

PERCEPTION OF SMOOTH AND PERTURBED VECTION IN SHORT-DURATION MICROGRAVITY

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Short title: Vection in microgravity

Abstract

Successful adaptation to the microgravity environment of space and re-adaptation to gravity on earth requires recalibration of visual and vestibular signals. Recently, we have shown that adding simulated viewpoint oscillation to visual self-motion displays produces more compelling vection (despite the expected increase in visual-vestibular conflict experienced by stationary observers). Currently it is unclear what role adaptation to gravity might play in this oscillation based vection advantage. The vection elicited by optic-flow displays simulating either smooth forward motion or forward motion perturbed by viewpoint oscillation was assessed before, during and after microgravity exposure in parabolic flight. During normal 1-g conditions subjects experienced significantly stronger vection for oscillating compared to smooth radial optic flow. The magnitude of this oscillation enhancement was reduced during short-term microgravity exposure, more so for simulated interaural (as opposed to spinal) axis viewpoint oscillation. We also noted a small overall reduction in vection sensitivity post-flight. A supplementary experiment found that 1-g vection responses did not vary significantly across multiple testing sessions. These findings: (i) demonstrate that the oscillation advantage for vection is very stable and repeatable during 1-g conditions, and (ii) imply that adaptation or conditioned responses played a role in the post-flight vection reductions. The effects observed in microgravity are discussed in terms of the ecology of terrestrial locomotion and the nature of movement in microgravity.

Keywords: self-motion, vision, vection, vestibular, sensory conflict, parabolic flight, perception, optic flow

Introduction:

The eyes and vestibular sensors in the inner ears are both known to play important roles in the perception of self-motion (Dichgans and Brandt 1978; Howard 1982). However, since the otolith organs in the inner ear are specialised for detecting high-frequency head accelerations (Benson 1990), the vestibular system cannot distinguish between self-motion at a constant linear velocity and remaining stationary. Fortunately, the visual system is sensitive to both constant velocity self-motions and low-frequency self-accelerations (Berthoz et al. 1979; Berthoz et al. 1975). Thus, vision is able to detect most self-motions based on the optical flow presented to the moving observer (Gibson 1966). In fact, it has long been known that optic flow alone can induce compelling visual illusions of self-motion in physically stationary observers (Mach 1875), known asvection.

Typically the notion of 'sensory conflict' (e.g. Oman 1990; Reason and Brand 1975) is used to explain how the visual and vestibular systems interact to inducevection (Zacharias and Young 1981). These sensory conflict theories predict that: (i) the bestvection will be induced by displays simulating constant velocity linear self-motion (because they should generate only minimal/transient visual-vestibular conflict), and (ii)vection will be degraded by displays simulating large/frequent heading and egospeed changes (because they should generate significant and sustained visual-vestibular conflicts - Palmisano et al. 2011; Zacharias and Young 1981). To test these predictions, Palmisano and colleagues (2000; 2003; 2008) showed stationary observers displays simulating either: (1) constant velocity forward self-motion (smooth radial optic flow), or (2) constant velocity forwards self-motion combined with random horizontal/vertical simulated viewpoint jitter (jittering radial flow), or (3) constant velocity forwards self-motion combined with horizontal/vertical simulated viewpoint oscillation (oscillating radial flow). Contrary to the notion that sensory conflict impairsvection, we demonstrated that both jittering and oscillating radial flow produced visual illusions of self-motion that started sooner and lasted longer (i.e. more compellingvection) than those produced by smooth radial flow.

These jitter and oscillation advantages forvection both pose strong challenges for traditional theories of visual-vestibular interaction. For example, while sensory conflict theories appear able to explain the occurrence and severity of motion sickness symptoms (Palmisano et al. 2007), they clearly do not predict thevection induced by jittering/oscillating patterns of optic flow. One popular explanation for these twovection advantages is that jittering and oscillating radial flow are more ecological than smooth radial optic flow (Palmisano et al. 2011). In fact, smooth radial flow rarely occurs during natural terrestrial self-motions. Walking and running both generate radial optic flow that contains random and oscillatory components (Cutting et al. 1992; Hirasaki et al. 1999). Importantly, we can only partially compensate for the effects of head jitter and oscillation by making eye-movements (Grossman et al. 1989; von Grünau et al. 2007). Thus, it has been proposed that simulated viewpoint jitter/oscillation taps into the visual processes used to perceive self-motion from naturally occurring patterns of optic/retinal flow. Consistent with this ecological interpretation,vection magnitude was found to be larger and latency shorter when viewing video sequences recorded with a handheld camera

(thus containing gait information) compared to smooth motion recorded with the camera on a rolling cart (Bubka and Bonato 2010).

Previous research examining simulated viewpoint jitter and oscillation effects on vection was always conducted on earth under normal gravity conditions. Here we examine the effects of simulated viewpoint oscillation on vection in microgravity for the first time. Successful adaptation to microgravity requires a recalibration of the interaction between the visual and vestibular signals. Weightlessness poses a special challenge for the vestibular system. The otolith organs cease to provide a “down” reference signal when free floating in microgravity (Cheung et al. 1990; Young et al. 1993). Instead, they respond only to linear self-accelerations, such as when one propels oneself by pushing off from any surface of the plane, shuttle or space station. As part of this complex adaptation process, there appears to be an increased dependence on visual information about self-motion and head orientation and a decreased dependence on vestibular information (compared to earth gravity conditions) (Cheung et al. 1990; Young and Shelhamer 1990). Some evidence suggests that the onset of these changes is rapid. For example, research has shown that circular vection is enhanced (relative to preflight 1-g and in-flight 1.8-g conditions) even during very brief exposures to microgravity (Cheung et al. 1990).

Our main experiment examined the vection before, during and after microgravity exposure (short-duration microgravity exposures were generated during parabolic flight). On the one hand, we might predict that the oscillation advantage for vection will be more pronounced during microgravity (compared to both 1-g during straight-and-level flight and 1-g on earth) due to the release of the restraining force of gravity. However, the dynamics of self-motion in microgravity differ greatly from those of terrestrial locomotion (movements can be much smoother than during travel over the ground). Thus, it is also possible that if the terrestrial oscillation advantage for vection is based on oscillating displays being more ecological, then this advantage might be reduced, or even destroyed, during exposure to microgravity.

Methods:

Subjects: A total of eight subjects (6 men, 2 women) participated in the ground studies and parabolic flights. These included the four authors and four naïve observers; two of the subjects had previously experienced parabolic flight. All had normal or corrected to normal visual acuity, stereopsis and colour perception and no reported history of visual, vestibular, or neurological disorders. None were taking medications known to impair neurovestibular or visual function. All subjects gave their prior informed written consent according to research ethics protocols approved by York University and the National Research Council of Canada. These protocols were in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Microgravity Flights: The in-flight experiments were performed on the National Research Council of Canada airborne microgravity facility. A modified Falcon 20 business jet was used to perform high-speed climbs which terminated in parabolic trajectories that approximated the ideal path of a free-falling projectile. During these segments the flight controls were adjusted to achieve precise control over the gravito-

inertial acceleration (GIA or g level), which is the vector sum of gravitational and inertial forces on the subjects' bodies (Figure 1). Each segment resulted in approximately 20 s of greatly reduced g interspersed with periods of approximately 2-g forces while the plane pulled out of the high-speed dive and accelerated into the next parabola (Haber and Haber 1950; Karmali and Shelhamer 2008). We will refer to those periods where the subject has the subjective and sensory experience of weightlessness as 'microgravity' segments although it is important to note that technically they are segments of free-fall and the earth's gravity is still present and effective. On a typical flight the pilots executed three blocks of six of these micro-g segments (Figure 2) with 2-5 minutes between blocks to reorient the aircraft for another block. Within each block, parabolas were executed sequentially one after another (each micro-g phase initiated and followed by 2-g phases).

***** Figure 1 and Figure 2 about here *****

Six flights occurred between April, 12th and 15th, 2010 out of Ottawa International airport. Two flights per day were planned over three days, each targeting 18 parabolic arcs (and associated weightless segments). Turbulence experienced on one day required running one pair of flights over two days necessitating a fourth day. The first flight was terminated early after 15 parabolas due to equipment issues and subject malaise and motion sickness. Each flight carried six subjects and an experimenter who conducted the experiment, as well as the normal microgravity crew of two pilots and an instrumentation engineer. The seated subjects did not have a normal view of the cabin. They were loosely strapped into their seats with seatbelts so that they could free float during the micro-g phases while maintaining a safe position and orientation relative to seats for safety during the 2-g pull up phase (see movie in Online Resource 1).

There are occasionally small longitudinal accelerations of the aircraft during microgravity flights, as well as pitch movements of the aircraft, which are normally near or below sensory thresholds (Karmali and Shelhamer 2008). To control and test for these effects we oriented three of the subject seats facing forward and three facing aft.

On the first flight, data from two subjects was not obtained due to motion sickness and/or equipment failure.

Apparatus and stimuli: Stimuli were generated on a Lenovo T61p laptop and displayed on the laptop's display panel (15.4-inch WUXGA TFT LCD display with 1920 x 1200 resolution). The laptop was powered by an Intel Core Duo processor and driven through the nVidia Quadro FX 570M built-in graphics adapter. The laptop was attached to an aluminum frame and an aperture panel and shroud were mounted with machine screws to the frame, over the display. Also mounted to the frame was an inertial measurement unit (PhidgetSpatial, Phidgets Inc., Calgary, AB) which served as a local 3-axis g monitor for comparison with the accelerometer instrumentation on the aircraft. A Logitech R Dual Action Gamepad was connected through the laptop's USB interface. The aluminum frame supporting this equipment was placed on a block of high-density foam, which was in turn placed on the seated subject's lap and secured there with nylon webbing. The

foam was angled so that it raised the display to eye level and square to the face when the head was put up to the viewing shroud.

The aperture panel was placed over the display and fixed to the frame. This panel was made of black opaque plastic machined with a circular aperture centered on the display subtending 39° and set off from the display surface by 1.5 cm, giving the impression of looking at the display through a circular porthole. Attached to the aperture panel was a cylindrical shroud made of semi-rigid neoprene. The subject put his/her head into the shroud so that it blocked peripheral light and set the viewing distance of 30 cm. The shroud and the aperture defined the field of view and prevented the subject from seeing extraneous stimuli.

The virtual camera generating the graphics was configured to be congruent with the perspective projection of the virtual scene, at the cyclopean eye, onto the 'window' formed by the display screen. The scene consisted of a 3D rendering of 600 blue spheres (diameter 15 cm) moving against a black background. The spheres were distributed throughout a virtual volume of space extending 30 m in depth from the observer, with the constraint that no object laid directly along the simulated path of the observer. Object size, density and velocity varied with the simulated position in depth as in real scenes. As objects disappeared off the edge of the screen, they were replaced at the far end of the space at the same horizontal and vertical 'world' coordinates.

Our visual displays either simulated constant velocity forward self-motion at 1.33 m/s through this virtual world, or the same self-motion combined with simulated viewpoint oscillation. The forward self-motion was simulated by radially expanding optic flow, which contained both motion parallax cues and the looming of individual elements. When present, the simulated viewpoint oscillation was sinusoidal at 2.0 Hz and had a peak velocity of 0.28 m/s along either the spinal or interaural axis. Thus there were three conditions: (1) radial flow, (2) radial flow with horizontal (interaural axis) oscillation and 3) radial flow with vertical (spinal axis) oscillation.

Procedure: In all cases the subject's task was to monitor their sensation of self-motion and rate its strength relative to a standard using magnitude estimation (Stevens 1975). A smooth radial flow pattern simulating 1.33 m/s motion through the virtual environment was presented during level flight. Subjects were told to: (i) assign this standard stimulus a magnitude of '50' (the modulus), and (ii) make estimates of vection strength proportionally relative to this modulus. For instance if they experienced vection that was twice as strong as the standard they were to report 100, if vection was only half as strong they were to report 25.

On a given flight session, four seated subjects performed vection estimations during the microgravity phases. Each experimental session was divided into four blocks. At the beginning of each block, subjects were presented with the standard stimulus during level flight (1-g) and told to assign the vection it elicited a value of 50 (While there was an option to indicate that they did not experience vection, subjects always reported experiencing vection on these standard stimulus trials). On subsequent test trials, subjects

reported the presence (or absence) of vection by pressing and holding (or releasing) one of the front buttons on the gamepad. The state of the button was recorded on each frame of the simulation and used to calculate the latency to vection from stimulus onset. Following each test trial, a screen appeared and the subject used button presses to enter their magnitude estimate. This was displayed graphically on both a bar indicator and as a number. The bar indicator was initialized to 50 and could be incremented or decremented from there in steps of 5 units over the range 0-100.

In the first block, subjects performed 12 test trials (3 motion types times four repeats) in random order during level flight to provide an in-flight 1-g baseline. The subsequent three blocks corresponded to the three sets of six parabolas. In these blocks, six trials were run, one per parabola with two repeats of each motion condition in random order. To synchronize with the parabola, subjects were given a verbal cue from the experimenter for the start of the trial. Each trial was 20 s and subjects monitored vection continuously throughout the micro-g phase. The 20-s trial ended and the magnitude estimate was entered during the transition out of this phase.

To provide additional 1-g baselines on earth, two sessions of preflight and two sessions of post-flight baseline data collection were performed for each task in the laboratory (using the same apparatus and timing as in parabolic flight). These tests were separated by at least three days from the microgravity flights.

Analysis: The constraints of parabolic flight preclude large numbers of subjects and trials. To allow for testing the experimental hypotheses while maintaining statistical power analyses were restricted to tests of contrasts associated with explicitly planned comparisons (with corrections made for multiple comparisons). These comparisons examined whether: (i) overall vection was modulated by the g-level; (ii) oscillation effects on vection differed in micro-g and 1-g; and (iii) the effects of g-level were more pronounced for vertical compared to horizontal oscillation.

Control for longitudinal effects: A supplementary study was performed on earth to evaluate the stability of the vection response measures over repeated testing. This study included stimuli comparable to those used in the main experiment and results for these conditions are reported here. Eight members of the York University community (4 men and 4 women, mean age 31 ± 10.2 SD) participated in the experiment. Stimuli and apparatus were as described in the main experiment except that: (i) a modified viewing shroud set a viewing distance of 41.6 cm with an aperture of 40° horizontally and 25° vertically, and (ii) stimuli were presented for 30 s rather than 20 s since we were not constrained by the duration of a parabolic segment. Participants were required to complete a 25-minute test session every 3 weeks over 6 months for a total of 8 sessions.

Results:

Linear mixed effects (lme) regression models were fitted for both the vection strength rating and vection onset latency measures with g-state, optic flow condition and their interaction as predictors and the subject treated as a random effect in a repeated-measures analysis. Similar models were used to compare preflight, post-flight and in-

flight 1-g data. The vection onset data were logarithmically transformed to reduce heteroscedasticity and improve the model fit. Corrections for multiple comparisons were made and adjusted p-values are shown for the results of the planned comparisons.

Main Experiment (preflight 1-g, in-flight 1-g and 0-g, post-flight 1-g)

Subjects reported reliable vection during preflight and post-flight 1-g baseline testing conditions. During the in-flight testing, vection was reported on all but four trials. All four non-vection trials were from the same observer during smooth radial flow conditions (three were occurred during level flight and one during micro-g).

A.) Vection Strength Rating Data

Preflight and Post-Flight. Consistent with previous research, adding horizontal or vertical simulated viewpoint oscillation to the radial flow displays increased reported vection strength ratings compared to smooth radial flow conditions (mean vection enhancement for interaural-axis oscillation = 13.15 ± 0.926 (mean \pm standard error), $p < 0.001$; enhancement for spinal-axis oscillation = 17.88 ± 0.925 , $p < 0.001$) with the spinal-axis oscillation effect being larger than the interaural-axis ($p < 0.001$). There was a small but significant decline in vection strength ratings from the preflight baseline to the post-flight baseline (mean decrease in ratings = 3.68 ± 0.764 , $p < 0.001$). This post-flight vection impairment was not correlated with time elapsed after the flights and appeared to be mainly driven by the effects in two subjects. Interestingly, these two subjects were the most affected by motion sickness and the only subjects who needed to discontinue the experiment, due to malaise, on their first flight. There was no significant difference in the oscillation enhancement effects between preflight and post-flight ($p = 0.95$ and $p = 0.80$ for interaural-axis and spinal-axis, respectively).

In-Flight. The data obtained during level flight were consistent with the preflight findings. There was no significant difference between preflight and in-flight 1-g vection strength ratings ($p = 0.910$). Figure 3 shows the mean vection strength ratings as a function of g-level and optic-flow condition. The oscillation based vection advantage found during preflight was also found in both level flight and in micro-g conditions (interaural-axis oscillation rating enhancement = 10.7 ± 1.17 (mean \pm standard error), $p < 0.001$; spinal-axis oscillation rating enhancement = 15.9 ± 1.18 , $p < 0.001$). However, vection strength ratings were lower in micro-g conditions than in level flight (average reduction across motion conditions and subjects = 4.82 ± 0.96 , $p < 0.001$). This reduction in vection strength ratings was more pronounced for oscillating compared to smooth radial flow conditions and was particularly true for the interaural-axis oscillation (mean reduction = 8.6 ± 2.34 , $p = 0.002$) with only a non-significant trend toward for the spinal-axis oscillation (mean reduction = 6.0 ± 2.36 , $p = 0.066$). This difference in g-level effect was indicated by a significant difference between the interaural-axis and spinal-axis oscillation vection strength ratings under micro-g conditions (mean difference = 6.5 ± 1.56 , $p < 0.001$) even though there was no significant difference at 1-g (mean difference = 3.9 ± 1.77 , $p = 0.180$).

***** Figure 3 about here *****

B.) Vection Latency Data

Figure 4 shows the mean onset latency (time between the start of the trial and the vection button being pressed) as a function of g-level and optic-flow condition. The small but significant reduction in vection latency with the addition of oscillation found on earth was also found in both level flight and in micro-g conditions (interaural-axis oscillation latency reduction = 1.84 ± 0.250 s, $p < 0.001$; spinal-axis oscillation latency reduction = 1.80 ± 0.250 s, $p < 0.001$). Reduction in g-level from normal 1-g to micro-g had a significantly different effect for spinal-axis oscillation and radial flow with reduction in g-level increasing latency in the former case and reducing it in the latter ($p = 0.005$).

***** Figure 4 about here *****

Longitudinal Control Study

For the longitudinal control study, repeated-measures ANOVA showed no significant effect of session for rating ($F(7,1) = 2.952$, $p = 0.421$) or onset latency of vection ($F(7,1) = 0.332$, $p = 0.936$). Online Resource 2 shows the time course of the average vection ratings across multiple testing sessions. Individual data did not show any session effects. Trends for other conditions were similarly flat across sessions. As in the main experiment, an oscillation effect was found as vection ratings with interaural-axis and spinal-axis oscillation were significantly larger than with the radial flow pattern trials across all subjects.

Discussion:

Here we report that the well-known oscillation based enhancement of vection is diminished by short-term exposure to microgravity¹. When deprived of the normally omnipresent down signal during micro-g phases of parabolic flights, subjects reported less vection from oscillating stimuli than in level flight. Previous research has suggested an effect of microgravity on spinal axis self-motion. Specifically, Kornilova et al (Kornilova et al. 1995) reported vection asymmetry and vection inversion for vertical linear vection in a cosmonaut during the initial few days of microgravity flight. We had predicted that when freed from the constraints of gravity, subjects might experience increased vection for spinal but not interaural oscillation (because the force of gravity normal acts along the spinal axis in erect observers). According to this notion, the lack of the normal gravity signal (vertical linear acceleration) would indicate possible vertical self-motion, which in turn should support vection along the spinal axis. However, we found no such preferential increase in vection responses for vertical oscillation. On the contrary, microgravity conditions degraded vection for oscillating self-motion displays but not for smooth self-motion displays. One possible explanation is that this degradation

¹ It is important to acknowledge that the micro-g phases were interleaved with salient hyper-g phases. Our protocol did not allow for estimation of the separate effects of the hyper-g phase. While the responses we measured were obtained during the micro-g phase, it is possible that exposure to the hyper-g state might have had effects that persisted through the micro-g phase.

arose because the unchanging head acceleration input signals experienced in microgravity were inconsistent with the display oscillation.

Another possible interpretation of the reduction in the oscillation effect under microgravity involves the reliability of vestibular cues in micro-g and 1-g environments. In micro-g, even though vestibular acceleration along the spinal axis does not signal the direction of gravity, it is still interpreted as self-motion (Young et al. 1984). In this situation, the ‘missing’ vestibular signals concomitant with oscillation could not result from a tilt response masking the linear acceleration. This reduced ambiguity should, in turn, increase sensory conflict as the unchanging otolith signal unambiguously signals a lack of head motion. According to sensory conflict theory (Young et al. 1984), increased conflict should promote the reliability of the conflicting vestibular signal and thus might be expected to reducevection. Supporting the idea that sensory re-interpretation occurred in the present study, two subjects reported feeling prone or supine (rather than erect) during at least some micro-g phases. This phenomena has been reported forvection before, particularly when the visual but not vestibular signal indicates tilt with respect to gravity, and is presumably a sensory re-interpretation of the lack of vestibular ‘down’ or ‘tilt’ signal (Allison et al. 1999; Cheung et al. 1990; Young and Shelhamer 1990). Under this interpretation, microgravity would have to differentially affect the reliability of horizontal and vertical vestibular signals, in order to explain our findings that the interaural oscillation effect was diminished more than the spinal-axis oscillation effect. The sensitivity of the utricle is usually considered to be higher than that of the saccule (Benson et al. 1986; MacNeilage et al. 2010; Rosenhall 1972; although this does not seem to be due to differences in peripheral afferent signal-to-noise ratio, see Yu et al. 2012) and the saccule is also loaded by the superimposed gravitational acceleration in the erect subject, factors that may explain why erect humans appear relatively insensitive to vertical compared to lateral motion (Malcolm and Melvill Jones 1974). Another possibility is that the reliability difference may reflect differences in the sensitivity to normal gravitational signals. When the head is tilted, the gravitational inertial acceleration can be decomposed into horizontal and vertical components with respect to the head. The magnitude of the horizontal component varies with the sine of the tilt angle (and thus is linearly sensitive to tilt for modest tilt angles) while the vertical component varies with the cosine (and thus is little affected by tilt at small angles). In either of these scenarios the expected vestibular signal corresponding to the vertical oscillation might remain less reliable or more ambiguous even with the release of gravity.

As noted in the introduction, one popular explanation for the terrestrial oscillation based advantage forvection is that oscillating radial flow displays are more ecological, and as a result visual self-motion perception is tuned for these types of optic flows (Guterman et al. in press; Palmisano et al. 2011). Such arguments apply only to locomotion in earth’s normal gravity field. The dynamics of self-motion in microgravity differ greatly from those of terrestrial locomotion (movements can be much smoother than during travel over the ground). Similarly, in free-fall conditions, the otoliths no longer signal the direction of gravity but instead respond only to linear self-accelerations. It seems unlikely that our subjects could have adapted to either their new ecology of movement or the reduced ambiguity of their vestibular signals given they had limited microgravity exposure (20 s

intervals) and they did not actively move. However, as discussed in the introduction, some changes in visual-vestibular interaction can be observed even during very brief exposures to microgravity. For example (Cheung et al. 1990) found a rapid increase in dependence on vision during rollvection when entering the micro-g phase of parabolic flight. However, in this earlier study, the increased visual dependence likely arose directly from the removal of conflicting vestibular tilt signals rather than adaptation to micro-g per se. It is possible that in the current study, micro-g exposure removed the ecological validity of the oscillating flow and hence thevection advantage without requiring adaptation to the new ecology. However, it is unclear how to explain the horizontal vertical oscillation differences under micro-g based on such an explanation.

The post-flight decrease invection responses could reflect persistent perceptual adaptation to the microgravity and/or hypergravity states. Such adaptation persisted for at least several days after the parabolic flights, which would indicate a remarkably strong adaptation to brief microgravity exposures. Furthermore, unlike the micro-g conditions the effects onvection did not appear to be selective for oscillating versus smooth optic flow conditions. These features of the post-flight decrease suggest that perhaps conditioned responses were a factor. Conditioned responses have often been reported to develop to environments or stimuli associated with motion sickness and other nauseogenic stimuli (Carey and Burish 1988; Klosterhalfen et al. 2005). Context specific adaptation to vestibular stimuli has been demonstrated in the oculomotor system (Shelhamer and Zee 2003). Similar context dependent modification ofvection responses may be involved in the post-flight response changes. Interestingly, the post-flight decrease invection only appeared to occur in the subjects that experienced the most motion sickness and emesis during the flights (i.e. that needed to discontinue at least one session due to frank sickness with emesis and a score of >16 on the Graybiel et al. (1968) motion sickness scale). It is possible that the subjects associated both the reducedvection experienced during microgravity and the nausea with the experiment through classical conditioning. At least one of the subjects anecdotally reported that preparing for the post-flight experiments in the apparatus produced (slight) anticipatory nausea after the flights. If the reducedvection was also learned as a conditioned response it could explain the post-flight reductions in susceptible observers².

If these changes reflect immediate responses and short-term adaptive behaviour to microgravity then the results may have importance for manned spaceflight. Adaptation to the visual-vestibular challenges of microgravity is important for astronaut performance and well being. In addition to disturbances to self-motion perception and disorientation, 70-80% of astronauts experience space motion sickness when in orbit (Harm and Schlegel, 2002). The demands of visual-vestibular recalibration in microgravity are considered a likely cause of this space motion sickness (Oman 1998; Young 1993). Sensory recalibration or compensation has been previously reported for forward self-

² Importantly,vection ratings for smooth flow were not altered in micro-g. This implies that despite some subjects feeling unwell, their ability to perform the task reliably did not seem to be affected.

motion of the kind used in the present study (Harris et al. 1981; Wallach and Flaherty 1975). Analogously, Brandt and colleagues (Brandt et al. 1974) have found that circular vection responses habituate and that long periods of adaptation can produce inverted vection percepts and lead to negative vection aftereffects. Harris and colleagues found that motion aftereffects were larger following inconsistent compared to consistent visual and vestibular self-motion stimuli and attributed the difference to sensory recalibration in the former case. Recalibration requires adapting to the novel inertial dynamics of space travel – lack of constant gravity and movements that are typically much smoother than during travel over the ground. While visual self-motion perception may be tuned to the jittering/oscillating optic flow typical of earthly movements, astronauts appear to rapidly adapt to the smoother visual motion typical of movements in space over the course of several days. We have demonstrated that even during brief exposures to microgravity there seems to be a modulation of this tuning. It remains to be seen how the visual-vestibular system adapts to smooth and perturbed visual motion during extended exposure to microgravity.

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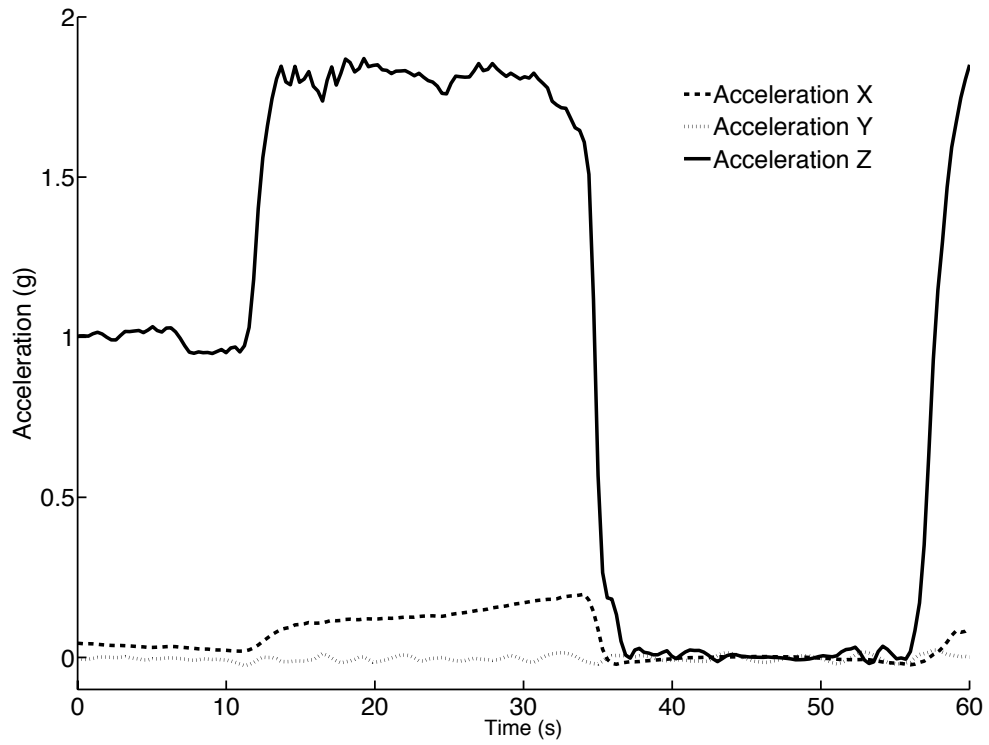


Figure 1 – Example parabolic flight segment acceleration levels. The curves plot the acceleration in the aircraft coordinate system along the longitudinal (Acceleration X), lateral (Acceleration Y) and vertical (Acceleration Z) axes.

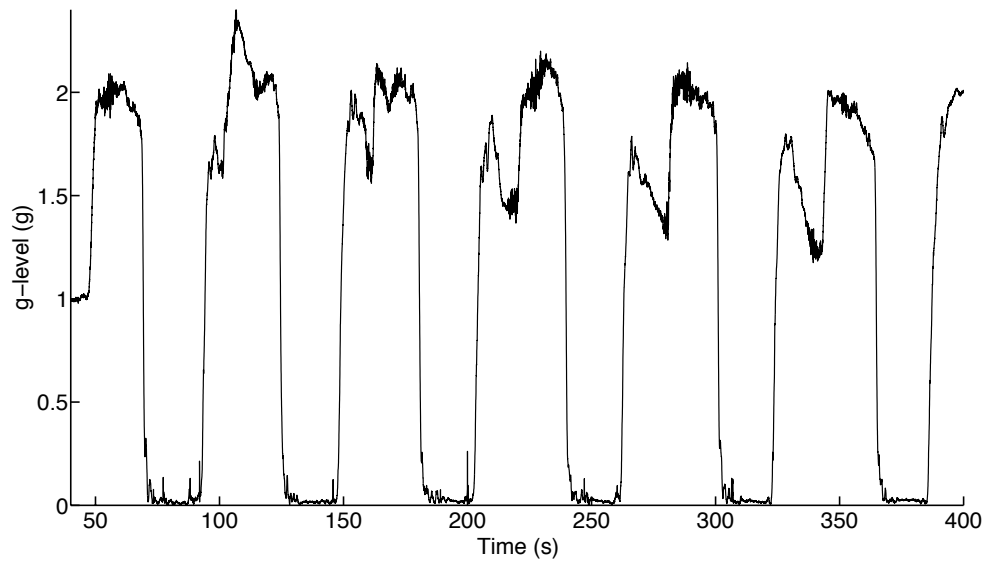


Figure 2 – Variation in g-level during the parabolic flight trajectory. Microgravity data collection took place during the peak of the parabola when g-level (GIA) was nearly zero (troughs in the g-level curve).

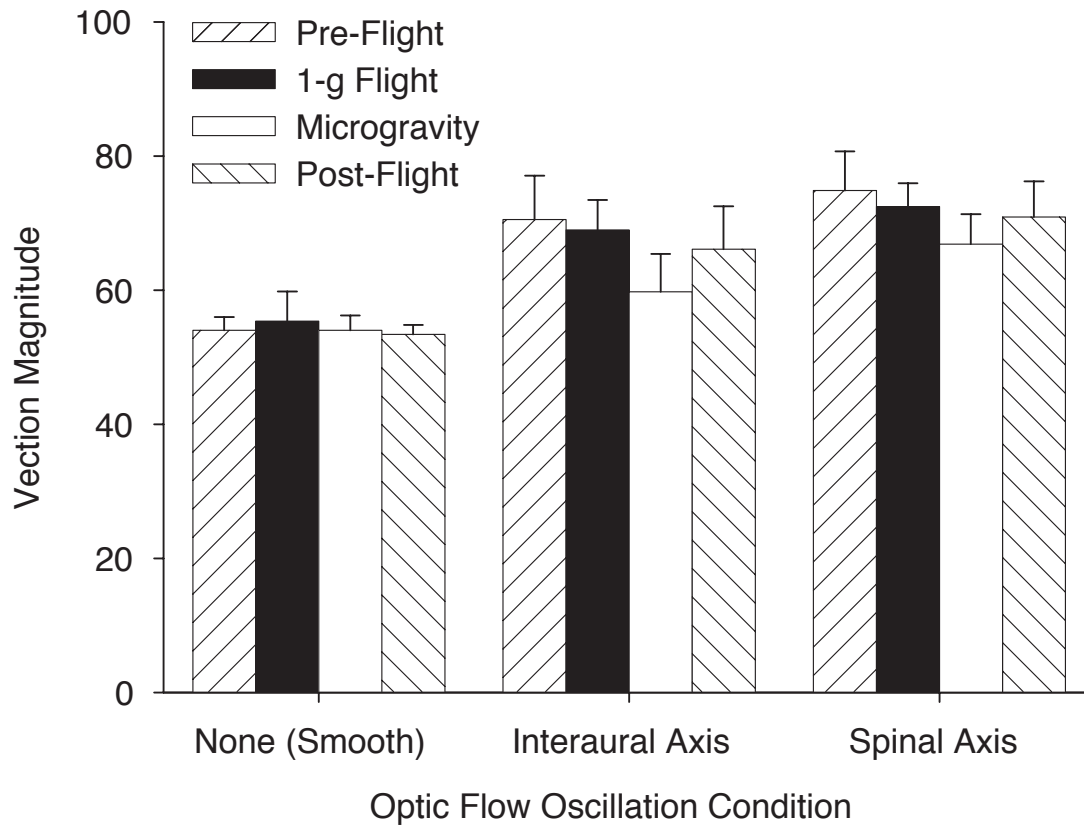


Figure 3- Vection ratings (mean \pm s.e.m.) as a function of g-level and optic flow condition before, during and following parabolic flights.

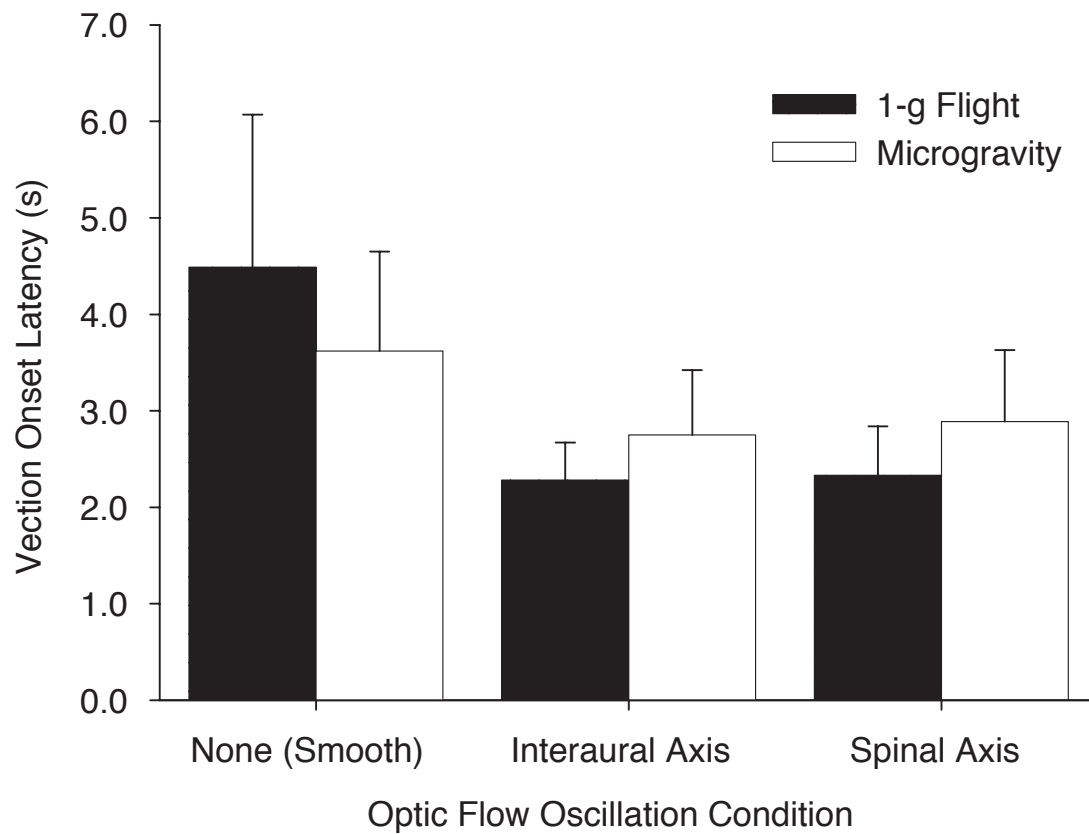
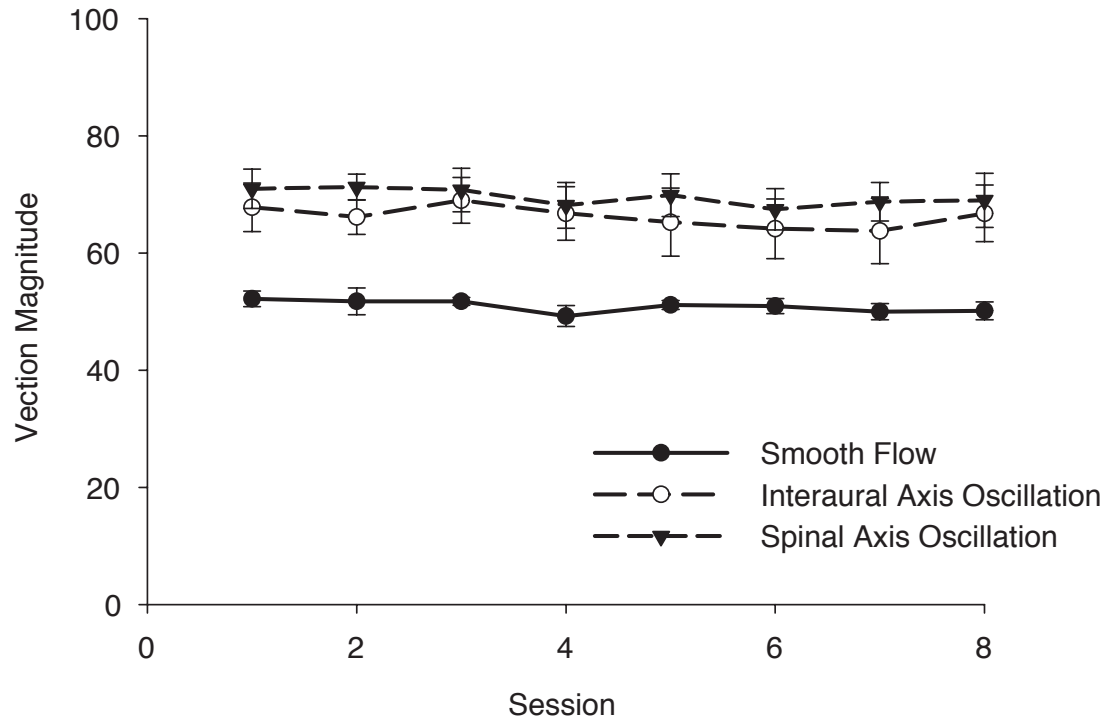


Figure 4- Vection onset latency as a function of g-level and optic flow condition during parabolic flights.



Online Resource 2: Average vection ratings (\pm s.e.m.) across repeated testing sessions for 8 subjects.