Horizontal fixation point oscillation and simulated viewpoint oscillation both increase vection in depth

Stephen Palmisano
School of Psychology, University of Wollongong, Wollongong, Australia

Juno Kim
School of Psychology, University of Sydney, Australia

Tom C. A. Freeman
School of Psychology, Cardiff University, Cardiff, UK

Previous research has shown that vection can be enhanced by adding horizontal *simulated viewpoint oscillation* to radial flow. Adding a horizontally oscillating fixation target to purely radial flow induces a superficially similar illusion of self-motion, where the observer's perceived heading oscillates left and right as their eyes pursue the moving target. This study directly compared the vection induced by these two conditions for the first time. Adding *fixation point oscillation* and *simulated viewpoint oscillation* to radial flow were both found to improve vection (relative to *no oscillation* control displays). Neither vection advantage could be explained in terms of differences in perceived scene rigidity or motion adaptation. Our findings also provided little support for the notion that pursuit eye-movements were essential for the *simulated viewpoint oscillation* advantage for vection (since observers successfully fixated a stationary, centrally- placed target during these conditions in the current experiments). The strongest support was found for the proposal that *fixation point oscillation* and *simulated viewpoint oscillation* both improve vection by increasing the observer's global retinal motion.

Keywords: vection, self-motion, optic flow, Motion-3D, heading, eye-movements, space and scene perception

Citation: Palmisano, S., Kim, J., & Freeman, T. C. A. (2012). Horizontal fixation point oscillation and simulated viewpoint oscillation both increase vection in depth. *Journal of Vision, 12*(12):15, 1–14, http://www.journalofvision.org/content/12/12/15, doi:10.1167/12.12.15.

Introduction

Self-motion can be detected by a variety of senses, including vision, the vestibular system of the inner ear, proprioception, somatosensation, and audition (Benson, 1990; Gibson, 1966; Howard, 1982; Johansson, 1977). Of these senses, vision and the vestibular system play particularly important roles in self-motion perception (Dichgans & Brandt, 1978; Fetsch et al., 2007; Howard, 1982; Lishman & Lee, 1973). Vision can detect both accelerating and constant velocity self-motions from the optical/retinal flow generated by our movement through the world (Gibson, 1966; Mach, 1875). By contrast, the vestibular system only detects self-accelerations, based on the inertia of the fluid in the semicircular canals and the otoconia of the otolith organs (Benson, 1990; Howard, 1986; Lishman & Lee, 1973).

Research has shown that it is possible to induce compelling visual illusions of self-motion in physically stationary observers, a condition known as "vection" (e.g., Fischer & Kornmüller, 1930; Tschermak, 1931). Given the above-mentioned differences in visual-vestibular specialization, it had long been thought that: (a) visually simulated constant velocity self-motions should induce the most compelling vection (since these optic flow displays would be expected to produce only minimal or transient visual-vestibular conflicts in a stationary observer [Dichgans & Brandt, 1978]); and (b) visually simulated self-accelerations should impair vection (since the vestibular stimulation which would normally accompany these optic flow patterns would be absent [Zacharias & Young, 1981]).

Contrary to both ideas, it has recently been shown that simulated self-acceleration actually enhances the vection induced by optic flow displays simulating constant velocity self-motion (Bubka & Bonato, 2010; Kim & Palmisano, 2008; Kitazaki & Hashimoto, 2006; Nakamura, 2010; Palmisano, Allison, & Pekin, 2008; Palmisano, Bonato, Bubka, & Folder, 2007; Palmisano, Burke, & Allison, 2003; Palmisano & Chan, 2004; Palmisano, Gillam, & Blackburn, 2000; Palmisano & Kim, 2009). Despite introducing potentially salient visual-vestibular conflicts in stationary observers, adding horizontal/vertical *simulated viewpoint jitter* has been found to significantly decrease the latencies, and increase the durations and strengths, of the vection induced by radial flow (e.g., Palmisano et al., 2008;

doi: 10.1167/12.12.15 Received September 18, 2012; published November 26, 2012 ISSN 1534-7362 © 2012 ARVO

Palmisano, Burke, & Allison, 2003; Palmisano et al., 2000). Interestingly, adding periodic *simulated viewpoint oscillation* produces a very similar vection advantage to adding random *simulated viewpoint jitter* (Palmisano et al., 2008; Palmisano et al., 2007). Research has shown that *simulated viewpoint jitter* and *oscillation* do not improve vection simply by making the simulated environment appear more 3D (e.g., by providing additional motion parallax-based information about distance/depth). Palmisano and Chan (2004) found that while horizontal/vertical *simulated viewpoint jitter* improved the vection in depth induced by their radial flow patterns, it had little effect on ratings of the perceived 3D layout. Similarly, Nakamura (2010) found that horizontal *simulated viewpoint oscillation* could still improve the vertical vection induced by purely 2D (as opposed to 3D) patterns of lamellar flow.

Currently there are four popular explanations of the *simulated viewpoint jitter and oscillation* advantages for vection; see Palmisano, Allison, Kim and Bonato (2011) for a recent review. S*imulated viewpoint jitter/oscillation* improves the vection in depth induced by radial flow by either: (a) making the visually simulated environment appear more rigid (Nakamura, 2010); (b) reducing the adaptation to the radial component of the flow (Palmisano et al., 2000); (c) generating pursuit eye-movements which indirectly stimulate the vestibular cortex of physically stationary subjects (Kim & Palmisano, 2008); or (d) producing more global retinal motion (Kim & Palmisano, 2010a; Palmisano & Kim, 2009).

First, Nakamura (2010) has proposed that *simulated viewpoint jitter* and *oscillation* might improve vection by making the visually simulated environment appear more rigid. In support of his proposal, Nakamura found that: (a) horizontal display oscillation which was both coherent and uniform (i.e., simulated viewpoint oscillation) enhanced vertical vection; (b) horizontal display oscillation that was incoherent impaired vertical vection; and (3) vertical vection appeared to decline as subjects' ratings of the perceived rigidity of their simulated (2D) environment decreased.

The second explanation of the *simulated viewpoint jitter* and *oscillation* advantages for vection is reduced motion adaptation. When observers are presented with purely radial flow simulating constant velocity self-motion in depth, their experience of vection should decrease over time as they adapt to the local 1D motion arising from this flow (Denton, 1971; Salvatore, 1968; Schmidt & Tiffin, 1969). Palmisano et al. (2000, 2008) proposed that *simulated viewpoint jitter* and *oscillation* should reduce the observer's adaptation to the local motion arising from this radial flow. Consistent with this proposal, radial flow displays with horizontal s*imulated viewpoint oscillation* have been found to induce significantly longer vection durations and significantly shorter motion aftereffects (MAEs) than non-oscillating control displays (Seno, Palmisano, & Ito, 2011).

The third explanation of the *simulated viewpoint jitter* and *oscillation* advantages for vection is based on recent findings that very similar compensatory eye-movements are generated when: (a) head-tracked observers generate their own horizontal display oscillation by physically moving their heads from side-to-side while viewing radial flow displays; and (b) they later view playbacks of these same horizontally oscillating radial flow displays while sitting still (Kim & Palmisano, 2008; 2010b). Not only did these active and playback display oscillation conditions both induce superior vection to non-oscillating control conditions, but they also generated similar ocular following responses (or OFRs – see Miles & Kawano, 1986; Miles, Busettini, Masson, & Yang, 2004), which were absent in the non-oscillating control conditions. Kim and Palmisano (2008) proposed that these OFRs may have improved vection in passive playback conditions by indirectly stimulating the vestibular cortex of stationary observers (e.g., via the mid-brain oculomotor pathways). Consistent with this notion, there is evidence that both visual and vestibular cortical areas associated with self-motion processing are excited when stationary observers are presented with visual displays simulating self-acceleration (Nishiike et al., 2002).

The fourth possible explanation for these previously demonstrated vection advantages is that adding horizontal/vertical *simulated viewpoint jitter* and *oscillation* to 3D radial flow increases the observer's global retinal motion. In general, this should be the case irrespective of whether the observer maintains stable gaze (e.g., by fixating a physically stationary target lying in the centre of the screen) or engages eye-movements to pursue moving objects in the self-motion display. In the former case, all of the *simulated viewpoint jitter* and *oscillation* will be added to the observer's retinal flow. In the latter case, the observer's pursuit eye-movements should compensate for some (but not all) of the display motion—retinal motion will only be nulled for moving objects at one particular depth, and tracking errors will generate additional retinal motion. Palmisano and Kim (2009) examined the role that increased retinal motion plays in vection by instructing observers to either alternate their gaze between the center and the periphery of their 3D radial flow displays every 5 s, or maintain stationary gaze at the center of these displays (the desired gaze location was indicated by a fixation target, which was briefly flashed every 5 s). Consistent with the notion that increased retinal motion improves vection, they found that: (a) in stationary gaze conditions, *simulated viewpoint oscilla-*

tion produced more compelling vection than *no oscillation*; and (b) when purely radial flow displays were shown, gaze alternation produced more compelling vection than stationary central gaze conditions. Also consistent with this idea, recent research by Kim and Palmisano (2010a) provided evidence suggesting that vection onset latencies and subsequent improvements in vection strength/speed were both temporally contiguous and contingent on declines in the gain of OFRs. These declines in OFR gain have the consequence of increasing global retinal motion and possibly vection.

The aim of the current study was to further test these competing explanations of the *simulated viewpoint oscillation* advantage for vection. We used three experimental conditions to examine induced vection, perceived scene rigidity, and any potential MAEs. Our seated and head-restrained observers either: (a) fixated a stationary central target while viewing purely radial optic flow (*No oscillation*); or (b) tracked a horizontally oscillating pursuit target while viewing purely radial optic flow (*Fixation point oscillation*); or (c) fixated a stationary central target while viewing radial flow combined with simulated horizontal viewpoint oscillation (*Simulated viewpoint oscillation*).

According to the Nakamura's theory of "increased rigidity," any condition which increases the perceived rigidity of the environment represented by optic flow should also increase vection (and vice versa). Thus, we tested this prediction by comparing our subjects' ratings of vection strength (in Experiment 1) and perceived scene rigidity (in Experiment 2) for each of the above experimental conditions. Similarly, we also tested the "reduced motion adaptation" theory by measuring the durations of the MAEs produced directly after viewing these three types of radial flow displays (in Experiment 3). The "indirect vestibular stimulation" and "increased retinal motion" theories have different predictions in terms of the relative effectiveness of the two different types of oscillation in generating vection – these specific predictions are outlined in the introduction of Experiment 1 below.

Experiment 1: Effects of gaze and simulated viewpoint oscillation on vection

In the *fixation point oscillation* conditions described above, the perceived direction of self-motion is known to oscillate to the left and right as the observer's eyes track the horizontal motion of the pursuit target[1] (Freeman, Banks, & Crowell, 2000). Perceived self-motion in these *fixation point oscillation* conditions appears superficially similar to the self-motion perceived in *simulated viewpoint oscillation* conditions - even though the oscillating retinal flow in the former case simulates combined whole body forwards translation and rotation about yaw, whereas the oscillating retinal flow in the latter case simulates combined whole body forwards and lateral translation. To our knowledge, no previous study has measured the vection induced in *fixation point oscillation* conditions. Therefore, one initial goal of Experiment 1 was to determine whether horizontal *fixation point oscillation* produces a comparable vection advantage to horizontal *simulated viewpoint oscillation* (given their superficial similarities in appearance and perceived self-motion trajectories).

However, the main purpose of Experiment 1 was to test the indirect vestibular stimulation and the increased global retinal motion accounts of the previous *simulated viewpoint oscillation* advantages for vection. According to the indirect vestibular stimulation theory, pursuit eye-movements should be essential for any oscillation-based advantage for vection. Unlike previous free-view vection studies (e.g., Palmisano et al., 2008), subjects were forced to maintain stationary central fixation while viewing displays with *simulated viewpoint oscillation* in Experiment 1. Thus, this indirect vestibular stimulation theory predicts that: (a) *simulated viewpoint oscillation* will produce little or no vection advantage in the current experiment; and (b) only the *fixation point oscillation* conditions will improve vection (i.e., above that induced by the *no oscillation* control).

By contrast, the increased global retinal flow theory predicts that both types of oscillation should improve vection – since we expect that *fixation point oscillation* and *simulated viewpoint oscillation* conditions will both generate more global retinal motion than the *no oscillation* control conditions. In *fixation point oscillation* conditions, this global retinal flow should be generated not only by the radially expanding display motion but also by the observer's smooth pursuit eye-movements. However, we assume that the observer's eyes will be reasonably stationary in *simulated viewpoint oscillation* and *no oscillation* conditions, and that, as a result, the global retinal flow will be generated primarily by their optic flow displays. The *simulated viewpoint oscillation* conditions should then generate more global retinal motion than the *no oscillation* control, as they contain both horizontally oscillating and radially expanding optic flow components, whereas the non-oscillating control displays only contain the radial expanding flow component. In order to fully test this 'increased global retinal motion' hypothesis, we tracked the eye-movements of a subset of the subjects while they performed this experiment.

Method

Participants

Ten male and four female postgraduate psychology students and staff at the University of Wollongong participated in this experiment (mean age 32.5 years; *SD* 6.7 years). All had normal or corrected-to-normal vision, were clear of any visual or vestibular impairment, and presented no obvious signs of oculomotor or neurological pathology. The University ethics committee approved the study in advance and each subject had to provide written informed consent before participating in the study.

Design

Two independent variables were manipulated in this experiment. (1) *Oscillation Type*. The *no oscillation, fixation point oscillation,* and *simulated viewpoint oscillation* conditions were created as follows. The visual displays used in this experiment all simulated constant velocity forward self-motion in depth either with or without horizontal simulated viewpoint oscillation. When viewing these displays, subjects were instructed to fixate a target whose position either oscillated sinusoidally from the left to the right of the screen or remained fixed at the centre of the screen. (2) *Oscillation Frequency*. Three different frequencies of *fixation point oscillation* and *simulated viewpoint oscillation* were examined: 0.58, 0.75, and 1 Hz. The dependent variable measured was the overall vection strength rating for each trial (0-100).

Every subject ran through four blocks – each of which consisted of nine experimental trials (36 trials in total). The standard stimulus (the *no oscillation* control stimulus) was shown before each block. From then on, trial order in the block was random. Each of the six oscillating conditions was tested once per block (four times in total). In addition to acting as the standard stimulus (i.e., for the modulus), the *no oscillation* control stimulus also served as an experimental condition – this condition was randomly intermixed with the six oscillating conditions and rated three times per block (12 times in total).

Apparatus

Optic flow displays were generated on a Dell Optiplex GX620 PC and rear projected onto a 1.48 m wide × 1.20 m high flat projection screen using a color data projector (Model XD400U, Mitsubishi Electric; refresh rate 72 Hz). Each display subtended a visual area which was 47° wide × 37° high when viewed through a large, rectangular viewing tube attached to a head-and-chin rest at a distance of 1.9 m from the display. The tube blocked the subject's view of his/her stationary surroundings (which included the screen's frame).

Visual displays

Prior to presenting each self-motion display, a stationary green fixation target (a cross which was 0.5° wide × 0.5° high; luminance 1.8 cd/m^2) was initially presented in the centre of the black screen. In *simulated viewpoint oscillation* and *no oscillation* trials, this fixation point remained stationary at the centre of the screen for the entire 15 s of the visually simulated self-motion. However, in *fixation point oscillation* trials, its position oscillated left-right on the screen throughout the entire 15 s self-motion display. The amplitude of this horizontal *fixation point oscillation* was 8 units (0.23 m or 6.8°). Self-motion display durations were kept brief so that subjects did not become fatigued in these active pursuit conditions.

Each of the self-motion displays simulated constant velocity forwards self-motion over a ground plane consisting of 600 randomly positioned blue circular objects (luminance 1.8 cd/m^2) on a black background (luminance 0.04 cd/m^2). Objects were distributed uniformly across this ground plane, which was simulated to be 170 units wide × 600 units deep. This resulted in a visible horizon being formed 2° below the fixation target. The simulated speed of the forwards self-motion was always 4 units/s. The optical size of each circular object increased from 0.0006° to 0.03° as the virtual camera approached it. When this virtual camera moved past an object, it was immediately replaced at the opposite end of space (i.e., 600 units away). This not only ensured a smooth and continuous simulation of self-motion, but it also minimized processing costs in terms of scene rendering. In addition to simulating constant velocity forward self-motion, some displays also contained a global optic flow component simulating horizontal viewpoint oscillation. As with the horizontal *fixation point oscillation*, the amplitude of this *simulated viewpoint oscillation* was 8 units (0.23 m or 6.8°).

Eye tracking

Eye tracking allowed us to examine the pursuit eye movements made during *fixation point oscillation* conditions. Importantly, it also allowed us to verify that stationary central fixation was being maintained during *no oscillation* and *simulated viewpoint oscillation* conditions. We calculated horizontal eye-velocity (in °/s) from the changes in horizontal eye position recorded (from 8 of our 14 subjects) using 3D video oculography. Optic flow display generation and eye-movement acquisition were handled by the same computer, which ran both software programs in parallel. Subjects wore a form-fitting ski mask (with the anti-glare filter removed) which had an infrared LED, a hot mirror and a FIREFLY-MV 120 Hz Firewire camera mounted to it. The infrared opaque mirror was used to reflect images of the left eye toward the laterally positioned acquisition camera. This mirror was transparent to natural light, which allowed our subjects to view the self-motion displays with minimal invasiveness. Prior to testing, eye position in degrees was calibrated over a ± 15° angular range in the horizontal and vertical directions. During testing, 320 × 240 pixel images of the subject's left eye were analyzed online using custom eye tracking software. The conversion from 2D pixel deviations of the pupil to angular rotations was achieved via simple geometric transformations (see Kim, 2004). Horizontal eye position data was recorded at a rate of 45 Hz.

Procedure

Subjects were initially informed that they would be shown displays of moving objects and told that "sometimes the objects may appear to be moving towards you; at other times you may feel as if you are moving towards the objects." Since the method of magnitude estimation was used, the first optic flow display of each testing session was used to set the modulus for the subject's speed ratings (Stevens, 1957). This standard stimulus was a non-oscillating pattern of radial flow with a stationary, central fixation target (i.e., a *no oscillation* control display). After 15 s exposure to this display, subjects were asked whether they felt as if they were moving or stationary. If they responded that they were moving, they were told that the strength of their feeling of self-motion corresponded to a value of 50 (with 0 representing stationary). Following each subsequent self-motion display, an interval scale was presented on the screen (from 0-100 in 5 point intervals) with a default position of 50 (the modulus). Subjects made their vection strength ratings by using the "up" and "down" arrow keys to position a needle along the bar chart and pressing the "enter" key to record their vection strength setting. After several practice trials, the experimental trials were presented in a random order. Each had a duration of 15 s and an inter-trial interval of 5 s. There were four blocks of nine experimental trials; the standard stimulus was always presented prior to each of these experimental blocks of trials to set/reset the modulus.

Results

Vection strength ratings

Vection was induced by all of the experimental conditions tested – with only the rated strength of this experience being found to vary. Specifically, all 14 subjects reported experiencing self-motion on every trial (No 0 vection strength ratings were recorded).

We first looked at which types of horizontal oscillation could produce a vection advantage (i.e., compared with the *no oscillation* control). Accordingly, we analyzed the average vection strength ratings for the *no, fixation point,* and *simulated viewpoint oscillation* conditions using a one-way repeated measures ANOVA. Vection ratings for the latter two conditions were collapsed across oscillation frequency. The *means* and *SEMs* of the vection ratings for these different conditions are presented in Figure 1. The main effect of Oscillation Type was found to be significant, $F(2, 26) = 38.76$, $p < 0.0001$. Pairwise comparisons revealed that *fixation point* and *simulated viewpoint oscillation* both produced significantly stronger vection ratings than the *no oscillation* control ($p < 0.05$ in all cases)—indicating that both types of horizontal oscillation produced measurable vection advantages.

Next we used a two-way repeated-measures ANOVA to examine the effects of Oscillation Frequency on vection for the two different types of Horizontal Oscillation (*fixation point oscillation* and *simulated viewpoint oscillation*). The *means* and *SEMs* of the vection strength ratings for these two types of horizontal oscillation at the three different oscillation frequencies (0.58, 0.75, and 1 Hz) are presented in Figure 2. We found a significant interaction between Oscillation Type and Oscillation Frequency, $F(2, 26) = 9.96$, $p < 0.001$. As can be seen from Figure 2, while vection strength ratings increased with frequency in *simulated viewpoint oscillation* conditions, they de-

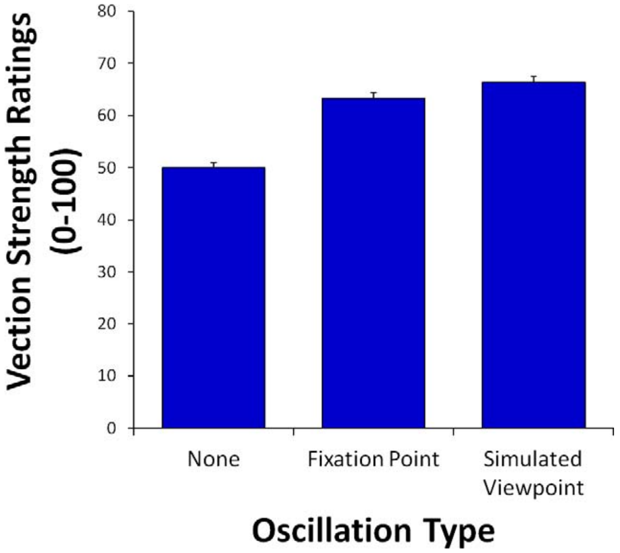

Figure 1. Effects of oscillation type (*none, fixation point,* and *simulated viewpoint*) on vection strength ratings induced by radially expanding patterns of optic flow. Error bars depict standard errors of the *mean* (*SEMs*).

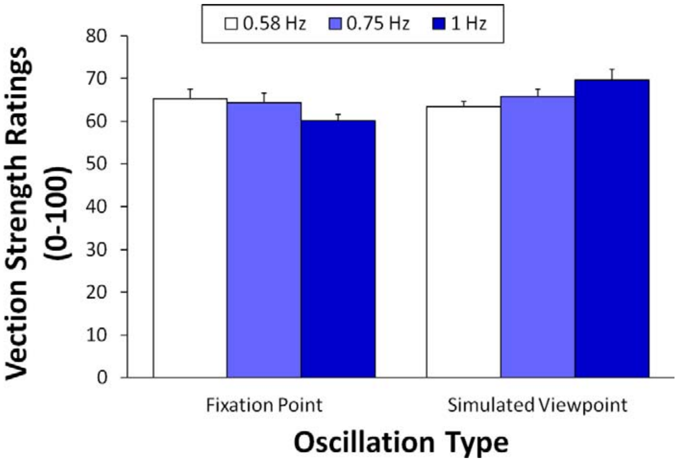

Figure 2. Oscillation type (*fixation point* and *simulated viewpoint*) and oscillation frequency (0.58, 0.75, and 1 Hz) effects on vection strength ratings induced by radially expanding patterns of optic flow. Error bars depict *SEMs*.

creased with frequency in *fixation point oscillation* conditions. We also found a main effect of Oscillation Type, $F(1, 13) = 5.27$, $p < 0.04$. These data (which were collapsed over frequency) revealed that *simulated viewpoint oscillation* produced significantly stronger vection ratings than *fixation point oscillation*.

Eye tracking data

Horizontal eye position data were digitally smoothed and derived to obtain pursuit eye velocity (first derivative), acceleration (second derivative) and jerk (third derivative). Saccades were detected using a jerk threshold of $100{,}000°/s^3$ (see Wyatt, 1998) and replaced via linear interpolation between the sample just before and just after the detected saccade.

As can be seen from the representative example eye-velocity plots in Figure 3, subjects tracked the horizontally moving fixation target with smooth pursuit movements during *fixation point oscillation* (Figure 3 Left) conditions. However, their eyes were close to stationary during both the *simulated viewpoint oscillation* (Figure 3 Right) and *no oscillation* conditions; this was expected since both of these conditions had a stationary fixation target located 2° above the horizon of the moving ground plane.

Since smooth pursuit eye-movements were only generated during the *fixation point oscillation* trials, we calculated the eye-velocity amplitudes for each of these trials by fitting a sinusoidal function of the given temporal frequency (i.e., 0.58, 0.75, and 1 Hz) to the desaccaded eye-velocity data, while leaving its amplitude and phase free to vary. The *mean* eye-velocity amplitudes (and *SEMs*) for the different frequencies of *fixation point oscillation* are presented in Figure 4. We examined the effects of Fixation Point Oscillation Frequency (0.58, 0.75, and 1 Hz) on this eye-velocity amplitude data using a one-way repeated measures ANOVA. The main effect of Oscillation Frequency was found to approach significance, $F(2, 14) = 3.12$, $p = 0.07$.

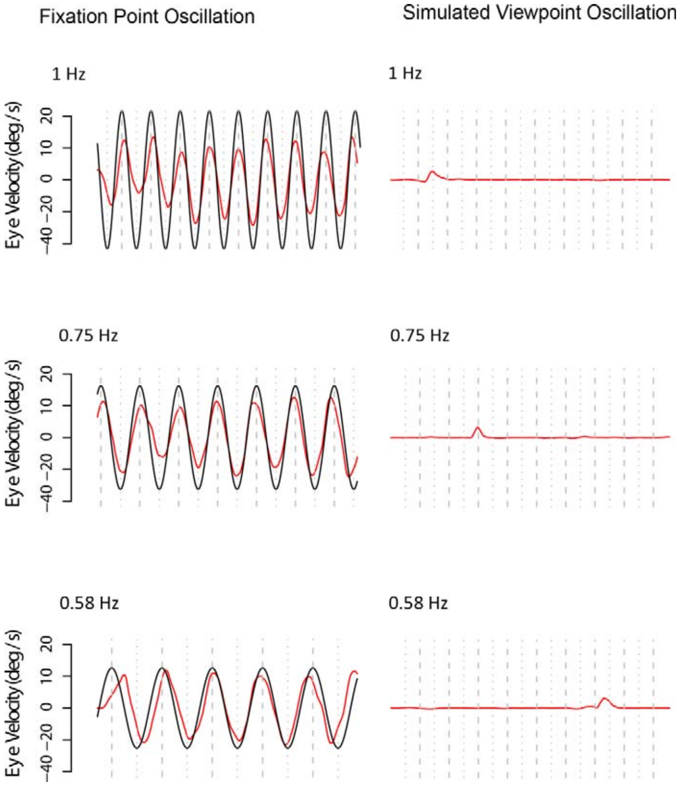

Figure 3. The horizontal eye velocities of one representative subject in *fixation point oscillation* (plots in left column) and *simulated viewpoint oscillation* (plots in right column) conditions. The red trace in each case represents the subject's eye-velocity and the black trace represents the velocity of the fixation target (if it moved). The oscillation frequency was either 1 Hz (top row), 0.75 Hz (middle row), or 0.58 Hz (bottom row). In each case, these are single eye-movement traces.

Relationship between vection strength and eye-velocity amplitude

We also analyzed the correlation between these eye-velocity amplitudes and the vection strength ratings for the eight eye-tracked subjects. For each of the eight subjects, we calculated the average vection strength rating and the average eye-velocity amplitude for all 3 frequencies of *fixation point oscillation*. Average vection strength was found to be positively correlated with average eye-velocity amplitude in *fixation point oscillation* conditions ($r = +0.71$, $n = 8$, $p < 0.049$, 2-tailed).

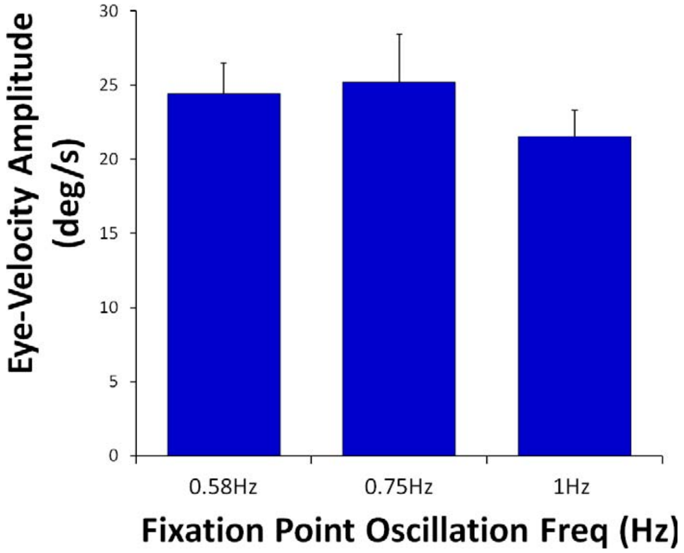

Figure 4. *Mean* eye-velocity amplitudes (in degrees/second) for each of the *fixation point oscillation* frequency conditions (0.58, 0.75 or 1 Hz). Error bars depict *SEMs*.

Discussion

According to the indirect vestibular stimulation theory outlined in the Introduction, *simulated viewpoint oscillation* would only be expected to improve the vection induced by radial flow during free view conditions – since pursuit eye-movements are assumed to be essential for any oscillation-based advantage for vection. However, during the *simulated viewpoint oscillation* conditions tested in the current experiment, subjects always fixated a stationary, centrally-located target while viewing these self-motion displays. Since this stationary fixation target proved to be highly successful in preventing optokinetic eye-movements (confirmed by eye-tracking), the indirect vestibular stimulation theory predicts that only the *fixation point oscillation* conditions should have improved vection. Contrary to these predictions, we found that both *fixation point oscillation* and *simulated viewpoint oscillation* significantly improved vection strength ratings compared to the *no oscillation* controls.

These findings are generally consistent with the predictions of the increased global retinal motion explanation of the simulated viewpoint oscillation advantage for vection. According to this theory, the *fixation point oscillation* and the *simulated viewpoint oscillation* conditions used in the current experiment were both expected to generate more global retinal motion than the *no oscillation* control. Our observation that both types of oscillation did in fact produce stronger vection ratings than the *no oscillation* control is directly consistent with this theoretical proposal.

Further supporting the increased global retinal motion explanation, we found that vection strength ratings increased with the frequency of the *simulated viewpoint oscillation*. Since our subjects' eyes were nearly stationary in these conditions (confirmed by eye-tracking), almost all of this (3D) horizontal display oscillation would have been added to the (3D) radially expanding retinal flow. Thus, the global retinal flow should have increased with the frequency of this *simulated viewpoint oscillation*, which could explain why the vection increased as well.

In the *fixation point oscillation* conditions, all of the added (2D) horizontal retinal motion was generated by the subjects' eye-movements. This added retinal motion would have been proportional to the pursuit eye-velocity amplitudes shown in Figure 4. Unfortunately, only 8 of the 14 subjects were able to have their eyes tracked while viewing these self-motion displays (as the remaining six subjects required optical correction for the viewing distance used). However, the eye-velocity amplitude data of these eight subjects tested does suggest a trend in the right direction, with both horizontal eye-velocity amplitudes and vection strength ratings increasing together as the fixation point oscillation frequency decreased (from 1 to 0.58 Hz). Furthermore, we did find that average vection strength was significantly correlated with the average horizontal eye-velocity amplitudes in these active pursuit conditions, which is also consistent with the increased global retinal motion theory.

In summary then, the results of Experiment 1 were inconsistent with the indirect vestibular stimulation theory and generally consistent with the predictions of the increased global retinal motion theory. It should be noted that by itself, Experiment 1 cannot rule out either the increased rigidity or the reduced adaptation theories of these oscillation based advantages for vection. Experiments 2 and 3 were specifically designed to test these two theories.

Experiment 2: Perceived scene rigidity

Nakamura (2010) recently proposed that *simulated viewpoint oscillation* might act to increase both the perceived rigidity of the 3-D environment and the vection in depth induced by radial flow. Experiment 2 therefore used the same conditions as Experiment 1 but this time had observers judge the rigidity of the ground-plane. Nakamura's (2010) theory predicts that viewing conditions that make the simulated environment appear more rigid should also induce more compelling vection. From the results of Experiment 1, we therefore predict that *fixation point oscillation* and *simulated viewpoint oscillation* conditions should both be rated as being more rigid than the *no oscillation* control.

Method

In this experiment, the rating scale was used to make judgments of scene rigidity not vection strength. All other details were identical to Experiment 1.

Participants

Six male and four female postgraduate psychology students and staff at the University of Wollongong participated in this experiment (*mean* age 35.9 years; *SD* 6.4 years). All had previously participated in Experiment 1.

Results

We first looked at the effects that *fixation point oscillation* and *simulated viewpoint oscillation* had on perceptions of scene rigidity compared to the *no oscillation* control. Rigidity ratings for these three different display types (collapsed across oscillation frequency) were examined using a one-way repeated measures ANOVA. The *means* and *SEMs* of these ratings are presented in Figure 5. We found a significant main effect of Oscillation Type, $F(2, 18) = 9.92$, $p < 0.001$. Pairwise comparisons revealed that: (a) *simulated viewpoint oscillation* produced significantly less rigid ratings of the ground plane than *no oscillation* ($p < 0.05$); and (b) *fixation point oscillation* did not produce significantly different rigidity ratings to *no oscillation* ($p > 0.05$).

The *mean* rigidity ratings for the two different types of horizontal oscillation at the three different oscillation frequencies (0.58, 0.75, and 1 Hz) are shown in Figure 6. These rigidity rating data were analyzed using a two-way repeated measures ANOVA (Greenhouse-Geisser corrections were applied whenever the assumption of sphericity was violated). We failed to find either a main effect of Oscillation Frequency, $F(2, 18) = .31$, $p > 0.05$, or an interaction between Oscillation Type and Oscillation Frequency, $F(1.12, 17.32) = 1.12$, $p > 0.05$. However, we did find a main effect of Oscillation Type, $F(1, 9) = 9.16$, $p < 0.01$. These data (collapsed over frequency) revealed that *simulated viewpoint oscillation* produced significantly less rigid ratings than *fixation point oscillation*.

Discussion

Taken together with the results of Experiment 1, the judgments of rigidity obtained in Experiment 2 provided little support for Nakamura's general explanation of the simulated viewpoint oscillation advantage for vection. Even though *fixation point oscillation* conditions produced stronger vection ratings than the *no oscillation* conditions in Experiment 1, *fixation point oscillation* conditions did not produce significantly different rigidity ratings to the *no oscillation* conditions in Experiment 2. *Simulated viewpoint oscillation* also produced stronger vection ratings than *no oscillation* conditions in Experiment 1. However, rather than increasing the perceived rigidity of the simulated ground plane, adding *simulated viewpoint oscillation* to radial flow was actually found to significantly decrease it (relative to the *no oscillation* conditions). Finally, in Experiment 1, vection strength ratings were found to increase with the frequency of the *simulated viewpoint oscillation* and decrease as the frequency of the *fixation point oscillation* increased. No corresponding frequency effects were observed in Experiment 2 in terms of the rigidity ratings, a result which suggests that the vection advantages observed in Experiment 1 depended primarily on information other than perceived scene rigidity.

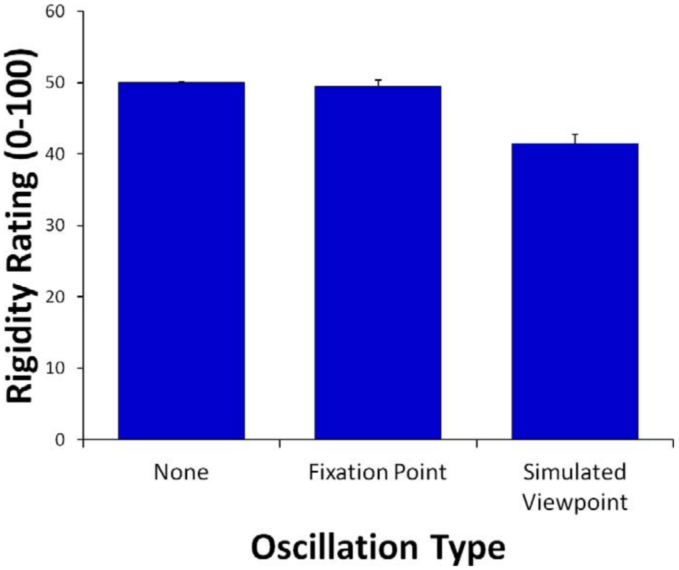

Figure 5. Effect of oscillation type (*none, fixation point,* and *simulated viewpoint*) on scene rigidity ratings for radially expanding patterns of optic flow. Error bars depict *SEMs*.

Experiment 3: Motion aftereffects (MAE)

In principle, reduced motion adaptation could also explain the vection advantages found in Experiment 1 for the *fixation point oscillation* and *simulated viewpoint oscillation* conditions (compared to *no oscillation* conditions). Experiment 3 was designed to test this reduced motion adaptation explanation. This experiment measured the time courses of the vection during,

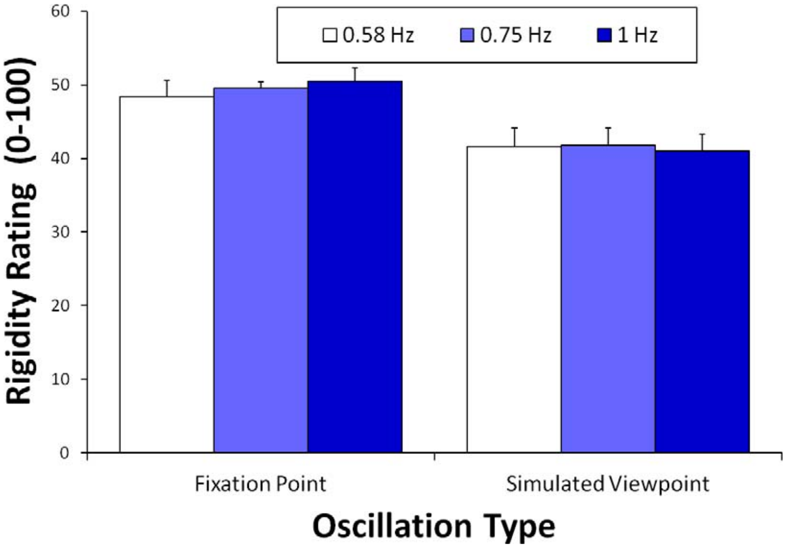

Figure 6. Oscillation type (*fixation point* and *simulated viewpoint*) and Oscillation Frequency (0.58, 0.75, and 1 Hz) effects on ground rigidity ratings induced by radially expanding patterns of optic flow. Error bars depict *SEMs*.

and the motion aftereffects (MAEs) directly following, exposure to these 15 s optic flow displays.

Method

Only the 0.58 Hz frequency was tested in Experiment 3 for both types of oscillation. Seno, Ito, and Sunaga (2010) have recently reported that following short adaptation periods (e.g., 20 and 60 s), MAEs and vection aftereffects (VAEs) experienced with a static test stimulus last longer than those experienced with either a blank screen or 10-75 Hz dynamic test stimulus. Our pilot testing confirmed the former MAE finding, and thus, we always used a static (as opposed to a dynamic) test stimulus in Experiment 3.

Participants

Four male and 10 female postgraduate psychology students and staff at the University of Wollongong participated in this experiment (*mean* age 27.6 years; *SD* 5.8 years). All fourteen subjects had previously experienced MAEs in a laboratory setting. None of them had participated in Experiments 1 and 2.

Procedure

The methodology used in this experiment was modified from Seno, Ito, and Sunaga (2010). Our 15 s radial flow displays–with either *no*, *fixation point* or *simulated viewpoint oscillation*–were used as the adaptation stimuli. As in Experiment 1, the subjects were instructed to maintain fixation on the stationary/moving target at all times during the adaptation phase of each trial. The time courses of the vection during, and the MAE after, each type of self-motion display were measured in separate blocks of trials.

During the self-motion measurement trials, the subject's instructions were as follows: "You will be shown a variety of 15 s displays simulating forwards self-motion in depth. Sometimes the objects may appear to be moving towards you; at other times you may feel as if you are moving towards the objects. Your task is to press the left mouse button down when you feel as if you are moving and hold it down as long as the experience continues. If you don't feel that you are moving, then don't press the mouse button" (instructions modified from Palmisano et al., 2000).

During the MAE measurement trials, all of the display motion ceased after the 15 s presentation of the adaptation stimulus, producing a static test stimulus (i.e., 600 blue objects on a black background with their screen sizes and positions frozen). This test stimulus remained on the screen until the subjects indicated that their MAE had been completely extinguished. For these MAE measurement trials, the subject's instructions were as follows: "You will be shown a variety of displays simulating forwards self-motion in depth. After 15 s, all physical display motion will cease. At this time, your task is as follows: press the left mouse button when/if you perceive any motion and hold it down as long as this illusory motion continues. If such a decision becomes difficult, or if this motion percept disappears, please release the mouse button" (instructions modified from Seno et al., 2010). Subjects were asked to double check that the MAE was completely extinguished by blinking.

Results

Vection was experienced on every trial by all but 1 of our 14 subjects. This subject did not experience vection on two trials (indicated by vection onset latencies that were longer than the 15 s presentation duration of the optic flow display). Both of these "no vection" trials occurred in the *no oscillation* condition.

Separate one-way repeated measures ANOVAs were performed on the vection onset latency, total vection duration, and the MAE duration data. Greenhouse-Geisser corrections were applied whenever the assumption of sphericity was violated.

Vection onset latency

The *mean* vection onset latencies (and *SEMs*) for the three different Oscillation Types (*none*, *fixation point,* and *simulated viewpoint*) are provided in Figure 7. We found a significant main effect of Oscillation Type on vection onset latency, $F(2, 26) = 8.27$, $p < 0.002$. Pairwise comparisons revealed that: (a) *simulated viewpoint oscillation* produced significantly shorter vection onsets than *no oscillation* ($p < 0.05$); and (b) *fixation point oscillation* also produced significantly shorter vection onsets than *no oscillation* ($p < 0.05$) and similar vection onsets to *simulated viewpoint oscillation* ($p > 0.05$).

Total vection duration data

The *mean* vection durations (and their *SEM*s) for the three different Oscillation Types (*none*, *fixation point,* and *simulated viewpoint*) are provided in Figure 8. We found a significant main effect of Oscillation Type on vection duration, $F(2, 26) = 7.76$, $p < 0.002$. Pairwise comparisons revealed that: (a) *simulated viewpoint oscillation* produced significantly longer vection durations than *no oscillation* ($p < 0.05$); (b) *fixation point oscillation* also produced significantly longer vection durations than *no oscillation* ($p < 0.05$) and similar vection durations to *simulated viewpoint oscillation* ($p > 0.05$).

MAE duration data

The *mean* MAE durations (and their *SEMs*) obtained following adaptation to the three different Oscillation Types (*none*, *fixation point,* and *simulated viewpoint*) are presented in Figure 9. We failed to find a significant main effect of Oscillation Type on MAE duration, $F(1.19, 15.48) = 1.90$, $p = 0.17$. It should also be noted that based on our subjects' reports during debriefing, the subjective experience of these MAEs was generally more similar to scene deformation than to motion in depth.

Discussion

Consistent with the findings of Experiment 1, both *fixation point oscillation* and *simulated viewpoint oscillation* improved the vection induced by our radial flow displays. However, the main purpose of this experiment was to test the reduced adaptation explanation of the *fixation point oscillation* and *simulated viewpoint oscil-*

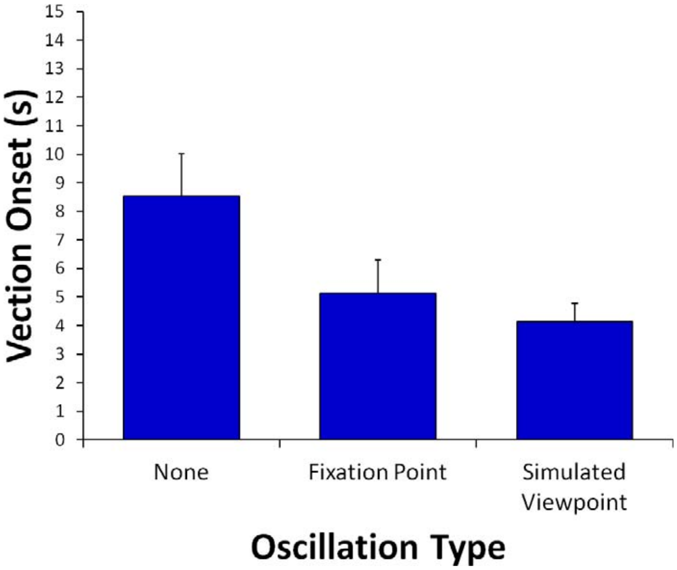

Figure 7. Effects of oscillation type (*none, fixation point,* and *simulated viewpoint*) on the vection onset latencies induced by radial flow. Error bars depict *SEMs*.

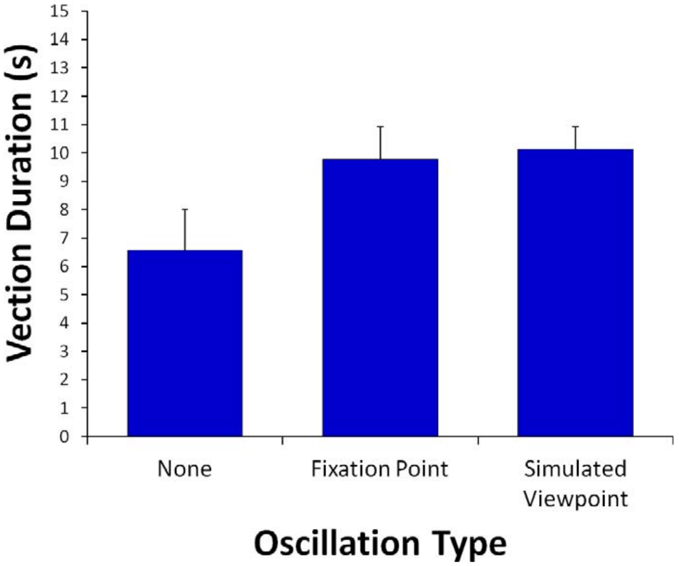

Figure 8. Effects of oscillation type (*none, fixation point,* and *simulated viewpoint*) on the total duration of the vection induced by radial flow. Error bars depict *SEMs*.

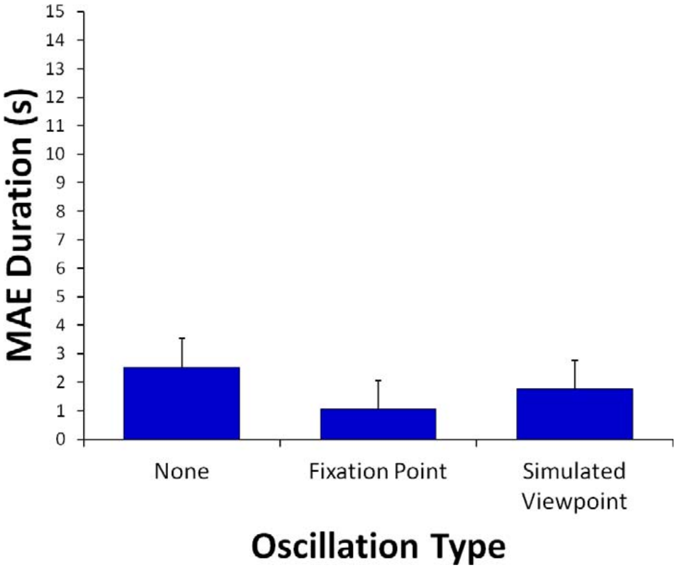

Figure 9. Effects of oscillation type (*none, fixation point,* and *simulated viewpoint oscillation)* during adaptation on the duration of the subsequent static MAE. Error bars depict *SEMs*.

lation advantages for vection. The MAE duration data obtained provided little support for this reduced adaptation theory. Exposure to 15 s of ground plane optic flow generally produced short duration MAEs. Even though *fixation point oscillation* and *simulated viewpoint oscillation* conditions both produced more compelling vection (i.e., shorter vection onset latencies and longer total vection durations) than *no oscillation* conditions, neither of these types of oscillation were found to produce significantly different MAE durations to the *no oscillation* condition.

General discussion

Previous studies have proposed that *simulated viewpoint jitter/oscillation* might improve the vection in depth induced by radial flow by either: (a) making the visually simulated environment appear more rigid (Nakamura, 2010); (b) reducing the adaptation to the radial component of the flow (Palmisano et al., 2000); (c) generating pursuit eye-movements which indirectly stimulate the vestibular cortex of physically stationary subjects (Kim & Palmisano, 2008); or d) generating more global retinal motion (Kim & Palmisano, 2010a; Palmisano & Kim, 2009). The current experiments were designed to test these four explanations of the *simulated viewpoint oscillation* advantage for vection. In the process of testing these explanations, we discovered a novel oscillation-based advantage for vection: *Fixation point oscillation* can also improve the vection induced by purely radial patterns of optic flow.

Little support was found for the increased perceived rigidity explanation of the *simulated viewpoint oscillation* advantage for vection. As in previous studies, Experiments 1 and 3 found that *simulated viewpoint oscillation* significantly improved the vection induced by radial flow by strengthening vection ratings, shortening vection onset latencies and prolonging vection durations. However, in Experiment 2 we found that instead of this display oscillation increasing the perceived rigidity of the simulated environment, it actually decreased it (compared to the *no oscillation* control). Perceived rigidity also did not appear to explain the vection advantages observed in *fixation point oscillation* conditions. In Experiments 1 and 3, *fixation point oscillation* was found to produce significantly stronger vection ratings, shorter vection onsets, and longer vection durations than the *no oscillation* control. However, in Experiment 2, *fixation point oscillation* produced very similar ratings of perceived scene rigidity to the *no oscillation* control.

Based on the current findings, it is possible that the previously reported relationship between increased vection and increased scene rigidity might be restricted to 2D optic flow stimuli (i.e., displays without any simulated depth variation). Nakamura's 2010 study used 2D optic flow stimuli, either with or without *simulated viewpoint oscillation.* All of the dots in these displays were simulated to lie on a frontal plane surface and as a result they all moved at the same speed (at least in his coherent-and-uniform display oscillation and non-oscillation conditions). By contrast, our simulations represented self-motion with respect to objects lying on a ground plane receding in depth, and as a result, objects simulated to be nearer to the subject moved further and faster than those simulated to be farther away. Thus, it is possible that the effects of display oscillation on perceptions of scene rigidity were stronger with Nakamura's 2D frontal wall stimuli (compared to our 3D ground plane stimuli), and perhaps, as a result, they had a greater influence on the vection that was induced.

Our experiments also did not find clear support for the reduced adaptation and the indirect vestibular stimulation explanations of the *simulated viewpoint oscillation* advantage for vection. Contrary to the reduced adaptation theory, Experiment 3 found that while adding *simulated viewpoint oscillation* to radial flow significantly reduced vection onsets and increased vection durations, it had no significant effect on the durations of the subsequent MAEs. The MAE duration data were also unable to explain the *fixation point oscillation* advantage for vection. However, it is worth noting that unlike recent studies by Seno et al. (2010, 2011), we were unable to obtain measurable vection aftereffects (VAEs) with our 15 s ground plane optic flow displays. So while we did not find support for the reduced adaptation hypothesis in the present study, it is likely that motion adaptation plays a more important role in vection (e.g., Seno et al., 2011) when the stimulus conditions are favorable for the generation of MAEs and VAEs.[2]

According to the indirect vestibular stimulation theory (or at least a strong version of this theory), only conditions which generate pursuit eye-movements should improve vection. Contrary to these predictions, Experiment 1 found that *simulated viewpoint oscillation* conditions (which produced negligible eye-motion thanks to the stationary fixation target) actually produced stronger vection ratings than *fixation point oscillation* conditions (which generated sizeable pursuit eye-movements). Also contrary to these predictions, Experiment 3 found that adding *simulated viewpoint oscillation* to radial flow reduced vection onsets and increased vection durations in a very similar fashion to *fixation point oscillation*.

Thus, of the four theories outlined in the Introduction, the most support was found here for the increased global retinal flow explanation. Since both *fixation point oscillation* and *simulated viewpoint oscillation* increased the observer's global retinal flow, this theory predicts that they should both generate vection advantages (compared to the *no oscillation* control). Consistent with this prediction, both *fixation point oscillation* and *simulated viewpoint oscillation* produced stronger vection ratings, shorter vection onsets, and longer vection durations than the *no oscillation* control (see Experiments 1 and 3). Also consistent with this theory, vection strength ratings increased with the frequency of the *simulated viewpoint oscillation*. Since our subjects' eyes were close to stationary in these *simulated viewpoint oscillation* conditions: (a) almost all of this display oscillation would have been added to their retinal flow; and (b) as a result, their global retinal flow should have increased with the frequency of this *simulated viewpoint oscillation*, which could explain why their vection increased as well. The increased global retinal motion hypothesis was also supported by the finding of a significant positive correlation between our subjects' vection ratings and their horizontal eye-velocity amplitudes in the *fixation point oscillation* conditions. However, in order for this theory to also explain the effects of *fixation point oscillation* frequency on vection (observed in Experiment 1), the subjects' eye-velocity amplitudes needed to increase as the frequency of the *fixation point oscillation* decreases. In partial support for this prediction we did find a trend in the predicted direction for the 8 eye-tracked subjects examined in Experiment 1.

It should be noted that simply adding more global retinal motion to a self-motion display does not always improve vection (even if the resulting combined retinal flow pattern is consistent with self-motion). For example, Palmisano, Allison, and Pekin (2008; Experiment 2) found that adding simulated *constant velocity* horizontal/vertical self-motion to radial optic flow (in free-view conditions) had no significant effect on vection in depth. Thus, it is possible that the simulated viewpoint jitter/oscillation advantages for vection are due (in part at least) to the fact that the resulting retinal flow patterns are superficially similar to those generated by actual walking and running (e.g., Bubka & Bonato, 2010). In order to test this possibility, future studies should directly compare the vection enhancements provided by realistic and artificial simulated viewpoint jitter/oscillation. Real head jitter/oscillation during walking has six degrees of freedom and contains both linear and rotary components, producing a rich and complex mix of jitter amplitudes and frequencies. The artificial head jitter stimuli required for this type of study should, by necessity, match the characteristics of real head jitter as closely as possible, while still serving as fair comparison stimuli. One cannot simply create artificial head jitter stimuli by scrambling real head position and orientation data, since the resulting frequencies and amplitudes of this artificial jitter would differ dramatically from those of the real head jitter. One potential solution to this problem might involve phase shifting. For example, one could make pseudo-artificial head jitter stimuli by phase shifting the different linear and rotary components of the real head jitter along/about the three different axes.

In conclusion, we have found that *fixation point oscillation* and *simulated viewpoint oscillation* both improve the vection induced by radial flow (relative to *no oscillation* radial flow control displays). The current vection findings cannot be easily explained by increased perceived rigidity, reduced motion adaptation, or indirect vestibular stimulation theories. The strongest support was found for the proposal that *fixation point oscillation* and *simulated viewpoint oscillation* both improve vection by increasing the observer's global retinal motion.

Acknowledgments

This study was funded by an Australian Research Council (ARC) Discovery Project grant (DP1093493) awarded to SP.

Commercial relationships: none.

Corresponding author: Stephen A. Palmisano.
Email: stephenp@uow.edu.au.
Address: School of Psychology, University of Wollongong, Wollongong, Australia.

Footnotes

[1] Referred to as the "slalom illusion," due to its similarity to the self-motion perceived when downhill slalom skiing, this effect is thought to arise due to mismatches between the amplitudes of retinal and extra-retinal motion estimates (Freeman et al., 2000; Souman & Freeman, 2008). Mismatches in the timing between these extraretinal and retinal components are thought to be small.

[2] There were a number of stimulus differences which might account for our failure to induce VAEs in the current experiment. First, we used shorter 15 s adaptation periods than Seno et al. (2010, 2011), who used adaptation periods up to 60 s. Second, we had much sparser and smaller optic flow displays. Our ground plane optic flow (consisting of 600 dots) covered less than half the screen and subtended 47° × 37°. Seno et al.'s cloud optic flow (consisting of 1,240 dots) covered the whole screen and subtended 72° × 57°.

References

Benson, A. J. (1990). Sensory functions and limitations of the vestibular system. In R. Warren & A. H. Wertheim (Eds.), *Perception and control of self-motion*, pp. 143–170. Hillsdale, NJ: Erlbaum.

Bubka, A., & Bonato, F. (2010). Natural visual-field features enhance vection. *Perception, 39*, 627–635.

Denton, G. G. (1980). The influence of visual pattern on perceived speed. *Perception, 9*, 393–402.

Dichgans, J., & Brandt, T. (1978). Visual-vestibular interaction: Effects on self-motion perception and postural control. In R. Held, H. Leibowitz, & H. L. Teuber (Eds.), *Handbook of sensory physiology: Vol. 8. perception*, pp. 755–804. New York: Springer-Verlag.

Fetsch, C. R., Wang, S., Gu, Y., Deangelis, G. C., & Angelaki, D. E. (2007). Spatial reference frames of visual, vestibular, and multimodal heading signals in the dorsal subdivision of the medial superior temporal area. *The Journal of Neuroscience, 27*(3): 700–712.

Fischer, M., & Kornmüller, A. (1930). Optokinetisch ausgelöste bewegungswahrnedhmungen und optokinetischer nystagmus [Translated: Optokinetically induced motion perception and optokinetic nystagmus]. *Journal of Psychological Neurology, 41*, 273–308.

Freeman, T. C. A., Banks, M. S., & Crowell, J. A. (2000). Extraretinal and retinal amplitude and phase errors during Filehne illusion and path perception. *Perception & Psychophysics, 62*, 900–909.

Gibson, J. J. (1966). *The senses considered as perceptual systems*. Boston: Houghton Mifflin.

Howard, I. P. (1982). *Human visual orientation*. Chichester, Sussex: Wiley.

Howard, I. P. (1986). The vestibular system. In K. R. Boff, L. Kaufman, & J. P. Thomas (Eds.), *Handbook of perception and human performance* (Vol. 1)*: Sensory processes and perception*, pp. 11-1–11-28. New York: Wiley.

Johansson, G. (1977). Studies on the visual perception of locomotion. *Perception, 6*, 365–376.

Kim, J. (2004). A simple pupil-independent method for recording eye movements in rodents using video. *Journal of Neuroscience Methods, 138*, 165–171.

Kim, J., & Palmisano, S. (2008). Effects of active and passive viewpoint jitter on vection in depth. *Brain Research Bulletin, 77*, 335–342.

Kim, J., & Palmisano, S. (2010a). Eccentric gaze dynamics enhance vection in depth. *Journal of Vision, 10*(12):7, 1–11, http://www.journalofvision.org/content/10/12/7, doi:10.1167/10.12.7. [PubMed] [Article]

Kim, J., & Palmisano, S. (2010b). Visually-mediated eye-movements regulate the capture of optic flow in self-motion perception. *Experimental Brain Research, 202*, 355–361.

Kitazaki, M., & Hashimoto, T. (2006). Effects of perspective jitter on vection and visual control of posture are dissociated. *Journal of Vision, 6*(6): 149a, http://www.journalofvision.org/content/6/6/149, doi:10.1167/6.6.149. [Abstract]

Lishman, J. R., & Lee, D. N. (1973). The autonomy of visual kinaesthesis. *Perception, 2*, 287–294.

Mach, E. (1875). *Grundlinien der Lehre von den Bewegungsempfindungen* [Translated: Elements of the doctrine of the movement sensations]. Leipzig: Engelmann.

Miles, F. A., Busettini, C., Masson, G. S., & Yang, D. S. (2004). Short-latency eye movements: Evidence for rapid, parallel processing of optic flow. In L. M. Vaina & S. K. Rushton (Eds.), *Optic flow and beyond*, pp. 79–107. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Miles, F. A., & Kawano, K. (1986). Short-latency ocular following responses of monkey. III. Plasticity, *Journal of Neurophysiology, 56*, 1381–1396.

Nakamura, S. (2010). Additional oscillation can facilitate visually induced self-motion perception:

The effects of its coherence and amplitude gradient. *Perception, 39*, 320–329.

Nishiike, S., Nakagawa, S., Nakagawa, A., Uno, A., Tonoike, M., Takeda, N., et al. (2002). Magnetic cortical responses evoked by visual linear forward acceleration. *Neuroreport, 13*, 1805–1808.

Palmisano, S., Allison, R. S., Kim, J., & Bonato, F. (2011). Simulated viewpoint jitter shakes sensory conflict accounts of self-motion perception. *Seeing & Perceiving, 24*, 173–200.

Palmisano, S., Allison, R. S., & Pekin, F. (2008). Accelerating self-motion displays produce more compelling vection in depth. *Perception, 37*, 704–711.

Palmisano, S., Bonato, F., Bubka, A., & Folder, J. (2007). Vertical display oscillation effects on forward vection and simulator sickness. *Aviation, Space and Environmental Medicine, 78*, 951–956.

Palmisano, S., Burke, D., & Allison, R. S. (2003). Coherent perspective jitter induces visual illusions of self-motion. *Perception, 32*, 97–110.

Palmisano, S., & Chan, A. Y. C. (2004). Jitter and size effects on vection are robust to experimental instructions and demands. *Perception, 33*, 987–1000.

Palmisano, S., Gillam, B. J., & Blackburn, S. (2000). Global perspective jitter improves vection in central vision. *Perception, 29*, 57–67.

Palmisano, S., & Kim, J. (2009). Effects of gaze on vection from jittering, oscillating and purely radial optic flow. *Attention, Perception & Psychophysics, 71*, 1842–1853.

Salvatore, S. (1968). Velocity sensing. *Highway Research Record, 292*, 79–91.

Schmidt, L., & Tiffin, J. (1969). Distortion of drivers' estimates of automobile speed as a function of speed adaptation. *Journal of Applied Psychology, 53*, 536–539.

Seno, T., Ito, H., & Sunaga, S. (2010). Vection aftereffects from expanding/contracting stimuli. *Seeing and Perceiving, 23*, 273–294.

Seno, T., Palmisano, S., & Ito, H. (2011). Independent modulation of motion and vection aftereffects revealed by using coherent oscillation and random jitter in optic flow. *Vision Research, 51*, 2499–2508.

Souman, J. L., & Freeman, T. C. A. (2008). Motion perception during sinusoidal smooth pursuit eye movements: Signal latencies and non-linearities. *Journal of Vision, 8*(14):10, 1–14, http://www.journalofvision.org/content/8/14/10, doi:10.1167/8.14.10. [PubMed] [Abstract]

Stevens, S. S. (1957). On the psychophysical law. *Psychological Review, 64*, 153–181.

Tschermak, A. (1931). Optischer raumsinn [Optical sense of space]. In A. Bethe, G. Bergnann, G. Emden & A. Ellinger (Eds.), *Handbuch der normalen und pathologischen physiologie* (pp. 824–1000). Leipzig: Springer.

Wyatt, H. J. (1998). Detecting saccades with jerk. *Vision Research, 38*, 2147–2153.

Zacharias, G. L., & Young, L. R. (1981). Influence of combined visual and vestibular cues on human perception and control of horizontal rotation. *Experimental Brain Research, 41*, 159–171.