

ACUITY FOR FINE-GRAIN MOTION AND FOR TWO-DOT SPACING AS A FUNCTION OF RETINAL ECCENTRICITY: DIFFERENCES IN SPECIALIZATION OF THE CENTRAL AND PERIPHERAL RETINA

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Abstract—The brief presentation in the peripheral field of two closely spaced luminous point stimuli, in rapid sequence, induces the illusion of a single dot moving over an extended path. This fine-grain movement illusion (FGMI) is particularly compelling under conditions of dark adaptation. The strength of the motion percept, assessed by a rating-scale procedure, was found to correlate well, over different flash–flash onset delays, with an objective measure of the illusion requiring discrimination of the direction of the flash–flash sequence. A direction–discrimination measure was used to determine the minimum dot separation that would reliably elicit an FGMI at retinal eccentricities of 5–25 deg. For comparison, measures of static spatial acuity was made based on the minimum angle of resolution of two simultaneous dot flashes, and on the threshold for discriminating the separation of two simultaneous dot flashes with variable initial spacing. The spatial threshold for FGMI was lower than that for each of the static measures at all peripheral eccentricities, and it increased more slowly with eccentricity than the other spatial thresholds, suggesting the involvement of separate visual pathways for generating percepts of motion and percepts of shape or location. The finding that in the periphery the grain for motion detection was finer than that for spatial discrimination constrains a class of motion-perception models that form an initial spatial description of the stimulus and then compute a temporal derivative.

Acuity	Motion	Hyperacuity	Fine-grain movement	Short-range apparent motion
Peripheral retina		Scotopic vision		

INTRODUCTION

A potent, minimum stimulus for motion perception is provided by the sequential flashing of two spatially unresolved points of light in the peripheral visual field (Exner, 1875a; Thorson, Lange & Biederman-Thorson, 1969). The resulting illusion, called the “fine-grain movement illusion” (FGMI) by Thorson et al. (1969), is of a dot travelling linearly for several degrees of visual angle. In the dark-adapted eye, where the effect is particularly pronounced, the extent of the illusion may be 30 times as great as the separation of the two retinal points being stimulated (Foster, Thorson, McIlwain & Biederman-Thorson, 1981). It is not an artefact of eye-movements for the FGMI occurs with stabilized retinal images (Biederman-Thorson, Thorson & Lange, 1971). The FGMI may represent the spatiotemporal two-impulse response of the peripheral movement-detection system (Biederman-Thorson et al., 1971), and a theoretical treatment of the illusion has been offered based

on the dynamics of neural arrays (von Seelen, 1973).

In the method of its generation and in its perceived form, the FGMI is quite distinct from classical apparent motion induced by the sequential flashing of stimuli that may be separated by up to 18 deg of visual angle (Zeeman & Roelofs, 1953). It is also distinct from the effects produced by simply displacing a continuously illuminated point stimulus (Biederman-Thorson et al., 1971; Scobey & Horowitz, 1976).

If two FGMI are presented close to each other they tend to interact. The interaction depends on their relative orientations and positions, and it is only when they are *co-directional* that they do not interfere with each other (Foster et al., 1981). This rule governing the local interactions of two, or more, FGMI may form the basis of the global motion percepts produced by alternating certain complex random-dot pattern (kinematogram) displays (Julesz, 1971; Braddick, 1974; Baker & Braddick, 1982;

Williams & Sekuler, 1984). Motion signals derived from "illegal" dot-pairings in the two displays are demonstrably suppressed by these local interactions.

The punctate nature of the FGMI stimulus makes it possible to investigate the effects of selective excitation of rods and cones. The illusion has thus been shown to be obtained by rod-rod excitation, by cone-cone excitation, and, providing the different latencies of rod and cone pathways are taken into consideration in the stimulus timing, by rod-cone excitation also (Foster, 1977). Although the illusion can be elicited dichoptically, it is only weakly obtained under conditions of monocular dichogeniculate presentation (stimuli to separate hemiretinae; Thorson et al., 1969; Biederman-Thorson et al., 1971).

Because the two stimulus points or dots of light when flashed simultaneously may be spatially unresolved, the characteristics of the FGMI have traditionally been measured objectively—by using the illusion to estimate the direction of the flash-flash sequence, e.g. "leftwards" or "rightwards" for a horizontally aligned dot-pair (Thorson et al., 1969; Biederman-Thorson et al., 1971). Direct estimates of the strength of the illusion as a motion percept have not previously been reported. It is shown here that discriminating the direction of the flash-flash sequence correlates well with subjective judgements of the strength of the motion percept, over a range of flash-flash onset delays and stimulus eccentricities.

The FGMI may be used to test directly the old speculation that the peripheral retina is organized more for the detection of motion than of form or location (Exner, 1875b). There are, however, surprisingly few quantitative data in the literature—some reviewed later—that bear properly on the issue. An important experimental prerequisite is that the motion- and form-detection tasks should, as far as possible, be spatially equivalent—that is, differ only in their temporal aspects. For the FGMI, there is an obvious measure of spatial acuity: the minimum separation of the two dots that will reliably elicit the illusion. For the detection of the form or location of the stimulus, there are two appropriate measures: the spatial threshold for discriminating two dots from one, that is two-dot spatial resolution, also known as the minimum angle of resolution (MAR); and the spatial threshold for discriminating pairs of dots differing in their centre-to-centre separations, the two dots being

initially spatially resolved. The MAR can be regarded as a degenerate case of the threshold for separation discrimination in which the two dots are initially coincident, but, because of the different levels of performance known to be obtained in the two types of task, it has been usual to treat MAR and separation-discrimination threshold differently, the latter being placed in the special class of "hyperacuity" measures (Westheimer, 1975) because of its fineness in relation to the retinal mosaic. MAR is an appropriate measure of static acuity because the comparison is direct: the stimulus to be resolved is, apart from the simultaneity of the dot-flashes, identical with the stimulus for an FGMI. The generation of an FGMI does not, however, require the spatial resolution of the dot-stimuli, and separation-discrimination threshold provides a measure of spatial sensitivity for the location of one dot in relation to the other.

The first, preliminary, experiment established the critical temporal parameters for generating the illusion at various retinal eccentricities: performance in discriminating the direction of the flash-flash sequence was determined as a function of onset delay. The second experiment compared these objective measurements with rating-scale estimates of the strength of the motion percept, independent of its direction. In the last two experiments, direction-discrimination measurements were used to determine spatial acuity for FGMI as a function of stimulus eccentricity; this FGMI acuity was compared with the two corresponding measurements of static spatial acuity, MAR and separation-discrimination threshold, the latter evaluated over a range of dot-dot spacings.

Some findings preliminary to this study have been reported previously (Foster, Gravano & Thorson, 1982; Foster, Thorson & Tomoszek, 1986).

EXPERIMENT 1: TEMPORAL RESPONSE CHARACTERISTICS OF FGMI SEQUENCE DISCRIMINATION AS A FUNCTION OF RETINAL ECCENTRICITY

As defined by performance in discriminating the direction of the illusion vs flash-flash onset delay, the temporal response characteristics of the FGMI have been shown to be band-pass: at very short or very long onset delays, no illusion is elicited and performance falls to chance levels. Thus, in the peripheral field, at 21-deg eccentric-

ity along a horizontal meridian, direction-discrimination performance under mesopic conditions was found (Thorson et al., 1969; Biederman-Thorson et al., 1971) to peak at onset delays of 25–65 msec. In other experiments (Foster, 1977) performed at 15-deg eccentricity, direction-discrimination performance under scotopic conditions was found to peak at approx. 100 msec.

This experiment determined temporal response characteristics of the FGMI at three stimulus eccentricities, 5, 15 and 25 deg, along a horizontal meridian in the temporal retina of the dark-adapted eye. The spatial separations of the two dot-flashes had to satisfy the requirement that they were less than the minimum necessary for spatial resolution (MAR) and greater than the minimum necessary for generation of an FGMI (FGMI spatial threshold). Two methods for setting dot-dot separations were used at each eccentricity: details are given in the following section.

Methods

Stimuli. The FGMI stimulus consisted of two, vertically aligned, circular white dots, with approximately Gaussian intensity profiles and half-height diameters of approx. 0.04-deg visual angle; duration of each dot-flash was less than 1 msec (see Apparatus). Flash-flash onset delays ranged from 0 to 500 msec. The stimuli were presented monocularly, to the right eye, at various eccentricities ranging from 5 to 25 deg along a horizontal meridian in the left visual field (temporal retina). The centre-to-centre separation of the dots was fixed at each eccentricity according to two methods, taken in turn: (1) spacing was set midway between MAR and the FGMI spatial threshold; (2) spacing was set a constant 0.02 deg larger than the FGMI spatial threshold. These dot-dot separations, which are indicated in Fig. 1 by circular and square symbols respectively (and which for subject SG were identical at 5 deg eccentricity), were computed from separate acuity estimates obtained with a fixed, optimal, flash-flash onset delay of 100 msec, a value based on previously published data (Foster, 1977). The details of these spatial determinations are given in full in the Methods section of expt 3. The stimuli appeared on zero background and their intensities were adjusted for each subject at each eccentricity to be 1.0 log₁₀ unit above absolute luminance threshold (see Procedure), where detection was dominated by the rod system.

Apparatus. The dot-flashes were produced on the screen of an X-Y display CRT (Hewlett-Packard, Type 1321A), with P4 sulphide phosphor (90–10% decay time approx. 100 μ s), controlled by a minicomputer (CAI Alpha LSI-2) with graphics interface (Sigma Electronic Systems QVEC 2150). The centres of the stimulus dots could be located on the screen at intervals of 0.01 deg vertically and 0.03 deg horizontally. The screen was viewed through a view tunnel at a distance of 0.75 m. The subject used the right eye and head position was stabilized with a chin-rest and head-rest. Because of the possible geometrical-optical problems associated with obliquely incident light, an artificial pupil was not used. The left eye was occluded. A dim, yellow, light-emitting diode fixed to the face of the CRT formed the fixation target. Subjects made their responses on a hand-held push-button box connected to the computer. The geometry of the display was calibrated at the beginning of each experimental session after at least 20-min warm-up of the CRT.

The intensity-modulation signal of the CRT was locked to the 50-Hz mains (line) supply; intervals between the onsets of dot-flashes were thus multiples of 20 msec. The intensity profiles of the dot-flashes on the CRT were measured at 0.1-mm intervals by means of a travelling microscope, with vernier adjustment, coupled to a photodiode detector and linear, low-noise amplifier. Half-height diameter of each dot flash was 0.47 mm.

Procedure. Each observation session was preceded by 20-min dark adaptation. At each eccentricity, dot-flash intensities were set for each subject at 1.0 log unit above absolute luminance detection threshold. (This setting was achieved by the experimenter placing a 1.0-log-unit neutral density filter over the screen, adjusting the intensity of the flashes to absolute threshold, and then removing the filter.) Subjects had the choice of initiating trials themselves or of the computer initiating trials automatically, a few seconds after each response. All subjects chose the latter course. No feedback concerning trial-to-trial performance was given to subjects. FGMI dynamics were determined as follows. The magnitude of the onset delay between the two dot-flashes was chosen pseudorandomly from 10 values between 0 and 500 msec; for each such setting, the direction of the stimulus sequence, "upward" or "downward", was also chosen pseudorandomly. (The trial sequence is schematized in Fig. 1.) Subjects indicated their

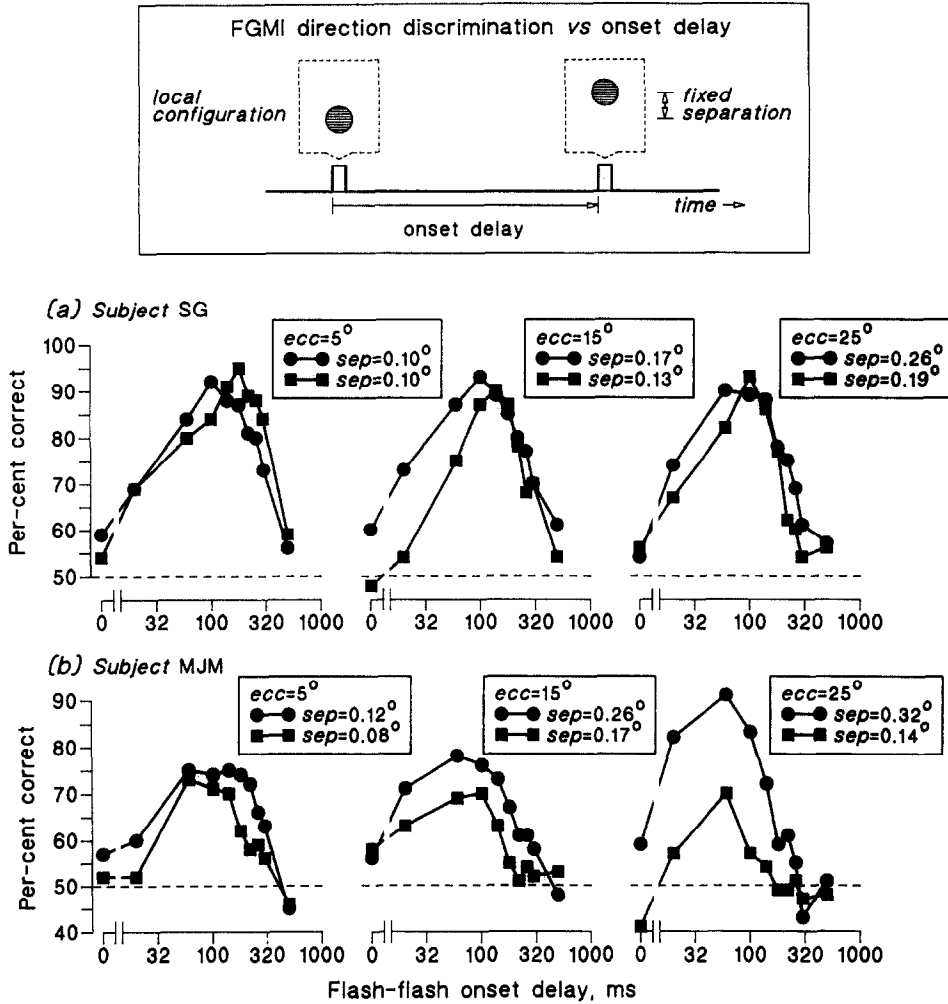


Fig. 1. Temporal direction-discrimination characteristics of the fine-grain movement illusion. For each subject (a) and (b), the percentage of correct estimates (in 100 trials) of the direction of the flash-flash sequence is plotted against flash-flash onset delay, for three stimulus eccentricities and a range of dot-dot separations (●: dot-dot spacings midway between MAR and FGMI spatial threshold; ■: dot-dot spacings 0.02 deg greater than FGMI spatial threshold). Chance-level performance is shown by the horizontal broken line. The trial sequence is schematized in the inset to the figure.

estimate (forced-choice) of the actual direction of the onset sequence on each occasion. Subjects were instructed that they could base their estimates on the direction of any perceived motion if it occurred. The ordering of flash-flash onset delays was determined by a randomized block design that was balanced for order and carry-over effects (see e.g. Wright, 1965). At each eccentricity, a run of 100 trials was performed, 10 trials in all for each of the 10 onset delays. Each experimental session, lasting 45–60 min, comprised three such runs, one run each at eccentricities of 5, 15 and 25 deg, in either ascending or descending order (the order being reversed from session to session). Each subject participated in 10 sessions. Each estimate of

direction-discrimination performance at each onset delay at each eccentricity was therefore based on 100 trials.

Subjects. Two subjects participated in the experiment: MJM was male, aged 25 yr, and had normal uncorrected vision, with Snellen acuity in the right eye of 6/4; SG (coauthor) was male, aged 22 yr, and had normal, uncorrected vision, with Snellen acuity in the right eye of 6/4. Both subjects were experienced psychophysical observers. MJM was unaware of the purpose of the experiment.

Results and comment

Figure 1 (a, b) shows FGMI temporal response characteristics for the two subjects. Per-

cent correct direction discrimination is plotted against flash–flash onset delay, on a logarithmic scale except at 0 msec, for the three stimulus eccentricities. Data points for the (larger) dot–dot spacings obtained by Method 1 are shown by the circular symbols, and those for the (smaller) dot–dot spacings obtained by Method 2 are shown by the square symbols. Chance-level performance is indicated by the horizontal broken line.

There were some differences between subjects in mean performance level and in variation in performance with stimulus eccentricity; these effects are shown later to be attributable mainly to differences in dot–dot spacing. Nevertheless, there were certain common features in the response characteristics. They were all band-pass, with performance declining rapidly for flash–flash onset delays below 60 msec and above about 180 msec, a finding consistent with previous studies (Biederman-Thorson et al., 1971; Foster, 1977). There was also a small shift in the positions of the peaks in the response characteristics towards smaller onset delays as eccentricity increased, an effect which was statistically significant* with the larger dot–dot separations (for both subjects, $z \geq 5.34$, $P < 0.0001$, 2-tailed tests here and elsewhere). There were no systematic effects of dot–dot separation on the positions of the peaks over the range of stimulus eccentricities tested (for both subjects, $z \leq 0.74$, $P > 0.1$).

The marked differences in mean levels of performance could be explained by differences in eccentricity and in dot–dot spacing (for both subjects, the proportion of variance accounted for was not less than 85%, $z \geq 2.76$, $P < 0.01$). Over the range of dot–dot separations tested, all of which were set below the MAR limit, mean performance (%) decreased slowly with eccentricity (deg) (for SG, $-0.96 \pm 0.20\% \cdot \text{deg}^{-1}$; for MJM, $-0.73 \pm 0.20\% \cdot \text{deg}^{-1}$) and increased rapidly with dot–dot separation (for SG, $89 \pm 29\% \cdot \text{deg}^{-1}$; for MJM, $74 \pm 20\% \cdot \text{deg}^{-1}$).

Although dot–dot spacing increased with eccentricity, the optimal onset delay for flash–flash direction discrimination decreased with eccentricity; in terms of the spatial and temporal parameters of the stimulus, this effect

may be interpreted as a shift in optimal stimulus velocity towards higher values. Using drifting sinewave grating stimuli, Koenderink, Bouman, Bueno de Mesquita and Slappendel (1978b) also found that the velocity that corresponded to an optimum spatiotemporal grid pattern (with respect to contrast sensitivity) was a monotonically rising function of eccentricity. Johnston and Wright (1985) also reported that lower temporal-frequency thresholds for grating motion increased with increase in stimulus eccentricity.

These effects were calculated for distances measured in (angular) retinal coordinates, and a more appropriate space might be the cortical projection of the retinal image based on the cortical magnification factor, which varies with eccentricity (Daniel & Whitteridge, 1961; Koenderink, Bouman, Bueno de Mesquita & Slappendel, 1978c; Rovamo & Virsu, 1979; Foster et al., 1981; Virsu, Rovamo, Laurinen & Näsänen, 1982; Pointer, 1986; see also General Discussion). When dot–dot separations were here expressed as fractions of MAR at each eccentricity, under the assumption that MAR defined an appropriate functional scale for the retinal image, the transformed dot–dot separations (from Fig. 1) then *decreased* with eccentricity. (For SG and MJM respectively, the plot of MAR-scaled values of the larger dot–dot separations (i.e. $\text{separation} \cdot \text{MAR}^{-1}$; $\text{deg} \cdot \text{deg}^{-1}$) vs eccentricity (deg) had gradients -0.005 ± 0.003 and $-0.004 \pm 0.003 \text{ deg}^{-1}$ and of the smaller dot–dot separations -0.015 ± 0.008 and $-0.010 \pm 0.005 \text{ deg}^{-1}$.) After this scaling, the shift in optimal velocity towards higher values was no longer evident. An effect of stabilizing responses to moving gratings by *M*-scaling was also described by Koenderink et al. (1978c, d) and by Johnston and Wright (1985).

EXPERIMENT 2: DOES FLASH-FLASH SEQUENCE DISCRIMINATION DEPEND ON SEEING MOTION?

Descriptions of classical apparent movement have been in terms of “simultaneity”, “optimal movement”, and “successivity” (Wertheimer, 1912). Although studies of the FGMI, cited earlier (and of displacement detection, Legge & Campbell, 1981) have depended on subjects’ using the direction of the motion illusion to infer the sequencing of the stimulus flashes, we decided, as a control, to ask them to report simply on the presence or absence of perceived

*The positions of the peaks in the response characteristics were estimated by transforming the per-cent-correct data by an empirical logistic transform (Cox, 1970), and then least-squares fitting the transformed data by two linear sections forming an inverted “V”, the position of the apex being allowed to vary in the fitting procedure.

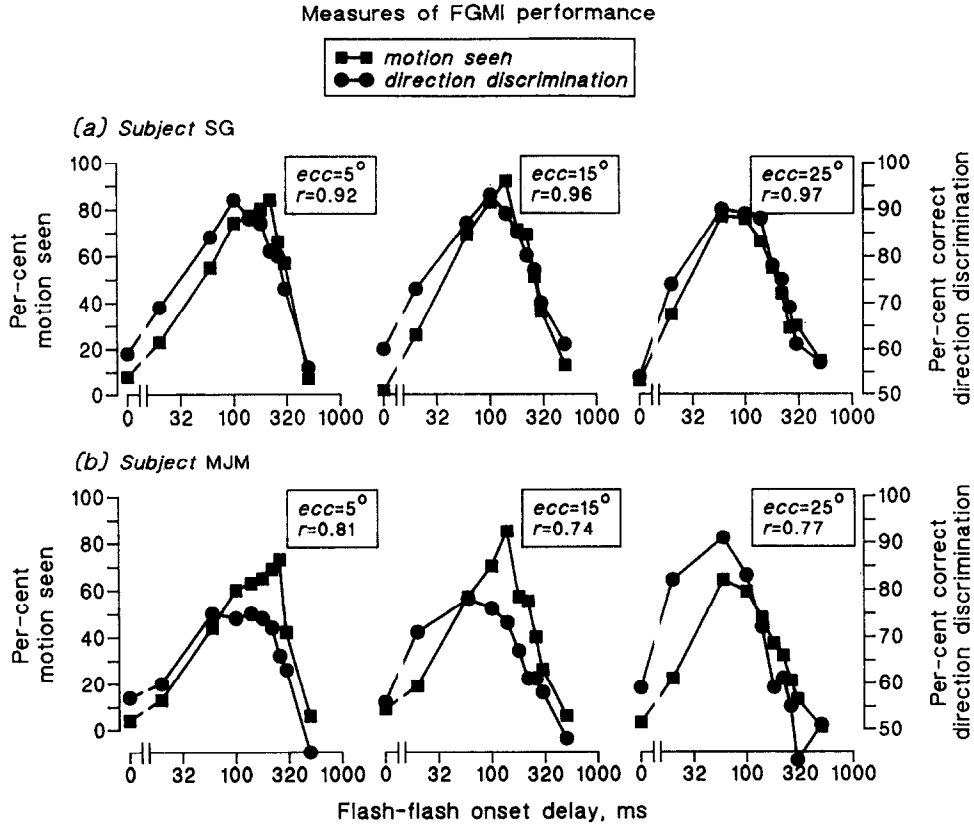


Fig. 2. Motion ratings of the fine-grain movement illusion. For each subject (a) and (b), the percentage of responses "motion seen" (in 100 trials) is plotted against flash-flash onset delay, for the three stimulus eccentricities and range of dot-dot separations used in expt 1 (Method 1). Data for direction discrimination have been replotted from Fig. 1 (●).

movement vs flash-flash delay to ascertain whether motion percepts so determined correlated closely with more objective measures of performance.

Methods

Apart from the definition of the task that subjects were required to perform, the methods and procedure were identical with those of expt 1 (with dot-dot spacings set according to Method 1). Responses were recorded as "1" for "motion seen", and "0" for "no motion seen". The subjects were the same as in expt 1.

Results and comment

Mean rating responses for motion seen (averaged over 100 trials per flash-flash onset delay, eccentricity, and subject) ranged from 0 to 100%. Figure 2 (a) and (b) shows the results plotted against flash-flash onset delay on a logarithmic scale (except at 0 msec), for the two

subjects and three stimulus eccentricities. Direction-discrimination data from Fig. 1 (solid circles) have been replotted to facilitate direct comparison.

Correlations between rating and discrimination performance were high: coefficients (Pearson product r) ranged from 0.74 to 0.97 (Fig. 2), and all were significantly different from zero (each $z \geq 2.49$, $P < 0.01$).

Previous assumptions about subjects' direction-discrimination performance (Thorson et al., 1969; Biederman-Thorson et al., 1971; Foster, 1977; Foster et al., 1981) were confirmed: the correctness of subjects' direction-discrimination estimates were closely related to the strength of the induced motion illusion. Moreover, the temporal response characteristics defined by the rating performances showed the same shift towards smaller flash-flash onset delays with increasing stimulus eccentricity as was detected in the direction-discrimination measurements of expt 1.

EXPERIMENT 3: COMPARISON OF ACUITY FOR FINE-GRAIN MOTION WITH MINIMUM ANGLE OF RESOLUTION

Measurements first made by Exner (1875a) and subsequently by Thorson et al. (1969), Biederman-Thorson et al. (1971), and Foster (1977) have shown that reliable flash-flash direction discrimination, determined by the induced FGMI, may be made with dot-flash pairs spaced so closely that when flashed simultaneously they are spatially unresolved. It was this basic property of the FGMI that made possible the original objective determination of the temporal response characteristics of the illusion (Thorson et al., 1969). What was not determined in those measurements, however, was how close the two dot-flashes may be placed without destroying the motion percept.

This experiment determined values for the minimum spatial separation of the sequentially flashed dots that would induce an FGMI, and, for comparison, the minimum angle of resolution (MAR) for the two dots flashed simultaneously. On the basis of the temporal response characteristics determined in expt 1, flash-flash onset delay was fixed at 100 msec.

Spatial thresholds were obtained by a procedure that measured (per-cent correct) flash-flash direction-discrimination performance, in a two-alternative forced-choice regime, over a range of dot-dot separations controlled by a sequential testing algorithm (PEST: Taylor & Creelman, 1967; modified by Hall, 1981). A sigmoidal performance curve (psychometric function) subsequently fitted to the data defined the stimulus threshold as the dot-dot separation corresponding to a performance level of 75%.

Methods

Stimuli and apparatus. The FGMI stimulus, with variable dot-dot spacing, was as in expt 1. The MAR stimulus consisted of two simultaneously flashed dots, also with variable spacing, which were spatially and temporally, apart from their zero onset delay, identical with those used in the FGMI measurements.

Procedure for FGMI acuity. Each trial consisted of two presentations, each containing two vertically aligned dot-flashes presented se-

quentially. The onset order of the dot-flashes was opposite in the two presentations, and the choice of direction ("downward" in first or second presentation) was determined pseudorandomly. The spatial separation of the dot-flashes was always equal in the two presentations and was controlled by the PEST procedure. The onset-delay between the two dot-flashes in each presentation was fixed at 100 msec. The two presentations in each trial were separated by an interval of 1.5 sec. (The trial sequence is schematized in the inset to Fig. 3.) The task of the subject was to report the presentation in which the upper dot-flash preceded the lower dot-flash. Subjects were aware that they could base their decision on the direction of any perceived motion.*

Procedure for MAR. Each trial consisted of two presentations, the one containing two vertically aligned dot-flashes presented simultaneously, the other containing a single dot-flash of twice the luminance of each of the dot-flashes in the other presentation. The choice of which presentation occurred first was determined pseudorandomly. The spatial separation of the dot-flashes in the two-dot presentation was controlled by the PEST procedure. The two presentations in each trial were separated by an interval of 1.5 sec. (The trial sequence is schematized in the inset to Fig. 3.) The task of the subject was to report which presentation contained the two dots.

Observations were made at five retinal sites, of 5, 10, 15, 20 and 25 deg eccentricity, in the temporal retina, in either ascending or descending order. Each experimental session consisted of five runs of trials, one run at each eccentricity, each run comprising 36 preliminary trials and 72 (or two independent sets of 36) recorded trials to which performance functions were fitted. Other details were as in expt 1. Subjects participated in two or four experimental sessions for each type of spatial threshold; mean thresholds were based on four separate estimates.

Subjects. There were four subjects: MJM and SG who had participated in expts 1 and 2; RSS who was female, aged 25 yr, and had normal, corrected vision, with Snellen acuity in the right eye of 6/6; and DHF (coauthor) who was male, aged 37 yr, and had normal, corrected vision, with Snellen acuity in the right eye of 6/4. All subjects were experienced psychophysical observers. MJM and RSS were unaware of the purpose of the experiment.

*It was noted by some observers that at very small spatial separations of the dots the FGMI percept was sometimes ambiguous, appearing to go in one direction and then immediately in the opposite direction. This effect may have been due to small involuntary shifts in fixation.

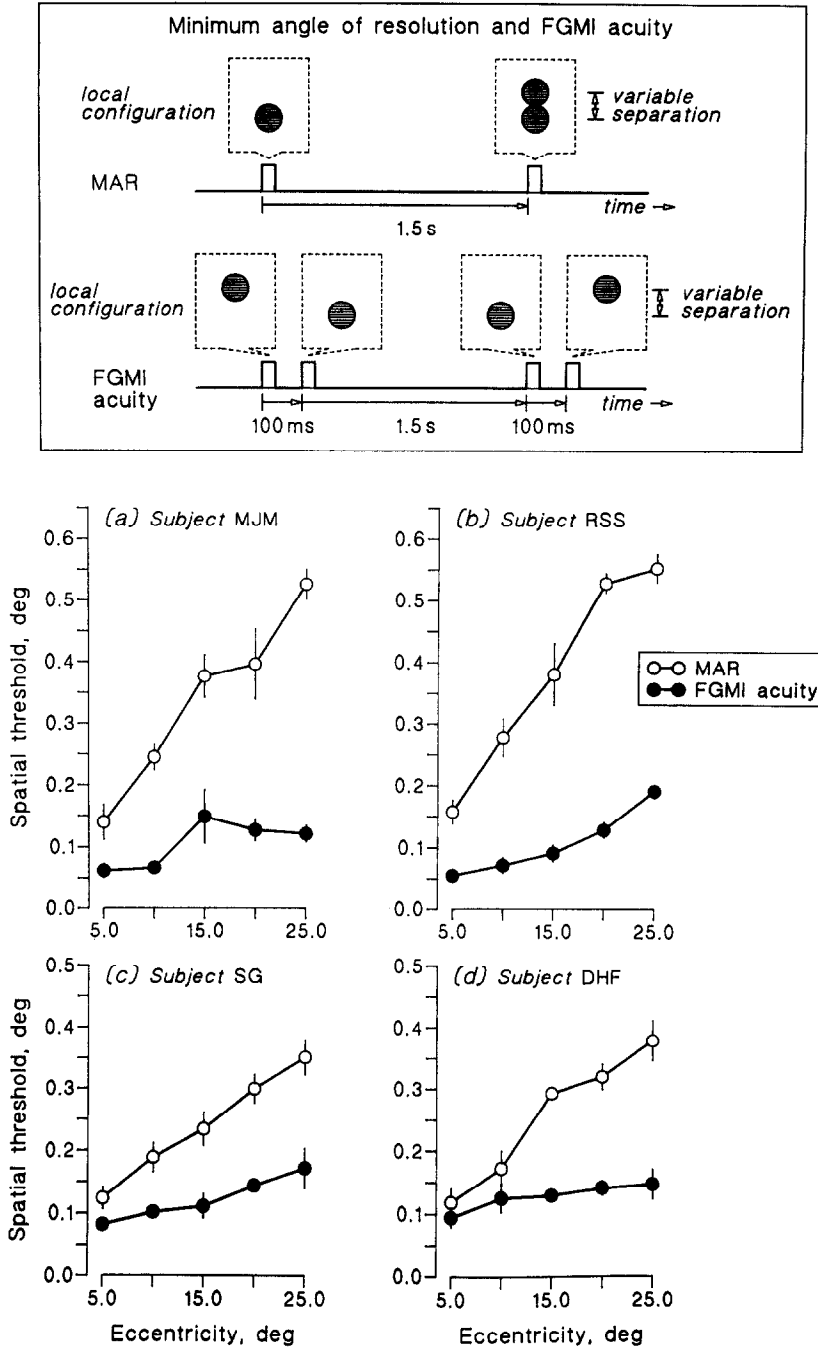


Fig. 3. Acuity for FGMI and for two-dot spatial resolution. Spatial thresholds for FGMI (●) and two-dot spatial resolution, MAR (○) are plotted against stimulus eccentricity for each of four subjects (a)–(d). Each point is the mean of four estimates, each based on 36 or 72 individual trials, and the vertical bars show ± 1 SEM where sufficiently large. The trial sequences are schematized in the inset to the figure, the regions within the broken lines illustrating the local stimulus configuration.

Data analysis. The performance data from each run were fitted by a logistic psychometric function of the form

$$P(x) = 1/n + (1 - 1/n)/(1 + \exp[-(x - M)/S]),$$

where $P(x)$ was the predicted probability of a correct response at stimulus level (dot-dot separation) x , $n = 2$ was the number of alternatives in the forced-choice task, M was the mid-point of the distribution, corresponding to the 75% performance level and the defined spatial

threshold, and S was the "spread" (Hall, 1981) of the distribution. The function was fitted by maximizing the likelihood. Details are given in Foster (1986). The reliabilities of individual thresholds thus derived were determined according to their estimated standard deviations (SDs), computed by a Taylor-series expansion technique (Foster, 1986). Weighted and unweighted mean thresholds (over the four independent runs in each condition) were compared to test for possible extreme values (which occasionally occur in automated threshold estimation procedures with fixed numbers of trials). In this experiment, only five threshold estimates out of 160 (3%), each with estimated SDs exceeding expected values by a factor of more than 10^3 , were thus rejected. (Similar results were obtained in other experiments.)

Results and comment

Figure 3 (a)–(d) shows for each of the four subjects the dependence on retinal eccentricity of the spatial thresholds for direction discrimination with sequentially flashed dots (FGMI) (solid symbols) and for two-dot spatial resolution (MAR) (open symbols). Vertical bars show ± 1 SEM (based on $N = 4$ individual thresholds) where sufficiently large.

The differences between the eccentricity dependencies of MAR and acuity for FGMI are obvious. Thresholds defined by two-dot resolution were greater than those for FGMI at 5-deg eccentricity, and they increased more rapidly with eccentricity than FGMI thresholds; in all cases, the variation of spatial threshold with eccentricity was well approximated by a linear function (there were in fact no significant departures from linearity: $F(3, 25) < 2.3$, $P > 0.1$, for each of the two types of threshold measure and four subjects). The mean gradient (± 1 SEM) over subjects of the increase in MAR (deg) with eccentricity (deg) was 0.016 ± 0.002 , whereas for acuity for FGMI it was 0.0045 ± 0.0008 ; the mean ratio of the two gradients was 3.73 (± 0.57).

Although both types of spatial threshold varied approximately linearly with eccentricity, the ratio of FGMI threshold to MAR was not constant with eccentricity (for subjects MJM, RSS, DHF, $F(4, 15) \geq 10.6$, $P < 0.001$; for SG, $F(4, 15) = 4.4$, $P < 0.05$). Acuity for FGMI therefore could not be made invariant with eccentricity by scaling according to MAR. Some implications of this result are considered after the next experiment.

Spatially, the stimuli used for two-dot resolution and for generating the FGMI were identical: they differed only in the onset delay between the dot-flashes. The measured performances showing that at all peripheral eccentricities MAR was much larger than FGMI threshold quantify and extend the earlier observations by Exner (1875a), Biederman-Thorson et al. (1971), and Foster (1977). They also make it possible to reject a simple model of fine-grain motion in which the separate parts of the spatially resolved image are labelled first by spatial location and then by time of excitation, an operation that would form the basis of a logical implication: "if upper dot flashed first, then direction downwards".

Some models of human motion perception are, of course, neutral with respect to the implications of static spatial resolution (e.g. the correlator models, Foster, 1971; but see van Santen & Sperling, 1984; Wilson, 1985). There are, however, other models (e.g. Marr & Ullman, 1981; Bischof & Groner, 1985) that perform comprehensive spatial analyses. Typically (Marr & Ullman, 1981) there is assumed to be an early extraction of spatial contours in the stimulus, after which a motion signal is generated by an operation of temporal differentiation. For the present purposes, no assumption need be made about the specific nature of the early spatial analysis; indeed, stimulus features such as centre of mass may be more appropriate descriptors (Westheimer & McKee, 1977a; Watt & Morgan, 1984). The critical point is that for movement perception to occur, some measure of stimulus position must be obtained before temporal differentiation is applied. The next experiment, then, considered performance in judging the position of one dot flash in relation to another, simultaneous, dot-flash.

EXPERIMENT 4: COMPARISON OF ACUITY FOR FINE-GRAIN MOTION WITH ACUITY FOR DIFFERENCES IN DOT SEPARATION

This experiment determined sensitivity to changes in spatial location, as a function of retinal eccentricity, to ascertain whether the spatial thresholds obtained were such that they could explain the spatial acuity associated with the FGMI. Detecting a change in the position of a light dot in relation to another light dot constitutes a hyperacuity task (Westheimer, 1975; Westheimer & McKee, 1977b), and per-

formance is known to depend strongly on the initial spacing of the dots both in the fovea and perifovea (Westheimer, 1982). In this experiment, thresholds for detecting an increase in spatial separation (separation-discrimination threshold) of two dots flashed simultaneously were determined for various initial (reference) values of the dot-dot separations, including values above and below MAR. Values of the minimum spatial separation of the dots flashed sequentially, thus inducing the FGMI, were obtained afresh.

Methods

Stimuli and apparatus. The stimuli and apparatus were similar to those of expt 3, except that the viewing distance was 0.5 m and the fixation target was formed by a computer-generated dot on the screen of the CRT. A small modification was made to the procedure for adjusting the intensities of the dot-flashes for one of the subjects (AT) participating in this experiment. The intensities of the dot-flashes were adjusted for that subject to be 1.0 log unit above absolute luminance threshold at the (dark-adapted) fovea. This intensity level was maintained over all eccentricities for that observer. As a result, in the periphery the dot-flashes were between 1.8 and 2.0 log unit more intense than at absolute threshold. For the other subject participating in this experiment, flash intensities were adjusted at each eccentricity to be 1.0 log unit above absolute luminance threshold. As shown later, however, minimum values of the spatial thresholds for the two subjects were very similar.

Procedure for separation-discrimination acuity and for FGMI acuity. Each trial consisted of two presentations in which two vertically aligned dot-flashes were presented simultaneously. (The trial sequence is schematized in the inset to Fig. 4.) The spatial separation of the dot-flashes had a fixed value in one presentation (the reference value), and a larger, variable value in the other presentation. The increase in separation was controlled by the PEST procedure. The choice of which presentation occurred first was determined pseudorandomly. The two presentations in each trial were separated by an interval of 1.5 sec. The task of the subject was to report which presentation contained the two dots with the larger spatial separation. The procedure for determining FGMI acuity was precisely as in expt 3.

Measurements were made at five retinal sites,

of 5, 10, 15, 20 and 25 deg eccentricity, in the temporal retina of the right eye, in either ascending or descending order. At each eccentricity, a run of 65 trials was performed comprising 5 preliminary trials and 60 recorded trials to which the performance function was fitted as in expt 3. Trials were initiated automatically by the computer for subject AT, but were initiated manually by subject DHF. Other details were as in expt 3. Subjects participated in two or three experimental sessions for each type of spatial threshold; mean thresholds were based on six separate estimates.

Subjects and data analysis. The two subjects participating in the experiment were DHF (see expt 3), and AT (coauthor), who was female, aged 26 yr, and had normal corrected vision, with Snellen acuity in the right eye of 6/6. Both subjects were experienced psychophysical observers. Data analysis was done as in expt 3.

Results and comment

Figure 4 (a) and (c) shows for each of the two subjects the dependence on retinal eccentricity of spatial thresholds for separation discrimination with simultaneously flashed dots (open symbols) and for direction discrimination with sequentially flashed dots (FGMI) (solid symbols). Vertical bars show ± 1 SEM ($N = 6$) where sufficiently large. The reference values of dot-dot separations used in the separation-discrimination measurements are indicated.

Most of the separation-discrimination threshold values were lower than the corresponding values of MAR. (Compare data for subject DHF in Fig. 4c with those in Fig. 3d). Nevertheless the general pattern of performance was similar to that for MAR determined in expt 3. Thus, at 5-deg eccentricity, separation-discrimination threshold was close to (but never smaller than) the spatial threshold for FGMI and, as eccentricity increased, separation-discrimination threshold increased more rapidly than FGMI threshold. All the sets of data except two of those for separation discrimination were adequately described by a linear dependence of spatial threshold on retinal eccentricity (departures from linearity: $F(3, 25) < 2.5$, $P > 0.05$). Even for the smallest separation-discrimination thresholds, the rate of increase in threshold (deg) with eccentricity (deg) (for AT, 0.0091 ± 0.0024 ; for DHF, 0.0092 ± 0.0012) was about twice the rate for FGMI (for AT, 0.0050 ± 0.0006 ; for DHF, 0.0040 ± 0.0009).

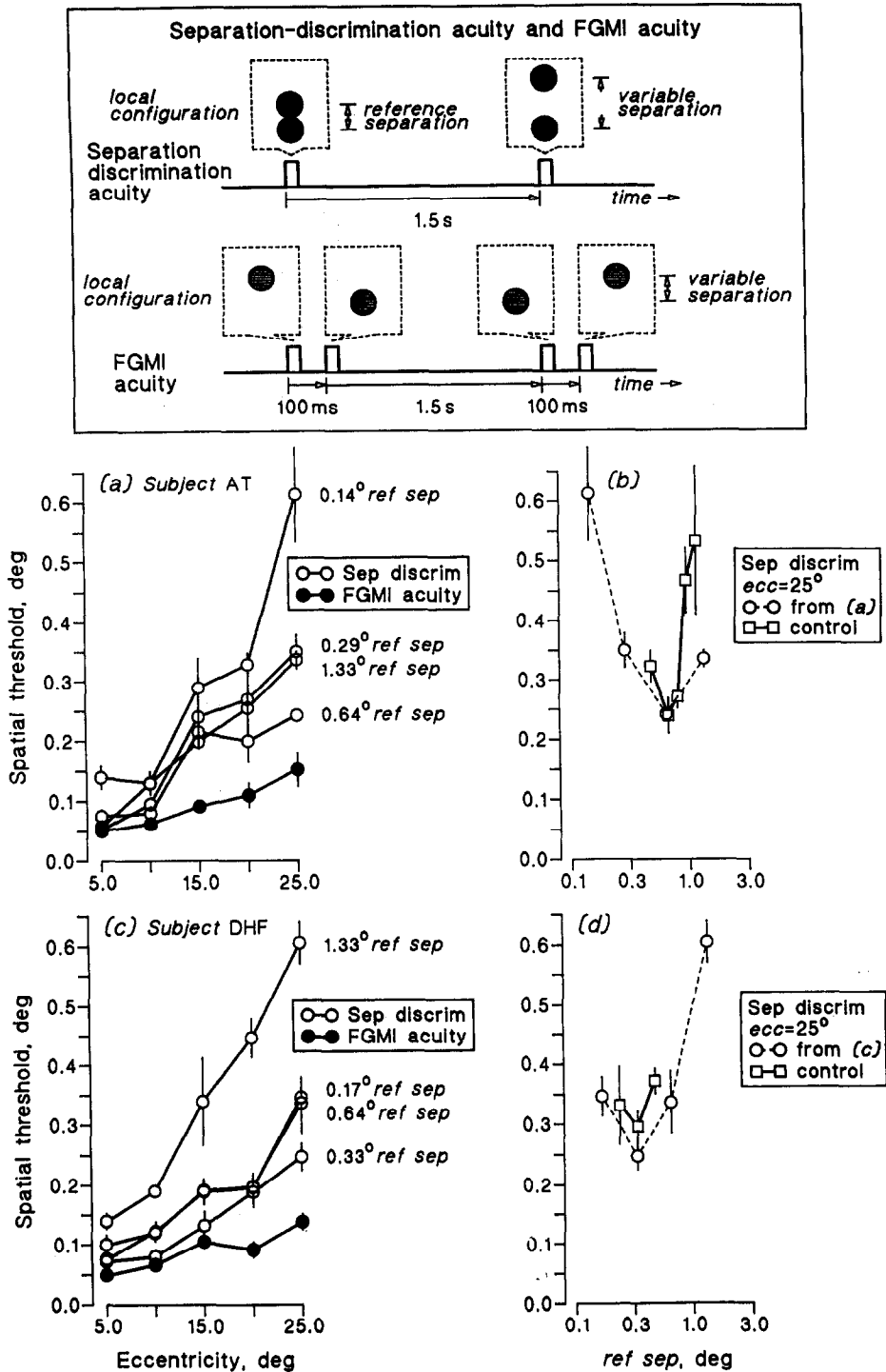


Fig. 4. Acuity for FGMI and for two-dot separation discrimination. (a) and (c) Spatial thresholds for FGMI (●) and two-dot separation discrimination (○) are plotted against stimulus eccentricity for each of two subjects. Reference values of the dot-dot separations for the separation-discrimination measurements are indicated. Each point is the mean of six estimates, each based on 60 individual trials, and the vertical bars show ± 1 SEM where sufficiently large. (b) and (d) Variation in separation-discrimination threshold with reference value of dot-dot separation at 25 deg stimulus eccentricity. Points shown by (○) are replotted from (a) and (c) respectively; those shown by (□) are the results of separate control measurements. The trial sequences are schematized in the inset to the figure, the regions within the broken lines illustrating the local stimulus configuration.

To assess more precisely the effects of reference value of dot-dot separation in determining separation-discrimination threshold at the largest stimulus eccentricity (shown by the open circles in Fig. 4 (b) and (d), which have been replotted from (a) and (c) respectively), a control experiment was performed in which a finer sampling was made of reference-separation values. Results are shown by the additional open squares in Fig. 4 (b) and (d). The values of the reference separation giving the smallest separation-discrimination thresholds were unaltered: 0.64 deg for AT (Fig. 4a, b) and 0.33 deg for DHF (Fig. 4c, d). These minimum separation-discrimination thresholds at 25-deg eccentricity were still 1.6–1.8 times greater than the corresponding spatial threshold for FGMI.

Could the smallest separation-discrimination threshold be rendered invariant with eccentricity if scaled according to magnification factor? In fact, the ratio of that threshold to MAR showed significant departures from constancy over the range of stimulus eccentricities (for each subject, $F(4, 25) \geq 3.5$, $P \leq 0.02$). In the light-adapted eye, departures from constancy have also been reported: thresholds for two-dot offset detection have been found to increase much faster, on a log scale, than MAR over the range 0–10 deg (Westheimer, 1982).

GENERAL DISCUSSION

In the peripheral field, the grain for motion detection appears to be finer than the grain for spatial discrimination. Spatial thresholds for the fine-grain movement illusion have been shown to be less than those obtained in comparable static acuity tasks, including the minimum angle of resolution of two simultaneously presented dots and less than the minimum detectable change in separation of two simultaneously presented dots, with optimal initial spacing. In addition to being smaller, FGMI spatial thresholds increased far less rapidly than these other measures as stimulus eccentricity was increased, the rate being about one half of that for the best static thresholds.

In the following sections we review evidence bearing on the notion of a peripheral superiority for the detection of motion over form, consider some implications for a class of motion-perception models that require the formation of an initial spatial description of the retinal image, and examine the relevance of *M*-scaling in fine-grain motion phenomena.

Grain for motion and for form in the peripheral field

The idea that stimulus motion is detected better than form or location in the periphery may be traced back at least to Exner (1875b, pp. 162, 164) (see Finlay, 1982, for a review of the early literature). Evidence comes from a variety of approaches. Thus the best temporal thresholds for temporal order detection, in two sequentially presented, resolvable lines of variable spacing, have been found to be substantially constant across the visual field (up to 20 deg eccentricity) and, outside the fovea, are obtained over a similar range of line spacings (Westheimer, 1983); the equivalent upper velocity limit (for a classical stroboscopic movement percept) therefore depends on stimulus eccentricity in a different way from other measures of spatial acuity (Westheimer, 1982, 1983). Measurements of the spatial limits on apparent motion produced by random-dot kinematograms (Braddick, 1974) show that the increase in maximum permissible pattern shift with eccentricity is much greater than the increase in minimum permissible shift, suggesting that the range of velocities that can be accommodated by the visual system increases in the peripheral retina (Baker & Braddick, 1985).

Some studies relating to a possible peripheral selectivity have, however, been equivocal or have led to the conclusion that the peripheral retina is *not* preferentially organized for motion detection, although, as in some of the investigations cited earlier, when stimuli were spatially extended, in one or two dimensions, measured sensitivities may have been influenced by variations in the eccentricity dependence of areal-summation effects. The problem was considered quantitatively by Koenderink et al. (1978c). A number of measurements have been made of contrast thresholds for moving, spatially sinusoidal gratings, as a function of spatial and temporal frequency. When these stimuli, presented at different eccentricities, are spatially normalized for similar cortical representations, the different temporal contrast sensitivity functions overlap closely, forming a single function (Koenderink et al., 1978a–c; Virsu et al., 1982). The similarity of foveal and peripheral behaviour at all cortical spatial frequencies did not support the assumption of differences in this form of spatiotemporal processing over the visual field (Virsu et al., 1982). Likewise, the relationship of “pattern” and “movement” contrast thresholds for stationary and drifting grat-

ing stimuli is also the same in central and peripheral vision (Murray, MacCana & Kulikowski, 1983). Instead of estimating absolute thresholds for the detection of motion, McKee and Nakayama (1984) obtained differential (velocity discrimination) thresholds using random-dot and line stimuli, and suggested that "motion sensitivity is not any more remarkable than the static ability to localize points in space" (p. 31), in clear distinction to the present findings.

Constraints on models of movement perception

Some models of local motion detection produce a motion signal derived independently from the light distribution falling on the receptor array, for example, the logical-unit schemes for the rabbit and human visual system (Barlow & Levick, 1965; Barlow, 1981), and the correlator schemes for beetle and locust visual systems (Reichardt and Varjú, 1959; Thorson, 1966a, b; Reichardt & Poggio, 1979) and for the human visual system (Foster, 1971; van Santen & Sperling, 1984; Wilson, 1985). The present data suggest constraints on the temporal characteristics of the constituent mechanisms (e.g. the temporal filters associated with the cross-multiplication paths) in these models, rather than on their organization and logical structure. More fundamental constraints, however, are implied for a different class of model, as is now shown.

An approach to the modelling of motion detection was proposed by Marr and Ullman (1981) in which the analysis of motion was combined with a spatial analysis, specifically of stimulus contours. There were two stages to this process: first, detection of sharp intensity changes in the retinal image such as would occur at a contour; and, second, detection of the sign of the (orthogonal) motion of this sharp intensity change. The locations of the sharp intensity changes were defined by oriented zero crossings—zero values in the convolution $\nabla^2 G * I$ of the retinal image I with a size-tuned filter or mask of profile $\nabla^2 G$, where G is a two-dimensional Gaussian distribution and ∇^2 is a two-dimensional Laplacian operator. Two kinds of unit were supposed to carry information about the convolved image: S^+ ("on-centre") dealing with positive values and S^- ("off-centre") dealing with negative values. If the two units were separated by about the width of a central excitatory region between them, each was maximally stimulated by an edge placed midway

between them. The sign of the temporal derivative $\partial(\nabla^2 G * I)/\partial t$ of the convolution unambiguously determined the direction of the motion component orthogonal to the edge. Like the S unit, a temporal T unit was defined with positive T^+ and negative T^- components. If the combination of units $S^+ T^+ S^-$ were active simultaneously then motion was in the direction of S^+ to S^- ; if the combination $S^+ T^- S^-$ were active simultaneously then motion was in the direction of S^- to S^+ . Experimental measurements of the direction of apparent rotation of sequentially presented, rotated random-dot displays have been found to be in good quantitative agreement with the predictions of this model (Bischof & Groner, 1985), except for low-density patterns and large displacements where perception seemed to be dominated by the operation of classical apparent-motion effects.

Marr and Ullman (1981) offered a number of reasons why the T units should have larger receptive fields than those of the S units, although they recognised that under certain conditions this arrangement would lead to problems. Because the model required an initial spatial analysis of the stimulus image and then a temporal derivative, its sensitivity to the motion of an edge should be no better than its sensitivity to the location of an edge. Indeed, because the measurement of the temporal derivative $\partial(\nabla^2 G * I)/\partial t$ is more complex and involves a delay, it should be *less* reliable than the measurement of $\nabla^2 G * I$ (from Prediction (iv), p. 174, of Marr and Ullman, 1981).

The present results showing that sensitivity to differences in the location of a stimulus is worse than sensitivity to its motion appear to be incompatible with this model. A plausible explanation is that motion information and form information are *not* combined in the manner proposed by Marr and Ullman (1981); although motion signals may be generated by STS units, the initial spatial descriptions $\nabla^2 G * I$ derived in these computations may not be accessible for spatial discriminations with static stimuli.

Invariance scaling and magnification factor

A considerable body of data has now accumulated showing the identity of a number of measures of visual performance over the retina, providing that these measures are scaled spatially by a factor such as minimum angle of resolution. Under photopic conditions, MAR correlates well with cortical magnification fac-

tor, M , expressed in mm of central map per degree of visual angle (Daniel & Whitteridge, 1961; Cowey & Rolls, 1974; Drasdo, 1977). In particular, spatiotemporal contrast sensitivity functions become invariant with eccentricity after M -scaling (Koenderink et al., 1978c, d; Rovamo & Virsu, 1979; Virsu & Rovamo, 1979). Spatial thresholds for detecting square-wave oscillatory motion of a sinusoidal grating also scale according to M (Wright & Johnston, 1985; see also Johnston & Wright, 1985), as do "critical velocities" for the detection of coherent motion in checkerboard random-dot patterns (van de Grind, Koenderink & van Doorn, 1986), and critical flicker frequency, providing that both area and retinal illuminance are scaled (Rovamo & Raninen, 1984). Although the dependence of MAR (or its equivalent) on eccentricity varies with the state of retinal adaptation (Mandelbaum and Sloan, 1947; Koenderink et al., 1978d), the scaling procedure, defined in its most general form (Koenderink et al., 1978c), may be applied to scotopic stimuli if the principle of measuring distances in MAR acuity units is extended to the specification of retinal illumination (Koenderink et al., 1978d).

Despite this concordance, there are several other measures of visual performance that do not scale properly with magnification factor. As already noted, measures of two-dot offset hyperacuity (Westheimer, 1982) and two-dot separation-discrimination threshold (expt 4) fail to become invariant with retinal eccentricity after MAR scaling; and discrimination of M -scaled mirror-symmetric patterns is poorer in eccentric vision than in central vision (Rentschler & Treutwein, 1985; Saarinen, 1988). Spatial acuity for fine-grain motion (expts 3 and 4) is also clearly an exception to the M -scaling principle. There is, however, one property of the FGMI that does not violate this principle. Previously reported data (Foster et al., 1981) on the spatial extent of the illusion under dark-adapted conditions showed that the illusion, after M -scaling, corresponded to a cortical distance of about 3 mm, independent of retinal eccentricity over the range 10–24 deg. (Over that range, standard M -scaling and scotopic MAR-scaling did not differ appreciably in their effects.) For reasons analogous to those offered by Westheimer (1983) for the separate visual processing of temporal order and spatial order, the finding of different spatial scales for these different aspects of the FGMI suggests that there may be distinct processes or pathways for generating fine-grain

motion percepts and their perceived spatial properties.

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