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# Effects of simulated viewpoint jitter on visually induced postural sway

# Abstract

In this study we examined the effects of simulated horizontal and vertical viewpoint jitter on the vection and postural sway induced by radial patterns of optic flow. During each trial, observers were exposed sequentially to 20 s periods of radially expanding flow, radially contracting flow, and static visual scenes. For half the trials, simulated viewpoint jitter was added to the radially expanding/contracting optic flow patterns. In experiment 1, we found that, while this jitter increased the backward postural sway induced by radial expansion, it actually decreased forward postural sway induced by radial contraction. However, in experiment 2 we found that jitter increased both the forward and backward vection induced by radially expanding and contracting flow patterns. We conclude that the processes involved in postural control are more sensitive to the sensory conflicts generated by viewpoint jitter than those involved in the perception of self-motion, and that the observed asymmetries in forward and backward sway are ecological in origin.

# Keywords

Effects, simulated, viewpoint, jitter, visually, induced, postural, sway

# Disciplines

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

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# EFFECTS OF SIMULATED VIEWPOINT JITTER ON VISUALLY INDUCED POSTURAL SWAY

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Keywords: self-motion, optic flow, postural sway, vection, jitter

**Abstract.** This study examined the effects of simulated horizontal and vertical viewpoint jitter on the vection and postural sway induced by radial patterns of optic flow. During each trial, observers were exposed sequentially to 20 s periods of radially expanding flow, radially contracting flow and static visual scenes. For half the trials, simulated viewpoint jitter was added to the radially expanding/contracting optic flow. In Experiment 1, we found that while this jitter increased the backward postural sway induced by radial expansion, it actually decreased forward postural sway induced by radial contraction. However, Experiment 2 found that jitter increased both the forward and backward vection induced by radially expanding and contracting flow (respectively). We concluded that the processes involved in postural control were more sensitive to the sensory conflicts generated by viewpoint jitter (compared to those involved in the perception of self-motion), and that the observed asymmetries in forward and backward sway were ecological in origin.

# **1** Introduction

While self-motion can be perceived and controlled via several senses, vision and the vestibular sense have been shown to play particularly important roles (Benson 1990; Howard 1982; Lishman and Lee 1973). Vision can detect all types of selfmotion, including active/passive, linear/rotary, accelerating/constant velocity selfmotions, from the optic flow presented to the moving observer (Lishman and Lee 1973). However, most studies suggest that vision is primarily sensitive to optic flow patterns that have low temporal frequencies or simulate constant velocity self-motions (Berthoz, Pavard and Young 1975; Previc 2004). Conversely, the vestibular system of the inner ear can only detect accelerating self-motions, based on the inertia of fluid in the semicircular canals and otolith organs (Benson 1990; Howard 1986). Unlike vision, this sense is primarily sensitive to brief high-frequency stimulations (i.e. greater than 1 Hz; Diener et al 1982; Melville-Jones and Young 1978). Two other non-visual senses provide particularly useful information about active self-motions. The proprioceptive system, including muscle and joint receptors, registers selfacceleration based on the inertia of a person's limbs, whereas the somatosensory system registers self-motion relative to the surface of support based on the pressure and shear forces acting on an individual's skin (Lishman and Lee 1973).

Most explanations of how these different senses interact to perceive self-motion are based on the notion of sensory conflict (Bles et al 1998; Reason 1978; Zacharias and Young 1981). Consider the following situation, which focuses primarily on the interaction between visual and vestibular self-motion information. When we accelerate a stationary car forward, both our visual and vestibular systems signal this acceleration. However, once the car reaches a constant linear velocity, vision alone is responsible for self-motion perception. According to Zacharias and Young's (1981) version of sensory conflict theory, if we viewed a video of the same driving sequence, initially we would feel that we were stationary due to the visual-vestibular conflict (optic flow would indicate self-acceleration but the vestibular activity that would normally accompany this motion would be absent). Illusory self-motion (known as vection) would only occur later, during the video segment simulating constant velocity self-motion, as we would not expect vestibular input to accompany this type of optic flow (i.e. little or no visual-vestibular conflict).

Recent findings by Palmisano and colleagues provide a challenge to these sensory conflict accounts of self-motion perception (Palmisano, Gillam and Blackburn 2000; Palmisano, Burke and Allison 2003; Palmisano and Chan 2004). In these studies, stationary observers were shown computer-generated displays simulating either: (i) constant velocity forward self-motion through a 3-D cloud of objects (expected to produce minimal/transient visual-vestibular conflict); or (ii) constant velocity forward self-motion combined with continuous, random horizontal and/or vertical impulse self-accelerations (designed to produce a situation of sustained visual-vestibular conflict in a stationary observer). In the case of the latter display, the horizontal and/or vertical simulated viewpoint jitter was similar to the effects of 'camera shake'. Most sensory conflict theories would predict that these jittering patterns of radiall expanding flow should produce more sensory conflict and therefore weaker vection than non-jittering patterns of radially expanding flow. However, contrary to these predictions, we found that jittering displays produced stronger vection, which started sooner and lasted longer than that produced by non-jittering displays.

Research has demonstrated that optic flow not only plays an important role in the perception of self-motion (e.g. vection), but also in the control of postural sway during standing (van Asten et al 1988; Berthoz et al 1975; Dichgans and Brandt 1978; Lee

and Aronson 1974; Lee and Lishman 1975; Lestienne et al 1977; Lishman and Lee 1973; Stoffregen 1985). Studies have shown that if an upright observer is presented with a large frontal display of radially expanding flow, he/she will typically sway backward (posterior sway) to compensate for the perceived forward self-motion<sup>i</sup>. Similarly, if the observer is presented with a large frontal display of radially contracting flow, he/she will typically sway forward (anterior sway) to compensate for the perceived backward self-motion. It is generally assumed that the goal of this visually induced sway is to minimise radial expansion or contraction of the frontal surface so as to maintain an upright posture (e.g. Lee and Lishman 1975).

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Several recent studies suggest that the experience of vection might actually increase visually induced postural sway. For example, Kuno and colleagues (1999) found that participants who perceived vection when exposed to radial flow simulating back-and-forth self-motions, swayed more than participants who perceived that they were stationary throughout the trial. Thurrell and Bronstein (2002) also noted that sway amplitudes increased when their participants experienced transient periods of roll vection (compared to periods when they correctly perceived that they were stationary and viewing a large rotating disk). As we have previously shown that simulated viewpoint jitter increases the strength of the forward vection induced by radial expanding flow, it is possible this jitter will also increase the postural sway induced by radially expanding and contracting flow. To test this hypothesis, we measured the anterior-posterior and medial-lateral postural sway induced in standing observers by jittering and non-jittering patterns of radially expanding and contracting flow.

#### 2 Experiment 1: Effect of jitter on visually induced postural sway

#### 2.1 Method

2.1.1 *Participants*. Eight males and five females, aged between 23 and 38 years, participated in this experiment. All had normal or corrected-to-normal vision and had not previously experienced visual illusions of self-motion in the laboratory.

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2.1.2 Apparatus. Displays were generated on a Power Mac G4 personal computer and rear projected onto a mylar screen by a Sanyo XGA 2200 Projector (resolution 1024 H x 768 V). This display subtended a visual angle of 80° H x 65° V at a distance of 1.10 m. However, as the standing participant viewed the display monocularly through a pair of googles, the visible display area was restricted to approximately 60° H x 60° V (which blocked his/her view of the screen's stationary frame and surroundings). Figure 1 shows the experimental setup. Participants stood on a 600 mm x 400 mm Kistler Multichannel force platform (Model 9281B) connected to a Kistler Multichannel Charge Amplifier (Type 9865A). The force platform was secured on four steel mountings embedded on a concrete base and covered so the surface was flush with the surrounding floor. Ground reaction forces were transduced, amplified and digitised before being sampled by a Pentium III computer at 200 Hz. Centre of foot pressure (COP) measurements, calculated from the ground reaction force data, were derived independently along the participant's medial-lateral and anterior-posterior axes. Back-and-forth body sway led to posterior and anterior displacements of the COP, whereas side-to-side sway resulted in medial and lateral displacements of the COP.

#### <INSERT FIGURE 1 ABOUT HERE>

2.1.3 *Visual Displays.* Each visual display consisted of 400 blue filled-in square objects (with a luminance of  $3 \text{ cd/m}^2$ ) on a black background (0.03 cd/m<sup>2</sup>). The 400 objects, which were placed symmetrically with respect to both the horizontal and vertical axes, were visible throughout each 120 s trial. Each trial had the following six discrete phases: (1) 'pre-motion phase 1' had no scene motion for 20 s (the first 10 s of which served as a baseline for the following phases); (2) 'self-motion phase 1' simulated either forward or backward observer motion for 20 s; (3) 'post-motion phase 1' had no scene motion for 20 s (sway should be minimal at this stage, similar to 'pre-motion phase 1'); (5) 'self-motion phase 2' simulated self-motion in the opposite direction to 'self-motion phase 1' for 20 s; and finally (6) 'post-motion phase 2' had no scene motion for 20 s and was used to examine postural after-effects.

Both the jittering and non-jittering display types used in this experiment were identical during the pre- and post-motion trial phases (consistent with the observer being stationary with respect to a frontal surface covered with squares of various sizes). (1) *Non-jittering-radial* displays simulated constant velocity (4 m/s) forward or backward self-motion through a 3-D cloud of randomly-positioned objects. These displays were radially expanding or contracting patterns of optic flow, which also contained local changing-size cues to motion in depth. Opposite directions of self-motion in depth were simulated in the two self-motion phases, by either progressively increasing or decreasing each object's velocity and total area (0.07°-1.21°). In order to maintain a constant display density, objects were replaced as soon as they disappeared off the edge of the screen, at their horizontal and vertical start coordinates but at the opposite end of space (a simulated distance of 20 m). (2) *Jittering radial* 

displays were identical to the non-jittering radial displays, with the sole exception being that random horizontal and vertical simulated viewpoint jitter was also added to the optic flow (simulating self-motion in depth through a 3-D cloud on a platform that oscillated both horizontally and vertically). Jitter magnitude was randomly selected from a uniform distribution ranging between  $\pm 1/3$  of the simulated displacement in depth for the frame. This jitter was updated 30 times per second (unlike the radial flow component, which was updated 85 times per second). However, since the sign and magnitude of this jitter varied randomly from frame to frame, it is best represented as a range of frequencies (i.e. both high and low) limited by the jitter update rate.

2.1.4 *Design.* Two independent variables were manipulated in this experiment: (i) *Display type.* In different trials, we used two different types of visual self-motion displays: jittering radial flow and non-jittering radial flow; and (ii) *Trial Phase.* As outlined above, each 120 s trial was broken into 6 discrete phases: "pre-motion 1", "self-motion phase 1", "post-motion phase 1", "pre-motion phase 2", "self-motion phase 2" and "post-motion phase 2" <sup>ii</sup>. During each of these phases, we measured both the participant's medial-lateral (COP displacement relative to baseline) and anterior-posterior sway biases (COP displacement relative to baseline; see Figure 2A).

#### <INSERT FIGURE 2 ABOUT HERE>

2.1.5 *Procedure*. Prior to the experiment, the participant's height, weight, and foot location and placement on the force platform were measured. Each participant stood with the medial borders of their feet touching and aligned in a direction that was

perpendicular to the orientation of the screen. They were told that: (i) during each trial a visual scene would be projected onto the screen in front of them and at some times this scene would be stationary and at others it would be moving; and (ii) they were to keep their feet stationary and maintain an upright posture with their arms kept by their sides throughout each 120 s trial. After several practice trials, participants began the experimental trials, which presented three replications of each of the visual display conditions. As a check for vection, at the end of the trial, participants were asked whether they felt that they were moving backward and forward during the second and fifth (i.e. the self-motion) phases of the trial.

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#### 2.1.6 Data Analysis.

We examined the anterior-posterior and medial-lateral postural sway of 13 participants using the COP data obtained from the force platform. We calculated the postural sway bias for each of the six 20 s trial periods as the mean COP displacement for the phase relative to the mean COP location during the first 10 s of 'pre-motion phase 1' (i.e. when subjects were standing still with no display motion). These sway bias estimates were analysed using the following set of planned contrasts, which controlled the familywise error rate at 0.05 (via Bonferroni correction). In terms of the trial phase factor, we compared: (T1) the COP during pre-motion phases 1 and 2 to check for equivalent levels of postural sway; (T2) the COP during radial expansion and contraction to confirm that they predominantly produced posterior and anterior sway, respectively, as has been shown in previous studies; and (T3) the COP directly following radial expansion and contraction to check for postural after-effects. To test for possible interactions between jitter type and trial phase, we compared: (JT1) the COP during jittering and non-jittering expanding flow; (JT2) the COP during jittering

and non-jittering contracting flow; (JT3) the COP after-effects following jittering and non-jittering patterns of expanding flow; and (JT4) the COP after-effects following jittering and non-jittering patterns of contracting flow.

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# 2.2 Results

2.2.1 Anterior-Posterior Sway. Mean anterior-posterior COP displacement was not significantly different during the two pre-motion trial phases ( $F_{1,60} = 0.62$ , p > 0.05). However, significance differences emerged during the two self-motion trial phases ( $F_{1,60} = 7.55$ , p < 0.05). Specifically, radially expanding flow was found to produce a marked posterior sway bias, whereas radially contracting flow produced a marked anterior sway bias (see Figure 3). However, mean anterior-posterior COP displacement did not differ significantly in the two post-motion phases ( $F_{1,60} = 1.38$ , p > 0.05).

Importantly, the viewpoint jitter used in our study was found to significantly alter anterior-posterior COP displacement (see Figure 3). Consistent with previously observed jitter effects on vection, simulated viewpoint jitter was found to significantly *increase* the posterior sway induced by radially expanding flow ( $F_{1,60} = 8.64$ , p <0.05). However, we found that simulated viewpoint jitter significantly *decreased* the anterior sway produced by radially contracting flow ( $F_{1,60} = 7.96$ , p < 0.05). Simulated viewpoint jitter had no significant effect on the short-lived postural aftereffects experienced following these radially expanding ( $F_{1,60} = 3.39$ , p > 0.05) and contracting flow displays ( $F_{1,60} = 1.33$ , p > 0.05).

# <INSERT FIGURE 3 ABOUT HERE>

2.2.2 *Medial-Lateral sway.* Medial-lateral COP displacement was relatively unaffected by the predominantly forward/backward self-motions simulated in our experiment. Mean medial-lateral COP displacement was not significantly different during either the two pre-motion trial phases ( $F_{1,60} = 0.003$ , p > 0.05), during the two self-motion trial phases ( $F_{1,60} = 0.263$ , p > 0.05), or during the post-motion trial phases ( $F_{1,60} = 1.16$ , p > 0.05). The combined horizontal and vertical viewpoint jitter also had little effect on medial-lateral COP displacement. This jitter did not significantly alter the mean medial-lateral COP displacement induced by either radially expanding ( $F_{1,60} = 0.61$ , p > 0.05) or contracting flow ( $F_{1,60} = 0.45$ , p > 0.05). Nor did it significantly alter the COP after-effects following radially expanding ( $F_{1,60} = 3.39$ , p > 0.05) or contracting flow ( $F_{1,60} = 1.33$ , p > 0.05).

2.2.3 *Vection Check.* All 13 participants reported experiencing vection during each self-motion phase on every experimental trial.

#### **2.3 Discussion**

Consistent with the findings of previous studies (e.g. Flückiger and Baumberger 1988; Lestienne et al 1977; Stoffregen 1985), non-jittering patterns of radially expanding and contracting flow were found to produce significant back-and-forth postural sway in our standing observers. These visual self-motion displays, however, were not found to significantly alter participants' side-to-side sway (relative to that observed in the pre-motion trial phases). As expected, radially expanding flow (simulating forwards self-motion) was found to produce a backward/posterior sway bias, whereas radially contracting flow (simulating backwards self-motion) was found to produce a forward/anterior sway bias. Although simulated viewpoint jitter was

shown to significantly increase the backward sway bias produced by radial expansion, this jitter was actually found to decrease the forward sway bias produced by radial contraction.

What could account for the asymmetrical effects of viewpoint jitter on visually induced backward and forward postural sway? Recent psychophysical research has provided evidence that we are more sensitive to radial contraction than to radial expansion, for both large and small patterns of optic flow (Edwards and Badcock 1993; Edwards and Ibbotson 2007). This reported asymmetry in motion sensitivity also appears to be reflected in the visually induced sway produced by radially expanding and contracting flow. For example, Lestienne, Soechting and Berthoz (1977) used a tunnel-like optic flow stimulus to induce back-and-forth postural sway in their standing participants. They found that the amplitude of the backward sway induced by radial expansion was 25% less than the forward sway produced by radial contraction. If one looks at the mean COP displacement data for our non-jittering conditions, it can be seen that, consistent with this earlier finding, the amplitude of the backward sway bias induced by expansion was 29% less than the forward sway bias induced by contraction. Interestingly, this trend reversed for jittering displays, where the amplitude of the sway produced by contraction was 93% less than the backward sway bias produced by expansion.

Given these previously reported sensitivity differences to radial contraction and expansion, it was possible that the addition of simulated viewpoint jitter acted to increase the vection-inducing potential of the radially expanding flow used in our study, but had little effect on the vection-inducing potential of our radially contracting flow patterns (as observers should already have been more sensitive to pure radial contraction than they were to pure radial expansion). If this was the case, then jitter should only have been expected to increase the compensatory backward sway in response to radial expansion (as opposed to the compensatory forward sway in response to radial contraction).

#### 3 Experiment 2: Effect of jitter on forwards and backwards vection

Previous research has shown that simulated horizontal and vertical viewpoint jitter increases the forward vection induced by constant velocity patterns of radially expanding flow (Palmisano et al 2000; 2003; Palmisano and Chan 2004). However, to date, no study has examined the effect that this jitter has on the strength of the backward vection induced by constant velocity patterns of radially contracting flow. As observers appear to be more sensitive to radially contracting flow, the possibility arises that jitter might only improve the forward vection induced by radially expanding flow. Experiment 2 tested this explanation by measuring the strength of the vection induced in seated observers by jittering and non-jittering patterns of radially expanding and contracting flow.

#### 3.1 Method

The hardware and software for generating and presenting our visual displays were identical to those used in Experiment 1, with one exception. In addition to the 6-phase jittering and non-jittering test stimuli used in Experiment 1 (i.e. "pre-motion 1", "self-motion 1", "post-motion 1", "pre-motion 2", "self-motion 2", "post-motion 2"), we also used a 40 s display of radially expanding flow as the standard stimulus for our vection strength ratings (Stevens 1957). This visual display represented constant velocity forward self-motion at 4 m/s (i.e. it was identical to the expanding flow used

in the non-jittering test stimulus, except that it was displayed for an extra 20 s longer). Furthermore, unlike Experiment 1, participants sat throughout each trial.

3.1.1 *Participants*. Six males and sixteen females, aged between 16 and 29 years, participated in this experiment. All had normal or corrected-to-normal vision and had not previously experienced illusions of self-motion in the laboratory (i.e. none of them had participated in Experiment 1).

3.1.2 *Procedure*. As the method of magnitude estimation was used, the first display was used to set the modulus for each participant's verbal vection strength ratings. This standard stimulus was a non-jittering, radially expanding pattern of optic flow, which simulated forward self-motion at 4 m/s. After 40 s had elapsed, participants were asked whether they felt as if they were moving or stationary. If they responded that they felt that they were moving forward, they were told that the strength of this forward self-motion corresponded to a value of '+50' (with '0' representing stationary and negative values representing backward self-motion). The practice and experimental trials followed – each had the same six 20 s phases as the trials examined in Experiment 1. At the end of each of the two self-motion trial phases participants were prompted for a verbal rating of the strength and direction of their perceived self-motion (relative to the standard stimulus). After several practice trials, participants began the experimental trials, which consisted of four replications of each of the visual display conditions (pure radial expansion, pure radial contraction, jittering radial expansion and jittering radial contraction). At the half-way point, participants were re-exposed to the standard stimulus to prevent drifts in their strength and direction ratings.

# **3.2 Results**

Vection was reported by all 22 participants during each of the 'self-motion' trial phases. Radially expanding flow was always found to induce forward vection and radially contracting flow was always found to produce backward vection<sup>iii</sup>. We performed a repeated measures ANOVA on our participants' mean (unsigned) vection strength ratings (see Figure 4 for the signed means, which indicate both vection strength and vection direction). We found a significant main effect of viewpoint jitter ( $F_{1,21} = 9.95$ , p < 0.005). That is, consistent with earlier research, the vection in depth induced by jittering radial flow. However, the main effect of flow direction did not reach significance ( $F_{1,21} = 3.48$ , p > 0.05), indicating that the strength of the backward vection induced by radial contraction was not significantly different to the strength of the forward vection induced by radial expansion. Importantly, there was also no significant interaction between display type (i.e. jitter versus no-jitter) and flow direction ( $F_{1,21} = 2.20$ , p > 0.05), indicating that viewpoint jitter had similar effects on the strength of both forward and backward vection.

#### <INSERT FIGURE 4 ABOUT HERE>

#### **3.3 Discussion**

Contrary to the differential sensitivity explanation of the asymmetrical jitter effects on back-and-forth postural sway, we found that: (i) radially expanding and contracting flow that simulated equivalent speeds of forward and backward self-motion produced similar vection strength ratings; and (ii) the addition of simulated viewpoint jitter

significantly increased the vection-inducing potential of both radially expanding and contracting flow.

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#### 4 General Discussion

Experiment 1 found that adding random horizontal and vertical simulated viewpoint jitter to radial flow displays significantly altered the back-and-forth, but not the side-to-side, sway of our standing observers (as determined by the COP displacement data). The nature of these jitter effects on back-and-forth sway was shown to vary with the simulated direction of self-motion in depth. Whereas viewpoint jitter significantly increased the backward/posterior sway bias produced by radially expanding displays (that simulated forward self-motion), it also significantly decreased the forward/anterior sway bias produced by radially contracting displays (that simulated backward self-motion).

As was noted in the introduction, several studies appear to show that standing observers sway more when they perceive their optic flow as being due to self-motion (i.e. experience vection) compared to when they perceive it to be due solely to object motion (Kuno et al 1999; Thurrell and Bronstein, 2002). This led us to propose that, as adding horizontal and vertical viewpoint jitter to radial flow displays induces a more compelling experience of vection in depth, it might also induce greater back-and-forth postural sway. The findings of Experiments 1 and 2 provided only partial support for this proposal. As predicted, simulated viewpoint jitter was found to increase both the forward vection and the backward sway bias induced by radially expanding optic flow. However, contrary to predictions, simulated viewpoint jitter actually decreased the forward sway induced by radially contracting optic flow, even though it significantly increased the rated strength of the backward vection.

It should be noted that, unlike observers in the Thurrell and Bronstein (2002) and Kuno et al (1999) studies, participants in our study appeared to experience significant vection throughout all of the optic flow or display motion trial sequences (in both Experiment 1 and 2). The random horizontal and vertical viewpoint jitter manipulation we used led to quantitative differences in vection strength (with vection ratings ranging from modest to strong) as opposed to all-or-none differences (i.e. vection being experienced at some times, object motion being perceived at others). Kitazaki and Hashimoto (2006) examined the relationship between vection strength and sway amplitude under similar conditions to those of our study. In their experiment, standing observers viewed displays that simulated back-and-forth selfmotion relative to a 3-D cloud of dots. They found that adding vertical viewpoint oscillation (0.96 Hz) to the radial flow component of these displays significantly reduced vection onset latencies, but did not significantly alter postural sway. In fact, based on our findings, it is possible that their vertical viewpoint oscillation also had asymmetrical effects on sway. That is, the presence of viewpoint oscillation-based increases in backward sway might have been cancelled/masked by corresponding viewpoint oscillation-based decreases in forward sway.

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It seems clear then that horizontal and/or vertical viewpoint jitter have different effects on vection and visually-induced body sway. Our findings, and those of Kitizaki and Hashimoto, suggest that the processes involved in postural control are more sensitive to sensory conflicts than those involved in the perception of selfmotion. As in previous experiments, we found that the visual information provided by radially expanding and contracting patterns of optic flow dominated the perception of self- (versus object-) motion. For example, in Experiment 2, observers always experienced vection even though their non-visual information correctly indicated that they were both seated and stationary throughout the trial. Increasing the sensory conflict, by adding random simulated viewpoint jitter to the radial flow, was found to enhance both forward and backward vection equally - providing further evidence of the apparent dominance of visual self-motion perception in this situation and its surprising tolerance to sensory conflict.

Sensory conflict, however, appeared to have a greater impact on the postural sway of our upright observers (relative to their seated counterparts in Experiment 2). Without viewpoint jitter, both radially contracting and expanding patterns of optic flow were found to produce significant forward and backward sway, with non-jittering contraction generating more sway than non-jittering expansion. Interestingly, this asymmetrical response to expansion and contraction reversed when jitter was added, with jittering expansion generating more sway than jittering contraction. While compensatory backward postural sway was increased by adding jitter to radially expanding flow, compensatory forward postural sway was reduced by adding jitter to radially contracting flow – even though the viewpoint jitter should have increased the sensory conflict between visual and non-visual cues in both situations.

What could account for the above asymmetrical effects of visual expansion, contraction and viewpoint jitter on postural sway? Edwards and Ibbotson (2007) have argued that in order to maintain our balance, it is more important to accurately perceive and minimise any backward sway than forward sway. They have noted that because our feet project forwards: (i) it is easier for us to avoid pitching forwards than backwards; and (ii) we can lean/sway forward to a greater degree than we lean/sway can backward. Edwards and Ibbotson (2007) have also shown that we are more sensitive to radial contraction (the visual indicator of backward sway) than to radial expansion (the visual indicator of forward sway). As noted earlier, this difference in

sensitivity might explain why the amplitude of the compensatory forward sway produced by non-jittering contraction was larger than the amplitude of the compensatory backward sway produced by non-jittering expansion. However, such sensitivity differences cannot by themselves account for the finding that the asymmetry in forward and backward sway reverses when viewpoint jitter is added (i.e. when the sensory conflict is increased).

Thus, the nature of our postural responses to visual information indicating backand-forth self-motion seems to vary with the level of sensory conflict. The current findings can potentially be explained as follows, based on ecological constraints arising from the shape and orientation of our feet. When the vection and sensory conflict generated by the optic flow are not excessive (e.g. as was the case with nonjittering radial flow), the observer's automatic response to this visual stimulus will be to attempt to minimise the perceived small/modest deviations from upright (because the benefit of maintaining an upright stance, outweighs the acceptable cost of making a small error). In this situation, the postural responses to radial contraction will typically be greater than those to radial expansion, due to the differences in sensitivity to these two types of flow pattern. However, when the vection is more compelling and the sensory conflict generated is greater (as was the case with jittering radial flow), postural responses to this optic flow can be markedly different. Observers will continue to respond automatically to visual information indicating large forward sways, even in the absence of confirmatory non-visual information, because such selfmotions are both possible and even likely based on the shape and orientation of our feet. However, observers will be less likely to respond automatically to visual information indicating large backward sways, which are implausible given both the

shape and orientation of our feet and the absence of confirmatory non-visual information.

Future studies could further test the above account by reducing the simulated speed of self-motion in depth induced by the radial component of the optic flow. As noted above, the ecological constraints imposed by foot shape and orientation should be reduced, or even removed, when the simulated speed of self-motion in depth is slow and the jitter-based advantage for vection is modest. Under these circumstances, viewpoint jitter should act to increase not only the forward postural sway bias induced by contracting flow, but also the backward postural sway bias induced by expanding flow.

We conclude that the processes involved in postural control are more sensitive to sensory conflicts (in this case arising from stationary observers viewing optic flow simulating random viewpoint jitter) than those involved in the perception of selfmotion. Our results suggest that visual information can be weighted quite differently (relative to non-visual information) in terms of self-motion perception and the active control of an upright posture. These differences become more evident in situations that both induce more compelling vection and generate greater sensory conflict. It seems that under these specific circumstances, non-visual information (arising from vestibular, proprioceptive and somatosensatory inputs) plays a more dominant role in postural control.

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# FIGURES AND FIGURE CAPTIONS



**Figure 1.** The participant stood on a Kistler force platform in front of a large screen. His/her foot location on the platform was marked with tape so that he/she could return to this position after rest periods between trials. The projector's height was physically adjusted so that the centre of the image was at the participant's eye-height. Visual displays of 400 square objects, which were either stationary or moving during the various trial phases, were then rear projected onto the screen.



**Figure 2.** (A) This plot shows anterior-posterior COP displacement (mm) for a single participant (GP) during a 120 s 'no viewpoint jitter' trial. There were six different 20 s trial phases: "pre-motion 1", "forward self-motion" (i.e. radial expansion), "post-motion 1", "pre-motion 2", "backward self-motion" (i.e. radial contraction), "post-motion 2". Mean COP displacement data is shown for each 2 s time interval. (B) We also obtained data about anterior-posterior ankle and trunk sway for a subset of our participants. Two MEL optical displacement sensors were aligned to the centres of their backs and to the midlines of their calves (the setup of these sensors is also visible in Figure 1). This lower plot shows the anterior-posterior ankle and trunk angle changes for participant GP during this same 6-phase trial. As can be seen, the optic flow presented in the self-motion phases had very similar effects in terms of COP displacements, ankle angle changes and trunk angle changes. The above traces in both (A) and (B) also show that postural bias/instability could potentially last for a substantial time after display motion had ceased.



**Figure 3.** Mean anterior-posterior COP displacement (mm) produced during the premotion, self-motion and post-motion trial phases (each lasting 20 s). As can be seen, radially expanding flow (simulating forward self-motion) produced a significant posterior sway bias, whereas radially contracting flow (simulating backward selfmotion) produced a significant anterior sway bias. Simulated viewpoint jitter significantly increased the former bias and significantly decreased the latter bias. Error bars represent the standard error of the mean.



**Figure 4.** Mean vection strength ratings produced by jittering and non-jittering patterns of optic flow that simulated either forward (radial expansion) or backward (radial contraction) self-motion. Error bars represent the standard error of the mean.

<sup>&</sup>lt;sup>1</sup>Radial flow was presented to the observer in the current experiment because our displays only stimulated the central 60° of the visual field. When an observer sways back-and-forth, radially contracting and expanding flow will be presented to his/her central visual field. However, lamellar optic flow will be presented to his/her peripheral vision in both situations (Stoffregen, 1985).

<sup>&</sup>lt;sup>ii</sup>Our method was based on a previous study by Flückiger and Baumberger (1988). Their 100 s trials consisted of 20 s pre-motion, 20 s forwards-self-motion, 20 s post-motion, 20 s backwards-self-motion, and 20 s post-motion. However, in our pilot study, we observed that a substantial period of postural bias/instability could follow the simulated self-motion phases (see Figure 2A and 2B). Thus, we also included the second 20 s pre-motion phase, before the second self-motion sequence, to obtain a new baseline after the postural aftereffects had subsided.

<sup>&</sup>lt;sup>iii</sup>This is not always the case in vection studies. For example, Kuno et al (1999) found that 60% of their participants perceived vection in the predicted direction when exposed to pure radial flow which simulated observer oscillation in depth. However, another 20% of their participants experienced no vection and the remaining 20% actually experienced reversed vection.