Mathematical Derivations

(Appendix to Carandini and Heeger, *Science* 1994)

Our model is analytically tractable when the stimuli are sinusoidal gratings. Here we derive formulas for response amplitude and response phase as functions of stimulus contrast and temporal frequency.

In our model, the "linear" inputs satisfy the following two constraints:

$$\begin{aligned} g_e V_e + g_i V_i + g_{leak} V_{leak} &= L \\ g_e + g_i + g_{leak} &= g_0, \end{aligned}$$

where g_0 is a constant, and L is the underlying linear response of the cell. Without loss of generality, we take $V_{rest} = V_{shunt} = 0$. Then the "driving current" to the cell is equal to the underlying linear response:

$$I_d = g_e V_e + g_i V_i + g_{leak} V_{leak} + g_{shunt} V_{shunt} = L.$$

The underlying linear response of each cell varies over time. However, the linear weighting functions are designed so that for drifting sinusoidal grating stimuli, summing the rectified and squared linear responses yields a signal that is constant over time:

$$\sum \lfloor I_d \rfloor^2 = k^2 c^2.$$

Here k is a constant, I_d is the "driving current" a cell, c is the contrast of the grating stimulus, and $\lfloor x \rfloor = \max(0, x)$ means halfwave-rectification, and the summation is taken over all the cells in the normalization pool.

The shunting conductance depends on the pooled activity of the cells in the normalization pool:

$$g_{shunt} = \frac{g_0}{\sqrt{1 - k' \sum R}} - g_0,$$

where k' is a constant and R denotes the firing rate a cell, and the summation is again taken over all the cells in the normalization pool. It follows from the above equations that the total conductance of the cell is given by:

$$g = g_e + g_i + g_{leak} + g_{shunt} = \frac{g_0}{\sqrt{1 - k' \sum R}}.$$

Firing rate, in the model, is proportional to the rectified and squared membrane potential:

$$R \propto \lfloor V \rfloor^2.$$

For drifting grating stimuli, the model reaches a "steady state" condition. Once in this condition the pooled activity, $\sum R$, is constant over time and it depends on the sum of the squared "driving currents":

$$k' \sum R = \frac{\sum \lfloor I_d \rfloor^2}{g_0^2 + \sum \lfloor I_d \rfloor^2} = \frac{k^2 c^2}{g_0^2 + k^2 c^2}.$$

It follows that the conductance g is also constant over time once the model has reached this "steady state" condition:

$$g^2 = g_0^2 + k^2 c^2$$

The model reaches this "steady state" condition because the underlying linear weighting functions are designed in quadruples: four cells with the same amplitude response but with phases in steps of 90°. For a drifting sine grating stimulus, the sum of the responses is proportional to the squared contrast of the stimulus, and it is constant over time (independent of the stimulus phase). The phase independence is a simple consequence of the 90° phase offsets, analogous to the trigonometric identity: $\sin^2(\theta) + \cos^2(\theta) = 1$. There is, in fact, evidence that adjacent simple cells exhibit either 90° or 180° phase relationships [D. Pollen and S. Ronner, *Science* 212, 1409 (1981); K. H. Foster *et al.*, *J. Physiol.* 365, 331 (1983); L. A. Palmer and T. L. Davis, *J. Neurophysiol.* 46, 260 (1981); Liu *et al.*, *Vis. Res.* 32, 1193 (1992)]

The membrane equation may now be rewritten as:

$$C \frac{d}{dt}[V(t)] + g\, V(t) = I_d(t),$$

where g is constant over time. Taking the Fourier transform of this expression gives:

$$i\, C\, \omega\, V(\omega) + gV(\omega) = I_d(\omega)$$

i.e.,

$$V(\omega) = \frac{I_d(\omega)}{g + i\omega C},$$

where ω is the temporal frequency of the stimulus. This last equation gives the amplitude and phase of the membrane potential:

$$[\text{amplitude}(V)]^2 = \frac{[\text{amplitude}(I_d)]^2}{g^2 + (\omega C)^2},$$

and

$$\text{phase}(V) = \text{phase}(I_d) + \text{atan}(\omega C/g).$$

Here amplitude(I_d) and phase(I_d) denote the amplitude and phase of the fundamental Fourier component of the "driving current" (i.e., for frequency ω equal to the temporal frequency of the stimulus). Likewise, amplitude(V) and phase(V) denote the fundamental component of the membrane potential.

Since the "driving current", $I_d(t) = L(t)$, is a linear sum of the stimulus intensities, the amplitude of its fundamental Fourier component is proportional to stimulus contrast, and the phase is not affected by contrast:

$$\text{amplitude}(I_d) \propto c, \quad \text{and} \quad \text{phase}(I_d) = \text{constant}.$$

Firing rate is proportional to the halfwave-rectified and squared membrane potential. Hence, the amplitude of the fundamental Fourier component of the response is proportional

to the square of the amplitude of the membrane potential. The phase of the response is equal to the phase of the membrane potential since halfwave-rectification and squaring do not affect phase:

$$\text{amplitude}(R) \propto [\text{amplitude}(V)]^2, \quad \text{and} \quad \text{phase}(R) = \text{phase}(V).$$

Response amplitude and phase are therefore given by:

$$\text{amplitude}(R) = K \frac{c^2}{g^2 + (\omega C)^2},$$

and

$$\text{phase}(R) = \phi + \text{atan}(\omega C / g)$$

where K, k, and ϕ are constants, $g = \sqrt{g_0^2 + k^2 c^2}$ is conductance, g_0 is the membrane conductance at rest (zero contrast), C is the membrane capacitance, c is stimulus contrast, and ω is the temporal frequency of the stimulus.