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Investigating the Time Course of Verticality Sensitivity Changes During Visuo-vestibular Conflict

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Abstract

Verticality perception is a multisensory process that relies primarily on visual and vestibular input. Previous studies show that sensory conflict induced by optic flow causes increased errors in verticality perception. However, the time course over which sensory conflict alters verticality perception, and the processes through which perceptual stability is subsequently restored, remain unknown. Experiment 1 aimed to examine how verticality perception changes over time in response to sensory conflict and Experiment 2 aimed to determine whether verticality perception recovers following the removal of a sensory conflict. Sensory conflict was induced using optic flow, such that visual cues signalled self-motion while vestibular input provided no self-motion signal. Sensitivity to verticality was measured using a Vertical Detection Task (VDT) in which participants judged whether lines were vertically oriented or not. Signal detection theory was used to analyse responses, where d' was an index of perceptual sensitivity to verticality and criterion was a measure of response bias. In Experiment 1 participants completed the detection task whilst either roll optic flow or randomly moving dots were presented in the background. Results showed that d' was significantly lower in the roll optic flow condition, with this effect varying as a function of time. Specifically, d' was significantly lower in the roll vs random visual stimulation condition for up to 6 minutes of exposure. Experiment 2 extended these findings by examining recovery from sensory conflict, comparing VDT performance during roll optic flow with performance at successive timepoints following its removal. Consistent with Experiment 1, d′ was significantly reduced during optic flow exposure. However, d′ returned to baseline levels by the first post-flow timepoint, indicating a rapid recovery of verticality sensitivity. Together, these findings demonstrate that sensory conflict reduces verticality sensitivity in a time-dependent manner, followed by rapid recovery within minutes after the conflict is removed.

Keywords: Sensory conflict, Verticality, Vestibular System, Optic Flow, Multisensory Integration

1. Introduction

The perception of self-motion is constructed from multiple sensory modalities including visual, vestibular, proprioceptive and somatosensory inputs. Visual input from optic flow and vestibular input regarding acceleration of the head are particularly important for self-motion integration, and typically both modalities provide complementary information about our own movements (Laurens & Angelaki, 2011). Visual and vestibular signals are thought to be integrated by reliability-based optimal multisensory integration, a process which reduces the variance in the multisensory estimate, increasing its precision relative to unimodal estimates precision (Ernst and Banks, 2002; Ernst and Bülthoff, 2004). Unimodal signals are weighted based on their reliability with more reliable information receiving higher weight, thereby contributing more to the multisensory estimate (Butler *et al.,* 2010; Ernst and Banks, 2002; Ernst and Bülthoff, 2004; Gu *et al.,* 2008; MacNeilage *et al.,* 2007). Crucially, visuo-vestibular integration plays a large role across many perceptual processes beyond self-motion perception alone, including spatial orientation (Ellmore and McNaughton, 2004) and verticality perception – our perception of what is "up" and what is "down" within the gravitational environment (Dakin and Rosenberg, 2018).

However, conflict between visual and vestibular modalities regarding self-motion can result in changes to perceptual functioning. Conflict between visual and vestibular modalities can occur in situations such as Virtual Reality (VR). In VR, optic flow signals that the body is moving in a certain direction with a certain acceleration while the vestibular system signals that the body is stationary. Therefore, both sensory signals have conflicting information regarding self-motion. This visuo-vestibular conflict is proposed as one explanation for motion sickness more broadly, and cybersickness in VR users (Gallagher and Ferrè, 2018; Rebenitsch and Owen, 2016; Reason and Brand, 1975).

Moreover, it has been proposed that re-weighting of unimodal signals occurs in response to visuo-vestibular conflict (Weech *et al.,* 2018; Weech *et al.,* 2020), which may result in a variety of changes to perceptual and behavioural functioning. For example, previous studies have shown that sensory conflict induced using VR reduces postural stability suggesting a down-weighting of vestibular cues (Chander *et al.,* 2019; Pujiartati *et al.,* 2020). Furthermore, Gallagher *et al.* (2020) found that four

minutes of roll optic flow in VR significantly reduced participants' ability to detect Galvanic Vestibular Stimulation (GVS) reflecting a reduction in vestibular sensitivity. However, they found no effect of linear optic flow suggesting that visual and vestibular input need to be in the same plane of motion to cause vestibular down-weighting. Optic flow in VR has also been found to affect vestibular reflexes. For example, Di Girolamo *et al.* (2001) found reduced vestibular-ocular reflex gain following exposure to visuo-vestibular conflict in VR indicating a down-weighting of vestibular signals. Similarly, Gallagher *et al.* (2019) found one minute of linear optic flow in VR increased the amplitude of the vestibular-evoked myogenic potential (VEMP) and significantly altered the VEMP asymmetry ratio. The increased amplitude may reflect an up-weighting of vestibular input which occurred after exposure to visuo-vestibular conflict. Moreover, Warchoł *et al.* (2024) examined the effects of a rollercoaster simulation in VR on postural responses, in which vision signals self-motion in the absence of corroborating vestibular cues. They reported that postural stability improved following VR exposure relative to baseline, and proposed that this effect reflected an increased weighting of vestibular signals in response to sensory conflict (Warchoł *et al.,* 2024). Together, these findings highlight that visuo-vestibular conflict results in altered vestibular perceptual and reflex functioning.

In addition to directly affecting vestibular function, visuo-vestibular conflict can also influence the perception of multimodal percepts that rely on vestibular input. Verticality perception – the ability to tell up from down in a gravitational environment – may be particularly affected by such conflict, given its dependence on vestibular and visual inputs. For example, studies that use roll optic flow have found that it increases errors in the Subjective Visual Vertical (SVV; Lubeck *et al.*, 2016; Park *et al.*, 2021) and that this effect is reduced when using linear optic flow (Park *et al.*, 2021) or having the presence of an Earth-fixed frame (Lubeck *et al.*, 2016). Additionally, visuo-vestibular conflict also affects sensitivity to verticality signals. For instance, roll optic flow reduces verticality sensitivity in a Vertical Detection Task (VDT) more than GVS on its own or combined GVS and roll optic flow (Schoenmaekers *et al.,* 2025). Furthermore, Arshad *et al.* (2023) examined the effect of roll optic flow on verticality sensitivity using a signal detection approach. They found that one minute of roll optic flow significantly decreased verticality sensitivity.

As well as visuo-vestibular conflict induced by optic flow, exposure to microgravity can also create sensory conflicts which affect perception of verticality. In microgravity, the otolith organs no longer receive gravitational signals, while semicircular canals and visual cues are still able to signal self-movement, creating sensory conflict. Such gravitational conflicts are thought to cause space motion sickness (SMS) which is defined as having feelings of nausea, vomiting, dizziness and headaches when exposed to microgravity (Heer and Paloski, 2006). Interestingly astronauts who had been in the International Space Station (ISS) for a mean duration of 168 days had increased variance in the SVV after returning to Earth (Harris *et al.,* 2017), suggesting that sensory conflict in microgravity reduces verticality perception.

1.1 Research gap and present study

Despite extensive investigation of long-term adaptation to sensory conflict, the temporal dynamics and mechanisms of short-term adaptation remain poorly understood. Fransson *et al.* (2019) examined adaptation to a VR roller coaster simulation and observed an initial reduction in postural stability, followed by progressive improvement across repeated exposures. This suggests that multisensory weighting mechanisms supporting postural control undergo adaptive recalibration over time in response to visuo-vestibular conflict. Additionally, Niehof *et al.* (2019) examined the effect of bias induced by either GVS or optokinetic stimulation and found them to affect SVV performance which was measured continuously. They reported that SVV deviations followed an exponential time course, characterised by rapid initial change and a subsequent plateau. The time constant of this process was approximately 4 seconds for GVS and 7 seconds for optokinetic stimulation. This suggests multisensory integration processes to be altered within seconds after a bias is introduced. Furthermore, the studies that examine the effects of visuo-vestibular conflict have only looked at short and immediate effects (Arshad *et al.*, 2023; Schoenmaekers *et al.,* 2025). As a result, the temporal dynamics of adaptation to

visuo-vestibular conflict, and the extent to which perceptual function recovers following its removal, remain poorly understood.

The present study aims to investigate the time course of changes in verticality sensitivity in response to visuo-vestibular conflict. In Experiment 1 we aim to see how verticality sensitivity changes over time during exposure to visuo-vestibular conflict. We hypothesized that verticality sensitivity will be lower when a participant is presented with roll optic flow in comparison to random visual stimulation and that verticality sensitivity will progressively decrease in the roll optic flow condition over time. We further hypothesized that there will be no significant changes in response bias. Experiment 2 examines the recovery of verticality sensitivity following the removal of visuo-vestibular conflict. Roll optic flow was used to induce a visuo-vestibular conflict in the first half of the experiment, followed by a post-exposure period in which optic flow was absent. We hypothesized that verticality sensitivity would progressively increase over time following the removal of roll optic flow. We also hypothesized that response bias will not significantly change over time.

Experiment 1

2. Methods

2.1 Participants

The study was approved by the University of Kent Psychology Ethics board. There were 36 participants in total recruited from the University of Kent's research participation scheme with students completing the study for course credit. Six participants were excluded from analysis, resulting in a final sample of n = 30. Participants were excluded if their average d' < 0 in the random condition, indicating task confusion (n = 5) or if over 50% of their data was missing responses (n = 1). Individual trials were

also excluded if the reaction time was <250ms. This exclusion criteria followed that used by Arshad *et al*. (2023). The mean age of the final sample was 21.13 (*SD* = 4.02) with 22 female and 8 male.

2.2 Stimuli

Optic flow was created using MATLAB R2024b with Psychtoolbox (Version 3.0.19) and exported as videos (1920x1080 resolution, 30 FPS). Roll optic flow consisted of a field of 1000 white dots on a black background moving in an anti-clockwise roll-rotation at 90°/s. Random visual stimuli consisted of 1000 dots presented as a limited-lifetime random dot kinematogram. Each dot persisted for 10 frames, after which it was randomly repositioned. Dot locations were sampled from a projected surface of a static 3D sphere and updated stochastically on each frame. This resulted in a dynamic motion field with no coherent dot trajectories. Each video was played continuously in the background for nine minutes during the vertical detection task.

The vertical detection task involved presentation of white lines (0.2 x 4.5 cm) presented with a black circular aperture (diameter 6.5cm). A tube (diameter 25.5cm) was fixed to the screen (Fig. 1a) to eliminate any visual cues for verticality, as an earth fixed frame significantly decreases the effects of roll optic flow on verticality perception (Lubeck *et al.,* 2016). Participants were seated approximately 30 cm from the monitor, resulting in a field of view of ~ 46 degrees. Each block consisted of 30 vertical stimuli, 15 clockwise-tilted stimuli (+2.5°) and 15 anti-clockwise-tilted stimuli (-2.5°), each presented for 500ms with a 1s response interval (Fig. 1b). Blocks lasted for 90 seconds, with six blocks in total presented consecutively for the nine minutes of visual stimulation. The task was created and run through Psychopy (version 2024.2.5).

Figure 1

Presentation of the VDT

(Fig. 1 here)

2.3 Data Analysis

Data was analysed using RStudio (version 4.2.0). Packages "lme4" (version 1.1-37; Bates *et al.,* 2015), "lmerTest" (version 3.1-3; Kuznetsova *et al.,* 2017) and "emmeans" (version 1.11.2-8; Lenth, 2025) were used for analysis. Packages "dplyr" (version 1.1.4; Wickham *et al.,* 2023) and "ggplot2" (version 4.0.0; Wickham, 2016) were used for descriptives and graphs respectively. A within-subjects design was used where the first factor was optic flow with two levels including roll and random. The second factor was time where measures of d' and criterion were calculated every 90 seconds over six time windows.

The signal detection approach was used for data analysis (Macmillan, 2002). Data was organised into hits (responding "yes" to vertical stimulus), misses (responding "no" to vertical stimulus), false alarms (FA; responding "yes" to tilted stimulus) and correct rejections (CR; responding "no" to tilted stimulus). After this the proportion of hits and FA's were calculated using this formula:

$$PropHit = \frac{nHits}{nVerticalStim} \tag{1}$$

$$PropFA = \frac{nFA}{nTiltedStim} \tag{2}$$

In cases where the number of hits were equal to the number of vertical stimuli or if the number of FA's were equal to the number of tilted stimuli a corrected proportion was used by using this formula:

$$PropHit = nHits - \frac{0.5}{nVerticalStim}$$

(3)

$$PropFA = nFA - \frac{0.5}{nTiltedStim}$$

(4)

In cases where the number of hits were 0 or the number of FA's were 0 this corrected proportion was used:

$$PropHit = \frac{0.5}{nVerticalStim}$$

(5)

$$PropFA = \frac{0.5}{nTiltedStim}$$

(6)

Verticality sensitivity was measured with d' which was calculated by:

$$d' = Z(PropHit) - Z(PropFA)$$

(7)

Response bias was measured with criterion which was calculated by:

$$C = -\frac{Z(PropHit) + Z(PropFA)}{2}$$

(8)

2.4 Linear Mixed Models

Linear mixed models were used to investigate the impact of time and condition on sensitivity to verticality and response biases. These models were chosen above a standard ANOVA approach to firstly account for the potential for significant individual variability in verticality sensitivity and responses to visuo-vestibular conflict, and secondly to allow modelling of potential non-linear changes in sensitivity over the duration of exposure. Random intercepts were used to account for differences in baseline verticality sensitivity, while random slopes were used to account for variation across individuals over time. This is theoretically motivated by previous reports of individual variability in vestibular sensitivity and motion sickness (Gallagher et al., 2023). A quadratic time component was included as a predictor in the model to investigate the possibility that the change in sensitivity over time may be non-linear. For example, participants could have experienced a period of recovery following prolonged exposure to visuo-vestibular conflict, which would not have been accounted for by a simple linear decrease alone. Likelihood ratio tests were used to determine the best fitting model structure, first comparing models with and without random slopes and intercepts, then comparing linear time models with quadratic models. Model selection was also guided by minimisation of AIC, indicating the most parsimonious model with the best predictive power. There were 360 observations in each model (30 participants x 2 conditions x 6 timepoints). Bonferroni-corrected planned pairwise comparisons were used to see at which time points there were significant differences between random and roll optic flow, with a new significance threshold of $p < .008$.

2.5 Procedure

Participants were first given information sheets containing details of the experiment and consent forms to sign prior to the start of the study. They were then instructed to remain seated and place their head into the large cardboard tube which was attached to the computer screen. Participants were instructed to judge whether each line was vertically oriented, pressing "Y" on the keyboard to indicate vertical and "N" not vertical. They were also told to hold their gaze to the green fixation dot (0.6 x 0.6cm) in the centre of the screen throughout the task and to keep their heads still. They were first given an opportunity to practice the task where they completed eight trials with a black background. After this the instructions were re-presented, and participants were informed that the real task was about to begin. They completed the verticality detection task with optic flow in the background moving continuously. The task and the optic flow lasted for nine minutes per condition. The order of roll optic flow and random visual stimulation was randomized across participants. After completing the first condition, participants notified the experimenter. The experimenter then initiated a five-minute break to minimise potential carry-over effects between conditions. Participants then repeated the task but with either roll optic flow or random visual stimulation in the background depending on the counterbalanced condition order. After completing the experiment, participants were debriefed.

3. Results

3.1 Sensitivity

It was hypothesized that d' would change over time however, no specific predictions were made regarding whether this change would follow a linear trajectory. For this reason, a likelihood ratio test was conducted comparing a linear model (d' = Condition * Time) and a quadratic model (d' = Condition * Time + Condition * Time^2). Including a quadratic term had a significantly better fit (*AIC* = 868.33) than the linear mode (*AIC* = 873.09) $\chi^2(2) = 8.76$, $p < .05$ suggesting the effect of visuo-vestibular conflict on d' over time was non-linear. A likelihood ratio test revealed that a random intercept model

(*AIC* = 886.18) provided a significantly better fit than a fixed-effects model (*AIC* = 1153.39) $\chi^2(1) = 269.21$, $p < .001$. Furthermore, it was revealed that a full model which had a random slope and intercept (*AIC* = 868.33) had a significantly better model fit than a model with only a random intercept (*AIC* = 886.18) t $\chi^2(2) = 21.85$, $p < .001$. Therefore, a random slope and intercept was selected for the final model.

The final model was fitted using restricted maximum likelihood estimation (REML). Scaled residuals ranged between -3.15 and 2.63 with a median of -0.02. There was no main effect of Condition ($b = 0.029$, $SE = 0.306$, $t = 0.096$, $p = .924$), Time ($b = 0.042$, $SE = 0.144$, $t = 0.291$, $p = .771$) or the Quadratic time term ($b = -0.020$, $SE = 0.020$, $t = -1.036$, $p = .301$). However, the analysis revealed a significant interaction between Condition and Time ($b = -0.492$, $SE = 0.200$, $t = -2.459$, $p < .05$) as well as a significant interaction between Condition and the Quadratic time term ($b = 0.075$, $SE = 0.028$, $t = 2.694$, $p < .01$). This suggests that the effect of visuo-vestibular conflict on vestibular sensitivity are time-dependent and non-linear.

Pairwise comparisons were used to determine time points with a significant difference between roll optic flow and random visual stimulation. Comparisons were evaluated at each time point using estimated marginal means from the quadratic model, using 296 degrees of freedom. Bonferroni correction was applied, giving a new significance threshold of $p < .008$. Significant differences between roll and random conditions were apparent at each time point up to 6 minutes however, there were no significant differences at 7.5 minutes and 9 minutes (Table 1). In particular, d' was significantly lower in the roll condition compared to the random condition at each time point (Table 2 and Fig. 2). The results from the quadratic model suggests that verticality sensitivity rapidly decreases immediately after exposure to visuo-vestibular conflict and then plateaus. At later timepoints, sensitivity in roll and random conditions converge, driven by the decrease in sensitivity in the random condition at these later time points, perhaps as a result of practice or fatigue.

Table 1

Results of the pairwise comparisons for the quadratic time term

Time (mins)	b	SE	t(296)	p-value	Significance
1.5	1.617	0.402	4.018	<.001	*
3	1.390	0.320	4.345	<.0001	*
4.5	1.014	0.186	5.448	<.0001	*
6	0.486	0.074	6.610	<.0001	*
7.5	-0.192	0.284	-0.677	.499	
9	-1.021	0.587	-1.740	.083	

Table 2

Means and standard deviations of d' for roll optic flow and random visual stimulation conditions at each timepoint.

Condition	Time (mins)	Mean	Std. Deviation
Roll	1.5	1.31	1.15
	3	0.87	1.15
	4.5	0.75	1.10
	6	0.77	1.19
	7.5	0.85	1.28
	9	0.86	1.20
Random	1.5	1.56	1.07
	3	1.74	1.30
	4.5	1.60	1.21
	6	1.36	1.24
	7.5	1.26	1.07
	9	1.18	1.35

Figure 2

d' Over Time by Condition

(Fig. 2 here)

Note. A measure of d' was calculated every 90 seconds. The graph shows the mean d' at each 90 seconds for the roll and random conditions. The shaded area shows the minimum and maximum standard deviation at each time point.

3.2 Response Bias

For criterion, likelihood ratio tests revealed that having a random intercept and slope (*AIC* = 466.29) did not significantly improve model fit in comparison to a model with only a random intercept

(*AIC* = 467.94) $\chi^2(2) = 5.64$, $p = 0.059$. It was also found that a model with only a random intercept (*AIC* = 467.94) provided better fit than a model with fixed-effects (*AIC* = 655.70) $\chi^2(1) = 189.76$, $p < .001$ meaning the final model had a fixed slope and random intercept. It was also found that having a quadratic time term (*AIC* = 467.94) significantly improved fit compared to linear (*AIC* = 472.33) $\chi^2(2) = 8.07$, $p < .05$. The final linear mixed effects model was fitted with REML with scaled residuals ranging from -3.40 to 4.73 with a median of 0.02. There was no significant effect of Condition ($b = -0.151$, $SE = 1.889$, $t = -0.800$, $p = .425$) however, there was an effect of Time ($b = -0.222$, $SE = 0.087$, $t = -2.539$, $p < .05$) and Quadratic time ($b = 0.025$, $SE = 0.012$, $t = 2.018$, $p < .05$) where participants became more liberal the longer the time (Fig. 3). There were no significant interactions between Condition and Time ($b = 0.016$, $SE = 0.124$, $t = 0.129$, $p = .897$) or Condition and Quadratic time ($b = -0.000$, $SE = 0.017$, $t = -0.017$, $p = .986$).

Figure 3

Criterion Over Time by Condition

(Fig. 3 here)

Note. Criterion was calculated every 90 seconds. The graph shows the mean criterion every 90 seconds for roll and random conditions. The shaded area shows the minimum and maximum standard deviation at each time point.

4. Discussion

Experiment 1 was designed to examine the time course of verticality sensitivity during sustained exposure to visuo-vestibular conflict. Overall, the findings indicate that the effect of sensory conflict on verticality sensitivity is time-dependent and quadratic. Specifically, visuo-vestibular conflict caused an initial reduction in verticality sensitivity, followed by a gradual recovery over time, such that performance approached levels observed in the absence of sensory conflict. Previous studies have established that visuo-vestibular conflict reduces verticality sensitivity after <5 minutes of exposure,

however few studies have examined adaptation across longer durations or systematically characterised its temporal dynamics (Schoenmaekers *et al.,* 2025; Lubeck *et al.,* 2016). These findings therefore provide novel evidence that verticality sensitivity undergoes dynamic adaptation during sustained visuo-vestibular conflict.

Consistent with the present findings, Niehof *et al.* (2019) examined the effects of roll optic flow and GVS on SVV perception and observed an exponential time course that rapidly reached a plateau. Specifically, the time constant of this effect was approximately 4 seconds for GVS and 6 seconds for optokinetic stimulation. This time-course parallels the pattern in the present study, albeit on a shorter time scale where a sensory conflict results in an initial exponential decrease in verticality perception which then slowly plateaus. The quadratic effect found in the present study could be a result of adaptation to the visuo-vestibular conflict, with verticality sensitivity converging towards performance observed under non-conflict conditions. There is existing evidence to suggest that people are able to recover from a visuo-vestibular conflict. For instance, Fransson *et al.* (2019) investigated adaptation to a VR rollercoaster simulation and found that postural stability, which relies on vestibular multisensory integration, decreased substantially within minutes of exposure to VR, but progressively improved over time. This pattern is consistent with the present findings and supports the interpretation that multisensory weighting mechanisms adapt over time in response to sensory conflict. However, the time course over which verticality sensitivity recovers following the removal of visuo-vestibular conflict remains unknown. Therefore, Experiment 2 examined the recovery of verticality sensitivity following exposure to roll optic flow.

Experiment 2

5. Methods

5.1 Participants

A new sample of 39 participants was recruited from the University of Kent's research participation scheme with students completing the study for course credit. Nine participants were excluded leaving the final sample size at n = 30. Participants were excluded if they pressed only one response button across the experiment or within any individual condition (n = 2). They were also excluded if their average d' < 0 (n = 2) or if over 50% of their data was missing responses (n = 5). Individual trials were also excluded if the reaction time was <250ms. The sample had a mean age of 20.63 (*SD* = 4.55) with 23 female, 6 male and 1 non-binary participant.

5.2 Stimuli

The roll optic flow condition was presented exclusively, using the same video stimulus as in Experiment 1. The video lasted nine minutes (1920x1080 resolution, 30 FPS) with dots moving in an anti-clockwise roll-rotation at 90°/s. The task was created and presented using Psychopy (version 2024.2.5). The VDT stimuli were the same as in Experiment 1, with white lines presented within a black circular aperture to eliminate any verticality cues. Each block contained 30 vertical stimuli, 15 clockwise-tilted stimuli (+2.5°) and 15 anti-clockwise-tilted stimuli (-2.5°), each presented for 500ms with a 1s response interval.

5.3 Data Analysis

A within-subjects design was used with two factors. The first factor was optic flow which had two levels including during and post-exposure. As Experiment 1 demonstrated that roll optic flow causes a decrease in verticality sensitivity, only roll optic flow was used for this study. The second factor was time with a measure of d' and criterion calculated every 90 seconds across six time windows.

As in Experiment 1, data was analysed using RStudio (version 4.2.0) using a signal detection approach with data organised into hits, misses, false alarms and correct rejections in order to calculate measures of d' and criterion using the same formula as in Experiment 1.

5.4 Procedure

All participants provided informed consent prior to inclusion. Consistent with Experiment 1, participants remained seated throughout the experiment and placed their heads into a large cardboard tube attached to the computer screen. Participants were instructed to keep their gaze fixated on the green fixation dot in the middle of the screen and to keep their heads still. Participants judged whether each line was vertically oriented by pressing "Y" to indicate vertical and "N" to indicate tilted. Participants were given an opportunity to practice the task before the experiment started whilst the VDT was presented with a black background. Following the practice trials, the on-screen instructions were re-presented and participants were informed that the real task was about to begin.. The first half of the experiment comprised the "during" condition, which lasted nine minutes and involved presentation of roll optic flow in the background of the VDT. Following this, the roll optic flow was removed, and the task continued without interruption with a black background. This constituted the "post" condition, during which participants completed the VDT for a further nine minutes. Participant were debriefed at the conclusion of the experiment.

6. Results

6.1 Sensitivity

As in Experiment 1 there were no specific predictions on whether verticality sensitivity would recover following a linear trajectory after exposure to a visuo-vestibular conflict. Therefore, a likelihood ratio test was used to see if adding a quadratic time term (d' = Condition * Time + Condition * Time^2) improved model fit compared to a linear time term (d' = Condition * Time). However, in contrast to Experiment 1, the quadratic time term (*AIC* = 951.72) did not significantly improve model fit in comparison to the linear time term (*AIC* = 952.08) $\chi^2(2) = 4.35$, $p = .113$ meaning a linear model was used. Likelihood ratio tests also revealed that a random intercept model (*AIC* = 951.72) provided a better fit to the data than a fixed-effects model (*AIC* = 1113.39) $\chi^2(1) = 163.66$, $p < .001$. However, adding a random slope (*AIC* = 955.65) did not improve model fit $\chi^2(2) = 0.07$, $p = .965$ meaning a model with random intercept and fixed slope was used.

The final model was a linear mixed effects model was fitted using restricted maximum likelihood estimation (REML). The median scaled residuals were -0.04 with a maximum of 3.08 and minimum of -3.71. A significant main effect of Condition was found ($b = -0.520$, $SE = 0.194$, $t = -2.675$, $p < .01$) such that participants in the post condition had higher verticality sensitivity ($M = 1.56$, $SD = 1.30$) than those in the during condition ($M = 0.86$, $SD = 0.95$; see Table 3). There was also a significant effect of Time ($b = -0.070$, $SE = 0.035$, $t = -1.973$, $p < .05$), but no significant interaction between Time and Condition ($b = -0.065$, $SE = 0.050$, $t = -1.296$, $p = .196$). These findings indicate that visuo-vestibular conflict produces a linear decrease in verticality sensitivity, which subsequently increases following the removal of the conflict. In addition, time was associated with a linear decrease in verticality sensitivity irrespective of the presence of sensory conflict.

Table 3

Mean and standard deviation d' for the during and post conditions

Condition	Time (mins)	Mean	Std. Deviation
During	1.5	1.29	1.01
	3	0.98	1.11
	4.5	0.73	1.02
	6	0.70	0.83
	7.5	0.61	0.83
	9	0.58	0.69
Post	1.5	1.54	1.03
	3	1.91	1.41
	4.5	1.53	1.21
	6	1.58	1.34
	7.5	1.56	1.39
	9	1.26	1.38

Figure 4

d' Over Time by Condition

(Fig. 4 here)

Note. A measure of d' was calculated every 90 seconds. The graph shows the mean d' every 90 seconds up to nine minutes for during and post optic flow conditions. The shaded area shows the minimum and maximum standard deviation at each time point.

6.2 Response Bias

For criterion likelihood ratio tests were also conducted to determine the best-fitting model. The full model did not significantly improve model fit (*AIC* = 382.52) when compared with a model with only a random intercept (*AIC* = 379.90) $\chi^2(2) = 1.37$, $p = .503$. Furthermore, having a random intercept model (*AIC* = 379.90) significantly improved fit relative to a fixed-effects model (*AIC* = 469.01) $\chi^2(1) = 91.11$, $p < .001$. Therefore, a model with a random intercept and fixed slope was used. A quadratic time term (*AIC* = 379.90) also significantly improved model fit compared to linear (*AIC* = 384.57) $\chi^2(2) = 8.67$, $p < .05$.

The final linear mixed effects model was fitted using REML. The median scaled residuals was 0.05 with a maximum of 3.53 and minimum of -2.89. There was a significant effect of Condition on criterion ($b = 0.376$, $SE = 0.172$, $t = 2.184$, $p < .05$) such that participants adopted a more liberal response bias post optic flow (M = -0.27, SD = 0.47) compared to during optic flow (M = -0.25, SD = 0.46). There was no significant effect from Time (b = -0.080, SE = 0.080, t = -1.000, p = .318) or Quadratic time (b = 0.016, SE = 0.011, t = 1.424, p = .156). There were no significant interactions between Condition and Time (b = -0.156, SE = 0.112, t = -1.384, p = .167) or Condition and Quadratic time (b = 0.013, SE = 0.016, t = 0.814, p = .417).

Figure 5

Criterion Over Time by Condition

(Fig. 5 here)

Note. Criterion was calculated every 90 seconds. The graph shows mean criterion every 90 seconds up to nine minutes for post and during optic flow conditions. The shaded area shows the minimum and maximum standard deviation at each time point.

7. Discussion

Experiment 2 examined the recovery of verticality sensitivity following the removal of visuo-vestibular conflict. The findings indicate that verticality sensitivity increased once the conflict was removed, with recovery occurring rapidly within the first few minutes. This suggests that the reduction in sensitivity observed during optic flow exposure is not sustained, but instead reflects a reversible change in perceptual processing. There was also a significant main effect of condition, with overall higher verticality sensitivity observed post optic flow offset compared to during exposure. In addition, a significant linear effect of time was observed, indicating that verticality sensitivity gradually declined over time across both conditions. Together, these findings suggest that while visuo-vestibular conflict

transiently disrupts verticality sensitivity, perceptual function recovers quickly once the conflict is resolved, consistent with adaptive recalibration of multisensory weighting mechanisms.

8. General Discussion

Across two studies, we investigated how visuo-vestibular conflict influences verticality sensitivity over time and how perceptual sensitivity recovers following the removal of such conflict. The findings demonstrate that visuo-vestibular conflict reduces sensitivity to vertical signals, with the magnitude and trajectory of this effect depending on both the presence of the conflict and the duration of exposure. Experiment 1 showed that the effect of visuo-vestibular conflict followed a quadratic time-course, with the greatest reduction in verticality sensitivity occurring within the first six minutes of exposure, followed by gradual recovery towards levels observed in the non-conflict condition. Experiment 2 expands on this finding by demonstrating that once a visuo-vestibular conflict is removed, there is an immediate and quick recovery. Unlike Experiment 1, the effect of visuo-vestibular conflict was linear with verticality sensitivity gradually declining over time. While the quadratic effect observed in Experiment 1 was not observed in Experiment 2, both experiments consistently demonstrated time-dependent modulation of verticality sensitivity, indicating robust adaptation to visuo-vestibular conflict. These findings suggest that further research is needed to more precisely characterise the temporal dynamics underlying this adaptive process.

The present findings demonstrating the influence of visuo-vestibular conflict on verticality sensitivity are consistent with previous research. For example, Arshad *et al.* (2023) compared roll optic flow to random visual stimuli and found that verticality sensitivity was reduced after one minute of visuo-vestibular conflict. Furthermore, Lubeck *et al.* (2016) found increased errors in the SVV in the presence of roll optic flow. Schoenmaekers *et al.* (2025) also used optokinetic stimulation in the roll plane as well as GVS to manipulate visual and vestibular signals while doing the VDT similar to that used in the present study. They found that both optokinetic stimulation and GVS reduced verticality

sensitivity with optokinetic stimulation having a more pronounced effect. Collectively, these findings support the present results demonstrating reduced verticality sensitivity during visuo-vestibular conflict relative to non-conflict conditions, as observed in both Experiments 1 and 2. Importantly, the present study extends prior work by demonstrating that this disruption is time-dependent and that verticality sensitivity recovers rapidly following the removal of sensory conflict, indicating dynamic and reversible changes in perceptual processing.

Moreover, the present experiments are consistent with previous findings demonstrating time-dependent effects on visuo-vestibular conflict. For example Niehof *et al.* (2019) found that optokinetic stimulation in the roll plane and GVS increased errors in the SVV. These effects followed an exponential time course, characterised by a rapid initial change that reached a plateau after approximately 4 seconds for GVS and 7 seconds for optokinetic stimulation. This temporal profile is consistent with the present findings from Experiments 1 and 2, in which verticality sensitivity showed a marked initial reduction during early exposure to visuo-vestibular conflict, followed by stabilisation over time.

Furthermore, studies have shown that repeated exposure to visuo-vestibular conflict leads to adaptation, with postural responses stabilising over time. This suggests that vestibular weighting mechanisms undergo adaptive recalibration in response to sustained sensory conflict (Fransson *et al.,* 2019). While Experiment 1 suggests the idea of a slight recovery near the later parts of exposure, Experiment 2 does not replicate this effect by showing a more linear decrease over time. This brings into question whether we adapt to sensory conflict and in what conditions this occurs. A key difference between Fransson *et al.* (2019) and the present study is that they outline the need for repeated exposure where there are multiple sessions with breaks. The present study had no repeated sessions meaning the adaptation seen in Fransson *et al.* (2019) requires multiple sessions over time. It is more likely that the unreplicated quadratic effect seen in Experiment 1 is a result of random variance between samples and hints at the idea that some people are in fact able to adapt to a conflict. This would make sense since there are individual differences in reactions to VR where some are more susceptible to cybersickness and disorientation than others (Kourtesis *et al.,* 2024).

In both experiments, verticality sensitivity decreases in the non-conflict condition across time. Experiment 2 also found a main effect of time where verticality sensitivity decreases across time regardless of the presence of a visuo-vestibular conflict. While fatigue would be a likely explanation for this natural decrease, this does not explain why verticality sensitivity rapidly increased once the visuo-vestibular conflict was removed in Experiment 2. In Experiment 2, roll optic flow was always presented first, followed by the post-exposure condition. If fatigue were responsible for the observed decline in verticality sensitivity over time, sensitivity would be expected to remain reduced during the post-exposure period. However, verticality sensitivity increased following the removal of optic flow, suggesting that fatigue alone cannot account for the observed time-dependent changes. This indicates that other mechanisms, such as perceptual adaptation or changes in sensory weighting, may underlie the temporal dynamics of verticality sensitivity, although further research is needed to clarify these processes.

A range of brain regions are implicated in the processing of visuo-vestibular conflict and its impact on verticality sensitivity. Visual motion activates regions in the temporal lobe, including the middle temporal area (MT/V5) and the medial superior temporal area (MST; Chen *et al.,* 2011; Smith *et al.*, 2006). In particular, while human MT was equally activated for all types of visual motion, including random dot patterns, MST was most strongly activated by complex optic flow which included rotation, expansion and contraction. Similarly, self-motion perception and heading perception which involves the integration of visual and vestibular cues, activate dorsal MST (MSTd) and multiple areas associated with vestibular processing including ventral intraparietal area (VIP), and the visual posterior sylvian area (VPS; Gu *et al.,* 2008; Sulpizio *et al.,* 2024). Accordingly, such regions are likely to be implicated when viewing the visual flow patterns in the present study.

Interestingly, Brandt *et al.* (1994) propose that when confronted with conflicting sensory information, there is a reciprocal inhibitory interaction mechanism where both sensory inputs compete to inhibit one another so that only one sensory input determines the sense of self-motion. According to this theory, it can be assumed that areas more strongly associated with optic flow would compete with brain areas strongly associated with vestibular input, potentially resulting in lower sensitivity to vertical

stimuli. In support of this idea, Roberts *et al.* (2017) found that incongruent visuo-vestibular input resulted in preferential activation in PIVC which they suggest was an attempt to resolve conflict by weighting vestibular input. Conversely, a visuo-vestibular congruent condition resulted in increased activation in primary and secondary visual areas. Given the decrease in sensitivity to verticality observed in the present study, it is likely that visuo-vestibular multisensory cues are re-weighted in response to visuo-vestibular conflict. Accordingly, it is possible that similar activation in PIVC and regions which represent verticality such as the inferior parietal lobule (IPL), inferior frontal gyrus (IFG) and superior temporal gyrus (STG) are also implicated in the re-weighting observed in the present study (Brandt *et al.,* 1994; Saj *et al.,* 2019; Baier *et al.,* 2012; Hegemann *et al.,* 2004). Future studies should therefore explore the use of neuroimaging to fully understand the neural mechanism driving decreased sensitivity to verticality following visuo-vestibular conflicts.

8.1 Limitations and future directions

In the present study, we did not measure participants' experiences of vection during exposure to optic flow stimuli. We chose not to measure vection as we wanted participants to focus entirely on the vertical detection task, rather than splitting their attention between the task and monitoring self-motion sensations. Nonetheless, it is possible that the experience of vection, rather than the optic flow alone, could also play a role in the changes to verticality sensitivity seen in the roll condition. Accordingly, future research could consider adding measures of vection, such as intensity or latency (Kooijman *et al*., 2024), to investigate the relationship between the sensations of self-motion and verticality sensitivity.

Moreover, while our study expands the timespan over which verticality sensitivity was measured, we also did not investigate longer-term effects or repeated exposure. It would be interesting, for example, to explore whether repeated exposure to roll optic flow would mediate the initial drop in sensitivity similar to how individuals adapt to visuo-vestibular and gravitational conflicts in settings

such as VR exposure and exposure to microgravity (Harm *et al*., 2008; Tays *et al.,* 2021). In addition, we focused on roll optic flow using a simplistic environment on a single plane of rotation. Accordingly, more complex visuo-vestibular conflicts using combined axes/planes of motion or more realistic environments may yield different results, giving new directions for future research.

8.2 Conclusion

Overall, the present studies show that visuo-vestibular conflict affects verticality sensitivity in a time-dependent manner. Experiment 1 demonstrated a quadratic effect on verticality sensitivity during visuo-vestibular conflict which may be evidence of adaptation. However, this effect should be interpreted with caution since Experiment 2 did not replicate the quadratic effect. Experiment 2 demonstrated that verticality sensitivity recovers rapidly within minutes following exposure to visuo-vestibular conflict, and that visuo-vestibular conflict produces a linear decrease in verticality sensitivity over time. Visuo-vestibular conflict has important implications for real-world contexts, including virtual reality (VR) use and exposure to microgravity, where sensory conflict can lead to motion sickness and space adaptation syndrome. By characterising the time course of disruption and recovery in verticality sensitivity, the present findings provide insight into the adaptive processes underlying sensory conflict and may inform strategies to minimise perceptual disruption and facilitate recovery in applied settings.

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