

Ocular Counter-Rolling During Centrifugation and Static Tilt

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ABSTRACT

Activation of the gravity sensors in the inner ear—the otoliths—generates reflexes that act to maintain posture and gaze. Ocular counter-rolling (OCR) is an example of such a reflex. When the head is tilted to the side, the eyes rotate around the line of sight in the opposite direction (i.e., counter-rolling). While turning corners, undergoing centrifugation, or making side-to-side tilting head movements, the OCR reflex orients the eyes towards the sum of the accelerations from body movements and gravity. Deconditioning of otolith-mediated reflexes following adaptation to microgravity has been proposed as the basis of many of the postural, locomotor, and gaze control problems experienced by returning astronauts. Evidence suggests that OCR is reduced postflight in about 75% of astronauts tested; but the data are sparse, primarily due to difficulties in recording rotational eye movements.

During the Neurolab mission, a short-arm human centrifuge was flown that generated sustained sideways accelerations of 0.5-G and one-G to the head and upper body. This produces OCR; and so for the first time, the responses to sustained centrifugation could be studied without the influence of Earth's gravity on the results. This allowed us to determine the relative importance of sideways and vertical acceleration in the generation of OCR. This also provided the first test of the effects of exposure to artificial gravity in space on postflight otolith-ocular reflexes.

There was little difference between the responses to centrifugation in microgravity and on Earth. In both conditions, the induced OCR was roughly proportional to the applied acceleration, with the OCR magnitude during 0.5-G centrifugation approximately 60% of that generated during one-G centrifugation. The overall mean OCR from the four payload crewmembers in response to one-G of sideways acceleration was 5.7 ± 1.1 degree (mean and SD) on Earth. Inflight one-G centrifugation generated 5.1 ± 0.9 degree of OCR, which was a small but significant decrease in OCR magnitude. The postflight OCR was 5.9 ± 1.4 degree, which was not significantly different from preflight values. During both 0.5-G and one-G centrifugation in microgravity, where the head vertical gravitational component was absent, the OCR magnitude was not significantly different from that produced by an equivalent acceleration during static tilt on Earth. This suggests that the larger OCR magnitude observed during centrifugation on Earth was due to the larger body vertical linear acceleration component, which may have activated either the otoliths or the body tilt receptors. In contrast to previous studies, there was no decrease in OCR gain postflight. Our findings raise the possibility that inflight exposure to artificial gravity, in the form of intermittent one-G and 0.5-G centripetal acceleration, may have been a countermeasure to deconditioning of otolith-based orientation reflexes.

INTRODUCTION

The otolith organs of the inner ear, the utricle and saccule, are the primary gravity sensors of the body. Activation of the otoliths by linear acceleration (including that of gravity) generates various spinal and ocular reflexes that act to maintain posture and gaze. Ocular counter-rolling (OCR) is one example of an otolith-ocular reflex in response to activation of the otoliths. When the head is tilted laterally, the eyes rotate around the line of sight. Termed OCR, this torsion is an orienting reflex that tends to align the eyes with the spatial vertical. During centrifugation, during side-to-side head movements, and while turning corners, the OCR reflex orients the eyes towards the sum of the imposed accelerations from body movements and gravity. For example, when walking or driving around a bend, there is an inward linear (centripetal) acceleration that sums with gravity to create a vector that is tilted into the turn (Figure 1). This is called the gravitoinertial acceleration (GIA) vector. Recent work has shown that rolling the head and eyes towards alignment with this tilted GIA vector plays a role in maintaining balance and gaze when walking around sharp turns.

The semicircular canals in the inner ear, which sense angular acceleration of the head, also induce torsional eye movements during rapid head movements; but these responses are transient. In contrast, otolith-induced OCR responses are sustained during static tilts of the head or the GIA vector, with a gain (amount of ocular torsion/head tilt angle) of approximately 0.1. The magnitude of OCR is related to the angle of head tilt.

Deconditioning¹ of otolith-mediated spinal and ocular reflexes following adaptation to microgravity has been proposed as the basis of many of the postural, locomotor, and gaze control problems experienced by returning astronauts. Consequently, OCR has been used in many postflight studies to gauge the effect of microgravity exposure on otolith function. There is evidence that OCR is reduced postflight in about 75% of astronauts tested; but the data are sparse, primarily due to difficulties in recording torsional eye movements. OCR was reduced in two cosmonauts for 14 days after landing (Yakovleva, 1982). Following the 10-day Spacelab-1 mission, OCR to leftward roll tilts was reduced by 28–56% in three subjects and was unchanged in one subject (Vogel, 1986). Asymmetries in the OCR response to left and right static roll tilts were also observed. OCR was reduced by 57% in one astronaut for five days after the 1992 Russian Mir mission (Hofstetter-Degen, 1993). OCR was also reduced in two subjects during postflight side-to-side oscillations at 0.4 and 0.8 Hz (Arrott, 1986). OCR gain was depressed in four subjects following the two-week SLS-2 mission (Young, 1998). In addition, asymmetries in OCR to left/right roll tilt were observed in all subjects studied on SLS-2. The development of video-oculography (see Moore, 1996, for a review) has led to significant improvements in OCR measurements in humans,

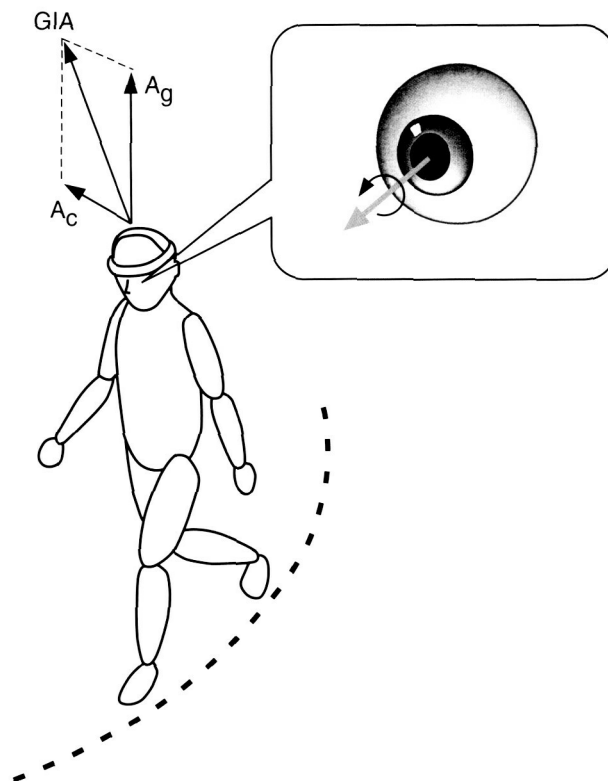


Figure 1. When walking around a turn, there is an inward centripetal linear acceleration, A_c , that sums with gravity, A_g , to form the GIA vector. To maintain balance and gaze during turns, the head, body, and eyes (inset) tend to roll towards alignment with the GIA. Rolling of the eyes around the line of sight towards a GIA vector that is tilted with regard to the head is termed OCR.

compared to the techniques used in the results cited above. OCR gain, measured using video-oculography following a 30-day Mir mission, decreased in one astronaut but increased in two other astronauts who had been in space for 180 days (Diamond, 1998).

Strong evidence for deficits in postflight otolith function was obtained from two monkeys following a 14-day COSMOS mission (Dai, 1994). Torsional eye position was measured postflight using a robust and accurate measure of ocular torsion (search coils). The eye movements were measured both during static roll tilt and during off-vertical axis rotation (OVAR). OVAR presents a sinusoidal linear acceleration stimulus to the otoliths suitable for averaging. There was a highly significant (70%) reduction (>2 SD) in OCR gain, which persisted over the 11 days of postflight testing. In addition, vergence of the eyes, an otolith-mediated response to front-to-back linear acceleration, was also reduced during this 11-day period. Thus, although the data are not entirely consistent, the majority of subjects tested have exhibited a decrease in their OCR response following short-duration missions. In this paper, we present a direct comparison of the OCR responses during preflight, inflight, and postflight centrifugation, as well as during pre- and postflight static tilt.

¹Defined as a decrease in gain of otolith-mediated reflexes.

METHODS

Centrifugation

Four payload crewmembers of the Neurolab STS-90 Space Shuttle mission served as subjects and as inflight operators for this experiment. Over the 16-day mission, the astronauts were exposed to inflight one-G centrifugation on flight days (FDs) 2, 5, 10, 11, and 16. Two crewmembers were also exposed to 0.5-G centrifugation on FDs 7 and 12. Approximately 80% of the exposure to sustained one-G linear acceleration was in the form of centripetal acceleration directed along a line connecting the ears (Figure 2). In addition, subjects underwent centrifugation where the centripetal acceleration was directed along the spine (see technical report by Cohen et al. in this publication). Cumulative flight exposure times to one-G centripetal acceleration were 50 minutes, 62 minutes, 37 minutes, and 62 minutes for the four subjects. Three subjects had their first exposure to centrifugation on FD2, less than 24 hours into the mission. One subject did not experience inflight centrifugation until FD5. In addition, due to mission operational constraints, this subject's exposure time was limited to approximately half that of the other payload crew's.

Baseline one-G data using the same paradigms as in flight were collected at Johnson Space Center in Houston 90, 60, and 15 days prior to launch (L-90, L-60, and L-15) on a centrifuge that was a replicate of the flight centrifuge (see technical report by Cohen et al. in this publication). The same tests were repeated in Houston 24 hours after return (R+1) and on subsequent days (R+2 and R+9). Baseline 0.5-G data were obtained from all four subjects on L-30 and R+4.

In each run, subjects were accelerated at 26 degrees/second² in darkness to a constant angular velocity of 254 degrees/second or 179 degrees/second, which generated a one-G or 0.5-G centripetal acceleration along a line connecting the ears. Subjects were oriented with their left ear facing away from the center of rotation (left-ear-out (LEO)), as in Figure 2A) or right-ear-out (REO). After 65 seconds at constant velocity in darkness, subjects were presented with a centering display dot for 9.5 seconds and instructed to fixate the dot. Eye movement data recorded during this period were used to calculate OCR. Subjects were then decelerated at 26 degrees/second² to rest in darkness either immediately following the center display, or after optokinetic and smooth pursuit stimuli were displayed (not considered in this report). A typical trial consisted of clockwise (CW) LEO centrifugation (facing-motion), counterclockwise (CCW) LEO (back-to-motion), and CCW and CW REO (facing- and back-to-motion). The video eye monitors were calibrated by having the subject fixate on 25 points at known gaze angles prior to the first LEO and REO runs. For a complete description of the methodology, refer to the technical report by Cohen et al. in this publication.

Static Tilt

Full-body static roll tilt was performed in Houston using the tilt mode of the ground centrifuge, and at Kennedy Space Center in Cape Canaveral using a static tilt chair developed at Mount

Sinai Medical Center. After subjects were positioned in the tilt chair and the video system was calibrated, subjects were roll-tilted from the upright (zero degree) to 60 degrees left-ear-down in 15-degree increments. The chair was locked in place at each tilt angle, and after 60-second video images were recorded for approximately 10 seconds while the subject viewed a centering dot on the visual display. This segment was used to measure OCR. Preflight baseline data collection was carried out 60 and 30 days prior to launch (L-60 and L-30) in Houston. Postflight data were obtained on the day of return (R+0) two to four hours after landing at Kennedy Space Center, and in Houston on R+1, R+4, and R+9.

RESULTS

OCR during centrifugation

During constant angular velocity sideways centrifugation (Gy centrifugation), there is a radial inward linear (centripetal) acceleration, A_c , regardless of the direction of rotation (Figure 2A) along a line connecting the ears (the interaural axis). On Earth, the equivalent acceleration of gravity, A_g , is aligned with the head vertical axis. The sum of A_g and A_c , known as the GIA vector, is tilted with respect to the head vertical axis as shown in Figure 2A. Ground-based centrifugation with one-G of centripetal acceleration generated a GIA vector with a magnitude of 1.4-G tilted 45 degrees with respect to the head. As a result, the subjects felt like they were tilted 45 degrees while rotating at this speed on Earth. Gy centrifugation at 0.5-G on Earth generated a GIA magnitude and tilt of 1.1-G and 27 degrees, respectively. In microgravity, however, the gravitational component was negligible, and the GIA was equivalent to the centripetal acceleration; i.e., it was directed along the interaural axis with a magnitude of either one-G or 0.5-G.

Robust torsional movements of the eyes were induced during Gy centrifugation both on Earth and inflight. The OCR was characterized by dynamic and static components (Figure 2C). The dynamic component, shown in Figure 2C, decayed at the onset of constant velocity and was dependent on the direction of rotation (Figure 2D). For example, a LEO CCW angular acceleration (back-to-motion) generated CW torsional eye movements in which the upper pole of the eye rolled to the subject's right. CW rotation (facing-motion) initially generated CCW ocular torsion. Thus, the dynamic component added to the static component of OCR when moving back-to-motion and subtracted from it when facing-motion.

When back-to-motion, ocular torsion developed rapidly during angular acceleration, reaching a maximum of 10 degrees at the onset of constant-velocity rotation before decaying to a steady-state value of approximately six degrees after 10 seconds at constant velocity. During facing-motion centrifugation, the eye initially torqued in the CCW direction then rolled back in the CW direction, reaching a plateau of approximately six degrees following 10 seconds of constant velocity rotation—as it did for back-to-motion centrifugation. Since the OCR had the same polarity for facing- and back-to-motion, the dynamic

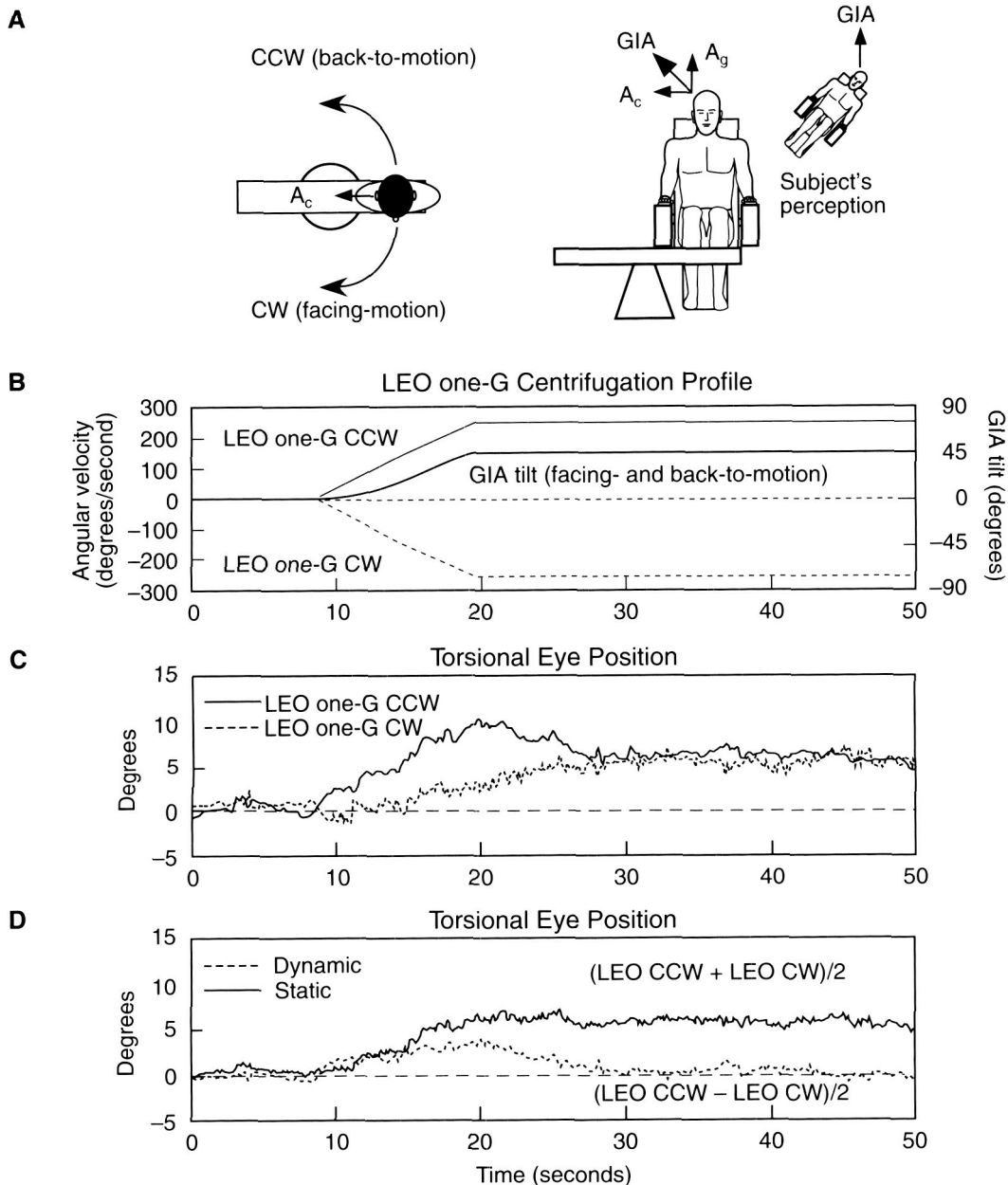


Figure 2. (A) Positioning of the subject for LEO centrifugation, which directs the centripetal linear acceleration along a line connecting the ears (also known as the interaural axis). This sideways acceleration is termed Gy centrifugation. LEO constant velocity centrifugation generates a centripetal acceleration, A_c , that sums with the equivalent acceleration of gravity, A_g , to tilt the GIA vector in the roll plane relative to the subject's head. Subjects tend to perceive the GIA as the spatial vertical, and feel tilted in the roll plane away from the rotation axis (inset). (B) Rotation velocity profiles for LEO back-to-motion (CCW) and facing-motion (CW) centrifugation that generated a one-G centripetal acceleration at steady state and a 45 degree roll-tilt of the GIA. The direction of GIA tilt was CW during LEO centrifugation (from the subject's point of view), regardless of the direction of rotation. During REO centrifugation (not shown), the roll-tilt of the GIA was CCW. (C) Torsional right eye position data from one subject during LEO one-G centrifugation on Earth. During angular acceleration, there was a dynamic ocular torsion component whose direction was dependent on the direction of rotation. Upon reaching constant angular velocity, this dynamic component decayed, and static OCR was generated by the otoliths in response to the tilted GIA. We sampled the OCR magnitude approximately 65 seconds into rotation, long after the dynamic torsional eye movements had ceased. (D) The dynamic and static components of the ocular torsion response could be isolated by superposing the torsional eye position records during facing- and back-to-motion centrifugation. The dynamic torsional response to angular acceleration (dashed trace) reached a maximum at onset of steady state and decayed over the following 10 seconds. The static OCR component (solid trace) rose in a linear fashion with the GIA tilt, reaching a plateau of approximately six degrees at onset of constant velocity. (From Moore, 2001, with permission; reproduced from *Experimental Brain Research*.)

component could be isolated by subtracting the two torsional eye position traces and halving the result (Figure 2D). Dynamic torsional eye position reached a peak of approximately four degrees at the onset of constant-velocity centrifugation and then decayed with a time constant of approximately six seconds. The directional dependence of the dynamic ocular torsion response has previously been observed during on-center rotation and is likely a semicircular canal response.

The static OCR component was generated by the otoliths in response to the tilt of the GIA with regard to the head, reaching a plateau during constant-velocity centrifugation after 10 seconds. In contrast to the dynamic component, static OCR was in the same direction (towards the GIA vector) for a given subject orientation (LEO or REO) regardless of the direction of rotation. This was because the centripetal acceleration, and therefore the GIA tilt, was in the same direction during facing- and back-to-motion centrifugation. The static OCR response was extracted by averaging the facing- and back-to-motion traces, which cancelled the oppositely directed dynamic components. The static OCR response followed the tilt of the GIA, reaching a maximum of approximately six degrees where the GIA tilt reached a plateau of 45 degrees at onset of constant velocity. We obtained our measures of OCR magnitude after approximately one minute of constant velocity rotation, when the dynamic contribution had ceased.

Torsional eye position showed little difference between the responses in microgravity and on Earth (Figure 3). The OCR response was roughly proportional to the applied interaural linear acceleration, with OCR magnitude during 0.5-G centrifugation approximately 60% of that generated during one-G centrifugation. The overall mean OCR response was determined by combining LEO and REO OCR data from the four payload crewmembers (Figure 3). On Earth, one-G Gy centrifugation elicited an OCR response of 5.7 ± 1.1 degrees (mean and SD). During inflight one-G centrifugation there was a small but significant ($p=0.0025$) 10% decrease in OCR magnitude to 5.1 ± 0.9

degree. The magnitude of OCR during postflight one-G centrifugation was 5.9 ± 1.4 degrees, which was not significantly different from preflight values. A similar trend was observed during 0.5-G Gy centrifugation. Preflight centrifugation generated 3.3 ± 0.9 degree of OCR. There was an 11% decrease observed in OCR during inflight 0.5-G centrifugation to 3.0 ± 0.8 degree (mean and SD of two subjects only), but this was not statistically significant. Postflight 0.5-G centrifugation generated a weak but significant ($p=0.02$) increase in postflight OCR to 4.1 ± 1.5 degrees as compared to preflight values.

It is interesting to note that, in contrast with the other three subjects whose responses were symmetrical, one subject developed a marked OCR asymmetry in response to left/right tilts of the GIA during inflight centrifugation. This subject exhibited a significant ($p=0.0002$) 26% decrement in mean OCR inflight relative to preflight values during one-G REO centrifugation, but had only a 7.5% decrease during LEO centrifugation. This asymmetry was maintained after landing. In response to postflight one-G REO centrifugation, OCR magnitude returned to preflight values, but there was a highly significant 28.9% increase relative to preflight ($p=0.0001$) during one-G LEO centrifugation. The asymmetry was also apparent during postflight 0.5-G centrifugation, where the OCR was also larger when in the LEO orientation.

OCR during static tilt

The OCR response was further investigated by tilting the body left-ear-down (LED) in a chair during pre- and postflight testing. Consistent with the centrifugation results, there was no significant change ($p>0.05$) in OCR two to four hours after landing (R+0) and on subsequent postflight test days as compared to preflight values (Figure 4A). It is interesting to note that the magnitude of OCR generated by 45-degree LED static tilt (three to four degrees) was significantly less than that induced by a 45-degree tilt of the GIA during preflight one-G Gy centrifugation (5.7 degrees). Previous studies have suggested that OCR is linearly related to the magnitude of interaural linear acceleration. Our OCR data exhibited a linear relationship with interaural linear acceleration during static tilt (mean of all pre- and postflight data), with a slope of 5.04 degrees/G ($R=0.995$) (Figure 4B). The magnitude of OCR during preflight centrifugation followed this linear relationship, but still had a significantly larger magnitude than for static tilt at an equivalent interaural linear acceleration (0.5-G centrifugation: $p=0.03$; one-G centrifugation: $p=0.01$). During both 0.5-G and one-G centrifugation in microgravity, where the head dorsoventral gravitational component was absent, the magnitude of OCR was not significantly different from that induced by static tilts on Earth with equivalent interaural linear acceleration.

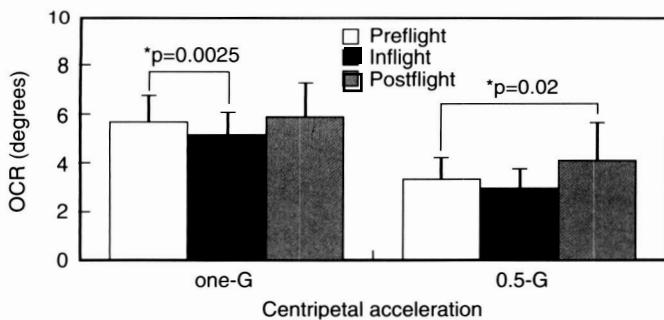


Figure 3. (A) OCR (mean and SD; combined LEO and REO data) of all four subjects. Relative to preflight OCR, there was a significant 10% decrease in inflight OCR but not in postflight OCR during one-G Gy centrifugation. (B) There was a similar inflight decrease in mean OCR during 0.5-G Gy centrifugation, but this did not reach significance due to the small number of inflight subjects ($N=2$). Postflight OCR was slightly but significantly increased during 0.5-G centrifugation from preflight values. (From Moore, 2001, with permission; reproduced from *Experimental Brain Research*.)

DISCUSSION

The OCR reflex in response to sustained interaural linear acceleration induced by Gy centrifugation was essentially maintained in microgravity. In addition, the OCR magnitude was proportional to the magnitude of the applied interaural linear

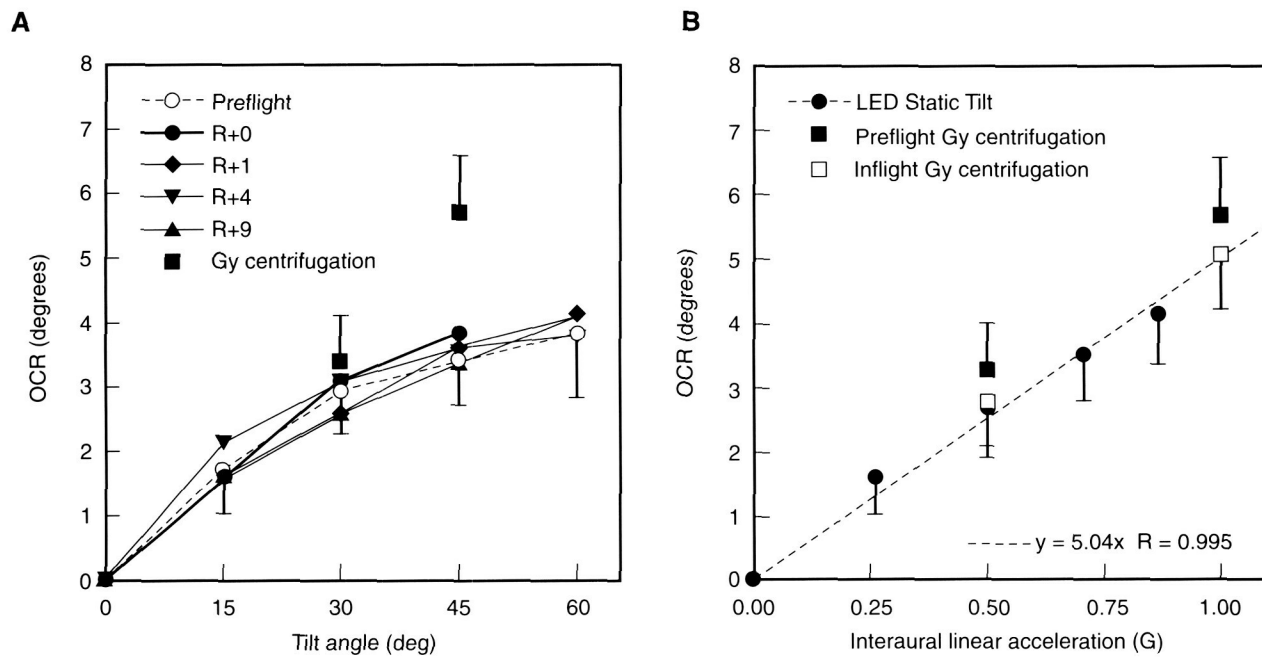


Figure 4. (A) Magnitude of OCR in response to static left-ear-down (LED) tilts during pre- and postflight testing. Each point is mean of the OCR of the right eye of the four payload crewmembers. Consistent with the results of centrifugation, there were no significant postflight changes in OCR on the day of landing (R+0) and on subsequent postflight test days (R+1, R+4, and R+9). The preflight data are the mean of OCR measures obtained 60 and 30 days prior to launch. For clarity, the SD is shown only for the preflight data. Superimposed on the plot is OCR measured during preflight Gy centrifugation (filled squares; mean and SD). OCR measured at a 45-degree static tilt angle was significantly less than that generated by a 45-degree GIA tilt during centrifugation. (B) OCR during LED static tilt (mean and SD of all test sessions) exhibited a linear relationship with interaural linear acceleration (filled circles – dashed line). OCR generated by preflight Gy centrifugation was significantly larger than that induced by a static tilt with equivalent interaural linear acceleration (filled squares). In contrast, there was no difference between OCR produced by inflight Gy centrifugation and by static tilt with equivalent interaural linear acceleration (open squares). This suggests that the larger vertical acceleration component during centrifugation on Earth (i.e., gravity) contributed to the OCR response. (From Moore, 2001, with permission; reproduced from *Experimental Brain Research*.)

acceleration. Mean values of inflight OCR were slightly lower (10%) than preflight values. In contrast to previous studies, there was no significant difference in OCR generated during pre- and postflight testing, suggesting that in the Neurolab astronauts' adaptation to microgravity and re-adaptation to gravity did not alter the gain of OCR. Consistent with this, there was no change in the OCR induced by static tilt before and after flight.

Our finding that preflight OCR during static tilts and Gy centrifugation were approximately linear functions of interaural acceleration up to one-G are in accord with previous studies. Our data are also consistent with findings that Gy centrifugation on Earth generates significantly greater OCR than during static roll tilt with an equivalent interaural acceleration. This difference has been attributed to the larger head vertical linear acceleration (one-G) during centrifugation. Centrifugation in space gave us a unique opportunity to test this hypothesis in that it generated the same interaural linear acceleration as on Earth, but with no head vertical gravitational component. During both 0.5-G and one-G Gy centrifugation in microgravity, OCR was generated with the same magnitude as that induced by static roll tilts on Earth with an equivalent interaural linear acceleration. These data are consistent with the hypothesis that OCR is pri-

marily generated in response to interaural linear acceleration. The increased OCR during terrestrial centrifugation was likely due to the larger vertical linear acceleration, which contributed approximately 10% of the total OCR magnitude. This could be attributed to activation of either the saccules, which lie approximately orthogonal to the utricles, or to activation of the body tilt receptors in response to the larger GIA magnitude during centrifugation.

Although there is some variability, in previous studies approximately 75% of subjects tested have exhibited a decrease in postflight OCR (Arrott, 1986; Diamond, 1998; Hofstetter-Degen, 1993; Vogel, 1986; Yakovleva, 1982; Young, 1998). Our finding—that there was no reduction in postflight OCR magnitude compared to preflight values in all four Neurolab payload crewmembers—raises the possibility that inflight exposure to artificial gravity, in the form of intermittent one-G and 0.5-G centripetal acceleration, may have been a countermeasure to oppose the deconditioning of otolith-based orientation reflexes. The only subject to exhibit signs of alteration in otolith responses—i.e., a substantial asymmetry in OCR to right and left tilts of the GIA—was not centrifuged until five days into the mission, and was exposed to significantly less artificial gravity than the

other payload crew. This subject's OCR asymmetry developed in space and persisted throughout the nine days of postflight testing. Asymmetries in low-frequency otolith sensitivity to roll-tilts of the GIA have previously been observed in astronauts postflight (Vogel, 1986; Young, 1998) and may have a significant impact on postural control, especially when turning corners. If intermittent inflight centrifugation did in fact act to prevent otolith-ocular deconditioning, the results suggest that any countermeasure effect may be reliant on early and/or cumulative exposure to artificial gravity.

Acknowledgements

We gratefully acknowledge the efforts of the payload crew, Drs. Rick Linnehan, Dave Williams, Jay Buckley, and Jim Pawelczyk, for serving as subjects and operators during the mission; the alternate payload specialists, Drs. Alex Dunlap and Chiaki Mukai; Dr. Mel Buderer, Dan Harfe, Gwenn Sandoz, and Nasser Ayub (JSC); Jacqui Van Tweste (KSC); Mike Cork and Dr. Thierry Dewandre (ESA/ESTEC); and Frederic Bellossi (Aerospatiale). Supported by NASA Contract NAS 9-19441 (Drs. Cohen, Moore and Raphan) and the Centre National d'Etudes Spatiales (Dr. Clément).

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