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EVIDENCE FOR EDGE AND BAR DETECTORS IN HUMAN VISION

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Abstract—The structure of receptive fields of human visual detectors was investigated by studying their phase response. Observers were required to discriminate between pairs of periodic stimuli that differed in phase by 180° (reversed in contrast). The stimuli comprised 256 harmonics, smoothly filtered in amplitude, and congruent in phase at the origin. Reversal discrimination thresholds were measured as a function of the phase of the harmonics. Thresholds were slightly higher for phases around 45°, consistent with the idea that all discriminations were mediated by independent detectors with 0 or 90° phase response (assuming probability summation between them). Discrimination thresholds were also measured with a pedestal stimulus, of phase complementary to that of the test gratings. For discriminations between 0 and 180° (cosine phase), or 90 and 270° (sine phase), the complementary pedestal had little effect, implying independence of detectors in sine and cosine phase. However, for discrimination between 45 and 225° (stimuli containing both sine and cosine components) the complementary pedestal, which also contained both sine and cosine components, facilitated greatly discrimination thresholds. The results suggest that there exist two classes of detectors, one with a Fourier phase spectrum of 0, the other with a Fourier phase spectrum of 90°. This implies that the receptive fields are symmetric, one class having even-symmetry (line-detectors), the other odd-symmetry (edge-detectors).

Receptive fields Edge detectors Symmetry Phase

INTRODUCTION

One of the fundamental questions for vision research is how key image features, such as lines and edges, are detected and identified. A current idea is that visual detectors may take advantage of the symmetry of these two features: a line or bar is an even-symmetric function ($f(x) = f(-x)$), choosing the bar centre as origin); an edge is an odd-symmetric function ($f(x) = -f(-x)$). Several researchers (Tolhurst, 1972; Shapley and Tolhurst, 1973; Kulikowski and King-Smith, 1973) have suggested that human visual detectors may have even- and odd-symmetric receptive fields specialized to respond either to lines or to edges. Visual detectors with odd-symmetric receptive fields will respond maximally when centred on an edge; detectors with even-symmetric receptive fields will respond maximally when centred on a line. This idea received support from the electrophysiological studies of Hubel and Wiesel (1962, 1977), who reported that receptive fields of simple cells in cat and monkey cortex had either even- or odd-symmetry.

At present direct evidence about the symmetry of receptive fields in the human visual system is scant and open to problems of interpretation. Experiments demonstrating selective adaptation to edges of differing polarity (Tolhurst, 1972), facilitation experiments (Stromeyer and Klein, 1974) and measurements of sensitivity to drifting gratings (Stork *et al.*, 1985) imply the existence of detectors tuned to edges (odd-symmetric). At contrasts near detection threshold, observers can discriminate accurately the polarity of edges and lines, consistent with the idea of detectors specialized for these features (Kulikowski and King-Smith, 1973; Tolhurst and Dealy, 1975). A series of summation experiments also supports this view (Kulikowski and King-Smith, 1973; Shapley and Tolhurst, 1973). However, none of these experiments preclude the possibility that there exist other classes of detectors with non-symmetric receptive fields.

For psychophysical studies it is often more convenient to measure the frequency response of a detector (the Fourier transform of its receptive field) rather than to probe directly the

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receptive field itself. In the frequency domain, the symmetry of the receptive field is reflected in the phase response. Choosing the centre of the field as origin, an even-symmetric receptive field can be expanded to a series of cosine components: the amplitude of sine components is zero. An odd-symmetric field expands to a series of sine components, all cosine components having zero amplitude. By convention, Fourier phase is expressed as the arctangent of the ratio of the sine to cosine amplitudes: so an even-symmetric field will have a constant phase spectrum of 0°, and an odd-symmetric field a constant phase spectrum of 90°. Any other phase spectrum implies an asymmetric receptive field.

Field and Nachmias (1984) investigated the phase response of visual detectors by measuring contrast thresholds for phase discrimination. Observers were required to discriminate between two compound gratings, one the negative of the other. The gratings comprised two Fourier harmonics, added together, in variable phase. The results were consistent with a model of two classes of detectors, in $\pm$ cosine (0 and 180°) phase and $\pm$ sine (90 and 270°) phase (receptive fields of even- and odd-symmetry). Other experiments, and the observations of strategies used by observers, provided further support for this assertion.

However, the interpretation of Field and Nachmias' experiments are open to criticism. Their major assumption was that discrimination should occur at only four points of the waveform: the peaks, troughs and zero-crossings of the fundamental. They argue that the response of cosine detectors is stronger at the peaks and troughs, and sine response strongest at the zero crossings. While this is true, it is not sufficient reason to ignore the responses at the rest of the waveform. The choice is based more on the mathematical description of the stimulus, rather than on a realistic model of the visual system.

A further limitation with Field and Nachmias' experiment is that they used stimuli comprised of only two cosinusoidal components, the fundamental and its second harmonic. Although this simplifies the mathematical analysis, it is clearly restrictive. Stimuli with only two harmonics cannot be considered to be representative of natural scenes, and certainly not of lines and edges. Furthermore, the discrete number of harmonics of high amplitude causes ringing and other artefacts (such as the Gibbs phenomenon: Hewitt and Hewitt, 1979), which could provide cues for discrimination. Indeed Badcock (1984a, b) has evidence that phase discrimination may be based on local contrast under similar conditions.

Local energy model

Morrone and Burr (1988) have recently developed a new model of edge and line detection. The model has two stages, one for detection of features (edges and lines), the other for identification of the detected feature. It avoids the origin problem of the Fourier approach, is strictly local in operation and allows the use of multiple harmonic stimuli in experimental research.

The first stage of the model is a linear convolution of the image by pairs of filters with receptive fields, matched in size, having even- and odd-symmetry (i.e. matched bandpass filters of identical amplitude response, in cosine and sine phase). The output of the convolutions are squared separately and summed, to give the square of the local energy profile. They have demonstrated that, for a wide range of patterns, visually salient features such as lines and edges, and other structures perceived by observers as lines or edges (such as Mach bands), cause peaks in the local energy profile (Morrone et al., 1986; Morrone and Burr, 1988; Ross et al., 1989). Furthermore, recent results suggest that detection of complex patterns can be predicted from the magnitude of local energy peaks (Morrone and Burr, 1989). Having defined the conditions for definition and detection of features, there is a firm basis for supposing that discrimination of feature type also occurs at those points. Thus it is reasonable to consider the response of detectors only at the peaks in local energy.

According to the Morrone–Burr model, the nature of the feature can be determined by considering the strength of the even- and odd-symmetric response at the peaks of the energy function. For a line, even-symmetric detectors respond maximally at that point; for an edge, odd-symmetric detectors respond maximally. Figure 1 illustrates the application of the model to two waveforms, a line and an edge. Note that only at the peaks of local energy is the response of odd-symmetric detectors to a line zero; elsewhere it is non-zero, and can be greater than the even-symmetric response.

Although the energy operator is a local operator, based on convolution, it relates well to a global Fourier description of periodic stimuli. It

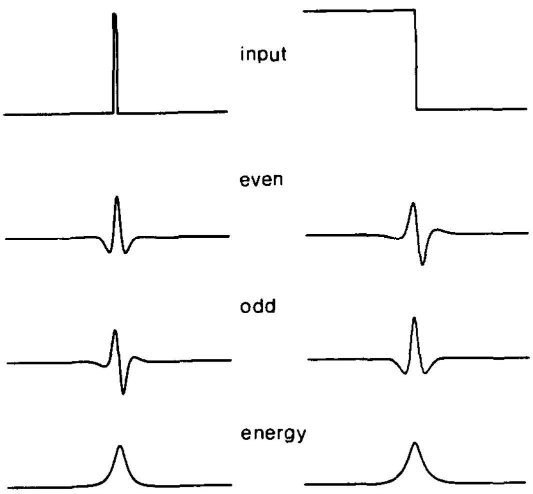

Fig. 1. Output of the various stages of the local energy model to two stimuli, a bar and an edge. Immediately under the stimuli are the responses of detectors with even-symmetric receptive fields, and under those the responses of detectors with odd-symmetric fields. The bottom traces show the output of the local energy operator, defined as the squareroot of the sum of the squared even-symmetric and squared odd-symmetric outputs (the pythagorian sum). For both stimuli, the peaks in local energy correspond to the position of the "feature". Note that the response to the bar (which approximates a delta function) is similar to the line spread function, or receptive fields of the detectors.

has been proven mathematically that peaks in local energy correspond to points of the image where the arrival-phases of harmonic components are most similar, or congruent (Morrone and Owens, 1987; Morrone and Burr, 1988). For a line, the arrival-phases of all cosine harmonics are 0 or 180° at the local energy peak; for an edge they are all congruent at 90 or 270°.* Thus, by defining the origin of a periodic stimulus as a peak in local energy, the phase of any arbitrary number of harmonics can be conveniently defined at that point. The choice of origin is no longer arbitrary.

The experiments reported in this study were designed to test further the hypothesis that human detectors have symmetric receptive fields. Contrast sensitivity was measured for discrimination of stimulus pairs, one phase shifted by 180° from the other (i.e. reversed in contrast). The stimuli were constructed by summing 256 harmonic cosine components, smoothly filtered in amplitude. The phase of the cosine components was such that all harmonics had the same arrival-phase at two points on the waveform, causing strong peaks in local energy, and hence visually salient features. The arrival-phase at the point of phase congruence was varied to change the nature of the feature (see Fig. 2 for examples). With these stimuli phase can be varied precisely without changing the amplitude spectrum (simple lines and edges have very different amplitude spectra). Ringing and other stimulus artefacts inherent in many of the previous studies of phase do not present a problem here, as the amplitude spectra taper off smoothly.

METHODS

Stimuli

The stimuli for the experiments of this study comprised 256 cosine harmonics, whose amplitude varied inversely with frequency. The amplitude spectrum was further multiplied by a Difference-of-Gaussian (DoG) function, to attenuate smoothly both the high frequencies (to avoid ringing) and the low frequencies (that could give luminance cues for discrimination). The general equation of the luminance profile $L(x)$ was:

$$L(x) = l_0 + a \sum_{K=1}^{256} \cos((2\pi k \cdot x/T) - \phi)\cdot \mathrm{DoG}(k)/k; \quad (1)$$

for k odd integer. l_0 is the mean luminance, a a constant related to contrast, T the period (equal to 512 points) and ϕ the phase at the origin. The Difference of Gaussian function is given by:

$$\mathrm{DoG}(k) = \exp(-k^2/2\sigma_h^2) - \exp(-k^2/2\sigma_L^2); \quad (2)$$

where σ_L and σ_h are the frequency constants (equal to 4 and 128 cycles/period respectively).

Note that the phases of all the harmonics are congruent and equal to ϕ at the origin ($x = 0$) and for $x = nT$, for n integer. They are also congruent for $x = nT + T/2$, where they are equal to $\pi + \phi$. At these points local energy is maximal, and features are seen (see Figs 1 and 2).

Equation 1 can be decomposed into its sine and cosine components by trigonometric expansion to give:

$$L(x) = l_0 + a \sum_{K=1}^{256} (\sin(\phi)\cdot\sin(2\pi k \cdot x/T) + \cos(\phi)\cdot\cos(2\pi k \cdot x/T))\cdot \mathrm{DoG}(k)/k. \quad (3)$$

*In this study we develop the Fourier series with cosine components, following the convention of most studies on phase. In a previous paper (Morrone *et al.*, 1986) we have developed the series with sine components. For the sine basis set, harmonics are in 0 or 180° phase at an edge and ±90° phase at a line.

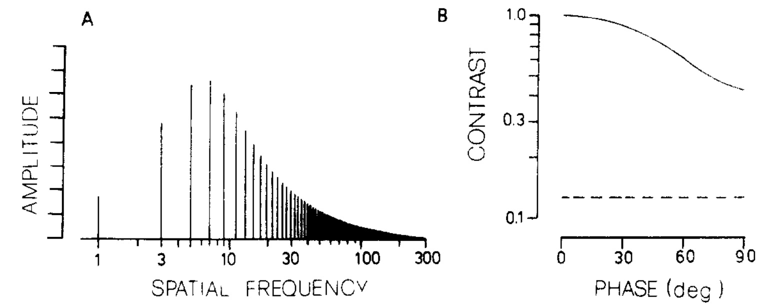

Fig. 3. (A) Amplitude spectra of the stimuli used in this study. (B) Contrast of stimuli, as a function of phase ϕ. The amplitude spectrum of all stimuli was identical. The top curve is the Michaelson contrast (ratio of peak amplitude to mean). This varies with phase, from the theoretical maximum of 1 for 0° phase (peaks add), to 0.43 to 90° phase (peaks subtract). The lower dashed curve shows contrast defined as the ratio of standard deviation of the luminance profile to mean luminance. This definition of contrast does not vary with phase (from Parseval's theorem), and was therefore used throughout this paper.

This representation is useful for describing the relative response of detectors of sine and cosine phase.

Figure 2 shows examples of the stimuli. Although they are periodic gratings, only 1 period is shown, positioned so that the origin ($x = 0$) is at about a quarter the width of the photograph. At this point the phases of all harmonics are ϕ, and features are seen. Features are also seen where $x = T/2$, where all harmonics have phase $\pi + \phi$. For Figs 2(A), (B) and (C) respectively, $\phi = \pi/2$, $\pi/4$ and 0 rad (90, 45 and 0°): i.e. only sine components, sine and cosine components of equal amplitude, and only cosine components. For $\phi = 90°$, the features seem to be edges, one positive going, the other negative going. For $\phi = 0°$, the features are lines, one bright and the other dark. For $\phi = 45°$, the features seem to be a combination of edge and line. Note that in Fig. 2A, there appears to be a brightness difference between the three panels, even though the luminances are identical except at the border. This is an example of the well known Craik–O'Brien–Cornsweet illusion (Craik, 1966; O'Brien, 1958; Cornsweet, 1970; see also Burr, 1987).

Figure 3A shows the amplitude spectrum of the stimuli. The 1st and 3rd harmonics are heavily damped, and the higher harmonics attenuate smoothly to zero at 256, the Nyquist rate. Figure 3B shows the contrast of the stimuli, expressed in two ways. The solid curves show the Michaelson contrast, defined as the luminance amplitude (at peak) divided by mean luminance. Michaelson contrast varies by more than a factor of two from 90° phase (peaks subtract) to 0° phase (peaks add). The dashed lines show the ratio of the standard deviation of the luminance profile to mean luminance (a standard definition for complex waveforms such as noise). This definition of contrast does not vary with phase (from Parseval's theorem). Therefore, throughout this paper, contrast is defined as the ratio of standard deviation to mean. In a separate study (Morrone and Burr, 1989) it has been shown that contrast detection thresholds for these patterns is constant for all phases if this definition of contrast is used.

Stimuli were generated by Micro-vax computer and transferred to a smaller computer (Cromemco-Z2D). The Cromemco displayed stimuli on a Joyce Electronics oscilloscope via an 8 bit D/A port, at 100 frames/sec, 624 lines/frame. The signal passed through a logarithmic digital attenuator (under computer control), then multiplied analogically by a Gaussian envelope (generated by a second D/A) to produce a temporal vignette. 1.2 periods of stimulus were displayed. Cycle width was 24.6 cm, on an oscilloscope face 30 cm wide by 20 cm high. The screen was surrounded by white card 1X1 m, floodlit to the same mean luminance as the screen (400 cd/m^2). All measurements were made at 3.5 m, where the spatial frequency of the fundamental was 0.25 c/deg.

For some experiments, a pedestal of fixed contrast was added to the test stimuli, and faded in and out with the test. The pedestal was also a periodic stimulus constructed from equation 1. It was generated via a third D/A converter, with conversion synchronized to the D/A generating the test. The signal was attenuated by a manually controlled logarithmic attenuator (Hewlett Packard), added to the attenuated test signal, then multiplied by the Guassian temporal window.

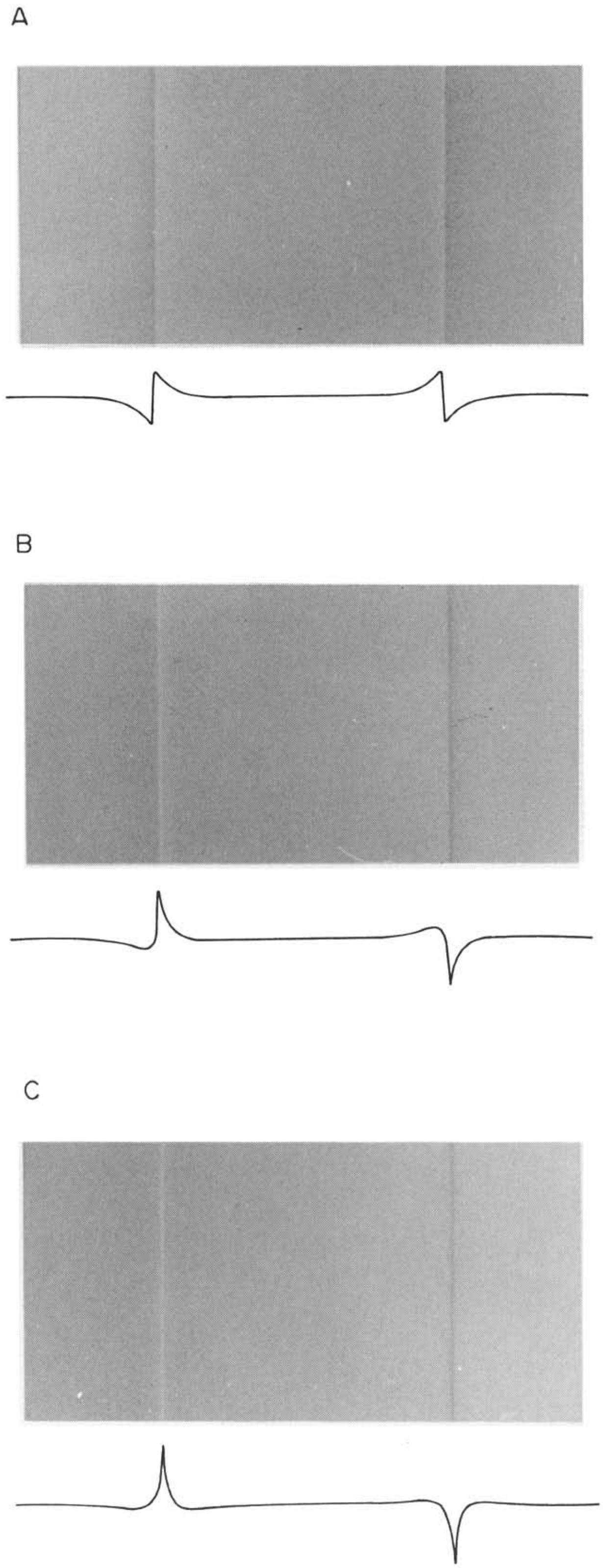

Fig. 2. Examples of the stimuli used throughout this study. All three comprise the sum of 256 cosinusoidal harmonics, whose amplitude spectrum is given by Fig. 3A. For all three figures, the arrival phases of all the harmonics are congruent at two points, where the features are seen. For the upper figure ϕ (of equation 1) is $\pi/2$, or 90°, producing arrival-phase congruence at 90° at one feature and 270° at the other. These features appear to be edges, producing an apparent change in brightness (although there is no accompanying change in luminance). For the middle figure ϕ is 45°, creating features that appear to be both edge and bar. For the lower figure ϕ is 0, creating light and dark bars at the points of phase congruence.

Procedure

Observers were required to discriminate between stimulus pairs, one the negative of the other. The phase of one stimulus (the "target") was ϕ, the other $\phi + 180°$ For each trial, the two test stimuli were presented successively, faded in and out within a temporal Guassian envelope of time constant 100 msec. Each presentation was marked by a tone, and lasted 500 msec. In the first experiment the test stimuli were presented alone, in the second experiment they were superimposed on a pedestal of phase $\phi + 90°$. Both test and pedestal were faded in and out together.

The order of presentation was randomized from trial to trial. Observers were required to indicate in which period the target stimulus appeared, by pressing the appropriate response button. Errors were signalled by a tone. Observers were allowed several sessions for each condition to familiarize themselves with the stimuli, and learn which stimulus was defined as "target": they were given no instructions on how to perform the task, but after experimentation, learned appropriate response strategies.

Within each trial, both test stimuli had the same contrast. Contrast varied from trial to trial, guided by the QUEST procedure (Watson and Pelli, 1983), which homed in on the contrast at which 82% of the responses were correct (taken as threshold). Within each session, ϕ and the contrast of the pedestal (where applicable) was constant. A fixed number of 40 trials were run for each session, and sessions where the confidence level of the maximum likelihood estimate was less than 95% were discarded (see Watson and Pelli, 1983). In practice this seldom occurred after observers were practiced at the task. A minimum of five sessions were run for each condition, yielding a mean and standard error.

The stimuli were positioned so that the first point of phase congruence fell roughly at 1/4 of the width of the oscilloscope face (like the photographs of Fig. 2). The exact position was varied randomly between presentations over a range of $T/16$. The random variation of position, combined with the heavy filtering of low spatial frequencies, reduced the possibility that observers discriminate between stimulus pairs on the basis of fixed local luminance cues. Observers were permitted to fixate at will. They usually chose to fixate the average position where one or other feature appeared.

Three observers (the authors) were used for all experiments. In all figures except Fig. 6 (the main experiment), the results of only two observers are shown, as the third observer gave substantially similar results. All observers had vision corrected to 6/6.

RESULTS

Sensitivity to contrast reversal

This experiment was similar to that of Field and Nachmias (1984). Observers were required to discriminate between pairs of stimuli (described by equation 1), one stimulus the negative of the other (all harmonics phase shifted by 180°). For the "target" stimulus, the phase at the points of phase congruence was ϕ or ($\phi + 180°$), where ϕ varied between 0 and 90° in 15° steps. Contrast thresholds for discrimination were determined by the QUEST procedure (Watson and Pelli, 1983).

Figure 4 shows the results for two observers. Contrast sensitivity (inverse of contrast thresholds) is reported on a logarithmic axis. For both observers, sensitivty for discrimination was similar for 0 and 90°, and slightly lover (1 or 2 dB) at intermediate phases. As peak-to-peak contrast of the stimuli vary by more than a factor of two (see Fig. 2), it would seem unlikely that the discriminations were based on local contrast (cf. Badcock, 1984b). Interestingly, this result differs from that of Field and Nachmias, whose data indicated higher sensitivity for 0–180° discrimination than for 90–270° discriminations. Possible explanations for this discrepancy, which becomes more exagerated with peripheral viewing, are discussed in the companion paper (Morrone *et al.*, 1989).

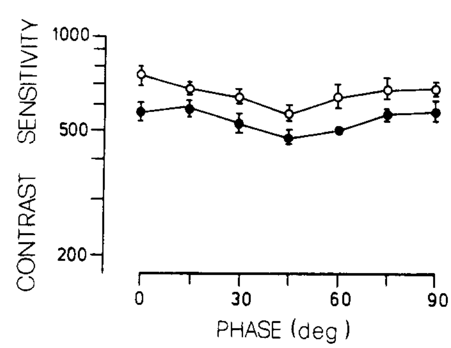

Fig. 4. Contrast sensitivity for discriminating multi-harmonic stimuli from their negative, as a function of the phase of one test stimulus. The spatial frequency of the fundamental harmonic was 0.25 c/deg. Results are shown for two observers, MCM (open symbols) and DS (solid symbols). For both observers, discrimination sensitivity was similar at 0 and 90°, but slightly less around 45°. Error bars indicate ±1 standard error.

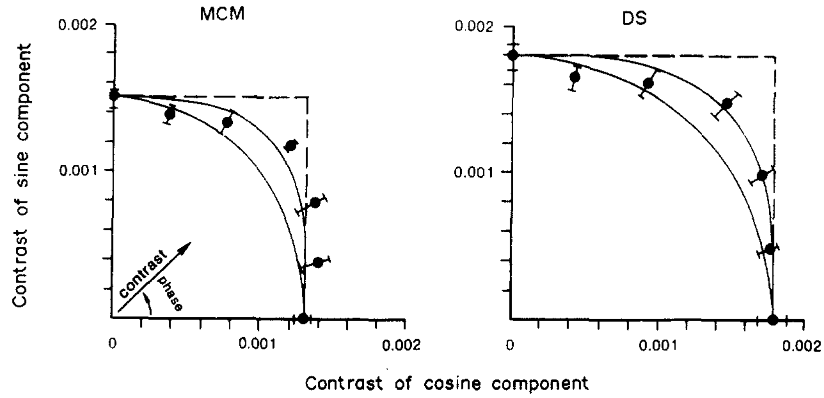

Fig. 5. Polar plot of the discrimination thresholds of Fig. 4. The data of Fig. 4 have been replotted, representing phase by the angular co-ordinate, and threshold contrast by vector length (with ± 1 standard error). The cartesian co-ordinates give the contrast of the sine and cosine components. The three curves represent the predicted thresholds of various discrimination hypotheses (see text for description). Inner ellipse: detectors of similar sensitivity tuned to all phases. Middle curve: independent detectors tuned to only sine and cosine phase, allowing for probability summation between detectors (see Appendix). Outer rectangle: detectors in only sine and cosine phase, neglecting probability summation.

A better insight of the action of detectors may be achieved by plotting the results of Fig. 4 on polar coordinates (Fig. 5), representing phase as vector angle, and contrast threshold (in linear units) as vector length. With this plot, the cartesian co-ordinates reflect the sine and cosine components of all the harmonics in the stimulus. Given the definition of ϕ in equations 1 and 3, stimuli of 0° phase have only cosine components, and those of 90° phase have only sine components. Those of intermediate phase will have both sine and cosine components, with the amplitude of the sine component proportional to $\sin(\phi)$ and that of the cosine component proportional to $\cos(\phi)$ (see equation 3).

The continuous lines show how various assumptions about detection predict thresholds. The central curve is an ellipse (almost circular), anchored at the thresholds for 0 and 90° phase. Thresholds should follow this curve if detectors existed at all phase angles, with roughly equal sensitivity. The outer rectangle is the prediction of Field and Nachmias, based on only two classes of detectors, in $\pm$ sine and $\pm$ cosine phase (odd- and even-symmetric receptive fields). They argue that if detectors with only these phases existed, then either the sine or the cosine component must reach its independent threshold for discrimination of intermediate phases. The rectangle passes through the thresholds for $\phi = 0$ and 90°.

The difference between these two curves is maximal around 45°, where the predicted thresholds differ by a factor of $\sqrt{2}$, about 3 dB. This difference is not great, but measurable. However, the data tend to fall between the two curves, giving support to neither theory.

The central curve shows predicted thresholds assuming only two classes of independent detectors, in sine and cosine phase, but allowing for probability summation between them. Probability summation is the slight increase in sensitivity resulting from the increased probability of a response if more than one detector is recruited (see for example Sachs et al., 1971). Appendix 1 gives details of the calculations. If probability summation between hypothetically independent detectors is considered, the predicted differences between the two-detector model and multiple-detector model become much smaller, about 1 dB at most. The data do tend to follow the middle curve, but the predicted effects are too small to allow any firm conclusions to be drawn.

The strategies used by observers for the discrimination tasks are of interest. For phases near 0°, discriminations were made by searching for a bar, in either the left or the right half of the screen, and deciding if it was bright or dark. For example, in Fig. 2C, the left bar would be judged as bright. For phases near 90°, the discrimination tended to be based on apparent brightness of the centre panel: the central panel of Fig. 2A would be judged brighter than the background. Near 45°, discrimination could be based on either strategy: polarity of bar or brightness of the central region. Observers claimed to search for both cues and use the most compelling. These observations are consistent with the hypothesis of two classes of detectors,

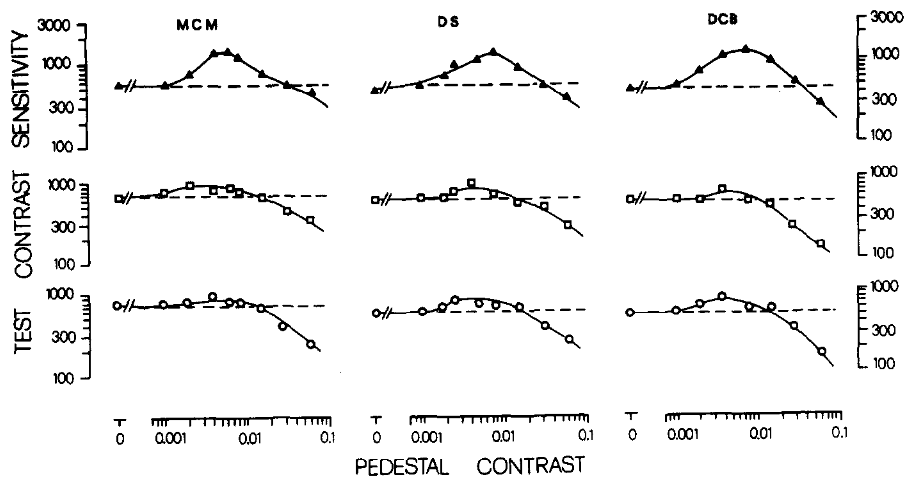

Fig. 6. Contrast sensitivity for discriminating test stimuli in the presence of a pedestal of phase orthogonal to that of the tests. The spatial frequency of the test and pedestal stimuli was 0.25 c/deg. Upper curves: test phases 45 and 225°, pedestal 315°; middle curves: test phases 0 and 180°, pedestal phase 90°; lower curve: test phases 90 and 270°, pedestal 0°. Contrast sensitivity is plotted as a function of pedestal contrast, with the dashed lines showing sensitivity with no pedestal. Strong facilitation occurred only for the 45–225° discrimination (see text for implications).

and also lends support to the idea that probability summation could be occurring between the two classes of detectors.

Facilitation

While the results of the previous experiment are consistent with a model of two classes of detectors with even- and odd-symmetric fields, they are far from conclusive. The following experiment was designed as a more direct test, taking advantage of an effect known as facilitation.

Nachmias and Sansbury (1974) showed that thresholds for detecting a grating superimposed on a pedestal grating of appropriate contrast can be lower than thresholds for detecting the grating when presented alone. There exist several plausible explanations for the effect, including thresholding non-linearities (Nachmias and Sansbury, 1974) and signal uncertainty (Pelli, 1985, 1987); however, for the purposes of this experiment a full understanding of the mechanisms of facilitation is not essential. Facilitation is merely used as a tool to probe the independence of visual detectors of differing phase response.

As with the previous experiment, contrast thresholds were measured for discriminating periodic stimuli from their negative. Three phases (ϕ) of test stimulus were used, 0, 45 and 90° (with negatives 180, 225 and 270°). To each test stimulus (both positive and negative) was added a pedestal, also constructed from equation 1, with phase ϕ orthogonal to that of both test stimuli. For the 0–180° discrimination, the phase of the pedestal was 90°; for the 45–225° discrimination it was 315°; and for the 90–270° discrimination it was 0°.

Figure 6 reports the thresholds of the three observers for the three discrimination tasks, as a function of pedestal contrast. The dashed lines on each curve show the threshold with no pedestal. For the discrimination of 45 from 225°, there was a marked facilitation in sensitivity over a wide range of pedestal contrasts. At the peak, sensitivity increased by more than a factor of 2 (more than 6 dB). At higher pedestal contrasts, sensitivity to the test began to decrease, falling to a level below that measured with no pedestal. The pattern of results for the 0–180° and 90–270° discrimination, however, was different. Facilitation was much less, about 1 or 2 dB at most. Again, sensitivity began to decrease with increased pedestal contrast for contrasts higher than those that cause maximum facilitation.

Figure 7 illustrates diagrammatically the test and pedestal stimuli for the 45–225° and 90–270° test stimuli. Like Fig. 5, the cartesian coordinates give the amplitudes of the sine and cosine components of the stimuli, and the polar co-ordinates give the contrast and phase. The values of test and pedestal contrast were taken from threshold data of observer MCM.

Consider first the 45° condition. With no pedestal, the test stimuli are represented by

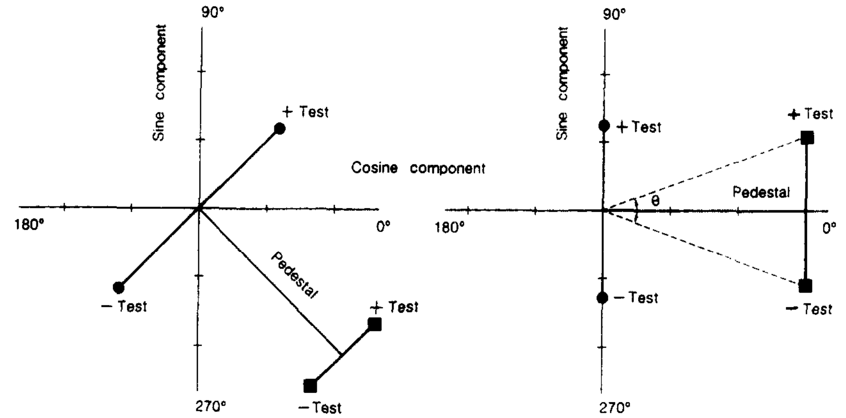

Fig. 7. Schematic representation of the phase and contrast of the stimuli of the pedestal experiment. On the left the test stimuli have 45 and 225° phase, with pedestal 315°; on the right the tests have 90 and 270° phase, with pedestal 0°. The solid circles represent contrast thresholds (from Fig. 6) with no pedestal and the squares with the pedestal that facilitated maximally discrimination. It is argued that only for the 45–225° discrimination does the pedestal add to sine and cosine components of the test, explaining the facilitation in this condition (see text).

circles at 45 and 225°, with vector length equal to contrast discrimination threshold. Both stimuli contain both sine and cosine components (in equal amplitude). The pedestal of 315° adds vectorially to both stimuli, affecting the amplitudes of both the sine and cosine components (squares). Detectors in sine and cosine phase should be facilitated by the pedestal. If, on the other hand, discriminations were achieved exclusively by detectors tuned to 45 and 225°, then adding the pedestal of 315°, orthogonal to both these detectors, should not facilitate discrimination. That thresholds are considerably lower in the presence of a pedestal implies the existence of detectors in sine and cosine phase, or at least in phases other than 45 and 225°.

The diagram on the right illustrates the effect for the 90–270° discrimination. The test stimuli alone contain only sine components, and should therefore be detected by detectors in sine phase. The pedestal of 0°, however, contains only cosine components, which should not facilitate detection of sine components. If, however, there existed detectors in other phases (such as 45°), these would respond to both sine and cosine components, and should be facilitated by the pedestal. The fact that strong facilitation occurs only for 45° test stimuli, and not for 0 or 90° tests suggests that the discrimination at all phases are mediated by detectors of sine or cosine phase response.

DISCUSSION

The results of this paper suggest that phase discrimination is achieved by two classes of detectors, one with even-symmetric fields, the other with odd-symmetric fields. The main evidence for this conclusion is the facilitation experiment (Fig. 6). A pedestal of orthogonal phase facilitated discriminations of 45–225°, but not 0–180° or 90–270°. It is argued that the pedestal adds to the sine and cosine components of the test only for the 45–225° discrimination, and therefore only in this condition is discrimination facilitated strongly (see Fig. 7).

The major assumption underlying these experiments was that phase discrimination occurs at the point where all phases are maximally similar, the point where local energy is maximal. This assumption is well justified by previous work. For a wide variety of patterns, including Mach bands, noise stimuli and stimuli that cause "monocular rivalry", visual salient features coincide with local peaks of local energy (Ross *et al.*, 1989; Morrone and Burr, 1988). Furthermore, detection thresholds can be well predicted by the local energy at the peaks (Morrone and Burr, 1989).

Although orthogonal pedestals did produce some facilitation for the 0–180° and the 90–270° discriminations, the effect was much smaller than for the 45–270° discrimination. There could be several explanations for the small facilitation. It may result from the increase in stimulus contrast when the pedestal is added, which should aid detection. Reducing the uncertainty of detection may cause a slight improvement in discrimination. Another possible explanation is that information for discrimination is available at points on the waveform other than at the peaks of local energy. At points away from the peaks, the phases of harmonics shift systematically. For example, for test stimuli in sine phase (and pedestals in cosine phase) both test and pedestal will have both sine and cosine components at points away from the peak. Facilitation may occur at those points. However, the fact that facilitation was weak in these conditions would suggest that the off-peak responses are weak compared with those at the peaks. Finally, it is possible that the small facilitation may imply the existence of detectors of intermediate phase of higher threshold than those in sine or cosine phase: these would be facilitated by the pedestal, but being less sensitive, the facilitation would not markedly affect discrimination threshold. However, irrespective of the reason for the 1 or 2 dB facilitation with the sine and cosine test and mask, the effect is clearly much less than that observed with tests and pedestals of $\pm 45°$, suggesting a predominance of detectors in sine and cosine phase in central vision.

At very high contrasts, the pedestal lowered contrast sensitivity for all three conditions, including the 45–270° discrimination. This could imply masking of even- by odd-symmetric filters and vice versa or that gain is set by local energy levels (pythagorian sum of even- and odd-symmetric output). The latter suggestion is appealing, but it would be premature to draw that conclusion at this stage.

The basic discrimination thresholds (Fig. 4) were also consistent with the odd- and even-symmetric field model, when probability summation between the two classes of detectors is considered. However, the predicted differences in threshold between the two-detector and multi-detector model are too small for any firm conclusions to be drawn from these data. It is surprising that Field and Nachmias (1984) found no evidence of probability summation, with a similar experiment. If discriminations of intermediate phases are based on the output of either even- or odd-symmetric detectors as they suggest, one would expect that the increased probability of response from one or other of the two classes of detectors would cause a slight decrease in threshold (e.g. Sachs *et al.*, 1971; Watson, 1979). A possible explanation is that the discrimination task with only two harmonics may have been more difficult than that reported here, so observers tended to concentrate on one or another strategy (searching for either lines or edges), rather than taking advantage of both responses.

In this study, the reported strategies of observers were consistent with the conclusion that all discriminations were based on responses of line and edge detectors. For phases near 90 or 270°, observers attempted to discriminate light from dark lines. For phases near 0 or 180°, they attempted to discriminate light from dark regions, divided by apparent edges. For other phases, judgments were based on either one or other, or both, of these cues. This suggests that if there exist detectors with asymmetric receptive fields tuned to phases between 0 and 90°, there is no perceptual outcome corresponding to their response.

The most likely neural mechanism for discrimination of contrast reversal are the simple cortical cells. These cells exhibit linear spatial summation across their receptive fields, except for half-wave rectification (e.g. Movshon *et al.*, 1979). The half-wave rectification (resulting from the fact that the cells have no resting discharge and cannot give a negative response) means that four cell types would be necessary: even-symmetric receptive fields with centre ON and centre OFF, and odd-symmetric fields with ON flanked by OFF regions and vice-versa. Hubel and Wiesel (1962, 1977) reported the existence of all four types of cells, in roughly equal quantities. Kulikowski and Bishop (1981) also claim that simple cell receptive fields are roughly symmetric (even and odd), approximating Gabor functions (Gaussians multiplied by sine or cosine functions). Pollen and Ronner (1981) reported that neighbouring simple cells tend to differ in phase response by 90°. While this does not provide information about the absolute phase response of simple cells, it does suggest, that if only two classes of cells exist, in sine and cosine phase, they tend to be grouped together.

Field and Tolhurst (1986), however, failed to confirm this finding, either by measurements of the phase response or from mapping of the receptive fields of simple cells of cat cortex. One possible explanation for the discrepancy between the two sets of electrophysiological results could be the temporal frequencies employed. Kulikowski (personal communication) asserts that the phase response is sine or cosine only if the appropriate temporal frequency is used.

In any event it would be unlikely that biological filters should be tuned to exactly 0 and 90°. Given sampling and other constraints, one would not expect receptive fields to be exactly symmetrical. However, the results of this paper suggest that while the division may not be exact, two broad types of detectors exist in the human brain, with even-symmetric and odd-symmetric receptive fields.

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APPENDIX

Probability Summation

The human visual psychometric function $P(C)$, describing the probability of a correct response as a function of contrast C, is usually well fit by a Weibull function (Weibull, 1951; Quick, 1974; Graham, 1977):

$$P(C) = 1 - (1 - \gamma)\exp - (C/\alpha)^{\beta}; \qquad \text{(A1)}$$

where C is signal contrast, γ is the guessing rate (equal to 0.5 for a two alternate forced choice experiment), α threshold contrast and β a parameter determining the log–log steepness of the function. The proportion correct at threshold, where $C = \alpha$, is given by $1 - (1 - \gamma)/e$. Thus $P(\alpha) = 0.816$ for $\gamma = 0.5$.

For several conditions of Expt 1, psychometric curves were measured and fitted with the Weibull function, using the program QUICK (Watson, 1979). The fit was generally good, and gave estimates of β around 3.5, consistent with most previous studies.

Probability summation refers to the increased probability of a response as more detectors are recruited. The probability of at least one response is given by 1 minus the probability that no detectors respond. If we assume only two classes of detectors, in cosine and sine phase, each of these detectors will give a response proportional to cos (ϕ) and sin (ϕ) respectively, where ϕ is the phase of the stimulus.

For any phase, ϕ the probability of a response to a stimulus of contrast C is given by:

$$P(C) = 1 - \tfrac{1}{2}\exp\{-[(\cos\phi)/(\alpha_c)C]^\beta - [(\sin\phi)/(\alpha_s)C]^\beta\}; \quad \text{(A2)}$$

where α_c is the contrast threshold for a stimulus of cosine phase and α_s the threshold for sine phase. At threshold

$$P(\alpha) = 1 - \tfrac{1}{2e} = 1 - \tfrac{1}{2}\exp\{-[(\cos\phi)/(\alpha_c)C]^\beta - [(\sin\phi)/(\alpha_s)C]^\beta\}. \quad \text{(A3)}$$

Solving for C gives

$$C = \left[\left(\frac{\cos\phi}{\alpha_c}\right)^\beta + \left(\frac{\sin\phi}{\alpha_s}\right)^\beta\right]^{-\frac{1}{\beta}}. \quad \text{(A4)}$$

The middle curves of figure 5 were calculated by this equation. β was fixed at 3.5 for both observers, and α_c and α_s fixed by the contrast thresholds of each observer for cosine ($\phi = 0°$) and sine ($\phi = 90°$) stimuli.