

## Chapter 4 Retinal Spatiotemporal Dynamics: A Physical Model

To discover how the retina implements bandpass spatiotemporal filtering, and to understand the tradeoffs that it makes in the face of severe wiring limitations, I analyze the spatiotemporal behavior of a simple dynamic model of the retina. This model is a physical one: It is built out of resistors, capacitors, and transconductances. It is based on the neurocircuitry of the vertebrate retina; it includes several major synaptic interactions in the outer plexiform layer (OPL). My goal is synthesize the minimal amount of machinery required to reproduce the observed qualitative behavior, rather than to provide detailed quantitative predictions of retinal responses.

In particular, I seek the simplest linear physical model that reproduces the salient features of retinal spatiotemporal dynamics, and I employ circuit theory and Fourier methods to obtain closed-form analytical descriptions of its behavior. These analytical expressions are indispensable to understanding the tradeoffs inherent in this simplified retina model. To the extent that these tradeoffs arise from fundamental physical limitations—such as the inseparability of spatial and temporal processing—they carry over to the real retina, or at least to those parts of the retinal structure that the model includes.

This approach is part of an overarching layered-complexity strategy that I have adopted, where we reverse-engineer the retina by peeling away one level of complexity at a time. Once we know the tradeoffs inherent in the design of a piece of neurocircuitry, we can see how to introduce an additional layer of complexity to improve its performance. Although a linear model cannot include adaptation mechanisms, such as gain control, we can often achieve the desired result by varying the parameters of the linear circuit, such as its gain or its time and space constants, appropriately.

Adaptation matches the gain of the filter to the mean signal level, and matches

the tuning of the filter to the signal-to-noise ratio. Since the linear filter’s tradeoffs are stated in terms of these very same parameters, studying the linear case helps us understand how adaptation affects system performance. By relating these parameters to the values of resistors, capacitors, and transconductances in the model, the linear analysis can guide the design of these adaptation mechanisms.

Layering adaptation on top of filtering in this fashion is valid, since these two mechanisms act on disparate spatial and temporal scales. Filtering occurs over tens of milliseconds of time and tens of minutes of visual angle, whereas adaptation occurs over hundreds of milliseconds of time and degrees of visual angle.

## 4.1 Assumptions of the Model

I construct linear electrical-circuit models of the retinal neurocircuitry by simplifying the latter’s biophysical elements in three ways:

1. *Gap-junction–coupled cell syncytia are isotropic resistive grids.* I abstract the fine physical structure of these cells into a **characteristic lateral resistance** and a **characteristic vertical conductance**. The former models the gap junctions, and the latter models the parallel combination of synaptic and leakage conductances; voltage dependencies, calcium dependencies, and nonlinearities of the membrane channels are ignored.
2. *Synaptic inputs are variable current sources.* I treat chemical synapses, which are usually modeled by conductance changes, as variable current sources. These model synapses are characterized by a **transconductance**: the additional current injected across the postsynaptic membrane per unit change in the presynaptic voltage.<sup>1</sup>
3. *Synaptic transmission is instantaneous.* I ignore the time dependencies of neurotransmitter release and diffusion, and those of the channel-gating mechanisms.

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<sup>1</sup>Synapse models based on conductance changes are characterized by a conductance per unit voltage. Multiplication of this parameter by the voltage across the channel gives the equivalent transconductance.

Hence, the model’s temporal dynamics arise solely from the membrane capacitances, and are characterized by the time constants of the cells.

Ignoring the fine details of cell morphologies and treating syncytia as isotropic resistive networks is justified by virtue of the dense, strong, local electrical connectivity in these cell syncytia. As the receptive fields are larger than the extent of the cells’ dendritic arbors, the relay of signals from cell to cell across gap junctions appears to play a dominant role in shaping the cells’ receptive fields—not the fine details of the dendritic arbor.

Ignoring voltage and calcium dependencies, and other nonlinearities, and treating synapses as current sources, is justified because the retina responds linearly for contrasts less than 10% [91]. Given that the threshold is 0.5% contrast, the retina is linear over a 20-fold range. For these small signal changes, the nonlinear voltage–current relationships of the ion channels, and of the gap junctions, can be replaced by their slope conductances, and the conductance changes due to activating more ion channels are negligible compared to the conductance of the cell.

Ignoring the time-course of synaptic transmission is justified because synaptic transmission occurs much faster than the cell responds, due to the large capacitance of the cell membrane.

Several researchers have used resistive networks to model gap-junction–coupled syncytia, going back to the work of Torre and Owen on rod coupling [103]. Chemical synapses have also been modeled previously as transconductances by Yagi and his colleagues [104]. Yagi and colleagues included time dependencies in their synapse model by using complex transadmittances, instead of real transconductances [104].

The model that they obtained by making these simplifications is discrete in space, but continuous in time; it is described by a difference equation in space and a differential equation in time. We can analyze such discrete–continuous systems by taking the Laplace transform in time, and obtaining a solution to the difference equation in space in terms of geometrically weighted Laplace transforms terms, as Yagi and his colleagues did [104]. Another approach is to work with discrete spatial frequencies and continuous temporal frequencies, using the  $z$ -transform and the Fourier transform,

respectively, as Beaudot has shown [105]. Both of these approaches work, but they produce unweildly solutions that are difficult to grasp intuitively.

To obtain simple and intuitive results, I analyze the model in the continuum limit, where second-order spatial differences become second-order spatial derivatives. As

$$V_{i+1} - 2V_i + V_{i-1} = \varepsilon^2 \frac{d^2V}{dx^2} + \frac{1}{12} \varepsilon^4 \frac{d^4V}{dx^4} + \dots$$

where  $V(\varepsilon i) \equiv V_i$ .<sup>2</sup> The error that we incur by taking the continuous approximation is

$$\xi_{xx} \approx \frac{\pi^2}{12} \left( \frac{f_x}{f_{\text{Nyq}}} \right)^2,$$

when expressed as a fraction, where  $f_x$  is the spatial frequency and  $f_{\text{Nyq}} \equiv (2\varepsilon)^{-1}$  is the Nyquist limit. It is negligible for spatial frequencies  $f_x^2 \ll (12/\pi^2)f_{\text{Nyq}}^2$ . We can use this expression to calculate the total error, if we know the power spectrum of the input signal. When most of the signal energy is at low frequencies—as it is for a step edge—the error is small. Hence, we do not lose much precision by taking the continuous approximation, and we gain much clarity by treating space and time uniformly.

Another concern that we have to address when we simulate a discrete network with a continuous one is the frequency limitations imposed by Nyquist’s sampling theorem. To prevent aliasing, the discrete network is prohibited from seeing any frequencies higher than the Nyquist limit ( $f_{\text{Nyq}}$ ). The continuous network, on the other hand, has no such restriction, and may produce frequencies higher than the Nyquist limit. We must filter out these frequencies before we can make valid predictions about the discrete network that we are simulating.

The continuous-space approximation has been used previously by Chen and Freeman [106]. They drew the analogy between gap-junction-coupled syncytia and a cable; this insight enabled them to apply results obtained for cables by Jack and others [107] to analyze the spatiotemporal dynamics of their retina model [106]. However,

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<sup>2</sup>I obtained this result by using the Taylor series expansion for  $V(x)$  at  $x = \varepsilon i$  to obtain expressions for  $V_{i-1}$  and  $V_{i+1}$

their analysis focused on the overall spatiotemporal behavior of the retina, from the cornea to the ganglion cells. My analysis is restricted to the outer retina, and reveals more about the contribution of the cone–horizontal-cell circuit to the retina’s response to spatiotemporal signals.

## 4.2 Linear Model of the Outer Plexiform Layer

The OPL circuit model is shown in Figure 4.1. Models more or less identical to this one have been proposed previously by Chen and Freeman, and by Yagi and colleagues [104]. As stated in Section 4.1, I use an analytical approach that is similar to that of Chen and Freeman by taking the continuous approximation, whereas Yagi analyzed the discrete case.

In the continuum limit, we have

$$I_o + \nabla^2 V_c / r_{cc} = g_{c0} V_c + c_{c0} \dot{V}_c + g_{ch} V_h, \quad (4.1)$$

$$g_{hc} V_c + \nabla^2 V_h / r_{hh} = g_{h0} V_h + c_{h0} \dot{V}_h, \quad (4.2)$$

where current per unit area, sheet resistance, conductance per unit area, and capacitance per unit area are used. The voltages  $V_c$  and  $V_h$  are continuous functions of space,  $(x, y)$ , and time,  $t$ ;  $\nabla^2 f$  is the spatial Laplacian of  $f$  (i.e.  $\partial^2 f / \partial x^2 + \partial^2 f / \partial y^2$ ), and  $\dot{f}$  is the temporal derivative of  $f$  (i.e.  $\partial f / \partial t$ ).

Assuming infinite spatial extent and homogeneous initial conditions, we can take Fourier transforms in space and time. Transforming the equations and solving, we obtain the following transfer functions between inputs and outputs.

$$\tilde{H}_c(\rho, \omega) \equiv \frac{\tilde{V}_c}{\tilde{I}_o} = \frac{1}{g_{ch} (\ell_c^2 \rho^2 + i\tau_c \omega + \epsilon_c) (\ell_h^2 \rho^2 + i\tau_h \omega + \epsilon_h) + 1}, \quad (4.3)$$

$$\tilde{H}_h(\rho, \omega) \equiv \frac{\tilde{V}_h}{\tilde{I}_o} = \frac{1}{g_{ch} (\ell_c^2 \rho^2 + i\tau_c \omega + \epsilon_c) (\ell_h^2 \rho^2 + i\tau_h \omega + \epsilon_h) + 1}, \quad (4.4)$$

where  $\tilde{f}(\rho, \omega)$  denotes the Fourier transform of  $f(x, y, t)$ ;  $\rho = \sqrt{(\rho_x^2 + \rho_y^2)}$  is the magnitude of the spatial frequency, and  $\omega$  is temporal frequency (both are in radians). Here,

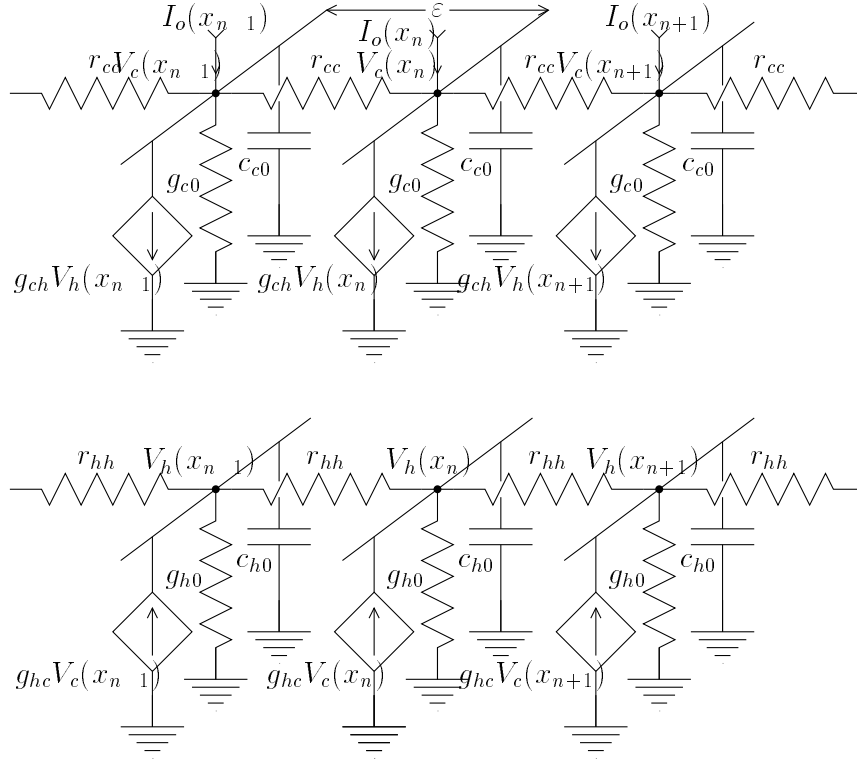


Figure 4.1: PHYSICAL MODEL OF THE OUTER RETINA

The two resistive networks model the cone and horizontal-cell synchia. The voltages  $V_c$  and  $V_h$  represent the membrane potentials, and the current  $I_o$  represents inputs from the cone outer segment. The diamonds are symbols for current sources controlled by voltages in another part of the circuit; they model chemical synapses. The direction of current flow, indicated by the arrow, is into the network for an excitatory synapse. The membrane capacitances of the cells are included to model dynamic behavior. The parameter  $\epsilon$  is a measure of cell sizes; it links the modeled quantities that are in current per unit area, sheet resistance, conductance per unit area, and capacitance per unit area to the physiological ones.

$\tau_c = c_{c0}/g_{ch}$  and  $\tau_h = c_{h0}/g_{hc}$  are the time constants of the cells;  $\ell_c = (r_{cc}g_{ch})^{-1/2}$  and  $\ell_h = (r_{hh}g_{hc})^{-1/2}$  are the space constants of the decoupled syncytia, with transconductances replaced by conductances to ground; and  $\epsilon_c = g_{c0}/g_{ch}$ ; and  $\epsilon_h = g_{h0}/g_{hc}$  are the ratios of membrane-leakage conductance to synaptic transconductance. The reciprocal of  $\epsilon_c$  is equal to the change in voltage that occurs in the cone for a unit change in voltage in the horizontal cell. I call this ratio the voltage gain from the horizontal cell to the cone; the voltage gain from cone to horizontal is defined similarly.

The inputs to the model are currents per unit area, and the responses of the cell are voltages, so the transfer functions have units of resistance times area, or the reciprocal of transconductance per unit area. To obtain a dimensionless measure of frequency sensitivity, I shall multiply the transfer function by  $g_{ch}$ . I define this dimensionless measure as the gain:  $\tilde{A}(\rho, \omega) \equiv g_{ch}\tilde{V}/\tilde{I}_o$ . That is, the gain is the ratio between the voltage response and the input current when the transconductance  $g_{ch}$  is 1 unit.

The transfer functions  $\tilde{H}_c(\rho, \omega)$  and  $\tilde{H}_h(\rho, \omega)$  give the responses of the cones and the horizontal cells to sinusoidal spatiotemporal patterns, like the one shown in Figure 4.2. The voltage response of the model is given by  $\tilde{H}(\rho, \omega)I \sin(\rho_x x + \rho_y y + \omega t)$ ; it is simply a scaled and shifted version of the signal. The scaling is given by the magnitude of  $\tilde{H}$ , and the phase shift is given by the argument of  $\tilde{H}$ . Since these quantities do not depend on the orientation of the grating, the model does not have orientation or direction selectivity.

Any moving image can be expressed as a sum of sinusoidal spatiotemporal patterns. Hence, by using the frequency-response function  $\tilde{H}$  to shift and scale each frequency component, we can obtain the model's response to motion. This is our primary motivation for studying the model's spatiotemporal-frequency response.

For illustrative purposes, we use the following set of parameters:  $\ell_c = 0.05^\circ$ ;  $\ell_h = 0.2^\circ$ ;  $\tau_c = 30\text{ms}$ ;  $\tau_h = 200\text{ms}$ ;  $\epsilon_c = 0.3$ ;  $\epsilon_h = 0.1$ ;  $g_{ch} = 0.2\text{pA/mV}$ . Unless otherwise stated, all model responses shown were obtained with these parameters.

In presenting the results from the model, I shall use typographical conventions to distinguish between model and reality. For example, a cone is a node in the circuit model; whereas a **cone** is a biological photoreceptor. The cone's response is given by

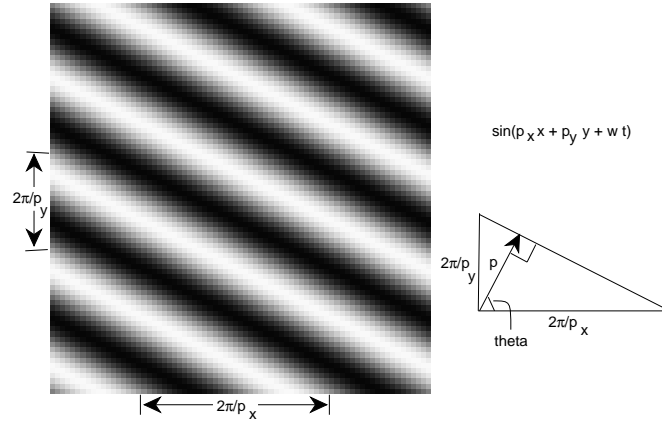


Figure 4.2: SINUSOIDAL SPATIOTEMPORAL SIGNALS

The values of this signal change over time and space according to the expression  $I \sin(\rho_x x + \rho_y y + \omega t)$ , where  $I$  is the peak amplitude. When time is frozen, the signal is just a sinusoidal grating, like the one shown here. The grating's orientation,  $\theta$ , is given by the direction of the spatial-frequency vector:  $\theta = \tan^{-1}(\rho_y/\rho_x)$ . The grating's wavelength,  $\lambda$ , is given by the magnitude of the spatial-frequency vector:  $\lambda = 2\pi/\sqrt{(\rho_x^2 + \rho_y^2)}$ . When time is running, we can track a particular point, with intensity  $I_p$ , and find that it appears to move with speed  $v = \omega/\sqrt{(\rho_x^2 + \rho_y^2)}$ , in a direction opposite to the spatial frequency vector, due to the constraint that  $\rho_x x + \rho_y y + \omega t = \sin^{-1}(I_p/I)$ . Because this constraint applies to all points, the whole grating moves with the same velocity. Actually, the motion of such a pattern is ambiguous; for example, moving the grating in the  $x$  direction at a higher speed  $\omega/\rho_x$  will produce the same spatiotemporal pattern. The model's response to such patterns is derived in the text.

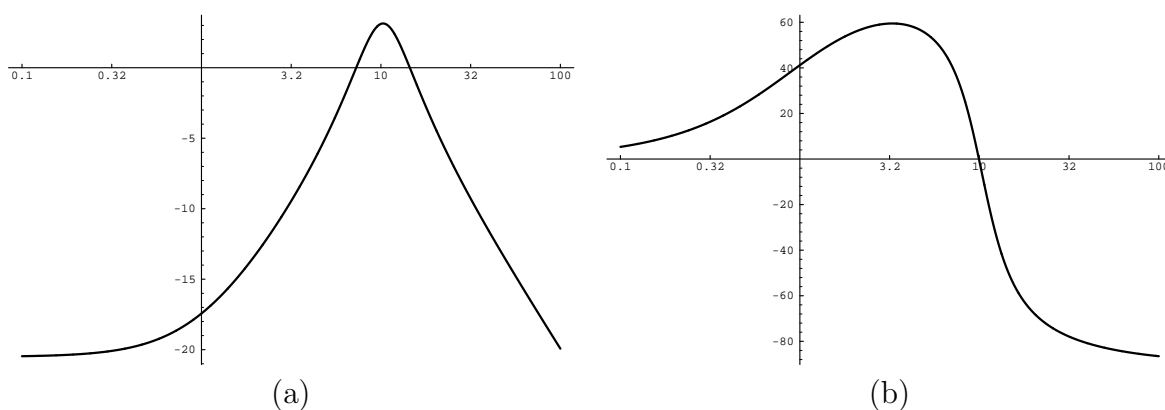


Figure 4.3: SENSITIVITY OF CONES TO FULL-FIELD FLICKER

Amplitude (a) and phase (b) of cone responses to temporal frequency from OPL circuit model. For the parameters values chosen, the cone's response peaks at 10cps, and levels off below 0.33cps.

the voltage of that node, and is the analog of the membrane potential of the cone. I will also plot frequency responses on a logarithmic scale, in dB<sup>3</sup>; spatial frequency in is units of cpd (cycles per degree), and temporal frequency is in units of cps (cycles per second).

### 4.3 Responses to Flicker and Gratings

Full-field flicker and stationary sinusoidal gratings are used by physiologists and psychophysicists to characterize the temporal and spatial responses of the visual system. In the same vein, I present analytical expressions that describe the model's response to these classic stimuli. I describe the salient features of these responses, and relate them, quantitatively, to the model's parameters. I validate the model by comparing its responses to biological measurements.

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<sup>3</sup>20dB is equivalent to a tenfold increase in amplitude.