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Original Contribution

THE EFFECT OF HEAD-TO-TRUNK POSITION ON THE DIRECTION OF ARM MOVEMENTS BEFORE, DURING, AND AFTER SPACE FLIGHT

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□ Abstract — This contribution deals with the examination of the consequences of different head-to-trunk positions on arm movements under normal gravity and during prolonged space flight. One of the objectives of this study was to investigate the influence of weightlessness on the condition of the spatial analysis system. Aimed arm movements in the horizontal plane (pointings towards two visual targets) were recorded, first with eyes open, head straight (learning part), then with eyes closed, head straight and during yaw or roll position of the head (performance part). Measurements related to these different head-to-trunk-positions were taken in one short-term and nine long-term cosmonauts preflight, inflight, and postflight. Terrestrial control experiments were carried out with an extended experimental design in 14 healthy volunteers. The analysis of these experiments revealed that, with eyes closed and the head in yaw position, cosmonauts before flight and control subjects exhibit significant slants of the movement plane of the arm. Contrary to terrestrial measurements, in space experiments roll tilt of the head to the right is correlated with considerable counterclockwise slant of the movement plane. This slant of the movement plane of the arm was interpreted as tilt of the internal representation of the horizontal coordinate. The effect is larger with greater distortion induced by the changed head position and with larger muscular involvement to keep this position. This effect is also increased by the reduction of information (for example, in microgravity). The amount and the direction of the horizontal offset of the arm movements are shown to be dependent on the head-to-trunk position, too. Additionally, we have found changes in the amplitude and in the duration of the arm movement, in the vertical offset, and in the curvature of the movement paths, depending on the experimental conditions. © 1998 Elsevier Science Inc.

□ Keywords — arm movements; weightlessness; head-to-trunk position; subjective horizontal.

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Introduction

The control of posture and motion is morphologically as well as functionally adapted to gravity. Therefore, staying in microgravity produces a variety of deficits in man. The disturbances reported inflight, but also postflight, range from impairment of simple sensorimotor skills (for example, 1–3) to changes in postural control (4–6), disorders in functions of the musculoskeletal system, coordination disturbances, and changes in the systems of motor regulation (7–9). Weightlessness causes modifications in the central interpretation of afferent signals from the otolithic organ, from proprioception and from exteroception. The reference system used for spatial orientation based on gravity is lost. In evaluating spatial coordinates, the perception relies mainly on the stable, gravitationally independent sensory systems. The visual information as well as the signals from skin and joint receptors are not modified during the exposure to microgravity. Therefore they are preponderant at the beginning of space missions for the recalibration of other sensory cues affected by weightlessness.

Nevertheless, in orbit, perception of the position of head, trunk, and arms relative to each other and to the environment is impaired (10–13), but not dramatically. This might be due to an internal cognitive image of the body called body scheme (14). This body image establishes the central motor program that controls the maintenance of a given posture. A postural control system that is based on such a hypothetical body scheme may be more resistant to changes in the environment and to loss of information (4). In spite of this body scheme, our motor system needs to be regularly updated by sensory information. Experiments with a deafferented man showed that it was possible to execute a large repertoire of learned manual motor tasks with both speed and accuracy, despite lacking any useful feedback of the hand (15). Although the patient was successful in laboratory tasks, his hands were virtually useless to him in everyday life. Spacelab-I and D-I astronauts reported degraded perception of limb position when the individuals were relaxed with their eyes closed. They did not know "where their limbs are." If they tensed, their muscles "got back" information (16). Subjects experienced the same phenomenon in prolonged body tilt. They were not aware of their position in space if they did not tense their muscles (17). Joint afferents seem to possess a very limited capacity to provide kinesthetic information. They appear to be important only in situations when muscle spindle afferents cannot contribute to kinesthesia (18).

To understand the complex adaptive process of human spatial orientation, an "optimal estimator" has been postulated that mixes external cues detected by the sense organs with internal model representations of body dynamics and constantly updates its estimate of spatial orientation (19). It was concluded from experiments that internal sensorimotor models provide a common reference for both spatial orientation and postural control (20).

Perception of one's body spatial configuration originates from information processing from gravireceptors like the otolith organs and exteroceptors and proprioceptors. For estimating the trunk position in space, messages from neck receptors must be added to information about the deviation of the head from the vertical. Thus, a measure of the deviation of the trunk from the vertical results (21). Proprioceptive neck muscle afferents gain direct access to vestibulospinal, vestibulo-ocular, and other secondary and even higher order vestibular neurons. On these neurons there is an extensive convergence of proprioceptive neck and labyrinthine afferents (22). The neck afferents inform about the head-to-body position and are important for the ideotropic body reference. It is known that changing the position of the head relative to the trunk affects the perception of the subjective vertical and the subjective horizontal (23–26). With the head in yaw or roll position, the precise adjustment of the visual or postural subjective vertical is more difficult (27,28). Therefore, the special aim of our experiments was to study the influence of microgravity on the spatial localization of arm pointings following yaw or roll position of the head.

Material and Methods

Nine cosmonauts, one of them had been in orbit twice, were investigated in preflight, inflight and postflight tests. The inflight time of the cosmonauts (8 male, 1 female; age range 31 to 47 years; mean age: 41 years) was 1 week (1 cosmonaut), 4 to 8 months (mean value 5.3 months), and 14 months (1 cosmonaut). The short-term cosmonaut carried out the tests on the 2nd and 5th day of flight, the other cosmonauts after the first 3 weeks inflight. The following measurements were performed inflight approximately once a month during prolonged exposure to microgravity. The postflight tests were on the 2nd and 5th days after landing. Fourteen healthy, paid volunteers (students, age range 20 to 28 years) served as controls in terrestrial experiments. All subjects gave informed consent to participate in these experiments.

The aimed arm movements were pointings towards two visual targets, presented on a LED-matrix in front of the subject (11.7° to the left and to the right in the horizontal plane, distance 1.6 m, Figure 1) (9). The arm pointer was always placed on the right hand, and the subjects were right-hand dominant. Visual feedback regarding pointing accuracy during eyes-open conditions was provided by a laser beam. The position of the arm was measured using a MONIMIR 3D registration system, consisting of an armlamp with 3 IR-LED's, and two IR scanning cameras (sampling rate 25 Hz). The subject carried a helmet equipped with IR-LED's in order to register three-dimensional head movements. It was not possible to record the final static head position throughout the test because after tilting the head to the right shoulder more than 30° and after rotating the head to the right shoulder more than 50° the sensors were out of range. The device was constructed for other experiments to register dynamic head movements in minor ranges. But the continuance of the correct head position was controlled by the second cosmonaut in space or by the experimenter on Earth. Biosignal amplifiers were recording electro-oculography (EOG).

On Earth the subjects were sitting upright on a chair; in the space lab MIR they were fixed in supine position on the floor by belts (pelvic, thoraxic) with the head moving freely. The test subject was asked to localize the two alternately flashing LED's (frequency 0.25 Hz) as accurately as possible and, after closing the eyes, to repeat this learned movement from memory. No other instruction was given to the subject, especially not which coordinate (head, trunk, or gravity) should be used as reference. Thus, a test was divided into two parts: after 6 pointings with eyes open (learning phase), the subject had to close the eyes, to change the head position if required, and to repeat the movement 10 times (performance phase).

These movements of the arm in the horizontal plane were executed in three head positions: head straight (HS), head rotated to the right shoulder (Yaw, range 50° and more), and head tilted to the right shoulder (Roll, range 30° and more). In the experiments with the cosmonauts, only head positions to the right were tested, and the eyes were always closed in the performance part. In the control experiments, head position to the right was compared to head position to the left. The eyes were either open or closed in the performance part (Table 1). Therefore, the input to the visual and the proprioceptive system was not always changed simultaneously, as it happened in the space experiments. One test lasted about 45 s. In the experiments with the cosmonauts, 3 tests were done in 1 session; in the control measurements, 2 times 10 tests were carried out randomly mixed.

The pointing arm movements were divided into sequences, in left-directed (negative) and

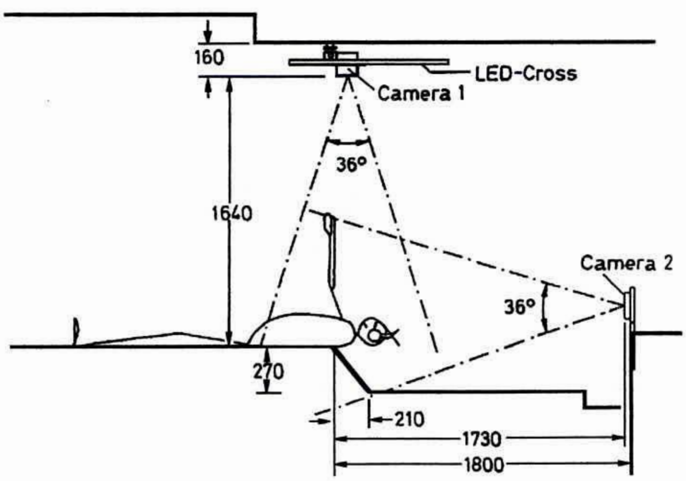

Figure 1. Schematic drawing of the test situation in the MIR Space Station. Cameras are mounted in front of the face (camera 1) and in the longitudinal axis of the body (camera 2). The visual targets are presented on a LED matrix mounted with camera system 1.

Table 1. Experimental Design of the Preflight, Inflight, and Postflight Experiments (10 Cosmonauts) and of the Terrestrial Control Experiments (14 Volunteers): Learning Phase (6 Arm Pointings) and Performance Phase (10 Arm Pointings).

	Experimental Design			
	Cosmonauts		Control Group	
	Learn. Ph.	Perform. Ph.	Learn. Ph.	Perform. Ph.
Eyes open				
Head yaw				+ (R and L)
Head straight	+		+	+
Head roll				+ (R and L)
Eyes closed				
Head yaw		+ (R)		+ (R and L)
Head straight		+		+
Head roll		+ (R)		+ (R and L)

R = head to the right side; L = head to the left side.

right-directed (positive) movements. These sequences were treated by vectors, which were the difference between final and initial position of the laser spot on the target plane. A special marker program was created to determine these vectors autonomously. The amplitude (length) of the movement and the duration, the angle between the horizontal LED-line and the movement plane of the arm (slant), the amount of vertical and horizontal offset, and the curvature of the movement were evaluated. Curvature is the amount of vertical deviation of the curved movement trajectory from the straight line connecting start and end point of the movement.

x_{initial} = *horizontal component of initial position.*

y_{initial} = *vertical component of initial position.*

t_{initial} = *time at initial position.*

x_{final} = *horizontal component of final position.*

y_{final} = *vertical component of final position.*

t_{final} = *time at final position.*

y_0 = *vertical component of position at time* $\frac{1}{2}(t_{\text{initial}} + t_{\text{final}})$.

$$\text{Amplitude} = \sqrt{(x_{\text{final}} - x_{\text{initial}})^2 + (y_{\text{final}} - y_{\text{initial}})^2}\,.$$

$$\text{Slant} = \arctan\frac{y_{\text{final}} - y_{\text{initial}}}{x_{\text{final}} - x_{\text{initial}}}\,.$$

$$\text{Duration} = t_{\text{final}} - t_{\text{initial}}\,.$$

$$\text{Vertical Offset} = \frac{1}{2}(y_{\text{initial}} + y_{\text{final}})\,.$$

$$\text{Horizontal Offset} = \frac{1}{2}(x_{\text{initial}} + x_{\text{final}})\,.$$

$$\text{Curvature} = y_0 - \frac{x_{\text{final}}y_{\text{initial}} - x_{\text{initial}}y_{\text{final}}}{x_{\text{final}} - y_{\text{initial}}}\,.$$

Multiple analyses of variance were done to indicate any significant differences among the experimental sets. In this article, the spatial parameters are of primary interest. These are the slant, the horizontal and the vertical offset, and the curvature of the memorized movement (Figure 2).

Results

Flight Data in Comparison to Preflight and Postflight Data

Slant. After closing the eyes, variability increases in all cases, markedly pronounced inflight. Multiple analyses of variance (MANOVA) showed that there are highly significant ($P < 0.001$) differences in the slant, depending on the head-to-trunk position, on the gravity level, and on the target position. There is also a highly significant ($P < 0.001$) interaction between the first two

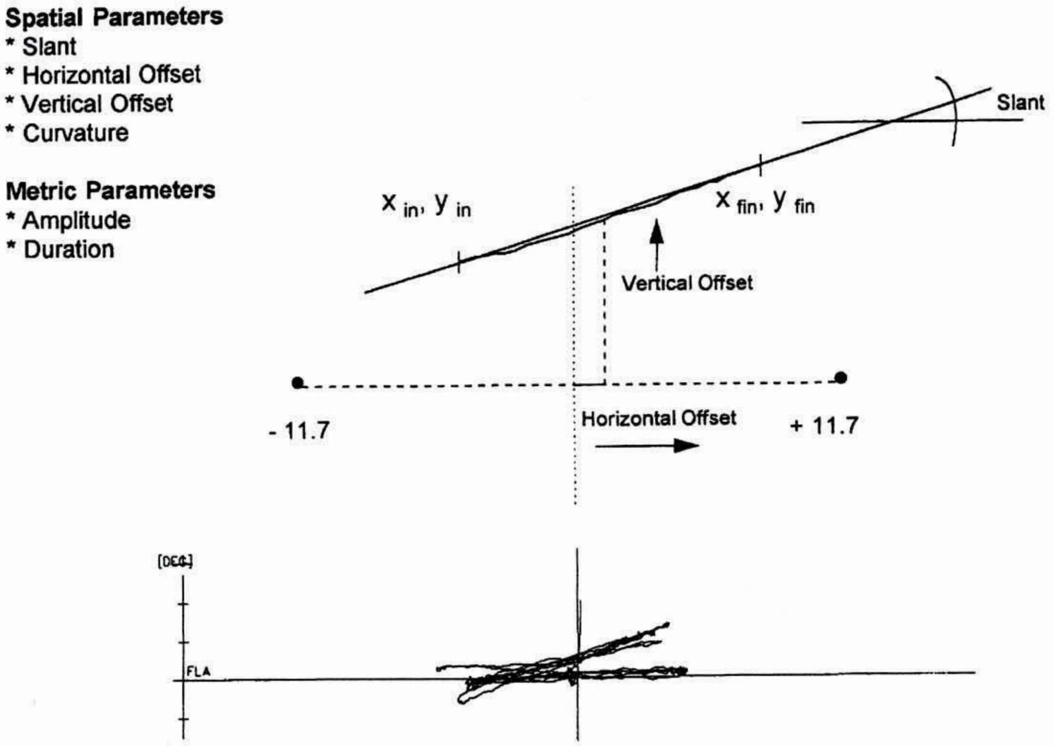

Figure 2. The upper graph shows the explanation of the spatial parameters as indicated by the formulas in the text. The lower graph presents original movement sequences (head in roll position, inflight for 13 months, the horizontal pointings were done in the learning phase, the tilted ones in the performance phase with eyes closed).

factors (Table 2). When head position is changed, the slant increases, that is, the counterclockwise roll of the movement plane gets strongly marked. In the preflight sessions, yaw of the head to the right shows a highly significant effect; roll of the head enlarges the slant to a lesser degree (Figure 3). Inflight, there is an opposite effect: a highly significant slant of the movement plane of the arm is produced by roll of the head. The difference in the response between yaw- and roll-position decreases in the postflight sessions, and there is a tendency towards preflight dominance of yaw (Figure 4a).

Horizontal offset. Additionally, the arm movements may shift laterally. Preflight, there is a remarkable shift of the arm movements to the left with yaw head position to the right, which decreases inflight and enhances again postflight. Inflight, with head roll tilt to the right and eyes closed, a contrary tendency is found: roll position of the head correlates with shifting of arm movements to the right (Figure 4b). The MANOVA (Table 2) shows highly significant differences ($P < 0.001$) in the horizontal offset, depending on head-to-trunk position and target position, and a significant interaction between head-to-trunk position and gravity level.

In comparing the short-term cosmonaut VF (5 days in weightlessness) with long-term cosmonauts, some remarkable facts can be seen: Figure 5 presents the slant of the arm movements of the short-term cosmonaut. Pointing movements on the second and on the fifth day of spaceflight indicate the largest slants ever seen in all experiments, especially in roll tilt of the head. But the large effect is limited to the inflight condition; on the 2nd day after landing no after-effect is measured. The time constant of readaptation seems to be shorter after short du-

Table 2. Results of Analysis of Variance: Experiments with 10 Cosmonauts Preflight, Inflight, and Postflight Data of the Performance Part Only.

	A: Head-to-trunk Position					B: Gravity Level					C: Target Position				
Dep. Variable	SS	df	MS	*F*-Ratio	Sig. lev.	SS	df	MS	*F*-Ratio	Sig. lev.	SS	df	MS	*F*-Ratio	Sig. lev.
Amplitude (Length)	1375.65	2	687.83	22.9	0**	360.35	2	180.18	6	0.0025**	91.67	1	91.67	3.05	0.0808
Duration	0.54	2	0.27	6.93	0.001**	9.72	2	4.86	125.23	0**	0.02	1	0.02	0.5	0.4879
Slant	1557.4	2	778.7	21.96	0**	415.08	2	207.54	5.85	0.0029**	420.91	1	420.91	11.871	0.0006**
Horizontal Offset	405.74	2	202.87	34.56	0**	8.19	2	4.09	0.7	0.5	274.84	1	274.84	46.82	0**
Vertical Offset	52.19	2	26.1	5.39	0.0046**	267.09	2	133.54	27.6	0**	1.96	1	1.96	0.41	0.531
Curvature	63.94	2	31.97	5.91	0.0027**	126.99	2	63.49	11.75	0**	34.65	1	34.65	6.41	0.01**
Interaction															
Slant	A × B				0**										
	B × C				0**										
Horizontal Offset	A × B				0**										
Vertical Offset	A × B				0.0117*										
Curvature	B × C				0**										

* Difference in mean-values significant at the .05 level.
** Difference in mean-values significant at the .01 level.

ration flights, but by testing after postflight day 1, important transient effects might have been missed. In the 14-month space flight, there is a tendency to increased slants with roll tilt of the head towards the end of the flight, which cannot be seen in the yaw-position.

Vertical offset. The values differ significantly ($P < 0.001$) according to head-to-trunk position and gravity level (interaction: $P = 0.012$). Roll and HS inflight cause ascending movement paths, just as in postflight yaw and roll. No dependency on the direction of movement is found (Figure 4b).

Curvature. As well as for head-to-trunk position, gravity level, and target position, there is a significant difference ($P < 0.001$) in the amount of curvature. Postflight A and postflight B are the highest values, with maximal standard deviations (Figure 4b). The direction of movement influences the amount of straightness, but only inflight (gravity level and target position, interaction of $P < 0.001$). Right-directed movements have significantly higher positive values than left-directed movements, above all, in the roll position of the head.

Amplitude. The amplitude depends significantly on the head-to-trunk position and on gravity level ($P < 0.001$). The amplitudes are reduced after closing the eyes and changing the head position. The head-straight position produces the highest values of amplitude, preflight, inflight, and postflight; the yaw position of the head produces the lowest.

Although there is a tendency to reduce the amplitude in change-over situations (preflight to inflight, eyes open to eyes closed, head straight to head in yaw or roll), there are a few cosmonauts who augment the amplitude in these conditions (Figure 6). The difference (amplitude eyes-closed minus amplitude eyes-open) includes all experiments of a cosmonaut (eye-effect); the difference (amplitude preflight minus amplitude inflight) includes only the performance phase with eyes closed (flight-effect). Positive values indicate "augmenter"; negative values indicate "reducer". There is a correlation between the behavior of the cosmonauts in these two different situations.

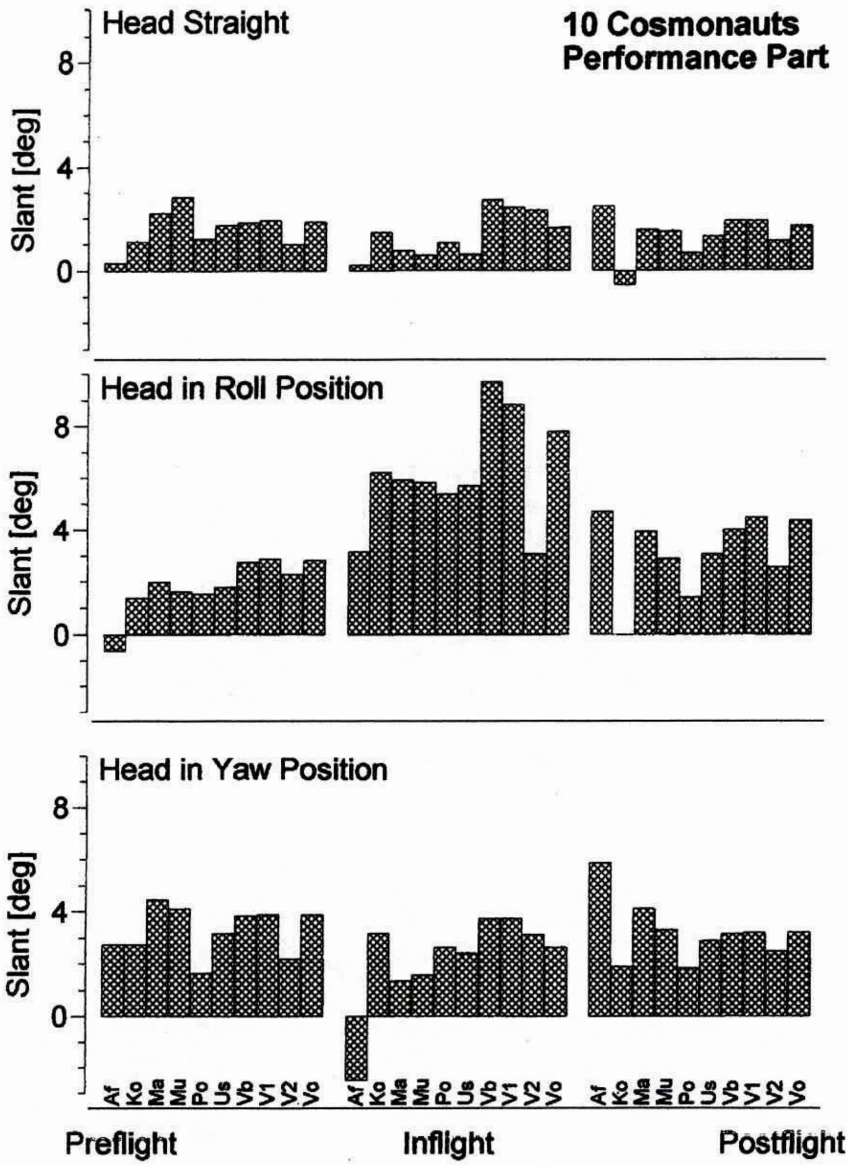

Figure 3. Slant of the movement plane of the arm for each cosmonaut preflight, inflight and postflight for 3 different head-to-trunk positions (Head straight = HS; Roll tilt of the head to the right = RollR; Yaw position of the head on the right side = YawR) in the performance phase with eyes closed. Positive values correspond with counterclockwise slant, negative values with clockwise slant of the movement plane.

Duration. The analysis of variance reveals that inflight the movements take a significantly longer time. The increase in duration after closing the eyes is very similar preflight, inflight, and postflight and independent of the position of the head and of the target. After landing, there is a highly significant decrease in duration (Figure 4a).

Terrestrial Experiments in Comparison with Preflight, Inflight, and Postflight Data

These experiments with 14 subjects have not been planned as a control led study in the strictest sense, for it was not possible to achieve correspondence in the test intervals. They were

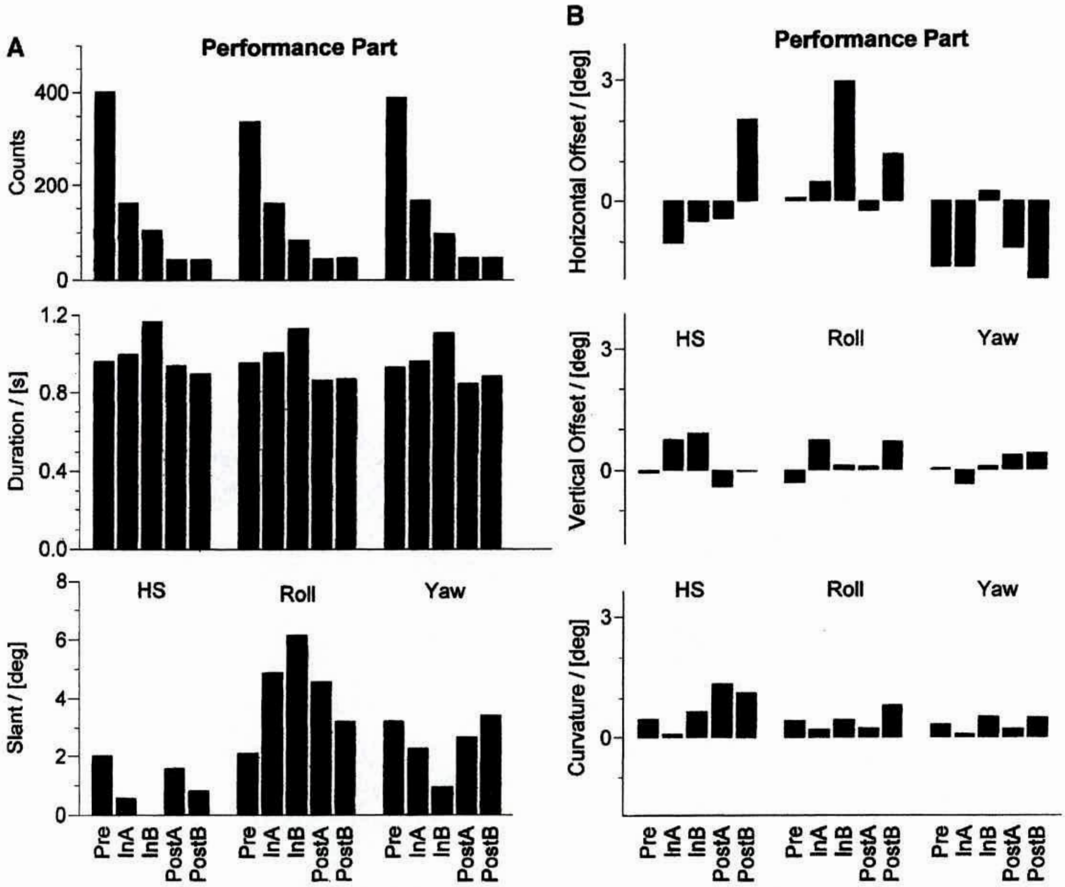

Figure 4. (A) Number of single arm movements, duration, and slant (B) Horizontal offset, vertical offset, and curvature of these movements as a function of the different head-to-trunk positions and 5 flight phases: Preflight, Inflight A (<90 days in orbit), Inflight B (>90 days in orbit), Postflight A (2nd day after landing), Postflight B (5th day after landing).

carried out to test the hypothesis that the slant that we found contralateral to head-position right would be consistent for head positions on the left side.

In comparing head direction right to head direction left, the MANOVA (Table 3) shows a highly significant ($P < 0.001$) difference in slant, amplitude, and duration and a significant ($P < 0.01$) difference in horizontal offset and curvature. The most pronounced effect concerning the slant is seen in yaw to the right. Movement towards the direction of head position generates a larger slant than movement opposite to head direction (Figure 7 and Table 4). The results are similar to the preflight data of the cosmonauts. Yaw to the right side (YawR-Perform) generates a significant horizontal offset to the left; roll to the right side (RollR-Perform) generates a significant deviation to the right. The results of the tests with head-left mirror the head-to-the-right data.

Discussion

The Slant of the Plane of the Arm Movements

In comparing the test situation with changed head–trunk position to the one with head straight, it is evident that the task of accurate horizontal pointing gets more difficult with the

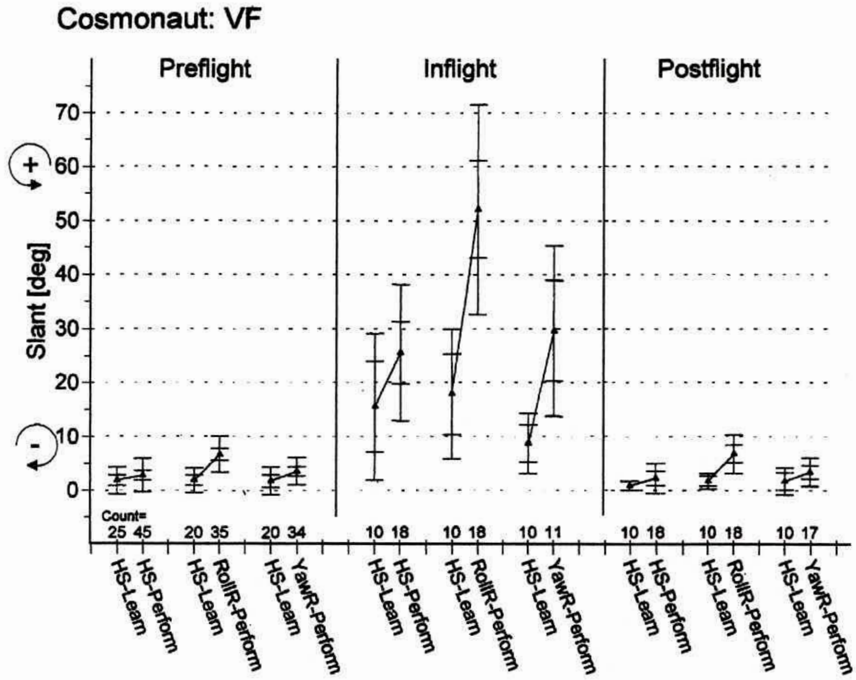

Figure 5. Slant of the movement plane of the arm as a function of the different test conditions for the short-term cosmonaut. Tests on the 2nd and the 5th day of flight. Learning part of the test (HS-Learn), performance part (HS-Perform, RollR-Perform, YawR-Perform).

head in yaw- or roll-position. Performance is worst inflight with eyes closed in the roll position of the head. Our findings confirm earlier experience that the head-to-trunk position is important for encoding target position in space, above all, the orientation of the head towards the target (29,30). Disturbances in head-position sense led to mislocations of objects in space and to misdirection of visuomotor behavior (31,32). Other studies showed that a shift of the trajectory to the right was induced in all subjects when they had their left neck muscles stimulated by vibration (33).

The reason why the slant of the movement plane of the arm is more pronounced in yaw than in roll head position under 1 G, may be explained by the different stimulus situation. During normal behavior on Earth, humans tend to experience more head roll tilt than extreme changes in yaw head position. The roll position of the head is a well-trained interaction of otoliths and neck receptors, so that even with eyes closed, space constancy is better maintained. Changes in yaw position are mostly not affected by gravity. But there is a difference in quality between small and marked rotation. Small rotation occurs mainly between atlas and axis and is purely in the horizontal plane. But after about 30°, rotation is carried out by the cervical spine in the form of a coupled movement of rotation–inclination (due to the inclination of the cervical zygapophysial joints). At this certain degree of rotation, a postural reaction can probably be produced that brings about this compensating countermovement of the pointing arm to keep balance, although normally the sitting or the supine position requires very little demand on postural control mechanism. In yaw this extreme head position on the side must be kept by muscle involvement, and there is a strong stimulation of the neck receptors. Therefore, the errors in pointing should be larger because there is a pronounced change in the cervical spine, with information processing that is not so well trained as the otolith-neck-receptor interaction in roll tilt.

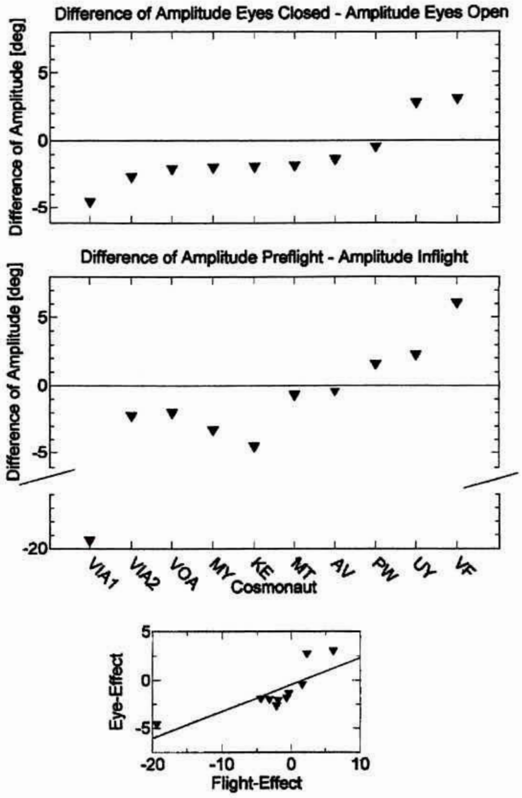

Figure 6. Difference of Amplitudes: (Amplitude Eyes-closed) − (Amplitude Eyes-open) ≥ (a, "eye-effect"), the difference (Amplitude Preflight) − (Amplitude Inflight) ≥ (b, "flight-effect") and the correlation of both. Experiments with 10 cosmonauts.

In space the stimulus situation is contrary to that on Earth. For roll tilt the well-trained stimulus–reaction pattern has changed, for there is neither reasonable information from the otoliths nor the accustomed afferent pattern from the neck. Instead of an objective vertical, there is a subjective vertical in, or close to, the direction of the person's longitudinal axis of the body (34). In this case, without dependable otolith information in space, all subjects generally become increasingly dependent on their internal body reference cues (down is where the feet are) (35). Because otolith signals are missing in space in the roll position of the head to the right, the stimulation of the neck receptors is not extinguished by opposite (reciprocal) information from the otoliths, in accordance with Mittelstaedt and Glasauer (36). Thus, in microgravity, the stimulation of the neck receptors is misinterpreted as a tilt of the trunk instead of the tilt of the head. In relation to the surroundings, the trunk seems to be tilted to the right. The cosmonauts know that there is a stable relationship between LED-row and trunk position. With eyes closed, they will try to align the plane of arm movement with a line in vague orthogonal relation to the longitudinal axis of the perceived trunk position. If the trunk is subjectively tilted counterclockwise, the same counterclockwise-roll of the movement plane of the arm results. This finding is in accordance with results of experiments done by de Graaf and colleagues (26). There, with stimulation of the neck, the subjects without labyrinthine function take their trunk as the reference frame, while normal subjects take their head. Experiments in weightlessness, which examined the cognitive processes of spatial coordinate assignment, showed that subjects, in this case free-floating, predomi-

Table 3. Effect of Eye Status and Head Direction Right or Left [Results of Analysis of Variance: Terrestrial Experiments (14 Control Subjects), Data of the Performance Part]

	Control Exp. Earth (Performance Phase Only)										Interaction A × B
	A: Visual Control: Eyes Closed vs. Open					B: Head Direction: Head Right vs. Left					
	SS	df	MS	F-ratio	Sig. Lev.	SS	df	MS	F-ratio	Sig. lev.	Sig. lev.
Dep. Variable											
Amplitude (Length)	1219.64	1	1219.64	120.1	0**	500.26	2	250.13	24.63	0**	0.1162
Duration	8.41	1	8.41	168.73	0**	0.73	2	0.36	7.3	0.0007**	0.0006**
Slant	262.42	1	262.42	40.7	0**	738.61	2	369.3	57.28	0**	0**
Horizontal Offset	366.07	1	366.07	38.16	0**	93.87	2	46.94	4.89	0.0076**	0**
Vertical Offset	218.96	1	218.96	27.94	0**	42.72	2	21.36	2.73	0.0657	0.0135*
Curvature	83.95	1	83.95	174.8	0**	4.59	2	2.3	4.78	0.0085**	0.0628

* Difference in mean-values significant at the .05 level.
** Difference in mean-values significant at the .01 level.

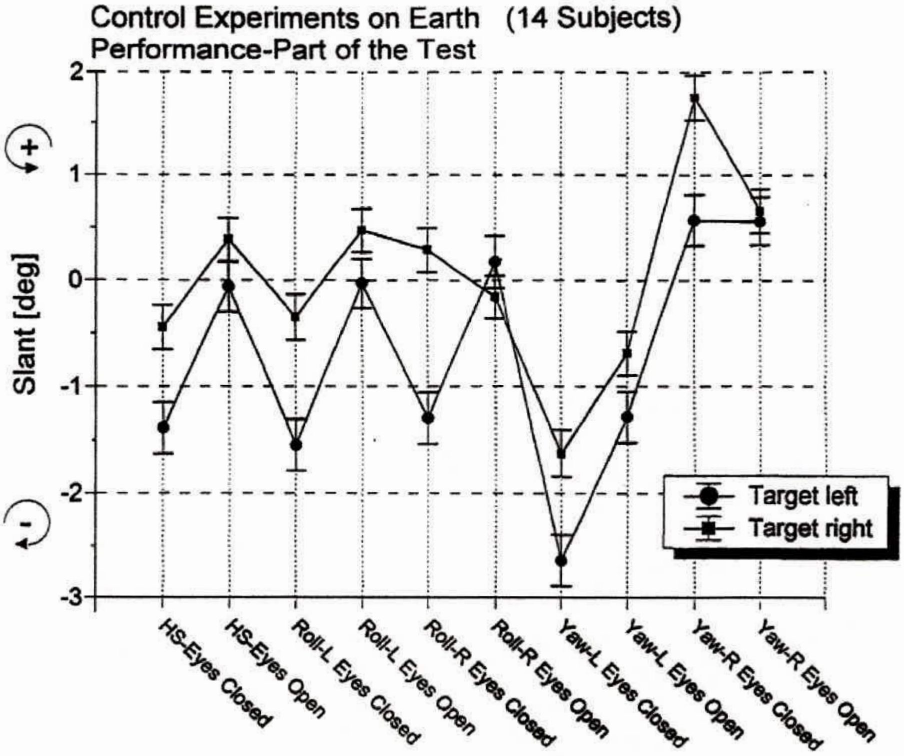

Figure 7. Slant in terrestrial control experiments for different test conditions, either for left-directed movements (Target left) or right-directed movements (Target right). Data from the performance part of the tests.

nantly used the retinal (head) vertical as a reference, whereas on Earth they preferred the gravitationally defined vertical (37).

Tests carried out earlier indicated that the more force is necessary to get into position and to maintain it, the more subjective deviation from the spatial reference system is perceived. This results from tests in which the amount of movement and the deviation from the true vertical is overestimated in active maintained positions (38). This fact brings about another possible explanation for the incorrect direction of the movement plane of the arm after closing the eyes. We could assume that in a cognitive process

Table 4. Influence of Head-to-Trunk Position and the Target Position on 6 Dependent Variables [Results of Analysis of Variance: Terrestrial Experiments (14 Control Subjects), Data of the Perfomance Part]

	Control Exp. Earth (Performance Phase Only)										
	A: Head-to-trunk Position					B: Target Position					
	SS	df	MS	*F*-ratio	Sig. Lev.	SS	df	MS	*F*-ratio	Sig. lev.	Sig. lev.
Dep. Variable											
Amplitude (Length)	2258.45	9	250.94	25.02	0**	5.17	1	5.17	0.516	0.4803	0.7779
Duration	9.03	9	1	20.7	0**	0.01	1	0.01	0.115	0.7383	0.9075
Slant	1852.99	9	205.89	34.34	0**	309.71	1	309.71	51.65	0**	0.0004**
Horizontal Offset	4022.38	9	446.93	54.75	0**	193.88	1	193.88	23.75	0**	0.5989
Vertical Offset	467.62	9	51.96	6.63	0**	0.98	1	0.98	0.125	0.7276	0.9997
Curvature	118.49	9	13.17	27.69	0**	0.01	1	0.01	0.013	0.9104	

* Difference in mean-value significant at the .05 level.

** Difference in mean-value significant at the .01 level.

of mental representation of space the subjective horizontal is estimated in relation (orthogonal) to the subjective vertical. The rationale behind this is the fact that normal subjects tend to slightly overestimate the degree of their head tilt. In compensating for this perceived deviation, the tendency is for the subjective vertical to show a counterclockwise-roll with head tilt to the right. If the subjective horizontal is put orthogonal to this subjective vertical, this would be an explanation for the slant of the plane of arm movement contrary to the direction of head tilt in our experiments. This hypothesis needs further inspection in planned experiments.

Horizontal Offset of the Arm Movements

With roll tilt of the head and after closing the eyes, lateral shifting of the movement frame into the direction of head tilt is found. This may be explained by the hypothesis that the new spatial location corresponds to the subjective visual straight ahead, which is close to the subject's head (39). According to the otolith-tilt–translation-reinterpretation hypothesis (40), in space the otolith signals, produced by roll tilt to the right, elicit horizontal eye deviation and are perceived as linear motion to the right. As a consequence of this reinterpretation (3), the subjective straight ahead would be shifted to the right more in space than on Earth, in accordance with our results.

In yaw, deviation of the arm movements contralateral to the head position may be either a kind of reflex movement as a reaction to the increasing tension in the neck during the test or some overcompensation in error correction.

Patients with problems in the cervical spine show the same movement patterns in the HAUTANT-Test (41). This test is part of the routine examination of patients who suffer from joint dysfunction of the cervical spine. Sitting in a chair, they have to close their eyes and to hold their arms stretched out in front of them. With a positive test, a deviation to the contralateral side of the lateral movement restriction is observed. Retroflexion of the head enlarges the deviation, anteflexion corrects it. An additional head rotation contralateral to the observed deviation enlarges the effect. The deviation is inhibited with head rotation in the direction of the lateral deviation (42).

Thus, in the final lateral head positions (yaw, roll) as well as in patients with cervical spine problems, the afferent input seems to be disturbed. This causes a changed perception of the space and of the head–arm coordinate, thus movements cannot be programmed and executed in a correct manner. The deviation from the horizontal plane is not recognized by the subject and is therefore not corrected.

Vertical Offset

Soechting and colleagues concluded from their findings (43) that both a head-centered and a shoulder-centered representation of target location exists within the central nervous system. They hypothesized that one step in the sensorimotor process that leads to a pointing movement of the arm involves the following transformation: the co-ordinate system in which the location of points in extrapersonal space is represented has to move the origin from the center of the head (the eyes) towards the shoulder. Additionally, the orientation of the arm may involve a system, serving gravity perception, which is independent of that of the labyrinth: Muscle afferents and joint receptors give information about the direction of gravity, the direction in which the unsupported arm is sinking (44,45). Forearm proprioception influences the visually perceived position or visual direction, for vibration of an arm muscle causes a rotation of visual space or of the visual frame of reference (46). It is concluded that goal-directed movements to remembered target locations are organized on the basis of internal representation of the external space (37) as well as weight/mass-inertial properties of the moving arm (47). The motor control system can compensate changes of arm mass more easily than it can compensate altered gravity. Only a few movements executed with a changed weight recalibrate the parameters of the motor program (12,48).

Analysis of the behavior of the cosmonauts showed that it was essential for them to control the upward component of the horizontal movement during space flight. The ascending arm trajectories that we found inflight could be the consequence of overestimation of the arm weight. The arm movements were planned too high. Bock obtained similar results (49) in an elbow-matching task. The right forearm, when immersed in water, deviated systematically upwards, especially in near horizontal forearm positions. On the ground, however, we found a tendency to descending movement paths during the test according to the weight of the arm, which was probably due to insufficient correction.

Curvature

Postflight, with head straight, pronounced curved, fast movements were measured. Although the vertical component took more effort on the ground, the arm trajectories looked like the path of a windshield-wiper. In the same manner as cosmonauts who were tested after landing, they might have overestimated the pull of gravity and therefore planned the upward component wrongly. Bock and colleagues reported (12,50) the same behavior in subjects who were brought from 1 G to hyper-G. There the final response positions were generally too high.

Taking all this into account, spatial orientation is impaired in weightlessness, and the central interpretation of the physical properties of the arm is modified. Additionally, yaw or roll position of the head disturbs the hypothesized body image and changes the central program of motor control, more in space than on Earth. The loss of background information, on the one hand due to the missing visual feedback, on the other hand due to reduced proprioception inflight, causes the development of a changed strategy for movement control. Minor mean velocities and in most cases a reduced amplitude of the arm movements were found. Cosmonauts inflight need more time for smaller movements, as it appears to take more time to get all the necessary information to perform the movement. In order to avoid countermovement of the whole body and overshooting, more control and feedback is necessary to preserve subjective accuracy. Velocity might be involved in calibrating the final location of the moved arm, because inflight and postflight mean velocity is kept constant in all head positions, regarding the mean values of all cosmonauts. Whether the error of pointing is mainly generated by the head-centered or by the body-centered system is an open question.

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