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# Listing's plane and the 3D-VOR in microgravity – The role of the otolith afferences

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**Abstract.** The study addresses the question as to what extent the otolith-mediated gravity vector maintains the stability of the coordinate frames of the vestibulo-ocular reflex and the oculomotor system, described by Listing's Plane. Under normal 1 G conditions it has been demonstrated in the monkey that Listing's Plane (LP) and the 3D vestibulo-ocular response (3D-VOR) are close to collinear [10].

In the present study the coordinate frames of the oculomotor system and the three-dimensional vestibulo-ocular reflex (3D-VOR) system were measured under one-g gravity conditions and during a period of prolonged microgravity, on-board the International Space Station (ISS). To this end, the coordinate frame of the oculomotor system is described in Listing's coordinates and that of the 3D-VOR system by the minimal gain vector.

The findings demonstrate that under Earthbound, one-g conditions the two coordinate frames diverge by approximately 20° in the human. In the absence of the gravity vector the radical loss in the otolith-mediated contribution to the dynamic VOR leads to a reduction of the torsional VOR component and in turn to a forward tilt of the oculomotor coordinate frame, described by the minimal gain vector. In contrast, the torsional component of LP during horizontal and vertical saccades was found to increase, resulting in a backward tilt of LP. Together with the backward tilt of LP a small but consistent change in LP vergence was observed.

The thickness of LP did not appear to change in the absence of gravity. The changes in coordinate frame orientation persisted over the six-month periods spent in zero gravity. The postflight measurements demonstrate that re-adaptation to preflight values proceeds over several days to weeks.

The findings demonstrate that the gravity vector represents a common reference for vestibular and oculomotor responses. They also support the idea that the gravity vector provides a central reference for the entire sensorimotor complex.

Keywords: Listing's plane, vestibulo-ocular reflex, microgravity, three-dimensional eye tracking, gravity vector

## 1. Introduction

Under Earthbound, one-g conditions the otolith organs transduce a combination of gravity and linear acceleration. Thus, mediated by the vestibulo-ocular reflex (VOR) or otolith-ocular reflex (OOR) a static tilt about the roll axis under one-g conditions, causes an alteration in the stimulation of the otolith organs by the gravitational force, and in turn an ocular counterroll (OCR) is elicited.

In microgravity, the otolith organs are no longer loaded by the 1 G vector and accordingly, torsional eye movements can be expected to occur only during dynamic head roll movement or during translatory acceleration. Similarly, in the initial hours and

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days in microgravity, head rotation about the naso-occipital axis will generate vestibular afferent patterns that differ distinctly from those under normal, one-g conditions. During orbital flight, which provides prolonged microgravity, it has been shown [5] that the three-dimensional vestibulo-ocular reflex (3D-VOR) is altered due to the radical loss of stimulation to the otolith organs during head movement and the resultant reduction of OCR. The resultant sensory discrepancy is instrumental to the occurrence of altered perception and malaise, as experienced by the majority of space-flight travellers. Fortunately, vestibular adaptation to the microgravity environment alleviates these complaints. Following their return to one-g, Earthbound conditions after spaceflight the process is reversed [29, *cf.*].

Spatial aspects of the 3D-VOR can be evaluated by measuring the orientation vectors associated with slow phase eye velocity generated by the VOR. The requirements for the formal representation of the 3-D aspects of this response were first addressed by Robinson [31] who discussed the idea of 3-D gain matrices for the angular VOR. This approach has been extended by rotation vector and quaternion representations of eye position and velocity [34] and has been examined experimentally for passive rotation of humans around the three orthogonal axes [10,35] and in spaceflight during active movement by Clarke et al. [6]. A further, related study has re-examined the misalignment of the 3D-VOR and the head axis frame of reference [14].

Since the late 19th century (e.g. Helmholtz [18]), it has been known that under normal visual conditions the torsional orientation of the eye is independent of the path that the eye takes to reach any secondary or tertiary eye position. This restriction implies a reduction from three to two degrees of freedom for the eyeball, and is known as Listing's law; thus, all axes about which the eye rotates from the so-called primary position lie in one plane, called Listing's plane (LP). LP can be visualised by plotting 3D eye positions as quaternions [34] or as rotation vectors [17]. Numerous investigations have verified the validity of Listing's law during fixations, saccades and smooth pursuit, e.g. [33], and it has been argued that LP is primarily under visuomotor control [19]. Furthermore it was previously held that LP was head-fixed and independent of head orientation to gravity, e.g. unchanged in different head positions relative to Earth gravity vector. One exception is related to the occurrence of OCR, which leads to a translation of Listing's plane along the x-axis. In addition, a number of LP studies in humans indicated that its orientation is slightly tilted (1–2°) in different head-pitch positions [2,13]. This effect appears to be stronger in the monkey [15], as supported by further studies investigating the gravity dependence of the primary position [20].

In a further study in the monkey [10], Crawford and Vilis showed that LP is near collinear with the co-ordinate frame of reference of the 3D-VOR. As indicator for the orientation of the 3D-VOR these authors introduced the concept of the minimal gain vector (MGV). This is defined as that vector parallel to the head axis around which the VOR has minimal gain i.e. representing the effective axis for torsional rotation of the eye. In an earlier study [5] it was demonstrated the 3D-VOR is altered during spaceflight, and in a more recent parabolic flight study [8] the orientation of Listing's Plane was measured in 10 healthy subjects during short-term changes in the gravito-inertial vector between one and zero gravity. It was found that in the zero-gravity condition LP orientation was consistently altered. LP elevation was tilted backwards on average by approx. $10°$ ($p = 0.003$). The azimuth angles of the left and right eyes also diverged in zero-G, with a vergence angle between 6.1 and $11.8°$($p = 0.04$). Dissociation in torsional eye position between 1G and 0G was also observed ($p = 0.03$). Corresponding changes in LP orientation have also been reported for hypergravic conditions during centrifuge experiments [28].

The present study examines the influence of prolonged microgravity during spaceflight, i.e. in the effective absence of the gravity reference, on the orientation of LP and the 3D-VOR coordinate frames, and their behaviour after return to Earthbound, one-g conditions. Examination of the collinearity between the Listing and VOR co-ordinate systems is necessary to determine whether a uniform representation of three-dimensional space exists in those CNS areas related to spatial orientation.

The report describes a series of single-case longitudinally studies over the course of 6-month spaceflight missions on-board the International Space Station (ISS), and the subsequent postflight period of up to 60 days.

## 2. Methods

### *2.1. Subjects*

LP and the 3D VOR were examined in ISS crewmembers ($n = 6$) who spent six months on-board the

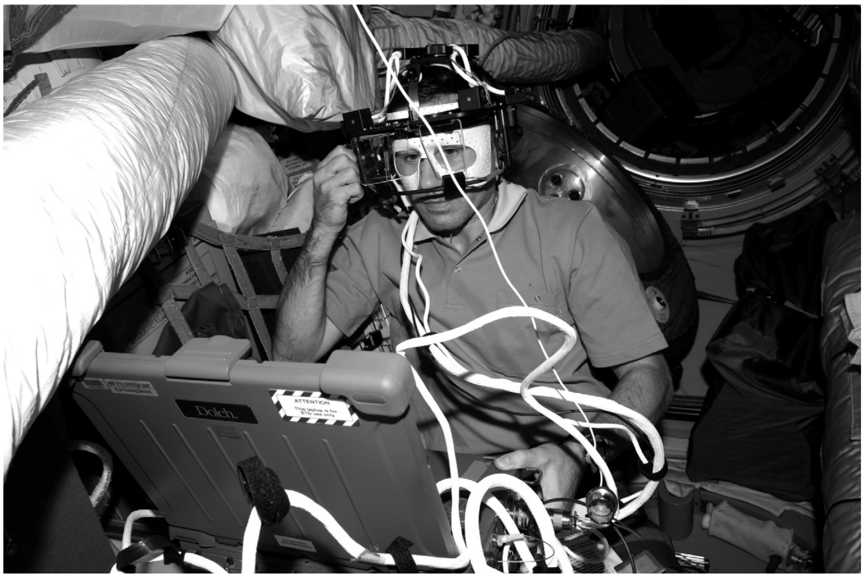

Fig. 1. ISS crew member wearing the eye and head tracker with individually moulded facemask. The inflight measurements were performed in a one-man subject/operator scenario. Identical equipment was employed for the pre- and postflight measurements.

International Space Station (ISS). Measurements were performed during the preflight, inflight and postflight phases of each spaceflight. During the spaceflight, testing was performed by each of the six-month subjects at three-week intervals over the course of their stay onboard the ISS, yielding between 4 and 8 inflight data points.[1]

Each spaceflight subject was tested three times – nominally at 20, 15, and 5 days before launch.[2] After returning to Earth, measurements were performed with all subjects on Day 0 (i.e. within 12 hours after landing), then again on postflight days 2, 5, 8, 10 and 12. In most subjects an additional measurement was made approximately 60 days after landing.

Due to artefacts and lid closure the inflight video recordings from one of the long-term six subjects were unable to be analysed so that the results from only five subjects are presented here.

During the preflight sessions the spaceflight subjects were also trained thoroughly to operate the measurement equipment and to perform the test procedure, in order that they could carry out the experiment protocol autonomously on-board the space station.

Prior to each measurement session, all participants were required to refrain from alcohol consumption and medications that could impact visual/vestibular responses for 48 hours. In addition, any exposure to flight simulator and centrifuge training was excluded for the 24-hour period prior to testing.

### 2.2. *Eye and head movement measurement*

For the determination of the orientation of Listing's plane, 3D eye movement recordings of sequences of saccades, with the test subject fixating at random a number of target points spaced over a $20^\circ \times 20^\circ$ field of view at 2 meters distance, were recorded over a period of 40 seconds. To evaluate the 3D-VOR coordinate frame of reference, recordings of eye and head movement were made during active head movements around the yaw, pitch and roll axes. An acoustic metronome signal running at 0.8 Hz was employed to trigger saccades for the LP recordings and likewise to synchronise the oscillations of the head for the 3D-VOR recordings.

Binocular eye images and head movement sensor signals were recorded throughout the experiment protocol. A three-dimensional eye tracking device (ETD, Chronos Vision, Berlin) was used for video and data recording. In addition to online monitoring of eye and head movement, the eye tracker system provides for digital storage of the video image sequences, head sensor data, and voice commentary for comprehen-

[1] Due to the restrictions imposed by operational requirements during spaceflight, the number of successfully performed measurements varied from 4 to 8. Unfortunately there was no opportunity to repeat unsuccessful or cancelled trials.

[2] This also applied to preflight and postflight experiment sessions.

| | $H_x$ | $H_y$ | $H_z$ |
|---|---|---|---|
| $E_x$ | -0.15 | -0.06 | 0.04 |
| $E_y$ | -0.12 | -0.89 | 0.11 |
| $E_z$ | 0.19 | 0.02 | -0.87 |

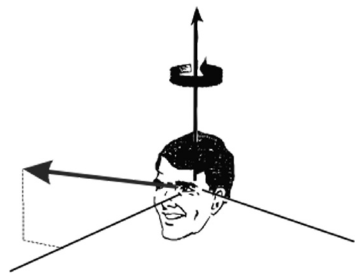

Fig. 2. Example of a 3×3 gain matrix for the VOR under 1 g conditions and the resultant minimal gain vector (MGV).

sive offline evaluation. Video recordings are made of each eye under infrared illumination. A six degree-of-freedom inertial sensor (triaxial linear accelerometer, triaxial angular rate sensor), fixed to the visor of the head-mounted eye tracker, provided continuous measurement of head movements. In order to reduce slippage of the device, and improve comfort, individually moulded facemasks clipped to the ETD headband were employed. The ETD thus permits online synchronous recording of the binocular eye video sequences and head movement sensor data to hard disk. After completion of each spaceflight, the hard disk with the recordings was returned to the investigators and all measurement sequences were subsequently analysed offline in the laboratory. The spatial and temporal resolution ($< 0.1°$, 200 Hz) permits accurate estimation of Listing's Plane and the 3D VOR. A detailed description of the ETD has been published previously [6].

Calibration of eye movements was performed by evaluation of a sequence of fixations to a set of target dots projected at $\pm$ 8.75° left/right and up/down. The target pattern was generated by a head-mounted laser diode and projected onto a target board affixed to the wall.

### 2.3. Data analysis

The video eye recordings were processed offline using custom-designed software. On a frame-by-frame basis, the centre of pupil was determined by geometric analysis of the binarised eye image. The centre of pupil was determined using the generalised Hough transform, which is insensitive to artefacts such as partial lid closure and shadowing effects. This provided the horizontal and vertical co-ordinates of eye-in-head position. Based on the current centre of pupil, the coordinates of two or more annular extracts (typically 40 deg. arc) within the iris were calculated and their luminance profiles extracted. These polar samples permit calculation of the torsional eye position by calculating the cross correlation function between the current sample and a zero reference [16]. The necessary numerical routines for conversion of image coordinates to Euler angles (respectively Fick coordinates) and the subsequent transformation into quaternions [27] were implemented in the acquisition software.

To calculate *Listing's Plane* the three-dimensional eye position sequence in Fick co-ordinates was transformed into quaternions. A principal components analysis was employed to calculate the best-fit plane for each data set. This provides the elevation, azimuth and thickness of the displacement plane. Examples are illustrated in Fig. 3. Details of the methods are described in Clarke and Haslwanter [8].

For the estimation of the *3D-VOR* co-ordinate frame of reference, the three components of eye movement recorded during the head oscillation trials were desaccaded using order statistic filtering techniques and 5 to 10 cycles of the resultant slow-phase eye velocity was processed.

The orthogonal components of head velocity were obtained from the head tracking rate sensor data. The $3 \times 3$ gain matrices relating head velocity and eye velocity were computed by stepwise least square regression, starting from the main diagonal components.

$$\omega^e = G\omega^h$$

where $\omega^e = (\omega^e_x, \omega^e_y, \omega^e_z)$ and $\omega^h = (\omega^h_x, \omega^h_y, \omega^h_z)$ represent the angular velocity of eye and head respectively. The resultant minimal gain vector is defined as the head angular velocity unity vector $\omega^h$ such that $G\omega^h$ is minimal in the Euclidean norm. An example is shown in Fig. 2.

The data from the preflight recordings were also examined to determine to what extent the MGV and LP coordinate frames of reference prove to be collinear, as a previous report [10] has demonstrated in the monkey.

The examination and test procedures employed were in accordance with the ethical standards of the Ethics

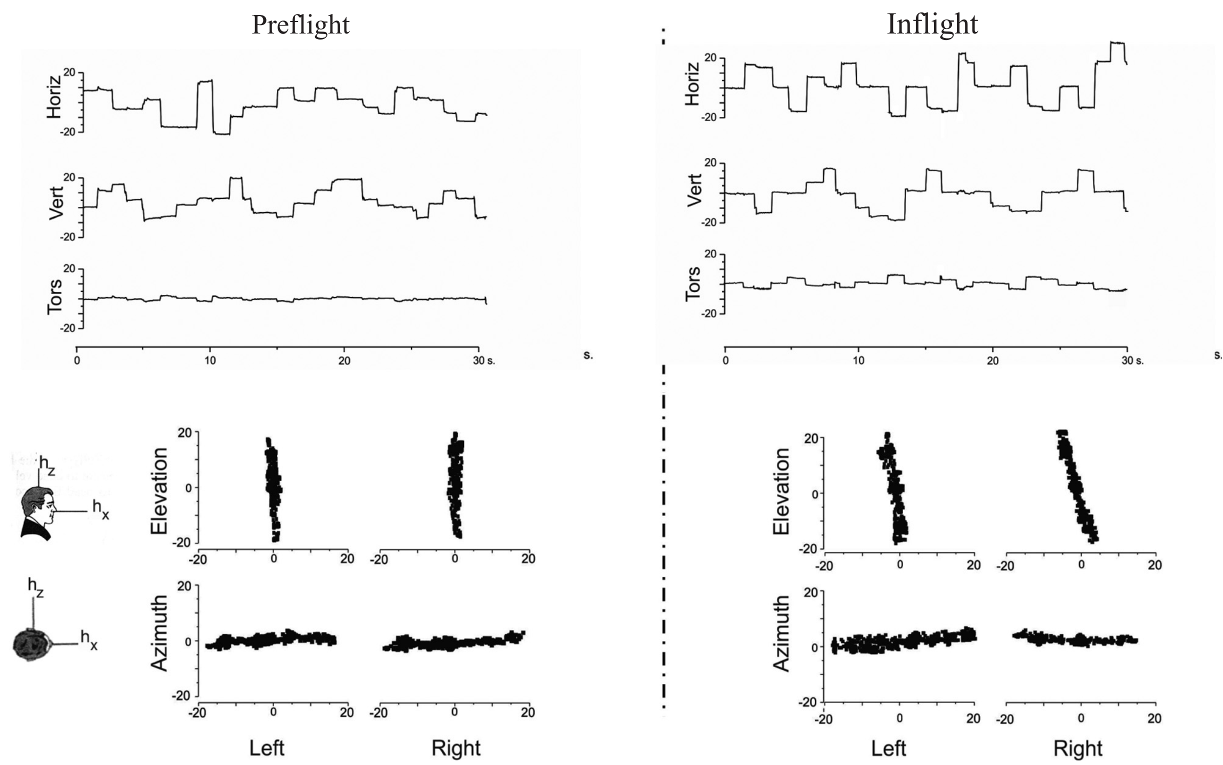


Fig. 3. Top: Examples of three-dimensional recordings (right eye) of saccade sequences from preflight (one-g) and inflight (zero-g) sessions. Bottom: Corresponding LP elevation (X-Z) and azimuth (Y-Z) projections for right and left eyes. Ordinate units are degrees for all plots. The inflight data illustrate the increased torsional component and resultant backward tilt and change in vergence.

Table 1

Comparison of preflight baseline values for the elevation of MGV and LP relative to head coordinates in five spaceflight subjects. For each individual median values were calculated across 3–4 preflight baseline sessions. In turn, the median across subjects yielded a divergence of 21.01°

| Elevation | MGV(°) | LP(°) | MGV-LP(°) |
|---|---|---|---|
| SL1 | 26.5 | 7.1 | 19.5 |
| SL2 | 24.4 | 10.9 | 13.5 |
| SL3 | 30.8 | 9.5 | 21.4 |
| SL4 | 32.6 | 11.6 | 21.1 |
| SL5 | 13.7 | −8.4 | 22.1 |
| Median | 26.5 | 9.5 | 21.1 |

Table 2

Preflight-to-inflight differences in MGV elevation, LP elevation and LP vergence (left – right azimuth). Data from five spaceflight subjects are shown. Median values were calculated across 3–4 preflight baseline sessions and across the available inflight sessions. Postflight values are not included, due to the adaptive modification of the responses during the two-week postflight test period

| | Elevation | | Vergence |
|---|---|---|---|
| | MGV(°) | LP(°) | LP(°) |
| SL1 | −23.1 | 6.5 | −1.7 |
| SL2 | −18.4 | 21.5 | −1.9 |
| SL3 | −20.6 | 14.1 | −1.9 |
| SL4 | −21.3 | 7.5 | −0.3 |
| SL5 | −16.6 | 7.9 | −2.7 |

Committee of the Charité Medical School, Berlin and the Medical Board of the European Space Agency on human experimentation and with the Declaration of Helsinki.

## 3. Results

The elevation of the MGV and LP frames of reference, relative to head coordinates, for each of the five tested subjects are listed in Table 1. The results indicate that in the human, the two frames of reference deviate by approximately 20°.

The preflight and inflight examples from one subject shown in Fig. 3 illustrate the increased torsional component under prolonged zero-g conditions. The corresponding LP projections demonstrate the backwards tilt in elevation and divergence in azimuth observed under zero-G conditions. The individual values are listed in Table 2.

The longitudinal course of the co-ordinate frames of reference of the MGV and LP, as represented by

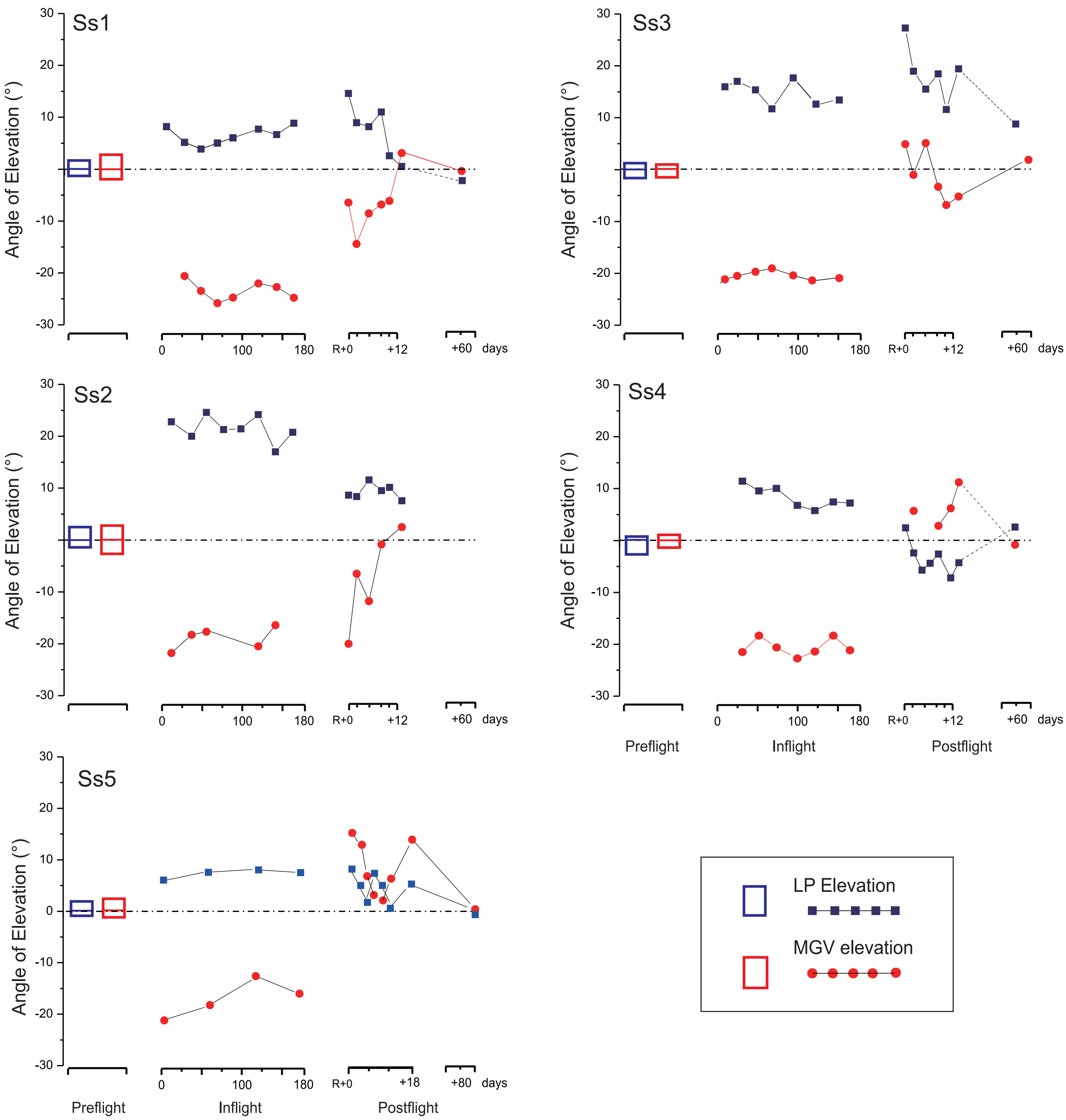


Fig. 4. Longitudinal course of the elevation of LP and MGV as measured in 5 subjects who spent a six-month period on the International Space Station (ISS). For each subject mean values were calculated over the preflight data sets (cf Table 1). For clarity, each plot is normalised to this mean value. The boxes represent + 1sd over the preflight tests. A positive (backward) tilt of LP elevation was consistently observed in all subjects. In contrast a negative (forward) tilt of MGV elevation was observed in all subjects. After return to Earthbound conditions a distinct re-adaptation to preflight values-proceeding over weeks – was observed. (Colours are visible in the online version of the article; http://dx.doi.org/10.3233/VES-130476)

the change in elevation, is shown in Fig. 4 for the five spaceflight subjects tested over a six-month period in microgravity. These demonstrate the consistent forward tilt of the MGV, coupled with the backward tilt of LP. A corresponding change in the LP vergence angle, as determined from the LP azimuth angles was found. These findings are summarised in Table 2, which lists the median values of the preflight-to-inflight differences in the elevation angle of MGV and LP, together with LP vergence. These findings are also reflected in

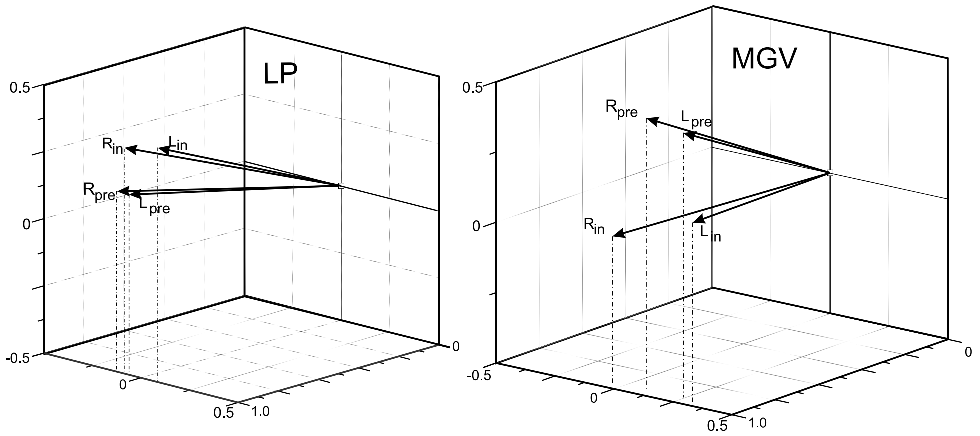


Fig. 5. Illustration of reorientation of LP and MGV in microgravity. Median values for preflight vs. inflight testing, determined across all five subjects are shown as unit vectors, presented in head coordinates. Left: primary positions of right and left eye during preflight and inflight testing. Right: MGV determined for right and left eye data from preflight and inflight testing. The vectors illustrate the opposite reorientation of LP (backward tilt) and the MGV (forward tilt).

Table 3
Statistics for LP thickness for the left and right eyes, calculated within and across subjects. LP thickness is obtained from the best-fit calculation based on the quaternion data during the fixation sequence and after transformation into Listing's coordinates. The data from preflight sessions, respectively 4–8 inflight sessions were averaged. Mean values and standard deviations are presented (all values in degrees)

| Subj No/Eye | Preflight | Inflight | Postflight |
|---|---|---|---|
| SL1 Left | $0.55 \pm 0.06$ | $0.55 \pm 0.03$ | $0.55 \pm 0.04$ |
| SL1 Right | $0.56 \pm 0.14$ | $0.49 \pm 0.03$ | $0.72 \pm 0.06$ |
| SL2 Left | $0.38 \pm 0.05$ | $0.47 \pm 0.04$ | $0.44 \pm 0.01$ |
| SL2 Right | $0.39 \pm 0.13$ | $0.57 \pm 0.07$ | $0.54 \pm 0.11$ |
| SL3 Left | $0.78 \pm 0.02$ | $0.85 \pm 0.03$ | $0.81 \pm 0.02$ |
| SL3 Right | $0.76 \pm 0.10$ | $0.81 \pm 0.06$ | $0.90 \pm 0.03$ |
| SL4 Left | $0.55 \pm 0.07$ | $0.52 \pm 0.03$ | $0.53 \pm 0.04$ |
| SL4 Right | $0.68 \pm 0.12$ | $0.64 \pm 0.06$ | $0.54 \pm 0.05$ |
| SL5 Left | $0.62 \pm 0.04$ | $0.62 \pm 0.02$ | $0.62 \pm 0.02$ |
| SL5 Right | $0.62 \pm 0.05$ | $0.61 \pm 0.03$ | $0.59 \pm 0.02$ |
| Mean | $0.59 \pm 0.13$ | $0.61 \pm 0.13$ | $0.62 \pm 0.14$ |

the MGVs and LP vectors representing the averages across all subjects, as shown in Fig. 5.

This divergence of the two co-ordinate frames of reference persisted throughout the six-month period in microgravity. After returning to Earth, the re-adaptation pattern to one-g conditions fluctuated diversely among subjects, but consistently recovered with a time constant of several days. Testing after 60 days indicates comparable values to preflight.

The calculated LP thicknesses for each of the eyes of the five tested long-term subjects are listed in Table 3. These data demonstrate that LP thickness does not change in microgravity. The difference in values within and across the five tested subjects does not prove statistically significant ($p = 0.12$, Wilcoxon matched pairs test).

## 4. Discussion

As can be seen from the present results, the co-ordinate frame of reference of the 3D-VOR is consistently tilted forward in the absence of the gravity vector. This can be understood as reflecting the absence of the gravity-induced, otolith-mediated component of the VOR during head movements around the roll axis in microgravity; only the canal-induced component persists, i.e. the torsional component is significantly reduced as compared to normal Earth-gravity conditions. This confirms the findings of a previous study [5] where the 3D VOR was examined during prolonged microgravity on the MIR space station.

In contrast to the VOR, the LP recordings from the spaceflight experiments reveal a consistent backward tilt of the LP frame of reference relative to the Earthbound values. This is consistent with the results of equivalent LP measurements performed during the short durations of microgravity available in parabolic flight [8]. After onset of the microgravity phase of each parabolic manoeuvre a backward tilt and a divergence in the azimuth angles of LP was observed. This finding is clearly in contrast to the previous Earthbound studies where only a slight change in LP orientation ($< 2°$) was observed with changes of head pitch position [2,13,20]. Under Earthbound conditions the gravity vector, and its perception by the otolith apparatus, persists regardless of head position. On the other hand, the absence of the otolith-mediated gravity vector in space represents a radical loss for the entire sensorimotor complex. It is proposed that this vector provides a basic reference for the CNS and effectively stabilizes the various mechanism of the sensorimotor complex.

In summary, in contrast to the case of LP where the torsional component during horizontal and vertical saccades and fixations is increased, resulting in a backward tilt, in the case of MGV the reduction of the torsional component, due to the loss of the otolith-mediated contribution to the VOR, results in the observed forward tilt.

The backward tilt of LP observed in microgravity may be interpreted as a disinhibition in the control of torsional eye position. Thus it appears that the otolith-mediated gravity vector has a stabilising, or inhibitory, influence on torsional eye position in the human. Further, the changes in orientation of LP and the 3D-VOR occur directly after removal of the gravity vector, and as such cannot be regarded as an adaptive mechanism. Further the re-orientation of both co-ordinate frames of reference remains throughout the inflight period in microgravity, indicating that no substitute for the gravity vector is made. After returning to one-g conditions, however, a re-adaptation to preflight values was observed in each individual. In comparison to the responses measured during parabolic flight, where no adaptation to 0-g occurs, the re-adaptation observed here proceeded over the postflight, two-week test period and beyond. This observation supports the idea of a CNS adaptation to altered gravity conditions.

The concept of a stabilizing, or inhibitory, function of the otolith afferences is in line with various findings of gravity specific adaptation of the canal-mediated VOR [9,39] and earlier reports of a modulation of velocity storage parameters by the otolith afferences [3, 30,37]. It has been determined that this otolith-canal interaction most likely occurs in the nodulus and uvula [1,37].

This is also supported by clinical evidence from patients with cerebellar lesions in this area, and in whom a gravity-dependent drift component in downbeat nystagmus was determined. It was concluded that lesions in the nodulus and uvula lead to a dysfunction of the otolith-ocular pathways [24]. In a previous report we proposed the concept of an inhibitory function of the otolith afferences on the SCC-driven torsional VOR [7]. The present findings provide evidence that such an inhibitory function assists in the maintenance of LP. Further evidence of such a coupling between the gravity reference and the oculomotor control circuitry is the gravity-dependent bias component on neural signals described by Frens et al. [12] who found that the oculocentric coordinate system is biased in the direction of gravity.

In contrast to the previous study in the monkey [10], where the MGV and LP axes were found to be near collinear to within approximately 2°, the present findings in the human indicate a consistent deviation on the order of 20°. This discrepancy may be due to the fact that active head rotations were performed in the present study, in contrast to the passive rotations performed with the monkey in [10]. It can also be speculated that this difference is due to the differing posture and/or behaviour patterns in the two species.

The thickness of LP did not alter significantly between one-g and zero-g conditions. On first glance this seems to contradict the findings of Diamond and Markham [11] from a previous microgravity study where they reported an increase in the torsional component of eye movement under microgravity conditions. However their analysis yielded eye position relative to head, rather than in Listing co-ordinates. A backward tilt of LP elevation would explain the increased thickness when projected onto a head co-ordinate frame of reference.

It appears that given the lack of voluntary control of ocular torsion, the tonic otolith afferences and the resultant generation of an internal gravity reference stabilise torsional eye position during normal oculomotor tasks. In this sense, the otolith-mediated gravity vector provides for a coupling of the frames of reference of LP and the 3D VOR.

Consideration of the OCR gain per se is warranted here. In an earlier report Leigh et al. [22] demonstrated that those factors that influence horizontal and vertical VOR gain, – visual fixation, the smooth pursuit and optokinetic systems, and mental set – have little or no effect on torsional VOR gain. Similar to reorientations of the head (and eye) around the horizontal and vertical axes, it can be presumed that under natural circumstances the head is actively tilted in order to direct attention to some visual scene. In the case of horizontal or vertical rotation, visual fixation would override the VOR and the eyes would be aligned to the intended target.

On the other hand, since the torsional VOR is not normally cancelled by visual fixation, it would make sense to keep the OCR gain as low as possible so that the meridians of the retina remain aligned as well as possible with the main axes of the intended visual target. In the case of sports and artistic performers, for example, who intuitively keep their head upright, the visual surround would thus be near optimally aligned with the orientation-specific organisation of the visual system so that visual acuity and processing would function most efficiently.

The findings of a recent experimental study [25] demonstrate such an effect during mental rotation tasks. Accuracy proves to be highest when the direction of mental and physical body rotation are congruent. A separate study [38] where subjects were required to update computer displays, reported an improved performance when subjects mentally rotated themselves compared to when they mentally rotated the display. It is postulated that such behaviour results from the so-called "oblique effect", i.e. the fact that visual acuity is highest along the vertical and horizontal meridians of the retina. This "oblique effect" and its neural substrate are well documented in the literature on the visual system (see [23] for review). Of particular interest is the narrow tuning width ( $\pm$ 17°) of those cells in the primary visual cortex sensitive to horizontal and vertical orientations, which matches well with the range of ocular counterroll that occurs during natural head tilting. It follows that a low torsional gain effectively restricts torsional eye position to correspond to this tuning width.

More generally, it appears that the absence of the otolith-mediated gravity vector represents a radical change for the sensorimotor complex. A number of microgravity studies, e.g. [4] have indicated that the entire sensorimotor complex is reliant on the gravity reference, and as such, undergoes adaptive modification during prolonged microgravity in spaceflight. Given the omnipresence of Earth's gravity some authors have postulated that Newton's laws are internalized in the CNS [21,26].

In many natural situations, e.g. during locomotion, the torsional VOR component is useful in correcting for fluctuations of the roll position of the head. All told, this synergy can be regarded as complementing the trade-off between the restrictions to torsional eye position as dictated by Listing's Law and VOR-elicited compensation for head rotations [36]. This is supported by the recent study by Roy and Cullen [32] who present neurophysiological evidence that in the case of the horizontal VOR, gain is altered to be maximal for gaze stabilisation and reduced when the behavioural goal is to redirect visual attention.

Contrary to speculations that the torsional VOR in humans be considered as some evolutionary relic, it is more likely to have resulted from an adaptive process, optimised to accommodate the various sensorimotor requirements of eye and head movement coordination in frontal-eyed species.

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