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The effects of contrast on the linearity of spatial summation of simple cells in the cat's striate cortex

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Summary. Non-linearities of spatial summation were examined in simple cells in the cat's striate cortex. The degree of non-linearity was assessed from an examination of the waveforms of the responses to moving sinusoidal gratings and was quantified by a measure called *relative modulation.* Relative modulation was affected little by changes in contrast at either optimal or non-optimal spatial frequencies. The non-linearities of spatial summation exhibited by some simple cells are, therefore, essential. Those simple cells which exhibit linear spatial summation are no less linear at high stimulus contrasts. These results support a 'push-pull' model of simple cell receptive field organization in which ON and OFF centre l.g.n. input is combined both additively and subtractively.

Key words: Visual cortex – Contrast – Spatial summation – Cat

Introduction

Hubel and Wiesel (1962) defined simple cells as those neurones in the cat's visual cortex for which the spatial configuration of the optimal visual stimulus could be predicted qualitatively from a map of the receptive field. The responses of simple cells to line, edge and grating stimuli have since been compared *quantitatively* (Movshon et al. 1978; Andrews and Pollen 1979; Maffei et al. 1979; Glezer et al. 1980; Kulikowski and Bishop 1981; Dean and Tolhurst 1983). The dimensions and relative responsiveness of the receptive field regions of simple cells can be predicted by performing a Fourier transform of the spatial frequency tuning curve (but see Field and Tolhurst 1986); this implies that the influences of light falling in different parts of the receptive field are summed linearly. In some simple cells, linear spatial summation has been demonstrated directly by examining the interaction between two line stimuli presented in different parts of the receptive field (Tolhurst and Dean 1987).

Nevertheless, application of the tests used by Enroth-Cugell and Robson (1966) to distinguish retinal X- and Y-cells shows that some simple cells do exhibit non-linearities of spatial summation which are evident in the responses to sinusoidal gratings (Movshon et al. 1978; Kulikowski and Bishop 1981; Dean and Tolhurst 1983). While most simple cells show pronounced modulation of response in time with the bars of a moving grating (Maffei and Fiorentini 1973; Ikeda and Wright 1975; De Valois and Tootel 1983), some simple cells give responses which are less modulated and which, at high spatial frequencies, consist largely of an unmodulated elevation of activity (Movshon et al. 1978). The responses to flashed lines also reveal the nonlinearity of spatial summation (Henry 1977; Movshon et al. 1978; Kulikowski and Bishop 1981; Palmer and Davis 1981; Dean and Tolhurst 1983; Heggelund 1986; Tolhurst and Dean 1987); between receptive field regions giving pure ON responses or pure OFF responses, there are transitional regions where ON/OFF (non-linear) responses are evoked.

Non-linearities of spatial summation might arise in a number of ways and it may be possible to distinguish between mechanisms by examining the way in which the non-linearities are influenced by stimulus contrast (see Shapley and Victor 1978, 1980). For instance, an *essential* non-linearity would be evident over the whole range of stimulus contrast, whereas a *non-essential* non-linearity would appear only at high contrasts. In this paper, we

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show that the non-linearities of spatial summation of simple cells are essential.

Methods

The preparation and the methods of recording, stimulus presentation and data collection have been described previously (Movshon et al. 1978; Dean 1981; Dean and Tolhurst 1983, 1986).

Adult cats were anaesthetized during surgery by i.v. injection of Althesin (Lilley); during recording they were anaesthetized by hyperventilating them with $N_2O:O_2:CO_2$ (75:23.5:1.5), supplemented by i.v. infusion of pentobarbitone sodium (0.5–1.5 $mg.kg^{-1}.hr^{-1}$). The level of anaesthesia was assessed as described by Dean and Tolhurst (1986). At the end of an experiment, the cat was killed with an overdose of barbiturate. Recording sites were shown histologically to be within the striate cortex.

Some definitions

Relative modulation. We have examined the responses of cortical simple cells to moving sinusoidal gratings of a variety of spatial frequencies and contrasts. We use a measure called relative modulation to assist in receptive field classification and to quantify the degree of non-linearity evident in the response waveforms (Movshon et al. 1978; Dean 1981; Dean and Tolhurst 1983). Relative modulation is calculated by performing a discrete Fourier transform of the response waveform, and then dividing the amplitude of the response component whose frequency is the same as the temporal frequency of the stimulus by the average level of activity (zero frequency component of response). Values can range from 0.0, when there is no modulation in the response, up to 2.0. Exact half-wave rectification yields a value of 1.57.

A simple cell. Hubel and Wiesel (1962) described two important features of simple cells that distinguish them from complex cells. First, simple cell receptive fields have discrete ON and OFF regions. Secondly, the dimensions of these regions allow a prediction of the spatial configuration of the neurone's optimal visual stimulus; the optimal width of bar should be the same as the width of the dominant region within the receptive field. In the present study, we have classified receptive fields according to quantitative indices of spatial summation (see Dean Tolhurst 1983).

Contrast. The contrast of a sinusoidal grating is:

$$\frac{L_{max}-L_{min}}{L_{max}+L_{min}}$$

where L is the luminance of a point on the display.

Results

We have determined the degree of non-linear spatial summation from the waveforms of the responses to moving sinusoidal gratings. Distortions in response waveform are quantified as *relative modulation* (see Methods). This is obviously indirect, but we have shown previously that there is a close association between relative modulation and direct measures of spatial summation (Tolhurst and Dean 1987).

The response of a linearly summating neurone to a moving sinusoidal grating should consist of a sinusoidal modulation of activity about the spontaneous level of activity. However, the majority of simple cells have little or no spontaneous activity. Thus, the *overt* response should appear as a rectified sine-wave. When the spontaneous level is exactly zero, the neurone should be silent for half of the stimulus cycle and the relative modulation should be close to 1.57. However, some simple cells behave as if they have a negative level of spontaneous activity (Movshon et al. 1978; Tolhurst and Dean 1987): the neurone will be overtly active for less than half the stimulus cycle and the relative modulation will exceed 1.57. Thus, values above about 1.5 are consistent with linear spatial summation (Tolhurst and Dean 1987). However, a relative modulation of less than 1.57 (overt activity for more than half the stimulus cycle) *must* indicate a non-linearity of summation, whenever the cell has no spontaneous activity.

Grating contrast and the response waveforms of simple cells

Figure 1A shows how two simple cells responded to moving gratings of near-optimal spatial frequency at a variety of contrasts. Following a threshold, the relation between response amplitude and contrast was roughly linear (Dean, 1981; Tolhurst et al. 1981; Albrecht and Hamilton 1982). Relative modulation (Fig. 1B) was affected little by changes in contrast or, for that matter, by large changes in response amplitude. Neither neurone had significant spontaneous activity; thus, if they had been responding truly linearly, the lowest relative modulation that could have been achieved would be 1.57 (*dashed line*), when the response waveforms would resemble half-wave rectified sine-waves. This was the case for one cell (*filled circles*); spatial summation did not become non-linear at high contrasts. The other cell (open circles) had consistently lower values than 1.57, over virtually the entire contrast range, thereby revealing an *essential* non-linearity of spatial summation.

Figure 2 confirms these results for a third cell; the values of relative modulation are the means of the estimates from 6 separate experiments. Standard errors are shown. As might be expected, these are largest at low contrasts when response amplitudes were small. However, it is still clear that relative modulation was consistently at a level of about 1.3 down to the lowest contrasts. The non-linearity of spatial summation was essential.

Slight increases in relative modulation at the lowest contrasts (evident in Fig. 1) can be explained by a 'negative' level of spontaneous activity

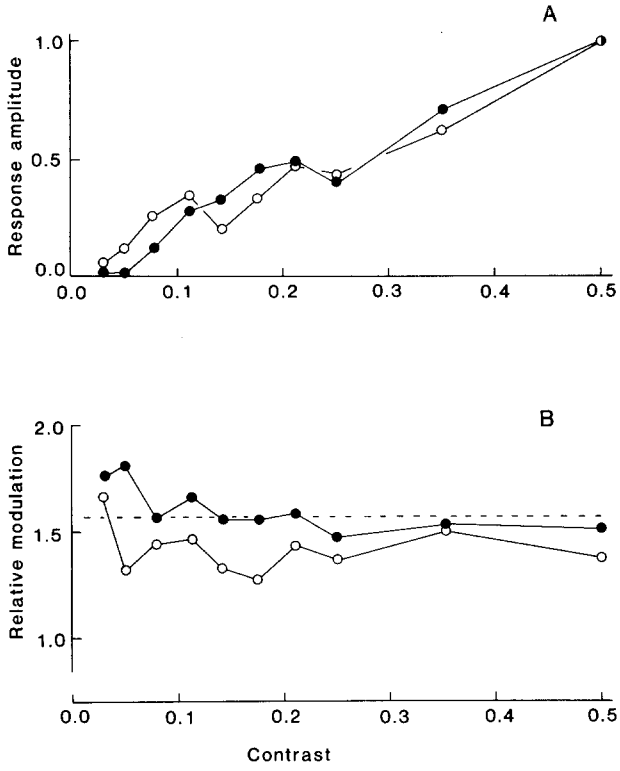

Fig. 1. **A** Response amplitude is plotted against grating contrast for two simple cells which had no spontaneous activity. The gratings were of near-optimal spatial frequency and orientation. Response amplitude (total activity in the presence of the grating) has been normalized to that at a contrast of 0.5. **B** For the same two cells, relative modulation is plotted against contrast. The dashed line shows a value of 1.57, the *lowest* value that could be achieved by a neurone which was responding linearly and which had no spontaneous activity

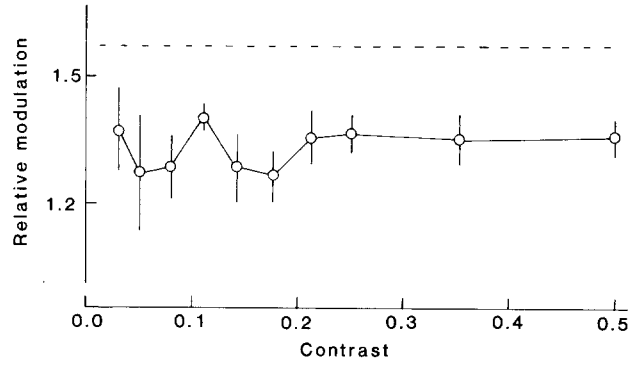

Fig. 2. For a third simple cell with no spontaneous activity, relative modulation is plotted against the contrast of a grating of near-optimal spatial frequency. The experiment was performed 6 times; the means and standard errors are shown. The dashed line shows a value of 1.57, the *lowest* value that could be achieved by a neurone which was responding linearly and which had no spontaneous activity

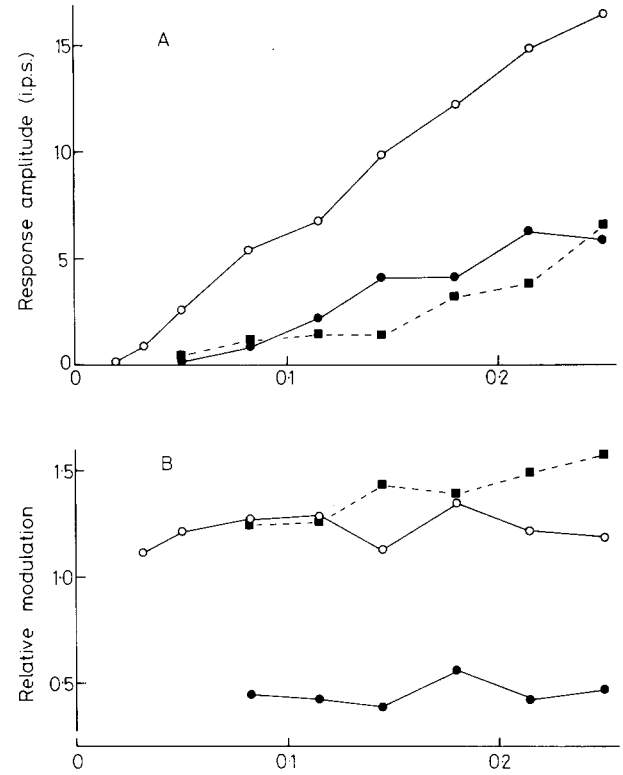

Fig. 3A, B. The amplitude of response (**A**) and the relative modulation (**B**) of a simple cell to gratings of three different spatial frequencies as a function of contrast. The open circles show the behaviour at near-optimal spatial frequency (0.67 c/deg); the filled circles show the behaviour at 1.33 c/deg; the filled squares at 0.33 c/deg

(Movshon et al. 1978; Tolhurst and Dean 1987); this would impose a threshold which must be exceeded before any *overt* response is elicited.

Figure 3 illustrates the dependence of response amplitude (A) and relative moduation (B) on contrast for both optimal (open circles) and non-optimal spatial frequencies for a single simple cell. The filled squares are for a frequency lower than the optimum, while the filled circles are for a frequency higher than the optimum. Relative modulation was highest at low spatial frequencies and was lowest at high frequencies (Movshon et al. 1978). At all three spatial frequencies, relative modulation was affected little by changes in contrast.

Figure 4 illustrates the behaviour of two relatively unusual simple cells: they had significant levels of spontaneous activity. As discussed above, if the neurones were responding linearly, the responses should have been sinusoidal modulations of activity about the spontaneous level, as is found in retinal X-cells (Enroth-Cugell and Robson 1966). At low contrasts, when the modulated response is small compared to the spontaneous level, relative modulation will also be small. As contrast is increased, the response waveform will 'hit bottom' (as the firing

rate cannot go negative) and relative modulation will increase, asymptoting to a value of 1.57 when the response waveform will resemble a half-wave rectified sine-wave. However, since response amplitude often saturates at high contrasts (Ikeda and Wright 1974; Dean 1981; Tolhurst et al. 1981; Albrecht and Hamilton 1982), one might anticipate that, for some cells, the relative modulation will never reach 1.57.

Figure 4A shows that both neurones behaved qualitatively as expected: relative modulation increased with contrast until it asymptoted at high contrasts. One of the neurones asymptoted close to the ideal of 1.57 (*dashed line*); the other asymptoted to a lower value. Whether the presence of spontaneous activity and of response saturation can account *quantitatively* for this behaviour was examined by computer simulation of the behaviour of a linear neurone. Response waveforms were calculated as:

$$R(t) = S + A.\sin(2\pi ft) \qquad \text{Eqn. 1}$$

where S is the spontaneous level, A is the amplitude of the modulation in the response and f is the temporal frequency of the stimulus. In order to simulate the rectification shown by real neurones, negative values of $R(t)$ were set to zero. The truncated waveforms were Fourier analyzed over one period of the temporal sine-wave in the same way as real data. Figure 4B plots, for the same two neurones, the relative modulation against response amplitude, which has been normalized by dividing by the spontaneous level of activity. Saturation of response amplitude is indicated by the bunching of data at high amplitudes. The continuous line shows the results of the computer simulation and is a reasonable description of the behaviour of one neurone (*open circles*) over the entire response range. However, relative modulation in the other neurone was consistently lower than that expected of underlying linear behaviour for normalized response amplitudes greater than 1. Clearly, these low values cannot be attributed only to spontaneous activity; there was also an essential non-linearity of spatial summation.

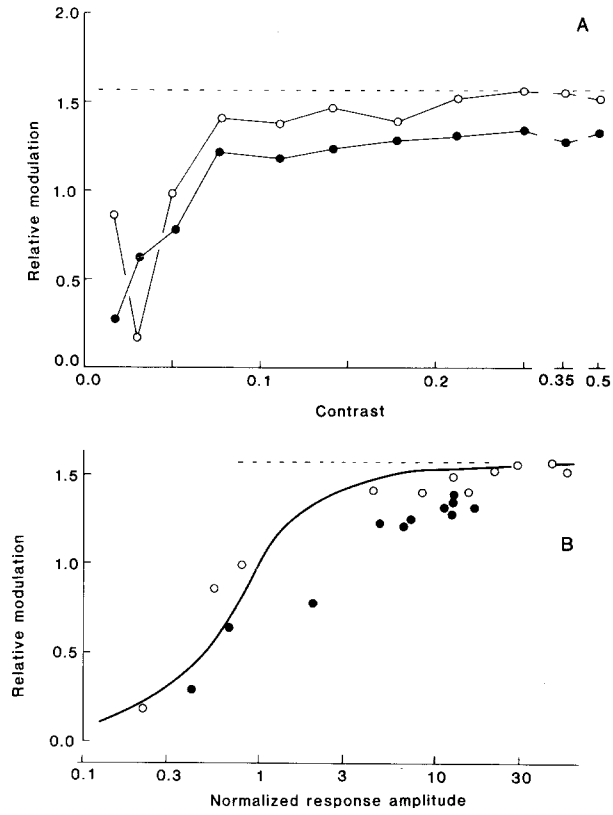

Fig. 4. **A** Relative modulation is plotted against the contrast of gratings of optimal spatial frequency and orientation for two simple cells which had spontaneous activity. The value of 1.57 (*dashed line*) is the *highest* value that could be achieved by a neurone which was responding linearly and which had spontaneous activity. **B** For the same two neurones, relative modulation is plotted against normalized response amplitude, defined as the amplitude of the modulated component of the response divided by the spontaneous level of activity. The dashed line again shows 1.57; the continuous curve is the behaviour expected of a neurone which responds linearly (see text)

Discussion

In this paper, we have examined how the linearity of spatial summation in simple cells is affected by stimulus contrast. We have used relative modulation as an index of non-linearity because it can be measured easily and accurately, and the values obtained correlate well with the results of a more formal assessment of the linearity or otherwise of spatial summation in simple cells (Tolhurst and Dean 1987).

The waveforms of the responses to moving sinusoidal gratings were relatively independent of the grating contrast. Any non-linearities revealed by the measure of relative modulation are essential. Those simple cells which showed low values of relative modulation indicative of non-linearities of spatial summation were as non-linear at low contrasts as they were at high. It is just as significant that simple cells with a high relative modulation (consistent with linear spatial summation) were as linear at high contrasts as they were at low. Both of these observations are inconsistent with one popular class of model of the organization of the simple cell receptive field: the simple cell is excited by a row of ON centre l.g.n cells to provide the ON region, and is excited by a row of OFF centre l.g.n cells to provide the

OFF region (e.g. Tanaka 1983). The problem arises from the surprising fact that the input to the cortex from the l.g.n. is mostly non-linear, even when derived from X-cells. While it is true that l.g.n. X-cells show linear spatial summation (Shapley and Hochstein 1975), their outputs are not a linear reflection of that linear sum: l.g.n. cells have only modest spontaneous activity so that their responses to moving sinusoidal gratings will be sinusoidal modulations about the spontaneous level only at low contrasts. At higher contrasts, the responses will 'hit bottom' and the responses will be partially rectified. This would suggest that a simple cell could show linear spatial summation only at very low contrasts; summation would appear to be progressively more non-linear as stimulus contrast was raised. This is not consistent with our data.

Figure 5 (A,B) illustrates the argument schematically for a simple cell that sums the activity of two neighbouring l.g.n. X-cells, one ON-centre and other OFF-centre; the responses are shown to low (A) and high (B) contrast stimulation. The stimulus is a moving sinusoidal grating of such a spatial frequency that the responses of the two l.g.n. cells differ in temporal phase by 90°. Other spatial frequencies would lead to other phase differences and the degree of non-linearity evident from the response waveforms would vary considerably, being least at 0° and greatest at 180°. A threshold must be introduced to the model to explain the simple cell's absence of spontaneous activity. The threshold may be generated after summation of the l.g.n. inputs (model 1) or there may be separate thresholds on each input (model 2).

Model 1. At very low contrasts, each l.g.n. cell will give a response which is a sinusoidal modulation about the spontaneous level of activity. The simple cell sums two true sinusoids and the sum will itself be a sinusoid; the response of the simple cell, after accounting for threshold behaviour, will be a half-wave rectified sine-wave (Fig. 5A). This response waveform, with relative modulation of 1.57 (indicated beside the histogram), is indicative of linear spatial summation. However, at moderate and high

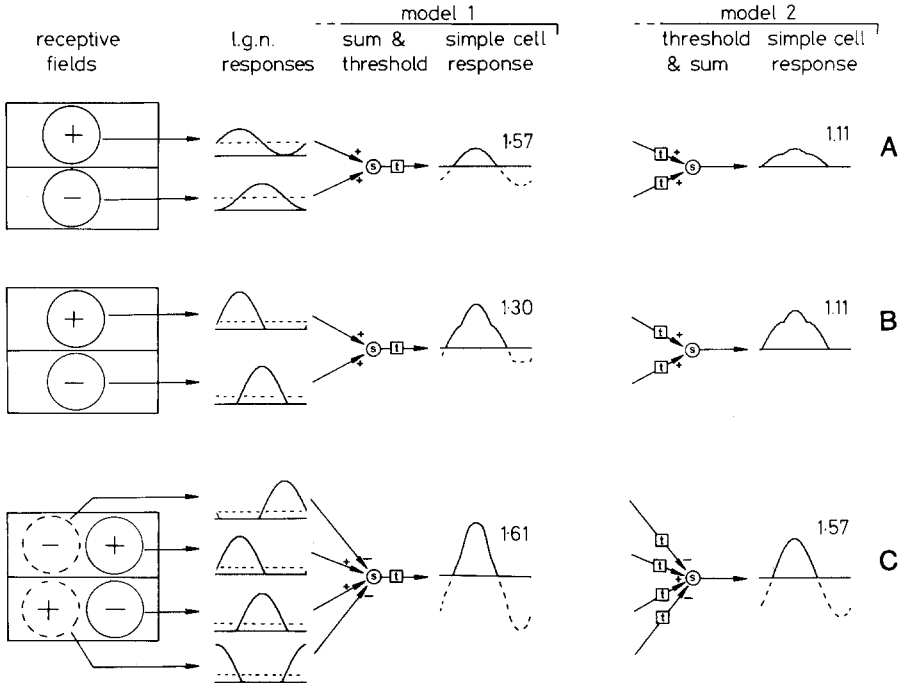

Fig. 5. A, B A model of a simple cell, responding preferentially to horizontal stimuli. On the left is the receptive field map: ON region above an OFF region. The circles within the field show the centres of the fields of two l.g.n. cells. The second column shows waveforms of the responses of these l.g.n. cells to a moving horizontal sinusoidal grating of such a spatial frequency that the responses differ in temporal phase by 90°. The dashed lines show the spontaneous level of activity. The responses are summed and then subjected to a threshold non-linearity (third column). The result, the overt response of the simple cell, is shown in the fourth column; the dashed lines show the sub-threshold response. The number beside the histogram shows the relative modulation of the simple cell's response. The fifth and sixth columns show an alternative model: the individual responses of the l.g.n. cells (column 2) are subject to a threshold before summation by the simple cell. **A** Low contrast grating; **B** moderate contrast. **C** The model is extended to include inhibitory connections. The dashed circles on the left show l.g.n. cells which inhibit the simple cell. Within one region of the simple cell field, the ON-centre and OFF-centre l.g.n. cells would have co-extensive receptive fields.

contrasts, the output non-linearities of the l.g.n. cells become evident. Their responses are no longer sinusoidal modulations about the spontaneous level; the responses have 'hit bottom'. The sum of the two rectified sinusoids will not be a sinusoid so that the simple cell's response will no longer be a half-wave rectified sine-wave (Fig. 5B). Thus, non-linear spatial summation is evident (low relative modulation) except at low contrasts. The predicted non-linearity is non-essential, which is inconsistent with our data.

Model 2. Each l.g.n. input may be subjected to a threshold (to delete the spontaneous level) before summation by the simple cell. This model predicts a greater degree of non-linearity, as evidenced by the lower values of relative modulation, and also that the non-linearity is independent of contrast. This more nearly mimics the essential non-linearity of real simple cells.

Model 2 may be able to explain the essential non-linearities of spatial summation shown by some simple cells. However, it fails in an important respect: it suggests that *all* simple cells will show non-linearities of spatial summation or, conversely, that no simple cell should exhibit linear summation. This is clearly incorrect. We have to turn to a model which was first considered by Hubel and Wiesel (1959) and which has been developed by Palmer and Davis (1981), Glezer et al. (1982) and Tolhurst and Dean (1987): the ON regions of the simple cell receptive field must be excited by ON-centre l.g.n cells and must also be inhibited (presumably via interneurones) by OFF-centre l.g.n. cells; the excitatory drive would *add* to the cell's firing rate while the inhibitory drive would *subtract* from it. The converse must be true of the OFF regions. This 'push-pull' arrangement would allow the simple cell to behave as if it linearly sums the influences of light from all parts of its receptive field, even though it is driven by non-linear rectified inputs. Figure 5C illustrates two versions of this model. For either version, the simple cell's response would be strictly linear at very low contrasts. At high contrasts, summation would be strictly linear only if each l.g.n. input were subject to a threshold before summation by the simple cell (model 2, Fig. 5C). If there were only one threshold point, after summation (model 1, Fig. 5C), the responses at high contrast would not be strictly linear, but the deviations from linearity would be small compared to those evidenced in Fig. 5A and B.

The model overcomes the non-linearity of rectification in the l.g.n. inputs, and it may be noted that it would remove any even-order non-linearities such as those which are characteristic of retinal and l.g.n. Y-cells. The proposed 'push-pull' antagonism of ON and OFF centre l.g.n. cells is reminiscent of retinal circuitry, where depolarizing and hyperpolarizing bipolar cells synapse antagonistically onto ganglion cells (McGuire et al. 1986). It may be that such synaptic arrangements are widespread.

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