A Learning Model for L/M Specificity in Ganglion Cells

al.ahumada@nasa.gov

Outline

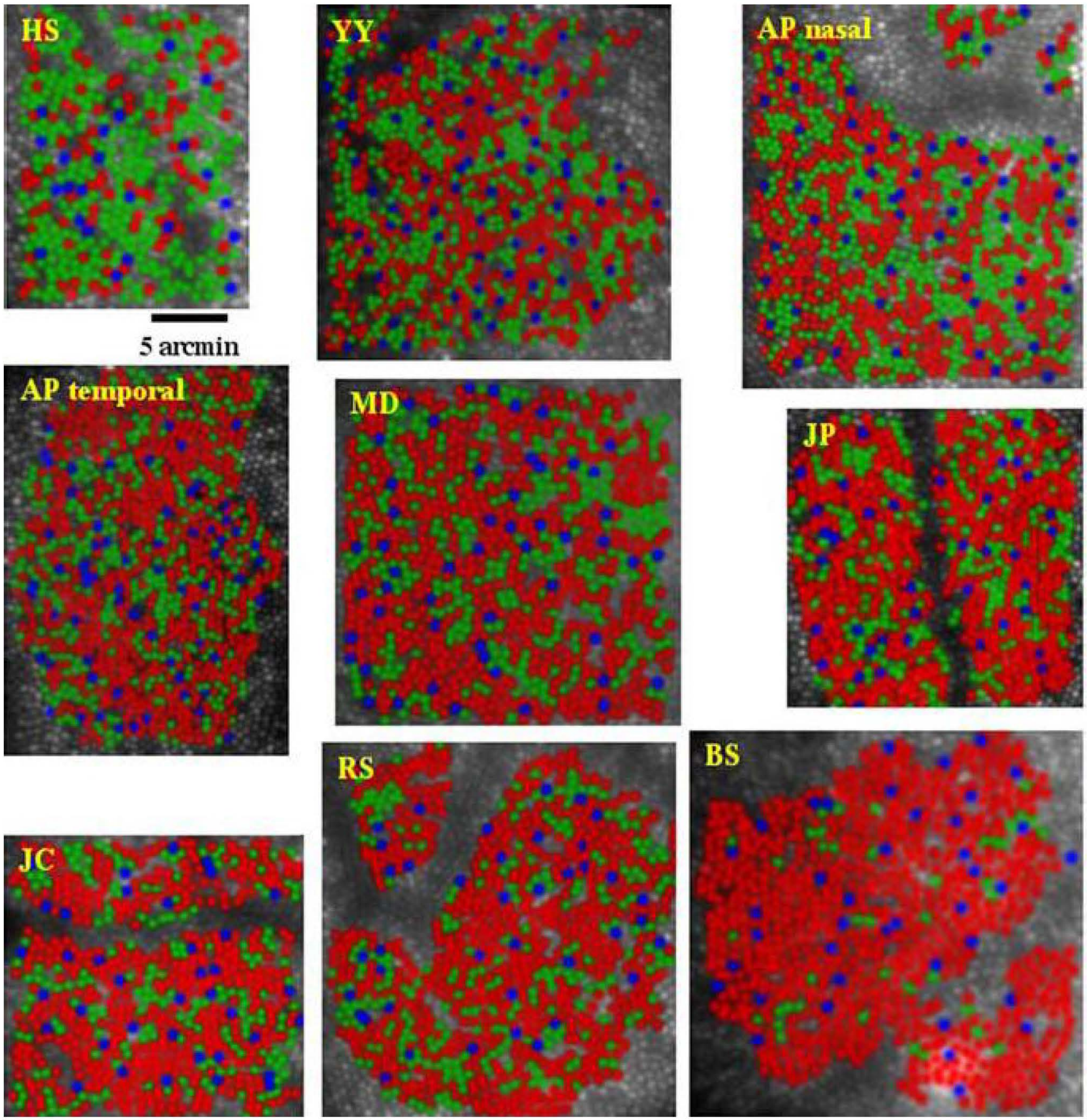
Review the cone-indiscriminate wiring model for ganglion cells.

Describe the resulting signal-to-noise issue.

Show how associative learning in the retina could generate cone-specific ganglion cells.

Discuss some implications.

Hofer, Carroll,Neitz, Neitz & Williams (2005) JNS



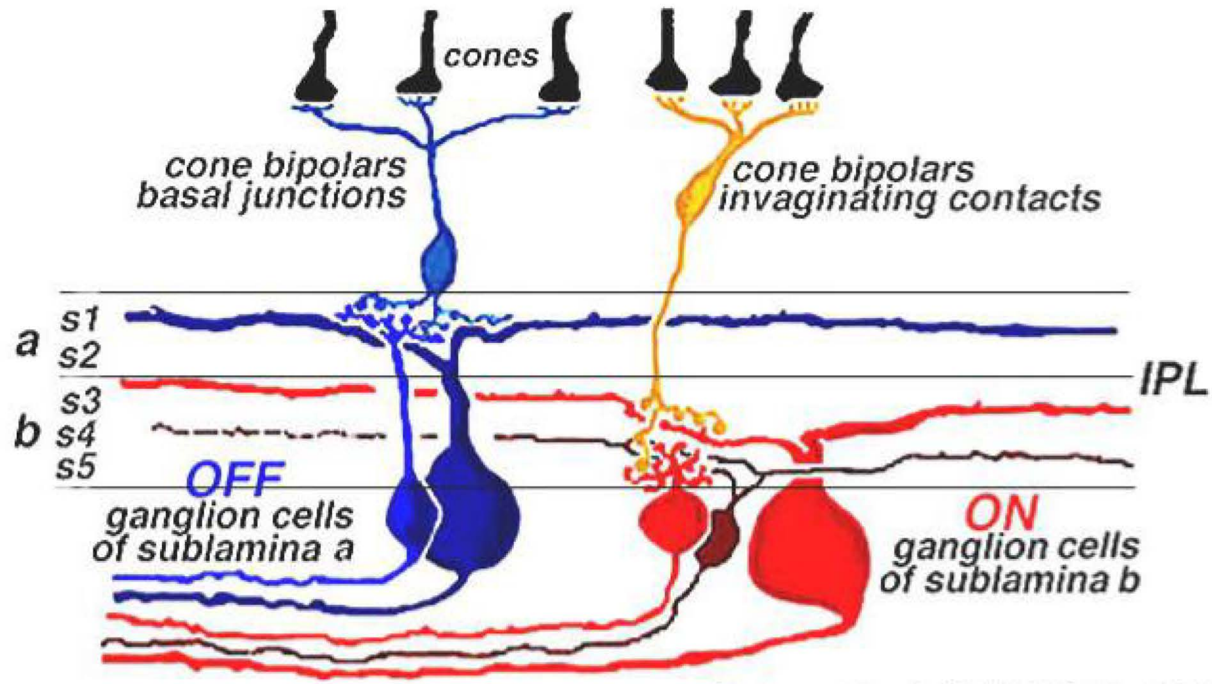
L/M Cone Array Model

Spatially random array of cones with a proportion p_L of L cones and $p_M = 1 - p_L$ of M cones.

$c_{L,\,i}$ is the signal from L cone i;

$c_{M,\,j}$ is the signal from M cone j.

Retinal Ganglion Cells



Nelson, Famiglietti & Kolb, 1978

Ganglion Cell Model

g_L , output of an L-center ganglion cell

$$g_L = c_{L,\,0} - \left(\sum_i w_{L,\,i}\, c_{L,\,i} + \sum_j w_{M,\,j}\, c_{M,\,j}\right)$$

$$w_{L,\,i}\,,\ w_{M,\,j} \geq 0$$

$$W_T = W_L + W_M$$

$$= \sum_i w_{L,\,i} + \sum_j w_{M,\,j} \leq 1$$

A balanced cell is color pure for a uniform stimulus .

Paulus & Kröger-Paulus (1983 VR).

"A new concept of retinal colour coding."

$$g_L = c_{L,0} - \left(\sum_i w_{L,i}\, c_{L,i} + \sum_j w_{M,j}\, c_{M,j}\right)$$

$$g_L = L - \left(\sum_i w_{L,i}\, L + \sum_j w_{M,i}\, M\right)$$

$$= L(1 - W_L) - M\, W_M$$

$$= L(1 - W_T + W_M) - M\, W_M$$

$$= W_M\, (L - M), \quad \text{if } W_T = 1.$$

Cone Noise Effects

Suppose we add to cone i an independent noise e_i with $E[e_i] = 0$ and $E[e_i^2] = \sigma_C^2$.

If there are N surround cones with N_M M cones, and $w_{L,i}$, $w_{M,j} = 1/N$,

$$W_M = N_M/N .$$

The signal to noise ratio, $s/n = E[g_L] / std[g_L]$

$s/n = ((L-M) N_M/N) / (\sigma_C \, sqrt(1+1/N))$

Cone-specific Case

If we delete the connections from the same type of cone, and there is a least one cone of the opposite type, the signal to noise ratio is that when $N = N_M$

$$s/n = (L-M) / (\sigma_C \, \mathrm{sqrt}(1+1/N_M))$$

The ratio of the signal-to-noise ratio for the indiscriminate case to that of the cone specific case is

$$N_M(N_M+1) / (N(N+1))$$

Loss Ratio Table

N = 6, p_L = 2/3

ratio	2/42	6/42	12/42	20/42	30/42	42/42
dB	-26	-17	-11	-6	-3	0
Prob	0.18	0.25	0.22	0.16	0.10	0.03

Prob all surrounds same as center = 0.06

Average loss = -13 dB

Goals

Review the cone-indiscriminate wiring model for ganglion cells and describe its signal-to-noise problem.

➨ Show how associative learning in the retina could generate cone-specific ganglion cells.

Discuss some implications.

Cone Images for Training

The cones are presented with a sequence of training images that provide each of the cone types in each position a series of values.

The average behavior of the learning process depends on certain average properties of the images.

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Cone Images for Training

Simplifying assumptions:
The inputs are locally uniform,
$c_{L,\,i} = L$, $c_{M,\,j} = M$.

The average over images of the cone inputs squared is
$E[L^2] = E[M^2] = \sigma^2$.

The average cross correlation is
$E[L\,M] = \rho\,\sigma^2$

Hebbian Learning Rule

$x = (x_i)$ = a list of random variables with covariance matrix $C = (c_{i,\,j}) = (E[x_i\, x_j])$

$$y = \Sigma\, w_i\, x_i$$

The Hebbian associative learning rule

$$\Delta\, w_i = a\, y\, x_i$$

can compute the principle component of the covariance matrix, i. e. find the weights that maximize the variance of y if

$$\Sigma\, w_i^{\,2} = 1$$

Ganglion Cell Learning Rule

$\Delta w_{L,i}(t) = w_{L,i}(t+1) - w_{L,i}(t) = -a\, g(t)\, c_{L,i}(t)$

Constraints: $w_i >= 0$,

$\Sigma w_i = W_L + W_M = W_T$.

For a g_L cell, the learning rule will result in W_L going to zero if a is small enough to average out the random variations and

$E[\Sigma \Delta w_{L,i} - \Sigma \Delta w_{M,j}] = E[\Delta W_L - \Delta W_M] < 0$

Ganglion Cell Learning

$\Delta\, w_{L,\,i}(t) = w_{L,\,i}(t+1) - w_{L,\,i}(t) = -a\, g_L(t)\, c_{L,\,i}(t)$

For the balanced, noise-free case

$g_L(t) = W_M(t)\,(L - M);\;\; c_{L,\,i}(t) = L;\; c_{M,\,i}(t) = M$

$E[\Delta\, w_{L,\,i}(t)\,] = -a\, W_M(t)\, E[L^2 - L\,M]$

$E[\Delta\, w_{L,\,i}(t)\,] = -a\, W_M(t)\, \sigma^2(1-\rho)$ [decreasing]

$E[\Delta\, w_{M,\,i}(t)\,] = -a\, W_M(t)\, E[L\,M - M^2]$

$E[\Delta\, w_{M,\,i}(t)\,] = a\, W_M(t)\, \sigma^2(1-\rho)$ [increasing]

Ganglion Cell Learning

For the balanced, cone noise case

$E[\Delta\, w_{L,\, i}(t)\,] = -a\,(W_M(t)\,\sigma^2(1-\rho) + w_{L,\, i}(t)\,\sigma_C^{\,2})$

$E[\Delta\, w_{M,\, j}(t)\,] = a\,(W_M(t)\,\sigma^2(1-\rho) - w_{M,\, j}(t)\,\sigma_C^{\,2})$

Learning depends on $\sigma^2(1-\rho)$ dominating $\sigma_C^{\,2}$.
For cones, ρ is close to 1, but for bipolars it should be small.

Finally

If L and M cells can only be distinguished by their responses to light, and
if ganglion cells have cone-specific connections,
learning must occur in the retina.

The CNS must have processes for pruning useless connections.
The retina could have such processes.
Associative learning is a good candidate.