Image Cover Sheet

CLASSIFICATION UNCLASSIFIED	**SYSTEM NUMBER** 152604

TITLE

DYNAMICS OF TORSIONAL OPTOKINETIC NYSTAGMUS UNDER ALTERED GRAVITOINERTIAL FORCES

System Number:

Patron Number:

Requester:

Notes:

DSIS Use only:

Deliver to:

Exp Brain Res (1995) 102:511–518

ORIGINAL PAPER

Bob S.K. Cheung · Ken E. Money · Ian P. Howard

Dynamics of torsional optokinetic nystagmus under altered gravitoinertial forces

Received: 25 July 1993/Accepted: 8 August 1994

Abstract The purpose of the present study was to investigate the influence of varying gravitoinertial forces on torsional optokinetic nystagmus during parabolic flights. Using the scleral search-coil technique, we measured the gain and phase lag of torsional optokinetic nystagmus (OKN) induced by a hemispherical visual display rotating about the roll axis either at constant velocity or sinusoidally at various frequencies during level flight, hypogravity, and hypergravity. Compared with level flight, there was a significant increase in slow-phase eye velocity during hypogravity and an increase in nystagmic frequency. An absence of well-developed torsional optokinetic afternystagmus was observed in all three gravity conditions. Other characteristics included a lack of a slow rise component. These data suggest that otolith inputs do affect torsional OKN. The absence of well-developed torsional optokinetic afternystagmus suggests that the velocity storage pathways do not contribute significantly to the torsional OKN system in humans.

Key words Nystagmus · Torsion
Torsional optokinetic nystagmus · Parabolic flights
Eye movements · Human

Introduction

When a person views a moving display, the eyes automatically execute a series of pursuit movements interspersed with saccadic returns. This alternating series of slow and quick movements is known as optokinetic nystagmus (OKN). The movements can occur around a horizontal axis (vertical optokinetic nystagmus) or a vertical axis (horizontal optokinetic nystagmus), or around the visual (roll) axis, in which case they are called torsional optokinetic nystagmus (TOKN). In normal circumstances OKN is evoked by image motion associated with movements of the head and thus is accompanied by an appropriate vestibulo-ocular response.

There is considerable evidence that the otoliths are involved in the optokinetic system. Buizza et al. (1980) have demonstrated that if a subject is presented with a constant-velocity optokinetic stimulus, lateral acceleration causes a direction-nonspecific increase in OKN slow-phase velocity. Surgical removal of the utricle and saccule decreases the gain of horizontal OKN (Takahashi et al. 1977) and significant improvement of the slow-phase eye velocity of vertical OKN in the monkey was observed (Igarashi et al. 1978). The finding that the gain and time constant of downward OKN are influenced by head position suggests that activity arising in the otolith organs exerts an effect on the discharge time constant of the velocity storage mechanism for nystagmus (Matsuo and Cohen 1984) A downward shift of the beating field of vertical OKN and a reversal of vertical OKN asymmetry was observed during microgravity generated by parabolic flights and space flight (Clement et al. 1986). More recently, studies of three-dimensional aspects of velocity storage suggested that the mechanism is modified by the action of gravity on the otolith organs (Dizio and Lackner 1992; Wei et al. 1994).

Although horizontal and vertical OKN have been well studied, continuous TOKN has not been studied until recently. Cheung and Howard (1991), using the scleral search-oil technique, were able to measure the gain and phase lag of optokinetic torsion induced by stimuli rotating at constant velocity and by stimuli oscillating sinusoidally at various frequencies about the roll axis. In addition, Morrow and Sharpe (1989) reported that there were no significant differences in TOKN

B.S.K. Cheung (✉)
Defence and Civil Institute of Environmental Medicine,
1133 Sheppard Avenue W., P.O. Box 2000, North York,
Ontario, Canada, M3M 3B9

K.E. Money · I.P. Howard
Human Performance in Space Laboratory,
Institute for Space and Terrestrial Science, Room 103,
Farquharson Building, York University, 4700 Keele Street,
North York, Ontario, Canada, M3J 1P3

DCIEM No. 93-27

provoked by constant velocity stimulation in the upright and supine positions. Measurement of ocular torsion during constant optokinetic stimulation about the roll axis in the course of parabolic flights indicated that, in some subjects, ocular torsion shifted markedly in the direction of field motion when the subject reported the onset of vection (Young et al. 1981). However, the method employed does not have the sampling rate to measure slow-phase velocities nor to see all the high-frequency components of the induced torsion (T.A. Crites, unpublished work). Ocular torsion associated with large-field optokinetic stimulation was measured in Spacelab 1 (Young et al. 1986); however, it is inconclusive that there was an enhancement of TOKN after a few day's adaptation in microgravity.

It has been hypothesized that gravitoinertial force (Gz) initiates an otolith-ocular response that manifests itself primarily in the modulation of OKN slow-phase velocity. Evidence for this hypothesis stems from lesion experiments in the monkey, as previously described (Takahashi et al. 1977; Igarashi et al. 1978). This study investigates the effect of increased dependence on visual input to TOKN. Under normal gravitational conditions, a standing or seated subject with the visual field rolling clockwise about the visual axis would tend to respond as if the body were rolling counterclockwise. However, otolithic information would indicate that such a bodily roll was not taking place, since the direction of gravity relative to the head would not be changing. The otolith input would contradict the visual input. It has been reported that during the microgravity phase of the parabolic flight, subjects experienced strong self-rotation, sometimes paradoxical and often continuous (Young et al. 1986; Cheung et al. 1990). Our hypothesis predicts that, on entering microgravity, the lack of contradiction of the visual input by the otolith could also lead to enhancement of optokinetic effects.

Materials and methods

Parabolic flight profile

A NASA KC-135 aircraft was flown in a parabolic path to generate alternating periods of microgravity 0.02–0.03 *g* (along the *z*-axis of the aircraft) at the tops, lasting about 20 s, and 1.4–1.8 *g* during the pull-ups, lasting 38 s. Ten parabolas were flown in succession, followed by a 5-min break. This manoeuvre was repeated until 40 parabolas were flown. The parabolic flight induced a change in the magnitude of the Gz vector acting at right angles to the floor of the aircraft. The change in this vector is directed mostly along a seated subject's spinal axis.

Subjects

Seven men and one woman ranging in age from 23 to 57 years, without prior history of neurologic or otologic disease, participated in the study. All had passed the USAF class III physical requirements test and received high-altitude indoctrination as a prerequisite for the parabolic flights. All but two of the subjects had previous experience in parabolic flight manoeuvres. Two of the subjects are myopic (less than 4 diopters); however, they were able to see the fixation point using corrective lenses on the non-recording (left) eye.

For some subjects, parabolic flights could induce motion sickness symptoms such as nausea and vomiting. The rotating visual field tends to heighten this discomfort. Two of the subjects premedicated themselves with 0.4 mg of scopolamine and 5 mg of dextroamphetamine sulphate (Dexedrine), the standard anti-motion sickness treatment recommended by NASA for the parabolic flight.

Visual stimulus

Randomly spaced black circular discs of 3.8 cm and 1.9 cm in diameter covered the inside surface of a white translucent plastic sphere 61 cm in diameter. Subjects were instructed to look into the sphere through a circular opening as shown in Fig. 1. The ratio of black to white area was approximately 25%. The display was trans-illuminated at a contrast of 95% and the mean luminance of the white background was 18 cd/m^2, of the black discs $<$ 1 cd/m^2. A small red disc in the centre of the display served as the fixation point, 51 cm from the subject's right eye. The sphere was rotated about a horizontal axis passing through the fixation point and a point midway between the subject's eyes (the sphere rotated about the subject's roll axis).

Eye movement recordings

Torsional eye movements were recorded by the electromagnetic scleral search-coil technique with phase-locked amplitude detection (Robinson 1963). The system employed was identical to that used in a previous experiment investigating ocular counter-rolling during microgravity (Cheung et al. 1992) . The subject was seated upright, facing the front of the aircraft, and restrained on the floor at the centre of a cubic frame containing vertical and horizontal induction coils 1 m in diameter (CNC Engineering, Seattle, Wash.). A scleral annulus designed for measuring horizontal, vertical and torsional eye movements (Skalar Medical, The Netherlands) was placed on the right eye during level flight, after topical anaesthetic (0.5% of proparacaine hydrochloride was applied. During the experiment, the subject was positioned so that his/her right eye was approximately at the centre of the magnetic field-generating coils and the subject's head was immobilized by a den-

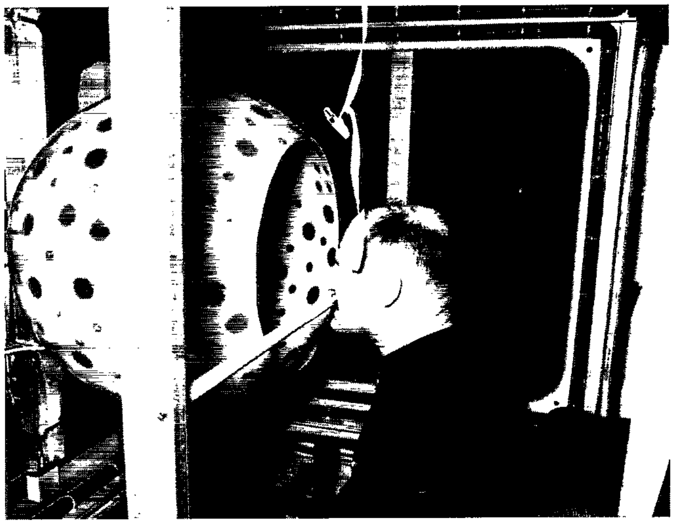


Fig. 1 Apparatus to induce torsional optokinetic nystagmus in flight. Subject was seated upright, facing the front of the aircraft, with his head immobilized by a dental bite-bar attached to the horizontal rod

tal bite-bar, as shown in Fig. 1. The subject viewed the stimulus binocularly and recordings were made monocularly from the subject's right eye.

Each search coil was calibrated horizontally, vertically and torsionally by mounting it on a protractor device which could be rotated about each of the three orthogonal axes. We checked the deviation of the torsional signal from linearity and symmetry. Within a radius of 7.5 cm from the centre of the magnitude field-generating coil, less than 1% variation for angles of torsion up to 30° was observed. The precision of the scleral coil system was investigated in our laboratory and reported in a previous article (Cheung et al. 1992). The absence of significant slippage of the annulus on the eye around the torsional axis was checked after each stimulus condition to make sure that there was no drift in the zero position. Any significant slip would have appeared as discontinuities in the recordings and irregular changes in the zero position.

Since the torsion-sensitive scleral annulus is not as flexible as the standard annulus, only subjects with satisfactory adherence were used. Once mounted, the annulus had no tendency to loosen and could not be shifted or rotated on the eye unless deliberately by mechanical means. At the beginning of each session, the subject was asked to gaze at the fixation point, to ensure that the scleral annulus stay within the acceptable range of previously calibrated zero. In the event of a large deviation, the scleral annulus was rotated until the zero offset matched the previously calibrated position. Eye movements were recorded simultaneously on polygraph paper and onto a TEAC PCM recorder for later analysis. In addition, horizontal and vertical eye positon were monitored on the strip chart recorder.

Procedure

We conducted the experiment during level flight and repeated it during the parabolic manoeuvres. In the first part of the study the visual stimulus was rotated at three different constant velocities and two directions of rotation: 30°/s clockwise (cw), 30°/s counterclockwise (ccw), 45°/s cw, 45°/s ccw, 60°/s cw and 60°/s ccw. For each rotation, torsional eye movements were recorded for 20 s. Visual stimulus was provided for the first 15 s, the subject was asked to close their eyes for the next 5 s, and the light was turned off. In the second part of the study, sinusoidal optokinetic stimulation was applied at frequencies of 0.2 Hz, 0.5 Hz, 1.0 Hz, 1.5 Hz and 2.0 Hz, all at a fixed total amplitude of 20°. The subjects were instructed to close their eyes until the simulus reached the prescribed velocity or frequency of oscillation. During the recording period, subjects were instructed to refrain from blinking to the best of their ability. During level flight, each of the stimuli lasted 60 s (approximately the time from the beginning of the microgravity phase in one parabola to the beginning of the microgravity in the next parabola). For the parabolic flight period, each stimulus began at the beginning of a microgravity phase: visual stimulus was provided for the first 15 s and then the subjects were instructed to close their eyes for the next 5 s the light was turned off, and the rotation of the stimulus was terminated. The subjects were instructed to keep their eyes closed until the pull-out. This sequence was repeated during the hypergravity phase, the stimulus was provided for the first 15 s and terminated for the next 5 s.

Data-analysis

Eye position and the position signal of the visual stimulus were recorded on a strip chart recorder and a TEAC pulse-code-modulated recorder simultaneously. Analog eye position signals were digitized off-line onto a Masscomp computer, sampling at a rate of 100 Hz/s, digitized with 12-bit precision over a 30° peak-to-peak range, using ±5 V/channel. Digitized data were then displayed on a graphics monitor for review and subsequent analysis. The fast components or saccades were identified by their direction and characteristic velocity profile and discarded. Velocity of each slow phase was calculated with an algorithm which selected and analysed the slope of each eye position (slow-phase eye velocity) over a continuous period of nystagmus of 15 s. The slow-phase velocity averaged over 15 s and its standard deviation was then calculated and expressed as gain. The TOKN gain was computed as the ratio between the mean slow-phase eye velocity and the velocity of the visual stimulus. The overall reliability was checked with calibrated signals and also compared with graphical analysis by hand. The statistical significance of the microgravity effect was tested by analysis of variance. For the sinusoidal data, after fast components were identified and removed, the gaps in the remaining slow-phase eye velocity were filled by connecting points on each side of the segment with a quadratic regression line. Fast-Fourier transform was performed, giving the magnitude and phase of the fundamental and first two harmonics. All measurement were based on an average of at least 2 cycles with less than 10% harmonics distortion. The gains were calculated as peak eye velocity/peak stimulus velocity.

Results

In parabolic flight, an ideal free fall provides very low relative accelerations. However, the ideal is rarely achieved, even at the centre of gravity of the aircraft. Unexpected accelerations could act on the aircraft throughout the free-fall phase owing to air turbulence, and uncontrolled accelerations could also result from perturbations in manual control of the aircraft. Disturbances from the ideal free fall occurred in all three axes and measurement revealed that the accelerations during our free falls were 0.03–0.04 *g* vertically (*z*-axis), 0.005–0.02 *g* longitudinally (*y*-axis), and approximately 0.01 *g* laterally (*x*-axis; Tryggvason 1991).

Figure 2 illustrates a typical recording of the acceleration level in the *z*-axis. The microgravity phase lasts 20 s and the hypergravity phase lasts 38 s. However, the magnitude of the hypergravity experienced had a much greater variability, from 1.7–1.8 *g* during the smoothest

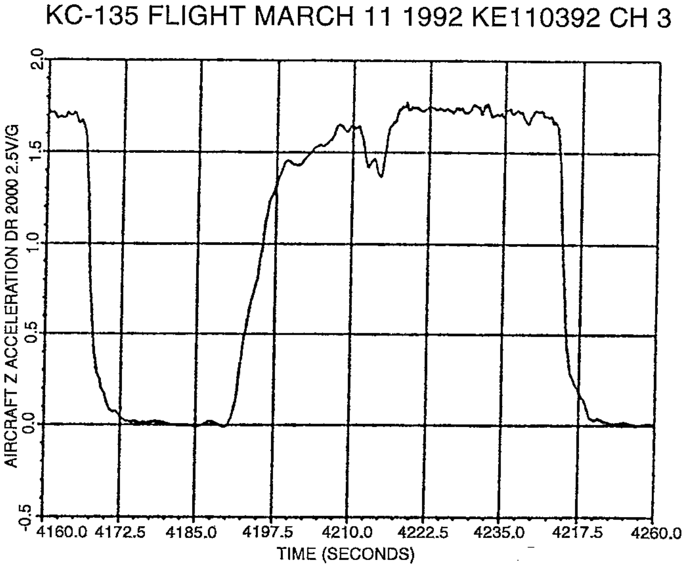


Fig. 2 Gravitionertial acceleration profile of the KC-135 flight during parabolic manoeuver

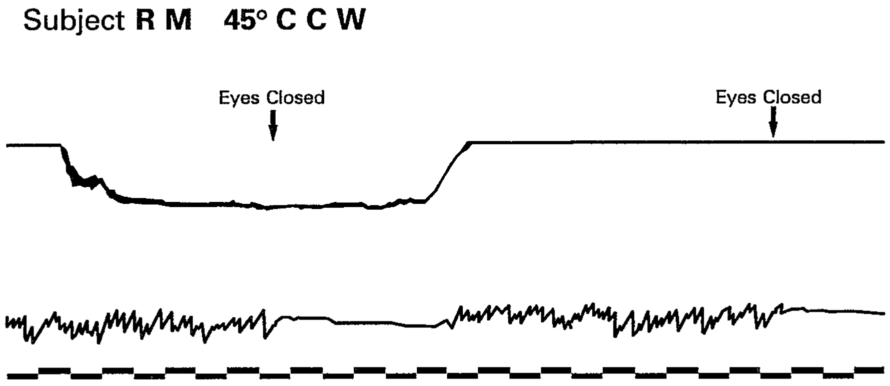


Fig. 3 Representative tracings of eye position (*middle trace*) versus time (*lower trace*) during a parabolic manoeuvre (45° counter-clockwise) in subject R.M. under constant-velocity stimulation

10–20 s. The investigation of ocular torsion under hypergravity might be done better under sustained Gz in a centrifuge.

Our subjects were located towards the back of the cabin at 5 m from the centre of gravity of the aircraft. The constant rate of translation could be calculated as follows. The microgravity phase starts at 30° above the horizontal during pull-up and ends at 30° down, for a change of 60° in 20 s or 0.052 radians/s. At 5 m the centripetal acceleration is therefore approximately 0.0013 g, an acceleration that will be hidden in the disturbance (noise) that occurs naturally in a non-ideal free fall. Under this condition the canal stimulation was also insignificant.

Owing to motion sickness in one subject and the slippage of the scleral annulus in another, their data were not included in the analysis. Coincidentally, these two subjects were the only two that were premedicated (with scopolamine and dexedrine).

Constant-velocity stimulation

The torsional nystagmus was symmetrical; there was no significant difference in the gain measured between clockwise and counter-clockwise directions. We took the mean of the data from clockwise and counter-clockwise direction in our analysis. There was no slow-rise component in TOKN; the peak torsional velocity was achieved within 500–600 ms of stimulus onset. When the eyes were closed and the light was off, there were no indications of torsional optokinetic afternystagmus (OKAN), except in one subject with a slight but not measurable variation (Fig. 3).

Figure 4 shows the plot of slow-phase eye velocity versus time in one subject with a stimulus velocity of 30°/s under all three gravity conditions. The peak velocity in this subject is 4.9%, 2.9% and 2.8°/s for microgravity, level flight and hypergravity, respectively. For this subject, the mean slow-phase velocities were 4.21°/s ±0.25 for level flight and 2.4°/s ±0.21 for the hypergravity phase. Similar results were obtained for the rest of the four subjects. We did not observe significant variation in the measurements from different epochs of the eye movement recording of 15 s. Owing to the time constraints, we did not have the opportunity to repeat each trial condition within the same subject.

During microgravity the mean slow-phase eye velocities under constant-velocity stimulation were 3.93°/s, 4.23°/s and 4.20°/s for stimulus velocities of 30°/s, 45°/s and 60°/s, respectively. We compared the gain of TOKN under different gravity conditions by averaging the

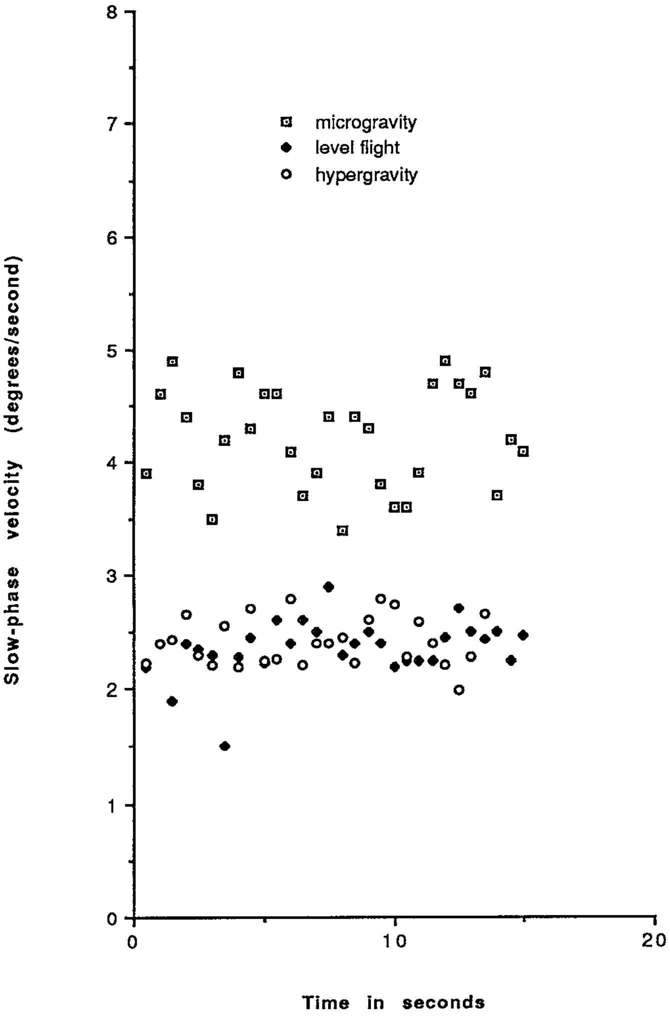


Fig. 4 Plot of slow-phase eye velocity versus time in one subject with a stimulus velocity of 30°/s under three gravity conditions

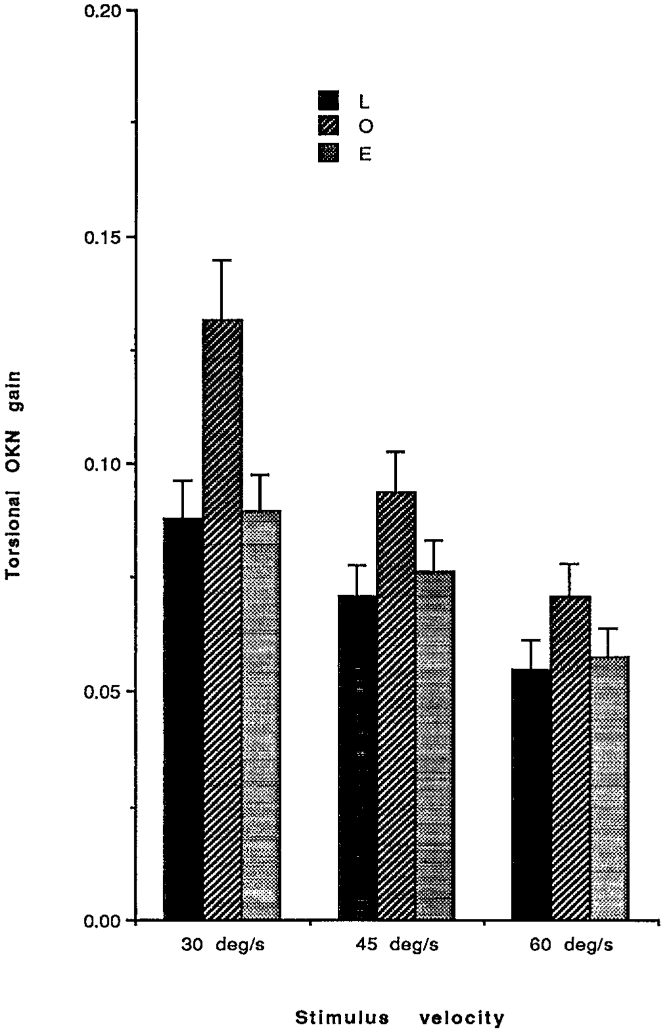


Fig. 5 Mean gain of torsional optokinetic mystagmus versus stimulus velocities during level flight (*L*), hypogravity (*O*) and hypergravity (*E*). There were no significant differences observed between level flight and hypergravity

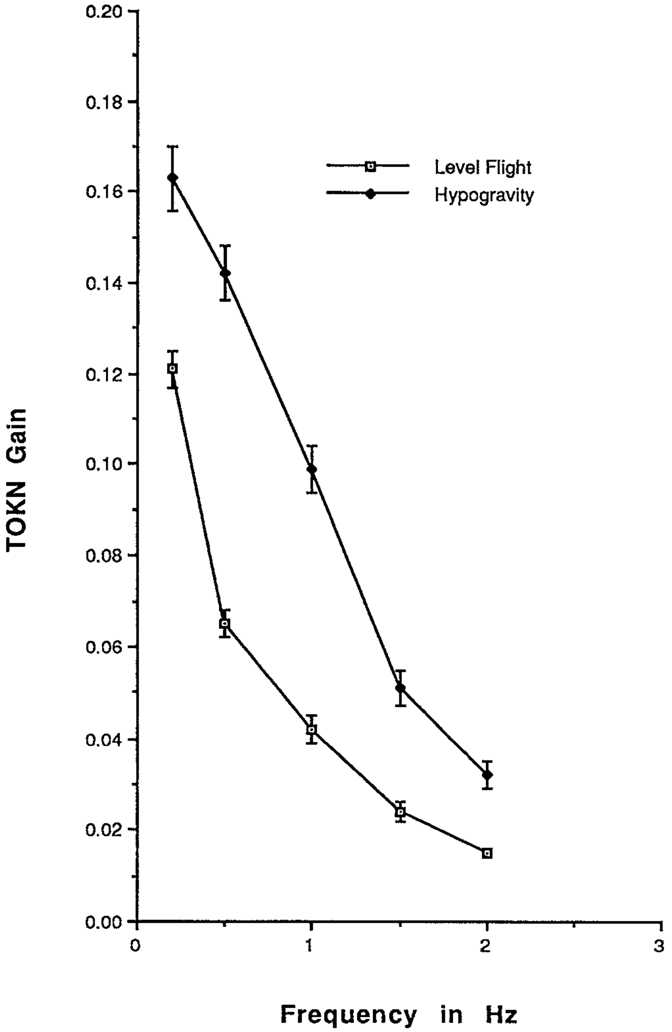
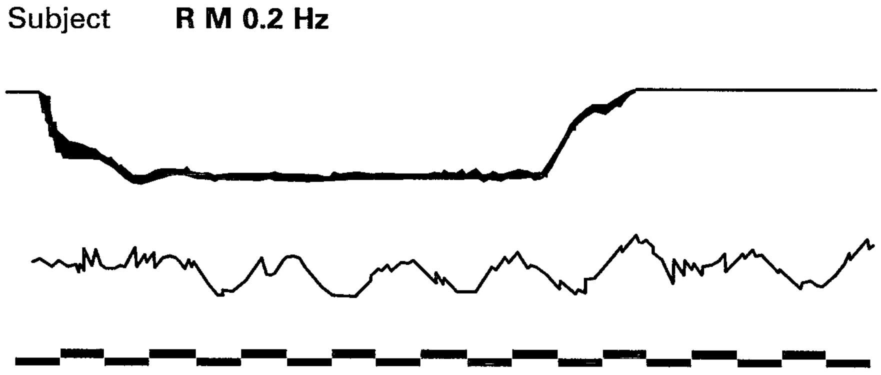


Fig. 7 Mean gain of torsional optokinetic mystagmus (*TOKN*) under various frequencies of sinusoidal stimulus motion (mean of clockwise and counter-clockwise rotation) and a fixed amplitude of 20°

slow-phase velocity obtained from all subjects under each gravity conditions and dividing by the given stimulus velocity. The gain of torsional nystagmus obtained from constant-velocity optokinetic stimulation was greater in microgravity than in the normal 1 *g* conditions. During level flight the mean gains were 0.088, 0.07 and 0.055 for 30°/s, 45°/s and 60°/s, respectively. In microgravity, the corresponding mean gains were 0.131, 0.094 and 0.07 (Fig. 5). Analysis of variance repeated measure revealed that TOKN gain increases in micro-

Fig. 6 Representative tracings of eye position (*middle trace*) versus time (*lower trace*) during a parabolic manoeuvre in subject R.M. under sinusoidal stimulation of 0.2 Hz



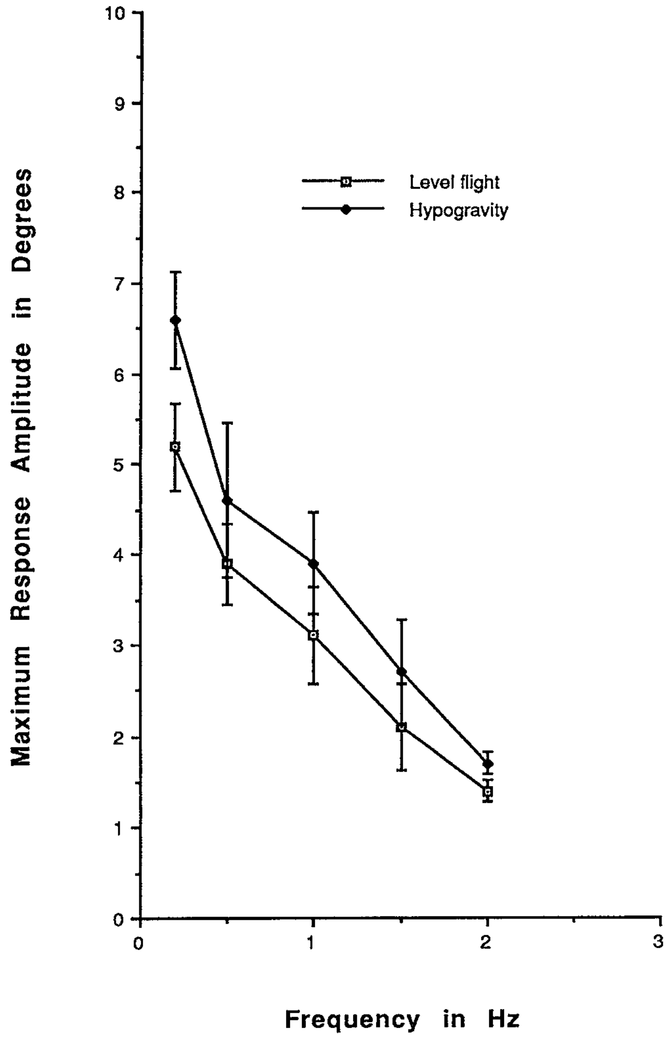


Fig. 8 Maximum response amplitudes versus frequencies of sversusinusoidal stimulus motion during level flight and hypogravity. Response amplitude increased with increase in stimulus amplitude, but dod not reach significance

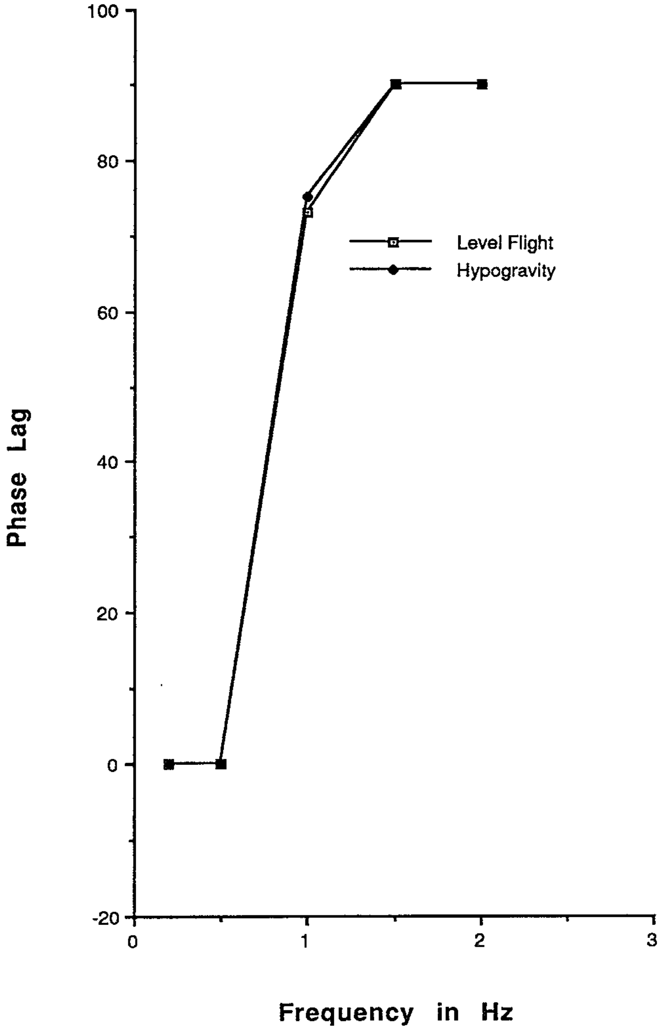


Fig. 9 Phase shift versus frequencies of sinusoidal stimulus motion. Phase lag became noticeable from 1.0 Hz

gravity were significant ($F_{2,10}=12.93$, $P<0.001$). Under all gravity conditions, torsional eye velocity decreased with increasing stimulus velocity, but the ratio of eye velocity to stimulus velocity (gain) was consistently greater in microgravity.

The mean gain calculated from the first 20 s of hypergravity did not differ significantly from the level flight data (Fig. 5). All subjects experienced a sensation of self-rotation about the roll axis for some of the time during the optokinetic stimuli in level flight, and also a paradoxical sensation of body tilt. However, some subjects reported a sensation of continuous self-rotation in roll during the microgravity stimulation.

Sinusoidal stimulation

A representative tracing of eye position in one subject during sinusoidal oscillation of the stimulus is shown in Fig. 6. The gains averaged across subjects for each frequency are plotted in Fig. 7. As expected, the gains using sinusoidal stimulation are higher than those obtained from constant-velocity stimulation. Under all gravity conditions, means gain decreased and the maximum response amplitude also decreased as the stimulus frequency increased (Fig. 8). For most subjects, the eye motion and stimulus motion were in phase at 0.2 Hz and 0.5 Hz, and phase lag became noticeable from 1.0 Hz onwards (Fig. 9). The gains were consistently greater in microgravity than in level flight. Under both visual stimulus conditions, the horizontal and vertical eye positon were also monitored throughout the optokinetic stimulation, and there were no indications of slow-phase eye velocity outside the "roll" plane of visual stimulation (no evidence of cross-coupling of eye movements to other axes). Also there was no evidence of afternystagmus in any of the three planes.

Discussion

Previous studies of horizontal OKN have revealed that, for a step increase in visual-surround velocity there is a quick rise in slow-phase eye velocity followed by a slow rise to a steady state level (Howard 1982). In TOKN under all gravity conditions, there was no slow-rise component; the peak torsional velocity was achieved within 500–600 ms of stimulus onset. This observation is consistent with our previous study of the dynamics of TOKN on the ground (Cheung and Howard 1991) and consistent with previous findings by Morrow and Sharpe (1989). The gain of TOKN is small compared with those of horizontal and vertical nystagmus.

Our data show that under constant velocity and sinusoidal stimulation there is a higher gain of TOKN in microgravity than in level flight. There is an obvious interpretation of these data. On entering microgravity there is no downward force acting on the otolith, and the lack of contradiction of the visual stimulus by graviceptors might be expected to result in a more vigorous TOKN. However, it has been found that under 1 *g* condition, there is no increase in TOKN as induced by constant-velocity rotation upon assuming a supine versus upright posture (Morrow and Sharpe 1989). This result appears to contradict the interpretation of our present findings, as one would expect that in the supine position the visual stimulus axis is coincident with the gravity axis (the sphere is rotated about the optic axis, *x*-axis, with the subjects looking straight up at the centre of rotation), the visual, semicircular canal, otolithic and somatosensory activity patterns are consistent with self-rotation or with visual motion about the same axis. However, previously unreported observations on TOKN induced by constant velocity and sinusoidal stimulus in the supine and upright positions in our laboratory were ambiguous. In two subjects, the TOKN gain in the supine position was significantly higher than in the upright position, but there was no significant difference in two other subjects. It should be emphasized that the gravity conditions of the parabolic flight study and the laboratory study were very different; in the supine position only the direction of the gravitational force relative to the head was altered, whereas at the height of the microgravity phase, the gravity level (Gz) was reduced to 0.02–0.03 *g*.

There were no significant differences observed between the slow-phase velocities in hypergravity and those in level flight. The strength of the otolithic influence on TOKN could be at its maximum at 1 *g*, so that any level over 1 *g* does not exert further effect. However, extreme care should be taken in the interpretation of the hypergravity data, because, as mentioned, the magnitude of acceleration due to gravity varies during the hypergravity phase, and even the peak level of hypergravity varies from one parabola to the next, making it difficult to compare with the data obtained from 20 s of microgravity and 20 s of level flight (1 *g*). The investigation of TOKN under hypergravity would be best served if the study were conducted under constant Gz in a centrifuge with a large radius.

OKAN is thought to reflect the discharge of neural activity from “a velocity storage mechanism” in the brain stem, which has been charged up during optokinetic stimulation (Cohen et al. 1977). Previous studies have presented evidence that otolith-mediated activity can be coupled to velocity storage in humans (Lafortune et al. 1989). A common velocity storage integrator is utilized in OKAN and post-rotatory nystagmus. The velocity storage can be activated by semicircular canal, otolithic and visual inputs, and it is capable of storing information to produce compensatory eye movements in a wide range of planes (Raphan and Cohen 1985). A recent study (Dizio and Lackner 1992) showed that horizontal OKAN and vestibular nystagmus both showed no effect of the level of acceleration due to gravity on their intitial or peak slow-phase velocities, but their decay rates were quicker in 0 *g* and 1.8 *g* than in 1 *g*. Vertical vestibular nystagmus also showed no effect of level of acceleration due to gravity on peak velocity but decayed faster in 0 *g* relative to 1 *g*. These findings indicated that the effective decay rate and three-dimensional organization of velocity storage are dependent upon body orientation relative to gravity and also are influenced by Gz level (Dizio and Lackner 1992). In monkeys, optokinetic stimulus which is not aligned with gravity elicits afternystagmus which shifts away from the stimulus axis towards the gravitational vertical (Raphan and Cohen 1988). The result of this study confirmed previous conclusions (Morrow and Sharpe 1989; Cheung and Howard 1991) that the absence of well-developed torsional OKAN and the lack of a slow-rise component under all gravity conditions indicate that the velocity storage mechanism does not contribute significantly to the TOKN system in humans. It appears that the underlying mechanisms of velocity storage and otolithic modulation of the storage could be complex and that the effects of variations of level of acceleration due to gravity on velocity storage are limited to the plane of stimulation.

It has been suggested that the velocity of image slip across the central retina produced by eye torsion is much less than that produced by vertical or horizontal ductions (Melvill-Jones 1966). In this study, we have provided further evidence of the otolithic influence on the optokinetic system. The different effects on horizontal, vertical and torisonal eye movements could be due to the directional characteristics of vestibular and visual interaction relative to the direction of gravity.

References

Buizza A, Leger A, Droulez J, Berthoz A, Schmid R (1980) Influence of otolithic stimulation by horizontal linear acceleration on optokinetic nystagmus and visual motion perception. Exp Brain Res 39:165–176

Cheung BSK, Howard IP, Money KE (1990) Visually induced tilt during parabolic flights. Exp Brain Res 81:391–397

Cheung BSK, Howard IP (1991) Optokinetic torsion: dynamics and relation to circularvection. Vision Res 31 (7, 8):1327–1335

Cheung BSK, Money K, Howard I, Kirienko N, Johnson W, Lackner J, Dizio P, Evanoff J (1992) Human ocular torsion during parabolic flight: an analysis with scleral search coil. Exp Brain Res 90(1):180–188

Clement G, Vieville T, Lestienne F, Berthoz A (1986) Modifications of gain asymmetry and beating field of vertical optokinetic nystagmus in microgravity. Neurosci Lett 63:271–274

Cohen B, Matsuo V, Raphan T (1977) Quantitative analysis of the velocity characteristics of optokinetic nystagmus and optokinetic after-nystagmus. J Physiol (London) 321–344

Dizio P, Lackner JR (1992) Influence of gravitoinertial force level on vestibular and visual velocity storage in yaw and pitch. Vision Res 32(1): 111–120

Howard IP (1982) Human visual orientation. John Wiley & Sons, Chichester New York Brisbane Toronto

Igarashi M, Takahashi M, Kubo T, Levy JK, Homick JL (1978) Effect of macular ablation on vertical optokinetic nystagmus in the squirrel monkey. Otorhinolaryngol 40:312–318

Lafortune SH, Ireland DJ, Jell RM (1989) Interaction of otolith organ activity with horizontal optokinetic afternystagmus (OKAN) in humans. Acta Otolaryngol (Stockh) [Suppl] 468:277–282

Matsuo V, Cohen B (1984) Vertical optokinetic nystagmus and vertical nystagmus in the monkey: up-down asymmetry and effects of gravity. Exp Brain Res 53:197–216

Melvill J (1966) Interactions between optokinetic and vestibulo-ocular responses during head rotation in various planes. Aerospace Med 37:172–177

Morrow MJ, Sharpe JA (1989) Torsional optokinetic nystagmus in upright and supine positions in human. Invest Opthalmol Vis Sci [Suppl 3] 30:51

Raphan T, Cohen B (1985) Multidimensional organization of the vestibulo-ocular reflex (VOR). In: Keller EL, Zee DS (eds) Adaptive processes in visual and oculomotor systems. Pergamon, New York, pp 285–292

Robinson DA (1963) A method of measuring eye movement using a scleral search coil in a magnetic field. IEEE Trans Biomed Elect 10:137–145

Takahashi M, Igarashi M, Homick J (1977) Effect of end organ ablation on horizontal optokinetic nystagmus and optokinetic afternystagmus in the squirrel monkey. Otorhinolaryngol 39:74–81

Tryggvason BV (1991) Acceleration levels in the KC-135. Conference Proceedings of Spacebound '91, Canadian Space Agency, Ottawa, April 1991

Young LR, Lichtenberg BK, Arrott AP, Crites TA, Oman CM, Edelman ER (1981) Ocular torsion on earth and in weightlessness. Ann NY Acad Sci 374:80–92

Young LR, Shelhamer M, Modestino S (1986) M.I.T./Canadian vestibular experiments on the Spacelab-1 mission. 2. Visual vestibular tilt interaction in weightlessness. Exp Brain Res 64:299–307

Wei G, Lafortune SH, Ireland DJ, Jell RM (1994) Human vertical optokinetic nystamus and after-response, and their dependence upon head orientation with respect to gravity. J Vest Res 4:37–47