456.2

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

Dario Ringach

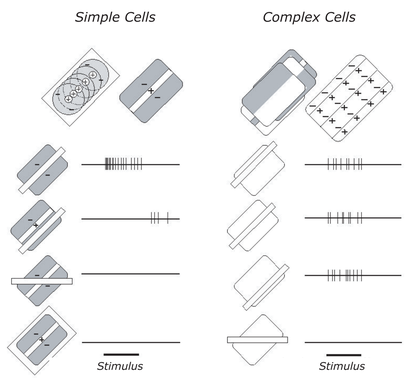
Dept of Neurobiology, David Gefen School of Medicine
Dept of Psychology & Brain Research Insititute, UCLA
Email: dario@ucla.edu

Ferenc Mechler

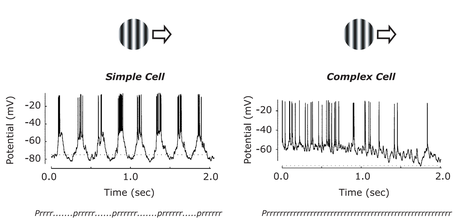
Dept of Neurology & Neuroscience
Cornell Univ Medical College
Email: fmechler@med.cornell.edu

1 Definition of simple and complex cells

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



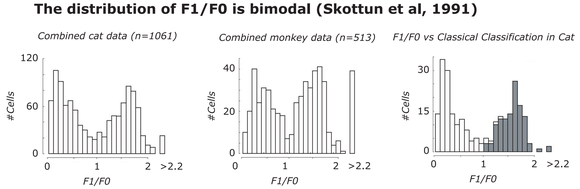
b) Linearity of spatio-temporal summation (Skottun et al)



Carandini & Ferster (2000)

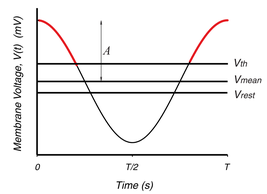
F1 = Amplitude of the temporal modulation of spike rate at the grating frequency (1st harmonic)
F0 = Mean spike rate of the response (or DC)

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



2 The Rectification Model

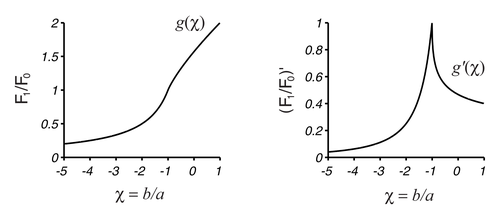
a) Mean firing rate is proportional to the suprathreshold membrane voltage



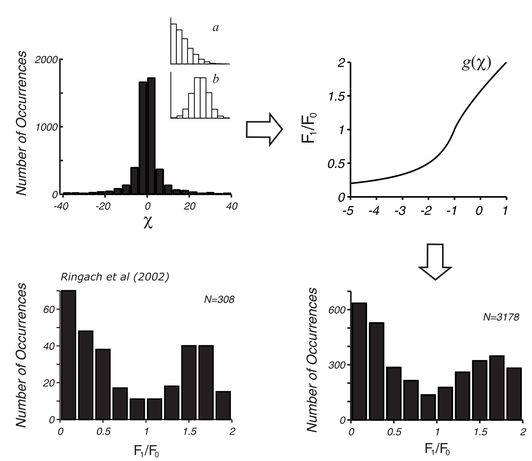
$$r(t) = G\left[V_{mean} + A\cos(2\pi ft) - V_{th}\right]^{+} = \left[a - b\cos(2\pi ft)\right]^{+}$$

$$a = GA \quad b = G(V_{th} - V_{mean})$$

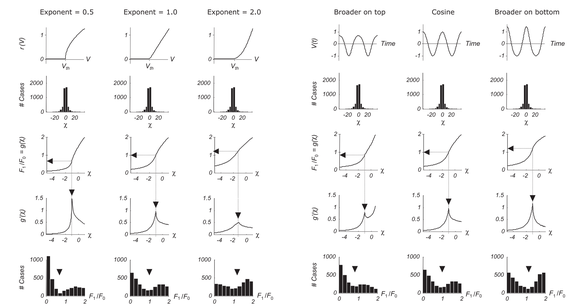
b) F1/F0 is a nonlinear function of $\chi = b/a$



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

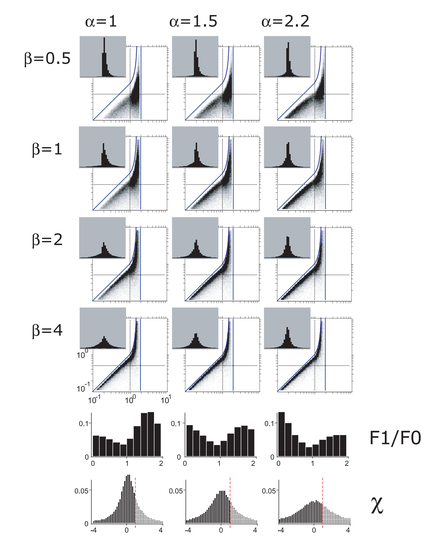


3 The Phenomenon is Robust

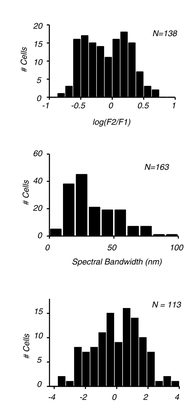


4 Distributions of the extracellular F1/F0 and the intracellular f1/f0 do not have to be consistent

$$\alpha = \sigma_b / \sigma_a \quad \beta = \sigma_a / (V_{th} - V_{rest})$$



5 We think the remaining evidence is weak



Hawken & Parker (1987)

Thorell et al (1984)

Schiller, Finlay & Volman (1976)

6 What do you think?

Our colleagues 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.

No. The null-hypothesis is that of a continuum. The existence of discrete classes requires falsifying this null-hypothesis. We showed that the main evidence thought to falsify the null hypothesis (the bimodality of F1/F0) is problematic.

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 play different roles in visual processing. Corroborating evidence, which must come independently and in a different form, is yet to be found.

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

A subset of Hubel and Wisel's criteria were defined in terms of "summation" within and "antagonism" between subfields. The equivalent mathematical concepts are called homogeneity and additivity, which together imply linearity. Skottun et al. correctly pointed this out. They also showed that, in cat, the classification based on "linearity" (i.e., on F1/F0) correlated with H&W's classification (see our point 1.b)

The "key" among Hubel and Wisel's classical criteria might be the spatial segregation of ON and OFF sub-fields. The F1/F0 is not a measure of subfield segregation. It is possible that such measure will show bimodality.

We agree that this is an open question. Bimodal distributions of such a measure have been reported by some studies (Schiller et al, 1976; Kogan, Gur & Snodderly, unpublished data; Livingstone & Conway, unpublished data) but not by others (Tolhurst & Dean). We are presently measuring the degree of overlap of the subfields identified by sparse bright/dark spots. For a model-based definition of a "complexity" index see Poster 557.13. Finally, The F2/F1 ratio, measured with contrast reversed stationary gratings, may be a quantity more related to subfield segregation than F1/F0. However, the currently available evidence for discrete cell classes based on the F2/F1 ratio is at best equivocal.

The existence of discrete classes of "simple" and "complex" cells is supported not only by the F1/F0 ratio, but by the significant difference in the mean value of other receptive field properties between the classes, such as their spontaneous rate, receptive field size, etc.

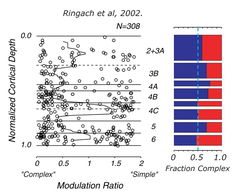
One must be careful in comparing the mean of two distributions of receptive field properties *after* using F1/F0 to classify cells into simple and complex. The means can be statistically different, but this result by itself does not demonstrate the existence, nor provides independent support, for two discrete classes of cells (see Fig. 10 in the paper).

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 as categories they are no more useful than "thin" and "fat". A hierarchical model should definitely not depend on such categories.

A hierarchy is obvious in 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 on 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 layer 4C and 6), 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 all the physical paramters are unimodally distributied (Tao, et al, unpublished).

You are ignoring the work of X who showed that the distribution of Y is clearly bimodal. Or, you are ignoring the important data of Z.

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