

ON THE EXISTENCE
OF NEURONES IN THE HUMAN VISUAL SYSTEM
SELECTIVELY SENSITIVE TO THE ORIENTATION AND
SIZE OF RETINAL IMAGES

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SUMMARY

1. It was found that an occipital evoked potential can be elicited in the human by moving a grating pattern without changing the mean light flux entering the eye. Prolonged viewing of a high contrast grating reduces the amplitude of the potential evoked by a low contrast grating.

2. This adaptation to a grating was studied psychophysically by determining the contrast threshold before and after adaptation. There is a temporary fivefold rise in contrast threshold after exposure to a high contrast grating of the same orientation and spatial frequency.

3. By determining the rise of threshold over a range of spatial frequency for a number of adapting frequencies it was found that the threshold elevation is limited to a spectrum of frequencies with a bandwidth of just over an octave at half amplitude, centred on the adapting frequency.

4. The amplitude of the effect and its bandwidth are very similar for adapting spatial frequencies between 3 c/deg. and 14 c/deg. At higher frequencies the bandwidth is slightly narrower. For lower adapting frequencies the peak of the effect stays at 3 c/deg.

5. These and other findings suggest that the human visual system may possess neurones selectively sensitive to spatial frequency and size. The orientational selectivity and the interocular transfer of the adaptation effect implicate the visual cortex as the site of these neurones.

6. This neural system may play an essential preliminary role in the recognition of complex images and generalization for magnification.

INTRODUCTION

Recently, attempts have been made to apply Fourier theory in describing the transmission of spatial information through the visual system. Using this approach it has been possible to compare and contrast, quantitatively, the role in this process of the retinal, geniculate and cortical neurones, as well as the preceding optics.

Not only has this simple approach been of value in the quantitative study of single units, it has also proved useful in the treatment of psychophysical responses from human observers, providing a unifying mathematical description of the threshold for non-repetitive patterns, such as lines and bars (Campbell, Carpenter & Levinson, 1969), as well as for gratings of simple and complex wave form (Campbell & Robson, 1968).

These studies raise the question of how the brain deals with spatial information and interprets the retinal image. Campbell & Robson (1968) have proposed that there may exist in the visual nervous system a number of elements each selectively sensitive to a limited range of spatial frequency i.e. a system of neurones encoding the dimensions of retinal images. However, they made no attempt to measure quantitatively the properties of these elements. But such measurements have been made on single units in the cat cortex and these are presented in the preceding article, where it is reported that the cat does possess cells each of which responds to a narrow range of spatial frequency (Campbell, Cooper & Enroth-Cugell, 1969).

In this paper we attempt to measure the properties of these neurones in man and compare them with those found previously in the cat. To achieve this we have used a recently discovered, spatial-adaptation effect.

Gilinsky (1968) found that an observer's acuity for a striped pattern is lowered by adaptation to a pattern of identical orientation and bar width but of higher mean luminance. She also found that this adaptation effect decreases as the orientation of the acuity grating is altered relative to the adapting grating.

Blakemore & Campbell (1969) noticed this adaptation phenomenon during a study of the occipital evoked potential and went on to confirm its orientation selectivity psychophysically. They used gratings with sinusoidal light distribution and measured the elevation in threshold by varying the contrast of the grating while keeping its space-average luminance constant. In addition, they discovered that the effect is maximal when the test and adapting gratings are identical in spatial frequency. Pantle & Sekuler (1968) also found that this psychophysical adaptation is frequency dependent.

This phenomenon cannot be due to a conventional after-image, because

it occurs even when the subject does not fixate steadily upon the high contrast grating but permits his gaze to roam over the pattern. Furthermore, under those conditions no after-image of the grating is perceived when a uniform surface is viewed after adaptation.

In Part I of this paper we establish the characteristics of this adaptation effect and in Part II we use the phenomenon to detect the presence and measure the properties of neurones selectively sensitive to spatial frequency.

METHODS

Stimulus. Gratings, the luminance profile of which varied sinusoidally along the horizontal meridian, were generated on an oscilloscope using a method described by Campbell & Green (1965). The space-average luminance was kept constant at about 100 cd/m². The pattern could be switched on and off, or its phase displaced by 180°, without changing the mean luminance. The contrast was varied by a logarithmic attenuator and a potentiometer in series. The contrast was monitored by measuring the amplitude of the signal to the oscilloscope by means of a logarithmic converter (Hewlett-Packard, type 7561 A). The output of the log converter was monitored by a digital voltmeter or displayed on a *x-y* plotter. The viewing distance was 114 in. and the diameter of the screen 3 in. (subtending 1.5 deg. at the eye) except for the experiment described in the legend of Fig. 12.

During all psychophysical measurements of contrast threshold the pattern was turned on and off twice per second, without change in mean luminance.

Recording of evoked potential. One electrode was applied to theinion and the other 2½ cm temporally. Signals were differentially amplified with an earthed electrode applied to the forehead. High and low pass filters with corner frequencies of 8 and 25 c/sec were used in the amplifier and the output was led to a computer of averaged transients (Enhancetron). The evoked potential was averaged for 200 sweeps. To provide a time-dependent patterned stimulus which would evoke a potential, the phase of the grating was changed by 180° at a rate of 8 times per second. Care was taken to avoid signals arising from nearby muscles by suitable positioning and training of the subject.

RESULTS

Part I

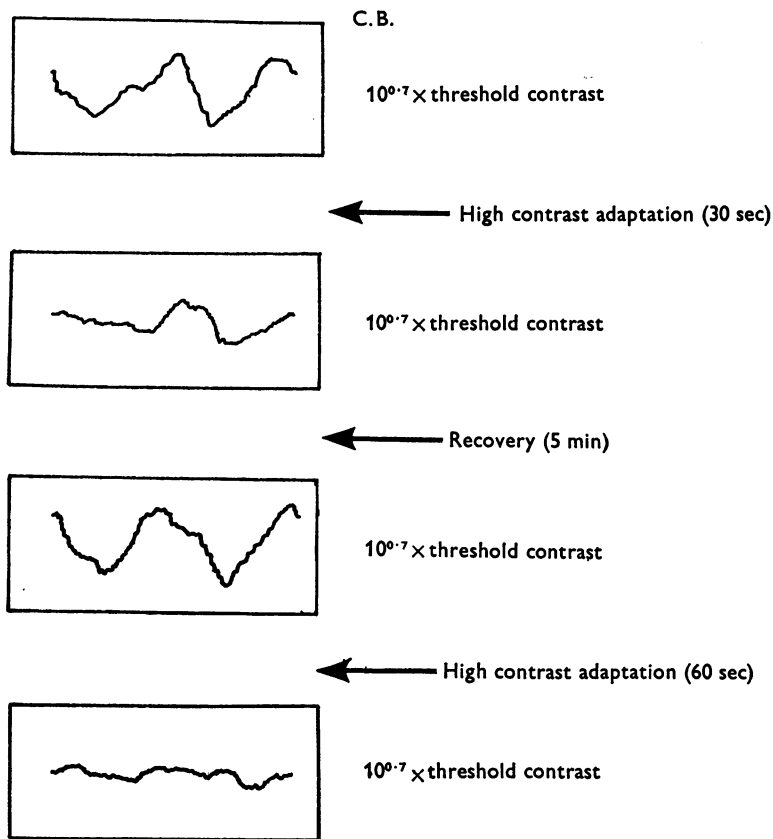
The pattern adaptation effect

Evoked potential evidence

It is important to note that, in this experiment, the flux of light reaching the eye did not change as the phase of the stimulus was switched. An evoked potential can, therefore, be generated solely by a change in retinal position of a pattern, as reported by Cobb, Ettliger & Morton (1968).

During this study of the human occipital potential evoked by a moving patterned stimulus, we discovered that the amplitude of the potential generated by a low contrast moving grating is markedly reduced if the subject has recently viewed a similar pattern of high contrast. The results are shown in Text-fig. 1. The failure to record objectively an evoked potential after adaptation to a high contrast grating was accompanied by

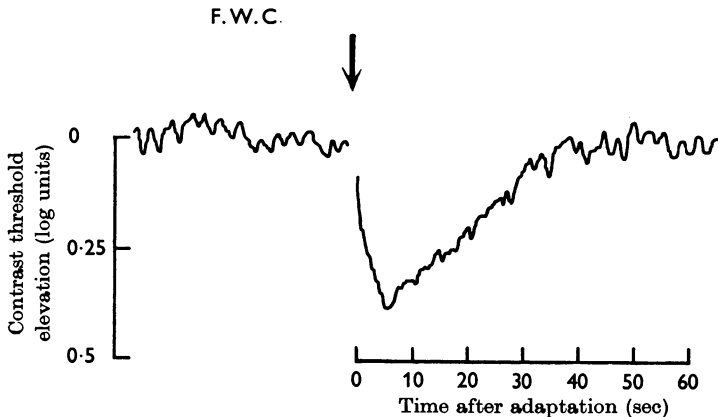
subjective fading of the low contrast pattern. We found it impracticable to collect detailed information about this effect using the evoked potential technique and we therefore decided to study it using psychophysical methods.



Text-fig. 1. The effects of spatial adaptation on the evoked potential for subject C.B. A sine-wave grating pattern (12 c/deg.) was shifted in phase by 180° , eight times per second, and the occipital potential evoked was summed 200 times on the Enhancetron to produce the records shown in boxes on the left. The stimulus was identical for each record. Each trace shows the potential for two phase shifts. The first record is for a low contrast grating, $10^{0.7}$ times the threshold contrast for this spatial frequency. C.B. then viewed a high contrast grating (1.5 log units above threshold) for 30 sec and the potential for the same low contrast grating was immediately re-measured. This second trace is clearly rather lower in amplitude than the first. After 5 min recovery the low contrast grating produced a record (3rd box) very similar to that of the original. The final record taken after 60 sec exposure to the high contrast grating has no distinguishable signal. The failure to record the potential was accompanied by subjective elevation of threshold.

Psychophysical evidence

Time course of recovery. The subject used a potentiometer to set the contrast of the grating on the oscilloscope to his own threshold before and after adapting to a high contrast pattern. After logarithmic conversion the contrast settings were displayed against time. A typical result is shown for subject F.W.C. in Text-fig. 2. The record to the left of the arrow was obtained before adaptation. The fluctuations represent the subject's



Text-fig. 2. The time course of recovery from adaptation. F. W. C. turned a potentiometer to adjust the contrast of the grating (12.5 c/deg.) until it was just visible. His searching movements oscillate around threshold in the first part of this record from an x - y plotter, after logarithmic conversion. The arrow indicates a period of 60 sec during which the record was stopped and F.W.C. viewed a high contrast grating (1.5 log units above threshold). The trace re-starts as he searches for his elevated threshold and gradually tracks the recovery back to normal contrast sensitivity, which is complete in about 60 sec.

attempts to estimate and re-estimate the contrast at which the grating appeared and disappeared. Their amplitude is about 0.05 log units and they clearly oscillate about some steady threshold value. The arrow indicates the lapse of 60 sec during which the contrast of the pattern on the screen was increased by the experimenter to 1.5 log units above the subject's threshold. The subject viewed this adapting pattern continuously, allowing his eye to wander over the screen to avoid the formation of an after-image.

At the end of this period, the experimenter reduced the contrast of the grating and instructed the observer again to set the contrast to threshold. The record to the right of the arrow describes the time course of the recovery of the contrast sensitivity. It will be noted that initially, the subject took a few seconds to locate his elevated threshold and thereafter

he steadily tracked the slow recovery until he reached the original threshold setting where the record reaches a plateau.

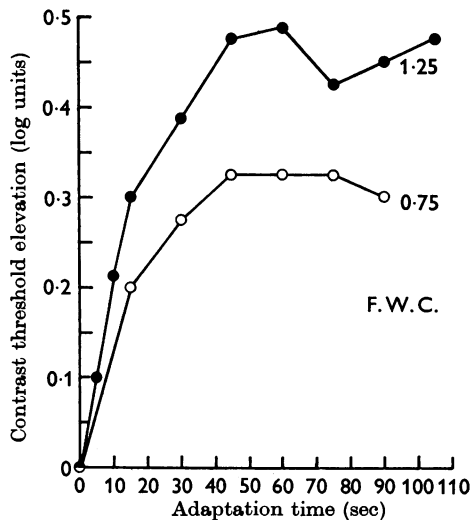
The logarithm of the contrast is being recorded and, since the recovery phase is approximated by a linear slope, we conclude that the recovery function is exponential. The time constant of this function in this example is about 20 sec. There was no significant variation in this time constant for five subjects nor over a wide variety of stimulus conditions, with the short adaptation times used here.

For most of the remaining experiments we found it unnecessary to record the complete recovery phase and instead decided that it was convenient and sufficient to measure the initial, elevated threshold, immediately after the adapting period. The subject was therefore instructed to adjust the contrast as quickly as possible to his new threshold. Thereupon, he pressed a switch and the output of the logarithmic converter was displayed on a 4-digit voltmeter.

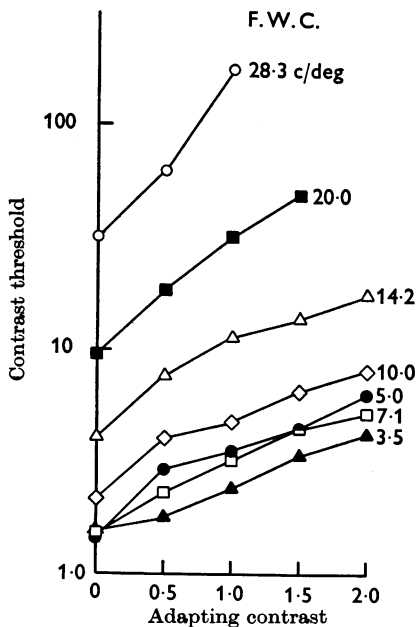
Time course of induction. The results shown in Text-fig. 3 were obtained by having an observer (F. W. C.) view a sinusoidal grating of 15 c/deg. (cycles per degree subtended at the eye) for various periods of time and determining his rise of threshold immediately after each adaptation period. A recovery time of at least 3 min was allowed between each reading. For the upper curve the adapting grating was set at a contrast of 1.25 log units above the normal contrast threshold for this grating. For the lower curve the grating was 0.75 log units above threshold. It is evident that, although the effect is greater for the higher contrast grating, the time course is similar for the two examples and that in both cases the adaptation effect reaches a plateau after viewing for about 1 min.

Therefore in all subsequent experiments an initial adaptation period of at least 60 sec was used in order to reach the equilibrium level. In cases where a number of threshold determinations were required under the same adaptation conditions, the subject viewed the screen continuously, the first reading being made after initial adaptation for 1 min. Subsequent estimates were made after at least 10 sec of re-adaptation each time. After the initial adaptation the low contrast test pattern was exposed and a threshold setting made as quickly as possible. The high contrast pattern was then substituted for the periods of re-adaptation between subsequent readings. This period was found to be sufficient to maintain the adaptation at the equilibrium level.

The contrast of the adapting pattern. Text-fig. 4 shows the result of an experiment in which pattern adaptation was measured for gratings of a number of spatial frequencies over a range of adapting contrast. The points are joined for each spatial frequency. These slopes are approximately parallel for all but the highest spatial frequencies (20 c/deg.,

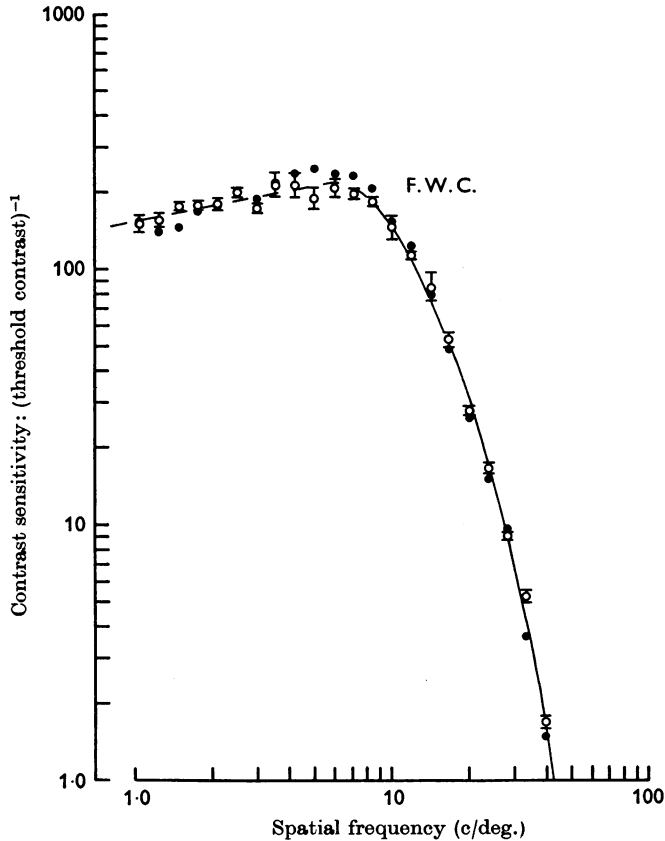


Text-fig. 3. The effect of adapting time. The initial elevation of threshold for F.W.C. is plotted against the adaptation time. For the filled circles the adapting grating of 15 c/deg. was 1.25 log units above threshold. For the open circles it was 0.75 log units above threshold.



Text-fig. 4. The effect of adapting contrast. The initial contrast threshold for F.W.C., after a period of adaptation, is plotted, on an arbitrary logarithmic scale, against the contrast of the adapting pattern in log units. Results are shown for a number of spatial frequencies: in each case adapting and test gratings were of the same frequency. The data points for zero adapting contrast are, of course, the normal contrast threshold values.

28.3 c/deg.). However, since there was only a limited range of supra-threshold contrast available for these frequencies too much significance should not be attached to this finding. The first point on each curve is the contrast threshold for that spatial frequency with no previous adaptation.



Text-fig. 5. The contrast sensitivity function for F.W.C. Contrast sensitivity is plotted on an arbitrary logarithmic scale against spatial frequency. The open circles and vertical bars show initial threshold estimates with 1 s.e. ($n = 6$). The filled circles are repeat determinations at the end of the series of adaptation experiments. The continuous curve is the function e^{-f} and the interrupted portion was fitted by eye to the low frequency data points. During threshold determinations the pattern was turned on and off twice per second, without changing mean luminance.

The position of each curve on the ordinate is clearly directly related to the more familiar contrast sensitivity function, an example of which is shown in Text-fig. 5.

In the experiments described in Part II we chose to adapt with gratings at 1.5 log units above their contrast threshold. This was done in order to

produce as large an effect as possible without excluding comparable measurements at all but the highest spatial frequencies.

Binocular transfer of pattern adaptation. To find out whether this adaptation effect transfers from one eye to the other we performed the following experiment.

Initially the contrast threshold of each eye was independently determined in subject F.W.C. for a spatial frequency of 10 c/deg. The left eye alone was then adapted as in the previous experiment to a grating of this frequency, 1.5 log units above the left eye's threshold. The contrast threshold was then re-determined for each eye separately. Ten readings were taken for each eye, the high contrast grating being substituted in the left eye between each reading to maintain adaptation.

As expected, there was the usual elevation of threshold in the adapted eye. Moreover, there was a significant rise of threshold ($P < 0.001$) in the right eye which had not been adapted. However, the rise of threshold in the adapted eye was 1.6 times greater than that in the unadapted.

We therefore conclude that there is definite, but incomplete, interocular transfer of the adaptation phenomenon.

Part II

Spatially selective channels

Contrast sensitivity characteristic before adaptation

Initially we determined the contrast sensitivity for a series of spatial frequencies spaced at one quarter octave intervals. These results are shown in Text-fig. 5 as open circles, which are the mean of six readings, with vertical lines representing 1 s.e. At the end of the experiments described below contrast sensitivity was redetermined in order to assess any possible equipment drift or change in the observer's threshold criterion. These second determinations are shown as filled circles and it is evident that no consistent difference has occurred. The high frequency portion of the curve drawn through the data is the best fitting value of e^{-f} (f = spatial frequency), a function which previous studies have shown to be appropriate (Campbell, Kulikowsky & Levinson, 1966). The interrupted portion of the curve, through the low frequency data, was fitted by eye.

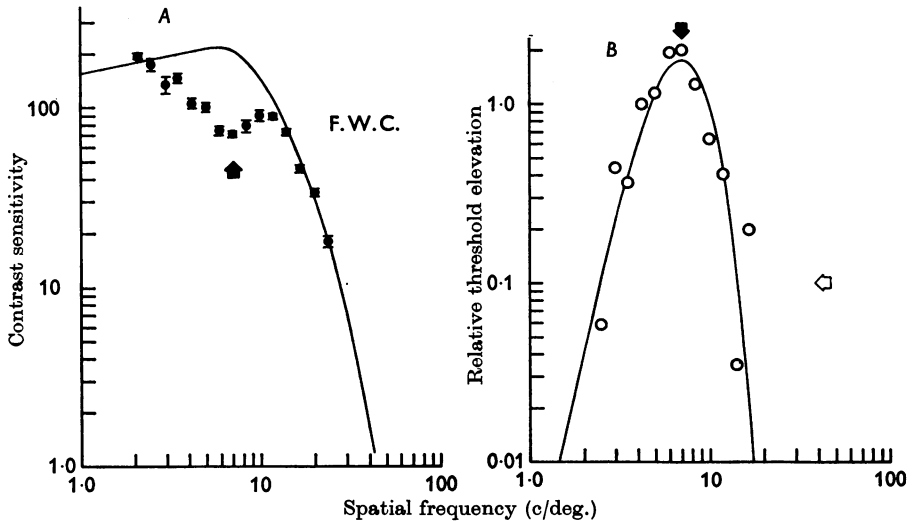
Contrast sensitivity characteristic after adaptation

The curve fitted to the data in Text-fig. 5 is reproduced in Text-fig. 6A.

As described earlier the subject continually viewed a grating of 7.1 c/deg., 1.5 log units above threshold for that frequency. While this adaptation was maintained, the contrast threshold for frequencies from 2.1

to 23.8 c/deg., at one quarter octave steps, was determined by briefly interpolating the low contrast test grating which the subject set to threshold.

The results are shown with their s.e. ($n = 6$). It is clear that the sensitivity has been dramatically depressed in the region of 7.1 c/deg. but that there is practically no effect beyond the frequencies 2.5 and 11.9 c/deg.



Text-fig. 6. The effect of adapting at 7.1 c/deg. *A*. The continuous curve from Text-fig. 5 is reproduced. The filled circles and vertical bars are the means and s.e. ($n = 6$) for re-determinations of contrast sensitivity at a number of spatial frequencies while F.W.C. was continuously adapting to a grating of 7.1 c/deg., 1.5 log. units above threshold. The exact procedure is described in the text.

B. The depression in sensitivity due to adaptation at 7.1 c/deg. is plotted, with open circles, as relative threshold elevation against spatial frequency. The vertical difference between each point and the smooth curve in Text-fig. 6 *A* is the ratio of sensitivity before and after adaptation. The relative threshold elevation is the anti-logarithm of this difference minus 1, so that no change in threshold would give a value of zero on the ordinate. The continuous curve is the function $[e^{-f^2} - e^{-(2f)^2}]^2$, fitted by eye to the data points. The filled arrows show the adapting frequency of 7.1 c/deg. The open arrow marks the value on the ordinate for a threshold elevation equivalent to $2/\sqrt{2}$ times an average s.e. for determining contrast sensitivity.

It is conceivable that adaptation at one specific frequency might have affected contrast threshold at all measurable spatial frequencies. If such were the case the over-all contrast sensitivity curve should have been uniformly lowered. This is not so, and we therefore conclude that the adapting pattern is principally depressing the sensitivity of some 'channel', independently of others, and that this channel is adapted by a limited range of spatial frequency.

In order to define its characteristics more specifically we have reduced

the data as follows. We took the difference between each data point and the smooth curve in Text-fig. 5, at each spatial frequency. This difference is the ratio of sensitivity before and after adaptation (since the ordinate is logarithmic). If there be no effect of adaptation on the contrast sensitivity then this ratio should theoretically be 1. If there is a depression of sensitivity after adaptation the ratio will be greater than 1. For example, at 7.1 c/deg. in Text-fig. 6 the ratio was 3.0 as the depression in contrast sensitivity was 0.48 log units. For mathematical convenience in describing the effect, we subtracted 1 from each ratio in order to express the depression as a positive increment above zero, so in this example the relative threshold elevation at 7.1 c/deg. is 2.0. In Text-fig. 6B we plot the log adaptation effect, derived in this manner, against log spatial frequency.

Naturally, due to the statistical variations in determining the mean contrast sensitivity, both before and after adaptation, some of the ratios which have values close to zero will be negative after this transformation. As no negative values of statistical significance were found, these points do not help us to define the shape of the curve and they have therefore been omitted. Indeed, probably some of the positive values which are plotted between 0.01 and 0.1 may not be significantly different from zero and little emphasis should be placed on them. An average standard error for re-determining contrast sensitivity without adaptation was about 0.02 log units. The ratio of twice the standard error of the difference to the original mean would give a value of about 0.1 on the ordinate of Text-fig. 6B. An open arrow marks this average significance level on the graph.

The curve fitted to these results is the simple function

$$[e^{-f^2} - e^{-(2f)^2}]^2.$$

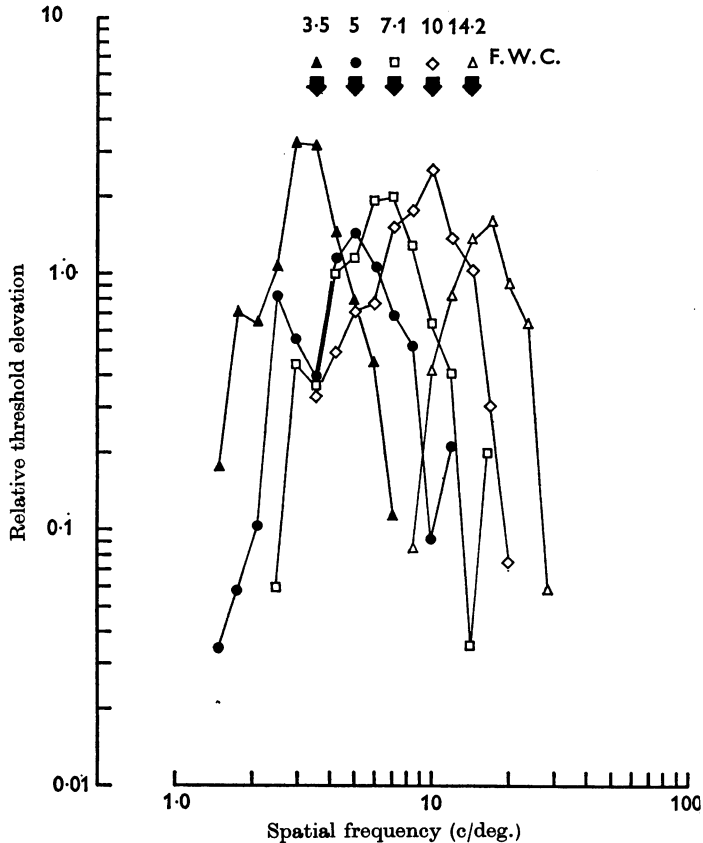
Adaptation characteristics at other spatial frequencies

The middle frequencies. The above experiment was repeated using adapting gratings of the following spatial frequencies, 3.5, 5.0, 7.1, 10.0 and 14.2 c/deg. These results are shown in Text-fig. 7, plotted as in Text-fig. 6B. It is clear that the effect is maximal at the spatial frequency used for adaptation and that the magnitude, that is the position on the ordinate, is similar in all cases.

To express the similarity of shape for these curves we reproduce the results normalized for the spatial frequency of the adapting grating. This transformation is shown in Text-fig. 8. This method of pooling the data illustrates that the individual curves are very similar and that good superposition of the results does not require displacement of these individual curves on the ordinate. Because of the similarity of functions relating threshold elevation to the contrast of the adapting grating, whatever the

spatial frequency of the letter (see Text-fig. 4), this result was not unexpected. The maximum elevation of threshold is determined by the contrast of the adapting grating, whatever its spatial frequency. It can be seen that the function

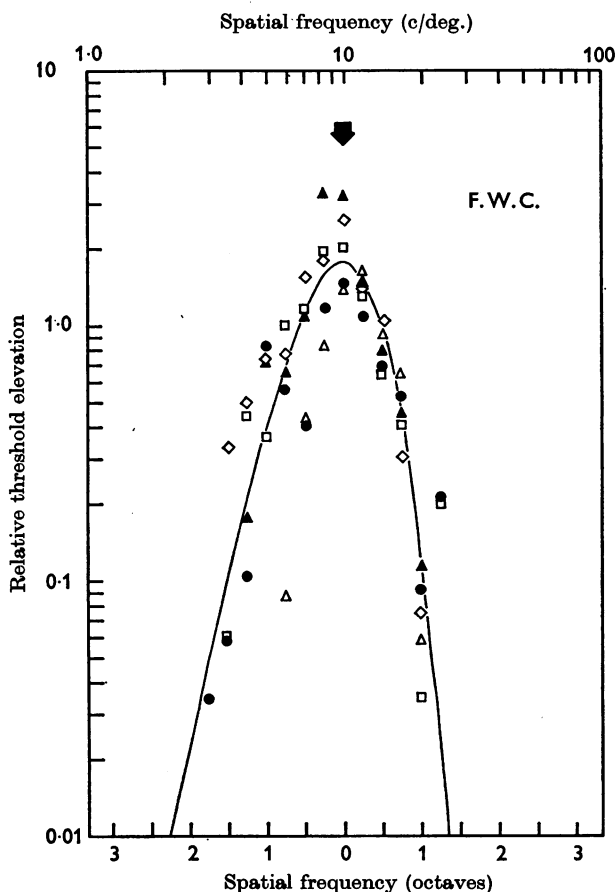
$[e^{-f^2} - e^{-(2f)^2}]^2$ fits all the pooled data.



Text-fig. 7. Adaptation characteristics derived as in Text-fig. 6 for five adapting spatial frequencies. Each arrow marks the frequency of adaptation and above it is the symbol used for the relative threshold elevation caused by the adaptation. Points are joined in order of spatial frequency. The adapting frequencies were 3.5, 5.0, 7.1, 10.0 and 14.2.

High spatial frequencies. At higher spatial frequencies the contrast sensitivity decreases rapidly (see Text-fig. 5) and inevitably there is little reserve of suprathreshold contrast available for adaptation. Thus we were unable to adapt with gratings of 1.5 log units above threshold, as in the preceding experiments, and we were forced to use only 1.25 log units for

adaptation at 20 c/deg. and 1.0 log units for 28.3 c/deg. Therefore these results, shown in Text-fig. 9, cannot strictly be compared with the results of the previous section. In this Text-fig. the adaptation data for these two high spatial frequencies are displayed as in Text-fig. 7. The smooth curves

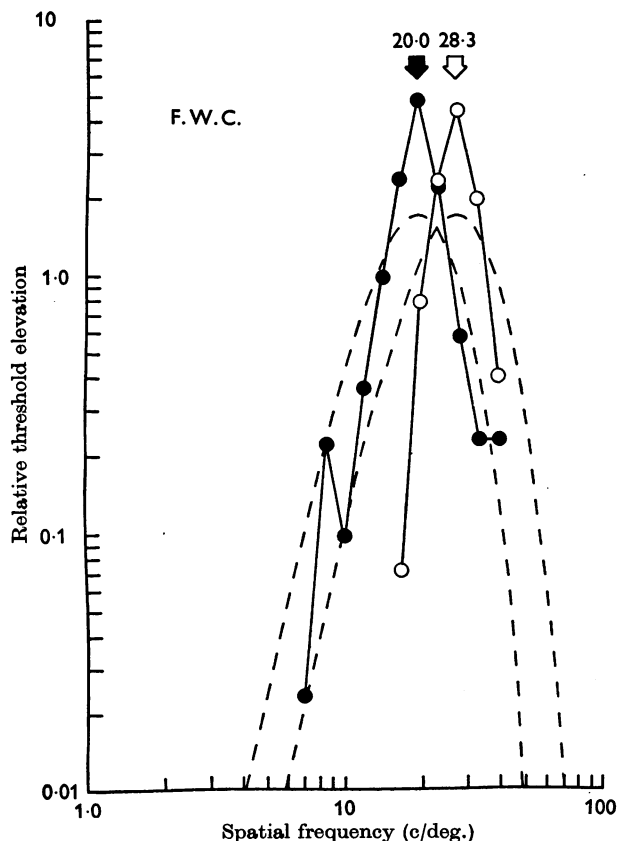


Text-fig. 8. Adaptation characteristics normalized for spatial frequency. The data points of Text-fig. 7 have been shifted along the abscissa so that all the adapting frequencies superimpose at 10 c/deg., shown by the arrow. The abscissa is also expressed, on the lower scale, as octaves of spatial frequency on either side of the adapting frequency. There is no normalization on the ordinate and the continuous curve is the function fitted in Text-fig. 6B, at the same position on the ordinate.

are the same function fitted to all the previous results, at the same position on the ordinate. Clearly this function does not fit these high frequency data. The adaptation characteristics appear to be narrower and the maximum effect greater than at lower spatial frequencies, despite the lower adapting contrasts used. This latter point is illustrated in another

way in Text-fig. 4 where it may be seen that the threshold elevation *versus* adapting contrast functions are steeper for 20 and 28.3 c/deg. than for other spatial frequencies.

Low spatial frequencies. The low spatial frequency results must be treated separately because of an unexpected observation. We found that for adapting frequencies lower than 3 c/deg. the maximum adaptation



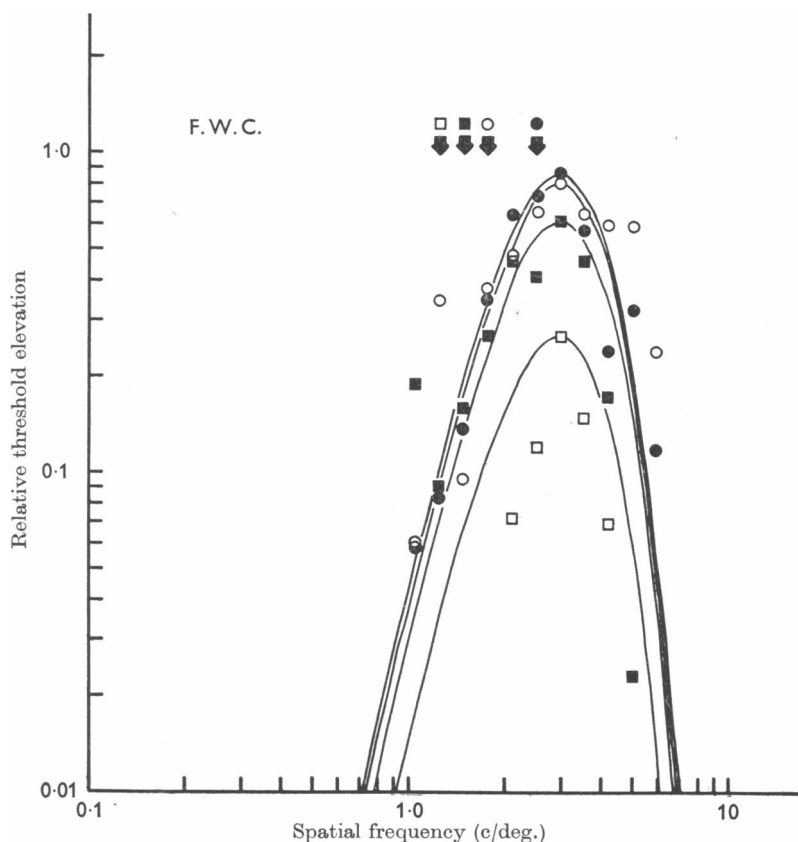
Text-fig. 9. Threshold elevation for adaptation at 20 c/deg. (filled circles) and 28.3 c/deg. (open circles). The symbols are joined. The interrupted curves are the same function fitted in Text-fig. 6B at the same position on the ordinate as in Text-fig. 6B, 7 and 8, and with the peak at the adapting frequency.

effect did not occur, as in the previous experiments, at the same frequency as the adapting grating. Text-figure 10 shows the effect of adapting to gratings of 2.5, 1.8, 1.5 and 1.3 c/deg. It will be noted that, as the spatial frequency of the adapting grating is lowered the magnitude of the adaptation effect is decreased without, however, its position changing on the frequency scale. All the curves peak at about 3 c/deg. When we attempted

to adapt to spatial frequencies less than 1.3 c/deg. there was no significant elevation of threshold at any spatial frequency.

The effect of contrast on spatial selectivity

In the prior experiments, the contrast of the adapting grating was usually set at 1.5 log units above threshold at each discrete spatial frequency. It is evident from Text-fig. 4 that the elevation of threshold at the same spatial

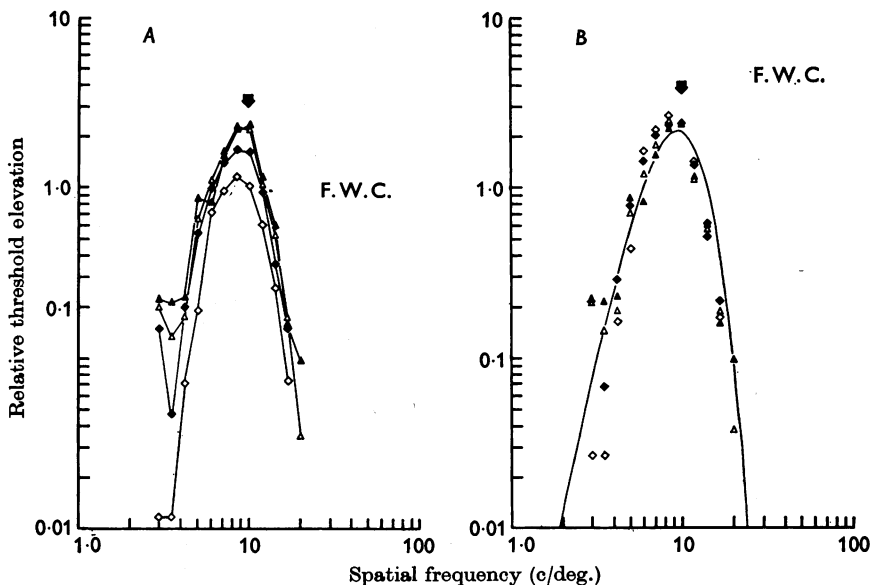


Text-fig. 10. The effect of adapting at 2.5 (●), 1.8 (○), 1.5 (■) and 1.3 (□) c/deg. Arrows with appropriate symbols above show these frequencies. The smooth curves are the function fitted in Text-fig. 6B, normalized on the abscissa and with the peak passing through the data point at 3.0 c/deg., since this is the frequency of maximum threshold elevation for all these adapting frequencies.

frequency as the adapting pattern increases with the contrast of the latter. Could it be that the shape of the whole adaptation characteristic depends upon the contrast of adaptation? We tested this speculation at a frequency of 10 c/deg. by adapting at contrast levels of 0.5, 1.0, 1.5 and 2.0 log units

above threshold, and measuring the change of threshold for neighbouring frequencies as in the previous experiments.

The results are shown in Text-fig. 11 *A*. It may be seen that the position of each curve on the ordinate does depend, as we expected, on the contrast of the adapting pattern. However, the shape appears to be remarkably similar in each instance. This point is better illustrated by normalizing on the ordinate for data points at the central spatial frequency (10 c/deg). This transformation is shown in Text-fig. 11 *B*. The continuous curve is the function previously found to give a good fit (Text-fig. 8).



Text-fig. 11 *A*. Each set of points shows the effect of adapting at 10 c/deg. The different symbols refer to different contrasts of the adapting pattern, as shown below. Symbols are joined. The arrow marks the adapting frequency.

B. The data points for adapting contrasts of 1.5, 1.0 and 0.5 log units above threshold have been shifted up until the points at the adapting frequency all superimpose on that for 2.0 log units of adapting contrast. The smooth curve is the function from Text-fig. 6 *B*, at the same position on the ordinate and centred at 10 c/deg.

▲, 2.0 log units; △, 1.5 log units; ◆, 1.0 log units; ◇, 0.5 log units.

It thus appears that within the middle frequency range the shape of the adaptation characteristic is independent of both the frequency of the adapting pattern (Text-fig. 8) and its contrast (Text-fig. 11).

Contribution of individual mechanisms to contrast sensitivity characteristic

It is clear from Text-fig. 5 and Text-fig. 8 that the adaptation characteristic is restricted to a narrow band of spatial frequency compared with the broad band of frequencies that can be detected by the visual system.

Consider the hypothesis that the adaptation characteristics established in Text-fig. 7 reflect the presence of neurones each selectively sensitive to a limited range of spatial frequency. If this be so, the shape of the over-all contrast sensitivity could be due to the combination of the sensitivity characteristics of individual narrow-band detectors.

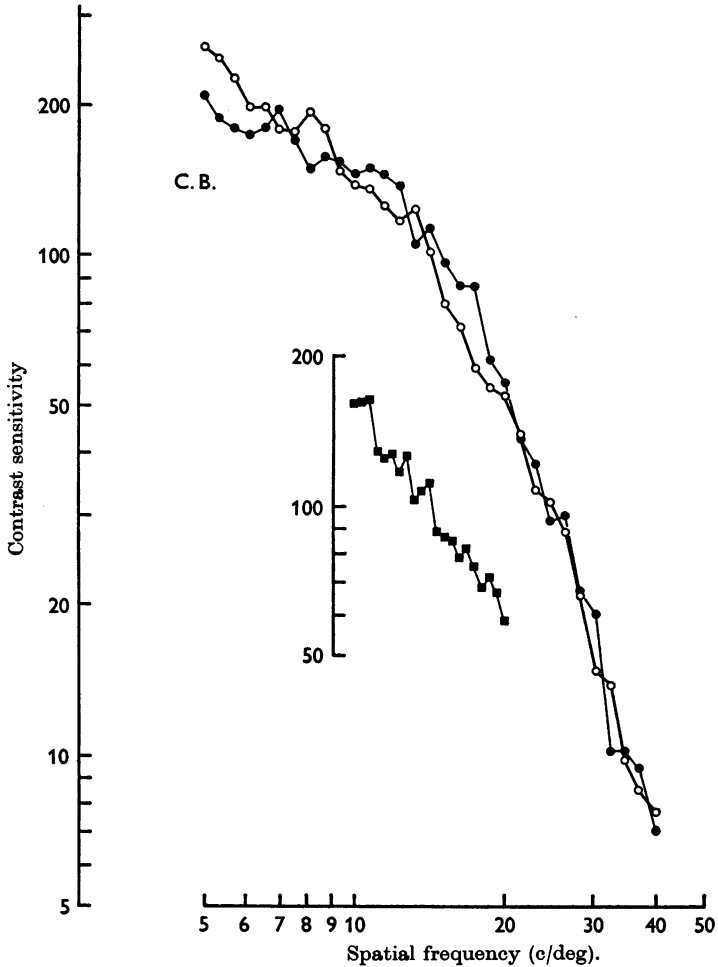
The presence of these narrow band detection characteristics dispersed throughout the spectrum of spatial frequency might lead to minor irregularities in the contrast sensitivity function, particularly if they were few in number or regularly spaced along the frequency domain. Indeed Patel (1966) has suggested that the contrast sensitivity function of man may have such irregular 'bumps' and Nye (1968) has reported them on the contrast sensitivity function of the pigeon.

In order to be confident of such excursions in the over-all sensitivity function it is necessary to sample contrast sensitivity at much closer frequency intervals than has been used heretofore. It is also essential to avoid small instrumental artifacts in generating gratings of different spatial frequency which might arise, for example, from small variations in the time-base trigger point. We chose, therefore, to measure contrast sensitivity initially at frequency intervals of $\frac{1}{10}$ octave and to produce these various spatial frequencies by changing the viewing distance for a pattern of constant frequency generated on the oscilloscope. Two runs were made at $\frac{1}{10}$ octave intervals over a range of 3 octaves from 5 to 40 c/deg. with six readings at each frequency for each run. The means are plotted in Text-fig. 12. It can be seen that although there are slight excursions in the contrast sensitivity within one run, these bumps are not correlated on the frequency scale in the two runs. We therefore conclude that there are no significant excursions from a smooth contrast sensitivity function.

To be doubly sure of this conclusion, in a third run, we sampled a one octave range (from 10 to 20 c/deg.) at $\frac{1}{20}$ octave intervals. The results are shown in Text-fig. 11 as squares and, to avoid confusion, they have been displaced downwards from the data for the first two runs by one half a log unit on the contrast sensitivity ordinate. These results again indicate that, if there are significant bumps, they are very small in amplitude, or closer than about one tenth of an octave in frequency, and therefore not detected by us.

Adaptation with a square-wave grating

Campbell & Robson (1968) and Robson & Campbell (1964) have shown that if contrast sensitivity is measured with a square-wave grating, the

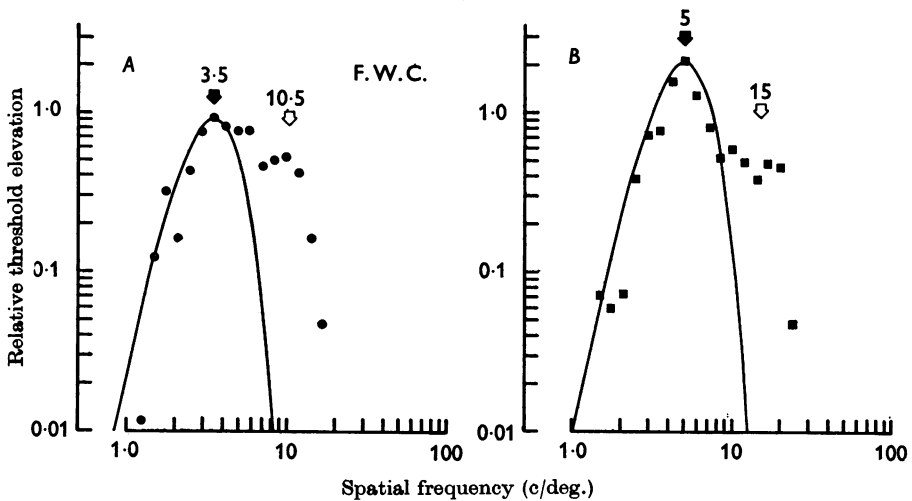


Text-fig. 12. Normal contrast sensitivity for C.B. The frequency on the screen was fixed at 13.3 c/in. and the screen diameter was 3 in. Spatial frequency at the eye was varied in one tenth octave steps by changing the viewing distance. This manoeuvre also altered the angular subtense of the screen at each spatial frequency. The filled circles are the means of initial determinations ($n = 6$) of contrast sensitivity, plotted on an arbitrary logarithmic scale. The open circles are means of redeterminations under identical conditions ($n = 6$). The filled squares are further estimates of contrast sensitivity from 10 to 20 c/deg., at one twentieth of an octave steps. These points have been displaced downwards by half of one log unit and the inset ordinate is appropriate.

harmonic content plays an essential role in determining the contrast sensitivity for such gratings. The first higher harmonic in a square-wave grating is the third and it has an amplitude of one third that of the fundamental frequency; this third harmonic, three times the spatial frequency of the fundamental, is the only one which need be considered here, for the higher odd harmonics have a relatively small effective magnitude.

We might predict that the elevation of threshold for a sine wave at the third harmonic frequency might be substantially elevated after adaptation to a square-wave grating, if indeed these spatially selective mechanisms are operating independently. We measured the adaptation characteristic in the normal way after adapting to square-wave gratings of 3.5 c/deg. (Text-fig. 13A) and 5 c/deg. (Text-fig. 13B).

In each case the usual curve is fitted to the data, normalizing it to the fundamental frequency on the abscissa and the data point at that frequency on the ordinate. These results should be compared with Text-fig. 8, where sine-wave gratings were used for adaptation. The arrows



Text-fig. 13. Adaptation with a square-wave grating. In each case the filled arrow marks the spatial frequency of the square-wave grating, 1.5 log units above threshold, which was viewed for adaptation. The open arrow shows the third harmonic frequency, three times the fundamental frequency. In Text-fig. 13A the fundamental is 3.5 c/deg., in 13B it is 5.0 c/deg. The function from Text-fig. 6B is positioned with its peak at the data point for the fundamental frequency.

indicate the fundamental and third harmonic frequencies. Clearly the harmonic component of the square wave pattern has caused a substantial elevation of threshold in the region of the third harmonic frequency.

DISCUSSION

In the previous paper (Campbell *et al.* 1969) cells were found in the visual cortex of the cat each of which responded to a relatively narrow range of spatial frequency. A neurone responds to a limited band of spatial frequency and the position of this range varies over 4 octaves from unit to unit. In the present study on man we have found that prolonged viewing at one spatial frequency causes a depression of contrast sensitivity over a limited range of neighbouring frequencies. We suggest that the spatially sensitive mechanisms revealed by this adaptation reflect the properties of neurones in the human visual system, similar to those found in the cat, which are involved in the encoding of the spatial characteristics of the retinal image. Moreover, our initial observations on the human evoked potential clearly suggest that the adaptation phenomenon is associated with depression of neural activity.

In the cat cortex it was found that the spatial sensitivity function was surprisingly similar, at its high frequency end, from neurone to neurone whatever its position in the frequency spectrum. Likewise, psychophysically, we have found that for adapting spatial frequencies of 3.5–14.2 c/deg. the adaptation characteristic is remarkably constant. At very high spatial frequencies (20 and 28.3 c/deg.), beyond the resolution of the cat visual system, the human adaptation characteristic is somewhat narrower (Text-fig. 9). The functional significance of this latter finding is not yet clear.

On the evidence we have it is not possible to argue quantitatively from the response characteristics of the cat cortical neurones to the human adaptation characteristic, since we do not know, for example, how the responses of individual neurones combine when more than one neurone is activated by a particular spatial frequency. Therefore, at this stage no particular emphasis should be placed on the function we have arbitrarily chosen to fit the data and to compare one set of data with another. The striking finding is that one function describes so well the adaptation characteristic for a wide variety of adapting frequencies and contrasts.

This study of spatial adaptation has, in effect, been restricted to the fovea by the use of a centrally fixated field of 1.5° diameter. Under these experimental conditions the results of Text-fig. 10 suggest that there are no adaptable channels which have peak sensitivities of lower than 3 c/deg. It seems unlikely that the field size alone accounts for this observation since, at 3 c/deg., there were nearly 5 cycles of the grating present on the screen. It therefore appears that the size-detecting channels of central vision are handling a range of 3–4 octaves of spatial frequency.

A number of properties of the adaptation effect point to its central origin in the visual system. First, the adaptation is orientationally specific

(Blakemore & Campbell, 1969), matching the orientation selectivity of units in the cat and monkey cortex (Hubel & Wiesel, 1962, 1968; Campbell, Cleland, Cooper & Enroth-Cugell, 1968). Secondly, we have shown that spatial adaptation through one eye causes threshold elevation through the other, suggesting that the effect occurs after binocular combination. We therefore suggest that the adaptation effect exposes the properties of central human neurones beyond the optic radiation. Strength would be added to this argument by evidence that individual neurones in the cat or monkey cortex do indeed adapt in a manner that would be predicted by this phenomenon.

Adaptation phenomena of this type might be of value in crossing the species barrier and allowing a description of the neurophysiology of man for many stimulus-coding mechanisms. An elegant example of this approach is Barlow & Hill's (1963) comparison of the after effect of seen motion and the depression of spontaneous activity after exposure to moving stimuli in the direction-selective units of the rabbit retina.

In this study we have intentionally used the simplest optical stimulus (Hopkins, 1962). The sine-wave grating is simple because it contains only one spatial frequency presented in one meridian. The most complex stimulus in Fourier terms is a single sharp disk of light for it contains a very wide band of spatial frequencies and they are present at all orientations. The 'bandwidth' of the individual spatial mechanisms revealed by adaptation is quite narrow (about 1 octave at half amplitude; see Text-fig. 6*B*). Therefore any complex pattern of light on the retina, containing a wide spectrum of Fourier components, will cause activity in many mechanisms. We should like to suggest that the pattern of responses from the family of mechanisms may serve to encode the spatial content of the particular retinal image and thus lead, in an unknown manner, to its identification.

Is there any evidence to support this hypothesis? The experimental results shown in Text-fig. 13, where a square wave was used to produce adaptation, indicate that the sensitivity of two mechanisms was depressed (one at the fundamental spatial frequency and one at the third harmonic) by a single grating pattern.

The reader may perform the complementary experiment by viewing Plate 1 from a distance of about 1 m. The lower half of the upper square consists of a square-wave grating and directly above it is a sine wave of the same spatial frequency. At their contrast levels the difference is clearly distinguishable. The lower square is a high contrast grating with a spatial frequency three times that of the upper pair. The reader should view this high contrast grating, allowing his gaze to wander around the fixation circle. After about 45 sec the gaze should be transferred to the fixation

point in the centre of the upper square and it will be noted that sine- and square-wave gratings are temporarily indistinguishable.

A further piece of evidence which supports the idea that spatially selective mechanisms contribute to the perception of complex spatial patterns is described by C. Blakemore & P. Sutton (1969, in preparation). They find that adaptation to one spatial frequency causes disturbance in the appearance of neighbouring frequencies, lower spatial frequencies appear to decrease and higher to increase their apparent frequencies. This suggests that adaptation of one mechanism disturbs the distribution of activity in the population of such mechanisms activated by a nearby spatial frequency.

An advantage of a system based on frequency analysis might be that it simplifies recognition of familiar objects presented at unfamiliar magnifications. Consider a child who has just learned to differentiate the letters of the alphabet and suppose that it is asked to recognize letters presented at quite different magnifications. It does this readily even although it has never observed the letters at these specific magnifications. We know that if we are so close to an object that we cannot perceive it in entirety it cannot be readily identified; 'we cannot see the wood for the trees'. Conversely, an object that subtends too small an angle cannot be recognized. Sutherland (1968) has lucidly reviewed the literature on size invariance and concludes 'that many species have the capacity to classify a shape as the same shape regardless of changes in size, at least over a considerable range, and that this capacity is innate'.

There must be a limited range of spatial dimensions which the visual system can handle with facility and speed. If it analyses the distribution of spatial frequencies in an object into independent channels covering its range of operation and then uses the ratios of these frequencies to identify the object, it would render the absolute size of the object redundant for the purpose of image recognition, for the relative harmonic content is independent of absolute size. Only the harmonic content would have to be stored in the memory system and this would require a much smaller store than if the appearance of every familiar object had to be learned at every common magnification. This generalization for size, and therefore distance, would greatly facilitate the process of learning to recognize images in our natural environment. This system might then be analogous to the auditory system where we can identify a musical interval (frequency ratio) independently of its position in the auditory spectrum (Helmholtz, 1877).

Such a mechanism for analysing spatial frequencies would be difficult to envisage if it had to operate simultaneously in two dimensions. It may well be significant that the visual system also transmits the input signal through a number of separate orientationally selective channels, each of

which can then analyse the spatial frequency content of the object over a narrow range of orientations (Campbell & Kulikowski, 1966). Although this arrangement would lead to a further economy in the size of the memory store it would also carry the penalty that one would be restricted to recognizing familiar objects only if they were presented at the learned orientation.

HERE IS THE EVIDENCE

We cannot generalize for orientation as we can do so remarkably well for magnification.

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EXPLANATION OF PLATE

The upper section consists of two low contrast gratings, one with a sinusoidal and the other a square-wave form. From a distance of about 1 m the wave forms should be clearly distinguishable. The lower section is a high contrast square-wave grating with a spatial frequency three times that of the upper.

The high contrast grating should be viewed for about 45 sec, allowing the gaze to wander around the circle. The dot in the upper section should now be fixated and an attempt made to discriminate the low contrast sine and square wave forms.

The low contrast gratings are photographs of the oscilloscope face. The high frequency pattern has been drawn with maximum contrast to facilitate adaptation.

