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Visually-induced tilt during parabolic flights

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Summary. A helmet-mounted visual display system was used to study visually induced sensations of self-motion (vection) about the roll, pitch and yaw axes under normal gravity condition (1g) and during the microgravity and hypergravity phases of parabolic flights aboard the NASA KC-135 aircraft. Under each gravity condition, the following parameters were investigated: (1) the subject's perceived body vertical with eyes closed and with eyes open gazing at a stationary random dot display; (2) the magnitude of sensations of body tilt with respect to the subjective vertical, while the subject viewed displays rotating about the roll, pitch and yaw axes; (3) the magnitude of vection; (4) latency of vection. All eleven subjects perceived a definite "up and down" orientation throughout the course of the flight. During the microgravity phase, the average magnitudes of perceived body tilt and self-motion increased significantly, and there was no significant difference in vection latency. These results show that there is a rapid onset of increased dependence on visual inputs for perception of self-orientation and self-motion in weightlessness, and a decreased dependence on otolithic and somatosensory graviceptive information. Anti-motion sickness drugs appear not to affect the parameters measured.

Key words: Visual-vestibular interaction – Parabolic flight – Circularvection – Human

Introduction

Circularvection is a sensation of self-rotation induced in a stationary subject exposed to a rotating visual field: it is a well established phenomenon of visual-vestibular interaction. This visually induced sensation is sometimes indistinguishable from a sensation of real self-motion, involving stimulation of the vestibular and somesthetic systems. In the cat and rhesus monkey, it has been found that optokinetic stimulation can induce a direction-specific modulation of resting discharge in neurons of the vestibular nuclei, neurons that also respond to vestibular stimulation (Keller and Precht 1979; Waespe and Henn 1977). The directional specificity of these neurons is opposite for visual and vestibular stimuli which corresponds to the natural condition in which a rotation of the animal in one direction is accompanied by relative motion of the visual environment in the opposite direction.

Roll vection is induced by a scene rotating about an axis in the sagittal plane of the head perpendicular to the spinal axis (x axis). Pitch vection is induced by a scene rotating about an axis running from ear to ear in the mid-frontal plane (y axis) and yaw vection is induced by a scene rotating about the spinal axis (z axis). A simple sensation of continuous self-rotation, with occasional "dropouts", is experienced if the axis of scene rotation is aligned with gravity. "Dropouts" are occasional losses of vection which occur suddenly and without warning during constant velocity stimulation. When the axis of scene rotation is Earth-horizontal (orthogonal to the gravity axis), the sensation of continuous self-rotation is usually accompanied by a paradoxical sensation of more or less constant body tilt (Dichgans et al. 1972; Held et al. 1975; Young et al. 1975; Howard et al. 1988). Limited sensations of body tilt have been attributed to conflict between the visually induced vection, and information from the otolith organs and somatosensory graviceptive senses (Dichgans et al. 1972). This interpretation is supported by the finding that visually induced tilt increases markedly when the utricules are placed in an orientation in which their sensitivity is reduced, for example, when the head is tilted laterally or when the observer is upside-down (Dichgans et al. 1972; Young et al. 1975). The idea that the visual inputs may substitute for otolith inputs is supported by the finding that otolith-dependent units in the cat's vestibular nucleus respond to translational self-motion and also to translational movement of a large visual field relative to the stationary animal (Daunton and Thomsen 1979).

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Microgravity changes the usual relation between bodily orientation and sensory stimulation: it is a form of stimulus rearrangement to which people adapt. For example, as a consequence of the absence of gravity, graviceptors (otoliths) do not respond to static pitch or roll, however they do respond to linear acceleration (translation). This has been referred as the otolith tilt-translation reinterpretation hypothesis (Parker et al. 1985). Roll vection has been studied by Young et al. (1986) on four crew members during weightless conditions in the Space Shuttle and during the microgravity phase of parabolic flights. The most surprising aspect of roll vection in space flight, where conflicting otolith and gravitoinertial cues are absent, was that it was not completely saturated for all subjects; that is the subjects perceived, from time to time, that the visual field was moving (field motion in addition to self-motion). Also during ground study, with the subject lying supine and viewing the field above rotating about the Earth vertical axis, all subjects reported a sensation of continuous self-rotation with occasional "dropouts". It is not reported in these studies how microgravity conditions affected the perceived vertical and sensations of illusory body tilt. Furthermore, pitch and yaw vection have not been studied in weightlessness because mechanical displays used to induce vection about these axes are too bulky for use in conditions of weightlessness. We have overcome this limitation by using video displays presented in a helmet-mounted optical system.

The purpose of this study was to investigate the effects of visual fields rotating about the roll, pitch and yaw axis, on the perception of self-motion and illusory body tilt during the microgravity and hypergravity phases of parabolic flights. There are two possibilities concerning the effects of microgravity on vection and illusory body tilt. In the first one, it is assumed that on arrival in microgravity, subjects use the floor to represent a subjective "gravitational" horizontal and that the perceptual system does not immediately "realize" that there would be no change in stimulation of the otolith organs or somesthetic senses if the body were actually to rotate about the "horizontal" axis. Accordingly, weightless subjects should expect the same experiences of vection and body tilt that they have under normal gravity (1 g) conditions, until they have learned through actual body rotation not to expect normal otolith and somesthetic sensations. Thus, if weightless subjects believe that the body is upright (relative to gravity) when it is at right angles to the floor, and supine (relative to gravity) when on the floor, as our subjects did, they should expect the same vection and illusory tilt as in the equivalent postures on the ground. Previous ground studies (Howard et al. 1988) have demonstrated that, for visual motion about roll, pitch and yaw axes, when the axis of visual rotation is coincident with the gravity axis, only a sensation of self-motion is experienced. However, when the axis of visual rotation is orthogonal to the gravity axis, the sensation of self-motion is coupled with a paradoxical sensation of body tilt.

The second possibility about the effects of weightlessness is that subjects immediately realize that the otolith organs and somesthetic senses would not respond were the body to actually rotate about an axis parallel to the floor. Accordingly, subjects in both the upright and supine postures should experience more vection as soon as they arrive in the microgravity state, and they should feel that they are tumbling fully through 360° whatever the axis of scene rotation.

Methods

Parabolic flight profile

The flight profile used in our experiments is illustrated in Fig. 1. A KC–135 aircraft was flown in a parabolic path to generate alternating periods of microgravity (0.0001–0.01 g) lasting 20–25 s and increased gravitoinertial force (1.8–2.0 g) lasting 20–30 s. The microgravity phase is also referred to as 0 g phase, free fall, and weightlessness. Ten parabolas were flown in succession followed by a five-minute break. This was repeated until 40 parabolas had been flown. As the aircraft approached the top of the parabola, the pilots put it into a condition of free fall by reducing the lift on the wings to zero and by matching the thrust generated by the engines to the drag caused by the airflow striking the aircraft. The aircraft then freely accelerated towards the Earth's surface by Earth's gravity. Objects within the aircraft did not have any tendency to move with respect to each other, and any objects floating in the aircraft continued to float. With respect to the surface of the Earth, the floor of the plane pitched through a considerable angle as it executed its parabolas. However, centrifugal forces ensured that the resultant gravitoinertial field was always at right angles to the floor of the plane. Therefore, the major effect of parabolic flight was a change in the magnitude of the gravitoinertial force vector acting at right angles to the floor of the aircraft.

Subjects

Five men participated in a preliminary study, their bodies were restrained but not their heads. Twelve subjects (9 males and 3 females) participated in the main experiment which was carried out in two subsequent sets of flights three months apart, with the subjects' bodies as well as their heads restrained. Most subjects (all except two) had previous experience with parabolic flights. Three of the subjects from the preliminary study also participated in the

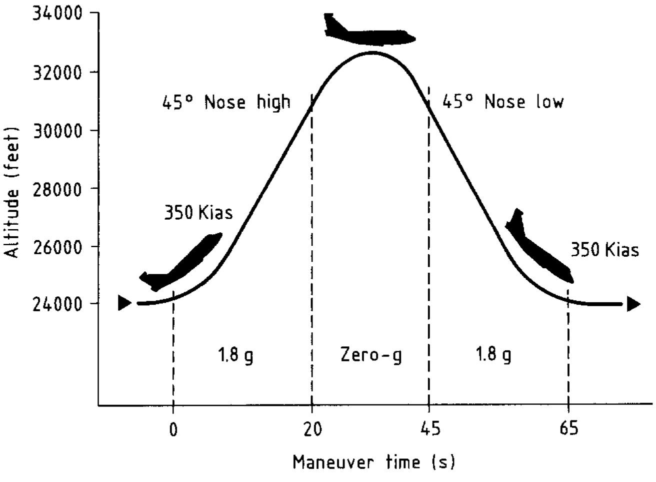

Fig. 1. NASA KC–135 aircraft trajectory

main experiment. None of the subjects had a known history of oculomotor or vestibular disorders.

Due to the unpleasant "roller-coaster" nature of the parabolic flight, some passengers experience motion sickness symptoms such as nausea and, in the extreme case, vomiting. The rotating visual field tends to heighten this discomfort. Six subjects therefore used anti-motion sickness drugs: four of the subjects were premedicated with 0.4 mg of scopolamine and 5 mg of dexedrine; two of the subjects used a combination of 0.25 mg of scopolamine, 5 mg of dexedrine, 25 mg of promethazine and 25 mg of ephedrine. One subject became violently sick mid-way through the trials, despite the medication, and her incomplete data were therefore not included in the analysis. In order to study the effect of anti-motion sickness drugs on the parameters measured, those subjects that were medicated for the flight were tested on the ground with and without the same medication.

Visual stimulus

The visual stimulus was a video film taken by a camera at the centre of a sphere 3 m in diameter lined with randomly positioned black dots of various sizes on a white background. The sphere was rotated at 45 degrees per second about the roll, pitch and yaw axes in clockwise and counter-clockwise directions, making a sequence of six visual stimulus conditions. Two video films each with a different sequence of the six visual conditions were recorded and presented to different subjects randomly. At the beginning of the sequence there was a stationary stimulus of random dots. The stimuli were presented on two miniature television monitors (6.9 cm) mounted one before each eye on a helmet (supplied by the CAE company of Canada) and viewed through a combination of lenses and prisms. The subject saw a 70 degree-wide binocularly fused display at optical infinity. The helmet was attached to a rigid framework and adjustable so as to immobilize the subject's head when the subject was either supine or seated upright on the floor of the aircraft (Fig. 2a, b respectively).

Procedure

For each sequence of visual stimulation, the subject was tested sitting upright for the first set of 10 parabolas, and lying supine for the second set of 10 parabolas. During the first of the ten parabolas (during both the microgravity and the high g periods) the subject was presented with a visual display that was stationary and during the second parabola the eyes of the subject were closed. During both these parabolas the subject pointed a finger in the direction perceived as "up" and also pointed in a direction perceived to be parallel to the spinal axis. The subject set the joystick to indicate the angle at which the body (spinal axis) was perceptually inclined with respect to this perceived "vertical".

A given visual stimulus was presented to the subject at the start of a microgravity phase, continued through the hypergravity phase and ended just before the next microgravity phase, at which time the stimulus changed to the next in the sequence. The subject was instructed to look straight ahead and focus on the display and attend to sensations of self-motion and body tilt.

The technique of magnitude estimation was used to quantify vection and perceived body tilt. Subjects indicated the self-motion sensation by pressing one of five buttons positioned under the fingers of the left hand. The thumb button represented zero vection in which the display seemed to be moving but the body seemed to be stationary. The fifth digit finger button represented a value of four, or full vection, in which only the body seemed to be moving. The other buttons represented intermediate degrees of vection with the middle finger button signifying that the visual scene and body seemed to be rotating at the same velocity in opposite directions. Subjects indicated the degree of subjective body tilt by deflecting the joystick through an appropriate angle, one way or the other from its central position. The joystick sprung back to its central position when released and deflection angles of 30°, 45°, 60° and 90° were indicated tactually by ball catches. Subjects pressed a button to one side of the joystick whenever they experienced a sensation of body tumbling through 360° (cart wheeling in the roll axis, tumbling in the pitch axis when the subject was sitting upright or barbecue rotation in the yaw axis when the subject was supine.) Subjects' verbal reports and comments were also recorded when available.

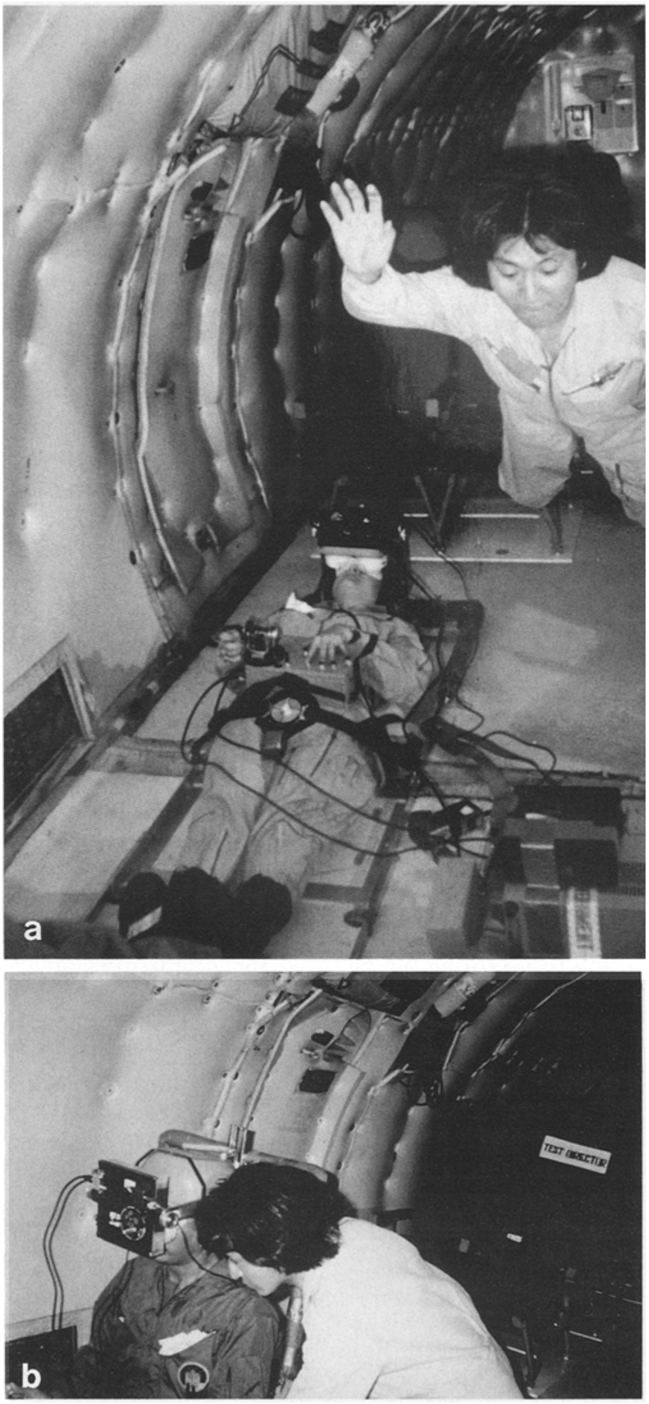

Fig. 2. a The helmet-mounted display in the supine position. **b** The helmet-mounted display in the upright position

The data were analyzed with biomedical statistical software. They were subjected to analysis of variance (2v) followed by multiway description of group (9d) and multiple comparisons program. Scheffe's test (two-tailed) was used to test for significance.

Results

The results of the preliminary study, in which the subjects' heads were not restrained, are as follows. During the microgravity phases the magnitude of vection increased and its latency decreased. In the roll and pitch axes two subjects experienced an unambiguous 360° rotation of the body through an upside-down orientation when seated upright. During the hypergravity phases, the visually induced sensation of body tilt increased in two subjects and decreased in two subjects. These contradictory results could have been due to changes in the posture of the subject's head as the weight of the helmet fluctuated with changing gravity.

In the main experiment, we avoided unwanted changes of head posture by attaching the helmet to a rigid frame. The mean sensation of body tilt under all conditions during the "ground" test, from the 6 medicated subjects with and without drugs is shown in Fig. 3. The mean vection magnitude from the same group under the same condition is shown in Fig. 4. Statistical analysis showed that anti-motion sickness drugs had no effect on the parameters measured.

Almost all subjects indicated a strong "up and down" orientation with respect to their particular posture. In the upright sitting position, during both the microgravity and hypergravity phase, all of the subjects reported that their perceived vertical was perpendicular to the floor of the aircraft, despite the fact that the aircraft was engaging in pitch movement, and their spinal axis (except in two subjects) was perceived to be coincident with their perceived vertical. In the supine position, in which subjects were on their backs on the floor of the cabin, their perceived vertical was also indicated as perpendicular to the floor of the aircraft, but their spinal axis was reported to be parallel to the floor. In the two subjects who deviated from this trend during the microgravity phase in the upright sitting position: one subject indicated the spinal axis as inclined forward 45° with respect to the perceived vertical and the other indicated a forward incline of 5°. In both cases, the perceived vertical was normal to the floor of the aircraft. In these two cases, the reported inclination was subtracted from the perceived body tilt reported during visual stimulation.

Overall, the mean vection magnitude during the microgravity condition was significantly stronger than during the 1.8 *g* condition ($p < 0.001$) and was also stronger than in 1 g ($p < 0.0025$), as shown in Table 1. There was no significant difference in vection magnitude between the roll, pitch and yaw axes.

Similarly, the mean sensation of body tilt increased during the microgravity phase. Quantitatively, in the upright posture about the roll axis, the sensation of sideways body tilt was significantly stronger during the microgravity phase than during 1 *g* and 1.8 *g* ($p < 0.005$ in both cases), as tabulated in Table 1. For the pitch axis, in both the upright and supine postures, the sensation of body pitch in microgravity was significantly stronger than in 1 *g* ($p < 0.01$) or in 1.8 *g* ($p < 0.005$). For the yaw axis with the subject supine, the sensation of body tilt during microgravity was significantly stronger than in 1 *g* ($p < 0.025$) and stronger than in 1.8 *g* ($p < 0.001$). Five subjects reported unambiguous 360° rotation of the body in the roll and pitch conditions during 0 *g*. In the supine-roll, and upright-yaw conditions, there were no reports of body tilt with respect to the subjective vertical.

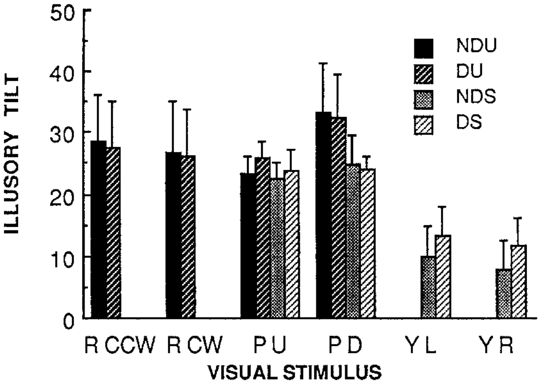

Fig. 3. Effect of anti-motion sickness drugs on illusory body tilt under 1 g condition. NDU = no drug, upright; DU = drug, upright; NDS = no drug supine; DS = drug, supine; RCCW = roll axis, counterclockwise; RCW = roll, clockwise; PU = pitch up; PD = pitch down; YL = yaw left; YD = yaw right

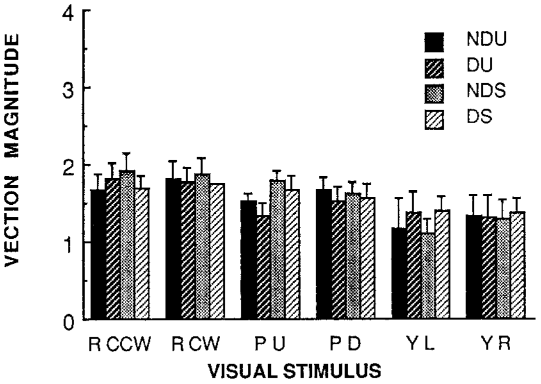

Fig. 4. Effect of anti-motion sickness drugs on visually induced self-motion, (abbreviations are the same as in Fig. 3)

Table 1. Mean vection magnitude[a], sensation of body tilt under the three gravity conditions (1 *g*, 0 *g*, 1.8 *g*)

	1 *g*	0 *g*	1.8 *g*
Vection magnitude	1.53 ± 0.16	1.98 ± 0.21	1.27 ± 0.20
Roll tilt	27.13 ± 4.79	138.27 ± 40.9	27.37 ± 5.43
Pitch tilt	32.17 ± 6.42	127.85 ± 42.74	22.04 ± 6.12
Yaw tilt	15.75 ± 4.65	25.74 ± 5.66	10.71 ± 4.07

[a] Vection magnitude is the group mean of the roll, pitch and yaw axes. Sensation of body tilt were subjectively indicated in degrees

In all cases, there was no significant difference between the 1 *g* and 1.8 *g* conditions in vection magnitude or sensation of body tilt. The mean value of latency to vection across subjects was less during the microgravity phase (7.40 ± 3.11 s) than the 1 *g* condition (8.63 ± 0.70 s) but this difference did not reach significance.

Discussion

Otolith cues concerning the direction of gravity are temporarily eliminated during free fall in parabolic flight, and interpretation of graviceptor signals as tilt is meaningless. Therefore, we are interested in the sensation of body tilt estimated with respect to the subject's perceived vertical. Our data demonstrate that in the absence of external visual cues in the microgravity phase, subjects retain a perceived notion of "up and down". This is consistent with previous findings that perceived orientation is dependent on available patterns of stimulation (Lackner and Graybiel 1983). In our case, during microgravity, it is dependent on the subject's knowledge of his posture relative to the aircraft and on tactile cues. Thus, the subjective vertical is the result of a compromise between a tendency to perceive it in the direction indicated by the gravity receptors and a tendency to perceive it in or close to the direction of a person's longitudinal axis (Mittelstaedt 1985).

Our results demonstrate that during brief periods of microgravity in parabolic flight, the magnitude of perceived self-motion and body tilt induced by visual stimuli moving around roll, pitch and yaw axes increase significantly above their 1 *g* or 1.8 *g* values. These findings suggest that the lack of contradiction of the visual inputs by graviceptor inputs was immediately appreciated by the perceptual system. However, not all subjects experienced full body rotation when vection was about an assumed horizontal axis in microgravity, and even those subjects who experienced full body tumbling on some trials experienced only a limited degree of body tilt on others. Thus, although the sense of "up" and "down" was weakened when subjects entered the microgravity state, some sense of direction was retained. This residual sense of "up" and "down" presumably arose from the pressure cues of being restrained in a sitting-upright or lying-supine position or from memory of orientation relative to the floor of the aircraft. It could also be from an impression carried over from the preceding hypergravity phase. Note that the sense of "up" and "down" could not have been provided by visual cues since the visual display was radially symmetrical.

We had hoped to run trials with subjects in a free-floating position out of contact with any surfaces. This was too difficult to achieve, since unrestrained weightless subjects tend to rotate and translate in the aircraft and holding them by hand complicates the sensory input.

The conflicting effects of changing g levels on illusory tilt obtained in the preliminary study were apparently due to the fact that the subjects' heads were not restrained. During free fall, one has no sensation of weight, the head and body are rarely maintained in precisely the same posture during any parabola, and head position varies unpredictably. There is no constant relationship between the pattern of the aircraft motion and the subject's head, so that the changing force patterns acting on the body are not always stimulating the vestibular and somatosensory receptor systems in the same way for the same phase of the parabola. Furthermore, an increase in g level along an axis which is tilted with respect to the head stimulates the otolith organs in much the same way as a change in the orientation of the head relative to gravity. This conclusion is strengthened by the fact that when the subjects' heads were restrained (in the main experiment), the effects of changing g forces on illusory tilt were consistent in sign from subject to subject.

In pitch vection in the normal 1 g environment, there is a distinct asymmetry in illusory body tilt in response to moving visual fields, with the sensation of self-motion pitching backwards much stronger than forward in most subjects (Howard et al. 1988). This asymmetry was also present during the microgravity phase in subjects who exhibited such asymmetry during the ground study. Morphologically, the plane of the utricular macula is approximately parallel to the plane of the horizontal semicircular canal with the anterior third curled up slightly. The asymmetry of illusory pitch of the body may be associated with the varying degree of this upward tilting of the utricular macula among individuals, and hence with asymmetries in otolith sensitivities.

Two of the subjects reported an occasional inversion illusion in both the upright and supine posture during the microgravity phase, while concentrating on the prescribed task. An inversion illusion is a sensation of being upside-down while exposed to weightless conditions of orbital flight, first reported by the Russian cosmonaut Titov. The sensation is relative to the surface of the earth or relative to floor of the aircraft (Graybiel and Kellogg 1975). It was also reported by Graybiel and Kellogg that labyrinthine-defective subjects do not experience this illusion when exposed to weightless conditions, and they concluded that the inversion illusion is due to the way normal subjects interpret the absence of otolithic inputs in the weightless state. More recently, Mittelstaedt defined an inversion of world and/or self which is experienced in spite of or in the absence of external cues for the vertical as "cue free inversion". He further contended that, in weightlessness, the direction as experienced in the external world and the perceived position of one's body to the vertical depend primarily on the "saccular bias", the difference between the mean resting discharge of saccular units polarized towards $+z$ and $-z$ direction (Mittelstaedt 1987). However, this hypothesis does not explain the inversion illusion experienced by two of our subjects who reported inversion in the supine posture, since the saccule mainly determines the magnitude of the gravity vector in the upright position. Alternatively, the "saccular bias" could occur along the subjects' x axis. It is of interest to note that circularvection and the inversion illusion could occur simultaneously.

The perception of body orientation, although relying on various sensory inputs, is heavily influenced by a number of cortical functions, including alertenss, expectation and habituation to a particular stimulus sequence. It is known that scopolamine and promethazine can produce side effects that affect human performance. Promethazine and scopolamine are associated with drowsiness, amnesia and fatigue. Interference with cholinergic transmission by scopolamine, a cholinergic blocking-agent capable of crossing the blood-brain barrier, results in a "scopolamine dementia" characterized by major interference with memory storage as well as other disorders of cognitive functioning (Drachman 1977). The sympathomimetic action of dexedrine and ephedrine have been hypothesized to counteract the CNS depressant effects of scopolamine and promethazine respectively. Ross and Schwartz (1984) reported that a significant deterioration in mass discrimination was found for oral scopolamine and dexedrine combination but that the deterioration is much less than that found under microgravity. The authors suggested that the deleterious effect of scopolamine lies more in sensorimotor coordination than in cognitive function. Scopolamine was also found to disrupt visual vigilance performance by lowering stimulus sensitivity (Wesnes and Warburton 1983). Our data suggest that the selected doses and combinations of anti-motion sickness drugs did not affect the magnitude estimation of vection and sensation of body tilt. Other findings have also shown no significant decrement in various human performance tasks, as measured by tests of cognitive and psychomotor skills, when low dosages of the above anti-motion sickness treatments were used (Gray et al. 1983; Wood et al. 1985; Schmedtje et al. 1988).

A limitation of this study is that the alternating periods of microgravity and increased gravitoinertial force were short, each lasting approximately 20–30 s. The illusory body tilt could depend on the time of exposure in microgravity or on the preceding exposure to hypergravity. The normal function of the otolith organ depends on the presence of a gravitational force vector of 1 *g* directed towards the centre of the earth. This system therefore malfunctions when the amplitude of the combined gravitoinertial load varies from 1 *g*. The exact time course and response dynamics of the "un-loading" of the otolith organ is unknown.

There is some evidence that the response of the otolith organs decreases during a period of microgravity in orbital flights. For instance, the resting activity of single otolith units in the vestibular nucleus of the bull frog has been shown to decrease within 4–5 days of exposure to microgravity (Bracchi et al. 1975). Humans have shown remarkable adaptation of both orientation perception and postural control during several days of exposure to the weightless conditions of space flight. Approximately 50% of all Shuttle crew members experience motion sickness of some degree in the first 72 h. Lack of congruence among signals from spatial orientation systems leads to sensory conflict which appears to be the primary cause of space motion sickness. After the initial 72 h, the crew members adapted to weightlessness as indicated by reduced subjective disturbance (symptom free) to voluntary motion. An increase of proprioceptive and somesthetic influence on their perception of spatial relationships during and early after the mission. Physiological reflex changes such as the gain of optokinetic nystagmus, and ocular counter-rotation during flight, reentry and immediately after landing, all demonstrate neural adaptability in man (von Baumgarten et al. 1986). It would be of interest to study vection and the visually induced sensation of body tilt about the roll, pitch and yaw axes over a prolonged period of weightlessness using apparatus like that used in this study.

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