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Mechanisms of Normalization in Primary Visual Cortex

Responses of neurons in primary visual cortex (V1) display a number of nonlinearities, many of which are well captured by the normalization model (1) in which local activity within V1 is pooled and then acts divisively on neuronal responses within the network. The biological mechanism underlying this divisive normalization signal is unknown, although shunting inhibition has been proposed as a possible candidate (2,3). We consider three mechanisms of inhibition: inhibitory current, a shunt conductance, and a varying "background" of noisy excitatory and inhibitory synaptic activity. The first two forms of inhibition are thought to be subtractive (4-6, but see 7) while the last form has been described as divisive (6, 8-9). We examine which of these forms of inhibition best reproduces normalization effects observed in V1, specifically contrast-dependent saturation and masking of neuronal responses by sub-optimal stimuli. In a computational study using leaky integrate-and-fire neurons, we find that all three mechanisms of inhibition can produce contrast-dependent saturation of responses like that observed *in vivo*. Masking, however, is best reproduced when the normalization signal is a background of mixed excitatory and inhibitory inputs.

[1] Heeger DJ (1992) Normalization of cell responses in cat striate cortex. Vis. Neurosci. 9: 181-197.

[2] Carandini M & Heeger DJ (1994) Summation and division in V1 simple cells. Science 264: 1333-1336.

[3] Carandini M, Heeger DJ & Movshon JA (1997) Linearity and normalization in simple cells of the macaque primary visual cortex. J. Neurosci. 17: 8621-8644.

[4] Gabbiani F, Midtgaard J & Knopfel T (1994) Synaptic integration in a model of cerebellar granule cells. J. Neurophysiol. 72: 999-1009.

[5] Holt GR & Koch C (1997) Shunting inhibition does not have a divisive effect on firing rates. Neural Comput. 9: 1001-1013.

[6] Chance FS, Abbott LF & Reyes AD (2002) Gain modulation from background synaptic input. Neuron 35: 773-782.

[7] Mitchell SJ & Silver RA (2003) Shunting inhibition modulates neuronal gain during synaptic excitation. Neuron 38: 433-445.

[8] Doiron B, Longtin A, Berman N & Maler L (2001) Subtractive and divisive inhibition: effects of voltage-dependent inhibitory conductances and noise. Neural Comput. 13: 227-248.

[9] Prescott SA & De Koninck Y (2003) Gain control of firing rate by shunting inhibition: roles of synaptic noise and dendritic saturation. Proc. Natl. Acad. Sci. USA 100: 2076-2081.