Identifying Falsifiable Predictions of the Divisive Normalization Model of V1 Neurons

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Abstract: The divisive normalization model (DNM, Heeger, 1992) accounts successfully for a wide range of phenomena observed in single-cell physiological recordings from neurons in primary visual cortex (V1). The DNM has adjustable parameters to accommodate the diversity of V1 neurons, and is quite flexible. At the same time, in order to be falsifiable, the model must be rigid enough to rule out some possible data patterns. In this study, we discuss whether the DNM predicts any physiological result of the V1 neurons based on mathematical analysis and computational simulations. We identified some falsifiable predictions of the DNM. The main idea is that, while the parameters can vary flexibly across neurons, they must be fixed for a given individual neuron. This introduces constraints when this single neuron is probed with a judiciously chosen suite of stimuli. For example, the parameter governing the maintained discharge (base firing rate) is associated with three characteristic observable patterns: (A) the existence of inhibitory regions in the receptive fields of simple cells in V1, (B) the super-saturation effect in the contrast sensitivity curves, and (C) the narrowing/widening of the spatial-frequency tuning curves when the stimulus contrast decreases. Based on this fact, it is predicted that the simple cells can be categorized into two groups: one shows A, B, and widening (C) and the other one shows not-A, not-B, and narrowing (C). We will also discuss roles of other DNM parameters for emulating the V1 neurons in physiological experiments.

Keywords: Divisive normalization model; Primary visual cortex (V1); Simple cell; Complex cell; Falsifiability

Additional details: A general form of the divisive normalization model (Heeger, 1992) can be written as follows:

$$R(I) = M \frac{\lfloor \beta + E_{tuned}(I) \rfloor^{n_N}}{\alpha^{n_D} + \sum_i w_i E_i(I)^{n_D}}$$

where M, n_N, n_D, α, and β are constants and I is a retinal image. The parameters M, n_N, n_D and α, are positive but β can be either positive or negative. The half-wave rectification operator $\lfloor E \rfloor$ equals E if $E > 0$ and 0 otherwise. $E_{tuned}(I)$ and $E_i(I)$ are 2D Gabor filters and their responses are linear to the contrast of I. The Gabor filter of $E_{tuned}(I)$ determines tuning of the model in the orientation, spatial frequency, and phase domains and $E_{tuned}(I)$ becomes maximum if I is a grating that is consistent with the tuning of the model and the contrast of the grating is maximum. If the retinal image is in uniform gray, both $E_{tuned}(I)$ and $E_i(I)$ become 0 and the response of the model is called the maintained discharge. The observed maintained discharge is closely associated with the parameter β.

Usually, a response of a V1 neuron increases monotonically as the contrast of the tuned grating increases. However, at high stimulus contrasts, the response of some V1 neurons has been observed to decrease as the contrast gets even higher (Li & Creutzfeldt, 1984). In that case, the contrast sensitivity curves of those neurons are unimodal but are not monotonic. This *super-saturation effect* can be emulated by the model if the maintained discharge parameter is high enough:

$$\beta > \frac{n_N}{n_D}\left(1 + \alpha^{n_D}\right) - 1$$