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SEPARATE CHANNELS FOR THE ANALYSIS OF THE SHAPE AND THE MOVEMENT OF A MOVING VISUAL STIMULUS

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SUMMARY

1. The effects of temporal modulation on the properties of spatial frequency channels have been investigated using adaptation.

2. Adapting to drifting sinusoidal gratings caused threshold elevation that was both spatial frequency and direction specific. Little systematic difference was found between the band widths of the elevation curves for drifting and stationary gratings.

3. It was confirmed that adaptation fails to reveal channels at low spatial frequencies when *stationary* gratings are used. However, channels were revealed at frequencies at least as low as 0·66 c/deg when the test gratings were made to move. These channels are adapted only a little by stationary gratings, confirming their dependence on movement.

4. The existence of movement-sensitive channels at low spatial frequencies explains the well known observation that temporal modulation greatly increases the sensitivity of the visual system to low spatial frequencies.

5. Temporal modulation was effective at revealing these channels only when the flicker or movement of the test patterns was apparent to the observer; only at low spatial frequencies did patterns, modulated at low rates, actually appear to be temporarily modulated at threshold. At higher spatial frequencies, they were indistinguishable from stationary patterns until the contrast was some way above the detection threshold.

6. It is suggested, therefore, that the movement-sensitive channels are responsible for signalling the occurrence of movement; the channels at higher spatial frequencies give no information about temporal changes. These two systems of channels are compared to the Y- and X-cells respectively of the cat.

INTRODUCTION

The sensitivity function of the human visual system to sinusoidal gratings is not that of a single detecting mechanism but should be regarded as the envelope of the sensitivity functions of many channels, each responsive to only a narrow band of spatial frequencies (Campbell & Robson, 1968; Sachs, Nachmias & Robson, 1971). Pantle & Sekuler (1968) and Blakemore & Campbell (1969) demonstrated adaptation phenomena which are consistent with the existence of spatial frequency channels. If one views a high contrast sinusoidal grating for several minutes, the detection threshold for that grating is elevated; at neighbouring spatial frequencies there is less elevation, and none is measurable at frequencies differing by more than about an octave from that of the adapting grating.

Blakemore & Campbell (1969) found evidence for channels over most of the visible range of spatial frequencies: the adaptation curves peaked at the adapting frequencies. However, at low spatial frequencies, adaptation experiments indicated an absence of channels: when the adapting frequency was less than 3 c/deg, the adaptation characteristic did not peak at the adapting frequency but rather it peaked at 3 c/deg.

In their experiments, the adapting patterns had been stationary on the screen and the test gratings were switched on and off at a low rate. It is of interest to consider what effects more pronounced temporal modulation would have on this lowest adaptable frequency channel, as it is well known that such modulation makes low spatial frequency gratings considerably more visible (Robson, 1966; Van Nes, Koenderick, Nas & Bouman, 1967). It is possible that the loss of the low frequency cut is due to a change in the low frequency sensitivity of the individual channels, perhaps due to differences in the temporal properties of excitatory and inhibitory mechanisms. Graham (1972), using adaptation, examined the effects of movement on channels at medium spatial frequencies; there was a slight broadening of the threshold elevation curves but the low frequency cut was still pronounced.

Low spatial frequencies were not examined and it is conceivable that only channels near the last lose their low frequency cut, but a second hypothesis should be considered: that, at low spatial frequencies, there are channels which are insensitive to stationary patterns but are highly sensitive to temporally modulated patterns.

In this paper, evidence is presented for the existence of such channels. It is suggested that these channels belong to a system different from that examined by Blakemore & Campbell and that their role in perception is the analysis of temporal changes in the contrast or position of an object rather than the analysis of the structure of the object itself (Keesey, 1972). The proposed existence of distinct movement-analysing and pattern-analysing channels is compared with the *X* and *Y* classification of cat retinal ganglion cells (Enroth-Cugell & Robson, 1966; Cleland, Dubin & Levick, 1971).

METHODS

Vertical sinusoidal gratings were generated on the face of an oscilloscope screen (P 31 phosphor) by a television technique. The screen was circular (diameter = 13 cm) and, viewed from a distance of 180 cm, subtended 4·1 deg of arc at the eye. The gratings could be stationary on the screen, could be caused to drift steadily in one direction or could be turned on and off repetitively. Subjects set their contrast thresholds by adjusting the contrast of the patterns with a logarithmic attenuator having steps of 0·025 log units. *Contrast* is defined as the peak-to-trough amplitude of the luminance profile divided by twice the mean luminance, which was 100 cd/m^2 and was unaffected by changes in the contrast.

Five threshold settings were made for each type of grating and the standard error of each mean was about 0·0125 log units. The results are expressed as *contrast sensitivity* which is the reciprocal of the threshold contrast. In terms of contrast sensitivity, the average standard error was about 3 %.

The conventional detection threshold is the contrast at which the subject could just detect that the screen was not spatially and/or temporally uniform. Threshold was reached at the lowest contrast at which flicker or movement was apparent or at which a spatial grating became visible. At threshold, the drifting gratings actually appeared to be moving, but this was not always so with the stimuli which were turned on and off. Under some circumstances, the temporal modulation was evident as soon as the stimulus was visible; but, often, the stimulus appeared to be stationary at the conventional threshold and the contrast had to be increased somewhat before it became clear that the pattern was being temporally modulated; the contrast at which the modulation was just apparent was termed the flicker threshold. This threshold was used only in the experiments described in Fig. 9.

The subject viewed the centre of the screen with both eyes, and natural accommodation was employed. When the gratings were drifting steadily, the subject was asked to fixate a small spot in the centre of the screen. But his eyes were allowed to roam when the gratings were stationary, so that the images did not fade and after-images were not generated. The author acted as subject for all the published data but the main findings were confirmed on a naive subject. Both subjects were emmetropic.

RESULTS

Temporal modulation and contrast sensitivity

The most obvious effect of temporal modulation is a marked increase in the sensitivity to sinusoidal gratings of low spatial frequencies (e.g. Robson, 1966). This is illustrated in Fig. 1 where the open circles show the contrast sensitivity to stationary gratings and the filled circles show that to gratings drifting steadily past the fixation spot at a rate of 5 c/sec. It is clear that the greatest effect of this type of temporal modulation is an increase in sensitivity to gratings below 4 c/deg. The low frequency cut is not abolished, but is delayed until lower frequencies. Robson (1966) found a total abolition of the low spatial frequency cut when the contrast of stationary gratings was sinusoidally modulated in time. This is not a real difference between the two types of temporal modulation: the filled squares in Fig. 1 show the sensitivity to gratings sinusoidally modulated at 5 c/sec. The low frequency cut is just as pronounced, suggesting differences between the subjects or the stimulus display. The sensitivity to drifting gratings is marginally, though significantly, greater than that to sinusoidally modulated gratings; the importance of this difference remains to be assessed.

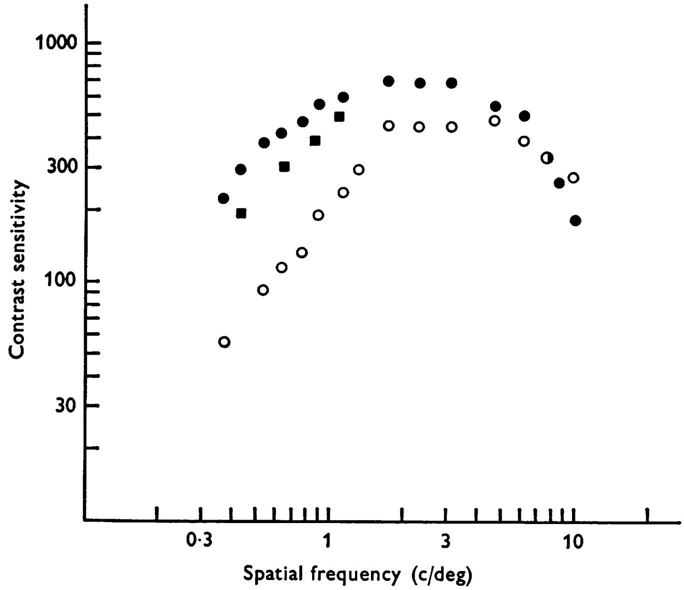

Fig. 1. The contrast sensitivity to stationary (○) and temporally modulated sinusoidal gratings. Two types of modulation, both at 5 c/sec, are illustrated: continuous lateral drift (●) and sinusoidal modulation of the contrast of a stationary grating (■).

Spatial frequency channels and movement

Temporal modulation causes an increase in sensitivity to low spatial frequency gratings. Is this due to a change in the low frequency characteristics of the individual channels? The problem has been examined by using the method of spatial adaptation. Fig. 2 shows typical threshold elevation curves.

The subject initially made five threshold settings at each of several spatial frequencies of sinusoidal grating, all of which drifted steadily to the left at 5 c/sec. He then viewed a grating of 0·9 c/deg, also drifting to the left at 5 c/sec; its contrast was 0·1, about forty times its threshold contrast. After 3 min adaptation, five threshold settings were made at each test spatial frequency, with a further 20 sec of adaptation between each setting. The detection thresholds for gratings close to 0·9 c/deg were considerably elevated, and this finding is quantified as *relative elevation* (Blakemore & Campbell, 1969), which is defined as:

$$\text{Rel. elev.} = \frac{\text{sensitivity before adapting}}{\text{sensitivity after adapting}} - 1.$$

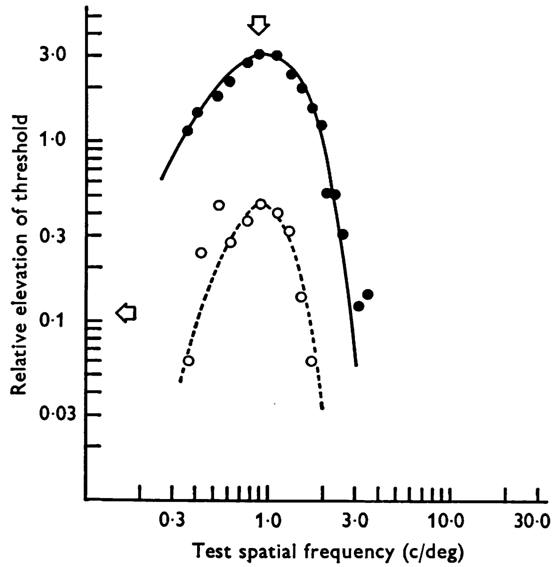

Fig. 2. Relative elevation of thresholds for gratings drifting to the left at 5 c/sec after adapting to a grating of 0·9 c/deg drifting to the left (●) and a grating of 0·9 c/deg drifting to the right (○). The adapting spatial frequency is indicated by the vertical arrow; both adapting gratings drifted at 5 c/sec and had a contrast of 0·1. The lines drawn through the points are described in the text. The horizontal arrow indicates the smallest elevation that can be considered statistically significant (95 %).

In Fig. 2, relative elevation is plotted as filled circles against the spatial frequency of the test gratings; the adapting frequency is indicated by the vertical arrow. The continuous curve drawn through these points is a function of the type:

$$(e^{-f^2} - e^{-4f^2})^n, \tag{1}$$

where f is the spatial frequency and n is an integer. In this case, n is one and the curve peaks very close to the adapting spatial frequency.

If the S.E. of each mean of five threshold settings is about 0·0125 log units, then the threshold elevation can be considered statistically significant (95 %) if it is greater than about 0·046 log units. This is equivalent to a relative elevation of 0·11, a value indicated by the horizontal arrow in Fig. 2.

The open circles in Fig. 2 are the results of a similar experiment but with the difference that the adapting grating drifted steadily to the right, the direction opposite to that of the test gratings. Again, the threshold elevation curve peaks at the adapting frequency, but there is considerably less effect, suggesting that the channels being investigated are directionally specific (Sekuler & Ganz, 1963). The dashed curve is again of the form of equation 1 but with $n = 2$; this function is considerably narrower than that drawn through the filled symbols, but is much the same as that used by Blakemore & Campbell (1969) to describe their results.

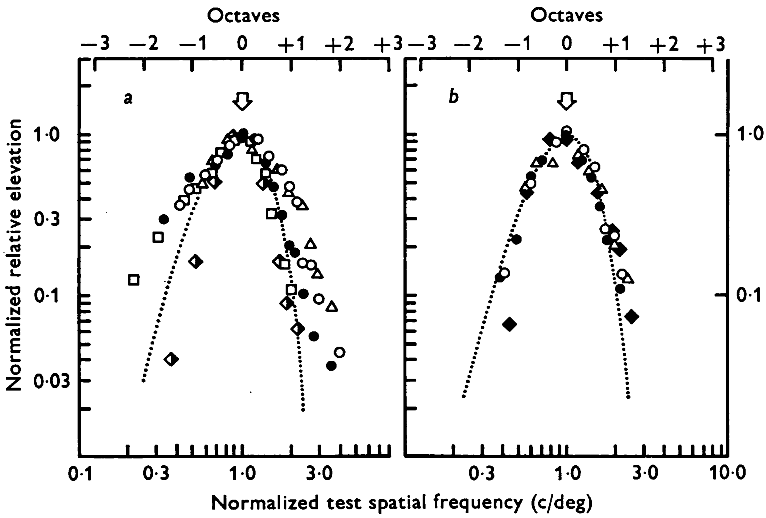

Fig. 3. Collected threshold elevation curves for several adapting spatial frequencies: 0·66 c/deg (△), 0·9 c/deg (○), 1·12 c/deg (●), 1·75 c/deg (□), 4·0 c/deg (◆) and 4·75 c/deg (half-filled ◆). The data have been normalized so that the adapting frequency is termed 1·0, and the relative elevation obtained at the same test frequency is also 1·0. The upper abscissa scale shows the difference between the test and adapting frequencies in octaves. All gratings drifted at 5 c/sec, and the adapting gratings had a contrast of 0·1. In the left-hand picture, the adapting gratings drifted continuously in one direction, that of the test gratings; in the right-hand picture, the adapting gratings reversed their direction of drift every 1·5 sec.

In Fig. 3*a*, threshold elevation curves for five adapting spatial frequencies are collected. All gratings drifted at 5 c/sec and the adapting gratings drifted in the same direction as that of the test gratings. The results have been normalized so that the adapting frequency is termed 1·0 and the elevation obtained at that frequency is also 1·0. The dashed curve is the above function with $n = 2$. The five sets of data are not describable by one function: the elevation curves are considerably broader at low spatial frequencies. This differs from the finding of Blakemore & Campbell (1969) whose data for stationary gratings could usually be described by one function. However, the elevation curves after adapting to gratings drifting in the opposite direction could be described by one narrow function (these are not illustrated).

After adapting to gratings moving in one direction, a subsequently viewed stationary pattern appears to move in the opposite direction (the waterfall effect). The subject felt that the apparent-motion after-effect made it difficult to set his thresholds, especially at low spatial frequencies and for gratings moving in the direction opposite to the illusory motion, perhaps causing spuriously large threshold elevation in these situations. Thus an adapting pattern was used that did not generate overt apparent-motion after-effects: the adapting grating drifted steadily at 5 c/sec but its direction of drift was reversed every 1·5 sec. The threshold elevation data for this adapting stimulus are pooled in Fig. 3*b* where the results for four adapting spatial frequencies are normalized as in Fig. 3*a*. This stimulus caused about 0·3 log units less elevation than a grating drifting continuously in one direction. It can be seen that one function describes all the data; the dashed curve is again of the form of eqn. (1) with $n = 2$, the function used to describe the data for the highest spatial frequency in Fig. 3*a* (◆) and the opposite direction data in Fig. 2 (○). Whatever the explanation for this narrowing of the threshold elevation curves when the adapting grating drifted backwards and forwards, the fact that all the data lay along one curve was taken as justification for using this type of adapting stimulus for the rest of the experiments.

The results in Fig. 3*b* suggest that movement does not affect the low spatial frequency characteristics of individual channels. Those in Fig. 3*a* might indicate a broadening of the channels but this is unsystematic and is not restricted to the low spatial frequency region of each elevation curve.

Spatial frequency or velocity channels?

Although the gratings in the previous experiments all drifted at 5 c/sec, their spatial frequencies varied from about 0·4 to 10 c/deg and the gratings thus drifted at different velocities, ranging from 12·5 to 0·5 deg/sec. The supposed spatial frequency specific threshold elevation in Figs. 2 and 3 might, in fact, be a velocity-specific effect. This has been ruled out by adapting to gratings drifting at one rate in c/sec and testing gratings drifting at another rate.

The filled circles in Fig. 4 show the relative elevation of threshold for gratings drifting at 5 c/sec after adapting to a grating of 0·9 c/deg (indicated by the filled arrow) and drifting at 2·5 c/sec. The adapting grating drifted continuously in one direction, and had a contrast of 0·1. The threshold elevation curve peaks at the adapting spatial frequency. If the elevation had been velocity-specific, the curve would have peaked at 1·8 c/deg.

The open circles in Fig. 4 illustrate a similar experiment: the adapting grating had a spatial frequency of 4 c/deg (open arrow) and drifted at 5 c/sec, while the test gratings all drifted at 10 c/sec. The adapting grating drifted backwards and forwards, and had a contrast of 0·1. Again, the maximum elevation is at the adapting frequency and not the adapting velocity (1·25 deg/sec at 8 c/deg).

The 'lowest adaptable spatial frequency channel' and movement

Blakemore & Campbell (1969), using stationary gratings, found that the peaks of the threshold elevation curves were at their respective adapting spatial frequencies except at low spatial frequencies. When the adapting spatial frequency was less than 3 c/deg, it was found that the

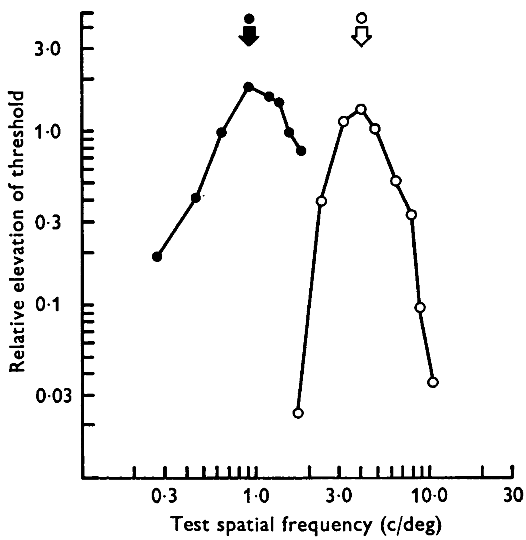

Fig. 4. The effects of adapting to gratings drifting at one rate and testing the thresholds of gratings drifting at another rate. The filled symbols are for an adapting grating of 0·9 c/deg drifting at 2·5 c/sec and test gratings drifting at 5 c/sec. The open circles are for an adapting grating of 4 c/deg drifting at 5 c/sec while the test gratings drifted at 10 c/sec.

maximum elevation was always at 3 c/deg; the lower the adapting spatial frequency, the less the effect at 3 c/deg. It will have been noticed that the adapting spatial frequencies used so far in this paper have usually been much less than 3 c/deg, but the elevation curves have all peaked at the adapting frequencies. There are several possible explanations for this difference in findings. In this study the gratings were moving, while

Blakemore & Campbell used stationary gratings. The subjects were, of course, different and the stimulus display in the present experiment was at least twice as large. The following experiments investigate these possibilities.

Fig. 5 illustrates the effects on the thresholds for stationary gratings of adapting to stationary gratings. During the adaptation periods, the subject was asked to move his eyes about to prevent the generation of after-images. The filled circles show the relative elevation of threshold after adapting to a grating of 0·9 c/deg and contrast 0·31, while the open circles are for an adapting grating of 0·66 c/deg and the same contrast. The con-

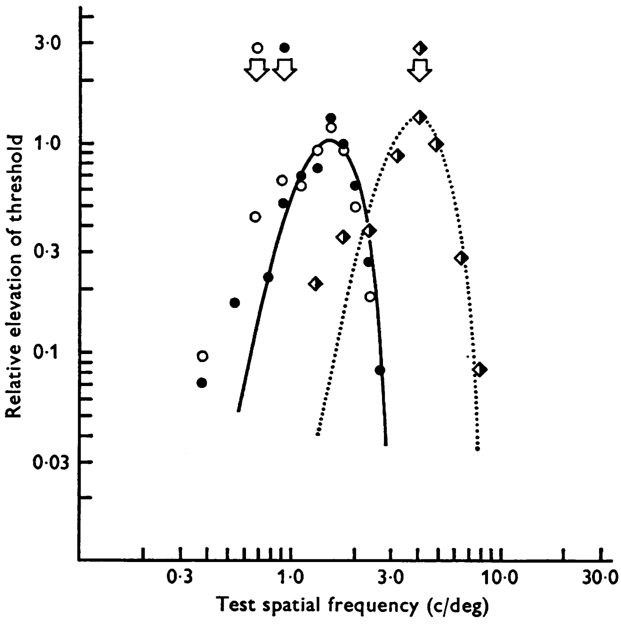

Fig. 5. The last spatial frequency channel. Relative elevation of threshold for stationary test gratings is shown after adapting to stationary gratings of 0·66 c/deg (○), 0·9 c/deg (●), and 4·0 c/deg (◆).

tinuous line drawn through the points has the form of equation 1 with $n = 3$. It peaks at 1·5 c/deg, which is thus the position of the lowest adaptable spatial frequency channels for this subject and stimulus display, and, of course, stationary gratings.

For comparison, the effects of adapting to a higher spatial frequency (4 c/deg——◆) are illustrated. The elevation curve now peaks at the adapting frequency. Adapting to frequencies between 1·5 c/deg and 4 c/deg also caused elevation that was maximal at the adapting frequency.

The position of the 'lowest channel' in this study was at 1·5 c/deg, while Blakemore & Campbell found a similar phenomenon at 3 c/deg. This shift is probably due to the size of the stimulus display: the screen size was reduced to a square with sides of 1·5 deg and the position of the 'lowest channel' shifted to 2·7 c/deg.

The position of the lowest adaptable spatial frequency channel appears to depend on the size of the stimulus display, but its actual existence depends on the use of stationary gratings. When the adapting and testing gratings both moved, the threshold elevation curves always peaked at the adapting spatial frequencies, suggesting that there are channels for

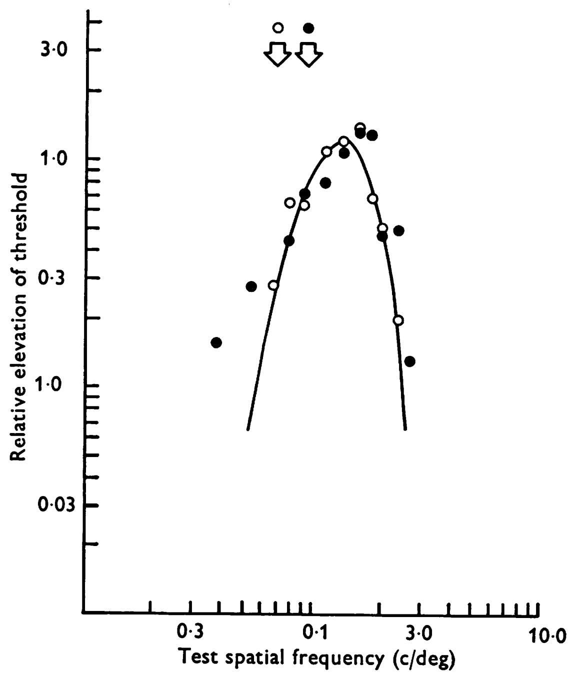

Fig. 6. The relative elevation of threshold for stationary test gratings after adapting to gratings drifting at 5 c/sec and reversing direction every 1·5 sec. The adapting spatial frequencies were 0·66 c/deg (○) and 0·9 c/deg (●).

low spatial frequencies which are somehow movement-dependent. Is this demonstration of low spatial frequency channels due to the movement of the adapting grating, test gratings or of both? Figs. 6 and 7 illustrate experiments that distinguish between these possibilities.

In the experiments illustrated in Fig. 6, the adapting gratings drifted steadily at 5 c/sec, the direction of drift being reversed every 1·5 sec; the test gratings were all stationary. The open circles show the effects of adapting to a grating of 0·66 c/deg and contrast 0·31, while the filled circles are the effects of adapting to a grating of 0·9 c/deg. Neither set of points peaks at the adapting frequency, but both peak near to the lowest adaptable channel for stationary gratings. Thus movement of the adapting grating alone does not reveal low spatial frequency channels. It should be noted that the amount of elevation for stationary test gratings obtained by adapting to moving and stationary gratings was much the same (cf. Figs. 5 and 6).

Fig. 7 shows the results of the inverse experiment: the test gratings moved steadily at 5 c/sec, while the adapting gratings were stationary. The open circles show the effects of adapting to a grating of 0·66 c/deg and contrast 0·56, while the filled circles show the effects of adapting to

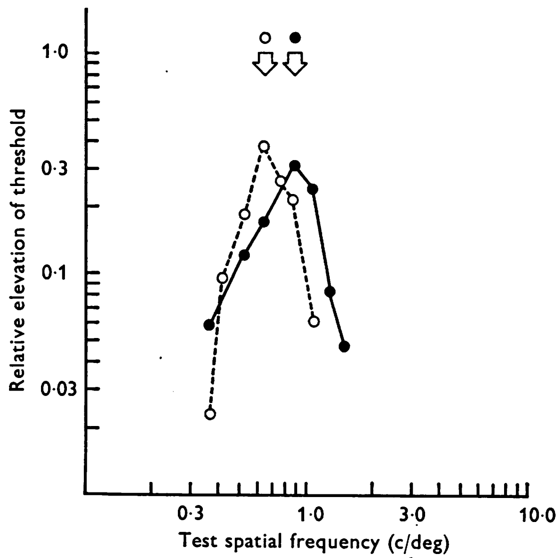

Fig. 7. The relative elevation of threshold for gratings drifting at 5 c/sec after adapting to stationary gratings of 0·66 c/deg (○) and 0·9 c/deg (●).

a grating of 0·9 c/deg and contrast 0·31. Both sets of data points peak at their adapting spatial frequencies, and it can be concluded that channels sensitive to low spatial frequencies can be revealed if the test patterns alone move. It is important to note that the thresholds for drifting gratings were affected much less by adaptation to stationary gratings than to moving gratings even though the former were of much higher contrast (cf. Figs. 2 and 7).

The role of low spatial frequency channels

Channels sensitive to low spatial frequencies of sinusoidal grating can be demonstrated if the test patterns move. Considerably more elevation of threshold for these drifting patterns is obtained when the adapting patterns also move. It can be concluded that these channels are especially sensitive to moving patterns but are relatively insensitive to stationary patterns.

Kulikowski (1971) noted that sinusoidal gratings of low spatial frequency, whose phase was shifted repetitively by 180 deg appeared to

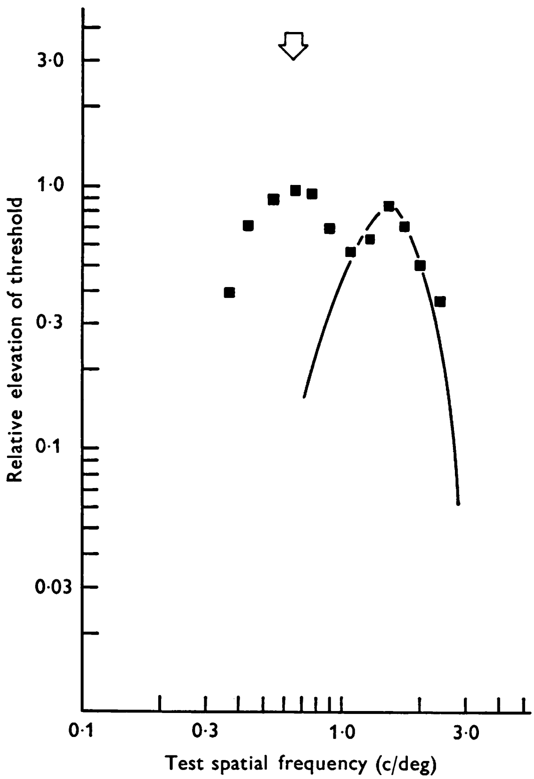

Fig. 8. The relative elevation of the detection threshold for gratings turned on and off at 1 c/sec. The adapting grating had a spatial frequency of 0·66 c/deg (vertical arrow) and drifted at 5 c/sec, reversing direction every 1·5 sec; its contrast was 0·1. Note that the elevation curve has two peaks: one at the adapting spatial frequency, and one at the position of the 'lowest adaptable channel' (1·5 c/deg). The curve is that describing the 'lowest channel' in Fig. 5.

flicker or to have discontinuous lateral movement (phi phenomenon), even at the detection threshold. Gratings of higher spatial frequency, however, appeared to be stationary at threshold, a higher contrast being required to perceive the temporal changes. Thus, temporal modulation causes an increase in sensitivity to low spatial frequencies and also an important change in their appearance; at higher spatial frequencies, modulation has little effect on sensitivity or appearance. Similar spatial frequency dependent changes in appearance can be seen when the gratings are turned on and off.

All the temporally modulated gratings so far examined in this paper had pronounced lateral movement, and this modulation was always evident to the subject at the detection threshold. Using adaptation, it has been shown that there is a characteristic difference in behaviour of moving and stationary test gratings at low spatial frequencies. Is this difference in behaviour dependent on whether or not the stimulus is really changing in time, or is it dependent on whether or not the subject can see that it is changing? In other words, does the temporally modulated pattern behave like a stationary pattern when the temporal changes are not evident?

To answer this question, the test gratings were turned on and off at 1 c/sec (500 msec on, 500 msec off repetitively). These patterns appeared to be stationary at threshold when their spatial frequency was greater than about 1·2 c/deg; at lower spatial frequencies, they appeared to be flickering at threshold. The elevation of the thresholds for such stimuli was examined after adapting to drifting gratings at low spatial frequencies. In Fig. 8, the adapting grating had a spatial frequency of 0·66 c/deg and drifted steadily at 5 c/sec, changing direction every 1·5 sec. Before and after adapting, the test gratings appeared to be flickering at threshold only when their spatial frequency was less than about 1·2 c/deg. The curve drawn through the points describes the 'lowest channel' (Fig. 5), peaking at 1·5 c/deg. It can be seen that the curve fits the data only above 1 c/deg, the region over which the test gratings seemed to be stationary. When gratings *appear* to be stationary, the lowest adaptable channel phenomenon is evident.

On the low spatial frequency side, there is divergence from the theoretical curve: there is a second peak at the adapting frequency. The divergent frequencies are those at which the gratings appeared to flicker at threshold.

A similar experiment is illustrated as filled symbols in Fig. 9, the adapting grating had a spatial frequency of 0·9 c/deg. The peak elevation at the lowest adaptable channel is pronounced, but the divergence at lower spatial frequencies is slight. This can be explained by a change in the appearance of the test gratings after adaptation; only below 0·5 c/deg did they now appear to be flickering at threshold. Keesey (1972) proposes that the suprathreshold contrast at which flicker can just be detected represents the threshold of an independent set of flicker-detecting channels. The hypothesis was tested by examining the flicker thresholds for those gratings in the above experiment which appeared to be stationary at the conventional detection threshold. The open symbols in Fig. 9 show that the elevation of the flicker thresholds is maximal at the adapting spatial frequency.

In conclusion, it can be said that temporal modulation reveals channels sensitive to low spatial frequencies, but that this modulation is effective only when the test patterns can actually be seen to be changing in time.

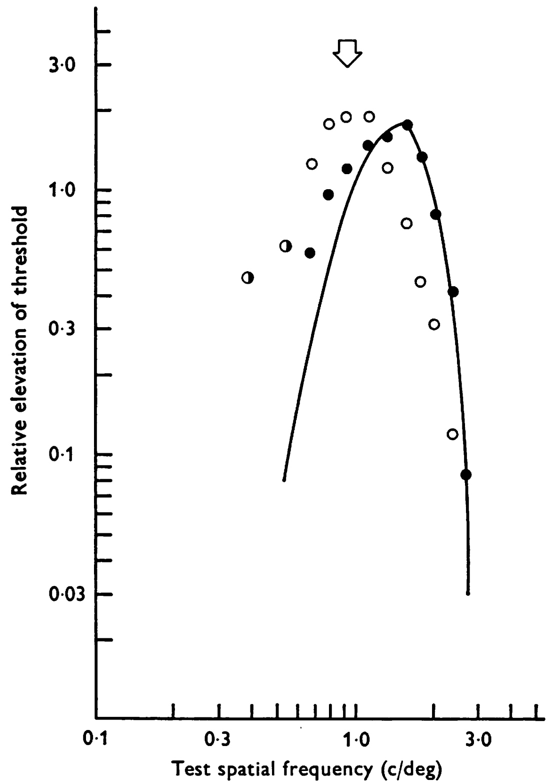

Fig. 9. The relative elevation of thresholds for gratings turned on and off at 1 c/sec after adapting to a drifting grating of 0·9 c/deg. The adapting grating drifted at 5 c/sec, reversing direction every 1·5 sec; its contrast was 0·1. The filled and half-filled circles show the elevation of the threshold for detecting a stimulus, which was maximal at the position of the 'lowest channel' (continuous curve). The open and half-filled circles show the elevation of the threshold for perceiving that the stimulus was flickering. The flicker threshold was most elevated at the adapting spatial frequency.

This suggests that the movement-sensitive channels are involved in the signalling of temporal changes. Patterns that appear to be stationary at threshold are detected by a separate system of channels, that exhibiting the 'lowest channel' phenomenon.

DISCUSSION

Adapting to a stationary sinusoidal grating produces a spatial-frequency dependent elevation of the thresholds for such gratings; the elevation is maximal at the frequency of the adapting grating. The frequency dependency presumably reflects the existence of channels in the human visual system which each respond to limited ranges of spatial frequency (Blakemore & Campbell, 1969). Graham (1972) demonstrated adaptation effects with moving gratings which seemed to be similar to those obtained with stationary gratings. The present paper shows that there are some marked differences between the effects of adapting to stationary and moving stimuli.

The experiments described in this paper provide evidence for a division of spatial-frequency selective channels into two classes: movement-dependent channels which respond only to temporally changing stimuli, and movement-independent channels which respond to both stationary and moving gratings. Furthermore, it seems that excitation of the movement-dependent channels is a necessary requirement for the perception of movement; the movement-independent channels will respond to moving stimuli, but, if they are excited alone, the stimuli appear to be stationary. The role of the latter class of channel is probably in the analysis of the spatial structure of the stimulus, whether stationary or moving. The two classes of channel cover different ranges of the visible spectrum of spatial frequency. Movement-independent channels are scarce at low spatial frequencies while the movement-dependent channels are very sensitive at these frequencies and are also found at higher frequencies. The relative insensitivity of the movement-independent channels at low spatial frequencies explains the well known increase in detectability of a low frequency grating when it is temporally modulated (Robson, 1966).

Over most of the visible range of spatial frequency, the effects of adaptation to a stationary grating are maximal at the frequency of the adapting grating. However, Blakemore & Campbell (1969) were unable to produce this effect at low spatial frequencies (below about 3 c/deg), using stationary gratings; they found that the frequency-dependent elevation was maximal at 3 c/deg, irrespective of the spatial frequency of the adapting grating. This observation might suggest that there are no adaptable channels below 3 c/deg. But it has now been demonstrated that, when the test gratings move, the elevation is maximal at the adapting frequency even at very low frequencies. Also, when the adapting grating moves, the magnitude of the threshold elevation is very much greater than when it is stationary. It would seem that the dominant channels at low spatial frequencies are movement-dependent, responding only when the stimuli move.

It might be argued that the movement-dependent channels at low frequencies are not really different from the channels demonstrated by Blakemore & Campbell at higher frequencies with stationary gratings. All channels could be movement-dependent, the necessary image movement being provided at high spatial-frequencies by eye movements. But this supposition seems unlikely since the frequency below which it becomes necessary to move the test gratings is found to depend on the size of the screen; if eye-movements are to be invoked as the explanation for adaptation at high spatial frequencies, it must be proposed that the pattern of eye-movements depends on screen size. Further, Tolhurst & Hart (1972) found that the threshold for a moving grating at a high spatial frequency was hardly affected by adapting to a stationary grating, although a moving grating was, of course, a very effective adapting stimulus. The effects of eye movements at this spatial frequency could not have been very great.

The threshold for a stationary grating is markedly elevated by adapting to either a stationary or a moving grating, at all spatial frequencies. The channels detecting stationary gratings seem to respond well over a range of temporal frequency, so that they could be involved in the analysis of the spatial structure of moving and stationary stimuli (Keesey, 1972; Kulikowski & Tolhurst, 1973).

As well as having different temporal characteristics and optimal spatial frequencies, the two classes of channel could have very different roles in perception. The conclusions drawn so far are derived from experiments in which the gratings either were stationary or had very pronounced lateral movement, which was always apparent to the observer. Some interesting phenomena arise when the stimuli are turned on and off at a low temporal frequency. At high spatial frequencies, the stimuli appear to be stationary at low contrast while, at low spatial frequencies, the temporal modulation is the most notable feature of the stimulus (Kulikowski, 1971). It is significant that, at low spatial frequencies, the movement-dependent channels are the dominant kind, and it is probable that these channels are responsible for the perception of temporal changes. This idea has been tested by examining the effects of adaptation on the thresholds for gratings which were turned on and off at a low temporal frequency. After adapting to a low spatial frequency drifting grating, threshold elevation showed *two* maxima: one at the adapting spatial frequency (just as with drifting gratings) and one at the frequency of the lowest channel adaptable with stationary test gratings (representing the movement-independent channels). The dual behaviour of the test grating was correlated with the spatial-frequency dependent changes in its subjective appearance. At medium spatial frequencies, it appeared to be stationary and behaved like a stationary grating while, at low frequencies, it appeared to flicker and the adaptation experiment suggested that it was detected by the movement-dependent channels.

There are two distinct thresholds for a temporally modulated stimulus: at one contrast, the temporal changes just become evident while, at a second contrast (which may be higher or lower), the spatial structure becomes distinct (Van Nes *et al.* 1967). Keesey (1972) has suggested that these independent thresholds represent the activity of two independent sets of neurones which have different roles in perception. Again, this suggestion is supported by the present experiments with slowly modulated gratings: the two thresholds were affected independently by adaptation.

Thus, it would seem that the movement-dependent channels alone carry information leading to the sensation of movement. The movement-independent channels might be largely responsible for the analysis of the spatial structure of the stimulus, whether moving or stationary; the excitation of these channels is never interpreted as arising from movement. As well as demonstrating the separate existence of these two types of channel, this paper has shown that they operate over different parts of the visible spatial frequency spectrum. The movement-dependent channels are distinctly dominant at low spatial frequencies while the movement-independent channels are the more sensitive at higher frequencies. The value in information processing of this difference is not immediately obvious, but it provides an interesting link with recent neurophysiological research.

It is well established that there are two distinct classes of neurone in the retina and Lgn of the cat: X-cells and Y-cells (Enroth-Cugell & Robson, 1966; Cleland *et al.* 1971). Amongst the several differences in the properties of these two classes of neurone (reviewed by Ikeda & Wright, 1973) two may be mentioned. Firstly, X-cells give sustained responses to prolonged presentation of a stimulus, while Y-cells give only transient responses at the onset and offset of the stimulus. The step responses suggest that X-cells are responsive to stationary stimuli, while Y-cells require that the stimulus be temporally modulated. Secondly, X-cells have, on average, smaller receptive field centres than have Y-cells in the same part of the retina so that Y-cells tend to respond to lower spatial frequencies than do X-cells. More recently, Maffei & Fiorentini (1973) have examined the temporal and spatial properties of cat cortical neurones. Two classes of cell were distinguished according to their responses to moving stimuli. Movement-dependent neurones responded to lower spatial frequencies of sinusoidal grating than did the second class of neurone, whose excitation did not depend so critically on the movement of the stimulus.

The temporal properties of neurones in the cat visual system are correlated with their optimal spatial frequencies in the same way as are the temporal characteristics of the two classes of human channel demonstrated in this paper.

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