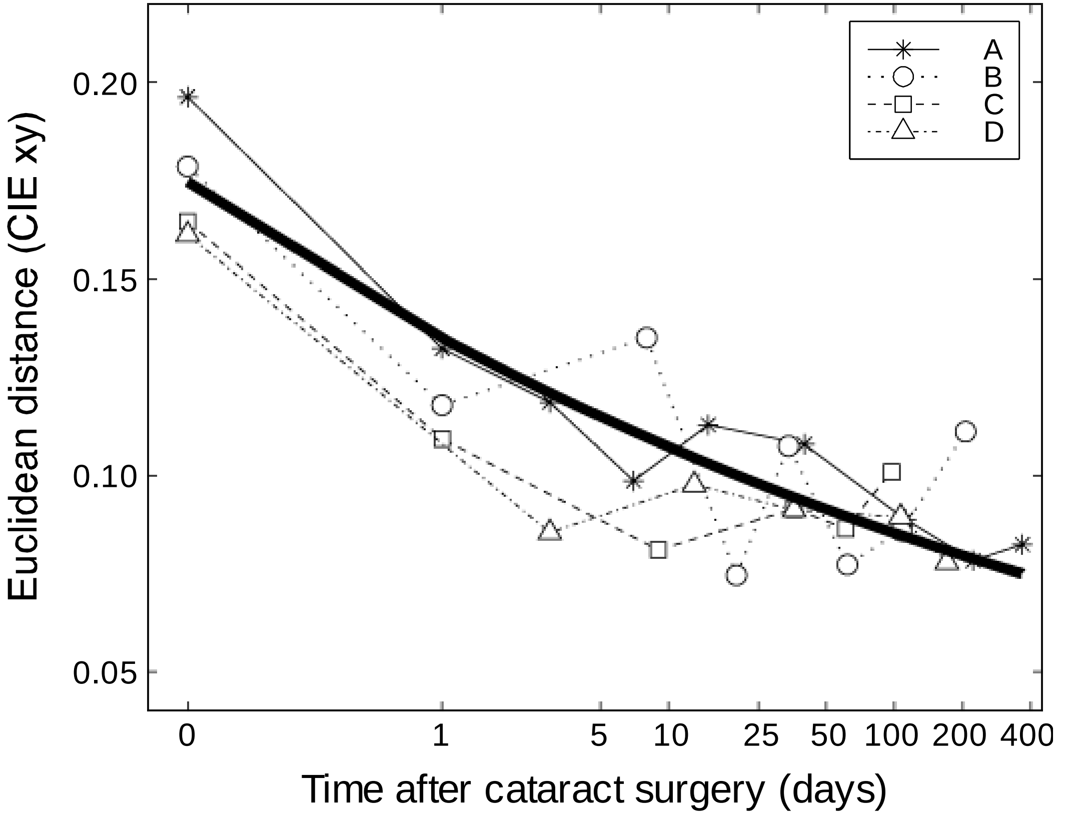
as seen by older observer
adapted to their lens

Spectral sensitivity before (red) and after (green) cataract surgery



Delahunt et al. Visual Neuroscience 2004

Changes in the achromatic locus following surgery reveal a very slow recovery.



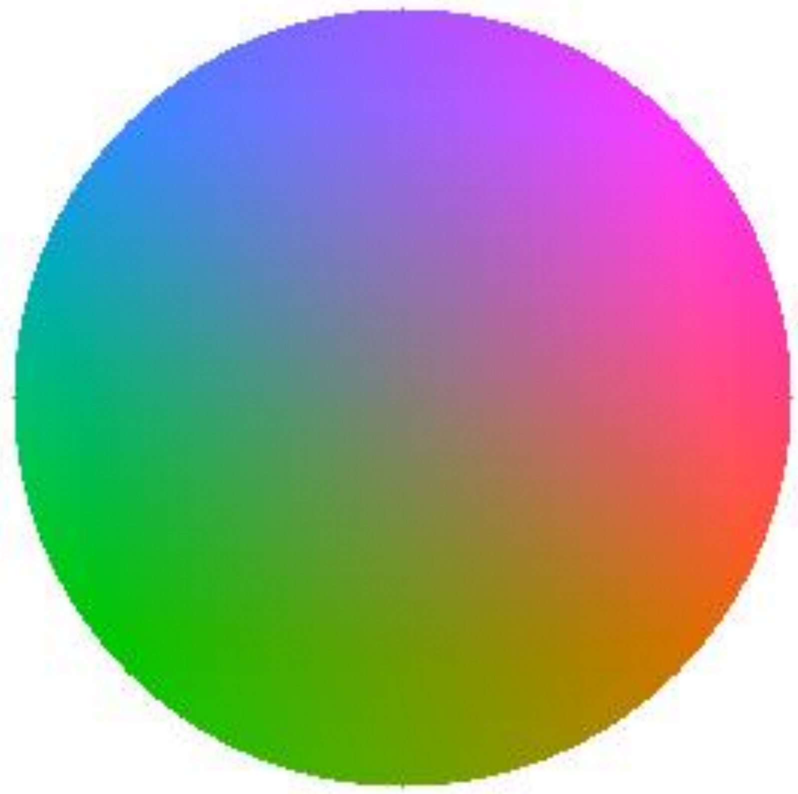
Discounting the mean: e.g. compensating for macular pigment

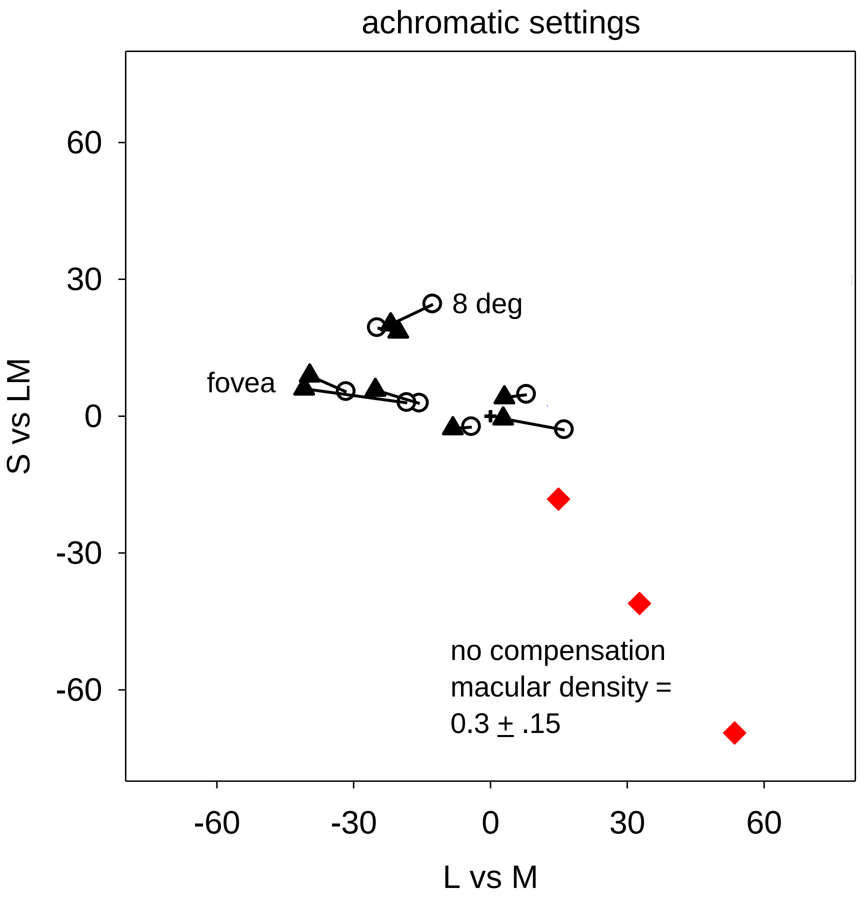
As seen by the fovea

As filtered by the periphery

Peripheral percept assuming adaptation

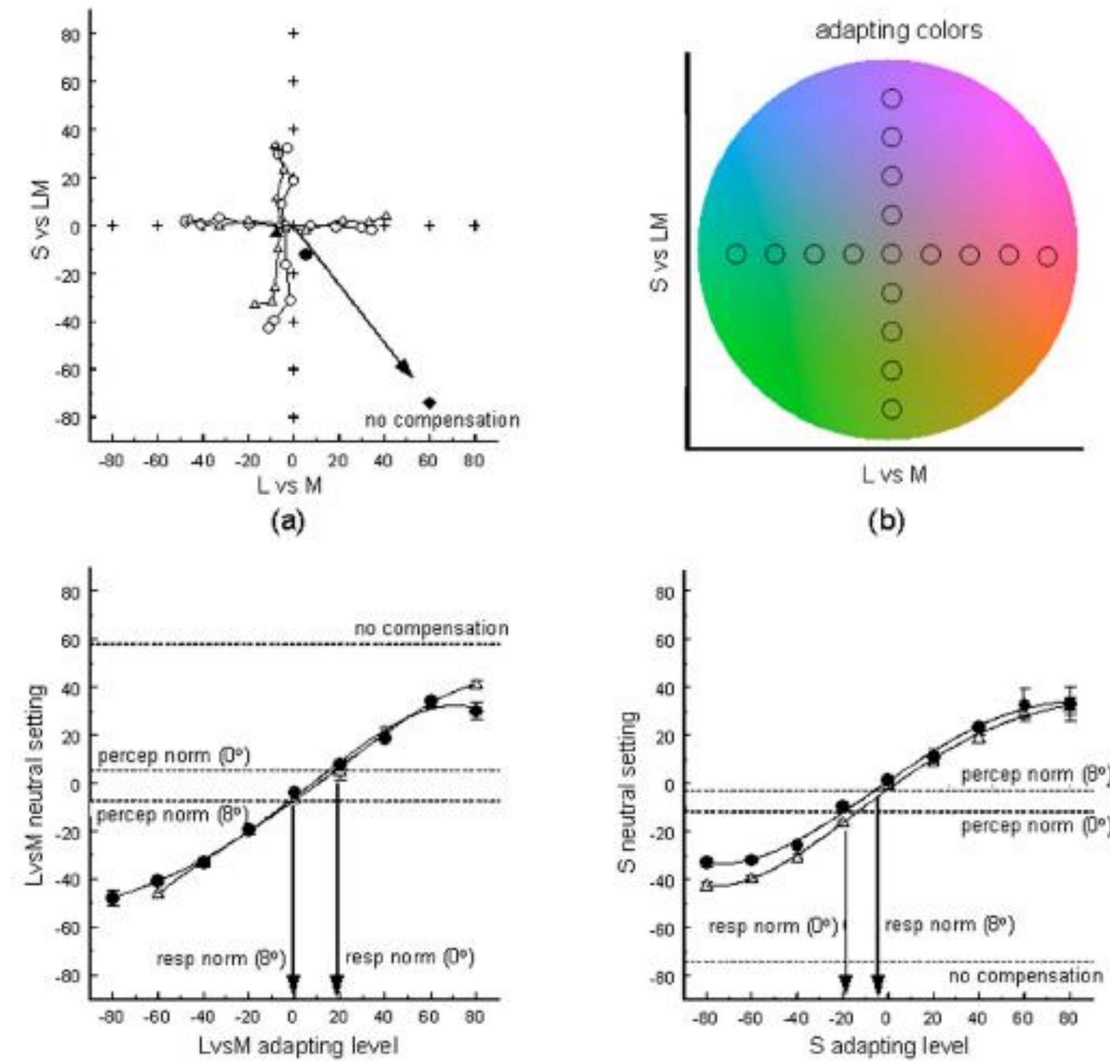
White settings in the fovea and periphery:
Nearly complete compensation for the macular pigment density, consistent with local receptor adaptation





Beer et al. JOV 2005; Webster and Leonard JOSA A 2008

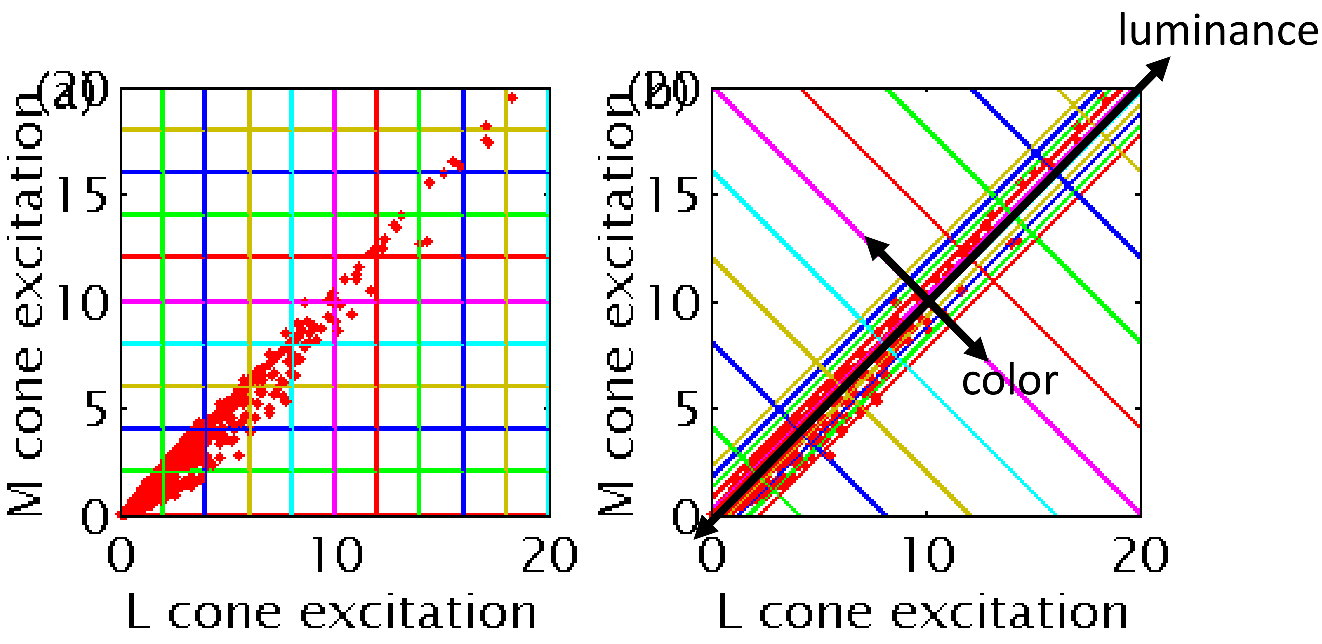
Adaptation in the fovea and periphery is adjusted to the same physical stimulus, not the same retinal stimulus



Webster and Leonard JOSA A 2008

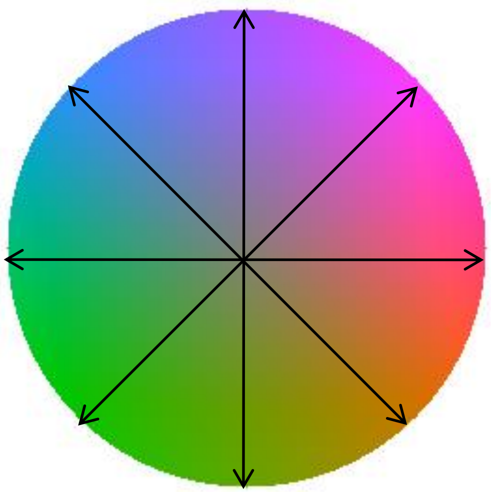
Compensating for the variance

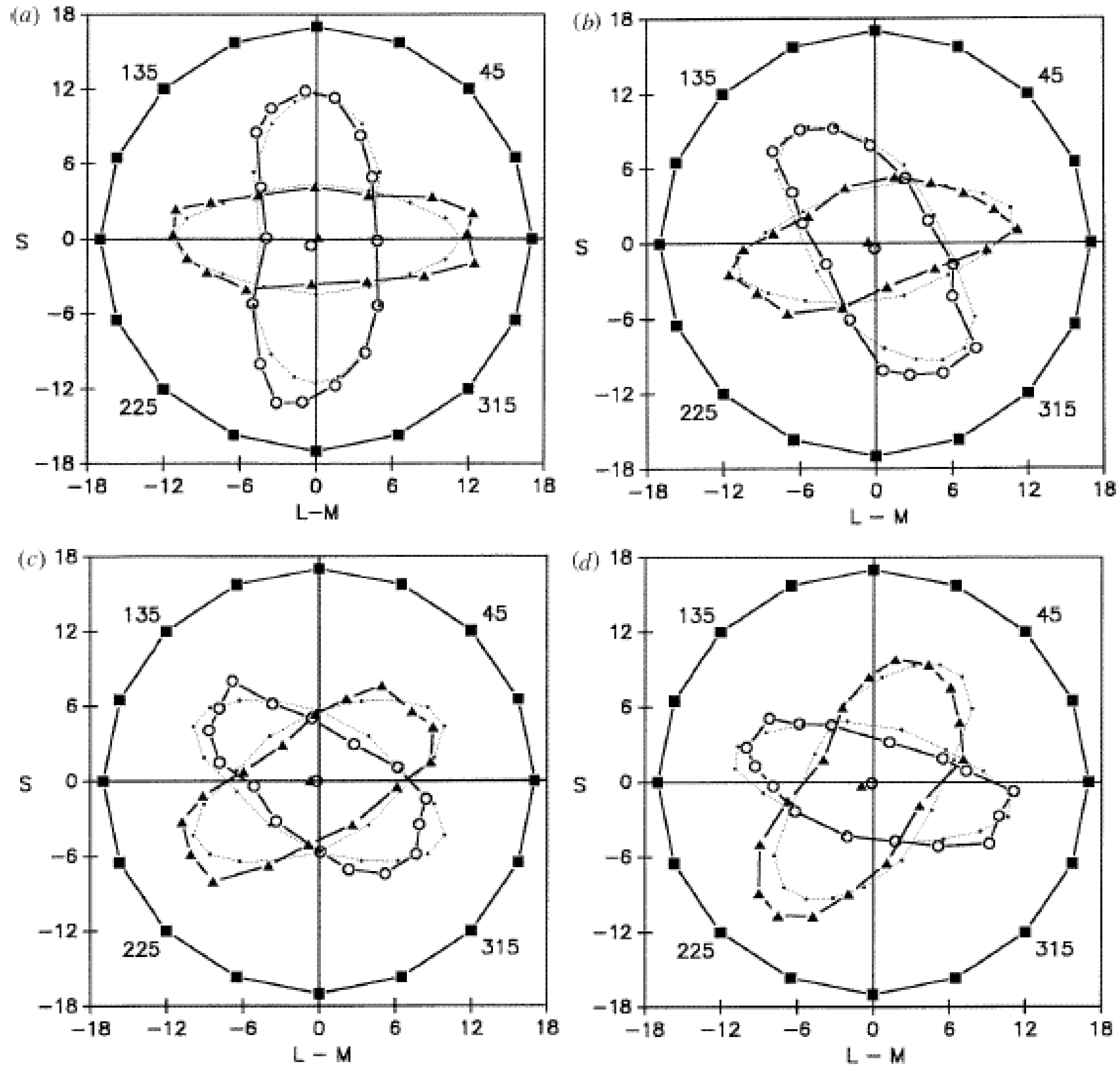
Chromatic signals are weaker than luminance but perceived contrast is similar



MacLeod and von der Twer *Colour Perception: Mind and the physical world* 2003;

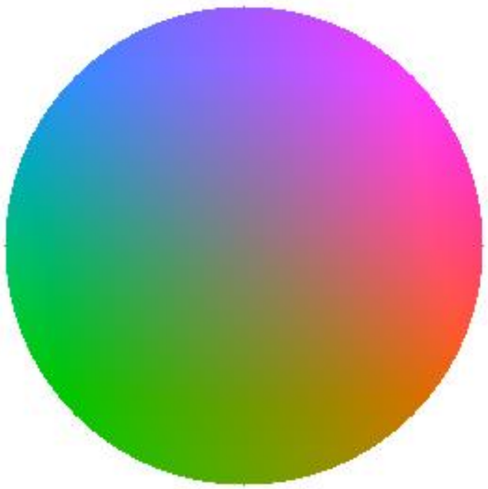
Adaptation can adjust to biases along different color directions

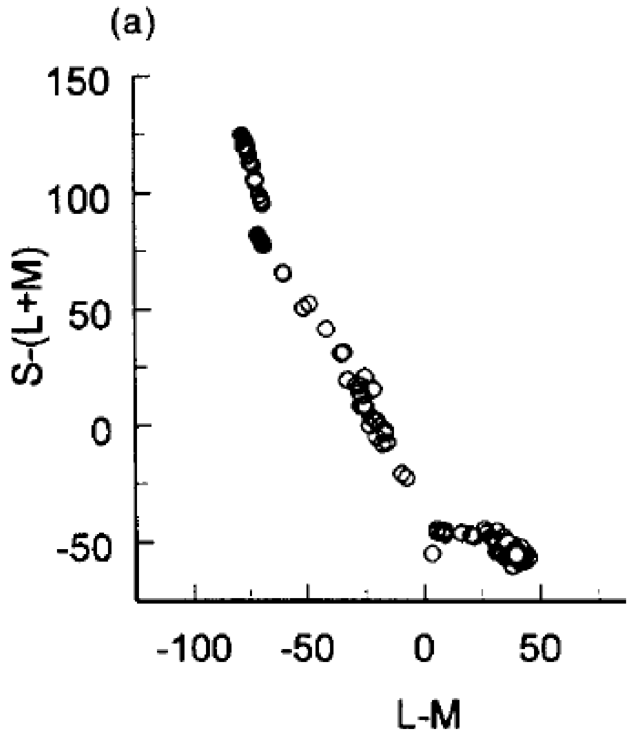


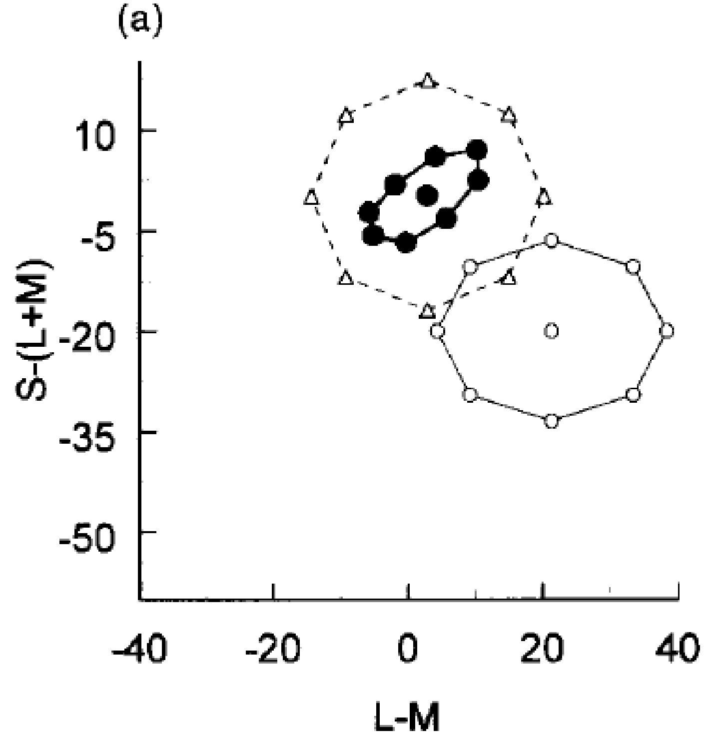


Krauskopf et al. Vision Res 1986; Webster and Mollon Nature 1991

And thus can adjust to the biases in natural color distributions



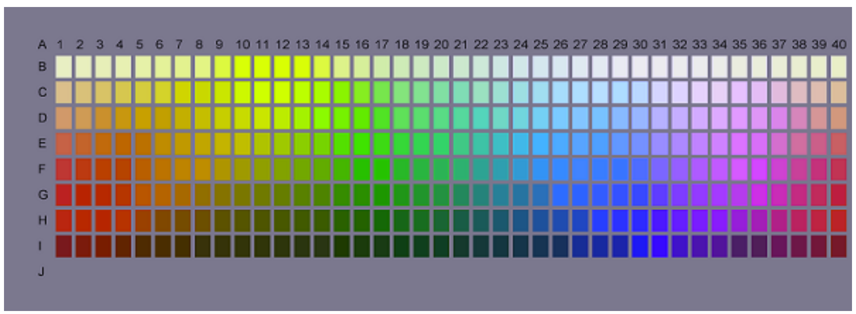


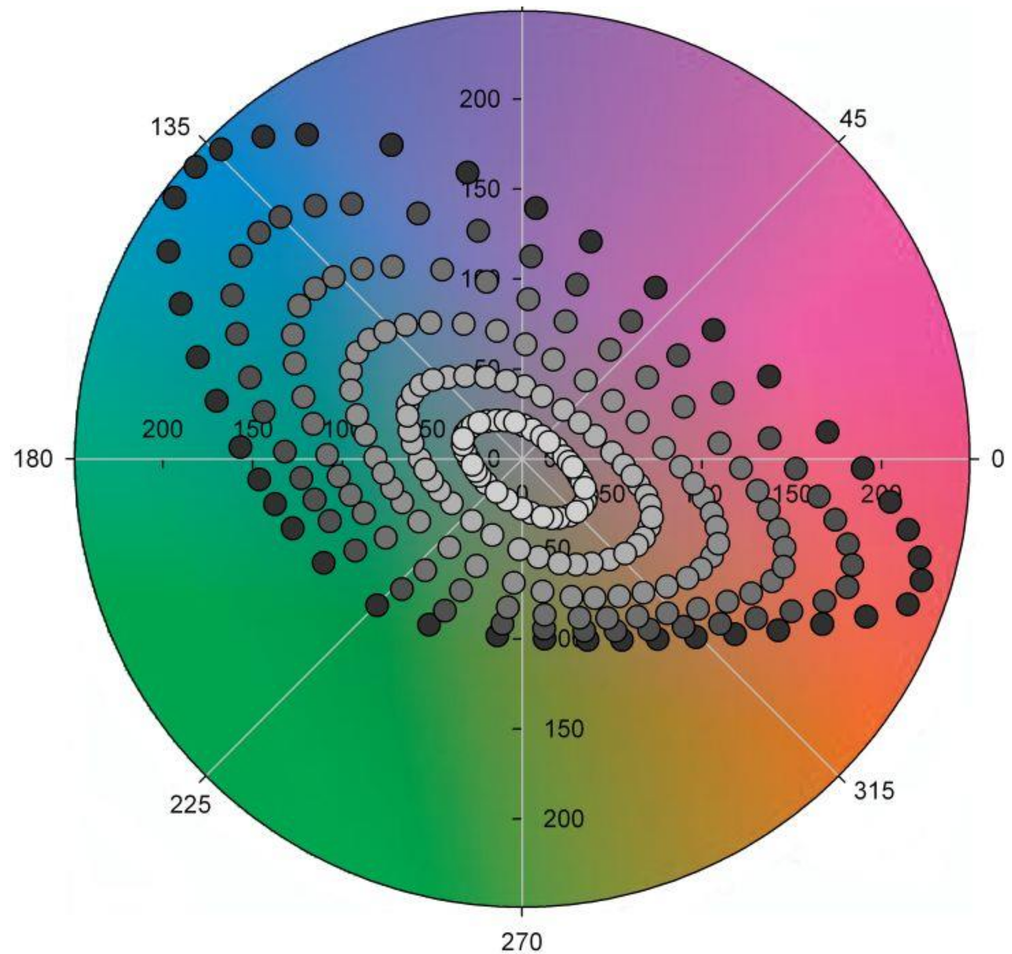


Webster and Mollon Vision Res 1997; Webster et al. JOV 2002

Environments implied by uniform color spaces

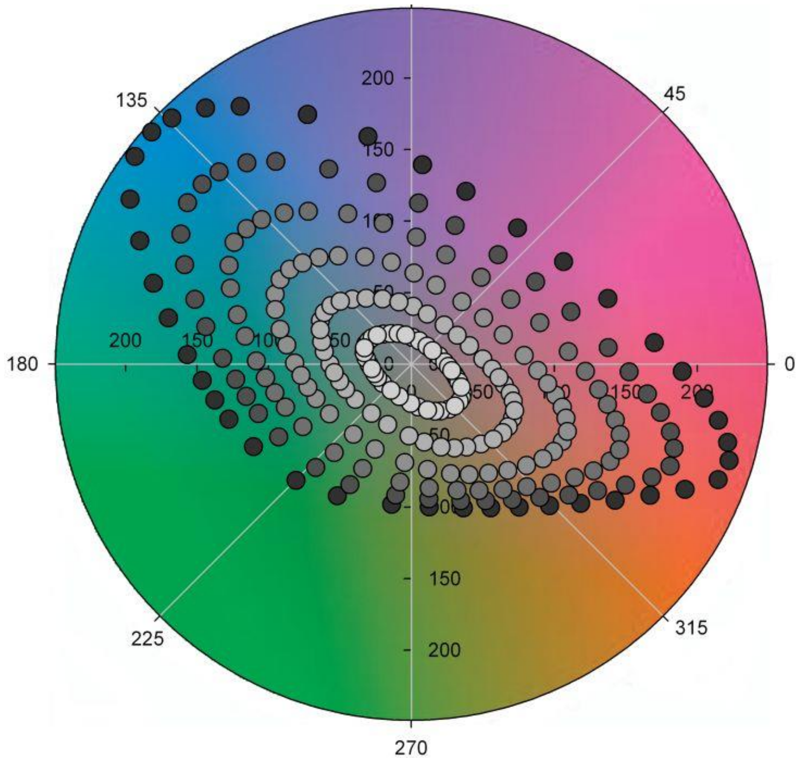
e.g. distribution of Munsell hues in cone-opponent space

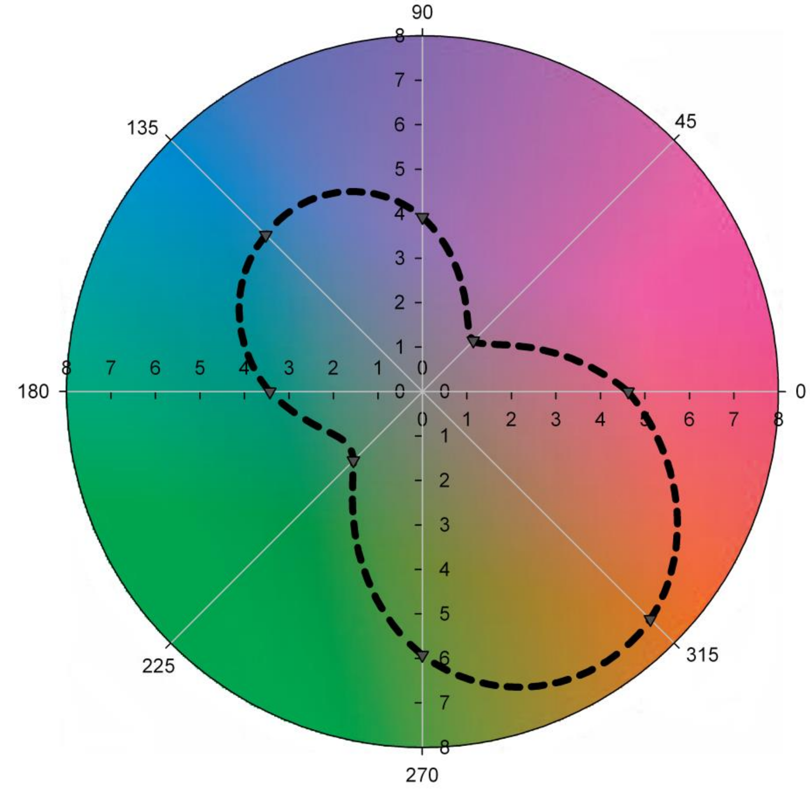




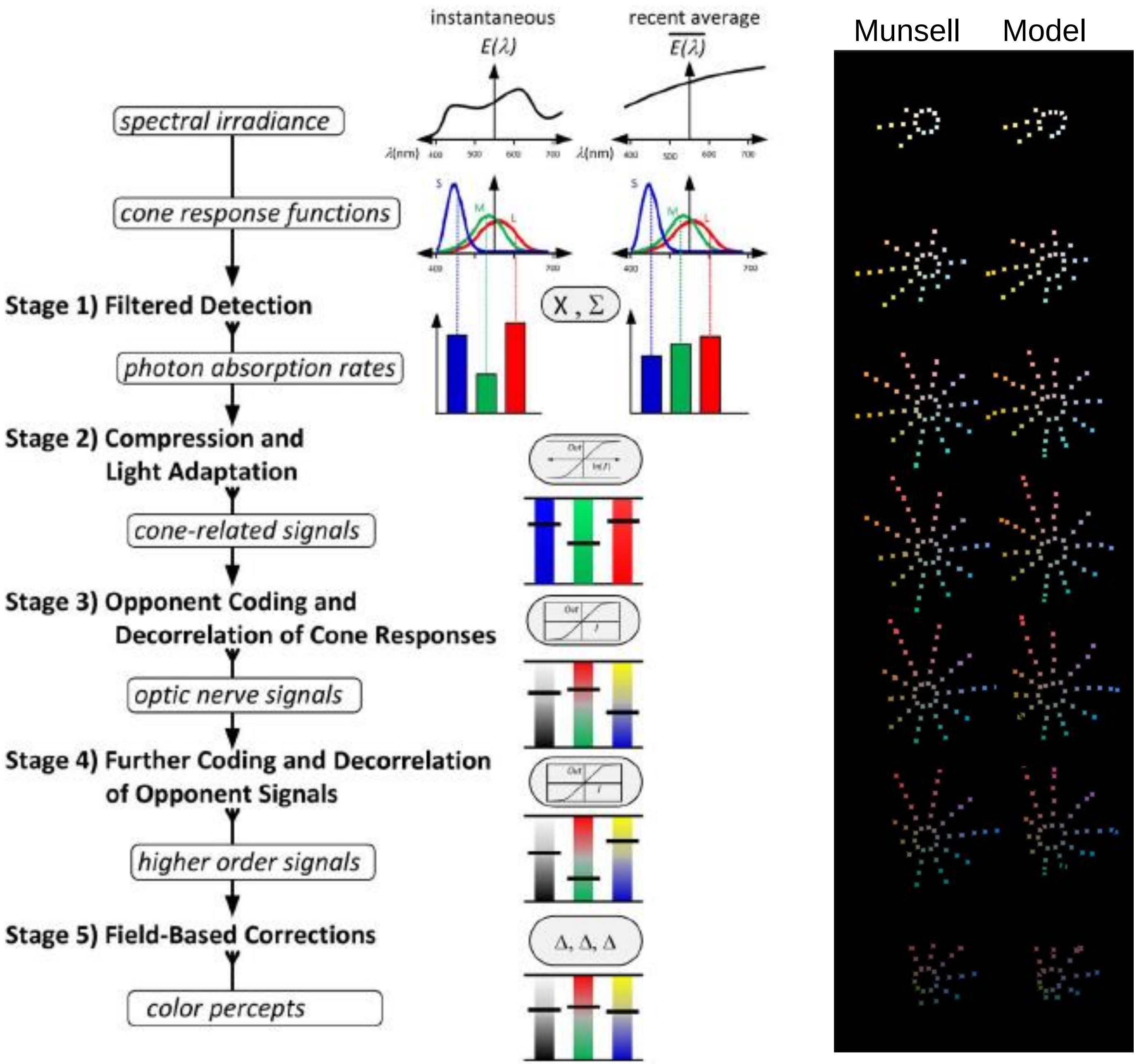
McDermott and Webster JOSA A 2012

Constant chroma requires greater cone-opponent contrasts along the blue-yellow axis, consistent with adaptation to greater blue-yellow variation in the world





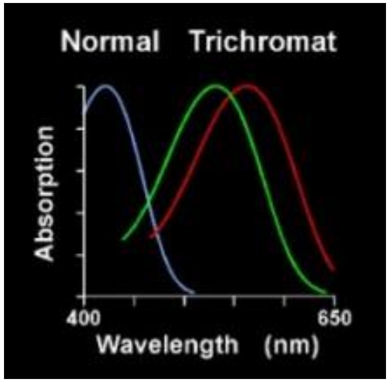
A uniform color metric based on visual coding of the color environment

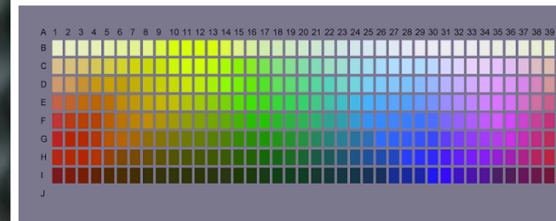


Smet, Webster and Whitehead JOSA 2016

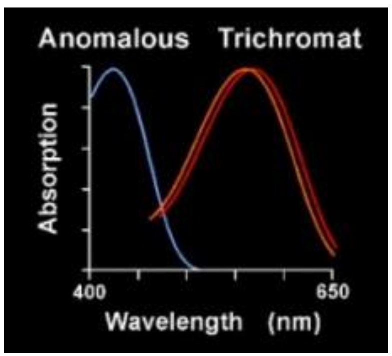
Compensation for color deficiencies

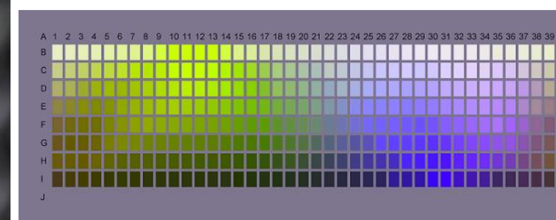
trichromat



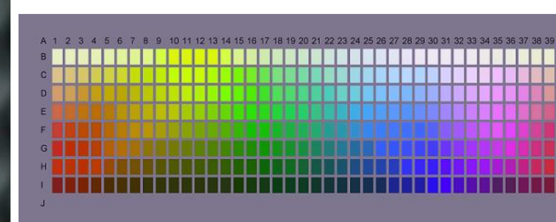


anomalous pigments

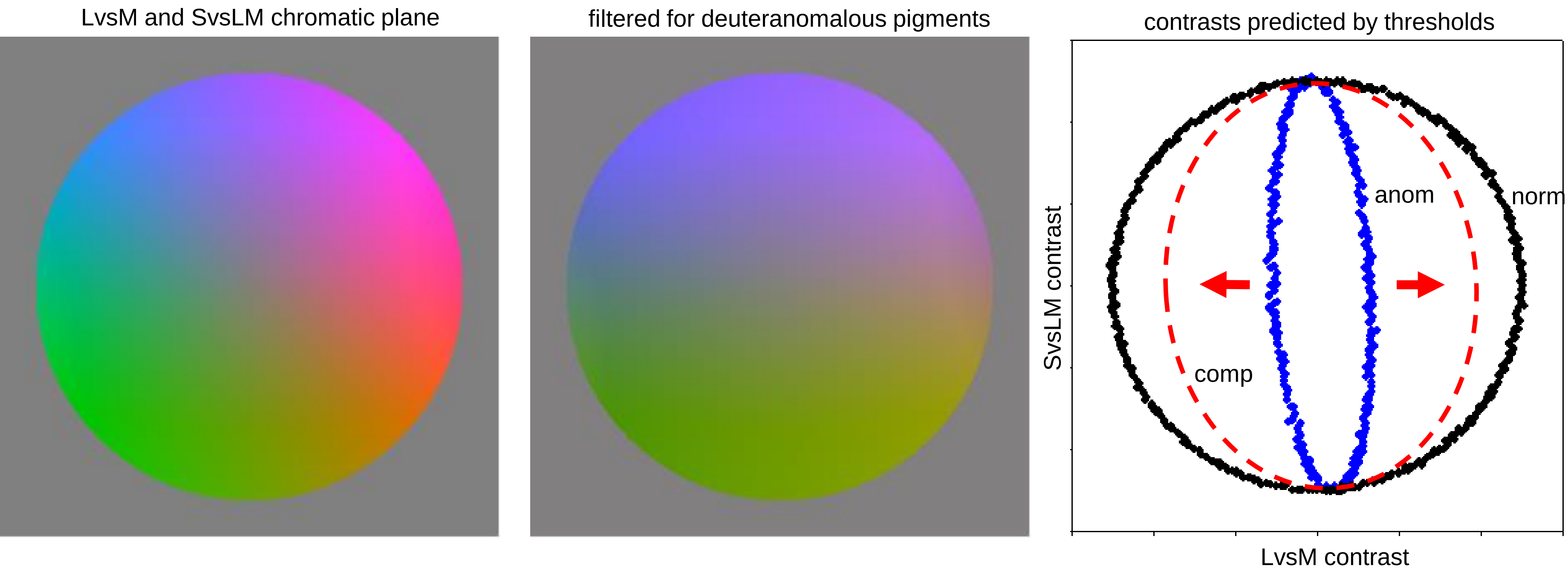




color percepts
compensated for
reduced LM contrast

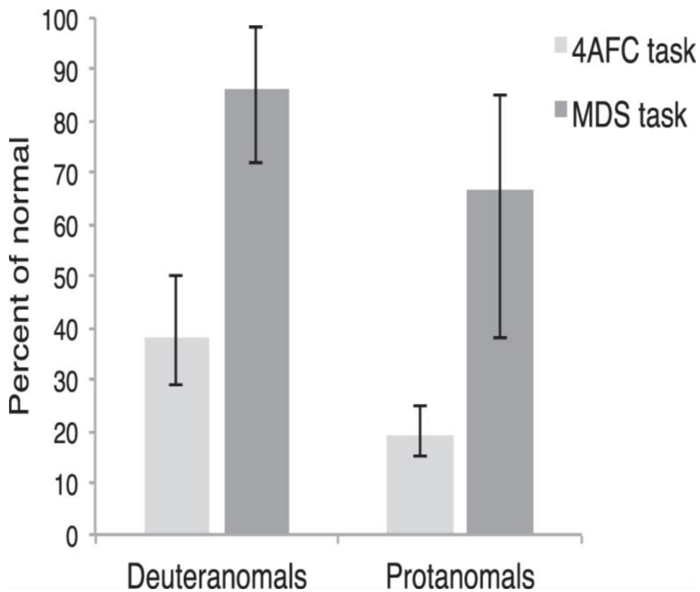


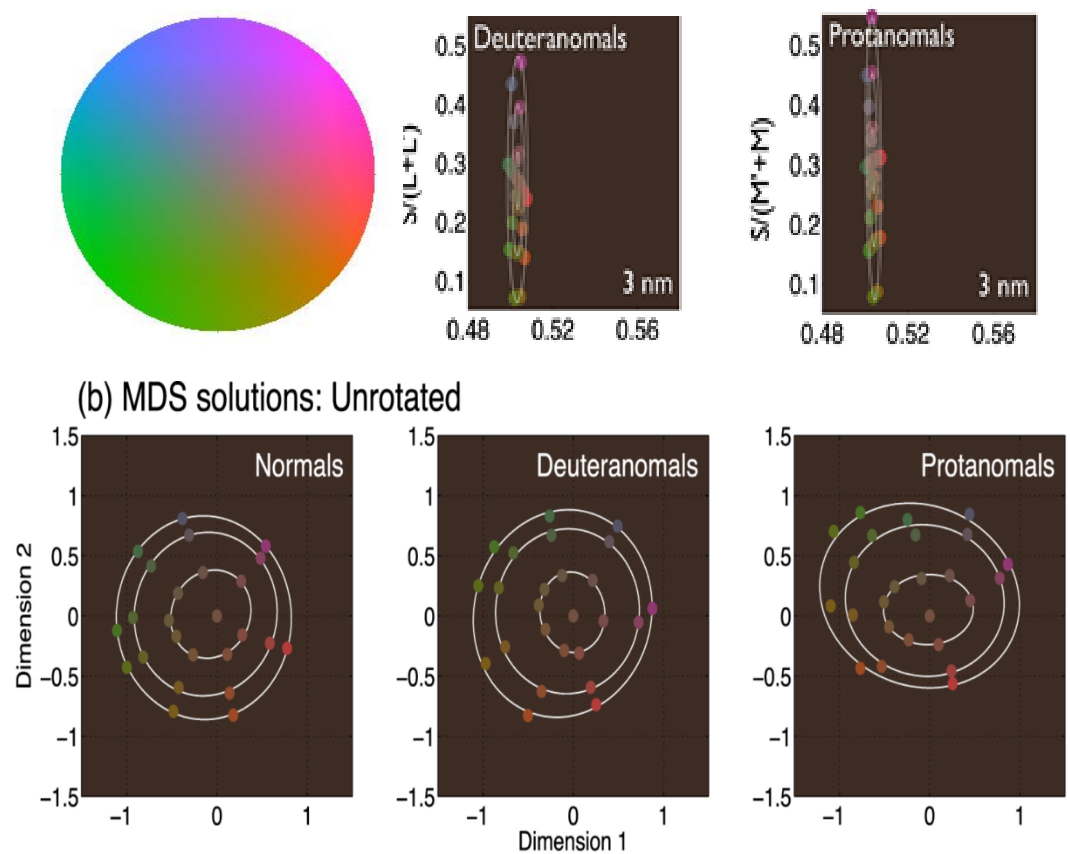
Webster et al. 2010


LvsM and SvsLM chromatic plane
filtered for deuteranomalous pigments
contrasts predicted by thresholds
anom
norm
comp
SvsLM contrast
LvsM contrast

Anomalous trichromats and contrast scaling

Anomals weight L-M contrasts more than their cone sensitivity predicts

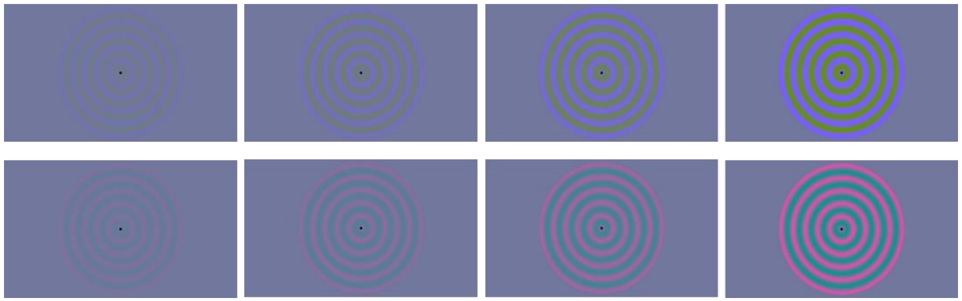


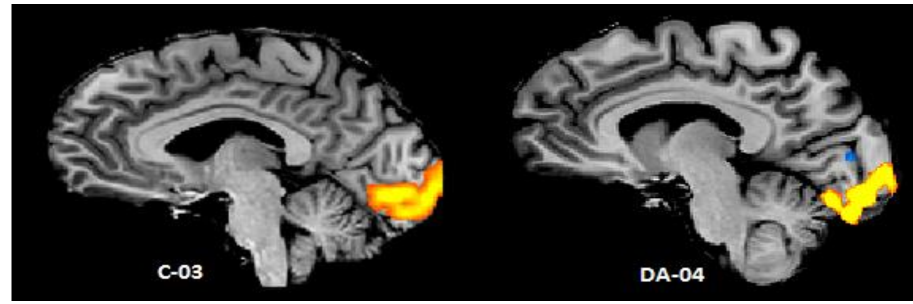


Boehm et al. JOV 2014; Bosten Cur Op Beh Sci 2019; Knoblauch et al. JOSA A 2020

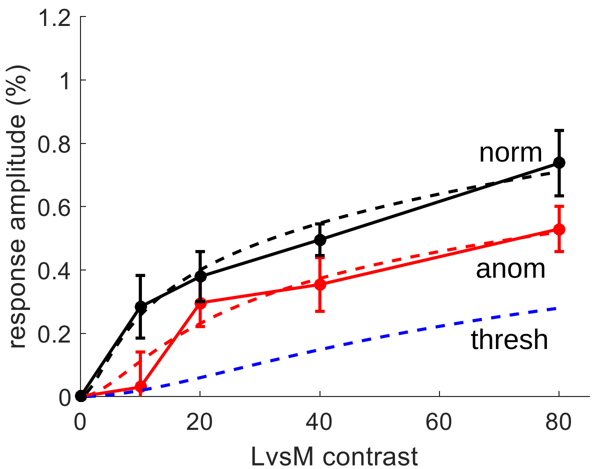
Neural correlates of contrast compensation

BOLD responses to LM or S chromatic contrast

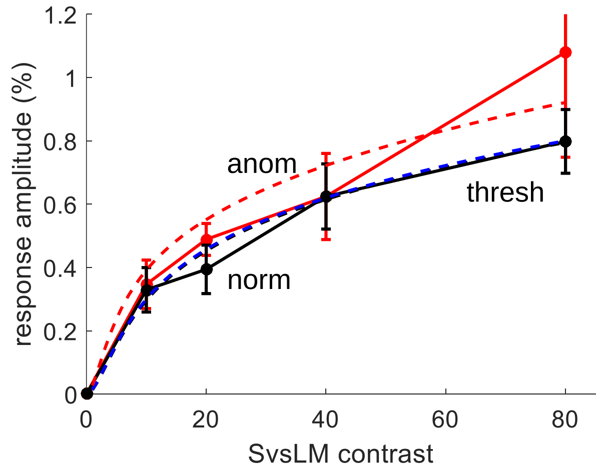




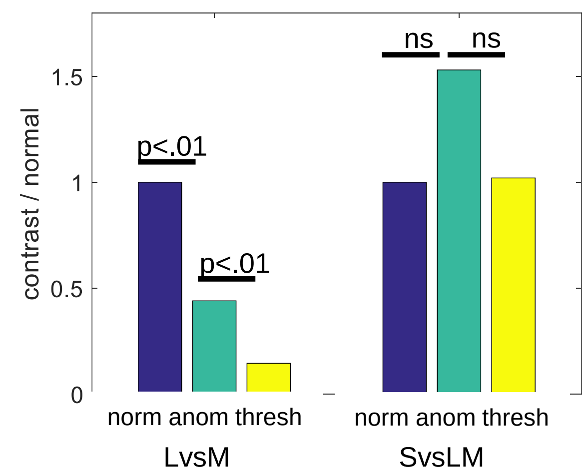
LvsM: predicted vs observed



SvsLM: predicted vs observed



contrast ratio



Tregillus et al., in preparation

Interim Summary

1. Adaptation compensates for the sensitivity variations in the observer

2. This tends to maintain a high degree of color constancy within the observer

3. It should also promote “inter-observer” constancy to the extent that different observers are adapted to the same environment

Adaptation and individual differences

But if adapting different observers to the same environment leads to converging perceptual experiences

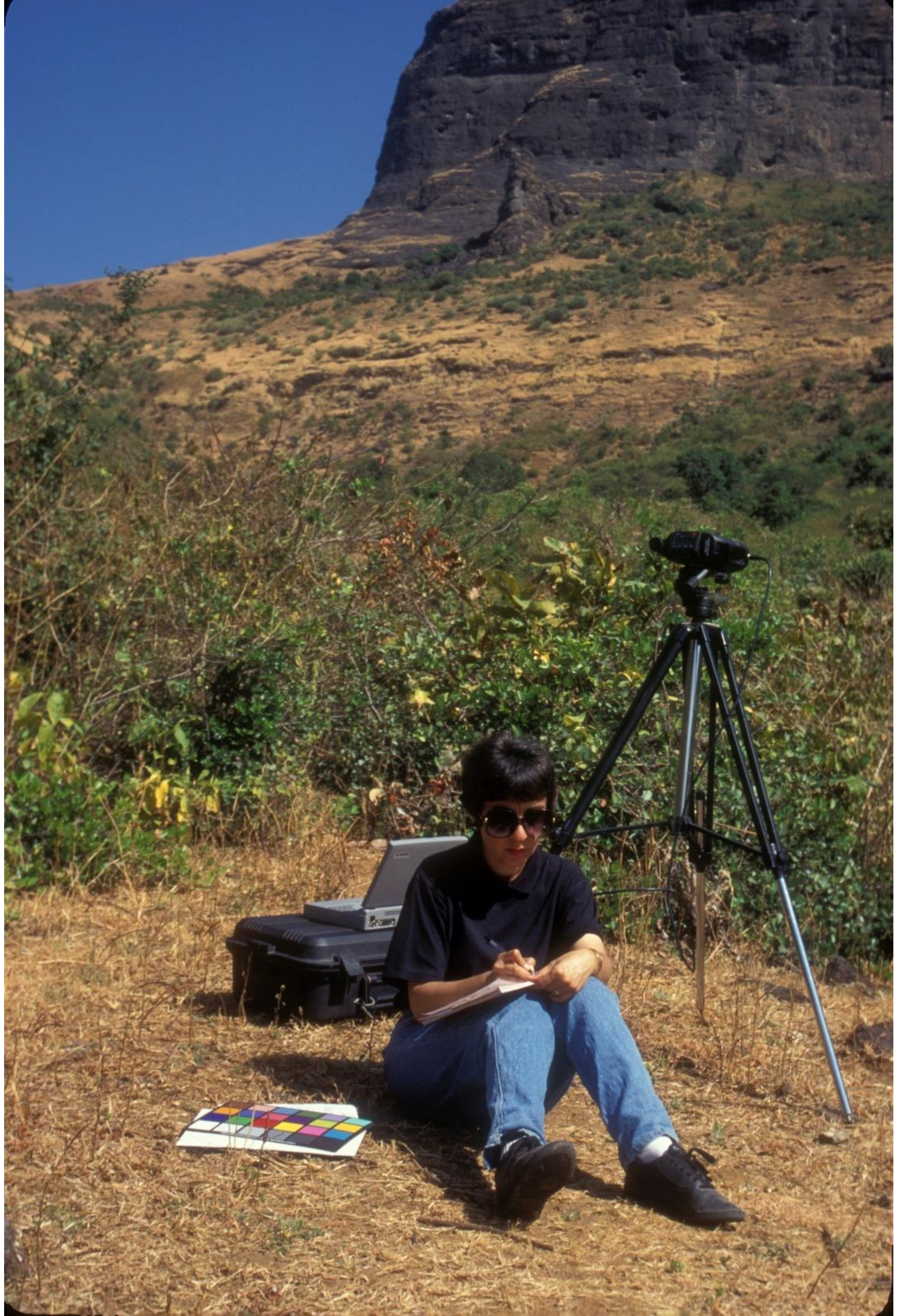
Then adapting similar observers to different environments should lead to diverging percepts

Adaptation and natural color distributions

Monsoon - September

Winter - January

Webster and Mollon Vision Res 1997; Webster et al. Network 2007



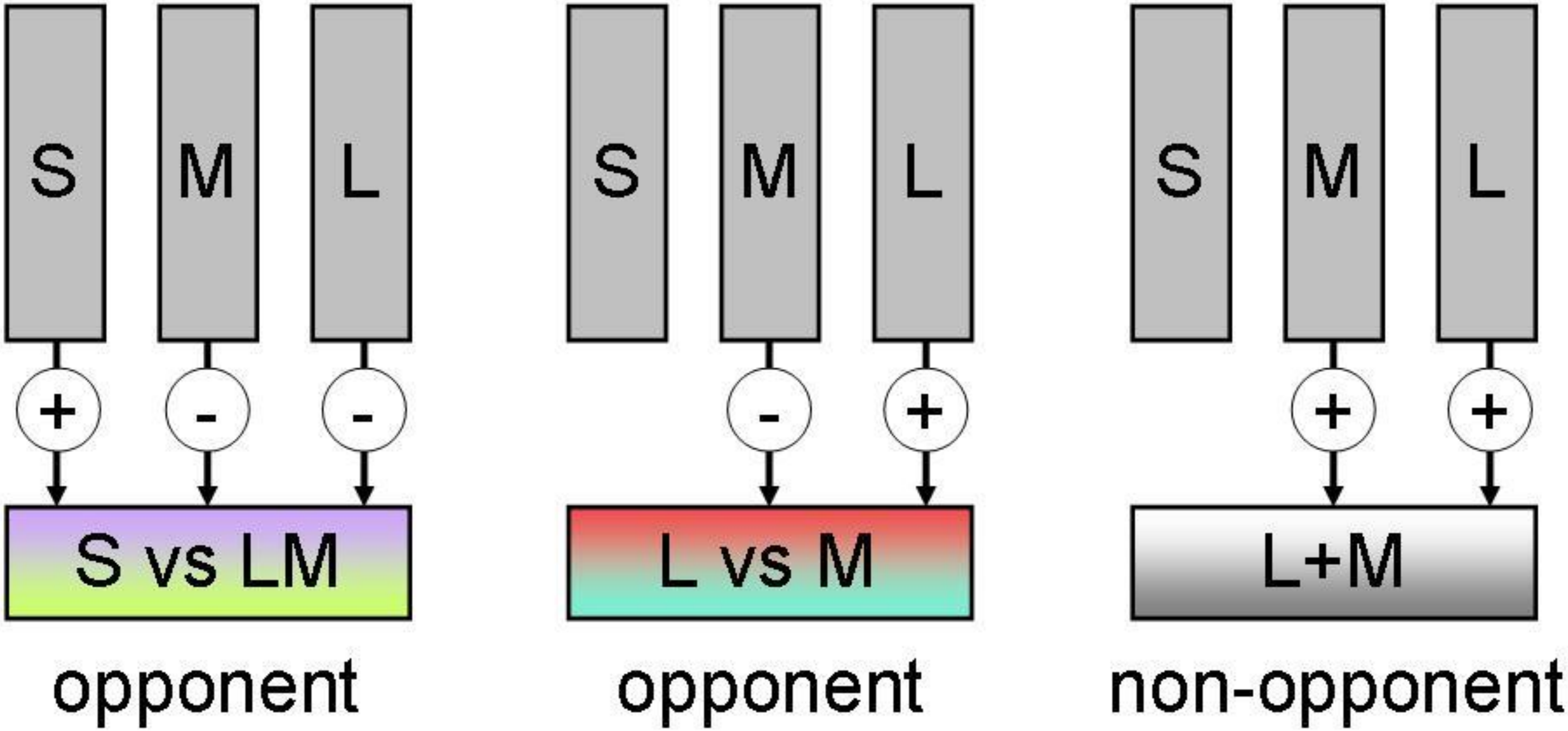
Predicting adaptation to different environments

To the extent that we understand the processes of color adaptation, we can simulate how scenes should look under different states of adaptation

Webster Vision Res 2014

Adaptation modeled by gain control in the receptors (to match the mean)

And gain control in multiple cortical color channels (to match the contrasts)



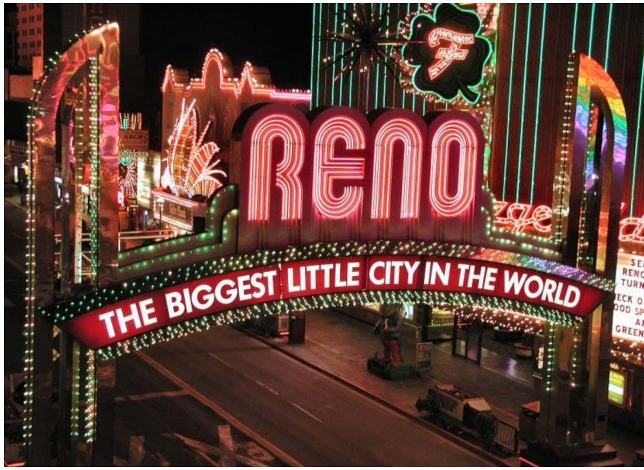
examples of natural environments

examples of other environments

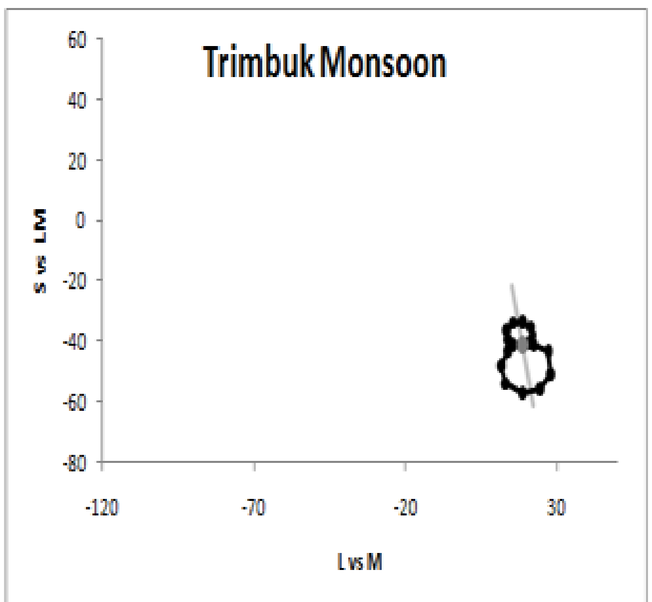
uncharacteristic

unnatural

uncivilized

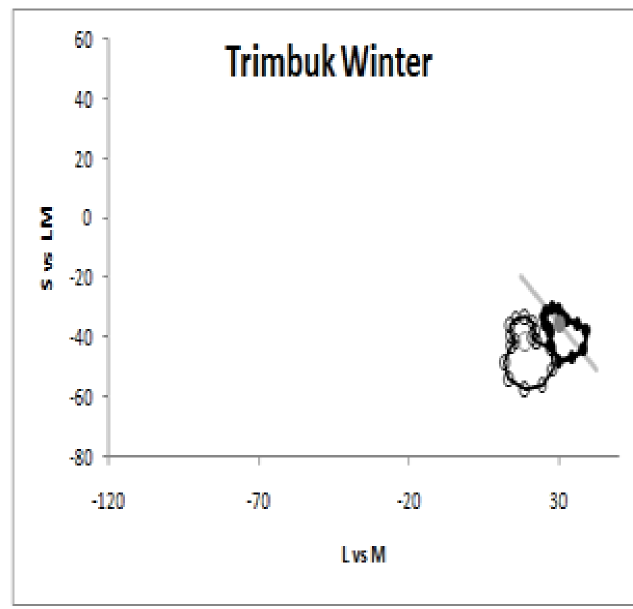


lush environment

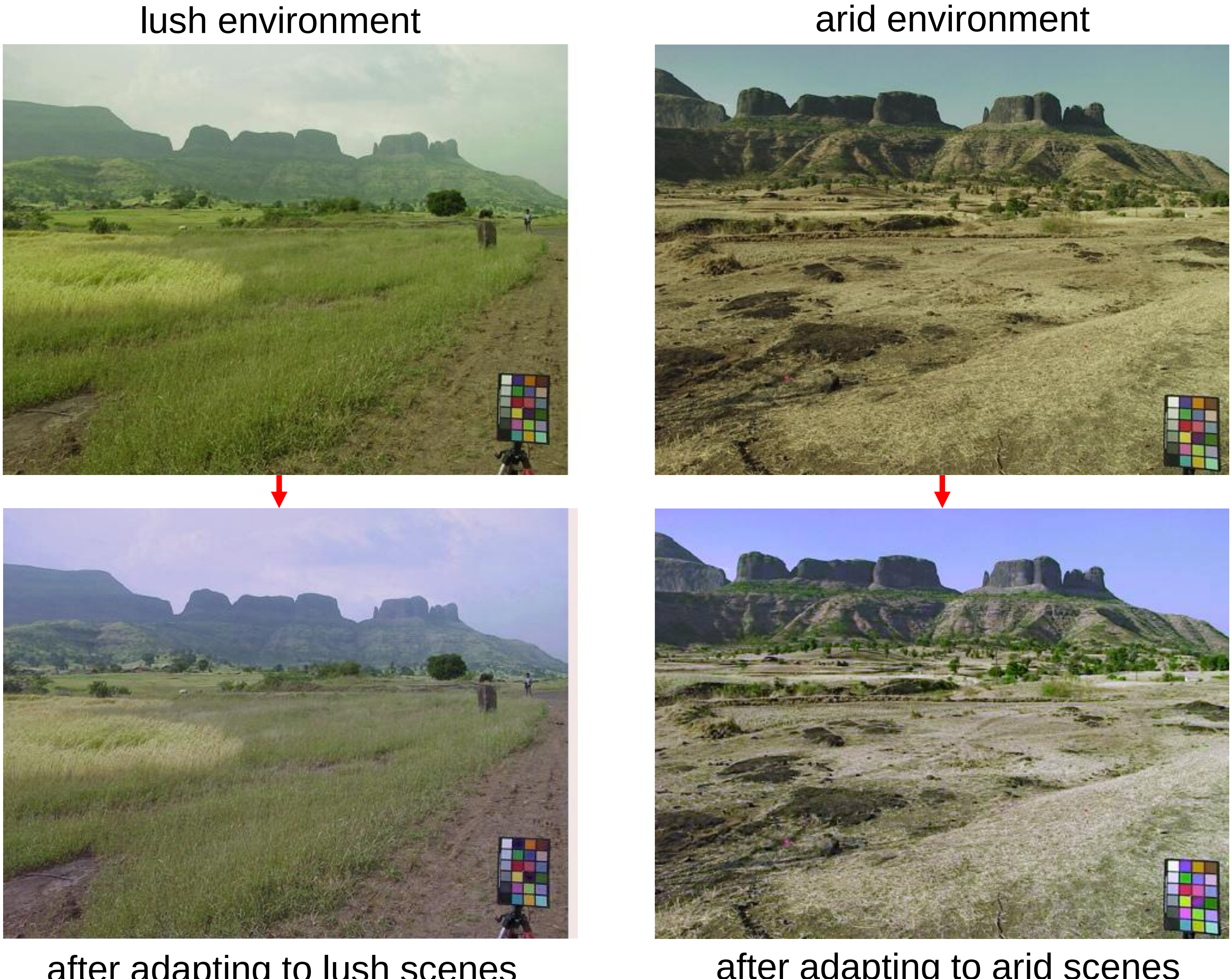


mean responses to lush scenes

arid environment



mean responses to arid scenes


lush environment
arid environment
after adapting to lush scenes
after adapting to arid scenes

Adaptation to more extreme environments
e.g. seeing “red” on Mars

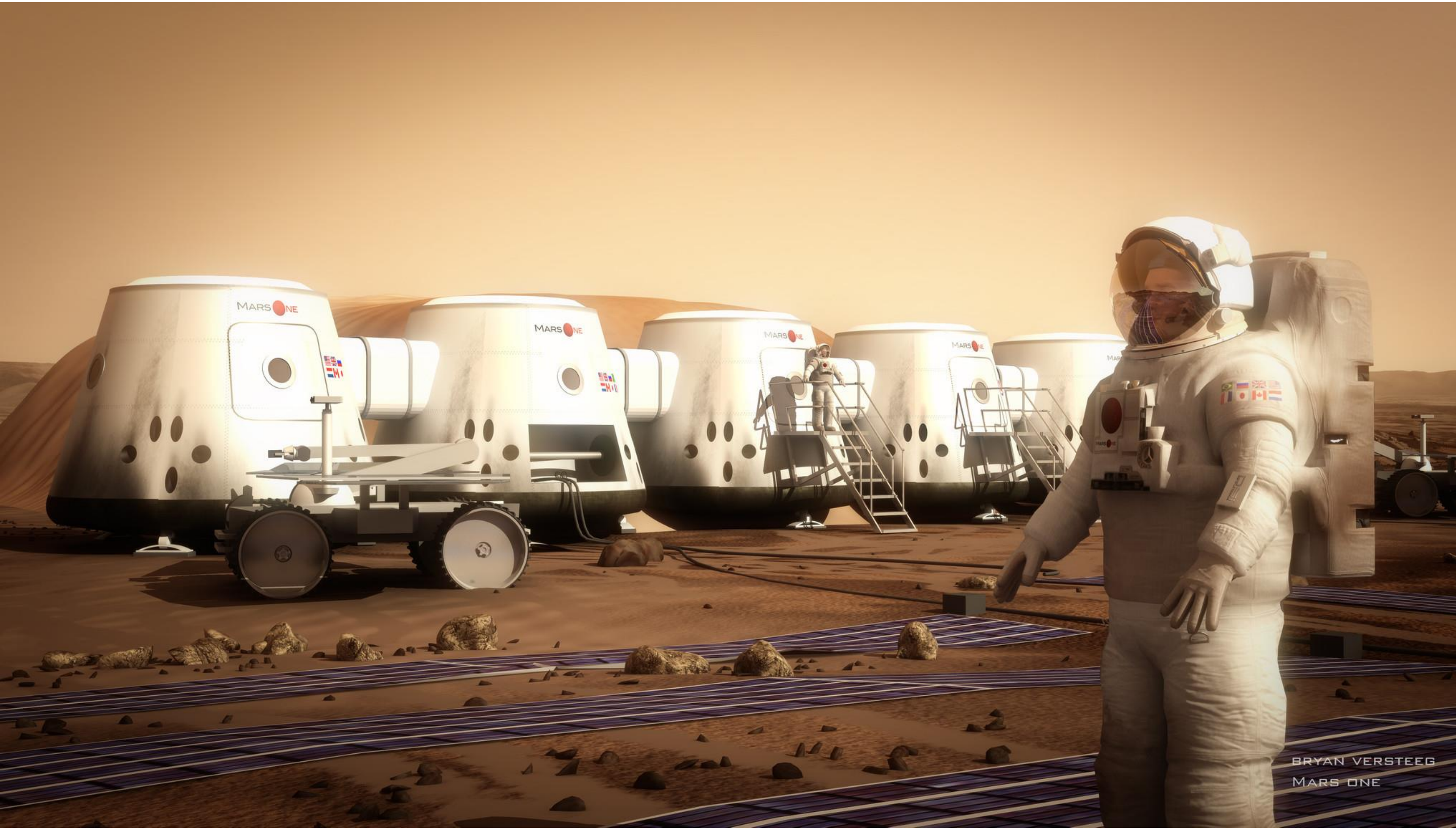
adapted to earth

adapted to mean

adapted to contrasts

Webster, Glimpse 2009

Mars One



Kay Radzik Warren from Reno 1 of 100 finalists
from more than 200,000 applicants!

Adaptation to more extreme environments
e.g. seeing “red” on Mars

adapted to earth

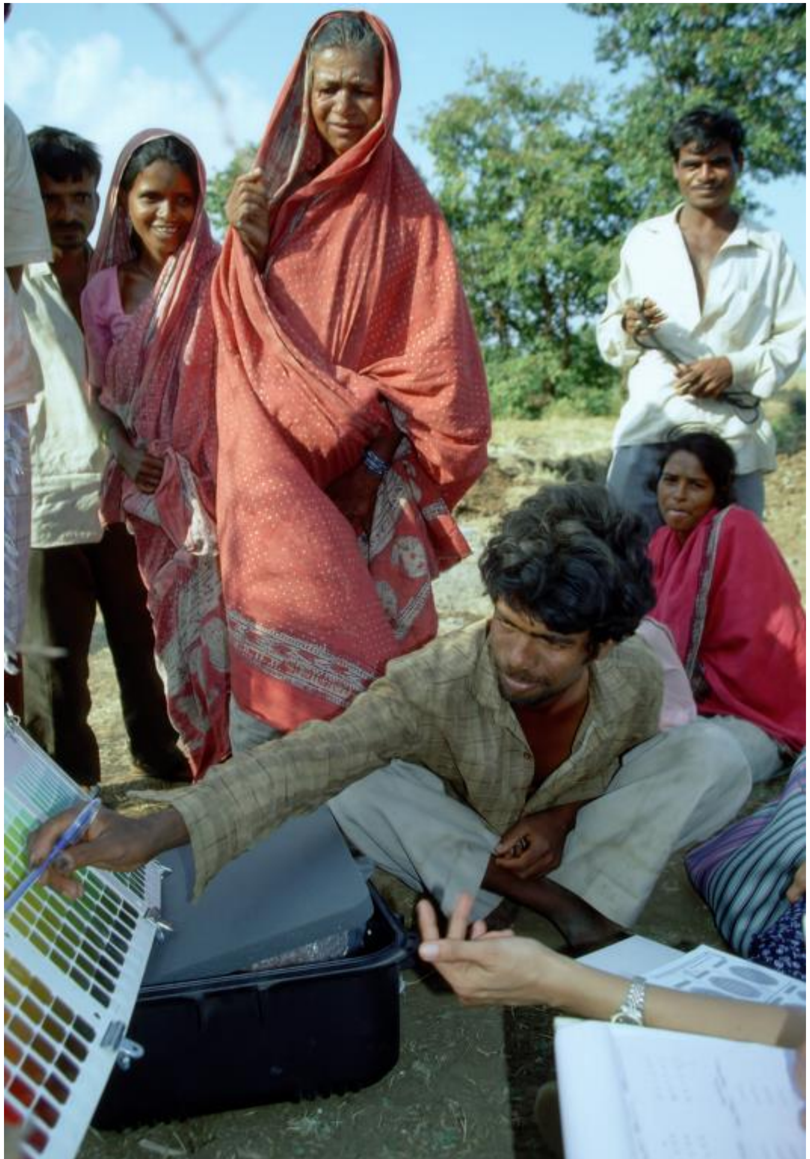
adapted to mean

adapted to contrasts

Webster, Glimpse 2009

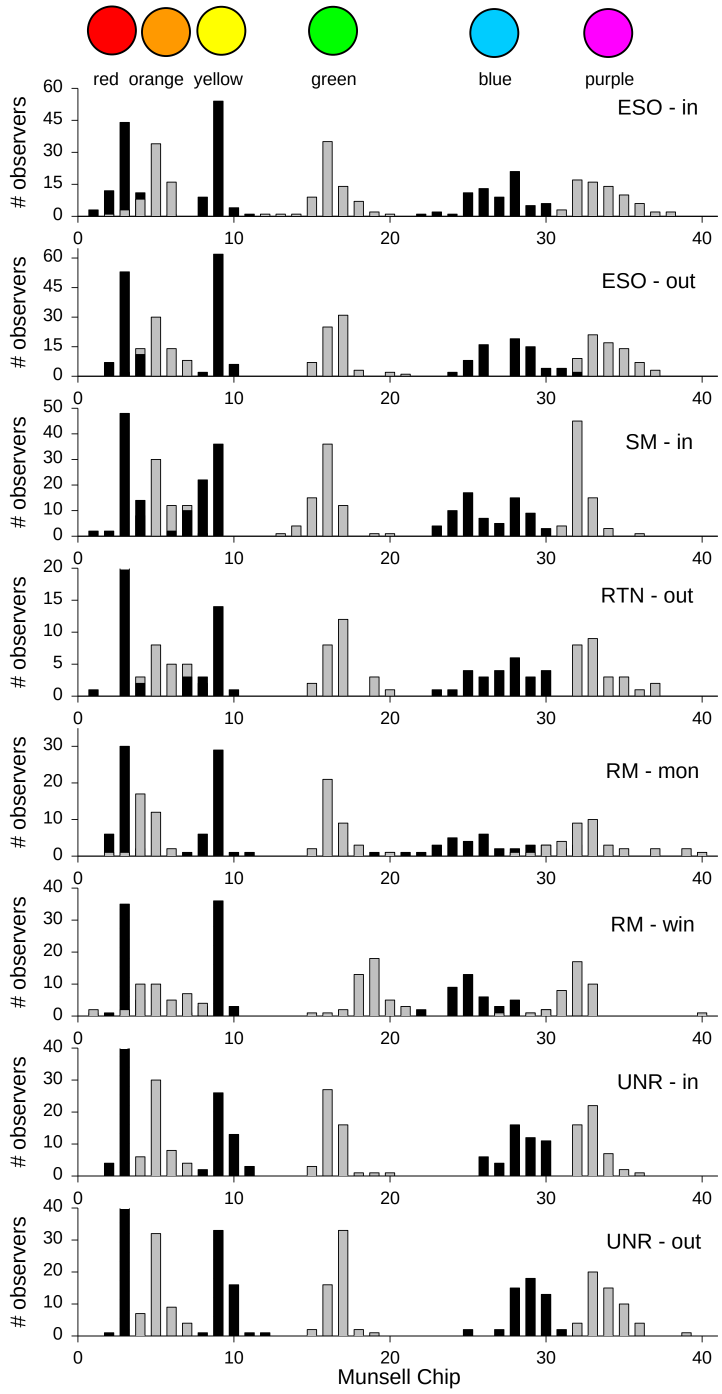
Testing color percepts in different environments

Webster et al. JOSA A 2004



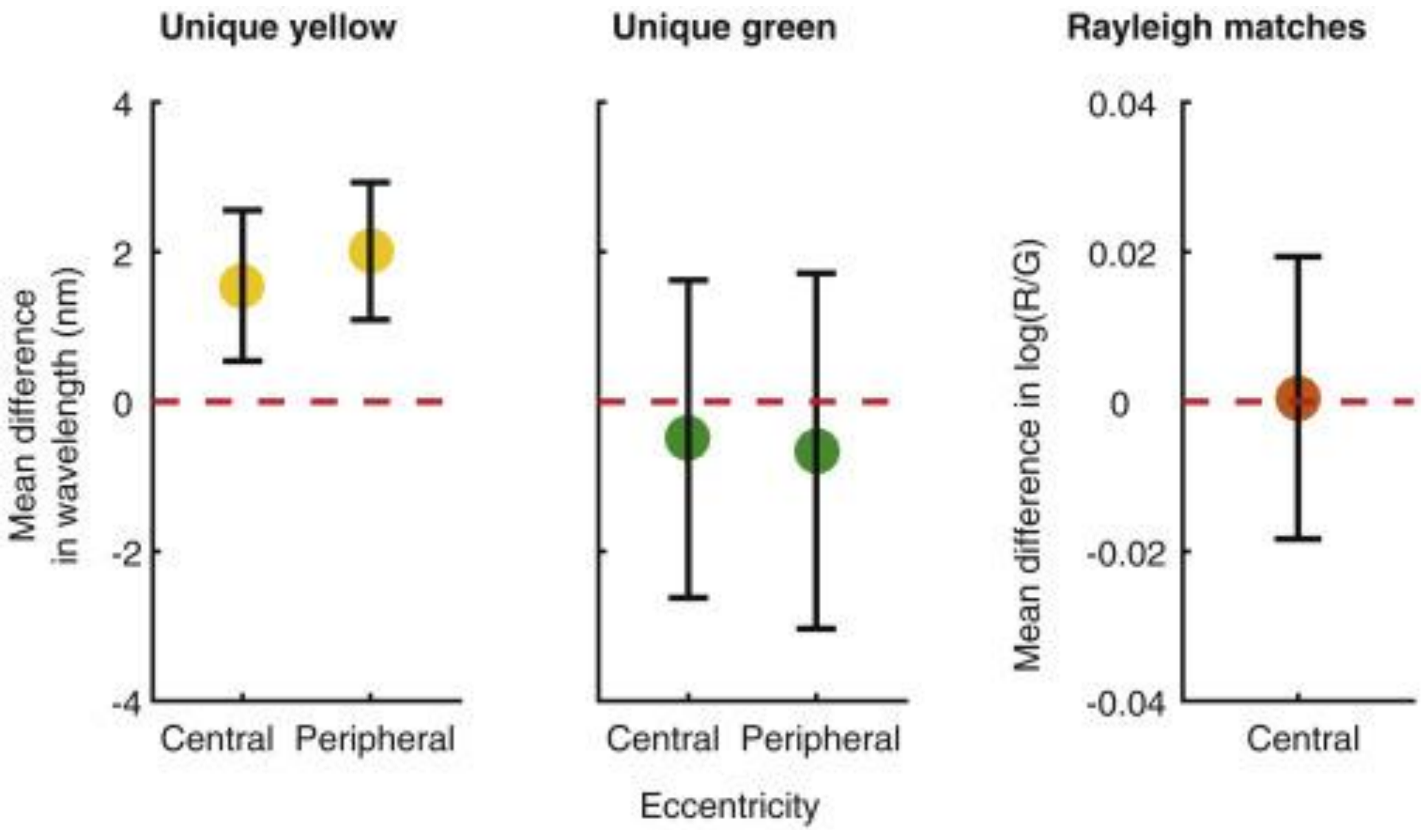

A
B
C
D
E
F
G
H
I
J
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19
20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40

Focal hues in Munsell chips



Webster et al.
JOSA A 2004

Seasonal changes in unique yellow



Welbourne et al. Current Biology 2015

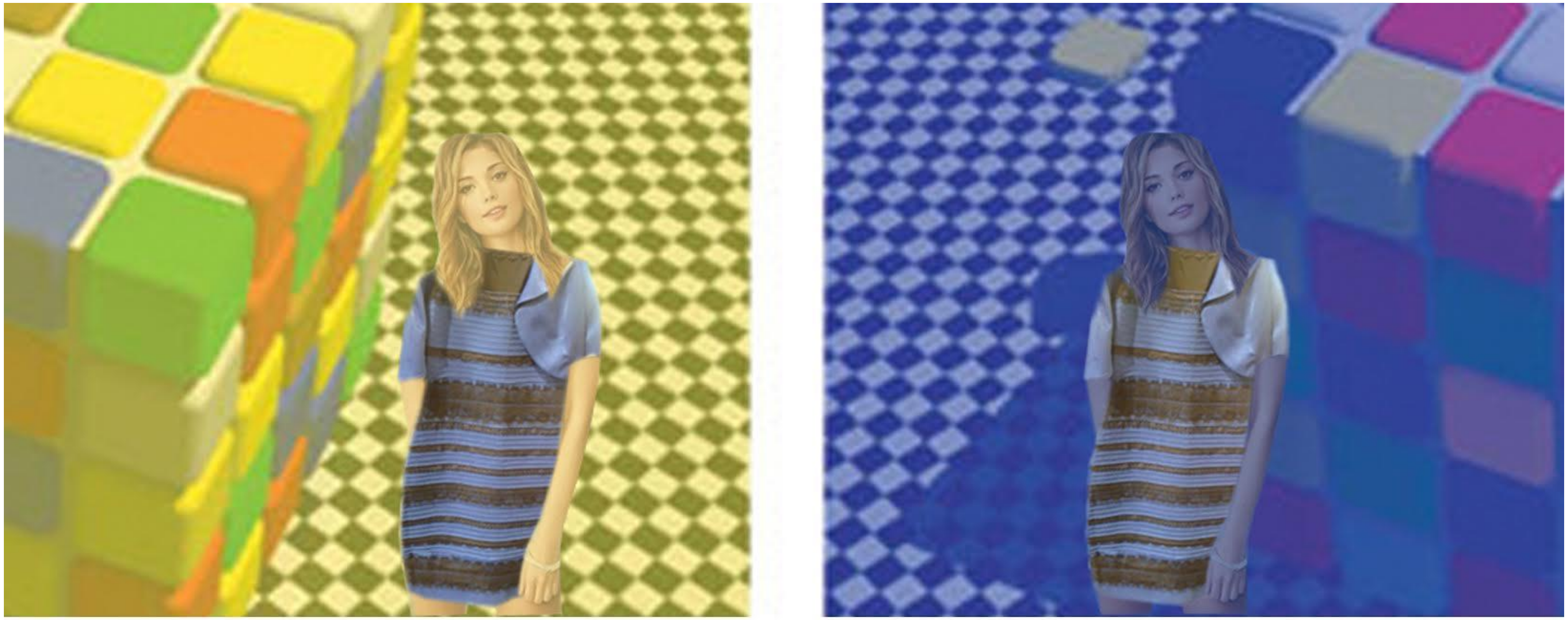
Interim Summary

1. Adaptation adjusts color perception for the observer's color environment

2. As a result individuals exposed to different environments should tend to see and experience color differently

Individual differences and higher-level factors: Color inferences

Accounts of the dress illusion point to whether you perceive the dress in bright light or shade



Rosa Lafer-Sousa (background by Beau Lotto)

Yukiyasu Kamitani

Why does the blue image appear less colorful than the yellow?

Occures even for uniform fields

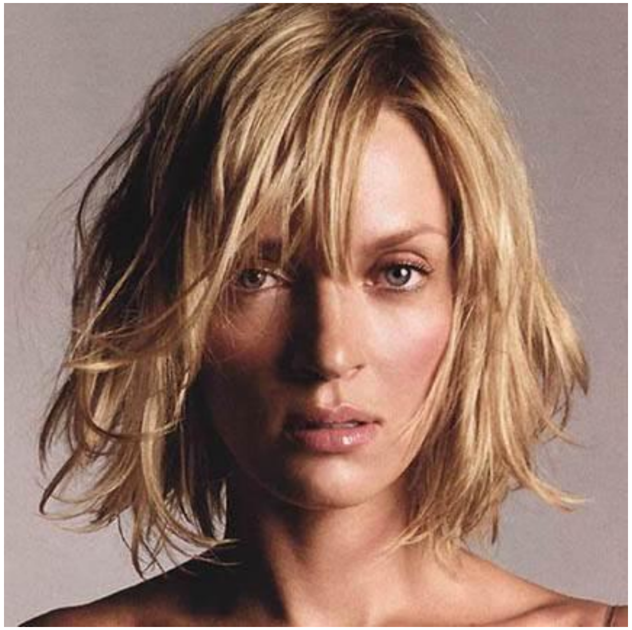
~specific to blue-yellow axis

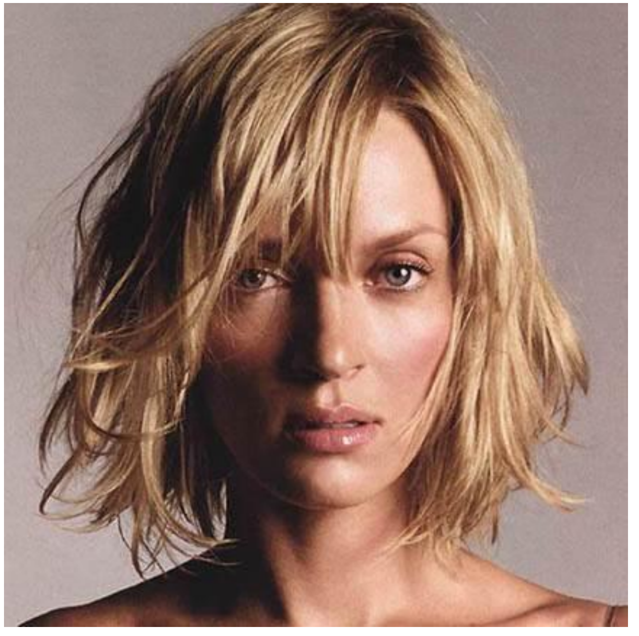



Inverting the color removes the ambiguity in the dress

Winkler et al. Cur Bio 2015; Gegenfurtner et al. Cur Bio 2015; Lafer-Sousa Cur Bio 2015

Blue-yellow and material percepts: inverting color can change steel to bronze

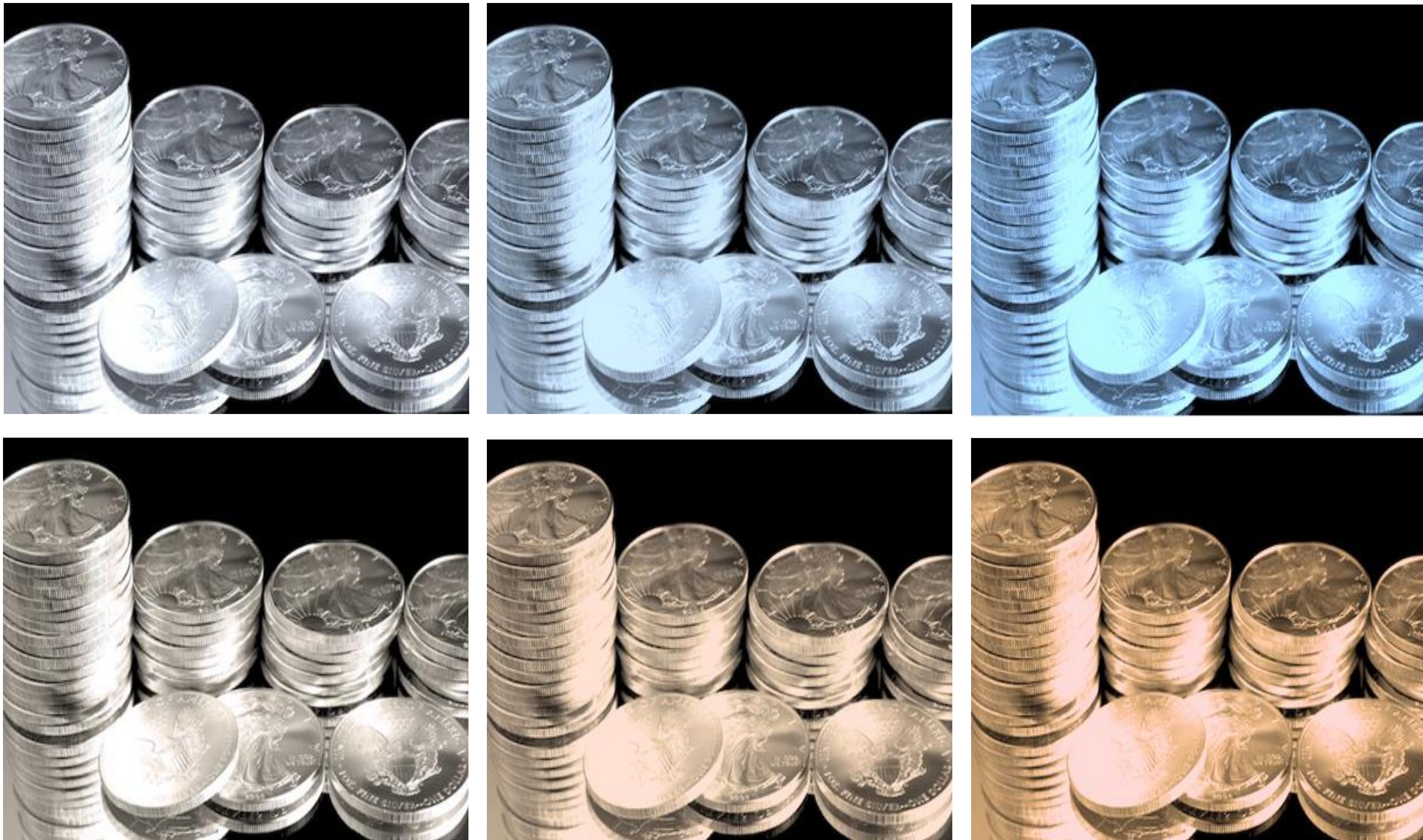


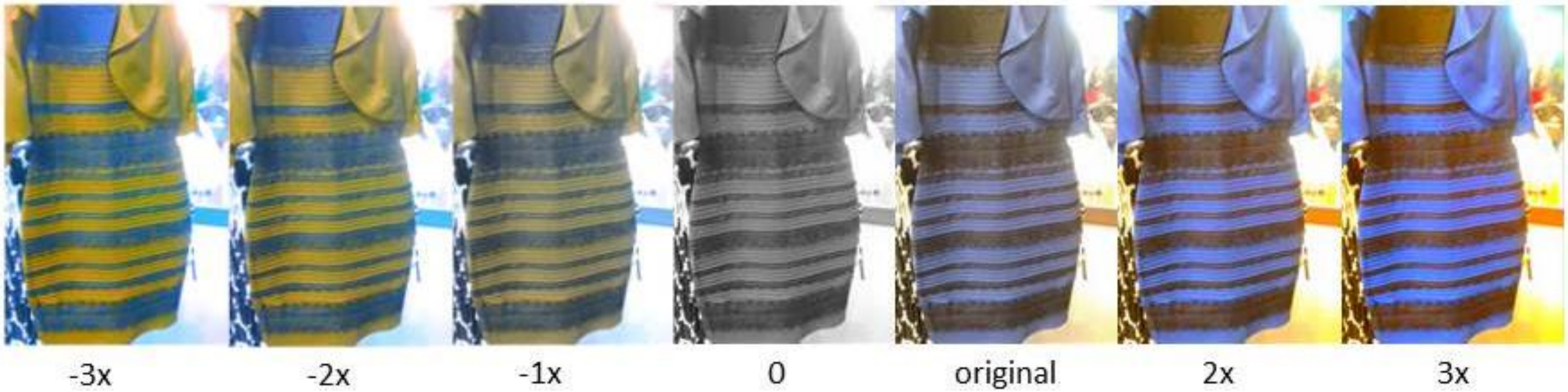

Shadows are from indirect light and tend to be blue: just as we discount their brightness we may discount their color.

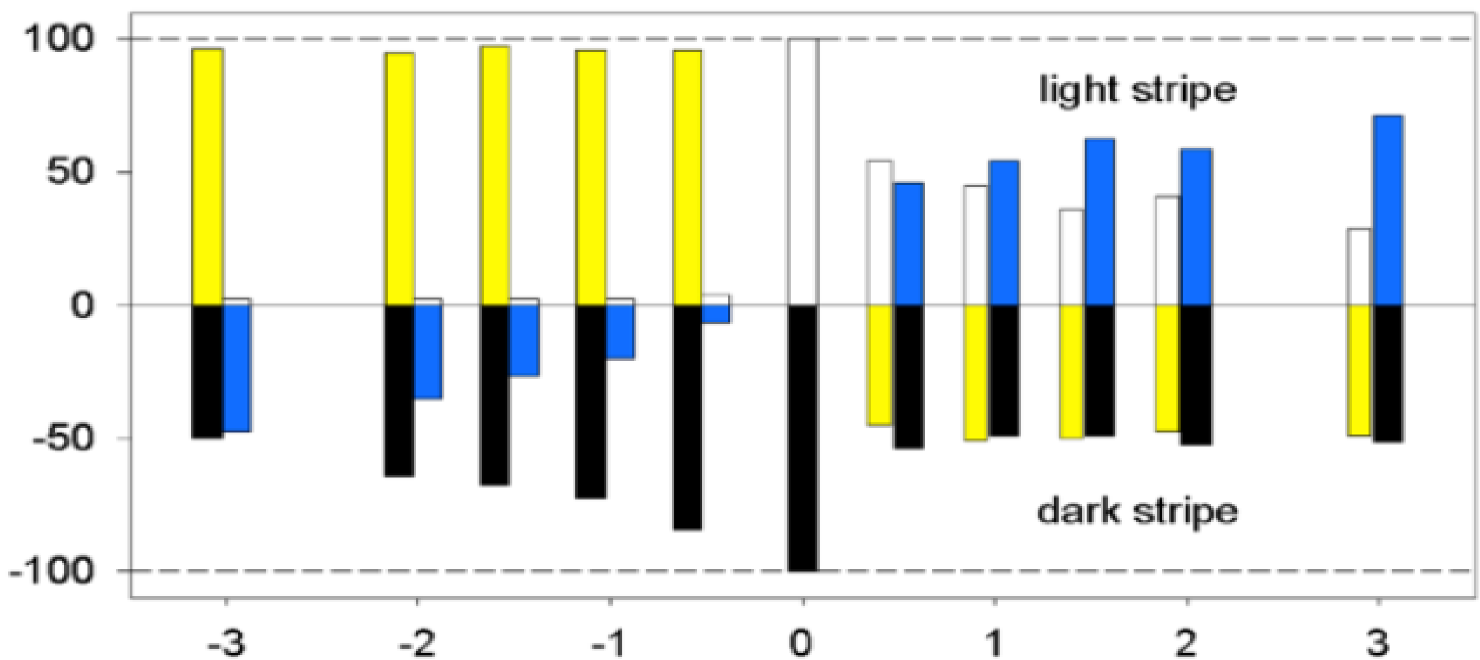
Surface color vs illumination color with Ivana Ilic

Blue tends to be attributed to the lighting, yellow to the object



Thus inverting the colors eliminates the ambiguity, while amplifying it doesn’t





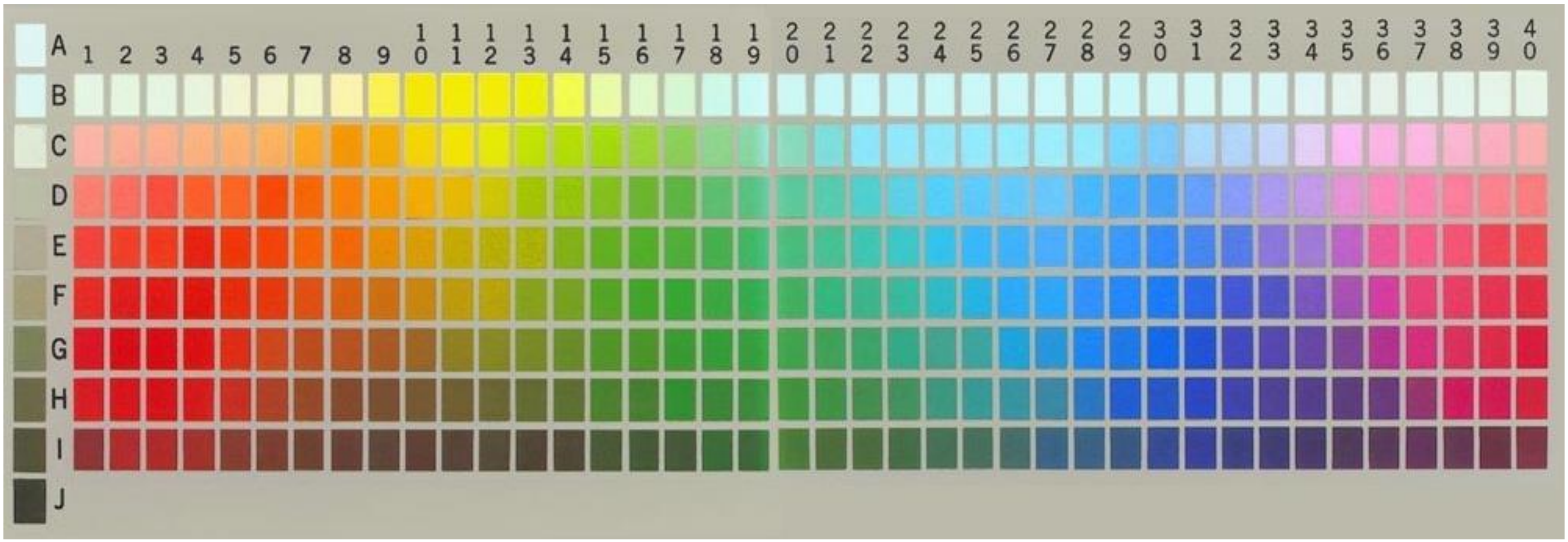
SEVENTEEN.COM

MAY 15, 2015

#TheDress Is Back: Scientists Finally Know Why It Was So Messed Up

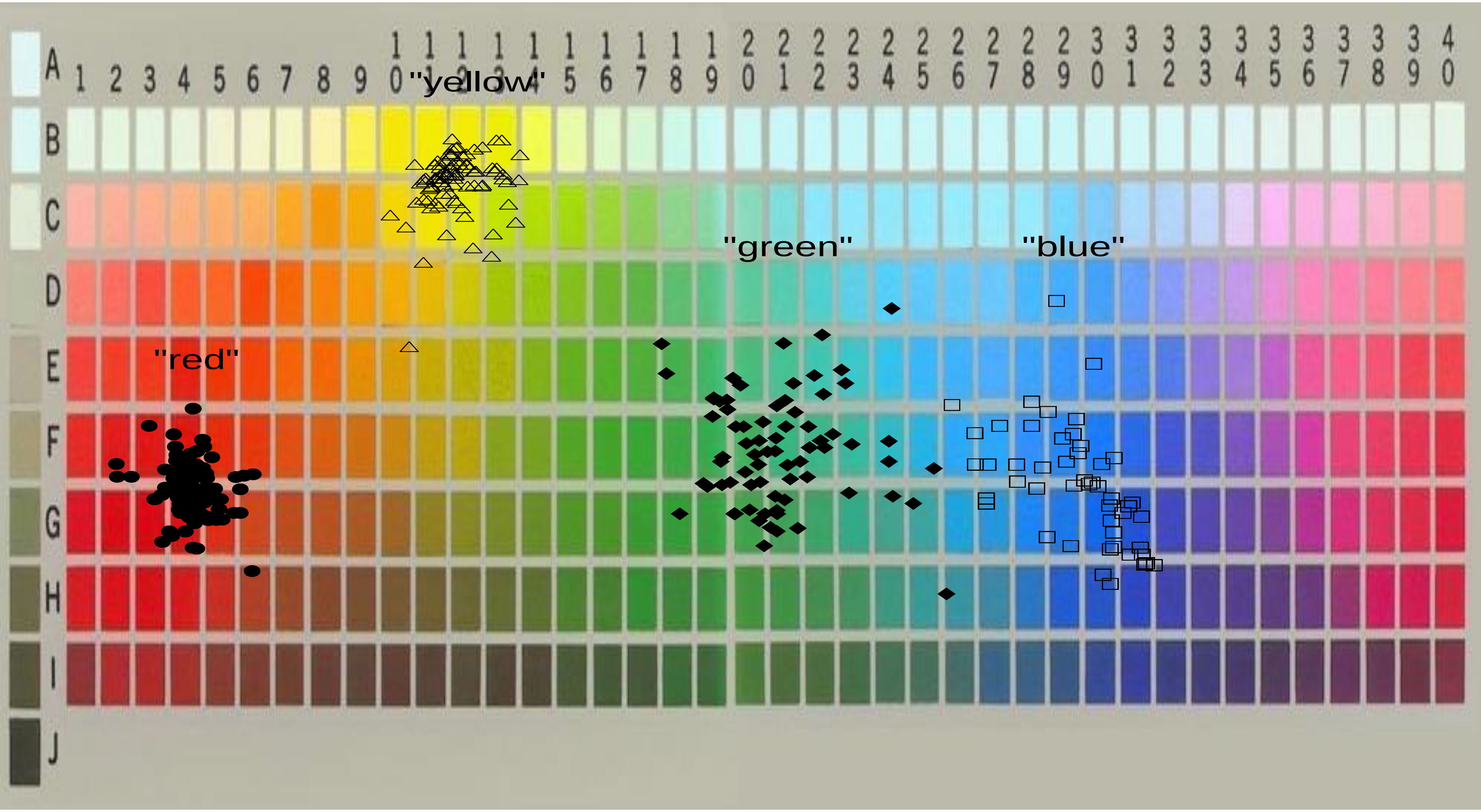
Individual differences and higher-level factors: Color naming and color categories

The World Color Survey



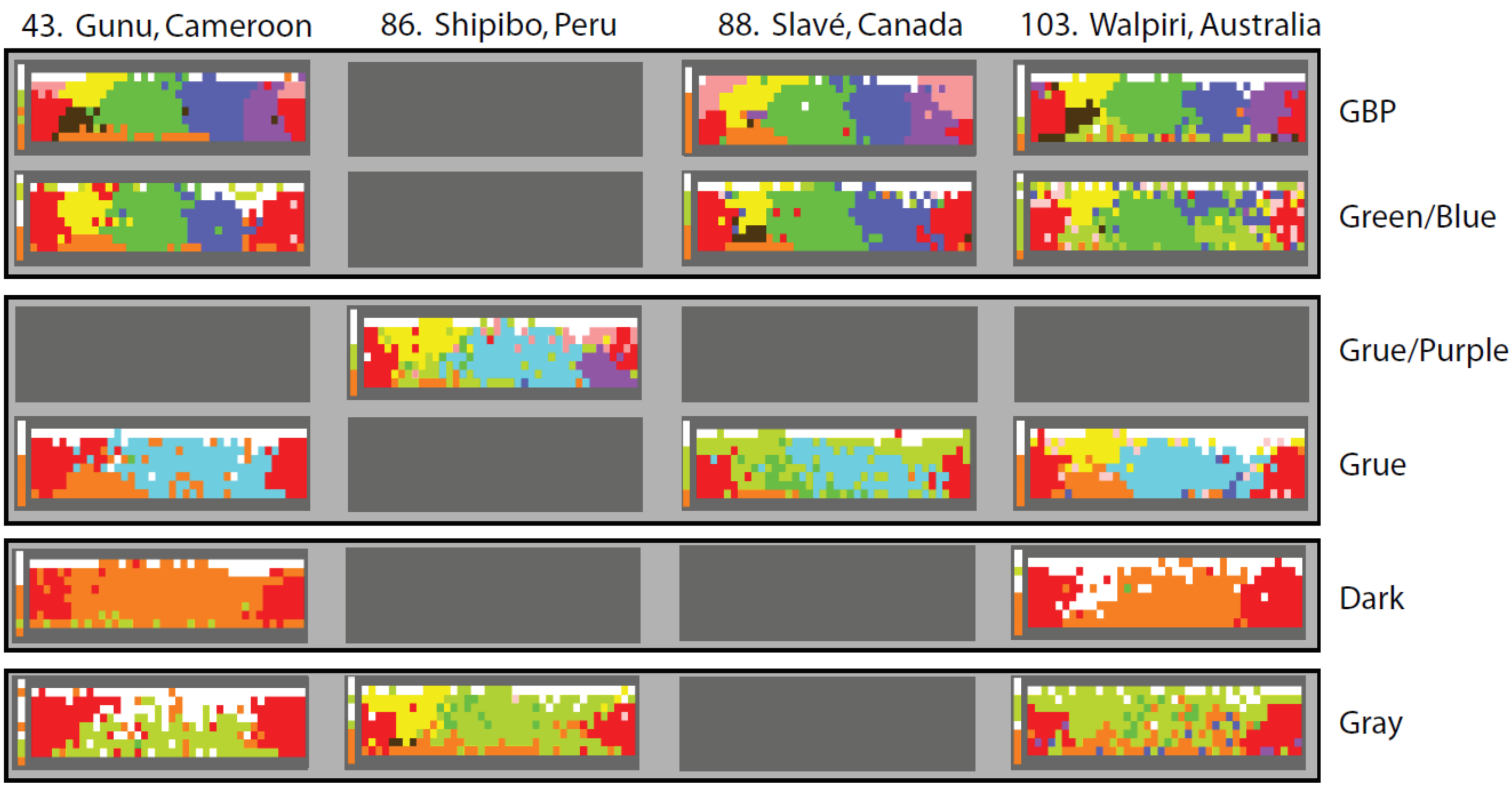
Berlin and Kay *Basic color Terms: Their Universality and Evolution* 1969

Mean focal stimuli for red, green, blue, and yellow in different languages



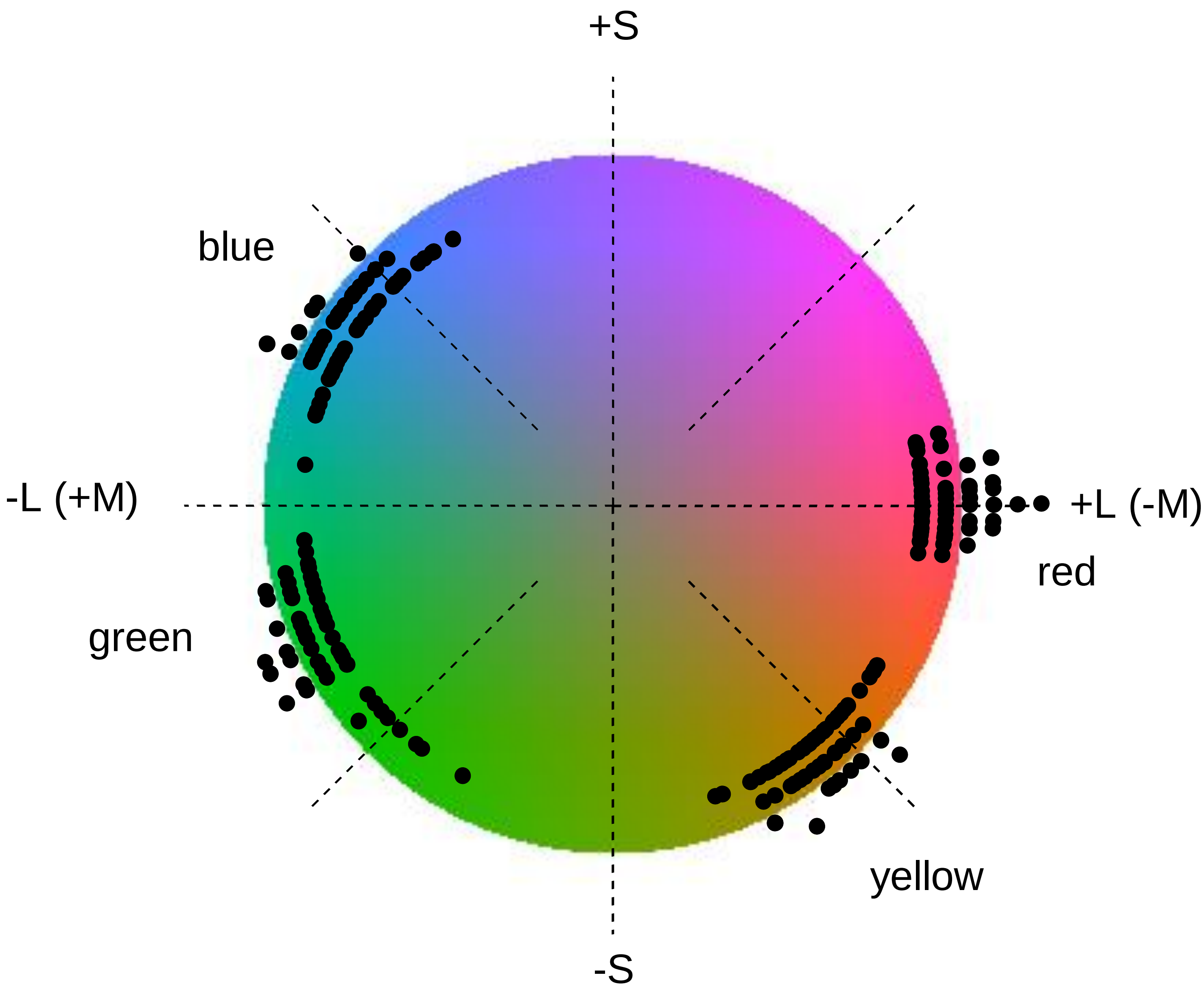
Webster and Kay *Anthropology of Color* 2007

There are also large individual differences in color naming within languages
Color categories vary widely from one individual to the next, and
speakers from different languages can be more similar than from the same language



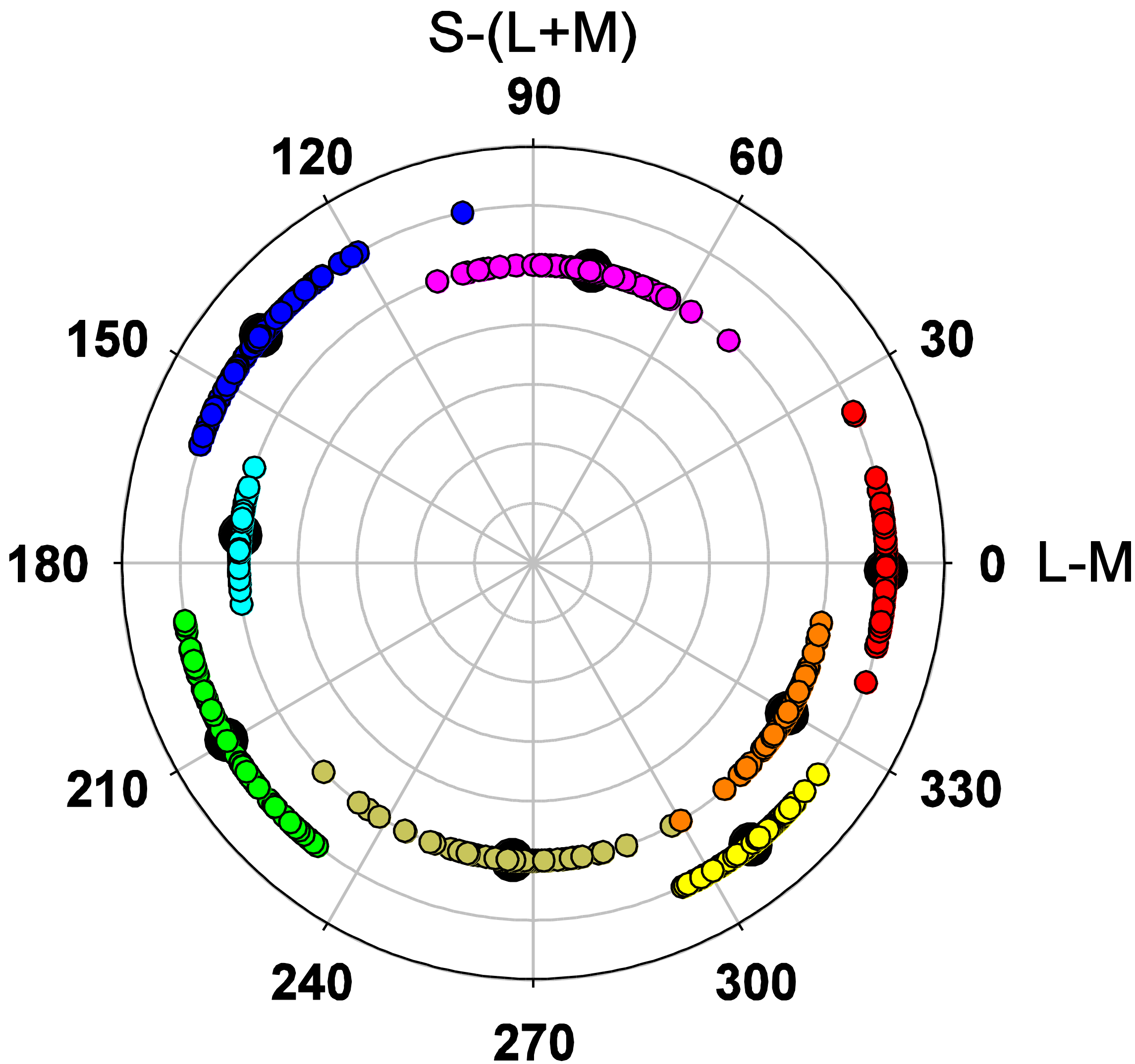
Lindsey and Brown PNAS 2009; Lindsey et al. Cur Bio 2015; Gibson et al. PNAS 2017

Individual differences in color appearance:
Differences in unique hue settings are large and uncorrelated with each other



Webster et al. JOSA 2000

Unique and binary hues are also uncorrelated

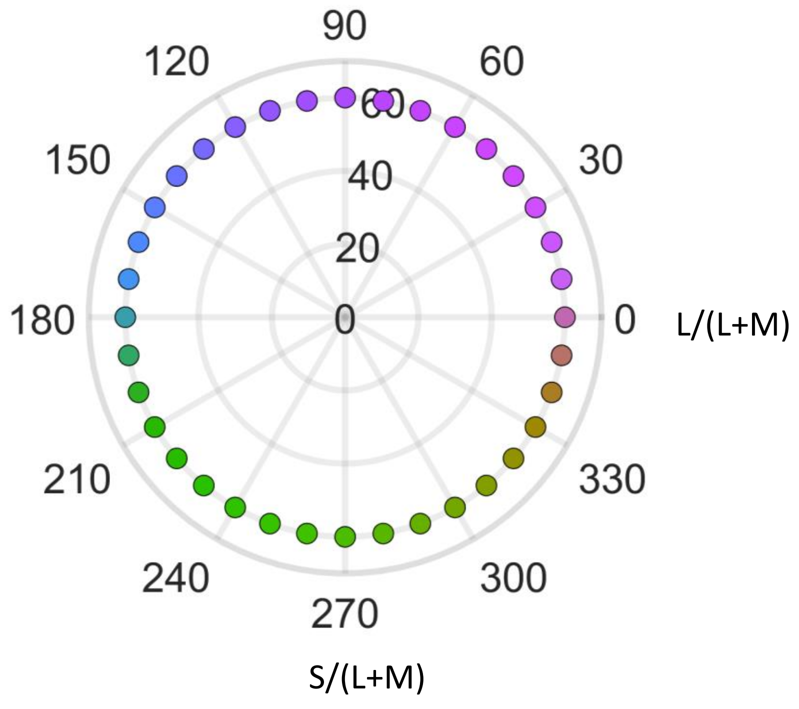


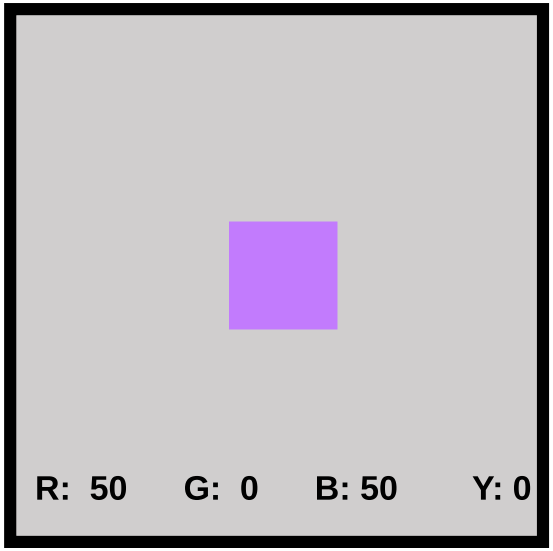
Malkoc et al. JOSA 2005

Using individual differences to explore the perceptual representation of color

Hue scaling

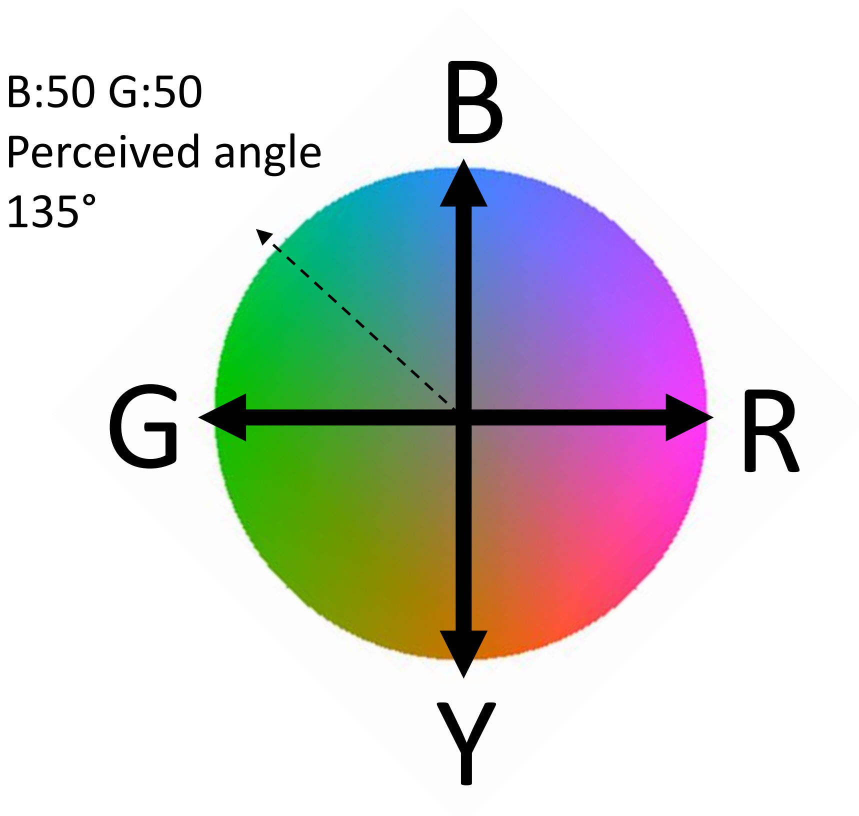
"Describe the proportion of color that is red/green and blue/yellow"





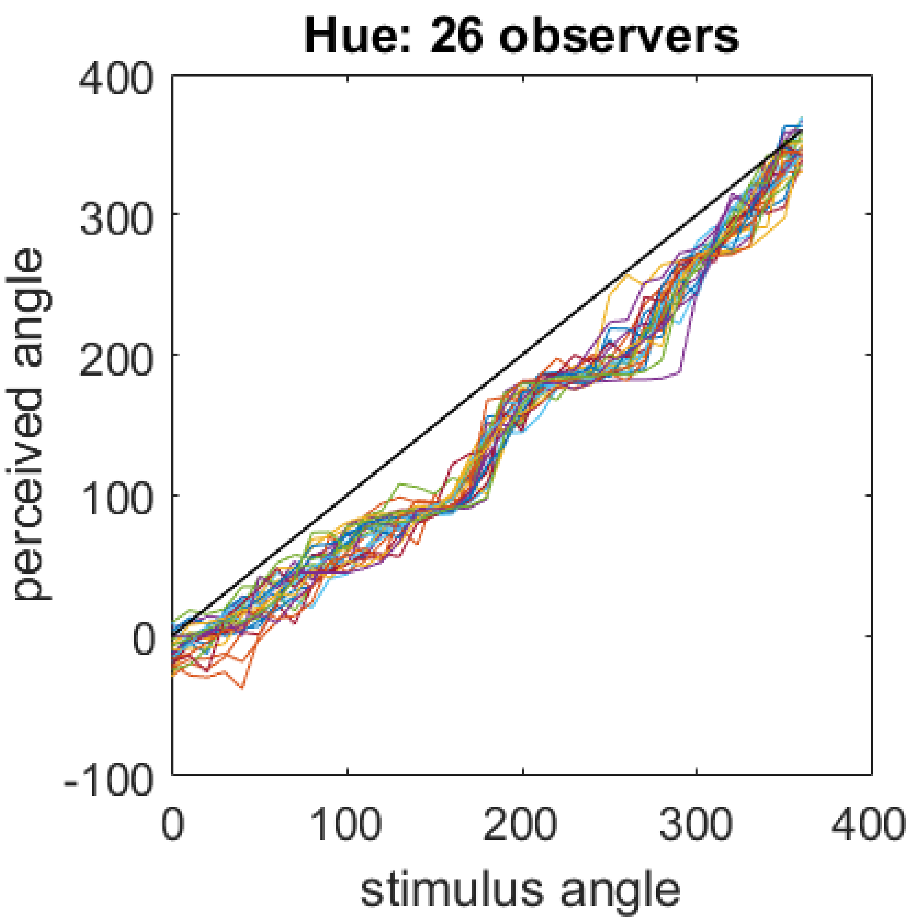
Emery et al. JOSA A 2017a, 2017b; Matera et al. JOSA A 2020

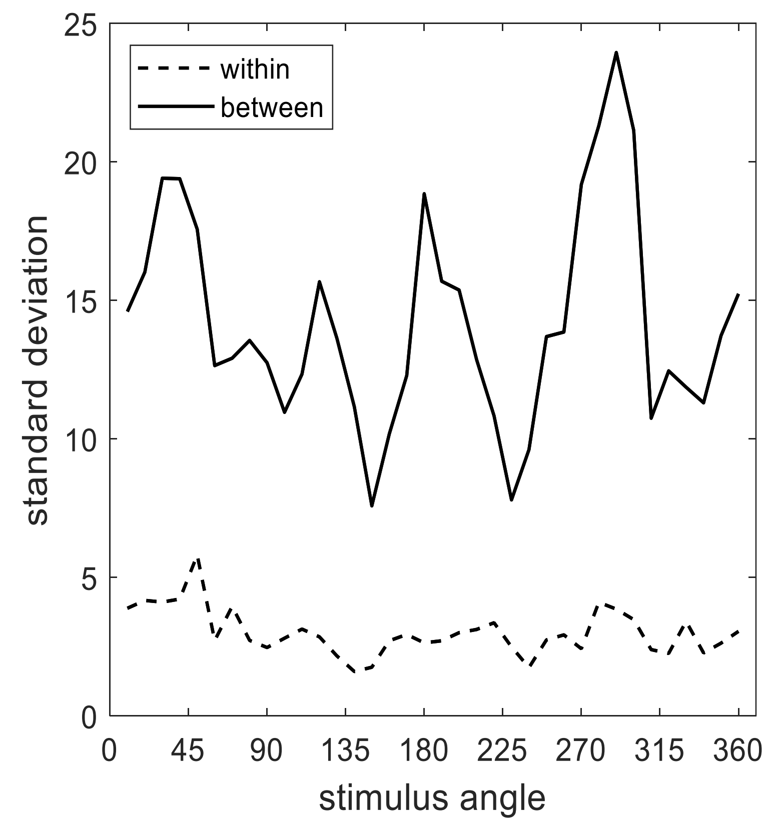
Responses coded as "perceptual angle"



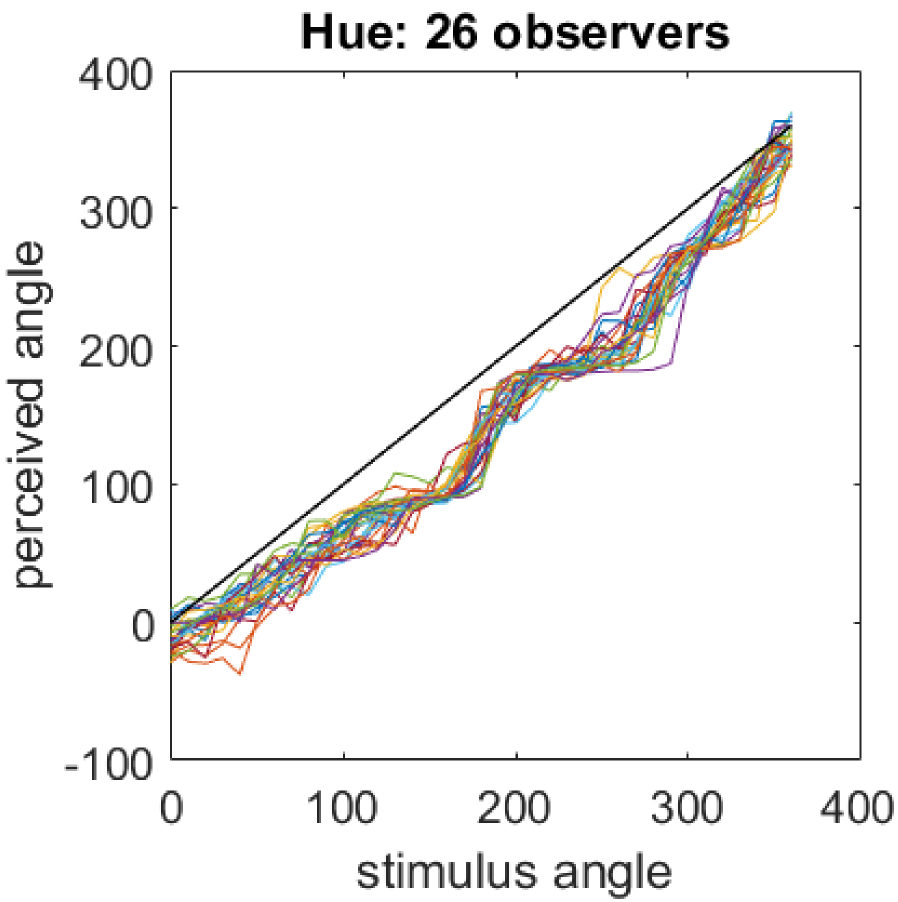
Individual hue scaling functions (perceptual angle vs stimulus angle)

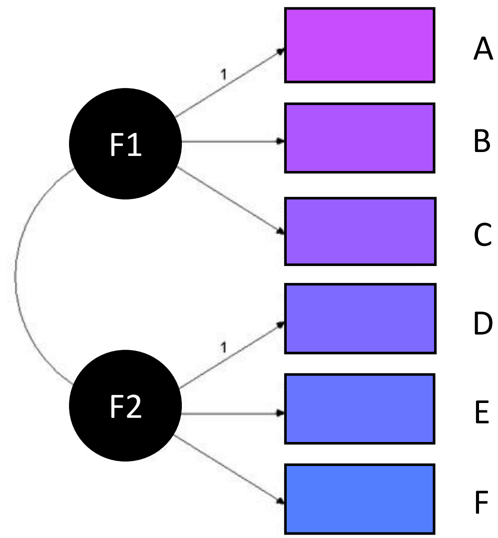
Between/within observer variability = 2:1





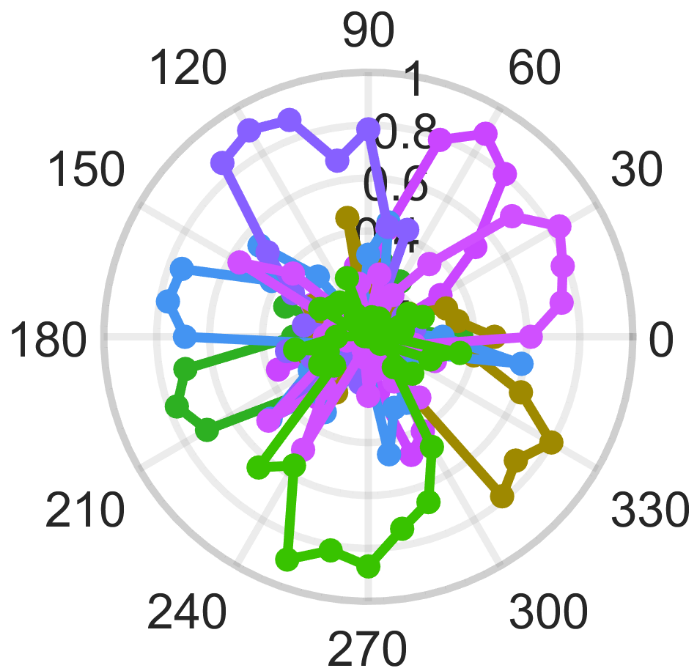
We can again explore the processes contributing to hue-scaling differences by analyzing the pattern of correlations

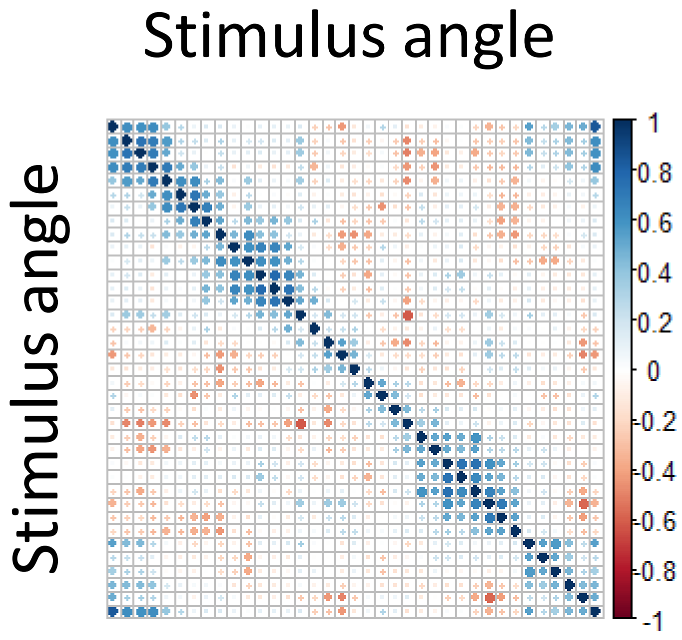




Only nearby stimulus angles are correlated indicating narrowly tuned factors

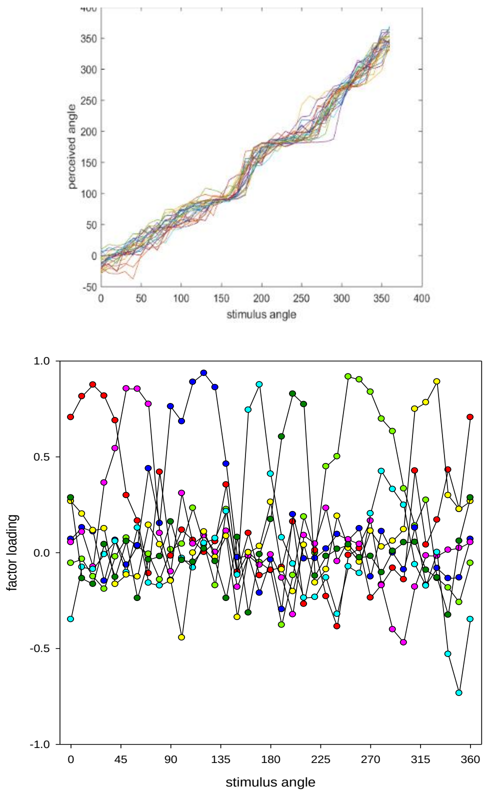
Cumulative variance: 72%



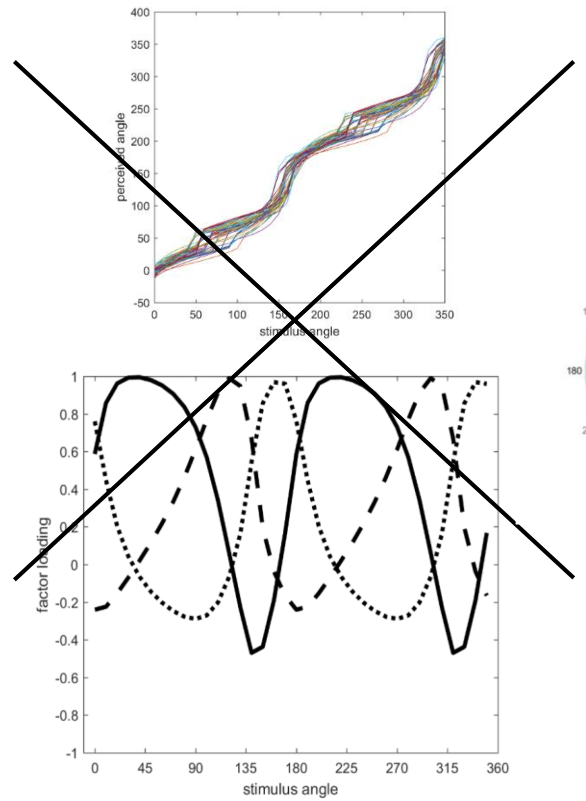


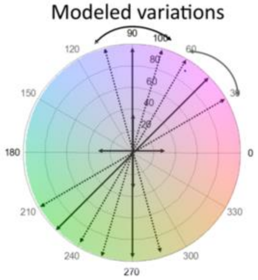
Narrow factors are not predicted by variations in conventional opponent processing

Observed

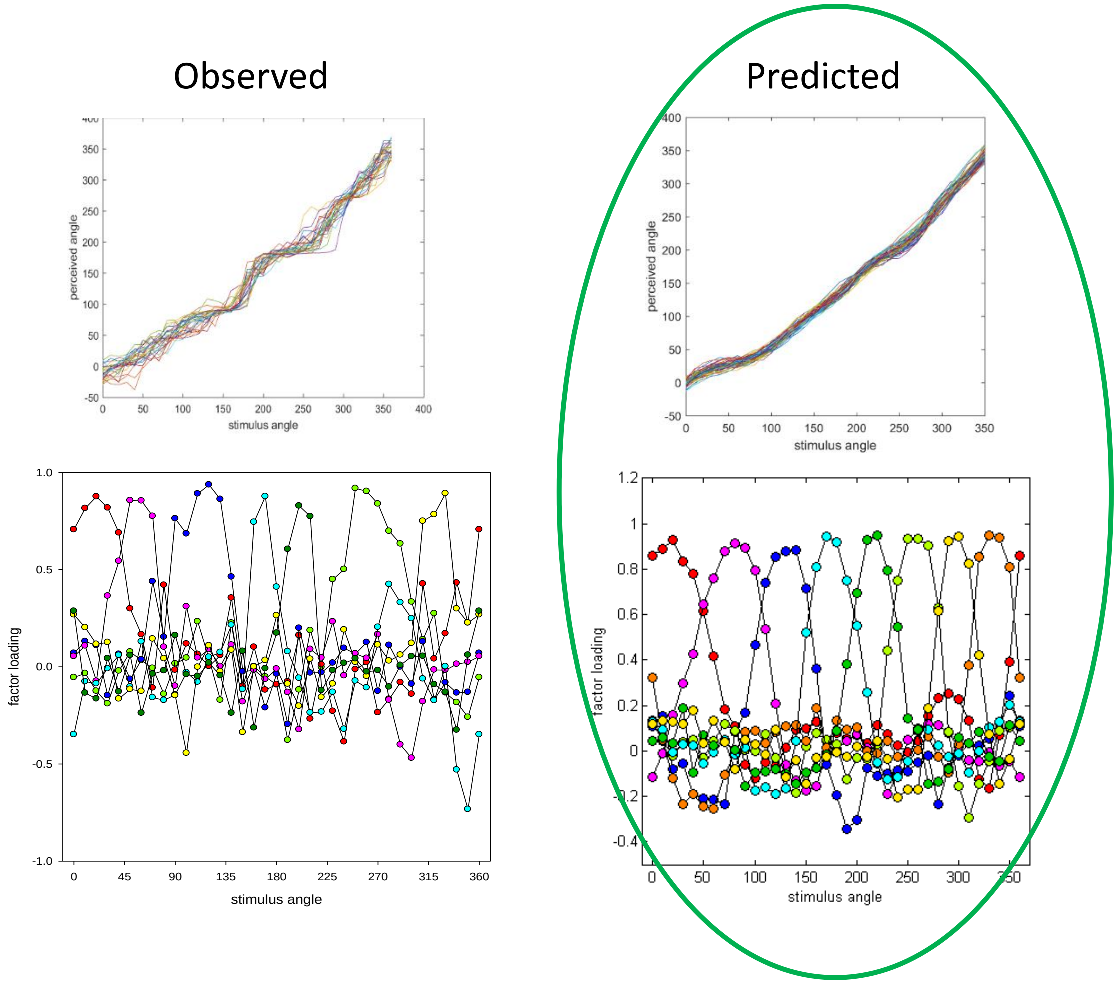


Predicted

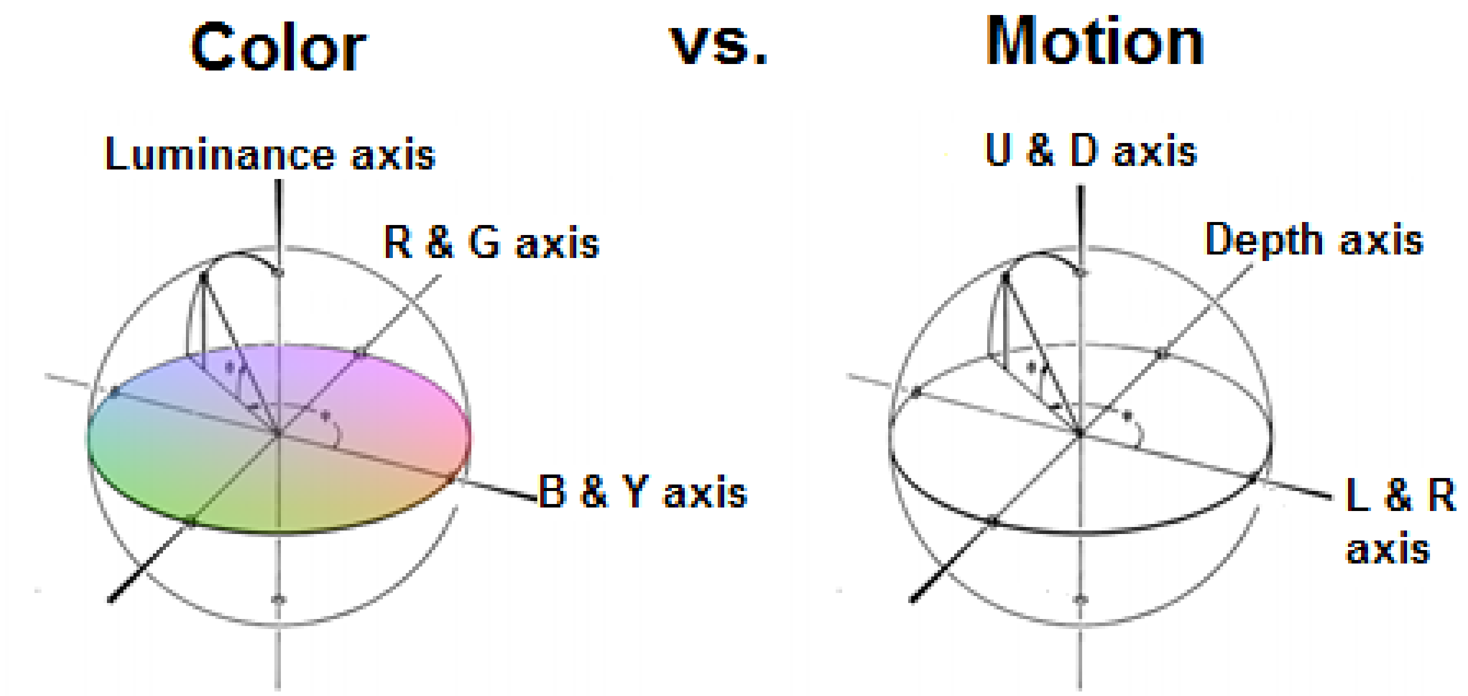




But are consistent with a population code for color categories

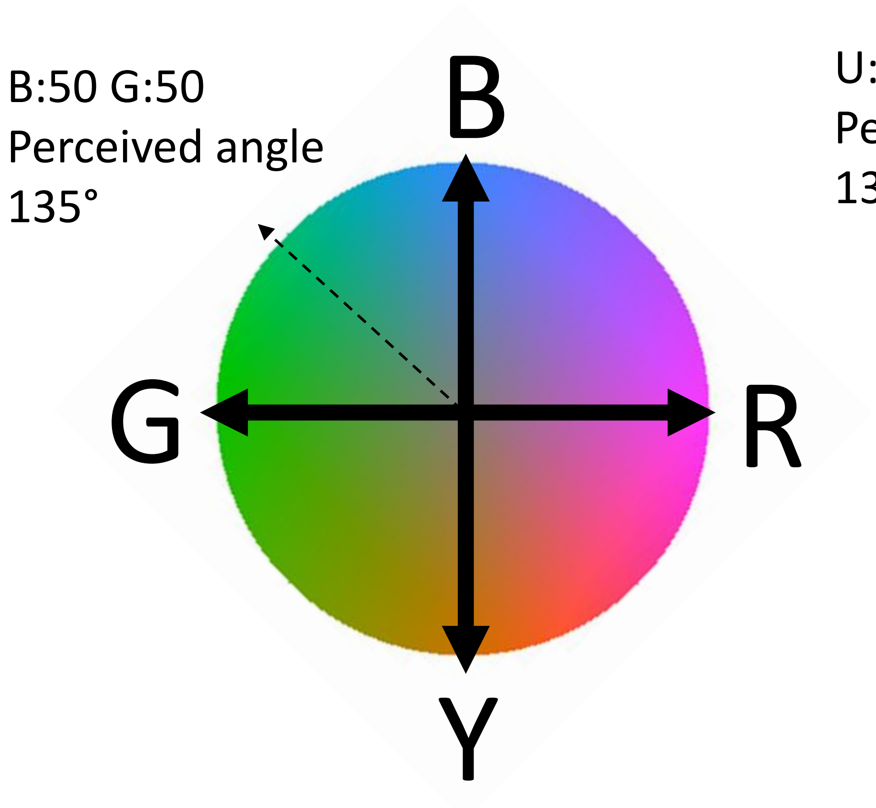


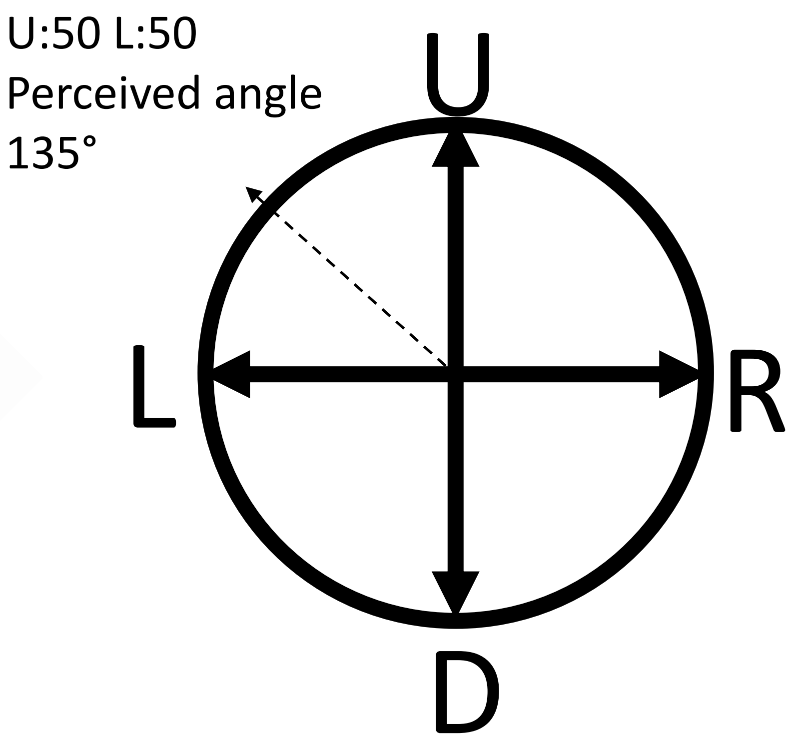
To what extent do these factors reveal the underlying representation of color, rather than the properties of the task?



Emery et al. in preparation

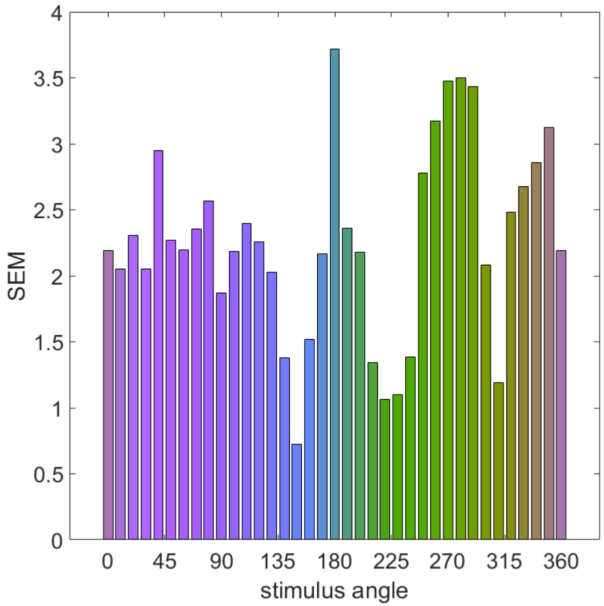
Perceptual angle in color or motion space

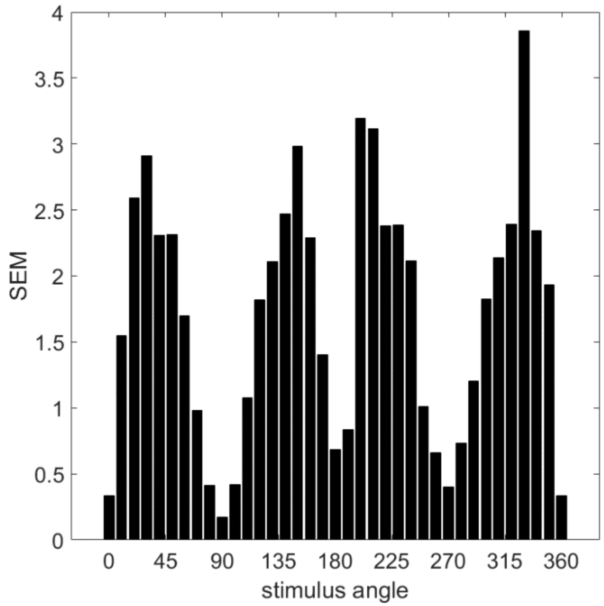




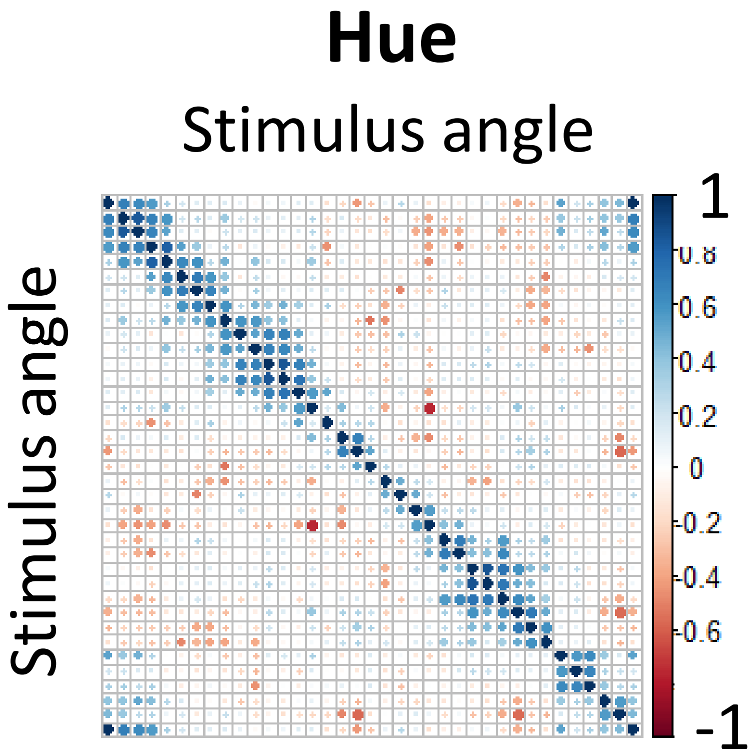
variability vs. stimulus angle

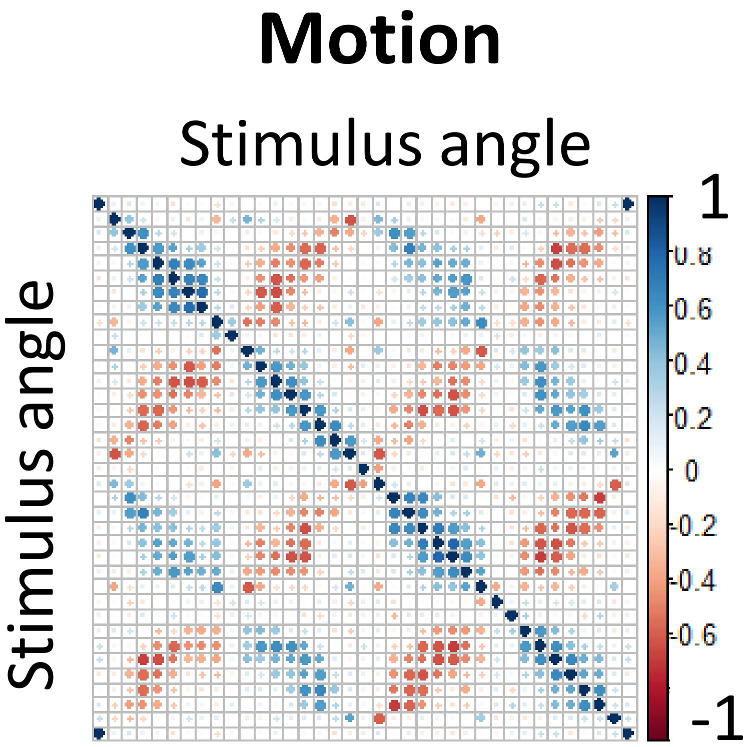
Stronger evidence for special (unique) directions for motion



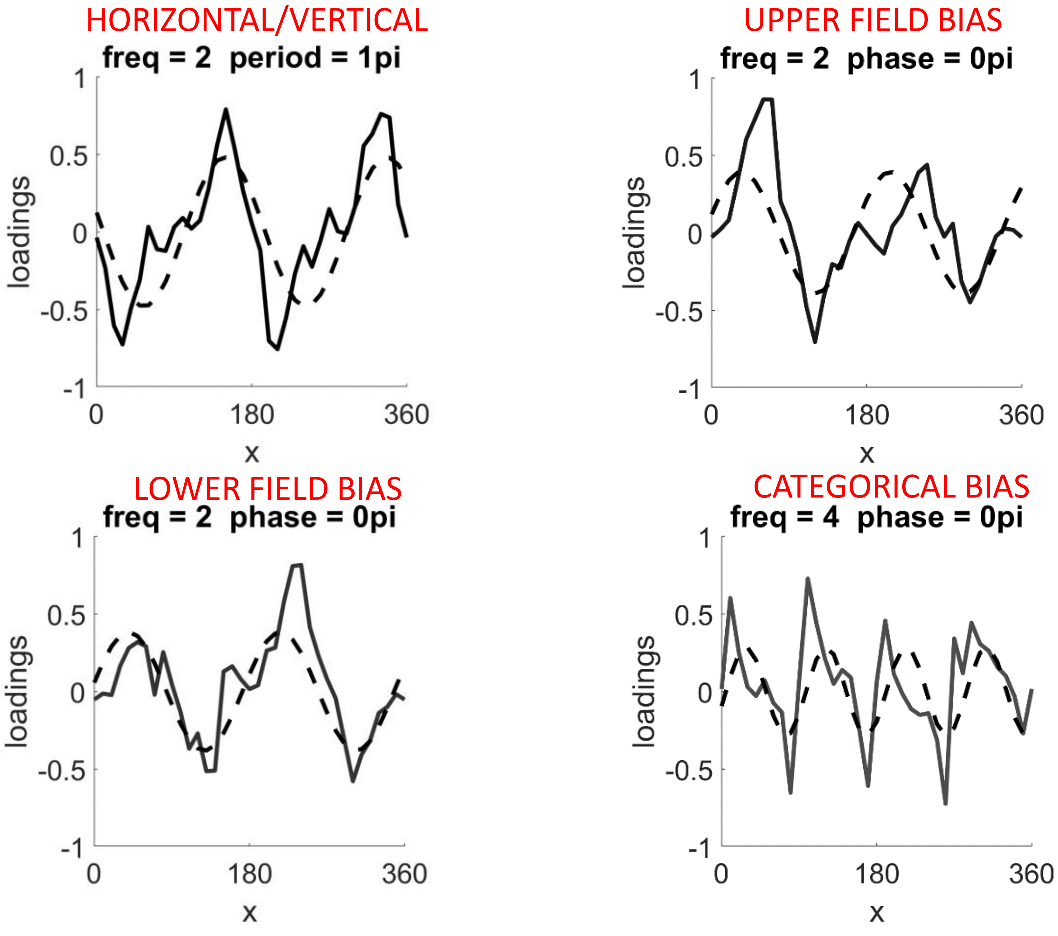


Variability in motion judgments correlates over very different stimulus angles





Motion factors vary roughly sinusoidally – consistent with variations in underlying cardinal axes

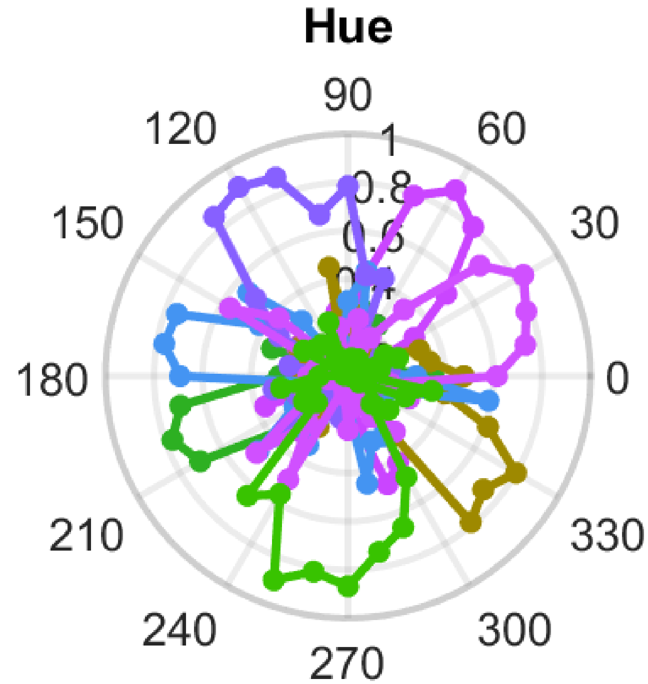


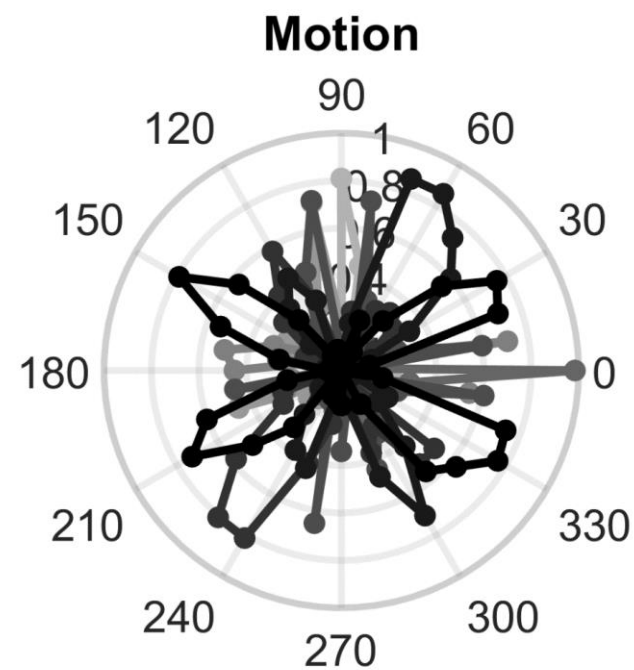
Summary

Color and motion percepts reflect very different patterns of individual differences:

Color: multiple, narrowly-tuned processes, with no evidence for opponent axes, and only weak evidence for privileged directions (e.g. unique hues)

Motion: differences consistent with a metrical code in terms of the cardinal axes





Conclusions

1. Individual differences are a prominent feature of color vision and affect all aspects of color perception

2. These differences are important to account for in both color research and color applications

3. Differences in sensitivity often have little effect on color appearance, which may be strongly shaped by experience and adaptation to the color environment

4. For both sensitivity and perception, the patterns of inter-observer variation can provide important clues about the mechanisms and processes of color vision

Thank you!

To many mentors, students, and colleagues and to NIH

Integrative Neuroscience
Center of Biomedical Research Excellence

Visual Perception Lab
University of Nevada Reno

NIH
National Eye Institute

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