

Higher-order cognitive processes moderate body tilt effects in vection

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Abstract

Changing head orientation with respect to gravity changes the dynamic sensitivity of the otoliths to linear accelerations (gravitational and inertial). We explored whether varying head orientation and optic flow direction relative to gravity affects the perception of visually induced self-motion (vection) in two experiments. We confirmed that vertical optic flow produces stronger vection than horizontal optic flow in upright observers. We hypothesized that if this was due to aligning the simulated self-motion with gravity, then interaural (as opposed to spinal) axis motion while lying on the side would provide a similar vection advantage. Alternatively, motion along the spinal axis could enhance vection regardless of head orientation relative to gravity. Finally, we hypothesized that observer expectation and experience with upright locomotion would favour horizontal vection, especially when in upright posture.

In the first experiment, observers stood and lay supine, prone, left and right side down, while viewing a translating random dot pattern that simulated observer motion along the spinal or interaural axis. Vection magnitude estimates, onset, and duration were recorded. Aligning the optic flow direction with gravity enhanced vection in side-lying observers as reflected by either a bias for interaural rather than spinal flow or by an elimination/reduction of the spinal advantage compared to upright. However, when overlapping these signals was not possible—as in the supine and prone

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posture—spinal axis motion enhanced vection. Furthermore, perceived scene structure varied with head orientation (e.g., dots were seen as floating bubbles in some conditions).

To examine the influence of scene structure, in the second experiment we compared vection during simulated motion with respect to two environments: a rigid pipe structure that looked like a complex arrangement of plumbing pipes, and a field of dots. Interestingly, vertical optic flow with the pipes stimulus produced a similar experience to that of riding an elevator and tended to enhance vection.

Overall, we found that vection depended on the direction of both the head orientation and visual motion relative to gravity, but was also influenced by the perceived scene context. These findings suggest that, in addition to head tilt relative to gravity, that higher-order cognitive processes play a key part in the perception of self-motion.

Keywords: vection, tilt, self-motion, gravity, scene structure, cognitive effects

1. Introduction

2 The act of moving in an environment generates a pattern of optical flow
3 that can indicate the direction and magnitude of self-motion. As well, a
4 stationary observer viewing a similar flow pattern can experience compelling
5 illusions of self-motion. This illusory percept of self-motion has been termed
6 “vection” [1]. A common experience of vection is the “train illusion”, in
7 which a passenger in a stationary train observes another train moving on an
8 adjacent track and experiences a strong sense of self-motion in a direction
9 opposite to the moving train. Determining self-motion depends on feedback
10 from multiple sensory cues, including visual, vestibular, proprioceptive, tac-
11 tile [2], and interoceptive [3, 4]. Of these self-motion senses, vision and the
12 vestibular system play dominant roles.

13 In natural surroundings, it would be unusual for a stationary observer
14 to see a large portion of their surroundings move [5]—i.e, to be presented
15 with global optic flow. Accordingly, when a large segment of our visible
16 surroundings are moving, we tend to attribute this motion to self-motion [6].

17 The vestibular system also signals self-motion. The otolith organs and
18 semicircular canals sense linear and angular accelerations of the head, re-
19 spectively [7]. In the case of an upright and translating observer, vertical

20 self-translation is predominantly sensed by the saccules and horizontal trans-
21 lation by the utricles— though both are sensitive to motion in all directions
22 [8, 9, 10]. Additionally, the vestibular organs are mechanical inertial sensors,
23 and therefore cannot distinguish between being stationary and constant ve-
24 locity motion [11, 12, 13].

25 Together, the visual and vestibular systems inform us about self-motion,
26 and the direction of gravity—a constantly imposed acceleration [11, 31]. The
27 visual system is able to estimate the gravitational “up/down” by static and
28 dynamic orientation cues, which are grounded in assumptions about the phys-
29 ical world—e.g., a tree trunk is rooted in the ground, and a tossed object
30 falls toward the earth. Likewise, the otolith organs detect linear acceleration
31 due to gravity, and hence signal the direction of gravity.

32 In most natural situations the visual and vestibular self-motion signals
33 provide consistent information about the direction and magnitude of self-
34 motion. Invection stimuli, the visual system signals motion while the vestibular
35 system signals no motion and the occurrence, magnitude and time course
36 of thevection percept are generally believed to reflect the resolution of this
37 intersensory conflict (e.g. [14]). This intersensory integration is likely to
38 depend on (1) the relative reliability of the senses, (2) the ambiguity of
39 the signals, and (3) the ecological relevance and likelihood of the motion
40 [6, 15, 16, 14, 17], all of which vary with the orientation of the stimuli with
41 respect to gravity.

42 *1.1. Differences in signal reliability: head-centric differences in otolith sen-* 43 *sitivity.*

44 Many theories of multi-sensory integration propose that signals are com-
45 bined according to their reliability. For example, maximum likelihood esti-
46 mation combining commensurable and unbiased signals predicts weighting of
47 cues proportional to their precision [18, 19]. Similarly, Bayesian approaches
48 model the precision of sensory signals in making a posteriori estimates and
49 effective robust estimators need to discount unreliable signals [20, 21]. In
50 a cue-conflict situation such asvection, the strength of the percept should
51 depend on the relative reliability/sensitivity of the visual and otolithic linear
52 self-motion signals.

53 While the otoliths are each sensitive to head-centric linear acceleration
54 stimuli in many directions, the anatomy of their respective maculae make
55 the saccule more sensitive to vertical acceleration and the utricle to hori-
56 zontal acceleration. Physiological, anatomical and psychophysical evidence

57 also suggests that the human utricle is more sensitive than the saccule [22,
58 23, 24, 25, 26]. Some of the earlier studies of relative sensitivity only ma-
59 nipulated posture or used a single plane of motion and thus confounded
60 head-centric and gravitational directions. MacNeilage et al. [25] systemati-
61 cally varied posture and motion direction and confirmed that sensitivity for
62 motion detection and heading discrimination was lower for up-down (spinal
63 axis) compared to left-right (interaural) motions. The direction of motion
64 with respect to gravity did not affect sensitivity (although observers were
65 generally less sensitive in recumbent posture).

66 Due to the head-centric nature of this directional vestibular sensitivity,
67 during vection stimuli the conflicting vestibular signal indicating no motion
68 should be more reliable for horizontal than vertical motion [27, 28]. In turn,
69 based on this mechanism, vision should be weighted more heavily and vection
70 should be stronger (larger magnitude, faster onset and longer duration) for
71 spinal motion than interaural motion regardless of the orientation of the
72 head¹.

73 *1.2. Ambiguity of the signals in our gravitational context*

74 Accurately estimating self motion requires determining which components
75 of the visual and vestibular signals indicate self motion. The distinction
76 between object and self motion is an inherent ambiguity in the visual signal
77 that was discussed above. The otolithic self-motion is also ambiguous as
78 the otoliths detect all forms of self-acceleration including gravity. Thus the
79 self-motion signal must be estimated from the ‘gravito-inertial acceleration
80 (GIA) vector’ —the sum of the acceleration vectors due to self-motion and
81 gravity [32]. Conceptually, this extraction could be done by subtracting the
82 gravity (1-g) vector from the GIA.

83 To perform such a vectorial subtraction the direction and magnitude of
84 the 1-g gravitation signal need to be known. The instantaneous vestibular
85 estimate of the GIA is ambiguous as the signal can result from various com-

¹Note that, as this discussion is based on relative cue reliability, similar considerations would hold if sensitivity to visual motion differed between vertical (spinally-directed) and horizontal (interaurally-directed) optic flow. Vertical and horizontal visual motion sensitivity have generally been reported as similar (e.g., [29]). Small anisotropies favouring horizontal motion have been reported for the visually-induced optokinetic response to optic flow [30] but, to be consistent with the upright vection data, vertical visual motion should be favoured.

86 binations of a 1-g signal orientation and motion directions and amplitudes.
87 The problem is simplified if the head orientation relative to gravity can be
88 determined (the perceptual upright). Evidence suggests that the perceptual
89 upright is formed by combining visual, vestibular and other sensory signals
90 to orientation with assumptions or priors such as the expectation that the
91 head is generally upright [31, 32, 33].

92 When the gravity and self-motion vectors are parallel, the resulting gravito-
93 inertial vector only changes in magnitude, but when self-acceleration is or-
94 thogonal to gravity it affects the direction and the magnitude of the gravito-
95 inertial vector. Thus, if one moves vertically an earth-vertical acceleration
96 signal would be added in the same direction as a larger gravitational ac-
97 celeration [28]. There is evidence that human vestibular discrimination of
98 self-translation obeys [35] or approximates [36] Weber’s law and thus should
99 become less sensitive when loaded by gravity. This would predict stronger
100 vection in the direction of gravity, regardless of posture. Evidence of gravi-
101 tational effects on self-motion were reported by [34], who found asymmetries
102 and inversions in vertical linear vection when observers were in microgravity.

103 *1.3. Ecological considerations.*

104 Our experience with moving through a constant 1-g environment has
105 likely shaped the evolution and development of our our perceptual systems.
106 The saccular and utricular signal processing have evolved and developed to
107 deal with a predominantly erect posture and thus a superimposed gravity
108 signal and tilt sensitivity respectively, If the peripheral and central vestibular
109 system has evolved to be optimized (tuned) for upright posture in 1-g
110 environment then we might expect it to be less effective in other postures
111 (e.g. as found in [25]) and, in turn, vection should be generally less restrained
112 and thus stronger in lying compared to erect posture.

113 Our environment also determines the likelihood of the type of movements
114 we make. Typically the sustained movements we make are mainly perpen-
115 dicular to gravity except when climbing or falling. Thus extended periods
116 of horizontal motion are more ecologically relevant than vertical motion. As
117 discussed above, vestibular, visual and cognitive factors all influence the per-
118 ception of upright. If directional biases in vection depend on perceived ori-
119 entation with respect to gravity then we may find they vary with the relative
120 saliency of these factors in the stimulus.

121 Similarly, apart from special situations such as swimming, traveling while
122 supine, prone or lying on one’s side are all unusual (i.e. non-ecological).

123 Therefore, we might expect that vection will be stronger when the observer
124 is upright as opposed to lying down.

125 *1.4. The role of posture with respect to gravity on linear vection*

126 The role of posture with respect to gravity on linear vection sensitivity has
127 received relatively little experimental attention. Kano [37] reported that vec-
128 tion onset latencies were shorter for simulated up-down (spinal) motion than
129 for forward/backward (naso-occipital) motion in upright observers (a finding
130 replicated in [27]). However, in another experiment using supine observers,
131 vection latency was shorter when the self-motion was perceived to be either
132 towards the feet or gravitationally downward towards the back (compared
133 to when self-motion was perceived to be toward the head or gravitationally
134 upward towards the front). In contrast, while Guterman et al. [28] con-
135 firmed postural modulation of vection using a within-subjects design, they
136 found that the effects of optic flow type direction (expanding versus con-
137 tracting along the naso-occipital direction) remained relatively constant in
138 various postures. In all these previous experiments, it is possible that any
139 directional effects reflect the difference between the looming flow typical of
140 forward/backward motion compared to the lamellar flow produced by ver-
141 tical motion. To address this issue we note that lamellar flow can also be
142 produced by lateral self motion, which could be compared more directly with
143 vertical flow. To our knowledge, no one has studied the effects of posture on
144 vection from lamellar flow either aligned with or orthogonal to gravity (but
145 see [39] for experiments measuring heading perception in the coronal plane
146 in various postures).

147 The factors outlined in sections 1.1–1.3 suggest that vection should de-
148 pend on the direction of motion with respect to the head and/or gravity. By
149 varying motion direction we can make the direction of simulated self-motion
150 congruent with or orthogonal to the gravity vector. By also varying posture
151 we can dissociate the head centric and gravity centric directions of vection.
152 Table 1 shows the relationship among postures, gravity, motion direction,
153 and principal otolith sensitivity (see Figure 1 for an illustration). Left-side
154 and right-side down postures (roll tilt 90°) are interesting in that the roles of
155 the utricle and saccule in sensing motion along the gravity axis are swapped
156 compared to the erect posture. Conversely, in supine/prone posture, both
157 the interaural and spinal axes are orthogonal to gravity. Several compet-
158 ing predictions can be formed about the relative potency of these stimuli

Table 1: A summary of the relationship between body-centric and gravito-centric frames of reference in different postures. Body axis convention was chosen to follow the computer graphics camera-space convention where z is in the view direction (thus the x-axis is interaural or left-right, y is spinal or up-down, and z is nasal-occipital or forward-backward). 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 directions of head motion 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)	Head-centric linear flow relative to gravity		Otolith sensitivity bias to gravity	
		Interaural (x-axis)	Spinal (y-axis)	Utricle	Saccule
Upright	y-axis	orthogonal	aligned	-	*
Supine/Prone	z-axis	orthogonal	orthogonal	-	-
Left/Right Side	x-axis	aligned	orthogonal	*	-

159 in various postures based on potential mechanisms underlying the reported
160 enhanced vection for spinal motion:

- 161 1. *Differences in otolith sensitivity, a head-centric mechanism.* If the sac-
162 cule is less sensitive than the utricle then, during vection stimuli, the
163 conflicting vestibular signal signalling no motion should be more reli-
164 able for horizontal than vertical motion. Thus, we hypothesize that
165 vection will be stronger (larger magnitude, faster onset and longer du-
166 ration) for spinal motion than interaural motion regardless of the ori-
167 entation of the head.
- 168 2. *A direct gravity dependence.* If the spinal axis advantage for vection in
169 upright posture is related to directly to gravity (for example resulting
170 from alignment of the motion with a large gravity signal) then the
171 advantage should switch to the gravitationally-aligned interaural axis
172 in roll and disappear in prone/supine postures.
- 173 3. *Specialization for locomotion over the ground plane in normal gravity.*
174 If the peripheral and central vestibular system has evolved to be opti-

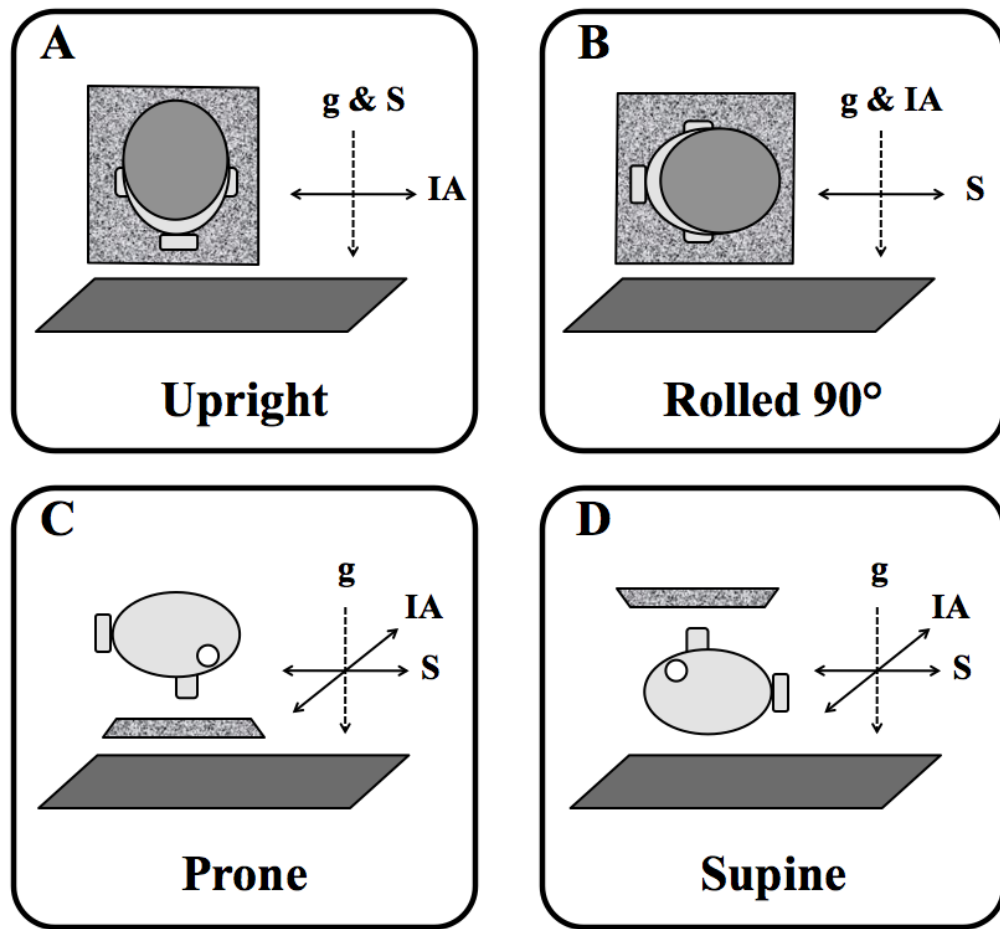


Figure 1: Visual schematic of the spinal (S) and interaural (IA) stimuli directions relative to gravity (g), for the upright (A), tilted (B), prone (C), and supine (D) postures. The solid gray and textured polygons represent the ground plane and display, respectively. For each posture, visual motion was presented along the spinal or interaural axes. As shown above, the direction of the stimulus motion and gravity could be aligned when participants were upright (g & S) or roll-tilted (g & IA), but not when lying supine or prone.

175 mized (tuned) for upright posture then we might expect it to be less
176 sensitive in other postures. In turn, vection should be generally less
177 restrained and thus stronger in lying compared to erect posture.

178 4. *Cognitive/Ecological considerations.* Extended periods of horizontal
179 motion are more ecologically relevant than vertical motion and thus
180 horizontal vection should be easier to evoke than vertical vection. Vi-
181 sual, vestibular, and cognitive factors all influence the perception of
182 upright and directional biases in vection may vary with the relative
183 saliency of these factors in the stimulus. We also predict that vection
184 will be stronger when the observer is upright as opposed to lying down
185 as travelling while lying down is unusual.

186 In this paper, we show that vertical optic flow produces stronger vection
187 than horizontal optic flow in upright observers. We also examined whether
188 this effect is due to gravitational alignment or to alignment to the spine
189 or trunk of the body. Observers viewed the same stimuli in various body
190 orientations, including positions in which visual motion was along an axis
191 in a plane that was orthogonal to gravity. In Experiment 1, we show that
192 vection is influenced by both gravity-centric and body-centric direction. We
193 then show in Experiment 2 that gravity and spinal effects in vection may
194 be modulated by scene structure that influences the perceived context of a
195 scene.

196 2. General Methods

197 2.1. Subjects

198 Participants included eight observers (four males, four females; mean age
199 = 30.88, SD = 9.96) in Experiment 1, and six observers (three males, three
200 females; mean age = 26.5, SD = 3.56) in Experiment 2. All subjects had
201 normal or corrected-to-normal vision and reported no vestibular impairment.
202 Participants had prior experience with illusions of self-motion in a laboratory
203 setting. Written informed consent was obtained in accordance with a protocol
204 approved by the York University Research Ethics Board.

205 2.2. Apparatus

206 Subjects stood upright on stable foot blocks or lay on a foam mattress
207 with a headrest to appropriately orient and center the head with a com-
208 puter screen. The mattress enabled observers to maintain a full-body tilt

209 of $\pm 90^\circ$ (left and right side down) about the naso-occipital (roll) axis, or to
210 lay prone or supine. The stimuli were displayed on an IBM Lenovo T61p
211 15.4-inch TFT laptop with a resolution of 1280 (horizontal) x 800 (vertical)
212 and refresh rate of 60 Hz. The laptop was mounted to a rigid frame with the
213 screen frontal-parallel to the subject. Extraneous stimuli were masked us-
214 ing a circular viewing tube, cloth shroud, and a matt-black opaque aperture
215 panel offset 1.5 cm from the screen. This aperture system set the observer-
216 to-screen distance of 30 cm and the field of view of 39° . The aperture and
217 viewing tube also promoted the sense of self-motion by (1) occluding extrane-
218 ous peripheral stimuli and (2) providing a frame of reference for both relative
219 motion and for perceiving the display as background - both stimulus factors
220 have been shown to improve thevection induced by optic flow [40, 41, 17, 42].
221 This provided the strong impression of looking through a window at the dis-
222 play beyond. This manipulation generated more compellingvection illusions,
223 despite the relatively small central display.

224 Responses were recorded using a Logitech R Dual Action Gamepad (see
225 Fig. 2). Subjects wore earplugs (model 1100, 3M) to mute extraneous audi-
226 tory orientation cues.

227 *2.3. Stimuli*

228 The self-motion displays were generated using custom Python software
229 with open-source Pyglet libraries (Experiment 1), Autodesk Maya and Adobe
230 Media Encoder (Experiment 2). Stimuli were 3-D animations (non-stereoscopic)
231 of vertical and horizontal translation through a computer-generated scene.
232 The virtual camera for the experiments had a vertical field of view of 39° to
233 match the display.

234 In Experiment 1, the scenes consisted of a volumetric (3-D) optic flow field
235 of 8500 randomly distributed blue dots (16.72 cd/m^2) on a black background
236 (0.64 cd/m^2). The cloud of dots extended 30 m along the depth or visual axis.
237 The dots had a simulated radius of 7.5 cm and were uniformly translated in
238 3-D space at 1.33 m/s to produce a lamellar flow pattern. The dots moved
239 vertically or horizontally with respect to the display. When any dot moved
240 beyond the field of view (off screen), it was redrawn at the same original
241 vertical (or horizontal for vertical motion) and depth coordinates on the
242 opposite side of the virtual scene. Stimulus duration was 30 s in Experiment
243 1.

244 In Experiment 2, the scenes contained the same 3-D dot scene as in Ex-
245 periment 1, or a blue, rigid 3-D pipe structure of randomly distributed and

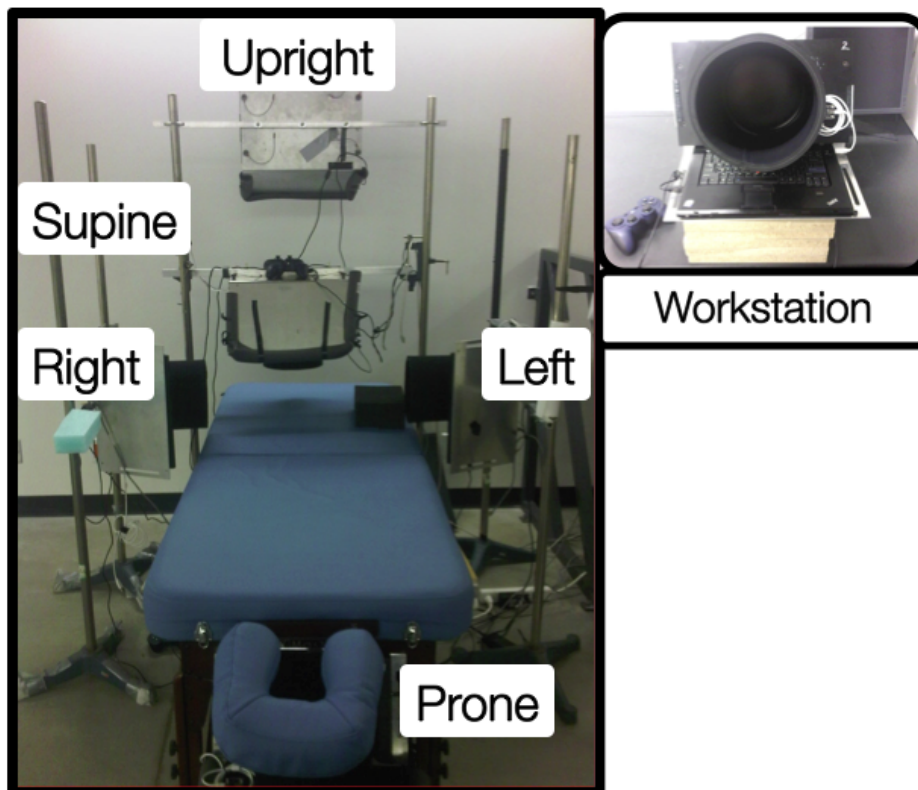


Figure 2: Photograph of the apparatus for the upright (standing), tilted (lying on the left and right side), supine and prone postures. Foot blocks and a foam headrest were used for height adjustment and support.

246 intersecting virtual pipes in a volume of black space (See Fig. 3). The
247 pipes were oriented vertically and horizontally with respect to the display.
248 Self-motion was simulated by translating a virtual camera through the pipe
249 structure. The rendered animation frames were rotated to produce the stim-
250 ulti for both the vertical and horizontal translation. Stimulus duration was
251 20 s. The motion sequences were rendered with a frame rate of 30 frames
252 per second as in Experiment 1, and the translation speed was 1.33 m/s.

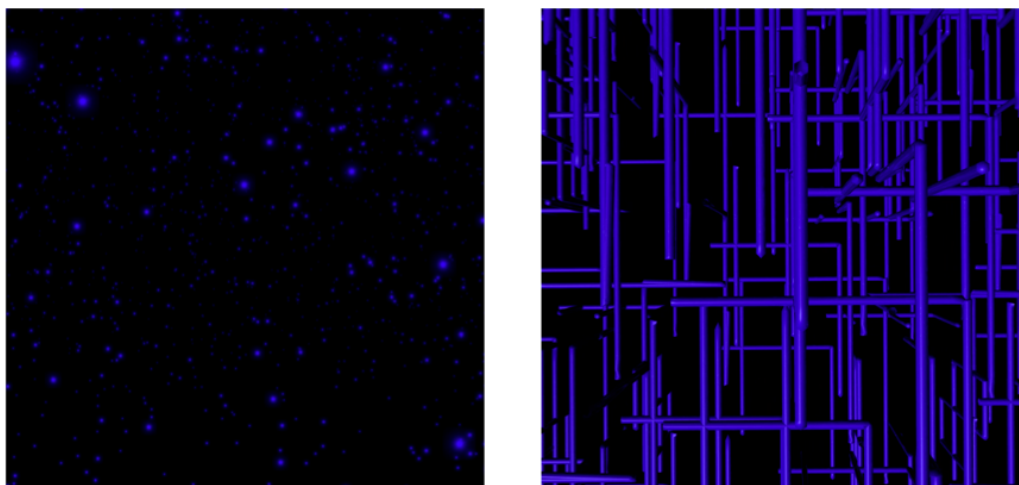


Figure 3: Screenshots of the dot (A) and pipe (B) stimuli. Camera motion through these scenes was upward, downward, leftward or rightward depending on the condition.

253 *2.4. Posture Conditioning*

254 While viewing the displays in the upright and lying postures, the head
255 was aligned with the trunk of the body and the legs were extended. Only in
256 the upright, left and right side down postures, was one of either the spinal or
257 interaural body axes aligned with the direction of gravity; these body axes
258 were orthogonal to gravity in the supine or prone postures. Figure 1 shows
259 the direction of the body axes relative to the direction of gravity. The trials
260 began after approximately 60 s in the given posture.

261 *2.5. Procedure*

262 The procedure was similar for the two experiments. Observers viewed a
263 series of self-motion displays while casually looking about the display and
264 attending to their perception of self-motion. In Experiment 1, observers first
265 tested in the standing posture followed by testing in lying postures, which in-
266 cluded lying left and right side down, supine and prone. In each session, they
267 first stood upright and viewed a 30 s lamellar dot motion display (vertical
268 or horizontal motion as appropriate for the block) while attending to their
269 sensation of self-motion. Observers were told to assign a vection magnitude
270 of 50 to the vection sensation produced, which served as a reference stimulus
271 for subsequent trials.

272 During each trial, observers viewed the dot displays and pressed one of
273 the shoulder buttons on a gamepad as soon as they experienced vection, and
274 continued to hold the button until that sensation or trial ended. If vection
275 ceased and reoccurred during a trial, the shoulder button was to be pressed
276 again. Each trial was followed by a response screen prompting observers
277 to use the gamepad to indicate their overall sensation of self-motion on a
278 rating scale of 0-100 relative to the reference stimulus. The rating scale had
279 a resolution of 5 units. If the observer’s feeling of self-motion was twice as
280 strong (or more) than the reference stimulus, they were told to give a rating
281 of 100. If observers did not experience self-motion, they were asked to provide
282 a rating of 0.

283 In Experiment 2, observers stood and lay left side down, while viewing
284 20 s lamellar motion displays consisting of either the same dot motion as in
285 Experiment 1, or motion across a scene of pipes. Each display was followed
286 by a black, blank screen, during which observers verbally reported their sen-
287 sation of self-motion on a rating scale of 0-100. Observers were told to give a
288 rating of 100 for maximal/saturated vection (i.e., they perceived themselves
289 as moving in a world of stationary dots/pipes), and 0 if they did not expe-
290 rience vection (i.e., they perceived themselves as stationary with dots or the
291 pipe structure moving past them).

292 For each trial, the motion direction (vertical or horizontal) and stimulus
293 type (dots or pipes for Experiment 2) were randomly selected and blocked
294 by posture. Within each posture block, trials were randomly ordered. The
295 blocks were ordered using a counterbalanced design.

296 Qualitative reports of observers’ vection experiences were collected during
297 the experiment debriefing. Participants were asked the open-ended question
298 “How would you describe your experience of self-motion?” to potentially
299 reveal any unintended or unexpected perceptions or sensations during or
300 following the experiment.

301 *2.6. Data analysis*

302 Linear mixed effect model data analyses were performed using the R
303 package nlme [43] with RStudio. Outlying points were identified through
304 regression diagnostics (using the function influence.measures in R) confirmed
305 with visual inspection of the response measures. Points were excluded based
306 on (1) DFFIT which identifies an influential outlying data point based on
307 the difference between the fitted values for the data point in the full dataset
308 compared to the fitted value after deleting the data point [44, 45] and (2) the

309 covratio which estimates the change in the covariance matrices for the fixed
310 effects if an observation is deleted [46, 47]. We confirmed that results were
311 qualitatively similar if these outlying points were included in the analysis.

312 We adopted backward stepwise selection based on Akaike’s Information
313 Criterion (AIC) to select the final regression models. Separate statistical
314 models were fitted for each of the response measures, which were vection
315 onset, duration, magnitude (Experiment 1 only) and saturation (Experiment
316 2 only). A goodness-of-fit test based on the analysis of deviance was used
317 to evaluate the fit the model. Planned comparisons for the main hypothesis
318 of spinal versus interaural vection differences were run using linear contrast
319 tests of the models. Family-wise error was controlled for with Bonferroni-
320 Holm correction and the adjusted p-values are shown for post-hoc analyses.
321 Trials in which vection was not reported were excluded from the analysis.
322 Effect sizes for the linear mixed effect model parameters were computed as
323 f^2 as described in Selya et al [48].

324 **3. Experiment 1**

325 In the first experiment, we examined whether the relative alignment of
326 the direction of head tilt and simulated self-motion modulates vection. We
327 dissociated these body and display vectors from gravity by varying body
328 posture with respect to gravity. In the upright posture, the display-vertical
329 (and spinal axis) was aligned with the direction of gravity. In contrast, in
330 the on-side conditions the interaural axis was aligned with gravity. As shown
331 in Figure 1, the visual motion and gravity do not align at all in the prone
332 and supine posture.

333 *3.1. Methods*

334 There were three independent variables Reference (4 levels: up, down,
335 left, right), Posture (5 levels: upright, left side down, right side down, supine
336 and prone), and stimulus Direction (4 levels: up, down, left, right, relative to
337 the display). Trials were sessioned and blocked by the direction of the refer-
338 ence stimulus, and within these reference blocks blocked further by posture
339 (20 blocks of 4 ref. x 5 postures). Prior to a testing block, subjects stood
340 and viewed a reference stimulus moving in one of the four motion directions
341 (up, down, left, and right). They then moved to the appropriate posture
342 for the first block and viewed one test stimulus for each of the four motion
343 directions. After each trial, they rated their vection relative to the reference

344 stimulus. After these four trials, they moved to the posture for the next
345 block.

346 3.2. Results and Discussion

347 Vection was reported for nearly all of the trials (approximately 97% of
348 the total responses, comparable to other recent studies [38]). Data points
349 that were identified as outlying or where vection was not obtained were re-
350 moved included 33 data points (across response measures). To confirm that
351 removing this data did not affect the outcome, we also repeated the analysis
352 assuming the limits of the stimulus (e.g. onset latency of 30 and duration of
353 0 s) and the pattern of results was unchanged.

354 Figure 4 shows the vection ratings averaged across all subjects. As shown
355 in Figure 4A, there were no significant vection differences between the op-
356 posing motion directions for vertical (up/down) or horizontal (left/right)
357 motion for the reference and stimulus directions (p 's $> .05$), so these lev-
358 els were collapsed into the two head-centric reference directions "Interaural"
359 and "Spinal." There were also no significant differences between laying left
360 and right side down (p 's $> .05$), or supine and prone (p 's $> .05$), so these
361 conditions were combined and noted as "Rolled 90°" and "Pitched 90°"
362 postures, respectively (see Figure 4B). The results shown in subsequent figures
363 are from data collapsed across these motion directions and postures.

364 Following this grouping of levels, the experimental design consisted of the
365 following three factors: Reference (4 levels: up, down, left, right), Posture (3
366 levels: upright, rolled 90° and pitched 90°), and stimulus Direction (2 levels:
367 interaural and spinal). Model selection began with the fully factorial model
368 with subject as random factor (models expressed in Wilkinson notation [49]):

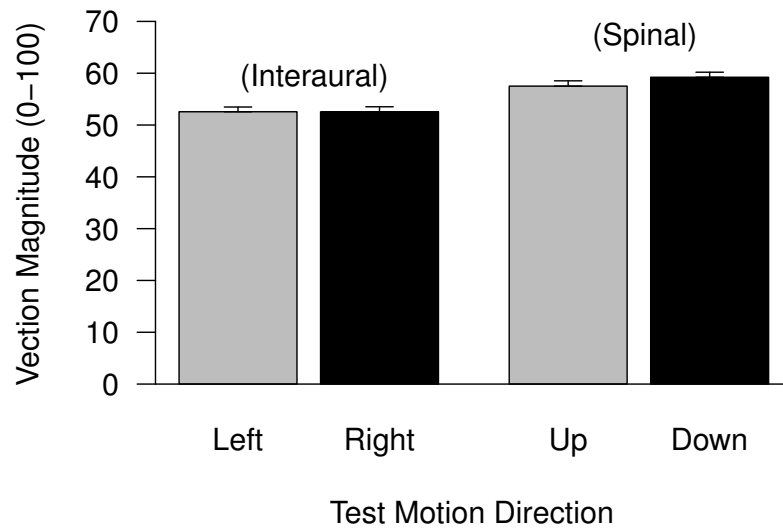
$$369 \quad \text{measure} \sim \text{posture} * \text{direction} * \text{reference} + (1|\text{subject}).$$

370 The model selection process attempted to produce simpler models based
371 on the AIC. This resulted in a model for the three measures that was used
372 for further analysis:

$$373 \quad \text{rating} \sim \text{posture} * \text{direction} + (1|\text{subject})$$
$$374 \quad \text{onset} \sim \text{posture} * \text{direction} + (1|\text{subject})$$
$$375 \quad \text{duration} \sim \text{posture} * \text{direction} + (1|\text{subject})$$

376 Consistent with predictions, visual motion that was aligned with grav-
377 ity enhanced vection. However, when the motion axis was orthogonal with

A)



B)

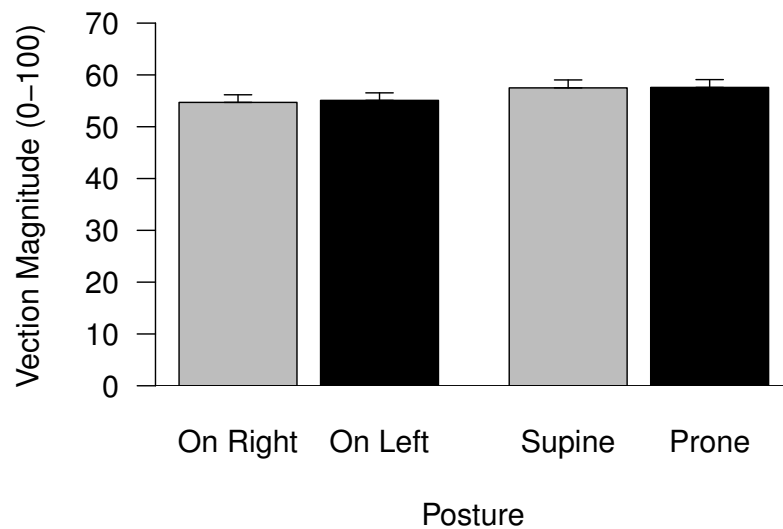


Figure 4: Mean vection magnitude ratings (± 1 standard error of the mean (SEM), 8 observers) for (A) opposing motion directions across postures, and (B) opposing body tilts. Ratings for both types of opposing conditions were not significantly different (p 's $> .05$). Observers based their magnitude estimates on a reference stimulus with a given vection rating of 50, corresponding to one of the four reference motion directions before each block of trials.

378 gravity (in the pitched postures), motion along the spinal axis resulted in
379 more compelling vection than interaural motion. Figures 5-7 show the mean
380 vection ratings, onsets, and durations across all subjects. Specifically, body
381 orientation significantly influenced vection ratings, $F(2, 947) = 10.33$, $p <$
382 $.0001$, $f^2 = 0.007$; onset, $F(2, 947) = 3.31$, $p = .0370$, $f^2 = 0.019$; and du-
383 ration, $F(2, 947) = 11.04$, $p < .0001$, $f^2 = 0.073$. Vection durations were
384 larger and onsets shorter in upright compared to lying posture (upright-roll
385 duration $t(7) = 8.09$, $p = .0005$; upright-pitched 90° duration $t(7) = 4.43$,
386 $p = .0150$; upright-roll onset $t(7) = -3.80$, $p = .0268$; upright-pitched 90°
387 onset was marginal $t(7) = -2.94$, $p = .0655$). The test motion axis also had
388 a significant impact on vection ratings, $F(1, 947) = 64.51$, $p < .0001$, $f^2 =$
389 0.044 ; onset, $F(1, 947) = 4.57$, $p = .0328$, $f^2 = 0.007$; and duration, $F(1,$
390 $947) = 12.16$, $p = .0005$, $f^2 = 0.014$. While there was a significant posture x
391 motion axis interaction for observer vection ratings, $F(2, 947) = 16.42$, $p <$
392 0.0001 , $f^2 = .035$, this was not the case for vection onsets or durations (p 's
393 $> .05$).

394 In directly comparing interaural and spinal motion by posture, we found
395 that when observers were upright, vection ratings and durations were sig-
396 nificantly higher for visual motion that was presented along the spinal axis
397 compared to interaural motion (ratings: $t(7) = 8.06$, $p < .0001$, $d_{rm} = .85$;
398 durations: $t(7) = 3.50$, $p = .0100$, $d_{rm} = .16$) but while onsets were also
399 shorter the difference was not significant ($t(7) = -2.14$, $p = .0692$, $d_{rm} = .06$).
400 In contrast, when observers lay on the side (rolled 90°), interaural motion did
401 not produce significantly stronger vection than spinal motion (neither larger
402 ratings, shorter onsets nor longer durations, all p 's $> .05$). While not sig-
403 nificant, the interaural motion produced larger average vection ratings than
404 spinal motion when observers lay on the side, suggesting if anything the ef-
405 fect had switched to interaural enhancement. However, when observers were
406 supine or prone (pitched 90°), visual motion along the spinal axis resulted
407 in significantly higher vection ratings ($t(7) = 3.02$, $p = .0192$, $d_{rm} = .31$)
408 and marginally longer duration ($t(7) = 2.21$, $p = .0630$, $d_{rm} = .13$), with no
409 significant difference in vection onset ($t(7) = -1.59$, $p = .1554$, $d_{rm} = .07$).

410 Our finding that the relative direction of the body and visual motion axis
411 significantly influenced vection, is consistent with that of previous vection
412 studies in which these factors enhanced the feeling of illusory self-motion
413 in observers [27, 37]. However, consider that in the upright posture, the
414 head-centric vertical/up was the same as gravity, so it is unclear whether the
415 vection advantage for vertical motion with respect to the display was due to

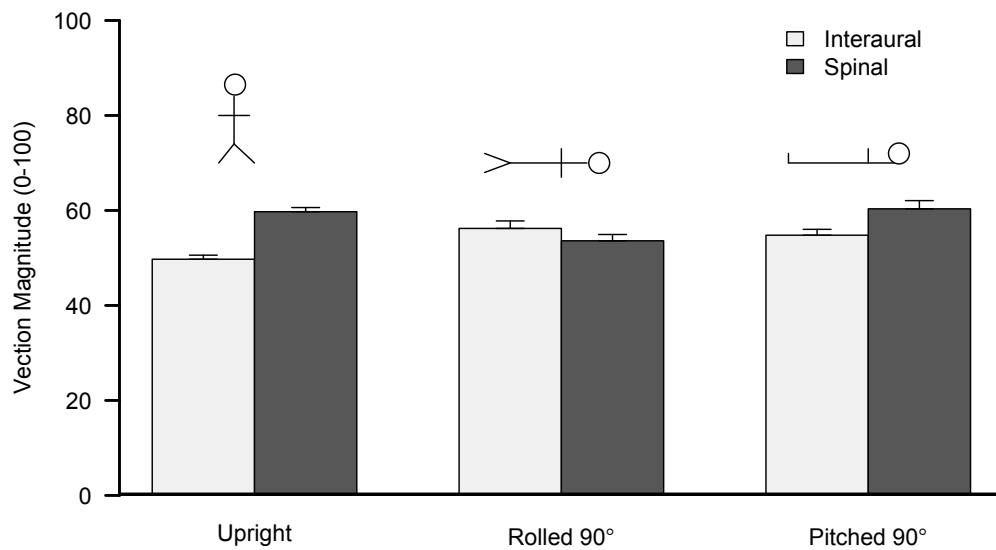


Figure 5: Mean vection magnitude ratings for the upright posture (Experiment 1, far left) compared with the tilted, prone, and supine postures (± 1 SEM, 8 observers). Ratings for the opposing motion directions for vertical (up/down) and horizontal (left/right) test and reference stimuli were not significantly different ($p > .05$) and so were collapsed and coded into the two head-centric reference frames Interaural and Spinal. The vection magnitude ratings for the left and right side down, and supine and prone postures, were also not significantly different ($p > .05$) and so were collapsed into the “Rolled” and “Pitched” body orientation conditions.

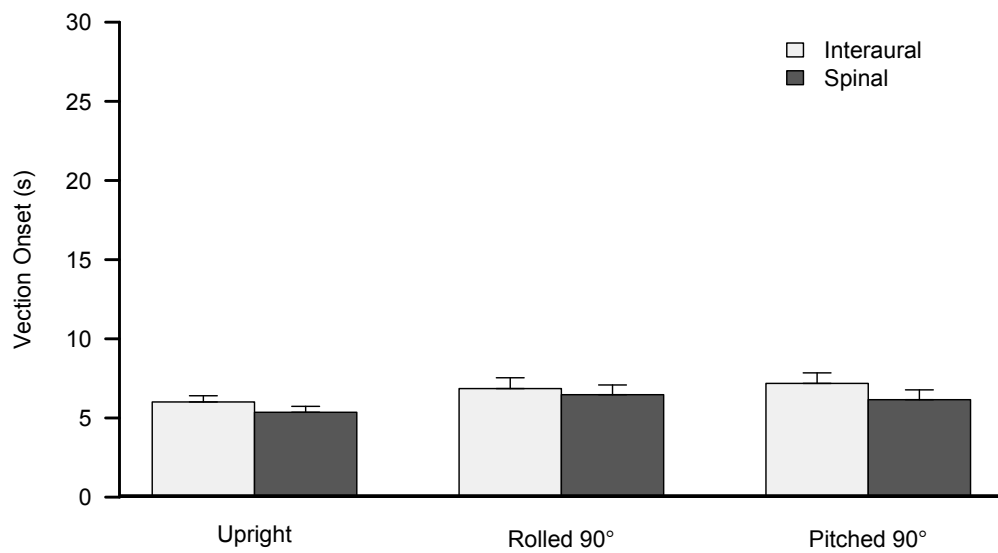


Figure 6: Mean vection onset (± 1 SEM, 8 observers). Onsets for the opposing motion directions for vertical (up/down) and horizontal (left/right) motion were collapsed into the head-centric axis directions Interaural and Spinal.

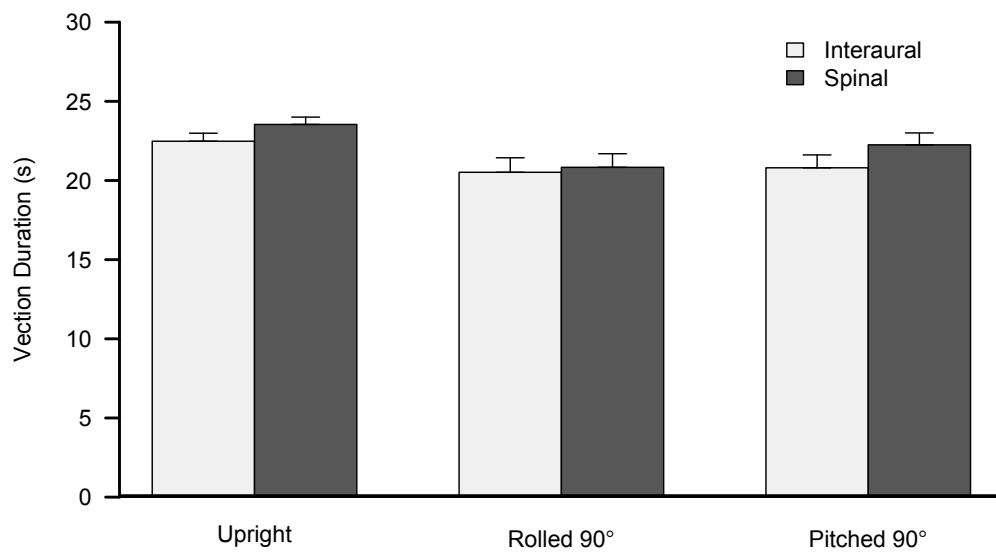


Figure 7: Mean vection duration (± 1 SEM, 8 observers). Durations for the opposing motion directions for vertical (up/down) and horizontal (left/right) motion were collapsed into the head-centric stimulus axis directions Interaural and Spinal.

416 alignment with the spinal axis or the gravity axis. Thus, from the data for
417 the upright posture, it may be argued that (a) gravity reinforced the visual
418 signal in vertical vection, (b) there is a preference for motion along the trunk
419 of the body, or (c) both the gravity and body vectors influence vection. The
420 results from the rolled and pitched postures suggest that the latter conclusion
421 is most correct, that both gravity and body influence vection. In other
422 words, the strength of visually-induced self-motion depends on the axis of
423 visual motion relative to both gravity and the body. In particular, this is
424 evident in (1) our finding that in roll-tilted observers vection was relatively
425 enhanced for interaural motion eliminating the spinal advantage found in
426 upright observers, (2) preservation of the spinal motion advantage for pitched
427 observers. This pattern was found for all of the response measures, but to a
428 lesser degree for vection onset and duration than magnitude.

429 The similarity of responses for vection from flow in opposing motion di-
430 rections (vertical up/down and horizontal left/right), suggests that these
431 alignment effects are not due to a simple vector summation of the visual and
432 gravity signals. Furthermore, the lack of a significant vection difference be-
433 tween the supine and prone postures is consistent with the similar pressure
434 sensitivities of the chest and back of the body [50].

435 During the session debriefing, three observers spontaneously reported that
436 when they were roll-tilted, the stimulus motion appeared to be moving along
437 a tilted axis with respect to the vertical and horizontal axis of the display—a
438 possible A-effect (for a review see [51, 52, 53]). One of these observers also
439 reported illusory scene shearing/distortion during the perceived self-motion.

440 Additionally, some observers reported that the dots stimulus looked like
441 stars and that this resulted in sensations of flying through outer space. For
442 other observers, the dots sometimes appeared as moving bubbles or snowfall,
443 and this created the impression that they were stationary and viewing a
444 moving stimulus, or more commonly moving through elements that are also
445 moving.

446 The fact that vection can be incomplete or dropout during the optic flow
447 stimulus and produce object motion percepts are well-known phenomena (for
448 review see [11]). The interesting observation here is that the interpretation
449 of the object motion percept during unsaturated vection appeared to vary
450 with posture. That is, that the object motion in the same stimulus could be
451 perceived in different ways depending on posture and motion direction. As
452 these phenomena were brought to light during the debrief, it was unclear as
453 to the role that the perceived scene context or scene structure might have in

454 influencing the effects of motion-gravity alignment in vection.

455 4. Experiment 2

456 While much of the research on self-motion perception has taken a “bottom-
457 up” approach and focused on the roles of the visual and vestibular system
458 [54, 14, 55], vection and other self-motion studies using virtual reality have
459 demonstrated that cognitive or “top-down” mechanisms can affect the in-
460 tensity, onset, and realism, of visually-induced self-motion. Accordingly, [56]
461 used a flight simulator simulating linear and circular self-motion and found
462 that vection saturation was enhanced when the motion in the scene was more
463 naturalistic. Similarly, Riecke et al. [6] presented observers with naturalistic
464 (coherent and incoherent/scrambled) and unnaturalistic 3D scenes of simu-
465 lated self-motion using a dome projection setup, and found that scenes that
466 were both coherent and naturalistic enhanced vection and “convincingness”
467 of the illusory sensation of self-motion. Riecke et al. posited that such scenes
468 provide the viewer the impression of a more stable visual environment, and
469 thus the visual motion is more likely to be attributed to self-motion than
470 external motion.

471 In the second experiment, we examined whether the influence of body ori-
472 entation and motion direction with respect to gravity might depend on scene
473 structure. To explore how the structure of a scene influences the percep-
474 tion of self-motion, observer posture was varied relative to gravity while they
475 viewed motion along the spinal and interaural axis. The displays simulated
476 self-motion across a 3-D volume of dots as in Experiment 1, or a 3-D scene
477 that contained a single, solid pipe-like structure; we refer to these stimuli as
478 “dots” and “pipes” respectively.

479 4.1. Methods

480 The procedure was the same as Experiment 1, except observers viewed
481 lamellar global optic flow displays while standing upright and lying down.
482 There were three independent variables: (1) Body posture: standing (up-
483 right) and lying left side down (roll-tilted 90°); (2) Simulated self-motion
484 direction: up, down, left, and right (relative to the display); and (3) Scene
485 type: dots and pipes. Trials were divided into two blocks by posture, to limit
486 the number of postural changes required given the four motion directions and
487 differently-structured stimuli. For each of the two postures, the 8 factorial
488 combinations (4 motion directions x 2 scene types) were repeated 4 times for

489 a total of 32 trials per block an overall total of 64 trials per subject. For each
490 trial, we recorded the vection saturation (rating of 0-100). A vection satura-
491 tion response of 0 meant the scene was perceived as moving and the self as
492 fully stationary, and 100 meant that the scene was perceived as stationary
493 and the self as fully moving.

494 4.2. Results and Discussion

495 Figure 8 shows the mean vection ratings across subjects. There were
496 no significant differences between the opposing motion directions for vertical
497 (up/down) or horizontal (left/right) motion, so these levels were collapsed
498 into the two head-centric motion directions Interaural and Spinal.

499 Using this two-level direction factor, the model selection began with the
500 fully factorial model with subject as random factor:

$$501 \quad \textit{rating} \sim \textit{posture} * \textit{direction} * \textit{sceneType} + (1|\textit{subject}).$$

502 The model selection process attempted to produce simpler models based
503 on the AIC. This resulted in a model without the non-significant three-way
504 interaction that was used for further analysis:

$$505 \quad \textit{rating} \sim \textit{posture} + \textit{direction} + \textit{sceneType} + \textit{posture} : \textit{direction} + \\ 506 \quad \textit{posture} : \textit{sceneType} + \textit{direction} : \textit{sceneType} + (1|\textit{subject}).$$

507 As in Experiment 1, body orientation had a significant effect on vection,
508 $F(1, 367) = 10.50$, $p = .0013$, $f^2 = .0002$, and so did the direction of visual
509 motion, $F(1, 367) = 4.29$, $p = .0390$, $f^2 = 0.1237$. The scene/stimulus
510 type (dots or pipes) did not have a significant main effect on vection, $F(1,$
511 $367) = 0.43$, $p = .5090$, $f^2 = .0265$; however, interactions indicated that
512 the effect of stimulus type depended significantly on body orientation, $F(1,$
513 $367) = 5.32$, $p = .0217$, $f^2 = .0139$, but not on visual motion direction (p
514 $= .76$, $f^2 = .0002$). There was also an interaction between body orientation
515 and motion direction, $F(1, 367) = 12.84$, $p = .0004$, $f^2 = 0.0345$. As in
516 the first experiment spinal motion produced significantly stronger vection
517 in upright observers $t(5) = 7.46$, $p = .0027$, $d_{rm} = .95$; however, in tilted
518 observers, there was no significant difference in vection between interaural
519 and spinal motion, $p > .05$, but rather, a trend towards stronger vection for
520 motion along the spinal axis. Thus, consistent with experiment 1, there was
521 a significant vection advantage for spinal motion in erect observers but when

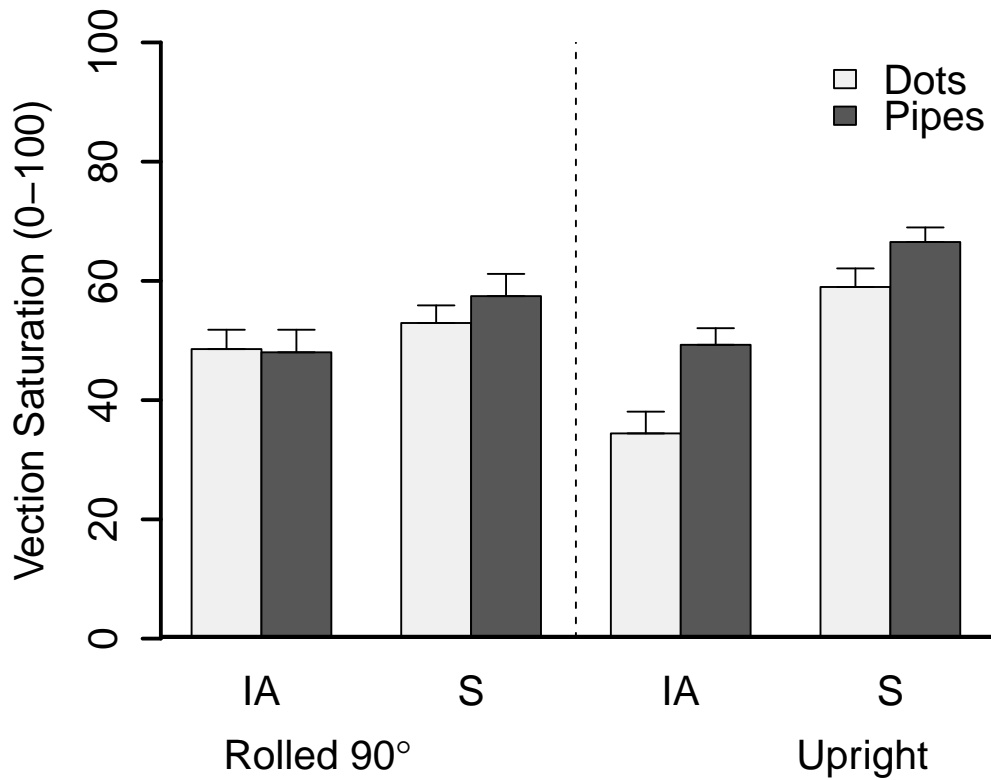


Figure 8: Mean vection saturation rating (± 1 SEM, 6 observers). Ratings for the opposing motion directions for vertical (up/down) and horizontal (left/right) motion were not significantly different ($p > .05$) and so were collapsed into two motion directions (vertical and horizontal) and coded into the head-centric reference frames Interaural and Spinal. Here, the “Rolled 90°” posture represents the left side down body orientation.

522 the interaural axis was aligned with gravity by lying on the side there were
523 no significant differences in vection between interaural and spinal motion.

524 Additionally, upright observers experienced stronger vection when view-
525 ing the pipes than the dots ($t(5) = 3.89$, $p = .0115$, $d_{rm} = .46$). When
526 participants were roll-tilted left side down, vection strength for the dots and
527 pipes stimuli were not significantly different ($t(5) = 0.59$, $p = .5787$, $d_{rm} =$
528 0.07).

529 Interestingly, in the debriefing observers reported that the pipes stimulus
530 gave the impression of being in a moving elevator and this effect tended to
531 enhance vection; however, this “elevator effect” was reduced when observers
532 lay tilted, as some felt that this effect seemed less natural when they lay on
533 the side given the atypical posture for that perceived context. Therefore,
534 the perceived context and naturalness of the scene had the potential to both
535 enhance and inhibit vection. Such observer anecdotes demonstrate the effects
536 of scene interpretation on illusory self-motion, and suggest that higher-order
537 cognitive processes may be involved in vection.

538 5. General Discussion

539 Varying head orientation allowed us to partially dissociate the effects of
540 the direction of gravity with respect to the head, visual motion direction,
541 and otolith sensitivity, on vection. Varying posture has been shown to mod-
542 ulate experiences of visually-induced self-motion [37, 28] and we confirmed
543 this in the present study. In the Introduction, we discussed potential mech-
544 anisms that could underlie a postural modulation of linear vection based
545 on vestibular (otolith) sensitivity, resolving ambiguity in the context of a
546 1-g environment, and ecological considerations including specialization for
547 locomotion over the ground plane and the role of expectations.

548 5.1. Differences in signal reliability: head-centric differences in otolith sen- 549 sitivity.

550 Anisotropies in the sensitivity of the otolithic system to linear accelera-
551 tion predict head-centric biases in linear vection. As the utricle is generally
552 considered more sensitive than the saccule to translation [22, 23, 24, 25, 26]
553 we expected the otolithic conflict to be stronger and thus the vection sensa-
554 tion weaker for interaural compared to spinal vection, regardless of posture.
555 We confirmed that this anisotropy held for erect observers. Based on simi-
556 lar logic, Giannopulu and Lepecq [27] predicted and confirmed that vection

557 along the naso-occipital axis (sensed more by the utricle) would generate
558 greater sensory conflict and thus longer onset latency than vection along the
559 spinal axis (where the saccular response predominates) in erect observers.
560 However, in [27] the optic flow differed in the two conditions with the naso-
561 occipital flow being mainly looming flow and the vertical translation pro-
562 ducing lamellar flow. Our flow conditions were both lamellar thus we can
563 attribute the enhanced vection for spinal motion to the direction of simulated
564 motion rather than the flow pattern produced.

565 Importantly, this hypothesis predicts that the anisotropy will be deter-
566 mined by the head-centric direction of simulated self-motion regardless of
567 posture. We have evidence for this head-centric dependence in our supine
568 and prone conditions in Experiment 1 where, as in upright posture, spinal
569 flow produced significantly stronger vection (larger magnitude, shorter onset
570 and longer duration) than interaural flow. In these pitched 90° conditions
571 gravity is orthogonal to the motion and thus we expect that any head-centric
572 dependence would not be affected by gravity. Anisotropies in sensitivity
573 for vestibular motion detection and vestibular heading discrimination show
574 an analogous head-centric dependence regardless of posture [25] consistent
575 with the hypothesis that vection anisotropy reflects the reliability of the con-
576 flicting vestibular cue. Interestingly, the same study found no head-centric
577 dependence of visual heading judgements. This is interesting since there
578 is significant evidence for optimal visual-vestibular cue integration (in an
579 either an MLE or Bayesian sense) that would predict performance would
580 reflect the reliability of the underlying vestibular cue [60, 61, 62, 63, 64].
581 It is likely that visual heading direction discrimination and vection reflect
582 different vestibular-visual integration processes (see [15] for discussion) and
583 this may explain why our vection results reflect the anisotropy in vestibular
584 motion sensitivity while the visual heading results [25] do not.

585 *5.2. Ambiguity of the signals in our gravitational context*

586 A pure head-centric difference in sensitivity as discussed in the previous
587 section cannot be the entire story as the spinal versus interaural anisotropy
588 diminished or reversed in the on-side postures in Experiments 1 and 2. This
589 suggests a gravity dependence as well as a head-centric anisotropy, consistent
590 with previous studies [28, 34, 37].

591 In upright posture, both head-centric and world/gravity-centric frames
592 are aligned and so we cannot dissociate the role of these factors. Side-lying
593 postures make these components orthogonal (see Table 1). If the anisotropy

594 found in upright posture were a purely gravitational effect then we would
595 expect a full reversal of the anisotropy when rolled 90° and a significant en-
596 hancement for interaural compared to spinal motion. In both Experiment 1
597 and 2, adopting the roll postures reduced or eliminated the spinal advantage
598 consistent with a relative enhancement of the interaural axis stimulus that
599 was aligned with gravity. However, in neither experiment was there a full
600 reversal of the effect. Any remaining anisotropy in on-side posture was much
601 smaller than the spinal advantage in upright observers. Thus, while we have
602 evidence that alignment with gravity modulated the directional anisotropy
603 it cannot fully explain it. Combined with our clear evidence for a spinal ad-
604 vantage in pitched 90° postures, the most parsimonious interpretation is that
605 both gravitational and body centric factors play an important role in the
606 perception of self-motion. Similar conclusions were reached by Kano [37] for
607 forward and verticalvection and by Burrell et al. [65] for heading estima-
608 tion in pitched observers, respectively. In our experiments, head-centric and
609 gravito-centric factors appeared to reinforce each other in upright posture
610 providing a strong spinal advantage but approximately balanced each other
611 in on-side postures nulling this advantage.

612 One possible factor underlying the gravitational dependence in our re-
613 sults could be the fact that gravitationally vertical motions must be inter-
614 preted in the context of a large and omnipresent 1-g gravity signal. Thus,
615 signal-noise ratios should be significantly different for gravitationally verti-
616 cal compared to horizontal self-motion. Human vestibular discrimination
617 thresholds for self-translation increase with stimulus intensity [35, 36] and
618 thus the vestibular system should become less sensitive when loaded by
619 gravity (the gravity-pedestal hypothesis). This reduced sensitivity predicts
620 strongervection along the direction of gravity, regardless of posture. How-
621 ever, McNeilage et al [25] found that vestibular thresholds did not depend
622 on orientation to gravity which is inconsistent with the hypothesis that a
623 gravitational-pedestal reduces sensitivity—remarkably the vestibular system
624 seems to maintain sensitivity in the presence of a 1-g pedestal [36]. Achieving
625 such gravity-independence requires that the self-motion system estimate and
626 compensate for the 1-g signal and this compensation process may underlie the
627 gravitational sensitivity ofvection even it is not reflected in vestibular sensi-
628 tivity. An omnipresent 1-g signal leads to a tilt-translation ambiguity in the
629 interpretation of changes in otolith signals (e.g., [72, 73]) and to qualitative
630 differences in the signals for vertical and horizontal motion [72, 74]. Detec-
631 tion of horizontal motion with respect to gravity depends on discrimination

632 in the orientation of the resulting gravito-inertial vector whereas detection
633 of vertical motion requires estimating changes in its magnitude.

634 Related to this 1-g pedestal effect is potential for up-down asymme-
635 tries [66, 67, 23, 36]. Unlike Seya et al [68] who reported larger vection
636 ratings for self-motion downward toward the feet than upward toward the
637 head, we found no up-down biases—in either head-centric or world-centric
638 coordinates—for vection ratings, onset latencies or duration. Our findings
639 are consistent with other vection studies [17, 69, 70] and with other reports
640 of no up-down asymmetry in vestibular sensitivity [25, 71].

641 *5.3. Specialization for locomotion over the ground plane in normal gravity.*

642 Self-motion sensitivity to head tilt was examined by [59] who found that
643 tilting the head during roll or pitch vection stimuli enhanced visually-induced
644 sensations of self-pitch and roll. They attributed this to reduced otolith sen-
645 sitivity [57, 58], and hence reduced cue conflict restraining vection, due to a
646 less sensitive orientation of the macular planes relative to gravity. For lin-
647 ear motion, MacNeilage et al. [25] reported that vestibular sensitivity was
648 generally reduced in on-side lying compared to upright posture. Thus in the
649 present experiments, if tilting or pitching the head with respect to gravity
650 makes the vestibular system less effective, then we would have expected in-
651 creased vection when lying down due to the reduced cue conflict. However,
652 consistent with prior studies [37, 28], the erect posture produced vection with
653 longer durations and shorter onsets than the lying postures. Interestingly,
654 [25] reported that visual heading judgements were also less precise when tilted
655 on side compared to upright posture (but [39] found no differences between
656 supine and upright posture). These effects of tilt suggest a more general ef-
657 fect of posture reflecting that the combined self-motion system (rather than
658 only the vestibular component) might be particularly tuned for self-motion
659 in upright individuals.

660 *5.4. Ecological and cognitive considerations*

661 Here, we have demonstrated that the perception of self-motion can be in-
662 fluenced by the alignment of visual motion with both gravity and the body,
663 and is also dependent on the perceived context of the scene. These findings
664 may reflect ecological considerations as well as low-level sensory sensitivity
665 differences. Typically the sustained movements we make are mainly perpen-
666 dicular to gravity except when climbing or falling. Since vestibular, visual
667 and cognitive factors all influence the perception of upright it is perhaps not

668 surprising that these factors all influence vertical-horizontal anisotropies in
669 vection. The vection advantage for lamellar motion along the spinal axis
670 when in supine and prone postures, may be because in an upright observer,
671 this axis would also be along the “up/down” direction of the body. The body
672 is typically aligned (during real locomotion) with both the visual and gravi-
673 tational up and we evolved to deal with this predominantly upright posture
674 for self-motion. Our prediction that horizontal vection should be favoured
675 over vertical vection based on ecological relevance was not supported. This
676 ecological view is consistent with our finding that vection had longer duration
677 in upright posture compared to in lying postures (where such self-motion is
678 unlikely) although the effects were modest. These types of ecological consid-
679 erations could be incorporated in cue combination models, for instance by
680 determining appropriate priors for Bayesian visual-vestibular cue integration
681 models [60, 61, 63, 64]. However, our finding that the perceived context of
682 the visual motion also had an impact on vection, suggests that a simple op-
683 timally weighted sum of sensory signals is not a complete model, but that
684 these dynamics should include influences of higher-level cognitive processes.

685 More recent studies have shown that, contrary to simple summation
686 models, cognitive factors can influence perceived self-motion. For example,
687 Wright et al [75] conducted a study to similar to earlier vection papers [55, 76]
688 but used simulated, naturalistic visual displays that were either spatially or
689 temporally in or out-of-phase with the motion of an oscillating seat. They
690 found that visual scenes that were consistent with the physical surround-
691 ings tended to dominate the vestibular inputs in the perceived self-motion.
692 They also found that oppositely directed visual and vestibular motion did
693 not reduce or cancel out the perceived self-motion.

694 The role of naturalism/realism in vection has also been reported by [77]
695 who reported that holding of an umbrella while perceiving moving stimuli
696 as rain or snow inhibited vection. Interestingly, our finding of enhanced
697 vection for the pipes stimuli in the upright postures—for which observers
698 reported feeling like they were riding an elevator—provides further evidence
699 that cognitive factors not only help shape our perceptual experience of self-
700 motion, but may also depend on other ecological factors.

701 The fact that vection can be incomplete or dropout during the optic flow
702 stimulus and produce object motion percepts are well-known phenomena
703 [78, 11, 55, 79]. It is possible that these differences in these cognitive effects in
704 different postures could explain the effects we observed. In the present study,
705 the perceived context of the visual scene varied with head orientation and

706 motion direction relative to gravity. The resulting interpretation of the scene
707 could have produced enhanced or inhibited vection. For instance, observers
708 reported “flying” through the dots defining the space (i.e., the dots perceived
709 as stars) and that this enhanced their vection experience, whereas viewing the
710 dots as bubbles or snow falling tended to reduce their sensation of self-motion.
711 The pipes scene was intended to produce a stronger context for a stationary
712 environment with the expectation that this would stabilize these cognitive
713 interpretations. With the pipes scene, observers who reported that they felt
714 like they were riding an elevator also added that they experienced stronger
715 vection. However, the lack of a main effect for stimulus type (i.e., dots versus
716 pipes) but rather, an interaction of stimulus type with head orientation,
717 suggests that both cognitive and ecological factors may be determinants in
718 perceived self-motion.

719 The varied interpretations of our stimuli might be explained by the fact
720 that, unlike in the studies by [75] and [6], our pipes stimulus was not a real
721 image or virtual simulation of a naturalistic scene, but rather was more ab-
722 stract. Interestingly, the interpretations of the dots stimulus varied more
723 and seemed to influence vection both positively and negatively, while the
724 pipes scene provided a more consistent and positive effect on vection. We
725 predicted and found that the rigid pipe structure—which consisted of geo-
726 metric objects and frame-like structures—might be more comparable to real
727 scenes. Observer reports seemed to indicate to greater sense of presence and
728 enhanced vection with the pipe stimulus. Notably, most of our observers in
729 their debrief reports related their experience of the pipes stimulus to that of
730 riding in an elevator. It is possible that this elevator interpretation was due
731 to expectations of being upright based on everyday experiences with elevators
732 (despite the fact that the scenario was similar to riding in a glass elevator
733 rather than the more commonly experienced enclosed elevator). These expec-
734 tations might partially explain the increased influence of spinal orientation
735 on vection for the pipes stimulus. Furthermore, lying on the side places
736 pressure on the side of body and therefore may not only be less comfortable
737 than being postured upright, but could also draw further attention to the
738 unnatural condition and percept of riding an elevator while roll-tilted. Thus,
739 the significant interaction between the scene and body orientation seems to
740 indicate both higher-order cognitive processes and ecological factors in the
741 perception of self-motion.

742 *5.5. Summary and conclusions*

743 Here, we have demonstrated that the perception of self-motion can be
744 influenced by the alignment of visual motion with gravity and the body, and
745 is also dependent on the perceived context of the scene. In Experiments 1 and
746 2, aligning the direction of visual motion with the gravitational vertical in
747 upright observers resulted in vection enhancement. Yet, in postures in which
748 the visual motion was orthogonal to the gravity vector, observers experienced
749 stronger vection when motion was along their spinal axis, suggesting that
750 the preference for the vertical direction may be based more on the trunk of
751 the body or a head-based coordinate system, rather than the orientation of
752 the body relative to gravity. The illusory self-motion also depended on the
753 perceived context of the visual scene, which was found to be influenced by
754 posture. Finally, when we changed the structure of the visual scene, this
755 too impacted their experience of self-motion. Taken together, these findings
756 support earlier findings that gravity, body orientation, and cognitive (“top-
757 down”) processes are involved in the perception of self-motion.

758 **6. Acknowledgements**

759 This research was supported by a National Science and Engineering Re-
760 search Council of Canada Discovery Grant RGPIN-06732-2015 to R. Allison
761 and a contract 9F007-091472 from the Canadian Space Agency.

762 **7. References**

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