

Motion selectivity and the contrast-response function of simple cells in the visual cortex

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Abstract

The responses of simple cells were recorded from the visual cortex of cats, as a function of the position and contrast of counterphase and drifting grating patterns, to assess whether direction selectivity can be accounted for on the basis of linear summation. The expected responses to a counterphase grating, given a strictly linear model, would be the sum of the responses to the two drifting components. The measured responses were not consistent with the linear prediction. For example, nearly all cells showed two positions where the responses approached zero (i.e. two “null phase positions”); this was true, even for the most direction selective cells. However, the measured responses were consistent with the hypothesis that direction selectivity is a consequence of the linear spatiotemporal receptive-field structure, coupled with the nonlinearities revealed by the contrast-response function: contrast gain control, halfwave rectification, and expansive exponent. When arranged in a particular sequence, each of these linear and nonlinear mechanisms performs a useful function in a general model of simple cells. The linear spatiotemporal receptive field initiates stimulus selectivity (for direction, orientation, spatial frequency, etc.). The expansive response exponent enhances selectivity. The contrast-set gain control maintains selectivity (over a wide range of contrasts, in spite of the limited dynamic response range and steep slope of the contrast-response function). Rectification conserves metabolic energy.

Keywords: Visual cortex, Receptive fields, Direction selectivity, Contrast gain control, Contrast response function, Motion

Introduction

The ability to sense motion is crucial for vision and visually guided behavior. Neurons in the visual cortex of monkeys and cats play a fundamental role in motion sensitivity and most are, to some extent, selective for the direction of motion (Hubel & Wiesel, 1962; 1968). The investigations of Barlow and Levick (1965) in the rabbit retina led them to propose that the basic mechanism of direction selectivity could be the result of “summation” over “simple excitatory and inhibitory connections” (pp. 498–500). However, other studies have approached the problem under the general assumption that direction selectivity is inherently nonlinear: for example, that it might involve a multiplicative or divisive interaction between inputs (for general reviews of this topic, see Nakayama, 1985; Hildreth & Koch, 1987).

Direction selectivity can be produced through strictly linear addition and subtraction of inputs (see for example the initial linear stages of the quadrature models developed by Watson & Ahumada, 1985; Adelson & Bergen, 1985). We have tested the

usefulness and validity of a linear model (the linear quadrature model) for describing the properties of motion-sensitive neurons recorded from the visual cortex of monkeys and cats (Hamilton et al., 1989). The spatiotemporal transfer function of simple cells was measured using sine-wave grating patterns of variable spatial and temporal frequency, drifting first in one direction of motion and then in the opposite direction. The results of these experiments, using drifting gratings, showed that both the amplitude and the phase satisfied several strong constraints implied by the linear quadrature model. Quantitative measurements of the spatiotemporal receptive fields of simple cells provide further experimental support for the linear mechanism (McLean & Palmer, 1989).

On the other hand, the responses of direction-selective simple cells to stationary flickering grating patterns do not appear to be entirely consistent with a linear mechanism. Reid et al. (1987) developed a model of motion sensitivity based upon linear summation of lateral geniculate nucleus (LGN) inputs. The model was used to predict direction selectivity from the responses to stationary flickering gratings. For the 19 cells tested, they concluded that “about half of the direction selectivity is due to mechanisms that sum in a linear fashion (p. 8742).” Hamilton (1987) developed and tested similar predictions based upon a linear model of direction selectivity. From a sample of 27 cells, he showed examples of some cells which did agree with

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the predictions and some which did not and then concluded that both linear and nonlinear mechanisms contribute to direction selectivity.

In many respects, simple cells are quite linear (for recent reviews, see Shapley & Lennie, 1985; De Valois & De Valois, 1988; Skottun et al., 1991). However, the contrast-response functions of simple cells reveal nonlinear behavior. Specifically, as the contrast increases, the response generally increases rapidly with a power-function exponent greater than 1.0 (the average for cat simple cells being approximately 2.5), and then saturates; furthermore, when measured at different spatial frequencies, the contrast-response functions shift vertically (on log-log coordinates) indicating a "contrast-set gain mechanism" (Albrecht & Hamilton, 1982). Although these nonlinear behaviors may not be inherent to the mechanism responsible for establishing direction selectivity, they may well influence the final output of a direction-selective mechanism, even if the direction-selective mechanism is based solely upon the simple principle of linear summation. Thus, it would seem reasonable to incorporate these contrast-response nonlinearities into any attempt to understand the responses of simple cells.

In the present study, we measured the responses of simple cells to stationary gratings and drifting gratings to quantitatively evaluate the linear and nonlinear components of direction selectivity. We also performed independent measurements of each cell's contrast-response function. We developed and tested the predictions of the linear model and found, in agreement with Reid et al. (1987) and Hamilton (1987), that linear summation alone cannot account for the responses to stationary flickering gratings. However, if the nonlinearities revealed in the contrast-response function are combined with a linear spatiotemporal receptive field, then the predicted responses are consistent with the measured responses, for both drifting and counterphase stimuli.

Methods

The procedures for electrophysiological recording, stimulus display, and measurement of neural responses using linear systems analysis have been described in detail elsewhere (Albrecht & Hamilton, 1982; Albrecht et al., 1984; Hamilton et al., 1989). Briefly, several days prior to an actual experiment, under deep barbiturate anesthesia, a preformed rigid plastic pedestal containing a recording chamber was attached to the animal's skull. On the day of the recording, the animal was initially anesthetized with 20 mg/kg of the short-acting barbiturate thiamylal sodium and then maintained throughout the experiment on 75% NO₂/25% O₂ along with 1 mg/kg/h of thiamylal sodium. The head was held rigid in stereotaxic coordinates (without ear and eye bars) using the plastic pedestal. The eyes were immobilized by continuous infusion of gallamine triethiodide (10 mg/kg/h) and the animal was artificially respired through an endotracheal throat tube. Single neurons were recorded using glass-coated tungsten or platinum-iridium microelectrodes.

The stimuli in the present set of experiments were spatial sine-wave grating patterns (presented on a Conrac studio monitor at a frame rate of 100 Hz), either drifting at a fixed temporal frequency or flickering in a stationary position at a fixed temporal frequency. The different stimulus conditions were randomly interleaved. One presentation consisted of a block of ten contiguous temporal cycles. Each block was separated by a pe-

riod of time equal to the block length; during these separations, the animal viewed mean luminance with no contrast. A minimum of four blocks were obtained, which resulted in 40 repeated presentations of each stimulus condition. Action potentials were collected into 1-ms time bins and the resulting average peristimulus-time histograms were Fourier analyzed. The response measure was the amplitude and phase of the first harmonic component.

Once a single neuron was isolated and classified as a simple cell, its optimal orientation was determined, and held constant throughout the experiment. The spatial-frequency tuning, temporal-frequency tuning, and contrast-response function were quantitatively measured. Direction selectivity was determined by measuring the responses to the optimal grating drifting in the preferred and nonpreferred directions. The direction-selectivity index was the ratio of the measured responses subtracted from one (1 - nonpreferred/preferred). Thus, for a cell which only responded to movement in one direction, the index would be 1.0; for a cell which responded equivalently to movement in both directions, the index would be 0.0. The responses as a function of contrast, $R(C)$, were fitted using least-squares criteria to the following function: $R(C) = R_{\max} \cdot C^n / (C^n + C_{50}^n)$, where R_{\max} is the maximum response rate, C_{50} the semi-saturation contrast (the contrast required to produce 50% of the cell's maximum response), and n the power-function exponent. This saturating power function provides a good description of the contrast-response function of neurons in the visual cortex.

Following these preliminary experiments, the responses to stationary counterphase flickering gratings were then measured at 12 different spatial/phase positions in 30-deg steps. The contrast, $(L_{\max} - L_{\min}) / (L_{\max} + L_{\min})$, of the counterphase pattern was modulated sinusoidally. The spatial and temporal frequencies of the gratings were held constant at the optimal values. The full set of measurements were performed at a contrast level near the midpoint of the dynamic response range for the specific cell and then, as time allowed, at other contrasts around the midpoint. For ease of viewing, the graphs (of the responses as a function of the position of the counterphase flickering grating) were normalized in the following three ways: (1) the amplitude and phase responses were shifted horizontally so that the amplitude functions peaked at 90 and 270 deg, (2) the phase functions were shifted vertically so that they passed through the origin, and (3) the amplitudes were expressed as a percentage of the maximum response.

Results

The initial goal of this study was to assess whether the motion-sensitive properties of simple cells could be accounted for on the basis of a linear mechanism for direction selectivity. The basic strategy was to measure the direction selectivity of each cell using drifting gratings and then assess the degree to which the linear model could predict the responses to stationary counterphase flickering gratings.

Counterphase gratings are composed of two gratings of equal contrast moving in opposite directions. Given a linear mechanism for direction selectivity, and the principle of additivity in linear systems, the response to a counterphase grating would be a weighted sum of the responses to the individual components present in the stimulus. Although the weight of each component in the stimulus is equal, the weight of each

component in the response will depend upon the degree of selectivity. For example, given a linear cell that is completely direction selective (i.e. no response in the nonpreferred direction), the weight given to the component drifting in the nonpreferred direction would be zero, and the weight given to the component drifting in the preferred direction would be one. As the direction selectivity changes from cell to cell, the weight given to each component in the counterphase stimulus would vary accordingly.

Linear summation

This section describes the expected responses to counterphase gratings presented in different spatial positions, given a strictly linear model, where the direction selectivity is simply due to linear summation of inputs (see eqns. (A1–A5) in the Appendix). These expectations are then compared to the measured responses of 41 simple cells. (Note that adding halfwave rectification does not affect the predictions described in this section.)

The solid lines in Fig. 1A plot the predicted amplitude and phase of response for a linear nondirection selective cell, as a

function of the position of a counterphase flickering grating. From the work of Enroth-Cugell and Robson (1966; see also, Hochstein & Shapley, 1976; Movshon et al., 1978; De Valois et al., 1982), we know that the amplitude of the response should be a sinusoidal function of spatial position with two "null phase positions," where the response is zero. (We have adopted the convention of plotting all amplitudes as positive, with the phases ranging from 0–360 deg.) The temporal phase of the response should consist of two values separated by 180 deg: 90 over half of the range of spatial position (0–180 deg) and 270 over the other half (180–360 deg). The filled circles in Fig. 1A plot the measured amplitude and phase responses for a representative nondirection-selective simple cell with a direction selectivity index of 0.08. As can be seen, the expectations from a linear model provide an adequate fit for this cell. The measured amplitude varies as a function of position in a fashion which is similar to the absolute value of a sine function, with two positions where the response is near zero; the phase responses cluster around the two expected values, 90 and 270.

The solid lines in Fig. 1B plot the predicted amplitude and phase for a totally direction-selective cell. Given strict linearity,

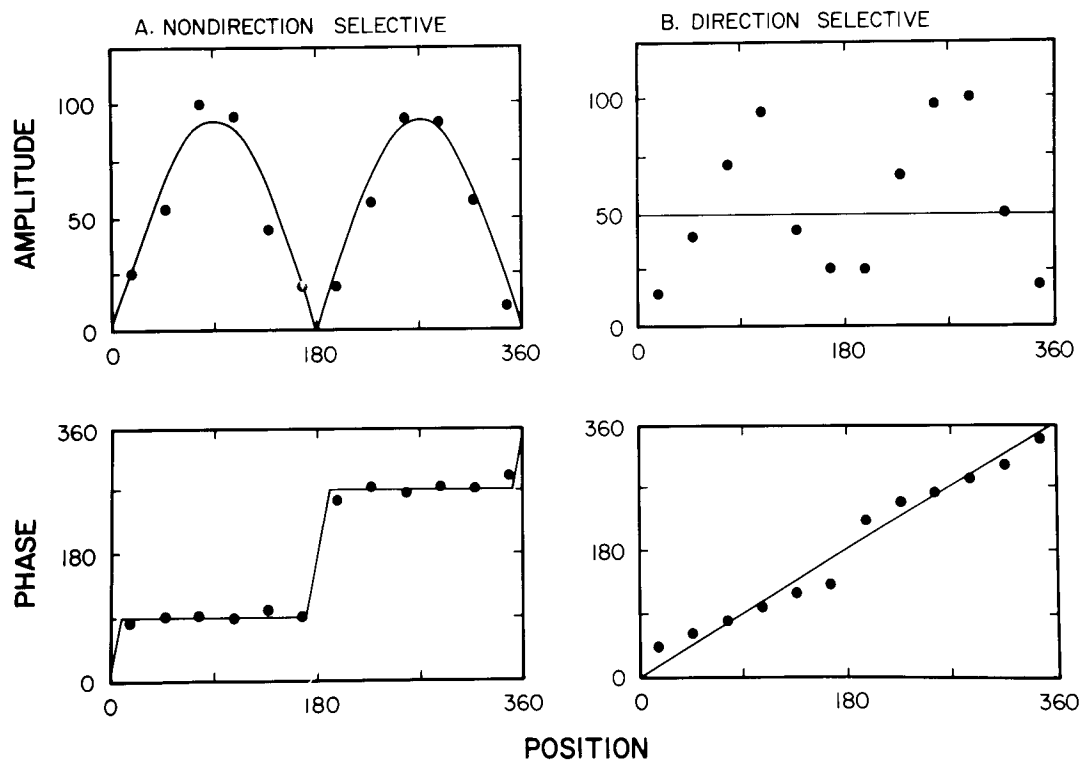


Fig. 1. Measured responses of a nondirection selective cell (A) and a highly direction-selective cell (B) as a function of the position of a counterphase flickering stationary grating pattern. The amplitude of the response is plotted in the upper panels and the phase in the lower panels (note that 0 and 360 are the same point). The solid lines are the predictions from the model which assumes strict linearity, including the mechanisms responsible for direction selectivity. The strictly linear model provided a reasonably good fit to the measured responses of the nondirection-selective cell (direction index 0.08). The predicted and measured amplitudes varied much like the absolute value of a sine function. The predicted phases are 90 deg for half the positions (0–180) and 270 for the other half (180–360); the measured phases clustered around these two values with a slope near zero. On the other hand, the strictly linear model provided a very poor fit to the measured responses of the direction-selective cell (direction index 0.95). The predicted amplitudes are constant, whereas the measured amplitudes varied in a fashion similar to the absolute value of a sine function. The predicted phases changed continuously with a slope of 1.0, whereas the measured phases clustered into two groups separated by 180 deg, and the slope within each group was approximately 0.6. (Stimulating contrast/peak response for (A) is 0.1/55.6, and for (B) is 0.08/47.5.)