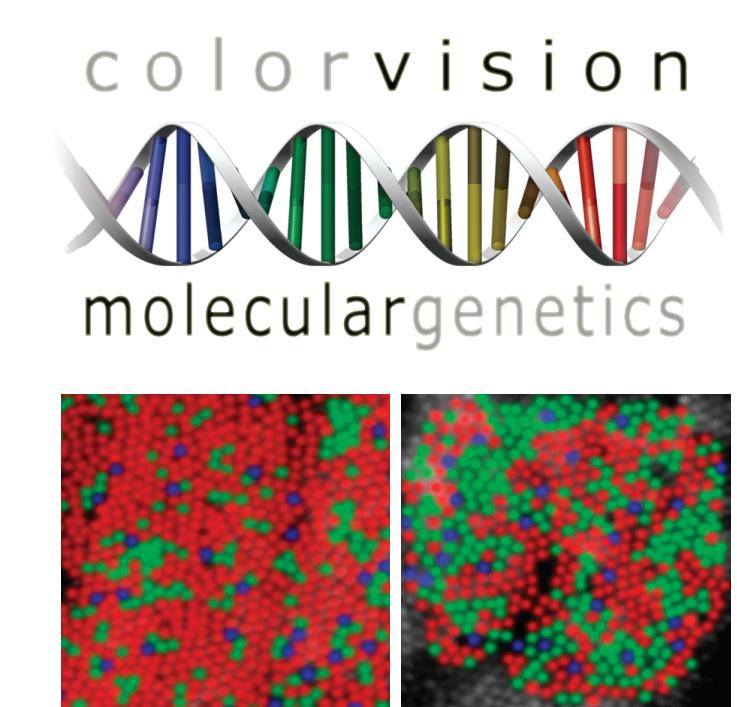




The neurobiological explanation for color appearance and hue perception

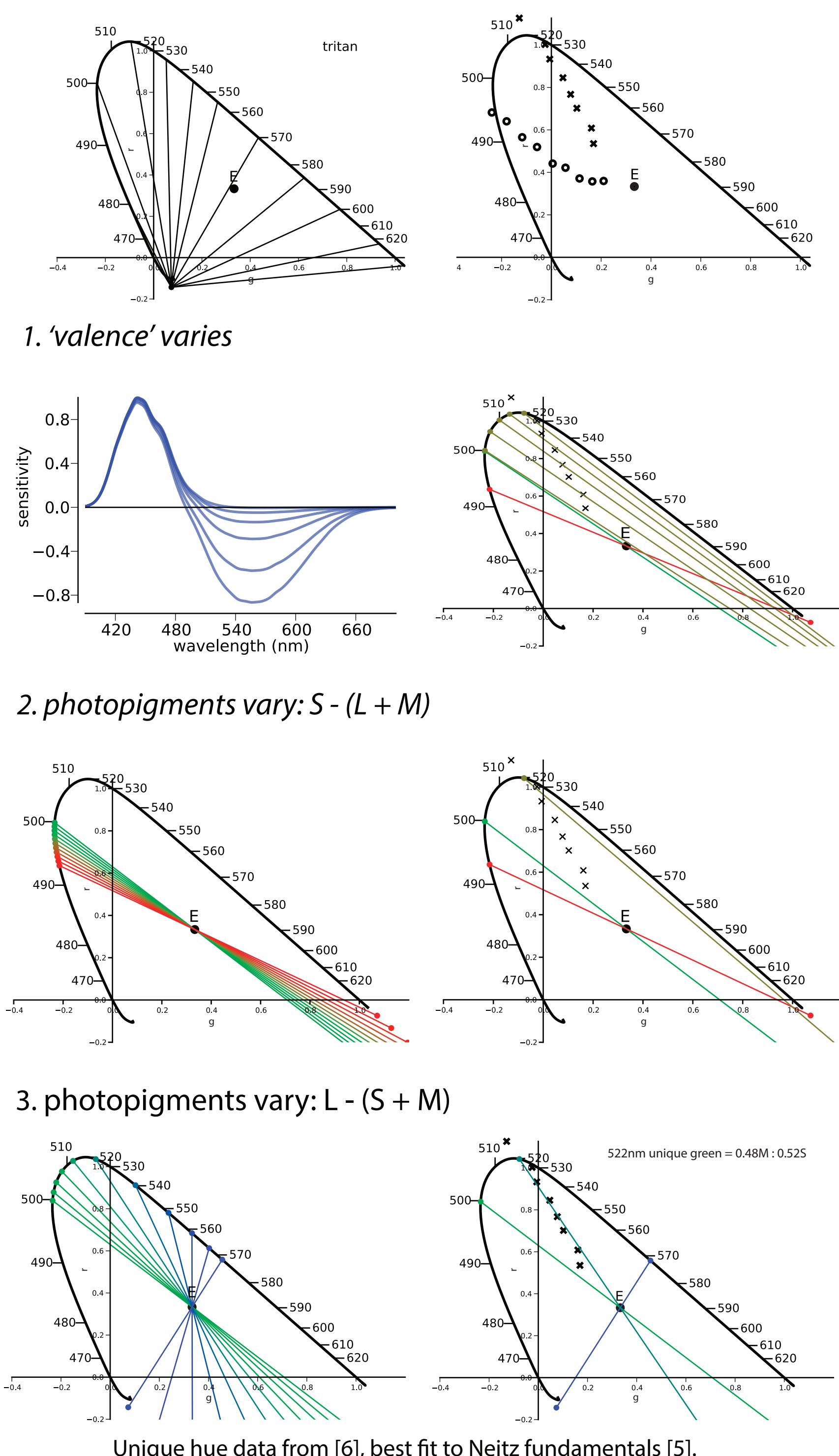
Brian P. Schmidt, Maureen Neitz, and Jay Neitz

Neurobiology and Behavior and the Department of Ophthalmology, University of Washington



INTRODUCTION: The spectral position of unique hues across a population of observers has received significant attention in color science. The standard model in which small bistratified cells that receive S-(M+L) cone input are the retinal origin of a blue-yellow channel underlying hue perception does not provide a parsimonious explanation for the spectral location and distribution of monochromatic lights identified as unique green. However, recordings from large samples of cells in the lateral geniculate nucleus have identified another group of cells, about equal in number to S-(M+L) cells, that have input from M-cones with the same sign as S-cones, i.e., they are (S+M)-L cells [1]. Because the only cells in the retina known to carry opponent signals from M vs. L cones are midget ganglion cells, this second class of blue sensitive cells appears to reflect the existence of a small subclass of midget ganglion cells that could be the substrate for blue-yellow (B-Y) color vision. These putative B-Y midget ganglion cells presumably receive S-cone input via H2 horizontal cells. The B-Y midget ganglion cell theory predicts that variation in L:M cone ratio will produce variation in unique green.

Variability in unique green



METHODS: The first stage of our model, inspired by DeValois and DeValois [4], consists of spectral sensitivity functions [5] corrected for optical filtering. The second stage, taken to be at the level of ganglion cells, linearly combines cone signals ($L(\lambda)$, $M(\lambda)$, $S(\lambda)$):

$$g(\lambda) = \omega [\rho S(\lambda) + (1-\rho)L(\lambda) + lM(\lambda)] - C(\lambda)$$

where $\rho=1.3$, $C(\lambda)=L(\lambda)$ or $M(\lambda)$ and l is the proportion of L vs M in the surround. Our only assumption is that at this second stage, responses of chromatically opponent cells null to equal energy white, requiring that ω is adjusted such that:

$$0 = \int_{\lambda=390}^{750} g(\lambda) d\lambda$$

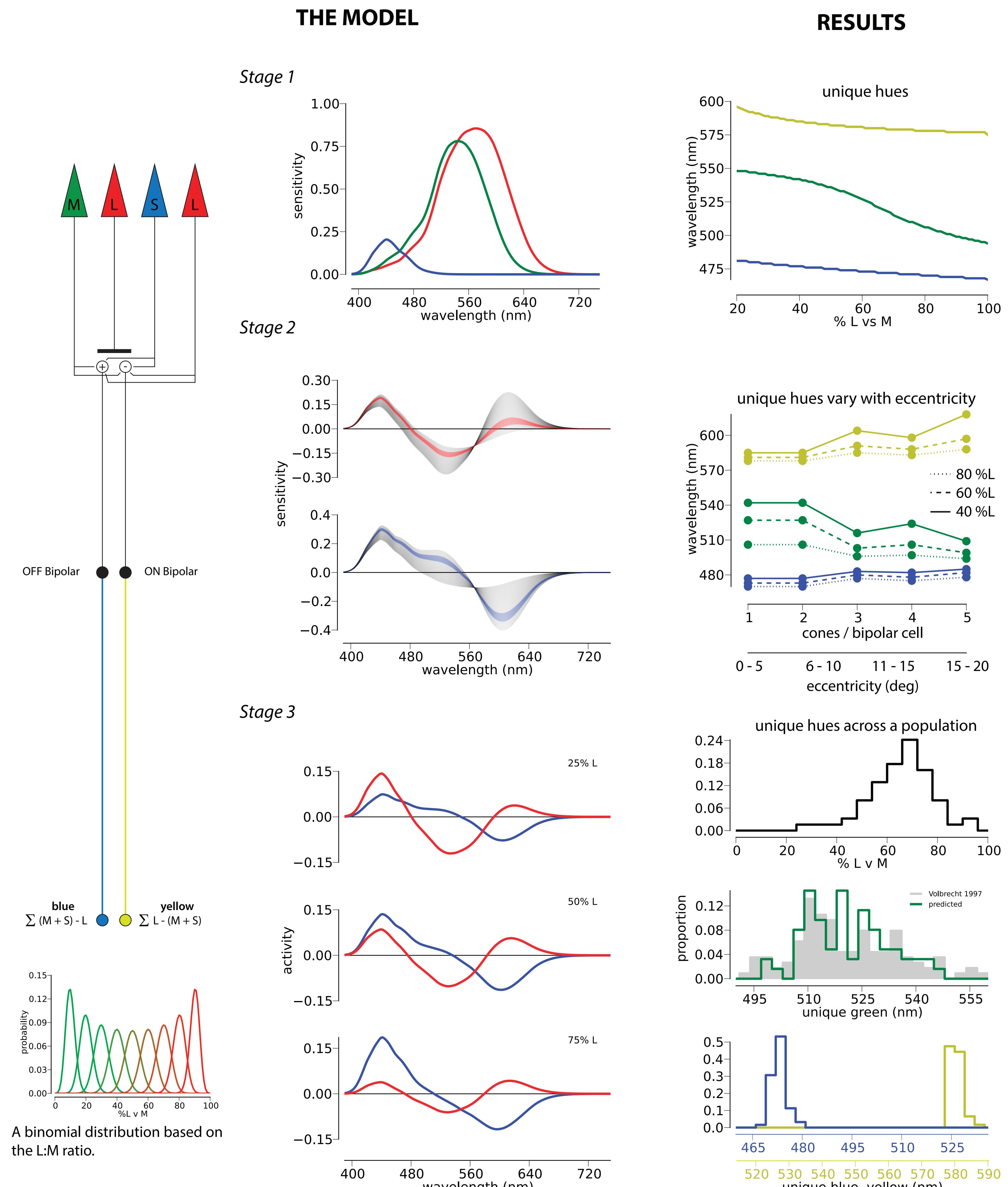
The third stage sums these ganglion cell units:

$$\alpha(\lambda) = \sum_{r=0}^{100} g_r(\lambda) P(S|r)$$

with l in each case equal to $r/100$. The weighting is based on the probability of occurrence, when P_L is the L:M ratio across the retina:

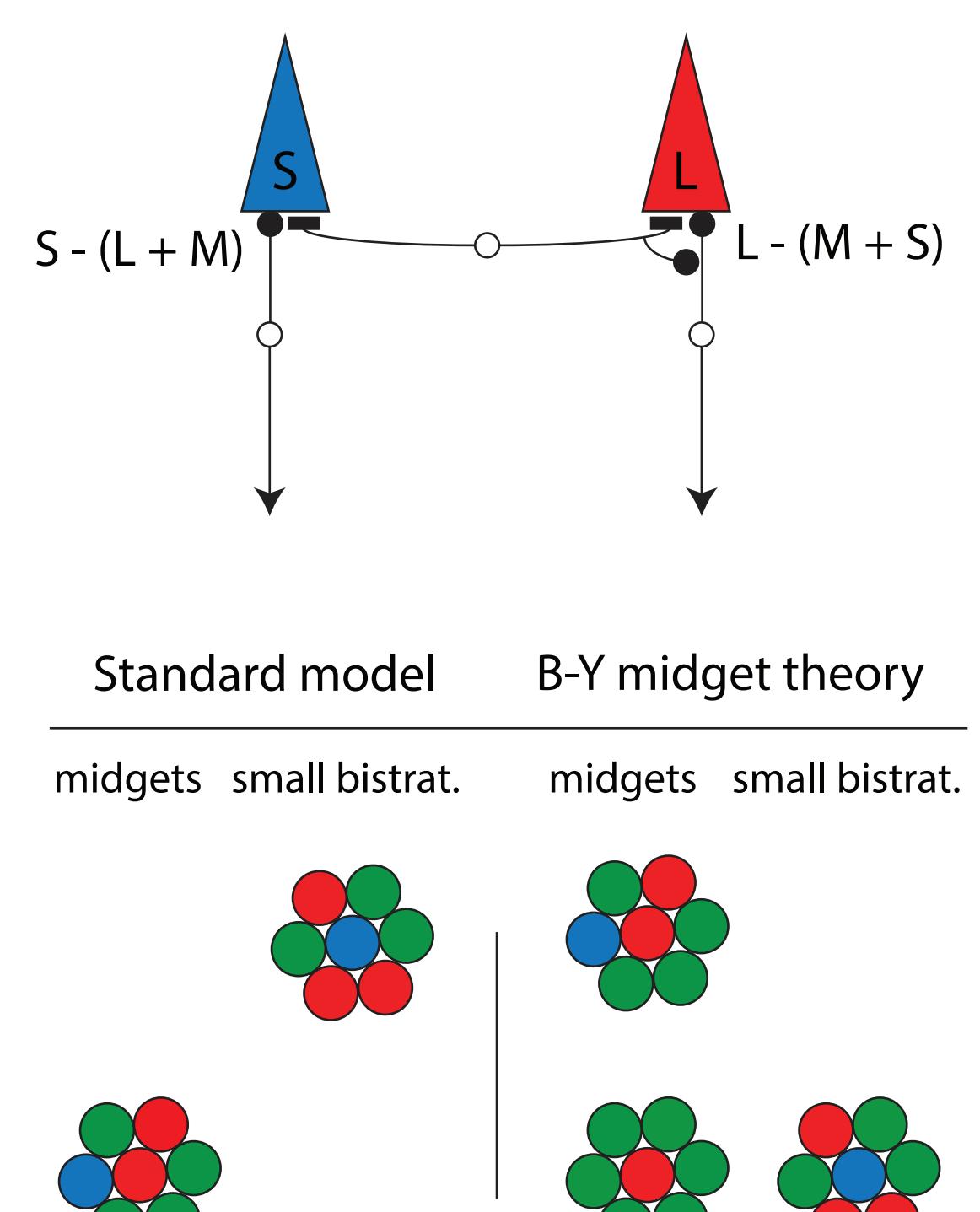
$$P(S|r) = \binom{n}{r} P_L^r (1-P_L)^{n-r}$$

Source code can be freely obtained from:
<https://github.com/bps10/color/tree/ICVS>



RESULTS: Using the spectral sensitivities of the cones and a previously measured distribution of L:M ratios [5], the theory predicted a range of 495 to 555 nm for unique green that almost perfectly matches the distribution of Volbrecht et al. [2]. The parallel idea that red-green hue perception is based on a second subset of midget ganglion cells with (S+L) vs. M-cone inputs accurately predicts narrow distributions for unique blue and yellow centered around 473 and 580 nm respectively as observed experimentally. Finally, due to the increasing number of cones contacting each midget ganglion with increasing eccentricity, we find a large shift in unique green towards shorter wavelengths as reported by Nerger et al. [3].

CONCLUSION: The current model accounts for the wide variability in L:M cone ratio known to exist in the human population and accurately predicts variation in unique hues, a previously unexplained phenomena. Further, the proposed retinal circuitry satisfies the necessary constraint that the addition of a third cone would immediately confer an advantage, without the need to evolve a separate circuitry. The B-Y midget ganglion cell theory is, therefore, a complete, biologically accurate and parsimonious account of hue perception and variation.



References

- Tailby, Solomon & Lenny. 2008. Functional Asymmetries in Visual Pathways Carrying S-Cone Signals in Macaque. *J Neuro* 28(15): 4078–4087.
- Volbrecht, Nerger & Harlow. 1997. The bimodality of unique green revisited. *Vis Res.*, 37: 407-416.
- Nerger, Volbrecht & Ayde. 1995. Unique hue judgments as a function of test size in the fovea and at 20-deg temporal eccentricity. *JOSA A*, 12(6): 1225-32.
- DeValois & DeValois. A multistage color model. 1993. *Vis Res* 33(8): 1053-65.
- Carrol, Neitz & Neitz. 2002. Estimates of L:M cone ratio from ERG flicker photometry and genetics. *JoV*, 2: 531-542.
- Ayama, Nakatsue & Kaiser 1987. Constant hue loci of unique and binary balanced hues at 10, 100 and 1000 Td. *JOSA A*, 4(6): 1136-44.

Acknowledgments NIH EY021242.