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Visuo-vestibular conflicts within the roll plane modulate multisensory verticality perception

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ABSTRACT

The integration of visuo-vestibular information is crucial when interacting with the external environment. Under normal circumstances, vision and vestibular signals provide corroborating information, for example regarding the direction and speed of self-motion. However, conflicts in visuo-vestibular signalling, such as optic flow presented to a stationary observer, can change subsequent processing in either modality. While previous studies have demonstrated the impact of sensory conflict on unisensory visual or vestibular percepts, here we investigated whether visuo-vestibular conflicts impact sensitivity to multisensory percepts, specifically *verticality*. Participants were exposed to a visuo-vestibular conflicting or non-conflicting motion adaptor before completing a Vertical Detection Task. Sensitivity to vertical stimuli was reduced following visuo-vestibular conflict. No significant differences in criterion were found. Our findings suggest that visuo-vestibular conflicts not only modulate processing in unimodal channels, but also broader multisensory percepts, which may have implications for higher-level processing dependent on the integration of visual and vestibular signals.

1. Introduction

Moving through the environment elicits a host of information across multiple sensory modalities. For example, walking down the road elicits visual signals from optic flow, vestibular signals from head acceleration, and proprioceptive signals from movement of the limbs. While one could estimate heading direction or movement speed from any individual modality, the integration of multiple signals is advantageous in that it provides a more precise estimate of self-motion than any sensory cue alone [1–3]. Multisensory integration has been demonstrated across a number of tasks and modalities, including visuo-vestibular self-motion perception, audio-visual localisation, and visuo-haptic size perception [1,4–6]. Unlike the integration of audio-visual or haptic-visual cues for object recognition [4,6], visuo-vestibular integration occurs constantly in order to provide us with accurate estimates of where we are in 3D space. However, little is known about the impacts of multisensory conflicts on perceptual processing, particularly within sensory modalities which are typically integrated automatically.

The interaction of visual and vestibular sensory information is crucial for a wide range of behaviours. Low-level visuo-vestibular interactions are necessary for maintaining balance and posture, while reflexes such as the Vestibulo-Ocular Reflex (VOR) enable automatic head-eye coordination to conserve gaze and visual stability during head movements. Visual and vestibular signals are also integrated for higher-level percepts. During self-motion, for example, visual optic flow signals indicate the direction and speed of movement, while vestibular signals indicate the acceleration and rotation of the head [7,8]. Visual and vestibular cues are also constantly integrated for the perception of the gravitational vertical. *Verticality* defines what is “up” and what is “down” and deviations thereof (i.e., tilts away from the vertical) in a gravitational field [9]. Humans are very accurate in perceiving verticality, estimating the vertical to within 2° of the physical gravitational vertical [10,11]. Visual cues provide stable references for verticality, for example from buildings and trees, while vestibular signals indicate the location of the head with respect to gravity via the otoliths [12,13]. In addition, proprioceptive and somatosensory signals about the position of the neck and the trunk indicate the position of the longitudinal body axis (i.e., the ‘idiotropic vector [14]’) and contribute to a prior that the

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head is usually upright [10,14–19]. Previous studies have demonstrated that tilting either the head or the trunk biases the *Subjective Visual Vertical* (SVV, [20]). Specifically, higher degrees of roll tilt (greater than 45-60°) tend to bias the SVV in the same direction of the body tilt, the so-called Aubert or A-effect [16,21–23], while smaller roll tilts induce a Müller or E-effect [24], with biases away from the direction of tilt [10,19]. Thus, the perception of verticality relies on effective integration of coherent sensory information to create up-to-date representations of the external environment.

While visuo-vestibular signals are usually integrated seamlessly, under some circumstances sensory conflict can arise. Visuo-vestibular conflicts have been shown to dramatically alter subsequent vestibular processing and perception. For example, one minute of exposure to optic flow in virtual reality altered both vestibular reflexes [25] and perceptual sensitivity to vestibular stimulation [26]. Similarly, conflicting motion profiles presented in visual and vestibular modalities led to altered sensitivity to optic flow signals [27,28] (but see [29] for contrasting findings). Crucially, changes in vestibular processing seem to occur only within the plane of motion containing the conflict. Specifically, while sensitivity to roll motion induced by vestibular stimulation was reduced after exposure to visuo-vestibular conflict in the roll plane, a decrease in sensitivity to roll was not found when adapted to visuo-vestibular conflicts in the linear plane [26].

While previous studies have shown that exposure to visuo-vestibular conflicts modulates processing in each modality directly, it is unclear whether such conflicts alter processing of stimuli requiring the integration of multiple cues. Here we investigated whether adaptation to rotating optic flow in the absence of corresponding vestibular signals could change participants' sensitivity to a visuo-vestibular integration process, such as the perception of verticality. Since the vestibular system continually signals the acceleration of the head in space and is usually in agreement with optic flow signals, exposure to a visual rotating stimulus in the absence of corroborating vestibular signals creates a visuo-vestibular conflict. We used a Vertical Detection Task based on the Signal Detection approach [30,31] to assess *sensitivity* to vertical stimuli following exposure to visuo-vestibular conflict. This approach is a standard psychophysical technique to assess the ability of individuals to distinguish signals from noise. Accordingly, it provided us with a measure of how sensitive participants were to the presence of a vertical versus tilted stimuli. Importantly, this approach allowed us to distinguish between changes in sensitivity versus changes in response bias (criterion). Sensitivity refers to the ability of the observer to distinguish sensory signals from random noise. In our Vertical Detection Task, high sensitivity indicates that the observer can distinguish slightly tilted and vertical stimuli, while low sensitivity indicates that tilted and vertical stimuli are almost indistinguishable. Criterion in contrast reflects the participant's response strategy. Those with a liberal bias (i.e., a lower criterion) indicate the presence of a signal in the absence of strong evidence for it, resulting in a greater number of hits (responding 'vertical' to a vertical stimulus) and false alarms (responding 'vertical' to a tilted stimulus). Those with a conservative bias (i.e., a higher criterion) report the presence of the signal only when sure of signal presence, resulting in a greater number of correct rejections (responding 'not vertical' to a tilted stimulus) and misses (responding 'not vertical' to a vertical stimulus). It is important to note that our Vertical Detection Task does not assess the subjective visual vertical bias itself (i.e., the amount that a vertical stimulus appears tilted after exposure to vestibular and/or visual stimulation) [15,16,32–34]. While the subjective visual vertical bias is dependent on visual rotation direction – with the vertical appearing to deviate in the direction of visual rotation – changes in sensitivity to vertical stimuli are not direction-dependent. Specifically, we anticipated changes in sensitivity to the detection of a vertical stimulus due to downweighting of visuo-vestibular cues, which would be of the same magnitude irrespective of whether the adapting stimulus rotates to the left or right. Accordingly, we expected no direction-specific effects related to the adaptation stimulus, and subsequently used only anticlockwise roll rotation.

Given that the perception of the gravitational vertical requires the integration of visual and vestibular signals, a change in sensory weighting induced by exposure to visuo-vestibular conflict may reduce sensitivity to the vertical by reducing the ability of participants to distinguish between tilted and upright stimuli. As previous research suggests that only conflicts within a motion plane reduce sensitivity to processing within the same plane [26], we investigated participants' sensitivity to vertical vs roll-tilted lines after exposure to visuo-vestibular conflict in the roll plane. We predicted that participants would be less sensitive to verticality following adaptation to roll-rotating versus random motion stimuli. We predicted no differences in criterion.

2. Methods

2.1. Participants

Forty-nine participants completed the online study. Six were excluded as they did not meet the exclusion criteria of any history of neurological, psychiatric, or vestibular disorders. Of the remaining 43 participants, 42 were right-handed, 35 identified as female. Mean age was 19.77 years (SD = 2.49).

2.2. Ethics

The experimental protocol was approved by Royal Holloway University of London. All participants gave written informed consent before participating in the study. The study was conducted in line with the Principles of the Declaration of Helsinki.

2.3. Stimuli and procedure

The study was conducted online with Gorilla (https://www.gorilla.sc/). After completing informed consent procedures, participants were given task instructions. Participants were asked to maintain an upright posture and keep their head still during the task. They were told to fixate on the fixation point throughout the experiment. During the adaptation phase, a rotating or random motion adaptor was presented for one minute. The motion adaptors were constructed in MATLAB 2020b and Psychtoolbox (Version 3) and exported to video (960x540 resolution, 30 FPS). Both adaptors consisted of grey dots on a white background. The dots were presented inside a circular aperture to minimise cues for verticality. A green fixation point marked the centre of the aperture. For the rotating adaptor, all dots moved anticlockwise in roll at 90° per second. We have used only one direction of visual rotation, as we anticipated no direction-specific effect on response biases or sensitivity. The random adaptor dots each moved in a random trajectory, giving no coherent sense of motion (Fig. 1A). Participants saw the roll-rotating or random adaptor first in a counterbalanced order. Following the adaptation phase, the Vertical Detection Task commenced (Fig. 1B). Participants were asked to decide whether a visual stimulus was vertical or not by responding "YES" or "NO" using a keypress. Stimuli were grey lines in a circular aperture, either perfectly vertical or tilted 2.5° clockwise or anticlockwise. Participants were presented with 30 vertical and 30 tilted (15 clockwise, 15 anticlockwise) stimuli in a random order. Each stimulus was displayed for 1 s. A 60 s break was given to participants before the beginning of the second adaptor and verticality detection task to prevent carry-over effects.

2.4. Data analysis

Data were analysed in RStudio version 1.4.1106. Responses were missed if no button was pressed or if the reaction time was < 150 ms. Participants were excluded if they missed more than 10 of each trial type ($n = 3$), if they did not follow task instructions ($n = 12$), or if their data

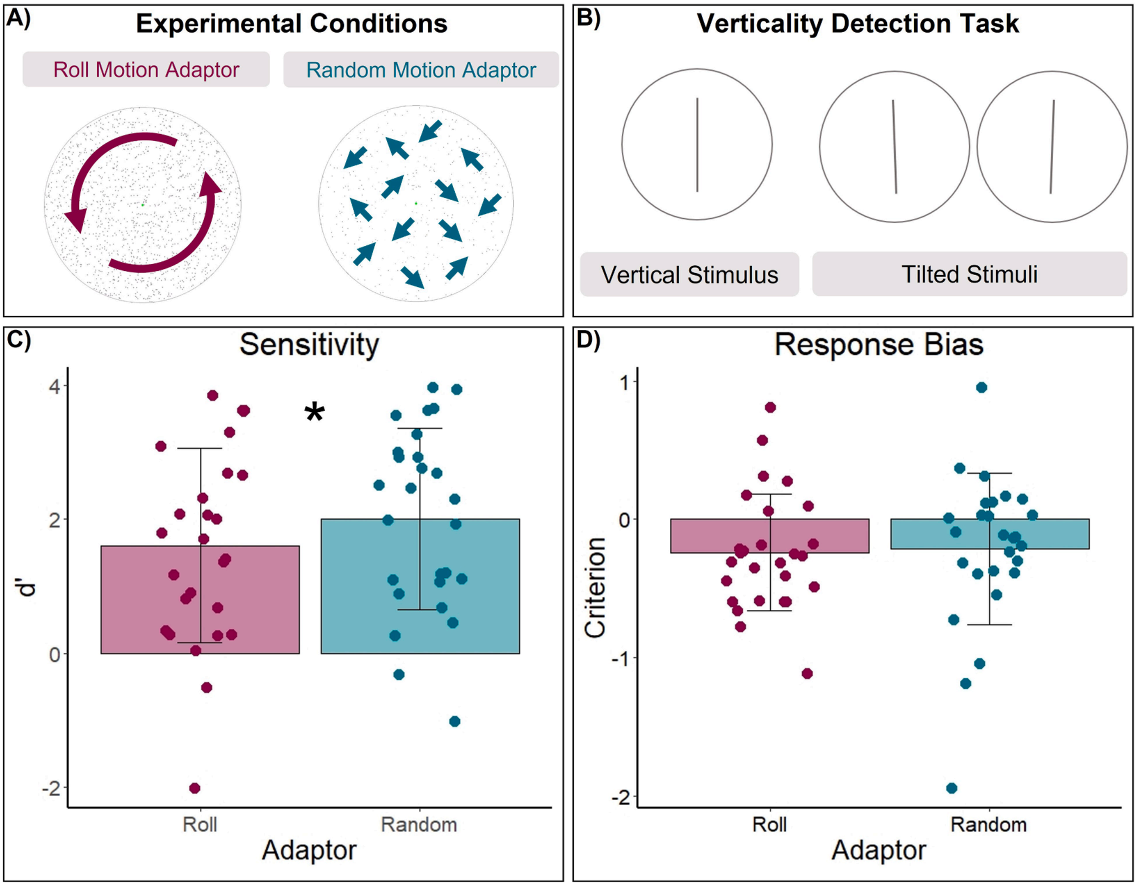

Fig. 1. Experimental stimuli and results (A) Roll and random adaptor stimuli. (B) Verticality detection task stimuli (C) d' results. (D) Criterion results.

was more than 2.5SD from the mean (n = 1). The final sample size for analysis was 27.

Data were analysed using a Signal Detection approach [30,31]. Responses were classed as 'Hits' (responding YES to a vertical stimulus), 'Misses' (responding NO to a vertical stimulus), 'False alarms' (FA, responding YES to a tilted stimulus) and 'Correct rejects' (CR, responding NO to a tilted stimulus). The proportion of Hits and FAs were calculated as:

$$Prop_{Hit} = \frac{n_{Hits}}{n_{VerticalStim}} \qquad Prop_{FA} = \frac{n_{FA}}{n_{TiltedStim}} \tag{1}$$

In order to calculate sensitivity (d') and criterion (C), a standard corrected proportion was used if $n_{Hit} = n_{VerticalStim}$ or $n_{FA} = n_{TiltedStim}$, with corrected proportions given by:

$$Prop_{Hit} = \frac{n_{Hits} - 0.5}{n_{VerticalStim}} \qquad Prop_{FA} = \frac{n_{FA} - 0.5}{n_{TiltedStim}} \tag{2}$$

Similarly, if $n_{Hits} = 0$ or $n_{FA} = 0$, proportion calculations were corrected to:

$$Prop_{Hit} = \frac{0.5}{n_{VerticalStim}} \qquad Prop_{FA} = \frac{0.5}{n_{TiltedStim}} \tag{3}$$

Sensitivity (d') was then calculated as:

$$d' = Z(Prop_{Hit}) - Z(Prop_{FA}) \tag{4}$$

Criterion (C) was calculated as:

$$C = \frac{-(Z(Prop_{Hit}) + Z(Prop_{FA}))}{2} \tag{5}$$

Paired t-tests were then used to compare d' and C following the random and rotating adaptors.

3. Results

3.1. *Verticality sensitivity (d')*

Mean d' following the random adaptor was 2.00 (SD = 1.36). Mean d' following the roll-rotating adaptor was 1.61 (SD = 1.45). A paired *t*-test revealed a significant difference between the two motion adaptor conditions (t(26) = 2.13, *p* =.04, Cohen's d = 0.41). Thus, subjects were less sensitive to verticality following adaptation to roll motion (Fig. 1C).

3.2. *Criterion (C)*

Mean C following the random adaptor was −0.22 (SD = 0.55). Mean C following the rotating adaptor was −0.24 (SD = 0.42). A paired *t*-test revealed no significant difference in C between the two motion adaptor conditions (t(26) = 0.19, *p* =.85; Fig. 1D).

3.3. *Influence of motion Aftereffect?*

Our findings suggest that the decrease in sensitivity to verticality is driven by multisensory down-weighting due to exposure to visuo-vestibular conflict. However, it is also possible that adaptation to roll motion may have induced a motion-aftereffect (MAE), in which vertical stimuli appear tilted post-adaptation [35–37]. To exclude this possibility, we conducted a post-hoc analysis on FA and CR rates for clockwise and anticlockwise tilted stimuli. If a MAE drove participant responses, we would expect that anticlockwise stimuli would appear less tilted, resulting in more FAs/fewer CRs following adaptation to roll-rotation versus random motion. Moreover, clockwise-tilted stimuli would appear further tilted if affected by a MAE, resulting in more CRs/fewer FAs following adaptation to roll-rotation versus random motion.

Rates of FAs/CRs were calculated by taking the percentage of each response type by stimulus and adaptor type (e.g., $\frac{N_{FA}}{15} \times 100$). Repeated measures ANOVAs tested for an interaction between motion adaptor (Roll versus Random) and stimulus type (Anticlockwise versus Clockwise).

Mean FA percentages for each adaptor and stimulus type can be seen in Table 1. No significant main effect of adaptor was found ($F(1, 26) = 0.756$, $p = .392$, $\eta_p^2 = 0.028$), with similar mean rates of FAs across roll (31.11) and random adaptors (27.16). A significant main effect of stimulus type was found ($F(1, 26) = 16.06$, $p < .001$, $\eta_p^2 = 0.382$), with greater FA rates for anticlockwise (40.86) versus clockwise-tilted (17.41) stimuli. Crucially, however, no significant interaction was found between adaptor and stimulus type ($F(1, 26) = 0.924$, $p = .345$, $\eta_p^2 = 0.034$). Accordingly, while FA rates were higher for anticlockwise stimuli, this was the same irrespective of adaptor type, and likely did not result from a motion after-effect.

Mean CR percentages for each adaptor and stimulus type can be seen in Table 1. A significant main effect of adaptor was found ($F(1, 26) = 4.38$, $p = .046$, $\eta_p^2 = 0.144$), with higher CRs for random (68.77) versus roll (58.52) adaptors. A significant main effect of stimulus type was also found ($F(1, 26) = 17.38$, $p < .001$, $\eta_p^2 = 0.401$), with greater CR rates for clockwise (76.17) versus anticlockwise-tilted (51.11) stimuli. However, no significant interaction was found between adaptor and stimulus type ($F(1, 26) = 0.531$, $p = .473$, $\eta_p^2 = 0.020$), suggesting that a MAE did not drive differences in responses to each stimulus type.

The results of this analysis suggest that the perception of stimuli displayed in this task were not affected by a MAE, suggesting that this did not drive the decrease in verticality sensitivity. We suggest that exposure to visuo-vestibular conflicts leads to sensory reweighting resulting in altered multisensory processing. It is important to note that this post-hoc analysis was exploratory, and consequently future studies should be designed to specifically investigate the role of the MAE in verticality perception following adaptation to roll-rotating stimuli.

4. Discussion

The interaction between vision and the vestibular system occurs over multiple levels, such as the vestibulo-ocular reflex and more complex integrated percepts for self-motion. The integration of visuo-vestibular cues provides more precise perceptual estimates, such as heading direction or verticality perception [1–3,12,13,16]. However, conflicts between visual and vestibular signals can alter subsequent processing in either modality. For instance, sensitivity to optic flow signals is altered following exposure to visuo-vestibular conflicting motion profiles [27,28], and vestibular sensitivity is reduced when exposed to optic flow when stationary [25,26]. While these studies showed conflict-induced modulation of processing within each sensory channel, our findings suggest that visuo-vestibular conflicts also alter the processing of multisensory percepts. Here we found reduced sensitivity to verticality following exposure to optic flow in the absence of corroborating vestibular inputs. As such, we show for the first time, that the sensitivity to integrated multisensory percepts – such as the gravitational vertical - is also modulated by sensory conflict.

Integration of sensory cues is achieved via reliability-based cue weighting [4,5,38]. Signals are weighted according to their reliability, with more reliable cues given a higher weighting than less reliable ones. Multisensory estimates are then computed as a sum of these weighted cues [4,5,38]. During self-motion, vision and the vestibular system provide redundant information regarding the direction and acceleration of motion, and are therefore integrated according to the above principles [1,39,40]. In this study, we exposed participants to optic flow while they remained stationary, inducing a cue-conflict with visual information signalling roll rotation, while vestibular cues signalled that the participant was stationary. To resolve this conflict, we suggest that vestibular cues are down-weighted in favour of the more salient optic flow [26,41]. Previously, we have shown that this reweighting results in lower sensitivity to vestibular self-motion signals [25,26]. Here, we extend this mechanism to broader visuo-vestibular processing, specifically the perception of verticality.

Table 1
Mean (SD) false alarm and correct reject rates by stimulus and adaptor type.

Stimulus type	Adaptor	
	Random	Roll
False Alarm		
Anticlockwise	37.77 (37.80)	43.95 (33.14)
Clockwise	16.54 (25.84)	18.27 (21.92)
Correct Reject		
Anticlockwise	57.04 (38.00)	45.19 (34.06)
Clockwise	80.49 (26.79)	71.85 (25.78)

Verticality perception requires integration of multisensory information, with biases in verticality perception when the head or body are tilted [10,16,19–20,22–24,42]. Moreover, rotating visual stimuli biases the subjective visual vertical towards the direction of rotation [15,34,43,44]. We found that exposure to visuo-vestibular conflict resulted in reduced sensitivity to vertical stimuli, suggesting that visual cues override both vestibular and somatic signals when estimating verticality. Importantly no differences were reported in the criterion. Crucially, the reduction in sensitivity occurred after adaptation to the roll-rotating stimulus – verticality judgements were made in the absence of visual motion stimuli. We do not believe therefore that our results reflect a conventional subjective verticality bias induced by dynamic visual stimuli, as this bias is unlikely to persist once the adapting stimulus is removed [45].

Here, participants were exposed to one minute of adaptation to visual stimuli. It is therefore possible that participants experienced a motion aftereffect (MAE, i.e., illusory rotation in the opposite direction to the adapting stimulus) which could interfere with the detection of vertical stimuli [35–37]. Post-hoc exploratory analysis suggested however that our findings could not be driven by a MAE alone, as rates of false alarms and correct rejects remained similar for each stimulus type across random and roll conditions. As this analysis was exploratory, future studies should be designed to investigate the role of the MAE in verticality detection, and possible interactions with multisensory reweighting after visuo-vestibular conflict. Moreover, here we investigated adaptation to anticlockwise roll rotation only. As we were interested in verticality *detection*, we did not anticipate any direction-dependent differences on our results. Our previous research has also shown that vestibular down-weighting occurs only for the plane in which the visuo-vestibular conflict occurred [26]. Accordingly, we did not investigate changes in vestibular detection following rotation in another direction or axis. However, it would be interesting to explore whether visuo-vestibular conflicts on other axes (such as yaw or pitch) could influence verticality judgements in these planes.

A number of brain areas have been identified to be involved in processing heading and self-motion perception. Specifically, the medial superior temporal sulcus (MSTd) has been shown to be sensitive to optic flow [46–48], while the cerebellar nodulus and uvula are highly involved in the processing of visuo-vestibular information [49]. The communication of these brain regions with parietal [50,51] and insula areas [52] may suggest sensory conflict is minimised through feedback loops. However, the mechanisms, connectivity and interactions of brain areas for self-motion, and in particular verticality perception, are still little understood [53].

Overall, we found that exposure to visuo-vestibular conflict reduces sensitivity to verticality. Crucially, our findings suggest that vestibular down-weighting results not only in reduced sensitivity to vestibular signals directly, but also to multisensory percepts requiring the integration of vestibular signals with other modalities. Given the vestibular system's pervasive influence on a range of higher and lower-level processes, the broader implications of visuo-vestibular sensory conflict should be further explored.

Author contribution

IA, MG, and ERF conceptualisation and design of study. MG generation of stimuli. IA programming experiment. MG data analysis. MG and IA drafting of manuscript. MG, IA and ERF revision of manuscript. All authors approved the final version of the manuscript.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data has been made available

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neulet.2022.136963.

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