Pergamon

PII: S0042-6989(96)00204-0

Vision Res., Vol. 37, No. 5, pp. 573–590, 1997
Published by Elsevier Science Ltd
Printed in Great Britain

Human Heading Estimation During Visually Simulated Curvilinear Motion

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Received 24 October 1995; in revised form 20 May 1996

Recent studies have suggested that humans cannot estimate their direction of forward translation (heading) from the resulting retinal motion (flow field) alone when rotation rates are higher than ~1 deg/sec. It has been argued that either oculomotor or static depth cues are necessary to disambiguate the rotational and translational components of the flow field and, thus, to support accurate heading estimation. We have re-examined this issue using visually simulated motion along a curved path towards a layout of random points as the stimulus. Our data show that, in this curvilinear motion paradigm, five of six observers could estimate their heading relatively accurately and precisely (error and uncertainty < ~4 deg), even for rotation rates as high as 16 deg/sec, without the benefit of either oculomotor or static depth cues signaling rotation rate. Such performance is inconsistent with models of human self-motion estimation that *require* rotation information from sources other than the flow field to cancel the rotational flow. Published by Elsevier Science Ltd

MST   Navigation   Self-motion perception   Vection   Optic flow

INTRODUCTION

It has long been known that a compelling illusion of self-motion can be elicited by a purely visual stimulus, a phenomenon called vection (e.g. Berthoz *et al.*, 1975; Sauvan & Bonnet, 1993). The question that we address in this study is: can such visual stimuli also support accurate estimation of the direction of self-motion? Over 40 years ago, Gibson (1950) postulated that humans could use the visual motion experienced during locomotion to determine their motion relative to a stationary environment. The retinal motion resulting from self-motion is commonly referred to as "optic flow".§ Much of the information in the optic flow is captured in the "flow field", the vector field consisting of the velocity of each point in the three-dimensional (3D) environment projected onto the two-dimensional (2D) retina. If locomotion is pure forward translation, then a "translational" flow field is generated: a radially expanding pattern with all of its vectors emanating from a single point. This point, the focus of expansion (FOE), indicates the direction of translation or heading [see Fig. 1(A, B)]. Therefore, to determine one's heading, one need simply locate the FOE. It has been shown that human observers are generally able to estimate their heading to within ~1 deg of visual angle during simulated translation (Warren *et al.*, 1988). However, it is not clear that such performance is necessarily an indication of 3D self-motion perception as the task could easily be performed by merely identifying the center of the simple 2D expansion pattern without any 3D interpretation. Furthermore, in most real-world situations, eye movement or self-motion along a curved path produces "rotational" flow which, when combined with the translational flow, shifts and disrupts the FOE. The net result is a singularity (an imperfect FOE) which is no longer in the same direction as heading [see Fig. 1(C, D)]. Estimating heading from the flow field then becomes more complicated (Regan & Beverly, 1982).

The question of how humans might estimate their self-motion has been the subject of many theoretical analyses. As human self-motion perception appears dominated by vision (see Henn *et al.*, 1980), a number of investigators have examined the visual cues that could provide information about self-motion (Gibson, 1950, 1966; Calvert, 1954; Llewellyn, 1971; Johnston *et al.*, 1973; Lee, 1974; Nakayama & Loomis, 1974; Koenderink & van Doorn, 1975, 1987; Warren, 1976; Regan & Beverly, 1979, 1982; Longuet-Higgins & Prazdny, 1980; Prazdny, 1981; Rieger, 1983; Rieger & Lawton, 1985; Verri *et al.*, 1989; Zacharias *et al.*, 1985; Cutting *et al.*, 1992; Hildreth, 1992; Perrone, 1992; Heeger & Jepson, 1992; Lappe & Rauschecker, 1993; Perrone & Stone, 1994; Royden, 1994; Vishton & Cutting, 1995). Most have focused on the visual problem in its simplest form, i.e.,

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§Gibson (1950) made a distinction between retinal and optical flow. However, we use the terms retinal and optic flow synonymously.

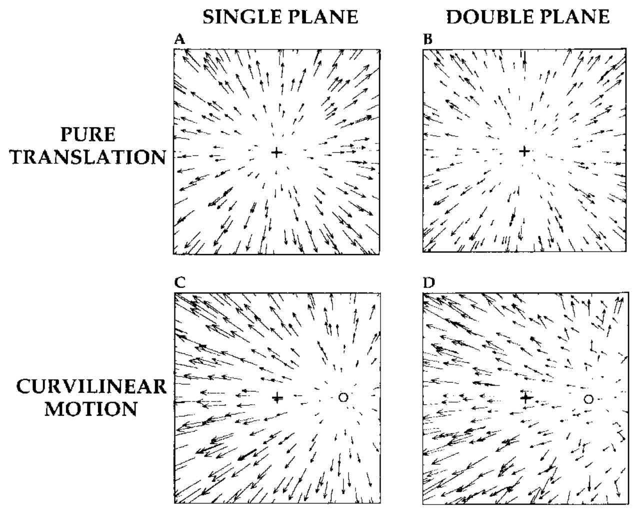

FIGURE 1. Examples of flow fields produced by self-motion, with either no yaw (A, B) or rightward yaw (C, D) rotation, towards either one frontoparallel plane at 12.5 m (A, C) or two at 12.5 and 25 m (B, D). These examples illustrate the flow field at the onset of trials in Expts 1 and 2. The crosses indicate heading (which is along the line-of-sight). The open circles in (C) and (D) show the location of the singularity of the 12.5 m plane.

the input is limited to a single instant of 2D retinal velocity (a single flow field) without other sources of visual information (e.g. disparity, perspective, occlusion, higher-order derivatives, etc.) or contributions from the oculomotor, vestibular, and other sensory systems. Although all of these cues may play an important role in human self-motion perception, if noise is neglected and there are no independently moving objects, it is mathematically possible, under most circumstances, to recover one's exact instantaneous direction of self-motion with respect to the line of sight (retinocentric heading) from the flow field alone (e.g. Longuet-Higgins & Prazdny, 1980; Zacharias *et al.*, 1985). This fact led to the development of a number of models of human self-motion perception which estimate retinocentric heading from a single flow field (e.g. Rieger & Lawton, 1985; Perrone, 1992; Heeger & Jepson, 1992; Hildreth, 1992; Lappe & Rauschecker, 1993; Perrone & Stone, 1994). The question we address in this paper is how well can humans perform this task.

Over the last decade, a number of investigators (Rieger & Toet, 1985; Cutting, 1986; Warren & Hannon, 1988, 1990; Warren *et al.*, 1988, 1991a,b; Cutting *et al.*, 1992; Warren & Kurtz, 1992; van den Berg, 1992, 1993; van den Berg & Brenner, 1994a,b; Royden *et al.*, 1992, 1994; Turano & Wang, 1994; Banks *et al.*, 1996) have examined human heading estimation. In all of these studies, the stimuli consisted of visually simulated self-motion which included rotation. The earlier studies (Rieger & Toet, 1985; Warren & Hannon, 1988, 1990) concluded that humans can visually estimate their heading from the flow field even in the presence of rotational flow, but they only examined rotation rates below 2 deg/sec. However, Banks and colleagues (Royden *et al.*, 1992, 1994; Banks *et al.*, 1996) have presented evidence that humans cannot estimate heading accurately from visual cues alone in the presence of rotational flow. They conclude that accurate visual heading estimation may be restricted to stimuli in which the rotation rate is less than 1 deg/sec and argue that, for higher rotation rates, oculomotor cues are "required". van den Berg and colleagues (van den Berg, 1992, 1993; van den Berg & Brenner, 1994a,b) have also challenged the view that heading can be estimated from the flow field alone and claim that static depth cues are "essential" for robust heading estimation. The above discrepancies invite a re-examination of the issue.

Several important methodological issues must be taken into consideration when interpreting the above results, particularly, the self-motion scenario, the layout, and, most importantly, the frame of reference. First, a number of different scenarios can introduce rotational flow into the flow field. Three common scenarios are self-motion along a curved path, self-motion along a straight path while tracking a moving object in the scene (translation + pursuit), and self-motion along a straight path while fixating a stationary point in the scene (translation + gaze-stabilization). Second, the layout (the positions and depths of the environmental points) can either be pseudorandom (e.g. a cloud or multiple planes of random dots) providing no static cues for motion in depth, or can have recognizable structure (e.g. a ground plane) providing depth information through perspective and/or texture gradients. Third, the frame of reference for the psychophysical judgments can be egocentric (with respect to the moving observer) or exocentric (with respect to a reference point in the stationary environment). Although it should be noted that there are a number of possible egocentric reference frames: with respect to the line of sight or gaze (retinocentric), with respect to the head (craniocentric), or even with respect to the body. If the three are not aligned, eye-position and head-position information can be used to move from one egocentric coordinate to another.

While each of the three scenarios (or combinations thereof) described above expose the observer to different optic flow, the instantaneous flow field (and therefore retinocentric heading) can be identical in any of these cases. However, the conditions differ over time, e.g., retinocentric heading systematically changes in the translation + pursuit and the translation + gaze-stabilization cases, but can be fixed during self-motion along a curved path. Therefore, while a single flow field defines an unambiguous and unique instantaneous retinocentric heading, either higher-order spatio-temporal information in the optic flow, integration over time, or information from sources other than optic flow is *required* to distinguish between the various possible exocentric trajectories (Rieger, 1983; Warren *et al.*, 1991a,b; Royden, 1994).

In this study, we re-examine the issue of whether humans can estimate retinocentric heading from flow fields in the presence of rotation. However, we designed our experiments to address issues left unresolved by previous studies. First, to address the criticism by Royden and colleagues (Royden *et al.*, 1992) that previous studies had only examined the effect of rotation rates at or below 2 deg/sec, we examined higher rotation rates. Second, to determine if static-depth cues, such as perspective, texture-gradient, or horizons, are essential (van den Berg, 1992; van den Berg & Brenner, 1994b), we used double planes of random points at different depths so that such cues were not available. Third, to generate retinocentric headings that do not change over time, we used visual stimuli that simulated a special case of self-motion along a curved path, curvilinear motion, which consists of rotation around the vertical axis through the observer (yaw) plus translation in a fixed direction with respect to the rotating line of sight. Fourth, to avoid the problem of the potential ambiguity of exocentric heading and to allow direct comparison of our results with the predictions of current models, we asked observers to make retinocentric judgments. Preliminary results were presented at annual meetings of the Association for Research in Vision and Ophthalmology (Perrone & Stone, 1991) and the Society for Neuroscience (Stone & Perrone, 1991, 1995).

GENERAL METHODS

Curvilinear paradigm

We simulated curvilinear motion by rotating the observer's line-of-sight at a constant rate around the yaw axis, while simultaneously translating the observer in a fixed direction with respect to the current line-of-sight. This allowed us to generate stimuli with rotational flow, but with constant retinocentric heading over the entire trial. This is equivalent to generating circular trajectories with the observer's line of sight fixed at some angle with respect to the tangent of the path (the direction of instantaneous translation). Figure 2(A, B) illustrate the principle behind our stimuli by showing circular trajectories that would result if trials were allowed to last for several tens of seconds, while Fig. 2(C, D) show examples of actual trajectories. The two trajectories in (A) and (B) were both generated with a translation rate of 2 m/sec and a rotation rate of 2 deg/sec, but are for two different headings. They are circles of radius of ~53 m and observers would take 180 sec to make a full revolution.* The solid arrows show the line-of-sight at the beginning of the trial and at two later time points. The curvature (and size) of the circular path is set by the translation and rotation rates (independent of heading angle) and therefore provides no cue for heading. Heading changes are produced by resetting the line-of-sight with respect to the tangent of the path, which is equivalent to changing the location of the axis of rotation in 3D space. In trials where heading was 0 deg [Fig. 2(A)], the observer translated along the circular path always looking straight ahead along the tangent of the path (in the direction of their instantaneous direction of translation). On the other hand, if heading was rightward (leftward), then the observer also moved along a circular path, but was always looking in a fixed direction leftward (rightward) from where they were going [Fig. 2(B)]. Throughout a given trial, retinocentric heading, the instantaneous direction of translation with respect to the line-of-sight, remained constant, although exocentric heading (direction of translation with respect to the virtual stationary world) was changing over time as observers experienced a simulated turn. In the case of zero rotation, curvilinear motion reverts to translation along a straight path which is equivalent to a circle of infinite radius.

Our actual stimuli were nearly two orders of magnitude shorter than those shown in Fig. 2(A, B): the trajectories were in fact small circular arcs (always <2.5% of a full circle). Our intent was to generate a brief stimulus, close to a single flow field within the constraints of the finite temporal integration time of human motion processing (see e.g. Watson & Turano, 1995). Eighteen examples of trajectories used in Expt 2 are shown in Fig. 2(C, D). Note the greatly expanded scales. Figure 2(C) illustrates the 0 and ±6 deg heading conditions, each for 0 and ±2 deg/sec of yaw. For the +6 deg heading trajectories (dotted lines), instantaneous translation was always 6 deg to the right of the line-of-sight. For the 0 deg heading trajectories (solid lines), instantaneous translation was always along the line-of-sight. For the −6 deg heading trajectories (dashed lines), instantaneous translation was always 6 deg to the left of the line-of-sight. In the 0 deg/sec rotation case (the straight paths), both retino-

*The absolute values of translation rate and distance, here and elsewhere, are arbitrary. Only the ratio of the two can be recovered from optic flow (i.e., 1 m/sec toward a point 10 m away will produce the same flow as 10 m/sec toward a point 100 m away). The specific values are provided for clarity: to provide the reader with a more concrete sense of the trajectories.

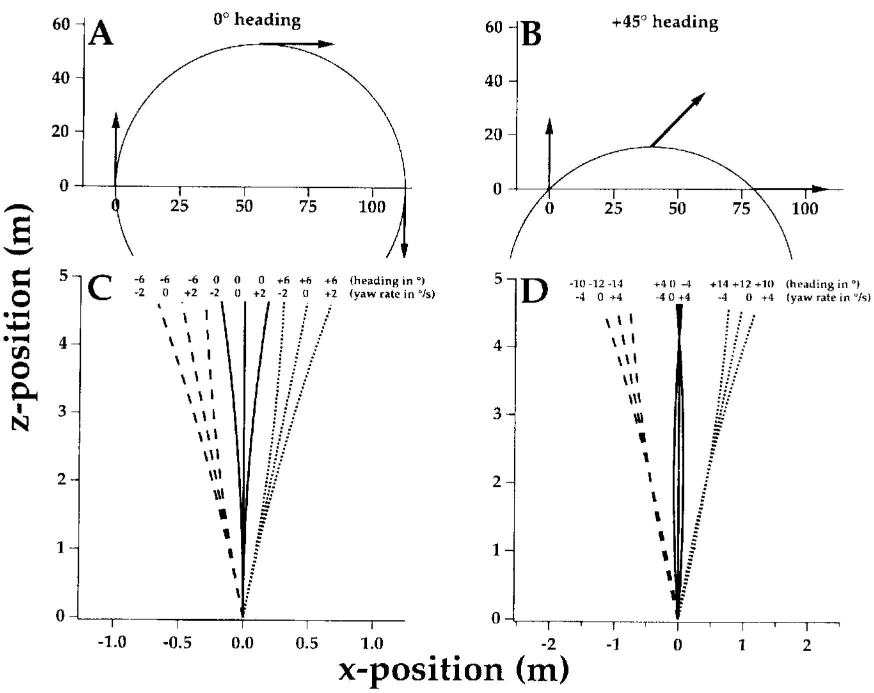

FIGURE 2. The curvilinear paradigm. (A, B) Illustrations of circular paths for 0 and 45 deg heading, respectively. (C, D) Actual trajectories in Expt 2. The heading and rotation values are shown at the top of each trace.

centric and exocentric heading remained constant. In the −2 and +2 deg/sec rotation conditions (the curved paths), exocentric heading slowly turned leftward or rightward, although retinocentric heading remained constant throughout the trial (either −6, 0, or +6 deg). Figure 2(D) shows the trajectories for the −4, 0, and +4 deg/sec rotation conditions as the three dashed lines for −10, −12 and −14 deg headings, as the three solid lines for −4, 0 and +4 deg headings, and as the three dotted lines for +14, +12 and +10 deg headings. Each of these triplets illustrates that even when the exocentric trajectories are similar (except possibly at the end of the trial), retinocentric heading can be quite different. It should also be emphasized that the trajectories were not directly visible in the stimuli.

The curvilinear scenario reduces visual–oculomotor conflict. It assumes that the eyes remain fixed in the head (no eye movements). This was true for all our experimental conditions, so there was no conflict with the lack of eye rotation reported by the oculomotor system. Furthermore, curvilinear motion assumes en-bloc rotation of the body/head/eyes, so all egocentric coordinates remained equivalent and we need not worry about differences between retinocentric, craniocentric, and body-centric coordinates.

The layout did not provide static-depth cues. Simulated motion was always towards one or two transparent frontoparallel planes of randomly distributed points (single pixels that did not change size with depth), yielding flow fields like those shown in Fig. 1. The planes were perpendicular to the line of sight at the beginning of the trial and remained fixed in space throughout the trial. They always extended to the margins of the field of view and the dot densities were balanced such that the number of dots on each plane was the same, at the beginning of the trial. Distance information could only be derived from motion. We systematically investigated the effect of rotation rates between 0 and 16 deg/sec with translation rates between 2 and 16 m/sec toward two planes 12.5 and 25 m or 14.4 and 26.4 m away. Details are found in the specific Methods sections for each experiment.

Observers were asked to make retinocentric heading judgments. They were told to fixate a stationary cross (0.3 by 0.3 deg in Expts 1 and 2; 1 by 1 deg in Expt 3) located at the center of a screen which appeared at stimulus onset and remained on throughout the stimulus presentation. In Expts 2 and 3, the cross was not immediately adjacent to moving points. In addition, its lack of motion was inconsistent with it being interpreted as part of the layout. It was provided for three reasons: (1) to enhance fixation (i.e., to allow observers to suppress eye movements); (2) to align the observer's real and virtual lines-of-sight; and (3) to provide a *directional* reference which defined the line-of-sight (not a positional reference in the scene). At the end of each trial, they were asked to respond whether the direction of their translation was to the left or right of their line-of-sight. We further explained the task by pointing out that it is similar to determining whether they were instantaneously skidding to the right or to the left of straight-ahead gaze while making a turn. To discourage

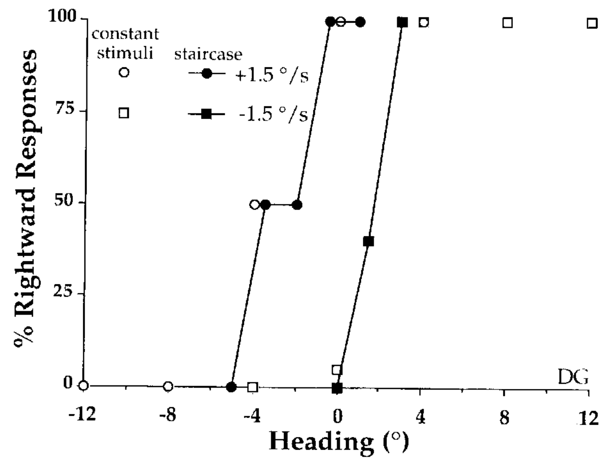

FIGURE 3. Raw psychometric data for observer DG. The solid symbols represent data obtained using a staircase method while the open symbols represent data obtained using the method of constant stimuli. The circles indicate data for rightward rotation and the squares for leftward rotation.

observers from being influenced by their exocentric path, we instructed them to ignore the direction of the turn (their exocentric heading) and to respond to the direction of the skid. We emphasized that the small translation signal was hidden in and independent of the large rotational mask. Despite these explanations, the task is difficult and casual observers are generally not able to perform well. Just as with many traditional 2D motion tasks, practice (see below) was required to achieve asymptotic performance (e.g., speed-discrimination Weber fractions asymptote at ~5% after practice, but can be up to an order of magnitude higher in unpractised observers).

Data collection

From trial to trial, the horizontal heading angle (azimuth) was varied in response to the observer's previous judgment using randomly interleaved up–down staircases for multiple conditions in which other parameters (layout, rotation rate, translation rate, and stimulus duration) were fixed. Vertical heading angle (elevation) was always fixed at 0 deg, as heading was varied only along the horizontal meridian. In Expts 1 and 2, the starting values of the staircases were randomly assigned heading directions from −6 to −8 deg for positive or from +6 to +8 deg for negative rotation (positive values of heading and rotation are rightward). For the 0 deg/sec rotation case, the starting values were randomly assigned between −4 and +4 deg. These values were selected to minimize the number of trials needed for convergence, as pilot studies indicated that staircases tended to converge on heading values somewhere between veridical and that predicted by the singularity. Four preliminary trials were presented at the start of each staircase, with the staircase step size initially set to 3 deg. The step size was then reduced to 1.5 deg and 26 additional trials were run per staircase (one staircase/condition or 26 trials/condition/run). Although the less than optimal randomization initially biased the staircases towards *larger* errors than those shown in Figs 4–5, the uncertain starting point together with the interleaved staircasing eliminated any bias in the final heading measurements. Furthermore, the naïve observers were unaware of the constraints on initial staircase position, the number of conditions, and of the specifics of the staircasing. Finally, Expt 3 explicitly controls for this issue. In Expt 3, we ran two randomly interleaved staircases per condition which started at random heading values between −14 and +14 deg. The initial step size was 4 deg, and was reduced by a factor of 2 after each reversal until it reached a minimum of 1 deg. Five preliminary trials were presented at the onset of each staircase followed by an additional 20 trials per staircase (40 trials/condition/run).

Data analysis

The psychophysical responses were tabulated into psychometric curves (Fig. 3) consisting of plots of percent rightward responses vs stimulus retinocentric heading direction. We fit the data with cumulative Gaussians using a least-squares procedure based on Probit Analysis (Finney, 1971) to yield "perceived straight-ahead" as the mean and "heading uncertainty" as the standard deviation (SD) of the underlying Gaussian. On the rare occasion that a fit had a correlation coefficient of less than 0.5 (<5% of the time, except for DD whose data could not be properly fit 30% of the time), the unreliable parameters were not included in the averaged data.

To illustrate our analysis, Fig. 3 shows the raw data from the ±1.5 deg/sec rotation conditions (filled symbols) for naïve observer DG. The fit to the −1.5 deg/sec condition had a mean (perceived straight-ahead) of +1.6 deg, while that for +1.5 deg/sec had a mean of −2.7 deg. Each psychometric curve is shifted in the direction opposite to that of the rotation. Note that

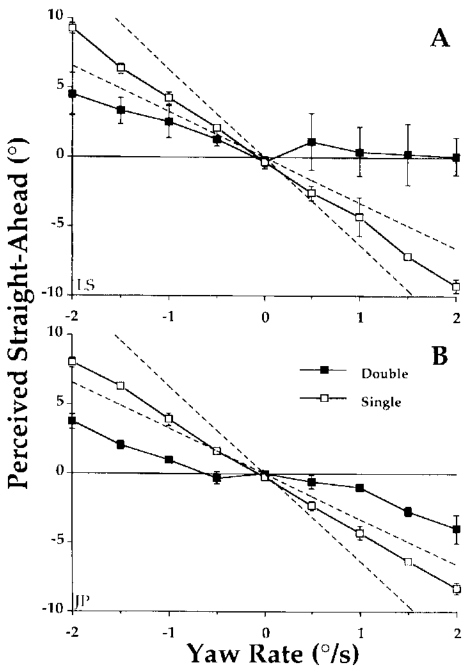

FIGURE 4. Perceived straight-ahead for the two observers in Expt 1. The open symbols indicate data for single-plane condition and the solid symbols for the double-plane condition. The solid horizontal line indicates perfect performance and the dashed lines performance using singularity-based strategies (see text). Error bars indicate standard deviation over three or four runs. (A) Data for observer LS. (B) Data for observer JP.

perceived straight-ahead is only an indirect measure of rotation-induced bias: it is the heading which cancels the bias caused by the rotation. Given that perceived straight-ahead is biased toward the direction opposite that of the rotation, we can therefore conclude that heading is biased toward the rotation direction. Although we cannot be sure of its magnitude, it is likely to be approximately equal and opposite to the measured perceived straight-ahead. Because of the underlying symmetry of the stimuli, in Figs 5–7, the data from both rotation directions were combined. Indeed, in all experiments, five of the six observers (all but LS) produced symmetric data. We therefore defined "heading error" as the perceived straight-ahead for leftward rotation minus that for rightward divided by two. Positive values of heading error, therefore indicate that perception is biased toward the direction of rotation.

To control for the possibility that multiple headings might be perceived as straight-ahead, we ran one naïve observer (DG) using the method of constant stimuli. The stimulus parameters remained the same as in Expt 2, except that only the ± 1.5 deg/sec rotation rates at a fixed range of headings (-12, -8, -4, 0, 4 deg for leftward rotation and -4, 0, 4, 8 and 12 deg for rightward rotation) were tested in pseudorandom order, with 20 trials per candidate heading (two runs of 10 trials/heading). The data are plotted as open symbols in Fig. 3 and are consistent with this observer's staircase data (solid symbols). The monotonic nature of the constant-stimuli data show that, under these conditions and within the limited heading range tested, this observer responded as if there were only a single heading that was perceived as straight-ahead. In all subsequent experiments, we used a staircase method for efficiency. The constant-stimuli method necessitated a coarse step size (4 deg) to cover the full range of possible heading responses and required 200 trials to generate the data shown by the open symbols. The staircase method, using a smaller step size (1.5 deg), took only 60 trials (including the eight discarded preliminary trials) to provide the more precise measure of performance shown by the solid symbols.

Visual display

In Expts 1 and 2, the stimuli were generated using an HP1345A vector graphics unit controlled by a SUN 3 workstation. The graphics unit was used to drive an HP1310B monitor with a P31 phosphor. The display had a resolution of 2024×2024 addressable points and a refresh rate of 15 Hz. The area between the screen and the observer was enclosed in a hood to minimize stray light. The edges of the display were masked off by a 38×28 cm rectangular aperture located directly in front of the screen to minimize glow from the edge of the monitor. The display was viewed binocularly through natural pupils from a distance of 0.71 m, thereby allowing a field of view of 30 deg by 22 deg.

In Expt 3, the stimuli were generated using a SPARC10 GT workstation driving a SUN 21-in monitor with a P22 Phosphor. The display had a resolution of 1024×1024 pixels and a refresh rate of 76 Hz. As described above, the area between the screen and observer was enclosed to minimize stray light and the edges of the display were masked off by an aperture 30 by 30 cm directly in front of the screen. Observers viewed the display binocularly through natural pupils from a distance of 0.36 m with a field of view of 45 by 45 deg.

Observers

We used six observers between the ages of 24 and 38 yr, four of whom (DG, DD, CN, DH) were naïve as to the purpose of the experiments, as well as inexperienced psychophysical observers. No trial-by-trial feedback was ever provided to observers LS, JP, DD, and DG. Nonetheless, prior to gathering the data for Expts 1 and 2, these four observers required a variable number of practice runs performing the task without feedback before their data became reliable (defined as correlation coefficients higher than 0.5 for the Gaussian fits), although DD's performance remained relatively noisy. In an effort to expedite the practising process for Expt. 3, two naïve observers (CN and DH) received trial-by-trial feedback in three runs of a special training task. The layout consisted of four large opaque colored cubes at different positions and depths, toward which we simulated 1.4 sec of curvilinear motion at 8 m/sec with either −8, 0, or +8 deg/sec of yaw rotation. Such stimuli provide powerful static perspective, relative displacement, and looming cues as well as motion cues about self-motion. Under these conditions, the richness of the stimuli together with the feedback enabled CN and DH to develop a stable response criterion quickly without ever receiving feedback with random-dot stimuli. Unlike the training stimuli, the stimuli in Expt 3 were brief (400 msec), the rotation and translation rates were varied, and the random-dot layout was rerandomized on a trial-by-trial basis. Therefore, any simple trial-by-trial association between stimuli and rewarded responses learned during training would be of minimal benefit during Expt 3.

RESULTS

Experiment 1: Confirming the need for depth in the layout

Methods. We simulated 3 sec (45 frames at 15 Hz) of curvilinear motion (translation rate of 2 m/sec and yaw rotation at rates up to 2 deg/sec) towards two different layouts: a single frontoparallel plane or two such planes at different depths. The two observers (LS and JP), while not naïve, were not yet highly practiced in heading estimation when this experiment was run.

In the double-plane condition, one vertical plane was located at 12.5 m from the observer and the other at 25 m (both perpendicular to the line-of-sight) at the start of the trial. Approximately 336 points were visible at the start of each trial (168 on each plane). In the single-plane condition, a single vertical plane of points was located at 12.5 m at the start of the trial. The points were randomly distributed on the image plane with approximately 250 points visible at the start of the trial. Examples of flow fields generated by the single- and double-plane stimuli under either pure translation or curvilinear motion (rightward yaw rotation) are shown in Fig. 1. Heading direction is along the line of sight (towards the cross) in all four panels. Note, however, that in the lower panels [Fig. 1(C and D)], the singularity (open circle) is displaced rightward, in the rotation direction. In the single-plane condition [Fig. 1(C)], a single singularity, very similar to a simple FOE shifted to the right, is largely indistinguishable from a true rightward heading.* In the double-plane condition [Fig. 1(D)], rotation produces a singularity for each of the two planes. The singularity of the closer plane is indicated by the open circle while that of the further plane is shifted further to the right and is not visible as it is outside the field of view. The two issues being investigated in Expt 1 are: (1) in response to a sequence of flow fields such as those in Fig. 1, can observers see that they are going straight-ahead or do they believe they are headed towards the singularity; and (2) is their ability to make this distinction different for the two stimuli shown in Fig. 1(C and D)? In particular, we wish to determine if previous findings related to point (2) are applicable to the curvilinear scenario.

We measured perceived straight-ahead for both the single- and double-plane layouts with rotations ranging from −2 to +2 deg/sec in steps of 0.5 deg/sec. Because of the large number of conditions (9 rotations × 2 layouts = 18), the experiment was split into a set of four separate runs with five conditions each to reduce the number of trials per run, while keeping layout and rotation counterbalanced: each run had four conditions balanced for rotation direction (two left, two right) plus one additional zero-rotation condition, three rotation rates (either 0, 0.5, and 1 deg/sec, or 0, 1.5, and 2 deg/sec), and either three single- and two double-plane layouts or vice versa. Additional conditions reported elsewhere were also included (Perrone & Stone, 1991; Stone & Perrone, 1991). The set of four runs was repeated three or four times to produce the data shown in Fig. 4.

Results. Figure 4 shows two plots of perceived straight-ahead as function of simulated rotation rate in both the single- (open squares) and double-plane (solid squares) conditions for the two observers. The locations of the headings that would make the singularity of the closer plane appear straight-ahead at the beginning and end of the trial are shown by the steeper and shallower dashed lines, respectively. Perfect heading estimation is indicated by the solid horizontal line. In the single-plane condition, perceived straight-ahead for both observers lies approximately in the middle of the singularity range. This suggests that both observers were unable to distinguish true heading from the singularity and that they responded to the location of the singularity near the midpoint of the trial.

Both observers performed better in the double-plane condition. One observer (JP) showed heading consistently biased towards the direction of the rotation, but these errors were less than half those in the single-plane condition, and always less than those predicted by the strategy of responding to the singularity of the closer plane at the end of the trial. Responding to the singularity earlier in the trial or to the singularity of the more distant plane would produce even larger errors. The other observer (LS) showed asymmetric responses to rightward and leftward rotations. For left rotations, LS showed performance similar to that of observer JP. For rightward rotations, LS showed nearly veridical performance.

Conclusions. These results indicate that humans are able to compensate, at least partially, for the rotation in estimating heading during simulated curvilinear motion towards the double-plane layout. However, they show no evidence of this ability for motion towards the single-plane layout. We conclude, for the restricted field-of-view (30 by 22 deg) used, that (1) humans require variation in the distance of the points in the layout to distinguish rotational from translation flow during curvilinear motion; and (2) when provided with such depth

*As the field of view increases, the flow field becomes increasingly different from a shifted expansion pattern. Perhaps, for a sufficiently large field of view, observers might be able to distinguish straight-ahead translation plus rightward rotation [e.g., Fig. 1(C)] from a true rightward heading.

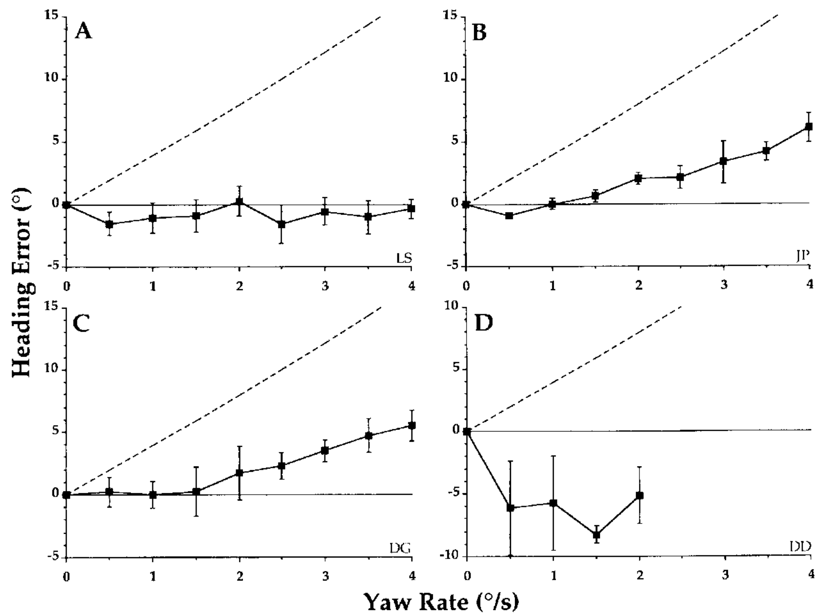

FIGURE 5. Heading error for the four observers in Expt 2. The solid horizontal line indicates perfect performance and the dashed lines performance predicted from responding to the closer singularity at the end of the trial. Error bars represent the standard deviation of the average over rightward and leftward conditions and over three or four runs. (A) Data for observer LS. (B) Data for observer JP. (C) Data for naïve observer DG. (D) Data for naïve observer DD (note that the y-axis is shifted).

variation, they can estimate their heading with errors <5 deg in the presence of 2 deg/sec of yaw. If they merely confused their heading with the nearer singularity at mid-trial, one would expect errors for 2 deg/sec to be ~10 deg as was found in the single-plane condition. These results confirm those of others (Rieger & Toet, 1985; Warren & Hannon, 1988, 1990), who have previously shown that distance variation in the layout is needed to estimate heading in the presence of rotation, and extend them to our curvilinear scenario. However, Expt 1 and these previous studies used low rotation rates, at or below 2 deg/sec. To examine the question of whether visual heading estimation can be performed at rotation rates >2 deg/sec, without oculomotor or static depth cues, we performed two more experiments using higher rotation rates and naïve observers.

Experiment 2: Higher rotation rates at fixed translation rate

Methods. The stimuli consisted of 2.33 sec of 2 m/sec curvilinear motion towards two sets of vertical half-planes above and below the horizontal meridian. The layout was, therefore, merely the double-plane condition of Expt 1 with a gap along the horizontal meridian (height jittered around 6 deg) to allow easier fixation. Another effect of the gap was that the singularities were no longer visible: their extrapolated locations were always along the horizontal meridian. As in Expt 1, at the onset of the trials, the closer two half-planes were at 12.5 m while the more distant half-planes were at 25 m. Three observers (including one naïve) were tested with rotation rates from 0 to 4 deg/sec in steps of 0.5 deg/sec. Because of the large number of conditions (including some not reported here), as in Expt 1, the experiment was split into a set of eight shorter runs. Initially only rotation rates of 0.5, 1.0, 1.5, and 2 deg/sec were tested. Subsequently, we tested 2.5 and 3 deg/sec, and finally 3.5 and 4 deg/sec. Observers therefore had more experience by the time they were tested with the rotation rates above 2 deg/sec. An additional naïve observer (DD) was only tested with rotation rates between 0 and 2 deg/sec (in a set of four runs). The runs were repeated three or four times to yield the data shown in Figs 5–6.

Results. Taking advantage of the exact symmetry of the leftward and rightward conditions, Fig. 5 plots heading error (see General Methods) as a function of rotation rate for the four observers, with positive errors indicating biases in the direction of the rotation. The heading error that would result from confusing heading with the extrapolated location of the closest singularity at the end of the trial is shown as a dashed line. Responding to this singularity would be the best simple singularity-based strategy, as the singularity is further away from the heading point earlier in the trial and the singularity of the more distant half-planes is even further out. The solid horizontal line indicates perfect heading estimation. Three of the four observers performed the task reliably. Two of these three observers (JP and DG) showed small positive errors which increased with increasing rotation rate but remained about one-third of those expected from

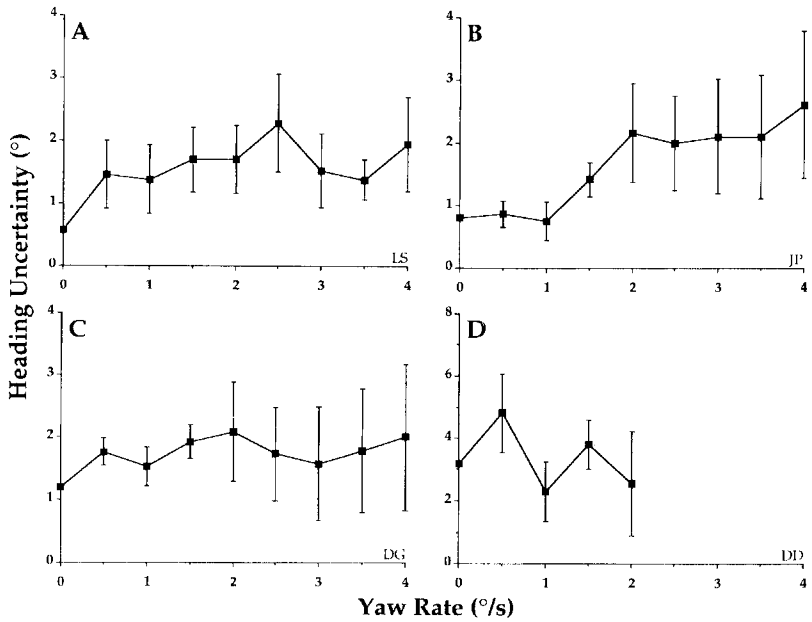

FIGURE 6. Heading uncertainty for the four observers in Expt 2. Error bars represent the standard deviation of the average over rightward and leftward conditions and over three or four runs. (A) Data for observer LS. (B) Data for observer JP. (C) Data for naïve observer DG. (D) Data for naïve observer DD (note that the y-axis scale is compressed by a factor of 2).

responding to the nearest singularity. The last of these three observers (LS) showed even smaller errors, largely unrelated to rotation rate. One of the four observers (DD) showed large biases away from the direction of rotation and considerable variability, suggesting an unstable response criterion.

At 4 deg/sec of yaw, the location of the closer half-plane's singularity was 22.6 deg at the middle of the trial, while the average (unsigned) heading error for the three reliable observers ($\pm$SD) was 4.0 ± 3.1 deg [Fig. 5(A, B, C)]. Therefore, their errors were, on average, $\sim$5 times smaller than if they were simply responding to the singularity at mid-trial, as two of them (LS and JP) apparently did in the single-plane condition of Expt 1 (Fig. 4, open squares). However, their heading errors were larger than in the no-rotation condition (average unsigned error 0.5 ± 0.5 deg).

Figure 6 shows plots of the heading uncertainty (see General Methods) as a function of rotation rate. The three observers (LS, JP, and DG) who made reliable heading judgments made relatively precise heading judgments, even at rotation rates as high as 4 deg/sec. The average uncertainty for these three observers was 2.2 ± 0.4 deg at 4 deg/sec of yaw. In the no-rotation condition, it was only 0.9 ± 0.3 deg, which is similar to that found previously by others (Warren *et al.*, 1988). Subject DD [Fig. 6(D), note scale difference] showed higher uncertainty in all conditions, including the no-rotation case.

Conclusions. All four observers made heading judgments unlike those expected if they were simply unable to distinguish rotational from translational flow and responded to the closest singularity as if it were an FOE. Three of the four observers made relatively precise (<3 deg uncertainty) and accurate (<6 deg bias) judgments at all rotation rates tested (up to 4 deg/sec) without the benefit of a rotation signal from either the oculomotor system or static depth cues, although not as precise and accurate as in the no-rotation condition (uncertainty and bias $\sim$1 deg).

In both Expts 1 and 2, the display system could not generate a frame rate higher than $\sim$15 Hz. This likely led to small but potentially visible temporal quantization artifacts. Furthermore, the stimuli lasted several seconds, so significant temporal integration could have contributed to performance accuracy and precision. Finally, in Expt 2, the gap was part of the layout so its height increased during the trial. Although the increase in gap-height did not provide a direct heading cue, it did provide information about forward speed which could indirectly have facilitated heading estimation. To eliminate these potential problems, we therefore performed a third experiment using a faster (76 Hz refresh rate) display system.

Experiment 3: Higher rotation rates with covarying translation rates

Methods. The stimuli consisted of 400 msec of simulated curvilinear motion towards two sets of frontoparallel planes. For three of the four observers (all but DG), a 45 by 6 deg virtual mask, equiluminant with the background, was placed over the horizontal

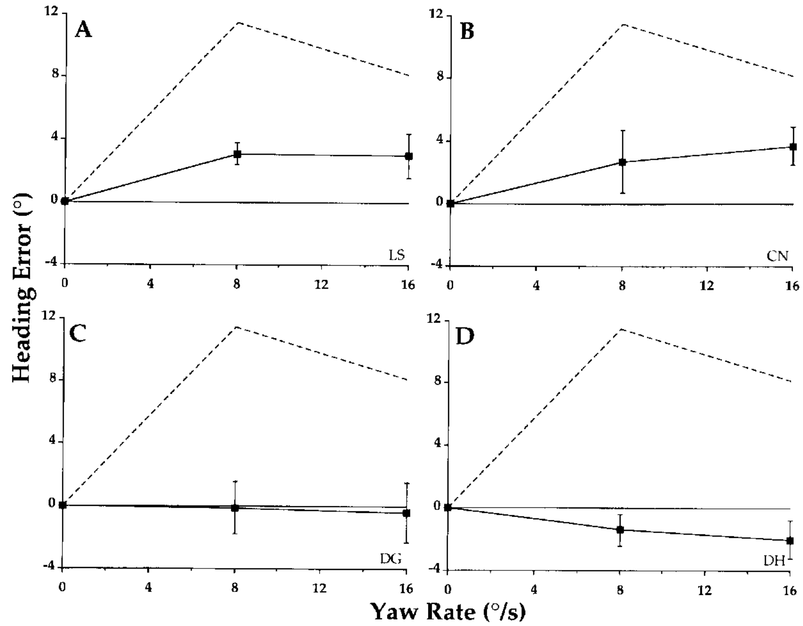

FIGURE 7. Heading error for the four observers in Expt 3. The solid horizontal line indicates perfect performance and the dashed lines performance predicted from responding to the closer singularity at the end of the trial. Error bars represent the standard deviation of the average over rightward and leftward conditions and over two to five runs. (A) Data for observer LS. (B) Data for naïve observer CN. (C) Data for naïve observer DG. (D) Data for naïve observer DH.

meridian. This had the same effect as the gap in Expt 2, except that the mask did not change size during the trial. At the onset of the trials, the closer plane was at 14.4 m, while the more distant plane was at 26.4 m. Four observers (including three naïve) were tested with six interleaved conditions: (1) −16 deg/sec of rotation and 16 m/sec of translation; (2) −8 deg/sec and 8 m/sec; (3) 0 deg/sec and 16 m/sec; 4) 0 deg/sec and 8 m/sec; (5) +8 deg/sec and 8 m/sec; and (6) +16 deg/sec and 16 m/sec, with positive rotation indicating rightward yaw. Two to five repeated runs were performed to yield the data in Fig. 7. The purpose of this experiment was to test higher rotation rates, to use brief presentations to minimize temporal integration, to use a 45 deg FOV to enhance performance, to use a 76 Hz refresh rate to make temporal quantization artifacts invisible, and to eliminate the "growing" gap.

Results. Figure 7 plots heading error as a function of rotation rate for all four observers. The dashed lines indicate the performance predicted by a strategy of responding to the singularity of the closer plane at the end of the trial. The solid horizontal line indicates perfect heading estimation. All observers tested were able to make heading judgments with better than 4 deg of accuracy, even with a stimulus presentation of only 400 msec, despite rotation rates as high as 16 deg/sec. Observers LS and CN showed small biases towards the direction of the rotation [Fig. 7(A, B)] while observers DG and DH showed small biases away from the direction of the rotation [Fig. 7(C, D)]. The location of the singularity of the closer plane at mid-trial was 13.3 and 11.5 deg for the 8 and 16 deg/sec conditions, respectively. The average (unsigned) heading error (±SD) for the four observers was 1.8 ± 1.3 and 2.3 ± 1.5 deg at 8 and 16 deg/sec, respectively, or ~5 times smaller than that predicted from responding to this mid-trial singularity, as observers apparently did in the single-plane condition of Expt 1 (Fig. 4, open squares). However, the average (unsigned) error in the no-rotation condition was even smaller (0.4 ± 0.1 deg). The average uncertainty (±SD) was 1.1 ± 0.8, 3.7 ± 0.8 and 3.2 ± 1.0 deg at 0, 8, and 16 deg/sec, respectively.

To examine the possibility that the fixation cross was influencing our results, we ran an additional control experiment on two observers (LS and CN) with the ±16 deg/sec conditions, but extinguished the fixation cross 500 msec before the onset of the flow-field stimulus. The results were qualitatively unchanged. The average (unsigned) heading error was 1.8 deg and average uncertainty was 2.1 deg, showing that our basic finding does not depend on the presence of a fixation cross.

Conclusions. Our observers were able to make relatively accurate (<4 deg errors) and precise (<4 deg uncertainty) heading estimates during simulated curvilinear motion, even when the rotation rate was as high as 16 deg/sec. This shows that accurate human visual heading estimation is not limited to conditions with rotation rates below ~1 deg/sec. This finding is consistent with the theoretical expectation that, for a fixed

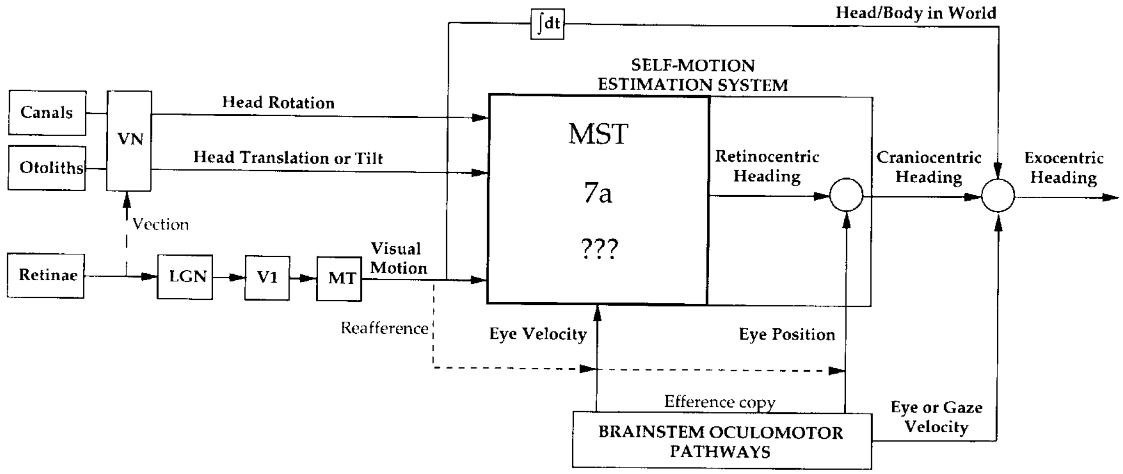

FIGURE 8. Multisensory fusion underlying human self-motion perception. This diagram illustrates the potential contributions of visual, vestibular, and oculomotor signals in primate heading estimation. Note that visual signals are in retinocentric coordinates at least up to area MT, while vestibular information is craniocentric. To facilitate the combination of vestibular and flow-field heading information, visual signals might be converted to craniocentric coordinates using an eye-position signal. Given that eye-position modulation of visual-motion responses has been found both in areas MST and 7a, as well as vestibular signals, perhaps the retino-to-craniocentric transformation occurs within MST or 7a concurrently with the incorporation of non-visual signals. Additional signals are necessary to convert instantaneous craniocentric heading into the exocentric information most likely needed for navigation. VN, vestibular nucleus; LGN, lateral geniculate nucleus; V1, primary visual cortex; MT, middle temporal cortex; MST, medial superior temporal cortex.

layout, the ratio of rotation to translation rates rather than the absolute rotation rate should limit precision (Koenderink & van Doorn, 1987) and with preliminary results in experiments where we varied this ratio (Stone & Perrone, 1996; see also Turano & Wang, 1994).

DISCUSSION

Multimodal strategies for self-motion estimation

In the real world, human self-motion estimation is a multisensory task with possible contributions from a number of visual, vestibular, oculomotor, and even auditory and proprioceptive inputs (Fig. 8). In addition to flow-field information, the visual system could use disparity (van den Berg & Brenner, 1994a), perspective or texture gradients (van den Berg, 1992; van den Berg & Brenner, 1994b), and cognitive cues (Vishton & Cutting, 1995) to support navigation. The vestibular system could also provide separate measures of both self-rotation and self-translation (albeit confounded with tilt with respect to gravity) from the canals and otoliths, respectively (Goldberg & Fernandez, 1971; Fernandez & Goldberg, 1976).* Information about eye-movements could be derived from the visual system (reafference) and/or from the oculomotor system (efference copy) (von Holst, 1954). The auditory system might provide cues about motion (e.g. Lackner, 1977) and/or displacement with respect to localized stationary sound sources (for a review, see Middlebrooks & Green, 1991). Proprioception might also contribute by providing head/neck or body motion information (e.g. Hlavacka *et al.*, 1992). We and others have previously suggested that at least some of this multimodal self-motion information might be combined in area MST or 7a (see Perrone & Stone, 1994). Although a study of the effects of lesions and/or microstimulation of MST and 7a on heading estimation will be needed to test the above hypothesis directly, there is, nonetheless, considerable evidence for oculomotor (Newsome *et al.*, 1988; Erickson & Thier, 1991; Bremmer & Hoffmann, 1993; Duffy & Wurtz, 1994), vestibular (Kawano *et al.*, 1984; Thier & Erickson, 1992), and disparity (Roy & Wurtz, 1990), as well as visual-motion signals within MST. To facilitate this sensory fusion, visual information could be transformed from retinocentric (eye-centered) coordinates in which visual motion is encoded in the retinae through area MT (for a review see Maunsell & Newsome, 1987) into craniocentric (head-centered) coordinates in which vestibular and auditory inputs are coded. For navigation through a complex environment, heading information might ultimately be further converted from craniocentric into exocentric (world-centered) coordinates to generate estimates of future paths using oculomotor signals related to eye or gaze velocity (Newsome *et al.*, 1988; Stone & Lisberger, 1990), integrated proprioceptive or vestibular signals (Israël & Berthoz, 1989; Brotchie *et al.*, 1995), higher-order visual-motion information (Rieger, 1983), integrated flow-field information (Warren *et al.*, 1991a), or displacement with respect to identified landmarks (Vishton & Cutting, 1995).

*Preliminary observations using oscillations in the *xz*-plane in darkness suggest that human heading estimation using vestibular cues is imprecise (Stone and Tomko, unpublished results).

If a retino-to-craniocentric coordinate transformation occurs along the primate visual-motion processing pathway, it is not clear where. However, there is recent evidence that eye position can significantly modulate responses in both MST (Bremmer & Hoffmann, 1993) and area 7a (Siegel & Read, 1994). It has been shown that such modulation could be used to perform a retino-to-craniocentric transformation (Andersen *et al*., 1985). If MST and/or 7a are in fact involved in heading estimation, these recent findings suggest that the retino-to-craniocentric transformation may occur prior to, or concurrently with, heading estimation. This scenario is represented by the thin-lined extension of the self-motion estimation system in Fig. 8. Recently, evidence for a cranio-to-exocentric coordinate transformation has been found in posterior parietal cortex with the discovery of neurons whose responses are modulated by both eye and head-position, such that collectively they could encode location in exocentric coordinates (Brotchie *et al*., 1995).

Retinocentric vs exocentric heading

Current computational models of human heading estimation are limited to estimating the instantaneous retinocentric heading from a single flow field (e.g. Rieger & Lawton, 1985; Heeger & Jepson, 1992; Hildreth, 1992; Perrone, 1992; Lappe & Rauschecker, 1993; Perrone & Stone, 1994). We have, therefore, designed our stimulus paradigm to measure the ability of humans to estimate instantaneous retinocentric heading from optic flow under circumstances similar to those used to test models. Our data are qualitatively consistent with the above models. Rieger (1983, p. 339), however points out that "the instantaneous direction of motion (tangential to a curved path of observation) tells an observer little about his motion relative to the environment". Additional information beyond a single flow field is needed to estimate exocentric heading or one's path through the environment.

Although the visual information that could be used to judge exocentric heading has been examined (e.g. Rieger, 1983; Warren *et al*., 1991a,b; Cutting *et al*., 1992; Royden, 1994; Vishton & Cutting, 1995), no general computational model of human exocentric heading estimation from optic flow has as yet been proposed, although the issue of temporal integration has been addressed in the machine-vision community (e.g. using Kalman filtering). The problem is two-fold. First, given that the same instantaneous flow field can be produced in a number of possible scenarios, visual processing across time is needed to distinguish visually between rotational flow caused by a curved path and that caused by an eye movement. Second, even if one can determine that one is on a curved path (as opposed to translation + eye-rotation) visually or otherwise, exocentric heading along a curved path is inherently ambiguous as it changes over time and depends on a world reference point.

The actual conditions under which humans can disambiguate translation + eye-rotation from motion along a curved path have been investigated (Warren & Hannon, 1988, 1990; Royden *et al*., 1992, 1994), but this question is orthogonal to the issue of how and if the flow field is visually processed accurately. It is distinctly possible that human visual cortex has the capacity to process instantaneous flow fields accurately to yield retinocentric heading by integrating noisy motion information from across the visual field, yet lacks the necessary machinery to keep track of the small differences in the trajectories of individual points over time or the small differences in local velocity necessary to discriminate between optic flow generated by a curved path and that generated by translation + eye-rotation. Therefore, despite our observers' ability to estimate their retinocentric heading, it is unclear if they recovered their exocentric trajectories accurately. However, a previous study (Warren *et al*., 1991b) provides evidence that some observers can estimate exocentric (circular) heading with <2 deg of bias during curvilinear motion (rotation rate <2.7 deg/sec) through a random cloud of points with retinocentric heading fixed along the line-of-sight and practice trials with feedback.

Because current models estimate retinocentric heading, distinguishing between retinocentric and exocentric heading is particularly important when testing models. Direct comparisons of simulations of *retinocentric* heading models with human *exocentric* heading perception (Banks *et al*., 1996; Crowell, 1996) are inappropriate, unless one further postulates how retinocentric heading might be transformed into exocentric judgments. Royden (1994) did such an analysis and showed that the earlier apparently large errors (Royden *et al*., 1992, 1994) could indeed be explained by a veridical flow-field analysis, followed by an exocentric judgment based on the assumption of a curved path (see her Fig. 5), yet could not be quantitatively explained by an extra-retinal model which relies on an eye-velocity signal to remove rotation (see her Fig. 3). While these analyses do not prove that the flow field is processed accurately, they illustrate how data on exocentric heading judgments have not resolved the issue.

Advantages of our stimulus paradigm

We chose the curvilinear paradigm for a number of reasons. First, it generates little visual–oculomotor conflict (except with vergence and accommodation). During actual curvilinear motion, eye position remains stationary in the head and our observers maintained fixation straight-ahead.* Therefore, if the oculomotor system plays a role in our judgments (see below), it would provide synergistic rather than conflicting information. Second, we asked observers to judge their retinocentric heading, which remains constant during curvilinear motion, but varies during the translation + eye-movement scenarios used by others (e.g. Rieger &

*Strictly speaking, to be sure that fixation was properly maintained, one would need to monitor eye position. However, the gap and fixation cross make it likely that fixation was indeed well maintained.

Toet, 1985; Cutting, 1986). Therefore, observers are not required either to track mentally a moving heading nor to convert the visual retinocentric information into exocentric coordinates. Furthermore, if heading estimation is actually performed in craniocentric coordinates, because there is no oculomotor conflict, the available eye-position signal (which reported fixed straight-ahead gaze) could support an accurate conversion back to retinocentric coordinates. Third, our stimuli contained no static depth cues. The double-plane layout provides no static information about the relative depths of our random points (i.e., individual frames have no depth information). Fourth, unlike a random-cloud layout, the double-plane layout allows a direct quantitative comparison of the errors expected from 2D singularity-based strategies and actual human performance, and ensures a sufficient number of close points.

Caveats

While we wished to make conclusions about the use of instantaneous flow fields in heading estimation and therefore made our presentation brief (400 msec in Expt 3), our stimuli were in fact sequences of flow fields. Observers therefore could have either integrated instantaneous heading information over time or performed a more sophisticated spatio-temporal analysis. The initial flow field might only allow an uncertain estimate of heading which is then made more precise over time as additional flow-field information arrives and is processed. However, we have preliminary evidence that precise heading judgments can be made with only 250 msec presentations (Stone & Perrone, 1991) and, in Expt 3, we found apparently asymptotic performance at 400 msec. Therefore, if such temporal processing is occurring, its integration time is short.

Although the data in Fig. 3 suggest that perceived heading is a monotonic function of actual heading, our staircase procedure only measures one point on this curve, perceived straight-ahead (the x-intercept). We have presented no data related to the slope of the curve and cannot be sure it is near one. Our data merely show that the x-intercept is near zero. Future experiments using a pointer or a reference direction off of the line-of-sight will be necessary to measure the whole curve.

Most studies of human "visual" heading estimation, including this one, have used pure visual stimuli to simulate self-motion and to isolate, supposedly, the visual-motion contribution. Unfortunately, our results and those of others must be interpreted with caution because we have actually measured heading estimation in a visual–vestibular conflict situation: our observers' canals and otoliths told them that they were, in fact, not moving. There was also visual–visual conflict with disparity (because binocular viewing was used) and looming cues, as well as conflict with vergence and accommodation signals. Although we have focused in this study on the visual contributions to heading estimation, sensorimotor conflict may have influenced our observers' responses.

Task difficulty

Our task was difficult and required practice. There are at least three possible causes: (1) we did not provide trial-by-trial feedback (the standard method for establishing stable criteria); (2) the FOV of our display was restricted; and (3) the difficulty was inherent to our paradigm.

It is critical not to provide trial-by-trial feedback so that observers cannot use a simple 2D lookup-table strategy to respond accurately. It is equally critical that observers be given the chance to develop a stable criterion. For instance, our naïve observers were initially confused by the fact that they could be translating instantaneously leftward along a path that curves to the right. While their retinocentric heading remained constant, their exocentric heading could indeed become more rightward over time. It therefore remains unclear whether DD has an inherent and insurmountable difficulty in performing the task, or merely remained unsure about the retinocentric nature of the task. Although in the experiments presented here, five of the six observers tested were able to perform well, we have subsequently found more observers whose performance is unreliable. We have no clear explanation for the observed inter-subject variability and are presently examining training paradigms to explore whether more reliable performance can be obtained from all observers given sufficient practice.

The limited FOV of our set-up may have contributed to the difficulty of the task and to the inter-subject variability. Observers experienced variable amounts of vection (visually driven sense of movement) and their performance therefore may have been differentially affected by vestibular conflict. Poor performers were perhaps not visually challenged, but rather unable to ignore the conflicting lack of vestibular input. The use of larger FOVs would likely reduce the severity of this potential problem by increasing both translational (Telford & Frost, 1993; but see also Andersen & Braunstein, 1985) and rotational (Post, 1988; Stern *et al.*, 1990) vection. Vection is likely caused by the confusion of subcortical visual and vestibular signals as early as the vestibular nucleus (Daunton & Thomsen, 1979; Henn *et al.*, 1980). If vection were experienced more consistently, perhaps performance would improve, as conflicting vestibular signals would be suppressed prior to their arrival in cortex (Fig. 8).

It could be argued that heading is more naturally perceived exocentrically. If heading perception is indeed experienced exclusively in exocentric coordinates, then it might be difficult to convert it back to retinocentric coordinates. The conflict between the visually simulated head/body rotation and the lack of vestibular stimulation might further hamper conversion back to egocentric coordinates (Fig. 8). However, this explanation is not supported by previous studies of circular exocentric heading estimation (Warren *et al.*, 1991a,b) which found that up to 25% of observers were unable to perform the task. This suggests that the retinocentric nature of our task is not the culprit.

Finally, it is also possible that the task was difficult because humans do not have the capability to process flow fields produced by arbitrary combinations of rotation and translation. However, they could use their ability to process a wide (but incomplete) range of rotation/translation combinations to make relatively accurate heading estimates, even when confronted with a flow field outside the repertoire of those that can be processed perfectly. We have previously proposed that human flow field processing for heading estimation might be specialized for that subset of flow fields generated during gaze-stabilization (Perrone & Stone, 1994) and have shown that the performance of this template model decays gracefully for non-gaze-stabilized flow fields and can yield performance consistent with our data (Figs 10 and 13 of Perrone & Stone, 1994).

The role of the flow field

The literature contains conflicting conclusions as to whether humans can indeed estimate heading from a flow field that contains rotational flow without the benefit of other visual or non-visual cues. Early studies that addressed this issue found evidence that humans can indeed do so in the translation + pursuit and translation + gaze-stabilization cases. Rieger and Toet (1985) simulated translation towards one or two vertical planes combined with simulated pursuit in a random direction. They found that humans could estimate their retinocentric heading accurately in the double- but not the single-plane condition. Rotation rates, however, were at or below 1.8 deg/sec and retinocentric heading changed over time. Warren and Hannon (1988, 1990) similarly showed that humans can in fact estimate exocentric heading during visually simulated translation + gaze-stabilization as long as there is depth variation in the layout. However, they only tested rotation rates at or below 0.7 deg/sec. Cutting (1986) also found that humans could make precise retinocentric heading judgments (thresholds <4 deg) during simulated translation and curvilinear motion plus gaze stabilization, but the retinocentric heading was changing over time, there was no vertical component to optic flow, and rotation direction provided a heading cue. In addition, in all of these studies, observers were given practice trials with trial-by-trial feedback, so the results are open to the criticisms discussed previously.

More recently, investigators have argued that either extra-retinal or depth information is needed for accurate visual heading estimation. Banks and colleagues (Royden *et al.*, 1992, 1994; Banks *et al.*, 1996) have argued that humans require oculomotor information for accurate heading estimation during translation plus eye movements. Their observers were asked to make exocentric heading judgments in translation+eye-rotation conditions using either real or simulated eye movements to generate the rotational flow. They reported large errors (up to ~18 deg) in heading estimation in the simulated eye-movement condition but only small errors (< ~4 deg) in the actual eye-movement condition (Royden *et al.*, 1992, 1994). They originally concluded (abstract, Royden *et al.*, 1992) that "humans require extra-retinal information about eye-position to perceive heading accurately in the presence of rotation rates >1 deg/sec". They later pointed out (Royden *et al.*, 1994) that a conflicting oculomotor cue, signaling no eye movement, might have hampered performance in the simulated eye-movement condition, so their results are not conclusive on this issue.

van den Berg (1992) examined the role of static depth cues in visual heading estimation and concluded (abstract, van den Berg, 1992) that "recognizable points at infinity (like the horizon) appear essential for robust heading perception in the presence of ego-rotations". He compared exocentric heading estimation during simulated gaze-stabilized motion over a ground plane which provides a wealth of static visual cues (a horizon at or near infinity, *a priori* knowledge that all points are constrained to lie in a plane, a texture gradient that indicates relative depth because dot density increases with depth) with that through a cloud of random points which provides no extra-flow-field cues. He argued that static cues are needed because "using translation through a cloud of points, most observers can determine their heading direction relative to their environment with little precision or not at all" (van den Berg, 1992, p. 1293). This statement is at odds with the no-noise data in his Fig. 7. Without added noise, the precision of both naïve observers tested appears statistically indistinguishable in the cloud and ground-plane conditions and ranged from 2 to 4 deg in the cloud condition for all three observers. In a subsequent experiment using disparity cues for depth, van den Berg and Brenner (1994a) again conclude that "(w)ithout static depth information, visual heading judgements are more vulnerable to noise and the confounding effects of eye and head rotation" (p. 702). While their data do support the first point, again they do not support the latter. In fact, with the lowest added noise, all three observers showed no reliable difference in either precision or accuracy between performance in the stereo and non-stereo cloud conditions (their Fig. 3).

The accurate and precise exocentric heading judgments during the simulated eye-movement conditions (with up to ~4 deg/sec of rotation) for self-motion through a cloud in these experiments of van den Berg and colleagues (van den Berg, 1992; van den Berg & Brenner, 1994a) are in conflict with those of Royden *et al.* (1992, 1994). A recent attempt to reconcile this discrepancy (Fig. 12a; Banks *et al.*, 1996) is unconvincing for two reasons. First, Banks and colleagues only compare their data with the worst observer from van den Berg and Brenner (1994a). The other two observers' appeared to show little systematic error at any rotation rate in the range ± ~4 deg/sec, although intercept data were unfortunately not provided. Second, their data on simulated eye-rotation plus translation through a 3D cloud (Banks *et al.*, 1996), show much smaller errors (~6–8 deg at 5 deg/sec) than the ~15–18 deg at 5 deg/sec reported in their earlier studies (see Royden *et al.*, 1994, Fig. 13). Although the different conditions and observers may be the explanation, recently, Banks and colleagues (Ehrlich *et al.*, 1996) have shown that a wide range of error values can be obtained simply by manipulating the distance of the reference probe. This illustrates the difficulty in the quantitative interpretation of exocentric data.

In summary, our results and those of others (Rieger & Toet, 1985; Cutting, 1986; Warren & Hannon, 1988, 1990; van den Berg, 1992; van den Berg & Brenner, 1994a) support the view that neither oculomotor nor static depth cues (from either perspective or disparity) are *necessary* to provide the rotational signal for accurate retinocentric heading estimation.

The role of oculomotor signals

Our data should not be construed to suggest that oculomotor signals do not play an important role in human heading estimation. Indeed the presence in MST of eye-movement signals (Newsome *et al.*, 1988; Erickson & Thier, 1991; Duffy & Wurtz, 1994) together with visual-motion responses ideal for processing self-motion (Saito *et al.*, 1986; Tanaka *et al.*, 1986, 1989; Tanaka & Saito, 1989; Roy & Wurtz, 1990; Duffy & Wurtz, 1991a,b, 1995; Orban *et al.*, 1992; Graziano *et al.*, 1994; Stone & Perrone, 1994) argue strongly for such a role. Our findings do not even rule out a direct role for oculomotor signals in retinocentric heading estimation. An input signaling ~0 deg/sec eye velocity may have influenced the visual processing of our stimuli. Nonetheless, under our curvilinear conditions, because eye velocity was ~0 deg/sec but simulated rotation was up to 16 deg/sec, simply vector-subtracting the eye-velocity signal from the flow field and then locating the resulting singularity would have generated performance equal to or worse than that shown by dashed lines in Figs 5 and 7.

Previous studies of exocentric heading judgments have not determined the exact role of oculomotor inputs. Regardless of where cortical heading signals are converted into exocentric coordinates, current exocentric experimental designs do not distinguish between oculomotor inputs at the level of the retinocentric flow-field analysis from those at the level of the transformation from retinocentric to craniocentric and exocentric coordinates: exocentric heading is downstream from both (Fig. 8). However, recent findings (Warren *et al.*, 1996) show that putting recognizable objects in the layout supports accurate exocentric heading estimation during simulated eye movements, suggesting that oculomotor information is not *required*, even for exocentric judgments.

Banks and colleagues (Banks *et al.*, 1996) argue for a direct role of oculomotor signals in the flow-field processing. They conclude that their data are inconsistent with retinal-image models and most consistent with an extra-retinal model in which rotational flow is subtracted using an extra-retinal signal. They claim that, for an extra-retinal model, "(i)t is a relatively simple matter to subtract the indicated rotational flow, compute the translational flow components, and then estimate heading" (p. 432), presumably using a flow-field model which assumes no rotational flow such as that proposed by Hatsopoulos and Warren (1991). However, the view that rotational flow is exclusively handled by subtracting an oculomotor signal would lead to heading being confused with the singularity during simulated rotation. This view is at odds with our data as well as those of others (Rieger & Toet, 1985; Warren & Hannon, 1988, 1990; van den Berg, 1992; van den Berg & Brenner, 1994a). Our findings do not prove that eye-velocity is not subtracted from the flow field, nor do they preclude other direct effects of an eye-rotation signal on flow-field processing such as the eye-velocity weighting of heading detector responses (Perrone & Stone, 1994). They merely revive those retinal models that Banks and colleagues (Banks *et al.*, 1996) deemed inconsistent with their data and rule out visual models that ignore rotation (e.g. Hatsopoulos & Warren, 1991). Considering that rotational flow is introduced without a concurrent oculomotor eye-rotation signal whenever a human moves along a curved path or if the oculomotor signal is imperfectly calibrated, it is not surprising that humans would have this visual ability. Oculomotor signals may also assist in the proper conversion from retinocentric to exocentric coordinates. While the findings of Banks *et al.* (1996) show that such an oculomotor signal cannot merely be a binary (eye movement vs curved path) trigger, they do not rule out more elaborate versions of the conversion hypothesis.

In summary, Banks and colleagues (Royden *et al.*, 1992, 1994; Banks *et al.*, 1996) have found evidence that oculomotor signals play a role in exocentric heading estimation. However, except possibly for their single-plane experiment (Royden *et al.*, 1994), their data do not resolve the issue of whether oculomotor inputs play that role in the determination of retinocentric heading from the flow field or in the conversion from retinocentric to exocentric coordinates or both.

Alternate hypotheses

While a parsimonious explanation of our results is that our observers used a visual algorithm to make relatively accurate estimates of their retinocentric heading directly from the flow field (e.g. Perrone, 1992; Lappe & Rauschecker, 1993; Perrone & Stone, 1994), there are other possible explanations.

First, observers could have estimated their axis of rotation and determined whether it was in front or behind them, albeit to the side [see Fig. 2(A, B)]. Such a strategy would require knowing that their path was exactly circular (i.e., had a single center of rotation), a fact not given to our naïve observers. Furthermore, it would yield better performance at higher rotation rates as the axis would be closer and the distance between centers of rotation larger for the same step in heading angle. We and others (Warren *et al.*, 1991b), however, observed the opposite trend.

Second, observers could have estimated their exocentric heading and worked backwards to generate their retinocentric heading. Although we eliminated static depth cues from our stimulus and used a random layout, because the random structure of our layout did not change over time (i.e., the same random dots remained present throughout a given trial), *dynamic* depth estimation (from the accurate processing of the flow field, e.g. Heeger & Jepson, 1992; Perrone & Stone, 1994) could have supported accurate heading estimation from exocentric displacement over time. The finding of successful exocentric heading estimation with short dot lifetimes argues against this possibility (Warren *et al.*, 1991a; van den Berg & Brenner, 1994a).

Third, observers might ignore our instructions and make exocentric judgments using an approach proposed by Royden (1994), whereby exocentric heading is estimated without extracting the 3D self-motion parameters from the flow field. This algorithm finds the largest flow vector on the vertical meridian at mid-trial, determines its intersection with the horizontal meridian, computes the angle between the intersection point and the line of sight, and divides this angle by two (her Fig. 6). This *ad hoc* algorithm depends critically on the assumed depth of the point that generated the original flow vector and it is difficult to believe that a naïve observer would have adopted such a complex strategy. Nonetheless, it provides an existence proof for a 2D algorithm that could have been used to generate the data in Royden *et al.* (1994). However, if our observers adopted this strategy and, despite our instructions, made exocentric heading judgments, they would have generated biases in the rotation direction larger than observed (e.g. ~ 11 deg at 4 deg/sec in Expt 2 and ~ 6 deg for both 8 and 16 deg/sec in Expt 3). Even if our observers applied this algorithm at the end of the trial, their errors would still have been larger than those observed. Furthermore, because this algorithm does not derive either the curvature or tangent to the path, it is difficult to see how exocentric heading derived using this algorithm could then be used to estimate retinocentric heading without going back to the flow field to estimate their 3D motion. It must be emphasized that, during curvilinear motion, retinocentric heading is not merely exocentric heading in retinal coordinates (Fig. 4 of Royden, 1994).

CONCLUSION

We conclude that at least some humans can disambiguate the rotational and translational components of flow fields to make largely accurate and precise judgments of retinocentric heading, without static depth cues. Therefore, humans do not simply rely on an eye-velocity signal to cancel the rotational flow.

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Acknowledgements—The authors would like to thank Andrew Watson, Preeti Verghese, and Brent Beutter for comments on an earlier draft, Philippe Stassart for programming support on Expt 3, the other members of the Vision Group for their ongoing intellectual contributions, and an anonymous third reviewer for helpful comments. This study was supported by NASA RTOPs No. 199-12-06-24 and 199-16-12-37 (to LS), and 505-64-53 (to the Vision Group).