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Input-specific adaptation in complex cells through synaptic depression

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Abstract

A number of experiments have reported that neurons in primary visual cortex can adapt in a stimulus-dependent manner. Synaptic depression is a plausible mechanism for this type of adaptation because its synapse specificity allows modification of particular inputs while allowing others to remain unaffected. Furthermore, a form of synaptic depression measured in slice experiments sets in and recovers over appropriate time scales to account for such an effect. We show that synaptic depression on feedforward, but not on recurrent, inputs can produce a fast form of spatial-phase-specific adaptation in a complex cell model.

Keywords: Adaptation; Synaptic depression; Visual cortex; Complex cell

1. Introduction

Recently, a fast form of orientation-specific adaption has been reported for complex cells in primary visual cortex [9]. This augments earlier reports of various stimulus-specific adaptation effects [2,7,8,10]. This form of adaptation operates over a time scale of hundreds of milliseconds, and acts in a stimulus-specific manner. Such a mechanism could play a critical role in visual processing because it acts to suppress responses to stimuli similar to the adapting stimulus. As a result, the system is, in effect, sensitized to changes in stimuli.

Synaptic depression in cortical slices has been measured operating over several different time scales [1,6,11,12]. An important computational feature of synaptic

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depression is that, in response to an adapting stimulus, particular inputs to a neuron may be depressed while others are left intact. Furthermore, the faster form of depression seen in cortical slices operates at a time scale similar to the input-specific adaptation reported by Müller et al. [9]. Therefore, synaptic depression is a candidate mechanism for input-specific adaptation [3].

Müller et al. [9] report that the stimulus-specific adaptation they see occurs only in complex cells, not simple cells. Complex cells are thought to receive input from simple cells, which are tuned for orientation. If complex cells receive input from simple cells with a wide range of orientation tunings, the orientation-specific effects of adaptation could be dramatic. However, if the inputs to a complex cell arise from simple cells with similar orientation tuning, adaptation to a grating of a particular orientation could easily result in some degree of depression on all input synapses. As a result, using orientation tuning of complex cells to distinguish between depression of similarly tuned inputs and more global adaptation mechanisms might be difficult. On the other hand, complex cells receive inputs with a wide range of spatial phase selectivities. This gives rise to the invariance of their responses to spatial phase. For this reason, we chose to look at input-specific adaptation of spatial phases, rather than input-specific adaptation of orientation, and we suggest this would be an interesting area for experimental investigation.

2. The model

The recurrent complex cell model used to study input-specific adaptation is identical to the firing-rate model discussed in Chance et al. [4]. Briefly, complex cells in the model receive two classes of inputs, feedforward and recurrent. The feedforward input to each model complex cell is well described by the response of a simple cell with a Gabor receptive field and is strongly tuned for spatial phase, although the spatial phase tuning of the feedforward inputs to the network cover a wide range of preferences. The recurrent synapses between model complex cells are strong and spatial-phase independent. This arrangement amplifies a spatial-phase-invariant population response and causes the neurons in a strongly coupled network to respond as complex cells, despite the spatial-phase tuning of their feedforward inputs.

We incorporate synaptic depression using a previously developed model [1,12]. The input transmitted through a synapse is $D_i r_i^{\mathrm{pre}}$, where $0 \leqslant D_i \leqslant 1$ represents the level of depression for the synapse denoted by index i, and r_i^{pre} describes the presynaptic firing rate. D_i is determined by

$$\tau_D \frac{\mathrm{d}D_i}{\mathrm{d}t} = 1 - D_i(1 + \tau_D r_i^{\mathrm{pre}}(1 - d)),$$

where d and τ_D control the rate of depression onset and the time constant of recovery from depression. We examined the effects of depression at both feedforward and recurrent synapses, and took $d = 0.75$ and $\tau_D = 300$ ms when synaptic depression was

present in the feedforward synapses and $d = 0.99$ and $\tau_D = 100$ ms when synaptic depression was present in the recurrent synapses of the model.

We have also considered a purely feedforward complex cell model [5]. In this case, complex cells arise from convergent input from simple cells with different spatial phase selectivities. This model uses a standard integrate and fire neuron. The membrane potential (V) is determined by $\tau_m dV/dt = V_{rest} - V + g_E(V_E - V)$, where g_E is an excitatory synaptic conductance resulting from feedforward input. If V crosses a predetermined threshold, $V_{th} = -55$ mV, an action potential is fired, and V is reset to $V_{reset} = -58$ mV. In addition, $\tau_m = 30$ ms, $V_{rest} = -58$ mV, and $V_E = 0$ mV.

The feedforward inputs are again equivalent to the responses of simple cells with Gabor receptive fields. Poisson spike trains are generated from the firing rates calculated in this manner, and these spikes are used to determine the excitatory synaptic conductance in the model neuron. With each presynaptic spike, the total excitatory conductance is increased by an amount reflecting the overall strength of the synapse, G_i, and the amount of depression in the synapse, D_i, $g_E \to g_E + G_i D_i$. Between presynaptic action potentials, the total excitatory synaptic conductance exponentially decays towards zero with a time constant $\tau_E = 2$ ms.

The parameter D_i, which defines the amount of depression in each synapse to the model complex cell, decreases with each presynaptic spike, $D_i \to d_i D_i$. As in the case of synaptic depression on the feedforward synapses of the recurrent model of a complex cell, $d_i = 0.75$ and in between presynaptic action potentials D_i recovers exponentially towards one with a time constant of 300 ms. In all models, the overall strengths of the synapses are chosen so that the maximum unadapted response of the model neuron to a grating is between 60 and 65 Hz.

3. Results

When synaptic depression is included on the feedforward input synapses of the recurrent model, the synapses activated by the stimulus depress during the adaptation period. Subsequently, the input through these synapses is much weaker than input through other feedforward synapses. The spatial-phase tuning curves for a model neuron after adaptation to a grating at 0° spatial phase for 215 ms (open symbols) and 27 ms (closed symbols) recovery periods are shown in Fig. 1b. Note that the response, which is approximately flat (independent of spatial phase) before adaptation (solid line), develops spatial-phase sensitivity after adaptation. Thus, the model predicts that, after adaptation to a stationary grating, a complex cell should briefly display a modulated response to a drifting grating reflecting its temporary, adaptation-induced, spatial-phase tuning.

When the synaptic depression is only on the recurrent synapses, the effect of adaptation is different. The input transmitted through the recurrent synapses is spatial-phase invariant. As a result, adaptation due to synaptic depression on recurrent synapses is not stimulus-specific, at least for spatial phase. This is illustrated in panel (c) of Fig. 1. Although adaptation dramatically decreases the responses of the

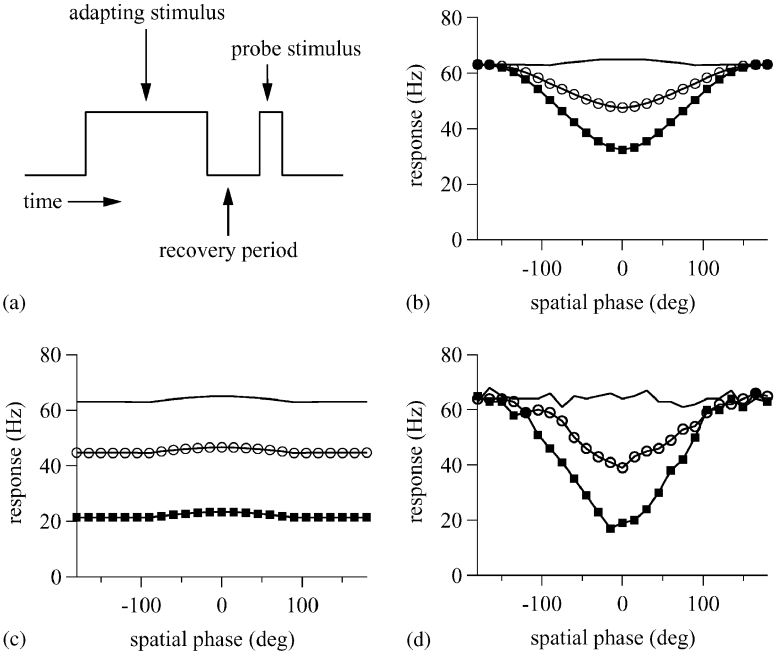

Fig. 1. Adaptation through synaptic depression. (a) The experimental protocol used by Müller et al. and also in the simulations. A 0.5 s adapting stimulus (a sinusoidal grating of 0° spatial phase) is followed by a recovery period, and then a probe stimulus to test the neuron's response. (b), (c), and (d) describe the spatial-phase tuning curves of model complex cells before (solid lines) and after (lines with symbols) adaptation. Filled squares represent responses after a recovery period of 27 ms, and open circles represent responses after a recovery period of 215 ms. (b) Synaptic depression is included only on the feedforward synapses of the recurrent network model of a complex cell. (c) Synaptic depression is present only on the recurrent synapses. (d) The responses of a feedforward complex cell with synaptic depression included. Because the underlying model is based on spikes rather than firing rates, the curves in this panel are slightly irregular.

neuron, the decrease in response does not depend on the spatial phase of the probe stimulus or the adapting stimulus.

When synaptic depression is included in the feedforward model of complex cells proposed by Hubel and Wiesel [5], spatial-phase-specific adaptation occurs (see panel (d) of Fig. 1) that is similar to that in panel (b). If experimental data demonstrate that spatial-phase-specific adaptation occurs in complex cells, this would not distinguish between the two models. However, if adaptation to a stimulus of a particular spatial phase results in spatial-phase-independent adaptation, this would suggest the presence of synaptic depression on recurrent, but not feedforward, synapses.

The global suppression of responses arising from synaptic depression in the recurrent connections of the recurrent model occurs because the inputs carried through those recurrent connections are relatively spatial-phase invariant. However, these

connections can be tuned for other stimulus characteristics, such as orientation and spatial frequency. Thus, stimulus-specific adaptation to orientation or spatial frequency could arise even if the depression is only on the recurrent synapses and there is no spatial-phase dependence in the adaptation.

4. Discussion

We propose that the synapse specificity of synaptic depression underlies stimulus-specific adaptation in the primary visual cortex. For stimulus-specific adaptation to occur with this mechanism, the input must be tuned, but not too narrowly. An advantage of using spatial phase as the relevant stimulus characteristic is that such an experiment distinguishes between whether synaptic depression occurs on recurrent or feedforward synapses. Only when synaptic depression is on the feedforward synapses are the resulting adaptation effects spatial-phase specific.

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