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Our Sense of Motion

During spaceflight, the linear acceleration due to gravity is reduced from 1-g on the Earth's surface to about 10^{-6} -g in Earth orbit, but the linear and angular accelerations associated with translation and turning are unaffected. Human adaptation to spaceflight therefore entails selective reorganization of the body's response to the relative absence of the linear acceleration due to gravity. Associated with this reorganization, astronauts experience nausea and disorientation during flight. After their flight, they experience walking and vision (gaze control) difficulties that could pose a serious problem if they had to function efficiently in a normal gravitational environment immediately after a long-duration spaceflight.

Although such difficulties have long been a source of concern, they are as still far from being fully understood. The otoliths, which are calcareous elements located in our inner ear that sense gravity and acceleration, act as linear accelerometers and drive various reflexes to maintain our gaze and posture when linear accelerations are acting on our bodies. This includes the linear acceleration due to gravity, the high-frequency linear acceleration associated with translation produced by forward/back, up/down or side-to-side movements, and the centripetal linear acceleration experienced when turning about a distant axis, such as when turning corners, driving or walking along a circular path.

The sum of these different linear accelerations is termed 'gravito-inertial acceleration', abbreviated to GIA. In the absence of translation and centripetal accelerations, gravity is the sole GIA. If the head is tilted with respect to gravity, or if the GIA is tilted with regard to the head, the otoliths sense the linear acceleration and orient the bodily posture or the eyes towards the GIA. In particular, the ocular counter-rolling (OCR) of the eyes tends to maintain the position of the retina with respect to the spatial vertical.

The VVIS Experiment on Neurolab

Although eye and perceptual responses to linear accelerations have been tested before and after spaceflight, the orientation

of the eyes to the GIA had never been directly tested in space before the Neurolab mission in 1998. During that 16-day Shuttle mission, a series of investigations were carried out in the Spacelab module. One of the main items of equipment onboard was the ESA-developed Visual and Vestibular Investigation System (VVIS), designed to investigate the role of the inner ear in detecting changes in linear acceleration and hopefully provide a new approach to diagnosis back on Earth for disease or trauma in our inner-ear vestibular system.

One technique for generating GIA in space is to rotate the test subject about a distant axis in a centrifuge to generate centripetal linear acceleration. Until the Neurolab experiment, the human response to centrifugation had not been formally

studied in space. One of the aims of the study was therefore to generate artificial gravity by centrifugation and examine whether low-frequency otolith function, as determined from OCR measurements during and after flight, is altered by the body's adaptation to microgravity.

Another measure of otolith function, albeit indirect, is our perception of the upright. During centrifugation on Earth, the sum of the gravitational and centripetal accelerations (i.e. the GIA vector) is perceived by the human body as the spatial vertical. Consequently, we experience a roll tilt of the body when we are upright

The Neurolab human centrifuge (VVIS) mounted in Spacelab's centre aisle generated linear accelerations of 0.5 g and 1.0 g along the astronauts' interaural axis for several minutes every other day.



When supine on the centrifuge arm, centrifugation was directed along the vertical axis of the astronauts' bodies. A linear acceleration of 1 g gave the astronauts the illusion of standing on their head.



during centrifugation. For example, test subjects in the left-ear-out position (see accompanying figure) who are exposed to 1-g of centripetal acceleration at the head during centrifugation on Earth will experience a GIA of magnitude 1.4-g tilted 45° towards the rotation axis with respect to the vertical. They perceive the GIA as the vertical and therefore feel tilted to their left in the roll plane by approximately 45°. Similarly, they sense a backward pitch of the body when they are supine with the head off-centre (see accompanying figure). This perception of tilt during centrifugation, which has been called the 'somatogravic illusion', is present in test subjects with an intact vestibular system. Whether the GIA is still perceived as the spatial vertical during in-flight centrifugation had never been tested and was the second major aim of the NeuroLab experiment.

Since the otoliths are not activated during static pitch or roll tilts of the head or the body in space, but are still activated by high-frequency translational head movements, it has been proposed that adaptation to weightlessness entails a reinterpretation of the signals from the otolith organs, so that pitch or roll of the head with respect to the vertical would be sensed as fore-aft or left-right translation upon return to Earth. Maintenance of this so-called 'Otolith Tilt-Translation Reinterpretation' (OTTR) in the post-flight period has been believed to be responsible for the imbalance and gaze instability observed in returning astronauts. This reinterpretation was also believed to be responsible for the amelioration of space motion sickness, which afflicts roughly half of all space travellers during their first few days in orbit. A third aim of the VVIS

experiment was to test this hypothesis by delivering sustained linear acceleration in microgravity. If OTTR had taken place, astronauts should incorrectly interpret the signals from the otoliths as translation, rather than correctly perceiving a static tilt.

Prior to the NeuroLab experiments, the effects of artificial gravity on our body-orienting responses in space had only rarely been addressed. During the Gemini-11 flight in 1966, the spacecraft was tethered to an Agena target vehicle by a long Dacron line, causing the two vehicles to spin slowly around each other for several minutes. According to the Gemini commander, a TV camera fell 'down' in the direction of the centrifugal force, but the crew did not sense any changes at that moment. Subjects sitting on the ESA-built linear Sled flown during the Spacelab-D1 mission in 1985 perceived linear acceleration, but not tilt. Similarly, during off-axis rotation on the Spacelab IML-1 mission, the test subjects perceived only rotation, not tilt. In these experiments,

however, the linear accelerations were less than 0.22-g, which ground-based studies have since shown to be insufficient to yield a perception of tilt.

The Results from NeuroLab

There was found to be little difference between the eye responses to centrifugation in microgravity and on Earth. In both cases, the induced OCR was roughly proportional to the inter-aural linear acceleration being applied, with the OCR magnitude during 0.5-g centrifugation approximately 60% of that generated during 1-g centrifugation. The OCR magnitude in space was not significantly different from that induced by equivalent inter-aural linear acceleration during static tilt on Earth. In contrast to previous studies, there was no decrease in OCR gain post-flight. These findings raise the possibility that in-flight exposure to artificial

gravity, in the form of intermittent 1-g and 0.5-g centripetal accelerations, may have acted as a countermeasure to the deconditioning of otolith-based orientation reflexes.

Before the NeuroLab mission, astronauts had never been exposed to sustained linear accelerations of 0.5 and 1-g in space. The results showed that they perceived a body tilt relative to a perceived spatial vertical when exposed to 0.5 and 1-g, and that the magnitude of this tilt adapted throughout the mission. During their first test session, on flight day 2, the astronauts perceived a 45 deg roll tilt when subjected to a 1-g inter-aural linear acceleration. After two weeks in space, they perceived a tilt of almost 90°, which was essentially veridical in that it represented the actual level of linear acceleration experienced by the otoliths. This suggests that the otoliths were operating normally in space when exposed to sustained 0.5 and 1-g linear accelerations, after the initial period of adaptation.

The ESA Visual and Vestibular Investigation System (VVIS)

The VVIS, of which one flight and one training model were built by ESA, included a human-rated centrifuge, a visual display, and binocular video-oculography. The test subjects were seated with the body's vertical axis parallel to the axis of rotation at a radius of 0.5 m, either facing or with their back to the direction of motion, and either left-ear-out or right-ear-out. In this configuration, rotations at constant velocities of 254°/sec and 180°/sec provided centripetal accelerations of 1 and 0.5-g, respectively, directed along the test subject's interaural axis. They could also be positioned so that they lay supine along the centrifuge arm with their head 0.65 m from the axis of rotation. Centripetal acceleration was then directed along the body's vertical axis. A restraint system, consisting of a five-point harness, thigh, shoulder and neck pads, and a knee strap, held the body firmly in place. A custom-made facemask restrained the subject's head. A set of headphones provided a masking noise that eliminated external audio cues.

An LCD screen was mounted in a unit directly in front of the test subject's face on the centrifuge chair. Sequences of dots were displayed at known gaze angles to enable calibration of the eye movements. The display was also used to present optokinetic patterns (sequences of 5° stripes that moved horizontally, vertically and diagonally across the screen at 30°/sec) and smooth pursuit targets (small dots that moved horizontally and vertically across the screen). The pattern illumination was adjusted for each test subject for best viewing of the visual targets.

Binocular video recordings were obtained using two miniature video cameras mounted on the LCD visual display unit. Near-infrared LEDs attached to each camera were used to illuminate the test subject's eye. Images of the latter were directed into the video camera via a beam-splitter, which was transparent to light in the visible range and allowed the subject a clear view of the visual display. Two videotape recorders mounted at the opposite end of the rotator beam to the chair were used to store the images of the eyes, as well as centrifuge velocity and timing information.

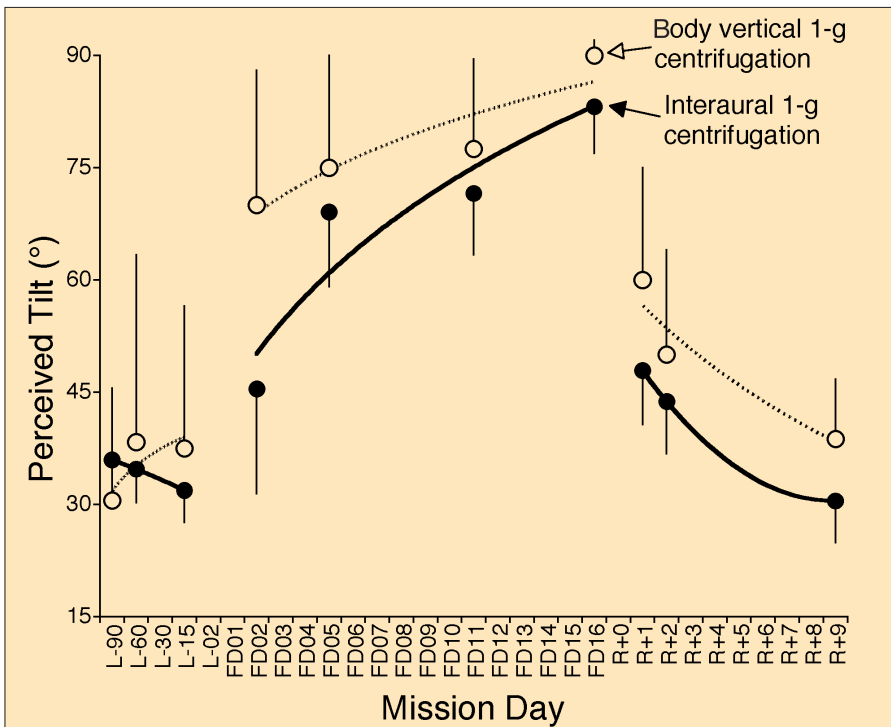
The finding that none of the astronauts felt translation instead of tilt in response to the constant 0.5 or 1-g linear accelerations in space indicates that the OTTR hypothesis is incorrect. Tilt is perceived as tilt, regardless of whether the test subjects are in microgravity or the 1-g environment of Earth, and is not sensed as translation. A model that references perception of tilt with regard to a weighted sum of all linear accelerations and body vertical as the perceived spatial vertical could explain these results. The underestimation of tilt on entry into microgravity suggests that the test subjects continue to weight their internal estimate of body vertical for computing the direction of the GIA. As flight progresses, the weight of this internal representation of body vertical would gradually decrease and the subjects finally adopt the centripetal acceleration as the new spatial vertical reference. This would carry over to the post-flight period and be responsible for a transient exaggerated sense of tilt on returning to Earth.

Eye movements during centrifugation in darkness and during horizontal visual stimulation also shifted towards the centripetal acceleration in space, consistent with the perceptual data.

Lessons Learned

There were a number of innovations in the research equipment developed for the Neurolab flight. In addition to being the first use of binocular, three-dimensional, video-based, eye-movement recordings during controlled vestibular stimulation in space, it was also the first use of visual stimuli to study visual-vestibular interactions during centrifugation, either on Earth or in space.

The information from this research could be used to develop countermeasures to overcome lags in adaptation or the



Mean magnitudes of the tilts perceived by the four Neurolab crew members during interaural and body vertical 1-g centrifugation (L-: pre-flight; FD: flight day; R+: post-flight).

changes in gaze and balance that occur after astronauts return from space. Such countermeasures will be critical for the long-duration spaceflights associated with planetary exploration. When astronauts go to Mars, for example, they will have to fend for themselves immediately after landing on a planet with substantial gravitational force, although they will have been travelling in a microgravity environment for many months. Anything that could hasten their re-adaptation to a stronger gravitational environment will therefore be very valuable in overcoming gaze, posture, and walking difficulties.

One consequence of our findings is that if low-frequency linear acceleration is always perceived as tilt, whether we are in the weightlessness of space or on Earth, long-duration missions can proceed in the expectation that the astronauts will respond normally to artificial gravity or to the gravitational fields of other planets when they are encountered.

These experiments also have substantial clinical implications for those of us back on Earth. We still have little understanding of exactly which part of the human vestibular system is damaged or not operating correctly when we experience balance problems. We also do not yet understand why older people are so prone to falling. Alignment of the body axis to the GIA during walking or turning is likely to be an important factor in this imbalance. Consequently, evaluation of the perceived tilt during centrifugation might prove to be a useful test of the brain's ability to evaluate the direction of the GIA in a dynamic situation.

Ground-based Clinical Studies


After the Neurolab flight, the training model of the VVIS was moved to the MEDES Flight Clinic in Toulouse's Rangueil Hospital, where it has been used for several studies of patients with vestibular disorders.

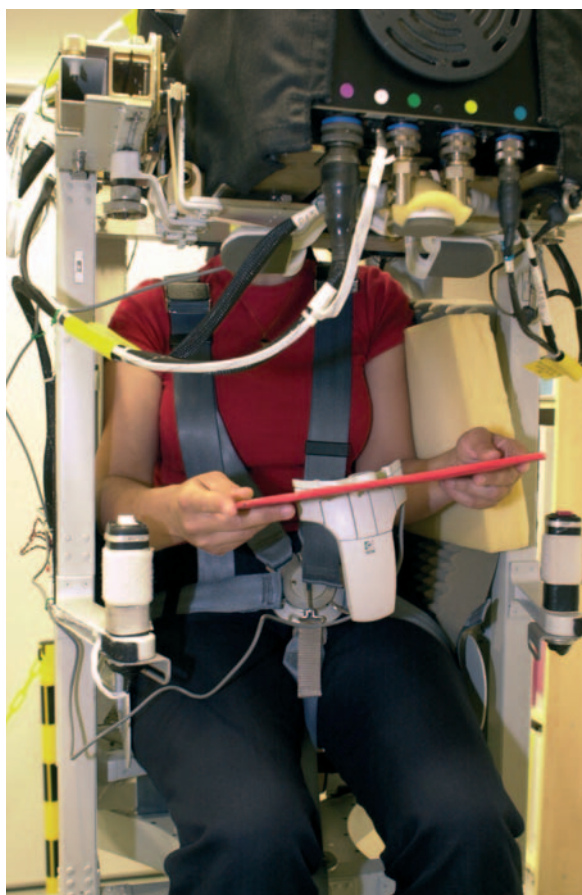
A study performed at the MEDES clinic on 20 normal subjects allowed roll and pitch tilt perception during centrifugation at various g-levels to be characterized. It revealed an asymmetry in the perceptive roll response between acceleration and deceleration, and in the pitch response between forward or backward motion. These results were also used to confirm that the baseline data collected from the four Neurolab crew members were normal.

Another MEDES study has recently begun to study the tilt perception and OCR during centrifugation of 20 other patients with various vestibular problems. The causes for these deficiencies in some patients are already known (e.g. surgical

the perceptions and eye movements captured with the VVIS training model can be used for the diagnosis of disorders in the otolith organs. Programmes for 'vestibular rehabilitation' will also be tested using the VVIS centrifuge,

Conclusion

The human centrifuge experiments conducted in space during the Neurolab mission provided a unique opportunity to evaluate the adaptation of the human spatial orientation system to an unfamiliar environment. The fact that the astronauts perceived tilt rather than translation during centrifugation in space proved that the theory based on a reinterpretation of the otolith signals in microgravity is incorrect. Instead, the results showed that the otolith organs respond normally to a linear acceleration in space, and that both eye movements and perception align to the GIA both on Earth and in space. These findings have helped to identify new possibilities for the testing of the otolith function and the diagnosis of the causes of imbalance-related medical problems in patients here on Earth, and as well as for evaluating the efficacy of artificial gravity during long-duration spaceflights to Mars and beyond. 



A test subject undergoing centrifugation, holding a plate in an orientation that she believes to be 'horizontal', i.e. perpendicular to gravito-inertial acceleration (GIA)

lesions). For others, the 'classical' clinical vestibular evaluation methods show no abnormalities in recorded response, although the patients themselves still complain about vertigo and balance problems. Indeed, most clinical vestibular tests do not address the malfunctioning of the otolith organs per se. It is hoped that