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Computational Models of Neural Retina

Socrates Dokos*
Graduate School of Biomedical Engineering, University of New South Wales, Sydney, NSW, Australia

Synonyms

Computational models of retinal function; Retinal network models

Definition

Computational models of the neural retina simulate the response of the retina to input light. In their most detailed form, the models yield neural output as a spatially varying pattern of spike trains which fully encode the incident dynamic image. In vivo, this retinal output is relayed to higher vision processing centers in the brain such as the lateral geniculate nucleus and the primary visual cortex in humans and primates. Neural retinal models assist not only in the understanding of normal and abnormal retinal function, but are useful for investigating retinal response to artificial stimuli such as electrical stimulation by a vision prostheses.

Detailed Description

The vertebrate retina consists of a thin layer of neural tissue which lines the back of the eye. It acts to transduce incoming light signals sensed by rod and cone photoreceptor cells into neural spike patterns output by retinal ganglion cells (RGCs), whose axons together form the optic nerve. The ratio of photoreceptor cells to RGCs is approximately 100:1 (dependent on eccentricity from the fovea), indicating that considerable neural processing occurs in the retina itself prior to the transfer of visual information via the optic nerve to the brain.

Each RGC is centered on an approximately circular receptive field of photoreceptors within an associated annular surround. Incident light falling within these regions will have opposite effects on RGC activation, eliciting two main types of response depending on the cell type. On-center RGCs are activated by light falling within their receptive field and inhibited by light falling in their surround, while the reverse holds for off-center RGCs. Both these spatial RGC responses can be mathematically modeled using a simple difference of Gaussians (DoG) (Rodieck 1965).

Computational models of the retinal response to light may be broadly classified into *integrate and fire*, *block-structured*, and *network models*. The models vary in complexity from simulating the response of a single retinal output neuron to incident light, through to simulating a spatiotemporal neural response to a 2D time-varying image.

Integrate and Fire Models

The simplest neural retina models are of the *integrate and fire* type (Gestri et al. 1980; Reich et al. 1997), shown in Fig. 1 fully generalized to the spatiotemporal domain. For a given input light

*Email: s.dokos@unsw.edu.au

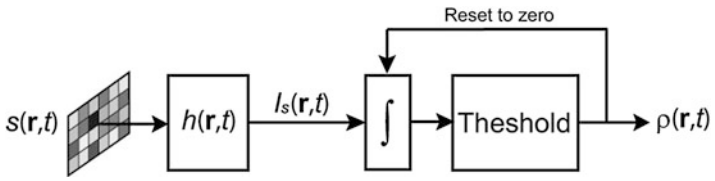

Fig. 1 Generalized spatiotemporal integrate and fire retinal model

stimulus $s(\mathbf{r},t)$ ($\mathbf{r}$ denotes the 2D spatial position and t time), an RGC stimulus current $I_s(\mathbf{r},t)$ is generated according to a linear convolution operation:

$$I_s(\mathbf{r},t) = \int_{\mathbb{R}^2}\int_0^\infty h(\boldsymbol{\xi},\tau)s(\mathbf{r}-\boldsymbol{\xi},t-\tau)d\boldsymbol{\xi}d\tau$$

where $h(\boldsymbol{\xi}, \tau)$ denotes the spatiotemporal convolution kernel which may feature a DoG spatial characteristic (McLaughlin et al. 2000). The spatial integral in the variable $\boldsymbol{\xi}$ is carried out over $\mathbb{R}^2$, and the lower bound of the time integral in variable τ is zero, since the kernel is assumed to be *causal*: that is, future values of the light stimulus do not affect the output at time t. The stimulus current $I_s(\mathbf{r},t)$ represents total RGC synaptic input at position $\mathbf{r}$ and time t. This input is integrated with respect to time and when the integrated signal exceeds a given threshold, an RGC spike is generated and the integrator is reset to zero. The resulting RGC output *neural response function* consists of a train of unit impulses given by

$$\rho(\mathbf{r},t) = \sum_{i=1}^{\infty}\delta\left(t - t_{\mathbf{r},i}\right)$$

where $\delta(t)$ is the Dirac delta function and $t_{\mathbf{r}, i}$ is the time of the ith spike at position $\mathbf{r}$. Some level of stochasticity in spike timing can be obtained by updating the integrator threshold after each spike from a random distribution of values. Furthermore, to account for a finite RGC memory, $I_s(\mathbf{r},t)$ can be pre-multiplied by an exponentially decaying time window function prior to integration: this is the basis of *leaky integrate and fire* models. In such models, I_s values further back in time contribute less to the generation of a subsequent output spike.

Block-Structured Models

Block-structured models of the retina simulate the response of output retinal neurons to input light using a combination of linear and nonlinear input/output functional block elements. In contrast to integrate and fire models, no block has its output reset when a neural spike is triggered. In one such model, the input light signal $s(t)$ is passed through a linear filter to produce a generator potential $g(t)$, which corresponds to the RGC membrane voltage (Keat et al. 2001). An output spike is triggered whenever a positive-going $g(t)$ value crosses a fixed threshold. A feedback loop in the form of negative after potentials can be used to ensure that the model produces clustered spikes, as observed in the real retina.

A more complex block-structured architecture of the retina is shown in Fig. 2 (Wilke et al. 2001). In this model, a spatiotemporal light stimulus $s(\mathbf{r},t)$ is transformed through linear convolution into a neural activation signal $u(\mathbf{r},\mathrm{t})$ according to $u(\mathbf{r},t) = \int_{\mathbb{R}^2}\int_0^\infty h(\boldsymbol{\xi},\tau)s(\mathbf{r}-\boldsymbol{\xi},t-\tau)d\boldsymbol{\xi}d\tau$. This signal

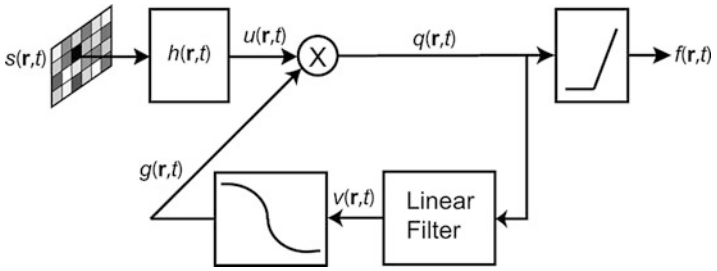

Fig. 2 Block-structured spatiotemporal model of Wilke et al. (2001)

is then multiplied by a local modulation factor $g(\mathbf{r},t)$ between 0 and 1, scaled, and rectified to produce the output local RGC firing rate $f(\mathbf{r},t)$:

$$q(\mathbf{r},t) = g(\mathbf{r},t)u(\mathbf{r},t)$$
$$f(\mathbf{r},t) = \begin{cases} Aq(\mathbf{r},t), & \text{if } Aq(\mathbf{r},t) > B \\ 0, & \text{otherwise} \end{cases}$$

where A is the output rate scaling factor and B the basal firing rate. The $g(\mathbf{r},t)$ modulation factor itself is determined by a linear convolution of $q(\mathbf{r},t)$ with a low-pass temporal filter to determine an intermediate signal $v(\mathbf{r},t)$, which is then fed through a static nonlinearity to yield $g(\mathbf{r},t)$:

$$v(\mathbf{r},t) = \int_0^\infty Ce^{-\frac{\tau}{D}} q(\mathbf{r},t-\tau)d\tau$$
$$g(\mathbf{r},t) = \begin{cases} \dfrac{1}{1+[v(\mathbf{r},t)]^4}, & \text{if } v(\mathbf{r},t) > 0 \\ 1, & \text{otherwise} \end{cases}$$

where C and D are parameters governing the low-pass temporal filter characteristics. Modulation of neural activation by $g(\mathbf{r},t)$ corresponds to the phenomenon of *contrast gain control*, whereby RGCs fire with increased frequency when the input light stimulus changes rapidly (Wilke et al. 2001).

The output of this retinal model is the RGC scalar firing rate $f(\mathbf{r},t)$, expressed as the number of spikes per unit time. This rate can be converted into an output spike train by assigning the interspike interval τ to a random variable drawn from an inhomogeneous Poisson distribution with probability density function:

$$p(\mathbf{r},\tau)|_t = f(\mathbf{r},t)e^{-f(\mathbf{r},t)\tau}$$

A remaining class of block-structured models of the retina is based on a cascaded architecture consisting of a dynamic linear convolution input/output block followed by a static nonlinearity, also known as a *Wiener system* (Juusola et al. 1995; Chichilnisky 2001). An advantage of these models is that several iterative techniques are available to identify constituent block characteristics from input/output experimental data (Westwick and Kearney 2003).

Network Models

Network models of the retina consist of coupled systems of discrete neural elements whose outputs modulate other elements through excitation or inhibition. The simplest such retinal network model is

the Hartline-Ratliff formulation (Hadeler and Kuhn 1987), in which the firing rate of neuron j, f_j, is given by

$$f_j = b_j \max\left(0, \quad e_j - \sum_{k=0}^{n} \beta_{jk} f_k\right)$$

where e_j is the excitatory input to neuron j due to incident light, b_j is a scaling factor, and coefficient β_{jk} characterizes the inhibitory action of neuron k on neuron j. The max() function acts as a rectifier, preventing negative values of firing rate.

More complex retinal network models are based on ionic membrane conductance formulations of discrete neurons and their synaptic interconnections (Rekeczky et al. 2001; Cottaris and Elfar 2005; Wohrer and Kornprobst 2009). Despite the fact that biophysically detailed ionic RGC models are available (Fohlmeister and Miller 1997), network models of the whole retina adopt simplified ionic formulations for computational efficiency. Such complex network models can incorporate multiple neural layers of the retina with up to 100,000 or more discrete neurons.

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Further Reading

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