Lateral excitation in the vertebrate retina

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1 The vertebrate retina

- There are five broad classes of neurons:
  - receptor, bipolar, ganglion (three layers)
  - horizontal and amacrine (lateral connectivity)

- In these five broad classes, there many cell types (60 in the cat), distinguished by morphology, function, neurochemistry, connections.

- There are considerable species differences. For example, "lower" animals do more visual processing in the retina, while mammals have simpler retinas and do more processing in the brain.

- The vertebrate retina is much more complex than the Limulus retina, and is not understood as well. The receptive field of ganglion cells shows center-surround structure, but its mechanisms are very different than in Limulus.

2 The neurons

- There are about 100 million photoreceptors. The two types are rods, which are specialized for night, and cones, which are specialized for day.
  - Bipolar
  - There are 1.25 million ganglion cells

- A simplified model of the outer plexiform layer: photoreceptor takes log of intensity horizontal cells form resistive network that smooths signal inhibitory chemical synapses to other neurons bipolars subtract the two

3 Resistive network model

- Since the horizontal cells are connected by gap junctions, we can model them as a network of resistors.
The voltages at the nodes of the network are \( V_n \).

Let \( R \) be the axial resistance between nodes.

Each node is connected to ground by a conductance \( G \) and a capacitance \( C \).

Let \( I_n \) be the current from node \( n \) to \( n + 1 \). Current balance gives us

\[
C \frac{dV_n}{dt} + GV_n = I_{n-1} - I_n + I_{n+1}^{ext}
\]

Ohm’s law tells us that \( I_n R = V_n - V_{n+1} \) and \( I_{n-1} R = V_{n-1} - V_n \), yielding

\[
RC \frac{dV_n}{dt} + GRV_n = V_{n-1} - V_n - V_n + V_{n+1} + I_{n+1}^{ext}
\]

This is interesting, because it looks like the network equations that we derived for chemical synapses, even though these synapses are electrical. Such equations have actually implemented in VLSI (silicon retinas). The lateral interactions are excitatory.

We can make a continuum approximation. Let the position of the \( n \)th node be \( x_n = n \Delta x \), where \( \Delta x \) is the spacing between nodes. Then

\[
\frac{\partial V}{\partial x} \approx \frac{V_{n+1} - V_n}{\Delta x} \approx \frac{V_n - V_{n+1}}{\Delta x}
\]

\[
\frac{\partial^2 V}{\partial x^2} \approx \frac{V_{n+1} - 2V_n + V_{n-1}}{(\Delta x)^2}
\]

So the continuum approximation is

\[
RC \frac{\partial V}{\partial t} + GRV = (\Delta x)^2 \frac{\partial^2 V}{\partial x^2} + I_{n+1}^{ext}
\]

### 4 Steady-state impulse response

- Discrete case
  
  intuition: peak in middle, decay solve homogeneous equation by guessing the solution \( V_n = \gamma^n V_0 \) match boundary conditions at input

- Continuous case. Same thing with exponential \( V = V_0 e^{-x/L} \). In two dimensions, the solution is a Bessel function.

### 5 Time-dependent impulse response

impulse response analogy with diffusion equation
6 Modeling the outer plexiform layer

• What is the mechanism of center-surround?
  – In the simplest model, the horizontal cells form a resistive network, and convolve the photoreceptor signal by the impulse response function. The bipolar cell takes the difference of the receptor and horizontal cell signals, to yield center-surround.
  – A more detailed model takes the gap junctions between the cones into account.

\[
c_{c0} \frac{dV_c}{dt} + g_{c0} V_c = I_o + \frac{1}{r_{cc}} \nabla^2 V_c - g_{ch} V_h \\
c_{h0} \frac{dV_h}{dt} + g_{h0} V_h = g_{hc} V_c + \frac{1}{r_{hh}} \nabla^2 V_h
\]

• Is there an advantage of using lateral excitation to build up the surround? The radius of the surround can be larger than the radius of lateral connectivity. The wiring is shared.