Nonlinear Analysis of Spatio-Temporal Receptive Fields: V. Dot, Bar, and Grating Response of Gabor-wavelets

Thomas Wennekers [1]

Max-Planck-Institute for Mathematics in the Sciences, Inselstr. 22–26, D-04103 Leipzig, Germany

Abstract

We calculate the convolution of two Gabor-wavelets, one a simple cell receptive field (RF), the other one a stimulus that contains dots, bars, and gratings as limiting cases. Assuming alpha-functions and damped sine-waves as temporal response functions, the spatio-temporal spectrum of a non-separable RF is also given. Effects of threshold nonlinearities are further estimated. Results provide tuning functions for orientation, spatial and temporal phase and frequency, and direction tuning indexes. The formulas should turn out useful in experimental fitting and model analysis.

Key words: Receptive field; Neural field equation; Gabor wavelets;

1 Introduction

In previous work we analysed mathematically the impact of feedforward and recurrent synaptic connections on tuning properties of neurons in nonlinear neural field equations [7,8]. This work from scratch assumed that input into cortical cells is Gaussian tuned in some feature dimension as the orientation of a bar or grating stimulus. Therefore, in the present paper, we consider the feedforward projection from LGN- to cortical simple cells assuming a field of cells with receptive fields (RFs) defined by a space-time kernel $k(r,t)$

$$\phi(r,t) = \int k(r-r', t-t') I(r', t') dt' d^n r' \tag{1}$$

$$\stackrel{sep}{=} \int h(r-r') I_r(r') d^n r' \cdot \int g(t-t') I_t(t') dt' \; . \tag{2}$$

[1] Tel.: +49-341-9959-533; Fax: +49-341-9959-555, wenneker@mis.mpg.de

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In (1) $\phi(r,t)$ is the membrane response for stimulus $I(x,t)$. The second form in (2) holds for space-time separable kernel $k(r,t) = h(r)g(t)$ and input $I(r,t) = I_r(r)I_t(t)$. For $h(r)$ we take n-dimensional Gabor-wavelets [1,3,5]

$$h(r;\Sigma_0,k_0,\psi_0) = e^{-\frac{1}{2}r^T\Sigma_0^{-1}r}\cos(k_0^T r - \psi_0)\ . \tag{3}$$

In section 2 we first compute the convolution of two arbitrary Gabor functions. This yields spatial responses of Gabor-type RFs to dots, bars, and gratings for special parameter choices. Section 3 considers temporal frequency spectra if $g(t)$ are combinations of alpha-functions and damped sine-waves. The spatial and temporal spectra are combined in section 4 to expressions for the amplitude and phase-transfer function of a non-separable RF. Finally, section 5 considers the impact of threshold non-linearities.

2 Convolution of two Gabor-wavelets

The (complex) Fourier-transform, H_0, of a Gaussian, h_0, reads

$$h_0(r;\Sigma_0) = e^{-\frac{1}{2}r^T\Sigma_0^{-1}r} \leftrightarrow H_0(k;\Sigma_0) = (2\pi)^{n/2}|\Sigma_0|^{1/2}e^{-\frac{1}{2}k^T\Sigma_0 k}\ , \tag{4}$$

where Σ_0 is the (symmetric) variance-matrix and $|\Sigma_0|$ its determinant. Because $\cos(k^T r - \psi) = \frac{1}{2}(e^{jk^T r - j\psi} + e^{-jk^T r + j\psi})$ one gets from (5) and (4)

$$H(k;\Sigma_0,k_0,\psi_0) = \frac{1}{2}\left(e^{j\psi_0}H_0(k+k_0;\Sigma_0) + e^{-j\psi_0}H_0(k-k_0;\Sigma_0)\right) \tag{5}$$

as the Fourier-transform of a general Gabor-wavelet (3). Now, consider the convolution of two n-dimensional Gabor-wavelets, a "filter" or "receptive field", and a "stimulus". Using (5) one derives

$$\phi(r) := \int_{R^n} h(r-r';\Sigma_0,k_0,\psi_0)\ h(r';\Sigma_1,k_1,\psi_1)\ d^n r' \tag{6}$$

$$\begin{aligned} &= \frac{(2\pi)^{n/2}|\Sigma_0|^{1/2}|\Sigma_1|^{1/2}}{2|\Sigma|^{1/2}} e^{-\frac{1}{2}k_0^T\Sigma_0 k_0}\ e^{-\frac{1}{2}k_1^T\Sigma_1 k_1}\ e^{-\frac{1}{2}r^T\Sigma^{-1}r}\ \cdot \\ &\quad \cdot\Big\{e^{-\frac{1}{2}k_+^T\Sigma^{-1}k_+}\cos(k_+^T\Sigma^{-1}r - \psi_0 - \psi_1) \\ &\quad + e^{-\frac{1}{2}k_-^T\Sigma^{-1}k_-}\cos(k_-^T\Sigma^{-1}r - \psi_0 + \psi_1)\Big\} \end{aligned} \tag{7}$$

where $\Sigma := \Sigma_0 + \Sigma_1$ and $k_\pm = \Sigma_0 k_0 \pm \Sigma_1 k_1$. As (7) shows, the spatial response of a Gabor-type receptive field to a Gabor-type stimulus is a sum of two

Gabor-wavelets (in r). The spatial Gaussian parts of both responses have the same variance, $\Sigma = \Sigma_0 + \Sigma_1$, but their amplitudes are different, and in especially, the spatial modulation in the cosine terms reveal wave-numbers $\Sigma^{-1}k_\pm = \Sigma^{-1}(\Sigma_0 k_0 \pm \Sigma_1 k_1)$ usually neither aligned to k_0 nor k_1. However, as one would expect, in the limit of a grating stimulus, $\Sigma_1^{-1} \to 0$ (cf. (3)), one has $\Sigma^{-1}k_\pm \to \pm k_1$ and (7) consist of two differently weighted, phase shifted left and right going waves with the same wave-number as the stimulus. In that limit one recovers results already given by others for grating stimuli [1,3,5]. Equation (7), however, is much more general, because it contains graiting, dot, bar, and Gaussian patch stimuli as special cases for different parameter choices. In particular, it suggests experiments, where the stimulus morphs smoothly in parameter space from one type, e.g., a grating, to another one, e.g., a bar or Gaussian patch. Deviations from responses predicted by (7) may yield insight into non-classical and/or non-linear receptive field effects.

Note, that several of the amplitude factors in (7) depend on stimulus properties like spatial frequency, k_1, or the orientation of Σ_1 and k_1 (which need not be aligned with the principal axes of Σ_1). It is possible, though somewhat tedious, to write down explicit formulas for spatial frequency and orientation tuning curves. The functional form of both depends on the precise stimulus (bar, grating, etc). In particular, orientation tuning curves are composed of several components, including von Mises functions, $e^{a \cos 2\theta}$, where θ is stimulus angle and a some modulation amplitude. As Swindale has shown [4], simple cell tuning curves can often be fitted better by von Mises functions than Gaussians.

3 Temporal response functions

A typical choice for $g(t)$ in (2) are "alpha-functions", $g_0(t) = t^\nu e^{-\lambda t}\Theta(t)$, which represent the impulse response of an $\nu + 1$ order low-pass with time-constant $1/\lambda$. The Fourier transform is (with Γ the gamma-function)

$$G_0(\omega) \equiv G_0(\omega; \nu, \lambda) = \frac{\Gamma(\nu+1)}{(\lambda^2 + \omega^2)^{(\nu+1)/2}} \exp\left[-j(\nu+1)\arctan\frac{\omega}{\lambda}\right] . \quad (8)$$

Responses with different time-constants (e.g., rise- and fall-times) can be treated by products of filters of the form (8). Experimental evidence shows that simple cell RFs are often not strictly low-pass, but oscillatory modulated [3,2]. This suggests taking $g(t)$ as $g_1(t) = g_0(t)\cos(\omega_0 t - \phi_0)$ which contains the decaying exponential, alpha-functions, damped sine and cosines, and their combination as special cases. The Fouriertransform of $g_1(t)$ is (cf. also (5))

$$G_1(\omega) \equiv G_1(\omega; \nu, \lambda, \omega_0, \phi_0) = \frac{1}{2}[G_0(\omega + \omega_0)e^{j\phi_0} + G_0(\omega - \omega_0)e^{-j\phi_0}] . \quad (9)$$

The spectrum (9) is of low-pass type for alpha functions and band-pass (resonance) for damped sine-waves. Amplitude and phase of K are easily obtained: If $z_\pm = |z_\pm| e^{j\phi_\pm}$ and $z := z_+ + z_- = |z| e^{j\phi}$ one first derives

$$|z|^2 = |z_+|^2 + |z_-|^2 + 2|z_+||z_-|\cos(\phi_+ - \phi_-), \tag{10}$$

$$\phi = \arg z = \tan^{-1}\left(\frac{|z_+|\sin(\phi_+) + |z_-|\sin(\phi_-)}{|z_+|\cos(\phi_+) + |z_-|\cos(\phi_-)}\right) . \tag{11}$$

Amplitude and phase of K result if one identifies $z_\pm$ with the two terms in (9). Absolute values $|z_\pm|$ and phases $\phi_\pm$ follow directly from (8) and (9). Observe also, that the spatial filter (5) can be treated in the same way.

4 Spatio-temporally non-separable receptive fields

DeAngelis et al. [2] presented experimental examples of inseparable simple cell receptive fields. We approximate those as a first choice by (12) which has the advantage that it can be written as a sum of two separable fields (14).

$$k(r,t) = h(r)\ \cos(k_0 r - \omega_c t - \psi_0)\ g(t)\ = \tag{12}$$

$$h(r)\cos(k_0 r - \psi_0) g(t)\cos(\omega_c t)\ +\ h(r)\sin(k_0 r - \psi_0) g(t)\sin(\omega_c t) \tag{13}$$

$$= h_c(r)\ g_c(t) + h_s(r)\ g_s(t)\ =:\ k_c(r,t) + k_s(r,t)\ . \tag{14}$$

If we choose for h a Gaussian h_0 as in (4) and for g an alpha-function g_0 as in (8) the Fourier tranform of h_c is exactly (5) whereas that of g_c is given by (9) with $\omega_0 = \omega_c, \phi_0 = 0$. Amplitudes and phases of these filters result from (10) and (11), and the amplitude of $K_c(k,\omega) = H_c(k)G_c(\omega)$ clearly is $|K_c| = |H_c||G_c|$. For the phase one gets $\arg K_c(k,\omega) = \arg H_c(k) + \arg G_c(\omega)$. To calculate the Fourier transform of $k_s(r,t) = h_s(r)\ g_s(t)$ observe that $\sin(x) = \cos(x - \pi/2)$. So, the Fourier transform $H_s(k,\omega)$ of $h_s(r,t) = h_0(r)\sin(k_0 r - \psi_0) = h_0(r)\cos(k_0 r - \psi_0 - \pi/2)$ is equal to $H(k;\Sigma_0, k_0, \psi_0 + \pi/2)$ in (5). Moreover, $G_s(\omega)$ equals $G_1(\omega; n, \lambda, \omega_c, \pi/2)$ in (9). We now have computed the amplitudes and phases of $K_c(k,\omega)$ and $K_s(k,\omega)$. The amplitude and phase of $K(k,\omega)$ finally result from (10) and (11) with $z_+ = K_c$ and $z_- = K_s$. K, as usual, describes the linear response of the inseparable receptive field (12) to moving gratings. The response to a counter-phase grating can be obtained from $K(k,\omega)$ as in [3,5]. If ψ is the spatial phase of the grating the response results from (10) for $z_\pm = K(\pm k,\omega)e^{\pm j\psi}$. Thus, $|z(\psi)|$, is an ellipse in polar coordinates. Obviously, direction tuning indexes (cf. [5]) can also be derived explicitly from $K(\pm k,\omega)$ for non-separable receptive fields of the form (12). If $g(t) = g_1(t)$ in (12) all calculations can be done as above (see Fig. 1).

5 Threshold non-linearities

Some of the results for graiting stimuli derived above have also been given by others [1,3,5]. Comparison with experiments were overall confirmative, but have also shown some non-linear effects, mostly due to thresholds. To estimate the rough influence of such effects, consider the following functional

$$\int_{-T/2}^{T/2} \{[r + I\cos(\omega t)]_+ - (F_0 + F_1\cos(\omega t))\}^2 \stackrel{!}{=} Min. \ , \tag{15}$$

where $[x]_+ = x$ if $x > 0$ and 0 else. r sets the baseline firing rate of a cell, and I is stimulus intensity. The best least square fit (15) of $F_0 + F_1\cos(\omega t)$ to the thresholded firing rates of the cell, $[r + I\cos(\omega t)]_+$, is obtained for

$$F_0 = 2r\frac{T_1}{T} + \frac{I}{\pi}\sin\left(2\pi\frac{T_1}{T}\right) \tag{16}$$

$$F_1 = 2I\frac{T_1}{T} + \frac{2r}{\pi}\sin\left(2\pi\frac{T_1}{T}\right) + \frac{I}{2\pi}\sin\left(4\pi\frac{T_1}{T}\right) \tag{17}$$

$$\text{where } T_1 = \frac{T}{2\pi}\arccos(-r/I) \text{ if } I \geq r \text{ and } T_1 = T/2 \text{ else.} \tag{18}$$

In (18) T_1 is the smallest time where $[r + I\cos(\omega t)]_+$ becomes zero for $I \geq r \geq 0$. For $I \leq r$ one gets $F_0 = r$, $F_1 = I$ from (16) and (17), but F_1 and F_0 both grow almost linearly in I as soon as $I >\approx 2r$ (see Fig. 1I and [6]). If the threshold non-linearity is interpreted as that of LGN-cells, F_0 approximates the level of untuned baseline input into cortical cells, whereas F_1 provides tuned, i.e. modulated, input. Conversely, if one considers simple cell non-linearities, the factors may account for suppressive effects at small signal strength for $r < 0$ (i.e., a positive firing threshold).

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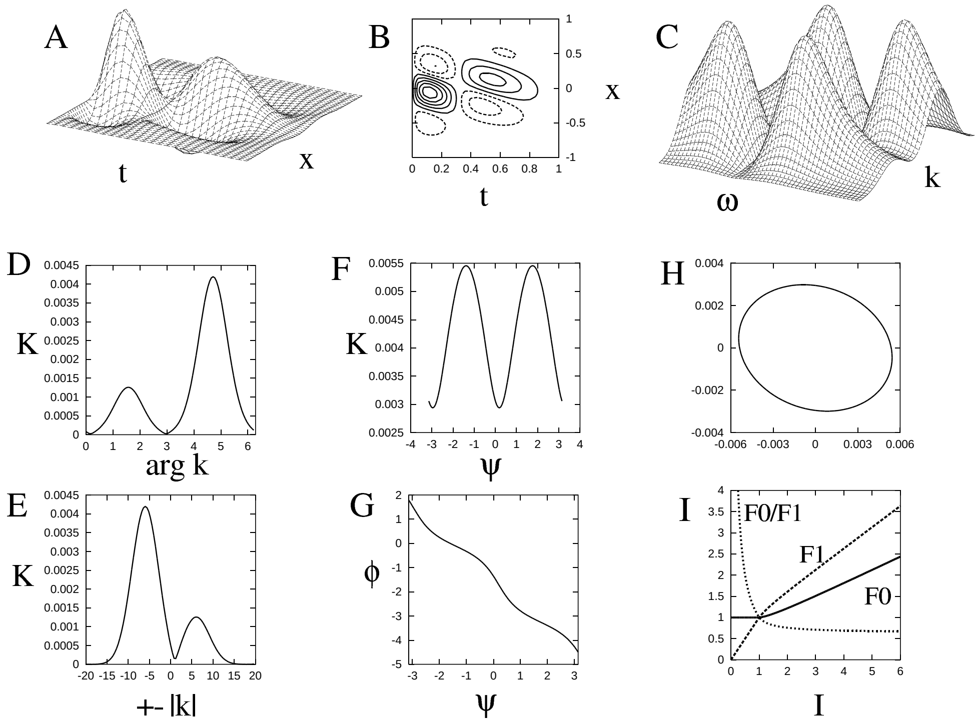

Fig. 1. A) Inseparable RF, $k(x, y = 0, t)$, with $r = (x, y), h(r) = h_0(r), g(t) = g_1(t)$ in (12). B) Contourplot and C) amplitude spectrum, $|K(k, 0, \omega)|$, of the kernel in A. D) Orientation tuning curve ($\omega = \omega_0, |k| = |k_0|$). E) Spatial frequency tuning curve ($\omega = \omega_0, arg k = arg k_0$). F) and G) Phase response to counter-phase gratings at phase ψ. H) $K(\psi)$ as in F and G as polar plot. I) F_0 and F_1 as in (16) and (17) for $r = 1$. (Kernel-parameters: $n = 2, \nu = 1, \lambda = 5, \omega_0 = 5, \omega_c = -4, \psi_0 = \phi_0 = 0$.)

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