Perceiving heading with different retinal regions and types of optic flow

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We examined the ability to use optic flow to judge heading when different parts of the retina are stimulated and when the specified heading is in different directions relative to the display. To do so, we manipulated retinal eccentricity (the angle between the fovea and the center of the stimulus) and heading eccentricity (the angle between the specified heading and the center of the stimulus) independently. Observers viewed two sequences of moving dots that simulated translation through a random cloud of dots. They reported whether the direction of translation—the heading—in the second sequence was to the left or right of the direction in the first sequence. The results revealed a large and consistent effect of heading eccentricity: Judgments were much more accurate with radial flow fields (small heading eccentricities) than with lamellar fields (large heading eccentricities), regardless of the part of the retina being stimulated. The results also revealed a smaller and less consistent effect of retinal eccentricity: With radial flow (small heading eccentricities), judgments were more accurate when the stimulus was presented near the fovea. The variation of heading thresholds from radial to lamellar flow fields is predicted by a simple model of two-dimensional motion discrimination. The fact that the predictions are accurate implies that the human visual system is equally efficient at processing radial and lamellar flow fields. In addition, efficiency is reasonably constant no matter what part of the retina is being stimulated.

As an observer moves through the environment, a moving pattern of light falls on the retina. This pattern, which Gibson (1950, 1966) called the optic flow field, can produce a compelling sensation of self-motion (Berthoz, Pavard, & Young, 1975), can be used to control posture (Lestienne, Soechting, & Berthoz, 1977), and can be used to determine the direction in which the observer is moving with respect to objects in the environment (Warren & Hannon, 1988).

In this paper, we examine how the perception of heading is affected by the region of the retina stimulated and the type of flow field presented. In regard to retinal eccentricity effects, the current literature suggests three possibilities. The first, which has been called the *peripheral dominance hypothesis* (see, e.g., Held, Dichgans, & Bauer, 1975), is that the retinal periphery dominates the perception of self-motion and presumably predicts more accurate heading perception when the retinal periphery, rather than the fovea and parafovea, is stimulated. The second possibility is that *retinal invariance* holds so that heading perception is independent of the part of the retina being stimulated. The third, which has been called the *functional sensitivity hypothesis* (Warren & Kurtz, 1992), is that "cen-

tral vision accurately extracts radial ... and lamellar flow, whereas peripheral vision extracts lamellar flow but is less sensitive to radial ... flow" (p. 451). Therefore, heading perception should be accurate when radial or lamellar flow is presented centrally or when lamellar flow is presented peripherally.

The peripheral dominance hypothesis claims that peripheral stimulation is more influential than central stimulation in the perception of self-motion (Berthoz et al., 1975; Brandt, Dichgans, & Koenig, 1973; Held et al., 1975) and the visual control of posture (Amblard & Carblanc, 1980; Lestienne et al., 1977). More recent experimental evidence, however, contradicts this hypothesis. For instance, stimulation of the central visual field (defined roughly as the part of the visual field within 10° of the fovea) is quite effective in producing a sensation of self-motion (Andersen & Braunstein, 1985; Telford & Frost, 1991); when the areas of stimulation are equated, the central and peripheral visual fields lead to similar sensations of circular (Post, 1988) and linear vection (Delorme & Martin, 1986). Similarly, both central and peripheral stimulation affect postural control; the effects are similar in magnitude as long as the areas of stimulation are roughly the same (Paulus, Straube, & Brandt, 1984). There may be some cases in which stimulation of the central visual field is even more effective than peripheral stimulation; Stoffregen (1985, 1986) has shown, for example, that a radial pattern of flow centered on the fovea leads to more postural sway than does a radial pattern centered on the periphery. In sum, little evidence favors the peripheral dominance hypothesis.

The retinal invariance hypothesis is plausible because the ability to discriminate some aspects of moving patterns is essentially invariant across the visual field. McKee and Nakayama (1984), for example, found that a constant difference of 5% was required for discrimination of the speeds of two spots, regardless of retinal eccentricity. The Weber fraction was constant at 5% for a large range of base speeds (increasing for slower and faster speeds; Orban, Van Calenbergh, De Bruyn, & Maes, 1985), but the range shifted to higher speeds as eccentricity increased. The similarity of thresholds and the shifting to higher velocities suggest that the mechanisms underlying velocity discrimination are similar in central and peripheral vision except that they are smaller in the fovea. Koenderink, van Doorn, and van de Grind (1985) examined the ability to use differential motion to segment the visual image into different patches. They found that the size of the smallest segmentable patch was similar from 0° to 48° of eccentricity, provided that fairly high velocities were used. At lower velocities, the smallest segmentable patch was similar for the fovea and parafovea, but larger for the periphery. These observations are also consistent with the idea that motion-sensing mechanisms are similar across the visual field, except that the fovea has some smaller mechanisms than the periphery does.

The functional sensitivity hypothesis—that the central retina is specialized for processing radial and lamellar flow, and the periphery, for processing lamellar flow (Kelly, 1985; Stoffregen, 1985; Warren & Kurtz, 1992)—is supported by two observations. First, such specialization would reflect the sorts of flow to which the central and peripheral visual fields are most frequently exposed. Locomoting observers tend to look near their heading or to fixate objects off to the side. In the former case, the fovea receives radial flow and the periphery lamellar flow, and in the latter case, the fovea receives complicated flow with radial and lamellar components while the periphery receives mostly lamellar flow (Warren & Hannon, 1988). Thus, better sensitivity when the central retina receives radial or lamellar flow or when the periphery receives lamellar flow might be an adaptation to the most likely of everyday situations. Stated another way, one would predict poorer sensitivity when the periphery is exposed to radial flow than when it is exposed to lamellar flow. Second, physiological observations from areas MT and MST in the macaque—areas that are widely believed to be involved in optic flow processing—suggest that most cells in the central retina are tuned to radial flow (Duffy, 1992; Wurtz, Duffy, & Roy, 1992), and most cells in the periphery, to lamellar flow directed away from the fovea (Albright, 1989).

Although Warren (1976) considered the effects of eccentric viewing, the only directly relevant psychophysical evidence concerning heading perception comes from Warren and Kurtz (1992).[1] In three experiments, they examined the role of central and peripheral vision in the perception of heading. In the first experiment, circular displays of a three-dimensional cloud of dots were presented. The motions of the dots simulated forward move-

ment (translation) of the observer. The observers made two-alternative forced-choice judgments about the horizontal position of the simulated heading. Because the flow fields simulated forward translation, there was a focus of expansion near the center of the display, indicating the heading. Two of the three experimental conditions are schematized in Figure 1. In the *central* condition, only the center of the display was presented, so the focus of expansion was visible (Figure 1A); the radius of the visible portion of the flow field was varied from 10° to 25°. In the *peripheral* condition, the center was masked so that only the peripheral portion of the display was visible (Figure 1B); the dimensions of the external contour of the visible portion were always 32° × 40°, while the radius of the internal diameter varied from 10° to 25°. In the *combined* condition, the whole display was presented. Warren and Kurtz reported heading thresholds (half of the angular difference between alternatives corresponding to 75% correct performance) of about 0.5° in the combined and central conditions, regardless of the size of the displayed flow field. In the peripheral condition, however, heading thresholds rose from 0.8° to 1.4° as the internal radius increased from 10° to 25°. The results suggested, therefore, that central stimulation is required for the most accurate discriminations of heading.

In their second experiment, Warren and Kurtz (1992) again presented a three-dimensional cloud of dots and asked observers to make judgments of the heading with respect to a target line. The retinal eccentricity of the focus of expansion (which was always visible) was varied from 0° to 15° while the observers fixated the center of the display. Their third experiment was the same, except that
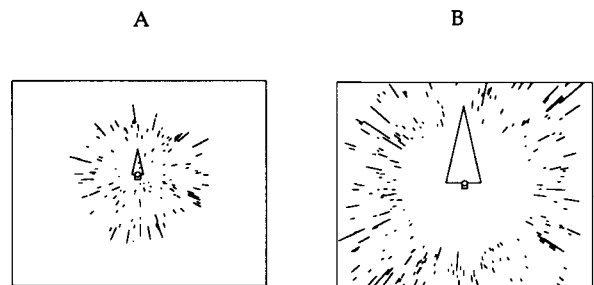

Figure 1. The stimuli used in Experiment 1 of Warren and Kurtz (1992). Dot motions simulated forward motion through a cloud of dots at random positions. (A) The stimulus in the central condition. The fixation point (indicated by the box) and focus of expansion (indicated by the circle) were near the middle of the aperture. The outer diameter of the visible portion of the stimulus was varied from 10° to 25°. (B) The stimulus in the peripheral condition. The fixation point and focus of expansion (indicated by the box and circle, respectively) were again near the middle of the stimulus. The inner diameter of the visible portion of the stimulus was varied from 10° to 25°. In A and B, the triangles show the effect of errors in estimating the direction of a single flow vector on the estimate of the focus of expansion; the angle at the apex of each triangle represents the directional error, and the length of the base represents the resulting heading error. The range displayed is for an error of 30°; the real error is much smaller at 1°–2°.
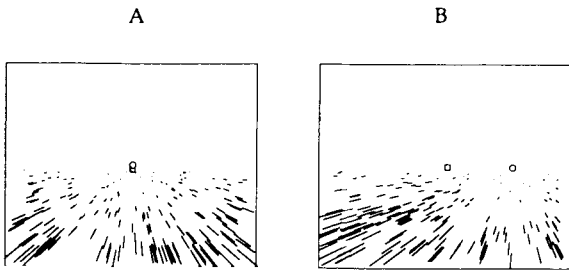
A   B

Figure 2. The stimuli in Experiment 3 of Warren and Kurtz (1992). Dot motions simulated forward translation across a ground plane. The boxes and circles represent the fixation points and foci of expansion, respectively. (A) Retinal eccentricity of 0°; translation toward the middle of the display. (B) Retinal eccentricity of 15°; translation toward the edge of the display.

the stimulus simulated a ground plane. Two versions of the display in this experiment are shown in Figure 2, one with the focus at 0° eccentricity (Figure 2A) and one with the focus at 15° (Figure 2B). With these displays, the same retinal regions were always stimulated, but the position of the focus of expansion was moved about. In the second experiment, heading thresholds rose from about 0.5° at an eccentricity of 0° to about 2° at an eccentricity of 15°. The effect of varying the eccentricity of the heading was larger in the third experiment, rising from roughly 0.5° at an eccentricity of 0° to roughly 2.7° at an eccentricity of 15°. They concluded again that the most accurate heading judgments occur when the focus of expansion is visible and near the fovea.

Warren and Kurtz (1992) argued that their results are consistent with the hypothesis that the central visual field is specialized to judge the direction in which an observer is moving through an otherwise stationary scene. We believe that their conclusion is plausible, but there are reasonable, though untested, alternative explanations that do not invoke a special role for the central retina.

In Warren and Kurtz's (1992) first experiment, the retinal eccentricity of stimulation was confounded with the visual angle between the visible flow and the heading. This is illustrated in Figures 1A and 1B for the central and peripheral conditions, respectively. Because the observer was asked to make a discrimination involving the horizontal component of the simulated heading, the most informative flow was above and below the focus of expansion. An isosceles triangle is drawn above the focus in each panel representing the possible range of errors in sensing the direction of an individual vector in that region. The widths of the triangles where they intersect the horizontal plane through the focus of expansion are $2r \cdot \tan(a/2)$, where r is the distance from the vector to the plane and a is the angular error in sensing the vector.[2] Thus, assuming that angular errors in perceived direction of motion are constant as a function of retinal eccentricity, the error in estimating the focus of expansion is proportional to its distance from the focus (Koenderink & van Doorn, 1987). Clearly, these errors would be larger in Warren

and Kurtz's (1992) peripheral condition than in the central condition because the visible flow vectors are always more distant from the focus of expansion in the peripheral condition. Consequently, one cannot determine from their first experiment whether greater sensitivity in the central condition was due to the part of the retina being stimulated or to the geometric consequences of errors in estimating the direction of individual flow vectors. Warren and Kurtz (1992) argued that they had circumvented "triangulation errors" by presenting flow all the way around the focus of expansion, but this argument does not bear on the point we are making; increasing the distance of the visible flow from the focus of expansion should have the effect of increasing thresholds, no matter what the shape of the stimulus is.

Warren and Kurtz's (1992) second and third experiments provide more persuasive evidence for a special role of the central retina in heading perception, but they too suffer from a confounding of retinal position and the pattern of flow. In these experiments, the stimulated portion of the retina was held constant (the observers fixated the center of the display) while the heading was varied. Heading thresholds increased with the retinal eccentricity of the focus of expansion. As eccentricity increased, however, the average distance between a dot and the focus also increased. This increase in average distance would tend to inflate heading threshold for the reasons described in the critique of the first experiment. In addition, when the eccentricity of the focus of expansion increased, the average angle between the horizontal axis and the line connecting a dot and the focus of expansion decreased; this point is illustrated graphically in Figure 3. This decrease in the average angle should also elevate the horizontal error in the heading estimate, because angular errors in estimating a dot's direction of motion have the smallest effect when this angle is largest (which occurs when the dot's motion is vertical). These considerations indicate that, if they were using all of the information
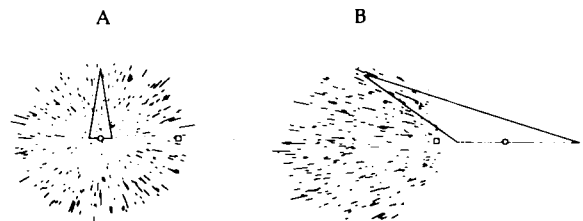
A   B

Figure 3. The stimuli in the present experiments. Dot motions simulated translation in various directions or heading eccentricities through a three-dimensional cloud of dots at random positions. The circles represent the simulated headings; the boxes, the fixation points. The diameter of the display was 10°. (A) Heading eccentricity = 0°, and retinal eccentricity = 5°. (B) Heading eccentricity = 10° and retinal eccentricity = 5°. The triangles are similar to those in Figure 1; the fact that the base of the triangle is longer in 3B than in 3A indicates that heading thresholds should increase with increases in heading eccentricity because of changes in the stimulus geometry alone.

available in the display, observers should have performed worse with an eccentric focus of expansion even if all parts of the retina were equally sensitive. Even though it has not been rigorously demonstrated, Warren and Kurtz's hypothesis is still plausible, because observers probably do not use all the information in the display.

To study how useful different parts of the retina are for the perception of heading, one needs to separate two variables: (1) the eccentricity of the stimulus patch with respect to the fovea, a variable we refer to as *retinal eccentricity*, and (2) the eccentricity of the heading with respect to the stimulus patch, a variable we refer to as *heading eccentricity*.[3] In the experiments reported here, we manipulated retinal eccentricity and heading eccentricity independently. We found a consistent and large effect of heading eccentricity: Observers' heading thresholds increased monotonically with heading eccentricity, regardless of the part of the retina being stimulated. In other words, radial flow fields were more effective than lamellar fields in specifying the direction of self-motion. There was also a smaller and less consistent effect of retinal eccentricity: Heading thresholds with radial flow fields were lower around the fovea than in the periphery.

EXPERIMENT 1

Method

Three observers participated. The first author, J.A.C., was a 7-diopter myope corrected to normal, who had extensive experience with optic flow displays. Observer G.L. was a 3.5-diopter myope who had some experience with similar displays and tasks. Observer H.F.C. was emmetropic and had no prior experience in psychophysics. G.L. and H.F.C. were both unaware of the experimental hypotheses.

The observers viewed moving dots on a CRT that simulated translation (straight-line motion) through a cloud of random dots. An example stimulus is shown in Figure 3; the fixation point and heading are indicated by a box and circle, respectively (they and the triangles were not in the stimulus). The depths of the dots varied from 50 to 1,050 cm at the beginning of a stimulus presentation, and the cloud was limited to a circular region 10° in diameter (generated in software), as if one were viewing it through a circular window. The number of visible dots ranged from 425 to 575 and decreased slightly over the course of a sequence; the maximum decrease was about 10% (for a heading eccentricity of 0°). The viewing distance was 50 cm; at this distance, each pixel subtended ~1.8′. Each dot was one pixel, so dot size did not change appropriately with simulated depth. Dot positions were updated every 33 msec on every other frame of the 66-Hz, noninterlaced display (Sony Trinitron, Sun Model GDM-1604-15). The limit of temporal integration for three-dimensional translational displays is approximately 300 msec (Crowell, Royden, Banks, Swenson, & Sekuler, 1990); in order to be safely above this limit, we used a stimulus duration of 800 msec. The mean speed of the translation was constant at 200 cm/sec when the focus of expansion was visible on the screen; for larger heading eccentricities, it was varied so that the mean angular velocity at the center of the stimulus remained roughly constant. Thus, for heading eccentricities of 10°, 20°, 40°, and 70°, the mean translation speeds were 200, 100, 50, and 37 cm/sec, respectively. The translation speed also had a random component (taken from a uniform distribution with width equal to half the mean) so that observers would not be able to respond on the basis of simple speed cues. Viewing was always monocular, all observers using the right (dominant) eye.

Heading eccentricity was varied in a horizontal plane through the fixation point. On any given trial, the observer saw two motion sequences separated by an interval of 400 msec; the last frame of the first sequence remained on screen for 200 msec, at which point it was replaced by the first frame of the second sequence. In one sequence, the heading eccentricity was set at the base value; in the other, heading was slightly to the left or the right of the heading in the first interval. The order of presentation was randomized, so the base heading eccentricity was presented with equal probability in the two intervals. The observer's task was to judge whether the heading in the second interval was to the left or the right of the heading in the first interval; feedback was given after each trial. The angle between the two headings was varied by using a two down/one up staircase that terminated after 12 reversals. Threshold, which corresponded to 71% correct, was defined by the mean of the last 10 reversals.

Our task was slightly different from Warren and Kurtz's (1992): Instead of judging the heading in a single interval with respect to a target, our observers judged the difference in heading between two successive intervals. This procedure allowed us to present a much broader range of heading eccentricities (without having to place a target many degrees from the display screen). In addition, with this procedure, thresholds are not affected by the ability to localize a static target (Levi, Klein, & Aitsebaomo, 1985) and are thus more likely to reflect the precision of heading perception rather than the precision of target localization.

Retinal eccentricity was independently varied, with a movable fixation point. Fixation was set at 0°, ±5°, ±10°, and ±40° from the center of the screen, with negative values indicating that the nasal retina was stimulated.

Results

The data from this experiment are plotted in Figures 4-6. In Figure 4, the observers' heading thresholds are plotted as a function of heading eccentricity with a separate panel for each retinal eccentricity. Each data point represents the mean of two to four staircase runs. Error bars represent ±1 *SD* (in some cases, they could not be displayed in the available space). All observers show a large effect of heading eccentricity: The lowest threshold of about 0.2° (at a heading eccentricity of 0° and a retinal eccentricity of 0°, Figure 4A) is 2 log units lower than the highest threshold of about 20° (at a heading eccentricity of ±70° at any retinal eccentricity). The 3 observers' thresholds differ in magnitude, but the shapes of their functions are quite similar. Observers H.F.C. and G.L. did not complete the entire experiment (both moved out of state), but given the similarity in the shapes of the functions over the range of completed conditions, there is no reason to believe that they would have shown a different pattern of results over the remaining conditions.

The graphs of threshold versus heading eccentricity can be divided into two categories: those in which fixation was within the stimulus patch (0° retinal eccentricity, Figure 4A) or at the edge of the patch (±5°, Figure 4B), and those in which fixation was outside the patch (±10° and ±40°, Figures 4C and 4D). In the figures in the former category, there is some heading eccentricity at which the focus of expansion was visible and centered on the fovea; this point is marked by an arrow. There is always an improvement in performance at this heading by 0.3-0.5 log units, and this produces a sharp dip in the func-
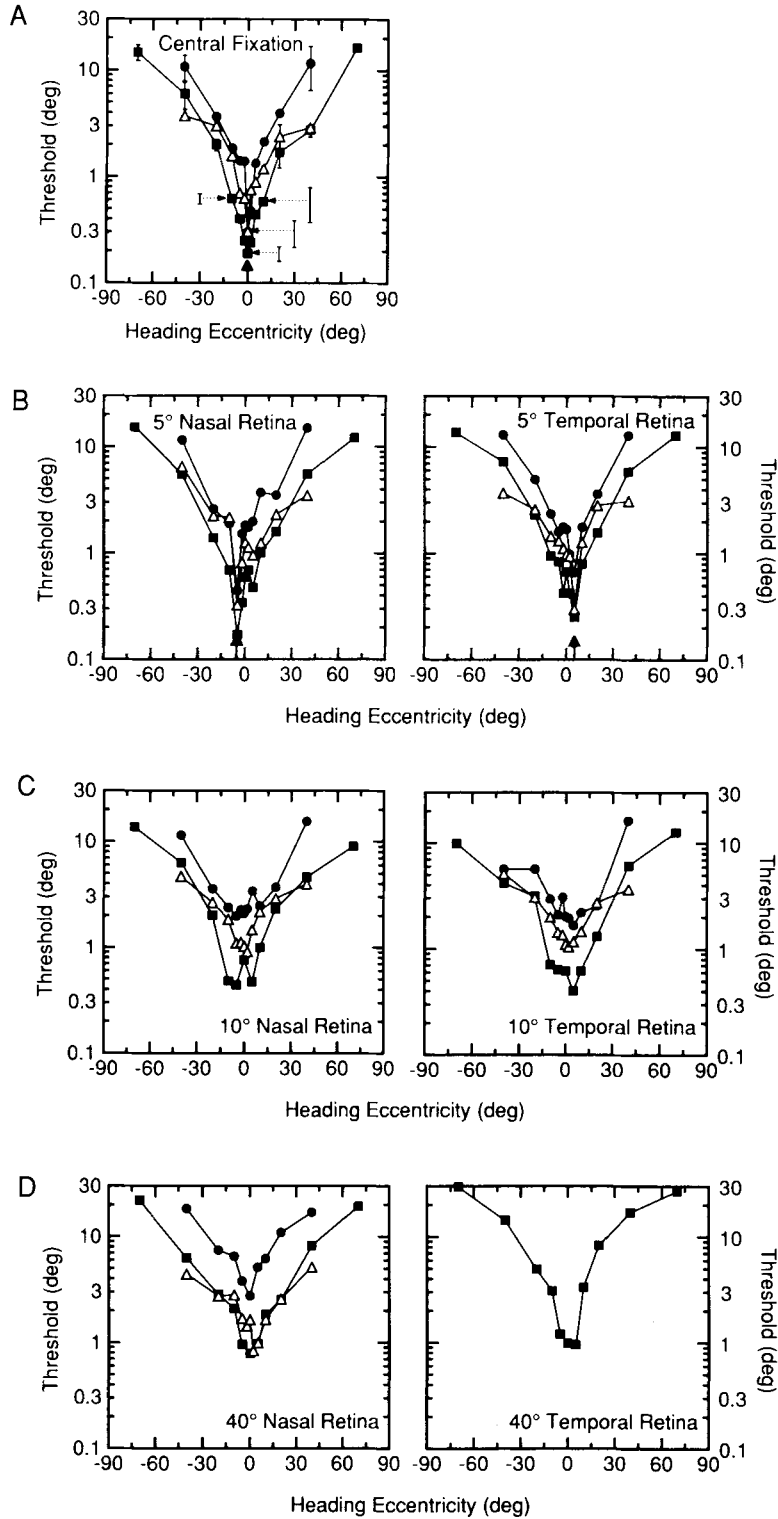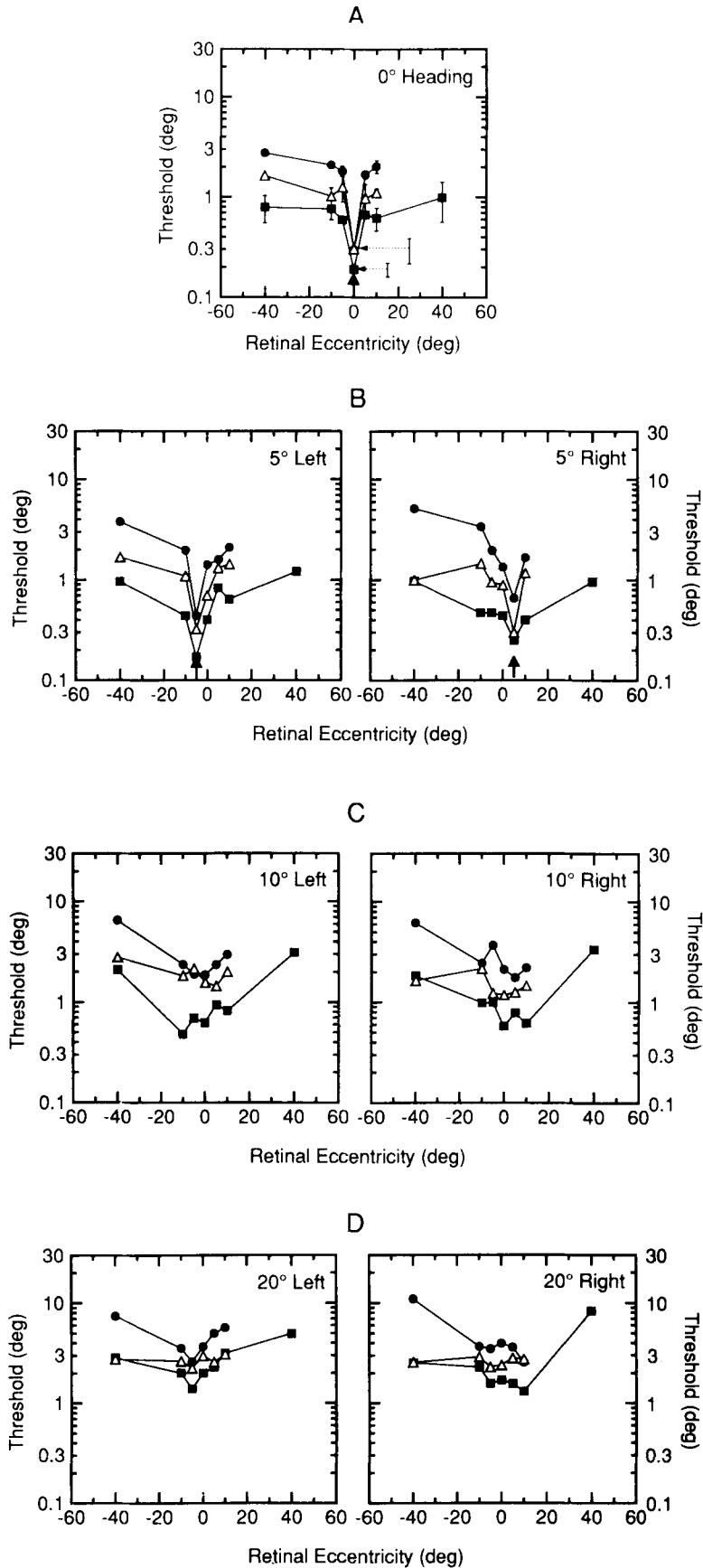
Figure 4. Heading thresholds as a function of heading eccentricity. Each panel represents a different retinal eccentricity. The squares, triangles, and circles represent mean thresholds for Observers J.A.C., H.F.C., and G.L., respectively. (A) Central fixation (retinal eccentricity = 0°). The arrow indicates the heading eccentricity that placed the focus of expansion on the fovea. (B) Retinal eccentricity = 5°, nasal and temporal retina. The arrows indicate the heading eccentricity that placed the focus of expansion on the fovea. (C) Retinal eccentricity = 10°, nasal and temporal retina. (D) Retinal eccentricity = 40°, nasal and temporal retina.
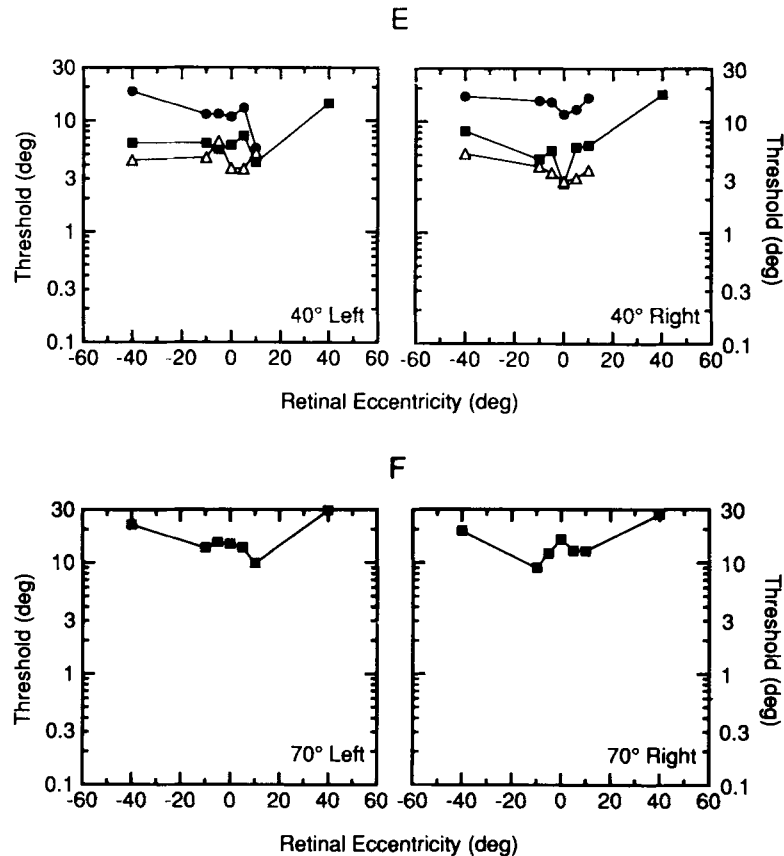
A

B

C

D

E

F

Figure 5. Heading thresholds as a function of retinal eccentricity (opposite page and above). Each panel represents a different heading eccentricity. The squares, triangles, and circles represent mean thresholds for Observers J.A.C., H.F.C., and G.L., respectively. (A) Heading eccentricity of 0° (radial flow). The arrow indicates the condition that placed the focus of expansion on the fovea. (B) Heading eccentricity of 5°, left and right of center. The arrows indicate the conditions that placed the focus of expansion on the fovea. (C) Heading eccentricity of 10°, left and right. (D) Heading eccentricity of 20°, left and right. (E) Heading eccentricity of 40°, left and right. (F) Heading eccentricity of 70°, left and right.

tions. When the focus of expansion was visible at the larger retinal eccentricities, it was not close to the fovea, and no sharp dip is observed. This difference between the functions indicates that central vision can make better use of the information in a radial flow field than can peripheral vision. The narrowness of the dips in Figures 4A and 4B indicate that this region of greater sensitivity extends only a couple of degrees from the center of the fovea.

Figure 5 contains the same thresholds plotted as a function of retinal eccentricity, with a separate panel for each heading eccentricity. These functions are generally quite flat, which indicates that all parts of the retina are almost equally sensitive to the information for heading. There is a tendency for thresholds to increase slightly between ±10° and ±40° retinal eccentricity; the ratios of the thresholds at these two retinal eccentricities range between 0.9 and 6.3, with a mean of 2.0. However, there is no correlation between magnitude of the increase and the heading eccentricity. In addition, with the exceptions de-

scribed below, there are no consistent trends at retinal eccentricities below 10°. Some of the functions (Figures 5A and 5B) contain noticeable dips like those in Figures 4A and 4B. These figures represent conditions in which the focus of expansion was visible in the stimulus; its position is again marked by an arrow. In each of these conditions, there is a retinal eccentricity at which fixation is on or close to the focus of expansion, and this leads to the dips in the data. There appears to be a foveal advantage with purely radial flow fields; the far periphery (retinal eccentricity greater than 10°) tends to be slightly less sensitive, but the sensitivity loss is not consistent. At intermediate retinal eccentricities (2°-10°), there are no systematic variations in sensitivity.

Figure 6 shows all of the data plotted as a function of heading eccentricity, with a separate panel for each observer. The functions are generally quite similar, with the exceptions of the dips described above. This means that the major determinant of threshold is the heading eccen-
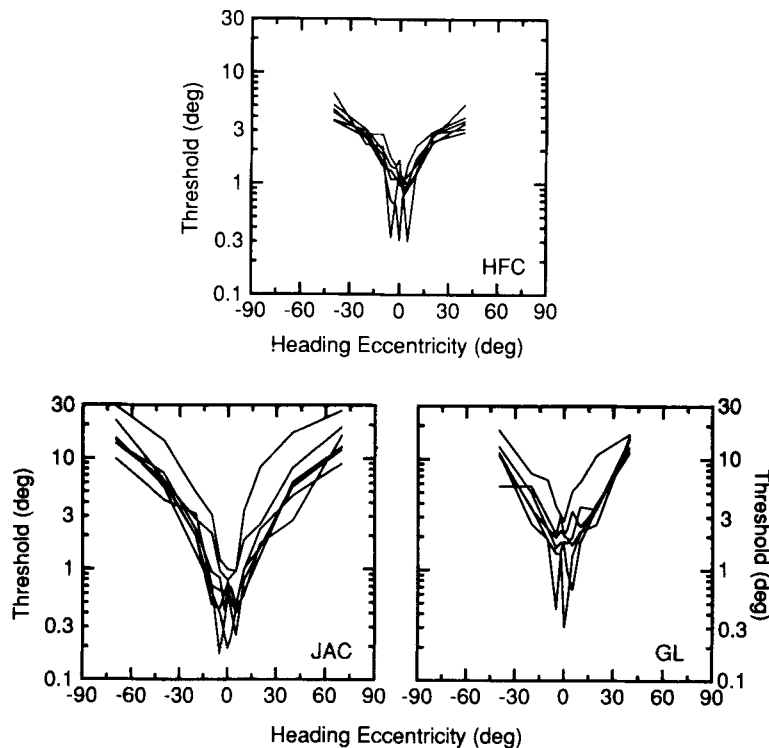
Figure 6. Heading thresholds as a function of heading eccentricity for all retinal positions. The panels display separately all the data from Observers J.A.C., G.L., and H.F.C.

tricity, not the retinal eccentricity, of the stimulus except when the focus of expansion is visible and centered on or near the fovea. Thus, retinal eccentricity effects in heading judgments are relatively small and mostly restricted to within a degree or so of the fovea.

There was a small nasal-temporal asymmetry at 40°, the largest retinal eccentricity tested. This is illustrated in Figure 7, where heading thresholds are plotted sepa-

rately for 40° nasal retina and 40° temporal retina. Notice that thresholds are 0.3-0.5 log units lower in the nasal retina for nonzero heading eccentricities. We observed this asymmetry only at 40°. It is similar to the nasal-temporal asymmetry observed in grating acuity (Rovamo, Virsu, Laurinen, & Hyvarinen, 1982) and in the density of retinal neurons (Curcio & Allen, 1990).

EXPERIMENT 2

The psychophysical literature on velocity discrimination suggests that the fovea is better suited for discriminating slow targets (McKee & Nakayama, 1984; Orban et al., 1985). Such specialization raises the possibility that retinal eccentricity effects on heading perception depend on stimulus speed. To examine this possibility, we presented central and peripheral targets at a variety of simulated translation speeds.

Method

Observer J.A.C. and 1 new observer, W.B.D., participated. W.B.D. was unaware of the experimental hypotheses. The stimuli were presented at two retinal eccentricities: 0° and 40° nasal. In each case, two heading eccentricities were presented: 0° and 70°. The former generates a radial flow pattern and the latter a mostly lamellar pattern. The simulated translation speed was varied by about 1.4 log units. The stimulus duration was 400 msec. In all other respects, the stimuli and procedures were identical to those in Experiment 1.
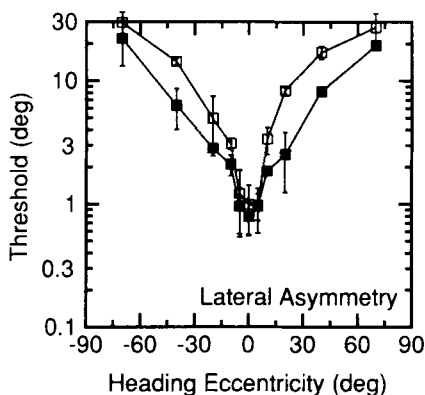

Figure 7. Heading thresholds as a function of heading eccentricity for the nasal and temporal retina. Observer J.A.C.'s thresholds for 40° nasal and temporal retina are represented by the filled and unfilled symbols, respectively.
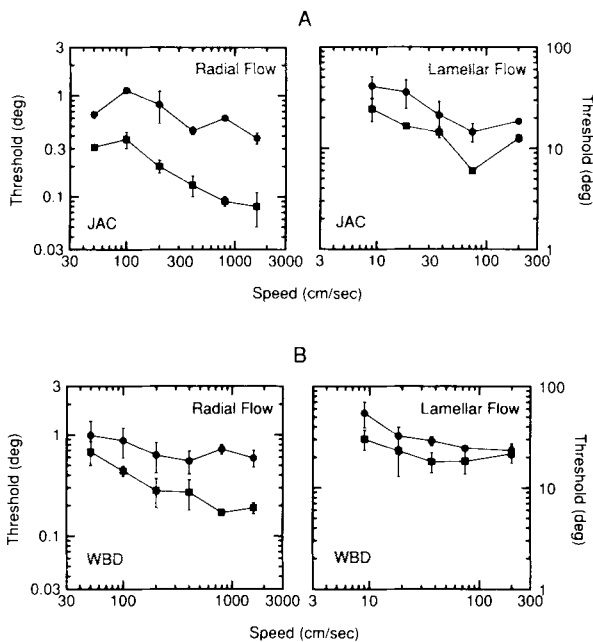
Figure 8. Heading thresholds as a function of translation speed for central and peripheral fixation. The upper (A) and lower (B) parts of the figure represent the data from Observers J.A.C. and W.B.D., respectively. The squares and circles represent thresholds for retinal eccentricities of 0° and 40° nasal, respectively. The left panels display thresholds for radial flow patterns; heading eccentricity was 0°. The right panels display thresholds for lamellar flow patterns; heading eccentricity was 70°. Note the difference in horizontal and vertical scales between the two panels.

Results

Figures 8A and 8B display the heading thresholds for the 2 observers at various translation speeds. The left panel of each figure shows thresholds for radial flow patterns, and the right panel, thresholds for lamellar patterns; note the difference in the scales for both axes between the two panels. The squares and circles represent foveal and peripheral (40° nasal) fixation, respectively. Heading thresholds decreased monotonically with increasing translation speed for all conditions tested. Most interestingly, however, the speed effect was essentially the same for foveal and peripheral viewing. This similarity suggests that the relatively small variation in performance that we observed at different retinal eccentricities does not depend significantly on stimulus speed.[4]

DISCUSSION

We have reported two main observations: (1) there is a fairly small and inconsistent effect of retinal eccentricity on the ability to perceive heading, and (2) there is a large and consistent effect of heading eccentricity on heading perception. In this section, we compare these observations with other findings in the literature and discuss their theoretical relevance.

Spatial Scaling and Peripheral Vision

The observation of nearly constant performance as a function of retinal eccentricity is consistent with the retinal invariance hypothesis and inconsistent with the peripheral dominance hypothesis (e.g., Held et al., 1975). Our results also seem to be at odds with another theoretical position originating in the psychophysical literature: the spatial scaling hypothesis. Rovamo, Virsu, and Nasanen (1978), among others, have argued that performance in a wide variety of visual tasks can be rendered equivalent across different retinal regions if a spatial scaling factor is employed. As an example, the spatial contrast sensitivity function varies greatly with retinal eccentricity mostly because contrast sensitivity to high spatial frequencies worsens with increasing eccentricity; the highest detectable frequency declines from 60 cycles/degree (cpd) in the fovea, to 15 cpd at 5°, and to 2 cpd at 40° (Banks, Sekuler, & Anderson, 1991). Rovamo et al. (1978) showed, however, that contrast sensitivity functions are constant across the visual field if the stimulus is scaled according to a cortical magnification factor (Van Essen, Newsome, & Maunsell, 1984). In other words, sensitivity is constant if stimulus size is increased in the periphery and the spatial frequency is expressed in scaled units. This spatial scaling hypothesis predicts how visual performance varies with retinal eccentricity in several tasks (Gordon & Abramov, 1977; Levi et al., 1985; Virsu & Rovamo, 1979), but our data imply that no such scaling is required to render performance similar in heading tasks. Possibly the targets were too large in our experiments to reveal any underlying spatial scaling effects, but we found in earlier work (Crowell et al., 1990) that stimulus scaling according to cortical magnification (Van Essen et al., 1984) leads to more accurate judgments in the periphery than in the fovea and parafovea.

Speed discrimination in central and peripheral vision is constant over a range of base speeds, but that range occurs at higher speeds in the periphery (McKee & Nakayama, 1984; Orban et al., 1985). There have been no measurements of direction discrimination as a function of speed in different retinal regions, but it seems plausible that a similar finding would be observed in that task. Thus, one might expect heading judgments, which are limited by speed and direction discrimination, to improve with increasing speed in the periphery but not in the central visual field. In contrast to this expectation, the results of Experiment 2 showed that heading judgments at higher speeds improve in both peripheral and central vision. This finding is probably a consequence of the fact that we presented dots at a wide variety of simulated depths, so a wide range of dot speeds was always present. Observers probably weighted most heavily the dots moving at speeds for which their speed and direction discrimination was best.[4]

In summary, it appears that our data are more consistent with the retinal invariance hypothesis than with the spatial scaling hypothesis. Heading perception is unusual in that sensitivity with unscaled stimuli is similar in central and peripheral vision.

Are Different Retinal Regions Specialized for Different Types of Flow?

Warren and Kurtz (1992) found that heading judgments were more accurate when the flow field stimulated the central rather than the peripheral retina (Experiment 1) or when the focus of expansion was near the fovea (Experiments 2 and 3). These results, they argued, suggest that central and peripheral vision are differentially sensitive to the types of flow that normally occur in those regions of the visual field (see also Kelly, 1985). Specifically, they hypothesized that the fovea and parafovea are better adapted for processing radial flow fields than the periphery is. Our observation of a small foveal advantage with radial flow patterns is consistent with this hypothesis, but we hasten to point out that the effect is small.

We argued earlier that the studies of Warren and Kurtz (1992) did not allow an independent assessment of how sensitive different parts of the retina are to the heading information in optic flow fields, because they confounded variations in retinal eccentricity with variations in heading eccentricity. Our experiments were designed to eliminate this confounding in order to reveal the true effect of retinal eccentricity. One can still compare their results to ours, however, as we have done in Figure 9, which plots heading thresholds as a function of retinal and heading eccentricity. Warren and Kurtz's data are from their Experiment 2, in which fixation was always in the center of the stimulus patch (so the same part of the retina was exposed for all conditions), but heading eccentricity was varied. Our data are from Experiment 1; the data points represent the average thresholds across 3 observers. The left panel plots our data at a heading eccentricity of 0° (radial flow) for different retinal eccentricities. The right panel plots our data at a retinal eccentricity of 0° for different heading eccentricities. Warren and Kurtz's data are the same in both panels. Notice that the data from the two experiments are more similar when plotted in terms of heading eccentricity rather than retinal eccentricity. This
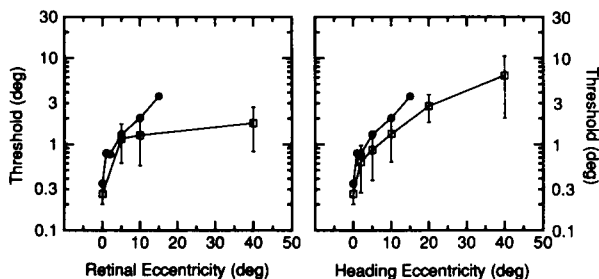

Figure 9. Heading threshold as a function of retinal eccentricity and heading eccentricity from the present study and from Warren and Kurtz (1992). In both panels, the squares represent heading thresholds (averaged across 3 observers) from Experiment 1 of the present report and the circles represent average thresholds from Experiment 2 of Warren and Kurtz. Error bars represent ± 1 SD of the averaged thresholds. The left panel plots the data as a function of retinal eccentricity, and the right panel plots them as a function of heading eccentricity.

observation suggests that the major determinant of performance in these experiments is the pattern of flow, not the retinal region being stimulated. We should note, though, that the effects of heading and retinal eccentricity should have been larger in our experiment than in Warren and Kurtz's, because our targets were significantly smaller (smaller displays allow better differentiation of one type of flow compared to another and better isolation of a retinal locus). Thus, it is somewhat puzzling that the data in the right panel of Figure 9 are so similar.

Are There Special Mechanisms for Processing Radial Flow?

The most consistent and significant determinant of heading judgments appears to be the position of the focus of expansion relative to the stimulus patch (the heading eccentricity) rather than the part of the retina onto which the patch falls (the retinal eccentricity). Figure 6 illustrates this: Heading thresholds increased monotonically by nearly 3 log units for heading eccentricities of 0°-70°. This effect does *not* necessarily imply a neural specialization for processing radial flow fields (De Bruyn & Orban, 1990; Regan & Beverley, 1979); it could equally well be a consequence of the variation with heading eccentricity of the fidelity of stimulus information specifying heading (Koenderink & van Doorn, 1987). To determine whether it reflects a neural specialization or not, one needs to estimate how efficiently human observers use the available stimulus information at different heading eccentricities. This is a very important point; to support a claim for neural specialization for one type of stimulus in comparison with another, one must demonstrate variations in *efficiency*, not just variations in *sensitivity*. More efficient utilization of the available information with radial than with lamellar flow fields would suggest a neural specialization for radial flow field analysis; equal efficiency for radial and lamellar flow would suggest no such specialization. A rigorous calculation of human efficiency requires an ideal discriminator (Geisler, 1989) for this task, but an informative approximation is straightforward.

The focus of expansion is presumably localized by extrapolating flow vectors in the display in order to locate their source (see Figures 1 and 3). Some vectors, however, are more informative than others: Because the observer's task is to judge the relative horizontal position of the foci of expansion, vectors above and below the foci are much more informative than vectors on the horizontal meridian of the display. We present the results of a one-vector analysis here, to show how informativeness varies from one vector to another. Of course, human observers undoubtedly use a large number of vectors in these tasks, but our analysis still gives insight into how variations in stimulus information ought to affect heading estimates. The position of the focus of expansion can be estimated from the intersection of one vector, above or below the focus of expansion, with the horizontal plane through the focus. The triangles in Figures 1 and 3 represent the range of errors in estimating the direction of

such a vector and show how errors in estimating vector directions produce errors in estimating the horizontal position of the focus; the angle at the apex of each triangle represents the directional error, and the length of the base represents the resulting heading error. There are two important effects: (1) As can be seen in Figures 1A and 1B, the error in estimating the horizontal position of the focus should increase with the distance from the flow vector to the focus of expansion. (2) As can be seen in Figures 3A and 3B, estimation errors should increase as the focus of expansion becomes more eccentric with respect to the center of the stimulus. Therefore, if heading were judged by finding the point of intersection of an informative vector with the horizontal plane through the focus of expansion, there are two reasons why heading judgments should become systematically less accurate with increasing heading eccentricity. One can show that the angular error in heading judgments (δ) is given by

$$\delta = h - \sin^{-1}\left\{ \frac{\tan \gamma}{\tan\left[\tan^{-1}\left(\frac{\tan \gamma}{\sin h}\right)+\epsilon\right]} \right\},$$

where ϵ is the error in estimating the direction of the flow vector, γ is the angle between the vector and the center of the stimulus, and h is the heading eccentricity (the angle between the center of the stimulus and the focus of expansion).

Figure 10 shows the expected error in judging heading for a particular set of assumptions about the error in estimating the direction of individual vectors and the vertical position of the vectors. The predictions are for $\gamma = 5°$ (the radius of the stimulus) and $\epsilon = 1.5°$. The
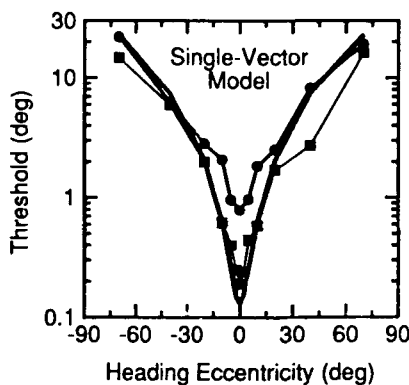

Figure 10. Observed and predicted thresholds as a function of heading eccentricity. The squares and circles represent Observer J.A.C.'s thresholds for retinal eccentricities of 0° and 40° nasal, respectively. The solid curves show the predictions of the single-vector model described in the text. The parameters of the model are ϵ (the error in estimating flow vector directions) = 1.5° and γ (the angular separation between the vector and the center of the stimulus) = 5°. Thus, the vector used to estimate heading is at the top of the display.

data are J.A.C.'s thresholds for retinal eccentricities of 0° (squares) and 40° (circles).

The predictions fit the foveal data well; they fit the peripheral data less well because the observed thresholds at small heading eccentricities are too high. Since this is not a proper ideal-observer analysis, this result suggests that humans, under conditions of foveal fixation, are equally efficient at using the available stimulus information across a wide range of heading eccentricities. In other words, human efficiency is generally similar for radial and lamellar flow fields presented in the central visual field. Constant efficiency implies that the mechanisms for processing radial flow are no better at using the available stimulus information than are the mechanisms for processing lamellar flow (see also De Bruyn & Orban, 1990).

The predictions do not fit the peripheral data as well because the observed heading thresholds at small heading eccentricities are too high. This implies, then, that human observers' efficiency, under conditions of peripheral fixation, is poorer for radial than for lamellar flow fields. Thus, our data are consistent with the following functional *efficiency* hypothesis: central vision processes all types of flow fields with equal efficiency; peripheral vision (starting at about 2° eccentricity) is as efficient as central vision with all types of flow fields except radial ones, with which it is somewhat less efficient.

There are three plausible interpretations of the observation that radial flow fields are processed more efficiently in the fovea than in the periphery. First, it could be the result of having more cells tuned to radial fields serving the fovea than in other parts of the visual field (Duffy, 1992). Second, it could be a consequence of having smaller receptive fields serving the fovea (Koenderink et al., 1985). In our task, the most informative vectors are at the very top and bottom of the display when the heading eccentricity is greater than 5° and are just above and below the focus of expansion when the heading eccentricity is less than 5° (see Figure 3). The availability of motion-sensing units with smaller receptive fields in the fovea might, therefore, be most advantageous for radial flow fields. One could test this possibility by blurring the displays to see if the foveal advantage depends on high spatial-frequency information. Third, it could be a consequence of the "crowding" effect. In the periphery, adding contours adjacent to a target diminishes the ability to identify the target; this effect is much smaller in the fovea (Levi et al., 1985). As mentioned above, the most informative vectors in a radial flow field are near the middle of the display; in a lamellar field they are at the top and bottom of the display. Thus, the crowding effect should be most detrimental with peripheral viewing at small heading eccentricities. The threshold elevation for radial flow fields viewed peripherally might, therefore, be a consequence of an inability to extract "crowded" information in the center of the display. One could test this possibility by decreasing dot density to see whether the peripheral disadvantage reflects crowding.

SUMMARY

Observers' ability to judge heading seems to depend more on the pattern of flow presented than on the part of the retina stimulated. More specifically, we observed a large and consistent effect of heading eccentricity: Judgments were much more accurate at small heading eccentricities (radial flow fields) than at large heading eccentricities (lamellar flow fields). There was a smaller and less consistent effect of retinal eccentricity: Judgments were more accurate with radial flow fields presented centrally rather than peripherally.

The fact that heading judgments are more accurate with radial than with lamellar flow seems to reflect the discrimination information provided by the stimulus rather than a neural specialization for processing radial flow fields. We conclude that the visual system is well adapted for extracting the information specifying heading in a variety of patterns of flow and from a variety of retinal regions.

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NOTES

1. Warren (1976) simulated translation across a ground plane and asked observers to indicate their perceived heading by pointing. He varied the visual angle between the heading and the center of the stimulus, but he allowed the observers to vary their fixation. Thus, he did not systematically vary retinal eccentricity.

2. This equation, which was presented in Warren and Kurtz (1992), specifies the heading error as a distance in the plane of the display. It

is more appropriate to specify the heading error as an angle, and we give the corresponding equation in the Discussion; it yields nearly the same result for small angles.

3. In both cases, eccentricity is expressed in spherical coordinates, with the origin at the center of the eye. Retinal eccentricity is the angular separation between the center of the stimulus and the fovea. Heading eccentricity is the angle between the center of the stimulus and the simulated heading.

4. It may not be obvious to the reader why speed discrimination is relevant in these heading tasks. To see how it is, consider forward translation (heading eccentricity = 0°) through our three-dimensional cloud of dots. The mean dot speed in each region of the stimulus is roughly proportional to the distance from the focus of expansion. In particular, a dot at the focus of expansion would have a speed of zero.

Thus, if the focus of expansion were visible, observers could identify simulated heading by detecting the region of lowest average speed. Because mean dot speeds were equated in Experiment 1 from one heading eccentricity to another, the simulated speed of observer translation was much higher at small than at large heading eccentricities. One might worry, therefore, that the observed effect of heading eccentricity was caused in part by this confounding. The results of Experiment 2 show that this is not the case; when observer speed was the same (e.g., 50-200 cm/sec), thresholds were still much lower at small heading eccentricities.