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Review

Simulated Viewpoint Jitter Shakes Sensory Conflict Accounts of Vection *

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Abstract
Sensory conflict has been used to explain the way we perceive and control our self-motion, as well as the aetiology of motion sickness. However, recent research on simulated viewpoint jitter provides a strong challenge to one core prediction of these theories — that increasing sensory conflict should always impair visually induced illusions of self-motion (known as vection). These studies show that jittering self-motion displays (thought to generate significant and sustained visual–vestibular conflict) actually induce superior vection to comparable non-jittering displays (thought to generate only minimal/transient sensory conflict). Here we review viewpoint jitter effects on vection, postural sway, eye-movements and motion sickness, and relate them to recent behavioural and neurophysiological findings. It is shown that jitter research provides important insights into the role that sensory interaction plays in self-motion perception.
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Keywords
Vection, sensory conflict, optic flow, eye-movements, postural sway, motion sickness

1. The Self-motion Senses

As we travel through the world, either actively (e.g., walking or running) or passively (e.g., sitting on a moving bus or train), we are consciously aware of our own self-motion. This conscious experience involves perceptions of the speed and direction of self-motion, as well as the times-to-contact with objects in the immediate environment. Multiple senses contribute to this perception of self-motion, including vision, the vestibular system of the inner ear, kinesthesia, somatosensation and

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even audition. The individual contributions of each of these self-motion senses are outlined below.

Vision can resolve both accelerating and constant velocity self-motions from the optic flow (see Note 1) presented to the moving observer (Gibson, 1966; Mach, 1875). The role that vision plays in self-motion perception has been known since the time of Helmholtz (1867/1925), who described a visual illusion of self-motion produced by viewing a large, quickly moving river from above. This type of experience has come to be known informally as the 'train illusion', since passengers sitting on a stationary train often experience a similar illusion of self-motion when they see a train on the adjacent track pulling out from the station. Such visual illusions of self-motion have also been successfully recreated in laboratory settings and are now referred to as 'vection' (Fischer and Kornmüller, 1930; Mach, 1875; Tshermak, 1931). This laboratory research has shown that optic flow can generate robust linear and rotational vection in physically stationary observers (Brandt *et al.*, 1973; Johansson, 1977).

The vestibular system of the inner ear can only detect active and passive accelerations of the head (Howard, 1982). These sensory organs have a 3-D arrangement, which allows them to transduce physical movements of the head with six degrees of freedom. Their inertial and viscous properties make them sensitive to accelerations of the head, which are converted into displacements of the cristae of the three semicircular canals (angular acceleration detectors) and the maculae of the two otolith organs, the utricle and the saccule (linear acceleration detectors), and are sensed by hair cell mechanoreceptors attached to these structures (Benson, 1990).

Kinesthesia, the sense of the movement and position of the limbs and joints, can indicate actual or intended self-motion. During active self-motions, expectations of motor action can be encoded to provide an internal representation of intended self-motion (von Holst and Mittelstaedt, 1950; Sperry, 1950). There is compelling evidence that the nervous system relies on these 'efference' copies for judgments of self-motion. Afferent kinesthesis from the proprioceptive system of muscle and joint receptors is able register the kinematics of self-motion, as well as active self-accelerations based on the inertia of a person's limbs (Lishman and Lee, 1973).

The somatosensory system of cutaneous receptors is able to register both active and passive self-motions relative to the surface of support, based on the pressure and shear forces acting on an individual's skin (Lee and Lishman, 1975) and even more subtle cues such as wind on the face during high-speed locomotion.

Finally, the auditory system can signal self-motion in certain situations. For example, auditory illusions of self-motion can be induced in blindfolded listeners by physically moving surrounding sound sources (Dodge, 1923; Lackner, 1977). Spatial audition can localize sound sources based on cues such as spectral shaping by the external ear, signal intensity, as well as interaural temporal/intensity differences. Changes to these cues can signal changes in the distance and direction of the observer with respect to his/her auditory environment.

1.1. Visual and Vestibular Self-motion Perception

Research shows that of the above self-motion senses, the visual and vestibular systems appear to play particularly important roles (Howard, 1982). Thus, while we will talk about sensory integration and sensory conflict throughout this review, the focus will be primarily on the role that the visual and vestibular systems play in the perception of self-motion. These two senses appear to be specialized for perceiving complementary types of self-motion (Dichgans and Brandt, 1978; Howard, 1982; Lishman and Lee, 1973). While vision can potentially detect all types of self-motions (both active and passive, linear and rotary, accelerating and constant velocity self-motions), it is thought to be most sensitive to low temporal frequency optic flow (i.e., below 1 Hz) and constant velocity self-motion (e.g., Berthoz *et al.*, 1975; Previc, 2003). Conversely, the vestibular system appears to be primarily sensitive to brief, high-frequency stimulations (see Note 2) (i.e., greater than 1 Hz: Diener *et al.*, 1982; Melville-Jones and Young, 1978) and is unable to distinguish between traveling at a constant linear velocity and remaining stationary (Lishman and Lee, 1973).

2. Sensory Conflict Theories of Self-motion Perception and Motion Sickness

In many situations, self-motion is redundantly specified by the information from all of the above sensory systems (Gibson, 1966). However, there are numerous situations where the self-motion information provided by one or more of these senses apparently conflicts with the others (Oman, 1982; Reason, 1978; Reason and Brand, 1975). While not all researchers accept the concept of 'sensory conflict' (Riccio and Stoffregen, 1991; Stoffregen and Riccio, 1991), it remains the most widely accepted explanation of motion sickness. According to Reason's (1978) original sensory conflict theory, motion sickness occurs when the signals from the different self-motion senses disagree either with each other or with what is expected from previous experience. Oman (1982) later provided a mathematical foundation for this neural mismatch model, where the degree of motion sickness experienced was determined by the difference between a vector representing all of the current sensory information and a vector representing the expected sensory information. Over the years, sensory conflict theories have been frequently modified and refined, with theorists defining sensory conflict in different ways. While most versions have focused on explaining motion sickness, they can and have been used to make strong predictions about self-motion perception and vection (e.g., Zacharias and Young, 1981).

2.1. Definitions of Sensory Conflict

In their critical review of sensory conflict theories, Stoffregen and Riccio (1991) identified three general types of conflict. (i) 'Input conflicts' generated when two or more sensory inputs are non-redundant (e.g., such a conflict could arise when optic flow indicates accelerating self-motion, but the lack of vestibular stimulation

suggests that the observer is stationary). (ii) 'Output conflicts' generated by intersensory differences in sensitivity (e.g., such a conflict could arise when both the visual and vestibular inputs signal the observer's self-acceleration, but the vestibular system is more sensitive to this acceleration than vision); and (iii) 'Expectancy violations' where, based on previous experience, we form expectations about the sensory inputs and outputs that should accompany most self-motions. Any differences between current and expected sensory inputs, or between current and expected sensory outputs, should therefore give rise to this type of sensory conflict.

It is worth noting that Stoffregen and Riccio themselves argue that there are in fact no situations of sensory conflict (Stoffregen and Riccio, 1991; Riccio and Stoffregen, 1991). Instead they refer to multisensory patterns of self-motion stimulation as either being 'redundant' or 'non-redundant'. They argue that each multisensory pattern of self-motion stimulation, irrespective of whether it is redundant or not, represents a specific type of self-motion (e.g., an alternating expanding and contracting optic flow without corresponding somatosensory information might specify sway on a non-rigid, as opposed to a rigid, surface).

2.2. Sensory Conflict and Self-motion Perception

In the 1970s, David Lee and his colleagues suggested that the simplest solution to most situations of sensory conflict would be for vision to dominate self-motion perception (Lee and Lishman, 1975; Lishman and Lee, 1973). Consistent with this notion of visual dominance, they found that vection could be quickly induced by swinging the walls and ceiling of an experimental room back and forth around a stationary, upright observer. This compelling back-and-forth vection occurred, and was even accompanied by compensatory postural sway, despite the presumably salient conflicts between the visual stimulus and the available non-visual self-motion cues.

While this 'visual dominance' solution to sensory conflict is attractive in its simplicity, it appears incompatible with much of the existing literature. Importantly, it has difficulty explaining the empirically observed time course for vection (Brandt *et al.*, 1973; Dichgans and Brandt, 1978; Held *et al.*, 1975; Telford and Frost, 1993; Young *et al.*, 1975). During their first few seconds of exposure to large patterns of optic flow, stationary observers typically perceive the visual motion as being entirely due to scene motion, followed shortly afterwards by perceptions of combined self- and object-motion, and finally by the experience of exclusive self-motion (if the other characteristics of the visual stimulus are also favorable for vection induction). A sensory conflict account of this vection time course is presented in the section below.

3. Sensory Conflict and Vection

Zacharias and Young's (1981) version of sensory conflict theory summarizes the most widely accepted account of the vection time course (see Fig. 1). According

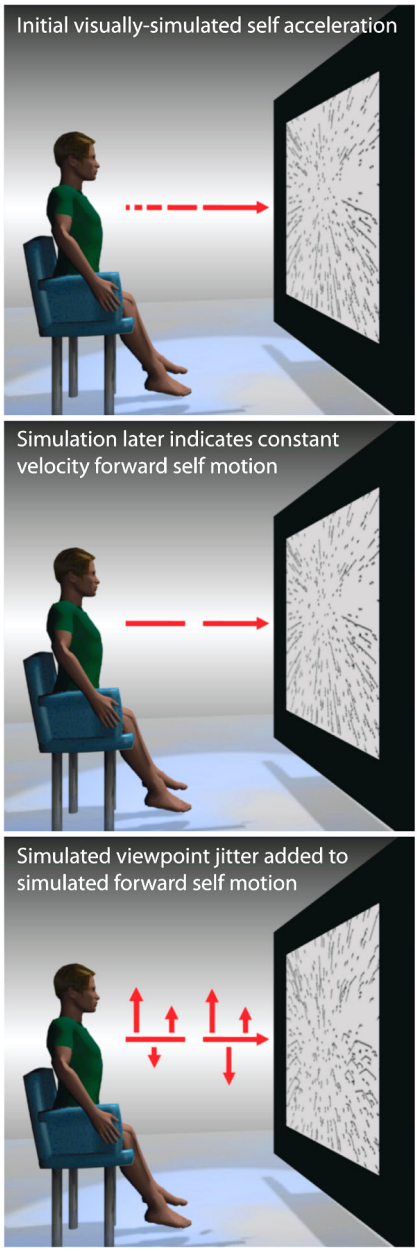


Figure 1. Sensory conflict account of vection and its time course. This figure is published in colour in the online version.

to this theory, a salient visual–vestibular conflict is generated when stationary observers are first exposed to a large pattern of optic flow and it is this sensory conflict which prevents them from experiencing exclusive (or any) vection straight away. This visual–vestibular conflict arises because: (i) these observers expect to be ac-

celerated up to the speed of self-motion specified by the optic flow; and (ii) the vestibular stimulation that would normally accompany this type of self-acceleration is absent. As a result, the optic flow is initially perceived as being due entirely to scene-motion. However, if the optic flow being presented to these stationary observers simulates constant velocity self-motion, then this initially salient visual–vestibular conflict should fade rapidly (as vestibular stimulation would no longer be expected), and from that time onwards observers should be free to experience compelling/exclusive vection. By contrast, visual–vestibular conflicts should persist and prevent the induction of compelling vection when the optic flow presented to stationary observers simulates large and frequent changes to the direction and speed of their self-motion, since significant and sustained vestibular activity would always be expected to accompany these types of accelerating optic flow patterns.

Support for the above sensory conflict account of the vection time course was initially provided by a series of studies on circular vection. Consistent with the notion that compatible visual–vestibular stimulation should improve vection, these studies showed that circular vection onset latency could be reduced by giving the observer a brief initial physical acceleration in the visually simulated direction of self-rotation (Brandt *et al.*, 1974; Melcher and Henn, 1981; Wong and Frost, 1981). Other studies showed that circular vection could be destroyed by briefly accelerating the observer in the opposite direction to the visually simulated self-rotation (Teixeira and Lackner, 1979; Young *et al.*, 1973).

Several studies on linear vection also appeared to provide support for this sensory conflict-based explanation of vection and its time course. For example, Giannopulu and Lepecq (1998) showed that the vestibular system was more sensitive to horizontal, than to vertical, physical head translations, and claimed that this difference in sensitivity was responsible for their finding that vertical vection had a shorter onset latency than horizontal vection. Similarly, Bonato and colleagues (2008) found that constantly expanding patterns of optic flow (expected to generate only minimal or transient sensory conflicts) induced more compelling vection in depth and less motion sickness in stationary observers than optic flow which alternated between expansion and contraction (expected to generate significant and sustained sensory conflicts).

4. Research on Simulated Viewpoint Jitter

A number of recent studies have produced vection results that are incompatible with the predictions made by sensory conflict theories. For example, most stationary, upright observers experience complete (360°) illusions of self-rotation when placed inside a large, fully-furnished room rotating about roll or pitch — despite significant conflicts between their visual, vestibular, somatosensory and proprioceptive information (Allison *et al.*, 1999; Howard and Childersen, 1994; Palmisano *et al.*, 2006). These studies show that compelling vection can still be induced in situations thought to generate very salient sensory conflicts. However, an even stronger

challenge to sensory conflict-based explanations of vection has been posed by the findings of a study by Palmisano *et al.* (2000) (see also Snowden's (2000) commentary of this paper). They found that a new type of visual self-motion display thought to generate greater conflicts actually produced *more compelling vection* than comparable self-motion displays thought to generate little or no conflict.

4.1. Effects of Simulated Viewpoint Jitter on Vection

According to sensory conflict theories, optic flow which simulates large and frequent changes to the direction and speed of self-motion should generate significant and sustained sensory conflicts in stationary observers, which in turn should prevent the induction of compelling vection. Palmisano *et al.* (2000) tested this prediction by presenting jittering and non-jittering patterns of optic flow to stationary observers (see the top two diagrams in Fig. 2).

Both types of optic flow contained an identical radial flow component, which simulated the same constant velocity forward self-motion in depth. However, jittering displays also contained an additional flow component, which simulated continuous, random horizontal and/or vertical jitter of the observer's viewpoint (similar to the effects of 'camera shake'). The amplitude of this random jitter, which occurred on every frame of these 30 Hz displays, ranged between 0–1/3 of the simulated forwards displacement (in Experiment 1 of this paper). Contrary to the predictions of sensory conflict theories, we found that the vection induced by: (i) jittering displays started sooner and lasted longer than that induced by non-jittering displays (even though the added display jitter was expected to substantially increase the level of sensory conflict); and (ii) displays simulating combined horizontal-and-vertical viewpoint jitter were not significantly different to that induced by displays which only simulated jitter along one axis (even though jitter along two axes should have generated more sensory conflict) (see Fig. 3).

Subsequent research has shown that simulated horizontal and/or vertical viewpoint jitter not only reduces vection onsets and increases vection durations, but it also increases the perceived strength and speed of the forwards (or backwards) vection induced by radial patterns of optic flow (Palmisano *et al.*, 2003, 2008, 2009; Palmisano and Chan, 2004). This simulated viewpoint jitter has even been shown to induce modest horizontal/vertical vection by itself (i.e., when presented without radial flow), which demonstrates that vection can be induced during extreme mismatches between actual and expected vestibular activity (Palmisano *et al.*, 2003). These jitter advantages for vection appear to be remarkably robust to changes to the amplitude (e.g., 0–1/3 to 0–1/5 of the forward speed) and/or the capping frequency (e.g., 0.5–15 Hz) of this simulated random viewpoint jitter (see Fig. 4), as well as the simulated forward speed (Palmisano *et al.*, 2000, Experiments 2 and 3; Palmisano *et al.*, 2008, Experiment 1).

While horizontal viewpoint jitter has been shown to improve vection in depth in a very similar fashion to vertical viewpoint jitter, viewpoint jitter in depth appears to have less (or sometimes no) effect on the experience of vection in depth

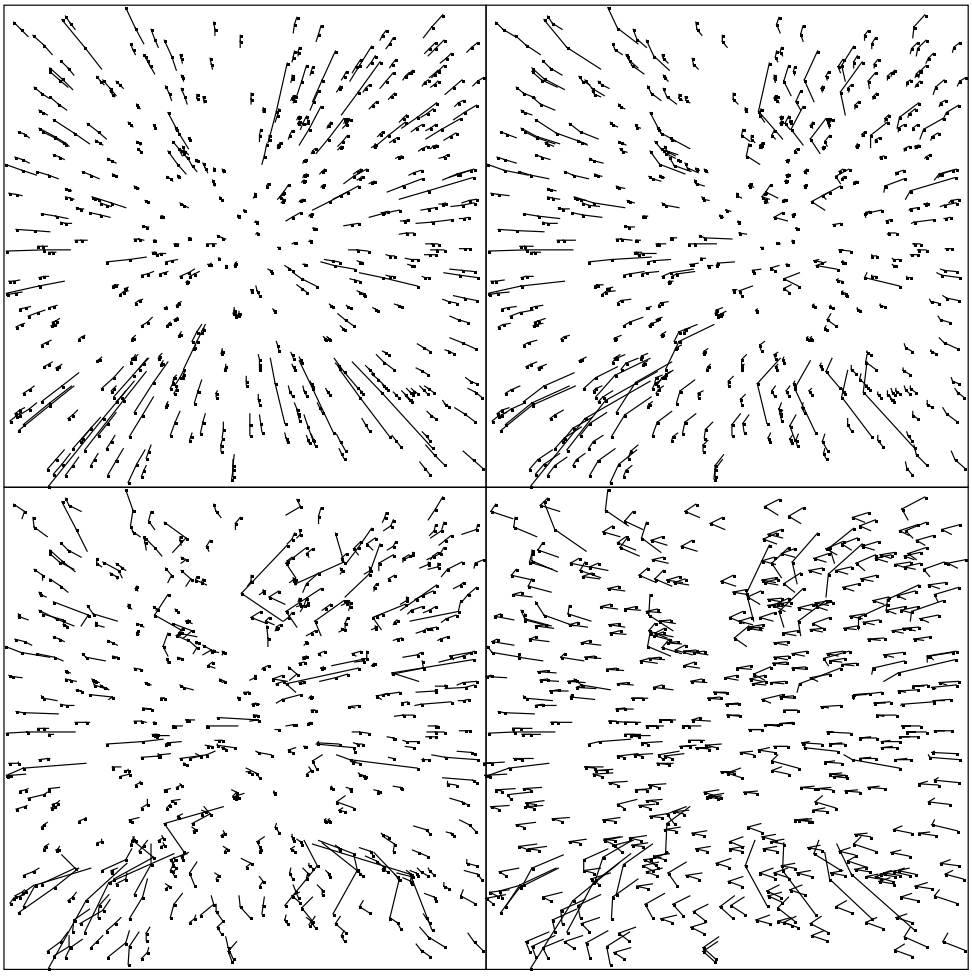


Figure 2. Velocity-field representations of the jittering and non-jittering optic flow used in Palmisano *et al.* (2003). Radial flow with no jitter (top-left) *versus* radial flow with either horizontal 'coherent perspective jitter' (top-right), horizontal 'incoherent perspective jitter' (bottom-left) or horizontal 'coherent non-perspective jitter' (bottom-right). Vertical jitter and combined horizontal and vertical jitter were also tested.

(Palmisano *et al.*, 2008). Thus, it appears that simulated viewpoint jitter has the greatest effect on vection when it is orthogonal to the main component of the visually simulated self-motion (Nakamura, 2010; Palmisano *et al.*, 2008; Palmisano and Keane, 2004). Consistent with this notion, simulated vertical and depth (but not horizontal) viewpoint jitter have both been found to improve the sideways vection induced by lamellar patterns of optic flow (Palmisano and Keane, 2004). For the rest of this section, the review will focus on the role that horizontal and vertical (not depth) jitter has on vection.

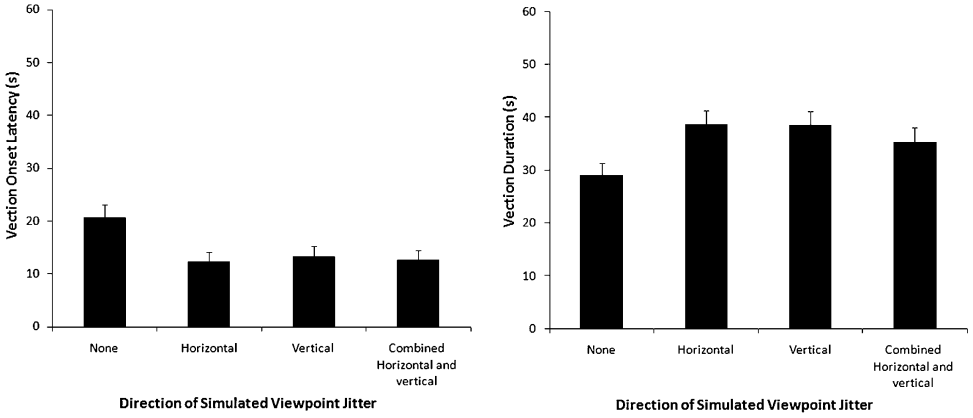


Figure 3. A replication of the original viewpoint jitter advantage for vection. Stationary observers viewed each self-motion display for 60 s (with a 20 s ISI between trials). As can be seen above, adding simulated horizontal and/or vertical viewpoint jitter to radial flow significantly reduced vection onset latencies and increased vection durations (compared to non-jittering patterns of radial flow). This new figure was created based on a subset of the data reported by Palmisano and Chan (2004).

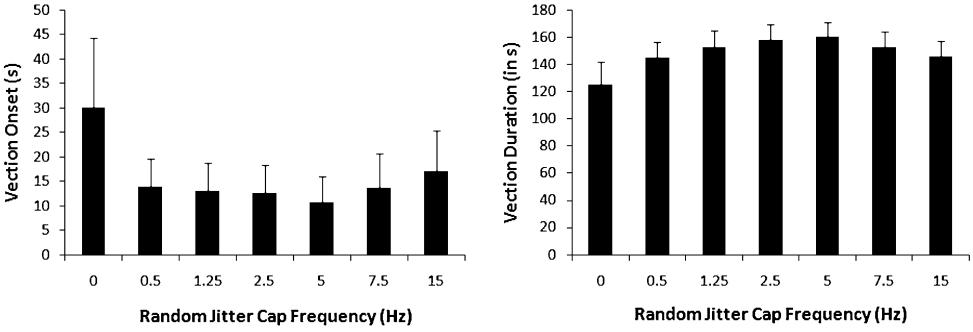


Figure 4. Effects of jitter capping frequency on vection onsets and durations (based on data from Experiment 3 of Palmisano *et al.*, 2000). Random simulated horizontal-and-vertical viewpoint jitter was added to radially expanding flow and stationary observers viewed these self-motion displays for 3 min. Since the sign and magnitude of this random jitter varied from one jitter frame to the next, it is best represented as a range of frequencies — both high and low — limited by the update rate (i.e., extending from zero to the capping frequency defined by the Nyquist limit of half of the update rate). Seven different random jitter capping frequencies were examined in this experiment: 0, 0.5, 1.25, 2.5, 5, 7.5 and 15 Hz. At one extreme (0), jitter was never applied to the display. At the other extreme (15 Hz), jitter was applied on every frame of the 30 Hz display. Please note that in the original paper these jitter frequencies were reported as the update rate rather than the capping frequency; thus they were double the frequencies used here (i.e., 0, 1, 2.5, 5, 10, 15 and 30 Hz *versus* 0, 0.5, 1.25, 2.5, 5, 7.5 and 15 Hz).

4.2. Effects of Other Types of Jitter on Vection

Palmisano *et al.* (2003) described simulated viewpoint jitter as 'coherent perspective jitter' in order to distinguish it from: (i) 'incoherent perspective jitter', where all of the objects jittered independently from each other (similar to the flow produced

when driving through a snow-storm — see Fig. 2, bottom-left); and (ii) 'coherent non-perspective jitter', where all of the objects were jittered by identical amounts irrespective of their simulated location in depth (similar to watching 3-D flow on a display that is being physically moved up-down or left-right — see Fig. 2, bottom-right). Unlike the original study, the random jitter in the Palmisano *et al.* (2003) study was capped at 37.5 Hz (not 15 Hz). We found that while incoherent jitter impaired the vection in depth induced by radial flow, coherent non-perspective jitter had little effect on this subjective experience (see Note 3). Thus, in this study (with its higher jitter capping frequencies), only coherent perspective jitter appeared to improve the experience of vection in depth induced by radial flow.

Similar vection advantages can be produced by adding horizontal/vertical simulated viewpoint oscillation to radial and lamellar patterns of constant velocity optic flow (Kitazaki and Hashimoto, 2006; Nakamura, 2010; Palmisano *et al.*, 2007, 2008; Palmisano and Kim, 2009). As with the simulated viewpoint jitter advantage for vection, this simulated viewpoint oscillation advantage is remarkably robust to changes in amplitude (0–1/3 to 0–1/5 of the forwards speed) and frequency (0.14–7.4 Hz). One study by Palmisano *et al.* (2008) compared the vection in depth induced by simulated horizontal/vertical viewpoint jitter (random, broadband simulated head perturbations capped at 15 Hz — see Fig. 5, middle) and simulated horizontal/vertical viewpoint oscillation (periodic 0.14 or 0.3 Hz simulated head perturbations — see Fig. 5, right). Despite the marked differences in these two types of simulated self-acceleration (in terms of predictability, amplitude and frequency), they were found to improve vection in depth in a remarkably similar fashion. Horizontal and vertical simulated viewpoint jitter and oscillation both significantly decreased the onsets and increased the speeds of the vection in depth induced by radially expanding optic flow (Fig. 5, left).

The above studies all looked at the effects of simulated *linear* head jitter and oscillation on vection. More recently, we and others have also examined the effects on vection of adding simulated *angular* eye oscillation to radial flow (Kim *et al.*, subm.; Kitazaki and Hashimoto, 2006). Kim and colleagues found that simulated

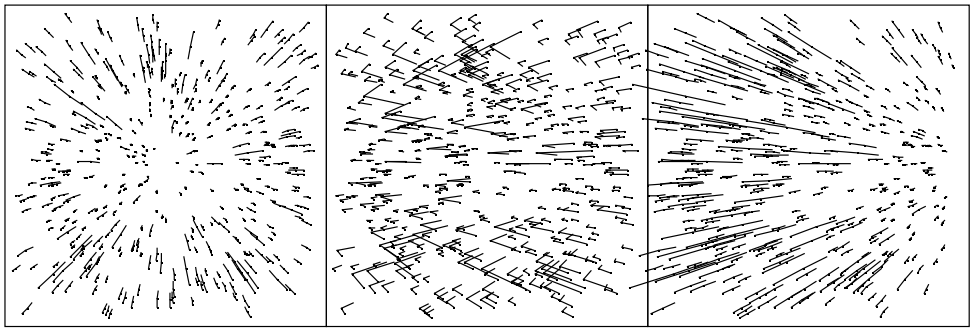


Figure 5. Velocity field representations of non-jittering, horizontally jittering and horizontally oscillating radial flow patterns similar to those examined by Palmisano *et al.* (2008).

horizontal eye oscillation improved vection in depth in a very similar fashion to horizontal linear head oscillation (even though simulated linear head oscillation would have provided additional motion parallax based information about the 3-D layout, whereas simulated eye oscillation would not). Similarly, Kitazaki and Hashimoto (2006) reported that simulated vertical eye oscillation improved vection in depth in a very similar fashion to simulated vertical linear head oscillation. Taken together, these findings suggest that while added jitter/oscillation generally needs to be coherent and orthogonal to the main component of the simulated self-motion, it does not necessarily need to be altered according to perspective in order to improve vection.

4.3. Multisensory Viewpoint Jitter and Vection

Several recent studies have presented computer-generated patterns of jittering optic flow to observers both when they were physically moving and stationary. In physical self-motion conditions, subjects either moved themselves or were moved, and their head motions were then tracked and used to adjust the locations of their simulated viewpoints in the virtual environment (i.e., updating the self-motion display in real-time — see Fig. 6). In control conditions, the now stationary subjects viewed playbacks of the displays generated by their own head motions in previous physical self-motion trials. In the first of these studies, Wright *et al.* (2005) found that synchronizing their display oscillation *in-phase* with (0.2 Hz, up to $\pm$0.8 m) whole-body vertical oscillation produced compelling experiences of self-motion. However, the perceived self-motion induced by this consistent multisensory stimulation was not significantly different to the vection induced by visual stimulation alone. Subsequent studies by Kim and Palmisano (2008, 2010a) used both actively-generated and passively-viewed displays which simulated horizontal viewpoint oscillation

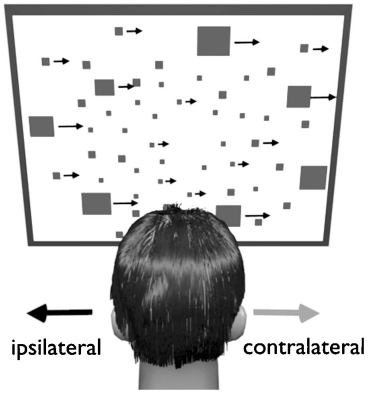


Figure 6. A representation of the *in-phase* and *out-of-phase* horizontal display oscillation conditions used in the Kim and Palmisano (2010a) study. When the observer moved his/her head, the display either moved in-phase (i.e., in the opposite/ipsilateral direction relative to the head) or out-of-phase (i.e., in the same/contralateral direction relative to the head). The amplitude of the display motion was determined by the size of the observer's tracked head motion.

combined with constant velocity forward self-motion. Consistent with the earlier findings of Wright *et al.* (2005), Kim and Palmisano (2008) found that actively generating *in-phase* (1 Hz, ±8 cm) display oscillation provided no further benefit to vection in depth. The experience of self-motion in these conditions was no different to the vection induced in the oscillating playback conditions (which were both superior to the vection induced by active and passive control conditions using non-oscillating patterns of radial flow). Even more recently, Kim and Palmisano (2010a) found that active conditions where the displays oscillated *out-of-phase* with the observer's physical head motion produced very similar vection ratings to *in-phase* display oscillation (see Fig. 6). Taken together, these findings suggest that visually jittering information about self-motion dominates vestibular and other non-visual information about self-motion (at least for the somewhat limited range of physical head jitter frequencies and amplitudes that have been tested so far).

4.4. Effects of Viewpoint Jitter on Postural Sway and Motion Sickness

Sensory conflict theories predict that simulated viewpoint jitter/oscillation should reduce the vection and increase the motion sickness induced by radial flow simulating constant velocity forwards self-motion. To test these predictions, Palmisano *et al.* (2007) examined the effects that simulated viewpoint oscillation had on the development of vection and simulator sickness in normal subjects. During 10 min trials (each run on a separate day), subjects rated the strength of their vection and simulator sickness at 2 min intervals — simulator sickness was measured using the Simulator Sickness Questionnaire (SSQ; Kennedy *et al.*, 1993) and the Subjective Symptoms of Motion Sickness scale (SSMS; Bubka and Bonato, 2003). Consistent with the predictions of sensory conflict theories, vertically oscillating radial flow was found to produce more simulator sickness than non-oscillating radial flow — with symptom severity increasing with the oscillation frequency from 1.8 to 7.4 Hz (see Fig. 7, right). However, contrary to the predictions of sensory conflict theories, vertically oscillating displays were still found to significantly increase vection (compared to non-oscillating displays) and there was no significant effect of oscillation frequency on vection (see Fig. 7, left). Thus, while sensory conflict may still be a viable explanation of motion sickness, it is clear that expectations about visual–vestibular conflict do not predict the vection induced by jittering/oscillating patterns of optic flow.

Current sensory conflict theories also appear unable to explain the effects of simulated viewpoint jitter/oscillation on visually induced postural sway. Kitazaki and Hashimoto (2006) showed their upright, standing subjects radial flow displays which alternated between expansion and contraction. They found that while adding 0.96 Hz simulated vertical viewpoint oscillation to these radial flow displays significantly increased their subjects' vection in depth, it appeared to have little effect on their visually induced (anterior–posterior) postural sway. By contrast, Palmisano and colleagues (2003, 2009) examined the anterior–posterior sway of upright, standing observers when simulated horizontal-and-vertical random viewpoint

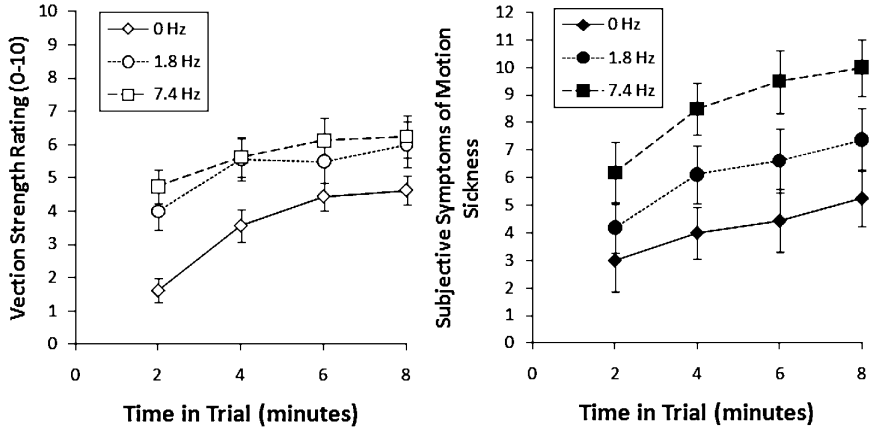


Figure 7. Mean vection strength (left) and subjective symptoms of motion sickness (right) ratings for radial flow displays with 0, 1.8 and 7.4 Hz simulated vertical viewpoint oscillation. This new figure was created based on a subset of the data reported by Palmisano *et al.* (2007).

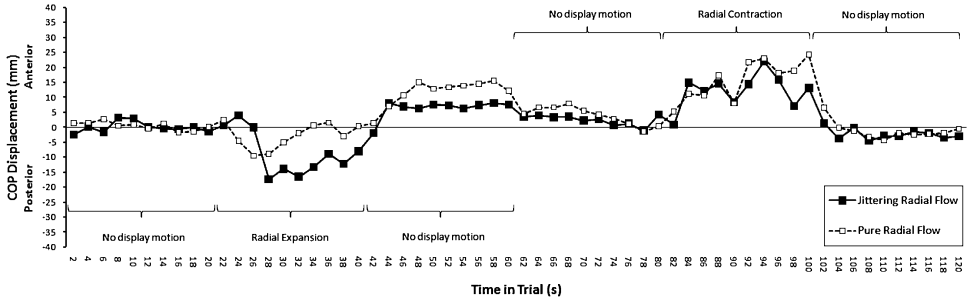


Figure 8. Anterior–posterior centre of foot pressure (COP) displacement data from a single representative subject (NM) during exposure to jittering and non-jittering patterns of radial optic flow. There were 6 different 20 s trial phases: no display motion (baseline 1), radial expansion (with/without jitter), no display motion (postural sway after-effects 1), no display motion (baseline 2), radial contraction (with/without jitter), and finally no display motion (postural sway after-effects 2). Mean COP data are shown for each 2 s time interval. This new figure was created based on a subset of the data reported by Palmisano *et al.* (2009).

jitter (capped at 15 Hz) was added to either constantly expanding or constantly contracting patterns of radial flow. We found that, compared to non-jittering trials, this random jitter: (i) increased both the backwards vection and the posterior sway produced by constant radial expansion; and (ii) increased the forwards vection, but not the anterior sway, produced by constant radial contraction (see Fig. 8).

We reconciled the results of these two sway studies by suggesting that the asymmetrical effects of oscillation on anterior–posterior sway may have cancelled each other out in the Kitazaki and Hashimoto study. That is, because their radial flow alternated between expanding and contracting, viewpoint oscillation-based increases in posterior sway might have cancelled or masked the viewpoint oscillation-based

decreases in anterior sway. A control experiment demonstrated that our asymmetrical sway findings could not be explained simply by differences in vection strength (simulated viewpoint jitter was found to increase forward and backward vection in a very similar fashion). Thus, we argued that these asymmetrical effects of jitter on postural sway were ecological in origin and could be explained by the biomechanical constraints of our feet (see Edwards and Ibbotson, 2007). This ecological or biomechanical explanation of jitter effects on postural sway is discussed in detail later in Section 4.8.

The jitter/oscillation findings outlined in this section suggest that the processes involved in postural control and motion sickness may be more sensitive to sensory conflicts than those involved in the perception of self-motion and vection. They also suggest that vection, motion sickness and postural control differ in their dependence on non-visual physiological processes underlying sensory conflict. These differences are likely to become more evident in situations that both induce more compelling vection and generate greater sensory conflict. We propose that under these specific circumstances, non-visual information (arising from vestibular, proprioceptive and somatosensatory inputs) appears to play a more dominant role in postural control and motion sickness.

5. Explanations of the Viewpoint Jitter Advantage for Vection

Viewpoint jitter effects on vection (and postural sway) cannot be explained by existing sensory conflict theories. However, over the last decade a number of alternative explanations have been proposed and tested. It has been shown that the viewpoint jitter advantage for vection persists even when experimental instructions and demands strongly bias participants towards object motion (Palmisano and Chan, 2004). Alternative perceptual and neurophysiological explanations are outlined below and the available evidence for and against each is discussed (see Table 1 for an overall summary of this evidence).

5.1. Viewpoint Jitter Makes the Simulated Environment Appear More 3-D

Andersen and Braunstein (1985) found that optic flow which appeared more 3-D (based on simulated dot speed and density) also induced more compelling experiences of vection in depth. Thus, it was possible that simulated horizontal/vertical viewpoint jitter might have increased the vection in depth induced in our studies by providing an additional motion parallax cue to the layout of the simulated 3-D environment. Palmisano and Chan (2004) tested this prediction by obtaining ratings of scene depth and vection strength from physically stationary observers viewing jittering and non-jittering patterns of 3-D radial flow. Contrary to this proposal, simulated horizontal/vertical viewpoint jitter significantly improved the forward vection induced by radial flow, but had no significant effect on the perceived depth represented by these computer-generated displays. Recently, Nakamura (2010) has shown that simulated horizontal viewpoint oscillation also improves the vertical

Table 1.
This table is an attempt to summarize the evidence for and against the main theories of the simulated viewpoint jitter advantage for vection. ✓: consistent with theory; x: inconsistent with theory; –: relationship to the theory is currently unknown. Display manipulations (unless explicitly stated added display motion is horizontal and/or vertical): SVJO: simulated viewpoint jitter and oscillation; IJO: incoherent jitter and oscillation; CVGM: constant velocity global motion; DSVJO: Simulated viewpoint jitter and oscillation in depth; SEJO: simulated eye oscillation (i.e., angular viewpoint oscillation); VID: vection in depth; VIFP: vection in the frontal plane

Theories	SVJO reduces VID onset	SVJO increases VID duration	SVJO increases VID speed	IJO impairs VID & VIFP	SVJO improves VIFP from 2-D flow	SVJO improves VID with stable central fixation	SVJO effects robust to large changes in both jitter amp & freq	SEJO also improves VID	CVGM does not improve VID	SVJO increases motion sickness	SVJO increases backward sway	SVJO reduces forward sway	SVJO does not make scene appear more 3-D	SVJO produces shorter MAEs & longer VAEs	Fixation point oscillation also improves VID	Active & Passive SVJO produce similar eye-motions	DSVJO increases PIVC activity
Sensory conflict theory	x	x	x	–	x	x	x	–	x	✓	x	✓	–	–	–	x	x
Scene appears more 3-D	–	–	✓	–	x	–	–	–	x	–	–	–	x	–	–	–	–
Scene appears more rigid	–	–	–	✓	–	✓	x	–	x	–	–	x	–	–	–	–	–
Reduced adaptation	x	✓	✓	x	✓	✓	✓	✓	✓	–	✓	x	–	✓	✓	–	–
Causes path integration errors	–	–	✓	–	✓	–	–	x	x	–	✓	x	–	–	✓	–	–
Vestibular suppression	–	–	–	–	–	–	–	–	–	x	–	x	–	–	–	–	x
Indirect vestibular stimulation	✓	✓	✓	–	✓	– or x	–	✓	✓	–	✓	x	–	–	✓	✓	✓
Increased retinal slip	✓	✓	✓	–	✓	✓	✓	✓	–	–	✓	x	–	–	✓	✓	–
Display is more ecological	✓	✓	✓	✓	✓	–	✓	✓	✓	–	✓	✓	–	–	–	✓	✓

vection induced by 2-D patterns of lamellar flow. Furthermore, several recent studies appear to show that simulated horizontal/vertical eye oscillation improves vection induced by radial flow in a similar fashion to simulated horizontal/vertical linear head oscillation (Kim *et al.*, subm.; Kitazaki and Hashimoto, 2006). Unlike linear head oscillation, this simulated eye oscillation provides little/no additional motion parallax based information about the 3-D layout of the environment. Taken together, the above findings conclusively demonstrate that simulated viewpoint jitter/oscillation does not improve vection by increasing the perceived 3-D layout of the optic flow display.

5.2. Viewpoint Jitter Makes the Simulated Environment Appear More Rigid

Simulated viewpoint jitter might have also improved vection indirectly by making the simulated environment appear more rigid. Nakamura (2010) tested this hypothesis using 2-D lamellar flow which simulated 15°/s downwards self-motion combined with horizontal/vertical oscillation (amplitude 12°/s; frequency 1 Hz). In his first experiment, Nakamura found that coherent (horizontal but not vertical) display oscillation improved the vertical vection induced by lamellar flow, whereas incoherent (horizontal and vertical) display oscillation impaired it. In a follow-up experiment, Nakamura examined the effects of display oscillation which was always coherent, but not uniform (oscillation amplitude varied across the display, determined by the horizontal position of the dots). Consistent with his rigidity account of the jitter advantage for vection, Nakamura found that as the amplitude gradient of the horizontal display oscillation increased, subjects' ratings of the perceived rigidity of the environment and vertical vection both decreased. Thus, it is possible that coherent perspective jitter might also have acted to increase the perceived rigidity of the 3-D environments and the vection in depth induced in our earlier experiments by radial flow. However, by itself, this 'rigidity hypothesis' would have difficulty explaining the asymmetric/different effects that simulated viewpoint jitter has on visually induced postural sway (Kitazaki and Hashimoto, 2006; Palmisano *et al.*, 2009). Importantly, the effects of jitter/oscillation on perceived rigidity have yet to be tested/confirmed with the 3-D radial flow stimuli typically used in most previous studies.

5.3. Viewpoint Jitter Produces Errors in Path Integration

It is possible that simulated horizontal/vertical viewpoint jitter may have improved vection in depth by producing path errors. In principle, adding linear simulated horizontal/vertical viewpoint jitter to radial flow might not only increase the perceived speed of self-motion in depth, but also the perceived speed of self-motion in the frontal plane (the end result being a perceived piece-wise 3-D curvilinear trajectory of self-motion). In our jitter/oscillation experiments, observers were typically instructed to report only the vection in depth component (rather than the net vection). Thus, it was possible that the vection advantage for viewpoint jitter might have occurred simply because path errors artificially increased the observer's perceived

speed of vection in depth (if they underestimated the magnitude of their simulated horizontal/vertical linear excursions and misattributed some of this display motion to self-motion in depth). Consistent with this notion, we have repeatedly found that horizontal/vertical jitter increases the perceived speed/strength of vection in depth, even though the simulated forward speed of self-motion was always identical in jittering and non-jittering displays (e.g., Kim and Palmisano, 2008; Palmisano *et al.*, 2008). However, the findings of several control experiments are inconsistent with this path error explanation. For example, Palmisano *et al.* (2008; Experiment 2) showed that adding constant velocity (as opposed to accelerating) horizontal/vertical simulated self-motion to radial flow had no significant effect on vection in depth (either in terms of vection onset latency or vection in depth speed ratings). Also contrary to this notion, we have recently found that adding simulated eye oscillation to radial flow improves vection in depth in a very similar fashion to adding simulated linear head oscillation — even though only the latter type of display resulted in horizontal excursions.

5.4. Viewpoint Jitter Suppresses Vestibular Cortical Activity

Several PET and fMRI studies have found evidence of reciprocal visual–vestibular interactions during perceived self-motion. When stationary observers view optic flow displays simulating constant velocity self-rotation (Brandt *et al.*, 1998) or self-translation (Deutschländer *et al.*, 2004), activity appears to increase in cortical areas implicated in visual self-motion processing (e.g., the dorsal medial superior temporal region or MSTd) and simultaneously decreases in an area implicated in vestibular self-motion processing (e.g., parieto-insular vestibular cortex or PIVC) — relative to conditions where the optic flow shown to the stationary observer was consistent with object/scene motion. In principle, such cortical suppression of any potential sensory conflict arising from vestibular signals could explain why simulated viewpoint jitter/oscillation does not impair the vection induced in stationary observers. However, by itself, it cannot explain why jittering/oscillating displays should produce more compelling vection in depth than non-jittering displays.

5.5. Viewpoint Jitter Indirectly Stimulates the Vestibular Cortex

Another problem for the above vestibular suppression account is that both visual and vestibular cortical areas appear to be excited when stationary observers experience visual illusions of linear self-acceleration (as opposed to visual illusions of constant velocity linear or rotary self-motion) — see Note 4. Nishiike *et al.* (2002) measured neuromagnetic responses in stationary observers when visually simulated self-acceleration in depth was intermittently added to a baseline constant-velocity radial flow pattern. They found that this visually simulated self-acceleration increased activity in a region of cortex that was anatomically consistent with the location of PIVC. Unlike vestibular suppression, this type of indirect vestibular stimulation has the potential to explain the viewpoint jitter advantage for vection. Since both the (direct) visual and the (indirect) vestibular cortical stimulation should

be compatible in this situation, we would expect that the resulting vection experience should be more compelling than that arising from visual cortical activation alone (e.g., by non-jittering radial flow simulating constant velocity self-motion).

One of our reviewers correctly noted that by itself, Nishiike *et al.*'s finding cannot fully explain our jitter/oscillation advantages for vection, since: (i) this indirect vestibular stimulation was produced when simulated depth jitter was added to a constant velocity radial flow display; and (ii) we have found that horizontal and vertical jitter improves the vection in depth induced by this type of radial flow more than depth jitter. However, Palmisano *et al.* (2008) did find that depth jitter and oscillation could still significantly improve the speed of vection in depth induced by constant velocity radial flow. Thus, it is possible that these more modest depth jitter and oscillation advantages for vection speed were due to indirect vestibular stimulation.

Further research using neurophysiological and neuroanatomical techniques is needed to determine whether simulated horizontal and vertical viewpoint jitter also produce indirect vestibular stimulation. For now, all we can say is that: (i) Nishiike *et al.*'s results show that indirect vestibular stimulation can occur using an experimental jitter manipulation that is somewhat similar to ours; and (ii) the so-called 'vestibular cortex' not only receives and processes vestibular information about self-acceleration, but it also receives and processes visual information about self-acceleration as well.

One way that this indirect vestibular stimulation might arise during vection is when the head-stationary observer makes compensatory eye-movements in response to the jittering/oscillating optic flow. Given that such eye-movements are often driven by a combination of visual and vestibular inputs, a relationship between optokinetic eye movements, vection and indirect vestibular stimulation is possible. Consistent with this notion, Kim and Palmisano (2008, 2010a) found that actively-generated and passively-viewed display oscillation not only produced very similar vection experiences, but they also produced very similar compensatory eye movements (see Fig. 9, left). Thus, one possible explanation for the jitter advantage in vection is that jitter-induced optokinetic responses (OKRs) indirectly stimulated the vestibular cortex of our stationary subjects (e.g., *via* the mid-brain oculomotor pathways). It should be noted, however, that this eye-movement based explanation would have difficulty accounting for why the jitter advantage for vection persists when the observer keeps his/her eyes stationary (e.g., Palmisano and Kim, 2009).

5.6. Viewpoint Jitter Increases Retinal Slip

The OKRs generated by simulated horizontal/vertical viewpoint oscillation are consistent with ocular following responses (or OFRs). While these OFRs operate at ultra-short latencies ($<$100 ms) when one initially views radial flow (Miles *et al.*, 2004), they are known to be reduced by repeated stimulation leading to adaptation (Miles and Kawano, 1986), and increased by the initiation of saccades (Lisberger, 1998). Hence, while these OFRs may initially stabilize the retinal image, their am-

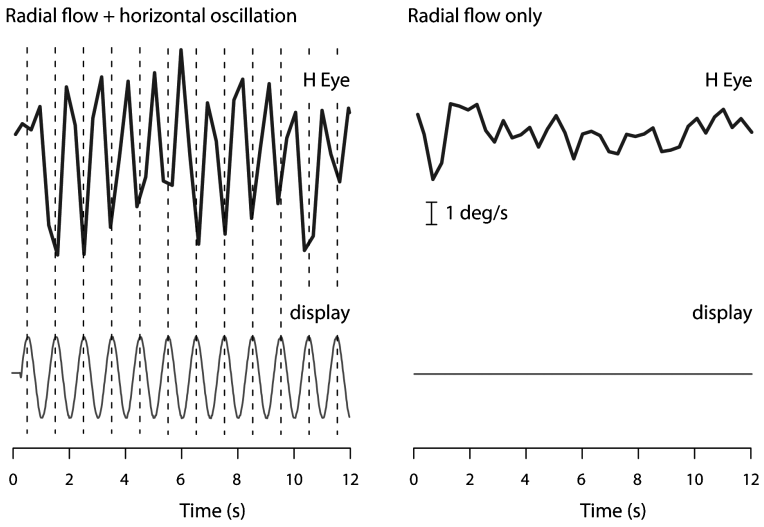


Figure 9. These traces show horizontal slow-phase eye velocity (dark gray traces, labelled 'H Eye') as a stationary observer freely views radial flow displays with (on the left) and without (on the right) simulated horizontal viewpoint oscillation (light gray traces, labelled 'display'). The time series each show 12 s of a 30 s trial from a representative subject (SAP).

plitude tends to fluctuate with prolonged viewing of oscillating radial flow (see Fig. 9, left). This should generate periods where retinal image stability is reduced, leading to retinal slip and possible consequences to vection.

To test the role that retinal slip plays in vection, Palmisano and Kim (2009) had their subjects engage in the following three different types of gaze while viewing jittering, oscillating and purely radial patterns of optic flow: (i) central/peripheral stationary fixation; (ii) central/peripheral directed looking; and (iii) gaze shifting from the centre of the display to the periphery. They found that simulated viewpoint oscillation always improved the vection in depth induced by radial flow, irrespective of whether instructions were to fixate, or look at, the centre or periphery of the display. However, simulated random viewpoint jitter only improved vection when central gaze was maintained (see Note 5). They found that vection could also be improved by instructing subjects to alternate their gaze between the centre and periphery of the display (relative to stable central gaze), with the greatest benefits in this case being observed for purely radial flow. These results were all consistent with the notion that retinal slip plays an important role in determining the time course and strength of vection. Palmisano and Kim proposed that increased retinal slip could not only be the mechanism responsible for the simulated viewpoint jitter/oscillation advantages for vection, but also for the gaze shifting advantage for vection observed with purely radial patterns of optic flow. Consistent with their proposal, Kim and Palmisano's (2010b) most recent eye-tracking study provides compelling evidence that vection onset latencies and subsequent improvements in vection strength/speed were both temporally contiguous and contingent on reduc-

tions in the gain of OKRs. These reductions in eye-movements would have led to increases in retinal slip, which may have contributed to the enhancements in vection strength.

5.7. Viewpoint Jitter Reduces Visual Adaptation to Optic Flow

When observers are presented with purely radial flow simulating constant velocity self-motion in depth, their experience of vection should decrease over time as they adapt to the flow (Denton, 1980; Salvatore, 1968; Schmidt and Tiffin, 1969). However, this adaptation to the radial flow may be reduced by adding either simulated random viewpoint jitter or simulated viewpoint oscillation to the display, which in turn may reduce the decline in vection in depth over time. While there should be little adaptation to the jitter/oscillation itself (since this flow component consists of opposite direction up–down/left–right motion signals), it may act as noise and prevent or reduce adaptation to the main radial component of the flow. Consistent with this proposal, radial displays with simulated horizontal/vertical viewpoint jitter have been found to induce longer vection durations and shorter motion after-effects than purely radial control displays (Palmisano *et al.*, 1997, 2000). More recently, Seno *et al.* (subm.) have found that simulated random viewpoint jitter increases both the vection experienced during, and the vection after-effects experienced after, adaptation to radially expanding flow (even though this jitter also simultaneously reduced the motion after-effects).

While these data are promising, we do not believe that reduced adaptation can fully explain all of our jitter/oscillation findings. For example, it has been consistently shown that adding simulated random viewpoint jitter/oscillation to radial flow reduces vection onset latencies. This particular jitter/oscillation advantage frequently emerges very early, before significant adaptation would be expected to occur to the radial flow (e.g., Palmisano *et al.* (2008) found a jitter advantage for vection onsets less than 4 s after the stationary observer's initial exposure to the optic flow). Furthermore, since random visual jitter is composed of a range of frequencies (both low and high), we might expect it to be more disruptive to adaptation than a single low frequency oscillation. However, we have consistently found that simulated random viewpoint jitter improves vection in a very similar fashion to simulated viewpoint oscillation (e.g., Palmisano *et al.*, 2008).

5.8. Viewpoint Jitter is More Ecological

To date, one of the most enduring explanations for the viewpoint jitter advantage for vection is that purely radial (or lamellar) flow rarely occurs in the real world. The acts of walking and running not only generate forward self-displacements, but also bob, sway and lunge self-displacements (Cutting *et al.*, 1992; Grossman *et al.*, 1988; von Grünau *et al.*, 2007; Hirasaki *et al.*, 1999; Lécuyer *et al.*, 2006). As a result, our retinal flow during self-motion typically contains both random and oscillatory components, often generated by head movement frequencies as high as 15 Hz, that can only be partially compensated for *via* eye-movements (Grossman *et*

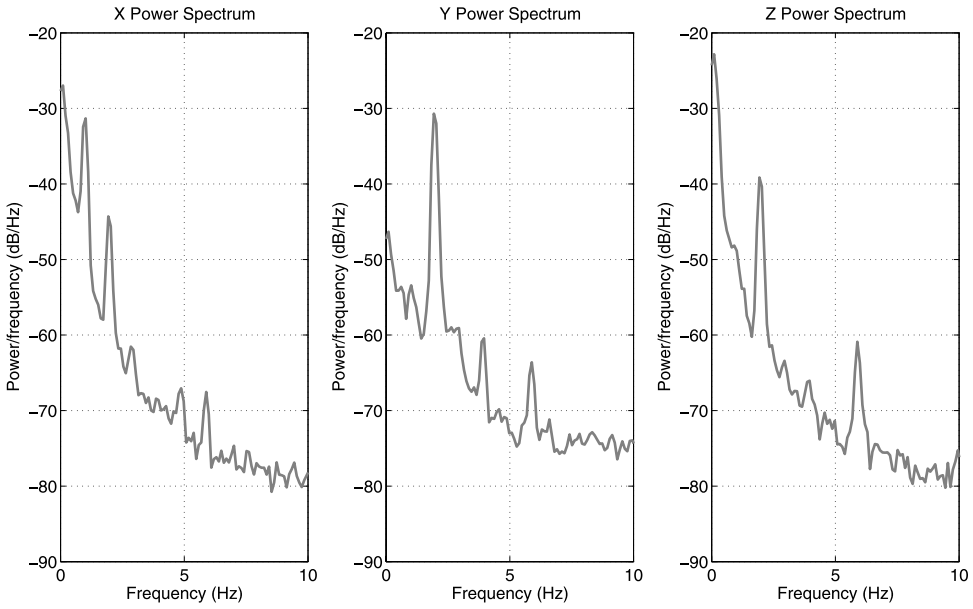


Figure 10. Distribution of head movement frequencies along the horizontal (X), vertical (Y) and depth (Z) axes during real walking on a treadmill. These head jitter data were obtained by tracking the first author's head movements as he walked on a treadmill while viewing a virtual self-motion display (treadmill belt speed was matched to the simulated forward walking speed). In the particular condition shown above, his tracked head movements were incorporated into the self-motion display in real-time.

al., 1989; von Grünau *et al.*, 2007) (see Fig. 10). Thus, it seems likely that simulated viewpoint jitter/oscillation taps into visual processes normally used to perceive self-motion from naturally occurring patterns of optic flow. Consistent with this notion, Lécuyer and colleagues (2006) have found that adding simulated head oscillation to their radial flow displays significantly increased reported sensations of walking by their subjects (relative to no-oscillation control displays). Similarly, a recent study by Bubka and Bonato (2010) has shown that first-person videos shot from a hand-held camera induce faster vection onsets and longer vection durations than comparable videos shot from a rolling cart.

Ecology might also be able to explain the asymmetrical effects that simulated horizontal-and-vertical viewpoint jitter have on the postural sway induced by radial flow. As noted in Section 3.4, Palmisano *et al.* (2009) found that this jitter increased the posterior sway produced by radial expansion and decreased anterior sway produced by radial contraction. Our ecological explanation of these results was as follows. Simulated viewpoint jitter acted to increase perceived observer sway induced by both types of radial flow (contraction and expansion). Observers responded automatically to jittering optic flow indicating large anterior sways because such self-motions are both possible and likely given the shape and orientation of our feet (Edwards and Ibbotson, 2007). However, they did not respond auto-

matically to jittering optic flow indicating large posterior sways in the absence of confirmatory non-visual inputs, because such self-motions were not only implausible but also quite dangerous given our biomechanical constraints.

In terms of future research, testing high frequency simulated viewpoint oscillation would provide a strong test of this 'jitter is more ecological' theory. To date, the type of simulated viewpoint change that has been tested the most thoroughly is random viewpoint jitter. This is best thought of comprising both high and low frequencies (generally capped at 15 Hz, which is still within the range of ecological head jitter). It is possible that the lower frequency components of this random jitter, common to all conditions tested, may have been responsible for the robustness of the jitter advantage for vection to our frequency manipulations (which simply altered the jitter capping frequency). By contrast, the effects of simulated viewpoint oscillation have been tested far less thoroughly. To date, the highest frequency simulated viewpoint oscillation that has been tested on vection is 7.4 Hz (Palmisano *et al.*, 2007).

Future studies testing this 'more ecological' theory should also try to directly compare the vection enhancements provided by real (e.g., see the tracked head jitter data in Fig. 10) and artificial jitter stimuli. Real head jitter has 6 degrees of freedom and contains both linear and rotary components, producing a rich and complex mix of jitter amplitudes and frequencies. Previous jitter studies have generated artificial head jitter stimuli by applying perspective shifts to the simulated viewpoint (along one, or at most two, axes) based on either random broadband noise or simple sinusoidal waveforms. However, the artificial head jitter stimuli required for this type of study should, by necessity, match the characteristics of real head jitter as closely as possible, while still serving as viable control stimuli. One cannot simply create artificial head jitter stimuli by scrambling real head position and orientation data, since the resulting frequencies and amplitudes of this artificial jitter would be dramatically different from those of the real head jitter on which they were based.

6. Conclusions

In everyday life there are many situations where the information provided by one or more of the known self-motion senses apparently is in conflict with the others. It is commonly believed that these sensory conflicts should impair the experience of self-motion and increase the likelihood of motion sickness. However, as Stoffregen and Riccio (1991) have previously noted, self-motions which provide redundant or complementary multisensory information about self-motion (i.e., little or no sensory conflict expected) are the exception rather than the rule. This is true for both natural and artificial environments. Their particularly insightful observation suggests that, rather than being disruptive and even dangerous, we must be able to tolerate and function well in most of the so-called sensory conflict scenarios.

Over the last decade, research from our laboratories and others has shown that simulated viewpoint jitter/oscillation significantly improves visual illusions of self-

motion induced by optic flow, despite expectations that this jitter should increase levels of sensory conflict. This jittering optic flow (expected to produce significant and sustained visual–vestibular conflicts) has been shown to induce vection in stationary observers that starts sooner, lasts longer and is perceived to be faster than comparable patterns of non-jittering optic flow (expected to produce minimal/transient visual–vestibular conflicts). These surprising findings — now replicated by independent groups from Japan, Europe and the US — cannot be explained by existing sensory conflict theories of self-motion perception.

The viewpoint jitter and oscillation advantages for vection suggest that the visual perception of self-motion must be much more tolerant to sensory conflict than has been previously thought. This notion is strongly supported by recent findings from our laboratory that moving and stationary observers experience very similar vection in depth when viewing horizontally jittering/oscillating optic flow (even though stationary observers only had visual information, whereas moving observers had consistent multisensory information, about the horizontal head oscillation). This notion is also highly consistent with neurophysiological evidence that sensory conflicts are actually reduced at the cortical level during vection — either by vestibular cortical suppression in the case of simulated constant velocity self-motion or by indirect vestibular activation in the case of simulated accelerating self-motion.

While the precise origins of the simulated viewpoint jitter/oscillation effects on vection are currently unclear, there appear to be several main front runners. Research suggests that viewpoint jitter and oscillation improve the vection experience by tapping into specialized processes used to perceive self-motion from naturally occurring patterns of optic flow (Bubka and Bonato, 2010; Palmisano *et al.*, 2009). While some recent research suggests that simulated viewpoint oscillation may improve vection by increasing the perceived rigidity of the optic flow (Nakamura, 2010), other evidence suggests that the mechanisms underlying these jitter/oscillation based improvements may be increased retinal slip (Palmisano and Kim, 2009) or reduced adaptation. Such studies have brought us tantalizingly close to a full understanding of the role of sensory conflict in the genesis of vection. We have every expectation that further neurophysiological, psychophysical, oculomotor and modeling studies will provide convergent evidence to unravel the remaining mysteries surrounding these surprising viewpoint jitter effects.

Notes

1. Moving observers actually receive retinal flow, generated not only by their whole body self-motion, but also by independent head and eye rotations (Regan and Beverly, 1982). However, we are reasonably successful at parsing out the flow generated by these head and eye motions, leaving the optic flow due to self-motion (e.g., Banks *et al.*, 1996).

2. The vestibular system end organs are inertial sensors which directly sense self-acceleration. Vestibular signals for egospeed and self-displacement arise from the frequency response of the system or neural processing.

3. It was conceivable that simulated viewpoint jitter could have improved vection by simply obscuring any 'jaggies' or pixel creep in our computer generated self-motion displays (i.e., artefactual object motions caused by limitations in spatiotemporal resolution). This possibility was discounted by Palmisano *et al.* (2003). While coherent-non-perspective jitter should have reduced the salience of any 'jaggies' in a very similar fashion, they found that this type of jitter provided no measureable advantage for vection. The visual effects of random coherent non-perspective jitter are quite similar to those of simulated eye rotation (in both cases, the added flow does not provide additional motion parallax information and approximates the retinal flow produced by head/eye rotations). We have subsequently found that 1 Hz simulated horizontal eye oscillation improves the vection induced by radial flow (Kim *et al.*, subm.). It is possible that the coherent non-perspective jitter used in Palmisano *et al.* (2003) did not improve vection because it contained extremely high (i.e., non-ecological) frequencies (it was capped at 37.5 Hz).

4. We believe that findings of vestibular suppression and indirect vestibular stimulation in different vection studies can be reconciled as follows. Research to date suggests that vestibular suppression is found in stationary observers when the optic flow simulates constant velocity self-motion. Since this is clearly a situation where visual self-motion perception should dominate, it is not surprising that the vestibular self-motion information is suppressed in favour of the visual self-motion information. By contrast, indirect vestibular stimulation has been found in stationary observers when the optic flow simulates self-acceleration. As noted in the introduction of this review, the vestibular system is specialized to detect self-acceleration, and in this situation the available vestibular input is consistent with the observer either being stationary or moving at a constant linear velocity. Based on Nishiike *et al.*'s (2002) findings, self-motion processing may attempt to reduce the sensory conflict generated during visually simulated self-acceleration by indirectly activating/stimulating the vestibular self-motion centres (e.g., PIVC). As stated here, one way that this indirect vestibular stimulation might arise is as a result of feedback arising from the stationary observer's optokinetic eye-movements.

5. It was argued that we failed to find a viewpoint jitter advantage for vection in these peripheral gaze conditions because the horizontal/vertical image velocities produced by the 10 Hz random jitter in the periphery of the display exceeded the visual limits for processing self-motion. This notion of visual limits relates to the 'more ecological' theory outlined in Section 4.8.

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