J. Physiol. (1973), **232**, *pp.* 149–162
With 8 *text-figures*
Printed in Great Britain

PSYCHOPHYSICAL EVIDENCE FOR SUSTAINED AND TRANSIENT DETECTORS IN HUMAN VISION

BY J. J. KULIKOWSKI AND D. J. TOLHURST*
From the University of Manchester Institute of
Science and Technology, Department of Ophthalmic Optics,
Manchester 1 and the Physiological Laboratory,
Cambridge CB2 3EG

(*Received 8 November 1972*)

SUMMARY

1. The sensitivity to temporally modulated sinusoidal gratings was determined. Two thresholds could be distinguished for the modulated gratings: the contrast at which flicker could be perceived and the contrast at which the spatial structure became distinct.

2. The flicker detection thresholds and pattern recognition threshold varied independently as functions of the spatial and temporal frequencies, suggesting that the two thresholds represent the activity of two independent systems of channels.

3. The channels detecting flicker prefer low and medium spatial frequencies. They have a pronounced decline in sensitivity at low temporal frequencies of sinusoidal modulation. They respond twice as well to gratings whose phase is alternated repetitively as to gratings turned on and off at the same rate.

4. The channels responsible for the discrimination of spatial structure are most responsive at high and medium spatial frequencies. There is no decline in sensitivity at low temporal frequencies. These channels respond equally well to alternating and on/off gratings up to about 8 Hz.

5. The temporal properties as revealed with sinusoidal modulation, suggest that the flicker-detecting channels would give transient responses to prolonged presentation of stimuli: the channels responsible for analysing the spatial structure would give sustained responses. The responses of the two types of channel to alternating and on/off gratings confirm this suggestion.

---

* Address for correspondence: D. J. Tolhurst, the Physiological Laboratory, Cambridge CB2 3EG.

INTRODUCTION

At its detection threshold, a temporally modulated spatial pattern often appears to be indistinguishable from a stationary pattern with the same spatial structure. This is especially obvious when the pattern is a sinusoidal grating whose spatial frequency is greater than 4 c/deg (Kulikowski, 1971*b*); if the contrast of such a stimulus is increased some way above its detection threshold, the flicker or movement becomes evident. Only if the grating has a low spatial frequency can the temporal modulation be detected at very low contrasts. At the detection threshold for such a pattern, flicker or movement is evident but the spatial structure of the modulated pattern is very indistinct. The contrast of the stimulus must be increased before it is possible to discern the position and width of the individual bars of the grating (Van Nes, Koenderick, Nas & Bouman, 1967).

There seem to be distinct flicker-detection and pattern-recognition thresholds, which are independent functions of the spatial frequency. Keesey (1972) found that these thresholds were also independent functions of the temporal frequency. She proposed that the two thresholds represent the activity of two independent types of detector in the human visual system. One type is especially sensitive to temporally modulated patterns, and, when excited, movement or flicker is perceived; the ability of this system to resolve spatial structure is poor. The second type of detector is responsive to stationary as well as to temporally modulated patterns. Its role in perception is the analysis of the shape and size of a stimulus; though it responds to temporal changes, the response is not interpreted as being due to a temporal change.

Tolhurst (1973), on the basis of adaptation experiments, has shown that channels at low spatial frequencies behave differently from those at higher spatial frequencies. The high frequency channels appeared to respond equally well to stationary gratings and to gratings drifting steadily at 5 Hz. Those at low spatial frequencies were very insensitive to stationary adapting gratings, but responded well to temporally modulated patterns. The patterns to which they responded were seen by the observer to be flickering at the detection threshold. The flicker thresholds, for those temporally modulated patterns which appeared stationary at the conventional detection threshold, were elevated in a very characteristic way at low spatial frequencies; the two thresholds were independently elevated and it was concluded that the flicker threshold represented the activity of one set of channels while the conventional threshold for these patterns was mediated by a second set of channels with very different spatial and temporal properties.

From the difference in the range of spatial frequencies over which the two types of channel operated, Tolhurst (1973) suggested that the movement-dependent and movement-independent channels were the human analogues of the transient and sustained (Y and X) neurones of the cat and monkey visual system (Enroth-Cugell & Robson, 1966; Gouras, 1968; Cleland, Dubin & Levick, 1971). It is important, therefore, to ascertain that the human channels can be classified as transient and sustained by methods which are more direct than adaptation. It would be expected that the properties of the flicker threshold would reflect the activity of transient neurones, while the pattern recognition threshold would derive from sustained neurones.

By using a variety of temporal wave forms, it has been possible to show that these expectations are, in fact, correct.

METHODS

Sinusoidal gratings were generated on the face of a cathode ray tube (P31 phosphor) by means of a television technique. The amplitude of the gratings was quantified as contrast which is defined as

$$\frac{L_{\max}-L_{\min}}{L_{\max}+L_{\min}},$$

where L is the luminance of a point on the screen. Two stimulus displays were used. For the experiments illustrated in Figs. 1–4, the screen was square, subtending 4 deg of arc at the eye; its space-averaged mean luminance was 7 cd/m^2. The second screen had a mean luminance of 100 cd/m^2 and was circular (diameter – 6 deg of arc).

Three kinds of temporal modulation were employed. The stationary grating could be switched on and off repetitively (on/off gratings); e.g. a grating turned on and off at 5 Hz was present for 100 msec and was then replaced by a uniform field of the same mean luminance for the next 100 msec. Secondly, the phase of the sinusoidal grating could be shifted by 180° repetitively (alternating gratings). The positions of the bright and dark bars of the grating were continually being exchanged. Lastly, the contrast of the stationary grating could be sinusoidally modulated in time. The latter mode of presentation is somewhat similar to the alternating mode, which is effectively a square -wave modulation of the contrast with time. The mean luminance was unaffected by any type of temporal modulation or by changes in the contrast.

The subjects determined their thresholds for detecting the stimuli by adjusting the contrast of the gratings using a logarithmic attenuator having steps of 0·05 log units. Five threshold readings were made for each point and the standard error of the mean was about 5–10 %. The results are expressed as *contrast sensitivity*, the reciprocal of the threshold contrast.

The reported data were obtained with the authors acting as subjects, but the main findings were confirmed on several naive subjects. The subjects were either emmetropic or wore corrective lenses. Binocular vision was employed and the centre of the screen was viewed. Artificial pupils were not used.

RESULTS

Dependence of sensitivity on spatial frequency

Kulikowski (1971*a*) compared the sensitivity to gratings switched on and off repetitively with that to gratings whose phase was shifted by 180° at the same rate. At the moment of switching, the change in luminance of each point on the screen is twice as great when the grating is alternated as when it is switched on and off. Kulikowski argued, therefore, that an observer should be twice as sensitive to the alternating patterns. However, the prediction was borne out only at spatial frequencies below about 2·5 c/deg. At frequencies greater than about 6 c/deg, the observer was equally sensitive to the two kinds of presentation. At intermediate spatial frequencies, the sensitivity ratio progressed steadily from 1·0 to 2·0.

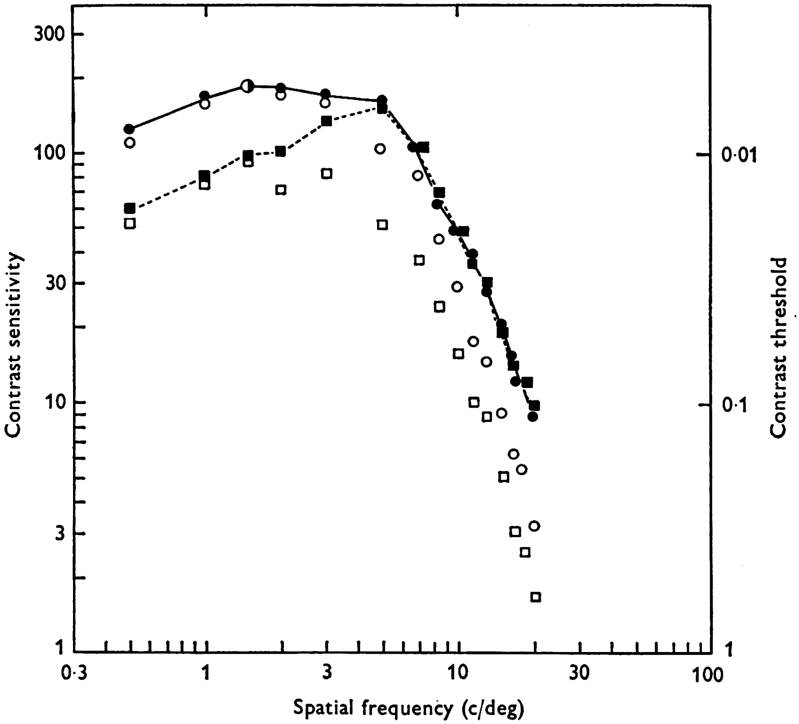

Fig. 1. Contrast sensitivity to sinusoidal gratings alternated in phase and switched on and off at 3·5 Hz. The filled symbols show the sensitivity for detecting a stimulus irrespective of its appearance: alternating (●) and on/off (■). The open symbols show the sensitivity for detecting that the stimuli were flickering: alternating (○) and on/off (□). The alternating grating was seen better than the corresponding on/off grating only when the alternating grating appeared to be flickering. Mean luminance 7 cd/m^2. Subject J.J.K.

In Fig. 1, the filled symbols show the sensitivity to gratings turned on and off or alternated in phase at 3·5 Hz as a function of the spatial frequency. Only below about 5 c/deg, is the alternating pattern (circles) seen better than the corresponding on/off pattern (squares). The sensitivity ratio (alternating: on/off) is plotted against the spatial frequency in Fig. 2 as filled symbols. The results of Kulikowski (1971*a*) are confirmed.

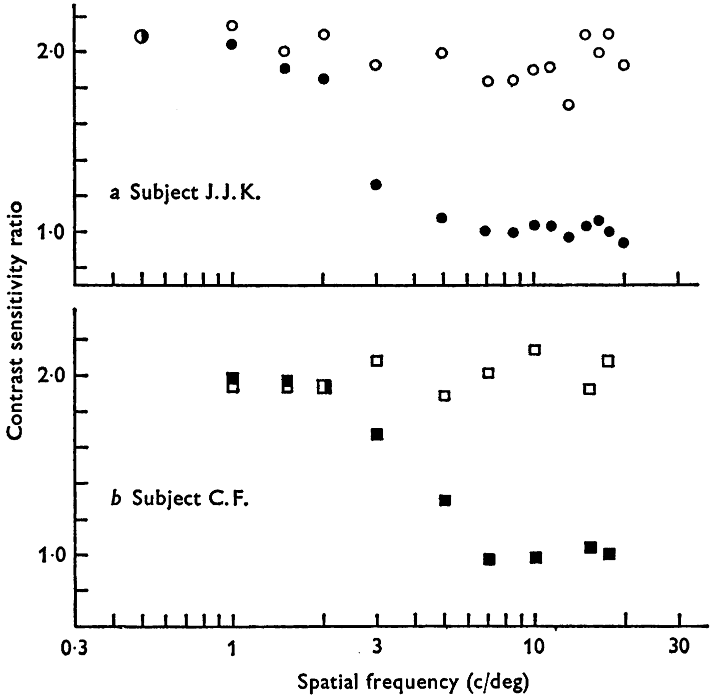

Fig. 2. The ratio of the sensitivity to the alternating gratings divided by the sensitivity to the corresponding on/off gratings. The upper graphs show the results of Fig. 1 replotted; the lower graphs are for a second subject and a modulation rate of 8 Hz. The filled symbols show the sensitivity ratio for detecting the stimulus irrespective of its appearance; the ratio varies between 1·0 and 2·0 depending on the spatial frequency. The open symbols show the ratio of the sensitivities for detecting that the gratings were flickering; the ratio is close to two at all spatial frequencies.

Kulikowski (1971*b*) found that alternating gratings appeared to be stationary at threshold when the spatial frequency was greater than about 4 c/deg. It is unlikely that the similarity of the spatial frequency ranges of the two effects is accidental. Thus the appearance of the patterns has been examined in more detail. The subject was required to say whether or not he considered that the stimulus appeared to be flickering at his threshold for the stimulus. If it did not, he was required to increase the contrast until the flicker was just apparent – his *flicker threshold*. The conventional threshold, when the subject was required only to decide whether or not the screen was uniform (spatially or temporally or both), is termed the *stimulus detection threshold*. The open symbols in Fig. 1 show the flicker sensitivity for the alternating and on/off patterns; the repetition rate was again 3·5 Hz. The alternating gratings which were seen better than the corresponding on/off gratings all seemed to be flickering at threshold; if the alternating grating appeared to be stationary, it was seen just as well as the on/off pattern. On/off gratings appeared to be stationary down to lower spatial frequencies (about 1·5 c/deg). The sensitivity ratio for stimulus detection was equal to 2·0 only when both the alternating and on/off gratings appeared to flicker at threshold. The ratio was intermediate when the appearance of the two types of grating was different. The sensitivity ratio for flicker detection is illustrated as open symbols in Fig. 2. Over the whole range of spatial frequency tested (and at two rates of modulation), the flicker of the alternating grating is detected twice as well as the flicker of the on/off grating. By using the flicker

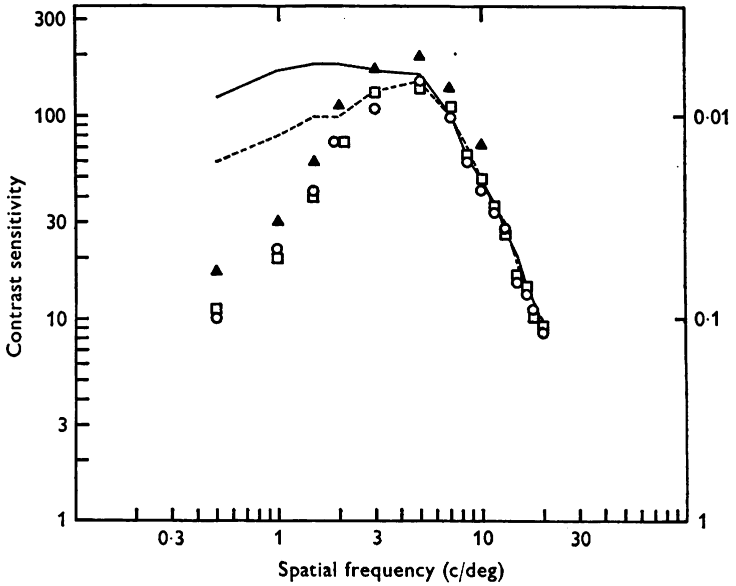

Fig. 3. The sensitivity for pattern recognition as a function of spatial frequency. The gratings were either alternated in phase at 3·5 Hz (○) or were switched on and off at the same rate (□). The continuous and interrupted lines show the sensitivities for detecting the stimulus irrespective of its appearance, reproduced from Fig. 1. The filled triangles show the sensitivity for detecting stationary sinusoidal gratings. Mean luminance 7 cd/m^2. Subject J.J.K.

threshold, it is possible to make the ratio equal to 2·0 at all frequencies. Can the ratio be made equal to 1·0 at all frequencies also?

Van Nes *et al.* (1967) and Keesey (1972) noted that, if a pattern appeared to be flickering at threshold, then its spatial structure was not evident or was very indistinct. The contrast could be increased to a point at which the individual bars of the grating (or the edges of Keesey's bar) could readily be discriminated – the *pattern recognition threshold.* How does the recognition threshold depend on the spatial frequency and the mode of temporal modulation?

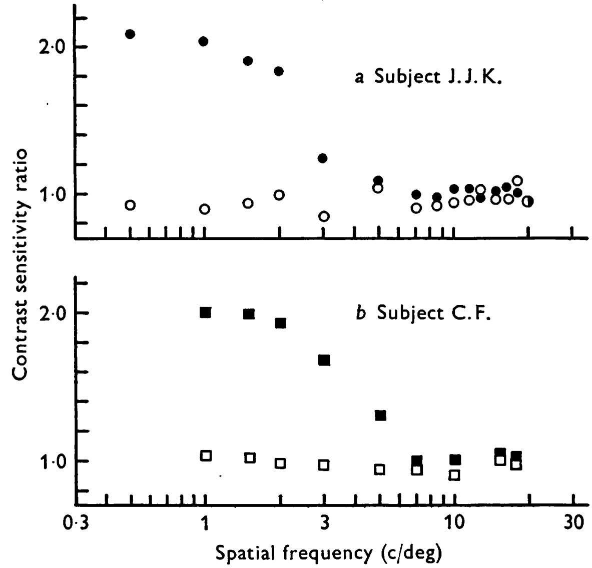

Fig. 4. The sensitivity ratio for pattern recognition as a function of spatial frequency. The filled symbols are reproduced from Fig. 2 and represent the sensitivity ratio for detecting the stimulus irrespective of the appearance. The open symbols show the ratio for the pattern recognition task; it is close to 1 over the whole range of spatial frequency. The data in the upper graph are replotted from Fig. 3; those in the lower graph are for a second subject and a repetition rate of 8 Hz.

The open symbols in Fig. 3 show that the recognition sensitivity is much the same as the stimulus detection threshold above about 5 c/deg; i.e. those spatial frequencies at which the gratings did not appear to flicker at threshold. There is a very pronounced decline in sensitivity at low spatial frequencies, reminiscent of that obtained with stationary gratings (e.g. Tolhurst, 1973). The filled symbols show that the sensitivity curve for detecting stationary gratings is, indeed, the same shape but it is slightly shifted on the sensitivity axis; this suggests that the neurones which detect stationary patterns are also responsible for analysing the structure of a temporally modulated pattern. In Fig. 4, the open symbols show that the sensitivity ratio for the recognition task is close to 1·0 over the whole range of spatial frequency.

The different shapes of the sensitivity curves for the flicker and recognition tasks suggest that the two tasks are mediated by different sets of neurones.

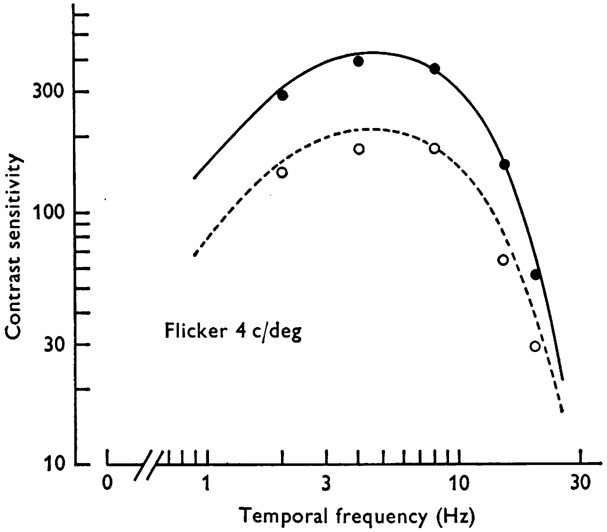

Fig. 5. The sensitivity for detecting the flicker of gratings of 4 c/deg alternated in phase (●) or turned on and off (○) repetitively. The curves show how the flicker threshold depends on the rate of repetition. The continuous curve was drawn by eye through the filled circles and was then shifted down the sensitivity axis by a factor of two to fit the data for the on/off gratings. Mean luminance 100 cd/m^2. Subject D.J.T.

Temporal frequency dependence of flicker and recognition tasks

The sensitivity ratio for the conventional stimulus detection task is dependent on the spatial frequency, and the change in ratio is explicable by the existence of two sets of channels having different spatial frequency ranges and different sensitivity ratios. Some results of Kulikowski (1971*b*) suggest that the ratio also depends on the temporal frequency. Fig. 5 shows how the flicker sensitivity depends on the temporal frequency and on the mode of presentation. The sensitivity ratio is close to 2·0 at all temporal frequencies. Fig. 6 shows how the recognition sensitivity for the two types of temporal modulation depends on the temporal frequency. At low temporal frequencies (up to about 10 Hz), the recognition sensitivity is much the same for the two modes of presentation. But, at higher

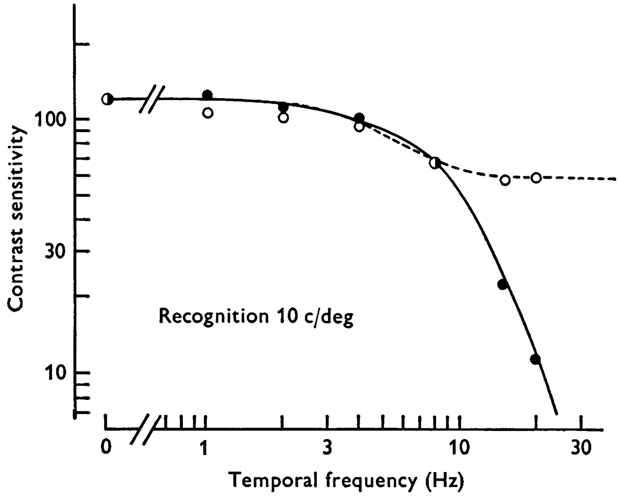

Fig. 6. The sensitivity for pattern recognition as a function of the repetition rate for gratings of 10 c/deg alternated in phase (●) or turned on and off (○) repetitively. Up to about 8 Hz, the sensitivities for the two types of modulation are much the same. At higher rates the curves diverge; the curve for on/off gratings flattens at a level about half that for a stationary grating. Mean luminance 100 cd/m². Subject D.J.T.

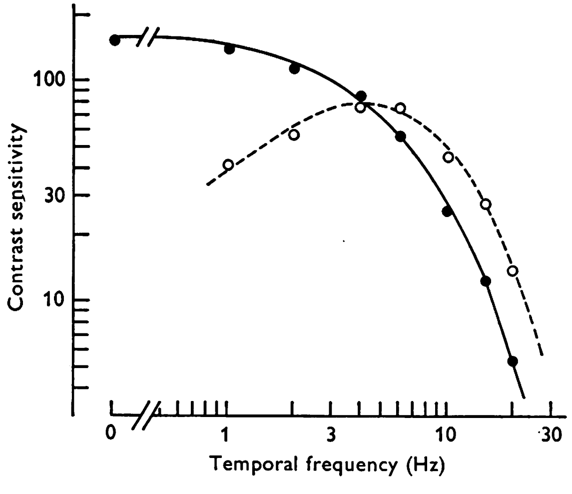

Fig. 7. The sensitivity for flicker detection and pattern recognition as functions of the frequency of *sinusoidal* modulation. The spatial frequency of all the gratings was 12 c/deg. The continuous line was drawn by eye through the points for pattern recognition (●); and the dashed curve was drawn by eye through the points for flicker detection (○). Mean luminance 100 cd/m². Subject D.J.T.

temporal frequencies, the curves begin to diverge. There is a very pronounced high frequency cut when the gratings are alternated, but the recognition sensitivity for the on/off mode flattens at a level which is half the sensitivity to a stationary grating. The significance of this divergence will be assessed in the Discussion.

If one wishes to know the temporal characteristics of a system, the most useful type of stimulus is one which changes sinusoidally in time. Thus flicker and recognition thresholds were determined for stationary gratings whose contrast was sinusoidally modulated in time. Figs. 7 and 8 show the results of two such experiments, at 12 and 0·8 c/deg respectively. The flicker sensitivity and recognition sensitivity are different functions of the temporal frequency (cf. Keesey, 1972). The flicker sensitivity curve shows a pronounced low temporal frequency decline and peaks at about 5 Hz. The recognition sensitivity is maximal when the gratings are stationary, and its high frequency decline begins at about 4 Hz. The curves were drawn by eye through the data points in Fig. 7 and have been indepen dently adjusted on the sensitivity axis to fit the points in Fig. 8. Thus the relative sensitivity of the neurones mediating flicker detection and pattern recognition depends on the spatial frequency, confirming the findings of Figs. 1 and 3.

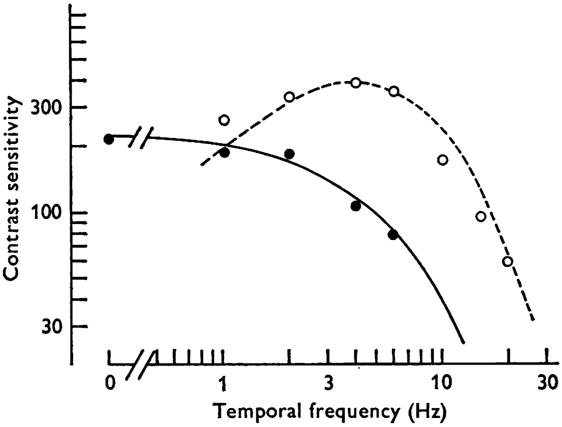

Fig. 8. As for Fig. 7, except that the spatial frequency of all the sinusoidal gratings was 0·8 c/deg. The data for the recognition task (●) are reasonably well fitted by the continuous curve of the previous Figure; the curve has been shifted up the sensitivity axis to fit the points. The flicker detection data (○) are reasonably fitted by the dashed curve of the previous Figure; again the curve has been shifted up the sensitivity axis, but by a larger factor. Mean luminance 100 cd/m^2. Subject D.J.T.

DISCUSSION

There are two distinct detection thresholds for a temporally modulated spatial stimulus: at one contrast, the temporal character becomes evident and, at a second contrast, the spatial structure becomes distinct. The two thresholds vary independently with changes in the temporal or spatial frequencies. The simplest explanation is that the two thresholds are mediated by two independent sets of neurones with different spatial and temporal properties (Keesey, 1972; Tolhurst, 1973). Rashbass (1968) has proposed the existence of two such sets of neurones. Those neurones responsible for flicker detection we will term movement-analysers, and those mediating pattern recognition will be termed form-analysers.

Our results show that the movement-analysers respond optimally to patterns which are temporally modulated at about 5–6 Hz. They are optimally responsive to gratings of about 2 c/deg and there is little low spatial frequency attenuation; the highest spatial frequency to which they respond is about 30 c/deg. When these analysers are excited, they give information about the nature of temporal changes. The form-analysers differ in the stimuli to which they are most sensitive. In the temporal frequency domain, they show no low frequency cut, being most responsive when the patterns are stationary. It must be remembered that these images were not stabilized on the retina, and so the image would have been in continual motion due to fixational eye-movements. The optimal spatial frequency is about 3·5 c/deg and the low spatial frequency cut is very pronounced; the maximum detectable spatial frequency is about 50 c/deg. Their role in perception is very different from that of the movement-analysers. They provide useable information about the shape, size and relative position of a stimulus; they respond to moving stimuli but, if they are excited alone, no movement is perceived.

The movement-analysers are much the more sensitive of the two systems at low spatial frequencies, explaining the marked increase in sensitivity to sinusoidal gratings at low spatial frequencies when some kind of temporal modulation is applied. This conclusion was reached from adaptation experiments by Tolhurst (1973) but the present experiments provide more direct evidence. The alternative explanation is that temporal modulation tends to abolish inhibition so that the low spatial frequency cut is also abolished (Kelly, 1971). The present experiments make this explanation very improbable: Fig. 4 shows that the pronounced low spatial frequency cut of the form-analysers is unaffected by temporal modulation.

The present experiments add to those of Tolhurst (1973) in that they show how far up the visible spatial frequency spectrum the movement-analysers operate. They operate up to about 30 c/deg, well into the spatial frequency range where eye movements would be expected to interfere with the analysis of object movements (Kulikowski, 1971*a*), although their sensitivity decreases very quickly. On the other hand, the pattern detectors are most sensitive over the range of operation of eye movements. Below this range (below 3 c/deg) their sensitivity decreases very quickly. It is a common experience that subjects setting thresholds at low spatial frequencies move their eyes to scan the pattern.

Sustained and transient responses

The temporal frequency sensitivity curves of the form-analysers and movement-analysers differ in a very important way: the presence or absence of a low temporal frequency cut. At present, we do not know whether the movement-analysers respond to truly stationary stimuli; our experiments have not gone lower than 1 Hz. But let us assume that they are unresponsive to stationary patterns.

From the sine-wave sensitivity curves, it should be possible to predict the responses of each system to other types of temporal change. There are two reasons why our results cannot be used quantitatively. First, the sine-wave sensitivity curve is not necessarily the response curve of one detector. There may be channels which respond to limited but different ranges of temporal frequency (Pantle & Sekuler, 1968). Secondly, and more important, we have no experimental information on the phase delays imposed on the sinusoidal inputs by the human detectors. We can draw qualitative conclusions, however.

Consider the response to a stimulus which is suddenly switched on and then kept motionless for an extended period of time. If the detector has a pronounced low temporal frequency cut and is unresponsive to stationary patterns, its response to the step input will be transient, returning to the resting level rapidly. When the stimulus is finally removed, there will be a transient off response of opposite sign. If, on the other hand, the detector has no low temporal frequency cut, the response will be sustained at a steady level until the pattern is removed. Thus, the movement-analysers should give transient responses and the form-analysers should give sustained responses.

We have no direct evidence for sustained and transient behaviour, but the way in which the detectors respond to on/off and alternating patterns gives some evidence. Consider first the responses of a sustained detector. When the pattern is turned on and off, the response will vary between the resting level (R_0) and some sustained level (R_0+x). When the pattern is alternated, the response will vary between R_0-x and R_0+x. Thus the peak response is the same for the two types of modulation, although the depth of modulation of the response is doubled when the pattern is alternated. Consider now the response of a transient detector. Its response to an on/off pattern would vary between the peak of the on-response ($R_0 + x$) and the minimum of the off-response ($R_0 - x$); the response to an alternating pattern would vary between $R_0 + 2x$ and $R_0 - 2x$. Both the amplitude of initial transient and the depth of modulation are doubled.

Let us assume that threshold is determined by the peak value of the response rather than the depth of modulation. Thus, the supposedly sustained form-analysers should detect on/off and alternating patterns equally well, while the supposedly transient movement-analysers should detect the alternating patterns twice as well as the on/off patterns. The first four Figures of this paper show that these predictions are borne out at rates up to 8 Hz.

The preceding argument applies to sustained neurones only at low and moderate rates of modulation. The transient neurone will have a sensitivity ratio of 2·0 at all rates (Fig. 5). At high rates, approaching the flicker fusion frequency, the sustained detector will hardly respond to an alternating grating, but will respond well to the on/off pattern. There would be little temporal modulation of the response, which would be maintained at a level half the response to a stationary grating of the same contrast. Fig. 6 shows that human form-analysers behave in just this way.

Neurophysiological correlates

Tolhurst (1973) proposed that human form-analysers and movement-analysers are analogous to the *X*- and *Y*-cells respectively of the cat visual system (Enroth-Cugell & Robson, 1966; Cleland *et al.* 1971; Maffei & Fiorentini, 1973). At various levels in the cat visual system, two distinct types of neurone can be distinguished. The most obvious difference in their properties is that the *X*-cells give sustained responses to prolonged stimulation while the *Y*-cells respond only transiently. The *X*-cells tend to respond to higher spatial frequencies of sinusoidal grating than do *Y*-cells in the same part of the visual field. This correlation between temporal and spatial properties is entirely consistent with the conclusions of this paper, but there is a problem as to what is meant by 'sustained'.

The cat *X*-cells show a considerable transient response before attaining a steady discharge level, especially in the lateral geniculate (Cleland *et al.* 1971). The psychophysical experiments in this paper could tolerate a 10% difference between the peak response and the steady level; this is within the standard error of the threshold settings. A larger difference (as shown by cat neurones) would cause the alternating gratings to be detected significantly better than the on/off gratings. The contrast of the stimuli used by Cleland *et al.* (1971) was high and it is possible that the responses would be more sustained at low contrasts (i.e. near threshold): Shapley, Enroth-Cugell, Bonds & Kirby (1972) found that the degree of transience of the responses of retinal cells was dependent on the intensity of the stimulus. The neurophysiology should be repeated using low contrast stimuli to assess how sustained are the X-cells and how transient are the Y-cells. At present, the human form-analysers seem to be too sustained to be completely consistent with the neurophysiology.

We should like to thank Drs J. G. Robson, R. M. Shapley and P. E. King-Smith for their helpful discussion and criticism and Mr C. French for acting as a subject. D. J. Tolhurst is in receipt of a research scholarship from the Medical Research Council.

REFERENCES

CLELAND, B. G., DUBIN, M. W. & LEVICK, W. R. (1971). Sustained and transient neurones in the cat's retina and lateral geniculate nucleus. *J. Physiol.* **217**, 473–496.

ENROTH-CUGELL, CHRISTINA & ROBSON, J. G. (1966). The contrast sensitivity of retinal ganglion cells of the cat. *J. Physiol.* **187**, 517–552.

GOURAS, P. (1968). Identification of cone mechanisms in monkey ganglion cells. *J. Physiol.* **199**, 533–547.

KEESEY, ULKER (1972). Flicker and pattern detection: a comparison of thresholds. *J. opt. Soc. Am.* **62**, 446–448.

KELLY, D. H. (1971). Theory of flicker and transient responses, II: counterphase gratings. *J. opt. Soc. Am.* **61**, 632–640.

KULIKOWSKI, J. J. (1971*a*). Some stimulus parameters affecting spatial and temporal resolution of human vision. *Vision Res.* **11**, 83–93.

KULIKOWSKI, J. J. (1971*b*). Effect of eye movements on the contrast sensitivity of spatio-temporal patterns. *Vision Res.* **11**, 261–273.

MAFFEI, L. & FIORENTINI, ADRIANA (1973). The visual cortex as a spatial frequency analyser. *Vision Res.* (in the Press).

PANTLE, A. J. & SEKULER, R. W. (1968). Velocity-sensitive elements in human vision: initial psychophysical evidence. *Vision Res.* **8**, 445–450.

RASHBASS, C. (1968). Spatio-temporal interaction in visual resolution. *J. Physiol.* **196**, 102–103*P*.

SHAPLEY, R. M., ENROTH-CUGELL, CHRISTINA, BONDS, A. B. & KIRBY, A. (1972). Gain control in the retina and retinal dynamics. *Nature, Lond.* **236**, 352–353.

TOLHURST, D. J. (1973). Separate channels for the analysis of the shape and the movement of a moving visual stimulus. *J. Physiol.* **231**, 385–402.

VAN NES, F. L., KOENDERICK, J. J., NAS, H. & BOUMAN, M. A. (1967). Spatiotemporal modulation transfer in the human eye. *J. opt. Soc. Am.* **57**, 1082–1088.