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Multisensory Interactions in Virtual Reality: Optic flow reduces vestibular sensitivity, but only for congruent planes of motion

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Abstract

During exposure to Virtual Reality (VR) a sensory conflict may be present, whereby the visual system signals that the user is moving in a certain direction with a certain acceleration, while the vestibular system signals that the user is stationary. In order to reduce this conflict, the brain may down-weight vestibular signals, which may in turn affect vestibular contributions to self-motion perception. Here we investigated whether vestibular perceptual sensitivity is affected by VR exposure. Participants' ability to detect artificial vestibular inputs was measured during optic flow or random motion stimuli on a VR head-mounted display. Sensitivity to vestibular signals was significantly reduced when optic flow stimuli were presented, but importantly this was only the case when both visual and vestibular cues conveyed information on the same plane of self-motion. Our results suggest that the brain dynamically adjusts the weight given to incoming sensory cues for self-motion in VR; however this is dependent on the congruency of visual and vestibular cues.

Keywords

Vestibular system, multisensory integration, self-motion perception; virtual reality.

1. Introduction

Moving through the world elicits a host of sensory information. Images moving across the retina provide an optic flow, while linear acceleration and angular rotation signals are detected via the vestibular organs in the inner ear. Typically, when moving through the external environment visual and vestibular inputs are perfectly matching and therefore the brain integrates them to form a coherent percept of the direction and speed of self-motion (Butler *et al.*, 2010; Fetsch *et al.*, 2009; Greenlee *et al.*, 2016; Gu *et al.*, 2008). According to Bayesian optimal integration accounts, multisensory integration reduces uncertainty and noise regarding the source percept (Ernst and Banks, 2002; Knill and Pouget, 2004). As such, more reliable cues are given a higher weighting than unreliable ones, and consequently bimodal sensory estimates are more precise than estimates obtained from a single sensory modality (Ernst and Banks, 2002; Ernst and Bülthoff, 2004). Evidence suggests that visuo-vestibular integration for self-motion follows exactly this Bayesian optimal integration framework: estimates of self-motion tend to be more precise when both visual and vestibular cues are available (Angelaki *et al.*, 2011; Gu *et al.*, 2008). Importantly, the weight given to vestibular cues increases as the coherence of the visual cues decreases (Fetsch *et al.*, 2009). Moreover, this reliability-based cue weighting is also apparent when visual and vestibular cues for heading direction are in conflict, with sensory estimates biased towards the more reliable cue, although integration may be sub-optimal with greater conflict (Ramkhalawansingh *et al.*, 2018).

Multisensory neurons coding for visual motion and vestibular motion were found in the macaque Middle Temporal (MT) complex: neurons in the dorsal Medial Superior Temporal area (MSTd), a subregion of this complex, strongly respond to retinal motion associated with optic flow (Duffy and Wurtz, 1991; Tanaka and Saito, 1989) and to vestibular stimulation arising from actual movement (Bremmer *et al.*, 1999; Fetsch *et al.*, 2007). Vestibular neurons responding to conflicts between predicted and actual inputs from active and passive movements have been described in the vestibular nuclei and brainstem (Carriot *et al.*, 2013; Oman and Cullen, 2014). Neuroimaging studies have confirmed cross-modal visual and vestibular convergence of cues to self-motion in the human homologue of MT and in the cingulate sulcus visual areas (Smith *et al.*, 2012). Reciprocal visuo-vestibular interactions are fundamental for self-motion (Brandt *et al.*, 1998). Positron Emission Tomography (PET) studies using artificial vestibular stimulation demonstrated not only an activation of the cortical vestibular network but also a decrease in regional Cerebral Blood Flow (rCBF) of the visual cortex (Deutschländer *et al.*, 2002; Wenzel *et al.*, 1996). Similarly, Bense *et al.* (2001) showed bilateral deactivation of the occipital visual cortex induced by artificial vestibular stimulation, suggesting a neural basis for visuo-vestibular integration for self-motion.

However, there are some circumstances, such as Virtual Reality (VR), in which visual and vestibular cues for self-motion may not be available and even potentially in conflict (Bos; *et al.*, 2008; Reason and Brand, 1975). This is the case when VR users feel the sensation of travelling through a virtual environment, while actually remaining stationary in the real world. Consider a typical VR scenario in which the user is driving a car while actually sitting on a chair: optic flow signals that the user is moving in a certain direction with a certain acceleration, however as the user is not physically moving, the vestibular organs signal that the user is stationary. This visuo-vestibular sensory conflict seems to be the underlying mechanism for the frequently experienced *cybersickness*, a form of motion sickness induced by exposure to VR (Kennedy *et al.*, 2010; Keshavarz *et al.*, 2014; Rebenitsch and Owen, 2016; Stanney *et al.*, 1997). As such, understanding how visuo-vestibular integration for self-motion occurs in VR may provide further insights to prevent cybersickness, and potentially improve the VR user experience.

According to Bayesian optimal integration frameworks (Ernst and Banks, 2002; Ernst and Bülthoff, 2004; Gu *et al.*, 2008; Angelaki *et al.*, 2011), when exposed to an environment in which visual cues are present and vestibular cues are uncertain or conflicting, such as VR, the weighting of the vestibular cues may be decreased, and the brain extracts self-motion information primarily from visual signals (Gallagher and Ferrè, 2018; Gallagher *et al.*, 2019). In other words, the brain adapts to extract self-motion information from visual cues and disregard vestibular signals. This dynamic reweighting process reduces visuo-vestibular conflict in VR, and eventually cybersickness. Accordingly, Weech *et al.* (2018) demonstrated that noisy artificial vestibular stimulation reduced the reliability of vestibular information in VR, decreasing symptoms of cybersickness. Similarly, Bos (2015) reported reduced motion sickness when vibration was applied to the head to decrease vestibular reliability, suggesting that a sensory reweighting may be implicated in different forms of motion sickness.

Critically, the ability to perceive self-motion by an optic flow may be altered by concomitant vestibular inputs (Edwards *et al.*, 2010; Holten and MacNeilage, 2018; Shirai and Ichihara, 2012). The detection of optic flow stimuli was reduced when participants viewed an expanding optic flow stimulus coupled with incongruent backwards physical motion, compared to congruent visuo-vestibular conditions, i.e., expanding optic flow with forward physical motion (Edwards *et al.*, 2010). However, findings are still somewhat mixed and evidence appears contrasting. Recent studies, indeed, reported a better detection of optic flow in incongruent visuo-vestibular conditions (Shirai and Ichihara, 2012), or even no differences between congruent or incongruent visuo-vestibular signalling (Holten and MacNeilage, 2018).

While vestibular input seems to modulate the perception of optic flow, it is not yet clear whether optic flow may affect vestibular processing. Importantly, the dynamic reweighting process described above clearly predicts a reduction in vestibular perceptual sensitivity during exposure to VR applications that generate visuo-vestibular conflicts. It has been shown that adaptation to vection, the illusory sensation of motion induced by optic flow exposure, leads to motion aftereffects which bias vestibular processing such that a greater physical motion is required to cancel the perceived illusory motion (Cuturi and MacNeilage, 2014). Additionally, a decrease in the gain of vestibulo-ocular reflexes (VORs) has been reported after exposure to VR (Di Girolamo *et al.*, 2001). Specifically, around 20 minutes of VR exposure dramatically decreased VOR gain by approximately 41% (Di Girolamo *et al.*, 2001). Here we investigated whether exposure to full-field VR optic flow affects participants' sensitivity to vestibular input. In Experiment 1, we administered low-intensity, short-duration Galvanic Vestibular Stimulation (GVS) while participants viewed patterns of rotating dots, which signal self-motion on the roll axis, or randomly moving dots, which do not signal any self-motion. Binaural GVS delivered between the mastoids activates the peripheral vestibular organs, i.e., the otoliths and semicircular canal afferents (Cullen, 2019; Kwan *et al.*, 2019; Stephan *et al.*, 2005), producing a polarity-dependent *virtual roll-rotation vector* (Cathers *et al.*, 2005; Fitzpatrick and Day, 2004). GVS-induced self-motion percepts are polarity-dependent: left-anodal and right-cathodal GVS mimics an inhibition of the left and an activation of the right ear vestibular peripheral organs, decreasing the firing rate of the vestibular nerve on the left side and increasing it on the right side, which is perceived as a movement towards the right (Goldberg *et al.*, 1984). In contrast, right-anodal and left-cathodal GVS induces the opposite effect. We hypothesised a reduction in perceptual sensitivity to vestibular input while viewing Optic Flow vs Random Motion stimuli. Further, we investigated whether the presence of optic flow on any axis may be enough to modulate vestibular sensitivity or whether visual and vestibular cues for self-motion must be congruent in order to interact. In Experiment 2, we therefore explored whether the modulation of vestibular sensitivity is *generally* induced by optic flow, or whether it is *specifically* caused by the congruency of visual and vestibular cues for self-motion.

2. Experiment 1: Congruent Visuo-Vestibular Cues for Self-Motion in VR

2.1. Methods

2.1.1. Ethics

The experimental protocol was approved by the ethics committee at Royal Holloway, University of London. The experiment was conducted in line with the Declaration of Helsinki. Written informed consent was obtained prior to commencing the experiment.

2.1.2. Participants

Twenty-four naïve participants (8 male, age $M = 20.71$, SD = 2.27) completed the experiment. All participants were right-handed according to their Edinburgh Handedness Inventory (Oldfield, 1971) scores. Exclusion criteria were any history of neurological, psychiatric, or vestibular disorders, epilepsy or family history of epilepsy. All participants had normal or corrected-to-normal vision.

2.1.3. Galvanic Vestibular Stimulation (GVS)

Bipolar GVS was applied to deliver a boxcar pulse of 0.7 mA with 250 ms duration, based on our previous study (Cabolis *et al.*, 2018). We used GVS parameters that induced a relatively faint virtual sensation of roll rotation. Individual thresholds for GVS-induced roll-rotation sensations range from 0.4 to 1.5 mA (Kerkhoff *et al.*, 2011; Oppenländer *et al.*, 2015), with one recent study suggesting average thresholds of approximately 1.8 mA for short (500–2000 ms) boxcar GVS pulses (Ertl *et al.*, 2018).

Electrodes (approx. 4 cm^2) were coated with NaCl gel and affixed to each of the mastoid processes. Left-anodal/right-cathodal stimulation (L-GVS) induced a sensation of roll rotation towards the right, whereas the reverse polarity (R-GVS) induced a sensation of roll rotation towards the left. Sham stimulation was also used as a control. Two electrodes were placed on the neck, approximately 5 cm below the upper electrodes, using both left-anodal/right-cathodal stimulation (L-SHAM) and right-anodal/left-cathodal stimulation (R-SHAM). The sham stimulation controlled for cutaneous sensations experienced during GVS, as well as the knowledge that an unusual stimulation was occurring. No sensations of self-motion were experienced during this type of stimulation. GVS and sham stimulation waveforms were generated by a custom-written code in LabView (LabView 2012, National

Instruments, Austin, TX, USA) and conveyed to a commercial stimulator (Good Vibrations Engineering Ltd., Nobleton, ON, Canada) over the serial port.

2.1.4. Experimental Design and Procedure

Data from each participant were gathered in a single session. Verbal and written instructions about the task were given to participants at the beginning of the session. Participants were asked to wear an Oculus Rift CV1 (Oculus VR, Menlo Park, CA, USA) head-mounted display (HMD). To reduce the postural consequences of the GVS pulse, the experiment was conducted in a comfortable sitting position and participants were asked to rest their head on a chinrest and place their arms on the table in front of them.

Our design factorially combined vection and vestibular signals. The *Vestibular Detection Task* (VDT) was designed to follow a signal detection approach (Macmillan and Creelman 1991) (Fig. 1). It consisted of a 2 (vestibular stimulus present/absent) × 2 (optic flow stimulus present/absent) design, with the following trial types: 30 vestibular-only trials (vestibular stimulus present and optic flow stimulus absent); 30 vestibular and optic flow trials (vestibular stimulus present and optic flow stimulus present); 30 optic flow-only trials (vestibular stimulus absent and optic flow stimulus present); and 30 no stimulus trials (vestibular stimulus absent and optic flow stimulus absent). Thus, a total of 120 trials were performed divided into four blocks.

Half of the vestibular- present trials was presented with L-GVS and the other half with R-GVS. Sham stimulation (L-SHAM and R-SHAM) was administered in the vestibular-absent trials. In the optic flow-present trials, full-field visual dots were presented on the Oculus HMD. Approximately 500 dots rotated anticlockwise at 90°/s, suggesting self-motion on the roll axis, and potentially inducing a sensation of roll vection. Crucially, this optic flow is congruent with the self-motion sensation induced by GVS. In the optic flow-absent trials the dots moved randomly, inducing no sensations of self-motion. All visual trials included a fixation cross at the centre of the HMD, and participants were asked to always fixate on the fixation cross. The visual stimulus was presented for 60 s prior to completing the detection task and continued throughout the entire block (total presentation of approximately four minutes). Optic flow-present and -absent stimuli were presented in separate blocks. Participants were informed that they may experience a sensation of vection when viewing the optic flow stimulus. Vection was described as the illusion one experiences when watching a neighbouring train move while sitting stationary (Keshavarz *et al.*, 2015). In particular, participants were told that it might feel as if they were rotating to one side or the other.

On each trial, participants heard a beep to indicate that they should pay attention to any potential GVS-induced roll sensations, but ignore any non-specific vestibular sensations, such as tingling under the electrode surfaces. A second beep 500 ms later indicated that participants should verbally respond ‘yes’ if they felt roll sensations or ‘no’ if they did not. GVS/SHAM stimulation was delivered between these two sounds. The visual stimulus remained on the HMD throughout the experimental trials. A custom LabView program was used to trigger the stimuli and record participant responses.

2.1.5. Data Analysis

A signal detection approach was used to analyse the VDT data (Macmillan and Creelman, 1991). The number of hits (the number of trials in which L-GVS/R-GVS was present and the participant responded ‘yes’), misses (the number of trials in which L-GVS/R-GVS was present and the participant responded ‘no’), false alarms (the number of trials in which L-SHAM/R-SHAM stimulation was present and the participant responded ‘yes’), and correct rejections (the number of trials in which L-SHAM/R-SHAM stimulation was present and the participant responded ‘no’) were calculated. Hit rates [P(‘yes’|GVS)] and false alarm rates [P(‘yes’|SHAM)] were used to calculate perceptual sensitivity (d’), the difference between z-transformed probabilities of hits and false alarms [$d' = z(\text{Hit}) - z(\text{False Alarm})$]. The response bias ($C$), the tendency for participants to report the GVS stimulus as present, was also calculated [$C = -[z(\text{Hit}) + z(\text{False Alarm})]/2$]. Both d’ and C were calculated for each GVS polarity (with L-SHAM false alarm rates paired with L-GVS hit rates and R-SHAM false alarm rates paired with R-GVS hit rates) and visual condition for each participant. Data from two participants were excluded as they were above two standard deviations from the mean in at least one condition.

2.2. Results

Means and SDs of hits, misses, false alarms and correct rejections by Visual Condition and GVS Polarity can be seen in Table 1.

*2.2.1. Perceptual Sensitivity (*d*’)*

A 2 × 2 repeated-measures ANOVA was conducted on d’ values, with factors GVS Polarity (L-GVS vs. R-GVS) and Visual Condition (Optic Flow vs Random Motion). This analysis revealed a significant main effect of Visual Condition ($F_{1,21} = 36.03$, $p < 0.001$, $\eta_p^2 = 0.63$)

(Fig. 2). Participants' sensitivity to vestibular stimulation was significantly lower during Optic Flow (*M* = 0.69, SD = 0.67) compared to Random Motion (*M* = 1.88, SD = 1.09) trials. No significant main effect of GVS Polarity ($F_{1,21} = 0.19$, $p = 0.67$, $\eta_p^2 = 0.01$) was found. No significant interaction between Visual Condition and GVS Polarity was found ($F_{1,21} = 0.32$, $p = 0.58$, $\eta_p^2 = 0.02$).

*2.2.2. Response Bias (*C*)*

A 2 × 2 repeated-measures ANOVA conducted on *C* values, with factors GVS Polarity (L-GVS vs R-GVS) and Visual Condition (Optic Flow vs Random Motion), revealed no significant main effects of Visual Condition ($F_{1,21} = 0.07$, $p = 0.79$, $\eta_p^2 = 0.004$) or GVS Polarity ($F_{1,21} = 0.01$, $p = 0.91$, $\eta_p^2 = 0.001$) (Fig. 2). No significant interaction between Visual Condition and GVS Polarity was found ($F_{1,21} = 2.31$, $p = 0.14$, $\eta_p^2 = 0.10$).

2.3. Discussion

Sensitivity to vestibular signals was significantly reduced following exposure to visual cues signalling self-motion compared to randomly moving visual stimuli. Response bias was not influenced by exposure to optic flow in VR. Thus, our results suggest that exposure to optic flow in VR reduces the weighting placed on vestibular cues for self-motion. Importantly, the self-motion sensations induced by GVS and the self-motion signals provided by optic flow were congruent: both vestibular and visual cues signal a sensation of motion on the roll axis. Thus, it is not clear whether the presence of optic flow itself may be enough to modulate vestibular sensitivity or whether visual and vestibular cues must be congruent in order to interact. We hypothesised that the reduction in vestibular sensitivity is selective for exposure to optic flow congruent with the type of movement evoked by GVS. To further investigate this hypothesis, in Experiment 2 we administered GVS during exposure to linear optic flow or randomly moving dots. This allowed us to explore whether the decrease in vestibular sensitivity is *generally* due to the presence of optic flow, or whether it is *specifically* caused by the congruency of visual and vestibular cues for self-motion.

3. Experiment 2: Incongruent Visuo-Vestibular Cues for Self-Motion in VR

3.1. Methods

3.1.1. Ethics

The experimental protocol was approved by the ethics committee at Royal Holloway, University of London. The experiment was conducted in line with the Declaration of Helsinki. Written informed consent was obtained prior to commencing the experiment.

3.1.2. Participants

Twenty-four naïve participants (eight male, age M = 21.63, SD = 5.13) completed the experiment. None of the participants had taken part in the previous experiment. All participants were right-handed according to their Edinburgh Handedness Inventory (Oldfield, 1971) scores. Exclusion criteria were as Experiment 1. All participants had normal or corrected-to-normal vision.

3.1.3. Experimental Design and Procedure

In order to investigate whether the effects of optic flow on vestibular sensitivity were generic or specific to the plane of self-motion evoked by GVS (i.e. roll rotation), here the participants were administered with a full-field linear optic flow stimulus during optic flow trials (Fig. 3). Each of the approximately 500 dots were assigned a random scaling factor between 0.01 and 1.5. On each frame, each dot expanded in size by its scaling factor in pixels from a minimum of one to a maximum of nine pixels in diameter. Once the maximum size was reached, the size reset to one-pixel diameter. The location of the dot on each frame was determined by multiplying its default X and Y coordinates by:

$$\text{Location} = \frac{(\text{Scaling Factor})^3}{1.5^3} \times 1.5$$

Thus, dots nearer the centre travelled less distance than dots farther from the centre, creating an expanding pattern, signalling forward self-motion and potentially inducing a sensation of linear vection. The optic flow stimulus was presented for 60 s, and remained on screen throughout the detection task (approximately four minutes total presentation time). Vection was described as in Experiment 1, but participants were told that this might feel like a sensation of moving forward through space, rather than a sensation of rotation. The experimental design and procedure were otherwise identical to Experiment 1.

3.1.4. Data Analysis

Data were analysed as in Experiment 1. Data from two participants were excluded as they were more than two standard deviations from the mean in at least one condition.

3.2. Results

Means and SDs of hits, misses, false alarms and correct rejects by Visual Condition and GVS Polarity can be seen in Table 2.

*3.2.1. Perceptual Sensitivity (*d'*)*

A 2 × 2 repeated-measures ANOVA was conducted on *d*' values, with factors GVS Polarity (L-GVS vs R-GVS) and Visual Condition (Optic Flow vs Random Motion). This analysis revealed no significant main effects of Visual Condition ($F_{1,21} = 0.21$, $p = 0.65$, $\eta_p^2 = 0.01$) or GVS Polarity ($F_{1,21} = 0.05$, $p = 0.82$, $\eta_p^2 = 0.002$) (Fig. 4). No significant interaction between Visual Condition and GVS Polarity was found ($F_{1,21} = 3.18$, $p = 0.09$, $\eta_p^2 = 0.13$).

*3.2.2. Response Bias (*C*)*

A 2 × 2 repeated-measures ANOVA was conducted on C values, with factors GVS Polarity (L-GVS vs. R-GVS) and Visual Condition (Optic Flow vs Random Motion); it revealed no significant main effects of Visual Condition ($F_{1,21} = 0.12$, $p = 0.73$, $\eta_p^2 = 0.01$) or GVS Polarity ($F_{1,21} = 1.52$, $p = 0.23$, $\eta_p^2 = 0.07$) on response bias (Fig. 4). No significant interaction between Visual Condition and GVS Polarity was found ($F_{1,21} = 0.55$, $p = 0.47$, $\eta_p^2 = 0.03$).

3.2.3. Between-Experiments Comparison

Our results suggest that vestibular sensitivity is reduced by optic flow in VR only when both visual and vestibular cues for self-motion provide information regarding the same plane of motion. To investigate this hypothesis, we directly compared the effect of congruent (Experiment 1) vs incongruent (Experiment 2) optic flow on vestibular sensitivity. As no effects of polarity of GVS were found in either experiment, we averaged across L-GVS and R-GVS conditions. A *Vestibular Sensitivity Index* was estimated by subtracting the random motion from the optic flow conditions, such that positive values corresponded to greater sensitivity during optic flow and negative values corresponded to lower sensitivity during optic flow.

An independent *t*-test revealed a significant difference in the Vestibular Sensitivity Index between Visuo-Vestibular Congruent and Visuo-Vestibular Incongruent planes of motion [$t(42) = 4.44$, $p < 0.001$, Cohen's $d = 1.34$, 95% CI (0.69, 1.99)]. Specifically, vestibular sensitivity was significantly lower during exposure to Visuo-Vestibular Congruent motion, i.e. roll optic flow ($M = -1.19$, SD = 0.93) compared to Visuo-Vestibular Incongruent motion, i.e. linear optic flow ($M = -0.07$, SD = 0.73).

3.3. Discussion

Incongruent visuo-vestibular motion signals did not influence vestibular sensitivity. Participants' sensitivity to roll-rotation vestibular signals was not affected by exposure to linear optic flow. However, vestibular sensitivity was significantly reduced if optic flow was generated on the roll plane. Thus, alterations in vestibular processing following optic flow in VR are dependent on the congruency between visual and vestibular cues for self-motion.

4. General Discussion

When moving through the world, optic flow and vestibular cues are integrated to form a coherent percept of self-motion (DeAngelis and Angelaki, 2012). During visuo-vestibular conflict, such as in VR, sensory signals may be reweighted, with more reliable sensory cues given a higher weighting (Ernst and Banks, 2002; Greenlee *et al.*, 2016). In particular, vestibular signals may be down-weighted during VR exposure, so that the brain extracts self-motion information predominantly from visual cues (Gallagher and Ferrè, 2018; Weech and Troje, 2017). This dynamic reweighting may alter how the brain subsequently processes vestibular inputs. Here we found that participants were less able to detect vestibular signals following exposure to visuo-vestibular congruent motion in VR. Thus, changes in vestibular sensitivity occurred only when optic flow and vestibular sensations were congruently experienced as roll rotation. No changes in vestibular sensitivity were found after exposure to visuo-vestibular incongruent motion. Importantly, our results indicate a specific modulation of vestibular processing induced by optic flow: response bias was not affected by either congruent or incongruent motion in VR. Taken together our results seem to suggest a modulation of vestibular sensitivity following exposure to optic flow in VR, and that this modulation depends on the specific plane of motion presented.

Aftereffects of VR exposure are often reported, but this remains a relatively under-explored area (Gallagher and Ferrè, 2018; Stanney and Kennedy, 1998). Altered vestibular experiences may be present in the hours or days following VR exposure (Di Girolamo *et al.*, 2001; Harm *et al.*, 2008; Stanney and Kennedy, 1998; Stanney *et al.*, 1999). For example, disorientation scores immediately following 15 minutes of exposure to VR were 143 times higher than before VR, and remained 95 times higher 60 minutes post-exposure (Stanney and Kennedy, 1998). Sensorimotor coordination has been shown to be dramatically poorer after exposure to VR, approaching recovery only six hours post VR (Harm *et al.*, 2008). Similarly, alterations in the vestibulo-ocular reflex have been reported after VR use (Di Girolamo *et al.*, 2001). The precise causes of VR-induced aftereffects are not entirely clear, but it is possible that these aftereffects result from altered vestibular processing following exposure to visuo-vestibular conflict. In VR scenarios that induce visuo-vestibular conflicts, for example when optic flow is presented to a VR user who is not moving, visual cues signal that the user is moving while vestibular cues signal that they are stationary. As a result, the vestibular cues for self-motion may be down-weighted, resulting in altered vestibular processing. Here we found a decrease in vestibular perceptual sensitivity during exposure to optic flow in VR, but importantly, this decrease was observed only when the experienced visuo-vestibular self-motion was congruent. That is, vestibular sensitivity was poor when both visual and vestibular cues for self-motion provided information about roll rotation, while no changes in vestibular sensitivity were found when vestibular cues signalled roll rotation and vision provided linear acceleration signals. Thus, our findings suggest that a dynamic reweighting of vestibular cues may impact vestibular processing during VR exposure. Future work should explore whether this dynamic reweighting carries over after VR exposure, potentially explaining VR-induced aftereffects.

Here we found decreases in vestibular sensitivity during exposure to visuo-vestibular congruent motion in VR. Previous studies have focused on the inverse interaction, i.e., whether optic flow detection may be modulated by vestibular stimulation (Edwards *et al.*, 2010; Holten and MacNeilage, 2018; Shirai and Ichihara, 2012). Interestingly the results are somewhat mixed. For example, Edwards *et al.* (2010) found that detection of optic flow was reduced when participants were exposed to incongruent vestibular stimulation. By contrast, Shirai and Ichihara (2012) found reduced detection of optic flow when it was paired with a congruent vestibular stimulus, while Holten and MacNeilage (2018) found no difference in optic flow detection between congruent and incongruent visuo-vestibular stimuli. The differences in visual and vestibular stimuli between these three studies could potentially account for these mixed findings. In particular, Edwards *et al.* (2010) used much faster visual stimuli and a constant acceleration vestibular stimulus, while Shirai and Ichihara (2012) and Holten and MacNeilage (2012) used slower visual stimuli and more complex vestibular motion profiles.

Thus, further research is necessary to explore the relationship between stimulus types and modulation of optic flow sensitivity.

We investigated vestibular sensitivity during exposure to only a few minutes of optic flow in VR. Specifically, participants viewed the visual stimulus for 60 s prior to commencing the detection task and continued viewing the visual stimuli throughout the task, resulting in approximately four minutes of visual stimulation. It is likely that the changes in vestibular sensitivity may differ according to the duration of VR exposure: for instance, sensitivity to vestibular stimuli may be higher during the first few seconds of exposure to congruent optic flow, declining only over time as the vestibular cue is gradually down-weighted. Interestingly, both vection sensations and optokinetic after-nystagmus have been demonstrated to change with habituation to optic flow (Brandt *et al.*, 1974). Specifically, the velocity of vection slows or ceases with longer durations of optic flow (between 4 and 12 minutes, depending on individual variability). In addition, the amplitude of the optokinetic after-nystagmus increases up to 60 s of exposure to optic flow, declining after three and up to 15 minutes (Brandt et al., 1974). Thus, further exploration of the time-course of vestibular sensitivity across shorter and longer periods of time will be an important step. Moreover, while we assumed that participants would experience vection during exposure to the optic flow stimuli designed to evoke self-motion sensations, we did not directly assess self-motion perception through measures such as vection latency or intensity. Potentially, vestibular processing may be impacted differently depending on the participants' subjective experience of vection. For instance, vestibular sensitivity might correlate with the strength of perceived vection. Thus, participants experiencing strong sensations of vection might show a further reduction in vestibular sensitivity compared to participants experiencing weaker vection.

Curiously, while we found significant changes in vestibular sensitivity only during visuo-vestibular congruent motion, the congruency between the direction of GVS polarity and roll optic flow had no impact on vestibular sensitivity. This may be due to different reasons. First, GVS parameters were set in order to induce a very mild motion sensation. Thus we cannot exclude that the stimulation would have been too weak to trigger a conflict between the perceived direction of GVS motion and the direction of roll optic flow. Second, binaural GVS induces a polarity-dependent virtual roll-rotation vector (Cathers *et al.*, 2005; Fitzpatrick and Day, 2004)*:* left-anodal/right-cathodal GVS is perceived as a movement towards the right, while right-anodal/left-cathodal GVS is perceived as a movement towards the left (Goldberg *et al.*, 1984). However, when the stimulation is off, a motion aftereffect is easily perceived by participants. That is left-anodal/right-cathodal GVS generates a movement towards the right and an aftereffect towards the left. It might therefore be possible that the short duration of our GVS pulses might make the direction of movements unclear. Mandatory fusion accounts might explain the decrease in vestibular sensitivity induced by congruent optic flow stimuli: when congruent visual and vestibular cues for self-motion are integrated, perceptual access to the unimodal estimates is lost, potentially resulting in lower sensitivity for the unimodal stimulus alone (Prsa *et al.*, 2012; Zhang *et al.*, 2019). This account might have predicted that vestibular sensitivity would be reduced only for the direction-congruent polarity if mandatory fusion were the underlying mechanism. Thus, the observed modulation of vestibular sensitivity for both L-GVS and R-GVS polarities suggests a more general mechanism of down-weighting vestibular cues. However, given the previously described stimulation factors (i.e., weak stimuli and motion aftereffects), further exploration of this possibility is necessary.

The integration of vestibular and visual cues for self-motion is underpinned by a complex network of brain regions. When viewing optic flow stimuli, activity is increased in MT+, Cingulate Sulcus Visual Area (CSv) and Ventral Intraparietal Area (VIP), suggesting that these regions are involved in the processing of visual cues for self-motion (Cardin and Smith, 2010; Kovács *et al.*, 2008; Wall and Smith, 2008). Several studies report that activity in the parieto-insular vestibular cortex (PIVC) is decreased when experiencing vection in the absence of vestibular cues (Brandt *et al.*, 1998; Kleinschmidt *et al.*, 2002). However, increased activity in PIVC has also been described (Kirollos *et al.*, 2017; Uesaki and Ashida, 2015). It is possible that differences in optic flow stimuli account for these apparently discrepant findings: while constant velocity stimuli across one axis were used in studies describing decreased PIVC activity (Brandt *et al.*, 1998; Kleinschmidt *et al.*, 2002), much more complex optic flows were used in studies reporting increased PIVC activity (Kirollos *et al.*, 2017; Uesaki and Ashida, 2015). Thus, the effects of vection and optic flow on PIVC are not yet entirely clear. Nevertheless, it seems likely that the activity in PIVC, MT+, CSv, and VIP may be implicated in the dynamic reweighting process. Here we investigated sensitivity to vestibular stimuli during exposure to constant velocity stimuli on one axis. Thus, our findings should be extended to more complex forms of motion.

Different patterns of cortical activity may be elicited by linear compared to roll vection. Deutschländer *et al.* (2004) reported increased activity in visual areas during linear vection, while roll vection led to increased activity in parietal regions. Moreover, while both roll and linear vection decreased activity in vestibular regions, this vestibular deactivation was much stronger for linear vection (Deutschländer *et al.*, 2004). Given these differences between roll and linear vection, it may be possible that our results may be a by-product of the type of optic flow (roll vs linear), rather than visuo-vestibular congruency. However, several factors count against this explanation. Firstly, while previous studies suggest that optic flow on combined axes results in increased vection strength (Keshavarz *et al.*, 2019, however see Diels and Howarth, 2011 for contrasting results), optic flow presented on one axis, such as that used in the present study, has been reported to elicit vection of similar magnitude on both linear and roll axes (Deutschländer *et al.*, 2004; Diels and Howarth, 2011). Thus, it is unlikely that participants experienced different intensities of vection across our two experiments. Secondly, Deutschländer *et al.* (2004) suggest that vestibular regions are more strongly deactivated by linear, rather than roll vection. Accordingly, if the difference between optic flow types were to play a role in the present findings, we might expect that vestibular sensitivity would be lower following exposure to linear optic flow vs roll optic flow. However, this explanation does not account for our observed results. Here we used bipolar binaural GVS to stimulate the vestibular organs. This GVS configuration is known to elicit a sensation of roll motion (Cathers *et al.*, 2005; Fitzpatrick and Day, 2004). As such, we were not able to investigate visuo-vestibular congruent motion in the linear plane. More complex forms of vestibular stimulation would therefore be necessary to fully explore the relationship between optic flow types and visuo-vestibular congruency on vestibular sensitivity. Given the reported stronger PIVC deactivations during linear vection (Deutschländer *et al.*, 2004), we might predict that vestibular sensitivity would be reduced when visual and vestibular cues for self-motion are congruent, with visuo-vestibular congruent motion on the linear plane resulting in further reductions in sensitivity relative to visuo-vestibular congruent motion on the roll plane.

The uses of VR in everyday life are becoming more apparent. While the utility of VR for training, rehabilitation, gaming, and research is clear, questions regarding its effect on our sensory processing remain outstanding. Previous research has documented aftereffects of VR exposure; however, a thorough investigation of these aftereffects is lacking. Here we found that exposure to optic flow in VR reduced sensitivity to incoming vestibular stimulation. Crucially, this reduction in sensitivity depended on the plane of visual motion presented, with reductions following visuo-vestibular-congruent, but not -incongruent, motion stimuli. Our findings therefore highlight how exposure to optic flow in VR can modulate incoming vestibular information, and provide further insights into mechanisms of visuo-vestibular integration for self-motion perception.

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Competing interests

The authors declare no conflicts of interest regarding this work.

Data accessibility

Data are available online as supplementary material.

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Figure captions:

Figure 1. Experiment 1 Methods. Vestibular sensitivity during congruent optic flow in VR.We used a 2 (vestibular stimulus present/absent) × 2 (optic flow stimulus present/absent) design. GVS induced a sensation of roll rotation to the left or right, while a full field of dots in VR rotated to signal roll motion. Sham stimulation and random motion were used as controls.

Figure 2. Experiment 1 Results. Vestibular sensitivity was significantly reduced following exposure to roll optic flow. Response bias was unaffected by exposure to roll optic flow.

Figure 3. Experiment 2 Methods. Vestibular sensitivity during incongruent optic flow in VR. We used a 2 (vestibular stimulus present/absent) × 2 (optic flow stimulus present/absent) design. GVS induced a sensation of roll rotation to the left or right, while a full field of expanding dots in VR signaled linear motion. Sham stimulation and random motion were used as controls.

Figure 4. Experiment 2 Results. No changes were found on vestibular sensitivity or response bias following exposure to linear optic flow.

Table 1.

Mean (SD) percentage hits, misses, false alarms, and correct rejects per Visual Condition and GVS Polarity.

	L-GVS		R-GVS	
	No Motion	Roll Optic Flow	No Motion	Roll Optic Flow
Hits	31.59 (13.37)	23.41 (13.14)	32.35 (12.64)	22.35 (12.83)
Miss	18.41 (13.37)	26.59 (13.14)	17.65 (12.64)	27.65 (12.83)
False Alarm	5.08 (6.16)	13.26 (11.48)	7.20 (9.64)	12.27 (10.73)
Correct Reject	44.92 (6.16)	36.74 (11.48)	42.80 (9.64)	37.73 (10.73)

Table 2.

Mean (SD) percentage hits, misses, false alarms, and correct rejections per Visual Condition and GVS Polarity.

	L-GVS		R-GVS	
	No Motion	Linear Optic Flow	No Motion	Linear Optic Flow
Hits	26.89 (10.78)	27.88 (10.46)	28.03 (13.16)	24.47 (12.36)
Miss	23.11 (10.78)	22.12 (10.46)	21.97 (13.16)	25.53 (12.36)
False Alarm	6.89 (7.42)	6.82 (8.40)	5.98 (6.76)	6.74 (8.06)
Correct Reject	43.11 (7.42)	43.18 (8.40)	44.02 (6.76)	43.26 (8.06)