Mathematical models for the spatial receptive-field organization of nonlagged X-cells in dorsal lateral geniculate nucleus of cat

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Abstract
Spatial receptive fields of relay cells in dorsal lateral geniculate nucleus (dLGN) have commonly been modeled as a difference of two Gaussian functions. We present alternative models for dLGN cells which take known physiological couplings between retina and dLGN and within dLGN into account. The models include excitatory input from a single retinal ganglion cell and feedforward inhibition via intrageniculate interneurons. Mathematical formulas describing the receptive field and response to circular spot stimuli are found both for models with a finite and an infinite number of ganglion-cell inputs to dLGN neurons. The advantage of these models compared to the common difference-of-Gaussians model is that they, in addition to providing mathematical descriptions of the receptive fields of dLGN neurons, also make explicit contributions from the geniculate circuit. Moreover, the model parameters have direct physiological relevance and can be manipulated and measured experimentally. The discrete model is applied to recently published data (Ruksenas et al., 2000) on response versus spot-diameter curves for dLGN cells and for the retinal input to the cell (S-potentials). The models are found to account well for the results for the X-cells in these experiments. Moreover, predictions from the discrete model regarding receptive-field sizes of interneurons, the amount of center-surround antagonism for interneurons compared to relay cells, and distance between neighboring retinal ganglion cells providing input to interneurons, are all compatible with data available in the literature.

Keywords: Mathematical model, Lateral geniculate nucleus, Receptive-field organization, Spatial summation, Retino-geniculate transmission

Introduction
Ever since the pioneering work by Hartline and Ratliff (1957, 1958), mathematical modeling of receptive fields has been common practice among neuroscientists working on the visual system. Rodieck (1965) introduced the difference of two circularly symmetric and concentric Gaussians as a model for the receptive field of retinal ganglion cells. This choice is mathematically convenient, and Rodieck was able to derive an analytical solution for the response to moving bars with this type of receptive field. Later, Enroth-Cugell and Robson (1966) gave a solution to the spatial-frequency response for the same model. This solution is the basis for the spatial-frequency analysis method which has been widely applied in the study of receptive fields the last 25 years (Shapley & Lennie, 1985). Later extensions of the difference-of-Gaussians (DOG) model have included temporal delays between the center and surround Gaussians (Enroth-Cugell et al., 1983) as well as nonconcentric (Dawis et al., 1984) and elliptical Gaussians (Soodak, 1986). Even though the DOG model was originally suggested for retinal ganglion cells, it has also been used (Kaplan et al., 1979; So & Shapley, 1981; Dawis et al., 1984; Norton et al., 1989; Mukherjee & Kaplan, 1995; Uhlrich et al., 1995) to describe receptive fields in dorsal lateral geniculate nucleus (dLGN).

Dayan and Abbott (2000) distinguishes between descriptive and mechanistic models. Descriptive models are used to summarize experimental data compactly yet accurately, while mechanistic models try to account for nervous system activity on the basis of neuronal morphology, physiology, and circuitry. The use of the DOG model in the visual system falls in the category of descriptive modeling. In this work, we investigated mechanistic models for spatial transfer characteristics of dLGN using the the DOG model as a descriptive model for the retinal input. The aim was thus not to find the simplest mathematical model which can describe particular experimental data. Instead, our aim was to use mathematical modeling to try to understand how the geniculate circuitry modifies the retinal input signal. In our approach, we summed appropriately weighted DOGs corresponding to ganglion-cell inputs,
and derived analytical formulas for receptive fields and responses to circular spot stimuli for neurons in dLGN.

Several models for how the inhibitory input to relay cells is organized spatially have been suggested in the literature. For a short overview of different types of models, see Ruksenas et al. (2000). Here we focused on different versions of the model suggested by the experimental data from Ruksenas et al. (2000). We derived mathematical formulas both for a model with a discrete number of retinal ganglion-cell inputs to dLGN neurons and simplified models with input from an infinite number of retinal ganglion cells represented by a continuous geniculate coupling function. The parameters in the model can be given direct physiological interpretations, testable in different types of experiments. We focused solely on the spatial organization of the receptive field. Since the model was compared with experimental data for spike counts, the present versions of the model were developed for modeling spike counts. The models can thus be labeled spike-count models (Rieke et al., 1997). However, the formalism is straightforwardly extended to a (time-dependent) rate-code scheme (Einevoll et al., 2000).

Ruksenas et al. (2000) recorded action potentials of nonlagged X-cells in dLGN as well as so-called S-potentials to study the spatial organization of the receptive fields of the dLGN cells and their retinal input. An S-potential is assumed to be a postsynaptic potential that reflects a single action potential in the retinal afferents (Bishop et al., 1958; Hubel & Wiesel, 1961; Cleland et al., 1971; Kaplan & Shapley, 1984). Circular light or dark spots were used to determine response versus spot-diameter functions. They suggested that the observed spatial receptive-field properties could be explained by a simplified circuit model where a relay cell receives (1) direct excitation from a single retinal ganglion cell, and (2) indirect feedforward inhibition from several retinal ganglion cells via intrageniculate interneurons. This corresponds directly to the discrete mathematical model presented here. The results of Ruksenas et al. (2000) were used to test the applicability of the present mathematical models. This was done by fitting mathematical formulas to the experimental response curves. Predictions that could be checked by other data in the literature were also derived from this fitting procedure.

In the present work, we chose to focus on the discrete model suggested by the experiments of Ruksenas et al. (2000), rather than the mathematically simpler continuous model. The reason is that the discrete model, most likely, is biologically most realistic. As a consequence of this, the predicted model parameters are more directly comparable with data from other types of experiments. This is important since a model is of less value if it is limited to the experimental data upon which it is based. It should also be noted that some of the simplifying assumptions inherent in the present discrete model are not as restrictive as they may initially appear. In fact, some of the results derived here for circular spot stimuli turn out to be identical for many choices of spatial arrangements and weight distributions of inputs to interneurons. Furthermore, mathematical expressions for neuronal responses in dLGN to circular spot stimuli may be constructed from the present results for essentially any choice of feedforward model. The model can also be used with other types of visual stimuli, for example, drifting gratings. Preliminary accounts of some of the results presented here have been presented previously (Fjeld et al., 1997; Einevoll & Heggelund, 1998).

Mathematical models

Mathematical expressions were derived for the receptive-field function of relay cells and intrageniculate interneurons in the dLGN, and response functions for retinal ganglion cells, relay cells, and interneurons. The receptive-field function describes the responsivity profile across the receptive field. The response function corresponds to the time-averaged firing activity in a neuron as a response to a circular light (for an ON-center cell) or dark (for an OFF-center cell) spot with diameter \( d \). In the present application, the time average is taken over the duration of the spot stimulus, and the resulting quantity is proportional to the average number of spikes occurring during the time the spot is on. Our model thus corresponds to a spike-count model (Rieke et al., 1997).

First, we present the so-called discrete model that is based upon a finite number of retinal ganglion-cell inputs to a dLGN neuron. Thereafter, we explore the so-called continuous model where an infinite number of ganglion-cell inputs to dLGN neurons are included. While the discrete model evidently is biologically more realistic, some formulas found with the continuous model are mathematically simpler. The continuous model may therefore be useful in more extended network calculations.

Discrete model

Retinal ganglion cells

We assume that the response to a visual stimulus of a retinal ganglion cell with it receptive-field center centered at a position \( r = [x, y] \) can be expressed as (Heeger, 1991)

\[
R_g(r) = S_g \left[ \int_{r_0} \tilde{g}_s(r_0 - r) s(r_0) \, dr_0 \right],
\]

where \( \tilde{g}_s(r) \) is the receptive-field function, \( s(r) \) represents the stimulus, and the spatial integral is over the whole visual field, that is, over all two-dimensional space. To account for possible nonlinear effects in the ganglion-cell response, the ganglion-cell transfer function \( S_g[x] \) is introduced. To avoid negative firing rates in the model, we here use \( S_g[x] = x \theta(x) \) where \( \theta(x) \) is the Heaviside step function given by \( \theta(x < 0) = 0, \theta(x > 0) = 1 \).

For X-class retinal ganglion cells, the receptive field is commonly described as a difference of Gaussians (DOG) (Rodieck, 1965). In the following, we use the form

\[
\tilde{g}_s(r) = \frac{A_1}{\pi a_1^2} e^{-r^2/a_1^2} - \frac{A_2}{\pi a_2^2} e^{-r^2/a_2^2},
\]

where the first term corresponds to the center and the second term to the surround (Fig. 1A). Here \( A_1 \) and \( A_2 \) are the strengths of the center and surround, respectively, and \( a_1 \) and \( a_2 \) are corresponding width parameters. Length unit is degrees of visual field angle.

Response versus luminance curves for photoreceptors are typically sigmoidal (Keener & Sneyd, 1998). This relationship will be reflected in the neuronal activity of the retinal ganglion cells. It is thus convenient to represent the visual stimulus via an (unspecified) sigmoidal function of the luminance \( L(r) \), that is, \( s(r) = s(L(r)) \) (Dayan & Abbott, 2000). With this representation, the sigmoidal nonlinearity is shifted from the receptive-field function to the input function (stimulus function, \( s(r) \)), and the assumption of linear spatial summation of visual inputs via the weight function \( \tilde{g}_s(r) \) becomes more plausible.

The response function for a stimulating spot with luminance \( L \) and diameter \( d \) for a retinal ganglion cell with its receptive-field center located a distance \( r_s \) from the spot center, is then given by
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where the dimensionless parameter \( \omega = A_2 / A_1 \) represents the relative strength between surround and center.

Note that even though the integrand in eqn. (1) depends on the position vector \( \mathbf{r} \), and not just the radial distance \( r \), the ganglion-cell response to a circular spot [eqn. (3)] will, for reasons of circular symmetry of \( g_0(\mathbf{r}) \), depend only on the distance \( r_g \).

Note also that eqn. (3) assumes that the neuronal firing activity is due to the stimulating spot only. A contribution from the surround will be added in the brackets of eqn. (3) when our model is compared with experiments.

The integral in eqn. (3) can be evaluated analytically (cf. Appendix A), and one finds

\[
R_g(d; r_g) = S_g \left[ l(L) \left( e^{-r_g^2/\omega^2} \sum_{m=0}^{\infty} \frac{1}{m!} \left( \frac{r_g}{a_1} \right)^{2m} \gamma(m + 1, d^2/4\omega^2) \right) - \omega e^{-r_g^2/\omega^2} \sum_{m=0}^{\infty} \frac{1}{m!} \left( \frac{r_g}{a_2} \right)^{2m} \gamma(m + 1, d^2/4\omega^2) \right].
\]

(5)

where \( \gamma(m, x) \) is the so-called incomplete gamma function given by

\[
\gamma(m, x) = \frac{1}{(m-1)!} \int_0^x u^{m-1} e^{-u} \, du.
\]

(6)

when \( m \) is an integer larger than zero. For the special case when the stimulation spot and receptive-field are concentric, that is, \( r_g = 0 \), eqn. (5) simplifies to

\[
R_g(d; 0) = S_g \left[ l(L) \left( 1 - e^{-d^2/4\omega^2} - \omega(1 - e^{-d^2/4\omega^2}) \right) \right].
\]

(7)

Fig. 1B shows examples of ganglion-cell response functions for the receptive-field function in Fig. 1A both when the spot stimulus and receptive-field are concentric, and when they are nonconcentric. In Appendix A, it is found from eqn. (5) that

\[
R_g(d \to \infty, r_g) = S_g \left[ l(L)(1 - \omega) \right],
\]

(8)

that is, the infinite spot-size response depends essentially only on the difference between the strengths of the center and surround. For the special case with \( r_g = 0 \), this result also follows straightforwardly from eqn. (7).

The theoretical expression in eqn. (8) shows that \( l(L) \) is proportional to the ganglion-cell response to diffuse illumination. The form of \( l(L) \) can thus be assessed by measuring the diffuse-illumination response as a function of luminance. For ON-center cells this response increases monotonically with increasing luminance \( L \), while for OFF-center cells this response decreases monotonically with increasing \( L \) (Fig. 2).

**Relay cells and intrageniculate interneurons**

To obtain analogous mathematical expressions for the relay-cell response functions \( R_s \), we need to combine the expressions for the response functions for the retinal ganglion cells with knowledge about the pattern of functional neuronal couplings in dLGN (reviewed by Sherman & Guillery, 1996). Relay cells receive excitatory input from a single or a few retinal ganglion cells (Cleland et al., 1971; Coenen & Vendrik, 1972, Cleland & Lee, 1985; Mastronarde, 1987a, b, 1992). They also receive feedforward inhibition from intrageniculate interneurons which in turn receive excitation from a few retinal ganglion cells (Dubin & Cleland, 1977; Mas-
In addition there are feedback inputs from the perigeniculate nucleus (PGN) and cortex, as well as modulatory inputs from the brain-stem reticular formation. Here we consider a simplified neuronal circuit involving only the feedback contributions.

In this model, the relay-cell response function is given by

\[ R_g(d) = S_j \left[ \sum_{\mathbf{r}_{g,e}} B_1(\mathbf{r}_{g,e}) R_g(d; \mathbf{r}_{g,e}) - \sum_{\mathbf{r}_{g,i}} B_2(\mathbf{r}_{g,i}) R_g(d; \mathbf{r}_{g,i}) \right] , \]

where \( \mathbf{r}_{g,e} \) denotes position vectors of centers of receptive fields of retinal ganglion cells with excitatory inputs to the relay cell in question, and \( B_1(\mathbf{r}_{g,e}) \) denotes the corresponding weights. Correspondingly, \( \mathbf{r}_{g,i} \) denotes the positions of the centers of the receptive field of the retinal ganglion cells which indirectly inhibit the relay cell via interneurons. The positive weight parameters \( B_j(\mathbf{r}_{g,j}) \) give the indirect inhibitory coupling between the retinal ganglion cells located at \( \mathbf{r}_{g,j} \) and the relay cell. This parameter depends on the strengths of both the excitatory coupling between the retinal ganglion cell and the interneuron, and the inhibitory coupling between the interneuron and the relay cell. As relay-cell transfer function \( S_j[x] \), we will also use the “rectification function” \( x\theta(x) \).

The retinal ganglion cells summed over in eqn. (9) are assumed to be of the same class (X) and type (ON-center, OFF-center). These cells may have varying receptive-field properties. However, in the following we will assume that they are identical, an assumption partially justified by the similar retinal positions of their receptive fields.

For the case with a single excitatory input from a retinal ganglion cell with its receptive-field center concentric with the circular spot \( r_{g,e} = 0 \), the response function simplifies to

\[ R_g(d) = S_j \left[ B_1 R_g(d;0) - \sum_{j=1}^n B_2(\mathbf{r}_j) R_g(d; \mathbf{r}_j) \right] \] (10)

The point \( r = 0 \) is defined by the center point in the receptive field of the retinal ganglion cell providing the excitatory input to the relay cell, and the shorthand notation \( B_1 = B_1(0) \) has been introduced. The sum in eqn. (10) goes over all \( n \) inputs to interneurons from retinal ganglion cells with position vectors \( \mathbf{r}_j, j = 1, \ldots, n \). (In the following, we use the short notation \( \mathbf{r}_{1,\ldots,n} \) for these \( n \) position vectors.)

The corresponding relay-cell receptive-field function is given by

\[ g_r(r) = B_1 g_g(|r|) - \sum_{j=1}^n B_2(\mathbf{r}_j) g_g(|r - \mathbf{r}_j|) \] (11)

Note that \( g_g \) is not circularly symmetric, even for the special case when the inhibitory weights depend only on radial distance, \( B_2(\mathbf{r}_j) = B_2(r_j) \). This is in contrast to the circularly symmetric receptive-field function for retinal ganglion cells, \( g_g \) [eqn. (4)].

We now assume that the inhibitory relay-cell input comes from a single interneuron. The formulas for the shape of the response function of this interneuron and the corresponding receptive-field function are found directly from the above expressions for relay cells by omitting the direct excitatory term, that is, setting \( B_1 = 0 \), and by replacing \( B_2(\mathbf{r}_j) \) with \( -B_2(\mathbf{r}_j) \). For the receptive-field function, the shape is given by

\[ g_i(r) = \sum_{j=1}^n B_2(\mathbf{r}_j) g_g(|r - \mathbf{r}_j|) \] (12)

Note that the absolute magnitudes of the interneuron response function and receptive-field function cannot be determined since the weights \( B_2(\mathbf{r}_j) \) also involve the strength of the connection between the interneuron and the relay cell.

To simplify the expression for the relay-cell response function further, one has to make assumptions about the distribution of ganglion-cell inputs \( \mathbf{r}_j \) to the interneurons as well as the weights \( B_2(\mathbf{r}_j) \). A simple choice is to assume that (1) the retinal ganglion cell which provides the excitatory input to the relay cell is also functionally coupled to this interneuron (this input is hereby labeled \( j = 1 \) and its weight is labeled \( B_2(\mathbf{r}_1) \)), (2) all excitatory inputs to this interneuron have the same strength, that is, \( B_2(\mathbf{r}_{1,\ldots,n}) = B_2 \), and (3) all inputs to interneurons, except the input that also give the direct excitatory input to the relay cell, have receptive fields centered at the same distance \( r_a \) from the relay-cell receptive-field center. Thus, in mathematical terms, we have \( |\mathbf{r}_1| = 0 \) and \( |\mathbf{r}_2,\ldots,n| = r_a \). In the following, the ganglion-cell input labeled \( j = 1 \) is called the central input, while the other ganglion-cell inputs are called noncentral. A natural conjecture could be that these \( n \) inputs correspond to an assembly of nearest-neighbor cells of the same type in the disordered grid of retinal ganglion cells (Wässle et al., 1981a,b). Fig. 3 shows these assumptions for the choice \( n = 5 \) which is used throughout the paper.

With these assumptions the relay-cell response function simplifies to

\[ R_g(d) = S_j \left[ B_1 R_g(d;0) - B_2(R_g(d;0) - (n-1)R_g(d;r_a)) \right] \]

\[ = S_j \left[ (B_1 - B_2) R_g(d;0) - (n-1) B_2 R_g(d;r_a) \right] \] (13)

where \( R_g(d;r_a) \) and \( R_g(d;0) \) are given by eqns. (5) and (7), respectively. For large spot sizes, the function simplifies to \( R_g(d \to \infty) = S_j \left[ (B_1 - nB_2) S_g[l(L)(1 - \omega)] \right] \).
tion in eqn. (11) can be rewritten as

\[ f_d(r_0) = -\sum_{j=1}^{n} B_2(r_j) \delta(r_0 - r_j). \]  

(15)

Here \( \delta(r) \) is the two-dimensional Dirac delta function which is zero everywhere except for \( r = 0 \) where it is infinite in such a way that \( \int_0^{\infty} f_d(r) \delta(r) \, d\theta \, dr = 1 \). Therefore, in eqn. (15), \( f_d(r_0) \) is zero everywhere except at the positions of the ganglion-cell inputs to the interneuron, \( r_0 = r_j, j = 1, \ldots, n \). The function \( f_d(r) \) represents the inhibitory functional coupling between a finite number of retinal ganglion cells and a relay cell. If one hypothetically considers a large number of densely and evenly distributed ganglion-cell inputs to the interneuron, the discrete geniculate coupling function \( f_d(r) \) can as an approximation be replaced in eqn. (14) with a continuous geniculate coupling function \( f_c(r) \). Two choices of continuous geniculate coupling functions are considered, namely a Gaussian and a square well.

**Gaussian geniculate coupling function**

The continuous Gaussian geniculate coupling function representing the indirect inhibitory functional coupling between retinal ganglion cells and relay cells in dLGN is given by

\[ f_c^G(r) = -B_5 \frac{1}{\pi b_2^2} e^{-|r|^2/b_2^2}. \]  

(16)

Here \( B_5 \) is a dimensionless inhibitory weight, and the parameter \( b_2 \) determines the spatial width of the distribution of inhibitory weights. To assure the same normalization as for the discrete coupling function \( f_d(r) \), that is,

\[ \int_0^{\infty} \int_0^{2\pi} f_d(r) \, d\theta \, dr = \int_0^{\infty} \int_0^{2\pi} f_c^G(r) \, d\theta \, dr, \]  

(17)

\( B_5 \) is set to be \( B_5 = nB_2 \). With the coupling function \( f_c^G(r) \), the integral in eqn. (14) can be evaluated (cf. Appendix B), and the result is

\[ \int_0^{\infty} \int_0^{2\pi} g_c(|r_0 - r|) f_c^G(r_0) \, d\theta \, dr = \int_0^{\infty} \int_0^{2\pi} g_c^G(r_0) \, d\theta \, dr, \]

where we have labeled the excitatory weight \( B_1 \) to distinguish it from the corresponding parameter in the discrete model. It should

\[ g_c^G(r) = B_1 \left( \frac{1}{\pi a_1^2} e^{-r^2/(a_1^2 + b_1^2)} - \frac{\omega}{\pi a_1^2} e^{-r^2/(a_1^2 + b_1^2)} \right), \]  

(18)

The relay-cell receptive-field function \( g_c^G(r) \) is then given by

\[ g_c^G(r) = B_1 \left( \frac{1}{\pi a_1^2} e^{-r^2/(a_1^2 + b_1^2)} - \frac{\omega}{\pi a_1^2} e^{-r^2/(a_1^2 + b_1^2)} \right), \]  

(19)

\[ -B_5 \left( \frac{1}{\pi (a_2^2 + b_2^2)} e^{-r^2/(a_2^2 + b_2^2)} - \frac{\omega}{\pi (a_2^2 + b_2^2)} e^{-r^2/(a_2^2 + b_2^2)} \right), \]  

where we have introduced the geniculate coupling function \( f_d(r_0) \) given by

**Continuous models**

The continuous and discrete models differ only in their description of couplings between retinal ganglion cells and neurons in dLGN. The sum in the expression for the relay-cell receptive-field function in eqn. (11) can be rewritten as

\[ -\sum_{j=1}^{n} B_2(r_j) g_s(|r_j - r|) = \int_0^{\infty} \int_0^{2\pi} g_s(|r_0 - r|) f_d(r_0) \, d\theta \, dr, \]  

(14)

where we have introduced the geniculate coupling function \( f_d(r_0) \) given by

\[ f_d(r_0) = -\sum_{j=1}^{n} B_2(r_j) \delta(r_0 - r_j). \]  

(15)
be noted that due to the circular symmetry of the geniculate coupling function \( f_C^G(r) \), \( g_C^G(r) \) is also circularly symmetric, in contrast to the corresponding discrete receptive-field function in eqn. (11). A striking feature of the receptive-field function is that it consists of a sum of two positive and two negative Gaussians, that is, a pair of DOGs. The width constants in the last two Gaussians in eqn. (19) are given as square roots of sums of squares of the width constants of the ganglion cell receptive-field function \( (a_1,a_2) \) and the geniculate coupling function \( (b_2) \).

Here we have considered excitatory relay-cell input from a single retinal ganglion cell which in the continuous model would have been represented by a Dirac delta function as geniculate coupling function. A more spatially extended excitatory input to relay cells represented by a Gaussian function with width parameter \( b_1 \) would still give a pair of DOGs as receptive-field function. Then the parameter \( b_1 \) would have entered the terms in the first line of eqn. (19) the same way as \( b_2 \) in the second line.

The relay-cell response function for a spatial point concentric with the receptive-field center of the central retinal ganglion cell is then found from eqn. (19) by straightforward integration to be

\[
R_C^G(d) = S_r \left[ l(L) \int_0^{d/2} \int_0^{2\pi} g_C^G(r_0) \, dr_0 \, dr_0 \right],
\]

\[
= S_r \left[ l(L) \left( B_2^G \left( 1 - e^{-d^2/4a_1^2} - \omega \left( 1 - e^{-d^2/4a_1^2} \right) \right) \right) \right.
\]

\[
- \left. B_2^G \left( 1 - e^{-d^2/4(a_1^2+b_1^2)} - \omega \left( 1 - e^{-d^2/4(a_1^2+b_1^2)} \right) \right) \right].
\]

(20)

Since the receptive-field function in eqn. (19) is simply a sum over four Gaussians, it is also straightforward to derive relay-cell response functions for the case where the stimulus spot is nonconcentric with the receptive-field center of the relay cell (and central ganglion cell). In direct analogy with eqn. (5), this gives a formula involving four sums over incomplete gamma functions. We do not show this formula here, however.

Note that the response-function formula eqn. (20) has been derived with the assumption that all retinal ganglion cells considered are linear. Within our model this requires that the summed input is positive in the expressions for the ganglion-cell responses in eqn. (5).

**Square-well geniculate coupling function**

The Gaussian coupling function assumes a gradual reduction of inhibitory weights with increasing distance from the central retinal ganglion cell. An alternative continuous model is to assume that only retinal ganglion cells within a radius \( b_2 \) from the central ganglion cell are coupled to the relay cell, and that these inhibitory connections carry identical weights. This translates into the so-called square-well geniculate coupling function

\[
f_C^{SW}(r) = -B_2^G \frac{1}{\pi b_2^2} \theta(b_2 - |r|),
\]

(21)

where \( \theta(x) \) is the Heaviside step function introduced previously. The two different coupling functions \( f_C^{SW}(r) \) and \( f_C^G(r) \) are illustrated in Fig. 4.

With the square-well geniculate coupling function, the relay-cell receptive-field function is found to be (cf. Appendix B)

\[
g^{SW}_C(r) = B_2^G \frac{1}{\pi a_1^2} e^{-r^2/a_1^2} - \omega \frac{1}{\pi a_2^2} e^{-r^2/a_2^2}
\]

\[
- B_2^G \left( \frac{1}{\pi b_2^2} e^{-r^2/b_2^2} \sum_{m=0}^{\infty} \frac{1}{m!} \left( \frac{r}{a_1} \right)^{2m} \gamma(m+1,b_2^2/a_1^2) \right)
\]

\[
- \frac{\omega}{\pi b_2^2} e^{-r^2/b_2^2} \sum_{m=0}^{\infty} \frac{1}{m!} \left( \frac{r}{a_2} \right)^{2m} \gamma(m+1,b_2^2/a_2^2) \right] .
\]

(22)

The corresponding relay-cell response function for a circular spot concentric with the receptive-field center of the central retinal ganglion cell is then found by integration to be

\[
R_C^{SW}(d) = S_r \left[ l(L) \int_0^{d/2} \int_0^{2\pi} g^{SW}_C(r_0) \, dr_0 \, dr_0 \right],
\]

\[
= S_r \left[ l(L) \left( B_2^G \left( 1 - e^{-d^2/4a_1^2} - \omega \left( 1 - e^{-d^2/4a_1^2} \right) \right) \right) \right.
\]

\[
- \left. \left( B_2^G \left( \frac{a_1^2}{b_2^2} \sum_{m=0}^{\infty} \gamma(m+1,d^2/4a_1^2) \gamma(m+1,b_2^2/a_1^2) \right) \right) \right],
\]

(23)
Fit of model to experimental response curves

Retinal input

We assume that the total neuronal input is a sum of the inputs caused by the spot with luminance $L_{\text{spot}}$ and by the surround luminance $L_{\text{bkg}}$. For a retinal ganglion cell with its receptive-field center concentric with the spot stimulus, it then follows from eqns. (7) and (8) that the response function is

$$
R_{g,\text{model}}(d) = S_g[l(L_{\text{bkg}})(1 - \omega) + l(L_{\text{spot}}) - l(L_{\text{bkg}})] \\
\times [1 - e^{-d^2/4a^2} - \omega(1 - e^{-d^2/4a^2})], 
$$

(24)

where $S_g[x] = x\theta(x)$. Thus, the background activity, that is, activity without a stimulating spot ($d = 0$), is assumed to be due to an overweight of excitation over inhibition in the receptive field when the whole field is uniformly stimulated by the background luminance.

The five parameters $l(L_{\text{bkg}}), l(L_{\text{spot}}), \omega, a_1$, and $a_2$ were determined by fitting this theoretical function to a set of data points for the retinal input to a dLGN cell from Ruksenas et al. (2000). The fit was obtained by minimizing the sum of quadratic deviations between the experimental and theoretical values using the computer program MATLAB (Biran & Breiner, 1995). An example is shown in Fig. 5 (upper curve).

The fitting error is defined as

$$
\Delta R_g = \left(\sum_{n_{\text{exp}}} (R_{g,\text{model}} - R_{g,\text{exp}})^2/n_{\text{exp}}\right)^{1/2},
$$

(25)

where the sum goes over all $n_{\text{exp}}$ experimental data points. For the example cell pair in Fig. 5, the fit was quite good with $\Delta R_g < 2$ spikes/s. These fitted parameters are listed in the legend of Fig. 5.

Discrete model: Relay cells and interneurons

When we sum the contributions caused by the stimulating spot and by the surround, we find from eqn. (13)

$$
R_{r,\text{model}}(d) = S_g \left[(B_1 - B_2)S_r[l(L_{\text{bkg}})(1 - \omega) + l(L_{\text{spot}}) - l(L_{\text{bkg}})] \\
\times [1 - e^{-d^2/4a^2} - \omega(1 - e^{-d^2/4a^2})] \\
- (n - 1)B_2S_g[l(L_{\text{bkg}})(1 - \omega) + l(L_{\text{spot}}) - l(L_{\text{bkg}})] \\
\times \left(1 - e^{-\omega^2S_g} \sum_{m=0}^{m_{\text{max}}} \frac{1}{m!}\left(\frac{r_s}{a_1}\right)^{2m} \gamma(m + 1,d^2/4a^2)d \right) \\
- \omega e^{-\omega^2S_g} \sum_{m=0}^{m_{\text{max}}} \frac{1}{m!}\left(\frac{r_s}{a_2}\right)^{2m} \gamma(m + 1,d^2/4a_2^2)\right]\right], 
$$

(26)

where $S_g[x] = S_r[x] = x\theta(x)$. The remaining three unknown parameters $B_1, B_2$, and $r_s$ can be determined by fitting eqn. (26) to the experimental relay-cell response data keeping the five ganglion-cell parameters fixed. The relay-cell fit for cell pair 2 is shown in Fig. 5 (lower curve). The fit was good with an average deviation of 2.6 spikes/s.

The two infinite sums in eqn. (26) must in the numerical procedure be approximated by finite sums over the summing index $m$. By varying the maximum value of $m$, we found $m_{\text{max}} \approx 30$ to be sufficient to obtain fitted parameters with the accuracy listed in the legend of Fig. 5.

The ganglion-cell, relay-cell, and interneuron receptive-field functions for the cell pair in Fig. 5 are shown in Figs. 6A–6C. The theoretical shape of the interneuron response curves for the example cell pair in Fig. 5 is shown in Fig. 7 (solid curve). The maximum of the interneuron response curve in Fig. 7 gives the width of the center of the circularly averaged interneuron receptive field in Fig. 6C. In this example, the diameter of the center was 3.1 deg which is nearly twice the widths of the ganglion-cell (1.8 deg) and relay-cell (1.6 deg, circularly averaged) receptive-field center. As seen in Fig. 7, this center width does not correspond exactly to the maximum of the curve for the difference between the ganglion-cell and relay-cell responses (Fig. 7, dashed line).

Ruksenas et al. (2000) reported response curves from 22 pairs of X-cells (17 ON-cells and 5 OFF-cells). The fitted parameters to these data are listed in Table 1. We have listed the quantities $l(L_{\text{bkg}})(1 - \omega)$ and $l(L_{\text{spot}})(1 - \omega)$ instead of $l(L_{\text{bkg}})$ and $l(L_{\text{spot}})$. These quantities are the summed input to the retinal ganglion cell for diffuse stimulation with the luminances $L_{\text{bkg}}$ and $L_{\text{spot}}$, respectively. This corresponds to the zero spot-size and infinite spot-size ganglion-cell responses, respectively (except when the summed input is negative and the response consequently is zero). These quantities have a more evident physiological meaning than the fitting parameters $l(L_{\text{bkg}})$ and $l(L_{\text{spot}})$.  

Fig. 5. Example of comparison of experimental response data with fitted theoretical curves for the OFF-center cell pair 2. In the experiment, dark spot stimuli were shown for a period of 500 ms. Data points correspond to the time-averaged firing rates during this period. Open dots correspond to retinal ganglion-cell response (S-potentials), while filled dots correspond to relay-cell response (action potentials). Upper line corresponds to the best fit of the theoretical ganglion-cell response function in eqn. (24), while lower line corresponds to the best fit of the theoretical relay-cell response function in eqn. (26). Fitted parameter values are $\omega = 0.85$, $l(L_{\text{bkg}})(1 - \omega) = 36.8$ spikes/s, $l(L_{\text{spot}})(1 - \omega) = 56.5$ spikes/s, $a_1 = 0.62$ deg, $a_2 = 1.26$ deg, $B_1 = 0.72$, $B_2 = 0.095$, and $r_s = 0.99$ deg.
Table 2 shows the fitting errors $\Delta R_g$ and $\Delta R_r$ for all cell pairs. To facilitate an evaluation of the fit, maximum experimental responses $R_g^{\text{max}}$ and $R_r^{\text{max}}$ are also listed. Overall, we observe small fitting errors.

The receptive fields of the relay cells and interneurons are not completely circular in our discrete model, and the values listed in Table 3 for the center sizes ($d_c^{\text{relay}}$ and $d_c^{\text{inter}}$) correspond to the spot diameters at the response maxima.

A quantity of interest is the degree of center-surround antagonism which has been observed to be larger for relay cells than for retinal ganglion cells (Hubel & Wiesel, 1961). Center-surround antagonism $\alpha$ was defined as

$$\alpha = \frac{R^{\text{max}} - R^{\text{min}}}{R^{\text{max}}} \cdot 100\%,$$  \hspace{1cm} (27) 

where $R^{\text{max}}$ is the maximum neuronal response (for spots filling exactly the receptive-field center, $d = d_c$), and $R^{\text{min}}$ is the minimum response for spot diameters in the range $d > d_c$. For the fitted parameters for the 22 cell pairs, we found the following average antagonisms: $\alpha_{\text{gang}} = 53 \pm 15\%$, $\alpha_{\text{relay}} = 81 \pm 17\%$, and $\alpha_{\text{inter}} = 40 \pm 16\%$. For the average values, we thus found $\alpha_{\text{inter}} < \alpha_{\text{gang}} < \alpha_{\text{relay}}$.

**Continuous model:** Relay cells and interneurons

The experimental relay-cell data of Ruksenas et al. (2000) were also fitted to the theoretical response functions for the continuous model assuming either a Gaussian or a square-well geniculate coupling function. For the Gaussian case, the formula to fit is

$$R_r^{\text{model}}(d) = S_r [l(L_{\text{spec}}) (1 - \omega)(B_1^r - B_2^r) + (l(L_{\text{spec}}) - l(L_{\text{back}})) B_1^r ((1 - e^{-d/\alpha_1^h}) - \omega(1 - e^{-d/\alpha_2^h})) + (l(L_{\text{spec}}) - l(L_{\text{back}})) B_2^r ((1 - e^{-d/\alpha_1^h}) - \omega(1 - e^{-d/\alpha_2^h})].$$

(28)

This formula for the response to a concentric circular stimulus with diameter, $d$, is found by, in analogy with eqn. (26), summing the contributions caused by the stimulating spot and by the surround using eqn. (20). The corresponding expression for the square-well coupling function is derived analogously from eqn. (23). The formula is not shown here. Since the above expression for the Gaussian case does not involve sums over incomplete gamma functions, the numerical fitting procedure takes significantly less computation time than for the discrete model (and the continuous square-well model). Fig. 8 shows results of the relay-cell fitting procedures.

---

**Fig. 6.** Predicted receptive-field functions for the neurons generating the response curves shown in Fig. 5 (cell pair 2). (A) Retinal ganglion cell [eqn. (4)]. (B) Relay cell [eqn. (11)]. (C) Shape of receptive-field function for intrageniculate interneuron [eqn. (12)].

**Fig. 7.** Predicted shape of response function for the intrageniculate interneuron corresponding to the example cell pair 2 in Figs. 5 and 6 (solid). The curve is obtained by setting $B_1 = 0$ and replacing $B_2$ with $-B_2$ (i.e., $B_2 = -0.095$) in eqn. (26). Note that only the shape and not the absolute magnitude of the interneuron response can be determined from our model and the experiments of Ruksenas et al. (2000). Dashed curve shows the difference between the fitted theoretical ganglion-cell and relay-cell response curves shown with dotted lines.
for cell pair 2. For this example, both the Gaussian and square-well model fit the experimental relay-cell data equally well as the discrete model in Fig. 5. The calculated average errors were 2.7 spikes/s for both the Gaussian and square-well models (cf. 2.6 spikes/s for the discrete model). Fig. 9 shows the receptive-field functions for the relay cell and interneuron for both continuous models.

**DISCUSSION**

Novel mathematical formulas have been derived for receptive-field functions and response functions to circular spot stimuli for neurons in dLGN. The advantages of our models are (1) that they take into account known functional properties of the geniculate circuit, and (2) that parameters in the models have specific physiological meaning. Different receptive-field functions for the dLGN neurons were found for the different model versions, but none of the functions corresponded to the commonly used difference-of-Gaussians model (Rodieck, 1965; Kaplan et al., 1979; So & Shapley, 1981; Troy, 1983; Davis et al., 1984; Norton et al., 1989; Uhlrich et al., 1995). It can be noted, however, that for the continuous model with a Gaussian geniculate coupling function, the relay-cell receptive-field function corresponds to a sum over two positive and two negative Gaussian, that is, a pair of difference-of-Gaussians.

**Table 1. Fitted parameters for the 22 pairs of experimental response curves for nonlagged X-cells from Ruksenas et al. (2000)**

<table>
<thead>
<tr>
<th>Cell no</th>
<th>(\omega_l)</th>
<th>(l(L_{bg})/(1 - \omega_l))</th>
<th>(l(L_{ps})/(1 - \omega_l))</th>
<th>(a_1)</th>
<th>(a_2)</th>
<th>(B_1)</th>
<th>(B_2)</th>
<th>(r_a)</th>
</tr>
</thead>
<tbody>
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<td>29.7</td>
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<td>0.87</td>
<td>0.43</td>
<td>0.048</td>
<td>0.57</td>
</tr>
<tr>
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<td>0.85</td>
<td>36.8</td>
<td>56.5</td>
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<td>0.72</td>
<td>0.095</td>
<td>0.99</td>
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<td>0.68</td>
<td>0.097</td>
<td>0.60</td>
</tr>
<tr>
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<td>2.49</td>
<td>0.80</td>
<td>0.066</td>
<td>1.94</td>
</tr>
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<td>0.70</td>
<td>0.062</td>
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</table>

The parameters \(\omega_l\), \(l(L_{bg})\), \(l(L_{ps})\), \(a_1\), and \(a_2\) are found from fitting the ganglion-cell response curve to eqn. (24), while \(B_1\), \(B_2\), and \(r_a\) are found from fitting the relay-cell response curve to eqn. (26). Mean values and standard deviations (sd) are also listed. The unit for \(l(L_{bg})\) and \(l(L_{ps})\) is spikes/s. The unit for \(a_1\), \(a_2\), and \(r_a\) is degrees, while \(\omega_l\), \(B_1\), and \(B_2\) are dimensionless. For cell pair no. 21, \(m_{max} = 100\) was used, while for the other cell pairs \(m_{max} = 30\) was sufficient to approximate the infinite sums in eqn. (26) sufficiently well to not affect the values of the listed parameters for the numerical accuracy used in the table.

**Fig. 8.** Comparison of relay-cell data (dots) with fitted theoretical curves for continuous relay-cell models for the example cell pair 2. Solid line corresponds to Gaussian geniculate coupling function [eqn. (28)] while dashed line corresponds to square-well geniculate coupling function. Fitted geniculate parameters are \(B_1 = 0.81, B_2 = 0.56, b_2 = 0.88\) deg for Gaussian coupling function, and \(B_1 = 0.72, B_2 = 0.47, b_2 = 1.28\) deg for square-well coupling function. Fitted ganglion-cell parameters are listed in the legend of Fig. 5.
The discrete model gave good fits to the data of Ruksenas et al. (2000) with the average of errors found to be less than 5 spikes/s. Moreover, none of the fitted parameter values in Table 1 were clearly unphysiological. Also the fits to the continuous models were good, although only the results for one example cell pair were presented here.

Retinal ganglion cells

Since the sizes of ganglion-cell receptive fields vary systematically with visual eccentricity (Cleland et al., 1979; Peichl & Wässle, 1979), and the data used to derive Table 1 were from cells within a range of eccentricities, a considerable variation in the width parameters $a_1$ and $a_2$ in Table 1 might be expected. We found $a_1 = 0.42 \pm 0.23$ deg and $a_2 = 1.40 \pm 0.73$ deg. The width ratio $a_2/a_1$ might be expected to be less dependent of visual eccentricity and therefore have a smaller scatter, but we found a larger relative scatter, that is, $a_2/a_1 = 4.32 \pm 3.79$. On the other hand, the ratio between the surround and center weights for retinal ganglion cells was observed to have a rather small variation, that is, $v = 0.79 \pm 0.12$.

Rodieck (1965) determined ganglion-cell parameters by fitting theoretical formulas for responses to moving bars to experimental data. Even though he did not specify mean and standard deviation of the fitted parameters, a parameter set presented as “typical” was $v = 0.8$, $a_1 = 0.59$ deg, and $a_2/a_1 = 3$. These are close to our mean values.

The fitted values for $l(L_{bg})/(1 - \omega)$ for two OFF-center cell pairs (4 and 5), but none of the ON-center pairs, were negative. This may reflect a very low background activity for these two

<table>
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<th>Cell no</th>
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<th>$\Delta R_r$</th>
<th>$R_{rmax}$</th>
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Mean 4.6 135 4.5 68

sd 2.9 54 2.7 28

*The unit is spikes/s.

Table 3. Receptive-field center sizes derived from the fitted parameters for the 22 cell pairs in Table 1

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<tr>
<th>Cell no</th>
<th>$d_{gang}$</th>
<th>$d_{relay}$</th>
<th>$d_{inter}$</th>
<th>$d_{relay}/d_{gang}$</th>
<th>$d_{inter}/d_{gang}$</th>
<th>$r_a/d_{gang}$</th>
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<td>0.78</td>
<td>1.65</td>
<td>0.93</td>
<td>2.12</td>
<td>0.68</td>
</tr>
<tr>
<td>2</td>
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Mean 1.39 1.29 2.87 0.94 2.31 0.77

sd 0.75 0.65 1.34 0.10 0.41 0.29

*The unit for $d_{gang}$, $d_{relay}$, and $d_{inter}$ is degrees, while the ratios $d_{relay}/d_{gang}$, $d_{inter}/d_{gang}$, and $r_a/d_{gang}$ are dimensionless.
retinal ganglion cells, presumably due to strong inhibition induced by the diffuse surround illumination. Therefore, the best theoretical fit for these two retinal ganglion cells were found to have a zero ganglion-cell response to the smallest spots (and the fitted model was thus nonlinear).

Our modeling gave predictions regarding the grid of retinal ganglion cells. Assume (1) that the noncentral ganglion-cell inputs to the interneurons come from the nearest neighbors of the same type (X, ON-center or OFF-center) and not from more distant retinal ganglion cells, and (2) that the receptive-field centers of all retinal ganglion cells providing the noncentral inputs to the interneuron, are approximately a distance $r_a$ away from the central retinal ganglion cell. Then our fitting procedure can predict this nearest-neighbor distance. Although both ganglion-cell density and receptive-field center size vary systematically with eccentricity, the coverage factor $c$, which is the number of receptive-field centers from cells of a certain type overlapping a single point, is fairly constant for X-cells over a wide range of eccentricities except close to the area centralis (Peichl & Wässle, 1979). The coverage factor is found by multiplying the local cell density with the receptive-field center size. The true ganglion-cell grid is disordered (Hughes, 1975, 1981; Wässle et al., 1981a, b). If we, however, assume an approximation a square ganglion-cell grid with nearest-neighbor distance $r_a$, we find the coverage factor to be $c = \pi (d_{gang}^2)^2/4 r_a^2$, that is, $r_a/d_{gang} = (\pi/4)^{1/2}$. For a hexagonal grid, we find $c = \pi (d_{gang}^2)^2/4 \sqrt{3} r_a^2$, that is, $r_a/d_{gang} = (\pi/4\sqrt{3})^{1/2}$. Since $r_a/d_{gang}$ only depends on the coverage factor, this ratio is well suited for comparison with our theoretical findings based on experiments from a range of eccentricities. After averaging, we found (cf. Table 3) $r_a/d_{gang} = 0.77 \pm 0.29$. Ruksenas et al. (2000) preferentially sampled cells located outside the area centralis. For this part of the visual field, Peichl and Wässle (1979) measured $c \approx 3.5–5$. With $c = 4$, we find $r_a/d_{gang} = \sqrt{\pi}/4 = 0.44$ for the square grid and $r_a/d_{gang} = \sqrt{\pi}/4(3)^{1/4} = 0.34$ for the hexagonal grid. This is approximately half of the average predicted ratio from our modeling. Note, however, that Peichl and Wässle (1979) used the so-called area thresholds method to measure the receptive-field center sizes. There the so called equivalent center diameter was found from the data by determining the intersection of two straight lines drawn through the data points in a log–log plot. Since this method of evaluating the receptive-field center sizes is significantly different from ours, these results is not straightforwardly comparable to ours. When one considers the approximations and uncertainties in our modeling effort, even a factor of two deviation might not be unexpected. Nevertheless, one possible reason for the observed deviation may be that the interneurons do not receive all inputs from the neighboring ganglion cells, but that more distant retinal ganglion cells also contribute to the excitation of interneurons. More studies are needed to clarify this point. In particular, a model which includes more distant neighbors than the nearest-neighbor ganglion cells as inputs to the inhibitory mechanism should be explored.

Fig. 9. Predicted shapes of receptive fields for the dLGN cells in the example cell pair 2 using continuous models with the parameters listed in the legend of Fig. 8. (A) Gaussian coupling function: Relay cell [eqn. (19)]. (B) Gaussian coupling function: Intrageniculate interneuron [eqn. (19) with $B_1 = 0$ and $B_2 = -0.56$]. (C) Square-well coupling function: Relay cell [eqn. (22)]. (D) Square-well coupling function: Intrageniculate interneuron [eqn. (22) with $B_1 = 0$ and $B_2 = -0.47$].

Mathematical models for receptive fields in cat dLGN
Relay cells

On average, we observed slightly smaller receptive-field centers for relay cells than for retinal ganglion cells. In Table 3, we observed $d^{\text{rel}}_c / d^{\text{gang}}_c$ to vary between 0.66 and 1.08 with an average value of 0.94. The cell pairs with $d^{\text{rel}}_c > d^{\text{gang}}_c$ (cell pairs 11, 12, 14–17, 21) were found to have the largest values for $r_a / d^{\text{gang}}_c$ (see Table 3).

In the discrete model, five retinal ganglion cells ($n = 5$) were assumed to indirectly inhibit a relay cell. This choice was motivated by physiological studies (Mastronarde, 1992), and by anatomical studies by Wässle et al. (1981b) which revealed a disordered grid of retinal ganglion cells with typically 4–6 nearest neighbors of the same type. However, other choices of $n$ would have given exactly the same theoretical fits of the relay-cell response curves, except that the predicted values for $B_1$ and $B_2$ would have differed. This is seen directly in eqns. (13) and (26) where the total weight from the central retinal ganglion cell is seen to be $B_1 - B_2$ while the total inhibitory weight from the noncentral ganglion cells is seen to be $(n - 1)B_2$. Thus, the important parameters in the fitting procedure are $B_1 - B_2$ and $(n - 1)B_2$, and the theoretical response curves will be identical for different choices of $n$ as long as these quantities are unchanged. It is not even necessary to assume that all inhibitory inputs have the same weight. For instance, the weight of the central inhibitory input $B_2(r_1)$ can be chosen differently from the weights of the noncentral inputs. Moreover, the theoretical response curve will remain unchanged even if the weights of the $n - 1$ noncentral inputs $B_2(r_2,...,r_n)$ are unequal or if they are not symmetrically positioned as long as the inputs are equidistant from the center and their sum is conserved. The theoretical relay-cell response curve depends only on the total central ($B_1^* = B_1 - B_2(r_1)$, $B_2^* = \sum_{j=2}^{n} B_2(r_j)$), (29)

which can readily be calculated for the 22 cell pairs by using the parameters listed in Table 1.

Retinal ganglion cells and relay cells of the X class are known to have linear-response properties to a large extent (Enroth-Cugell & Robson, 1966; Hochstein & Shapley, 1976; So & Shapley, 1979). Here we addressed the question of linearity of X-cells by considering the results of the fitting to the data of Ruksenas et al. (2000). In the theoretical functions used for the fit to the relay-cell response data, the nonlinear transfer functions $S_g[x] = S_r[x] = x^2(1 + x)$ were used. However, for the fitted discrete model the arguments of $S_g[x]$ and $S_r[x]$ were found to always be positive for 15 of the 22 cell pairs so that the rectification functions could be replaced simply by $S_g[x] = S_r[x] = x$ making the model fully linear. Thus, for these 15 X-cell pairs the purely linear model represented the best fit to the experimental data.

A key decision made at the dLGN is whether action potentials received from the retina will generate action potentials in the relay cells that project to visual cortex. To elucidate geniculate transmission the transfer ratio, defined as the ratio between output and input firing rates, have been used (Coenen & Vendrik, 1972; Fukuda & Stone, 1976). From Fig. 5, it follows that the transfer ratio when plotted against the input firing rate, will not be unique, that is, one has different output firing rates, and thus different transfer ratios, for different spot sizes even when the input firing rates are identical. This was a general feature for all cell pairs, not just the example cell pair 2, and demonstrated that there must be a spatial component involved in the variation of the transfer ratio. Even the most complicated choice of nonlinear transfer functions $S_g[x]$ and $S_r[x]$ cannot account for these dependencies alone. Note, however, that this result is based on the spike-count code used in the present work. Effects from the temporal structure, which have not been considered here, could also play a role in explaining the observed variation in transfer ratio observed for identical input firing rates (Funke & Wörgötter, 1997; Reich et al., 1997).

In our models, we have assumed a single excitatory ganglion-cell input to a relay cell. Mastronarde (1992) found that 85% (87/102) of the relay X-cells had single ganglion-cell inputs ($X_g$) while 15% (15/102) had multiple ganglion-cell inputs ($X_{gt}$). The present model could easily be extended to handle also relay cells with inputs from several retinal ganglion cells.

The only application of the continuous relay-cell model presented here was to the example cell pair 2. For this example, we saw in Fig. 9D that the size and shape of the interneuron receptive field for the square-well model had some qualitative similarity with the discrete model with five ganglion-cell inputs shown in Fig. 6C. This is not surprising since the square-well model can be viewed as a continuous version of the equal-weight discrete model when the inputs are evenly distributed in space. This is demonstrated further when the values for the fitted parameters are compared. For cell pair 2, one finds the same values for the fitted parameters (for the numerical accuracy used in the parameter listing in the legend of Figs. 5 and 8), that is, $B_1 = 0.72 = B_1$ and $B_2 = 0.47 = 5 \times B_2$. However, this extremely close agreement was not observed for all cell pairs.

Intrageniculate interneurons

From the fitted parameters listed in Table 1, we found the average predicted size of the receptive-field centers of the interneurons to be $d^{\text{inter}} = 2.87 \pm 1.34$ deg. A substantial part of this variation is expected to come from the range of eccentricities of the cells sampled in the experiments. The ratio between the widths of the interneuron and relay-cell receptive fields is expected to vary less with eccentricity, and this is supported by our calculations which gave $d^{\text{inter}} / d^{\text{rel}} = 2.31 \pm 0.41$. Mastronarde (1992) estimated the width of the receptive fields of putative interneurons from responses to a moving slit, or from responses to handheld discs of varying diameter. Response to moving slits suggested an average center width for interneurons ($N = 5$) that was 2.1 times the average center width for nonlagged X relay cells ($N = 50$). Responses to the discs showed an average center width for the interneurons ($N = 19$) that was 1.5 times the center width of the relay cells ($N = 97$). Although our theoretical result was slightly larger than the largest estimate of Mastronarde (1992), it is reasonable to say that our result is compatible with Mastronarde’s results, considering the significant spread in measured $d^{\text{inter}} / d^{\text{rel}}$ for the different experimental methods. Note, however, that other choices of distributions of weights of ganglion-cell inputs to the interneuron would give somewhat different model predictions for the interneuron center width.

The predicted mean center-surround antagonism for interneurons in the discrete model was found to be $\alpha_{\text{inter}} = 40 \pm 16\%$ which is smaller than both the retinal ganglion-cell and relay-cell antagonisms ($\alpha_{\text{gang}} = 53 \pm 15\%$, $\alpha_{\text{rel}} = 81 \pm 17\%$). This agrees with the qualitative observation of Mastronarde (1992) that X-class
interneurons showed weaker surround suppression for the largest disks than the relay cells.

It should be noted that our model for the relay-cell response does not require that the inhibitory afferents providing the spatial convergence to the relay cells come from the same interneuron. In principle, these afferents could come from different interneurons, each with inputs from, for example, a smaller number of retinal ganglion cells.

**Model evaluation**

We have derived new mathematical formulas for the spatial receptive-field functions and responses to circular spot stimuli for neurons in the dLGN. The model can also be used with other types of visual stimuli (Einevoll et al., 2000). Furthermore, the model may be extended to include different spatial arrangements and weight distributions of inputs to interneurons and relay cells. The mathematical response expressions for other models may be constructed based on the mathematical formulas derived here.

Both relay cells and interneurons receive afferents from the cortex and perigeniculate nucleus (PGN) (Sherman & Guillery, 1996). These feedback connections have not been incorporated in our simplified neuronal circuit used to explain the data of Rukse nas et al. (2000). The approximation of neglecting cortical feedback might be justified by the observation that the layer VI cortical cells providing the corticothalamic afferents to dLGN are not well activated by the circular spot stimuli used here (Sillito & Jones, 1997). The neglect in our model of the afferents from the GABAergic neurons in PGN is supported by observations that PGN cells have a less clearly defined receptive field with mixed ON–OFF response (Ahlsén et al., 1983; Dubin & Cleland, 1977) in anesthetized preparations used by Ruksenas et al. (2000). In recent experiments, Funk and Eyssel (1998) found the PGN cells to respond best to circular spots much larger than the relay-cell receptive-field center, and this may suggest that the error in neglecting the PGN feedback in our models for the spatial receptive-field organization will be largest for these largest spots. Our model can be extended to incorporate feedback from PGN and cortex.

In conclusion, we found our purely feedforward models to account well for the results from the nonlagged X-cells in the experiments of Ruksenas et al. (2000) with circular spot stimuli. Moreover, confidence in the use of the discrete model to this experimental situation is supported by predictions regarding (1) receptive-field sizes of interneurons, (2) amount of center-surround antagonism for interneurons compared to relay cells, and (3) distance between neighboring retinal ganglion cells providing input to interneurons, which all are found to be compatible with data available in the literature.

**Acknowledgments**

We thank A. Kocbach and P.C. Hemmer for useful discussions on mathematical aspects of this work.

**References**


Appendix A

This appendix shows the derivation of the ganglion-cell response functions for the cases when the spot stimulus is nonconcentric [eqn. (5)] and concentric [eqn. (7)] with the receptive-field center.

The integral in eqn. (3) consists of two integrals of the type

\[ R = \frac{1}{\pi a^2} \int_0^{\pi/2} \int_0^{\pi/2} e^{-(\rho_0 - r_0)^2/a^2} \rho_0 d\rho_0 dr_0 \]

\[ = \frac{1}{\pi} \int_0^{\pi/2} \int_0^{\pi/2} e^{-t^2} e^{n_0 \cos(\theta_0 - \theta_0')} d\theta_0 d\theta_0', \quad (A1) \]

where we have introduced the dimensionless variables \( t = d/2a, \rho_0 = r_0/a \), and \( t_0 = r_0/a \). Note that the position vectors are given in polar coordinates via \( r_0 = (r_0, \theta_0) \) and \( r_0 = (r_0, \theta_0') \).

The angular integrations can be performed to give (Bender & Orzag, 1978)

\[ \int_0^{\pi/2} e^{n_0 \cos(\theta_0 - \theta_0')} d\theta_0 = \int_0^{\pi/2} e^{n_0 \cos \theta} dx = 2 \pi J_0(2n_0 t_0), \quad (A2) \]

where the modified Bessel function \( J_0(x) \) is given by

\[ J_0(x) = \sum_{m=0}^{\infty} \frac{1}{(m!)^2} \left( \frac{x}{2} \right)^{2m}. \quad (A3) \]

Then the integral simplifies to

\[ R = 2 \int_0^{\pi/2} e^{-t^2} \sum_{m=0}^{\infty} \frac{1}{m!} t^{2m} \frac{e^{2m+1}}{m!} \rho_0 d\rho_0 \\
= e^{-t^2} \sum_{m=0}^{\infty} \frac{1}{m!} t^{2m} \int_0^{\pi/2} e^{-t^2} \rho_0 d\rho_0 \\
= e^{-t^2} \sum_{m=0}^{\infty} \frac{1}{m!} t^{2m} \int_0^{\pi/2} \frac{e^{t^2} u^m}{m!} e^{-u} du, \quad (A4) \]

In the final step, we have made the substitution \( u = t_0^2 \). By introduction of the incomplete gamma function given as

\[ \gamma(m, x) = \frac{1}{(m-1)!} \int_0^x u^{m-1} e^{-u} du, \quad (A5) \]

the integral can be compactly written as

\[ R = e^{-t^2} \sum_{m=0}^{\infty} \frac{1}{m!} \frac{1}{t^2} \gamma(m + 1, t_0^2) \\
= e^{-t^2} \sum_{m=0}^{\infty} \frac{1}{m!} \left( \frac{r_0}{a} \right)^{2m} \gamma(m + 1, d^2/4a^2). \quad (A6) \]

The result in eqn. (5) is obtained by adding the contributions from the center and the surround.

The results for the concentric case, that is, the special case where \( r_0 = 0 \), can be straightforwardly obtained from the above result. When \( r_0 = 0 \) in eqn. (A6), the only contribution from the sum comes from \( m = 0 \), and one finds

\[ R = \gamma(1, d^2/4a^2) = \int_0^{d^2/4a^2} e^{-u} du = 1 - e^{-d^2/4a^2}. \quad (A7) \]

By adding the contributions from the center and surround one obtains eqn. (7).
In the infinite spot-size limit, \( d \to \infty \), the incomplete gamma function \( \gamma \) approaches 1, and one obtains from eqn. (A6)

\[
\lim_{d \to \infty} \tilde{R} = e^{-r_i^2/a^2} \sum_{n=0}^{\infty} \frac{1}{m!} \left( \frac{r_i}{a} \right)^{2m} = e^{-r_i^2/a^2} e^{r_i^2/a^2} = 1.
\]

(A8)

Addition of the center and surround contributions then gives the infinite spot-size response as \( R_g(d \to \infty; r_c) = S_g[I(L)(1 - w)] \) as listed in the main text.

Appendix B

This appendix shows the derivation of formulas related to the continuous version of the relay-cell model.

Gaussian geniculate coupling function

The double integral in eqn. (18) consists of two integrals of the type

\[
B_0^2 \int_0^2 \int_0 e^{-i(\theta_0 - \theta_0')/a^2} e^{-i\theta_0' b_0} d\theta_0 r_0 dr_0
\]

\[
= \frac{B_0^2}{\pi^2 b_0^2} e^{-r_i^2} \int_0^\infty e^{-a^2/|b_0|^2} e^{-i\theta_0} 2\pi I_0(2t_0) d\theta_0, \quad (B1)
\]

where we have introduced the dimensionless variables \( t = r/\alpha, t_0 = r_0/\alpha, \) and performed the same angular integration as in Appendix A. With the series expansion of \( I_0(x) \) in eqn. (A3) inserted into eqn. (B1), one obtains

\[
\frac{B_0^2}{\pi^2 b_0^2} e^{-r_i^2} \sum_{m=0}^{\infty} \frac{1}{(m!)^2} \int_0^\infty \frac{1}{1 + a^2/|b_0|^2} e^{-a^2/|b_0|^2} d\theta_0
\]

\[
= \frac{B_0^2}{\pi^2 b_0^2} e^{-r_i^2} \sum_{m=0}^{\infty} \frac{1}{m!} \left( \frac{b_0^2 r_i^2}{a^4 + b_0^4} \right)^m \sum_{n=0}^2 \frac{1}{m!} \left( \frac{b_0^2 r_i^2}{a^4 + b_0^4} \right)^m
\]

\[
= \frac{B_0^2}{\pi^2 b_0^2} e^{-r_i^2} \sum_{m=0}^{\infty} \frac{1}{m!} \left( \frac{b_0^2 r_i^2}{a^4 + b_0^4} \right)^m
\]

\[
\int_0^\infty \frac{1}{m!} \left( \frac{b_0^2 r_i^2}{a^4 + b_0^4} \right)^m = \frac{B_0^2}{\pi^2 b_0^2} e^{-r_i^2} \sum_{m=0}^2 \frac{1}{m!} \left( \frac{r_i^2}{a^4 + b_0^4} \right)^m.
\]

(B2)

Here we have used that \( \int_0^\infty u^m e^{-u} du = \Gamma(m + 1) = m! \) when \( m \) is an integer, and that \( \sum_{n=0}^\infty x^n/m! = \exp(x) \). The result in eqn. (18) is then obtained directly by summing the center and surround contributions.

An alternative approach for solving the integral in eqn. (18) is to introduce the two-dimensional Fourier transforms of the retinal ganglion-cell receptive-field function and coupling function, respectively. Then according to the standard convolution theorem, the Fourier transform of the relay-cell receptive-field function is essentially given by the product of these two Fourier transforms. Since the Fourier transform of a Gaussian function is a Gaussian function itself, and the product of two Gaussian functions is also a Gaussian function, the result in eqn. (B2) follows readily. This approach can also be used for other choices of coupling functions. An advantage of this is that the problem of evaluating the Fourier transform and its inverse maps over to evaluating the so-called Hankel transform and its inverse. One might then reduce the effort of solving the integrals by exploiting the collection of functions for which the Hankel and inverse Hankel transforms have been tabulated (Magnus & Oberhettinger, 1949).

Square-well geniculate coupling function

In analogy to the Gaussian model above, the contribution to the receptive-field function from the inhibitory square-well geniculate coupling function consists of two integrals of the type

\[
B_0^2 \int_0^\infty \int_0 e^{-i(\theta_0 - \theta_0')/a^2} e^{-i\theta_0' b_0} d\theta_0 r_0 dr_0
\]

\[
= \frac{B_0^2}{\pi^2 b_0^2} e^{-r_i^2} \int_0^\infty t_0 e^{-t_0^2} 2\pi I_0(2t_0) d\theta_0
\]

\[
= \frac{B_0^2}{\pi^2 b_0^2} e^{-r_i^2} \sum_{m=0}^2 \frac{1}{m!} \int_0^\infty u^m e^{-u} du
\]

\[
= \frac{B_0^2}{\pi^2 b_0^2} e^{-r_i^2} \sum_{m=0}^2 \frac{1}{m!} \left( \frac{r_i^2}{a^4 + b_0^4} \right)^m.
\]

(B3)

The result in eqn. (22) then follows in a straightforward manner.