Optic flow asymmetries bias high-speed steering along roads

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How do animals and insects use visual information to move through the world successfully? Optic flow, the pattern of motion at the eye, is a powerful source of information about self-motion. Insects and humans are sensitive to the global pattern of optic flow and try to maintain flow symmetry when flying or walking. The environments humans encounter, however, often contain demarcated paths that constrain future trajectories (e.g., roads), and steering has been successfully modeled using only road edge information. Here we examine whether flow asymmetries from a textured ground plane influences humans steering along demarcated paths. Using a virtual reality simulator we observed that different textures on either side of the path caused predictable biases to steering trajectories, consistent with participants reducing flow asymmetries. We also generated conditions where one textured region had no flow (either the texture was removed or the textured region was static). Despite the presence of visible path information, participants were biased toward the no-flow region consistent with reducing flow asymmetries. We conclude that optic flow asymmetries can lead to biased locomotor steering even when traveling along demarcated paths.

Introduction

Controlling locomotion is a fundamental behavior for humans exploring and interacting with their environment. Gibson (1958) proposed that humans control locomotion using optic flow, the pattern of relative motion that occurs at the eye when moving through a world containing textured surfaces. Gibson's original theory proposed that the mobile animal will ensure that its desired direction of travel aligns with the point from which the optic flow field expands (the focus of expansion). Though elegant, this theory has proven insufficient to describe the behavior of humans who, evidently, use eye movements to sample visual information from the scene during locomotion (Wilkie & Wann, 2003).[1] Various patterns of eye movements have been observed during driving (Land & Lee, 1994), but our previous work has shown that during locomotion, gaze tends to be directed to points in the world you wish to pass through (Robertshaw & Wilkie, 2008; Wilkie, Kountouriotis, Merat, & Wann, 2010; Wilkie & Wann, 2003). This leads to a particular pattern of eye movements: a saccade toward a point 1–2 s ahead, followed by smooth pursuit to track this point as it approaches, followed by a further saccade ahead

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(Wilkie et al., 2010). A series of saccade/pursuit/saccade eye movements has been observed when steering to a series of waypoints (Wilkie, Wann, & Allison, 2008) and also when steering along bending roadways (Wilkie et al., 2010). The role of these eye movements seems to be to ensure that useful visual and nonvisual information is available to aid the control of steering (Wilkie & Wann, 2005). A number of sources of information may be used to control steering, e.g., splay angle (Beall & Loomis, 1996; Li & Chen, 2010), visual direction (Llewellyn, 1971; Rushton, Harris, Lloyd, & Wann, 1998), and extraretinal sources (Wilkie & Wann, 2005). As a result, it has been proposed that the human central nervous system (CNS) relies upon a weighted combination of information to generate steering behaviors (Wilkie & Wann, 2002, 2003; Wilkie et al., 2008). For example, it has been shown recently that the quality of road edge information alters the extent to which other sources are used to control steering (Kountouriotis, Floyd, Gardner, Merat, & Wilkie, 2012). What is currently unclear is the extent to which optic flow information is used by humans when steering along a demarcated path such as a road.

A demarcated path can provide two broad classes of information: (a) immediate error feedback about the current position relative to the path boundaries, and (b) prospective information about the upcoming steering requirements to maintain the current position. Salvucci and Gray (2004) successfully modeled human steering control solely relying upon two points of information: a near point and a far point, both of which could be supplied by the visible road boundaries. This model could be used to suggest that optic flow is simply not an important information source for controlling steering when a visible path is present. Similarly, Land and Lee (1994) suggested that one can successfully steer around a bend using only the tangent point of the inside road edge. There is supporting evidence to suggest that high-quality road edge information is predominantly used when steering (Kountouriotis et al., 2012; Robertshaw & Wilkie, 2008).[2] However, we propose that the human CNS carries out skilled actions in a robust fashion by relying upon multiple information sources that are combined to steer successfully (Kountouriotis et al., 2012). The focus for the present paper is to test this assertion and investigate whether optic flow information will influence human steering along demarcated paths.

Optic flow field asymmetries

One method to determine whether optic flow is being used to control steering is by selectively biasing this information and observing the resulting trajectories. Previous research that manipulated the flow field properties has revealed that humans seem to use flow when controlling walking (Prokop, Schubert, & Berger, 1997; Warren, Kay, Zosh, Duchon, & Sahuc, 2001) and controlling high speed steering (Wilkie & Wann, 2002, 2003, 2005). One interesting phenomenon is that insects (Srinivasan, Lehrer, Kirchner, & Zhang, 1991; Tammero & Dickinson, 2002) and humans (Chou et al., 2009; Duchon & Warren, 2002; Sarre, Berard, Fung, & Lamontagne, 2008) have been shown to be sensitive to the global properties of the flow field. When traveling down a straight tunnel, if one wall translates in the direction of travel, the insect or human drifts away from the faster wall. This adjustment essentially reduces the difference in magnitude between the velocity vectors across the two parts of the flow field, and provides evidence that during straight-line locomotion, global optic flow influences steering.

While the evidence suggests that optic flow is often important for maintaining a straight-line trajectory, it remains unclear the degree to which this is true when other cues are available. Duchon and Warren (2002) found that optic flow asymmetry effects disappeared when a path was visible, but this experiment only examined the case of straight-line walking. It is difficult to generalize from maintaining a straight-line course to actively controlling changes in direction to steer along a demarcated bending path. While textured or moving corridor walls (as used by Duchon & Warren, 2002) are excellent for maintaining precise control over the optical properties of left and right visual fields, these walls would act as solid barriers and so steering biases may have been underestimated due to participants avoiding collisions. For a human, a more general high-speed locomotor scenario is moving across a textured ground plane (be it running, cycling, or driving; Wilkie & Wann, 2002). A demarcated path acts as a natural boundary around which textures often vary, but without acting as a solid object or obstacle (with the associated risk of collision with that boundary). Kountouriotis et al. (2012) demonstrated that when controlling steering at higher-than-walking speeds, road edge information was highly weighted by the visual system, but the relative contribution of optic flow was not examined.

To determine whether optic flow can influence steering control in the presence of a visible road, we carried out three experiments that used a computer-simulated virtual environment containing a textured ground and a bending roadway. We altered the textures applied to the road and to the regions either side of the road, in order to manipulate optic flow properties and create flow asymmetries. This allowed us to determine whether optic flow influenced high-speed locomotor steering when a visible bending path was present.

Methods

Participants

Participants were recruited from a university participant pool. All had normal or corrected-to-normal vision. In Experiments 1 and 2 we recruited 14 naive participants (eight females) with a mean age of 20 years. They all held a valid driving license (on average for three years). In Experiment 3 we recruited nine new naive participants (four females), with a mean age of 24 years. All but one held a valid driving license (on average for five years). All participants gave their informed consent to take part in these experiments. The experiments were approved by the University of Leeds Ethics Committee, and the studies complied with all guidelines as set out in the Declaration of Helsinki.

Apparatus

Participants steered along a series of bending roads using a fixed-base driving simulator traveling at a constant speed of 13.8 m/s (~30 mph or 50 kph). The simulated environments were created using WorldViz Vizard 3.0. A PC with Intel i7 950 (3.07 GHz) processor generating images at 60 Hz with a resolution of 1280 × (WorldViz, Santa Barbara, CA) 1024 pixels was used, and as well as rendering the simulated scene, this machine read and recorded the steering and gaze responses of participants. Locomotor steering was controlled by participants using a force-feedback wheel (Logitech G27, Logitech, Fremont, CA). Rendered images were projected using a Sanyo Liquid Crystal Projector (PLC-XU58, Sanyo, Watford, UK) onto a back projection screen with dimensions of 1.98 × 1.43 m. Participants sat 1 m away from this screen, making the total field of view 89.42° × 71.31°. A height-adjustable racing-style driving seat was used to maintain eye-height 1.2 m above the ground, which was also the simulated eye height used to render the display image. Perspective projection then meant that the ground surface matched the real-world slant of the ground that ran horizontally from the observer 1.2 m below the eye-height (an effective height of 0 m). Participants sat in a matte black booth so that the projection screen provided the only source of light.

Stimuli and procedure

A perspective-correct projection simulated the virtual driving environment, which consisted of a 3-m wide road with an initial 9-m straight section followed by a bend of constant curvature (either 60- or 90-m radius). Locomotor speed was kept constant (13.8 m/s) in all trials, and participants were asked to fixate a cross located at the center of the road, always 16.1 m ahead (approx. 1.5 s on the desired curved trajectory) in order to ensure that any bias in trajectories were not due to changes in the gaze patterns (Wilkie et al., 2010). Participants were instructed to steer smoothly to maintain their position in the middle of the road. The road, the inside, and the outside regions of the bend could be textured independently to contain elements of different size (Experiment 1), or a blank texture (Experiment 2), and these regions could also be rotated (Experiment 3).

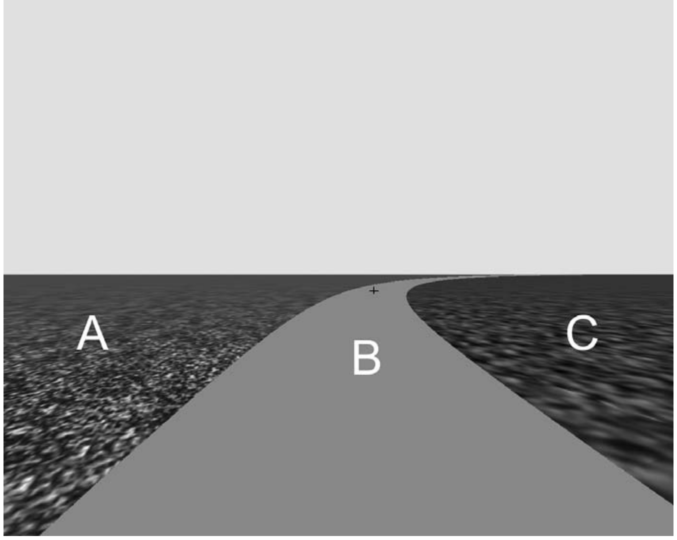

Figure 1. Example trial with road bending to the right. The small texture elements are placed on the outside region (A), no texture is on the road (B), and large texture elements are on the inside of the bend (C). The regions inside and outside of the road had a green tint, but no tint was applied to the gray road so they could always be distinguished. The fixation cross was positioned on the road approximately 1.5 s ahead of the driver to ensure eye movements did not change between different texture conditions.

In Experiments 1 and 2, three ground textures were used: no texture elements (blank), large texture elements, and small texture elements (Figure 1). The large texture was created from a manipulated version of the small texture to retain the same essential tiling properties. The manipulation was such that if both textures were applied to a fronto-parallel plane they would appear equivalent when the large texture was placed at the eye-height distance in front of the observer (1.2 m) and the small texture placed ¼ of the eye-height distance away. Of course in the visual scene, the textures were applied to the plane that ran horizontally from the viewer, and so depth and perspective caused transformations to the relationship between the textures (for example at the horizon, the textures appeared identical since there were essentially no texture elements visible for either large or small textures). The textures had no tint applied to the road (grayscale) and a green tint applied to both the inside and the outside regions. This meant that the road could always be distinguished from the inside and outside zone irrespective of which texture was applied. The blank texture was only used on the road in Experiment 1, but in Experiment 2 it was used on the outside or inside regions.

The following conditions were created for Experiments 1 and 2 (with trials for each condition repeated four times):

Experiment 1: *Texture Type (Large, Small)* × *Region (Inside, Road, Ouside)* × *Radius (60 m, 90 m)* × *4 trials*
Experiment 2: *Texture Type (Large or Small, Blank)* × *Region (Inside, Outside)* × *Radius (60 m, 90 m)* × *4 trials*

In Experiment 3 we created two types of flow asymmetry condition: While one of the regions always had the small texture elements, the other was either: (a) a blank region as per Experiment 2, or (b) a textured region that had no apparent motion (remained static). The second manipulation effectively moved the manipulated region along with the observer so it produced no contribution to flow. Because we found no effect of road texture type in Experiment 1, the road was always left blank in Experiment 3. We also used only tight bends (60-m radius) allowing us to run six repeated trials for each condition (randomized) as follows:

Experiment 3: Texture Manipulation (Blank Texture, Static Texture) × *Region (Inside, Outside)* × *6 trials*

In all three experiments participants were initially given five practice trials to familiarize themselves with the task, and they were instructed to always attempt to steer in the middle of the road. These instructions are crucial because they allow steering bias to be measured relative to a clear reference trajectory (i.e., the invisible midline of the road).

Data analysis

For each trial we calculated steering bias, taking the position of the participant in the world for each frame and finding the closest distance to the (invisible) centerline of the road. This measure indicates whether participants spent most of the trial at the correct road position (zero bias), or whether steering caused drift towards the inside road edge (positive bias) or towards the outside road edge (negative bias). We only analyzed steering bias for the curved section of roadways since we wished to ignore performance associated with the initial straight section of trials where no steering was required and no bias was expected (this avoided diluting any effect of asymmetries). Each experimental condition was repeated four times (Experiments 1 and 2 were collapsed across the 60- and 90-m radii conditions to get eight repetitions of the main conditions) or six times (Experiment 3) and the mean signed steering error was calculated for each person to provide an estimate of steering bias for each condition. Statistical evaluation of steering bias was then carried out using a repeated-measures ANOVA using SPSS 20 (IBM, Hampshire, UK).

Results

Experiment 1: The effect of asymmetric textures on steering

In the first experiment we investigated whether steering around bends was affected by the size of the texture elements on either side of the road. A virtual environment was generated that contained a ground plane and a bending road. The regions inside of the bend or outside of the bend could be textured with the same size elements (symmetrical conditions) or different size elements (asymmetrical conditions; example shown in Figure 1). The 3-m-wide road was either blank (no texture), or textured with the same elements as used on the inside or outside of the road. Preliminary analysis suggested there was no difference if the road was blank or had texture, so we averaged across these conditions.

A repeated-measures 2 (Symmetry) × 2 (Element Size) ANOVA was used to test steering bias (Figure 2a), which revealed a significant interaction, $F(1, 13) = 19.46$, $p = 0.001$, $\eta^2_p = 0.60$. During asymmetric texture conditions, participants steered away from the region with larger elements towards the region with smaller ones, $t(13) = 3.83$, $p = 0.002$, whereas there was no difference in steering bias for symmetrical conditions, $t(13) = 1.08$, $p = 0.302$. When textures were symmetrical, the size of the texture elements had no effect on steering (Figure 2a, black line). When textures were asymmetrical, participants steered towards the region with smaller elements (Figure 2a, gray line). Across all conditions there was a general tendency to oversteer (positive steering bias, Figure 2a), which is consistent with previous studies examining steering bends (Kountouriotis et al., 2012; Robertshaw & Wilkie, 2008); however, participants cut the corner most when there were large texture elements in the outside region and small elements on the inside (and they stayed closest to the road center when there were small elements in the outside region and

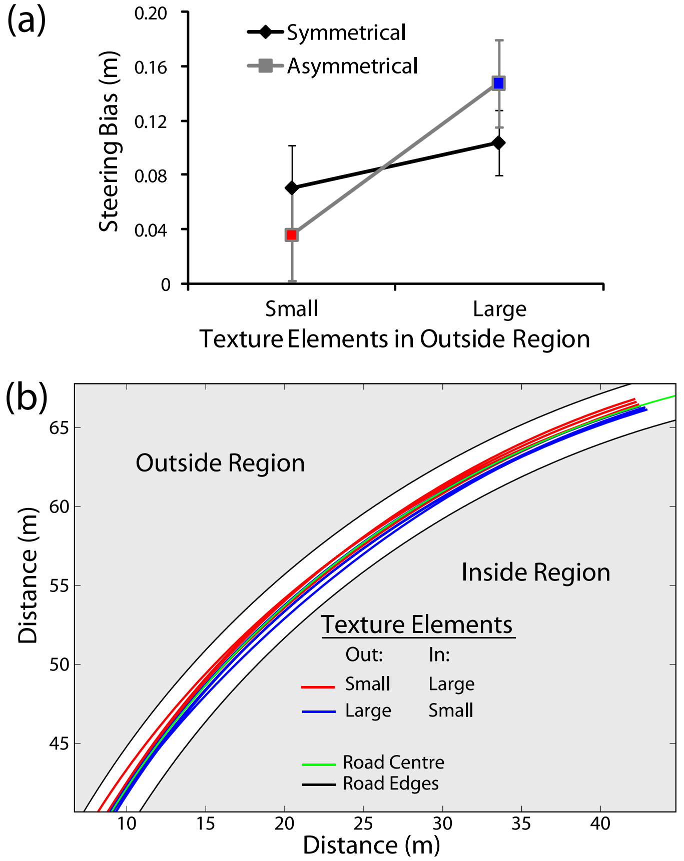

Figure 2. (a) The interaction between texture element size and symmetry. Positive bias indicates steering toward the inside region, while negative bias indicates steering towards the outside region. The bias values represent means across all participants steering down roads of two curvatures (radius of 60 m or 90 m). Bars = *SEM*. (b) All steering trajectories from a single participant in the two asymmetric conditions (four trajectories for each condition) along a tight (60-m radius) bend.

large elements on the inside). This effect can be seen across single trials; Figure 2b shows example trajectories for one individual steering during the different texture conditions. The steering bias towards smaller texture elements and away from larger texture elements is in line with an optic flow equalization strategy, but shows a much stronger effect than previously observed when information from a visible path was present (Duchon & Warren, 2002). Crucially, these results demonstrate that optic flow is being used despite the presence of a visible path.

Experiment 2: The effect of asymmetric removal of texture on steering

The steering biases that occurred due to asymmetric textures in Experiment 1 can be explained in terms of balancing the global flow field. In the real world, however, a region may be very sparsely textured and contribute little to optic flow. For instance when driving at night, some parts of the road surface will be illuminated so the texture will be visible, whereas dark regions (perhaps a drop off at the road edge) will have no visible texture. In such cases it seems difficult a priori to predict whether steering will be biased by the flow asymmetry since changes in road position would not alter the properties of flow generated by moving across untextured surfaces. At one extreme, the untextured region could be treated by the visual system as a single very large texture element, in which case, based on Experiment 1, we would expect steering to be biased toward the remaining textured region to expand those elements and thereby reduce asymmetries. Alternatively, the untextured region could be treated as a very slow-moving (i.e., static) surface that may cause steering to be biased toward it (as in moving wall experiments by Srinivasan et al., 1991). To examine whether asymmetric flow created by untextured regions also leads to biased steering when traveling along demarcated paths, we created conditions where either the inside or outside region was left blank (untextured).

Figure 3a shows the mean steering biases for all three conditions. As in Experiment 1, we found a significant effect of asymmetric flow, $F(2, 26) = 30.05$, $p < 0.001$, $\eta^2_p = 0.70$, with participants steering away from the textured region towards the blank untextured region (all pairwise comparisons between the three means were significant at the $p < 0.05$ level). This result confirms that asymmetric flow can influence steering even when a visible demarcated path is present. Participants steered more toward the inside region when it was blank than when both regions were textured. Similarly, when the outside region was blank, participants steered more toward the outside than when both regions were textured. In Experiment 1, there was a clear tendency to oversteer even when there were no flow asymmetries, but the flow asymmetries either increased or decreased the degree of oversteer depending on which region was textured in which element—this was also the case in Experiment 2 (Figure 3). The direction of the steering bias is consistent with participants steering toward the slower moving region and away from the faster moving region.

Even though the road was always clearly distinguished from inside and outside regions (using different colored tints) we wanted to see if the presence or absence of texture on the road altered the quality of road edge information (i.e., an untextured road may have led to a more salient road "edge"). To examine this issue we compared conditions where the road was left blank (untextured) with the conditions where the road was textured as elsewhere in the scene. Our analysis showed that there was no differential effect of blank/textured road on steering bias, $F(1, 13) = 0.268$, $p = 0.61$, and we found no interaction between the road

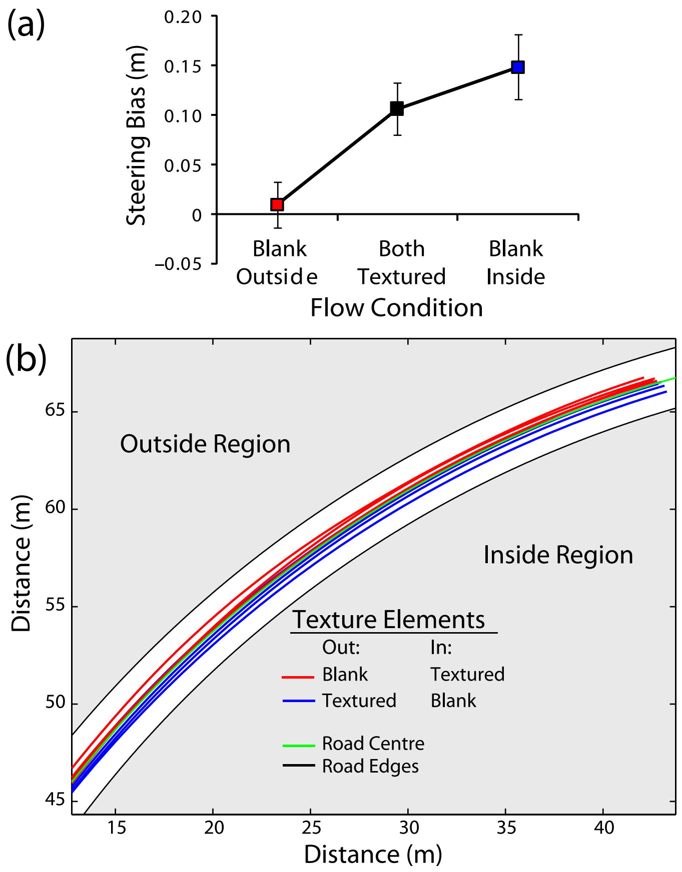

Figure 3. Steering behaviors in the presence of asymmetric flow caused by one blank region and one textured region. (a) The pooled means for all participants across two road curvatures, two texture element sizes, and two road textures (road textured or left blank) when flow was symmetric (both regions textured) or asymmetric (the outside or inside left blank). Error bars = ±*SEM*. (b) All trajectories for a single participant around a tight bend (60-m radius). Red trajectories are trials when the inside was textured and the outside and road were blank, and blue trajectories are trials when the outside was textured and the inside and road were blank.

texture and the region that was textured, $F(2, 26) = 1.34$, $p = 0.28$. We also examined whether the size of texture elements (large or small) affected the degree of steering bias, and there were no significant differences, $F(1, 13) = 0.107$, $p = 0.75$. We therefore conclude that a blank region can lead to significant flow asymmetries that will bias steering even when visible road edges are present.

Experiment 3: The effect of asymmetric optic flow velocity on steering

In Experiment 2, when participants steered toward the region without flow, they effectively reduced the perceived speed of the remaining textured region.

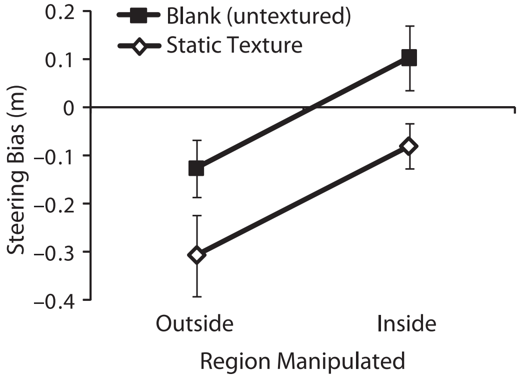

Figure 4. Experiment 3 examined steering in the presence of blank regions (filled squares), or textured regions that were static and had no flow vectors (open diamonds). The mean steering bias for all participants across six repetitions of each trial are shown, and the bars are ±*SEM*. Both asymmetry manipulations caused steering bias of the same magnitude, although there was a greater general tendency to understeer when one textured region was static (indicated by the negative steering bias).

Previous studies on insects and humans have shown that when there is an inconsistency between the speed of two tunnel/corridor walls, a trajectory is taken that reduces the difference between those regions (i.e., drift toward the slower moving wall). In order to test whether speed equalization can explain the results of Experiment 2, we ran one final experiment. We recruited nine new participants and asked them to steer in conditions where, although both regions had the same texture (only the "small" texture was used), one of the regions was kept static (as if attached to the observer) in order to remove any visible flow vectors from that region. We also included a separate subset of the blank texture conditions to compare performance between static textured regions and blank regions. If steering bias is caused by asymmetric flow speed, we would expect to see the same pattern and magnitude of bias for both types of asymmetry manipulation (with participants steering toward the region without flow).

The results confirmed the hypothesis that steering towards the blank region with no texture can be explained by unequal velocity vectors in the flow field (Figure 4). We found a significant effect of the region manipulated, $F(1, 8) = 32.28$, $p < 0.001$, $\eta^2_p = 0.80$, with participants steering towards the region that did not contribute to flow (either because of blank or static texture manipulations). We also found a significant effect of the type of manipulation, $F(1, 8) = 17.72$, $p = 0.003$, $\eta^2_p = 0.69$, with greater understeer overall when both regions were fully textured. No significant interaction was found between these two factors, $F(1, 8) = 0.001$, $p = 0.98$, suggesting the same relative degree of steering bias in both asymmetric flow conditions. This further confirms the power of optic flow to influence steering even when visible path information is available, and indicates that symmetric velocity vectors remain critical under these conditions.

Discussion

We have found that asymmetries in optic flow can bias steering at driving speeds when a visible path is present. Previous studies have shown that both insects (Srinivasan et al., 1991; Tammero & Dickinson, 2002) and humans (Chou et al., 2009; Duchon & Warren, 2002; Sarre et al., 2008) try to equalize the perceived speed of optic flow. When asymmetries are introduced to corridor walls, the insect or human adopts a position further away from the faster flow. Research on humans by Duchon and Warren (2002) has also suggested that asymmetric flow patterns may have a small effect when walking down corridors, but only in the absence of splay angle information (i.e., when there is no path). Here we demonstrate for the first time large effects of flow asymmetry from a ground plane when texture is manipulated, despite the presence of visible path boundaries. The magnitude of bias observed in the present studies were much larger than those reported previously. This could be because there were no walls acting as a potential collision risk (though the road edges constrain steering to some degree) or because the locomotor speeds were faster than walking pace (magnifying the errors resulting from steering bias). Ideally it would be possible to estimate the degree to which optic flow is being equalized and the extent to which the road edges were moderating steering errors. Unfortunately the present methods were unsuitable for distinguishing between an increased weighting of road edges versus a decreased weighting of flow asymmetries. Despite this our findings are generally consistent with an optic flow equalization strategy (Chou et al., 2009; Duchon & Warren, 2002; Sarre et al., 2008; Srinivasan et al., 1991; Tammero & Dickinson, 2002). In Experiment 1 participants drifted away from the texture with larger elements (effectively decreasing their optical size) while moving toward the texture with smaller elements (effectively expanding their optical size). In Experiments 2 and 3, when we introduced asymmetries by creating a region without flow (either using a blank texture or by keeping the textured region static), participants were biased towards the region without flow. This region would have zero perceived speed, and thus it would appear to be moving slower than the textured region. The observed steering bias away from the textured region would, therefore, reduce the difference in perceived speed. These experiments suggest that humans are sensitive to both spatial and temporal asymmetries in optic flow, and adjust steering to reduce such asymmetries.

Our findings raise interesting questions about the neural basis of steering control using optic flow. It has been reported that the medial temporal/media superior temporal (MT/MST) cortex areas are dominated by speed coding (Lingnau, Ashida, Wall, & Smith, 2009), whereas the ventral intraparietal/cingulate sulcus visual (VIP/CSv) cortex areas are particularly involved in coding egomotion (Wall & Smith, 2008). Given the similar behaviors observed in our study when optic flow contained spatial or temporal asymmetries, it would be interesting to examine whether there is a common underlying asymmetry signal propagated from MST, or whether there are different functional bases to the observed steering biases.

Whilst the data presented are consistent with flow equalization, we should highlight another possible explanation for the observed steering biases. The reduction or removal of flow vectors from a region could lead to a lower overall perceived locomotor speed because of whole field averaging. Indirect evidence for such an explanation is given by Chou et al. (2009); when they changed the flow speed of one half of the visual field, participants not only veered towards the slower moving wall, but they also slowed down their walking speed and reduced stride frequency as the overall flow speed increased. These observations are consistent with previous experiments that have shown that bilateral flow speed is negatively correlated with walking speed (Prokop et al., 1997; Schubert, Prokop, Brocke, & Berger, 2005; Varraine, Bonnard, & Pailhous, 2002). In our experiments we might expect that a reduction in perceived speed would lead to greater understeer since a less rapid steering response would usually be appropriate for slower locomotor speeds. Our results show that there was indeed a tendency to understeer when one of the regions was static; however, we do not believe this fully explains our results. Firstly, we observed no differences in steering when the road was textured or untextured in Experiment 1 (a global speed explanation would predict greater understeer when it was untextured). Experiment 1 also showed that there was greater oversteer when the inside region had smaller texture elements compared to when both regions were textured (Figure 2a), which is also inconsistent with a global speed explanation. In any case it remains true that visible path information was not sufficient to support unbiased steering when flow was manipulated, highlighting the importance of the global flow field for locomotor steering control even when demarcated paths are present.

These findings have implications for studies examining human control of driving. For example both real world and simulator experiments have used visual conditions where ground textures are asymmetric

(Land & Lee, 1994; Mars, 2008) without considering the potential impact of flow asymmetries on steering behaviors. Steering control is usually robust to degraded visual information (Wilkie & Wann, 2002), and it seems likely that humans would readily adapt to environments that are consistently asymmetric; however, future experiments should investigate the degree of adaptation to flow asymmetries (and the time course of this adaptation) in order to determine whether there are particular flow asymmetry conditions that would put a motorist at high risk of error.

Keywords: locomotion, steering, optic flow, asymmetries

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Footnotes

[1] Eye movements add a rotation component to the optic flow pattern at the back of the eye (retinal flow) so the focus of expansion is often masked (Regan & Beverley, 1982).

[2] This is consistent with the work of Wilkie and Wann (2002) who showed that when steering to a single eccentric target (i.e., when there is no road) the contribution of retinal flow to steering was only 20%–35% depending upon the availability of other information.

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