

Influence of head orientation and viewpoint oscillation on linear vection¹

Pearl S. Guterman^{a,*}, Robert S. Allison^a, Stephen Palmisano^b and James E. Zacher^a

^a*Centre for Vision Research, York University, Toronto, ON, Canada*

^b*School of Psychology, University of Wollongong, Wollongong, NSW, Australia*

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Abstract. Sensory conflict theories predict that adding simulated viewpoint oscillation to self-motion displays should generate significant and sustained visual-vestibular conflict and reduce the likelihood of illusory self-motion (vection). However, research shows that viewpoint oscillation enhances vection in upright observers. This study examined whether the oscillation advantage for vection depends on head orientation with respect to gravity. Displays that simulated forward/backward self-motion with/without horizontal and vertical viewpoint oscillation were presented to observers in upright (seated and standing) and lying (supine, prone, and left side down) body postures. Viewpoint oscillation was found to enhance vection for all of the body postures tested. Vection also tended to be stronger in upright postures than in lying postures. Changing the orientation of the head with respect to gravity was expected to alter the degree/saliency of the sensory conflict, which may explain the overall posture-based differences in vection strength. However, this does not explain why the oscillation advantage for vection persisted for all postures. Thus, the current postural and oscillation based vection findings appear to be better explained by ecology: Upright postures and oscillating flow (that are the norm during self-motion) improved vection, whereas lying postures and smooth optic flows (which are less common) impaired vection.

Keywords: Vection, sensory conflict, head orientation, posture, optic flow, linear, oscillation

1. Introduction

As we move through the world, multiple sensory systems provide feedback about our self-motion, with vision and the vestibular system playing dominant roles in this process but providing complimentary information. Based on the optical/retinal flow, vision is sensitive to most self-motions, including constant velocity motion [6,32]. By contrast, the vestibular system of the inner ear only senses self-accelerations – with its otolith organs and semicircular canals being specialized for the detection of linear and angular accelerations

respectively [13]. When the body is upright, vertical acceleration is mainly sensed by the saccule, whereas horizontal acceleration is predominantly sensed by the utricle, although the maculae of both have some sensitivity to motion in all directions [4,5,29]. Importantly, the vestibular system cannot distinguish between travelling at a constant linear velocity and remaining stationary (as these two conditions are indistinguishable to an inertial sensor [12,20,32]).

The visual and vestibular systems also provide information about the direction of gravity, the most pervasive linear acceleration we encounter (for review see Howard [13]). The visual perception of the gravitational “up/down” is derived by static and dynamic visual orientation cues which are available in our optic array (e.g. [2,14]). Similarly, since the otolith organs of the vestibular system register forces related to linear acceleration including gravity, they are also sensitive to static/dynamic head tilt [11]. However, since the

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*Corresponding author: Pearl S. Guterman, Centre for Vision Research, York University, 4700 Keele Street, Toronto, ON, M3J 1P3, Canada. Tel.: +1 416 736 2100 x20192, Fax: +1 416 736 5872; E-mail: pearljam@cse.yorku.ca.

force of gravity acts on all parts of the body, non-visual signals to its direction and magnitude are provided not only by the vestibular system, but also by the skin [15], gut [16], baroreceptors [30], and other proprioceptive and somatosensory sources. Thus, in the case of these non-visual senses, ambiguity can sometimes arise on account of having two sources of linear acceleration (self-motion and gravity).

Many real world situations, such as walking or driving a car, provide consistent visual and vestibular information about our self-motion. However, fixed-based simulators, which display visual motion to physically stationary observers, can also evoke (sometimes compelling) sensations of self-motion. Such visually-induced illusions of self-motion are known as “vection” [7]. Sensory conflict is often assumed to play a critical role in vection [35]. For instance, visual-vestibular conflicts should be transient when vection displays simulate constant velocity self-motion, since the vestibular system does not respond to this type of motion. However, the initial acceleration from a stationary position up to the constant speed represented by this display would normally be detected by the vestibular system during real (as opposed to simulated) self-motion. Thus, it has been proposed that this type of visual-vestibular conflict might be responsible for the observed latency of vection – with the vestibular system initially suppressing vection induction for a brief period after visual stimulus onset [35].

Sensory-conflict based models of visual-vestibular interactions in vection typically posit that vection responses should be modulated by the degree and saliency of the conflict. For example, in Zacharias and Young’s [35] model, vestibular self-motion signals are compared with a visually-derived, high-pass filtered analogue to estimate inter-sensory conflict. The vestibular signal is proposed to be dominant during situations of significant sensory conflict since it is a more reliable indicator of high-frequency head motion. Consistent with this theory, Lepecq and his colleagues [19] found that erect subjects’ vection onset latencies to unidirectional upward or downward visual self-motion displays were significantly (but weakly) correlated with their vestibular detection thresholds for equivalent real self-motion stimuli.

Similarly, since physiological, anatomical and psychophysical evidence suggests that the human utricle is more sensitive than the saccule, Giannopulu and Lep-ecq [8] predicted that vection along the naso-occipital axis (sensed more by the utricle) would generate greater sensory conflict than vection along the spinal axis

(where the saccular response predominates) in erect observers. In agreement, they found that vection onset latencies were shorter for up or down motions along the spinal axis than for forward or backward motions along the naso-occipital axis. One complication in interpreting the data from this study arises from the fact that the translations along the naso-occipital and spinal axes – besides preferentially stimulating the utricles and saccules, respectively, of erect observers – also differed in orientation with respect to gravity; had observers been lying on their side (shoulder down), then both of the displays would have moved orthogonal to gravity.

This confound has several aspects worth considering including the facts that: 1) the vertical but not the horizontal acceleration signal is superimposed on a generally larger gravitational acceleration, 2) the saccular and utricular signal processing have evolved and developed to deal with a predominantly erect posture and thus a superimposed gravity signal and tilt sensitivity respectively, 3) gravity provides a constant acceleration signal in contrast to the limited periods of acceleration resulting from natural head movements, and 4) extended periods of horizontal motion are more ecologically relevant than vertical motion. By varying posture one can partially (but not completely) dissociate the direction of gravity with respect to the head, the direction of vection, and otolith sensitivity. For instance, in a supine posture the utricle becomes more vertical and thus sensitive to vertical acceleration but also becomes loaded by the superimposed gravitational acceleration.

Two previous studies have examined the roles that orientation with respect to gravity plays in linear vection. In the first of these studies, Kano [17] used pairs of displays that presented 2-D optic flow simultaneously to the left and right visual fields of his stationary observers, who were either seated upright (Experiment 1) or lay supine (Experiment 2). These peripherally viewed (constant velocity) optic flow displays moved together in a direction that was either parallel or orthogonal (in a naso-occipital direction) to the observer’s spinal axis in both postures. Like Giannopulu and Lepecq [8], Kano found that for upright seated observers, the latencies for vertical self-motions (up and down) were significantly shorter than those for horizontal (forward and backward) self-motions. However, a different pattern of results was found when supine. In these conditions, vection latency was shorter when the self-motion was perceived to be either towards the feet or gravitationally downward towards the back (compared to when self-motion was perceived to be toward the head or gravitationally upward towards the front).

Table 1

A summary of the relationship between body-centric and gravito-centric frames of reference in the different posture and oscillation conditions. For each posture the table shows: 1) the direction of gravity in body-centric terms, 2) the gravito-centric direction of x-axis and y-axis display oscillation and 3) the gravity sensitivity of the utricle and saccule. In the last two columns an asterisk indicates that the given macula is oriented for high sensitivity in the direction of gravity

Posture	Gravity relative to self	Display oscillation relative to gravity		Otolith sensitivity bias to gravity	
		x-axis	y-axis	Utricle	Saccule
Upright	y-axis	orthogonal	aligned	—	*
Supine	z-axis (+)	orthogonal	orthogonal	—	—
Prone	z-axis (-)	orthogonal	orthogonal	—	—
Left Side	x-axis	aligned	orthogonal	*	—

Kano concluded that vection latency is not determined by egocentric or gravitational direction alone. Instead there was an interaction between gravitational and body centric information.

Kano [17] reported that overall vection onset latencies were shorter in supine compared to upright posture, but that this effect was not significant. Tovee [31], however, analyzed Kano's results and noted that vection latency for simulated forward motion, along the naso-occipital axis, was shorter in supine than upright conditions (Kano did not comment on this comparison). Tovee argued that in the supine posture, the constant acceleration signal due to gravity should support rather than restrain this forward vection. To further investigate the influence of posture on forward vection, Tovee presented observers with simulated forward (along the naso-occipital axis) motion through a virtual hallway using a stereoscopic helmet-mounted display in both upright and supine postures. Contrary to expectations, subjects experienced vection more frequently and onset latencies were shorter (but only by about 500 ms on average for trials where vection occurred) for upright compared to supine conditions. Regardless of posture, the subjects tended to report feeling upright, travelling in the horizontal direction perpendicular to gravity through the hallway. Thus, visual and cognitive cues that promoted the percept of a hallway rather than an earth-vertical shaft seemed to overcome vestibular and proprioceptive signals indicating they were supine. The author argued that the conflict between visual and vestibular gravitational orientation cues might have caused the increased delay in the onset of vection in supine conditions.

As well as modifying vestibular sensitivity to assess the effects of sensory conflict and concordance on visual-vestibular interaction in vection, one can also vary the visual stimulus. Unlike constant velocity self-motion displays, optic flow indicating continuous variation in head velocity would normally be accompanied by significant and sustained vestibular activity.

According to sensory conflict theories, the absence of this expected vestibular activity should generate visual-vestibular conflict, which in turn should continue to impair vection induction. However, this notion has been strongly challenged by recent findings that adding simulated viewpoint jitter or oscillation to patterns of radial optic flow simulating constant velocity motion can enhance vection – decreasing vection latency and increasing both vection durations and strength ratings [24–28]. Viewpoint jitter or oscillation refers to perturbations of the viewpoint used to render the scene (virtual camera position) and hence the perspective image. The effect is similar to the flow resulting from the bob and sway of the head that typically accompanies locomotion or vehicular travel. These jitter and oscillation advantages for vection have always been tested when the observer was upright (typically seated) with the head and body aligned with the direction of gravity.

One goal of the present study was to see whether vection and the above mentioned simulated viewpoint oscillation advantage for vection change with observer posture and orientation with respect to gravity. Changing orientation with respect to gravity changes the dynamic response of the otoliths to gravity and linear acceleration. For instance, in a supine individual the saccular maculae should be more sensitive to oscillatory motion that is orthogonal to the gravitational axis than to motion parallel to gravity. By varying posture we can make the gravity vector congruent with or orthogonal to the main direction of simulated self-motion and/or to the oscillation component. Manipulation of these factors could modulate the effects of sensory conflict. Table 1 shows the relationship among postures, gravity, oscillation direction, and principal otolith sensitivity. The utricle is normally considered to be a more effective sensor of self-motion than the saccule [22,29]. In prone and supine postures the utricle is sensitive to vertical acceleration; however, it is also loaded by the superimposed gravitational acceleration. Of the postures to be tested, the left side down position is unique in that

the role of the utricle and saccule in sensing motion along the gravity axis is swapped compared to the erect posture. It is expected that these changes in sensitivity to gravity will inhibit vection since the vestibular apparatus may be particularly tuned for the dynamics of self-motion in upright observers.

Alternatively, an ecological account of vection would suggest that – apart from special situations such as swimming – traveling while supine, prone or lying on one’s side are all unusual (i.e. non-ecological). Therefore, we might expect to find that vection is stronger when the observer is upright as opposed to lying down. Consistent with this ecological account, it has been suggested that the jitter/oscillation advantage for vection may be due to jittering/oscillating optic flow mimicking the bob, sway and lunge common to walking/running [3,25]. Thus, it is possible that the oscillation advantage for vection may disappear when the observer is no longer upright if it is ecological in origin.

2. Method

2.1. Participants

Ten graduate students and staff (Main experiment: 3 males, 7 females; mean age = 30, SD = 8.88; Control experiment: 4 males, 6 females; mean age = 30.5, SD = 8.64) from the York University community participated in this study. All had normal or corrected-to-normal vision and reported no vestibular impairment. Four of the participants had no prior experience with illusions of self-motion in a laboratory setting and underwent several practice sessions to ensure they were comfortable with the task. This ensured that all subjects understood the task and had experienced the sensation of vection. Written informed consent was obtained in accordance with a protocol approved by the York University Research Ethics Board.

2.2. Apparatus

The optic flow displays were generated on an IBM Lenovo T61p laptop with a 15.4 inch TFT display with a resolution of 1280 (horizontal) x 800 (vertical) pixels and refresh rate of 60 Hz. A custom Python program using the open-source libraries Visual Python (VPython) for the visual displays and Pygame for gamepad control was installed on each laptop. Each laptop was attached to a rigid frame to form a workstation that could be

mounted and oriented to accommodate different body postures.

Posture was varied with respect to gravity. For the upright-seated posture, the observer’s head was aligned with the display using the height adjustment of the chair or wood blocks beneath the workstation (see inset in Fig. 1). For the upright-standing posture, subjects requiring height adjustment stood on appropriately sized, stable, wooden blocks. For lying postures, the subject was appropriately positioned so that the head was centered on the screen. A massage table was used for the lying postures and the displays were mounted on steel stands. The “prone” display was mounted below the headrest of the table, the “supine” workstation was mounted above the table, and the “left side down” display at the side of the table. All displays were aligned with the orientation of the head (see Fig. 1).

The viewing distance and visual angle were defined by a circular, black neoprene viewing tube that was fitted to the display. The tube had a length of 0.30 m (observer-to-screen distance) and subtended a visual angle of 39°. A secure fit of the tube prevented light leakage, and a matte interior limited reflections off the surface of the display.

Responses were recorded with a Logitech R Dual Action Gamepad. Observers wore earplugs to mute any environmental noise, which otherwise might have distracted them or provided orientation cues.

2.3. Visual displays

The self-motion displays were 3-D animations (frame rate of 60 Hz) of translation through a field of 600 randomly distributed, stationary, blue spheres (16.72 cd/m²) on a black background (0.64 cd/m²). The spheres had a simulated physical radius of 7.5 cm, and were randomly positioned in space to form a 3-D cloud of spheres that extended 30 m along the depth or visual axis and ± 5 m horizontally and vertically along the motion path. Spheres were not drawn inside a small circular region (radius 5 cm) at the centre of the display, so as to avoid simulated collisions with the observer’s head. Radially expanding or contracting flow was used to simulate smooth self-motion along the naso-occipital axis at 1.33 m/s through this stationary cloud. When simulated horizontal or vertical (with respect to the head) viewpoint oscillation was added to the display, this sinusoidal oscillation had an amplitude of 0.28 m/s peak velocity and a frequency of 2 Hz. When any sphere moved beyond the field of view (off screen) it was redrawn at the same horizontal and vertical coordinates but at the maximum depth represented by the cloud.

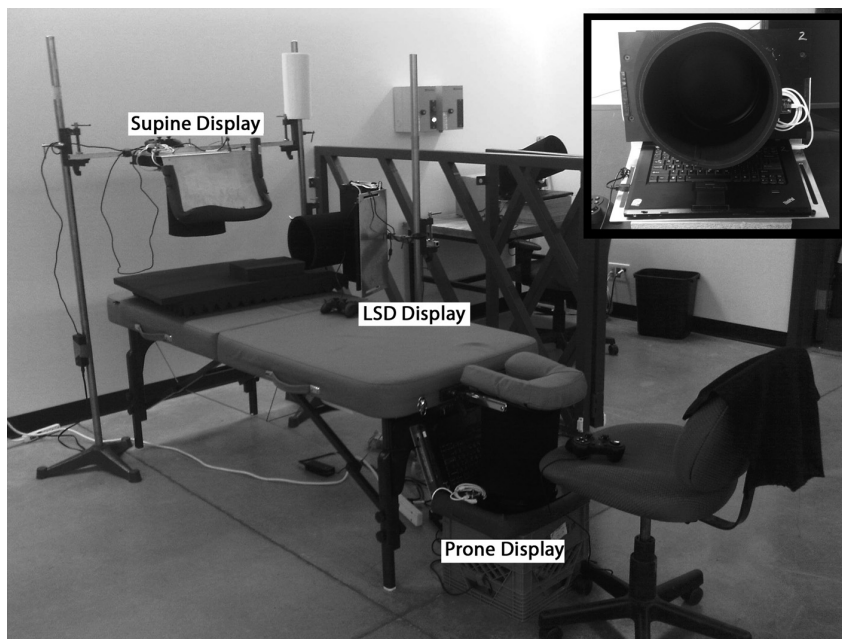


Fig. 1. Photograph of the display and table for the lying down body postures. The inset shows the workstation containing the laptop with shroud. The workstations for prone, supine and left side down postures are mounted to the table and labeled. For the prone position the subject viewed the display through the open face rest of the massage table and, to account for the thickness of the pillow, the shroud was adjusted to maintain viewing distance.

2.4. Design

There were three independent variables. (1) Body posture: upright (seated), and lying supine, prone, and left side down. (2) Optic flow type: smooth motion, smooth motion with added horizontal (x -axis) oscillation, or smooth motion with added vertical (y -axis) oscillation. The direction of oscillation was with respect to the head. (3) Optic flow direction: forward (radial expansion) or backward (radial contraction) self-motion (with respect to the head). Each of the 24 factorial combinations of these conditions was repeated 4 times for a total of 96 trials. The trials were blocked by posture and, within each posture block, blocked again by flow direction. Within each posture-direction block, the 12 trials for all combinations of the remaining variables (flow type and repeat) were pseudo-randomly ordered. The blocks were ordered using a counterbalanced Latin-Square design. In a separate control experiment with a similar design, we compared the seated (folded legs) and standing (extended legs) postures.

For each trial we obtained: 1) an overall vection strength rating, 2) the latency to vection onset, and 3) the total vection duration. Vection dropouts were identified by the release of the vection response button after the initial vection response on a trial (to count as

a dropout, releases were required to last at least 250 ms to filter out accidental releases). We calculated four vection dropout measures for each trial: 1) number of dropouts in a trial, 2) time of the first dropout, 3) mean dropout duration, 4) total dropout duration, and additionally we calculated the proportion of trials with dropouts.

2.5. Procedure

Participants were informed that they would be viewing a series of movies of blue spherical objects in a computer-generated world. They were told to freely look around the display while attending to their feeling of self-motion. For each posture block, the participant was appropriately positioned. For all postures, the head was aligned with the trunk of the body, and the legs were extended in all but the upright posture. After approximately 60 s in that posture, the first display they were shown was a smooth radial flow pattern (expanding or contracting as appropriate for the block), which served as a standard stimulus (which they were told was to be assigned a vection magnitude of 50) to base their responses upon. During all of the subsequent trials in the block, participants pressed one of the shoulder buttons on the gamepad if they experienced vection

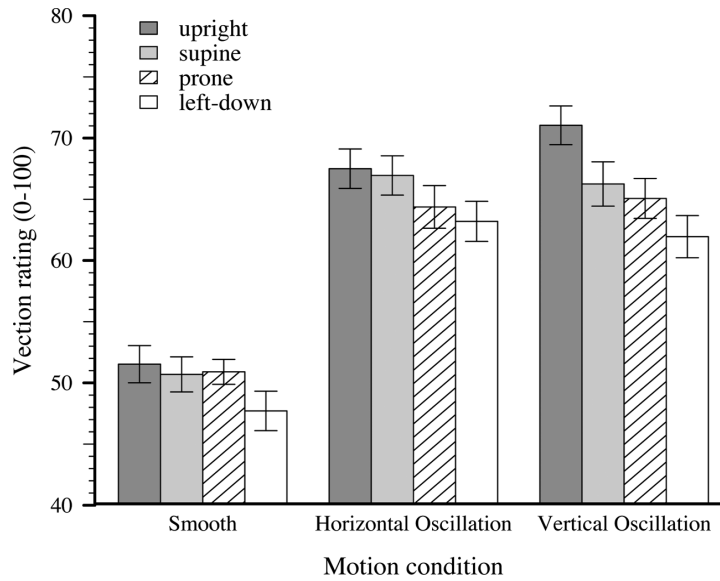


Fig. 2. Mean vection strength rating (± 1 standard error of the mean (SEM), 9 observers). The three motion conditions were smooth radial flow with no oscillation, or with horizontal or vertical oscillation (in display-centric coordinates). Observers based their magnitude estimates on a sample stimulus of smooth radial flow presented before each block of trials. Since the smooth radial flow displays were the same as the sample stimulus, it was expected that the ratings would have an approximate mean rating of 50.

(i.e., feeling of self-motion), and continued to hold this button down until the trial ended or the sense of vection disappeared.

Each experimental trial began with a 3-s inter-stimulus interval with the screen blank followed by the 30-s stimulus display. After each trial, observers rated their vection magnitude relative to the standard stimulus. If the feeling of self-motion was twice as strong (or more) than the standard, they were told to set the rating to 100. If the observer did not feel like they were moving, they were instructed to select a rating of 0. This rating scale had a resolution of 5 unit steps.

After the first block of 12 trials in one direction, observers were presented the standard and a set of 12 trials in the opposite self-motion direction. After blocks in both directions (24 trials) for a given posture, participants were placed into the next body posture and repeated the above procedure.

3. Results and analysis

One subject reported no self-motion (vection rating of 0) for 40% of the trials, particularly in the lying postures, and so was excluded from the dataset. In the remaining subjects, vection was reported for 861 of the 864 trials. Separate statistical models were fitted for each of the response measures.

Linear mixed effects (lme) regression models were fitted with fixed effects (namely body posture, 4 levels; optic flow type, 3 levels; and optic flow direction, 2 levels) and a random effect (to model inter-subject subject variability) using the R package *nlme* (<http://cran.r-project.org/web/packages/nlme/>). The response measures for vection onset, duration, dropout frequency, and mean and total dropout duration, were logarithmically transformed to reduce skew and improve normality. Normality of vection ratings was improved with a Box-Cox transformation. We adopted stepwise selection with Akaike's Information Criterion [1] to select the final models. The final regression model varied for each response measure. For the vection ratings, body posture, optic flow type, and optic flow direction were selected for the model. For vection onset and duration, only optic flow type and body posture were selected. Of the vection dropout measures, we only found significant effects on the number of dropouts in a trial (only optic flow type selected), and the proportion of trials with dropouts (flow type and posture selected in a logistic regression). Although we were interested in whether the oscillation enhancement of vection was modulated by posture, the stepwise selection indicated that there were no significant interactions between optic flow type and body posture. Family-wise error was controlled for with Bonferroni correction and the adjusted p-values are shown for post-hoc analyses.

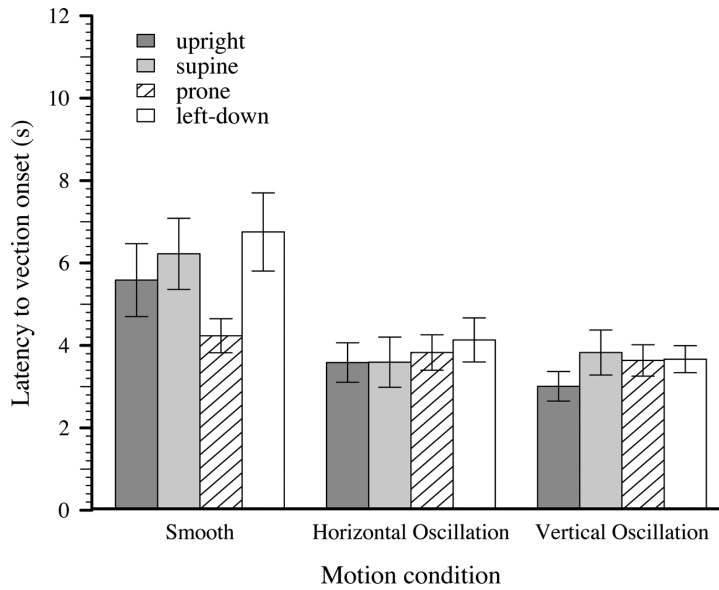


Fig. 3. Mean vection onsets (± 1 SEM, 9 observers). The three motion conditions were smooth radial flow with no oscillation, or with horizontal or vertical oscillation (in display-centric coordinates).

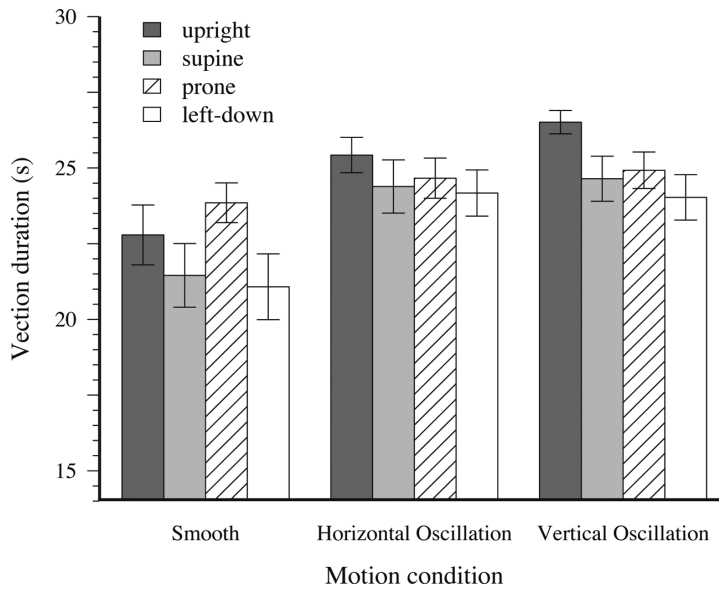


Fig. 4. Mean vection durations (± 1 SEM, 9 observers). The three motion conditions were smooth radial flow with no oscillation, or with horizontal or vertical oscillation (in display-centric coordinates).

The results for vection ratings, onsets, and durations are shown in Figs 2–4. Oscillating radial flow displays produced significantly stronger vection ratings, shorter vection onsets, longer vection durations, and fewer trials with vection dropouts than smooth radial flow (main effect of optic flow for ratings: $F_{2,846} = 197.05, p < 0.0001$; onset: $F_{2,850} = 10.43, p < 0.0001$; duration: $F_{2,850} = 13.47, p < 0.0001$; proportion of trials with

dropouts: $\chi^2_{2,861} = 6.51, p = 0.04$). Horizontal oscillation tended to result in more vection dropouts in a trial ($F_{2,850} = 3.77, p = 0.02$), otherwise, there were no significant differences between mean vertical oscillation and horizontal oscillation data for any response measure (p 's > 0.05).

Body posture also significantly affected vection strength ratings ($F_{3,846} = 10.66, p < 0.0001$), onsets

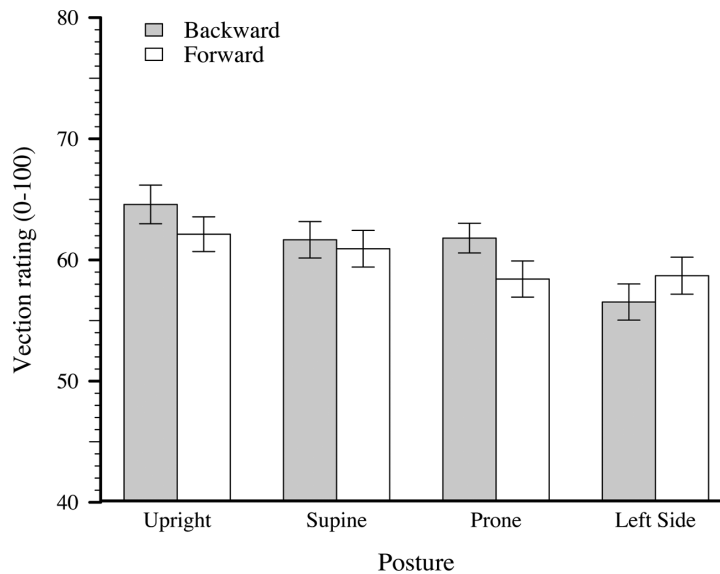


Fig. 5. Mean vection strength rating as a function of body posture and motion direction (± 1 standard error of the mean (SEM), 9 observers).

($F_{3,850} = 3.70, p = 0.0116$), durations ($F_{3,850} = 6.21, p = 0.0004$), the number of vection dropouts in a trial ($F_{3,850} = 8.71, p < 0.0001$), and the proportion of trials with dropouts ($\chi^2_{3,858} = 22.77, p < 0.0001$). Subjects generally experienced less compelling vection when lying down than sitting upright. The left side down condition – which oriented the head so that otolith sensitivity was reversed (utricle rather than saccule sensitive to motion along the gravity vector) – resulted in the weakest sensations of self-motion. Compared to erect posture data, when lying left side down, vection had a smaller magnitude ($z = 5.50, p = 0.003$), took longer to develop ($z = -3.15, p = 0.01$), had a shorter duration ($z = -4.20, p < 0.001$) and produced more trials with dropouts ($z = -4.81, p < 0.0001$). Similarly, vection had smaller magnitudes ($z = 3.48, p = 0.004$) when lying prone versus sitting upright. These effects were weaker for the supine posture and vection magnitude did not significantly differ from upright when supine ($z = 2.15, p = 0.2$). Although no interaction between optic flow type and body posture was selected with AIC, we observed that in the prone posture, subjects viewing smooth radial flow tended to have shorter vection onsets and longer vection durations than when upright.

While there was no significant main effect of optic flow direction (forward or backward), there was a significant interaction between optic flow direction and body posture but only for observers' ratings of vection strength ($F_{3,846} = 2.65, p = 0.048$). This effect was marginally significant and post-hoc analysis did

not provide any clear pattern except a trend that simulated backwards self-motion produced higher average vection ratings than simulated forwards self-motion in the prone posture ($z = -2.09, p = 0.07$). There was no difference between the supine and prone posture in mean vection magnitude for forward self-motion ($z = -1.06, p = 0.9$).

Although there was no interaction between optic flow type (smooth or horizontal/vertical oscillation) and body posture, we observed that prone subjects viewing smooth optic flow had shorter vection onsets and longer vection durations.

A control experiment compared upright seated with the upright standing posture to see if the above findings showing improved vection when upright compared to lying down, could be explained by differences in sensitivity to vection when the legs were extended (lying) compared to bent (seated upright). The results were mixed – compared to sitting, standing produced lower vection ratings ($F_{1,417} = 5.00, p = 0.03$), but significantly longer vection durations ($F_{1,419} = 26.08, p < 0.0001$) and fewer dropouts ($F_{1,419} = 8.56, p = 0.004$), with no difference in latency ($p > 0.05$). Furthermore, the magnitudes of the effects were much smaller than the postural effects reported in the main experiment. Unlike the main experiment, optic flow direction had a significant effect with forward vection displays producing higher vection estimates ($F_{1,417} = 5.19, p = 0.0232$), shorter latencies ($F_{1,422} = 7.52, p = 0.0063$) and slightly longer durations ($F_{1,419} = 3.68, p < 0.06$) compared to backwards vection (generated by radially

contracting flow), but conversely more frequent vection dropouts in a trial ($F_{1,419} = 14.79$, $p = 0.0001$) and a greater proportion of trials with dropouts ($F_{1,427} = 6.05$, $p = 0.01$) than backward vection. Some observers reported awareness of body sway and that vertical oscillation felt more natural while standing.

4. Discussion

We investigated whether vection, and the enhancement of vection by simulated viewpoint oscillation, were affected by head orientation with respect to gravity. Contrary to the predictions of sensory conflict theories, our results demonstrated that oscillating radial displays produced more provocative sensations of self-motion than smooth radial flow displays. Adding viewpoint oscillation to radial optic flow increased vection ratings for all postures. Viewpoint oscillation also increased vection duration and decreased vection latency compared to smooth radial flow for all postures. However, Figs 3 and 4 appear to show that the oscillation advantage was noticeably weaker in terms of the vection time course for the prone posture. It is interesting to note that of all the postures tested, the prone posture produced the shortest vection latency and the longest vection duration when smooth radial flow was shown. These observations may reflect changes in sensitivity due to the orientation of the otolith maculae, which would be angled downward (membrane side down) and toward the resultant force of gravity. Alternatively it may reflect sensitivity to the pressure placed on the front of the body, which is more sensitive than the back of the body [33]. Overall, the finding of an oscillation enhancement is consistent with Palmisano et al. [24,26,28], who first showed jitter and oscillation advantages for vection in upright observers. The persistence of this viewpoint oscillation advantage for vection, across all the postures and orientations tested here, further strengthens the challenge that these effects pose for sensory conflict theories.

In principle, one might expect differences in the vection advantages produced by horizontal and vertical oscillation, since upright observers have differential vestibular sensitivities to head motions along these vectors [22]. However, we found no significant differences in the vection magnitudes, latencies or durations induced by vertical and horizontal oscillation. Vestibular sensitivities to horizontal and vertical head motions should have been reversed in the left side down posture. This posture was also the only condition in which

the horizontal oscillation was orthogonal to the visual direction of self-motion but aligned with the gravity vector. If the perception of self-motion depends more on head orientation with respect to gravity, it might be posited that a swap in otolith sensitivity would result in both different responses to horizontal and vertical viewpoint oscillation, and reduced vection when left side down, compared to the upright posture. While we found lying left side down resulted in the weakest vection there were no differences in sensitivity to horizontal and vertical viewpoint oscillation. It is possible that this role reversal may have simply exceeded the tolerance for sensory conflict.

Consistent with prior studies, the erect posture produced vection with shorter latencies, longer durations, and larger reported magnitudes than most of the lying postures. Recall, that in discussing Kano [17], Tovee [31] suggested that in the supine posture the constant acceleration signal due to gravity should support rather than restrain forward vection (and by logical extension the prone posture should promote backward vection). However, contrary to this proposal we found no difference in the strength of the forward vection induced in supine and prone postures. Although there was a trend that backwards vection was improved when prone, this effect was not significant. Ecologically, there is little reason to expect that a constant acceleration due to gravity should support the perception of constant velocity motion in the same direction. Such an arrangement is not consistent with a real constant velocity translation along the naso-occipital direction, which would be accompanied by a transient otolith signal – a sustained otolith signal that is constant before, during and after the vection stimulus would indicate continuous acceleration which is most likely to be due to gravity. An erect observer should experience a transient change in the orientation of the resultant gravito-inertial vector at the start of motion and the utricle should be better positioned to sense the horizontal component of this change [22].

Our results share some similarities with Kano [17], reinforcing the notion that both gravitational and body centric information play an important role in the perception of self-motion. Based on cross-experimental comparisons, Kano concluded that vection was determined by an interaction between gravitational and body centric information. However, there was not strong support for this proposal from the current results – the upright posture consistently produced more compelling vection, and the effects of optic flow type remained relatively constant. As the vection in our study was

always simulated to be in a naso-occipital direction our results cannot be directly compared to those of Kano. It is however possible to compare our results with those of Tovee [31] who directly compared vection in upright and supine observers. In apparent contradiction to our finding of weakened vection in lying postures (and to a degree, Kano), she found no appreciable difference in the perceived vection magnitude between seated upright and supine subjects. This can be reconciled by noting that, in both the present study and that of Tovee, the reference stimulus was presented prior to each block. Any effect of posture on vection should also apply to the reference stimulus and, therefore, while vection magnitude is a useful measure of the effects of various parameters on vection strength within a block (posture), it does not permit meaningful direct cross-posture comparisons of vection magnitude. On the other hand, Tovee did report that the proportion of trials eliciting a vection response was lower in supine compared to upright postures. This measure does allow for cross posture comparisons and is consistent with our finding that vection dropouts were more frequent, vection latency longer and vection duration shorter in supine (and other lying postures) compared to the seated posture. Given that the method used to estimate magnitude should not allow for establishing inter-posture differences in vection magnitude our finding that it significantly affected the perceived magnitude requires discussion. It is likely that the variation in absolute vection strength influenced vection ratings despite presentation of a standard in each posture, or that subjects simply rated their experience relative to the previous postures

Additionally, changing the orientation of the head with respect to gravity affects vestibular sensitivity and can be used to modulate visual-vestibular conflict. Young et al. [34] reasoned that tilting the head away from upright reduces the sensitivity of the otoliths [9, 10] making them less effective in suppressing visual tilt information. However, if tilting or pitching the head with respect to gravity makes the vestibular signal a less reliable indicator of self-motion then we would have expected increased rather than reduced vection when lying down. Furthermore, it is possible that the weighing of the otolith signals is calibrated for the upright head.

Our pattern of results indicate that orientation with respect to gravity has a significant influence on linear vection. Oman et al. [23] investigated the role of gravity in looming linear vection while space shuttle astronauts were free-floating or restrained in micro-g lev-

els during orbital flight, as well as when placed in the supine and upright posture during pre- and post-flight (one-g) tests. Contrary to our findings, they reported that pre-flight latencies did not differ reliably between supine and upright postures. However, they did find that vection responses were significantly affected by micro-g with both latencies reduced and magnitude estimates increased in free-floating micro-g, compared to 1-g tests. This was consistent with a hypothesis of increased weight on visual cues after adaptation to micro-g conditions. Anchoring the subjects firmly to the floor of the spacelab with constant force springs to partially simulate loading of gravity on the lower limbs reduced vection in two of the three astronaut observers. Similarly, in the present study a control experiment to examine the possible effects of lower body extension showed that standing observers (body extended condition) experienced longer vection durations, but had an overall lower quality of vection than seated observers (reflected by weaker ratings and more vection dropouts) – although, it is possible that postural sway could account for the reduced vection while standing.

Several ecological factors could account for the erect posture and oscillation advantages for vection. For example, we are typically in an upright posture when translating naturally through the world when walking or driving. Also, it may be that oscillation mimicked the head bob, sway or other motion that occurs while walking [21]. The general lack of difference between horizontal and vertical oscillation may simply reflect that the body in motion moves (bobs and sways) along several axes of motion. Oscillation also enhanced vection in lying postures, supporting the notion that visually induced self-motion is dependent on the egocentric direction of motion in the stimulus regardless of posture.

Postural effects are also consistent with an ecological account of vection. Lying postures are less common during self-motion and were found to impair vection. An observation of stronger vection (in terms of onset and duration) for smooth radial flow in the prone posture than in the upright or other lying postures, may simply reflect that naso-occipital self-motion along the gravity axis typically occurs when falling, and it is possible that this association could have elicited a heightened response in our observers particularly for vection latencies [18].

Changing the orientation of the head with respect to gravity was expected to alter the degree/saliency of the sensory conflict, which may explain why vection tended to be stronger in upright postures than in ly-

ing postures. However, sensory conflict cannot explain why the oscillation advantage for vection persisted for both upright and lying postures. Furthermore, contrary to the notion that vection might vary based on the vestibular sensitivity to the type of self-motion being simulated, horizontal and vertical oscillation were both found to improve vection induced by our radial motion displays in a remarkably similar fashion. We conclude that the current postural and oscillation based vection findings are best explained by ecology. According to this view, the upright posture and oscillating flow display both facilitated vection because these are the norm during real self-motions. By contrast, lying postures and smooth optic flows reduced vection because they are unusual/atypical in our experience of self-motion.

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