Sensitivity loss in odd-symmetric mechanisms and phase anomalies in peripheral vision

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The ability to detect, discriminate and identify spatial stimuli is much poorer in the peripheral than in the central visual field. Some deficits are eliminated by scaling stimulus size. For example, grating detectibility is roughly constant across the visual field when spatial frequency and target extent are scaled appropriately[1,2]. Other deficits persist despite scaling. For instance, some readily detectable patterns are more difficult to identify peripherally than in the fovea[3,4]. This deficit is caused, at least partially, by a reduced ability to encode spatial phase (or relative position)[5–7]. To specify the properties of foveal and peripheral phase-encoding mechanisms, we measured discrimination thresholds for compound gratings at several eccentricities. Our observations are consistent with a two-channel model of phase encoding based on even- and odd-symmetric mechanisms[8] (see Fig. 1), but the sensitivity of the odd-symmetric mechanisms decreases dramatically with eccentricity. Thus, the loss of sensitivity in one type of mechanism may underlie the reduced ability to encode spatial phase peripherally.

We used a paradigm introduced by Field and Nachmias[8]. Observers were presented with two compound gratings composed of a fundamental (F) and second harmonic (2F) added in two phases differing by 180°. A 180° phase shift does not alter the peak-to-trough amplitude, or the contrast, of these waveforms (Fig. 1). Discrimination thresholds for several 180° phase shifts (for example, 0–180, 45–225) were measured by varying the contrast of 2F. These thresholds can be explained by the operation of two broad-band channels. One channel has positive and negative even-symmetric receptive fields, and the other has positive and negative odd-symmetric fields (Fig. 1). Only mechanisms located at particular points in the waveform contribute to phase discrimination: even-symmetric mechanisms centred on peaks and troughs of F and odd-symmetric mechanisms centred on zero-crossings of F. This assumption differs from the Field and Nachmias model[8]; they assumed that the computations were restricted to these points in the waveform when the contrast of 2F was low relative to the contrast of F. We assumed that the computations are spatially restricted in

this way for all 2F contrasts. As it turns out, this assumption is required to explain our results in the far periphery, a point we expand below.

Figure 1 illustrates how the model discriminates 180° phase shifts (for explanation see Fig. 1 legend). Two important features of the model need to be emphasized. First, a 0–180 (degree) phase shift does not change the responses of odd-symmetric mechanisms centred on zero-crossings in F. Second, a 90–270 phase shift does not change the responses of even-symmetric mechanisms centred on the peaks and troughs of F. Thus, discrimination thresholds for the 0–180 and 90–270 conditions reveal the sensitivities of the even and odd channels, respectively. From these thresholds, the two-channel model predicts thresholds for all other 180° phase shifts (Fig. 2). We hypothesized that the peripheral phase-encoding deficit is caused by the reduced sensitivity of one or both of these mechanisms.

The stimuli were generated on a Joyce Electronics display with P4 phosphor. The targets were presented in a 4.5 × 15 cm window surrounded by a dark field. Target size was held constant and viewing distance was varied to test different retinal eccentricities. This procedure allowed us to scale target size appropriately for each eccentricity. The gratings were vertically oriented and contrast was modulated by a gaussian envelope with a standard deviation of 1.5 cm. Space-average luminance was 95 cd m^{-2}. A light-emitting diode served as the fixation target when stimuli were presented peripherally. Observers fixated the centre of the window for foveal conditions.

Before the discrimination experiments, contrast sensitivity functions (CSFs) were measured at the fovea and at 5°, 10°, 20° and 40° in the temporal retina. In the discrimination experiments, the spatial frequency of F was set to the peak of the CSF, and its contrast was set about 1 log unit above detection threshold. Thus, F was equally visible at all eccentricities. In some experimental sessions the contrast of 2F was varied according to 2-down/1-up staircase rule. The method of constant stimuli was used in other sessions. Trials were started by the observer and consisted of two 250 ms intervals. Observers judged whether the patterns in each interval were the same or differed by a 180° phase shift of 2F relative to F. Auditory feedback indicated the accuracy of the response after each trial.

Two potential problems arise when using this procedure. First, a 180 deg phase shift changes the average luminance of a gaussian-damped grating. To ensure that the observers could not use average or local luminance cues to make discriminations, the waveform was displaced randomly within the gaussian envelope between intervals on each trial. Second, suprathreshold gratings are known to mask gratings of lower spatial frequency[9–11]. Thus, raising the contrast of 2F to obtain discrimination thresholds may reduce the visibility of F. In all sets of

Fig. 1 Receptive fields of the mechanisms and the luminance profiles of the stimuli. Inset, positive and negative even- and odd-symmetric mechanisms. Except for the requirement that each mechanism responds to F and 2F, the model's predictions are not dependent on the bandwidths of the mechanisms. The stimuli were pairs of compound gratings composed of a fundamental (F) and second harmonic (2F). The luminance profiles of the stimuli are shown with 2F added in 90° and 270° (*a*), 30° and 210° (*b*) and 0° and 180° (*c*) phase. The model uses changes in the response of mechanisms centred on the peaks, troughs and zero-crossings in F to discriminate phase shifts. To illustrate this process, we have represented the responses of even and odd mechanisms with light and dark arrows, respectively. Responses are computed by cross-correlating the stimulus with the receptive fields and half-wave rectifying; arrow length is proportional to response magnitude. Notice that a 0–180 (degree) shift (*c*) alters the responses of even-symmetric mechanisms, but not odd-symmetric mechanisms. This is illustrated by the lengths of the arrows in corresponding locations in the waveforms. The length of light arrows pointing upwards (positive even-symmetric response) decreases when 2F is shifted from 0° to 180° phase, whereas the length of light arrows pointing downwards (negative odd-symmetric response) increases when 2F is shifted from 0° to 180° phase. The lengths of all dark arrows (positive and negative odd-symmetric response) are the same in both waveforms. A 0–180 shift is discriminated, therefore, when the change in responses of even-symmetric mechanisms exceeds some threshold. In a 90–270 phase shift (*a*), the reverse is true: responses of odd-symmetric mechanisms, but not even-symmetric mechanisms, are altered. Again, this is illustrated by the lengths of arrows in corresponding locations in the two waveforms. A 90–270 shift is discriminated when changes in odd-symmetric mechanisms exceed some threshold. A 30–210 phase shift changes the responses of even and odd-symmetric mechanisms (*b*). The two-channel model predicts that a 30–210 shift is discriminated when changes in either the even-symmetric or the odd-symmetric mechanisms reach threshold (see Fig. 2). The 2F contrasts needed to discriminate 0–180, 30–210 and 90–270 phase shifts are plotted in Fig. 2 as M_0, M_{30}, and M_{90}, respectively.
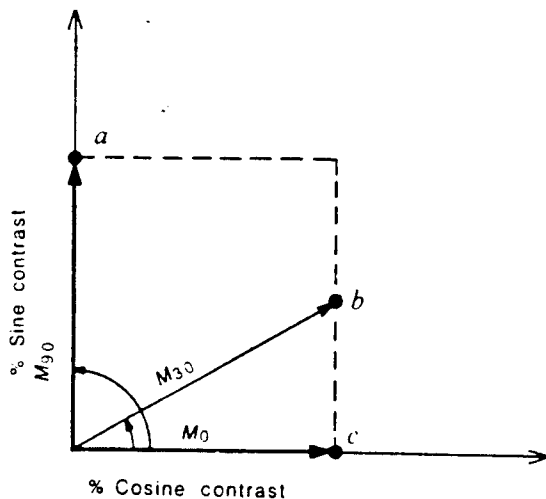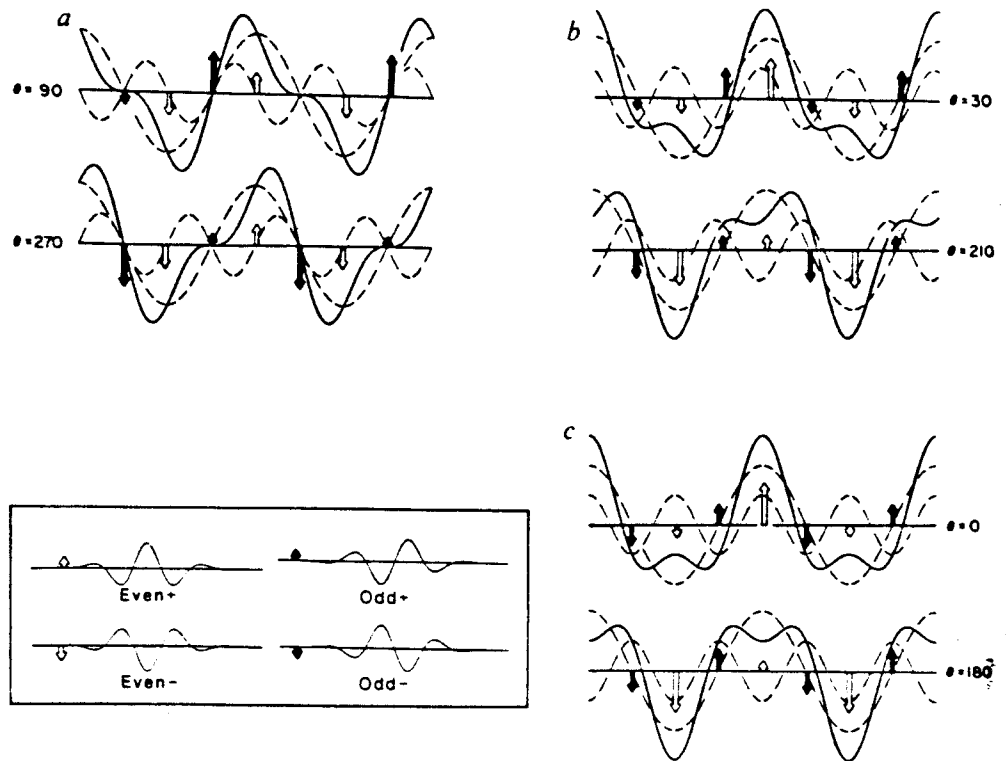

Fig. 2 Plot of predicted discrimination thresholds. The angle expansion formula $M \cos (2\pi 2F + \theta) = M \cos \theta \cos (2\pi 2F) - M \sin \theta \sin (2\pi 2F)$, is used to analyse 2F into its cosine and sine components. For any 180° shift, the predicted threshold is the contrast needed for the cosine amplitude to equal the 0–180 threshold, or for the sine amplitude to equal the 90–270 threshold. The predicted and observed thresholds are plotted as follows: the length of a vector is proportional to the contrast of 2F, and phase is represented by its angle. The 0–180 threshold (*c*) is plotted on the abscissa and the 90–270 threshold (*a*) on the ordinate. The model predicts that an 180° shift is discriminated when the cosine or sine components of 2F equal one of those thresholds. Thus, the predicted thresholds lie along the two dotted lines, the horizontal line representing 180° shifts discriminated by odd-symmetric mechanisms, and the vertical line representing shifts discriminated by even-symmetric mechanisms. The prediction for a 30–210 shift (*b*) is illustrated.

conditions reported here, however, F was clearly visible despite the presence of 2F. A failure to discriminate phase shifts cannot, therefore, be attributed to an inability to detect both grating components.

Discrimination thresholds were similar in the fovea for the 0–180 and the 90–270 phase shifts (Fig. 3*a*), and thresholds for the other phase shifts were quite consistent with the predictions of the two-channel model. This implies that two mechanisms with similar sensitivities operate in the fovea, replicating the results of Field and Nachmias[8]. With increasing eccentricity, the thresholds for the 0–180 shift rose slightly, but thresholds for the 90–270 shift rose monotonically and dramatically (Fig. 3*b–e*). At 20°, for example, the 90–270 threshold was ~10 times greater than the 0–180 threshold. Thus, two mechanisms also seem to operate in the peripheral visual field (with the possible exception of 40°), but their sensitivities are strikingly dissimilar.

The difficulty of the 90–270 discrimination in the periphery has an interesting implication for the model. Even-symmetric
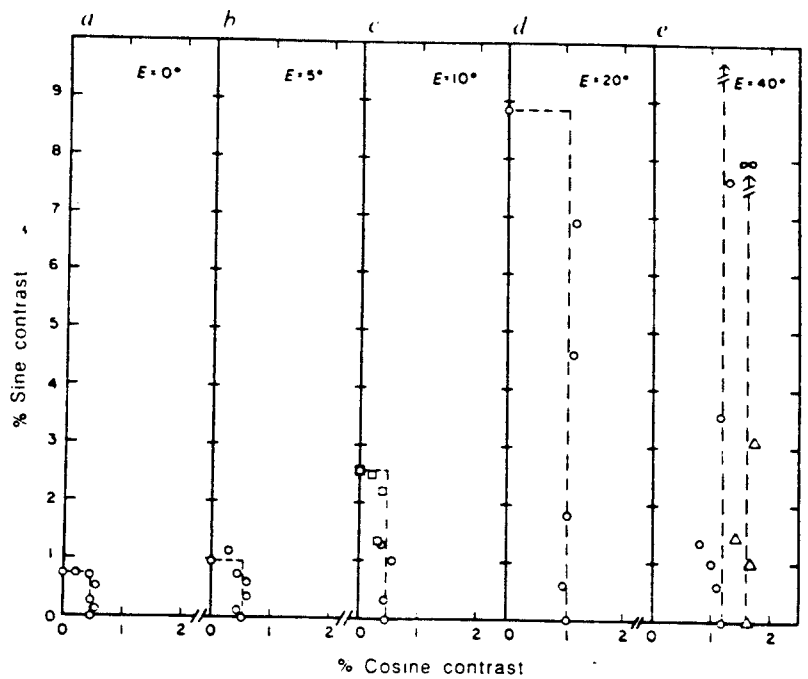
Fig. 3 Phase discrimination thresholds at five eccentricities (E): a, 0°; b, 5°; c, 10°; d, 20°; e, 40°. The circles represent the thresholds from one observer using a 2-down/1-up staircase procedure. Thresholds obtained with the method of constant stimuli are represented by the squares in c. Thresholds from a second observer, obtained with the staircase procedure, are shown as triangles in e. When the staircase procedure was used, threshold was defined as the geometric mean of the final 12 reversals. When the method of constant stimuli was employed, threshold was the 70% point on the psychometric function defined by 4 points with at least 100 trials per point. Both observers had normal vision, and viewed the stimuli monocularly with natural pupils. At an eccentricity of 40°, a 90–270 phase shift could not be discriminated. The predictions of the two-channel model are illustrated by the dotted lines in a-e. Values of F, the fundamental spatial frequency (in cycles per degree; c per deg) were: for a, 4; b, 2; c, 1.5; d, 1; e, 0.5. C_F, contrast of the fundamental, was 10% throughout.

mechanisms could readily discriminate these two phases if they made their computations at points other than the peaks and troughs of F. One can demonstrate this by computing the responses of the mechanisms by cross-correlating the F+2F waveform with an even-symmetric receptive field (Fig. 1). The difference between the responses to the 90° and 270° stimuli is a sinewave of frequency 2F, and the response differences are greatest at points distant from the peaks and troughs of F. Even-symmetric mechanisms positioned at such points should, therefore, be able to make the 90–270 discrimination at high contrasts of 2F. The fact that the 90–270 discrimination is impossible in the far periphery suggests that even-symmetric mechanisms make their computations only at or near the peaks and troughs of F where the differential response is zero.

The stimuli in this experiment were scaled to render them equally detectable at all eccentricities. The scaling factor was similar to previous estimates of the retinal magnification factor[2,12]. Livingston and Hubel[13] argued that a different scaling factor should be used in some phase discrimination tasks. We followed their suggestion by examining whether different scaling factors would reduce the disparities between foveal and peripheral performance. Discrimination thresholds were measured in the fovea and at 40° using a range of spatial frequencies. Again, the contrast of F was set about 1 log unit above detection threshold. We found that foveal thresholds for the 0–180 and 90–270 discriminations are similar to one another for all the spatial frequencies we tested (Fig. 4a). In the far periphery (Fig. 4b), thresholds for the 0–180 discrimination are similar at the two frequencies, and the 90–270 discrimination is impossible at both. Thus, the foveal-peripheral disparity is scale-invariant at least over the range of frequencies tested. We conclude that Livingston and Hubel's scaling hypothesis does not account for the differences we observe between foveal and peripheral phase discrimination.

Our findings are consistent with earlier reports of phase-encoding anomalies in the periphery[6,7], but they extend those reports by suggesting that the anomalies are caused primarily by sensitivity losses among odd-symmetric mechanisms. Consequently, our results are inconsistent with several models of how foveal and peripheral phase encoding differ[6,7,14]. For example, Rentschler and Treutwein[7] proposed that two processes mediate grating discrimination. One process, operating only in the fovea, registers the relative positions of features. A second process, operating in the fovea and periphery, registers changes

in pattern contrast. Therefore, only phase shifts that alter contrast should be discriminable in the periphery. Braddick's model[6] makes a similar prediction. The phase shifts we used did not alter contrast, so these models[6,7] predict that none of the shifts should be discriminable in the periphery. Our results are clearly inconsistent with this prediction. Watt's model[14] predicts that peripheral phase-encoding deficits will be reduced by increasing stimulus size. Again, our results are inconsistent with this prediction.

We examined whether the two-channel model can predict Rentschler and Treutwein's[7] findings. They measured phase discrimination thresholds in the fovea and near periphery with compound gratings composed of a fundamental (F) and third harmonic (3F). The contrast of 3F was fixed at one-third that of F, but the phase of 3F was shifted around a mean phase of 0°, 90°, or 180°. Foveal thresholds in the 0° and 180° conditions were somewhat higher than those in the 90° condition. In the near periphery, however, shifts about 0° and 180° could not be discriminated. Only shifts about 90° were discriminable. The two-channel model predicts the peripheral results accurately, but it also predicts that phase shifts around 0° and 180° should not be discriminated in the fovea. We can account for the foveal results by altering the model slightly. Instead of using the responses exclusively of mechanisms centred precisely on the peaks, troughs, and zero-crossings of the waveform, the responses of slightly decentred mechanisms were used. Mechanisms centred on points up to 40 s on either side of a peak, trough, or zero-crossing enable foveal phase discriminations about 0 and 180°. With this new (and more biologically plausible) assumption, the two-channel model predicts Rentschler and Treutwein's findings quite accurately. Specifically, it predicts that foveal discrimination thresholds in the 0° and 180° conditions should be somewhat higher than in the 90° condition, and that thresholds in the 0° and 180° conditions, but not in the 90° condition, should rise substantially in the near periphery. The added assumption does not alter the predictions for our experiment, provided that the decentring is small.

In summary, our experiments are consistent with previous reports of phase-encoding anomalies in the periphery. They suggest, however, that the anomalies stem from sensitivity losses among odd-symmetric, but not even-symmetric, mechanisms. It is interesting to speculate that many of the recognition and identification deficiencies observed in peripheral vision may be caused in large part by changes in the sensitivity of one type of
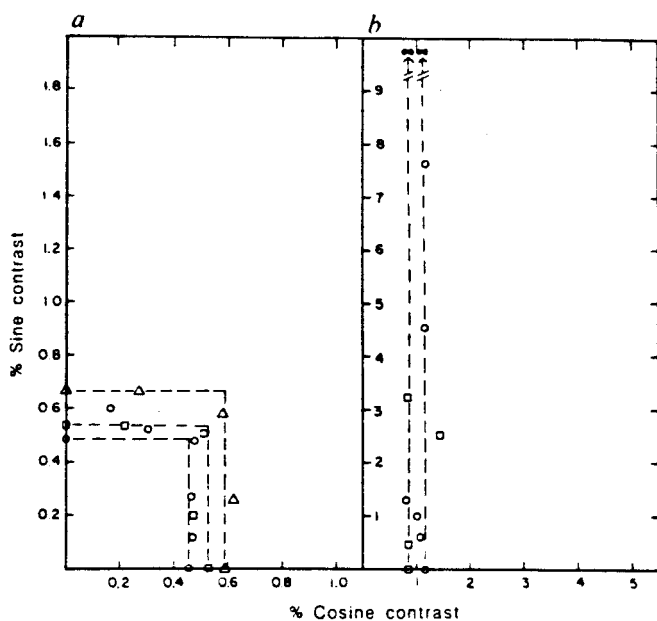
Fig. 4 The effect of spatial frequency on phase discrimination. *a*, Foveal phase discrimination thresholds: O, $F = 4$ c per deg, $C_F = 10\%$; □, $F = 8$ c per deg, $C_F = 12.5\%$; △, $F = 12$ c per deg, $C_F = 15\%$. Sensitivities to 0-180 and 90-270 shifts were approximately similar at all spatial frequencies. *b*, Discrimination thresholds at 40°: O, $F = 0.5$ c per deg, $C_F = 10\%$; □, $F = 0.167$ c per deg, $C_F = 15\%$. Lowering spatial frequency does not alter the pattern of results. In particular, it was impossible to discriminate a 90-270° phase shift at both spatial frequencies. Note the change of scale on both axes between *a* and *b*.

mechanism, and a corresponding inability to pick up one class of phase information. This hypothesis is difficult to test currently because recognition and identification models are not sufficiently detailed to make quantitative predictions. However, even and odd mechanisms have been postulated in quantitative models of foveal grating detection and discrimination[15-20], motion discrimination[21-23], and the perception of Mach bands[24]. If the mechanisms proposed in these models are the same as the even and odd mechanisms of our two-channel model, we predict that particular peripheral deficits will be observed in these visual processes. Such a prediction for the perception of Mach bands was confirmed recently[24]. It remains to be seen if the other predictions are confirmed.

1. Rovamo, J., Virsu, V. & Nasanen, R. *Nature* **271**, 54-56 (1978).
2. Koenderink, J. J., Bouman, M. A., Bueno de Mesquita, A. E. & Slappendel, S. *J. opt. Soc. Am.* **68**, 854-860 (1978).
3. Merchant, J. *J. opt. Soc. Am.* **55**, 1291-1295 (1965).
4. Loomis, J. *Vision Res.* **18**, 335-338 (1978).
5. Julesz, B. *Nature* **290**, 91-97 (1981).
6. Braddick, O. *Documenta ophth. Proc. Series* **30**, 255-262 (1981).
7. Rentschler, I. & Treutwein, B. *Nature* **313**, 308-310 (1985).
8. Field, D. J. & Nachmias, J. *Vision Res.* **24**, 333-340 (1984).
9. Stromeyer, C. F. & Julesz, B. *J. opt. Soc. Am.* **62**, 1221-1232 (1972).
10. Nachmias, J. & Weber, A. *Vision Res.* **15**, 217-224 (1975).
11. Tolhurst, D. J. & Barfield, L. P. *Vision Res.* **18**, 951-958 (1978).
12. Levi, D. M., Klein, S. A. & Aitsebaomo, A. P. *Vision Res.* **25**, 963-977 (1985).
13. Livingston, M. S. & Hubel, D. H. *Nature* **315**, 285 (1985).
14. Watt, R. J. *Nature* **313**, 266-267 (1985).
15. Stromeyer, C. F. & Klein, S. *Vision Res.* **14**, 1409-1420 (1974).
16. Stromeyer, C. F., Lange, A. F. & Ganz, L. *Vision Res.* **13**, 2345-2360 (1973).
17. Shapley, R. M. & Tolhurst, D. J. *J. Physiol., Lond.* **229**, 165-183 (1973).
18. Tolhurst, D. J. *Vision Res.* **12**, 797-804 (1972).
19. Lawton, T. B. *Vision Res.* **24**, 139-148 (1984).
20. Lawton, T. B. *J. opt. Soc. Am.* A **2**, 1140-1152 (1985).
21. Van Santen, J. P. H. & Sperling, G. *J. opt. Soc. Am.* A **2**, 185-321 (1985).
22. Nakayama, K. & Silverman, G. H. *J. opt. Soc. Am.* A **2**, 267-274 (1985).
23. Watson, A. B. & Ahumada, A. J. *J. opt. Soc. Am.* A **2**, 322-342 (1985).
24. Morrone, M. C., Ross, J., Burr, D. C. & Owens, R. *Nature* **324**, 250-253 (1986).