

Visual and Vestibular Integration Express Summative Eye Movement Responses and Reveal Higher Visual Acceleration Sensitivity than Previously Described

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PURPOSE. Acceleration plays a great impact on the vestibular system, but is attributed little influence over vision. This study aims to explore how visual and vestibular acceleration affect roll-plane oculomotor responses, including their additive effect.

METHODS. Seated in a mechanical sled, 13 healthy volunteers (7 men, 6 women; mean age 25 years) were exposed to a series of visual (VIS) optokinetic, vestibular (VES) whole-body, and combined (VIS + VES) rotations. This was carried out at two acceleration intensities. Subjects wore a video-based eye tracker, enabling analysis of torsional and skewing eye movement responses, which were used to evaluate the individual response to each trial. The tracker also contained accelerometers allowing head tracking.

RESULTS. Both ocular torsion and vertical skewing were sensitive to acceleration intensities for VES and VIS + VES. For VIS only, skewing exhibited such a response. An increased acceleration yielded a decreased torsion-skewing ratio for VIS, explained by the change in skewing, but remained unchanged for VES and VIS + VES. Torsion exhibited particularly reliable summative effect, yielding a relative contribution of 32% VIS and 75% VES during low acceleration, and 19% and 85%, respectively, during high acceleration.

CONCLUSIONS. The change in the skewing response to different intensities indicates that the visual system is more sensitive to visual accelerations than previously described. Eye movements showed reliable summative effects, indicating a robust visual-vestibular integration that indicates their integrative priorities for each acceleration, with the visual system being more involved during low accelerations. Such objective quantifications could hold clinical utility when assessing sensory mismatch in vertiginous patients.

Keywords: ocular torsion, vertical skewing, visual acceleration, visuovestibular integration, gaze control

Dizziness and vertigo are generally attributed to the mismatch theory; the vestibular, visual, and proprioceptive sensory inputs produce conflicting information about head movements to the brain leading to incongruent motion perception and balance discomfort.¹ Most clinical evaluations of dizzy patients tend to investigate these systems separately, with a focus on vestibular integrity.

Although vertigo is a subjective sensation due to mismatched perceptions of the world, there are methods aiming to objectively quantify the symptoms. Currently, eye movement analyses make up the foundation of objectively evaluating balance complaints, assessing reflexive arcs unrelated to subjective perceptions. This is primarily done through stimulating the vestibular system and measuring the vestibulo-ocular reflex (VOR), but also by looking for signs of pathological nystagmus or skew deviation.² One aspect of the VOR, when induced by a head tilt, is the rotation of the eyes in the contralateral direction in what is called ocular counter-rolling (OCR), induced by an activation of the semi-circular canals and maintained through otolithic signaling

during a static head tilt with the purpose of reducing the rotation of a visual scene on the retina as the head moves.^{3,4}

Rotation of the visual field will also produce a torsion response of the eyes.⁵ This visually induced ocular torsion is much smaller than the OCR, yielding a positional gain of only 1% to 4% relative to the visual rotation.⁶⁻⁸ This torsion can, however, be modified by the amount of visual clues present in the visual scene, with additional visual information resulting in a larger response.^{6,9} The amount of torsion exhibited to a rotating visual scene has also been positively correlated to poorer postural control and increased sympathetic signaling.¹⁰ Such a relationship may not be unexpected, as the connectivity of visual and vestibular input is well developed, with the systems sharing cortical areas for posture and self-motion.^{11,12}

In addition to the torsional response during a head tilt, the ipsilateral eye will move upward and the contralateral eye downward in the form of a vertical divergence (i.e. vertical skewing),^{13,14} the purpose of which is to avoid diplopia and increase the fusional range. This response is not to be



FIGURE 1. An illustration of the balance provoking trials. (A) Vestibular stimulation in which a vestibular activation is obtained due to changes in head position. The trial is performed in complete darkness with no visual clues. (B) Visual stimulation in which the visual scene is being tilted while the subject remains in a stationary, upright position. (C) Visual-vestibular stimulation in which the subject is being tilted. The visual scene is static and is, therefore, passively rotated in the opposite direction relative to the retina. Blue arrows represent the active rotation.

confused with the pathological *skew deviation*, as this example of vertical skewing is a physiologic response to head tilt.¹⁵ In contrast to the semicircularly induced OCR, vertical skewing is thought to primarily be a utricular motor-reflex.¹⁶

We have recently shown that rotational visual stimulation alone will result in the same type of vertical divergence, indicating a distinct ocular balance response in the combined eye movement response of ocular torsion and vertical skewing, which is common for both visual and vestibular systems.⁹ From a visual perspective, there is no apparent reason for inducing a vertical divergence response, given that the head and visual target has remained stationary. Consequently, the most plausible explanation could be that there exists a visual drive of this primarily vestibular reflex.

Animal studies have shown how rotational optic flow activate dedicated neurons in the vertebrate vestibulocerebellum, highlighting the intertwined relationship between vestibular and visual motion that would allow such a response.^{17,18}

Further investigation of this relationship could hold clinical utility in assessing patients suffering from non-vestibular vertigo, particularly visual motion hypersensitive, as these patients show increased visual dependency.¹⁹

The primary aim of this study was to explore the effect of stimulus acceleration on the visual and vestibular systems on the reflexive eye movement responses of ocular torsion and vertical skewing. The secondary aim was to investigate to what extent the visual and vestibular systems contribute to a conjoint visuovestibular trial, elucidating the relative importance of each system. This was made possible through performing combinations of visual, vestibular, and visuovestibular trials, and comparing the velocities for each eye movement response so that a relative percentage could be attributed to both the visual and vestibular systems.

MATERIALS AND METHODS

Subjects

Thirteen healthy volunteers (7 men and 6 women; mean age 25 years [23–34]) participated in the study. None had any disorder or drug use that would affect the central nervous system. All participants had normal or corrected visual acuity (VA; ≥ 1.0 using logarithm of the minimum angle of resolution [logMAR chart]), stereoscopic vision of at least 200" of arc (Lang II stereotest), and normal eye motility. Latent strabismus was precluded with the cover test. No participant had any history of vertigo. Normal vestibular function was assessed through a horizontal head impulse test revealing no refixation saccade, and balance through the

Romberg's test. This was regarded as an initial screening, as any undetected vestibular pathologies were expected to be identifiable during the baseline recordings in darkness, as the eye tracking software would reliably detect any nystagmus.

All participants signed informed written consent prior to their enrollment after explanation of the nature of the study, and having received written and oral information on the procedure. The research complied with the Declaration of Helsinki and was approved by the Regional Ethics Committee of Stockholm (EPN 2018-1768-31-1).

METHOD

The subjects were seated in a motorized sled in which they were exposed to three different balance-provoking stimulations (i.e. modalities: visual (VIS), vestibular (VES), and visual-vestibular (VIS + VES) (Fig. 1). All stimulations were carried out at two intensity levels and were performed with simultaneous recording of the subject's eye and head movements. Visual stimuli were selected based on a rigorous trial-and-error screening process during which several iterations were tried to assess the fidelity with which eye movement responses were produced. Together with the whole-body rotations during VES, stimulations have been implemented and characterized in a series of studies involving eye-tracking.^{9,10,20}

As to reduce the impact of learning effects due to repeated measurements, the test order was balanced according to intensity level and modality between subjects. The trials were preceded and followed by 20 seconds without active stimulation (i.e. with the static image presented), in order to establish baseline values. Furthermore, the subjects received short breaks of 2 to 4 minutes between every trial to allow recuperation of the sensory systems.

VISUAL STIMULATION

Subjects were seated in the motorized sled facing visual scenes presented on a projector screen (res 1024 × 768; contrast 2000:1; update frequency 60 hertz [Hz]) using a front video projector (NEC NP-M350X, NEC Display Solutions Ltd., Tokyo) at an eye-screen distance of two meters using a visual presentation program for Windows 10 (Powerpoint; Microsoft, Redmond, WA). The visual scenes consisted of oblique white lines on a black background together with a central white fixation point (Fig. 2). During the tracking phase, the scene was rotated around the central fixation point with a duration of 1 second at 2 intensity levels at

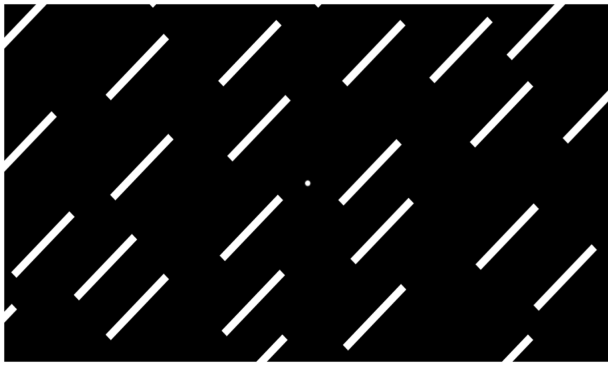


FIGURE 2. Visual scene presented on the projector screen during visual stimulation, covering circa 50 degrees of the subject's field of vision. The scene consists of a central fixation point (0.32 cm in diameter) surrounded by 38 inclined white lines tilted at 45 degrees (0.42 cm long, 3.25 cm wide, visual angle 0.93 degrees). During tracking phase, the lines rotated counterclockwise at low and high acceleration intensities. Reprinted from Wibble T, Pansell T. Vestibular eye movements are heavily impacted by visual motion and are sensitive to changes in visual intensities. *Invest Ophthalmol Vis Sci.* 2019;60:1021–1027. © 2019 The Authors. Published by the Association for Research in Vision and Ophthalmology (ARVO).

accelerations of 28 deg/s² (Supplementary Video S1) and 56 deg/s² (Supplementary Video S2), respectively; these were multiples of the vestibular accelerations, which is in line with previous experiments implementing this methodology.⁹ The rotation was performed counterclockwise, as previous studies have shown no effect of stimulation direction.^{9,10} Similarly to the aforementioned studies, the lines were presented tilted at an angle of 45 degrees, which in pigeons have been

show to provoke the strongest neural response to translational optic flow.²¹

Vestibular Stimulation

A motorized sled was constructed in house and moved on two separate belts, connected to two AC Brushless Servo Motors (Baldor BSM90C, 400 V; Fig. 3). It allowed exact full body rotation with the subject sitting, moving around the center of rotation, which in this study was predetermined to be between subjects' eyes in order to adjust for interindividual differences in height.

Subjects were instructed to look straight ahead at a reference point presented on the projector screen. The projector was then turned off in order to eliminate visual clues, which created a room of complete darkness. The stimulation (i.e. chair rotation), was then initiated 20 seconds after the switch-off, while the subjects remained fixating on the imagined target straight ahead to obtain a stable position for eye recording. The subjects' heads were immobilized using an extrication collar and hook-and-loop straps to ensure minimal proprioceptive impact (Fig. 3). The trial was performed once with an acceleration of 14 deg/s² and once with an acceleration of 28 deg/s².

Visual-Vestibular Stimulation

This modality was carried out by combining the visual and vestibular trials. The stimulation was performed as described for vestibular stimulation, whereas the visual addition was implemented through having subjects simultaneously view the static visual stimulus. Consequently, the body rotation caused an equivalent relative rotation of the visual field on the retina in the opposite direction of the head tilt.



FIGURE 3. Picture demonstrating passive whole-body movement during vestibular stimulation. Subject is positioned in a dark room without visual information and is wearing an eye tracker (Chronos C-ETD) for recording of the VOR response due to the head tilt. Extrication collar and hook-and-loop straps stabilized the movement as to obtain an isolated and stable vestibular activation through relieving neck muscles and minimizing proprioceptive input. Reprinted from Wibble T, Pansell T. Vestibular eye movements are heavily impacted by visual motion and are sensitive to changes in visual intensities. *Invest Ophthalmol Vis Sci.* 2019;60:1021–1027. © 2019 The Authors. Published by the Association for Research in Vision and Ophthalmology (ARVO).

TABLE. Descriptive Statistics (Mean [SD]) of Torsion and Vertical Vergence Velocities (Deg/Sec) to Each Modality and Intensity

| Intensity | Torsion | | Paired <i>t</i> -test | Vertical vergence | | Paired <i>t</i> -test on |
|-----------|-----------|------------|-----------------------|-------------------|------------|--------------------------|
| | Low | High | | Low | High | |
| VES | 6.9 (1.9) | 16.1 (5.6) | $t = 7.84; P < 0.001$ | 4.3 (1.9) | 10.4 (6.1) | $t = 5.14; P < 0.001$ |
| VIS | 2.8 (1.0) | 3.5 (1.4) | $t = 1.76; P = 0.10$ | 1.2 (0.4) | 2.2 (1.0) | $t = 3.90; P = 0.002$ |
| VIS + VES | 9.3 (2.6) | 19.1 (4.6) | $t = 9.34; P < 0.001$ | 5.7 (1.8) | 12.5 (5.0) | $t = 5.56; P < 0.001$ |

Paired *t*-tests were performed on logged data. Alfa (α) was Bonferroni corrected with the number of comparisons in the table and set to 0.008.

Eye and Head Movement Recording

The motorized sled was time-synchronized with a head-mounted eye tracker that recorded the eye movements in three dimensions (C-ETD; Chronos Inc., Berlin; Fig. 3). The Eye Tracker was a video-based device recording at a frame rate of 100 Hz and was part of a PC-based system with dedicated hardware and software. It allowed for binocular tracking of horizontal and vertical eye movements (spatial resolution <0.05 deg), and quantification of torsional eye movements through iris pattern recognition. The Chronos Eye tracker also contained a head tracking system measuring angular displacements to control for head position. Eye movements were calibrated into degrees rotation before the measurements by recording eye positions at five locations with known angular displacements. This type of video-based eye tracking has been proven reliable as implemented under the present methodology.⁹

ANALYSIS

In order to obtain values of horizontal and vertical pupil positions and torsional displacement of iris position, the recorded sequences were processed with the analysis software attached to the eye-tracking system (Chronos Vision GmbH, Berlin). From these values the vertical skewing response was calculated by subtracting the left vertical eye position with the right vertical eye position, whereas the torsional was taken from the eye exhibiting the best signal-to-noise ratio.

The average velocity of vertical skewing response, the average velocity of torsional response, and the ratio between these two outcomes were derived from these calculations having been plotted in the Origin software (OriginPro 2017; OriginLab, Northampton, MA). The velocity was calculated by retrieving the change in degrees between the beginning and end of the slow phase at one second into the stimulation, and dividing it with the change in time for the same period. As such, the eye movement slow-phase velocities could be put into the context of faster or slower relative to each other for each trial. The ratio was computed by dividing the torsional velocity over the skewing velocity. Additionally, the stimulus-gain of each eye movement was analyzed in order to further elucidate the nature of each response. The amount of false torsion for visual and vestibular trials has previously been shown to be insignificant for this methodology.⁹

To further investigate the inter-relationship between vestibular and visual response during visual-vestibular stimulation, calculations were made to determine their respective contributions. These calculations were based on the outcome of torsional velocity due to its stable and additive properties.⁹ The results from the isolated visual and vestibular trials were divided by the result from the visual-vestibular

trial, yielding a percentage of each modality's contribution to the motor response of the joint stimulation.

All statistical analyses were performed using IBM SPSS Statistics 25 for Windows, and the significance level (α) was set to 0.05. A One-way multivariate analysis of variance (MANOVA) for repeated measures was used to illustrate the impact of *intensity* (low/high) on the dependent variable *eye movement* (torsion or vertical vergence) and the torsion-skewing ratio for each *modality* (VES, VIS, and VES + VIS). The analysis had to be done separately for each modality because visual stimulation gave much smaller eye movement responses, leading to unequal variances in comparison to the vestibular and visual-vestibular stimulation. All comparisons are presented with Bonferroni corrected *P* values. A paired sample *t*-test was used to determine any significant differences between the two intensity levels with regard to modality and with the Bonferroni corrected alpha-value presented for a number of comparisons. The test of normality was obtained using Shapiro–Wilk's test.

RESULTS

The test of normality revealed a non-normal distribution for several variables. The data was log-transformed and again inspected to certify the data distribution to be suitable for running a parametric MANOVA analysis. The descriptive statistics presented are calculated on non-logged data.

Eye Movement Responses to Vestibular Stimulation

Head roll stimulation in darkness revealed significantly higher velocities for both ocular torsion and vertical vergence in response to the high intensity stimulation ($F [2, 11] = 30.59; P < 0.0001$; partial $\eta^2 = 0.848$). The univariate test revealed significant effects for both torsion ($F [1, 12] = 55.71; P < 0.0001$; partial $\eta^2 = 0.823$) and vertical vergence ($F [1, 12] = 26.55; P < 0.0001$; partial $\eta^2 = 0.689$). Stimulus gain (mean [SD]) for torsion were 0.49 (0.13) and 0.57 (0.20) ($t [12] = 1.52; P = 0.15$), and for vertical vergence 0.31 (0.14) and 0.37 (0.22) ($t (12) = 1.04; P = 0.32$) for low and high intensity, respectively, indicating that gain was unaffected by acceleration intensity. For descriptive data, see Table. One may note the summative characteristics of VIS and VES, which together reach the total VIS + VES value for each intensity of the eye movement responses. The eye movement responses to VES is illustrated in Figure 4.

Eye Movement Responses to Visual Stimulation

The repeated MANOVA revealed significantly higher eye movement velocities to high intensity stimulation ($F [2, 11]$

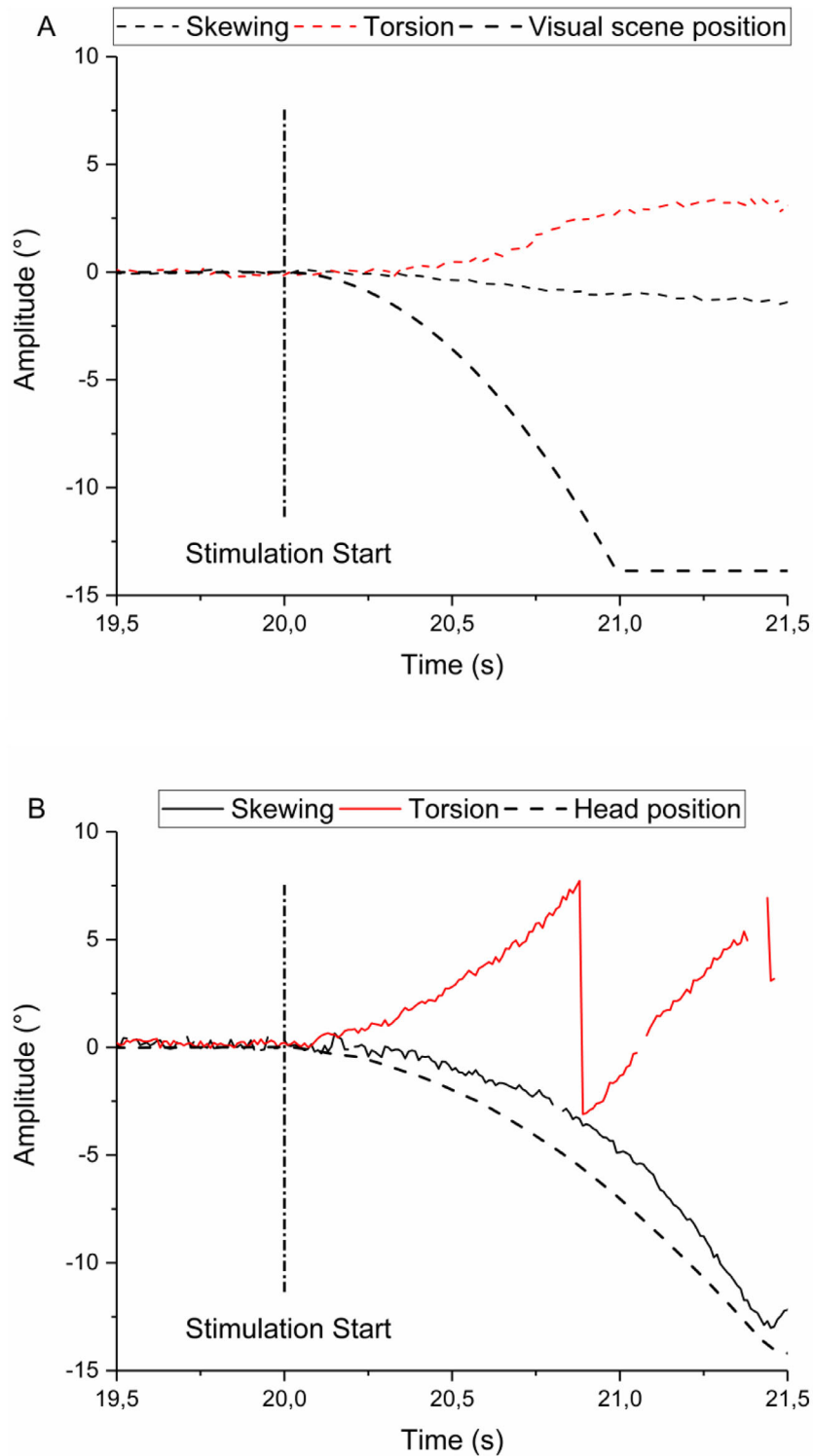


FIGURE 4. Raw signal of the torsional and skewing responses to the high intensity (A) VIS and (B) VES modalities for one test person. The VIS signals have been inverted so as to allow for clearer comparison to VES. The visual scene position and head position have been divided by a factor of two for fitting purposes.

= 6.90; $P = 0.011$; partial $\eta^2 = 0.557$). The univariate test revealed a nonsignificant effect on torsion ($F [1, 12] = 3.10$; $P = 0.10$; partial $\eta^2 = 0.205$), whereas vertical vergence was found to be significant ($F [1, 12] = 15.02$; $P = 0.002$; partial $\eta^2 = 0.556$). The high intensity induced both a torsional

and vertical vergence response (Fig. 4 and Table). Stimulus gain for torsion were 0.10 (0.03) for the low stimulus intensity and 0.06 (0.03) for the high, with a significant effect of stimulus intensity ($t [12] = 3.57$; $P = 0.004$). For vertical vergence, the corresponding figures were 0.04 (0.01) and

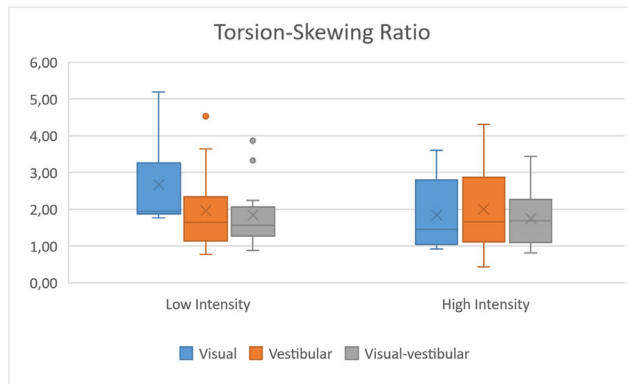


FIGURE 5. The effect of acceleration on the torsion-skewing ratio given as degrees of torsion per degrees of skewing.

0.04 (0.02) (t [12] = 0.19; P = 0.85) for low and high intensities respectively. Thus, the high intensity induced a higher velocity (see Table), albeit with a relatively lower stimulus gain.

Eye Movement Responses to Visual-Vestibular Stimulation

VIS + VES, produced a higher velocity than simply VES (F [1, 12] = 20.99; P = 0.001). The MANOVA revealed significantly higher eye movement velocities to high intensity stimulation (F [2, 11] = 54.19; P < 0.001; partial η^2 = 0.908). The univariate test revealed significant effects for both torsion (F [1, 12] = 88.56; P < 0.0001; partial η^2 = 0.881) and vertical vergence (F [1, 12] = 26.55; P < 0.0001; partial η^2 = 0.715). Torsional gain were 0.67 (0.19) for low stimulus intensity and 0.68 (0.17) for high, but expressing no effect of stimulus intensity (t [12] = 0.31; P = 0.76), and for vertical vergence gain 0.40 (0.13) and 0.45 (0.18) (t [12] = 0.70; P = 0.496) for low and high intensities, respectively.

Torsion-Skewing Ratio Response

The ratio of torsion and vertical skew remained relatively constant independently of changes in acceleration during vestibular and visual-vestibular stimulation. During visual stimulation the ratio was lower during exposure to the high intensity stimulation compared to low, reflecting a decreased torsion-skewing ratio (P = 0.036; Fig. 5). However, after applying Bonferroni correction for multiple comparisons, this P value was nonsignificant (α = 0.017).

Relative Contribution of Modality on Torsion Velocity

The absolute torsional velocity expressed robust additive properties of the visual and vestibular systems, allowing for comparisons of the relative impact of each modality on the VIS + VES trials for both accelerations (Table). Bonferroni-corrected alpha was calculated to 0.025. A paired t -test revealed a significant difference between visual contributions depending on the level of acceleration, with the low intensity yielding a visual relative contribution of 32% and the high intensity 19% (t [12] = 2.890; P = 0.014). When added together, a paired t -test showed that the visual and vestibular contributions did not differ from the correspond-

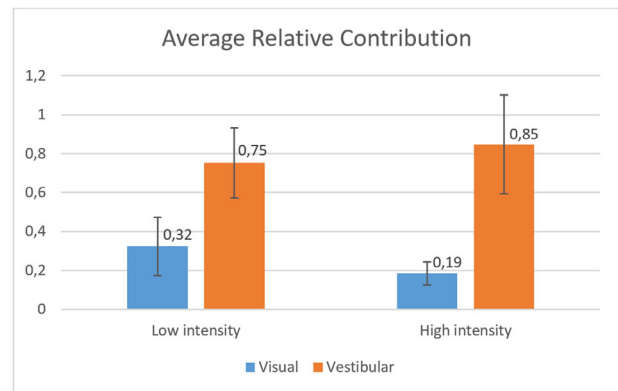


FIGURE 6. Relative contribution to torsional velocity. Mean relative contribution to torsional velocity for visual (VIS) and vestibular (VES) as given in proportions for low (14 deg/s²) versus high (28 deg/s²) acceleration intensities.

ing visual-vestibular output for either intensity (Fig. 6) (i.e. the combined contribution is not significantly different from 1 for either intensity).

As the accelerations for low intensity VIS was the same as those of high intensity VES and VIS + VES, corresponding calculations were performed as it would indicate how the eye movement parameters may differ between amplitude and acceleration. For ocular torsion, the relative contribution was 26% for VIS and 146% for VES, which differed significantly from the corresponding results for high intensity VIS + VES (t [12] = 2.944; P = 0.012). The corresponding numbers for vergence were 10% for VIS and 85% for VES, the summative effects of which were not different from the VIS + VES results (t [12] = 0.746; P = 0.47).

DISCUSSION

The purpose of this study was to explore to what extent eye movement responses of ocular torsion and vertical skewing are affected by visual and vestibular roll accelerations, and how the two sensory systems integrate their responses. Results revealed that the torsion-skewing ratio was significantly affected by stimulus acceleration, which also altered the relative contribution of visual and vestibular sensory information to the torsional response. The clear summative effect of visual and vestibular eye movement responses onto that of the visual-vestibular strengthens the notion that visual and vestibular information goes through a robust integration seen for both ocular torsion and skewing. Still, there are some limitations to this study that are revealed in the light of these results. The recording frequency of the eye-tracker was set to 100 Hz. The Chronos system allows for reliable recordings of up to 200 Hz. However, during the present study, we saw recurring data loss when processing the video files, leading to several retakes. It was revealed that the computer linked to the eye tracker was suffering from performance issues, and a decision was made to pursue the experiments at 100 Hz, which has proven sufficient in previous publications.^{10,20} This naturally limits the utility of the collected data, as any fast-acting eye movement is prone to a high signal dispersion. As can be seen in Figure 4, this still allowed for precise measuring of eye movement responses, particularly as this study does not deal with quick-phase analysis.

Additionally, there was a discrepancy among visual accelerations and the other modalities, which implement a multiple of the former. This was done in previous studies to technical limitations. As vision had been described as insensitive to accelerations, it was decided to set all stimuli to a fixed amplitude, which reliably produced stable and summative torsional eye movement responses. As this study found skewing to be sensitive to visual accelerations, this setup obviously produces a limitation to assessing the combined visuovestibular effect; this study does not allow for assessing the additive effects of visual and vestibular stimuli on the skewing response. This was further illustrated when performing the reverse analysis (i.e. when comparing low intensity VIS to high intensity VES and VIS + VES for both torsion and skewing), as this kept the acceleration constant between VIS and VES but instead meant that the amplitudes were different. In this scenario, torsion proved unreliable whereas skewing, having been shown to exhibit a certain sensitivity to accelerations, showed robust summative effects.

As a result, torsion was used for quantifying the relative contribution of VIS and VES onto VIS + VES, as only skewing was found sensitive to accelerations. This is, however, something that future studies need to take into consideration, and a proper format for matching amplitude and accelerations need to be implemented.

Eye Movement Responses to Visual and Vestibular Stimulation

As demonstrated in our previous study, there was an increase in eye movement velocities between modalities, with the vestibular response being significantly higher than the visual.⁹ Considering that the vestibular system is purported to be sensitive to accelerations, compared to the rather insensitive visual detection of acceleration, this response in eye movement velocities could be expected.

An increase in stimulation intensity resulted in increased torsional and skewing velocities for both vestibular and visual-vestibular trials. During VIS, only the change in skewing velocity was significant between stimulation accelerations (Table). For context: vertical skewing is generally considered a vestibular brainstem reflex, seen together with OCR in an ocular tilt reaction.²² The presence of a skewing response to visual stimuli indicate that either visual stimuli activate the vestibular nuclei, or there exists another neural mechanism responsible for producing vertical skewing. Although this eye movement response to visual stimuli had been described before,⁹ the present study adds that visually induced vertical skewing is sensitive to accelerations, contrary to the pre-existing notion that the visual system is rather poor at accommodating accelerations. This was exemplified further in the constant gain of the skewing response, which indicated that it accommodated the change in acceleration, unlike torsion, which evidently reached a peak velocity much earlier and consequently yielded a decreased gain. Considering that accelerations are known to produce a vestibular response, it is tempting to suggest that visual rotation may indeed activate the vestibular nuclei. Studies in monkeys have shown precisely such vestibular activation to optokinetic stimulation, with type I vestibular neurons being sensitive to accelerations up to 5 deg/s² and type II neurons up to 10 deg/s².²³ Later studies have supported the view that the visual system is rather insensitive to accel-

eration, being more dependent on the visual information density.²⁴

The current study implemented acceleration over the previously described limit for vestibular activity, yet still produced what is generally considered a vestibular motor response. Consequently, it would appear that the human vestibular nuclei may not be limited to an optokinetic acceleration of 10 deg/s², and that the visual system is sensitive to stimulus acceleration, as illustrated in Table, albeit to a lesser degree than the vestibular complex. Such a relationship might have been previously missed as vertical skewing has only recently been described as an optokinetic eye movement response.⁹ Considering that ocular torsion proved insensitive to acceleration changes, one might suggest that the two eye movement responses differ in their neural integration.

TORSION-SKEWING RATIO

It has been demonstrated that an increased amount of visual clutter leads to an increased torsion-skewing ratio during visual and visual-vestibular trials.⁹ The initial analysis saw this study revealed that an increased stimulus acceleration instead had a negative effect on the ratio, albeit only during the visual trials. With these two factors in mind, it seems reasonable to suggest that the torsion-skewing ratio reflects the motion characteristics in a viewed visual scene as it is dependent on both content and motion. However, after a Bonferroni correction, this was found to be nonsignificant, which limited this interpretation. Still, putting these results in context to previous findings in relation to a highly significant acceleration effect on skewing, which was absent for torsion, it may be that the corrections instead produced a type II error. Additionally, a torsion-skewing ratio sensitive to visual stimuli have been shown previously, albeit related to clutter levels rather than accelerations.⁹ In keeping with recent suggestions on adjusting *P* value significance levels,²⁵ we would call this finding suggestive rather than confirmatory, as it fits in well with the greater picture but falls short of reaching the adjusted alpha.

In the present study, a change in ratio between low and high intensity visual stimulations could be attributed to the relatively low skewing response during the low intensity. As shown in Table, ocular torsion proved insensitive to changes in acceleration, and so the change in torsion-skewing ratio can be attributed to the increase of the skewing response. Considering that the torsion-skewing ratio is both reflective of the visual information density and its acceleration, it presents an interesting approach to possibly quantifying subjective complaints to visual elements.

The vestibular and visual-vestibular stimulations produced no difference in the torsion-skewing ratio between stimulation intensities. The torsion-skewing ratio, therefore, seems to be more sensitive to changes in the visual field than movements of the head itself, and vestibular activation may even hide changes in the weaker visually induced eye movement responses. However, a more important aspect might be the disparities in optokinetic accelerations between VIS and VIS + VES, as the former adopted multiples of the latter, yielding a larger difference between accelerations within the VIS trials. It may well be that the ratio was only sensitive to the greater difference presented between VIS trials.

It is well described that visual information help calibrate the vestibular system, and vice versa during infancy.^{26,27}

Maladaptation of the vestibular system following brain trauma has been attributed as a possible cause of visually induced vertigo, and visual rehabilitation has yielded promising results for alleviating associated symptoms.^{28,29} It would consequently seem that the visual-vestibular system retains plasticity in how it integrates multisensory information. Vertigo, as well as motion-sickness, stem from a mismatch of sensory input, highlighting that visual and vestibular information relay different aspects of postural signalling.^{30,31} Considering the evidence for ocular torsion and skewing exhibiting different response patterns to visual acceleration and information density, it would be of great interest in investigating how the torsion-skewing ratio responds when multisensory integration is lacking. Visual information density has been shown to reflect the torsional component, whereas visual acceleration alters the skewing response. A testing kit involving visual stimulations of two density levels and two acceleration levels may, therefore, provide enough information so as to determine what components of the visual-vestibular integration is most affected, suggesting that vestibular integrity might be inferred from visually induced eye movement responses. As it stands, this hypothesis is based on trials in healthy subjects, so naturally future studies involving patients with vertigo of both visual and vestibular natures are in order to further develop the clinical feasibility of utilizing the torsion-skewing relationship.

Visual and Vestibular Contributions to Ocular Torsion Velocity

Similarly to our previous study, the combined effects of the torsional response to visual and vestibular stimulations reliably summated to the visual-vestibular results, indicating a robust summative nature of the two senses in its motor output. The reliability of the eye movement parameters was exemplified further in the constant gain between the two accelerations. Changes in visual information density has been shown to not affect the relative contribution of neither vision nor vestibular signalling.⁹ In comparison, this study shows that an increased acceleration leads to a greater vestibular impact over vision. Such a relationship could be expected as it is well-described that the vestibular system is more sensitive to accelerations than the visual. With regard to the robust nature of this type of approximation, ocular torsion can be considered a stable variable in assessing motion perception in the roll plane as an objective standard.

Furthermore, although the percentages here should not necessarily be taken as absolute truths on the relative importance of vestibular and visual signalling, they present an indication of how the two systems interact under different situations. The results also highlight how torsion remained insensitive to the differences in acceleration between VIS and VES, but was highly sensitive to the differences in amplitude when comparing low intensity VIS to high intensity VES. Reversely, skewing instead provided a robust summation effect when the accelerations were kept constant, in spite of the change in amplitude and, thus, further highlighting a sensitivity to acceleration.

Although these values do not necessarily reflect how perceptually aware an individual is of a visual or vestibular stimulus, it is conceivable that patients suffering from different kinds of motion-perception disorders would exhibit deviating sensory contributions depending on the nature

of the complaints; patients suffering from visual motion hypersensitive are known to be more visually dependent,¹⁹ and could consequently present a greater visual contribution that could be objectively quantified. Similarly, optic flow stimulation have been shown to persistently evoke balance problems in concussed patients.³² As such, comparing the torsional response in this fashion could hold both clinical and scientific utility as an indication of how the visual-vestibular integration may be effected by different disorders or drugs.

CONCLUSIONS

Based on how an increased acceleration led to a higher skewing velocity, producing a decreased torsion-skewing ratio, this suggests that visual acceleration has a stronger effect on vertical skewing than on ocular torsion, and that the visual system is more sensitive to acceleration than previously described. Considering how the torsion-skewing ratio shifts in relation to changes in a rotating visual scene, it could be of clinical interest assessing how patients suffering from visually induced vertigo, expressing a sensitivity to visual motion, may deviate from a healthy control group in terms of objective eye movement parameters.

This study also shows how vision plays a decreasing role as the acceleration during whole-body rotations is increased, indicating a robust neural integration of visual and vestibular sensory information, which can be reliably quantified through the eye movement response.

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SUPPLEMENTARY MATERIALS

SUPPLEMENTARY VIDEO S1.

SUPPLEMENTARY VIDEO S2.