

# Assessing the inherent nonlinearity of visual neurons: simple cells versus complex cells

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Neurons in primary visual cortex (area V1) vary in the nonlinearity of their response to visual stimuli. Neurons whose response can be approximately characterized as linear are classified as simple cells. Those whose response is more fundamentally nonlinear are classified as complex cells [7]. One challenge is to quantify the degree of nonlinearity or “complexity” based on measurements of spike times in response to experimentally controlled stimuli.

We explore the behavior of two measurements of complexity. The first is the  $F_1/F_0$  ratio, a measure of linearity of spatio-temporal summation, which was proposed by a number of investigators as an appropriate measure of cell complexity [8, 2, 5, 7]. The  $F_1/F_0$  measure represents the ratio between the amplitude of the first harmonic response and the mean spike rate when cortical neurons are stimulated with drifting sinusoidal gratings.

As an alternative to  $F_1/F_0$ , we present a new model-based measure of receptive field complexity [6]. The measure is based on the following observations of “ideal” simple and complex cells. Simple cells respond as quasi-linear filters [5]. If a bright bar flashed on the receptive field of a simple cell induces the cell to spike above baseline, a dark bar will tend to suppress its response. On the other hand, complex cells are inherently nonlinear and respond equally to a bright or dark bar flashed on their receptive fields. In other words, the responses of simple cells are sensitive to the contrast-sign of the stimulus while complex cells are insensitive to contrast-sign [4].

We propose a *quadratic complexity index*, denoted by  $\alpha$ , which is an estimate of the fraction of a cell’s response that is independent of contrast-sign.

The quadratic complexitiy index is based on the model where the probability of firing at any one time is given by

$$\Pr\{R = 1|\mathbf{x}\} = g(\sqrt{1-\alpha}\langle\mathbf{h}_1, \mathbf{x}\rangle + \sqrt{\alpha}\langle\mathbf{h}_2, \mathbf{x}^2\rangle). \quad (1)$$

Here,  $R \in \{0, 1\}$  represents the response of the cell (with one representing the occurrence of a spike),  $\mathbf{x}$  represents the recent spatio-temporal input,  $\langle\mathbf{h}, \mathbf{x}\rangle$  denotes the dot product between a kernel and the input,  $\mathbf{h}_1$  and  $\mathbf{h}_2$  represent the linear and quadratic kernels (normalized so that  $\langle\mathbf{h}, \mathbf{x}\rangle$  has a variance of one),  $\mathbf{x}^2$  represents component-wise squaring, and  $g(\cdot)$  is a static nonlinearity.

The parameter  $0 \leq \alpha \leq 1$  is called the quadratic complexity index because it determines the relative contribution of the linear and quadratic components to the response of the cell. When  $\alpha = 0$  the response of the model reduces to the standard linear-nonlinear model of simple cells,  $\Pr\{R = 1|\mathbf{x}\} = g(\langle\mathbf{h}_1, \mathbf{x}\rangle)$ . In this case, the model behaves as a quasi-linear filter. When  $\alpha = 1$  the response of the cell is dominated by the (sign-independent) energy of the signal and lacks a linear component,  $\Pr\{R = 1|\mathbf{x}\} = g(\langle\mathbf{h}_2, \mathbf{x}^2\rangle)$ . The response of this model is insensitive to contrast sign. Mixed responses between these ideal simple and complex cells are generated by intermediate values of  $\alpha$ . This phenomenological model captures in a concise form the contrast sign-dependent and independent response components of cortical cells. The model’s parameters, including the quadratic complexity index, can be estimated from the arrival times of each action potential elicited by a sequence random orthonormal images using the procedure detailed in Ref. [6].

We investigate the behavior of the  $F_1/F_0$  ratio and the quadratic complexity index via simulations of simplified neuron models and via analysis of single unit data from macaque V1. The simulations demonstrate that, while both  $F_1/F_0$  and  $\alpha$  behave equivalently under some circumstances, their behaviors diverge for more realistic models. We argue that  $\alpha$  is a better measure of the complexity of the underlying model because  $F_1/F_0$  is strongly affected by the rectification in the model. Moreover, the simulations demonstrate that the “complexity” of a given model neuron could depend strongly on the operating regime of neurons, which could change due to normalization effects in response to different stimulus conditions.

In the V1 single unit data, measurements of the  $F_1/F_0$  ratio and  $\alpha$  appear uncorrelated. This decoupling can be understood from the analysis of the

simulations. We also observe a bimodal distribution of  $F_1/F_0$  but a unimodal distribution of  $\alpha$ . Since our simulations demonstrate that  $\alpha$  better captures model complexity and the bimodal distribution of  $F_1/F_0$  is predicted by a rectification model of spike generation [3, 1], we argue that these results fail to demonstrate the existence of discrete classes of simple and complex neurons. Nonetheless, given the observation of the dependence of complexity measures on the normalization state of the neuron, we cannot rule out the possibility that a bimodal distribution could be observed under other stimulus conditions.

## References

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