

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

BY DUANE G. ALBRECHT AND RUSSELL L. DE VALOIS

From the Department of Psychology, University of Texas, Austin, Texas 78712, U.S.A. and the Department of Psychology, University of California, Berkeley, California, U.S.A.

(Received 25 February 1981)

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-Cugeil, 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 respired 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; accommodation was paralysed and the natural pupil dilated by applying cyclopentolate 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 triethiodide. 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

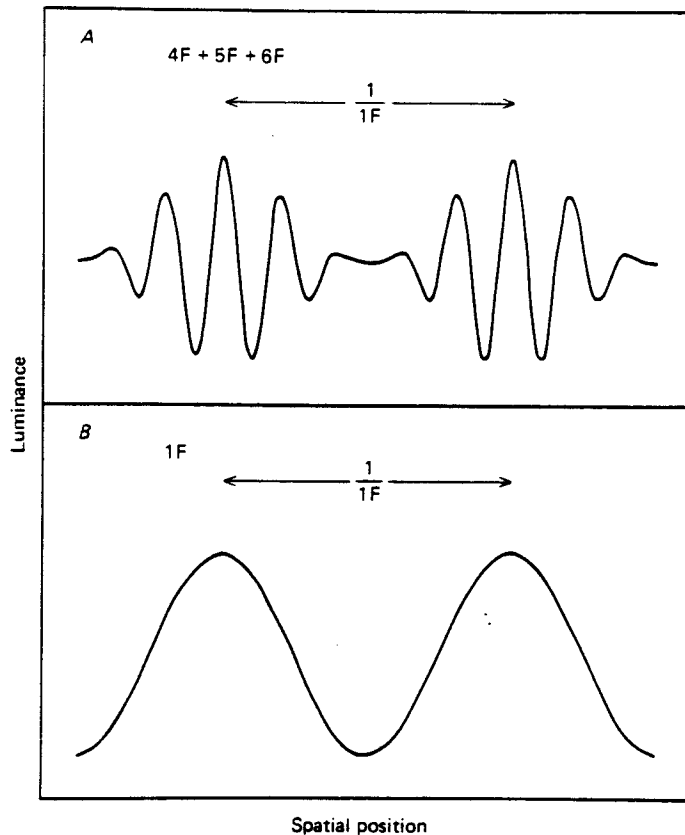


Fig. 1. *A* shows the distribution of luminance produced by summing the three harmonics $4F$, $5F$ and $6F$ in cosine phase at amplitudes of 0.25 , 0.5 and 0.25 respectively. The modulation of the pattern varies periodically (beats) with a period equal to that of the fundamental, $1F$, as can be seen by comparing it with *B* which shows the luminance distribution of the fundamental, $1F$.

roughly the same mean luminance level (27.4 cd/m^2). 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 $(\max - \min)/(\max + \min)$.

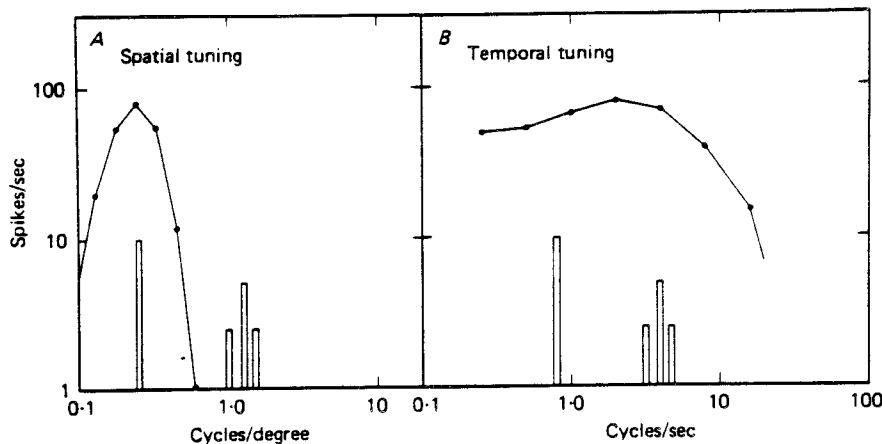


Fig. 2. *A* shows the spatial frequency tuning function for a cat striate simple cell as well as the location and relative amplitudes of the harmonics ($1F$, $4F$, $5F$, $6F$) of the stimulus used to test the cell in Experiment 1. As can be seen, the cell has a bandpass characteristic of about 1 octave 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

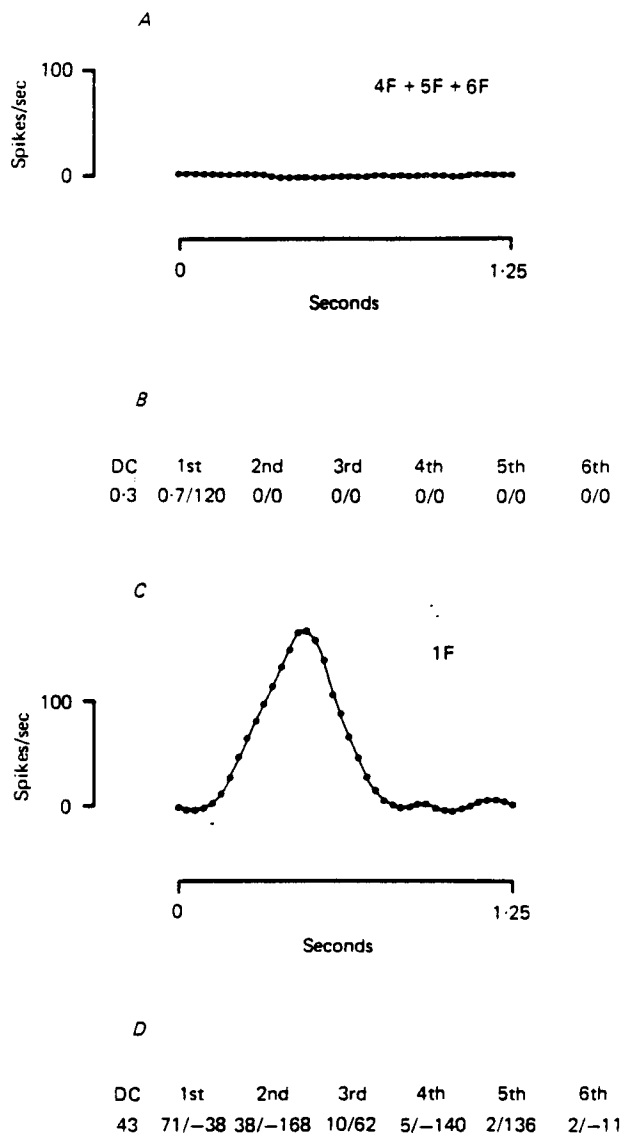


Fig. 3. *A* shows the PSTH of the cell shown in Fig. 2 when presented with the stimulus shown in Fig. 1*A* (that is, $4F + 5F + 6F$). As can be seen, the cell gives essentially no response to the high frequency harmonics even though the pattern has an 'apparent' low frequency periodicity equal to the period of the cell's best spatial frequency. *B* is a print-out 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.

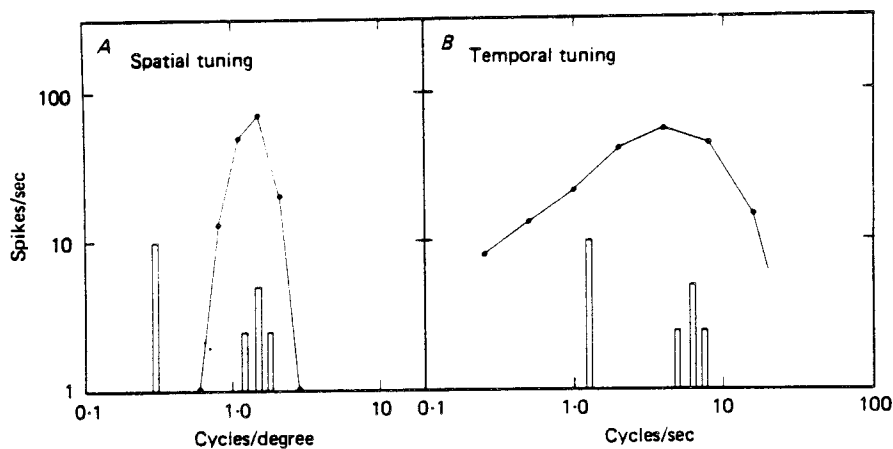


Fig. 4. *A.* spatial frequency tuning function of a cat striate simple cell in relation to the stimulus frequencies ($1F$, $4F$, $5F$, $6F$) used to test the cell in Experiment 2. Since only the higher harmonics fall within the spatial bandpass, they alone should influence the cell's response. *B.* temporal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