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Report

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**A synaptic explanation of suppression in visual cortex: Mathematical derivations**

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This is a mathematical appendix to our paper "A synaptic explanation of suppression in visual cortex" (Journal of Neuroscience, 2002). Here we derive approximate analytical expressions for the responses to certain stimuli of an individual depressing synapse and of the model V1 neuron. We first consider the responses of an individual depressing synapse to sinusoidal presynaptic currents (Figure 1) and then the responses of the model V1 neuron to grating and plaid visual stimuli (Figure 4).

**Synaptic responses to a sinusoidal current**

In Methods we have derived an expression for the postsynaptic current in response to a steady presynaptic current:

\[
I_{post} = I_{max} \frac{I_{pre}}{\sigma + I_{pre}}.
\]

We now generalize this expression to the case of a presynaptic current that modulates sinusoidally, with a goal to predict the curve in Figure 1F.

When stimulated with a constant presynaptic firing rate \(f^0\) the probability of release converges to a steady state value that, according to (1), is given by

\[
p^0 = \frac{u}{1 + u \tau R f^0}.
\]

(7)

If the presynaptic firing rate is sinusoidally modulated, \(f(t) = f^0 + f^1 \cos \omega t\), the probability of release \(p\) follows this modulation in a nonlinear way. As a consequence, the postsynaptic current \(I_{post}(t) = p(t) f(t)\) is nonlinearly distorted, (Figure 1B-D, third row). As derived elsewhere (Senn and Buchs 2002) the first order Fourier component (F1) of the postsynaptic current at the stimulation frequency, \(f^1\), is a product of the steady state release probability, \(p^0\), the first order Fourier component of the presynaptic firing rate, \(f^1\), and an additional factor \((1-c)\) that mainly compensates for the phase difference between presynaptic frequency \(f(t)\) and release probability \(p(t)\).

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In our case the presynaptic firing rate \( f \) is itself a nonlinear distortion of a sinusoidally modulated presynaptic current, \( I_{pre}^1(t) = I_{pre}^1 \sin(\omega t) \), injected into the LGN cell,

\[
f(t) = \left[ k I_{pre}^1 \sin(\omega t) - f_{rest} \right].
\] (9a)

As an example, Figure 1 shows the F1 component, \( f^1 \), of the LGN output firing rate \( f(t) \) at 2 Hz for parameter values \( k=300 \), \( \omega/2\pi = 2 \) Hz, and \( f_{rest} =10 \) spikes/s. To simplify the deduction we comprise the effect of the LGN rectification and the effect of the factor \((1-\varepsilon)\) in a single, empiric correction factor \( \rho \). In doing so we replace \( f^0 \) in the expression for \( p^0 \) given in (7) with \( \rho f^0 \), where \( f^0 \) is now the F0 component of the presynaptic firing rate, and where we put \( \rho =1.4 \). With such empirically corrected formulas we get from (7) and (8) the F1 component of the postsynaptic current,

\[
l_{post}^1 = \frac{uf^1}{1+u\tau_R \rho f^0}.
\] (9b)

This equation represents the desired generalization of the synaptic response from a constant to a sinusoidal input. As illustrated in Figure 1 the equation predicts closely the saturation produced by synaptic depression.

**Simple cell responses to plaids**

We now turn to our model V1 neuron, and consider the visual responses to plaids composed of two drifting gratings, a test grating with preferred orientation and an orthogonal mask grating. We show that suppression by the mask is divisive (as shown in Figure 4). In particular show that the membrane potential of the V1 neuron in response to the test and mask with contrasts \( c_{test} \) and \( c_{mask} \) has a modulation amplitude approximately equal to
\[ V^1 = V_{\text{max}} \frac{c_{\text{test}}}{c_{50} + \sqrt{c_{\text{test}}^2 + c_{\text{mask}}^2}} \]

which is the expression we have given in the Methods.

Our main result, which is proven later on, is that the F1 component of the simple cell depolarization at the stimulation frequency is given by

\[ V^1 = \frac{c_{\text{test}} V_{100}^1}{1 + \alpha \sqrt{c_{\text{test}}^2 + c_{\text{mask}}^2}}, \quad (10) \]

with

\[ \alpha = \frac{u \tau_k f_{\text{max}} l}{\sqrt{2\pi}} \rho \tau_k e^{-\left(\tau_k \omega\right)^2}. \]

Here, \( V_{100}^1 \) is the modulation amplitude of \( V \) in the absence of synaptic depression, in response to a test grating with 100% contrast (measured from peak to peak). The constant \( \alpha \) is composed of the use parameter \( u \), the synaptic recovery time constant \( \tau_k \), the maximal LGN firing rate \( f_{\text{max}} \), the empiric correction factor \( \rho \), a constant \( l = 1.4 \) taking into account the effect of the spatial LGN filter \( L_r \), the coefficient \( k_l \) and the fast time constant \( \tau_f \) of the temporal LGN filter, and the temporal frequency \( \omega/(2\pi) \) of the test and masking grating (which are assumed to be the same). For the present parameter values we get \( V_{100}^1 = 702 \text{ spikes/s} \) and \( \alpha = 10.3 \). Equation 10 is obtained by dividing numerator and denominator in (10) by \( \alpha \), yielding \( c_{50} = 1/\alpha \) and \( V_{\text{max}} = V_{100}^1/\alpha \).

The accuracy of the above approximation is shown in Figure II. In A we show the simple cell response in the absence of synaptic depression. The slight deviation from linearity at low contrasts is due to the LGN thresholding and a non-vanishing resting firing rate (3). In B we show the F1 component of the membrane potential for different test and mask contrasts, in the presence of synaptic depression. Dots represent the simulation results, the line is obtained from (10). Note that the denominator in (10) correctly estimates the effect of synaptic depression, as the maximal subthreshold response of 702 spikes/s is converted into a maximal response of roughly 55 spikes/s.

To predict the modulation amplitude of the simple cell firing rate we simply rectify the modulation amplitude

\[ R^1 = \int [V - V_{\text{thresh}}] G[V^1/2, V_\alpha](v) \, dv. \quad (11) \]

where \( V_{\text{thresh}} \) is the threshold and \( V^1 \) is given by (10). The idea is that the modulation amplitude of the firing rate roughly corresponds to the truncated half-modulation amplitude of the membrane potential. The factor \( \frac{1}{2} \) arises because, by convention, the modulation amplitudes of the subthreshold membrane potential \( V^1 \), and of the simple cell firing rate \( R^1 \), are given as the difference between the peak values, and therefore are twice as large as the corresponding F1 components. Figure IIc confirms that the approximation given by Eq. 11 is reasonable.

Essentially, the response amplitude \( R^1 \) is again sigmoidal:

\[ R^1 = R_{\text{max}} \frac{c_{\text{test}}}{c_{50} + \sqrt{c_{\text{test}}^2 + c_{\text{mask}}^2}}, \]
where, very roughly, $R_{\text{max}} \approx V_{\text{max}}/2 - V_{\text{thresh}}$ and $c_{50} = 1/\alpha$ with $\alpha$ given in (10).

![Graphs showing firing rate and membrane potential](image)

Figure II. Cross-orientation suppression. Responses to plaids composed of an optimally oriented test grating and an orthogonal mask grating. Curves correspond to different mask contrasts (0%, 25% and 50%). A: Modulation amplitude of the firing rate in the absence of synaptic depression. B: Modulation amplitude of subthreshold membrane potential in the presence of synaptic depression $V'$, according to simulations (dots) and analytical estimate in equation (10) (curves). C: Modulation amplitude of firing rate $R'$, according to simulations (dots) and analytical estimate in equation (11) (curves).

We now deduce the formula in (10).

We first estimate the mean LGN firing rates in response to a grating stimulus of the form

$$S(x, t) = c \cos(\mathbf{k} x - \alpha t),$$

where $c$ is local contrast, $\mathbf{k}$ is a 2-dimensional wave vector, and $\alpha/2\pi$ is temporal frequency. Integrating this stimulus over the LGN receptive field according to (2) gives a sinusoidally modulated LGN current, $I_{\text{pre}}$, with (half-) amplitude

$$I_{\text{pre}}' = c I \sqrt{\pi/2} k_f \tau_f \exp(-\tau_f \omega^2).$$

The constant $I$ depends on the spatial LGN filter $L_r$, and the parameters $k_f$ and $\tau_f$ characterize the dominant term of the temporal LGN filter $L_t$ given in Methods. The formula neglects the slow term in the temporal LGN filter. This is reasonable since $\tau_s < \tau_f$ and $k_s < k_f$. If we further assume that the resting firing rate of the LGN cell is small (Eq. 3), the firing rates of ON- and OFF-center cells become half-rectified sinusoids with amplitude $f_{\text{max}}/I_{\text{pre}}'$. Averaging over a cycle, $t=0...2\pi/\omega$, gives a mean LGN firing rate

$$f^0 = f_{\text{max}}/\sqrt{2\pi} \frac{c f_{\text{max}} I}{\sqrt{2\pi}} k_f \tau_f \exp(-\tau_f \omega^2).$$

We next apply the formula for the synaptic depression (9b) derived for sinusoidally modulated stimuli. This is possible since for plaid stimuli each individual LGN-cell is again driven by a sinusoidally modulated input, although with different amplitudes. Formally, this is seen by rewriting the plaid stimulus in the form...
\[ S(x, t) = \mathbf{c}_{\text{test}} \cos(\mathbf{k}_{\text{test}} x - \omega t) + \mathbf{c}_{\text{mask}} \cos(\mathbf{k}_{\text{mask}} x - \omega t) = \mathbf{c}(x) \cos(\psi(x) - \omega t), \]

with \( \mathbf{c}(x) = \sqrt{\mathbf{c}_{\text{test}}^2 + \mathbf{c}_{\text{mask}}^2 + 2 \mathbf{c}_{\text{test}} \mathbf{c}_{\text{mask}} \cos((\mathbf{k}_{\text{test}} - \mathbf{k}_{\text{mask}}) x)} \). Averaging over space yields a mean amplitude which is the root mean square of the test and mask contrasts,

\[ \bar{c} = \sqrt{c_{\text{test}}^2 + c_{\text{mask}}^2} . \quad (13) \]

The formula for \( V^1 \) in (10) is obtained from (9b) by first substituting \( f^0 \) according to (12), and by substituting current with membrane potential on both sides in (9b). Such a substitution is allowed because according to (5), \( V \) is a linearly filtered version \( I \). We then obtain

\[ V^1 = \frac{V^1_{\text{nd}}}{1 + \alpha c}, \quad (14) \]

with \( \alpha \) given in (10) and \( V^1_{\text{nd}} \) representing the F1 component of \( V \) in the absence of synaptic depression. Due to the push-pull mechanism, and because the mask does not contribute to the postsynaptic potential, the F1 component \( V^1_{\text{nd}} \) is a linear function of the test contrast, provided the resting LGN firing rate vanishes, \( f_{\text{rest}} = 0 \).

For small \( f_{\text{rest}} \) we still have approximately

\[ V^1_{\text{nd}} = c_{\text{test}} V^1_{100}, \quad (15) \]

with \( V^1_{100} \) denoting the response without depression at 100% test contrast. Substituting in the formula for \( V^1 \), Eq. 14, the contrast \( c \) given by (13) and the non-depressed response \( V^1_{\text{nd}} \) given by (15), we get the desired equation (10) for the membrane potential response of the simple cell to a plaid.