Extended difference-of-Gaussians model incorporating cortical feedback for relay cells in the lateral geniculate nucleus of cat

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Abstract A striking feature of the organization of the early visual pathway is the significant feedback from primary visual cortex to cells in the dorsal lateral geniculate nucleus (LGN). Despite numerous experimental and modeling studies, the functional role for this feedback remains elusive. We present a new firing-rate-based model for LGN relay cells in cat, explicitly accounting for thalamocortical loop effects. The established DOG model, here assumed to account for the spatial aspects of the feedforward processing of visual stimuli, is extended to incorporate the influence of thalamocortical loops including a full set of orientation-selective cortical cell populations. Assuming a phase-reversed push-pull arrangement of ON and OFF cortical feedback as seen experimentally, this extended DOG (eDOG) model exhibits linear firing properties despite non-linear firing characteristics of the corticothalamic cells. The spatiotemporal receptive field of the eDOG model has a simple algebraic structure in Fourier space, while the real-space receptive field, as well as responses to visual stimuli, are found by evaluation of an integral. As an example application we use the eDOG model to study effects of cortical feedback on responses to flashing circular spots and patch-grating stimuli and find

that the eDOG model can qualitatively account for experimental findings.

Keywords Relay cell · Thalamocortical · Difference-of-Gaussians · Feedback

Introduction

A striking feature of the early visual pathway is the significant feedback from primary visual cortex to cells in the dorsal lateral geniculate nucleus (LGN). This cortical feedback has been shown to switch LGN relay cells from burst to tonic firing modes (McCormick and von Krosigk 1992; Godwin et al. 1996) and to modify the response properties of LGN cells to visual stimuli both in cat (Geisert et al. 1981; Vidyasagar and Urbas 1982; Murphy and Sillito 1987; Sillito et al. 1993, 1994; Cudeiro and Sillito 1996; Wörgötter et al. 1998; Wang et al. 2006; Andolina et al. 2007) and monkey (Marrocco et al. 1982; McClurkin and Marrocco 1984; McClurkin et al. 1994; Marrocco et al. 1996). These studies reported both enhanced and reduced responses of LGN neurons due to cortical feedback, and the identification of a particular functional role of this feedback has been difficult (Briggs and Usrey 2008, 2011). Cortical feedback has been shown to affect the length tuning of relay-cell responses (Murphy and Sillito 1987) and the response to patch-grating stimuli (Sillito et al. 1993; Cudeiro and Sillito 1996; Sillito and Jones 2002).

Relay cells receive synaptic inputs from a variety of sources (Sherman and Guillery 2001): excitatory input from retinal ganglion cells, feedforward inhibition from intrageniculate interneurons, inhibitory feedback from the thalamic reticular nucleus (TRN) and excitatory feedback

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from the striate cortex. Intrageniculate interneurons and TRN cells also receive feedback from cortex. When trying to decipher the properties of such a complex neural network, mathematical modeling is an essential tool, and a few mathematical models have been constructed to elucidate effects of cortical feedback on LGN neurons. They have focused on the effect of cortical feedback on visual latency (Köhn and Wörgötter 1996), synchronization of thalamocortical oscillations (Destexhe et al. 1998; Destexhe 2000; Mayer et al. 2007), temporal structure of spike trains (Wörgötter et al. 1998), synchronization of LGN-cell firing (Kirkland and Gerstein 1998; Kirkland et al. 2000), object segmentation based on motion cues (Hillenbrand and van Hemmen 2000), LGN responses to bipartite drifting grating stimuli (Hayot and Tranchina 2001), and on LGN impulse responses (Yousif and Denham 2007). These modeling efforts have typically been based on grids of neurons representing the different populations in the early visual pathway (retinal, LGN, TRN, and cortical cells), and results for the question at hand have been found by numerical simulations.

In this article we present a new firing-rate-based model of spatiotemporal LGN relay-cell responses to visual stimuli incorporating cortical feedback. In this *extended DOG model (eDOG)* the feedforward response is modeled by means of the standard difference-of-Gaussians (DOG) model (Rodieck 1965), and the corticothalamic feedback is assumed to have a phase-reversed push-pull organization (Wang et al. 2006): e.g., inhibitory feedback influence from a cortical ON-cell onto an LGN cell is accompanied by an excitatory feedback influence from a cortical OFF cell. While the resulting model has a more complicated mathematical structure than the DOG model, it is still linear. This means that responses to arbitrary visual stimuli can be calculated by evaluating integrals, though numerical evaluation is generally required. In the eDOG model, characteristics of cortical feedback such as strength, spatial spread and temporal properties are parameterized in a straightforward manner, and possible effects on LGN cells from cortical feedback can be studied more easily—both conceptually and methodologically—than with extensive numerical simulations of networks of neurons.

In section “[Impulse response and receptive field](#)” we introduce impulse-response functions and receptive fields. In section “[Receptive-field models incorporating phase-reversed push-pull cortical feedback](#)” a general expression for the linear response of relay cells incorporating cortical feedback from a full set of orientation-selective cortical populations is derived, while the eDOG model is presented in section “[Extended difference-of-Gaussians model](#)”. An example application is given in section “[Example application: patch-grating stimuli](#)” where we use the eDOG model to describe the effects of cortical feedback on

responses to flashing circular spots and patch-grating stimuli and compare with experimental findings (Sillito et al. 1993; Cudeiro and Sillito 1996; Sillito and Jones 2002). We discuss our findings in the final section.

Preliminary accounts of some of the results presented here have been presented in abstract form previously (Einevoll and Plesser 2003).

Impulse response and receptive field

Impulse-response functions

For a cell in the early visual pathway located at position $\mathbf{r}$ in the visual field, the response, i.e., the firing rate, can be written as

$$R(\mathbf{r}, t) = \int_{\tau} \iint_{\mathbf{r}_0} G(\mathbf{r} - \mathbf{r}_0, \tau) s(\mathbf{r}_0, t - \tau) d^2 \mathbf{r}_0 d\tau, \quad (1)$$

if one assumes (i) linearity, (ii) time invariance, and (iii) local spatial homogeneity. Here $G(\mathbf{r}, \tau)$ is the spatiotemporal *impulse-response function* (Heeger 1991). In Eq. 1 $s(\mathbf{r}, t)$ represents the visual stimulus presented at position $\mathbf{r} = (x, y)$ at time t . The spatial integral over $\mathbf{r}_0$ goes over all two-dimensional space. For mathematical convenience we have chosen the temporal integration to go from $\tau = -\infty$ to ∞ . From causality it follows that $G(\mathbf{r}, \tau < 0) = 0$, so the lower integration boundary for τ could also be set to zero.

The integral in Eq. 1 is a *convolution* between the stimulus and the impulse-response function, i.e.,

$$R(\mathbf{r}, t) = G(\mathbf{r}, t) * s(\mathbf{r}, t). \quad (2)$$

From the theory of Fourier transforms it follows that the integral in Eq. 1 can be reformulated as an integral over temporal and spatial frequencies (Bracewell 1986),

$$R(\mathbf{r}, t) = \frac{1}{(2\pi)^3} \int_{\omega} \iint_{\mathbf{k}} e^{i(\mathbf{k}\mathbf{r} - \omega t)} \tilde{G}(\mathbf{k}, \omega) \tilde{s}(\mathbf{k}, \omega) d^2 \mathbf{k} d\omega. \quad (3)$$

Here $\tilde{G}(\mathbf{k}, \omega)$ and $\tilde{s}(\mathbf{k}, \omega)$ are the complex Fourier transforms of the impulse-response functions G and stimulus s , respectively. The complex Fourier transform we use, and its inverse, are given by

$$\tilde{y}(\mathbf{k}, \omega) = \int_t \iint_{\mathbf{r}} e^{-i(\mathbf{k}\mathbf{r} - \omega t)} y(\mathbf{r}, t) d^2 \mathbf{r} dt, \quad (4)$$

$$y(\mathbf{r}, t) = \frac{1}{(2\pi)^3} \int_{\omega} \iint_{\mathbf{k}} e^{i(\mathbf{k}\mathbf{r} - \omega t)} \tilde{y}(\mathbf{k}, \omega) d^2 \mathbf{k} d\omega. \quad (5)$$

The physiological interpretation of the real-space impulse-response function $G(\mathbf{r}, t)$ is that it corresponds to the

response to briefly flicking test spots positioned at different positions $\mathbf{r}_{\text{test}}$ which are both very small ($\sim \delta(\mathbf{r} - \mathbf{r}_{\text{test}})$) and narrow in time ($\sim \delta(t - t_{\text{test}})$). Mathematically this corresponds to a stimulus function given by $s(\mathbf{r}, t) = L_{\text{test}} \delta(\mathbf{r} - \mathbf{r}_{\text{test}}) \delta(t - t_{\text{test}})$ where L_{test} is the luminance of the test spot. Inserting into Eq. 1 and using the sifting property of the δ -function (Bracewell 1986), we obtain the response $R(\mathbf{r}, t) = L_{\text{test}} G(\mathbf{r} - \mathbf{r}_{\text{test}}, t - t_{\text{test}})$. The impulse-response function is thus in principle given by the measured firing rates of neurons at various positions $\mathbf{r}$ and times t following a δ -pulse at position $\mathbf{r}_{\text{test}}$ at time zero. In practice it is easier to keep the electrode position fixed and measure from a particular cell and instead move the test spot. Therefore the *receptive-field function* (or *point-spread function*) is often considered instead. The impulse-response function and the receptive-field function are intimately related: the receptive-field function is the impulse-response function with $\mathbf{r}$ replaced with $-\mathbf{r}$ and t with $-t$ in the spatial and temporal arguments, respectively (Heeger 1991).

The Fourier-transformed impulse-response $\tilde{G}(\mathbf{k}, \omega)$ also has a clear physiological interpretation. In Eq. 3, the response to the stimulus s is essentially written as an infinite sum (integral) over contributions from drifting sinusoidal gratings specified by $\mathbf{k}$ and ω . Here $\mathbf{k}$ is the so called *wave vector* which is related to the more familiar *spatial frequency* ν via $|\mathbf{k}| = 2\pi\nu$. Correspondingly the *angular frequency* ω is related to the *temporal frequency* f via $\omega = 2\pi f$. The weight and phase of each different grating required to represent the stimulus s are given by $\tilde{s}(\mathbf{k}, \omega)$, while $\tilde{G}(\mathbf{k}, \omega)$ gives the response to a sinusoidal drifting grating specified by $\mathbf{k}$ and ω .

Example impulse-response function: DOG model

The choice of model for the receptive field can now be incorporated into the expression for the impulse-response function $G(\mathbf{r}, t)$. For retinal ganglion cells and relay cells in LGN a simple and common choice is to assume the impulse-response function to be spatiotemporally separable ($G(\mathbf{r}, t) = f(\mathbf{r})h(t)$), and to model the spatial part with the difference-of-Gaussians (DOG) model (Rodieck 1965), i.e.,

$$G(\mathbf{r}, t) = f_{\text{DOG}}(\mathbf{r})h(t) = \left(\frac{A_1}{\pi a_1^2} e^{-r^2/a_1^2} - \frac{A_2}{\pi a_2^2} e^{-r^2/a_2^2} \right) h(t), \quad (6)$$

with the accompanying Fourier transform

$$\tilde{G}(\mathbf{k}, \omega) = \tilde{f}_{\text{DOG}}(\mathbf{k})\tilde{h}(\omega) = \left(A_1 e^{-k^2 a_1^2/4} - A_2 e^{-k^2 a_2^2/4} \right) \tilde{h}(\omega). \quad (7)$$

The DOG model is an example of a filter model or *descriptive* model (Dayan and Abbott 2001) where the

main goal is to account mathematically for experimental data (see, e.g., Jing et al. (2010)). *Mechanistic* models, in contrast, aim to explain experimental data in terms of the underlying neurons and neuronal circuitry (see, e.g., Wang and Zhang 2007; Saglam et al. 2009; Liang et al. 2010).

General mechanistic receptive-field models

In Einevoll and Plesser (2002), we investigated a linear mechanistic model for the impulse-response function for cat relay cells taking both feedforward and feedback aspects of the geniculate circuit into account. Generally, the Fourier-transformed impulse response of geniculate relay cells has the form

$$\tilde{G}_r(\mathbf{k}, \omega) = \tilde{T}_{\text{rg}}(\mathbf{k}, \omega) \tilde{G}_g(\mathbf{k}, \omega) \quad (8)$$

where $\tilde{G}_g(\mathbf{k}, \omega)$ is the Fourier-transformed impulse-response function for retinal ganglion cells providing the feedforward input to the geniculate cells. The *geniculate transfer function* $\tilde{T}_{\text{rg}}(\mathbf{k}, \omega)$ describes the transfer ratio for each sinusoidal grating (specified by $\mathbf{k}$ and ω).

In Einevoll and Plesser (2002) we further derived a general expression for $\tilde{T}_{\text{rg}}(\mathbf{k}, \omega)$ in terms of properties of the neurons and the neuronal connections in the LGN circuit as reviewed in Sherman and Guillery (2001): The relay cells receive excitatory input from retinal ganglion cells as well as feedforward inhibition from intrageniculate interneurons both via dendro-dendritic structures (triads) and presumably axonal output. The interneurons in turn receive excitation from a few retinal ganglion cells. In addition the relay cells receive inhibitory feedback from the thalamic reticular nucleus (TRN) and excitatory feedback from the striate cortex. The intrageniculate interneurons and TRN cells also receive excitatory feedback from cortex. These connections were all incorporated in a general mathematical expression for $\tilde{T}_{\text{rg}}(\mathbf{k}, \omega)$. In combination with a model expression for the (Fourier-transformed) impulse-response function for the retinal ganglion cells $\tilde{G}_g(\mathbf{k}, \omega)$, such expressions for $\tilde{T}_{\text{rg}}(\mathbf{k}, \omega)$ can be used to derive mechanistic expressions for the relay cell impulse response $\tilde{G}_r(\mathbf{k}, \omega)$, cf Eq. 8.

Receptive-field models incorporating phase-reversed push-pull cortical feedback

General expression with several cortical populations providing feedback

The main focus of this paper is the derivation of receptive-field models for cat relay cells (i.e., impulse-response functions G_r) which explicitly account for feedback effects

from a set of orientation-selective cortical populations under the following assumptions: We consider both the four feedforward pathways (X/Y, ON/OFF) and the X and Y cortical feedback pathways to be decoupled (Briggs and Usrey 2009, 2011), while we take the cortical ON and OFF feedback channels to be coupled (Wang et al. 2006).

The corticogeniculate feedback comes from orientation-tuned cells in layer 6 in cortex. We thus consider a set of N orientation-selective cortical populations c_n , for $n = 1, \dots, N$. Each population c_n responds preferably to stimuli (bars, gratings) with orientation θ_n . We assume in our model that (i) all cortical populations receive direct input from relay cells, (ii) provide direct excitatory feedback or indirect inhibitory feedback (via intrageniculate interneurons or TRN neurons) to the relay cells in LGN, and (iii) are mutually uncoupled. The full model circuit is illustrated in Fig. 1; only two cortical populations are drawn even though an arbitrary number of cortical populations is considered in the mathematical analysis.

To be specific, we focus on the ON pathway in the derivation below, but a completely analogous derivation can be done for the OFF pathway. The firing-rate responses of the various ON cells in the early visual pathway are assumed to be governed by the following set of equations (Einevoll and Plesser 2002; Norheim et al. 2011):

$$R_g^{\text{ON}}(\mathbf{r}, t) = G_g^{\text{ON}}(\mathbf{r}, t) * s(\mathbf{r}, t) \quad (9)$$

$$\begin{aligned} R_r^{\text{ON}}(\mathbf{r}, t) = & K_{rg}^{\text{ON}}(\mathbf{r}, t) * R_g^{\text{ON}}(\mathbf{r}, t) \\ & + K_{ri}^{\text{ON}}(\mathbf{r}, t) * R_i^{\text{ON}}(\mathbf{r}, t) \\ & + \sum_{n=1}^N K_{rc_n}^{\text{ON}}(\mathbf{r}, t) * R_{c_n}^{\text{ON}}(\mathbf{r}, t) \\ & + \sum_{n=1}^N K_{rc_n}^{\text{X}}(\mathbf{r}, t) * R_{c_n}^{\text{OFF}}(\mathbf{r}, t) \end{aligned} \quad (10)$$

$$R_{c_n}^{\text{ON}}(\mathbf{r}, t) = F_c^{\text{ON}}\left(K_{c_r}^{\text{ON}}(\mathbf{r}, t) * R_r^{\text{ON}}(\mathbf{r}, t)\right), \quad n = 1, \dots, N \quad (11)$$

$$R_{c_n}^{\text{OFF}}(\mathbf{r}, t) = F_c^{\text{OFF}}\left(K_{c_r}^{\text{OFF}}(\mathbf{r}, t) * R_r^{\text{OFF}}(\mathbf{r}, t)\right), \quad n = 1, \dots, N. \quad (12)$$

R_g , R_r , and R_{c_n} represent the responses of retinal ganglion cells, relay cells, interneurons, and cortical cells, respectively. $s(\mathbf{r}, t)$ represents the visual stimulus, i.e., s is zero in the background state. $K_{jk}^{\text{ON}}(j, k: g, r, c_n)$ represents the linear coupling from ON neurons of type k onto ON neurons of type j . The real-space functions $K_{jk}^{\text{ON}}(\mathbf{r}, \tau)$ are the spatiotemporal coupling functions which tell how the firing rate of a cell of type k at position $\mathbf{r}_0$ and time zero affects the firing of a cell of type j at position $\mathbf{r}$ a time τ later. The coupling function K_{rg}^{ON} from retinal ganglion cells to relay cells, e.g., will thus depend both on the ganglion-cell

Fig. 1 **a** Schematic view of present model of the geniculate circuit for the ON X pathway in cat comprising ON retinal ganglion cells (g), ON geniculate relay cells (r), and cells from several cortical cell populations, both ON (c_n) and OFF (c_n^{OFF}). The feedback cross-connections (from OFF to ON) are shown as *dashed lines*. For the sake of clarity, only two populations ($n = 1, 2$) are shown, even though an arbitrary number of populations N are considered in our mathematical analysis, and input to OFF is not shown. The cortical OFF cells are driven by relay OFF cells not depicted in the figure. **b** Illustration of the mathematical model of the geniculate circuit. $R_g^{\text{ON}}, R_r^{\text{ON}}, R_i^{\text{ON}}, R_{c_n}^{\text{ON}}, R_{c_n}^{\text{OFF}}$ ($n = 1, 2$) represent the responses of ON retinal ganglion, ON relay, ON cortical, and OFF cortical cells respectively. K_{jk} ($j, k = g, i, r, c_n$) represents the coupling from ON neurons of type k onto ON neurons of type j . $K_{rc_n}^{\text{X}}$ represents the cross-connection in the cortical feedback (*dashed arrows*), and K_{rig} represents the indirect feedforward inhibition via intrageniculate interneurons (*dotted arrow*)

synapses on relay cells and how the firing of action potentials in relay cells is governed by synaptic inputs. The coupling function K_{rig}^{ON} represents the indirect feedforward inhibition (via intrageniculate interneurons) from ON ganglion cells onto ON relay cells.

In the above equation set $K_{rc_n}^{\text{X}}$ represents the cross-coupling feedback from cortical OFF cells onto relay ON cells.

Further, $K_{c_n r}^{\text{OFF}}$ represents the coupling from the relay OFF cells onto these cortical OFF cells. Also, $F_c^{\text{ON}}(x)$ and $F_c^{\text{OFF}}(x)$ are firing-rate functions converting the input onto the cortical ON and OFF cells, respectively, to firing rates (Norheim et al. 2011).

In the following we only model the *time-dependent* part of the relay-cell and cortical responses, i.e., $R_r(\mathbf{r}, t)$ and $R_{c_n}(\mathbf{r}, t)$ correspond to true firing rates minus the background firing rates. Thus the stimulus function $s(\mathbf{r}, t)$ represents the variation of stimulus luminance around the background luminance.

Assumption of phase-reversed push-pull cortical feedback

We now make the following additional assumptions:

1. The firing-rate functions of the cortical cells are assumed to be half-wave rectified functions $F_c^{\text{ON}}(x) = F_c^{\text{OFF}}(x) = [x]_+$ (Troyer et al. 1998; Dayan and Abbott 2001; Norheim et al. 2011), so that Eqs. 11 and 12 become

$$R_{c_n}^{\text{ON}}(\mathbf{r}, t) = [K_{c_n r}^{\text{ON}}(\mathbf{r}, t) * R_r^{\text{ON}}(\mathbf{r}, t)]_+, \quad (13)$$

$$R_{c_n}^{\text{OFF}}(\mathbf{r}, t) = [-K_{c_n r}^{\text{OFF}}(\mathbf{r}, t) * R_r^{\text{OFF}}(\mathbf{r}, t)]_+, \quad (14)$$

with $n = 1, \dots, N$. This assumption can be well fulfilled if the inputs to the cortical cells are close to zero in the background state.

2. The OFF pathway is not modeled explicitly. Instead we take the input to the half-wave rectifying functions for the cortical OFF cell to be exactly the negative of the input to the ON half-wave rectifying function (Troyer et al. 2002; Norheim et al. 2011):

$$R_{c_n}^{\text{OFF}}(\mathbf{r}, t) = [-K_{c_n r}^{\text{ON}}(\mathbf{r}, t) * R_r^{\text{ON}}(\mathbf{r}, t)]_+. \quad (15)$$

3. The feedback cross-connection (OFF to ON) is phase-reversed compared to the “same-sign” feedback, i.e.,

$$K_{rc_n}^{\text{X}}(\mathbf{r}, t) = -K_{rc_n}^{\text{ON}}(\mathbf{r}, t). \quad (16)$$

The assumption of phase-reversal, i.e., the negative sign, is supported by the experimental study of Wang et al. (2006). As the inhibitory feedback connections will go through one more synapse than the excitatory feedback connections, one may expect that the inhibitory feedback by necessity will be delayed compared to the excitatory feedback, at odds with the assumption inherent in Eq. 16 of identical temporal kernels. However, a study of Ahlsén et al. (1982) found the difference in latency for IPSPs and EPSPs arriving onto relay cells following electrical stimulation of the corticogeniculate feedback pathway, to be less than a

millisecond. This suggests that the delay due to the extra synapse may be on the order of one millisecond and thus small compared to the overall time it takes the signal to pass around the thalamocortical loop and thus also small compared to the overall time constant in the final temporal loop kernels derived below.

With these three assumptions, and use of the mathematical identity $[x]_+ - [-x]_+ = x$, we then find

$$R_r^{\text{ON}}(\mathbf{r}, t) = K_{rg}^{\text{ON}}(\mathbf{r}, t) * R_g^{\text{ON}}(\mathbf{r}, t) + K_{rg}^{\text{ON}}(\mathbf{r}, t) * R_g^{\text{ON}}(\mathbf{r}, t) + \sum_{n=1}^N K_{rc_n}^{\text{ON}}(\mathbf{r}, t) * K_{c_n r}^{\text{ON}}(\mathbf{r}, t) * R_r^{\text{ON}}(\mathbf{r}, t). \quad (17)$$

This expression for $R_r^{\text{ON}}(\mathbf{r}, t)$ is completely linear, and the Fourier-transformed impulse response of ON relay cells, $\tilde{G}_r^{\text{ON}}(\mathbf{k}, \omega)$, can now be found using the approach of Einevoll and Plesser (2002):

$$\begin{aligned} \tilde{G}_r^{\text{ON}}(\mathbf{k}, \omega) &= \tilde{T}_{rg}^{\text{ON}}(\mathbf{k}, \omega) \tilde{G}_g^{\text{ON}}(\mathbf{k}, \omega) \\ &= \frac{\tilde{K}_{rg}^{\text{ON}}(\mathbf{k}, \omega) + \tilde{K}_{rg}^{\text{ON}}(\mathbf{k}, \omega)}{1 - \sum_{n=1}^N \tilde{K}_{rc_n}^{\text{ON}}(\mathbf{k}, \omega) \tilde{K}_{c_n r}^{\text{ON}}(\mathbf{k}, \omega)} \tilde{G}_g(\mathbf{k}, \omega). \end{aligned} \quad (18)$$

Even though this expression for the geniculate impulse response is quite involved, it has a simple structure. The direct feedforward excitation and the indirect feedforward inhibition via interneurons are represented by the first and second terms in the numerator, respectively. The feedback effects are accounted for in the denominator. Here the sum in the second term represents the effects of the excitatory feedback loop between relay cells and the N cortical populations (relay cell $\rightarrow$ cortex $\rightarrow$ relay cell).

Each of the terms in the denominator (of the type $\tilde{K}_{rc_n}^{\text{ON}}(\mathbf{k}, \omega) \tilde{K}_{c_n r}^{\text{ON}}(\mathbf{k}, \omega)$) will *not* be circularly symmetric. Rather, their dependence on spatial wave vector $\mathbf{k}$ will reflect the orientation-preference of the cortical cells in the particular population n and the synaptic footprint of the corticogeniculate feedback to LGN from this particular population. Equation 12 gives an expression for the response of the cortical orientation-selective cell populations (c_n). The coupling kernel $K_{c_n r}^{\text{ON}}(\mathbf{r}, t)$ describes the transformation from the (roughly) circular receptive fields of relay cells to the elongated receptive fields of cortical cells (Hubel and Wiesel 1962); it is thus anisotropic. Likewise, there is evidence for an anisotropic organization of the corticothalamic synaptic input to LGN cells (Murphy and Sillito 1996; Murphy et al. 1999) which will be reflected in anisotropic corticogeniculate coupling kernels $K_{rc_n}^{\text{ON}}(\mathbf{r}, t)$.

However, as seen in the denominator of Eq. 18, the total effect of cortical feedback on the response of LGN relay cells is a sum over contributions from *all* N cortical

orientation-selective populations. Since the cortical populations cover all orientation angles, the net feedback effect is expected to be essentially isotropic, i.e., circularly symmetric. This is supported by experimental observations of cortical feedback effects on relay cells using bipartite grating stimuli (Sillito et al. 1993; Cudeiro and Sillito 1996). There, the feedback effects were found to be independent of the *absolute* orientation of the gratings.

Net effect of feedback from several cortical populations

We now go on to demonstrate that the net feedback effect on relay cells may effectively be circularly symmetric when all cortical populations are included. First, the coupling kernels involved in the thalamocortical loops ($K_{c_n r}^{\text{ON}}(\mathbf{r}, t)$, $K_{c_n r}^{\text{OFF}}(\mathbf{r}, t)$) are assumed to be spatiotemporally separable, i.e., $K^{\text{ON}}(\mathbf{r}, t) = f(\mathbf{r})h(t)$. Then the terms in the sum in the denominator of Eq. 18 will be of the form

$$\tilde{K}_{c_n r}^{\text{ON}}(\mathbf{k}, \omega) \tilde{K}_{c_n r}^{\text{OFF}}(\mathbf{k}, \omega) = \tilde{f}_{c_n r}(\mathbf{k}) \tilde{f}_{c_n r}(\mathbf{k}) \tilde{h}_{c_n r}(\omega) \tilde{h}_{c_n r}(\omega).$$

The spatial coupling kernel $f_{c_n r}(\mathbf{r})$ must have an elongated shape in order to assure the orientation-selectivity of the cortical population c_n . Likewise, an elongated shape of $f_{c_n r}(\mathbf{r})$ also qualitatively captures experimental findings regarding the anisotropic and topographic organization of the corticothalamic feedback (Murphy and Sillito 1996; Murphy et al. 1999).

In our model we assume that the spatial coupling for the loop is elongated and strongest at the the same position in the visual field, i.e., for $r = 0$. A simple mathematical choice is to model the spatial coupling for the excitatory loop involving cortical population c_n ($\tilde{f}_{c_n r}(\mathbf{k}) = \tilde{f}_{c_n}(\mathbf{k}) \tilde{f}_{c_n r}(\mathbf{k})$) as a an elliptic Gaussian, i.e.,

$$f_{c_n r}(\mathbf{r}) = \frac{C_{c_n r}}{\pi \sigma_l \sigma_n} e^{-(x \cos \theta_n + y \sin \theta_n)^2 / \sigma_l^2 - (y \cos \theta_n - x \sin \theta_n)^2 / \sigma_n^2}, \quad (19)$$

or, equivalently, in Fourier space,

$$\tilde{f}_{c_n r}(\mathbf{k}) = C_{c_n r} e^{-(k_x \cos \theta_n + k_y \sin \theta_n)^2 \sigma_l^2 / 4 - (k_y \cos \theta_n - k_x \sin \theta_n)^2 \sigma_n^2 / 4}. \quad (20)$$

Here σ_l and σ_n are the parameters determining the spatial widths of the loop kernel along its long and narrow axes, respectively ($\sigma_l > \sigma_n$), $C_{c_n r}$ is the loop coupling strength, and θ_n is the angle the long axis of the ellipse makes with the x -axis. Contour plots of an example spatial-loop kernel are shown in Fig. 2 (left panels). Here the coupling kernel is chosen to be significantly elongated, reflecting both the oriented relay-cell input to orientation-selective cortical cells and a possibly oriented feedback from cortex to LGN.

In Fig. 2 (right panels) we also show an example of a model input to the cortical cell, i.e., its “subthreshold” receptive field, for our simplified thalamocortical projection pattern. In Fourier space this spatial impulse-response function $\tilde{f}_{c_n}(\mathbf{k})$ is the product of the relay-cell response (modeled as a DOG, i.e., $\tilde{f}_{\text{DOG}}(\mathbf{k})$, cf. Fig. 2 (middle panels)) and an elliptical coupling function from relay cells to cortical cells $\tilde{f}_{c_n r}(\mathbf{k})$ of the form in Eq. 20. As seen in the figure, the real-space cortical receptive field $f_{c_n}(\mathbf{r})$ has an elongated shape characteristic for orientation-selective cells. This receptive-field also exhibits both ON and OFF subfields, but a mix of ON and OFF inputs from LGN (not included in our simplified model for $f_{c_n r}(\mathbf{r})$) would presumably give a more realistic simple-cell receptive field structure (Reid and Alonso 1995). In Fig. 2 the parameters of the DOG model are chosen so that the relay-cell receptive field has a center diameter of 0.8° , and the resulting model cortical receptive-field length is seen in the figure to be about 4° . These numbers are similar to the mean optimal summation sizes (0.9° and 3.6°) observed for LGN cells and visual cortical cells, respectively, in cat (Jones et al. 2000).

If the relay cell only received feedback from a single cortical population c_n , the feedback effect would clearly be orientation selective. However, the relay cell appears to receive inputs from all cortical populations (Sillito et al. 1993; Cudeiro and Sillito 1996). If we assume the temporal coupling kernels to be the same for all thalamocortical loops (i.e., $\tilde{h}_{c_n r}(\omega) \tilde{h}_{c_n r}(\omega) = \tilde{h}_{rc}(\omega) \tilde{h}_{cr}(\omega)$ for all c_n), the loop term in the denominator of Eq. 18 simplifies as follows:

$$\begin{aligned} \sum_{n=1}^N \tilde{K}_{c_n r}^{\text{ON}}(\mathbf{k}, \omega) \tilde{K}_{c_n r}^{\text{OFF}}(\mathbf{k}, \omega) \\ = \sum_{n=1}^N \tilde{f}_{c_n r}(\mathbf{k}) \tilde{f}_{c_n r}(\mathbf{k}) \tilde{h}_{rc}(\omega) \tilde{h}_{cr}(\omega) = \tilde{f}_{rc}^N(\mathbf{k}) \tilde{h}_{fb}(\omega), \end{aligned} \quad (21)$$

where we have introduced the temporal feedback kernel $\tilde{h}_{fb}(\omega) \equiv \tilde{h}_{rc}(\omega) \tilde{h}_{cr}(\omega)$ and the summed spatial kernel

$$\tilde{f}_{rc}^N(\mathbf{k}) = \sum_{n=1}^N C_{c_n r} e^{-(k_x \cos \theta_n + k_y \sin \theta_n)^2 \sigma_l^2 / 4 - (k_y \cos \theta_n - k_x \sin \theta_n)^2 \sigma_n^2 / 4}. \quad (22)$$

There is no *a priori* reason why one cortical orientation population should have stronger feedback connections than any other, and we thus assume the loop weight $C_{c_n r}$ to be the same for all populations c_n . If so, the summed spatial kernel $\tilde{f}_{rc}^N(\mathbf{k})$ will approach a circularly symmetric form when the number of cortical populations N increases and the preferred angles θ_n of these orientation-selective cortical populations are assumed to be equidistant in

Fig. 2 Contour plots illustrating spatial part of loop kernel (a, b) and model impulse-response functions (c, d) for relay-cell (DOG model) and impulse-response “input” to cortical cell (e, f). Functions are shown in Fourier-space in the left column (a, c, e) and in real space in the right column (b, d, f). (a) Fourier-space loop kernel for cortical feedback loop modeled as a Gaussian ellipse, $\tilde{f}_{rc,r}(\mathbf{k})$ in Eq. 20 ($\theta_n = \pi/4$, $\sigma_n = 0.1$ deg, $\sigma_l = 1.4$ deg, $C_{rc,r} = 1$). (b) $f_{rc,r}(\mathbf{r})$ Eq. 19 corresponding to $\tilde{f}_{rc,r}(\mathbf{k})$. (c) Fourier-space relay-cell DOG model $\tilde{f}_{DOG}(\mathbf{k})$ from Eq. 7 ($A_1 = 1$, $a_1 = 0.25$ deg, $A_2 = 0.85$, and $a_2 = 0.83$ deg). (d) $f_{DOG}(\mathbf{r})$ (from Eq. 6) corresponding to $\tilde{f}_{DOG}(\mathbf{k})$. (e) Fourier-transformed input to cortical cell $\tilde{f}_c(\mathbf{k}) = \tilde{f}_{c,r}(\mathbf{k})\tilde{f}_{DOG}(\mathbf{k})$. The spatial parameters for the feedforward coupling kernel $\tilde{f}_{c,r}(\mathbf{k})$ are chosen a factor $\sqrt{2}$ smaller than for the loop kernel $\tilde{f}_{rc,r}(\mathbf{k})$, i.e., $\sigma_n = 0.07$ deg, $\sigma_l = 0.99$ deg, while $C_{c,r} = 1$. With the same spatial parameters for a similarly modeled feedforward coupling kernel $\tilde{f}_{rc,n}(\mathbf{k})$, one would get the loop kernel $\tilde{f}_{rc,n}(\mathbf{k})$ in panel (a). (f) $f_c(\mathbf{r})$ found by an inverse Fourier-transform of $\tilde{f}_c(\mathbf{k})$. In panels (a), (b), (c) and (e) white corresponds to the zero level; in panels (d) and (f) white corresponds to a negative value to illustrate the negative lobes of the LGN (DOG) receptive fields and input to cortical cells (subthreshold receptive fields)

angular space. This is illustrated in Fig. 3 for our model with elliptical Gaussian coupling kernels distinguished only by their orientation θ_n . As seen in the figure, a sum over eight populations gives essentially a circularly symmetric spatial feedback-loop kernel.

For our model we can in fact find a closed-form expression for the net summed coupling kernel from N angular equidistant and equally weighted populations in the limit $N \rightarrow \infty$. In this “continuous” limit we have with $\theta_n = (n - 1)\pi/N$

$$\lim_{N \rightarrow \infty} \frac{1}{N} \sum_{n=1}^N e^{-(k_x \cos \theta_n + k_y \sin \theta_n)^2 \sigma_l^2 / 4 - (k_y \cos \theta_n - k_x \sin \theta_n)^2 \sigma_n^2 / 4} \\ = \frac{1}{\pi} \int_0^\pi e^{-(k_x \cos \theta + k_y \sin \theta)^2 \sigma_l^2 / 4 - (k_y \cos \theta - k_x \sin \theta)^2 \sigma_n^2 / 4} d\theta. \quad (23)$$

This angular integral can be solved analytically to give the net spatial feedback kernel for this continuous model

Fig. 3 Example contour plots of the summed spatial loop kernel including several excitatory cortical feedback loops, Eq. 22, for different numbers of cortical populations N . The Gaussian width parameters are chosen as in Fig. 2, i.e., $\sigma_n = 0.1$ deg, $\sigma_l = 1.4$ deg. Here we use $C_{rcnr} = 1/N$ which assures the same overall coupling strength (summed over all k -space) in the set of examples. (a) $N = 1$, (b) $N = 2$, (c) $N = 3$, (d) $N = 4$, (e) $N = 8$, (f) $N = \infty$, Eq. 24

$$\tilde{f}_{rcr}^{\infty}(\mathbf{k}) = \tilde{f}_{rcr}^{\infty}(k) = C_{rcr}^{\infty} e^{-k^2(\sigma_l^2 + \sigma_n^2)/8} I_0(k^2(\sigma_l^2 - \sigma_n^2)/8), \quad (24)$$

where $I_0(x)$ is the zeroth-order modified Bessel function (Abramowitz and Stegun 1965), $k^2 = k_x^2 + k_y^2$, and we have introduced $C_{rcr}^{\infty} = \lim_{N \rightarrow \infty} N C_{rcnr}$, implicitly assuming that the loop weight C_{rcnr} for each cortical population is inversely proportional to N .

An example of $\tilde{f}_{rcr}^{\infty}(k)$ in Eq. 24 and the real-space equivalent $\tilde{f}_{rcr}^{\infty}(r)$ (found by an inverse Fourier transform, cf. Eq. 5) is shown in Fig. 4. For small k , the modified Bessel function

$I_0(k^2(\sigma_l^2 - \sigma_n^2)/8)$ is close to one, and the exponential prefactor $C_{rcr}^{\infty} \exp(-k^2(\sigma_l^2 + \sigma_n^2)/8)$ dominates. For large k (and $\sigma_l \neq \sigma_n$) we can use the asymptotic expansion $I_0(x) \sim \exp(x)/\sqrt{2\pi x}$ (Abramowitz and Stegun 1965) to obtain

$$\tilde{f}_{rcr}^{\infty}(k) \sim C_{rcr}^{\infty} \frac{2e^{-k^2\sigma_n^2/4}}{\sqrt{\pi k^2(\sigma_l^2 - \sigma_n^2)}}. \quad (25)$$

As seen in Fig. 4 the two approximate, but more mathematically transparent, expressions valid in the small- k and large- k regimes, respectively, together describe the function $\tilde{f}_{rcr}^{\infty}(k)$ in Eq. 24 quite well.

Fig. 4 **a** Example plot of net spatial loop kernel in k -space in the limit of infinitely many orientation-selective cortical populations ($N \rightarrow \infty$), i.e., $\tilde{f}_{\text{rcr}}^{\infty}(k)$ in Eq. 24 (solid line). The dashed line corresponds to the exponential prefactor $C_{\text{rcr}}^{\infty} \exp(-k^2(\sigma_l^2 + \sigma_n^2)/8)$ of Eq. 24, while the dotted line shows the asymptotic expansion of Eq. 25, valid for large k . Gaussian width parameters are as in Fig. 2 ($\sigma_n = 0.1$ deg, $\sigma_l = 1.4$ deg, $C_{\text{rcr}}^{\infty} = 1$). **b** Real-space version of coupling kernel in left panel, $\tilde{f}_{\text{rcr}}^{\infty}(r)$, found by a numerical inverse Fourier transform of $\tilde{f}_{\text{rcr}}^{\infty}(k)$ (solid line). The dashed and dotted lines show the coupling kernel $f_{\text{rcr}}(r)$ in Eq. 19 along the narrow and long axes, respectively (with $C_{\text{rcr}} = 1$)

The main point of the mathematical analysis above is not the particular functional form of the summed “continuous” loop kernel $\tilde{f}_{\text{rcr}}^{\infty}(k)$, which is based on modeling the loop kernel for each cortical population as an elliptical Gaussian. Other loop kernels incorporating, for example, mixed ON/OFF input from LGN to cortical cells (Hayot and Tranchina 2001) would have given different summed “continuous” loop kernels. The crucial point—that this summed loop kernel is independent of the direction of $\mathbf{k}$ and only depends on the magnitude $k = |\mathbf{k}|$ —however, only relies on the summation of identical contributions from sufficiently many angularly equidistant cortical populations covering all orientations. The net effect of the cortical feedback can thus be incorporated in the model via a single (and presently unspecified) term $\tilde{f}_{\text{fb}}(k)\tilde{h}_{\text{fb}}(\omega)$ regardless of the detailed form of the loop kernel for individual cortical populations. The Fourier-transformed impulse response of relay cells $\tilde{G}_{\text{r}}(\mathbf{k}, \omega)$ in Eq. 18 can then be rewritten as,

$$\begin{aligned} \tilde{G}_{\text{r}}(\mathbf{k}, \omega) &= \tilde{T}_{\text{rg}}(\mathbf{k}, \omega) \tilde{G}_{\text{g}}(\mathbf{k}, \omega) \\ &= \frac{\tilde{K}_{\text{rg}}(\mathbf{k}, \omega) + \tilde{K}_{\text{rig}}(\mathbf{k}, \omega)}{1 - \tilde{f}_{\text{fb}}(k)\tilde{h}_{\text{fb}}(\omega)} \tilde{G}_{\text{g}}(\mathbf{k}, \omega), \end{aligned} \quad (26)$$

corresponding to the expression assuming a single (hypothetical) cortical population with circularly-symmetric and linear response properties (Einevoll and Plesser 2002).

Note that the assumption of lumping the feedback effect of all orientation-selective cortical populations into a single term without orientation selectivity does not hinge on the assumption of spatiotemporally separable thalamocortical coupling kernels (as long as the coupling kernels are identical except for an angular rotation).

Extended difference-of-Gaussians model

Eq. 26 only determines the overall mathematical structure for the mechanistic model for the relay-cell impulse-response function. To make a model one must make specific choices for the Fourier-transformed retinal ganglion cell impulse-response function $\tilde{G}_{\text{g}}(\mathbf{k}, \omega)$ and coupling kernels ($\tilde{K}(\mathbf{k}, \omega), \tilde{f}(k), \tilde{h}(\omega)$). These choices will in practice depend on the goal of the modeling. Here we will consider a simple model, which we call the *extended difference-of-Gaussians model* (eDOG), aimed at elucidating some salient features of effects of cortical feedback.

Spatiotemporal eDOG model

We first replace the numerator of Eq. 26, i.e., the feed-forward contribution, with the simple DOG model expression in Eq. 7,

$$\tilde{G}_{\text{DOG}}(k, \omega) = \tilde{f}_{\text{DOG}}(k)\tilde{h}_{\text{ff}}(\omega). \quad (27)$$

Here we have added the subscript “ff” for “feedforward” to the unspecified temporal function h . We have also removed the bold face on “ k ” to stress that the spatial DOG function only depends on the magnitude of the wave vector $\mathbf{k}$. Eq. 26 then simplifies to

$$\tilde{G}_{\text{r}}(k, \omega) = \tilde{T}_{\text{rg}}(k, \omega) \tilde{G}_{\text{g}}(k, \omega) = \frac{\tilde{f}_{\text{DOG}}(k)\tilde{h}_{\text{ff}}(\omega)}{1 - \tilde{f}_{\text{fb}}(k)\tilde{h}_{\text{fb}}(\omega)}. \quad (28)$$

A natural choice for modeling, e.g., the summed spatial loop kernel $\tilde{f}_{\text{fb}}(k)$, could be to use the derived loop-kernel function $\tilde{f}_{\text{rcr}}^{\infty}(k)$ in Eq. 24. However, this loop-kernel function was derived based on the somewhat arbitrary choice of using elliptical Gaussians to model elongated spatial loop kernels involving individual cortical populations. With other choices the result would be different. In lack of physiological observations aiding the specification, we therefore presently use the mathematically simpler circularly symmetric Gaussians (Einevoll and Plesser 2002),

$$\tilde{f}_{\text{fb}}(k) = Ce^{-k^2 c^2/4}. \quad (29)$$

Here the weight parameter C will be negative if the in-phase (i.e., ON to ON) cortical feedback is inhibitory and positive if this in-phase feedback is excitatory. The parameter c parameterize the spatial spread of the thalamocortical feedback loop; a large value of c would indicate that the thalamocortical loop is involved in more global information processing (Murphy and Sillito 1996).

A similarly simple model choice for the temporal coupling functions $h(t)$ could be the delayed exponential coupling kernel (Einevoll and Plesser 2002; Norheim et al. 2011). For the moment, however, we keep the choice of $h(t)$ open; the only constraint we impose is that it should be normalized, i.e., $\tilde{h}(0) = 1$.

Then the (Fourier transformed) relay-cell impulse-response function of the *extended DOG* (eDOG) model, is reduced to

$$\tilde{G}_{\text{eDOG}}(k, \omega) = \frac{\tilde{f}_{\text{DOG}}(k)\tilde{h}_{\text{ff}}(\omega)}{1 - Ce^{-k^2 c^2/4}\tilde{h}_{\text{fb}}(\omega)}. \quad (30)$$

A first observation is that in the general case $\tilde{G}_{\text{r}}(k, \omega)$ is not spatiotemporally separable, i.e., $\tilde{G}_{\text{r}}(k, \omega) \neq \tilde{f}_{\text{r}}(k)\tilde{h}_{\text{r}}(\omega)$.

The *space-time impulse-response function* $G_{\text{eDOG}}(r, t)$ can be found by taking the inverse Fourier transform of $\tilde{G}_{\text{eDOG}}(k, \omega)$, i.e.,

$$G_{\text{eDOG}}(r, t) = \frac{1}{(2\pi)^3} \int_{\omega} \int_{\mathbf{k}} e^{i(\mathbf{k}\mathbf{r} - \omega t)} \tilde{G}_{\text{eDOG}}(k, \omega) d^2\mathbf{k} d\omega. \quad (31)$$

In the general case this integral must be evaluated numerically.

Fast-loop limit

In many experiments with sinusoidally drifting stimuli (full-field grating or bipartite stimuli) the temporal frequencies have been chosen to be in the range 1–3 Hz (Sillito et al. 1993; Cudeiro and Sillito 1996; Cheng et al. 1995). The shortest propagation time around the thalamocortical loop can be less than ten milliseconds (Sillito and Jones 2004; Briggs and Usrey 2007), much shorter than the experimental oscillation period of up to a second (for $f = 1$ Hz). This suggests that a low-frequency, or “fast-loop”, approximation can be used where $\tilde{h}_{\text{fb}}(\omega)$ may be approximated as unity, in the modeling of the experiments.

To illustrate the approximation we assume for simplicity that the temporal thalamocortical loop kernel $h_{\text{ff}}(t)$ is described as a delayed δ -function, i.e., $h_{\text{fb}}(t) = \delta(t - \tau_{\text{loop}})$. This corresponds to assuming the signal taking a time τ_{loop} to pass around the thalamocortical loop. The Fourier-transformed kernel is then given by

$$\tilde{h}_{\text{fb}}(\omega) = \int_{-\infty}^{\infty} \exp(i\omega\tau) h_{\text{fb}}(\tau) d\tau = \exp(i\omega\tau_{\text{loop}}). \quad (32)$$

A temporal frequency $f = 1$ Hz corresponds to an angular frequency of $\omega = 2\pi f \sim 6$ Hz. For $\tau_{\text{loop}} = 10$ ms we thus have $\omega\tau_{\text{loop}} = 0.06$, so that $\tilde{h}_{\text{fb}}(\omega) = \exp(i\omega\tau_{\text{loop}})$ will be close to unity. In this “fast-loop” limit where $\tilde{h}_{\text{fb}}(\omega) \approx 1$ the eDOG relay-cell impulse-response function in Eq. 30 simplifies to

$$\tilde{G}_{\text{eDOG}}(k, \omega) = \frac{\tilde{f}_{\text{DOG}}(k)}{1 - Ce^{-k^2 c^2/4}} \tilde{h}_{\text{ff}}(\omega) = \tilde{f}_{\text{eDOG}}(k) \tilde{h}_{\text{ff}}(\omega), \quad (33)$$

where we have introduced the *spatial eDOG function* $\tilde{f}_{\text{eDOG}}(k)$ via

$$\tilde{f}_{\text{eDOG}}(k) \equiv \frac{\tilde{f}_{\text{DOG}}(k)}{1 - Ce^{-k^2 c^2/4}} = \frac{A_1 e^{-k^2 a_1^2/4} - A_2 e^{-k^2 a_2^2/4}}{1 - Ce^{-k^2 c^2/4}}. \quad (34)$$

The corresponding real-space impulse-response function describing the spatial receptive field is now given by an inverse Fourier transform of $\tilde{f}_{\text{eDOG}}(k)$, i.e.,

$$\begin{aligned} f_{\text{eDOG}}(r) &= \frac{1}{(2\pi)^2} \iint_{\mathbf{k}} e^{i\mathbf{k}\mathbf{r}} \frac{A_1 e^{-k^2 a_1^2/4} - A_2 e^{-k^2 a_2^2/4}}{1 - Ce^{-k^2 c^2/4}} d^2\mathbf{k} \\ &= \frac{1}{2\pi} \int_0^{\infty} k J_0(kr) \frac{A_1 e^{-k^2 a_1^2/4} - A_2 e^{-k^2 a_2^2/4}}{1 - Ce^{-k^2 c^2/4}} dk. \end{aligned} \quad (35)$$

Here we have exploited that $\tilde{f}_{\text{eDOG}}(k)$ does not depend on orientation and that $\int_0^{2\pi} \exp(ix \cos \theta) d\theta = 2\pi J_0(x)$, where $J_0(x)$ is the zeroth-order Bessel function (Abramowitz and Stegun 1965).

In Fig. 5 we show example plots of $\tilde{f}_{\text{eDOG}}(k)$ and the corresponding real-space expression $f_{\text{eDOG}}(r)$. For the case where the in-phase feedback is excitatory, i.e., $C > 0$, (and the anti-phase feedback thus is inhibitory) we see that the impulse-response function is amplified. We call this situation *push-pull excitation*. For the opposite case where the in-phase feedback is inhibitory, i.e., $C < 0$, the impulse-response is correspondingly reduced, and we call this situation *push-pull inhibition*. In Fig. 5 we also show spatial impulse-response functions for a modified eDOG model where the Gaussian function in the denominator of Eq. 34 is replaced with a function of the type $\tilde{f}_{\text{rcr}}^{\infty}(k)$ (cf. Eq. 24) derived by summing over many elliptical Gaussian loop kernels in section “Net effect of feedback from several cortical populations”. In the example plot σ_n is set to zero, i.e., to the anisotropic limit. To compare with the Gaussian

Fig. 5 Examples of eDOG spatial receptive fields (spatial impulse-response function) in the “fast-loop” limit. **a** eDOG function in Fourier space, $\tilde{f}_{\text{eDOG}}(2\pi\nu)$, in Eq. 34 plotted as a function of spatial frequency ν ($k = 2\pi\nu$). Solid line: $C = 0$, i.e., standard DOG. Dash-dotted line: Push-pull excitatory feedback for $C = 0.5$, $c = 0.83$ deg. Dashed line: Push-pull inhibitory feedback for $C = -1.5$, $c = 0.83$ deg. Dotted line: Modified push-pull inhibitory-feedback eDOG model with the Gaussian loop-function replaced with a function of the type in Eq. 24 with the constant C_{ref}^{∞} set to -1.5 , $\sigma_l = \sqrt{2}c = \sqrt{2} \cdot 0.83 \text{ deg} \simeq 1.17 \text{ deg}$ and $\sigma_n = 0$. **b** Real-space eDOG functions, $f_{\text{eDOG}}(r)$, corresponding to the Fourier-space functions in left panel. The DOG parameters used are $A_1 = 1$, $a_1 = 0.25$ deg, $A_2 = 0.85$, and $a_2 = 0.83$ deg

push-pull inhibitory eDOG model, the parameters in the plot are chosen so that the prefactor in Eq. 24 corresponds to the Gaussian eDOG model example. As seen in the left panel, for this example the inhibitory feedback in this modified eDOG model gives, except for the smallest and largest spatial frequencies, a larger reduction of the Fourier-space impulse response compared to the Gaussian push-pull inhibitory eDOG model.

When the cortical feedback is small or moderate, i.e., $|C| < 1$, the integral expression for $f_{\text{eDOG}}(r)$ in Eq. 35 can be significantly simplified, as shown in Appendix 1.

Example application: patch-grating stimuli

To clearly elucidate the effects of cortical feedback on response properties of LGN cells, comparison of data from identical experiments done with and without cortical feedback is preferable. This requires removal of cortical feedback to LGN (e.g., by surgical or pharmacological means), and such experiments are scarce in the literature.

Sillito and co-workers have, however, measured the effect of cortical feedback on the response properties of LGN relay cells (Murphy and Sillito 1987; Sillito et al. 1993; Cudeiro and Sillito 1996; Andolina et al. 2002; Sillito and Jones 2002).

In one study, they compared responses of flashing circular spots to circular patches of drifting gratings (Andolina et al. 2002; Sillito and Jones 2002). For circular spots the center-surround suppression (i.e., the reduction of the response to large spots compared to the maximum response to a spot covering the receptive-field center) was found to be qualitatively the same with (normal) and without (decorticated) cortical feedback. For circular patches of drifting gratings, a similar center-surround suppression was found in the normal case, while it was significantly reduced in the decorticated case.

In another experiment they compared the spatial frequency tuning of responses to a patch of grating covering the receptive-field center with the responses to a similar full-field grating both for the normal and decorticated cases (Cudeiro and Sillito 1996). They observed lower responses to full-field gratings compared to patch-gratings, and the percentage response reduction was largest for the smallest spatial frequencies. However, the response reduction was generally smaller for the decorticated compared to the normal case, with the difference being more pronounced for the smallest spatial frequencies (particularly for X cells, cf. Figure 8 in Cudeiro and Sillito (1996)).

These studies indicate that cortical feedback provides extra inhibition of LGN relay cells under certain experimental conditions. Corticogeniculate terminals have been found to be preferentially located on LGN interneurons (Weber et al. 1989). A push-pull inhibitory eDOG model is thus a natural choice for a modeling investigation of these experiments. In the experiments a large grating contrast was used (0.36–0.72, cf. Cudeiro and Sillito (1996)). The eDOG model is by construction linear and cannot account for non-linear effects expected to be significantly evoked at such high contrasts. Nevertheless, results from our linear model may give qualitative insights into the observed phenomena.

For circular patches of drifting gratings, the stimulus can mathematically be described as

$$s_{\text{pg}}(\mathbf{r}, t) = C_{\text{pg}}(1 - \Theta(r - d_{\text{pg}}/2)) \cos(\mathbf{k}_{\text{pg}}\mathbf{r} - \omega_{\text{pg}}t), \quad (36)$$

where $\mathbf{k}_{\text{pg}}$ and ω_{pg} are the wave vector and the angular frequency of the patch-grating, respectively, $\Theta(x)$ is the Heaviside step function, d_{pg} is the diameter of the patch-grating spot, and C_{pg} is a measure of the patch-grating contrast; circular patches are obtained for $\mathbf{k}_{\text{pg}} = \omega_{\text{pg}} = 0$. It is mathematically convenient to introduce a complex version

of this stimulus function, $s_{pg}^c(\mathbf{r}, t)$, obtained by replacing the cosine-function in Eq. 36 with $\exp(i(\mathbf{k}_{pg}\mathbf{r} - \omega_{pg}t))$. The Fourier transform of this (complex) patch-grating stimulus is after some mathematical derivation found to be (Einevoll and Plesser 2005)

$$\tilde{s}_{pg}^c(\mathbf{k}, \omega) = 2\pi^2 d_{pg} C_{pg} \frac{J_1(|\mathbf{k} - \mathbf{k}_{pg}| d_{pg}/2)}{|\mathbf{k} - \mathbf{k}_{pg}|} \delta(\omega - \omega_{pg}), \quad (37)$$

where $J_1(x)$ is the first-order Bessel function.

The (complex) response to a patch grating for the eDOG model can now be found by insertion of $\tilde{s}_{pg}^c(\mathbf{k}, \omega)$ into the general response expression in Eq. 3 together with $\tilde{G}_{eDOG}(k, \omega)$ from Eq. 30. In the above-mentioned experiments by Sillito and co-workers the temporal grating frequency was between 1 and 2 Hz, and in this example application we will consider the “fast-loop” limit and use the simpler expression for $\tilde{G}_{eDOG}(k, \omega)$ in Eq. 33 instead. For a relay-cell with receptive field centered at the center of the patch grating ($r = 0$), the complex response then becomes

$$R_{pg}^c(t) = C_{pg} F_{pg}(d_{pg}, k_{pg}) \tilde{h}_{ff}(\omega_{pg}) e^{-i\omega_{pg}t}, \quad (38)$$

where

$$F_{pg}(d_{pg}, k_{pg}) \equiv \iint_{\mathbf{k}} \frac{d_{pg} A_1 e^{-k^2 a_1^2/4} - A_2 e^{-k^2 a_2^2/4} J_1(|\mathbf{k} - \mathbf{k}_{pg}| d_{pg}/2)}{4\pi (1 - C e^{-k^2 c^2/4}) |\mathbf{k} - \mathbf{k}_{pg}|} d^2\mathbf{k}. \quad (39)$$

In this model the patch-grating response will thus be harmonically oscillating with the amplitude determined by $F_{pg}(d_{pg}, k_{pg})$ and $\tilde{h}_{ff}(\omega_{pg})$. In the experiments from Sillito's group firing responses were measured as a function of spot diameter d_{pg} (Sillito and Jones 2002) or spatial frequency of patch grating $v_{pg} = |\mathbf{k}_{pg}|/2\pi$ (Cudeiro and Sillito 1996) with a fixed temporal frequency $f_{pg} = \omega_{pg}/2\pi$. Thus $\tilde{h}_{ff}(\omega_{pg})$ does not change in these experiments, and the relevant quantity to investigate is $F_{pg}(d_{pg}, k_{pg})$. Note that $F_{pg}(d_{pg}, k_{pg})$ only depends on the magnitude and not the direction of $\mathbf{k}_{pg}$. This is a consequence of the circular spatial symmetry of the eDOG model.

The integral in Eq. 39 must be solved numerically in the general case. However, for the special case where the spatial receptive field is described by a standard DOG (i.e., $C = 0$), an analytical solution to the integral can be found. The function $F_{pg}(d_{pg}, k_{pg})$ can then be written as an infinite series where each term in the series involves the confluent hypergeometric function (Einevoll and Plesser 2005).

To compare with the results of Sillito and Jones (2002) on the difference between patch-grating and flashing-spot responses, we also need a model expression for the

response to flashing spots. This we obtain by setting the spatial frequency to zero (i.e., $k_{pg} = 0$) in Eq. 39. This gives the response to harmonically oscillating spots, but for our spatiotemporally separable version of the eDOG model the flashing-spot response will be directly proportional to the amplitude $C_{pg} F_{pg}(d_{sp}, 0)$ of this oscillatory response.

To compare with the results of Cudeiro and Sillito (1996) we further need the response to full-field gratings. The amplitude of this response is simply given by $C_{pg} \tilde{f}_{eDOG}(k)$ where $\tilde{f}_{eDOG}(k)$ is given by Eq. 34. In Fig. 6 (upper left) we show an example plot of the diameter-dependence of the flashing-spot response of LGN relay cells, i.e., $F_{pg}(d_{sp}, 0)$. The solid line corresponds to the standard DOG model which in our case will correspond to the decorticated case (the DOG model is assumed to account for the feedforward processing). The dashed line corresponds to an eDOG model with the same DOG parameters but including a push-pull inhibitory thalamocortical loop. The eDOG model represents the LGN response when the cortical feedback is intact (normal case). We observe that the eDOG model response overall is reduced compared to the DOG model, but the shape and amount of center-surround suppression are qualitatively similar in the two cases.

In Fig. 6 (upper right) we show for the same example models plots of the diameter-dependence of the patch-grating response (i.e., $F_{pg}(d_{pg}, 2\pi v_{pg})$) with v_{pg} set to 0.3 cycles/deg. Here, the normal case (eDOG model) still has a sizable center-surround suppression, while this suppression is significantly reduced in the decorticated case (DOG model). Hayot and Tranchina (2001, Fig. 7) observed the same effect in network simulations of a similar system (although it was less pronounced in their model than in ours).

We thus find a qualitative similarity between the experimental observations by Andolina et al. (2002) and Sillito and Jones (2002) and the results for these example models with the eDOG model representing the normal case and the DOG model representing the decorticated case.

The qualitative effects of cortical feedback on the center-surround suppression can be elucidated by first considering the plots in Fig. 5 (left). Here the eDOG and DOG impulse-response functions in Fourier space $\tilde{f}(2\pi v)$, giving the response to full-field drifting gratings, are shown for the same model parameters used in Fig. 6. The response to full-field “flashing-spot” illumination corresponds to the special case $v = 0$, and for the DOG model in Fig. 5 (left) we have $\tilde{f}_{DOG}(0) = 0.15$, and for the push-pull inhibitory eDOG models we have $\tilde{f}_{eDOG}(0) = 0.06$. Since the peak values of the spot response are seen in Fig. 6 (upper left) to be 0.5 or larger, these low full-field responses imply a sizable center-surround suppression for flashing spots for both the DOG and eDOG models, cf. Fig. 6 (upper left).

Fig. 6 Example push-pull inhibitory eDOG model responses for flashing ($F_{pg}(d_{pg}, 0)$) and patch-grating ($F_{pg}(d_{pg}, 2\pi\nu_{pg})$) spots, cf. Eqs. 38–39. **a** Flashing-spot response as a function of spot diameter. *Solid line:* $C = 0$, i.e., standard DOG. *Dashed line:* $C = -1.5$, $c = 0.83$ deg. *Dotted line:* Variation of push-pull inhibitory eDOG model with the Gaussian loop-kernel replaced with a function of the type in Eq. 24 with the constant $C_{cr}^{\infty} = -1.5$, $\sigma_l = \sqrt{2}c = \sqrt{2} \cdot 0.83$ deg $\simeq 1.17$ deg and $\sigma_n = 0$; DOG parameters are $A_1 = 1$, $a_1 = 0.25$ deg, $A_2 = 0.85$, and $a_2 = 0.83$ deg. **b** Patch-grating response for $\nu_{pg} = 0.3$ cycles/deg as a function of spot diameter d_{pg} for the same models considered in upper left panel. **c** *Thin lines:* Full-field grating response as a function of spatial frequency ν of the grating. *Thick lines:* Patch-grating response for $d_{pg} = 0.8$ deg as a function of spatial frequency ν_{pg} of the patch grating. Same models and parameters as in upper panels

In Figure 6 (upper right) we see that the peak response values for the patch-grating case are still quite similar for the DOG and eDOG models. However, the large-patch responses $\tilde{f}(2\pi\nu_{pg})$ are now quite different for the two models: for $\nu = \nu_{pg} = 0.3$ cycles/deg we find $\tilde{f}_{DOG}(2\pi\nu_{pg}) = 0.49$ and $\tilde{f}_{eDOG}(2\pi\nu_{pg}) = 0.27$. As seen in Fig. 6 (upper right), the

center-surround suppression is reduced for both the DOG and eDOG models compared to the flashing-spot case in Fig. 6 (upper left). However, the reduction is seen to be much larger for the DOG model (decorticated case) than for the “Gaussian” push-pull inhibitory eDOG model (normal case), in qualitative agreement with the findings reported in Sillito and Jones (2002). Note that for larger spatial frequencies ν_{pg} the full-field grating response $\tilde{f}_{eDOG}(2\pi\nu_{pg})$ will be larger (cf. Fig. 5 (left)), and the patch-grating center-surround suppression will consequently become small also for the eDOG model (normal case).

In Fig. 6 (bottom) we show plots of the spatial-frequency dependence of both the full-field grating response and the patch-grating response for a patch covering the receptive-field center. The same model parameters as in Fig. 6 are used. A first observation is that for low spatial frequencies the full-field grating responses are significantly reduced compared to the corresponding patch-grating responses. For these low frequencies we further see that the percentage reduction is smaller for the decorticated case (DOG model, solid line) compared to the normal case (eDOG model, dashed line). This is in qualitative agreement with the observation for X-cells in Cudeiro and Sillito (1996). Since X-cells exhibit more linear response properties than Y-cells, it is to be expected that our linear models are more suited to account for the response characteristics of these cells.

Hayot and Tranchina (2001) observed a similar effect in network simulations on a similar system. In contrast to our results in Fig. 6 (bottom) and experimental observations of Cudeiro and Sillito (1996), their model predicts no effects of cortical feedback for the lowest spatial frequencies. This difference may be due to the mixed excitatory and inhibitory in-phase cortical feedback assumed in Hayot and Tranchina’s network model, in contrast to the inhibitory in-phase feedback incorporated in the push-pull inhibitory eDOG model.

Overall we conclude that the eDOG model, with the present choice of parameters, accounts qualitatively for the experimental findings by Cudeiro and Sillito (1996) and Sillito and Jones (2002).

Discussion

Scope of eDOG model

The present *extended DOG (eDOG)* receptive-field model for LGN relay cells predict *linear* responses, even though the cortical cells providing the thalamocortical feedback themselves have non-linear firing characteristics. This somewhat non-intuitive linearity stems from the assumption in the

model of a phase-reversed push-pull arrangement of cortical feedback, supported by recent experimental findings (Wang et al. 2006). The mathematical structure of the spatiotemporal eDOG model is similar to but somewhat more complicated than the purely spatial DOG model. In Fourier space (ω , $\mathbf{k}$ -space) the response function $\tilde{G}_{\text{eDOG}}(k, \omega)$ is given by a simple formula, while the real-space response function $G_{\text{eDOG}}(r, t)$, as well as responses to particular visual stimuli, in general must be found by numerical evaluation of integrals.

The LGN circuit as illustrated in Fig. 1 exhibits various non-linear effects beyond the non-linearity of the firing response of the cortical cells providing the corticothalamic feedback. Receptive-field models such as eDOG thus cannot be expected to account for all behavior of the circuit. Given that X relay cells in cat under certain conditions have been found to respond approximatively linearly (So and Shapley (1981), Cheng et al. (1995)), our formalism is expected to be particularly suitable for analysis of this pathway.

To model non-linear network effects one is generally forced to do computer simulations of networks of interconnected neurons. The equation set shown in Eq. (12) could be a starting point for such an endeavor. Simulations of sizable networks require significant computer power, however, and extended simulation times often prohibit comprehensive testing of the parameter-dependence of the model results. The use of the linear eDOG model (or variations thereof) to study properties of the thalamocortical circuit is both computationally and conceptually easier. The eDOG model can thus be used as a “linear starting point” for mathematical exploration where the results may function as guidelines for more detailed exploration of non-linear effects with extensive computer simulations.

Linear models cannot account for orientation-discontinuity effect

In experiments the response to a bipartite drifting grating stimulus was found to be independent of the *absolute* orientation of the grating of the inner and outer stimulus (Sillito et al. 1993; Cudeiro and Sillito 1996). This observation is incorporated in the eDOG model since the impulse-response functions are circularly symmetric, e.g., $\tilde{G}_{\text{eDOG}}(\mathbf{k}, \omega)$ depends only on the magnitude ($k = |\mathbf{k}|$) and not the orientation of $\mathbf{k}$.

The response to a bipartite drifting was, however, also found to depend on the *relative* orientation of the gratings in the inner and outer stimulus (Sillito et al. 1993; Cudeiro and Sillito 1996). This effect cannot be accounted for by a linear and circularly symmetric model such as the eDOG model: Consider a bipartite stimulus with an inner spot of radius R_i and grating wave vector $\mathbf{k}_i$ surrounded by an annulus with outer radius R_o and outer grating wave vector

$\mathbf{k}_o$. We further have $|\mathbf{k}_i| = |\mathbf{k}_o|$ since only the direction of the grating varies between the inner spot and outer annulus. This stimulus can be considered to be the linear sum of two circular grating-spots specified by $R_i, \mathbf{k}_i$ and $R_o, \mathbf{k}_o$, respectively, *minus* a circular grating-spot specified by $R_i, \mathbf{k}_o$. In a linear model the response to the bipartite stimulus will thus be given by the sum of the responses to two circular grating spots specified by $R_i, \mathbf{k}_i$ and $R_o, \mathbf{k}_o$ minus the response to a grating spot specified by $R_i, \mathbf{k}_o$. Since the response to a grating spot in a circularly symmetric model only depends on the magnitude of $\mathbf{k}$, the responses to the two spots specified by $R_i, \mathbf{k}_i$ and $R_i, \mathbf{k}_o$ will cancel since $|\mathbf{k}_i| = |\mathbf{k}_o|$. The total response will thus be given by the response to the grating-spot specified by $R_o, \mathbf{k}_o$ alone (which will only depend on the magnitude $k_o = |\mathbf{k}_o|$). Consequently, in a linear circularly symmetric model the response will be independent of the relative orientation of the inner and outer gratings. This effect was observed by Hayot and Tranchina (2001) in their neural network simulations of cortical feedback effects on LGN relay cells when the input-output relationships of cortical neurons and LGN neurons were linearized.

Note that in the experiments with bipartite drifting gratings, the orientation-alignment effect was found to be only about a quarter (24%) of the observed enhanced inhibition due to cortical feedback (Sillito et al. 1993). The remaining dominant part (76%) was found to be independent of the relative orientation so that the applicability of a linear model (such as eDOG) is not excluded *a priori*.

Stimulus dependence of cortical feedback effects

Cortical feedback effects also for non-oriented stimuli

It has been argued that since cortical cells predominantly respond to oriented stimuli, only such stimuli will evoke significant cortical feedback effects. As seen in Fig. 6 (upper left) significant cortical feedback effects can also be evoked by circular spot stimuli in our linear eDOG model. Compared to oriented stimuli, circular spot stimuli may not evoke a strong response in any particular cortical population. In our linear model Eq. 12, however, circular spots evoke a small but non-negligible response in all cortical populations c_n so that the overall summed cortical feedback effect becomes sizable. In contrast, an oriented stimulus may evoke a strong response in a few cortical populations but little response in the others. The cortical feedback effects from the few activated populations might be substantial, but the overall summed feedback is not necessarily larger than for a non-oriented stimulus.

Clear demonstrations of cortical feedback effects on visually driven relay-cell responses have come from experiments with oriented stimuli such as bipartite drifting

gratings and patches of drifting gratings (Sillito et al. 1993; Cudeiro and Sillito 1996; Sillito and Jones 2002). In our model example in Fig. 6 (upper right) we observed a significantly reduced response suppression for large patch-grating diameters when the push-pull inhibitory cortical feedback was removed, in qualitative agreement with experimental observations (Sillito and Jones 2002). Significant inhibitory cortical feedback effects are also present in our eDOG model with circular-spot stimuli (Fig. 6 (upper left)) or full-field grating stimuli (Fig. 5 (left)). However, in these cases the cortical feedback reduces the responses with modest change in the qualitative shape of the response curves, so the effects will be difficult to observe in experiments where the normal and decorticated response curves are measured for different cells.

Model assumptions and variations

Other choices for feedforward model

In the present eDOG model the feedforward aspects of the response of LGN relay cells are represented using the standard difference-of-Gaussians (DOG) model. This mathematically simple choice is motivated by our intention to highlight the effects of corticothalamic feedback.

In Einevoll and Heggelund (2000) and Einevoll and Plesser (2002) we have explored various mechanistic models for the spatial organization of the feedforward LGN circuitry, both with discrete (finite number of retinal inputs to LGN cells) and continuous connection patterns. These models could straightforwardly be implemented in a more comprehensive mechanistic receptive-field model incorporating both feedforward and feedback connections in the LGN circuit. For example, the numerator $\tilde{f}_{\text{DOG}}(k)\tilde{h}_{\text{ff}}(\omega)$ in Eq. 30 could be replaced by two terms, one representing the direct feedforward excitation on relay cells from retinal ganglion cells, and one representing the indirect feedforward inhibition via intrageniculate interneurons (Norheim et al. 2011). Such a comprehensive receptive-field model might be appealing since each term in the formula would be related to a particular synaptic connection between various neuron types. Even though one could explore how the relay cell response depends on the various connections, the large number of model parameters would make it difficult to compare with the limited experimental data available at present.

Other choices for cortical feedback model

The modeling of corticothalamic effects on LGN cells in terms of simple linear loops, each involving a single population of orientation-selective cells, is clearly a severe

simplification. The dominant input from LGN to primary visual cortex appears to arrive in layer 4. However, geniculate inputs also terminate in layer 6, where the neurons providing the corticothalamic feedback are located; cf. Ch. 2 in Sherman and Guillery (2001) and references therein. Simple cells have the most linear response properties of the cells in V1 and are the best candidates for providing corticothalamic feedback resembling the half-wave rectified, linear characteristics assumed in our model. In a study in cat, Grieve and Sillito (1995) found that 71 % of the layer VI cells projecting back to LGN are simple cells.

We derived an analytical expression for a circularly symmetric feedback loop kernel for a specific (and somewhat arbitrary) model for the thalamocortical and corticothalamic connection pattern (cf. Eq. 24), but the important qualitative conclusion regarding the circular loop-kernel symmetry does not depend on this particular model choice. In the absence of contradictory experimental data, we therefore chose to model the spatial part of the feedback loop-kernel as a simple Gaussian function in the present eDOG model. This function parameterizes the connection patterns in two presumably important parameters: coupling strength (C) and spatial spread (c). Other functions such as, e.g., the two-parameter exponential function $C \exp(-ck)$ or the three-parameter function $C \exp(-c_1 k^2) I_0(c_2 k^2)$ derived in Eq. 24, could equivalently have been chosen; examples of flashing-spot and patch-grating responses for a modified eDOG-model using the latter function are shown in Fig. 6. The advantage of choosing Gaussians is mainly that for moderate cortical feedback strength, the relay-cell receptive field in space-time coordinates can be written as a sum of DOGs (cf. Eq. 40), as shown in the Appendix 1.

Significance

The eDOG model has been constructed to elucidate salient features of visually evoked cortical feedback effects on LGN cells. The model has a simple mathematical structure: In Fourier space, the impulse-response function (essentially the receptive field) is given by a simple formula (Eq. 30), while the real-space expression in the general case involves a triple integral (Eq. 31), which must be numerically evaluated. However, for moderate cortical-feedback strengths, a closed-form expression for the spatial receptive field, involving an infinite sum over DOGs, can be found in the “fast-loop” limit (Eq. 40). The eDOG model response to arbitrary visual stimuli can also be found by evaluating a triple integral (Eq. 3).

The main virtue of the eDOG model compared to alternative network models focusing on cortical-feedback effects on LGN cells (Köhn and Wörgötter 1996; Wörgötter et al. 1998; Kirkland and Gerstein 1998; Kirkland et al. 2000; Hillenbrand and van Hemmen 2000; Hayot and Tranchina

2001; Yousif and Denham 2007) is the conceptual and methodological ease in using the model. In the example application to patch-grating stimuli in section “[Example application: patch-grating stimuli](#)”, the cortical feedback was described by two parameters, the feedback weight C and the spatial spread c . In comprehensive network simulations of the same problem, far more (and often uncertain) model parameters have to be specified, and the parameter-dependence of the results is much harder to assess, cf. Hayot and Tranchina (2001).

Since the eDOG model is much simpler to use and analyze than extended network models, it can be particularly useful as a “linear starting point” for the exploration of various possible scenarios for the organization of the cortical feedback system. One should in particular explore the interplay between the spatial and temporal coupling patterns, parameterized respectively by the push-pull feedback weight C and its spatial spread c and by the temporal kernel $\tilde{h}_{fb}(\omega)$.

The eDOG model can also be useful for finding visual stimuli which highlight effects of cortical feedback. In section “[Example application: patch-grating stimuli](#)” we found, for example, that for our inhibitory eDOG model the qualitative shape of the response curve for circular spots (cf. Fig. 6, upper left) was little affected by cortical feedback even if it reduced the overall response magnitude. For patch-grating spots the shape and the amount of center-surround antagonism was, however, found to be quite different for the cases with and without cortical feedback (cf. Fig. 6, upper right) making experimental testing for the effect easier (Sillito and Jones 2002).

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Appendix 1: eDOG model for small cortical feedback strengths

For $|C| < 1$, the denominator term of the integral expression for $f_{eDOG}(r)$ in Eq. 35 can be replaced by a series expansion, i.e., $1/(1-x) = \sum_{m=0}^{\infty} x^m = 1 + x + x^2 + \dots$. With $x = Ce^{-k^2 c^2/4}$ we find by insertion into Eq. 35:

$$\begin{aligned} f_{eDOG}(r) &= \frac{1}{(2\pi)^2} \iint \mathbf{k} e^{i\mathbf{k}\mathbf{r}} \frac{A_1 e^{-k^2 a_1^2/4} - A_2 e^{-k^2 a_2^2/4}}{1 - Ce^{-k^2 c^2/4}} d^2 \mathbf{k} \\ &= \frac{1}{(2\pi)^2} \iint \mathbf{k} e^{i\mathbf{k}\mathbf{r}} \left(A_1 e^{-k^2 a_1^2/4} - A_2 e^{-k^2 a_2^2/4} \right) \\ &\quad \times \sum_{m=0}^{\infty} C^m e^{-mk^2 c^2/4} d^2 \mathbf{k} \\ &= \sum_{m=0}^{\infty} \frac{C^m}{(2\pi)^2} \iint \mathbf{k} e^{i\mathbf{k}\mathbf{r}} \end{aligned}$$

$$\begin{aligned} &\left(A_1 e^{-k^2(a_1^2+mc^2)/4} - A_2 e^{-k^2(a_2^2+mc^2)/4} \right) d^2 \mathbf{k} \\ &= \sum_{m=0}^{\infty} C^m \left(A_1 \frac{e^{-r^2/(a_1^2+mc^2)}}{\pi(a_1^2+mc^2)} - A_2 \frac{e^{-r^2/(a_2^2+mc^2)}}{\pi(a_2^2+mc^2)} \right). \end{aligned} \quad (40)$$

The final expression in Eq. 40 has a relatively simple form: it consists of an infinite sum of DOGs. For small values of C , the higher terms vanish rapidly, so that only a limited number of terms need to be retained. The terms in the sum have increasing spatial extent ($\sqrt{a_1^2+mc^2}$, $\sqrt{a_2^2+mc^2}$) and alternating sign when C is negative.

The terms in the series have an intuitive interpretation as illustrated by the first three terms:

$$\begin{aligned} f_{eDOG}(r) &= \left(\frac{A_1}{\pi a_1^2} e^{-r^2/a_1^2} - \frac{A_2}{\pi a_2^2} e^{-r^2/a_2^2} \right) \quad (m=0) \\ &\quad + C \left(\frac{A_1}{\pi(a_1^2+c^2)} e^{-r^2/(a_1^2+c^2)} \right. \\ &\quad \left. - \frac{A_2}{\pi(a_2^2+c^2)} e^{-r^2/(a_2^2+c^2)} \right) \quad (m=1) \\ &\quad + C^2 \left(\frac{A_1}{\pi(a_1^2+2c^2)} e^{-r^2/(a_1^2+2c^2)} \right. \\ &\quad \left. - \frac{A_2}{\pi(a_2^2+2c^2)} e^{-r^2/(a_2^2+2c^2)} \right) \quad (m=2) \\ &\quad + \dots \end{aligned}$$

The first term corresponds to the “direct” feedforward DOG. The second term corresponds to the correction to this “direct” term due to one round of the feedforward DOG in the cortical feedback loop. The spatial extension of the Gaussians is larger since they have been “spread out” by the spatial spread of the corticogeniculate loop. Correspondingly, the third term corresponds to a “correction of the correction” after the direct term has gone through the thalamocortical loop twice. This term is spatially even more spread out after two rounds through the loop.

For $|C| < 1$, the series in Eq. 40 can be shown to be uniformly convergent assuring the validity of the mathematical derivation. If the feedback is positive with $C = 1$, the integrand in Eq. 35 has a singular point corresponding to a resonance in the thalamocortical loop (Einevoll and Plesser 2002).

Appendix 2: Numerical methods

Figures 2, 3 were created using Mathematica 7 (Wolfram Research), while Figs. 4, 6 were created using Matlab 7.10.0 (MathWorks) on a Lenovo T410i computer running Windows XP.

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