

## The Role of Visual and Non-Visual Information in the Control of Locomotion

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*Running Head: Control of Locomotion*

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## **Abstract**

During locomotion retinal flow, gaze angle and vestibular information can all contribute to our perception of self-motion. Their respective roles were investigated during active steering: retinal flow and gaze angle were biased by altering the visual information during computer-simulated locomotion and vestibular information was controlled through use of a motorised chair that rotated the participant around their vertical axis. Chair rotation was made appropriate for the steering response of the participant, or inappropriate by rotating a proportion of the veridical amount. Large steering errors resulted from selective manipulation of retinal flow and gaze angle, and the pattern of errors provided strong evidence for an additive model of combination. Vestibular information had little or no effect upon steering performance suggesting that vestibular signals are not integrated with visual information for the control of steering at these speeds.

## **Keywords**

Human Locomotion, Steering, Body Rotation, Vestibular Information, Semi-circular Canals, Optic Flow, Gaze Angle

## Introduction

Controlling self-motion is a fundamental ability for most living creatures, and in humans such control is primarily effected using vision, but supported by non-visual senses. Previous research has mainly focussed on the visual elements of steering, and in particular on retinal flow information. It is possible to judge your direction of motion from retinal flow under a wide range of conditions (Warren, Morris & Kalish, 1988; Warren & Hannon, 1990; Royden, Banks & Crowell, 1992; Van den Berg, 1993; Royden, Crowell & Banks, 1994; Stone & Perrone, 1997) and a number of methods for steering directly on the basis of retinal flow have been identified (Kim & Turvey, 1999; Wann & Land, 2000; Wann & Swapp, 2000). Despite abundant evidence for the importance of flow, it does seem that other sources of information can make a strong contribution. Rushton, Harris, Lloyd and Wann (1998) asked participants to walk directly towards a target when wearing prism glasses that introduced an offset ( $16^\circ$ ) to the egocentric visual direction of the target. The curved paths that resulted suggest that egocentric visual direction was the predominant source of information in a walking task. Retinal-flow information, however, may have been quite weak during the task of Rushton et al. Harris & Bonas (2002) tested whether quality of flow was an issue in the Rushton et al. task, by reproducing the visual direction offset experiment in a well-lit corridor with rich scene structure, and then repeating trials in darkness. Equivalent curved paths were followed in both cases, which indicated that biased visual direction information rather than flow was used, even when the environment was well illuminated. It is, however, possible that distortions in the lenses and limited field of view may have contributed towards reduced dependence upon retinal flow. Warren, Kay, Zosh, Duchon & Sahuc (2001) implemented “virtual prisms” using a head-mounted display with a wide field of view and found that path curvature was reduced in the presence of increased quality flow. In agreement with this Wilkie & Wann (2002) found that the reliance of flow information, in a curved steering task, increased as the salience of the ground flow improved (e.g. from twilight to daytime). Nevertheless, there are a number of models for more complex steering tasks that propose that steering adjustments can be used without recourse to retinal flow information (Land & Lee, 1994; Rushton, Wen & Allison, 2002; Salvucci & Gray, In Press). There is a range of non-visual sources that

could supply useful information when controlling locomotion, such as feedback from the vestibular system, skin receptors, muscles, and joints allowing the changing position in the world to be monitored. These inputs are often referred to as *extra-retinal* information.

Crowell, Banks, Shenoy and Anderson (1998) performed a series of experiments to quantify the effectiveness of different extra-retinal cues in mediating accurate self-motion judgments during head turns. As well as measuring performance during eye pursuit, three possible sources of extra-retinal information were examined independently and in conjunction: efferent information about motor commands to the neck muscles, proprioceptive information from the neck muscles and vestibular semi-circular canal information about head rotation. They found that neither neck proprioception nor vestibular information alone was sufficient for accurate perception of heading. The combination of all three extra-retinal sources, however, supported veridical judgements of direction of locomotion. Interestingly, combinations of only two sources yielded mixed results, probably due to the cue conflict conditions, which is an indication that the combined effect of the information was not simply additive.

Our own research (Wilkie & Wann, 2003; Wann & Wilkie, 2004) proposed that steering can be simplified by fixating the target that you wish to steer towards, since under these conditions retinal flow and extra-retinal signals provide very similar information (Wann & Land, 2000). They can be combined using, as a first approximation, an additive model that acts as a point attractor:

$$\ddot{\theta} = k(\beta_1 \text{eRF} + \beta_2 \text{eERD} + \beta_3 \text{eVD}) - b\dot{\theta} \quad (1)$$

Where  $\theta$  is the angle of the locomotor axis in world coordinates,  $\text{eRF}$  is a perceptual estimate of the rotation within the flow field and  $\text{eERD}$  an extra-retinal estimate of the rate of change of target direction (equivalent to gaze rotation for a fixated target). A third term  $\text{eVD}$  was included for situations in which there is a retinal estimate of the changing target direction, such as provided by the bodywork of a car (Wilkie & Wann, 2002).  $\beta_1$  -  $\beta_3$  are weights and should sum to 1.0. The parameters  $k$  and  $b$  determine response rate scaling and damping respectively. If  $\text{eRF}$ , or  $\text{eERD}$ , or  $\text{eVD}$

are above threshold they indicate that the observer is not travelling towards the point of fixation, and the direction of change in eRF, eERD, or eVD indicates the direction of steering error (understeer or oversteer). Equation 1 serves to describe a system where the perceptual information pushes steering towards an attractor state where the perceptual estimates of eRF, eERD, and eVD are below threshold. It has been shown (Wilkie & Wann, 2003) that precise pick up of these variables is not essential. In the absence of correct steering, eRF, eERD, and eVD scale exponentially with decreasing target distance, so the estimates can be severely quantized and a correct steering response can still occur. Poor sensitivity or a high threshold will just result in late steering, whereas early steering requires higher sensitivity to these variables. For the purposes of this study we will remove visual direction as a source of information (so  $\beta_3$  can be set to zero) and explore the role of eERD. There are two broad classes of non-visual information that may contribute to eERD, which we will manipulate independently: gaze angle direction and vestibular information about the rotation of the head in space.

#### *Gaze Angle Direction*

When steering towards and fixating an eccentric target, the angle of the head and eyes relative to the locomotor axis indicates the amount of closure needed to turn towards the intended destination (Figure 1). In this situation proprioceptive signals from head and eye rotations could supply gaze angle direction information. This information is not completely independent of visual function since in order to fixate the target some retinal processing is required, but the muscles of the eye and neck supply the gaze angle information rather than the retinal signal. These extra-retinal signals are the central components of the performer's estimate of egocentric visual direction as proposed by Rushton et al (1998) and Harris & Bonas (2002) for situations where the intended walking path was in a straight-line. Wilkie & Wann (2002) investigated the more complex case of steering curved paths at high speeds, and found that gaze angle could be used to steer when other visual information sources were absent, but gaze angle information was not directly manipulated.

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Insert Figure 1 here

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### *Vestibular Information*

The semi-circular canals (SCC) and otoliths of the vestibular system inform us about the orientation and localisation of our head in space (Ivanenko, Grasso, Israel & Berthoz, 1997). A number of studies have demonstrated integration of vestibular and proprioceptive signals during rotation events (Hlavacka, Mergner & Schweigart, 1992; Mergner, Nasios, Maurer & Becker, 2001), and even though proprioception often emerges as the dominant source (Jurgens, Boss & Becker, 1999), a strong role for vestibular information has been observed in some navigation related tasks: for example judging distance travelled (Harris, Jenkin & Zikovitz, 2000), and reconstructing the shape of the course travelled (Bertin & Berthoz, 2004).

In principle, information from the semicircular canals could assist steering control. At the coarsest level they could confirm that you are indeed rotating in the direction that you are trying to turn. A greater sensitivity to SCC signals would allow comparisons between the actual rate of change of turn specified from the SCC and that estimated from gaze angle or retinal flow. A situation where this information could be crucial during locomotion is where a skid (caused by loss of traction) results in motion that is inappropriate for the control input. Furthermore, in snowy/icy conditions, where skidding is common, poor visual information may exacerbate control errors.

Vestibular information could also provide direct feedback for steering control. Wann & Land (2000) noted that curved paths, towards a point of fixation, could be controlled by maintaining a constant rate of change for the angle of the target. This information could be derived from the angular velocity of the eye/head in tracking the target or from signals generated in the SCCs of the vestibular system during head rotation if the head (nose) is kept aligned with the target. Land (2004) has also highlighted the role of the vestibulo-colic reflex<sup>1</sup> in re-centering the head on the body following a manoeuvre at a road intersection. Within this feedback loop is information equivalent to that required by the Wann & Land (2000) proposal.

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<sup>1</sup> The vestibular mechanism for stabilizing the head against rotations of the body is known as the vestibulo-colic reflex. Signals from the vestibular system, indicating head rotations of greater than zero velocity, are fed back negatively to the neck muscles via the vestibulo-spinal and vestibulo-reticulo-spinal pathways Wilson, V. J. & Melvill Jones, G. (1979). Mammalian vestibular physiology.

Research using galvanic vestibular stimulation (GVS) has been used to assess the contribution of the visual and vestibular systems during walking. In quiet standing GVS can cause body motion that is not attenuated by vision, but as the phases of forward stepping progress the relative roles of visual and vestibular information change, possibly reflecting a complex form of integration that depends upon the stage of stepping (Bent, Inglis & McFadyen, 2002; Bent, McFadyen & Inglis, 2002; Kennedy, Carlsen, Inglis, Chow, Franks & Chua, 2003). Kennedy et al (2003) perturbed visual information in some conditions using prisms, and then examined the resulting walking trajectories when galvanic stimulation was present. Deviations in walking were observed, but despite some apparent visuo-vestibular integration, visual information appeared to be dominant in most cases. The galvanic stimulation technique, while effective in stimulating the vestibular system, acts equally upon SCC and otolith afferents, so the relative roles of these two modalities cannot be dissociated. When considering self-motion along smoothly curving paths, it is not obvious which aspects of the otolith response would be useful for generating or modifying a steering manoeuvre, so at this stage we have limited our experiments to investigating the signals available from simple body rotations around the yaw axis.

#### *Manipulating the available information*

We stimulated the SCCs by seating the participants in a motorised chair and rotating them around the vertical yaw axis. We introduced body rotation in two ways. Firstly, in *yoked* conditions, the chair moved through an angle that was proportional to that indicated by the steering device and the amount of rotation in the visual scene, and this was either be veridical (1), greater ( $>1$ ) or less ( $<1$ ) than the appropriate amount. This method has the advantage of being able to generate a bias from which we can predict specific directional errors in steering whilst also reproducing steering dynamics proportional to those presented visually to the participant. The limitation is that the magnitude of SCC stimulation cannot be controlled since it is dependent on the course that the participant follows. The second method for introducing body rotations was independent of the simulated locomotor trajectory. Here we rotated the motorised chair such that it moved towards or away from the steering target with constant acceleration, irrespective of steering behaviour.

In previous research prisms have been used to introduce a gaze angle offset; they cause errors when steering is based upon minimizing gaze angle. This technique is limited, however, since with a fixed prism you can only introduce a constant angular offset and our model (eqn 1) proposes that the rate of change of gaze angle is important. We wished to introduce a systematic directional bias closely matched to our retinal flow conditions, so we systematically moved the viewport<sup>2</sup>. This was equivalent to moving the whole visual display on each frame so that the fixated target moved relative to the body, but stayed in a fixed position relative to the rest of the scene. This had the effect of introducing a bias to the rate of change of gaze angle, without affecting the retinal flow information (Wilkie & Wann, 2002, 2003).

As well as manipulating non-visual sources of information (SCC & gaze angle) we examined their interaction with the visual flow information. To determine whether retinal flow information is used, a directional bias was introduced by rotating the ground plane around the point of fixation, which was also the steering target (see Method for details). This fixation point is the singularity of the retinal flow field, so rotation of the ground around this point (around an axis perpendicular to the ground) is not obvious to the observer, but the technique ensures that the perceived course is eccentric to the actual path. Rotation in one direction will create a percept of a course of reduced curvature, and therefore a steering response based upon retinal flow information will promote oversteer. Similarly rotation of the ground in the opposite direction will increase the perceived rotation within retinal flow, prompting a reduction in steering, or understeer. The magnitude of errors will be influenced both by the rate of bias ( $1^\circ/s$ ) relative to the translation and rotation components due to steering, and also the quality of retinal flow information (Wilkie & Wann, 2002).

Experiment 1 compared steering errors when either retinal flow or gaze angle information was directionally biased in order to determine the weighting of retinal flow and gaze angle during steering. We also examined the relative proportions of eye and head rotations involved in tracking the steering target. Land and Tatler (2001) have previously demonstrated a significant correlation between head rotation and

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<sup>2</sup> The viewport was a rectangular area of the otherwise black screen within which the scene was projected. Movement of the viewport therefore translated the whole scene into empty areas of the screen.

steering rate of a racing driver, so we have reason to expect that head rotations will contribute to gaze tracking and therefore bring neck proprioception and/or the SCC's into the target direction estimate

Experiment 2 then provided direct stimulation of the SCC system by introducing body rotations that were in agreement with the locomotor trajectory to allow comparison with performance when no rotation was available. Body rotation information may act as useful feedback that becomes available as a result of previously carried out steering manoeuvres. Bias in retinal flow or gaze angle will cause steering errors due to understeer or oversteer (depending upon the direction of bias). In principle both understeer and oversteer could be detected from SCC signals, by determining if the body rotation was inappropriate for the desired course. However, a further possibility is that the SCC system only detects oversteer errors due to insufficient sensitivity at low accelerations. In line with this we might expect a greater influence of body rotation information as rotation rates increase due to erroneous steering caused by biased information.

Experiment 3 then systematically altered the SCC stimuli while keeping the retinal flow and gaze angle information veridical. When cues have very different values, the nervous system will often exhibit 'robustness' by ignoring wayward values, as observed in the cue conflict conditions responsible for roll-off in the induced effect (Banks & Backus, 1998). To control for this we introduced a wide range of small and large body rotations that were 150%, 125%, 100%, 75%, 0%, -100%, -150% of what would be veridical. If SCC information were integrated with other sources during steering, then we would expect, at the coarsest level, a directional effect of body rotation. Rotation opposite to steering should result in the participants reducing their rate of turn. If participants are particularly sensitive to SCC information then too little rotation in the same direction as steering would also be perceived as an understeer, and steering rate may be increased to compensate. Too much body rotation, however, may cause a reduction in steering rate. If SCC information can be used then the overall pattern would show systematic directional errors due to over and understeer when biased SCC information was present.

## General Method

### *Image generation*

The visual scene comprised a ground plane seamlessly tiled with a gravel texture sourced from a library of natural photographic textures. A target (a yellow post) was placed in the scene 60m away from the observer's initial position. The observer was instructed to fixate the target which was eccentric to the observer's initial heading. The target moved in one of two ways: either as a result of observer's translation within the scene, (which caused changes in both retinal flow and gaze angle information), or due to artificial translation of the viewport in which the scene was projected, (which only had a direct effect upon gaze angle: see Figure 2). The observation point moved across the ground plane at  $8\text{ms}^{-1}$  for a duration of 6.32 seconds.

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Insert Figure 2 here

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### *Control of locomotion*

Control of simulated locomotion was through use of a Sidewinder Precision 2 joystick (Microsoft). Moving the joystick left and right provided analogue control over the direction of motion, modifying the rate of change of rotation during locomotion in the range 0-15°/s. We recorded the steering behaviour of participants when attempting to control locomotion towards the steering target. Locomotion was stopped 10m from the target to avoid the participant receiving precise feedback as to trial success, which in turn would make the experimental manipulations apparent. An early termination also has the advantage of avoiding the large rotations that occur close to the target if there is a steering error, which can sweep the target off the screen.

They also mean that binocular information is unlikely to have any impact on performance. To determine final performance the path was projected along an arc of constant curvature fitted to the final 1/3 of the trial. The lateral offset of the path from the target was then used to identify the amount of steering error for that trial.

### *Manipulating retinal flow and gaze angle*

To introduce bias to retinal flow we rotated the ground plane around the steering and fixation target. The rate of rotation was a function of the distance of the observer from the target and used a polar estimate of gaze rotation ( $\dot{\theta}$ ) that would result from a heading error of  $\alpha$ :

$$\dot{\theta} = V\sin(\alpha)/F, \quad (2)$$

V was locomotor speed (8m/s). F was the line of sight distance calculated at every frame (25Hz). The angular constant ( $\alpha$ ) was chosen to be 20°. Biased retinal flow (RF) information is directional, so -RF increases the amount of rotation in the flow field and should cause understeer (retinal flow rotates more than expected), whereas +RF should cause oversteer since it decreases flow rotation.

To introduce bias into the gaze angle information requires a two-step process. First of all we had to ensure there were no visual direction cues available by removing all invariant visual frames of reference that could supply retinally referenced direction information. Images were projected onto a screen 1m from the observer, and within this area a moveable viewport (29.6° x 27.6°) was displayed. The screen was edged with matt black tape, the room interior was matt black, and all incidental light was excluded from the projection booth. This prevented the participants from using the edge of the viewport like a car windscreen. In addition the participant wore a matte black cape to occlude the joystick and their body from view. Even though the orbit of the eye and the side of the nose are visible they do not supply useful visual direction information since they are not fixed relative to the locomotor axis. Once references to visual direction were removed we then biased gaze angle by moving the viewport rightwards or leftward at a constant rate (1deg/s), such that -gaze angle should cause understeer, whereas +gaze angle should cause oversteer. Horizontal viewport motion also translates all the flow elements, however maintaining fixation upon the steering target effectively undoes this with a horizontal eye rotation leaving retinal flow unaffected by gaze angle bias. Gaze angle manipulation constrained the eccentricity of steering targets since the use of shutters plus additional viewport motion displaces the viewing area laterally towards the edge of the projection area.

## Experiment 1: The role of retinal flow and gaze angle

The aim of this experiment was to evaluate the contribution of retinal flow and gaze angle information when steering a curved path towards a target. We introduce directional bias to both sources of information and examine the amount of steering error that results. This is similar to experiment 4 in Wilkie & Wann (2003) except here we are examining the role of gaze angle instead of retinally referenced direction.

## **Method**

### *Participants*

Six participants were recruited at the University of Reading, UK. All persons gave their informed consent prior to their inclusion in the study, and the studies themselves have been approved by the relevant ethics committee (The University of Reading) and have been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All participants had normal or corrected-to-normal vision and were unconnected with the study but they did have some general experience of viewing motion displays in addition to having at least 2 years driving experience. Observers used both eyes to view the non-stereo image (bi-ocular viewing), and head and body position were not stabilized.

### *Apparatus*

The platform used was a PC with dual Xeon (1500 MHz P4 processors; Intel Corporation, Santa Clara, CA) with Quadro 2 Pro Graphics card (nVidia) running Windows 2000 and DirectX 8.1 libraries (Microsoft Corporation, Redmond, WA) using custom written C++ code. A Hitachi Liquid Crystal Projector (1024 x 768 pixels) was viewed from 1m, and rendered a viewport with dimensions matched to those in later experiments (29.6° x 27.6°).

### *Procedure*

We manipulated the retinal flow or gaze angle information using the techniques outlined in the *general methods* section. In the University of Reading lab we were able to test a wide range of heading eccentricity using a 2m (90deg FoV) screen, so initial angles of motion relative to the targets were: 4, 8 12 & 16 degrees. We also measured head rotations (yaw) using a “flock of birds” magnetic head tracker (Ascension Technology Corporation). An error estimation procedure found the error

in angular information from the head tracker to be  $.3^\circ$ . The range of head motion during each trial was recorded, allowing the proportion of head:eye rotation to be calculated and an estimate to be made of the vestibulo-proprioceptive information associated with gaze angle. Participants controlled their trajectory in the manner described in the *general methods*.

## Results and Discussion

### *Steering errors*

Every trial stopped 10m before the target destination. To calculate the end steering error an arc of constant curvature was fitted to the final 1/3 of the trial and projected onwards from that point up to the depth of the target. We then calculated the lateral offset of the projected path from the target pole in metres. The mean end steering error was then calculated in two ways: the signed constant error (CE) which provided a measure of bias, and the unsigned root mean square (RMS) error which provided a measure of precision. Average bias and precision were calculated across participants and are displayed in Figure 3.

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Insert Figure 3 here

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The results show that there were systematic differences in the constant errors across levels of gaze angle ( $F(2,10) = 146.14, p < .001$ ) and retinal flow ( $F(2,10) = 13.76, p < .001$ ). When gaze angle information was veridical, bias in retinal flow caused steering errors that would be predicted from the direction of the ground rotation. Similarly when retinal flow was veridical, bias to gaze angle resulted in directional errors that demonstrated reliance upon the visual angle of the steering target. The overall patterns of constant steering errors do indicate that there is a tendency to understeer (a natural negative bias) even when retinal flow and gaze angle are unbiased, which is also reflected in reduced precision of RMS errors in negative gaze angle bias compared to positive bias.

When bias was present in both retinal flow and gaze angle information, the pattern of constant errors suggested a linear combination of information: when the direction of retinal flow and gaze angle bias conflicted, steering errors decreased in magnitude, whereas coordinated bias increased errors. This linear relationship was confirmed statistically by a non-significant interaction between retinal flow and gaze angle conditions ( $F(4,20) = 0.04$ , ns). This linear relationship need not be simply additive, since it is possible that under some bias conditions steering errors were augmented beyond the sum of the constituent biases. To determine whether the linear relationship could be predicted from summation we compared the differences in steering errors due to gaze angle bias across three levels of retinal flow bias, then repeated this analysis, examining error differences due to retinal bias across three levels of gaze angle bias. There was no significant difference in the size of the steering error change for either the gaze angle ( $F(2,10)=1.17$ , ns) or retinal flow ( $F(2,10)=.46$ , ns) suggesting that the linear combination was indeed additive. We therefore propose that retinal flow and gaze angle information are combined in a similar manner to retinal flow and visually specified direction, and that the model presented in Eq.1 holds. It should be noted that in this experiment we did not explicitly test the combination of visual direction (VD) with retinal flow and gaze angle.

We can calculate the relative weights of retinal flow and gaze angle by modelling the steering behaviour of the human observer and then biasing the informational inputs to the model in a manner commensurate with that used for the experimental stimuli. Assuming veridical estimates we can then adjust the weights of retinal flow and gaze angle information until the modelled steering errors match observed steering errors. This process reveals that gaze angle is weighted .85, and the  $\beta$  weight for retinal flow is .15. This weighting highlights the importance of gaze angle information, and the relatively weak influence of retinal flow, though the weighting of retinal flow seems reduced in comparison to previous experiments that explored retinal flow and gaze angle (Wilkie & Wann, 2002). This could be partly due to the restricted FoV of the viewport, since the display used by Wilkie & Wann (2002) subtended  $64.8^\circ \times 50.7^\circ$ , which revealed more peripheral ground information and they estimated a retinal flow weighting of .35. Bear in mind that these weights merely describe the general influence of each information source as captured at the end steering error, rather than

representing the dynamic use of information that could fluctuate throughout each steering event.

We have demonstrated the importance of gaze angle information when steering a course, but what are the constituents of gaze angle? To determine this we can examine head rotations during steering to see what proportion of gaze angle information was encoded by head and eye movements.

### *Head Rotation*

Each trial began with the steering and fixation target offset by one of a range of initial headings (4, 8, 12 or 16 degrees). Due to the active nature of the task, and the influence of erroneous information, the gaze fixation angle could increase to almost double the initial angle over the course of the steering manoeuvre before being minimized. The angle of the target, and of the participant's head was recorded at each frame (25Hz) and the proportion of gaze angle that was made up of head rotation was then calculated (the remainder being generated by eye rotation). Movements of the head ranged from 47% of gaze angle when the target offset was small down to 8% for larger offsets. This is quite different from the patterns observed when negotiating a series of tight and winding bends where 92% of the gaze angle was controlled by head motion (Land & Tatler, 2001). In pilot work we have recorded head movements of participants driving on a simulated curved roadway around a number of bends and we also observed extensive use of head rotations to direct gaze. In the current task participants did not need to move their heads a great deal to keep the target comfortably fixated when steering a single curved path, however head rotations sometimes reached upwards of  $\sim 20^\circ$ , with average rotations of  $\sim 2.8^\circ$ . Since some conditions encoded a proportion of the gaze angle with the head, it therefore seems prudent to examine further those sources of information available to a mobile head and gaze, and determine what aspects of head rotation supply useful information.

## **Experiment 2: The role of body rotation in the presence of biased retinal flow or gaze angle**

We have shown that gaze angle, including head rotation, is a useful source of information whilst steering a course and demonstrated the additive combination of

retinal flow and gaze angle information. In the second set of experiments we wanted to test the role of body rotation information in the presence of biased and veridical retinal flow or gaze angle information. We sought to establish whether body rotation information, detected via the semicircular canals, were able to inform active steering in the conditions explored in Experiment 1.

## **Method**

### *Participants*

Six participants were recruited at the University of California, Berkeley, US. All persons gave their informed consent prior to their inclusion in the study, and the studies themselves had been approved by the relevant ethics committee (The University of Reading) and have been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All participants had normal or corrected-to-normal vision and were unconnected with the study but they did have some general experience of viewing motion displays in addition to having at least 2 years driving experience. Observers used both eyes to view the non-stereo image (binocular viewing), and head and body position were not stabilized.

### *Apparatus*

Real time images were generated on an X200 Dell Laptop (930 MHz P3 processor; Intel Corporation, Santa Clara, CA) with an Intel 82830M Graphics Controller Card running Windows XP. The images were projected onto a screen using a Boxlight DLP Projector (800 x 600 pixels). The screen was fixed to a motorized rotating chair and moved with it as it rotated. The viewport subtended  $29.6^\circ \times 27.6^\circ$  and was viewed from a distance of 0.6m. The display was limited to this size to allow manipulation and control of gaze angle information (Figure 2, lower panel). Frame rate of the display and rate of update of chair rotation speed was 25Hz. Stepper motors with fine angular resolution were used to rotate the chair. New step rates were streamed to the stepper motor through a Panther Microstepper Controller (Intelligent Motor Systems, Hartford, CT). Due to slow ASCII communication protocols no specific frame-by-frame positional feedback was possible, but in constant acceleration trials the final location of the chair matched the final world location with a mean error of  $0.29^\circ$  (SD:  $0.19^\circ$ ). The number and size of steering adjustments influenced this figure since rapid

oscillating direction changes of large magnitude would compound inaccuracies. To minimise adjustments, participants were encouraged to steer smooth paths toward the target, though the priority was to ensure the greatest degree of steering accuracy possible. The six participants were given practice trials to become familiar with the procedure, the display, and the mapping of the input device to control smooth paths.

The motors of the chair emitted an audible whine as they rotated. To prevent the pitch of the motor noise being used as a cue to rotation rate, Bose acoustic noise cancelling headphones were provided, and music was played to the participants during trials. Because the position of the chair needed to be reset to the origin after each rotation event, different time gaps occurred between trials as the chair recentered itself at a subthreshold rate. To inform the participant when the next trial was ready to be commenced, a chime was played through the headphones.

### *Procedure*

We manipulated the retinal flow or gaze angle information using the techniques outlined in the *general methods* section (viewport motion was used to alter gaze angle information and a rotating ground plane biased retinal flow information). For each visual condition we introduced two levels of body rotation: 0% and 100%. To keep the number of conditions manageable, there were no visual conditions that biased both retinal flow and gaze angle simultaneously. The 0% rotation condition displayed visual motion with no accompanying body rotations, as tested in Experiment 1, but provides a useful baseline measure of accuracy when compared to 100% rotation since we would expect equivalent or better performance when appropriate body rotation was available. To generate 100% rotation the motorised chair was moved at a rate commensurate with the steering implemented by the participant through joystick, and therefore it also matched the amount of rotation present in the visual scene when retinal flow was veridical.

Gaze angle information was biased in one of two directions (left or right) but the rate and direction of gaze angle bias was independent of the rate and direction of body rotation (which was controlled by the steering behaviour). The net effect of these conditions meant that in some conditions gaze angle moved in the opposite direction to the body rotation and in others it moved in the same direction as body rotation. In

an equivalent manner retinal flow information was biased by rotating the ground texture to the left or right around the point of fixation, independent of the rate and direction of body rotation.

Two initial target angles ( $4^\circ$  &  $8^\circ$ ) were used to cause varying amounts of SCC (labyrinthine) stimulation within the range of the chair and display. There were 4 trials at each initial angle for the 6 visual conditions, repeated under two levels of body rotation (0% & 100%) making a total of 96 trials per participant. The maximum rotation angle of the chair was  $\pm 25^\circ$ , and the maximum viewport size ( $29.6^\circ \times 27.6^\circ$ ) ensured there was room for lateral motion across the projector screen. The participants' head motion was unmonitored, and though a headrest was present in the chair, this was to provide support rather than restrict head rotations. We would expect head rotation rates similar or smaller than those present in Experiment 1, since the maximum heading angle of the target on the screen ( $8^\circ$ ) meant that the target would have remained within the comfortable viewing zone of eye movements for the majority of trials.

The threshold of the human vestibular system for detecting accelerations can range from  $0.02^\circ/s^2$  (for the sensitive oculo-gyral illusion to be exhibited) up to  $1\text{--}2^\circ/s^2$  for nystagmus or body sensations or to be detected (Howard, 1982). It is not clear how long the SCC signals need to remain within a detectable range to be useful to the steering system. The rates of rotation generated in our conditions depend upon the initial angle of the steering target, distance of target, and the speed at which you are travelling. These parameters are limited by the size of display used to control for information supplied by screen edges (by centring the target in the viewport at all times). Additionally when we bias gaze angle information we need to translate the viewport, so there is conflicting demand for space within the projection area. A final limitation is the range and rate of the chair; from centre it can move  $\pm 25^\circ$ . These various constraints meant that active control body-rotation trials caused average rotation accelerations of  $\sim 3.65^\circ/s^2$  with maximum rotation accelerations of  $> 10^\circ/s^2$ . All participants reported experiencing physical body rotations suggesting supra-threshold stimulation throughout some section of each trial. Many navigation tasks investigating vestibular inputs have simulated large ( $> 90^\circ$ ) and rapid changes in orientation, so we should also emphasise that we are trying to simulate the properties

of an everyday locomotor situation, with travel velocities, rotation rates, and information sources that would be available to a driver or cyclist moving across an unmarked tarmac environment, with the ultimate aim of determining which information sources are used under these conditions. Participants controlled their trajectory in the manner described in the *general methods*.

## Results and Discussion

When retinal flow information was biased (Figure 4) we again saw systematic directional errors in steering ( $F(2,12) = 7.07, p < .01$ ), however veridical body rotation did not significantly affect steering errors ( $F(1,6) = .07, ns$ ).

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Insert Figure 4 here

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The same patterns can be observed when gaze angle information is biased (Figure 5). Steering behaviour is highly influenced by gaze angle information ( $F(2,12) = 127.71, p < .001$ ) but unaffected by the presence or absence of body rotation information ( $F(1,6) = 1.66, ns$ ).

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Insert Figure 5 here

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The results demonstrate that the veridical body rotation information was not utilised by participants to improve the accuracy of their steering performance when retinal flow (Figure 4) or gaze angle (Figure 5) were biased. The pattern of results seem to demonstrate that body rotation information was not used to reinforce either visual retinal flow or non-visual gaze angle and thereby offset errors in the other source of information. The observation that the system can operate in a similar manner whether vestibular information is absent or available, may just reflect that we are accustomed to performing smooth steering tasks where SCC stimulation drops close to or below threshold. To establish whether the steering system actually excludes vestibular

information in this type of task we create settings in experiment 3 where the SCC information directly conflicts with gaze angle and retinal flow information.

### **Experiment 3: The effect of biased body rotation in the presence of retinal flow and gaze angle**

We observed no influence of veridical body rotation in the presence of biased retinal flow & gaze angle, in experiment 2, suggesting that body rotation information was not additively combined with either source in these situations. Our aim in experiment 3 was to see if biased body rotation information could influence steering in the presence of veridical retinal flow and gaze angle information.

#### **Method**

The participants and apparatus were the same as described in experiment 2.

#### *Procedure*

To further test whether SCC stimulation influences steering we introduced two types of bias to this source of information. The first method was to rotate the chair proportional to the correct amount of rotation. In this way the participant would feel rotations that were linked to their steering manoeuvres, but the information supplied by those rotations would be greater or less than that specified visually. Veridical information can be labelled as 100% rotation of the chair. Bias was introduced by rotations of either lesser or greater proportions. Initially we tested a small range of biases ( $\pm 25\%$ ), centred around 100% veridical body rotation information: 75%, 100%, and 125%. For each of these conditions we tested 2 initial headings (4&8°) with 4 trials per heading, making a total of 24 trials per participant. We then examined a more extreme range of rotations that were larger and could also be in the wrong direction (indicated by '-'): -150%, -100%, 0%, 100%, 150%. We tested 3 initial headings (4,6,8°) with 6 trials per heading, making a total of 90 trials per participant. Using a bias of 150% unfortunately limits the maximum initial angle of the steering target to be 8°. To minimize the initial angle at a constant rate would require steering at 1.27 deg/s. The general pattern of steering, however, consisted of an initial turning phase with an accelerating rate of steering, followed by a period of constant turning,

and finally deceleration. The average accelerations resulting from steering to the target were  $\sim 3.65^\circ/s^2$  with maximum accelerations of  $>10^\circ/s^2$ .

One concern was that the rotation rates resulting from active control of locomotion may have been sub-threshold for significant periods of the locomotor event. To address this issue we implemented a second technique to ensure that the highest accelerations possible were reached within the physical constraints of the chair and the limitations of the stimuli generation (screen size and viewport motion). One of two constant accelerations were produced either in the correct (+) or opposite (-) direction relative to the initial offset of the target, so rate of rotation was not dependent on the steering behaviour of the participant: -1.2, -0.6, 0, +0.6, +1.2 $^\circ/s^2$ . This will demonstrate whether a constant strong SCC signal can upset steering behaviour when there are 2 veridical visual sources available. For each of the 5 conditions we tested 2 initial headings (4&8 $^\circ$ ) with 4 trials per heading (except 0 bias which had 8 trials per heading) randomly interleaved, making a total of 48 trials per participant. Participants controlled their trajectory in the manner described in the *general methods*.

## Results and Discussion

As in experiment 2, there is little evidence for the influence of body rotation on steering. Small body rotation biases, that were 75% or 125% of the veridical rotation amount, resulted in no change in steering behaviour (Figure 6a:  $F(2,10)=2.9$ , ns). For medium body rotation biases (-150%, -100%, 150%) changes in steering bias are minor (Figure 6b), and analysis of variance reveals no significant effect of body rotation bias on constant errors ( $F(4,20)=1.44$ , ns) or precision ( $F(4,20)=.87$ , ns). In all trials where body rotation was yoked to steering, across conditions and participants, there were no consistent trends, significant changes in precision or systematic patterns of bias. It therefore appears that our sensitivity to body rotation information is not sufficient for useful integration with retinal flow and gaze angle information when generating steering responses. This reinforces the findings of experiment 2 that observed no benefit of veridical body rotation information in the presence of biased retinal flow or gaze angle.

To determine whether body rotation biases of constant acceleration could influence steering we introduced body rotations that were not yoked to steering behaviour, and so were guaranteed to stimulate the SCC's throughout the trial. These conditions resulted in the broadest range of steering errors (Figure 6c) and even caused significant changes in constant errors ( $F(4,20) = 6.4, p < .01$ ). Closer examination of the results revealed that only some biased body rotation conditions influenced steering behaviour. When body rotations were in the correct direction neither precision ( $F(2,10) = 1.19, ns$ ) nor constant errors ( $F(2,10) = .97, ns$ ) were significantly different from the unbiased condition, despite a mismatch between the rate of accelerations specified by body rotation and those from retinal flow and gaze angle. Only body rotations in the opposite direction to steering caused steering errors, where persistent SCC signals were inconsistent in both direction and magnitude. Even under these circumstances constant errors due to body rotation bias were small when compared to the magnitude of those observed in biased visual conditions in experiment 1 & 2.

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Insert Figure 6 here

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## General Discussion

In these experiments we estimated the contribution of visual and non-visual sources of information to steering behaviour: retinal flow, gaze angle direction and vestibular, semi-circular canal (SCC) information. In experiment 1 we introduced systematic biases to retinal flow and gaze angle information and examined the resultant steering behaviour. Bias to either source caused predictable directional steering errors, and simultaneous bias to both sources resulted in errors consistent with a linear combination of information. The relative weightings of this information were generated by modelling the steering performance using the Wilkie & Wann (2003) steering model, and revealed a much stronger influence of gaze angle upon steering than would have been predicted from our previous work. The general result argues against the sole use of either retinal flow or gaze angle and provides further evidence for the combined influence of these information sources (in line with Wilkie & Wann, 2002).

It is worth noting here that the influence of each term in the steering equation (Eq.1) is a product of the strength of signal and the gain applied to that signal (the weight). The weightings within a system are often related to the variability of each environmental property, which can be estimated using a maximum-likelihood estimation strategy (Ernst & Banks, 2002). We estimate the weighting of information by modelling biased information and its effect upon steering rather than factoring in signal strength since there is no single way to measure the strength or variability of rotation estimates. For example, we could estimate retinal flow strength on the basis of ground textures, edge rate, contrast, or field of view, and each would supply a different result. An additional issue with calculating weights for these information sources is whether these weights remain constant across the time series of a steering manoeuvre. It may well be that over the course of an approach to a target steering control shifts towards use of gaze angle (or visually specified direction information if available) to allow precise alignment with the target. On this basis we are unable to identify the statistically optimal method of processing the relevant information to generate steering performance.

In experiment 2 & 3 we sought to examine the role of vestibular stimulation, provided through body rotation, when controlling locomotion. Firstly we made veridical SCC information available when either retinal flow or gaze angle was biased, but the presence of body rotation had no effect upon steering behaviour. We can infer from this that gaze angle information does not rely upon a vestibular input to determine the rate of change of the gaze angle. We then examined whether a biased SCC input could influence steering performance when veridical retinal flow and gaze angle were present. Again, no influence of body rotation was observed when the rotations were yoked to steering behaviour, and though a significant bias was observed in the most extreme case of a constant body rotation in the wrong direction, the effect was still minor. This suggests that participants appeared generally to disregard SCC inputs when controlling steering and rely predominantly on retinal flow and gaze angle. Only when the both the dynamics and direction of body rotation conflicted with the other sources was any disruption to steering observed, and even then the magnitude of influence was small. These results are consistent with the findings of Crowell et al. (1998) who found that pure vestibular stimulation did not influence path extrapolation judgements.

Kemeny and Panerai (2003) reviewed the current evidence for the use of vestibular information during driving, and concluded that its role in vehicle control still needed to be examined. In line with this we have aimed to generate a situation consistent with everyday driving, following curving paths, with information that is available for instant online control rather than for observation and report. For this task, under these speeds and rotational rates, no effect was found of proportional vestibular information. Although the vestibulo-collic reflex is involved in coordinating head movement with trunk rotation (Land, 2004) the vestibular information does not appear to be used in online steering control. Our results would seem to contradict recent evidence indicating the importance of vestibular inputs for perception of self-motion (Bertin & Berthoz, 2004), however we have addressed the issue of closed-loop control of steering rather than the general percept of position in space. It might be argued that higher rates of SCC stimulation would show more of an effect, but the rates we used were appropriate for everyday steering manoeuvres. We would expect an increased role for vestibular information if we altered the nature of the task to be more dependent on position and orientation *within the world*, for example looking behind you then pivoting on one foot to turn around (Land, 2004).

Wilkie & Wann (2002) showed the additive combination of retinal flow and retinally referenced direction information. Here we confirm that retinal flow and gaze angle direction information also combines in an additive manner, but that vestibular information plays little or no part in prospective steering behaviour. These results provide further support to the growing evidence in multi-modal integration that between-sense information can be separated more easily than tightly grouped within-sense information (Hillis, Ernst, Banks & Landy, 2002). The intriguing issue arising from this is whether such separation can have an impact upon the use of gaze angle information. It could be considered a cross-modal source, relying upon both retinal and extra-retinal information, and as such may be more susceptible to exclusion when further retinal information sources (such as retinally referenced direction) are available in addition to retinal flow.

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<http://www.rdg.ac.uk/ar1> and <http://john.berkeley.edu/>.

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## Figure Captions

Figure 1. a) Strategies for steering towards a target: Holding the target at a constant visual angle  $\theta$  (as shown) would result in a curved path that overshoots the end location (though it may eventually approach the target when the path tightens into a spiral). Reducing the visual angle at a constant *rate* would result in a curved path that intercepted the target. Fixating the target and steering to maintain a constant rate of body rotation would result in an equivalent path. A similar path can also result from fixating the target and steering to null any rotation that arises in the retinal flow field. See Wann & Land (2000) for details. b) A bicyclist approaching a bend whilst fixating the point on the ground. The cyclist's head and eyes are offset from her locomotor axis supplying gaze angle information, and body rotation information results from the curved path around the bend. c) Cyclists eye view from the bicycle with the point of fixation marked with a white spot. Not only is gaze angle direction information made available by fixating the eccentric point on the ground, but this fixation also shapes the retinal flow information so that flow-lines for ground elements remain straight if current steering is appropriate to ensure you pass through that point (Wann & Swapp, 2000).

Figure 2: Two types of experimental setup. In experiment 1 (Top Panel) we used a wide field of view projection screen containing a large viewport that could be translated to manipulate gaze angle information. Steering was controlled with a joystick, and head rotations were measured with a magnetic head tracker. In experiments 2 & 3 (Bottom Panel) the screen still contained a moveable viewport, but this was of smaller size than experiment 1. The whole projection system was attached to a motorised chair which could be rotated around the yaw axis to introduce body rotations of varying magnitudes.

Figure 3: Bias (a) and precision (b) of steering performance for combinations of biased retinal flow (x-axis) and gaze angle (grey, white, black: positive, zero, negative bias respectively). Data averaged across six participants from Experiment 1.

Figure 4: Bias (a) and Precision (b) of steering in the presence of veridical and erroneous retinal flow information, and either no body rotation (BR0) or veridical body rotation (BR1). Data averaged across six participants from Experiment 2.

Figure 5: Bias (a) and Precision (b) of steering in the presence of veridical and erroneous gaze angle direction information, and either no body rotation (BR0) or veridical body rotation (BR1). Data averaged across six participants from Experiment 2.

Figure 6: Biased body rotation (BR) in the presence of veridical retinal flow and gaze angle direction. Data averaged across six participants from Experiment 3.

- a) Small BR Bias (25%)
- b) Medium BR Bias
- c) Constant acceleration of .6 or 1.2 deg/s/s

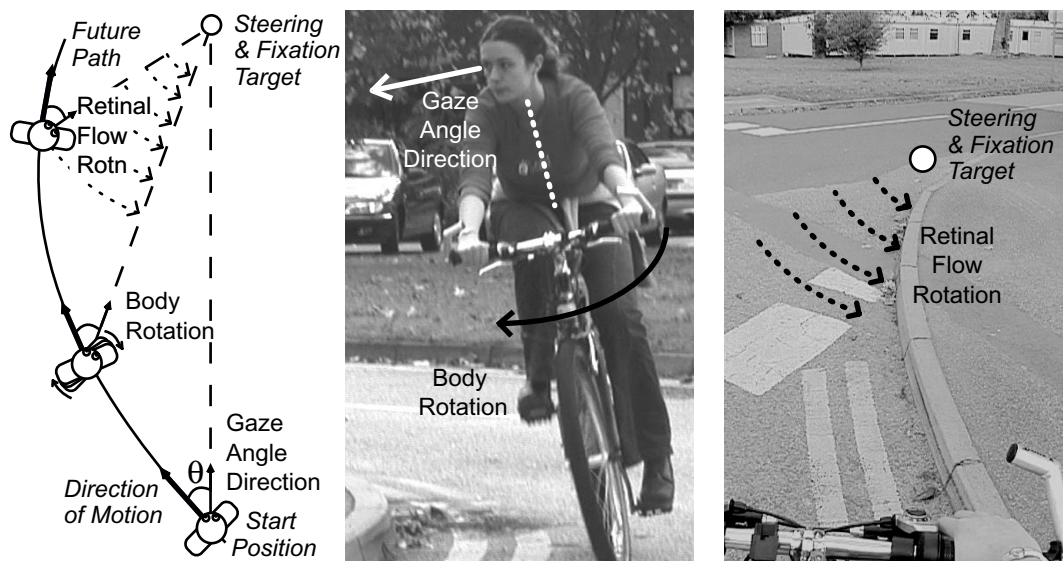


Figure 1

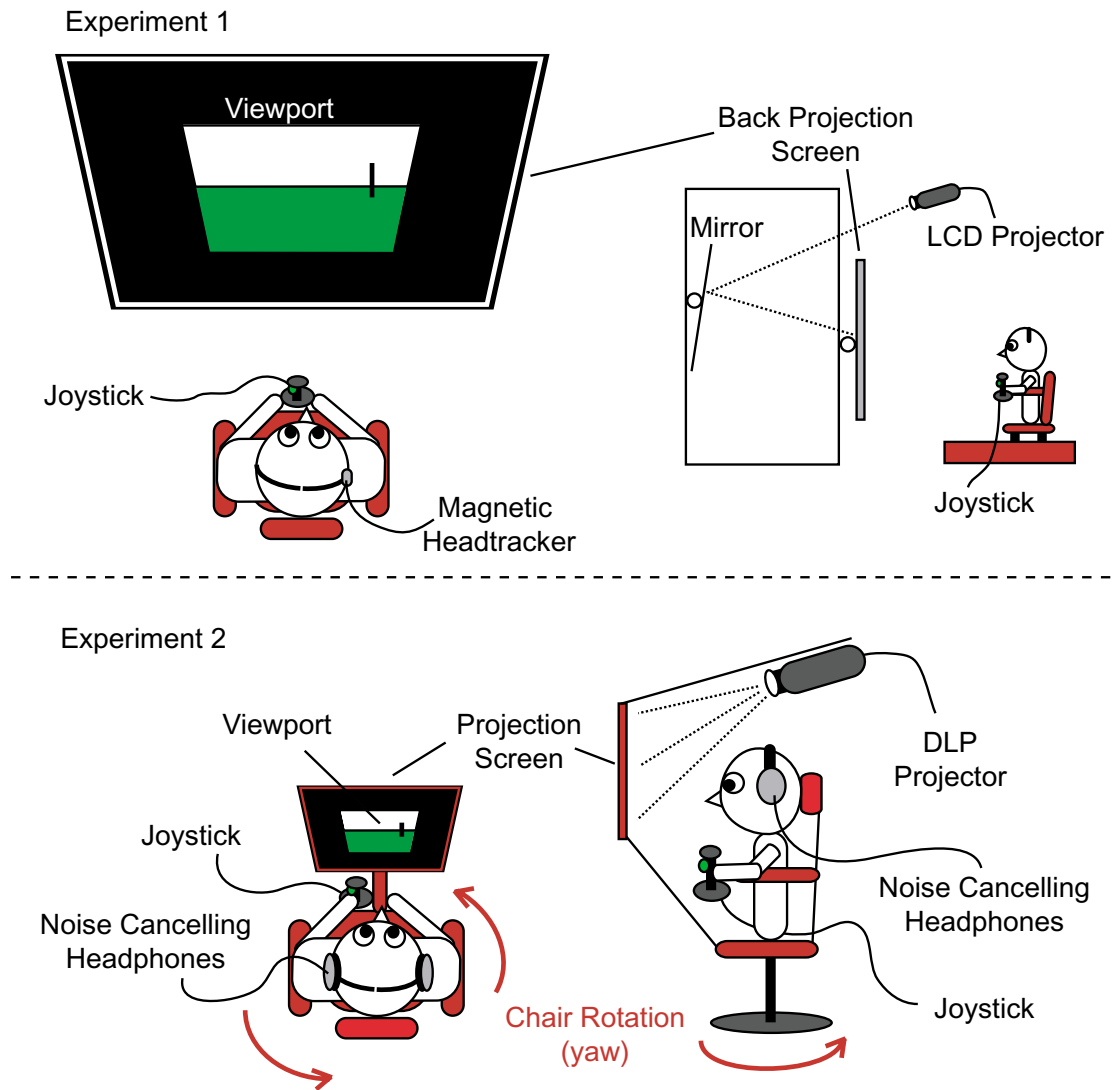


Figure 2

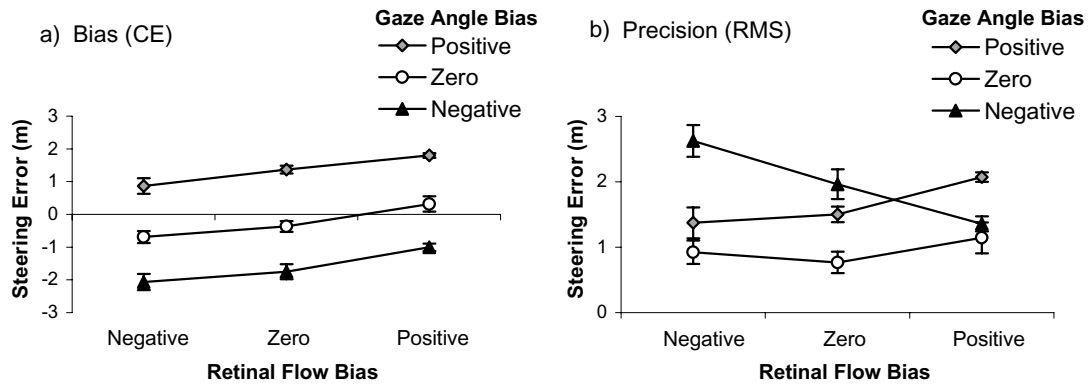


Figure 3

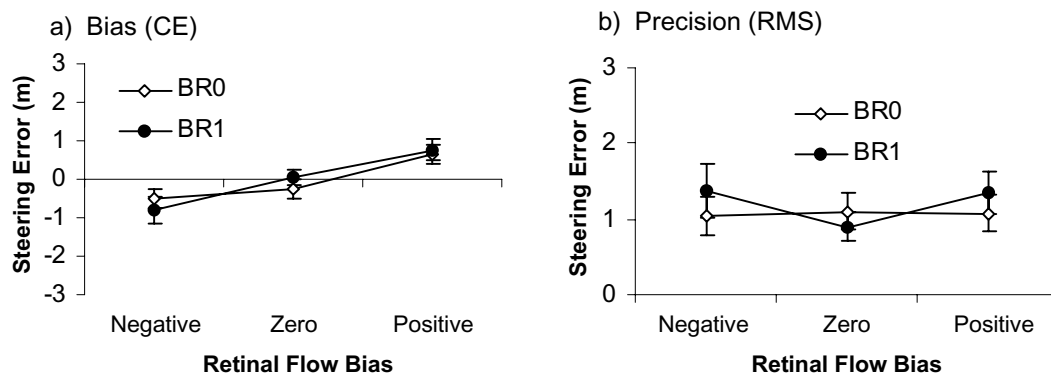


Figure 4

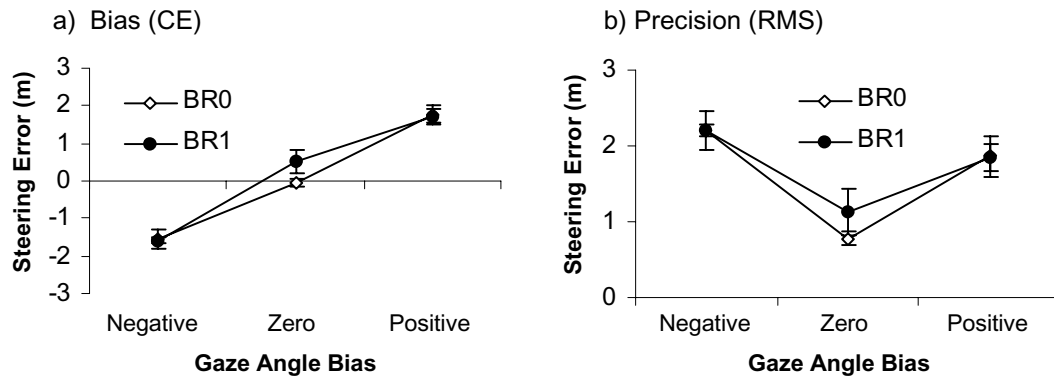


Figure 5

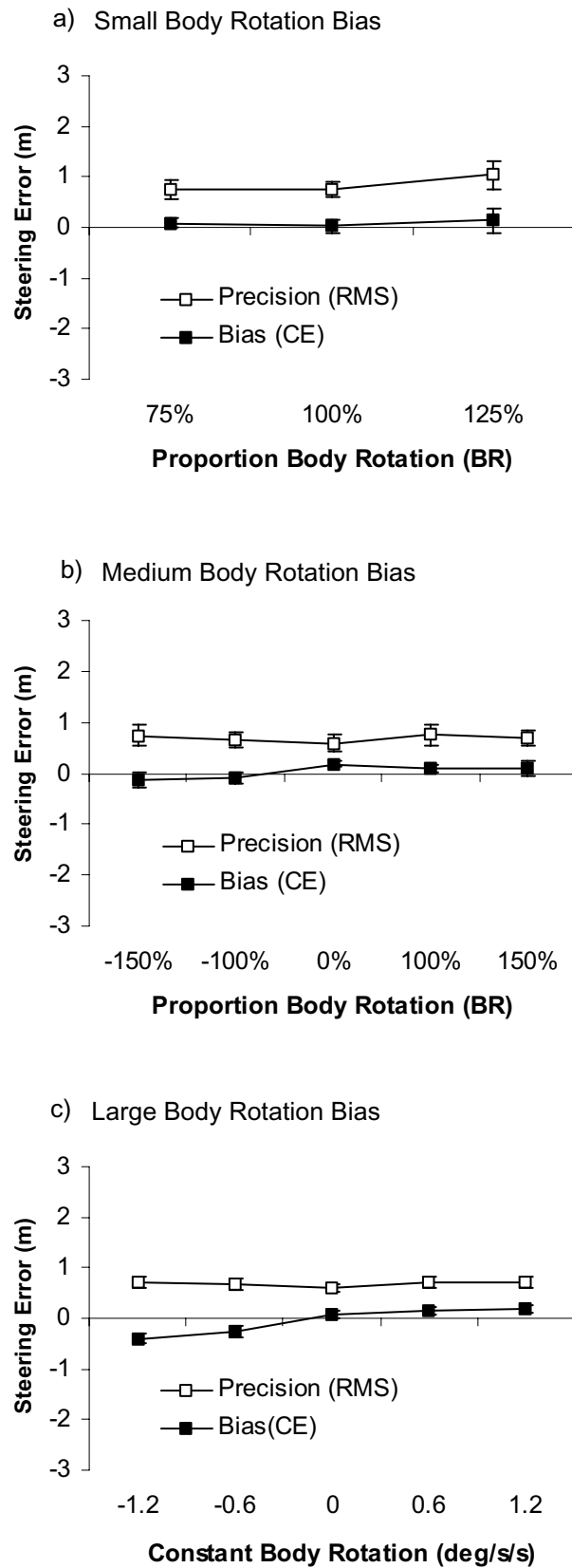


Figure 6