

## **Analysis of ON/OFF Subfield Overlap in Macaque V1**

Dario Ringach  
Departments of Neurobiology and Psychology  
Jules Stein Eye Institute  
David Geffen School of Medicine  
University of California, Los Angeles

In their pioneering studies of primary visual cortex, Hubel and Wiesel described the existence of two classes of cells, which they termed "simple" and "complex". The original classification scheme was based on partly subjective tests of linear spatial summation, later replaced by the F1/F0 ratio – the ratio between the first harmonic and the mean spike rate when the neuron is stimulated with a drifting sinusoidal grating. The distribution of F1/F0 in V1 is bimodal and divides neurons into two classes that correspond closely to the classical definition by Hubel and Wiesel. We have recently showed, however, that a bimodal distribution of F1/F0 is predicted by a simple rectification model when the distribution of the intracellular response modulation and rate are unimodal. Thus, the bimodality of F1/F0 does not necessarily imply two classes of cells.

While the F1/F0 represents a measure of receptive field linearity it fails to capture one of the key aspects in the classical definition of simple and complex cells: the degree of spatial overlap between the ON and OFF subfields of the receptive field. Hubel and Wiesel described simple cells as having non-overlapping subfields, while complex cells responded with and ON and OFF responses everywhere within their receptive field. Thus, it could be the case that the degree of overlap between the subfields is the key element that would differentiate between these neuronal classes.

To test this possibility we measured the ON/OFF subfields in macaque V1 via reverse correlation with sparse noise stimulation. We found "simple" cells which have segregated ON/OFF subfields with push-pull responses in each sub-region, and "complex" cells with nearly complete overlap between the ON and OFF subfields. However, we also observe a very heterogeneous population of neurons that exhibited partial degrees overlap. Four different measures of overlap failed to show a bimodal distribution over our V1 population. Thus, at least in monkey V1, "simple" and "complex" cells appear to represent the ends of a continuum instead of discrete cell classes. I will discuss how this fact may influence our understanding of cortical function.