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Vernier Acuity for Edges Defined by Flicker

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We investigated the effects of contrast and temporal frequency on vernier edge alignment thresholds. Edges were defined by the presence of a 180 deg phase difference in the temporal modulation waveform of adjacent rectangles with spatially uniform luminances. Thresholds of 10 arc sec or less could be obtained at high contrasts, and flicker rates up to 8 Hz. Above this range, thresholds increased rapidly with decreasing contrast and increasing rates of flicker. Thresholds also increased with increasing temporal frequency over the range 0–20 Hz for contrasts normalized to thresholds for the detection of either flicker or the edge. Linear regression on log–log plots of threshold vs contrast at different temporal frequencies showed that the relationship between threshold and contrast was well described by a power law with an exponent of about −0.5 at temporal frequencies of 8 Hz or lower. About 8 Hz the slope more than doubled and thresholds increased. Thresholds also increased when the relative phase (i.e. the instantaneous sign of the contrast) of the upper and lower edges was reversed, and this effect was observed at all temporal frequencies. Measurements of threshold as a function of the size of a gap between the upper and lower edges suggested that the integration region was larger at 16 Hz or above than at 8 Hz. The results suggest that the channels which mediate vernier hyperacuity are phase sensitive and attenuate frequencies higher than 8 Hz.

Magnocellular pathways Parvocellular pathways Parallel pathways Hyperacuity Temporal frequency

INTRODUCTION

Humans are able to detect the presence of extremely small vernier misalignments of abutting lines or edges. Unpractised subjects can detect offsets of as little as 10–15 arc sec, which is about half of the spacing between adjacent foveal cones, while a skilled observer may do as well as 4 arc sec. This ability has been termed "hyperacuity" because the distances involved are smaller than the minimum angle of resolution, which is typically around 30–60 arc sec. The factors which permit such high acuities have been extensively investigated (Westheimer, 1981). It has been found for example that acuities increase with stimulus contrast up to high contrast levels (Watt & Morgan, 1983; Mather, 1987; Wehrhahn & Westheimer, 1990), that they are independent of line length for lengths of 5 min arc or greater (Westheimer & McKee, 1977) and that acuity is highest in the fovea and declines with eccentricity more rapidly than the corresponding decline in resolution (Weymouth, 1958; Westheimer, 1982). Performance is also about as good for a briefly flashed stimulus as it is for one moving at a velocity of 4 deg/sec (Westheimer & McKee, 1975).

While the influence of these and many other spatial and luminance defined parameters on vernier acuity has been explored, relatively little attention has been paid to the temporal properties of the underlying mechanisms. Flashed or moving stimuli contain a spectrum of temporal frequencies and so do not allow one to specify which temporal channels may have contributed to performance. We have attempted to study the temporal characteristics of the mechanisms subserving vernier acuity, by measuring acuities for the detection of offsets between edges defined by contrast-reversing flicker. Information about the presence of an offset in this stimulus is sharply localized in the temporal frequency domain. We studied the effects of varying both the contrast and the temporal frequency of the flicker on offset thresholds. Our results show that while acuity is best at high contrasts and low temporal frequencies, thresholds of 10 arc sec or less could be obtained at flicker rates as high as 8 Hz. A brief description of these results has been published (Fendick & Swindale, 1992).

METHODS

Apparatus

A Tektronix 608 monitor with a P31 green phosphor driven by a computer controlled Picasso image synthesizer (Innisfree) was used to generate the stimuli. The display area was divided into four spatially uniform quadrants, and the luminance of each quadrant was sinusoidally modulated in time with a given contrast,

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phase, and temporal frequency. In some experiments (e.g. Expt 1) an edge between two adjacent quadrants was produced by keeping the luminance of one quadrant fixed and temporally modulating the luminance of the adjacent quadrant, keeping the mean luminances the same. In other cases (e.g. Expt 3) both quadrants flickered, and a 180 deg temporal phase difference in the modulation waveforms produced an apparent edge.

By varying the relative position of flicker-defined edges in the upper and lower halves of the display, we produced a vernier stimulus. Normally, the phase of the adjoining quadrants in the upper and lower halves of the display was the same, so that only the vertical boundary between the left and right quadrants was visible. Because the mean brightness of all four quadrants was the same, the phase difference in the flicker was the only cue to the existence of an edge. At 0 Hz, our stimulus was the same as that used by Wehrhahn and Westheimer (1990): a static edge with the same sign of contrast in the upper and lower halves of the display.

Testing procedure

The display screen subtended 2 × 2.45 deg and was viewed binocularly in a dimly lit room from a distance of 2.8 m. The subjects, with head supported by a chinrest and forehead bar, had no difficulty under these conditions maintaining steady gaze in the center of the screen without the aid of a fixation spot. Thresholds were determined using a two-alternative forced-choice method of constant stimuli. In the experiments which measured vernier thresholds, the subject's task was to signal the direction of displacement of the upper edge relative to the lower one by pressing one of two buttons. In experiments which measured threshold contrast for detection of flicker or an edge, the subject similarly signaled in which half of the display the stimulus appeared. There was no error feedback. Each threshold was determined by probit analysis (Finney, 1971) of the responses to 12 presentations of each of nine different stimulus values, equally spaced on a linear scale, given in pseudo-random order. Appropriate ranges were chosen on the basis of preliminary trials in each case. On each trial, a stimulus was presented for 3 sec, with the contrast linearly ramped between zero and the maximum desired level over 500 msec at the beginning and end of each presentation. The stimulus was thus visible at maximum contrast for a period of 2 sec. In the interval between presentations the screen had a spatially and temporally uniform luminance equal to the mean of the presentations. The edges of the screen were clearly visible and provided a cue for fixation and accommodation.

Flicker contrast was defined as $(L_{\max} - L_{\min})/(L_{\max} + L_{\min})$ where $L_{\max}$ and $L_{\min}$ represent the maximum and minimum intensities of the sinusoidally modulated screen intensity. Maximum and minimum screen luminances (i.e. the maximum modulation depth) were 11.1 and 3.28 cd/m^2 respectively. Although low, these values are well above the scotopic/photopic boundary at around 0.1 cd/m^2. Between 3 and 12 (most often 5 or 6) separate determinations of each threshold were made and the mean and standard deviation of these measurements was used for analysis. Because of the possibility that a bisection cue might be used under conditions where large vernier offsets had to be used to obtain correct responses, we generally did not attempt to repeat initial measurements where thresholds of greater than about 300 arc sec (about 3% of the display width) were obtained; and have omitted these data from the analysis of results. We attempted to reduce loss of flicker contrast sensitivity due to adaptation, by periodic brief rests every 30–50 presentations, and by counterbalancing the order of presentation of frequencies in successive tests.

Although vernier thresholds are known to improve with practice, repeated determinations of thresholds under the same conditions showed no consistent trend towards lower thresholds in either subject.

Subjects

The subjects were the authors, who have normal binocular vision when corrected for refractive error, as here. MGF is experienced in vernier tasks, and NVS is not.

EXPERIMENT 1: EFFECT OF TEMPORAL FREQUENCY ON VERNIER ACUITY AT A FIXED CONTRAST LEVEL

Results

In this experiment we measured alignment thresholds as a function of modulation frequency at the maximum contrast level our apparatus could provide (0.54). For this experiment the luminance of the upper and lower left quadrants of the display was constant in time, and the luminance of the upper and lower right quadrants flickered in phase. The results for both subjects, which are similar, are shown in Fig. 1. Thresholds were about 10–12 arc sec at 0 and 4 Hz, and showed a rapid increase above 10 Hz. At frequencies of 16 Hz and above, thresholds were > 30 arc sec; i.e. no longer in the hyperacuity range.

Discussion

Subjectively, the increasing difficulty of the task above 10 Hz seemed to correlate with a loss both in the visibility and in the apparent sharpness of the edge. We also had the impression that judgments were easier with slightly eccentric fixation at higher frequencies, although we always strove to maintain steady central fixation. Because the increase in vernier offset thresholds at higher temporal frequencies might simply be due to a decline in the target's visibility, we attempted to control for this (Expt 2) by setting the contrast of the stimulus at a fixed ratio above each subject's measured threshold for detection of (a) the flicker and (b) the edge.

EXPERIMENT 2: EFFECT OF TEMPORAL FREQUENCY AFTER NORMALIZATION FOR DETECTABILITY

In this experiment we normalized the stimulus contrast for equal visibility at each temporal frequency in two different ways: (a) by normalizing to the threshold contrast required for detection of flicker and (b) by normalizing to the threshold contrast required for detecting the edge.

Results

Normalizing for detection of flicker. Threshold contrast for the detection of flicker was measured by sinusoidally modulating the luminance of either the right or the left half of the screen at a given temporal frequency while the luminance of the other half was held constant at the mean level. The subject's task was to signal whether the left or the right side of the display was flickering. After determination of threshold contrasts for a variety of temporal frequencies [Fig. 2(a)], we measured vernier offset thresholds using contrast levels set at 6 times the flicker detection level for each temporal frequency. The results are shown in Fig. 2(b). Thresholds were higher overall because of the relatively low contrasts used. Both subjects showed an approximately four-fold increase in thresholds as temporal frequency increased from 0 to 12 Hz, with little further increase between 12 and 20 Hz.

Normalizing for detection of the edge. Since detecting and localizing a flicker-defined edge is distinct from the task of merely detecting flicker it could be argued that it would be more appropriate to normalize contrasts for detection of the edge rather than flicker. We therefore repeated the previous procedures and measured threshold contrast required for detecting the presence of the edge. Both the left and right quadrants of either the upper or lower half of the screen were modulated in counterphase. The left and right quadrants of the other half were modulated in phase at the same temporal frequency. The subject's task was to signal whether the edge appeared to be in the upper or lower half of the display. Contrast thresholds for this task varied differently with frequency than did flicker detection thresholds, and are shown in Fig. 2(c). Thresholds remained unaffected by flicker up to 6 Hz, and thereafter increased linearly (on a log contrast scale). For the subsequent vernier experiment we set the contrast modulation level in each subject to be 5 times higher than the edge detection threshold at each temporal frequency. The results are shown in Fig. 2(d). Despite equating the stimuli for edge visibility, both subjects showed an approximately 3–4 fold increase in vernier thresholds between 0 and 16 Hz, with the lowest thresholds (of around 30 arc sec) obtained at 0 Hz, as in Expt 2a.

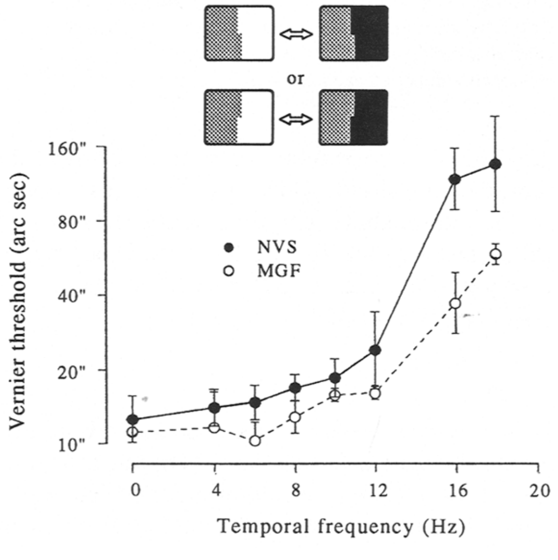

FIGURE 1. Vernier acuity thresholds in arc seconds as a function of temporal frequency for flicker-defined edges at a constant contrast level of 0.58. Data for the two subjects (NVS and MGF are shown). Each point in this and subsequent graphs shows the mean of 3–12 (typically 5) separate determinations of threshold, and the error bars show the standard deviation of these values. In this and subsequent figures, the left and right panels of the inset diagram the instantaneous appearance of the display at 0 and 180 deg phases respectively, while the upper and lower panels indicate the discrimination the subject was asked to make.

Discussion

It is unlikely that the increase in thresholds with increasing temporal frequency observed in Expt 1 can be fully ascribed to reduced visibility because the increase remained, although reduced in magnitude, when contrasts were normalized to either those required for detection of the flicker [Fig. 2(a)] or for detection of the edge [Fig. 2(b)]. Normalizing for edge detection may provide a better control for stimulus visibility in these two experiments because edge detection requires phase sensitive channels whereas flicker detection does not. Although the particular procedure that we used for measuring the detectability of the edge was, in fact, a localization task (since the observer had to signal whether the edge appeared in the upper or lower half of the screen) it required an accuracy of only about a degree of visual angle (since the screen was 2 deg high). Thus the measured thresholds were probably very close to the absolute detection thresholds.

Two additional problems arise in interpreting the results of Expt 2. The first is that a 5- or 6-fold increase in contrast above the detection threshold (whether for an edge or flicker) may not produce equal increases in the responses of channels responding at different temporal frequencies. This would frustrate our objective of normalizing for visibility. However, one interpretation of the results of Expt 3 (presented below) is that the contrast gain of the channels involved in fine-grain localization increases with increasing temporal frequency. This means that a given increase in contrast above detection threshold would have the effect of making the stimulus more visible at higher temporal frequencies than at low ones. If visibility were the only factor determining thresholds then thresholds in Expt 2 would have been expected to decrease, rather than increase with frequency.

EXPERIMENT 3: EFFECTS OF CONTRAST AT DIFFERENT TEMPORAL FREQUENCIES

Vernier acuity is known to exhibit a power-law relationship with stimulus contrast, with the exponents

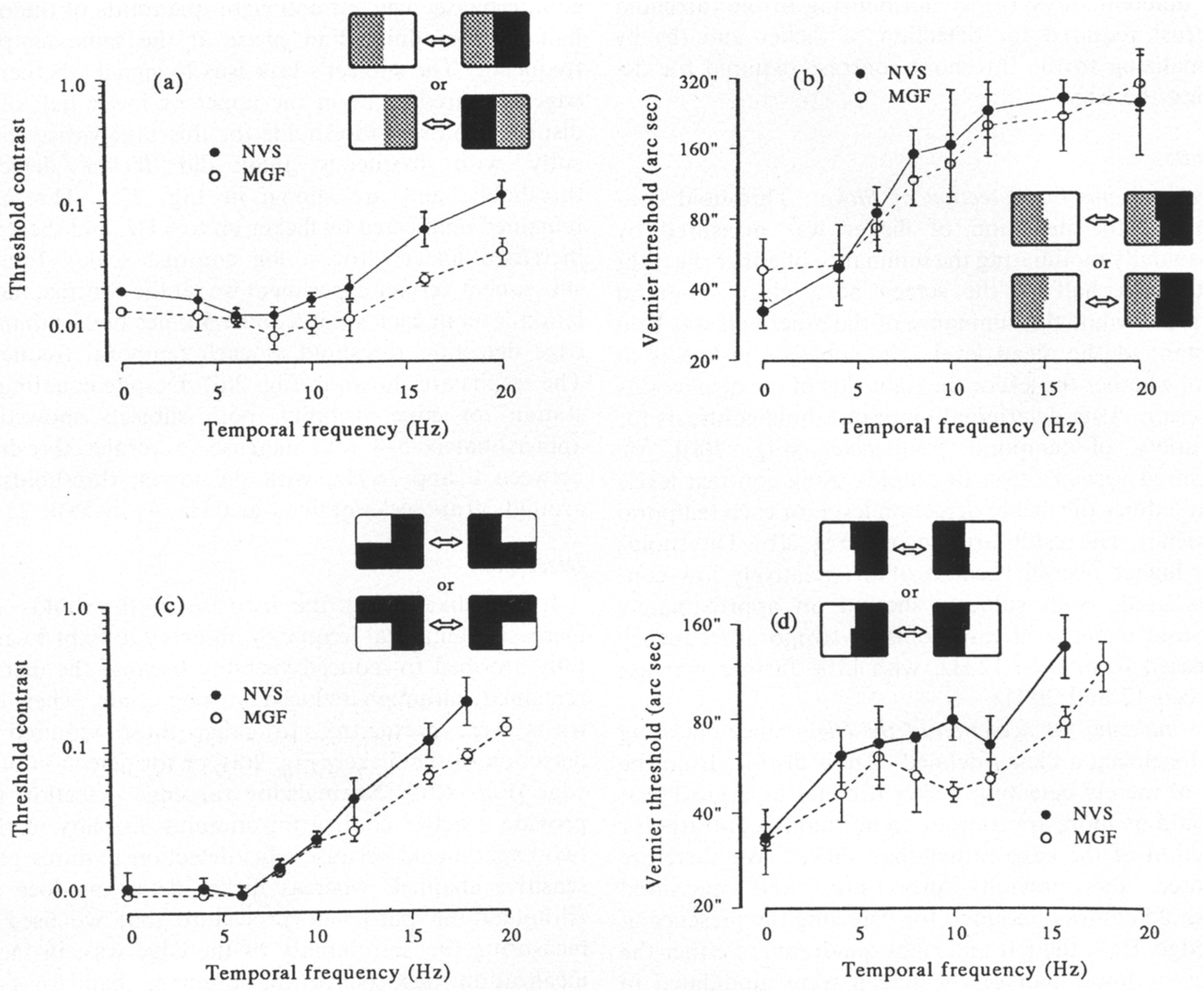

FIGURE 2. (a) Contrast thresholds for detection of flicker as a function of temporal modulation frequency. (b) Vernier thresholds as a function of temporal frequency for contrast levels set to 6 times the flicker detection thresholds for each subject at each temporal frequency shown in (a). (c) Contrast thresholds for correctly locating a flicker-defined edge in the upper or lower half of the display, as a function of temporal frequency. (d) Vernier thresholds as a function of temporal frequency for contrast levels set to 5 times the edge detection thresholds for each subject at each temporal frequency.

found in different studies ranging between −0.5 and −0.94 (Mather, 1987; Watt & Morgan, 1983; Wehrhahn & Westheimer, 1990). In Expt 3 we studied the impact of temporal frequency on this dependence.

Results

Vernier thresholds were measured as a function of flicker contrast, for a range of temporal frequencies. Data from the two subjects are shown in Fig. 3(a, b) on log–log plots. At 0 Hz we found, as have other observers (Watt & Morgan, 1983; Wilson, 1986; Bradley & Skottun, 1987), that the relationship between vernier acuity and contrast was well described by a power law. In our case, the exponent (determined by linear regression) had a value of −0.44 (MGF) and −0.43 (NVS). For subject MGF both the thresholds and the slope (i.e. the exponent) of the contrast-threshold functions remained approximately the same up to 8 Hz (where the exponent had a value of −0.56). Above 8 Hz, both thresholds and exponents increased. At 16 Hz, the exponent was −0.90 and at 20 Hz it was −1.72. Results for subject NVS were similar except that, for this subject, the contrast-threshold functions gradually steepened across the intermediate temporal frequencies (4–10 Hz). Overall, however, the functions changed in much the same way as for observer MGF, with slopes of −0.99 and −1.1 at 10 and 12 Hz respectively.

Discussion

The increase in slopes to a value of −1.0 or greater at temporal frequencies above 10 Hz suggests the involvement of different mechanisms at high and low temporal frequencies. At high temporal frequencies (i.e. > 10 Hz) the responses in whatever channels are involved seem to change much more rapidly with contrast than at low temporal frequencies. Increasing the contrast beyond the highest level we used here (0.58) should, therefore, cause a greater improvement in thresholds at high frequencies than at low frequencies. If we extrapolate our data (by assuming lines of constant slope on a log–log plot) to predict thresholds for a maximum contrast value of 1.0 there is, nevertheless, still a substantial worsening of vernier thresholds with increasing temporal frequency. For example, subject MGF would have thresholds of 6.7 arc sec at 0 Hz, 6.8 arc sec at 8 Hz, 13.8 arc sec at 14 Hz and 30 arc sec at 20 Hz. A difference is likely to remain even if the contrast threshold functions flatten out more at low temporal frequencies than at high ones.

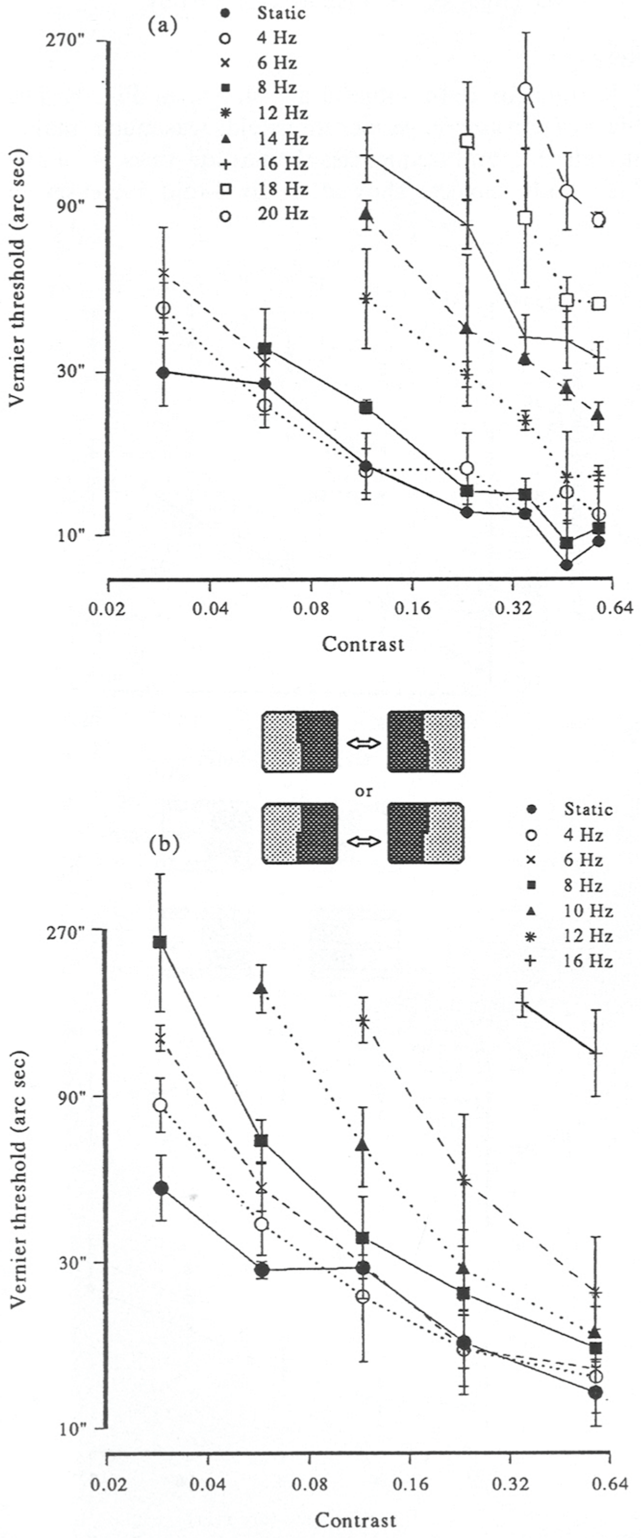

FIGURE 3. Vernier thresholds in arc seconds as a function of contrast, at a variety of different temporal frequencies. Data from subject MGF are shown in (a) and from NVS in (b).

EXPERIMENT 4: EFFECTS OF RELATIVE PHASE OF THE UPPER AND LOWER EDGES

Vernier thresholds are known to increase by a factor of 2–3 if the sign of the contrast of the two bars or edges whose positions are being compared is different (Mather & Morgan, 1986; O'Shea & Mitchell, 1990). To investigate the possible dependence of this effect on temporal frequency, we introduced a 180 deg phase difference between the flicker in the adjoining upper and lower quadrants of the display. At 0 Hz this stimulus is similar to that used by Mather and Morgan. Because adjoining left and right quadrants were also 180 deg out of phase when temporal modulation was introduced, the upper left and lower right quadrants flickered in phase, as did the lower left and upper right quadrants. This had the unavoidable effect of introducing a horizontal edge bisecting the vernier, and the effects of this additional contour on acuity have to be considered.

Results

The results of this experiment are shown in Fig. 4. Both subjects showed a small and nearly uniform elevation in thresholds at all temporal frequencies tested. Subject NVS showed an average increase in thresholds of 1.46 across all frequencies, while subject MGF showed a somewhat larger average increase of 1.82 with some indication of a smaller increase at higher temporal frequencies.

Discussion

These results show that the mechanism comparing the positions of flicker defined edges is sensitive to their relative phase up to at least 18 Hz (the highest frequency tested). This is surprising given the lack of any subjective impression of edge polarity at frequencies of 10 Hz or greater (where the edge had an illusory quality). Although phase information is necessarily required for the detection of the edge, it is possible that, following detection, edge positions are compared by a phase-insensitive mechanism. Our results suggest that below 18 Hz this is not the case. An alternative explanation is that a constant elevation in thresholds was caused by the horizontal edge resulting from the phase difference between vertically adjacent upper and lower quadrants of the display. This would imply that phase information is unimportant at all frequencies, including 0 Hz. However, this would be inconsistent with the rise in thresholds reported by O'Shea and Mitchell (1990) for static bar stimuli of opposite contrast where a horizontal edge was not present. In addition, results from the following experiment (Expt 5), in which a horizontal gap between the upper and lower halves of the display was present (resulting in the presence of horizontal edges) did not, for small gaps, produce significant increases in vernier thresholds.

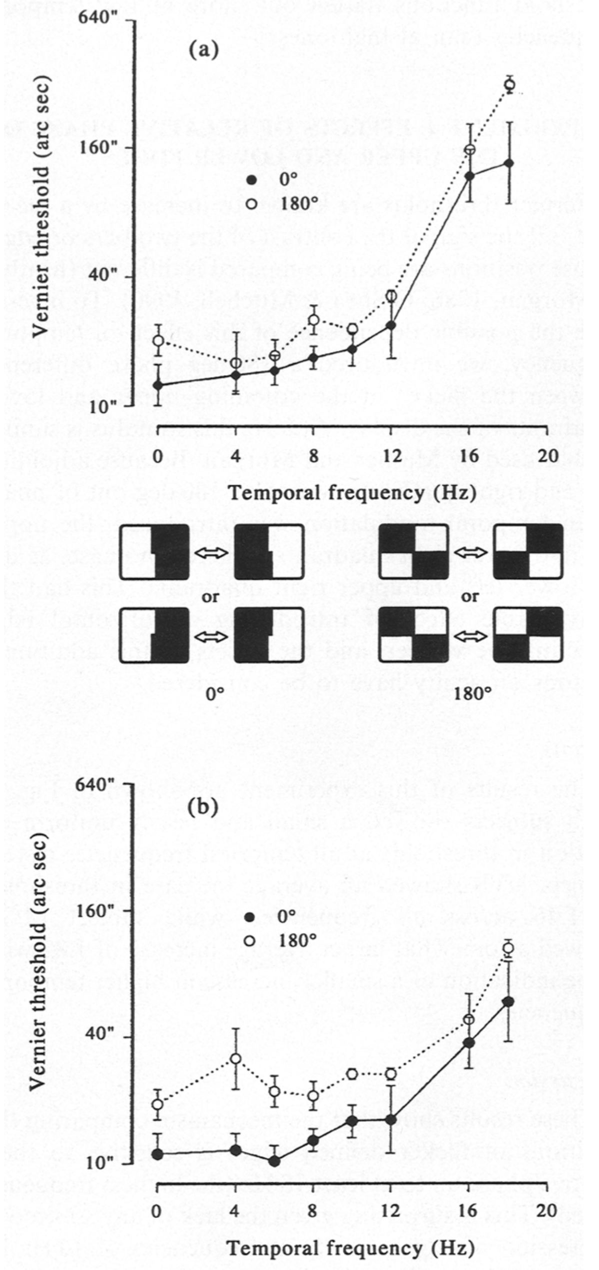

FIGURE 4. The effect on vernier threshold of reversing the instantaneous sign of edge contrast in the upper and lower halves of the display. This was done by introducing a 180 deg phase difference in the flicker waveform of adjoining quadrants in the upper and lower halves of the display. Diagonally adjacent quadrants thus flickered in phase. Solid symbols show the 0 deg phase (i.e. normal) condition (data are the same as in Fig. 1) and open circles show the 180 deg (phase reversed) condition. Data in (a) are from subject NVS and in (b) from MGF.

EXPERIMENT 5: EFFECTS OF VERTICAL SEPARATION

Vernier thresholds increase when two vertical bars are separated by a vertical gap of greater than about 5 min arc (Westheimer & McKee, 1977) and this has been used to define an "integration region" for vernier offset detection. We studied the effect of gap size on vernier thresholds at different temporal frequencies to see if the size of this integration region varied. In order to keep the lengths of the edges the same for different gap sizes, the length of each edge was reduced to 40 arc min. We measured vernier offset thresholds for each of five vertical gap sizes (2, 4, 8, 16 and 32 arc min) at modulation frequencies of 0, 8 and 16 Hz (for subject NVS) or 0, 8 and 18 Hz (for subject MGF). At the largest gap size the upper edge of the top bar, and the lower edge of the bottom bar coincided with the upper and lower edges of the display respectively.

Results

Results for both subjects are shown in Fig. 5. The effect of gap size on vernier thresholds was much smaller at high temporal frequencies than at low ones. At 0 and 8 Hz both subjects showed 2- to 4-fold increases in

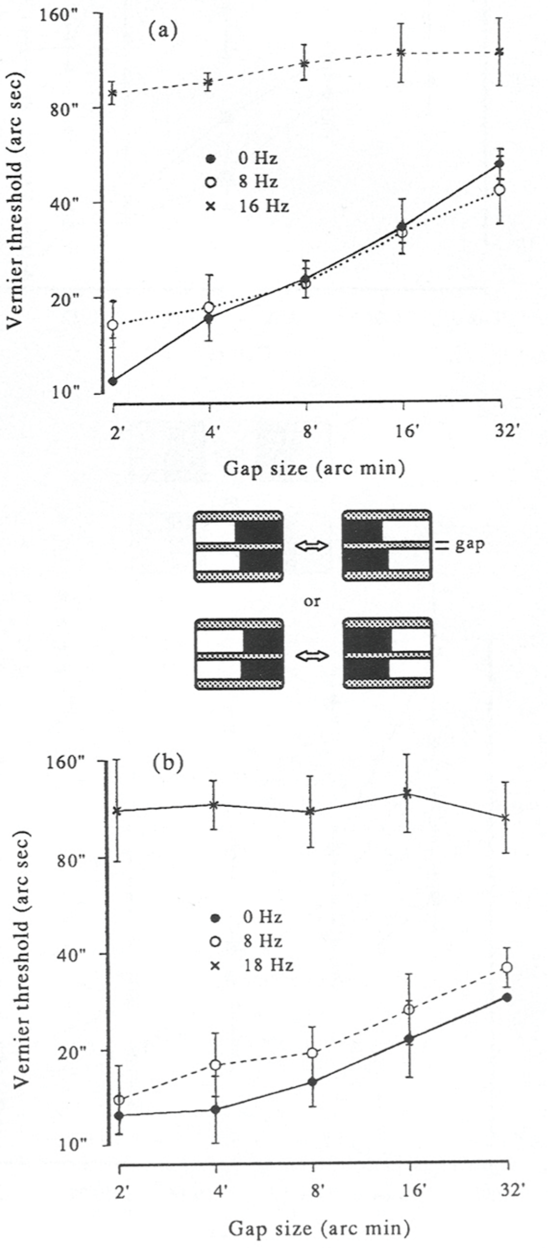

FIGURE 5. The effect of gap size on vernier threshold for subjects NVS (a) and MGF (b) at temporal frequencies of 0, 8 and 16 Hz (NVS) or 18 Hz (MGF).

thresholds as the size of the vertical gap between the edges increased from 2 to 32 arc min. However at 16 Hz, subject NVS showed only a slight increase in thresholds for a gap size of 32 arc min, while at 18 Hz subject MGF's thresholds were unaffected by gap size over the range tested.

Discussion

The result of Expt 5 suggests that the integration region for vernier offset judgments increases in size with temporal frequency. This is not surprising given that vernier acuity is so much worse at high temporal frequencies. If the integration region is 20–60 times the size of the threshold (as it is for normal vernier acuity) then at 18 Hz where a threshold of about 2 arc min was measured, the corresponding integration region might be up to a degree in size, or about twice the size of the largest gap tested here.

GENERAL DISCUSSION

Localization of flicker-defined edges

We have found that the accuracy with which contrast-reversing edges can be localized by the visual system is strongly dependent on both the temporal frequency of the phase reversal and its contrast, and, to a lesser extent, on the relative phases (or instantaneous contrast polarity) of the two edges. Although this report has emphasized the *loss* of positional acuity for flicker defined edges, it is worth stressing that, at high contrasts, positional acuity remains surprisingly good up to moderately rapid rates of contrast reversing flicker. For example, at the highest contrasts used (0.58) both subjects showed little change in thresholds between 0 Hz (i.e. for a static edge) and 8 Hz (Fig. 4). MGF's threshold at 8 Hz was around 10 arc sec, and, on the basis of extrapolation, might have been as small as 6.8 arc sec at a contrast of 1. (The overall difference in thresholds between the two subjects may be attributable to MGF's previous extensive experience as a subject in vernier tasks.) Although our display could not produce contrasts higher than 0.58, it is possible that at a contrast of 1, thresholds might have remained unchanged up to perhaps 10 or 12 Hz.

This comparison may underestimate performance at temporal frequencies above 0 Hz to some extent, since it can be argued that the r.m.s. (root-mean-square) value of the contrast for a sinusoidally flickering stimulus would be a better way of expressing its effective contrast than the measure we used (which expresses contrast in terms of the maximum and minimum values of the sinusoidal temporal variation in luminances). If we rescale the contrasts in this way (by dividing all the contrast values for frequencies > 0 Hz by $\sqrt{2}$) the functions shown in Fig. 4 (with the exception of those at 0 Hz) are shifted to the right by a constant amount. The differences in the contrast threshold functions between 0 and 8 Hz (Fig. 4) then become even smaller than they already are, further reinforcing the lack of effect of contrast flicker at frequencies up to 8 Hz. Moderately rapid rates of contrast reversal can therefore be added to the list of stimulus perturbations (such as image motion) which have little or no effect on hyperacuity thresholds (Westheimer, 1981).

At flicker rates above 8 Hz, vernier offset thresholds increase, the increases being much greater at low contrast levels than at high ones. At a contrast of 0.58 MGF's threshold at 20 Hz was about 90 arc sec. An optimistic estimate of his threshold at a contrast of 1 (obtained by extrapolating the data obtained at two lower contrast levels) is 30 arc sec. NVS (who was unable to do the task at 20 Hz) had a threshold at 16 Hz of about 180 arc sec, and extrapolation gives an optimistic estimate in his case of a threshold of 84 arc sec at a contrast of 1.

Temporal integration and vernier acuity

It has been demonstrated that vernier hyperacuity involves a summation of information present in a spatial window, or integration region, roughly 5 min arc in size. Thresholds rise when the dots or lines whose positions are being compared are more than a few minutes of arc apart (Westheimer & McKee, 1977) or when irrelevant stimuli are placed within this region (Westheimer & Hauske, 1975; Williams & Essock, 1986). Our results support the existence of an analogous temporal integration window for vernier hyperacuity. An edge whose contrast is flickering sinusoidally at 8 Hz is continuously present at $> 50\%$ of its maximum contrast for periods of about 40 msec, with contrast reversals occurring every 62.5 msec, and this is sufficient to support nearly normal hyperacuity. The decline in vernier acuity at higher temporal frequencies might be caused by contrast reversals at intervals of < 60 msec, which we suppose could interfere with vernier acuity in much the same way that a flanking line does in the spatial domain (Westheimer & Hauske, 1975; Williams & Essock, 1986). Previous estimates of a temporal integration period for vernier hyperacuity are also in this range. Fahle and Poggio (1981) and Morgan and Watt (1983) studied spatio-temporal interpolation for moving stimuli which were discretely sampled in space and time, and estimated that the temporal filters involved had time constants of the order of 20–50 msec. The notion of the existence of both a spatial and a temporal integration window for vernier hyperacuity is also consistent with the observation that offset thresholds are unaffected by image velocities up to 4 deg/sec (Westheimer & McKee, 1975) since a stimulus moving at 4 deg/sec will take about 20 msec to cross a region 5 arc min in size. In other words, a necessary condition for vernier hyperacuity seems to be that the stimulus be continuously visible within a region roughly 5 arc min in size for a period of around 20–40 msec. The explanation for this is most likely to be found in the properties of foveal visual cortical neurons, which are likely to have receptive fields of about this size, and to respond poorly to stimulus velocities > 4 deg/sec.

Effects of temporal frequency on contrast dependence

Our results show that the dependence of vernier acuity on contrast varies with temporal frequency, indicating the involvement of different neural mechanisms at low vs high temporal frequencies. At frequencies of 8 Hz and lower we found that the data followed a power-law relationship with an exponent of about −0.44. Above 8 Hz, the value of the exponent more than doubled, reaching a value of −1.72 at 20 Hz for subject MGF and −1.1 at 12 Hz for NVS. Our results at low temporal frequencies are in agreement with previous studies which used static stimulus presentations (Watt & Morgan, 1983; Wehrhahn & Westheimer, 1990) and which also found exponents with a value close to −0.5. Several other studies have found somewhat larger values: e.g. with flashed presentations Wilson (1986) found values between −0.67 and −0.94 in different subjects, and Bradley and Skottun (1987), using gratings of different spatial frequencies, found a value of −0.8 which was relatively independent of spatial frequency. The reasons for these differences are not entirely clear. However Wilson (1986), suggested that transient presentation of test stimuli would produce higher exponents, while Regan (1989) found that orientation discrimination thresholds were more highly dependent on contrast for contours defined by relative motion than for those defined by luminance. This is consistent with the effects of temporal frequency observed in the present study and suggests that tasks mediated by motion pathways generally show a higher contrast dependence than those which involve processing of contour information at low temporal frequencies.

Relative involvement of M and P pathways in vernier actuity

Since M cells are known to have a higher contrast gain than P cells (Kaplan & Shapley, 1986) our finding of an increasing contrast gain with temporal frequency suggests, at first sight, that M pathways mediate hyperacuity at high temporal frequencies and P pathways at low temporal frequencies. This would be consistent with the fact that the ratio of M cell to P cell response is likely to increase at frequencies above 10 Hz (Derrington & Lennie, 1984) and, at 16–20 Hz, the M cell response may well predominate. Unfortunately for this interpretation, however, the high contrast gain of M cells is most obvious at low contrasts (e.g. below 0.1) and, because responses tend towards saturation at higher contrasts, M cell responses at high contrasts are likely to change *less* rapidly with contrast than those of P cells. This would lead to a flattening, rather than a steepening of the threshold contrast function at high contrasts and temporal frequencies. It can likewise be argued that the relatively higher contrast thresholds of P cells (at all temporal frequencies) would lead to M cell responses dominating at low contrasts (Purpura, Kaplan & Shapley, 1988), with a corresponding increase in the slope of the threshold contrast function at low contrasts. Although one subject did show evidence of a steepening of the function for low contrasts and intermediate temporal frequencies, there was no evidence for any change of slope for either subject at 0 Hz down to contrasts of about 0.03. Other studies which extended the range of stimulus contrasts down to low levels also failed to find a change in slope at low contrasts (Bradley & Skottun, 1987; Wehrhahn & Westheimer, 1990). Overall, therefore, it is hard to find a simple correspondence between our results and the contrast–response characteristics of either the M or the P pathways at the retinal and LGN levels.

Although the slopes of the threshold contrast functions do not provide a clear answer to the question of the relative involvement of M and P cells in vernier acuity, our data show that acuity is poor at low contrasts and high temporal frequencies, and good at high contrasts and low temporal frequencies. This suggests that P cells are more likely to be responsible for high acuities than are M cells. Anatomical and physiological data from macaque monkey retinas appear to lend support to this belief. Foveal P cells are about an order of magnitude more numerous than M cells (Perry, Oehler & Cowey, 1984), and have smaller cell bodies (Perry *et al.*, 1984; Grünert, Greferath, Boycott & Wässle, 1993) and smaller receptive fields (Derrington & Lennie, 1984). The difference in field sizes may be especially large in the fovea (where few, if any, physiological recordings appear to have been carried out) since recent anatomical data (Grunert *et al.*, 1993) show that the cone to ganglion cell convergence ratio is about 1 : 1 for foveal P cells, and around 30–50 : 1 for foveal M cells. The relative preponderance of M cells increases with distance from the fovea (Malpeli, Lee & Baker, 1993), whereas vernier acuity thresholds decline more rapidly with eccentricity than spatial resolution (Westheimer, 1982), which is almost certainly determined by P cell density.

In spite of these considerations, we cannot exclude the possibility that M cells cooperate with P cells in carrying out vernier acuity at low temporal frequencies, or even that M cells are solely involved. M cells probably responded in all of the stimulus conditions used in the present experiments. Although they give poor responses at low temporal frequencies, eye movements would ensure that M cells were well stimulated even in the 0 Hz condition. While P cells have higher spatial resolution than M cells, vernier acuity is best at intermediate spatial frequencies of about 16 c/deg (Bradley & Skottun, 1987). Individual parafoveal M cells have been reported to have resolutions this high or greater (Crook, Lange-Malecki, Lee & Valberg, 1988) although the Nyquist limit of the foveal M cell mosaic may be as low as 15 c/deg (Grünert *et al.*, 1993). The loss of hyperacuity at temporal frequencies and contrasts at which M cells should be responding well, may simply reflect a loss of either frequency or phase sensitivity in cortical pathways receiving M cell inputs. Although M cell responses saturate at moderate to high contrast levels, improvement in vernier thresholds at high contrasts might be explained by increased recruitment of retinal units with receptive fields along the fringes of the edge, and exposed to lower contrast levels than that of the edge itself (Watt & Morgan, 1983). Thus, the lower contrast thresholds of M cells would mean that the area of M cells responding to a high contrast edge would exceed the area of responding P cells. This might, to some extent, compensate for the effects of their lower density.

It has been suggested (Parker & Hawken, 1985; Shapley & Victor, 1986) that the neural factors which limit hyperacuity thresholds can be measured by finding the smallest change in the position of an edge in a receptive field which can provoke a statistically significant change in firing rate. Lee, Wehrhahn, Westheimer and Kremers (1994) showed that the sensitivities of parafoveal M cells measured this way were greater than those of P cells at the same eccentricity and are close to human psychophysical thresholds for brief motion at the same location. For this reason these authors suggest that P cells lack the positional sensitivity required for hyperacuity judgments. Similar conclusions were reached based on a calculation of the theoretical sensitivities of human foveal ganglion cells (Wachtler, Wehrhahn & Lee, 1993). These measurements may however underestimate the positional acuities of foveal P cells, which receive inputs from single cones. Nor is it clear that detection of brief motion will utilise similar mechanisms to those involved in detecting vernier offsets. In addition, it is likely that the limits to vernier hyperacuity are set by the performance of the cortex rather than the retina (Geisler, 1984; Klein & Aitsebaomo, 1985). If so, then studies of the differential sensitivities of individual retinal M and P cells to hyperacuity stimuli may not resolve the issue of how each cell type might be involved in such tasks.

Recent behavioral measurements of vernier acuity in monkeys with retinal P-cell lesions produced by acrylamide exposure (Lynch, Silveira, Perry & Merigan, 1992) might have been expected to resolve the issue, but appear not to. Although thresholds were elevated in one of two lesioned animals, providing some support for the role of P cells, thresholds were unchanged in the other animal, supporting exactly the opposite conclusion. More significantly perhaps, none of the treated or normal monkeys used in the study showed vernier offset thresholds of less than about 50 arc sec. These values are well outside the range of most human hyperacuities, and arguably do not qualify as a hyperacuity. Ideally these experiments should be repeated on monkeys able to discriminate vernier offsets of < 30 arc sec.

CONCLUSIONS

Our results suggest the existence of two visual mechanisms, one active at high temporal frequencies with relatively poor positional acuity and a high contrast gain (exponent of -1 or greater), and the other active at low temporal frequencies with a lower contrast gain (exponent of -0.5) and positional acuities in the hyperacuity range. Although these mechanisms may reflect the separate behaviors of M and P pathways, another possibility is that they correspond to parietal (dorsal) and temporal (ventral) processing streams (Ungerleider & Mishkin, 1982) which diverge at levels above that of Vl, and do not receive exclusively M or P cell inputs (Maunsell, Nealy & Ferrara, 1992). Further understanding of the roles of the M and P pathways in flickering vernier acuity might be achieved by studying the contrast–response functions of visual cortical neurons to phase-reversing edges at different temporal frequencies, coupling this with a study of their retinal inputs. As there is now much evidence supporting the involvement of orientation selective mechanisms in vernier offset detection (Sullivan, Oatley & Sutherland, 1972; Andrews, Butcher & Buckley, 1973; Watt, Morgan & Ward, 1983; Beck & Halloran, 1985; Wilson, 1986; Swindale & Cynader, 1986; Waugh & Levi, 1992; Waugh, Levi & Carney, 1993), another approach would be to study the contributions of M and P cell inputs to orientation selectivity in cortical neurons.

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