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European vestibular experiments on the Spacelab-1 mission: 6. Yaw axis vestibulo-ocular reflex

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Summary. In two Spacelab-1 crew members the lateral eye movements evoked by active angular oscillation of the head in yaw at 1 Hz were recorded in-flight and post-flight. In one, the responses to passive angular oscillation in yaw at 0.2–1 Hz were also studied pre- and post-flight. In the absence of visual fixation there was no significant change in the gain of either the active or passive vestibulo-ocular reflex (VOR) attributable to exposure to microgravity. However, when the subject fixated on a visual target that moved with his head the suppressed VOR gain was lower on the first post-flight test (performed 16 h after landing) than that obtained pre-flight or on subsequent post-flight tests.

Key words: Vestibulo-ocular reflex – Semicircular canals – Visual-vestibular interaction – Microgravity

Introduction

The role of the semicircular canals in the stabilisation of eye position, and hence the preservation of visual activity, during active and passive head movements has long been recognised. In contrast, the contribution of the otoliths to the vestibulo-ocular reflex (VOR) is relatively poorly understood. Modulation of the VOR in the horizontal plane by a changing linear acceleration vector has been demonstrated (Benson 1970, 1974), as has the induction of horizontal nystagmus by high intensity ($\pm$ 5 ms^{-2}) linear oscillation in the Y axis of the skull (Niven et al. 1966).

Evidence for the modification of lateral (horizontal) canal responses by relatively sustained changes in the force environment is, however, more ambiguous. Experiments in parabolic flight have shown either no change in the nystagmus evoked by Z axis rotational stimuli (Jackson and Sears 1965; Oosterveld and van der Laarse 1969; Bludworth et al. 1982; Vesterhauge et al. 1984) or a reduction in the response (Lackner and Graybiel 1981; Vesterhauge et al. 1982) during the period of weightlessness. In the sustained microgravity afforded by orbital flight psychophysical experiments did not reveal any consistent change in the threshold for detection of yaw (Z) axis angular acceleration (Graybiel et al. 1977).

In view of the relative paucity of information about the behaviour of semicircular canal driven oculomotor responses in microgravity, and possible changes in VOR gain and canal-otolith interaction which may feature in vestibular adaptation to weightlessness, experiments employing active stimulation of the lateral (horizontal) semicircular canals were carried out in orbital flight. The vestibulo-ocular responses elicited by both active and passive angular oscillation in the normogravic environment of a terrestial laboratory were also recorded. The experiment, involving passive rotational stimulation, was planned several years before the flight of Spacelab-1. It employed centric and eccentric angular oscillation of the subject in order to study the possible modification of the nystagmic response to the rotational stimulus by the changing linear acceleration vector that the subject experienced during eccentric oscillation. In addition, tests were carried out with the subject fixating on a visual target that moved with the head in order to assess the suppression of the VOR response by vision. The experiment in which the VOR elicited by voluntary (active) head oscillation in yaw was studied, lacked the benefit of pre-flight, base-line, measures because it was not part of the

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formal protocol of the flight experiments. This ad hoc experiment was introduced only when time became available during flight due to the failure of other experimental hardware. Despite the deficiences the results are here reported as they complement the observations made on the passive VOR responses.

Methods

Passive VOR

Apparatus. The apparatus employed for pre- and post-flight tests was a manually operated turntable on which the subject sat in a cross-legged position. He was restrained by a harness and his head was located by lateral pads within a box-like helmet that excluded ambient light. Tests were conducted with the subject in each of two positions on the turntable, one in which the longitudinal (Z) axis of his head was close (i.e. within 50 mm) to the axis of rotation of the turntable (Centric mode), the other in which the Z axis of the head was parallel to but 1 m distant from the rotation axis (Eccentric mode). Lateral eye movements were recorded by a conventional DC electro-oculographic (EOG) technique and were visualised by an infra-red TV camera that was mounted, as were collimated calibration LEDs, on the helmet assembly. The EOG signal and turntable velocity were recorded on magnetic tape for subsequent analysis.

The motion stimulus was an angular oscillation, of approximately sinusoidal form at nominal frequencies of 0.3 and 1.0 Hz, that was achieved by the experimenter moving the turntable by hand in time to an audio signal. The mean peak angular velocity of the stimulus in the centric mode was ± 64°/s and ± 53°/s, and in the eccentric mode ± 46°/s and ± 27°/s at 0.3 Hz and 1.0 Hz respectively. The linear acceleration experienced by the subject's vestibular apparatus during angular oscillation was low (i.e. < 0.3 ms^{-2}) when the subject was in the centric position, but when the head was 1 m from the axis of rotation (eccentric position) changes in the force environment were appreciable. The calculated mean peak tangential acceleration (i.e. acting in the Y axis of the head) was ± 1.51 ms^{-2} and ± 2.96 ms^{-2}, and the peak radial acceleration (X axis) was 0.64 ms^{-2} and 0.22 ms^{-2} during oscillation at 0.3 Hz and 1 Hz respectively.

Procedure. The same protocol was followed for all pre- and post-flight tests, the order in which the oscillatory stimuli were delivered being: centric oscillation at 0.3 Hz and 1 Hz, with eyes open in darkness, followed by eccentric oscillation at 0.3 Hz and 1 Hz in darkness. Subsequently, a single central fixation light (a collimated green LED subtending approx. 0.3°) was illuminated and oscillatory stimuli at 0.2 Hz and 1 Hz were given. On each test, the operator increased the amplitude of the oscillatory motion of the turntable in time with an audio signal until a steady rhythm and amplitude were established (typically over 4–5 cycles) and then attempted to maintain this level of stimulation for at least 10 cycles. Calibration eye movements of ± 10° were made at the beginning and end of the test procedure and between each change in the stimulus mode (i.e. centric, eccentric, fixation).

VOR gain (i.e. slow phase eye velocity head velocity) was determined using the interactive computer technique developed by Barnes (1982). Ten successive stimulus cycles were analysed from which, in addition to a measure of mean VOR gain, mean phase error and asymmetry of the oculomotor response were obtained for each test condition: the exception being the response recorded during oscillation at 0.2 Hz with fixation where nystagmus was suppressed to an amplitude (circa 1°) that was within the noise level of the EOG recording system.

The experiment was performed on astronauts C and D. Baseline measures were taken 120, 64, 43 and 11 days before the flight of SL-1 (STS9). Post-flight the subjects were first tested 16 h after landing and subsequently on the 2nd, 4th and 6th post-flight day.

Active VOR

The equipment and procedure employed for the recording of the oculomotor response to active angular oscillation of the head in yaw was similar to that used for the study of the pitch VOR and is fully described by Berthoz et al. (1986) in this issue. The essential difference was that the subject was required to shake his head in yaw, rather than in pitch, at a nominal frequency of 1 Hz. As with the pitch VOR experiment, recordings of eye movements were made when the subject experienced no oscillopsia with eyes open, and when he made angular head movements of comparable amplitude with the eyes closed. An approximate measure of dark VOR gain was obtained by comparison of the eye movements made with the eyes open, (when the gain of the response – eye movement in head/head movement in space – was assumed to be close to unity) and with the eyes closed. As with the pitch VOR responses two methods of analysis were employed to determine VOR gain. In one the peak to peak amplitudes of the EOG signal were compared between samples of record in which a head mounted accelerometer indicated that the oscillatory movement was of similar amplitude with eyes open and eyes closed. In the other, the amplitude of the eye displacement was determined from the reconstructed sinusoidal component after elimination of saccades.

As noted earlier, the experiment was first performed in orbital flight, so there are no pre-flight base line measures. Tests in flight were carried out on subject C on the 5th day in orbit and subject D on the 7th day. The timing of the post-flight tests on subjects C and D was similar to that of the passive VOR tests (*vide supra*).

Results

Passive VOR

Reliable data were obtained only from subject C, the EOG records of subject D being of consistently poor quality with numerous traces in which there was no recognisable nystagmus or cyclical eye movement from which slow phase velocity could be computed. An almost complete set of pre- and post-flight measures of VOR gain were obtained from subject C (Fig. 1), the exceptions being the 0.33 Hz centric test on post-flight day 2, when the EOG record was dominated by large amplitude pendular eye movements, characteristics of a low arousal (drowsy) behavioural state, and the 0.33 Hz eccentric test on post-flight day 4 when there was a recorder malfunction (or mal-operation).

Inspection of the base-line VOR gain data of subject C failed to show any significant difference in the response evoked by centric and eccentric oscillation in darkness, though as is to be expected (Barnes 1980), the gain at 1 Hz (mean 0.65, range 0.51–0.79)

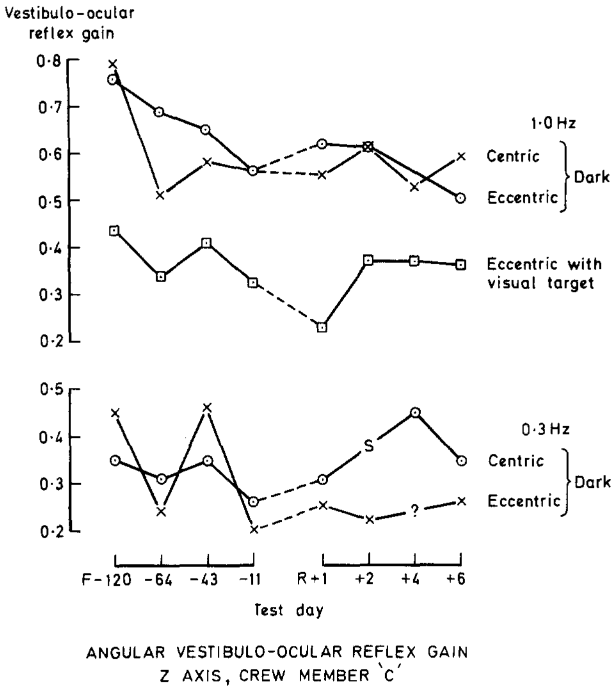

Fig. 1. Yaw axis vestibulo-ocular reflex gain of subject C during passive angular oscillation at 0.3 Hz and 1 Hz in centric and eccentric positions with eyes open in darkness, and during eccentric oscillation at 1 Hz when fixating on a head-fixed visual target. F-120 to F-11 indicate the test days before launch, R + 1 to R + 6 the test days after landing

Table 1. Measures of phase and asymmetry of vestibulo-ocular response of subject C during angular oscillation in yaw (Z axis). Zero phase error indicates perfect phase compensation of eye movement on head movement

	Pre-flight		*Post-flight*	
	Phase deg	Asymmetry deg/s	Phase deg	Asymmetry deg/s
0.3 Hz Centric	2.1	–0.3	3.3	–0.7
1.0 Hz Centric	3.1	–0.7	2.9	0.9
0.3 Hz Eccentric	–0.2	0.6	–2.3	–0.6
1.0 Hz Eccentric	0.5	0.2	3.7	–1.5
1.0 Hz Eccentric with fixation	7.9	0.9	3.9	0.6

was higher than at 0.3 Hz (mean 0.33, range 0.20–0.46). With repetition of the test procedure, VOR gain tended to decrease, a feature that probably reflects the increasing familiarity of the subject with the procedure and his more relaxed behavioural state.

The values obtained post-flight were, with one exception comparable to the pre-flight measures, the mean VOR gain being 0.58 (range 0.50–0.62) at 1 Hz and 0.32 (range 0.22–0.55) at 0.3 Hz. Only the

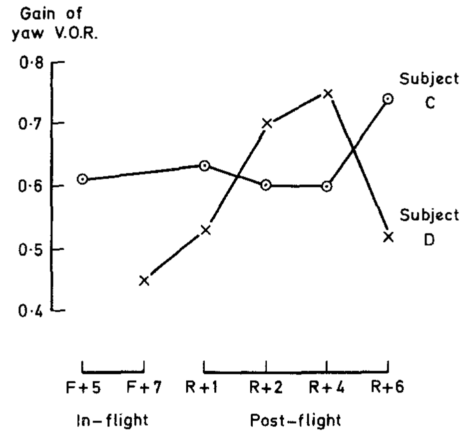

Fig. 2. Vestibulo-ocular reflex gain of subjects C and D during voluntary head oscillation in yaw at 1 Hz with eyes closed

response in the 0.3 Hz centric condition on the fourth post-flight day was greater than the baseline measures and this is not outside the range of values obtained during eccentric oscillation at 0.3 Hz. Notably, all responses obtained in darknes on the first post-flight test, when any change attributable to adaptation to microgravity should be most manifest, yielded measures of VOR gain that were within the range of those obtained pre-flight. Likewise, measures of phase and asymmetry of the slow phase velocity of the oculomotor response (summarised in Table 1) failed to show any significant difference between pre- and post-flight.

In contrast, the gain of the VOR at 1 Hz, when reduced by the presence of a single visual target, was 0.23 on the first post-flight test. This value is significantly ($p = 0.05$) lower than the pre-flight suppressed VOR gain of 0.38 (range 0.32–0.44) or the subsequent post-flight measures, all of which yielded gains of 0.37.

Active VOR

The estimates of the gain of the VOR during active head movements in yaw of subjects C and D, both in-flight and post-flight are shown in Fig. 2. For subject C the gain of 0.61 obtained on the fifth day in flight is comparable to that recorded on the first three post-flight tests (range 0.60–0.63). The test performed on the sixth post-flight day yielded a gain of 0.74, but all these values fall within the range of gains obtained with passive oscillation in darkness at 1 Hz. The data obtained from subject D suggest en enhancement of VOR gain in the post-flight period, especially on post-flight days two and four, with a return towards the value obtained in flight on the sixth day after landing. However, the lack of information on the variability of this subject's VOR gain pre-flight, precludes the conclusion being drawn that the change in gain was a significant effect attributable to exposure to microgravity.

Discussion

Measures of the vestibulo-ocular reflex elicited by Z axis angular oscillation in only two subjects are hardly sufficient to draw statistically reliable conclusions. However, the limited data yielded by these experiments do not suggest that exposure to microgravity and adaptation to this atypical force environment has any appreciable effect on the magnitude and velocity of the compensatory eye movements that are evoked, in the absence of vision, by stimulation of the lateral (horizontal) semicircular canals. It is to be regretted that measures of VOR acitivty in flight were not obtained until the subjects had adapted to microgravity, though observations of Bludworth et al. (1982) and the more recent studies of Vesterhauge et al. 1984) in contrast to their earlier experiments (Vesterhauge et al. 1982), failed to demonstrate a significant change in yaw VOR gain during the transient weightlessness of parabolic flight.

Thus our findings are in agreement with most of the investigators who have recorded the yaw VOR in weightlessness (Jackson and Sears 1965; Oosterveld and van der Laarse 1969; Bludworth et al. 1982; Vesterhauge et al. 1984). The exception is the study of Lackner and Graybiel (1981) who reported a reduction of VOR gain during zero G and an increase at 2 G. However, these authors employed intense angular stimuli (acceleration at $15°/s^{-2}$ to 300°/s with a sudden stop after 30 s) in which the nystagmic response to deceleration was confounded with that induced by the acceleration. Furthermore, they did not compute VOR gain in an acceptable manner (e.g. Slow phase eye velocity/Head velocity) but inferred changes in gain from an averaged measure of slow phase velocity during the period of angular acceleration. The published eye movement records do show a more irregular nystagmus during zero G than during 2 G, but in those sections of the trace obtained in weightlessness in which the nystagmus is well defined, the slow phase velocity is not overtly lower than in the corresponding 2 G record. The claim of Lackner & Graybiel (1981) that the gain of the VOR is decreased in microgravity is therefore questionable.

The gain of the VOR elicited by both active and passive angular oscillation at 1 Hz has a mean value of 0.63, which is lower than most of the yaw axis VOR gains reported in the literature. With passive oscillation the mean VOR gain is, typically, 0.8 (Barnes 1980); the mean gain during active head movement is slightly higher, at 0.84 (Jell et al. 1982). However, in the experiments of Jell et al. (1982) the subjects attempted to fixate an imagined stationary point with eyes open in darkness, whereas our two subjects received no specific instruction in this respect, except in the one experimental condition when a fixation light that moved with the head was presented. It is quite possible that this requirement for the subjects to suppress their VOR in one phase of the test procedure was responsible for the low gain obtained in the absence of fixation. Barnes (1983), for example, found a mean VOR gain of 0.6 at 1 Hz during passive oscillation in darkness in an experiment which investigated suppression of the VOR as the function of the retinal location of visual targets. The progressive reduction in gain with repetition of the test procedure exhibited by subject C is a manifestation of the involuntary modification of the VOR that is probably consequent upon increased familiarity with the experiment which entailed, *inter alia*, the partial suppression of reflex eye movements.

Whereas exposure to microgravity does not appear to modify the yaw VOR in the absence of vision, the demonstration of a greater suppression of the VOR post-flight, when the subject attempted to fixate a visual target that moved with the head, implies that adaptation to weightlessness involves an increased dependence on visual as opposed to vestibular mechanisms in the stabilisation of the retinal image during head movement. While it would be hazardous to attach undue weight to this finding in one experimental subject, it accords with other observations, in early post-flight tests, of a greater dominance and utilisation of visual cues for spatial orientation; notably the more powerful influence of optokinetic stimuli (Benson et al. 1984) and of a tilted visual frame of reference (Rod and Frame test, Young et al. 1984).

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