

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.

1 Introduction

The primary visual cortex of higher mammals encodes visual scenes by extracting - and 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 feature at a location is signalled independently of its strength, a property which might be a neural correlate of low-level perceptual constancy. For example, the orientation tuning of simple orientation-selective cells in cat area 17 is independent of the contrast of the presented stimulus [1], meaning that simple cells will only be active if the orientation of a stimulus possesses the feature to lie within a fixed interval. This property is signalled independently of the contrast (the feature strength), which is implicitly encoded in the strength of the activity. Mean-field-models [2, 3] of cortical function have demonstrated that contrast-invariant orientation tuning can be the result of local recurrent cortical information processing ([4, 5], for a review see [2]).

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 [6]. Grating cells respond selectively to repetitive bar patterns (gratings), but not to individual bars (figure 1a, adapted from [6]). 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. In short, they seem to selectively represent the presence of a grating with a certain orientation and spatial frequency.

But perhaps the most important property of grating cells is their well-expressed constancy in representation of oriented texture. Figure 1b (adapted from [6]) shows, how the response of a typical grating cell increases gradually and progressively 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). In other words: 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.

Grating selective response and selected other grating-cell properties have been modeled by a two-stage feed-forward-model [7], and this model has been proposed as a nonlinear operator for oriented texture extraction in image processing [8]. Lang and colleagues [9, 10] have demonstrated that

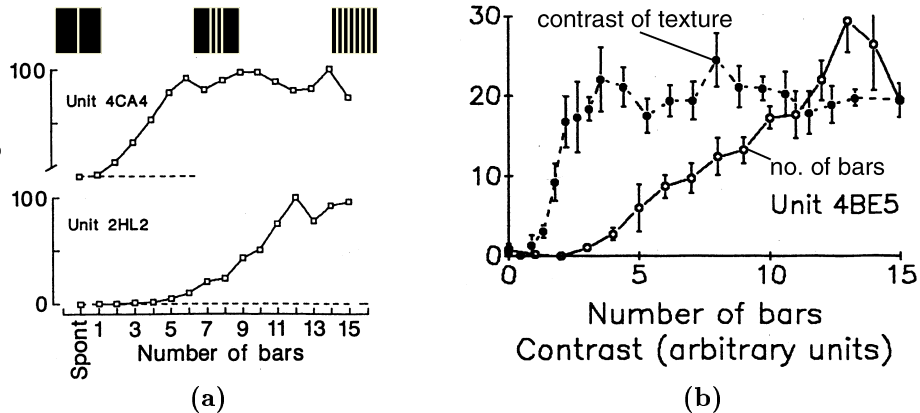


Figure 1: **(a)** Relative response (% of maximum) of two typical grating cells as a function of the number of bars of a square grating. The activity increases progressively from a zero response for a single bar, before it saturates. **(b)** Texture constancy of grating cells. The spike rate (1/s) increases 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). The response is nonlinear (many dim bars are not the same as few bright ones): the cell signals the presence of a texture irrespective of its contrast (results adapted from [6])

a neuronal feed-forward circuitry with grating-cell properties can emerge from Hebb-like synaptic plasticity. These feed-forward approaches successfully explain several grating cell properties, but do not address either the role of the ubiquitous intracortical wiring or the property of contrast-invariant grating detection.

In this contribution we present a recurrent mean-field neuronal model 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 [11, 12]. 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 [4] or spiking neurons [2], respectively, the mean output m of a neuronal pool in the presence of a mean synaptic input h is given by

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

where the activation function $g(h)$ is typically taken as a rectified semi-linear activation function. Because it is known that local inhibitors (e.g., cortical stellate cells) can cause contrast saturation

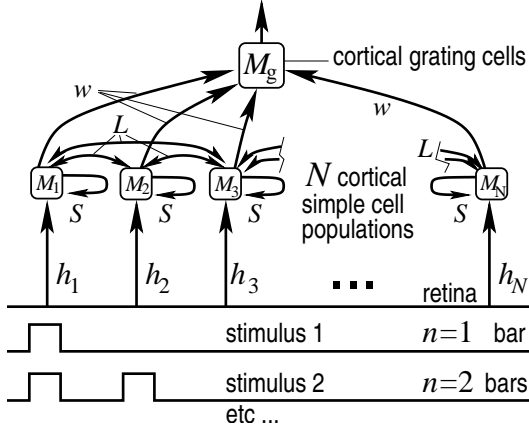


Figure 2: Model architecture for a grating cell. N retinotopic input channels feed N pools of simple cells, which self-amplify with connection strength S and are mutually coupled by long-range intracortical connections of strength L . Grating cells sum the responses from the simple cell pools. Each simple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

in neural models [13] – a phenomenon which is widely observed experimentally in the visual cortex – inhibitory pools are not explicitly modeled here, but instead the saturation is incorporated in the activation function, which allows activation above a threshold T and saturates at unity activation:

$$g(h, \beta, T) = \begin{cases} 0 & h \leq T \\ \beta(h - T) & T < h \leq T + 1/\beta \\ 1 & h \geq T + 1/\beta \end{cases} \quad (2)$$

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 of the simple cells and with optimal spatial frequency. Likewise, phase dependencies are assumed to be eliminated by jitter of the receptive field centers at the level of the simple cell afferents, and are ignored here as well. 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 i th simple cell pool evolves according to

$$\tau \frac{d}{dt} m_i = -m_i + g \left((S m_i + L \sum_{j \neq i}^N m_j + h_i), \beta, T \right), \quad (3)$$

and the mean activities of the grating cells evolve according to

$$\tau \frac{d}{dt} m_g = -m_g + g \left(w \sum_{i=1}^N m_i, \beta_g, T_g \right). \quad (4)$$

The central proposed operation for the grating cell network is the following: If an optimal grating stimulus is presented, each of its bars activates one of the simple cell pools. Given this assumption, the number of bars influences the activity of the grating cells in a nonlinear way and differently from the contrast. This asymmetry between number of bars and their contrast yields the basis for texture-constancy. In the following section this will become explicit from the steady-state activities of simple cell pools and the grating cells for various grating stimuli.

3 Results

We wish to derive the stationary activities of the i th 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 that all simple cell pools receive suprathreshold input, either directly or

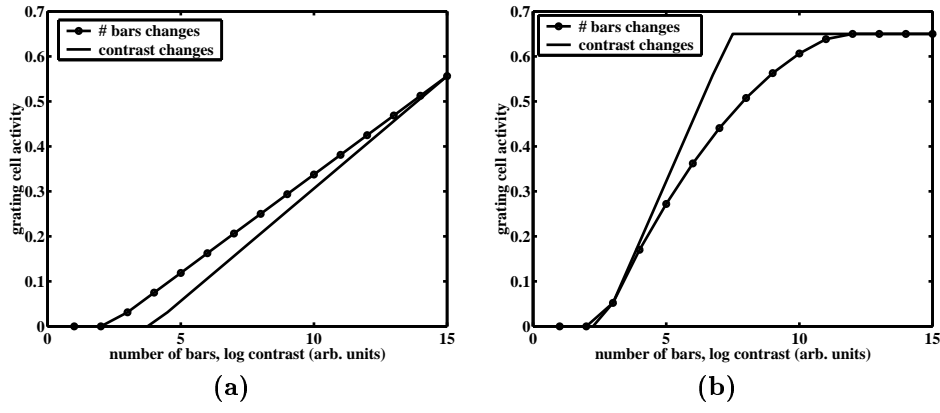


Figure 3: Grating cell response (a. u.) as a function of the number of bars (log contrast = 2, circles) and as a function of log contrast (number of bars $N = 15$, solid line). The common stimulus was used to rescale the log contrast axis. **(a)** Feed-forward system without recurrent connectivity, $L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

indirectly, but remain below saturation: in other words, we assume that the system remains in the linear part of the activation function. Then, by setting the time-derivative in eq. (3) to zero and replacing the activation function by its linear part, one obtains

$$\begin{aligned}
 M_i &= \beta((S - L)M_i + L \sum_{j=1}^N M_j + c - T), \quad i \leq n, \\
 M_i &= \beta((S - L)M_i + L \sum_{j=1}^N M_j - T). \quad i > n
 \end{aligned} \tag{5}$$

Because the stimulated and unstimulated pools receive identical inputs each, the activities must be identical as well for each group. By using the definitions $M_i \equiv M$, $i = 1, \dots, n$ and $M_i \equiv M_0$, $i = n + 1, \dots, N$ for the activities and collecting the coefficients, eq. (5) can be transformed to yield the following analytical expression for the simple cell activities:

$$\begin{pmatrix} M \\ M_0 \end{pmatrix} = \begin{pmatrix} 1 - \beta(S + (n - 1)L) & -\beta(N - n)L \\ -\beta nL & 1 - \beta(S + (N - n - 1)L) \end{pmatrix}^{-1} \begin{pmatrix} c - T \\ -T \end{pmatrix} \tag{6}$$

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. (4).

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

$$M = \min \left(\frac{\beta(c - T)}{1 - \beta(S + (n - 1)L)}, 1 \right). \tag{7}$$

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

$$M_g = g \left(\frac{nw\beta(c - T)}{1 - \beta(S + (n - 1)L)}, \beta_g, T_g \right). \tag{8}$$

Equation (8) 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.

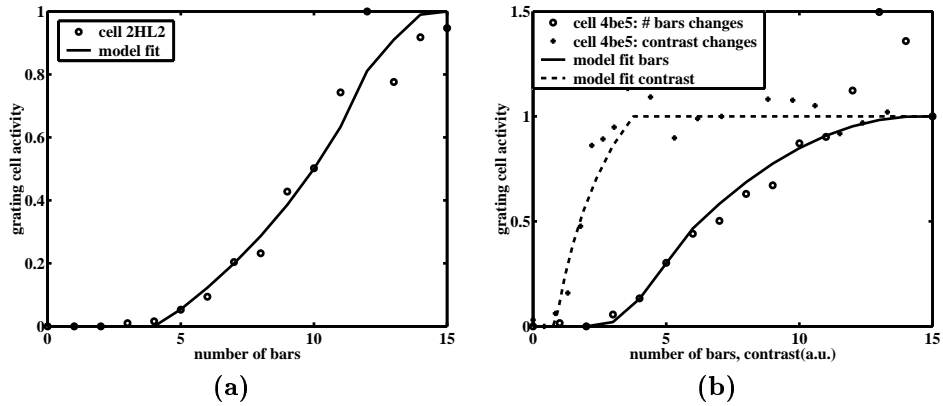


Figure 4: Model fit of measured response profiles. **(a)** Unit 2hl2 of figure 1 (parameters: $T = 1$, $L = 0.09$, $w = 0.083$ and $T_g = 0.2$). **(b)** Unit 4be5 of figure 1 (parameters: $T = 0.25$, $L = 0.09$, $w = 0.05$, $T_g = 0.1$). Solid line: Number of bars changes (contrast: 42 %), dashed line: 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.

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 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 shown by the cell in 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. (6) 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 that three bars - it is grating-selective. However, its response increases linearly with the number of bars (other than the progressive increase of the biological counterpart, figure 1). Moreover, 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 an accelerating and then saturating response of the grating cell. In addition, the response is independent of the contrast over some range: As the biological counterpart the model neuron signals the presence of a grating unambiguously: it shows texture-constancy.

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 Discussion

We propose a tow-stage recurrent network, which can unambiguously encode the presence of an oriented texture in a local part of a visual scene. In the simple setup chosen here the input processing by simple cells is not explicitly modeled. We hypothesize, that many other properties which distinguish grating cells from other neuron types are based on the properties of the simple cell receptive fields and how they are connected to each other. Also, because of the symmetry of

the lateral connections L , the present system is sensitive only on the number of bars, but cannot distinguish between different bar arrangements. This spurious symmetry of the model can be broken by assigning a space-dependence on the lateral connectivity.

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 intracortical long-range patchy connections. Although the model grating cells are collected in a pool, this does not imply any geometrical distribution of the cells in the visual cortex: The model only assumes that grating cells should receive a convergent set of fibers which proceed from mutually exciting populations of simple cells.

Using this wiring scheme, the present model describes the response properties of grating cells. Because these cells form only a very small fraction of visual cortical neurons, one might ask why it is important to consider these neurons. As mentioned, one important reason is that we can learn how to represent textures invariantly in image processing. In addition, however, we hypothesize that the current two stage model is suitable to model a whole variety of coding properties of cortical neurons like bar-selectivity [6] or cortical contextual effects [5] from natural variations in the local connectivity.

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