



Vernier Acuity During Image Rotation and Translation: Visual Performance Limits

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Our capacity to detect spatial misalignments a fraction of the distance between retinal receptors in the presence of image motion challenges our understanding of spatial vision. We find that vernier acuity, while robust to image translation, rapidly degrades during image rotation. This indicates that orientation is a critical cue utilized by the visual system in vernier acuity tasks. Moreover, vernier acuity is robust to translational motion only at high target strengths. Vernier acuity for translating 3-dot targets over midrange velocities can be predicted from vernier acuity data derived from static targets of different presentation durations. However, the degradation observed at higher velocities is greater than predicted. The high velocity degradation reveals that performance is limited by a 1 msec asynchrony sensitivity. The moving vernier stimulus appears to constitute an optimal configuration for the visual system to achieve a 1 msec asynchrony sensitivity by making use of an orientation cue.

Vernier acuity Motion Acuity Orientation

INTRODUCTION

The optics of the eye and retinal receptor spacing limit normal visual acuity to about 0.5 minarc (Helmholtz, 1909; Westheimer, 1976; Williams & Coletta, 1987). However, we can detect vernier offsets of a few seconds of arc, or about 1/10 the receptor spacing. Exactly how the visual system achieves hyperacuity levels of performance remains an enigma though several physiologically plausible models have been proposed to explain this phenomenal sensitivity (Klein & Levi, 1985; Wilson, 1986). Investigators have proposed the use of cues such as local orientation, orthoaxial size, shape and relative position (Sullivan, Oatley & Sutherland, 1972; Findlay, 1973; Westheimer, 1981; Watt, 1984; Watt, Morgan & Ward, 1983; Klein, Casson & Carney, 1990) to explain vernier acuity. While static vernier acuity is impressive, all the more remarkable is the finding of Westheimer and McKee (1975) that for brief presentations, vernier acuity is not degraded by motion for velocities of up to 3 deg/secarc (see also Morgan, Watt & McKee, 1983). Given the presumed coarse temporal resolution of the visual system, the neural image of the vernier stimulus should appear smeared at these velocities. For example, assuming a 50 msec integration time and 3 deg/sec target velocity, the image would be smeared over 9 minarc or 10-20 times normal resolution acuity.

The importance of achieving good acuity in the pres-

ence of object and eye motion provides strong evolutionary pressure to develop mechanisms for "deblurring" the motion smeared image (Burr, 1980). Velocity selective neurons of the type found in cat visual cortex (Emerson, Citron, Vaughn & Klein, 1987) could provide a means for neural tracking to reduce motion blur (Burr, Ross & Morrone, 1986). While neural shifter circuits (Van Essen & Anderson, 1990) or velocity tuned mechanisms may exist to reduce motion blur, they do not readily explain why vernier acuity is less sensitive to motion blur than interval discrimination (Morgan & Benton, 1989). One physiologically plausible explanation is based on the use of the local orientation cue present in the vernier stimulus. This cue persists under motion and is less likely to be degraded than other cues. Orientation selective neurons in cat visual cortex respond to moving vernier acuity offsets in a manner consistent with their orientation tuning properties (Swindale & Cynader, 1986; 1989). We will examine how these mechanisms can maintain their orientation tuning as velocity increases. The problem is, how can cells with sluggish temporal impulse responses maintain the high temporal resolution implied by an orientation tuning which is independent of velocity?

To examine the role of orientation we have compared vernier acuity under translation with vernier acuity under rotation. If vernier acuity depends on an orientation cue during image translation then image rotation should degrade performance. The orientation cue is constant during translation, however, it is constantly and rapidly changing during image rotation. Assuming the assessment of object orientation takes some time, during rotation the orientation information will be

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blurred along the orientation dimension and vernier acuity will suffer.

Even if the orientation cue accounts for the relative robustness of vernier acuity to motion up to about 3 deg/sec, the question remains as to what limits performance at high stimulus velocities. One potential limiting factor which we examine is the role of stimulus intensity. The results of our experiments are consistent with the utilization of the orientation cue during image translation when we include limits due to stimulus intensity and an intrinsic temporal uncertainty.

EXPERIMENT 1: THREE-DOT VS TWO-LINE VERNIER ACUITY UNDER MOTION

Previous investigators have assessed the effects of translation on vernier acuity using line targets. However, 3-dot vernier targets are ideal for comparing vernier acuity during rotation and translation. Our first task was to verify that 3-dot vernier acuity is similar to line vernier acuity in the presence of image motion.

Methods

A single well-practised but experimentally naive subject participated in this first experiment. Detection thresholds were determined for static line and dot targets so that vernier acuity thresholds using these two types of targets could be compared at similar target strengths. The detection and vernier targets were presented on a Tektronix 608 monitor under the control of a Venus pattern generator. Viewed from 4 m, the pixel size was 0.32 minarc. A centroid based method was used to achieve spatial shifts of less than a pixel (see Klein *et al.*, 1990). For example, a two-pixel wide line having a pixel luminance profile of 0.0, 0.5, 0.5 and 0.0, can be shifted by one-quarter of a pixel by using the luminance profile; 0.0, 0.25, 0.75 and 0.0. The background luminance was 20 cd/m² and the frame rate was 278 Hz. Detection thresholds ($d' = 1$) for 6 minarc long lines and single pixel dot targets were determined using a self-paced rating scale method of constant stimuli using four stimulus strengths, one of which was zero. The individual detection thresholds are based on at least three runs of 100 stimulus presentations per run. Auditory feedback that indicated the intensity of the stimulus was provided on each trial.

Three-dot vernier and abutting line vernier thresholds were determined at several target strengths and velocities. Vernier acuity thresholds ($d' = 1$) were determined using the same rating scale method of constant stimuli but with five stimulus offsets as described in Klein and Levi (1987). After each presentation the observer indicated the perceived stimulus offset. For 3-dot vernier targets the location of the central dot was either collinear or displaced one or two units to the right or left relative to the surrounding two dots on each trial. The line vernier targets, abutting 6 minarc long lines, were similarly either collinear or the bottom line was displaced to the left or right, from trial to trial. Line targets, when static, were either 2.2, 8 or 49 times their

detection thresholds. The dot targets were either 3.4 or 14 times their static detection thresholds. Target velocities ranged from 0 to 8 deg/sec for a total of 30 stimulus conditions. The stimulus duration for both the detection threshold and vernier acuity task was 200 msec. The use of a short stimulus duration prevented the observer from tracking the moving stimuli. In addition, the direction of target motion, left or right, was randomly varied from trial to trial to prevent anticipatory tracking eye movements.

Results and discussion

In Fig. 1, the results for 3-dot (open symbols) and line vernier (closed symbols) acuity targets are presented. The intersection points of the dashed lines with the ordinate indicate the thresholds for the static target conditions. The stationary line and 3-dot vernier acuities were similar for high target strengths, about 8 secarc (corresponding to about 5 secarc if threshold is defined as 75% correct, $d' = 0.68$), a reasonable value for such brief stimulus presentations (Westheimer & McKee, 1975; Hadani, Meiri & Guri, 1984). For stationary targets, the finding that vernier acuity improved with increasing target strength is consistent with previous findings (Morgan & Aiba, 1986; Wilson, 1986; Klein *et al.*, 1990). The robustness of line and 3-dot vernier acuity to motion blur was dependent on target strength. For high target strengths, 49 times the line detection threshold, line vernier acuity was unchanged up to about 3 deg/sec. For low target strengths, thresholds increased at much lower velocities. Vernier acuity for the bright 3-dot target did begin to degrade before 3 deg/sec. This degradation is probably due to the reduced strength in terms of how many times it is above threshold (14 times) relative to the bright line target strength. In fact, as can be seen in the figure, the velocity at which performance starts to deteriorate increases with increasing stimulus strength, irrespective of the stimulus type, line or 3-dot.

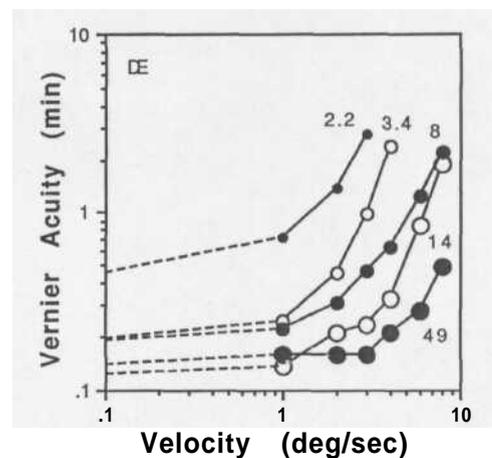


FIGURE 1. Vernier acuity for 3-dot and 2-line targets for a range of target strengths as a function of image velocity. Line targets () were either 2.2, 8 or 49 times the detection threshold of the 6 minarc lines. The dots in the 3-dot targets were separated by 6 minarc. The dot targets (O) were either 3.4 or 14 times the dot detection threshold. The larger the symbol the greater the target strength. Dashed lines connect thresholds for the lowest velocity tested with the zero velocity thresholds along the ordinate.

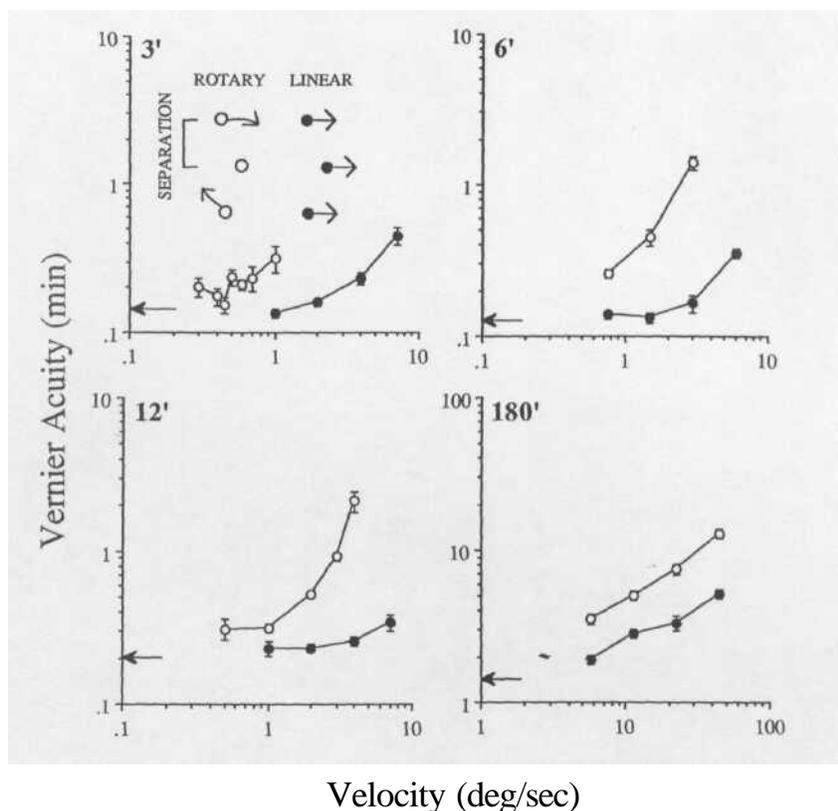


FIGURE 2. Vernier acuity for one subject (DS) using 3-dot targets under translation and rotation at four dot separations: 3, 6, 12 and 180 minarc. The stimulus geometry for translation and rotation are depicted in the upper left. \circ and \bullet indicate target translation and rotation conditions respectively. At modest velocities vernier acuity is disrupted during rotation whereas translation has little effect. The arrow on the ordinate of each plot indicates the vernier acuity for the zero velocity condition.

When stimulus strength is taken into account (see Experiment 3), the similarity between 3-dot and line vernier performance under motion indicates that similar visual mechanisms are likely involved.

EXPERIMENT 2: THREE-DOT Vernier ACUITY, TRANSLATION VS ROTATION

The advantage of the 3-dot stimulus is that it allows the comparison of vernier thresholds during image translation with thresholds during image rotation. For translation both line or dot stimuli have a unique velocity. However, for image rotation, it is not reasonable to assign a single velocity to a line vernier target. The velocity of points along the line depends on their distance from the center of rotation. In the case of the 3-dot stimulus rotating about the center dot, assigning a unique velocity is straightforward, it is simply the instantaneous tangential velocity of the outer dots. Therefore, the appropriate comparison of vernier acuity thresholds during translation and rotation for a range of velocities is clear for the 3-dot targets but ambiguous for line targets.

As mentioned earlier, the orientation cue in a vernier target remains invariant under translational motion. However, under rotation of the image the orientation cue is changing at a rate dependent on the rate of rotation. If local orientation is an important cue for vernier acuity then performance should degrade under

rotation as a result of the changing orientation information. If, on the other hand, vernier processing is performed by position or curvature mechanisms then the rotation thresholds should be approximately the same as the translation thresholds.

Methods

Three subjects, two experimentally naive and one of the authors, participated in this experiment. All had normal or corrected visual acuity of 20/20 or better. An Amiga computer driving an HP 1345A vector scope was used to produce both the rotating and translating 3-dot vernier targets used in this experiment. The intensity of each individual dot was about 41 times the dot detection threshold, the same as the dots used in the high intensity condition of Experiment 3. Details on estimating dot strength are provided in the methods section of Experiment 3.

As in Experiment 1, the method of constant stimuli was used to determine vernier thresholds, but this time only three stimulus offsets were used for both the linear and rotary conditions. The 3-dot stimulus configuration is shown in the upper left panel of Fig. 2 for the two types of stimulus motion. Dot separation is the distance from the center dot to either of the outer dots. At stimulus onset, the center dot was either aligned or to the left of the surrounding dots by one or two offset units. Unidirectional offsets were used to disambiguate stimulus conditions in cases where the rotations were over

180 deg. The center of image rotation coincided with the center dot. The two outside dots were equidistant from the center dot (see inset of Fig. 2). The vernier offset was defined as the distance from the center dot to the midpoint of the two outside dots. Rotation velocity is expressed as the tangential velocity of the outer dots. Each subject performed the experiment at four or five dot separations ranging from 3 minarc to 180 minarc for both the rotary and linear motion conditions.

Results and discussion

The translation and rotation vernier acuity results from one subject (DS) are shown in Fig. 2 at four dot separations and over a range of velocities. The arrow along the ordinate of each panel indicates the vernier threshold for the static vernier target at that particular dot separation (note the change of scale for the 180 minarc dot separation data). There is a striking difference in velocity at which thresholds become elevated for the two tasks. Under rotation, performance is severely degraded at velocities as low as 1 deg/sec. Whereas, under translation, performance is unaffected by velocities up to about 2-3 deg/sec. These results, along with findings of Welch and McKee (1985), contradict the idea that the visual system can effectively take an orientation independent snapshot of the image to make spatial judgments. The use of a snapshot at any instant should be equally effective under both linear and rotary motion.

Morgan and Benton (1989) have shown that 2-line interval discrimination tasks are much less robust to image motion than vernier acuity. This finding indicates that vernier acuity tasks make use of a stimulus cue which is not present in the interval discrimination task and little effected by motion. The likely candidate cue is orientation which is invariant with respect to translation. The rapid orientation changes that occur during rotation should disrupt performance, as was observed.

Models of vernier acuity based on mechanisms compatible with known cortical physiology have shown how the visual system could use an orientation cue for static vernier acuity (Wilson, 1986). Moreover, physiological data from cat area 17 cortical cells indicate that the sensitivity of orientation selective cells to vernier offsets persists over a broad range of stimulus velocities (Swindale & Cynader, 1989). A cell's vernier acuity is often not effected by a log unit change in velocity. It is estimated that cortical cells with receptive fields in area centralis have vernier acuity of 1.5 minarc, a hyperacuity range for cats (Swindale & Cynader, 1986). Cat orientation discrimination thresholds approximate thresholds estimated for single cells in cat area 17 cortex (Bradley, Skottun, Ohzawa, Sclar & Freeman, 1987). Our psychophysical results and these physiological observations

from cat cortical cells are consistent with orientation being an important cue in vernier acuity.

Our subjects reported that for a 3-dot vernier task, during image rotation, the dots were noticeably smeared compared with image translation. Burr (1980) has reported that the apparent length of dots translating at 3-15deg/sec and presented for less than 30 msec increases with velocity. Surprisingly, this smearing of the dot decreases in length for longer stimulus presentations, indicating a mechanism for deblurring moving images (Burr, 1980). This mechanism that minimizes blur apparently does not function when stimulus motion has an acceleration as in the rotation case.

With increasing dot separation, the minimum (or baseline) threshold increases, causing an increase in the velocity at which thresholds start to become elevated (Fig. 2). In Fig. 3(A) the effects of dot separation and velocity are shown. The data for different separations are plotted together for each of the three subjects. The results for the linear (filled symbols) and rotary (open symbols) motion conditions are similar except for a horizontal shift of about a factor of four. The baseline or minimum thresholds for large dot separations (> 12minarc) are about 1% of the dot separation; for smaller separations this fraction increases. This 1% Weber fraction is typical for static 3-dot vernier tasks (Klein & Levi, 1987). A 1% Weber fraction corresponds to about 1 deg of angular bend irrespective of the dot separation*, which is compatible with orientation discrimination thresholds for lines (Westheimer, Shimamura & McKee, 1976; Paradiso & Carney, 1988; Paradiso, Carney & Freeman, 1989).

Since thresholds increase with separation, the data were replotted in screen coordinates [Fig. 3(B)] by converting velocity in degrees per second to revolutions per second for image rotation, and vernier thresholds in minutes to angular bend in "clock-degrees" (which will be described). Velocity in revolutions per second (*VR*) is defined as:

$$VR_{(rev/sec)} = V_{(deg/sec)} * 60_{(min/deg)} / (S_{(min)} * 2\pi_{(rad/rev)}), \quad (1)$$

where *V* is dot velocity and *S* is dot separation. Vernier acuity in clock-degrees (*VC*) is defined as:

$$VC_{(deg)} = 2 * VA_{(min)} * (360/2\pi)_{(deg/rad)} / S_{(min)}, \quad (2)$$

where *VA* is vernier acuity and *S* is dot separation. The same data transformation was made for the linear motion conditions. The following example is provided to clarify the expression of vernier thresholds as angular bend in clock-degrees. Imagine an analog clock at 2:20 in the afternoon. The angle between the minute and hour hand is 50 deg (do not forget the hour hand is past 2). A 3-dot vernier target with a 50 deg threshold would have the dots positioned at the center of the clock and at the ends of equal length hour and minute hands. To express this threshold in terms of the familiar visual angle requires knowledge of the viewing distance.

When thresholds in clock-degrees as a function of velocity in revolutions per second are plotted [Fig. 3(B)], the data scatter is reduced and two functions emerge,

*A 3-dot stimulus with 1 deg of bend defines a triangle with a 179 deg angle at the center dot vertex. A line drawn from the center dot perpendicular to the opposite side generates two equivalent right angle triangles. The angle at the upper and lower dot vertices is one-half degree which is 0.0087 rad or a 0.87% Weber fraction.

one for image rotation and another for image translation. The optimal performance at low velocities appears to be constrained by an orientation discrimination limit of between 1 and 2 clock-degrees. At high

velocity, thresholds increase with increasing velocity. An orientation discrimination task (vernier acuity) at high stimulus velocities can be thought of as detecting a temporal asynchrony between two detectors. Consider

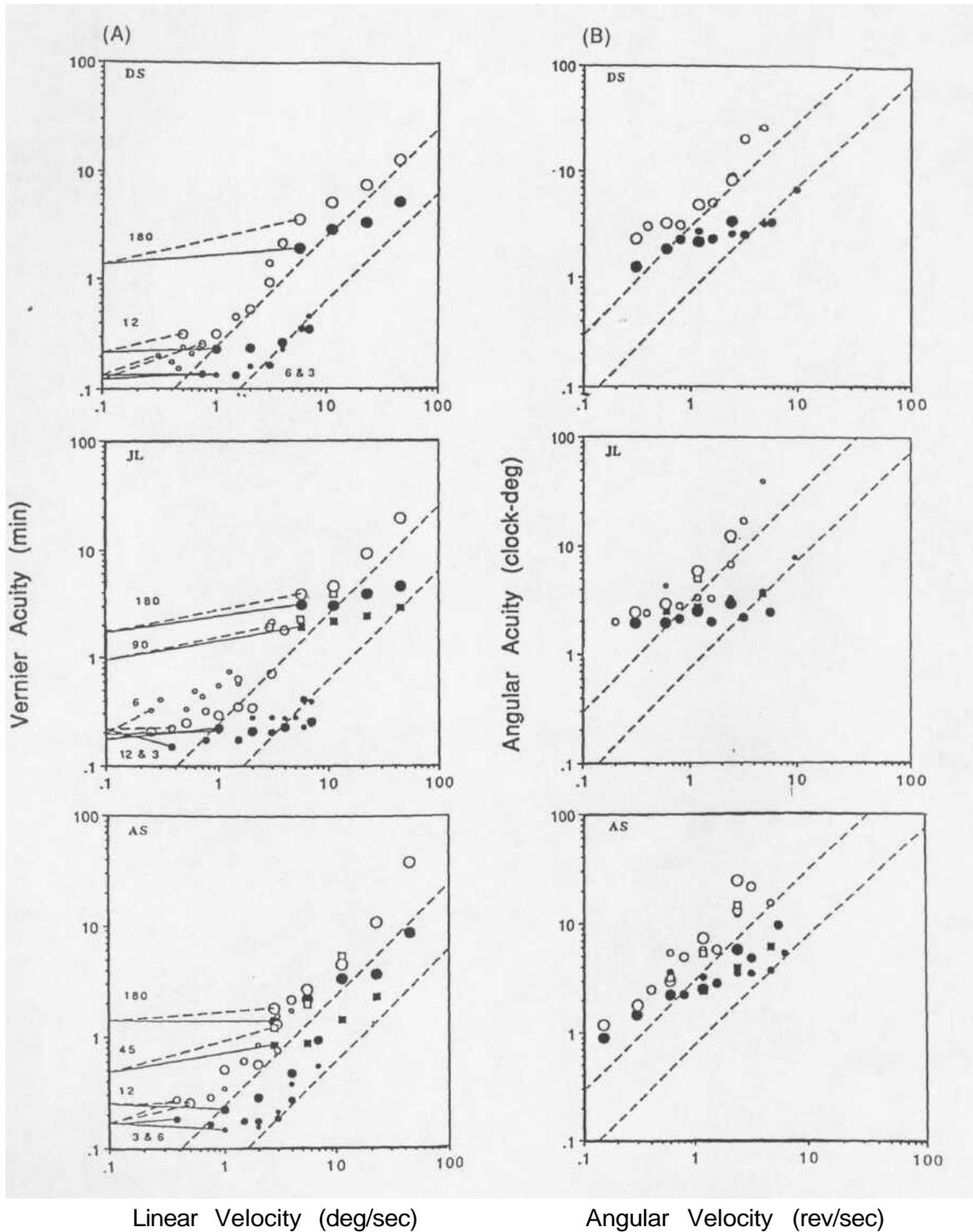


FIGURE 3. Vernier acuity for 3-dot targets under image translation and rotation, combined on a single plot. Each panel contains the data from one subject for several dot separations. O and \bullet indicate image rotation and translation conditions respectively. Larger circles reflect larger dot separations: 3, 6, 12 and 180 minarc. \square and \triangle indicate dot separation unique to particular observers; DS-90 minarc, AS-45 minarc and JL-90 minarc. The 1 and 4 msec constant temporal asynchrony limits are indicated by the two parallel dashed lines. (A) Vernier acuity in minarc as a function of velocity in deg/sec. Dashed and solid lines connect the low velocity datum for each separation with the zero velocity thresholds along the ordinate. (B) The same data are replotted with thresholds expressed as the angle of bend, in clock-degrees, as a function of velocity in revolutions/sec. For the image translation conditions, velocity is expressed in equivalent revolutions/second. The data for 3 minarc separations are not plotted since scaling is not expected to occur at small separations.

a pair of moving dots aligned vertically. They will simultaneously stimulate a pair of vertically aligned photo detectors with the same separation as the dots. If one of the stimulus dots is delayed or, equivalently, the dots are oriented off vertical, the photo detectors will respond asynchronously. After combining the responses of the two dots this mechanism would be selective for both orientation and temporal asynchrony.

For our moving 3-dot targets, a spatial offset (corresponding to the vernier threshold) can be expressed as a temporal delay (t): $t = x/v$ where x is spatial offset and v is velocity. In Fig. 3, constant asynchrony thresholds of 1 and 4msec are indicated with dashed lines. Actual vernier thresholds for image translation and rotation appear to be limited by temporal asynchrony sensitivities of about 1 and 4 msec, respectively. While other factors such as stimulus intensity may prevent thresholds from reaching these limits, we suggest these limits are fundamental constraints on optimal performance. The 1 msec asynchrony limit is consistent with other studies involving vernier judgements based on temporal asynchronies (Fahle & Poggio, 1981; Burr, 1979; Morgan & Watt, 1983). The 1 msec limit does not imply that a specialized asynchrony detector performs the task, we believe that an orientation tuned mechanism achieves this level of performance by using the orientation information. The asynchrony limit of 4 msec likely involves the need to make rapid orientation comparisons between two "line" segments, each of which is undergoing rapid orientation changes. Not surprisingly, relative orientation judgements during rotation, resulting in motion blur along the orientation dimension, are degraded. During image translation either "line" segment could be compared with an internalized vertical reference or the orientation of the two segments could be compared directly. In either case, the orientation information is constant over time during translation.

EXPERIMENT 3: STIMULUS DURATION AND VERNIER ACUITY

The difference in vernier thresholds between the rotation and translation conditions indicates the use of an orientation cue. Why vernier thresholds in minutes of visual angle or clock-degrees appears to be limited by a 1 msec asynchrony line for velocities where thresholds are increasing remains a mystery. The limit may reflect a fundamental temporal uncertainty of the inputs to orientation tuned mechanisms. However, it might reflect the visibility of the particular stimulus targets used in Experiment 2. In fact from Experiment 1, we see (Fig. 1) that the apparent temporal asynchrony limit does change with stimulus intensity.

In Experiment 3 we address two questions. First, as stimulus intensity increases, do we reach a point where the temporal asynchrony limit becomes independent of intensity? Second, can we predict thresholds for moving vernier targets based on thresholds obtained using static vernier targets of variable duration? In the case of the

visibility of static vs moving dots, detection thresholds are the same for velocities up to 8 deg/sec and temporal summation is complete in both cases up to 100msec (Burr, 1981). Perhaps by using a simple spatio-temporal model we can predict moving vernier acuities from static vernier acuities.

Methods

Two experimentally naive subjects participated in this experiment. Both had normal or corrected visual acuity of 20/20 or better. The display system described in Experiment 2 was used to produce both the static and translating 3-dot vernier targets used in this experiment. To facilitate the comparison between static and moving targets the frame rate was a constant 179 Hz. The method of constant stimuli was used with either three or five stimulus offsets to determine vernier thresholds. Thresholds were based on three or more runs of 100 trials per point. Pilot data from one subject indicated that dot separations around 6 minarc achieved the lowest static threshold so all runs were performed at this separation. Four stimulus intensities were used for the static and moving conditions.

To estimate the stimulus intensities we measured the detectability of a single dot at each of the intensities for observer DE, by optically reducing its effective intensity. A -16 diopter spherical lens was placed at a small distance (A) in front of the display screen with the subject seated 4 m from the display. The distance of the lens (A) from the screen was adjusted until the dot was at its detection threshold ($d' - l$). At the threshold distance, A , the number of times a dot is above its detection threshold without the lens being present is given by the equation:

Dot strength (threshold units) =

$$[1 - AP(1 - A/D)]^2 \quad (3)$$

where D is the distance of the observer from the screen in meters and P is the lens power in diopters. This equation neglects the transmission inefficiencies of the lens and luminance masking due to reflection off the front surface of the lens, which we attempted to minimize. The stimulus duration was 150 msec for determining the detection thresholds. Using this method, the single dot intensities were estimated to be 1.2, 2.4, 9 and 41 times the observer's detection threshold for the four intensities used in the vernier stimuli of Experiment 3. Using these numbers for relative stimulus strength estimates of 3-dot targets is appropriate. However, the absolute number of times threshold is an underestimate of the visibility of the 3-dot vernier target with 6 minarc separation because the intensities of the three dots appeared to summate. The underestimate of threshold is also evident from the fact that vernier acuity could be obtained for the low strength target for a stimulus duration of 56 msec.

For the static vernier acuity conditions, stimulus duration ranged from a single frame (5.6msec) to 320 msec. For the two low intensity conditions the minimum duration was increased so that target visibility was sufficient for the vernier task to be performed.

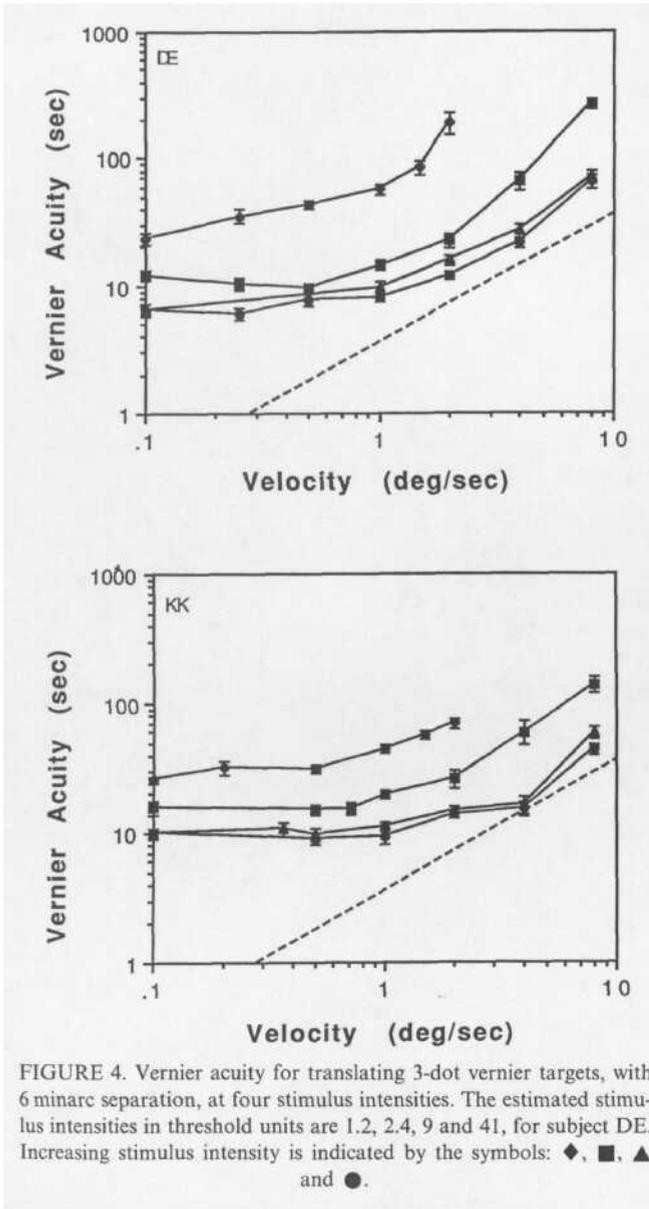


FIGURE 4. Vernier acuity for translating 3-dot vernier targets, with 6 minarc separation, at four stimulus intensities. The estimated stimulus intensities in threshold units are 1.2, 2.4, 9 and 41, for subject DE. Increasing stimulus intensity is indicated by the symbols: \diamond , \square , \triangle and \bullet .

Vernier acuity under translation was determined for a range of velocities, from 0.1 to 8.0 deg/sec. The poor visibility of the low intensity stimulus at high velocities prevented threshold assessment for part of the range. The stimulus duration was always 150msec for the moving targets.

Results and discussion

The translating 3-dot vernier thresholds at four stimulus strengths are shown in Fig. 4 for the two observers. The dashed line indicates the 1 msec asynchrony limit as described in the previous experiment. As expected, the lowest thresholds are achieved with the highest intensity targets. The two low stimulus intensity functions for each subject never reach the 1 msec limit. However, the more intense of the two stimuli clearly had a lower asynchrony sensitivity. Both of the high stimulus intensity functions approached the 1 msec limit and there was no improvement in going from 9 to 41 times the stimulus detection threshold. These data support the idea of a 1 msec asynchrony sensitivity limit (Fahle & Poggio,

1981; Burr, 1979; Morgan & Watt, 1983) which we assume is detected using an orientation cue.

The static vernier thresholds are presented in Fig. 5. Thresholds continue to decline with duration of presentation up to the longest duration tested, 0.36 sec. At the shorter durations thresholds could not be reliably determined for the two low intensity targets. For the two highest intensities, a single 5.6 msec frame was of sufficient strength to determine threshold. These data, and data from other investigators, clearly demonstrate that vernier thresholds depend on stimulus strength and duration (Hadani *et al.*, 1984). As seen in Fig. 6 (a replot of Fig. 5, subject DE) the data conform to Bloch's law, where vernier acuity is plotted as function of stimulus energy, which is the actual duration times the stimulus intensity relative to the low intensity condition. Identical symbols were used to indicate the same stimulus intensities in Figs 5 and 6. The similarity of the four functions is consistent with the Hadani *et al.* (1984) finding that 3-dot vernier targets of constant energy have constant thresholds for stimulus durations of 2-200 msec.

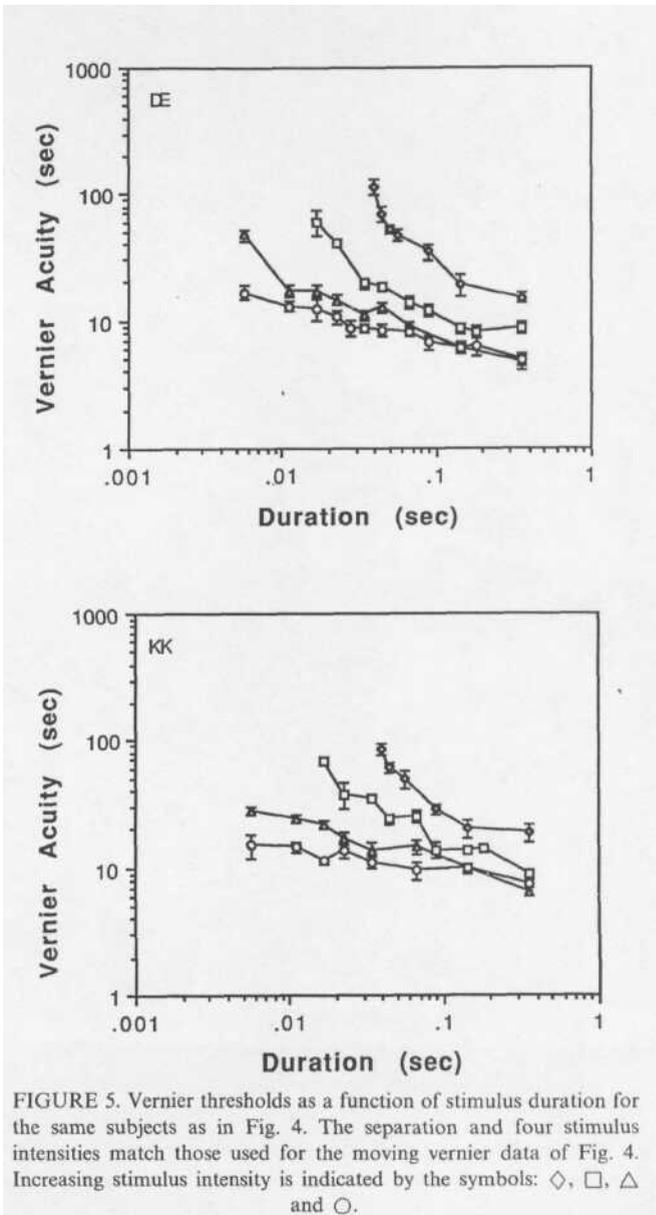


FIGURE 5. Vernier thresholds as a function of stimulus duration for the same subjects as in Fig. 4. The separation and four stimulus intensities match those used for the moving vernier data of Fig. 4. Increasing stimulus intensity is indicated by the symbols: \diamond , \square , \triangle and \circ .

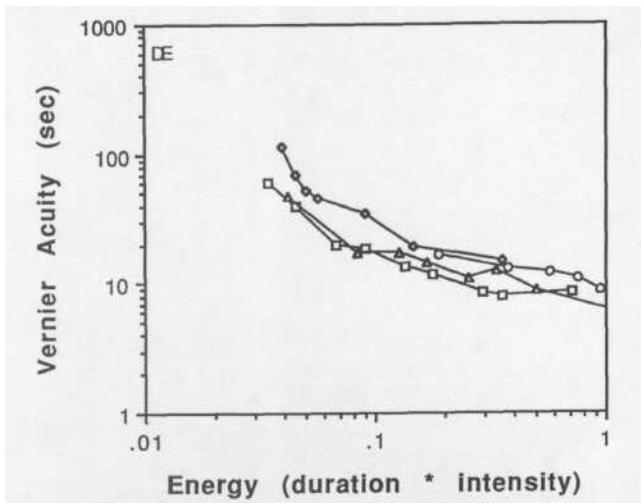


FIGURE 6. Vernier acuity is replotted from Fig. 5, subject DE, as a function of scaled energy for the four stimulus intensities. The symbols are the same as used in Fig. 5. Actual stimulus duration was scaled by the intensity of the stimulus in terms of how many times stronger it was than the low intensity condition. For example for the nine times detection threshold targets, the actual stimulus duration was multiplied by nine and divided by 1.2, the number of times the low intensity target was above threshold. This plot demonstrates the tradeoff between stimulus intensity and stimulus duration, Bloch's law, for 3-dot vernier acuity.

A simple model

The question remains, can the dependence of vernier acuity on stimulus intensity be used to predict the translating vernier acuity thresholds? Our admittedly simplistic approach to the problem is to assume a fixed receptive field center size with a rectangular sensitivity profile. Not very realistic, but very easy to calculate. To compare the static and the moving 3-dot vernier acuity thresholds we could calculate an effective stimulus duration for each of the moving vernier targets by determining how long each would reside within a fixed size receptive field. In this way the moving vernier thresholds, with velocity expressed as effective duration for a fixed receptive field size, could be directly compared with the static vernier thresholds of similar duration. Alternatively, we could transform the stimulus duration of the static vernier data into effective velocities for a fixed receptive field size and make the comparison. We have chosen the latter approach. By doing this, the abscissa is velocity, which is consistent with most of the previous graphs. It also allows for the inclusion of the 1 msec asynchrony limit line of Figs 3 and 4. For each static vernier target duration (Fig. 5) an effective velocity was calculated. For each stimulus duration the effective velocity is the velocity the stimulus would have to be traveling to just traverse the fixed size receptive field center. Therefore, to convert the durations of the static vernier acuity thresholds into velocities, simply divide the receptive field size by the stimulus duration. If the receptive field size is chosen correctly and performance is limited by the temporal integration time (stimulus intensity), the four curves derived from the static vernier thresholds should match the four curves for each subject

in Fig. 4 (which were obtained using actual moving targets).

Vernier acuity is not likely to be based on the smallest of visual mechanisms. It is known that for two-dot targets separated by 6 min, blurring them enough to remove spatial frequencies above 10 c/deg has minimal effect on vernier acuity (Williams, Enoch & Essock, 1984; see also Stigmar, 1971). A study of visual masking of abutting line vernier acuity tasks (Waugh, Levi & Carney, 1992) found that the underlying mechanisms are likely tuned to about 15 c/deg. Since we assume mechanisms with lower peak spatial frequency tuning would be involved in a moving vernier task, we have chosen a relatively large 4 minarc receptive field center for our effective velocity calculations. Moreover, Westheimer and McKee (1977a) used similar methods and found that information for making a vernier acuity judgement was gathered over a zone that extended about 4 minarc along the direction of motion, another good reason for assuming a 4 minarc receptive field center.

In Fig. 7, vernier acuity based on actual moving targets (from Fig. 4) are plotted using solid symbols (solid lines). The open symbols (dashed lines) indicate the vernier thresholds for variable duration static targets from Fig. 5 after assuming a 4 minarc receptive field to calculate effective velocity. The static data accurately predicts thresholds for different target strengths for a mid-range of velocities of the translating 3-dot vernier targets. Performance deterioration with velocity may indeed be limited by stimulus energy for most conditions. However, the predictions fail at the highest and lowest velocities.

Part of the failure at low velocities is a result of our having limited the stimulus duration of the moving vernier targets to 150 msec. To traverse a 4 minarc (0.067 deg) receptive field center within the 150 msec stimulus duration the stimulus would have to be traveling at 0.44 deg/sec (velocity = 0.067 deg/0.150 sec). It is not surprising that the predicted thresholds are too low for velocities less than 0.44 deg/sec (vertical line in Fig. 7) since at these effective velocities the static stimuli actually lasted longer than the 150 msec duration of the comparison moving target data. At the lowest stimulus intensity predicted thresholds were lower than predicted even for velocities somewhat above 0.44 deg/sec (less than 150msec).

The more important discrepancy is at the high velocities where the predicted vernier acuities based on static thresholds are much lower than that observed using moving targets. Better agreement at high velocities can be achieved by assuming a smaller receptive field, thereby shifting the curves to the right. However, for a very small 1 minarc receptive field, thresholds based on this effective velocity computation do not fit the actual moving target thresholds. The change to a 1 minarc receptive field just shifts all the points in Fig. 7, which are connected with dashed lines, to the left by a factor of four. In this case the thresholds for actually moving stimuli are generally too low to be achieved using such small receptive fields. A 2 minarc receptive field would

improve the high velocity fit but it would disrupt the fits for the two lower intensity targets.

Rather than a fixed 4 minarc receptive field, perhaps the size of the critical mechanism changes with velocity. Shifting to small receptive fields at higher velocities would provide a better fit with the data but it seems backward for the visual system to use smaller mechanisms as stimulus velocity increases.

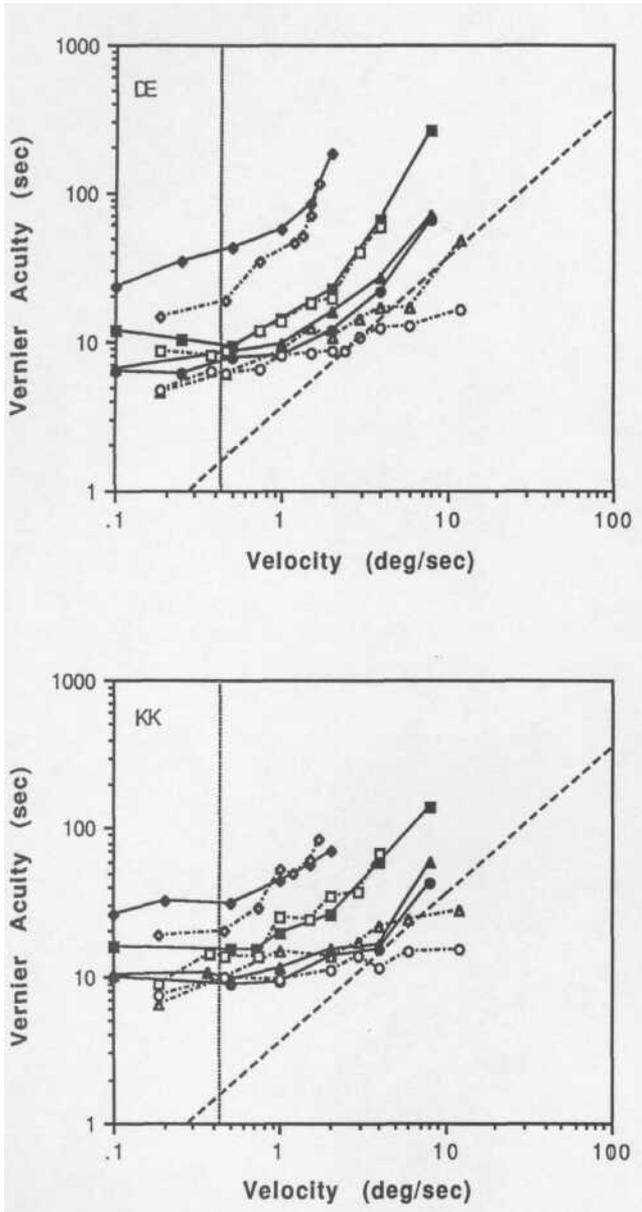


FIGURE 7. Vernier threshold as a function of stimulus velocity for two subjects. Solid symbols are the vernier acuity data for moving targets presented in Fig. 4. Open symbols are predictions derived from the static vernier data of Fig. 5 assuming a 4 minarc receptive field center. For the static vernier data an effective velocity was calculated by dividing the estimated receptive field center size of the mechanism by the stimulus duration. This calculation gives the target velocity needed to cross the 4 minarc receptive field within the target's duration. As in previous plots, the dashed line indicates the 1 msec asynchrony threshold. Open symbols to the left of the vertical dotted line are static targets which lasted longer than the 150 msec duration of the moving targets. For the middle velocities the static data can adequately predict the moving vernier data. Some discrepancies occur at very low and high velocities and are discussed in the text.

Ultimately, any scheme for explaining the high velocity data based purely on stimulus intensity would fail for stimuli of much higher intensities. Given Bloch's Law behavior, a static stimulus 10 times as intense but presented for 1/10 as long should produce the same threshold as what is currently the high intensity stimulus. However, assuming a 4 minarc receptive field, the effective velocity for such a stimulus would be well over 100 deg/sec. Vernier acuity for an intense stimulus moving at 100 deg/sec would be severely degraded relative to the static predictions. The data (as well as this armchair experiment) indicate that optimal vernier acuity at high velocities is not limited by target visibility for high intensity targets. Rather, performance appears to be limited by the visual system's inability to detect less than a 1 msec temporal asynchrony for stimuli in a vernier acuity spatial configuration. This 1 msec limit is indicated by the diagonal dashed lines in Fig. 7.

GENERAL DISCUSSION

Before considering the implications of these results for modeling vernier acuity we first summarize the critical points of the three experiments. In Experiment 1, it was demonstrated that vernier thresholds for line and 3-dot targets are similarly effected by target velocity and intensity. The more intense the stimulus the more robust vernier acuity is to motion for both 3-dot and line targets. The similar results obtained for line targets, as used by Westheimer and McKee (1975), and 3-dot targets justifies our use of dot targets in Experiment 2 to compare the effects of target translation and target rotation on vernier acuity.

In Experiment 2, the use of 3-dot targets enabled the assignment of an appropriate velocity to the rotating motion (which could not be done for line targets). For all observers, performance in the rotating vernier target conditions quickly deteriorated with increasing velocity as compared to the translating vernier target condition. This difference indicates the utilization of an orientation cue in the translating vernier acuity task. The difference between translation and rotation also argues against the use of curvature detectors in 3-dot vernier acuity. When vernier thresholds are expressed in clock-degrees all the data for different separations coalesce into two curves, one for rotation and the other for translation. The translation curves shifted toward higher velocities. The translation data exhibits a 1 msec temporal asynchrony limit (Fig. 3). This reveals an important temporal factor in vernier acuity under motion.

Experiment 3 demonstrates that the 1 msec limit was not a result of the particular stimulus strength used in experiment two. Most of the threshold changes obtained using vernier targets at different intensities and different velocities can be accounted for based on effective stimulus strength derived from static target thresholds. Assuming a 4 minarc receptive field center, the static thresholds were sufficient for predicting midrange to high velocity vernier acuity, except for the high-strength high-velocity vernier targets (Fig. 7). For these latter

targets, performance was limited by a 1 msec temporal asynchrony sensitivity as indicated by the dashed line in Fig. 7. A 4 minarc receptive field mechanism would likely be optimally selective for 7.5 c/deg gratings. Using sine wave gratings in a vernier acuity task, Bradley and Skottun (1987) found thresholds were lowest for stimuli in the range of about 6-12 c/deg (see also Hu, Klein & Carney, 1993). While a 4 minarc receptive field is within reason, we are not necessarily proposing that such a mechanism is responsible for vernier acuity. Rather it demonstrates that a rather simple model is adequate to predict moving vernier thresholds from static vernier thresholds. The interesting point is how the model fails for high-velocity high-intensity targets where vernier acuity is limited to a 1 msec asynchrony, irrespective of intensity or velocity.

Performance limits of vernier acuity

Vernier acuity as a function of stimulus velocity exhibits three performance limiting floors. The first floor is evident in the flat limb (constant threshold) portion of the curve (Fig. 3) present at low velocities. The height of this limb depends on the dot separation and dot intensity, with thresholds between about one and two clock-degrees (1-2% Weber fraction) for bright dots with a separation of 12 minarc or greater. For a 6 minarc separation, the constant threshold floors of Fig. 4 were no lower than about 8 secarc. Morgan *et al.* (1983) have shown that lower thresholds at slow velocities can be obtained by increasing the number of exposures to a brief vernier stimulus before the subject is required to make a decision. Their multiple presentation method lowered the threshold from 10 secarc (single 150 msec static presentation) down to 3.8 secarc (see their Fig. 1). Lower thresholds with multiple presentations were also obtained for targets moving at 1.5 and 3.0 deg/sec. In general the lower thresholds for moving targets did not violate the 1 msec limit of the second limb. However, for their high velocity target of 6 deg/sec the threshold suggests a 0.5 msec asynchrony sensitivity. Moreover, for the same subjects, the threshold for a single presentation of a target moving at 6 deg/sec suggests an asynchrony sensitivity of about 0.75 msec. One of our own subjects was also able to perform better than the 1 msec limit (Fig. 3, subject JL), so individual differences are an important factor. The impressive 0.5 msec sensitivity in the multiple exposure condition could be due to a combination of factors: the individual differences just mentioned, improved performance due to probability summation across the multiple exposures and finally the possible use of stimulus onset and/or offset cues present in the 6 deg/sec target. Morgan *et al.* (1983) tried in various ways to determine if cues at the start and end of a target's trajectory were being used and found them not to be significant. However, the tests were only performed at 3 deg/sec and not at the 6 deg/sec condition that achieved the 0.5 msec asynchrony sensitivity.

The second performance floor is responsible for the limb which approximates a temporal asynchrony limit of 1 and 4 msec for the translation and rotation conditions,

respectively. Westheimer and McKee (1977b) were the first to describe the 1 msec asynchrony sensitivity of vernier acuity. The temporal asynchrony floor is only reached by stimuli of sufficient intensity, otherwise the second floor is never reached. As we describe below, the low asynchrony limit does not require a special visual mechanism for detecting asynchrony. Rather, with this particular stimulus configuration, the utilization of an orientation cue during motion can be used to achieve an apparent 1 msec sensitivity. The moving vernier task appears to constitute an optimal configuration for achieving the 1 msec asynchrony limit. The data in Fig. 4 shows that the 1 msec limit is not determined by stimulus intensity and Fig. 3 demonstrates the limit for a range of dot separations.

The third floor, evident in the right most data of Fig. 1 and 4, reflects a visual sensitivity limit. At very fast velocities or at lower dot intensities the dots are barely detectable and performance rapidly deteriorates with increasing velocity (greater than unity slope).

Orientation tuning of cortical mechanisms

Static vernier acuity has been modeled using spatial mechanisms that resemble the receptive fields of cortical simple cells (Wilson, 1986). The fact that optimal vernier acuity is roughly constant for image velocities up to about 3 deg/sec offers new challenges for the modeling of vernier acuity using physiologically plausible mechanisms. Our modeling efforts have focused on the problem: can (and do) cortical cells have the capacity to signal orientation changes at high image velocities at the level required for vernier acuity? We have approached the problem in two steps. The first is to characterize the orientation tuning of cortical cells for moving targets. The motion blur resulting from a sluggish temporal impulse response might be expected to broaden the typical cell's orientation tuning characteristics. The second step is to estimate if the responsiveness of sharply tuned cells at higher velocities is sufficient for the cell's output to reliably signal 1-2 deg orientation changes.

Is it reasonable to expect that the orientation tuning of a cortical cell remains constant with stimulus velocity? Although it is unknown if orientation tuning is constant with velocity in primate cortical cells tuned to high spatial frequencies (> 7 c/deg), it is not unreasonable to expect that the temporal blurring due to the sluggish behavior of most cortical cells (Foster, Gaska, Nagler & Pollen, 1985) might broaden orientation tuning. However, it is possible that the sluggish temporal characteristics of most cortical cells results from a late stage of temporal integration, while local integration of signals in the dendrites could follow a much shorter time constant than the cell as a whole. A nonlinear peripheral dendritic integration with a 1 msec asynchrony sensitivity (Softky, 1994) might enable the cell to maintain orientation tuning in the presence of motion. However, before seeking an exotic explanation for how orientation tuning could be constant with velocity based on mechanisms with little empirical support (Shadlen & Newsome, 1994), it behooves us to see just how well we might

expect a cortical cell to perform based on estimates of their overall spatial and temporal sensitivity.

A simple cortical cell model. Using typical functions for describing the spatio-temporal characteristics of cortical mechanisms we will try to find a mechanism whose behavior is consistent with the psychophysical data on moving vernier acuity. We begin with a spatio-temporally separable receptive field given by $S(x)T(t)$. We chose a separable receptive field to be conservative. A velocity tuned mechanism constructed from the sum of two separable subunits (Adelson & Bergen, 1985) could perform the task only slightly better. The separable receptive field can be thought of as composed of a rightward plus a leftward subunit and only the rightward subunit responds well to the rightward moving stimulus. The separable receptive field should have about the same response, as the motion receptive field. Since for the moment we are considering the response to a single moving dot we do not need to introduce the y dependence of the receptive field. The activation of the mechanism to a moving dot the instant it is at receptive field location, x , can be described as:

$$R(x) = \int_{-\infty}^0 S(x - vt)T(t) dt, \quad (4)$$

where $S(x)$ is the spatial receptive field, v is the velocity of the target and $T(t)$ is a temporal function that obeys causality [$T(t) = 0$ for $t > 0$]. Within the integral t is negative since we are integrating over what has happened prior to the target reaching its current position x .

The total integrated activation of a cortical cell to two dots traversing the receptive field with a temporal delay, δ , can be crudely modeled as the integral of the product of the response to either dot alone, the autocorrelation function of equation (4)*.

$$O(\delta) = \int_{-\infty}^{\infty} R(x)R(x + v\delta) dx \quad (5)$$

*This is indeed a simple model, both equations (4) and (5) make no mention of stimulus strength or mechanism sensitivity. The responses are normalized. While response amplitude decreases with velocity this could be compensated for by increasing the overall stimulus strength. As will be discussed, the orientation bandwidth of this simple model may not change with velocity but the number of spikes would go down with velocity. The product model of equation (5) is similar to a sum of the two inputs followed by a squaring operation followed by a threshold.

†Orientation bandwidth will be determined for a range of stimulus velocities. Normally the direction of stimulus motion is orthogonal to the stimulus orientation when mapping a cell's orientation tuning. In our model the direction of motion is always horizontal with orientation changes produced by delaying one of the dots. Therefore the velocity reported for our stimuli will differ somewhat from what would be obtained using standard cortical mapping procedures. The differences will be small except for large offvertical orientations. For example, the reported velocity for a moving dot stimulus oriented at 45 deg from vertical would differ from standard methods by a factor of 1.4. This effect is seen in Fig. 8, for the cell with the slow temporal impulse response, as a saturation at high velocities which is a consequence of the atan function in equation (6).

Using equation (5) we can determine the cell's orientation tuning in terms of δ , the temporal delay between two dots moving with velocity, v , which are separated in the y dimension. The peak response is at $\delta = 0$, corresponding to a vertically oriented cell presented two vertically aligned dots that are moving horizontally. As the temporal delay increases (a change in stimulus orientation) the response decreases. We define the orientation bandwidth as that delay for which the response decreases by one-half.†

Since the orientation bandwidth in units of temporal delay is unfamiliar we have converted to the common unit of degrees of tilt by assuming a fixed dot separation. The temporal delay, δ , in msec converted into an orientation in degrees for a particular dot separation (s) in deg and velocity (v) in deg/sec is shown in equation (6):

$$\text{orientation(deg)} = \frac{360}{2\pi} \text{atan}\left(\frac{\delta v}{1000s}\right). \quad (6)$$

For example, when $\delta = 1$ msec, $s = 6$ min and $v = 3$ deg/sec the orientation is 1.7 deg.

To model the spatial receptive field (S) of our mechanism we have chosen a Gabor function (Baker & Gynader, 1986; Kulikowski & Bishop, 1981) where the y dimension is ignored since the response is just to a single dot:

$$S(x) = \exp(-x^2/2\sigma^2)\cos(2\pi fx), \quad (7)$$

where x is position in degrees, f is spatial frequency in c/deg and σ is the envelope standard deviation in degrees. Since the data of experiment three suggest a 4 minarc receptive field center, we have chosen a mechanism tuned to 7.5 c/deg ($f = 7.5$). The envelope was chosen to have $\sigma = 2.3/60$ deg to produce the spatial receptive field shown in Fig. 8(A).

The temporal function we employ is that used by Adelson and Bergen (1985) as the basis for physiologically plausible motion mechanisms:

$$T(t) = (kt)^n \exp(-kt) \left[\frac{1}{n!} - \frac{(kt)^2}{(n+2)!} \right] \quad (8)$$

where t is time in msec and $n = 3$ in this case. The parameter k was varied to explore the effects of different center frequencies. The temporal impulse responses for $k = 0.05$ and $A = 0.14$ are shown in Fig. 8(B). Both are bandpass functions with center frequencies of about 4 and 11 Hz, respectively. A 4 Hz frequency peak is common for primate cortical cells, a 11 Hz peak is unusual but within reason (Foster *et al.*, 1985).

Using these two temporal functions and the spatial function described earlier, we have determined the mechanism's orientation tuning as a function of velocity. First the response to single dot targets for a range of velocities, 0.3-10.0 deg/sec was calculated. Using the single dot responses, we then determined the mechanism's response to two-dot targets with different temporal delays [equation (5)] for the same range of velocities. The mechanism's orientation tuning bandwidth as a function

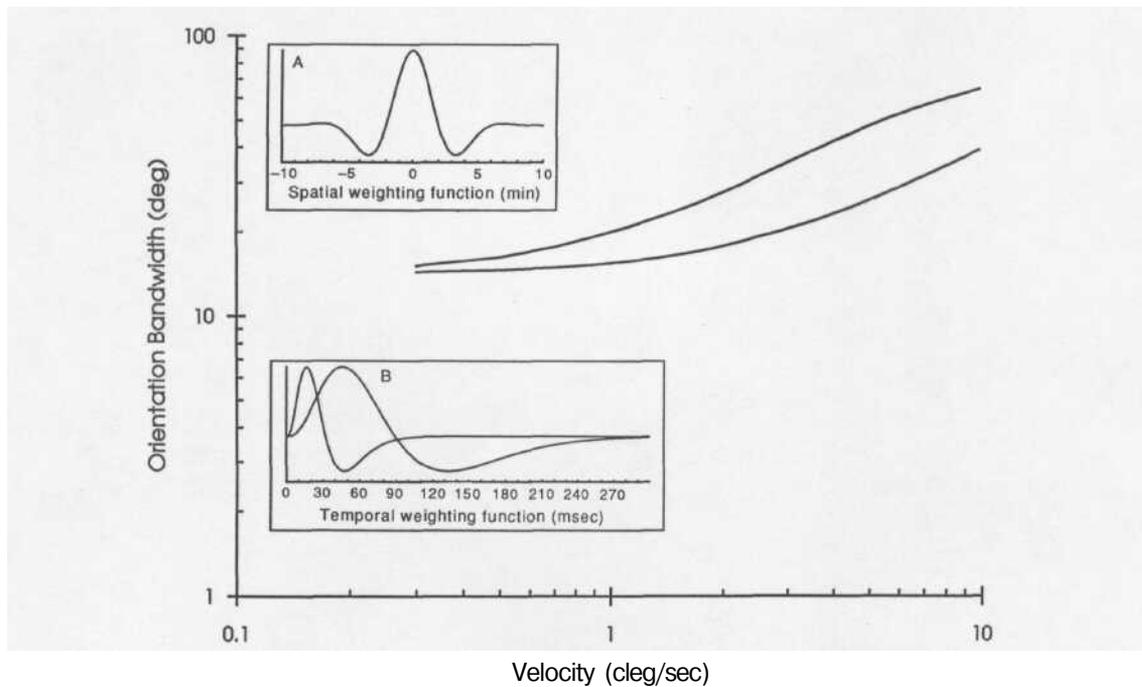


FIGURE 8. The model mechanism's orientation bandwidth at half-height is plotted as a function of stimulus velocity. The stimulus targets were two dots separated by 6 minarc [from equations (5) and (6)]. The rapidly increasing function (upper curve) was based on a mechanism having the sluggish temporal impulse with a peak frequency of about 4 Hz. When an impulse response with a 11 Hz peak frequency was used (lower curve) the mechanism orientation bandwidth remains almost constant for velocities under 3 deg/sec. Inset (A) Mechanism's spatial weighting function as defined in equation (7) with $\sigma = 2.3$ min and center spatial frequency of 7.5 c/deg. The spatial frequency was based on the 4 min receptive field center size that fit the data from Experiment 3. Inset (B) Two temporal impulse functions based on equation (8) with sensitivity plotted as a function of time in msec. The transient function has a bandpass center frequency of about 4 Hz and the slower function peaks at about 11 Hz. Primate cortical cells have been identified with peak frequencies throughout the range.

of velocity is the temporal delay for each velocity at which the response decreases by one-half. The results are plotted in Fig. 8 where orientation bandwidth is given in degrees, based on the 2-dot targets having a 6 minarc separation [equation (6)]. For the low temporal frequency tuned mechanism (4 Hz), as the 2-dot vernier target velocity increases, spatio-temporal blurring results in a rapid increase in orientation tuning bandwidth. The orientation bandwidth changes from 15 deg at 0.3 deg/sec to about 33 deg at 3 deg/sec. This type of cortical mechanism tuned to 4 Hz could not account for the robust nature of vernier acuity to image motion. However, the orientation bandwidth of the mechanism tuned to about 11 Hz only increased about 5 deg over the same velocity range so it is a possible mechanism that might account for our data. In general the orientation bandwidths are related to the autocorrelation of the mechanisms spatial profile for low velocities (< 1 deg/sec) and to the autocorrelation of the mechanisms temporal impulse response function at high velocities.

Orientation bandwidth does not strictly determine a mechanism's orientation discrimination threshold. Other issues such as response amplitude and variability are critical (Bradley *et al.*, 1987; Burr & Wijesundra, 1991). However, other things being equal a narrower bandwidth mechanism will result in improved vernier acuity (Swindale & Cynader, 1989). Our theoretical cortical mechanism (which has physiological plausibility) can

approximate the behavioral data of a roughly constant threshold at low velocities. This model implicitly assumes that at higher velocities the stimulus intensity can be increased to maintain a criterion response level or signal to noise ratio. Is this a viable assumption about a cell's performance at high velocities?

From orientation bandwidth to vernier acuity

Our hypothetical cell has an orientation bandwidth of about 15 deg at low velocity, while it is a reasonable bandwidth for a simple cell it must be remembered that this value is a direct consequence of the 6 minarc separation chosen for converting the spatial offset tuning to orientation tuning in equation (6). The sharpest orientation tuning reported for primate VI cells is 9 deg, half-width at half-height (Henry, Michalski, Wimborne & McCart, 1994). The question remains, how might a cell with 9 deg orientation tuning and the spatio-temporal frequency characteristics of our model be able to achieve vernier acuity levels of 1-2 deg orientation sensitivity. While the information from a population of such cells could easily be used to achieve this level of performance (Paradiso & Carney, 1988), some *individual* cortical simple cells are able to provide a reliable response change to orientation changes in the 1-2 deg range (Bradley, Skottun, Ohzawa, Sclar & Freeman, 1985). The factors that limit a cell's potential for signalling a change in stimulus orientation are firing rate, slope of the orientation tuning function and the

variability of the cell's response. Earlier, in the photocell detector example, we assumed the orientation discrimination task was performed along the primary axis of the two detectors, vertical in the example. In the case of actual cortical neurons the best orientation discrimination performance occurs some distance from the peak of the cell's orientation tuning function (Bradley, *et al.*, 1987; Scobey & Gabor, 1989).

The cell with the best orientation selectivity observed by Bradley *et al.* (1985) had an orientation bandwidth of 9.5 deg (half-width at half-height) and a peak firing rate of about 23 spikes per stimulus presentation (one cycle at one hertz of a drifting grating) and could reliably discriminate a change of 1.8 deg in orientation. The average orientation tuning of cat simple cells is 17 deg (Henry *et al.*, 1994), the sharp 9.5 deg tuning of this cell is one factor that makes this cell unusual. Another factor is its unusually low ratio of response variance to mean response. Along the steep part of the tuning function the mean response was about 8 spikes per stimulus presentation, the variance was about 5 spikes², which is a variance to mean ratio of 0.63. Typical ratios observed by Bradley *et al.* (1987) for cat cortical neurons were from 1.5 to 2.0.

Might we anticipate reliable response changes to 1-2 deg orientation changes of rapidly moving targets in primate cortical cells? We know some primate cortical cells have orientation tuning characteristics comparable to the cell reported by Bradley *et al.* (1985) and there is no reason to assume optimal variance to mean response ratios are larger. The problem in obtaining reliable response changes is the weak response strength. Consider our model cortical cell with peak spatial frequency tuning of 7.5 c/deg and a peak temporal frequency tuning of about 11 Hz, an optimally oriented pair of spots traversing the cells receptive field at 3 deg/sec will only be in the receptive field center for about 22 msec. At best the cell is only likely to elicit a few independent spikes in that brief period, especially to a stimulus at a non-optimal orientation. Therefore, vernier acuity under motion probably involves a population of responding cells rather than a single best cell. On the other hand, there may exist cortical cells that are tuned to much higher temporal frequencies than are commonly reported* or have other response features that might be important, such as time of response onset. In those cases model based on just a few cells might ultimately be correct.

The psychophysically observed 1 msec asynchrony sensitivity probably reflects the size of the neural integration pool which determines performance. If, on the other hand, cortical units are ever found that can reliably signal a change of 1-2 deg in orientation up to the 1 msec limit, the limit may reflect a 1 msec temporal uncertainty of the units' inputs. The data from Levick and Klein

(Klein, 1992) and that of Crognale and Jacobs (1991) suggest that an ideal detector could obtain information from a few ganglion cells with a temporal uncertainty of about 1 msec.

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*Hawken, Shapley, Gordon, Grosf and Mechler (1994) have recently reported that a few primate parafoveal V1 cells respond as well as LGN cells at high temporal frequencies. Perhaps cortical cells will eventually be found with comparable spatial and higher temporal frequency tuning than that of our model cortical cell.

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