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Vection in depth during consistent and inconsistent multisensory stimulation

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Vection in depth during consistent and inconsistent multisensory stimulation

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Abstract. We examined vection induced during physical or simulated head oscillation along either the horizontal or depth axis. In the first two experiments, during active conditions, subjects viewed radial-flow displays which simulated viewpoint oscillation that was either in-phase or out-of-phase with their own tracked head movements. In passive conditions, stationary subjects viewed playbacks of displays generated in earlier active conditions. A third control, experiment was also conducted where physical and simulated fore – aft oscillation was added to a lamellar flow display. Consistent with ecology, when active in-phase horizontal oscillation was added to a radial-flow display it modestly improved vection compared to active out-of-phase and passive conditions. However, when active fore – aft head movements were added to either a radial-flow or a lamellar-flow display, both in-phase and out-of-phase conditions produced very similar vection. Our research shows that consistent multisensory input can enhance the visual perception of self-motion in some situations. However, it is clear that multisensory stimulation does not have to be consistent (ie ecological) to generate compelling vection in depth.

1 Introduction

Vision is able to provide information about many types of body movement (active or passive, linear or rotary, constant-velocity or accelerating self-motions — Dichgans and Brandt 1978; Johansson 1977; Lee and Lishman 1975; Lishman and Lee 1973). However, useful non-visual information about self-motion is also provided by the vestibular, auditory, somatosensory, and proprioceptive systems (Benson 1990; Johansson 1977; Siegler et al 2000). Of these non-visual senses, the vestibular system of the inner ear appears to play a particularly important role in self-motion perception. This sense is thought by many to dominate the perception of self-acceleration (Benson 1990), as it appears to be more sensitive to high-temporal-frequency self-motions than vision (ie 1 Hz or greater — van Asten et al 1988; Berthoz et al 1975, 1979; Melvill-Jones and Young 1978). However, unlike vision, the vestibular system cannot distinguish between travelling at a constant linear velocity and remaining stationary (Benson 1990; Lishman and Lee 1973).

Visually induced illusions of self-motion (or vection) have often been used to explore the relationship between visual and non-visual self-motion perception. Traditionally, it had been thought that conflicting non-visual information about self-motion would always impair one's experience of vection (see Zacharias and Young's 1981 sensory-conflict theory of vection). Therefore, most vection studies have tended to use optic-flow displays simulating constant-velocity self-motion as these are thought to produce only transient or minimal visual – vestibular conflicts (Andersen and Braunstein 1985; Palmisano 1996, 2002; Telford and Frost 1993). Consistent with sensory-conflict theory, Wong and Frost (1981) showed that a brief period of acceleration that was consistent with one's simulated direction of self-rotation resulted in faster circular-vection onset times. Also consistent with sensory-conflict theory, several studies have shown that a brief period of acceleration in the opposite direction to the visually simulated self-rotation can impair

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one's experience of circular vection (Melcher and Henn 1981; Teixeira and Lackner 1979; Young et al 1973). However, in contrast to the latter studies (and sensory-conflict theory), Wong and Frost (1981) also found that circular vection was unaffected by a brief period of acceleration in the opposite direction (ie inconsistent vestibular stimulation) to the visually simulated self-rotation. Furthermore, Palmisano et al (2000, 2003, 2008) found that adding horizontal/vertical simulated viewpoint jitter to a radial-flow display simulating constant-velocity self-motion in depth could significantly improve the experience of vection in depth in stationary observers. These vection improvements occurred even though this continuous display jitter should have generated significant and sustained visual – vestibular conflicts (since the expected vestibular stimulation that would have normally accompanied the visually simulated viewpoint jitter was absent).

Most previous studies on the role that visual jitter plays in vection have simulated viewpoint changes in physically stationary observers. In this situation, only visual information indicates that the observer is accelerating. By contrast, the available non-visual information is consistent with the observer either being stationary or moving at a constant linear velocity (the latter possibility is compatible with the non-jittering radial-flow component — Palmisano et al 2000, 2008). However, several recent studies have synchronised this visual-display jitter/oscillation with the observers' own movements, thereby creating consistent visual and non-visual information about their self-acceleration.

Studies by both Wright et al (2005) and Kim and Palmisano (2008) tracked their subjects' oscillatory linear head movements in real-time. These movements were then used to continually adjust the subject's simulated viewpoint in the self-motion display throughout the entire duration of the trial (as opposed to earlier studies that only briefly provided consistent vestibular stimulation — eg Wong and Frost 1981). In the Wright et al study, passive subjects were physically moved vertically by an automatic device, which generated 0.2 Hz whole-body oscillation (ie these active whole-body movements were involuntary). Wright et al's study also varied visual (both high and low) and inertial (0.2 – 1.6 m) amplitudes during light and dark conditions. In the Kim and Palmisano study, their active subjects made voluntary horizontal physical head movements at approximately 1 Hz. The computer-generated oscillatory optic flow generated by these head movements was then added to a radial-flow component, which simulated constant-velocity forwards self-motion in depth. Irrespective of whether this horizontal/vertical display oscillation was generated by voluntary or involuntary movements, both studies found that ecological/in-phase display oscillation (ie conditions in which the display moved in the opposite direction to the observer's head/whole-body movements) did not significantly improve the experience of self-motion (ie above the levels experienced when the observer viewed display oscillation while stationary). Even when this physical/active oscillation was voluntary and in-phase (in Kim and Palmisano 2008), the perception of self-motion was very similar to that induced by conditions that only provided visual information about self-acceleration.

Interestingly, Wright et al (2005) also found that, depending on the level of inertial amplitude, increasing visual input appeared to suppress or enhance the experience of illusory self-motion (with vision dominating the perception of self-motion in most cases). Also of interest, Kim and Palmisano (2008) found that their observer's compensatory eye-movements (identified as ocular following responses or OFRs — see Miles et al 2004) were very similar in both active and passive playback conditions. The OFR essentially serves as a backup to the otolith-ocular reflex. The OFR is the mechanism responsible for regulating compensatory eye movements for maintaining a stable retinal image of the world during linear head translation. They suggested that these OFRs may have acted to reduce potential visual – vestibular conflicts in passive playback conditions by indirectly stimulating the vestibular system.

It should be noted that Kim and Palmisano (2008) compared the vection induced by consistent multisensory stimulation with that induced by only one situation of sensory conflict. That is, they examined a situation where vision indicated self-acceleration and non-visual stimulation indicated that the observer was either stationary or travelling at a constant linear velocity. A more recent study by Kim and Palmisano (2010) compared the effects of consistent and inconsistent visual – vestibular information about horizontal self-acceleration on the vection in depth induced by radial flow. The design was similar to that of Kim and Palmisano (2008) but, in this case, the updated visual displays moved either in the same (out-of-phase display oscillation) or the opposite (in-phase display oscillation) direction to the observer's head. Interestingly, Kim and Palmisano (2010) found no difference in the vection-in-depth strength ratings obtained for these consistent (in-phase) and inconsistent (out-of-phase) multisensory self-motion stimulation conditions.

In the current study we again investigate the vection experienced in the presence of sensory consistency and sensory conflict. As in the Kim and Palmisano (2008, 2010) studies, observers either oscillated their heads or sat still while viewing radial-flow displays simulating constant-velocity forwards self-motion in depth. Novel sensory conflict situations were generated by systematically altering both the phase and the gain/amplitude of the visual display oscillation with respect to the observer's physical head movements. While in experiment 1 we re-examined the effects of left – right head movements and horizontal display oscillation in further detail, in experiment 2 we investigated, for the first time, the effects of fore – aft head movements and simulated depth oscillation. As the fore – aft head oscillation was simulated along the same axis as the simulated constant velocity self-motion in depth in experiment 2, a third control experiment was conducted. In this experiment we investigated the effects of physical and simulated fore – aft head oscillation on rightwards vection using a lamellar-flow stimulus. Since recent studies on the effects of multisensory stimulation on vection have produced null results, we used much larger sample sizes (twenty-five, twenty-four, and seventeen subjects in experiments 1, 2, and 3, respectively) and included conditions with much larger display oscillation amplitudes than those tested previously.

2 Experiment 1. Effects of multisensory stimulation about horizontal head oscillation on vection in depth

In this experiment we compared the vection in depth induced by radially expanding optic-flow displays, which also moved in either the opposite (active in-phase display oscillation) or the same (active out-of-phase display oscillation) horizontal direction to the subject's physical head movements. Display gain was either appropriate for the subject's physical head movements or twice as large as would be expected for them. The large and small oscillation amplitude optic-flow displays generated by these active conditions were later played back to the same subjects when they were stationary.

2.1 *Method*

2.1.1 *Subjects.* Twenty-five naive undergraduate psychology students (eighteen females and seven males; mean age $= 21.78$ years, $SD = 3.02$ years) at the University of Wollongong received course credit for their participation in this experiment. All had normal or corrected-to-normal vision. None of them had any existing vestibular or neurological impairments.

2.1.2 *Apparatus.* Computer-generated displays were rear-projected onto a flat projection screen (1.48 m wide $\times$ 1.20 m high) with a Mitsubishi Electric (Model XC400U) colour data projector [with a 1024 (horizontal) $\times$ 768 (vertical) pixel resolution]. Subjects viewed these displays from a distance of 2.2 m in front of the screen through custom-made monocular goggles (see figure 1), which reduced their field of view to approximately 45°.

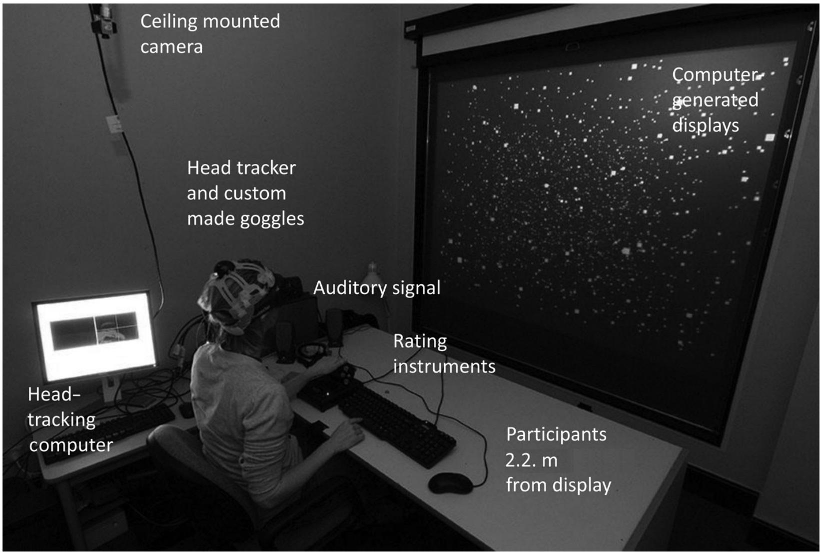

Figure 1. The setup for experiments 1 – 3.

In active conditions, the subjects were asked to move their heads in time with a computer-generated metronome. A ceiling-mounted digital firewire camera was used to track their head position/motion. These tracked head movements: (i) were incorporated into the visual display during active (head moving) conditions, and/or (ii) used to check subject compliance with experimenter instructions (in terms of head motion direction, frequency, and amplitude) during active and passive (ie head stationary) conditions. At the end of each trial, subjects moved a linear throttle (Pro Throttle USB) along a sliding scale to represent the perceived strength of their experience of vection in depth during that trial. That is, subjects were asked to rate the perceived strength of their vection in depth and instructed to ignore any horizontal self-motion/vection. A rating of 0% indicated no experience of self-motion (the visual display motion was attributed solely to scene motion) and a rating of 100% indicated complete/saturated vection (the visual display motion was attributed solely to self-motion). Subjects made these ratings relative to a standard reference stimulus, which they were told represented a rating of 50% self-motion. This standard stimulus was a non-oscillating pattern of radially expanding optic flow. It simulated constant-velocity forwards self-motion in depth and was viewed while the subject was stationary.

2.1.3 *Visual displays.* Each optic-flow display consisted of 2592 randomly placed blue square objects (1.8 cd m^{-2}) on a black background (0.04 cd m^{-2}). These objects were uniformly distributed within a simulated 3-D environment, which was 12 units wide by 12 units high and 18 units deep (object density was one dot per cube unit). Each optic-flow display also had a single green fixation dot (20 cd m^{-2}) located precisely in the centre of the screen. Subjects were asked to fixate on this stationary green dot for the entire 30 s duration of the trial.

All of the optic-flow displays simulated the same constant-velocity (1.5 m s^{-1}) forward self-motion in depth (ie all displays had the same radially expanding flow component). During active conditions, the subject oscillated his/her head left to right and information about his/her changing head position was incorporated into the self-motion display in real-time. Five combinations of visual display phase and gain were tested during these active conditions: '+2', '+1', '0', '−1', or '−2'. During active in-phase display oscillation conditions (indicated by a '+' sign), the visual display always moved in the opposite direction to the subject's head movement so that it provided consistent visual – vestibular information about horizontal self-acceleration. By contrast, in the active out-of-phase display oscillation conditions (indicated by a '−' sign), the visual display always moved in the same direction as the subject's head movement. This provided inconsistent visual – vestibular information about horizontal self-acceleration. Finally, in the active no-display oscillation ('0' gain) condition, the subject's physical head movements were simply ignored. This should have also provided inconsistent visual – vestibular information about horizontal self-acceleration. The gain of the additional horizontal display motion (with respect to the subject's physical head movement) was twice as large in '+2' and '−2' conditions as in '+1' and '−1' conditions.

During the passive viewing conditions, the now stationary subjects viewed either: (i) playbacks of the horizontally oscillating radial flow generated by their own head movements on previous active trials; or (ii) purely radial optic-flow displays. As subjects were stationary (ie not oscillating their head) during these passive playback conditions, the display oscillation had no phase. Therefore, passive display oscillation conditions only varied in terms of oscillation amplitude with display amplitudes of '2' being twice as large as display amplitudes of '1'.

2.1.4 *Procedure.* Prior to testing, the experimenter briefed the subjects on the experiment and made sure that they were familiar and comfortable with the experimental requirements. Subjects were first run through a practice block of active (head movement) trials and then given feedback about the frequency and amplitude of their head movements. They were told to oscillate their heads left and right at 1 Hz by: (i) moving at the waist, rather than at the neck; and (ii) timing their movements to a computer-generated auditory tone that sounded, every half-cycle, at 0.5 s intervals (the aim being to produce a physical head movement frequency of ~ 1 Hz). Subjects were then run through the three experimental blocks of trials. These consisted of two identical active blocks of trials with one passive block of trials run in-between them. There were 10 trials within each block (2 repetitions of each experimental condition). During passive blocks, the now stationary subjects viewed playbacks of the displays generated by their own head movements on previous active trials. Subjects' head-position data were still recorded during these playback conditions to ensure that physical head motion was minimal.

2.2 *Results*

2.2.1 *Active viewing conditions (with or without horizontal-display oscillation).* We first performed Bonferroni-corrected planned contrasts on our active viewing data (controlling the family-wise error rate at 0.05). Active in-phase ($F_{1,24} = 31.76$, $p < 0.05$) and active out-of-phase ($F_{1,24} = 18.75$, $p < 0.05$) display oscillation conditions were both found to significantly improve vection-in-depth strength ratings compared to active no-display oscillation conditions (see figure 2). While there was a trend for active in-phase oscillation to produce stronger vection ratings than active out-of-phase oscillation, this effect did not reach significance ($F_{1,24} = 7.07$, $p > 0.05$). However, we did find a significant phase type by gain type interaction. In active in-phase oscillation conditions, displays with larger, '+2', gains induced significantly stronger vection than those with smaller, '+1', gains ($F_{1,24} = 8.1$, $p < 0.05$). By contrast, there was no significant effect of display gain on vection strength ratings for the active out-of-phase oscillation conditions ($F_{1,23} = 0.87$, $p > 0.05$).

2.2.2 *Passive viewing conditions (with or without horizontal-display oscillation).* We next performed Bonferroni-corrected planned contrasts on the passive viewing data (controlling the family-wise error rate at 0.05). As in previous studies, passive display oscillation conditions resulted in significantly stronger vection-in-depth ratings compared to passive no-display oscillation conditions ($F_{1,24} = 12.61$, $p < 0.05$—see figure 3). However, the vection generated by displays with larger, '2', oscillation amplitudes was not found to

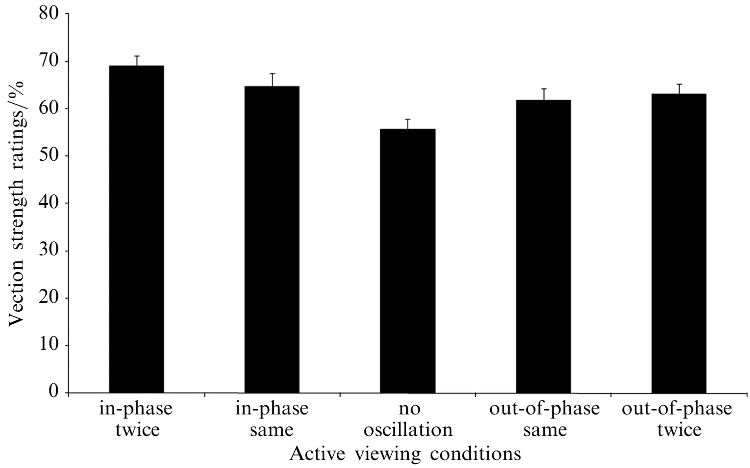

Figure 2. Effect of active horizontal-display oscillation on vection-in-depth strength ratings as a function of both display gain (either at the same or twice the amplitude expected from the subject's head movements) and phase (either in-phase with, out-of-phase with, or unaffected by, the subject's head movements). Error bars depict 1 SEM.

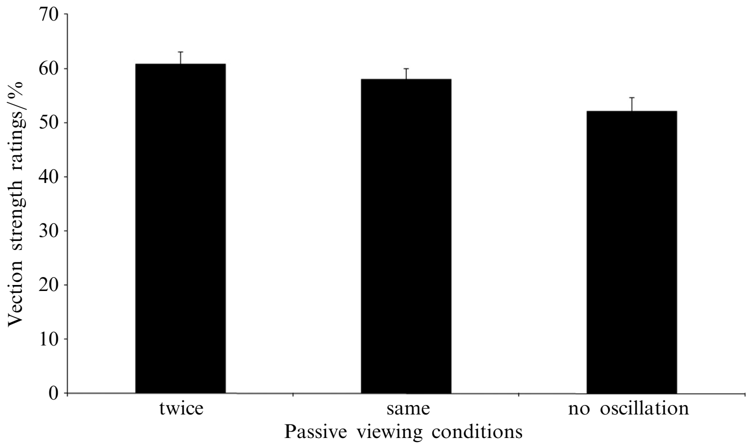

Figure 3. Effect of passive horizontal-display oscillation (at the same and twice the amplitude as subject's physical head movements) on vection-in-depth strength ratings compared to passive no-display oscillation conditions. Error bars depict 1 SEM.

differ significantly from that generated by displays with smaller, '1', oscillation amplitudes ($F_{1,24} = 2.18$, $p > 0.05$).

2.2.3 *Active versus passive conditions (with or without horizontal-display oscillation).* Finally, we performed Bonferroni-corrected planned contrasts to compare the active and passive viewing data (controlling the family-wise error rate at 0.05). Contrary to Kim and Palmisano (2008), active in-phase display oscillation was found to produce significantly stronger vection-in-depth ratings than passive display oscillation conditions ($F_{1,24} = 12.73$, $p < 0.05$—see figure 4). However, active out-of-phase display oscillation was not found to produce significantly different vection-in-depth ratings than passive display oscillation conditions ($F_{1,24} = 2.41$, $p > 0.05$).

2.2.4 *Head movement analyses.* Subjects moved their heads in a similar fashion for all of the active conditions tested (there was negligible head movement in passive conditions). Head movement frequencies and amplitudes in active conditions were on average

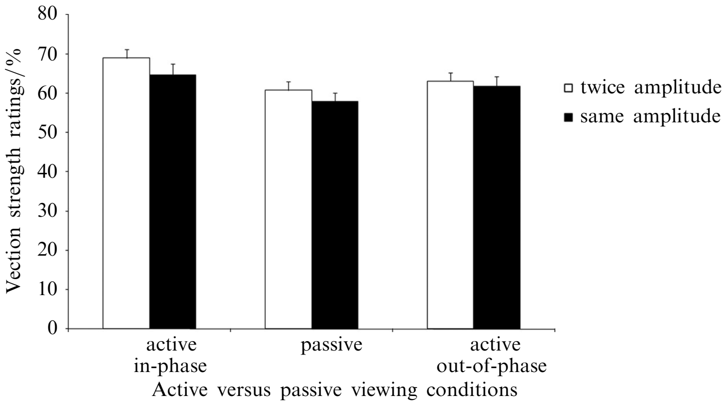

Figure 4. Effect of active in-phase, passive, and active out-of-phase horizontal-display oscillation on vection-in-depth strength ratings. Error bars depict 1 SEM.

0.73 ± 0.06 Hz and 7.80 ± 3.33 cm, respectively. The correlation between head movement amplitude and vection strength ratings was non-significant ($r = -0.04$, $p > 0.05$). Similarly, the correlation between head movement frequency and vection strength ratings was also non-significant ($r = -0.02$, $p > 0.05$). Head amplitude was not significantly different for the active '+2' ($M = 7.9$ cm, SE $= 3.52$ cm) and active '+1' ($M = 8.02$ cm, SE $= 3.33$ cm) display oscillation conditions ($t_{21} = 0.51$, $p = 0.62$). It was also not significantly different for the active '−2' ($M = 7.7$ cm, SE $= 3.07$ cm) and active '−1' ($M = 7.85$ cm, SE $= 3.32$ cm) display oscillation conditions ($t_{21} = 0.68$, $p = 0.50$).

2.2.5 *Eye movement analyses.* We also collected peak-to-peak horizontal eye-velocity data for twelve of our twenty-five subjects. As in previous studies (Kim and Palmisano 2008; Palmisano and Kim 2009), gaze relative to the display appeared to be regulated by OFR activation in both active and passive display oscillation conditions. Peak-to-peak horizontal eye velocity was not found to be significantly different for the active '+2' ($M = 0.21$ deg s^{-1}, SE $= 0.06$) and active '+1' ($M = 0.23$ deg s^{-1}, SE $= 0.06$ deg s^{-1}) display oscillation conditions ($t_{11} = 0.22$, $p > 0.05$). Similarly, peak-to-peak horizontal eye velocity was not found to be significantly different for the active '−2' ($M = 0.45$ deg s^{-1}, SE $= 0.18$ deg s^{-1}) and active '−1' ($M = 0.39$ deg s^{-1}, SE $= 0.09$ deg s^{-1}) display oscillation conditions ($t_{11} = 0.33$, $p > 0.05$). However, peak-to-peak horizontal eye velocity was significantly faster for the passive '2' ($M = 0.14$ deg s^{-1}, SE $= 0.05$ deg s^{-1}) compared to the passive '1' ($M = 0.07$ deg s^{-1}, SE $= 0.03$ deg s^{-1}) display oscillation conditions ($t_{11} = 2.50$, $p < 0.05$).

2.3 *Discussion*

Unlike in the earlier studies by Kim and Palmisano (2008, 2010), consistent multisensory information about self-motion was found to produce significantly stronger vection ratings than conditions which provided only visual information about self-motion. While active in-phase display oscillation was found to produce significantly more compelling vection than passive display oscillation, active out-of-phase display oscillation did not. Thus, as would be predicted by most theories of sensory interaction in self-motion perception, it does appear that consistent vestibular stimulation can (sometimes) enhance the visual perception of self-motion.

One reason why we might have found this modest vection advantage for active in-phase (compared to passive) display oscillation conditions, while Kim and Palmisano (2008, 2010) did not, was that these earlier studies used much smaller numbers of subjects (only nine and fourteen, respectively, compared to twenty-five subjects tested in experiment 1). Another possible reason why we may have found an advantage for active in-phase conditions was that Kim and Palmisano's (2008, 2010) studies used older subjects (ie mean age of 32 and 28.5 years, respectively, compared to a mean age of only 21.78 years in the current study). Therefore, it is possible that the younger subjects in the current study had better vestibular sensitivity (see Haibach et al 2009; Howard et al 2000) and were thus more sensitive to visual–vestibular conflicts. A further possible explanation for our apparently discrepant results was based on the fact that the self-motion displays used in these earlier studies always had the same gain/oscillation-amplitude. In addition to using comparable conditions in the current experiment ('+1' and '1'), we also tested larger horizontal gains/oscillation-amplitudes ('+2' and '2'). It is likely that these larger gains/oscillation amplitudes contributed to the significant vection-in-depth improvements observed in our active in-phase display oscillation conditions.

It was also possible that the improved vection in depth found in the in-phase oscillation conditions was purely the result of the observer actively generating his/her own display oscillation. That is, the benefits of active in-phase oscillation could have been due to the observer being physically active (as opposed to passive). However, a study conducted in our laboratory (unpublished) found that actively generating horizontal display oscillation without vestibular stimulation (by moving a joystick in-phase or out-of-phase via hand and wrist movements) provided no further improvement compared to viewing this display oscillation while seated completely stationary. Therefore, it does not appear as though the vection advantage for active in-phase display oscillation resulted simply from the observer being active or controlling the display. Rather, it appears that this vection advantage was due to the multisensory pattern of self-motion stimulation (ie visual, vestibular, proprioceptive, and somatosensory) generated when the subjects moved their heads in a consistent manner relative to the self-motion display.

Overall, we found that vection was more compelling in: (i) active display oscillation conditions compared to active no-display oscillation conditions; and (ii) passive display oscillation conditions compared to passive no-display oscillation conditions. Both of these findings provide support for a simulated viewpoint jitter/oscillation advantage for vection in depth. That is, the vection-in-depth experience is always more compelling when the radially expanding inducing flow contains additional horizontal display oscillation compared to when it does not (see Palmisano et al 2000). This simulated viewpoint oscillation advantage for vection was even present in active conditions where the visual display moved in a non-ecological direction. Even though active out-of-phase display oscillation and active no-display oscillation conditions should both have generated significant and sustained visual–vestibular conflicts (head oscillation was simulated by only one sense in each case), the former was consistently found to produce stronger vection than the latter.

Therefore, physical head oscillation without matching display oscillation does not appear to improve vection strength ratings. However, we did still find a vection advantage for display oscillation in passive conditions. That is, when the observer was stationary, radial flow with horizontal display oscillation improved vection strength ratings compared to pure radial flow. Therefore, it appears as though the presence of display oscillation is particularly important (irrespective of whether this display oscillation is consistent with one's physical head movements or not). This vection advantage for passive display oscillation provides further evidence for the importance of the visual system to self-motion perception. It may indicate that the vestibular system was relatively insensitive to the direction of the observer's oscillating head motion in the current experimental conditions (compared to vision). Alternatively, it may indicate that, when an observer is experiencing vection, inconsistent vestibular information about the direction of self-motion is more likely to be ignored or downplayed.

The latter notion is consistent with a number of neuropsychological (Brandt et al 1998; Kleinschmidt et al 2002) and experimental (Berthoz et al 1975; Wong and Frost 1981) studies. For example, a positron emission tomography (PET) activation study by Brandt et al showed that visual stimulation during circular vection (CV) simultaneously activates the visual cortex (and associated areas) and deactivates/inhibits the processing centre for vestibular inputs (ie the parieto-insular vestibular cortex or PIVC for short). Similarly, an fMRI study by Kleinschmidt et al also showed deactivation of the PIVC during vection. The findings of these studies both suggest that there is a reciprocal inhibitory interaction between the visual and vestibular systems during visually induced self-motion perception. They suggest that, depending on the type and nature of stimulation, the visual system may dominate the perception of self-motion from optic flow, resulting in the vestibular sense being deactivated/inhibited (or, as suggested in the current study, being downplayed or ignored).

Interestingly, we did find a significant interaction between the phase of the display oscillation and its gain/amplitude. In active in-phase display oscillation conditions, displays with larger gains were found to induce significantly stronger vection than those with smaller gains.(1) However, in active out-of-phase and passive oscillation conditions, displays with larger gains/oscillation-amplitudes did not induce significantly different vection from those with smaller gains/oscillation-amplitudes. These findings also suggest that there was an additional benefit for consistent (as opposed to inconsistent) multisensory information about self-motion.

It may be possible to explain these oscillation phase and amplitude effects on vection using the head and eye movement data. In active in-phase display oscillation conditions, head movements and horizontal eye velocities were similar for large and small gains. Therefore, large gains should have generated more retinal slip (as the eyes were not compensating effectively for differences in display amplitudes) and this in turn may have generated the more compelling experiences of vection (see Palmisano and Kim 2009). By contrast, OFR velocities in passive oscillation conditions were significantly faster when displays simulated larger oscillation amplitudes (compared to smaller oscillation amplitudes—see section 2.2.5). Since eye movements in these passive conditions appeared to do a good job at compensating for both levels of the passive display oscillation, we would have expected the retinal slip (and thus vection) to have been similar irrespective of the oscillation amplitude. This retinal-slip-based explanation does, however, have difficulty accounting for the lack of a gain effect on vection in active out-of-phase display oscillation conditions. That is, since head motions and horizontal eye velocities were always similar, larger gains should have also produced more retinal slip and superior vection in these conditions. However, as noted above, these active out-of-phase conditions were not ecological. It is, therefore, possible that the increased sensory conflict generated by active '-2' conditions cancelled the vection advantage that would have otherwise been generated by the increased retinal slip (relative to active '-1' conditions). Alternatively, because the head moved in the same direction as the visual display motion in out-of-phase display oscillation conditions,

(1) One reviewer suggested that this finding may have been the result of our subjects not being able to break their vection down into cardinal directions (ie their vection-in-depth ratings were contaminated by their lateral vection). This could explain why active in-phase conditions with more lateral display motion produced stronger vection-in-depth ratings than active in-phase conditions with less lateral display motion. However, if this explanation had been valid, we should have also found a similar benefit for larger display gains in active out-of-phase and passive display oscillation conditions (we did not). Also, we have previously shown that adding simulated constant-velocity (as opposed to accelerating) horizontal self-motion and horizontal non-perspective (as opposed to perspective) jitter both have no effect on ratings in depth induced by radial flow (Palmisano et al 2003, 2008). These findings appear to show that observers can ignore the lateral component of self-motion and make consistent estimates of self-motion in depth (at least when they are stationary).

less eye motion should have been required to maintain a stable retinal image. For this reason, retinal motion may have been greater for in-phase display oscillation conditions and this could have been responsible for the vection advantage in these conditions.

3 Experiment 2. Effects of multisensory stimulation about fore – aft head oscillation on vection in depth

In experiment 2 we examined the effects of physical and simulated fore – aft head oscillation on the vection in depth induced by radial flow. Unlike in experiment 1, the subject's physical head motion and the visually simulated self-motion all occurred along the same axis. The visually simulated fore – aft self-motions, generated by incorporating the subject's tracked head motion into the display, were combined with the visually simulated forwards self-motion generated by the constantly expanding radial-flow component. There are a number of reasons why physical/simulated fore – aft head oscillation might have different effects on the experience of vection in depth (compared to the physical/simulated horizontal head oscillation examined in experiment 1). First, Palmisano et al (2008) have previously shown that, in passive (ie head-stationary) viewing conditions, horizontal simulated viewpoint jitter/oscillation improves vection in depth significantly more than the equivalent simulated self-accelerations in depth. Second, fore – aft viewpoint oscillation generates different types of compensatory eye movements than horizontal viewpoint oscillation. As noted earlier, the real/simulated horizontal head oscillation examined in experiment 1 generated OFRs. By contrast, the real/simulated fore – aft head oscillation in experiment 2 should have generated radial-flow vergence eye movements (eye movements that are dependent on both target distance and eccentricity—Busettini et al 1997).

3.1 *Method*

The apparatus, visual displays, and procedure were similar to those of experiment 1 (see figure 1). In active conditions, before the subject started moving his/her head in depth, displays simulated forwards self-motion in depth at 1.5 m s^{-1} (radially expanding optic flow). However, when the subject began to oscillate his/her head fore-and-aft, an additional (alternately expanding and contracting) radial-flow component was generated. The simulated speed of forward self-motion in depth was thus determined by the combination of these constant and alternating radial-flow components. Importantly, the average speed of the visually simulated self-motion in depth was always the same in comparable conditions (ie '1', '+1', '−1' and '2', '+2', '−2'). As in experiment 1, the sign in active conditions indicated whether the display moved in the same or the opposite direction to one's physical head movements (ie '−' indicated that the visual display moved in the same direction and '+' indicated that the display moved in the opposite direction). The gain of the additional in-depth display motion (with respect to the subject's physical head movement) was twice as large in '+2' and '−2' conditions than in '+1' and '−1' conditions. In passive playback conditions, since the head was stationary during these trials, the display oscillation had no phase or sign. So, for example, the display oscillation generated by active '+2' or active '−2' conditions was simply referred to as '2'.

3.1.1 *Subjects.* Twenty-four naive undergraduate psychology students (nineteen females and five males; mean age = 22.12 years, SD = 3.02 years) participated in this experiment. Other selection criteria were the same as those for experiment 1.

3.2 *Results*

3.2.1 *Active viewing conditions (with or without fore – aft display oscillation).* Both active in-phase ($F_{1,23} = 44.99$, $p < 0.05$) and active out-of-phase ($F_{1,23} = 38.12$, $p < 0.05$) display oscillations were found to significantly increase vection-in-depth strength ratings

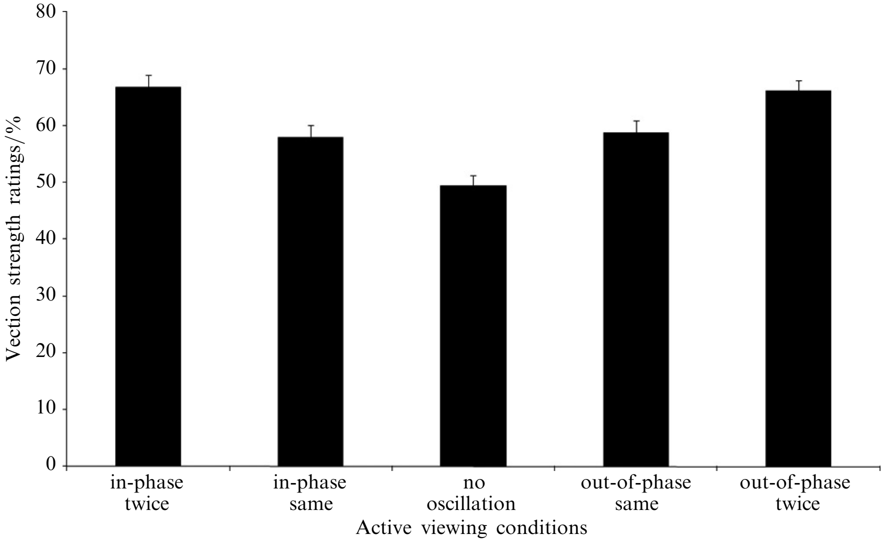

Figure 5. Effect of active fore – aft display oscillation on vection-in-depth strength ratings as a function of both display gain (either the same or twice the amplitude expected from the subject's physical head movements) and phase (either in-phase with, out-of-phase with, or unaffected by, the subject's head movements). Error bars depict 1 SEM.

above those produced in active no-display oscillation conditions (see figure 5). Larger fore – aft display gains were found to produce significantly stronger vection ratings than smaller fore – aft display gains for both active in-phase ($F_{1,23} = 22.33$, $p < 0.05$) and active out-of-phase ($F_{1,23} = 14.63$, $p < 0.05$) conditions.

3.2.2 *Passive conditions (with or without fore – aft display oscillation).* The vection-in-depth strength ratings produced by passive display oscillation were not found to differ significantly from those produced by passive no-display oscillation ($F_{1,23} = 1.41$, $p > 0.05$— see figure 6). Furthermore, larger display oscillation amplitudes were not found to produce significantly different vection strength ratings compared to smaller display oscillation amplitudes ($F_{1,23} = 2.75$, $p > 0.05$).

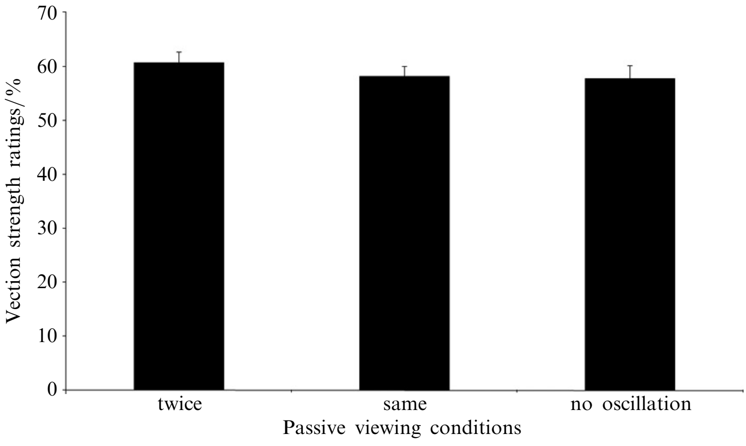

Figure 6. Effect of passive fore – aft display oscillation (at the same and twice the amplitude as the subject's head movements) on self-motion strength ratings compared to passive no-display oscillation conditions. Error bars depict 1 SEM.

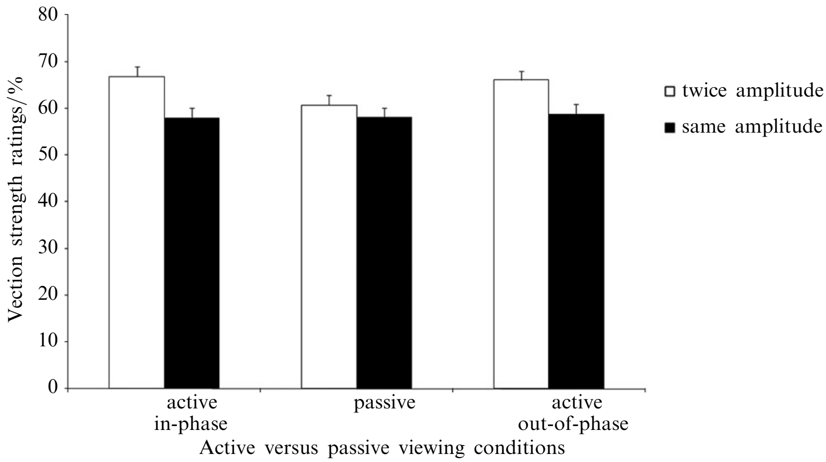

Figure 7. Effect of active in-phase, passive and active out-of-phase display oscillation (at the same or twice the amplitude as the subject's head movements) on self-motion strength ratings. Error bars depict 1 SEM.

3.2.3 *Active versus passive conditions (with or without fore – aft display oscillation).* Active display oscillation did not produce significantly different vection-in-depth strength ratings from passive display oscillation (in-phase versus passive: $F_{1,23} = 2.715$, $p > 0.05$; out-of-phase versus passive: $F_{1,23} = 3.146$, $p > 0.05$—see figure 7). Active display oscillation also did not induce significantly different vection from passive no-display oscillation ($F_{1,23} = 4.224$, $p > 0.05$).

3.2.4 *Head movement verification.* Subjects moved their heads in a similar fashion in all of the active conditions tested (there was negligible head movement in passive conditions). Mean head frequency and amplitude in active conditions was 0.79 ± 0.1 Hz and 7.45 ± 2.39 cm, respectively. As expected, there was no significant difference in physical head amplitudes for the '+2' ($M = 7.9$ cm, SE = 2 cm) and '+1' ($M = 7.5$ cm, SE = 2.31 cm) conditions ($t_{19} = 0.87$, $p = 0.4$). There was also no significant difference in physical head amplitudes for the '−2' ($M = 6.9$ cm, SE = 2.61 cm) and '−1' ($M = 7.3$ cm, SE = 2.35 cm) conditions ($t_{19} = 1.72$, $p = 0.1$). The correlations between the amplitude ($r = 0.08$, $p > 0.05$) and the frequency ($r = -0.07$, $p > 0.05$) of our subjects' head movements and their resulting vection strength ratings were both found to be non-significant.

3.3 *Discussion*

As predicted, the effects of fore – aft display oscillation on vection were quite different from the effects of horizontal display oscillation observed in experiment 1. When subjects were stationary in the previous experiment, horizontal display oscillation was found to significantly increase the vection in depth induced by radial flow. However, when subjects were stationary in the current experiment, adding fore – aft display oscillation appeared to have little or no effect on vection in depth (even with the larger oscillation amplitude). This replicates Palmisano et al's (2008) null finding for vection in depth with purely computer-generated (as opposed to head-tracking playback) simulated fore – aft viewpoint oscillation. Interestingly, in the current experiment we found that adding fore – aft display oscillation improved vection only in active viewing conditions.

Both active in-phase and active out-of-phase fore – aft display oscillation produced significantly stronger vection in depth than active no-display oscillation. As in experiment 1, the advantage of this display oscillation for vection in active conditions was largely independent of the direction of the visual display movement relative to the head.

This suggests that the non-visual senses were: (i) rather insensitive to the direction of the head motion [at least with the relatively low temporal frequencies ($\sim$0.8 Hz) tested/generated in this study]; and/or (ii) that this non-visual information was ignored or vetoed. The latter notion was further supported by findings that vection-in-depth ratings increased with display gain in both active in-phase and active out-of-phase depth-oscillation conditions.

4 Experiment 3. Effects of multisensory stimulation about fore – aft head oscillation during rightward vection

In experiment 1 we examined the effects of horizontal head and display oscillation on the induction of vection in depth, whereas in experiment 2 we examined the effects of fore – aft head and display oscillation on the induction of vection in depth. The former experiment showed that in-phase head and display oscillation improved vection more than out-of-phase conditions, while the latter showed similar effects for in-phase and out-of-phase oscillation. A potential issue in experiment 2 was that the physical/simulated head oscillation (fore – aft oscillation) was always along the same axis as the main component of the visual display motion (which simulated constant-velocity-forwards self-motion in depth). Several previous studies have found that, with stationary observers, simulated head oscillation improves vection in depth only when it is along an orthogonal axis to the main/constant velocity component of the optic flow (Nakamura 2010; Palmisano et al 2008). This may have been the reason why we obtained different patterns of results in experiments 1 and 2. To test this possibility, in experiment 3 we examined the effects of physical and simulated fore – aft head oscillation on rightwards vection using a lamellar-flow stimulus (instead of the radial-flow displays used in experiments 1 and 2).

4.1 *Method*

The apparatus, visual displays, and procedure were similar to those in experiments 1 and 2 (see figure 1). However, the main optic-flow component of all of the display conditions tested simulated leftward lamellar flow (ie rightward vection) at 1.5 m s^{-1}. During active conditions, subjects were asked to oscillate their heads fore-and-aft throughout the trial. These head position data were then either updated into the self-motion display or ignored. In conditions in which the subject's physical head movements were updated into the display, the expanding/contracting display motion was either the same ('1') or twice ('2') the amplitude expected from the subject's head movements. Passive playback conditions were also tested. Unlike in experiments 1 and 2, subjects were only asked to rate their experience of rightward vection (and were instructed to ignore any vection along the depth axis). Subjects made these ratings relative to a standard reference stimulus, which they were told represented a rating of 50% self-motion. This standard stimulus was a non-oscillating pattern of lamellar flow (ie 0 gain) and was viewed while the subject was stationary.

4.1.1 *Subjects.* Seventeen naive undergraduate psychology students (eleven females and six males; mean age = 22.15 years, SD = 3.18 years) participated in this experiment. Other selection criteria were the same as those for experiment 1.

4.2 *Results*

4.2.1 *Active viewing conditions (with or without fore – aft display oscillation).* As in experiments 1 and 2, both active in-phase ($F_{1,16} = 25.789$, $p < 0.05$) and active out-of-phase ($F_{1,16} = 12.19$, $p < 0.05$) display oscillations were found to significantly increase vection strength ratings compared to active no-display oscillation conditions (see figure 8). In contrast to experiment 1, but similar to experiment 2, we did not find a significant difference between active in-phase display oscillation and active out-of-phase display

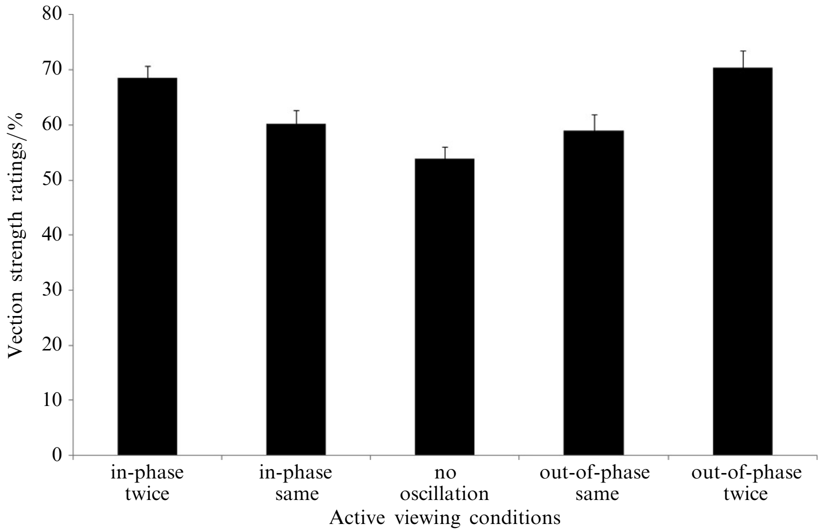

Figure 8. Effect of active fore – aft oscillation on vection strength ratings for rightward vection as a function of both display gain (either at the same or twice the amplitude expected from the subject's head movements) and phase (either in-phase, or out-of-phase with, or unaffected by, the subject's head movements). Error bars depict 1 SEM.

oscillation ($F_{1,16} = 0.027$, $p > 0.05$). As in both experiments 1 and 2, larger fore – aft display gains were found to significantly improve vection compared to smaller fore – aft display gains for both active out-of-phase oscillation ($F_{1,16} = 23.08$, $p < 0.05$) and active in-phase oscillation ($F_{1,16} = 10.94$, $p < 0.05$) conditions.

4.2.2 *Passive viewing condition (with or without oscillation).* As in experiment 1, but not experiment 2, vection strength ratings for passive display oscillation conditions were significantly greater than those for passive no-display oscillation conditions ($F_{1,16} = 15.50$, $p < 0.05$—see figure 9). This confirms that display oscillation has to be in an orthogonal direction to improve the vection induced by the main/constant velocity component of the optic flow. Contrary to both experiments 1 and 2, larger display oscillation conditions were found to significantly differ from smaller visual display oscillation conditions ($F_{1,16} = 15.40$, $p < 0.05$).

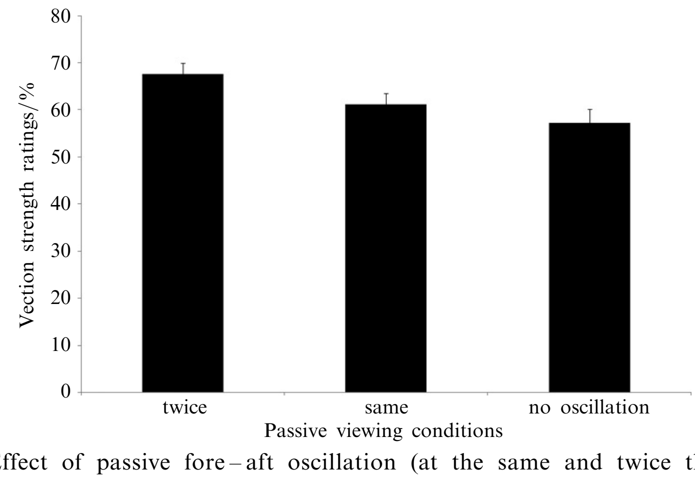

Figure 9. Effect of passive fore – aft oscillation (at the same and twice the amplitude as the subject's head movements) on horizontal self-motion strength ratings compared to passive no-display oscillation conditions. Error bars depict 1 SEM.

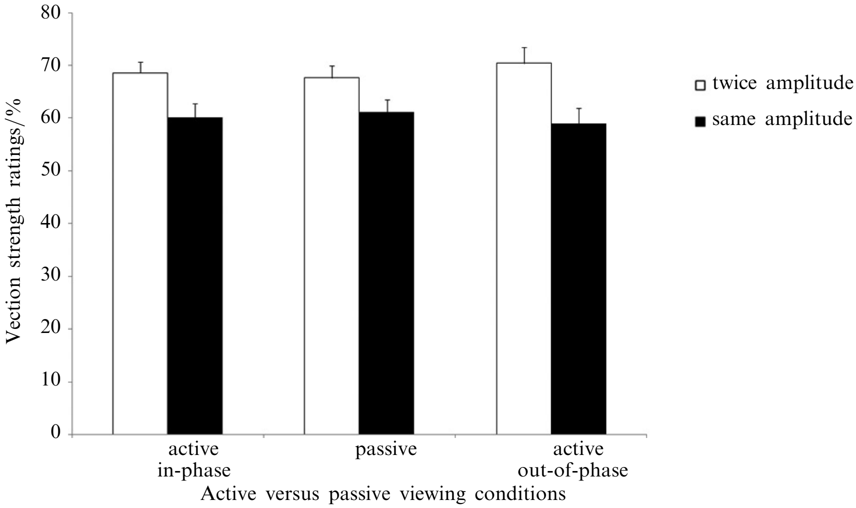

Figure 10. Effect of active in-phase, passive, and active out-of-phase display oscillation (at the same and twice the amplitude as the subject's head movements) on horizontal self-motion strength ratings. Error bars depict 1 SEM.

4.2.3 *Active versus passive viewing conditions (with or without display oscillation).* As in experiment 2, active display oscillation did not produce significantly different vection strength ratings from passive display oscillation (in-phase versus passive: $F_{1,16} = 0.00$, $p > 0.05$; out-of-phase versus passive: $F_{1,16} = 0.02$, $p > 0.05$—see figure 10). Also, as in experiment 2, active display oscillation did not induce significantly different vection from passive no-display oscillation (in-phase versus no-display oscillation: $F_{1,16} = 5.60$, $p > 0.05$; out-of-phase versus no-display oscillation: $F_{1,16} = 5.97$, $p > 0.05$).

4.2.4 *Head movement verification.* Subjects moved their heads in a similar fashion for all active conditions tested (there was negligible head movement in passive conditions). On average, head movement frequencies and amplitudes in these conditions were 0.72 ± 0.17 Hz and 6.36 ± 2.57 cm, respectively.

4.3 *Discussion*

As in the earlier experiments, active in-phase and active out-of-phase oscillation conditions were both found to improve vection compared to active no-display oscillation conditions. Interestingly, as in experiment 1 (but not experiment 2), passive display oscillation conditions were also found to improve vection strength ratings compared to passive no-oscillation conditions. Taken together the findings of all three experiments support the notion that only simulated head oscillation along an orthogonal axis to the display's main motion improves vection induced in stationary/passive observers. That is, in experiment 2, when simulated fore–aft head oscillation was played back along the same axis as the display's main motion, it did not improve the vection in depth compared to stationary viewing of non-oscillating radial flow. However, when the observer actively generated this display oscillation, both active in-phase and active out-of-phase display oscillation conditions improved vection compared to active no-display oscillation conditions. Therefore, as suggested by Nakamura (2010) and Palmisano et al (2008), added display oscillation may need to be simulated along an orthogonal axis in order to improve vection in stationary observers (but not when this display oscillation is actively generated by the observer).

As in experiment 2 (but not experiment 1) we found no vection advantage for active in-phase oscillation compared to active out-of-phase oscillation and passive display oscillation. Vection strength ratings were similar for both active in-phase and active out-of-phase conditions in experiments 2 and 3. However, in experiment 1, we found that vection strength ratings were significantly higher for active in-phase conditions compared to active out-of-phase conditions. One important difference between these experiments was that the subjects moved their heads along the horizontal axis in experiment 1 and along the depth axis in experiments 2 and 3. Therefore, one possible reason for the differential effects of display phase on vection in these experiments may have been that subjects were more sensitive to visual – vestibular conflicts arising from side-to-side head movements than those arising from fore – aft head movements.

5 General discussion

In the current experiments we examined the vection in depth induced by radial flow during physical/simulated head oscillation along the horizontal (experiment 1) or depth (experiment 2) axis. A control experiment (experiment 3) was also performed to examine the sideways vection induced by lamellar flow during physical/simulated fore – aft head oscillation. Unlike previous studies (eg Kim and Palmisano 2008, 2010), experiment 1 showed that active observer conditions (consistent visual – vestibular information about horizontal self-acceleration) generated more compelling experiences of vection in depth than passive observer conditions (only visual information about horizontal self-acceleration). Based on the null findings of previous studies, it seems likely that this consistent advantage of multisensory vection only reached statistical significance in our study due to: (i) the large sample sizes used; (ii) the younger subjects tested; and/or (iii) the larger display gains that were examined (compared to Kim and Palmisano 2008, 2010). Evidence of a similar consistent multisensory vection advantage for self-acceleration in depth was absent in experiments 2 and 3, suggesting that this advantage may be unique to actively generated horizontal head movements and/or horizontal display oscillation.

Experiment 1 showed that active in-phase horizontal-display oscillation significantly improved the vection in depth induced by radial flow compared to passive horizontal-display oscillation, passive no-display oscillation, and active no-display oscillation. That is, ratings of vection in depth were stronger when the visual and vestibular inputs both indicated the same direction of horizontal self-acceleration (compared to conditions when only visual input or only vestibular input indicated this horizontal self-acceleration). This vection advantage for active in-phase display oscillation (relative to the active no-display oscillation control) was greater for the larger of the two gains/oscillation-amplitudes tested (ie '+2' as opposed to '+1'). However, it is worth noting that compelling vection in depth could still be induced by inconsistent patterns of multisensory self-motion stimulation: that is, when visual and vestibular inputs indicated opposite directions of horizontal self-acceleration or when only vision indicated horizontal self-acceleration. Active out-of-phase and passive horizontal-display oscillation both induced significantly more compelling vection in depth relative to comparable conditions without display oscillation (ie active no-display oscillation and passive no-display oscillation conditions).

In experiment 1, the superiority of active in-phase horizontal-display oscillation on vection may be explained (in part) on the basis of differences in retinal motion produced by uncompensated eye movements. During this experiment, subjects attempted to fixate at, or near to, the centre of the display. This required the execution of compensatory eye movements that were equal and opposite in velocity to the velocity of the visual scene. Rather than increasing proportionally with increases in the velocity of visual motion, the compensatory eye movements in these active in-phase conditions remained statistically invariant across the amplitudes of display oscillation we used. In these active in-phase conditions the subjects' compensatory eye movements would have been relatively less effective at maintaining stable central fixation with larger amplitudes of display oscillation. These (high-gain) display oscillations occurring in-phase with the head movement would have resulted in greater retinal slip of the visual scene. Recent evidence from our laboratory suggests that increases in retinal slip may enhance the strength of vection in depth (Kim and Palmisano 2010). It is possible that the increased retinal motion in active in-phase horizontal-display oscillation conditions may account for the enhancement in vection strength produced in these conditions.

Differences in degrees of retinal motion may also account for the weaker vection reported during active out-of-phase horizontal-display oscillation. Because the head moved in the same direction as visual display motion in active out-of-phase conditions, less eye motion would have been required to maintain a stable retinal image compared to active in-phase horizontal-display oscillation. The overall amount of retinal motion would have been comparatively smaller for these out-of-phase compared to in-phase conditions, explaining the relatively weaker vection in out-of-phase viewing conditions. By contrast, in passive horizontal-display oscillation conditions, the velocity of the subject's compensatory eye movements increased proportionally with increases in the velocity of display oscillation. Thus, it appears that eye movements were more effective at compensating for both levels of the passive horizontal-display oscillation. This would have produced similar amounts of retinal slip and vection for large and small display oscillation amplitudes.

While in experiment 1 there was a modest vection advantage for active in-phase (compared to active out-of-phase) horizontal-display oscillation, the effects of active in-phase and active out-of-phase depth oscillation were similar in experiment 2 (despite the former condition being more ecological). Similar to the findings of experiment 1, the vection induced by both active in-phase and out-of-phase depth oscillation was still significantly stronger than that induced by active no-display oscillation conditions.

Thus, one consistent finding that was common to both experiments 1 and 2 was that the vection in depth induced by radial flow was always superior when the observer's physical head oscillation was accompanied by visual display oscillation. Irrespective of whether the visual display oscillation was in-phase or out-of-phase with the head movements, or along the horizontal or depth axis, active display oscillation always induced more compelling vection in depth than active no-display oscillation. This advantage of head-and-display oscillation over head-only oscillation might indicate that: (i) the vestibular system was less sensitive to the direction of head oscillation than vision under the current experimental conditions; or (ii) inconsistent vestibular information about head direction was ignored or downplayed because the observer was experiencing vection; or (iii) the absence of expected visual display motion in active no-display oscillation conditions inhibited the vection more than visual display oscillation that moved in a non-ecological direction. Both (ii) and (iii) may be explained by recent neurophysiological findings of reciprocal inhibitory visual – vestibular interactions during self-motion perception (eg Brandt et al 1998). In the case of (ii), contradictory vestibular information about the direction of self-motion may have been suppressed by the visual system and visual information about self-motion may have dominated. In the case of (iii) vestibular stimulation would have dominated the perception of self-acceleration (in the absence of visual oscillation) and this in turn may have suppressed information provided by the visual system about constant-velocity self-motion.

Unlike in experiment 1, vection was found to increase with the display gain in both active in-phase and active out-of-phase depth oscillation conditions in experiment 2. Only vection in the passive depth oscillation conditions was unaffected by the display oscillation amplitude. Head movements were similar in both active conditions and negligible in passive conditions. However, we could not examine the retinal-slip/eye-movement based explanations for the vection data in this experiment, as we were unable to record the binocular radial vergence eye movements generated by its depth oscillating radial optic-flow displays (see Miles et al 2004). This would have required a binocular eye-tracking system, rather than the monocular eye-tracking system used in experiment 1. However, similar effects of display gain were found for the vection obtained in both active in-phase and active out-of-phase depth oscillation conditions. This suggests that the inconsistent vestibular stimulation in out-of-phase conditions was playing less of an inhibitory role in this experiment.

One reason why we might have obtained a different pattern of results in experiment 2 (compared to experiment 1) was that the active/passive display oscillation (fore–aft) was generated along the same axis as the display motion (which simulated forwards self-motion in depth). Therefore, in experiment 3, we added fore–aft display oscillation to a lamellar flow display simulating leftward motion (ie induced rightward vection). As in experiments 1 and 2, we found vection improvements for active in-phase oscillation and active out-of-phase oscillation compared to active no-display oscillation conditions. Interestingly, we also found vection improvements for passive display oscillation conditions (similar to experiment 1, but not experiment 2). The vection improvements found for passive display oscillation conditions in experiments 1 and 3 suggest that added display oscillation should be simulated along an orthogonal axis in order to improve vection in stationary observers (but not when the observer actively generates this display oscillation). The above notion is consistent with recent findings of Nakamura (2010) and Palmisano et al (2008). Furthermore, unlike in experiment 1 (but as in experiment 2), we did not find an advantage for active in-phase oscillation compared to passive display oscillation. Therefore, in combination, these results suggest that subjects were more sensitive to visual–vestibular conflicts arising from side-to-side head movements than to those arising from fore–aft head movements.

Overall, our research shows that consistent non-visual information can enhance the visual perception of self-motion in some situations. However, the current and previous findings (Kim and Palmisano 2008, 2010; Palmisano et al 2000, 2003, 2008; Wright et al 2005) also suggest that: (i) conflict between the visual and vestibular systems often does not impair the experience of illusory self-motion (even when this is generated via non-visual channels—Reicke et al 2005); and (ii) discordant vestibular information may sometimes enhance this experience (Wright 2009). Therefore, it is clear that the pattern of multisensory stimulation does not always have to be consistent to induce compelling vection and generate substantial vection improvements. However, it should also be noted that, in addition to the contribution of retinal and extra-retinal information, higher-level cognitive (see Palmisano and Chan 2004; Wertheim et al 2001) and contextual factors (see Wright et al 2006) have also been suggested to play a role in the suppression and/or enhancement of illusory self-motion. Therefore, future research should further examine the contribution of the different sensory systems as well as the relative importance of cognitive and contextual information to the perception of self-motion and vection.

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