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Limits of Precision for Human Eye Motor Control

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Abstract

If the two segments of a vernier target are presented to different eyes, i.e., dichoptically, thresholds are three to four times higher than with presentation to the same eye. This increase in thresholds is mainly due to uncorrelated movements of both eyes, such as tremor and drifts, that occur even under steady fixation. The psychophysically measured thresholds allow one to calculate an upper estimate for the amplitudes of uncorrelated eye movements during fixation. This estimate matches the best results from direct eye position recording, with the calculated mean amplitude of eye tremor corresponding to roughly one photoreceptor-diameter. The combined amplitude of both correlated and uncorrelated eye movements was also measured by delaying one segment of the vernier relative to its partner under monocular or dichoptic conditions. Fixation proved to be relatively stable, and trained observers could sustain eye position within a few arcmin.

This report describes research done within the Artificial Intelligence Laboratory and the Center for Biological Information Processing (Whitaker College) at the Massachusetts Institute of Technology E25-201 Cambridge, Massachusetts 02139, USA and at the Department of Neuroophthalmology of the University Eye Clinic in D7400 Tübingen, West Germany. Support for the A.I. Laboratory's artificial intelligence research is provided in part by the Advanced Research Projects Agency of the Department of Defense under Office of Naval Research contract N00014-85-K-0124. Support for this research is also provided by a grant from the Office of Naval Research, Engineering Psychology Division. Dr. M. Fahle holds a Heisenberg Stipend from the Deutsche Forschungsgemeinschaft (Fa 119/5-1 and Fa 119/3-2).

Introduction

Humans can identify relative spatial position with a precision far below the diameter of single photoreceptors. Detection of vernier displacement, curvature, orientation, relative motion, depth and spatio-temporal interpolation belong in this class of so-called hyperacuity tasks (e.g. Westheimer, 1979; Ogilvie & Daicar, 1967; Burr, 1979; Watt & Andrews, 1982; Nakayama & Tyler, 1981). In most hyperacuity tasks, relative positional information within one eye is evaluated. One important exception is stereoacuity, the perception of depth from binocular disparity. The relative thresholds for stereoacuity can be as low as 3" (e.g. Westheimer & McKee, 1977), hence the visual system compares the relative locations of features in both eyes with a precision of about one tenth of a photoreceptor diameter.

This study investigates dichoptic vernier acuity, or nonius alignment (McKee & Levi, 1987), another type of binocular hyperacuity, in which one segment of a vernier target is presented to one eye, and the other segment to the other eye. All uncorrelated movements of the eyes shift the retinal positions of the segments of the vernier relative to each other and this increase in positional noise increases thresholds in proportion to the amplitude of the motion. Therefore, the amplitude of disjunctive (Rashbass & Westheimer, 1961) or uncorrelated movements of the eyes during steady fixation can be inferred from the thresholds for dichoptic vernier acuity. In a further series of experiments, the presentation of the second segment of a monocular vernier target was delayed. Movements of the eye during the delay shift the retinal position of the delayed segment relative to the first one. Hence, this delayed vernier task allows one to measure the combined amplitude of correlated and uncorrelated eye movements during fixation.

Methods

Apparatus and Procedure

The vernier targets consisted of two vertical or horizontal bars. They were created by a digital computer (PDP 11/73) and fed to fast (>100 kHz) linear 16 bit D/A converters which allowed accurate control of exposure duration and vertical and horizontal position. The targets were presented on the screens of two Tektronix 608 oscilloscopes with P31 phosphor. Surface-silvered mirrors in front of the eyes routed the image of each monitor to only one eye. In pilot experiments, two Tektronix 602 with P4 phosphor were used. The ray paths were separated by crossed polarizing filters in front of the oscilloscope screens with matched filters in front of the eyes. A beam splitter superimposed the two images.

The segments of the vernier target were 60' (arcmin) long and 2' wide. The spatial gap between the upper and the lower segment of the vernier was always 7' wide. The two segments of the vernier were presented either to one or to both eyes (monocular or binocular condition), or each segment was presented to a different eye (dichoptic condition). Presentation time was 10, 100 or 1000 msec in the first set of experiments. In the second set of experiments, each segment of

the vernier was presented for 10 msec, and one segment was delayed relative to its partner by between 10 and 1000 msec. Stimulus luminance, as measured by a luminance meter (Gossen), was always about 100 cd/m^2 on a homogeneous surround of 30 cd/m^2 produced by overhead incandescent lighting. The only exception was some control experiments performed in a completely dark room. Stimuli were presented at a luminance 2.5 log units above detection threshold and faded to invisibility within less than 1 msec after the end of presentation time.

A bright rectangle, subtending 4x5 deg, was presented to both eyes whenever no vernier stimulus was present. It served both as a fusion aid to enable stable fixation and as a spatial reference in addition to the screen surrounds which were always visible. In control experiments, this rectangular pattern remained on the screen during presentation of the vernier targets without any noticeable effect on the results. The rectangle was presented in peripheral vision to ensure that no reference lines were available near the vernier targets which might have acted as cues for a bisection task (see discussion). In another control experiment, only the lower bar was presented to test its sensitivity as a bisection cue.

The subjects sat at an observation distance of 1.4 m. Additional control experiments were performed at observation distances of 0.5 and 3.0 m, to make sure that thresholds were not limited by noise in the apparatus. If noise were a limiting factor, thresholds in degrees of visual angle should have decreased with increasing observation distance. This, however, was not the case. At the longer observation distances, the vernier targets were either 30' or 60' long. Their width was between 1' and 6', depending on observation distance.

Threshold Measurements

Vernier displacements of three different sizes and different directions (to the right or to the left) were randomly interdigitated in any one session, according to a method of constant stimuli. Presentations followed each other at an interval of 3 sec and the subject had to decide whether the lower line was to the left or right of the upper one, and signal this by setting a switch appropriately. During most of the experiments, an error signal provided feedback information (not for subject M.F.). Responses were collected by the computer and fits to the data were obtained using the probit method (Finney, 1971). Responses displaced to the right as a function of vernier offset, are distributed from 0% for large offsets to the left, through 50% at the point of subjective equality (PSE), to 100% for large offsets to the right. The threshold was defined as half the distance between the points of 17% and 83% responses 'to the right'. If the point of subjective equality does not coincide with perfect physical alignment of the vernier lines, this will - to a first approximation - only shift the distribution sideward rather than changing its slope or form. Hence, the distance between the two points for 17% and for 83% on the curve stays constant and thresholds are not greatly influenced. However, the PSE may not correspond to perfect physical alignment especially in the dichoptic case because of factors like fusional disparity (Mitchell & Ellerbrock, 1955). Before the main experiments, the PSE was measured for each subject in a dichoptic pilot experiment, to estimate fusional disparity. Any fusional disparity found in the pilot experiment was compensated for in the dichoptic experiments

by an additional fixed offset of one vernier segment. Thus, the PSE usually fell in the middle of the range of offsets tested in the experiments proper.

In additional control experiments, an adaptive estimate of thresholds similar to APE (Watt & Andrews, 1981) or a staircase method similar to PEST (Taylor & Creelman, 1967) were used. The results from these different methods of measurement were typically within one standard deviation of each other.

Observers

The six subjects, not all of which participated in all experiments, were experienced observers without any visual defects as revealed by standard ophthalmological investigation. Their uncorrected visual acuity was at least 1.0 (20/20). No artificial pupils were used. Vernier thresholds can reduce with practice. To minimize the influence of practice on the results, two observers had experienced more than 10 000 presentations of vernier targets before the experiments proper (HW,MF). One observer was slightly less experienced (AH) and two further observers were much less experienced. The latter were two paid students who were not selected for good vernier thresholds.

Each of the thresholds shown in the graphs was obtained under the standard conditions outlined above, and is based on at least 200 stimulus presentations, typically obtained in two runs at different sessions. The order of testing was pseudo-random between conditions for all subjects. The basic results have been confirmed in three additional subjects who participated in only some of the experiments.

Results

Simultaneous vernier thresholds

In the first set of experiments, dichoptic as well as monocular vernier acuity was measured for presentation times of 10, 100, and 1000 msec, to assess the amplitude of uncorrelated eye movements.

For vertical stimuli, vernier targets presented monocularly yielded thresholds of about 10 - 15" for the best observers under optimal conditions (cf. the lowest thresholds in Fig. 1, left column). Binocular conditions yielded very similar results (not shown here). When the vernier targets were presented dichoptically (Fig. 1, right column), i.e., the upper segment to the right eye and the lower segment to the left eye (or vice versa), thresholds increased quite considerably. The average threshold of 64" for 1 sec presentation time was about four times higher than the corresponding monocular thresholds. Subjects often reported that the relative positions of the vernier targets changed during the longest presentation time of 1 sec. These changes are most probably caused by vergence eye movements, in an attempt to fuse the stimuli. The observers were asked to base their decisions about the relative positions of the segments on their first impression, when uncertain.

Changing the orientation of the vernier target to horizontal improved results only slightly (Fig.1b_2 and 1c_2). Also, the point of subjective equality, that is the physical displacement between the two segments that yielded equal numbers of the two possible responses (e.g. right and left) was, in general, no closer to physical alignment with horizontal than with vertical verniers.

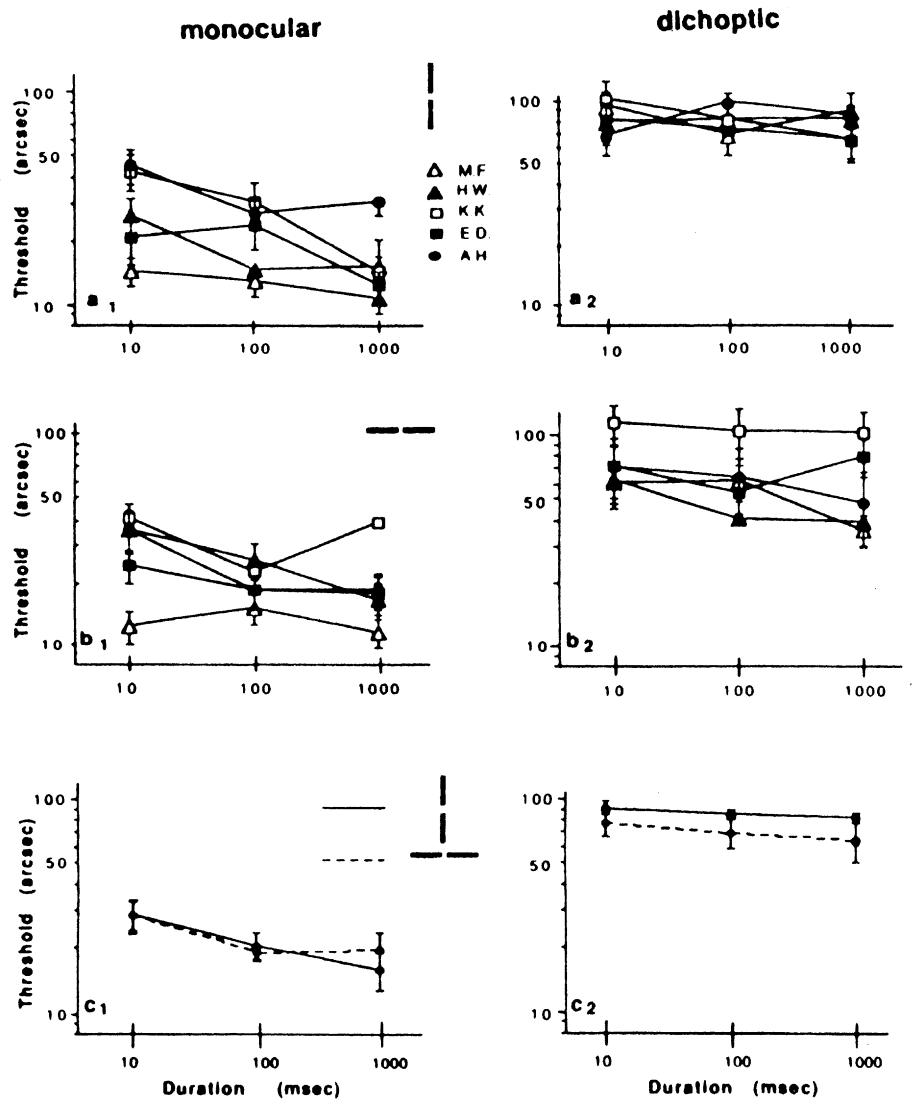

Fig. 1 Thresholds for vernier acuity with monocular presentation (left column) and with dichoptic presentation (right column) for five observers. The vernier target was presented for 10, 100 or 1000 msec (see abscissa). Fig. 1a shows results for vertical vernier targets, whereas Fig. 1b shows those for horizontal targets. Fig. 1c shows the means and standard errors of Figs. 1a and 1b.

Thresholds for monocular vernier acuity tended to decrease with presentation duration: from an average value of 26" for 10 msec, to 20" for 100 msec and 13" (vertical) or 21" (horizontal) for 1 sec (Fig 1c_1). These results are similar to those of Foley and Tyler (1976). Average dichoptic vernier thresholds decreased by a comparable amount on a logarithmic scale (Fig. 1c_2).

The large difference between observers in experience with vernier tasks was also reflected in the results. Thresholds differed by a factor of three between the most experienced (and probably most motivated) subject (MF) and one of the unexperienced observers. The difference, however, between monocular and dichoptic thresholds was evident for both experienced and less experienced observers.

Linear regression lines (not shown) through the data points of Fig. 1, i.e., for thresholds as a function of stimulus duration, have slopes not significantly different from zero but correlation coefficients of r=0.84 for vertical and r=0.57 for horizontal orientations (means of all observers). The same holds true for the dichoptic condition, but here the correlation coefficients are r=0.83 and r=0.79. Hence, no significant influence of target duration upon the thresholds appears in this (limited) set of data on simultaneously presented vernier targets.

It is important to notice that a strong and highly significant difference exists between the thresholds for monocular and dichoptic presentation at all presentation times as is evident from the means and standard errors shown in Figs. $1c_1$ and $1c_2$ ($p << 0.01$; $U= 0$ for Mann-Whitney U-test).

Delayed vernier thresholds

In a second set of experiments, thresholds for monocular and dichoptic vernier targets were measured with presentation times of 10 msec. A variable delay of 0, 50, 100, 200, 500 or 1000 msec was introduced between the presentations of the two segments of the vernier to indirectly measure the amplitude of both correlated and uncorrelated eye movements during fixation. These thresholds are limited by both correlated and uncorrelated eye movements. Results are shown in Fig. 2.

As would be expected for identical stimuli, results for the 0 msec delay were very similar to those of the first set of experiments at the shortest presentation time. For longer delays, thresholds increased quite considerably both under monocular and dichoptic conditions. As can be seen from the left column in Fig. 2, monocular thresholds with delays between 50 and 100 msec reached the level of simultaneous dichoptic thresholds (cf. Fig $2c_1$ at 100 msec delay with Fig. $2c_2$ at 0 msec delay).

The increase of monocular vernier thresholds with increasing delay between the segments of the stimulus was steepest around 100 msec delay (left column of Fig. 2). For longer delays, monocular (and dichoptic) delayed thresholds began to asymptote at about 200" to 300". Thresholds from zero and one second delay differed by a factor of about ten for monocular presentation.

Thresholds for dichoptic delayed vernier acuity, on the other hand, do not show this steep increase for delays between 0 and 100 msec (right column of Fig. 2; logarithmic scale). Thus, dichoptic thresholds increase only by a factor of about 4 between zero and one second delay. The difference between the monocular and dichoptic thresholds was much larger with no delay than with a delay of 1 sec. The remaining difference at delays of 1 sec was mostly due to the results of one

observer (AH) who showed a distinct difference between monocular and dichoptic thresholds even at delays of 1 second.

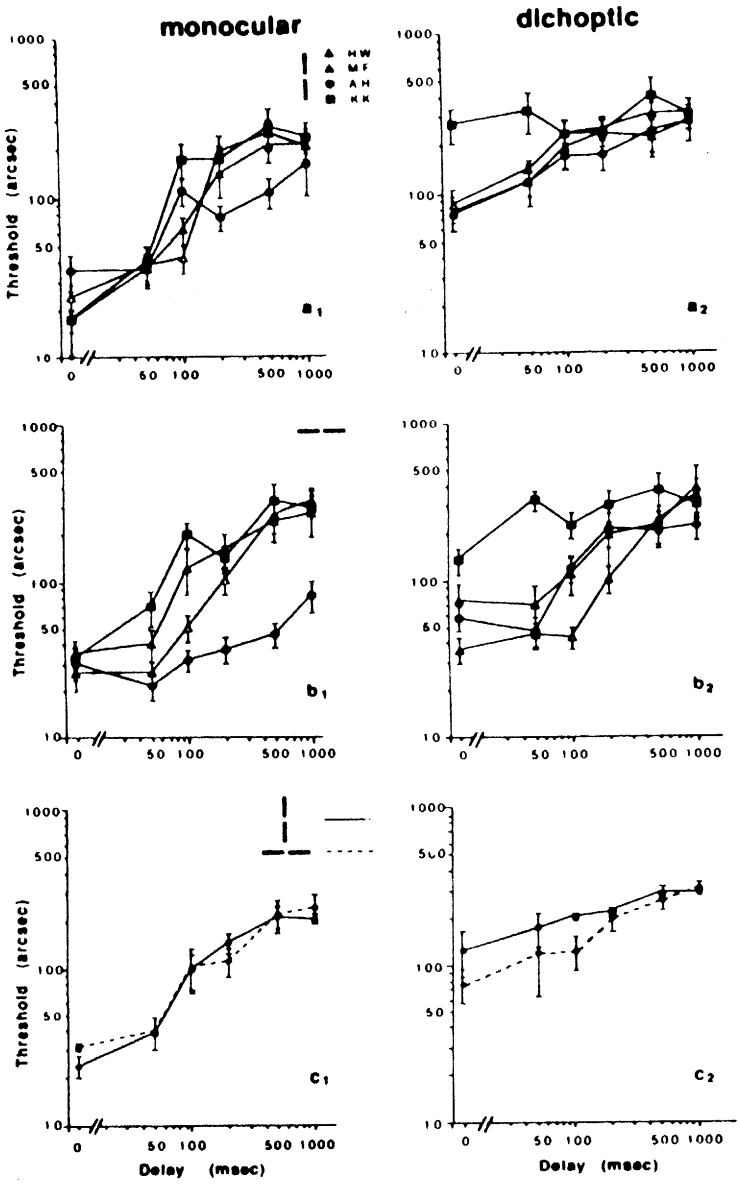

Fig. 2 Thresholds for monocular (left column) or dichoptic (right column) vernier targets as a function of the delay between the presentation of the upper and lower segments. a) vertical targets; b) horizontal targets; c) means and standard errors of the four observers.

Linear regression lines (not shown) through the data points for the delayed vernier presentations (Fig. 2), both in the monocular and dichoptic conditions, have slopes that are significantly different from zero at the 5% level ($p = 0.015$ to 0.001; U-test). The correlation coefficients for the individual curves in Fig. 2 range between $r=0.81$ and $r=0.99$.

Control Experiments: the possible role of a bisection cue, extravisual feedback, and memory.

The first control experiment addressed the problem that increasing the delay between the presentations of the two vernier segments may lead the observer to change his or her system of reference. Rather than comparing the two segments relative to each other, the observer might rely upon a reference that is further away in space, but nearer in time, namely the fusion rectangle and the borders of the monitor, and judge whether the second segment is nearer to the right or to the left border of the monitor. This switch of strategy would change the task into a bisection experiment, so that perceptual thresholds would be independent of eye movements. The same is true for simultaneous dichoptic thresholds: observers might compare the bisection-ratio in both eyes to infer the positions of the two segments relative to each other. In the first control experiment, only the lower segment of the vernier was presented. All other parameters were identical to the previous experiments on simultaneous monocular vernier thresholds. At a stimulus duration of 10 ms, the mean of all observers was 403" (+-81" s.e.). Longer presentation times did not improve results dramatically; the mean threshold at 1 sec stimulus duration was 275" (+-23"). A regression line through the means of all observers was calculated as y= 382 - 0.11 x (r= 0.96). The results show that the fusion rectangle and the surround of the monitor were a less efficient system of reference than the other segment of the vernier. Thresholds were significantly higher without the second segment under otherwise identical conditions (cf. Fig. 3 at 10 msec duration with Fig. 2 c_1; p= 0.002 at 0 delay to p= 0.02 at 1000 ms delay; one-tailed t-Test). Only thresholds for dichoptic delays above 200 msec (Fig. 2c_2) were not significantly different from bisection thresholds (p=0.13).

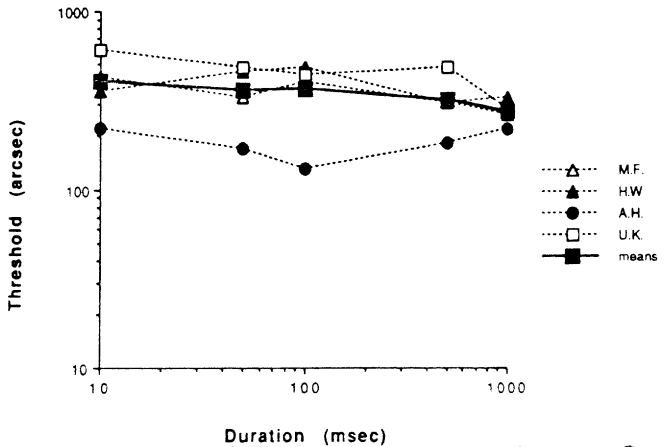

Fig. 3 Displacement thresholds in a bisection experiment. Conditions were similar to those for Fig. 2, but only the lower segment of the vernier was presented. The task was to indicate whether this segment was nearer to the left or to the right border of the monitor. These thresholds give the displacement required for detection. As both segments were always displaced into opposite directions, but only one segment was actually shown here, absolute bisection thresholds would be lower by a factor of 2. These experiments, however, were intended to rule out bisection as a possible cue in the previous experiments. Therefore, thresholds were calculated in a way corresponding to the previous experiments.

The second control experiment tested the possibility that the detrimental effect of eye movements upon thresholds might be compensated for by extravisual information, such as a corollary discharge or by proprioceptive afferents. As a control, simultaneous dichoptic vernier thresholds were measured for 100 msec presentation times - but this time in the dark, without any visual system of reference or a fusion pattern. The fusion pattern was switched off 10, 20, 50, 100, 200, 500 or 1000 msec before the presentation of the vernier. During that time, the subjects were in complete darkness. Without a fusion pattern, larger eye movements are to be expected. Thresholds rose with the duration of this dark interval (Fig. 4), indicating that extravisual information cannot compensate for eye movements under these conditions. A regression line through the means of all observers was calculated according to the least mean square method: $y = 184 + 0.17 x$ ($r= 0.93$). The slope of this line differs significantly from zero ($p= 0.002$).

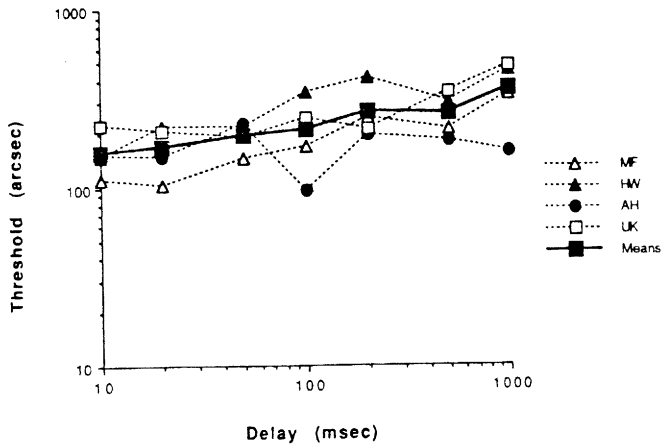

Fig. 4 Dichoptic vernier thresholds, as in the right column of Fig. 1, but measured in an otherwise dark room without a visual system of reference for different time intervals between offset of fusion pattern and presentation of the dichoptic stimulus. Both segments of each target were displaced by identical amounts in opposite directions.

A third control experiment investigated the possible role of positional memory in the experiments with delayed vernier targets. The increase in thresholds might have been due in part to 'forgetting' the position of the first segment rather than to eye movements. To assess the contribution of any decay of positional memory, pairs of complete vernier targets were presented for 10 msec each, separated by a variable temporal interval (ISI). The first vernier target was always offset by 400" (Fig.5a), 100" (5b) or 25" (5c) to the left or right ('standing offset'). The second vernier of a pair was offset relative to the first one. The observers' task was to indicate the change of offset between the two targets. In this experiment, the shape of the first target had to be memorized and compared with the second target after the delay. Small eye movements should not increase thresholds under these conditions. A bisection version of this task has been used by Badcock and Westheimer (1990). Lowest thresholds were obtained not with zero delay, but with a delay of around 50 msec (Fig. 5). This delay also induced the strongest impression of apparent motion, whose strength diminished both for longer and shorter ISIs. Due to this dip in thresholds, linear regression lines could not well fit the data ($r= 0.1$ to 0.5). Thresholds increased with delay far less for this

'memory-test' (Fig. 5) than for the comparison of single vernier segments (Fig. 2). Indeed, thresholds even (nonsignificantly) decreased with delay for small standing offsets: from 49" (+-8.1 s.e.) to 33.5" (+-7.7) for 25" standing offset (Fig. 5c), and from 57" (+-13.4) to 55.3" (+-7.5). Only for a standing offset of 400", thresholds increased from 63" (+-16") to 91" (+-7.2) within a second (p= 0.02). Hence, the role of memory seems not to be crucial for the increase of thresholds in Fig. 2 (see Discussion).

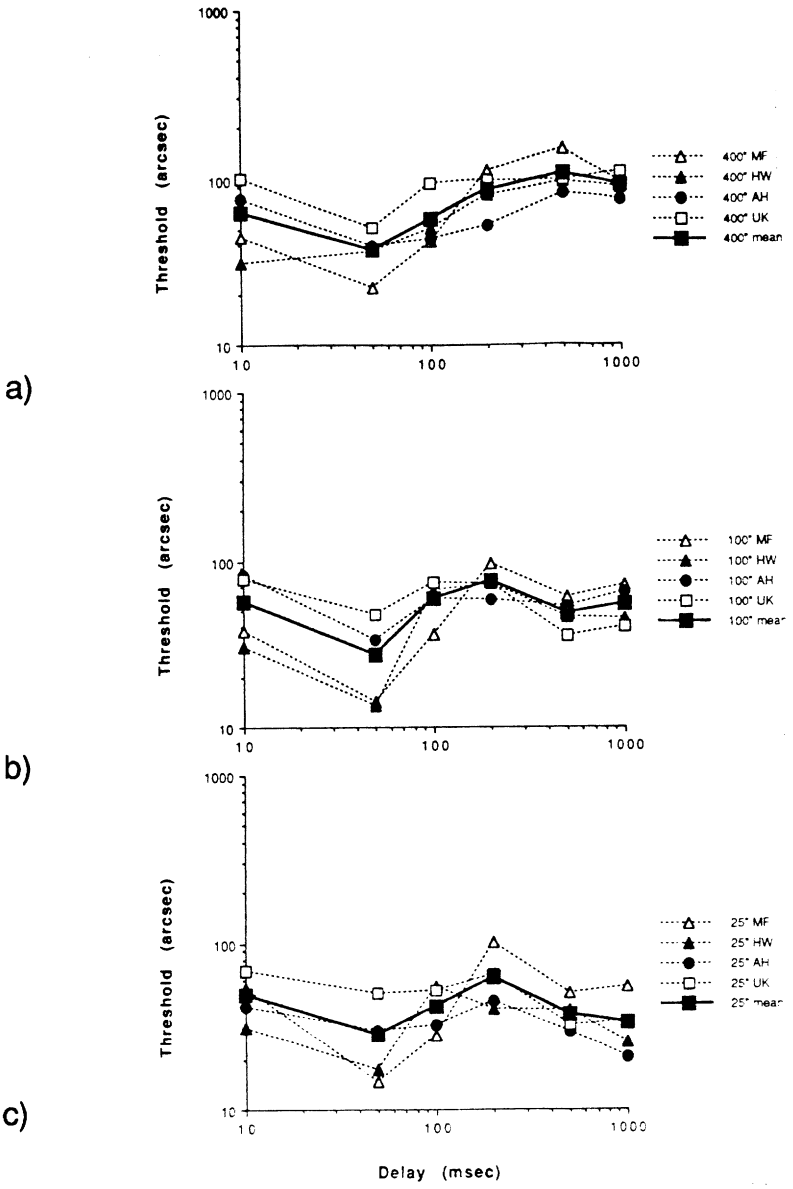

Fig. 5 Monocular vernier thresholds for comparing two vernier targets in the presence of a standing disparity of a) 400", b) 100", c) 25" in the first vernier of each pair. The second vernier followed after the time indicated on the abscissa. Thresholds represent the difference in vernier offset between the first and second verniers.

Discussion

Acuity for simultaneous verniers: Differences between monocular and dichoptic results.

The thresholds for monocular and dichoptic vernier acuity with no delay between the segments, and presentation times of 10 and 100 msec, are in close agreement with the results of McKee and Levi (1987). Monocular thresholds are all above 10" (arcsec) - clearly higher than the best results that have been reported in the literature (Klein & Levi, 1985). This might be partly because the observers in this study are not especially good at vernier acuity tasks, partly because of the relatively large gap of 7' between the upper and the lower segment of the vernier target and partly because of the rather short presentation time of 10 msec in most experiments. This large gap size was chosen to decrease the amount of possible inhibitory interaction between the vernier segments under dichoptic conditions (see below).

All the thresholds for dichoptic vernier acuity are much higher than those for monocular vernier acuity - and this difference is even greater if they are compared with stereoscopic thresholds. However, it should be kept in mind that even some of the dichoptic thresholds of about 35" for horizontal stimuli (Fig. $1b_2$) are not much larger than the photoreceptor diameter and hence not far above the hyperacuity range. Obviously, the visual system can detect the relative positions of neighboring features in one retinal image rather accurately; but why is dichoptic acuity so much worse than stereo acuity ?

Three possible answers spring to mind: First, inhibitory interactions are known to occur between corresponding retinal areas of the two eyes whenever fusion is not achieved (e.g. Breese, 1899; Fahle, 1982) - and fusion is certainly not possible with the dichoptic vernier targets. But inhibitory interactions between the eyes need around 100 msec to build up (Kaufman, 1963; Bower & Haley, 1964; Bokander, 1966), and so, with the 10 msec presentation times, inhibition should not exert an important influence upon the results.

Second, there may be no neural mechanism that can identify the relative positions of the two segments when they are presented to different eyes. It is true that stereoscopic thresholds (which rely upon the disparities between picture elements in the two eyes) can be below 3´´, but it is still possible that the visual system is able to recover depth information from this cue but is not able to recover displacement information. This possibility, improbable as it is, cannot be disproved at this point. Some calculations, however, suggest that a very precise neural mechanism for comparison of features in different eyes is available (see Conclusions).

Third, disjunctive eye movements certainly introduce a systematic error through failure of fixation and increase the positional noise by relative motion between the retinal images of the vernier segments in both eyes. This third factor will influence only dichoptic vernier acuity, and not relative stereoscopic thresholds where two stimuli have to be compared with each other. (In the latter case, both stereoscopic stimuli are affected in an identical way by eye movements, i.e., the

absolute disparity of the stimuli changes while their relative disparity and hence their stereoscopic distance is not affected and so the impression of depth is constant; cf. Westheimer, 1979; Erkelens & Collewijn, 1985.)

Simultaneous dichoptic verniers: Calculation of the amplitude of uncorrelated eye movements from thresholds.

Disjunctive or uncorrelated eye movements seem to be the most important reason for the increase of thresholds (T) in dichoptic vernier acuity as compared with monocular vernier acuity (McKee & Levi, 1987; Fahle, 1988a). Thus, the dichoptic vernier thresholds are limited by two factors: 1) by the precision of the monocular spatial localization and binocular comparison mechanisms for both segments of the vernier stimulus (C) and 2) by the size of involuntary disjunctive eye movements during steady fixation (D). In what follows, these two sources of error are assumed to be independent.

The overall performance of the observers (thresholds - T) is normally distributed: The distribution of correct responses as a function of displacement size was a good approximation to a normal distribution, when compared using χ^2 tests. Hence, the contribution of both the neuronal mechanisms of localization and comparison (C) and the disjunctive eye movements (D) to thresholds can be treated to a first approximation as a gaussian normal distribution.

When two independent normal distributions are superimposed, then their variances add (e.g. Lindgren, 1968; Sokal & Rohlf, 1981). Hence, the following relation holds: $T^2=D^2+C^2$, where T is the dichoptic threshold actually measured as defined by the standard deviation of the gaussian fit through the data points (83% correct responses; Finney, 1971). For the present data, this threshold is around 40" under optimal conditions for the best observers, hence $T^2 \approx 1600$. If we assume the dichoptic comparison-mechanism to have the same precision as the monocular one (10" under optimal conditions), this factor has a variance of about 10^2, i.e., 100. The disjunctive eye movements therefore have a standard deviation of $D= \sqrt{1600-100}$, hence D= 39". This value represents the sum of the uncorrelated movements of both eyes. The amplitude of the movement of each eye must be smaller by a factor of $\sqrt{2}$, leading to calculated amplitudes around 28" for the sum of uncorrelated drifts and tremor of one eye. This value fits nicely with reports of eye tremor amplitude around 25" to 45" and is below the values given for drifts of 2' to 5', suggesting very stable fixation in my subjects (Riggs & Ratliff, 1951; Barlow, 1952; Ditchburn & Ginsborg, 1953; Ditchburn, 1955; Yarbus, 1967; Alpern, 1972; Findlay, 1974; cf. also Riggs, Armington & Ratliff, 1954). There are, however, large individual differences, with mean eye movement amplitudes of up to about 80" (roughly 1.5') in some subjects when estimated in this way. The amplitude of eye movements during steady fixation was measured in one subject (MF) by means of a monocular SRI eyetracker. Maximal amplitudes of eye tremor were estimated to be below around +- 2' to 4'.

McKee and Levi (1987) found dichoptic vernier thresholds of 0.65', comparable to those reported here, when they added spatial noise to the position of a monocular vernier target. They needed an average amplitude of 1.5' of the noise

they used to increase monocular thresholds to the level of dichoptic ones and estimated that this specific kind of noise added less than 0.9' mean error to vernier position.

Saccades should not make a large contribution to the size of the disjunctive movements, as they are of identical size in both eyes by definition, and should not occur during steady fixation. Also the microsaccades that occur during steady fixation are simultaneous in both eyes, and have the same direction and similar amplitudes in most instances (Riggs & Ratliff, 1951; Ditchburn & Ginsborg, 1953; Krauskopf, Cornsweet & Riggs, 1960).

Possible sources of error: Feedback of eye movements and bisection cue.

Two potential sources of error in the experiments with simultaneous verniers were identified: The possible use of a bisection cue inherent in the stimulus and of extravisual information about eye position.

Uncorrelated eye movements can increase thresholds for dichoptic vernier acuity, but only up to a certain limit. If the eye movements become too large, observers might not use the vernier cue, but another cue inherent in the dichoptic vernier stimulus, namely the relative lateral distances between the vernier and the peripheral fusion pattern. A comparison between the bisection ratios of the two vernier segments could convey information about the direction of the vernier offset: If the upper segment was displaced more to the right than the lower one, the vernier offset of the lower segment must be to the left, and vice versa. The sensitivity for such a bisection cue depends critically upon the distance between the three targets that represent the bisection cue - larger distances result in higher thresholds. With the present displays, bisection thresholds were around 150" to 600", depending on stimulus duration and on observer (Fig. 3). The mean bisection threshold was significantly above the thresholds for simultaneously presented verniers ($p= 0.02$ to 0.002). The distance between both the peripheral fusion pattern and the surround of the monitor and the vernier stimuli is obviously too large to yield the thresholds obtained for dichoptic verniers with simultaneous presentation of both segments (Fig. 1). Thus, this cue cannot have determined the thresholds.

A basic assumption underlying the calculation of eye movement amplitudes from the vernier thresholds is that the observer does not have precise extra visual information on the direction and amplitude of his or her own eye movements, e.g. from proprioceptive afferents or from an efference copy or corollary discharge. If this were the case, the eye position would be known with a precision of around 2μm, corresponding to one photoreceptor diameter or to the best dichoptic vernier thresholds. This information could be used to make very precise dichoptic vernier judgements in spite of much larger eye movements. Computational compensation for these movements could achieve spatial localization far beyond the amplitude of eye movements under these conditions. Extra visual information about the precise positions of the eyes is, however, not available to the brain. Thresholds for dichoptic vernier targets increased significantly when the fusion pattern was turned off before the presentation of the target (Fig. 4). The longer the dark interval between the extinction of the fusion pattern and the presentation of

the vernier, the higher were the thresholds for dichoptic vernier acuity. Very short intervals, at identical background luminance, yielded significantly lower thresholds: mean thresholds were 159" (+-24) for 10 msec delay and 352" (+-73) for 1 sec delay. As this difference is significant (p= 0.02; t-Test), and as the slope of the regression line through the data differs significantly from zero (p= 0.002), the increase of thresholds was not merely due to decreased performance under scotopic conditions.

The most straightforward interpretation is that eye movements occur during the dark interval, of which the observer is not aware and for which he is unable to compensate by means of extravisual information. Thus, these movements increase the perceptual thresholds for dichoptic verniers. This finding agrees well with reports on the influence of a visual frame of reference upon delayed monocular vernier acuity (e.g. Findlay, 1974; Badcock & Westheimer, 1990; cf. also Matin, Pola, Matin & Picoult, 1981). In these experiments, thresholds typically increased with delay much more strongly when the fusion pattern was removed. The effect of a fusion pattern is also consistent with the phenomenon that a single stationary bright point in an otherwise dark room seems to move - observers perceive the movements of their own eyes as movements of the object ('autokinetic motion'; cf. Aubert, 1886; Crone, Verdun & Lunel, 1969; Levy, 1972). Obviously, the visual system needs a fusional pattern to stabilize eye position and cannot use extravisual information to assess exact eye position and to compensate for small (involuntary) eye movements such as drifts and tremor. High positional stability of eye position seems to be attained through a feedback mechanism, whose afferent path is based on visual information.

Dichoptic vernier thresholds and different frequencies of tremor and drifts.

The perceived position of a target is determined by the sequence of positions it occupies during its presentation time. Extended presentation times offer the possibility of spatial averaging. The longer the presentation time, the lower are the temporal frequencies that can be eliminated by averaging. At the shortest presentation time of 10 msec, only the highest frequency components of eye tremor can be eliminated, i.e., those beyond 50 Hz. Longer presentation times decrease the influence of progressively lower frequencies of eye tremor but do not decrease dichoptic thresholds dramatically. Simultaneous monocular thresholds would not be affected by the elimination of tremor. Since the slight decrease in thresholds with increasing presentation time was similar for monocular and for dichoptic presentations, the decrease in dichoptic thresholds is not primarily due to an averaging of position over time and to an elimination of the high frequencies of eye tremor. Hence, the high frequency components of eye tremor seem not to be the limiting factor in fixation instability.

For longer presentation times, the beneficial effect of averaging over time is probably to some extent counteracted by drifts, by the uncorrelated portions of microsaccades and by fusional eye movements beginning shortly after the onset of each presentation of the dichoptic vernier target. The drifts are largely uncorrelated between the eyes (StCyr & Fender, 1969) and decrease the precision of dichoptic vernier alignment. But the detrimental effect of such drifts might also be counteracted by averaging over time.

The decrease of monocular vernier thresholds with presentation time might be attributed to greater signal-to-noise problems at short presentation durations.

Delay can increase monocular vernier thresholds far above simultaneous dichoptic thresholds.

The thresholds for delayed monocular vernier acuity (Fig. 2, left column) approach those for simultaneous dichoptic vernier acuity (Fig. 1, right column) for delays around 100 msec. For longer delays, thresholds increase up to several arcmins. The shapes of the curves for delayed monocular thresholds closely resemble the ones found by Foley (1976) and by Findlay (1974) in their 'light' conditions, i.e., with a system of reference for fusion. Thresholds, however, are about a factor of 2 lower in the present experiments. This is in accordance with thresholds that Barlow (1952) measured with an afterimage technique for delays below 100 msec, and of Westheimer and Hauske (1975) for delays of 250 and 500 msec, who found even lower thresholds. The difference between the present results and those of Foley and of Findlay might be due partly to the different stimulus configurations, as well as to the experience of the observers. Matin, Pola, Matin & Picoult (1981) found an even greater increase in vernier discrimination thresholds with increasing delay (called ´dark interval` in their paper) between the presentation of the two segments of the vernier targets, e.g., a threshold of roughly 1200" at a delay of 800 msec. These very high thresholds are probably caused by larger eye movements, partly due to the lack of a fusion pattern (cf.,however, also the present Fig. 4 and Fig. 2 of Findlay, 1974). When they subtract the results of direct eye movement recording from the psychophysical thresholds, Matin et al. indeed obtain thresholds for retinal localization of around 300-720" for a monocular delay of 800 msec, which is not much higher than my results. This is another indication that the visual system cannot use extravisual information on eye movements or eye position to compensate for the effects of small drifts or tremor (cf. Fig. 4).

Thresholds for delayed verniers increase due to correlated and uncorrelated eye movements.

Delayed monocular and dichoptic vernier acuity are influenced by all kinds of eye movements, while simultaneous dichoptic vernier acuity is influenced only by disjunctive (vergence) or uncorrelated eye movements. This difference arises because movements that are correlated in direction and amplitude in both eyes — as saccades are — will shift the stimuli in both eyes by identical amounts. Thus, the relative positions of the vernier segments are not influenced by correlated movements. The opposite is true for delayed vernier thresholds. There, the position of the second segment is compared with the position of the first segment presented earlier. It is evident for monocular delayed presentation that, unlike in the case of simultaneous dichoptic presentation, all kinds of eye movements (not only uncorrelated ones) will shift the position of the second element relative to the first one. This is also true (though perhaps less obvious) for dichoptic delayed thresholds. Hence, the increase in delayed monocular and

dichoptic thresholds can be attributed primarily to the effect both of uncorrelated and of correlated eye movements (i.e., movements performed simultaneously by both eyes). Correlated movements of both eyes - which do not influence the results on simultaneous dichoptic vernier acuity - are the probable reason for the thresholds for delayed vernier acuity increasing beyond those for simultaneous dichoptic acuity. Another factor increasing delayed vernier thresholds is a fading of positional memory for the location of the first segment during the interstimulus interval (see below).

Direct recordings of eye position during steady fixation show that in addition to the movements that are correlated in both eyes, there are a number of uncorrelated movements such as vergences, drifts and part of the saccades (flicks) that can be of different amplitude for each eye. The amplitude (either convergent or divergent) of these components is often up to 5' , but in a study by StCyr and Fender (1969), the mean amplitudes for the more stable of two subjects were around 1.5' for flicks and 1.7' for drifts under optimal conditions. In this study, the subjects were instructed to gaze as steadily as possible, but in such a manner as to keep the target visible at all times. It is therefore to be expected that the subjects performed regular small voluntary eye movements to prevent the stimulus, that was continuously presented, from fading due to local adaptation. Given these voluntary eye movements, and the fact that large individual differences appear in fixation stability, the values calculated here of amplitudes between 0.4' and 1.5' are in good agreement with the results of StCyr and Fender. Also the subjective impression of perceptual fading even of foveal targets, for trained observers, during the present experiments indicated that fixation must have been very stable, to within about one photoreceptor diameter.

Loss of spatial memory is not crucial in the 'delayed' vernier task, but the bisection cue might be.

In addition to the two possible sources of error in simultaneous vernier tasks, there is a third one with delayed verniers, namely the loss of spatial memory. While the possibility of compensation by extravisual information for possible larger eye movements could be ruled out above, the possibility that the bisection cue inherent in the vernier targets might be used in delayed verniers must be considered here, too.

The peripheral fusion stimuli are too distant to allow bisection thresholds comparable to vernier thresholds (cf. Figs. 3 and 1). Thresholds in the bisection task were between 150" and 600". These values are clearly beyond all thresholds for simultaneously presented verniers and correspond roughly to the thresholds for delayed vernier acuity at long delay times. Observers could in principle have relied on the bisection cue for delays of 500 msec and longer, but not for shorter delays (and certainly not for simultaneously presented monocular or dichoptic verniers). The psychophysical method of measuring uncorrelated eye movements by means of delayed vernier acuity is therefore, strictly speaking, only valid for delays below approximately 500 msec under the conditions used here. The bisection cue represents a major limitation of the method, as every visual stimulus aimed at stabilizing eye position can be used as a system of reference. The only remedy is to place these stabilizing stimuli as far in the periphery as

possible; the more peripheral they are, the less precise a bisection localization they allow. Without feedback, observers will not usually use bisection information but will rather concentrate on the vernier cue. But the limitation of the method in accurately measuring large, relatively slow, correlated movements of the eyes should be kept in mind. These movements can be better measured by means of conventional methods based on the EOG (electrooculogram) or on infrared oculography.

Another possible source of error in the experiments with delayed vernier targets is fading of positional memory. In the experiments with a delay between the presentations of the two segments of the vernier, not only eye movements, but also a fading of memory about the position of the first vernier segment at the presentation time of the second segment might cause an increase of thresholds. For three reasons, however, it seems that loss of spatial memory is not an important factor in these experiments. First, a number of experiments make it plausible that the visual cortex has a kind of temporal resolution around 10 Hz, corresponding to 100 msec integration time (e.g., thresholds for stereoscopic depth perception are only marginally influenced if the stimuli to both eyes are delayed by as much as 50-100 msec relative to each other; Foley, 1976; cf. also Guilloz, 1904; Ewald & Gross, 1906; Ogle, 1963; Herzau, 1976). This is to say that all events occuring within 100 msec are more or less ´simultaneous` for a number of visual tasks.

Second, the thresholds for dichoptic delayed vernier stimuli increased far less as the delay was increased from 0 to 100 msec than did the monocular delayed ones (on a logarithmic scale). If forgetting of position were the important factor, then the dichoptic thresholds should also have increased in a similar fashion. But as is obvious from Fig. 2, the dichoptic thresholds increased by a factor of only about 3. Hence, this is an upper limit for the influence of loss of spatial memory.

Third, Badcock and Westheimer (1990) have determined the precision of spatial memory by measuring the increase in thresholds for the comparison of two different bisection intervals with varying delays between the presentations of the two bisection targets. They conclude that there is a true decrement of the localization signal, confined largely to the first 200 msec of the delay and amounting to a factor around three during the first second. Badcock and Westheimer used a presentation time of 300 msec in their experiments, i.e., a shortest total stimulus duration of 600 msec (at 0 sec delay), whereas my vernier targets were presented for only 10 msec, i.e., a shortest duration of 30 msec (at 10 msec delay). This difference of stimulus duration probably explains why these authors did not find the increase in thresholds that is apparent for the shortest delays shown in Fig. 5. One could speculatively attribute the very low thresholds at 50 msec interstimulus interval (ISI) to the subjective impression of apparent motion that was experienced with these stimuli, and hence to the stimulation of some motion detector. Apparent motion might have been an additional cue, which disappeared at shorter or longer delays. But the results agree in the main point: thresholds below 100" can be obtained even with delays of 1 sec!

Thus, the increase in thresholds is probably not primarily due to an inability of the visual cortex to remember the correct location of the first vernier segment at the

presentation time of the second segment (Matin, Matin & Pearce, 1970; Findlay, 1974; Foley, 1976; cf. also Matin, Pearce, Matin & Kibler, 1966; Kinchla & Smyzer, 1967; Kinchla & Allan, 1969; Matin et al, 1981). As this idea suggests, one of the observers (AH) does seem to be able to stabilize her eye position over longer periods of time - at least for horizontal targets under monocular conditions (Fig. 2 b_1) and to remember the positions well at least for 500 msec.

Conclusions

In summary, I suggest that the thresholds for simultaneous dichoptic vernier acuity obtained in the present experiments were severely degraded by involuntary disjunctive eye movements during fixation. The results demonstrate that there must be a cortical mechanism which can detect relative positional differences between the eyes that are in the hyperacuity range, perhaps with the same precision as monocular positional differences. This further supports the idea of the cortical origin of vernier acuity, since dichoptic vernier acuity tasks would be impossible if vernier acuity were of retinal origin (cf. McKee & Levi, 1987; Fahle, 1988b).

The experiments on delayed vernier acuity reflect the effects of eye movements of all types while the results on simultaneous dichoptic vernier acuity are influenced only by uncorrelated movements of the eyes.

Vernier thresholds could in principle be increased by a number of additional sources of noise. However, to incorporate such additional sources of positional noise in simultaneous dichoptic vernier thresholds, one would have to reduce the assumed noise in one or both of the sources considered so far, namely the neuronal comparison mechanism and eye position control. And this is not an easy task, as the dichoptic neuronal comparison mechanism is already assumed to be as precise as the monocular one (an assumption not usually made). The amount of noise to be expected from this source cannot be decreased. The same holds true for the second source of positional noise, namely eye movements. When the dichoptic vernier thresholds of the best observers are considered, we have to postulate a minimal amplitude of (uncorrelated) eye movements during steady fixation that corresponds to the most optimistic, i.e., smallest estimates from the literature on direct eye movement recordings and that is of the order of the diameter of foveal photoreceptors. Thus, most estimates of the amplitude of this factor also would have been much larger than mine.

On the basis of these results, an upper limit can then be calculated both for the precision of the neuronal mechanism comparing local signs from both eyes in dichoptic vernier acuity and for the mean amplitude for involuntary eye movements during steady fixation. For both of these factors, the estimates we arrive at on the basis of the experimental results are at the lower edge of the range of values expected from the literature and we can conclude that the neural mechanisms which compare the relative positions of features in different eyes are about as precise as the mechanisms that compare monocular features. On the other hand, the experiments support the view that the positional noise recorded with these techniques was not an artifact caused, for example, by slip between the contact lens and the eye.

The psychophysical method of measuring fixation stability via vernier thresholds also provides a relatively easy means of assessing to what extent a subject´s fixation stability is affected by uncorrelated eye movements. This measure might be of interest in a variety of investigations, given the high inter-individual variation of the dichoptic thresholds, and for assessing eye tremor in patients with different disturbances of the central nervous system.

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If the two segments of a vernier target are presented to different eyes, i.e., dichoptically, thresholds are three to four times higher than with presentation to the same eye. This increase in thresholds is mainly due to uncorrelated movements of both eyes, such as tremor and drifts, that occur even under steady fixation. The psychophysically measured thresholds allow one to calculate an

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upper estimate for the amplitudes of uncorrelated eye movements during fixation. This estimate matches the best results from direct eye position recording, with the calculated mean amplitude of eye tremor corresponding to roughly one photoreceptor-diameter. The combined amplitude of both correlated and uncorrelated eye movements was also measured by delaying one segment of the vernier relative to its partner under monocular or dichoptic conditions. Fixation proved to be relatively stable, and trained observers could sustain eye position within a few arcmin.

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