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A recurrent network model for the phase invariance of complex cell responses

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Abstract

Cortical amplification is a mechanism for modifying the selectivity of neurons through recurrent interactions. Although conventionally used to enhance selectivity, cortical amplification can also broaden it, de-tuning neurons. Here we show that the spatial-phase invariance of complex cell responses in primary visual cortex can arise using recurrent amplification of feedforward input. Neurons in the model network respond like simple cells when recurrent connections are weak and complex cells when they are strong. Simple or complex cells can coexist in such a network, and they can have a range of selectivities for image characteristics such as spatial frequency. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Complex cell; Simple cell; Recurrent amplification; Visual cortex

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1. Introduction

Recurrent connections are a prominent feature of primary visual cortex (V1), suggesting that these connections play a critical role in cortical information processing. A number of investigators have proposed that recurrent connections amplify weak input [5] to enhance tuning for stimulus attributes such as the orientation or direction of motion of a grating [2,5,11,12]. The idea of cortical amplification through recurrent connections is supported by experiments in which cortex is either cooled and shocked. However, these experiments did not reveal the increases in orientation or direction selectivity expected in models with cortical amplification [4,6]. Recurrent

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circuitry can also decrease selectivity through the amplification of non-selective modes of activity. It can thereby generate responses that are invariant with respect to certain stimulus features. An example is the spatial-phase invariance of complex cell responses, which we suggest arises from a broadening of spatial-phase tuning through cortical amplification [3].

Simple and complex cells in V1 can be distinguished by a number of criteria, for example on the basis on their responses to counterphase and drifting sinusoidal gratings. Simple cells are selective for the orientation, spatial frequency, and spatial phase of a grating [9]. Complex cells are also orientation and spatial frequency selective, but are insensitive to spatial phase [10]. Complex cell responses can arise through converging feedforward inputs with a wide variety of spatial-phase preferences but similar orientation and spatial-frequency selectivities [7,8]. Such models do not include recurrent connections between complex cells, which are known to be strong [13]. In contrast, recurrent connectivity produces complex cell behavior in the model we present.

2. Model

We model a population of neurons within a single orientation column of primary visual cortex. As such, all neurons have the same orientation tuning. In addition, each neuron, denoted by a subscript i, is labelled by a spatial-phase preference, ϕ_i, and a spatial-frequency preference, k_i, which it inherits from its feedforward input.

A firing rate, r_i, describes the activity of each neuron and is determined by the sum of feedforward and recurrent inputs, as described by

$$\tau_r \frac{\mathrm{d}r_i}{\mathrm{d}t} = -r_i + I_i + \sum W_{ij} r_j,$$

with $\tau_r = 1$ ms. The feedforward input is comparable to the output of a single simple cell,

$$I_i = \left[\int_{-\infty}^{\infty} \mathrm{d}x\, G_i(x) \int_0^{\infty} \mathrm{d}t'\, H(t') s(x, t-t') \right]_+,$$

where $s(x,t)$ represents the visual stimulus and $[\ ]_+$ indicates rectification. The spatial filter is a Gabor function,

$$G(x) = \exp\left(-\frac{x^2}{2\sigma_i^2} \right) \cos(k_i x - \phi_i).$$

The parameters ϕ_i, k_i, and σ_i range over values which reflect the distributions of spatial-phase and spatial-frequency preferences and tuning curve bandwidths for simple cells in the primary visual cortex. Within the network, ϕ_i ranges over $[-180°, 180°)$, k_i ranges from 0 to 3.5 cycles/deg, and $\sigma_i = 2.5/k_i$. The temporal response function is [1]

$$H(t') = \exp(-\alpha t')\left(\frac{(\alpha t')^5}{5!} - \frac{(\alpha t')^7}{7!}\right),$$

where we use $\alpha = 1/\text{ms}$.

The recurrent weight matrix, which determines the strength of coupling between neurons, is chosen so that each element is a function of the difference between the spatial-frequency selectivities of the feedforward inputs of the coupled neurons, but is independent of their spatial-phase selectivities. Specifically, the strength of recurrent coupling from neuron j to neuron i is

$$W_{ij} = \frac{g_i}{(N-1)}\left[2\exp\left(-\frac{(k_i-k_j)^2}{2\sigma_c^2}\right) - \exp\left(-\frac{(k_i-k_j)^2}{2\sigma_s^2}\right)\right],$$

for all $i \neq j$. N is the number of neurons in the network, $\sigma_c = 0.5$ cycle/deg, $\sigma_s =$ 1 cycle/deg, and $0 \leq g_i < g_{\max}$. $g_{\max}$ is the value of g_i for which the network becomes unstable. In Figs. 1 and 2, g_i is the same for all cells in the network. In Fig. 3, g_i is chosen randomly within the allowed range.

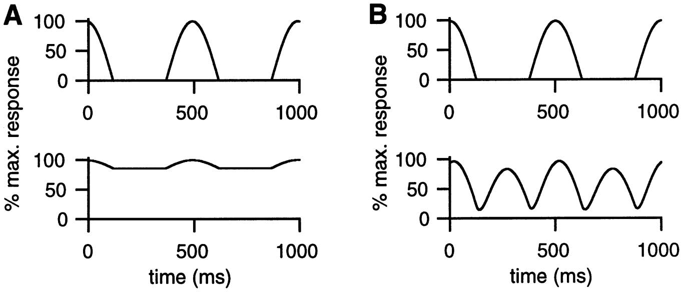

Fig. 1. The gain of a neuron affects the responses to visual stimuli. The responses of one neuron to a 2 Hz drifting grating (A) and to a 2 Hz counterphase grating (B) are shown for a neuronal gain of one (top panels) and 20 (bottom panels).

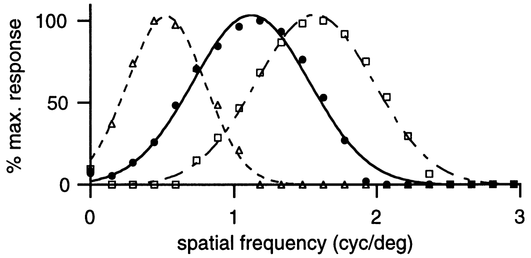

Fig. 2. Neurons in a high-gain network can be selective for spatial frequency while remaining insensitive to spatial phase. Above are the spatial frequency tuning curves of three representative high-gain neurons.

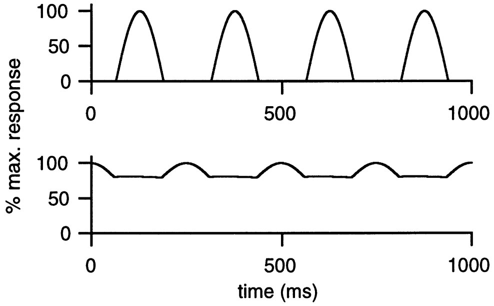

Fig. 3. Responses of two neurons from a network consisting of neurons with varying levels of gain. The top trace represents simple cell behavior and the bottom trace complex cell behavior in response to a 4 Hz drifting grating.

3. Results

The gain of each neuron, or the degree of amplificaton of its feedforward input, is related to the strengths of the recurrent synapses in the network (with $g_i = g$ for all i) by the equation $1/(1 - g/g_{\max})$. We examine the responses of model neurons with various gain to visual stimuli and compared these with the types of responses seen in primary visual cortex.

For visual stimuli, we use drifting and counterphase sinusoidal gratings. In a sinusoidal grating, the luminance varies sinusoidally over one spatial dimension and is uniform in the other. The orientation of the stimulus in the x–y plane is assumed to be optimal for the neurons in the network. For a drifting grating, the spatial phase varies over time, $L(x) = C\sin(Kx + \omega t) + A$, where L represents the luminance at position x, C is the overall contrast of the stimulus, and A is its mean luminance. The response of a simple cell to a drifting grating is highly modulated at frequency ω [9], while the response of a spatial-phase invariant complex cell is elevated but relatively unmodulated [10]. When recurrent connections are weak or absent, the responses of the neurons in the model network are like those of simple cells (Fig. 1A, top). When recurrent connections are strong, the behavior resembles that of complex cells (Fig. 1A, bottom).

To create a counterphase grating, the contrast is modulated sinusoidally with time, $L(x) = C\sin(\omega t)\sin(Kx + \Phi) + A$. In response to a counterphase grating, the activity of a simple cell is modulated at frequency ω, the frequency of the stimulus [9]. A complex cell's activity, however, oscillates at twice the frequency of the stimulus, 2ω. At low gain, the model neuron's activity is modulated at the frequency of the stimulus (Fig. 1B, top) while at high gain the neuron's response is frequency-doubled (Fig. 1B, bottom). These changes in response behavior arise because the strong recurrent interactions effectively broaden the spatial-phase selectivity of the neurons in the network. At low gain, the neurons are strongly tuned for spatial phase, while at high gain they exhibit little sensitivity to spatial phase. Intermediate behavior is exhibited by neurons with intermediate levels of gain.

The recurrent weight matrix of this model amplifies a mode which is insensitive to spatial phase but is tuned for spatial frequency. As a result, neurons within the network, while insensitive to spatial phase, are selective for spatial frequency. In Fig. 2, high-gain neurons which are insensitive to spatial phase show a variety of selectivities for spatial frequency.

If g_i varies from neuron to neuron, the gain of each neuron and hence the behavior varies across the network. Complex and simple cell responses from neurons within one network are shown in Fig. 3. Neurons with intermediate levels of gain have intermediate response characteristics and can also coexist within the network.

4. Conclusion

In this model of V1 neurons, responses characteristic of complex cells are generated by the recurrent amplification of simple cell input. Unlike previous models, which use recurrent amplification to sharpen tuning, here recurrent amplification acts to de-amplify selectivity for spatial phase while leaving selectivity for other stimulus characteristics, such as spatial frequency, intact. In this way, recurrent connections can be used to construct invariant representations of input data. Given the importance of invariant representations in cortical processing, similar mechanisms may have extensive application within cortical circuitry.

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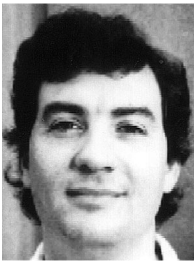

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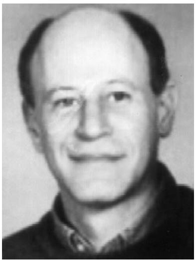

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