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# STRIATE CORTEX RESPONSES TO PERIODIC PATTERNS WITH AND WITHOUT THE FUNDAMENTAL HARMONICS

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SUMMARY

1. The visual system has been modelled as a set of independent linear channels each tuned to a limited band of spatial frequency with the average bandwidth being approximately 1 octave. A great deal of psychophysical and physiological evidence supports this basic notion. However, Henning, Hertz & Broadbent (1975) have shown reciprocal masking between a fundamental frequency (1F) and a complex grating composed of higher harmonics several octaves removed ((4+5+6)F); their results clearly indicate a lack of independence.

2. We recorded the activity of cells in the striate cortex of monkeys and cats using stimuli similar to those of Henning *et al.* to make comparisons with their psychophysical data and to test specific physiological predictions.

3. We found that cells tuned to the fundamental frequency did not produce an excitatory response to the (4+5+6)F pattern. However, the response of such cells to 1F could be reduced by simultaneous presentation of (4+5+6)F. Similarly, the response of cells tuned to high frequencies, when presented with (4+5+6)F, was reduced by simultaneous presentation of 1F. However, this reciprocal inhibition could be produced between single harmonics (e.g. 1F and 4F) and was not dependent upon a special relationship between 1F and (4+5+6)F.

4. When cells tuned to high frequencies were presented with the (4+5+6)F pattern they generated predictable responses in the higher harmonics (4, 5, 6) but they also generated an unexpected, non-linear, response at the fundamental frequency, 1F, even though no such low frequency component was present in the stimulus. This effect is due to the response rectification which striate cells show.

5. In support of the linear independent spatial frequency channel model, we find (*a*) striate cells provide an excitatory response to only a limited range of frequencies, (*b*) they do not provide such responses to the 'apparent' yet 'missing' fundamental in the (4+5+6)F beating pattern, and (*c*) the response wave form to complex stimuli like (4+5+6)F is reasonably predictable (at least for simple cells) from the model. Against the model we find that (*a*) frequencies outside the excitatory bandpass can produce inhibition and (*b*) the rectification of the response wave form introduces harmonics not present in the stimulus.

## INTRODUCTION

Campbell & Robson (1968) first proposed that the visual system could be modelled as a set of independent spatial frequency tuned channels. Since then, considerable evidence has accumulated which supports this basic notion (for general reviews see: Sekular, 1974; Robson, 1975; Braddick, Campbell & Atkinson, 1978; De Valois & De Valois, 1980). For example, Blakemore & Campbell (1969) have shown psychophysically that prolonged adaptation to a single spatial frequency grating pattern causes a loss in sensitivity to only a limited range of spatial frequencies centred around the adaptation frequency. Physiological studies have shown that single cells in the striate cortex of both monkeys (Schiller, Finlay & Volman, 1976; De Valois, Albrecht & Thorell, 1977, 1978; Albrecht, 1978; Albrecht, De Valois & Thorell, 1980) and cats (Campbell, Cooper & Enroth-Cugell, 1969; Maffei & Fiorentini, 1973; Ikeda & Wright, 1975; Albrecht, 1978; Movshon, Thompson & Tolhurst, 1978*a*, *b*) respond to only a limited range of spatial frequencies within a given localized retinal area. These studies, and others, indicate that the visual system up through the striate cortex may be performing a patch-wise spatial frequency filtering of the visual information, segregating the visual stimulus into a set of quasi-linear independent channels.

However, several psychophysical studies have now demonstrated that under some circumstances the spatially selective channels in the human visual system are not totally independent. Henning *et al.* (1975) have shown that the detection of a low frequency grating pattern can be masked by simultaneous presentation of a specific set of harmonically related frequencies more than two octaves removed and vice versa. Tolhurst (1972) and Nachmias, Sansbury & Vassilev (1973) have shown that adaptation to a square wave grating does not produce the appropriate loss in sensitivity at the third harmonic which would be expected from totally independent channels. Other psychophysical studies (De Valois, 1977; 1978*a*; Tolhurst & Barfield, 1978) have shown that detection of a single spatial frequency can be enhanced by prior adaptation to a grating pattern several octaves removed. This type of evidence imposes clear limitations on the generality of the independent channel hypothesis.

Henning *et al.* (1975) used a specific set of harmonically related grating patterns which has an interesting perceptual property. A stimulus consisting of the 4th, 5th and 6th harmonics of a particular fundamental has an 'apparent' periodicity at that fundamental frequency even though there is no 'physical' energy present at the fundamental. They showed that this 4F + 5F + 6F stimulus increased the detection threshold of the fundamental harmonic component (1F). Reciprocally, the fundamental harmonic component increased the detection threshold of the complex pattern. This led Henning *et al.* to propose that low spatial frequency channels might be sensitive to this apparent low frequency periodicity, that is, that low frequency channels might somehow respond to a periodic contrast modulation of a high frequency grating.

In the present study we asked how single cells in the striate cortex behave when presented with the stimuli used by Henning *et al.* (1975). Specifically, we first asked whether cells tuned to low spatial frequencies would respond to a combination of the 4th, 5th and 6th harmonics (of the cell's characteristic frequency) alone, even though no low spatial frequency components were present in the stimulus. Secondly, we asked

how cells tuned to high frequencies would respond to the complex pattern when the 4th, 5th and 6th harmonics all fell within the cell's bandpass. Thirdly, we asked whether the response of a low frequency cell to its best frequency, 1F, is perhaps enhanced or inhibited by the simultaneous presentation of 4F + 5F + 6F. Finally, we asked whether the low frequency beat is actually the necessary condition for producing interactions, or whether perhaps individual harmonics by themselves are sufficient.

The predictions one would make from a linear spatial filter model are quite straightforward. After measuring the response of a particular cell to single spatial frequency sine waves across the entire range of spatial and temporal frequencies, one should have a good estimate of the 'bandpass characteristic' of that cell (which frequencies excite the cell and what their weighting factors are). If the spatial frequencies present in a particular stimulus fall within the bandpass of the cell, then they should excite the cell by predictable amounts; if the frequencies present in a stimulus fall outside of the cell's bandpass, then they should produce no response. Thus, for example, a cell tuned to frequency 1F should not respond to a pattern composed of 4F + 5F + 6F if these frequencies are all outside of the excitatory bandpass of the cell. These linear predictions are quite contrary to the explanation of Henning *et al.* (1975) of their psychophysical findings.

## METHODS

*Preparation.* The apparatus and general recording procedures are similar to those more fully described elsewhere (Albrecht, 1978; De Valois, De Valois & Yund, 1979). Briefly, macaque monkeys (*Macaca fascicularis*) and domestic cats were prepared for chronic experiments some days before the first neurophysiological recording; under deep barbiturate anaesthesia a rigid plastic pedestal containing a recording chamber was cemented to the animal's skull. The actual experiments ran for about 12 hr (1 hr preparation, 9 hr recording, 2 hr recovery).

On the day of an experiment, the animal was anaesthetized with a short-acting barbiturate (thiamylal sodium) and maintained throughout the experiment on 75% $N_2O$/25% $O_2$ analgesia. Since no ear, eye, or mouth bars were used, discomfort was minimal. The animals showed no increased aversion to the experimenters or the experimental room as a result of this treatment; those previously tamed remained friendly. During the recording session, the animal rested on a foam-rubber pad with its head held by a plate screwed into the pedestal. It was respirated through an endo-tracheal throat tube, with the respired $CO_2$ being maintained at 4·5%. Temperature was maintained within normal limits by means of a thermostatically controlled heating pad; the heart rate was monitored throughout the experiment.

The eyes were covered with contact lenses; accomodation was paralysed and the natural pupil dilated by applying cylopentolate hydrochloride (Cyclogyl HCl). The animal was refracted by streak retinoscopy, corrective lenses were used to focus the stimuli on the retina, and an artificial pupil was introduced (3 mm for monkey, 4 mm for cat). The eyes were immobilized by continuous infusion of gallamine triethiodiode. Action potentials were recorded from area 17 neurones using glass coated platinum-iridium micro-electrodes. The action potentials were amplified and converted by a window discriminator to standard pulses which were fed into and analysed by an on-line NOVA 1220 computer.

*Display.* Visual stimuli were displayed on a Tektronix 654 oscilloscope and were digitally generated line-by-line from a NOVA 1200 computer. A table of luminances to specify each pattern was stored in the computer and sent to the D/A controlling scope luminance one line at a time, synchronized to the raster scan of the monitor. The pattern was drifted across the scope by changing the starting position in the stimulus array on each successive frame. To rotate the patterns, we placed the scope in a 56 cm diameter steel drum which rested on wheels, and rotated the whole unit. The scope face was viewed through a circular aperture in a large white screen maintained at

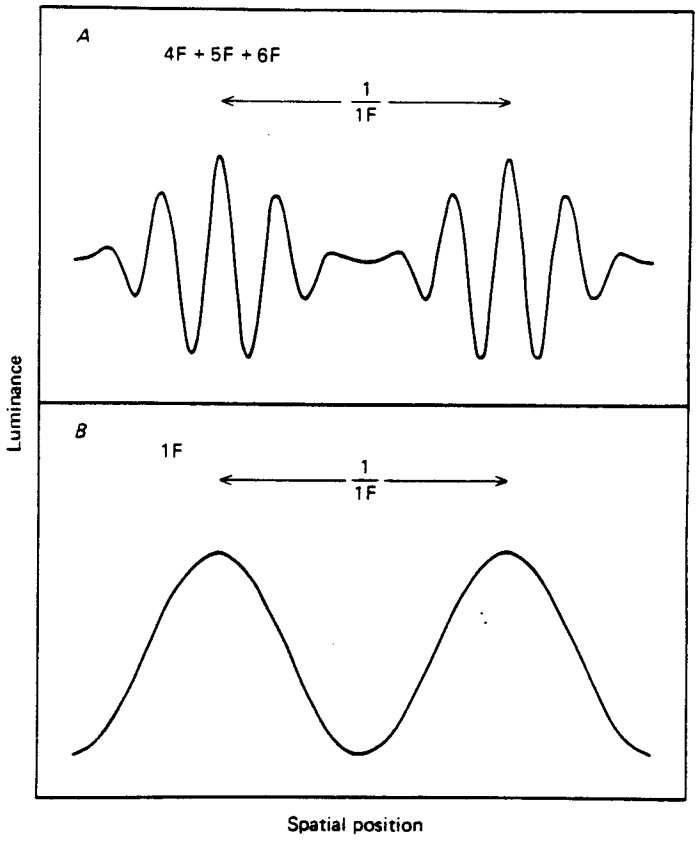



Fig. 1. *A* shows the distribution of luminance produced by summing the three harmonics 4F, 5F and 6F in cosine phase at amplitudes of 0·25, 0·5 and 0·25 respectively. The modulation of the pattern varies periodically (beats) with a period equal to that of the fundamental, 1F, as can be seen by comparing it with *B* which shows the luminance distribution of the fundamental, 1F.

roughly the same mean luminance level (27·4 cd/m²). The aperture subtended 18 degrees at the 57 cm viewing distance used for cats, and 6 degrees for monkeys at a viewing distance of 172 cm.

*Experimental procedure.* Once the response of a single cell was clearly isolated, its receptive field was located and centred on the display scope. Its preferred orientation, direction of movement, spatial frequency, and temporal frequency were approximately determined by listening to the spike trains while varying these parameters. Bar stimuli were then used to classify the cell as simple or complex according to the criteria of Hubel & Wiesel (1962). On the basis of these preliminary measurements, the responses of the cell to various spatial and temporal frequencies were quantitatively assessed with the orientation and direction of motion held constant at the optimum. These measures provided us with the cell's spatial and temporal frequency contrast sensitivity function.

Upon completion of these preliminary experiments, we presented varying combinations of 1F, 4F, 5F, and 6F to each of the fifty-three cells studied. Except for the relative locus on the spatial frequency axis, we observed no clear differences between the samples of cells recorded from the cat (thirty cells) and monkey (twenty-three cells); we thus grouped them together. For cells tuned to low spatial frequencies (twenty-four cells), the spatial harmonics were chosen such that 1F was near the peak of the spatial bandpass and the temporal harmonics were chosen such that they all

fell within the temporal bandpass. For cells tuned to high frequencies (twenty-nine cells), the spatial harmonics were chosen such that 4F, 5F and 6F were centred near the peak of the spatial bandpass and the temporal harmonics all fell within the temporal bandpass. In general, each cell was tested with the following patterns presented in random order: (*a*) 1F, (*b*) 4F, (*c*) 5F, (*d*) 6F, (*e*) 4F + 5F + 6F, (*f*) 1F + 4F + 5F + 6F, (*g*) 1F + 4F, (*h*) 1F + 5F. The relative amplitudes of the individual components in the patterns (*e*) to (*h*) inclusive were as follows: (*e*) 0·25, 0·50, 0·25, (*f*) 0·5, 0·12, 0·25, 0·12, (*g* and *h*) 0·5, 0·5. The harmonics were added together in cosine phase. The various patterns were each presented at several contrast levels ranging from 2 to 20 % where contrast (for each individual harmonic) is defined as (max − min)/(max + min).

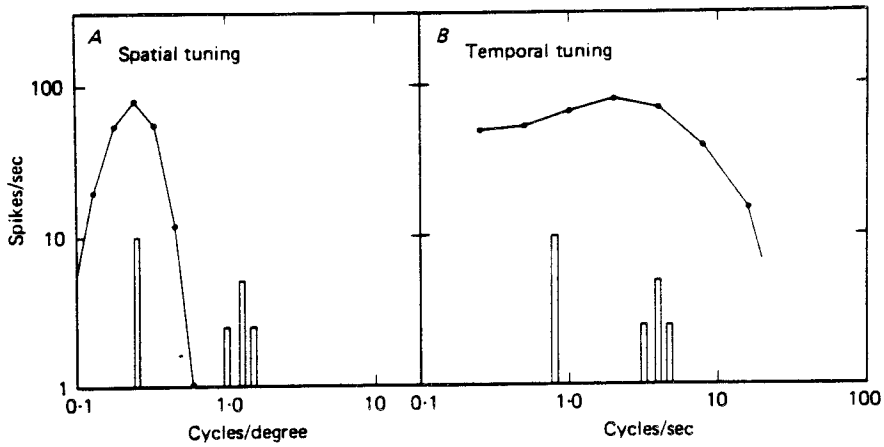



Fig. 2. *A* shows the spatial frequency tuning function for a cat striate simple cell as well as the location and relative amplitudes of the harmonics (1F, 4F, 5F, 6F) of the stimulus used to test the cell in Experiment 1. As can be seen, the cell has a bandpass characteristic of about 1 octave and is tuned to relatively low spatial frequencies. Since only the fundamental frequency component of the stimulus lies within the tuning curve of the cell, linear filter theory would predict that the cell should respond only to the fundamental frequency. *B* shows the temporal frequency tuning of the same cell as well as the location and relative amplitudes of the stimulus frequencies. Since the cell has a relatively flat low pass temporal tuning curve, all of the temporal frequency components of the stimulus are passed with little attenuation.

*Data analysis.* Peristimulus time histograms (PSTH) averaged over twenty to forty repetitions of each periodic stimulus were collected in 5 msec time bins. From these averaged histograms an on-line Fourier harmonic analysis was computed relative to the fundamental temporal frequency of the stimulus. The mean response rate (or DC) and the amplitudes and phases of the first six harmonic components were printed out on-line.

## RESULTS

The two primary stimulus conditions used in this study are shown in Fig. 1: *A*, the sum of 4F + 5F + 6F (in cosine phase with relative amplitudes of 0·25, 0·50 and 0·25), and *B* a single low spatial frequency grating, 1F.

*Experiment 1.* In the first experiment we asked whether cells tuned to low spatial frequencies would respond to the complex pattern composed of 4F, 5F and 6F (where 1F is the frequency to which that particular cell responded best). As shown in Fig. 1*A*, the luminance profile of this pattern has an 'apparent' low frequency oscillation

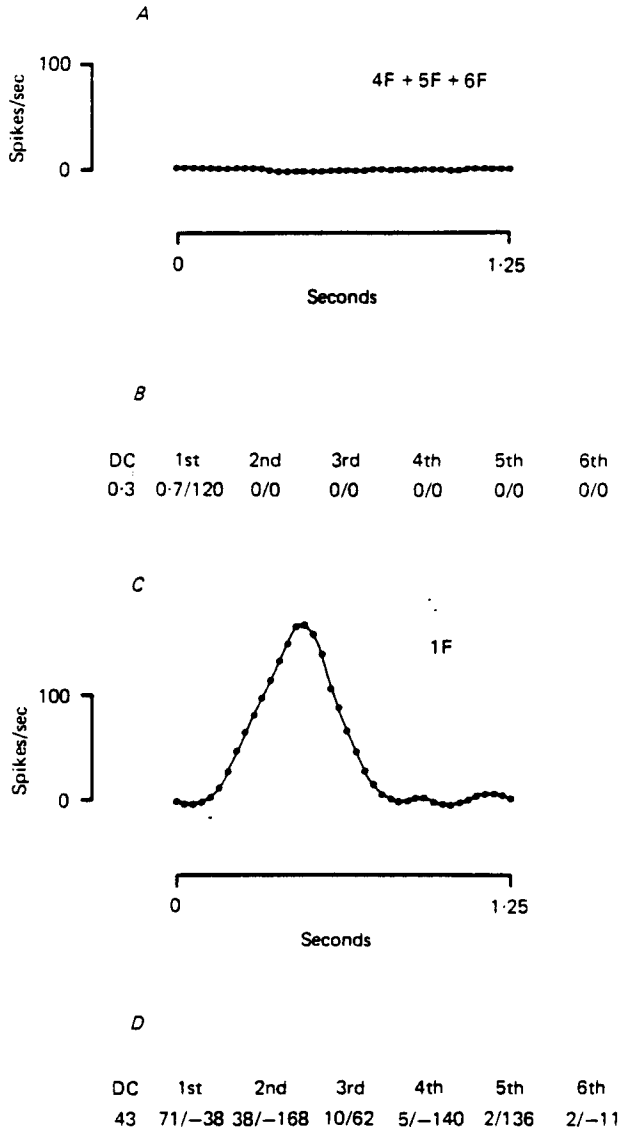



Fig. 3. *A* shows the PSTH of the cell shown in Fig. 2 when presented with the stimulus shown in Fig. 1*A* (that is, 4F+5F+6F). As can be seen, the cell gives essentially no response to the high frequency harmonics even though the pattern has an 'apparent' low frequency periodicity equal to the period of the cell's best spatial frequency. *B* is a printout of the amplitude/phase of the first six harmonics of the response shown in *A* above. *C* shows the response of the same cell to the fundamental (1F) frequency. As is typical for simple cells, the cell produces a half-wave rectified discharge pattern which modulates in synchrony with the input. The cell thus responds strongly when presented with a 'real' low frequency component within its bandpass. In *D* is the printout of response harmonics. The lack of a maintained discharge produces energy in the higher harmonics as well as in the fundamental.

whose period is equal to the difference between the adjacent higher harmonics (in this case the oscillation is at the lowest common multiple, or 1F). The psychophysical experiments of Henning *et al.* suggested to them that low frequency channels in the visual system might respond to the 'missing' (yet 'perceptually apparent') low frequency periodicity. If this were so, it would be a major (first order) non-linearity of visual function: a linear spatial filter tuned to low frequencies would not be expected to respond to this pattern, since it is composed of only high frequencies outside the bandpass of the filter.

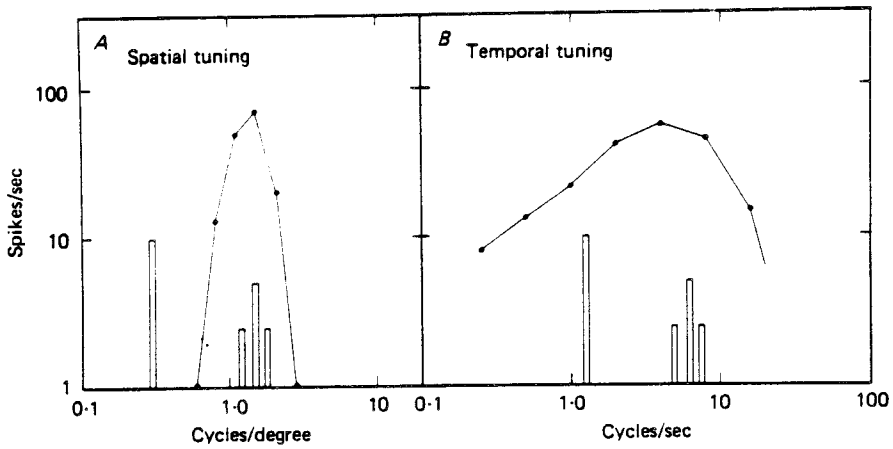



Fig. 4. *A*, spatial frequency tuning function of a cat striate simple cell in relation to the stimulus frequencies (1F, 4F, 5F, 6F) used to test the cell in Experiment 2. Since only the higher harmonics fall within the spatial bandpass, they alone should influence the cell's response. *B*, temporal frequency tuning function for the same cell and the location of the stimulus frequencies.

Fig. 2 shows the spatial frequency tuning (2*A*) and the temporal frequency tuning (2*B*) of a particular striate simple cell in cat which was tuned to low spatial frequencies. The location of the stimulus frequency components (1F, 4F, 5F, 6F), with respect to the cell's sensitivity range, are shown by the bars. Since the higher harmonics (4, 5, 6) are all outside the spatial bandpass of this cell, linear filter theory would predict that the cell would not respond to the pattern. The response (PSTH) of this cell when presented with the high frequency pattern, 4F + 5F + 6F is shown in Fig. 3*A*. As can be seen, this low frequency cell did not respond to the complex periodic pattern composed only of higher harmonics. Fourier analysis of the cell's response (shown in Fig. 3*B*) demonstrates that there were no responses at any of the higher harmonics (2F through 6F) nor did the cell show any response at the 'apparent' low frequency fundamental (1F). We tested a total of twenty-four cells tuned to low frequencies under similar conditions and found that not one cell responded to this complex high frequency grating pattern.

Fig. 3*C* shows the response (PSTH) of the same cell (described above) to a grating of its best or characteristic frequency (that is, 1F). The corresponding harmonic analysis of the PSTH is shown in Fig. 3*D*. As can be seen from the responses in Fig.

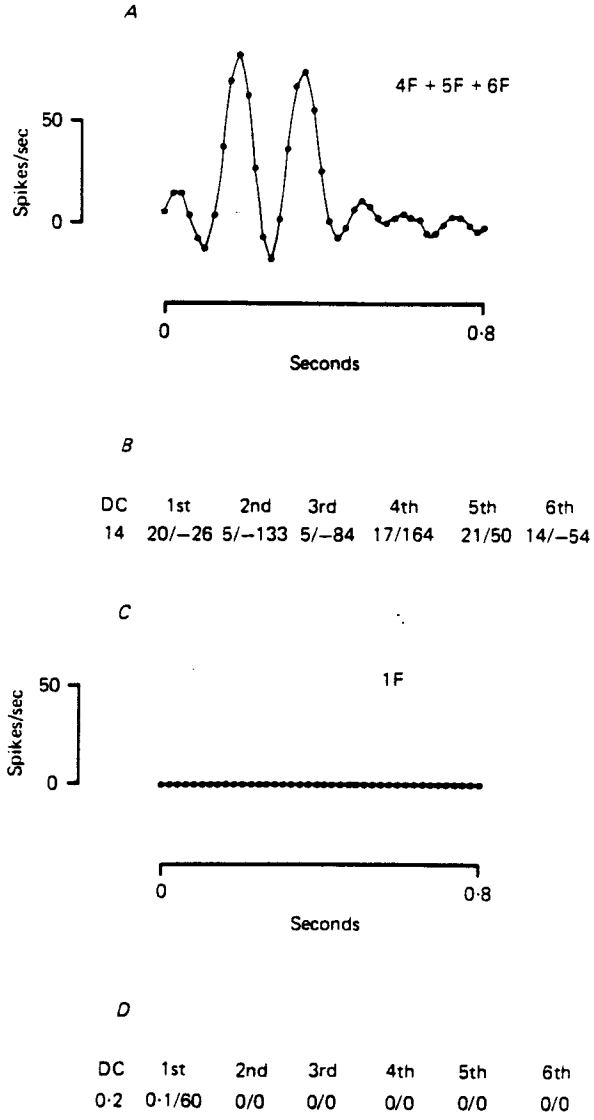



Fig. 5. *A*, PSTH of the cell shown in Fig. 4 to the stimulus shown in Fig. 1 *A* (4F + 5F + 6F). As can be seen, this cell responds quite vigorously to this pattern composed of high frequency harmonics; further, the shape of the response is very similar to the shape of the stimulus luminance profile. The response is what one would expect from a linear filter given the stimulus–response relationships depicted in Fig. 4. Note however that the response is inverted (due to the particular receptive field organization) and that the response is largely half-wave rectified (due to the lack of a maintained discharge). *B*, corresponding distribution of the response harmonics. As expected, there are sizable responses in the 4th, 5th and 6th harmonics. There is also, however, a response at the fundamental (1F) due to half-wave rectification: the lack of maintained discharge forces a modulation at the fundamental harmonic in addition to the higher harmonics. *C*, PSTH of the same cell to the fundamental frequency (1F) alone, which shows that the cell provides no excitation. *D*, corresponding distribution of the response harmonics.

3, this cell responds quite vigorously to a 'real' low frequency pattern but does not respond at all to an 'apparent' low frequency pattern.

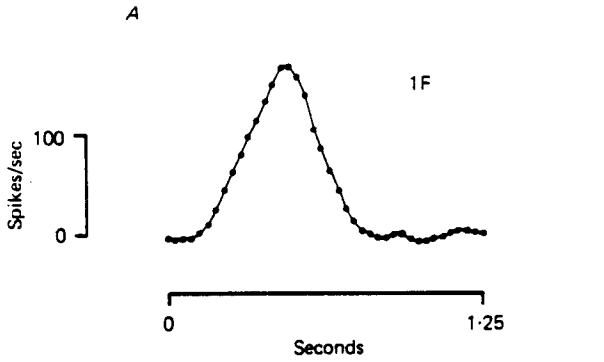
*Experiment 2.* In the second experiment we presented the same stimulus patterns to a total of twenty-nine cells tuned to higher spatial frequencies. The patterns were generated such that 4F, 5F and 6F were centred near the peak frequency of the particular cell under examination.

Fig. 4 shows the spatial frequency tuning (4*A*) and the temporal frequency tuning (4*B*) of a particular striate simple cell tuned to high frequencies, along with the location of the stimulus frequencies used to test it. As can be seen, 4F, 5F and 6F all fall within the spatial bandpass of this cell, whereas 1F is well outside its response range. Given this information, linear filter theory would predict that the cell should respond to 4F, 5F and 6F. Fig. 5 shows that the cell does respond quite well to this combination of high frequency components. In fact, if the PSTH is Fourier analysed into harmonic components (Fig. 5*B*), one finds striking agreement between the predicted and the observed amplitudes in the 4th, 5th and 6th harmonics. However, unlike what one would expect from a linear filter, this cell shows a large amplitude response in the 1st harmonic component despite the fact that there is no such low frequency component present in the stimulus. As discussed below, this response to the low frequency beat can be explained by the response rectification which striate neurones show (due to the lack of a maintained discharge). Such rectification will necessarily introduce a low frequency component into the response which is not present in the stimulus.

It is worth noting that, other than showing half-wave rectification, this simple cell gives quite linear responses: the PSTH looks very similar to the actual input (compare Figs. 1*A* and 5*A*). The receptive field of this cell was organized such that the central region was excited by a black line and inhibited by a white line; the two flanking regions responded in just the opposite fashion (excited by white and inhibited by black). This receptive field organization has the net effect of inverting the stimulus pattern so that (given half-wave rectification) the cell's response follows only those parts of the stimulus which fall below the mean luminance level.

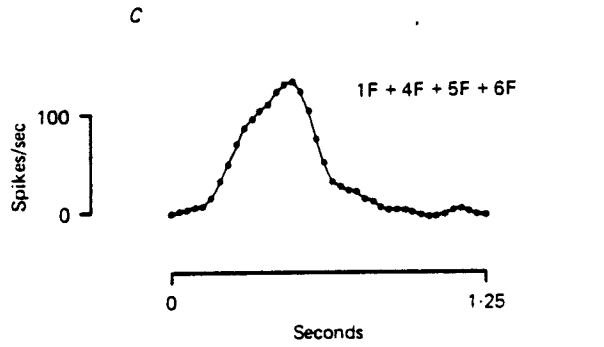
*Experiment 3.* While experiment 1 clearly demonstrates that cells tuned to low spatial frequencies do not produce an excitatory response to the 'apparent' low frequency periodicity of 4F + 5F + 6F, it does not rule out the possibility that their response to 1F would be enhanced or inhibited by the simultaneous presence of 4F + 5F + 6F. Therefore, in Experiment 3 we compared the response of low frequency cells to 1F alone *vs.* their response to 1F + 4F + 5F + 6F. The psychophysical experiments of Henning *et al.* showed that 1F was more difficult to detect in the presence of 4F + 5F + 6F. One might therefore expect that the presence of higher harmonics could reduce the response of a particular cell to a grating of frequency 1F.

Fig. 6*A*, *B* shows the response (PSTH and corresponding harmonic analysis) of a typical low frequency simple cell to its best frequency (1F) when presented alone. As is true for most simple cells, the discharge pattern modulates in synchrony with the fundamental frequency of the stimulus such that most of the power appears in the 1st harmonic component. Due to response rectification, however, some power appears in the higher harmonics as well. Fig. 6*C*, *D* shows the response of the same cell when presented with the same low frequency, 1F, but now combined with




B

| DC | 1st | 2nd | 3rd | 4th | 5th | 6th |
|---|---|---|---|---|---|---|
| 43 | 71/−38 | 38/−168 | 10/62 | 5/−140 | 2/136 | 2/−11 |




D

| DC | 1st | 2nd | 3rd | 4th | 5th | 6th |
|---|---|---|---|---|---|---|
| 36 | 56/−33 | 27/−150 | 9/92 | 5/−108 | 5/97 | 4/−37 |

Fig. 6. *A*, PSTH and *B*, printout of the harmonics of the cell shown in Fig. 2 when presented with 1F (its best frequency) alone. *C*, PSTH and *D*, printout of the harmonics of the same cell when 1F is presented in combination with the higher harmonics 4F, 5F and 6F. As can be seen, the cell's response is reduced; the peak response was reduced from 165 to 130 spikes/sec..

4F + 5F + 6F. Qualitatively the response (to 1F + 4F + 5F + 6F) looks very similar to the response to 1F alone. The discharge modulates in synchrony with the fundamental frequency of the stimulus and the relative distribution of the harmonics (shown in Fig. 6*D*) is virtually the same. However, the overall amplitude of the response is reduced by approximately 20 %. The presence of the higher harmonics in the stimulus, then, has reduced the amplitude of the response of the cell to its characteristic low frequency without significantly changing its wave form.

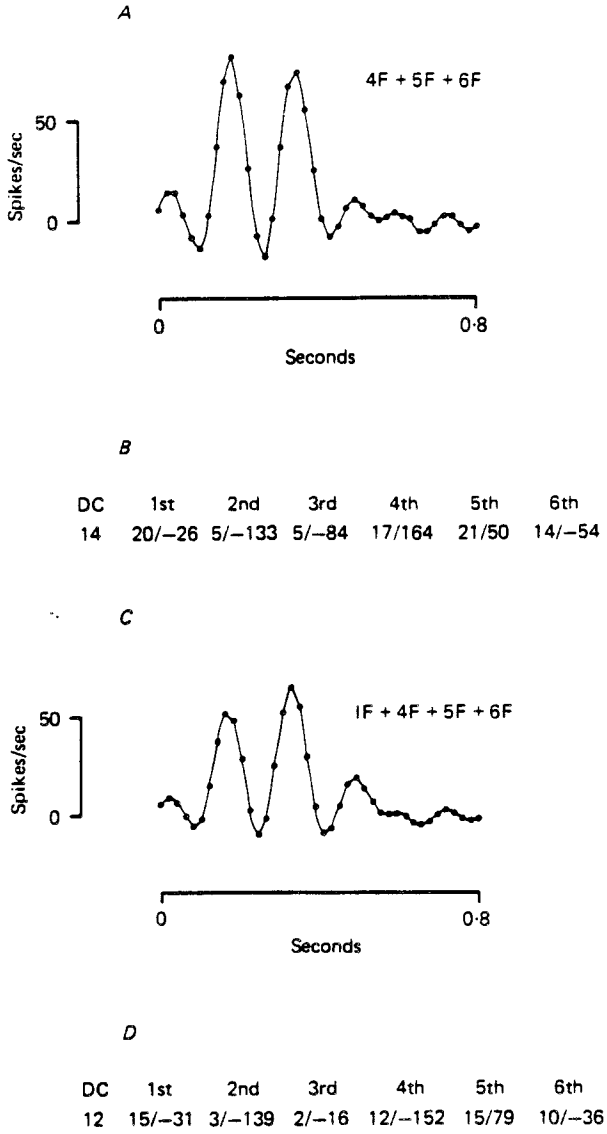



Fig. 7. *A*, PSTH and *B*, printout of the harmonics of the cell shown in Fig. 4 when presented with the three harmonics 4F, 5F and 6F, without the fundamental 1F. *C*, PSTH and *D*, printout of the harmonics of the same cell's response to these higher harmonics plus the fundamental (that is, the sum of 1F+4F+5F+6F). The addition of the fundamental harmonic decreases the response to the higher harmonics without changing the overall shape of the wave form.

Fig. 7 shows an analogous experiment performed on a cell tuned to high frequencies. The results are quite comparable: the response of this cell to 4F + 5F + 6F (Fig. 7*A*, *B*) is greater by approximately 30% than its response to these frequencies plus 1F (Fig. 7*C*, *D*).

Not all cells showed inhibition by frequencies well outside their excitatory bandpass. Fig. 8 shows a quantitative distribution of the magnitude of this (masking)

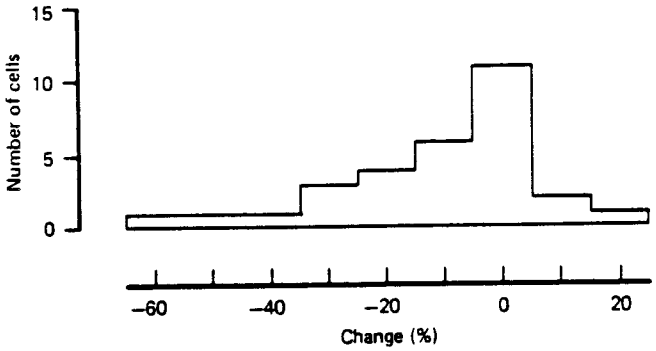



Fig. 8. Histogram showing the percent change in response to patterns within their spatial bandpass when frequencies outside of the excitatory spatial bandpass are added to the pattern. It can be seen that most of the cells are inhibited to some extent by these outside frequencies.

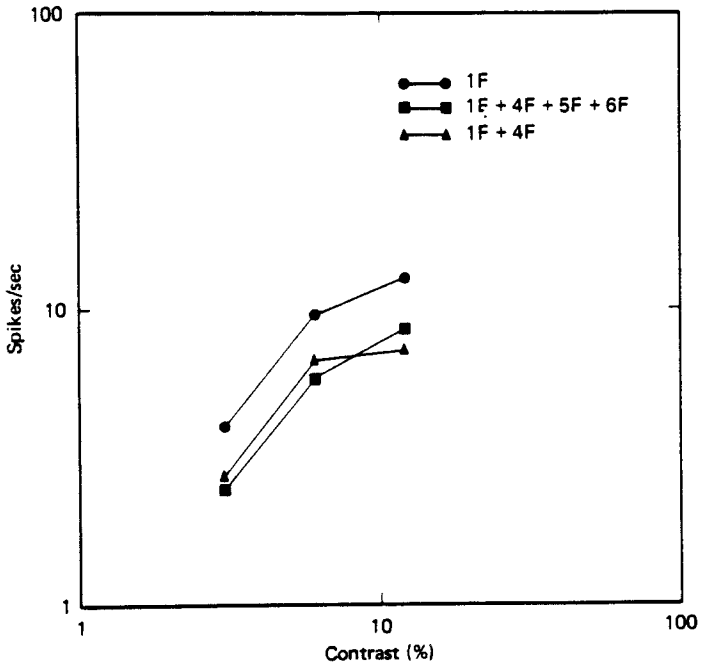



Fig. 9. Responses as a function of contrast of a monkey striate cell tuned to low spatial frequencies when presented with (i) the fundamental frequency alone, (ii) the fundamental with the three higher harmonics, (iii) the fundamental with only one higher harmonic. As can be seen, the size of the response to 1F was decreased by the simultaneous presentation of the three higher harmonics (4F, 5F, 6F) or by only one higher harmonic (4F), equated for contrast.

effect for a sample of thirty cells. Some 37 % of the cells showed no such interaction between 1F and the sum of 4F + 5F + 6F; about 10 % showed an enhancement by the distant frequencies; and the remaining 53 % of the cells showed an antagonistic interaction. The magnitude of the inhibitory interaction varied from cell to cell; among those showing the effect, the average decrease was approximately 25 % of the original response (the range was from 5 to 60 % inhibition).

*Experiment 4.* Henning *et al.* chose to examine the effect of 4F + 5F + 6F on 1F because the 4, 5, 6 pattern beats at 1F and might therefore be expected to mask a pattern of frequency 1F. Our results above raise the possibility that the masking effect may not be related to this (4 + 5 + 6)F beating at all. We therefore set up this final experiment to specifically test whether the antagonistic interaction, produced by frequencies well outside of the excitatory bandpass of the cell, was a consequence of the unique relationship this particular combination of high frequencies has with the low frequency fundamental, or whether the antagonistic interaction was produced by a generalized inhibition from high frequencies. As noted above, the sum of 4F + 5F + 6F produces an 'apparent' low frequency component whose period is equal to the period of the fundamental harmonic. We asked whether a single high frequency harmonic could, by itself, interact with the low frequency fundamental. Recent reports by De Valois (both psychophysical, 1977, and physiological, 1978*a*, 1979) indicate that single frequencies outside of the excitatory bandpass of a channel can produce net inhibition.

To examine this question, we presented cells tuned to low frequencies the following stimuli: (*a*) 1F alone, (*b*) 1F + 4F + 5F + 6F and (*c*) 1F + 4F. Cells tuned to high frequencies were tested with: (*a*) 4*F* + 5*F* + 6*F*, (*b*) 5F alone, (*c*) 1F + 4F + 5F + 6F, and (*d*) 1F + 5F.

Fig. 9 shows the response of a low frequency cell to these different stimulus patterns as a function of contrast. At all contrasts, the largest responses are to 1F alone. When 4F + 5F + 6F is added to 1F, the responses are decreased. However, this same decrease in responsiveness can be produced by adding 4F (without 5F and 6F) to 1F. Fig. 10 shows the results of performing the analogous experiment on a high frequency cell. As is shown, the largest responses at all contrasts are to 4F + 5F + 6F, or to 5F alone. When 1F is added to either one of these stimuli, the responses are decreased. It therefore appears that the masking interaction can be produced by single frequencies alone and is not a result of the unique relationship of 1F with the sum of its harmonic components 4F, 5F, and 6F.

## DISCUSSION

A great deal of evidence, both psychophysical and physiological, supports the basic spatial frequency channel model of the visual system. Neurones in the striate cortex of both monkeys and cats, when presented with single spatial frequency grating patterns, only produce excitation over a limited band of spatial frequencies. In the human visual system, many psychophysical experiments have demonstrated band-limited spatial frequency channels. The model, if valid, has the virtue of allowing numerous predictions from a relatively small set of observations and assumptions. The linear spatial filter model allows one to predict the responses to complex stimuli

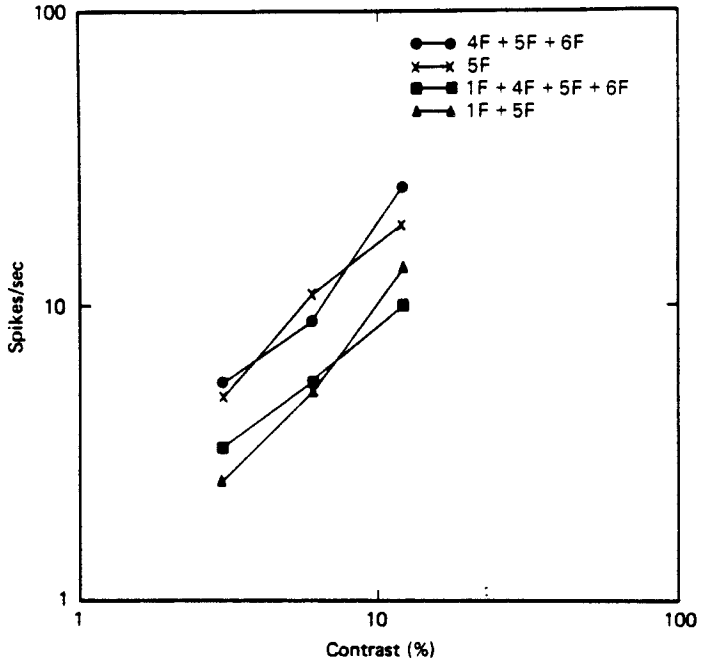



Fig. 10. Responses as a function of contrast of a monkey striate cell tuned to high spatial frequencies when presented with frequencies inside and outside its excitatory spatial bandpass. As can be seen, the presence of 1F (which is outside the cell's spatial bandpass) decreased the responses to 5F alone, as well as the responses to 4F + 5F + 6F.

from a knowledge of the bandpass characteristic of the channel and the frequency characteristics of the stimulus. The usefulness of the model for making such predictions has in fact been demonstrated both psychophysically (Campbell & Robson, 1968; Kelly, 1976) and physiologically (Albrecht, 1978; De Valois *et al.* 1979). There have however been several reports which indicate that the channels are perhaps not completely linear or independent.

The results of the experiments reported here provide some evidence for and some against the spatial frequency filter model of the visual system. In support of the model we find (as others have) that many striate neurones are fairly narrowly tuned for spatial frequency. Two examples of this tuning can be seen in Figs. 2*A* and 4*A*. Further, some of the cells demonstrate considerable linearity in that the excitatory response to a complex stimulus can be predicted solely from a knowledge of the stimulus frequency components present within the particular cell's spatial bandpass. The striate simple cell shown in Figs. 4 and 5 is a particularly good example of a linear cortical cell; the shape of the PSTH shown in Fig. 5*A* is remarkably similar to the luminance profile of the stimulus (Fig. 1*A*). Finally, as would be expected from a linear filter, cells tuned to low spatial frequencies only produce excitation when the stimulus contains a 'real' low frequency component in its spectrum, and not when only an 'apparent' low frequency is present. That is, the cells were not excited by the low frequency periodicity produced by the sum of the higher harmonics, 4F + 5F + 6F. To a first approximation, then, the visual system behaves as a linear multiple-channel system.

However, these experiments reveal two types of non-linearities that are second order but nonetheless important. One is that frequencies well outside the excitatory filter characteristic can often inhibit a cell's responses: the reduction in the responses shown in Figs. 7–10 cannot be accounted for from a strict, linear, independent-filter model. One cell we studied showed as much as 60 % reduction in response to its best spatial frequency when that frequency was presented together with a set of distant frequencies (which by themselves produced no measurable response from the cell). We would describe this as a second order non-linearity because it only quantitatively reduces somewhat the cells' predicted responses to stimuli rather than producing responses to stimuli at which there is no power, as a major non-linearity (such as that postulated by Henning *et al.* 1975) might do.

The other non-linearity revealed in these experiments is that the responses of cortical cells are, to a large extent, rectified due to their lack of spontaneous discharge. Such rectification introduces harmonics into the cells' responses which are not present in the stimulus. These non-linear aspects of striate cells may well account for many of the psychophysical demonstrations of non-linearity.

The human psychophysical experiments of Henning *et al.* (1975) are inconsistent with the hypothesis that the visual system analyses patterns into completely independent spatial frequency channels: their experiments clearly demonstrate a lack of independence in that channels tuned to low frequencies can be influenced by an appropriate combination of high frequencies (two octaves removed). To account for their results Henning *et al.* proposed a hypothetical model which, if true, would considerably weaken the notion that cells in striate cortex are acting like bandpass spatial frequency filters (each producing excitation to only a limited range of frequencies). The model they propose (as diagrammed in their Fig. 13) suggests that channels tuned to low frequencies receive excitatory inputs from channels tuned to high frequencies; given this arrangement, low frequency channels would produce excitation not only to low frequency sinusoidal variations in *luminance* but would also produce excitation to low frequency variations in the contrast of high frequency gratings. Our physiological results presented here do not support their model and in fact suggest a quite different explanation for their psychophysical findings.

On the basis of their model (described above) one would predict that a striate cell tuned to a band of frequencies centred around 1F should produce an excitatory response when presented with a pattern composed of 4F + 5F + 6F, since the latter has a beat frequency, or contrast modulation, with a period equal to 1F. The prediction was not fulfilled. As illustrated in Fig. 3, cortical cells tuned to low frequencies (centred around 1F) do not produce excitation to the higher harmonic stimulus pattern (4 + 5 + 6)F. Such low frequency cells were affected by the high frequency pattern; the effect, however, was inhibitory rather than excitatory. As shown in Fig. 6, such a cell's response to 1F (its best frequency) was clearly reduced, rather than enhanced, when 4F + 5F + 6F was added.

The inhibition produced by the 4F + 5F + 6F pattern on a cell tuned to 1F could account for the masking shown by Henning *et al.* (1975). However, the implication from the psychophysical experiments that the effect is dependent upon the 'apparent' low frequency beat is not supported by our experiments. As illustrated in Fig. 9, we found that 4F alone could reduce the response as much as 4F + 5F + 6F. This result suggests that the masking is caused by a generalized inhibition from frequencies