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MINIREVIEW

CLASSIFYING SIMPLE AND COMPLEX CELLS ON THE BASIS OF RESPONSE MODULATION

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Abstract—Hubel and Wiesel (1962; *Journal of Physiology, London, 160,* 106–154) introduced the classification of cortical neurons as simple and complex on the basis of four tests of their receptive field structure. These tests are partly subjective and no one of them unequivocally places neurons into distinct classes. A simple, objective classification criterion based on the form of the response to drifting sinusoidal gratings has been used by several laboratories, although it has been criticized by others. We review published and unpublished evidence which indicates that this simple and objective criterion reliability divides neurons of the striate cortex in both cats and monkeys into two groups that correspond closely to the classically-described simple and complex classes.

Simple cells Complex cells Striate cortex Gratings Spatial frequency Response modulation Linear systems

INTRODUCTION

In their early recordings from the striate cortex, Hubel and Wiesel (1962) distinguished two main types of cells: simple and complex. They described four characteristics of simple cells (pp. 109–110).

(1) Spatially separate ON and OFF regions:

> "Like retinal ganglion and geniculate cells, cortical cells with simple fields possessed distinct excitatory and inhibitory subdivisions. Illumination of part or all of an excitatory region increased the maintained firing of the cell, whereas a light shone in the inhibitory region suppressed the firing and evoked a discharge at 'off'."

(2) Summation within each region:

> "A large spot confined to either area produced greater change in rate of firing than a small spot, indicating summation within either region."

(3) Antagonism between ON and OFF subregions:

> "... the two types of region within a receptive field were mutually antagonistic. This was most forcefully shown by the absence or near absence of a response to simultaneous illumination of both regions ..."

(4) Response properties can be predicted from receptive field maps:

> "From the arrangement of excitatory and inhibitory regions it was usually possible to predict in a qualitative way the responses to any shape of stimulus, stationary or moving."

Complex cells were defined by exclusion as cells that failed to display the stated characteristics of simple cells. Hubel and Wiesel (1968) found that the cell classification originally defined in cats could be used equally well to