Human monochromatic light discrimination explained by optimal decoding of cone absorptions

Li Zhaoping, Wilson S. Geisler, and Keith A. May (Paper in PLoS One 2011)

Presented on June, 9, 2011, at the Gatsby external seminar.

Motivation: Decoding from real physiological signals for real behavioral data

Sensory signal: S, neural responses r, perception: S'
Encoding: P(r|S) --- likelihood
Decoding: P(S'|r) ~ P(r|S) P(S)
Prior: P(S).

In most decoding work so far, one or more of the followings apply:

1. P(r|S) is assumed, not quantitatively known (e.g., noise is unknown)
2. r is not neural response, but artificial by experimental design
3. S' is not the behavioral perception, but modeler's toy.

e.g., **Pillow et al**, decoding visual inputs from retinal ganglion responses.
many parameters in P(r|S) are assumed, S' is not for behavioral

e.g., **Koerding & Wolpert**,
inferring motor target position S' from noisy position seen r, with prior P(S).
S: actual target position invisible to subjects
r: not neural response, but fake target position shown to subjects with likelihood P(r|S), --- typical of many behavioral studies of Bayesian inference.
P(S): prior, controlled by experimenter, experienced by subjects.
S': Subject's estimate of target position, manifested in their motor responses

Motivation: Decoding from real physiological signals for real behavioral data

Sensory signal: S, neural responses r, perception: S'
Encoding: P(r|S) --- likelihood
Decoding: P(S'|r) ~ P(r|S) P(S)
Prior: P(S).

Some exceptions:

Paradiso (1988),human orientation discrimination from V1 neural responses.

Fisher Information

$$I_F = \sum_i \int dr_i P(r_i \mid S)[-\partial^2 \ln P(r_i \mid S) / \partial S^2]$$

$$\propto \text{number of neurons}$$

However, used several free parameters

3 parameters: Orientation tuning function and response amplitude,

2 parameters: Neural noise

1 parameter: total number of neurons.

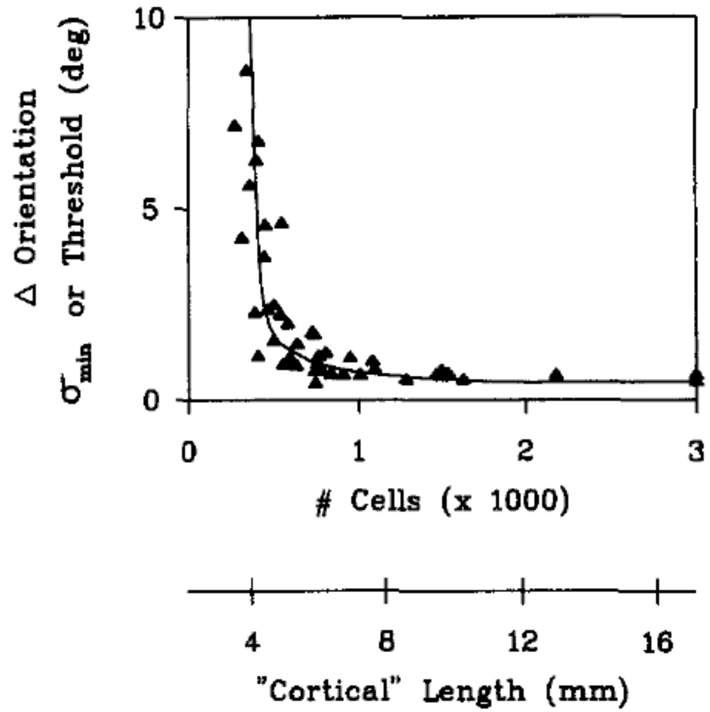


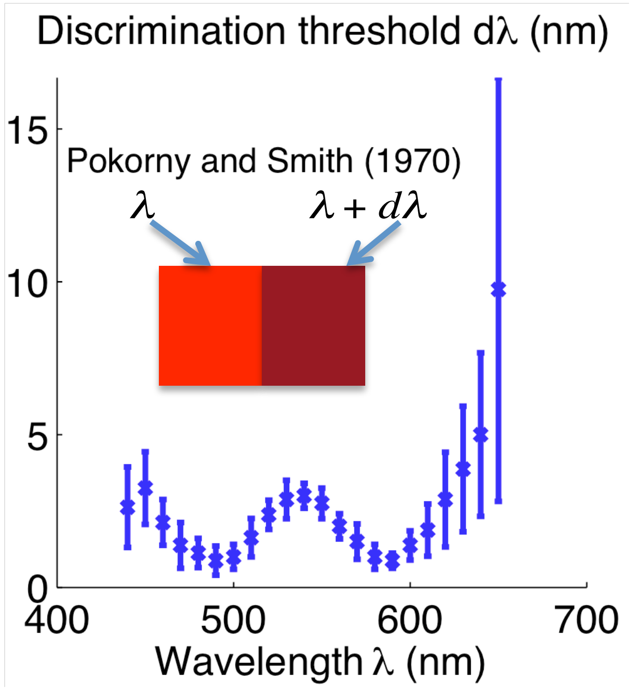
Fig. 8. A comparison of psychophysical data with the theoretically predicted relationship between σ_{min} and the number of cells (HN). The experimental data is from a study of orientation discrimination threshold as a function of the retinal eccentricity and size of a line target (Paradiso and Carney 1986). The theoretical curve was fit to the data by assuming the number of cells is proportional to the "cortical" length (see Appendix) where "cortical" length = (cortical magnification factor) × (actual target line length)

Motivation: Decoding from real physiological signals for real behavioral data

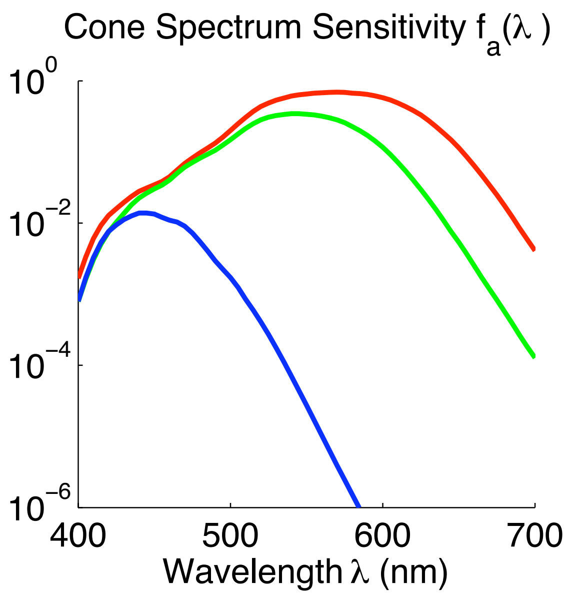
Sensory signal: S, neural responses r, perception: S'
Encoding: P(r|S) --- likelihood
Decoding: P(S'|r) ~ P(r|S) P(S)
Prior: P(S).

Current work:
Color perception from cone responses, only one free parameter (input intensity)

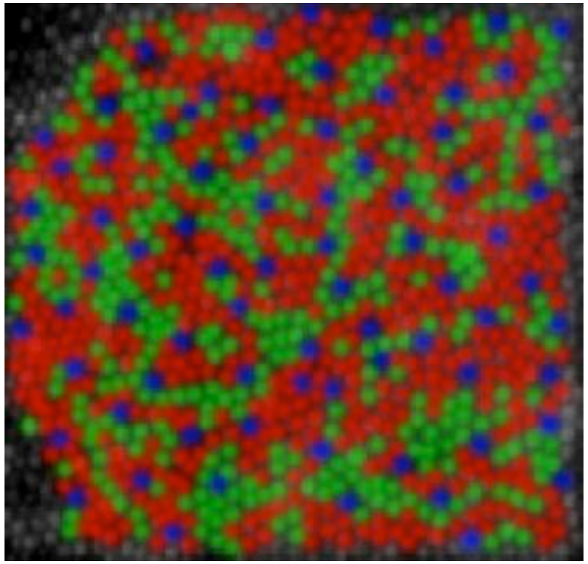
Behavior



Physiology P(r|S),
Poisson noise.



Number of cones.



(1) Other than different sensitivities to wavelength, different cones give equal electrical responses to light after photon absorption--- physiologically known.

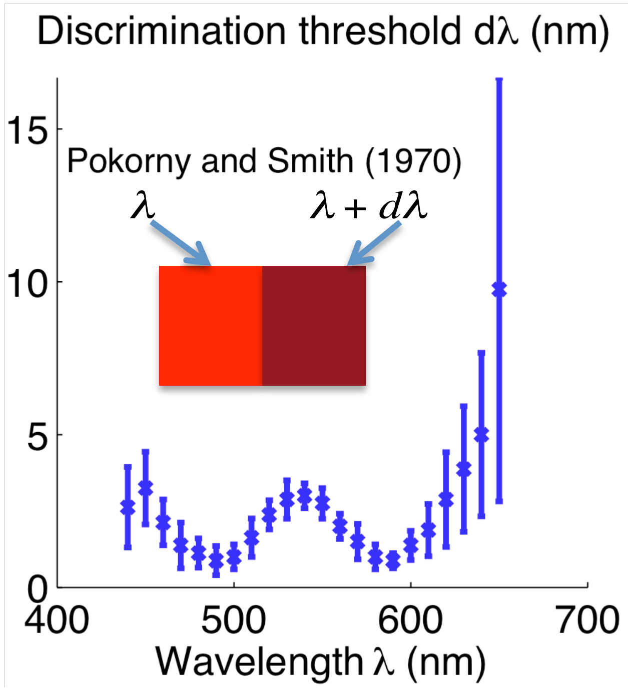
(2) N_a red cones, each Poisson, each with tuning function $f_a(\lambda)$, equivalent to one single giant red cone, Poisson, with tuning function $N_a f_a(\lambda)$.

Hence, different amplitudes of cone tuning curves reflect different cone densities and pre-receptor optical absorption

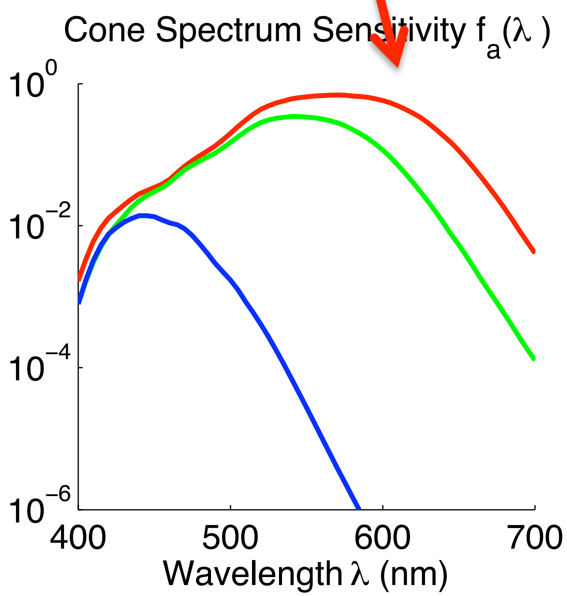
Current work:

Color perception from cone responses, only one free parameter (input intensity)

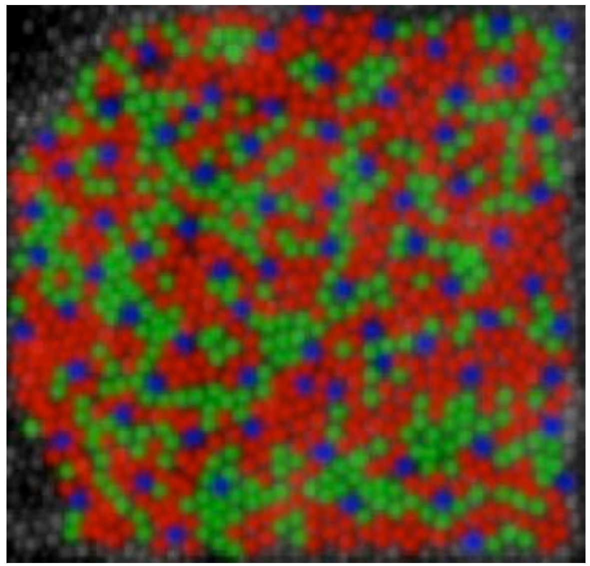
Behavior



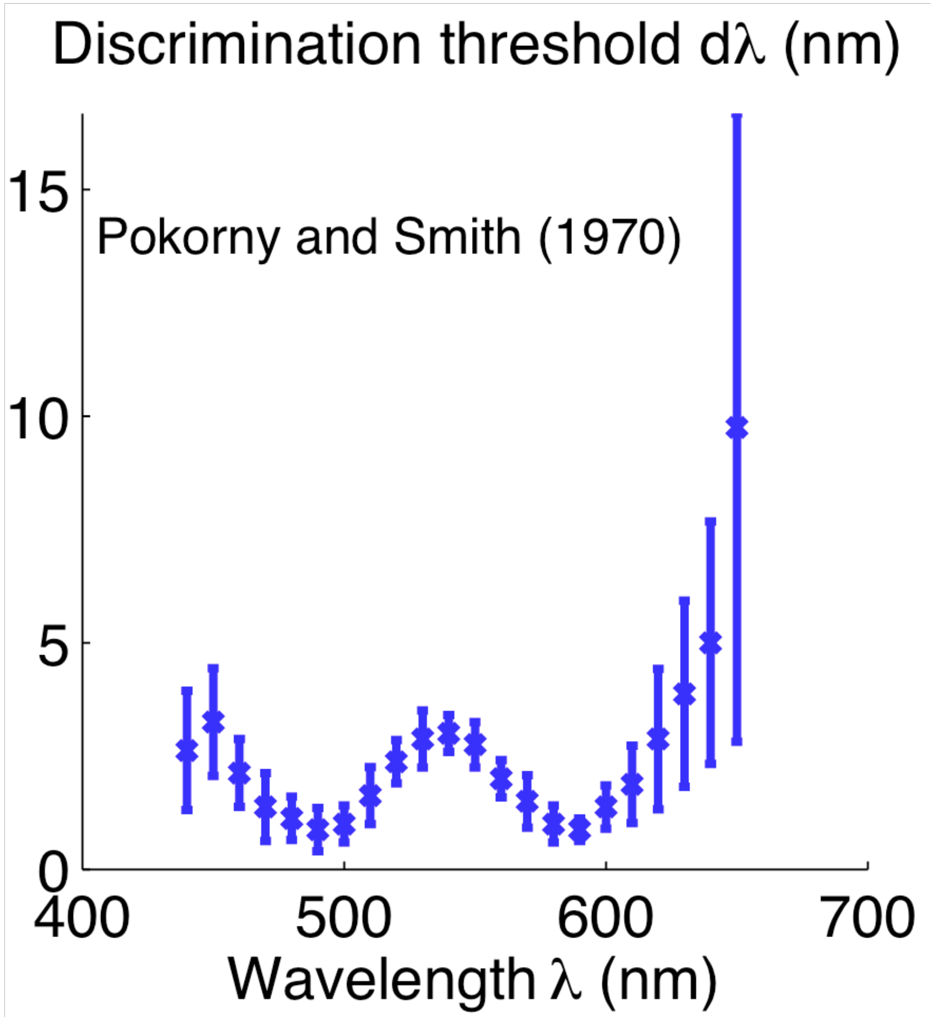
Physiology P(r|S),
Poisson noise.

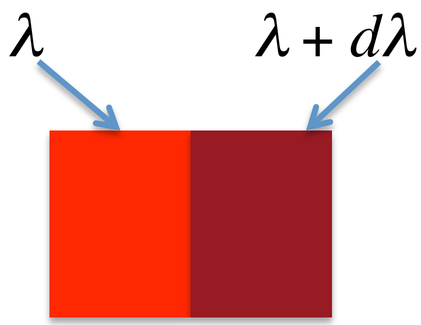


Number of cones.



Monochromatic discrimination threshold depends on wavelength (Pokorny and Smith, 1970)

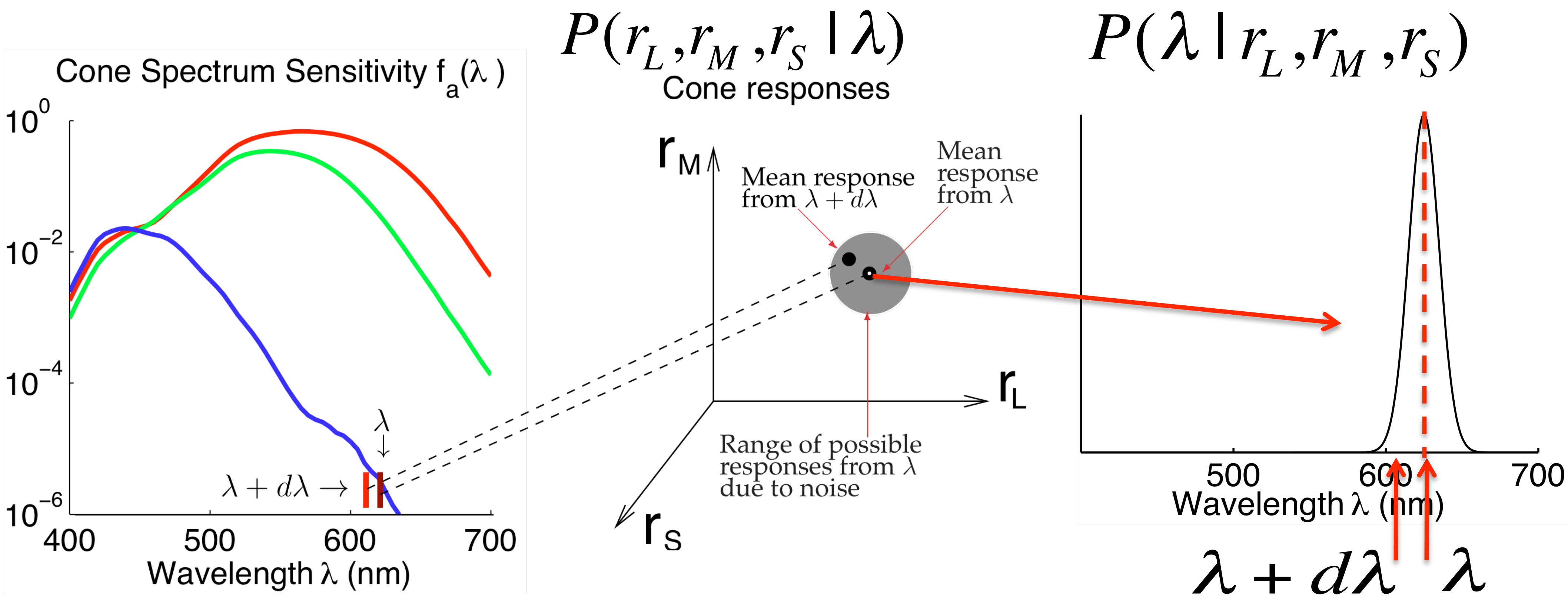




Subject adjust the intensity of the test field to make it appear identical to the standard field, threshold is reached when this is impossible

Why? Can we understand this from the information in the cone absorptions regardless of the post-receptor mechanisms (like an ideal observer's approach)

Due to noise, cone response (absorption) as a probability distribution --- finite discrimination threshold



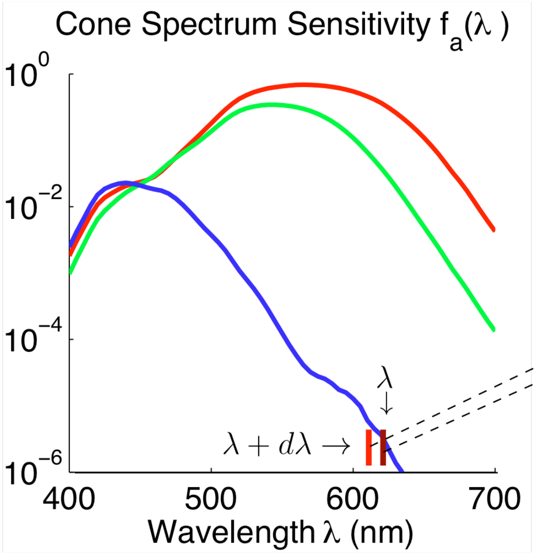
$$P(r_L, r_M, r_S \mid \lambda) \longrightarrow P(\lambda \mid r_L, r_M, r_S)$$ By Bayesian:

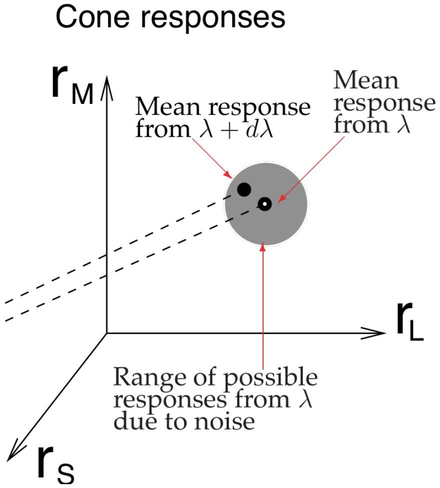
$$P(\lambda \mid r_L, r_M, r_S) = P(r_L, r_M, r_S \mid \lambda) P(\lambda) / P(r_L, r_M, r_S)$$

Maximum likelihood: $P(\lambda \mid r_L, r_M, r_S) \propto P(r_L, r_M, r_S \mid \lambda)$

Cone response noise is Poisson noise

$$P(r_L, r_M, r_S \mid \lambda)$$



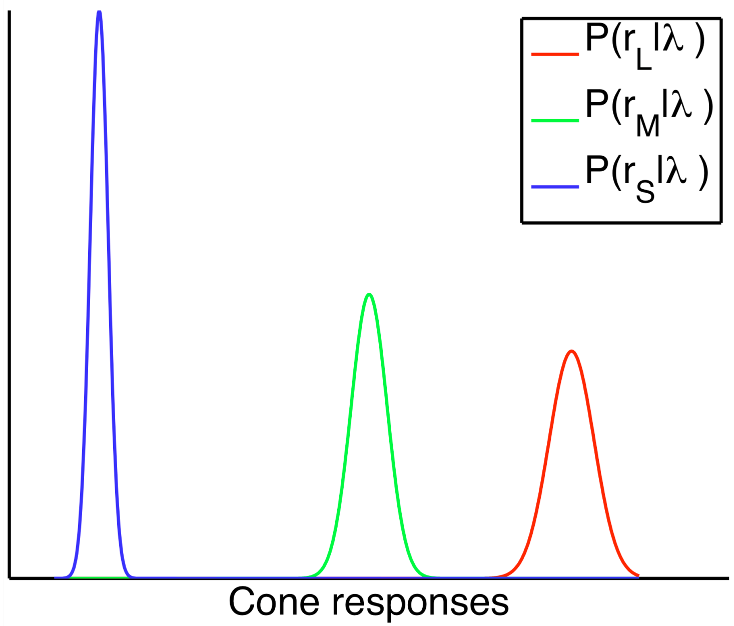


Mean cone response

$$\bar{r}_a = I \bullet f_a(\lambda)$$

Input light intensity

Spectral sensitivity



$$P(r_a \mid \lambda) = \frac{\bar{r}_a^{\,r_a}}{r_a!} \exp(-\bar{r}_a)$$

$$P(r_L, r_M, r_S \mid \lambda) = P(r_L \mid \lambda) P(r_M \mid \lambda) P(r_S \mid \lambda)$$

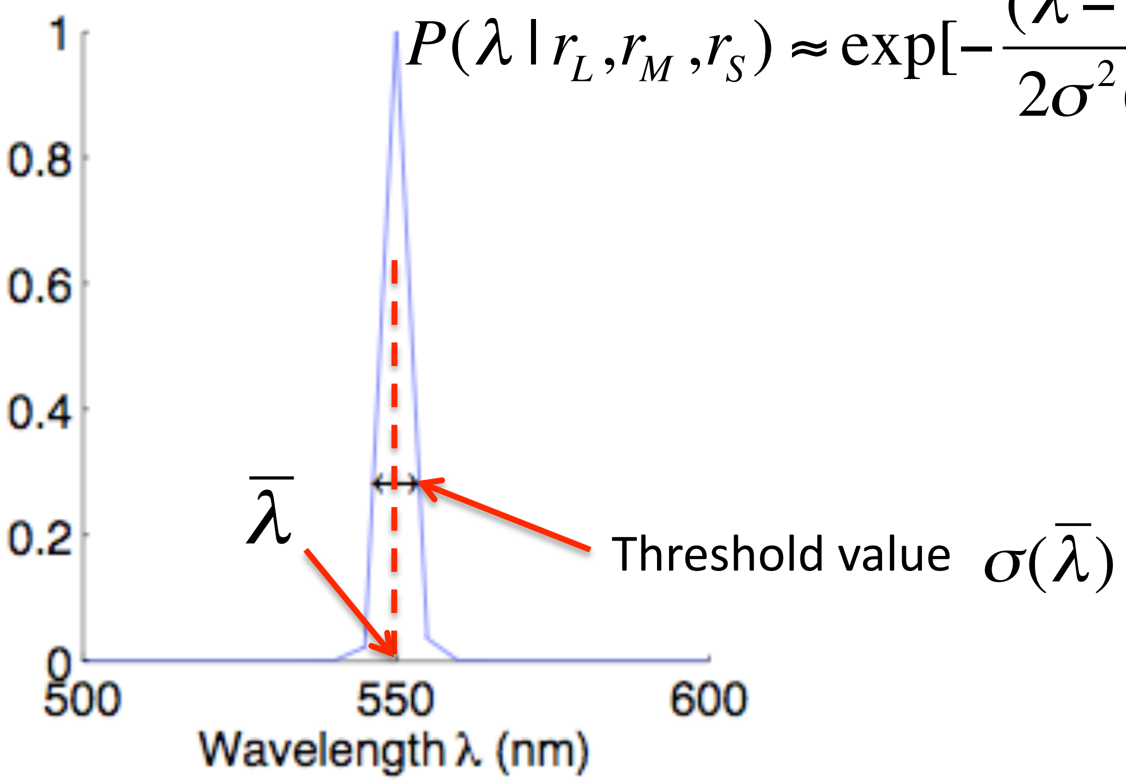
An example of maximum likelihood decoding, given (r_L, r_M, r_S)

get $P(\lambda \mid r_L, r_M, r_S) \propto P(r_L, r_M, r_S \mid \lambda)$

$$\bar{r}_a = I \bullet f_a(\lambda)$$

Responses generated by wavelength at 550 nm

$$P(\lambda \mid r_L, r_M, r_S) \approx \exp[-\frac{(\lambda - \bar{\lambda})^2}{2\sigma^2(\bar{\lambda})}]$$

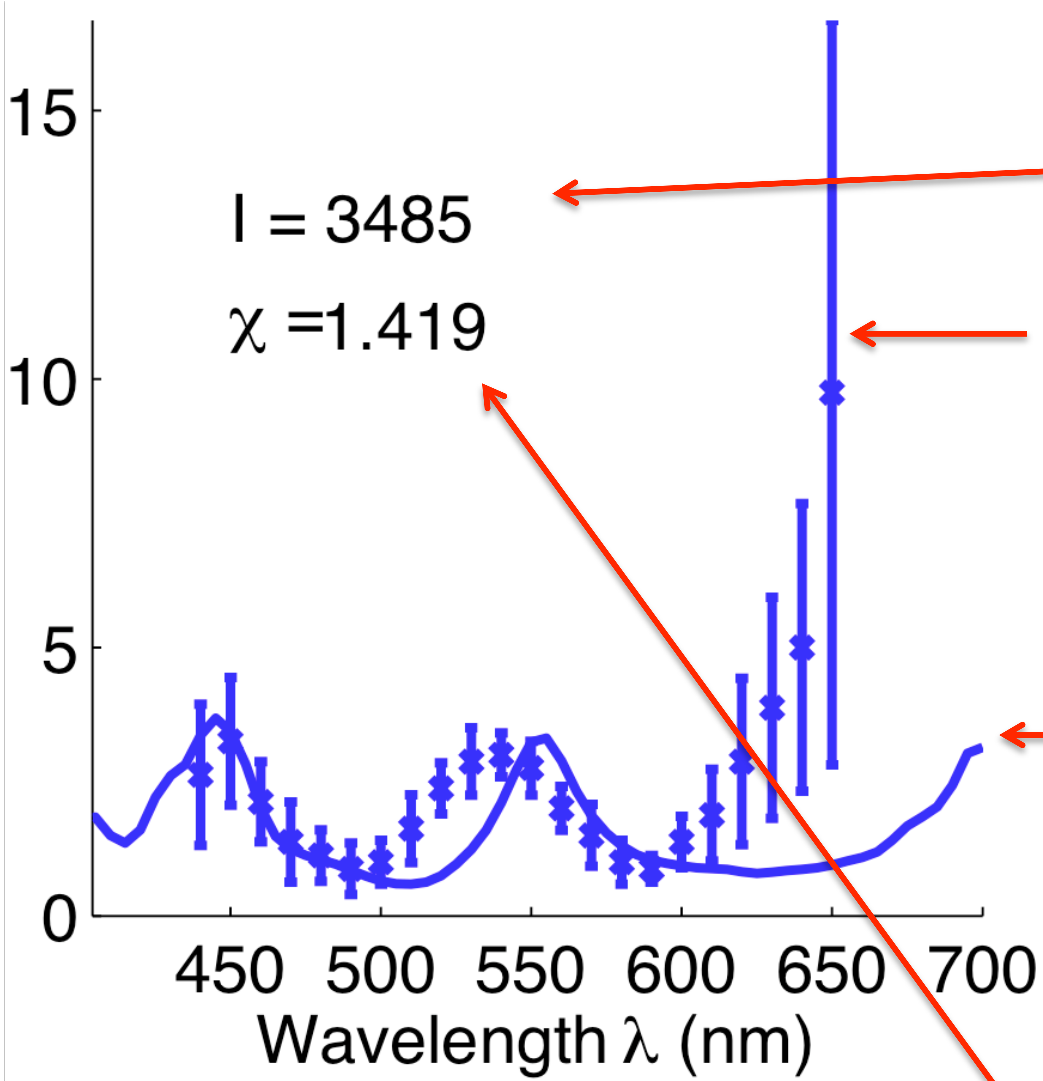


$$\text{Fisher Information } I_F(\lambda) = \sum_a I[f'_a(\lambda)]^2 / f_a(\lambda)$$

$$\text{threshold } \sigma(\lambda) = I_F^{-1/2}$$

Repeat this for all wavelength to find the wavelength discrimination threshold

Threshold σ (nm) $\sigma(\lambda) = \{\sum_a I[f'_a(\lambda)]^2 / f_a(\lambda)\}^{-1/2}$



I chosen to minimize fitting error χ

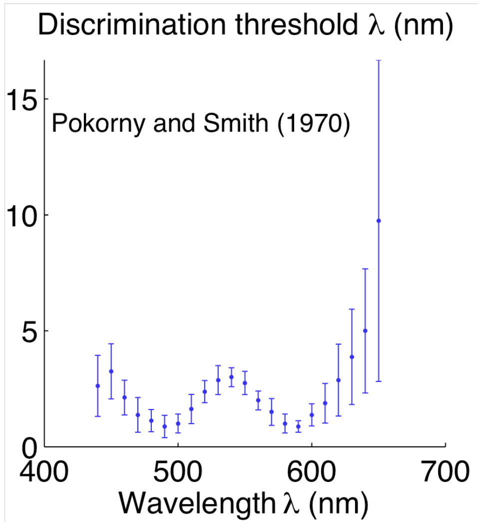
Data $\sigma_{\text{data}}(\lambda)$

Why large discrepancy χ?

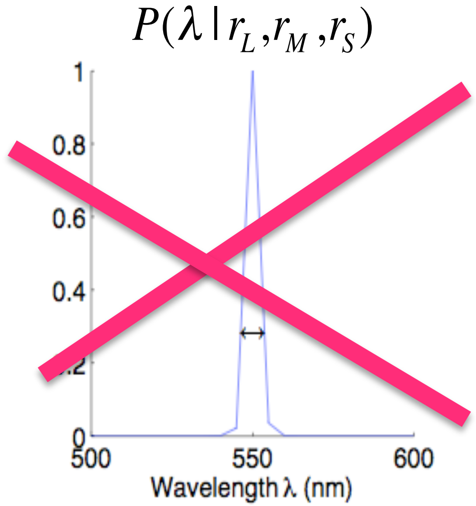
Model prediction $\sigma_{\text{model}}(\lambda)$

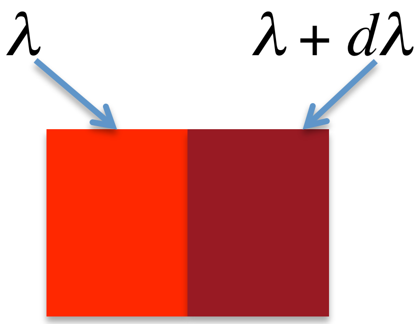
$$\chi^2 = \sum_\lambda \frac{[\sigma_{\text{model}}(\lambda) - \sigma_{\text{data}}(\lambda)]^2}{[\Delta\sigma_{\text{data}}(\lambda)]^2} \Bigg/ \sum_\lambda 1$$

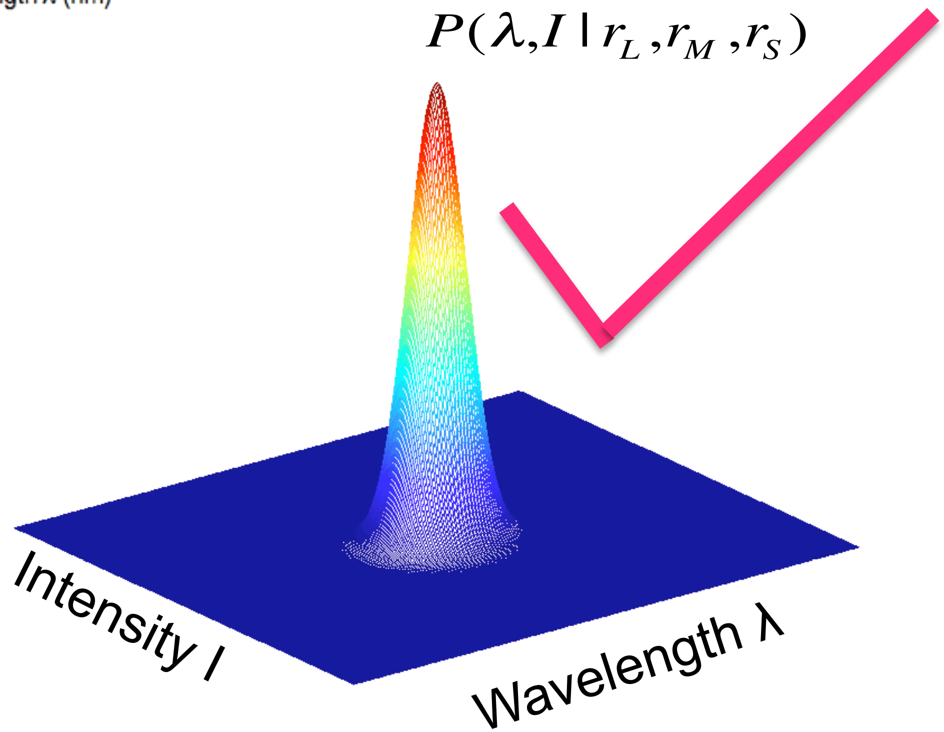
Back to the original measurements (Pokorny and Smith, 1970)



Both input intensity I and input wavelength λ are changed in matching.



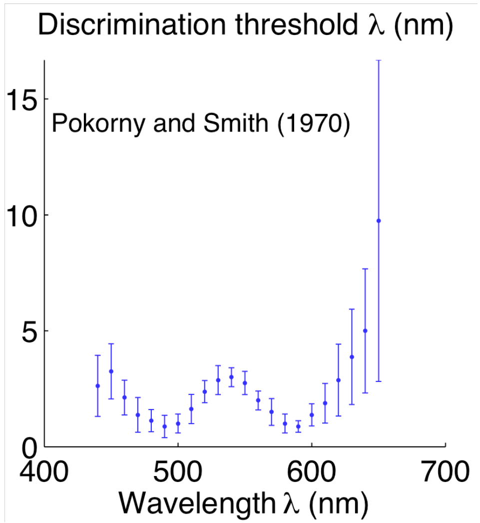


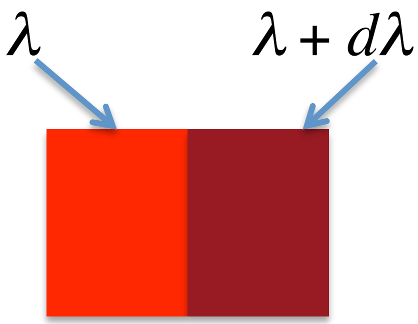


Subject adjust the test field by intensity I to make it appear identical to the standard field, threshold is reached when this is impossible

Back to the original measurements (Pokorny and Smith, 1970)

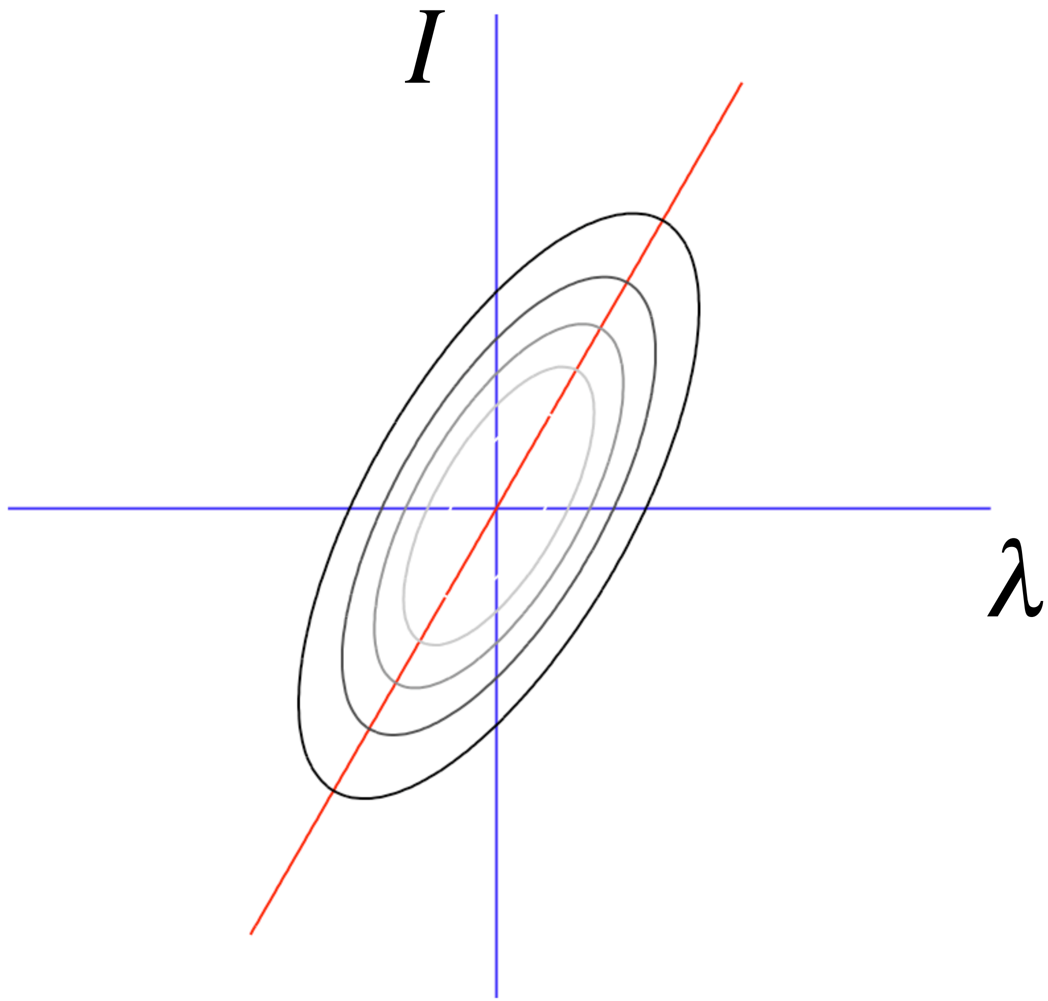
Both input intensity I and input wavelength λ are changed in matching.





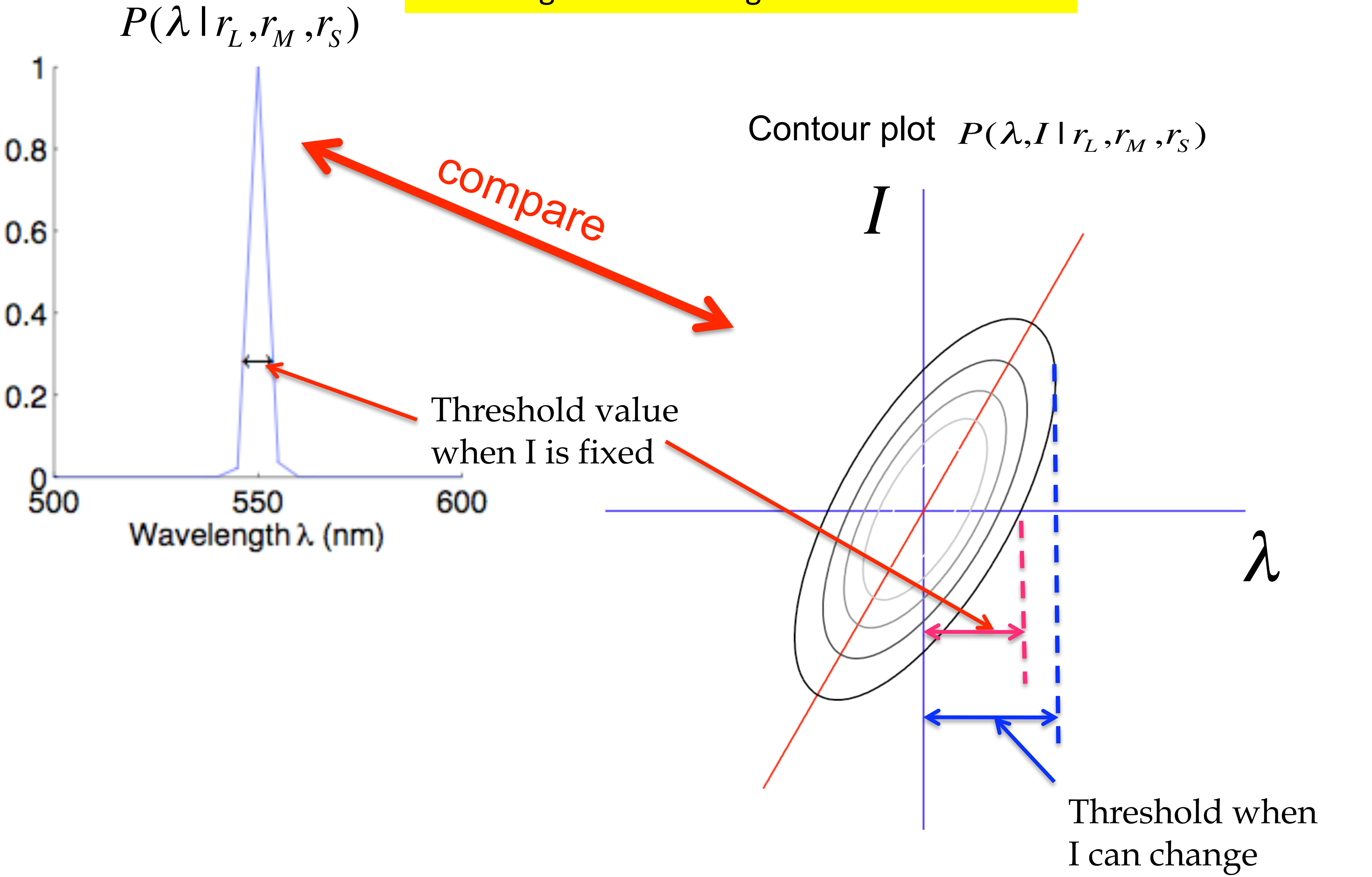
Subject adjust the test field by intensity I to make it appear identical to the standard field, threshold is reached when this is impossible

Contour plot $P(\lambda, I \mid r_L, r_M, r_S)$

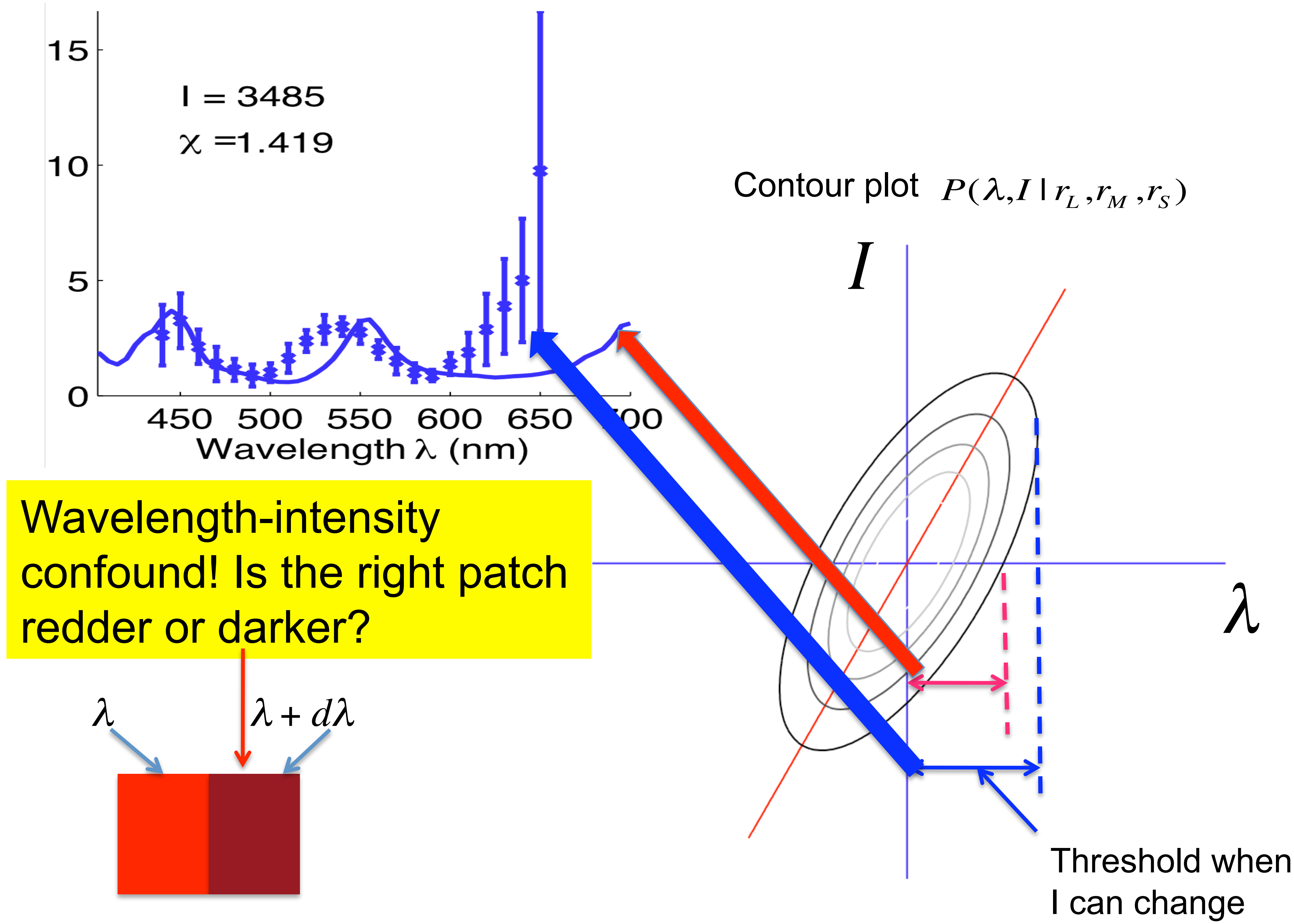


Back to the original measurements (Pokorny and Smith, 1970)

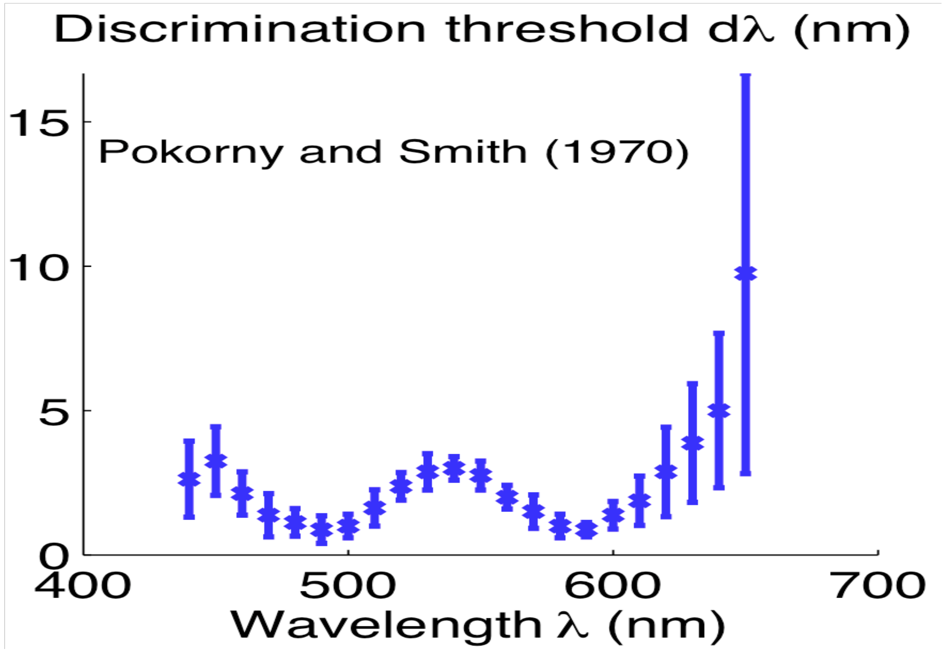
Both input intensity I and input wavelength λ are changed in matching.

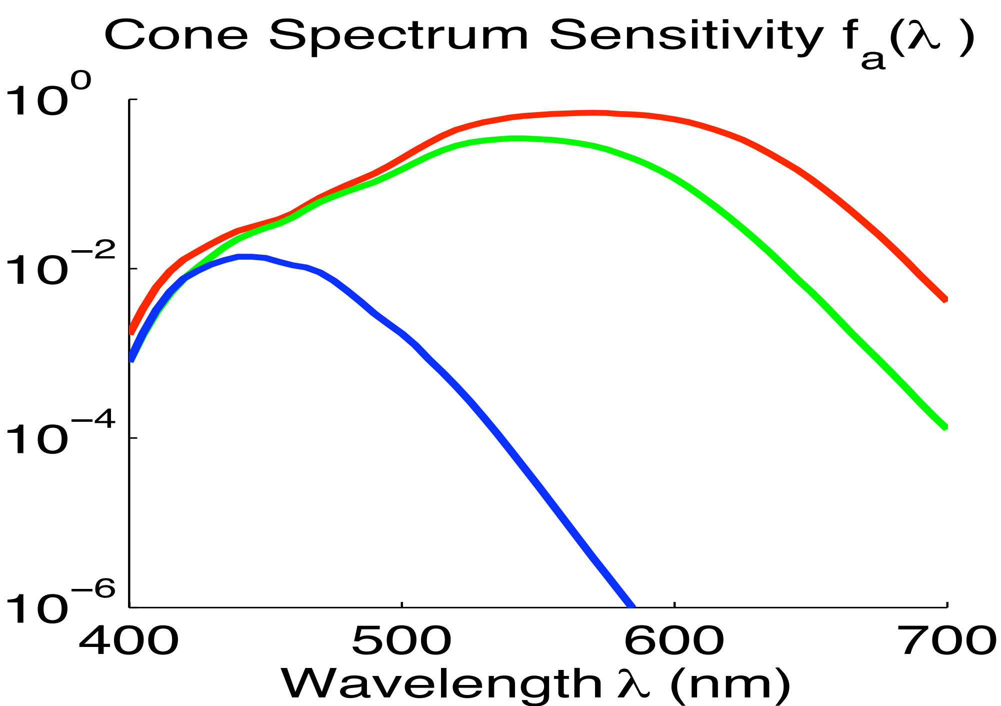


Back to the original measurements (Pokorny and Smith, 1970)

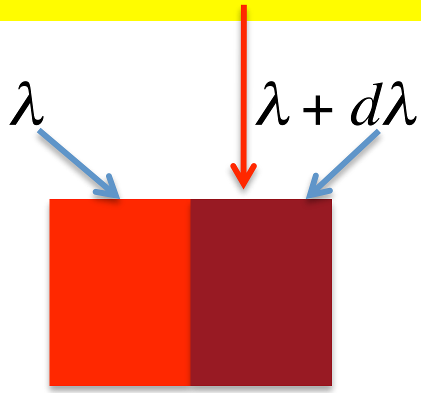


Back to the original measurements (Pokorny and Smith, 1970)





Wavelength-intensity confound! Is the right patch redder or darker?



At long λ, increasing λ decreases responses from all 3 cones, difficult to tell whether the input is redder or darker, the confound is stronger, hence larger threshold.

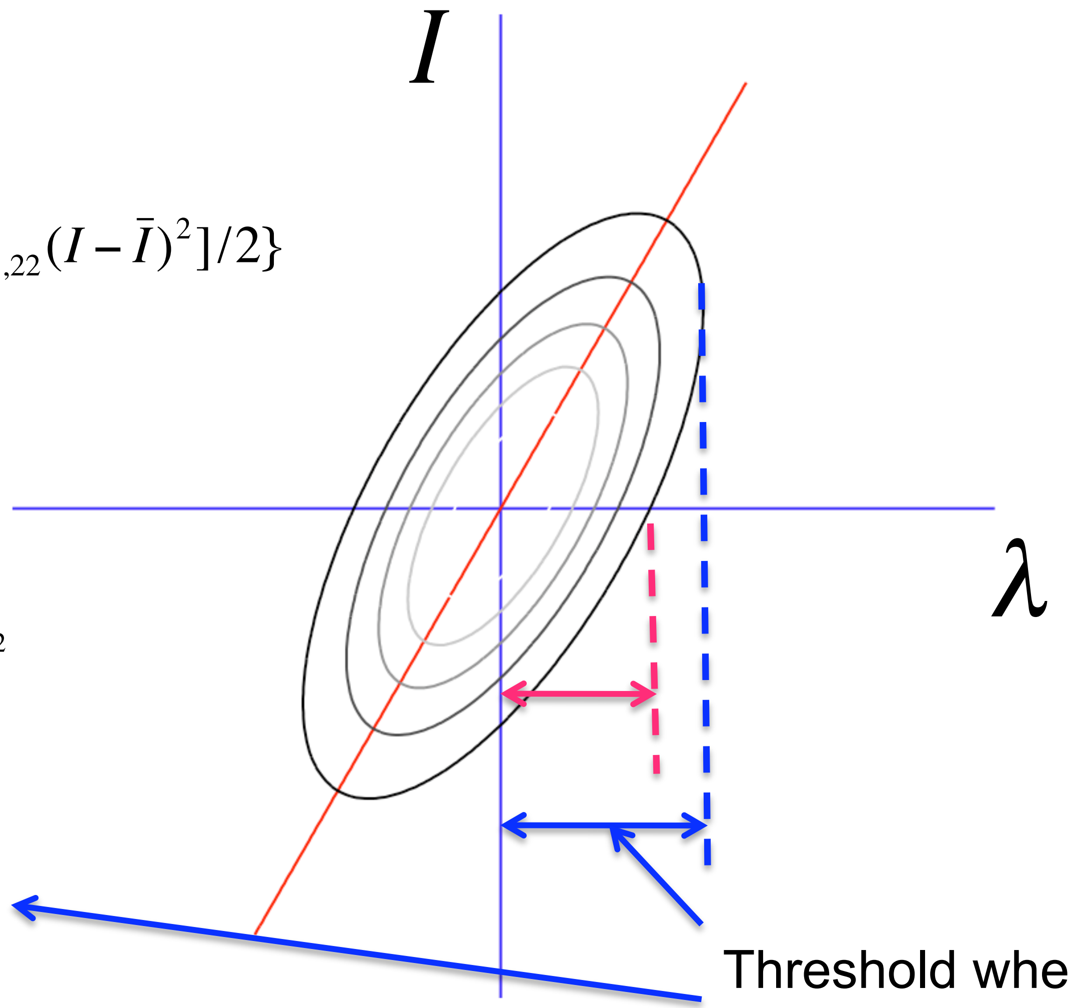
At medium λ, increasing λ increases response from some cone and decreases response from other cones, easier to tell wavelength change. The confound is weaker, hence smaller threshold.

2-d Fisher information formulation

$$I_F(\lambda, I) = -\begin{pmatrix} \left\langle \dfrac{\partial^2 \ln P(r \mid \lambda, I)}{\partial \lambda^2} \right\rangle & \left\langle \dfrac{\partial^2 \ln P(r \mid \lambda, I)}{\partial \lambda \partial I} \right\rangle \\ \left\langle \dfrac{\partial^2 \ln P(r \mid \lambda, I)}{\partial \lambda \partial I} \right\rangle & \left\langle \dfrac{\partial^2 \ln P(r \mid \lambda, I)}{\partial I^2} \right\rangle \end{pmatrix}$$

Contour plot $P(\lambda, I \mid r_L, r_M, r_S)$

$$P(\lambda, I \mid r) \approx$$
$$\exp\{-[I_{F,11}(\lambda - \bar{\lambda})^2 + 2I_{F,12}(\lambda - \bar{\lambda})(I - \bar{I}) + I_{F,22}(I - \bar{I})^2]/2\}$$

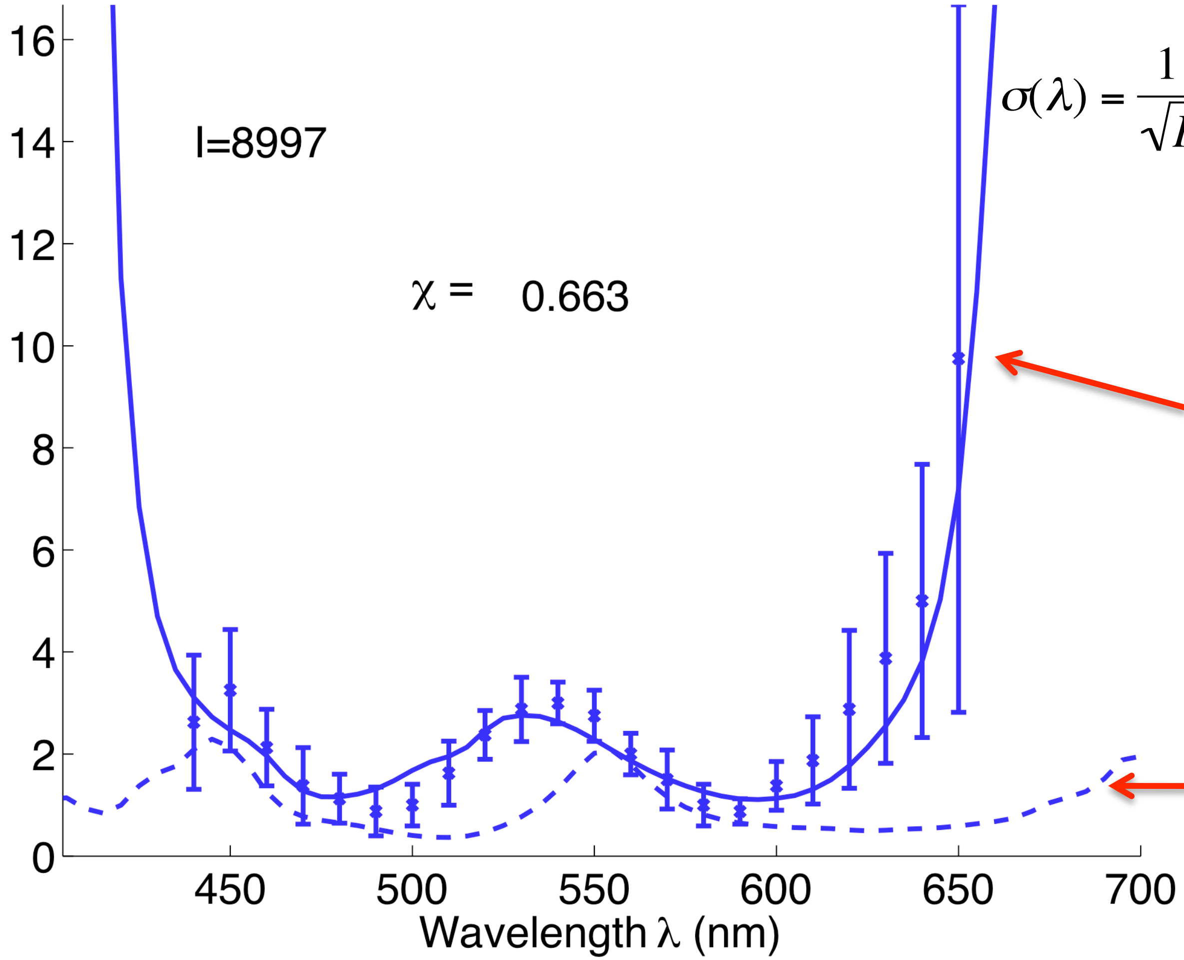


Result:

$$\sigma(\lambda) = \frac{1}{\sqrt{I}} \left\{ \frac{\sum_a f_a(\lambda)}{\sum_b \frac{[f'_b(\lambda)]^2}{f_b(\lambda)} \sum_c f_c(\lambda) - [\sum_d f'_d(\lambda)]^2} \right\}^{1/2}$$

Threshold when
I can change

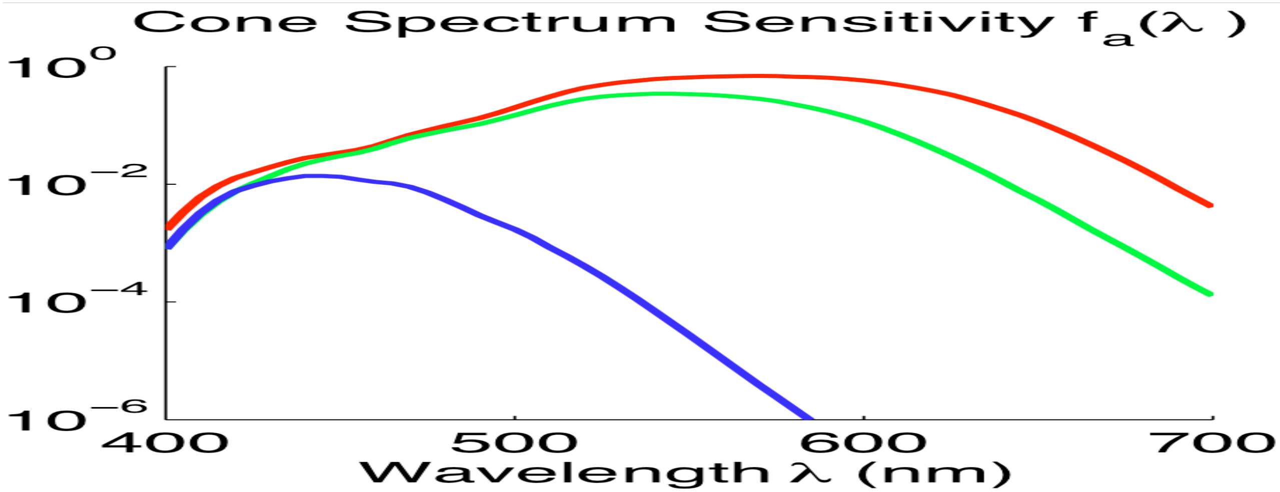
Better explanation of data!



$$\sigma(\lambda) = \frac{1}{\sqrt{I}}\left\{\frac{\sum_a f_a(\lambda)}{\sum_b \frac{[f'_b(\lambda)]^2}{f_b(\lambda)}\sum_c f_c(\lambda) - [\sum_d f'_d(\lambda)]^2}\right\}^{1/2}$$

When input intensity is adjusted in color matching

otherwise



Interim Summary:

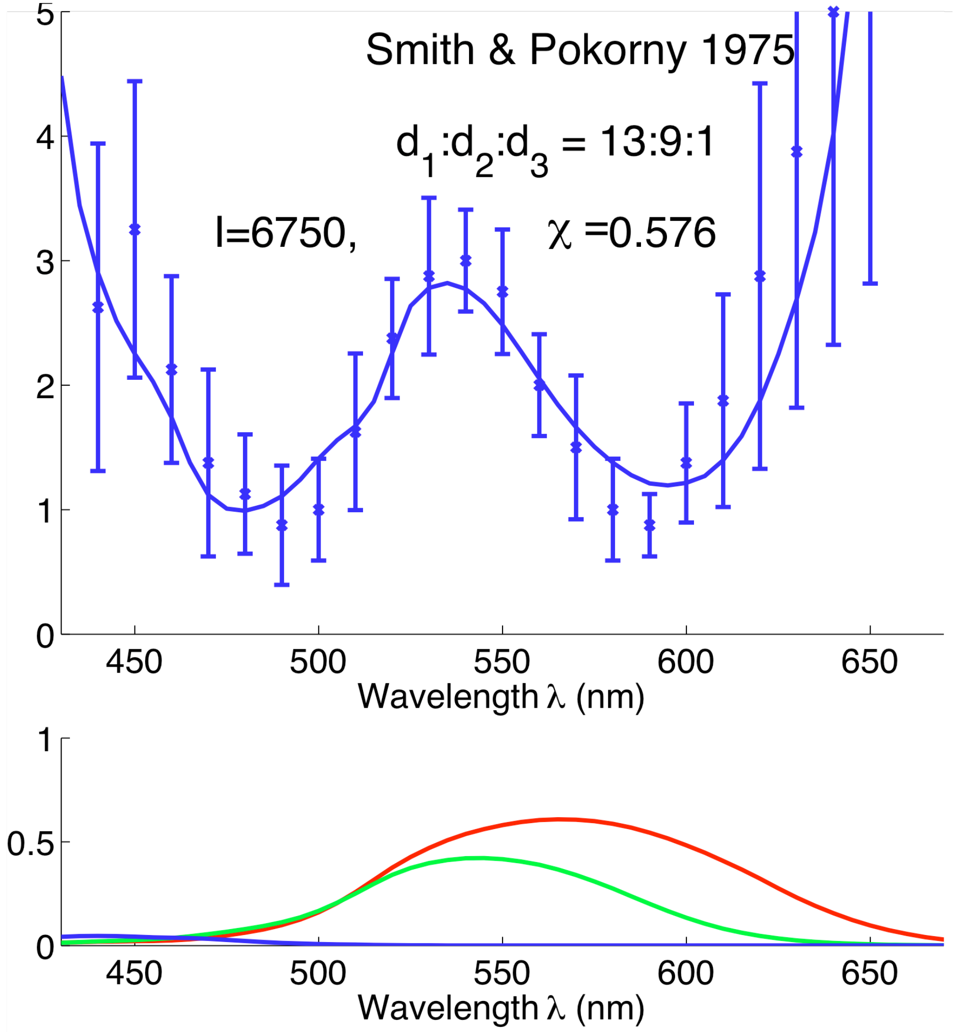
Monochromatic light wavelength discrimination explained by optimal decoding based on signals in the cones.

Suggest that efficiency in information processing efficiency in post-receptoral mechanisms is a constant regardless of wavelength.

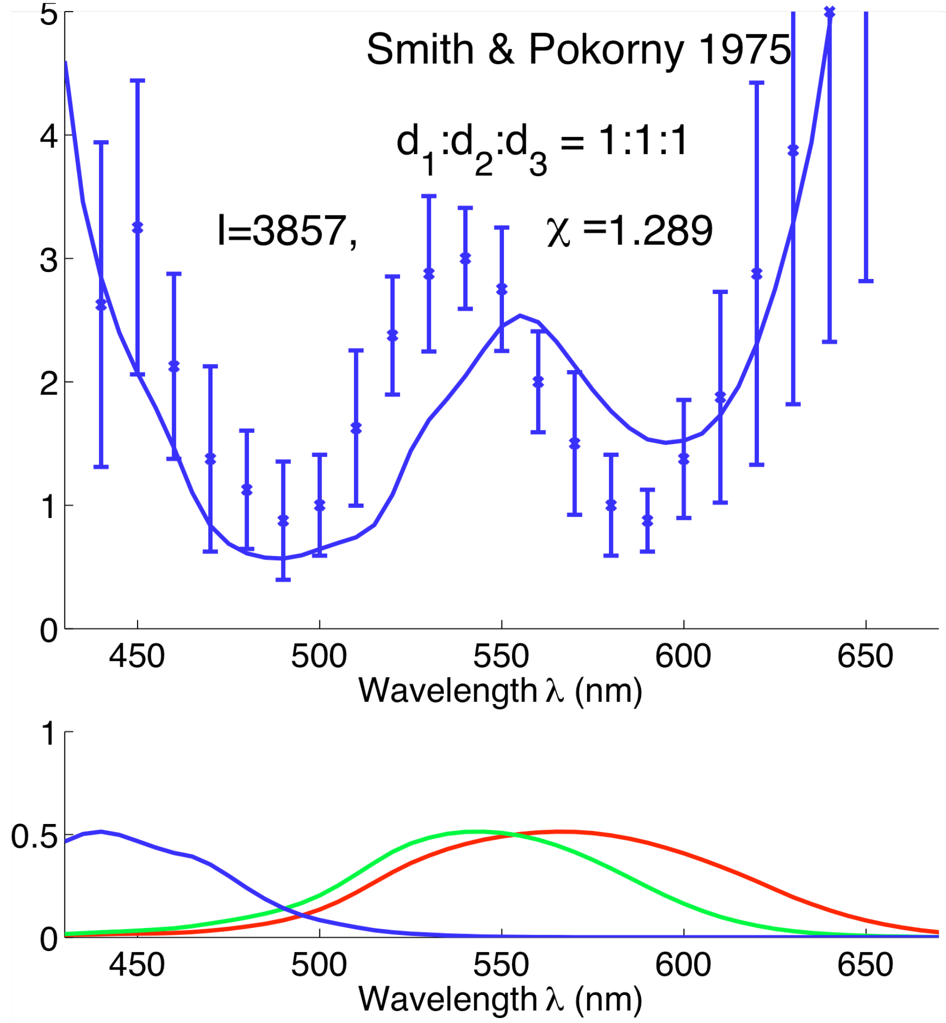
Model has to match with experimental methods to account for data.

Prediction --- smaller threshold when input intensity is fixed in threshold assessments

Relative cone densities for L, M, S cones influence model prediction accuracy



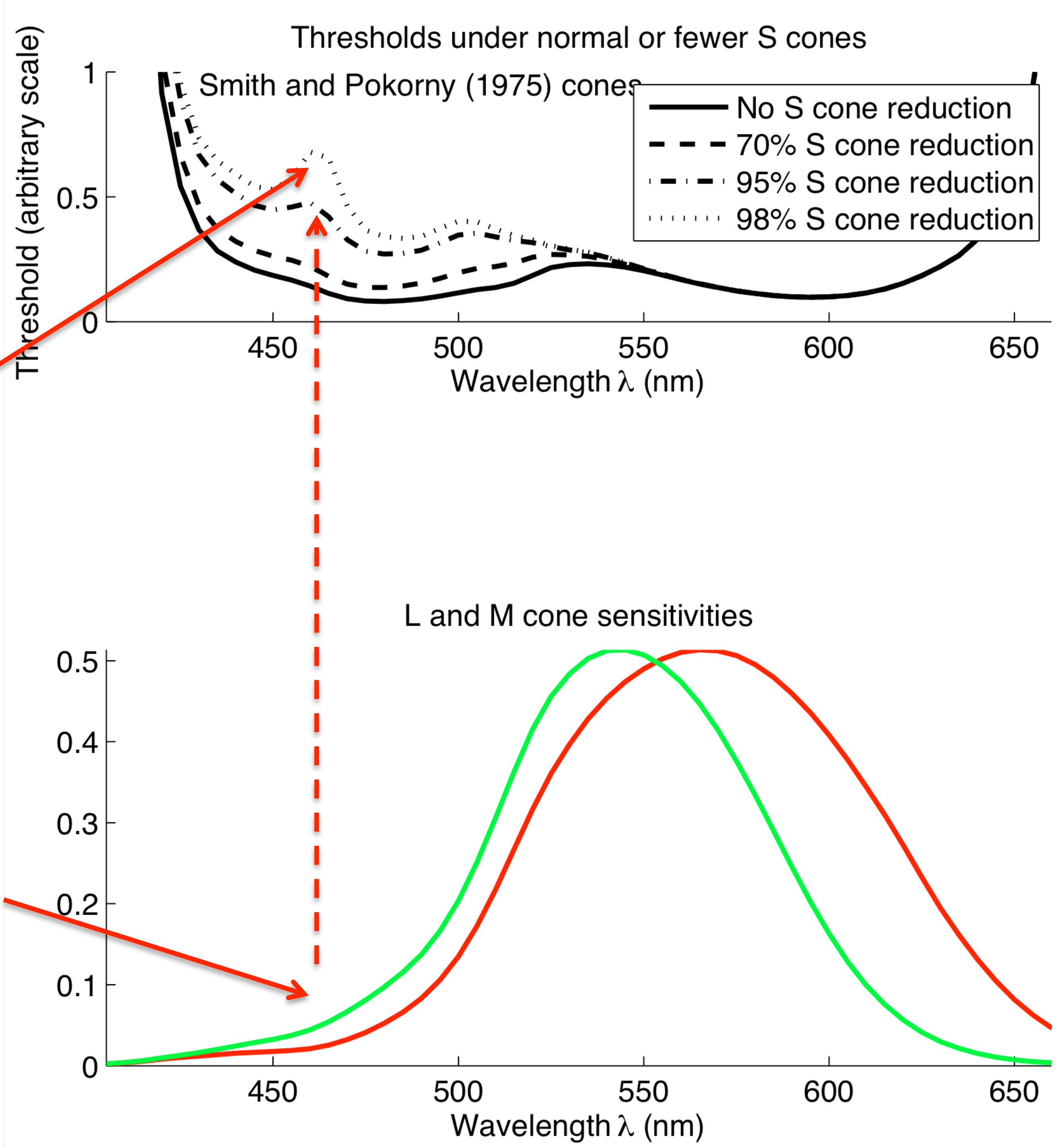
normal amount of S cones



S cones too numerous

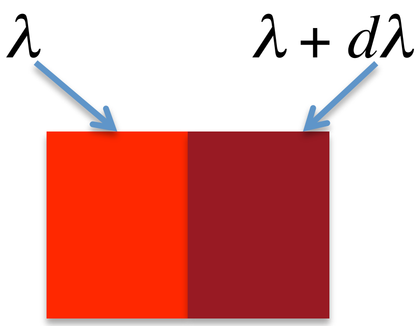
When S cones are too few …

An extra peak… as seen in some data (Bedford and Wyszecki 1958)when the input field is too small, too few S cones



L & M cone co-vary here … becoming color blind.

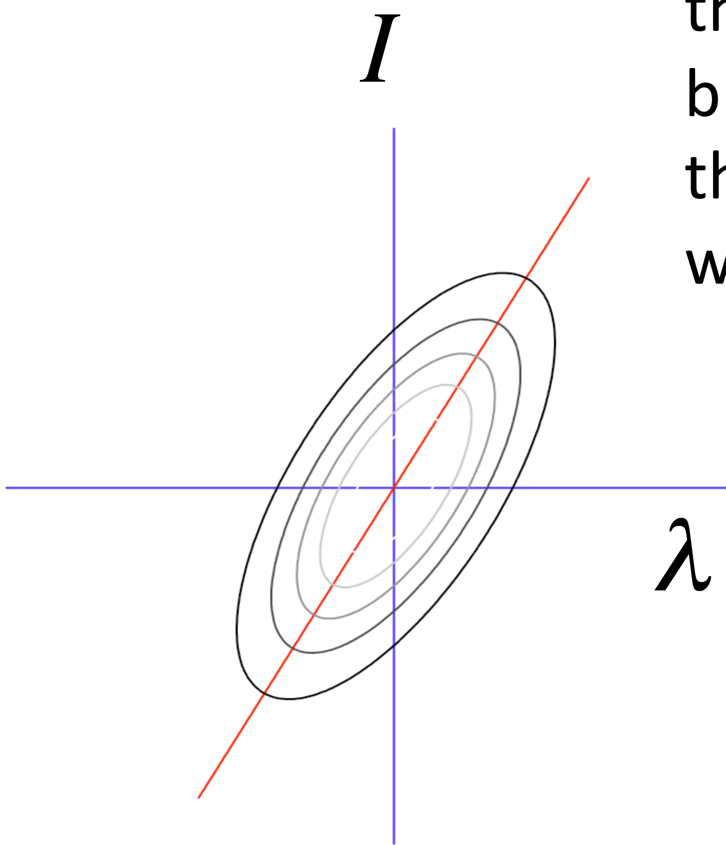
Importance of proper experimental procedures:



Two kinds of procedures in the literature:

Pokorny and Smith (1970): Subject adjust the test field by intensity I to make it appear identical to the standard field, threshold is reached when this is impossible

Bedford and Wyszecki (1958): Subject adjust the test field by intensity I to match the brightness of the two fields, and then see if there is a hue difference. Threshold is reached when there is a hue difference.



Wavelength-intensity confound means that it is difficult to ask subjects to match the brightness of two color fields while checking whether they differ in hue.

Summary:

Human wavelength discrimination can be understood as optimal decoding from cone absorptions (with constant efficiency)

This model reveals the reliability of data from different experimental procedures.