

Fraction of excitatory inputs required by a visual neuron to fire.

Guido Bugmann

School of Computing Communications and Electronics
University of Plymouth, Drake Circus, Plymouth PL4 8AA, United Kingdom
gbugmann AT plymouth.ac.uk

The properties of visual neurons are often quantified in terms of sharpness of orientation tuning, direction selectivity, etc. How do these quantifiers translate in terms of input/output function of a spiking neuron? In this paper, we attempt to estimate the fraction of active excitatory inputs required by a visual neuron to fire on the basis of orientation selectivity data and V1 cells connectivity data.

The mean tuning width of the firing rate response of V1 cells to a drifting sinusoidal grating is around 20° orientation, however the tuning of its membrane potential variations is closer to 40° (Carandini & Ferster, 2000). This difference is an effect of the firing threshold. The orientation selectivity is due to LGN inputs corresponding to areas aligned in the visual space, as originally proposed by Hubel and Wiesel (1962). More specifically, V1 neurons receive inputs from selected centre-ON and centre-OFF neurons in the LGN in such a way as to exhibit elongated receptive fields with ON and OFF areas. A neuron is excited by bright spots falling in the ON area and dark spots (darker than the background illumination) falling on the OFF area. It is however be inhibited by the reverse pattern of stimulation (dark on ON and bright on OFF). This is termed the push-pull mechanism. Inhibition is shown to arise via intra-cortical relay cells (Hirsch et al., 1998). When a grating stimulus made of dark and bright bars is moved over the receptive field, it successively activates and inhibits the V1 cell. If the grating has the optimal orientation and is moved at the optimal speed, the cell will firing strongly during the phases of excitation (Carandini & Ferster, 2000). It is possible that inhibitory rebound also contributes to the spiking. At a less than optimal orientation, ON and OFF receptive field are exposed to a mixture of dark and bright parts of bars and are never highly excited or highly inhibited. Firing is then less vigorous during excitation. Beyond a given angle of mismatch, the current I_+ generated by excitatory inputs to the V1 cell can no longer compensate for the loss I_- due to inhibitory inputs and the cell stops firing. We try to estimate the fraction of active excitatory inputs at that point.

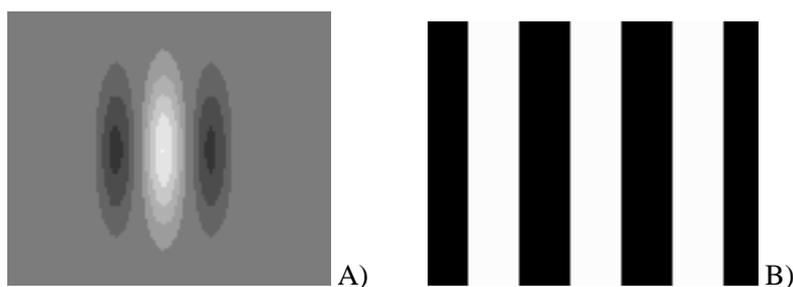


Figure 1. **A.** Receptive field of the modeled simple cell. **B.** Portion of a square-wave grating with optimal spatial frequency used as a stimulus.

The approach chosen here is to run a numerical simulation of inputs generated by a high contrast grating exciting the LGN inputs to a V1 cell with a Gabor receptive field (figure 1A), then to note for what input condition the orientation tuning reaches 20° . With such a stimulus it is reasonable to assume that LGN inputs are either strongly active or silent. Then, the input current becomes proportional to the difference between the number of active excitatory and inhibitory inputs.

It is assumed that the Gabor function reflects the spatial density of LGN inputs. The total net current I_{tot} generated by inputs cells in the Gabor receptive field is then proportional to:

$$I_{tot} \approx \iint G(x, y) SM(x, y) dx dy \quad (1)$$

where $G(x,y)$ is a 2-dimensional Gabor function (Jones and Palmer, 1987). The stimulus matching functions $SM(x,y)$ is defined as:

$SM(x,y) = 1$	if $G(x,y) < 0$ and grating(x,y) = dark or if $G(x,y) > 0$ and grating(x,y) = bright
$SM(x,y) = -\beta$	otherwise

where β represents the relative strength of inhibition versus excitation. Physiological data generally show a stronger increase in membrane potential due to excitation than a decrease during inhibition phases. From figure 2b in Carandini and Ferster (2000), β can be estimated to be around 0.25. We have experimented with various values of β in our simulations. Intracortical inputs are assumed not to affect orientation tuning (Chung and Ferster, 1998) and are absorbed as proportionality constant in (1). Figure 2 shows the tuning curve of input currents in the case $\beta=0$, $\beta=0.25$ and $\beta=1$ for a stimulus with the ideal phase (bright on ON and dark on OFF at the ideal orientation). To account for a tuning of the firing rate of 20° , the firing threshold must here be reached with respectively 70%, 63% and 42% of active excitatory inputs. This gives an indication of how to set the weight/threshold relation in simulated neurons.

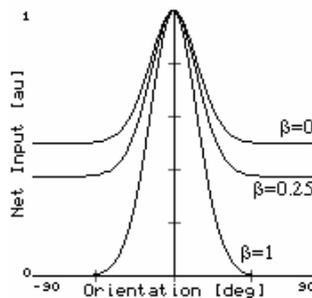


Figure 2. Net input fraction $(N+-N-)/N_{tot}$ in dependence on the difference of orientation between the grating and the receptive field.

All the above is based on observations that visual neurons are highly orientation selective when stimulated with bars or gratings. This leads to the conclusion that neurons can fire only if more than around two third of the excitatory inputs are active. Yet receptive fields mapping measurements are routinely performed with flashed stimuli of sizes much smaller than the receptive field (see e.g. Gardner et al., 1999). How can this puzzle be resolved?

References

- Carandini M. and Ferster D. (2000) Membrane potential and firing rate in cat primary visual cortex. *J. of Neuroscience*, 20:470-484.
- Chung S. and Ferster D. (1998) Strength and orientation tuning of the thalamic input to simple cells revealed by electrically evoked cortical suppression. *Neuron*, 20: 1177-1189.
- Gardner J.L., Anzai A., Ohzawa I., and Freeman R. (1999) Linear and nonlinear contributions to orientation tuning of simple cells in the cat's striate cortex. *Visual Neuroscience* 16: 1115-1121.
- Jones J.P. and Palmer L.A. (1987) An evaluation of the two-dimensional Gabor filter model of simple receptive fields in cat striate cortex. *J. Neurophysiology*, 58:1233-1258.
- Hubel D.H. and Wiesel T.N (1962) Receptive fields, binocular interaction and functional architecture in the cat visual cortex. *J. Physiol. (London)*, 160:106-154.