Response of the difference-of-Gaussians model to circular drifting-grating patches

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Abstract
Forty years ago R.W. Rodieck introduced the Difference-of-Gaussians (DOG) model, and this model has been widely used by the visual neuroscience community to quantitatively account for spatial response properties of cells in the retina and lateral geniculate nucleus following visual stimulation. Circular patches of drifting gratings are now regularly used as visual stimuli when probing the early visual system, but for this stimulus type the mathematical evaluation of the DOG-model response is significantly more complicated than for moving bars, full-field drifting gratings, or circular flashing spots. Here we derive mathematical formulas for the DOG-model response to centered circular patch gratings. The response is found to be given as the difference between two summed series, where each term in the series involves the confluent hypergeometric function. This function is available in commonly used mathematical software, and the results should thus be readily applicable. Example results illustrate how a strong surround suppression in area-summation curves for iso-luminant circular spots may be reversed into a surround enhancement for circular patch gratings. They also show that the spatial-frequency response changes from band-pass to low-pass when going from the full-field grating situation to the situation where the patch covers only the receptive-field center.

Keywords: Receptive field, Difference-of-Gaussians model, Circular patches, Drifting gratings

Introduction
Forty years ago R.W. Rodieck (1965) introduced the Difference-of-Gaussians (DOG) model to quantitatively account for spatial receptive-field properties in cat retinal ganglion cells. Ever since, this model has been widely applied by the neuroscience community and is now maybe the best known mathematical model in visual neuroscience. The model’s popularity stems partially from the mathematical simplicity of applying it: responses to different visual stimuli can be obtained by standard integration and simple formulas for the stimulus dependence of responses are available in many cases.

In the DOG model, the spatial receptive field is modeled as the difference of two circularly symmetric and concentric Gaussians. 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) derived the spatial-frequency response for the same model, that is, the response to full-field drifting sinusoidal gratings. 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 (Stoodak, 1986). Even though the DOG model was originally suggested for retinal ganglion cells, it has also been used to describe receptive fields in lateral geniculate nucleus (LGN) (Kaplan et al., 1979; So & Shapley, 1981; Troy, 1983; Dawis et al., 1984; Norton et al., 1989; Mukherjee & Kaplan, 1995; Uhlrich et al., 1995).

Due to limited spatial extents of visual displays, large patches of drifting gratings have commonly been used as a substitute for genuine full-field gratings. As long as the patch size is larger than the spatial extent of the receptive field of the probed cell, the response will be little affected by the finite size of the grating. Lately, however, circular patches of drifting gratings of a variety of sizes have deliberately been chosen as visual stimuli, in particular in studies of cortical feedback effects on cells in the LGN (Sillito et al., 1993; Cudeiro & Sillito, 1996; Sillito & Jones, 1997, 2002; Andolina et al., 2002; Allito & Usrey, 2004).

In one set of experiments, the stimulus consisted of a circular patch grating chosen to cover the receptive-field center of the cat LGN cells in question, often in combination with a patch-grating annulus (with a different grating orientation) covering the surround (Sillito et al., 1993; Cudeiro & Sillito, 1996). The purpose of these experiments was to study effects of cortical feedback on LGN cell response properties, and one motivation for using patch gratings...
instead of, say, flashing circular spots was that layer VI cortical cells providing feedback to LGN cells are more vigorously driven by grating stimuli (Sillito & Jones, 1997). By selective use of patches and annuli of gratings covering the receptive-field center and/or surround instead of full-field gratings, the relative contributions from these two parts of the receptive field could be assessed. As an example, Cudeiro and Sillito (1996) compared responses to patch gratings covering the receptive-field center with responses to full-field gratings. For LGN X cells they observed that the characteristic band-pass spatial-frequency response for the full-field case was changed to low-pass when the patch grating only covered the receptive-field center.

In other experiments, patch-grating area-summation curves have been recorded for cat LGN cells. Here responses to circular patch gratings were measured for a range of patch diameters spanning from sizes much smaller than to much larger than the receptive-field center (Sillito & Jones, 2002; Andolina et al., 2002). In the area-summation curves reported by Sillito and Jones (2002), a strong surround suppression, that is, significantly reduced response for the largest diameters compared to the peak value, was observed in the normal case both for flashing spots and their patch gratings. However, with cortical feedback removed, the surround suppression was found to be strongly reduced for the patch gratings while it was essentially unaltered for flashing spots.

For patch diameters much larger than the receptive field, the response will correspond to the well-known full-field grating response. When the patch diameter is much smaller than the wavelength of the patch grating, the stimulus is essentially a sinusoidally modulated iso-luminant spot. However, in the intermediate regime where the patch-grating diameter, patch-grating wavelength and spatial extent of the receptive field are comparable, the situation is more complicated. As for other visual stimuli, a comparison with the well-established DOG model is a natural strategy when interpreting patch-grating data. Such comparisons have been pursued (Andolina et al., 2002; Allito & Usrey, 2004), but for circular patch-grating data encompassing this intermediate regime the mathematical evaluation of the DOG-model response is significantly more complicated than for moving bars, full-field drifting gratings, or circular flashing spots.

The main purpose of this article is to derive general mathematical formulas for the DOG-model response to circular patch gratings (here also simply called patch gratings). These formulas can then immediately be used to compare and fit the DOG model to experimental data. We show that the DOG-model response to circular patch gratings centered at the origin of the DOG receptive field, is given by the difference between two summed series where each term in the series involves the so called confluent hypergeometric function \( F_1(\alpha; \gamma; x) \) (Gradshteyn et al., 2000). This is a less familiar function than the Gaussian function describing the response to drifting gratings (Enroth-Cugell & Robson, 1966) and flashing spots (Einevoll & Heggelund, 2000), or the error function describing the response to moving bars (Rodieck, 1965). However, confluent hypergeometric functions are available in commonly used mathematical software such as MATLAB and Mathematica. Our results should thus be readily applicable.

In the next section, we describe receptive fields, linear neural responses, and the DOG model. We then derive formulas for the DOG-model response to circular patch gratings. We further give some example results illustrating some qualitative effects stemming from the interplay between the different lengths in the problem (patch-grating diameter and wavelength; spatial extents of DOG center and surround). In the final section our results are summarized and discussed.

### Receptive fields and neural responses

#### Impulse-response functions and linear response

For cells in the early visual pathway the response \( R(r, t) \) to a stimulus \( s(r, t) \) can be written as

\[
R(r, t) = \int G(r - r_0, \tau) s(r_0, t - \tau) \, dr_0 \, dy_0 \, \, dr,
\]

if one assumes (1) linearity, (2) time invariance, and (3) local spatial homogeneity. Here \( G(r, \tau) \) is the impulse-response function (Heeger, 1991), \( s(r, t) \) represents the visual stimulus presented at position \( r = [x, y] \) at time \( t \), and \( R(r, t) \) is the firing rate for a neuron located at \( r \). The spatial integral over \( r_0 \) goes over all two-dimensional space. For mathematical convenience, we have chosen the temporal integration to go from \( \tau = -\infty \) to \( \infty \). From causality, it follows that \( G(r, \tau < 0) = 0 \), so the lower integration boundary for \( \tau \) could also be set to zero.

The integral in eqn. (1) is essentially a convolution between the stimulus and the impulse-response function, that is,

\[
R(r, t) = G(r, t) * s(r, t).
\]

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

\[
R(r, t) = \frac{1}{(2\pi)^3} \int_{\omega} \int_{k} e^{i(kx - \omega t)} \bar{G}(k, \omega) \bar{s}(k, \omega) \, dk \, dk_y \, \, d\omega.
\]

Here \( k = [k_x, k_y] \) is the wavevector, and \( \omega \) is the angular frequency. Further, \( \bar{G}(k, \omega) \) and \( \bar{s}(k, \omega) \) are the complex Fourier transforms of the impulse-response function \( G \) and stimulus \( s \), respectively. The complex Fourier transform we use, and its inverse, are given by

\[
\hat{y}(k, \omega) = \int_{r} \int_{t} e^{-i(kx - \omega t)} \gamma(r, t) \, dx \, dy \, dt,
\]

\[
y(r, t) = \frac{1}{(2\pi)^3} \int_{\omega} \int_{k} e^{i(kx - \omega t)} \hat{y}(k, \omega) \, dk \, dk_y \, \, d\omega.
\]

The physiological interpretation of the real-space impulse-response function \( G(r, t) \) for a particular cell is that it is given directly by the response to test spots positioned at different positions \( r_{\text{test}} \) in the receptive field of the cell. These test spots must both be very small \( [\Delta(r - r_{\text{test}})] \) and narrow in time \( [\Delta(t)] \). Mathematically, this corresponds to a stimulus function given by \( s(r, t) = L_{\text{test}} \delta(r - r_{\text{test}}) \delta(t) \) where \( L_{\text{test}} \) is the luminance of the test spot. Then insertion in eqn. (1) yields the response \( R(r, t) = L_{\text{test}} G(r - r_{\text{test}}, t) \) for a neuron with the receptive field centered at \( r \). [Here we have used the sifting property of the \( \delta \)-function (Bracewell, 1986).]

Thus, the response depends only on the difference between the position vectors of the test spot and the receptive-field center.
The impulse-response function is thus in principle given by the measured firing rates of neurons at various positions \( r \) following a \( \delta \)-pulse at position \( r_{\text{test}} \) at time zero. In practice, it is easier to measure from a particular cell and move the test spot. Therefore, the receptive-field 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 \( r \) replaced with \(-r\) and \( t \) with \(-t\) in the spatial and temporal arguments, respectively (Heeger, 1991).

The Fourier-transformed impulse-response expression \( \tilde{G}(k, \omega) \) also has a clear physiological interpretation. In eqn. (3), the response to the stimulus \( s \) is essentially written as an infinite sum (integral) over contributions from drifting sinusoidal gratings specified by their wavevector \( k \) and angular frequency \( \omega \). The wavevector is related to the spatial frequency \( v \) via \( |k| = 2\pi v \), while the angular frequency 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 \( \delta(k, \omega) \). \( \tilde{G}(k, \omega) \) tells how much a particular sinusoidal drifting grating (specified by \( k \) and \( \omega \)) contributes to the response of a cell. To see this, we consider the modulatory part of a drifting grating stimulus,

\[
s_{\text{dg}}(r, t) = C_g \cos(k_d r - \omega_d t),
\]

where \( k_d \) and \( \omega_d \) are the wavevector and angular frequency of the drifting grating, respectively, and \( C_g \) is a measure of the grating contrast (Eimevoll & Plesser, 2002). We now use the standard mathematical trick of replacing the real function \( \cos(k_d r - \omega_d t) \) with the complex quantity \( \exp[i(k_d r - \omega_d t)] \) and, correspondingly, the real stimulus function \( s_{\text{dg}}(r, t) \) with the corresponding complex quantity \( s'_{\text{dg}}(r, t) \). These mathematical representations of the stimulus are related via \( s_{\text{dg}}(r, t) = \Re \{s'_{\text{dg}}(r, t)\} \) where \( \Re \{z\} \) represents the real part of the complex number \( z \). The Fourier transform of the (complex) drifting grating stimulus is now given by

\[
\tilde{s}^{\text{c}}_{\text{dg}}(k, \omega) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} e^{-i(k \cdot r - \omega t)} s'_{\text{dg}}(r, t) \, dx \, dy \, dt,
\]

\[
= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} C_g e^{i(k_d r - \omega_d t)} e^{-i(k \cdot r - \omega t)} \, dx \, dy \, dt
\]

\[
= C_g (2\pi)^3 \delta(\omega - \omega_d) \delta^2(k - k_d),
\]

where we have used the mathematical relationships

\[
\int_{-\infty}^{\infty} e^{iut} \, dt = 2\pi \delta(\omega), \quad \text{and} \quad \int_{-\infty}^{\infty} e^{-ikx} \, dx = (2\pi)^2 \delta^2(k).
\]

We can now insert eqn. (7) into the response integral in eqn. (3). Since we use the complex stimulus \( s'_{\text{dg}}(r, t) \) instead of its real counterpart \( s_{\text{dg}}(r, t) \), we obtain the complex response

\[
R^{\text{c}}_{\text{dg}}(r, t) = \left( \frac{1}{2\pi} \right) \int_{|k| = 2\pi} \int_{\omega} e^{i(k \cdot r - \omega t)} \tilde{G}(k, \omega) C_g (2\pi)^3 \delta(\omega - \omega_d) \times \delta^2(k - k_d) \, dk \, d\omega,
\]

\[
= C_g \tilde{G}(k_d, \omega_d) e^{i(k_d \cdot r - \omega_d t)}
\]

\[
= C_g \tilde{G}(k_d, \omega_d) e^{i(k_d \cdot r - \omega_d t + \Phi)},
\]

where we have used the general relationship \( \tilde{G}(k_d, \omega_d) = |\tilde{G}(k_d, \omega_d)| e^{i\Phi} \) in the final step. The real-valued cell response is thus given by

\[
R_{\text{dg}}(r, t) = \Re \{R^{\text{c}}_{\text{dg}}(r, t)\} = C_g |\tilde{G}(k_d, \omega_d)| \cos(k_d r - \omega_d t + \Phi).
\]

This shows that the complex Fourier-transformed impulse-response function \( \tilde{G}(k, \omega) \) gives both the amplitude of the response to a drifting sinusoidal stimulus \( (|\tilde{G}(k, \omega)|) \) and the phase-shift (\( \Phi \)) of the response compared to the sinusoidal stimulus.

**Difference-of-Gaussians (DOG) model**

The recipe for calculating linear responses described above applies to any choice of receptive-field model \( G(r, t) \). The present focus is on the Difference-of-Gaussians (DOG) model. Following Rodieck (1965), we assume the impulse-response function to be spatiotemporally separable \( [G(r, t) = f(r) h(t)] \) and model the spatial part as the difference of two Gaussians, that is,

\[
G_{\text{DOG}}(r, t) = f_{\text{DOG}}(r) h(t) = \left( \frac{A_1}{\pi a_1^2} e^{-r^2/a_1^2} - \frac{A_2}{\pi a_2^2} e^{-r^2/a_2^2} \right) h(t),
\]

where \( A_1 \) and \( A_2 \) (defined to be positive) are the strengths of the center and surround, respectively, and \( a_1 \) and \( a_2 \) are corresponding width parameters. Rodieck (1965) chose a particular model for the temporal part \( h(t) \), but here we leave it unspecified. The corresponding Fourier-transformed impulse response is found to be (Emroth-Cugell & Robson, 1966)

\[
\tilde{G}_{\text{DOG}}(k, \omega) = \tilde{f}_{\text{DOG}}(k) \tilde{h}(\omega) = (A_1 e^{-k^2/a_1^2} - A_2 e^{-k^2/a_2^2}) \tilde{h}(\omega).
\]

With the parameters \( A_1, A_2, a_1, \) and \( a_2 \) [as well as the temporal function \( h(t) \) specified, \( G_{\text{DOG}}(r, t) \) and \( \tilde{G}_{\text{DOG}}(k, \omega) \) immediately give the DOG-model responses to a “delta-spot” and a full-field drifting grating, respectively. To predict the responses to other visual stimuli, an integral must be evaluated, and it is a matter of convenience whether the real-space [eqn. (1)] or Fourier-space [eqn. (3)] expression is used.

As a simple example, we consider the DOG-model response to flashing circular spots centered at the receptive-field center of the cell. Here a spot with diameter \( d \) is turned on at time \( t = 0 \) and kept on for a duration \( \Delta t \). The mathematical expression for this stimulus is given by

\[
s_{\text{spw}}(r, t) = C_s [1 - \Theta(r - d/2)][\Theta(t) - \Theta(t - \Delta t)],
\]

where \( C_s \) is a constant reflecting the spot luminance, and \( \Theta(x) \) is the Heaviside step function defined by \( \Theta(x < 0) = 0 \), \( \Theta(x \geq 0) = 1 \).

For a neuron positioned at \( r = 0 \), the firing rate due to this stimulus is then predicted by the DOG model to be [eqn. (1)]
where the temporal function $H(t)$ comes from evaluating the temporal integral. If one is interested in the total number of action potentials during a time period, an integral over $H(t)$ must be performed. This gives a constant which together with $C_d$ typically is absorbed into redefined values of the weights $A_1$ and $A_2$.

**DOG-model response to circular patch gratings**

For a circular patch of drifting grating (specified by $k_d$ and $\omega_d$, the diameter $d$, and the constant $C_d$), the stimulus can be mathematically described as [cf. eqns. (6) and (13)]

$$s_{pg}(r, t) = C_d[1 - \Theta(r - d/2)]\cos(k_dr - \omega_dt). \tag{15}$$

To evaluate the DOG-model response to this stimulus, we will use the Fourier expression in eqn. (3), and we thus need to evaluate the Fourier transform of $s_{pg}(r, t)$.

**Fourier expression of patch-grating stimulus**

As in the full-field grating case above, it is convenient to consider the “complex” version of the patch-grating stimulus in eqn. (15), that is,

$$s^c_{pg}(r, \omega) = C_d[1 - \Theta(r - d/2)]e^{(ik_dr - \omega_d)t}. \tag{16}$$

The Fourier transform of the (complex) patch-grating stimulus is then given by eqn. (4):

$$\mathcal{F}\{s^c_{pg}(r, \omega)\} = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} s^c_{pg}(r, \omega) e^{-i(\mathbf{k} \cdot \mathbf{r} - \omega_d t)} \, dx \, dy$$

$$= C_d \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} e^{(ik_dr - \omega_d t)[1 - \Theta(r - d/2)]} e^{-i(\mathbf{k} \cdot \mathbf{r})} \, dx \, dy$$

$$= C_d \int_{r=d/2}^{\infty} \int_{r=d/2}^{\infty} e^{-i(k_dr)} \, dx \, dy$$

$$= 2\pi C_d \delta(\omega - \omega_d) \int_{r=d/2}^{\infty} e^{-i\mathbf{k} \cdot \mathbf{r}} \, dx \, dy \tag{17}$$

where we have used eqn. (8) and introduced $\mathbf{K} = \mathbf{k} - \mathbf{k}_d$ to compress the notation. The spatial integral is solved by using polar coordinates:

$$\int_{r=d/2}^{\infty} e^{-i\mathbf{k} \cdot \mathbf{r}} dx \, dy = \int_{0}^{d/2} \int_{0}^{2\pi} e^{-i\mathbf{k} \cdot \mathbf{r}} \cos \theta \, d\theta \, dr,$$

$$= \frac{\pi d}{K} J_1(Kd/2). \tag{18}$$

Here $J_0(x)$ and $J_1(x)$ are the zeroth- and first-order Bessel functions, respectively, and we have used the relations (Butkov, 1968; Bracewell, 1986)

$$J_0(x) = \frac{1}{2\pi} \int_{0}^{2\pi} e^{-ix\cos \theta} \, d\theta$$

$$sJ_0(x) = \frac{d(J_1(x))}{dx}. \tag{19}$$

When we substitute back $\mathbf{k} - \mathbf{k}_d$ for $\mathbf{K}$, we thus find

$$\tilde{s}^c_{pg}(\mathbf{k}, \omega) = C_d 2\pi^2 \delta(\omega - \omega_d) d^2 \frac{J_1((\mathbf{k} - \mathbf{k}_d)d/2)}{|\mathbf{k} - \mathbf{k}_d|d}$$

$$= C_d \delta(\omega - \omega_d) \frac{\pi^2 d^2}{2} S_1(|\mathbf{k} - \mathbf{k}_d|d/2), \tag{20}$$

where we have introduced a function $S_1(x)$ defined via

$$S_1(x) = \frac{2J_1(x)}{x}. \tag{21}$$

The function $S_1(x)$ is shown in Fig. 1. It has a maximum value of 1 for $x = 0$, while its roots coincide with those of $J_1(x)$, the first being located at $x \approx 3.832$ (Butkov, 1968).

Typical experimental values for patch-grating spatial frequencies $\nu_d$ have been in the range 0.5–1 cycles/deg (Sillito et al., 1993; Cudeiro & Sillito, 1996). This corresponds to $k_d = |\mathbf{k}_d| = 2\pi\nu_d$ in the range 3.14–6.28 deg$^{-1}$. In Fig. 1, we further plot the function $S_1(|\mathbf{k} - \mathbf{k}_d|d/2)$ for different diameter values $d$ for $k_d = 3.14$ deg$^{-1}$. We see that the smaller the spot diameter $d$, the broader the peak around $k_d$. In the limit $d \to \infty$, the only contribution will come from $\mathbf{k} = \mathbf{k}_d$, reflecting that the patch grating approaches a full-field grating in this limit. In Fig. 1, we finally show a contour plot of the function $S_1(|\mathbf{k} - \mathbf{k}_d|d/2)$ for an example patch grating with a diameter of $d = 1.5$ deg.

Fig. 1 illustrates the simple functional form of $\tilde{s}^c_{pg}(\mathbf{k}, \omega)$ in eqn. (20). The diameter of the patch determines the shape of the circularly symmetric envelope in $k$-space ($S_1(x)$) while $k_d$ determines where in $k$-space this envelope is positioned.

**Integral expressions for DOG-model response**

We can now insert the result for $\tilde{s}^c_{pg}(\mathbf{k}, \omega)$ from eqn. (20) into the general response expression in eqn. (3). This gives
in time with the angular frequency which shows that the response of the neuron will vary sinusoidally.

The (Fourier transformed) impulse-response function \( \tilde{G}(k, \omega) \) of choice (i.e., the model of choice) can now be inserted into this two-dimensional integral over \( k \) to obtain both the amplitude and the phase shift of the sinusoidal modulation as a function of \( k_d \) and patch diameter \( d \). In the general case, this integral must be computed numerically (Einevoll & Plesser, 2003), but for the DOG model it can be transformed to a one-dimensional integral.

For the case where the patch and the DOG receptive field are concentric (\( r = 0 \)), it follows from eqns. (12) and (22) that the patch-grating response is given by

\[
R^c_{pg}(r, t) = \frac{1}{(2\pi)^3} \int_\omega \int_k \frac{\pi^2 d^2}{2} S_i(|k - k_d|/d) \, dk_x \, dk_y \, dw, \\
= C_d \frac{d^2}{16\pi} e^{-i \omega t} \int_k e^{i \omega t} \tilde{G}(k, \omega_d) \\
\times S_i(|k - k_d|/d) \, dk_x \, dk_y.
\]

which shows that the response of the neuron will vary sinusoidally in time with the angular frequency \( \omega_d \) of the drifting grating inside the patch.

\[
R^c_{pg}(t) = \frac{C_d d^2}{16\pi} \tilde{h}(\omega_d) e^{-i \omega_d t} \int_k (A_1 e^{-k^2 \hat{a}_1^2/4} - A_2 e^{-k^2 \hat{a}_2^2/4}) \\
\times S_i(|k - k_d|/d) \, dk_x \, dk_y.
\]  

In the Appendix we show that this response expression can be transformed to

\[
R^c_{pg}(t) = C_d \hat{h}(\omega_d) e^{-i \omega_d t} \left[ A_1 X \left( \frac{a_1}{d}, a_1 k_d \right) - A_2 X \left( \frac{a_2}{d}, a_2 k_d \right) \right],
\]  

where \( X(y, z) \) is a two-dimensional function given by the one-dimensional integral

\[
X(y, z) = e^{-z^2/4} \int_0^\infty e^{-y^2 x^2} I_0(yz) J_1(x) \, dx.
\]

Here \( I_0(x) \) is the zeroth-order modified Bessel function (Abramowitz & Stegun, 1965).

We see that the spatial part of the expression for \( R^c_{pg}(t) \) depends on four relationships between the four length scales \( a_1 \), \( a_2 \), \( d \), and \( 1/k_d \): \( a_1/d \), \( a_2/d \), \( a_1 k_d \), and \( a_2 k_d \). We further see that the response only depends on the magnitude of the spatial fre-
frequency \(k_z/2\pi\) and not the orientation of the grating. This is a consequence of the circular symmetry of the DOG model.

**Series representation of DOG-model response**

The function \(X(y, z)\) given in an integral representation in eqn. (25) can also be represented as a series. This is done by using a series expansion of the modified Bessel function \(I_0(x)\) in the integrand. From Abramowitz and Stegun (1965), we have

\[
I_0(x) = \sum_{n=0}^{\infty} \frac{(x^2/4)^n}{n!(n+1)} = \sum_{n=0}^{\infty} \frac{(x^2/4)^n}{(n!)^2},
\]

(26)

where we have used that \(\Gamma(n+1) = n!\) for \(n \geq 0\). We now insert a series expression for \(I_0(x)\) into eqn. (25) and interchange the order of integration and summation:

\[
X(y, z) = e^{-z^2/4} \int_{0}^{\infty} e^{-y^2x^2} \sum_{n=0}^{\infty} \frac{1}{(n!)} \frac{1}{n} \int_{0}^{\infty} e^{-y^2x^2/4} J_n(x) \, dx,
\]

\[
= e^{-z^2/4} \sum_{n=0}^{\infty} \left( \frac{1}{4} \right)^n \frac{1}{n!} \int_{0}^{\infty} e^{-y^2x^2/4} J_n(x) \, dx.
\]

(27)

The integral in this final expression can be found in Gradshteyn et al. (2000):

\[
\int_{0}^{\infty} e^{-y^2x^2} x^{2n} J_n(x) \, dx = \frac{n!}{4y^{2n+1}} F_1(n+1; 2; -1/4y^2),
\]

(28)

where \(F_1(\alpha; \gamma; x)\) is the confluent hypergeometric function given by (Gradshteyn et al., 2000)

\[
F_1(\alpha; \gamma; x) = 1 + \frac{\alpha x}{\gamma} + \frac{\alpha(\alpha+1) x^2}{\gamma(\gamma+1) 2!} + \frac{\alpha(\alpha+1)(\alpha+2) x^3}{\gamma(\gamma+1)(\gamma+2) 3!} + \ldots
\]

(29)

For \(X(y, z)\), we thus have the series representation

\[
X(y, z) = e^{-z^2/4} \sum_{n=0}^{\infty} \frac{1}{(n!)} \frac{1}{n} \int_{0}^{\infty} e^{-y^2x^2/4} J_n(x) \, dx\times F_1(n+1; 2; -1/4y^2) = e^{-z^2/4} \sum_{n=0}^{\infty} \frac{1}{(n!)} \int_{0}^{\infty} e^{-y^2x^2/4} J_n(x) \, dx.
\]

(30)

which can be used when evaluating the DOG-model response to patch gratings using eqn. (24).

From the form of this series expression, it can be seen that as \(z \rightarrow 0\), fewer terms have to be included in a numerical evaluation of the series. In eqn. (24), it is seen that this second argument to the function \(X(y, z)\) is \(k_x a_i\) and \(k_y a_i\), respectively, that is, proportional to the magnitude of the patch-grating wavevector. In the “no-grating” limit where the spatial frequency is zero, that is, \(k_x a_i = 0\) \((i = 1, 2)\), only the first term \((n = 0)\) in the series in eqn. (30) will be nonzero, and we have

\[
X(y, 0) = \frac{1}{4y^2} F_1(1; 2; -1/4y^2),
\]

(31)

which can be recognized as (Abramowitz & Stegun, 1965)

\[
\frac{1}{4y^2} F_1(1; 2; -1/4y^2) = \frac{1}{4y^2} \frac{\epsilon^{-1/8y^2}}{(-1/8y^2)} \sinh^{-1}(1/8y^2) = 1 - \epsilon^{-1/4y^2}.
\]

(32)

Thus, we have \(X(a_i, d, 0) = 1 - \epsilon^{-d^2/4a_i^2} (i = 1, 2)\) in agreement with the previous result for a (flashing) iso-luminant spot in eqn. (14).

**Example results**

In Fig. 2, we show the spatial impulse-response function \(f_{\text{DOG}}(r)\) and the corresponding Fourier transform \(\tilde{f}_{\text{DOG}}(k)\) of the DOG model considered in the following example applications.

In Fig. 3 (upper left), we plot area-summation curves, that is, patch-grating response \([A_1 X(a_1/d, a_1, k_y) - A_2 X(a_2/d, a_2, k_y); cf. eqn. (24)]\) vs. diameter for our example DOG model in Fig. 2 using...
both the series expression for \(X(y, z)\) in eqn. (30) and the integral expression in eqn. (25). With a sufficient number of terms, the series converges to the correct result; for this particular example with \(k_d = 3.14\) deg\(^{-1}\) five terms (\(n_{\text{max}} = 4\) ) are seen to be sufficient to assure convergence. For larger values of \(k_d\), more terms must be included in the series summation to obtain an accurate numerical value for \(X\).

In Fig. 3 (upper right), we show corresponding area-summation curves for a set of different values of patch-grating wavevector magnitudes \(k_d\). The series expression for \(X(y, z)\) in eqn. (30) is used and up to 16 terms are included in the series summation for the largest considered value of \(k_d\). This plot illustrates the significant role played by the wavevector magnitude \(k_d\) in determining the diameter dependence of the patch-grating response. The area-summation curve for the iso-luminant spot (\(k_d = 0\), solid line) shows a strong surround suppression for this example model. For relatively small values of \(k_d\), for example, \(k_d = 2\) deg\(^{-1}\) (dashed line), the response curve follows the iso-luminant spot curve closely for small diameters, but lies significantly above for larger diameters. The response peak near the receptive-field center size, \(d = 0.85\) deg, is hardly discernible for \(k_d = 4.4\) deg\(^{-1}\) (dot-dashed line), and it is clearly lower than the response obtained for the largest patch diameters. Thus in this case, stimulation of the surround enhances rather than suppresses the response. For \(k_d = 10\) deg\(^{-1}\) the response is significantly reduced all over. Even though it displays some minor oscillations for diameters \(d\) between 0.5 and 2 deg, the response varies little over most of the diameter range (\(d > 0.5\) deg). Fig. 3 (lower), showing a contour plot of the patch-grating response versus diameter and wavevector magnitude, highlights these points. The two main qualitative features are immediately apparent: for large diameters (\(d > 2\) deg) the response is largest for \(k_d \approx 4\)–\(5\) deg\(^{-1}\) and the iso-luminant (\(k_d = 0\)) response peak around \(d \approx 0.85\) deg is lowered with increasing \(k_d\).

The observed strong response for large diameters for \(k_d \approx 4\)–\(5\) deg\(^{-1}\) is easily understood by looking at the Fourier-transformed receptive field \(f_{\text{DOG}}(k)\) in Fig. 2 (right). Our example DOG model is seen to have its maximum of \(f_{\text{DOG}}(k)\) at \(k = 4.4\) deg\(^{-1}\), and for large diameters the patch grating will approach a full-field grating where the response is given by \(f_{\text{DOG}}(k)\). For smaller spot diameters, the spread in \(k\)-space around \(k_d\) of the stimulus Fourier
shown in Fig. 2. Contributions to the response integral in eqn. (23) will thus come from larger parts of $k$-space where $f_{\text{DOG}}(k)$ is smaller, and the band-pass peak for $k = 4.4 \text{ deg}^{-1}$ will become smaller and eventually vanish.

The interplay between and relative contributions from the center $[A_1X(a_1/d,a_1,k_d)]$ and surround $[A_2X(a_2/d,a_2,k_d)]$ terms in eqn. (24) are illustrated in Fig. 4. Here we plot the response as a function of the magnitude of the patch-grating wavevector $k_d$ for four different patch-grating diameters. The upper left panel corresponds to a large diameter, and the DOG-model response essentially is identical to the full-field grating response shown in Fig. 2 (right). This panel further demonstrates the well-known and characteristic band-pass feature of the DOG model, and how it arises from subtracting the surround contribution from the center contribution.

The upper right panel shows the result for $d = 1.5 \text{ deg}$ corresponding to nearly twice the diameter of the receptive-field center. The frequency characteristic is still band-pass, but it is less prominent. We also see that this change mainly follows from a qualitatively different frequency response imposed by the patch on the spatially more extended DOG surround term: the magnitude has been reduced for small spatial frequencies and increased for large spatial frequencies. The contribution from the narrower DOG center term is much less affected.

The lower left panel of Fig. 4 shows the situation where the patch diameter equals the receptive-field center size, $d = 0.85 \text{ deg}$. Here the band-pass feature of the full-field grating has vanished and has been replaced by a low-pass response characteristic, that is, maximum for $k_d = 0$.

The lower right panel corresponds to a very small patch diameter, $d = 0.3 \text{ deg}$, where the frequency response of both the center and surround DOG terms is dominated by the patch. The net result is a weak response with a low-pass characteristic. In the small-diameter limit $d \to 0$ the function $S_1([k - k_d]/d/2)$ widens out and approaches unity for all values of $k$, and the integral over $k$-space in eqn. (23) can be done analytically. In this limit, we find that the contributions from the center and surround DOG terms are $A_1d^2/4a_1^2$ and $A_2d^2/4a_2^2$, respectively, and the relative weight of the surround compared to the center term is thus $A_2a_1^2/A_1a_2^2$. For the example DOG model in the figure, this ratio is 0.225. This is not too different from the numerical value 0.247 found for $k_d = 0$ for the small (but not infinitely small) diameter value $d = 0.3 \text{ deg}$ considered in the lower right panel of Fig. 4.

The upper right and lower left panels of Fig. 4 also illustrate that center and surround responses to patch gratings can switch sign (corresponding to a 180 deg phase change of the oscillating response) when stimulus parameters are varied. In the upper right panel ($d = 1.5 \text{ deg}$), the contribution from the surround $[A_2X(a_2/
Likewise, the total DOG-model response becomes (barely) negative for \( k_d \sim 18–20 \text{ deg}^{-1} \). The sign switch of the surround contribution for \( k_d \sim 7–10 \text{ deg}^{-1} \) can be understood mathematically by considering the response integral expression in eqn. (23). For \( d = 1.5 \text{ deg} \) and \( k_d \sim 7–10 \text{ deg}^{-1} \), there will be relatively little overlap between the positive central lobe of \( S_1([k - k_d]/d/2) \) and the surround Gaussian \( A_2 \exp(-k^2/2) \) (cf. Fig. 1 (upper right, dashed line) and Fig. 4 (upper left, dot-dashed curve)). However, the first negative lobe of \( S_1([k - k_d]/d) \) will overlap substantially with the surround Gaussian, and as a consequence the spatial integration over \( k \)-space will end up giving a negative number.

Compared to the full-field grating situation in the upper left panel of Fig. 4, we see that the patch-grading data in the other panels have a larger high-frequency cutoff. The relative weight of the high frequencies will be largest for smaller patch gratings where \( S_1([k - k_d]/d) \) has the largest extension in \( k \)-space. Then the spatial integral in eqn. (23) can become nonnegligible even when \( k_d \) is larger than the high-frequency cutoff for the full-field grating case.

Fig. 4 further illustrates that with patch gratings stimulation of the surround does not necessarily reduce the response compared to stimulation of only the receptive-field center. By comparison of the results in the upper left and lower left panels, we can infer that for \( k_d \) in the range \( \sim 3.5–8 \text{ deg}^{-1} \) the full-field grating response is relatively constant, in fact larger than the response from stimulating only the receptive-field center. Such a wavevector-dependent transition between surround suppression and spatial enhancement for patch gratings was observed for an LGN X cell reported by Cudeiro and Sillito (1996, Fig. 2).

Discussion

The main result of this article is the mathematical formula for the DOG-model response to centered circular patch gratings in terms of two summed series. From eqns. (24) and (30), we have that the spatial part of this response is given by

\[
\bar{R}_{\text{pp}}(d, \nu) = A_1 X\left(\frac{a_1}{d}, 2\pi a_1 \nu_d\right) - A_2 X\left(\frac{a_2}{d}, 2\pi a_2 \nu_d\right),
\]

\[
X(y, z) = e^{-z^2/4} \frac{1}{4\pi} \sum_{n=0}^{\infty} \frac{1}{n!} \left(\frac{z}{2}\right)^{2n} iF_1(n + 1; 2; -1/4y^2),
\tag{33}
\]

where \( \nu_d \) and \( d \) are the spatial frequency and diameter of the circular patch grating, respectively, and \( A_1, a_1, A_2, \) and \( a_2 \) are DOG-model parameters.

This formula encompasses two well-known limiting cases: full-field drifting grating and iso-luminant (flashing) spot. A full-field grating is obtained in the large-diameter limit \( d \to \infty \), where the response expression is given by [cf. eqn. (12)]

\[
\bar{R}_{\text{dd}}(\nu_d) = A_1 e^{-\pi^2 a_1^2 \nu_d^2} - A_2 e^{-\pi^2 a_2^2 \nu_d^2}. \tag{34}
\]

An iso-luminant spot is obtained in the zero spatial-frequency limit \( \nu_d \to 0 \), and in this case the response is given by [cf. eqns. (14) and (32)]

\[
\bar{R}_{\text{spud}}(d) = A_1 (1 - e^{-d^2/4a_1^2}) - A_2 (1 - e^{-d^2/4a_2^2}). \tag{35}
\]

Each term in the series representation for \( X(y, z) \) in eqn. (33) involves the confluent hypergeometric function \( iF_1 \) (Gradshteyn et al., 2000). Although unfamiliar to some, this special function is available in commonly used mathematical software such as MATLAB and MATHEMATICA. Application of this formula for comparison and fitting of the DOG model to experimental data should therefore be straightforward.

The contour plot in Fig. 3 (lower) for our example DOG model illustrates that the interplay between the four length constants in the system (DOG spatial widths \( a_1, a_2 \), patch-grating diameter \( d \), patch-grating wavelength \( 2\pi/k_d \)) can give a variety of qualitatively different response characteristics even for the simple DOG model.

One characteristic feature is the dependence of the surround suppression in area-summation curves (response vs. patch diameter) on the patch-grating wavevector. In Fig. 3 (upper right), we observed in our example model a significant surround suppression for the iso-luminant spot, less so for \( k_d = 2 \text{ deg}^{-1} \), while for \( k_d = 4.4 \text{ deg}^{-1} \) a surround enhancement was observed. This feature agrees qualitatively with the observation for decorticated LGN cells by Sillito and Jones (2002) where a significant reduction of surround suppression was seen for patch gratings compared to flashing spots.

Another characteristic feature is the transition from the full-field band-pass response to a low-pass response when the patch diameter equals the receptive-field center size (cf. Fig. 4). This is in qualitative agreement with experimental observations of cat LGN X cells in Cudeiro and Sillito (1996, Fig. 4).

While two length constants \((d, 2\pi/k_d)\) characterize the patch-grating stimulus, full-field drifting gratings and flashing spots are characterized by only a single length constant \((2\pi/k_d \text{ and } d)\), respectively. Thus, as demonstrated here a richer set of qualitatively different response characteristics can be obtained for patch gratings, and this can be helpful when probing the system. If such experiments are pursued and a comparison with the DOG model is wanted, the necessary mathematical apparatus is provided here.

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References


\[
\int_{\mathbf{k}} e^{-i k \cdot x / a} \frac{d^2}{16\pi} S_1(|\mathbf{k} - \mathbf{k}_d|/d) \, dk_x \, dk_y = X(a/d, ak_d).
\]

From the definition of \(S_1(x)\) in eqn. (21), it follows that the left side of eqn. (36), labeled \(I\), is given by

\[
I = \int_{\mathbf{k}} e^{-i k \cdot x / a} \frac{d^2}{16\pi} 2 J_1(|\mathbf{k} - \mathbf{k}_d|/d) \, d(k_x \, dk_y)
\]

\[
= \int_{\mathbf{k}} e^{-i k \cdot x / a} \frac{d}{4\pi|\mathbf{k} - \mathbf{k}_d|/d} \, dk_x \, dk_y.
\]

We introduce \(\mathbf{K} = \mathbf{k} - \mathbf{k}_d\) and change the integration variable from \(\mathbf{k}\) to \(\mathbf{K}\), and obtain

\[
I = \int_{\mathbf{K}} e^{-i \mathbf{K} \cdot \mathbf{x} / a} \frac{d^2}{4\pi} \frac{J_1(K_d/2)}{4\pi K} \, dK_x \, dK_y
\]

\[
= \int_{\mathbf{V}} e^{-i \mathbf{v} \cdot \mathbf{x} / a} \frac{d^2}{2\pi} \frac{J_1(V/2)}{2\pi V} \, dV_x \, dV_y,
\]

where we in the last step have introduced the dimensionless variables \(\mathbf{V} = \mathbf{K}d/2\) and \(V_d = \mathbf{k}_d d/2\). We further introduce the dimensionless parameter \(y = a/d\) as well as polar coordinates for \(\mathbf{V}\):

\[
I = \int_{0}^{\pi} \int_{0}^{\infty} e^{-V^2 + V_y^2 + 2V_y \cos \theta} \frac{J_1(V)}{2\pi V} \, dV \, d\theta
\]

\[
= e^{-V_y^2 / 4} \int_{0}^{\infty} e^{-V^2 / 4} \left( \int_{0}^{\pi} e^{-V_y \cos \theta} \cos \theta \right) \frac{J_1(V)}{2\pi} \, dV
\]

\[
= e^{-V_y^2 / 4} \int_{0}^{\infty} e^{-V^2 / 4} J_1(2V_y d^2) J_1(V) \, dV.
\]

Here we have introduced the modified Bessel function \(I_0(x)\) by use of the relation (Abramowitz & Stegun, 1965)

\[
I_0(x) = \frac{1}{2\pi} \int_{0}^{2\pi} e^{ix \cos \theta} \, d\theta.
\]

With another dimensionless parameter \(z = ak_d = dy_k = 2V_y d\), we can write the final integral as

\[
I = e^{-z^2/4} \int_{0}^{\infty} e^{-V^2 / 4} I_0(Vy_c) I_1(V) \, dV
\]

which is identical to \(X(y, z)\) in eqn. (25).