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## Simulated angular head oscillation enhances vection in depth

### Abstract

Research has shown that adding simulated linear head oscillation to radial optic flow displays enhances the illusion of self-motion in depth (ie linear vection). We examined whether this oscillation advantage for vection was due to either the added motion parallax or retinal slip generated by insufficient compensatory eye movement during display oscillation. We constructed radial flow displays which simulated 1 Hz horizontal linear head oscillation (generates motion parallax) or angular head oscillation in yaw (generates no motion parallax). We found that adding simulated angular or linear head oscillation to radial flow increased the strength of linear vection in depth. Neither type of simulated head oscillation significantly reduced vection onset latencies relative to pure radial flow. Simultaneous eye-movement recordings showed that slow-phase ocular following responses (OFRs) were induced in both linear and angular viewpoint oscillation conditions. Vection strength was significantly reduced by active central fixation when viewing displays which simulated angular, but not linear, head oscillation. When these displays with angular oscillation were viewed without stable fixation, vection strength was found to increase with the velocity and regularity of the OFR. We conclude that vection improvements observed during central viewing of displays with angular viewpoint oscillation depend on the generation of eye movements.

### Keywords

vection, oscillation, depth, simulated, enhances, angular, head

### Disciplines

Arts and Humanities | Life Sciences | Medicine and Health Sciences | Social and Behavioral Sciences

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# Simulated angular head oscillation enhances vection in depth

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**Abstract.** Research has shown that adding simulated linear head oscillation to radial optic flow displays enhances the illusion of self-motion in depth (ie linear vection). We examined whether this oscillation advantage for vection was due to either the added motion parallax or retinal slip generated by insufficient compensatory eye movement during display oscillation. We constructed radial flow displays which simulated 1 Hz horizontal linear head oscillation (generates motion parallax) or angular head oscillation in yaw (generates no motion parallax). We found that adding simulated angular or linear head oscillation to radial flow increased the strength of linear vection in depth. Neither type of simulated head oscillation significantly reduced vection onset latencies relative to pure radial flow. Simultaneous eye-movement recordings showed that slow-phase ocular following responses (OFRs) were induced in both linear and angular viewpoint oscillation conditions. Vection strength was significantly reduced by active central fixation when viewing displays which simulated angular, but not linear, head oscillation. When these displays with angular oscillation were viewed without stable fixation, vection strength was found to increase with the velocity and regularity of the OFR. We conclude that vection improvements observed during central viewing of displays with angular viewpoint oscillation depend on the generation of eye movements.

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

## 1 Introduction

Multiple senses are stimulated when we move through the world. However, the perception of self-motion does not always require these different senses to provide compatible sensory information. The vestibular system responds to physical head acceleration, but strong visual illusions of self-motion (or vection) can still occur when completely stationary observers view displays that simulate head accelerations in the absence of accompanying vestibular stimulation (Palmisano et al 2000, 2003, 2007, 2008). The experience of self-motion in the presence of conflicting multisensory stimulation suggests that visual information alone is sufficient to generate the perception of self-motion (eg Kim and Palmisano 2008; Lishman and Lee 1973). Here, we examine the potential roles of different forms of visual information in the generation of linear vection in depth.

Previous studies have shown that simulated horizontal and vertical head jitter/oscillation significantly improves the vection in depth induced by radial patterns of optic flow (Palmisano and Chan 2004; Palmisano et al 2000, 2003, 2007, 2008; Palmisano and Kim 2009). These studies added horizontal or vertical simulated linear head accelerations (either as random head jitter or predictable head oscillation) to radial-flow displays that simulated constant-velocity self-motion in depth through a 3-D cloud of small objects. In both cases, the addition of this simulated horizontal/vertical head acceleration was found to significantly decrease the onset latencies, lengthen the durations, and strengthen the experience of vection induced by radial patterns of optic flow.

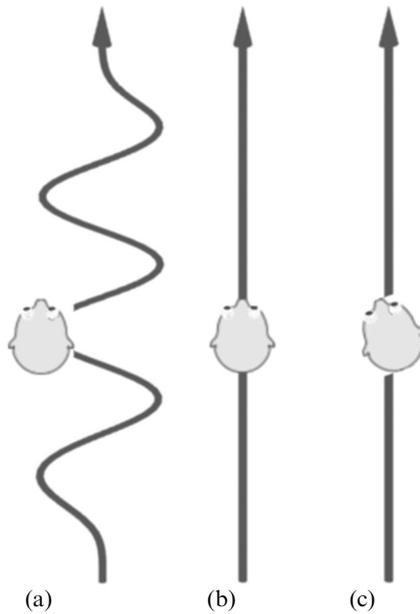
To date, one of the most enduring explanations for these simulated head jitter and oscillation advantages for vection is that purely radial (or lamellar) optic flow rarely occurs in the real world. Walking and running not only generates whole body forward self movement, but also smaller-scale “bob”, “sway” and “lunge” head movements (Cutting et al 1992; Grossman et al 1988; Hirasaki et al 1999; Lécuyer et al 2006; von Grünau et al 2007). These oscillatory head movements are both linear and angular in nature, and change the scene in ways that can only be partially compensated by eye movements (Grossman et al 1989; von Grünau et al 2007). Thus, one intriguing explanation of the so-called jitter and oscillation advantages for vection is that simulated head jitter/oscillation taps into visual processes normally used to perceive self-motion from naturally occurring patterns of optical/retinal flow. Consistent with this notion, Lécuyer and colleagues (2006) have found that adding simulated linear head oscillation to their radial-flow displays significantly increased reported sensations of walking by their subjects (relative to their no-head-oscillation control displays). Similarly, a recent study by Bubka and Bonato (2010) showed that first-person videos shot from a hand-held camera (which contained both linear and angular simulated head jitter) induce faster vection onsets and longer vection durations than comparable videos shot from a rolling cart (which did not contain any linear or angular head jitter).

Not only could this simulated linear head jitter and oscillation have served as an ecologically consistent cue to self-motion, its motion parallax should have generated information about the layout of the simulated environment in depth. There is some evidence to suggest this motion-parallax information might enhance vection by making the radial flow appear more 3-D (Andersen and Braunstein 1985; Palmisano 1996, 2002). Andersen and Braunstein found that radial flow which appeared more 3-D (based on simulated dot speed and density) also induced more compelling experiences of vection in depth. Similarly, Palmisano found that adding consistent stereoscopic and changing-size cues to the depth of the radial-flow field also improved the experience of vection in depth; vection onset latencies were reduced, while vection durations and strength ratings were increased, compared with same-size patterns of radial flow viewed monocularly.

Contrary to the notion that vection strength depends on the perceived depth of radial-flow displays, Nakamura (2010) recently showed that adding simulated horizontal linear head oscillation also improves the vection induced by 2-D patterns of vertical lamellar flow. This finding suggests that simulated viewpoint jitter and oscillation advantages for vection may not depend on the presence of motion parallax, but on other potential factors.

One physiological factor that is known to influence vection strength is the generation of eye movements when viewing optic flow displays (de Graaf et al 1991; Kim and Palmisano 2008, 2010a, 2010b). When observers view displays containing motion parallax or any other form of simulated head translation in space, display-induced eye movements, known as ocular following responses (or OFRs), occur to maintain retinal image stability (Miles et al 1986). In a recent study, Kim and Palmisano (2010b) instructed their observers to push a throttle whenever they experienced vection while viewing the peripheral edge of a radial optic-flow pattern simulating self-motion in depth. They found that increases in vection strength tended to be contingent upon decreases in OFR velocity (increased central/foveal retinal motion). The corresponding increases in foveal retinal motion may contribute to vection by increasing the perceived speed of object motion. Consistent with this notion, the perceived speed of moving objects is known to increase with the rate of retinal motion generated when viewing visual motion (Aubert 1887; Fleischl 1882).

It is also possible that adding simulated linear head jitter/oscillation to radial flow may enhancevection by increasing the perceived speed of self-motion along a 3-D curvilinear trajectory. As shown in figure 1, self-motion displays which simulate horizontal head translations (figure 1a) should produce greater perceived instantaneous oblique velocities of self-motion, compared with conditions that only simulate constant-velocity self-motion in depth (figure 1b). If the observer underestimates the magnitude of these simulated horizontal linear excursions of the head, some of the horizontal velocity may be misattributed to self-motion in depth. This may artificially increase the perceived speed of simulated forward self-motion, and enhance the strength ofvection in depth—sincevection strength has been shown to correlate strongly with increases in perceived speed of self-motion in depth (eg Dichgans and Brandt 1978; Kim and Palmisano 2008). However, adding simulated angular head oscillation to radial-flow displays should not affect either the simulated 3-D linear trajectory (moving forward) or the perceived speed of self-motion (figure 1c). These simulated angular head oscillations are also devoid of the motion parallax that provided strong additional cues to depth in the previousvection studies.



**Figure 1.** (a) When simulated linear horizontal head oscillation is added to a display simulating constant-velocity self-motion in depth, an ideal observer should perceive fast oblique traversal along a curvilinear path. (b) Pure constant-velocity self-motion in depth simulated with the head in a fixed orientation. (c) Pure constant-velocity self-motion in depth simulated with added angular head oscillations.

In this study, we examined whether angular changes in simulated head orientation (within the horizontal plane) can also enhance linearvection in depth. If simulated head oscillation enhancesvection simply because it is more ecologically consistent with the visual feedback received during natural head movement, then adding either angular or linear display oscillation to radial flow should enhancevection in depth. If, however, additional motion parallax information, or errors in path integration are crucial for producing these jitter/oscillation advantages, then adding simulated angular head oscillation to radial flow should yield no advantage forvection in depth. We also recorded eye movements from our observers to ascertain whether any effects of adding angular display oscillation could be explained by the retinal motion generated by these eye movements.

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## 2 Materials and method

### 2.1 Observers

Fifteen undergraduate students (age range 18–34 years) enrolled in courses administered by the School of Psychology participated in the study. All had normal or corrected-to-normal vision and no reported neurological pathology. All procedures were approved by the Human Ethics Committee at the University of Wollongong.

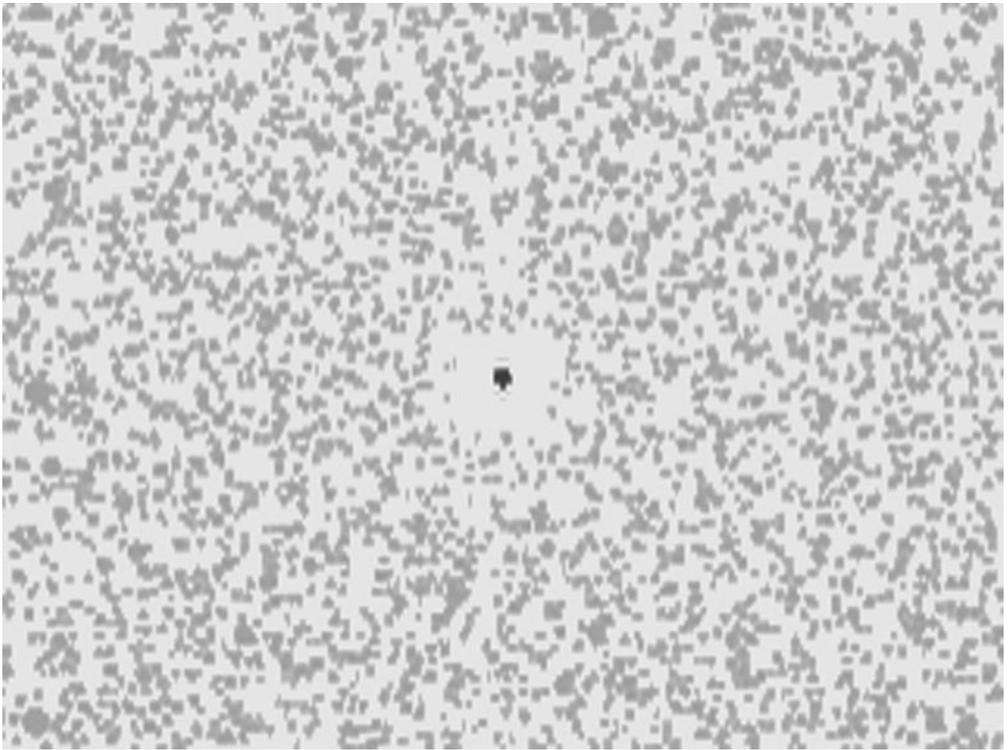
### 2.2 Visual displays

Optic flow was rear-projected onto a large screen (1.6 m × 1.2 m) situated precisely 2.1 m in front of the observer. The observer's head was restrained with a chin-rest rigidly clamped to the edge of the desk at which he/she sat for the duration of each experimental session. Observers viewed the display through a large circular plastic tube mounted on the chin-rest, which served to occlude the peripheral field of view (>16 deg), removing any global reference-frame cues. The restricted field of view was sufficient to generate compelling vection in our previous studies (Kim and Palmisano 2010b; Palmisano and Kim 2009). In some conditions a stable central fixation point was provided (luminance = 42 cd m<sup>-2</sup>).

The 3-D rendering of random-dot optic flow was performed using standard OpenGL calls from custom software written in Visual C++ 6.0 (Microsoft Corporation). Previous studies (eg Kim and Palmisano 2010a, 2010b) have distributed simulated objects within the boundary of a cube environment, but this leads to noticeable variations in the local density across the optic array. Rather than arranging our square objects within a cube, we constrained the distribution of objects to a spherical cloud centred at the simulated location of the observer. A total of 1152 blue square objects (0.1 to 1.0 deg diameter; luminance = 18 cd m<sup>-2</sup>) were generated with approximately 70% of these objects visible to the observer at any one time. All the objects moved towards the simulated viewpoint at a speed of approximately 2 m s<sup>-1</sup>. In each trial, visual simulations of self-motion in depth were presented for 55 s. The simulated depth of the display was approximately 3 m.

The spherical arrangement of objects was performed by occluding the objects that fell outside a specified visual radius from the 3-D simulated location of the camera. Constant-velocity self-motion in depth was simulated by translating the scene toward the camera. Once objects passed behind the camera, their horizontal and vertical planar locations were re-randomised before their approach recommenced from a distant simulated location in front of the camera. The resulting visual simulation was both uniform in density across the visual field and uniform across changes in simulated head translation.

Horizontal head translation was simulated by moving the virtual camera to the left or right in the environment. The centre of the spherical occluder was maintained at the new simulated horizontal location of the camera. Head rotations were simulated by rotating the virtual camera around the vertical axis relative to the simulated environment. Figure 2 shows the static layout of the visual stimuli used in the present study. Pure radial-flow control conditions simulated constant-velocity self-motion in depth. No motion parallax information was provided by the simulated 1 Hz angular head oscillations. However, significant motion parallax was generated by the simulated 1 Hz linear head oscillations. All of the display conditions tested contained the same radially expanding optic-flow component, which simulated constant-velocity self-motion in depth. In different experimental trials, simulated horizontal angular or linear head oscillation was added to this radial flow pattern and the resulting vection was compared to that induced by non-oscillating radial flow.



**Figure 2.** Layout of the visual stimulus used in the present study. A cloud of small squares formed a tunnel with a square fixation point in the centre during half the trials.

### 2.3 *Eye and head movement recording*

We recorded two-dimensional changes in eye position using 120 Hz digital infrared video oculography, as in previous vection studies (Kim and Palmisano 2008, 2010a, 2010b; Palmisano and Kim 2009). The raw positional resolution of the system was better than 0.25 deg, and was calibrated over a horizontal visual angle of 20 deg with two separate horizontal fixations.

The observer's head was restrained on a chin-rest, and any potential changes in head position were determined by tracking LEDs rigidly mounted to a plastic form-fitting headband. This allowed changes in head position to be determined (see also Kim et al 2010) in order to ensure the head remained stable throughout testing and that no detectable display-induced head movements occurred.

### 2.4 *Procedure*

We examined the vection induced by four display types/conditions: (i) pure radial flow; (ii) radial flow with simulated small 1 Hz horizontal angular head oscillation ( $\pm 10$  deg); (iii) radial flow with simulated large 1 Hz horizontal angular head oscillation ( $\pm 20$  deg); and (iv) radial flow with simulated 1 Hz horizontal linear head oscillation ( $\pm 15$  cm). All of these optic flow conditions were presented in randomised block order and each observer performed at least 2 repeats of each stimulus condition.

Observers were seated at a distance of 2.1 m in front of the display and stared at a fixation point located at its centre 5 s prior to each experimental trial. Half of the trials were viewed with active fixation and the remaining trials were viewed freely. In the active fixation trials, observers were instructed to maintain fixation on the stationary central fixation target, which was sustained during the presentation of optic-flow displays. In the free-viewing trials, the fixation point disappeared after the initial 5 s fixation period and observers were instructed to maintain their gaze at the centre

of the display. Observers held a joystick and were instructed to push a button on it when they experienced any illusion of self-motion in depth. Specifically, the experimenter requested the observer to press a button on the joystick button if the sensation increased at any time and hold down the button while the experience was sustained. Observers were instructed to stop pressing/release the joystick if vection ceased. At the end of each trial, observers used the same joystick for reporting the overall perceived strength of vection strength in depth. The rating was obtained using a vertical scale (0–10 in magnitude) presented at the end of each 55 s trial, where a modulus of 5 was used to indicate the strength of vection generated by pure radial flow.

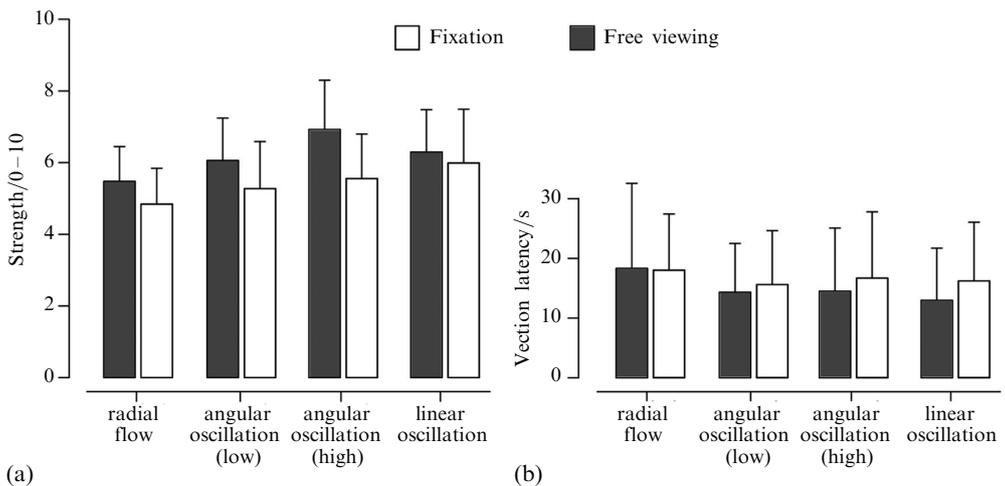
### 2.5 Data analysis

Saccades were removed from eye-movement traces using a simple desaccading algorithm similar to a previous method (Holden et al 1992). Position traces were further smoothed using a mean filter with a sliding window of 10 ms in the *R* statistical package (<http://www.r-project.org>). A cubic-spline interpolation was used to resample the eye-movement data to 220 Hz. Eye velocity was then determined by computing the change in eye position over finite intervals of time (30 ms). Differences between consecutive eye velocities occurring at opposite phase angles of display oscillation were also determined, and the median of these values over the course of each 55 s trial was taken as a stable estimate of the OFR. Mean vection strength ratings and onset latencies were also determined for each observer performing each of the experimental conditions. Both psychophysical and physiological recordings of eye movements were analysed using within-subjects ANOVAs.

## 3 Results

### 3.1 Vection strength and latency

Mean vection-strength ratings and 95% confidence intervals are shown in figure 3a. Across all conditions, vection-strength ratings generated during active fixation ( $M = 5.4$ ,  $SD = 0.9$ ) were found to be significantly lower than vection-strength ratings generated during free-viewing conditions ( $M = 6.2$ ,  $SD = 0.8$ ), as indicated by a two-way within-subjects ANOVA ( $F_{1,14} = 21.57$ ,  $p < 0.0005$ ).



**Figure 3.** Means and 95% confidence intervals showing overall vection-strength ratings (a) and vection onset latencies (b). White bars show responses obtained in conditions with fixation and dark bars refer to conditions with free viewing.

The same ANOVA model also indicated a significant effect of display type ( $F_{3,42} = 5.29$ ,  $p < 0.005$ )—see figure 3a. A posteriori contrasts indicated that: (i) both of the angular display oscillation conditions ( $M = 6.2$ ,  $SD = 1.2$ ) produced significantly stronger vection ratings than the pure radial flow ( $M = 5.2$ ,  $SD = 0.9$ ) ( $p < 0.05$  in both cases); (ii) high-amplitude angular display oscillation conditions produced stronger vection ratings than low-amplitude angular display oscillation conditions ( $p < 0.05$ ); and (iii) while the linear display oscillation conditions ( $M = 6.1$ ,  $SD = 1.2$ ) also produced significantly stronger vection ratings than the pure radial-flow condition, they did not produce significantly different vection ratings to the angular display oscillation conditions ( $p > 0.05$ ). There was a marginal interaction effect on vection strength between display and fixation conditions ( $F_{3,42} = 2.66$ ,  $p = 0.06$ ). This interaction was possibly due to the significant effect of fixation on the vection induced by angular oscillation conditions ( $p < 0.05$ ), since fixation had no significant effect on the vection induced by linear oscillation ( $p > 0.05$ ).

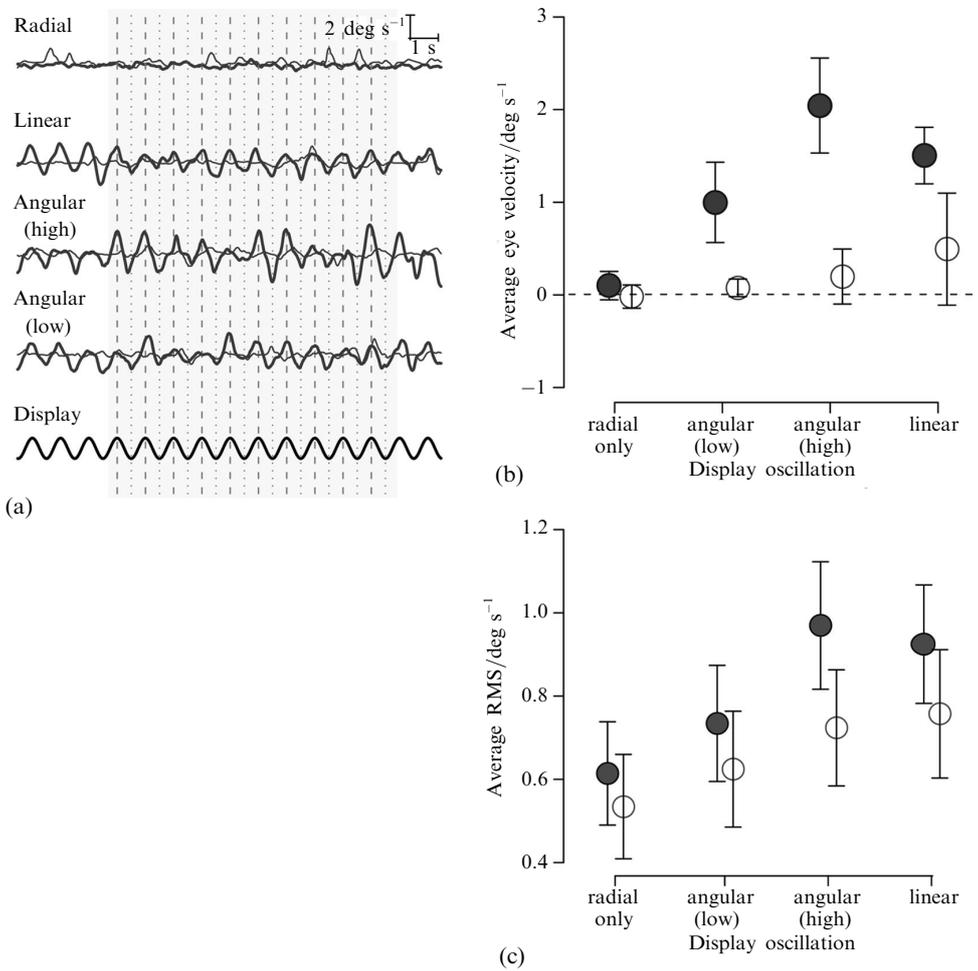
Mean vection onset latencies and their 95% confidence intervals are shown in figure 3b. A two-way ANOVA found no main effects on vection onset latency with changes in display type ( $F_{3,42} = 2.45$ ,  $p = 0.08$ ) or fixation type ( $F_{1,14} = 1.05$ ,  $p = 0.32$ ). There was no interaction effect on vection onset latency between display and fixation conditions ( $F_{3,42} = 0.62$ ,  $p = 0.61$ ).

### 3.2 Eye movement responses to visual displays

Figure 4a shows the raw time series of the horizontal slow-phase eye-velocity responses for one observer over a 5 s period of a 55 s trial. Vertical dashed and dotted lines show the phase relationship between eye movements in relation to the simulated horizontal changes in either angular or linear head position. The median amplitude of peak-to-peak slow-phase eye velocities was computed for each subject in each of the four conditions, the means and 95% confidence intervals of which are shown in figure 4b. The root-mean-squared (RMS) error of peak slow-phase eye velocities was computed for each subject in each of the four conditions, the means and 95% confidence intervals of which are shown in figure 4c.

Median peak-to-peak slow-phase eye velocities were found to increase with the amplitude of the angular display oscillation (above those induced by linear display oscillation). Stationary central fixation reduced optokinetic eye movements in all of the display oscillation conditions, even in the linear display oscillation condition ( $t_{14} = 2.80$ ,  $p < 0.05$ ). In free-viewing conditions, high-amplitude angular display oscillation produced faster eye velocities ( $M = 1.8$ ,  $SD = 1.0$ ) than linear display oscillation ( $M = 1.2$ ,  $SD = 0.5$ ), as indicated by a repeated-measures  $t$ -test ( $t_{14} = 2.80$ ,  $p < 0.05$ ). However, low-amplitude angular display oscillation produced slower eye velocities ( $M = 0.8$ ,  $SD = 0.9$ ) compared to linear display oscillation, although this difference was not significant ( $t_{14} = 1.16$ ,  $p = 0.27$ ).

RMS eye-velocity errors were also found to increase with the amplitude of the angular display oscillation ( $t_{14} = 3.70$ ,  $p < 0.005$ ). Stationary central fixation reduced optokinetic eye movements in all display oscillation conditions, including the high-amplitude angular display oscillation condition ( $t_{14} = 2.48$ ,  $p < 0.05$ ). Mean RMS errors were similar between the high-amplitude angular oscillation condition ( $M = 0.97$ ,  $SD = 0.30$ ) and the linear oscillation condition ( $M = 0.92$ ,  $SD = 0.28$ ), as indicated by a repeated-measures  $t$ -test ( $t_{14} = 0.74$ ,  $p = 0.47$ ). However, the low-amplitude angular oscillation condition produced significantly smaller RMS errors ( $M = 0.73$ ,  $SD = 0.28$ ) compared with linear display oscillation ( $t_{14} = 3.21$ ,  $p < 0.01$ ).



**Figure 4.** (a) Time-series plots of horizontal slow-phase eye velocity responses from one representative subject during free viewing (thick contours) and fixation (thin contours) conditions. Peak-to-peak differences in eye velocity were temporally synchronised with display oscillations for the four display oscillation conditions. Positive values of the display trace are leftward eye-movements and negative values are rightward eye-movements. (b) Means of median peak-to-peak eye velocities across all fifteen subjects in each of the four display conditions. (c) Average root-mean-squared (RMS) error in eye velocity across all fifteen subjects in each of the four display conditions. In (b) and (c), solid points refer to eye data for free-viewing conditions, whereas open points refer to eye velocities for fixation conditions. Error bars are 95% confidence intervals of the averages. Display trace indicates timing of display oscillations where amplitude is arbitrary.

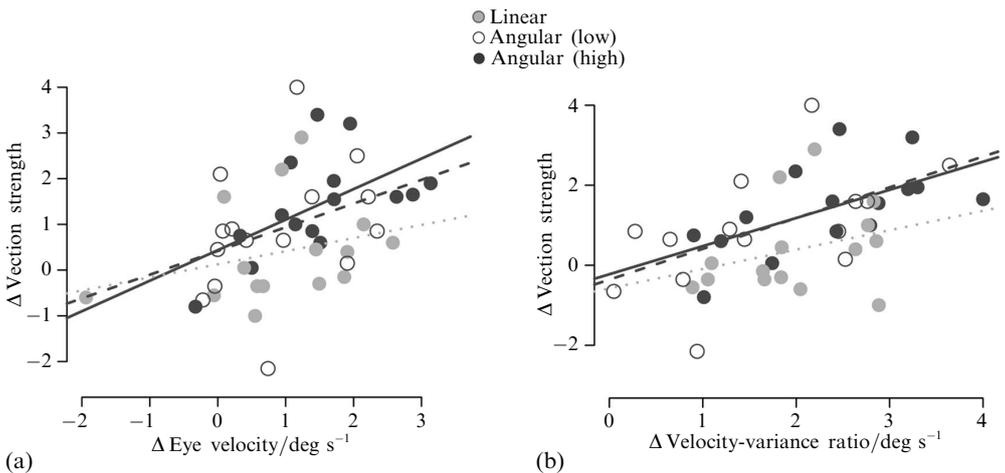
### 3.3 Relationship between the OFR and vection strength

We computed individual difference scores for vection-strength ratings between free viewing and fixation conditions with display oscillation. We also computed the differences in slow-phase eye velocity for these same free-viewing and fixation conditions. Figure 5a plots vection-strength differences as a function of differences in median peak-to-peak slow-phase eye velocity for conditions with added linear oscillation (solid grey circles), conditions with low-amplitude angular oscillation (open white circles), and conditions with high-amplitude angular oscillation (solid black circles). Pearson product-moment correlations performed on these data revealed a significant relationship between vection strength and slow-phase eye velocity when viewing radial flow with added high-amplitude

angular display oscillation ( $r = 0.57$ ,  $t_{13} = 2.51$ ,  $p < 0.05$ ). However, there were no significant correlations between vection and eye velocity in either the low-amplitude angular display oscillation condition ( $r = 0.33$ ;  $t_{13} = 1.26$ ,  $p = 0.23$ ) or the linear display oscillation condition ( $r = 0.29$ ;  $t_{13} = 1.08$ ,  $p = 0.30$ ).

Further Pearson product-moment correlations found no significant relationship between vection strength increases and RMS eye velocity alone in the high-amplitude angular display oscillation condition ( $r = -0.23$ ;  $t_{13} = 0.85$ ,  $p = 0.41$ ), the low-amplitude angular display oscillation condition ( $r = 0.22$ ;  $t_{13} = 0.81$ ,  $p = 0.43$ ) and the linear display oscillation condition ( $r = -0.11$ ;  $t_{13} = 0.41$ ,  $p = 0.69$ ). However, given that RMS error tends to increase with median eye velocity ( $r = 0.44$ , based on data in figure 4), a measure of eye velocity that is independent of variance was devised to examine the relationship between changes in vection strength and central tendencies in eye velocity. We normalised eye movements by dividing each median peak-to-peak slow-phase eye velocity by the RMS error computed over a given trial, obtaining an index we refer to as the Velocity Variation Ratio. The relationship between increases in vection strength and Velocity Variation Ratio ( $\text{deg s}^{-1} \text{RMS}^{-1}$ ) is shown in figure 5b for the three different display oscillation conditions. Based on this model, there were significant correlations between increases in vection strength and normalised eye velocity in the high-amplitude angular display oscillation condition ( $r = 0.59$ ;  $t_{13} = 2.66$ ,  $p < 0.05$ ) and the low-amplitude angular display oscillation condition ( $r = 0.55$ ;  $t_{13} = 2.38$ ,  $p < 0.05$ ), but not the linear display oscillation condition ( $r = 0.30$ ;  $t_{13} = 1.12$ ,  $p = 0.28$ ). These normalised eye-movement responses suggest that the overall velocity and (in-)variance of eye movements accounts for a significant proportion of the increases in vection generated by radial flow displays with added angular display oscillation.

Taken together, these results suggest vection improvements obtained in angular display oscillation conditions depend on the effective engagement of smooth eye movements with high consistency (ie little variability). These eye movements appear to improve vection by maintaining retinal image stability, where most of the residual salient motion generated by the display on the retina will be radial flow simulating motion in depth.



**Figure 5.** Mean difference in vection strength between free viewing and fixation plotted as a function of (a) the difference in median eye velocity ( $\text{deg s}^{-1}$ ) between free viewing and fixation conditions; and (b) the normalised velocity-variance ratio ( $\text{deg s}^{-1} \text{RMS}^{-1}$ ) for each of the fifteen observers viewing the three types of display oscillation (linear, in mid-grey circles; angular high-amplitude, in dark circles; and angular low-amplitude, in open circles).

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## 4 Discussion

In this study we investigated whether simulated horizontal angular head oscillation influences the strength of linear vection generated by radial-flow simulating self-motion in depth. We found that adding simulated horizontal angular and linear head oscillation to radial-flow displays produced comparable enhancements to vection in depth. Interestingly, the strength of linear vection in depth increased with the amplitude of these simulated head rotations, even though both low-amplitude and high-amplitude angular display oscillation simulated identical physical velocities of self-motion in depth. We also obtained supplementary video eye-movement recordings that indicated OFRs were induced by both simulated horizontal angular and linear head oscillations. The velocity of these OFRs was found to increase with the velocity of the display oscillation. Of particular interest, the overall strength of vection was found to increase as a function of horizontal OFR velocity and its regularity (ie lack of variability).

Our finding that simulated horizontal head rotation can improve the vection induced by radial flow was unexpected on the basis of the findings of earlier research. Previously, Palmisano et al (2003) found that adding non-perspective viewpoint jitter (as opposed to oscillation) to radial flow had no effect on vection (it did not significantly improve/impair vection compared to that induced by non-jittering radial flow). The visual effects of adding non-perspective viewpoint oscillation to radial flow should be quite similar to those of adding simulated angular head oscillation (which does not provide any additional motion parallax information and approximates the retinal flow produced by head/eye rotations). It is possible that the coherent non-perspective jitter used in Palmisano et al (2003) study did not improve vection because this broadband random noise contained extremely high (ie non-ecological) frequencies (it was capped at 37.5 Hz).

The vection strength advantages we obtained with simulated angular head oscillation were highly similar to the increases in vection strength obtained with simulated linear head oscillation/jitter in the current and previous studies (eg Nakamura 2010; Palmisano et al 2000, 2008). Palmisano et al found that vection in depth could be improved by adding horizontal/vertical simulated linear head jitter/oscillation to radial-flow displays. However, this simulated linear head oscillation/jitter would always have increased the amount of motion-parallax information in the display (above and beyond that provided by the available motion perspective in the 3-D radial component of the optic flow). Interestingly, the simulated angular head oscillations used in the current study still generated comparable vection strength advantages, even though they did not provide any additional motion-parallax information. We also observed a decline in vection onset latency with increased angular oscillation, but this trend failed to reach significance. It is possible that a larger visual display may be necessary to enhance the effects of simulated head oscillation on the time course of vection. Thus, it would appear unlikely that the previous viewpoint oscillation/jitter advantages for vection were solely due to these oscillating/jittering displays providing additional motion-parallax information. For this reason, the current findings are quite consistent with recent work by Nakamura (2010), who showed that vection strength can be improved by simulated linear head oscillation that does not generate any motion parallax (eg where all the scene elements fall within the same depth plane and simulated self-motion is vertical or horizontal).

Contrary to the prediction that increased retinal motion should increase vection (de Graaf et al 1991; Kim and Palmisano 2010b), we found that vection induced by simulated angular viewpoint oscillation appeared to decrease as retinal slip increased during central viewing. Vection strength increased when OFRs had low variability and higher slow-phase velocities. These results are consistent with Brandt et al (1974) who found support for the notion that the onset of circular vection coincides with increases

in optokinetic nystagmus. Further, consistent with this view, in the current study we found that free-viewing conditions produced significantly stronger vection than conditions where eye movements were suppressed by active fixation. However, these fixation conditions still generated vection that was comparable to that induced by radial flow alone, which is consistent with the view that eye movements are not essential to generate vection (Howard 1982). It appears that the engagement of display-induced eye movements may account for the vection enhancement caused by angular viewpoint oscillation, as these eye movements should help stabilise the flow field on the retina.

Unlike simulated angular head oscillation, simulated horizontal linear head oscillation generates motion parallax, where the horizontal optical velocity of 3-D objects scales inversely with increasing simulated distance into the display. The vection in these simulated linear head oscillation conditions appeared to be relatively unaffected by the observer's eye movements. Our failure to find a significant effect of fixation versus free viewing on the vection induced by linear oscillation suggests that it did not depend on display-induced eye movements per se. However, a recent study shows that simulated linear viewpoint oscillation increases vection strength during, but reduces the motion aftereffect experienced following, presentations of radial optic flow (Seno et al 2011). This finding suggests that simulated linear viewpoint oscillation may reduce adaptation to the foveal retinal motion generated during central viewing of radial displays. This reduced adaptation to the radial flow may be driven by eye movements and may be responsible for the simulated linear viewpoint oscillation advantage for vection.

The vection advantages obtained with adding angular display oscillation may not just depend on lower adaptation to the radial flow component simulating self motion in depth, but also on ecologically consistent eye-movement motor command signals. Compared with viewing pure radial flow, we found that vection was greater in angular oscillation conditions when eye movements occurred to hold the fovea at the centre of the radial flow (ie the so-called focus of expansion of the optic flow, which coincides with the simulated destination point). The visual stimulation this generates would be similar in both oscillating and non-oscillating conditions, but the motor command (and corresponding efference copy) signals for horizontal changes in eye position would have been stronger in angular oscillation conditions. It is possible that the vection advantages we observed in angular oscillation conditions depended on the increased strength of these efference copy signals.

The results of the current study with central viewing appear to differ from those reported during peripheral viewing of optic flow displays. An earlier study by Kim and Palmisano (2010b) found that perceptually noticeable increases in the strength of linear vection in depth were temporally contiguous and contingent upon declines in OFR velocity. Because OFR eye movements serve to reduce the amount of retinal slip, any decline in their velocity will increase the amount of foveal retinal motion generated when viewing the edge of the radial-flow display. However, the angular display oscillations added to the radial flow in the current study were viewed with the observer's gaze held near the focus of expansion. Counter-phase eye movements generated by the angular display oscillation caused the observer's gaze to track the change in the position of this focus of expansion, and thus minimised the retinal motion generated by visual motion. These central OFRs would have helped the retina capture information about radial flow simulating self-motion in depth, which is a factor known to influence vection during central viewing (Kim and Palmisano 2010a).

In summary, we found that simulated angular display oscillation enhances the vection in depth induced by radial flow. This is contrary to the notion that increases in motion parallax and/or errors in path integration are responsible for the simulated viewpoint jitter/oscillation advantages for vection. Rather, vection strength often appears to depend on the reliable engagement of eye movements that serve to capture the retinal motion

generated by optic flow during central viewing. Together with evidence from previous studies, the current findings are consistent with the view that simulated linear and angular head oscillations both enhance the strength of vection, which depends in part on the generation of display-induced eye movements.

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