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SPATIAL ARRANGEMENT OF LINE, EDGE AND GRATING DETECTORS REVEALED BY SUBTHRESHOLD SUMMATION

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INTRODUCTION

KULIKOWSKI (1969) has shown that the contrast threshold (determined by a method of limits) for a fine dark line (1·5′ wide) may be reduced by superimposing it on a dark striation of a *subthreshold* sinusiodal grating having a spatial frequency of 5 cycles per degree (c/deg). If the dark line was superimposed on a bright striation of the grating, the contrast threshold for the dark line was found to be raised by a similar amount.

However, a subthreshold grating of 20 c/deg did not affect the threshold for the superimposed line. It is therefore clear that the reduction in contrast threshold for the line is not simply due to the physical addition of the grating modulation to the line contrast. Our interpretation is therefore that the "detector" (or detectors) which responds to the fine line at threshold is also sensitive to the 5 c/deg grating. When the dark line is placed on a dark striation of the grating, the responses to the two stimuli add together and so a lower contrast of the line is needed for a threshold response; when the dark line is placed on a bright striation, the two responses oppose each other and a greater line contrast is needed for threshold. We propose that the reason why the 20 c/deg grating has no effect on the contrast threshold for the line is that the "line detector" is entirely insensitive to a 20 c/deg grating.

Using this interpretation, *the change in the contrast threshold for the line due to the subthreshold grating, is a measure of the sensitivity of the line detector to a grating of that frequency*. If certain assumptions are made, the contrast threshold of the line detector for gratings of different spatial frequencies may be determined from such measurements. The term "grating sensitivity" will be used to denote the contrast sensitivity (i.e. the reciprocal of contrast threshold) to gratings.

The above analysis may therefore be used to investigate some of the spatial properties of the line detector. Is this detector responsible for the detection at threshold of all stimuli (with the same position and orientation) or are there separate detectors for, say, edges and gratings? This question may be tested by using other "test" stimuli (e.g. edges or gratings) instead of the line and, again, superimposing these stimuli on subthreshold gratings of different spatial frequencies. In this way, the "grating sensitivity" functions for "edge" and "grating" detectors may be determined and compared to the grating sensitivity of the line detector. It will thus be shown that all these detectors are quite distinct from each other.

In the above experiments, the "test" stimulus (line, edge or grating) has always been superimposed on a subthreshold "background" consisting of a sine wave grating. It is, however, possible to use other types of background pattern designed to investigate the spatial properties of the detector. Particularly valuable patterns are those consisting o lines or edges. In a corresponding manner, we can then derive the sensitivity (for the detector of the test stimulus) for these different types of background; in particular the sensitivity to lines placed at various distances from the test stimulus will be called the "line sensitivity" of the detector, and "edge sensitivity" will be used to denote the sensitivity of the detector to edges as a function of their distance of the edge from the centre of the test stimulus.

The models that are used in this analysis and the corresponding assumptions and predictions are described in the Theory section. In brief, we intend to demonstrate:

1. That there is evidence for several types of detectors acting in parallel.
2. That these detectors are based on spatial "filters" which process the test and background patterns in a *linear* manner (in the conditions of our experiments, i.e. at threshold).
3. That the results obtained using one type of subthreshold background pattern (e.g. gratings) may be used to predict the results obtained with other backgrounds (e.g. lines or edges).

For a given test pattern, it is therefore reasonable to suppose that only one type of detector is used and that the properties of this detector is *not* influenced by the presence of the subthreshold backgrounds.

METHODS

Patterns were generated on the face of a Solartron CD 1400 oscilloscope using a television technique based on that of SCHADE (1956) and CAMPBELL and GREEN (1965). The lines, edges and gratings used were all vertical, i.e. the luminance was modulated along the horizontal direction.

The circular display region subtended 2½ degrees in diameter at the viewing distance of 114 cm. The pale green display had a space-average luminance of 5 cd/m^2 and it was surrounded by a uniform square screen with a side of 6 degrees and with approximately the same luminance and colour. A small black mark on the display screen was used to help the subject locate the stimuli.

Most of the experimental results were obtained on subject J.J.K. (37 years, corrected myope) and checked on E.K.S. (32 years, corrected myope). Both are experienced subjects. Some of the results were checked on another subject who was not initially aware of the purpose of the experiment. Binocular vision was used throughout with natural pupils.

Test and background patterns

The display generally consisted of two superimposed patterns:

1. A background pattern which was set at a constant subthreshold contrast during any measurement.
2. A test pattern whose contrast was adjusted by the subject until the combined pattern was at threshold.

The patterns were derived from electronic function generators whose outputs (after attenuation and, if necessary, inversion) were added electronically and were then used to modulate the luminance of the display.

Experimental procedure

A PDP-12 computer was used in the determination of the relation between test contrast threshold and background contrast, as follows:

1. The computer set the background contrast at random to one out of a number of prespecified subthreshold levels. (The background contrast could be attenuated and/or inverted by means of the relay ouputs from the computer.)
2. The subject then adjusted the test contrast to threshold by means of a potentiometer. (He was, of course, totally unaware of which background contrast had been chosen.) This contrast setting was then "read" and stored by the computer; a new background contrast was then set and the above cycle repeated many times.
3. When each background contrast had been set a certain number of times (usually 10 occasionally 20 or 30), the computer printed out the mean and standard error of the test contrast thresholds for each background contrast level.

Derivation of the contrast sensitivity of a detector to a background pattern

It will be shown in the Theory section that the contrast threshold (and hence the contrast sensitivity) of the detector under study for the background stimulus is given by the intersection of the "contrast interrelation" line with the axis of background contrast (cf Figs. 1b and 1c). In general, there was not sufficient time to measure the test contrast threshold for many background contrasts and so two simplified techniques have been used:

1. The test contrast threshold, C_+, was found for a certain background contrast, C_b, and the test threshold was also found (C_-) when the background contrast was reversed ($-C_b$). For this "contrast reversal" technique, the contrast sensitivity (reciprocal of contrast threshold) of the detector for the background pattern may be shown to be

$$S = (C_- - C_+)/(C_- + C_+).C_b.$$

2. When the test pattern was a grating, contrast reversal of the background may not be used for reasons to be discussed later. In this case the test contrast threshold was determined with and without a certain background contrast C_b. The sensitivity is then given by

$$S = (C_{0t} - C_+)/C_{0t}.C_b$$

where C_{0t} is the contrast threshold for the test stimulus by itself, and C_+ is the contrast threshold in the presence of the background.

THEORY

The multi-channel model

There is considerable experimental evidence that visual processing occurs in a large number of parallel "channels" as represented in Fig. 1(a) (after Sachs, Nachmias and Robson, 1971). The first part of each channel is a "filter" which performs some sort of processing on the retinal image (as, for example, a "simple" cortical cell does—Hubel and Wiesel, 1962); the output from the filter is fed to a "threshold device" which responds only when the filter output reaches a threshold level. The outputs from all the threshold devices are fed to a logical "or" circuit; thus, in this model, a subject will report the presence of a stimulus if any of the threshold devices are activated.

In contrast, Campbell, Carpenter and Levinson (1969) showed that some of the spatial properties of vision may be predicted on the assumption of only a single channel (for a given orientation and retinal position). Despite the elegance of their analysis, we believe that their model cannot now be maintained. Firstly, it is difficult to believe that the visual system may

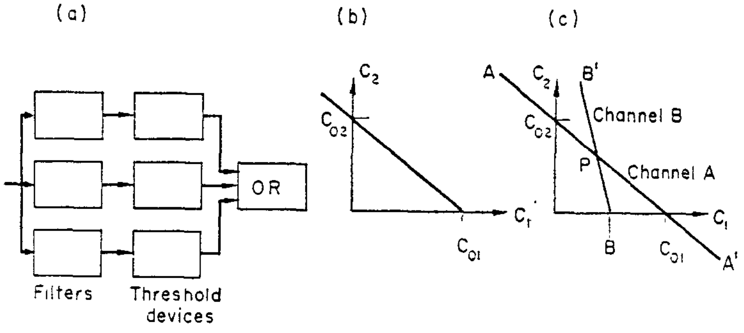

Fig. 1. (a) A representation of the multi-channel hypothesis. The visual input (i.e. the pattern of activity in the photoreceptors) is first processed in a number of parallel "filters". The output from each filter passes to a "threshold device" which only signals the presence of a stimulus if the filter response exceeds a certain threshold value. A "channel" or "detector" corresponds to the series combination of filter and threshold device. The outputs from all the channels feed to a logical "or" circuit; thus a stimulus is seen if any threshold device responds. (b) The contrast interrelation for a single channel predicted by the linear filter hypothesis. C_1 and C_2 are the contrasts of two patterns whose combination is just at threshold for the channel. C_{01} and C_{02} are the contrast threshold of the channel for each pattern on its own. (c) The contrast interrelations for two channels, A and B. See text for discussion.

be treated as a single channel of the sort they describe, when there is neuro-physiological evidence that visual cells have a considerable range of shapes and sizes of receptive fields. Secondly, the psychophysical measurements of CAMPBELL and ROBSON (1968), BLAKEMORE and CAMPBELL (1969) and SACHS *et al.* (1971) can only be fitted by a multi-channel model. Our present measurements are also quite inconsistent with the single channel model.

The linear filter hypothesis

The second basic assumption that we have used in our analysis is that the filters in the multi-channel model respond in a *linear* manner to light stimuli, in the conditions of our experiments (i.e. at levels near threshold). Specifically, we postulate two things:

1. The response, R, of a particular filter for a particular stimulus pattern (e.g. line, edge or grating) is directly proportional to the contrast, C, of the pattern. For convenience, we will define R to be unity for a threshold stimulus. The above postulate may then be expressed by

$$R = C/C_0 \qquad (1)$$

where C_0 is the contrast threshold of the filter for that pattern. The contrast of a pattern is defined here as $(L_{max} - L_{min})/(2\bar{L})$ where L_{max}, L_{min} and $\bar{L}$ are respectively the maximum, minimum and space-average luminance of the pattern.

If, however, the pattern is reversed in contrast (as in a photographic negative), the contrast will be defined to be *minus* the above quantity; in this situation we postulate that equation (1) still holds, i.e. the response to this pattern will be of opposite sign.

2. The response of a filter to two superimposed stimuli is equal to the algebraic sum of the responses to each stimulus separately. Thus, as the response, R_1, to the first pattern of contrast C_1 may be written (cf. equation 1)

$$R_1 = C_1/C_{01}$$

where C_{01} is the threshold for pattern 1 alone, and similarly for pattern 2,

$$R_2 = C_2/C_{02}$$

then the response to the combined pattern will be

$$R = R_1 + R_2$$
$$= C_1/C_{01} + C_2/C_{02}$$

Thus, for a threshold response ($R = 1$), we may derive the following important relation:

$$C_1/C_{01} + C_2/C_{02} = 1. \qquad (2)$$

This relation may be represented graphically by a contrast interrelation diagram such Fig. 1(b). Two points should be noted:

1. The contrast interrelation plot is a straight line.
2. This straight line intersects the two axes at C_{01} and C_{02} respectively—i.e. at the *individual* contrast thresholds for patterns 1 and 2.

The above predictions and Fig. 1(b) apply to only a single channel. Call this channel A. Suppose now that there is a second channel (B) which is more sensitive to the combined pattern in some circumstances, e.g. when pattern 1 predominates over pattern 2. The contrast interrelation plots for the two channels will be two straight lines, e.g. AA′ and BB′

in Fig. 1c. The threshold for the combined system of channels will be determined by whichever channel is more sensitive for a particular pattern combination.

The following predictions should now be noted:

1. When 2 (or more) channels are involved in the detection of pattern combinations, the contrast interrelation plot for the whole system is not a single straight line (as in Fig. 1b) but contains 2 (or more) straight line segments (AP and PB in Fig. 1c).
2. For a range of conditions in which only *one* channel is stimulated at threshold, the contrast interrelation for the whole system is represented by a straight line (e.g. AP for channel A in Fig. 1c). Conversely, if it is found that, over a certain range, the observed human visual contrast interrelation plot is a straight line, then this is strong (but not conclusive) evidence *both* that only one channel responds at threshold within this range *and* that this channel is linear under threshold conditions.
3. We may derive the contrast threshold of a channel for a particular pattern *even if it is less sensitive to this pattern than are other channels*. Thus in Fig. 1(c), channel A is less sensitive to pattern 1 than channel B. However, the contrast threshold of channel A to pattern 1 may be determined from the intersection of the line AA′ (i.e. AP extended) with the abscissa.

In this way, we may determine for example the contrast sensitivity (i.e. the reciprocal of contrast threshold) of a "line detector" to gratings even though there are other detectors (the "grating detectors") which are more sensitive to gratings than the line detector.

RESULTS

Part I—Evidence for the linear filter hypothesis

In the theory section, it was demonstrated that one prediction of the linear filter hypothesis is that, for a combination of patterns that are at threshold for a particular detector, there should be a linear interrelation between the contrasts of the two patterns (as in Fig. 1b).

This prediction has been tested for a variety of pattern combinations and some results are illustrated in Fig. 2. In all measurements, one pattern ("the background") was set to a certain subthreshold contrast and the contrast of the other pattern (the "test" stimulus) was adjusted until the combination was at threshold. In Fig. 2(a) the test pattern was a dark line (0·3 min wide) and background gratings of 5 and 7·6 c/deg were used. Positive values of background contrast correspond to the dark line being placed on the centre of a dark striation of the background grating. The "contrast interrelation" is seen to be linear, within the accuracy of the measurements, for both background frequencies; similar results (not shown) have been found using an edge as a test stimulus.

The linear superimposition principle. Measurements were made to test a further prediction of the linear filter hypothesis; namely that the combined effect of two backgrounds in reducing (or increasing) the test contrast threshold should be the algebraic sum of the effect of each background separately. An equivalent prediction is that the reduction (or increase) in test contrast threshold due to one background should be independent of the presence of another background.

A test of this prediction is represented by the large symbols in Fig. 2(a). In this experiment both 5 c/deg and 7·6 c/deg backgrounds were used; large circles indicate that a 5 c/deg grating was present and large squares correspond to a 7·6 c/deg grating. Both symbols together indicate that both background gratings were present simultaneously. The abscissa corresponds only to the contrast of the 5 c/deg grating; the contrast of the 7·6 c/deg grating,

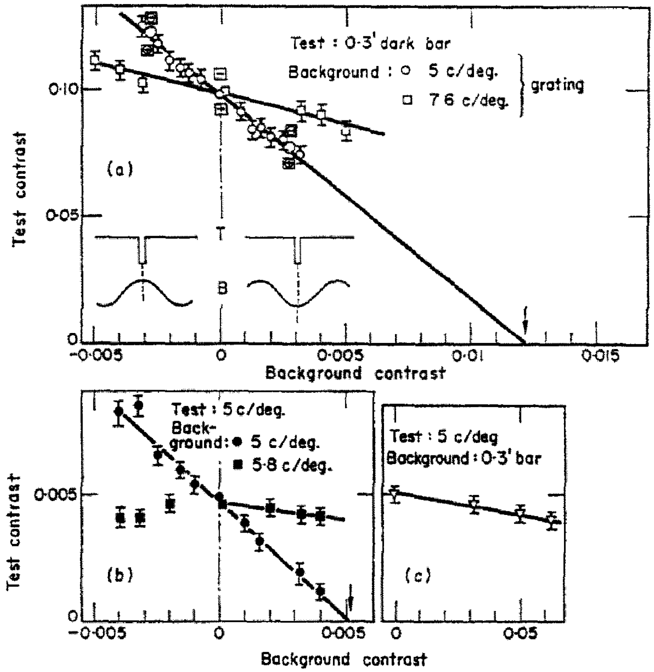

FIG. 2. Evidence for the linear filter hypothesis. (a) The contrast interrelation (relation between the "test" and "background" contrast at visual threshold) for a 0·3′ dark line (test stimulus) on a sinusoidal grating (background). Positive background contrasts correspond to the dark test line superimposed on a dark striation of the grating. The circles correspond to a 5 c/deg grating and the squares to 7·6 c/deg. The linearity of the relationship between test contrast threshold and background contrast is evidence for the linear filter hypothesis. (The arrow represents the deduced contrast threshold of the "threshold-line" detector for a 5 c/deg grating). Large symbols: these represent a test of a linear superimposition principle. Large circles indicate that a 5 c/deg background grating was present and large squares correspond to a 7·6 c/deg background grating. Both symbols together indicate a combination of the two backgrounds. For these measurements, the abscissa represents the contrast of the 5 c/deg grating; the contrast of the 7·6 c/deg grating, when present, was either +0·0028 (plus sign) or −0·0028 (minus sign). The reduction (or increase) in the test contrast threshold due to the 7·6 c/deg grating is seen to be independent of the contrast of the 5 c/deg grating—in accordance with the linear superimposition principle. (b) The contrast interrelation for a 5 c/deg test grating on a 5 c/deg background grating (circles) and on a 5·8 c/deg grating (squares). (c) The contrast interrelation for a 5 c/deg test grating and a 0·3′ dark line as background. The dark line was positioned at the centre of a dark striation. Triangles indicate means of 20–30 repetitions. The subject was J.J.K. for all experiments. Continuous lines are regression lines fitted through the means. Vertical bars here and subsequently represent ± S.E.

when present, was either +0·0028 (plus signs) or −0·0028 (minus signs). It can be seen that the results are consistent with the prediction that the effect (reduction or increase in test contrast threshold) of the 7·6 c/deg grating is independent of the contrast of the 5 c/deg grating. This prediction is, indeed, just the prediction made above for the linear superimposition principle and is, therefore, further evidence for the linear filter hypothesis.

Grating test patterns. The very simple case where both test and background stimuli are 5 c/deg gratings is illustrated in Fig. 2(b) (filled circles). As expected, the reduction in the test contrast threshold due to the background is equal to the background contrast (within experimental error).

The situation is more complex when a different background frequency is used (e.g. 5·8 c/deg, Fig. 2(b)—squares). The gratings were aligned so that maxima of the two gratings coincided at a point near the centre of the screen (for "positive" background contrast). In this case, a straight line may be fitted to the points for positive background contrast, but it is evident that the points for negative background contrast do not lie on this line. The reason is that although, for negative contrasts, the background is out of phase with the test stimulus at the *centre* of the screen, there are other regions where the background is in phase with the test stimulus and thus lowers the contrast threshold of the test grating.

Thus there is a linear contrast interrelation for the two gratings only when the background contrast is positive. Similarly, when a test grating is superimposed on a background line, the contrast interrelation (Fig. 2c) is only of interest when the background contrast is "positive" (i.e. when a dark striation is superimposed on a dark line). If the background contrast is "negative", it does not cause a significant increase in the grating contrast threshold because the observer can look at a different region of the grating where the effect of the background line is negligible.

It should be emphasized that the present evidence *only* demonstrates that the filters may be considered to be linear under the conditions of our experiments, i.e. *at threshold.* It is probable that this linearity is observed because the signals are relatively small; with much larger (suprathreshold) signals, it is very likely that significant non-linearity will occur within the filters.

Further evidence for the linear filter hypothesis will be described in later sections.

Part II—The spatial properties of detectors

The spatial properties of the "threshold-line" detector

"Grating sensitivity". The linearity of the relation between the contrast threshold for a test line and the contrast of a background grating (Fig. 2a) is evidence both for the linear filter hypothesis *and* that only one detector is active at threshold for the range of background contrasts used (see Theory). We will call this detector the "threshold-line" detector because it must be the detector which responds to a fine line *at its threshold contrast.* We have not used the more obvious term "fine line" detector, because it will be shown later that there are other line detectors, some of which might also be described as fine line detectors. According to our assumptions, we may derive the contrast threshold of this detector for the background grating; this corresponds to the intersection of the regression line (e.g. in Fig. 2a) with the grating contrast axis (cf. Fig. 1b). Thus, the contrast threshold of the threshold-line detector for a 5 c/deg grating is seen to be 0·0121 (arrow in Fig. 2a). We will define "grating sensitivity" (contrast sensitivity to a grating) as the reciprocal of threshold contrast; thus, for this detector, the grating sensitivity at 5 c/deg is $1/0{\cdot}0121 = 83$ (slightly higher values were found for J.J.K. on other occasions). Because the measurement of test contrast thresholds for a range of background contrasts (as in Fig. 2a) is very time consuming, grating sensitivities were normally determined by a simple "contrast reversal" technique; the background contrast was either plus or minus a certain contrast level which was generally about half the visual threshold contrast for that grating (see Methods). The linearity of the contrast interrelation was often checked by measuring the contrast threshold of the test stimulus with no background; this threshold should be the average of the contrast thresholds set for positive and negative background contrasts.

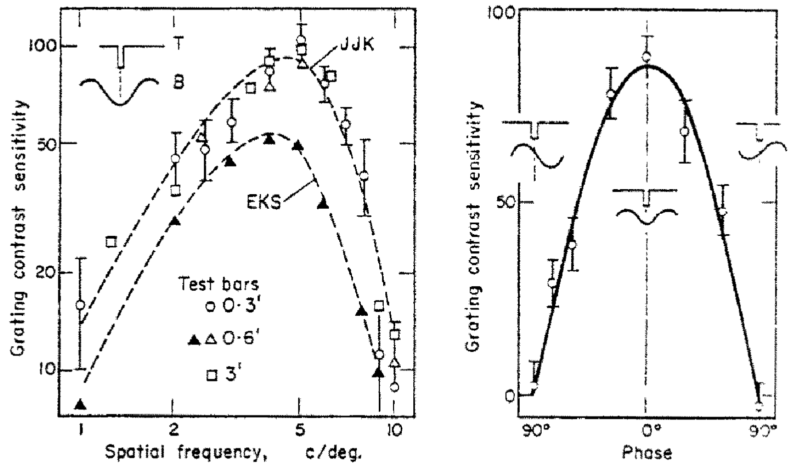

FIG. 3. The grating and phase sensitivity of the threshold-line detector. (a) The grating sensitivity (i.e. contrast sensitivity to gratings) of the "threshold-line" detector, derived by subthreshold summation. Open symbols refer to subject J.J.K., filled symbols to E.K.S. Circles, triangles and squares correspond to 0·3, 0·6 and 3′ wide test bars. (b) The variation of the grating sensitivity of the threshold-line detector as a function of the phase of the (5 c/deg) background grating—(subject J.J.K.). Zero phase corresponds to the dark test line aligned at the centre of a dark striation of the grating. The curve corresponds to a sensitivity proportional to the cosine of the phase angle.

Grating sensitivities of the threshold-line detector are represented in Fig. 3(a). J.J.K. was consistently found to be rather more sensitive than E.K.S. Maximum grating sensitivity is found to be at 4 to 5 c/deg which is close to the frequency for maximum grating sensitivity of the whole visual system. However, the maximum grating sensitivity of the line detector (about 100 for J.J.K.) is only about one half of the maximum grating sensitivity of the visual system as a whole. Further, the grating sensitivity function for the line detector falls off more rapidly at high spatial frequencies than that for the whole visual system (see also Fig. 11). The grating sensitivity function of the line detector is similar in shape to the grating sensitivity functions of ganglion cells (ENROTH-CUGELL and ROBSON, 1966) and of many cortical cells (CAMPBELL, COOPER and ENROTH-CUGELL, 1969).

Grating phase sensitivity. In Fig. 3b, the grating sensitivity of the threshold-line detector to a 5 c/deg grating has been measured as a function of the phase of the grating. The phase was defined to be zero when the dark line fell on the centre of a dark striation; as in the previous measurements, the contrast-reversal technique was used. It is seen that the sensitivity varies as the cosine of the phase angle; this result is again consistent with the linear filter hypothesis.

"Line sensitivity". If the grating sensitivity of a linear system is known as a function of spatial frequency and phase angle, it should be possible to use Fourier transformation to predict the sensitivity of the system to any other luminance distribution (cf. CAMPBELL *et al.*, 1969). In particular, we may predict the "line sensitivity" of the system—i.e. the contrast sensitivity to a fine line as a function of the position of the line (see Appendix 1).

The curves in Fig. 4 are line sensitivities of the threshold-line detector derived by Fourier transformation from the grating sensitivity data of Fig. 3(a) (assuming a cosine type transformation consistent with the phase data of Fig. 3b). Note that this and all subsequent

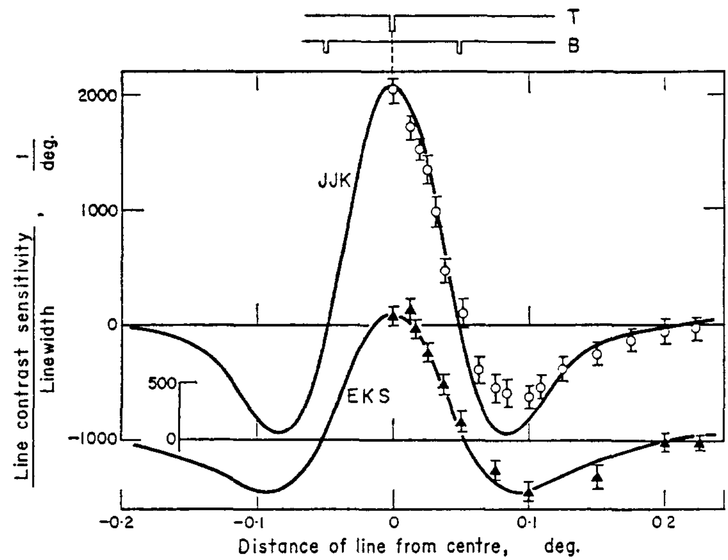

FIG. 4. The line sensitivity of the threshold line detector. The curves correspond to the line sensitivities (reciprocal of the product of contrast threshold and line width) calculated from the grating sensitivity data (Fig. 3a) using the Fourier transform method (Appendix 1). The upper curve refers to J.J.K. and the lower curve to E.K.S. The symbols (circles—J.J.K., triangles—E.K.S.) refer to direct determinations of the line sensitivities using a thin dark test line on a subthreshold background of two additional lines spaced on either side of the test line. T and B represent the luminance distribution of the test line and of the background (for positive background contrast).

curves calculated by the Fourier transform method are derived *without* any arbitrary scaling factor. The predicted maximum line sensitivity for J.J.K. is about 2000 deg^{-1}; for a line width of 0·3′ (1/200°) this corresponds to a contrast sensitivity of about 10 or a contrast threshold of 0·1—in good agreement with the observed contrast threshold for that line (Fig. 2a).

The line sensitivity of the threshold-line detector may be derived by an independent method as follows: the line test stimulus is placed on a background of two equal subthreshold fine lines placed at equal distances on either side of the central test line (see Fig. 4). By observing the effect of contrast reversal of the background lines on the contrast threshold of the test line, the sensitivity of the line detector to the background lines (i.e. the line sensitivity) may be determined in the same way as the grating sensitivity was determined above. The results of this method are represented by the symbols in Fig. 4 and it is seen that they are in reasonable agreement with the Fourier transform predictions. Both methods demonstrate a region of inverted line sensitivity beyond about 3′ from the centre of the "receptive field" with greatest negativity at about 5′ from the centre. For this spacing, a subthreshold background of two dark lines *increases* the threshold for a central dark test line; this lateral region of inverse line sensitivity is reminiscent of the lateral inhibition of many visual cells (BARLOW, 1953; KUFFLER, 1953; HUBEL and WIESEL, 1962). However, there is no evidence in our results for any region of "disinhibition" surrounding the inhibitory region (cf. MAFFEI and FIORENTINI, 1972, HAMMOND, 1972).

"*Edge sensitivity*". The edge sensitivity (contrast sensitivity to an edge as a function of

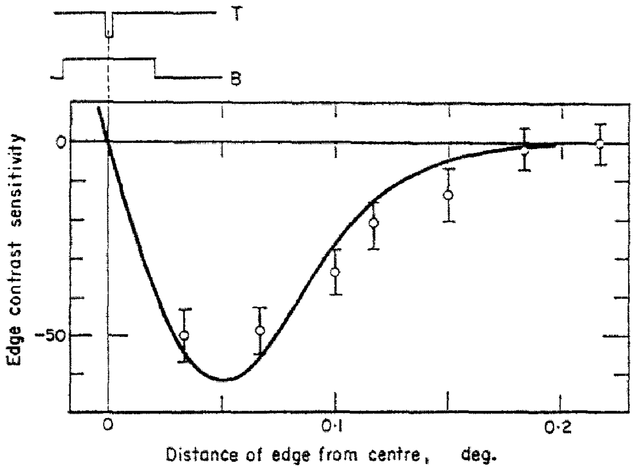

FIG. 5. The edge sensitivity of the threshold-line detector. The curve represents the edge sensitivity of the threshold-line detector calculated from the grating sensitivity data (subject J.J.K.). The circles correspond to a direct determination of the edge sensitivity using a thin dark test line and a background of two flanking edges (see T and B in inset).

edge position) may also be derived from the grating sensitivity and phase data by Fourier transformation (Appendix 1). The results of this calculation for the threshold-line detector are represented by the curve in Fig. 5.

The edge sensitivity of this detector may also be determined directly from the effect on the contrast threshold of a test line, of superimposing two subthreshold edges at equal distances on either side of the test lines (see Fig. 5). The edge sensitivity may be derived in a similar way to the direct derivation of the line sensitivity described above. The observed edge sensitivity (circles in Fig. 5) is again in good agreement with the Fourier transform calculation.

As plotted in Fig. 5, the edge sensitivity at point x is equivalent to the integral of the line sensitivity between that point and plus infinity. Thus, if there were a significant region of disinhibition (positive line sensitivity) above, say, 15′ from the centre, there would be a corresponding positive edge sensitivity at 15′. This is not observed and so we deduce that there is little or no disinhibition in these conditions (but see Discussion).

The spatial properties of the "threshold-edge" detector

Grating sensitivity and phase sensitivity. We will define the "threshold edge" detector as the detector which signals the presence of an edge at the visual threshold. There may, of course, be other edge detectors which are less sensitive to edges, but we have not yet investigated them.

The grating sensitivity of the "threshold edge" detector may be determined in the way discussed above for the "threshold-line" detector, i.e. by observing the effect of subthreshold background gratings on the threshold contrast for a test edge. The results are plotted in Fig. 6(a) for the case where the edge is placed on a node of the background grating (see inset to Fig. 6a).

The curves are similar in shape to those for the threshold-line detectors (Fig. 3). The maximum grating sensitivity, for J.J.K. is seen to be about 75 at about 3 c/deg. The grating sensitivity of the edge detector is found to vary as the sine of the phase angle (Fig. 6b), if the phase angle is defined to be zero when the edge is placed on a maximum of the grating luminance distribution. SHAPLEY and TOLHURST (1973) obtained similar results.

Line sensitivity. In Fig. 7(a), the curve represents the line sensitivity of the threshold-edge detector determined by Fourier transformation of the grating sensitivity data of Fig. 6(a) assuming a "sine type" transformation consistent with Fig. 6(b) (see Appendix 1). The symbols represent direct determinations of the line sensitivity using a background of two

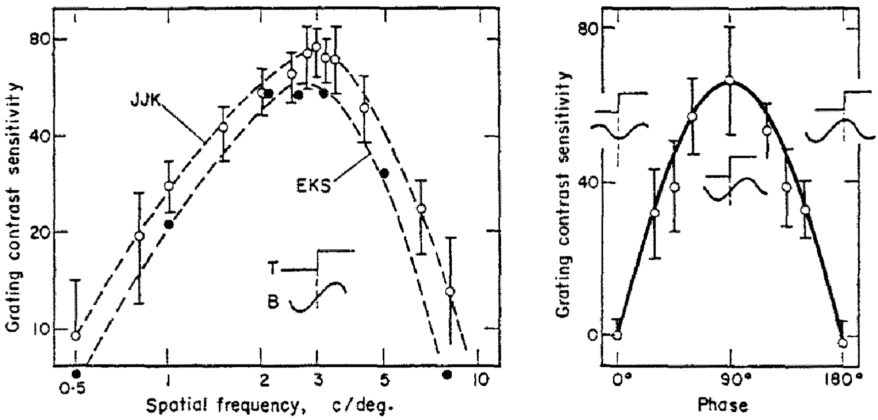

FIG. 6. The grating and phase sensitivity of the threshold edge detector. (a) The grating sensitivity of the threshold-edge detector as a function of spatial frequency, determined by subthreshold summation (open circles—J.J.K., filled circles—E.K.S.). (b) The phase sensitivity of the threshold-edge detector for a 3 c/deg background grating (subject J.J.K.). Zero phase corresponds to the test edge being placed on a maximum of the subthreshold background grating. The curve corresponds to a sensitivity proportional to the sine of the phase angle. (Note the difference in the scale of phase between Figs. 3b and 6b).

subthreshold lines (see Fig. 7a, inset); again, reasonable agreement is found between the direct determination and the Fourier transform curve. The most important components of the line sensitivity function are the regions of positive and negative line sensitivity on either side of the centre (Fig. 7a); the amplitude of the line sensitivity reaches about 1000 degrees^{-1} (about half the maximum for the threshold-line detector) at 3 min from the centre. Above about 11 min from the centre, there are less important regions where the line sensitivity is inverted compared with the more central regions.

Edge sensitivity. In Fig. 7(b), the curves represent the edge sensitivity function of the threshold-edge detector calculated by the Fourier transform method (Appendix 1) and the symbols represent direct determinations using a subthreshold background of two edges equally spaced on either side of the test edge (see inset to Fig. 7b). The direct determinations tend to be slightly greater than the calculated values for J.J.K. and slightly less for E.K.S.; these differences are probably due to slight changes in the sensitivity of the subjects between the grating sensitivity and the edge sensitivity measurements.

The maximum edge sensitivity of the edge detector (about 80 for J.J.K.) corresponds, of course, to the edge sensitivity of the whole visual system. A region of inverted edge sensitivity is found, for both subjects, at distances above 6′ from the centre of the receptive field.

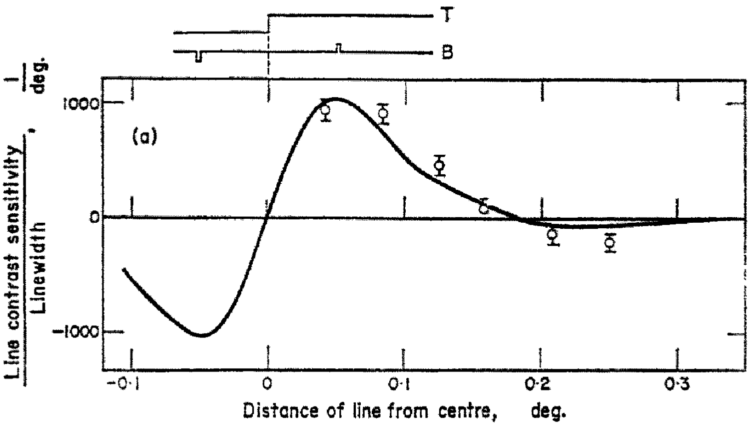

FIG. 7(a)

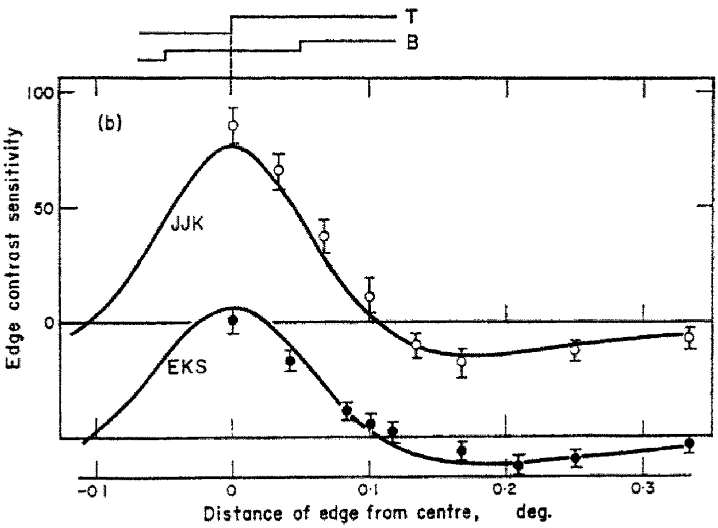

FIG. 7(b)

FIG. 7. The line and edge sensitivity of the threshold-edge detector. (a) Line sensitivity: The curve was derived by the Fourier transform method from the grating and phase sensitivity data of Fig. 6. The circles represent a direct determination of the line sensitivity by subthreshold summation using a test edge superimposed on a background of two lines (represented by T and B in the inset). The subject was J.J.K. (b) Edge sensitivity. The curves were derived by the Fourier transform method from the grating and phase sensitivity data of Fig. 6. The upper curve refers to J.J.K. and the lower to E.K.S. The circles (open—J.J.K., filled, displaced vertically—E.K.S.) correspond to direct determinations of the edge sensitivities using a test edge on a subthreshold background of two flanking edges (see T and B in inset).

The spatial properties of the 5 c/deg grating detector

Grating sensitivity. In this section, we examine the properties of the detector which signals the presence of a 5 c/deg grating at the visual threshold. The grating sensitivity of this detector can be determined in the normal way, i.e. a study is made of the effect on the contrast threshold of a 5 c/deg grating of different subthreshold background gratings. It should be noted, however, that it is not possible to make use of "negative" background contrasts because a background grating which is out of phase with the test grating at the centre of the screen may be in phase at some other region; thus the grating sensitivity was derived from test contrast thresholds for only zero and "positive" background contrasts (i.e. background in phase with the test at the centre of the screen). The background contrasts were generally set at about half their visual threshold level.

The following point should be emphasized. At the visual threshold, the combination of test and background gratings looked like a simple sinusoidal grating (for background gratings in the range 4–6 c/deg). In fact, the subject was generally unaware of whether the background grating was present or not. These observations support the idea that the combined pattern was in fact detected by a grating detector, and not by some other sort of detector which happened to be "tuned" to some element of the interference pattern generated by the two gratings.

The grating sensitivity determinations for J.J.K. are represented by the circles in Fig. 8(a). The sensitivity curve fitted to these points corresponds to the Gaussian function

$$S = S_0\, e^{-(f - f_0)^2/2\sigma^2}$$

where S is the grating sensitivity at the spatial frequency f, S_0 is the maximum grating sensitivity corresponding to frequency f_0 and σ is a constant proportional to the width of the curve. The curve plotted in Fig. 8a corresponds to $\sigma = 0{\cdot}38$ c/deg, but a small correction has been made to the curve for the following reason—when the 5 c/deg test grating is superimposed on a background grating of different frequency (e.g. 5·5 c/deg) it is likely that the combined pattern may be detected at threshold by a detector with an intermediate optimum frequency (e.g. 5·2 c/deg). The correction to the curve is derived in Appendix 2.

It is seen that the grating detector is sensitive only to a narrow range of frequencies (cf. SACHS *et al.*, 1971).

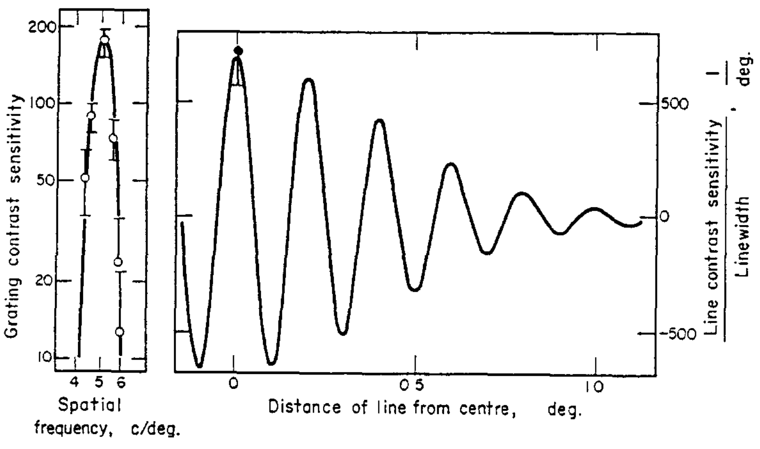

FIG. 8. The spatial properties of the 5 c/deg grating detector. (a) The grating sensitivity for subject J.J.K. The curve through the points corresponds to a Guassian variation of grating sensitivity as a function of spatial frequency, with the correction described in Appendix 2. (b) The curve corresponds to the line sensitivity of the grating detector derived by the Fourier transform method from the grating sensitivity data in (a). The circle represents a direct determination of the maximum line sensitivity by subthreshold summation using a 5 c/deg test grating superimposed on a dark background line (cf. Fig. 2c).

The maximum grating sensitivity of 175 at 5 c/deg corresponds, of course, to the sensitivity of the visual system at this frequency; it should be noted that this value is approximately double the maximum grating sensitivities of the line and edge detectors (J.J.K. Figs, 3a and 6a).

Line sensitivity. The curve in Fig. 8(b) shows the line sensitivity of the 5 c/deg grating detector derived by Fourier transformation from the grating sensitivity data of Fig. 8(a) (Appendix 1). The curve is symmetrical about the centre line because a "cosine type" transformation was used; however, a "sine type" transformation yields a line sensitivity curve which is very similar in amplitude and lateral extent. The line sensitivity function is, in fact, the product of a cosine term and a Gaussian function of the form $e^{-x^2/2 \cdot \sigma_x^2}$ where x is the angular distance from the centre; the value of constant σ_x is 0·42°.

The maximum line sensitivity of the grating detector can be checked by determining the effect of a subthreshold dark line in reducing the contrast threshold for a 5 c/deg grating (as in Fig. 2c, the dark line being placed at the centre of a dark striation). The circle in Fig. 8(b) is the maximum line sensitivity derived by this direct method and it is seen to be in good agreement with the Fourier transform prediction.

Of the three detectors considered so far, the grating detector is the least sensitive to fine lines. Its maximum line sensitivity (i.e. contrast sensitivity divided by line width) is about 700 deg^{-1} (Fig. 8b) compared with about 2000 deg^{-1} (Fig. 4) for the line detector and 1000 $degrees^{-1}$ (Fig. 7a) for the edge detector. Comparing Fig. 8(b) with Figs. 4 and 7(a), it can be seen that the grating detector has the greatest lateral spread of the three detectors.

Other line detectors

The "threshold-line" detector was defined to be the detector which responds to a fine line at the visual threshold. The properties of the threshold-line detector (Figs. 3, 4 and 5) were determined by subthreshold summation using a fine line as a test stimulus.

There are, however, other line detectors which have qualitatively similar properties to the threshold-line detector, but which have a lower contrast sensitivity for a fine line. These other detectors have been studied by using two other types of test stimuli; one of these consisted of a blurred bar with luminance distribution corresponding to one cycle of a 2·5 c/deg sine wave (see inset to Fig. 9a); the other test pattern consisted of a dark line of width two minutes flanked on both sides by bright lines of equal modulation and with width of one minute (see Fig. 9a).

Grating sensitivity measurements for these patterns are represented in Fig. 9(a), and the line sensitivities calculated by Fourier transform (Appendix I) are represented in Fig. 9(b). It can be seen that the "receptive fields" of the two new detectors are respectively broader and narrower than that for the threshold-line detector. As expected, the calculated maximum line sensitivity for the two new line detectors is less than that for the threshold-line detector. In summary, it seems that there are line detectors corresponding to a continuous range of sizes; the threshold-line detector is intermediate in this range.

Contrast sensitivity of the visual system to bars of different widths

Grating sensitivity measurements derived using a 3 min wide test bar are indistinguishable from those derived using finer test bars (Fig. 3a). This suggests that bars up to at least 3 min wide are detected at visual threshold by the same detector, i.e. the threshold-line detector.

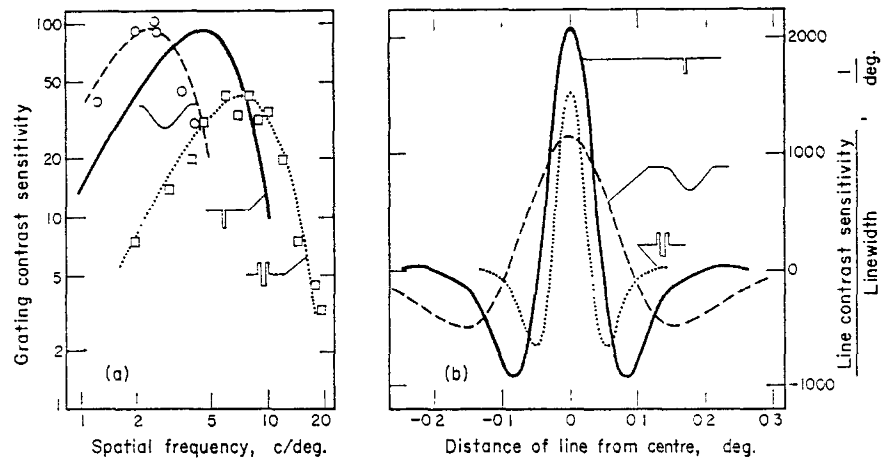

FIG. 9. The spatial properties of coarse and fine line detectors. (a) Grating sensitivity: The continuous curve represents the grating sensitivity of the threshold-line detector (from Fig. 3a). The open circles (dashed curve) correspond to grating sensitivity measurements using a blurred bar (one cycle of a 2·5 c/deg grating—see inset) as test stimulus. The squares (dotted curve) correspond to a composite test stimulus consisting of a 2 min central dark line flanked on either side by 1 min bright lines (see inset). The subject was J.J.K. in all cases. (b) Line sensitivity: The continuous curve is the line sensitivity of the threshold-line detector from (Fig. 4). The dashed and the dotted curves are derived from the corresponding curves in (a) using the Fourier transform technique. They thus correspond to the line sensitivities of detectors which are respectively coarser and finer than the threshold-line detector. Insets (not to scale) as in Fig. 9(a).

To what extent may the contrast thresholds for bars of different widths be predicted from a knowledge of the spatial properties of detectors? In Fig. 10, contrast thresholds are plotted as a function of bar width for two sorts of bars—bars with sharp edges (whose

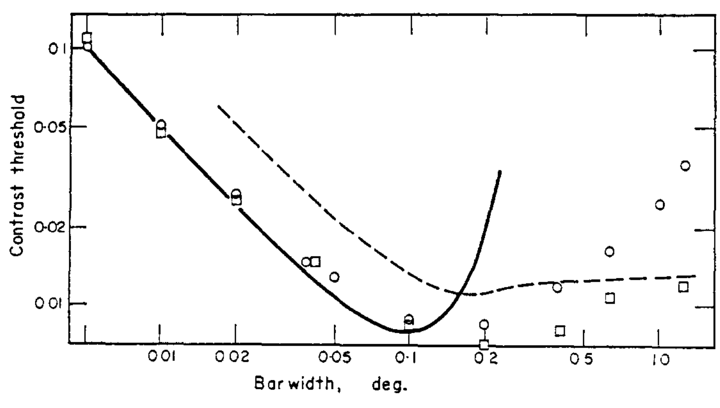

FIG. 10. The visual contrast threshold for bars as a function of their width. The squares represent the visual contrast threshold for sharp bars (i.e. having a luminance distribution corresponding to a rectangular pulse) as a function of their width. The circles correspond to similar measurements for blurred bars (one cycle of a sinusoidal grating) as a function of half the cycle period. The subject was J.J.K. The continuous curve represents the calculated contrast threshold of the threshold-line detector for sharp bars; the dashed curve is the corresponding prediction for the threshold-edge detector.

luminance distribution corresponds to a rectangular pulse) and blurred bars (with a luminance distribution corresponding to one cycle of a sine wave—see inset to Fig. 9; the width in this case is taken to be one half of the cycle period). The curves represent the contrast thresholds for rectangular bars predicted for the threshold-line and threshold-edge detectors.

It is seen that the visual threshold corresponds to the predicted threshold for the threshold line detector up to 6′ bar width. Similarly, the threshold for *rectangular* bars over 60′ is in reasonable agreement with the calculated threshold for the edge detector. In the intermediate range, 6–60′, we presume that other detectors are involved. Note that the thresholds for the blurred (sinusoidal) bars are much higher than for sharp bars at widths of one degree or more; thus wide rectangular bars are not detected by broad line detectors (e.g. of the type in Fig. 9b) but they would appear to be detected by their edges.

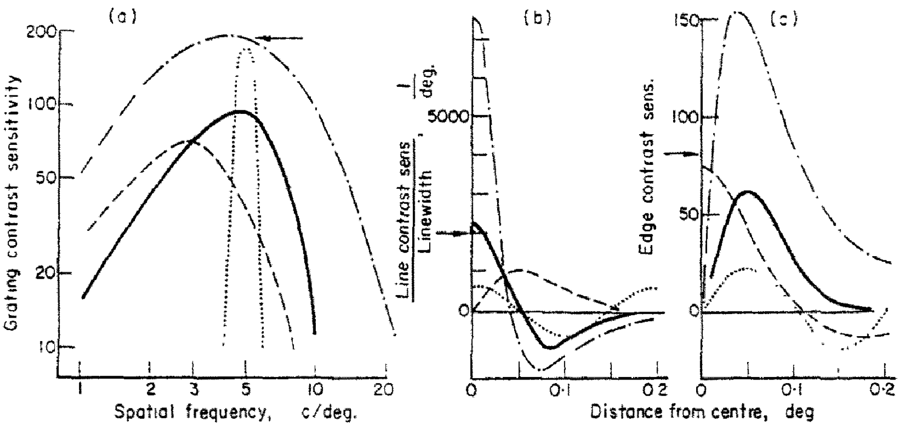

FIG. 11. Comparison between the multi-channel and single channel models. (a) Grating sensitivity curves: the continuous curve corresponds to the measured grating sensitivity function for the threshold-line detector (from Fig. 3). Similarly, the dashed and the dotted curves correspond respectively to the threshold-edge and 5 c/deg grating detectors (from Figs. 6a and 8a). The dot–dashed curve corresponds to the visual contrast sensitivity to gratings; note that, as there is only *one* detector in the single channel model, this curve must correspond to the grating sensitivity of that detector. The visual contrast sensitivity for a 5 c/deg grating is indicated by the arrow and this is consistent (within experimental error) with the grating sensitivity of the 5 c/deg grating detector (dotted curve) and of the detector in the single channel model (dash–dotted curve). All curves in Fig. 11 refer to J.J.K. (b) Line sensitivities: the curves represent line sensitivity functions for the multi-channel and single-channel models derived from the grating sensitivity functions of Fig. 11(a) by using Fourier transformation. Continuous, dashed and dotted curves correspnding to the threshold-line, threshold-edge and 5 c/deg grating detectors of the multi-channel theory. The dash–dotted line represents the calculated line sensitivity for the one detector of the single channel model (whose grating sensitivity is equal to the visual contrast sensitivity to gratings—dash–dotted line in Fig. 11a); a cosine type transformation has been assumed. The arrow indicates the observed visual contrast sensitivity for fine lines; it is seen that the predicted maximum line sensitivity for the threshold-line detector is in reasonable agreement with the observed contrast sensitivity, but that the line sensitivity predicted by the single channel model is much too high. (c) Edge sensitivities: the curves represent edge sensitivities, derived by the Fourier transform method, for the threshold-line (continuous curve), threshold-edge (dashes) and 5 c/deg grating (dots) detectors and also for the single channel model (dots and dashes). It is seen that the calculated maximum edge sensitivity of the threshold-edge detector is in reasonable agreement with the observed visual contrast sensitivity for edges (arrow) but that the maximum edge sensitivity calculated for the single channel model is again too great.

DISCUSSION

Grating, edge and line sensitivities for the multi-channel and single-channel models

Figure 11(a) summarizes, for observer J.J.K., the "grating sensitivity" data for the "5 c/deg grating", "threshold-line" and "threshold-edge" detectors. As already discussed, these data may be used to derive "line sensitivity" and "edge sensitivity" functions for the three detectors using Fourier transformation (Figs. 11b and 11c respectively).

On the "single channel" model (cf. CAMPBELL, CARPENTER and LEVINSON, 1969) it is proposed that the visual system may be treated as a *single* detector. If this assumption is made, then the contrast sensitivity to gratings for the whole visual system (also represented in Fig. 11a) must correspond to the "grating sensitivity" of this single detector. In this case, we may use this grating sensitivity function to derive corresponding line sensitivity and edge sensitivity functions using the Fourier transform method of Appendix 1. The latter sensitivity functions for the single channel model are represented in Fig. 11(b) and Fig. 11(c) (dot-dashed curves). An "even" (cosine type) Fourier transform has been assumed for the line sensitivity function (as was done by CAMPBELL *et al.*, 1969).

The arrows in Figs. 11(a), (b) and (c) represent the observed visual contrast sensitivities for a 5 c/deg grating, a fine line and an edge respectively. It is thus possible to compare these *observed* sensitivities with the sensitivities *predicted* by the single and multi-channel models. It can be seen, for example, that the observed sensitivity to a 5 c/deg grating is in good agreement with the predictions of both the single channel model (corresponding to the dot-dashed curve in Fig. 11(a)—see above) and the multi-channel model (for the 5 c/deg grating detector—dotted curve); however, in the case of the single channel model, this agreement is entirely trivial as the grating sensitivity of the detector in the single channel model has been *defined* to equal the visual contrast sensitivity to a grating.

The following points may now be noted from Fig. 11:

1. The maximum line and edge sensitivities predicted by the *single* channel model are considerably greater than the corresponding observed sensitivities. The predicted values would still be too great if we assumed a "peak to trough" detecting mechanism (see CAMPBELL *et al.*, 1969).

2. The observed line and edge sensitivities are however in good agreement with the predictions of the multi-channel model. Thus the observed visual contrast sensitivity to lines (Fig. 11b, arrow) corresponds to the calculated line sensitivity of the threshold-line detector (continuous curve); similarly the visual contrast sensitivity to an edge (Fig. 11c, arrow) corresponds to the calculated edge sensitivity of the threshold-edge detector (dashed curve). In summary, the visual contrast sensitivity for lines and edges may be predicted by the multi-channel model but not by the single-channel model.

3. As must be expected, the line detector has the highest line sensitivity of the three detectors, and, similarly, the edge detector has the highest edge sensitivity. Figure 11(a) illustrates that the grating detector has, of course, the highest grating sensitivity at 5 c/deg. These observations are further checks on the self-consistency of our model.

We conclude that, for these conditions, the predictive power of the multi-channel model is much better than that of the single channel model. The multi-channel model for the detection of *gratings* of different frequencies was suggested by CAMPBELL and ROBSON (1964) and further evidence for this model has been provided by CAMPBELL and ROBSON (1968), BLAKEMORE and CAMPBELL (1969), GRAHAM and NACHMIAS (1971) and SACHS, NACHMIAS and ROBSON (1971). THOMAS, ROURKE and WILDER (1968) have proposed the existence of units "tuned" to different widths of slits and our results (Fig. 9) confirm this idea. We may thus suggest an extended multi-channel model with a range of detectors both for gratings of different frequencies and for slits (or bars) of different widths.

Some related studies on line and edge detectors

THOMAS (1968) and THOMAS *et al.* (1968) have derived weighting functions which are similar to the line sensitivity function for the threshold-line detector (Fig. 4); their weighting functions were derived from the effects of suprathreshold adapting stimuli and it is interesting that their results are in reasaonble agreement with ours despite the non-linearity of the interactions which they demonstrated for their procedure. SULLIVAN, GEORGESON and OATLEY (1972) have shown that the threshold for a thin bar is elevated after adaptation to a 5·5 c/deg but not a 16 c/deg grating. This is because the threshold-line detector is almost insensitive to a 16 c/deg grating (Fig. 3). Other studies (CARTER and HENNING, 1971, BODIS-WOLLNER, 1972) are also consistent with our model.

TOLHURST (1972) has provided evidence for the existence of edge detectors in the human visual system and some similar subthreshold summation experiments for the edge-detector have been performed by SHAPLEY and TOLHURST (1972).

The two dimensional arrangement of the detectors

The term "line detector" has been used although we have only presented evidence on its spatial arrangement in the one dimension perpendicular to the line used as test stimulus. However, there is good reason to believe that the "receptive field" of the line detector extends a considerable distance in the direction parallel to the test line, because:

1. The threshold contrast for a thin line decreases as the length of the line is increased up to at least one degree (KULIKOWSKI, 1967).

2. If a line is superimposed on a subthreshold grating which is orientated at an angle to the line, the effect of the grating on the line threshold contrast decreases rapidly for angles

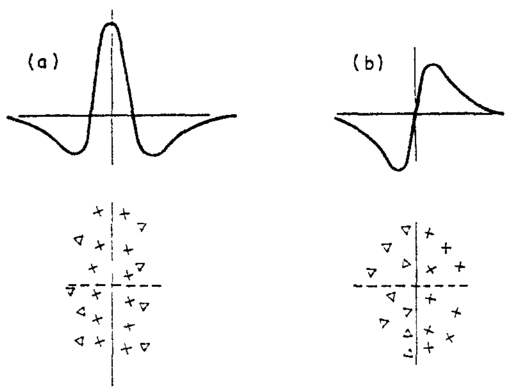

FIG. 12. Comparison between psychophysical detectors and visual neurons. (a) The curve represents the line sensitivity of the threshold-line detector. Beneath this is shown (not to the same scale) the receptive field map of a cortical cell in the cat (after HUBEL and WIESEL, 1962; crosses represent excitatory ('on') responses and triangles represent inhibitory ('off') responses). There is an evident similarity between the spatial properties of the line detector and the cortical cell. (b) The curve represents the line sensitivity of the threshold-edge detector; again, there is an evident similarity to the spatial properties of the cortical cell represented underneath.

above a few degrees (KULIKOWSKI, ABADI and KING-SMITH, 1973). These measurements are also consistent with a receptive field extent of above one degree along the axis of the test line.

The relation between visual neurons and psycho-physical detectors

Figure 12 illustrates the similarities between the line sensitivities of line and edge detectors and the receptive fields of "simple" cortical cells responding to lines (slits) and edges (HUBEL and WIESEL, 1962). Particularly remarkable is the resemblance between the "surround inhibition" of the line detector and that of the corresponding cortical cell (Fig. 12a). It has already been noted that the "grating sensitivities" of the line and edge detectors are very similar to the grating sensitivities of retinal ganglion cells (ENROTH-CUGELL and ROBSON, 1966) and many cortical cells (CAMPBELL, COOPER and ENROTH-CUGELL, 1969).

It is, therefore, very tempting to speculate that the detectors we describe correspond to cortical neurons. This is certainly plausible for simple patterns such as lines or edges. Yet the psychophysical detectors of complex patterns such as gratings may perhaps not correspond to single cells. There is no evidence, as yet, of any visual cell with properties like the grating detector described here and by SACHS, NACHMIAS and ROBSON (1971).

Disinhibition

MAFFEI and FIORENTINI (1972) and HAMMOND (1972) have described a region of disinhibition surrounding the inhibitory surround region of the receptive fields of lateral geniculate cells. It is perhaps surprising, therefore, that, by subthreshold summation, we have found no evidence for disinhibition in the line detector. However, we have found that two dark lines which are (even slightly) *suprathreshold* and spaced 12′ on either side of a central dark test line will lower the test threshold contrast, i.e. disinhibition seems to occur for suprathreshold conditions. This observation could be interpreted as a *lateral facilitation* effect between detectors of similar type and orientation; thus, if one detector is stimulated, the threshold for some similar surrounding detectors may be lowered.

Lateral inhibition between detectors

The grating sensitivity curve which we obtain for the grating detector (Fig. 8) is in reasonable agreement with the sensitivity curve of SACHS, NACHMIAS and ROBSON (1971) derived from frequency of seeing curves for superimposed gratings. However, BLAKEMORE and CAMPBELL (1969) have shown that, after adapting to a grating of one spatial frequency, the contrast threshold for gratings is elevated over a considerably broader range of the spatial frequency spectrum than in Fig. 8. An even broader range was found by using simultaneous masking (KULIKOWSKI, 1969). The elevation of threshold in these cases is, therefore, probably not due solely to adaptation (fatigue) of the detectors which responded to the adapting grating. We propose that the observed threshold elevation may also be partly due to lateral inhibition between grating detectors of different optimal frequencies; thus the strong response of the grating detector corresponding to the adapting or masking frequency would inhibit grating detectors responding at higher and lower frequencies. This inhibition could continue after cessation of the adapting stimulus. Similar observations have been made for orientation selectivity; thus, simultaneous masking by a grating, or adaptation by a grating, elevates the contrast threshold for a test grating for a *wider* range of orientations than the range that is effective for subthreshold summation (see KULIKOWSKI, ABADI and KING-SMITH, 1973).

Considerable evidence has been obtained for such lateral inhibition between detectors, since it was suggested by ANDREWS (1965). BLAKEMORE, CARPENTER and GEORGESON (1970) have suggested that it may form the basis of the apparent broadening of acute angles. BLAKEMORE, CARPENTER and GEORGESON (1971) have suggested that the tilt aftereffect may also depend on lateral inhibition. The threshold contrast for a test bar or a grating superimposed on a (suprathreshold) background grating may sometimes be *reduced* by adding a second background grating (Kulikowski, unpublished). Presumably, the second background inhibits the first background detector which therefore causes less elevation of the test threshold. Similarly, TOLHURST (1972) has shown that the adapting effect of a grating may be reduced by adding a second grating. Finally, BLAKEMORE and TOBIN (1972) have demonstrated, in cortical cells, a lateral inhibition effect which is orientation specific: presumably, this inhibition must be derived from other cortical cells. Further evidence for lateral inhibition between cortical cells has been provided by BENEVENTO, CREUTZFELDT and KUHNT (1972).

The assumptions which have been used in the analysis of our data (i.e. the multichannel model of Fig. 1a and the linear filter theory) are, we believe, of value in understanding the behaviour of the visual system at *threshold*. But our model is evidently too simple at levels much above threshold. Thus, according to our model, a fine line with a contrast of, e.g. 5 times threshold will stimulate not only a variety of line detectors of various widths and orientations, but it will also stimulate edge and grating detectors. Despite these confusing signals, we have in fact no doubt that the stimulus is a fine line and not a coarse line or an edge or a grating. Further processing must occur (in addition to that in Fig. 1) and it is tempting to speculate that lateral inhibition between detectors may play an important part in two ways:

1. In general, one might expect that the most active detectors will strongly inhibit the less active detectors, e.g. in the above example, the optimally activated line detectors will strongly inhibit the edge and grating detectors and thus any confusion due to the simultaneous response of all three types of detectors will be reduced or eliminated.

2. In addition, there is a tendency for *finer* detectors to inhibit *coarser* detectors. Thus, as the contrast of a fine line is increased above threshold, the line appears to become sharper (or at least more sharply localized). Simultaneous masking experiments (KULIKOWSKI, 1969) also provide evidence that finer detectors inhibit more strongly than coarser detectors since a masking grating elevates contrast thresholds for coarser gratings more than for finer gratings. Again, it can be demonstrated that when useful information in a picture is contained mainly in low spatial frequencies, the picture cannot be analysed if there are too many irrelevant high-frequency components (HARMON, 1970; JULESZ, 1971). All these observations suggest that, for any retinal image, we tend to make most use of the finest detectors that are activated.

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APPENDIX 1

Derivation of the line sensitivity and edge sensitivity functions from the grating sensitivity function

If we know the sensitivity of a *linear* system to sinusoidal stimuli as a function of frequency and phase, then it is possible to predict the response of the system to any other stimulus using the Fourier transform method (see, for example, CORNSWEET, 1970). The data of Fig. 2 provide evidence that the "filters" of Fig. 1(a) behave linearly in the conditions of our experiments. We may therefore use the "grating sensitivity" data for a detector to predict its response (and hence its sensitivity) to any pattern; in particular, we may calculate its "line sensitivity" and "edge sensitivity" (i.e. the contrast sensitivity to thin lines and to edges as a function of their position) as follows:

According to the Fourier integral theorem, a luminance distribution, $L(x)$, may be expressed in terms of its frequency components as follows:

$$L(x) = \int_0^\infty (A(f) \cos 2\pi fx + B(f) \sin 2\pi fx)\, df \tag{A1}$$

where

$$A(f) = 2 \int_{-\infty}^{\infty} L(x) \cos 2\pi fx\, dx \tag{A2}$$

and

$$B(f) = 2 \int_{-\infty}^{\infty} L(x) \sin 2\pi fx\, dx \tag{A3}$$

(see, for example, STUART, 1961). The functions $A(f)$ and $B(f)$ correspond to the amplitude of the cosine and sine components for spatial frequency f.

We are particularly interested in two luminance distributions, $L(x)$:

1. A fine line at position x_0 with width Δx and luminance ΔL (above the surrounding luminance $\bar{L}$).
2. An edge corresponding to a step in the luminance distribution of height ΔL at position x_0.

For each of these stimuli we may calculate the cosine and sine components of luminance from equations A2 and A3. Then, if we know the grating and phase sensitivity of a detector, we can calculate the response of this detector to the line or the edge described above, and finally derive the line or edge sensitivity.

Note that some detectors (e.g. the line detector) are insensitive to gratings of sine type phase (Fig. 3b) so in these cases, the sine components (i.e. $B(f)$) of the stimulus need not be considered. Similarly, the cosine components, $A(f)$, need not be considered for the edge detector (Fig. 6b).

The line sensitivity of a "cosine-type" detector (e.g. the line detector)

The cosine components of the luminance distribution of the line may be derived from equation A2; thus

$$A(f) = 2\, \Delta L.\, \Delta x.\, \cos 2\pi f x_0.$$

The corresponding contrast components are $A(f)/\bar{L}$.

Note that grating sensitivity is defined as the reciprocal of the grating contrast threshold. If we define the response (R) of the "filter" (see Fig. 1a) to a grating to be the product of the grating contrast and the grating sensitivity of the detector, then a threshold stimulus must correspond to $R = 1$.

The response of the filter to the line will be the sum (integral) of the responses to the individual sinusoidal components, i.e.

$$R = \int_0^\infty S_g(f)A(f)/\bar{L}\,\mathrm{d}f$$

$$= \int_0^\infty S_g(f).2(\Delta L.\Delta x/\bar{L})\cos 2\pi f x_0\,\mathrm{d}f$$

where $S_g(f)$ is the grating sensitivity of the detector.

The line sensitivity $S_l(x_0)$ is defined as the reciprocal of (contrast threshold times line width), i.e.

$$S_l(x_0) = 2\bar{L}/(\Delta L.\Delta x)$$

for a threshold stimulus ($R = 1$). Thus, finally we obtain

$$S_l(x_0) = 4\int_0^\infty S_g(f)\cos 2\pi f x\,\mathrm{d}f.$$

In a similar way, the edge sensitivity $S_e(x_0)$ for a cosine-type detector may be shown to be

$$S_e(x_0) = -(2/\pi)\int_0^\infty S_g(f)\sin 2\pi f x_0\,\mathrm{d}f/f.$$

Corresponding formulae may be derived for sine-type (e.g. edge) detectors.

Appendix 2. The observed sensitivity curve for the grating detector

It is assumed that the grating sensitivity function of a grating detector has the form

$$S = S_0\,\mathrm{e}^{-(f-f_0)^2/2\sigma^2} \qquad \text{(A4)}$$

(see Results section).

Let C_{0t} be the contrast threshold for a test grating (frequency f_1) by itself, and let C_+ be the test contrast threshold in the presence of a subthreshold background grating of contrast C_b and frequency f_2. Then the calculated grating sensitivity, S', for this background frequency will be

$$S' = (C_{0t} - C_+)/(C_{0t}.C_b) \qquad \text{(A5)}$$

(see Methods).

Assume that there is a continuous spectrum of grating detectors each tuned to a slightly different frequency f_0; then the combined grating pattern will presumably be detected, at threshold, by a detector with a tuned frequency, f_0, between f_1 and f_2. The frequency f_0 will be found to be fairly close to f_1, so we will assume that its maximum sensitivity, S_0, is the same as that at f_1 (i.e. $1/C_{0t}$).

If we define the response, R, of the detector filter as the product of contrast and sensitivity (thus $R = 1$ at threshold—see Appendix 1), then the response of the grating detector to the two gratings will be at threshold when (from equation A4)

$$R = 1 = S_0(C_+\,\mathrm{e}^{-(f_1-f_0)^2/2\sigma^2} + C_b\,\mathrm{e}^{-(f_2-f_0)^2/2\sigma^2})$$

Thus for an assumed value of σ, and knowing the values of f_1, f_2, S_0 ($= 1/C_{0t}$) and C_b, we can find (e.g. by trial and error) the detector frequency f_0 which gives the lowest test contrast threshold C_+. The prediction for the observed sensitivity is now given by equation A5.

Abstract—The present psychophysical experiments provide evidence for the existence of a variety of detectors responding optimally to lines, edges or gratings. Their existence is revealed by subthreshold summation measurements in which the effect of a subthreshold background on the contrast threshold of a test stimulus is determined. By suitable choice of test and background patterns, we have studied the sensitivities of the detectors tuned to a variety of patterns (e.g. lines, edges and gratings) to background patterns also consisting of lines, edges or gratings. The analysis of the measurements is shown to be self-consistent in a number of ways; for example, the measured contrast sensitivity of the line detector for gratings of different frequencies may be used to predict the sensitivity of this detector for fine lines as a function of their width and position.

Résumé—Les expériences psychophysiques connues prouvent l'existence d'une variété de détecteurs répondant électivement aux lignes, bords et réseaux. Leur existence est révélée par les mesures de sommation subliminale où l'on détermine l'effet d'un fond subliminal sur le seuil de contraste d'un stimulus test. Par un choix convenable des figures test et fond, nous avons étudié les sensibitités des détecteurs spécialisés pour certaines figures (lignes, bords et réseaux) à des fonds composés avec les mêmes figures. On peut montrer de diverses façons la cohérence interne de ces mesures; par exemple la sensibilité au contraste d'un détecteur de ligne mesurée avec des réseaux de diverses fréquences permet de prédire la sensibilité de ce détecteur de lignes fines en fonction de leur largeur et de leur position.

Zusammenfassung—Die gegenwärtigen psychophysikalischen Experimente weisen darauf hin, dass eine Vielzahl von Detektoren, die optimal auf Linien, Kanten oder Gitter reagieren, vorhanden sind. Ihr Vorhandensein zeigt sich aufgrund unterschwelliger Summation bei Messungen, in denen der Effekt eines unterschwellig dargebotenen Hintergrundes auf die Kontrastschwelle eines Testreizes bestimmt wird. Durch die geeignete Wahl von Test- und Hintergrundsmustern haben wir die Empfindlichkeit der Detektoren für eine Vielzahl von Mustern (z.B. Linien, Kanten und Gitter) auf Hintergrundsmuster, die auch aus Linien, Kanten oder Gittern, bestanden, untersucht.

Die Analyse der Messergebnisse zeigt, dass sie in sich konsistent sind. So kann z. B. die gemessene Kontrastempfindlichkeit des Liniendetektors für Gitter verschiedener Frequenzen dazu benutzt werden, die Empfindlickheit dieses Detektors für schmale Linien als Funktion ihrer Breite und Position vorherzusagen.

Резюме—Настоящие психофизические эксперименты доказывают существование различных детекторов, отвечающих оптимально на линии, края и решетки. Их существование обнаруживается путем измерения подпороговой суммации, которая определяет действие подпорогового фона на порог различения для тестового стимула. Путем соответствующего выбора тестового объекта и фона мы изучили чувствительности детекторов включенных в различные паттерны (например, линии, края и решетки), по отношению к фоновым паттернам, также состоящим из линий, краев и решеток.

Анализ результатов измерений показал, что они согласуются несколькими путями; например, результаты измерения контрастной чувствительности детектора линии для решеток различных частот может быть использовано с целью предсказания чувствительности этого детектора для тонких линий, в зависимости от их ширины и положения.