

Half-squaring in responses of cat striate cells

DAVID J. HEEGER

NASA-Ames Research Center, Moffett Field and Department of Psychology, Stanford University, Stanford

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Abstract

Simple cells in striate cortex have been depicted as rectified linear operators, and complex cells have been depicted as energy mechanisms (constructed from the squared sums of linear operator outputs). This paper discusses two essential hypotheses of the linear/energy model: (1) that a cell's selectivity is due to an underlying (spatiotemporal and binocular) *linear* stage; and (2) that a cell's firing rate depends on the *squared* output of the underlying linear stage. This paper reviews physiological measurements of cat striate cell responses, and concludes that both of these hypotheses are supported by the data.

Keywords: Striate (primary visual) cortex, Simple cells, Complex cells, Spatiotemporal linear operators, Energy mechanisms, Squaring, Direction selectivity

Introduction

For over thirty years, physiologists have been measuring response properties of simple and complex cells in primary (striate) visual cortex. A longstanding view of simple cells is that their responses can be characterized as a weighted sum (over local space and recently past time) of the intensity values in a visual stimulus (Hubel & Wiesel, 1962; Campbell et al., 1968, 1969). An ideal mathematical operator that computes a weighted sum of stimulus intensities is called a linear operator. A popular model of simple cells is that they act like halfwave-rectified linear operators, at least over a limited range of stimulus contrasts. In addition, it is widely believed that complex cells are constructed from linear subunits, and that the subunit outputs are rectified before being combined into the complex cell response. A popular model for complex cells is that they act like energy mechanisms that compute the sum of the squared outputs of a set of linear subunits (Pollen & Ronner, 1983; Adelson & Bergen, 1985).

The linear/energy model of striate physiology is attractive because the response of a linear/energy mechanism can be completely characterized with a relatively small number of measurements. Unfortunately, the linear/energy model falls short of a complete account of striate physiology.

One fault with the linear/energy model is the fact that cell responses saturate at high contrasts. The responses of ideal linear operators and energy mechanisms, on the other hand, increase with stimulus contrast over the entire contrast range. A second fault with the linear/energy model comes from experi-

ments that reveal nonspecific suppression in cortical cells. To explain nonspecific suppression and response saturation, Robson (1988) and Bonds (1989) have suggested that striate cells mutually inhibit one another, effectively normalizing their responses with respect to stimulus contrast.

A companion paper (Heeger, 1992a) attempts to reconcile the linear/energy model with physiological data by including a divisive normalization nonlinearity. The new model, with divisive normalization, explains a significantly larger body of physiological data. That paper (Heeger, 1992a) reviews physiological data on contrast-response curves, contrast adaptation, and nonspecific suppression. None of these results are consistent with the linear/energy model, but nearly all of them are consistent with the new model.

This paper reviews a variety of other experimental results, and elaborates two essential aspects of the new model. The first issue concerns the origin of selectivity of simple and complex cells. According to the model, a cell's selectivity is due to an underlying (spatiotemporal and binocular) linear stage. In reviewing the literature, surprisingly few experiments are found that actually test for the underlying linearity of simple cells. There are a number of qualitative tests, but very few direct quantitative tests of linearity. Most of the results are, however, consistent with the linear hypothesis (see Simple cell responses).

The second issue emphasized in this paper concerns the role of squaring in the model. Ideal energy mechanisms require a perfect squaring nonlinearity. In addition, given that the model complex cell outputs are squared, the model simple cell outputs must also be squared for the divisive normalization to work properly (see Heeger, 1992a). This paper reviews a variety of experimental results that provide evidence in support of the squaring hypothesis.

Some of the material in this paper has been reported previously (Heeger & Adelson, 1989; Heeger, 1990, 1991).

The model

A summary of the new model is diagrammed in Fig. 1. Linear operators of four different phases are applied to the stimulus. The outputs of these operators are then rectified and normalized to give the simple cell responses; i.e. simple cells are modeled as normalized, half-squared, linear operators. The complex cell responses are computed by averaging the simple cell responses; i.e. complex cells are modeled as normalized energy mechanisms.

This section reviews the basic building blocks of the model: linear operators, rectification, and energy mechanisms. Divisive normalization is explained in detail elsewhere (Heeger, 1992a).

Although divisive normalization is an important part of the model (see Heeger, 1992a), it is largely ignored in this paper. The emphasis in this paper is on squaring and on the underlying linearity of striate cells. The simulations and the discussion are kept simple by ignoring normalization as much as possible. On the other hand, normalization does have an important effect on some of the simulation results and it has been included in the simulations in those cases.

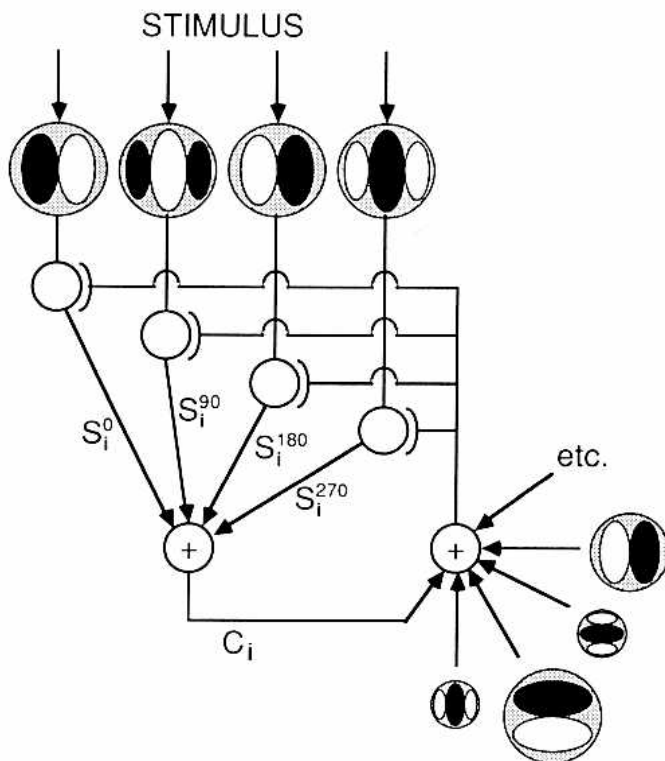


Fig. 1. Diagram of the various stages of the model. Linear weighting functions are depicted as circles, subdivided into excitatory (bright) and inhibitory (dark) subregions. The S_i^ϕ labels represent simple cell outputs, and the C_i label represents a complex cell output. The feedback signal is the combined energy at all orientations and nearby spatial frequencies, averaged over space and time. The feedback signal suppresses the simple cell responses by way of divisive suppression. See Heeger (1992a) for details.

Linear operators

The response of a linear operator is expressed as a weighted sum, over local space and recently past time, of the stimulus intensities. The response, $L(t)$, is the inner product in space and the convolution in time of a stimulus, $I(x, y, t)$, with the spatiotemporal weighting function of the operator, $f(x, y, t)$:

$$L(t) = \iiint_{-\infty}^{\infty} f(x, y, \tau) I(x, y, \tau - t) dx dy d\tau. \quad (1)$$

The triple integral in the above equation is simply a weighted sum of the stimulus intensities over space and time. The output response waveform, $L(t)$, is the model equivalent of a poststimulus time histogram (PSTH), a measure of a cell's average response per unit time.

The linear operators considered in this paper have weighting functions with positive and negative subregions. The positive and negative weights are balanced, so the operators give no output for a constant intensity stimulus. Rather, their responses are proportional to stimulus contrast, for stimuli that vary in intensity over space and/or time.

These linear operators could be built from a complementary arrangement of geniculate inputs, as proposed by Glezer et al. (1980, 1982), Palmer and Davis (1981), Tolhurst and Dean (1987), and others. An excitatory subregion of the receptive field would result from excitation by ON center geniculate cells and inhibition of OFF center cells. Likewise, an inhibitory subregion would result from inhibition by ON center geniculatcs and excitation by OFF center geniculatcs. Each simple cell subregion would receive complementary inputs both from ON center and OFF center geniculatcs. Assuming that the geniculate cells are themselves linear (Shapley et al., 1981; Troy, 1983; Derrington & Lennie, 1984), this complementary arrangement of inputs would yield a linear operator.

The spatiotemporal weighting function of a linear operator determines its selectivity (e.g. for orientation or direction of motion). Several researchers (Fahle & Poggio, 1981; Watson & Ahumada, 1983, 1985; Adelson & Bergen, 1985; Van Santen & Sperling, 1985) have pointed out that a linear operator is direction selective if its subregions are tilted along an oblique axes in space-time. Fig. 2B, for example, illustrates the weighting function of a direction-selective linear operator.

Rectification

Cell firing rates are by definition positive, whereas linear operators can have positive or negative outputs. A linear cell with a high maintained firing rate could encode the positive and negative values by responding either more or less than the maintained rate. Striate cells, however, have very little maintained discharge so they cannot truly act as linear operators.

The positive and negative outputs might rather be encoded by two halfwave-rectified operators; one mechanism encoding the positive outputs of the underlying linear operator, the other one encoding the negative outputs. Two such mechanisms are complements of one another; that is, the positive weights of one weighting function are replaced by negative weights in the other. Because of the rectification, only one of the two has a nonzero response at any given time.

This paper considers half-squaring and over-rectification as

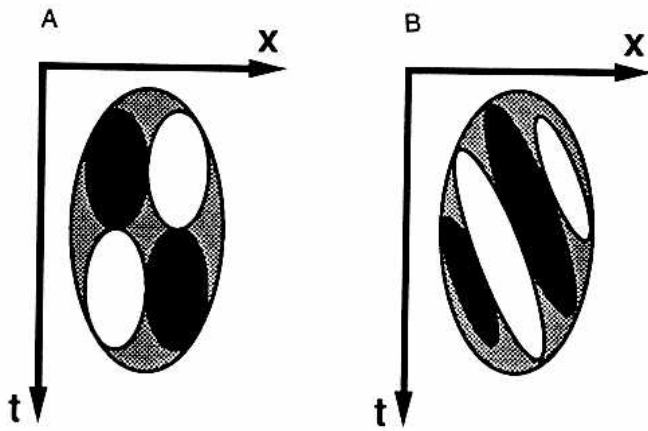


Fig. 2. Illustrations of linear spatiotemporal weighting functions, subdivided into excitatory (bright) and inhibitory (dark) subregions. A: Diagram of space-time slice through the weighting function of a biphasic, space-time separable, linear operator. B: Diagram of space-time slice through the weighting function of a non-separable, direction-selective, linear operator.

alternative forms for the rectification. Halfwave-rectification, over-rectification, and half-squaring are each special cases of the following:

$$A(t) = [L(t) - T]^n, \quad (2)$$

where $[x] = \max(x, 0)$ is halfwave-rectification, and $L(t)$ is the linear response defined in eq. (1). If T is negative, then the operator will have a nonzero maintained discharge. If T is positive, then the response of the linear operator must be greater than the threshold, T , to contribute to the output. Half-squaring corresponds to the case in which $n = 2$ and $T = 0$. Half-wave-rectification corresponds to the case in which $n = 1$ and $T = 0$. Over-rectification corresponds to the case in which $n = 1$ and $T > 0$.

Energy Mechanisms

Two linear operators with the same amplitude response, but with phases that are shifted 90 deg (in space and time), are called a quadrature pair (or Hilbert transform pair). A mechanism that sums the squared outputs of a quadrature pair is called an energy mechanism (Adelson & Bergen, 1985; Pollen & Ronner, 1983). For a drifting sine-grating stimulus, an energy mechanism's response is proportional to the squared contrast of the stimulus, and the response is constant over time (independent of the stimulus phase).

An energy mechanism can also be constructed as the average of the outputs of four half-squared linear operators, all four with the same amplitude response, but with phases in steps of 90 deg. The energy output, $E(t)$, is expressed as

$$E(t) = (1/4) [A^0(t) + A^{90}(t) + A^{180}(t) + A^{270}(t)], \quad (3)$$

where $A^\phi(t)$ is the response of a half-squared linear operator, and where the superscript ϕ specifies the operator's phase in degrees.

Weighting functions and transfer functions

The transfer function of a linear operator is defined as the Fourier transform of its impulse response,* and it is made up of two parts—the amplitude and the phase responses. A spatiotemporal linear operator is completely characterized by either its three-dimensional spatiotemporal impulse response or its three-dimensional spatiotemporal transfer function. A rectified (halfwave-rectified or half-squared) linear operator is also completely characterized by its impulse response or its transfer function. However, measurements of the impulse response and transfer function have different interpretations depending on the form of the rectification.

The weighting function of a linear cell is measured as the time-varying response to impulses flashed at each point in the visual field. For a halfwave-rectified linear operator, the weighting function of the underlying linear operator is measured using impulses of opposite polarity. Positive impulses (brighter than the mean intensity) are used to map the excitatory subregions of the spatiotemporal weighting function, and negative impulses (darker than the mean) are used to map the inhibitory subregions. The responses to dark impulses are interpreted with negative sign. For a half-squared linear operator, the weighting function of the underlying linear operator is measured in the same way, except that we use the square roots of all of the responses.

The spatiotemporal transfer function of a linear cell is measured using drifting sine-grating stimuli of all spatial and temporal frequencies. For each stimulus spatial and temporal frequency, the response, $L(t)$, is sinusoidal with frequency equal to the temporal frequency of the stimulus. The response amplitudes (peak heights) and the response phases (relative peak latencies) give the transfer function. For a halfwave-rectified linear operator, the transfer function of the underlying linear operator is measured in the same way. The response of a halfwave-rectified operator varies over time as a truncated sinusoid. The amplitude (peak height) and phase (relative peak latency) of the responses are unaffected by halfwave-rectification.

Although the term "amplitude response" is technically reserved for linear operators, it is used in this paper when describing half-squared operators and energy mechanisms as well. In both cases, the "amplitude response" is measured using drifting sine-grating stimuli. For half-squared operators, one measures the Fourier amplitude of the fundamental component of the response waveform (this is proportional to the peak height of the response waveform). Energy mechanisms give an unmodulated response to sine gratings so we measure the d.c. response. The "amplitude response" of an energy mechanism is the same as the "amplitude response" of each of its input half-squared operators. The square root of an energy mechanism's "amplitude response" equals the amplitude response of the underlying linear operator.

*The impulse response, $h(x, y, t)$, of a convolution filter is defined as the mirror image of its weighting function, $h(x, y, t) = (-x, -y, -t)$. However, the linear operators considered in this paper are not convolution filters. Their responses, according to eq. (1), are computed by convolving in time and by taking the inner product (not convolving) in space. It is natural to define the "impulse response" of such a linear operator to be the responses to impulses flashed at each location in the operator's receptive field. Using this definition, the "impulse response" is the mirror image of the weighting function only in time (not in space), $h(x, y, t) = f(x, y, -t)$.

Simple cell responses

The recent literature on simple cell physiology largely revolves around the issue of linearity. A number of researchers have proposed that simple cells behave like linear operators, and that selectivity of simple cells is determined by their linear weighting functions. However, since there are blatant violations of linearity, some researchers have argued that selectivity of simple cells must be due to nonlinear mechanisms.

This section attempts to reconcile the controversy regarding the origin of selectivity in simple cells. The model advocated in this paper is based on (spatiotemporal and binocular) linear operators that compute a linear sum of the stimulus intensities over local space and time. The outputs of the linear operators are rectified in some way (e.g. half-squared) and normalized. According to the model, cells are selective for orientation, scale, and direction of motion because of the underlying linear stage. Cell responses, according to the model, also depend on the nonlinearities (rectification and normalization).

This section reviews the physiology of simple cells and compares model simulations with experimental results. Some of the experimental results can be explained with the linear (or half-wave-rectified linear) model. For those cases, it is shown that the new model (with half-squaring and normalization) does just as well. In other cases, experimental results clearly refute the linear (and half-wave-rectified linear) model. It is shown that nearly all of those results can be explained by the new model (with half-squaring and normalization).

A number of experimental results are included in this review for the sake of completeness, but the focus is on two questions. First, is there a linear stage underlying simple cell responses? Second, assuming that there is an underlying linear stage, what is the form of the rectification (half-wave-rectification, half-squaring, or over-rectification)?

The first question would be most easily addressed by an experiment that tested for the underlying linearity of simple cells, independent of rectification and independent of divisive suppression. Although such an experiment can easily be designed (see Responses to temporally modulated bars), this experiment has not yet been performed. Even so, there are a number of experimental results that provide indirect evidence supporting the underlying linearity hypothesis.

Likewise, the second question would be most easily addressed by an experiment that measured the rectification, independent of suppression. Indeed, suppression (from divisive normalization) is largely irrelevant for many of the simulations described in this paper.* For these experiments, the normalization stage of the model is ignored and the experimental results are discussed in the context of rectified linear operators. This paper concludes that there is ample evidence to reject half-wave-rectification in favor of either over-rectification or half-squaring. It also concludes that the experimental results to date do not distinguish well between over-rectification and half-squaring. This latter conclusion

*Normalization is relevant for simulating some experiments but not for others. As an example, consider simulating responses to a drifting grating stimulus of fixed contrast. According to the model, a single drifting grating of fixed contrast yields suppression that is constant over time. Thus a normalized, half-squared, linear operator has the same behavior as an unnormalized operator. Regardless of normalization, the model gives the same predictions. On the other hand, some stimuli (e.g. counterphase gratings) yield suppression (from divisive normalization) that varies over time. In such cases, the normalized and unnormalized operators give different predictions.

is not surprising since these two nonlinearities (half-squaring and over-rectification) are approximately the same, particularly in the context of response saturation (see Heeger, 1992a).

Response to impulses

Many researchers have used impulses (flashed spots or bars) and white noise stimuli to map simple cell weighting functions (e.g. Hubel & Wiesel, 1962; Heggelund, 1981a; Jones & Palmer, 1987a; McLean & Palmer, 1989). This section reviews these experimental results and explains that they are consistent with a rectified linear model.

Hubel and Wiesel (1962) discovered that simple cells have clearly defined excitatory and inhibitory spatial subregions. Bright (brighter than the mean intensity) light in an excitatory region or dim (darker than the mean) light in an inhibitory region enhances the cell's response, whereas bright light in an inhibitory region or dim light in excitatory region inhibits its response. Simple cells rarely have much maintained discharge (Pettigrew et al., 1968; Rose & Blakemore, 1974), so the inhibition cannot be measured directly. Removal of an inhibitory stimulus (e.g. turning off a bright stimulus in an inhibitory subregion) yields a burst of activity that has often been assumed to be a reasonable measure of the magnitude of the inhibition. White noise stimuli can also be used to measure the inhibitory responses. The noise drives the cell to a nonzero firing rate, so that responses to individual bright or dark impulses are seen as spike rates either above or below the background activity.

These results are readily explained by a rectified (either half-wave-rectified, over-rectified, or half-squared) linear model. The underlying linear stage predicts that excitation to a bright light is complemented by inhibition to a dim light. Because of rectification, the inhibition can be measured only by first driving the operator to a nonzero response with an excitatory stimulus.

Simple cells have also been characterized as having ON and OFF subregions. Cells respond to light increment (the onset of a bright stimulus) in an ON region and to light decrement (the offset of a bright stimulus) in an OFF region.

The ON and OFF responses are also consistent with a rectified linear model. In particular, the ON and OFF responses can be explained by a linear operator that has a biphasic temporal response. The space-time weighting function of such an operator is illustrated in Fig. 2A. First consider stimulation within the ON subregion (the right half of the receptive field). At the onset of a bright light, the operator's output will first increase and then return to zero. At stimulus offset, the output will first decrease and then return to zero. Since the response is rectified, only the positive response (the response at onset in the ON subregion) will be seen. Now consider stimulation within the OFF subregion (the left half of the receptive field). At the onset of a bright light, the linear operator's output will first decrease and then return to zero. At stimulus offset, the output will first increase and then return to zero. Again, only the positive response (the response at offset in the OFF subregion) will be seen. The ON and OFF spatial regions of the linear weighting function are better thought of as biphasic *spatiotemporal* subregions. This explanation of ON and OFF responses is similar to previous accounts (e.g. Emerson, 1988; Wolbarsht et al., 1961).

According to the model, a cell's selectivity is due to an underlying linear operator. The existence of excitatory and inhib-

itory (ON and OFF) subregions is consistent with the hypothesis of an underlying linear stage, regardless of the form of rectification and regardless of normalization.

Flashed vs. drifting bars

According to the model, cells are direction selective because of the underlying linear stage. McLean and Palmer (1989) and Shapley et al. (1991) measured full three-dimensional spatiotemporal weighting functions of simple cells using white noise stimuli. They found some simple cells with space-time separable weighting functions, like that depicted in Fig. 2A, that can be expressed as the product of a spatial function multiplied by a temporal function. The model predicts that these cells be non-direction selective.

They also found some simple cells with weighting functions tilted along an oblique axis (inseparable) in space-time, like that illustrated in Fig. 2B. The model predicts that these cells be direction selective, that is, that they prefer motion in one direction over the other. In fact, since a spatiotemporal linear operator is completely characterized by its impulse response, the model allows one to predict a cell's preferred direction and speed of motion from the cell's spatiotemporal weighting function. When McLean and Palmer (1989) measured simple cell responses to moving bars, they could, for most cells, correctly predict the preferred bar motion from the weighting function. This result supports the hypothesis that direction selectivity is due to an underlying linear stage.

Baker (1988) performed a similar experiment. He measured the preferred velocity for a continuously drifting bar, and the preferred displacement for two bars flashed sequentially at nearby locations. Consistent with the model, he could predict the preferred velocity from the preferred displacement. Baker (1990) also measured the preferred spatiotemporal frequency of a drifting grating from which he could predict the preferred velocity of a moving bar. Again, these results are consistent with the underlying linearity of simple cells.

However, direction selectivity is unexplained in some simple cells. The weighting function of a direction-selective linear operator has subregions that are tilted along oblique axes in space-time (like Fig. 2B), and hence it is space-time inseparable. The model (regardless of the rectification and regardless of divisive normalization) predicts that cells with space-time separable weighting functions not be direction selective. Some cells, however, are direction selective even though they have space-time separable weighting functions (McLean & Palmer, 1989; Emerson & Citron, 1989). The behavior of these cells cannot be accounted for by a model, like that advocated in this paper, in which direction selectivity is due to an underlying spatiotemporal linear stage.

Responses to drifting gratings

The response of a spatiotemporal linear operator to a drifting grating varies sinusoidally over time with the same temporal frequency as that of the stimulus. A halfwave-rectified linear operator responds over only half of each cycle, remaining silent during the other half-cycle. A half-squared operator also responds over only half of each cycle, but the shape of the response waveform is distorted. Simple cells, like rectified linear operators, also respond over approximately half of each cycle (Movshon et al., 1978a; Andrews & Pollen, 1979; Kulikowski & Bishop, 1981a).

Distortion from rectification

The discussion here centers on the difference between the predictions of halfwave-rectification and half-squaring. Although the results to date cannot be used to discriminate between these two models, it might be possible to do further experiments that would discriminate between them.

For a linear operator, a frequency analysis of the response waveform reveals one frequency component at the temporal frequency of the grating stimulus. Nonlinearities like halfwave-rectification and half-squaring distort the response, so a frequency analysis of a halfwave-rectified or half-squared response will reveal more than one frequency component.

If the form of the output nonlinearity were known, then a simple method could be used to compensate for it. One can compensate for halfwave-rectification by stimulating cells with paired stimuli that have inversely related intensity profiles, and then differencing the resulting responses. This method was used by Pollen et al. (1988), as discussed below, to analyze responses to compound gratings. Note that this method also encompasses the procedure described above for mapping simple cell weighting functions (stimulating with bright and dark impulses, and interpreting the responses to dark impulses with negative sign). If the actual nonlinearity is halfwave-rectification, then this procedure gives the response of the underlying linear operator. If the actual nonlinearity is half-squaring, then this procedure gives the signed-square of the response of the underlying linear operator:

$$|(L(t))L(t)| = \begin{cases} L^2(t) & \text{if } L(t) > 0, \\ -L^2(t) & \text{if } L(t) < 0, \end{cases} \quad (4)$$

where $|L(t)|$ is the absolute value of $L(t)$, and $L(t)$ is the response of the underlying linear operator.

The signed-square of a sine wave of frequency f has an additional frequency component (of relatively low amplitude) at three times the base frequency, $3f$. A quantitative analysis of the responses could, in principle, discriminate between half-squaring and halfwave-rectification. Half-squaring predicts that this $3f$ component be present, whereas halfwave-rectification predicts that it be absent. However, the difference between the frequency distortions generated by halfwave-rectification and half-squaring are small, perhaps too small to be significant in noisy measurements.

Spatiotemporal transfer function

Hamilton et al. (1989) used drifting grating stimuli to measure the spatiotemporal "transfer functions" (both the "amplitude responses" and "phase responses") of simple cells. They confirmed that cell responses satisfy a number of properties implied by a spatiotemporal linear model. They computed spatiotemporal weighting functions from the transfer functions, assuming linearity, by inverse Fourier transformation. Their data is also consistent with a half-squared linear model. Under the assumption of half-squaring, Hamilton et al. (1989) should have taken the square root of the measured amplitude responses before computing the inverse Fourier transform.

A number of other researchers also measured the spatial-frequency tuning curves, temporal-frequency tuning curves, and orientation-tuning curves of striate cells. These measurements have been done for both simple and complex cells in both cat and monkey (Campbell et al., 1968; Maffei & Fiorentini, 1973;

Rose & Blakemore, 1974; Henry et al., 1974*a,b*; Ikeda & Wright, 1975*a,b*; Tolhurst & Movshon, 1975; Schiller et al., 1976; Movshon et al., 1978*c*; Andrews & Pollen, 1979; Holub & Morton-Gibson, 1981; Kulikowski & Bishop, 1981*a*; Tolhurst & Thompson 1981; DeValois et al., 1982; Berardi et al., 1982; Foster et al., 1985; Webster & DeValois, 1985; Jones et al., 1987; Robson et al., 1988; Baker, 1990; Hammond & Pomfrett, 1990). Unlike Hamilton et al. (1989), most of these researchers did not measure the phase response at all, and many of them measured only part of the amplitude response (either the spatial frequency-tuning curve, or the orientation-tuning curve, or the temporal-frequency tuning curve). Although these results are consistent with the linear/energy model of cortical cell responses, they are not in any way a test of the underlying linear stage.

Impulses vs. gratings

Many experimenters (Movshon et al., 1978*a*; Maffei et al., 1979; Andrews & Pollen, 1979; Glezer et al., 1980; Kulikowski & Bishop, 1981*a,b*; Dean & Tolhurst, 1983; Field & Tolhurst, 1986; Tadmor & Tolhurst, 1989; Shapley et al., 1991) have tested for linearity of simple cells by comparing the response to gratings with the response to impulses. The logic of these experiments is straightforward. The response of a linear cell to the sum of two stimuli is equal to the sum of the responses to each of the component stimuli. Since a grating is composed of the sum of a number of impulses, the response of a linear cell to a grating is predictable (*via* Fourier transform) from its response to impulses. Likewise, since an impulse can be thought of as the sum of a number of gratings, the response to an impulse is predictable (*via* inverse Fourier transform) from the response to gratings.

The results of these experiments show that the response to gratings and the response to impulses look very nearly like Fourier transforms of one another, up to an *arbitrary* scale factor. These results have been taken as evidence for linearity of simple cells.

Most of these researchers found, however, that the response to gratings and the response to impulses are not precise transforms of one another. In many cases, the inverse transform of the response to gratings gives a weighting function with additional side bands beyond those measured directly. In addition, the measured response to gratings is often more narrowly tuned for spatial frequency than predicted from the Fourier transform of the response to impulses.

Several experimenters (e.g. Tadmor & Tolhurst, 1989) have suggested that the discrepancy between the frequency and space-domain measurements can be explained by over-rectification.

These results are also predicted by half-squaring. In spite of the half-squaring nonlinearity, the inverse transform of the response to gratings still looks very similar to the response to impulses. In Fig. 3, the response to impulses was simulated as the signed-square, eq. (4), of the underlying linear weighting function. The response to gratings was simulated as the squared magnitude of the Fourier transform of the underlying linear weighting function. As shown in Fig. 3A, the inverse transform of the simulated response to gratings has some extra (low amplitude) side bands. As shown in Fig. 3B, the simulated response to gratings is more narrowly tuned than predicted from the simulated response to impulses. The half-squared linear model is, therefore, consistent with physiological data.

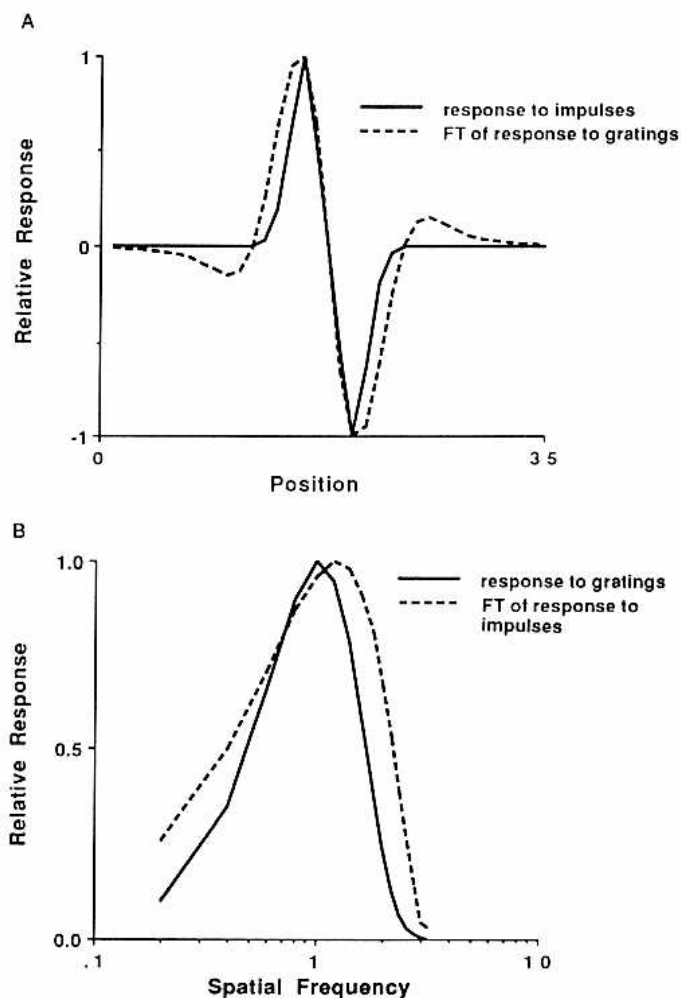


Fig. 3. Comparison between the response to impulses and the response to gratings of a half-squared operator. Since the operator is nonlinear, the response to impulses and response to gratings are not transforms of one another. A: Response to impulses superimposed with the inverse Fourier transform of response to gratings. B: Response to gratings superimposed with the magnitude of the Fourier transform of response to impulses. The response to gratings is more narrowly tuned than predicted from the response to impulses, and the response to impulses is more narrowly tuned than predicted from the response to gratings. Both A and B are consistent with physiological data.

In a related series of experiments, however, Jones and Palmer (1987*a,b*) and Jones et al. (1987) did *not* find a systematic mismatch between space and frequency-domain measurements. They tested for the linearity of simple cells by fitting Gabor functions to measurements in both domains. They found that the parameters of the fits in the two domains were highly correlated. Although the fits were not perfectly correlated, the errors were of both signs. For some cells the frequency bandwidths were greater than expected based on space-domain data. For other cells the bandwidths were less than expected. Half-squaring, however, predicts that the bandwidths always be less than expected.

Palmer (personal communication) also points out that the mismatch between space- and frequency-domain measurements might be an artifact of the experimental technique. The frequency-domain measurements typically make use of large stimuli and take advantage of spatial summation to bring out the

influence of the weaker sidelobes. This tends to make the tuning curves appear narrower than would be predicted from impulse responses.

In all these experiments, the space- and frequency-domain measurements were compared up to an arbitrary scale factor. If the data could be analyzed without this arbitrary scaling, then it would be a much more powerful test for discriminating between the different models. Enroth-Cugell and Robson (1966) and Enroth-Cugell et al. (1983) demonstrated linearity of retinal ganglion cells, by comparing space- and frequency-domain measurements, without needing a scale factor. Unfortunately, it is quite difficult to do this experiment in cortex without re-scaling the data, due to the cortical contrast gain control (e.g. Ohzawa et al., 1985; see Heeger, 1991 for review). One would have to "balance" the space- and frequency-domain stimuli in order to yield the same gain.

Two-bar interactions

For a linear operator, the response to a pair of bars equals the sum of the responses to each individual bar. Physiologists have tested linearity of simple cells by measuring responses to pairs of bars. The experiments to date yield conflicting results. Results from one experiment are consistent with halfwave-rectification, and results from another are consistent with half-squaring.

Ganz and Felder (1984) analyzed responses of simple cells to stimuli made up of pairs of bars flashed in sequence. They found that cell response to a pair of bars is less than the sum of the responses to each individual bar consistent with halfwave-rectification.

Emerson and Citron (1989) used white noise stimuli to study the interaction of pairs of bars. Like Ganz and Felder (1984), they found that cell response to a pair of bars is different from the sum of the responses to each individual bar. Unlike Ganz and Felder, however, their results favor half-squaring. They used a three stage (linear/nonlinear/linear) cascade model to fit the cell response data. They found that the second (nonlinear) stage is well described by half-squaring.

Simulation results are shown in Figs. 4 and 5. Fig. 4A is the response over time of a halfwave-rectified, direction-selective, linear operator, for an impulse flashed in the center of the operator's receptive field. Fig. 4B is the response of the same operator, but for an impulse flashed at a different position in the receptive field. Fig. 4C is the linear prediction, the sum of Figs. 4A and 4B. Fig. 4D is the actual response to the pair of impulses. Notice that the linear prediction (Fig. 4C) underestimates the actual response (Fig. 4D) because of the hidden (rectified) inhibition. The magnitude of the effect can be summarized as the integral of the difference between the actual response and the linear prediction.

This computation was repeated for a number of conditions, corresponding to a different spatial and temporal offset between the pair of impulses. One impulse was always flashed in the center of the receptive field. The second impulse was flashed at all different locations, either simultaneous with the first impulse, before it, or after it. Either both impulses were brighter than the background or both were darker than the background. For each stimulus condition (spatiotemporal offset, bright/dark polarity), the simulation computed the integral of the difference between the linear prediction and the actual response of the halfwave-rectified operator. For each spatial and temporal off-

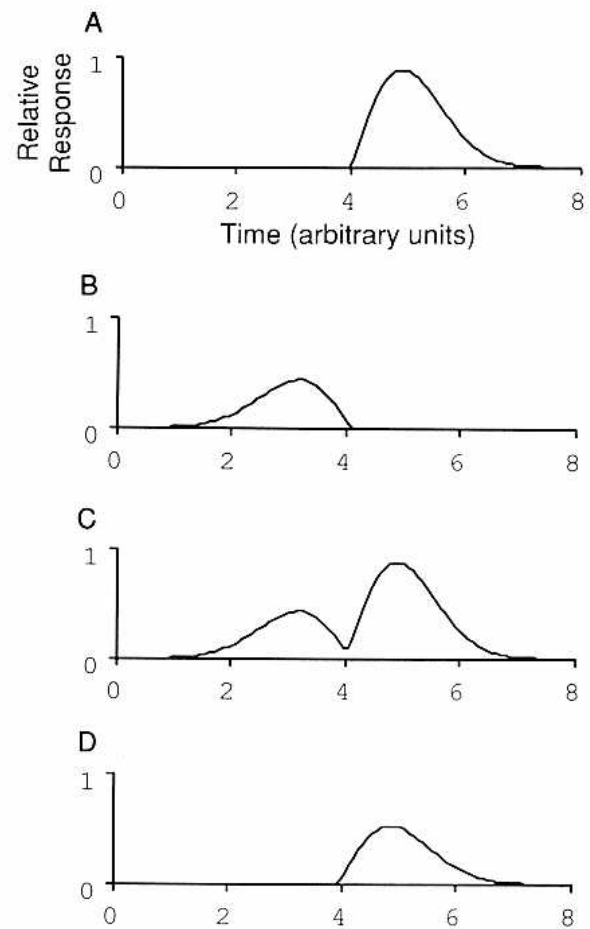


Fig. 4. A: Response of halfwave-rectified, direction-selective, linear operator for an impulse flashed in the center of the operator's receptive field. B: Response of same operator for impulse flashed at a different position in the receptive field. C: Linear prediction, sum of A and B. D: Actual response of operator to pair of impulses flashed simultaneously. Linear prediction overestimates actual response because of hidden (rectified) inhibition.

set, the computed results using bright and dark impulses were summed. Fig. 5A shows the mismatch between the linear prediction and the halfwave-rectified response. Brightness is proportional to the integral of the difference between the linear prediction and the actual response. Fig. 5B shows the result, analogous to Fig. 5A, when using half-squaring instead of halfwave-rectification. Using over-rectification can give a result similar to either Figs. 5A or 5B, depending on the choice of the threshold.

With halfwave-rectification (Fig. 5A), the actual response is always less than or equal to the linear prediction (like the results of Ganz & Felder, 1984). With half-squaring (Fig. 5B), the actual response is greater than the linear prediction for some conditions and less than the linear prediction for others.

Ganz and Felder (1984) concluded from their experiment that direction selectivity depends on inhibition. Several other physiologists (Goodwin et al., 1975; Sillito, 1977; Emerson & Gerstein, 1977; Tolhurst & Dean, 1991) have also reached that conclusion. In Figs. 4 and 5, however, both additive excitation and subtractive inhibition contribute to the selectivity. In these simulations, rectification (not inhibition) causes the mismatch between the linear prediction and the actual response.

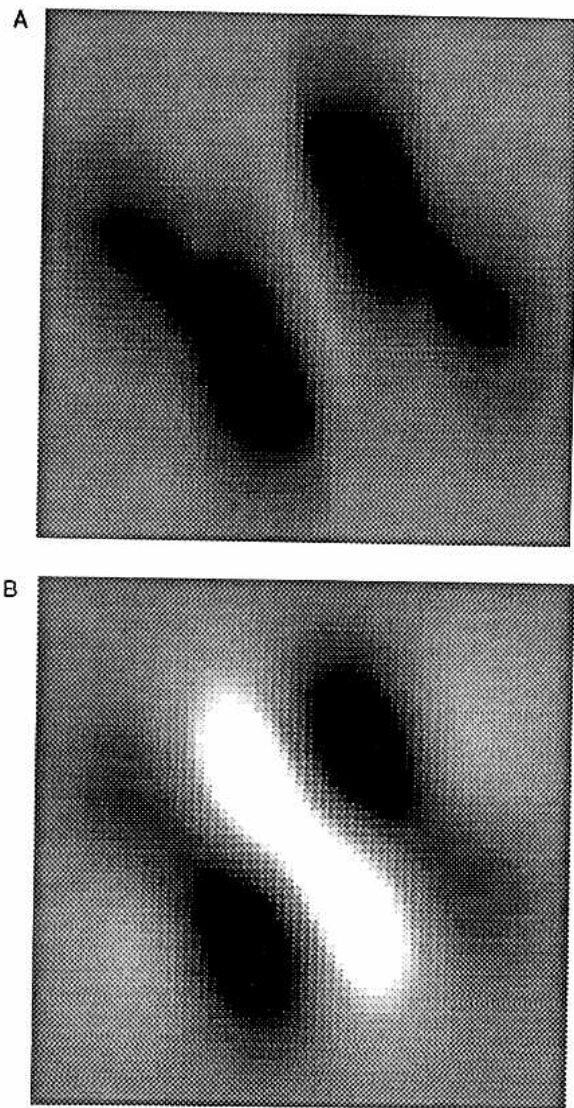


Fig. 5. Two-bar interactions (integral of the difference between actual response and linear prediction) for pairs of impulses flashed sequentially at different positions. One impulse always flashed in the center location. Second impulse flashed at all locations, either simultaneous with the first impulse, before it, or after it. Space is represented horizontally, and time along the vertical axis. Center of each image corresponds to location and time of the first (fixed position) impulse. Top half of each image corresponds to flashing the second impulse before the first. Bottom half of each image corresponds to flashing the second impulse after the first. Brightness is proportional to the mismatch between the actual response and the linear prediction. Mid-grey corresponds to a perfect linear prediction. **A:** Two-bar interaction of halfwave-rectified, direction-selective, linear operator. With halfwave-rectification, the actual response is always less than or equal to the linear prediction (like results of Ganz & Felder, 1984). **B:** Same as in **A**, but for a half-squared, direction-selective, linear operator. With half-squaring, the actual response is greater than the linear prediction for some conditions and less than the linear prediction for others.

Responses to temporally modulated bars

Tolhurst and Dean (1987) used pairs of temporally modulated bars to test for the underlying linear stage (see also Henry et al., 1978). They placed one bar in an ON subregion and the other in an OFF subregion. The intensities of both were modulated

sinusoidally over time. They found that the response to the pair of bars could be predicted from the responses to each individual bar, using a spatiotemporal linear model with over-rectification. Simulation results in Fig. 6 demonstrate that the new model (with half-squaring and divisive normalization) does just as well.

Data from one cell is replotted in Fig. 6A. There were three conditions. In the first condition, a single bar was modulated in an ON subregion of the receptive field. The middle curve in Fig. 6A is the cell's response (peak response amplitude) as a function of the bar's amplitude of modulation. In the other conditions, two bars were displayed simultaneously, one in an ON subregion and one in an OFF subregion. The amplitude of modulation of the second (OFF) bar was fixed, but that of the first (ON) bar was varied. Both bars had the same frequency of modulation. The second bar was either modulated in phase (bottom curve) or out of phase (top curve) with the first bar.

For a spatiotemporal linear operator, the response to a single modulating bar varies sinusoidally over time with the same temporal frequency as the stimulus. The response phase may be different for each bar placement. When both bars are displayed at once, the response still varies sinusoidally over time with the same temporal frequency as the stimulus. Varying the relative amplitudes or relative phases of the two bars affects the amplitude and phase of the response, but leaves the frequency of the response unchanged.

There are two notable aspects of the results shown in Fig. 6A. First, the middle curve (single bar condition) is near zero for low amplitudes and then rises more steeply. This is an indication of an accelerating nonlinearity (either over-rectification or half-squaring). Second, adding the second bar in phase with the first (lower curve) inhibited the cell's response, whereas adding the second bar out of phase (upper curve) enhanced the cell's response. This is an indication of the underlying linearity.

The new model, with half-squaring and divisive normalization, behaves similarly, as shown in Fig. 6B. Note that normalization is important in modeling these results because the amplitude of modulation was varied over a fairly wide range. The normalization factor was a constant, σ , plus a sum of the energy outputs, averaged over time (see Heeger 1998a, for details). The σ value was chosen by hand to approximate the shape of the single bar condition (middle curve), and the same σ value was used for all three conditions. The results demonstrate that the spatiotemporal linear model, with divisive normalization and half-squaring, is consistent with the data.

A variant of this experiment would prove to be a much more powerful test of the underlying linear stage. Consider stimuli made up of two spots (or bars) at fixed positions that are both modulated sinusoidally over time. Both spots have the same temporal frequency, but the amplitude and phase of modulation may be different. For a spatiotemporal linear operator, one can always choose the relative amplitude and phase of modulation, regardless of the positions of the two spots, to null the output. This is also true for a normalized, rectified linear operator. An experiment of this sort was performed by Spekreijse and van den Berg (1971) in goldfish retinal ganglion cells. It is surprising that this experiment has not yet been done in cortex.

Responses to compound gratings

Physiologists have used a variety of compound grating stimuli to test for linear superposition. DeValois et al. (1979) compared

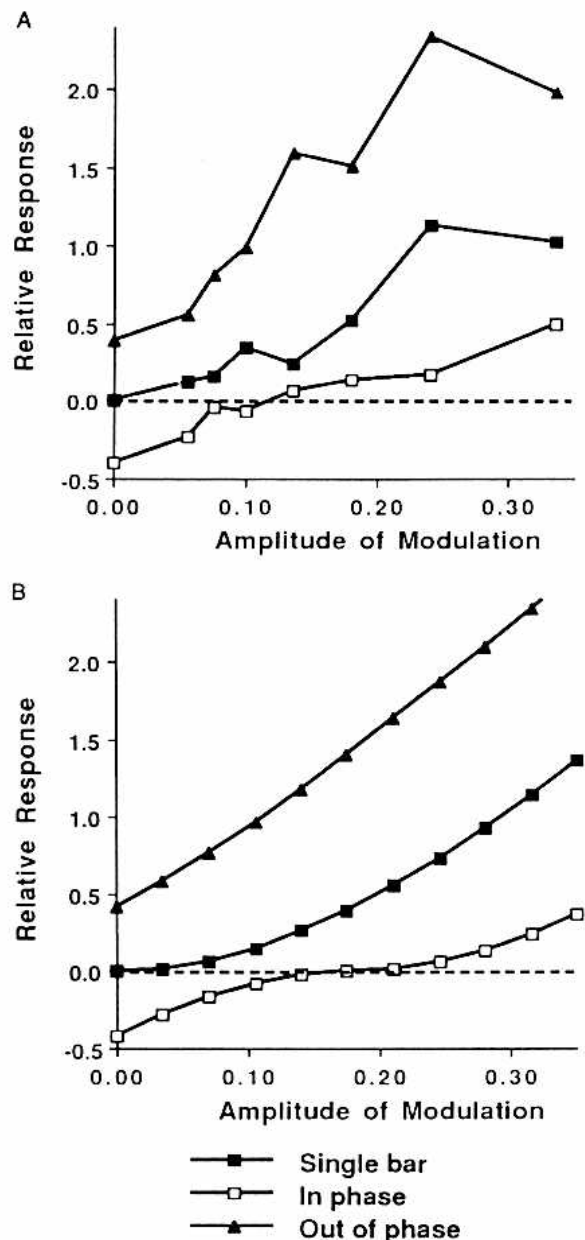


Fig. 6. Simple cell responses to pairs of temporally modulated bars. A: Data replotted from Tolhurst and Dean (1987). Middle curve shows responses as a function of a single bar's amplitude of modulation. Other two curves are responses to a pair of bars, both with the same frequency of modulation, one in an ON subregion and the other in an OFF subregion. Amplitude of modulation of the second (OFF) bar was fixed, but that of the first (ON) bar was varied. The second bar was either modulated in phase (bottom curve) or out of phase (top curve) with the first bar. Positive responses mean that cell activity occurred during the first half of the stimulus temporal cycle. Negative responses mean that activity occurred during the second half cycle. B: Model cell, with half-squaring and divisive normalization, behaves similarly.

responses to checkerboard stimuli with responses to sine gratings. Maffei et al. (1979) compared responses to sine gratings with responses to square waves and fluted square waves (square wave minus the fundamental) of various spatial frequencies. Pollen and Ronner (1982) compared responses to sine waves and square waves of various spatial frequencies. Pollen et al.

(1988) and DeValois and Tootell (1983) measured responses to pairs of gratings, while varying the phase offset between the two component gratings.* In all of these experiments, responses to single sine gratings were compared with responses to compound sine gratings; that is, sums of two or more sine gratings (of different spatial frequencies or orientations) were added together and drifted rigidly across the receptive field.

The following paragraphs concentrate on the results of Pollen et al. (1988). Simulation results in Fig. 7 show that half-squaring explains their data better than halfwave-rectification.

Pollen et al. (1988) stimulated simple cells with the sum of two gratings at frequencies of $1f$ and $2f$, and with four different choices for the phase of the $2f$ component. They assumed halfwave-rectification as the output nonlinearity of simple cells, and compensated for it by differencing responses to stimuli with inversely related intensity profiles. They measured the amplitude and the phase of both the $1f$ and $2f$ components of the response waveforms after compensating for halfwave-rectification. The linear prediction is that the $1f$ component of the response be entirely independent of the relative phase of the two component gratings. Although their results are generally consistent with this prediction, they found slight phase-dependent distortions in the response amplitudes. Their data is replotted in Fig. 7A.

Fig. 7B shows the predictions of half-squaring (filled symbols) and halfwave-rectification (open symbols). The prediction of half-squaring was computed as the $1f$ component of the signed-square of a compound grating, as a function of relative phase. Half-squaring results in a slight phase-dependent distortion, whereas halfwave-rectification yields no distortion. Half-squaring underestimates the magnitude of the effect (compare Figs. 7A and 7B), but half-squaring explains the experimental data better than halfwave-rectification.

Pollen et al. (1988) also found that the phases of both the $1f$ and $2f$ components of the output and the amplitude of the $2f$ component of the output are as predicted by the (halfwave-rectified) linear model. Half-squaring gives the same predictions for these measurements. The phases of both the $1f$ and $2f$ components of the output and the amplitude of the $2f$ component of the output are unaffected by squaring.

Responses to counterphase gratings

Simple cells exhibit characteristic responses to temporally modulated (i.e. counterphase) sine gratings. The response varies over time with the temporal modulation of the stimulus, and the amplitude and phase of modulation both depend on the spatial phase of the grating (Maffei & Fiorentini, 1987; Movshon et al.,

*Pollen et al. (1988) and DeValois and Tootell (1983) both measured responses to pairs of gratings while varying their relative phases. Pollen et al. (1988) explained that halfwave-rectification leads to distortions (introducing new frequency components) of the response waveform for the compound grating stimuli. These distortions in the response waveform were misinterpreted as phase-dependent inhibition by DeValois and Tootell (1983). By varying only the relative phase of the two component gratings, Pollen et al. (1988) controlled properly for any effect of divisive normalization. As discussed in the companion paper (Heeger, 1992a), varying the spatial frequency or orientation of either of the two gratings results in more complicated behavior. DeValois and Tootell (1983) varied the relative spatial frequency of the two gratings, and found what they called phase-independent inhibition. The companion paper (Heeger, 1992a) attributes this phase-independent inhibition to divisive normalization in the model.

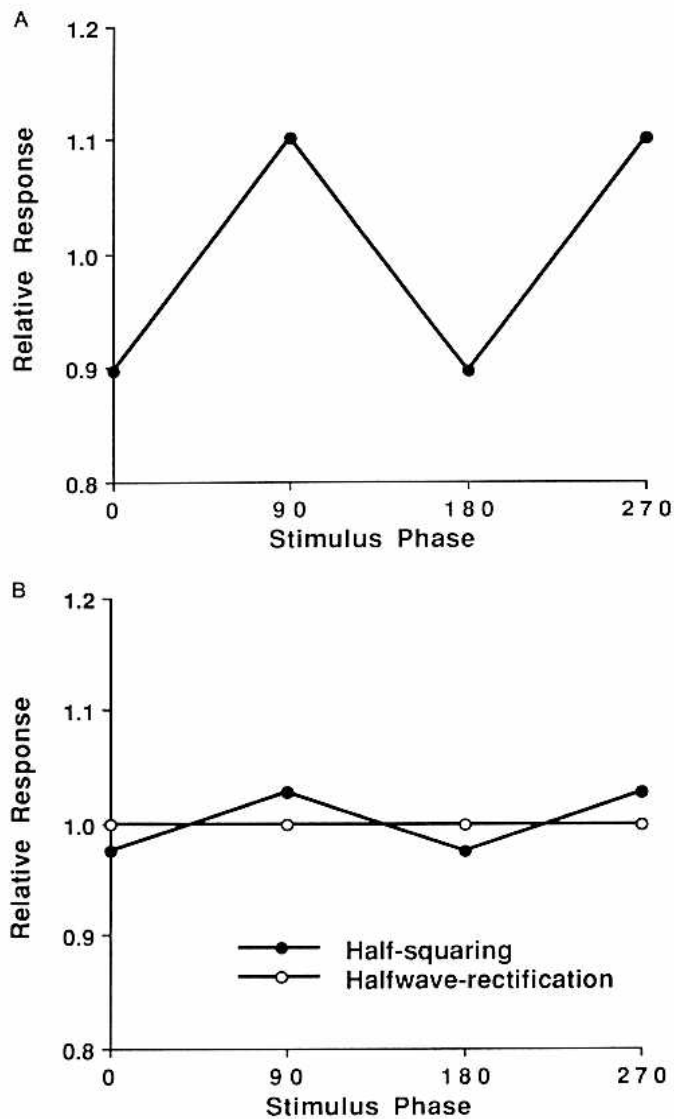


Fig. 7. A: Simple cell responses to the sum of two gratings with frequency components at $1f$ and $2f$, as a function of the phase of the $2f$ component. Data replotted from Pollen et al. (1988). B: Predictions of half-squared and halfwave-rectified linear models. Half-squaring gives a better explanation of the experimental data.

1978a; Kulikowski & Bishop, 1981a; Reid et al., 1987). A spatiotemporal linear operator followed by either halfwave-rectification or half-squaring behaves similarly.

This section points out that a rectified, spatiotemporal linear model is consistent with the results of counterphase grating experiments. It also shows that some of the results are explained better by half-squaring than by halfwave-rectification.

Counterphase nulling

For a linear mechanism, it is possible to balance the inputs to the excitatory and inhibitory subregions. For example, a counterphase grating with appropriately chosen spatial phase elicits no response in retinal ganglion cells (Enroth-Cugell & Robson, 1966; Enroth-Cugell et al., 1983). The presence of such a null point, a choice of spatial phase that yields no response, has been taken as evidence for the linearity of these cells. Some

striate cells, in both cat and monkey, have null points (Movshon et al., 1978a; Kulikowski & Bishop, 1981a; Kulikowski & Vidyasagar, 1986; Robson et al., 1988).

Counterphase nulling is not, however, a valid test for linearity in direction-selective cells, as explained by several authors (Movshon et al., 1978a; Dean & Tolhurst, 1986; Reid et al., 1987; Hamilton et al., 1989). Movshon et al. (1978a) and Reid et al. (1987) found that some cortical cells respond to all counterphase grating spatial phases. The spatiotemporal linear model (with either half-squaring or halfwave-rectification) suggests that these cells have space-time inseparable (direction-selective) weighting functions, and that cells with counterphase grating null points (for every stimulus spatial and temporal frequency) have space-time separable (not direction-selective) weighting functions. To date, this comparison between space-time separability and counterphase nulling remains to be done.

Response amplitude vs. response phase

Movshon et al. (1978a), Reid et al. (1987, 1991), and Tolhurst and Dean (1991) measured response amplitude and response phase of simple cells while varying the spatial phase of counterphase gratings. They have shown (mathematically) that for a halfwave-rectified spatiotemporal linear operator, a polar plot of the response amplitude as a function of the response phase is elliptical in shape. Their experimental results, however, are typically not quite elliptical. Rather the results are described as "wasp-waisted ellipses" since the amplitudes near the minor axes are smaller than they should be to fit an ellipse. An example, replotted from Tolhurst and Dean (1991), is shown in Fig. 8A.

Movshon et al. (1978a) proposed that the deviation from an ellipse could be explained by over-rectification. If the neuron has to reach a certain level of excitation before any activity is seen, there will be a disproportionate decrease in small responses.

The wasp-waisted elliptical shape is also predicted by half-squaring. The output of a spatiotemporal linear operator was computed for counterphase gratings of various spatial and temporal frequencies, and various spatial phases. The response waveforms were then half-squared, and the amplitude and phase of the fundamental Fourier component (equal to the temporal frequency of the stimulus) were measured. Figs. 8B and 8C show the wasp-waisted results for two different spatial and temporal frequencies.

Counterphase vs. drifting gratings

By comparing the responses to counterphase gratings with responses to drifting gratings, several researchers (Reid et al., 1987, 1991; Tolhurst & Dean, 1991; Albrecht & Geisler, 1991) found that there is a nonlinear contribution to simple cell responses. Specifically, they found that the linear prediction from counterphase gratings underestimates a directional index computed from drifting grating responses.

The following paragraphs present simulation results demonstrating that a half-squared linear model can account for this result. Indeed, a variety of accelerating nonlinearities (including half-squaring and over-rectification) give similar predictions (see Albrecht & Geisler, 1991, for a similar conclusion).

The directional index is defined as

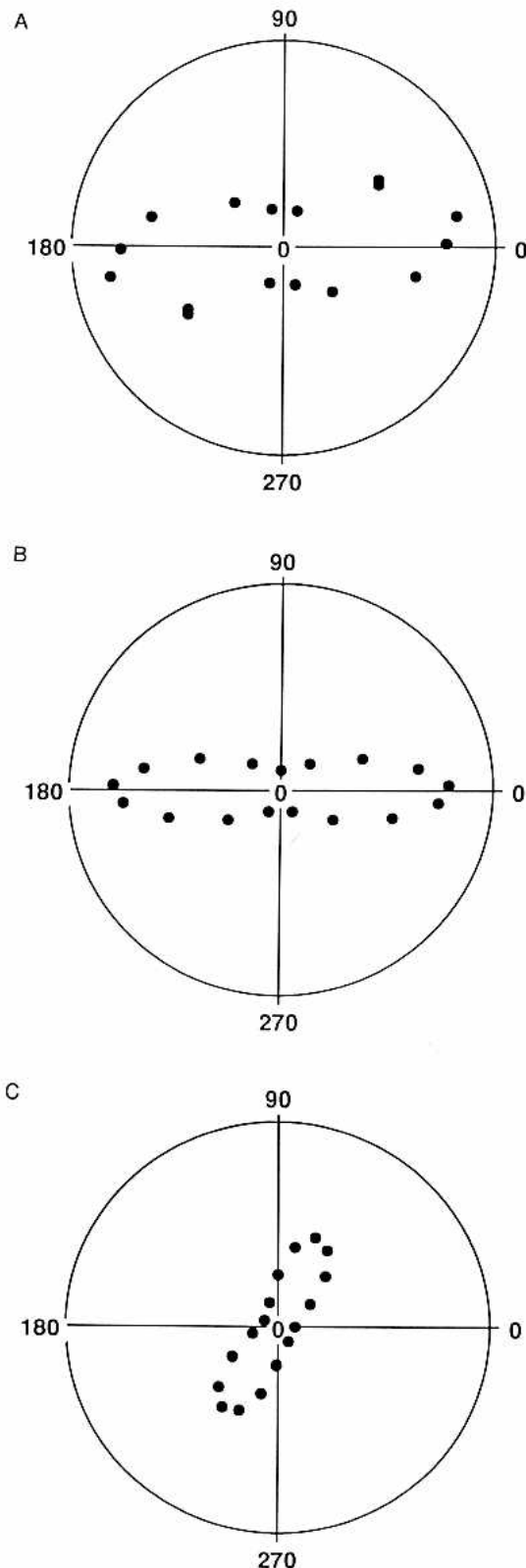


Fig. 8. A: Polar graph of responses to counterphase gratings; data replotted from Tolhurst and Dean (1991). Each data point represents a different stimulus spatial phase. The amplitude of the fundamental component of the response is represented radially, while the angular coordinate indicates the temporal phase of the response. B, C: Responses of a half-squared operator for counterphase grating stimuli to different spatial and temporal frequencies. Wasp-waisted ellipses resemble the physiological data.

$$\frac{R_p - R_a}{R_p + R_a}, \quad (5)$$

where R_p and R_a are, respectively, the responses for gratings drifting in the preferred and anti-preferred directions. Reid et al. (1987) showed that for a (halfwave-rectified) linear operator this directional index is predictable from the responses to counterphase gratings. Specifically, the directional index is equal to the ratio of the axes of the ellipse obtained, as described above, from counterphase gratings. However, the data do not agree with the linear prediction. The prediction from counterphase stimuli underestimates the index by about half.

Note that divisive normalization is totally irrelevant when simulating this experiment. Since the directional index is a ratio of responses, the normalization factors in numerator and denominator exactly cancel one another. Therefore, normalization was ignored in the model simulations.

Fig. 9A shows data replotted from Reid et al. (1987), and Fig. 9B shows results from model simulations. In both cases, the ratio of the axes of the best-fitting ellipse derived from counterphase stimuli is plotted against the directional index measured with drifting grating stimuli. Fig. 9B shows that for a half-squared operator, the prediction from counterphase stimuli underestimates the directional index, in a manner very similar to the experimental results.

Reid et al. (1991) and Tolhurst and Dean (1991) reported two additional results by comparing counterphase and drifting grating responses. First, the linear prediction from counterphase gratings underestimates responses to gratings drifting in the anti-preferred direction. Second, the linear prediction correctly estimates responses to gratings drifting in the preferred direction. In other words, the nonlinear behavior of cells is manifested primarily as suppression of the anti-preferred response, rather than as enhancement of the preferred response. Half-squaring alone does not explain these results.

However, the complete model (with both half-squaring and divisive normalization) can explain these results. Preliminary simulations suggest that including divisive normalization contributes to the discrepancy between responses to counterphase and drifting gratings, so as to suppress the anti-preferred response (Heeger, 1992b).

Although these preliminary simulation results are promising, some issues still need to be addressed. First, Tolhurst and Dean (1991) found some cells for which the linear prediction was particularly bad. For these cells, the ellipse axis ratio was very small (e.g. 0.05) but the directional index was very large (e.g. 0.95). It is not clear that this extreme mismatch can be explained by divisive normalization. In addition, Reid et al. (1991) found that the ellipse axis ratio underestimates the directional index even when the polar plots were well fit by ellipses (that were not wasp-waisted). According to the model, on the other hand, the wasp-waist and the directional-index mismatch are both due to half-squaring. Hence the two effects should go hand in hand.

Complex cell responses

The model of complex cells advocated in this paper is based on energy mechanisms that are constructed by averaging the outputs from four half-squared linear operators. This section briefly reviews experimental data on complex cell responses and compares them with simulations of the energy model. As in the

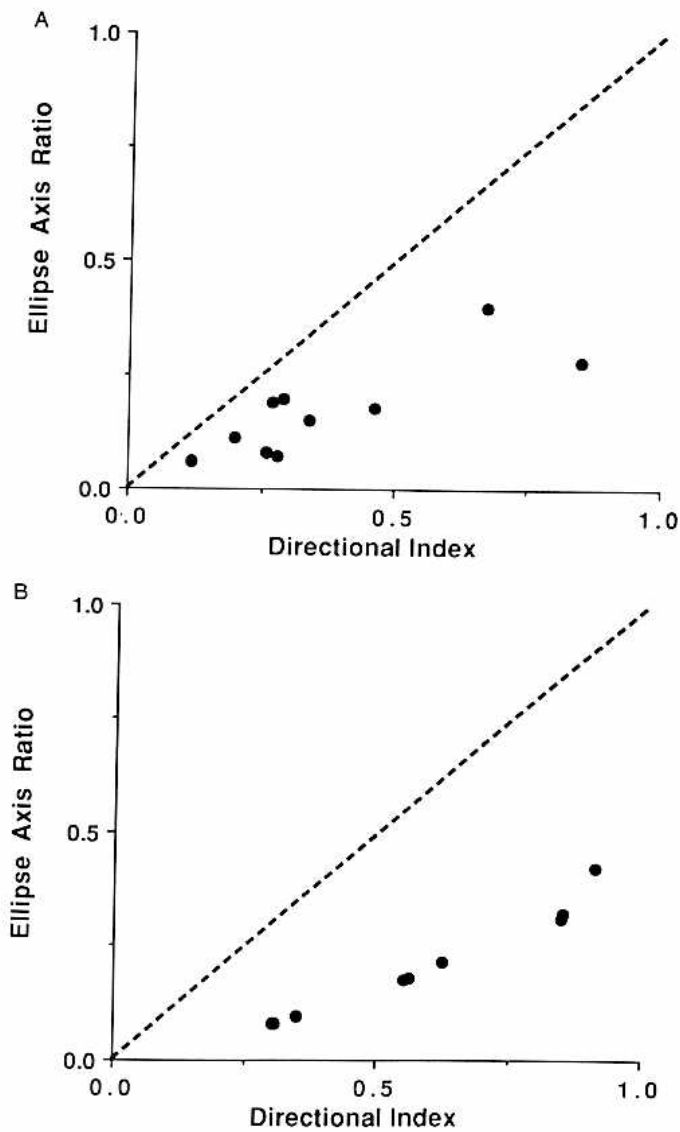


Fig. 9. Directional index predicted from counterphase grating stimuli vs. that measured directly from drifting gratings. **A:** Data for a direction-selective simple cell (replotted from Reid et al., 1987). Each point is for a different stimulus spatial and temporal frequency. The dotted line is the linear prediction. **B:** Simulation results for a half-squared spatiotemporal operator. For both model cells and real cells, the directional index predicted from counterphase stimuli underestimates that measured with drifting gratings.

previous section, divisive normalization is largely ignored in these simulations.

Quadrature phase

Energy mechanisms are constructed by averaging the outputs from four half-squared linear operators, with phases in 90 deg steps. Although simple cell weighting functions are not necessarily even or odd phase (Field & Tolhurst, 1986; Heggelund, 1986; Jones & Palmer, 1987a), there is evidence for pairs of cells in quadrature phase.

A quadrature-phase relationship can be established by comparing responses to drifting gratings. Two linear operators are

in quadrature phase only if they have identical receptive-field sizes and centers, identical amplitude responses, and response phases offset by 90 deg for all test gratings (all spatial and temporal frequencies).

Pollen and Ronner (1981) used drifting grating stimuli while recording simultaneously (with a single microelectrode placement) from pairs of nearby simple cells. By cross correlating the response waveforms, they found cell pairs with nearly the same receptive-field size, center, and orientation preference. In each case, they found that the response waveforms were offset by a quarter cycle. Foster et al. (1983) and Palmer and Davis (1981) subsequently found some additional cell pairs with responses that were offset by a half cycle (180 deg phase), also required by the model.

However, Pollen and Ronner (1981) did not compare the response amplitudes and phases for *all* test gratings. Rather, they compared responses only for stimuli that shared the cell's preferred orientation and motion direction. The cells may be offset by 90 deg for the tested stimuli, but not for all others. It would be worthwhile repeating these experiments using gratings of all spatial and temporal frequencies, drifting in both the preferred and anti-preferred directions.

Although the idealized energy model depends on having quadrature pairs of linear inputs, energy mechanisms might be approximated by summing a large number of operators with randomly distributed phases. The implementation of such a model is an interesting topic for future research, but it is beyond the scope of this paper.

Responses to pairs of impulses

Complex cells are clearly nonlinear as they respond to either a bright or a dim stimulus placed anywhere within their receptive fields. In experiments performed by Movshon et al. (1978b) (see also Rybicki et al., 1972), a bar fixed in one position was flashed simultaneously with a second bar, of the same or opposite polarity, that could appear in one of several positions around the location of the fixed bar. By measuring the influence of the second bar upon the response to the first, Movshon et al. were able to demonstrate that complex cell receptive fields are composed of subunits. The subunits have clearly defined spatial profiles with excitatory and inhibitory subregions. Movshon et al. hypothesized that the subunit outputs are rectified before being combined into the complex cell response. Later studies by Heggelund (1981b), Baker and Cynader (1986), Ohzawa and Freeman (1986b), Emerson et al. (1987), and Szulborski and Palmer (1990, 1991) provide further evidence for the existence of subunits.

The energy model is consistent with these results. The subunits of model complex cells are linear operators. The linear operators are half-squared and summed to give the energy mechanism outputs.

Citron and Emerson (1983) and Emerson et al. (1987, 1989, 1992a,b) analyzed responses of complex cells to white noise stimuli. Like the simple cell results discussed above (Two-bar interactions), the response of a complex cell to a pair of bars is different from the sum of the responses to each individual bar. Emerson et al. (1987) analyzed their data for a number of conditions, each corresponding to a different spatial and temporal offset between the pair of bars. Cell responses were greater than the linear prediction in about half of the conditions, and they

were less than the linear prediction in the other half (similar to Fig. 5B). Emerson et al. (1992a) showed that energy mechanisms behave similarly. Emerson et al. (1989, 1992b) used a three-stage (linear/nonlinear/linear) cascade model to fit the cell response data. They found that the second (nonlinear) stage is well described by squaring.

Watson (personal communication) and I have both done simulations using variants of the energy model in which squaring was replaced by other nonlinearities. If the input linear operators are halfwave-rectified (instead of half-squared), then the response to a pair of bars is always less than or equal to the sum of the individual responses (as in Fig. 5A). If the input linear operators are either half-squared or over-rectified, then the simulation results are similar to Fig. 5B. The latter is consistent with the experimental data (Emerson et al., 1987, 1992).

Responses to gratings

Movshon et al. (1978b) and Szulborski and Palmer (1991) measured complex cell responses to grating stimuli. They determined that the inverse Fourier transform of the response to gratings matches the spatial profile of the underlying subunits (up to a scale factor and with an appropriate choice of phase). This is also explained by the energy model. The "amplitude response" (response to gratings) of an energy mechanism is identical to the "amplitude responses" of its underlying half-squared linear operators. Thus, the inverse transform of the energy mechanism's response to gratings approximately matches the spatial profile of its subunits (see *Impulses vs. gratings*).

A variety of other grating experiments also indicate that energy mechanisms are reasonable models of complex cells. First, an energy mechanism exhibits unmodulated responses to drifting grating stimuli, as do the majority of complex cells (Maffei & Fiorentini, 1973; Ikeda & Wright, 1975a; Movshon et al., 1978b). Second, both complex cells and energy mechanisms exhibit responses to counterphase gratings that vary over time at twice the temporal frequency of the stimulus (Movshon et al., 1978b). Third, responses to counterphase gratings do not depend on the spatial phase of the stimulus (Maffei & Fiorentini, 1973; Movshon et al., 1978b). Fourth, both complex cells and energy mechanisms show a robust modulation to the difference frequency of compound gratings (Pollen et al., 1988).

However, the energy model is not completely consistent with all of the experimental results. Some complex cells give modulated responses for some drifting gratings, depending on the stimulus spatiotemporal frequency (Pollen et al., 1978; Movshon et al., 1978b; Glezer, 1980; Holub & Morton-Gibson, 1981; Kulikowski et al., 1981; Kulikowski & Bishop, 1982). It is possible that these cells are imperfectly constructed energy mechanisms. A nonlinearity other than half-squaring (e.g. halfwave-rectification) would predict modulated responses (Pollen & Ronner, 1983).

In addition, Spitzer and Hochstein (1985a,b) found that complex cells do not always give a frequency-doubled response to counterphase gratings, depending on the stimulus spatial frequency. They explain their results with a model, like the energy model, that combines inputs from two linear subunits. Unlike the energy model, however, they use halfwave-rectification instead of half-squaring, and the linear subunits are not in quadrature.

Responses to binocular stimuli

Freeman and Ohzawa (1990) have recently published a review of experiments that measured the manner by which striate cells combine inputs from the two eyes (see also Ohzawa & Freeman, 1986a,b; Ohzawa et al., 1990). Consistent with the view advocated in this paper, Freeman and Ohzawa explain their data (at least qualitatively) by modeling simple cells as binocular, rectified, linear operators and by modeling complex cells as disparity selective energy mechanisms.

Summary

For some years, simple cells have been characterized as halfwave-rectified linear operators, and complex cells have been characterized as energy mechanisms. A variety of experimental results provide evidence in support of the linear/energy model, but a variety of other experimental results cannot be explained by that model.

This paper and the companion paper (Heeger, 1992a) suggest two modifications to the linear/energy model. One modification is the use of half-squaring instead of halfwave-rectification at the output of the model simple cells. The other modification is to include a divisive normalization nonlinearity.

The companion paper (Heeger, 1992a) concentrates on the divisive normalization stage of the model. That paper is a review of experimental results on response saturation, contrast adaptation, and nonspecific suppression. None of those results are consistent with the linear/energy model, but nearly all of them are consistent with the new model.

This paper reviews a variety of other experimental results, and concentrates on the underlying linear stage of the model, and on the rectification stage of the model. The simulation results in this paper provide indirect evidence that supports the underlying linearity hypothesis. In addition, there is ample evidence to reject halfwave-rectification in favor of either over-rectification or half-squaring. A summary of the results leading to these conclusions follows.

Linearity of simple cell responses

The model advocated in this paper is based on spatiotemporal linear operators that compute a linear sum of the stimulus intensities. Although a variety of experimental results are consistent with the linear hypothesis, most of them are rather weak tests of this hypothesis.

For example, a number of researchers tested linearity of simple cells by comparing responses to gratings with responses to impulses (see *Impulses vs. gratings*). Unfortunately, the space- and frequency-domain measurements were compared only up to a scale factor. If the experiments were done without this arbitrary rescaling factor, then it would be a much more powerful test of the model. Unfortunately, it would be quite difficult to do this experiment without the scale factor, due to cortical contrast gain control.

There is, however, a simple way to test for the underlying linearity of simple cells, independent of rectification and independent of divisive suppression. Consider stimuli made up of two spots (or bars) at fixed positions that are both modulated sinusoidally over time. Both spots have the same temporal fre-

quency, but the amplitude and phase of modulation may be different. For a spatiotemporal linear operator, one can always choose the relative amplitude and phase of modulation, regardless of the positions of the two spots, to null the output. This is also true for a normalized, rectified linear operator. It is surprising that this experiment has not yet been done.

Half-squaring vs. halfwave-rectification in simple cell responses

Assuming that there is a linear stage underlying simple cell responses, the following experimental results provide evidence to reject halfwave-rectification in favor of half-squaring:

- A number of researchers (see *Impulses vs. gratings*) tested linearity of simple cells by comparing responses to gratings with responses to impulses. In many cases, the inverse transform of the response to gratings gives a weighting function with additional side bands beyond those measured directly. In addition, the measured response to gratings is often more narrowly tuned for spatial frequency than predicted from the Fourier transform of the response to impulses. These results are predicted by half-squaring (Fig. 3), but not by halfwave-rectification.
- Pollen et al. (1988) measured responses to compound gratings (see *Responses to compound gratings*). Half-squaring explains the data better than halfwave-rectification (Fig. 7).
- Several physiologists (Movshon et al., 1978a; Reid et al., 1987; Tolhurst & Dean, 1991) measured responses of simple cells while varying the spatial phase of counterphase gratings (see *Responses to counterphase gratings*). They found that polar plots of response amplitude vs. response phase are shaped like wasp-waisted ellipses. The wasp-waisted plot is predicted by half-squaring (Fig. 8), but not by halfwave-rectification.
- By comparing the responses to counterphase gratings with responses to drifting gratings, Reid et al. (1987, 1991), Tolhurst and Dean (1991), and Albrecht and Geisler (1991) demonstrated that there is a nonlinear contribution to simple cell responses (see *Counterphase vs. drifting gratings*). Half-squaring predicts a similar mismatch between the responses to counterphase and drifting gratings (Fig. 9).
- Emerson and Citron (1989), Emerson et al. (1989) and Mancini et al. (1990) used a three-stage (linear/nonlinear/linear) cascade model to fit simple cell responses to white noise stimuli. They found that the second (nonlinear) stage is well described by half-squaring.

There are two experimental results that favor halfwave-rectification over half-squaring:

1. Ganz and Felder (1984) analyzed responses of simple cells to stimuli made up of pairs of bars flashed in sequence. They found that cell response to a pair of bars is always less than the sum of the responses to each individual bar. This result is consistent with halfwave-rectification (Fig. 5A), not half-squaring.

2. The majority of experimental results indicate a systematic mismatch between space- and frequency-domain measurements (see *Impulses vs. gratings*). Jones et al. (1987), however, did not find a systematic effect. For some cells the frequency bandwidths were greater than expected based on space-domain data. For other cells the bandwidths were less than expected. The usual mismatch between space- and frequency-domain measurements might be an artifact of the experimental technique. The frequency-domain measurements typically make use of large stimuli and take advantage of spatial summation to bring out the influence of the weaker side lobes. This tends to make the tuning curves appear narrower than would be predicted from impulse responses.

The majority of data, thus, favors half-squaring over halfwave-rectification.

Half-squaring vs. over-rectification

The physiological results reviewed in this paper do not distinguish between half-squaring and over-rectification. Both half-squaring and over-rectification are consistent with much of the data. This is not surprising since the two nonlinearities are approximately the same (at least over a restricted operating range).

Half-squaring and over-rectification are particularly similar given saturation/normalization of cell responses. In the new model (with divisive normalization), cell responses are parameterized by a threshold, a gain, and an exponent (see Heeger, 1992a, for details). Varying the threshold and gain parameters simultaneously can look very much like a change in the exponent. For appropriate choices of the gain and threshold parameters, over-rectification (with an exponent of 1) closely approximates squaring.

Squaring is important in the new model for several reasons. First, ideal energy mechanisms require squaring to give truly phase-independent responses. Second, the underlying linear operators in the model tile the spatiotemporal-frequency domain; that is, that the sum of their *squared* responses gives the total Fourier energy of the stimulus. Third, given that the model complex cells outputs are squared, the model simple cell outputs must also be squared (half-squared) for the feedback normalization to work properly (see Heeger, 1992a, for details).

However, it is difficult to imagine how squaring could be implemented by neurons. Indeed, it is difficult to imagine how the brain could exponentiate responses to any power other than 1. One hypothesis is that the exponent is fixed at 1, and that the threshold and gain are set so as to approximate squaring (see Suarez & Koch, 1989, for a similar suggestion).

Squaring in complex cell responses

Complex cell receptive fields are composed of subunits (see *Complex cell responses*). A popular view is that the subunits are linear and that their outputs are rectified before being combined into the complex cell response. According to the energy model, the linear subunit outputs are squared and then summed. Assuming that there are linear operators underlying complex cell responses, the following experiments provide evidence in favor of the squaring hypothesis:

- Citron and Emerson (1983) and Emerson et al. (1987, 1989, 1992a,b) analyzed responses of complex cells to white noise stimuli. Their results are consistent with squaring in the energy model.
- Complex cells typically exhibit unmodulated responses to drifting grating stimuli (see Complex cell responses for references), a result that is consistent with squaring in the energy model.
- Complex cell responses to counterphase gratings do not depend on the spatial phase of the stimulus (see Complex cell responses for references), a result that is consistent with squaring in the energy model.

There is, however, some evidence against the squaring hypothesis. Some complex cells give modulated responses for some drifting gratings, depending on the stimulus spatial frequency. In addition, complex cells do not always give a frequency-doubled response for some counterphase gratings, again depending on the stimulus spatial frequency (see Complex cell responses for references). It is possible that complex cells are imperfectly constructed energy mechanisms; e.g. that the linear subunits are over-rectified (not half-squared) and that the threshold and gain are set so as to approximate squaring.

Selectivity of striate cell responses

There are a variety of experimental results that reveal nonlinearities in simple cell responses. Based on these results, some have rejected the hypothesis that a cell's selectivity is due to an underlying (spatiotemporal and binocular) linear operator.

To the contrary, results reported in this and other papers (Heeger, 1992a,b) support the linear model of selectivity. According to the model advocated in these papers, a cell's selectivity is attributed to an underlying (spatiotemporal and binocular) linear stage. Additive excitation and subtractive inhibition both contribute to selectivity. Nonlinearities in a cell's response are attributed to half-squaring and normalization.

This new model explains both the linear and nonlinear components of cell responses, thereby (1) attempting to reconcile the controversy regarding the origin of selectivity of simple and complex cells, and (2) attempting to reconcile the controversy regarding the role of intracortical suppression in striate cortex.

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