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THE RELATIONSHIP OF DISPLACEMENT THRESHOLDS FOR OSCILLATING GRATINGS TO CORTICAL MAGNIFICATION, SPATIOTEMPORAL FREQUENCY AND CONTRAST

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Abstract—The threshold amplitude for detecting square-wave oscillatory motion of a sinusoidal grating (contrast 0.3) was approximately 14 sec arc for foveal viewing, and was independent of spatial frequency in the range 2–16 c/deg. Threshold displacement amplitude (TD) was greater for eccentric stimuli; but when these were scaled inversely with the cortical magnification factor (M) it was found that TD was equivalent to a constant displacement in cortically-scaled units (0.03 mm). As grating contrast was reduced, invariance of TD over spatial frequency disappeared and consequently for a contrast of 0.03 TD was minimum at 6–8 c/deg. TD was systematically elevated at low contrast and low spatial frequency. Sensitivity to sinusoidal displacements was maximum at 2–10 Hz; for temporal frequencies below 1 Hz, TD was proportional to velocity. The results provide evidence that oscillatory displacement thresholds in the hyperacuity range depend on motion-detecting mechanisms whose spatial dimensions are correlated with M^{-1}.

Vision Psychophysics Motion threshold Cortical magnification Gratings Hyperacuity

INTRODUCTION

Under some conditions the smallest amplitude of detectable motion of a target is less than the two-point discrimination threshold or the intercone separation, and thus falls into the range of hyperacuities (Westheimer, 1982). Lateral sinusoidal displacement of a line can be detected at amplitudes as small as 10 arc sec (Tyler and Torres, 1972). Comparable values have been obtained for step displacements of a spot in the centre of an annulus (Legge and Campbell, 1981) and differential motion in random dot patterns or between separated bars (Nakayama and Tyler, 1981; McKee and Nakayama, 1984). The achievement of hyperacuity in these studies may depend on the presence of stationary contours within the field, or the detection of relative motion, since thresholds of the order of 1–2 min arc for foveal viewing of single step displacements of a line or spot are more usual (Johnson and Scobey, 1980; Scobey and Johnson, 1981; Legge and Campbell, 1981). Targets in differential motion tasks need not be contiguous but can be separated by distances at which positional hyperacuity is degraded (McKee and Nakayama, 1984) and relative motion thresholds depend on stimulus velocity as well as displacement magnitude (Tyler and Torres, 1972; Nakayama and Tyler, 1981). For these reasons, motion-sensitive mechanisms rather than spatial acuity or spatial hyperacuity mechanisms have been held responsible (McKee and Nakayama, 1984).

Westheimer (1978) investigated discrimination of the direction of phase displacements of sinusoidal gratings. He found that the smallest discriminable phase displacement was a linear function of spatial frequency in the range 3–25 c/deg; that is, threshold was constant in terms of lateral distance. Grating displacement thresholds were between 9–12 arc sec and equal to the lateral displacement threshold for a single line, thus falling into the hyperacuity range. Threshold displacement (TD) for gratings is thus comparable, in units and magnitude, with differential motion thresholds. The use of grating stimuli offers the possibility of simplifying the analysis of the spatial organisation of motion-detecting systems. However, because the visual field is not homogeneous for spatial organisation, it is desirable to extend such an analysis into the peripheral retina. A powerful approach for investigating such problems is to scale stimuli in the periphery in accordance with an estimated cortical magnification factor. Cortical magnification (M) is defined as the extent of (striate) cortex, in mm corresponding to a degree of visual angle (Drasdo, 1977). Many psychophysical measures, including acuity (Drasdo, 1977), contrast sensitivity (Virsu and Rovamo, 1979) and detection of coherent motion in dynamic random dot patterns (van der Grind *et al.*, 1983) are invariant with M-scaling, but a growing number of exceptions to this rule have been observed, for example vernier acuity (Westheimer, 1982) and relative motion of offset gratings (Levi *et al.*, 1984).

Johnston and Wright (1983, 1985) measured the lower threshold of continuous motion (LTM) for gratings whose spatial frequency decreased and area increased with increasing eccentricity in inverse relation with M (M-scaling). The threshold was equivalent to a constant cortical velocity, and was independent of spatial frequency and eccentricity for M-scaled gratings of moderate or high contrast. LTM is not expressible in purely spatial units and is not directly comparable with the differential motion and displacement thresholds reported by other investigators. In the present study variants of Westheimer's (1978) and Tyler and Torres' (1972) procedures were adopted.

We set out to determine whether grating threshold displacement (TD) like LTM, is constant in cortical units for eccentric viewing after M-scaling. Second, we determined the range of spatial frequencies and contrasts over which threshold displacement is independent from spatial frequency and the form of the relationship outside this range. Thirdly, we analysed the temporal frequency dependence of TD.

METHODS

The apparatus has been described in a previous paper (Wright and Johnston, 1983). A vertical sinusoidal grating was viewed monocularly through a semi-circular aperture in a concentric circular mask, diameter 10 cm, which was transversely illuminated and carefully matched to the mean luminance (100 cd/m^{-2}) and colour of the grating. The aperture had a horizontal base of 7 cm and the grating was fixated at the centre of the base for foveal viewing (no fixation dot), or using a series of fixation dots placed vertically below for eccentric viewing. The outer 0.5 cm border of the grating patch was covered by an overlay of translucent film which reduced the contrast, but not the mean luminance, of the grating edges and eliminated the sharp edge of the aperture. In some experiments a rectangular aperture was used (6.2 cm $\times$ 3.1 cm), and this gave almost identical results.

The oscillatory grating motion was produced by adding a square or sine wave (0.1–20 Hz) from a function generator to the time base of the display (128 Hz). The ends of the gratings were always hidden by the aperture mask so that the appearance to the observer was that of a phase shift. The square wave was synchronised to the time base so that displacements occurred between frames. The amplitude of the displacement was controlled by passing the square or sine wave through a digital attenuator, under computer control. Threshold displacement was measured in most experiments using a "yes/no" double interleaved staircase procedure identical with that used previously for measured contrast thresholds (Wright and Johnston, 1983); stationary gratings occurred on 50% of trials. Some experiments were also conducted using a two-interval forced choice procedure; this gave similar results.

The foveal viewing distance was 200 cm. TD was measured in peripheral vision with fixation displaced along the lower vertical meridian and viewing distance altered in accordance with M-scaling. This ensured that each spatial frequency presented decreased with eccentricity such that SF M (cortical spatial frequency) remained constant. Values of M for the vertical meridian at these eccentricities have been taken from Rovamo and Virsu (1979). In order to check that our procedures were comparable with those of previous workers, we first confirmed that contrast sensitivity functions were equivalent for our M-scaled stimuli (Virsu and Rovamo, 1979). The authors were subjects in all experiments, and in addition most observations were replicated using two naive observers (P.P., R.H.).

RESULTS

TD for oscillatory movement of gratings of moderate contrast (0.1, 0.3) was very low, within the hyperacuity range, and independent of spatial frequency in the range 2–16 c/deg for foveal viewing (Figs 1 and 2). The display was carefully designed to eliminate positional cues such as would be provided by sharp grating boundaries or fixation dots close to the target, and the first experiment was designed to test the adequacy of these precautions, TD was found to be almost identical for rectangular and semicircular grating patches of the same area. Therefore the shape of the aperture did not appear to be contributing significantly to the pattern of results. TD was raised for a semi-annular display with the same external diameter, particularly at low and high spatial frequencies (Fig. 1). Therefore "edge effects"

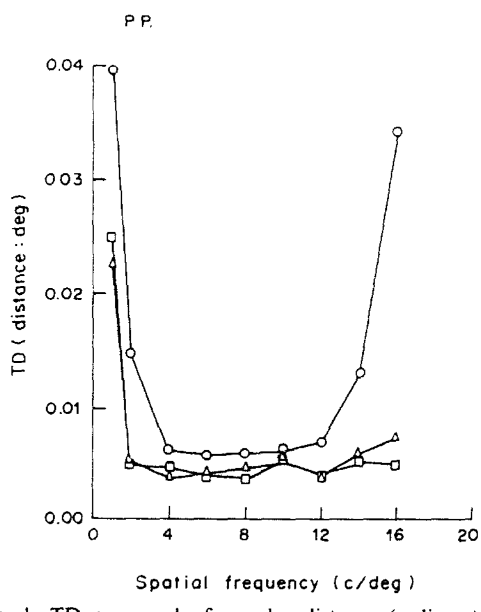

Fig. 1. TD expressed of angular distance (ordinate) for gratings of varying spatial frequency (abscissa). The shape of the grating patch has been varied. (□) Rectangular aperture, (△) semicircular aperture, (○) semi-annular aperture; outer diameter 7 cm, inner diameter 6 cm. Grating contrast, 0.1, eccentricity = 0 deg.

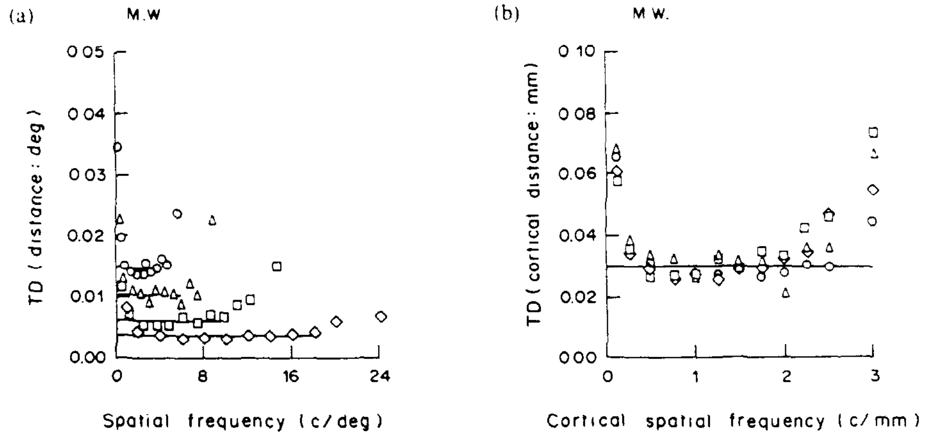

Fig. 2. (a) TD expressed as angular distance (ordinate) for M-scaled gratings of various spatial frequencies (abscissa) measured at four eccentricities (◇) 0 deg; (□) 1.5 deg; (△) 4 deg; (○) 7.5 deg. (b) The ordinate has been transformed to express TD in units of cortical displacement, and the abscissa in units of cortical spatial frequency. Contrast = 0.3.

cannot account for the constancy of TD over the middle range of spatial frequency.

TD increased with eccentricity [Fig. 2(a)]. When the data were converted into cortical distances, the curves for different eccentricities superimposed [Fig. 2(b)]. TD was equivalent to a constant cortical distance of 0.03 mm for the middle range of spatial frequencies for subject M.W. The equivalent figure for A.J. was 0.04 mm and for P.P. and R.H. it was 0.03 mm. For the lowest spatial frequency, at each eccentricity, TD was raised and this increase was constant in units of cortical distance for M-scaled stimuli. Cortical distance in this context is an abstract measure, and we do not necessarily imply a topographic correlate in the cortex. Unlike Westheimer (1978) we found that the threshold was also raised for cortical spatial frequencies above 2 c/mm, that is, above 16 c/deg for foveal viewing. At these high spatial frequencies, the task was very difficult and required particularly steady fixation. M-scaling failed above 2 c/mm performance being better in the periphery than the central field. A similar breakdown of M-scaling at high spatial frequencies was noted in preliminary measurements of contrast sensitivity; this is thought to be due to the greater optical attenuation of high retinal spatial frequencies (Rovamo and Virsu, 1979).

TD was identical for sine- and square-wave gratings (contrast 0.3) in the range 2–16 c/deg for foveal viewing, and for the equivalent M-scaled gratings viewed eccentrically. This was the case even though the amplitude of the fundamental of the square wave was $4/\pi$ times greater than the amplitude of the sine wave grating of the same contrast, and supports the conclusion of the previous experiment that spatial frequency does not affect TD in the middle range. We may add that spatial waveform and the amplitude of the fundamental Fourier component apppear to have little effect in this range. However, below about 2 c/deg TD increased with decreasing spatial frequency for sine-wave gratings whilst remaining constant for square-wave gratings (Fig. 3). For low spatial frequencies, TD for sinusoidal gratings increased regularly with decreasing spatial frequency, and was found to be constant in terms of spatial phase. The relationship of TD and spatial frequency is therefore very different at low spatial frequencies than in the middle range.

We measured TD as a function of grating contrast for gratings of two spatial frequencies (Fig. 4). TD increased at low contrast, but was nevertheless almost constant for contrasts above 0.5; the contrast functions for gratings of the two spatial frequencies tested were similar, as shown in Fig. 4.

As TD shows little variation in the middle to high contrast range, but increases quite rapidly at low contrast, the departures from constancy of TD at high and low spatial frequency might be due to loss of contrast sensitivity. This possibility was tested by determinations of the TD as a function of spatial frequency for four contrast levels [Fig. 5(a)] using foveal fixation. The greatest degree of independence of TD from spatial frequency was obtained at the highest contrast level, and the greatest degree of spatial frequency "tuning" of TD was obtained at the lowest contrast level.

Changes in TD do reflect changes in contrast sensitivity, but TD showed greater contancy at moderate and high contrasts than would be expected if thresholds were proportional to contrast sensitivity. At moderate and high contrasts, the TD/spatial frequency function was flatter than the contrast sensitivity function when the displacement data were plotted on log/log coordinates like contrast sensitivity data [Fig. 5(b)]. Apparent contrast, like TD, is also constant across spatial frequency for suprathreshold gratings (Georgeson and Sullivan, 1975). However the correspondence between TD and apparent con-

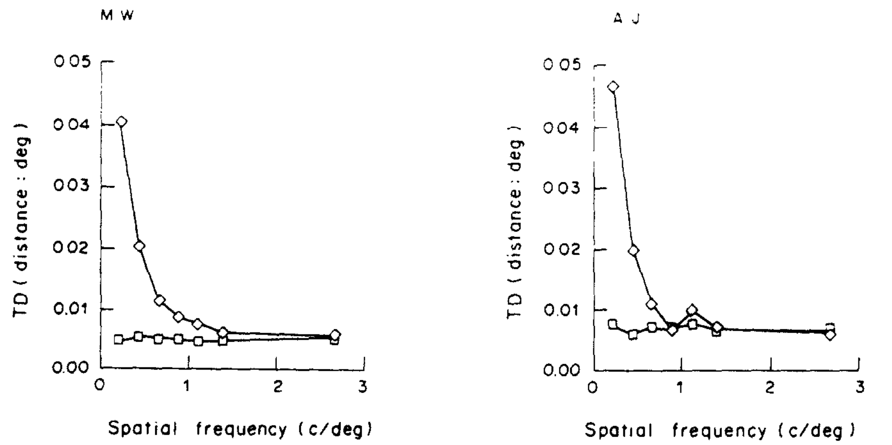

Fig. 3. TD expressed as angular distance (ordinate) for sine- (◇) and square-wave gratings (□) as a function of spatial frequency (abscissa). 1.5 deg eccentricity, 133 cm viewing distance, 12 cm diameter semicircular aperture. Contrast = 0.3.

trast is probably not exact since apparent contrast varied over the upper range of contrast whereas TD was nearly constant (Fig. 4).

At high spatial frequencies and high or moderate contrasts, TD was slightly elevated: at lower contrasts there was an abrupt high-frequency cut-off. The displacement threshold could not be measured above 18 c/deg at a contrast of 0.1 and above 14 c/deg at a contrast of 0.03; the grating was still clearly visible but appeared stationary. The maximum possible phase displacement of a grating is 180 deg, which is presumably below threshold at the high frequency cut-off. This half-cycle limit is shown in Fig. 5a. The shape of the low frequency cut was similar at all contrast levels (i.e. proportional to phase) but shifted up the frequency axis with decreasing contrast (Fig. 3, Fig. 5).

The threshold for detecting sinusoidal displacement of a grating was found to vary with temporal frequency (Fig. 6). A method of adjustment was used for this determination in order to provide a continuous temporal waveform. The shape of the function was consistent with that shown by Tyler and Torres (1972) for sinusoidal displacements of a single line. Peak sensitivity occurred at 2–8 Hz. Below 1 Hz, the graph of sensitivity versus temporal frequency had a slope of 1. This corresponds with a constant velocity; thus below 1 Hz sensitivity is limited by velocity rather than displacement. The maximum velocity of sinusoidal motion is $\pi/2$ times its mean velocity. The lower threshold of unidirectional motion (0.018 deg/sec for subject M.W. at 8 c/deg; Johnston and Wright, 1985) is equal (within experimental error) to the maximum velocity of sinusoidal oscillatory motion below 1 Hz (0.017 deg/sec). This similarity of threshold is consistent with the view that the same mechanism is responsible for detecting linear and low-frequency oscillatory motion.

Threshold amplitude for sinusoidal displacement at 1 Hz (16.6 sec arc) was higher than that for

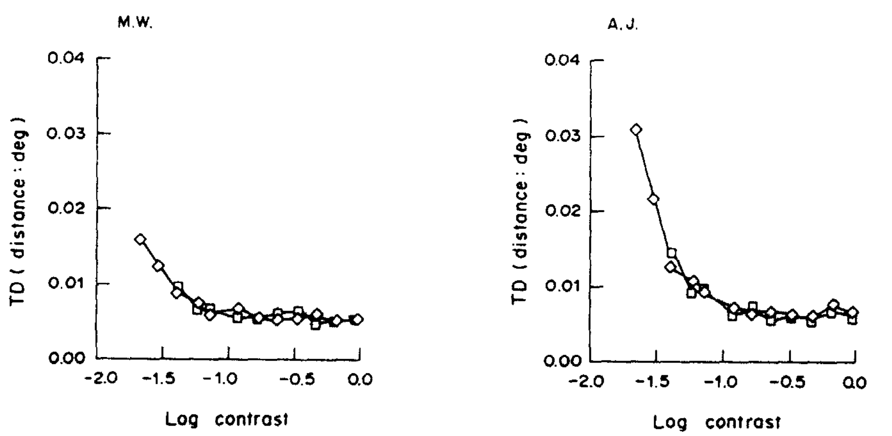

Fig. 4. TD expressed as angular distance (ordinate) for gratings of 4 c/deg (◇) and 6.7 c/deg (□) as a function of log contrast (abscissa). 1.5 deg eccentricity, 133 cm viewing distance, 7 cm diameter semicircular aperture.

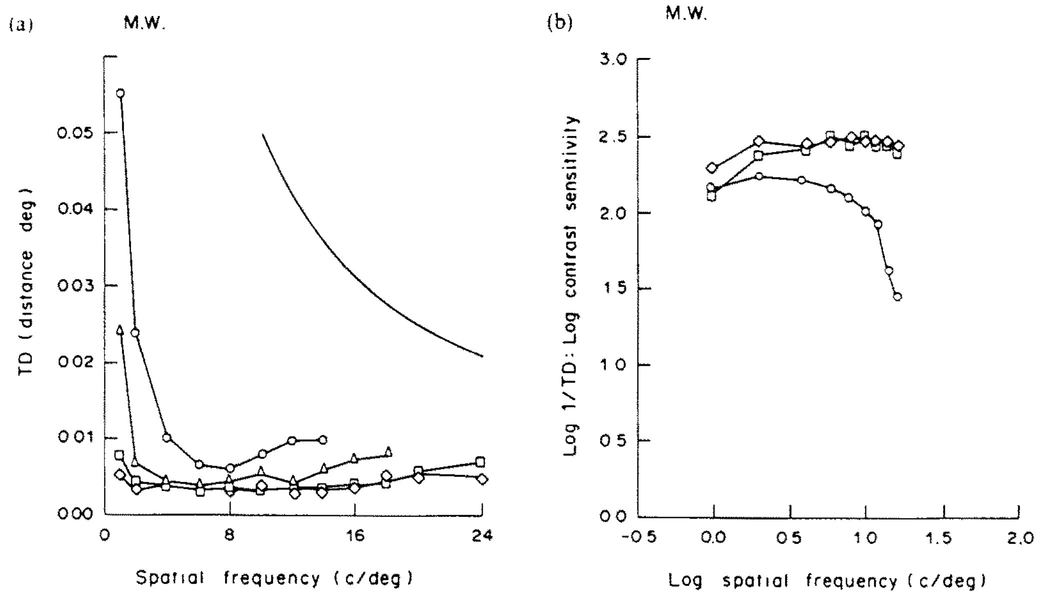

Fig. 5. (a) TD expressed as angular distance (abscissa) for gratings of varying spatial frequency at four different contrast levels. Eccentricity = 0 deg, rectangular aperture. Contrast (◇) = 1; (□) = 0.3; (△) = 0.1; (○) = 0.03. Continuous curve = theoretical cut-off at 180 deg phase displacement. (b) Log displacement sensitivity (log 1/TD) and log contrast sensitivity (log 1/threshold contrast) vs log spatial frequency. TD for contrast (◇) = 1; (□) = 0.3. (○) = contrast sensitivity for 2 Hz counterphase grating measured under same conditions.

square-wave displacements at the same temporal frequency (14 sec arc). The threshold amplitude for sine-wave displacements was higher than the 1 Hz square-wave value at all temporal frequencies. Therefore the threshold for oscillatory motion is not simply a function of the amplitude of displacement.

The equivalent velocity at threshold for square wave displacements is limited only by the frame rate of the display; that is, the displacement multiplied by frame frequency is equivalent to a real motion with a velocity of approximately 0.5 deg/sec at threshold. This value is nearly 30 times the threshold velocity for sinusoidal displacements, so threshold is not determined by the equivalent velocity of displacement. The loss of sensitivity at high temporal frequencies of sinusoidal oscillation confirms this supposition. The observed sine to square ratio of sensitivities at 1 Hz is consistent with filtering in the spatiotemporal domain of the displacement waveform in the detection of velocity.

DISCUSSION

Square-wave oscillatory motion of gratings can be detected at very small displacements (14 sec arc) comparable with those reported by Westheimer (1978) for discrimination of the direction of single step displacements, or by Tyler and Torres (1972) for detection of oscillatory motion of single lines. Like Westheimer, we found that the threshold displacement was independent of spatial frequency over a considerable range; that is the motion of the grating, at a given eccentricity, was detectable when it exceeded a fixed excursion, rather than being related to the periodicity of the grating. We showed threshold displacement amplitude to be constant in cortical (M-scale) dimensions rather than retinal ones; for M-scaled stimuli at different eccentricities (0–7.5 deg.), the minimum threshold displacement would be equivalent to approximately 0.03 mm at the cortex (though we need not suppose that the displacement actually is encoded in a topographic mapping).

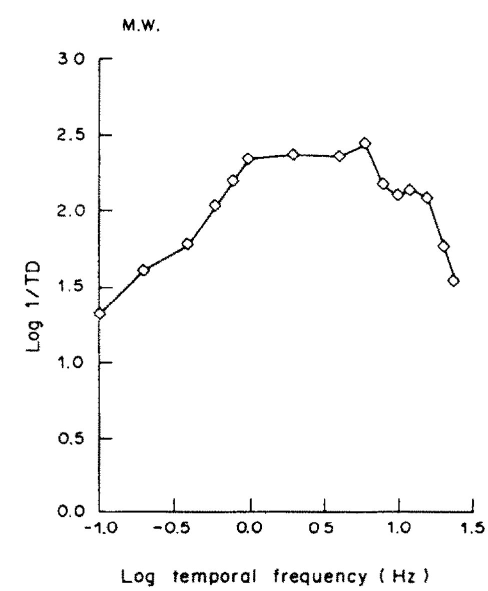

Fig. 6. Log displacement sensitivity (log 1/TD) as a function of log temporal frequency for sinusoidal oscillation of a grating. Rectangular aperture, 0 deg eccentricity, contrast = 0.3.

We found raised thresholds for low contrasts and low and high spatial frequencies delimiting the boundaries of the constant threshold displacement relationship. At a constant of 0.03, threshold displacement sensitivity was sharply tuned with a maximum at 6–8 c/deg. The results are consistent with the view that TD improves as a strongly decelerating function of contrast (Fig. 4). The saturating contrast function approaches the same minimum value for all spatial frequencies in the middle range (Figs. 4 and 5), so that there is a limit to TD which is independent of spatial frequency. This limit is not a fixed displacement, as was suggested by Westheimer (1978), since it varies with eccentricity. Nor is it a fixed M-scaled displacement (see above), since it varies with temporal frequency. Data on the temporal tuning of TD (Fig. 6) is consistent with the view that the limit on TD is a minimum detectable (M-scaled) velocity in a spatially and temporally filtered signal (Johnston and Wright, 1985).

Vernier hyperacuity thresholds, unlike TD in the present study, have been shown to rise faster than minimum angle of resolution (Westheimer, 1982). Though our measurements are within the range of hyperacuities, our display provides no vernier cues. Our results cannot be attributed to position-sensitive mechanisms; it was not possible to detect the grating displacement by noticing or remembering a spatial offset. First, the displays were constructed to eliminate stationary contrasts close to the grating which could have served as reference cues for positional hyperacuity, which is degraded at distances of 10 min arc at the fovea (Westheimer, 1982). Second, control experiments indicated that cues from the fuzzy borders of the grating were not the basis for threshold-setting (Fig. 1). Third, TD was tuned to temporal frequency, and was velocity-limited rather than displacement-limited at low temporal frequencies (Fig. 6). If it were possible to detect the stimulus motion by detecting some spatial offset, there would be no reason for degradation of performance at low temporal frequencies. Thus TD is a motion-detection task.

There is evidence that some motion hyperacuity thresholds which do not depend on vernier cues nevertheless increase with eccentricity more rapidly than does TD. Differential motion thresholds, defined as the minimum relative distance travelled at threshold by two targets, have been studied as a function of eccentricity by McKee and Nakayama (1984), and Levi *et al.* (1984). They found that the relative increase in differential motion threshold rose faster with eccentricity than visual acuity.

Although the detection of oscillatory motion of gratings produces thresholds in the hyperacuity range, there appears to be significant differences between our TD task and the referenced motion tasks employed by Nakayama and McKee (1984) and Levi *et al.* (1984). In our experiments, there was no reference bar or grating, and temporal integration over several cycles of oscillation was possible (Post *et al.*, 1984). Our experimental paradigm gives results which have a similar scaling function to the lower threshold of unidirectional motion (Johnston and Wright, 1983, 1985), and the data shown in Fig. 6 suggest that oscillatory and linear motion thresholds are similar given the appropriate metric and temporal frequency range.

There is moreover considerable similarity in the pattern of results obtained with grating TD and the lower threshold of motion (LTM) for gratings (Johnston and Wright, 1983, 1985). Both are invariant with retinal locus (for M-scaled stimuli) when expressed in cortical dimensions. Both are invariant with spatial frequency (2–16 c/deg foveal) and contrast (greater than 0.05). Both are invariant with spatial waveform (above 2 c/deg) and show similar behaviour at low spatial frequencies. The most parsimonious explanation for the similarity of results is that LTM and TD reflect the same motion-detecting mechanism, whose spatial dimensions are correlated with M^{-1}.

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