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Oculovestibular interactions under microgravity

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Summary. On a space mission in March 1992 a set of experiments were performed aimed at clarifying the interaction between visual, proprioceptive and vestibular inputs to the equilibrium system. Using the VESTA goggle facility from the European Space Agency we investigated the effect of pure neck receptor stimulation on eye position as measured by the flash afterimage method and on perception of a head-fixed luminous line in space. Space vestibular adaptation processes were measured by rotating pattern perception during prescribed head movements. It was found that static ocular counterrotation does not occur under micro gravity conditions. This result suggests that the neck receptors apparently do not contribute to a measurable extent. The subjective orientation of a vertical line was perceived correctly inflight. Obviously neck receptors on the perception level can fully substitute for the ineffective equilibrium organs of the inner ear within less than 4 days. The rotating pattern perception during different head motion patterns is not influenced by the absence of a gravity reference.

Key words: Visual vestibular interaction – Ocular counterrotation – Afterimage method – Luminous line – Neck position receptors

Orientation in man depends on an afferent information from various sense organs. It is influenced by information from the visual, vestibular, and proprioceptive system, including tactile cues from the skin, joint receptors, muscle spindles, and tendon organs. All movements of the body involve convergence of these sensory inputs followed by central processing. Among the numerous modalities permitting upright stance and gait the vestibular system, especially the otolith-macula system, plays an important role, in particular when the visual system does not provide sufficient information under poor illumination. Special importance must also be attributed to the neck position receptors. Since the head is pivoted in all directions on the trunk by the neck joints, the position of the trunk in relation to the gravity vector cannot be computed on otolith information alone; it must be calculated from at least two sources, the cervical position receptors and the otolithic system.

On earth, we are perfectly able to maintain our equilibrium when standing blindfolded in an upright position, even while keeping the head tilted 30° forward or to the side. This ability requires central computation of the otolithic and cervical signals to determine the verticality of the trunk. It was of interest to us to investigate what kind of reflexes or illusory sensations would occur if the function of one of the two systems is "eliminated" (as occurs in space with the otolith system). The situation is further complicated by the visual input. When standing upright and rolling the head laterally, for example, to the right, the visual environment as projected on the retina rotates to the same amount to the left side. However, the information from the otoliths enables us to distinguish whether the retinal shift is caused by self movement or by rotation of the environment.

In orbital weightlessness the result of this computation must be wrong and misleading since the otolith apparatus is disabled. One of the several consequences of neck deflection in space would be an illusory tilt sensation of the environment and of the trunk to the contralateral side [2]. A pilot study during the Spacelab D-1 mission showed that in space ocular torsion and illusory shifts of a head-fixed target cross can occur during active movements of the trunk in the roll axis while the head is fixed [4]. Neither ocular roll nor illusory roll of a target was reported before flight on the ground by the same subject [2]. If in space the distinction between self and object motion is impaired, temporary dizziness and disorientation occur. This is most likely caused by a mismatch between the signals from the otolith apparatus and the cervical position receptors [2, 3]. Informal observations of the D-1 crew indicated that illusory sensations of

Abbreviations: OCR = ocular counterrotation; VOR = vestibulo-ocular reflex self or object motion also occurred following active deflection in the foot joints [2]. This indicates an increased "weighting" of proprioceptive information after space vestibular adaptation, when the otolith system is disabled [3]. A similar report was available from one astronaut of the Spacelab International Microgravity Laboratory 1 mission who experienced instability of the visual surroundings during body motion.

Aside from subjective perception changes the lack of the gravitational force on the otoliths in space allows one to investigate the function and interaction between the visual, proprioceptive, and vestibular inputs to the equilibrium system in better isolation. Therefore a set of experiments were performed.

1 Ocular counterrotation experiment

The effect was determined of pure neck receptor stimulation on eye position as measured by the flash afterimage method. In normogravity static ocular counterroll appears after rolling the head and trunk together around a naso-occipital axis. Its magnitude is about 10% of the head roll angle for the first 30° of roll. This was measured, for example, with a scleral search coil technique by Collewijn et al. [9] when they tilted the head to steady positions up to 20° from the upright position. In keeping with this Kass et al. [21] arrived at a mean ocular counterrotation (OCR) angle of 3.8° for a 30° head and body tilt.

The OCR angle is commonly assumed to be otolith mediated. When one changes the otolith load, for example, on a centrifuge or in parabolic flight, the OCR magnitude can be expected to vary. Teiwes et al. [27] tested six subjects in parabolic flight and reported that OCR is linearly dependent on the force environment, yielding no OCR in microgravity. A presentation by Teiwes at the 1992 Montreal meeting of the International Astronautical Federation showed six subjects, with a mean OCR of about 0° in microgravity, 3° at normogravity and 5° at 1.8 g_z. These subjects rested on their side and had their heads immobilized from pull-up throughout the parabola until pullout, i.e., from hypergravity through microgravity and into hypergravity again. The body attitude corresponds to a head and body roll of 90°, i.e., without any neck bend. Interestingly, the amount of OCR is not markedly higher than that found already at 20°–30° of roll tilt.

Results by Kass et al. [21] furthermore suggested that neck position receptors do contribute an additional component to ocular counterroll. In their experiments, the OCR angle was found to be greater when otoliths plus neck receptors were stimulated, by rolling the head while the trunk remained stationary, as opposed to an otolith only stimulation by a roll of head and trunk together. The difference in five subjects was 5.0° versus 3.8°. This suggested a possible neck receptor mediated OCR component contributing in an additive manner.

After Teiwes et al. [27] had found no OCR under microgravity when head and trunk were tilted together, we were interested to look at a paradigm in which the neck was bent under weightlessness. The OCR experiment thus looked at the consequences on ocular roll movements of bending the neck. Under microgravity conditions the otolithic input is absent, and only the signals of the neck position receptors are present in tilted head positions. We expected that some amount of static OCR would still be present, but that it would be smaller than in the measurements under 1-g conditions.

This experiment was performed before and after the flight, with a slightly different hardware, already before and after the Spacelab 1 and D-1 missions [5, 21]. We were thus, in addition, setting out to increase the number of data points for OCR measurement under pre- and post-flight conditions. After the Spacelab 1 and D-1 missions the OCR gain of the astronauts was reduced compared to the preflight measurements, supporting the view that during space vestibular adaptation the otolithic gain diminishes.

2 Luminous line experiment

The effect was determined of pure neck receptor stimulation on perception of a head fixed luminous line. Under normal gravity subjects can set a luminous line to the true vertical with an error of almost 0 when upright [7]. The further they are tilted in the frontal plane from vertical, the less reliable their settings become, with the error increasing to an overcompensation (Müller, or E, effect) for tilt angles up to about 60° [13, 26, 28].

Changes in the vestibular processing were investigated by looking at the conscious effects of subjective orientation of a head-fixed luminous line. Ground-based studies have shown that such subjective roll of a luminous line occurs when the head is tilted in roll to an extent clearly surpassing any ocular roll effected [1, 10, 11, 29]. We hypothesized, as with ocular roll, that vestibular and neck impulses are additive. Therefore, and in accordance with other orientation experiments [4, 20, 23], we

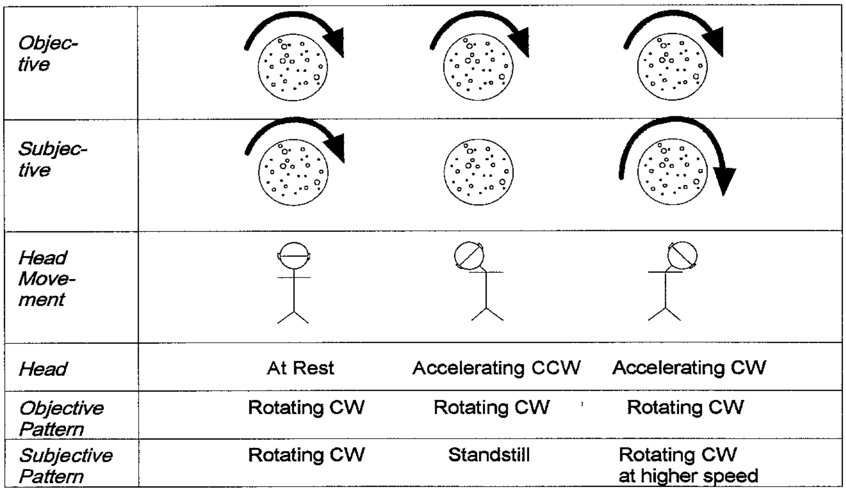

Fig. 1. Situation of visual scene during the minidome experiment *CW*, clockwise; *CCW*, counterclockwise

predicted that under 1g the combined cervical and vestibular stimulation by head roll allows the most exact resetting of the luminous line as subjective vertical to the true vertical. In the absence of otolithic information (0 *g*) the deviation of the subjective vertical from the true vertical would be more pronounced.

3 Minidome experiment

The subjective pattern movement cancellation speed was determined for a roll pattern. This experiment should determine the "weighting" of visual versus vestibular signals during self and object motion in space. While performing timed and standardized oscillating rolling movements of the head to the left and right shoulder, the rotating dotted visual pattern of a minidome was observed. The angular velocity of the minidome can usually be adjusted by the subject in such a way that the optokinetic pattern seems to be at rest when tilting the head against the pattern's turning direction (Fig.1). It can in fact be seen at appropriate head motion speed as moving twice as fast as the actual physical pattern speed in one direction and standing still in the other direction (under 1-g conditions). The ratio of pattern versus head movement speed is almost constant for any given subject [19].

Results of vestibular experiments obtained in the Spacelab 1 and D-1 missions suggest that space vestibular adaptation is accompanied by an increased weighting of visual and decreased weighting of vestibular signals [4, 22]. Concerning the minidome experiment this leads to the prediction that given the same head motion speed a decreased minimal rate of rotation of the minidome during which virtual standstill is achievable will be found initially. Changes in visuovestibular processing, found for linear pattern under microgravity [6], suggest, in addition, that the ratio and the absolute values vary over the course of adaptation to the microgravity state. Accordingly, when the gain of the visual system is increased during the course of the mission, the "standstill velocity" would be found to be decreased. In this way information about the respective contribution of otolith and canal apparatus on the standstill effect is expected.

Materials and methods

Subject

The subject was a 39-year-old male payload specialist. The space authorities confirmed that he was healthy and had no vestibular abnormalities throughout the test periods reported here.

Equipment

All experiments were performed using the VESTA goggle facility from the European Space Agency which is described elsewhere [14]. Basically the equipment consists of a head-fixed mask with various tubular inserts carried on a face plate in front of the subject's eyes. The inserts carry a camera for recording the eye position, allow generation of a rod-shaped afterimage for measurement of ocular roll, present a red luminous line for subjective alignment, and present the rotating dot pattern for the cancellation trial. All optical presentations were visible without other visual references. The head position in relation to the trunk position was

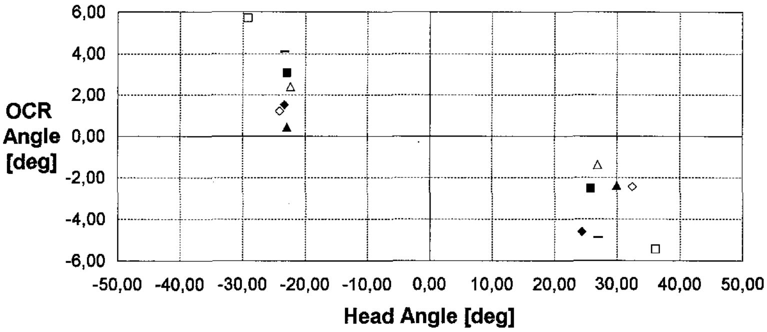

Fig. 2. Mean ocular counterroll settings for pre- and postflight sessions. Positive head roll and OCR angles are clockwise, as seen from the subject, negative are counterclockwise. ■ Mean OCR 12.02.; □ Mean OCR 17.02.; ◆ Mean OCR 10.03.; ◇ Mean OCR 26.03.; ▲ Mean OCR 28.03.; △ Mean OCR 30.03.; – Mean OCR 01.04.

measured by a goniometer. Eye pictures were recorded on videotape for postflight evaluation on the ground. Ocular roll angles measured by the afterimage method were accessible already during the mission on board, as were the luminous line data and the cancellation speed settings. These data were also stored on RAM cards of an Atari portfolio computer and taken back for postflight evaluation.

Procedure

All experiments were performed three times before the flight (35, 30, and 7 days before launch), three times inflight (1, 3 and 5 days onboard a space station) and four times after the flight (1, 3, 5, and 7 days after return). During all sessions the subject was sitting upright wearing the VESTA goggle.

For the OCR experiment the following procedure was conducted. In an upright head position the subject set the luminous line vertical and pushed a button which triggered a thin flash line coincident with the luminous line. He then tilted his head 30° to the left or right shoulder and reset the luminous line to his afterimage. Since the goggle was head fixed the difference of the two settings reflected the amount of OCR. This procedure was repeated five times for right and five times for left head tilt.

For the luminous line sessions the subject adjusted in an upright head position the luminous line to subjective vertical. Then he tilted his head 30° to his left or right shoulder and reset the luminous line back to the vertical position (where the subject thought "vertical" was; usually parallel to the vertical axis of his body) well after the motion has ceased. The difference of these two settings was measured. The procedure was carried out five times each for left and right head tilt.

For the minidome experiment the subject performed head movements 30° to the left and right shoulder in a rhythm of 0.2 Hz, 0.7 Hz, and 1 Hz. The rhythm was set by a metronome. The subject adjusted the angular velocity of the roll pattern to the maximum speed at which he still perceived the pattern as stationary during one-half of the cyclic head motion. The profile of the head movements and the adjusted pattern velocity were recorded. The pattern velocity found in this manner, i.e., the objective rotary velocity corresponding to subjective pattern arrest, is referred to here as pattern arrest speed. The measurements were taken during clockwise and counterclockwise rotation of the optokinetic pattern for each frequency.

Results

Ocular counterrotation

Nonzero data are available only for the pre- and postflight baseline data collection. During the flight our subject reported that he was unable reliably to align the luminous line with his flash afterimage because the afterimage turned on its own after 10–12 s to the previous position. This was the case even when he tried head movements with different amplitudes and velocities, varying the experiment of his own accord. Every time he could see the two lines became parallel again.

The results of the static OCR measurements are shown in Fig. 2. Each data point represents the mean OCR angle of five trials in relation to the angle of head tilt. Table 1 presents the angles and their standard deviations.

There appeared to be a slight tendency for smaller OCR angles upon left head tilts than for right tilts. The means over all left head tilts did not differ significantly from right tilts, however (2.86° versus 2.23°).

Figure 3 shows the ratio of OCR angle indicated in relation to the head tilt. This is a measure of "gain" of the processing of inputs. The first three values after landing were notably smaller, with a mean of -0.06, compared to the preflight mean of -0.14.

Table 1. Ocular counterroll values

Test date	Variable	Mean right	Mean left	SD right	SD left
12 February	Head roll angle	25.86	−22.92	3.44	1.75
	OCR angle	−2.53	3.08	3.11	3.83
17 February	Head roll angle	36.11	−29.21	4.38	2.23
	OCR angle	−5.45	5.70	1.96	0.66
10 March	Head roll angle	24.35	−23.33	1.71	1.64
	OCR angle	−4.61	1.53	2.64	5.15
26 March	Head roll angle	32.46	−24.11	4.22	2.64
	OCR angle	−2.44	1.22	1.84	2.88
28 March	Head roll angle	30.01	−22.89	5.43	2.17
	OCR angle	−2.39	0.45	1.22	3.15
30 March	Head roll angle	26.92	−22.35	2.86	4.25
	OCR angle	−1.36	2.41	2.53	1.98
01 April	Head roll angle	−27.00	−23.28	4.06	4.28
	OCR angle	−4.90	4.11	0.97	3.46

Luminous line

Figure 4 presents the settings of the pre-, in- and postflight measurements in relation to the angle of head tilt, and in Fig. 5 the ratios of these are shown. As can be seen, there was no significant difference between the pre- and postflight settings. At most there was a minute overshooting of the luminous line settings for left head tilts.

On flight day 1 (actually the first day on board the space station but the third day in microgravity) upon right head tilt a marked overcorrection occured. An average right head tilt of 10° – notably less than trained for – was answered by up to 30° of line correction, with a mean of 18°. On the left side the mean head roll angle was still below the trained range with 14°, the correction angle, however, was

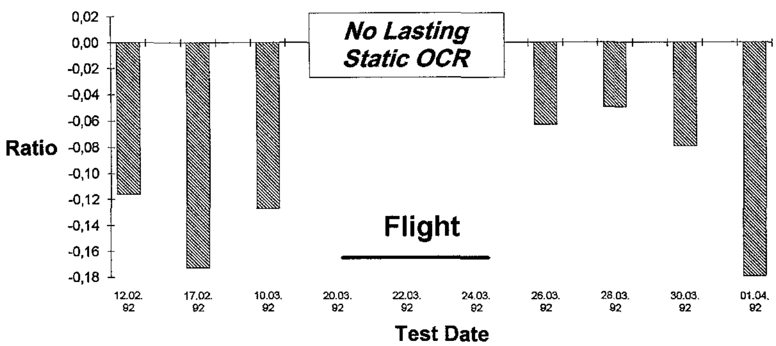

Fig. 3. OCR ratios for static head tilt. The ocular counterroll angle has been divided by the head roll angle. Data are the mean of left and right head rolls, each measured five times per test session

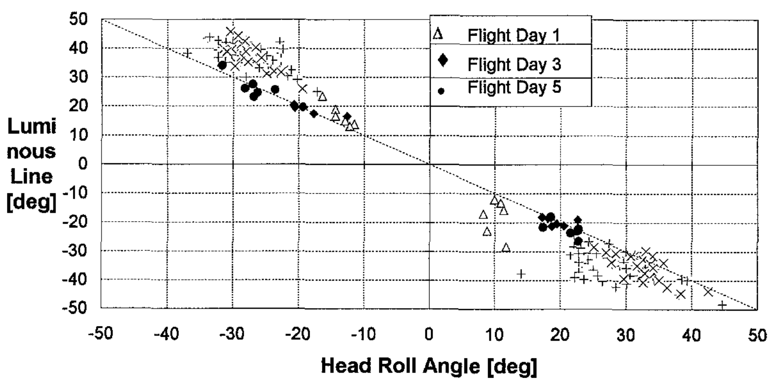

Fig. 4. Luminous line settings for static head tilt. Positive head roll and luminous line angles are clockwise, as seen from the subject, negative are counterclockwise. *Dotted line*, positions with head and line angle of equal magnitude (unity gain); + Preflight values; × postflight values. Note the data points for flight day 1 and right head tilt deviating more than average from the unity gain. The data point at about 15° head tilt and 37° line angle most likely is a spurious anomaly

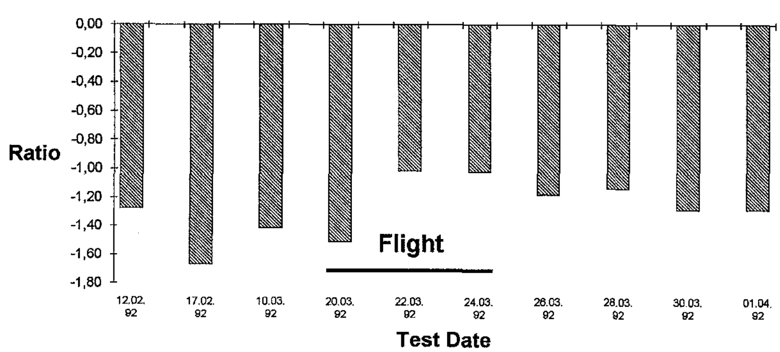

Fig. 5. Luminous line ratios for static head tilt. The luminous line correction angle has been divided by the head roll angle. Data are the mean of left and right head rolls, each measured five times per test session

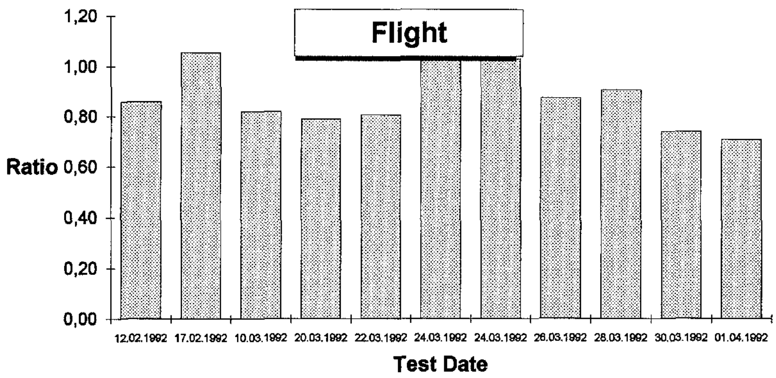

Fig. 6. Pattern arrest speed ratios for dynamic head roll. Data are means of three head movement frequencies (0.2, 0.7, and 1 Hz) and clockwise and counterclockwise rotating visual pattern

almost veridical with a mean of 17°. Flight days 3 and 5 were remarkable for their adherence to the unity gain line.

Looking at the ratios in Fig. 5, the mentioned overcompensation was apparent in ratios above 1 for all pre- and postflight tests and on flight day 1. On flight days 3 and 5, however, the subject was able to set the line almost perfectly; the ratio was close to 1.

Minidome

Head motion velocity and pattern velocity varied inflight from preflight values (not shown here). Since, however, the relevant parameter was less the absolute values than their relationships, only ratios are considered here. The ratios of the velocity of head movements and the "subjective standstill velocity" are presented in Fig. 6. These data are the mean values over the three frequencies and both clockwise and counterclockwise pattern directions. As can be noted, the subject performed the minidome experiment twice on the last inflight day.

On first sight one might find that this inflight day (24 March 1992) showed a 20° increase from 0.8 to 1.0 over the other flight days. However, a ratio of about 1 had already been found once before the flight.

In summary, there was no marked difference between the pre-, in- and postflight values.

Discussion

Ocular counterrotation

The OCR angles found before and after the flight corresponded well with the literature [10, 11, 15]. However, the expected neck receptor mediated OCR component inferred from the data of Kass et al. [21], did not materialize inflight.

The hypothesised reduction in OCR gain appeared to be present for at least 5 days after the flight. This confirms results found after Spacelab 1 and D-1 [4]. At that time, however, the re-adaptation may have occurred faster, reaching preflight values on the third day after the flight, whereas in this study it took 5 days. There is no apparent reason for this difference in time course, and it may well be that they represent the normal variations in biological experiments.

The firmness and precision of the comments by the subject appear to leave no doubt that under microgravity no static OCR at all remained. The dynamic OCR which occurred and vanished was most likely caused by the vertical semicircular canals. The time constant which our subject reported as 10–12 s agrees with the range found, for example, by Hain and Buettner [17] for 30° head rolls of 15.7 ± 4.0 s for the horizontal and 11.0 ± 1.4 s for the vertical vestibulo-ocular reflex (VOR) component.

Our initial assumption was that neck receptors add a component of their own to the OCR input, independent of the otoliths; this component would be unchanged by the gravity level. Assuming for the moment that data from one subject can be conclusive, one must most likely abandon this hypothesis. There clearly was no purely neck receptor mediated OCR component under microgravity. We are left then with the conclusion that the additional component stems from a mechanism resulting in a modification of the otolith information processing. This mechanism apparently arises in the neck receptors. The loss of the otolith information under microgravity would then make any modifier ineffective. Such a mechanism might take the form of an increase in gain of the otolith processor, as was made plausible by Dichgans et al. [12] for eye-head movements in the horizontal plane. On the other hand, it might consist of an otolith-gated addition of a neck receptor signal to the otolith signal. Which of these two it is will have to be investigated in future studies.

In the view of the results of OCR experiments carried out on labyrinthectomized patients or animals there are additional explanations for our findings. Krejcova et al. [24] found in healthy monkeys nearly the same amount of static OCR when the head or the whole body was tilted laterally. After bilateral labyrinthectomy smaller but definite amounts of static OCR were induced by head or whole body tilts. These authors thought that in an intact animal static OCR is induced mainly by the otolith organs. In the absence of the labyrinths, however, other types of somatosensory afferents responsive to gravity influence the steady angle of torsion of the eyes. Similar results from bilaterally labyrinthectomized subjects were reported by Bles and de Graaf [8]. In their patients head tilts and whole body tilts led to a considerable static OCR, demonstrating substitution of other sensory modalities for the lost vestibular function. This somatic gravity information could be mediated by mechanoreceptors that measure forces acting on the limbs and/or skin. From experiments with paraplegic patients Mittelstaedt [25] concluded that nonvestibular gravity reception should contain two distinct systems. One is located in the trunk, and the other one is probably stimulated by the influence of gravity on the cardiovascular system.

Comparing these findings with our data obtained in microgravity, we conclude the following. (a) The greatest part of the activity responsible for static OCR arises in the otolith organs. (b) There must be at least a second source of gravity receptors in the body which also influence the static OCR. (c) This second source cannot be the neck position receptors since they do not induce a significant amount of static OCR when stimulated alone. This situation occurs in microgravity where no force is acting either on the otoliths or on the body of the subject.

Luminous line

The pre- and postflight data were as expected [13, 15, 20]. Somewhat to our surprise, the subject was able to reset the line veridically on flight days 3 and 5. Apparently at this time the neck receptors were able to supply a sufficient signal to allow the computation of the trunk position with respect to head and retina. It appears plausible that at the level of perception the missing otolith input was totally supplanted by neck receptors.

We must note in passing that our subject, due to extensive training, including nauseogenic vestibular stimuli, had been deconditioned already before the mission from using the vestibular otolithic inputs at least under some circumstances (see Wetzig et al., this issue). It stands to reason that he then used other sensory cues, such as the neck inputs, with a greater facility and to a greater extent than would have been found in "naive" subjects.

Minidome

Based on experiments looking at cyclorotatory nystagmus (e.g., [9]) and linear VOR (e.g., [17]), we had initially assumed the pattern arrest to be an interaction between the visual system and the semicircular canals, modulated by the otoliths. This assumption was confirmed when we found a change in pattern arrest speed on a ground based rotary chair dependent on head and whole body position [18, 19]. Up to this point there appeared to exist a clear otolith influence on the pattern arrest speed. We were thus confident that we had a straightforward and well-controllable model for visual vestibular interaction at hand. In keeping with results found for linear VOR [6] we expected the visuo-vestibular interaction to change when the otolith influence was removed under microgravity.

The frequency dependence of the otoliths is well known (see, for example, the Bode plot in [16], p.73). Had there been a strong otolithic influence one would have found that the pattern arrest speed varies systematically with stimulus frequency under 0 *g*. The fact that it did not vary between ground-based and space experiments suggests that the hypothesized change in visuo-vestibular weighting does not take place measurably during this experiment. The variation of head movement frequency did not yield a consistent trend (it is not shown in detail above for this reason), supporting this view. Apparently the otoliths play a much smaller role than thought (but see the caveat concerning $n=1$ in the luminous line paragraph). The modulation of pattern arrest speeds seen on the ground under changing head positions [19] might, in view of the results reported here, result more from the changing constellation of the semicircular canals than from otolith inputs.

Complicating the interpretation of the results is the fact that the head acceleration was performed manually. Although our subject was well trained, manual head movements were sinusoidal in profile, thus presenting a constantly changing stimulus and subsequently a wider scatter of data.

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