Modeling Texture-Constancy of Cortical Grating Cells

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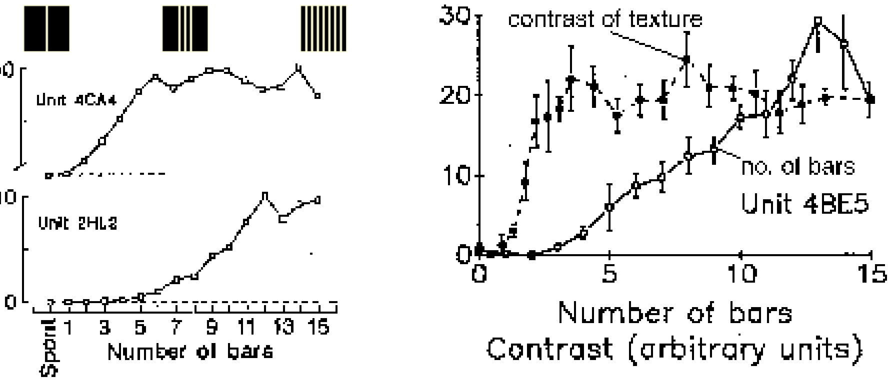
Abstract

Cortical grating cells respond only and in a contrast-independent way to repetitive bar stimuli (bar gratings), but not to individual bars: their responses behave like the neural correlate of perceptual texture-constancy. We present a recurrent mean-field model for grating response. A first stage consists of idealized simple cell pools with identical preferred orientations, which are coupled by intracortical long-range patchy connections. In the second stage, grating cells sum up the simple cell input. The proposed model shows texture-constancy, quantitatively reproduces the responses of macaque monkey grating cells and provides testable predictions of further cellular response properties.

Key words: Mean field model, texture-sensitivity, long-range patchy connections, recurrent cortical processing

1 Introduction

The primary visual cortex of higher mammals encodes visual scenes by indicating the presence of various kinds of local features such as orientation of contrast lines, color contrast, binocular disparity, direction of movement and others. Often, these features are represented such that the presence of the visual feature at a location is signalled independently of its strength or contrast, a property which might be a neural correlate of low-level perceptual constancy [9]. Here we consider the rare but important cell type of periodic-pattern-selective or *grating cells*, which have been found in V1 and V2 of alert macaque monkeys [5]. Grating cells respond selectively to repetitive bar patterns (gratings), but not to individual bars (figure 1a, adapted from [5]). Among other properties, they show a narrower spatial frequency and orientation tuning than comparable simple and complex cells, and they ignore higher harmonics in the stimulus. Some of these aspects have been modeled earlier both in function [6,7] and development from Hebb-like synaptic plasticity [4,1].



(a) **(b)**

Fig. 1 **(a)** Relative response (% of maximum) of two typical grating cells as a function of the number of bars of a square grating. The activity increases progressively from a zero response for a single bar, before it saturates. **(b)** Texture constancy of grating cells. The spike rate (1/s) increases gradually with the number of bars (open circles, 42 % contrast), but shows a switching behavior as the contrast of a grating goes down (filled circles, 15 bar grating).

But perhaps the most important property of grating cells is their well-expressed constancy in representation of oriented texture. Figure 1b (adapted from [5]) shows, how the response of a typical grating cell increases gradually with the number of bars (open circles), but for a given number of bars keeps the response independent of the stimulus contrast, sometimes all way down to the perceptual detection limit (filled circles). This is a nonlinear code, because many dim bars evoke a reponse different from few bright bars. By this, grating cells signal the presence of an oriented texture unambiguously, i.e. independent of its contrast: their responses behave like a neural correlate of texture-constancy.

In this contribution we present a recurrent mean-field neuronal model [2,10,11] for a grating-selective response which reproduces the important feature of contrast-independent texture signalling. The model is of minimal complexity and is in essence analytically tractable, yet its architecture is based on biological evidence for neuronal recurrent circuitry. We show that the model quantitatively reproduces the grating selectivity, the dependence of grating-cell response on the number of bars and the switching like contrast-response curve. The model can serve as a biologically inspired operator for the invariant extraction and encoding of oriented textures from images.

2 Model

The central part of the model is a set of N pools of simple cells with identical preferred orientations (figure 2). These pools receive local excitation of strength $S \geq 0$ and are recurrently coupled by long-range connections of strength $L \geq 0$. The receptive field centers of the pools are retinotopically arranged and are assumed to shift progressively along the direction orthogonal to the preferred orientation (the direction shown in figure 2). In V1, for example, the arrangement will correspond to an idealized set of orientation columns with similar preferred orientations, which are mutually coupled by collaterals of pyramidal neurons known to form long-range "patchy" connections [8,3]. In this arrangement, grating cells are units which sum up the output of all the simple cell pools.

According to the mean-field formulation introduced elsewhere for binary units [2] or spiking neurons [11], respectively, the mean output m of a neuronal pool in the presence of a mean synaptic input h is given by

$$\tau \frac{d}{dt} m = -m + g(h), \tag{1}$$

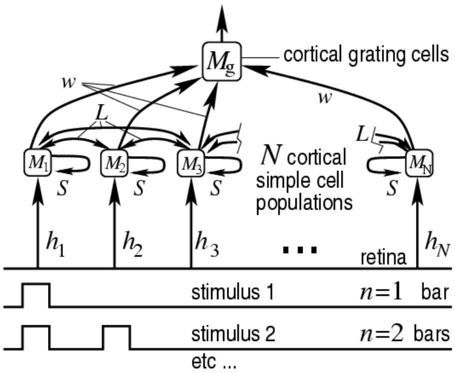


Fig. 2 Model architecture for a grating cell. N retinotopic input channels feed N pools of simple cells, which self-amplify with connection strength S and are mutually coupled by long-range intracortical connections of strength L. Grating cells sum the responses from the simple cell pools. Each simple cell pool is driven by one bar of a grating with optimal spatial frequency.

where the activation function $g(h)$ is typically taken as a rectified and saturating activation function with threshold T and slope β, $g(h) = g(h, \beta, T) = \min(\max(\beta(h - T), 0), 1)$. As we aim at a minimal model specifically for texture constancy, we assume for the present framework that gratings are always presented in the preferred orientation and optimal phase of the simple cells. In light of this we do not explicitly model the early visual pathway but assume a simple cell pool i to receive an input proportional to the logarithmic contrast $h_i = c$, if a bar of a grating with log contrast c crosses its aggregate field. If a stimulus is applied, the ith simple cell pool evolves according to

$$\tau \frac{d}{dt} m_i = -m_i + g\left((Sm_i + L \sum_{j \neq i}^{N} m_j + h_i), \beta, T \right), \tag{2}$$

and the mean activities of the grating cells evolve according to

$$\tau \frac{d}{dt} m_g = -m_g + g\left(w \sum_{i=1}^{N} m_i, \beta_g, T_g \right). \tag{3}$$

3 Results

We wish to derive the stationary activities of the ith simple cell pool, M_i and the grating cells, M_g, if a grating with $n \leq N$ bars and a suprathreshold contrast $c > T$ is presented. Under this condition, n simple cell pools, for example the first n ones, receive suprathreshold visual input, whereas the remaining pools are driven only by the intracortical recurrent connections. Let us assume first that all n simple cell pools receive suprathreshold input, either directly or indirectly, but remain below saturation. Because the stimulated and unstimulated pools receive identical inputs each, the activities must be idential as well for each group. By using the definitions

$M_i \equiv M,\ i = 1,..,n$ and $M_i \equiv M_0,\ i = n+1,..,N$ for the activities and collecting the coefficients, the fixed points of eq. (2) are given by:

$$\begin{pmatrix} M \\ M_0 \end{pmatrix} = \begin{pmatrix} 1-\beta(S+(n-1)L) & -\beta(N-n)L \\ -\beta nL & 1-\beta(S+(N-n-1)L \end{pmatrix}^{-1} \begin{pmatrix} c-T \\ -T \end{pmatrix} \quad (4)$$

where $\beta(S+(n-1)L) < 1$ has been assumed to assure invertibility of the matrix. The grating cell activity is given by inserting M and M_0 in the steady-state solution of eq. (3). This solution simplifies further, if we now assume that the long-range connectivity is modulatory, i.e., it is too weak to drive the unstimulated neurons (this is true for $L < T/(nM)$). In this case we find $M_0 = 0$ and the activities of the first n simple cell pools become

$$M = \min\left(\frac{\beta(c-T)}{1-\beta(S+(n-1)L)}, 1\right). \quad (5)$$

If the simple cells do not saturate, the steady state input of the grating cell, M_g, is given by

$$M_g = g\left(\frac{nw\beta(c-T)}{1-\beta(S+(n-1)L)}, \beta_g, T_g\right). \quad (6)$$

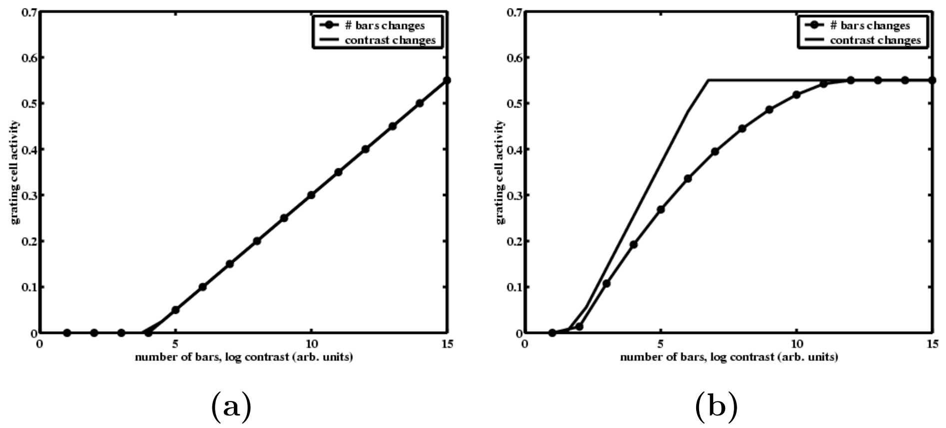
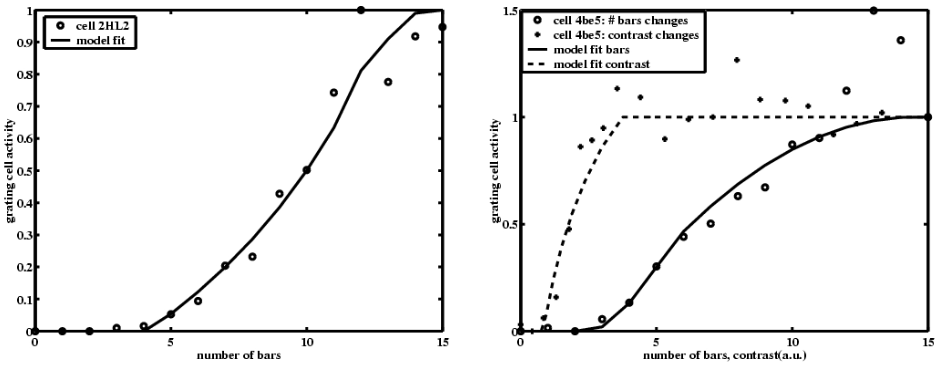


Fig. 3 Grating cell response (a. u.) as a function of the number of bars (log contrast = 2, circles) and as a function of log contrast (number of bars $N = 15$, solid line). The common stimulus was used to rescale the log contrast axis. **(a)** Feed-forward system without recurrent connectivity, $L = 0$. **(b)** recurrent system with connectivity, $L = 0.09$. Other parameters were: $\beta = 0.5$, $T = 0.25$, $S = 0$, $w = 0.05$, $T_g = 0.1$, $\beta_g = 1$.

Equation (6) demonstrates the asymmetry between the number of bars in a grating and their contrast. The contrast enters linearly into the equation, and therefore every contrast-response function for a fixed number of bars will be shaped piecewise linear, as the activation function g. As the number of bars increases, however, the grating cell response increases stronger than linear: First, the more bars are presented, the more terms sum up to the input of the grating cell. This linear summation is sufficient to model a bar-selective response, however it does not allow for contrast-independent texture selectivity. Second, with increasing n, more and more simple cell pools participate in the recurrent amplification which is mediated by the long range fibers. By this, the contrast gain of the whole system increases with the number



(a) (b)

Fig. 4 Model fit of measured response profiles. **(a)** Unit 2hl2 of figure 1 (parameters: $T = 1$, $L = 0.09$, $w = 0.083$ and $T_g = 0.2$). **(b)** Unit 4be5 of figure 1 (parameters: $T = 0.25$, $L = 0.09$, $w = 0.05$, $T_g = 0.1$). Solid line: Number of bars changes (contrast: 42 %), dashed line: contrast changes (number of bars $N = 15$). Other parameters as in figure 3. The mean response at maximum contrast/number of bars and the maximum model response was scaled to unity.

of bars present in the grating. As a consequence, cells in a system stimulated with many bars have a higher contrast gain compared to stimulation with few bars. This high contrast gain is responsible for the switch-like contrast-response of the model (cf. the cell in figure 1b). The simulations in Figure 3 illustrate this behaviour by showing, how a model grating cell responds to various grating stimuli. These and all other simulations were carried out by evaluating eq. (4) subject to the threshold and saturation constraints. In figure 3a, the recurrent connections are switched off, which leads to a feed-forward model for the grating cell. The cell does not respond to gratings with less than three bars - it is grating-selective. However, changing the contrast or changing the number of bars has the same effect: the cell cannot encode gratings independent of the contrast. In figure 3b, where the recurrent connectivity is switched on, increasing the number of bars leads to a gradually increasing and then saturating response of the grating cell. Moreover, the symmetry between the number of bars and bar contrast is broken: The response to a graing is contrast-independent over some range, and the model neuron shows texture-constancy-like activity.

Quantitative fits of the measured response profiles for two of the cells of figure 1 are shown in figure 4. The model can reproduce both the bar selectivity and progressive increase of the response of unit 2hl2, and this ability can be assigned to the effect of the recurrent connectivity. The fit of the data for unit 4be5 (Figure 4b) demonstrates, that the network reproduces correctly and quantitatively both the bar-response profile and the contrast-response profile of the neuron with a single consistent parameter set.

4 Summary and Conclusions

We propose a two-stage recurrent mean-field network model, which can unambiguously encode the presence of an oriented texture in a local part of a visual scene. In this model, grating cells are proposed to be cells that sum up input from pools of orientation selective cells of an earlier processing stage, which belong to different orientation columns of the same preferred orientation and which are mutually connected by recurrent excitatory connections. We propose intracortical long-range patchy connections as the biological substrate for these connections. Using this wiring scheme, the present model correctly describes nonlinear response properties of grating cells. We hypothesize, that the proposed current two stage model is suitable to model a whole variety of coding properties of cortical neurons like bar-selectivity [5] or cortical contextual effects [10] from natural variations in the local connectivity, depending on the recurrent lateral connectivity that guides the interplay between lateral facilitation and suppression.

Acknowledgments

The Autors gratefully acknowledge support through the German Ministery for Research, (BMBF grants 01IBC01A, 01IBC01D) and the European Union (IST-2001-38099)

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