Functional implications of cross-orientation inhibition of
cortical visual cells.

I. Neurophysiological evidence

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Simple and complex cells of striate cortex of anaesthetized and paralysed cats were stimulated with two superimposed one-dimensional grating stimuli of different orientations to investigate inhibitory effects of non-optimally oriented stimuli. We confirmed that a stimulus of orientation orthogonal to a cell's long axis significantly reduces the cell's discharge rate. Further experiments revealed the following. (i) The inhibition was typically stronger for simple than for complex cells. (ii) It is very broadly tuned for orientation, all orientations outside the cell's tuning band having a comparable inhibitory effect. (iii) Similarly, it is broadly tuned for spatial frequency. These last two results suggest that the inhibition arises not from a single cell but from a pool of cells. (iv) The pattern of the discharge of the inhibition in response to stimulation by phase-reversed sinusoidal gratings is consistent with the notion that the inhibition arises from complex cells. A second series of recordings of stimulation by visual noise patterns demonstrated how 'cross-orientation inhibition' prevents simple cells from responding to two-dimensional visual noise while allowing them to respond to comparable one-dimensional noise patterns. We suggest that this mechanism may serve to render simple cells selectively sensitive to one-dimensional stimuli, such as the contours or borders of visual objects.

Introduction

The classical finding of Hubel & Wiesel (1962), that cells of the striate visual cortex are selectively tuned for orientation, has generated much speculation about the role of these cells in the processing of visual information. There now exist many theories and computational models purporting to explain how the elongated receptive fields of the cortical cells serve to analyse the visual scene. Although the theories are widely diverse, they usually assume, following the original suggestion of Hubel & Wiesel, that the orientation selectivity of the cortical detector units derives from the spatial organization of the receptive fields of the lateral geniculate (l.g.n.) input: that is, that simple cortical cells receive a convergent excitatory input from several l.g.n. cells whose receptive fields are aligned so as to form a row, the direction of which establishes the orientation of the cell. However, Hubel & Wiesel

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(1962) also noted the possibility that inhibitory processes may be involved in the orientation selectivity, and indeed there is now considerable evidence that this is in fact the case, at least for simple cells (see, for example: Benevento et al. 1972; Blakemore & Tobin 1972; Bishop et al. 1973; Creutzfeldt et al. 1974a, b; Watkins & Berkley 1974; Sillito 1975; Tsumoto et al. 1979; Sillito et al. 1980; Burr et al. 1981).

In this study, we measure and characterize these inhibitory processes, and show how the inhibition creates a nonlinearity which severely restricts the cell's response to complex visual patterns. We go on to speculate on how orientation tuning generated by inhibition may serve in the analysis of visual scenes.

**Methods**

**Preparation**

We studied 56 simple and 43 complex cells, recorded from 19 adult cats. The first nine animals were operated on under halothane (2%) anaesthesia, halothane being replaced with althesin (1.5 ml/kg) for the later experiments. Surgery, which comprised insertion of an endotracheal tube, cannulation of a femoral or brachial vein, and removal of a small piece of skull and dura overlying area 17 (Horsly-Clarke p:1, 4), was generally completed within 30 min, whereupon the halothane (for the earlier experiments) was withdrawn and anaesthesia was maintained with forced ventilation of a humidified mixture of 70% N₂O and 30% O₂, at 29 strokes per minute with a stroke volume adjusted to maintain the end-tidal CO₂ within the range 3.8–4%. Anaesthesia was supplemented by periodic treatment of all wounds with a long-lasting local anaesthetic (xylocaine). Electroencephalogram, heart rate, end-tidal CO₂ and body temperature were continually monitored.

Eye movements were minimized by immobilizing the animal with a continuous intravenous infusion of Pancuronium. Both eyes were treated with atropine and phenylephrine to dilate the pupils and to retract the lids and nictitating membrane. Optically neutral contact lenses with 4 mm pupils were fitted to the eyes; refraction was corrected with additional lenses if necessary.

**Recording**

Action potentials were recorded from single units with glass micropipettes (tip diameter approximately 2 μm), advanced through the cortex by a micromanipulator driven by a stepping motor. The potentials were conventionally filtered, amplified and pulse-shaped, and monitored both by ear and by a Digital PDP-11/03 laboratory computer, which computed on-line response histograms.

On isolating a unit, we mapped its receptive field on a tangent screen, using stationary slits and spots. Simple/complex cell classification was based principally on whether the receptive field could be divided into separate excitatory and inhibitory zones (Hubel & Wiesel 1962; Gilbert 1977), but we also took account of spontaneous activity (Pettigrew et al. 1968) and the modulation pattern to drifting sinusoidal gratings. This latter method has been shown to reflect reliably the presence of separate antagonistic zones (Maffei & Fiorentini 1973; Movshon et al. 1978a, especially fig. 9), and has been described by many researchers as being
as reliable a method as any other in making the contentious simple/complex classification (see, for example: Schiller et al. 1976; Andrews & Pollen 1979). We made no attempt to subdivide the complex cells into the ‘standard’ and ‘special’ types of Palmer & Rosenquist (1974) and Gilbert (1977). Cells with either strong end inhibition (the hypercomplex cells of Hubel & Wiesel) or side flank inhibition (Maffei & Fiorentini 1976) were not studied.

**Figure 1.** Examples of the visual noise used in these experiments. The 1-D noise (right) was constructed from the 2-D noise (left) by smearing each dot vertically along the length of the display. The insets illustrate the power spectra of the patterns, obtained by optical means (see figure 2 for precise distribution). Note that, whereas the energy of the 1-D noise is contained principally along one orientation, that of the 2-D noise is distributed over 360°. However, the horizontal power spectra are identical.

After receptive field determination and cell classification, the grating and noise stimuli were oriented appropriately and positioned to cover the receptive field of the preferred eye, the other eye being occluded.

**Stimuli**

Three different stimuli were used in these experiments, two-dimensional (2-D) visual noise, one-dimensional (1-D) visual noise and sinusoidally modulated gratings. All stimuli had the same mean luminance of 5 cd/m².

Both the 2-D and 1-D noise (illustrated in figure 1) were generated by computer (PDP-11/10) and displayed on the screen of an oscilloscope (Tektronix 602) whose position, height and orientation could be readily varied. The 2-D noise comprised 800 dots randomly positioned, each briefly illuminated, produced by driving the X and Y inputs of the oscilloscope with the computer D/As, and the Z input with a 4 µs unblanking pulse. The pattern was caused to drift smoothly at any chosen velocity by incrementing the X coordinates of each dot every frame. Viewing
Figure 2. Luminance profiles, together with their Fourier transforms amplitude for the two noise patterns used in these experiments. The arrows indicate the mean luminance of each distribution. The luminance distributions were measured by projecting an image of the drifting pattern through a thin vertical slit onto a photometer (EG & G Model 450), which drove one of the computer A/Os. By masking down the size of the slit, the distribution was also obtained for the bottom half and quarter field. For the 1-D noise, which is homogeneous along its length, the three distributions are identical. However, for the 2-D noise, the contrast is considerably higher when the energy is being integrated for only a portion of the pattern. The purpose of these measurements is to show that if a cell receptive field is positioned so as to cover only a fraction of the screen, the contrast ($\sigma/\mu$) of the 2-D noise, integrated along the length of the receptive field, will be higher than that of the 1-D noise.
distance was typically 57 cm, so that the oscilloscope screen (10 cm x 10 cm) subtended 10° of visual angle, but this was sometimes varied in the experiments with 2-D noise.

The 1-D noise was constructed from the 2-D noise by replacing the Y computer drive with a triangle-wave raster (3 MHz), and the unblanking pulse with a direct-current voltage adjusted so that the luminous intensity was identical for the two stimuli. Thus, as the X input is left intact, and the intensity matched, the power spectra for the vertical integrals of the two stimuli were identical. We also confirmed the equality of the spectra by direct photometric measurements of the luminance distributions of the two patterns (see figure 2).

Sinusoidal gratings were displayed on the screen of another oscilloscope (HP1300A), also free to vary in position and orientation, by using the conventional television method of Schade (1956). The waveforms were generated by an analogue pattern generator, which also provided a synchronization pulse for the data acquisition computer (PDP-10/03) to allow histograms of response time to be synchronized to the passage of the grating bars.

The two oscilloscope screens were optically superimposed by a beam-splitting prism positioned directly in front of the cat's eye. A system of crossed polaroids in front of the two oscilloscopes and a rotatable polaroid in front of the cat's eye allowed the relative contrast of the two stimuli to be varied (following the square of the sine of the angle of rotation).

Contrast of noise is typically defined as the ratio of the standard deviation to the mean of its power spectrum ($\sigma/\mu$). Following this definition, the maximum contrast of our noise (as determined by local photometric measurement) was 0.31. Grating contrast is typically specified by the Michelson contrast, the ratio of the difference between the peak and trough luminances to their sum ($L_{\text{max}} - L_{\text{min}})/(L_{\text{max}} + L_{\text{min}}$). For convenience of comparison, we shall express noise contrast in terms of its 'equivalent Michelson contrast', calculated as being $\sqrt{6}\sigma/\mu$. (This constant is the inverse of $\sigma/\mu$ for a sine wave of Michelson contrast 1.)

**Results**

*Inhibition by grating stimuli*

We measured what may be termed *cross-orientation inhibition* of cortical cells with a relatively simple and direct technique. Cells were stimulated simultaneously by two stimuli whose orientation could be varied independently: a field of 1-D noise and a sinusoidal grating. Typically the noise was oriented at the cell's preferred orientation, to elicit a response from the cell (like the 'conditioning stimulus' of Bishop et al. 1973), and the grating was oriented at some non-optimal orientation, serving as the 'inhibiting stimulus'. The use of random noise together with sinusoidal gratings avoided phase problems. Both patterns were caused to drift continuously, the noise at the cell's preferred velocity, and the sinusoid at the same speed as the noise.

Figure 3 shows the basic inhibitory effect for representative simple and complex cells. When stimulated by drifting noise alone (superimposed on a homogeneous
field), both cells responded briskly. However, when the blank field is replaced by an orthogonally orientated grating of suitable spatial frequency and drift velocity, the response of both cells is drastically reduced. We observed this effect with every cortical cell that we examined. The magnitude of the inhibition varied somewhat from cell to cell, in general being more powerful for simple than for complex cells.

**Figure 3.** Example of cross-orientation inhibition for representative simple and complex cells. These two cells were from the same penetration, about 100 μm apart. Records (a) show the response to drifting 1-D visual noise (see figure 1) of optimal orientation (contrast 30%). Records (b) show the response to the same noise superimposed on an orthogonally oriented grating (spatial frequency 1 cycle/deg, temporal frequency 4 Hz and contrast 20%). Each histogram comprises 60 sums, bin width 19.5 ms, and is synchronized to the passage of the sinusoidal grating, extending over two grating cycles (shown on upper scale). Note that the magnitude of the inhibition is far stronger for the simple than for the complex cells, which is quite typical of the pattern of results. The resting discharge was 0 and 5 spikes per second for the simple and complex cells respectively.

**Optical artefacts?**

Although the average contrast of the noise is not affected by the superimposed grating, there will be local variation in contrast along the length of the noise, corresponding to the peaks and troughs of the grating. It may be argued that it is this local variation in contrast, not neural inhibition, that attenuates the response of the cell. To preclude this possibility, we replaced the drifting grating...
with a stationary grating reversed in phase every 1.3 s (square-wave counterphase of temporal frequency 0.38 Hz).

Figure 4 shows the response of a typical simple cell. The firing rate exhibits a short bout of depression only when the grating changes phase, otherwise being practically equal to that measured without the superimposed grating (depicted by the dotted line).

![Figure 4. Response of a representative simple cell to drifting, optimally oriented 1-D visual noise (contrast 25%), superimposed on an orthogonally oriented sinusoidal grating (spatial frequency 0.5 cycle/deg, contrast 20%) whose contrast was caused to reverse abruptly every 1.3 s. The broken line above the discharge record indicates the cell response to the noise alone. Note that the response is depressed below this level only when the grating changes phase, suggesting that it results from neural rather than optical factors. Sum 30. Bin width 26 ms.](image)

**Effect of contrast response function**

We next determined the effect of an orthogonal inhibiting stimulus on the contrast response function. For this experiment the grating was used as the conditioning stimulus (as its contrast could be varied conveniently) and noise, of two contrasts, was used to inhibit it.

Figure 5 summarizes the results. The three curves show the cell response as a function of stimulus contrast with no inhibiting stimulus (circles) and orthogonal noise at 18% contrast (triangles) and at 37% contrast (squares). The main effect of the inhibiting noise was to reduce the slope of the curve, suggesting that the action of the inhibition is *divisive*, rather than subtractive. Similar changes of slope have previously been observed for the contrast response functions of directionally selective simple cells in the presence of an inhibiting drifting grating (Dean et al. 1980), and for the orientation tuning curve of cortical cells on extracellular injection of γ-aminobutyric acid (GABA) (Rose 1977a), GABA being the putative inhibitory transmitter in the visual cortex (Iversen et al. 1971; Silito 1975).
Figure 5. Cross-orientation inhibition as a function of the contrast of the conditioning stimulus for a representative simple cell. The response (mean discharge) was elicited by a sinusoidal grating (spatial frequency 0.75 cycle/deg, velocity 2.7 deg/s, contrast 20%), and inhibited by orthogonally oriented noise of 0 (circular symbols), 18 (triangular symbols) and 37% (square symbols) contrast. Note that the effect of the inhibition is to reduce the slope of the curves, suggesting a division-like process.

Figure 6. Orientation tuning of intra-cortical inhibition for two representative simple cells, one uni- and one bidirectional. The response was elicited by a sinusoidal grating (spatial frequency 0.8 and 1.2 cycle/deg; velocity 2.8 and 1.5 deg/s; contrast 20%) and inhibited by 37% contrast 1-D visual noise, free to vary in orientation. The arrows indicate the response (mean discharge) to the grating alone, obtained by replacing the noise with a blank field. The insets show the orientation selectivity band of the cells, obtained by stimulating with the noise alone. Note that the inhibition arises over a wide range of orientations, being of comparable strength at all orientations outside the cells' selectivity bands.
Division-like processes have also been described in inhibitory synapses of moto-neurons (see, for example: Eccles 1964; Smith et al. 1967; see also Blomfield 1974).

**Orientation tuning**

The previous experiments all employed an inhibitory stimulus oriented orthogonally to that preferred by the cell. Here we employ a range of orientations.

A sinusoidal grating (of optimal orientation, spatial frequency and drift velocity) was used as the conditioning stimulus, and the noise, of variable orientation, as the inhibitory stimulus. This arrangement was chosen as, for reasons elaborated in the next section, the noise proved to be a more effective inhibitory stimulus than gratings of comparable contrast. We report results only for simple cells, as the complex cells that we examined showed an inhibition too small and a response variability too large for reliable tuning curves to be obtained.

Figure 6 shows the results for two simple cells, with insets showing each cell’s orientation tuning for excitation alone. For both cells, when the noise is orientated at or near the preferred orientation for the cell, that is within the cell’s orientation selectivity channel (depicted in the inset), it acts as a stimulant and raises the firing rate. However, as soon as the orientation is such that it ceases to be an effective stimulus, it begins to inhibit the cell. Although there were sometimes small variations in the strength of inhibition at different orientations (such as seen for the cell depicted on the right), in all the cells that we observed some inhibition could be evoked at all orientations outside the orientation selectivity channel of the cell. This result suggests that the inhibition arises not from a single cortical cell but from a pool of cells whose combined response encompasses all orientations to which the cell itself does not respond.

**Spatial frequency tuning**

Cortical cells are tuned not only for orientation but also for size (Hubel & Wiesel 1962). Size tuning is best described by spatial frequency response functions (Cooper & Robson 1968; Campbell et al. 1969). Here we measure the spatial frequency response curve of the inhibition.

Noise, oriented at the cell’s preferred orientation and caused to drift at the preferred velocity, provided the conditioning stimulus, and an orthogonally oriented sinusoidal grating served to inhibit it. The drift velocity was varied with spatial frequency so that the temporal frequency (the rate at which the bars pass a given point) was always 4 Hz, a suitable frequency (see Figure 8).

Figure 7 shows results for two simple cells, with the spatial frequency tuning shown on the left. The tuning curves are quite sharp, as typically observed in simple cells (Maffei & Fiorentini 1973; Movshon et al. 1978a). The inhibitory tuning curves, however, are far from sharp. Although there was some small variation of peak inhibition frequency from cell to cell, the inhibition tuning curves resemble more closely the spatial frequency transfer function of the entire visual cortex, as determined by recording mass action evoked potentials (Campbell et al. 1973), than they do the tuning curves of single cortical neurons.

Further evidence that the inhibition arises from cells tuned to a wide range of spatial frequencies is provided by the observation that a noise grating is a more
effective inhibitor than a sinusoidal grating of comparable contrast (that is, matched so that the grating is as effective a conditioning stimulus as the noise). Noise contains energy over a wide range of spatial frequencies (see power spectrum of figure 2), which presumably stimulates a larger pool of cells than the grating, which has energy at only one spatial frequency. Thus each simple cell is inhibited by many other cortical cells, tuned to a wide range of spatial frequencies as well as orientations.

Figure 7. Spatial frequency tuning of the inhibition for two simple cells. (a) The spatial frequency tuning curve of the two cells (mean discharge), obtained by stimulating with a sinusoidal grating (temporal frequency 2 Hz; contrast 30%) of varying spatial frequency. (b) The spatial tuning for the inhibition, obtained with a noise conditioning stimulus of 37% contrast, together with an orthogonally oriented grating (temporal frequency 4 Hz; contrast 30%) of variable spatial frequency. The arrows indicate the response to the conditioning noise alone. The inhibitory ‘tuning curves’ have nothing like the sharp bandpass characteristics of the excitation curves, suggesting that the inhibition arises from a wide range of spatial frequencies.

**Temporal frequency tuning**

As Hubel & Wiesel (1962) noted, cortical cells do not respond well to stationary stimuli, but require that they be moved, or at least flashed, to elicit a vigorous response. Cells vary somewhat in their temporal properties, but in general complex cells prefer higher drift speeds or flicker rates than simple cells (Pettigrew et al. 1969; Movshon 1975; our own observations; but see also Ikeda & Wright 1975). A convenient description of the temporal properties of cells is provided by their temporal frequency response function (Tolhurst & Movshon 1975; Movshon et al. 1978c). Here we measure the temporal frequency response function of the inhibition.

As in the previous experiment, the noise served as the conditioning stimulus, and an orthogonally oriented grating of appropriate spatial frequency as the inhibitory stimulus. Figure 8 reports the results. As for the spatial frequency
tuning, the temporal frequency tuning curves are rather broad. Note also that they extend into a rather high range of temporal frequencies, often above 15 Hz, a temporal frequency at which, in our experience, simple cells rarely respond. This is consistent with the suggestion that complex cells are involved in the inhibition process, which will be discussed in more detail later.

**Cross-orientation inhibition of visual cells**

![Figure 8. Temporal frequency tuning of the inhibition for two simple cells. The conditions were as for figure 7, except that the spatial frequency of the grating was fixed at the cells' preferred frequency (0.3 and 0.9 cycle/deg; contrast 25 %) and the temporal frequency was free to vary. The arrows indicate the cell discharge rate to the noise alone. Again these curves are quite broad, much broader than the typical temporal tuning curves for excitation. It is of interest that the inhibition extends into a quite high temporal frequency range (in one case 16 Hz), where simple cells rarely respond.]

**Patterning of cell discharge**

When stimulated by drifting or counterphased sinusoidal gratings, the discharge patterning of simple and complex cells exhibits certain distinguishing characteristics (Maffei & Fiorentini 1973; Movshon et al. 1978a, b). Typically, simple cells respond quasi-linearly to both drifting and counterphased gratings of appropriate spatial frequency, the discharge rate modulating in synchrony with the passage of grating bars (with 'half-wave rectification', as the response cannot go negative when the white grating bars fall on an 'off' zone or black bars on an 'on' zone). To counterphased gratings, the magnitude of the response varies with the spatial phase of the grating. Complex cells, however, show little modulation of their response to drifting gratings, but only an increase in firing rate. To counterphased gratings the discharge rate modulates, but to the second rather than the first harmonic of the stimulus ('full-wave rectification'), and is independent of the spatial phase of the grating. Thus, while simple cells are phase-sensitive, the response of complex cells depends only on the absolute power of the stimulus.

What then is the response patterning of the inhibition of simple and complex cortical cells? To drifting gratings, the firing rate neither of simple nor of complex cells shows any stimulus-synchronized modulation, but merely an overall depression (Figure 3). However, with counterphased gratings, the inhibition of both simple
Figure 9. Patterning of cell discharge in response to stimulation by phase-reversed sinusoidal gratings, for a typical simple and a typical complex cell. The cells were stimulated by a sinusoidal grating of optimal spatial frequency (0.75 cycle/deg for both cells), whose contrast was caused to modulate at 4 Hz (up to a peak of 30%). Each record is a stimulus-synchronized response histogram (60 sums; binwidth 12.5 ms), showing the response to two cycles of modulation. The sinusoids above the histograms indicate the variation in the contrast of the grating. Records (a) show the response of the cells to the grating alone, oriented at the cell’s preferred orientation. Records (b) show the response of the cells to combined stimulation by a noise conditioning stimulus and an orthogonally oriented counterphase grating. The dotted lines indicate average discharge to the noise alone. As had been previously demonstrated, on stimulation by a counterphased grating the simple cell modulated to the first harmonic of the stimulus, and the complex cell to the second harmonic. However, when the counterphased grating was used as the inhibition stimulus, the depression in discharge rate modulated with the second harmonic for both simple and complex cells. Note that the discharge modulation of records (b) is about 180° out of phase with the discharge of the complex cell of records (a), the peaks of the excitation corresponding to the troughs of the inhibition.

and complex cells modulates with the second harmonic of the stimulus (figure 9). Records (a) of figure 9 show two cycles of the stimulus-synchronized response histograms obtained with optimally oriented gratings counterphased at 4 Hz. In agreement with previous studies, the simple cell modulates to the first and the complex cell to the second harmonic of the stimulus. Records (b) of figure 9 show
the patterning of the inhibition, for simultaneous stimulation by noise and orthogonally oriented gratings. Here both the simple and the complex cell show a deep second harmonic modulation. Note also that for both cells this modulation is 180° out of phase with that of the complex cell when stimulated by an optimally oriented grating, the peaks of the excitation corresponding to the troughs in the inhibition, as may be expected.

These results are again quite consistent with the idea that complex cells are involved in intra-cortical inhibition. We cannot exclude, on the basis of these data alone, the possibility that the inhibition arises from a battery of simple cells whose receptive fields are positioned to cover 360° of phase. It may be argued that the combined inhibitory input of such a pool may produce a second harmonic modulation of the response. However, as the response of simple cells to counterphased gratings is weak, and indeed almost non-existent unless the phase of the grating is closely matched to that of the cell’s receptive field, it is unlikely that simple cells make a significant contribution to the inhibition under these conditions.

It is also interesting that the modulation of the response to the composite noise and grating pattern swings both below and above that of the response to the noise alone (indicated by the broken line of records (b), implying that the counterphased grating produces not only inhibition, but also disinhibition, or release from spontaneous inhibition. This would be expected if the inhibition were generated by complex cells whose response to counterphased gratings modulates above and below their resting discharge level. Indeed the high spontaneous activity of complex cells (particularly the ‘special’ type complex cells of Palmer & Rosenquist (1974) and Gilbert (1977)) may serve to provide a continuous tonic inhibition of both simple and complex cells.

Two-dimensional patterns

The results of the previous experiment were all obtained with 1-D grating type stimuli. However, one may ask whether these results can be generalized to more natural viewing conditions, where cells are typically stimulated by complex two-dimensional stimuli rather than one-dimensional gratings.

An appropriate complex two-dimensional visual stimulus is white visual noise. When correctly constructed, this stimulus contains energy at all orientations and over a wide range of spatial frequencies (see power spectrum of figure 2). Thus it should be both an excitatory and an inhibitory stimulus for cortical cells: a small subset of energy falling within the cell’s orientation and spatial frequency selectivity channel should excite the cell, and the rest of the energy inhibit it.

On the basis of the results of previous sections, simple cells, which are tightly tuned both for orientation (Watkins & Berkley 1974) and for spatial frequency (Maffei & Fiorentini 1973) and receive a strong inhibition from a wide range of orientations and spatial frequencies (figures 7, 8), should respond only weakly, if at all, to 2-D visual noise, while complex cells, which are much more broadly tuned for orientation and spatial frequency (Watkins & Berkley 1974; Maffei & Fiorentini 1973) and receive weaker intracortical inhibition (figure 3), should respond more vigorously.
This is in fact the case. Complex cells respond well to 2-D visual noise, while simple cells remain virtually silent (Hammond & MacKay 1975, 1977). Simple cells, however, do respond to 1-D visual noise of horizontal power spectrum identical to 2-D noise (Burr et al. 1981). As the 1-D noise of the experiment by Burr et al. (1981) was a mathematical subset of the 2-D noise (see figure 2), this confirms that the silence of simple cells results from inhibition rather than from a paucity of effective energy in the pattern.

![Figure 10](http://rspb.royalsocietypublishing.org/)

**Figure 10.** The response of a representative simple and a representative complex cell to various noise patterns: 1-D noise (depicted by vertical bars), 2-D random noise (circular symbols) and partially correlated 2-D noise, where the randomness of dot position was constrained to form pairs (triangular symbols) or triplets (square symbols). The complex cell responded well to all stimuli, particularly to the 2-D stimuli. The simple cell, however, responded well only to the 1-D noise; to stimulation by the 2-D random noise, it was virtually silent, and it responded only weakly to the partially correlated 2-D patterns. The power spectra of the stimuli were identical along the orientation of the cells' axis, but differed at other orientations. The difference in magnitude of response to the four stimuli presumably arises from inhibition generated by energy outside the cells' orientation passband.

The difference in the simple cell response to 1-D and 2-D noise is shown in figure 10. Although the cell failed to respond to the 2-D noise (circular symbols), it responded well to 1-D noise of matched power, the response increasing with contrast (bar symbols). As the cell responded over a contrast range of an order of magnitude, it seems unlikely that the failure to respond to 2-D noise results from saturation of the l.g.n. input.

It is interesting to note that, whereas simple cells do not respond to random textured patterns, they do respond to a more orderly pattern, the chessboard (De Valois et al. 1979). This response presumably occurs because the energy of the chessboard is much less dispersed than that of the noise, the bulk of it being contained within a few discrete spatial frequencies and orientations (see De Valois et al. 1979, fig. 2). Thus, when the orientation and spatial frequency are carefully adjusted to meet the requirements of the cell, the ratio of excitation to inhibition energy is far higher than that for random patterns.
Cross-orientation inhibition of visual cells

**Partially correlated noise**

The other two curves of figure 10 (square and triangular symbols) show the response of the cell to partially correlated noise patterns. These patterns consisted of a field of randomly positioned pairs or triplets of dots, constructed by positioning one member of the pair or triplet at random and the other(s) directly above (and below) this dot. Biasing the randomness in this way creates the percept of striations in the pattern, which results from an attenuation of stimulus energy at all orientations except that of the alignment of the pairs or triplets. One would expect that when the dots or triplets are aligned along the cell’s preferred orientation axis, these stimuli should produce less inhibition than white noise and hence permit a response from simple cells.

Figure 10 supports this prediction. The simple cell responded, albeit weakly, to the dot pair pattern and somewhat more strongly to the dot triplet pattern. Note that, as for the response curves of figure 5, the curves for 1-D, triplet and pair patterns show a progressive decrease in slope, again implying that cortical inhibition is a divisive rather than subtractive process.

**Homogeneity of simple cell response to texture**

Although Hammond & MacKay (1975, 1977) reported that no simple cell in their sample \( n = 120 \) responded to textured patterns, 12 of our 56 cells did respond to 2-D noise. Thus it is possible that simple cells are not a homogeneous class with respect to their inhibition-mediated tuning.

However, it is also possible that the variation in simple cell response results from the condition of the animal preparation. The preparations in which the cells responded to the noise often exhibited high spontaneous activity, weak orientation and spatial frequency tuning, and a more transient response. These symptoms have been reported to be related to the anaesthetic level of the animal (Robertson 1965; Ikeda & Wright 1974). It is possible that the difference in response of simple cells to textured noise reflects varying states of anaesthesia rather than the existence of a genuine subset of simple cells, but this must remain an open question at present.

**Discussion**

The experiments of this paper have shown that cortical cells, particularly simple cortical cells, are strongly inhibited by stimuli of non-preferred orientation. The inhibition occurs over a wide range of orientations and spatial frequencies, suggesting that it derives from a large pool of cells, rather than from a single cell. This result has several interesting implications for the role of simple cells in the processing of visual information.

**Lengthwise integration of simple cells**

It is generally accepted that simple cells summate or integrate energy along their long axis. This assertion is supported by several studies which show that on stimulation by thin bars the response of simple cells increases monotonically with
bar length up to a certain level, whereupon it either saturates or decreases depending on the end inhibition (Henry et al. 1974; Gilbert 1977; Rose 1977b).

However, the results of our experiments suggest that this demonstration of integration depends on the use of particular class of stimuli, such as bars or gratings, and cannot be generalized to more complex 2-D patterns. *Simple cells do not report the lengthwise integral of visual texture.* Were they to do so, the response to 2-D noise should be equal to or stronger than that to the 1-D noise, as the lengthwise integral of the 2-D noise is equal to or greater than that of the 1-D noise (see figure 2); indeed the 1-D noise was constructed from the 2-D noise by ‘smearing’ (i.e. integrating) along the cell’s long axis.

The apparently conflicting results of cell integration of bar and pattern stimuli can be readily reconciled by considering the action of cross-orientation inhibition. An inhibition-free system, in which orientation selectivity derives solely from the excitatory drive, is essentially linear, in the sense that the cell will respond equally well to a stimulus of given orientation irrespective of the presence of stimuli outside the orientation tuning of that cell. That is to say, it will respond equally well to a line or grating whether it be embedded among a mass of texture or stand alone. For an inhibition-driven system, however, the cell’s response can be conditioned by stimuli both of preferred and of non-preferred orientation. Here the cell is not a simple filter, extracting energy that falls within its passband, but responds rather to the ratio of energy within and without its orientation passband. Thus it will respond selectively to 1-D stimuli, such as lines and gratings, but not to patterns.

For 1-D stimuli, of course, where the inhibitional is minimal, it will demonstrate length summation, but this summation cannot be considered to demonstrate a general property of simple cells.

*Inhibition of simple by complex cells*

Our results also imply, in agreement with previous suggestions (Creutzfeldt et al. 1974b; Singer et al. 1975; Hammond & MacKay 1978; Lennie 1980), that complex cells may be principally responsible for the cross-orientation inhibition. This evidence derives from the transient nature of the inhibitory response, the second harmonic modulation to counterphased gratings, the evidence for spontaneous inhibition (figure 10), and the fact that simple cells, themselves unresponsive to textured patterns, are unlikely to create the inhibition that renders them unresponsive.

Complex cells are well suited as intra-cortical inhibition units. Spatially, they are less discriminative than simple cells, tending to have larger receptive fields, are insensitive to position or to spatial phase within their fields, and are less tightly tuned for both orientation and spatial frequency (Hubel & Wiesel 1962; Pettigrew et al. 1968; Maffei & Fiorentini 1973; Watkins & Berkley 1974). These characteristics, while rendering them less suitable for the transmission or analysis of specific spatial information, satisfy the broad-tuning requirements of an inhibitory system.

A second advantage is that complex cells receive a major drive from *Y*-type geniculate cells, which transmit through fast-conducting axons (Cleland et al. 1971; Hoffmann & Stone 1971; Stone & Dreher 1973). Thus the inhibition can arrive
in time to coincide with or even to precede the excitatory input, despite its having
to cross an additional synapse. Indeed, Singer et al. (1975) found that in response
to electrical stimulation of the l.g.n. the inhibitory postsynaptic potential (i.p.s.p.)
preceded the excitatory postsynaptic potential (e.p.s.p.), which frequently re­
ained subthreshold, for 44% of their cell sample.

Complex cells, particularly the ‘special’ type complex cells of Palmer &
Rosenquist (1974) and Gilbert (1977), usually have high resting discharge levels.
Our evidence suggests that this spontaneous discharge generates a spontaneous
inhibition of both simple and complex cells, which can be temporally disabled by
stimulation by sinusoidally counterphased gratings (see overswing of records (c)
and (d) in figure 9). The spontaneous inhibition could contribute to the silent
resting levels of simple cells (and also of some complex cells; cf. Gilbert 1977), and
may also contribute towards the mechanism of the response threshold of cortical
cells (Maffei & Fiorentini 1973).

Thus, the cortical scheme suggested by our results is one in which information is
processed not by a hierarchical sequence (Hubel & Wiesel 1962) but rather by a
cooperative inhibitory network (Creutzfeldt 1975) in which the complex cells subserve
the simple cells, shaping their spatial selectivity and suppressing background noise.

Psychophysical correlates

A reader who is well acquainted with the psychophysical literature may be
surprised that a neurophysiologically observed effect as large as cross-orientation
inhibition does not manifest itself in psychophysical measurements: high-contrast
gratings have almost no effect on the visibility thresholds of an orthogonal grating
(Campbell & Kulikowski 1966), and adaptation to high-contrast gratings (which
might weaken inhibition from that orientation) does not enhance sensitivity to
gratings of orthogonal orientation (Blakemore & Nachmias 1971). Threshold
elevation has been observed for orthogonally oriented flickering masking gratings
(which may be a more potent inhibitory stimulus), but the effects are small, about
0.1 logarithmic units (Gorea & Fiorentini 1982). However, all these measurements
are of contrast thresholds, which one would not expect to be affected greatly by
divisive inhibition. The results of our figure 4 indicate that inhibition decreases the
slope of the contrast response without raising substantially the response threshold.

For psychophysical correlates of divisive inhibition one must consider supra-
threshold effects. Although these effects can pose some problems of interpretation,
it is conceivable that phenomena such as the competitive visibility of orthogonal
gratings (the ‘monocular rivalry’ of Campbell et al. (1973)), Attneave’s (1971)
‘reversible triangles’ and the ‘indirect tilt after effect’ of Campbell & Maffei (1971)
may be consequences of cross-orientation cortical inhibition.

Preliminary measurements (in collaboration with M. Pirchio & D. Spinelli) also
suggest that the slope of the contrast function of visual evoked potentials of man
is reduced by the presence of orthogonally oriented dynamic 1-D noise, without
the response threshold being raised.
Functional implications?

What is the biological significance of inhibition shaped orientation tuning?

As we have seen, because of their strong cross-orientation inhibition, simple cells respond selectively to 1-D stimuli or stimuli whose energy is weighted along a particular orientation. In natural scenes, which are composed of patterns rather than gratings, 1-D structures often correspond to the contours or borders of visual objects. Thus it is possible that the inhibition shaped orientation selectivity of simple cells serves to render them selectively sensitive to the outlines of objects. Indeed Hoffmann & von Seelen (1978) have shown that simple cells respond to bars embedded in noise at much lower signal to noise ratios than complex cells.

A system selective to visual contours could form an important part of a visual pre-analysis, delineating visual scenes into discrete objects, which could then receive more extensive analysis by the complex cells and (if it really exists) the subclass of simple cells that do respond to 2-D stimuli. This pre-analysis would be somewhat akin to the idea of the 'primal sketch' proposed by Marr (1966). This idea will be pursued further in a later paper (paper II).

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