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Contrast normalization and a linear model for the directional selectivity of simple cells in cat striate cortex

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Abstract

Previous tests of the linearity of spatiotemporal summation in cat simple cells have compared the responses to moving sinusoidal gratings and to gratings whose contrast was modulated sinusoidally in time. In particular, since a moving grating can be expressed as a sum of modulated gratings, the response to a moving grating should be predictable (assuming linearity) from the responses to modulated gratings. However, these simple linear predictions have shown varying degrees of failure (e.g. Reid et al., 1987, 1991), depending on the directional selectivity of the neurons (Tolhurst & Dean, 1991). We demonstrate here that the failures of these linear predictions are, in fact, explained by the contrast-normalization model of Heeger (1993). We concentrate on the ratio of the measured to predicted moving grating responses. In the context of the contrast-normalization model, calculating this ratio turns out to be particularly appropriate, since the ratio is independent of the precise details of the linear front-end mechanisms ultimately responsible for directional selectivity. Hence, the contrast-normalization model can be compared quantitatively with this ratio measure, by varying only one free parameter. When account is taken both of the expansive output nonlinearity and of contrast normalization, the directional selectivity of simple cells seems to be dependent only on linear spatiotemporal filtering.

Keywords: Visual cortex, Simple cells, Directional selectivity, Contrast normalization

Introduction

Hubel and Wiesel (1959), in their pioneering study of simple cells in the cat's visual cortex, discovered one of the most prominent properties of these neurons: their directional selectivity. Most simple cells respond better to movement of a spatial stimulus in one direction through their receptive fields than to movement at the same speed in the opposite direction. The mechanism underlying directional selectivity has not yet been resolved, and there is debate as to whether it can be explained fully with a linear model or whether one also needs to invoke some nonlinear (probably inhibitory) neuronal interactions.

In that pioneering paper, Hubel and Wiesel (1959) speculated on the mechanism of directional selectivity. They proposed that the preferred direction for motion could be predicted in some instances from the asymmetrical spatial geometry of the ON and OFF regions within the receptive field. The neuron would respond best to a bright stimulus when it moved in the direction from the major OFF region of the receptive field into the major ON region, since the OFF response (caused as the stimulus left the OFF region) would coincide in time with the ON response (caused as the stimulus entered the ON region). This model of directional selectivity has many hidden assumptions about the spatiotemporal structure of the neuron's receptive field, but it is essentially a linear model; it is a forerunner of the linear model presently under debate (Reid et al., 1987, 1991; Albrecht & Geisler, 1991; Heeger, 1991, 1992, 1993; Tolhurst & Dean, 1991; DeAngelis et al., 1993*b*; Jagadeesh et al., 1993).

Hubel and Wiesel's model was soon criticized (Barlow & Levick, 1965; Pettigrew et al., 1968) on the grounds that it seemed to predict that the preferred direction for motion would reverse if the stimulus contrast polarity were changed from bright to dark, a simple prediction that was not borne out experimentally in most cases (Pettigrew et al., 1968; Goodwin et al., 1975; Emerson & Gerstein, 1977). Thus, the model was discarded and, with it, any consideration of more appropriate or exact linear models. Instead, a variety of essentially nonlinear models were proposed, following Barlow and Levick's (1965) work on rabbit retina. Most of these models supposed that a stimulus moving in the nonpreferred direction would provoke nonlinear (perhaps divisive) inhibition of the neuron's responses (Goodwin et al., 1975; Emerson & Gerstein, 1977; Sillito, 1977; Dean et al., 1980; Ganz & Felder, 1984).

Linear models of directional selectivity

A series of more recent theoretical papers has shown that it is possible to devise linear models in which the preferred direction

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does *not* reverse when the polarity of stimulus contrast is reversed; the observations of Barlow and Levick (1965) and Pettigrew et al. (1968) do *not* rule out all linear models. It was pointed out by Watson and Ahumada (1983, 1985) that useful directionally selective motion detectors *can* be constructed from purely linear mechanisms, confirming a point made by Fahle and Poggio (1981). Other models for directional selectivity have been proposed that are based upon linear mechanisms (Adelson & Bergen, 1985; Burr et al., 1986), while the Elaborated Reichardt Detectors of van Santen and Sperling (1985), although inherently nonlinear, are related.

The original criticism of linear models of directional selectivity assumed that the receptive fields of simple cells are space–time separable. Successful linear models, on the other hand, require that the receptive fields are space–time inseparable; that is, a neuron's temporal properties should be different at different spatial locations within the receptive field. Indeed, it has been found that the response time courses depend on where a stimulus is placed within the receptive field (Movshon et al., 1978; Dean & Tolhurst, 1986; McLean & Palmer, 1989; Reid et al., 1991; DeAngelis et al., 1993*a*; McLean et al., 1994).

The question then arises whether the spatiotemporal inseparability demonstrated experimentally for real simple cells could underlie their directional selectivity. If so, simple-cell directional selectivity would be dependent upon linear mechanisms after all.

This question was addressed by Reid et al. (1987, 1991), who measured the responses of simple cells to sinusoidal gratings moving in the preferred and nonpreferred directions. They compared these responses with those to stationary sinusoidal gratings of various spatial phases, whose contrast was modulated sinusoidally. A linear model of directional selectivity that relies on spatiotemporal inseparability would predict particular relationships [eqns. (2)–(4) in Appendix] among (1) the amplitudes of response in the two directions of motion, (2) the amplitudes of response to stationary gratings in the worst and best spatial phases, and (3) the directional index (a measure of the degree of directional selectivity). The predictions of the linear model were partially validated and Reid et al. concluded, therefore, that simple-cell directional selectivity is partially dependent on linear processes. The partial success of the linear predictions has been confirmed in other laboratories for both sinusoidal grating stimuli (Albrecht & Geisler, 1991; Tolhurst & Dean, 1991; DeAngelis et al., 1993*b*) and bar stimuli (McLean et al., 1994).

In general, the simple linear model correctly predicts the preferred direction (Reid et al., 1987, 1991) and even the optimal velocity (McLean & Palmer, 1989; McLean et al., 1994). However, the predicted value of the directional index is a significant underestimate of the measured one, and the amplitudes of the responses to moving gratings are poorly predicted from a knowledge of the amplitudes of the responses to stationary modulated gratings and *vice versa*. This partial success has led to the curious proposal that a linear mechanism for directional selectivity is augmented by a synergistic nonlinear mechanism, probably based upon inhibition in the nonpreferred direction (Reid et al., 1987, 1991; Tolhurst & Dean, 1991; McLean et al., 1994).

Effects of simple-cell output nonlinearities

While much of the behavior of simple cells can be modeled, to a first approximation, on the hypothesis that they sum their inputs linearly (Movshon et al., 1978), it is also obvious that the neurons' final response output (expressed as trains of action potentials) is *not* directly proportional to that linear sum. The output nonlinearity has been described either as a hard threshold at low contrasts followed by response saturation at high contrasts (Maffei & Fiorentini, 1973; Ikeda & Wright, 1974; Tolhurst et al., 1981; Tolhurst & Dean, 1987) or as an expansive nonlinearity at low contrasts (a soft threshold) leading sigmoidally [see eqn. (1)] to saturation at high contrasts (Albrecht & Hamilton, 1982; Heeger, 1991, 1992).

The tests for the linearity of directional selectivity employed by Reid et al. (1987, 1991) rely on the simple arithmetic manipulation of response amplitudes measured in units of action potentials per second. If these measured response amplitudes have been distorted by an output nonlinearity, then the simple arithmetic is almost certain to lead to the wrong answer. The calculations have to be performed, if possible, on the underlying supposedly linear responses. Indeed, there are numerous examples (starting with Movshon et al., 1978) where apparent deviation from linear summation seems to be resolved by supposing only that there is an output nonlinearity (see Heeger, 1992; Tolhurst & Heeger, 1997, for a variety of examples).

Jagadeesh et al. (1993) made intracellular recordings from simple cells and were able to record both the underlying continuous membrane potential fluctuations and the more usual trains of action potentials. As in previous extracellular recording studies, the linear model only partially succeeded when comparing the firing rate responses to moving and modulated gratings. However, the linear model succeeded quite satisfactorily when comparing the membrane potential fluctuations. While the underlying response (membrane potential fluctuation) does seem to behave linearly, the process of action potential generation leads to an output nonlinearity that confounds the otherwise simple predictions of a linear model of directional selectivity.

Heeger (1991, 1993) has shown theoretically that failure to take into account a sigmoidal output nonlinearity [eqn. (1) of Appendix] would, indeed, lead to the kinds of mismatch between linear prediction and actual measurement seen in the studies of Reid et al. (1987, 1991) and others. And Albrecht and Geisler (1991) and DeAngelis et al. (1993*b*) found very good agreement between measured and predicted directional index once the expansive output nonlinearity of the simple cell had been taken into account.

Thus, for many simple cells, the linear model based on spatiotemporal inseparability does seem to be able to explain the preferred direction of motion, the optimal speed, and the directional index (based on a *ratio* of response amplitudes), once the sigmoidal output nonlinearity has been taken into account. However, it is not clear yet whether the output nonlinearity is also capable of explaining the large discrepancies between the measured and predicted *amplitudes* of the responses to moving gratings found by Reid et al. (1987, 1991) and Tolhurst and Dean (1991). Heeger (1993) has shown qualitatively that the discrepancies may be attributable not only to the sigmoidal output nonlinearities, but also to contrast normalization where a neuron's output is rescaled with respect to the total contrast energy of a stimulus. In this paper, we will show quantitatively that this is indeed the case for the experimental data first published by Tolhurst and Dean (1991).

Methods

The details of the experimental procedures are given by Tolhurst and Dean (1991), where the data were first reported. Simple cells were recorded extracellularly from the *area centralis* representation of area 17 of adult cats using tungsten-in-glass microelectrodes. The cells were classified after Hubel and Wiesel (1959) using the quantitative criteria discussed by Dean and Tolhurst (1983). The cats were anesthetized by i.v. infusion of barbiturates, supple-

mented by ventilation with nitrous oxide. The animals were also paralyzed by i.v. infusion of gallamine triethiodide to prevent eye movements. The state of anesthesia was assessed by monitoring heart rate and the EEG.

Sinusoidal gratings of the optimal spatial frequency and orientation were presented on a bright monochrome raster display, and a computer compiled peri-stimulus time histograms (PSTH) of the action potentials generated in response. A particular stimulus was presented for only a few seconds or temporal cycles at a time, interleaved at random with short presentations of the other stimuli in the experiment. These short epochs were repeated several times, so that the final PSTH might represent the summed response to 50–200 temporal cycles. In an experiment, the responses were collected for 11 stimuli. One stimulus had zero contrast so that the neuron's spontaneous activity could be assessed. The remaining 10 stimuli all had the same Michelson contrast, which was usually between 0.25 and 0.7. Responses were measured to gratings that moved in the neuron's preferred direction and in its nonpreferred direction; the responses to stationary gratings whose contrast was sinusoidally modulated in time were measured at eight spatial phases. The temporal frequency of modulation or movement was usually 2 Hz.

The metric of response was usually the amplitude of the Fourier component in the PSTH whose frequency was the same as the temporal modulation frequency of the stimulus. Response is expressed as impulses per second (ips).

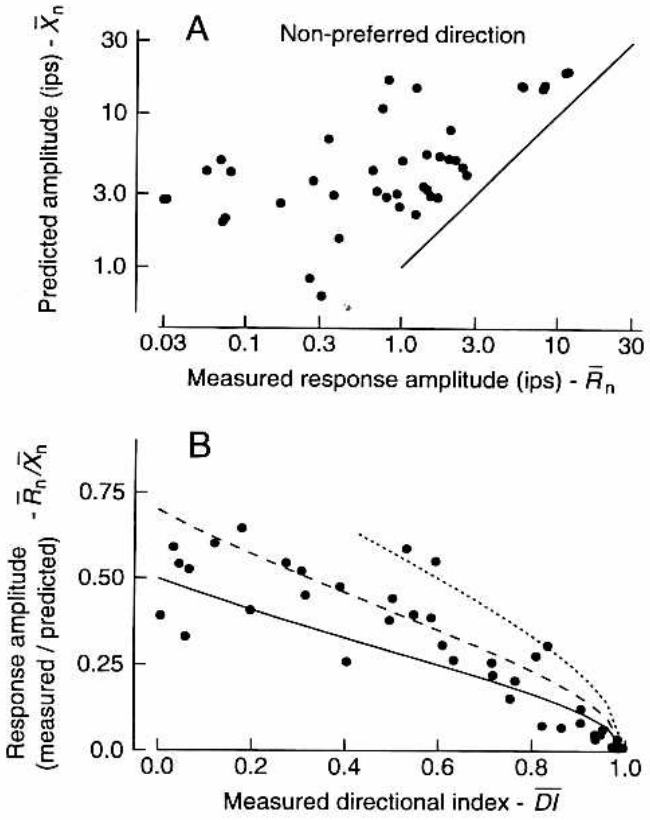

Fig. 1. A: For 41 simple cells recorded extracellularly in cat striate cortex, the predicted amplitude of the response to gratings moving in the nonpreferred direction ($\bar{X}_n$) is plotted on the ordinate against the experimentally measured response ($\bar{R}_n$), abscissa. The prediction is made from the responses to stationary modulated gratings in the best spatial phase ($\bar{R}_1$) and worst spatial phase ($\bar{R}_2$), assuming a simple linear model [eqn. (4b)]. The diagonal line shows where the data should have fallen if the measured and predicted responses were the same. B: For responses in the nonpreferred direction, the ratio measured/predicted response amplitude ($\bar{R}_n/\bar{X}_n$) is plotted against the measured directional index ($\overline{DI}$). The continuous curves are various solutions to the normalization model [eqn. (14)] for different values of the parameter s, which can take on values between 0.5 and 1 (solid line, $s = 0.5$; dashed line, $s = 0.7$; dotted line, $s = 1.0$). The data are replotted from Tolhurst and Dean (1991, their Fig. 4), who give full experimental details.

Results

Response in the nonpreferred direction

If a simple cell behaved linearly, the amplitudes of its responses to gratings moving in the nonpreferred direction would be predictable [eqn. (4) of Appendix] from the responses to stationary modulated gratings presented in the best and worst spatial phases. Fig. 1A shows how the measured amplitude of response to movement in the nonpreferred direction compares with that predicted from the responses to modulated gratings, for 41 simple cells recorded by Tolhurst and Dean (1991). It is quite clear that the simple linear model of spatiotemporal summation greatly overestimates the response in the nonpreferred direction. This observation led Tolhurst and Dean (1991) to propose that the major mechanism underlying directional selectivity must be nonlinear inhibition by movement in the nonpreferred direction.

However, it has been shown by Heeger (1993) that his contrast normalization model of simple-cell responses would predict just such a discrepancy. According to the normalization model, simple-cell responses are based on an underlying linear stage. The linear responses are then halfwave-rectified, squared, and normalized. In the normalization stage, each neuron's response to a stimulus is divided by a quantity proportional to the pooled activity of a large number of other neurons. Thus, the response of each neuron is no longer dependent solely on the contrast of stimulus components that it prefers; rather, the response is normalized or rescaled with respect to the *total* contrast or energy within the stimulus. In this model, the linear stage is responsible for directional selectivity. Unlike some proposals (cited in the Introduction) in which directional selectivity is attributed to nonlinear inhibition in the nonpreferred direction, the nonlinear inhibitory stage in the normalization model is not specific to any particular direction of movement.

One consequence of such normalization is that the otherwise-linear neuron will be subjected to a sigmoidal output nonlinearity [eqn. (1)]. This nonlinearity will contribute *per se* to the discrepancy between measurement and prediction in Fig. 1A, just as it does to the prediction and measurement of the directional index (see Introduction). But there is an additional consequence of normalization. The responses to moving gratings and to stationary modulated gratings are affected differently by normalization (see Appendix). The moving and modulated gratings have the same Michelson contrast, but different *time-averaged* contrast or energy. The moving grating is present continuously, but sinusoidal modulation causes the time-averaged energy to be halved. The resulting differences in the normalization signal [compare eqn. (1) with eqn. (20)] will also contribute to the discrepancy between measurement and prediction in Fig. 1A.

In the Appendix, we extend Heeger's (1993) analysis, and we show [eqn. (14)] that the linear predictions of response amplitude will fail to different degrees, depending upon the directional selectivity of the neuron and upon the stimulus contrast. Fig. 1B shows that the degree of failure of the linear model does indeed vary systematically with the neuron's directional index. The continuous curves show the behavior of the normalization model un-

der different conditions. The solid curve in Fig. 1B is the lower bound on the model's behavior; it corresponds to a situation in which the stimulus contrast is much greater than the semisaturation contrast [the contrast that evokes half the maximal response, σ in Eqn. (1)]. The dotted curve is the upper bound, when stimulus contrast is much less than the semisaturation contrast.

For neurons with little or no directional selectivity ($\overline{DI} \approx 0$), the measured response is only about half of that predicted on the simple linear model; this is exactly the discrepancy expected to result from contrast normalization for the high contrasts at which we generally performed our experiments. The failure of the linear model becomes worse as the neurons become more directionally selective until, for highly directionally selective neurons ($\overline{DI} \approx 1.0$), the measured response amplitude is only a small percentage of that predicted by the simple linear model. Again, this is just the behavior expected to result from contrast normalization. However, we should note that some of the data lie outside of the allowable bounds, especially for neurons that are highly directionally selective (see Discussion).

Response in the preferred direction

Fig. 2A compares the measured responses in the preferred direction of movement with the predictions of the simple linear model [eqn. (3b)] for the 41 simple cells of Tolhurst and Dean (1991). Although the measured and predicted responses seem quite similar on average, this is deceptive; the normalization model expects that the response in the preferred direction will sometimes be overestimated and sometimes underestimated, depending upon stimulus conditions (Heeger, 1993). In the Appendix [eqn. (18)], we show that the preferred direction responses should depend in a particular way on stimulus contrast and on the neuron's directional index.

Fig. 2B shows the degree of failure of the simple linear model plotted against directional index. The curves show the behavior of the normalization model under different conditions. The solid curve is the lower bound (stimulus contrast much higher than the semisaturation constant) and the dotted curve is the upper bound (low-contrast stimuli). The normalization model expects and the data show that, for neurons with little or no directional selectivity ($\overline{DI} \approx 0$), the measured response amplitude is only about half that predicted on the linear model. For highly directionally selective neurons ($\overline{DI} \approx 1.0$), the measured response amplitude is between one and two times that predicted, as expected by the normalization model. Again, we should note that some of the data do lie outside of the allowable bounds of the normalization model.

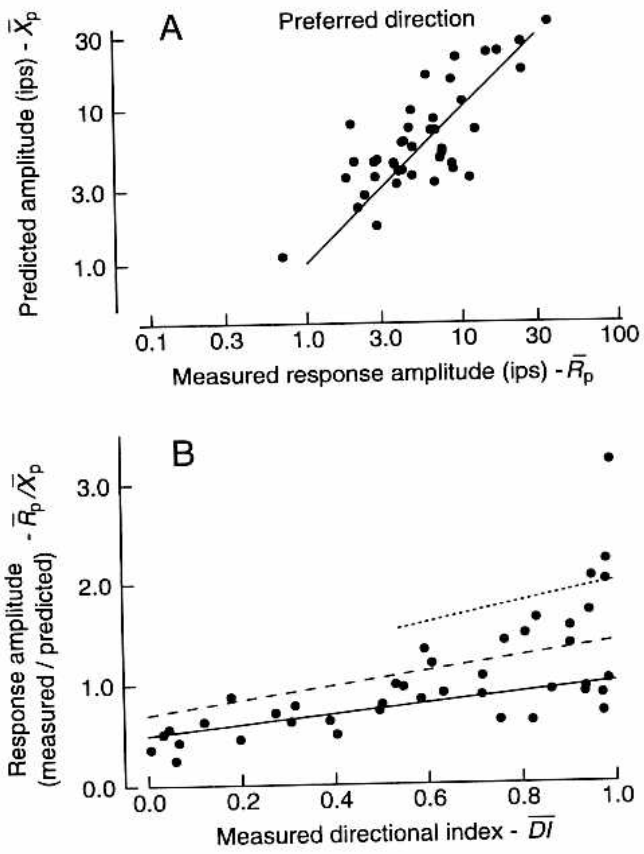

Fig. 2. A: For 41 simple cells, the predicted amplitude of the response to gratings moving in the preferred direction ($\bar{X}_p$) is plotted on the ordinate against the experimentally measured response ($\bar{R}_p$). The prediction is made on a simple linear model [eqn. (3b)]. The diagonal line shows where the data should have fallen if the measured and predicted responses were the same. B: For responses in the preferred direction, the ratio measured/predicted response amplitude ($\bar{R}_p/\bar{X}_p$) is plotted against the measured directional index ($\overline{DI}$). The continuous curves are various solutions to the normalization model [eqn. (18)] for different values of the parameter s, which can take on values between 0.5 and 1 (solid line, $s = 0.5$; dashed line, $s = 0.7$; dotted line, $s = 1.0$).

Discussion

Reid et al. (1987, 1991) and Tolhurst and Dean (1991) tested the proposition that simple-cell directional selectivity arises from linear mechanisms. They investigated the relationship between the responses to moving and modulated sinusoidal gratings. If directional selectivity were the result only of linear processes, then these responses should be related by rather simple equations [eqns. (2)–(4)]. In particular, if simple cell responses were due to linear processes then responses to modulated gratings could be used to predict: (1) the neuron's directional index, (2) the responses to gratings moving in the nonpreferred direction, and (3) the responses to gratings moving in the preferred direction.

In fact, these simple linear predictions were only partially fulfilled. However, this failure need not be due to a failure of linear spatiotemporal summation, as was first proposed. Rather, the linear predictions might well have failed because of a nonlinear output stage after the initial linear summation stage. Indeed, the first failure (the discrepancy between measured and predicted directional indices) can be explained by an expansive or squaring output nonlinearity (Albrecht & Geisler, 1991; Heeger, 1991, 1993; DeAngelis et al., 1993*b*; Emerson & Huang, 1996). Other forms of expansive nonlinearities (e.g. the hard threshold adopted by Tolhurst and Dean, 1991) might also be capable of explaining this result.

However, an expansive nonlinearity by itself cannot explain the other two failures, the discrepancies between the measurements and the linear predictions of the preferred and nonpreferred responses. We have now shown that the full contrast-normalization model (Heeger, 1991, 1992, 1993) would expect just such failures of the simple linear model.

The contrast-normalization model includes two nonlinear steps. First, the underlying linear responses are halfwave-rectified and squared. Second, the responses are normalized, divided by a quantity proportional to the total contrast energy in the stimulus. Although the moving and modulated gratings under comparison have the same nominal contrast, the time-averaged contrast energy is not the same in the two cases. The energy is lower for modulated gratings (since they are not present continuously), so that there is

less contrast normalization and higher overt responses. Since the directional index is computed as a *ratio* of preferred and nonpreferred responses, only the first (squaring) nonlinearity is involved in the failure of the linear predictions of the directional index (see Heeger, 1993). For the case of gratings moving in the nonpreferred direction, the two nonlinearities (squaring and normalizing division) in the normalization model work together, so that the predictions of the simple linear model become quite bad. On the other hand, the two nonlinearities tend to cancel when predicting responses in the preferred direction.

In this paper, we have concentrated on the ratio of the measured to predicted moving grating responses. By plotting this ratio as a function of directional index, Tolhurst and Dean (1991) found that the degree of mismatch between linear prediction and measurement was correlated with directional index (see Figs. 1B and 2B). In the context of the contrast-normalization model, calculating this ratio turns out to be particularly appropriate, since the ratio is independent of the precise details of the linear front-end mechanisms ultimately responsible for directional selectivity [see Appendix, eqns. (14) and (18)]. Hence, the contrast-normalization model can be quantitatively compared with this ratio measure, by varying only one parameter (the contrast-related scaling factor, s).

We believe that the normalization depends upon the *time-averaged energy* of the stimuli (Appendix; and Heeger, 1993). The validity of our present conclusions depends on this assertion, which should be amenable to direct test in neurophysiological experiments. We *must* be able to demonstrate that modulated gratings (which are present discontinuously) have less of a normalizing effect than do moving gratings (which are present continuously).

We have shown that, for many simple cells, their behavior falls within the bounds allowed by the normalization model. We suspect that the contrasts used in the experiments were probably high compared to σ, and so we would expect the data in Figs. 1B and 2B to lie closer to the theoretical lines for $s = 0.5$ and $s = 0.7$ than for $s = 1.0$. This does seem to be the case for the population of neurons as a whole. For 11 of the neurons, we were able to estimate σ (and thence s) from direct measurements of the relation between response amplitude and contrast, and in most cases, the detailed predictions of eqns. (14) and (18) *were* borne out. However, the results for three of these neurons (two of which were strongly direction selective) did not fit the predictions satisfactorily. Furthermore, for some other simple cells, the data of Figs. 1B and 2B lie outside the bounds allowed by the normalization model, especially for neurons with directional index close to unity. Although our model has not been fully successful in these cases, it may be that a small modification to the model might be sufficient to resolve the remaining discrepancy. In particular, Albrecht and Geisler (1991) argue that the exponent in the sigmoidal output function [eqn. (1)] can be higher than the value of 2 that we have allowed (see also Tolhurst & Heeger, 1997).

Finally, the behavior of some simple cells appears to be inconsistent with the linear model in a manner that cannot be explained by an output nonlinearity. Some simple cells exhibit pronounced directional selectivity even though their receptive fields seem to be spatiotemporally *separable* (Tolhurst & Dean, 1991; Emerson & Citron, 1992; McLean et al., 1994). For some other simple cells, there are pronounced asymmetries in the amplitudes and phases of the responses to modulated gratings (Emerson & Huang, 1996; Tolhurst & Heeger, 1997). Furthermore, the waveforms of the membrane potential fluctuations in response to sinusoidal modulation are sometimes distinctly not sinusoidal (Jagadeesh et al., 1993). These observations have led to the proposal that some neurons derive their directional selectivity from the nonlinear combination of two linear subunits (Kontsevich, 1995; Emerson, 1996; Emerson & Huang, 1996). The underlying subunits may be spatiotemporally *inseparable*, even in an overtly separable simple cell (Emerson & Citron, 1992), an idea that is reminiscent of the strictly linear model of Watson and Ahumada (1983, 1985).

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Appendix

Output nonlinearities

Consider a simple cell that sums its inputs linearly to give an *underlying* response (R) that is directly proportional to stimulus contrast, c. The underlying response is converted to an *overt* response ($\overline{R}$) that is subject to one or more output nonlinearities. We define the following (after Heeger, 1993):

	Underlying R	Overt $\overline{R}$
(a) *Moving gratings*		
Response in preferred direction	R_p	$\overline{R}_p$
Response in nonpreferred direction	R_n	$\overline{R}_n$
(b) *Stationary modulated gratings*		
Response in best spatial phase	R_1	$\overline{R}_1$
Response in worst spatial phase	R_2	$\overline{R}_2$
(c) *Directional index*	DI	$\overline{DI}$

The overt response ($\overline{R}$) depends upon the linear underlying response (R) according to Heeger's (1992, 1993) half-squaring and contrast-normalization relationship. This can be written in different ways and, when considering steadily moving gratings all of the same spatiotemporal frequency, it can be simplified as

$$\overline{R} = K\frac{R^2}{\sigma^2 + c^2} \tag{1}$$

where K and σ (the semisaturation contrast) are constants for the particular neuron. Since contrast (c) is also constant in the experiment under consideration, this can be rewritten as

$$\overline{R} = K'R^2 \tag{1a}$$

where K' is a new constant.

Since the neuron sums its inputs linearly, the *underlying responses* to moving and modulated gratings will obey the following relationships (Reid et al., 1987, 1991):

$$DI = \frac{R_p - R_n}{R_p + R_n} = \frac{R_2}{R_1} \tag{2}$$

$$R_p = R_1 + R_2 \tag{3}$$

$$R_n = R_1 - R_2 \tag{4}$$

However, because of the output nonlinearity, analogous attempts to predict the *overt* values $\overline{DI}$, $\overline{R}_p$, and $\overline{R}_n$ from the overt measurements $\overline{R}_1$ and $\overline{R}_2$ will fail (Heeger, 1993):

$$\overline{DI} = \frac{\overline{R}_p - \overline{R}_n}{\overline{R}_p + \overline{R}_n} \geq \frac{\overline{R}_1}{\overline{R}_2} \tag{2a}$$

$$\overline{R}_p \neq \overline{R}_1 + \overline{R}_2 \tag{3a}$$

$$\overline{R}_n \leq \overline{R}_1 - \overline{R}_2 \tag{4a}$$

Tolhurst and Dean (1991) calculated $\overline{X}_p$ and $\overline{X}_n$, predictions of $\overline{R}_p$ and $\overline{R}_n$ on the false assumption that linear rules *would* apply to the overt responses:

$$\overline{X}_p = \overline{R}_1 + \overline{R}_2 \tag{3b}$$

$$\overline{X}_n = \overline{R}_1 - \overline{R}_2 \tag{4b}$$

They then plotted the ratio $\overline{R}/\overline{X}$ (measured/"predicted" overt response) against $\overline{DI}$, and the results are reproduced in our Figs. 1 and 2.

Now, because of the output nonlinearity of half-squaring and contrast normalization [eqn. (1a)],

$$\overline{R}_p = K' \cdot R_p^2 \tag{5}$$

$$\overline{R}_n = K' \cdot R_n^2 \tag{6}$$

$$\overline{R}_1 = K' \cdot R_1^2/s \tag{7}$$

$$\overline{R}_2 = K' \cdot R_2^2/s \tag{8}$$

where s is a contrast-dependent scaling factor with a value between 0.5 and 1.0 (see below) that is imposed by contrast normalization. Although the moving and modulated gratings have the same nominal contrast, the *time-averaged* contrast is not the same in the two cases. The time-averaged contrast is lower for the modulated gratings, so that there will be less contrast normalization and higher overt responses (by the factor s).

The prediction ($\overline{X}_n$) of the response in the nonpreferred direction ($\overline{R}_n$)

If we substitute for $\overline{R}_1$ and $\overline{R}_2$ [eqns. (7) and (8)] in eqn. (4b), the definition of $\overline{X}_n$ in terms of the linear underlying responses become

$$\overline{X}_n = K' \cdot \frac{R_1^2}{s} - K' \cdot \frac{R_2^2}{s} \tag{9}$$

After substituting for $\overline{X}_n$ [eqn. (9)] and $\overline{R}_n$ [eqn. (6)], the ratio $\overline{R}_n/\overline{X}_n$ is given by

$$\frac{\overline{R}_n}{\overline{X}_n} = \frac{s \cdot R_n^2}{R_1^2 - R_2^2} \tag{10}$$

This factorizes very neatly

$$\frac{\overline{R}_n}{\overline{X}_n} = \frac{s \cdot R_n^2}{(R_1 - R_2)(R_1 + R_2)} \tag{11}$$

Looking to the definitions for R_p and R_n [eqns. (3) and (4)] and for $\overline{R}_p$ and $\overline{R}_n$ [eqns. (5) and (6)], we get

$$\frac{\overline{R}_n}{\overline{X}_n} = \frac{s \cdot R_n^2}{R_n \cdot R_p} = \frac{s \cdot R_n}{R_p} = s\sqrt{\frac{\overline{R}_n}{\overline{R}_p}} \tag{12}$$

Rearrangement of eqn. (2a) shows that

$$\frac{\overline{R}_n}{\overline{R}_p} = \frac{1 - \overline{DI}}{1 + \overline{DI}} \tag{13}$$

so that eqn. (12) becomes

$$\frac{\overline{R}_n}{\overline{X}_n} = s\sqrt{\frac{1 - \overline{DI}}{1 + \overline{DI}}} \tag{14}$$

Thus, the ratio between measured and predicted response in the non-preferred direction should depend upon s and upon the measured directional index. Fig. 1B shows this theoretical relationship for comparison with real experimental data.

The prediction ($\overline{X}_p$) of the response in the preferred direction ($\overline{R}_p$)

Now, if we substitute for $\overline{R}_1$ and $\overline{R}_2$ [eqns. (7) and (8)] into eqn. (3b), the definition of $\overline{X}_p$ in terms of the linear underlying responses becomes

$$\overline{X}_p = K' \cdot \frac{R_1^2}{s} + K' \cdot \frac{R_2^2}{s} \tag{15}$$

After substituting for $\overline{X}_p$ [eqn. (15)] and $\overline{R}_p$ [eqn. (5)], the ratio $\overline{R}_p/\overline{X}_p$ is given by

$$\frac{\overline{R}_p}{\overline{X}_p} = \frac{s \cdot R_p^2}{R_1^2 + R_2^2} \tag{16}$$

This does not factorize neatly, but we can substitute for R_1 and R_2 (obtained from rearranging eqns. (3) and (4) and, after simplification

$$\frac{\overline{R}_p}{\overline{X}_p} = \frac{2s \cdot R_p^2}{R_p^2 + R_n^2} = \frac{2s \cdot \overline{R}_p}{\overline{R}_p + \overline{R}_n} \tag{17}$$

Using eqn. (2a), this can be reduced to

$$\frac{\overline{R}_p}{\overline{X}_p} = s(1 + \overline{DI}) \tag{18}$$

Thus, the ratio between measured and predicted response in the preferred direction should also depend upon s and upon the measured directional index. Fig. 2B shows this theoretical relationship along with real experimental data.

The scaling factor, s

The contrast term (c^2) in eqn. (1) represents the energy of the grating stimulus. Although the moving and modulated gratings have the same nominal contrast (c), their time-averaged energy will *not* be the same: the moving grating is present all of the time, while the modulated grating has contrast changing sinusoidally with time. The sinusoidally modulated grating has r.m.s. contrast of $c/\sqrt{2}$ and an energy, therefore, of $c^2/2$. Alternatively, we can say that a modulated grating of contrast c can be considered as the sum of two moving gratings, each with contrast $c/2$. The total energy of the modulated gratings is the sum of the energies of the two component moving gratings:

$$\text{Modulated energy} = \left(\frac{c}{2}\right)^2 + \left(\frac{c}{2}\right)^2 = \frac{c^2}{2} \tag{19}$$

Thus, if eqn. (1) describes the overt response for a moving grating of contrast c, the overt response for a modulated grating of the same contrast is

$$\overline{R} = K\frac{R^2}{\sigma^2 + (c^2/2)} \tag{20}$$

Comparison of eqns. (1) and (20) shows that the scaling factor (s) in eqns. (7) and (8) must be

$$s = \frac{\sigma^2 + (c^2/2)}{\sigma^2 + c^2} \tag{21}$$

For high contrast gratings ($c \gg \sigma$), the scaling factor s will be 0.5; but at low contrasts or for an insensitive neuron with high σ ($c \ll \sigma$), the scaling factor will be 1.0.