Exp Brain Res (1993) 94:456–462

Experimental Brain Research

Effects of prolonged weightlessness on horizontal and vertical optokinetic nystagmus and optokinetic after-nystagmus in humans

G. Clément[1], **K. E. Popov**[2], **A. Berthoz**[1]

[1] Laboratoire de Physiologie de la perception et de l'action. CNRS-collège de France, 15 Rue de l'Ecole de Médecine, F-75270 Paris Cedex 06, France

[2] Institute for Problems of Information Transmission, Academy of Sciences, Ermolovoy Str. 19, SU-10351 Moscow, Russia

Received: 30 July 1992 / Accepted: 31 December 1992

Abstract. Horizontal and vertical optokinetic nystagmus (OKN) and optokinetic after-nystagmus (OKAN) provided by a partial-field, binocular optokinetic stimulator were recorded in one astronaut before, during, and after a 25-day space flight. A ground-based study was performed on six control subjects. During the flight experiment, performed on flight days 5, 18, 19, and 21, the subject either had their feet attached to the deck or was free-floating. Vertical OKN gain only slightly increased in weightlessness compared with ground data, but the center of interest (CI) during vertical OKN, evaluated by the eye position in the saggital plane at the end of the fast phases relative to the straight-ahead direction, was found to be significantly changed during long-term exposure to weightlessness. The horizontal CI showed very little change in-flight, but the gain was increased. The time constant for the astronaut was small for vertical OKAN, but there was an increase in slow-phase velocity (SPV) by the end of the flight, which returned to normal postflight. These results partly confirm the data obtained during head-tilt studies on the ground and are in accordance with the hypothesis of a gravity-dependent control of vertical gaze direction during orientation reflexes.

Key words: Optokinetic nystagmus – Optokinetic after-nystagmus – Otolith organs – Velocity storage – Weightlessness – Human

Introduction

The vestibulo-ocular reflex (VOR) in combination with the visual and proprioceptive systems stabilizes gaze in space as we move about, reducing retinal slip so that clear vision is ensured. Considerable insight into the detailed dynamics of the VOR has come from identifying a process in the central vestibular system which is hypothesized to "integrate" vestibular, visual, and proprioceptive information used in generating compensatory eye movements. This process, called the velocity storage integrator, is responsible for lengthening the time course of the VOR response, as compared to the change in activity seen in the peripheral units in the eighth cranial nerve (Raphan et al. 1979).

Velocity storage can also be activated by the visual system, using full-field optokinetic stimulation. An optokinetic drum rotating about a subject's yaw axis induces eye movements, known as optokinetic nystagmus (OKN). When the lights are extinguished, the eye movements do not disappear immediately but continue during optokinetic after-nystagmus (OKAN), decaying with a time course similar to that of VOR after rotation. The storage properties associated with both vestibulo-ocular compensation and optokinetic following were therefore suggested to be mediated by a common mechanism (Cohen et al. 1981). Studies done in parabolic flight (DiZio and Lackner 1992) have demonstrated that it is this common pathway that is affected upon exposure to brief periods of weightlessness.

In monkeys and humans, the asymmetry between upward and downward slow-phase velocity (SPV) during OKN and OKAN (Matsuo and Cohen 1984; Van den Berg and Collewijn 1988) has also been shown to be a function of gravity. This asymmetry (upward SPV higher than downward SPV) was modified by tilting the subject more than 90° (Clément and Lathan 1991; Leliever and Correia 1987) and was found to be reversed in one astronaut during the first days of orbital flight and during parabolic flight (Clément et al. 1986).

An important discovery in the last few years has been the realization that velocity storage has a three-dimensional structure. Horizontal optokinetic stimulation in monkeys tilted 90° from the upright on Earth was found to produce an oblique after-nystagmus, referred to as "cross-coupling" (Raphan and Cohen 1988). Recently, this cross-coupling has also been observed in human subjects during OKAN as well as during OKN (Clément and Lathan 1991). Raphan and Cohen suggested that the axis of rotation of the eyes during OKN and OKAN is

Correspondence to: A. Berthoz

brought to alignment with spatial vertical, i.e., gravity on Earth. Since there is virtually an absence of spatial vertical in weightlessness, the plane of the compensatory eye movements should be altered.

The present study was directed toward analyzing the data obtained with one astronaut before, during, and after a 25-day space flight and to compare them with ground-based data from control subjects. Priority was given to the study of adaptation of vertical eye movements to weightlessness, but we were fortunate to have the opportunity to also examine limited horizontal eye movement data. In addition, a concurrent experiment on visual-postural interaction allowed us a minimal comparison of the effects of postural conditions (free-floating and feet-fixed) and different instructions ("to look" or "to stare") on the characteristics of OKN and OKAN in weightlessness.

Materials and methods

Subjects

Data were obtained for one astronaut before, during, and after a 25-day space flight aboard the MIR space station in November, 1988. Six other subjects were tested on the ground as controls.

Apparatus

During the flight, the optokinetic stimulation was provided by means of a head-portable binocular stimulator.[1] This stimulator presented a black and red checkerboard pattern (4°/square) viewed through Fresnel lenses placed in front of each eye for focusing. The viewing range dimensions were approximately 115° horizontal by 110° vertical. Ground-based studies were performed using an exact duplicate of the flight stimulator. Constant-velocity optokinetic stimulation was provided preflight, in-flight, and postflight at 27, 39, 51, and 65°/s for the astronaut. However, the control subjects' data was taken at 15, 30, 45, and 60°/s before the final flight protocol had been determined.

The electro-oculographic (EOG) signals corresponding to horizontal and vertical eye movements, the velocity of the optokinetic stimulator, and the presence or absence of light, were digitized and recorded on a portable 12-analog-channel recording system built for this mission.[2] The EOG signals were amplified 4000 times with a bandwidth of d.c. to 100 Hz. The data were recorded at a sampling rate of 200 Hz.

Ground-based testing

In this study, the OKN and OKAN measured on the ground for the astronaut were compared with those obtained from the six control subjects. During both horizontal and vertical optokinetic stimulation, the subject was asked to look at the visual display attentively, and to try to count each stripe, without following them, as they went by. No instruction about the direction of gaze was given to the subject.

A standard test sequence was as follows: (a) the subject was instructed to look at the center of the stationary visual display, the EOG signals were reset to 0 V, and recording started at zero time ($T=0$ s); (b) at $T=5$ s, the visual display began moving at a constant velocity; (c) to evaluate EOG drift, at $T=10$ s, $T=20$ s, and $T=30$ s, a tone signal was delivered, and the subject had to track one dot per square across the entire visual field until it disappeared and then return to the OKN instruction; (d) at $T=35$ s, the light was switched off for OKAN recording; (e) recording stopped at $T=60$ s. This sequence test was then repeated with an optokinetic stimulation in the opposite direction at the same velocity. The interval between tests was about 10 s.

Calibrations of eye movements were obtained from voluntary saccades as the subject acquired visually the boundaries between black and red squares on the checkerboard pattern, which were separated by about 7°, or red light-emitting diodes (LED) placed 5° apart on the full-field screen.

Flight testing

The preflight experiment was performed on the astronaut 2 months (F-60), 1 week (F-7), and 4 days (F-4) before the launch. Unfortunately, the data collected on F-7 were discarded because of the poor quality of the eye movement recordings. During the flight, the experiment was performed on flight day (FD) 5, FD18, FD19, and FD21. After the flight, the first test was performed 29 h after landing (R + 1), and subsequent tests were carried out on days R + 3, R + 6, and R + 7.

The subject was given "look" OKN instructions in some conditions and in others was just instructed to stare through the visual stimulus. In-flight, the subject had his feet attached to the deck for both OKN instructions; "stare" conditions are indicated in the figures by an asterisk preceding the test day, e.g., *F-60 or *FD19. In addition, a test was performed on FD19 with the subject free-floating and under stare OKN instructions (**FD19 in the figures).

Data analysis

Calibration. The EOG drift was evaluated during the first 5 s of recording, i.e., when the subject was instructed to look at the center of the visual display, and also from the slope of the line linking the eye position at the end of each pursuit period (see "c" in the test sequence). In each trial raw data were first corrected for EOG drift and then calibrated. The nonlinearity of the vertical EOG was corrected by using a second-order polynomial function fitted to the calibration data.

Once calibrated, the eye position signals were differentiated by software. Slow phases (SPs) were then manually marked during OKN and OKAN from the eye velocity traces by selecting the beginning and the end of each SP. The computer analysis took each point within a marked SP and calculated the mean SP eye velocity. These values for each SP were then averaged to give a final mean SPV and standard deviation (SD).

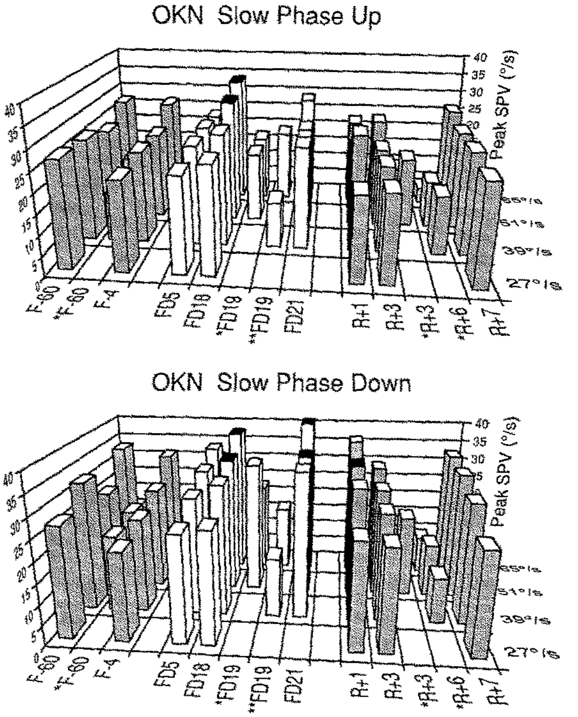
Optokinetic nystagmus. During the first 20 s of each trial, approximately 20 SPs with the highest velocities were averaged to calculate the mean peak SPV and SD. OKN gain was computed as the ratio between the mean peak SPV and the stimulus velocity. Also, during OKN the successive eye positions at the beginning of the SPs were averaged to calculate the mean eye deviation relative to the straight-ahead direction of gaze, referred to as the center of interest (CI) (Chun and Robinson 1978; Clément and Lathan 1991), and SD. Differences in mean peak SPV and CI for preflight (F-60) values versus in-flight and postflight values were statistically evaluated using a two-tailed t-test for correlated means.

Optokinetic after-nystagmus. For each trial, the OKAN peak SPV was approximated by extending the best-fitting exponential curve

---

[1] The binocular stimulator was designed by P. Simon (CNES), Y. Matsakis (CNRS), and M. Ehrette (CNRS), and built by AETA Company, Paris, France.

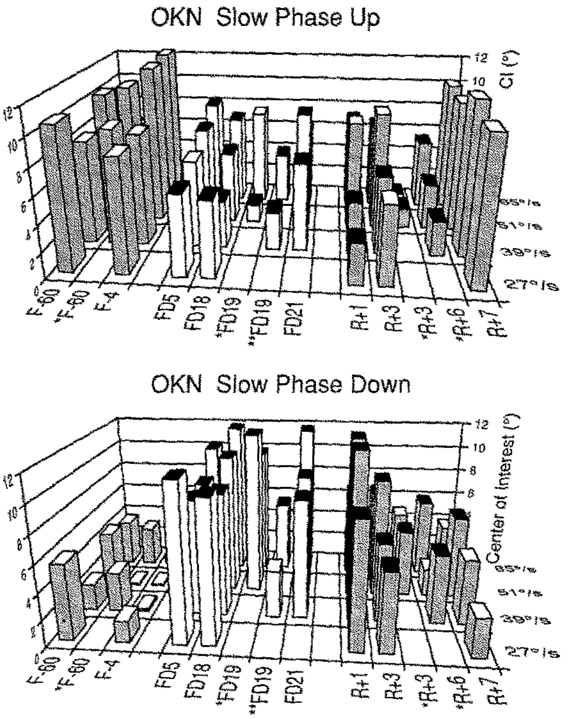
[2] The "Super-Pocket" system was designed by P. Simon (CNES) and O. Charade (CNRS), and built by EREMS Company, Toulouse, France.



OKN Slow Phase Up

OKN Slow Phase Down

Fig. 1. Peak slow-phase velocity (*SPV*) of vertical optokinetic nystagmus (*OKN*) for four stimulus velocities in one astronaut as a function of exposure to weightlessness. Sessions during which the subject was instructed "to stare" at the visual display are marked with an *asterisk*. During all other sessions, the subject was instructed "to look" at the visual display. On flight day 19 (***FD19*) the subject was free-floating and performing "stare" OKN. Each entry, mean value calculated for approximately 20 slow phases during one trial. Statistical difference ($P<0.05$) relative to preflight value is indicated by *black tops of bars*. *F* with *negative numbers*, preflight days; *R* with *positive numbers*, postflight days



OKN Slow Phase Up

OKN Slow Phase Down

Fig. 2. Center of interest (*CI*) of vertical optokinetic nystagmus (*OKN*) for four stimulus velocities in one astronaut as a function of exposure to weightlessness. Note that the CI was directed downward during OKN with slow phase up, and was directed upward during OKN with slow phase down. Each entry, mean value calculated for approximately 20 slow phases during one trial. Statistical difference ($P<0.05$) relative to preflight value is indicated by black tops of bars

back from the last OKAN SP through the preceding OKAN SPs. The time constant for decline of OKAN corresponds to the time when the area under the SPV curve equals 63% of the total area. This variation on the technique of Cohen et al. (1977) has the advantage of not being reliant on the initial OKAN peak SPV. Differences in OKAN parameters for preflight values versus in-flight or postflight values were evaluated by averaging the measurements over all velocities for each condition.

Results

Flight data – vertical OKN and OKAN

Both upward and downward peak SPVs saturated at 25–30°/s, resulting in very low gains for the higher velocities (Fig. 1). The vertical OKN peak SPV only increased for the highest velocities of optokinetic stimulation by the end of the flight for both directions of stimulation. The stare OKN peak SPV did not change significantly during the flight, with the subject restrained or free-floating.

The CI of vertical OKN, however, showed significant changes in-flight and during postflight tests, with the two instructions and two posture conditions (Fig. 2). When all values were averaged, preflight tests gave a mean CI of 9.47° (SD 1.77°, $n=11$) below the straight-ahead position during upward stimuli, and a mean CI of 2.16° (SD 1.78°, $n=11$) above the straight-ahead position during downward stimuli. In-flight, during upward stimuli the mean CI was in average 5.85° (SD 2.0°, $n=15$) below the straight-ahead position, whereas during downward stimuli the mean CI was 9.48° (SD 2.29°, $n=15$) above the straight-ahead position. These data indicate that the position of the eye at the end of the fast phase was about 4° higher than preflight during upward stimuli, and about 7° higher than preflight during downward stimuli. It is interesting to note that when free-floating (**FD19), the magnitude of the CI was approximately equal for both directions of stimulation (mean −3.5° during upward stimuli versus 4.5° during downward stimuli). Return to preflight CI values was only observed after postflight week 1 (R + 7).

When preflight values obtained for each velocity and direction of stimulation were averaged, the vertical OKAN mean peak SPV was 14.16°/s (SD 1.60°/s, $n=14$), whereas the average over FD18 and 21 gave a vertical OKAN mean peak SPV of 17.63°/s (SD 1.96°/s, $n=14$). Therefore, vertical OKAN peak SPV after look OKN at the end of the flight showed a 3.5°/s increase in the mean relative to the preflight mean (Fig. 3). Unfortunately, the decline of vertical OKAN was so fast (less than 2 s) with

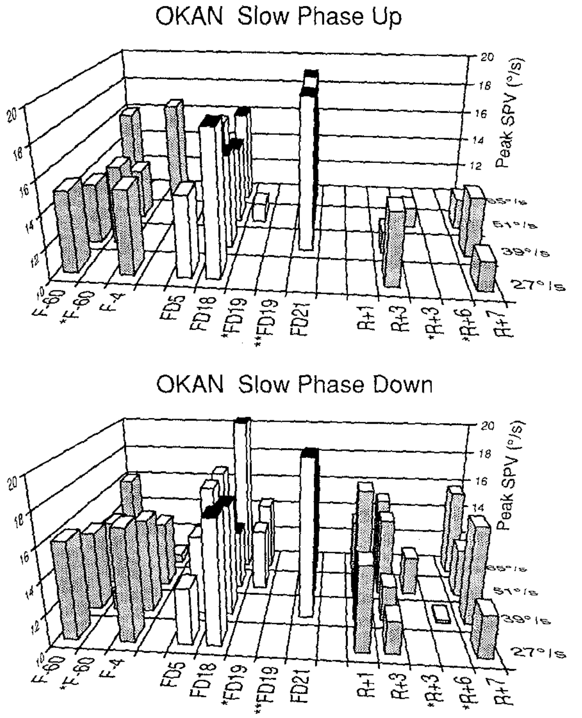


Fig. 3. Peak slow-phase velocity (*SPV*) of vertical optokinetic after-nystagmus (*OKAN*) for four stimulus velocities in one astronaut as a function of exposure to weightlessness. Each entry, single value calculated during one trial. Statistical difference ($P<0.05$) between averaged measurements over all velocities relative to preflight values is indicated by black tops of bars

this subject that accurate estimates of the vertical OKAN time constant were not possible.

Ground-based data – vertical OKN and OKAN

Characteristics of vertical OKN and OKAN measured during preflight tests are shown in Fig. 4. In the control group mean values for OKN gain with SP up were higher than those for OKN gain with SP down (Fig. 4A). In contrast, in the astronaut, the OKN gain with SP up was not significantly different from the OKN gain with SP down. However, the overall gain of vertical OKN in the astronaut was lower than the control group for stimulus velocity 39°/s and higher.

Although the CI was not measured in this control group, the astronaut's preflight values were similar to data obtained in other subjects tested with the same optokinetic stimulator (Clément and Lathan 1991, Fig. 2).

In the control group, vertical OKAN with SP up was stronger than vertical OKAN with SP down (Fig. 4B). No systematic asymmetry was observed with the astronaut subject as for the OKN gain above. The peak SPV of OKAN with SP up was followed by a gradual decline to zero over 2–6 s in the control group, but only over 1–2 s in the astronaut (Fig. 4C). The OKAN with SP down declined even faster in all the subjects, and secondary OKAN, i.e., nystagmus with SP up, was occasionally observed in the control subjects.

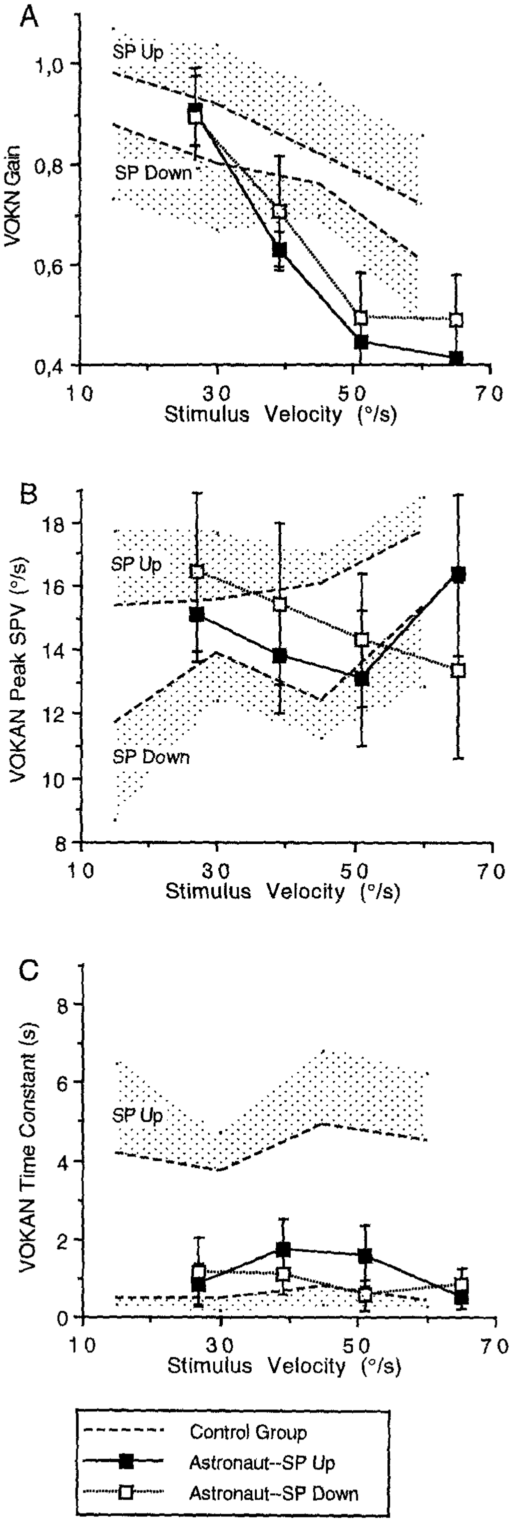


Fig. 4. Vertical optokinetic nystagmus (*VOKN*) gain (**A**), vertical optokinetic after-nystagmus (*VOKAN*) peak slow phase velocity (**B**), and VOKAN time constant (**C**) as a function of stimulus velocity with the astronaut and a control group of subjects on the ground. The control subjects' data was taken with slightly different velocities because the final preflight, in-flight, and postflight protocol had not been determined at the time of testing. All subjects were instructed "to look" at the visual display. Plots show responses obtained for each direction of stimuli. In the control group, data were also averaged among subjects – *shaded areas* represent means + SD for nystagmus with slow phase up, and means –SD for nystagmus with slow phase down

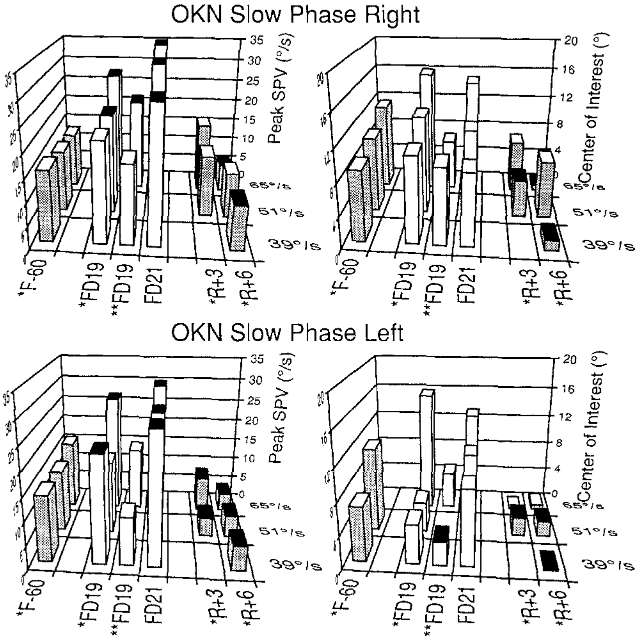


Fig. 5. Peak slow-phase velocity (*SPV*) and center of interest of horizontal optokinetic nystagmus (OKN) for three stimulus velocities in one astronaut as a function of exposure to weightlessness. Each entry, mean value calculated for approximately 20 slow phases during one trial. Statistical difference ($P<0.05$) relative to preflight value is indicated by black tops of bars

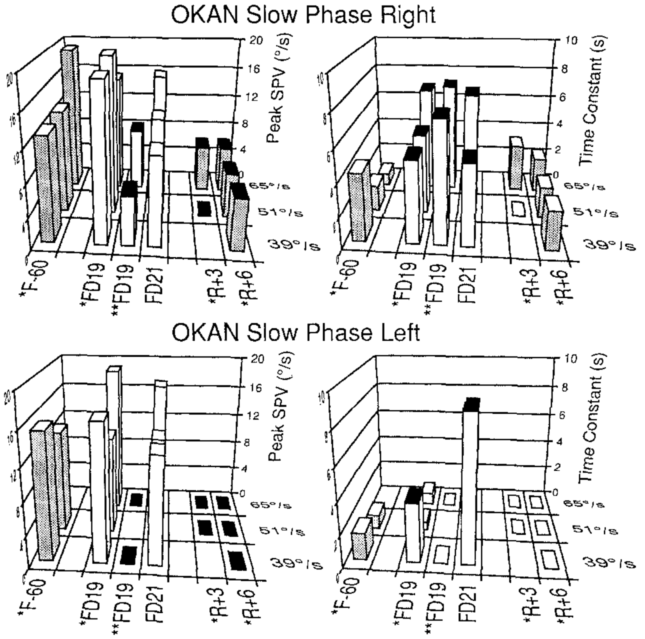


Fig. 6. Peak slow-phase velocity (*SPV*) and time constant of horizontal optokinetic after-nystagmus (*OKAN*) for three stimulus velocities in one astronaut as a function of exposure to weightlessness. Each entry, single value calculated during one trial. Statistical difference ($P<0.05$) between averaged measurements over all velocities relative to preflight values is indicated by black tops of bars

Flight data – horizontal OKN and OKAN

Measurements of the steady-state horizontal OKN during preflight, in-flight, and postflight tests are shown in Fig. 5. The peak SPV of OKN with SP right or left significantly increased by FD19 compared with preflight values in four out of six trials, when the subject was instructed to stare at the stimulus with the feet fixed and in only one out of four trials when the subject was free-floating (**FD19). The measurements of peak SPV during look OKN on FD21 were found to be higher than during stare OKN, although no preflight data was available. The postflight horizontal OKN peak SPVs were significantly less than the preflight data.

The measurements of the CI during horizontal OKN, i.e., the magnitude of the horizontal eye position relative to the straight-ahead direction at the end of the fast phase, are shown on the right part of Fig. 5. On the ground, CI ranged from 7 to 11° to the left or to the right during right- or left-directed optokinetic stimuli, respectively. During the flight, the mean values of CI ranged from 3 to 15°. However the variance about the mean values was very large, at least during the stare OKN, and in-flight measurements were not found to significantly differ from preflight values for the feet-fixed condition and in one out of four trials when the subject was free-floating. Postflight measurements of CI were, however, significantly smaller than preflight in six out of ten trials.

The horizontal OKAN peak SPV during the flight was similar to preflight values for the feet-fixed condition (Fig. 6). In the free-floating condition (**FD19), the OKAN peak SPV decreased. After the flight, no OKAN was observed after optokinetic stimulation directed to the left. The peak SPV of OKAN with SP to the right was considerably less than during preflight until at least R+6. Finally, the time constant of horizontal OKAN was increased in-flight relative to preflight.

Ground-based data – horizontal OKN and OKAN

Unfortunately, it was not possible to record the horizontal OKN during ground tests in the astronaut with the look instruction. However, with the stare instruction, the horizontal OKN gain of the astronaut was not significantly different from those of a control group of subjects. Horizontal OKAN peak SPV was also the same for all subjects, but the astronaut's horizontal OKAN response showed a faster decline over time.

Discussion

Only a few experiments have been designed to examine the adaptive effects of altered levels of acceleration due to gravity (g) on human vestibular and optokinetic systems (Kornilova et al. 1983, 1987; Von Baumgarten et al. 1984, 1986; Watt et al. 1985; Young et al. 1986). Experiments performed at the onset of microgravity or during brief exposures show a different set of results from those after longer exposure to weightlessness.

Modifications of horizontal and vertical optokinetic and VORs have been noted by Viéville et al. (1986) both in the weightlessness phase of parabolic flight and during

Earth orbit. Horizontal OKN gain was found to be significantly reduced on the first day in orbit but gradually recovered during the following flight days. Vertical OKN gain asymmetry seen in normal gravity was reversed in weightlessness, both in parabolic flight and on the first days in Earth orbit (Clément et al. 1986), progressively returning to ground values during the flight. Both horizontal and vertical OKAN time constants exhibited a transient, direction-specific increase just after insertion into weightlessness, followed by a decrement after 24 h in weightlessness (Clément and Berthoz 1990). However, the OKAN time constants recovered to preflight measurements by FD5. For the VOR, both horizontal and vertical gain also decreased at the beginning of the flight and returned to ground values by FD4. During parabolic flight, horizontal and vertical VOR gain in absence of gravity was also found to be lower than in normal gravity (DiZio and Lackner 1988), and both the OKAN and the VOR time constant of decay decreased in zero gravity conditions, with no change in peak SPV (DiZio and Lackner 1992).

OKN and OKAN

It has been proposed that the initial reversal of vertical OKN gain asymmetry in weightlessness might be due to the absence of saccular inputs which would normally (in normal gravity) play an inhibitory role on the optokinetic system (Viéville et al. 1986). This hypothesis was reinforced by results from recent lesion studies which found that, after bilateral sacculectomy, OKN downward SPV was increased whereas OKN upward peak SPV was decreased (Igarashi et al. 1987). In our data, a reversal of preflight vertical OKN gain asymmetry was not likely to occur, since: (a) no asymmetry was observed preflight, possibly due to the OKN saturation at 25–30°/s for both upward and downward optokinetic stimulation; and (b) our first measurement was performed late in-flight, on FD5.

It is possible, however, that saccular inputs influence vertical direction of gaze, which in turn affects the gain of visually oriented eye movements. This theory would suggest that modifications (or absence of modifications) of the vertical OKN gain might be just a consequence of changes in the vertical direction of gaze. On Earth, the asymmetry in the magnitude of the CI during vertical optokinetic stimulation has been found to be affected by head position relative to gravity (90° roll position), but the vertical OKN asymmetry was unchanged (Clément and Lathan 1991, Figs. 2, 4). A similar elevation of the eyes' CI during flight without a change in vertical OKN asymmetry was observed in the present study when the astronaut was exposed to weightlessness.

Further support for the above theory comes from evidence of a downward gaze deviation during the weightless phase of parabolic flight and on the first day in Earth orbit (Clément et al. 1986). This downward gaze deviation was interpreted as a transient effect of the release of the antigravity influence exerted by the sacculus, on Earth, on limb and eyeball musculature. Long-term adaptation to weightlessness could be directed toward canceling the downward trend observed during the acute stage, resulting in the elevation of the eyes' CI when the astronaut was tested late in-flight. The end result is to symmetrically equalize the CI in the vertical plane.

The horizontal CI changed very little during space flight, while the gains significantly increased. The OKAN time constant also increased on FD19. This result, together with the increase in vertical OKAN SPV after FD21, suggests a general increase in the stored activity related to SP eye velocity during adaptation to weightlessness.

Finally, the overall OKN gain with the stare instruction was lower than with look as expected. The instruction to stare is known to favor the subcortical OKN, which is associated with circular vection and OKAN, whereas the instruction to look mainly triggers cortical OKN (Brandt et al. 1974). Similar changes for both instructions were observed during adaptation to weightlessness, including large changes in-flight in the vertical CI and few or no changes in the vertical gain. This suggests that both pathways may be similarly affected by gravity.

Time course of adaptation

This 3-week space flight was the first opportunity to compare the characteristics of OKN and OKAN during long-term adaptation to short-term space flights.

The absence of cross-coupling in our present data contrasts with other observations made during the first hours of a space flight (Clément and Berthoz 1990; Reschke et al., in preparation). However, it may be that cross-coupling occurs only during the acute stage of adaptation, i.e., just after insertion into weightlessness, or until the system establishes a new frame of reference (Young et al. 1984, Mittelstaedt 1988).

Tactile cues probably play an important role in this new frame of reference, since the free-floating situation is accompanied by an overall decrease in the velocity storage (all eight trials). In agreement with this, and in contrast with a singular observation (Von Baumgarten et al. 1986), there was a decrease in SPV during OKN when the subject was free-floating.

After the flight, the system would return to the use of spatial vertical as a privileged axis for compensatory eye movements. However, the results of postural (Kenyon and Young 1986; Watt et al. 1986) and perceptual studies (Kozlovskaya et al 1983; Parker et al. 1985; Young et al. 1986) performed immediately after return to Earth have suggested that perception of the spatial vertical was altered as a consequence of adaptation to weightlessness. This alteration might be responsible for the decrease in horizontal velocity storage during postflight tests.

Acknowledgements. The authors are grateful to Anna Petropoulos and Corinna E. Lathan for their assistance, and to Jean-Loup Chrétien, Michel Tognini, and Alexander Volkov for their collaboration in this experiment. This research was supported by Centre National de la Recherche Scientifique, Paris, France, under grants 1218/520|061 and 1276/520|133 from the Centre National d'Etudes Spatiales.

References

Brandt T, Dichgans J, Buechele W (1974) Motion habituation: inverted self-motion perception and optokinetic after-nystagmus. Exp Brain Res 21:337–352

Chun KS, Robinson DA (1978) A model of quick phase generation in the vestibulo-ocular reflex. Biol Cybern 28:209–221

Clément G, Berthoz A (1990) Cross-coupling between horizontal and vertical eye movements during optokinetic nystagmus and optokinetic afternystagmus elicited in microgravity. Acta Otolaryngol (Stockh) 109:179–187

Clément G, Lathan CE (1991) Effects of static tilt about roll axis on horizontal and vertical optokinetic nystagmus and optokinetic afternystagmus in humans. Exp Brain Res 84:335–341

Clément G, Viéville 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 (Lond) 270:321–344

Cohen B, Henn V, Raphan T, Dennett D (1981) Velocity storage, nystagmus and visual-vestibular interactions in humans. Ann NY Acad Sci 374:421–433

DiZio P, Lackner JR (1988) The effects of gravitoinertial force level and head movements on post-rotational nystagmus and illusory after-rotation. Exp Brain Res 70:485–495

DiZio P, Lackner JR (1992) Influence of gravitoinertial force level on vestibular and visual velocity storage in yaw and pitch. Vision Res 32:123–145

Igarashi M, Himi T, Kulecz WB, Patel s (1987) The role of saccular afferents in vertical optokinetic nystagmus in primates. A study in relation to optokinetic nystagmus in microgravity. Arch Otorhinolaryngol [Suppl] 244:143–146

Kornilova LN, Yakovleva IY, Tarasov IK, Gorgiladze GI (1983) Vestibular dysfunction in cosmonauts during adaptation to zero-G and readaptation to one-G. The Physiologist 26: S35–S36

Kornilova LN, Bodo G, Kaspransky RR (1987) Sensory interaction in weightlessness. Physiologist 30: S85–S89

Kenyon RV, Young LR (1986) MIT/Canadian vestibular experiments on the Spacelab-1 mission. 5. Postural responses following exposure to weightlessness. Exp Brain Res 64:335–346

Kozlovskaya IB, Aslanova IF, Barmin VA, Grigorieva LS, Gevlich GI, Kirenskaya AV, Sirota MG (1983) The nature and characteristics of a gravitational ataxia. Physiologist 26: S108–S109

Leliever WC, Correia MJ (1987) Further observations on the effects of head position on vertical OKN and OKAN in normal subjects. Otolaryngol Head Neck Surg 97:275–281

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

Mittelstaedt H (1988) Determinants of space perception in space flight. Adv Otorhinolaryngol 42:18–23

Parker DE, Reschke MF, Arrott AP, Homick JL, Lichtenberg BK (1985) Otolith tilt-translation reinterpretation following prolonged weightlessness: implications for preflight training. Aviat Space Environ Med 56:601–606

Raphan T, Cohen B (1988) Organizational principles of velocity storage in three dimensions: the effect of gravity on cross-coupling of optokinetic after-nystagmus. Ann NY Acad Sci 545:74–92

Raphan T, Matsuo V, Cohen B (1979) Velocity storage in the vestibulo-ocular reflex arc (VOR). Exp Brain Res 35:229–248

Van den Berg AV, Collewijn H (1988) Directional asymmetries of human optokinetic nystagmus. Exp Brain Res 70:597–604

Viéville T, Clément G, Lestienne F, Berthoz A (1986) Adaptive modifications of the optokinetic nystagmus and vestibulo-ocular reflexes in microgravity. In: Keller EL, Zee DS (eds) Adaptive processes in visual and oculomotor systems. (Advances in the Biosciences, vol 57) Pergamon, Oxford, pp 111–120

Von Baumgarten RJ, Benson A, Berthoz A, Brandt Th, Brand U, Bruzek W, Dichgans J, Kass J, Probst T, Scherer H, Viéville T, Vogel H, Wetzig J (1984) Effect of rectilinear acceleration and optokinetic and caloric stimulations in space. Science 225:208–212

Von Baumgarten RJ, Benson A, Berthoz A, Bles W, Brandt T, Brenske A, Clarke A, Dichgans J, Eggertsberger R, Jurgens K, Kass J, Krakczyck s, Probst T, Scherer H, Thumler R, Viéville T, Vogel H, Wetzig J (1986) European experiments on the vestibular system during the Spacelab D-1 mission. In: Sahm PR, Jansen R, Keller MH (eds) Scientific results of the German Spacelab mission D1. ETEC, Noordwijk, pp 475–490

Watt DGD, Money KE, Bondar RL, Thirsk BB, Garneau M, Scully-Power P (1985) Canadian medical experiments on Shuttle flight 41-G. Can Aeronaut Space J 31:215–226

Watt DGD, Money KE, Tomi LM (1986) MIT/Canadian vestibular experiments on the Spacelab-1 mission. 3. Effects of prolonged weightlessness on a human otolith-spinal reflex. Exp Brain Res 64:308–315

Young LR, Oman CM, Watt DGD, Money KE, Lichtenberg BK (1984) Spatial orientation in weightlessness and readaptation to Earth's gravity. Science 225:205–208

Young LR, Oman CM, Watt DGD, Money KE, Lichtenberg BK, Kenyon RV, Arrott AF (1986) MIT/Canadian vestibular experiments on the Spacelab-1 mission. 1. Sensory adaptation to weightlessness and readaptation to one-g: an overview. Exp Brain Res 64:291–298