View rotation is used to perceive path curvature from optic flow

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In many natural situations like driving a car, path curvature is accompanied by observer rotation. The experiments reported here test whether such view rotation is necessary to perceive path curvature from optic flow. Displays simulated travel on a circular path along a random dot ground plane, with speeds of 4 m/s and curvature of ±2°/s. In the Rotating View condition, the view direction rotated with heading, as in previous studies. In the Non-rotating View condition, displays simulated travel along the same circular paths but without change in view direction. In Experiment 1, observers indicated positions on their perceived future path at various distances. Judgments were consistent with curved paths in the Rotating View condition, while in the Non-rotating View condition, judgments were consistent with straight paths. In Experiment 2, observers reported whether the simulated path was straight, curved leftward, or curved rightward. Judgments were accurate in the Rotating View condition, while in the Non-rotating View condition, curved paths were often reported to be straight, and observers did not reliably distinguish the sign of curvature. In both experiments, observers had difficulty perceiving path curvature from optic flow when it was not accompanied by view rotation.

Keywords: optic flow, self-motion, heading, locomotion

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Introduction

Optic flow provides a strong source of information about observer self-motion, and there is a large body of literature on perceptual use of optic flow (see Warren, 2004 for a review). Most studies of perceived self-motion from optic flow have focused on the case of observer travel along a straight path. Another important situation is observer travel on a circular path, as when driving a car. A number of studies have found that observers can reliably judge their future circular path along the ground (Fajen & Kim, 2002; Kim & Turvey, 1998; Turano & Wang, 1994; Warren, Blackwell, Kurtz, Hatsopoulos, & Kalish, 1991; Warren, Mestre, Blackwell, & Morris, 1991).

Circular path perception from optic flow is more challenging than the case of straight paths because it requires taking into account path curvature, which is not directly specified by an instantaneous velocity field. Observer heading and rotation can be computed from a velocity field (Longuet-Higgins & Prazdny, 1980), but curvature cannot be determined without further information or assumptions. To unambiguously compute curvature from optic flow, a model would have to analyze changes in optic flow over time (Rieger, 1983; Warren, Mestre et al., 1991). For example, a model by Wann and Swapp (2000) uses curvature in the extended visual trajectories of points to determine whether a circular path is headed to the left or right of fixation. A model that utilizes acceleration cues, like that of Wann and Swapp, could be capable of distinguishing different paths with the same instantaneous translation and rotation.

However, the results of Warren, Mestre et al. (1991) suggest that instantaneous optic flow is sufficient for perception of self-motion along a circular path, despite its formal ambiguity. Warren et al. used motion displays composed of limited-lifetime dots to test for an influence of acceleration cues. In the most extreme case, each dot was presented for only two frames before being replaced, thereby eliminating acceleration information that would otherwise be available from the extended trajectories of the dots. Warren et al. observed that dot lifetime had little effect on performance, and path judgments remained accurate even in the two-frame case.

There is also evidence that observers can have difficulty distinguishing the presence or absence of path curvature, suggesting insensitivity to acceleration cues. Numerous studies have reported that simulating travel on a straight path with rotating view can give the illusory percept of travel on a curved path (Banks, Ehrlich, Backus, & Crowell, 1996; Ehrlich, Beck, Crowell, Freeman, & Banks, 1998; Li & Warren, 2000, 2004; Royden, Banks, & Crowell, 1992; Royden, Crowell, & Banks, 1994; van den Berg, 1996). This illusion has been interpreted as evidence that the visual system does not effectively utilize acceleration cues (Ehrlich et al., 1998). As a number of researchers have noted, the instantaneous optic flow produced in this situation is the same as when an observer is traveling on a circular path while rotating their view with their heading (e.g., Ehrlich et al., 1998; Stone & Perrone, 1997; Warren, Blackwell et al., 1991). Travel on

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a circular path may be a default interpretation of the ambiguous instantaneous flow. Although optic flow over extended time could distinguish straight from curved paths, observers do not appear to take advantage of this information.

Visual insensitivity to path curvature cues, as evidenced by these results, raises a question about how we are able to accurately perceive movement along a circular path. The same velocity field can be produced by a variety of paths with differing curvature. To unambiguously determine curvature, the visual system would have to analyze changes in optic flow over extended time. However, the studies cited above suggest that acceleration cues are not utilized. Observers can misperceive a straight path to be a curved path, despite the fact that the optic flow produced in these situations diverges over time. Distinguishing the amount of path curvature when traveling on a circular path poses the same computational challenge as distinguishing whether a path is straight or curved. If instantaneous optic flow is ambiguous and acceleration cues are not used, how then are we still able to accurately judge future path along circular trajectories?

A possible solution is that visual analysis of optic flow uses an implicit assumption that path curvature is accompanied by view rotation. View rotation is specified by instantaneous optic flow. As discussed in the next section, rotation within optic flow that cannot be attributed to pursuit eye and head movements would typically provide a valid cue to curvature. The previous studies cited above demonstrate that the presence of rotation can cause a straight path to appear curved. The experiments reported here test whether the absence of view rotation conversely makes it difficult to perceive curvature when traveling on a circular path.

Rotation as a cue to path curvature

Rotation and path curvature are independent aspects of observer movement, but there is often a close relationship between body rotation and change in heading. When driving a car, the driver's body is generally fixed within the car and the instantaneous heading is fixed relative to the car, so changes in heading are tightly coupled to rotation of the body. The situation when walking is less constrained, but we still typically orient our body in the direction we are walking. Thus, body rotation would often be coupled with change in heading.

This relationship suggests a way that path curvature could be inferred from instantaneous optic flow. Body rotation introduces a rotational component to optic flow separate from the rotational component due to pursuit eye and head movements. Provided that there is depth structure in a scene, view rotation is well specified from instantaneous optic flow. Using extra-retinal information about pursuit eye and head movements, which is known to contribute to visual analysis of optic flow (e.g., Crowell, Banks, Shenoy, & Andersen, 1998; Royden et al., 1994), it would be possible to identify the residual rotational component that would typically be due to body rotation. To the extent that heading is coupled with body orientation, this rotational component would provide a cue to curvature. Because rotation can generally be determined from instantaneous optic flow, estimating path curvature based on rotation would not require analysis of optic flow over extended time. This would be advantageous for real-time feedback control.

An assumption that path curvature is accompanied by rotation could be utilized in different ways. Rotation that is not attributable to pursuit eye rotation might be used as a direct cue to rate of path curvature (Ehrlich et al., 1998; Saunders & Niehorster, 2010). This rotational component would typically be coupled with vestibular cues to head rotation, so visual and vestibular cues could be integrated to jointly estimate curvature. Rotation could also contribute to perception of self-motion along circular paths without being used to explicitly estimate curvature. If an observer rotates with their direction of heading while traveling on a circular path along the ground, the resulting optic flow is constant over time. As discussed later, this could allow a strategy based on extrapolating flow lines (Lee & Lishman, 1977).

Perception of path curvature from rotation

If the visual system infers path curvature from rotation, it would explain why observers were able to make accurate judgments in previous studies of circular path perception and why conditions with simulated rotation can cause an illusion of traveling on a curved path.

Previous studies that have tested the ability to judge future circular path from optic flow have used displays in which the simulated viewing direction rotated along with change in heading, as in Figure 1a (Fajen & Kim, 2002; Kim & Turvey, 1998; Turano & Wang, 1994; Warren, Blackwell et al., 1991; Warren, Mestre et al., 1991). Thus, in all these previous studies, view rotation provided a valid cue to path curvature. Strategies for using optic flow that depend on a coupling of rotation and curvature, such as use of flow lines (see Discussion section), would be applicable and produce accurate performance. This situation does present conflicting information about body rotation, because participants are physically stationary. However, it is representative of typical conditions in that it preserves the relationship between body orientation and heading. This consistency may be important for perception of circular travel.

If the visual system infers path curvature from rotation, then simulating travel on a straight path with rotation creates a cue conflict situation. This corresponds to "simulated eye movement" conditions tested in many previous studies, which generally create an illusion of travel on a curved path (Banks et al., 1996; Ehrlich et al.,

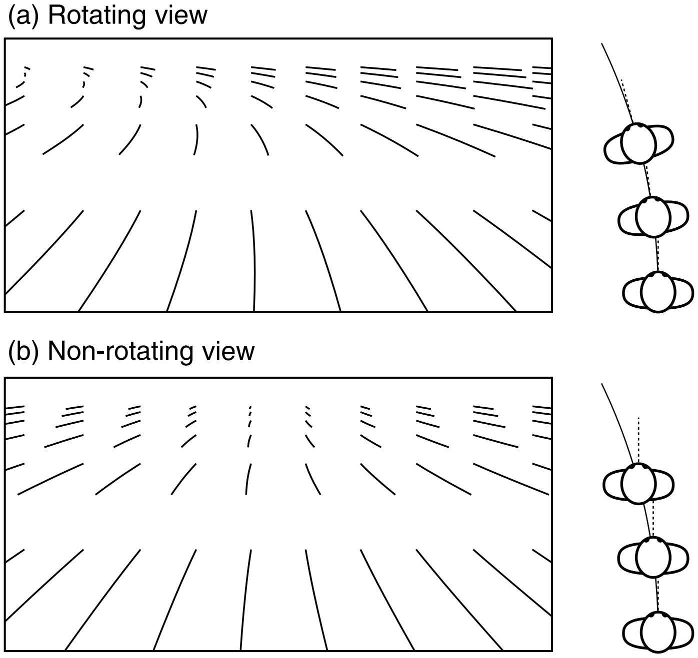

Figure 1. Examples of the view conditions. The curves plot the visual trajectories of points over 1 s of movement along a curved path. (a) In the Rotating View condition, the simulated viewing direction rotated at the same rate as the change in heading, 2°/s. Instantaneous heading remains constant in screen coordinates. (b) In the Non-rotating View condition, displays also simulated a curved path with heading changing by 2°/s, but the simulated viewing direction was held constant. Illustrations depict a 40° by 20° field of view, with horizon at the top (actual displays were 70° wide).

1998; Li & Warren, 2000, 2004; Royden et al., 1992, 1994; van den Berg, 1996). The previous literature has emphasized the cue conflict caused by the absence of extra-retinal eye and head movement signals. For example, the issue has been framed as whether the visual system can discount the rotational component within optic flow without extra-retinal information. The cue conflict in this situation could be interpreted in a different way. There is often a rotational component within optic flow that is not due to gaze rotations, but rather due to body rotation. This aspect of the simulated rotation condition is not unnatural. However, the additional rotational component would typically be accompanied by path curvature. Simulated rotation during travel on a straight path does not preserve this relationship, which could explain the illusory percept. A number of researchers have similarly argued that a circular path would be a sensible interpretation of the sensory information in this case (Ehrlich et al., 1998; Royden et al., 1994; Stone & Perrone, 1997).

The situation illustrated in Figure 1b likewise presents a cue conflict situation in which change in heading and view rotation are decoupled. It is the complement to the simulated rotation condition described above: the actual simulated path is circular, but simulated viewing direction does not rotate. If visual analysis assumes a coupling between rotation and curvature, the absence of rotation in this case would suggest a straight path. Observers might then have difficulty perceiving path curvature. This prediction has not yet been clearly tested.

Only two previous studies have tested the case of a simulated curved path without coupled rotation. Bertin and Israel (2005) and Bertin, Israel, and Lappe (2000) presented visual simulations of self-motion with various combinations of path curvature and rotation, including circular paths with absent or mismatched rotation, and observers attempted to reconstruct the perceived path of motion with a handheld object. In both studies, there was a general tendency for systematic errors in conditions where path curvature did not match rotation, in the direction toward interpreting rotation as curvature. However, in the case of travel along a full semi-circle without rotation, observers were able to perceive a curved path. Direct comparison of these results to other studies of path perception is difficult due to the novel task and other significant methodological differences.

The experiments presented here test perception of self-motion along circular paths on the ground for Rotating View and Non-rotating View conditions like those illustrated in Figure 1. In Experiment 1, observers judged locations on their future path at various distances. In Experiment 2, observers made qualitative judgments of perceived path curvature. Across both experiments, a general finding was that rotation is crucial to perceiving path curvature.

Experiment 1

In Experiment 1, judgments of future path were compared for the view conditions illustrated in Figure 1. Displays simulated travel along a circular path, with view direction either rotating along with change of heading or fixed straight ahead. Observers indicated points along their future path at various distances. The correct future paths in these two conditions were identical. However, if view rotation is necessary to perceive path curvature, judgments in the Non-rotating View condition would be consistent with a straight path of travel.

Methods

Participants

Twelve students at the University of Hong Kong participated in Experiment 1. All were naive to the purposes of the experiment and had normal or corrected-to-normal vision.

Apparatus

Stimuli were presented on large screen Mitsubishi WD-65736 DLP TV and viewed from a position 1 m away and centered relative to the screen. The image region of the display was 139 cm wide and 79 cm tall, corresponding to 70° by 42°. Participants viewed the displays monocularly with their right eye, and their heads were not constrained. The display has a resolution of 1776 × 1000 pixels and a refresh rate of 120 Hz. Images were generated using OpenGL on a Dell Vostro 200 computer with an ATI Radeon 3650 graphics card.

Stimuli

Stimuli were motion sequences that simulated travel along a curved path over a ground plane covered with randomly positioned dots. In all trials, simulated observer speed was 4 m/s, and simulated heading changed at a constant rate of ±2°/s. The initial heading was varied to be 0°, ±5°, or ±10° away from the center of the display.

The main experimental manipulation involved the relationship between view rotation and change in observer heading over time. In Rotating View trials, the simulated viewing direction was coupled to the heading, such that viewpoint rotated at the same rate and in the same direction (Figure 1a). For the case when initial heading is 0°, the viewing direction is the tangent of the path. This corresponds to the typical situation when driving in a car. In Non-rotating View trials, the simulated viewing direction remained constant relative to the environment while the heading varied (Figure 1b).

The random dots were uniformly distributed over the ground plane with a density of 0.8 dots/m^2, extending to a far clipping plane at 100 m away. Simulated eye height was 1.7 m, so the nearest visible portion of the ground was 4.3 m away. Approximately 6000 dots were visible on a given frame. Dots were anti-aliased and had a constant diameter of 4 pixels (0.18°) regardless of simulated distance (i.e., dot sizes were not scaled for depth).

At the end of a trial, pole with adjustable position was displayed for observers to indicate their future path. The probe pole was simulated to be 120 cm tall and 20 cm in diameter and was attached to the ground plane. The pole was rendered in accurate perspective, so its projected size varied as a function of distance. Three probe distances were tested for each heading and view condition: 7.5 m, 15 m, and 30 m. For these distances, the bases of the poles were initially 12.7°, 6.5°, and 3.2° away from the horizon. If responses were consistent with a curved path, the horizontal position of the probes would be expected to vary with distance. Thus, testing multiple probe distances allows perceived path curvature to be inferred.

Procedure

The participants' task was to adjust the horizontal position of a pole to lie on their future path of motion. On each trial, 1 s of simulated self-motion was presented and then the probe pole appeared. Participants were allowed free fixation and were given no instructions about where to look during the motion. The probe pole could be moved horizontally using the computer mouse along a range of positions that were constrained to have a constant simulated distance from the observer. Participants were instructed to position the probe so that it would be on their path if they had continued moving in the same manner as during the motion display. When the probe was adjusted to their satisfaction, they indicated by pressing a mouse button, and the next trial began after a 2-s delay. After the experiment, participants were asked whether they found the task difficult or confusing, and none reported any difficulty.

Participants performed two blocks of 240 trials. Each block consisted of three repetitions of each combination of view condition (Rotating vs. Non-rotating), direction of curvature (−2°/s or 2°/s), initial heading (−10°, −5°, 0°, 5°, or 10°), and probe distance (7.5 m, 15 m, or 20 m). All variables were fully randomized within blocks. Trials were self-paced, and each block took about 20 min to complete.

Results

Mean future path judgments

Figure 2 shows mean positions of probes relative to the initial observer position and heading, plotted as a top-down view. Raw responses were normalized by rotating the initial heading to be straight ahead, and conditions differing only by initial heading were combined for analysis. The graphs plot mean relative probe positions, averaged across observers, for leftward and rightward curved paths and the three probe distances tested. Dashed lines depict the correct future paths, and dotted lines show the heading at the end of a trial.

For the Rotating View conditions, judgments were strongly dependent on direction of simulated curvature (Figure 2a). Mean probe positions were to the left of the final instantaneous heading for trials with leftward curvature and to the right of final heading for trials with rightward curvature. Probe positions also varied with distance in a way consistent with a curved path. For the Non-rotating View condition (Figure 2b), in contrast, path curvature had little effect on judgments of future path. Leftward and rightward curved simulated paths yielded similar judgments, and mean probe position was less than 2° from the initial heading even for the largest probe distance.

Figure 3 replots mean probe positions as path angles: the horizontal visual angles between a probe and the final instantaneous heading. Leftward and rightward curved trials were normalized and combined for analysis. For negatively curved trials, the sign of initial heading was reversed to be consistent with a mirror reflection. If judgments were consistent with a curved path, path angle would be expected to systematically increase with probe distance.

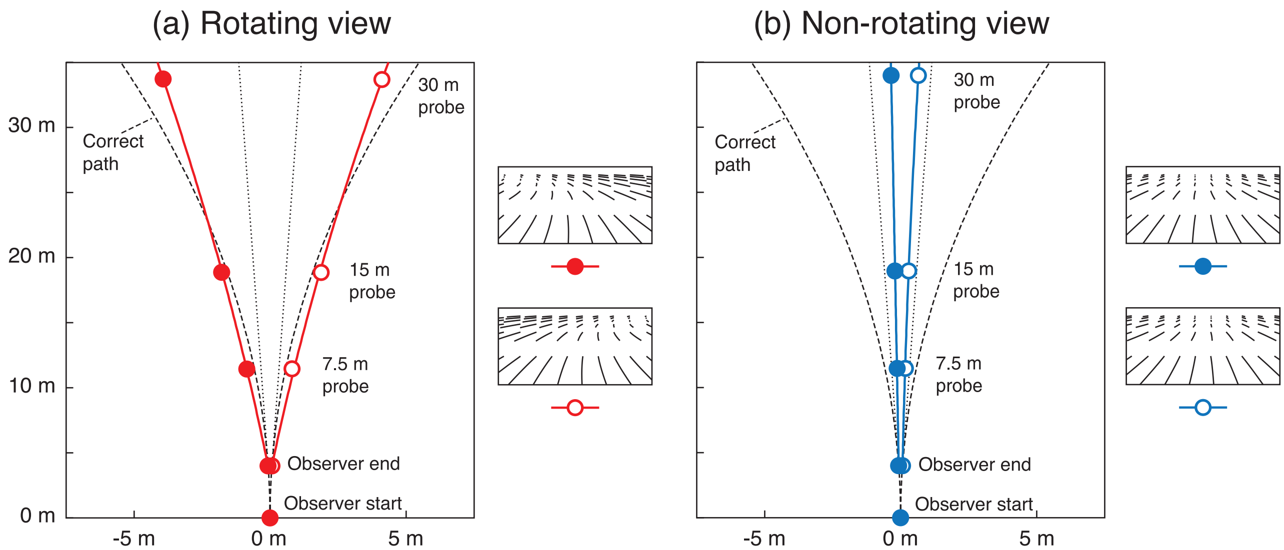

Figure 2. Mean probe settings from Experiment 1, plotted as points on the ground from a top-down view, for the (a) Rotating View and (b) Non-rotating View conditions. Data from conditions with different initial heading directions were normalized and combined for analysis. In normalized coordinates, the initial position of the observer is (0, 0) and the initial heading is vertical. At the end of a trial, the heading was ±2° from the initial heading, illustrated as dotted lines. Filled and open circles show the mean probe positions for leftward and rightward circular paths for various probe distances. The initial and final simulated observer positions are also plotted. Dashed lines depict the correct future paths.

To evaluate the increase in path angles statistically, I tested for linear trends as a function of probe distance. In the Rotating View condition, path angle significantly increased with probe distance ($F(1,11) = 20.3$, $p < 0.001$). The increase corresponded to about 30% of the expected increase if judgments were veridical (dashed lines). This suggests that paths were perceived as curved in the Rotating View condition but with less curvature than simulated. In the Non-rotating View condition, probe distance had no detectable effect. The trend in the Non-rotating View data was in the positive direction, but it was not significant ($F(1,11) = 3.0$, $p = 0.10$) and represented less than 5% of the expected increase for veridical performance. For all probe distances, path angles of mean judgments were between the initial heading (−2° in Figure 3) and the final heading (0°). Thus, judgments in the Non-rotating View condition were consistent with perceiving a future path that is straight and in the direction of the average heading experienced during a trial.

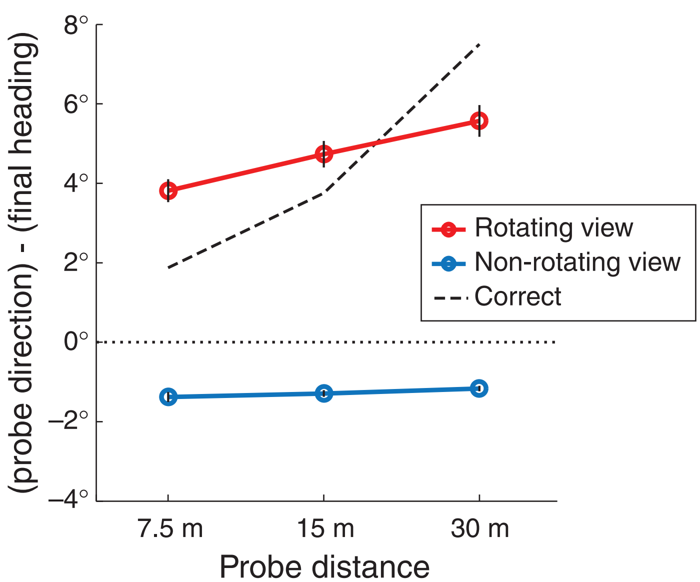

Figure 3. Results from Experiment 1 plotted as path angles. The graph plots the mean difference between the probe direction and the final heading as a function of probe distance. Conditions with different initial headings were normalized and combined for analysis. The dashed line shows correct responses. Error bars depict ±1 standard error.

Results in the Rotating View condition also suggest that perceived heading was biased in the direction of rotation. If curvature was underestimated but heading was perceived accurately, one would expect path angles to be reduced by a constant factor. At the nearest probe distance, however, the path angle of mean future path judgments was larger than veridical.

Estimates of perceived heading and curvature

To further analyze perception of instantaneous heading and path curvature, I computed best-fitting circular paths based on observers' judgments. Circular paths were fit separately for each observer and view condition. I computed which circular path, starting at the observer's end position, passed closest to the three mean normalized probe positions. Sum of squared distances from probes to the path was used as a measure of fit. The tangent of the best-fitting circle at the observer position was used as an estimate of perceived instantaneous heading. The radius of the best-fitting circle was used as an estimate of perceived rate of curvature, expressed as rate of change in heading (yaw).

Figure 4 plots the mean heading and curvature fits for the Rotating View and Non-rotating View conditions, averaged across observers. Veridical performance would correspond to heading of 0° and curvature of 2°/s. In the Rotating View condition, best-fitting paths had 0.5°/s curvature, corresponding to about 25% of the simulated curvature, and heading that was biased by 3.7° in the direction of curvature. Both heading bias and curvature were significantly different from zero (heading: $t(11) = 7.8$, $p < 0.001$, curvature: $t(11) = 2.76$, $p = 0.009$). In the Non-rotating View condition, curvatures of best-fitting paths were not significantly different from zero ($t(11) = 1.18$, $p = 0.13$ n.s.), and there was a significant heading bias of 1.4° in the direction opposite path curvature ($t(11) = 10.2$, $p < 0.001$).

Based on this analysis, perceived future paths in the Non-rotating View condition are almost straight, while in the Rotating View condition, perceived future paths are curved but with underestimated curvature and some bias in heading. These results are consistent with the analyses of path angle reported in the previous section.

Variable error

The consistency of path judgments was assessed by computing the standard deviation of probe positions across trials in each condition. Probe positions were coded as path angles, and mirror-symmetric conditions were combined for analysis after normalization. Standard deviations were computed separately for each initial heading condition and then averaged across conditions with the same view rotation and probe distance.

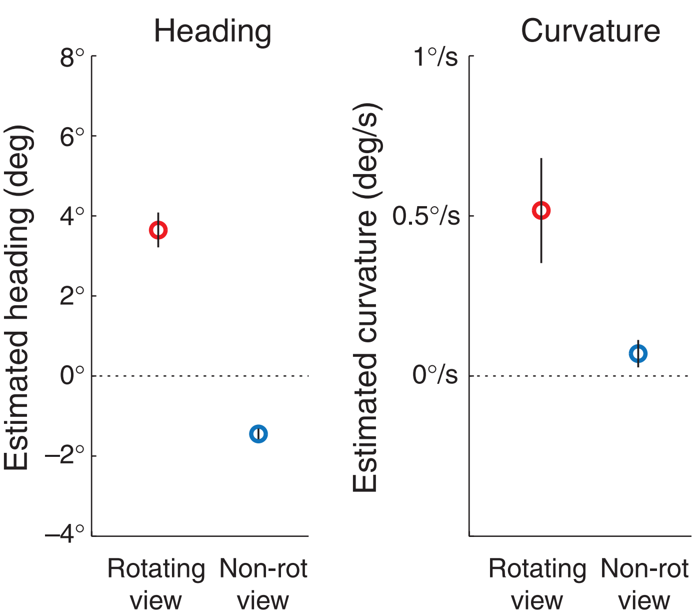

Figure 4. Mean estimates of perceived heading and path curvature derived from fitting circles to observers' responses at different probe distances. Accurate performance would correspond to heading of 0° and curvature of 2°/s. Error bars depict ±1 standard error.

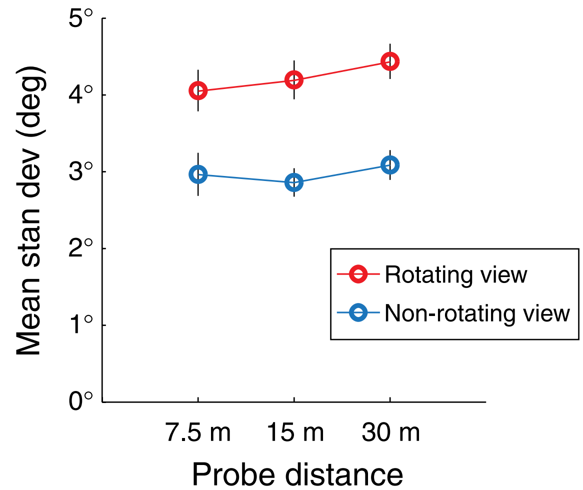

Figure 5. Variable error in subjects' judgments from Experiment 1. The graph plots mean standard deviation of path angles as a function of probe distance for the two view conditions. Error bars depict ±1 standard error.

Figure 5 shows the mean standard deviations of path angles, averaged across observers. Mean deviations in the Non-rotating View condition were around 3° for all probe conditions, while deviations in the Rotating View condition were higher, averaging 4.2°. An ANOVA confirmed that there was a significant overall difference between Rotating View and Non-rotating View conditions ($F(1,11) = 100$, $p < 0.001$). There was no significant main effect of probe distance ($F(2,11) = 0.84$, $p = 0.46$), nor an interaction between view condition and probe distance ($F(2,11) = 0.82$, $p = 0.45$). The deviations in the Rotating View condition suggest a trend toward increasing with probe distance, but this trend was not significant ($F(1,11) = 3.25$, $p = 0.09$).

The deviations of probe settings were larger overall than discrimination thresholds that have been observed in comparable conditions. For example, Warren, Blackwell et al. (1991) reported discrimination thresholds of 1–2°, which is a factor of two smaller than the deviations reported here. The probe adjustment task likely contributes additional variability, which could account for this difference.

Center bias

Circular paths were tested with five different initial headings, −10° to 10°. For the analyses described in the previous sections, responses were normalized and

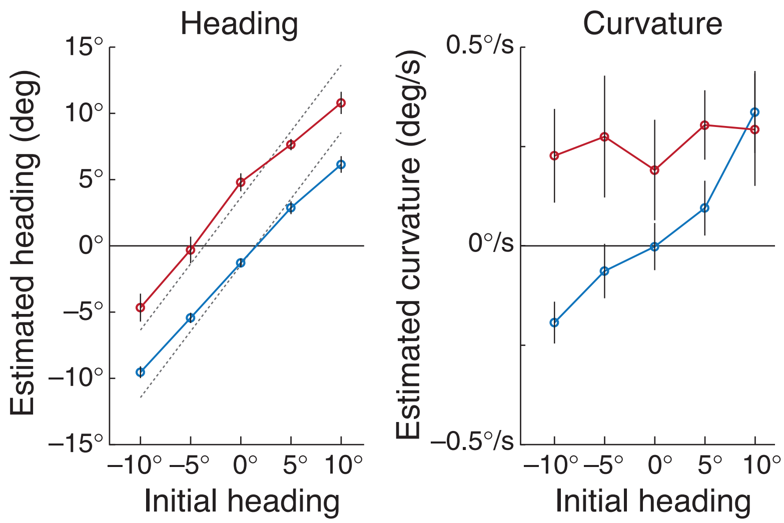

Figure 6. Mean heading and curvature of best-fitting circles as a function of initial heading. Error bars depict ±1 standard error. In the heading graph (left), dashed lines show predicted results if observers had a constant heading bias in each view condition, independent of initial heading. Compared to these predictions, heading estimates are biased toward the center. In the Non-rotating condition, initial heading also affects the estimate of curvature (right).

averaged across initial heading conditions. However, there is reason to expect that judgments could depend on initial heading. Heading judgments from simulated optic flow often show a general bias toward the center of the display (e.g., Ehrlich et al., 1998; Johnston, White, & Cumming, 1973; Warren & Saunders, 1995), and there are potential steering strategies based on motion of objects relative to the reference frame provided by the screen (Wann & Land, 2000; Wilkie & Wann, 2002).

To test for center bias or other screen effects, I computed circular fits separately for the five initial headings. Mirror-symmetric conditions with leftward and rightward curvatures were again combined for analysis. Figure 6 plots heading and curvature as a function of initial heading for the two view conditions. A center bias is revealed by the fact that heading estimates vary over a smaller range than initial heading. The dashed lines in the heading plots show the predicted results if observers had a constant heading bias that was independent of initial heading. Relative to these predictions, heading estimates were biased rightward when initial heading was to the left of center and leftward when initial heading was to the right of center. This center bias appears for both Rotating and Non-rotating View conditions.

In the Non-rotating View condition, estimates of perceived curvature were also affected by initial heading. This is due to an interaction between probe distance and center bias, illustrated in Figure 7. Judgments showed more bias toward the center at near probe distances than at far probe distances. Consequently, when initial heading was non-zero, mean probe positions were not aligned vertically (as expected for a straight path). When initial heading was to the left, the best-fitting circular path had a leftward curvature, and when initial heading was to the right, the best-fitting circular path had a rightward curvature. A possible explanation for this distance-dependent center bias is discussed later.

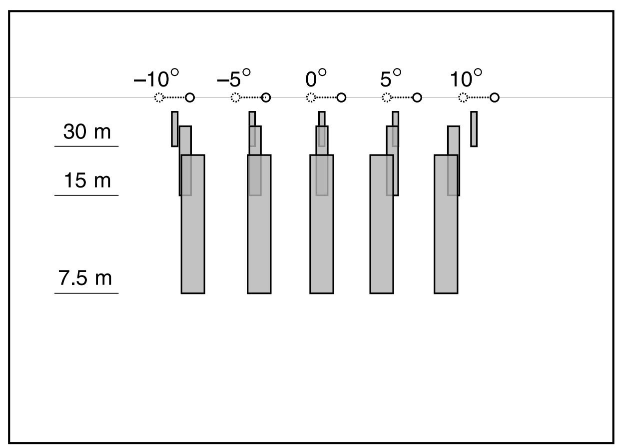

Figure 7. The interaction between center bias and distance in the Non-rotating View condition. The rectangles show mean probe positions, in perspective view, for each probe distance and initial heading. Actual curvature is rightward, so final heading (solid circles) is 2° to the right of initial heading (dashed circle). At the farthest distance, probes were placed approximately halfway between the initial and final headings. At nearer distances, probes were placed closer to the center. For a straight path, probes would be aligned vertical. Because of this distance-dependent center bias, the best-fitting circular path at −10° initial heading has leftward curvature, and the best-fitting circular path at 10° initial heading has rightward curvature.

Discussion

Although the same circular paths were simulated in the two view conditions, observers' path judgments were dramatically different. When path curvature was not accompanied by simulated rotation (the Non-rotating View condition), judgments were consistent with perceiving a straight path and showed little difference between leftward and rightward curved paths. Observers' future path judgments were reliable in the Non-rotating View condition, with lower variability than in the Rotating View condition, but deviated greatly from the simulated curved paths. In the Rotating View condition, judgments were strongly affected by the direction of simulated curvature and were closer to veridical overall. Thus, view rotation greatly facilitated perception of path curvature.

In the Non-rotating View condition, judgments were consistent with travel along a straight path in a direction between the initial and final headings. Relative to the actual heading at the end of a display, the heading implied by observers' judgments was biased. This heading bias depended on direction of path curvature, indicating that observers were sensitive to the change in heading over the course of a trial. Thus, leftward and rightward curved paths with the same initial heading were distinguishable. However, observers did not appear to use change in heading to infer curvature. The path angles of judgments did not change with distance as expected for a curved path. Rather, the pattern of results is consistent with integrating optic flow over the course of the trial and perceiving a straight path with intermediate heading. Integration over long time spans could interfere with detecting acceleration of visual trajectories, which would explain the poor accuracy in the Non-rotating View condition.

While the Rotating View condition was more effective in conveying perception of curvature, judgments suggested that perceived future paths were not accurate. The perceived curvature implied by responses was less than veridical, and the perceived heading was biased in the direction of curvature. There are a number of possible explanations for these biases. If the rotational component in optic flow were underestimated, one would expect this pattern of biases. Incomplete compensation for pursuit eye movements would also produce such biases, as discussed in a later section. Third, even if self-motion were perceived accurately, biases in the perception of probe distance could cause responses to deviate from veridical.

The biases in the Rotating View condition are consistent with results of Ehrlich et al. (1998) in an experiment that included simulated curved paths with view rotation. Ehrlich et al. similarly observed less effect of distance on responses than expected from accurate perception of curvature, and heading bias in the direction of curvature. Other previous studies of circular path perception did not include multiple probe distances, so it is difficult to directly compare accuracy. The present results suggest that both perceived heading and perceived path curvature may be biased. If path is judged relative to only one distance, as in most previous studies, errors in perceived heading and curvature cannot be separated.

An additional novel finding of Experiment 1 was an interaction between center bias and probe distance in the Non-rotating View condition. Overall, judgments were biased toward the center of the screen, as has been observed previously (Johnston et al., 1973; Warren & Saunders, 1995). The additional finding is that the center bias was larger when probes were near than far (Figure 7). I speculate that this bias is due to a misperception of spatial geometry rather than misperception of self-motion. In a perspective projection, radial lines along the ground from the observer's feet to the horizon project to parallel vertical lines on the screen. For a straight path, accurate judgments for probes at different distances would therefore align vertically. Subjectively, this may be counterintuitive. Observers may instead perceive radial lines along the ground as diverging from the bottom of the projected image, rather than being parallel and vertical, due to some influence of the display screen on the perceived spatial layout. Such a bias could account for the distance-dependent center bias observed here.

A potential concern is that the task used to assess perceived self-motion, judging locations on one's future path, could have accentuated the difference between conditions. In particular, the flow lines from instantaneous optic flow provide a valid cue for future path in the Rotating View condition but not the Non-rotating View condition (see General discussion section). Even if observers perceived their path to be just as curved in the Non-rotating View condition, they might have had more difficulty judging future path relative to the Rotating View condition. To confirm that the observed differences are not limited to future path judgments, Experiment 2 tested qualitative judgments of perceived path curvature.

Experiment 2—Curvature discrimination

Experiment 2 tested the ability to discriminate straight from curved paths and to discriminate direction of path curvature. In the previous experiment, perceived heading and curvature were inferred from judgments of future path. The observed differences between Rotating View and Non-rotating View conditions are consistent with their phenomenology: Rotating View stimuli appear to be curved paths, while Non-rotating View stimuli appear to have little or no curvature. However, it remains possible that differences in future path judgments are specific to the task. In this experiment, observers directly reported the perceived curvature of their path: whether they appeared to be curving leftward, curving rightward, or traveling on a straight path. Based on the results of Experiment 1, one would expect discrimination of path curvature to be difficult in Non-rotating View conditions and easy in Rotating View conditions.

Methods

Participants

Eight students at the University of Hong Kong participated in Experiment 2. All were naive to the purposes of the experiment and had normal or corrected-to-normal vision.

Apparatus

The display apparatus was the same as in the previous experiment.

Stimuli

The stimuli were identical to those of previous experiment, except that conditions with intermediate rates of curvature were included. The rate of change of heading was either −2°/s, −1°/s, 0°/s (straight path), 1°/s, or 2°/s. Each of these paths was tested in both Rotating View and Non-rotating View conditions. All other stimulus variables were the same as in the previous experiment (e.g., observer speed, initial headings, duration, etc.).

Procedure

Participants performed a three-alternative forced-choice task. On each trial, they judged whether the simulated path of motion appeared to be curving leftward, curving rightward, or straight. No feedback about their responses was given. Participants performed a short practice block, and then two experimental blocks of 180 trials each. Conditions were fully randomized within blocks. Trials were self-paced, and each block took about 15 min to complete.

Results and discussion

Figure 8 plots percent of trials judged leftward, rightward, and straight as a function of actual simulated curvature, averaged across observers and initial heading conditions. The left graph shows the Rotating View condition, and the right graph shows the Non-rotating View condition. In the Rotating View condition, observers were able to accurately judge curvature. When simulated curvature was ±2°/s, direction of curvature was correctly identified 80% of the time on average, and when simulated path was straight, observers correctly indicated a straight path 75% of the time. Accuracy was lower in the ±1°/s curvature conditions, but observers could still reliably distinguish between leftward and rightward curved paths, with 50% of trials judged correctly and less than 10% of trials judged to be curved in the opposite direction. Chi-squared tests for independence were conducted for each subject's data, and all revealed a significant effect of simulated curvature on judgments in the Rotating View condition (all $p < 0.001$).

Performance in the Non-rotating View conditions was markedly different. The majority of Non-rotating View trials, 65–75%, were judged to be straight paths regardless of amount and direction of simulated curvature. In the ±2°/s simulated curvature condition, less than 20% of

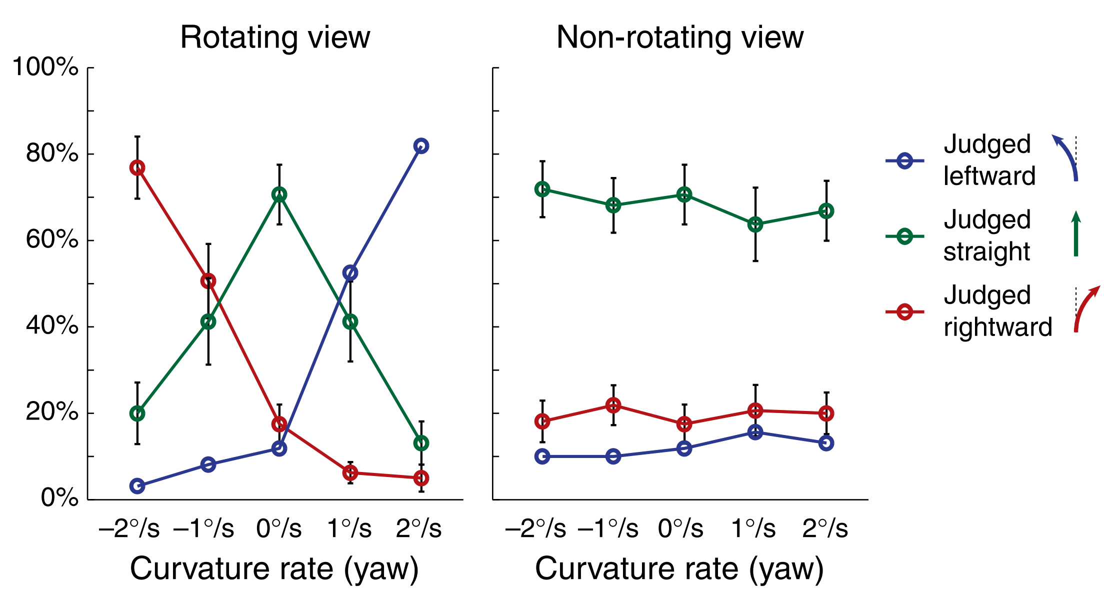

Figure 8. Mean results of Experiment 2. The three lines on each graph plot percent judged leftward, straight, or rightward as a function of simulated curvature. (a) The left graph plots results for the Rotating View condition, and (b) the right graph plots results for the Non-rotating View condition. Error bars depict ±1 standard error.

trials were judged to be curved in either direction. Mean judgments showed a slight overall bias toward judging curvature to be rightward rather than leftward, but this was a constant bias that was unrelated to the direction of simulated curvature. Chi-squared tests of independence found no evidence that simulated curvature influenced judgments in the Non-rotating View conditions for any of the subjects (all $p \geq 0.25$).

These qualitative judgments of perceived motion are consistent with the results of Experiment 1 and support the hypothesis that rotation is required to perceive path curvature. Observers were able to easily distinguish curved and straight paths and direction of curvature, when the simulated view rotates with change in heading. However, in the absence of view rotation, simulations of curved paths appeared to have little or no curvature.

General discussion

Importance of rotation for curvature perception

The two experiments demonstrate that rotation is important for perceiving circular path of motion from optic flow. In Experiment 1, quantitative judgments of future path positions were used to assess perceived self-motion. In Experiment 2, observers made qualitative judgments of presence and direction of path curvature. In both experiments, judgments were strongly dependent on whether viewpoint rotated along with the observer's changing heading. Observers could not accurately perceive path curvature in the absence of simulated view rotation.

The present results are generally consistent with those of Bertin and Israel (2005) and Bertin et al. (2000), in which observers attempted to reproduce simulated paths of self-motion with a handheld object. A variety of combinations of simulated path and observer rotation were tested, including situations in which rotation was not coupled with path curvature. In most such cases, observers made systematic errors in reconstructed paths, in a direction consistent with use of rotation as a cue for curvature. Bertin et al. interpret these results as evidence that the visual system assumes a coupling between rotation and curvature. One inconsistent finding was observed. In a condition that simulated travel on a circular path with no observer rotation, as in the Non-rotating View condition tested here, Bertin et al. found that observers were able to successfully identify their paths as circular, despite the lack of rotation. This would appear to conflict with the present results. However, an important difference is that the circular paths simulated in Bertin et al.'s study spanned an entire half-circle. They suggest that the sequence of forward, lateral, and then backward translational motion in this condition allowed observers to infer a circular path of travel, even if instantaneous curvature was not correctly perceived without coupled rotation. Due to task differences, it is hard to directly compare the results of Bertin and Israel and Bertin et al. to the present experiments. However, the general findings are consistent: observers have difficulty perceiving path curvature accurately when curvature is not coupled with rotation.

Many previous studies have found that simulating travel along a straight path with view rotation can produce the illusory percept of traveling on a curved path (Banks et al., 1996; Ehrlich et al., 1998; Li & Warren, 2000, 2004; Royden et al., 1992, 1994; van den Berg, 1996). The results of the experiments presented here complement these findings. Previous studies have demonstrated that adding rotation can cause a straight path to appear curved. The present results conversely demonstrate that in the absence of view rotation, a curved path can appear straight. If the visual system implicitly assumes that curvature is coupled with view rotation, then both rotation without curvature and curvature without rotation are unnatural cue conflict situations. In both situations, the typical coupling between rotation and curvature is not preserved. The resulting perceptual errors in these conditions are consistent with the hypothesis that rotation in optic flow is used to perceive path curvature.

Ivanenko, Grasso, Israel, and Berthoz (1997) observed analogous effects for perception of self-motion from vestibular cues. Observers were passively moved without vision along straight and circular paths and with or without simultaneous body rotation. Ivanenko et al. observed that linear translation while rotating was perceived as travel along a curved path, while movement along a circular path without rotation was perceived as traveling on a straight path. These are analogous to the perceptual errors observed for self-motion perception from optic flow, described above. Thus, use of rotation to infer curvature may be a general perceptual strategy, used across modalities.

Flow lines as cue to future path

In the situation where changes in heading are accompanied by observer rotation, flow lines could be used to perceive one's future path and the future trajectories of objects relative to the observer. In this section, I discuss a flow line strategy and how it could account for the results of Experiment 1.

If an observer rotates with change in heading, then the direction of heading remains constant in observer-relative coordinates. The optic flow generated from traveling on a circular path along the ground would then be a constant velocity field. In the case of a constant velocity field, the future visual trajectories of objects can be extrapolated over time by integrating the velocity field to obtain flow lines. This corresponds to assuming that the observer moves forward on a circular path with curvature equal to the current rate of rotation. Flow lines would then be the projections of concentric circles along the ground. An observer's future path would correspond to the flow line that passes under the observer. Lee and Lishman (1977) term this the *locomotor flow line* and propose that steering could be based on whether the locomotor flow line passes to the left or right of desired goal.

In the Rotating View condition tested here, the simulated path was circular and the view rotated with heading, so the locomotor flow line accurately specified the observer's future path (Figure 9a). In the Non-rotating View condition, however, visual trajectories of objects over time (Figure 9b) cannot be predicted by extrapolating the instantaneous velocity field. Because the velocity field has no rotational component, the flow lines form a purely radial pattern (Figure 9c). The locomotor flow line in this condition would incorrectly indicate a straight path toward the instantaneous heading, which is consistent with observers' judgments.

A locomotor flow line strategy could also account for center biases. To accurately judge future path based on flow lines, one would have to correctly identify the flow line that passes under the observer. In an artificial laboratory display with missing and conflicting cues to depth, observers may not accurately extrapolate trajectories on a screen into personal space. Specifically, I hypothesize that observers might perceive the locomotor flow line to be the flow line that passes through the bottom center of the projection screen (which would be incorrect), rather than the flow line that asymptotically approaches vertical (which would be correct). Figure 10 illustrates the biases that would result from incorrectly identifying the locomotor flow line in this way. If heading were to the right of center, path judgments would be biased to the left and vice versa. The bias would further depend on distance. At near distances, there is a large angular difference between the correct locomotor flow line and the line that passes through the bottom center of the screen. Thus, if one assumes that an inaccurate reference point is used to identify the locomotor flow line, it is possible to explain both an overall center bias and an interaction with distance. Heading estimates in both view conditions showed center biases, and in the Non-rotating View condition, the bias was distance dependent. The one inconsistency is that this explanation predicts a similar distance-dependent center bias for the Rotating View condition, which was not observed.

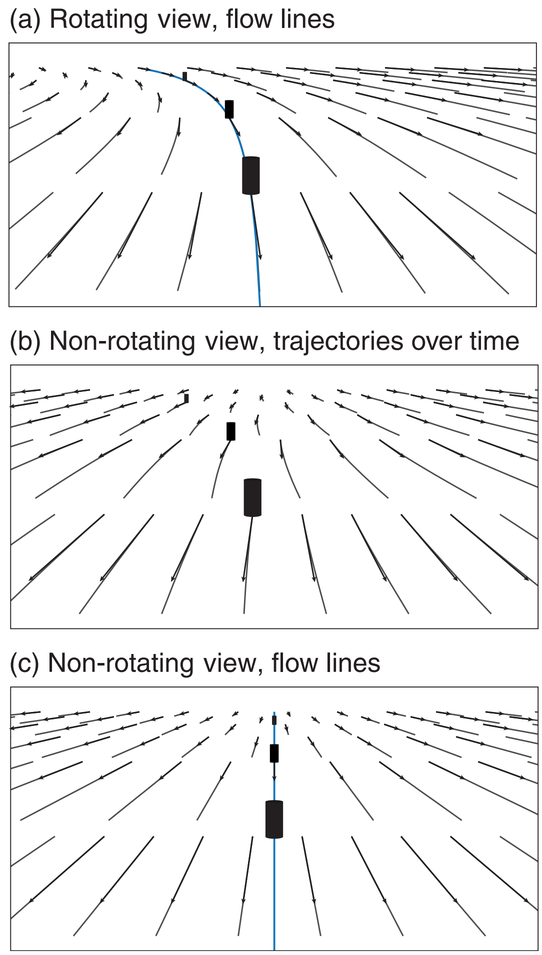

Figure 9. (a) In the Rotating View condition, the velocity field is constant in viewer-relative coordinates, so the visual trajectories of points over time (gray curves) correspond to the flow lines of the instantaneous velocity field (arrows). The locomotor flow line is the flow line that passes under the observer (blue line), which indicates points on one's future path (cylinders). (b) In the Non-rotating View condition, visual trajectories over time diverge from the flow lines of the instantaneous velocity field. The gray lines in the middle panel show visual trajectories over time. Cylinders indicate some points on the correct future path. (c) The flow lines of the velocity field in this condition form a radial pattern, shown by gray lines in the bottom panel. The locomotor flow line (blue line) specifies a straight path in the direction of heading, rather than the correct circular path. Path judgments based on the flow line (cylinders) would be inaccurate.

Role of pursuit eye and head movements

To use a strategy based on viewer-relative optic flow, such as using the locomotor flow line, the visual system would have to account for the effects of pursuit eye movements. When performing a path judgment task like that tested here, the natural tendency is for observers to fixate a point near the future path. If observers fixate a point in the scene, then the retinal flow produced in the Rotating View condition is identical to the retinal flow produced in the Non-rotating View condition. Distinguishing these situations requires extra-retinal information about eye movements.

Extra-retinal information has been demonstrated to contribute to self-motion perception for the case of travel on a straight path. Heading judgments are less affected by rotation due to active eye movements than equivalent simulated rotation (Banks et al., 1996; Li & Warren, 2000, 2004; Royden et al., 1992, 1994). It is reasonable to expect that extra-retinal information could similarly allow

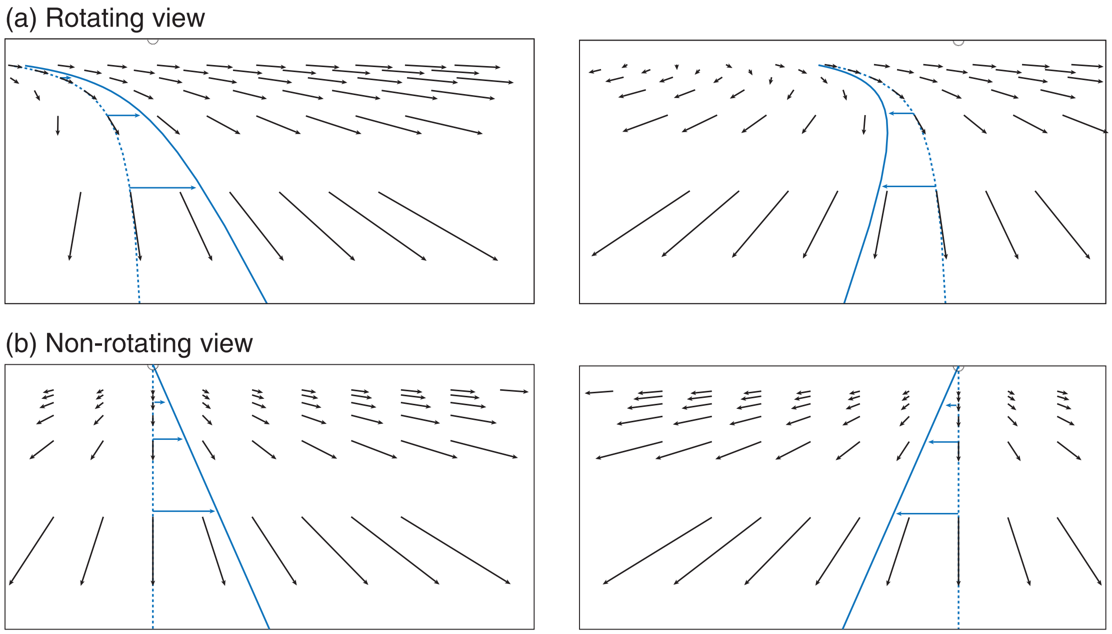

Figure 10. Illustration of the effect of incorrectly identifying the locomotor flow line. The graphs show instantaneous velocity fields for (top) Rotating View and (bottom) Non-rotating View conditions, with heading (left) to the left of center or (right) to the right of center. In each graph, the correct locomotor flow line is the flow line that asymptopically approaches vertical (dashed lines). If observers instead perceived the locomotor flow line to be the flow line approaching the bottom center of the screen (solid lines), path judgments would be biased toward the center, with larger bias at near distances.

the visual system to discount the effect of eye movements in the conditions tested here. However, this cannot be determined from the present results because eye movements were not controlled.

Previous evidence suggests that compensation for active eye movements is only partial (Freeman, 1999; Freeman & Banks, 1998). If self-motion perception is based on viewer-relative optic flow, incomplete compensation for eye movements could explain the heading bias and curvature underestimation observed in the Rotating View condition. Figure 11 illustrates the hypothetical consequences of incomplete compensation for eye movements. The locomotor flow line of the optic flow correctly indicates future path (Figure 11a). Fixating a point on the ground produces a retinal flow pattern with a singularity at the fixation point (Figure 11b). The retinal flow by itself does not directly specify the motion of the fixated point; extra-retinal information is required to recover optic flow. If optic flow is reconstructed from retinal flow using an underestimate of eye rotation rate (Figure 11c), the resulting optic flow is consistent with less curvature and a heading biased in the direction of curvature. These predicted errors are consistent with human judgments from Experiment 1. This explanation does not strongly depend on the location of fixation. The same qualitative effect would be expected for any fixation point that requires pursuit eye movements in the direction opposite to path curvature.

Crowell et al. (1998) tested the role of extra-retinal information about head movements and found that observers perceptually compensate for rotation due to active head movements, like in the case of rotation due to active eye movements. However, Crowell et al. found that passive rotation of the head or body did not elicit similar compensation. This difference between active pursuit and passive rotation is consistent with the framework proposed here. I have argued that visual system implicitly assumes that changes in heading are accompanied by body rotation, so any rotation within optic flow that is not due to pursuit would provide a cue to path curvature. Active head movements used to direct gaze would be like eye movements and have no reliable relationship to change in heading. On the other hand, body rotation generally would be a cue to path curvature. Thus, one would expect active and passive head rotations to have different perceptual effects, as observed by Crowell et al.

Role of acceleration cues

In principle, curvature could be unambiguously determined through analysis of optic flow over time. For example, Wann and Swapp (2000) proposed a method based on curvature of visual trajectories in retinal flow. Use of such acceleration cues could allow path curvature to be accurately perceived even if changes in heading were not coupled with rotation.

In the present experiments, however, observers did not appear to utilize acceleration to perceive path curvature. If observers fixated a point near their future path, which is

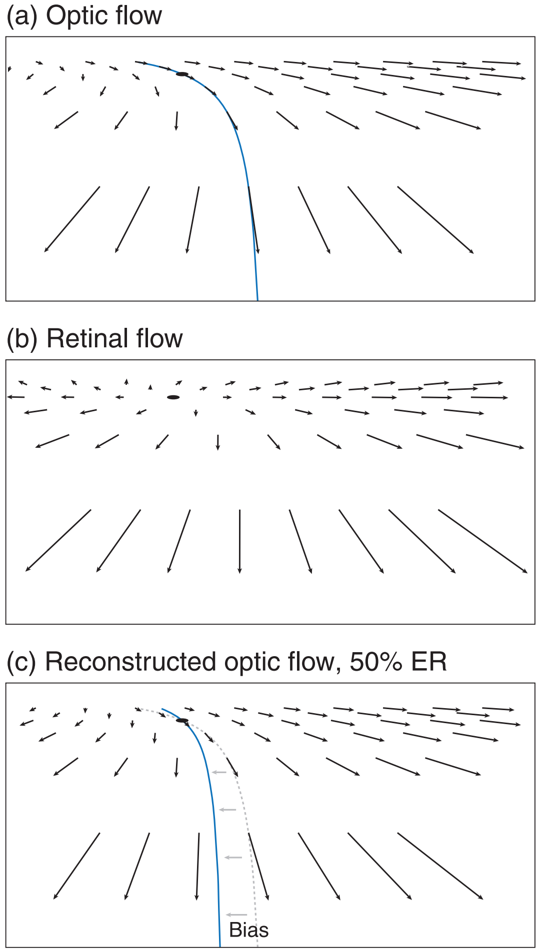

Figure 11. Illustration of the effect of incomplete compensation for pursuit eye movements in the Rotating View condition. (a) Optic flow for a circular path with 2°/s rotation and curvature. The locomotor flow line indicates the correct future path. (b) Retinal flow in the situation where an observer fixates a point on the future path. (c) Reconstruction of optic flow from retinal flow using an extra-retinal signal that underestimates rotation rate, with gain of 0.5. Lateral motion corresponding to 1°/s gaze rotation, rather than 2°/s rotation, was added to the retinal flow. The locomotor flow line of the reconstructed optic flow (solid blue line) corresponds to a path with half the curvature and an instantaneous heading shifted in the direction of curvature.

likely, then the acceleration cue identified by Wann and Swapp (2000) would have provided valid information for either of the view conditions tested here. Contrary to this prediction, performance was markedly different. In the Non-rotating View condition, the sign of path curvature had little effect on path judgments, and the small difference could be entirely explained by differences in mean heading over the course of a trial. Qualitative judgments further suggest that the Non-rotating View stimuli were often perceived as straight paths. Thus, I found no evidence that optical acceleration contributed to perception of path curvature.

Because I did not measure or control eye movements, the present study is not a strong test of the strategy proposed by Wann and Swapp (2000). Wann and Swapp emphasize the importance of fixating on the target of steering, and their proposed retinal flow cue specifies only whether the observer's future path passes to the left or right of the point of fixation. If observers did not reliably fixate points near their future path, conditions would not have been optimal for use of this strategy. To more directly test Wann and Swapp's strategy, one could use similar view conditions but with a target visible throughout motion. Judgments of future path relative to a visible fixated target might be more accurate than in direct estimates of future path, as tested here.

Another potential factor is the rate of curvature. The simulated paths tested here had modest curvature: heading changed by 2°/s at a speed of 4 m/s. In normal driving, the ratio of turning rate to speed would often be 2–4 times faster. At higher rates of curvature, the visual system might be better able to use information provided by optical acceleration.

Wilkie and Wann (2002, 2003) have observed effects of optic flow on steering that they interpret as use of the retinal flow cue proposed by Wann and Swapp (2000). However, these effects can alternatively be explained in terms of first-order optic flow. Their manipulation was to rotate the ground plane around the steering target. This alters Wann and Swapp's cue but also shifts the location of the instantaneous heading on the screen and changes the amount of simulated rotation in the displays. Either of these alternative factors could explain the effect of their manipulation on performance.

Results from a recent study by Li, Chen, and Peng (2009) might also appear to conflict with the present findings. Li et al. compared perceived self-motion along curved paths through random dot clouds for conditions where random dots were either static or dynamically replaced every 100 ms. If perceived path curvature is based on rotation in instantaneous optic flow, as hypothesized here, then one might expect little difference between the static and dynamic random dot conditions. However, Li et al. observed more accurate performance in the static dot condition, particularly when field of view was limited. They interpret their results as evidence that the extended visual trajectories of dots are important for path perception. Extended visual trajectories could potentially allow optical acceleration to be measured, which could explain the benefit observed by Li et al. This explanation would conflict with the present results. I have interpreted poor performance in the Non-rotating View condition as evidence that the visual system does not effectively utilize acceleration of visual trajectories over time.

An alternate explanation of Li et al.'s (2009) results is that extended visual trajectories allowed better estimation of first-order optic flow, thereby improving accuracy of judgments. Li et al. argue that the first-order optic flow in static and dynamic conditions was equivalent because local motion mechanisms have limited temporal integration. However, motion noise was not equated in these conditions because replacement of dots in the dynamic dot condition added spurious random motion signals. In their small field-of-view condition, the dot density was 2.6 per deg^2 and one-sixth of dots were replaced every 16 ms, so the additional noise was non-trivial. The difference between static and dynamic dot conditions observed by Li et al. could therefore be due to the differing amount of noise, rather than curvature of extended visual trajectories. Thus, it remains an open question whether optical acceleration contributes to the ability to perceive path curvature from optic flow.

Conclusion

The rotational component of optic flow that is not due to gaze pursuit provides a potential cue to path curvature. Path curvature is formally ambiguous from instantaneous optic flow, but curvature is often coupled to rotation of the viewer, so instantaneous rotation provides a potential cue to curvature. This cue has the advantage of being specified by instantaneous optic flow and therefore would not require analysis of optic flow over extended time.

The results presented here provide evidence that rotation is important for perception of self-motion along circular paths. The validity of rotation as a curvature cue requires that rotation and curvature be coupled, which is not always true. However, when this assumption does not hold, humans reveal predictable errors in their perceived self-motion. Previous studies have found that optic flow simulating travel on a straight path while rotating is perceived as a curved path (e.g., Ehrlich et al., 1998; Royden et al., 1992). The present results show that simulated travel on a curved path without rotation also leads to highly inaccurate perception. In this situation, observers were unable to account for curvature in judging their future path and often could not even determine whether the simulated path was curved or straight. These results demonstrate that view rotation is used to perceive path curvature from optic flow.

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