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THE INDEPENDENCE OF CHANNELS IN HUMAN VISION SELECTIVE FOR DIRECTION OF MOVEMENT

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SUMMARY

1. Human visual selectivity for direction of movement was determined using a subthreshold summation technique.

2. The threshold contrast for detecting a drifting sinusoidal grating was found to be independent of the contrast of an added subthreshold grating which moved in the opposite direction.

3. The detection threshold for a counterphase flickering grating is twice that for a moving grating, suggesting that the visual system analyses a counterphase grating as the sum of two half-contrast gratings which move in opposite directions.

4. Threshold for a counterphase grating may be linearly reduced by the addition of subthreshold background gratings drifting in either direction. Additivity between counterphase grating and moving background is complete.

5. After adaptation to a drifting grating, the behaviour of counterphase detection threshold as a function of the contrast of a moving subthreshold background depends upon the direction of background movement. When the background moves in a direction *opposite* that of the adaptation stimulus, complete linear additivity results. When the background moves in the same direction as the adapting grating, counterphase threshold is constant for low background contrasts, but drops linearly for higher background contrasts.

6. The results support the hypothesis that directionally selective channels in human vision are independent contrast detectors. Counterphase gratings are detected by one or the other of these direction-specific mechanisms, whichever is momentarily the more sensitive.

INTRODUCTION

Throughout the course of mammalian evolution, the visual response to moving objects has probably been of great survival value. It is not surprising, then, that mammalian visual systems contain structures which show high selectivity for direction of movement. Direction-specific neurones are abundant in the visual cortex of cat (Pettigrew, Nikara & Bishop, 1968; Henry, Bishop & Dreher, 1974) and of monkey (Hubel & Wiesel, 1968; Wurtz, 1969; Poggio, 1972). A directionally selective cell discharges strongly when its receptive field is traversed by a properly oriented stimulus drifting in one direction; the cell will fire at a reduced rate, however, if the stimulus moves in the opposite direction.

Directional selectivity has been found in human vision as well, primarily through psychophysical measurements of *direction-specific adaptation* (Sekuler & Ganz, 1963; Pantle & Sekuler, 1969). Prolonged exposure to a high-contrast adaptation grating moving in one direction elevates the contrast detection threshold *more* for a grating moving in the *same* direction than for one drifting in the opposite direction. Selectivity demonstrated using such an adaptation technique does not, of course, imply the existence of separate *detectors* for opposite directions of movement (Sekuler, 1974). Direction-specific adaptation might reflect activity in directionally selective neurones whose outputs are pooled at a non-direction-specific detection stage. One way to determine whether separate and independent channels detect movement in opposite directions is to measure the extent to which a threshold or subthreshold grating drifting in one direction can reduce the detection threshold for a superimposed grating moving in the opposite direction. This additivity, or *summation*, technique has been extensively utilized for measurements of channels in human spatial vision (Graham & Nachmias, 1971; Sachs, Nachmias & Robson, 1971; Kulikowski & King-Smith, 1973; Shapley & Tolhurst, 1973). In the present study we show that gratings moving in opposite directions do *not* add near threshold; channels in human vision selective for opposite directions of movement therefore operate independently.

THEORY

A vertical sinusoidal grating is generated by periodic spatial modulation of luminance along a horizontal axis. Such a grating may drift along the axis of modulation (i.e. perpendicular to the orientation of its bars); this movement is equivalent to a linear change in spatial phase as a function of time. The luminance of this moving grating as a function of time and of position along the horizontal axis is given by

$$L(x,t) = L_0\{1+m \cos (fx \pm \omega t)\}, \tag{1}$$

where L_0 is the average luminance, m is the contrast, defined as $(L_{\text{maximum}} - L_{\text{minimum}})/2L_0$, $f/2\pi$ is the spatial frequency in c/deg, x is horizontal position in the visual field, $\omega/2\pi$ is temporal frequency or drift rate in Hz, and

t is time. Equation (1) describes a grating moving to the left when the phase angle (ωt) is added; for a rightward-moving grating the phase angle is subtracted.

A stimulus in the present experiments can be represented as a combination of two gratings, drifting in opposite directions:

$$L(x, t) = L_0\{1+m_{\text{left}} \cos (fx+\omega t)+m_{\text{right}} \cos (fx-\omega t)\}. \tag{2}$$

The two moving gratings have the same spatial frequency and the same temporal frequency; only direction and contrast may be different. In most cases both f and ω are non-zero, although for a few control measurements we used stationary gratings ($\omega = 0$) or uniform flickering fields ($f = 0$). Equation (2) reduces to eqn. (1) when either m_{left} or m_{right} is zero.

A special case occurs when the contrasts of the two moving components are equal; substituting $m' = m_{\text{left}} = m_{\text{right}}$ into eqn. (2), and applying standard trigonometric identities, we have

$$L(x, t) = L_0\{1+m' \cos (fx+\omega t)+m' \cos (fx-\omega t)\} \tag{3}$$

$$= L_0\{1+2m' \cos (\omega t) \cos (fx)\}. \tag{4}$$

Equation (4) is the luminance profile for a *counterphase flickering grating* whose contrast, $2m'$, is twice that of either moving component alone. A counterphase grating alternates sinusoidally in phase; it does not drift in either direction. Counterphase gratings have frequently been used to measure the spatio-temporal contrast sensitivity of the human visual system. Implicit in several previous studies using such gratings (Kelly, 1971, 1972) has been the assumption that responses to a counterphase grating do not depend upon its moving components. The present experiments will show, on the contrary, that the counterphase grating is physiologically, as well as mathematically analysed in terms of its moving parts.

Let us now consider the mechanism which detects the presence (at threshold) of a stimulus such as that described by (2). Assume that this mechanism is a *linear* contrast detector; its response R is given by

$$R = m_{\text{left}}\, S_{\text{left}}+m_{\text{right}}\, S_{\text{right}}, \tag{5}$$

where S_{left} and S_{right} represent sensitivities to leftward- and rightward-moving gratings, respectively. Sensitivity for a particular type of stimulus is defined as the reciprocal of the threshold contrast required by the mechanism for detection of that stimulus, presented alone. For example,

$$S_{\text{left}} = (m^{\text{th}}_{\text{left}})^{-1}, \tag{6}$$

where $m^{\text{th}}_{\text{left}}$ is the threshold contrast for a leftward-moving grating. Substituting into eqn. (5), we obtain the threshold response of this mechanism (or of any other linear mechanism):

$$R = m^{\text{th}}_{\text{left}}\, (m^{\text{th}}_{\text{left}})^{-1}+0\cdot S_{\text{right}} = 1. \tag{7}$$

Imagine now that we can isolate and examine the mechanism which normally detects leftward-moving gratings when they are presented alone. Previous research (Pantle & Sekuler, 1969) has shown that contrast thresholds for gratings moving in opposite directions are approximately equal. If our mechanism's sensitivity for rightward motion were as great as its sensitivity for stimuli moving to the left ($S_{\text{right}} = S_{\text{left}} = S$), then the mechanism would be the sole detecting channel for both leftward and rightward movement. This *single-channel* hypothesis predicts complete additivity when observers must detect combinations of oppositely moving gratings (eqn. (2)): from eqns. (5) and (7),

$$1 = m_{\text{left}}\,S + m_{\text{right}}\,S = (m_{\text{left}} + m_{\text{right}})S, \tag{8}$$

or, at threshold $m_{\text{left}} + m_{\text{right}}$ is constant. On the other hand, if S_{left} is greater than S_{right} for this mechanism, then *separate channels* would exist for detecting leftward- and rightward-moving gratings, and incomplete summation between leftward and rightward components might occur. If $S_{\text{right}} = 0$, these direction-specific channels would be effectively *independent* at threshold, and no additivity might be expected (m_{left} = constant = $m_{\text{left}}^{\text{th}}$). The results of our experiments will support this idea, that independent channels detect gratings moving in opposite directions.

METHODS

Vertical sinusoidal gratings were generated on the face of a cathode-ray tube (P4 phosphor) using a television technique (Campbell & Green, 1965). A raster (1 kHz frame rate) was created which subtended 10 deg × 10 deg visual angle at a 57 cm viewing distance. The average luminance of the display was 3·4 cd/m^2. A small rectangular bar ($1 \times \frac{1}{2}$ deg) in the centre of the screen was provided to assist fixation.

Modulating voltages were obtained from a set of electronic wave-form generators. Gratings were made to drift by means of motor-driven synchro-resolvers, a modification of the method used by Enroth-Cugell & Robson (1966). The shafts of two synchro-resolvers were firmly fixed together, such that their rotation was precisely synchronized but in opposite directions. This arrangement allowed the simultaneous production of gratings moving in opposite directions at identical drift rates.

Counterphase flickering gratings were produced by directly multiplying a modulating signal by a low temporal frequency sinusoid (eqn. (4)). This guaranteed that the contrasts of the moving components would be equal, so that a 'true' counterphase grating could always be obtained. For some measurements the multiplication was electronically achieved; in other cases one of the ganged synchro-resolvers was used as a multiplier. Equivalent data were obtained using either technique.

Combinations of these modulating signals could be electronically summed before application to the brightness axis of the CRT. The contrasts of the components were independently adjustable. When two components were added, the contrast of one component (the 'test' grating) was under control of the observer, whereas the contrast of the other (the 'background' grating) was fixed at some subthreshold level.

Contrasts are always specified separately for test and background components; this means that when a counterphase grating as such is used as test stimulus, its *nominal* contrast is twice the actual contrast of each moving component (see eqns. (3) and (4)). When necessary, phase angles of the component gratings could be fixed relative to one another, making precise synchronization possible; great care was taken to ensure that such alignment was maintained throughout an experimental session.

The experiments were controlled by a small computer. The observer typically began a session by viewing the uniformly illuminated CRT screen (or in some cases a high-contrast adaptation grating) for 3 min. He was then presented with a test stimulus plus background grating for 1 sec, followed by another 4 sec of blank screen (or adaptation grating). This sequence (1 sec test plus background, 4 sec blank or adaptation) was repeated indefinitely while the observer turned a linear potentiometer which controlled the contrast of the test stimulus. The observer reduced the contrast of the test grating until he could no longer discriminate it from the unmodulated raster. He then signalled the computer to calculate and print the threshold contrast. Six such threshold settings constituted an experimental session. The S.E. of the mean of measurements within a session was generally less than 6 %. A different set of parameter values was used for each session, and the order of conditions was randomized. We emphasize that within a session only direction of movement and contrast varied; one spatial frequency and one temporal frequency was used for all stimuli (test, background and adapting gratings).

A few measurements were made using a two-interval forced-choice procedure, also under computer control. These observations increased our confidence that experimental results were not attributable to observer biases.

The authors served as observers. R.S. has normal vision and E.L. wore his normal spectacle correction. Monocular viewing was used throughout. E.L. viewed through a 2·3 mm diameter artificial pupil for all measurements except those in Fig. 3.

RESULTS

Subthreshold summation between opposite directions of movement

The degree of independence for direction-specific mechanisms may be assessed by measuring the detection threshold for a moving grating superimposed upon a fixed-contrast, subthreshold grating which drifts in the opposite direction. Imagine, for example, that an observer must detect a rightward-moving grating (contrast = $m^{\mathrm{v}}_{\mathrm{right}}$) added to a subthreshold background (of the same spatial frequency and drift rate) which moves to the left (contrast = $m^{\mathrm{b}}_{\mathrm{left}}$). We shall initially consider the implications of the single-channel hypothesis (i.e. $S_{\mathrm{right}} = S_{\mathrm{left}} = S$). The threshold response (from eqns. (5) and (7)) of the single detecting mechanism is

$$\begin{aligned} 1 &= m^{\mathrm{v}}_{\mathrm{right}}\, S + m^{\mathrm{b}}_{\mathrm{left}}\, S \qquad (9)\\ &= (m^{\mathrm{v}}_{\mathrm{right}} + m^{\mathrm{b}}_{\mathrm{left}})\, S. \end{aligned}$$

Rearranging eqn. (9) , we have the new threshold contrast of the rightward test, $m^{\mathrm{v}}_{\mathrm{right}}$, as a function of the subthreshold background contrast $m^{\mathrm{b}}_{\mathrm{left}}$

$$m^{\mathrm{v}}_{\mathrm{right}} = S^{-1} - m^{\mathrm{b}}_{\mathrm{left}} = m^{\mathrm{th}}_{\mathrm{right}} - m^{\mathrm{b}}_{\mathrm{left}}. \qquad (10)$$

The line described by eqn. (10) represents complete summation between opposite directions of motion; it is indicated by the dashed line (slope $= -1$) in Fig. 1. The line intercepts the ordinate (variable test contrast axis) at the threshold contrast for the rightward test stimulus alone, with no background present ($= m^{\mathrm{th}}_{\mathrm{right}}$). The function may be extrapolated to an intersection with the background contrast axis (abscissa), where the variable test contrast ($m^{\mathrm{v}}_{\mathrm{right}}$) is zero. At the abscissa intercept the entire stimulus package would still be at threshold, even though no test stimulus contrast would be present. The leftward background would therefore be driving the detector at a threshold level, and the value of background contrast at this point must represent the threshold of the detecting mechanism for the leftward background. Substituting $m^{\mathrm{v}}_{\mathrm{right}} = 0$ into eqn. (10), and rearranging terms, we see that the background contrast $m^{\mathrm{b}}_{\mathrm{left}}$ at the intercept equals $m^{\mathrm{th}}_{\mathrm{right}}$, the threshold for the test stimulus alone. Hence the detector's threshold for the leftward background is the same as its threshold for a rightward-drifting grating, satisfying the single-channel assumption ($S_{\mathrm{left}} = S_{\mathrm{right}}$). Data points should thus follow the steep dashed line in Fig. 1 if the single-channel model is correct.

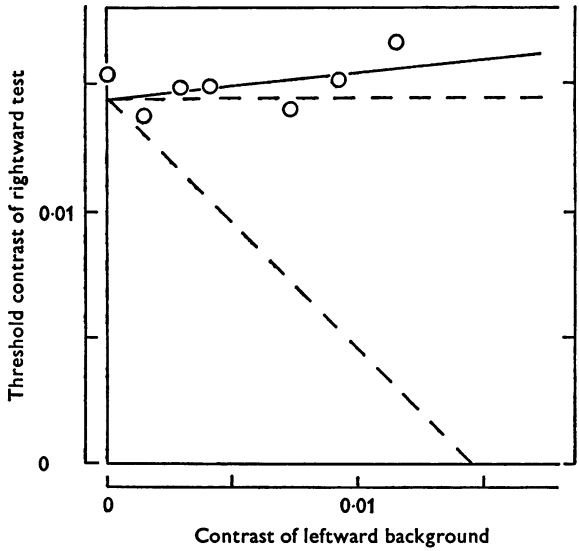

Fig. 1. Thresholds for rightward-moving test gratings added to subthreshold, leftward-moving background gratings. The continuous line is a least-squares estimate. The steep dashed line is a prediction based on the single-channel model, the horizontal dashed line a prediction of the independent-channels model. The observer was E.L., the spatial frequency 1·75 c/deg, the temporal frequency 7·9 Hz.

Now consider the independent-channels hypothesis ($S_{\text{left}} = 0$); this model predicts a response for the rightward-specific detector of

$$1 = m^{\text{v}}_{\text{right}}\, S_{\text{right}} + 0 . m^{\text{b}}_{\text{left}} = m^{\text{v}}_{\text{right}}\, S_{\text{right}}. \tag{11}$$

The test grating contrast at threshold is therefore constant ($= S^{-1}_{\text{right}} = m^{\text{th}}_{\text{right}}$, the threshold for the rightward test stimulus alone), and independent of leftward background contrast; a horizontal summation line (dashed line), indicative of no additivity, is predicted. Fig. 1 shows thresholds for rightward gratings with leftward backgrounds. The slope of the solid line (fitted by least squares) falls within the 95 % confidence limit for the horizontal. Similar results have been obtained using leftward movement on backgrounds drifting to the right. The data therefore support the independent-channels model; a direction-specific mechanism has virtually no sensitivity for its non-preferred direction.

Contrast sensitivity for moving and counterphase gratings

A comparison of contrast sensitivity for moving and counterphase gratings provides rather a more powerful test of the independent-channels hypothesis, because the counterphase grating, although formally a combination of two gratings moving in opposite directions, does not physically drift in either direction.

Equations (3) and (4) show that the sum of two gratings, one moving to the left, the other to the right, and each of contrast m', is a counterphase grating of contrast $2m'$. Assume that $2m' = m^{\text{th}}_{\text{c}}$, the *threshold* contrast for a counterphase grating. We would like to obtain an expression for m^{th}_{c} in terms of the threshold for a moving component itself, $m^{\text{th}}_{\text{left}}$ or $m^{\text{th}}_{\text{right}}$. The threshold response of the detecting mechanism (from eqns. (5) and (7)) can be written

$$1 = m' S_{\text{left}} + m' S_{\text{right}}. \tag{12}$$

Under the single-channel hypothesis ($S_{\text{left}} = S_{\text{right}} = S$) the counterphase threshold response of the single channel is given by substitution into eqn. (12):

$$1 = m'S + m'S = 2m'S = m^{\text{th}}_{\text{c}} S. \tag{13}$$

Threshold for a counterphase grating should then equal $S^{-1} = m^{\text{th}}_{\text{left}} = m^{\text{th}}_{\text{right}}$: moving and counterphase stimuli should have the *same* contrast threshold.

Now assume that the independent-channels hypothesis is correct. This means that the counterphase grating will be detected by one *or* the other direction-specific channel, whichever is momentarily the more sensitive to its preferred direction (the detecting channel might vary from moment to moment as a result of probabilistic fluctuations in noise levels, for example). Imagine that for one particular measurement the rightward-specific channel is the detector; S_{left} for this channel is zero. The threshold response to a counterphase grating is therefore

$$1 = m'S_{\text{left}} + m'S_{\text{right}} = m'S_{\text{right}} = \tfrac{1}{2}m_c^{\text{th}}S_{\text{right}}. \tag{14}$$

Therefore,

$$m_c^{\text{th}} = 2S_{\text{right}}^{-1} = 2m_{\text{right}}^{\text{th}}. \tag{15}$$

Similar reasoning applies when the leftward-specific channel happens to detect the counterphase ($m_c^{\text{th}} = 2m_{\text{left}}^{\text{th}}$). The counterphase threshold will be *twice* that for a moving grating.

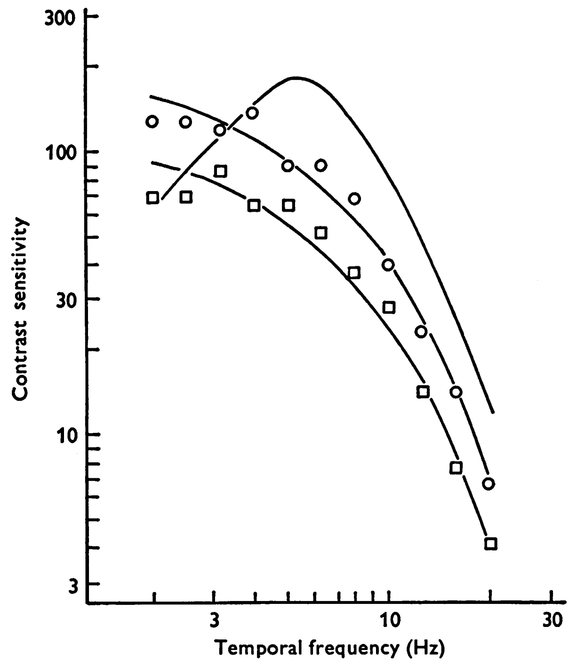

Fig. 2. Contrast sensitivity for rightward-moving gratings (circles) and counterphase gratings (squares). The curves through the data points are exponential functions (fitted by least-squares). The non-monotonic curve gives sensitivity for uniform flicker. The observer was E.L., the spatial frequency 1·75 c/deg.

Fig. 2 gives the contrast sensitivity (reciprocal of threshold contrast) of one observer for 1·75 c/deg gratings, moving to the right (circles) or flickering in counterphase (squares), as functions of temporal frequency (drift rate). The axes are logarithmically scaled, as is customary. Shown also for comparison is this observer's sensitivity to uniform flicker of the entire 10 deg raster (non-monotonic curve). The increased relative sensitivity at low temporal frequencies when spatial modulation is also present is typical of these sorts of measurements (Robson, 1966; Kulikowski & Tolhurst, 1973). The critical point is that sensitivity to moving gratings is about 0·3 log. unit greater than that for counterphase gratings (i.e. counterphase thresholds are twice those for motion).

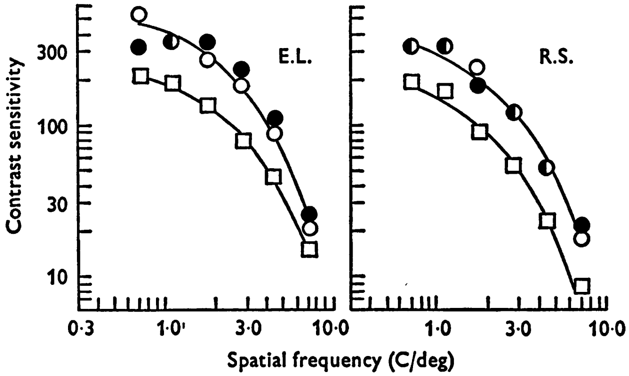

Fig. 3. Contrast sensitivities for rightward-moving gratings (open circles), leftward-moving gratings (filled circles), and counterphase gratings (squares). The curves are exponential functions; one function was fitted to the counterphase sensitivities, the other to the sensitivities for both directions of movement. The temporal frequency was 4·0 Hz for E.L., 7·9 Hz for R.S.

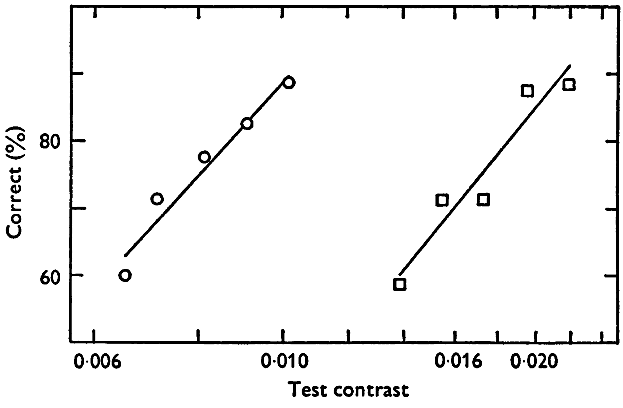

Fig. 4. Psychometric functions for forced-choice detection of rightward-moving gratings (circles) and counterphase gratings (squares). Lines are least-squares estimates. The observer was R.S., the spatial frequency 2·81 c/deg, the temporal frequency 7·9 Hz.

Similar results are obtained as functions of spatial frequency. Fig. 3 gives contrast sensitivity for counterphase gratings and for gratings moving left and moving right. The data for E.L. were collected at 4·0 Hz, while those for R.S. were at 7·9 Hz. No systematic differences are found in thresholds for opposite directions of movement, but counterphase sensitivity is again about half the sensitivity to moving stimuli. These are the results predicted by the independent-channels model.

Forced-choice measurements of this difference are displayed in Fig. 4 for observer R.S. (2·81 c/deg, 7·9 Hz). Five contrasts were chosen for each stimulus type (moving and counterphase) such that a previous estimate of threshold was bracketed; eighty trials were run at each contrast to obtain psychometric functions. The function for the counterphase grating is shifted by about 0·3 log unit toward higher contrasts. Again, the results are consistent with the idea of independent direction-selective channels.

Thresholds for counterphase gratings on subthreshold moving backgrounds

The preceding experiments do not eliminate the possibility that a counterphase grating is detected by a separate 'counterphase detector' which is itself non-direction-specific. This new mechanism might coincidentally be half as sensitive as are direction-selective channels; this could account for the observed difference in threshold between counterphase and moving stimuli. We therefore need to demonstrate that a counterphase grating is detected by the *same* mechanism which detects a drifting grating. We do this by measuring summation between a variable contrast counterphase test grating and a subthreshold background grating (of the same spatial and temporal frequency) moving leftward or rightward, exactly in phase with the corresponding moving part of the counterphase test grating. If the counterphase is detected by a moving grating detector, complete additivity should result.

Consider the case where the background drifts rightward. For clarity, we shall assume independence of direction-specific channels, although such an assumption is not essential for the present argument. The rightward-specific channel ignores the leftward component of the counterphase grating, and responds to the counterphase grating as though it were a grating drifting to the right. The rightward background grating is identical (except for its contrast) to this rightward component of the counterphase. Thus, for the stimulus package to remain at threshold, any increase in background contrast must be exactly balanced by a decrease in the rightward part of the counterphase. If we call the variable threshold contrast of the counterphase $m_c^v = 2m'$, and the rightward background contrast m_{right}^b, we can use eqns. (3), (4) and (5) to obtain the response of the rightward-specific mechanism:

$$1 = m'S_{\text{left}} + m'S_{\text{right}} + m_{\text{right}}^b S_{\text{right}}. \tag{16}$$

Assuming independence of direction-selective channels ($S_{\text{left}} = 0$) we have

$$1 = S_{\text{right}}(m' + m_{\text{right}}^b) \tag{17}$$

and

$$m_c^v (= 2m') = 2S_{\text{right}}^{-1} - 2m_{\text{right}}^{\text{b}} = 2m_{\text{right}}^{\text{th}} - 2m_{\text{right}}^{\text{b}}. \tag{18}$$

This means that counterphase test threshold should decrease linearly to an abscissa intercept (where variable test contrast is zero at threshold) which estimates $m_{\text{right}}^{\text{th}}$, the threshold contrast for the rightward-moving background, presented alone. Therefore, if the counterphase grating is detected by the same mechanism which detects moving gratings, this abscissa intercept should agree with an independent measurement of threshold contrast for a rightward-drifting grating. The reasoning is identical when the background moves to the left, only in that case the leftward-specific channel is the presumed detector, and the abscissa intercept of the summation line should agree with an independent measurement of *leftward* threshold.

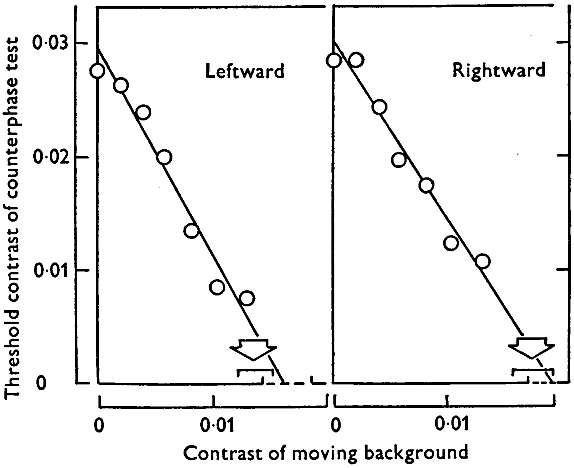

Fig. 5. Thresholds for counterphase test gratings added to subthreshold, leftward- or rightward-moving background gratings. Lines were fitted by least-squares; the dashed portions of the abscissas denote ± 2 S.E. of the intercept. Arrows represent independent measurements of threshold for detection of the background alone, and the horizontal bars are ± 2 S.E. of these estimates. The observer was E.L., the spatial frequency 1·75 c/deg, the temporal frequency 7·9 Hz.

In Fig. 5 we present the results of this manipulation (observer E.L.), the left- and right-hand panels for leftward- and rightward-moving background gratings, respectively. The solid lines have been fitted by least-squares; the small vertical lines marking the dashed portion of the abscissa show ± 2 S.E. of the intercept. Each arrow points to an independent threshold estimate for a grating, presented alone, which moves in the direction of the background. A horizontal bar gives ± 2 S.E. of the mean for each of these estimates. The abscissa intercept and the independent threshold estimate agree, within limits of experimental error, for both directions of background motion. Fig. 6 shows similar results for observer R.S. at a different pair of spatial and temporal frequencies.

The results thus show that counterphase flickering gratings *are* detected by the same mechanisms which detect moving gratings.

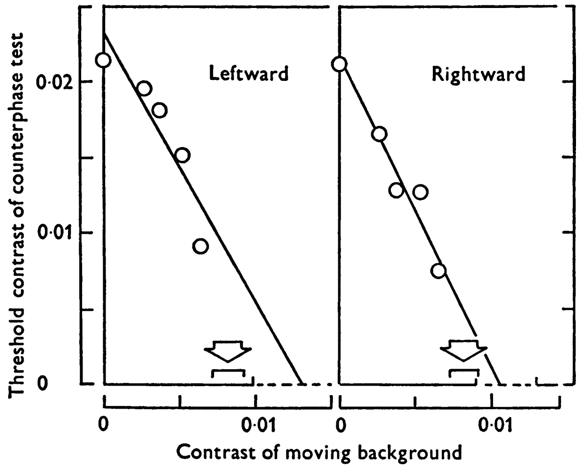

Fig. 6. Same as Fig. 5, except the observer was R.S., the spatial frequency 2·81 c/deg, the temporal frequency 7·9 Hz.

Summation following direction-specific adaptation

The independent-channels hypothesis asserts that prior to adaptation a counterphase grating is detected by one or the other directionally selective channel, whichever is temporarily most sensitive. A background grating moving in one direction contributes to the response of the mechanism selective for that direction, increasing the likelihood of that particular channel detecting the counterphase grating. As a final test of the independent-channels hypothesis, we would like to show that a *change* in the sensitivity of one direction-specific mechanism relative to the other can influence the detectability of a counterphase grating. Such a sensitivity difference can be produced by means of direction-specific adaptation. When an observer views for several minutes a high-contrast grating which drifts to the right, subsequent detection thresholds are elevated more for rightward- than for leftward-drifting gratings (Sekuler & Ganz, 1963; Pantle & Sekuler, 1969). Following rightward adaptation, then, the counterphase stimulus will be detected by the *leftward*-specific channel, since that channel will now be more sensitive than the rightward mechanism.

How will the response of the leftward-specific channel, as it detects a counterphase test grating, vary with changes in the contrast of a sub-threshold moving background? If the background drifts to the left (and is exactly in phase with the corresponding component of the counterphase test grating), it will be identical (except for contrast) to the leftward-moving part of the test grating. Since the leftward channel responds only to this leftward component, complete summation should result (in a manner analogous to that described in eqns. (16), (17) and (18)). The intersection of the summation line and the abscissa should estimate the threshold for the leftward-moving background itself.

This is exactly what does happen. The filled circles in Fig. 8 give threshold contrast for a counterphase grating as a function of contrast of a leftward-moving background grating. The data were obtained following adaptation to a rightward-moving grating of contrast 0·23 (same spatial and temporal frequencies). The intercept of the regression line on the background contrast axis agrees well with an independent estimate of threshold for the leftward background alone.

What might happen when the background moves rightward, in the same direction as the adaptation? Consider the response of just the leftward-specific channel. Under the independent-channels hypothesis this mechanism has no sensitivity for rightward motion ($S_{\text{right}} = 0$). Therefore the threshold *of the leftward mechanism* for the counterphase test grating should be constant and independent of background contrast. We should expect a horizontal summation line, similar to that in Fig. 1; one solid line in Fig. 7 represents such a hypothetical result.

The rightward-specific mechanism, although relatively less sensitive than the leftward because of adaptation, should still retain considerable sensitivity for the rightward background. We should thus find substantial additivity *for the rightward channel*; the steep continuous line in Fig. 7 indicates how counterphase threshold should decrease linearly with increasing background contrast (as in Figs. 5 and 6). The two hypothetical summation lines in Fig. 7 (one for each direction-specific mechanism) intersect when contrast of the rightward-drifting background is great enough to compensate for the differential effect of adaptation. For lower background contrasts the rightward channel will repond at a subthreshold level while the leftward mechanism is *at* threshold; for background contrasts greater than at the intersection point, the rightward channel is *at* threshold when the leftward is *below* threshold. Hence the actual measured thresholds for counterphase gratings might be expected to follow the 'lowest threshold' envelope of these two lines (dashed lines in Fig. 7); the horizontal branch would show detection by the leftward-specific channel, the steeper branch detection by the rightward-selective mechanism.

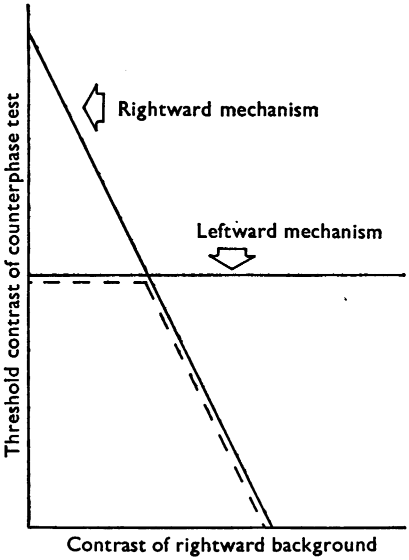

Fig. 7. Hypothetical summation lines for leftward- and rightward-specific channels following adaptation to a grating drifting rightward. The test grating is counterphase, the background moves rightward. The dashed line marks the 'lowest threshold' envelope for these mechanisms.

Data (Fig. 8, open circles) confirm this expectation. At low contrasts of rightward-moving background, no additivity can be measured; apparently the leftward-specific channel, with no sensitivity for rightward motion, detects the counterphase grating. For high background contrasts, the rightward-selective mechanism is presumably the detector, and substantial summation results. The continuous lines were separately fitted (by least-squares) to the two groups of data points; the intersection point was arbitrarily determined. The steep branch of the function does not agree very well with an independent measurement of threshold for the rightward background alone. We shall consider possible reasons for this discrepancy in the next section. The data do show, however, that a directionally selective channel may be 'forced' (via direction-specific adaptation) to continue detecting a counterphase grating even when a background drifts in the channel's *non-preferred* direction. The two-branched function of Fig. 8, then, demonstrates the existence of two independent direction-specific detectors.

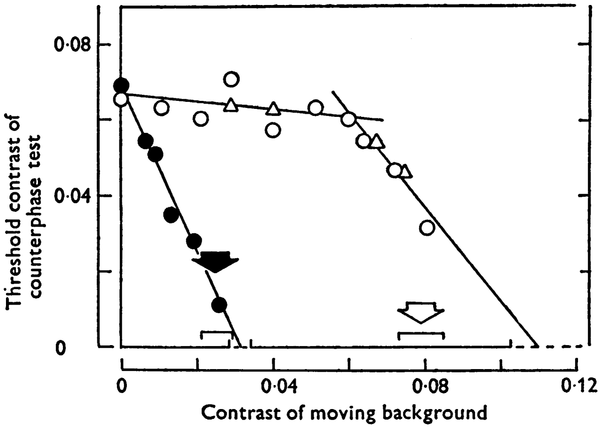

Fig. 8. Thresholds for counterphase test grating added to subthreshold moving background gratings, following adaptation to a rightward grating of contrast 0·23. Filled circles and arrow are for backgrounds moving to the left, open circles and arrow for rightward backgrounds. Triangles are points not included in the regression analysis. The observer was E.L. Other details are similar to those in Fig. 5.

DISCUSSION

The role of the counterphase grating. The present experiments show that direction-specific mechanisms in human vision operate as independent contrast detectors. In making these measurements we have emphasized the importance of the counterphase flickering grating; we have done this because a counterphase grating does not itself drift in either direction, although it is the sum of two gratings moving in opposite directions. A number of previous investigators (for example, Kelly, 1971, 1972) have implicitly assumed that detection of a counterphase grating does not depend upon its moving components. Our results indicate that a counterphase grating *is* analysed into moving parts, that a counterphase grating is detected by whichever direction-specific channel is momentarily the more sensitive. Other possible mathematical decompositions of the stimulus are inconsistent with at least some portion of the data, as are other assumptions regarding the appropriate measure of stimulus strength (e.g. average power rather than contrast).

It is instructive to consider our observers' descriptions of the appearance of a slightly suprathreshold counterphase grating before and after adaptation to a grating drifting rightward. Before adaptation the counterphase stimulus usually seems to oscillate, but not to move. Occasionally the grating appears to drift for a short while, its direction reversing at a slow, rather steady rate. Such 'monocular alternation' suggests that multiple mechanisms may be involved in the perception of the stimulus (Campbell & Howell, 1972). The presence of a *subthreshold* moving background may bias the percept in favour of the background direction; when such a background is very close to its own threshold, the counterphase grating seems consistently to move in the background direction.

Following rightward adaptation, the counterphase grating cannot be distinguished from a grating moving *leftward*; it continues to look like a leftward-drifting grating as long as the sensitivity of the rightward-specific channel is held far below that of the leftward mechanism. If a subthreshold rightward-drifting background is added (see Fig. 8), the counterphase grating still seems to drift leftward as long as the background contrast is *lower* than that at the inflexion point of the curve (i.e. for contrasts giving a horizontal summation line). At higher background contrasts (the steep regression line), the test grating seems once again to flicker or to move to the right. We emphasize that the movement seen in a counterphase grating appears to be *real* motion, not at all resembling the illusory sort of motion commonly called 'motion after-effect' or 'the waterfall illusion' (Wohlgemuth, 1911). The phenomenal qualities of the counterphase grating, then, are congruent with the measured independence of directionally selective mechanisms.

A minor discrepancy between the data and the prediction of the independent-channels model appears in Fig. 8, where the abscissa intercept of the steep regression line agrees poorly with the independent estimate of background threshold. A similar discrepancy was found on a second observer. This difference may result from the considerable uncertainty surrounding the proper choice of an inflexion point for the two-branched function. Up to now we have implicitly assumed that any noise affecting the two direction-specific channels is correlated. If, however,the noise in the channels were uncorrelated, a slight increase in detectability might be expected when each channel's response is very close to threshold, because of probability summation. Before adaptation, a counterphase grating provides these circumstances; following adaptation to a rightward grating, the intersection of the two branches in Fig. 8 is the point where each channel is driven near threshold. A very small amount of error near this point can produce rather large changes at the abscissa intercept.

We would expect to find some evidence for probability summation affecting counterphase grating thresholds in the psychometric functions of Fig. 4. Unfortunately, too few measurements were made to provide the precision necessary to measure such a small effect (somewhat less than 0·1 log unit). The situation is also complicated by the possibility that the direction-selective channels may display mutual inhibition (Levinson & Sekuler, 1974*b*, 1975), perhaps to some extent even near threshold.

Inhibition would work against probability summation in Fig. 4, but might contribute to the line-fitting error in Fig. 8. We shall return shortly to the question of direction-specific inhibition.

Sustained and transient mechanisms. The thresholds measured in this study are *absolute* detection thresholds: the observer is required to discriminate the test grating from a uniform field of the same average luminance. Recent experiments, however, have revealed two distinct thresholds for a moving or flickering grating, a threshold for detecting flicker and a threshold for recognizing pattern (Keesey, 1972; Tolhurst, 1973). These dual thresholds presumably represent responses from two separate groups of mechanisms, a 'sustained' (pattern) system and a 'transient' (movement) system. For intermediate drift or flicker rates, the absolute detection threshold for a low spatial frequency grating is the flicker threshold, a higher contrast being necessary for discernment of individual grating bars. At higher spatial frequencies, the pattern threshold is lower than the flicker threshold (Kulikowski & Tolhurst, 1973). Our observers report that motion or flicker is generally visible at the detection threshold for our moving or counterphase test targets. It would thus appear that the independent directionally selective channels which we have isolated are components of the 'transient' system. It is worth noting that adaptation to a moving grating is *not* direction-specific when *pattern* rather than flicker thresholds are measured (Levinson & Sekuler, 1974*a*; D. J. Tolhurst, personal communication). We might therefore expect the 'sustained' system to behave as a single channel, pooling all available contrast of a given spatial frequency, regardless of direction of movement. The recent experiments of Kulikowski & Tolhurst (1973) are consistent with this expectation, although they used flickering stimuli only, not moving gratings. An investigation of the directional selectivity of the 'sustained' system, using the techniques of the present study, is currently under way in our laboratory.

Relevance for measurements of direction-specific adaptation. Pantle & Sekuler (1969) found that adaptation to a grating moving in one direction *did* elevate threshold for a grating moving in the *opposite* direction (although somewhat less than for a same-directional test stimulus). The usual assumption in such a selective adaptation study is that adaptation is due to 'neural fatigue', and that the amount of threshold elevation obtained is proportional to the sensitivity of the detecting mechanism for the adaptation stimulus. Pantle & Sekuler's experiment thus implies that a direction-specific mechanism has some sensitivity for its non-preferred direction of motion. The present experiments show this to be incorrect, and force us to consider alternative explanations for opposite-directional threshold elevation. Pantle & Sekuler (1969) suggest that a moving grating may be processed by an initial non-direction-specific stage which provides input for a subsequent directionally selective mechanism. Some adaptation might occur in the initial stage as well as in the direction-specific channel; elevation of threshold for a test stimulus drifting in a direction opposite that of an adapting stimulus would correspond to this adaptation in the initial stage. Thus a direction-specific mechanism could be 'adapted' by a stimulus which does not directly excite it. This model is therefore consistent with Pantle & Sekuler's data and with the results of our study.

Recently the assumption that adaptation is a result of 'neural fatigue' has been challenged. Dealy & Tolhurst (1974) have made measurements which suggest that prolonged inhibition may be responsible for spatial frequency-specific threshold elevation. Such a process too would allow for threshold elevation induced by exposure to a stimulus which does not excite the detector in question. There is already evidence for inhibition between channels selective for opposite directions of movement. Levinson & Sekuler (1974*b*, 1975) have reported that threshold for detecting a moving grating is elevated more when an adaptation grating (moving in the same direction) is presented alone than when the same adaptation grating is viewed in combination with a grating moving in the *opposite* direction. Measurements for direction-specific adaptation comparable to those of Dealy & Tolhurst (1974) in the spatial domain might resolve this question.

Physiological analogues. The independent direction-specific channels uncovered in the present experiments may be similar in many of their properties to the directionally selective neurones observed frequently in the visual cortex of cat or monkey. Movement across a cell's receptive field in the non-preferred direction sometimes drops the neurone's discharge frequency below its maintained, unstimulated level, occasionally even eliminating spike activity entirely (Henry & Bishop, 1971). There is now evidence suggesting that this response inhibition may originate intracortically (Benevento, Creutzfeldt & Kuhnt, 1972; Pettigrew & Daniels, 1973), perhaps from cells selective for other directions of motion (Blakemore & Tobin, 1972). Our results are compatible with the speculation that similar direction-specific neurones in the human visual cortex mediate detection of moving gratings. The independence between channels which we have measured may in reality reflect subtle inhibitory interactions, possibly the same interactions responsible for the suprathreshold inhibitory effects reported by Levinson & Sekuler (1974*b*, 1975).

As for the responses to counterphase gratings, which we have so heavily stressed, Cooper & Robson (1968)provide some interesting data on single units in cat visual cortex. A non-direction-specific cell responds as well to a counterphase grating flickered in its receptive field as to a moving grating (either direction) of the same contrast. A directionally selective cell, on the other hand, responds about *half* as well to a counterphase grating as to an equal-contrast moving grating. The direction-specific cell, then, seems to respond only to the half-contrast component of the counterphase grating which drifts in its preferred direction, a result strikingly similar to our psychophysical observations.

If such direction-selective neurones really are analogous to the independent direction-specific mechanisms of human vision, then we should be able to manipulate the responses of these cells via adaptation much as we can manipulate threshold of the human mechanisms. In particular, it should be possible to adapt such cells by exposing them to their *non-preferred* directions of movement, even though they do not respond to the adapting stimuli. That this is plausible has been indicated by Maffei, Fiorentini & Bisti (1973), who were able to adapt a cat cortical neurone using a grating which did not cover the central excitatory area of the cell's receptive field. The demonstration that cat cortical neurones display properties so similar to those of human direction-specific mechanisms would provide strong evidence that similar neurones in the human cortex form the independent directionally selective channels of human vision.

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REFERENCES

BENEVENTO, L. A., CREUTZFELDT, O. D. & KUHNT, U. (1972). Significance of intracortical inhibition in the visual cortex. *Nature, New Biol.* **238**, 124–126.

BLAKEMORE, C. & TOBIN, E. A. (1972). Lateral inhibition between orientation detectors in the cat's visual cortex. *Expl Brain Res.* **15**, 439–440.

CAMPBELL, F. W. & GREEN, D. G. (1965). Optical and retinal factors affecting visual resolution. *J. Physiol.* **181**, 576–593.

CAMPBELL, F. W. & HOWELL, E. R. (1972). Monocular alternation: a method for the investigation of pattern vision. *J. Physiol.* **225**, 19–21 *P*.

COOPER, G. F. & ROBSON, J. G. (1968). Successive transformations of spatial information in the visual system. *IEE/NPL Conference on Pattern Recognition, IEE Conference Publication* **42**, 134–143.

DEALY, R. S. & TOLHURST, D. J. (1974). Is spatial adaptation an after-effect of prolonged inhibition? *J. Physiol.* **241**, 261–270.

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

GRAHAM, N. & NACHMIAS, J. (1971). Detection of grating patterns containing two spatial frequencies: A comparison of single-channel and multiple-channel models *Vision Res.* **11**, 251–259.

HENRY, G. H. & BISHOP, P. O. (1971). Simple cells of the striate cortex. In *Contributions to Sensory Physiology*, vol. 5, ed. NEFF, W. D. New York: Academic Press.

HENRY, G. H., BISHOP, P. O. & DREHER, B. (1974). Orientation, axis and direction as stimulus parameters for striate cells. *Vision Res.* **14**, 767–777.

HUBEL, D. H. & WIESEL, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *J. Physiol.* **195**, 215–243.

Keesey, U. T. (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.

Kelly, D. H. (1972). Adaptation effects on spatio-temporal sine-wave thresholds. *Vision Res.* **12**, 89–101.

Kulikowski, J. J. & King-Smith, P. E. (1973). Spatial arrangement of line, edge and grating detectors revealed by subthreshold summation. *Vision Res.* **13**, 1455–1478.

Kulikowski, J. J. & Tolhurst, D. J. (1973). Psychophysical evidence for sustained and transient detectors in human vision. *J. Physiol.* **232**, 149–162.

Levinson, E. & Sekuler, R. (1974*a*). Direction-specific adaptation in human vision: measurements using isotropic random dot patterns. Presented at the meetings of the Psychonomic Society, Boston, Massachusetts.

Levinson, E. & Sekuler, R. (1974*b*). Inhibition between direction-specific mechanisms. Presented at the meetings of the Association for Research in Vision and Ophthalmology, Sarasota, Florida.

Levinson, E. & Sekuler, R. (1975). Inhibition and disinhibition of direction-specific mechanisms in human vision. *Nature, Lond.* **254**, 692–694.

Maffei, L., Fiorentini, A. & Bisti, S. (1973). Neural correlate of perceptual-adaptation to gratings. *Science, N.Y.* **182**, 1036–1038.

Pantle, A. & Sekuler, R. (1969). Contrast response of human visual mechanisms sensitive to orientation and direction of motion. *Vision Res.* **9**, 397–406.

Pettigrew, J. D. & Daniels, J. D. (1973). Gamma-aminobutyric acid antagonism in visual cortex: different effects on simple, complex and hypercomplex neurons. *Science, N.Y.* **182**, 81–83.

Pettigrew, J. D., Nikara, T. & Bishop, P. O. (1968). Responses to moving slits by single units in cat striate cortex. *Expl Brain Res.* **6**, 373–390.

Poggio, G. F. (1972). Spatial properties of neurons in striate cortex of unanesthetized macaque monkey. *Investve Ophth.* **11**, 368–376.

Robson, J. G. (1966). Spatial and temporal contrast-sensitivity functions of the visual system. *J. opt. Soc. Am.* **56**, 1141–1142.

Sachs, M. B., Nachmias, J. & Robson, J. G. (1971). Spatial-frequency channels in human vision. *J. opt. Soc. Am.* **61**, 1176–1186.

Sekuler, R. (1974). Spatial vision. *A. Rev. Psychol.* **25**, 195–232.

Sekuler, R. & Ganz, L. (1963). Aftereffect of seen motion with a stabilized retinal image. *Science, N.Y.* **139**, 419–420.

Shapley, R. M. & Tolhurst, D. J. (1973). Edge detectors in human vision. *J. Physiol.* **229**, 165–183.

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.

Wohlgemuth, A. (1911). On the after-effect of seen movement. *Br. J. Psychol. Monogr.* Suppl. 1.

Wurtz, R. H. (1969). Visual receptive fields of striate cortex neurons in awake monkeys. *J. Neurophysiol.* **32**, 727–742.