

Probing the retino-geniculate circuit in cat using circular spot stimuli

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Abstract

Spatial receptive fields of relay cells in the dorsal lateral geniculate nucleus (dLGN) have commonly been modeled as a difference-of-Gaussians. Recently, we presented an alternative receptive-field model which incorporates the known functional couplings between retina and dLGN. The model gave good fits to recently published experimental data on responses to circular spot stimuli. Moreover, predictions from the modeling compared well with other experimental data available in the literature. Here we derive the connection between these purely spatial receptive-field functions and the spatiotemporal impulse response functions measured in experiments using drifting gratings or white noise analysis. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

The difference-of-Gaussians (DOG) model [10] has been the model of choice when describing the spatial receptive-field organization of retinal ganglion cells and relay cells in the dorsal lateral geniculate nucleus (dLGN). Even though a DOG model may be able to describe the spatial receptive-field properties of dLGN neurons, this model provides little insight into the detailed workings on *how* the geniculate circuit modifies the retinal input signals. Recently we have investigated a model [3] which includes

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excitatory input, modeled as a DOG, from a single retinal ganglion cell and feedforward inhibition via intrageniculate interneurons. The response of neurons in the dLGN to circular spot stimuli was calculated. Recent experimental data [11] were used to test the applicability of the model. The model compared well with the results for the 22 pairs of recordings for nonlagged X cells reported in [11] (an example is shown in Fig. 1). Moreover, predictions regarding receptive-field sizes of interneurons and distance between neighboring retinal ganglion cells were found to be compatible with other data available in the literature [7,8].

In the present paper we investigate the connection between the purely spatial receptive-field functions modeled in [3] and the general spatiotemporal impulse response function used in linear systems analysis [5]. The spatiotemporal impulse response function for neurons in the visual system is commonly measured using the drifting-grating method [4] or by using white-noise stimuli [9]. A good approach to investigate models for the geniculate circuitry would be to record the response of single neurons to different kinds of visual stimuli. Then a mathematical model fitted to experimental results for one type of stimuli would make testable predictions for experiments with another type of stimuli. Such testing would increase the constraints on the mathematical modeling and make it easier to falsify a proposed general quantitative model for the signal processing in dLGN. One thus needs to relate the

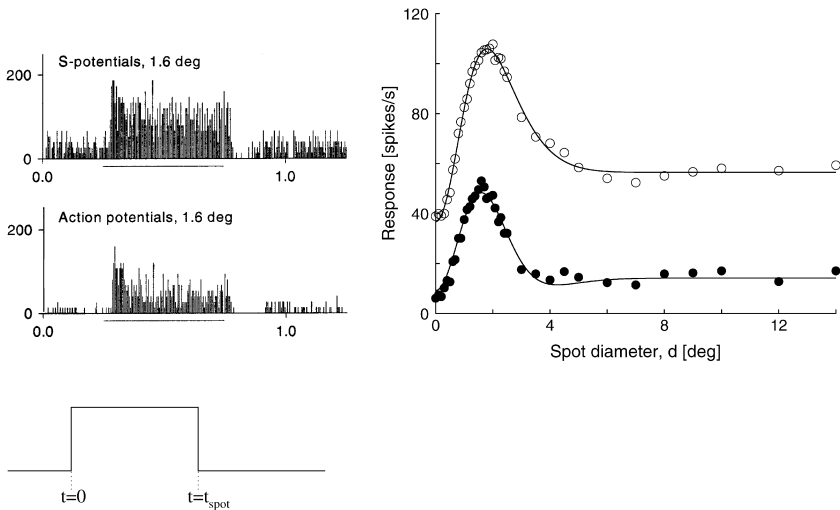


Fig. 1. Example of results for a nonlagged off-center X cell measured in dLGN from Ruksenas et al. [11]. Peri-stimulus time histograms (PSTHs) for spot diameter $d = 1.6^\circ$ for retinal input (S-potentials, top left) and action potentials (middle left), and temporal profile of spot stimulus (bottom left). Time-averaged PSTHs (right) during 500 ms stimulus period as functions of spot diameter (open dots correspond to retinal input, filled dots to action potentials). Upper and lower lines correspond to the best fits of the theoretical ganglion-cell and relay-cell spot response functions, respectively, which are derived in [3].

quantities measured in the different types of experiments. Here we derive the relation between the spatial receptive-field function measured in the circular-spot experiments by Ruksenas et al. [11], and the spatiotemporal impulse response function measured using drifting gratings or white noise stimuli. If the spatiotemporal impulse response function is assumed to be spatiotemporally separable, these quantities are trivially related. However, retinal ganglion cells and geniculate relay cells seem to have spatiotemporally connected impulse response functions [1], and in this case the connection is not so direct.

2. Results

With the assumptions of linearity and time invariance the response of a retinal ganglion cell at a position $\mathbf{r} = [x, y]$ can generally be expressed as

$$R_g(\mathbf{r}, t) = \iint_{r_0} \int_0^\infty G_g(\mathbf{r} - \mathbf{r}_0, \tau) s(\mathbf{r}_0, t - \tau) d\tau d^2r_0, \quad (1)$$

where $G_g(\mathbf{r}, \tau)$ is the spatiotemporal impulse response function [5] of the retinal ganglion cell, which is not necessarily spatiotemporally separable [1]. $s(\mathbf{r}_0, t - \tau)$ represents the visual stimulus presented at position \mathbf{r}_0 at time $t - \tau$. The spatial integral is over the whole visual field, i.e., over all two-dimensional space.

The luminance profile corresponding to the experiments by Ruksenas et al. [11] is mathematically expressed as

$$L(\mathbf{r}_0, t) = L_{\text{bkg}} + (L_{\text{spot}} - L_{\text{bkg}})\theta(d/2 - r_0)(\theta(t) - \theta(t - t_{\text{spot}})),$$

where L_{bkg} is the background luminance, L_{spot} is the spot luminance, $r_0 = |\mathbf{r}_0|$, t_{spot} is the duration of the spot stimuli (500 ms), and $\theta(t)$ is the Heaviside step function given as $\theta(t < 0) = 0, \theta(t > 0) = 1$. The temporal profile of the stimuli for a point inside the spot ($r_0 < d/2$) is shown in Fig. 1.

The response of photoreceptor cells adapts to the background light level and has a sigmoidal response curve to applied visual stimuli [6]. This sigmoidal response will be reflected in the activity of the retinal ganglion cells. It is thus convenient to represent the stimulus via an (unspecified) sigmoidal activity function $l(\mathbf{r}, t)$, i.e., $s(\mathbf{r}_0, t - \tau) = l(L(\mathbf{r}_0, t - \tau))$ [3]. With this stimulus representation, the sigmoidal non-linearity is removed from $G_g(\mathbf{r}, \tau)$, and the assumption of a linear spatiotemporal impulse response function becomes more plausible. If the stimulus contrasts are sufficiently small, so that the system operates within a linear region of the sigmoidal response curve (which is often assumed), the activity function will be represented by a linear function.

To compare with the experimental results of Ruksenas et al. [11] we only need the response during the time the circular spot is on ($0 < t < t_{\text{spot}}$). In this time period the expression for the response of a retinal ganglion cell with its receptive field centered at

a position \mathbf{r} away from the center of the stimulating spot with diameter d , can be split into parts and reorganized according to

$$\begin{aligned}
 R_g(\mathbf{r}, t; d) &= l(L_{\text{bkg}}) \iint_{r_0} \int_0^\infty G_g(\mathbf{r} - \mathbf{r}_0, \tau) d\tau d^2r_0 \\
 &\quad + (l(L_{\text{spot}}) - l(L_{\text{bkg}})) \iint_{r_0 < d/2} \int_0^t G_g(\mathbf{r} - \mathbf{r}_0, \tau) d\tau d^2r_0 \\
 &= l(L_{\text{bkg}}) \iint_{r_0} g_g(\mathbf{r}_0 - \mathbf{r}) d^2r_0 \\
 &\quad + (l(L_{\text{spot}}) - l(L_{\text{bkg}})) \iint_{r_0 < d/2} g_g^t(\mathbf{r}_0 - \mathbf{r}, t) d^2r_0. \tag{2}
 \end{aligned}$$

Here we have introduced a spatial receptive-field function g_g^t which depends on time t after onset of spot stimulus,

$$g_g^t(\mathbf{r}_0 - \mathbf{r}, t) \equiv \int_0^t G_g(\mathbf{r} - \mathbf{r}_0, \tau) d\tau, \tag{3}$$

and a steady-state receptive-field function g_g given by

$$g_g(\mathbf{r}_0 - \mathbf{r}) \equiv \int_0^\infty G_g(\mathbf{r} - \mathbf{r}_0, \tau) d\tau. \tag{4}$$

g_g^t and g_g only differ in their upper limits for their temporal integration. In the special case of spatiotemporal separability of the impulse response function, i.e., $G_g(\mathbf{r}, \tau) = f(\mathbf{r})h(\tau)$, g_g^t and g_g will have identical spatial shapes given by $f(\mathbf{r})$ and the temporal integration will only contribute a multiplicative constant (which will be different for g_g^t and g_g).

Ruksenas et al. [11] presented measured spot-responses averaged over the duration of the spot. In mathematical terms this corresponds to

$$\overline{R_g(\mathbf{r}; d)} = \frac{1}{t_{\text{spot}}} \int_0^{t_{\text{spot}}} R_g(\mathbf{r}, t; d) dt, \tag{5}$$

which by straightforward integration of Eq. (2) is seen to be given as

$$\overline{R_g(\mathbf{r}; d)} = l(L_{\text{bkg}}) \iint_{r_0} g_g(\mathbf{r}_0 - \mathbf{r}) d^2r_0 + (l(L_{\text{spot}}) - l(L_{\text{bkg}})) \iint_{r_0 < d/2} \overline{g_g^t(\mathbf{r}_0 - \mathbf{r})} d^2r_0. \tag{6}$$

Here $\overline{g_g^t(\mathbf{r}_0 - \mathbf{r})} = \frac{1}{t_{\text{spot}}} \int_0^{t_{\text{spot}}} g_g^t(\mathbf{r}_0 - \mathbf{r}, t) dt$ corresponds to a spatial receptive-field function (5). Note that the temporal average over the steady-state receptive-field is the steady-state receptive-field itself, i.e., $\overline{g_g(\mathbf{r}_0 - \mathbf{r})} = g_g(\mathbf{r}_0 - \mathbf{r})$.

The shapes of $\overline{g_g^t(\mathbf{r})}$ and $g_g(\mathbf{r})$ are in general different since the strong transient response at stimulus onset gives a contribution to $\overline{g_g^t(\mathbf{r})}$ while $g_g(\mathbf{r})$ describes only the tonic response. For increasingly longer durations of the spot stimuli the short transient effect will give a relatively smaller contribution to $\overline{g_g^t(\mathbf{r})}$, and in the limit $t_{\text{spot}} \rightarrow \infty$, $\overline{g_g^t(\mathbf{r})}$ and $g_g(\mathbf{r})$ would become identical.

In the application in (3) it was assumed as an approximation that $\overline{g_g^t(\mathbf{r})}$ and $g_g(\mathbf{r})$ in Eq. (6) were identical, and they were both described by the same difference-of-Gaussians [10]. Then the response vs. spot diameter curves for the retinal ganglion cells were found by straightforward spatial integration of Eq. (6).

To obtain analogous mathematical expressions for the average relay-cell response $\overline{R_r(\mathbf{r}; d)}$ in [12], the expression for the response function for the retinal ganglion cells was combined with knowledge about the pattern of functional neuronal couplings in dLGN (reviewed in [12]). Relay cells receive excitatory input from a single or a few retinal ganglion cells (see [3] and references therein). They also receive feedforward inhibition from intrageniculate interneurons which in turn receive excitation from a few retinal ganglion cells [2,7]. In addition there are feedback inputs from the perigeniculate nucleus (PGN) and cortex, as well as modulatory inputs from the brain stem reticular formation. In (3) a simplified neuronal circuit involving only the feedforward contributions was considered. We further (i) assumed that the average response for the relay cell was a weighted sum over the averaged ganglion-cell responses including both feedforward excitation and indirect feedforward inhibition (via intrageniculate interneurons), and (ii) neglected the temporal delay in transporting the signal from ganglion to relay cells. The latter approximation is supported by the fact that the axonal and synaptic time delays are significantly shorter than the duration of the spot stimulus in the experiments in [11].

3. Conclusion

In the derivation in [3] of the mathematical formulas for the time-averaged responses of retinal ganglion cells and geniculate relay cells to circular spot-stimuli, our starting point was a purely spatial receptive-field function for retinal ganglion cells (difference-of-Gaussians) combined with knowledge about the geniculate circuitry. Here we have derived mathematical relations between the spatiotemporal impulse response function measured using drifting gratings or white noise stimuli, and these spatial receptive-field functions. The derivation does not invoke the approximation of assuming spatiotemporal separability for the retinal ganglion cells. The derived relations are useful when comparing experimental data from different kinds of visual stimuli (circular spot, drifting gratings, white noise) on the same neuron. When such experimental data are available, the relations make it possible to increase the

constraints on proposed mathematical models describing the receptive-field structure of neurons in the dLGN.

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