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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% NO_2/25% O_2 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 triethiodiode (10 mg/kg/h) and the animal was artificially respirated 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 period 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,

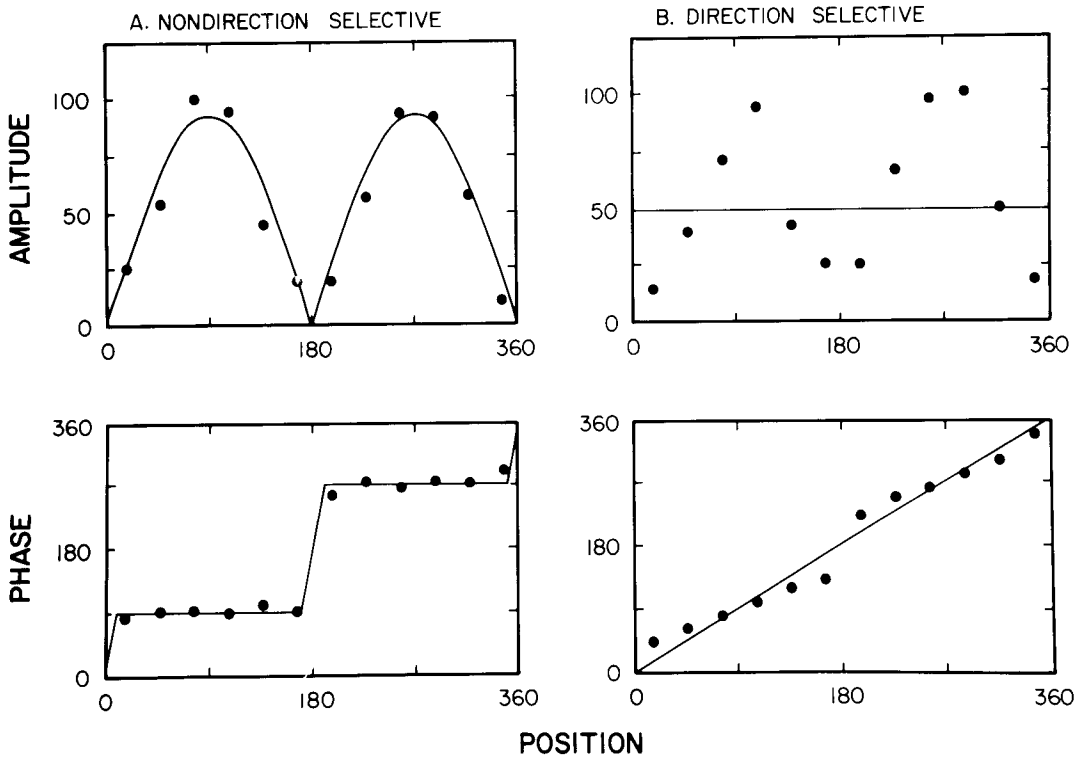

Fig. 1. Measured responses of a nondirection selective cell (A) and a highly direction-selective cell (B) as a function of the position of a counterephase flickering stationary grating pattern. The amplitude of the response is plotted in the upper panels and the phase in the lower panels (note that 0 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.)

the amplitude would not change as a function of position, and the phase would change continuously, with a slope of one. As noted above, these linear predictions are a simple consequence of the fact that while the stimulus is actually composed of two gratings drifting in opposite directions, a linear direction-selective cell will only be affected by the component moving in the cell's preferred direction. If the cell is only responding to one of the drifting components, changing the position of the counterphase grating would be equivalent to changing the starting position of that component. Hence, changing position would not affect the response amplitude (only the response phase).

The filled circles in Fig. 1B plot the measured amplitude and phase responses for a representative direction-selective simple cell with a direction index of 0.95. As can be seen, the expectations from a strictly linear model do not provide an adequate fit for this cell. Like the nondirection-selective cell, the measured amplitude varies as a function of position in a fashion which approximates the absolute value of a sine function, and there are two locations where the response is near zero. The phase responses do change continuously, as expected from the linear model; however, they cluster into two distinct groups separated by 180 deg, and the slope within each group is closer to 0.5 than 1.0.

In order to quantify these response patterns for the total population of cells, we indexed the size of the change in amplitude as a function of position by taking the maximum and minimum values of the response and computing the following ratio: (max − min)/(max + min). The value of this amplitude index was then compared to the direction-selectivity index. In general, given a linear model, the amplitude index should be equal to one minus the direction-selectivity index.

Consider the expected changes in the amplitude index for cells with different degrees of direction selectivity. Given a completely nondirection-selective linear cell, there will be two positions of the grating where the inputs sum to a maximum value and two positions where the inputs sum to a minimum value (the "null phase positions"). Thus, for a cell with a direction index near 0.0, the amplitude changes would be large: the amplitude index would approach 1.0. Given a totally direction-selective linear cell, the response amplitude will be constant independent of position. Thus, for a cell with a direction index near 1.0, the amplitude changes would be small: the amplitude index would approach 0.0. Given a direction-selective linear cell between these two extremes, the amplitude will change with position; however, the differences between the maximum and minimum values will decrease as the direction selectivity increases. (Note that, strictly speaking, the term "*null* phase position" would be inappropriate for a linear cell with any degree of direction selectivity because the inputs do not perfectly cancel at any position of the counterphase grating; "*minimum* phase position" would be perhaps a more accurate term.)

Figure 2A shows the distribution of the amplitude index for the total sample of cells. The amplitude for most cells shows sizable changes as a function of the position of the counterphase grating (only four cells had an index less than 0.5). The mean of the distribution was 0.79. Figure 2B shows the scatter plot for the amplitude index *vs.* the direction index for all cells. The solid line, with a slope of −1.0, is the prediction of the linear model. As can be seen, nearly all of the cells in this sample showed larger changes in amplitude than was expected from a linear filter. The slope of the regression line for the data points was −0.21; the coefficient of correlation was −0.32. Even the most direction-selective cells showed sizable changes in amplitude as a function of position. For example, the direction-selective cell illustrated in Fig. 1B had an amplitude index of 0.76, yet its direction-selectivity index was 0.95.

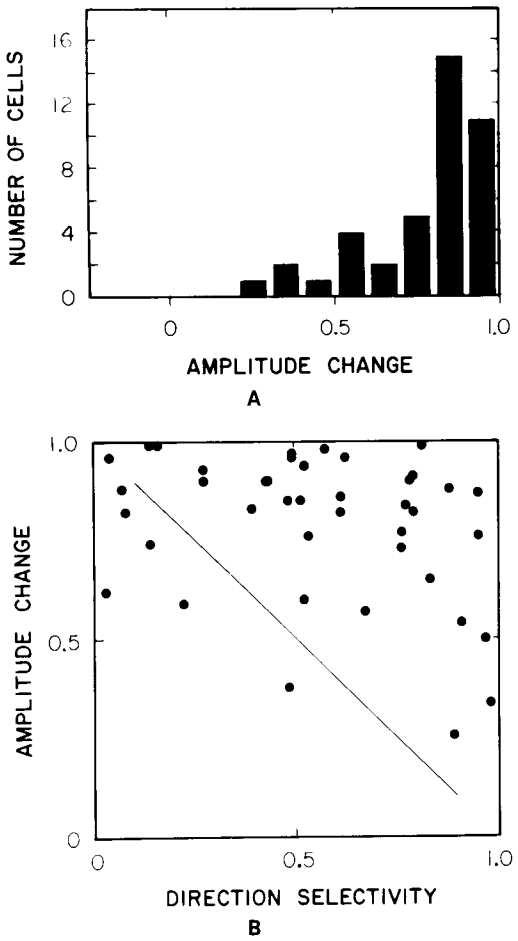

Fig. 2. A: Distribution of the amplitude change index for the entire population of cells. To provide a quantitative indication of the change in amplitude as a function of the position of the counterphase grating, the following ratio was computed from the maximum and minimum responses: (max-min)/(max+min). For linear nondirection-selective cells, the amplitude index should be close to one; for linear direction-selective cells, the amplitude index should be close to zero. As can be seen, all cells showed large changes in amplitude as a function of grating position. The mean amplitude index was 0.79. B: Scatter plot of the amplitude index *vs.* the direction-selectivity index. In general, given a strictly linear model for simple cells, the amplitude index should be equal to one minus the direction-selectivity index. This expected relationship is indicated on the scatter plot by the straight line, with a slope of −1.0. As can be seen, the changes in amplitude were much larger than expected from the strictly linear model and the degree of direction selectivity was only weakly correlated with the amplitude index. The slope of the regression line for the data points was −0.21; the coefficient of correlation was −0.32.

The slope of the phase function was measured for the total population of cells and then compared to the direction-selectivity index. (The slope was determined by fitting separate straight lines to the data points which fell within the x axis ranges of 20–160 deg and 200–340 deg.) As noted above, for a linear nondirection-selective cell, the phases should cluster into two distinct groups separated by 180 deg and the slope within each group should be

0.0. For a totally direction-selective cell, the phases should change continuously from 0–360 with a slope of 1.0. In general, given a strictly linear filter, the slope of the phase function would be equal to the direction-selectivity index.

Figure 3A shows the distribution of the slope for the total sample of cells. For 70% of the population, the slope was less than 0.5; only two cells had a slope greater than 0.7. The average slope for the distribution was 0.35. Figure 3B shows the scatter plot for the slope *vs.* the direction selectivity. As can be seen, the majority of cells fall below the value expected from a strictly linear mechanism (indicated by the solid line with a slope of 1.0). The slope of the regression line for the data points was 0.52; the coefficient of correlation was 0.70. Even the most direction-selective cells did not have a slope of 1.0; for example, the slope of the direction-selective cell shown in Fig. 2B was 0.61.

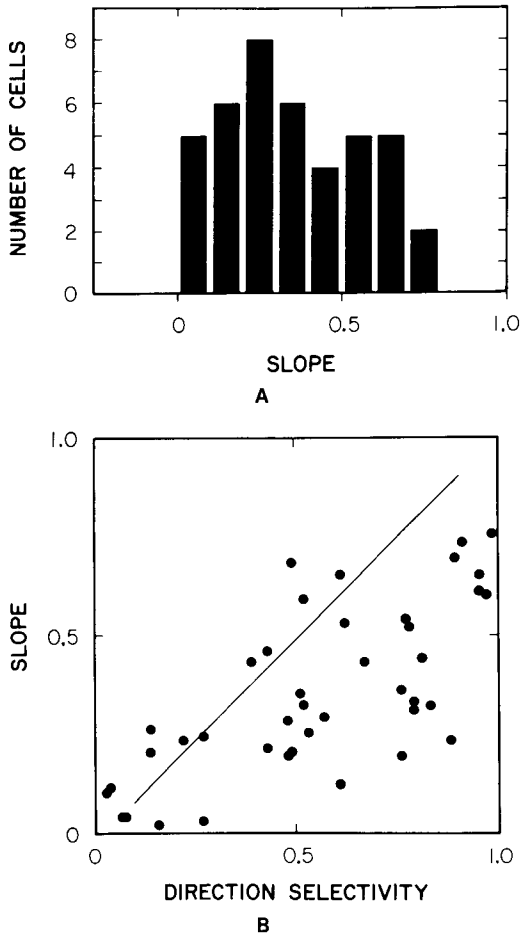

Fig. 3. A: Distribution of the phase index. To provide a quantitative index of the change in the phase responses, as a function of the position of the counterphase gratings, the average slope was computed. For linear nondirection-selective cells, the slope should be close to zero; for linear direction-selective cells, the slope should be close to one. As can be seen, for most cells the slope was well below 0.5; the largest value was 0.75. The mean slope was 0.35. B: Scatter plot of the slope of the phase responses *vs.* the direction-selectivity index. In general, given a strictly linear model of simple cells, the slope should be equal to the direction-selectivity index. This expected relationship is indicated in the scatter plot by the straight line with a slope of 1.0. As can be seen, the slopes were less than expected from the strictly linear model and the degree of direction selectivity was moderately correlated with the slope. The slope of the regression line for the data points was 0.52; the coefficient of correlation was 0.70.

Linear summation, rectification, and response exponent

The results presented above clearly indicate that simple cells cannot be described as strictly linear filters. One possible explanation is that the direction-selective mechanism itself is nonlinear. Another explanation, one that we consider in the Discussion, is a phase-specific direction-selective inhibition: a nonlinear silent inhibition from the nonpreferred component. However, these types of explanations require postulating relatively complicated and undocumented (although see Dean et al., 1980) nonlinear processes. A more parsimonious approach is to first consider other well-known nonlinearities.

One obvious nonlinearity of simple cells is seen in the responses to sine-wave stimuli: because simple cells have little or no maintained discharge, and they cannot produce negative responses, the response waveform is "halfwave rectified." Any realistic model of simple cells should include this nonlinearity and thus in the sections which follow, the models incorporate halfwave rectification. However, halfwave rectification following linear summation of inputs cannot account for the results presented in the section above because the responses to both drifting and counterphase gratings are merely diminished by a fixed amount (the amplitude of the fundamental harmonic is diminished by 50%).

Another prominent nonlinear property of simple cells is the expansive power-function growth in response to contrast, before the onset of compression and saturation (Albrecht & Hamilton, 1982; Sclar et al., 1990). The power-function exponent varies from cell to cell; it is generally greater than 1.0; the average value is 2.5. If the exponent reflects an expansive nonlinearity occurring after linear summation, it could potentially explain the discrepancy between the responses to drifting *vs.* counterphase gratings. In this section, we develop and test the hypothesis that simple cell direction selectivity is based upon linear summation of inputs and that this linear summation is then followed by halfwave rectification and an expansive nonlinearity—the *exponent model* (cf. Heeger, in press, for a similar proposal). The *exponent model* is presented formally in the Appendix (see eqns. (A6–A11)).

Consider the potential effects of an expansive nonlinearity on the responses to counterphase flickering gratings presented in different positions. Recall that given a strictly linear filter, the magnitude of variation in the counterphase amplitudes (as a function of position) is inversely related to the degree of direction selectivity (the amplitude index is 1.0 minus the direction index). If the output of a linear direction-selective mechanism passes through an expansive nonlinearity, the variation in the counterphase amplitudes would be enhanced—the stronger responses at the peaks (90 and 270 deg) would be disproportionately increased relative to the weaker responses at the troughs (0 and 180 deg). Similarly, the direction selectivity of the cell would be enhanced; the stronger responses in the preferred direction would be disproportionately increased relative to the weaker responses in the nonpreferred direction. The phases would be unaffected by the expansive nonlinearity and thus the slopes of the phase functions would directly reflect the linear direction-selective mechanism.

To illustrate the basic effect of an expansive nonlinearity on

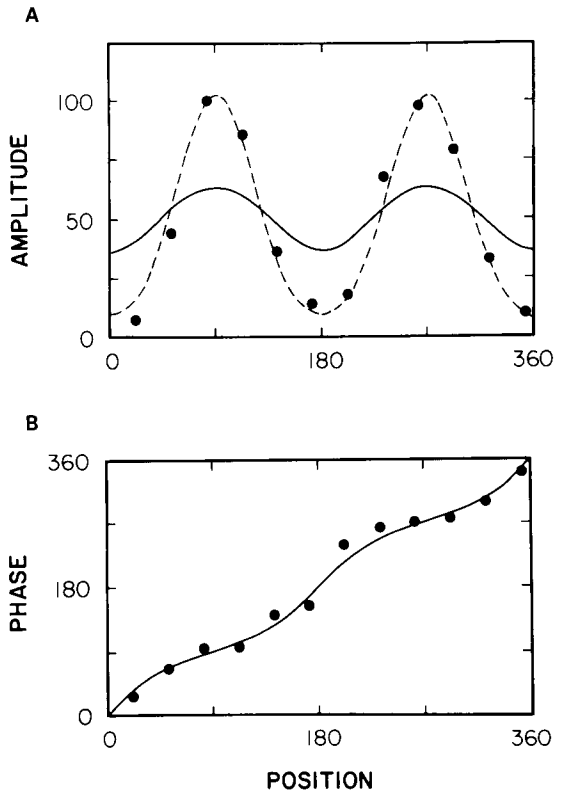

Fig. 4. The effect of applying an expansive response exponent after linear summation is illustrated for a highly direction-selective cell (direction index 0.95). The solid line in (A) shows the amplitudes expected from a strictly linear direction-selective cell with a direction index of 0.72. A cell with this degree of direction selectivity shows some variation in amplitude (amplitude index 0.28) and the phases cluster into two groups with a slope equal to the direction index. The dashed lines in (A) show the effect of applying a power-function exponent of 4.2 (taken from the contrast-response function for this cell) to the expected responses. As can be seen, the exponent considerably enhances the variation in the amplitude and increases the peakedness. Furthermore, the exponent enhances the expected direction selectivity from 0.72–0.99. The solid line in (B) shows the expected phases before and after applying the exponent: the exponent has no effect on the phases. (Stimulating contrast/peak response = 0.1/65.9.)

the responses to counterphase flickering stimuli, Fig. 4 plots the measured amplitudes and phases of a direction-selective cell (direction index of 0.95, amplitude index of 0.87, and slope index of 0.65). The solid curve in Fig. 4A shows the predicted amplitudes of a strictly linear model with a direction index of 0.72; the dashed curve shows what happens to the predicted amplitudes if they are passed through an exponentiation stage (the exponent for this particular cell, taken from its contrast-response function, was 4.18). Note that the expansive nonlinearity results in a nonsinusoidal relationship between response amplitude and position (an exponentiated sinusoidal relationship); specifically, the exponent increases the difference between the maximum and minimum values, narrows the width of each half-cycle, and increases the peakedness. For this cell, the exponent enhanced the predicted variation in the amplitude from 0.28–0.83, which more closely matches the measured variation of 0.87. The exponent also enhanced the predicted direction selectivity from 0.72–0.99, which more closely matches the measured direction selectivity of 0.95. Because the exponent has no effect on the phases, the solid line in Fig. 4B shows the predicted phases with and without the exponent; the predicted slope, 0.72, is similar to the measured slope, 0.65.

In the *exponent model*, the predictions for normalized counterphase responses are completely determined by two parameters: (1) the direction selectivity of the linear mechanism (which determines the weight given to each of the drifting components) and (2) the nonlinear exponent (which determines the degree of response expansion). Both of these parameters can be estimated from the responses to drifting gratings. Specifically, by measuring the exponent n of the contrast-response function and by measuring the ratio of the responses in the two directions, it is possible to make a parameter-free prediction of the normalized counterphase responses as a function of position for both amplitude and phase. (The direction selectivity of the linear mechanism is given by the nth root of the ratio of the responses in the preferred and nonpreferred directions; see eqns. (A9) and (A10) in the Appendix.)

Figure 5 replots the measured responses to counterphase gratings shown in Fig. 1; the nondirection-selective cell is shown in Fig. 5A and the direction-selective cell is shown in Fig. 5B. The expansive exponent (taken from the contrast response function) was 1.86 for the nondirection-selective cell and 3.22 for the direction-selective cell; the measured direction-selectivity indices were 0.08 and 0.95. The smooth curves through the data points represent the parameter-free predictions expected from these measured exponents and direction selectivities. As can be seen, the fit to both the amplitude and the phase data is quite good.

Figure 6 shows the results of this analysis for nine typical cells. For each cell, the exponent and the direction selectivity of the linear mechanism were predetermined as described above and thus there were no free parameters. The measured direction selectivity d, along with the exponent n and the direction selectivity of the linear mechanism D, are shown in the lower right corner of each plot. These nine cells were chosen to illustrate a range of direction selectivities and a range of contrast-response exponents. From left to right, the measured direction selectivity decreases; this is reflected as a reduction in the slope of the phase functions. From top to bottom the exponent decreases; this is reflected as a reduction in the amplitude variation and, as expected, the effect of the exponent is more evident for the cells with a greater degree of direction selectivity. The fit to all 41 cells was quite good: for over half of the cells the predictions accounted for more than 90% of the variance (the average value was 83%).

An alternate approach to evaluating this model (similar to the approach taken by Reid et al., 1987) is to compare the direction selectivity measured from the responses to drifting gratings with the direction selectivity expected from the responses to stationary gratings. This analysis was also performed on the entire sample of cells. Specifically, for each cell, the amplitude and phase responses (as a function of the position of the counterphase flickering grating) were fitted using the linear-summation model, followed by rectification and the exponent of the contrast-response function. The exponent for each cell was fixed (from the independent set of measurements of the contrast-response function); however, the direction selectivity of the linear mechanism was free to vary. The optimized value of the linear direction selectivity, along with the measured exponent of the contrast-response function, were then used to predict the

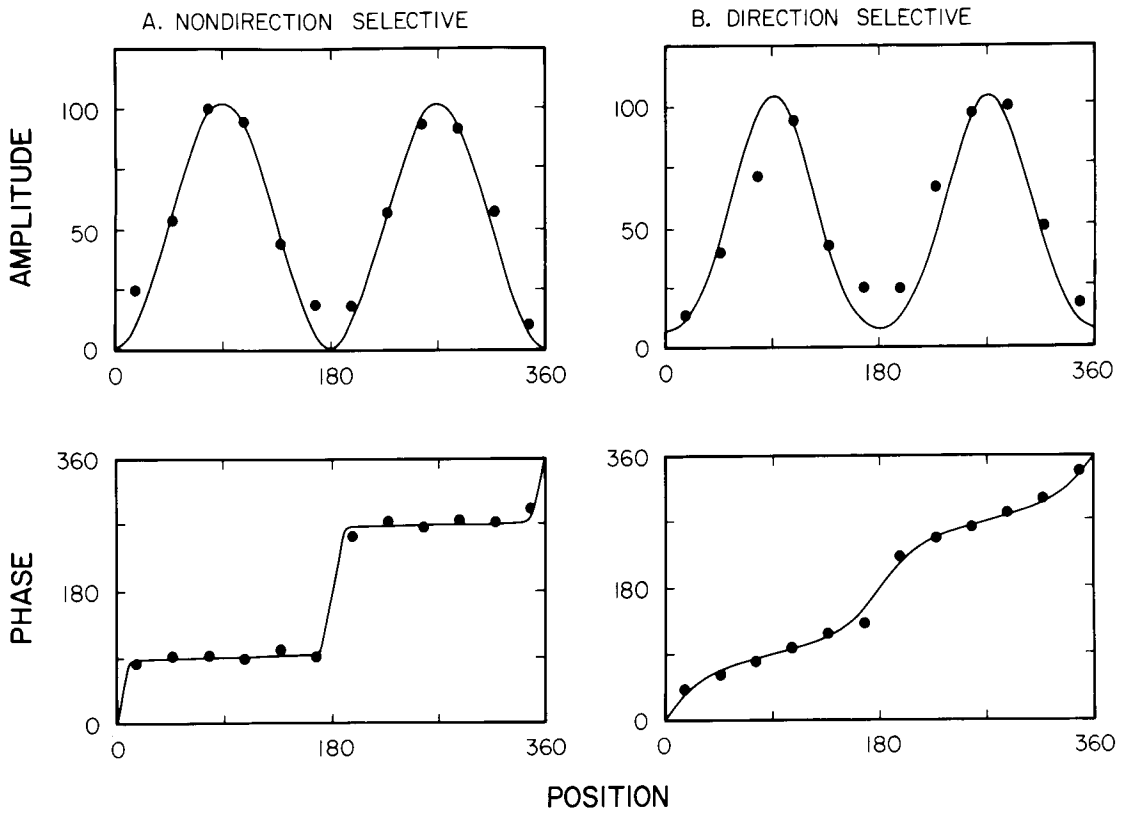

Fig. 5. Measured responses of a nondirection-selective cell (A) and a direction-selective cell (B) as a function of the position of a counterphase grating. These are the same data points shown in Fig. 1; however, the smooth curves are the expected responses from a model which assumes a linear-summation mechanism for direction selectivity followed by an expansive nonlinear exponent (the *exponent model*). The exponent for each cell was determined from an independent measurement of the contrast-response function. For the cell shown in (A) the exponent was 1.86 and for the cell shown in (B) the exponent was 3.22. As can be seen, the responses expected from linear summation followed by the nonlinear exponent provide a good fit to the measured counterphase responses of both the nondirection-selective cell and the direction-selective cell.

measured direction selectivity of each cell (see eqn. (A10) in the Appendix).

The scatter plot shown in Fig. 7 illustrates the results of this analysis for all 41 cells; the direction selectivity predicted from the responses to stationary flickering gratings is plotted as a function of the direction selectivity measured from the responses to drifting gratings. As can be seen, the predicted and measured values were, on average, quite similar. The straight line, with a slope of 1.0, illustrates perfect correspondence. The slope of the regression line for the data points was 0.86; the coefficient of correlation was 0.89.

Contrast gain, linear summation, rectification, and response exponent

The model described above (linear summation followed by an expansive exponent) provides a good description of the responses to counterphase gratings presented at a fixed contrast (within the dynamic range of a cell). However, it does not take into account response compression and saturation. A more accurate model will have to include saturating nonlinearities.

The simplest hypothesis is that the expansive behavior at lower contrasts and the compressive behavior at higher contrasts are due to the same response nonlinearity—the *response nonlinearity model*. However, this hypothesis seems unlikely, based upon the results of previous studies. Albrecht and Hamilton (1982) measured the contrast-response function of striate cells at different spatial frequencies. As they argue, if the saturation were due to a final response nonlinearity, then saturation would occur at higher contrasts for nonoptimal spatial frequencies, the magnitude of the saturated response would be the same for all frequencies, and the spatial frequency tuning would change with contrast. Instead, they found that saturation occurred at approximately the same contrast for all spatial frequencies, the magnitude of the saturated response was different for each frequency, and the spatial-frequency tuning remained relatively invariant. They point out that this behavior would be produced if a saturating "contrast-set gain" mechanism preceded response generation. This earlier work, in conjunction with the results presented above, lead us to propose that there are two separate nonlinearities, a contrast-gain control nonlinearity that is responsible for saturation and a final response-exponent nonlinearity, that is responsible for expansion—the *contrast-gain/exponent model*.

These two alternative hypotheses (the *response nonlinearity model* and the *contrast-gain/exponent model*) can be discriminated by measuring contrast-response functions for counterphase gratings presented at different spatial positions. On the one hand, if the saturation and expansion are part of the same final response nonlinearity, then the contrast-response functions

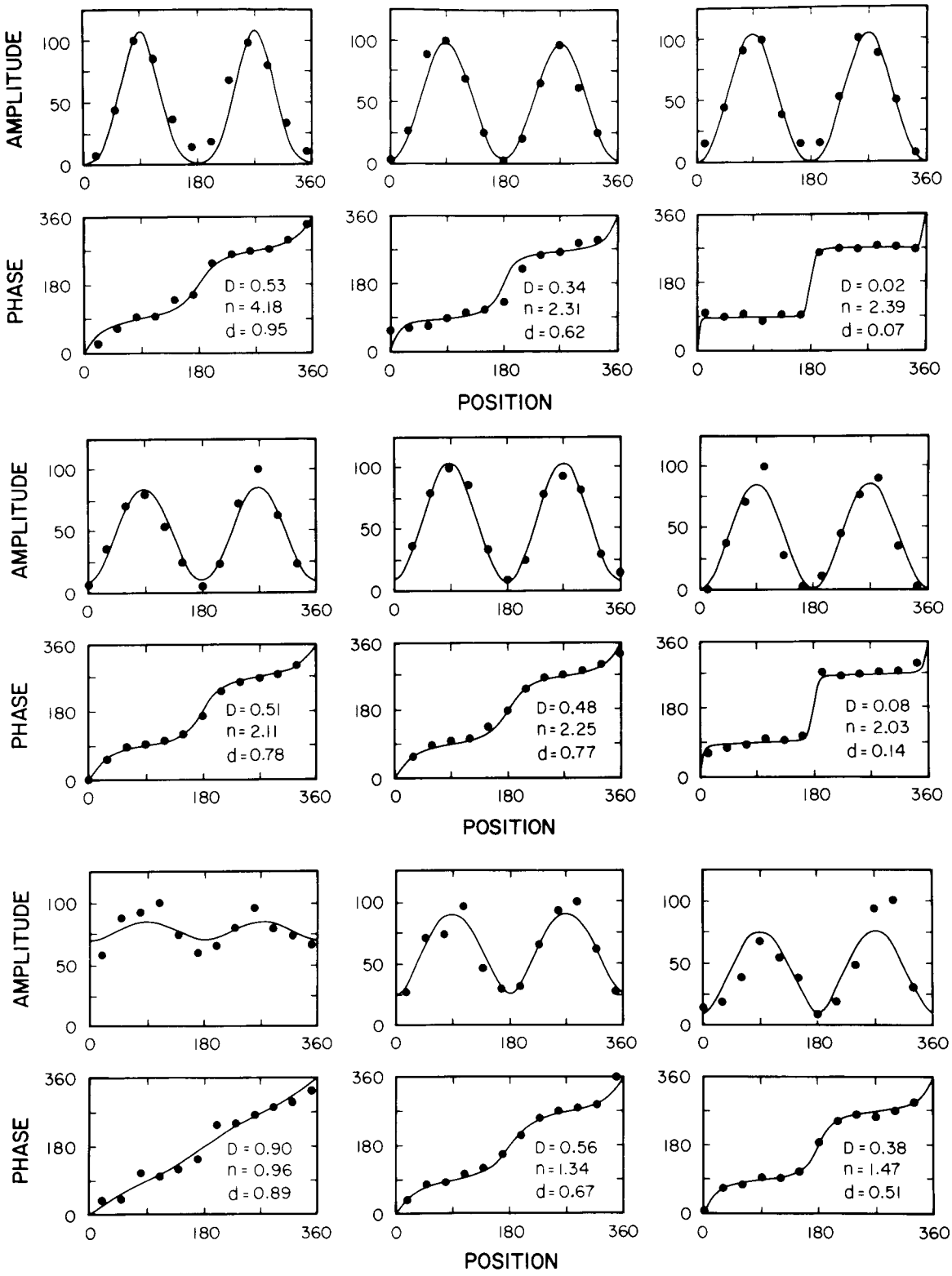

Fig. 6. Measured responses of nine different cells as a function of the position of a counterphase grating pattern. The smooth curves through the data points are the predictions from the model which assumes a linear mechanism for direction selectivity followed by a nonlinear response exponent (the *exponent model*). The exponent for each cell was determined from an independent measurement of the contrast-response function. As can be seen, the linear-summation model for direction selectivity, followed by the contrast-response exponent, provides a good fit to the measured responses for these nine cells. The nine cells were organized in this figure such that from left to right direction selectivity decreases and from top to bottom the exponent decreases. As would be expected, the slopes of the phases tend to decrease from left to right, and the amplitude change tends to decrease from top to bottom. In the lower right corner of each graph, the following three values are listed: n = measured exponent of the contrast response function, d = measured direction selectivity, and D = the direction selectivity of the linear mechanism. The direction selectivity of the linear mechanism (D) was determined by removing the effect of the exponent on the measured direction selectivity (d). (Stimulating contrast/peak firing rate for each cell: from left to right, top row, 0.1/65.9, 0.15/77.5, 0.05/57.0, middle row, 0.15/49.5, 0.04/47.5, 0.13/74.8, and bottom row, 0.2/24.5, 0.12/30.4, 0.06/27.3.)