

ORIENTATION TO GRAVITY

Oculomotor and perceptual responses in man

**Orientatie op zwaartekracht
oogbewegingen en waarneming bij de mens
(met een samenvatting in het Nederlands)**

PROEFSCHRIFT

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General introduction

The work described in this thesis concerns aspects of human spatial orientation, in particular the orientation with respect to gravity. By its invariant direction and strength, gravity provides a reference for “up” and “down” in our daily environment, which has significance for the control of posture, locomotion, and vision. Spatial orientation is a multisensory process, integrating information from the vestibular system, visual system, and somatosensory system. Usually, the information provided by these sensory systems is concordant, and we remain spatially oriented without great exertion. However, there are many situations where the information is discordant, and where an adequate sense of “uprightness” is not self-evident. For instance, when we are inside a ship compartment, our vestibular system registers the motion of the ship, whereas our eyes detect a stable environment. Vice versa, when we watch a wide-screen cinema or a flight simulator, we may get the sensation that we are moving from what we see, without corresponding stimulation of the vestibular and somatosensory system. These examples show that the perception of self-orientation and self-motion relative to the external world is determined by the interaction between sensory systems that do not necessarily contribute to the same extent.

With the progress of spaceflight, man has created another challenge for the orientation senses. In weightlessness, there is no gravitational “down” and one can move about in three dimensions. Obviously, this has important consequences for perceptual and sensorimotor responses. The judgment of body orientation becomes strongly dependent of the visual frame of reference. Because the visual cues provided by the interior of the spacecraft can be rather ambiguous, there is a tendency to perceive the surface seen beneath the feet as the subjective “floor”. Visual reorientation illusions may occur when familiar objects are recognized that normally maintain a constant orientation to gravity, such as other people. This is nicely illustrated by reports that astronauts, while oriented truly “upright” with respect to the spacecraft interior, may suddenly feel “upside down” when they observe a crewmember floating “upside down”, and perceive the other person as being the right side up (Oman *et al.* 1986).

During the first several days of a mission in space astronauts often suffer from space sickness (Space Adaptation Syndrome, SAS) with symptoms such as nausea, vomiting, stomach awareness, belching, yawning, apathy, and impaired concentration (Homick *et al.* 1984; Oman *et al.* 1986). Although these symptoms are normally associated with common forms of motion sickness (air sickness, sea sickness etc.), there seems to be no correlation between the individual susceptibility to regular motion sickness and to space sickness. Correspondingly,

standard motion sickness provocation tests seem to have no predictive value for the incidence of space sickness. As a result, there has been some debate about whether space sickness can be explained in terms of the widely accepted “sensory conflict theory”, which states that motion sickness generally arises when the motion signals from the orientation senses are in conflict with each other or with anticipated signals based on previous experience (Reason and Brand 1975). Alternative theories have suggested that the discomfort in zero-gravity (0G) is caused by changes in the cardiovascular system, related to the shift of blood from the legs to the upper part of the body.

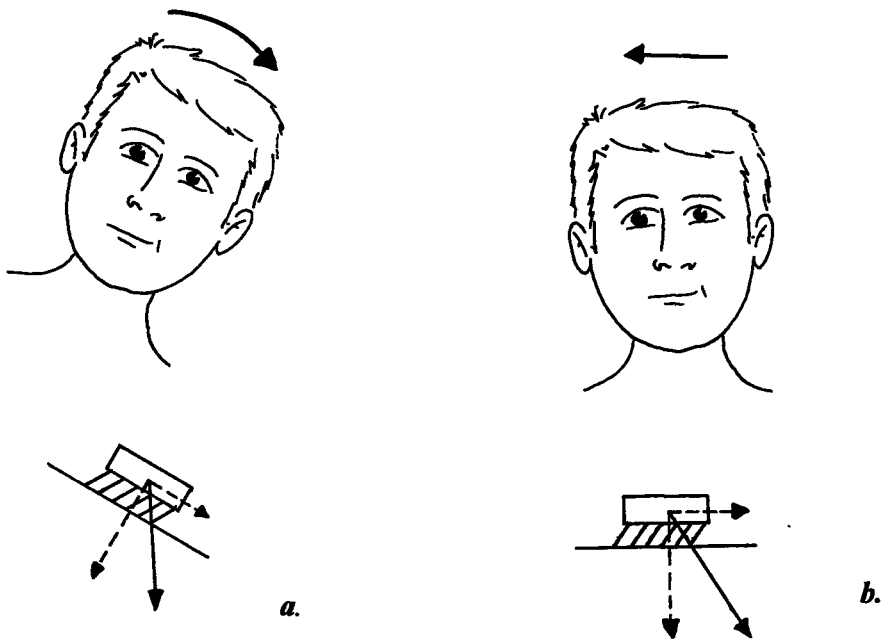


Figure 1. Representation of how the sensory haircells in the utricular macula are deflected by displacement of the otolith membrane (solid black) due to (a) tilt of the head relative to gravity or (b) linear acceleration in lateral direction. This shows that during the dynamic phase of head tilt in an 1G environment the activation of the semicircular canals is accompanied by stimulation of the otolith organs. In weightlessness, the pull of gravity is missing, so that the otolith organs only respond to the translational component of head movements, and no longer to the rotational component. Obviously this may disturb the tight coupling between the two vestibular subsystems.

Certain findings point to an explanation for space sickness that entails the central processing of vestibular information. First, there is a clear cause-and-effect relationship between head movements and the appearance of symptoms, which is stronger with the eyes open than with the eyes closed (Oman *et al.* 1986). Second, astronauts have noted that visual reorientation illusions are potentially provocative, even though the subjective reorientation is not accompanied by actual motion. Thus, problems seem to arise from inconsistencies in the spatial orientation information, probably due to unusual stimulation of the otolith organs of the vestibular system. Under circumstances of normal gravity (1G), the otolith organs not only detect linear accelerations resulting from translational motion of the head, but also continuously register the direction of gravity relative to the head (see Figure 1). Without the constant stimulation from gravity, the otoliths still respond to translational aspects of head motion, but they no longer provide a reference to vertical. Obviously, this will affect the sensory interactions during head movements. It is assumed that the otolith function must adapt to the novel state of gravity (0G) as to reestablish the congruity between the orientation senses. In the same way it is assumed that, once adapted to 0G, the otolith system must re-adapt to 1G on return on Earth. The latter would explain the reappearance of symptoms after spaceflight (similar to the “mal d'embarquement” which is observed on the shore after adaptation to sea sickness). Money (1992) has suggested three possible paradigms by which otolith adaptation to weightlessness can take place: 1) suppressing the otolith system (gain reduction); 2) the interpretation that all otolith signals arise from head translations (tilt-translation reinterpretation); 3) the substitution of other senses for the otolith information (higher weighting of visual inputs). In general, studies in spaceflight seem to support the view that all three mechanisms may contribute to adaptation to 0G, although the evidence is sporadic and sometimes contradictory. The difficulty with research in space is that it is hampered by high expenses and small numbers of subjects.

Recently it was suggested that otolith adaptation may be studied after prolonged exposure to *hypergravity* in a human centrifuge (Bles *et al.* 1989; Albery and Martin 1994). After a centrifuge run with a G-load of 3G, postural instability and symptoms of motion sickness were found (Bles and De Graaf 1993), similar to the effects observed in astronauts on the first day post-flight (Kenyon and Young 1986; Bles and Van Raay 1988). The centrifuge run itself was not experienced as very stressful by the subjects, but symptoms emerged afterwards. Interestingly, European astronauts who participated in these experiments reported striking similarities with sensations in space (Ockels *et al.* 1990). Head movements induced illusory motion of the visual surround (oscillopsia) and, analogous to space sickness, triggered attacks of discomfort or nausea (Sickness Induced by Centrifugation, SIC). Especially head movements that changed the orientation of the head to vertical were provocative (“pitch” and “roll”, see Figure 2 for

convention on rotation axes). The subjects walked very carefully in an attempt to minimize head movements (resulting in a “robot walk”). In addition, it was found that the rank order in the astronauts’ susceptibility for SIC was the same as that for SAS, implying a common mechanism. Medical monitoring during and after the centrifuge run has shown that a cardiovascular cause was highly unlikely (Bles *et al.* 1989; Krol 1994), which is in favor of a vestibular mechanism.

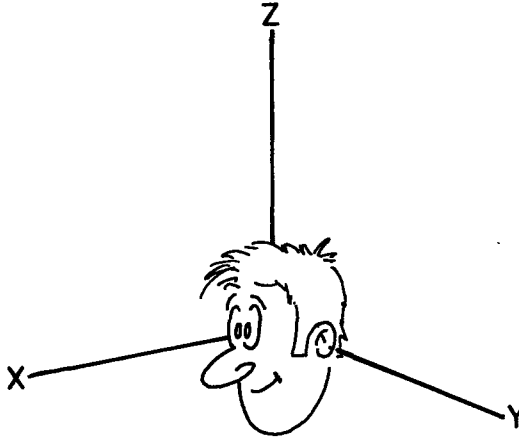


Figure 2. The three main rotation axes with respect to the head. Rotation about the x-, y-, and z-axis are designated as “roll”, “pitch”, and “yaw”, respectively.

Otolith adaptation to hypergravity

The first aim of the work presented in this thesis was to identify vestibular adaptation in human subjects after an one-hour centrifuge run with a G-load of 3G. Of special interest was adaptation of the otolith system. Otolith signals play a role in sensing the inclination of the head relative to vertical, and in controlling postural responses and eye movements. As mentioned above, previous studies have shown that a long duration centrifuge run produces destabilizing effects on postural balance. In addition, subjects noted a compelling sensation of illusory body tilt immediately after the run (Bles and De Graaf 1993), and also showed a measurable bias in the judgment of body orientation in a post-test about 30 minutes later (Bles *et al.* 1989). These findings provide indirect evidence for otolith adaptation.

A new study was designed to expand the body of evidence with more “objective” tests. In this study, the effect of centrifugation on the ocular torsion response to

static tilt was evaluated. When the head or the whole body is tilted laterally (roll), the eyes rotate in the opposite direction about the line of sight. This is referred to as ocular counterroll or, more generally, ocular torsion (OT)¹. In general, an important vestibular function is to generate compensatory eye movements (vestibulo-ocular reflex, VOR) during movements of the head, so as to minimize retinal blur. The OT response observed during static tilt is considered a static equivalent of this, which probably is used for orientation. It has been shown that static OT reflects the functioning of the otolith organs (Miller 1962; Colenbrander 1963; Miller and Graybiel 1971; Diamond and Markham 1981; Collewyn *et al.* 1985), and the response also has clinical relevance (Diamond and Markham 1983; Gresty and Bronstein 1992). It was hypothesized that a hypergravity-induced change in the sensitivity of the otolith system would be visible in the magnitude of static OT. In addition to the static measurements, the dynamic OT response was also measured during sinusoidally body roll, in order to evaluate changes in the interaction between the semicircular canals and the otolith organs. The results of this study are described in **Chapter 2** of this thesis.

Video-oculography

The magnitude of static OT in humans is rather small: on average, the maximum response amounts to about 6°. OT can not be detected by standard electro-oculography (EOG), because rotations about the visual axis do not produce changes in the electrical potential. Accurate measurements of OT can be achieved with the scleral search coils technique. However, this technique was discarded because it requires the subjects to wear contact lenses containing a small coil, that firmly adhere to the sclera and soon become uncomfortable. The OT measurements took about 45 min and were performed twice (once before and once after the centrifuge run), which was considered too long for the use of search coils. Furthermore, the metal frame of the rotating chair was considered unsuitable to contain the large Helmholtz coils, needed to generate a homogeneous magnetic field around the subject.

An alternative, non-invasive approach to measure OT was offered by the video-based technique described by Bos and De Graaf (1994). This comprises the recording of eye movements on video tape and quantification of OT afterwards by matching the iris patterns between one image of the eye and another image which serves as a reference. In the original method, the matching is performed semi-automatically by visual inspection of iris patterns that are digitized and displayed

¹ Although the definition of ocular torsion *de facto* depends on the coordinate system that one uses to describe eye position (eg. Helmholtz, Fick or Listing's coordinates), in the vestibular literature torsion usually refers to the rotation of the eyes about the visual axis.

on a computer monitor. Because this procedure is too time consuming for time series analysis, an automatic pattern recognition algorithm was developed and implemented on a PC system, that automatically digitizes consecutive images from video tape into the computer memory, selects significant structures in the iris of a reference image, and relocates these landmarks by a method of template matching. The use of several landmarks, uniformly distributed over the iris, allows for correction of errors that result from miscalculation of the rotation center of the eye. This feature is usually not accounted for in other video-oculography methods. The new video-oculography method is described in **Chapter 1** of this thesis.

Otolith-canal interaction in ocular torsion response

To a great extent, the information concerning spatial orientation provided by the different sensory systems is redundant. On the other hand, sensory systems also differ in their characteristics so that they can supplement each other. For instance, the visual system operates in a low-frequency range, whereas the vestibular system operates at higher frequencies. This can be verified by a simple test: when you keep your head still and wave your hand in front of your face, the image of your hand will soon become blurred with increasing frequency; when you keep your hand still and oscillate your head, the image of your hand will remain clear up to much higher frequencies due to the VOR. This frequency dependency is reflected in the contribution of the visual and vestibular senses to orienting responses (as we will see in Chapter 5).

A similar interaction may exist within the vestibular system, between the semicircular canals and the otolith organs. The semicircular canals respond to angular accelerations of the head and are responsible for the generation of the angular VOR. The operational range of the semicircular canals is adjusted to frequencies of natural head movements. At very low frequencies, the canal-induced response becomes less effective (Carpenter 1988), and it was hypothesized that the otolith system may help to improve the low-frequency response dynamics for rotations about an off-vertical axis. The torsional VOR was considered appropriate for this purpose, especially because of the association of the otolith organs with OT. From studies on a linear track which applied linear accelerations along the interaural axis, it is known that otolith-induced OT can be characterized as a low-frequency response, being maximal in a frequency range up to about 0.3Hz (Young 1985; Hannen *et al.* 1966; Lichtenberg *et al.* 1980). Nevertheless, whereas otolith-induced OT has been well-studied during static tilt, its usefulness during dynamic tilt has received little attention. This is due to the simultaneous activation of the semicircular canals, which complicates examination of the otolith component. In **Chapter 3** a study is presented in which the OT response was

measured during sinusoidal body roll in a frequency range of 0.05-0.4Hz. By comparing the response to rotation about an earth-horizontal axis with that to rotation about an earth-vertical axis, some specific otolith contributions to the response were revealed.

The coupling between semicircular canals and the otolith organs is of interest for another reason as well. There is a fundamental difference between the two vestibular subsystems. Functionally, the semicircular canals can detect the rate of rotation of the head, but they can not detect the plane of rotation relative to gravity. Signals from the semicircular canals are coded in head egocentric coordinates. The otolith system, however, is able to detect the plane of rotation relative to gravity. Signals from the otoliths therefore may help to link the egocentric canal-induced VOR to an exocentric frame of reference. This issue will also be evaluated in Chapter 3.

Vestibular-visual interaction in judgments of self-tilt

Most of us are familiar with the experience that, sitting in a stationary train, watching a neighboring train leave may produce a sensation as if our train is moving. This example shows that our visual system plays an important, and often dominant, role in the perception of self-motion. In general, motion of the visual surroundings induces a sensation of self-motion (“vection”) in the opposite direction. This is particularly true for yaw rotation about the vertical axis. An upright observer viewing rotation of a visual scene about an earth-horizontal axis, however, experiences a limited degree of self-tilt in the opposite direction, paradoxically combined with a sensation of continuous self-rotation. It has been shown that the magnitude of visually induced self-tilt is to some extent a function of stimulus area and also of stimulus velocity (Held *et al.* 1975; Howard *et al.* 1988). Nevertheless, the tilt effects seldomly exceed 20°, which is ascribed to the restraining influence of the otolith organs which do not register any change in the direction of gravity relative to the head. This hypothesis is supported by the observation that visually induced self-tilt increases when the head is inclined 90° or inverted, so that the utricles are out of their most sensitive position (Young *et al.* 1975; Bishof 1978; Howard *et al.* 1988).

Recently, Howard and Childerson (1994) distinguished that the sense of body orientation depends on three types of visual information: visual motion, visual frame, and visual polarity. The visual frame refers to a set of lines and surfaces (such as walls and floors) which are normally horizontal or vertical. Even a simple stationary tilted visual frame may lead to perceived self-tilt in the opposite direction (Asch and Witkin 1948c). Visual polarity is found in objects with a distinct top and bottom, indicating “up” and “down”, such as chairs, tables, and

people. When all polarized objects visible are tilted relative to gravity, the effect is a compelling illusion of self-tilt, especially if the objects are part of a tilted frame (Asch and Witkin 1948a). The usual stimulus in studies on visually induced self-tilt is a simple display of dots lacking visual frame or polarity cues, so that the effects are due to mere visual motion information. Using a rotating 7-foot cubic room with replaceable walls, Howard and Childerson (1994) showed that motion of a polarized visual frame elicited larger effects than visual frame motion, which in turn elicited larger effects than visual motion alone. They noted that erect subjects even experienced sensations of head-over-heels rotation when seated inside the “furnished” room (the polarized visual frame), while it rotated at constant velocity about the subjects’ roll-axis. Apparently, when certain requirements are met, a visual stimulus can completely dominate the conflicting otolith information in a stationary observer.

The so-called “Tumbling Room” of Dr. Howard’s laboratory (York University, Toronto, Canada) was later replaced by a larger and more realistic one, containing an even richer variety of polarized objects. **Chapter 4** of this thesis describes a study that was performed in this new Tumbling Room to determine the percentage of subjects that perceive “full tumbling” (through 360°) about an earth-horizontal axis. Another objective of the study was to examine the effects of body orientation with respect to gravity (upright or inclined 90°) and with respect to the fixed rotation axis of the room (roll, pitch, and yaw). These variables have been shown to affect illusory self-tilt and vection, using displays that consisted only of dot patterns. It was expected that these factors become less important when the effectiveness of the visual stimulus increases.

Flight simulators, among other virtual reality applications, exploit visually induced self-motion and self-tilt. As long as the simulated motion is smooth and in horizontal direction, a visual display can be sufficient. However, when the simulated motion comprises fluctuations in velocity or direction (that is, linear and angular accelerations, respectively), the lack of confirming vestibular information will undermine the fidelity of the intended sensations. Flight simulators with a motion base therefore employ vestibular “onset” cues to reinforce the visual motion. For instance, the vestibular cue arising from forward linear acceleration in an aircraft can be recreated by pitching the motion base backwards, stimulating the utricles in a way that is approximately comparable to horizontal linear acceleration. Vestibular onset cues may also be useful to enhance visually induced self-tilt. As was mentioned above, illusory self-tilt is larger when the body is inclined 90°. However, a motion base has limited travel and must return to its original position. Despite the widespread use of motion base simulators, there seem to be no documented studies on the effects of a vestibular onset cue on illusory self-tilt. The experiment presented in **Chapter 5** addresses the question whether sensations of self-tilt and self-rotation can be enhanced by actual body tilt at the onset of

rotation of the visual scene. The original plan was to use the Tumbling Room (of Chapter 4) for this experiment but this room generated complete illusory self-rotation through 360° in most subjects even without a vestibular onset cue. Therefore, a less powerful stimulus was needed which only produces limited illusory self-tilt, so that any effects of an onset cue could be assessed. Such a stimulus was the rotating sphere of Dr. Howard's laboratory, which had been shown before to generate a mean illusory self-tilt of about 20° (Howard *et al.* 1988).

Chapter 1

Video-oculography

Introduction

During head movements, the vestibular system generates compensatory eye movements for stabilization of the retinal image. In the case of head rotation about the roll-axis, this results in rotation of the eyes about the visual axis, generally referred to as ocular torsion (OT). The sustained OT response to static tilt of the head is attributed to stimulation of the otolith organs (Cheung *et al.* 1992; Miller 1962; Miller and Graybiel 1971; Woellner and Graybiel 1959), whereas OT during dynamic head tilt is primarily generated by the semicircular canals (Collewijn *et al.* 1985). Non-vestibular inputs, however, such as proprioception from the neck, may contribute as well (De Graaf *et al.* 1992). In addition to the field of basic research, OT measurement may also find clinical applications in the field of oto-neurology (Diamond and Markham 1981; Dieterich and Brandt 1993 Gresty and Bronstein 1992).

Several techniques for OT determination have been described, varying from photographic procedures (Miller 1962; Graybiel and Woellner 1959; Melvill Jones 1962), to the semi-invasive and accurate search coil method (Robinson 1963; Collewijn *et al.* 1985). Expanding on photographic methods, advanced video-based techniques offer great flexibility: the approach is non-invasive, no calibration is needed and images are directly available for analysis. Like photographic methods, video-based techniques commonly measure OT by tracking iris structures. Hatamian and Anderson (1983) described an algorithm for OT measurement in digitized video images based on cross-correlation of a sampled iris pattern encircling the pupil. Such an algorithm was implemented in automatic methods developed by Clarke *et al.* (1989) and Bucher *et al.* (1990). The apparatus of Clarke *et al.* allowed for analysis of the vestibulo-ocular reflex in all directions: vertical and horizontal gaze direction on-line, and OT off-line.

Recently, Bos and De Graaf (1994) introduced a semi-automatic method for OT quantification, especially designed for the correction of errors that arise from incorrect assessments of the pupil center (which is assumed to coincide with the rotation axis of the eye). It was shown that this type of error varies sinusoidally in tangential direction and may amount to 1-2°, which is sometimes on the order of OT

Adapted from: Groen E, Bos JE, Nacken PFM, De Graaf B (1996) Determination of ocular torsion by means of automatic pattern recognition. *IEEE Trans Biomed Eng* 43:471-479.

itself. By averaging OT values determined in opposite segments of partitioned annular iris strips, this type of error can largely be corrected for, yielding a practical accuracy of about 0.25° . In the implementation of this method, OT determination was carried out by matching iris patterns visually on a computer monitor. Consequently, the method was appropriate for *static* OT measurements, involving a small number of images, but not very efficient for OT measurements under *dynamic* conditions, involving larger series of images. Therefore a fully automatic system was developed which made use of the error analysis of Bos and De Graaf. As a prerequisite, the method should take as many as possible iris segments into account for a reliable estimate of OT. A procedure of tracking 36 distinct landmarks, well spread over the iris, was considered appropriate for this purpose. An algorithm for template matching was derived from In den Haak *et al.* (1992) which allows for automatic *selection* and *relocation* of the most salient iris structures in two directions. The procedure and its implementation will be described in this chapter. The system's reliability will be evaluated in both an *in vitro* and an *in vivo* study. The results show that two-dimensional template matching is a useful alternative for the common one-dimensional cross-correlation between iris strings.

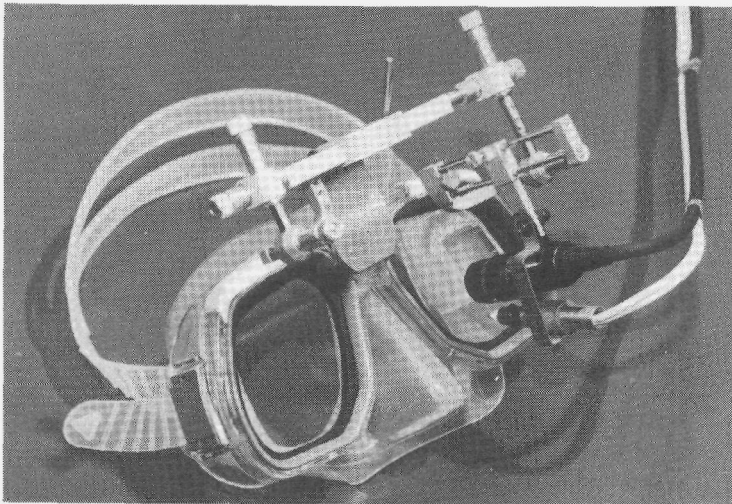


Figure 1.1. The head set with one lipstick CCD-camera (another camera can be mounted in front of the other eye). The aluminum frame allows for careful adjustments of the camera.

Configuration

The system hardware consists of two small CCD-cameras mounted on a pair of diving goggles (Figure 1.1). The cameras are placed in front of the eyes at a distance of about 1-2 cm, the optical axes aligned with the visual axes. Each eye is illuminated by a small white light emitting bulb, closely fixed to the camera. To avoid artifacts by movement of the headset relative to the head, the headset can be attached to a dental frame. Both eyes are recorded separately on S-VHS tape, mixed with an analogue time code signal for synchronization. For off-line analysis, the video recorder (Panasonic AG-6730) is controlled by an RS232-interface protocol. Recordings are made using European video standard PAL (25 frames/s, each frame consisting of two interlaced fields). By playing one field at a time, a temporal resolution of 20 ms is realized. The fields are digitized into 512*512 pixel images with a depth of 8 bits by a PC-Vision Plus frame-grabber (Imaging Technology Inc., Bedford

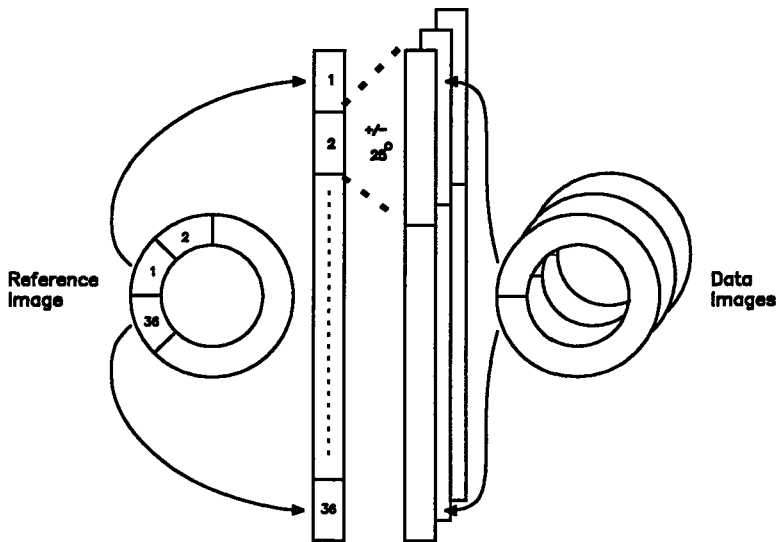


Figure 1.2. Schematic representation of the total procedure. In a reference image, the pupil is identified, and a ring-shaped iris area is selected and converted into polar coordinates (so that it projects on a rectangular grid). After gray value normalization, the iris area is divided tangentially in 36 segments of 10° , in each of which one landmark is selected. These landmarks then are relocated in the corresponding iris areas in consecutive data images.

Method

The OT determination is based on tracking a set of distinct landmarks in the iris in a number of data images relative to *one* reference image (Figure 1.2). In the analysis, six steps can be identified: 1) pupil detection, 2) polar transformation, 3) normalization, 4) selection of significant points, 5) matching, and 6) OT estimation.

Pupil detection

The software automatically determines the pupil center, which is assumed to lie on the axis of rotation. The pupil is the largest dark area in the image and is separated from the surrounding iris by simple thresholding at a value just beyond the first clear peak in the gray value distribution. Eventually, some additional smaller dark regions, like eyelashes or shadows, remain after thresholding and the pupil is distinguished from these by connected area labeling (Sedgewick 1984).

To obtain the center of rotation, the imaged pupil edge is approximated by a circle (the subject is looking straight into the camera). To compute the parameters of the circle (center (x_0, y_0) , and radius R), we applied the method of Chaudhuri and Kundu (1993). This method is based on minimizing the least square error J , with

$$J = \sum w_i [(x_i - x_0)^2 + (y_i - y_0)^2 - R^2]^2 \quad (1)$$

(where the summation is over all edge points (x_i, y_i) with $i = 1..n$). This can be done by setting the derivative of J with respect to x_0, y_0 , and R to zero. Then x_0, y_0 , and R are given by:

$$x_0 = \frac{B_y C_x - B_x C_y}{A_x B_y - A_y B_x}, \quad y_0 = \frac{A_y C_x - A_x C_y}{A_y B_x - A_x B_y} \quad \text{and} \quad R^2 = \frac{1}{W} \sum w_i [(x_i - x_0)^2 + (y_i - y_0)^2] \quad (2)$$

where

$$\begin{aligned} W &= \sum w_i, & \bar{x} &= \frac{1}{W} \sum w_i x_i, & \bar{y} &= \frac{1}{W} \sum w_i y_i, \\ A_x &= \sum w_i (x_i - \bar{x}) x_i, & B_x &= \sum w_i (x_i - \bar{x}) y_i, & C_x &= \frac{1}{2} \sum w_i (x_i - \bar{x}) (x_i^2 + y_i^2), \\ A_y &= \sum w_i (y_i - \bar{y}) x_i, & B_y &= \sum w_i (y_i - \bar{y}) y_i, & C_y &= \frac{1}{2} \sum w_i (y_i - \bar{y}) (x_i^2 - y_i^2) \end{aligned} \quad (3)$$

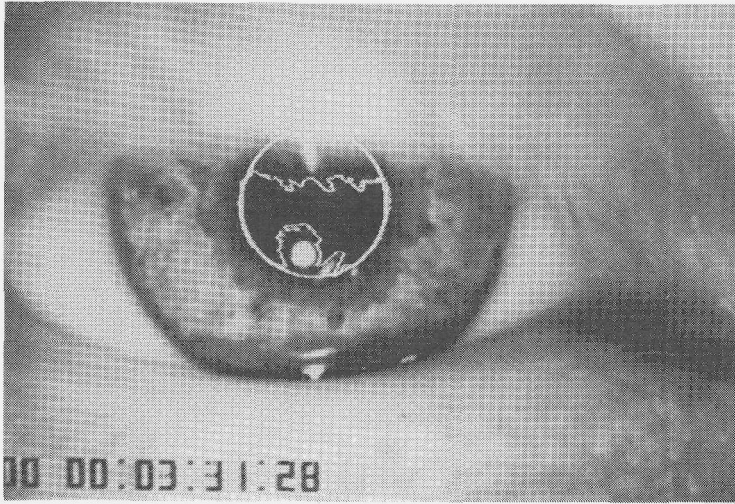


Figure 1.3. Despite deformations of the pupil edge, caused by reflection artifacts and a partial eye blink, the pupil has been localized successfully by means of a reweighted least squares circle approximation to the edge points. The raw thresholded pupil edge is marked by the frayed line, whereas the fitted circle is shown as the thick solid line.

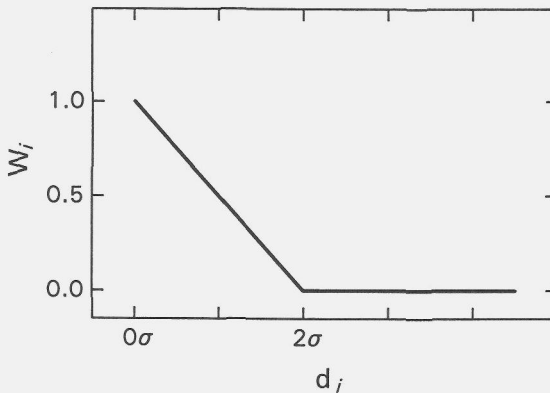


Figure 1.4. Weights w_i are assigned to the pupil edge points according to their distance $|d_i|$ to the previous circle fit, expressed in terms of the standard deviation of these distances (σ_{n-1}). Dubious edge points with a distance $|d_i|$ of more than 2σ are excluded by setting the weight to zero.

Illumination artifacts and eyelids may cause deformations of the imaged pupil edge (Figure 1.3). The influence of these artifacts on the analysis can be reduced by giving dubious edge points low weight values w_i . Initially, it is not known which edge points are dubious, and all weights are set to unity. Then, all edge points are reweighted depending on their deviation from the fitted circle, and the calculation of x_0, y_0 and R is repeated. The most natural choice for the weights is the reciprocal of the squared distance from the individual points (x_i, y_i) to the previously fitted circle, i.e. $w_i = 1/d_i^2$ with $d_i = \sqrt{((x_i - x_0)^2 + (y_i - y_0)^2) - R}$. It is even better to exclude points that clearly do not belong to the true pupil edge completely. An appropriate weighing, as depicted in Figure 1.3, is then given by $w_i = 1 - d_i/(2\sigma)$ for $|d_i| < 2\sigma$, and $w_i = 0$ otherwise, where the overall standard deviation σ is considered explicitly ($\sigma^2 = \sum d_i^2 / (n-1)$). This procedure of fitting and weighing is executed eight times.

Polar transformation

Once the center and radius of the pupil have been determined, an annular iris area of fixed width is selected (Figure 1.5A). The distance of this iris ring to the pupil border can optionally be adjusted in the reference image to overcome reflection artifacts. Once chosen, the distance to the pupil border is invariable for all consecutive data images, so that the same iris area will be selected automatically, irrespective of expansion or constriction of the iris due to variations in pupil size. After Gaussian smoothing to avoid aliasing, the selected region is transformed into polar coordinates, so that it is represented on a rectangular grid (Figure 1.5B): *rotation* (OT) in the original image then corresponds with *translation* in the converted image (translation is computationally less expensive).

Let (r, ϕ) denote the polar coordinates to which the points of the selected iris region will be projected, r being the radius and ϕ the azimuth angle of each point, and (x_0, y_0) be again the center of the pupil in Cartesian coordinates. Then the relation between the transformed image $I(r, \phi)$ and the original image $F(x, y)$ is determined as follows:

$$I(r, \phi) = F(x_0 + r \cos \phi, y_0 + r \sin \phi) \quad (4)$$

The angle ϕ is quantized into 0.25° bins (rounded to the nearest pixel index), and the radial extent of the annulus is sampled in 39 steps, which covers nearly half of the iris width. Finally, the iris strip projects on a rectangle of 39×1440 bins (hereafter treated as pixels again).

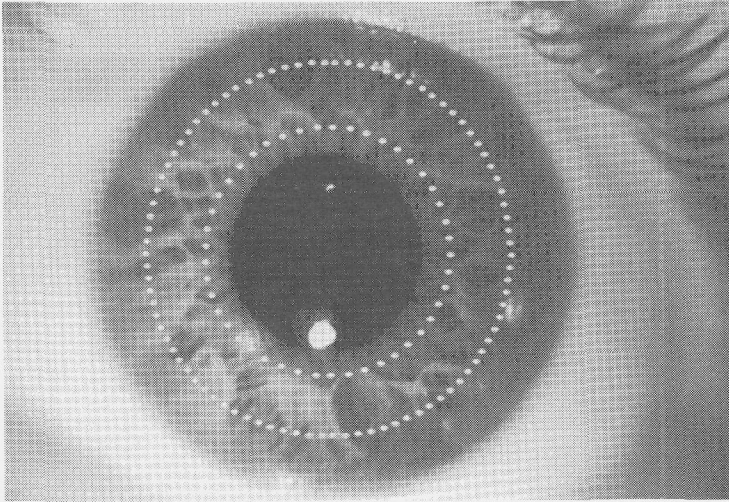


Figure 1.5a. Selection of the area of interest. After the pupil center and radius have been estimated, an annular band of fixed width is selected around the pupil (between dotted circles). The distance between this band and the pupil edge can be adjusted manually in the reference image, and will be held constant for all data images.

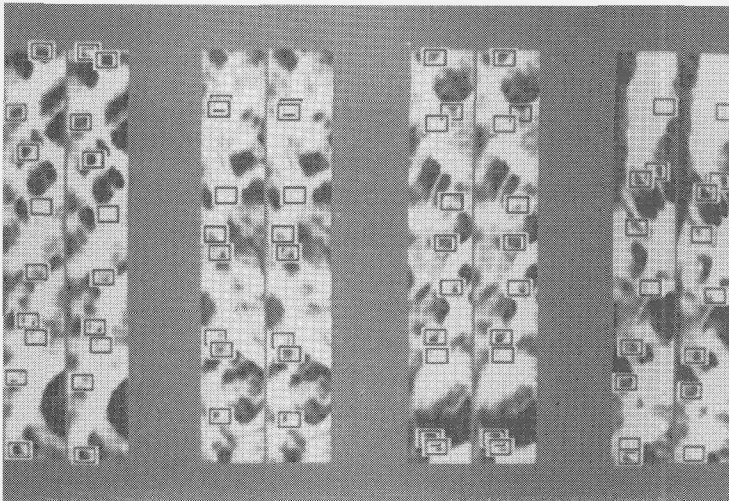


Figure 1.5b. After transformation into polar coordinates the annular iris band is represented by a rectangle. Here the rectangles of both a reference (left) and a data image (right) are shown of real eyes. For practical reasons the rectangles are displayed in 4 segments of 90° . Adjacent segments correspond with respect to their position in Cartesian coordinates. OT is calculated by the translation of 36 landmarks (square masks) between these rectangles. OT is -0.9° in this example.

Normalization

Although great care is taken to guarantee constant illumination of the eye, the use of a small light bulb may result in an illumination gradient (Figure 1.5A). Luminance differences can also occur, e.g., by reflections from the headset. To eliminate these luminance differences between images and to facilitate relocation of significant points, two procedures are applied on the polar transformed iris images. First, the gradient that occurs with radiant illumination is largely removed by a high-pass moving average filter covering 40° , moving unidirectional along ϕ , and effectively eliminating structures larger than 63° (c.f. Faes *et al.* 1994). Second, by means of a parameter-free histogram equalization, gray values are stretched to include the entire gray scale, with exception of the maximum gray value. The latter is reserved for identification of reflections, defined as pixels with original gray values above the 80th percentile of the gray scale. In the following analysis reflection areas will be excluded. Because the same iris area is selected in all images, this normalization procedure will equalize gray values of corresponding structures.

Selection of significant points

In the iris of the reference image, significant points are selected which are to be recognized in successive data images. A suitable method to find unambiguous patterns was presented by In den Haak *et al.* (1992). Their method selects points at junctions of distinct dark and bright structures (Figure 1.6). Following a path along the sides of a small square (a "mask", typically between 10×10 and 20×20 pixels) centered at those points, the number of times the gray value increases or decreases is counted (Figure 1.7). To be independent of noise, gray value transitions must exceed a certain noise level. We chose the noise level to be the standard deviation of gray values of the entire iris strip (which is a constant after the normalization step²). The significance of a mask is defined as the number of gray value transitions greater than this noise level. We chose a mask size of 15×15 pixels, which is in correspondence with the general size of the iris patterns as can be judged from Figure 1.4b. To achieve a fairly homogeneous distribution of landmarks, the iris is divided into 36 sectors of 10° each, and for each sector the most significant structure is determined. Masks which cover a reflection are ignored.

² For an optimal histogram equalized image with gray values I_i in the range $[0, m]$ and i in $[1, N]$, each I occurs exactly $n = N/m$ times, and the average gray value $I = \frac{1}{2}m$. Then

$$\sigma_N^2 = \frac{1}{N} \sum_{i=1}^N (I_i - \bar{I})^2 = \frac{1}{N} n \sum_{I=0}^m (I - \frac{1}{2}m)^2 \approx \frac{n}{N} \int_0^m (I - \frac{1}{2}m)^2 dI = \frac{nm^3}{12N} = \frac{m^2}{12}$$

In our case, $m = 254$, and thus σ a constant of 73.3.

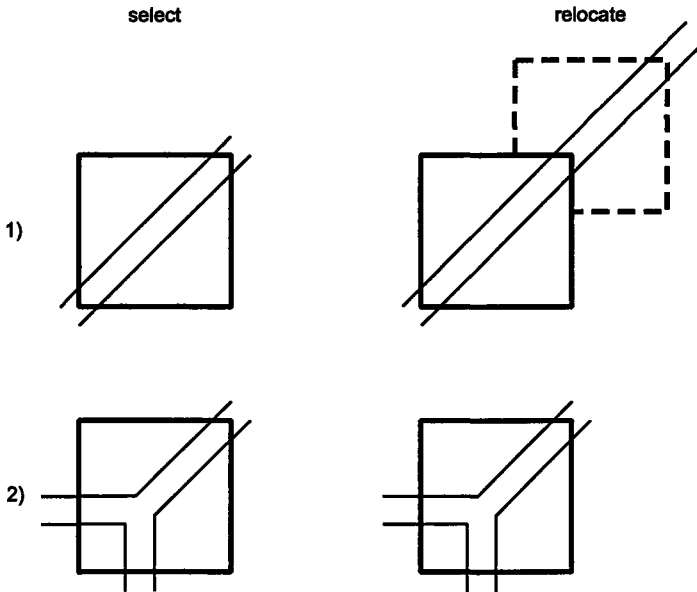


Figure 1.6. This drawing shows that a mask covering a multiple ramification of iris structures (b) can be successfully relocated because the precise location of gray value transitions under the mask prevent it to move in any direction, as opposed to a mask covering a more ambiguous structure such as an edge (a).

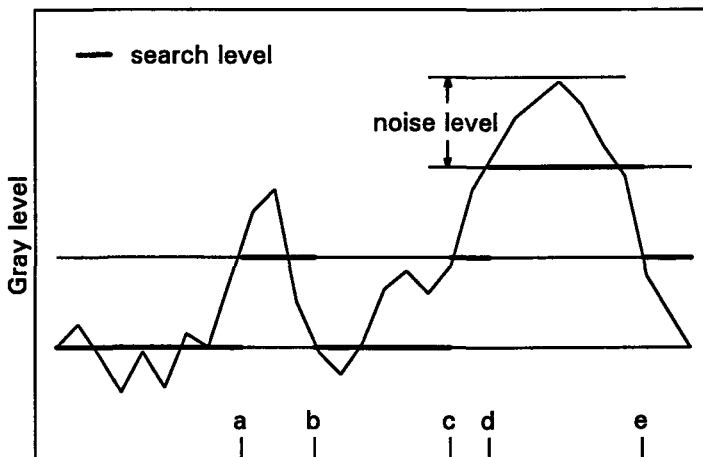


Figure 1.7. The calculation of the significance of a mask. Following the gray value profile along the sides of the mask, the number of gray value transitions that exceed the noise level, are counted. The counted transitions here are a, b, d, and e. The "up" transition c is ignored, because it is followed by another "up" transition. (after: In den Haak et. al. (1992), by kind permission).

Matching

Significant structures from the reference image are recognized in the data image by template matching. Let M denote the border of a 15×15 square mask, centered at some point in an iris image. Let I_u and I_v denote the gray values of the iris of the reference image and data image iris respectively, as defined in equation 1. Then the match error, E , for a significant point $u=(r_u, \phi_u)$ in the reference image and a point $v=(r_v, \phi_v)$ in the data image, is defined as

$$E(u,v) = \sum_{z \in M} |I_u(u+z) - I_v(v+z)| \quad (5)$$

This match error is simpler and computationally faster than the normalized cross-correlation used by In den Haak *et al.* (1992). It is permitted because gray values of corresponding iris structures in reference and data images have been normalized beforehand by the histogram stretch. Furthermore, as a consequence of the transformation to polar coordinates, iris structures retain their orientation in spite of changing torsion angle.

For each point u in the reference image, a point v in the data image is determined for which E is minimal. The difference in ϕ -coordinates $\Delta\Phi = \phi_v - \phi_u$ of each pair yields a measured torsion angle. In this way, up to 36 $\Delta\Phi$ -values are obtained. To reduce analysis time, searching is restricted to intervals of $\Delta\Phi$ between $\pm 25^\circ$, since OT never exceeds this range.

OT estimation

In determining the true torsion angle from these measurements, two problems arise. First, mismatches should be excluded from the estimation process. Second, as indicated by Hatamian and Anderson (1983) and Bos and De Graaf (1994), misalignment of the pupil center with the true rotation center results in a measured torsion angle, $\Delta\Phi$, that varies sinusoidally with the angular position ϕ of the landmark around the rotation center (Figure 1.8). The same problem occurs when the imaged pupil shape is not circular, due to gaze shifts with respect to the camera position. We can thus characterize the estimation problem as a sinusoidal fit, eventually corrupted by outliers. Analogous to the circle fit procedure in the pupil detection, we apply an iterative reweighted least squares approximation to the measurements $(\phi_i, \Delta\Phi_i)$, $i=1..36$ (see e.g. Hogg 1979):

$$\Delta\Phi(\phi) = \Theta + C \sin(\phi + \delta) = \Theta + A \cos(\phi) + B \sin(\phi) \quad (6)$$

in which the regression coefficient Θ estimates true torsion, C depends on the amount of misalignment of the pupil center, and δ depends on the direction of the misalignment. Because of the linearity of the second notation, we estimate the regression coefficients Θ , A and B instead of Θ , C and δ . Estimates $(\phi_i, \Delta\Phi_i)$ are mutually independent, as opposed to the edge points in the least squares fit of the pupil circle. Therefore, a slightly different weighing rule is applied here. To make a first estimate of the parameters in (6) without interference of outliers, an initial unweighted fit is performed only to the central 50% of the ordered measurements. Next, weights, w_i , are assigned to all 36 measurements depending on their distance, d_i , to the last fitted sinusoid, where here $d_i = \Delta\Phi(\phi_i) - \Delta\Phi_i$. The relationship between d_i and w_i is given in Figure 1.7B. Weights are limited to unity when $|d_i|$ is smaller than σ ($\sigma^2 = \sum d_i^2 / (n-1)$). Obvious outliers with $|d_i|$ greater than 3σ are rejected ($w_i=0$). The reweighted measurements are input for another estimate of the variables Θ , A and B given in equation 6. This procedure of weighting and fitting is iterated three times, which is sufficient to achieve convergence.

The method was implemented on a PC (Intel 486, 66MHz), in which the analysis took about 7 s per image: digital image processing needed 4 s, where the remaining time was consumed by operation of the video recorder, and storage and displaying of the results.

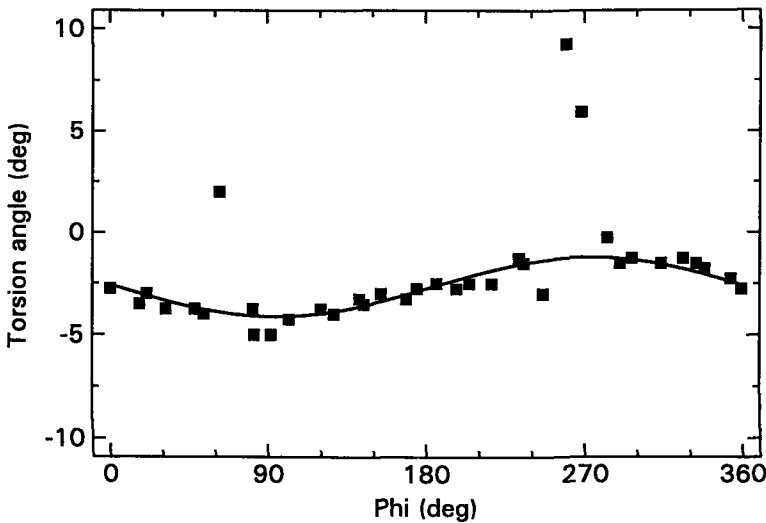


Figure 1.8. Robust estimation of OT from individual determined torsion angles. The 36 measured torsion angles (squares) depicted against the angular position in the iris (ϕ) of the corresponding landmarks. Misjudgment of the rotation center results in a sinusoidal variation of the measured torsion angles about OT. Therefore, a robust sinus fit procedure is applied on the measurements to estimate OT. In this figure OT amounts to -3.0 deg.

Validation

The accuracy of the automatic system was first validated using the same set of prepared images of an *artificial eye* as was used by Bos and De Graaf. The torsion angle of this artificial eye could be set with an accuracy of 0.1° . The torsion angle was varied in steps of 5° from -10° to $+10^\circ$, and the angle between the line of sight and the camera's optical axis was either 0° or 10° . In this way, ten data images were prepared. The error in the computed OT for each image is shown in Figure 1.8. At the most, this error was 0.11° , i.e. on the order of the precision of the setting of the artificial eye itself.

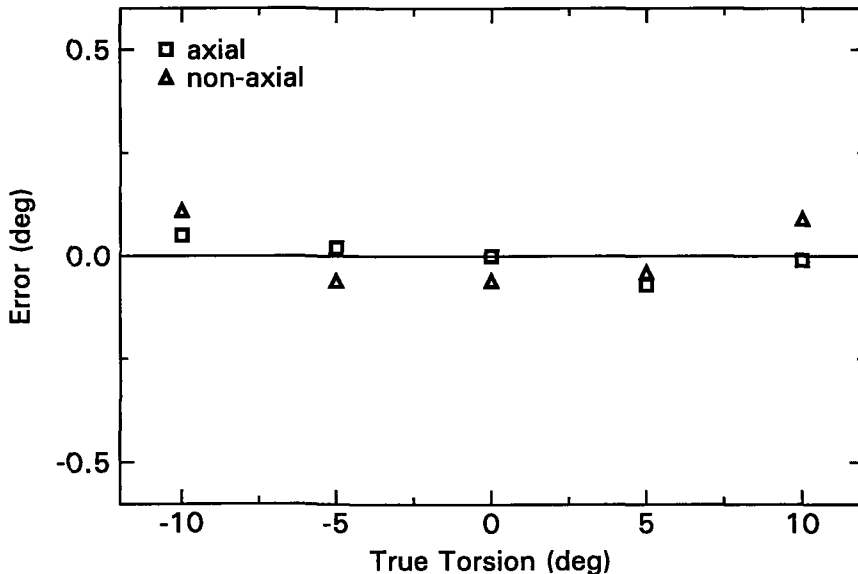


Figure 1.9. The error in automatically reproduced torsion angles in ten images of an artificial eye. The squares and triangles denote that the camera-visual axis was 0° (axial) and 10° (non-axial), respectively.

Second, the system was validated by applying it to a set of 256 images of *real eyes* obtained from 8 different subjects who had been positioned at various angles of lateral body tilt. The system's reliability was evaluated by comparing the automatically determined OT values with the results of three examiners who used the semi-automatic method Bos and De Graaf (1994), which served as a reference. Figure 1.9 shows that the results of both methods are in close agreement for the entire series of observed torsion angles from -11.4° to 8.9° (for graphical representation, the data have been sorted according to the mean of the OT values estimated by the three examiners). Comparing the system's value with the

examiners' average, the inter-examiner variability should be taken into account. In 94% of the images, the difference between the automatically computed torsion angles and the examiners' average was within two times the examiners' standard deviation (σ_{n-1}). In the remaining 6% of the images, the automatic system failed to find a reasonable match, resulting in a difference with the examiners' average of 1° or more (Figure 1.10). This increased variability could be attributed to inadequate focusing in these specific images, caused by large gaze shifts of the eye with respect to the camera. In most of these cases, the inter-examiner variability exceeded the practical accuracy of the semi-automatic method (0.25°) as well.

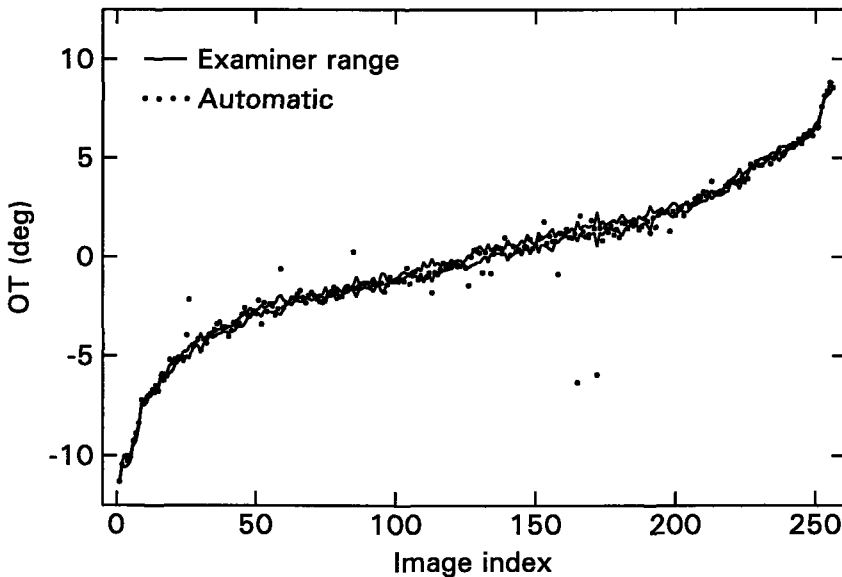


Figure 1.10. Validation results with images of real eyes. OT was estimated by both the automatic system and three examiners using the semi-automatic system. The images have been sorted by the examiners' average. The automatically computed OT values are depicted by dots, whereas the results of the semi-automatic method are shown by the examiners' average plus and minus the standard deviation (upper and lower solid line, respectively).

In conclusion, these results demonstrate that the automatic system determines OT in an accurate and reliable way. Based on the overall correspondence with the semi-automatic method, we conclude that with real human eyes, the practical reliability of the system is 0.25° . The performance of the automatic system does not depend on the amount of torsion itself. Coincidental mismatches can be detected as outliers in time-series analysis because of the coherence of such an OT signal.

Discussion

Automated video-based techniques described previously quantify ocular torsion with cross-correlation of a *narrow* circular sampled iris pattern (Clarke *et al.* 1989; Bucher *et al.* 1990). The method presented here uses an alternative strategy by tracking a set of 36 landmarks, uniformly distributed over a *wide* annular iris strip. As a result, the method is robust with respect to variations in pupil size, and it enables correction for systematic errors due to misdefined pupil centers. Another important feature of the system is that it autonomously selects landmarks as areas of high interest, facilitating the relocation in the data images. Applied in this way, pattern recognition by template matching is an effective tool for automatic determination of ocular torsion. Although not real-time, the analysis is performed automatically (hands-free) and considerably faster than the semi-automatic method described by Bos and De Graaf (1994).

Because In den Haak *et al.* (1992) applied their algorithm of template matching in Cartesian coordinates, the masks became distorted by rotation of the image, thereby reducing the match performance. This problem does no longer exist in polar coordinates. This was demonstrated by the consistency of the OT measurements through a wide range of torsion angles in the validation studies.

To assess the accuracy of an OT measurement technique explicitly, the torsion angle should be known. This was the case in the *in vitro* study with an artificial eye, and the automatic system reproduced the torsion angle accurate to 0.1°. The question whether the results are reliable in a practical sense was addressed by an *in vivo* validation study taking real human eyes into consideration. Apart from some mismatches, the computed results were indistinguishable from those of the reference method with a general variability of 0.25°. This observation concerns individual images, and may be improved by time-series analysis. Mismatches can be recognized as outliers and rejected by postprocessing. Consequently, also in static conditions it is preferable to analyze a series of consecutive images, rather than a single snap shot, to avoid the risk to rely on a coincidental mismatch.

Acknowledgments

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Chapter 2

Vestibular adaptation to sustained hypergravity

Introduction

The aim of this experiment was to identify vestibular adaptation to hypergravity by comparing ocular responses to body tilt and rotation, before and after an one-hour +3Gx centrifuge run. Because the otolith organs are being stimulated by gravito-inertial force, we expected to find changes in otolith-induced eye movements due to adaptation to the new 3G level. For this purpose we measured the ocular torsion (OT) response to static lateral body tilt (roll). This response, also indicated as ocular counterrolling, is considered to reflect the function of the otoliths (e.g. Colenbrander 1963; Miller 1962; Miller and Graybiel 1971). Hence it would suffice to examine otolith adaptation in static conditions only. However, previous experiments with prolonged centrifugation have shown that subjects experienced the strongest after-effects during head movements, in particular when these head movements were about an off-vertical axis (Bles *et al.* 1989; Bles and De Graaf 1993; De Graaf and De Roo 1996). This suggests a disturbed otolith-canal interaction. Therefore we also registered the dynamic OT response (or torsional VOR) during sinusoidal body roll, stimulating the otoliths and the semicircular canals simultaneously. To distinguish the contribution of the otolith organs from that of the semicircular canals, we measured the response to the same roll stimulus in two conditions, once about an earth-horizontal axis (body upright), and once about an earth-vertical axis (body supine). Thus the two conditions differed with respect to stimulation of the otoliths. In the upright condition, the otolith input from gravity was modulated because of the continuously changing head tilt. Conversely, in the supine condition the otolith input remained constant since the rotation was orthogonal to gravity.

In addition to these OT measurements we studied two more variables. First, in another static tilt condition we asked the subjects to align a visual line with the apparent vertical. This was done to relate possible otolith adaptation to alterations in perception of the body orientation with respect to gravity. Second, we examined

Results of this study have been published in: Groen E, de Graaf B, Bles W, Bos JE (1996) Ocular torsion before and after 1 hour centrifugation. *Brain Res Bull* 40(5/6):331-335.

the horizontal VOR during earth-vertical rotation (yaw) to make sure that we did not overlook adaptation in the semicircular canals. We had the notion that such could be the case, since subjects previously reported illusory surround motion during head movements about all three major axes, including the yaw axis.

Our hypothesis was that the centrifuge run would primarily affect otolith-induced responses, ie. in conditions of static body tilt and body roll about an earth-horizontal axis. More specifically, we expected that the sensitivity (gain) of the otoliths would be reduced due to adaptation to the sustained high G-load. Nevertheless, we did not rule out to find changes in canal-induced eye movements.

Methods

Centrifuge

The centrifuge was located at the Netherlands Aerospace Medical Centre (NLRGC), next to the TNO Human Factors Research Institute where the measurements took place. It had a free swinging gondola suspended to a 4 m long arm. For the purpose of these experiments, the aircraft seat inside the gondola was removed and replaced by a mattress, supporting the subject in supine position. This was done to prevent blood pooling in the legs during the long duration centrifuge run. The body was inclined forward over about 10° due to the dimensions of the gondola. The centrifuge accelerated at 0.1 G/s^2 up to a resultant G-force vector of 3G. Since the subject was supine and the free-swinging gondola remained collinear with the resultant force, the stimulation was directed along the subject's x-axis (Figure 2.1). The subjects was asked to avoid head movements during the run.

All subjects gave their informed consent before the experiment. Each subject underwent a medical checkup. Details on medical monitoring during and after the run were reported elsewhere (Bles *et al.* 1989). There was continuous verbal contact possible between subject and operator, who could also observe the subject on a video screen. At any time the subject had the possibility to end the centrifuge run by himself, or by asking the operator. Transportation between the TNO and the NLRGC was done by car, although the subjects had to walk about 50 m inside each institute, which included two staircases. In total 18 healthy subjects participated in this experiment. Maximally two subjects were tested each day. The first subject started between 9:00 and 9:30 am at the TNO institute, where OT was measured in the tilt chair. These measurements took about one hour, so that the centrifuge run could start around 11:00 am. During this run the tilt chair session with the second subject was carried out, so that this subject's centrifuge run could start shortly after completion of the first.

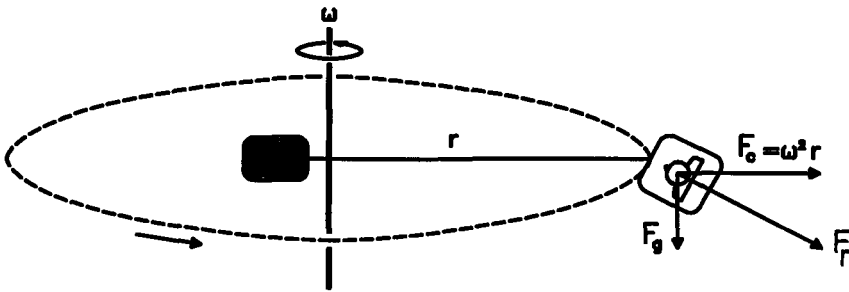


Figure 2.1. Diagram showing the supine position of the subject in the gondola of the centrifuge. Because the gondola is free-swinging it aligns itself with the resultant force F_r , which is the vector sum of gravity F_g and centrifugal force F_c .

OT during static and dynamic tilt

OT was measured during passive static and dynamic body tilt about the naso-occipital axis (roll, or x-axis). Subjects were seated in the TNO tilt chair, the rotation axis being centered between both eyes. The subject's head was supported by a head rest, and the body was firmly strapped to the chair. Ocular torsion measurements were performed once before ("pre-test") and once after ("post-test") the centrifuge run. The post-test generally took place 20 min. after the centrifuge run.

In the static tilt condition, subjects were seated upright and tilted to successive angles of 10, 20, 30, 42, and 57° to the right (clockwise). OT was recorded on videotape (see next section) after 20s of constant tilt, when the influence of the semicircular canals was considered to have subsided. A video image of each eye taken in the erect subject served as reference for the quantification of OT in tilted positions. In the dynamic condition, OT was registered during ten cycles of passive sinusoidal body roll at the frequency of 0.25 Hz and an amplitude of 45°. First, this stimulus was applied in an upright body orientation (roll axis parallel to the earth horizontal), and after a 5 min. rest, in a supine body orientation (roll axis

parallel to the earth vertical). In the upright condition, oscillation was symmetrical about the vertical (0° offset).

Video-oculography (VOG)

Eye movements of both eyes were recorded simultaneously on video tape by means of two small CCD video cameras mounted to a head set and placed 2 cm in front of the eyes, the optical axes approximately aligned with the visual axes. Except for a point source of light, fixed to each camera for illumination of the eyes, the measurements were performed in darkness under a hood. Subjects were asked to look straight into the cameras, using a reflection dot on the camera lens for fixation, so that horizontal and vertical eye movements were negligible. There were no visual cues for orientation to vertical. The subjects were encouraged to keep their eyes open and refrain from eye blinks during the actual eye movement recordings.

For analysis of single shot images in the static condition, the semi-automatic method described by Bos and De Graaf (1994) was used. The time series recordings in the dynamic paradigm were analyzed with a sample frequency of 50 Hz, using the automatic method that we developed especially for this purpose (Groen *et al.* 1996), as described in Chapter 1 of this thesis. For the analysis of the dynamic OT response the first three cycles were disregarded to allow for build up of the response. From the remaining seven periods two parameters were calculated. First, the torsional VOR gain was calculated by dividing the amplitude of the slow component velocity (SCV) by the amplitude of the stimulus velocity ($V_{\max} = 70^\circ/\text{s}$). The SCV amplitude was obtained by a sinusoidal fit on the OT signal after digital differentiation and interactive saccade removal (see Figure 2.4). Second, the mean amplitude of the original OT signal was calculated to quantify the total excursion range of torsional eye position, which we will refer to as OT-range³. Whereas the SCV gain is related to the dynamics of the slow component only, the OT-range also concerns the influence of saccades.

Subjective vertical during static body tilt

In nine subjects we measured the subjective vertical during static tilt in clockwise direction. In this case, the camera in front of the right eye was replaced by a miniature computer monitor. On this monitor a red line was presented at a virtual

³ In the original paper of Groen *et al.* (1996b) we incorrectly used the term “beating field” for the mean amplitude of the nystagmus. The term beating field refers to the average size of the saccades (“beats”), whereas we were interested in the *displacement* of the beating field (analogous to the gaze shift in optokinetic nystagmus). The displacement of the beating field is the result of the combined effects of slow component and saccades, which causes the eyes to move within a certain torsional excursion range. In Chapter 3 we will argue that this modulation of eye position more correctly reflects an “offset” for the beating field.

distance of 60 cm in front of the subject's eye. The length of the line subtended a visual angle of about 10°. The line could be rotated by means of a tracker ball mounted on the armrest of the tilt chair. At each angle of static body tilt the subject was asked to set the line parallel to the apparent vertical. The initial position of the line was always upright in the coordinates of the monitor, which was head-fixed and thus aligned with the subject's z-axis. The angle between this null position and the final setting by the subject will be referred to as the "subjective vertical". In this way, the subjective vertical gives a direct estimate of the perceived body tilt. Because visual judgments of the vertical are confounded by OT (Howard 1982; De Graaf *et al.* 1992), we corrected for the amount of torsion that was measured in the right eye during the static OT trial.

Horizontal VOR during yaw rotation

Finally, we measured the horizontal eye movements in response to a velocity step rotation about the vertical yaw in nine subjects. Horizontal eye movements were recorded using Electro-oculography (EOG), as described by Bos and De Graaf (1997). The stimulus profile consisted of an acceleration of 90°/s² up to a constant velocity of 90°/s ("velocity step"), which was maintained for 1 min. followed by a deceleration to a stop. This profile was done for leftward and rightward rotation, respectively, with a few minutes rest in between. The gain and dominant time constant for the per-rotatory and post-rotatory phase were estimated by fitting a single exponential function to the velocity signal after saccades had been removed by means of a median filter with a time window of 500 ms.

<i>Score</i>	<i>(Dis)comfort</i>
0	No problems
1	Dizzy
2	Stomach awareness
3	Nausea
4	Very nauseated (edge)
5	Vomiting

Table 2.1. Miscery scale (MISC)

Motion sickness symptoms (SIC)

From previous centrifuge experiments it is known that about 40-50% of all subjects develop symptoms of motion sickness after a prolonged exposure to 3G. This phenomenon was designated Sickness Induced by Centrifugation (SIC: Bles

et al. 1989; Ockels *et al.* 1990; De Graaf and De Roo 1996). Since in the present study we looked for the vestibular mechanism underlying the aftereffects of centrifugation, including SIC, we asked the subjects to report their subjective (dis)comfort at regular time intervals, before and after the centrifuge run. For this we used a six-point scale (Miscery SScale, MISC), as shown in Table 1 (De Graaf *et al.* 1992; Wertheim *et al.* 1992). A subject was considered to suffer from SIC, when their maximum score was 3, 4, or 5.

Results

All 18 subjects who underwent the centrifuge run mentioned visual motion illusions during head movements (oscillopsia) afterwards, similar to earlier reports (Bles and De Graaf 1993). Six subjects developed serious symptoms of SIC after the run, lasting between 2-6 hours. Due to technical problems with the tilt chair we were not able to perform vestibular testing in two subjects after the centrifuge run. Moreover, the dynamic OT could not be determined accurately in an additional five subjects, because of various artifacts, such as “droopy” eye lids or indistinct iris structures (dark brown eyes)⁴. The data of these subjects was excluded from the analyses, so that the torsional VOR of 11 subjects will be presented. This group included four of the subjects who suffered from SIC.

OT response during static tilt

The amplitude of OT showed large intersubject variability, which is common for this response. Effects were tested using an ANOVA within subjects design (factors: pre-post; left-right eye; tilt angle). There was a main effect for tilt angle ($F=61.33$; $df=4,40$; $p<0.001$), and a main effect for pre/post-test ($F=7.88$; $df=1,10$; $p<0.05$). The mean OT curves from the pre-test and the post-test are shown in Figure 2.2 (pooled for both eyes, since the response was the same for both eyes). On average, OT was 10% smaller in the post-test with respect to the pre-test.

Subjective vertical during static tilt

Figure 2.3 shows the mean setting of the visual line of nine subjects as function of static clockwise body tilt. On the whole, subjects underestimated the angle of body tilt (A-effect). More importantly, the performance did not change as a result of

⁴ The experiment was performed, and OT data were recorded while the software for OT analysis was still in development. Therefore we did not know the criteria for successful OT quantification, one of which is to illuminate brown pigmented eyes with infrared light so that iris structures become more distinct.

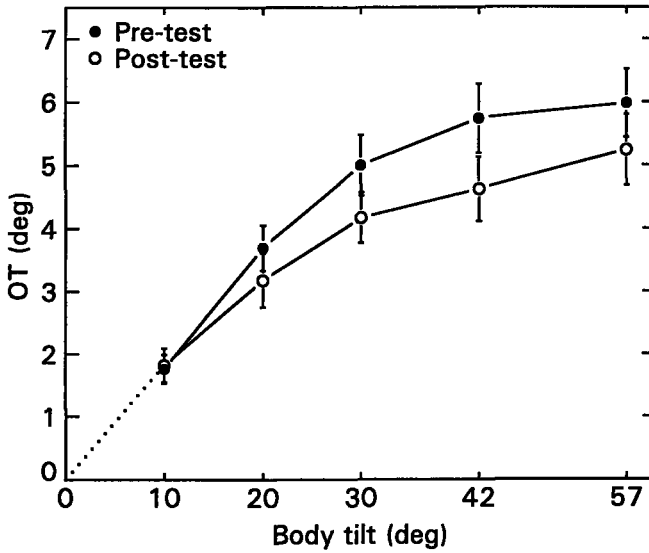


Figure 2.2. Mean OT response as a function of clockwise static body roll, before and after the one hour centrifuge run. Positive OT values denote anti-clockwise rotation (ie. compensatory to the tilt). The OT response was about 10% smaller in the post-test than in the pre-test. The bars indicate standard errors of the mean ($n=11$).

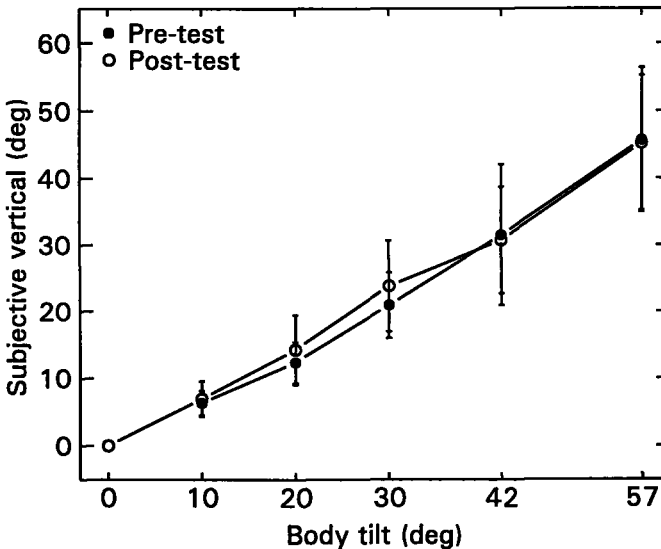


Figure 2.3. The mean subjective vertical as indicated by the setting of a line to the apparent vertical, before and after centrifugation. The bars are the S.E.M. ($n=9$). Line settings under the dotted line denote underestimation of tilt (A-effect).

centrifugation. Correction of the line settings with the corresponding OT data did not change this result. The only main effect was for body tilt ($F=105.12$; $df=4.32$; $p<0.001$).

OT response during dynamic tilt

The OT response to sinusoidal body roll in both body orientations is shown in Figure 2.4 for one subject. The recordings show a compensatory “slow component”, which appears to be interrupted by saccades more frequently in the supine than in the upright orientation. This aspect will be discussed in more detail in Chapter 3 of this thesis.

For all calculations, data from both eyes have been averaged. The group’s mean values and standard errors of the mean are listed in Table 2.2. The pre-test SCV gain was smaller in the upright condition than in the supine condition (Student’s t-test, $p<0.05$). The mean gain was 0.31 in upright and 0.35 in supine. On the other hand, the mean OT-range in upright was twice as large as in supine, due to a difference in saccadic activity. In both conditions there was a mean phase lead of about 40° of the response relative to the inverted stimulus (to account for the fact that an ideal compensatory response would be in anti-phase with the stimulus).

	Gain <i>tVOR</i>		OT-range ($^\circ$)		Gain <i>hVOR</i>		<i>Tc hVOR</i> (s)	
	Upright	Supine	Upright	Supine	Per-rot	Post-rot	Per-rot	Post-rot
Pre-test	0.31 \pm 0.01	0.35 \pm 0.01	7.8 \pm 0.5	3.9 \pm 0.5	0.59 \pm 0.20	0.61 \pm 0.18	15.7 \pm 1.7	18.7 \pm 2.2
Post-test	0.34 \pm 0.02	0.35 \pm 0.02	8.2 \pm 0.7	3.0 \pm 1.8	0.60 \pm 0.15	0.63 \pm 0.15	12.8 \pm 1.1	15.2 \pm 1.6

Table 2.1. Means and S.E.M. of the gain and OT-range of the OT response (*tVOR*) to sinusoidal body roll, and the gain and time constant (*Tc*) calculated from the horizontal VOR (*hVOR*) to yaw rotation.

Neither the OT-range nor the phase of the response were different between pre-test and post-test. In the upright condition, all but one subjects showed a larger response in the post-test than in the pre-test. The mean SCV gain increased from 0.31 to 0.34 (Figure 2.5a). In the supine condition, the averaged gain remained the same (0.35). The individual responses, however, showed divergent behavior: the gain increased in six subjects, remained constant in one subject, and decreased in four other subjects. As a result, the apparent interaction in Figure 2.5a between upright/supine and pre-test/post-test was not statistically significant ($p=0.18$). It is interesting to note that the four subjects who showed a reduced gain, were also the ones who suffered from SIC. In Figure 2.5b the same data are plotted again, but now differentiated between those subjects with SIC symptoms and those without. It can be seen that the gain increase was approximately parallel in both conditions, except for the four SIC subjects.

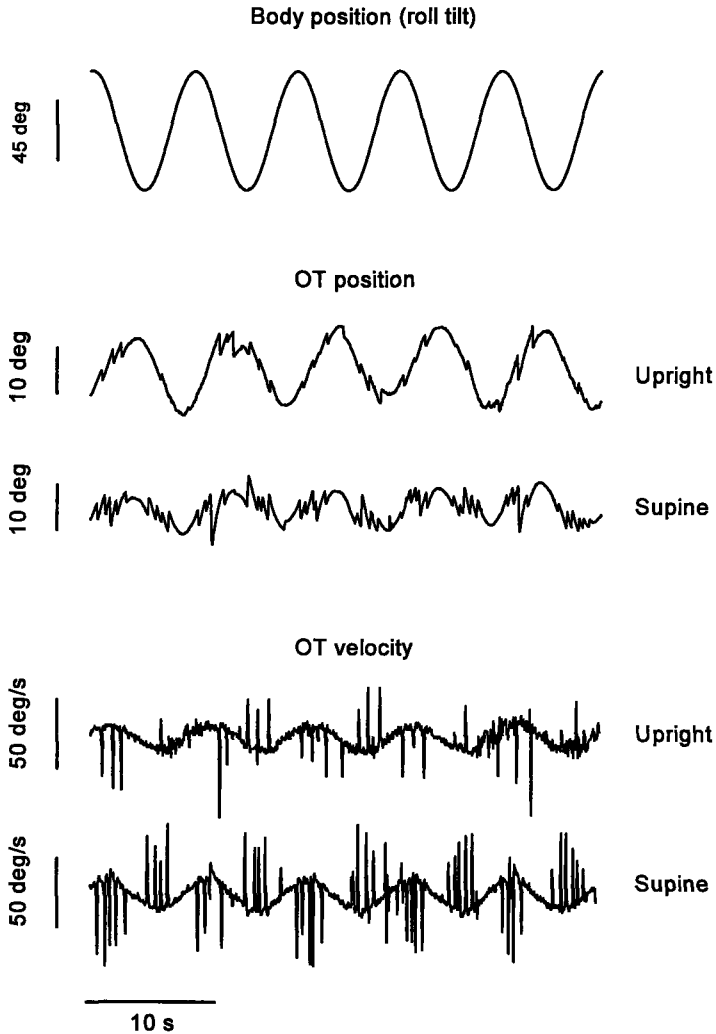


Figure 2.4. OT response of one subject to passive sinusoidal body roll (at the frequency of 0.25Hz) about an earth-horizontal axis (“Upright”) and about an earth-vertical axis (“Supine”). The original nystagmus (OT position) is shown during five cycles, together with the corresponding differentiated signal (OT velocity). The upper trace represents the stimulus (body tilt versus time).

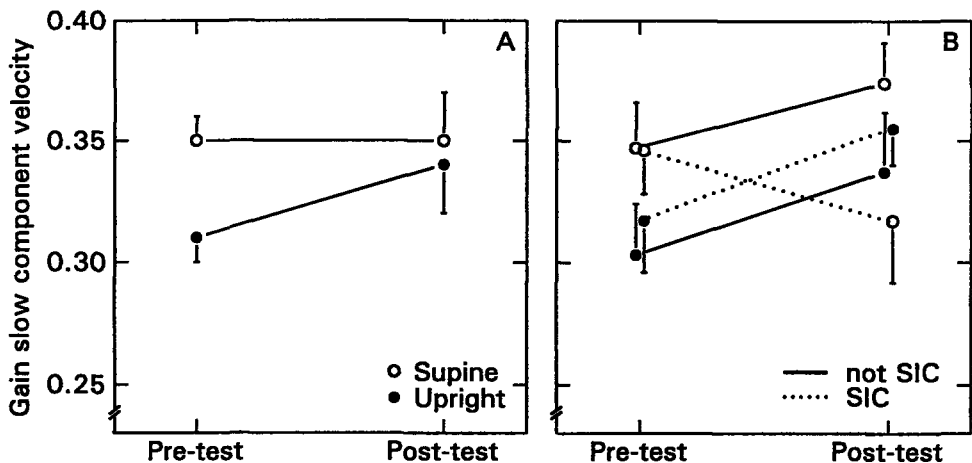


Figure 2.5. a. Gain of slow component velocity of torsional VOR. Mean values of 11 subjects in pre-test and post-test for upright and supine body orientation (with contribution and without contribution of the otoliths, respectively). The bars denote the S.E.M. In the pre-test the upright gain was higher than the supine gain. The upright gain was significantly increased in the post-test. The mean supine gain, however, remained constant. **b.** The same torsional VOR data as in Fig. 2.5, but now distinguished between the four SIC subjects (dotted lines) and seven non-SIC subjects (solid lines). It appears that the SIC and non-SIC subjects showed the same gain increase in the upright condition, but that the mean gain of the SIC subjects dropped in the supine condition after centrifugation, whereas the mean gain of non-SIC subjects showed a slight increase. Bars are the S.E.M.

Horizontal VOR during rotation about yaw-axis

The mean gain and mean time constant of the per- and post-rotatory phase of the horizontal VOR measured in nine subjects are listed in Table 1. The mean gain was about 0.60 in the per- and post-rotatory phase, and was the same before and after the centrifuge run. The dominant time constant (Figure 2.6), on the other hand, was on average 3 s longer in the pre-test than in the post-test ($F=29.21$; df 1,14; $p<0.001$). Also, the time constant observed in the post-rotatory phase was

generally longer than that observed in the per-rotatory phase ($p < 0.01$). No differences were found between subjects with SIC and subjects without.

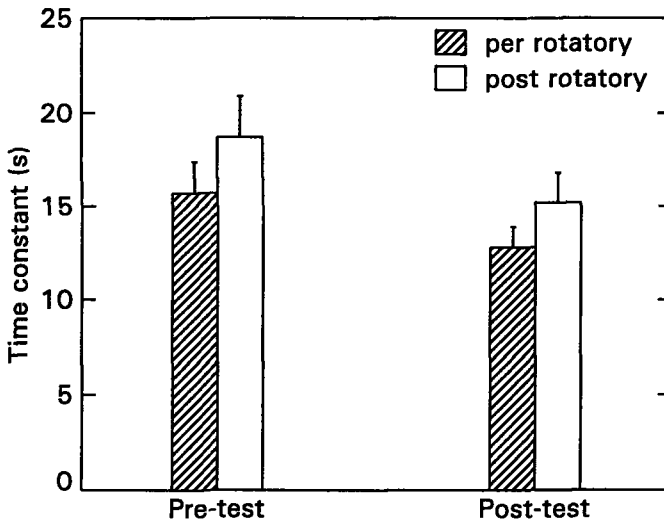


Figure 2.6. *The time constant for the per- and post-rotatory phase of the horizontal VOR induced by a velocity-step rotation about a vertical yaw-axis. Data from leftward and rightward rotation have been averaged. The mean time constant was 3s shorter in the post-test than in the pre-test. Although the time constant was longer in the post-rotatory phase than in the per-rotatory phase, both decreased by the same amount after centrifugation.*

Discussion

In this study we examined changes in vestibular parameters due to sustained exposure to hypergravity in human subjects. In this way, we hoped to substantiate the effects of postural instability and motion sickness which have been observed after one hour centrifugation at 3G (Bles *et al.* 1989; Ockels *et al.* 1990; Bles and De Graaf 1993; Albery 1994; Bles *et al.* 1995; De Graaf and De Roo 1996). Because we expected that a high G-load would especially influence the otolith function, we measured the OT response to static body tilt. Previous observations pointed to alterations in the canal-otolith interaction, which is why we included the OT response to dynamic body tilt. To verify that no direct changes in the

functioning of the semicircular canals occurred, we also investigated canal-induced horizontal eye movements. The major finding was that the gain of the static OT response was consistently reduced by 10% after the centrifuge run of one hour. The results from the dynamic OT measurements were less explicit. In both body orientations the gain of the compensatory slow component was higher in the post-test by about 10% in all subjects, except in the four subjects who suffered from SIC. These subjects showed the same trend in the upright condition, but their response was reduced in the supine condition. Finally, the gain of the horizontal VOR remained constant after centrifugation, but the time constant was on average 3 s shorter in the post-test compared to the pre-test.

Unfortunately we had to disregard the OT data from five of the eighteen subjects, mainly because the automatic pattern recognition algorithm to determine OT was still in development at the time of the data collection, and we did not know the exact criteria for accurate analysis. All data were collected using a visible light source, while dark brown pigmented eyes should preferably be illuminated by infrared light, so that iris structures become more distinct.

Static OT

The OT response to static tilt suggests that the otolith function adapted to a higher G-load by a gain reduction. It seems reasonable that otolith adaptation would occur, since this sensory system must detect small linear accelerations against relatively large background stimulation by gravity. Normally, the otolith system operates in an invariant force field of 1G, with an optimally adjusted basic activity ("set-point") and sensitivity. Changing the background level of 1G will shift the set-point away from its ideal position. Adaptation will restore the operational range of the system within its normal limits. Thus, in a 3G environment the otoliths would shift their set-point to a higher value. Assuming that re-adaptation to normogravity is not immediately, the higher setting is likely to result in a smaller response after centrifugation. The direction of the OT change (a decrease in amplitude) in this experiment is in agreement with this.

From this reasoning we would expect that the static OT response would increase after exposure to 0G (weightlessness). Previous studies on vestibular adaptation to spaceflight, however, suggest the opposite (Vogel and Kass 1985; Arrot and Young 1986; Hofstetter-Degen *et al.* 1993; Dai *et al.* 1994). This discrepancy may be explained by the unique property of weightlessness that there is no effective gravitational force to support spatial orientation. On earth, otolith-induced OT is considered an orientational response which tends to maintain the eye position with respect to gravity. In space, the otolith organs no longer register gravity, but only receive stimulation from linear accelerations induced by head movements. It has been postulated that in weightlessness all otolith signals

become interpreted in terms of head translation. This is known as the “tilt-translation reinterpretation theory” (Parker *et al.* 1985). Accordingly, the OT response to head tilt is strongly reduced or absent in spaceflight (Hofstetter-Degen *et al.* 1993; Clarke *et al.* 1993). Moreover, linear motion along the subject’s y-axis, which normally induces OT, primarily produces horizontal eye movements after spaceflight (Arrot and Young 1986). Hence, the effects of weightlessness on the OT response presumably result from sensory-rearrangement which is related to the reduced demand for orientational responses. The reduction in OT gain observed in the present study may be based on a different mechanism, because in hypergravity there is a gravitational force to allow for orientational responses. The fact that we measured an effect during tilt *about* the subject’s x-axis, whereas the resultant G-load was directed *along* the x-axis, implies that a central mechanism is involved.

The effect on the OT response was not mirrored in the settings of a visual line to vertical. Theoretically, a reduction in the sensitivity of the otolith system could have consequences for the perceived angle of body tilt, and thus for the judgment of the verticality of a line. According to the following reasoning, the perceptual effect could even be larger than the oculomotor effect. Imagine that the subjective vertical would depend entirely on the information provided by the otolith system. Imagine also that a certain OT angle would strictly correspond to a certain angle of body tilt specified by the otolith system. Then the expected change in the perceived angle of body tilt could be obtained by looking at the post-test value of static OT at a certain angle of body tilt, and finding the angle of body tilt which produced the same amount of OT in the pre-test (by drawing a horizontal line through an OT value in the post-test curve in Figure 2.2, and determining at which angle of tilt the line crosses the pre-test curve). Nevertheless, there was no connection between the two measures, as can be seen by comparing Figure 2.2 and 2.3. Other sensory senses, such as non-vestibular proprioceptors (De Graaf *et al.* 1992), may have compensated for the reduced otolith gain in the determination of the subjective vertical. Previous centrifuge experiments have established an effect on the control of postural balance, so that we can not eliminate the possibility that reduction of the otolith gain (even if this is only 10%) has larger impact in situations that require more active behavior than does passive static body tilt. From this perspective dynamic SV measurements would have been useful.

Torsional and horizontal VOR

The profile of the centrifuge run consisted of a 30s acceleration up to a constant velocity of about 150°/s, which was sustained for one hour before the centrifuge was decelerated to a stop in 30s. Thus there were only two brief periods of angular acceleration, and we did not expect main changes in the functioning of the

semicircular canals due to the centrifuge run. We did find a 10% increase of the slow component gain of the torsional VOR. In all but the four SIC subjects this trend was apparent in both body orientations, which excludes an otolithic origin and argues for a change in the canal-induced VOR. The latter was not confirmed by a change in the gain of the horizontal VOR. Spaceflight studies have provided inconclusive evidence on the effects of an altered G-environment on the canal-induced VOR. In the Spacelab-1 mission, Benson and Vieville (1986) did not observe changes in the horizontal VOR gain in human subjects (during active and passive oscillation). In monkeys, neither the horizontal VOR gain (Cohen *et al.* 1992), nor the vertical VOR gain (Dai *et al.* 1994) was found to be affected by weightlessness. On the other hand, Berthoz *et al.* (1986) measured an increase of the vertical VOR in humans on the first day after spaceflight. Clarke *et al.* (1993) measured a reduction in the active torsional VOR in human subjects during the first four days in flight, although Cheung *et al.* (1992) did not find any differences in the torsional VOR during parabolic flight. One factor contributing to these variable results may be the restricted number of subjects that is typical for studies in space. Another explanation is that possible adaptation processes in the sensory system may be concealed by the high plasticity of the VOR, as was suggested by Dai *et al.* (1994). They did not find changes in the horizontal and vertical VOR gain in monkeys after a two week spaceflight, while the activity of the primary afferents of the semicircular canals was found to be increased in the same animal in an accompanying study (Correia *et al.* 1994).

It is unlikely that the different post-test gain of the torsional VOR observed in the SIC subjects in the present study, reflects a causal factor in the etiology of SIC. First, the stimulus itself was not experienced as provocative. Second, the response of the SIC subjects only differed from the other subjects in the supine roll condition, in which the rotation was about an earth-vertical axis, whereas motion sickness symptoms were induced by head movements about an off-vertical axis. For that reason, a difference in the upright roll condition would have been more compatible with the subjective reports. It is possible that the torsional VOR gain in the SIC subjects was related to their state of alertness. Even though subjects were encouraged to stay alert in all conditions, the measurement in a supine body position in the dark may have invoked drowsiness especially in these subjects. In contrast, the upright position may have provided sufficient arousal for a normal response.

Surprisingly, the SCV gain of the torsional VOR in the pre-test appeared higher in the upright condition than in the supine condition, suggesting that the otolith function counteracted the canal-induced response. In view of the low gain of the torsional VOR (the highest mean gain that we found was about 0.37) we had expected that the combination of canal and otolith stimulation would yield a larger response than canal stimulation alone. In another experiment we investigated this

response in more detail. The results of this experiment are described in Chapter 3 of this thesis. For now we will conclude that the otolith inputs have small and variable effects on the magnitude of the slow component of the torsional VOR. More important effects include modulation of the phase of the response at frequencies below 0.2 Hz, and modulation of the OT range. Since both parameters were unchanged after centrifugation, these otolith components provided no evidence for otolith adaptation.

Finally, the decrease in the time constant of the horizontal VOR is interesting with regard to a possible canal-otolith interaction. In general, the falling time constant of the VOR for rotations about an earth-vertical yaw axis is longer than the time constant of the signals from the semicircular canals, due to a brainstem circuitry designated “velocity storage” mechanism (Raphan *et al.* 1979). The time constant of velocity storage is affected by inputs from the otoliths. It can be considerably reduced when the head is suddenly tilted (“tilt dumping”), and it is shorter during off-vertical axis rotations (Dai *et al.* 1991; Tweed *et al.* 1994b). It is tempting to attribute the reduced time constant in the post-test to altered otolith inputs that feed into the velocity storage mechanism. The static OT data may confirm this. An interesting hypothesis is that, after the centrifuge run, the velocity storage is inaccurately informed about the orientation of the rotation axis, and erroneously “assumes” that the rotation is not about a vertical axis, resulting in a shorter time constant. This can be visualized as if the system is incorrectly spatially oriented because it is aligned with the resultant vector sum of actual gravity and some “residual” +3G_x vector from the centrifuge run (like an inverted G-excess phenomenon), until re-adaptation is complete. Psychophysical evidence for this is provided by the sensation reported by most subjects, that they feel inclined forward in the gondola after deceleration from a prolonged centrifuge run (Bles and De Graaf 1993). This sensation normalizes only after a couple of minutes, although even after 30 minutes a few subjects showed a measurable bias of backward tilt when they were asked to align their body with vertical (Bles *et al.* 1989). Moreover, Dai *et al.* (1994) demonstrated in a spaceflight study that the spatial orientation of the velocity storage mechanism is indeed capable to adjust to the G-environment. At any rate, the shortened time constant is a strong indication that the centrifuge run had consequences for the canal-otolith interaction.

Model for SIC

So far the only difference found between subjects who suffered from SIC and those who did not, concerned the response to supine body roll. As explained above, we do not see how this can play a role in the etiology of SIC. Instead, it is likely that this difference was a consequence of their malaise, and not a cause. All other parameters examined in the present study do not differentiate between SIC and

non-SIC subjects, and therefore have no predictive value for the susceptibility for SIC. Although the changes in ocular responses that we measured were relatively small, they may explain the illusory surround motion during head movements. On the other hand, the difference in magnitude of the effects that were subjectively reported and the effects that were objectively registered may be due to different time scales by which perceptual changes take place as compared to sensorimotor changes. Indeed, it has been shown in human subjects living in an enclosed rotating room, that perceptual and oculomotor reactions did not follow the same course (Guedry 1991).

Based on the observation that after centrifugation visual motion illusions may be induced by all head movements (including yaw-motion), but that motion sickness symptoms are only provoked when the orientation of the head is changed relative to gravity (roll and pitch), it was proposed that SIC is generated by discrepancies in the internal representation of the vertical (the subjective vertical; Bles and De Graaf 1993; Bles *et al.* 1997). This probably is a more accurate interpretation than the commonly accepted “conflict theory” on motion sickness, which states that motion sickness arises when the information from different sensory systems is “at variance with one another or with what is expected from previous experience” (Reason and Brand 1975).

The new model assumes that motion sickness only arises when there is a conflict about the direction or magnitude of the subjective vertical. The subjective vertical is determined based on the integrated information from the eyes, the vestibular system and the non-vestibular proprioceptors. Normally the information from these systems is congruent. However, when one or more of these systems adapt to earth-anomalous gravity, this expectedly influences the computation of the subjective vertical. It should be noted that an inaccurate subjective vertical does not implicitly produce motion sickness. For instance, the present study demonstrated that passive body roll in the dark was not experienced as provocative, whereas active roll motion of the head in the light was. Furthermore, static situations were not provocative at all. Apparently some self-generated action is needed to perceive the discrepancy between the subjective vertical and the reafferent feedback obtained by this action (De Graaf *et al.* in press). But even then it is still unclear why some subjects suffer from SIC while others don't. A possible explanation is that, despite comparable physiological changes, subjects may assign different relative weightings to the information provided by the various sensory systems, leading to perceptual differences.

An alternative theory on the generation of space sickness is based on the assumption that there are minor anatomical and physiological differences between the left and right utricle (Baumgarten and Thümler 1978). On earth, these differences would be fully compensated for, but under hypo- and hypergravity these differences would become pronounced, requiring new adjustments. During

this process motion sickness may result. The asymmetry measured in OT during parabolic flights may be a manifestation of this utricular imbalance (Markham and Diamond 1991). We did not find (a change in) the asymmetry between the left and right eye. Moreover, the OT response to static body tilt was similar in SIC and non-SIC subjects, so that we did not verify an effect of hypergravity on utricular imbalance, as a possible cause in the generation of SIC.

Conclusions

The results from this study suggest that the sensitivity of the otolith function was reduced by 10% after a long duration +3Gx centrifuge run. This was observed by a decrease in static OT amplitude. Although the effect was not present in the corresponding static subjective vertical, it seems likely that a reduced otolith gain has larger impact in dynamic situations, provoking postural instability and SIC. According to a significant decrease of the time constant of the velocity storage mechanism, centrifugation affected the otolith-canal interaction at a central level. Admittedly speculative, this fits in the assumption that an earth-anomalous level of gravity has consequences for the determination of the subjective vertical. The gain of the torsional VOR was found to be augmented by 10% after centrifugation, irrespective of body orientation with respect to gravity. Possibly, the observed effects on the VOR may explain the sensations of illusory surround motion during head movements. It is unclear, however, whether these small effects could induce severe symptoms of SIC for several hours afterwards. The vestibular parameters did not have any predictive value for the susceptibility to SIC.

Acknowledgments

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Chapter 3

Otolith contribution to the human torsional vestibulo-ocular reflex

Introduction

The vestibular system contributes to the stabilization of the retinal image during head movements by means of the vestibulo-ocular reflex (VOR). Whereas the semicircular canals are clearly involved in the control of the angular VOR during head rotation, the role of the otolith organs is more difficult to interpret. The otoliths respond to linear accelerations, which may result from head translation, but also from head tilt relative to gravity. Accordingly, “*translational*” and “*tilt*” otolith-ocular responses (OOR) have been identified, each with different spatiotemporal properties. It is illustrative for the ambiguity of linear acceleration and tilt as stimulus for the otoliths, that tilt responses can be elicited by linear head motion, and translational responses can be elicited by head rotation relative to gravity. For instance, Paige and Tomko (1991a,b) distinguished translational OORs and tilt OORs in squirrel monkeys during horizontal oscillation along various body axes on a linear track. Translational responses included horizontal and vertical eye movements during motion along the interaural axis and the dorso-ventral axis, respectively. These eye movements were most sensitive to high-frequency oscillations and were functionally compensatory to the linear motion of the stimulus. Tilt responses included torsional and vertical eye movements during motion along the interaural axis and the naso-occipital axis, respectively. In contrast to the translational responses, the tilt responses were most sensitive to lower stimulus frequencies and were not functionally compensatory to the motion itself. This category of eye movements was designated “*tilt*” OORs because they are normally associated with inclination of the head. In man, a well-studied tilt OOR is ocular torsion in response to static head tilt in the roll plane (Miller 1962; Belcher 1964; Bucher *et al.* 1992; Collewijn *et al.* 1985; Cheung *et al.* 1992). The low-frequency dynamics of this response have been established in more detail using linear acceleration along the interaural axis (Woellner and Graybiel 1959; Colenbrander 1963; Hannen *et al.* 1966; Lichtenberg *et al.* 1982; De Graaf *et al.* 1996).

Adapted from: Groen E, Bos JE, De Graaf B. Contribution of the otoliths to the human torsional vestibulo-ocular reflex. Submitted to Journal of Vestibular Research.

It has been assumed that ocular torsion is determined exclusively by the shear force along the maculae of the utricles, and not by the “swinging” of the resultant gravito-inertial force relative to the head. Recently, however, it was suggested that the ocular torsion response to interaural oscillation in man can be divided into a component responding to linear motion and a component responding to the swinging resultant gravito-inertial force (Merfeld *et al.* 1996). Correspondingly, the steady state nystagmus observed during constant velocity rotation about an off-vertical axis has been recognized as a third type of OOR, which reflects the ability of the otoliths to estimate angular velocity from the rotation of the gravito-inertial vector relative to the head (Guedry 1965; Benson and Bodin 1966; Angelaki and Hess 1996a).

Basically, linear motion and constant velocity rotation about an off-vertical axis are unnatural conditions for tilt OORs such as ocular torsion. The findings obtained with these methods suggest that otolith-induced ocular torsion does exist during rotations of the head in the roll plane, when the semicircular canals are activated simultaneously. Nevertheless, there seems to be no decisive evidence that such is the case in humans. Collewijn *et al.* (1985) studied ocular torsion during active head roll, but did not determine the contribution of the otoliths. Vierville and Masse (1987) made an attempt to isolate the contribution of the otoliths from that of the semicircular canals, by measuring ocular torsion during voluntary head movements in the roll plane (in only one subject), once with the head erect, and once with the head prone. In the head-erect condition the motion was about an earth-horizontal axis, modulating inputs from the otoliths and the semicircular canal. In the head-prone condition the motion was orthogonal to gravity, only stimulating the semicircular canals. In a frequency range from 0.1 to 0.4 Hz, the response gain was slightly higher and the phase lead smaller when the head was erect compared to when the head was prone. Conversely, Tweed *et al.* (1994) did not find a difference in three-dimensional VOR dynamics for oscillations of 0.3 Hz about an earth-horizontal axis and about an earth-vertical axis. However, taking the low-frequency characteristics of tilt OORs into account, a frequency of 0.3 Hz may have been too high to reveal an otolith effect.

The goal of the present study was to investigate whether the otoliths improve the low-frequency dynamics of the torsional VOR in human subjects. We focused on the torsional VOR because it is considerably weaker than the horizontal and vertical VOR (Crawford and Vilis 1991; Tweed *et al.* 1994), suggesting that especially ocular torsion could benefit from assistance of the otoliths. We compared the response to passive sinusoidal body roll about an earth-horizontal axis and an about earth-vertical axis (in upright and supine body orientation, respectively) in the frequency range from 0.05 to 0.4 Hz. At very low frequencies the canal-induced VOR normally becomes less effective, showing a smaller gain and a progressive phase lead (Carpenter 1988). Our main hypothesis was that the

otoliths would enhance the gain and reduce the phase lead of the response in the lower end of the frequency range.

In a previous study we measured ocular torsion during sinusoidal body roll at 0.25 Hz about an earth-horizontal and about an earth-vertical axis, and observed that the torsional nystagmus contained less anti-compensatory saccades in the former condition, which corresponded to larger amplitudes of ocular torsion (Groen *et al.* 1996b). A similar finding has been reported for the vertical VOR in rabbits (Barmack 1981). We believe that modulation of the saccadic activity in vestibular nystagmus offers the possibility for the otoliths to control the position of the eyes in space, and that this may be independent of effects on the slow component (velocity) of the response. In addition to the slow component dynamics, we therefore investigated the saccadic activity and the amplitude of torsional eye position in the original nystagmus.

Methods

Subjects

Each of five healthy subjects, one female and four male, 28-37 years old, participated in one experimental session of an hour with their informed consent. Seated in a rotating chair, the subjects were sinusoidally rotated about their naso-occipital (roll) axis. The subjects' head was supported by a head rest, and the body was firmly harnessed to the chair.

Stimuli

In total, there were six different stimuli of sinusoidal roll motion. Four of them varied in frequency (0.05, 0.1, 0.2, and 0.4 Hz), but had a fixed amplitude (25°), allowing for evaluation of the frequency response. Moreover, at the frequency of 0.2 Hz there were two additional stimuli with an amplitude of 12.5° and 50°, respectively, so that the linearity of the response could be examined. Responses were measured during ten cycles at most, with a maximum duration of one minute (that is 3 cycles at 0.05 Hz, 6 cycles at 0.1 Hz, and 10 cycles at 0.2 and 0.4 Hz).

The same set of stimuli was applied in two different body orientations (Figure 3.1). In upright position, the rotation axis was earth-horizontal. Here, the stimulus modulated semicircular canal and otolith inputs. In supine position, the rotation axis was earth-vertical. Here, only the canal input was modulated. Thus, there were 12 different conditions (six motion stimuli in two body orientations). To save time of rearranging the chair between the two orientations, conditions were not randomly applied. Instead, the stimuli were divided into two blocks of three, each

of which was carried out in the upright orientation first, followed by the same block in the supine orientation.

Eye movement recording

With two small synchronized CCD-cameras mounted on a head set, movements of both eyes were simultaneously recorded on video with a sample frequency of 50 Hz. To avoid artifacts from movement of the cameras relative to the head, the head set was attached to a dental frame with individual fit. Except for a point source fixed to the camera, the measurements were performed in darkness. The subjects were asked to gaze straight ahead into the cameras, using a reflection spot on the camera lens for fixation. Thus “pure” torsional movements were measured. The video recordings were digitized and analyzed off-line by means of the method described in Chapter 1. The angle of ocular torsion was determined relative to a reference image, arbitrarily chosen from the recording just prior to the stimulus onset. The eye position signals were stored in separate datafiles, synchronized with the corresponding stimulus signals (the actual rotation angle of the chair).

Analysis of the slow component

The datafiles were analyzed using an interactive computer program. First, we determined gain and phase of the slow component velocity (SCV). For this, the position signal was differentiated digitally, and saccades were removed by a moving median filter with a window of 500 ms (the saccades were typically 100 ms of duration, or less). Subsequently, the amplitude and phase of the component with the stimulus periodicity were estimated by means of discrete Fourier transformation. The SCV gain was computed as the amplitude ratio of eye velocity and stimulus velocity. The SCV phase was determined relative to the stimulus. Positive values were used for a phase lead, where zero phase indicated perfect compensatory eye velocity.

Although the gain and phase are interdependent parameters, we examined them separately. This implies that an ambiguous phase of a small response may have a disproportionate weight in the group’s average. Anticipating the results, however, no data had to be excluded for this reason. First, all individual responses were distinct enough to allow for reliable parameter estimation. And second, the between-subject variability was small.

Analysis of eye position

In the absence of saccades, the behavior of the eye position would be directly described by the SCV parameters. But in any nystagmus the excursion range of

eye position is modified by saccades. To examine the effects of saccades, we therefore determined the gain of torsional eye position, by averaging a number of cycles of the original nystagmus (including saccades) and measuring the amplitude of the approximately sinusoidal result. Analogous to the determination of the SCV gain, this amplitude then was divided by the stimulus amplitude to obtain the eye position gain.



Figure 3.1. Two pictures showing the orientation of the TNO tilt chair for whole body roll about (a) an earth-horizontal axis and about (b) an earth-vertical axis. To illustrate the camera equipment for OT recordings, the hood was removed in (a). The roll axis was more or less centered between the eyes.

The saccades themselves were characterized by their amplitude and incidence (frequency). In general, the saccade amplitude is monotonously increasing with peak velocity (Bahil *et al.* 1975, Lebedev *et al.* 1996), a rule which also holds for torsional saccades (Collewyn *et al.* 1985). For technical reasons we took the *saccade peak velocity* as a measure for their amplitude. The *saccade frequency* was expressed as the number of saccades per second.

In general, the above analyses were performed on the entire response, with disregard of the first cycle to allow the response to build up. Incidentally, one or more cycles had to be ignored because of artifacts (e.g. eye blinks).

Hypothetical otolith response

Assuming additive contributions of the semicircular canals and the otoliths to the slow component, we calculated a hypothetical otolith response as the difference between the upright and the supine response. Instead of actually subtracting the original signals, we calculated averages of the individual vector differences using the available gains and phases of the SCV.

Results

Figure 3.2 shows 20 s periods of torsional nystagmus of one subject at different stimulus frequencies, with a fixed amplitude of 25°. Data are shown in both the upright and supine conditions. Similarly, Figure 3.3 shows data of the same subject at different stimulus amplitudes, where the frequency is fixed at 0.2 Hz. All responses feature an obvious sinusoidal “slow” component sharing the periodicity of the stimulus. The amplitude of the nystagmus appears to increase with increasing stimulus frequency and amplitude. In the next paragraphs the contribution of the slow component and the saccades will be quantified.

Slow component velocity

In Figure 3.4a the SCV dynamics (gain and phase), averaged over all subjects, are plotted versus stimulus frequency (with an amplitude of 25°). The data of both eyes have been combined. The SCV gain increases significantly with stimulus frequency (within subjects design ANOVA: $F=34.87$; $df=3,12$; $p<0.01$). Furthermore, the average gain is significantly higher in upright than in supine orientation ($F=29.80$; $df=1,4$; $p<0.01$). The linear relationship between the SCV gain and the logarithm of the stimulus frequency (f) is demonstrated by the two regression lines, plotted in the upper diagram of Figure 3a: $y_{\text{upright}} = 0.50 + 0.26 \log(f)$, and $y_{\text{supine}} = 0.37 + 0.21 \log(f)$.

The corresponding phase characteristics, as presented in the lower diagram of Figure 3.4a, reveal a significant interaction between body orientation and stimulus frequency ($F=11.07; df=3,12; p<0.01$). In the supine orientation, at 0.05 Hz the response leads the stimulus on average by 78° , which decreases slightly at 0.1 Hz, and increases again up to 101° at 0.4 Hz. In the upright orientation, the average phase lead is only 29° at 0.05 Hz, and successively increases to 99° at 0.4 Hz. From 0.2 Hz and above, the phase leads in both body orientations are identical.

The hypothetical "otolith only" response, the vector difference of the upright and supine response, is also depicted in Figure 3.4a (dotted line). The gain of this response is about 0.1 for all frequencies, where the phase changes from a lag of about 15° at 0.05 Hz into a lead of 90° at 0.4 Hz.

In Fig. 3.4b, the SCV gain and phase are plotted versus stimulus amplitude (with frequency fixed at 0.2 Hz). There was no effect of amplitude, which implies that the response behaves linearly in both body orientations for amplitudes from 12.5° to 50° . Again, there is a main effect of body orientation on the SCV gain, which is consistently higher in upright than in supine ($F=59.87; df=1,4; p<0.01$).

Eye position

The three parameters describing eye position behavior are plotted in Fig. 3.5a for increasing stimulus frequency, and in Fig. 3.5b for increasing stimulus amplitude. The excursions of torsional eye position are invariably smaller than the corresponding SCV gains. This confirms that the saccades are oppositely directed to the slow component, reducing the maximum amplitude of torsion. This is best seen by comparing the upper diagrams of Figures 3.4b and 3.5b: the eye position gain decreases significantly ($F=64.78; df=1,4; p<0.01$), whereas the gain of the SCV remains constant with increasing stimulus amplitude. Parallel to this, the average saccade frequency increases significantly with stimulus amplitude ($F=15.76; df=2,8; p<0.01$), as does the peak velocity ($F=49.84; df=2,8; p<0.01$). Similarly, the saccade frequency increases with stimulus frequency ($F=29.28; df=3,12; p<0.01$), as does the peak velocity ($F=23.24; df=3,12; p<0.01$). In this case, however, the gain of the eye position still increases, due to the increase in SCV gain. From the original recordings, as shown in Figures 3.2 and 3.3, it is evident that the saccadic activity is higher supine than upright. In fact, the saccades seem to operate around an "offset", which appears sinusoidally modulated in the upright conditions, but seems about zero in the supine conditions. Figure 3.5 shows that this can be attributed to a difference in the saccade frequency, which is significantly higher in the supine than in upright orientation ($F=26.76; df=1,4; p<0.01$). On the other hand, the saccade amplitude (or "beating field") is independent of body orientation, as is indicated by the average peak velocity, which does not differ between upright and supine conditions.

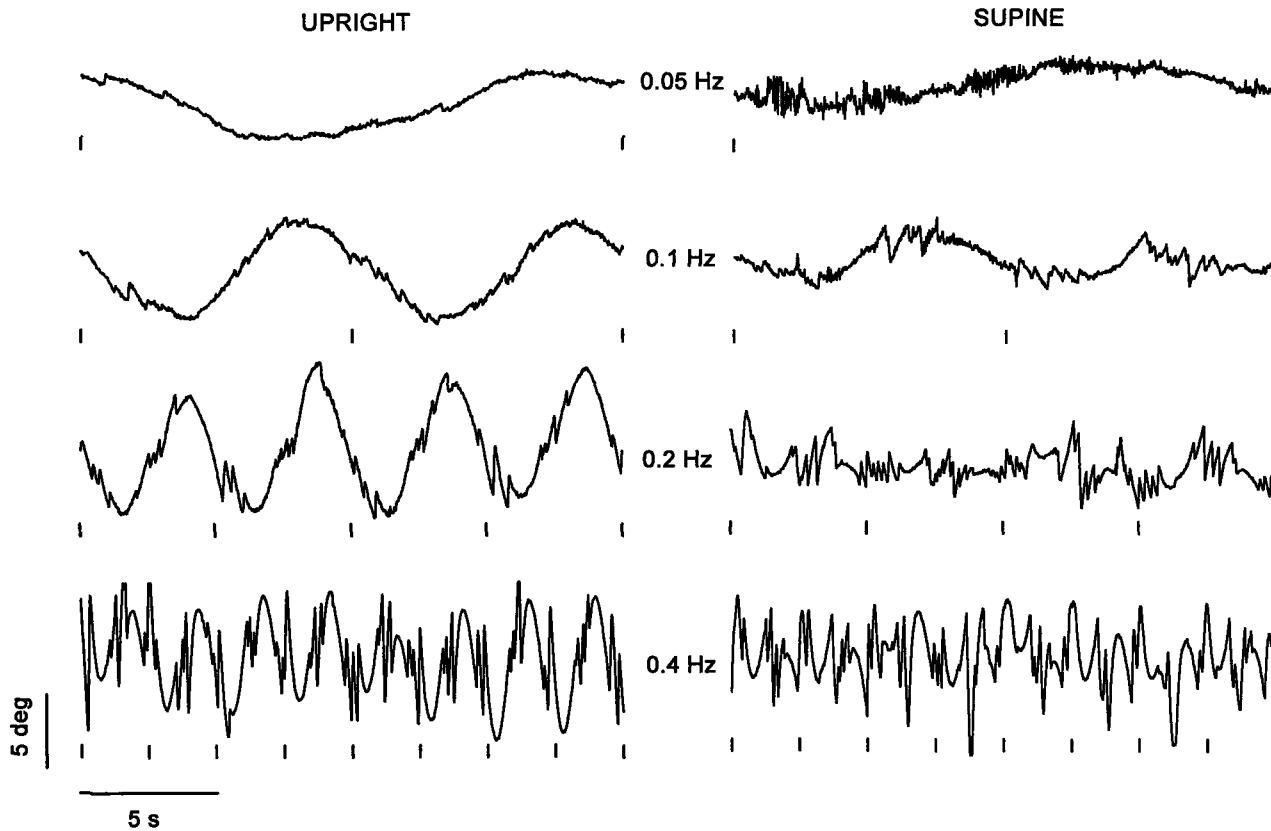


Figure 3.2. Twenty seconds of torsional nystagmus of one subject at four stimulus frequencies (fixed amplitude 25 °) in the upright (left) and supine (right) orientation. The small markers below each trace indicate the moment of maximum clockwise body tilt. Upward deflection of the eye position signal corresponds to counter-clockwise rotation.

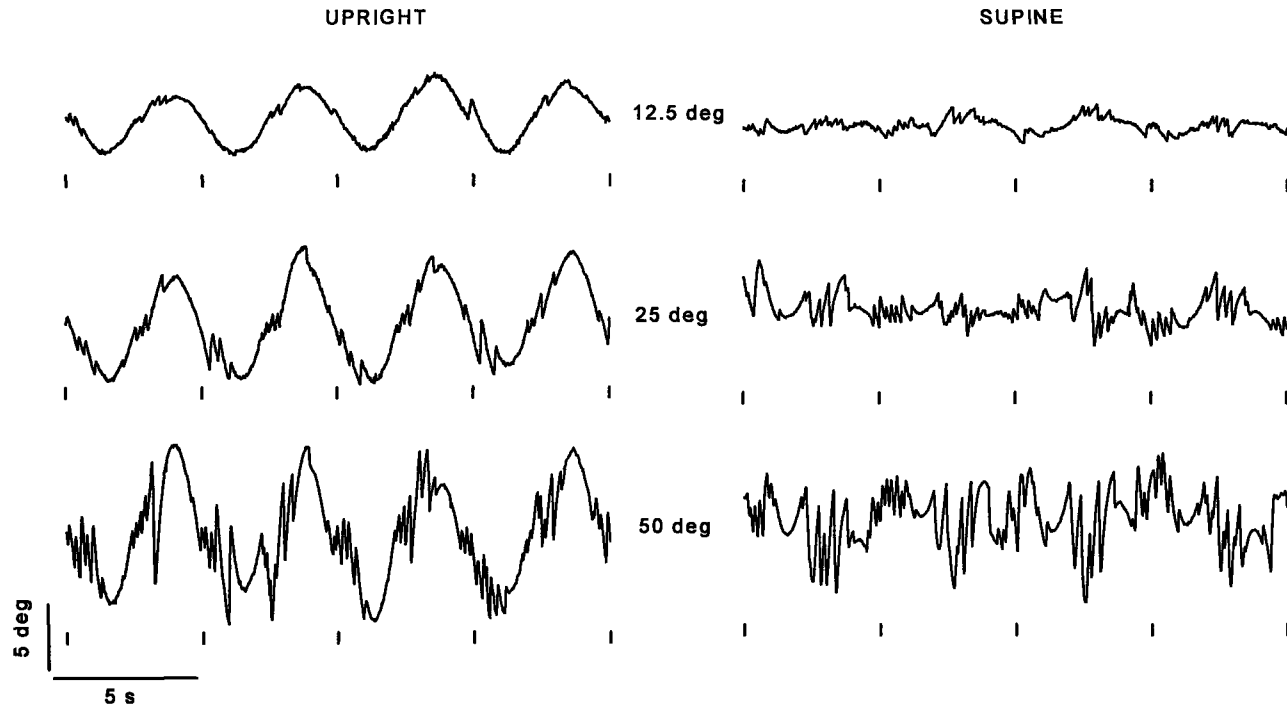


Figure 3.3. *Twenty seconds of torsional nystagmus at three different stimulus amplitudes (with frequency fixed at 0.2Hz) in upright (left) and supine (right). Data are from the same subject as in Figure 3.2. The small markers below the traces correspond to maximum clockwise body tilt.*

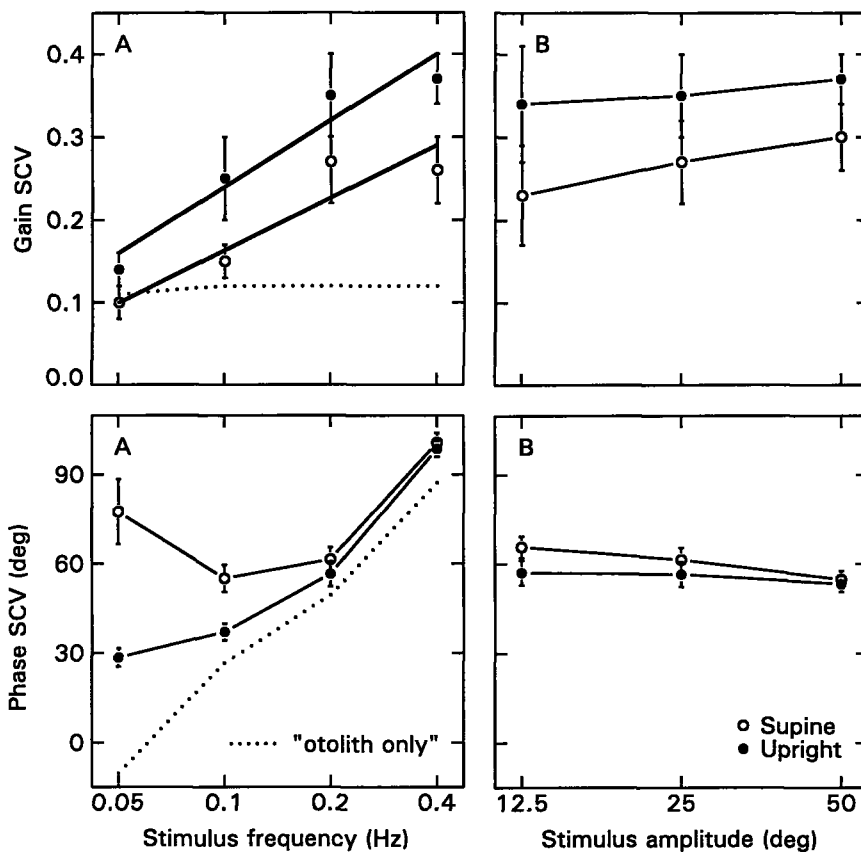


Figure 3.4. The SCV dynamics, binocular data averaged over five subjects, for the upright (filled circles) and supine conditions (open circles). In the left column (a) the SCV gain and phase are depicted versus log stimulus frequency. Here, the dotted line shows the hypothetical "otolith only" response, calculated as the vector difference between upright and supine. The solid lines in the gain plot (upper left diagram) are the fitted regression lines: $y_{\text{upright}} = 0.50 + 0.26 \log(f)$, and $y_{\text{supine}} = 0.37 + 0.21 \log(f)$. In all other plots the connecting lines between data points are drawn. In the right column (b) gain and phase are shown for the log stimulus amplitude. Positive phase values indicate phase lead relative to a perfect compensatory response. Error bars indicate S.E.M.

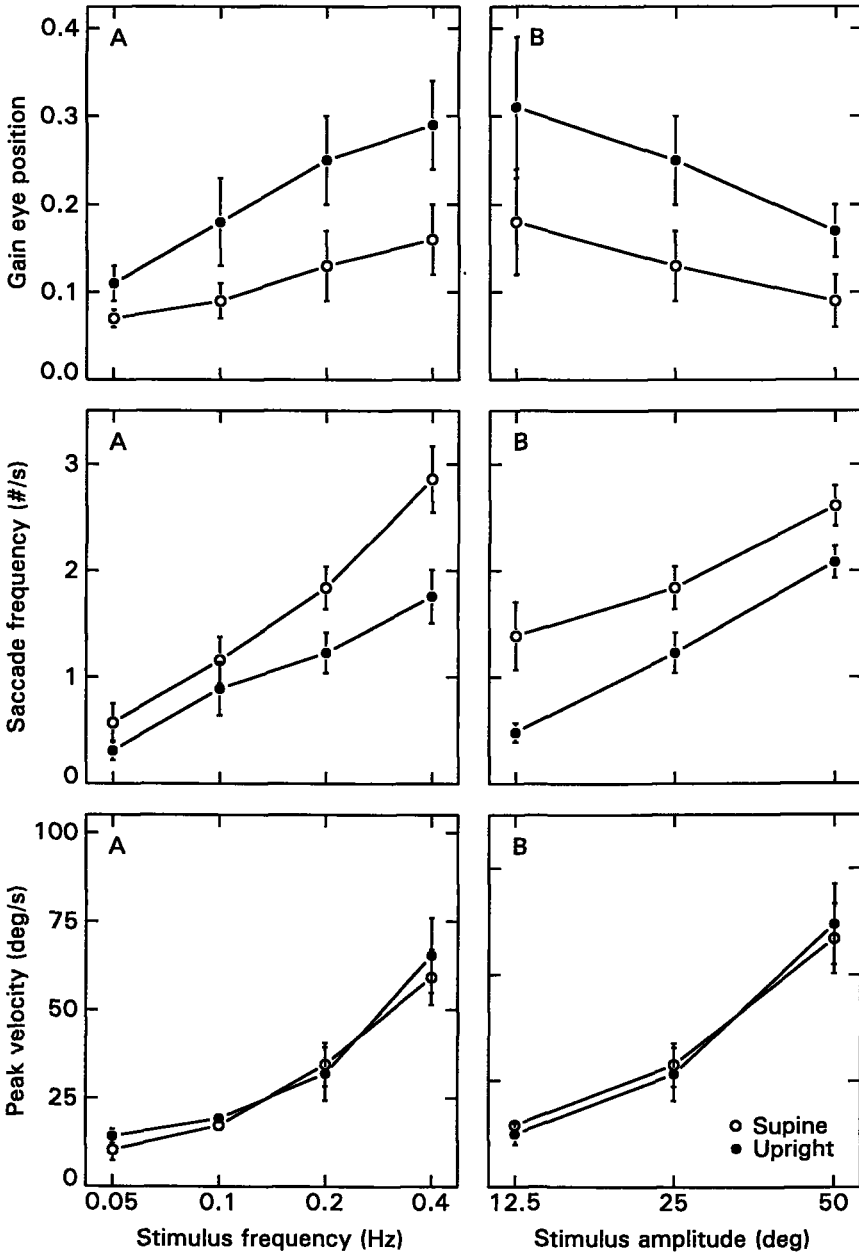


Figure 3.5. The eye position parameters as they vary with log stimulus frequency (a, left column) and amplitude (b, right column). The mean eye position gain (upper diagrams), saccade frequency (middle diagrams), and saccade peak velocity (lower diagrams) are shown for upright (filled circles) and supine conditions (open circles). Error bars indicate S.E.M.

Discussion

In this study we compared the torsional VOR during oscillations about an earth-horizontal and an earth-vertical roll axis, that is with varying and invariant otolith input, respectively. We used passive body roll in order to minimize inputs from the neck receptors. Therefore, the response differences between the two body orientations were attributed to the contribution of the otoliths.

Slow component velocity

We found that in both body orientations the gain of the slow component velocity increased with stimulus frequency. The gains observed were within the common range of the human torsional VOR. For instance, the average SCV gain of 0.37 at 0.4Hz in the upright condition is similar to the value measured by Tweed *et al.* (1994) at 0.3Hz. A further increase of the torsional gain up to 0.7 has been reported for active head movements of 1 Hz (Collewyn *et al.* 1985; Vieville and Masse 1987). The logarithmic relation between the SCV gain and the stimulus frequency, suggested by our data, confirms these results.

In the present study, the gain was consistently higher, by an amount of 0.1, in the upright orientation than in the supine orientation. In a previous study we measured the torsional response in exactly the same way at the frequency of 0.25 Hz (Groen *et al.* 1996b). We then observed a higher gain in the supine conditions compared to the upright conditions. Among the 11 subjects of the previous experiment were the same five subjects of the present study. Although the difference between the two conditions was significant for the entire group of 11 subjects, it was not for the subgroup of five subjects. Later we collected more (unpublished) data of the same subjects, again at the frequency of 0.25 Hz, which were consistent with the results described here. Considering these variable results within subjects and the small effects, we do not believe that the otoliths contribute significantly to improve the *gain* of the (torsional) VOR in humans. Other studies have also failed to show a difference in SCV gain between earth-horizontal and earth-vertical rotation (Tweed *et al.* 1994; Seidman *et al.* 1995). In this, humans differ from lateral-eyed species, such as rabbits, where the otoliths almost completely compensate for the reduced gain of the canal-induced VOR at very low stimulus frequencies (Barmack 1981).

We adhere to a different conclusion with respect to the *phase* of the response: in the lower frequency range, contribution of the otoliths had a significant effect on the phase lead. At the frequency of 0.05 Hz the response to earth-vertical rotation showed a phase lead of about 80°, which was only 30° in the response to earth-horizontal rotation. Similarly, Vieville and Masse (17) reported that the phase lead of ocular torsion during active head roll in their (only) subject was larger when the

head was prone than when the head was erect. There is evidence that otolithic control of the phase is not restricted to the torsional VOR. The same effect was reported for the phase of the horizontal VOR in humans during barbecue spit rotation (Benson 1970). Optimizing the phase therefore seems to represent a general mechanism of the otoliths to improve the VOR dynamics.

In the present study, there are two otolith-induced responses under consideration: a (position-dependent) response to head *tilt*, and a (position-independent) response to the rotation of the gravito-inertial force relative to the head (“*tilt velocity*”). With our experimental design however, it is difficult to discriminate the two components in the calculated “otolith only” response. This may explain why this response did not show the typical low-pass filter characteristics, which have been described for tilt OORs (Paige and Tomko 1991a; Hannen *et al.* 1966; Lichtenberg *et al.* 1982; De Graaf *et al.* 1996; Merfeld *et al.* 1996). It is possible that the observed otolith effect on the phase of the slow component exclusively resulted from the response to tilt velocity, as was argued by Angelaki and Hess (1996a). Using sinusoidal rotation with an amplitude of more than 360°, these authors demonstrated that it was the “tilt velocity” information by which the otoliths improved the low-frequency dynamics of the angular VOR in monkeys.

Theoretically, the reduction of the phase lead of the slow component may be accomplished via the neural integrator (Robinson 1971), which converts eye velocity signals into position signals. In their physiological range, the canal afferents encode for angular head velocity, which is suitable to drive the movements of the eyes, but needs to be integrated to hold the eyes in their new position after cessation of the movement. At lower frequencies, the canal signal is shifted toward acceleration (Férez and Goldberg 1971), as becomes clear in the progressive phase lead of the VOR. To hold eye position then, the signal would have to be integrated twice. Our data suggest that the otoliths provide supplementary (tilt) velocity information that can be used to achieve this extra integration step.

Eye position

Due to anti-compensatory saccades the eye position gain was invariably smaller than the gain of the slow component. This effect was most noticeable in the response to earth-vertical rotation: at all stimulus frequencies the nystagmus consisted of more saccades in the supine condition than in the upright condition, even though the corresponding SCV gain was higher in the latter. The amplitude of the saccades was equally large in both body orientations, indicating that the beating field itself was unaffected. Instead, it was the *offset* of the beating field

that was sinusoidally modulated during earth-horizontal rotation. This resulted in larger accumulation of ocular torsion in the upright orientation, illustrated by the higher eye position gain. This confirmed our assumption that the otoliths modulate torsional eye position by influencing the saccadic behavior. In contrast to the observed effect on the phase of the slow component, the effect on the saccade frequency reached over the entire frequency range, so that presumably the two effects are independent.

We believe that modulation of the beating field offset is an instrument for the otoliths to maintain eye position in space. It may well be that this is common to any system associated with gaze stabilization, since it has been reported that the incidence of anti-compensatory saccades in the ocular torsion response is reduced in the presence of a visual scene (Collewijn *et al.* 1985). By the same token, our results indicate that stabilization of the eyes-in-space is less important when the rotation is independent of gravity. Here, the system seems inclined to compensate for head velocity, irrespective of the orientation of the eyes. From this we conclude that the canals are primarily concerned with stabilization of the retinal image in head-centric coordinates, whereas the otoliths tend to anchor the oculomotor coordinate system with respect to gravity.

Listing's law

Although our study concerned one-dimensional eye movements, the above described effects are relevant in the light of Listing's law, which applies to three-dimensional eye movements. According to this law, the eyes usually assume positions that can be reached from a certain reference position by rotation about an axis laying in a head-fixed plane. When this reference position is the primary position, these axes lie in a plane (Listing's plane) perpendicular to the gaze direction (Tweed *et al.* 1990). As a result of the strategy as described by Listing's law, the oculomotor system tries to avoid torsional eye positions. This implies that there is a conflict between minimizing the degree of ocular torsion and stabilizing the position of the eyes in space. This raises an alternative explanation for the low torsional gain of the VOR. Originally, it has been argued that a low torsional gain is not necessarily inadequate, because torsional movements do not alter the direction of gaze and thus preserve fixation on a stationary target (Seidman *et al.* 1989; Ferman *et al.* 1987). As a result, there would be little retinal slip in the foveal area. However, these assumptions only hold when ocular torsion is regarded as rotation about the line of sight, that is relative to the eye. There is reason to believe that the torsional VOR should be regarded in head-fixed coordinates, or, more precisely, in Listing's coordinates (Crawford and Vilis 1991; Tweed *et al.* 1994). In the view of these authors, the low torsional gain signifies a trade-off between perfect (co-axial) compensation for head rotations and obeying

Listing's law. The compensatory slow component tilts the rotation axes of the eyes out of Listing's plane, which is subsequently restored by anti-compensatory saccades. Our data confirm this behavior for the supine position. During earth-horizontal rotation, however, the (now) varying otolith contribution complicates the matter. It is questionable whether this otolith-induced ocular torsion should be considered as a violation of Listing's law. In fact, it may establish the link between the eye in its head-centric orientation (according to Listing's law) and the eye in the orientation to the environment (i.e. to gravity). It has been hypothesized that the static ocular torsion during head tilt may result from a shift of Listing's plane (Vilis 1993). Indeed, the rotation axes of voluntary saccades have been shown to lie in a plane shifted in torsional direction when the subject is tilted laterally (Crawford and Vilis 1991). Similar observations have been made for static tilt in pitch (Haslwanter *et al.* 1992). Recently, Angelaki and Hess (1996a,b) found that in monkeys the otoliths did not only influence the slow component but also the saccades of vestibular nystagmus. They argued that the orientation of primary position is dynamically modulated by the otoliths. The modulation of the beating field offset, observed in the present study, indicates that the otoliths serve this function also in humans.

In conclusion, our data showed that the dynamic contribution of the otoliths improved the human torsional VOR dynamics at low stimulus frequencies, mainly by keeping the response in phase with the stimulus motion. In addition, the otoliths reduced the number of anti-compensatory saccades in the nystagmus, increasing the excursion range of torsional eye position. Through these effects the otoliths achieve better stabilization of the eyes-in-space.

Acknowledgments

This work was supported by the Foundation for Behavioral and Educational Sciences of the Netherlands Organization for Scientific Research. The dental frames with individual fit were provided by ACTA (Academisch Centrum Tandheelkunde Amsterdam). We are grateful to Astrid de Vries for her contribution to the data analysis. We also thank Dr. Doug Crawford for his helpful discussions.

“Those who are to participate in the apparent gyrations of the swing - and there may be quite a number who enjoy it simultaneously - are ushered into a small room. From a bar crossing the room, near the ceiling, hangs a large swing, which is provided with seats for a number of people. After the people have taken their places, the attendant pushes the car and it starts into oscillation like any other swing. The room door is closed. Gradually those in it feel after three to four movements that their swing is going rather high, but it is not at all. The apparent amplitude of the oscillations increases more and more, until presently the whole swing seems to whirl completely over, describing a full circle about the bar on which it hangs. To make the thing more utterly mysterious, the bar is bent crank fashion, so that it seems demonstrably impossible for the swing to pass between bar and ceiling. It continues apparently to go round and round this way, imparting most weird sensations to the occupants, until its movements begin gradually to cease and the complete rotation is succeeded by the usual back and forth swinging, and in a few seconds, as the children say, “the old cat dies.” The door of the room is opened and the swinging party leaves. Those who have tried it say the sensation is most peculiar and the deception perfect.”

“The haunted swing”

(from A.A. Hopkins. 1976. Magic, stage illusions, special effects and trick photography. A.A. Hopkins. Dover Publications, New York)

Chapter 4

Illusory self-tilt in a “Tumbling Room”

Introduction

Rotation of a visual display about an earth-horizontal axis induces a sensation of continuous self-motion accompanied by a sensation of self-tilt in the opposite direction, or equivalently an apparent tilt of the subjective vertical in the same direction (Dichgans and Brandt 1978). The degree of illusory self-tilt is determined by several factors. First, the effect increases with the area of the rotating display, especially when the stimulus motion expands to the retinal periphery (Held *et al.* 1975). Second, illusory self-tilt is a function of stimulus velocity, but only up to about 40°/s (Held *et al.* 1975; Howard *et al.* 1988). Third, the strength of the effect depends on the orientation of the head relative to gravity. The effect is stronger when the head is tilted 90° to the side, or inverted, as compared to erect (Young *et al.* 1975; Dichgans *et al.* 1975). Additionally, the axis of rotation relative to the subject may be important too. It was found that illusory self-inclination is larger for backward rotation of the scene about the subjects' y-axis (pitch) compared to forward pitch motion (Young *et al.* 1975). In general, the average maximum illusory body inclination does not exceed 20°, which is attributed to the restraining influence of the otolith organs.

Furthermore, illusory self-tilt depends on the type of visual information in the display. Three types of visual cues contribute to the sense of body orientation with respect to gravity: visual motion, visual frame, and visual polarity. A visual frame is a set of lines and surfaces that constitute a frame which is normally aligned with gravity. Visual polarity comprises objects which show a identifiable “up” and “down”. Visual motion alone can be obtained by rotation of a display with a texture lacking visual frame and visual polarity cues. Most studies on visually induced self-tilt have applied rotating displays textured with non-polarized dot patterns. Recently, Howard and Childerson (1994) used a 7 feet cubic room, which contained distinct cues for visual frame and visual polarity, and which rotated about the subjects' roll-axis. In total, 60% of the upright subjects reported a compelling sensation of complete self-rotation, meaning that the information of the graviceptive sensors was completely overridden by the dominant visual stimulus. The other 40% of the subjects experienced a limited degree of self-tilt, either

Results of this study have been reported in: Howard IP, Cheung B, Groen E (1997) Disorientation training in non-motion based simulator. DCIEM report W7711-5-7256.

constant or alternating. During the latter, the subjects perceived self-tilt with the body becoming erect each time a surface became horizontal. Some subjects noted the feeling that they were supine and experienced self-rotation about a vertical roll-axis.

The so-called "Tumbling Room" used by Howard and Childerson was rebuilt to make it more realistic and provide it with a richer variety of polarized objects. The study described here was performed using this new Tumbling Room, with the following objectives: (1) Determine the percentage of subjects that perceive full self-rotation when immersed in a highly polarized scene. (2) Examine the effects of body posture on illusory self-tilt produced by rotation of the room (in the previous study the subjects sat in an erect posture). (3) Compare the effects of rotation of the room for different viewing directions of the subject relative to the room (roll, pitch, or yaw). Because the results showed that the rotating Tumbling Room was very effective in producing sensations of complete self-rotation, it was of interest to know whether (4) static tilt of the room could induce sensations of self-tilt which exceeded previously reported illusory self-tilt in response to static tilt of visual scenes. This question was addressed in an additional experiment by testing erect subjects with rotation about the roll axis only.

Methods

Furnished room

The furnished room consisted of an 8 foot cubic frame lined with plywood on the floor and foam plastic sheets on the walls and ceiling (Figure 4.1). One side wall had a window with a lighted outdoor scene, a valance curtain and plants. The opposite wall had an interior house door that allowed access to the room. The walls were papered and decorated with pictures, hanging objects, and a bookcase holding books, a teddy bear and three cups hanging from cup hooks. There was a small kitchen table screwed to the floor, set with cutlery, plates, cups and saucers, a bread basket and a box of tissues. Two wicker chairs either side of the table completed the scene. The floor was carpeted and there were baseboards against the walls, and additional floor details included waste baskets and slippers. All objects were carefully held in place by either hidden bolts, glue or Velcro, so that they stayed in place when the room rotated. In the center of the ceiling was a simple 60W fluorescent light fixture with a plastic cover. Thus, the room provided a clear visual frame and a rich variety of visual information about which direction was up and which direction was down.

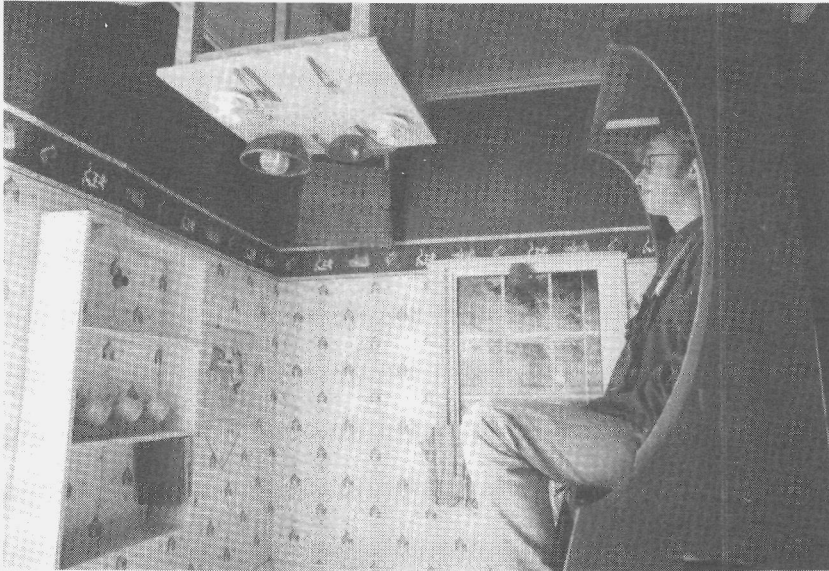


Figure 4.1. The interior of the furnished Tumbling Room (upper picture) tilted 180°. A variety of objects was fastened to the walls and floor. The room rotated about a fixed earth-horizontal axis (lower picture). By changing the orientation of the chair, the effective rotation axis relative to the subject could be varied between roll, pitch, or yaw.

Bearings were placed on the centers of an opposite pair of walls and the whole structure was mounted on external brackets so that it could be rotated about a horizontal axis passing through the center of the room. Room rotation was generated by a computer controlled DC servomotor. The subject was strapped into a seat supported on a 10 inch square boom which protruded through one wall along the axis of rotation of the room. The chair could be removed and replaced by a bed, which was suspended between the boom on one side and a shaft on the other side of the room.

Constant velocity rotation of room

Profile

The room rotated about an earth-horizontal axis at a constant velocity of $30^\circ/\text{s}$ for 4 cycles over a period of 48 s. The initial acceleration and final deceleration were $5^\circ/\text{s}^2$ applied over a period of 6 s. The lights were on all the time and the subjects looked straight ahead at the center of the wall in front of them.

The first experimental variable was the **rotation axis** with respect to the subject. The subject was placed in each of three postures so that the room rotated about the subject's roll, pitch, or yaw axis. For roll, the subject was looking along the axis of room rotation. For pitch, the chair was turned so that the subject was facing the side wall with the door. For yaw, the chair was replaced by the bed with the subject lying along the axis of rotation of the room. The second variable was **body orientation**. In roll, the subject was seated upright, tilted left ear down or right ear down. In yaw, the subject was lying either in supine position, or with left ear down or right ear down. In pitch, the subjects were seated upright or pitched backwards 90° into supine posture, but they were not pitched forward, since this would have been an awkward position. Finally, the **direction** of room rotation was either clockwise or anti-clockwise. The 16 conditions were arranged in blocks per rotation axis. The order of conditions within each block and the order of blocks was counterbalanced over subjects. Additionally, conditions were alternated for direction.

Responses

Thirty-two subjects (of whom 12 were familiar with the purpose of the experiment) were tested in each of 16 conditions. Subjects were asked to report their sensations of self-tilt according to the following categories (Howard and Childerson 1994): (a) "Full tumbling", subjects felt as if they had rotated completely through 360° . (b) "Alternating self-tilt", subjects felt that they were rotating opposite to the room

to a certain angle of self-tilt, then felt suddenly upright, and then began tilting again. (c) "Constant self-tilt", subjects felt inclined at a more or less constant angle in the opposite direction of room motion. (d) "Supine", subjects felt as if they were lying supine, looking up at the rotating display that now appeared to be rotating in a horizontal plane. (e) "No effect", subjects did not experience self-tilt but felt veridically upright.

The subjects were also asked to rate the magnitude of their sensations of self-motion (vection) on a seven point scale (0 - only room motion; 1 - much more room motion than self; 2 - more room than self; 3 - equal room and self; 4 - more self than room; 5 - much more self than room; 6 - only self-motion).

Static tilt of room

Profile

The subject sat erect in the chair with the head near the center of the furnished room. The room rotated about the subject's roll axis and brought to rest at one of four angles with respect to the vertical. While the room was moving, subjects kept their eyes closed for a fixed time so that the duration of eye closure could not indicate how far the room had moved. The angles of scene tilt were 0, 40, 80, and 120°, either clockwise or anti-clockwise. There were thus seven conditions, each repeated four times per subject.

Response

Subjects indicated their subjective vertical by aligning two black one-inch diameter discs ("indicator") with the apparent vertical. The discs were placed on a transparent circular disc about 1 foot in diameter which was mounted at its center on a horizontal shaft protruding from the axis of room rotation in the facing wall, about five foot in front of the subject. The setting of two dots was preferred to the setting of a line because of possible tilt contrast effects between a line and the room. The subject could set the disc to the desired angle by means of a servo device which controlled a motor attached to the disc shaft. There was some overshoot each time the disc rotated. However, subjects quickly learned to handle the rotating device with a minimum of overshoot. Six subjects were tested in each condition, making 168 randomized and counterbalanced trials.

Results

Constant velocity rotation

The rotating room induced compelling sensations of self-rotation about an earth-horizontal axis. Subjects were aware that the pressure sensations acting on the five-point harness were not what they expected from full self-rotation but this did not prevent them from feeling that they had rotated through 360°. After completing the experiment, several subjects found it difficult to believe that they had remained stationary and the room had been rotated. The percentages of the different kinds of sensations produced by room rotation are set out in Figure 4.2 for each axis of rotation. There were no significant effects of the factors rotation axis, body orientation, or direction of rotation on the type of self-rotation (tested with Pearson's Chi-square). In total, 83.8% of the 512 responses were "full tumbling"; 8.4% were "alternating self-tilt"; 5.5% were "constant self-tilt"; and 2.3% were "no effect". The number of subjects that accounted for these percentages are shown above the bars in Figure 4.2 (in fact, these numbers indicate how many subjects experienced the regarding sensation in at least one of the trials). There were no "supine" responses.

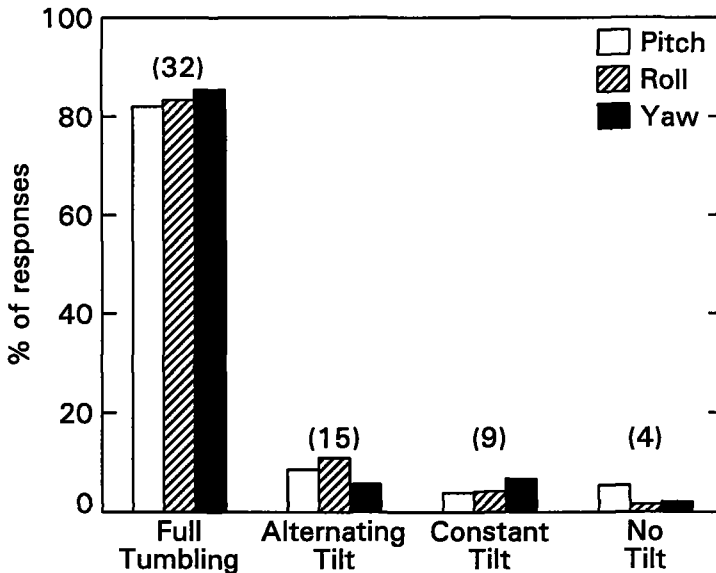


Figure 4.2. Percentage of all 512 responses (32 subjects in 16 conditions) for each category of illusory self-tilt in the tumbling room for each axis of rotation with respect of the subject's body for a constant room velocity of 30°/s. The numbers above the bars indicate the number of subjects who experienced the corresponding sensation at least once.

Mean vection magnitude over the 32 subjects for room rotation about the subject's roll, pitch, and yaw axes are shown in Fig. 4.3. Vection data were subjected to an ANOVA (within subjects design). There were no significant effects of rotation axis, body orientation, or direction of rotation. Vection was on average relatively well saturated with an average of 4.6 (st. dev.1.8), which means that - except for some residual sensation of room motion - most of the visual motion was attributed to self-motion.

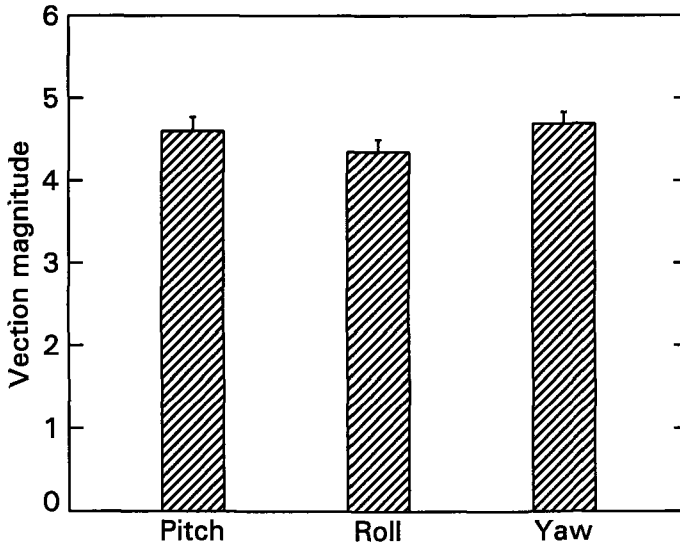


Figure 4.3. Mean vection magnitude in the tumbling room for each axis of rotation with respect to the subject's body during constant room velocity of 30°/s. Bars are standard errors of the mean (n=32).

Static tilt

The mean subjective vertical (constant error from true vertical) and the mean variable errors (standard deviation) are shown in Figure 4.4. There was a significant main effect of scene tilt angle on the subjective vertical ($F=4.99$; $df=3$; $p<0.05$), but only between 0° and 40° (post-hoc Tukey: $p<0.05$). There was a non-significant trend for the effect of room tilt on the variable error between the four repetitions per condition ($F=3.0$; $df=3$; $p=0.06$). The data from the condition in which the room was vertical show that the accuracy of the settings was quite good. On average, the visual stimulus was set at -1.1° , that is, slightly anti-clockwise from the true vertical. The precision was 1.5° (mean standard deviation).

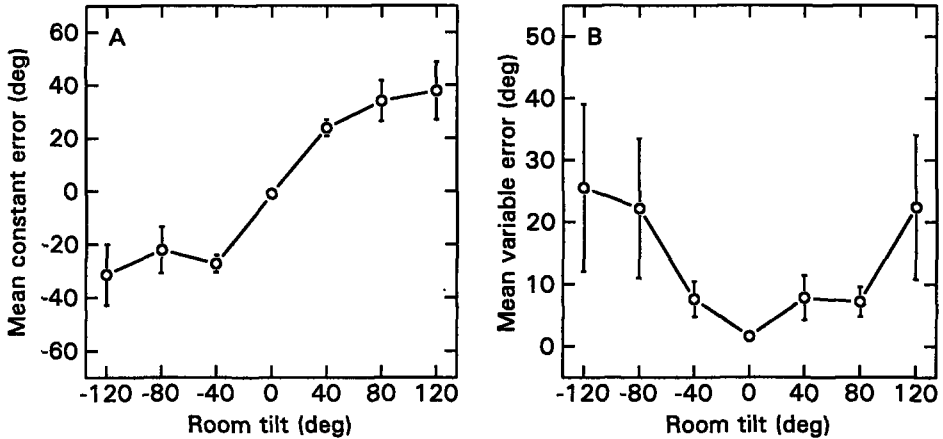


Figure 4.4. Mean constant error (a) of the vertical setting of the indicator (subjective vertical) for each angle of room tilt (six subjects with four measures per condition). Corresponding mean variable errors (b) of the subjective vertical for each angle of room tilt. Bars are the standard errors of the mean.

Figure 4.5 shows the distribution of all settings of the indicator to vertical. For 40° of room tilt, some subjects aligned the indicator with the room, while others showed only a tendency to align it with the room. In only one trial of one subject was the indicator set in the opposite direction of the room. For larger angles of room tilt, 80° and 120°, the response varied greatly between subjects. One subject (S6) aligned the two dots almost exactly with the tilted room in all conditions. Another subject (S4) sometimes reported that the indicator appeared vertical when it was close to being aligned with the room and sometimes when it was close to the actual vertical. There was no time limit in setting the indicator, and this subject kept rotating it over large angles before making a decision. As a result, his settings for 80° and 120° scene tilt were rather scattered. Two other subjects (S1, S3) consistently set the indicator close to the true vertical. Finally, two other subjects (S2, S5) seemed to use either the real floor or the surface that was closest to horizontal as the apparent floor. This resulted in a bimodal distribution of their responses which is reflected in the mean distribution settings over subjects in Figure 4.6. The settings of the indicator for each subject are shown in Figure 4.5.

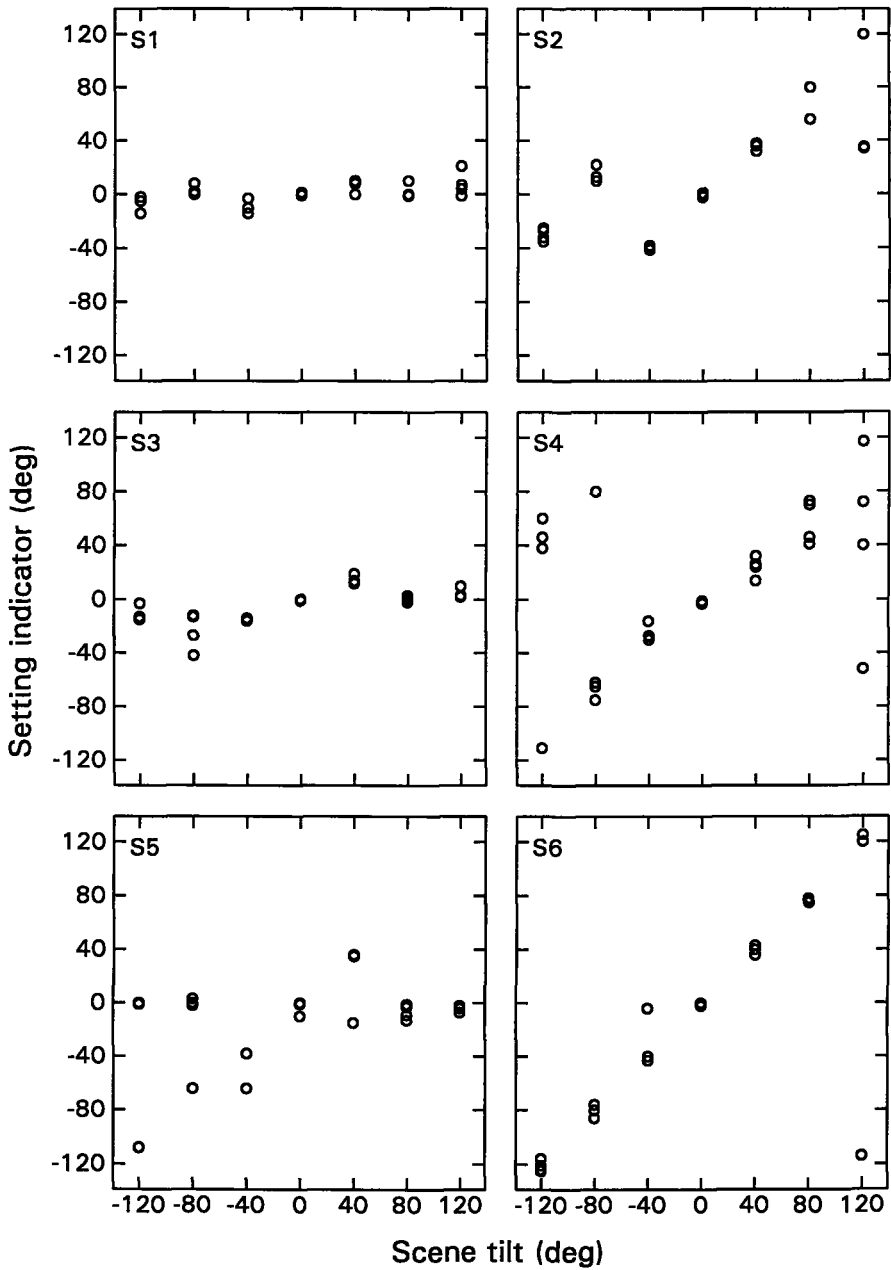


Figure 4.5. Settings of the indicator to the apparent vertical for each subject.

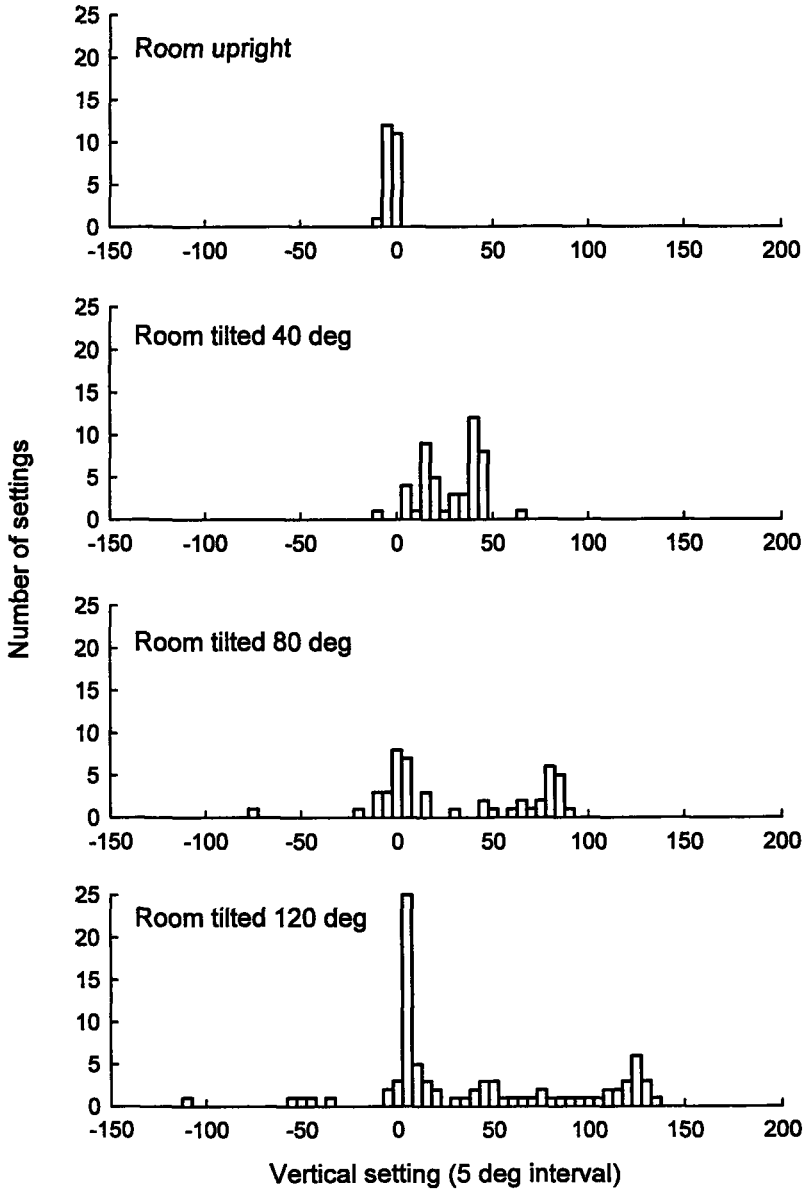


Figure 4.6. Distribution of vertical setting of the indicator for each angle of room tilt, collected in 5° intervals. Data from clockwise and anti-clockwise trials collapsed ($n=6$; 4 repetitions for each angle of room tilt). Positive angles indicate that the stimulus was rotated from the true vertical in the direction of the room (with the exception of the upright room condition, where the sign is not related to the room tilt, but illustrates the accuracy of the indicator setting).

Discussion

Constant velocity rotation

All subjects experienced complete self-rotation (self-tilt through 360°) in most of the trials when exposed to rotation of the furnished room. Over 80% of the responses were “full tumbling”. Subjects also experienced strong sensations of self-motion (vection) whether or not they experienced full self-rotation. In the furnished room used by Howard and Childerson (1994), 60% of subjects reported full self-rotation. This room was smaller and contained less polarized visual features. There have been no other scientific reports of sensations of full self-rotation produced by visual stimulation alone in the presence of restraining information from the otolith and somatosensory organs. People experienced full tumbling in the “haunted swing”, a fairground device that was built towards the end of the last century (Wood 1895). The room rotated about the pitch axis, while the observers sat in a stationary gondola with their heads several feet below the axis of rotation. In this case, the information of the otolith organs was not necessarily contradictory with the simulated motion, since the resultant G-force would have stayed approximately in line with the body axis when the gondola were to have actually rotated. In the present study the observer’s head was near the axis of rotation, so that during actual body rotation the otolith organs would have indicated self-tilt. The high rate of full tumbling therefore demonstrates that immersion in a rotating polarized scene can fully override the restraining otolith organ and semicircular canal inputs.

There was no difference in incidence of self-rotation sensations between the three axes of rotation: roll, pitch, and yaw. Nor was there a measurable effect of body orientation with respect to gravity. Previous reports showed that vection magnitude is larger for yaw rotation than for pitch, which in turn is larger than for roll (Howard *et al.* 1988). Moreover, visually induced self-tilt and self-rotation normally increase when the body is inclined to gravity (Young *et al.* 1975). The reason that these effects were not found in the present study must be due to the general effectiveness of the furnished room. Presumably the response was already saturated in an upright body posture, and tilting the body could not add to this.

Static tilt

Subjects were most consistent in setting the visual display to the apparent vertical when the furnished room was upright. The variable errors were comparable to those reported by Witkin and Asch (1948). When the room was tilted 40° the position of the apparent vertical shifted in the direction of room tilt and was equal to room tilt for some subjects. For tilt angles of 80° and 120°, responses became

highly variable. Subjects became confused and their disorientation sensations were less stable. Some subjects fluctuated between two criteria of verticality: the room, as indicated by the visual polarity, and the actual direction of gravity as signaled from the otolith and somatosensory sense organs.

Asch and Witkin (1948a) had subjects stand in the laboratory and look into a furnished room tilted 22°. Settings of a rod inside the room to the apparent vertical were displaced on average 15° in the direction of room tilt. A simple tilted frame produced an apparent tilt of only 6°. In the present experiment subjects were immersed in the tilted room, and the angles of scene tilt were larger. This resulted in larger effects. In a similar study, Howard and Childerson (1994) observed on average only 15° at 40° of room tilt, with a maximum of 60°. At larger angles of scene tilt, there was a strong tendency of the subjects to use the surface-closest-to-horizontal as subjective floor. In the same study, results were compared to the effects of a framed room without any polarity. The results were similar, except for 40° of room tilt, where subjects in the framed room took the diagonal (a 45° tilted square frame may be seen as an erect diamond with a “vertical” at 45° intervals).

Conclusion

It is concluded that a static, richly polarized visual scene in which the subject is immersed can induce illusions of self-tilt far greater than previously reported. However, for most subjects, a static polarized room is not as effective as a rotating room in inducing strong illusory self-tilt. The full self-rotation experienced by most people when immersed in a richly polarized and moving visual environment, such as the rotating furnished room, must represent the combined effect of motion, visual frame and the polarity features in the room. With the rotating room subjects were generally consistent in their responses and did not report the ambiguity that they experienced in the static tilted room.

Acknowledgments

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Chapter 5

Influence of body roll on visually induced self-tilt

Introduction

A stationary observer exposed to a rotating scene experiences self-rotation, or circularvection in the opposite direction and perceives the scene as stationary (Fischer and Kornmüller 1930). It generally takes 20-30 s for vection to reach its full strength, which is ascribed to the absence of the vestibular inputs that would accompany actual self rotation during this initial period (Dichgans and Brandt 1978). Because the semicircular canals do not respond to steady rotation of the body, the relative motion of the visual surroundings is the only cue to steady passive rotation about a vertical axis. Therefore, during circularvection about a vertical axis there is a visual-vestibular conflict only at the onset of the visual motion. Accordingly, the latency of circularvection can be shortened by an impulsive rotation of the body in the same direction (Brandt *et al.* 1974).

Circularvection about a horizontal axis is more complicated, because it affects the perceived orientation of the body with respect to gravity. This not only involves inputs from the semicircular canals, but also from the otolith organs. The otoliths register the steady state orientation of the head relative to gravity, and thus contradict visually induced sensations of self-tilt in a stationary observer. As a consequence, rotation of the visual surroundings about a horizontal axis typically produces a sensation of continuous self-rotation accompanied by constant illusory self-tilt with a mean value of about 20° (Dichgans *et al.* 1972; Held *et al.* 1975). Moreover, the magnitude of circularvection has been found to be smaller for rotations about a horizontal axis than for rotations about a vertical axis (Held *et al.* 1975; Howard *et al.* 1988). Because of the persisting visual-otolith conflict, it is questionable whether passive body rotation at the onset of the visual motion can enhance visually-induced sensations of self-rotation and self-tilt about a horizontal axis, as it does for circularvection about a vertical axis. In the present study we addressed this question for rotation about the line of sight (roll axis) in an upright observer.

In flight simulators with a motion base, vestibular onset cues are applied to enhance sensations of self-motion. A motion base has limited travel and must be

Adapted from: Groen E, Howard IP, Cheung B. Effects of actual body roll on visually induced self-tilt. Submitted to Journal of Vestibular Research.

returned to its original position after a maneuver without disturbing the sensation of self-motion. This is done by an acceleration below the vestibular threshold, a procedure known as washout. We examined the effects of washout temporally separated from the onset by delaying the restoration of the body position. The effective vestibular stimulus to body roll can be decomposed into a rotation component and a tilt component. It was hypothesized that the magnitude of circularvection primarily depends on initial body acceleration in the washout maneuver, whereas the extent of perceived self-tilt primarily depends on the angle of body tilt. To investigate this hypothesis we exposed subjects to whole-field visual rotation about the horizontal roll axis and superimposed two acceleration levels of body roll, one above the vestibular threshold and one in the threshold region.

Method

Stimulus

The subject sat inside a 9-foot diameter sphere lined with black dots on a white surface. The seat was padded with “slow recovery” plastic foam and the subject was constrained by a five-point harness and head rest with the head upright and close to the center of the sphere. The sphere was illuminated by a 60 watt light bulb placed above and behind the subject's head. The sphere and chair could be rotated independently about the same earth-horizontal axis. The rotation axis passed through the center of the sphere and was parallel to the subject's roll axis centered on the subject's head. There were seven conditions (Table 5.1). The effect of visual motion itself was investigated in one condition in which the sphere alone rotated (“visual motion”). The effect of body motion was investigated in two conditions, in which the subject alone rotated (“subject motion”). The effect of washout was investigated in three “washout conditions”, in which both the sphere and the subject rotated. In two washout conditions the washout was delayed for 40s (“delayed-washout”), and in the third condition the washout immediately followed the onset (“immediate-washout”). Finally, the effect of body tilt without washout was investigated in a condition in which the subject was tilted before the sphere was accelerated, and restored to upright after deceleration of the sphere (“pre-tilt”). The sphere accelerated at $3^\circ/s^2$ until it reached a terminal velocity of $18^\circ/s$ which was maintained for 80 s before deceleration. The subject was accelerated at either $0.7^\circ/s^2$ (“subthreshold”) or $3^\circ/s^2$ (“suprathreshold”). We selected an acceleration of $0.7^\circ/s^2$ because it is in the threshold region for detection of self rotation about the roll axis and takes over 1 s to detect. An acceleration of $3^\circ/s^2$ is detected in under 0.1 s (Gundry 1978).

<i>Condition</i>	<i>Onset</i>	<i>Washout</i>
1 Visual-motion	Sphere accelerated at $3^\circ/s^2$ to constant velocity of $18^\circ/s$. Chair stationary.	After 80s sphere decelerated at $3^\circ/s^2$ to stop.
2 Subject-motion suprathreshold	Chair accelerated/decelerated at $3^\circ/s^2$ to 15° of tilt (in 4.5s). Sphere stationary and visible.	After 40s chair accelerated/decelerated in reverse to the vertical.
3 Subject-motion subthreshold	Chair accelerated/decelerated at $0.77^\circ/s^2$ to 15° of tilt (in 8.8s). Sphere stationary and visible.	After 40s chair accelerated/decelerated in reverse to the vertical.
4 Delayed-washout suprathreshold	Chair motion as in 2. Synchronous acceleration of sphere to constant velocity of $18^\circ/s$ (acceleration of sphere relative to chair was $3^\circ/s^2$).	Chair motion as in 2. Sphere motion relative to the chair kept constant at $18^\circ/s$ and maintained for a further 40s.
5 Delayed-washout subthreshold	Chair motion as in 3. Synchronous acceleration of sphere to constant velocity of $18^\circ/s$ (acceleration of sphere relative to chair was $3^\circ/s^2$).	Chair motion as in 3. Sphere motion relative to the chair kept constant at $18^\circ/s$ and maintained for a further 40s.
6 Immediate-washout	Chair motion as in 2. Synchronous acceleration of sphere to constant velocity of $18^\circ/s$ (acceleration of sphere relative to chair was $3^\circ/s^2$).	Immediately after onset phase, the chair accelerated/decelerated at $0.77^\circ/s^2$ back to the vertical. Sphere motion relative to the chair kept constant at $18^\circ/s$ and maintained for a further 40s.
7 Pre-tilt	Chair motion as in 2. After 20s the sphere accelerated at $3^\circ/s^2$ to constant velocity of $18^\circ/s$.	Sphere motion maintained for 40s and stopped. Subject remained tilted 15° for a further 30s.

Table 5.1. Acceleration profile of chair and sphere in onset-phase and washout-phase in the concordant motion conditions. Chair tilt was achieved by constant acceleration up to half the final tilt angle of 15° , followed by constant deceleration of equal magnitude.

The subject was accelerated and then decelerated to a tilt angle of 15° . This is designated the onset phase of the washout trial. In the onset phase the sphere accelerated in the opposite direction so that the acceleration of the sphere relative to the subject was always $3^\circ/\text{s}^2$. In the delayed-washout conditions, the body tilt of 15° was maintained for 40s while the sphere rotated at a constant velocity of $18^\circ/\text{s}$. This is the post-onset phase of the trial. After 40s the subject returned to the vertical with the same acceleration/deceleration sequence as in the onset phase. Simultaneously, the sphere was accelerated/decelerated to keep its velocity relative to the subject constant. This is the washout phase of a trial. After the subject came to a stop in the upright position, the sphere continued to rotate at $18^\circ/\text{s}$ for a further 40s. This is the post-washout phase of the trial. In the immediate-washout condition, the suprathreshold onset phase was immediately followed by a subthreshold washout phase, so that the subject was upright for the remaining 80s of sphere rotation at $18^\circ/\text{s}$. This condition most closely resembles washout sequences used in flight simulators. Finally, in the “pre-tilt” condition the subject was tilted to 15° about the roll axis with the sphere stationary. After 20s the sphere motion was initiated and maintained at $18^\circ/\text{s}$ for 40s and stopped while the subject remained tilted.

In the above washout conditions, the sphere and the subject rotated in opposite directions. This was designated “concordant motion”, because both motions produced sensations of self-motion in the same direction. We added two “discordant motion” conditions, in which the sphere and the body moved in the same direction. To keep the relative acceleration between the subject and the sphere comparable to that in the concordant conditions, the sphere accelerated faster than the chair, which created self-tilt in the opposite direction to the subject motion. In one discordant condition the body was tilted at subthreshold acceleration, and in the other at suprathreshold acceleration.

The velocity profiles of the subject and sphere for the concordant conditions are set out in Figure 5.1. The corresponding position profiles of the subject are shown in Figure 5.2. All conditions were performed with the light on. Each condition was run twice, once for clockwise and once for anti-clockwise motion of the sphere. The order of conditions was counterbalanced over subjects.

Responses

Subjects were asked to report verbally the magnitude of perceived body tilt and vection. The reports were taken 20 s after each acceleration-deceleration onset phase or restoration phase during the time of constant body posture and constant sphere rotation. It was assumed that the post-acceleration effects of the semicircular canals had faded after 20 s. The angle of self-tilt was expressed in degrees by all but two subjects, who preferred to use a scale based on half-hour

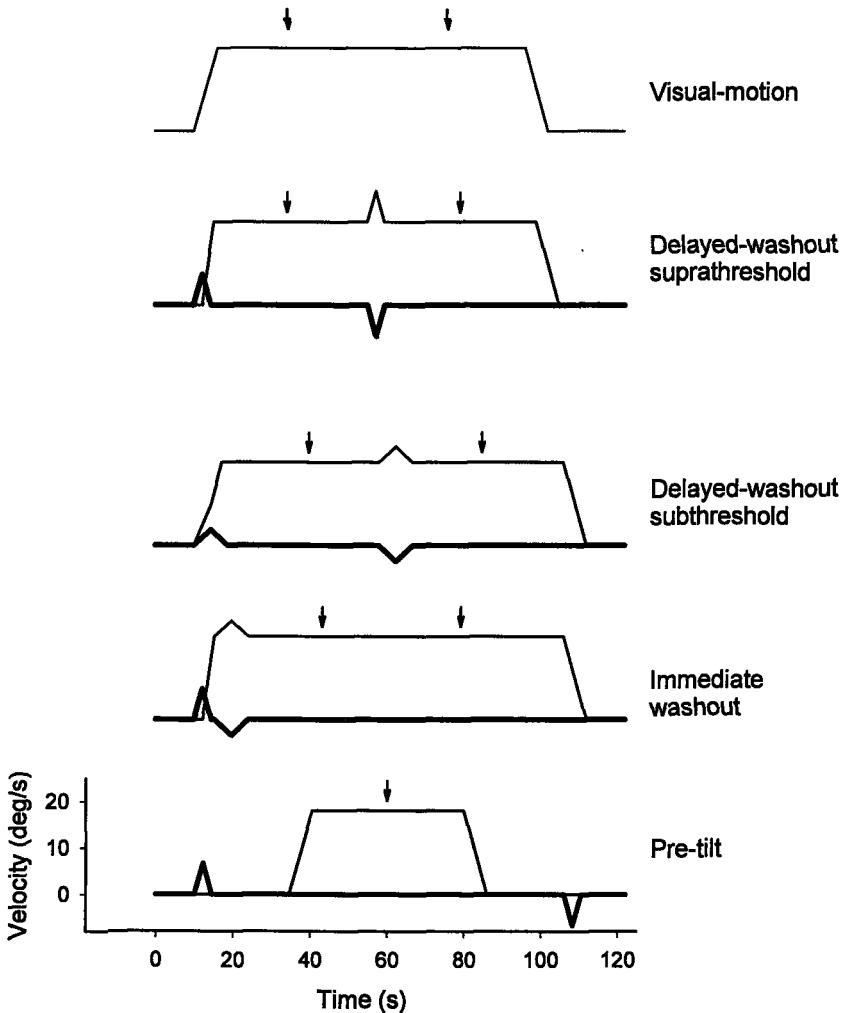


Figure 5.1. Velocity profiles of sphere (thin line) and chair (bold line) for concordant conditions. To indicate relative velocity, the same sign is used for sphere and chair velocity, although they rotated in opposite directions. The supra- and subthreshold subject-motion conditions are not shown, but the velocity profiles of the chair were the same as in the supra- and subthreshold delayed-washout conditions, respectively. The arrows indicate when the subject reported perceived self-tilt and vection. In all but the pre-tilt condition, there were two test phases.

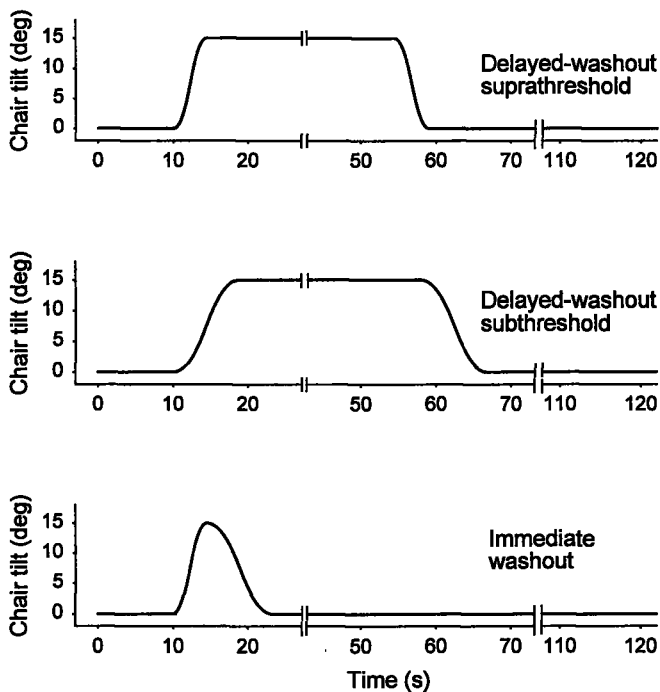


Figure 5.2. Position profiles of the chair. In the supra- and subthreshold conditions, the chair was tilted to 15° and kept in that position throughout the 40 s post-onset phase, before the upright position was restored. In the immediate-washout condition the chair was tilted at a suprathreshold acceleration, and immediately tilted back to upright at a subthreshold acceleration.

intervals of the hour hand of a clock. Vection was expressed by a five-point scale as shown in Table 5.2. Subjects were also asked to keep a tactile rod aligned with the perceived vertical. The rod was 20 cm long and placed to the side of the subject's right knee. The rod was not quite out of sight but subjects were asked not to pay visual attention to it. The first movement of the rod indicated the latency of illusory self-tilt at the beginning of each trial and the magnitude of rod tilt provided a measure of the perceived vertical which could be related to the verbal estimates.

<i>Vection value</i>	<i>Experience</i>
0	All motion in the sphere
1	Sphere moves faster than subject
2	Subject and sphere move at same velocity in opposite directions
3	Subject moves faster than sphere
4	All motion in subject

Table 5.2. The five-point vection scale

Results

Twelve subjects participated in the experiment, seven men and five women between ages of 24 and 60. One subject had to withdraw because of developing nausea. The data from another subject were excluded from the analysis because she experienced full self-rotation in all conditions, probably because she confused vection with illusory self-tilt. A third subject felt supine in about half of the conditions, and the perceived tilt data were entered as missing. Her vection and latency data were used.

Latency

The mean values and standard errors of the 10 subjects are shown in Figure 5.3 for the latency of perceived tilt, as indicated by settings of the tactile rod. The latency in the visual-motion condition was significantly longer than in the washout conditions (within subjects design ANOVA; $F=9.91$; $df=3,6$; $p<0.01$). A post-hoc Tukey test revealed a difference between the visual-motion condition and suprathreshold delayed-washout condition and between the visual-motion condition and the immediate-washout condition ($p<0.05$), but not between the visual-motion and the subthreshold delayed-washout condition. There was no difference in latency between the visual motion and the pre-tilt condition. The latency was longer in the subthreshold subject-motion and washout conditions than in the suprathreshold subject-motion and washout conditions ($F=47.13$; $df=1,4$; $p<0.01$). There was no difference between the suprathreshold delayed-washout condition and the immediate-washout condition.

There was no main effect of acceleration level of the subject on the angle of perceived self-tilt in the post-onset phase of both subject-motion and delayed-washout conditions. The magnitude of perceived self-tilt was greater in a tilted

body position than in an upright body position, according to a significant difference between the delayed-washout conditions and the visual-motion condition (tactile rod: $F=6.37$; $df=2,18$; $p<0.01$; verbal estimate: $F=7.22$; $df=2,18$; $p<0.01$). In the pre-tilt condition the angle of perceived tilt as indicated by the tactile rod (but not the verbal estimate) was significantly greater than in the visual-motion condition ($F=20.15$; $df=1,9$; $p<0.01$) and also greater than in the delayed-washout conditions ($F=4.47$; $df=2,18$; $p<0.05$). However, in neither the delayed-washout conditions nor in the pre-tilt condition, was perceived self-tilt greater than the sum of the visual-motion condition and the suprathreshold or subthreshold subject-motion condition, respectively. Perceived tilt in the immediate-washout condition was not different from that in the visual-motion condition, indicating that the effect of actual body tilt disappeared after washout.

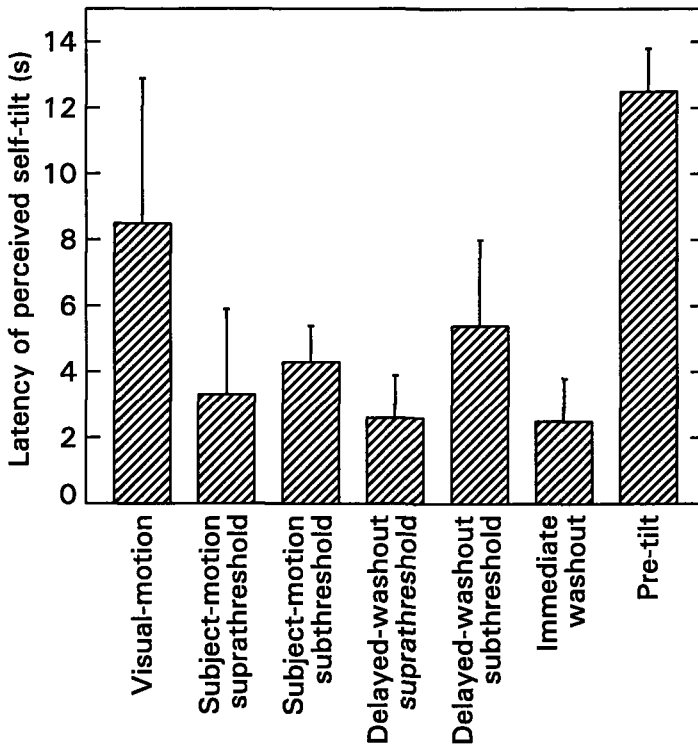


Figure 5.3. Mean latency of perceived self-tilt in the concordant-motion conditions. The bars indicate standard errors of the means ($n=10$).

Perceived self-tilt

The results for the magnitude of perceived self-tilt, as indicated by settings of the tactile rod and by the verbal estimate, are shown in Figs. 5.4a and b, respectively. Verbal estimates were consistently higher than estimates derived from settings of the tactile rod. For instance, in the post-onset phase of the subject-motion conditions the mean perceived tilt indicated by the settings of the tactile rod was 10.3°, while the verbal estimate amounted to 21.9° ($F=15.12$; $df=1,9$; $p<0.01$). In general, the two measures varied in a similar way with experimental conditions.

In both subject-motion conditions, restoration of the subject to vertical resulted in a significant decrease in perceived self-tilt to about zero (tactile rod: $F=17.44$; $df=1,9$; $p<0.01$; verbal: $F=27.96$; $df=1,9$; $p<0.001$). In the delayed-washout conditions, the perceived tilt was smaller in the post-washout phase than in the post-onset phase for both verbal ($F=20.0$; $df=1,8$; $p<0.01$) and tactile judgments ($F=6.14$; $df=1,9$; $p<0.05$), and was no longer different from the judgments in the visual-motion condition. There was no effect of acceleration level on the perceived tilt in the post-washout phase.

Magnitude of vection

The mean vection magnitudes are shown in Figure 5.5. In the post-onset phase there were no differences between the various conditions. On average, vection magnitude was about 2.5, indicating that the subjects experienced slightly more self motion than sphere motion. Washout seemed to reduce the vection magnitude: in the suprathreshold and subthreshold delayed-washout condition, the mean values before washout were 2.4 and 2.7, respectively, and became 1.8 and 1.9 after washout. This difference, however, did not reach significance.

Discordant conditions

Subjects were very confused in the discordant conditions. According to the verbal reports, the direction of perceived body tilt was initially determined by the tilting chair, but then quickly changed sign and became determined by the visual stimulus. But even during the constant velocity phase, subjects did not have much confidence in their judgments. They felt tilted to one side (visually induced) and pressure to the other side. As a consequence, the subjects indicated that they were guessing when they set the tactile rod to the vertical, and they often failed to move it. Therefore, only verbal estimates were analyzed.

The magnitude of estimated self-tilt in the post-onset phase varied around zero (1.9 ± 3.5 in suprathreshold condition; -2.4 ± 7.0 in subthreshold condition). This suggests that the visual stimulus roughly canceled the self-tilt induced by the body

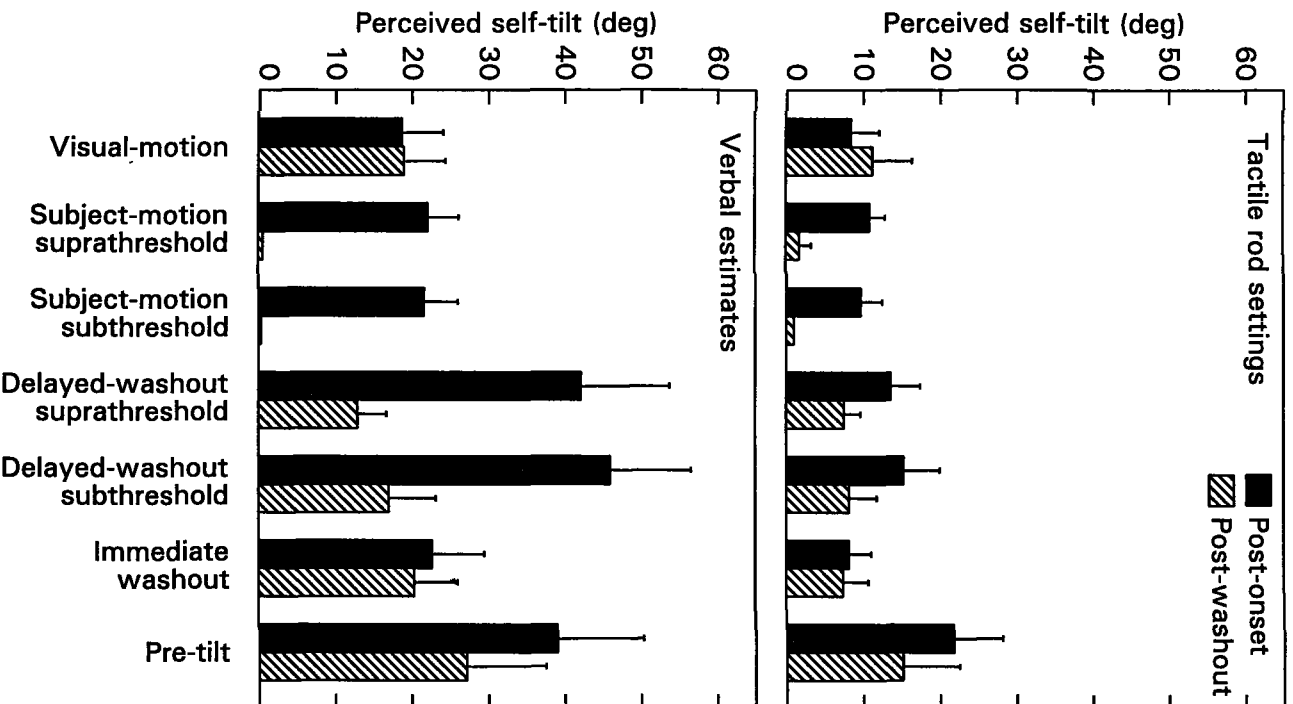


Figure 5.4. Mean angle of perceived self-tilt during the post-onset and post-washout phases in the concordant-motion conditions. Settings of the tactile rod (upper) and Verbal estimates of tilt (lower). Bars are standard errors of the means ($n=9$).

tilt, which is about 20° according to the verbal estimate in the subject-motion conditions. This value is similar to the experienced self-tilt in the visual-motion condition. Thus, as in the concordant washout conditions, the combination of body tilt and visual motion induced an effect no greater than the sum of effects produced by the corresponding visual-motion and the subject-motion conditions. After washout of the subject to the vertical, estimated self-tilt changed in the same direction and was no longer different from that in the visual-motion condition (9.7 ± 3.2 in suprathreshold condition; 19.1 ± 4.2 in subthreshold condition).

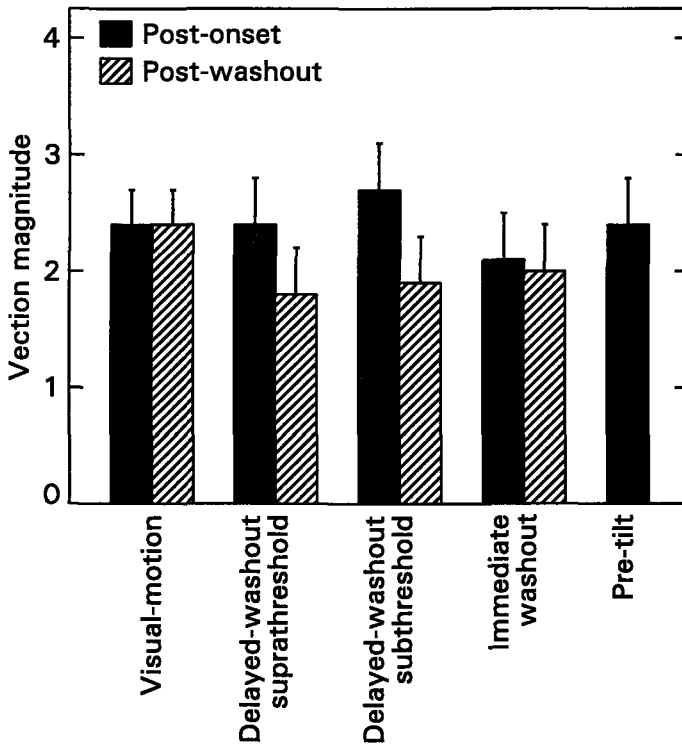


Figure 5.5. Mean vection magnitude in the post-onset and post-washout phases of the concordant-motion conditions. Vection was scored on a scale of zero to four. The bars are standard errors of the means ($n=10$).

There were no significant differences in vection magnitude between the concordant and discordant combined-motion conditions. In the post-onset phase the mean vection magnitude was 2.5 ± 0.3 in the discordant suprathreshold condition, and 2.3 ± 0.3 in the discordant subthreshold condition. After washout these values were 2.0 ± 0.3 and 2.35 ± 0.3 , respectively, which is not significantly different from the post-onset values.

Discussion

In this study we investigated whether passive body motion accompanying motion of a visual scene about the horizontal roll axis affects the latency and magnitude of sensations of self-tilt and self-motion (vection). The magnitude of perceived tilt was greater when visual motion was accompanied by concordant tilt of the subject than when there was only visual motion or only subject tilt. This is what one would expect from addition of the response to body tilt and that to visual motion. Because the magnitude of perceived tilt did not depend on the level of subject acceleration, we conclude that the increase in perceived tilt was merely due to the tilt component of the subject roll stimulus - and not to the rotation component. Sensations of self-motion, as opposed to self-tilt, were not much affected by whether visual motion was or was not accompanied by real self-motion or real self-tilt.

There seem to have been few studies on the additivity of visual and vestibular contributions to perceived self-tilt. It has been shown that the effects of a rotating or tilted display on sensations of vection and self-tilt are larger when the head is in a tilted position (Asch and Witkin 1948; Held *et al.* 1975; Bishof 1978; Young *et al.* 1975). This non-linearity is attributed to the sensitivity of the utricles being higher when the head is erect than when it is tilted. As a result otolith inputs would be less reliable when the head is tilted, resulting in a lower weighting of otolith inputs relative to visual inputs. We did not find that actual tilt facilitated visually-induced self-tilt. When corrected for the response to real body tilt, perceived tilt in the washout conditions was not different from that in the visual-motion condition. It is likely that the angle of 15° was too small to produce sufficient change in otolith sensitivity.

For rotation about the vertical yaw axis Zacharias and Young (1981) found that the threshold for detection of self-motion was reduced when visual motion was accompanied by real self-motion. With vertical yaw motion, however, semicircular canal inputs are involved but not otolith inputs. They proposed a model in which visual and vestibular inputs are combined with weightings which depend on whether visual inputs are consistent with vestibular inputs. Inconsistent vestibular inputs were assigned higher weightings than consistent vestibular

inputs. Our results showed signs of linear addition when visual and vestibular inputs were consistent. However, when the two inputs were in conflict, the results were so variable that the additive model could not be tested.

When the body was rotated along with the visual stimulus and then returned to vertical, perceived self-tilt in the erect observer was the same as it would have been if the body had not moved. Thus the effects of real self-tilt on the magnitude of sensations of self-tilt persist when the body remains in a tilted position but do not persist after the body has returned to the vertical. In the typical washout sequence in a motion-base flight simulator, the body is returned to the vertical at near threshold acceleration immediately after being accelerated with the visual scene, as in our immediate-washout condition. Under these conditions, washout produces only a momentary potentiation of sensations of self-tilt while the body is tilted, but the effect does not outlast the washout procedure. From these results we expect that when a motion base executes a series of washout movements in close succession, the magnitude of illusory self-tilt will be larger than that produced by visual motion alone.

The main effect of body roll was a reduction of the latency of detection of self-motion. The latency of tilt sensations was shorter when suprathreshold body motion and visual motion were combined compared with when the visual scene alone was rotated, and was similar to the latency of indicating real body motion alone. A reduction in latency in a flight simulator means that the subject will show less phase lag in his response to the simulated motion. Gundry (1977) distinguished between "maneuver motion" arising from the pilot's control of the aircraft, and "disturbance motion" arising from turbulence or aircraft failure. There has been conflicting evidence about whether motion bases in flight simulators improve pilot training, as reflected in transfer from simulator to actual flight. In general, performance has been found to improve under disturbance motion, but not under maneuver motion. When performance improved, pilot reactions were more rapid and accurate with motion-based training than without motion-based training (Caro 1979). In addition, learning time and error rate of a visual tracking task improved when visual motion was accompanied by concordant body motion. Since disturbance motion is imposed on the subject without warning, responses should have longer latency than those to maneuver motion. In maneuver motion, subjects can anticipate the motion of the aircraft and, under these circumstances, latency will be short without a motion base. Also, with disturbance motion, reaction time should be longer in the absence of real self motion than in the presence of real self motion.

We used body roll as the vestibular onset cue for self-tilt. This paradigm is not appropriate to simulate the vestibular stimulation arising from banked turns. A banked turn of a real aircraft generates a centrifugal force in excess of 1g to which the pilot's body and the otolith organs remain aligned (Gilson *et al.* 1973). In real

tilt of a motion base the otolith organs are displaced relative to gravity and there is no g-excess. Similar differences between real flight and motion-base simulation exist in pitch maneuvers (Cramer and Wolfe 1970). Differences of this type probably account for why the pilot's ratings of fidelity of motion sensations in a flight simulator were not related to large changes in the motion of a motion base (Bussolari *et al.* 1987).

The visual display used in the present study was lined with dots which gave no indication of "up" and "down" (visual polarity). Visual motion alone of a whole-field stimulus does not completely override the contradictory information from the otolith organs in an erect observer, resulting in combined sensations of continuous vection and limited self-tilt (Howard *et al.* 1988). To override the otolith inputs completely, one needs a visual stimulus containing clear horizontal and vertical lines (visual frame) and features with a top and bottom, such as chairs and tables. Howard and Childerson (1994) showed that more than 60% of erect observers reported sensations of head-over-heels rotation (360° of self-tilt) when placed inside an 7-foot cubic furnished room with abundant visual polarity cues, rotating about the line of sight. However, when exposed to static tilt of the furnished room up to 120°, the mean perceived self-tilt was at most 15°. The larger effects produced by the moving room are presumably due to the combined effects of motion, the visual frame and visually polarized objects. It therefore seems that the most effective visual stimulus to induce apparent self-tilt in an upright observer is a moving polarized scene. We conclude that apparent self-tilt can be enhanced by a typical washout sequence of real body tilt, but only during the actual tilt. More importantly, the latency of perceived self-tilt is greatly reduced when visual motion is accompanied by suprathreshold body rotation. We found no effects of actual body tilt on sensations of self-rotation.

Acknowledgments

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Summary

Chapter 1

In this chapter a new and automatic method was described to determine ocular torsion (OT) from digitized video images (Video-oculography). We developed this method based on the tracking of iris patterns. Instead of quantifying OT by means of cross-correlation of circular iris samples, which is commonly applied, this new method automatically selects and recovers a set of 36 significant patterns in the iris by a technique of template matching. Each relocated landmark results in a single estimate of the torsion angle. A robust algorithm estimates OT from this total set of individually determined torsion angles, thereby largely correcting for errors which may arise as due to misjudgments of the rotation center. In a prepared set of images of an artificial eye the new method reproduced OT with an accuracy of 0.1° . In a sample of 256 images of human eyes, a practical reliability of 0.25° was achieved.

Chapter 2

The objective of this experiment was to assess evidence for vestibular adaptation to prolonged hypergravity in human subjects as to substantiate previously described effects, such as postural imbalance and motion sickness (Sickness Induced by Centrifugation, SIC). We measured the ocular torsion response in eleven subjects during static and dynamic body tilt, once before and once after an one-hour centrifuge run of $+3G_x$. The OT response to static tilt (in the range of 0 to 57° to either side) showed a 10% decrease, suggesting a reduced otolith gain. The otolith-canal interaction was examined by comparing the dynamic OT response to sinusoidal body roll (frequency of 0.25 Hz and amplitude of 25°) about an earth-horizontal rotation axis (stimulation of both otoliths and canals) and about an earth-vertical rotation axis (stimulation of canals). After centrifugation, the gain of the slow component velocity increased in both conditions in all but four subjects, who showed a decrease in the supine condition (but not in the upright condition). These four subjects developed symptoms of SIC, so that the different behavior of their SCV gain was likely due to a declined state of alertness which specifically may have occurred in the supine condition. In addition to the OT data, the horizontal VOR was measured in response to a velocity step rotation about the vertical yaw axis. The mean gain of the horizontal VOR was unaffected by centrifugation, but the dominant time constant was significantly reduced. Because

the time constant of the horizontal VOR is centrally controlled by the velocity storage mechanism, this result provides evidence for vestibular adaptation at a central level.

Chapter 3

In the experiment of Chapter 2 the dynamic OT response (or torsional VOR) was measured to study possible effects of centrifugation on the canal-otolith interaction. However, the response did not show a clear otolith contribution. Supposedly, the stimulus frequency of 0.25 Hz had been too high to reveal an otolith component. The response was therefore studied in more detail at a wider frequency range. The ocular torsion response was examined during passive sinusoidal body roll in five human subjects. To separate the otolith organ and semicircular canal contributions, again the axis of rotation was varied between earth-horizontal and earth-vertical. At a fixed amplitude of 25° , the stimulus frequency was varied from 0.05 to 0.4 Hz. Additionally, at a fixed frequency of 0.2 Hz, the response was also measured at the amplitudes of 12.5° and 50° . The results showed that the gain and phase of the slow component velocity (SCV) did not depend on stimulus amplitude, indicating a linear response. Contribution of the otoliths affected the ocular torsion response in three different ways. First, the gain of the SCV was slightly but consistently higher during earth-horizontal rotation than during earth-vertical rotation. In the supine orientation the average gain increased from 0.10 to 0.26. In the upright orientation the average gain increased from 0.14 to 0.37. Second and more substantially, modulation of the otolith inputs improved the response dynamics by reducing the phase lead at frequencies up to 0.2 Hz. Third, the nystagmus showed considerably less anti-compensatory saccades in upright conditions than in supine conditions, even though the SCV gain was lower in the latter. As a consequence, the average excursion of torsional eye position was highest during earth-horizontal rotation. This effect was observed in the entire frequency range. Thus, the otoliths did not only control the torsional VOR at low stimulus frequencies by keeping the slow component in phase with head motion, but also in a wider frequency range by modulating the saccadic behavior as to increase the excursion range of torsional eye position. We conclude that, during head tilt, the primary concern of the otolith-oculomotor system is to stabilize eye position in space, rather than to prevent retinal blur. This confirms that tilt otolith-induced ocular responses subserves spatial orientation.

Chapter 4

This chapter describes a study on the effectiveness of a highly polarized visual environment to induce sensations of self-motion and self-tilt in a stationary observer. The subject were immersed in an 8 foot cubic room which could be fully rotated about an earth-horizontal axis. The interior of the room was filled with common visual features such as a door, a window, and a great variety of objects which indicated up and down (visual polarity). When the room was tilted about the roll axis of an erect observer it produced illusory self-tilt by virtue of its visual polarity alone. Although the effect was larger than is known from the literature, the experienced self-tilt did not linearly increase with room tilt. At higher angles of room tilt (80 and 120°) the judgment of verticality became more variable and depended less on the visual scene. The room induced complete self-rotation in more than 80% of the cases when it was rotated at constant velocity about a stationary subject in various body positions. This strong effect was attributed to both its motion and its visual polarity.

Chapter 5

This chapter describes a study on the visual-vestibular interaction in the judgment of the body orientation relative to gravity. Illusory self-tilt and self-motion (vection) produced by rotation of a full-field non-polarized visual scene about the subject's roll axis was measured as a function of the presence or absence of actual rotation of the subject during visual acceleration. Subject rotation was at two levels of acceleration and with or without a delay between initial rotation and subsequent return (washout) to the vertical position. In one set of conditions, visual motion and self-motion were in opposite directions (concordant) and in another set they were in the same direction (discordant). For concordant motion the main effect of body rotation was to reduce the time taken by the subject to indicate self-rotation. The magnitude of self-tilt was increased by actual body tilt as could be expected from addition of the perceived actual body tilt and illusory body tilt induced by visual rotation. This effect of augmented body tilt did not persist after the body was returned to the vertical. The magnitude of vection was not influenced by body rotation and washout. For discordant motion of the body and the visual scene, subjects were confused and their responses were very variable. This suggests a non-linear visual-vestibular interaction, in which perceived self-tilt and self-motion are strongly determined by visual inputs, except for discordant accelerations of the body and the visual surroundings. Then the perception is determined by the vestibular inputs.

Concluding remarks

In our daily lives, the omnipresent force of gravity helps the perceptual system to integrate egocentric information arising in the eyes, head, and body into an exocentric frame of reference. With the otolith organs in our inner ear, we possess a sensory system that is specialized to detect gravity and thus to register the orientation of our head in space. Still, the otolith organs do not have the exclusive rights to graviceptive information. The visual and somatosensory system also provide important “down” cues. In normal situations, these sensory systems cooperate as silent partners, making it difficult to determine to what extent each of them is responsible for our sense of orientation. In this thesis I examined the contribution of the otolith system and the visual system to oculomotor and perceptual behavior in two situations where these systems provide discordant information.

First, in the centrifuge experiment described in Chapter 2, the approach was to specifically modify the contribution of the otolith system by exposing subjects to prolonged hypergravity. It was assumed that the vestibular system - the otolith organs in particular - would adapt to this higher G-environment. Accordingly, the otolith system would be “maladapted” to normal gravity for some duration afterwards, thus providing incorrect information about the direction and magnitude of gravity. This view was based on previous observations that centrifugation causes postural imbalance and perceptual changes which may result in motion sickness, similar to the symptoms of the space adaptation syndrome seen during the first days of spaceflight. In the centrifuge experiment presented here, the emphasis was on changes in the otolith-induced ocular torsion response in the need of a quantification of vestibular adaptation. Eye movements were recorded on video tape, and before I was able to “digest” the increasing pile of ocular torsion data in a reliable way, a new automatic method for video-oculography had to be developed first (Chapter 1). Typically, the amplitude of ocular torsion is rather small in man. Hence, using this response in an attempt to relate the perceptual consequences of centrifugation to vestibular adaptation felt like looking for a needle in a hay stack, while in search of the hay stack itself. Nevertheless, the measurements before and after the centrifuge run yielded consistent evidence for otolith adaptation. Additional VOR measurements indicated that this adaptation affected the canal-otolith interaction. Unfortunately I did not observe a direct relationship between oculomotor and perceptual variables. This presumably stems from the fact that the VOR was recorded during passive vestibular testing, while

the perceptual consequences were most outspoken during self-generated movements.

The second situation of discordant graviceptive information was created by rotating the visual surroundings of a stationary observer about an earth-horizontal axis (Chapter 4). Static tilt of the visual stimulus resulted in a limited degree of illusory self-tilt, even though the subjects were actually immersed in a tilted environment which was detailed with a rich variety of familiar and polarizing objects. In the case of continuous rotation of the same visual stimulus, however, subjects reported compelling sensations of head-over-heels rotation, irrespective of their actual body orientation. Thus, to completely override the restraining otolith inputs one needs a *rotating* polarized scene, i.e. a combination of visual motion and visual polarity information. In the rotating non-polarized sphere of Chapter 5, it was shown that sensations of self-tilt are temporarily enhanced by real body tilt. These effects do not persist after washout in which the body is returned to vertical.

The former two situations were basically concerned with *intersensory* processes. Chapter 3, on the other hand, dealt with *intrasensory* interaction within the vestibular system itself. It focused on the relative contribution of the semicircular canals and the otolith organs to the torsional VOR during sinusoidal body roll. Here I learned that there is something peculiar about the torsional component of eye movements. Several workers in the field of eye movements have spent the last century or so to prove that during voluntary saccades the eyes only assume positions which involve no torsion. This restriction is generally known as Listing's law. All situations which elicit ocular torsion have consequently been labeled as violations of this law. That is bad news for someone who spent more than a year developing a technique to measure ocular torsion! But the case may not be lost yet. It has been argued that the low gain of the torsional VOR in man reflects a conflicting situation for the oculomotor system. On one hand the vestibular system demands to generate a collinear VOR (even if this involves torsion), while on the other hand some "Listing's operator" demands to avoid torsion. The validity of Listing's law has essentially been tested during static conditions. The results of Chapter 3 indicate that we should consider the possibility that, during head movements, Listing's coordinates are dynamically modulated by the otolith system. The otolith-induced component to the response consisted of a modulation of torsional eye *position*, compensating for head position, while the canal-induced component was clearly charged with the compensation for head *velocity*. This finding reflects an important functional difference between both vestibular subsystems: the semicircular canals operate in head-centric coordinates, whereas the otolith organs provide a link to exocentric coordinates by registering the orientation of the head relative to gravity. In

conclusion, the semicircular canals can be considered as velocity detectors, whereas the otolith organs can be described to be primarily position detectors.

To me, the most remarkable finding is that *both* the oculomotor *and* the perceptual responses showed this position-velocity dichotomy. For instance, in the torsional VOR this was visible as the modulation of the beating field (position), superimposed on the slow component (velocity). Similarly, in the rotating sphere, subjects simultaneously experienced a limited degree of self-tilt (position) and a sensation of continuous self-motion (velocity). I believe that the effects observed after centrifugation, or during spaceflight for that matter, can be attributed to the otolith organs providing different position signals than would be anticipated based on previous experience in the normal 1G environment. In this sense, the situations of hypergravity and hypogravity are not essentially different. Until adaptation to the new situation has taken place, which may last from several hours to several days, both sensorimotor and perceptual responses will be inappropriate. It is, however, important to note that adaptation in hypergravity may be accomplished in a different way than adaptation in weightlessness. In hypergravity, there is still a gravitational “down” - which is even stronger than normal - to allow for (intrasensory) adaptation of the otolith system itself. For example, this can be done by reducing the sensitivity, as is suggested by the results of the centrifuge experiment in this thesis. In weightlessness, on the contrary, there is no gravitational “down”, and position signals from the otolith organs are completely missing. Here, (intersensory) adaptation may take place by replacing the otolith signals by other sensory signals, for instance from the visual system. No matter how adaptation is achieved, the result will be that the subject is able to function optimally in the new environment. The sensory systems have become silent partners again.

Bibliography

- Albery WB, Martin ET (1994) Development of space motion sickness in a ground-based human centrifuge for human factors research. *45th Congress of the International Astronautical Federation, Jerusalem*; October 9-14, 1994.
- Angelaki D, Hess B (1996a) Three-dimensional organization of otolith-ocular reflexes in rhesus monkeys. II. Inertial detection of angular velocity. *J Neurophysiol* 75(6):2425-2440.
- Angelaki D, Hess B (1996b) Three-dimensional organization of otolith-ocular reflexes in rhesus monkeys. I. Linear acceleration responses during off-vertical axis rotation. *J Neurophysiol* 75(6):2405-2424.
- Arrot AP, Young LR (1986) M.I.T./Canadian vestibular experiments on the Spacelab-1 mission. 4. Vestibular reactions to lateral acceleration following ten days of weightlessness. *Exp Brain Res* 64:347-357.
- Asch SE, Witkin HA (1948a). Studies in space orientation. I. Perception of the upright with displaced visual fields. *J Exp Psychol* 38:325-337.
- Asch SE, Witkin HA (1948b). Studies in space orientation. II. Perception of the upright with displaced visual fields and with body tilted. *J Exp Psychol* 38:455-477.
- Bahil AT, Clark MR, Stark L (1975) The main sequence, a tool for studying human eye movements. *Math Biosci* 24:191-204.
- Barmack NH (1981) A comparison of the horizontal and vertical vestibulo-ocular reflexes of the rabbit. *J Physiol* 314:547-564.
- Baumgarten RJ, Thümler R (1987) A model for vestibular function in altered gravitational states. *Life Sci Space Res* 17:161-170.
- Belcher SJ (1964) Ocular torsion. *Brit J Physiol Optics* 21:1-20.
- Benson AJ, Bodin MA (1966) Effect of orientation to the gravitational vertical on nystagmus following rotation about a horizontal axis. *Acta Oto-Laryngol (Stockh)* 61:517-526.
- Benson AJ (1970) Interactions between semicircular canals and graviceptors. In: Busby DE, ed. *Recent Advances in Aerospace Medicine*; 249-261.
- Bishop N. (1975) Optic-vestibular orientation to the vertical. In: HH Kornhuber, ed. *Handbook of Sensory Physiology. Vol. 6. Vestibular system part 2*. Berlin: Springer-Verlag:155-190.
- Bles W, Bos JE, Furrer R, De Graaf B, Hosman RJA, Kortschot HW, Krol JR, Kuipers A, Marcus JT, Messerschmid E, Ockels WJ, Oosterveld WJ, Smit J, Wertheim AH, Wientjes CJE (1989) Space Adaptation Syndrome induced by

-
- a long duration +3Gx centrifuge run. *Report TNO/IZF 1989-25*; TNO Factors Research Institute, Soesterberg, The Netherlands.
- Bles W, De Graaf B (1993) Postural consequences of long duration centrifugation. *J Vestibular Res* 3(1):87-95.
- Bles W, De Graaf B, Krol JR (1995) Space Adaptation Syndrome and Sickness Induced by Centrifugation: Vestibular consequences of earth anomalous gravity. *Report TNO-TM 1995 B-12*, TNO Factors Research Institute, Soesterberg, The Netherlands.
- Bles W, De Graaf B, Bos JE, Groen E, Krol JR (1997) A sustained hyper-G load as a tool to simulate space sickness. *J Gravitational Physiol* (in press).
- Bos JE, De Graaf B (1994) Ocular torsion quantification with video images. *IEEE Trans Biomed Eng* 41:351-357.
- Bos JE, De Graaf B (1997) VOR parametrisering: Oogbewegingsanalyse bij draai-stopproeven rond een aard-horizontale en een aard-verticale as in "yaw", "pitch" en "roll". *Rapport TNO-TM-97-A019*.
- Brandt T, Dichgans J, Büchele W (1974) Motion habituation: Inverted self-motion perception and optokinetic after-nystagmus. *Exp Brain Res* 21:337-352.
- Bucher UJ, Heitger F, Mast F, Bischof N (1990) A novel automatic procedure for measuring ocular counterrolling: A computeranalytical method to determine the eye's roll angle while the subjects work on perceptual tasks. *Beh Res Meth Instrum Comput* 22:433-439.
- Bucher UJ, Mast F, Bischof N (1992) An analysis of ocular counterrolling in response to body positions in three dimensional space. *J Vestibular Res* 2:213-220.
- Bussolari RR, Young LR, Lee AT (1987) The use of vestibular models for design and evaluation of flight simulator induced sickness. *AGARD Proceedings*:433.
- Caro PW (1979) The relationship between flight simulator motion and training requirements. *Human Factors* 21:493-501.
- Carpenter RHS (1988) *Movements of the eyes*. London: Pion.
- Chaudhuri BB, Kundu P (1993) Optimum circular fit to weighted data in multidimensional space. *Pattern Recognition Letters* 14: 1-6.
- Cheung BSK, Howard IP, Money KE (1990) Visually-induced tilt during parabolic flights. *Exp Brain Res* 81:391-397.
- Cheung BSK, Money K, Howard I, Kirenko N, Johnson W, Lackner J, Dizio P, Evanoff J (1992) Human ocular torsion during parabolic flights: an analysis with scleral coil. *Exp Brain Res* 90:180-188.
- Clarke AH, Teiwes W, Scherer H (1989) Video-oculography: An alternative method for measurement of three dimensional eye movements. In: *5th European Conf. on Eye Movements*, R. Schmidt and D. Zambambieri, Eds., 1989.

- Clarke AH, Teiwes W, Scherer H (1993) Vestibulo-oculomotor testing during the course of a spaceflight mission. *Clin Invest* 10:740-748.
- Colenbrander A (1963) The influence of G-forces on the counterrolling of the eye. *Ophthalmologica* 146:309-313.
- Collewijn H, van der Steen J, Ferman L, Jansen TC (1985) Human ocular counterroll: assessment of static and dynamic properties from electromagnetic scleral coil recordings. *Exp Brain Res* 59:185-196.
- Cramer RL, Wolfe JW (1970) Effects of pitch and coriolis illusions upon adjustment of pitch angle. *Aerospace Med* 41:644-646.
- Crawford JD, Vilis T (1991) Axis of eye rotation and Listing's law during rotations of the head. *J Neurophysiol* 65:407-423.
- Dai M, Raphan T, Cohen B (1991) Spatial orientation of the vestibular system: dependence of optokinetic after nystagmus (OKAN) on gravity. *J Neurophysiol.* 66:1422-1439.
- Dai M, McGarvie L, Kozlovskaya I, Raphan T, Cohen B (1994) Effects of spaceflight on ocular counterrolling and the spatial orientation of the vestibular system. *Exp Brain Res* 102:45-56.
- De Graaf B, Bekkering H, Erasmus C, Bles W (1992) Influence of visual, vestibular, cervical, and somatosensory tilt information on ocular rotation and perception of the horizontal. *J Vestibular Res* 2:15-30.
- De Graaf B, Bos JE, Groen E (1996b) Saccular impact on ocular torsion. *Brain Res Bulletin* 40(5/6):321-330.
- De Graaf B, De Roo AJ (1996) Effects of long duration centrifugation on head movements and a psychomotor task. *J Vestibular Res* 6(1):23-29.
- De Graaf B, Bos JE, Bles W, Groen E (in press) Sensory conflict, perceptual weighting and motion sickness. *Brain Res Bulletin*.
- Diamond SG, Markham CH (1981) Binocular counterrolling in humans with unilateral labyrinthectomy and in normal controls. *Annals of New York Academy of Sciences* 374: 69-79.
- Diamond SG, Markham CH (1983) Ocular counter-rolling as an indicator of vestibular otolith function. *Neurology* 3:1460-1469.
- Diamond SG, Markham CH (1991) Prediction of space motion sickness susceptibility by disconjugate eye torsion in parabolic flight. *Aviat Space Environ Med* 62(3):201-205.
- Dichgans J, Held R, Young LR, Brandt T (1972) Moving visual scenes influence the apparent direction of gravity. *Science* 178:1217-1219.
- Dichgans J, Brandt T, Held R (1975) The role of vision in gravitational orientation. In: *Mechanisms of spatial perception and orientation as related to gravity*. Schöne H (ed). Fortschr. Zool. 23: 255-263.
- Dichgans J, Brandt T (1978) Visual-vestibular interaction: Effects on self motion, perception and postural control. In: R Held, H W Leibowitz, H-L Teuber,

-
- eds. *Handbook of Sensory Physiology. Vol. 8 Perception*. New York: Springer:755-804
- Dieterich M, Brandt T (1993) Ocular torsion and tilt of subjective visual vertical are sensitive brainstem signs. *Ann Neurol* 33:292-299.
- Faes TJC, Govaerts HG, Tenvoorde BJ, Rompelman O (1994) Frequency synthesis of digital filters based on repeatedly applied unweighed moving average operations. *Med Biol Eng Comp* 32: 698-701.
- Ferman L, Collewijn H, Jansen TC, Van den Berg AV (1987) Human gaze stability in the horizontal, vertical and torsional direction during voluntary head movements, evaluated with a three dimensional scleral induction coil technique. *Vision Res* 27:811-828.
- Férendez C, Goldberg JM (1971) Physiology of peripheral neurons innervating semicircular canals of the squirrel monkey. II. Response to sinusoidal stimulation and dynamics of peripheral vestibular system. *J Neurophysiol* 34:661-675.
- Fischer MH, Kornmüller AE (1930) Optokinetisch ausgelöste Bewegungswahrnehmungen und optokinetischer Nystagmus. *J für Psychologie und Neurologie (Leipzig)* 41:273-308.
- Gilson RD, Guedry FE, Hixon WC, Niven JI (1973) Observations on perceived changes in aircraft attitude and attending head movements made in a 2g bank and turn. *Aerospace Medicine* 44:90-93.
- Graybiel A, Woellner RC (1959) A new and objective method for measuring ocular torsion. *Am J Ophthalmol.* 47:349-352.
- Gresty MA, Bronstein AM (1992) Testing otolith function. *Brit J Audiol* 26:125-136.
- Groen E, Bos JE, Nacken PJM, de Graaf B (1996a) Determination of ocular torsion by means of automatic pattern recognition. *IEEE Trans Biomed Eng* 43:471-479.
- Groen E, Graaf de B, Bles W (1996b) Ocular torsion before and after 1 hour 3G centrifugation. *Brain Res Bulletin* 40 (5/6); 331-335
- Guedry F (1965) Orientation of the rotation axis relative to gravity: Its influence on nystagmus and the sensation of rotation. *Acta Otolaryng (Stockh)* 60:30-48.
- Gundry AJ (1977) Thresholds for roll motion in a flight simulator. *J Aircraft* 14:624-630.
- Gundry AJ (1978) Experiments on the detection of roll motion. *Aviat Space and Environ Med* 49:657-664.
- Hannen RA, Kabrinsky M, Replogle CR, Hartzler VL, Roccaforte PA (1966) Experimental determination of portion of the human vestibular response through measurement of eyeball counterroll. *IEEE Trans Biomed Eng* 13:65-70.

- Haslwanter T, Straumann D, Hess BJM, Henn V (1992) Static roll and pitch in the monkey: shift and rotation of Listing's plane. *Vision Res* 32:1341-1348.
- Hatamian M, Anderson DJ (1983) Design considerations for a real-time ocular counterroll instrument. *IEEE Trans Biomed Eng* BME-30:278-288.
- Held R, Dichgans J, Bauer J (1975) Characteristics of moving visual areas influencing spatial orientation. *Science* 141:722-723.
- Hogg RV (1979) An introduction to robust estimation. Eds: Launer RL and Wilkinson GN. *Robustness in Statistics*: 1-17.
- Homick JL, Reschke MF, Vandenploeg JM (1984) Space Adaptation Syndrome: Incidence and operational implications for the Space Transportation System Program. In: *Motion Sickness: Mechanisms, prediction, prevention and treatment. Agardograph* 372 (36):1-6.
- Howard IP (1982) Human Visual Orientation. John Wiley, ed. Chichester Sussex.
- Howard IP, Cheung BSK, Landoldt J (1988) Influence ofvection axis and body posture on visually-induced self rotation. *Advisory Group for Aerospace Research and Development* 433:15-1 to 15-8.
- Howard IP, Childerson L (1994) The contribution of motion, the visual frame and visual polarity to sensations of body tilt. *Perception* 23:753-762.
- In den Haak MD, Spoelder HJW, Groen FCA (1992) Matching of images by using automatically selected regions of interest. Eds: Dietz JLG. *Computing Science in the Netherlands*: 27-40.
- Junker AM, Replogle CR (1975) Motion effects on the human operator in a roll axis tracking task. *Aviat Space Environ Med* 46:819-822.
- Krol JR (1994) Cardiovascular measurements during long duration +Gx load. *Memo no. 1994-M-4*, Netherlands Aerospace Medical Centre, Soesterberg.
- Lebedev S, Van Gelder P, Tsui WH (1996) Square-root relations between main saccadic parameters. *Invest Ophthalmol Vis Sci* 37:2750-2758.
- Lichtenberg BK, Young LR, Arrot AP (1982) Human ocular counterrolling induced by varying linear accelerations. *Exp Brain Res* 48:127-136.
- Melville Jones G (1962) Ocular nystagmus recorded simultaneously in three orthogonal planes. *Acta Otolaryngol* 56.
- Merfeld D, Teiwes W, Clarke AH, Scherer H, Young LR (1996) The dynamic contributions of the otolith organs to human ocular torsion. *Exp Brain Res* 110:315-321.
- Miller II, EF (1962) Counterrolling of the human eyes produced by head tilt with respect to gravity. *Acta Otolaryngol* 54:479-501.
- Miller II EF, Graybiel A (1971) Effect of gravito-inertial force on ocular counterrolling. *J. Applied Physiol* 31:697-700.
- Money KE (1991) Space sickness. In: *Motion sickness: Significance in aerospace operations and prophylaxis. AGARD LS175*: 6.A1-6.A5.

-
- Ockels WJ, Furrer R, Messerschmid E (1990) Space sickness on earth. *Exp Brain Res* 79:661-663.
- Oman CM, Lichtenberg BK, Money KE, McCoy RK (1986) M.I.T./Canadian vestibular experiments on the Spacelab-1 mission: 4. Space motion sickness: symptoms, stimuli, and predictability. *Exp Brain Res* 64(2):316-334.
- Paige GD, Tomko DL (1991a) Eye movement responses to linear head motion in the squirrel monkey. I. Basic characteristics. *J Neurophysiol* 65(5):1170-1182.
- Paige GD, Tomko DL (1991b) Eye movement responses to linear head motion in the squirrel monkey. II. Visual-vestibular interactions and kinematic considerations. *J Neurophysiol* 65(5):1183-1196.
- Parker DE, Reschke MF, Arrott AP, Homick JL, Lichtenberg BK (1985) Otolith tilt translation reinterpretation following prolonged weightlessness: implications for preflight training. *Aviat Space Environ Med* 56:601-607.
- Raphan T, Matsuo V, Cohen B (1979) Velocity storage in the vestibulo-ocular reflex arc (VOR). *Exp Brain Res* 35:229-248.
- Robinson DA (1963) A method of measuring eye movement using a scleral search coil in a magnetic field. *IEEE Trans Biomed Eng* 10:137-145.
- Robinson DA (1971) In: Bach-y-Ritas P, Collins CC, Hyde JE, eds. *The Control of Eye Movements*. New York: Academic Press; 519-538.
- Schöne H (1964) On the role of gravity in human spatial orientation. *Aerospace Med* 35:764-772.
- Schöne H (1984) *Spatial Orientation*. Princeton NJ: Princeton University Press.
- Sedgewick R (1984) *Algorithms* Reading Addison-Wesley. Eds: Harrison MA and DeWolfe JT. Chapter 30: 389-406.
- Seidman SH, Leigh RJ (1989) The human torsional vestibulo-ocular reflex during rotation about an earth-vertical axis. *Brain Res* 504:264-268.
- Seidman SH, Leigh RJ, Tomsak RL, Grant MP, Dell'Osso LF (1995) Dynamic properties of the human vestibulo-ocular reflex during head rotations in roll. *Vision Res* 35 (5):679-689.
- Tweed D, Cadera W, Vilis T (1990) Computing three-dimensional eye position quaternions and eye velocity from scleral coil signals. *Vision Res* 30: 97-110.
- Tweed D, Sievering D, Misslisch H, Fetter M, Zee D, Koenig E (1994a) Rotational kinematics of the human vestibuloocular reflex I. Gain matrices. *J Neurophys* 72(5):2467-2479.
- Tweed D, Fetter M, Sievering D, Misslisch H, Koenig E (1994b) Rotational kinematics of the human vestibuloocular reflex II. Velocity steps. *J Neurophysiol* 72(5):2480-2489.
- Vieville T, Masse D (1987) Ocular counter-rolling during active head tilt in humans. *Acta Otolaryng (Stockh)* 103:280-290.

- Vilis T (1993) Interactions between the angular and translational components of vestibulo-ocular reflex. In: Sharpe JA and Barber HU, eds. *The vestibulo-ocular reflex and vertigo*. New York: Raven Press
- Woellner RC, Graybiel A (1959) Counterrolling of the eyes and its dependence on the magnitude of gravitational or inertial force acting laterally on the body. *J Appl Physiol* 14:632-634.
- Wood RW (1895) The haunted swing illusion. *Psychol Review* 2:277-278.
- Young LR, Oman CM, Dichgans JM (1975) Influence of head orientation on visually induced pitch and roll sensation. *Aviat Space Environ Med* 46:264-269.
- Zacharias GL, Young LR (1981) Influence of combined visual and vestibular cues on human perception and control of horizontal rotation. *Exp Brain Res* 41:159-171.

**IK HEB NIKS
TEGEN
CENTRIFUGEREN
ALLEEN KRIJG JE ER
ZO'N DROGE BEK
VAN**

Loesje

Samenvatting

Zwaartekracht is een van de meest constante kenmerken in onze dagelijkse fysieke omgeving, zowel qua grootte (1G) als qua richting (verticaal). Door de aanwezigheid van zwaartekracht kunnen we “onder” en “boven” in onze omgeving onderscheiden. Een adequaat gevoel van oriëntatie op de zwaartekracht is van belang voor onder andere een goed houdingsevenwicht. Onze ruimtelijke oriëntatie ontstaat door de integratie van zintuiginformatie over de stand van de lichaamsdelen onderling, en over de stand van het lichaam in de omgeving. Deze informatie is afkomstig van verschillende zintuigsystemen. Bijvoorbeeld, de proprioceptoren in de nek signaleren de stand van het hoofd op de romp, maar niet de stand van het hoofd in de ruimte. Voor dat laatste zijn we aangewezen op de otolietorganen (kortweg “otolieten”) en voor een belangrijk deel ook op het visueel systeem. De otolieten maken onderdeel uit van het evenwichtsorgaan en kunnen worden beschouwd als gespecialiseerde zwaartekracht-sensoren. Zij registreren de hoek die het hoofd maakt met de verticaal. Doorgaans kan dit soort informatie ook worden ontleend aan de visuele omgeving, die meestal duidelijk horizontaal en verticaal georiënteerde structuren bevat. Dit proefschrift heeft betrekking op de rol die de otolieten en het visueel systeem spelen in de oriëntatie op de zwaartekracht. Dit gebeurt aan de hand van oogbewegingen (oogtorsie) en de waarneming van de verticaal. Een probleem hierbij is dat, onder normale omstandigheden, de oriëntatie-informatie van de verschillende zintuigen een grote mate van overlap vertoont. Dat maakt het moeilijk om de individuele bijdrage van elk zintuig vast te stellen. Daarom is een aantal experimentele situaties gecreëerd waarin de verschillende zintuigen als het ware tegen elkaar zijn uitgespeeld.

Het promotie-onderzoek begon met een experiment waarin specifiek de werking van de otolieten werd veranderd door ze te adapteren aan een hoger zwaartekracht-nivo (**hoofdstuk 2**). Proefpersonen werden in een zogenaamde mensen-centrifuge een uur lang blootgesteld aan een zwaartekracht van 3G, waarvan verondersteld werd dat het vooral de otolieten stimuleert en de andere zintuigsystemen ongemoeid laat. Eerder onderzoek had al uitgewezen dat een dergelijke centrifuge-run consequenties heeft voor het houdingsevenwicht, en dat zich naderhand bovendien symptomen van bewegingsziekte voordoen bij het maken van hoofdbewegingen (Sickness Induced by Centrifugation, SIC). Deze effecten werden toegeschreven aan otoliet-adaptatie, temeer daar hetzelfde soort verschijnselen optreedt tijdens de eerste dagen van gewichtloosheid in een ruimtevlucht. Dat is eveneens een situatie waarin de otoliet-informatie afwijkt van die onder normale 1G. De resultaten in hoofdstuk 2 laten zien dat er inderdaad

sprake is van otoliet-adaptatie aan een zwaartekracht-nivo van 3G. Centrifugeren leidt tot een reductie van de oogtorsie respons, achteraf gemeten in een draaistoel. Oogtorsie is de (compensatoire) rotatie van de ogen om de visuele as die wordt opgewekt door zijwaartse kanteling van het hoofd. De oogtorsie tijdens statische kanteling wordt toegeschreven aan stimulatie van de otolieten. Derhalve duidt de gevonden reductie in statische oogtorsie op een afgenomen gevoeligheid van de otolieten. Aanvullende metingen van de horizontale vestibulo-oculaire reflex (VOR) toonden voorts aan dat deze otoliet-adaptatie gevolgen heeft voor de interactie tussen de otolieten en de halfcirkelvormige kanalen. Er werd geen correlatie gevonden tussen veranderingen in oogbewegingen en het optreden van SIC. Dit houdt vermoedelijk verband met het feit dat de oogbewegingen werden gemeten tijdens een passieve draaistoel-test, terwijl de verschijnselen van SIC juist werden waargenomen tijdens actieve hoofdbewegingen.

In een ander experiment werd de interactie tussen otolieten en halfcirkelvormige kanalen in het genereren van oogtorsie nog eens apart onder de loep genomen (**hoofdstuk 3**). In de literatuur bestaat een grote hoeveelheid bewijs dat de otolieten verantwoordelijk zijn voor de statische oogtorsie tijdens statische kanteling van het hoofd. Daarentegen is het nauwelijks bekend welke rol de otolieten spelen bij de dynamische oogtorsie tijdens het roteren zelf. Deze respons wordt doorgaans geheel toegeschreven aan de halfcirkelvormige kanalen. Niet alleen vormen de kanalen het aangewezen zintuigstelsel om rotaties van het hoofd te detecteren, maar ook is de amplitude van otoliet-geïnduceerde oogtorsie relatief klein (de maximale statische oogtorsie bedraagt gemiddeld ongeveer 6-7° bij een kanteling van 60-90°). Om de otoliet-component in dynamische oogtorsie boven water te krijgen werd de respons gemeten tijdens oscillaties rond een horizontale as en rond een verticale as. In beide situaties is de stimulus voor de kanalen identiek. De stimulus voor de otolieten verschilt echter wel. Bij rotatie rond een horizontale as verandert de stand van het hoofd ten opzichte van de verticaal. Dit wordt waargenomen door de otolieten, zodat in deze situatie zowel de kanalen als de otolieten kunnen bijdragen aan de respons. Een rotatie rond een verticale as is echter indifferent met betrekking tot de otolieten, zodat in dit geval de respons volledig tot stand komt door stimulatie van de kanalen.

Vergelijking van beide situaties leert dat de dynamische oogtorsie respons op twee belangrijke manieren wordt beïnvloed door de otolieten. Allereerst zorgen de otolieten ervoor dat bij lage stimulus frequenties de respons beter in fase blijft met de beweging van het hoofd. Daarnaast blijkt het aantal snelle slagen (saccades) in de nystagmus onder invloed van de otolieten sterk verminderd: in de kanaal respons worden de ogen vaker naar een nul-positie teruggezet dan in de gecombineerde kanaal-otoliet respons. Het gevolg hiervan is dat er, ondanks een nagenoeg gelijke oogsnelheid, een grotere amplitude van oogtorsie wordt bereikt wanneer de otolieten "meedoen". Als we er rekening mee houden dat de

oogrotatie tegengesteld gericht is aan die van het hoofd (zeker omdat de otolieten het verschil in fase bij lagere frequenties teniet doen), betekent een grotere variatie van de oogstand in het *hoofd* een kleinere variatie van de oogstand in de *ruimte*. Op deze manier dragen de otolieten bij tot een betere stabilisatie van oogpositie ten opzichte van de omgeving. De kanaal respons lijkt er meer op gericht om beweging van het beeld op het netvlies (retinale slip) terug te dringen, ongeacht de positie van de ogen. Met andere woorden, de kanalen regelen de *oogsnelheid* in een egocentrisch coördinatenstelsel, en de otolieten bewaken de *oogpositie* in een exocentrisch coördinatenstelsel.

Het feit dat in de pure kanaal respons de amplitude van oogtorsie zo weinig varieert, weerspiegelt een fenomeen dat in de wereld van oogbewegingen bekend staat als de wet van Listing. Algemeen gezegd houdt deze wet in dat het oculomotor systeem ernaar streeft om oogtorsie te vermijden. Dat lijkt op gespannen voet te staan met bovenstaande conclusie dat de otolieten nu juist de amplitude van oogtorsie vergroten. Mijn interpretatie is dat deze otolietgeïnduceerde oogtorsie niet in strijd hoeft te zijn met de wet van Listing (zoals dat volgens de gangbare opvatting het geval is). Integendeel, het heeft er alle schijn van dat het "platform" (het coördinatenstelsel) voor oogbewegingen door de otolieten gestabiliseerd wordt ten opzichte van zwaartekracht.

In de experimenten van hoofdstuk 2 en 3 werden de oogbewegingen met behulp van kleine cameraatjes op videoband opgenomen (video-oculografie). Achteraf werden de opnames in de computer ingelezen om de oogtorsie te bepalen. Om dit betrouwbaar en efficiënt te kunnen doen, moest eerst een automatisch systeem worden ontwikkeld (**hoofdstuk 1**). De methode berust op een elegant algoritme dat zelfstandig een aantal karakteristieke structuren in de iris van een referentieplaatje opzoekt en deze vervolgens terugvindt in de iris van opeenvolgende dataplaatjes. Door informatie verspreid over de hele iris te benutten, biedt deze methode bovendien de mogelijkheid om te corrigeren voor fouten die ontstaan door het foutief bepalen van het rotatiecentrum. Hierdoor wordt een praktische betrouwbaarheid van 0.25° bereikt.

Tenslotte besteed ik in **hoofdstukken 4 en 5** aandacht aan de visueel-vestibulaire interactie bij de waarneming van de lichaamspositie ten opzichte van de verticaal. Beweging van de visuele omgeving rond een stationaire persoon leidt in het algemeen tot het gevoel van zelf-beweging ("vectie") in tegengestelde richting (zoals bekend van de sensatie dat onze trein vertrekt wanneer de trein op een naburig spoor zich in beweging zet). Rotatie van de visuele omgeving om een horizontale as leidt niet alleen tot een sensatie van continue lichaamsrotatie, maar tegelijkertijd lijkt het alsof het lichaam over een vaste hoek is gekanteld. Deze illusoire lichaamskanteling is doorgaans zeer beperkt, hetgeen wordt toegeschreven aan de conflicterende otoliet-informatie die aangeeft dat de lichaamspositie (ten opzichte van verticaal) in feite niet verandert. De resultaten

van het onderzoek in een zogenaamde “tuimelkamer” (hoofdstuk 4) wijzen uit dat de conflicterende otoliet-informatie kan worden overwonnen door het aanbrenge van duidelijk herkenbare horizontale en verticale structuren (“visueel frame”) en objecten met een duidelijke boven- en onderkant (“visuele polariteit”): in de gemeubileerde tuimelkamer, die met constante snelheid ronddraaide, had ruim 80% van 32 waarnemers het overtuigende gevoel volledig over de kop te draaien. Dit maximale effect komt overeen met een lichaamskanteling van 360°. Opvallend genoeg was het effect veel kleiner bij statische kanteling van de kamer. Bij kantelhoeken boven 40° bleken de proefpersonen zeer verward: nu eens gebruikten ze de echte kamervloer als referentie voor “onder”, dan weer beschouwden ze het oppervlak onder hun voeten als “vloer”. Concluderend, de otoliet informatie kan alleen overwonnen worden door een bewegende visuele stimulus die rijk is aan visuele polariteit (en frame).

Om het gevoel van zelf-beweging te versterken maakt men in “motion-base” vluchtsimulators vaak gebruik van kortstondige fysieke bewegingen aan het begin van een (visueel) gesimuleerde beweging. Deze “onset-cues” moeten het gemis aan vestibulaire stimulatie compenseren. Omdat een motion base simulator maar een beperkte slag heeft, moet de simulator na de beweging weer worden teruggebracht in de oorspronkelijke positie. Dit gebeurt meestal met een langzame beweging om het effect van de onset cue niet kwijt te raken. Deze manoeuvre heet “washout”. In hoofdstuk 5 wordt onderzocht of een onset cue het gevoel van visueel-geïnduceerde lichaamskanteling versterkt, en of dit effect beklijft na de washout. Het lag in de bedoeling dit experiment uit te voeren in de tuimelkamer van hoofdstuk 4, maar deze stimulus was zo krachtig dat er geen onset cue nodig was om een gevoel van kantelen te produceren. Daarom heb ik mijn toevlucht genomen tot een grote witte bol (diameter 3m), die aan de binnenkant is voorzien van een patroon van zwarte stippen. Rotatie van deze bol om een horizontale as bevat uitsluitend visuele bewegingsinformatie (en geen frame of polariteit) en leidt gemiddeld tot een sensatie van 20-30° lichaamskanteling. Het blijkt dat een onset cue (15° echte lichaamskanteling) de waargenomen zelf-kanteling niet verder vergroot dan zou worden verwacht op grond van optelling van de respons bij pure visuele beweging en de respons bij pure lichaamskanteling. Dit resultaat is onafhankelijk van de snelheid van de onset cue, en verdwijnt bovendien na de washout. De voornaamste verdienste van een onset cue is dat het de latentietijd voor zelf-kanteling sterk verkort.

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Curriculum Vitae

Eric Groen werd op 1 september 1964 te Utrecht geboren. Na het ongedeeld VWO aan het College Blaucapel te Utrecht studeerde hij Biologie aan de Universiteit Utrecht. Tijdens zijn hoofdvak bij de Vakgroep voor Vergelijkende Fysiologie verrichtte hij electrofysiologisch onderzoek aan de electroreceptor van de dwergmeerval, een zintuig voor ruimtelijke oriëntatie. Daarnaast behaalde hij de eerstegraads onderwijsbevoegdheid voor de biologie. Na het verkrijgen van het doctoraaldiploma in augustus 1987 was hij ruim een jaar verbonden aan de Vakgroep voor Humane Fysiologie, waar hij participeerde in inspanningsfysiologisch onderzoek. Vervolgens was hij twee jaar lang werkzaam als systeemontwerper in de automatisering. In 1992 begon hij als onderzoeker-in-opleiding bij de Stichting voor de Gedragwetenschappen (NWO) met het onderzoek naar de ruimtelijke oriëntatie bij de mens. Dit vond plaats bij Dr. B. de Graaf van TNO Technische Menskunde in Soesterberg. Hij ontwikkelde eerst een computersysteem voor het automatisch analyseren van oogbewegingen vanaf videoband, een essentieel gereedschap bij het vestibulaire onderzoek binnen het project. Gebruik makend van een buitengewoon verlot regeling werkte hij een jaar als "pre-doc" bij Prof. Dr. I.P. Howard in het Human Performance Laboratory in Toronto (Canada). Hier verrichtte hij de in dit proefschrift weergegeven studie naar visueel-vestibulaire interacties, en bouwde hij mee aan een mock-up van het Space Shuttle interieur. Deze moet gaan dienen als (des)oriëntatie-trainer voor astronauten.

Publications

- De Graaf B, Bos JE, Groen E (1994) Otolith function under hypo- and hypergravity conditions. Proceedings Scientific Workshop on Parabolic Flights, November 1994
- De Graaf B, Bles W, Bos JE, Groen E (1995). The otoliths under hypo- and hypergravity conditions. In: Experiment results of the ESA and CNES parabolic flights campaign: Tenth anniversary of first ESA parabolic flight campaign. ESA WWP-90 and CNES ED/MV-95-039
- Groen E, Nacken PFM, Bos JE, De Graaf B (1996) Determination of ocular torsion by means of automatic pattern recognition. IEEE Transactions on Biomedical Engineering 43(5); 471-479
- Groen E, De Graaf B, Bles W, Bos JE (1996) Ocular torsion before and after 1 hour centrifugation. *Brain Research Bulletin* 40(5/6): 331-335
- De Graaf B, Bos JE, Groen E (1996) Saccular impact on ocular torsion. *Brain Research Bulletin* 40(5/6): 321-330
- Bos JE, De Graaf B, Groen E (1995) Otolith directional sensitivity and ocular torsion (1995) *New York Academy of Sciences* 781: 583-584
- Bles W, De Graaf B, Bos JE, Groen E, Krol JR (in press) A sustained hyper-G load as a tool to simulate space sickness. *Journal of Gravitational Physiology*
- De Graaf B, Bos JE, Groen E, Tielemans W, Rameckers F, Clark J, Mead A, Guedry FE (in press). Otolith contribution to ocular torsion and spatial orientation during acceleration II. NAMRL Report.
- Groen E, Bos JE, De Graaf B (submitted to *J Vestib Res*) Contribution of the otoliths to the human torsional vestibulo-ocular reflex
- Groen E, Howard IP, Cheung B (submitted to *J Vestib Res*) Influence of body roll on visually induced self-tilt.
- Bles W, Groen E, De Jong V, Lok J (submitted to *Acta Otolaryngol*) Cervically induced ocular torsion: clinical and physiological aspects.