Extended DOG Model for Relay Cells in Cat Lateral Geniculate Nucleus

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Abstract

The early visual pathway (EVP) from retina via the visual thalamus to primary visual cortex is one of the best studied sensory pathways. Most models of the EVP, though, are focused on particular elements of the pathway, or specific issues. In particular, only few models have hitherto included feedback; see [1–3] for exceptions.

We propose to remedy this lack by a two-pronged approach:

1. A *Comprehensive Thalamocortical Model* (CoThaCo) based on spiking model neurons, implemented using the NEST neural network simulator [4, 5].
2. A linear filter model as we published recently [6].

Both models are *mechanistic* models, i.e., response properties are inferred from the known or proposed connectivity within the visual pathway, in contrast to *descriptive* models, which aim to characterize response properties parsimoniously. Mechanistic models thus allow us to test hypotheses on connectivity within neuronal networks.

On this poster, we use the linear filter model of the EVP to study the effect of cortico-thalamic feedback on the response properties of X-type relay cells in the dorsal lateral geniculate nucleus (dLGN). We argue in particular that

- the feedback impinging on any relay cell is isotropic;
- the resulting effective receptive field of the geniculate relay cell can be characterized by an extended difference-of-Gaussian (eDOG) model.

Filters

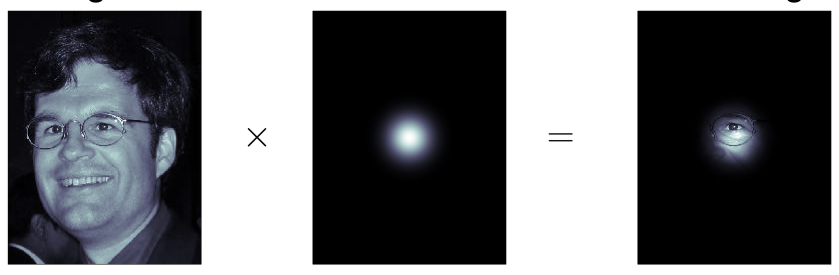
Masking

Masking is equivalent to multiplication of signal and mask in real space:

$$R(\mathbf{r}) = m(\mathbf{r}) \times S(\mathbf{r})$$

A Gaussian mask cuts out part of the image:

Signal × Mask = Masked signal



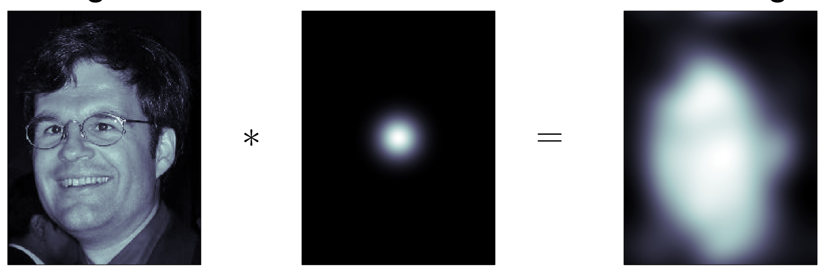
Filtering: Low-pass

Filtering is equivalent convolution in real space, or to multiplication in Fourier space:

$$r(\mathbf{r}) = \iint f(\mathbf{r}-\mathbf{r}')s(\mathbf{r}')d^2\mathbf{r}' \equiv f(\mathbf{r}) * s(\mathbf{r})$$

The same Gaussian, applied as filter, smoothes the image:

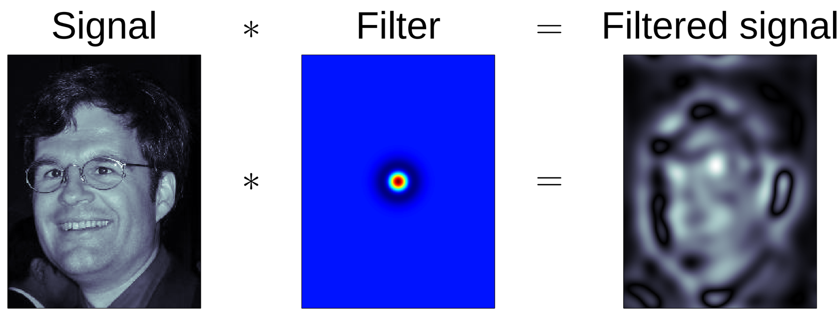
Signal * Filter = Filtered signal



Filtering: Difference-of-Gaussians

Difference-of-Gaussians filter highlights edges:

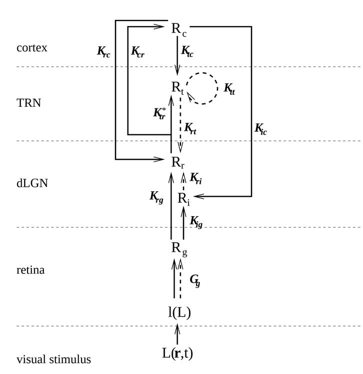
Signal * Filter = Filtered signal



Visual Pathway

In our model, we describe the early visual pathway as a sequence of linear filter $K(\mathbf{r}, t)$ connecting neuronal populations, represented by their firing-rate fields $R(\mathbf{r}, t)$, eg

- R_{r} geniculate relay cell population
- K_{cr} feedforward LGN $\longrightarrow$ cortex
- K_{rc} feedback cortex $\longrightarrow$ LGN
- L stimulus impinging on retina



Solid lines mark excitatory, dashed lines inhibitory coupling.

Transfer function

In linear approximation, one can completely describe the signal processing properties by its transfer function

$$\tilde{T}(\mathbf{k}, \omega) = \frac{\text{output at } (\mathbf{k}, \omega)}{\text{input at } (\mathbf{k}, \omega)}$$

In [6] we derived the following expression for the transfer function of geniculate relay cells

$$\tilde{T}_{\mathrm{rg}}(\mathbf{k}, \omega; L_0) = \frac{\tilde{K}_{\mathrm{rg}}(\mathbf{k}, \omega) + \tilde{K}_{\mathrm{ri}}(\mathbf{k}, \omega)\tilde{K}_{\mathrm{ig}}(\mathbf{k}, \omega)}{\left[1 - \tilde{K}_{\mathrm{rc}}(\mathbf{k}, \omega)\tilde{K}_{\mathrm{cr}}(\mathbf{k}, \omega) - \tilde{K}_{\mathrm{ri}}(\mathbf{k}, \omega)\tilde{K}_{\mathrm{ic}}(\mathbf{k}, \omega)\tilde{K}_{\mathrm{cr}}(\mathbf{k}, \omega) - \frac{\tilde{K}_{\mathrm{rt}}(\mathbf{k}, \omega)\tilde{K}^{*}_{\mathrm{tr}}(\mathbf{k}, \omega; L_0) + \tilde{K}_{\mathrm{rt}}(\mathbf{k}, \omega)\tilde{K}_{\mathrm{tc}}(\mathbf{k}, \omega)\tilde{K}_{\mathrm{cr}}(\mathbf{k}, \omega)}{1 - \tilde{K}_{\mathrm{tt}}(\mathbf{k}, \omega)}\right]}$$

We assume that the feedforward contribution (numerator) can be described as a difference of Gaussian $\tilde{f}_{\mathrm{DOG}}(\mathbf{k}, \omega)$, and focus on direct cortical feedback. The transfer function then simplifies to

$$\tilde{T}_{\mathrm{rg}}(\mathbf{k}, \omega) = \frac{\tilde{f}_{\mathrm{DOG}}(\mathbf{k}, \omega)}{1 - \tilde{K}_{\mathrm{rc}}(\mathbf{k}, \omega)\tilde{K}_{\mathrm{cr}}(\mathbf{k}, \omega) - \tilde{K}_{\mathrm{ri}}(\mathbf{k}, \omega)\tilde{K}_{\mathrm{ic}}(\mathbf{k}, \omega)\tilde{K}_{\mathrm{cr}}(\mathbf{k}, \omega)} \; . \qquad (1)$$

Cortical Feedback

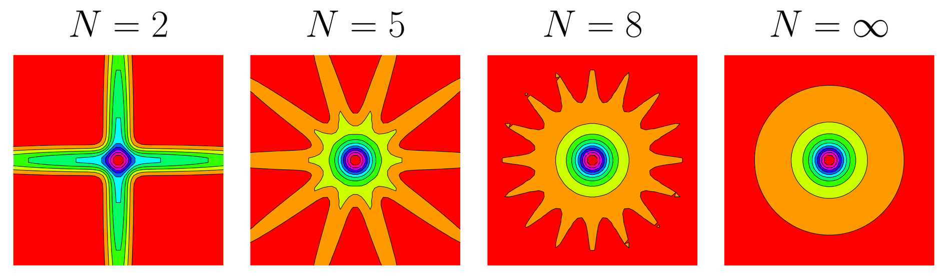
Thalamocortical projections are spatially structured to yield bar-shaped cortical receptive fields, and cortico-thalamic feedback appears to follow similar patterns. The excitatory feedback term in Eq. (1) should thus be written as

$$\begin{aligned} &\tilde{K}_{\mathrm{rc}}(\mathbf{k}, \omega)\tilde{K}_{\mathrm{cr}}(\mathbf{k}, \omega) \\ \longrightarrow\; &\frac{1}{N}\sum_{n=1}^{N} \tilde{K}_{\mathrm{rc}}(\mathbf{k}, \omega; \frac{2\pi n}{N})\tilde{K}_{\mathrm{cr}}(\mathbf{k}, \omega; \frac{2\pi n}{N}) \\ \longrightarrow\; &\int_0^{2\pi} \tilde{K}_{\mathrm{rc}}(\mathbf{k}, \omega; \theta)\tilde{K}_{\mathrm{cr}}(\mathbf{k}, \omega; \theta) d\theta \; , \end{aligned}$$

and likewise for the inhibitory term. Note that the total cortical feedback to a thalamic relay cell is *independent* of orientation, since all direction contribute to the feedback.

Examples for effective spatial feedback

$N = 2$ $N = 5$ $N = 8$ $N = \infty$



DOGs and Mirrors

Equation (1) describes a feedback *loop*: feedback will affect input to cortex, which affects feedback, which in turn affects input to cortex, etc ad infinitum. We make the following assumptions to facilitate analysis:

- slow stimuli $\longrightarrow$ ignore temporal filtering;
- excitatory and inhibitory feedback have circular Gaussian profile;
- feedback is weak.

The transfer function can then be written as

$$\tilde{T}_{\mathrm{rg}}(\mathbf{k}) = \frac{A_1 e^{-k^2 a_1^2} - A_2 e^{-k^2 a_2^2}}{1 - Ce^{-k^2 c^2} + De^{-k^2 d^2}} \; .$$

Using the series expansion $1/1{+}x \approx \sum_n (-x)^n$ and Fourier-transforming to real space, one obtains

$$T_{\mathrm{eDOG}}(r) = \frac{1}{\pi}\sum_{n=0}^{\infty}\sum_{m=0}^{n}(-1)^m \binom{n}{m} C^{n-m}D^m \left[\frac{A_1}{a_{1,nm}^2} e^{-\frac{r^2}{a_{1,nm}^2}} - \frac{A_2}{a_{2,nm}^2} e^{-\frac{r^2}{a_{2,nm}^2}}\right]$$

The first series terms represent

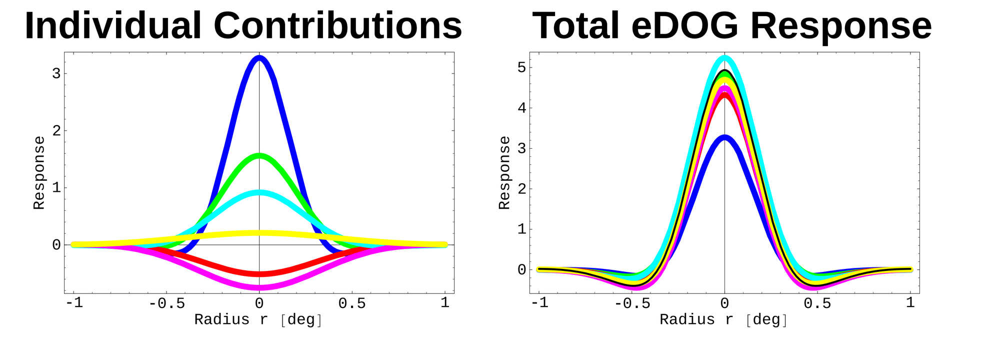
$$\frac{A_1}{a_1^2} e^{-r^2/a_1^2} - \frac{A_2}{a_2^2} e^{-r^2/a_2^2} \qquad \text{(feedforward)}$$

$$\frac{A_1}{(a_1^2+c^2)} e^{-r^2/(a_1^2+c^2)} - \frac{A_2}{(a_2^2+c^2)} e^{-r^2/(a_2^2+c^2)} \qquad \text{(excitatory FB)}$$

$$\frac{A_1}{(a_1^2+d^2)} e^{-r^2/(a_1^2+d^2)} - \frac{A_2}{(a_2^2+d^2)} e^{-r^2/(a_2^2+d^2)} \qquad \text{(inhibitory FB)}$$

$$\frac{A_1}{(a_1^2+2c^2)} e^{-r^2/(a_1^2+2c^2)} - \frac{A_2}{(a_2^2+2c^2)} e^{-r^2/(a_2^2+2c^2)} \qquad \text{(iterated exc. FB)}$$

Individual Contributions **Total eDOG Response**



Summary

We have presented a comprehensive analytical model of the early visual pathway, based on linear filters connecting neuronal populations at different stations in the pathway. From this model, expressions for response properties of thalamic relay cells can be derived in various approximations. We have shown in particular, that the influence of cortico-thalamic feedback on relay cell response properties can be characterized by a series of differences of Gaussians, i.e., by and *extended difference of Gaussians (eDOG)*.

We expect the eDOG representation to be applicable in the limit of not too fast stimuli ($\mathcal{O}(1Hz)$) and for stimuli with limited contrast.

References

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[6] G. T. Einevoll and H. E. Plesser, Network-Comp Neural **13**, 503 (2002).