



## Probing mechanistic models for the retinogeniculate circuit in cat using drifting gratings

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### Abstract

Experiments with drifting gratings are widespread in the study of neurons in the retina and dorsal lateral geniculate nucleus (dLGN). As an alternative to descriptive modeling based on the difference-of-Gaussians model, we show how mechanistic models for the retinogeniculate circuitry can be tested against drifting-grating data. As an example of this approach we (i) derive mechanistic expressions for the geniculate contrast gain for X-type relay cells in dLGN for a set of models with direct feedforward excitation and feedforward inhibition via intrageniculate interneurons, and (ii) compare the expressions with example data from the literature. © 2001 Elsevier Science B.V. All rights reserved.

*Keywords:* Receptive field; Lateral geniculate nucleus; Mechanistic modeling; Drifting grating

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### 1. Introduction

The use of stationary or drifting gratings [5] in investigations of the visual system has been widespread in the neuroscience community in the last few decades. In such experiments the first harmonic components of neuronal firing rates are typically measured for drifting sinusoidal gratings described by their spatial ( $v$ ) and temporal ( $f$ ) frequencies. For retinal ganglion cells and relay cells in the dorsal lateral geniculate nucleus (dLGN) the spatial receptive fields are approximately circular and exhibit the so-called center-surround antagonism. The standard theoretic analysis for these neurons has been to assume a difference-of-Gaussian (DOG) model [8] for the spatial

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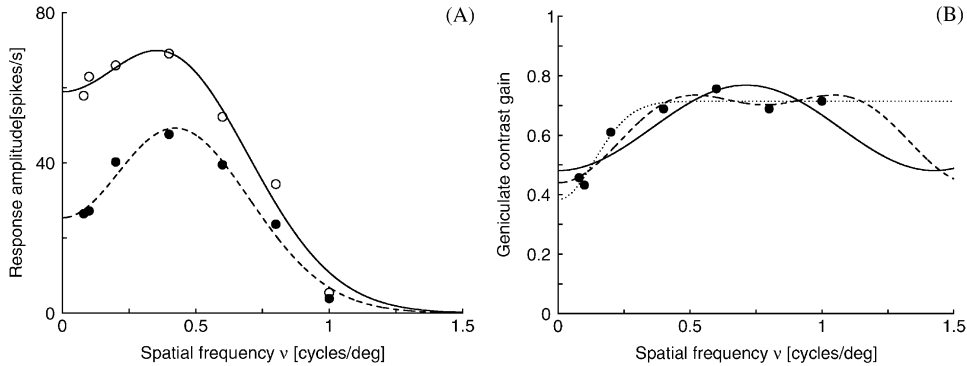


Fig. 1. A: Spatial frequency tuning curves of a dLGN X cell (filled dots) and its main retinal drive (S-potentials, open dots). Data replotted from Cheng et al. [1]. Amplitudes of first harmonic responses to drifting sinusoidal gratings are shown as functions of spatial frequency. Best fits to the DOG model,  $A_1 \exp(-\pi^2 a_1^2 v^2) - A_2 \exp(-\pi^2 a_2^2 v^2)$ , are shown [5]. B: Spatial frequency tuning curve for the geniculate contrast gain, i.e., ratio between response amplitudes for relay cells and retinal input, for the data in A. The best fits to the formulas for the geniculate contrast gain  $|\hat{T}(v)|$  for feedforward inhibition for square grid (see Fig. 2A) for the directions  $\mathbf{k}_1$  (Eq. (5)) and  $\mathbf{k}_2$  (Eq. (6)) as well as hexagonal grid (see Fig. 2B) for  $\mathbf{k}_2$  (Eq. (8)) are all given by the solid line. The dashed line corresponds to best fit for hexagonal grid for  $\mathbf{k}_1$  (Eq. (7)) while dotted line corresponds to the continuous Gaussian feedforward model (Eq. (9)).

receptive field and fit the Fourier transform of this function to the experimental data to provide estimates for model parameters [5]. An example of such an analysis, based on data for an example cell from Cheng et al. [1], is shown in Fig. 1A.

Even though the DOG-model is able to fit the data of Cheng et al. well, no insight is gained regarding what aspects of the retinogeniculate circuitry are responsible for the differences in neuronal responses between the retinal and geniculate level. This is an example of a *descriptive* model which is used to summarize large amounts of experimental data compactly, yet accurately [2]. In contrast, *mechanistic* models attempt to account for nervous system activity on the basis of neuronal morphology, physiology and circuitry [2]. In the present paper we describe how data from drifting-grating experiments can be used to test mechanistic models for the retinogeniculate circuitry in cat. This follows our earlier papers on the testing of such models using experiments with circular flashing spots [4] and the mathematical relation between spatial receptive fields measured with flashing spots and drifting gratings (or white-noise analysis) [3]. Here we consider only purely feedforward models for the retinogeniculate circuitry.

## 2. Mechanistic modeling

Our starting point is the observation that, given the responses  $R_g(\mathbf{r}, t)$  for the retinal ganglion cells feeding into the dLGN, an expression for the relay cell firing-rate can be

written as

$$R_r(\mathbf{r}, t) = \int_{\tau} \int_{\mathbf{r}_0} \int K(\mathbf{r} - \mathbf{r}_0, \tau) R_g(\mathbf{r}_0, t - \tau) d^2 r_0 d\tau, \tag{1}$$

where  $K(\mathbf{r} - \mathbf{r}_0, \tau)$  is the space–time retinogeniculate coupling kernel (coupling function) between a retinal ganglion cell at a position  $\mathbf{r}_0$  and a relay cell at  $\mathbf{r}$ . This assumes linearity and time-invariance [11] for the feedforward couplings between retinal ganglion cells and relay cells. The integral corresponds to a convolution in space and time, and from the convolution theorem it follows that the relationship  $\tilde{R}_r(\mathbf{k}, \omega) = \tilde{R}_g(\mathbf{k}, \omega) \tilde{K}(\mathbf{k}, \omega)$  holds for the complex Fourier transformed quantities of  $R_r(\mathbf{r}, t)$ ,  $R_g(\mathbf{r}, t)$ , and  $K(\mathbf{r}, t)$ . The complex transform for a quantity  $A(\mathbf{r}, t)$  is generally defined via

$$\tilde{A}(\mathbf{k}, \omega) \equiv \int_t \int_r e^{-i(\mathbf{k}\mathbf{r} - \omega t)} A(\mathbf{r}, t) d^2 r dt. \tag{2}$$

A crucial observation here is that while the drifting-grating response for a relay cell (given by  $\tilde{R}_r(\mathbf{k}, \omega)$  [5]) naturally depends on the responses for the retinal ganglion cells feeding into the relay cell (given by  $\tilde{R}_g(\mathbf{k}, \omega)$ ), the *ratio* between the first harmonic components,  $\tilde{T}(\mathbf{k}, \omega)$ , only depends on the retinogeniculate coupling kernel  $K$ , i.e.,

$$\tilde{T}(\mathbf{k}, \omega) \equiv \frac{\tilde{R}_r(\mathbf{k}, \omega)}{\tilde{R}_g(\mathbf{k}, \omega)} = \frac{\tilde{R}_g(\mathbf{k}, \omega) \tilde{K}(\mathbf{k}, \omega)}{\tilde{R}_g(\mathbf{k}, \omega)} = \tilde{K}(\mathbf{k}, \omega). \tag{3}$$

Here we will call  $\tilde{T}(\mathbf{k}, \omega)$  the *geniculate transfer function* [11], and the magnitude  $|\tilde{T}(\mathbf{k}, \omega)|$  for the *geniculate contrast gain* [6]. The experimental data points for the geniculate contrast gain for the example cell in Fig. 1A are shown in Fig. 1B.

To derive a mechanistic model for the retinogeniculate coupling kernel  $K$ , knowledge about the pattern of functional neuronal couplings in dLGN, reviewed in [9], is required. Relay cells receive excitatory input from retinal ganglion cells as well as feedforward inhibition from intrageniculate interneurons, which in turn receive excitation from a few retinal ganglion cells. In addition, the relay cells receive feedback from the perigeniculate nucleus (PGN) and striate cortex, but presently we will consider only the feedforward connections. Here we study simplified feedforward circuit models [4] where a relay cell receives (i) direct excitation from a single retinal ganglion cell, and (ii) indirect feedforward inhibition from several retinal ganglion cells via an intrageniculate interneuron. We assume that the (indirect) inhibitory influence from each of the contributing ganglion cells carry the same weight. If we further assume that retinogeniculate coupling kernel is space–time separable, i.e.,  $K(\mathbf{r}, t) = f(\mathbf{r})h(t)$ , the spatial part of the coupling kernel,  $f(\mathbf{r})$ , and the geniculate transfer function  $\tilde{T}(\mathbf{k}, \omega_0)$ , are given by

$$f(\mathbf{r}) = B_1 \delta(\mathbf{r}) - B_2 \frac{1}{n} \sum_{j=1}^n \delta(\mathbf{r} - \mathbf{r}_j), \tag{4}$$

$$\tilde{T}(\mathbf{k}, \omega_0) = \tilde{h}(\omega_0) \tilde{f}(\mathbf{k}) = \tilde{h}(\omega_0) \left( B_1 - B_2 \frac{1}{n} \sum_{j=1}^n e^{-i\mathbf{k}\mathbf{r}_j} \right).$$

Here  $B_1$  and  $B_2$  are the (positive) weights for the feedforward excitatory and inhibitory coupling, respectively and  $\omega_0 = 2\pi f_0$  with  $f_0$  being the fixed temporal frequency. With the prefactor  $1/n$  included in the inhibitory term,  $B_2$  corresponds to the total inhibition acting on the relay cell. Further,  $\mathbf{r}_j, j = 1, \dots, n$ , are the centers of the receptive fields of the retinal ganglion cells providing input to the interneuron (where the position  $\mathbf{r} = \mathbf{0}$  corresponds to the center of the receptive-field of the single excitatory afferent to the relay cell).  $\delta(\mathbf{r})$  is the Dirac delta function.

The X-type retinal ganglion cells of the same symmetry (on or off) form a disordered grid with typically four to six nearest neighbors [10]. Here we approximate this real disordered grid with periodically ordered grids, either quadratic or hexagonal, and in our models we assume that the inhibition is provided by (i) the retinal ganglion cell which provides the excitatory input to the relay cell (indirectly via an interneuron), and (ii) the four (quadratic case) or six (hexagonal case) nearest-neighbor same-symmetry ganglion cells located a distance  $r_a$  away (see Fig. 2). The relay cell response depends on the direction of the drifting grating, and in the present study we consider only the two high-symmetry directions labeled  $\mathbf{k}_1$  and  $\mathbf{k}_2$  (see Fig. 2). The geniculate contrast gain,  $|\tilde{T}(\mathbf{k})|$  (fixed  $\omega = \omega_0$  implicit), for the two models is then found from Eq. (4) to be

$$\text{square: } |\tilde{T}_{\mathbf{k}_1}(v)| = B \left[ 1 - \frac{\eta}{5}(3 + 2 \cos(2\pi v r_a)) \right], \quad (5)$$

$$|\tilde{T}_{\mathbf{k}_2}(v)| = B \left[ 1 - \frac{\eta}{5}(1 + 4 \cos(\sqrt{2}\pi v r_a)) \right], \quad (6)$$

$$\text{hexagonal: } |\tilde{T}_{\mathbf{k}_1}(v)| = B \left[ 1 - \frac{\eta}{7}(1 + 2 \cos(2\pi v r_a) + 4 \cos(\pi v r_a)) \right], \quad (7)$$

$$|\tilde{T}_{\mathbf{k}_2}(v)| = B \left[ 1 - \frac{\eta}{7}(3 + 4 \cos(\sqrt{3}\pi v r_a)) \right], \quad (8)$$

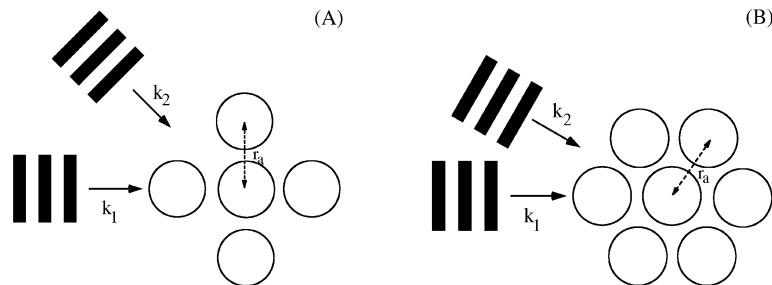


Fig. 2. Illustration of spatial distribution of retinal ganglion cells providing the indirect feedforward inhibition on the relay cell. A: Square grid. B: Hexagonal grid. The circles correspond to ganglion cell receptive-field centers which are set unrealistically small and non-overlapping for reasons of figure clarity. Only drifting gratings moving in the high-symmetry directions  $\mathbf{k}_1$  and  $\mathbf{k}_2$  are considered here.

where we have introduced  $B \equiv |\tilde{h}(\omega_0)B_1|$ , and  $\eta \equiv B_2/B_1$ . We have also replaced the wave vector  $\mathbf{k}$  with the more commonly used spatial frequency  $\nu$ , related to  $\mathbf{k}$  via  $\nu = |\mathbf{k}|/2\pi$ .

For comparison we also consider a *continuous* feedforward model [4] with an infinite number of inhibitory relay-cell afferents, and where the feedforward inhibition is assumed to decrease like a Gaussian as a function of spatial distance. Mathematically this corresponds to  $f(\mathbf{r}) = B_1\delta(\mathbf{r}) - B_2 \exp(-\mathbf{r}^2/b_2^2)/(\pi b_2^2)$ . Then the geniculate contrast gain for *all* directions of  $\mathbf{k}$  is given by the Fourier transform  $\tilde{f}(\mathbf{k})$ , and one finds

$$|\tilde{T}(\nu)| = \tilde{h}(\omega_0)\tilde{f}(\mathbf{k}) = B(1 - \eta e^{-\pi^2\nu^2 b_2^2}). \quad (9)$$

### 3. Comparison with experiment

These expressions for the geniculate contrast gain can now be compared with experimental data. To illustrate this, we consider the data from Cheng et al. [1]. Fig. 1B shows the best fit of the five expressions in Eqs. (5)–(9) to these experimental data. From Eqs. (5), (6), and (8) we see that both  $|\tilde{T}_{\mathbf{k}_1}(\nu)|$  and  $|\tilde{T}_{\mathbf{k}_2}(\nu)|$  for the square grid case and  $|\tilde{T}_{\mathbf{k}_2}(\nu)|$  for the hexagonal grid case are of the form  $|\tilde{T}(\nu)| = c_1 + c_2 \cos(c_3\nu)$ , where  $c_1$ ,  $c_2$ , and  $c_3$  are constants. This means that the best fits for these three expressions yield *identical* contrast-gain curves (solid line in Fig. 1B). The predicted parameter values of  $\eta$  and  $r_a$  will be different, however, and we find for these three cases  $B = 0.84$ ,  $\eta = 0.43$ ,  $r_a = 0.70$  deg (square,  $\mathbf{k}_1$ ),  $B = 0.66$ ,  $\eta = 0.27$ ,  $r_a = 0.99$  deg (square,  $\mathbf{k}_2$ ), and  $B = 0.73$ ,  $\eta = 0.34$ ,  $r_a = 0.81$  deg (hexagonal,  $\mathbf{k}_2$ ). Since these parameters have clear physiological interpretations, the different cases can be distinguished by comparing with other experimental data, e.g., other choices of stimuli. From Eqs. (5)–(8) we also see that all discrete models will predict oscillatory geniculate contrast gains as a function of spatial frequency  $\nu$  while the continuous Gaussian inhibitory model predicts a monotonically increasing geniculate contrast gain with increasing  $\nu$ .

The best fit for the present example data is provided by the continuous Gaussian model (mean square error = 0.025) followed by the hexagonal model for direction  $\mathbf{k}_1$  (mean square error = 0.031) and the three remaining cases (mean square error = 0.052 for all). Even though a comparison with the available data in the literature seems to indicate that the continuous Gaussian model yields fits better than discrete nearest-neighbor models [7], more experimental studies are needed to clarify this issue. Such experimental data may also make it possible to elucidate the relative role played by feedback afferents from the perigeniculate nucleus (PGN) and cortex compared to the feedforward afferents.

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