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.


“A new concept of retinal colour coding.”

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

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

\[
= L(1 - W_L) - M W_M
\]

\[
= L(1 - W_T + W_M) - M W_M
\]

\[
= W_M (L - M), \text{ if } W_T = 1.
\]
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, \( s/n = E[g_L] / \text{std}[g_L] \)

\[
s/n = ((L-M) N_M/N) / (\sigma_C \sqrt{1+1/N})
\]
Cone-specific Case

If we delete the connections from the same type of cone, and there is at least one cone of the opposite type, the signal-to-noise ratio is that when \( N = N_M \)

\[
\frac{s}{n} = \frac{(L-M)}{(\sigma_C \sqrt{1+1/N_M})}
\]

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

\[ N = 6, \ p_L = 2/3 \]

<table>
<thead>
<tr>
<th>ratio ( \frac{2}{42} )</th>
<th>( \frac{6}{42} )</th>
<th>( \frac{12}{42} )</th>
<th>( \frac{20}{42} )</th>
<th>( \frac{30}{42} )</th>
<th>( \frac{42}{42} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>dB</td>
<td>-26</td>
<td>-17</td>
<td>-11</td>
<td>-6</td>
<td>-3</td>
</tr>
<tr>
<td>Prob</td>
<td>0.18</td>
<td>0.25</td>
<td>0.22</td>
<td>0.16</td>
<td>0.10</td>
</tr>
</tbody>
</table>

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

The average cross correlation is
$E[L M] = \rho \sigma^2$.
Hebbian Learning Rule

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

\[ y = \sum w_i x_i \]

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

\[ \sum w_i^2 = 1 \]
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: \( w_i \geq 0 \),

\[ \sum w_i = W_L + W_M = W_T. \]

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

\[ E[\sum \Delta w_{L, i} - \sum \Delta w_{M, j}] = E[\Delta W_L - \Delta W_M] < 0 \]
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
\[ g_L(t) = W_M(t) (L - M); \quad c_{L, i}(t) = L; \quad c_{M, i}(t) = M \]

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

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

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

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

For the balanced, cone noise case

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

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

Learning depends on \( \sigma^2(1-\rho) \) dominating \( \sigma_C^2 \). For cones, \( \rho \) 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.