Consistency of Extracellular and Intracellular Classification of Simple and Complex Cells

An Luo, Marios Philiastides, Jim Wielaard and Paul Sajda*

Abstract

Using a rectification model and an experimentally measured distribution of the extracellular modulation ratio (F_1/F_0), we investigate the consistency between extracellular and intracellular modulation metrics for classifying cells in primary visual cortex (V1). We first demonstrate that the shape of the distribution of the intracellular metric χ is sensitive to the specific form of the bimodality observed in F_1/F_0. When the proper mapping between F_1/F_0 and χ is applied to the experimentally measured F_1/F_0 data, χ is weakly bimodal. We then use a two-class mixture model to estimate physiological response parameters given the F_1/F_0 distribution. We show, once again, that a weak bimodality is present in χ. Finally, using the estimated parameters for the two cell clases, we show that simple and complex cell class assignment in F_1/F_0 is more-or-less preserved in a heavy-tailed f_1/f_0 distribution, with complex cells being in the core of the f_1/f_0 distribution and simple cells in the tail (misclassification error in $f_1/f_0 = 19\%$). Class assignment in f_1/f_0 is likewise consistent (misclassification error in $F_1/F_0 = 15\%$). Our results provide computational support for the conclusion that extracellular and intracellular metrics are relatively consistent measures for classifying cells in V1 as either simple or complex.

*Department of Biomedical Engineering, Columbia University,New York, NY 10027; (al2082, mgp2101, djw21, ps629)@columbia.edu.
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Introduction

It has been observed that the ratio between the amplitude of the first harmonic of the response to the mean firing rate (F_1/F_0) when a cell is responding to drifting sinusoidal gratings is bimodally distributed over the V1 population. Furthermore, this bimodality is perceived as evidence for the existence of two discrete classes of cells [1]. Mechler and Ringach [2] however, have proposed that the bimodality of F_1/F_0 does not necessarily imply the existence of two cell classes. Using a rectification model, they show that a bimodal distribution in F_1/F_0 can be observed even when the distribution of a parameter χ, closely linked to the intracellular modulation ratio f_1/f_0, is unimodal. Since f_1/f_0 , and therefore χ, is more directly linked to the synaptic drive of the neurons, it can be argued that it is likely to be a better metric than F_1/F_0 for inferring the presence of underlying cell classes.

In this paper we investigate the issue of simple and complex cell classification with respect to the consistency of the extracellular and intracellular modulation ratios. Similar to [2], we model neuron responses using a rectification model. Somewhat differently, however, we use the experimentally observed data for F_1/F_0 reported in [2] to fit model parameters and estimate χ and f_1/f_0. We first show that the nonlinear mapping from F_1/F_0 to χ results in a weak bimodal distribution for χ if one uses the experimentally observed F_1/F_0 distribution. We next use a rectification model, similar to that used in [2], to estimate parameters for both a one class and two class model that best fit the experimentally observed distribution of F_1/F_0. Finally we use the estimated parameters for the two cell class model to investigate the consistency of simple and complex classification when labeling in F_1/F_0 and evaluating the class distribution in f_1/f_0, and vice versa.

The rectification model

We assume that a neuron's membrane potential in response to a sinusoidal drifting grating at preferred orientation and spatial frequency consists of a sinusoidal waveform driven at the temporal frequency of the stimulus, with amplitude A, and mean voltage potential V_m. A neuron's instantaneous firing rate, $r(t)$, is assumed to be proportional to the supra-threshold membrane potential and zero if the membrane potential remains below the threshold, V_t. Eqn. 1&2 summarize this rectification model.

$$v(t) = V_m + A\cos(2\pi f t) \tag{1}$$

$$r(t) = G[v(t) - V_t]^+ \tag{2}$$

In Eqn. 2, G is the gain related to the spike generator. The intracellular modulation ratio f_1/f_0 is defined as $A/(V_m - V_I)$, where V_I is the inhibitory reverse potential. The extracellular modulation ratio F_1/F_0 is given by $F_0 = \frac{1}{2\pi}\int_0^{2\pi} r(t)dt$ and $F_1 = \frac{1}{2\pi}\int_0^{2\pi} r(t)\cos(2\pi f t)dt$.

In their paper [2], Mechler and Ringach define an intracellular ratio parameter $\chi = (V_t - V_m)/A$, and prove that F_1/F_0 is a nonlinear monotonic function of χ,

$$F_1/F_0 = f(\chi) = \begin{cases} \frac{-\chi\sqrt{1-\chi^2}+\arccos(\chi)}{\sqrt{1-\chi^2}-\chi\arccos(\chi)} & \text{if } -1 \le \chi \le 1 \\ -1/\chi & \text{if } \chi < -1. \end{cases} \tag{3}$$

Non-linear mapping between F_1/F_0 and χ

Although a bimodal distribution in F_1/F_0 can be generated from a unimodal distribution in χ, as Mechler and Ringach propose, this bimodal distribution appears to be quite different from experimentally observed results (compare Fig. 1a & b). We calculate the distribution of χ from the F_1/F_0 distributions using the following,

$$p(\chi) = p_{F_1/F_0}(f(\chi))\left|\frac{d}{d\chi}f(\chi)\right|. \tag{4}$$

Results are shown in Fig. 1a & b for two distributions reported in [2]. When using the experimental data, the distribution in χ appears weakly bimodal, suggesting that the intracellular metric is consistent with the F_1/F_0 distribution in terms of inferring two underlying cell classes. As a second test of whether two cell classes are consistent with the distribution of F_1/F_0 and χ, we use the rectification model to estimate parameters for a two population mixture model of p(F_1/F_0) and p(χ).

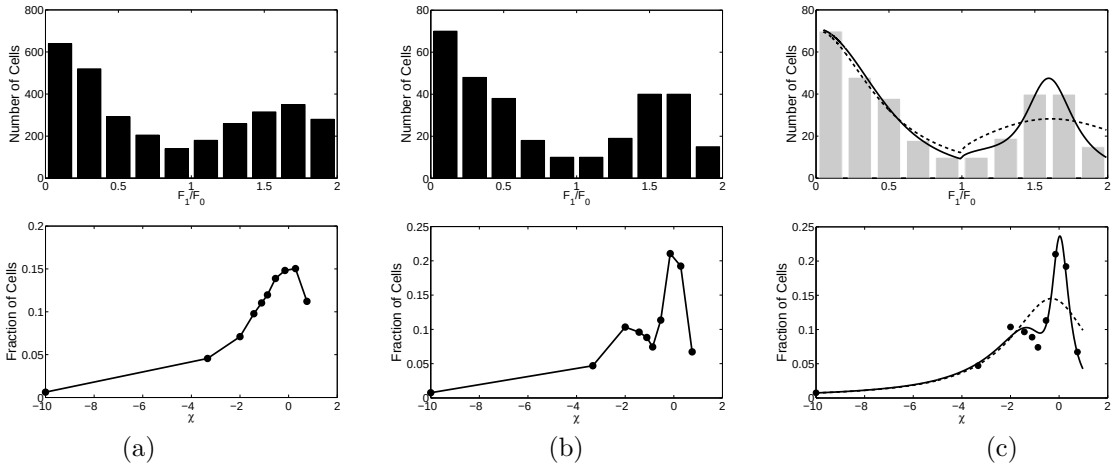

Figure 1: Relationship between the extracellular modulation index F_1/F_0 (top row) and the intracellular modulation metric χ (bottom row) for simulated and experimental F_1/F_0 data. a) Example simulated F_1/F_0 distribution taken from [2] and the corresponding distribution for χ using the non-linear mapping of Eqn. 4. For this simulated F_1/F_0 data χ is clearly unimodal. (b) F_1/F_0 experimental data for macaque reported in [2] and the corresponding distribution for χ given the non-linear mapping. Note that there is a weak bimodality in χ if the experimental data, rather than the simulated data, is used. (c) Model fits to the experimental data assuming one (dashed) and two (solid) classes of cells. Parameters for these fits are shown in Table 1. The two class fit better matches the non-linear mapping (black points) and is also weakly bimodal.

Two class mixture model for p(F_1/F_0) and p(χ)

We fit the rectification model and associated distributions for the parameters to the experimental data for F_1/F_0. Starting from the experimentally observed distributions of F_1/F_0 and the rectification model, we find the parameters (i.e. mean value μ and standard deviation σ) of V_m, V_t, and A. Specifically, we first estimate parameters for $V_t - V_m$ and the calculate the corresponding values for V_t and V_m.

We assume $V_t - V_m$ to be Gaussian distributed for both simple and complex cells, $\mathcal{N}(V_t - V_m; \mu_{V_t-V_m}, \sigma_{V_t-V_m})$. As the amplitude A is positive, we set its distribution to,

$$p(A) = \begin{cases} \frac{1}{\sqrt{2\pi}\sigma_A}(\exp(-\frac{(A-\mu_A)^2}{2\sigma_A^2}) + \exp(-\frac{(-A-\mu_A)^2}{2\sigma_A^2})) & \text{if } A \geq 0 \\ 0 & \text{if } A < 0 \end{cases} \tag{5}$$

For simplicity μ_A for complex cells is set to 0.

Additional constraints are included to make the model more realistic. For example we add a constraint on the membrane potential relative to the inhibitory reversal potential. For both simple and complex cells, we force

$$\mu_A + 1.5\sigma_A + \mu_{V_t-V_m} + 1.5\sigma_{V_t} + 1.5\sigma_{V_m} < \mu_{V_t} - V_I \tag{6}$$

μ_{V_t} is set at -55mV and σ_{V_t} to be 1.5mV for both types of cells [3].

We minimize the squared error between the F_1/F_0 data and the F_1/F_0 predicted by the model,

$$\underset{\alpha,\beta,C}{\text{argmin}} \; \|p(F_1/F_0) - p(f(\alpha,\beta,C))\|^2 \tag{7}$$

where $p(F_1/F_0)$ is the experimentally observed distribution given in Fig. 4c of [2]. α represents parameters for simple cells, which include $\mu_{V_t-V_m}$, $\sigma_{V_t-V_m}$ and σ_A; and β represents the counterparts for complex cells. In addition, C is a random variable representing cell type, with probability, $p(C = t)$, equal to the fraction of cells of type t. Since this is a nonlinear optimization, we perform exhaustive search to estimate the parameter values.

The parameters estimated for both a two class model and a single cell class model are given in Table 1, with fits for F_1/F_0 and χ shown in Fig. 1c. Clear is that the two class model is a better fit to the experimental F_1/F_0 data than the single class model. In addition we see that the two class modeling fitting yields a weakly bimodal distribution in χ, consistent with the non-linear mapping between F_1/F_0 and χ shown in Fig 1b.

Classifying simple and complex cells

We analyzed the extent to which classification is preserved in terms of the two cell classes (as defined by the parameter values of the two classes) as well as in terms of the classification of f_1/f_0 given cell labels from F_1/F_0 and vice versa.

	Two Classes		One Class
	Simple Cells	Complex Cells	
C	0.44	0.56	1.0
$\mu_{V_t-V_m}(mV)$	0.5	-14.6	0
$\sigma_{V_t-V_m}(mV)$	3.8	5.2	2.5
$\mu_A(mV)$	5.6	0	1(-1)
$\sigma_A(mV)$	6.8	6.3	0.5

Table 1: Results of optimizing the model parameters to fit experimental data for F_1/F_0.

We simulate 20,000 neurons, with distributions for F_1/F_0 and f_1/f_0 shown in Fig. 2. Misclassification error when class labels are defined by the parameters of the two cell classes in Table 1 is 9% for F_1/F_0 and 25% for f_1/f_0. When class labels are defined by criteria on the modulation index, misclassification error in f_1/f_0 is 19% and in F_1/F_0 is 15%. As can be seen, the distribution in f_1/f_0 is not weakly bimodality, as is χ, rather it is a heavy tailed distribution. Clear is that separability between cell classes is possible by observing that complex cells tend to lie in the core of the f_1/f_0 distribution while simple cells are in the tails. Recent intracellular recordings in cat [4] have shown a similar heavy-tailed distribution in f_1/f_0, and a misclassification error of 18% in f_1/f_0 when class labels are defined in F_1/F_0. Interestingly, when applying our model fitting techniques to this experimentally measured distribution of F_1/F_0 for cat, the fits are poor, largely because the shape of the F_1/F_0 in [4] is very different from what is seen in macaque [2]. It should be noted that the distribution of F_1/F_0 reported in [4] consists of about 1/3 as many cells as that reported in [2].

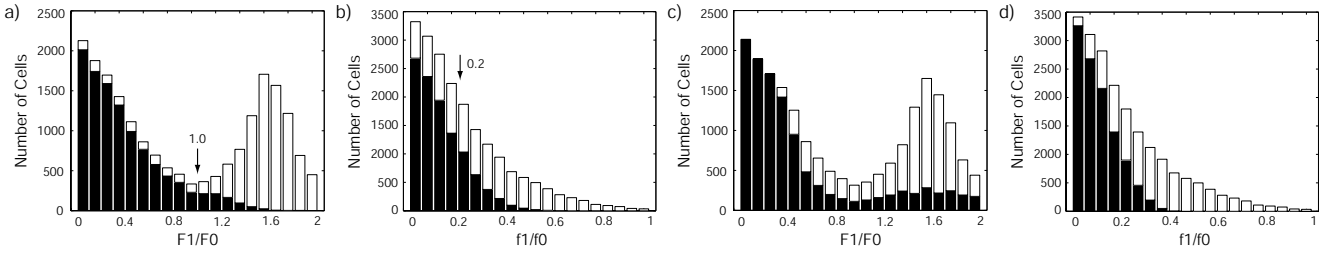

Figure 2: Simulation results showing classification of cell types given the two class model and parameters estimates in Table 1. (a) Distribution of F_1/F_0 where white bars indicate cells defined as "simple" in terms of their parameters values in Table 1 and black bars indicate "complex" cells in terms of these values. (b) Distribution of f_1/f_0 given the same labels of simple and complex cells as in (a). (c) Distribution of simple (white) and complex cells (black) when labels are defined by the modulation index criterion $F_1/F_0 > 1$ for simple, else complex. (d) Same as (c) except for f_1/f_0 where criterion is $f_1/f_0 > 0.2$ simple, else complex.

Conclusion

We conclude that extracellularly experimental data from primary visual cortex of macaque, assessed by a rectification model are consistent with a heavy-tailed distribution in f_1/f_0 and weakly bimodal distribution for χ. Even though our analysis does not provide conclusive evidence for multiple cell classes in V1 or microcircuitry differences between simple and complex cells, our analysis demonstrates that extracellular and intracellular modulation criteria are more-or-less consistent with one another and that the form of the intracellular criteria is consistent with two underlying cell classes.

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