

# Role of inhibition in the specification of orientation selectivity of cells in the cat striate cortex

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## Abstract

Mechanisms supporting orientation selectivity of cat striate cortical cells were studied by stimulation with two superimposed sine-wave gratings of different orientations. One grating (base) generated a discharge of known amplitude which could be modified by the second grating (mask). Masks presented at nonoptimal orientations usually reduced the base-generated response, but the degree of reduction varied widely between cells. Cells with narrow orientation tuning tended to be more susceptible to mask presence than broadly tuned cells; similarly, simple cells generally showed more response reduction than did complex cells.

The base and mask stimuli were drifted at different temporal frequencies which, in simple cells, permitted the identification of individual response components from each stimulus. This revealed that the reduction of the base response by the mask usually did not vary regularly with mask orientation, although response facilitation from the mask was orientation selective. In some sharply tuned simple cells, response reduction had clear local maxima near the limits of the cell's orientation-tuning function.

Response reduction resulted from a nearly pure rightward shift of the response *versus* log contrast function. The lowest mask contrast yielding reduction was within 0.1-0.3 log unit of the lowest contrast effective for excitation.

The temporal-frequency bandpass of the response-reduction mechanism resembled that of most cortical cells. The spatial-frequency bandpass was much broader than is typical for single cortical cells, spanning essentially the entire visual range of the cat.

These findings are compatible with a model in which weak intrinsic orientation-selective excitation is enhanced in two stages: (1) control of threshold by nonorientation-selective inhibition that is continuously dependent on stimulus contrast; and (2) in the more narrowly tuned cells, orientation-selective inhibition that has local maxima serving to increase the slope of the orientation-tuning function.

**Keywords:** Visual cortex, Visual receptive fields, Inhibition, Orientation selectivity

## Introduction

The response amplitude of cells in the striate cortex typically depends on the orientation of moving, one-dimensional stimuli (see Orban, 1984 for review). Two general models have been proposed to account for cortical orientation selectivity, one relying principally on excitation, the other on a combination of excitation and inhibition. Hubel and Wiesel (1962) hypothesized that the receptive field of a simple cell is constructed from the convergence of excitatory afferent fibers from lateral geniculate nucleus (LGN) cells whose receptive fields formed a roughly linear array. Bars oriented in parallel with these arrays would provide maximum excitation, while orthogonally oriented bars would excite minimally as well as invoke inhibition from LGN receptive-field surrounds. This hypothesis is attrac-

tive in its simplicity, but is insufficient by itself. A linear array is unlikely to be adequate to support tuning as narrow as 5 deg, which is seen in some cells (Orban, 1984). Even though LGN cells have been reported to show some innate orientation preference (Vidyasagar & Urbas, 1982; Soodak et al., 1987), they nonetheless respond vigorously to stimuli presented at all orientations. Suppression of some kind is required to account for the failure of most cortical cells to respond when stimulated by bars with orientations orthogonal to the optimal axis (Hubel & Wiesel, 1962).

The alternate model proposes that excitation of cortical cells is influenced minimally by stimulus orientation, and that selectivity is shaped instead by intracortical inhibition. The inhibition is itself considered to be orientation selective and is tuned in opposition to a cell's excitatory tuning function so that the inhibition would be greatest for orthogonal stimuli (e.g. Bishop et al., 1973; Creutzfeldt et al., 1974b; Sillito, 1975; Nelson & Frost, 1978). This hypothesis was first suggested by the observation that an artificially elevated maintained discharge could be

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