# THE EFFECTS OF CONTRAST, SPATIAL SCALE, AND ORIENTATION ON FOVEAL AND PERIPHERAL PHASE DISCRIMINATION

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Abstract—We examined the effects of contrast, spatial scale, and orientation, on phase discrimination thresholds. In expt I, the ratio of thresholds for 180 deg shifts in F + 2F gratings remained invariant across a wide range of fundamental contrasts. Experiment II demonstrated that random fluctuations in overall pattern contrast did not affect discrimination. Experiment III found that foveal, but not peripheral, thresholds were roughly independent of spatial scale; foveal-peripheral differences in phase sensitivity could not be eliminated by scaling stimulus size. Finally, expt IV found that thresholds for some phase shifts varied significantly with orientation in the periphery; in general, peripheral sensitivity was greatest for radially-oriented gratings. The implications of these findings for models of phase discrimination are discussed.

Spatial phase Peripheral vision Discrimination Cortical magnification

### INTRODUCTION

Spatial phase is thought to be an important source of information for discriminating and identifying complex natural images. Little is known, however, about the way that the visual system represents spatial phase. Therefore, we have undertaken an examination of the effects of contrast, spatial scale, and orientation on relative phase discrimination for compound gratings viewed in the fovea and periphery.

### EXPERIMENT I. THE EFFECTS OF CONTRAST ON PHASE DISCRIMINATION

The fact that human observers can discriminate patterns that differ only in phase demonstrates that the visual system represents spatial phase in some fashion. The representation of phase is remarkably precise in the fovea. Badcock (1984a, b), for instance, found that observers can discriminate relative phase shifts as small as 2.5 deg in compound gratings composed of a fundamental (F) and third harmonic (3F), which is equivalent to a shift of about 5 sec for the spatial frequencies used in Badcock's experiments. However, several studies have found that phase sensitivity is dramatically reduced in the periphery (Bennett & Banks, 1987;

Hess & Pointer, 1987; Klein & Tyler, 1985; Rentschler & Treutwein, 1985; Stephenson & Braddick, 1983). Rentschler and Treutwein measured phase discrimination thresholds for F + 3F gratings that were equally visible in the fovea and periphery. They found that all phase shifts were discriminable in the fovea, although shifts that changed overall contrast (i.e. the peak-to-trough amplitude) were slightly more discriminable than shifts that did not. In the periphery, however, only phase shifts that changed contrast were discriminable. On the basis of these and other findings, Rentschler and Treutwein (1985) and Braddick (1981) proposed that two processes subserve the discrimination of spatially complex patterns: one that encodes changes in contrast and another that encodes the relative positions of pattern features. According to these models, the contrast-encoding process operates everywhere in the visual field, but the position-encoding process operates reliably in foveal vision only. Both models predict that compound sinewave gratings that have equal contrasts should be difficult to discriminate in the periphery.

Bennett and Banks (1987) tested this prediction by measuring discrimination thresholds for compound gratings, composed of a fundamental (F) and second harmonic (2F), that differed

by a 180 deg relative phase shift. Thresholds were measured at the fovea and 5, 10, 20 and 40 deg along the horizontal meridian. The fundamental frequencies were scaled to make them equally visible at all eccentricities. A useful property of F + 2F gratings is that 180 deg relative phase shifts do not change the peak-totrough amplitude of the compound waveforms (Fig. 1), so the position-encoding processes of the Rentschler-Treutwein and Braddick models must be used to discriminate these phase shifts. Consequently, both models predict thresholds for all 180 deg phase shifts should rise with increasing eccentricity. Instead, Bennett and Banks (1987) found that thresholds for some phase shifts were roughly constant at all eccentricities, but thresholds for other shifts increased dramatically in the periphery. Specifically, foveal thresholds for 0-180 and 90-270 deg phase shifts were similar. At 20 deg in the periphery, however, the 0-180 deg threshold was only 0.3 log units greater than the foveal threshold but the 90-270 threshold was 1 log unit greater.

Bennett and Banks' results were consistent with a two-channel model of phase discrimination proposed by Field and Nachmias (1984). According to this model, phase shifts are encoded by two, and only two, channels. One channel consists of even-symmetric spatial filters and the other of odd-symmetric filters. Bennett and Banks proposed that foveal and

peripheral differences in sensitivity to spatial phase were caused by a loss of sensitivity in odd-symmetric filters. Because none of the phase shifts changed grating contrast, they concluded that the Rentschler-Treutwein and Braddick models of peripheral phase-encoding mechanisms were incorrect.

Bennett and Banks' conclusion may be premature because nonlinearities in the early stages of visual processing may have introduced effective contrast differences upon which observers based their judgments. There is, in fact, substantial psychophysical and physiological evidence for compressive nonlinearities early in visual processing that could conceivably introduce such contrast differences (e.g. Burkhardt & Gottesman, 1987; Cone, 1965; Naka & Rushton, 1966; Schneider & Zrenner, 1987; Wirth & Zetterstrom, 1954). Moreover, contrast differences introduced by such nonlinearities would be phase dependent. Consider the effects of a compressive nonlinearity on the waveforms in 0 and 180 deg phase (Fig. 1a, b). Although these stimuli have equal physical contrasts, a compressive nonlinearity causes the output contrast for the two waveforms to differ. If the nonlinearity is made more compressive, or if pattern contrast is increased, the output contrast difference increases. Nonlinearities do not introduce contrast differences between waveforms in 90 and 270 deg phase because they are mirror images of one another (Fig. 1g, h). Thus,

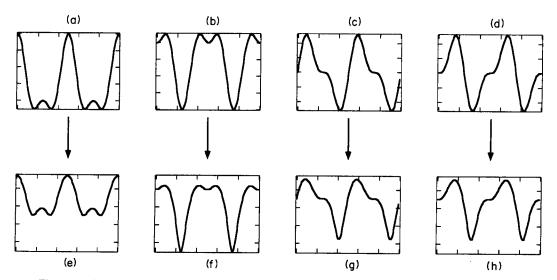


Fig. 1. Luminance profiles of F + 2F gratings are shown with 2F added in 0 (a), 180 (b), 90 (c), and 270 (d) deg phase. Space and luminance are represented on the abscissa and ordinate, respectively, in arbitrary units. Notice that a 180 deg phase shift does not change the peak-to-trough amplitude of the waveforms. The profiles of the waveforms, after being filtered through a compressive nonlinearity, are shown in (e-h). A 0-180 deg phase shift changes the amplitudes of the filtered waveforms (e vs f) but a 90-270 shift does

nonlinearities may produce effective contrast differences for 0–180 deg phase shifts, but not 90–270 shifts, prior to the site where phase-specific encoding occurs. The contrast-encoding process in the Rentschler–Treutwein and Braddick models could use such differences to discriminate 0–180 deg, but not 90–270, phase shifts, so those models might predict lower peripheral thresholds for 0–180 than for 90–270 phase shifts, as observed by Bennett and Banks (1987). Experiments I and II test this nonlinearity hypothesis.

### Methods

Stimuli. The stimuli were vertical F + 2F compound sinewave gratings:

$$L(x) = L_{avg}[1 + C_F \cos(2\pi F x) + C_{2F} \cos(2\pi 2F x - \theta)]$$
 (1)

where  $L_{\text{avg}}$  is the space-average luminance,  $C_F$ and  $C_{2F}$  are the Michelson contrasts of F and 2F, respectively, and  $\theta$  is the base phase of 2F. Pattern contrast was modulated horizontally and vertically by a Gaussian envelope with a radius (at half-amplitude) that equalled one period of F. Stimulus eccentricity was defined as the angle between the fixation point and the center of the Gaussian envelope. The waveforms were generated on a PDP-11/73 computer and passed through a 12-bit DAC and an adjustable step attenuator to a Joyce Electronics display with P4 phosphor. The frame rate was 83 Hz. Mean luminance was fixed at 100 cd/m<sup>2</sup>. All calibrations were done with a Pritchard spot photometer (model UDB) and care was taken to ensure that the display's response was linear at all contrasts used in these experiments.

Observers. Observers P.J.B. and M.S.B. are emmetropic with normal visual acuity; J.C. is a corrected-to-normal myope. The visual fields of all observers are normal. Observers P.J.B. and M.S.B. are the authors; J.C. was naive with respect to the aims of these experiments. Observers P.J.B. and J.C. received extensive practice (i.e. >20,000 trials) distributed across all conditions. M.S.B. received less practice (approx. 1200 trials) in the peripheral conditions.

Procedure. Discrimination thresholds for 180 deg relative phase shifts were measured by fixing the contrast of F at a suprathreshold value and then varying the contrast of 2F until the phase shift was just visible. Trials were started by the observer and consisted of two 250 msec intervals marked by tones and separated by 250 msec.

The first interval always contained F and 2Fadded in some base phase (e.g. 0 deg phase). The second interval contained either a pattern of the same base phase or one in which 2F had been shifted by 180 deg relative to F (e.g. either 0 or 180 deg phase). Observers judged whether the patterns in the two intervals were the same or different. Auditory feedback indicated the accuracy of the response after each trial. To ensure that observers could not use average or local luminance cues to make discriminations, the waveforms were displaced randomly within the Gaussian envelope from one interval to another. The fixation target was a small high-contrast dot when stimuli were presented peripherally. For foveal conditions, 4 dots were placed above, below, and to either side of the center of the stimuli. Viewing was monocular and chin and head rests were used to stabilize head position. To facilitate the detection of the high spatial frequency components, observers viewed the patterns through a 2 mm artificial pupil in foveal conditions. Viewing was through natural pupils (diameter approx. 4 mm) in all other conditions. Control experiments showed that the reduction in retinal illuminance caused by the 2 mm pupil did not affect the results.

Thresholds were determined using the method of constant stimuli (with 2F contrast presented in blocks of 25 or 50 trials) in most conditions. During a testing session, we measured a psychometric function defined by at least 3 points with at least 75 trials per point. The same conditions were always retested in a different session so that the cumulative psychometric functions were defined by at least 4 points and at least 150 trials per point. Probit analysis (Finney, 1971) was used to compute the best-fitting cumulative normal on the log-transformed data and threshold was defined as the 2F contrast yielding 75% correct.

In some conditions, 2F contrast was varied according to a 2-down/1-up staircase procedure (Levitt, 1971). Contrast was changed in steps of diminishing size as the number of reversals increased. Threshold was defined as the geometric mean of the final 12 reversals. The results from 2-5 staircase runs were averaged for the final threshold estimates. As one would expect, the staircase and constant stimuli procedures yielded very similar thresholds.

### Results and discussion

Previous studies have found that discrimination of 180 deg phase shifts in F + 2F gratings

occurs when either the change in the cosine or sine component of 2F exceeds some threshold (Bennett & Banks, 1987; Field & Nachmias, 1984; Morrone, Burr & Spinelli, 1989). The contrast of the fundamental differed among these studies, suggesting that this finding is not critically dependent on contrast. We tested this directly by measuring thresholds for 0-180, 90-270, and other 180 deg phase shifts at several F contrasts (Fig. 2). As in previous studies, the data were well-fit by a pair of vertical and

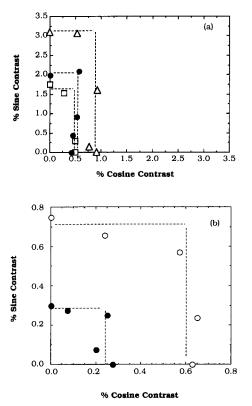


Fig. 2. Phase discrimination thresholds measured at 10 deg in the nasal visual field (a; observer P.J.B.) and in the fovea (b; observer J.C.) with different stimulus contrasts. In (a), the fundamental spatial frequency was  $1.5\,\mathrm{c/deg}$  and Fcontrast was 0.03 ( $\square$ ), 0.1 ( $\bullet$ ), or 0.51 ( $\triangle$ ). In (b), the fundamental was 4 c/deg and F contrast was  $0.10 \ ( \bigcirc )$  or  $0.3 \$ (O). Each point represents the threshold for a different 180 deg phase shift: threshold is represented as the length of a vector joining each point to the origin and base phase is represented as the vector's angle to the horizontal axis. Alternatively, each point can be considered as the vector sum of orthogonal cosine and sine components. In these plots, 0-180 thresholds are plotted on the horizontal axis, 90-270 thresholds on the vertical axis, and thresholds for other 180 deg shifts lie in-between. The dotted lines represent the predictions of the two-channel model. The vertical, constant-cosine line represents phase shifts discriminated by even-symmetric filters and the horizontal, constant-sine line represents shifts discriminated by oddsymmetric filters. Standard errors (not shown) are approx. 0.05 log units or 12%.

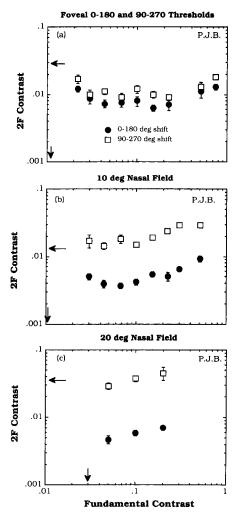


Fig. 3. 0-180 ( ) and 90-270 ( ) discrimination thresholds measured as a function of stimulus contrast in the fovea (a) and at 10 (b) and 20 (c) deg along the nasal horizontal meridian. All thresholds are for a single observer. In (a), the frequency of the fundamental was 8 c/deg. In (b) and (c), the fundamentals were 1.5 and 1.0 c/deg, respectively. The arrows on the abscissa and ordinate mark the detection thresholds for F and 2F, respectively. Error bars represent  $\pm 1$  SEM.

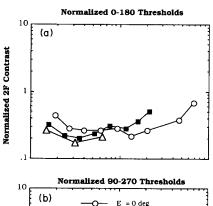
horizontal line segments (the vertical and horizontal segments representing equal cosine and sine components, respectively). These results, in combination with previous findings, demonstrate that two thresholds—for 0-180 and 90--270 shifts—are sufficient to predict thresholds for all other 180 deg shifts with reasonable accuracy (i.e. within 0.03 log units on average) for a wide range of F contrasts. In the following figures, therefore, only thresholds for 90-270 and 0-180 deg shifts are shown. Because the 90-270 and 0-180 deg shifts are thought to be encoded by odd-symmetric and even-symmetric filters, respectively, we will call

the ratio of these thresholds the *odd-even* ratio (Bennett & Banks, 1987; Field & Nachmias, 1984; Morrone et al., 1989).

The results from different observers were similar, so only thresholds from observer P.J.B. are shown here. (The results from observer M.S.B. are shown in Fig. 10). Figure 3 shows thresholds for 0–180 and 90–270 phase shifts measured at three eccentricities. Detection thresholds for F and 2F are indicated by arrows on the abscissa and ordinate of each panel.

First consider the foveal results. Discrimination thresholds for 0–180 and 90–270 deg phase shifts were nearly constant across a broad range of fundamental contrasts. Specifically, for contrasts of 0.015–0.75, thresholds for both phase shifts were 0.2–0.6 log units below the detection threshold for 2F; thresholds increased at the highest F contrasts. Thresholds measured at 10 and 20 deg in the periphery also varied little with F contrast but, unlike the foveal results, 90–270 thresholds were substantially higher than 0–180 thresholds.

The differences between foveal and peripheral 90–270 thresholds cannot be explained by differences in the detectability of the frequency components. This is shown most clearly in Fig. 4



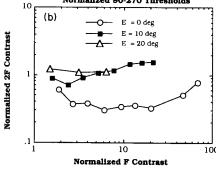


Fig. 4. Normalized 0–180 (a) and 90–270 (b) phase discrimination thresholds. Each threshold in Fig. 3 was shifted horizontally by dividing it by the detection threshold for F and vertically by dividing by the detection threshold for 2F. Foveal thresholds ( $\bigcirc$ ); 10 deg nasal field ( $\blacksquare$ ); 20 deg nasal field ( $\triangle$ ).

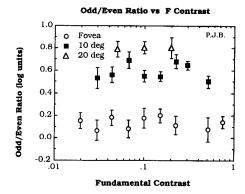


Fig. 5. The effects of stimulus contrast on odd-even ratios measured in the fovea (○), 10 deg (■), and 20 deg (△). Odd-even ratios are defined as ratio of 90-270 thresholds divided by 0-180 thresholds. All data are from observer P.J.B. Error bars represent ± 1SEM.

where the thresholds for all conditions are plotted in normalized contrast coordinates. The axes were normalized by dividing each value on the abscissa and ordinate by the detection threshold for F and 2F, respectively. Foveal and peripheral 0–180 thresholds collapse onto a single dipper-shaped function with this normalization, but the 90–270 thresholds do not.

The nonlinearity hypothesis outlined in the Introduction predicts that the odd-even ratio should rise with increasing stimulus contrast regardless of the form of the nonlinearity (e.g. compressive, accelerative, or sigmoidal). Foveal and peripheral odd-even ratios are shown in Fig. 5. Foveal 90-270 thresholds were on average 0.12 log units higher than 0-180 thresholds. Peripheral 90-270 thresholds were 0.6 and 0.8 log units higher at 10 and 20 deg. Figure 5 reveals no monotonic relationship between contrast and the odd-even ratio, a result that is clearly inconsistent with the nonlinearity hypothesis.

# EXPERIMENT II. CONTRAST RANDOMIZATION HAS NO EFFECT ON PHASE DISCRIMINATION THRESHOLDS

Phase discrimination thresholds measured in expt I did not vary substantially with pattern contrast. One interpretation of this result is that discriminations were based on changes in the shapes (or profiles) of the waveforms, rather than the brightness of particular features or overall contrast. If shape is used exclusively, then varying pattern contrast randomly should not affect discriminability. The nonlinearity hypothesis makes a different prediction: if 0–180, but not 90–270, shifts are discriminated on the

basis of overall contrast, then contrast randomization should increase thresholds for 0–180 phase shifts more than for 90–270 shifts. The effects of contrast randomization were examined in expt II.

### Methods

Stimuli. The stimuli were again vertical F + 2F compound sinewave gratings. The stimuli were generated on a Macintosh IIx microcomputer and passed through a 12-bit DAC and adjustable step attenuator to a Tektronix 608 CRT with P31 phosphor. The frame rate was 100 Hz with 500 lines per frame. Mean luminance was  $85 \text{ cd/m}^2$ . The CRT was the only source of illumination in the testing room. Stimulus contrast was vignetted horizontally and vertically by a square opaque mask placed over the CRT. Seven cycles of the fundamental were visible beneath the mask. All other aspects of the stimuli were identical to those in expt I.

Observers. Thresholds were measured for three observers. One observer from expt I (observer P.J.B.) also participated in expt II. Observers A.B.S. and B.A. have normal and corrected-to-normal visual acuity, respectively, and normal visual fields. Observer A.B.S. is highly experienced in spatial visual psychophysical tasks, but received minimal practice in the current experimental conditions. Observer B.A. received several hundred practice trials but was naive with respect to the experimental hypothesis.

Procedure. A 2 IFC procedure was used. One pattern was designated arbitrarily as the standard and the other (i.e. 180 deg phase-shifted pattern) as the target. Observers were allowed to inspect the patterns prior to each experimental run. Each trial consisted of two 250 msec stimulus intervals marked by tones and separated by 250 msec. Unlike the first experiment, however, the standard and the target were presented on every trial. The observer's task was to identify the temporal interval containing the target.

Phase discrimination thresholds were measured by fixing the contrast of F at 0.10 and varying the contrast of 2F. A 2-down/1-up staircase procedure was used to vary 2F contrast in steps of 0.05 log units. A staircase ended after 10 reversals, and threshold was defined as the mean of the final 8 reversal points. The results from 2–5 staircases were averaged to yield the final estimates of threshold and standard error.

Thresholds were measured in two conditions. In the *random-contrast* condition, the overall

contrast of the compound gratings was varied randomly from one stimulus interval to another. Contrast randomization was achieved by multiplying the patterns by a gain factor that was selected from a uniform distribution ranging from 0.3 to 3.0 in steps of 0.1. Thus, the contrast randomization procedure varied the amplitude of each frequency component (e.g. F contrast varied from 0.03 to 0.30) but did not alter the ratio of F and 2F contrasts. Thresholds in the random-contrast condition were expressed as 2F contrast measured prior to the multiplication by the gain factor. In the *fixed-contrast* condition, the gain factor was always 1.0.

#### RESULTS

Preliminary testing did not reveal any interaction between the effect of contrast randomization and the parameters of fundamental spatial frequency, bandwidth, and retinal eccentricity. We therefore arbitrarily set the fundamental to 2 and 1.5 c/deg for foveal and peripheral (i.e. 10 deg nasal visual field) viewing conditions, respectively. The results are presented in Figs 6 and 7.

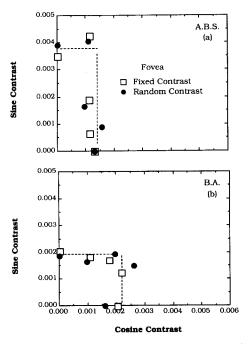


Fig. 6. The effect of contrast randomization of foveal phase discrimination thresholds measured in the fixed- (□) and random-contrast (●) conditions. Panels (a) and (b) show thresholds from two observers. The fundamental frequency was 2 c/deg and contrast was 0.10 (prior to multiplication by the contrast gain factor). The dotted lines are the predictions of the two-channel phase-encoding model. Standard errors (not shown) were approx. 0.04 log units.

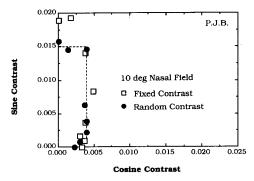


Fig. 7. Peripheral (10 deg) thresholds measured in one observer in the fixed- (□) and random-contrast (●) conditions. The fundamental frequency was 1.5 c/deg and contrast was 0.10 (prior to multiplication by the contrast gain factor). The dotted lines are the predictions of the two-channel phase-encoding model. Standard errors (not shown) were approx. 0.04 log units or 10%. Note that the scales differ from those in Fig. 6.

There are three important features of these data. First, phase discrimination thresholds in all conditions are consistent with the two-channel model of phase discrimination proposed by Field and Nachmias (1984). Second, foveal odd—even ratios varied significantly across observers (e.g. compare Fig. 6a and b). Subsequent testing of observer A.B.S. did not lower her odd-even ratio significantly, so it is unlikely that the individual differences were merely due to differences in practice. Finally, we found no consistent difference between thresholds in the fixed- and random-contrast conditions.

Badcock (1984a, b) has pointed out that some phase shifts alter the contrast between local maxima and minima in compound sine wave gratings. In a series of experiments that employed stimuli and procedures that differed significantly from the current ones, Badcock found that discrimination thresholds were accurately predicted by a model that discriminated phase shifts on the basis of such local contrast changes. In the current experiment, the only features on which to compute local contrast are the overall luminance maxima and minima. The local contrast model predicts, therefore, that contrast randomization should reduce sensitivity to phase shifts. We found no such sensitivity loss, however, and conclude that the local contrast model cannot account for the present results.

Experiment I demonstrated that the ratios of thresholds for a variety of 180 deg relative phase shifts are independent of fundamental contrast. Experiment II found that randomizing contrast over a 1 log unit range has no effect on discrimi-

nation thresholds. Both findings are inconsistent with the nonlinearity hypothesis. We are not claiming that nonlinearities do not affect phase discrimination thresholds. On the contrary, the fact that thresholds rise at high F contrasts (see Fig. 3) may well be a manifestation of a nonlinear contrast response. The current results simply demonstrate that the effects of nonlinearities are the same in the two conditions and that such effects do not account for the fact that thresholds in the 90–270 condition vary much more with eccentricity than thresholds in the 0–180 condition.

### EXPERIMENT III. THE EFFECTS OF SPATIAL SCALE ON PHASE DISCRIMINATION

Spatial vision generally worsens with increasing retinal eccentricity. For example, vernier acuity (Levi, Klein & Aitsebaomo, 1985; Westheimer, 1982; Yap, Levi & Klein, 1987a) and contrast sensitivity for sinewave gratings (Koenderink, Bourman, Bueno de Mesquita & Slappendel, 1978a, b; Robson & Graham, 1981) fall monotonically with increasing eccentricity. However, many differences between foveal and peripheral vision can be reduced or even eliminated by scaling stimulus size (i.e. an overall magnification of the simulus like that produced by changing viewing distance). For example, peak contrast sensitivity and the shape of the contrast sensitivity function are nearly invariant across the visual field when spatial frequency and target extent are scaled appropriately (Koenderink et al., 1978c; Rovamo, Virsu & Nasanen, 1978). Discrimination thresholds for contrast increments (Legge & Kersten, 1987; Maattanen, Koenderink & Nienhuis, 1988), orientation (Paradiso & Carney, 1988), spatial frequency (Thomas, 1987) and velocity (Johnston & Wright, 1986) are invariant too, once pattern size is scaled. One interpretation of these findings is that differences between foveal and peripheral pattern vision are caused only by quantitative differences in the density of sampling of the retinal image (Koenderink et al., 1978c; Rovamo et al., 1978; Virsu, Nasanen & Osmoviita, 1987; Virsu & Rovamo, 1979; Watson, 1987).

There are, however, some conspicuous exceptions to this scaling rule. Foveal and peripheral two-dot separation discrimination thresholds, for instance, cannot be equated by magnifying the stimulus (Westheimer, 1982; Yap, Levi & Klein, 1989). Relative phase discrimination

thresholds may be another such exception. Previous studies of phase sensitivity that used two-component grating stimuli found that scaling a target's spatial frequency and spatial extent did not eliminate the differences between foveal and peripheral thresholds (Bennett & Banks, 1987; Rentschler & Treutwein, 1985). However, Morrone et al. (1989) recently reported that differences between foveal and peripheral phase discrimination thresholds, measured with broad-band, multi-component gratings, can be

eliminated by scaling stimulus size. Morrone et al. also found that peripheral thresholds measured with F+2F gratings improved at very low spatial frequencies. Their findings raise the possibility that previous phase discrimination studies that used compound gratings failed to use the correct scaling factor needed to equate foveal and peripheral thresholds. Experiment III examined this hypothesis by measuring discrimination thresholds across a wide range of spatial scales.

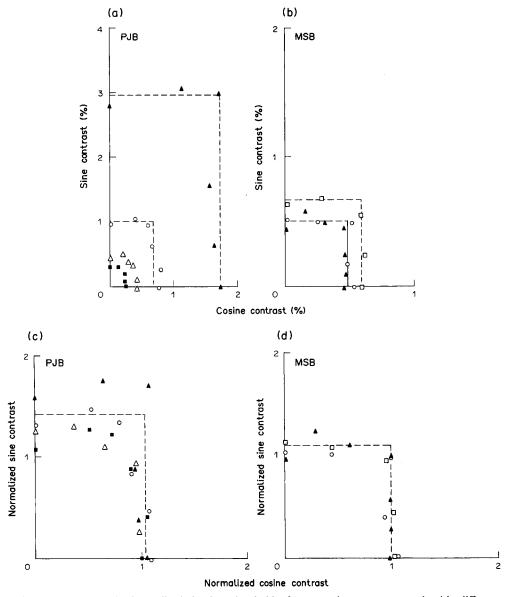


Fig. 8. (a, b) Foveal phase discrimination thresholds for two observers measured with different fundamental frequencies. Fundamental contrast was 0.2 in the 16 c/deg condition and 0.1 for all other conditions. Thresholds shown in (b) were reported previously (Bennett & Banks, 1987). Standard errors (not shown) are approx. 0.05 log units or 12%. Panels (c) and (d) show the data from (a) and (b) after each threshold was normalized by dividing it by the appropriate 0–180 threshold. Dotted lines in all panels are the predictions of the two-channel phase-encoding model. ( $\blacksquare$ ) F = 1 c/deg; ( $\triangle$ ) F = 4 c/deg; ( $\bigcirc$ ) F = 8 c/deg; ( $\bigcirc$ ) F = 12 c/deg.

#### Methods

Stimuli and procedure. In most conditions, the stimuli and general procedure were identical to those used in expt I. Observers viewed the stimuli monocularly through natural pupils (4 mm dia.) except in two foveal conditions when the spatial frequencies of the fundamental were 8 and 16 c/deg and we used an artificial pupil (2 mm dia.). Control experiments showed that the reduction in retinal illuminance caused by the artificial pupil did not affect the results.

Discrimination thresholds were measured for vertical patterns in the fovea and at 10 and 20 deg along the nasal horizontal meridian. Eccentricity was the angle between the fixation point and the center of the stimulus. The spatial scale of the stimulus was manipulated by fixing the pattern of the display and changing viewing distance. Thus, stimulus size was inversely proportional to the spatial frequency of F. In the fovea, thresholds were measured with fundamentals ranging from 1 to 16 c/deg. Peripheral thresholds were measured with fundamental frequencies ranging from 0.125 to 1.5 c/deg. Fundamental contrast was 0.10, except for the 16 c/deg pattern which had a contrast of 0.20. The results of expt I show that foveal phase discrimination thresholds are essentially invariant over this contrast range.

We remeasured thresholds in one observer over a broader range of spatial scales using the stimuli from expt II. In these conditions, eccentricity was defined as the angle between the fixation point and the nearest edge of the pattern. The results obtained with these stimuli were quantitatively similar to those obtained with the other patterns, so both sets of results are presented here. The two sets of data are clearly differentiated in the figures: condition 1 refers to the Gaussian-damped stimuli (from expt I) and condition 2 refers to the square-masked stimuli (from expt II).

Observers. The observers were P.J.B. and M.S.B. from expt I.

### Results and discussion

One goal of the current experiment is to determine how sensitivity to spatial phase varies across the visual field. Direct comparisons of foveal and peripheral phase discrimination thresholds are complicated by the fact that peripheral thresholds vary slightly as a function of stimulus contrast. Comparisons of *relative* thresholds are less problematic because the

ratios of phase thresholds are invariant across contrast. Therefore, we have used the odd—even ratio as an index of the relative sensitivity to different phase shifts at different eccentricities.

Figure 8a illustrates foveal discrimination thresholds for observer P.J.B. Thresholds for observer M.S.B., shown in Fig. 8b, were collected with a slightly different stimulus configuration and were reported previously (Bennett & Banks, 1987). The dotted lines are the bestfitting vertical and horizontal lines. Not surprisingly, discrimination thresholds increased with increasing spatial frequency. Of primary interest, however, is the finding that relative thresholds-the odd-even ratios-were not changed substantially by varying pattern size. This is shown more clearly in the bottom panels of Fig. 8, where thresholds at each spatial scale have been normalized by dividing by the appropriate 0-180 threshold. The odd-even ratio for observer M.S.B. was invariant across spatial scale, while that for observer P.J.B. increased slightly (from 0.0 to 0.20 log units) over a 16-fold range of spatial frequency. We conclude that varying spatial scale had only a small effect on the relative discriminability of 0-180, 90–270, and other 180 deg phase shifts in the fovea.

Results from the peripheral conditions are shown in Figs 9–11. Unlike what was found in the foveal conditions, peripheral odd—even ratios varied with spatial scale. For observer P.J.B., for example, the ratio at 10 deg decreased from 0.57 to 0.01 log units as the spatial frequency of F was reduced from 1.5 to 0.25 c/deg (Figs 9 and 11). At 20 deg, the odd—even ratio decreased from 0.69 to 0.36 log

### 10 deg Nasal Visual Field

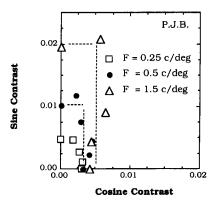


Fig. 9. Peripheral phase discrimination thresholds from one observer measured at 10 deg along the nasal horizontal meridian with three spatial frequencies. The contrast of the fundamental was always 0.1.

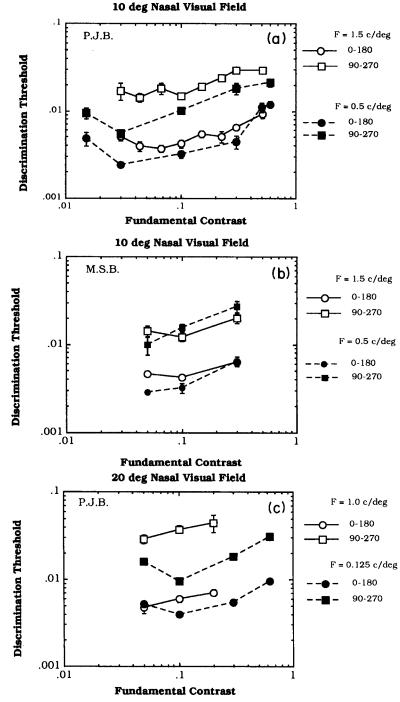
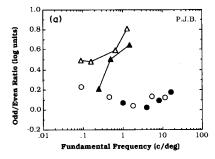


Fig. 10. Thresholds for 0–180 (circles) and 90–270 (squares) phase shifts at different stimulus contrasts. Panels (a) and (b) show thresholds from two observers measured at 10 deg in the periphery with the fundamental frequencies of 1.5 (open symbols) and 0.5 (solid symbols) c/deg. (c) Thresholds for one observer measured at 20 deg with frequencies of 1 (open symbols) and 0.125 (solid symbols) c/deg. The difference between 0–180 and 90–270 thresholds does not vary systematically with contrast. The error bars show  $\pm$  1 SEM.

units as spatial frequency was lowered from 1.0 to 0.125 c/deg (Fig. 10c). Peripheral thresholds were measured for a range of F contrasts to determine whether the effects of spatial scale

interacted with contrast. As was found in expt I, the ratio of thresholds in the 90–270 and 0–180 conditions was invariant over a 1 log unit range of contrast at both eccentricities (Fig. 10).



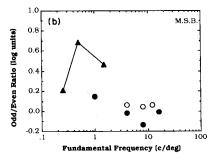


Fig. 11. (a, b) Odd-even ratios measured in the fovea (circles) and at 10 deg in the periphery (triangles) for two observers at a variety of spatial frequencies. Odd-even ratios are defined as ratio of 90-270 thresholds divided by 0-180 thresholds. Condition 1 (solid symbols) are thresholds measured with Gaussian-damped stimuli; condition 2 [open symbols in panel (a)] are thresholds measured with stimuli presented in a square-mask (see Stimulus section). Open symbols in (b) are the ratios of the thresholds presented in Fig. 8b. The average standard error (not shown) is 0.07 log

All of the patterns used in this experiment had equal bandwidths, so low spatial frequency targets were significantly larger than high frequency targets. For example, the diameter (at half-amplitude) of the 0.25 c/deg pattern was 8 deg but the diameter of the 1.5 c/deg pattern was only 1.3 deg. Thus, filters located on the halfamplitude locus of the larger pattern were only 6 deg from the fovea while those on the half-amplitude locus of the smaller pattern were 9.4 deg away. It is possible, therefore, that mechanisms closer to the fovea than the nominal eccentricity may have been used at low frequencies which let to the reduction in the odd-even ratio. We tested this possibility in a second set of experimental conditions. Thresholds for one observer (P.J.B.) were remeasured at the fovea and at 10 deg while maintaining a constant angle between the fixation point and the nearest edge (rather than the center) of the peripheral target. The patterns were presented in a square mask displaying 7 cycles of the fundamental (see Stimulus section).

The foveal odd-even ratios in this second set of conditions (open symbols in Fig. 11a) were quite similar to the foveal thresholds with the Gaussian-modulated patterns. The peripheral data differed in some ways from those obtained in the first set of conditions. Most importantly, the peripheral odd-even ratios at low frequencies were much higher than in the first set. This finding implies that the low odd-even ratios obtained in the first conditions (solid triangles in Fig. 11) were an artifact of our experimental procedure. Specifically, we propose that mechanisms closer than the nominal eccentricity contributed significantly to phase discrimination and therefore lowered the odd-even ratio to near foveal values.

In summary, our results are consistent with the report of Morrone et al. (1989) that there is a genuine improvement in peripheral phase sensitivity, indexed by the odd-even ratio, at very low spatial frequencies. Unlike Morrone et al., however, we find that peripheral phase sensitivity, again indexed by the odd-even ratio, is less than foveal sensitivity at all spatial frequencies.

The finding that foveal, but not peripheral, odd-even ratios are nearly constant across spatial scale implies that a single spatial scaling factor cannot eliminate differences in foveal and peripheral phase sensitivity. According to the scaling hypothesis, foveal and peripheral phase-encoding mechanisms differ only in size. If this hypothesis were correct, then it should be possible to superimpose the data presented in Fig. 11a, b simply by translating the curves along the log spatial frequency axis. Clearly, lateral shifting cannot superimpose the data, so the scaling hypothesis is disconfirmed for this task.

Although the scaling hypothesis fails to eliminate peripheral phase-encoding anomalies, it may be possible to do so by using a more complex scaling scheme. We have argued that even- and odd-symmetric filters are used to encode relative phase shifts. Suppose that the spatial scale of odd-symmetric filters increases more rapidly than that of even-symmetric filters: At least two scaling factors would be needed to equate phase sensitivity across the visual field. The following equations were used to test this idea:

$$T = a 1(1 + E/s 1)[(SF_{\text{scaled}})]^{p_1}$$

$$\{\text{when } SF_{\text{scaled}} < SF_{\text{min}}\}$$

$$T = a 2(1 + E/s 1)[(SF_{\text{scaled}})]^{p_2}$$

$$\{\text{when } SF_{\text{scaled}} \Rightarrow SF_{\text{min}}\}.$$
 (2)

In equation (2), T is threshold, E is eccentricity, and a1, a2, p1, p2,  $SF_{min}$ , and s1 are constants.  $SF_{\text{scaled}}$  is the fundamental spatial frequency multiplied by a scaling factor of the form 1 + (E/s2), where E is the stimulus eccentricity and s2 is a constant. When log thresholds are plotted as a function of log spatial frequency, parameters a1, a2, p1, p2 and  $SF_{min}$  define a v-shaped template that has been used successfully to fit foveal and peripheral position acuity data (Yap et al., 1989). Parameter s1 determines the vertical position of the template and therefore will be referred to as the *sensitivity* scaling factor. Parameter s2 determines the horizontal position and therefore will be referred to as the spatial scaling factor.

The values of the constants in equation (2) were estimated using nonlinear regression. The most complete set of data was obtained with observer P.J.B. in the fovea and at 10 deg in the periphery, so only those thresholds were used in the regression analysis. The estimated parameters in equation (2) for the 0–180 and 90–270 deg conditions are shown in Table 1.

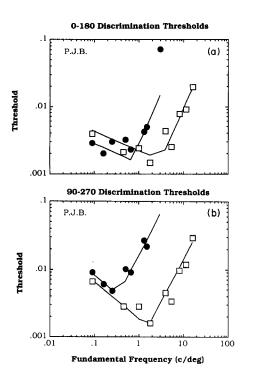


Fig. 12. Phase discrimination thresholds measured in the fovea ( $\square$ ) and periphery ( $\bullet$ ) of one observer. Thresholds for 0–180 phase shifts are shown in (a) and thresholds for 90–270 shifts in (b). The v-shaped templates are the functions estimated by non-linear regression (see text for details). Fundamental contrast was 0.1 at all spatial frequencies except 16 c/deg when it was 0.20. The average standard error of each threshold (not shown) was approx. 0.04 log units and did not vary systematically across conditions.

Table 1. Scaling parameters for v-shaped templates

Phase shift	90270	0-180
a1	0.002	0.002
<i>a</i> 2	0.0006	0.0003
s 1(deg)	5.51	>100
s2(deg)	2.47	2.88
p1	-0.49	-0.15
p2	1.32	1.5
SF <sub>min</sub>	2.3	3.25

and the data and best-fitting templates are shown in Fig. 12. The spatial scaling factor, s2, was similar for both conditions, but the sensitivity scaling factor, s1, differed markedly. In the 0-180 condition, the lowest threshold (i.e. peak sensitivity) was identical at 0 and 10 deg. In the 90-270 condition, however, the lowest threshold at 10 deg in the periphery was approx. 0.5 log units higher than in the fovea. The reader can gain an appreciation for these regression results by examining Fig. 12. The v-shaped templates in the 0-180 condition can be superimposed by shifting the peripheral curve horizontally by approx. 0.75 log units. The 90–270 templates are superimposed by shifting the peripheral curve horizontally by about 0.75 log units and downward by 0.5 log units. Thresholds for observer M.S.B. follow a qualitatively similar pattern: lateral shifting was sufficient to superimpose 0-180 thresholds, but lateral and vertical shifting was necessary for 90-270 thresholds.

The finding that the spatial scaling factors are similar in the 0-180 and 90-270 conditions is inconsistent with the idea that the spatial scale of odd-symmetric filters increases more rapidly in the periphery than that of even-symmetric filters. Thus, reduced sensitivity for peripheral 90-270 phase shifts is not due solely to changes in the spatial scale of phase-encoding mechanisms, and the increase in the odd-even ratio observed in the periphery cannot be eliminated simply by scaling stimulus size.

## EXPERIMENT IV. THE EFFECTS OF STIMULUS ORIENTATION ON PHASE DISCRIMINATION

Foveal contrast sensitivity and grating acuity are higher for vertical and horizontal gratings than for oblique gratings (Campbell, Kulikowski & Levinson, 1966; Mitchell, Freeman, & Westheimer, 1967). In the periphery, however, the oblique effect gives way to a meridional effect in which sensitivity and

acuity are higher for radially-oriented gratings (stripes parallel to the visual meridian) than for tangentially oriented gratings (Johnston, 1987; Rovamo, Virsu, Laurinen & Hyvarinen, 1982; Temme, Malcus & Noell, 1985). Position acuity (Yap, Levi & Klein, 1987b) and

curvature detection (Fahle, 1986) show similar radial-tangential differences in the periphery. None of these anisotropies are caused by optical differences (Rovamo et al., 1982; Yap et al., 1987b), so they must reflect meridional differences in the neural mechanisms underlying

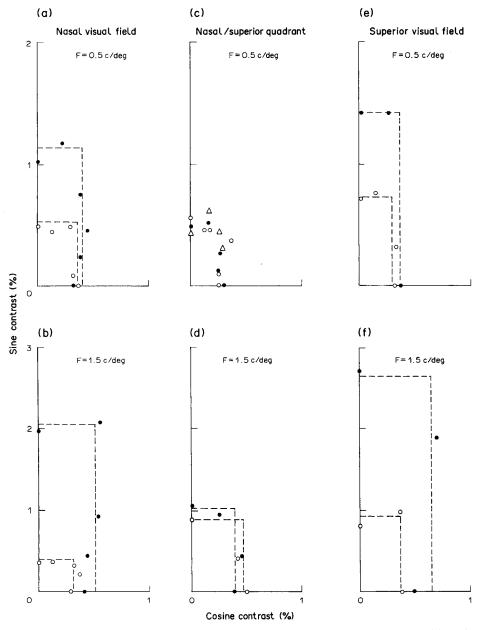


Fig. 13. Peripheral phase discriminations measured at 10 deg along three different meridians with gratings at different orientations. The panels in the top row (a, c, e) show thresholds measured with a fundamental frequency of 0.5 c/deg; panels in the bottom row (b, d, f) show thresholds measured with a fundamental of 1.5 c/deg. Contrast was always 0.1. Thresholds measured along the nasal (180 deg), oblique (135 deg), and superior (90 deg) half-meridians are shown in the left, middle, and right columns, respectively. Open circles show thresholds measured with radially-oriented patterns and solid circles show thresholds measured with tangentially-oriented patterns. The open triangles in (c) show thresholds measured with vertically-oriented patterns. Standard errors (not shown) were approx. 0.05 log units. The dotted lines in each panel represent the predictions of the two-channel phase-encoding model. Note that 90-270 thresholds are more orientation-dependent than 0-180 thresholds.

peripheral vision. Experiment IV examines whether similar anisotropies exist in peripheral phase perception.

### Methods

Stimuli, procedure and observers. The stimuli and procedure were identical to those used expt I. Stimulus orientation was varied by rotating the raster of the Joyce display.

The observers in expt I also participated in this experiment along with two new observers (S.A. and S.K.). All were emmetropes or corrected-to-normal myopes with normal visual fields.

### Results and discussion

Foveal phase discrimination thresholds were measured with vertical, horizontal, and oblique gratings. The spatial frequency of F was 8 c/deg and contrast was 0.10. The difference between 90–270 and 0–180 thresholds was approx. 0.2 log units for all orientations. Thus, stimulus orientation had no effect on foveal phase discrimination thresholds.

Figure 13 shows thresholds for one observer measured at 10 deg along the 90, 135 and 180 deg (i.e. the vertical-superior, left-oblique, and horizontal-nasal) meridians. Thresholds for sev-

eral 180 deg phase shifts were measured with tangentially- and radially-oriented gratings at each retinal locus. The spatial frequencies of F were 1.5 or 0.5 c/deg and contrast was 0.10. Thresholds at all locations and all orientations were consistent with the predictions of the twochannel model, but the odd-even ratio varied strikingly with the stimulus orientation and location. For tangential gratings, the ratios for patterns on the horizontal and vertical meridians were approx. 0.60 and 0.64 log units. For radial gratings, however, the ratios for patterns on the horizontal and vertical meridians were only 0.15 and 0.28 log units, values that are only slightly greater than those obtained with foveal targets. Thresholds measured on the oblique meridian were less dependent on orientation: the odd-even ratio was 0.4 log units for all orientations.

Odd-even ratios from three observers are shown in Fig. 14. Again, the ratios were generally higher for tangentially-oriented patterns, although there was considerable variability across observers and, within observers, across meridians. It it important to note that orientation-dependent changes in the odd-even ratio were caused by changes almost exclusively in the threshold for the 90-270 phase shift. To test the

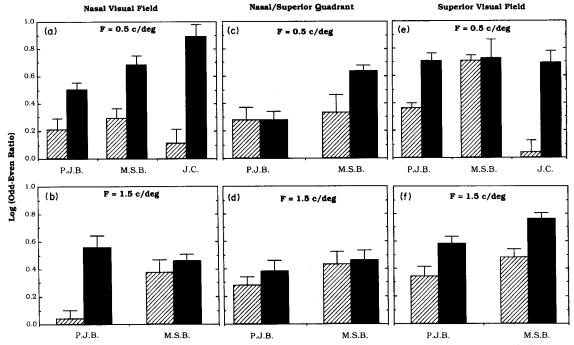


Fig. 14. Peripheral (10 deg) odd-even ratios measured for three observers with radially-oriented (hatched bars) and tangentially-oriented (solid bars) gratings. Panels (a), (c) and (e) show ratios measured with a fundamental of 0.5 c/deg. Ratios measured with a fundamental of 1.5 c/deg are shown in panels (b), (d) and (e). Fundamental contrast was 0.1. Ratios measured along the 180, 135 and 90 deg half-meridians are shown in the left, middle, and right columns, respectively. Error bars represent 1 SEM.

generality of this orientation-dependence of phase sensitivity, we measured sensitivity to 0-180 and 90-270 shifts in two additional observers. Figure 15 displays d-primes for 0-180 and 90-270 phase shifts at 10 deg along the nasal horizontal meridian. The spatial frequency of F was 0.5 c/deg and contrast was 0.10. Each observer received several hundred practice trials at each orientation for each phase shift. For both observers, rotating the patterns to a radial orientation raised sensitivity for 90-270 shifts more than for 0-180 shifts.

To determine if the orientation effects depended on contrast, 90–270 and 0–180 thresholds were measured for a range of contrasts using radial gratings at 10 and 20 deg in the periphery. As was found in expt I, odd–even ratios were virtually independent of F contrast.

Figures 13–15 reveal that the orientation effect varied across individuals. With a 1.5 c/deg fundamental, P.J.B.'s, but not M.S.B.'s, thresholds for 90–270 deg shifts varied considerably with orientation. Individual differences

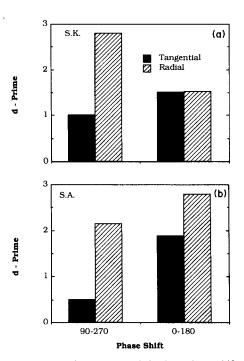


Fig. 15. d-Primes for 0-180 and 90-270 phase shifts at different orientations. Stimuli were presented at 10 deg along the nasal-horizontal meridian. Each d-prime is based upon 150 responses. The spatial frequency of the fundamental was 0.1. (a) d-Primes for observer S.K. The contrast of the 2F component was 0.05 in the 90-270 condition and 0.01 in the 0-180 condition. (b) Results from observer S.A. 2F contrast was 0.075 in the 90-270 condition and 0.01 in the 0-180 condition. Sensitivity for 90-270 shifts was more orientation-dependent than sensitivity for 0-180 shifts for both observers.

were less noticeable with 0.5 c/deg patterns: 90-270 deg thresholds for all observers varied significantly with stimulus orientation. The orientation effect also varied across visual meridians: the effect on 90-270 deg thresholds was larger for patterns on the horizontal and vertical meridians than on the oblique meridian. This amount of individual variability is consistent with previous reports of radial-tangential differences in spatial vision tasks. Rovamo et al. (1982), for instance, found that radial-tangential differences in grating acuity at 25 deg in the periphery ranged from 0.45 log units (on the horizontal meridian) to only 0.15 log units (on the left-oblique meridian; see their Fig. 2). Fahle (1986) reported similar meridional effects on curvature detection thresholds. Finally, Yap et al. (1987b) found radial-tangential differences in three-dot bisection tasks and these differences varied significantly across individuals: thresholds for the two orientations differed by 0.6 log units in one observer, but only a factor of 0.25 log units in the other.

The meridional differences in phase discrimination cannot be accounted for by meridional differences in the contrast sensitivity for F and 2F. Experiment I showed that changing the visibility of F raises thresholds for all phase shifts by identical amounts and therefore does not affect the odd-even ratio. The same would be true for differences in the visibility of 2F. Consequently, meridional differences in contrast sensitivity cannot explain why 90-270, but not 0-180, thresholds varied significantly with orientation. These findings also cannot be explained by assuming that the fixation point served as a spatial referent for radial, but not tangential, gratings (Morrone et al., 1989) because we found that the degree of orientationdependence varies across visual meridians. Also, the position of a feature relative to the fixation point provided no information for any of the phase shifts in this study because the gratings were randomly displaced between each interval on every trial. Finally, the orientation-dependent changes in phase sensitivity reported here cannot be due to orientation-dependent learning effects (Fiorentini & Berardi, 1981); observers P.J.B. and J.C. received thousands of trials of practice with patterns oriented tangentially along the horizontal meridian prior to viewing radial patterns. Nevertheless, both observers were significantly more sensitive to 90–270 shifts when tested with radial patterns for the first time.

Although previous demonstrations of radialtangential differences have a neural, rather than optical, basis, it is important to examine the possible effects of peripheral optics in our tasks. Oblique incidence causes astigmatism in the periphery (Ferree, Rand & Hardy, 1931; Millodot & Lamont, 1974; Rempt, Hoogerheide & Hoogenboom, 1971). This astigmatism causes tangential gratings to be more myopically focused than radial gratings in most eyes. To quantify such observations, Ferree et al. (1931) measured peripheral refractive errors in 12 emmetropic eyes. The average amplitudes of astigmatism were 0.5 (range = 0-1.25) and 1.0 (range = 0-2.0) D at eccentricities of 10 and 20 deg, respectively. We measured refractive errors at 10 and 20 deg in the nasal visual field in two of our observers using a method similar to that described by Rempt et al. (1971). Both observers exhibited astigmatism in amounts similar to those reported by Ferree et al. We used equations from Green, Powers and Banks (1980) to compute the largest change in retinal image contrast produced by this astigmatism: it was 0.13 log units for the spatial frequencies used in our experiment. Experiment I showed that varying F contrast by this amount does not affect the odd-even threshold ratio. We conclude, therefore, that the blur produced by peripheral astigmatism cannot explain the orientation-dependence of peripheral phase discrimination.

A second consequence of oblique incidence is lateral chromatic aberration, which increases in magnitude with increasing retinal eccentricity (Howarth, 1984; Thibos, 1987). Such aberrations cause the retinal images of monochromatic gratings to be displaced by an amount that is proportional to their wavelength, thus reducing the image contrast of spectrally broad-band gratings. This effect is quite small, though, at the spatial frequencies and eccentricities we tested, and therefore is unlikely to influence our results. For example, the highest spatial frequencies we used at eccentricities of 10 and 20 deg were 3 and 2 c/deg, respectively. The contrast loss due to lateral chromatic aberrations for these patterns (when tangentially-oriented) is less than 0.01 log units (Thibos, 1987).

The fact that the orientation dependence of the odd-even ratio is not significantly affected by optics implicates neural processes. Anatomical and physiological studies have found radialtangential differences in several parts of the visual pathway (Hubel & Freeman, 1977;

Leventhal, 1983; Leventhal, Schall & Wallace, 1984; Levick & Thibos, 1980; Schall, Vitek & Leventhal, 1986; Van Essen, Newsome & Maunsell, 1984). Psychophysical studies also provide indirect evidence that the linear density of sampling units is slightly higher along iso-eccentric contours than along iso-meridian contours: Coletta and Williams (1987) showed that orientation reversal, a psychophysical technique for estimating spacing in irregular sampling mosaics, occurs at a spatial frequency that is about 7-8% higher for radial than for tangential gratings at an eccentricity of 3.8 deg. This anisotropy, however, is much too small to account for our results: if receptor anisotropies caused the radial/tangential differences we observed, one should be able to eliminate them by changing the relative sizes of the radial and tangential stimuli by about 8%. We found instead that radial-tangential differences in odd-even ratios persisted even when tangential targets were three times the size of the radial targets. We conclude that differences in receptor density alone cannot explain our observations. Presumably, the radial/tangential differences are manifestations of more substantial anisotropies at subsequent visual processing stages.

### **GENERAL DISCUSSION**

Evaluation of the position-restriction assumption

The two-channel model outlined by Field and Nachmias (1984) and Bennett and Banks (1987) asserts that 180 deg phase shifts are encoded by two, and only two, channels; one channel consists of even-symmetric receptive fields and the other of odd-symmetric fields. A critical assumption in the model is that only the responses of mechanisms centered on the peaks, troughs, and zero-crossings of the fundamental are used to discriminate phase shifts. A model of feature detection and discrimination outlined by Morrone and Burr (1988) also utilizes the responses of even- and odd-symmetric mechanisms located only at particular points in the image. Most quantitative models (e.g. Klein & Levi, 1985; Nielsen, Watson & Ahumada, 1985; Watson, 1983; Wilson, 1986; Wilson & Gelb, 1984) assume that stimuli are discriminated whenever the differential response of any mechanism, regardless of its position, exceeds some criterion. In contrast, the Field and Nachmias, Bennett and Banks, and Morrone and Burr models do not assume that the information

(4)

contained in a pattern of differential responses is used efficiently. Here we examine whether models that use such information efficiency could account for our observations.

We start with a linear mechanism with a receptive field of arbitrary shape [RF(x)]. We also assume that these mechanisms sample stimuli densely. The responses of these mechanisms to two compound waveforms [i.e. S1(x) and S2(x)] differing by a relative phase shift of 180 deg are proportional to the cross-correlation of the waveforms and the receptive fields (equations 3 and 4):

$$S1(x)*RF(x) = [a1\cos(2\pi Fx) + a2\cos(2\pi 2Fx - \theta)]*RF(x)$$

$$= k1 a1\cos(2\pi Fx + p1) + k2 a2\cos(2\pi 2Fx - \theta + p2)$$

$$(3)$$

$$S2(x)*RF(x) = [a1\cos(2\pi Fx) - a2\cos(2\pi 2Fx - \theta)]*RF(x)$$

$$= k1 a1\cos(2\pi Fx + p1) - k2 a2\cos(2\pi 2Fx - \theta + p2)$$

where F is the spatial frequency of the fundamental,  $\theta$  is the base phase of 2F, a1 and a2 are the amplitudes of F and 2F, k1, k2, p1 and p2 are constants, and \* signifies cross-correlation. The differential response is:

$$\{S1(x) * RF(x)\} - \{S2(x) * RF(x)\}$$
  
=  $2k2 \cos(2\pi 2Fx - \theta + p2)$ . (5)

The differential response is identical (except for a spatial phase shift) for all phases of 2F. This result is unaffected by the form of the receptive field [RF(x)] as long as it responds to F and 2F. Thus, if phase discrimination occurs whenever the largest response difference exceeds some criterion, then thresholds for all phase shifts should be identical. Stated another way, the data in Figs 2, 6 and 7 should fall on quarter circles. The foveal data from observer B.A. in Fig. 6, as well as foveal thresholds reported by Field and Nachmias (1984) and Bennett and Banks (1987), are reasonably consistent with this prediction. However, foveal thresholds for some normal observers (A.B.S. in Fig. 6) and anisometropic amblyopes (Bennett, 1989), as well as peripheral thresholds are clearly inconsistent with this prediction. We conclude,

therefore, that models based on the efficient use of linear spatial filters (that is, use of information available at all points in the waveform) cannot explain the large differences we observe between peripheral 0–180 and 90–270 thresholds.

This conclusion does not depend on the sampling density of the underlying spatial filters. To show this we consider phase-encoding mechanisms positioned in a sampling lattice. Equation 6 describes the differential response of the mechanisms:

$$\{S1(x) * RF(x)\} \operatorname{samp}(\sigma, \phi)$$

$$-\{S2(x) * RF(x)\} \operatorname{samp}(\sigma, \phi)$$

$$= 2k2 \ a2 \cos(2\pi 2fx - \theta + p2) \operatorname{samp}(\sigma, \phi).$$
(6)

The sampling lattice is represented by samp  $(\sigma, \phi)$ , where  $\sigma$  is the sampling interval and  $\phi$ is the phase of the lattice relative to the stimulus. The magnitude of the differential response to the two stimuli depends only on the points sampled. For a fixed sampling interval,  $\sigma$ , the differential responses are simply sampled points of a cosinusoid with amplitude and phase shifts. If  $\phi$  varies randomly from trial to trial with respect to the pattern, then the maximum differential response will vary too. Notice, however, that changing base phase,  $\theta$ , will not influence the statistics of the maximum response; increasing  $\sigma$  only increases the variability of those responses regardless of  $\theta$ . Therefore, if sampling density is the sole limit on performance in the periphery, thresholds for 180 deg shifts will increase by identical amounts regardless of base phase.

We showed in expt I that the diminished sensitivity of the periphery to 90-270 shifts cannot be explained by use of distortion products caused by nonlinearities. Equation 5 in this section demonstrates that this phenomenon cannot be explained by models that use maximum differential responses among linear filters that sample the waveform densely. Equation 6 shows that increasing the sampling interval among linear filters in these models also cannot explain why 90–270 thresholds rise in the periphery. Instead it seem necessary to posit restrictions on the information the visual system uses in phase discrimination tasks. The two-channel phaseencoding model (Bennett & Banks, 1987; Field & Nachmias, 1984) and the energy-detection model (Morrone & Burr, 1988) restrict the

information by limiting computations to particular locations in the waveform.

The original proponents of the two-channel model used low-contrast stimuli in their

which can be used to evaluate the effects of uncertainty on real performance in any spatial discrimination task. Under conditions of position uncertainty, the ideal discriminator uses the following decision variable:

$$L = \frac{C \iint \exp\{\Sigma Z(xi, yi) \ln [\beta (xi - x, yi - y)]\} f(x, y) dx dy}{\iint \exp\{\Sigma Z(xi, yi) \ln [\alpha (xi - x, yi - y)]\} f(x, y) dx dy}$$
(7)

experiments (Field & Nachmias, 1984) in the hope of forcing the visual system to the limit the computations of even- and odd-symmetric mechanisms to the peak, troughs, and zero-crossings of the fundamental where their responses exceeded threshold. We have shown, however, that the high odd-even ratio in the periphery is observed at high contrasts where the responses of even- and odd-symmetric mechanisms positioned throughout the waveform should exceed threshold. Consequently, position restriction of computations relative to the waveform may be inherent to the processing involved in phase discrimination.

### The effects of position uncertainty

Visual patterns are encoded by arrays of topographically-organized receptive fields at several stages in the visual pathway. We have assumed that phase discrimination is based on changes in the responses of such receptive fields. Specifically, we have argued that the responses of only even- and odd-symmetric receptive fields are used to discriminate 180 deg relative phase shifts. In order to account for the difference 90-270 and 0 - 180peripheral between thresholds, we have suggested that the sensitivity of odd-symmetric receptive fields declines more rapidly than that of even-symmetric fields with increasing eccentricity. However, it is possible that other factors—position uncertainty, or an increase in the spatial disorder, or scrambling, of the peripheral sampling mosiac—contribute to decreased sensitivity to 90-270 shifts. In this section, we examine the effects of position uncertainty on phase discrimination. The effects of spatial scrambling are considered in the following section.

Geisler and Davila (1985) derived an ideal discriminator whose performance in visual discrimination tasks is limited only by optics, the sampling characteristics of the receptor lattice, and stimulus uncertainty. The performance of such an ideal discriminator provides a baseline

where L is the likelihood ratio, C is a constant, Z is the number of quanta absorbed by the ith receptor, f(x, y) is the probability of the stimulus being at location (x, y), and  $\alpha(x_i, y_i)$  and  $\beta(x_i, y_i)$  are the luminance distributions of the two stimulus alternatives. The ideal discriminator computes the cross-correlation between the stimulus (Z) and the logarithm of a receptive field  $(\alpha \text{ or } \beta)$ , passes the result through an accelerating nonlinearity, and then sums the resulting values across the region of uncertainty. Provided that stimulus position uncertainty is equal in all conditions, ideal sensitivity to a 180 deg shift is independent of the base phase of 2F. Thus, position uncertainty alone cannot explain the difference between peripheral 0-180 and 90–270 thresholds if the visual system efficiently utilizes the information contained in the photoreceptors.

Of course, real observers are not ideal observers, and it is important to consider whether stimulus uncertainty differentially affects 90-270 and 0-180 thresholds when nonoptimal processes are used. For optimal phase discrimination, stimuli must be filtered with receptive fields that have the same shape as the natural logarithm of the expected pattern [i.e.  $\alpha$  and  $\beta$ in equation (7)]. A more plausible model of real performance would restrict receptive field shape to a relatively small set of (possibly nonoptimal) shapes that are observed electrophysiologically. Such a model must also include the possibility that real observers combine information across different receptive fields in a nonoptimal manner. How would such deviations from ideal behavior affect phase discrimination thresholds? There are a variety of receptive fields shapes that could conceivably be used to discriminate phase shifts, but the precise shapes are unimportant so long as the deviation from the optimally-shaped filter is the same in the 0-180 and 90-270 conditions. For simplicity, we will consider the case where the visual system contains linear even- and odd-symmetric receptive fields. We will assume that observers discriminate 0-180

and 90-270 phase shifts on the basis of some combination of responses in an array of evenand odd-symmetric receptive fields, respectively, and that the size of the array spans the range of position uncertainty. We will also assume that even- and odd-symmetric fields have the same sensitivities to F and 2F. With these assumptions, the responses of odd-symmetric receptive fields to compound gratings in sine phase are identical (except for an absolute phase shift) to the responses of even-symmetric fields to gratings in cosine phase. Thus, if position uncertainty is equal in the 0-180 and 90-270 conditions and observers use the same rule for combining the responses of different receptive fields then discrimination thresholds for 0-180 and 90-270 shifts will be identical.

To account for differences between 0–180 and 90–270 thresholds, it is necessary to assume that: (a) the responses of odd-symmetric receptive fields are combined less efficiently and/or; (b) odd-symmetric fields are less numerous and/or less sensitive. We conclude that increased position uncertainty in the periphery alone cannot account for the difference between 0–180 and 90–270 thresholds.

### The effects of spatial scrambling

Although images are encoded by topographically-organized sampling arrays, anatomical and physiological (e.g. Hubel & Wiesel, 1974; Van Essen et al., 1984) and psychophysical (e.g. Hess & Watt, 1990) evidence suggests that disorder in the spatial structure of these arrays increases in the periphery. That is to say, regularity of receptive field positioning decreases in the periphery thereby decreasing the amount of spatial information contained in the sampling array (unless the receptive field positions are known). Spatial scrambling differs from stimulus position uncertainty: in the former case, the position of each sample is uncertain, but in the latter case, the position of the stimulus on the receptor array is uncertain. In this section, we consider whether spatial scrambling in the peripheral sampling mosaic can account for differences between 0-180 and 90-270 discrimination thresholds.

The effects of scrambling are model-dependent, so it is necessary to make some assumptions about the processes that discriminate phase shifts. We assume that visual stimuli are sampled by an array of linear receptive fields. Spatial scrambling (complete position uncertainty) is incorporated into the analysis by

assuming that the visual system accurately records the response of each receptive field, but that the location of each field is unknown. If the sampling array consists solely of even-symmetric receptive fields, then spatial scrambling renders 90-270 but not 0-180 shifts indiscriminable. The reverse occurs if the sampling array contains only odd-symmetric receptive fields. To see why this is so, consider first the case where all of the receptive fields are even-symmetric. 0-180, but not 90-270, phase shifts alter the first-order statistics of F + 2F gratings (see Fig. 1). After the stimuli are filtered with even-symmetric receptive fields, the maximum response in the sampling array will be greater for 0 deg patterns than for 180 deg patterns and therefore can be used as a discrimination cue. This cue is not available in the 90-270 condition, however, because the maximum responses of the evensymmetric sampling array to stimuli in 90 and 270 deg phase are identical. In order to discriminate 90-270 shifts it is necessary therefore to analyze the spatial distribution of responses in the sampling array. But if the spatial locations of individual receptive fields are not known due to scrambling, 90-270 shifts could not be discriminated. When all receptive fields are oddsymmetric, 90-270 but not 0-180 shifts are discriminable in the face of spatial scrambling because 90-270 shifts create changes in the first-order statistics of the filter outputs. If observers are able to attend selectively to the responses of even-symmetric receptive fields to discriminate 0-180 shifts and odd-symmetric fields to discriminate 90-270 shifts, and both kinds of receptive fields are equally sensitive. then complete spatial scrambling of the sampling arrays will not differentially affect thresholds in the two conditions. The same conclusion holds for different amounts of spatial scrambling. It seems necessary, therefore, to posit less sensitive odd-symmetric mechanisms, or to assume that their responses are used less efficiently, in order to account for the differential increase in 90-270 and 0-180 thresholds in the periphery.

Our review of the effects of position uncertainty and spatial scrambling assumes that patterns are encoded by linear filters. This assumption is undoubtedly too strong, and one might argue that differences between 0–180 and 90–270 thresholds are caused by nonlinearities in the responses of phase-encoding filters. Recall, however, that the results of expt I suggest that nonlinearities affect 0–180 and

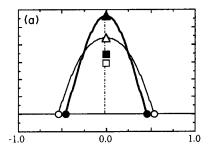
90–270 thresholds similarly. It is possible to show that incorporating nonlinear filters into our analyses of spatial uncertainty and scrambling would not alter the conclusions provided that the nonlinearities were identical.

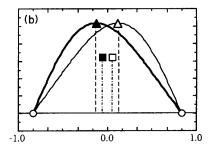
Our analyses suggest that position uncertainty and spatial scrambling cannot account for differences between peripheral 90-270 and 0-180 thresholds and contradict the argument of Morrone et al. (1989) that both factors should raise 90-270 thresholds more than 0-180 thresholds. Their argument rests on the assumption that it is necessary to localize pattern features in order to discriminate 90-270, but not other, phase shifts. Having assumed this, Morrone et al. argue that 90-270 thresholds are higher in the periphery because feature localization is degraded in the periphery. The assumption of qualitatively different strategies for different phase shifts is not well-founded. There is no reason to assume, a priori, that different strategies must be used to discriminate 0-180 and 90-270 shifts. Both phase shifts could be discriminated by simply measuring changes in the responses of an array of arbitrarilyshaped linear receptive fields. Moreover, our results do not provide evidence that qualitatively different processes are used to discriminate different shifts. The discrimination threshold increases more with eccentricity for the 90-270 condition, but the shapes of the psychometric functions in the 0-180 and 90-270 conditions are identical and both thresholds are affected similarly by changes in spatial contrast. Also,

the spatial scaling factor derived from comparisons of foveal and peripheral thresholds are similar for 0–180 and 90–270 shifts. Finally, all of the observers report using feature-localization cues in all of the discrimination conditions (see below). Thus, we see no need to invoke qualitatively different processes to explain our findings.

### Phase discrimination and feature localization

Badcock (1984a, b) has proposed that phase discrimination may be based on local analyses of contrast and the spatial arrangement of pattern features and that analyses of different stimulus properties can be used to discriminate different phase shifts. For example, changes in the arrangement of features might be the most salient aspect of 90-270 phase shifts, but local contrast or brightness cues are perhaps most important for discriminating 0-180 phase shifts. It is of interest, therefore, that our observers reported using featurelocalization cues to discriminate all 180 deg phase shifts. These position cues are illustrated in Fig. 16. Observers discriminating 0–180 shifts reported attending to changes in the widths of the individual bars in the grating (see Note 1). In the 90-270 condition, they said they attended to the location of luminance maxima (or minima) and determined whether the brightest (or darkest) part of an individual bar was to the right or left of the bar's center. According to the subjective impressions of the observers, then, the 0-180 condition is a type of width-

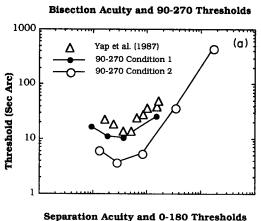




Position (arbitrary units)

Fig. 16. The spatial cues reportedly used to discriminate 0–180 and 90–270 phase shifts. The smooth curves in (a) and (b) are luminance profiles of a single bar of F + 2F compound gratings (i.e.  $\frac{1}{2}$ -cycle of F). For purposes of illustration, the profiles were drawn with the amplitude of 2F set to 12% of the amplitude of F (i.e. a value that is much higher than actual discrimination thresholds). Positions of zero-crossings  $(\bigcirc, \bullet)$ , centroids  $(\blacksquare)$ , and luminance maxima  $(\triangle)$  are shown. (a) Changes in feature positions caused by a 0–180 phase shift. The luminance profiles show a single bar when 2F is added in 0 deg (thick line) and 180 deg (thin line) phase. The lateral positions caused by a 90–270 phase shift. The luminance profiles show a single bar when 2F is added in 270 deg (thick line) and 90 deg (thin line) phase. The positions of luminance maxima and centroids, but not zero-crossings, are altered (see Note 1).

discrimination task and the 90-270 condition is a type of bisection task. We wondered whether phase thresholds were comparable to width discrimination and bisection thresholds measured with other stimuli. In order to compare our data to other measurements of position acuity, we assumed that observers discriminated phase shifts by noting changes in the relative locations of three features in each half-cycle of the compound gratings: zero-crossings, luminance maxima (or minima), and luminance centroids (see Fig. 16). In the 0-180 condition, we assumed that observers based discrimination on a change in the separation between the



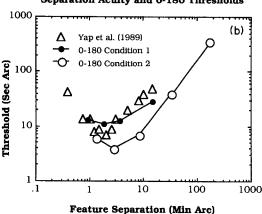
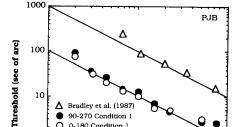


Fig. 17. Comparison of phase discrimination thresholds and position acuities. Condition 1 ( ) are thresholds measured Gaussian-damped stimuli; condition 2 (O) are thresholds measured with stimuli presented in a square mask (see Stimulus section, expt II). All thresholds are for observer P.J.B. (a) Foveal 90-270 thresholds and bisection (threedot) acuities measured with dots (△; Yap et al., 1987). For phase discrimination, feature separation refers to half the width of a single bar. For three-dot stimuli, feature separation is half the distance between the outermost dots. (b) Foveal 0-180 thresholds and separation acuities measured with small lines ( $\triangle$ ; Yap et al., 1989). Feature separation for two-line stimuli was defined as half the distance between the lines.



90-270 Condition 1

0-180 Condition 1

.oi

Comparison of Phase and Vernier Thresholds

Fig. 18. Comparison of the effects of contrast on phase discrimination and vernier acuity. Foveal thresholds for 0-180 and 90-270 phase shifts are shown by the open and solid circles, respectively. Vernier acuities (Bradley et al., 1987) are shown by the open triangles. Phase discrimination thresholds were measured with a fundamental frequency of 8 c/deg. Vernier acuities—the just-detectable offset in a sinewave grating—were measured with a spatial frequency fixed of 10 c/deg. The solid lines have a slope of -1.0.

.1 Contrast

centroid and zero-crossing. In the 90-270 condition, we assumed that discrimination was based on a change in the position of the centroid (i.e. to the left or right) relative to the center of each bar.

Feature displacements produced by 0-180 and 90-270 shifts at discrimination threshold are shown in Fig. 17. (Displacements of luminance maxima are similar to the displacement of the centroids. For clarity, only the latter are shown in Fig. 17a.) For phase discrimination tasks, feature separation was defined as onehalf of the distance separating adjacent zerocrossings in the fundamental (i.e. one-quarter of the spatial period). Also shown are twodot separation (Yat et al., 1989) and three-dot bisection (Yap et al., 1987a) acuities measured with dots and short lines, respectively. Obviously, one would not expect the thresholds to be the same because of the substantial differences between the stimuli used in the different experiments. Nonetheless, the thresholds are quite similar, particularly in terms of the variation of threshold with feature separation. Figure 18 shows how vernier acuity [measured with displaced sinewave gratings by Bradley and Skottun (1987)], 0-180, and 90-270 thresholds varied with contrast when the inter-feature separation was held constant. Although the vernier thresholds are higher than phase discrimination thresholds, all thresholds decreased by similar amounts with increasing stimulus contrast.

The similarity among the thresholds in the different tasks raises the possibility that common mechanisms underlie the discrimination of relative phase shifts and some hyperacuity targets. In particular, it is tempting to speculate that odd-symmetric and even-symmetric filters are used to make bisection and separation judgements, respectively. Such a linkage of these two kinds of thresholds leads to the prediction that three-dot bisection acuity measured in the periphery will be substantially more orientationdependent than two-dot separation acuity. Indeed, Yap et al. (1987b) report that peripheral bisection acuities in the radial and tangential directions differ significantly, but to our knowledge there is no published data comparing the orientation-dependence of bisection and separation acuities in a single observer. The "common mechanisms" hypothesis also predicts that peripheral bisection acuities will be elevated relative to separation acuities. Again, there is data consistent with this prediction: peripheral separation acuity, but not bisection acuity, constitutes a genuine hyperacuity because the former, but not the latter, is less than the resolution limit (Yap et al., 1987a, 1989; Westheimer, 1982). However, some evidence is inconsistent with the claim for common mechanisms. For instance, hyperacuity and phase discrimination tasks appear to require different scaling strategies to equate foveal and peripheral thresholds. Two scaling factors are needed to equate foveal and peripheral two-dot separation acuity (Westheimer, 1982; Yap et al., 1989), but only one factor is needed to equate three-dot bisection acuity (Yap et al., 1989). The reverse seems to be true of phase discrimination: two factors are needed for the 90-270 (i.e. "bisection") task and only one for the 0-180 (i.e. "separation") task. Also, it is not clear why bisection judgements should be mediated by odd-symmetric filters and separation judgements by even-symmetric filters. Despite such difficulties, the hypothesis that the even- and odd-symmetric mechanisms used to discriminate relative phase shifts (Bennett & Banks, 1987; Field & Nachmias, 1984) also are utilized in hyperacuity tasks deserves further study.

### Relationship to edge and bar discrimination

Morrone and Burr's (1988) feature-encoding model is somewhat similar to the model described here (see also Burr, Morrone, & Spinelli, 1989; Morrone et al., 1989; Morrone & Owens, 1987). Like the two-channel model, Morrone

and Burr's model has only even- and odd-symmetric mechanisms. Unlike the two-channel model, the even and odd mechanisms sample the entire waveform and then the responses of both mechanisms are combined to compute an energy function (see Note 2). The peaks in this energy function generally correspond to the locations of bars and edges in an image. At these points, the Morrone and Burr model uses the relative activities of even- and odd-symmetric mechanisms to identify features as either bars or edges. For example, if the even-symmetric response is high and the odd-symmetric response is zero, the feature is identified as a bar. The relative activity of positive and negative evensymmetric mechanisms is then used to discriminate bright and dark bars. The Morrone and Burr model places no restrictions on the locations of the maximum in the energy function but, for F + 2F gratings, the maxima occur at the peaks, troughs, and zero-crossings of F. When 2F is in 0 deg phase, for instance, the peaks of the energy function occur precisely at the peaks of F. When 2F is in 90 or 270 deg phase, on the other hand, the peaks are located precisely at the zero-crossings of F. Not surprisingly, the Morrone and Burr and two-channel model make similar predictions when applied to the grating stimuli used in the current study.

We have argued that the sensitivity of oddsymmetric mechanisms declines with increasing eccentricity. This has an interesting implication for the Morrone and Burr model. If edges are identified on the basis of the differential outputs of odd-symmetric filters, then they should be increasingly difficult to detect and/or identify in the peripheral visual field. Morrone et al. (1989) measured detection and discrimination thresholds for broad-band patterns consisting of light or dark bars (even-symmetric task) or left or right edges (odd-symmetric task). Contrary to our prediction, Morrone et al. found that bar and edge polarity was easily discriminated even in the periphery. They took this as evidence that even- and odd-symmetric mechanisms are roughly equally sensitive throughout the visual field.

We set up the Morrone et al. conditions in our laboratory and tested one observer (P.J.B.): edge and bar polarities were easily discriminated in the fovea and at 10 deg in the periphery, replicating their results. The similarity of edge and bar discriminability is clearly inconsistent with our interpretation of peripheral phase-encoding deficits. That is to say, the two-

channel model (or the local energy model) coupled with an assumption of lower sensitivity among odd-symmetric mechanisms in the periphery cannot predict this result. Of course our results are equally inconsistent with the assertion of Morrone et al. (1989) that peripheral even- and odd-symmetric mechanisms have similar sensitivities.

It is unclear at this point why these seemingly similar phase discrimination tasks behave so differently in the periphery. One possible explanation is that peripheral odd-symmetric and even-symmetric mechanisms have different spatial bandwidths. Our results suggest that odd-symmetric mechanisms are less sensitive to F and 2F compound gratings. However, if oddsymmetric mechanisms signal phase shifts across a broader range of spatial frequencies than do even-symmetric mechanisms, then the difference between thresholds for 90-270 and 0-180 shifts should decrease as the spatial bandwidth of the stimulus increases. This hypothesis predicts that odd-even ratios measured with broad-band stimuli, such as those used by Morrone et al., should be less than those measured with F and 2F gratings.

Morrone et al. (1989) suggested a second possible explanation based on lateral masking [i.e. the reduced detectability or discriminability of a feature caused by the presence of other nearby features (Andriessen & Bouma, 1976; Loomis, 1978]. One way of characterizing repetitive patterns, such as the gratings used in the current experiments and those used by Morrone et al., is as a set of several adjacent features (e.g. bars or edges). Morrone et al. suggested that peripheral phase-encoding deficits measured with compound gratings might be due to lateral masking effects on local feature analyses used to discriminate phase shifts (Badcock, 1984a, b). Lateral masking would have less of an effect on discrimination thresholds measured with the Morrone et al. stimuli because, unlike the compound gratings used in the current experiments, even high-frequency features are well-separated. In order to account for differences between peripheral 90-270 and 0-180 thresholds measured with compound gratings, lateral masking effects are presumed to be greater in the 90-270 condition. In expt III we found that differences between peripheral 90-270 and 0-180 thresholds persist over a wide range of spatial frequencies, so it is also necessary to assume that the spatial extent of lateral masking is inversely proportional to the spatial frequency of the targets.

One might be tempted to conclude that the peripheral discrimination deficits reported in this paper are restricted to repetitive, spatially-complex waveforms. Bennett and Banks (1988) have shown, however, that qualitatively similar effects are obtained with some aperiodic bar stimuli. Clearly, further work is needed to clarify the stimulus conditions that produce peripheral phase-encoding anomalies and to determine the extent to which the predictions of the two-channel model generalize to aperiodic waveforms.

### Relationship to texture discrimination

Many textures with identical second-order statistics (and, therefore, equal amplitude but different phase spectra) can be discriminated with scrutiny but are indistinguishable preattentively. Textures that can be discriminated pre-attentively and have identical second-order statistics differ in the density of particular local features, or textons (Caelli & Julesz, 1978; Caelli, Julesz & Gilbert, 1978; Julesz, Gilbert, Shepp & Frisch, 1973; Julesz, Gilbert & Victor, 1978). These observations suggest that preattentive mechanisms cannot in most cases encode phase information reliably.

Peripheral phase discrimination is, in some respects, similar to pre-attentive texture discrimination (Rentschler, Hubner & Caelli, 1988). For instance, relative phase shifts that produce mirror image compound gratings (and therefore, preserve second-order statistics) are difficult to discriminate in the periphery. Phase shifts that produce non mirror-image patterns, and that have different first- and second-order statistics, are easily discriminated peripherally. One can speculate, therefore, that pre-attentive texture discrimination failures and peripheral phase discrimination anomalies are manifestations of similar weaknesses in processing. This speculation was, however, not well-founded until recently. One reason is that previous phase discrimination studies, which manipulated relative phase in F and 3F compound gratings, confounded changes in first-order statistics with changes in grating contrast. The current experiments and those of Bennett and Banks (1987), which used F and 2F compound gratings, show unambiguously that phase shifts producing differences in first-order statistics alone are easily discriminated in the periphery. A second reason is that nearly all texture discrimination studies used black-and-white patterns whereas phase discrimination studies used gray-scale

images. Klein and Tyler (1985) provided a theoretical link between black-and-white textures and gray-scale images. They demonstrated that the third-order, zero-shift autocorrelation function (Z3) of F and 2F gratings, a measure that corresponds to the first-order statistics of a black-and-white texture, depends on the phase of 2F according to the equation:

$$Z3 = (1/8)a 1 a 2 \cos(\theta)$$

+ terms independent of  $\theta$  (8)

where a1 and a2 are the amplitudes of F and 2F, and  $\theta$  is the phase of 2F. A 0-180 deg phase shift changes Z3 (or first-order statistics), but a 90-270 deg shift does not. Klein and Tyler hypothesized that 180 deg phase shifts are discriminated by mechanisms sensitive only to changes in Z3. If so, then thresholds should fall along an equal-cosine contour when plotted as in Figs 6 and 7. The thresholds that are determined by the even-symmetric mechanisms in the two-channel model are consistent with this prediction. One can think of the even-symmetric mechanisms, therefore, as encoding changes in Z3. Thresholds determined by the responses of odd-symmetric mechanisms are, however. clearly inconsistent with the Klein and Tyler hypothesis: because 90-270 phase shifts do not alter Z3, observers should be completely unable to make such a discrimination if they relied on that statistic alone.

Although we have emphasized observers' relative insensitivity to 90-270 phase shifts in the periphery, it is obvious that they can make these discriminations at eccentricities of 20 deg or more. Thus, another mechanism that picks up information different from Z3 is needed (see also Bruce & Morgan, 1975; Rentschler et al., 1988; Morrone et al., 1989; Sarrinen, 1988). The hypothesized mechanism must provide information about the relative positions of features. Simple mechanisms are capable of doing this. As several recent texture discrimination models have demonstrated (Bergen & Adelson, 1988; Turner, 1986; Voorhees & Poggio, 1988), patterns that differ only in second- or third-order statistics can be transformed into patterns differing in first-order statistics by filtering the images appropriately. This is the strategy adopted in the two-channel model. The Z3, or first-order statistics, of the stimuli, are not changed by a 90-270 deg phase shift. However, the statistics of the outputs, or responses, of odd-symmetric filters are changed by such a

phase shift. In other words, filtering mirror image stimuli with odd-symmetric mechanisms (and half-wave rectifying the response) produces responses with different first-order statistics. Hence, the two-channel model simply uses differences in the first-order statistics of the filtered waveforms to discriminate all 180 deg phase shifts. Thresholds for 90–270 phase shifts are higher than for 0–180 shifts in the periphery because of a loss of sensitivity among odd-symmetric mechanisms rather than because of differences in the processes by which such discriminations are made.

Even-symmetric and odd-symmetric receptive fields in visual cortex

The results from the current experiments discrimination demonstrate that phase thresholds measured over a wide range of contrasts and spatial frequencies are consistent with that the two-channel model proposed by Bennett and Banks (1987) and Field and Nachmias (1984). In the two-channel model, even-symmetric and odd-symmetric filters encode relative spatial phase. Retinal and lateral geniculate neurons have only even-symmetric receptive fields, so the visual cortex is the earliest stage at which the proposed even- and odd-symmetric mechanisms could be observed. Indeed, it has been proposed that single cells in the visual cortex are either even- or odd-symmetric (Albrecht, Hamilton, & Farrar, unpublished manuscript: Foster, Gaska, Marcelja & Pollen, 1983; Pollen & Ronner, 1981, 1982), so the mechanisms of the two-channel model might correspond to single cells in V1 and V2. The fact that a major relative magnification occurs for foveal, as opposed to peripheral, striate cortex (e.g. Daniel & Whitteridge, 1961; Hubel & Wiesel, 1974; Van Essen et al., 1984; but see Curcio & Allen, 1991; Wassle, Grunert, Rohrenbeck & Boycott, 1989), is consistent with the development of odd-symmetric mechanisms mainly in the central cortical representation. Moreover, an under-representation of tangentially-oriented odd-symmetric mechanisms is consistent with radial-tangential anisotropies observed in the parts of the cat's cortex subserving vision outside the central 5 deg of the visual field (Leventhal, 1983; Leventhal et al., 1984). However, specific physiological support for a direct linkage between single neurons in the visual cortex and the even- and odd-symmetric filters in the two-channel model is insufficient at this point. First, we do not know if the

sensitivity (or number) of cortical cells having odd-symmetric receptive fields declines with increasing eccentricity. Second, there is no evidence that the sensitivities (or number) of odd-symmetric fields outside of the central visual field are orientation-dependent. Third, although the receptive fields of most cells in cat and monkey visual cortex are approximately even- or odd-symmetric, many are not (Field & Tolhurst, 1986; Hamilton, Albrecht & Geisler. 1985; Hubel & Weisel, 1962; Kulikowski & Bishop, 1981). The two-channel model does not incorporate the responses of asymmetric receptive fields. Finally, the two-channel model assumes that phase-encoding mechanisms have large bandwidths because they respond to both F and to 2F. Many cortical cells are in fact broadly tuned (DeValois, Albrecht, & Thorell, 1982), so there is some support for this assumption. A reasonable alternative hypothesis is that relative phase is encoded by comparing the outputs of narrow-band mechanisms, each responding to a single component (Lawden, 1983). An even-symmetric comparator might, for example, respond best when the peak responses of the two narrow-band mechanisms coincide. An odd-symmetric comparator, on the other hand, might respond best when the peak responses of the two narrow-band, even-symmetric mechanisms are displaced by 90 deg. These sorts of comparisons would require intracortical interactions among cells tuned to different spatial frequencies. DeValois and Tootell (1983) have reported just such interactions. Clearly, then, a better understanding of how cortical mechanisms encode relative spatial phase is necessary to delineate the linkage between mechanisms based on psychophysical evidence and cortical mechanisms observed electrophysiologically.

The origins of radial-tangential differences in phase processing

Perhaps the most surprising finding of the current experiments is that sensitivity to spatial phase shifts can vary substantially with stimulus orientation. Berardi and Fiorentini (1988) have reported a similar finding (see Note 3). How might such anisotropies arise? One intriguing hypothesis, suggested by Fahle (1986), is that the neural anisotropies may have been induced developmentally by peripheral astigmatism. Tangential gratings are more myopically focused than are radial gratings in most eyes (Ferree et al., 1931). According to Fahle's devel-

opmental hypothesis, radial-tangential differences in retinal blur may induce a local meridional amblyopia: differences in phase processing occur presumably because the development of odd-symmetric phase-encoding mechanisms is more adversely affected by blur than is the development of even-symmetric mechanisms. It is very difficult to evaluate this hypothesis because there are no data on the development of peripheral astigmatism in human eyes and, furthermore, very little is known regarding the development of phase sensitivity in human infants. However, there is some indirect evidence that supports the hypothesis. First, Bennett (1989) found that 6- and 12-week-old infants are capable of discriminating 0-180 shifts in compound sinewave gratings but obtained no evidence for discrimination of 90-270 shifts. This finding suggests that different phaseencoding mechanisms do indeed develop at different rates. Second, Bennett (1989) found that phase discrimination thresholds in the anisometropic amblyopic fovea are quantitatively similar to those obtained in the normal periphery, demonstrating that early retinal blur affects the putative odd-symmetric filters more than the even-symmetric filters.

Note 1—Inspection of Fig. 17 suggests an alternative cue that could be used to discriminate 0–180 phase shifts, namely changes in peak brightness or luminance. Observers do not report using this cue. Moreover, in expt II we found that randomly varying stimulus contrast (and, hence, the peak brightness of a single bar) has no effect on phase discrimination. This finding strongly suggests that 0–180 shifts are not discriminated on the basis of brightness/luminance differences.

Note 2—In the Morrone and Burr model, local energy is equal to the Pythagorean sum of a pair of broad-band evenand odd-symmetric filters. The complete energy function therefore can be modeled as a nonlinear computation that takes the modulus of a space-varying complex Gabor coefficient. Interestingly, Pollen, Gaska and Jacobson (1988) found that the same model accurately predicts the responses of complex cells in feline primary visual cortex. In other words, the time-varying response of a complex cell to a drifting compound grating is very similar to the energy function for that stimulus.

Note 3—Rentschler et al. (1988) noted that discrimination of 90–270 shifts improved when gratings were oriented radially instead of tangentially. However, they attributed the improvement to the fact that the fixation point served as an effective spatial referent for radially-oriented, but not tangentially-oriented, patterns. As was outlined in the Results section of expt IV, such an explanation cannot account for radial-tangential differences found in this study.

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### REFERENCES

- Albrecht, D. G., Hamilton, D. B. & Farrar, S. B. Visual cortex of monkey and cats; spatial phase preferences of simple cells. Unpublished manuscript, University of Texas, Austin.
- Andriessen, J. J. & Bouma, H. (1976). Eccentric vision: Adverse interactions between line segments. Vision Research, 16, 71-78.
- Badcock, D. R. (1984a). How do we discriminate spatial phase? Vision Research, 24, 1847-1857.
- Badcock, D. R. (1984b). Spatial phase or luminance profile discrimination? Vision Research, 24, 613-623.
- Bennett, P. J. (1989). An investigation of spatial phaseencoding mechanisms in human adults and infants. Doctoral Dissertation, University of California, Berkeley, 1988. Dissertation Abstracts International, 50(5), 2182-B.
- Bennett, P. J. & Banks, M. S. (1987). Sensitivity loss among odd-symmetric mechanisms and phase anomalies in peripheral vision. *Nature*, *London*, 326, 873–876.
- Bennett, P. J. & Banks, M. S. (1988). Peripheral phaseencoding deficits with aperiodic patterns. *Investigative* Ophthalmology and Visual Science (Suppl.), 29.
- Berardi, N. & Fiorentini, F. (1988). Lateralization and orientational bias in the discrimination of mirrorsymmetric complex gratings. *Perception*, 17, 364.
- Bergen J. R. & Adelson, E. H. (1988) Early vision and texture perception. *Nature*, *London*, 333, 363-364.
- Braddick, O. (1981). Is spatial phase degraded in peripheral vision and visual pathology? *Documenta Ophthalmolog*ica, 30, 255-262.
- Bradley, A. & Skottun, B. C. (1987). Effects of contrast and spatial frequency on vernier acuity. Vision Research, 27, 1817–1824.
- Bruce, V. G. & Morgan, M. J. (1975). Violations of symmetry and repetition in visual patterns. *Perception*, 4, 239-249.
- Burkhardt, D. A. & Gottesman, J. (1987). Light adaptation and responses to contrast flashes in cones of the walleye retina. Vision Research, 27, 1409-1420.
- Burr, D. C., Morrone, M. C. & Spinelli, D. (1989). Evidence for edge and bar detectors in human vision. Vision Research, 29, 419-431.
- Caelli, T. M. & Julesz, B. (1978). On perceptual analyzers underlying visual texture discrimination: Part I. Biological Cybernetics, 28, 167-175.
- Caelli, T. M., Julesz, B. & Gilbert, E. N. (1978). On perceptual analyzers underlying visual texture discrimination: Part II. Biological Cybernetics, 29, 201-214.
- Campbell, F. W., Kulikowski, J. J. & Levinson, J. (1966). The effect of orientation on visual resolution of gratings. *Journal of Physiology*, *London*, 187, 187, 427.
- Chandler, J. P. (1975). STEPIT, quantum chemistry pro-

- gram exchange, Department of Chemistry, Indiana University, Bloomington, IN 47401, U.S.A.
- Colletta, N. J. & Williams, D. R. (1987). Psychophysical estimate of extrafoveal cone spacing. *Journal of the* Optical Society of America A, 4, 1503-1513.
- Cone, R. A. (1965). The early receptor potential of the vertebrate eye. In Cold Spring Harbor symposia on quantitative biology. New York: Cold Spring Harbor.
- Curcio, C. A. & Allen, K. A. (1991). Topography of ganglion cells in human retina. *Journal of Comparative Neurology*, in press.
- Curcio, C. A., Sloan, K. R., Packer, O., Hendrickson, A. E. & Kalina, R. E. (1987). Distributions of cones in human and money retina: Individual variability and radial asymmetry. Science, 236, 579-582.
- Daniel, P. M. & Whitteridge, D. (1961). The representation of the visual field on the cerebral cortex in monkeys. *Journal of Physiology*, *London*, 159, 203-221.
- DeValois, K. K. & Tootell, R. B. H. (1983). Spatial-frequency-specific inhibition in cat striate cortex cells. Journal of Physiology, London, 336, 359-376.
- DeValois, R. L., Albrecht, D. G. & Thorell, L. G. (1982). Spatial frequency selectivity of cells in macaque visual cortex. Vision Research, 22, 545-559.
- Fahle, M. (1986). Curvature detection in the visual field and a possible physiological correlate. *Experimental Brain Research*, 63, 113–124.
- Ferree, C. E., Rand, G. & Hardy, C. (1931). Refraction for the peripheral field for vision. Archives of Ophthalmology, 5, 717-731.
- Field, D. J. & Nachmias, J. (1984). Phase reversal discrimination. Vision Research, 24, 333-340.
- Field, D. J. & Tolhurst, D. J. (1986). The structure and symmetry of simple-cell receptive-field profiles in the cat's visual cortex. *Proceedings of the Royal Society, London (Biology)*, 228, 379–400.
- Finney, D. J. (1971). Probit analysis. Cambridge: The University Press.
- Fiorentini, A. & Berardi, N. (1981). Learning in grating waveform discrimination: Specificity for orientation and spatial frequency. Vision Research, 21, 1149-1158.
- Foster, K. H., Gaska, J. P., Marcelja, S. & Pollen, D. A. (1983). Phase relationships between adjacent simple cells in the feline visual cortex. *Journal of Physiology, London*, 345, 22P.
- Geisler, W. S. & Davila, K. D. (1985). Ideal discriminators in spatial vision: Two-point stimuli. *Journal of the Optical* Society of America A, 2, 1483-1497.
- Green, D. G., Powers, M. K. & Banks, M. S. (1980). Depth of focus, eye size, and visual acuity. Vision Research, 20, 827–835.
- Hamilton, D. B., Albrecht, D. G. & Geisler, W. S. (1985). Receptive field organization of visual cortical neurons in monkey and cat: The phase and amplitude transfer functions. *Investigative Ophthalmology and Visual Science* (Suppl.), 26, 265.
- Hess, R. F. & Pointer, J. S. (1987). Evidence for spatially local computations underlying discrimination of periodic patterns in fovea and periphery. Vision Research, 27, 1343-1360.
- Hess, R. F. & Watt, R. J. (1990). Regional distribution of the mechanisms that underlie spatial localization. *Vision Research*, 30, 1021-1032.
- Howarth, P. A. (1984). The lateral chromatic aberration of the eye. *Ophthalmology and Physiological Optics*, 4, 223-226.

- Hubel, D. H. & Freeman, D. G. (1977). Projection into the visual field of ocular dominance columns in macaque monkey. *Brain Research*, 122, 336–343.
- Hubel, D. H. & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat visual cortex. *Journal of Physiology, London*, 160, 106-154
- Hubel, D. H. & Wiesel, T. N. (1974). Uniformity of monkey striate cortex: A parallel relationship between field size, scatter, and magnification factor. *Journal of Comparative Neurology*, 158, 295–306.
- Johnston, A. (1987). Spatial scaling of central and peripheral contrast-sensitivity functions. *Journal of the Optical Society of America A*, 4, 1583-1593.
- Johnston, A. & Wright, M. J. (1986). Matching velocity in central and peripheral vision. Vision Research, 26, 1099–1110.
- Julesz, B., Gilbert, E. N., Shepp, L. A. & Frisch, H. L. (1973). Inability of observers to discriminate between textures that agree in second-order statistics: Revisited. *Perception*, 2, 391–405.
- Julesz, B., Gilbert, E. N. & Victor, J. D. (1978). Visual discrimination of textures with identical third-order statistics. *Biological Cybernetics*, 31, 137-140.
- Klein, S. A. & Levi, D. M. (1985). Hyperacuity thresholds of 1.0 second: Theoretical predictions and empirical validation. *Journal of the Optical Society of America A*, 2, 1170–1190.
- Klein, S. A. & Tyler, C. W. (1985). Phase discrimination of compound gratings: Generalized autocorrelation analysis. *Journal of the Optical Society of America A*, 3, 868-879.
- Koenderink, J. J., Bouman, M. A., Bueno de Mesquita, A. E. & Slappendel, S. (1978a). Perimetry of contrast detection thresholds of moving spatial sine wave patterns—I. The near peripheral visual field (eccentricity 0-8). Journal of the Optical Society of America, 68, 845-849.
- Koenderink, J. J., Bouman, M. A., Bueno de Mesquita, A. E. & Slappendel, S. (1978b). Perimetry of contrast detection thresholds of moving spatial sine wave patterns—II. The far peripheral visual field (eccentricity 0-50). Journal of the Optical Society of America 68, 850-854.
- Koenderink, J. J., Bouman, M. A., Bueno de Mesquita, A. E. & Slappendel, S. (1978c). Perimetry of contrast detection thresholds of moving spatial sine wave patterns—III. The target extent as a sensitivity controlling parameter. *Journal of the Optical Society of America*, 68, 854–860.
- Kulikowski, J. J. & Bishop, P. O. (1981). Linear analysis of the responses of simple cells in the cat visual cortex. Experimental Brain Research, 44, 386-400.
- Lawden, M. C. (1983). An investigation of the ability of the human visual system to encode spatial-phase relationships. Vision Research, 23, 1451-1463.
- Legge, G. E. & Kersten, D. (1987). Contrast discrimination in peripheral vision. *Journal of the Optical Society of America A*, 4, 1594-1598.
- Leventhal, A. G. (1983). Relationship between preferred orientation and receptive field positions of neurons in cat striate cortex. *Journal of Comparative Neurology*, 220, 476-483.
- Leventhal, A. G., Schall, J. D. & Wallace, W. (1984). Relationship between preferred orientation and receptive field position of neurons in extrastriate cortex (area

- 19) in the cat. Journal of Comparative Neurology, 222, 445-451.
- Levi, D. M., Klein, S. A. & Aitsebaomo, A. P. (1985).
  Vernier acuity, crowding and cortical magnification.
  Vision Research, 25, 963-977.
- Levi, D. M., Klein, S. A. & Yap, Y. L. (1987). Positional uncertainty in peripheral and amblyopic vision. *Vision Research*, 27, 581-597.
- Levick, W. R. & Thibos, L. N. (1980). Orientation bias of cat retinal ganglion cells. *Nature*, *London*, 286, 389-390.
- Levitt, H. (1971). Transformed up-down methods in psychoacoustics. Journal of the Acoustic Society of America, 49, 467–477.
- Loomis, J. M. (1978). Lateral masking in foveal and eccentric vision. Vision Research, 18, 335-338.
- Maattanen, L. M., Koenderink, J. J. & Nienhuis, B. (1988).
  Contrast discrimination: Invariant to spatial parameters.
  Vision Research, 28, 811–818.
- Millodot, M. & Lamont, A. (1974). Refraction of the periphery of the eye. Journal of the Optical Society of America, 64, 110-111.
- Mitchell, D. E., Freeman, R. D. & Westheimer, G. (1967).
  Effect of orientation on the modulation sensitivity for interference fringes on the retina. *Journal of the Optical Society of America*, 57, 246-249.
- Morrone, M. C. & Burr, D. C. (1988). Feature detection in human vision: A phase dependent energy model. Proceedings of the Royal Society, London (Biology), 235, 221-245.
- Morrone, M. C. & Owens, R. (1987). Edge detection by local energy. *Pattern Recognition Letters*, 6, 303-313.
- Morrone, M. C., Burr, D. C. & Spinelli, D. (1989). Discrimination of spatial phase in central and peripheral vision. *Vision Research*, 29(4), 433–445.
- Naka, K. I. & Rushton, W. A. H. (1966). S-potentials from colour units in the retina of fish (Cyprinidae). Journal of Physiology, London, 185, 536-555.
- Nielsen, K. R. K., Watson, A. B. & Ahumada, A. J. (1985).
  Application of a computable model of human spatial vision to phase discrimination. *Journal of the Optical Society of America A*, 2, 1600–1606.
- Paradiso, M. A. & Carney, T. (1988). Orientation discrimination as a function of stimulus eccentricity and size: Nasal/temporal retinal asymmetry. Vision Research, 28, 867-874.
- Pollen, D. A. & Ronner, S. F. (1981). Phase relationships between adjacent simple cells in the visual cortex. *Science*, 212, 1409–1411.
- Pollen, D. A. & Ronner, S. F. (1982). Spatial computation performed by simple and complex cells in the visual cortex of the cat. *Vision Research*, 22, 101–118.
- Pollen, D. A., Gaska, J. P. & Jacobson, L. D. (1988).
  Responses of simple and complex cells to compound sine-wave gratings. Vision Research, 28, 25–39.
- Rempt, F., Hoogerheide, J. & Hoogenboom, W. P. H. (1971). Peripheral retinoscopy and Skiagram. *Ophthalmologica*, 162, 1-10.
- Rentschler, I. & Treutwein, B. (1985). Loss of spatial phase relationships in extrafoveal vision. *Nature*, *London*, 313, 308-310.
- Rentschler, I., Hubner, M. & Caelli, T. (1988). On the discrimination of compound Gabor signals and textures. *Vision Research*, 28, 279–291.
- Robson, J. G. & Graham, N. (1981). Probability summation and regional variation in contrast sensitivity across the visual field. *Vision Research*, 21, 409-418.

- Rovamo, J., Virsu, V. & Nasanen, R. (1978). Cortical magnification factor predicts photopic contrast sensitivity of peripheral vision. *Nature*, *London*, 271, 54-56.
- Rovamo, J., Virsu, V., Laurinen, P. & Hyvarinen, L. (1982).
  Resolution of gratings oriented along and across meridians in peripheral vision. *Investigative Ophthalmology and Visual Science*, 23, 666-670.
- Saarinen, J. (1988). Detection of mirror symmetry in random dot patterns at different eccentricities. Vision Research, 28, 755-759.
- Schall, J. D., Vitek, D. J. & Leventhal, A. G. (1986). Retinal constraints on orientation specificity in cat visual cortex. *Journal of Neuroscience*, 6, 823-836.
- Schneider, T. & Zrenner, E. (1987). The variable interdependence of amplitude and implicit-time in P III, b-wave, and optic-nerve responses of the cat. Experimental Eye Research, 45, 655-664.
- Stephenson, C. & Braddick, O. (1983). Discrimination of relative spatial phase in fovea and periphery. *Investigative* Ophthalmology and Visual Science (Suppl.), 24, 146.
- Temme, L. A., Malcus, L. & Noell, W. K. (1985). Peripheral visual field is radially organized. American Journal Opthalmology and Physiological Optics, 62, 545-554.
- Thibos, L. N. (1987). Calculation of the influence of lateral chromatic aberration on image quality across the visual field. *Journal of the Optical Society of America A*, 4, 1673–1680.
- Thomas, J. P. (1987). Effect of eccentricity on the relationship between detection and identification. *Journal of the Optical Society of America A*, 4, 1599-1605.
- Turner, M. R. (1986). Texture discrimination by Gabor functions. Biological Cybernetics, 55, 71-82.
- Van Essen, D. C., Newsome, W. T. & Maunsell, J. H. R. (1984). The visual field representation in striate cortex by the macaque monkey: Asymmetries, anisotropies, and individual variability. Vision Research, 24, 429-448.
- Virsu, V. & Rovamo, J. (1979). Visual resolution, contrast sensitivity, and the cortical magnification factor. Experimental Brain Research, 37, 475-494.

- Virsu, V., Nasanen, R. & Osmoviita, K. (1987). Cortical
  magnification and peripheral vision. *Journal of the Optical Society of America A*, 4, 1568-1578.
- Voorhees, H. & Poggio, T. (1988). Computing texture boundaries from images. Nature, London, 333, 364-367.
- Wassle, H., Grunert, U., Rohrenbeck, J. & Boycott, B. B. (1989). Cortical magnification factor and the ganglion cell density of the primate retina. *Nature*, *London*, 341, 643-645.
- Watson, A. B. (1983). Detection and recognition of simple spatial forms. In Braddick, O. J. & Slade, A. C. (Eds), Physical and biological processing of images. Berlin: Springer.
- Watson, A. B. (1987). Estimation of local spatial scale. Journal of the Optical Society of America A, 4, 1579–1582.
- Westheimer, G. (1982). The spatial grain of the perifoveal visual field. Vision Research, 22, 157-162.
- Wilson, H. R. (1986). Responses of spatial mechanisms can explain hyperacuity. *Vision Research*, 26, 453-469.
- Wilson, H. R. & Gelb, D. J. (1984). Modified line element theory for spatial frequency and width discrimination. Journal of the Optical Society of America A, 124-131.
- Wirth, A. & Zetterstrom, B. (1954). Effect of area and intensity on the size and shape of the electroretinogram: Exclusion of stray light effect. *British Journal of Ophthal-mology*, 38, 257-265.
- Yap, Y. L., Levi, D. M. & Klein, S. A. (1987a). Peripheral hyperacuity: Three-dot bisection scales to a single factor from 0 to 10 degrees. *Journal of the Optical Society of America A*, 4, 1554-1561.
- Yap, Y. L., Levi, D. M. & Klein, S. A. (1987b). Peripheral hyperacuity: Isoeccentric bisection is better than radial bisection. *Journal of the Optical Society of America A*, 4, 1562–1567.
- Yap, Y. L., Levi, D. M. & Klein, S. A. (1989). Peripheral positional acuity: Retinal and cortical constraints on 2-dot separation discrimination under photopic and scotopic conditions. Vision Research, 29, 789-802.