THE DETECTION OF MOTION IN THE PERIPHERAL VISUAL FIELD*

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Abstract—To assess the sensitivity of the periphery to motion, we measured differential motion detection and velocity discrimination as a function of eccentricity in the lower visual field. The differential motion threshold, a measure of the ability to detect relative motion (shear) between adjacent visual stimuli, is smaller than the minimum angle of resolution at all retinal loci tested. The target size required to produce the lowest differential motion threshold is surprisingly large, ranging from 1 deg in the fovea to about 20 deg at 40° eccentricity. When the peripheral thresholds for differential motion and for resolution are normalized against the fovea and plotted on linear axes, the eccentricity functions are linear. Velocity discrimination ($\Delta V/V$) is as precise in the periphery as it is in the fovea, amounting to about 6% for the optimum velocity range. In the fovea, the minimum Weber fraction is reached at velocities of 5 deg/sec or faster. In the periphery this minimum is found for a faster range of velocities (>30 deg/sec at 40° eccentricity). If target velocity is expressed in the resolution units/second appropriate to each tested eccentricity, the velocity discrimination functions coincide. Thus, while the spatial determinants of velocity discrimination follow the change in resolution found with eccentricity, peripheral temporal sensitivity must be nearly equal to foveal temporal sensitivity.

Motion   Acuity   Cortical magnification function   Peripheral vision   Eccentricity

INTRODUCTION

Most measures of visual sensitivity show a decline with retinal eccentricity. The thresholds for contrast, binocular disparity, vernier offset and, of course, spatial resolution are all markedly higher even at parafoveal distances (Hilz and Cavonius, 1974; Fendick and Westheimer, 1983; Westheimer, 1983; Johnson *et al.*, 1978). While there has been occasional speculation that the periphery might be particularly sensitive to motion, absolute motion thresholds rise with eccentricity at a pace comparable to the change observed with visual acuity (Tyler and Torres, 1972; Johnson and Leibowitz, 1976; Tynan and Sekuler, 1982). For this study of peripheral motion sensitivity, we chose to measure two thresholds which have not been examined systematically as a function of eccentricity: the threshold for differential motion and the threshold for velocity discrimination.

The differential motion threshold measures the ability to detect relative motion between adjacent visual stimuli. In the fovea, this ability is extremely fine. The spatial displacement required for threshold amounts to 5–10 arc sec, a value comparable to the spatial precision found with vernier acuity and other positional hyperacuities. But, the differential motion threshold depends on a different mechanism (Tyler and Torres, 1972). For one thing, this

threshold varies with the velocity of the spatial change as well as its magnitude, a finding consistent with the premise that the detection of these tiny displacements is mediated by motion sensitivity. Moreover, this motion threshold is unaffected if the compared targets are separated by distances which significantly degrade positional hyperacuity (Westheimer, 1979; Nakayama and Tyler, 1981; Legge and Campbell, 1981).

Foveal velocity discrimination is also fairly precise. Differences in velocity of 4–6% can be detected for a broad range of velocities (McKee, 1981). As there is considerable evidence that this discrimination depends on temporal properties of the visual system, it seemed possible that the periphery, known to be quite sensitive to flicker (Brown, 1965; Tyler, 1981), could respond delicately to velocity differences.

Any measurement of peripheral functioning is naturally enhanced if it can be related to the cortical magnification functions now emerging from physiological, anatomical, and psychophysical studies (Hubel and Wiesel, 1974; Koenderink *et al.*, 1978; Virsu and Rovamo, 1979). Visual acuity is thought to provide a psychophysical estimate of this magnification function, a view supported by several findings. Both the average receptive field size and the reciprocal of cortical magnification rise linearly with eccentricity (Hubel and Wiesel, 1974). So does the minimum angle of resolution (MAR) measured psychophysically (Weymouth, 1958). All conform to a single expression when normalized at the fovea

Receptive field size

$$= 1/\text{cortical magnification function}$$
$$= \text{MAR} = m\theta + 1 \qquad (1)$$

where $m = 0.33\,\text{deg}^{-1}$ and θ is eccentricity measured in degrees (Sakitt and Barlow, 1982). This simple equation supplies a dimensionless scaling factor; for example, the MAR at 21° eccentricity should be roughly eight times the foveal value. In order to compare the spatial limits of motion sensitivity with an estimate of the spatial grain, or its reciprocal, cortical magnification, we also measured grating acuity as a function of eccentricity. Scaling according to the acuity function would be consistent with a close link between motion processing and the spatial properties of primary visual cortex whereas deviations might suggest the importance of secondary projection areas with different magnification functions (Van Essen, 1979).

METHODS

Our objective was to obtain the lowest threshold possible at each retinal locus for three types of psychophysical judgments: differential motion detection, velocity discrimination and visual acuity. In addition to the difficulties associated with all peripheral judgments, we were faced with the special problems inherent in motion studies—the need for stimulus configurations which selectively address motion sensitivity instead of other competing detection systems. Thus the psychophysical procedures and stimuli were tailored to the joint requirements of retinal locus and the requisite isolation of motion or acuity mechanisms. Specific details of the apparatus and stimuli for each set of experiments are described below.

General procedures

Thresholds were measured either in the fovea or in the lower visual field. Targets were viewed binocularly with natural pupils at distances ranging from 35 to 400 cm, distances well within the accommodative range of both subjects. The fixation target for all peripheral measurements was a bright yellow disk 3 cm in diameter, on which was drawn a narrow horizontal line with a small gap. Subjects fixated on the gap in the line. Staring briefly at this target produced a bright colored afterimage. Because this afterimage remained superimposed on the fixation target during stimulus presentations, we could be sure that no undesired eye movements occurred. For all experiments in the periphery, the stimulus was presented at the same distance as the fixation target, the CRT screen being tilted so that the stimulus was displayed on a tangential plane.

The two authors served as subjects for these experiments. K.N. is a well-corrected myope ($+7.0$D) who wore his glasses for all experiments; SM is slightly hyperopic (-0.5D). We did not correct for peripheral refractive error. Millodot et al. (1975) found that existing errors in refraction did not influence peripheral visual acuity, but there has been a report that peripheral refractive error does elevate absolute motion thresholds, albeit most significantly at eccentricities greater than those we employed (Leibowitz et al., 1972). To check the effect of refractive error on the differential motion thresholds at one eccentricity (20 deg), we placed positive and negative lenses in front of the eyes of subject S.M. and measured her peripheral thresholds. We could find no lens power which produced much improvement in the differential motion threshold. In fact, this threshold seemed relatively immune to positive lens blur: $+6$ D produced no change in the thresholds of S.M. and removing the glasses of subject K.N., which introduced a $+7$ D error, did not alter his threshold.

Differential motion procedure

The basic differential motion stimulus consisted of two adjacent targets moving in opposite directions, the directions being randomized from trial to trial. The subject was asked to identify the direction moved by one of the two targets. Threshold was defined as the relative distance moved by both targets which led to a correct identification on 80% of stimulus presentations (approximately 200 trials for each threshold). Our problem was to determine whether the subject was responding to the shearing *motion* of the target or was merely recognizing that the two targets had changed position. Nakayama and Tyler (1981) successfully isolated motion sensitivity by using adjacent fields of moving random dots as their stimulus pattern, the random dots serving to obscure positional information. In the present study we intended to use this same random dot stimulus (see Fig. 1), but we discovered that the periphery was quite insensitive to motion in the random dots. Peripheral motion thresholds for line targets were much lower than the thresholds obtained with the random dot pattern, even when dot size was increased to compensate for the declining acuity of the periphery. Line targets, such as the vernier-like configuration diagram, Fig. 1, might be thought an ideal stimulus for position judgments. However, positional information is accurately encoded only over relatively small distances, distances of less than 10 min in the fovea and distances of less than 20 min at an eccentricity of 10 deg (Westheimer, 1982). Fine motion sensitivity operates over much larger distances. Thus we presented the line targets to the peripheral loci with a large standing offset, scaled according the Weymouth formula [equation (1)]. For example, the offset at 10° eccentricity was 1 deg (four times the value required in the fovea) and more than 3.5 deg at 40° eccentricity. In the fovea, shearing motion was more easily detected in the random dot pattern than in the line stimulus; thresholds for the dots were about half the values found with lines. Foveal measurements were thus made with random dots to obtain the lowest threshold at all loci.

A full technical description of the method for generating the random dot display has been presented elsewhere (Nakayama and Tyler, 1981).

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Briefly, the random picture elements (pixels) are presented on the face of a CRT (Hewlett-Packard 1332A). At the distance we used for the foveal measurements (103 cm), each pixel subtended 3.1 min arc and had a 50% probability of being light or dark. Mean luminance of the display was 20 cd/m² and the contrast was set at 80% The static random dot display appeared on the screen for 200 msec. Then a computer-generated ramp produced a vertical shearing motion causing the two halves of the display to move in opposite directions for 52 msec. After the motion ceased, the static display remained visible for another 200 msec. The line stimuli, which were presented on a larger CRT (Hewlett-Packard 1311A) at a luminance of approximately 40 cd/m², followed a temporal sequence identical to that used for the random dot display. The viewing distances for the tested retinal loci were: 10 deg, 57 cm; 20 deg, 52 cm; 30 deg, 45 cm; 40 deg, 35 cm.

Velocity discrimination procedure

The minimum detectable difference in velocity was determined by the method of single stimuli. In this method, a line target moves across a fixed distance at one of five velocities chosen from a narrow range. The subject must judge whether the single present-ation of velocity is faster or slower than the mean of the range. With a small amount of practice, a subject is quickly able to judge the velocity range and divide the velocities into the slow and fast categories with a 4–5% precision, comparable to the thresholds ob-tained with the method of constant stimuli where a standard is employed on each trial.

It is evident that if the targets move over a fixed distance, the subject could be responding to vari-ations in the total target duration, rather than to the velocity. To obscure this duration cue, we used three fixed distances chosen at random, the distances varying by ±15%. This random distance procedure eliminated the consistent relationship between target duration and velocity. For each tested velocity range, the three interspersed distances were chosen so that

the *average* stimulus duration was 200 msec and ranged from about 150 to 250 msec. The percentage of trials on which the subject responded "fast" was measured as a function of velocity and a cumulative normal function was fitted to the data by probit analysis. The criterion for threshold was the velocity difference which produced an 80% correct response rate.

The stimulus for this study was a long narrow line generated on the screen of a Hewlett-Packard 1311A CRT (see Fig. 1). The motion itself was created by a computer-generated ramp, and the target moved upward or downward on a random schedule. View-ing distances were the same as those used to measure the differential motion thresholds. The length of the target used for the velocity experiments at each eccentricity was determined by the measured sum-mation areas found for differential motion thresholds (Fig. 2). At 20 deg eccentricity, the summation length was about 20 degrees. Therefore, to confine the moving target to the smallest and most homogeneous region of the visual field, we were forced to move the targets vertically across a point centered on the eccentricity of interest. At the fastest velocity used for these experiments (50 deg/sec), the target moved over a 10 deg distance in 200 msec, or 5 deg on either side of the tested retinal locus.

Visual acuity measurements

The target used to measure visual acuity was a sinusoidal grating of horizontal bars presented at a mean luminance of 39 cd/m² which matched the homogeneous surround of the target. The target contrast was 71%. To avoid artifacts associated with abrupt contrast changes at the edge of the grating, a cosine envelope function (half-period 3.2 cm) modu-lated the sinusoidal stimulus so that the full contrast of the grating was reached only in the middle of the stimulus. The sinusoidal pattern was generated by a Daugman *Picasso* image generator and displayed on a Hewlett-Packard 1332A CRT.
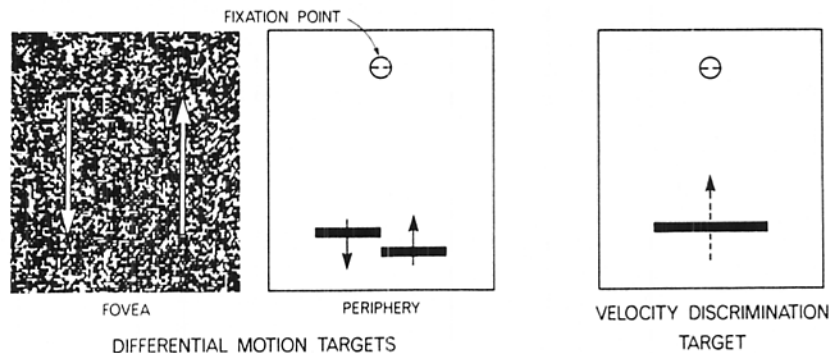

Fig. 1. Motion stimuli used in study. On the left are the targets used to measure differential motion hyperacuity in the fovea and periphery. On the right is the single line stimulus used for velocity discrimination.
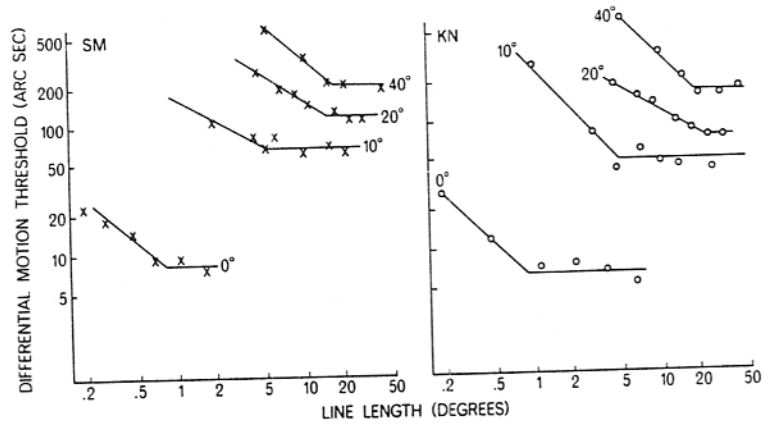
Fig. 2. Differential motion thresholds plotted as a function of stimulus width for four different retinal loci. Data from 30 deg eccentricity were not plotted to avoid crowding the other eccentricity data.

Stimuli presented to the periphery fade very quickly which impairs acuity. To prevent fading during the adjustment setting, the targets were presented for 500 msec followed by a 1500 msec presentation of a homogeneous field, the whole sequence repeating until the threshold setting was reached. Subjects adjusted the spatial frequency of the grating stimulus until the bar pattern just disappeared. Ten settings of the descending limit of spatial frequency were averaged to estimate grating acuity at each retinal locus. The viewing distance was scaled according to the Weymouth magnification function which was described above, assuming a viewing distance for the foveal threshold of 500 cm. If this function adequately describes the properties of the peripheral visual field, then the general spatial parameters of the stimulus (height, width, etc.) are increased to meet the exact requirements of the periphery. For example, 15 periods of the grating stimulus were visible within one half-cosine window for every eccentricity, a figure comparable to the total number of periods necessary to reach asymptotic contrast sensitivity (Virus and Rovamo, 1979; Howell and Hess, 1978). The foveal measurements were the only exception to this viewing distance rule; they were made at a distance of 400 cm, rather than 500 cm, because of the length of the room. The viewing distances for the other retinal loci were: 10 deg, 115 cm; 20 deg, 65 cm; 30 deg, 46 cm; 40 deg, 35 cm.

RESULTS

Our first experiment measured "areal summation functions" for the differential motion threshold. What target size is needed at each eccentricity to produce the lowest threshold? Typically, sensitivity in the periphery for almost any visual dimension is improved if the size of the target is enlarged (Johnson et al., 1978; Johnson and Scobey, 1980). Nakayama and Tyler (1981) found that the spatial dimensions necessary to produce the lowest motion threshold are

substantial even in the fovea. In their experiments the shearing motion superimposed on the random dot pattern shown in Fig. 1 was sinusoidal in form. The lowest thresholds were found at frequencies of less than 1 c/deg which corresponds to a spatial separation of 30 min arc or more between the "peak" and the "trough" of the opposing movements. For our foveal experiments we used a square-wave pattern of motion: half the field of dots moved upward, and half moved downward. We measured foveal thresholds as a function of the horizontal extent of the random dot field with the vertical extent held constant size at 4.7°. For the peripheral measurements, we increased the length of the offset horizontal lines until the minimum differential threshold was reached.

Figure 2 shows the effect of target size on the differential motion threshold for different retinal eccentricities. The size of the lines required to produce maximum sensitivity is everywhere quite large, even if the relevant summation region is treated as the half the indicated values (one summation area for each direction). In Fig. 3 we have plotted the length at which the curves in Fig. 2 reach their asymptotic values. The summation regions increase in size up to an eccentricity of 20 deg. and then remain roughly constant. At 20 deg eccentricity, the optimum length is nearly 20 deg, or 10 deg for each direction of motion.
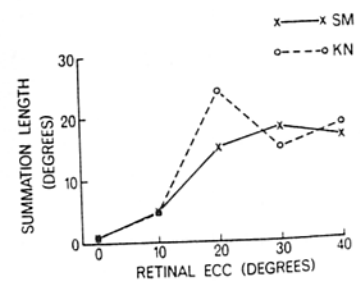

Fig. 3. Summation length of differential motion sensitivity as a function of stimulus eccentricity. Points were determined from the break points of functions shown in Fig. 2.
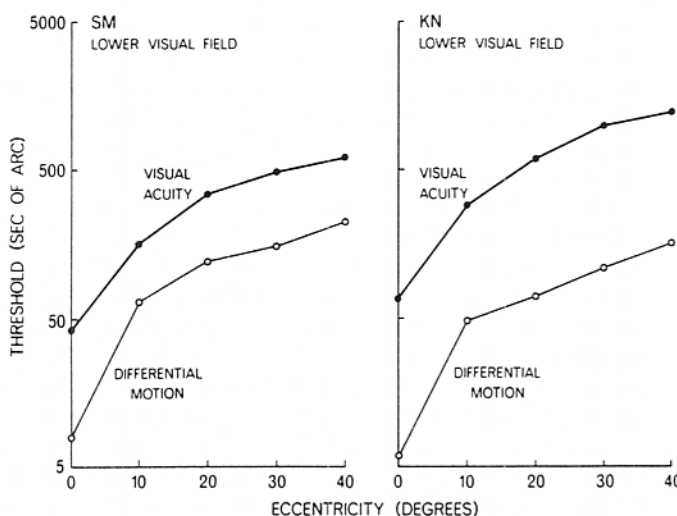
Fig. 4. Grating acuity and differential motion thresholds as a function of retinal eccentricity. Note the logarithmic scale on the ordinate.

How do the thresholds themselves vary with eccentricity? In Fig. 4, we have plotted the lowest thresholds found at five retinal locations. For comparison, visual acuity measurements are shown in the same figure (the ordinate in this figure is logarithmic). The spatial displacement detected by the motion system is considerably lower than the minimum angle of resolution at all retinal loci, similar to the relationship found between vernier acuity and the MAR. Nevertheless, differential motion and vernier thresholds are not based on the same spatial substrate, a point underlined by the target length needed to produce the best motion sensitivity. At 10 deg eccentricity, the half-length of

our ideal differential motion target is 2.5 deg, while the separation required between two dots to produce the lowest vernier threshold at eccentricity of 10 deg is about 10 min (Westheimer, 1982). The precise detection of line orientation is also a spatial hyperacuity. Westheimer (1982) found that the length requirement for the lowest orientation threshold is about 30 min at 10 deg eccentricity, one fifth of the half-length needed for the differential motion threshold.

In Fig. 5 we have replotted the data of Fig. 4 as ratios of the peripheral to the foveal thresholds. The normalized eccentricity functions, both for visual acuity and differential motion sensitivity show a
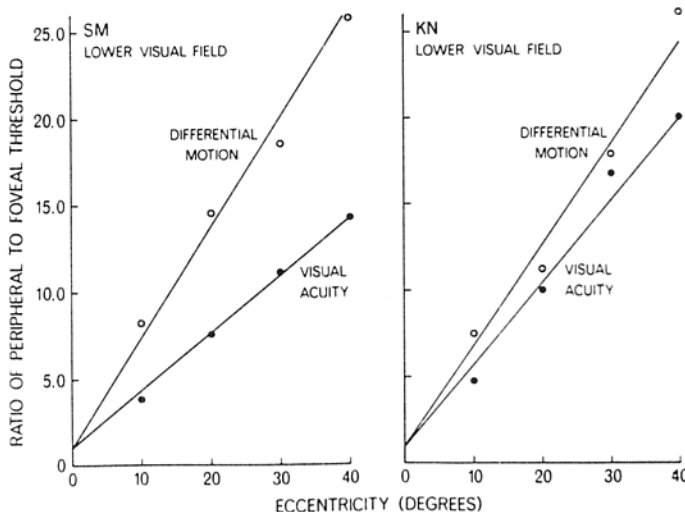

Fig. 5. Ratio of peripheral to foveal threshold for differential motion and for the minimum angle of resolution (visual acuity). The upper curves for differential motion (open circles) show the normalized functions for the lowest threshold that can be obtained at a particular locus; the stimulus for foveal thresholds was a moving random dot pattern and thresholds for the periphery were obtained with moving lines. Solid circles and the lower solid line denotes the normalized function for visual acuity. Note the linear scale on the ordinate.

rather striking linearity in each subject. In fact, S.M.'s fall-off in acuity conforms almost exactly to previous neurophysiological and psychophysical data (Hubel and Wiesel, 1974; Weymouth, 1958); the slope for her curve is 0.33. For both subjects, the differential motion thresholds rise more rapidly with eccentricity than does visual resolution.

From the slopes of these functions, it would seem that shearing motion is processed at a different location in the visual cortex than visual acuity. But the eccentricity function for motion is based on a peculiar amalgam of stimulus conditions chosen to produce the lowest differential motion thresholds. If line targets had been used consistently, the motion function would run closely parallel to the resolution function, because, in the fovea, the motion threshold is higher for lines than for random dot targets. On the other hand, consistent use of the random dots at all eccentricities would have produced a much steeper motion function than that shown in Fig. 5. Thus, the graphed function represents a compromise—a choice based on the criterion of maximum sensitivity. These results raise the intriguing possibility that sensitivity to moving lines is mediated by very different mechanisms than moving dots. We have some evidence that contradicts this notion. At 10° eccentricity we measured areal summation functions for both types of targets; the shape of the summation function found with random dots matches the shape shown in Fig. 2 for the line targets, differing only in the absolute sensitivity level.

We next measured the discrimination of velocity at three eccentricities. The left half of Fig. 6 shows the Weber fractions ($\Delta V/V$) as a function of velocity for the fovea and for a 20 and 40 deg eccentricity. Surprisingly, the minimum detectable difference in velocity is the same in the periphery as in the fovea—

about 6%. In the periphery, this minimum is found at a faster range of velocities. This shift with eccentricity toward a faster optimum velocity range is also characteristic of the velocity tuning of single units in the cat visual cortex (Orban *et al.*, 1981).

The peripheral curves are similar to the foveal curve in shape, but are spread laterally along the velocity axis. It occurred to us that some transformation might superimpose the three curves. A natural scaling factor in this context is our psychophysical measure of the cortical magnification function, the minimum angle of resolution with eccentricity. In the right half of Fig. 6, velocity has been transformed, using the resolution measurements from each subject, into the resolution-units/second appropriate to each retinal locus. To a first approximation, the plotted data points are now coincident.

What aspect of velocity processing is actually contingent on the cortical magnification function? We would have been unable to show the scaling of velocity discrimination if the curves were flat everywhere—if the measured Weber fractions had been constant at all velocities. The demonstrated coincidence depends significantly on the rising part of the functions, so the reason for the scaling must depend on the reason for the rise at slow velocities. One possible explanation involves the distance travelled by the target. Recall that our velocity thresholds are based on a short presentation time (average duration 200 msec). Clearly, slowly-moving targets move only a short distance in this brief period. The best velocity discrimination may require that the target move a minimum distance, and this minimum distance would undoubtedly increase systematically with eccentricity. If this speculation is correct, then the lateral position of the curves along the velocity axis should change with target duration. In a control
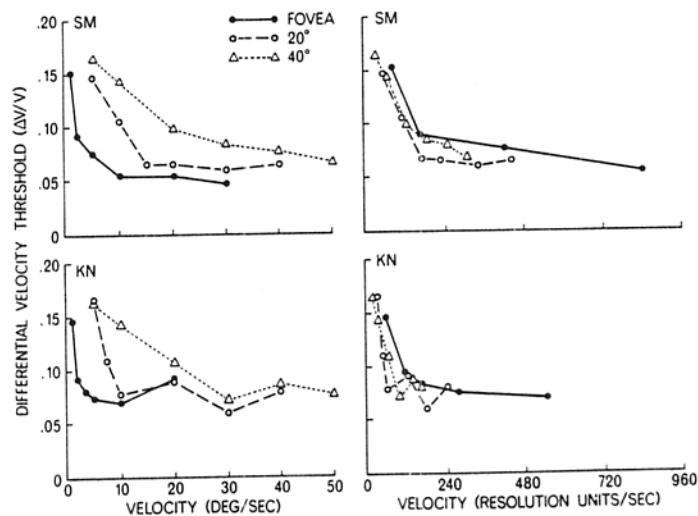

Fig. 6. Differential velocity thresholds. Mean Duration 200 msec. Left pair of graphs shows the differential velocity threshold as a function of velocity (in degrees per second). Right pair shows the same threshold replotted as a function of a cortically scaled velocity (resolution units/sec), calculated from the grating acuity data plotted in Fig. 4.

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experiment, we found that longer stimulus durations did improve the discrimination of slow velocities, so that the functions reached their asymptotic level at a slower velocity. However, stimulus duration cannot be the sole explanation for the shape of these functions, because the thresholds for very slow velocities are elevated no matter how long the duration or how far the targets move. Velocity discrimination is thus constrained by a more stringent requirement: the stimulus must move a minimum distance within some specified time period. It is probably this spatiotemporal requirement which follows the cortical magnification function. Incidentally, there is one interesting implication of this cortical scaling feature. The eccentricity curves for velocity are coincident for stimuli which move at similar velocities across the *cortex* when measured in millimeters/second.

DISCUSSION

The peripheral visual field has no special ability to detect motion. Peripheral thresholds for differential motion and for the discrimination of velocity are *not* better than foveal thresholds. Perhaps the more enlightening comparison is between the peripheral thresholds for motion and the peripheral thresholds for other dimensions. The differential motion threshold is much smaller than the minimum angle of resolution at all tested retinal loci. For example, at 10 deg eccentricity our resolution thresholds were 2.7 and 4.8 min arc; the comparable motion thresholds were less than 1 min arc. But vernier acuity and the other stationary hyperacuities are also smaller than the resolution limit when measured in the periphery. In this respect, motion sensitivity is not any more remarkable than the static ability to localize points in space.

The linear scaling functions, shown in Fig. 5, which relate visual acuity and motion sensitivity are of theoretical interest especially given the recent work on cortical magnification functions. The slope of the normalized eccentricity function for differential motion is steeper than the one measured for acuity. This result may indicate a degree of functional specialization in the fovea which is not revealed by simple estimates of the minimum angle of resolution. Contrast sensitivity functions, even if scaled for cortical magnification, generally have a higher peak sensitivity in the fovea (Virsu and Rovamo, 1979; Robson and Graham, 1981). Should the threshold for shearing motion be dependent on spatial frequency components lower than the cut-off frequency as is evident in other hyperacuity tasks (Westheimer and McKee, 1980), the fovea might be correspondingly more sensitive to displacement than the acuity estimates suggest.

Velocity discrimination is one aspect of motion processing which the periphery performs as well as the fovea, because the detection of differences in velocity does not depend on a fine spatial representation of the moving stimulus. In simplistic terms, the visual system can encode velocity by measuring the time a target takes to move between two physiologically-defined spatial landmarks. A fairly common model of motion processing consists of a "receptor stage" where a moving stimulus initiates impulses in a pair of spatially distinct receptive units, followed by a "comparison stage" which processes the outputs from the receptive units to determine the direction and velocity of the target (Reichardt, 1961; Foster, 1971). Typically, the comparison procedure involves a cross-correlation of the temporal impulse functions generated in each receptive unit. Velocity is thus translated into a time difference between the initiation of an impulse in one receptive unit and its initiation in the next. This temporal signal when processed in conjunction with the spatial separation between the units can provide an accurate estimate of the target velocity.

Suppose there is some factor, perhaps intrinsic noise within the receptive units, which limits the onset of the temporal impulses to an absolute precision of 2–3 msec (Westheimer and McKee, 1977). If the receptive elements which are joined in the comparator stage are very close together, then a stimulus moving at a high velocity would initiate impulses in adjacent units with a time interval comparable to this absolute limit. Consider a target which requires 5 msec to cross the distance separating the receptive units. Given an absolute precision of no better than 2 msec, this velocity could be encoded only to a precision of 40%. It becomes evident from such considerations why velocity, particularly high velocities, must be encoded by spatially-extended mechanisms.

Our results support this speculation: the periphery responds accurately to fast velocities. The scaling with eccentricity of the optimum velocity range, shown dramatically in Fig. 6, indicates that the *finest* spatial sampling of the moving stimulus is changing at a pace dictated by the cortical magnification function. Note, however, that a coarser sampling of the motion, appropriate to yet faster velocities, may exist at any retinal locus.

There is one other important implication of the precision of velocity discrimination in the periphery. In order to achieve this precision the periphery must be able to respond to the temporal dimensions of a moving stimulus with a precision comparable to the fovea. Two recent studies have shown that the peripheral sensitivity for one type of temporal signal, asynchrony, is very good (Westheimer, 1982; Happ and Pantle, personal communication). Confirming a wealth of anecdotal evidence, Tyler (1981) has recently demonstrated that the critical flicker fusion rate is actually higher in the periphery than in the fovea.

The precise response to velocity in the periphery may have some functional consequences. For the

moving observer, differences in the retinal velocities of stationary objects can provide information about their relative depth (Helmholtz, 1910; Gibson, 1950; Nakayama and Loomis, 1974; Rogers and Graham, 1979). In the fovea, binocular disparity supplies exquisitely precise information about depth, but disparity detection in the far periphery may be significantly degraded, particularly if the visual field is in motion. As one example, motion parallax in the peripheral visual field can provide information as to the layout of the ground plane ahead. An observer of average height looking straight ahead and walking at a pace of 2 m/sec will be exposed to optical velocities of 35°/sec from ground points two paces ahead. Thus he will be able to fixate points on the horizon plane and still have optimal registration of velocity information at a retinal eccentricity of 40°.

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