Are there distinct classes of simple and complex cells in V1? Bimodality of the F1/F0 ratio is predicted by a simple rectification model

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1 Definition of simple and complex cells

a) Sub-field segregation and antagonism (Hubel & Wiesel)

Simple Cells

Complex Cells

b) Linearity of spatio-temporal summation (Skottun et al)

c) Gaussian distributions of a and b generate a bimodel F1/F0

The distribution of F1/F0 is bimodal (Skottun et al. 1991)

The Rectification Model

a) Mean firing rate is proportional to the supathreshold membrane voltage

b) F1/F0 is a nonlinear function of \( \chi \)

c) Gaussian distributions of a and b generate a bimodal F1/F0

2 The Rectification Model

3 The Phenomenon is Robust

4 Distributions of the extracellular F1/F0 and the intracellular f1/f0 do not have to be consistent

5 We think the remaining evidence is weak

6 What do you think?

Our coauthors have expressed different opinions about these results. Below are some of their views, together with our thoughts on them:

The "simple" and "complex" classes are upheld because you show only the possibility, but not the existence, of a continuum.

The null hypothesis is that of a continuum. The existence of discrete classes is a stronger hypothesis. However, we show that the null hypothesis is not contradicted by the evidence (as expected from the bimodal distribution of F1/F0), which is consistent with the null hypothesis.

A bimodal/intracellular f1/f0 would prove the existence of simple and complex cells.

Yes, because f1/f0 is not subject to the nonlinear mapping described here. However, preliminary data from David Ferster's lab appear to show a unimodal f1/f0.

The bimodal distribution of F1/F0 defines a meaningful functional dichotomy, even if everything in the circuitry is unimodal.

The bimodality of F1/F0 does not by itself indicate how cells with high and low f1/f0 differs in visual processing. Correlating evidence, which must come independently and in a different form, is yet to be found.

The bimodality of F1/F0 has been investigated because Hubel & Wiesel did not base their definition of simple and complex cells on "linearity".

A subset of Hubel and Wiesel's criteria were defined in terms of "summation" within and "disruption" between subfields. The equivalent mathematical concepts are called homogeneity and antithesis, which together imply linearity. Skottun et al. correctly point out that these type of linearity (i.e., on f1/f0) correlated with Hubel's classification (see our point 1b).

The "key" among Hubel and Wiesel's criteria might be the spatial separation of ON and OFF subfields. The F1/F0 is not a measure of spatial separation. It is possible that such measures will show bimodality.

We agree that this is an open question. Bimodal distributions of such a measure have been reported in studies (Schiller et al. 1992; Kogon, Gyr & Srodowiski, unpublished data; Livingstone & O'Keefe, unpublished data) but not by others (Thaller & Dallas). We are presently measuring the degree of overlap of the excitatory and inhibitory responses of cells using both the gain factor (G) and the spatial frequency of the input, as well as its spatial frequency selectivity index (see Friston & Priebe, 1997). The F1/F0 ratio, measured with contrast reversed stimulation is linearly related to the spatial frequency of the stimulus. The F1/F0 ratio is a quantitatively more reliable single segregation than F1/F0. However, the currently available evidence for discrete cell classes based on f1/f0 ratio is not yet established.

The existence of discrete classes of "simple" and "complex" cells is supported not only by the F1/F0 ratio, but by other evidence that the cell's spatial receptive field properties between the classes, such as their spontaneous rate, receptive field size, etc.

One must be careful in comparing the mean of two distributions or receptive field properties after using a cutoff to classify cells into simple and complex. The means of the distributions may be significantly different even if the distributions have the same parameters. For instance, the mean of the receptive fields of complex cells is larger than that of simple cells, but these two distributions have the same parameters.

It makes sense to name the ends of the spectrum even if simple and complex cells form a continuum.

It may make sense to label the ends of a spectrum but categories are not more useful than "thin" and "thick". A hierarchical model should not depend on such categories.

A hierarchy is elusive to the distribution of simple and complex cells in the different layers of V1. Thus, it might be the case that the hierarchical model is correct and, therefore, simple and complex cells are clearly different.

As shown in the right, the distribution of F1/F0 across all layers in the monkey does not show a clear hierarchical structure. Yes, there is a tendency to see a larger fraction of cells with high F1/F0 in some layers (including V1 and 2), but "complex" cells are seen everywhere.

The rectification model is not biologically realistic.

A bimodal distribution of F1/F0 has also been observed in a large scale realistic model of V1 using conductance-based integrate-and-fire neurons where the physical parameters are unimodally distributed (Tan, et al., unpublished).

You are ignoring the work of X who showed that the distribution of Y is clearly bimodal. Dr. Y is the one who is ignoring the important data of Z.

We speculate that, because the relevant reference(s) in the envelope below, we will be happy to look at them. Keep in mind that we are looking for data reported as a distribution of a specific measure over a large population of V1 neurons.