Research Report

RETINAL FLOW IS SUFFICIENT FOR STEERING DURING OBSERVER ROTATION

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Abstract—*How do people control locomotion while their eyes are simultaneously rotating? A previous study found that during simulated rotation, they can perceive a straight path of self-motion from the retinal flow pattern, despite conflicting extraretinal information, on the basis of dense motion parallax and reference objects. Here we report that the same information is sufficient for active control of joystick steering. Participants steered toward a target in displays that simulated a pursuit eye movement. Steering was highly inaccurate with a textured ground plane (motion parallax alone), but quite accurate when an array of posts was added (motion parallax plus reference objects). This result is consistent with the theory that instantaneous heading is determined from motion parallax, and the path of self-motion is determined by updating heading relative to environmental objects. Retinal flow is thus sufficient for both perceiving self-motion and controlling self-motion with a joystick; extraretinal and positional information can also contribute, but are not necessary.*

Research over the past decade has shown that people can perceive their direction of self-motion, or *heading*, quite accurately from patterns of optic flow (Gibson, 1950; Warren, in press; Warren, Morris, & Kalish, 1988). This is even the case when the observer's eye is rotating while traveling on a straight path, as during a pursuit eye movement. However, there has been controversy over whether heading during rotation can be determined from the retinal flow pattern alone (Stone & Perrone, 1997; van den Berg, 1992; van den Berg & Brenner, 1994; Wang & Cutting, 1999; Warren & Hannon, 1988, 1990), or whether extraretinal signals about eye movements are necessary, particularly at high rotation rates (>1°/s; Banks, Ehrlich, Backus, & Crowell, 1996; Ehrlich, Beck, Crowell, Freeman, & Banks, 1998; Royden, Banks, & Crowell, 1992). Using displays that simulate an eye rotation, we recently found that either type of information is sufficient to perceive a straight path of self-motion (Li & Warren, 2000). In particular, one's path can be judged from retinal flow with an accuracy of a few degrees as long as dense motion parallax and reference objects are both present. This led us to propose that the visual system determines instantaneous heading from the motion parallax field, and recovers the path of self-motion over time by updating heading with respect to environmental objects.

Although people may be able to perceive their path from retinal flow, it remains an open question whether such passive judgments generalize to the active control of self-motion. There are two reasons to think they may not. First, there is evidence that walking toward a target relies on the egocentric position of the target rather than the flow pattern (Rushton, Harris, Lloyd, & Wann, 1998). However, when adequate flow is available, it dominates positional information (Harris & Carre, 2001; Warren, Kay, Zosh, Duchon, & Sahuc, 2001; Wood, Harvey, Young, Beedie, & Wilson, 2000). Second, it has been argued that visually controlled action involves neural pathways different from those underlying explicit perceptual judgments, leading to dissociations between perceptual and motor performance (Goodale & Milner, 1992; Milner & Goodale, 1995). In our view, perception and action are likely to be similar to the extent that the tasks used to assess them depend on the same visual information (Smeets & Brenner, 1995; Vishton, Rea, Cutting, & Nunez, 1999). Our aim in the present experiment was to determine whether the information used in perceptual judgments of self-motion is also used to control steering with a joystick.

Two previous studies investigated joystick steering under simulated-rotation conditions. Rushton, Harris, and Wann (1999) found that participants could successfully steer toward a target in random-dot displays, with final heading errors below 4°. Frey and Owen (1999) reported evidence that steering accuracy correlates with the magnitude of motion parallax between objects in the scene. However, both of these studies tested the special case of fixating the target toward which one is steering. Consequently, the simulated rotation rates were very low (<1.5°/s and <0.6°/s, respectively) and decreased to zero as the heading neared the target, so participants could have performed the task simply by zeroing out the small rotational component of flow. The question at issue here is whether retinal flow is sufficient for steering during higher, sustained rotation.

In the present study, we asked participants to steer toward a target while fixating a moving object elsewhere in the scene. The critical comparison was between displays of a textured ground plane, which contained motion parallax but no reference objects, and displays with an array of posts on the textured ground plane, which contained both. If active steering is based on the same information as passive perceptual judgments, we would expect large errors with the ground displays, but accurate steering with the displays that also included the posts.

The logic of the experiment was as follows. In the actual-rotation condition, the display depicted forward travel while the fixation point moved on the screen, inducing a pursuit eye movement. Any extraretinal signals thus corresponded to the actual eye rotation. In the simulated-rotation condition, the fixation point remained stationary on the screen while the display simulated the optical effects of an eye rotation. Any extraretinal signals thus specified no eye rotation. If performance was found to be comparably accurate in the two conditions, this result would indicate that retinal flow is sufficient for steering, even when conflicting extraretinal signals are present. However, if performance was found to be markedly worse in the simulated condition, this would imply that an extraretinal signal may be necessary.

Further, the simulated condition rendered positional information from the target and posts useless for steering control. Specifically, the mapping between the joystick and the resulting heading direction varied from trial to trial, so one could not steer by pushing the joystick in the direction of the target. Thus, successful performance would also imply that participants could rely on retinal flow rather than positional information.

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METHOD

Participants

Seventeen students and staff at Brown University were paid to participate. Five naive participants viewed the ground display, and 9 others viewed the ground-plus-posts display. Three experienced participants viewed both types of displays. There were no systematic differences between experienced and naive observers.

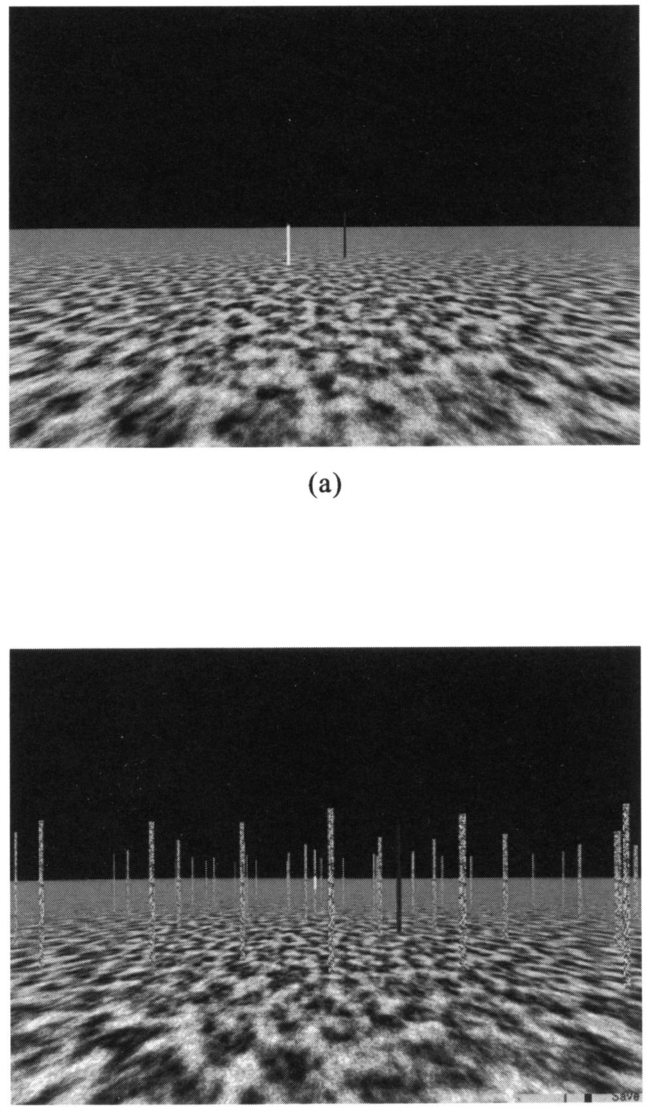
Displays

Displays depicted observer translation parallel to a ground plane. A blue target line appeared at a distance of 16 m (1 eye height = 1.6 m), and a red fixation point appeared at eye level on top of a white post, off to one side. The participant's task was to steer toward the target line while tracking the fixation point. The target was initially in a random position within ±10° from the center of the screen,[1] the initial heading was ±8° or ±12° from the target, and the fixation point was within ±10° of the initial heading. During a trial, the fixation point moved horizontally through the scene at a constant rotation rate (±3°/s or ±5°/s), and the target receded in depth to maintain a constant distance of 16 m. Thus, four initial headings were crossed with four rotation rates.

In the actual-rotation condition, the fixation point moved across the screen at the prescribed rotation rate while the depicted environment remained in place. In the simulated-rotation condition, the "camera" rotated about a vertical axis so that the fixation point remained in its initial screen location, simulating the effects of a pursuit eye movement. Consequently, the depicted environment, including the target and the heading point, moved horizontally on the screen; subsequent steering adjustments changed the heading direction and hence influenced the motion of the target. During accurate steering, the heading and target drifted together across the screen, opposite the simulated rotation.

Two environments were tested (see Fig. 1). In the *ground* condition, the ground plane (120 m in depth) was mapped with a green multiscale texture composed of a filtered noise pattern with a power spectrum of $1/f^2$ for the range of frequencies from 8 to 32 cycles per patch, anti-aliased with a mipmap-bilinear minification filter. The sky was black. Trial duration was 8 s. In the *ground-plus-posts* condition, 104 gray granite-textured posts were added on the textured ground surface, spanning a depth range of 2 to 25 m. The posts were planar, were 0.1 m wide, varied randomly in height (2.5–2.7 m), and were randomly rotated out of the frontal plane by −20° to 20° about a vertical axis. They were randomly positioned in eight rows, with 2 to 4 m between rows and 1.3 to 2.3 m between posts in a row. Trial duration was 6 s.

The displays were generated on a Silicon Graphics Crimson RE (SGI, Mountain View, California) at a frame rate of 30 Hz, and were rear-projected on a large screen (112° horizontal × 95° vertical) with a Barco 800 graphics projector (Barco N.V., Kortrijk, Belgium) with a 60-Hz refresh rate. They were viewed monocularly from a chin rest at a distance of 1 m. The lateral position of the joystick (CH Products Flightstick, Vista, California, with a HOTAS serial game-port converter, 30-Hz sampling rate) controlled the lateral component of velocity while the longitudinal component remained constant at 2 m/s. Thus, if the joystick were held in a fixed position, the observer would travel on a straight path through the environment. We recorded the time series of *heading error*, the angle between the instantaneous direction of motion and the direction to the target. In the simulated condition, positional information could not be used for successful steering because the joystick-display mapping depended on the rotation rate and initial heading. For example, on some trials, when the target appeared on the left of the screen (or drifted leftward), the participant had to push the joystick to the right to steer toward it. Moreover, one could not steer by canceling target drift, because successful steering made the heading drift with the target across the screen.



(a)

(b)

Fig. 1. Display conditions: (a) ground and (b) ground plus posts.

Procedure

Each subject participated in both the actual- and the simulated-rotation conditions, blocked in a counterbalanced order, with 256 test

1. Positive values are to the right, negative values to the left.

trials in each. In order to learn the joystick-display mapping, they first received 32 practice trials in each condition, with no explicit feedback on any trial.

RESULTS

Mean time series of heading error for the initial heading of ±8° appear in Figures 2 and 3; results for the initial heading of ±12° were similar. When the direction of rotation and initial heading were toward the same side of the target, the time series were symmetrical, so we collapsed these conditions (left column of each figure), and plotted them as though initial heading error were positive (to the right of the target) and rotation positive. We similarly collapsed the data when the rotation and initial heading were toward opposite sides of the target (right column of each figure), and plotted them as though initial heading error were positive and rotation negative. Thus, each panel in the figures represents one collapsed combination of rotation rate (±3°/s or ±5°/s) and initial heading (±8°), as indicated in the legend; positive heading errors are toward the same side of the target as the rotation, and negative heading errors are toward the opposite side.

With the ground display, heading errors in the simulated-rotation condition (Fig. 2a) increased sharply over time in the direction of simulated rotation, up to 40° when rotation and initial heading were toward the same side, and −20° when they were toward opposite sides. Clearly, retinal flow from the ground alone was not sufficient to steer toward the target. In the actual-rotation condition (Fig. 2b), in contrast, performance was quite accurate, with final heading errors smaller than 5° in all conditions. This confirms that extraretinal signals contribute to steering control during actual eye rotation.

With the ground-plus-posts display, performance in the simulated-rotation condition improved dramatically (Fig. 3a). Final heading errors were on the order of 5°, comparable to those in the actual-rotation condition (Fig. 3b). The mean heading error never rose from its initial value, indicating that steering adjustments correctly shifted heading toward the target, and standard errors were smaller than those for the ground display. This result demonstrates that participants can steer successfully as long as both motion parallax and reference objects are available. Moreover, the retinal flow is sufficient despite conflicting extraretinal signals (as in the simulated condition).

To analyze the results, we plotted the mean heading error in the last second of each trial as a function of the collapsed rotation rate, so positive rotations represent the data in the left columns of Figures 2 and 3, and negative rotations represent the data in the right columns. In the simulated condition (Fig. 4a), errors increased rapidly with rotation rate for the ground display, with steep slopes (5.93 and 5.32 for initial headings of 8° and 12°, respectively). In contrast, the slopes were much flatter for the ground-plus-posts display (1.23 and 1.12, respectively). A multivariate regression analysis revealed that the slopes for the two displays were significantly different, $t(76) = -13.12$, $p < .0001$, and $t(76) = -11.04$, $p < .0001$, respectively. This confirms that adding reference objects in the scene dramatically improves steering accuracy during simulated rotation. The slopes in the actual-rotation condition (Fig. 4b) were significantly shallower than the slopes in the simulated-rotation condition for the ground display (0.11 and 0.11), $t(60) = 12.97$, $p < .0001$, and $t(60) = 10.99$, $p < .0001$, confirming the contribution of extraretinal signals. The ground-plus-posts display also showed significantly shallower slopes in the actual-rotation condition (−0.05 and −0.14) than in the simulated-rotation condition, $t(92) = 10.59$, $p < .0001$, and $t(92) = 10.59$, $p < .0001$.

What were participants doing in the simulated-rotation condition without reference objects (Fig. 2a)? We can infer that they tried to cancel the target drift on the screen due to simulated rotation, for the predicted heading error (heavy lines in Fig. 4a) closely accounts for the data. The exception is the -5°/s rotation rate (collapsed data corresponding to Fig. 2a, bottom right panel), possibly because of the initial conditions at the start of a trial. The initial heading was on the side of the target opposite the direction of rotation, which induced a target drift in the same direction as the heading. To cancel the target drift, participants crossed in front of the target, coincidentally reducing heading error to zero (zero crossing in Fig. 2a, bottom right panel). In contrast, this was not the case for positive simulated rotations (Fig. 2a, bottom left panel). Participants may thus have accidentally discovered a strategy for steering toward the target, reducing the heading error in the -5°/s condition.

DISCUSSION

The results demonstrate that retinal flow is sufficient for joystick steering during observer rotation. When both motion parallax and reference objects were present, steering accuracy was on the order of 5° in the simulated-rotation condition, but when reference objects were removed, errors rose to as much as 40°. This clearly indicates that steering relative to objects in the environment can be based on retinal flow alone. At the same time, the high accuracy in the actual-rotation condition with the ground alone indicates that extraretinal signals also contribute to steering control. Taken together, these findings confirm that retinal flow and extraretinal signals are each sufficient to compensate for the effects of an eye rotation. However, successful steering during simulated rotation implies that retinal flow dominates when it is in conflict with extraretinal signals.

The results also show that positional information is not necessary for steering control. Participants were able to ignore the egocentric position of the target in order to steer successfully in the simulated condition. This confirms that optic flow, when it is available, dominates positional information during joystick steering as it does during walking (Warren et al., 2001).

These data allow us to conclude that the same information is used in passive perception and active control of self-motion under rotation. During simulated rotation, the combination of dense motion parallax and reference objects is sufficient for judgments of one's path of self-motion (Li & Warren, 2000) and for steering a path to the target. During actual eye rotation, extraretinal signals also contribute to accurate path judgments as well as to successful steering. Taken together, these results provide an example in which perceptual judgments and motor performance are comparable because they rely on similar information.

Why might reference objects be important? We believe that heading is perceived and controlled with respect to objects in the environment. Retinal flow is sufficient to determine *object-relative heading* (the visual angle between the heading direction and the direction of an object), but not *absolute heading* (the body's direction of travel in space). This is because the motion parallax field specifies one's instantaneous heading only in an oculo-centric reference frame, not in a body-centric frame. Further, to determine whether one is on a straight or curved path through the environment, one must integrate the instantaneous head-

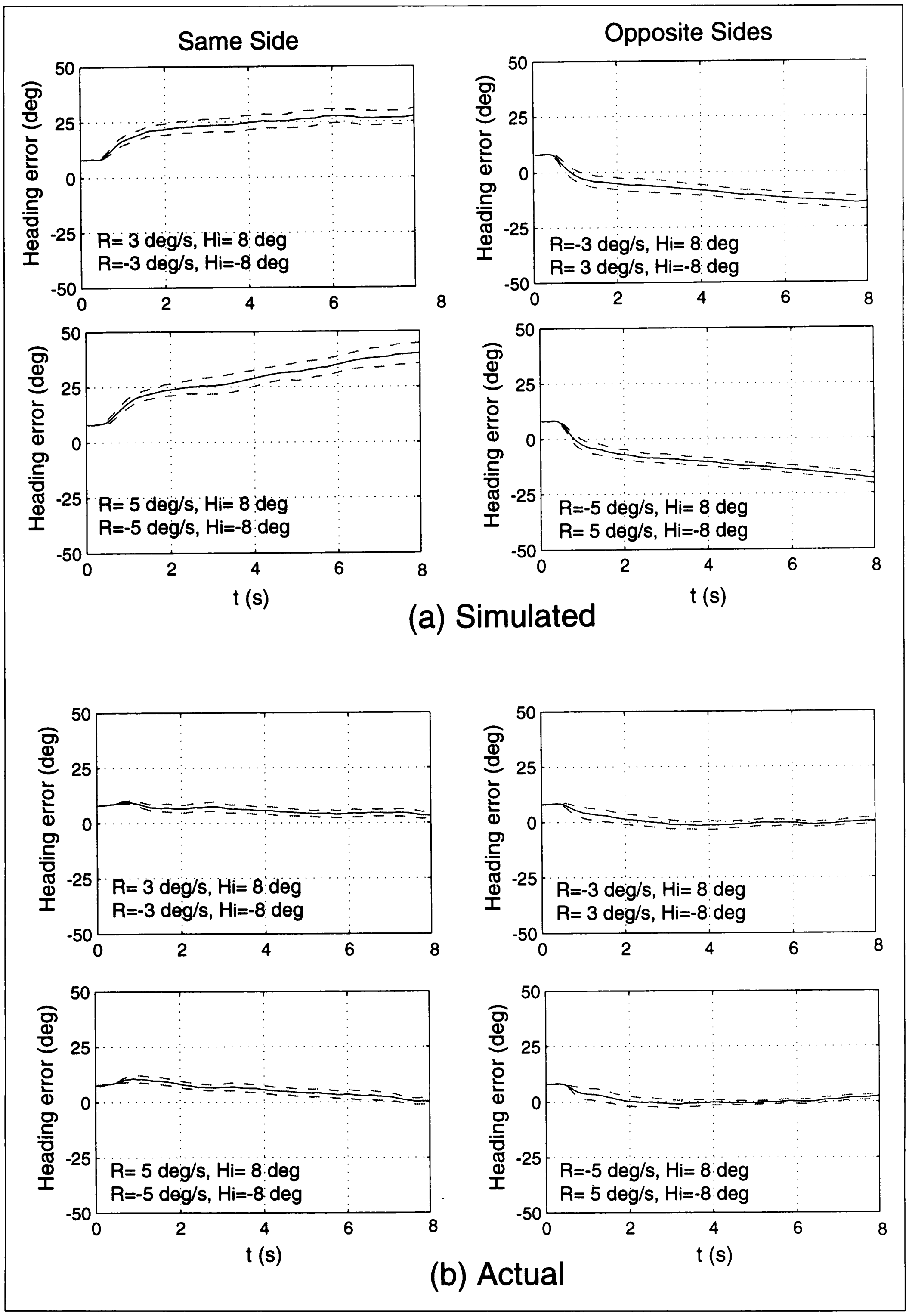


Fig. 2. Mean time series of heading error for the ground display, with an initial heading (Hi) of 8°. Results are shown separately for the simulated-rotation condition (a) and actual-rotation condition (b) with rates of rotation (R) of ±3°/s and ±5°/s. Data for initial heading and rotation toward the same side of the target are collapsed (left column), as are data for initial heading and rotation toward opposite sides of the target (right column). Data are plotted as though all initial headings were to the right of the target (positive heading error), as indicated by the top line of each legend. The dashed lines represent between-subjects standard error.

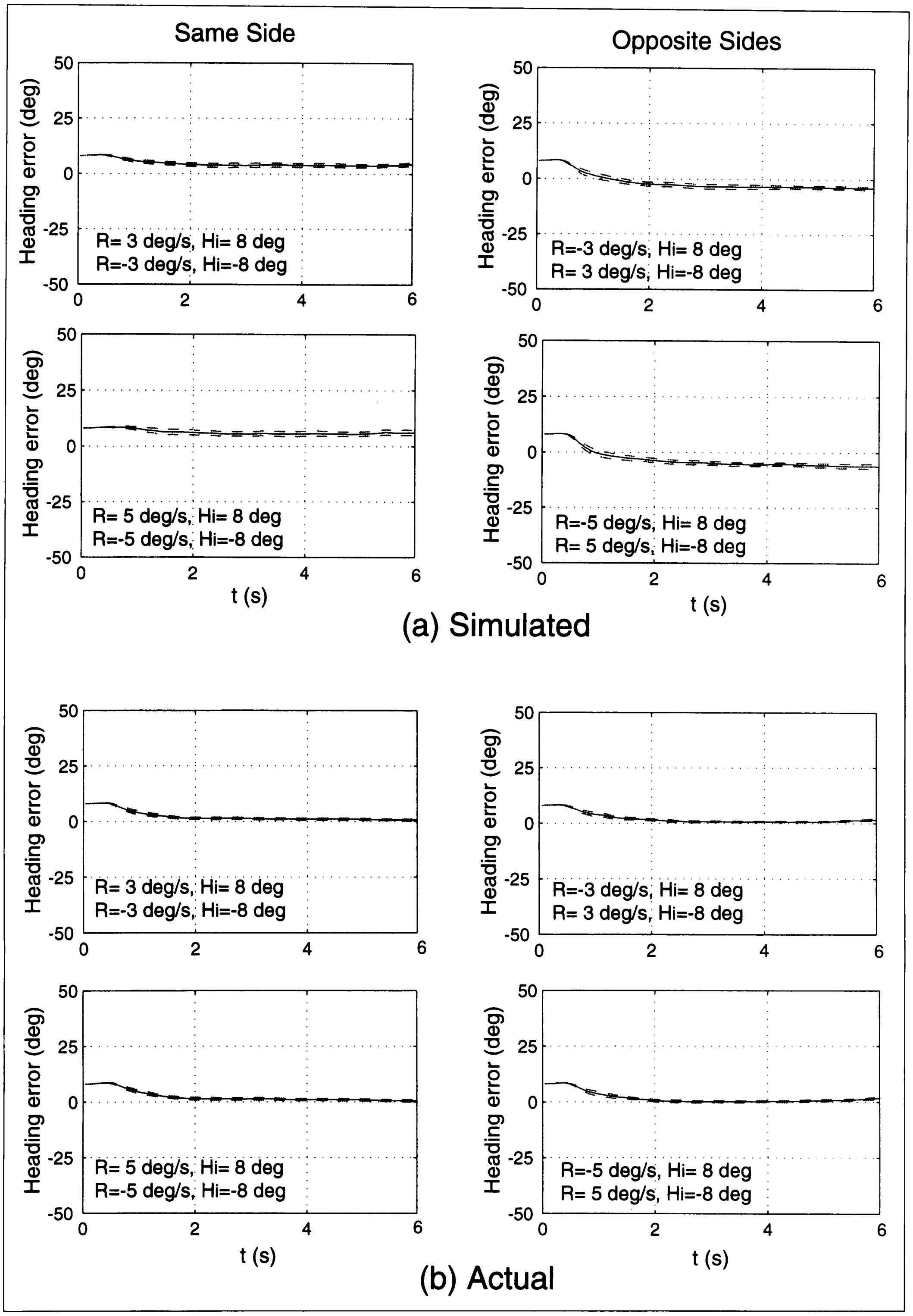


Fig. 3. Mean time series of heading error for the ground-plus-posts display, with an initial heading (Hi) of 8°. Results are shown separately for the simulated-rotation condition (a) and actual-rotation condition (b) with rates of rotation (R) of ±3°/s and ±5°/s. Data for initial heading and rotation toward the same side of the target are collapsed (left column), as are data for initial heading and rotation toward opposite sides of the target (right column). Data are plotted as though all initial headings were to the right of the target (positive heading error), as indicated by the top line of each legend. The dashed lines represent between-subjects standard error.

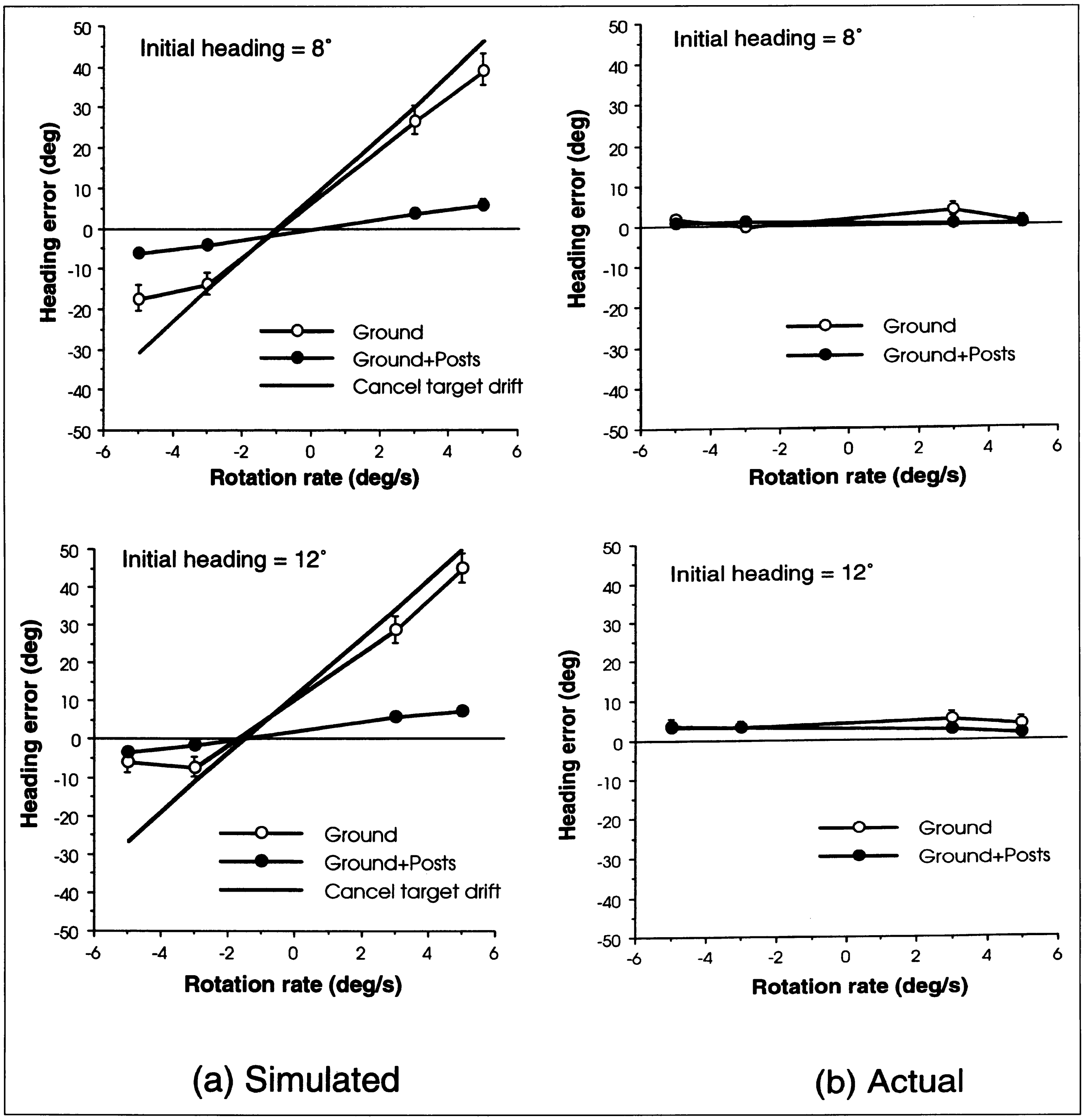


Fig. 4. Mean final heading error as a function of the (collapsed) rate of eye rotation in the simulated-rotation condition (a) and actual-rotation condition (b). Positive rotations are toward the same side of the target as the initial heading (corresponding to the left columns in Figs. 2 and 3), and negative rotations are toward the opposite side (corresponding to the right columns in Figs. 2 and 3). The heavy lines in (a) represent the predicted heading error for steering to stabilize the target on the screen.

ing over time. Reference objects allow the heading direction to be updated with respect to locations in the environment. The present findings are thus consistent with the proposal that one's instantaneous heading is determined from motion parallax, and one's linear path of self-motion is determined by updating heading with respect to objects in the scene (Li & Warren, 2000).

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