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SUMMATION AND DISCRIMINATION OF GRATINGS MOVING IN OPPOSITE DIRECTIONS*

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Abstract—We have measured the amount of summation occurring at threshold between gratings which move in opposite directions. The small amount of summation observed at low spatial and high temporal frequencies is approximately consistent with the action of direction-selective mechanisms, as proposed by Levinson and Sekuler (1975), provided that probability summation between such mechanisms is taken into account. However, at high spatial and low temporal frequencies much more summation is found, an amount approximately consistent with detection by directionally non-selective mechanisms.

We have also measured thresholds for identifying the direction of a moving grating. For those gratings which show little summation, direction of motion is judged correctly at the detection threshold, while for those gratings which show the most summation, the identification threshold is considerably above the detection threshold.

INTRODUCTION

Levinson and Sekuler (1975) have reported that the sum of two gratings of equal contrast and spatial frequency which move with equal velocity in opposite directions is little or no more visible than either grating alone. They have taken this lack of summation to indicate that mechanisms exist in the human visual system which respond to motion in one direction, but are insensitive to motion in the opposite direction. This same conclusion has also been drawn from many experiments on direction-specific adaptation and movement aftereffects. These studies have been reviewed by Sekuler (1975) and Thompson (1976).

The sum of two oppositely moving gratings (a counterphase grating) does not itself move, but varies in contrast sinusoidally in time. Since the time course of a grating stimulus may always be resolved into a collection of temporal sinusoids, it may also be resolved into a collection of moving gratings. If Levinson and Sekuler's result were obtained at all spatial and temporal frequencies, then all grating stimuli, whatever their time course and whether or not they moved, might be detected by direction-selective mechanisms. Furthermore, it has been shown that many spatially aperiodic stimuli are detected at contrasts at which one or another of their periodic constituents is at threshold (Graham, 1977), so it is possible that *all* visual stimuli are detected by mechanisms which are selective for direction of motion. This outcome would have important consequences for models of the spatial and temporal sensitivity of the eye, and we have therefore attempted to assess its validity. To do this we examined sensitivity to drifting and counterphase gratings with spatial frequencies of 2, 4 and 8 c/deg and temporal frequencies of 1.5, 3.1, 6.2 and 12.4 Hz.

The procedures used in these experiments differed in several ways from those of Levinson and Sekuler. First, we collected frequency-of-seeing data for discrete presentations rather than using the method of adjustment with continuous exposure of the stimulus. This technique allows precise control of the stimulus time-course, reduces the probability and magnitude of eye movements occurring during the stimulus, and allows for more rigorous tests of direction selective and non-selective models.

We have also examined the *informational* properties of the detecting mechanism. If the mechanism responds only or primarily to one direction of motion, and if the mechanism always indicates to the observer motion in that preferred direction, then the direction of a moving grating should be reported as accurately as its presence or absence. This test has been applied to a subset of the stimuli noted above.

THEORY

The stimuli used in both the Levinson and Sekuler study and in these experiments were vertical sinusoidal gratings. The luminance, L, at a point x in space and t in time of a stimulus consisting of some modulation, $M(x, t)$ about a mean level, L_0, is given by

$$L(x, t) = L_0[1 + M(x, t)], \quad -1 < M < 1 \qquad (1)$$

A vertical grating which moves with a constant leftward velocity is described by

$$M_L(x, t) = m\,g(t)\cos[2\pi(f_S x + f_T t)] \qquad (2)$$

* Some of these results were reported in May, 1978 at the meetings of the Association for Research in Vision and Ophthalmology (Nachmias *et al.*, 1978).

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where

m = contrast

f_S = spatial frequency in c/deg

f_T = temporal frequency in Hz

and where $g(t)$ is a *gating function*, normalized so that its maximum is unity, which governs the overall time course of the stimulus. The *velocity* of the stimulus in deg/sec is given by f_T/f_S. The sum of a grating of contrast m which moves to the left and one of equal contrast which moves right is then

$$M_L + M_R = mg(t)[\cos 2\pi(f_S x + f_T t) + \cos 2\pi(f_S x - f_T t)] \quad (3)$$

which reduces to

$$M_L + M_R = 2mg(t)[\cos(2\pi f_S x)\cos(2\pi f_T t)] \quad (4)$$

The expression on the right describes a counterphase grating, which does not move but whose contrast varies as a cosine function of time. If we denote a counterphase grating of contrast m by $M_C(x, t)$, then we have

$$M_L + M_R = 2\,M_C \quad (5)$$

In words, the sum of two gratings of contrast m which move in opposite directions is equal to a counterphase grating of contrast $2\,m$.

In the remainder of this paper, the "threshold contrast" for a counterphase grating will indicate *the contrast of either of its moving components*, rather than the overall contrast of their sum. For example, if the stimulus described by equation (5) was just visible, it would have a threshold contrast of m.

Levinson and Sekuler argued that if a counterphase grating were detected by mechanisms each of which responds only to one or the other of its moving components, then the sum of M_L and M_R would be no more visible than M_L or M_R alone. In other words, the threshold contrasts for moving and counterphase gratings would be equal. On the other hand, they reasoned, detectors which respond to both directions of motion would sum the contrasts of the oppositely moving components, so that the threshold contrast for a counterphase grating would be half that of a moving grating. This ratio of threshold contrasts, or equivalently, the decibel difference in sensitivity to counterphase and moving gratings thus provided a test of the two models: the direction-selective model predicts a difference of 0 dB, the non-selective model predicts a difference of 6 dB*. The results they reported were for the most part consistent with a difference of approximately 0 dB, and they therefore concluded in favor of the direction selective model.

Several features of these models are improbable, however. If, in the selective model, the two mechanisms sensitive to opposite directions of motion are independently perturbed by noise, then we might expect to observe the effects of probability summation between them. Effects of this sort have been observed by Sachs *et al.* (1971) and Graham *et al.* (1978), among others. Probability summation between direction-selective mechanisms would improve the visibility of a counterphase grating, which stimulates both mechanisms, relative to a moving grating, which stimulates only one.

Similarly, the non-selective model neglects the effects of probability summation over space (Robson and Graham, 1979) and time (Watson, 1979). Consider a collection of mechanisms, each having the same temporal impulse response, and each having a spatial weighting function of identical shape, whose centers are distributed densely and uniformly across the retina. Suppose that each mechanism is noisy, and that a stimulus is detected if and only if the response in at least one mechanism exceeds some magnitude. Threshold contrast for a stimulus will then reflect probability summation over space, that is, over the collection of spatially distributed mechanisms, and over time, that is, over the temporal response within each mechanism. Here, probability summation reduces the advantage of a counterphase grating over a drifting grating, since the drifting grating has contrast peaks at many points in space and time.

The differences in sensitivity to moving and counterphase gratings predicted by these noisy direction-selective and non-selective mechanisms are shown respectively as open and filled circles in Fig. 1. Both predictions depend upon a parameter β, which reflects the slope of the psychometric function, as described in Appendices A and B. Typically, estimates of β lie between 3 and 6, so that the remaining difference in the predictions of the two models is between 1.5 to 3.5 dB. The original predictions of Levinson and Sekuler, which neglect probability summation, are shown as filled and open arrows on the right margin.

METHODS

Two experiments were performed. In both, moving sinusoidal gratings were generated by a PDP 11/10 computer on the face of a Tektronix 604 oscilloscope at a frame rate of 200 Hz. Additional details of our method of stimulus generation are available elsewhere (Watson, 1979). The face of the oscilloscope was seen through a rectangular hole (2.5 by 1.9°) in an 8° dia circular screen whose color and brightness closely matched that of the oscilloscope (green P-31, 15 cd/m^2). A small central fixation spot was used. The display was viewed binocularly from a distance of 228 cm.

For all stimuli, the gating function, $g(t)$ in equation (2), was a raised cosine, that is,

$$g(t) = 0.5 - 0.5\cos(2\pi t/0.82) \quad 0 < t < 0.82$$
$$= 0 \quad \text{elsewhere.} \quad (6)$$

* By convention, decibels of contrast or of ratios of contrasts are given by $dB(x) = 20\log_{10}(x)$.

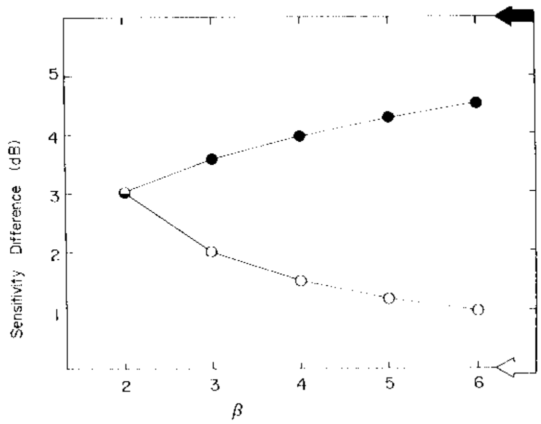

Fig. 1. Values of the decibel difference in sensitivity to moving and counterphase gratings predicted by noisy direction selective mechanisms ○ and noisy non-selective mechanisms ●, as a function of the psychometric function slope parameter β. Also shown as open and filled arrows are the simple predictions of Levinson and Sekuler.

Experiment 1

Yes no frequency of seeing data were collected for left-moving, right-moving, and counterphase gratings. For each of the three stimulus types, four contrasts, spanning 6 dB in 2 dB steps, were selected so as to bracket a previously estimated threshold. Within a session of 1300 trials, the spatial and temporal frequencies were fixed, and the three types of grating as well as 7.7% catch trials were randomly intermixed. Two observers participated in Experiment 1.

Experiment 2

In the second experiment each trial consisted of two observation intervals marked by tones. In a randomly selected one of the two intervals a left or a right-moving grating was presented. On each trial, the observer attempted to identify the interval containing the grating, *and* the direction in which it moved. Following each response, feedback tones indicated the interval in which the grating was presented and the direction in which it moved. As in Experiment 1, four contrast levels were used for each stimulus type, and all stimuli appeared with equal frequency in each session of about 480 trials. Again, the spatial and temporal frequencies were fixed within a session. Three observers took part in Experiment 2.

RESULTS

Experiment 1

Figure 2 shows sensitivity (defined as the reciprocal of the threshold contrast) of one observer to leftward moving (open circles), rightward-moving (solid circles) and counterphase gratings (squares) at spatial frequencies of 2 and 8 c/deg. Results for a second observer were very similar in all relevant respects. According to Levinson and Sekuler, at each temporal frequency the sensitivity to a counterphase grating should be equal to the sensitivity to a moving grating. It is clear that the actual sensitivities to counterphase gratings depart consistently from those to moving gratings: both observers are *more* sensitive to the counterphase grating than predicted by the simple direction-selective model which neglects probability summation.

The departures are most pronounced at 8 c/deg at the lower temporal frequencies. At 1.5 Hz, sensitivity to the counterphase grating is about 4 dB higher than to a moving grating.

Figure 3 provides a comparison of the sensitivity differences actually obtained (circles) with those predicted by noisy direction-selective (triangles) and non-selective mechanisms (squares). Each point is the mean of several sessions. Appendix C describes the derivation of these quantities. The right panel of Fig. 3 shows results for 2 c/deg. The obtained values are certainly better approximated by the predictions of the direction-selective mechanisms, though a discrepancy of 0.5 to 1 dB is present at all temporal frequencies. The data depart by about 2 dB from the simple prediction (0 dB) given by Levinson and Sekuler.

Results for gratings of 4 and 8 c/deg are shown in the center and left panels of Fig. 3. At 4 c/deg, the obtained sensitivity differences show a systematic trend away from the direction-selective predictions at the lower temporal frequencies, though they still remain below the non-selective predictions. At 8 c/deg the trend persists, so that at 1.5 Hz (a velocity of about 0.2 deg/sec) the obtained values are about 2 dB

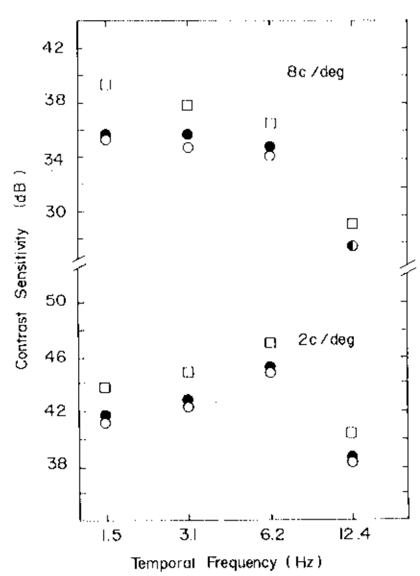

Fig. 2. Contrast sensitivity, defined as the inverse of threshold contrast, for leftward moving ○, rightward moving ● and counterphase gratings □, as a function of temporal frequency. For counterphase gratings, threshold is expressed in terms of the contrast of either of its moving components. The results of one observer (Peter) at two spatial frequencies are shown.

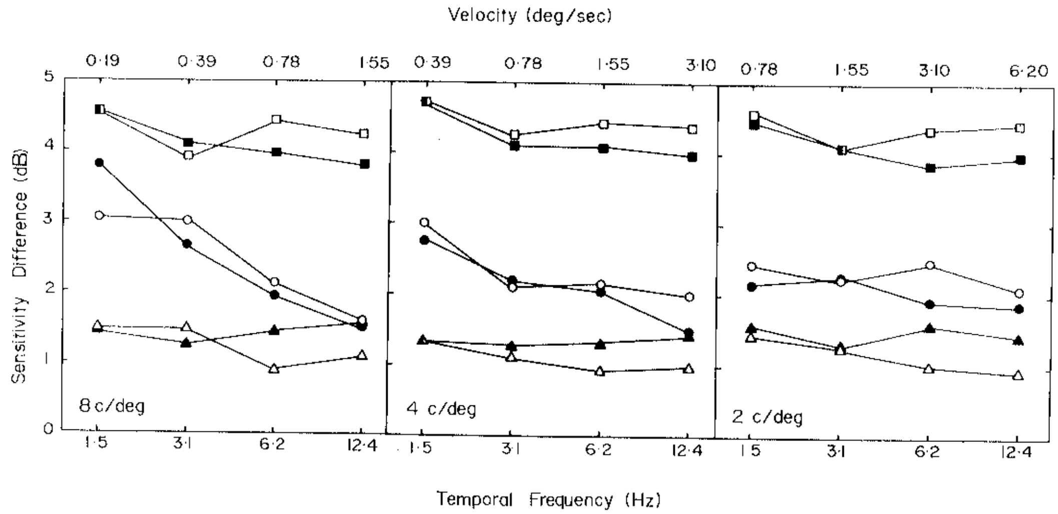

Fig. 3. Decibel difference in sensitivity to counterphase and moving gratings as a function of temporal frequency for gratings of 8 c/deg (left panel), 4 c/deg (center panel), and 2 c/deg (right panel). Circles represent experimentally obtained values, while triangles and squares represent the predictions of noisy direction-selective and non-selective mechanisms, respectively. See appendices for a fuller description of these quantities. Solid symbols are for Peter, open symbols for Sandy.

above the direction-selective prediction, but are reasonably approximated by the non-selective predictions.

Levinson and Sekuler reported that sensitivity to moving gratings was about equal (in our terms) to that for counterphase gratings. We find differences in sensitivity of between 1.5 and 4 dB. The discrepancies between these results may in part be explained by a difference in procedure. Our results were obtained by the method of constant stimuli, with a random ordering of presentations of counterphase, left-moving, and right-moving gratings, so that the observer was not able to predict the type of stimulus to be presented next. Levinson and Sekuler, on the other hand, used the method of adjustment with continuous exposure of each stimulus, so that the observer presumably was aware of the type of stimulus being presented. Suppose direction-selective mechanisms exist. In our procedure, the observer's attention to left- and right-selective mechanisms must be independent of which stimulus is presented. In the method of adjustment, the observer can ignore the right-selective mechanism when a leftward moving grating is presented, and vice versa. If there is a "direction uncertainty effect" as reported by Sekuler and Ball (1977), this strategy should improve performance with moving, but not with counterphase gratings, thereby inflating the measured sensitivity difference (See Graham *et al.* (1978) for a similar discussion of uncertainty effects.)

Stromeyer *et al.* (1978) have also compared thresholds for moving and counterphase gratings, using partly method of adjustment and partly a signal detection method with discrete stimulus presentations and intermixed stimuli. Their results are on the whole comparable to our own, though their adjustment thresholds at the higher temporal frequencies, like those of Levinson and Sekuler, show less summation than we have obtained.

In summary, the relative visibility of moving and counterphase gratings is never precisely consistent with the operation of channels sensitive to only one of two opposite directions of motion. This is so even when probability summation among these channels is taken into account. The inconsistency is modest for low spatial and high temporal frequencies (high velocities), but is severe at high spatial and low temporal frequencies (low velocities). At the lowest velocities, the results are in accord with the action of direction-

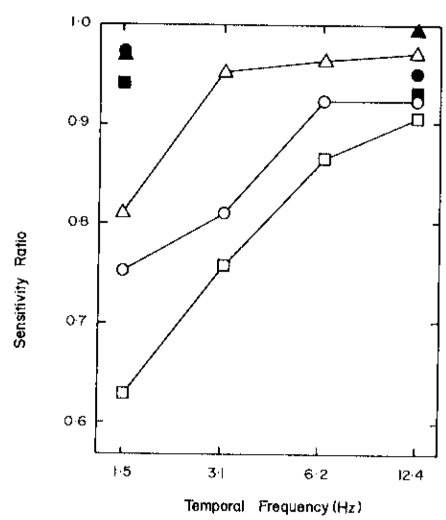

Fig. 4. Ratio of threshold for detection of a moving grating and for identifying its direction of motion, as a function of temporal frequency. Solid symbols are for a spatial frequency of 2 c/deg, open symbols, 8 c/deg. Triangles are for Peter; circles for Sandy; squares for Lucy.

ally non-selective mechanisms. This pattern of results agrees with the outcome of our second experiment.

Experiment 2

In this experiment the observer was required to identify which of two intervals contained a moving grating, *and* to identify the direction in which it moved. The data of each session have been converted to two thresholds, a *detection threshold*, an estimate of the contrast at which the correct interval is chosen on some fixed proportion of trials, and an *identification threshold*, a comparable measure for correct report of direction. (See Appendix C for the method of estimating these thresholds.)

The ratio of thresholds for detection and identification are shown for three observers in Fig. 4. The filled symbols are for gratings of 2 c/deg,, the open symbols for 8 c/deg. Each point is the mean of the ratios from several sessions. For the lower spatial frequency, the ratio is nearly unity at both high and low temporal frequencies. Apparently, whenever the stimulus is detected, its direction is known. This sort of performance would be expected of a mechanism which itself encodes direction.

The ratios for a spatial frequency of 8 c/deg are also near unity at a temporal frequency of 12.4 Hz, but decline systematically as the temporal frequency is reduced. At 1.5 Hz, between 2 and 4 dB more contrast is required before direction is reported as correctly as interval. Evidently the mechanisms which detect these low velocity stimuli do not themselves encode direction of stimulus motion.

DISCUSSION

At low spatial and high temporal frequencies (high velocities) gratings which move in opposite directions show very little summation, and are easily discriminated at threshold, consistent with detection and identification by direction-selective mechanisms. At high spatial and low temporal frequencies (low velocities), more summation is found, and discrimination of direction is poor. We shall consider several explanations of these results.

Direction tuning

It is possible that a left-selective mechanism might have some residual sensitivity to rightward motion; and this sensitivity, relative to that of the mechanism selective for rightward motion, might decline with velocity. Some summation would then occur at low velocities, but much less than at high, and only at low velocities would frequent confusions of direction at threshold occur. This means that a single mechanism might be selective or non-selective, depending upon the stimulus velocity.

Non-selective mechanisms

Alternatively, both selective and non-selective mechanisms might exist. Their sensitivities to velocity might be such as to favor the action of selective mechanisms at high velocities, and of non-selective mechanisms at low. Elsewhere, Watson (1977) has found failures of summation between high and low temporal frequencies, as would be expected of this model.

Note that there is a general correspondence between the presumed ranges of operation of direction-selective and non-selective mechanisms and the transient and sustained mechanisms proposed elsewhere (Kulikowski and Tolhurst, 1973).

Eye movements

Motions of the eye, even during 820 msec of fixation, may be sufficiently probable and large that their contribution to the results should be considered.

At low stimulus velocities, the retinal velocity may be dominated by motions of the eye. Hence gratings with opposite but low stimulus velocities may occasionally move in the same direction on the retina. Thus the lower the stimulus velocity, the more summation would be obtained, and the more frequent would be confusion of direction. The eye movements required to explain our results on this basis would seem more rapid or frequent than are ordinarily observed, but the most direct test of this idea is to conduct comparable experiments under stabilized image conditions. Efforts in this direction are now being made (Mansfield and Nachmias, 1979).

SUMMARY

Over a wide range of spatial and temporal frequencies, summation of gratings which move in opposite directions is consistent with detection by mechanisms which are strongly selective for direction of motion, as reported by Levinson and Sekuler (1975), provided that probability summation between such mechanisms is taken into account. Furthermore, for this range of stimulus parameters, the direction of a moving grating is correctly reported about as often as the stimulus is detected.

At low temporal and high spatial frequencies more summation is observed than expected from direction-selective mechanisms, and considerably less contrast is required to detect a stimulus than is required to correctly judge the direction in which it moves. For these stimuli, the amount of summation is consistent with detection by directionally non-selective mechanisms.

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APPENDIX A

In this appendix we derive the difference in sensitivity to moving and counterphase gratings predicted by noisy direction-selective mechanisms.

Suppose that the probability, P_L, that a leftward moving grating of contrast m_L is detected by the left-sensitive mechanism is given by

$$P_L = 1 - \exp[-(m_L/\alpha_L)^\beta] \qquad \text{(A1)}$$

where α_L is the "threshold contrast" of the mechanism (the contrast at which 63% of the stimuli are detected), and β is a parameter which governs the slope of the function. A psychometric function of this form was suggested in another context by Brindley (1960).

If left and right-sensitive mechanisms are independent, then the probability P, of a "yes" response to any combination of left and right moving gratings will be

$$P = 1 - (1 - \gamma)(1 - P_L)(1 - P_R) \qquad \text{(A2)}$$

where γ is the probability of a "yes" when both m_L and m_R are zero. Combining equations (A1) and (A2), we obtain the psychometric function

$$P = 1 - (1 - \gamma)\exp[-R^\beta] \qquad \text{(A3)}$$

where

$$R = [(m_L/\alpha_L)^\beta + (m_R/\alpha_R)^\beta]^{1/\beta}. \qquad \text{(A4)}$$

Note that a stimulus is at threshold when $R = 1$.

A simple prediction is now possible if we suppose that sensitivity is equal to both directions of motion, that is, that $\alpha_L = \alpha_R$. (α_L and α_R were approximately equal in our own and Levinson and Sekuler's results.) If we write α_C for the threshold contrast of a counterphase grating, that is, for the contrast of either moving component when the sum is at threshold, then

$$1 = [(\alpha_C/\alpha_L)^\beta + (\alpha_C/\alpha_L)^\beta]^{1/\beta} \qquad \text{(A5)}$$

Simplifying and converting to dB, we have

$$\mathrm{dB}(\alpha_L) - \mathrm{dB}(\alpha_C) = 6/\beta. \qquad \text{(A6)}$$

In summary, the decibel difference between sensitivities for moving and counterphase gratings predicted by probability summation between direction-selective mechanisms is given by 6 divided by the psychometric function slope parameter, β. This quantity is plotted as open circles in Fig. 1.

APPENDIX B

In this appendix we describe a model for the detection of moving and counterphase gratings by directionally non-selective mechanisms.

Consider a collection of mechanisms, each with a "receptive field" of fixed size, shape, and position on the retina, whose sensitivities, or gains, vary according to the function $a(x)$ where x is the distance of the receptive field center from the fovea in degrees of visual angle. Each mechanism has the same temporal impulse response, which is independent of position in the receptive field.

The receptive field properties are defined by two *weighting functions*, $w_S(x' - x)$ and $w_T(t' - t)$ which describe the contribution of modulation at a horizontal location x' in space and t' in time to the response at time t of the mechanism centered at x. The response is given by

$$r(x, t) = \iint M(x', t')a(x)w_S(x' - x)w_T(t' - t)\,dx'dt' \qquad \text{(B1)}$$

This is a convolution integral, so we may write

$$r(x, t) = a(x)M(x, t) * [w_S(-w)w_T(-t)] \qquad \text{(B2)}$$

By the convolution theorem, we may convert to a frequency representation

$$r(x, t) = a(x)\mathscr{F}^{-1}[\mathscr{F}[M(x, t)]\,W_S(2\pi f_S)\,W_T(2\pi f_T)] \qquad \text{(B3)}$$

where W_S and W_T are the spatial and temporal transfer functions of the mechanisms. It is reasonable to suppose that these functions have constant gain, linear phase, over the spectrum of the signal. Then we may write

$$r(x, t) = a(x)\,k\,M(x - a, t - b) \qquad \text{(B4)}$$

where, k, a and b are constants which depend only on the frequencies f_S and f_T.

Assume that the response of each mechanism is independently perturbed by noise, that each mechanism has a threshold, and that the probability that threshold is exceeded is given by

$$p(x, t) = 1 - \exp(-|r(x, t)|^\beta) \qquad \text{(B5)}$$

If the stimulus is detected whenever the response in at least one mechanism exceeds threshold, then for all stimuli at threshold,

$$1 = \left[\sum_{j=-n}^{n}\sum_{i=-m}^{m}|r(j\Delta x, i\,\Delta t)|^\beta\right]^{1/\beta} \qquad \text{(B6)}$$

Thus the ratio of thresholds for counterphase and moving gratings will be given by

$$\alpha_C/\alpha_L = \frac{1}{2}\left[\frac{\Sigma\Sigma\,|a(j\Delta x)g(i\Delta t)\cos 2\pi(f_S j\Delta x - f_T i\Delta t)|^\beta}{\Sigma\Sigma\,|a(j\Delta x)g(i\Delta t)\cos(2\pi f_S j\Delta x)\cos(2\pi f_T i\Delta t)|^\beta}\right]^{1/\beta}. \qquad \text{(B9)}$$

In the calculations whose results are shown in Fig. 1 the parameters used were: $n = 40$, $\Delta x = 0.025°$, $m = 40$,

$\Delta t = 0.01$ sec, $f_S = 8$ c/deg, $f_T = 12.4$ Hz. The actual values of spatial and temporal frequency and the duration of the gating function have very little effect upon the predictions, except that, if fewer than two periods of the temporal modulation are enclosed by the gating function, more summation will result. Thus the predictions for 1.5 Hz lie about 0.5 dB above those shown.

The function $a(x)$ was taken to be

$$a(x) = 10^{-|x| f_S 3/160} \qquad \text{(B10)}$$

This function was adopted from the data of Robson and Graham (1979) and describes a decline in gain of about 0.375 dB per period of the spatial waveform distant from the fovea.

APPENDIX C

In this appendix we describe a method of estimating threshold contrasts and psychometric function slopes from frequency-of-seeing data. We also provide a rule for estimating a single measure of the observed sensitivity difference from the thresholds for left-moving, right-moving and counterphase gratings.

Equation A3 specifies a form for the psychometric function. This expression, with $R = m/C$, may be fitted to the frequency-of-seeing results for each separate type of stimulus to provide maximum likelihood estimates of the threshold, α, the slope, β, and the guessing probability, γ (Watson, 1979). The thresholds plotted in Fig. 2 were estimated by this method. The detection and identification thresholds of Experiment 2 were estimated by fitting separately the frequency-of-detection and frequency-of-identification results. To fit these forced-choice results, γ was set at 0.5.

In experiment 1 the frequency-of-seeing results for left, right, and counterphase gratings from each session were also fit by a model in which the psychometric function for each type of stimulus has the form of equation A3 but in which all three functions share a common slope. This estimate of the slope, β, was used in the predictions of the models described in Appendices A and B which are plotted as triangles and squares in Fig. 1. A χ^2 statistic rejects the fit in 10 cases out of 69 at the 0.05 level.

To convert the three thresholds estimated in this way to a single value of the obtained sensitivity difference, we have supposed that the effects of left and right-moving gratings are combined by the rule

$$R = [(m_L/\alpha_L)^\sigma + (m_R/\alpha_R)^\sigma]^{1/\sigma}. \qquad \text{(C1)}$$

where R serves as the argument in equation A3. Here σ is an arbitrary parameter which is inversely related to the degree of summation that the rule expresses. When $\sigma = 1$, linear summation results, when $\sigma > 1$, less than linear summation occurs, and when $\sigma < 1$, more than linear summation takes place. When $\sigma = \beta$, the amount of summation is consistent with probability summation, since equations A4 and C1 are then identical.

When a counterphase grating is at threshold,

$$\alpha_C^{-\sigma} = \alpha_L^{-\sigma} + \alpha_R^{-\sigma} \qquad \text{(C2)}$$

Provided that $\alpha_L \geq \alpha_C \leq \alpha_R$, these three thresholds determine the value of σ. When $\alpha_L = \alpha_R$,

$$\text{dB}(\alpha_L) - \text{dB}(\alpha_C) = 6/\sigma. \qquad \text{(C3)}$$

Values of the sensitivity difference estimated in this way are plotted as circles in Fig. 3.