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Li L, Niehorster DC. Influence of optic flow on the control of heading and target egocentric direction during steering toward a goal. *J Neurophysiol* 112: 766–777, 2014. First published May 14, 2014; doi:10.1152/jn.00697.2013.—Although previous studies have shown that people use both optic flow and target egocentric direction to walk or steer toward a goal, it remains in question how enriching the optic flow field affects the control of heading specified by optic flow and the control of target egocentric direction during goal-oriented locomotion. In the current study, we used a control-theoretic approach to separate the control response specific to these two cues in the visual control of steering toward a goal. The results showed that the addition of optic flow information (such as foreground motion and global flow) in the display improved the overall control precision, the amplitude, and the response delay of the control of heading. The amplitude and the response delay of the control of target egocentric direction were, however, not affected. The improvement in the control of heading with enriched optic flow displays was mirrored by an increase in the accuracy of heading perception. The findings provide direct support for the claim that people use the heading specified by optic flow as well as target egocentric direction to walk or steer toward a goal and suggest that the visual system does not internally weigh these two cues for goal-oriented locomotion control.

optic flow; heading; target egocentric direction; locomotion control; self-motion

SUCCESSFUL CONTROL OF self-motion is essential for human survival. One important self-motion control task that we face frequently in our daily life is to walk or steer toward a goal successfully, such as when we travel to a place where we want to get, a person with whom we want to be, or a food source that we need to reach, etc. In the last two decades, the type of visual-control strategy that people use to accomplish this task has become a heated topic and attracted a lot of attention from researchers across many disciplines. Much research has centered on the use of the following four visual control strategies for goal-directed locomotion.

Heading Strategy

Gibson (1950, 1958) proposed that during locomotion, humans can use the projected image motion of the environment on the retina (optic flow) to perceive and control self-motion. For example, when we travel on a straight path with no body, head, or eye rotation (pure translation), the focus of expansion (FOE) in the resulting radial retinal flow indicates our instantaneous direction of travel (i.e., heading). To steer toward a target in the environment, we can thus align our heading specified by optic flow with the target (Fig. 1*A*). Previous studies have shown that during pure translation, we can perceive heading within 1° of visual angle to support the accurate control of locomotion toward a goal (Crowell and Banks 1993; Warren and Hannon 1988).

Under normal conditions, when we travel with eye, head, and/or body rotation (translation and rotation), the rotation shifts the FOE away from heading in retinal flow and complicates the process of extracting heading (Gibson 1950; Regan and Beverly 1982). Nevertheless, it has been shown that given sufficient optic flow information or extraretinal information about eye, head, and body movement, we can still estimate heading within 2° of visual angle to sustain successful control of locomotion toward a goal (Banks et al. 1996; Cutting et al. 1997; Grigo and Lappe 1999; Li et al. 2006b, 2009; Li and Warren 2000, 2004; Stone and Perrone 1997; van den Berg 1992; Warren and Hannon 1988).

Path Strategy

Lee and Lishman (1977) proposed that people can use the velocity vectors in the flow field to perceive their future path of travel directly without recovering heading. Mathematically, when traveling on a circular path, while fixating a target on the future path, the path of forward travel can be recovered by integrating all vertical flow lines in the flow field (Kim and Turvey 1999; Wann and Swapp 2000). Accordingly, Wann and Land (2000) proposed that we can use path, instead of heading, for the control of locomotion toward a goal. That is, we steer or walk to change path curvature to a set value, such that our path of forward travel would go through the target (Fig. 1*B*).

τ-Equalization Strategy

To steer toward a goal, we can also steer to render the simultaneous closure of two gaps: the target heading angle (θ) and the distance of the target along the heading direction (D; Fig. 1*C*); i.e., we steer to equalize the time to closure of the target heading angle (τ_θ) with the time to passage of the target (τ_p) (Kaiser and Mowafy 1993). τ_θ and τ_p are optically defined by the information in the flow field, and this strategy is thus called the τ-equalization strategy (Lee 1998; Fajen 2001). The use of the τ-equalization strategy for locomotion control would result in traveling on a spiral path with decreasing path curvature toward the target.

Egocentric Direction Strategy

In contrast to the above three strategies that rely on information from optic flow for locomotion control, it has been

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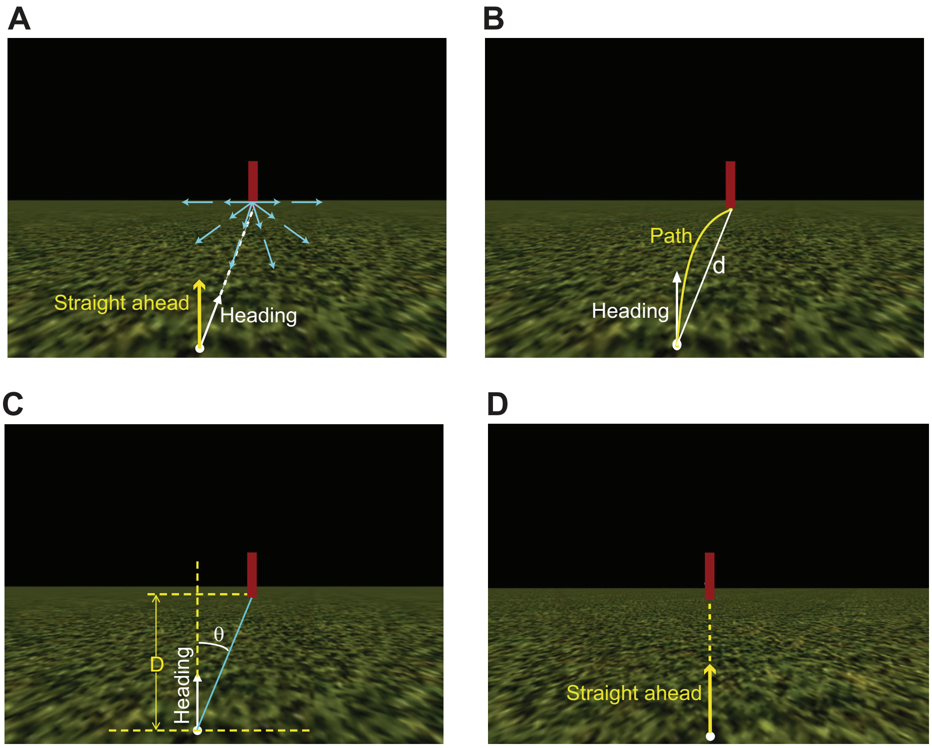

Fig. 1. Illustrations of the visual control strategies for goal-oriented locomotion. *A*: align the heading specified by optic flow with the target. *B*: align the future path with the target. d, distance. *C*: equate the time to closure of the target heading angle (θ) with the time to passage of the target distance along heading (D). *D*: center the target straight ahead.

proposed that people can walk or steer toward a goal using the target egocentric direction relative to their straight-ahead without relying on information from optic flow (Rushton et al. 1998; Warren 1998). For example, we can walk or steer toward a target by centering it straight ahead, which results in traveling on a straight-line course toward the target (Fig. 1*D*). We can also walk to cancel the target optical drift to keep the target at a fixed angle from the straight-ahead (Llewellyn 1971), which results in traveling on equal-angular spirals toward the target (Lee 1998; Rushton and Harris 2004).

Previous Studies

In previous studies that examined the flow-based strategies for the control of locomotion toward a goal, the target egocentric direction cue was also available. The availability of target egocentric direction could have affected the use of optic flow to perform the task, which most of these studies failed to consider [see also Harris and Rogers (1999)]. To examine systematically which flow-based strategy is used for goal-oriented locomotion control, Li and Cheng (2011) fixed the target's position on the screen, thus making the egocentric direction cue unavailable for steering to force participants to rely on information from optic flow to steer toward a target. They found that participants steered to align their instantaneous direction of travel (i.e., heading) but not their future trajectory of travel (i.e., path) with the target (see Fig. 1, *A* and *B*, respectively). Furthermore, participants did not steer toward the target by equalizing the τ_θ with the τ_p. This indicates that people do use heading specified by optic flow for goal-oriented locomotion control when target egocentric direction is unavailable. Chen et al. (2013) recently found that increasing travel speed increases participants' reliance on the heading strategy for locomotion control.

Under normal situations of traveling in the world, our heading and straight-ahead are aligned, such that walking or steering to align our heading with the target generates the same straight-line course to the target as walking or steering to center the target straight ahead. To decouple heading and the straight-ahead, Rushton et al. (1998) conducted a walking study, in which participants wore displacing prism glasses that shifted both heading and target visual direction away from the straight-ahead. If participants used the heading strategy and walked to keep their heading on the target, as heading and target visual direction were shifted together, then they should walk on a direct straight-line course to the target. Rushton et al. (1998) found that participants walked on a curved, spiral path toward the target, indicating that participants did not use optic flow to perform the task. Instead, their path was consistent with walking to center the target at their perceptual straight-ahead. However, as the prism glasses constantly shifted the target away from their straight-ahead during walking, participants could have also walked to cancel the target optical drift, which would result in the same walking trajectory toward the target.

Later studies, using prism glasses (Harris and Carré 2001; Turano et al. 2005; Wood et al. 2000) or head-mounted displays that mimicked the effect of the prism glasses (Bruggeman et al. 2007; Warren et al. 2001), found that participants walked on a straighter path with enriched optic flow displays. Specifically, Warren et al. (2001) displaced the heading specified by optic flow, 10° away from participants' physical walking direction with a head-mounted display, and found that when the display contained a complex, three-dimensional (3D) structure and dense optic flow, participants walked on a nearly straight path.

In the above walking studies, as the heading specified by optic flow was displaced from the physical walking direction, participants' visually perceived heading in the egocentric co-

Fig. 2. Experimental displays. *A*: sparse ground. *B*: sparse ground with foreground motion. *C*: dense ground with foreground motion. The target, shown as a red dot atop a gray post, was placed at optical infinity.

ordinate system is in conflict with their nonvisually perceived heading from the vestibular, proprioceptive, and motor information of the body and limb movements (Butler et al. 2010; de Winkel et al. 2010; Gu et al. 2008; Telford et al. 1995). To remove such a conflict and examine the contribution of visual information to the control of locomotion toward a goal, Li and Cheng (2013) had participants sit in front of a large screen that presented displays simulating their walking over a ground plane. Their simulated heading in the display was displaced 10° from the center of the screen that was aligned to their straight-ahead. Participants were instructed to use a joystick to control their simulated self-motion in the display to steer toward a target placed off to one side on the ground, to center the target straight ahead, or to minimize the target drift on the screen. Li and Cheng (2013) found that participants steered toward the target by centering it straight ahead instead of canceling the target optical drift. Regardless of the type of instructions received, the final heading errors were significantly smaller (~5°) with a textured ground than with an empty ground display, indicating that optic flow affects steering even when participants were explicitly instructed to steer using target egocentric direction alone.

Current Study

Although at present, it is unanimously agreed that optic flow affects the control of locomotion toward a goal, it is still in debate as to whether people use heading specified by optic flow when target egocentric direction is available for locomotion control. For example, Rushton and Salvucci (2001) proposed that when heading specified by optic flow is not aligned with one's straight-ahead, one's perceived straight-ahead can shift toward the displaced heading, thus affecting the perceived target egocentric direction. Accordingly, the effect of optic flow observed in previous walking studies could be due to the shifted perceived target egocentric direction rather than the use of heading. Indeed, it has been shown that after walking for a period of time with prism glasses that displaced heading specified by optic flow away from the straight-ahead, observers perceived their straight-ahead to be biased toward the displaced heading (Held and Bossom 1961; Herlihey and Rushton 2012; Morton and Bastian 2004; Redding and Wallace 1985). With the use of a visual control of steering task, Li et al. (2012) also found that the longer one steers toward a target with displaced heading, the larger the shift of the perceived straight-ahead.

To learn whether heading specified by optic flow is used in the visual control of locomotion, it is important to examine how increasing optic flow information in the display affects the control of heading and the control of target egocentric direction during goal-orientated locomotion. It is also important to examine whether the reduction of the heading target angle with added optic flow during locomotion control is directly linked to the improved accuracy of heading perception from optic flow, as this would show whether the improved control of heading is due to the improved heading perception.

To address the above issue, in the current study, we took a control, theoretical approach to separate the control response specific to heading and target egocentric direction cues in the visual control of steering toward a goal. We systematically varied optic flow information in the display to examine how the control of heading and the control of target egocentric direction were affected. In addition, we examined passive heading perception using the same rotation rates generated during active steering to find out whether the reduction in heading target angle with the added optic flow during active steering was coupled with the improved accuracy in heading perception.

Specifically, in the active steering experiment, the display simulated a participant steering a vehicle over a ground plane that contained sparse flow, sparse flow with foreground motion, or dense flow with foreground motion (Fig. 2). Participants used a joystick to control their simulated self-motion to steer toward a red post target placed at optical infinity, while facing random perturbations to both the vehicular heading and orientation (i.e., their virtual heading and gaze directions), consisting of two different sets of a harmonically independent sum of sines (Fig. 3*A*). As participants were seated, and the center of the display screen was calibrated to correspond to their straight-ahead, the vehicular heading perturbation shifted participants' heading specified by optic flow away from the target but did not affect the target visual direction relative to their straight-ahead, whereas the vehicular orientation perturbation shifted the target visual direction away from their straight-ahead but did not affect the heading target angle (Fig. 3*B*). The constant perturbation prevented any shift of the perceived straight-ahead reported by previous studies, due to walking or steering with heading displaced at a constant offset from the straight-ahead.

Participants had control of the vehicular heading but not the vehicular orientation. As a consequence, the control of heading was a closed-loop task, whereas the control of target visual

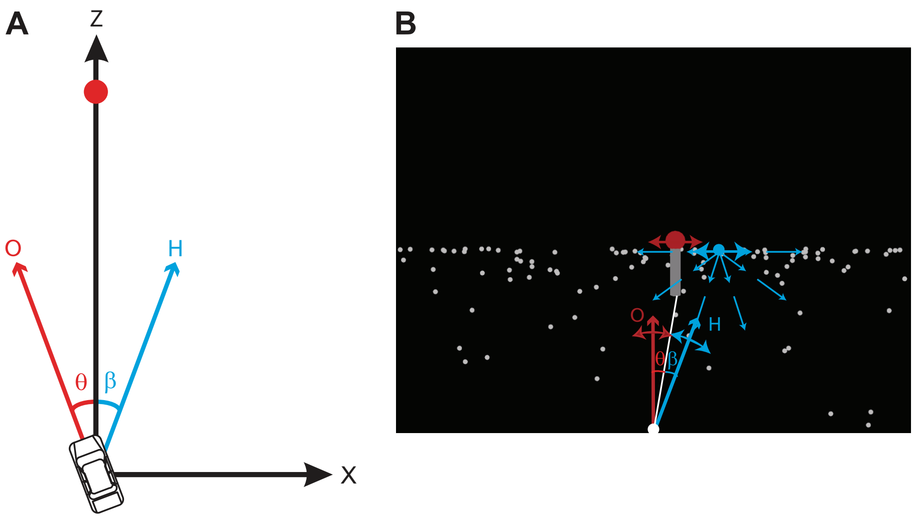

Fig. 3. Experimental setup. *A*: bird's-eye view showing the vehicle's heading (H) and its orientation (O) relative to the *z*-axis of the simulated environment, as well as the heading target angle (β) and the target visual direction relative to the straight-ahead (θ). *B*: front view showing the effects of the vehicular heading and orientation perturbations on the heading specified by optic flow and the target visual direction, respectively.

direction was an open-loop task (i.e., the control outputs affected heading specified by optic flow but not target visual direction). This has several benefits. First, the closed-loop control of heading task kept participants' control performance normal, due to the fact that their control outputs mattered, and they thus made an effort to performance as well as possible. As long as participants used target visual direction for steering, they would not be able to ignore this cue for their steering response. Instead, they would also respond to the perturbation to the vehicular orientation regardless of whether their response affected the input target visual direction. Both closed-loop and open-loop tasks can examine the control response specific to an input signal/cue and evaluate its effectiveness (Jagacinski and Flach 2003). Second, as the perturbations to the vehicular heading and orientation are nonharmonic, the control response specific to target visual-direction change, caused by the vehicular orientation perturbation, was separable from the control response specific to the heading change caused by the vehicular heading perturbation. This allowed an independent evaluation of the use of heading vs. target egocentric direction for steering control. The same technique has been used before to identify and model visual cue use in manual-control tasks (Sweet 1999; Sweet et al. 2003).

The display in the active steering experiment contained simulated gaze rotations, due to the perturbation to the vehicular orientation (i.e., the participant's virtual gaze direction). Accordingly, in the heading perception experiment, similar to the display used in previous studies that examined heading perception with simulated eye rotation (Cutting et al. 1997; Li and Warren 2000, 2004; van den Berg 1992), the display simulated a participant traveling on a straight path over a ground plane while looking at a target fixation point off to one side. Four mean-simulated, gaze-rotation rates ($\pm 2.5°$/s, $\pm 5.0°$/s, $\pm 7.5°$/s, or $\pm 10°$/s), spanning ~90% of the vehicular rotation in the active steering experiment, were tested. At the end of each 1-s trial, participants were asked to use a mouse to move a probe to indicate their perceived heading direction. The angle between the perceived and the actual heading at the end of the trial, defined as heading error, was measured.

The logic of the study is given as follows. If participants use their perceived heading from optic flow for steering control, then the change of the heading target angle with enriched optic flow display in the active steering experiment should reflect the change of the accuracy in heading judgment in the heading perception experiment. Specifically, we expect that with the increase of optic flow, both heading judgment and the control of heading would improve. Given that target egocentric direction is available immediately for locomotion control before participants initiate self-motion (Rushton et al. 1998; Warren et al. 2001), the control response time to target egocentric direction should be shorter than that to heading. If heading and target egocentric direction are used for steering control through an internal cue weighting (Wilkie and Wann 2003), as the control of heading improves with the added optic flow information, then the control of target egocentric direction should get worse.

MATERIALS AND METHODS

Participants

Fourteen students and staff at The University of Hong Kong, between the ages of 20 and 31, participated in the experiment. All had normal or corrected-to-normal vision and provided informed consent. Among them, seven (four women and three men; six naive to the specific goals of the study) participated in the active-control experiment, and 11 (four women and seven men; nine naive to the specific goals of the study) participated in the heading perception experiment. Four participants took part in both experiments, and both experiments were approved by the Human Research Ethics Committee for Non-Clinical Faculties at The University of Hong Kong.

Visual Stimuli and Control

Active steering experiment. The display simulated a participant steering a vehicle at the speed of 5 m/s over a ground plane (depth range: 1.4–100 m). During a trial, the vehicular traveling direction (i.e., the participant's virtual heading direction) and orientation (i.e., the participant's virtual gaze direction) were separately perturbed by a sum of seven harmonically independent sinusoids (Fig. 3*A*). A target, shown as a red dot (1.8° in diameter at eye height) atop a gray post (1.2° width × 2° height), was placed in infinity along the *z*-axis of the world. As the target was placed at optical infinity, the perturbation to the vehicular heading affected the target heading angle but did not affect the target visual direction on the screen. In contrast, the perturbation to the vehicular orientation affected the target visual direction but had no effect on the heading target angle (Fig. 3*B*).

Table 1. *Magnitudes (a_i) and frequencies (ω_i) of the 7 harmonically independent sinusoids in the input perturbations to the vehicular heading (H) and orientation (O)*

		Vehicular Heading (*H*)	Vehicular Orientation (*O*)
i	a_i	ω_i, Hz	ω_i, Hz
1	2	0.1	0.11
2	2	0.14	0.16
3	2	0.24	0.27
4	0.2	0.41	0.42
5	0.2	0.74	0.77
6	0.2	1.28	1.31
7	0.2	2.19	2.21

The input perturbation to the vehicular heading (*H*) and orientation (*O*) had the following form as a function of time (*t*)

$$I(t) = D \sum_{i=1}^{7} a_i \sin(2\pi\omega_i t + \rho_i) \quad (1)$$

Different values of ω_i were used to result in two different sets of seven nonharmonically related frequencies for the perturbations to the vehicular *H* and *O*. The perturbation spectra were chosen to conform to the guidelines for pilot frequency response identifications (McRuer and Krendel 1974). Table 1 lists the values of *a* and ω used for *H* and *O*, respectively. The use of two different sets of harmonically independent sums of sinusoids for the perturbations to the vehicular heading and orientation made them appear pseudo random, whereas the control response to each can be separated during data analysis. The disturbance gain (*D*) was set to values of 4.6° and 1.7° for the vehicular heading and orientation perturbations, respectively. The phase offset of each sine component (ρ_i) was randomly varied from $-\pi$ to π in each trial. The random phase offset of each frequency component ensured that each trial was different from the previous trials. When generating the perturbations, we searched for a point in the time series where the perturbation was zero and started the trial at that point. As such, both the vehicular heading and orientation direction offsets were zero at the beginning of each trial.

The average magnitude of the uncorrected heading target angle (β), due to the vehicular heading perturbation, was 9.2° (peak: 30.4°), and the average magnitude of the target visual direction relative to the straight-ahead (θ), due to the vehicular orientation perturbation, was 3.5° (peak: 11.4°). The larger perturbation magnitude used for heading made the control of heading more difficult but ensured that the control responses to both cues were stable and normal, given that the control of target visual direction was an embedded task. This practice is common in manual control studies (Sweet 1999) and should have no effect on the measurement of the gain of the control response as long as the perturbation is within the controllable range. This is due to the fact that the control gain is the ratio of the control response and the input perturbation specific to each cue. This was confirmed by the data from a pilot study in which we used the same average magnitude (3.5°) for both heading and target visual-direction perturbations.

Participants were asked to use a high-precision joystick (JF3; BG Systems, Palo Alto, CA) to control the vehicular heading (i.e., their virtual heading) to steer toward the target; i.e., the joystick's left-right displacement was proportional to the rate of change of the vehicular heading, whereas the traveling speed remained constant at 5 m/s. The control dynamics of the joystick (see Y_c in Fig. 4) were thus velocity control. The joystick position was sampled at 60 Hz. The largest joystick displacement corresponded to a peak heading movement velocity at 28.6°/s. As the control outputs affected heading but not target visual direction, the control of heading is a closed-loop task, whereas the control of target egocentric direction is an open-loop task. A simplified block diagram of the whole control system is shown in Fig. 4. The duration of each trial was 95 s. Following previous studies on manual control (Li et al. 2005, 2006a, 2011; Li WO et al. 2009), all chosen frequencies for the vehicular heading and orientation perturbations went through an integer number of cycles in 90 s, and we added 5 s in each trial, such that we could skip the initial transient response at the beginning of the trial.

Heading perception experiment. To examine heading perception in the active steering experiment that contained simulated gaze rotations due to the perturbation to the vehicular orientation (i.e., the participant's virtual gaze direction), the display in the perception experiment simulated a participant traveling on a straight path over a ground plane (depth range: 1.4–100 m) at 5 m/s, while looking at a target at eye height off to one side. Each 1-s trial was constructed as follows. The fixation point, a red circle (1.4° diameter) atop a gray post (0.8° width), was positioned at a distance of 15 m in the world with an initial heading angle up to 21.5° (final heading angle up to 31.3°). Following previous practice (Li and Warren 2000, 2004), this angle was chosen, such that the mean eye rotation rate over the course of each 1-s trial was ±2.5°/s, ±5.0°/s, ±7.5°/s, or ±10°/s [see General Method in Li and Warren (2000) for the computation of mean eye rotation rates]. Positive values indicate rightward eye rotation and negative values leftward eye rotation. These eye rotation rates spanned close to 90% of the simulated gaze/vehicular rotation rates in the active steering experiment.

The "camera" in the computer program was oriented such that the fixation point appeared in a random position within 8° of the center of the display. The heading direction thus appeared at an angle up to 29.5° (final angle up to 39.3°) from the center of the display. During the course of the trial, the camera rotated to keep the fixation point stationary on the screen, simulating the retinal effects of eye rotation during pursuit tracking of a target off to one side of the walking path. The flow pattern in the display was thus the sum of a translational component due to the simulated forward self-motion and a rotational component due to the simulated gaze rotation, similar to that in the active steering experiment.

At the end of each trial, a white horizontal line appeared at the center of the screen. Participants were asked to use the mouse to move a white vertical probe (3.7° height), which appeared in a random position within 20° from the center of the screen along the horizontal line to indicate their perceived heading. The angle between the perceived heading and the actual heading at the end of the trial, defined as heading error, was measured.

For both experiments, three display conditions providing an increasing amount of optic flow were tested. *1*) Sparse ground: the ground plane consisted of 100 white dots (0.5° diameter; luminance contrast 99+%) uniformly distributed on the ground. Due to the

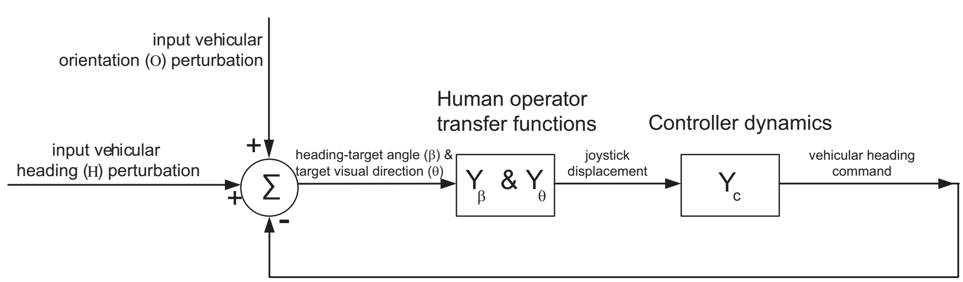

Fig. 4. Simplified block diagram of the active steering task. Human operator transfer functions, Y_β and Y_θ, capture the participant's control response to heading and target visual direction, respectively, and Y_c specifies the joystick control dynamics.

perspective projection, most dots were clustered near the horizon (Fig. 2*A*). This display provided almost no foreground motion and sparse motion parallax information. *2*) Sparse ground with foreground motion: the 100 dots were distributed on the ground plane, such that the same number of dots was placed at each distance in depth in the trapezoidal viewing frustum (Fig. 2*B*). As a result, the nearby ground plane was covered with the same number of dots as was the far ground plane; this display thus provided more foreground motion and motion parallax information than did the sparse ground display. *3*) Dense ground with foreground motion: the ground plane was composed of 300 white dots that were distributed, such that the same number of dots was placed at each distance in depth (Fig. 2*C*). This display provided dense global flow and motion parallax information due to the increased number of dots and foreground motion. For all three displays, the number of visible dots/frame and the dot distribution in depth were kept constant throughout the trial. The background sky was black in all three displays.

The visual stimuli were generated on a Dell Precision Workstation 670n with an NVIDIA Quadro FX 1800 graphics card at the frame rate of 60 Hz. They were rear projected on a large screen (109° horizontal × 94° vertical) with an Epson EMP-9300 liquid-crystal display projector (native resolution: 1,400 × 1,050 pixels; refresh rate: 60 Hz) in a light-excluded viewing booth. The screen edges were covered with matte black cloth to minimize the availability of an artificial frame of reference. To minimize the conflict between the simulated 3D self-motion and the binocular information about the flatness of the screen, participants viewed the displays monocularly with their dominant eye. The simulated eye height in the display was at 1.51 m, corresponding to the average eye height of participants sitting on a high chair with their head stabilized by a chin rest at 0.56 m away from the screen.

Procedure

Active steering experiment. Participants pulled the trigger of the joystick to start each trial. They were instructed to imagine that they were looking through the windshield of a vehicle that was traveling on a straight path while facing crosswind perturbations to both the vehicular heading and orientation. Their task was to use the joystick to steer toward the target. The vehicle initially moved according to the sum-of-sines heading perturbation input, but its movement was soon controlled as the participant moved the joystick leftward and rightward to control the vehicular heading to steer toward the target.

As the target was placed at optical infinity, a change in the vehicular heading did not affect the target visual direction on the screen but only changed the heading target angle in the display. In contrast, a change in the vehicular orientation did not affect the heading target angle but only changed the target visual direction on the screen. Accordingly, in the absence of optic flow, participants could only notice the change in the target visual direction and steer to maintain the target straight ahead. In the presence of optic flow, participants could perceive the vehicular heading and steer to minimize the heading target angle.

The experiment consisted of three blocks of six trials, with each block containing one display condition. Participants viewed all three display conditions, and the testing order of the display condition was counterbalanced among participants. To ensure that participants learned the controller dynamics of the joystick and could control their simulated self-motion to steer toward the target, they received practice trials before the experiment commenced. A different random dot ground with foreground motion display, in which the ground plane was composed of 200 dots, was used for the practice trials. Participants first received practice trials in which the initial heading was displaced 10° to the left or right of the target, and they used the joystick to steer toward the target with no crosswind perturbation. Then, participants received practice trials with only the vehicular heading perturbation. The practice continued until participants reported that they could comfortably steer toward the target, which required four to six trials. Last, participants received two practice trials with both the vehicular heading and orientation perturbations as in the experimental trials. Note that we used a different display and did not provide participants with any feedback about their control performance during practice; thus we did not encourage participants to use one cue or the other. The primary purpose of training was to stabilize their control and make their performance consistent across different trials to reduce the variance. The experiment lasted <2 h.

Heading perception experiment. In each trial, the first frame was frozen; participants were asked to fixate on the red circle atop the gray post and click the mouse to start the trial. Participants were asked to continue to fixate on the red circle throughout the 1-s trial. At the end of the trial, participants were asked to use the mouse to move a vertical probe along a horizontal line in the middle of the screen to indicate their perceived instantaneous direction of traveling. They then clicked the mouse to proceed to the next trial.

The experiment contained 360 randomized trials (three display conditions × eight rotation rates × 15 trials). Before the experiment started, participants received 72 randomized practice trials (three display conditions × 24 trials). To ensure that participants understood the instructions and were indicating their perceived heading but not path at the end of the trial (Li and Cheng 2011), feedback was provided in the practice trials. Accordingly, we used different translation (ranging from 4.6 to 5.3 m/s) and rotation rates (ranging from 2.3 to 10.6°/s) for the practice trials, such that participants could not rely on any artificial 2D cue to perform the heading task in the experimental trials. No feedback was given during the experimental trials. The entire experiment lasted ~30 min.

Data Analysis

For the active steering experiment, the time series of the input vehicular heading and orientation perturbations, the joystick control output, and the heading target angle were recorded. We analyzed the data, beginning 5 s after the start of the trial, to skip the initial transient response in each 95-s trial. Total performance error was measured as the mean (reflecting overall control accuracy) and root mean square (RMS; reflecting overall control precision) of the recorded time series of the heading target angle.

To examine participants' control response specific to heading and target egocentric direction cues, we performed Fourier transforms of the time series of the joystick control output (in percent of maximum displacement), the heading target angle (in degree of visual angle), and the target visual direction relative to the straight-ahead (also in degree of visual angle). Specifically, we took the ratios of the Fourier-transformed joystick displacement and the heading target angle to obtain the control gain (in percent of max/degree) and phase lag of the human operator transfer function for the control of heading (see Y_β in Fig. 4) and the ratios of the Fourier-transformed joystick displacement and the target visual direction relative to the straight-ahead to obtain the control gain and phase lag of the human operator transfer function for the control of target visual direction (see Y_θ in Fig. 4) at each perturbation frequency for each display condition. The control gain and phase lag measure the amplitude and the delay of the control response, respectively. Note that the gain and phase of the control response to heading and target egocentric direction were computed with respect to the input perturbation specific to that cue. As the input perturbation frequencies for heading and target egocentric direction cues are not harmonically related, the computed gain and phase of the control response to each cue show the control characteristic specific to that cue. Theoretically, the pattern of results should remain the same regardless of whether heading is closed-loop controlled and whether target visual direction is open-loop controlled or vice versa.

For both the active steering and heading perception experiments, the pattern of data from the experienced and naive participants was

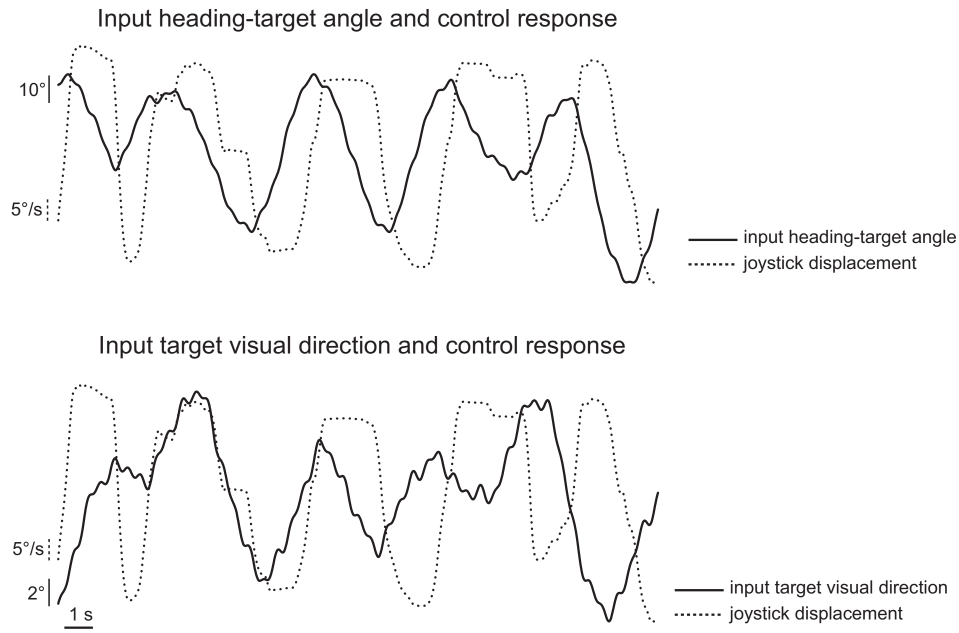

Fig. 5. Typical raw performance data from part of a trial. The solid lines depict the input heading target angle and target visual direction, respectively. The dotted lines depict the output joystick control displacement.

similar. The data from all participants were thus analyzed together. To examine the effect of display condition on the task performance, we conducted repeated-measures ANOVAs on the measured performance metrics.

RESULTS

Active Steering Experiment

Overall performance. Figure 5 plots typical raw performance data from part of a trial, depicting the input heading target angle and the output joystick control displacement, as well as the input target visual direction relative to the straight-ahead and the joystick control displacement. Note that the former is closed-loop control and the latter is open-loop control. As expected, the joystick response is a scaled and delayed version of both the input heading target angle and target visual direction, with a clear falloff in the response at the highest frequencies.

The overall control accuracy, measured as the mean heading target angle averaged across six trials, is plotted against display condition for each participant in Fig. 6*A*. A one-way repeated-measures ANOVA on the mean heading target angle revealed that the effect of display condition was not significant [$F(2,12) = 1.3$, $P = 0.31$], indicating that the overall control accuracy was similar across the three display conditions. Separate *t*-tests showed that the mean heading target angle was not significantly different from zero for all three display conditions [$t(6) < 1.06$, $P > 0.32$], indicating that participants could, in general, steer to align their heading with the target.

The overall control precision, measured as the RMS heading target angle averaged across six trials, is plotted against display condition for each participant in Fig. 6*B*. As heading could go off of the screen when participants ignored heading and responded only to target visual direction, the uncorrected RMS heading error can be very large. A one-way repeated-measures ANOVA on the RMS heading target angle revealed that the effect of display condition was highly significant [$F(2,12) = 29.36$, $P < 0.0001$]. Newman-Keuls tests further revealed that the mean RMS heading target angle for the sparse ground display (14.09°) was significantly larger than those for the sparse ground with foreground motion and the dense ground

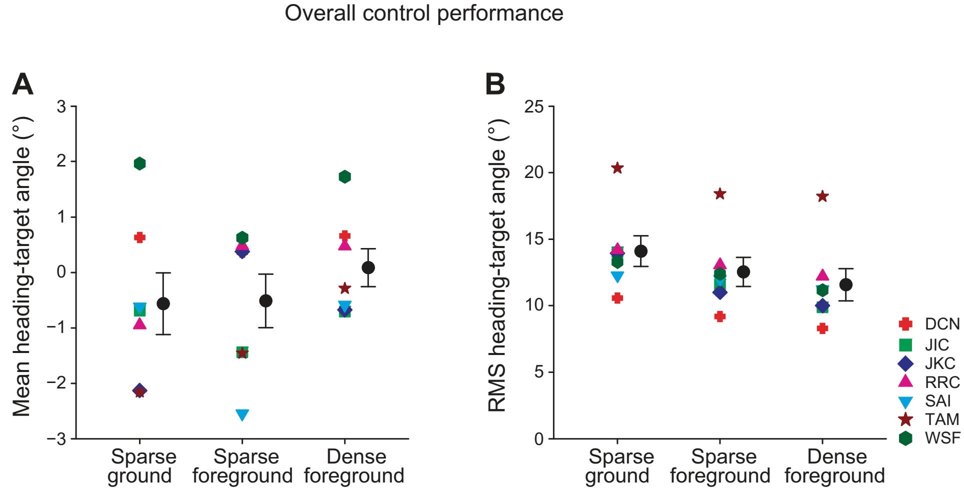

Fig. 6. Overall performance data from the active steering experiment. Mean (*A*) and root mean square (RMS; *B*) heading target angles against display condition for each participant along with the mean averaged across participants. Error bars represent SE across 7 participants.

with foreground motion displays (12.53°, $P < 0.001$, and 11.57°, $P < 0.001$, respectively), and the latter two were also significantly different from each other ($P < 0.05$). This indicates that the overall control precision improves with the addition of optic flow information in the display.

The mean and RMS heading target angle measure the total performance error that includes both the control response error driven by the input visual signals, as well as the noises in motor control not related to the input visual signals. The control response at the perturbation frequencies provides a better measure of the visually driven component of the control response. In the following section, we present the results from the Fourier analysis on the performance data to show how participants responded to the input heading target angle (β) and target visual direction relative to straight-ahead (θ) in each display condition at each vehicular heading and orientation perturbation frequency, respectively.

Frequency response performance. To analyze participants' response specific to heading specified by optic flow, we computed the human operator transfer function Y_β (i.e., the ratio of the Fourier transform of the output joystick displacement to that of the heading target angle; see Fig. 4). Figure 7*A* plots the gain and phase of Y_β, averaged across six trials and seven participants, as a function of the input vehicular heading perturbation frequency for the three display conditions. Consistent with the findings of previous manual control studies [Jagacinski and Flach (2003); McRuer et al. (1965); McRuer and Krendel (1974); Sweet (1999); see a review in Wickens (1986)], the control gain increases with frequency, with little phase lag at low frequencies (≤0.24 Hz). The phase then rolls off progressively with frequency, and the gain also decreases sharply at highest frequencies, due to the natural bandwidth of manual control.

To examine how the control of heading changes with display condition, we conducted a three (display condition) × seven (frequency) repeated-measures ANOVA on the gain and phase, respectively. For the gain, both the main effects of display condition and frequency were significant [$F(2,12) = 14.52$, $P < 0.001$, and $F(6,36) = 32.4$, $P \ll 0.0001$, respectively] and so was their interaction effect [$F(12,72) = 2.59$, $P < 0.01$]. The effect of display condition on the control gain was larger at the highest three frequencies than at the lower four frequencies (Fig. 7*A*). Newman-Keuls tests revealed further that the mean gain averaged across seven perturbation frequencies for the sparse ground display (5.28 dB) was significantly lower than those for the sparse ground with foreground motion and the dense ground with foreground motion displays (7.32 dB, $P < 0.05$, and 9.42 dB, $P < 0.001$, respectively), and the latter two were also significantly different from each other ($P < 0.05$; Fig. 7*B*). This indicates that the gain of the control of heading increases with the added optic flow information in the display.

For the phase, the repeated-measures ANOVA showed that both the main effects of display condition and frequency were significant [$F(2,12) = 7.41$, $P < 0.01$, and $F(6,36) = 488.61$, $P \ll 0.0001$, respectively], but their interaction effect was not [$F(12,72) = 0.55$, $P = 0.87$]. Newman-Keuls tests revealed that the mean phase lag averaged across seven perturbation frequencies for the dense ground with foreground motion display (148.2°) was significantly smaller than those for the sparse ground and the sparse ground with foreground motion displays (170.4°, $P < 0.01$, and 164.5°, $P < 0.05$, respectively), and the latter two were not significantly different from each other ($P = 0.34$; Fig. 7*B*). This indicates that the phase lag of the control of heading decreases when the display contains a dense flow field with foreground motion.

To analyze participants' response specific to target visual direction, we computed the human operator transfer function Y_θ (i.e., the ratio of the Fourier transform of the output joystick displacement to that of the target visual direction relative to the straight-ahead; see Fig. 4). Figure 8*A* plots the gain and phase of Y_θ, averaged across six trials and seven participants, as a function of the input vehicular orientation perturbation frequency for the three display conditions. Different from the control of heading, the control of target visual direction shows a phase lead at low frequencies (≤0.24 Hz), indicating that participants were predicting target visual direction for steering. The phase lead is coupled with the low gain at these frequencies to prevent overshooting in the control response. Both gain and phase then roll off progressively with frequency, due to the natural bandwidth of manual control responses. Note that if participants ignored the target visual-direction cue, then they

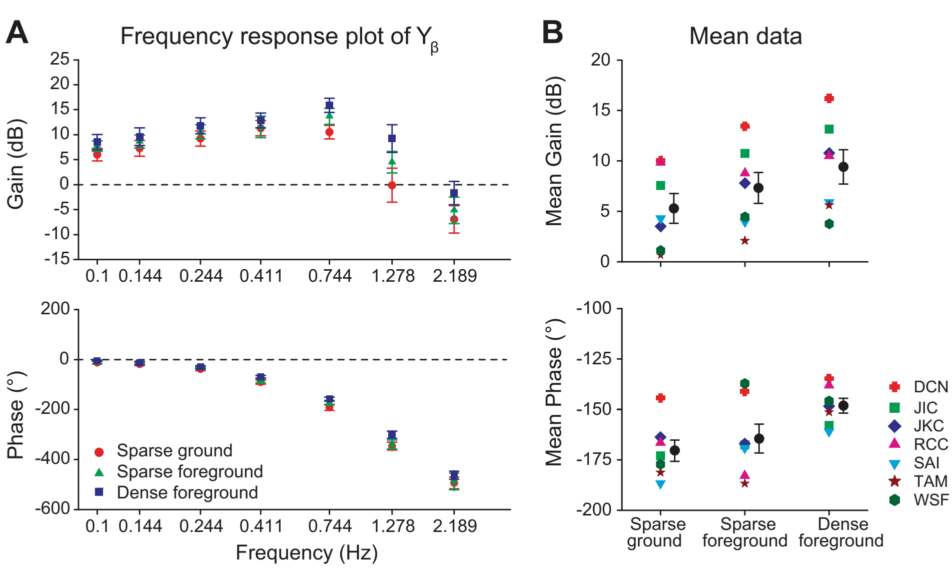

Fig. 7. *A*: frequency response (Bode) plot of Y_β. *Top*: mean control gain; *bottom*: mean phase averaged across 7 participants as a function of vehicular heading perturbation frequency. *B*: mean gain (*top*) and mean phase (*bottom*) averaged across 7 perturbation frequencies against display condition for each participant, along with the mean averaged across 7 participants. Error bars represent SE across participants (some of them are smaller than the data symbols).

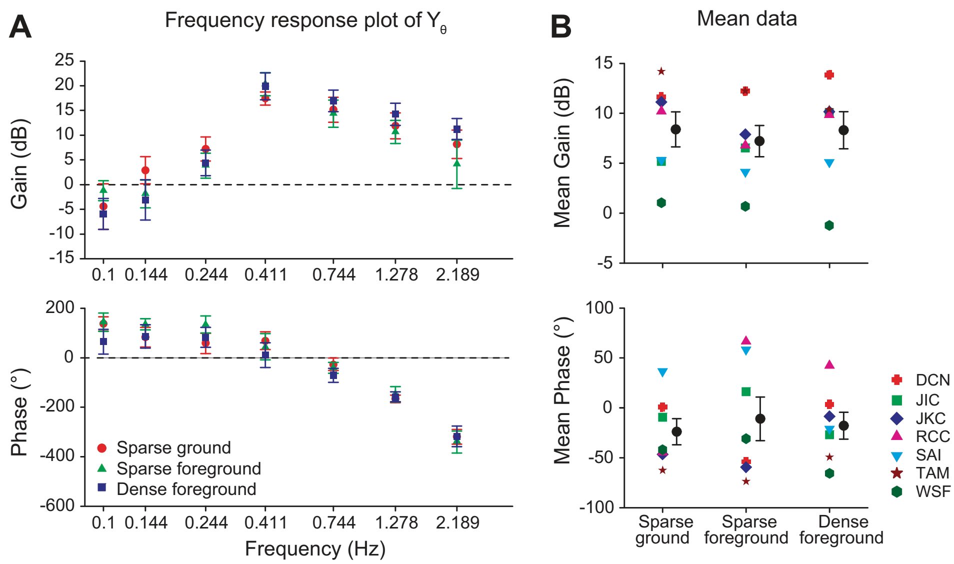

Fig. 8. *A*: frequency response (Bode) plot of Y_θ. *Top*: mean gain; *bottom*: mean phase averaged across 7 participants as a function of input vehicular orientation perturbation frequency. *B*: mean gain (*top*) and phase (*bottom*) averaged across 7 perturbation frequencies against display condition for each participant, along with the mean averaged across 7 participants. Error bars represent SE across participants (some of them are smaller than the data symbols).

would not have responded to the vehicular orientation perturbation, and the gains at all input vehicular orientation perturbation frequencies would have been similar and close to zero ($-\infty$ dB).

To examine how the control of target visual direction changes with display condition, we also conducted a three (display condition) × seven (perturbation frequency) repeated-measures ANOVA on the gain and phase, respectively. For the gain, whereas the main effect of frequency was highly significant [$F(6,36) = 17.55$, $P \ll 0.0001$], the main effect of display condition was not [$F(2,12) = 1.09$, $P = 0.37$]. Their interaction effect was marginally significant [$F(12,72) = 1.88$, $P = 0.051$]. There is a trend that the effect of display condition on the control gain differs at different perturbation frequencies, which, however, is not systematic (Fig. 8*A*). The mean gain averaged across seven perturbation frequencies is not different across the three display conditions (Fig. 8*B*), indicating that the gain of the control of target visual direction is not affected by the added optic flow information in the display.

For the phase, the repeated-measures ANOVA showed again that whereas the main effect of frequency was highly significant [$F(6,36) = 83.14$, $P \ll 0.0001$], the main effect of display condition was not [$F(2,12) = 0.24$, $P = 0.79$]. Their interaction effect was also not significant [$F(12,72) = 0.67$, $P = 0.77$]. Similar to the gain, the mean phase averaged across seven perturbation frequencies is not different across the three display conditions (Fig. 8*B*), indicating that the phase lag of the control of target visual direction is also not affected by the added optic flow information in the display.

Last, to compare directly the control of heading with the control of target visual direction, we conducted a three (display condition) × two (cue) repeated-measures ANOVA on the mean control gains and phases averaged across the seven perturbation frequencies (Fig. 9). For the gain, whereas the main effect of cue was not significant [$F(1,6) = 0.1$, $P = 0.76$], both the main effect of display condition and the interaction effect of display condition and cue were significant [$F(2,12) = 5.18$, $P < 0.05$, and $F(2,12) = 10.08$, $P < 0.01$, respectively]. Separate one-way repeated-measures ANOVAs revealed that whereas the main effect of display was significant for the control gain specific to heading [$F(2,12) = 14.52$, $P < 0.001$], it was not significant for the control gain specific to target visual direction [$F(2,12) = 1.09$, $P = 0.37$]. This indicates that whereas the overall control gain averaged across the three display conditions is comparable for the control of heading and the control of target visual direction, adding optic flow information in the display increases the control gain specific to heading but not target visual direction (Fig. 9*A*). Furthermore, a Newman-Keuls test revealed that for the sparse ground display condition that provided only a sparse flow field, the

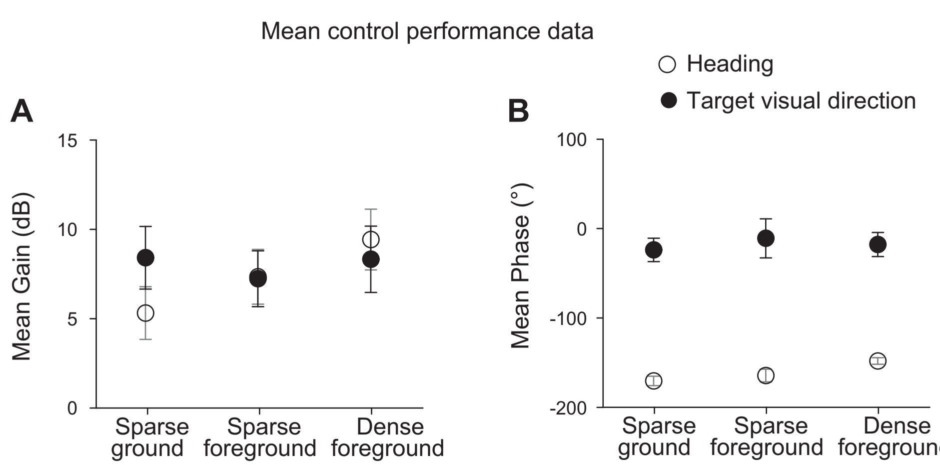

Fig. 9. Mean gain (*A*) and mean phase (*B*) of the control of heading and target visual direction against display condition. Error bars represent SE across 7 participants (some of them are smaller than the data symbols).

mean control gain specific to target visual direction (8.28 dB) is significantly larger than that to heading (5.28 dB, $P < 0.01$), indicating that participants' control response to target visual direction was larger than that to heading when the display contained impoverished optic flow.

For the phase, the three (display condition) × two (cue) repeated-measures ANOVA showed that only the main effect of cue was significant [$F(1,6) = 108.97$, $P < 0.0001$]; both the main effect of display condition and the interaction effect of display condition and cue were not [$F(2,12) = 1.07$, $P = 0.37$, and $F(2,12) = 0.72$, $P = 0.51$, respectively]. The overall phase lag averaged across the three display conditions was larger for the control of heading than the control of target visual direction, indicating that the response delay of the control of heading is larger than that of the control of target visual direction (Fig. 9*B*).

Heading Perception

Heading perception performance for the left and right rotation rates was symmetrical; thus the heading error data were collapsed over left and right rotation rates. Positive heading error indicates that the perceived heading is biased in the direction of the simulated eye rotation (i.e., toward the fixation point), and negative heading error indicates the opposite.

Figure 10*A* plots the mean heading error averaged across 11 participants against rotation rate for the three display conditions. A three (display condition) × four (rotation rate) repeated-measures ANOVA on the mean heading errors revealed that both the main effect of display condition and rotation rate were significant [$F(2,20) = 13.47$, $P < 0.001$, and $F(3,30) = 34.32$, $P \ll 0.0001$, respectively] and so was their interaction effect [$F(6,60) = 4.98$, $P < 0.001$]. Consistent with previous findings (Banks et al. 1996; Li and Warren 2000, 2004; Royden et al. 1994), whereas the mean heading error is biased in the direction of the simulated eye rotation and increases with rotation rate, the increase of heading error with rotation rate decreases with the addition of optic flow information in the display. Newman-Keuls tests revealed that the mean heading error averaged across the four rotation rates was significantly larger for the sparse ground display (5.6°) than for the sparse ground with foreground motion (4.72°, $P < 0.05$) and the dense ground with foreground motion displays (3.78°, $P < 0.001$), and the latter two were also significantly different from each other ($P < 0.05$; Fig. 10*B*). This indicates that the accuracy of heading perception with simulated rotation increases with the added optic flow information in the display.

DISCUSSION

The results from the active steering experiment show that adding optic flow information (such as foreground motion and global flow) in the display improves the overall control precision measured as the mean RMS heading target angle and the amplitude and response delay of the control of heading. As the gaze rotation rate constantly changes during the course of the trial in the active steering experiment, it is not possible to examine heading perception at all gaze rotation rates. We thus examined heading perception at four representative gaze rotation rates, spanning 90% of the gaze rotation rates generated during active steering. In the heading perception experiment, heading error increases with rotation rate, as shown by previous studies (Banks et al. 1996; Grigo and Lappe 1999; Li L et al. 2009; Li and Warren 2000, 2004), and the overall heading error across the four rotation rates tested decreases with the added optic flow information in the display. Although the heading judgment error at the rotation rate of 10°/s is ~10° for the sparse ground display, it is uncommon for us to experience such a sparse flow field and large rotation rate in our daily life. At low rotation rates, heading error is small for all display conditions (<2° at 2.5°/s and <4° at 5°/s). In fact, 74% of the rotation rates in the active steering experiment are below 7.5°/s, and the heading errors averaged across the lower three rotation rates (2.5°/s, 5°/s, and 7.5°/s) in the heading perception experiment are 4.01°, 3.56°, and 2.69° for the sparse ground, sparse ground with foreground motion, and dense ground with foreground motion display conditions, respectively. These are below the heading error limit for safe control of human locomotion (Cutting et al. 1992). Our heading perception data thus show how the accuracy of heading perception is affected by both rotation rate and the richness of the optic flow field in the display. The improvement in heading judgment with the added optic flow information in the display in the heading perception experiment corresponds to the improvement in the control of heading in the active steering experiment, thus lending support to the proposal by Gibson (1958) that people use their perceived heading from optic flow for goal-oriented locomotion control.

Consistent with our previous findings (Li and Cheng 2011, 2013), the findings of the current study also clearly show the use of target egocentric direction for steering control. Across

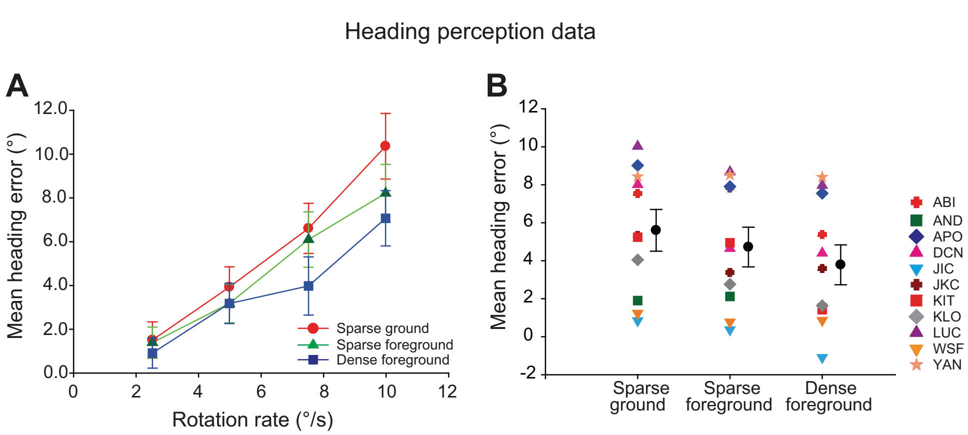

Fig. 10. Data from the heading perception experiment. *A*: mean heading error averaged across participants against rotation rate and (*B*) mean heading error averaged across rotation rates against display condition for each participant, along with the mean averaged across participants. Error bars are SE across 11 participants.

the three display conditions, the control gains specific to target egocentric direction are comparable with those specific to heading, and the control response delays are shorter for target visual direction than for heading. This is consistent with the fact that the target egocentric direction cue is available immediately (Rushton et al. 1998; Warren et al. 2001), whereas perceiving heading from optic flow requires 300–430 ms processing time (Crowell et al. 1990; Hooge et al. 1999). Furthermore, our results indicate that in the sparse ground display condition that provides little foreground motion and sparse motion parallax information, the control gain specific to target egocentric direction is larger than that to heading. However, whereas the control gain specific to target visual direction remains constant across the three display conditions, the control gain specific to heading increases with the added optic flow information in the display (see Fig. 8*A*), indicating an improvement in the control of heading with enriched optic flow displays.

Although previous studies have shown that people use optic flow to walk or steer toward a goal (Bruggeman et al. 2007; Harris and Carre 2001; Turano et al. 2005; Warren et al. 2001; Wood et al. 2000), no study, so far, has examined how varying optic flow information in the display affects the control of heading specified by optic flow and the control of target egocentric direction during goal-oriented locomotion. Our study is the first that showed that whereas adding optic flow information in the display has no effect on the control of target egocentric direction, it increases the amplitude and decreases the response delay of the control of heading. As the improvement in the control of heading with the added optic flow information is not coupled with any declined control of target egocentric direction, this suggests that the visual system does not internally weigh heading and target egocentric direction cues for goal-oriented locomotion control.

The lack of effect of optic flow on the control of target egocentric direction could be due to the fact that the perceptual salience of target egocentric direction is not affected by adding optic flow information in the display. It also shows that continuous perturbation successfully prevented perceptual shifts of the straight-ahead due to adaptation to steering with displaced heading (Li et al. 2012), which would presumably change the perceived target egocentric direction, thus affecting the control of target visual direction with enriched optic flow displays.

Last, in previous walking studies that found participants walking on a nearly straight path with enriched optic flow displays, the displays also contained nonflow information, such as complex 3D structure and change in static perspectives (Bruggeman et al. 2007; Warren et al. 2001). It is unknown whether optic flow information alone is sufficient to affect goal-oriented locomotion control. In the current study, we systematically manipulated optic flow information alone, such as foreground motion and global flow in the display, and the findings show that such optic flow information is sufficient to improve active steering toward a goal. To illustrate this, the addition of foreground motion in the display improves the control precision measured by the RMS heading target angle by 11% and the control gain specific to heading by 26%. The addition of both foreground motion and global flow in the display improves the control precision by a further 7% and the control gain specific to heading by a further 35%. The presence of both foreground motion and global flow in the display also reduces the control response delay specific to heading by 13%. As foreground motion and global flow increase the amount of motion parallax information in the flow field, we propose that dense motion parallax is the key optic flow information to improve the control of heading during goal-oriented locomotion. This is in line with previous findings showing that the presence of dense motion parallax in optic flow is important for accurate heading perception during translation and rotation (Li L et al. 2009; Li and Warren 2000).

Conclusion

This study used a control-theoretic approach and systematically examined how varying optic flow information in the display affects the control of heading specified by optic flow and the control of target egocentric direction during steering toward a goal. We conclude that: *1*) the addition of optic flow information, such as foreground motion and global flow in the display, improves the overall control precision, the amplitude, and the response delay of the control of heading but has no effect on the control of target egocentric direction; *2*) the improvement in the control of heading with enriched optic flow displays is due to the increased accuracy in heading perception from optic flow; and *3*) people use both heading specified by optic flow and target egocentric direction to steer toward a goal. However, the visual system does not internally weigh these two cues when performing the task. Future studies are needed to examine how visual information interacts with nonvisual information for the online control of locomotion toward a goal.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Author contributions: L.L. and D.C.N. conception and design of research; D.C.N. performed experiments; L.L. and D.C.N. analyzed data; L.L. and D.C.N. interpreted results of experiments; L.L. and D.C.N. prepared figures; L.L. drafted manuscript; L.L. and D.C.N. edited and revised manuscript; L.L. and D.C.N. approved final version of manuscript.

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