Eccentric gaze dynamics enhance vection in depth

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This study examined the role of eccentric gaze dynamics in the generation of visual illusions of self-motion (i.e., vection). In Experiment 1, observers maintained their gaze either upward, downward, leftward, or rightward with respect to the center of a radially expanding optic flow pattern, which simulated forward self-motion in depth through a 3D cloud of objects. Real-time vection strength ratings and changes in horizontal and vertical eye positions were recorded simultaneously. Vection strength was found to increase progressively over the course of each 30-s presentation of radial flow. Eye tracking revealed strong optokinetic responses, consistent with ocular following responses (OFRs). Reported increases in vection strength in all four gaze conditions were typically preceded by reductions in slow-phase eye velocity. Similar results were found in Experiment 2, where displays simulated self-motion over a ground plane, which provided superior perspective. We conclude in both cases that enhancements of vection strength over time were temporally contingent upon the changing character of OFR while viewing these displays.

Keywords: self-motion, vection, sensory integration, eye movements, gaze, optic flow


Introduction

The “optic flow” generated as we move through the world can provide us with important information about our speed and direction of self-motion (i.e., vection). In Experiment 1, observers maintained their gaze either upward, downward, leftward, or rightward with respect to the center of a radially expanding optic flow pattern, which simulated forward self-motion in depth through a 3D cloud of objects. Real-time vection strength ratings and changes in horizontal and vertical eye positions were recorded simultaneously. Vection strength was found to increase progressively over the course of each 30-s presentation of radial flow. Eye tracking revealed strong optokinetic responses, consistent with ocular following responses (OFRs). Reported increases in vection strength in all four gaze conditions were typically preceded by reductions in slow-phase eye velocity. Similar results were found in Experiment 2, where displays simulated self-motion over a ground plane, which provided superior perspective. We conclude in both cases that enhancements of vection strength over time were temporally contingent upon the changing character of OFR while viewing these displays.

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Introduction

The “optic flow” generated as we move through the world can provide us with important information about our speed and direction of self-motion (Gibson, 1950; Gibson, Olum, & Rosenblatt, 1955). However, optic flow alone is not sufficient to determine whether we are in fact physically moving. This is because identical patterns of optic flow will be generated when we move toward objects embedded in the scene and when the same group of objects moves toward us when we are stationary (refer to Movie 1). The visual system often interprets global patterns of optic flow as being due to self-motion, and as a result, it is possible to induce compelling visually induced illusions of self-motion in stationary observers, known as vection (Brandt, Dichgans, & Koenig, 1973). The effectiveness of vision in generating vection depends on how the visual information is acquired by our eye(s) and integrated with the available self-motion information arising from other senses. The present study examines the role that eye movements play in the capture of visual motion information in stationary observers and how they may influence visual distinctions between self- and object motions.

The brain can supplement visual information about linear self-motion in depth with inertial signals from the otolith receptors of the vestibular system located in the inner ear. These receptors respond to linear head acceleration and can help resolve the self- versus object motion ambiguity raised by optic flow. For example, otolith signals are generated when the head moves from rest and during changes in its linear velocity, such as the deceleration that occurs when the head achieves a new stationary position (red zones in Movie 2). However, these otolith projections do not signal head movements occurring at a constant linear velocity (green zone in Movie 2). This means that even with multi-sensory contributions from inertial and visual signals, a residual perceptual ambiguity will often persist, leading to the generation of vection.

Normally, when we move angularly or linearly through space, compensatory slow-phase eye movements are induced in an attempt to stabilize the retinal image. Both visual and vestibular inputs drive these eye movements, which are coordinated via convergent signals arising from the primary vestibular receptors and global retinal stimulation consistent with self-motion (Rucker, 2010). The present study examines the role that these compensatory eye movements play in the visual perception of self-motion.

Optokinetic nystagmus (OKN) is a compensatory eye movement induced by visual displays that simulate maintained angular head rotation. The earliest eye movement research on vection examined the role of OKN in the onset of circular vection. For example, Brandt, Dichgans, and Büchele (1974) found that the onset of vection...
correlated with the buildup of OKN over time. Taken by itself, this finding suggests that the engagement of compensatory eye movements might facilitate the onset of vection. However, as noted by Howard (1982), circular vection can still be induced when OKN is suppressed with active target fixation (p. 392), which suggests that OKN buildup over time is not necessary for the induction of circular vection.

Displays that simulate linear head translation also induce eye movements that facilitate the maintenance of a stable visual image. The ocular following response (OFR) achieves optimal activation at extremely short latencies (<100 ms) in response to motion parallax simulating linear head translations in 3D space (e.g., Kawano & Miles, 1986; Miles, 1998; Miles & Kawano, 1986; Miles, Kawano, & Optican, 1986; Schwarz & Miles, 1991). These visually mediated OFRs are similar to the early phase of OKN (i.e., OKNe) and scale inversely with perceived viewing distance (Busettini, Miles, & Schwarz, 1991; Busettini, Miles, Schwarz, & Carl, 1994), providing retinal image stability for a given depth of field. Recently, we found that pseudo-randomly directing the observer’s gaze around a radial flow display improved the overall strength of linear vection in depth (Palmisano & Kim, 2009). This gaze shifting advantage for vection may have been due to the increased OFR/OKNe that follows each saccade eye movement (e.g., Kawano & Miles, 1986; Lisberger, 1998).

However, the OFR/OKNe is also known to adapt rapidly during maintained viewing of radial flow (Miles et al., 1986). This will also lead to the repeated adaptation of the OFR over a series of gaze shifting events, which will increase the retinal slip of the visual scene. It is therefore possible that either the enhancement of the OFR during gaze shifting conditions or the retinal slip generated by its repeated adaptation may lead to increases in vection strength.

Previously, we found that stabilizing eccentric gaze with a stationary eccentric fixation point (increasing retinal slip) impaired vection, compared to free viewing conditions (Palmisano & Kim, 2009). It is possible that this finding may have been caused by differences in the retinal stimulation produced by the active versus passive engagement of eye movements. The present study examined the changes in eye movements that accompany changes in linear vection in depth as observers passively viewed radially expanding optic flow displays. We focused on eccentric, as opposed to central, viewing, since eccentric viewing produces the strongest OFR in passive observers due to the greater motion in the periphery of radial flow displays.

**Experiment 1**

**Experiment 1** examined the possible relationship between compensatory eye movements and vection. Observers were exposed to purely radial flow while they...
gazed at one of the four eccentric display locations (10 degrees from center out to the left, right, up, or down). They were instructed to maintain their gaze in this display location for the entire duration of each 30-s trial. Over the course of each trial, we simultaneously measured both our observers’ eye movements (OFRs) and their ratings of vection strength in real time. The goal of this experiment is to look for any eye movement changes that might lead to vection changes (e.g., from perceived scene motion to perceived self-motion).

In principle, there are three general ways that the OFR might alter the vection experience. The first possibility is that OFR engagement might be required to induce vection. If this is the case, then we would expect slow-phase eye velocity to increase prior to each increase in vection strength. The second possibility is that it is the adaptation of the OFR over time that is responsible for inducing vection and triggering subsequent vection enhancements. If it is this slowing of the OFR that triggers vection enhancements, then we would expect a decrease in slow-phase eye velocity to precede each increase in vection strength. Finally, it is possible that vection occurs independently of the pursuit characteristics of the observer’s eye movements, as proposed in the case of angular vection (Howard, 1982), in which case we should expect there to be no consistent relationship between changes in vection strength and changes in eye velocity.

**Methods**

**Observers**

Eight adults (four males and four females), who were naïve to the aims of the experiment, had normal or corrected-to-normal vision, and worked/studied at the University of Wollongong, participated in this study. All observers received a fee of $20 AUD for their contribution to the project. All procedures used were approved in advance by the Human Ethics Committee at the University of Wollongong.

**Optic flow displays**

Optic flow displays consisted of 2304 randomly positioned blue square objects (1.8 cd/m²) on a black background (0.04 cd/m²). Objects were distributed uniformly within a simulated 3D environment (approximately 3.0-m optical depth). These radially expanding patterns of flow simulated constant-velocity forward self-motion in depth by moving the square objects toward the camera viewpoint linearly at a rate of 1.0 m/s. After an object moved beyond the near clipping plane of the simulated space, its spatial configuration was rerandomized before reemerging from the far clipping plane in the distance. The size of each square object increased from 0.05° at the far clipping plane to 1.08° at the near clipping plane, appropriately simulating smooth and continuous self-motion in depth, while minimizing the processing cost of real-time scene rendering.

**Gaze tracking**

Horizontal and vertical eye movements were recorded from the eight head-restrained observers in real time using 3D video oculography (Figure 1). Image acquisition was performed using a FIREFLY-MV 120Hz Firewire camera secured to an aluminum frame inserted into a form-fitting ski mask after removal of its anti-glare filter. Images of the left eye (320 × 240 pixels) were acquired and analyzed online using custom eye tracking software. Eye position in degrees was calibrated over a ±15° angular range in the horizontal and vertical directions. The conversion from 2D pixel deviations of the pupil to angular rotations in horizontal and vertical directions was obtained using simple geometric transformations (see Haslwanter, 1995; Kim, 2004). Acquisition of eye movement data was handled by a dedicated PC, which transmitted time-stamped eye position signals to the stimulus generation machine via wireless Bluetooth UDP network messages (Kim & Palmisano, 2008). This hardware configuration formed a data acquisition pipeline that

![Figure 1. Schematic of the infrared video-oculography system used to record monocular changes in eye position. An occluder was placed over a hole made in the base of a plastic bucket to produce a rectangular aperture through which the observer viewed optic flow displays, while their head was immobilized on a chin rest.](https://jov.arvojournals.org/)
supported the direct temporal synchronization of ocular and visual-display events (Movie 3).

We used a right-handed coordinate system to characterize rotations of the eye. Horizontal eye movements were defined as those occurring around the cardinal $z$-axis, which had a positive direction that pointed upward from the top of the eye. Hence, leftward horizontal eye movements around the $z$-axis were indicated by positive (Euler) angular values (in degrees), whereas rightward eye movements around the $z$-axis were indicated by negative angles. Vertical eye movements were defined as those occurring around the cardinal $y$-axis, which had a positive direction that pointed leftward, from the perspective of the observer. Hence, downward vertical eye movements around the $y$-axis were indicated by positive angles, whereas upward eye movements around the $y$-axis were indicated by negative angles.

**Procedure**

Observers were instructed to manipulate a push–pull throttle throughout each optic flow display to indicate their instantaneous perceived self-motion in depth. They were informed that they would be presented with large visual motion displays and that they should indicate the strength of their illusory sensation of self-motion in depth as follows:

“Sometimes the objects may appear to be moving towards you, while at other times you may feel as though you are moving towards the objects. Your task is to push and pull on the throttle joystick to indicate any sensations of self motion you may experience. If your feel as though you are moving in depth or the sensation of self motion in depth increases, then push the throttle forward to an appropriate setting. If you feel as though you are not moving, or the sensation of self motion in depth decreases, then pull the throttle back toward either the zero/start position or an appropriately lower setting”.

Each 30-s trial began with the observer viewing a fixation point presented at the center of an otherwise darkened display for 4.8 s. An eccentric fixation cursor cross (luminance $\approx 20$ cd/m$^2$, 0.2-cm stroke width, $4^\circ$ visual angle—i.e., 13-cm diameter) was then randomly presented in one of the four cardinal display directions by $10^\circ$ for 200 ms, after which it was suppressed and the radial flow display commenced. Observers were instructed to maintain fixation at the approximate location they last saw the fixation cursor and to adjust a throttle control to indicate changes in vection strength over time. We were primarily concerned with examining the effects of gaze in standard viewing conditions, and so our observers performed the experiments with both eyes open.

**Data analysis**

Differential horizontal and vertical slow-phase eye velocities were determined for gaze at each of the four eccentric display locations. Eye velocity is numerically informative about gaze relative to the head during both visual and inertial stimulations, characteristic of physical self-motion (e.g., Kim, 2009; Kim & Palmisano, 2008, 2010). A cubic spline interpolation was used to resample these data to a temporal resolution of 250 Hz. This compensated for any missing samples and ensured data samples were equally spaced in time. Velocity was computed as the change in eye position over a 10-ms time period around each data sample acquired. This allowed us to characterize the pursuit characteristics of gaze relative to the center of the radial flow display. In order to remove contamination due to saccades and blinks, velocity traces were smoothed using locally weighted regression fitting over a 200-ms time span (see Cleveland, 1979).

Further analysis of eye movement responses in terms of their second derivative (acceleration) was performed (in the same manner as used to obtain velocity from position) to characterize any changes in these eye velocities. We computed acceleration profiles of eye movements to identify the presence of any adaptation in gaze control during maintained viewing of these optic flow displays. Eye acceleration prior to each indicated change in vection strength was averaged over a 1-s period ending 0.5 s before the real-time vection strength report. The mean of these values for each trial was computed to provide a stable estimate of acceleration. Repeated-measures ANOVAs were then performed on these acceleration estimates.

Movie 3. The radially expanding optic flow stimulus used in the present study to induce vection and the cursor presentation sequence used to direct observer gaze at the start of the trial.
Onset of vection was determined at the time the position of the throttle control moved from rest (i.e., velocity \( m \neq 0 \)). Overall vection strength was based on the final position of the throttle control at the end of each trial.

**Results and discussion**

**Effect of gaze direction on vection strength and latency**

Bar plots showing mean overall vection strength and associated standard errors are presented in Figure 2 (top). There appeared to be a trend for vection to be rated as stronger during downward gaze compared to the other three eccentric display locations. However, a repeated-measures one-way ANOVA performed on these data showed no significant difference in vection strength across the four viewing conditions \( (F(3, 21) = 1.37, p = 0.27) \).

Bar plots showing mean vection onset latency and standard errors are presented in Figure 2 (bottom). A repeated-measures one-way ANOVA on these data showed no significant difference in mean vection onset latency across the four gaze conditions examined \( (F(3, 21) = 1.80, p = 0.18) \).

**Effect of gaze direction on eye position and slow-phase eye velocity**

The mean displacement of the eye from the center of the display was similar for all four directions of gaze (up, down, left, or right; \( F(3, 21) = 0.32, p = 0.81 \)). The average gaze eccentricity, across all these conditions, was 12.9°. A Pearson’s product-moment analysis showed no significant correlation between average magnitude of eccentric eye position and overall vection strength pooled across observers \( (r = -0.24, p = 0.18) \). There was also no significant difference in overall eye velocity for the four directions of gaze, as indicated by a repeated-measures ANOVA \( (F(3, 21) = 0.63, p = 0.60) \). The mean eye velocity was determined to be approximately 5.0°/s based on the pooled data across these gaze conditions and observers.

**Slow-phase eye velocity and vection**

Figure 3A shows the time series of horizontal and vertical slow-phase eye velocities and vection strength buildup over time for one representative observer. Vection was observed to increase cumulatively over the course of each 30-s trial and tended to be temporally synchronized with reductions in slow-phase eye velocity (as indicated by the vertical dotted lines in Figure 3A). Observers rarely indicated a reduction in vection strength. We therefore examined the relationship between increases in vection strength and slow-phase eye acceleration. In order to identify the presence of any contingent relationship between vection increases over time and changes in slow-phase eye velocity, we averaged the acceleration of the eye movements over a 1-s window prior to each given change in vection. These data are shown in Figure 3B. Note that all bars indicate decelerations, due to the right-handed coordinate system used to describe angular eye rotations (see inset).

We had previously found that maintained eccentric gaze produced vection with similar onset latencies and rated strengths across the four eccentric directions we examined. In a similar fashion, a repeated-measures ANOVA performed on the signed-corrected data shown in Figure 3B revealed no significant differences in mean slow-phase eye deceleration across the four eccentric viewing conditions \( (F(3, 21) = 2.56, p = 0.08) \). Sign correction involved inverting the sign of accelerations for upward and rightward gaze conditions.

Further analysis found that increases in vection strength over time were temporally contiguous with reductions in slow-phase eye velocity at all of the eccentric gaze locations we tested. There was a significant bias toward
a reduction in slow-phase velocity immediately prior to reported enhancements in vection strength over time, irrespective of the eccentric direction of gaze ($t_f = -2.58$, $p < 0.05$). Thus, it is possible that the OFR reduction may have contributed to the enhancement of vection strength. In the next experiment, we examined this apparent relationship between OFR reduction and vection enhancement in further detail.

Vection strength tended to increase just after eccentric eye velocity decreased in Experiment 1. Although this reduction in eye velocity would lead to changes in retinal slip of the visual scene, the pattern of retinal stimulation generated when viewing these radially expanding optic flow patterns was rather complex. If an observer, who is looking at the left-hand side of such a display, engages in a leftward OFR, then the foveal retinal motion generated by these eccentric points will be reduced to near zero. However, the peripheral retinal motion generated by points in the center and other eccentric regions of the radial flow display will be quite different. For example, the peripheral retinal motion of points on the opposite (i.e., right-hand) side of the display would increase during leftward eye movements. One possible explanation for the findings of Experiment 1 was that the decreases in optokinetic eye velocity improved vection by increasing central retinal image velocity. If, as this explanation predicts, central retinal motion is more important to the generation of vection in depth, then similar findings should be obtained when only one side (as opposed to both sides) of the radial flow field is presented.

A second potential explanation for the findings of Experiment 1 was that decreases in eccentric eye velocity over time indirectly increased the perceived distance/depth represented by the inducing display. Nawrot (2003a, 2003b) showed that when observers viewed displays with lateral motion parallax, the perceived depth of the display increased inversely with engagement of the OKNe. As the gain of the OFR scales inversely with the perceived viewing distance (Busettini et al., 1994), any reduction in the OFR would be consistent with viewing objects at greater simulated distances and depths. This in turn may have increased the perceived speed of forward self-motion in depth induced by the 3D cloud displays used in Experiment 1 (i.e., due to a perceived increase in self-displacement over time). If such effects were responsible for the results of Experiment 1, then we would expect changes in the character of the observer’s eye movements to have less effect on the vection induced by ground plane optic flow. OFR reduction would be expected to increase perceived distance/depth in the cloud displays more than in ground plane displays, since the 3D layout is unambiguous in the latter type of optic flow. Unlike simulated self-motion through a 3D cloud, where optical velocities could be very different in the same eccentric display region, ground plane optic flow provides a locally smooth (i.e., interpolatable) gradient of optical velocity (an unambiguous cue to relative distance). Ground plane optic flow also provides additional texture gradient and horizon-based cues to relative/absolute distance (see Sedgwick, 1986). Thus, it was expected that the superior/additional distance information available in ground plane optic flow
would mitigate any effects of eye movements on the perceived display depth.

A final factor that could have also contributed to changes in eye and head velocities in Experiment 1 was the potential engagement of micro head movements at or around the time of increases in vection strength. Any micro head rotations would influence the amount of eye and head rotations required to null eccentric display motion. Therefore, to eliminate this possible artifactual explanation of our previous results, we tracked eye and head movements simultaneously in this experiment to determine gaze in space relative to a flat ground plane simulating linear self-motion in depth.

**Methods**

**Observers**

Twelve adults (nine females and three males) with normal or corrected-to-normal vision enrolled in first-year psychology. Observers participated for 30 min to earn 12.5% of their total course credit quota for the semester. All procedures used were approved in advance by the Human Ethics Committee at the University of Wollongong.

**Optic flow display**

Rather than simulating a 3D cloud of objects, as in the previous experiments, all of the objects in these displays were randomly structured into a flat ground plane that had a simulated vertical height that was close to the physical ground plane of the testing room (approximately 1.0 m below the lower edge of the display). All other display parameters were the same as in Experiment 1.

**Eye and head tracking**

Changes in angular pitch head position were determined using an optical marker array (Kim, 2004; Kim, Palmisano, Ash, & Allison, 2010) consisting of three LEDs embedded along the surface of a 5-cm plastic sphere secured to the head (Kim & Palmisano, 2008). One LED situated at the top of the headset was flanked by two other markers at an angle of approximately ±30° within the mid-sagittal plane. Angular displacements of the headset were referenced to a calibration where the relative pixel distance of the center marker from the midpoint of the two flanking markers was determined for known angular changes in the headset over a ±15° range of rotation.

A separate camera mounted to the ceiling acquired 320 × 240 images of the marker array at 120 frames per second. The same software used for determining changes in eye position was used to determine changes in angular pitch head position. This head position data were transmitted to the simulation computer along with the eye movement data.

**Procedure**

The directed looking task was performed as in Experiment 1, except that only the downward (not the upward, leftward, or rightward) eccentric gaze location was utilized. The trial started with the observer viewing a centrally located fixation point in an otherwise darkened display for 4.8 s. After this period elapsed, the radially expanding optic flow pattern was then presented to the observer for 29.5 s (the first 10 s of this trial phase is shown in Movie 4). As in the previous experiment, observers were again instructed to stare at the approximate location they last saw the fixation cursor and to adjust a throttle control to indicate changes in vection strength over time. We simultaneously recorded eye and head movements and vection strength ratings. Rear projection ceased 34.5 s after the start of the trial. However, the observer was instructed to continue gazing at the approximate point they last viewed the display for a further 5 s in darkness. This final phase was added to each trial in order to determine whether the eye movements induced by this display were consistent with OKNe, and did not result in optokinetic nystagmus (OKAN).

Adding data concerning pitch head position in degrees to vertical eye position data provided an indication of gaze relative to the center of the display. Eye velocity was determined as the derivative of eye position relative to the head or relative to the display (by adding pitch head rotation vectors to vertical eye rotations) using the statistical package R. Velocity data were smoothed in R using the same procedures as used in Experiment 1. The second derivative was again computed in order to obtain eye acceleration. Rate changes in reported vection strength over time were also computed, the peak of which
was traced back to determine the start of each discrete change in vection strength recorded.

Cross-correlation between eye acceleration and real-time rate changes in vection strength signals over the 29.5-s period of radial flow presentation (before the radial flow display was suppressed) allowed us to determine the average latency between changes in the character of eye movement relative to the display and the subsequent indication of a change in vection strength.

Results and discussion

Figure 4A shows time-series plots of changes in vertical eye velocity and vection strength for one trial with a representative observer. Individual reported changes in vection strength were almost always increases in strength during each 34.5-s presentation of radial flow. At the time when the visual display was suppressed (vertical dotted line), a decrease in vertical eye velocity was observed. Over this 5-s period in darkness, the average eye velocity \((M = 0.01, SD = 5.5)\) was found to be statistically equivalent to zero velocity according to a single sample \(t\)-test \((t_{11} = 0.06, p = 0.95)\).

Rate changes in vection strength and vertical eye acceleration over time are shown in Figure 4B. Individual changes in vection strength had an average duration of approximately 2 s. The acceleration of eye movements relative to the head (averaged over a 1-s period) just before (0.5 s) each reported increase in vection strength was found to be negative \((M = -0.28, SD = 0.32)\). This deceleration was statistically significant according to a single sample \(t\)-test \((t_{11} = -2.91, p < 0.05)\). Identical analysis based on data obtained with eye movements relative to the display (which accounted for head rotation) also showed a statistically significant negative vertical acceleration \((i.e., deceleration — M = -0.29, SD = 0.23)\) prior to the onset of reported changes in vection strength \((t_{11} = -2.91, p < 0.05)\).

The results of normalized cross-correlations between vection strength and eye acceleration are shown in Figure 5 over a range of temporal offsets of rate changes in vection strength from \(-6.0\) s to +3.0 s. At precisely \(-4.5\) s \((t_1)\), there was a peak positive cross-correlation between the acceleration of vertical eye movement and vection strength \([M(v.s) = +0.01, SD = 0.03]\), which was not significant according to a single sample \(t\)-test \((t_{11} = +1.74, p = 0.11)\). This was subsequently followed at \(-2.6\) s \((t_2)\) by a consistent peak negative correlation between vertical eye acceleration and vection strength \([M(v.s) = -0.03, SD = 0.04]\), which was found to be significant according to a single sample \(t\)-test \((t_{11} = -2.68, p < 0.05)\).

Thus, similar to Experiment 1, reported increases in vection strength were consistently found to follow decreases in slow-phase eye velocity when viewing ground plane optic flow. Specifically, these decreases in slow-phase eye...
velocity consistently occurred at approximately 1 to 3 s just prior to reported increases in vection strength.

In Experiment 1, it was possible that OFR reduction was simply a result of the engagement of vection-induced micro head movements (the potential causal relationship between OFR reduction and vection increases being simply the result of the temporal delay in reporting each increase in vection). However, Experiment 2 recorded real-time simultaneous head and eye movements. Combining these signals allowed us to determine gaze in space, which was unaffected by any changes in head movement. Based on these data, reductions in OFR relative to the visual display still consistently preceded increases in vection strength. This finding strongly suggests that the relationship between OFR change and vection change was not artifactual in nature. We examine the findings in further detail in the next section.

**General discussion**

The current experiments examined the effects of eccentric gaze on both the vection in depth and compensatory eye movements (OFRs) generated by purely radial patterns of optic flow. In Experiment 1, we found evidence for reported increases in vection strength being temporally contingent upon decreases in OFR velocity. These reductions in OFR velocity tended to precede each increase in vection, regardless of the eccentric direction in which gaze was maintained. Experiment 2 examined performance when displays simulated self-motion over a ground plane (as opposed to through a random 3D cloud of objects). These ground plane displays had locally smooth (as opposed to discontinuous) velocity gradients and provided strong static and dynamic cues to the 3D scene layout (unlike the ambiguous cloud stimuli used in Experiment 1). Since the relationship between reductions in OFR velocity and vection persisted with these ground plane displays, we conclude that vection increases were unlikely to be the indirect result of OFR-based changes to the perceived display depth. Real-time head and eye tracking in Experiment 2 also confirmed that this relationship between the change in OFR and vection was not artifactual in nature. Thus, taken together, our results suggest that the observed increases in vection strength were likely to have been due to reductions in slow-phase optokinetic activity.

Recently, Palmisano and Kim (2009) found that vection and its time course of onset were facilitated by the observer shifting his/her gaze from the center to the periphery of the display (compared to stable central gaze conditions). Because the OFR is known to receive post-saccadic gain enhancement (Lisberger, 1998), this gaze shifting advantage for vection could have been generated by either the initial post-saccadic gain enhancement of the OFR and/or its subsequent adaptation. Interestingly, Palmisano and Kim (2009) found that while peripheral “directed looking” increased vection, maintained peripheral fixation stabilized with a fixation point dramatically impaired vection (compared to central gaze with directed looking or stable central fixation). The latter finding would seem to suggest that increased retinal slip per se cannot explain vection induction and its subsequent enhancements (as according to this notion, peripheral “stationary fixation” conditions should produce more compelling vection than peripheral “directed looking” conditions).

The eccentric viewing conditions used in the present study were quite similar to free viewing conditions and did not actively restrict display-induced eye movements. The results of Experiment 2 suggest that reported increases in vection strength were preceded by both an initial increase in OFR velocity and then its subsequent decrease. Hence, we believe that the change in the observer’s eye movements and the inevitable changes in retinal image velocity both play an important role in enhancing vection.

**Gaze and perceived scene layout**

In the random 3D cloud stimuli used in Experiment 1, it was possible for objects in the same eccentric region of the display/scene to have very different optical velocities. Previously, Nawrot (2003a, 2003b) showed that perceived depth from motion parallax increases with viewing distance, and Busettini et al. (1994) showed that the OFR scales inversely with perceived viewing distance. Thus, decreases in OFR velocity should have produced retinal stimulation that was consistent with more distant viewing into a deeper scene. Studies have shown that the experiences of vection in depth and perceived display depth tend to be positively correlated (Andersen & Braunstein, 1985). Thus, it is possible that the adaptation of the eccentric OFR in Experiment 1 might have indirectly increased observer’s experience of vection in depth by increasing the perceived distance/depth of their 3D cloud inducing displays.

However, in Experiment 2 increases in vection strength were still found to be related to the adaptation of the OFR when self-motion was simulated relative to a ground plane. These ground plane displays provided unambiguous information about distances and depths within the scene. While the global flow of the ground plane still contained residual motion parallax information, it was unlikely to be sensitive to engagement of eye movements. Therefore, while changes in the perceived 3D layout mediated by eye movements may still contribute to the enhancement of vection in depth, they do not appear to account for vection and its time course of onset in the current experiments.

Thus, by a process of elimination, the current findings appear to be most consistent with the interpretation that decreases in optokinetic eye velocity improve vection in depth by increasing the central retinal image velocity. It is
important to note that the results of temporal cross-correlation suggested that there was an earlier tendency for eccentric eye velocity to increase. However, these increases in eye velocity were not as consistent as the decreases in eye velocity observed prior to increases invection strength.

Gaze and perceived speed

Another possible explanation for the findings of the current study is that decreases in eccentric eye velocity, which increase central retinal velocity, may have increased the perceived speed of object motion. Similar to an Aubert-Fleischl effect (Aubert, 1887; Fleischl, 1882), the perceived speed of objects moving in relation to the observer will decrease when their motion is tracked with the eyes, compared to when their motion is viewed with the eyes held stationary. Similar findings have been shown for objects moving in and out of depth (Nefs & Harris, 2007). If the perceived speed of object motion tends to be inversely related to the speed of the eye motion, this entails that perceived speed of object motion will be positively correlated with retinal motion generated by the object’s image. This was previously suggested in studies on circularvection (Becker, Raab, & Jurgens, 2002; Wertheim & Van Gelder, 1990). However, because Palmisano and Kim (2009) found that suppressing eccentric eye movements impaired vection, it would appear that retinal slip per se does not lead to increased vection. Therefore, engagement of eye movements and/or changes in the velocity of retinal motion produced by optic flow of the visual scene appears to lead to enhancements in vection strength.

Concluding remarks

In summary, we provide evidence that enhancements ofvection strength over time may be temporally related to the disengagement of eccentric pursuit eye movements that increase retinal motion. Similar to an Aubert-Fleischl effect, these findings may be broadly applicable to scenarios where we resist the physiological drive to pursue ground plane motion of the visual scene when we move through the world. In these situations, our perceived speed of ground plane motion (and attributions about self-motion) will be enhanced. The ecological advantage of this is that our heightened awareness of self-motion should facilitate most tasks of visual self-navigation.

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