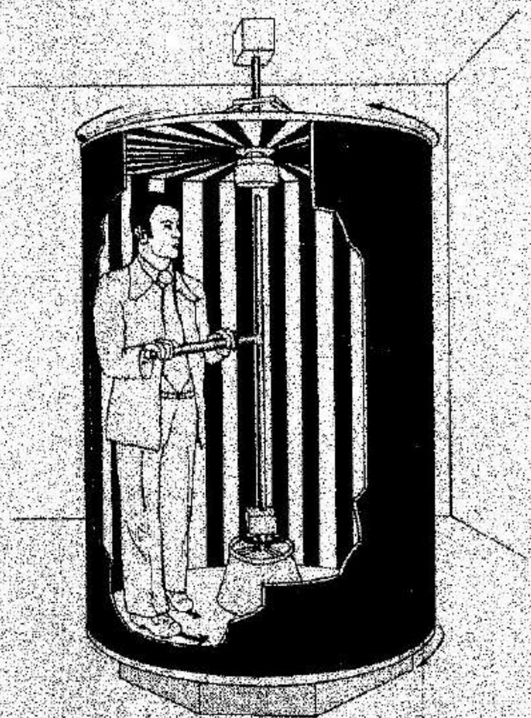
SENSORY INTERACTIONS AND HUMAN POSTURE

– an experimental study –



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VRIJE UNIVERSITEIT TE AMSTERDAM

Sensory interactions and human posture

an experimental study

ACADEMISCH PROEFSCHRIFT

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Aan Eloje en Jurriaan

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CONTENTS

INTRODUCTION

To keep control of postural balance at free stance or locomotion, an adequate spatial orientation is a necessary condition both in animal and man. Spatial orientation refers to the orientation of the body within a certain frame of reference (physically defined) and to the perception of the position within a spatial reference frame (psychophysically defined). Especially in man, because of his unstable equilibrium due to his upright stance, the central nervous system (CNS) has to be provided continuously with information about the actual as well as the expected position of the body with respect to the field of gravity and the supporting earth surface. The most important sensory systems which provide this information are the vestibular, the somatosensory and the visual system.

The vestibular system comprises the semicircular canals for detection of angular acceleration and the otoliths for detection of linear accelerations (therefore sensing the position of the head relative to the gravitational vector).

The somatosensory system refers to the sensors in the skin and underlying tissue (which record the contact and pressure of the body on the supporting surface), as well as to the sensory inputs from joints and tendons (signalling relative positions and movements of parts of the body). The somatosensory system and the vestibular system together will be called the proprioceptive system.

The visual system provides the CNS with an additional reference frame because directional structures in the visual field are preferentially perceived as vertical or horizontal. Moreover, the retinal periphery is important in deciding between self- and object-motion.

Both the vestibular apparatus and the eyes are situated in the head, and the fact that this can be moved relative to the trunk complicates matters considerably. Therefore an interaction between these two information sources and e.g. the somatoreceptors in the neck is necessary during head movements. For instance the deep somatic neck afferents have to neutralize the visual and vestibular signals, when a standing subject inclines his head on his shoulder, in order to prevent righting reactions which are not necessary then. From this simple example the necessity of an adequate integration of the sensory information for maintaining spaceconstancy is already evident Perceptual space orientation and postural balance are redundant mechanisms with some overlap between the functions of the single loops. Mutual calibration is required which then allows for one loop to compensate for a deficiency of the other. In case of intersensory mismatch (provided by incongruent visuo-vestibular or somatosensory-vestibular information) vertigo and nausea may occur. This is called motion sickness when the vertigo is induced by stimulation of the sensory systems, and clinical vertigo syndrom in patients suffering from lesions of the peripheral or central vestibular system. Therefore, experimentally induced vertigo by stimulation of the sensory systems not only increases the knowledge in sensory physiology but also leads to a better understanding of the pathogenesis of clinical vertigo syndroms. Extensive studies have been performed on effects of unimodal stimulation of either the visual or the vestibular system. However, recent work on visuo-vestibular-somatosensory interactions gave motivation for a study in which the perceptual as well as the oculomotor and postural consequences of multisensory motion stimulation were investigated. This required a combination of psychophysical methods (verbal report, magnitude estimation), electronystagmography (to quantitatively analyse eye movements) and posturography (to record the body sway).

The following questions have been investigated :

1. Are the somatosensory-vestibular interactions analogous to the visuo-vestibular interactions when dealing with rotation about a vertical axis ?

   From a functional point of view it must be primarily the somatosensory system involved in stepping around which should contribute to a sensation of circular self-motion (Circular Vection, CV). By means of a rotating bar and rotating drum combination the visuo-somatosensory-vestibular interactions during real or apparent stepping around have been investigated which will be described in chapter 1.

2. What is the influence of CV on Posture ?

   Since the after effects on active or passive rotation about a vertical axis were found to differ as to the direction of the CV and the direction of body torsion, perceptual and postural effects due to other rotatory vestibular and visual stimuli have been studied as well. These experiments will be described in chapter 2.

3. What is the effect of optic roll stimuli on posture ?

   Continuous rotation of the visual surround about a horizontal axis in the sagittal plane results in a sensation of roll motion in the opposite direction, which is called roll vection. In literature the perceptual and postural consequences of optic rolling with the rotation axis at eye-level have been described ; in chapter 3 therefore only one simple experiment will be described which deals with the effect of an optic roll stimulus at eye-level with its rotation axis fixed relative to the earth or fixed relative to the head. Chapter 3 can be seen as a prelude to the experiments in chapter 4.

4. What is the effect of tilting surroundings on posture ?

   Tilting surroundings are known to induce perceptual space transformations. These perceptual space transformations have been subject of investigation together with the postural consequences by means of a tilting room and a tilting platform. This is done for stationary and sinusoidally varying room tilt. The results are given in chapter 4.

5. What is the effect of different eye-object distances on posture ?

   Due to retinal deficiency body movement cannot be visually detected if the eye-object distance is too large. It will be shown in chapter 5 that this increase in eye-object distance may lead to a postural imbalance. In correspondence herewith a possible hypothesis for the mechanism of physiological height vertigo will be discussed.

In all experiments described in these chapters postural and perceptual consequences of stimulation of the sensory systems have been studied in healthy subjects. Therefore this approach is quite different from the original approach used by e.g. de Kleyn and Magnus (1913), Magnus (1924) or Rademaker (1924) who analysed the postural consequences of operative elimination of the labyrinth, unilaterally or bilaterally, or of central neural structures in animals. A similar study under the described test conditions of the perceptual and postural behaviour of patients with well defined peripheral or central vestibular lesions would enlarge the knowledge about the clinical vertigo syndrom (e.g. compensating mechanisms) and perhaps result in new examination methods for clinical use, but this would be beyond the scope of the present study. However, in chapter 6 the results of a preliminary study on patients are given. Some patients suffering from the post-concussional dizziness syndrom and patients devoid of vestibular function have been examined with the tilting room. These patients show a significant enhancement in the sensory weight given to vision in spatial orientation demonstrating the possible clinical use of the tilting room.

CHAPTER 1

CIRCULAR VECTION AND STEPPING AROUND

Summary

Reafferent somatosensory information from muscle and joint receptors is sufficient to induce an illusion of CV with concomitant nystagmus in an objectively stationary subject Apparently Stepping Around (ASA) on a rotating platform in the dark. A somatosensory-vestibular convergence underlying this phenomenon must be postulated. Active head tilts at ASA-induced CV may elicit Coriolis-like effects. It is shown by magnitude estimation of Coriolis-effects that intensity is strongest in case of incongruity of afferent motion signals.

1.1. INTRODUCTION

The horizontal semicircular canals within the vestibular labyrinths are detectors and transducers of angular accelerations applied to the head about the z-axis. The mathematical description of the cupula-endolymph system as a heavily damped torsion-pendulum system (Steinhausen, 1933 ; van Egmond et al.(1949) is widely accepted among physiologists.
For a survey of the psychophysical aspects and mathematical modelling of the vestibular system reference is made to Guedry (1974) and Mayne (1974). Of importance at this moment is that stimulation of the lateral semicircular canals results in a horizontal nystagmus and in CV.
However, the vestibular system is not the only system that detects self-motion, vision is also very important. Mach (1875) already observed that looking at moving visible surroundings induces self-motion sensation. Dichgans and Brandt (1978) have extensively investigated the optokinetically induced CV. Their most important finding is that in a stationary subject rotation of the entire visible surround invariably leads to an apparent self-rotation opposite in direction to pattern motion (optokinetic CV).

Using microelectrodes in neurophysiological studies in animals (fish, rabbit and monkey) it was found first by Klinke and Schmidt (1970), confirmed by Dichgans et al. (1973) and in recent years by Henn and associates that second order neurons in the vestibular nuclei exhibit a direction specific modulation of resting discharge evoked either by body acceleration or optokinetic stimulation. Waespe and Henn (1977) reported that more than 95% of the units recorded in the vestibular nuclei which could be influenced by stimulation of the horizontal semicircular canals, also showed consistent frequency changes when the animals were exposed to moving visual fields. These authors state that the visual pathway conveys the rather abstract information about velocity of the visual surround. The visual stimulus, however, must cover large areas of the peripheral visual field. After onset of stimulation (e.g. velocity step function) the visually induced modulation of the discharge rate has a latency of several seconds and it usually takes some more seconds until most units are maximally activated or inhibited by the visual stimulus.
When these neurophysiological findings are compared to human perception under these circumstances, the similarities are evident : exposed to a moving pattern, the initial experience is only that of object or surround motion relative to the ego (egocentric motion perception) ; after one to a few seconds the subject experiences a self-motion as well (combined ego- and exocentric motion perception) which is followed by a compelling sensation of pure self-motion (exocentric motion perception), in which the actually moving surround seems to be stationary (Dichgans and Brandt, 1972).
The finding that it was possible to induce Coriolis-like effects through head tilts during visually induced CV (the so-called Pseudo-Coriolis effects (Brandt et al., 1971)) provided further evidence for a functional visual-vestibular convergence. Because in the present section Coriolis effects are dealt with, some explanation is required here. Tilt of the head towards a shoulder during constant velocity rotation results in a typical cross-coupled vestibular stimulation. In literature this kind of vestibular stimulation together with its perceptual consequences is referred to as Coriolis effect. The perceptual aspects of the Coriolis effect are complex. The un-experienced subject reports at first a confused, unpleasant experience of motion. This is, however, often the case with sensation of

rotation about other axes than the vertical axis (cf. roll vection in chapter 3). The reports are mostly a combination of tilt and rotation which can be understood by mathematical examination of the stimulus. A comprehensive mathematical analysis of this matter has been given by Guedry (1974). The point is that at completion of the head movement there is a discrepancy between the head tilt indicated by the otolith- and neck-receptors and the direction of the angular velocity vector as sensed by the canals. When the head is tilted during optokinetically induced CV (Pseudo-Coriolis effect ; Brandt et al., 1971), the perceptual experience includes tilt and dizziness too and is indistinguishable from real Coriolis effects. Because the Coriolis and the Pseudo-Coriolis effect are qualitatively the same it is supposed that a common central integrator is mediating both vestibular and visual information.
The implication of these findings has been discussed in literature. Dichgans et al. (1973) state that the functional significance seems to be to provide the animal with an accurate velocity signal. Waespe and Henn (1977) predict from their experiments that congruent visual and vestibular stimulation would result in a function that accurately transfers velocity information over the whole frequency range up to about 1 Hz. They assume velocity to be the important parameter for the animal and that combination of the visual and vestibular cues would reduce the shortcomings of each transfer characteristic alone, i.e. the poor vestibular response at low frequencies and the poor visual performance at high frequencies. They assume that a combination of vestibular and visual input already at the level of the vestibular nuclei would ensure that motor reactions like nystagmus and postural changes should be the same, independent of the peripheral channel by which information about the velocity or acceleration has been obtained.
However, in view of the experimental results to be described in chapter 2, this assumption about postural changes cannot be maintained. When the subjects experience a CV certain discrepancies in the direction of the CV, nystagmus and postural sway were observed, especially in those conditions, where the subjects were standing or had been stepping around. This will be discussed in chapter 2 in more detail but is in fact the reason for the experiments described in this chapter. The question is whether the somatosen-

sory information about rotatory motion (in analogy to vision) also may be interpreted as either object-motion or self-motion. As real stepping around modifies the vestibular response after stopping (see chapter 2) the somatosensory information of stepping around might be a source of information about rotation. Stepping around in small circles provides a complex pattern of afferent somatosensory consequences in skin, muscle and joint receptors which in combination may represent the actual movement. Simultaneously, however, under natural conditions there may be redundant visual as well as vestibular information. For the study of the pure somatosensory contribution a dissociation of the various loops is a pre-condition. This can be achieved by the experimental situation of apparently stepping around on a rotating platform in the dark, a stimulus situation in which somatosensory stimulation is the same while the canals and vision are not activated. If under these conditions it were possible to induce CV, Coriolis-like effects and perhaps nystagmus, then a somatosensory-vestibular convergence similar to the visuo-vestibular convergence is highly likely.

1.2 APPARATUS

The instrument used in the experiments was a rotating chair and drum combination (Tönnies, Freiburg im Breisgau). The drum has a cylindrical shape, diameter 1.5 m the inner walls of which are painted with vertical black and white stripes each subtending 7^{0} of visual angle. The chair and the drum can be rotated separately or simultaneously at any desired speeds up to 180^{o}/sec in both directions. Chair and drum can be coupled to each other by means of a clutch for stimulation with identical movement patterns. The velocity and acceleration of the chair as well as the velocity of the drum and the relative chair-drum velocity (by means of a photocell stripe detection system) were recorded continuously.
The first part of the experiments was performed with the following arrangement : the subject walking on the floor of the drum beside the chair, with one hand on the back of the chair. In the second part the chair had been removed and replaced by a barconstruction as depicted in Fig. 1.1.: the subject is then walking with his hands on the bar. Also connected to

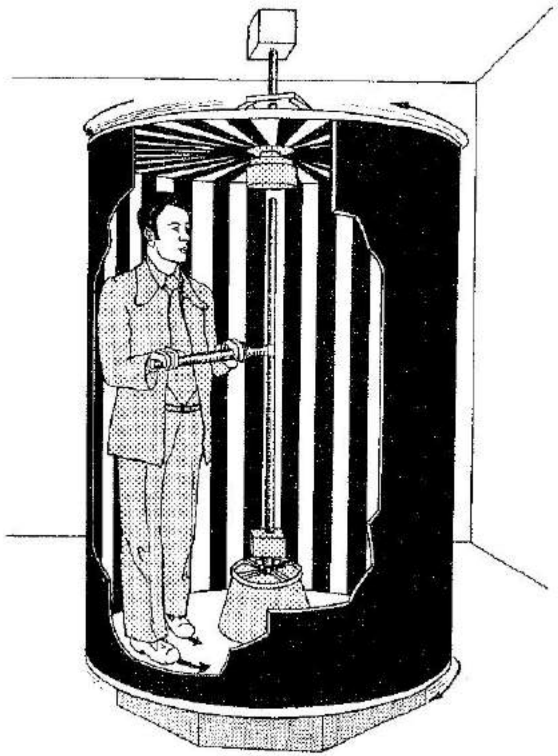

Fig. 1.1. Experimental equipment consisting of the rotating bar and drum. The bar and the drum can be rotated separately. The subject is stepping behind the bar on the floor of the drum.

this bar a small platform could be used on which the subject could stand upright, again with his hands resting on a bar. With this rotating bar-drum combination it is possible to play off the sensory systems against each other. However, stimulation of both vision and the somatoreceptors is always congruent. Subjects could indicate each subjective complete 360^{o} body

rotation by pushing a button on the bar. In some of the experiments horizontal eye-movements were recorded by means of electronystagmography (AC, time constant 5 sec).
All described signals were simultaneously recorded on a strip-chart recorder (Siemens EM 81.80). Under all experimental conditions a noise source was placed inside the drum in order to mask the faint motor noise. Because of the reflections on the walls the sound field was diffuse thus acoustic spatial orientation was impossible.

1.3. EXPERIMENTS AND RESULTS

The bar construction was used in all experiments except for the pilot experiment in which the chair was still used.

1.3.1. Pilot experiment : Real Stepping Around and Apparent Stepping Around

The subjects were standing beside the chair on the floor of the drum, resting with one hand on the back of the chair. They were instructed to maintain this position relative to the chair which meant that they had to walk, no matter whether it was the chair which rotated or the drum (chair and drum of course always rotated such that the subjects had to walk forward). Two stimulus conditions were used in this study (see Fig.1.2.) :
(1) chair rotation (which meant Real Stepping Around ,RSA : stimulation of both the somatoreceptors and the vestibular system) and
(2) drum rotation (which meant Apparent Stepping Around, ASA : stimulation of only the somatoreceptors.
These tests were performed in complete darkness, the subject having his eyes open. Perception of CV was reported verbally by the subject during the runs. Subjects were familiar with the experimental set up.
An important finding is that most of the test subjects could not distinguish between ASA and RSA :they believed they had to do with RSA, which means that they did not realise whether the vestibular system was involved or not.
The influence of acceleration, final velocity and deceleration was tried out too.

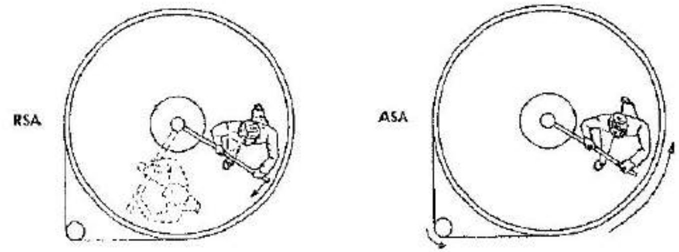

Fig. 1.2. Test conditions of the pilot experiment.
Left : Real Stepping Around, stimulation of both the vestibular system and the somatoreceptors.
Right: Apparent Stepping Around, stimulation of only the somatoreceptors.

These pilot experiments showed that it is important to avoid some unwanted cues for the test subjects : (1) only at velocities of over 80-90°/sec it is easy to distinguish between ASA and RSA. This is because of the centrifugal forces which become apparent in the case of RSA resulting in difficulties with stepping and requiring a firm grip on the bar. Up to 50 or 60°/sec these problems are not present.
(2) In case of ASA strong accelerations of the drum at the stimulus onset push the feet backward which makes it easy for the subjects to recognize this as drum rotation, so as ASA. This problem can be overcome by instructing the subjects to begin stepping before rotation is started, but even then too exessive accelerations should be avoided. This means also that it is difficult to measure exact latencies of CV induction.
(3) In these pilot experiments the subjects were also asked for possible after effects. In case of ASA there were reports of weak positive after effects (positive = sensation in preceding direction). In case of RSA the subjects mostly reported just a stop and not the (vestibular) negative after effect. It is possible that after the active stop the somatosensory signal "no movement" (because the subjects are standing still) dominates possible after effects originating within the vestibular system. In this way pure after effects like the optokinetic after effects cannot be expected. The ASA positive after effects were much stronger when the subjects stopped ASA abruptly by hopping on the elbow-rest on the chair, probably because in

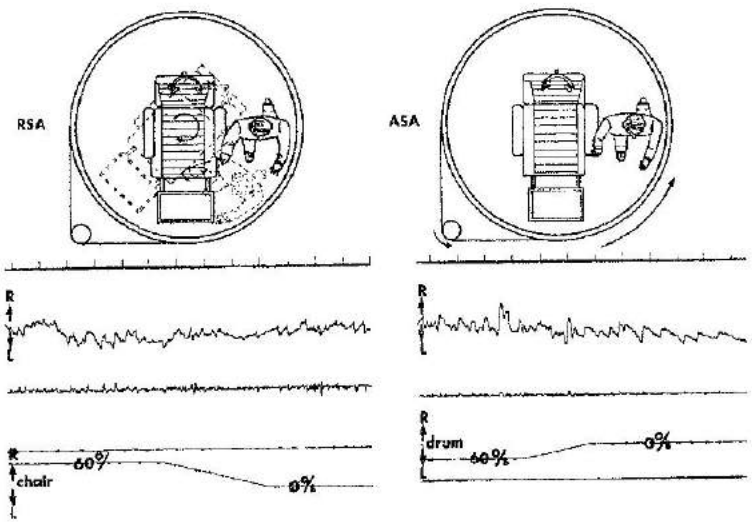

Fig. 1.3. Example of a nystagmus recording of a subject stepping RSA (a reversal of the nystagmus direction is seen) and stepping ASA (a positive after nystagmus is seen).

that situation there was no more somatosensory information about the movement in relation to the floor. These after effects lasted up to about 15 sec.

In these experiments the eye movements of several subjects have been recorded. Some subjects showed a nystagmus. However, in most cases the recordings were heavily disturbed by the stepping. Therefore, no quantitative evaluation can be given. A very nice example of such a nystagmus at the end of RSA and ASA is shown in Fig. 1.3. The ASA nystagmus pattern (fast phase toward the direction of stepping and perceived CV) with positive after effect is always seen when nystagmus is present at all.

1.3.2. Experiment 1.a.: Congruent sensory information and Circular Vection

Aim of this experiment was to compare the magnitude of the CV as induced by stimulation of the sensory systems, separately or in congruent combination. By using also the platform as described in 1.2. it was possible to generate the following stimulus conditions :

1. Vest		: subj. standing on plat.	- plat.	rotation	- light off
2. - vis -		: subj. standing on plat.	- drum	rotation	- light on
3. - - somatos		: subj. stepp. behind bar	- drum	rotation	- light off
4. Vest vis -		: subj. standing on plat.	- plat.	rotation	- light on
5. Vest - somatos		: subj. stepp. behind bar	- bar	rotation	- light off
6. - vis somatos		: subj. stepp. behind bar	- drum	rotation	- light on
7. Vest vis somatos		: subj. stepp. behind bar	- bar	rotation	- light on

The stimulus consists of an angular acceleration of $5^o/sec^2$ for 12 sec, up to an angular velocity of $60^o/sec$ which was maintained for a two minute period followed by a deceleration of $10^o/sec^2$. The bar, the platform or the drum rotated in such a way that the subjects should experience a CV to the left (rotation to the left means counterclockwise).

In order to obtain a reproducable stepping behaviour, the step frequency was fixed. The subjects were instructed to adjust their stepping rhythm to the clicks of a metronome, set to a repetition rate of 1 Hz. These clicks were also presented when the subjects were standing still on the platform. The third and fifth condition were presented with a 2 Hz stepping frequency as well (condition 8 and 9). The conditions were offered in random order. The subjects started stepping by command, 10 sec before motion stimulation took place. By pushing a button on the bar the subjects signaled each time they thought to have rotated through 360^o. In analysing the data the time between successive marks was used to calculate the mean subjective velocity. Horizontal eye movements were recorded by electronystagmography (AC, time constant 5 sec).

Ten subjects, without previous experience in such experiments, participated. They always had the eyes open.

Fig. 1.4. shows the results. In all conditions CV to the left has been reported. Only one subject did not experience a CV in condition 8 (ASA, 2 Hz). Because of the deficiency of the vestibular system to detect constant velocity, CV in the first condition was not maintained during the constant velocity rotation. The duration of the first experienced 360^o rotation (which had to be 12 sec) is underestimated except for the ASA conditions, indicating possible latency effects (cf. the latencies in optokinetic stimulation, 1.1.). In discussing the experiment with the subjects after

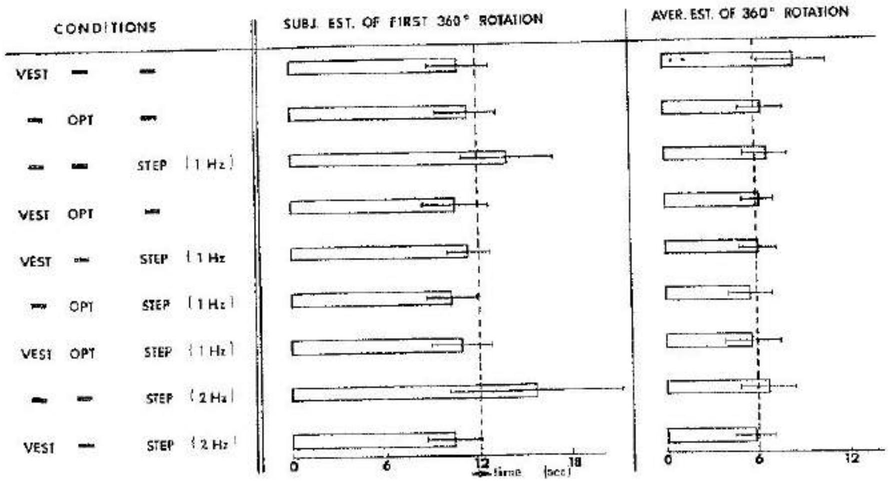

Fig. 1.4. CV magnitude estimation of 10 subjects during congruent stimulation of the sensory systems. For detailed information about the test conditions, see text. The mean estimates (± 1σ) of the first 360° rotation (acceleration period) are shown as well as the mean estimates during the 2 min period following the acceleration period. Of course from the vestibular stimulus only few data were available during the constant velocity period (about 2 completed rotations).

wards, three of them mentioned clear latencies in these conditions indeed. The differences in magnitude of the CV are not very obvious which means that stimulation of only one sensory system is already sufficient to obtain a correct CV. The results of condition 3 and 8 indicate that the stepping frequency is not decisive for the final magnitude of the CV. The nystagmus-tracings do not permit a quantitative evaluation because of the disturbance of the tracings during the stepping. From one subject the original recordings of condition 1, 5 and 3 respectively are depicted in Fig. 1.5. It shows the prolonged nystagmus in case of somatosensory involvement which was found also by Guedry et al. (1978).

1.3.3. Experiment 1.b.: Congruent sensory information and (Pseudo-) Coriolis effects

The aim of this experiment was to investigate (1) whether Coriolis-like

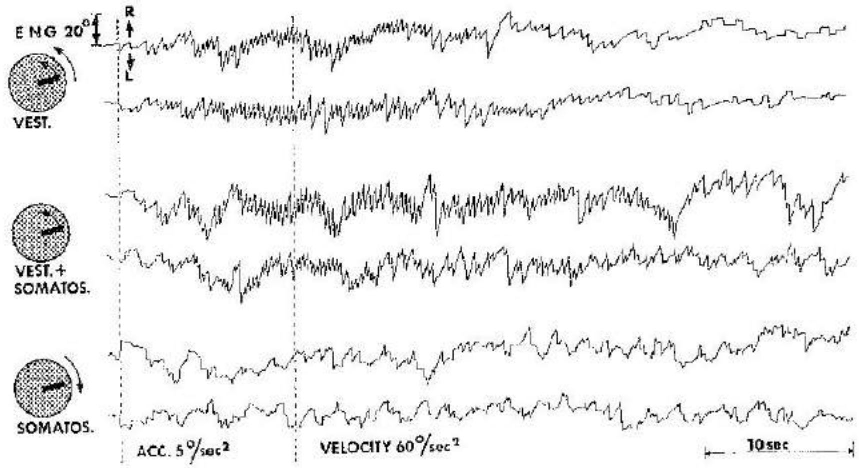

Fig. 1.5. Original nystagmus recordings during condition 1 (stimulation of the vestibular system), 5 (stimulation of the vestibular and the somatosensory system) and 3 (stimulation of the somatosensory system) respectively of one subject (tested twice).

effects can be induced during ASA and (2) whether the magnitude of the Coriolis effects is dependent on the different stimulus conditions 1-7 as described in experiment 1.a. The stimulus was again an acceleration of 5°/sec² up to a velocity of 60°/sec which was maintained for one minute ; then the subject moved his head and a few seconds later the deceleration began. Three more conditions (8, 9, 10) were incorporated in which the sequence of the head movements and the deceleration was reversed. In this way no Coriolis accelerations are involved ; only tilt of the head fixed rotation vector (Purkinje, 1820). Under each experimental condition the subject started with his head tilted towards the left shoulder. By command (after the one minute constant velocity rotation) he returned his head towards the normal position within about 1 second. Afterwards he was asked to scale his subjective sensation as compared with the purely vestibular Coriolis effect which served as a standard (with an arbitrary value of 5). No sensation at all had to be scaled 0. The method to return the head from tilted position (Purkinje, 1820) has been chosen because this permitted to get reproducable head movements as the initial head tilt was checked by the experimenter. The subject was stepping only when necessary and the stepping rhythm was left free. 11 Subjects participated. First they were trained to perform the correct head movements, after which they were exposed to the standard : the exclusively vestibular stimulation. Subsequently the other conditions were presented in random order with sufficient time between the conditions for the subjects in order to recover from the effects.

	STIMULUS CONDITIONS		MAGNITUDE ESTIMATION OF CORIOLIS-LIKE EFFECTS												
	DURING		SUBJ: 1	2	3	4	5	6	7	8	9	10	11	mean	σ
1	platform 60°/sec → le drum 0°/sec	light off	(5	5	5	5	5	5	5	5	5	5	5)	5.0	-
2	platform 0°/sec drum 60°/sec → ri	light on	2	1	3	1	2	2	1	1	4	3	0	2.4	1.9
3	bar 0°/sec drum 60°/sec → ri	light off	1	2	3	0	1	3	1	0	2	2	3	2.3	1.9
4	platform 60°/sec → le drum 0°/sec	light on	2	1	3	2	1	2	3	1	4	3	0	2.0	1.2
5	bar 60°/sec → le drum 0°/sec	light off	3	3	3	3	4	3	4	2	5	2	1	3.0	1.1
6	bar 0°/sec drum 60°/sec → ri	light on	2	3	3	2	2	2	1	2	6	4	3	2.7	1.3
7	bar 60°/sec → le drum 0°/sec	light on	1	2	2	0	0	1	1	0	2	2	0	1.0	0.9
	AFTER														
8	platform 60°/sec → le drum 0°/sec	light off	7	2	4	0	4	4	6	5	5	2	1	3.6	2.2
9	bar 0°/sec drum 60°/sec → ri	light off	0	2	1	1	0	0	0	0	0	0	1	0.5	0.7
10	bar 60°/sec → le drum 0°/sec	light off	4	1	2	1	1	5	4	5	7	0	0	2.7	2.4

Table 1.I. Magnitude estimation of Coriolis-like effects during and after congruent stimulation of the sensory system.

Table 1.I. shows the results. It is possible indeed to induce Coriolis-like effects during ASA conditions. Another important finding is that the vestibular Coriolis effect is scaled lower when the other sensory systems are also contributing with congruent motion information (condition 1 - con-

dition 4,5 - condition 7).

1.3.4. Experiment 1.c: Incongruent Sensory information and (Pseudo-) Coriolis effects

The experimental conditions were chosen in such a way that the vestibular stimulation was modified either by congruent or incongruent information from the other sensory channels as can be seen from Table 1.II.

	STIMULUS CONDITIONS		MAGNITUDE ESTIMATION OF CORIOLIS-LIKE EFFECTS										
	DURING		SUBJ: 1	2	3	4	5	6	7	8	9	mean	σ
A	bar 60°/sec → le drum 0°/sec	light off	1	2	1	2	2	2	2	2	0	1.6	0.7
B	bar 60°/sec → le drum 60°/sec	light off	4	3	4	3	2	3	5	5	5	3.9	1.1
C	bar 60°/sec → le drum 120°/sec	light off	5	7	7	5	3	5	7	6	7	5.8	1.4
D	bar 0°/sec drum 60°/sec → ri	light off	1	0	0	1	1	3	2	1	0	1.0	1.0
E	bar 0°/sec drum 0°/sec	light off	0	0	0	0	0	0	0	0	0	0.0	0.0
F	bar 0°/sec drum 60°/sec → le	light off	0	1	0	2	1	3	0	2	0	1.0	1.1
G	bar 60°/sec → le drum 0°/sec	light on	1	3	0	1	0	1	2	0	0	0.9	1.1
H	bar 60°/sec → le drum 60°/sec	light on	4	6	5	3	2	1	5	5	5	4.0	1.7
I	bar 60°/sec → le drum 120°/sec	light on	4	8	8	5	4	6	9	6	6	6.4	1.9
J	bar 0°/sec drum 60°/sec → ri	light on	2	6	4	4	2	3	3	2	5	3.4	1.4
K	bar 0°/sec drum 0°/sec	light on	0	0	0	0	0	0	0	0	0	0.0	0.0
L	bar 0°/sec drum 60°/sec → le	light on	0	6	2	0	3	5	2	5	6	3.2	2.4

Table 1.II. Magnitude estimation of Coriolis-like effects during incongruent stimulation of the sensory system.

The acceleration was chosen to be $3^{\circ}/sec^2$ for reaching the angular velocity of 60°/sec and $6^{\circ}/sec^2$ for the velocity of 120°/sec. This consequently means that the stepping acceleration forward or backward was always $3^{o}/sec^{2}$. The stepping was left free to the observers. Nine subjects participated. The same procedure was used as in experiment 1.b. which means that condition B served as standard (5). However, this time this condition was also included in the stimulus conditions. Again, the conditions were presented in random order.

Table 1.II. shows the stimulus conditions and the results. It turned out that the stepping direction determined the direction of the CV. The differences in magnitude of Coriolis effects in conditions A and C are impressive as is also the case when vision is present : conditions G and I introduce an even greater difference in Coriolis effect. By comparing the scaling in conditions B, A and G the same phenomenon is seen as already mentioned with experiment 1.b.: the more sensory systems provide congruent information, the less the vestibular Coriolis effect. Again it is seen that ASA (condition D) induces Coriolis-like effects, conform the findings of experiment 1.b.

1.4. DISCUSSION

From the previously described experiments it may be concluded that the complex somatosensory information of the stepping around is sufficient to induce a compelling illusion of self-motion. The finding that ASA is perceived as RSA, that during ASA nystagmus and Coriolis-like effects can be induced, that latencies and possitive after effects occur, strongly suggests similarities with the perceptual and motor effects of optokinetic stimulation. Nystagmus has been reported to occur also at stimulation of other parts of the somatosensory system as well, such as torsion of the cervical vertebral column (cervical nystagmus ; Bos and Philipszoon, 1963) or passive rotation of the extended arm about a vertical axis in the shoulder joint (arthrokinetic nystagmus ; Brandt et al., 1977). In both instances there is an direct stimulation of the vestibular system. Arthrokinetic nystagmus is accompanied by an ego-motion sensation, and both the nystagmus and the CV exhibit latencies and positive after effects. Torsion of the cervical

vertebral column shows that, apart from the cervical nystagmus, it is possible to induce a sensation of head movements as well[1]. So, obviously the role of the somatosensory system in dealing with rotation is very complex as stimulation of different parts of the somatosensory system already results in CV and nystagmus. This indicates that within the somatosensory system integration of afferent signals is performed, especially clear from the complex excitation of the different receptors during stepping around (cf. the fact that no difference in magnitude of the CV is obtained with the 1 and 2 Hz stepping frequencies, indicating integration of the stepsize and the bending of the feet).
It is highly probable that especially the joint receptors, which transfer information about position of the joint as well as the direction and speed of movement, are involved in the contribution to kinaesthesis (Skoglund, 1973). Four types of joint receptors are known : (1) Ruffini receptors in the capsule, (2) Golgi-tendon-organs in the ligaments, (3) Pacinian corpuscles and (4) free nerve endings. The nervous pathways of the joint afferents project to the cortical somatic area 1 and 2, probably espacially to area 2, very near to the vestibular projection field 2v (Frederickson, 1974). There is also a somatosensory projection to area 5, a cortical locus in which neurons respond to movements of several different joints, even from both sides of the body (Sakata, 1974). Convergence of vestibular and somatosensory signals at cortical level has been established several times (see Frederickson, 1974) and is functional because both systems give information about position and movements of the body (Büttner and Buettner, 1978). Since at the level of the vestibular nuclei a visual-vestibular convergence has been established (a.o. Dichgans et al., 1973 ; Waespe and Henn, 1977) as well as a somatosensory-vestibular convergence (Frederickson et al., 1966 ; Deecke et al., 1977 ; Rubin et al., 1978), and since it is possible to induce similar perceptual and oculomotor phenomena during ASA and optokinetic stimulation, a somatosensory-vestibular convergence at the level of the

1). The head of the subject, who is sitting on a rotating chair, is fixed onto an external reference frame. The chair is rotated over 120^{o} in 15 sec at a constant angular velocity of $8^{o}/sec$. Nystagmus is induced similar to the arthrokinetic nystagmus with latencies and possitive after effects. The subject initially experiences a movement of the body, which reflects the actual stimulation. After some seconds, however, a movement of the head is perceived relative to the seemingly stationary trunk. After effects are not clear, probably because the head remains fixed at the end, which means that probably 'no rotation' is signaled after the stop (cf.the ASA after effects).

vestibular nuclei and thalamus can be assumed for the stepping around as well (Bles and Kapteyn, 1977). It is interesting to note that the vestibular nuclei are under control not only of the vestibulo-cerebellum, but also of the anterior and posterior vermis which do not receive primary or secondary vestibular afferent information. These areas integrate impulses from several sources, especially spinal, acoustic and visual inputs (see Pompeiano, 1974). This fits in well with the present finding of self-motion sensation induced by the somatosensory and visual systems. An auditory induced CV and nystagmus have also been described in literature several times (Dodge, 1923 ; Hennebert, 1960). These auditory induced phenomena are not very impressive, probably because of the lack of spatial extensiveness of only one sound source, as discussed by Marme and Bles (1977). However, Lackner (1977) claims an induction of CV and nystagmus by means of 6 different sound sources which might be enough for spatial extensiveness.

From the foregoing it might be concluded that the function of the vestibular nuclei is much broader than the name suggests : it seems reasonable to assume that for self-motion perception induced by any movement sensitive system, a modulation of the discharge rate of second order neurons within the vestibular nuclei is a necessary condition. This fits in with the wellknown fact that the vestibular nuclei, the cerebellum and reticular formation together form the unit which is primarily concerned with the maintenance of postural equilibrium. So far, the neurophysiological findings fit in with the psychophysical data. An important feature of the ASA induced CV is the torsion of a.o. the feet. This seems to be essential for inducing CV because stepping on a "trottoir roulant" induces Linear Vection and not CV. The stimulation of the otolithic system is the same for both cases (vertical head movements) and the semicircular canals are not stimulated. On the other hand it is not the torsion of the feet alone, the stepsize is important too. This can be derived from the fact that the stepsize and the joint torsion are integrated during the 1 and 2 Hz stepping rate in such a way that the magnitude of the perceived velocity remains unaltered (cf. experiment 1.b., conditions 3-8 ; 4-9). Such an integration teleologically is of functional value for more complex movement patterns.

Also funtional is the result of experiment 1.b. that there is no difference

in magnitude of the CV as induced by the sensory systems individually or in congruent combination. In principle this offers the possibility to maintain an adequate spatial orientation, even in those situations in which not every sensory system is provided with information or in those cases in which systems are impaired somehow and therefore incapable to transfer information.

Congruent stimulation of the sense organs offers the possibility to get information about the space constancy mechanisms under normal daily-life circumstances. It is incongruent stimulation of the sense organs which provides the possibility to become informed about the interactions and the particular sensory weight of the different systems in the integration process and perhaps to get more insight into the (perceptual and/or postural) behaviour of patients with an impaired orientation system. The magnitude estimations of the Coriolis effects as obtained in experiment 1.b. and 1.c. are instructive in this respect.

The somatosensory-vestibular interactions in the Coriolis-like effects as found in experiment 1.c., condition A,B and C (Table 1.II.) show exactly the same behaviour as was found for the visual-vestibular interactions in the Coriolis-like effects (Brandt et al., 1971). It is interesting to note the considerable differences in magnitude between condition A and C despite the fact that the magnitude of the ASA induced Pseudo-Coriolis effect (condition D or F) is relatively small. When vision cooperates with the somatoreceptors the incongruity with the vestibular stimulus (condition I) results in a very vehement reaction. Some subjects had even serious difficulties to remain upright. However, the Coriolis effect is remarkably reduced when the three systems are in physiological agreement (condition G), which is the normal daily-life situation. These findings are in agreement with the findings of experiment 1.b.

In discussing Coriolis and Pseudo-Coriolis effects the Purkinje effect must be mentioned also. Purkinje (1820) induced similar sensations as associated with the Coriolis effect by bending his head, directly after a constant velocity rotation. In this case there is of course a different intersensory conflict as now the Coriolis forces are absent. In fact, it is only the

velocity vector fixed to the skull which changes its position according to the head movement ; a tilt of such a vector induces tumbling sensations and this is in conflict with the information of the graviceptors (Guedry, 1974). Guedry associates the Pseudo-Coriolis effect with this Purkinje effect, because in the Pseudo-Coriolis effect the Coriolis forces are absent too, cf. experiment 1.b., condition 8 and 10). However, care should be taken to call condition 8 or 10 a Purkinje effect since Purkinje performed his experiment after real stepping around with eyes open : in this case we are dealing with optokinetic as well as somatosensory after effects which are certainly playing an important role (Dichgans and Brandt, 1973 ; Bles and Kapteyn, 1977 ; see also chapter 2), so the real Purkinje effect is highly complicated. In experiment 1.b. this could not be demonstrated as can be seen by comparing condition 8 and 10, although it was possible in some cases to induce Purkinje-like effects after the Apparent Stepping Around (condition 9). However, Purkinje made a sudden stop which for mechanical reasons is impossible to realise with the drum : the maximal possible deceleration is $20^{\circ}/sec^{2}$, so the subject gradually slows down, reducing the after effects (cf. the lack of clear after effects in the pilot experiment). In terms of definition it is not only the Purkinje effect that may cause confusion : one might also question if condition 8 in experiment 1.c. is a purely vestibular Coriolis effect. One can argue that in that case the subject is standing still which means that the somatosensory signal of "no movement" may influence the vestibular information about acceleration. This explanation is supported by the finding that the CV as induced by caloric stimulation is dependent on the body position of the subject -standing or sitting- (Kapteyn and Bles, 1977 ; see also chapter 2).
In order not to add to the confusion, it is reasonable to speak of
(1) Coriolis effects when we are dealing with head movements performed by subjects sitting in complete darkness on a rotating chair which rotates at a constant velocity,
(2) optokinetically induced Pseudo-Coriolis effects when we are dealing with head movements performed by stationary sitting subjects viewing a rotating surround (cf. Dichgans and Brandt, 1973) and
(3) ASA induced Pseudo-Coriolis effects when we are dealing with head movements performed by subjects stepping in darkness on a rotating platform without stimulation of the semicircular canal system. This means that the last effect should not be called Pseudo-Purkinje effect as done by Bles and de Wit (1978).

CHAPTER 2

CIRCULAR VECTION AND HUMAN POSTURE

Summary

Rotatory vestibular and visual stimulation may result in postural changes such as body torsion and lateropulsion. It is found that the direction of the lateropulsion of the body is opposite to the direction of the nystagmus, whereas the body torsion is in the same direction as the CV. The results are compared with published data.

2.1. INTRODUCTION

It is a common experience in vestibular clinical routine examinations that the vestibulo-spinal tests ("Unterberger Tretversuch", Unterberger, 1938 ; "Fukuda Stepping Test", Fukuda, 1959) are less sensitive and subject to more voluntary control by the patient than are vestibulo-ocular methods. Extra-labyrinthine influence on the vestibulo-spinal reflexes is thought to cause considerable intra- and interindividual differences which restricts the clinical value of these ataxia tests as a diagnostic tool.
Still, postural reactions to vestibular stimulation have been studied in the laboratory. Several methods of stimulation have been used such as caloric irrigation (Fischer and Wodak, 1924 ; Aubry et al., 1968 ; Kapteyn, 1973) or stopping abruptly a constant velocity rotation (a.o. Purkinje, 1820 ; Fischer and Wodak, 1924). Visual stimulation by rotating surrounds also results in postural reactions (Kapteyn, 1973 ; Koitcheva et al., 1976 ; Miyoshi et al., 1978). The resulting postural behaviour on comparable vestibular or visual stimulation is, surprisingly enough, not always identical. The somatosensory, vestibular and visual convergence in inducing CV has been demonstrated in chapter 1 ; the influence of CV on postural behaviour

during visual and vestibular stimulation will be discussed in this chapter. In literature the subjective sensations are mostly disregarded, but just these sensations might be of interest the more so as it was found by chance that an abrupt stop after actively stepping around resulted in a similar nystagmus pattern as stopping a passive rotation, but that the CV was opposite in direction as also was the case with the body torsion.

2.2. APPARATUS AND METHODS

2.1.1. Caloric irrigation

Caloric irrigation is used as a routine examination in otoneurology to test the function of the horizontal (lateral) canals separately. Syringing water (30° or 44° C) into the external meatus results in an endolymph flow in the lateral semicircular canal if this is positioned in a vertical plane by head tilt. Water of 30° C elicits a nystagmus beating to the contralateral side of the irrigation and water of 44° C a nystagmus beating to the ipsilateral side, indicative of an ampullofugal and ampullopetal flow respectively. In the present tests caloric irrigation was performed with icewater (50 cc in 20 sec). Icewater was chosen in order to guarantee a clear reaction in spite of the not ideal position of the lateral canal (inclination of about 30° with respect to the horizontal plane). The head had to be in the normal position during standing because otherwise the stability is already affected (see also 5.3.1).

2.2.2. Visual Stimulation

The optic stimulus consisted of a stripe projection on a screen (horizontal visual angle 270°, radius of curvature 75 cm). The height of the screen was such that the screen covered the visual field completely. Stimulus velocities could be varied up to 120°/sec both to the left and to the right.

2.2.3. Body-rotation

It is known that, due to semi-circular canal mechanics, an abrupt stop following a constant angular velocity rotation results in a fast cupula deflection, followed by an exponential return to the resting position (van Egmond et al., 1949). This kind of vestibular stimulation was induced by two different methods : the "active" method, which means that the subject is stepping around on a spot for some time after which he stops by command, and the "passive" method, which means that the standing subject is rotated on a hand driven platform. In order to obtain an identical vestibular stimulus (∿ 90°/sec for ∿ 30 sec) in the active as well in the passive case, the subject was stepping around trying to make as smooth head movements as possible.

2.2.4. Recordings

In all situations the horizontal eye movements were recorded by means of an electronystagmograph (AC, time constant 5 sec). Apart from the visual stimulation all measurements were performed with eyes open in total darkness. The mean nystagmus slow phase velocity (SPV) was computed for each 10 or 20 sec recording period.
The body torsion was measured by a torsion meter, a device which registered the angle between the shoulders and the feet. It consists of a horizontal bar, the rotation angle of which is registered by a potentiometer. Two (parallel) elastic cords connect the ends of the bar to the shoulder of the subject. This permits free swaying of the body. With such a construction torsion of the body can be measured independently of a possible foreaft or lateral body sway. The mean torsion during each 10 or 20 sec recording period was computed.
The postural sway was recorded by means of a stabilometer which recorded the foreaft and lateral movements of the centre of pressure as exerted by the feet. The stabilogram consists of two plates (Ø 50 cm), the centres of which are connected to each other by means of a bar. When a subject is standing on the top plate, the pressure exerted on that plate is reflected in the bending of the bar. By means of straingauges the bending of the bar can be recorded as has been described elsewhere (Kapteyn and de Wit, 1972).

The version used in these experiments has been modified in such a way that the total height of the top plate from the floor is only 10 cm. The maximal bending of the bar is less then 5' (not perceptible by the subjects standing on the stabilometer) and a resonance frequency of over 70 Hz (van Waveren, 1978). The recording obtained of the body sway in two dimensions as a function of time is called stabilogram. As has been discussed extensively elsewhere (Kapteyn, 1973) such a stabilogram does not represent exactly the movements of the centre of gravity. However, apart from the very fast dynamic corrections, the stabilogram is a sufficient approximation of the movements of the centre of gravity. The mean position of the centre of gravity and the Root Mean Square value of both the foreaft and lateral stabilograms were computed each 10 or 20 sec recording period. For technical reasons neither the stabilogram nor the torsion meter could be used with the rotatory stimuli so the direction of the lateropulsion (= induced body tilt) or body torsion had to be derived from video recordings in those tests.
All experiments described in this chapter, including the verbal communication about the CV, were recorded completely on sound- and video-tapes.

2.3. EXPERIMENTS AND RESULTS

2.3.1. Caloric Irrigation

Eight subjects were submitted to irrigation with icewater of both ears subsequently while standing upright. Analyses were performed of each 10 sec recording periods.

The results are shown in Fig.2.1. The nystagmus beats into the expected contralateral (relative to side of irrigation) direction with a maximum reached about 60 sec after onset of irrigation. Body torsion is found to be into the ipsilateral direction. Rather unexpected the CV was reported to be in the ipsilateral direction (so opposite to the nystagmus) for ten cases ; five times a corresponding egocentric motion sensation was reported. Only once a CV into the contralateral direction was reported and in that case a body torsion was found to be also in the contralateral direction.

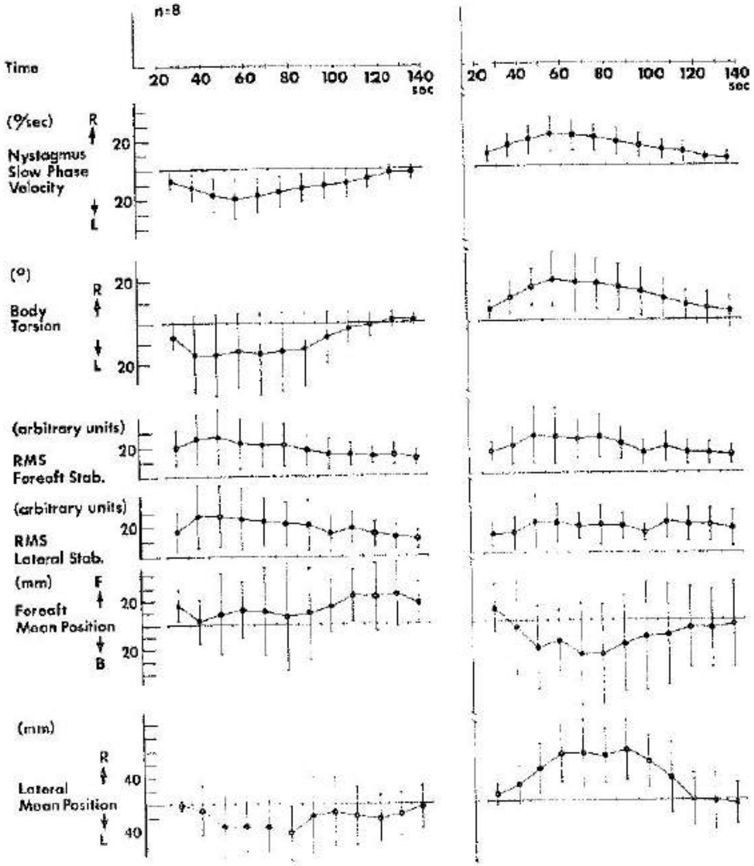

Fig. 2.1. Mean values ± 1 σ (N=8) of nystagmus Slow Phase Velocity (°/sec), body torsion (°), RMS of foreaft and lateral stabilogram (arbitrary units) and foreaft and lateral displacement of centre of gravity of the body (mm) over 10 sec periods following irrigation of the left and the right ear with cold water. The torsion and the displacement are referred to the level prior to the irrigation.

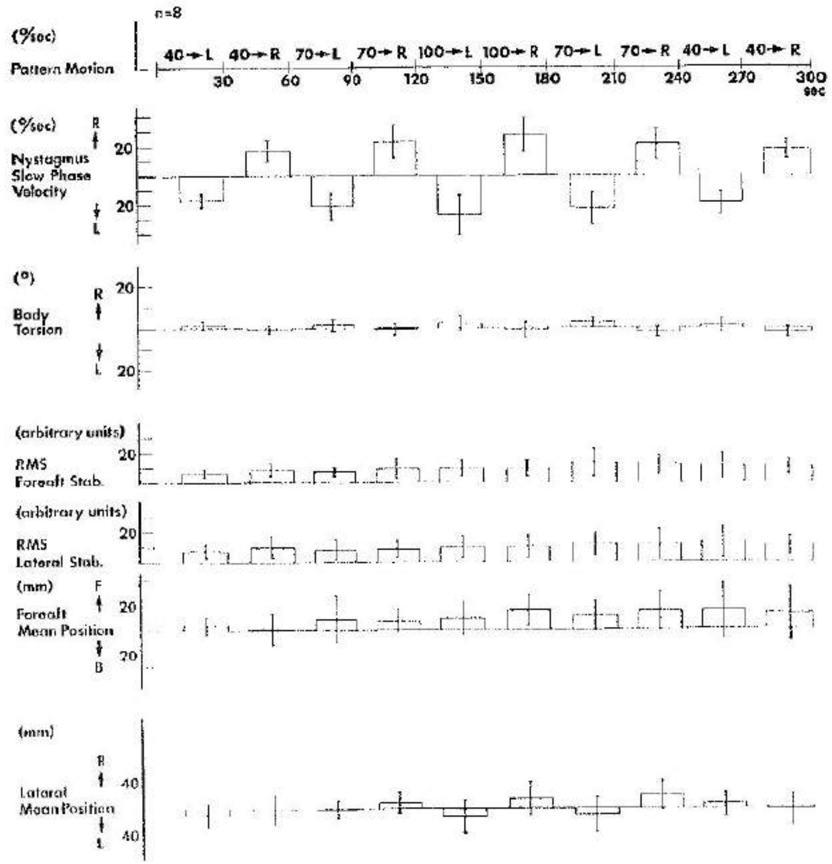

Fig. 2.2. Mean values ± 1 σ (N=8) of nystagmus Slow Phase Velocity (°/sec), body torsion (°), RMS of the foreaft and lateral stabilogram (arbitrary units) and foreaft and lateral displacement of centre of gravity of the body (mm) over 20 sec periods during optokinetic stimulation. The torsion and the displacement are referred to the level prior to onset of stimulation.

From the stabilogram analyses it is seen that the irrigation results in a decrease of stability of both foreaft and lateral body sway with the maximum instability about 50-60 sec after onset of the irrigation. Furthermore the analyses show a shift of the centre of gravity to the ipsilateral side.
A slight shift forward is seen after irrigation on the left side while a shift backward is seen after irrigation on the right side.
An analysis of the sound- and video- tapes taught that the extent of the body torsion was related to the intensity of the CV. The body torsion was mostly maintained up to the moment that the subject became aware of his torsion after which a correction was made : at the same time the CV had lost its compelling character and ended rather abruptly. From the video-tapes it was clear that the shift of the centre of gravity found from the stabilometric data was not only due to a torsion of the body but also due to lateropulsion.

These subjects were also submitted to calorization when sitting straight (same head position as in the "standing" condition). Because of the small postural reactions no analysis could be performed. The verbal reports of the subjects were uniform : all subjects experienced CV. However, the reported CV by caloric irrigation in the sitting position was in accordance with the nystagmus, i.e. to the non-irrigated side, so opposite to the direction as obtained in the standing position.

2.3.2. Visual stimulation

The eight subjects who participated in the foregoing experiment were also submitted to visual stimulation while standing upright. The movement of the stripes was alternately to the left and to the right. The speed was increased and decreased, maintaining each speed for 30 sec (40^{o}/sec → L, 40 → R, 70 → L, 70 → R, 100 → L, 100 → R, 70 → L, 70 → R, 40 → L, 40 → R).
The nystagmus SPV, mean body torsion, and the RMS and mean position of the foreaft and lateral stabilograms were computed from the last 20 sec of each stimulation period only in order to avoid the disturbances at the transition points.

The results are shown in Fig. 2.2. The torsion is seen to be in the same direction as the optokinetic nystagmus. The verbally reported CV was in accordance with the nystagmus, so opposite to the surround motion. Two subjects showed neither CV nor body torsion. The RMS for both the foreaft and lateral stabilograms showed an increase, but the values are considerably below the levels obtained with the caloric irrigation. The mean foreaft position shows a forward shift of the centre of gravity. The mean lateral position shows a shift into the direction of pattern motion. The video-tapes taught that this was mostly due to lateropulsion.

In the sitting position corresponding findings were recorded, but the body torsion and the lateropulsion were of course less intens.

2.3.3. Active and Passive Rotation

Eight test conditions were chosen as tabulated in Table 2.I. in which also vision was incorporated. These test conditions were presented in random order. Eight healthy subjects participated in this test. Four subjects always rotated to the left, the other four subjects to the right.

The results of the body torsion and the reported CV of the period after the stop are shown in Table 2.II. It is seen that the body torsion goes into the preceding direction after active rotation whereas it goes into the opposite direction after passive rotation. The same holds for the direction of the CV. The nystagmus recordings were not analysed but for the direction : the nystagmus always beat into the expected direction, i.e. opposite to the preceding movement. Lateropulsion following passive rotation was, if present at all, too weak to allow a correct description. After active rotation the lateropulsion was found to be in the same direction as the torsion, i.e. in the opposite direction as the nystagmus.

2.3.4. Summary of Experimental Results

If the experimental results are tabulated in such a way that the nystagmus

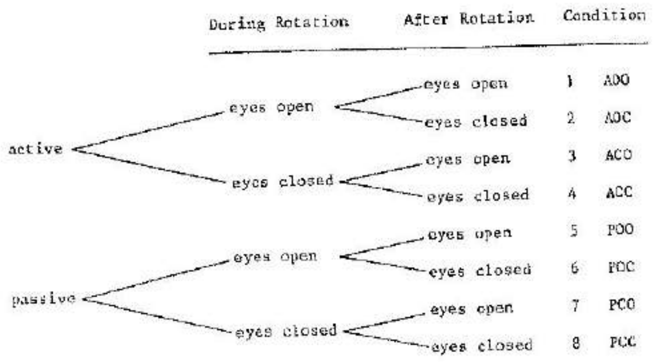

Table 2.I. Survey of the test conditions.

Subjects	Conditions							
	AOO	AOC	ACO	ACC	POO	POC	PCO	PCC
a	2 (1)	3 (0)	2 (2)	2 (2)	0 (-1)	0 (-1)	0 (-3)	0 (-2)
b	1 (2)	0 (0)	0 (0)	1 (2)	-1(1)	0 (0)	-1(-2)	-1(-3)
c	2 (-2)	2 (3)	0 (1)	2 (3)	-1(-3)	-2(-3)	-2(-3)	-2(-3)
d	2 (1)	2 (2)	3 (2)	3 (0)	0 (0)	0 (-3)	0 (-1)	0 (-2)
e	3 (3)	3 (3)	3 (3)	3 (3)	-1(-3)	-2(-3)	-1(-2)	-1(-2)
f	2 (2)	1 (0)	1 (1)	1 (1)	0 (0)	-1(-1)	0 (-3)	1 (1)
g	3 (1)	2 (3)	0 (0)	1 (1)	-1(0)	-2(-3)	-1(0)	-2(-3)
h	2 (0)	1 (0)	0 (0)	3 (1)	0 (0)	-2(-2)	0 (0)	-1(-2)
mean velocity	102.2	109.4	92.0	101.5	94.4	93.4	88.4	96.0
st. dev.	18.0	15.9	18.0	17.0	13.8	13.3	17.7	15.1

Table 2.II. Torsion and CV resulting from active and passive rotation.
Torsion : 0 = no torsion ; 1 = < 10° ; 2 = 10°–45° ; 3 = > 45°.
CV : (0) = no CV ; (1) = moderate CV ; (2) = medium CV ; (3) = strong CV.
+ = in preceding direction ; – = in opposite direction.
For explanation of the conditions see Table 2.I. The mean angular velocity ± 1 σ (°/sec) is shown as well.

	Caloric Irr. Standing	Caloric Irr. Sitting	Optokin. Standing	Optokin. Sitting	Following Active Rotation Standing	Following Passive Rotation Standing
Nystagmus	L	L	L	L	L	L
CV	R	L	L	L	R	L
Lateropulsion	R	-	R	R	R	-
Body Torsion	R	-	L	L	R	L

Table 2.III. Survey of experimental results tabulated in such a way that the nystagmus beats to the left.

beats to the left, the results can be summarized by table 2.III.
By inspection of Table 2.III. it is seen that on the one hand nystagmus and lateropulsion and on the other hand CV and body torsion seem to be related to each other.

2.4. DISCUSSION

Caloric irrigation causes postural changes which are described by Fischer and Wodak (1924) in detail : they distinguish two body movements known as body torsion ("Körperdrehreflex") and lateropulsion ("Körperneigungsreflex"). With trained subjects they found that irrigation with cold water resulted in body torsion and lateropulsion to the side of the irrigated ear and possibly a fall to this side and backward. The experiments described above support such a distinction between torsion and pulsion but the postural reactions were not as clear and longlasting as claimed by those authors (up to 30 min.!). The lateropulsion and the body torsion found in the present experiments are in accordance with the description given by Fischer and Wodak. From Fig. 2.1. it is seen that the foreaft movement of the centre of gravity is dependent on the side which was irrigated.
It is quite possible that these foreaft movements are caused by body torsion: body torsion may cause a shift of the centre of gravity in both foreaft and lateral direction but the direction of the resulting shift is individually determined. This explains perhaps the different conclusions drawn from stabilometric recordings by Aubry et al., (1968) and Kapteyn (1973) who did not take into account that body torsion per se already may result in a shift of the centre of gravity, the direction of which is individually determined.

Comparison of the induced body sway by visual stimulation with stabilometric data in literature (Kapteyn, 1973 ; Koitcheva et al., 1976 ; Miyoshi et al., 1978) is difficult because of the same contamination of the body torsion and lateropulsion in the stabilogram and because of the lack of information about the possibly present CV. In the present experiments the existence of CV determined more or less the presence of body torsion. The CV and torsion were found to be in the same direction too. From the stabilogram analyses an increase in RMS values can be seen both for the foreaft and lateral body sway indicating a visual destabilization of free stance. The instability, however, is less than the instability induced by calorization. It is also seen from Fig. 3.2. that the centre of gravity shifts forward, probably in order to improve stability. Furthermore, a lateral shift of the centre of gravity is seen in the direction of visual pattern motion which is in agreement with the experiments described in chapter 3 and 4.

The differences in direction of CV after active or passive rotation were also found by Correia et al. (1977) and Guedry et al. (1978).
The findings concerning the body torsion following active stepping around are in agreement with the findings of Purkinje (1820) ; Purkinje, however, did not mention a CV but reported about the sensation of a force which tried to rotate the body in the preceding direction (sensation of body torsion?). The direction of the body torsion after passive rotation in free sitting subjects should be in the preceding direction according to Fischer and Wodak, so different for free standing subjects.
Lateropulsion during angular acceleration in sitting subjects is described by Torok and Kahn (1960). From the experiments by Wapner et al. (1951) concerning the visual perception of the vertical during body torsion around the vertical axis, a lateropulsion may be deduced as well, because they showed a tilt of the subjective vertical during acceleration. By electric stimulation of the ampullary nerve of a lateral canal in alert cats and monkeys Suzuki and Cohen (1964) also obtained body and limb responses which can be described as body torsion and lateropulsion. The postural changes deduced from the cited literature as well as from the described experiments are summarized in Table 2.IV. Again, the results are arranged in such a way

	Caloric Irr.	Caloric Irr.	Optokin.	Optokin.	Following Active Rotation	Following Passive Rotation	Rotation Acceler.	Electric Stimul.
	Standing	Sitting	Standing	Sitting	Standing	Standing	Sitting	Standing
Nystagmus	L	L	L	L	L	L	L	L
CV	R	L	L	L	R	L	L	-
Lateropulsion	R	-	R	R	R	-	R	R
Body Torsion	R	-	L	L	R	L	-	R

Table 2.IV. Survey of experimental results. For explanation see text.

that the nystagmus is always to the left. In this table two interesting aspects are seen concerning the lateropulsion and the body torsion : the lateropulsion is always coupled with the nystagmus (i.e. they go into opposite directions, whereas the bodytorsion is always coupled with the CV (i.e. they go into the same direction). From a physiological point of view it was to be expected that the nystagmus and the CV should be in the same direction. However, from Table 2.IV. it is clear that there are three cases with unexpected direction of body torsion and CV (i.e. "following active rotation, standing" , "caloric irrigation, standing" and "electric stimulation, standing" although in the last case the CV of the monkeys is not known of course). From the findings in chapter 1 it might be deduced that the lack of the reversal of the CV in the case "following active rotation, standing" is due to a possitive after effect of the somatosensory system involved in the stepping around. What kind of somatosensory interference takes place in the other two situations is not yet clear : a similar somatosensory interference would not induce CV, as the subjects are standing only, and certainly no reversal of the direction of the CV. Obviously, further research is required before definite conclusions can be reached, the more so since in a recent study Fitger (personal communication) found a dissociation between body torsion and CV after passive rotation when working with a motor driven platform (abrupt stop after constant angular velocity rotation of 90°/sec). She confirmed, however, the CV findings of the present experiments.

In conclusion it can be stated that an important parameter in studying human posture by stimuli which might induce CV , is whether a CV is experienced indeed and, if so, in what direction. This might be helpful in explaining the sometimes completely opposite postural behaviour of some subjects since the direction of the CV (c.q. the torsion) is not always the same for each subject especially in the more complex (standing) situations.

CHAPTER 3

ROLL VECTION AND HUMAN POSTURE

Summary

Rotation of the visible surround about the line of sight results in roll vection and a shift of the centre of gravity in the direction of pattern motion.
As a prelude to the tilting room experiments in which the rotation axis is at ankle-height, one experiment is described in this chapter in which the rotation axis is at eye-level. It is shown that the postural behaviour is different when the position of the rotation axis is fixed in space or is fixed relative to the head. These findings are discussed and compared to data known from literature.

3.1. INTRODUCTION

Rotation of the visible surround about a sagittal axis coinciding with the line of sight of a subject in upright position (to be called "Optic Roll, may result in a sensation of rotation in the opposite direction, to be called Roll Vection. This is comparable with Circular Vection with, however, one important difference. In case of CV the axis of rotation coincides with the direction of gravity whereas in case of RV these directions are perpendicular to each other. It is therefore not surprising that the subjective experience in Roll Vection is rather complex, in fact paradoxical : one experiences a rotation but the upside down position is never reached. Such a sensation is often experienced as unpleasant (cf. the Coriolis effect in 1.1.).
Optic Roll has been used in order to study the influence on the subjective and postural vertical. For better understanding of the effects of the Optic Roll some of the publications on this subject will be reviewed briefly.
(a) Dichgans et al. (1975) and Held et al. (1975) in their experiments used

a rotating disk which was covered with circular dots of different sizes. This disk was monocularly viewed in such a way that the visual field was limited to 130° of visual angle. A coaxially mounted small disk, one half painted in black, one half in white, just in front of the disk's surface, could be rotated by the subject in order to adjust the partition of the white and black halves to his subjective vertical. Dichgans et al. (1975) found a systematic tilt of the subjective vertical in the stimulus direction. At a stimulus velocity of about 30°/sec the effect is saturated for healthy subjects with a tilt of about 15° (one subject even showed a tilt of over 40°). The effect reaches its maximum within 20 seconds. These findings were confirmed by Held et al. (1975).

(b) In a second experiment Dichgans et al. (1972) used a link-trainer. Via the trainer windows an Optic Roll was presented by means of a projector on top of the link-trainer. The subjects were asked to keep the link-trainer in a horizontal position by means of a hand-controlled stick, despite mechanically induced positional disturbances. It appeared that the subjects mismatches the position for 8.5° on the avarage, again in the direction of the Optic Roll.

(c) Dichgans et al. (1976) investigated the influence of the Optic Roll on posture too. In order to induce an Optic Roll they used a hemispherical dome with a radius of 40 cm, again covered with coloured patches. The average displacement of the centre of gravity in the stimulus direction was found to be about 6 mm with healthy subjects. Dichgans stated in another paper (Dichgans et al., 1975) that after a sufficient time of stimulation most observers were unable to avoid falling down in the direction of screen rotation.

The explanation of postural behaviour in (c) is given in terms of a conflict between vision (signaling Roll Motion) and the graviceptors (signaling no change in body position) but this would be true only if the roll axis had been at ankle-height. This can only be obtained with a dome with a diameter of at least 5 m, which is of course quite a construction : then the visual information in case of Roll Motion of the dome or Roll Motion (fall) of the subject would be exactly the same. The difficulty with the small dome is that

a lateral shift of the head of the subject in front of the dome results in a retinal shift of the whole dome, because the dome is fixed to the wall. Such a retinal shift might be perceived, indicating the shift of the head, resulting in a readjustment of the body. So with free standing subjects vision might play a stabilizing role as well. This argument is completely disregarded in literature. The aim of this chapter is to show the validity

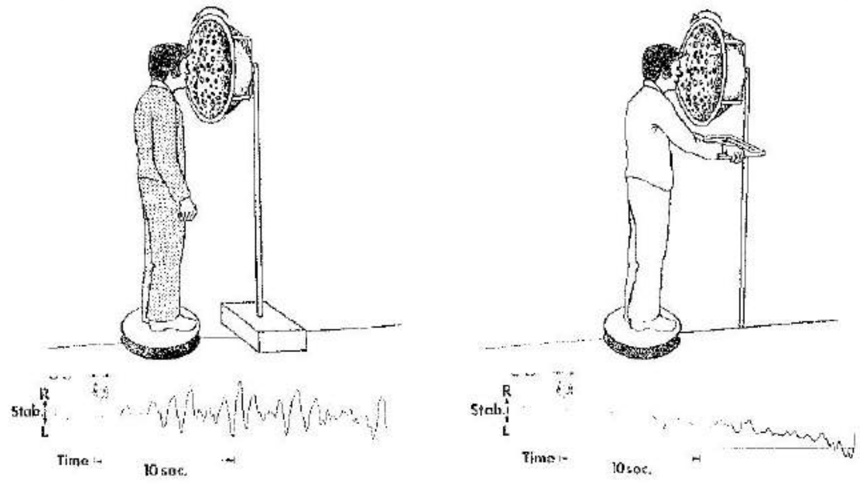

Fig. 3.1. Example of stabilograms of a subject under the conditions dome fixed-no foamrubber (le) and dome in hands-no foamrubber (ri).

of the argument. Without such a large dome (rotating axis at ankle-height, 5m in diameter) it is not possible to thoroughly investigate the influence of Roll Vection on posture as it should be done, but it is worth to be done in view of the tilting room experiments to be described in the next chapter.

3.2. APPARATUS AND METHODS

3.2.1. The Optic Roll

Roll vection was induced by means of a hand driven hemispherical dome, diameter 50 cm, the surface of which was covered with coloured dots. This very light device was connected to an aluminium bar construction (one-point stand) as depicted in Fig. 3.1. The construction was either fixed or standing with a point on the floor in which case the subjects kept holding it. In the latter case the dome remained in the same position relative to the head. Because the dome is hand driven it was decided to use the following procedure. The observer closed his eyes after which the dome was set into motion with a too high velocity. The time required for each revolution was recorded continuously and when the velocity had decreased to about 300^{o}/sec ($\pm$ 40^{o}/sec) the subject was asked to open his eyes. The stimulus was maintained for 30 seconds.

3.2.2. Posturography

The body sway was recorded by means of the stabilometer as described in 2.2.4. Part of the experiments was performed with a piece of foamrubber (height 10 cm, s.g. 40 kg/m^3) placed on top of the stabilometer and upon which a rigid plate was attached. In this way the position of the feet to one another does not alter which makes the exteroceptive information of the ankle joints even less effective. The position of the head with respect to the dome was continuously monitored with a videocamera. All proceedings were recorded on sound- en videotapes.

3.3. EXPERIMENT AND RESULT

In this experiment 23 healthy subjects without previous experience with such experiments participated. They were submitted to four testconditions :

A. Dome in hands - no foamrubber

B. Dome in hands - with foamrubber

C. Dome fixed - no foamrubber

D. Dome fixed - with foamrubber

10 of the subjects were submitted to a clockwise (CW), 13 of the subjects to a counterclockwise (CCW) Optic Roll. The four conditions were randomized.

The results are shown in Table 3.I.

Subjects	Conditions				Stimulus direction
	Dome in hands no foamrubber	Dome in hands with foamrubber	Dome fixed no foamrubber	Dome fixed with foamrubber	
1	-	→ ri, 19	-	→ ri, 14	CW
2	→ ri, 21	→ ri, 25	-	→ ri, 5	CW
3	-	→ le, 5	→ ri, 28	→ ri, 2	CW
4	→ ri, 24	→ le, 4	-	→ ri, 5	CW
5	→ ri, 4	→ ri, 4	→ ri, 5	→ ri, 6	CW
6	→ ri, 10	→ ri, 18	-	→ ri, 10	CW
7	-	-	-	→ ri, 15	CW
8	→ ri, 12	→ ri, 15	→ -	→ ri, 6	CW
9	→ ri, 7	→ ri, 4	→ ri, 10	→ ri, 10	CW
10	-	-	-	-	CW
11	→ le, 14	→ le, 10	-	→ le, 10	CCW
12	→ le, 5	→ le, 4	-	→ le, 5	CCW
13	→ le, 20	→ le, 13	-	→ le, 4	CCW
14	-	→ le, 20	→ le, 24	→ le, 20	CCW
15	→ le, 10	→ le, 11	→ le, 7	→ le, 7	CCW
16	→ le, 25	-	→ le, 25	-	CCW
17	→ le, 16	→ le, 15	→ le, 24	→ le, 13	CCW
18	-	→ le, 29	-	-	CCW
19	-	→ le, 4	-	→ le, 15	CCW
20	→ le, 28	→ le, 15	→ le, 6	→ le, 6	CCW
21	-	→ le, 10	-	→ le, 18	CCW
22	→ le, 10	→ le, 17	-	→ le, 7	CCW
23	→ le, 21	→ le, 22	-	-	CCW

Table 3.I. Fall direction and time before falling (in sec).

The effect of foamrubber on the stability during rolling is such that it does not matter whether the position of the head relative to the dome changes or not. In condition B 20 out of the 23 subjects fell over, and in condition D 19. This in strong contrast to the responses without foamrubber: in condition A 15 subjects fell over and in condition C 8.
No clear differences in time before falling over can be established by comparing condition A with C and condition B with D.
The stabilograms indicating the strong effect of a head-fixed stimulus as obtained in condition A and C can be described as follows. If the position of the dome is not changed with respect to the subject's head (condition A), the stabilogram is relatively quiet : the subject slowly falls over. If the dome position is not related to the head (condition C), the stabilograms are different. If the subject falls over, this is rather abruptly and if he doesn't fall, the centre of gravity shifts into the stimulus direction, but

the instability is considerable. Representative examples of the stabilograms in condition A and C (of the same subject) are shown in Fig. 3.1.

3.4. DISCUSSION

In their studies about the influence of tilted reference frames on the perception of verticality Witkin and Asch (1948) report about a sensation which can be described as Roll Vection, although they don't use this term. In their experiment a subject, lying horizontally on his side, views a frame rotating slowly over 360° in a vertical plane. This frame (a square frame, each side of which was 1 inch wide and 40 inch long) is the only visible object in an otherwise complotely dark room. This subject reported that the frame (as the consequence of experienced self-rotation) was always in a fixed position although he saw it rotating. This was not a continuous process. When the frame had rotated almost to the point were he felt his head hanging down vertically, he experienced a change of the base line of the frame to an altitude, and simultaneously the snapping back of his body to the horizontal position.
For more detailed information about the influence of the Optic Roll on the perception of verticality reference is made to Dichgans et al. (1972, 1976). They as well as Mauritz et al. (1977) give the following explanation for the effects of Optic Roll stimuli. A postural sway (e.g. to the right) results in a relative movement of the visible surround to the left. If such a relative movement is simulated under laboratory conditions, it results in a tilt of the subjective vertical to the left and a correcting body movement, also to the left. But as the initial body movement is missing, this causes falling, whereas under real life conditions this would have been a correct righting response.
This explanation, however, seems to be appropriate to an Optic Roll with the rotation axis at ankle-height. The main objection against the posturographic experiments with fixed Optic Roll stimuli with the rotating axis at eye-level, as already mentioned in the introduction 3.1., is substantiated by the results of the experiment described in 3.3, but in fact also by the link-trainer experiment as described in 3.1. sub (b).

The shift of the link-trainer position of 8.5° is much larger than that obtained with the posturographic experiments : a lateral tilt of the body is maximal ∿ 2° otherwise the subject falls over. In the link-trainer experiment the Optic Roll remained the same in spite of the tilt because the projector was positioned on top of the link-trainer.
So in posturographic experiments with a fixed dome vision has not only a destabilizing influence but stabilizes posture as well.
From the above mentioned considerations it can be derived that a fixed Optic Roll stimulus at eye-level with free standing subjects is a complex stimulus at the moment the subject moves his head. Therefore there is no stationarity so it is not permitted to Fourier-analyze the stabilograms under such circumstances and to draw conclusions by inspecting the power spectrum about the influence of vision especially in the lower frequency range (Dichgans et al., 1976). These low frequency components probably more reflect the time between the postural deviations as Dichgans et al. (1975) state that ".... intermittent loss of roll sensation occurs frequently and is accomplished by a simultaneous break-down of the induced postural deviation....".
Roll Vection and the shift of the subjective vertical are accounted for by assuming that neurally encoded signals of visual motion modulate signals from graviceptors at some level of the nervous system (Dichgans et al., 1972) analogous to the Circular Vection as described in chapter 1. In case of Roll Motion the involvement of the otolith system is a complicating factor ; the discussion about how the canal system or the otolith system might be involved will be postponed until the discussion in 4.4.

CHAPTER 4

TILTING SURROUNDINGS AND HUMAN POSTURE

Summary

Stationary tilting visual surroundings influence the perception of verticality, shifting the subjective vertical into the direction of the surround tilt. It is shown that for standing subjects this deviation is independent of the position or rigidity of the foot support. The upright position is also influenced by the tilting surroundings, resulting in a slight shift again in the direction of tilt. Sinusoidally tilt of the visual surroundings induces a sinusoidal body sway. This sway increases when the somatosensory information is reduced by the use of foamrubber on the foot support, thereby enhancing the sensory weight of vision.

4.1. INTRODUCTION

The information of the otolith system (the utricle-otoliths, which register the orientation of the head relative to the direction of gravity) together with the somatosensory information about the relative positions and the movements of parts of the body is sufficient to provide a correct gravitational orientation. Directional structures in the visual field (mostly horizontal or vertical) give additional information via the visual channel. Under everyday conditions the information of these sources is coherent. The induced perceptual space transformations by varying the body tilt and the tilt of the visual surroundings, separately or in combination, have been investigated extensively mostly with subjects in a sitting or lying position (literature reviewed by Howard and Templeton, 1966, and by Bischof, 1974). The influence of tilting surroundings on standing upright has been mentioned in literature only occasionally. According to Edwards (1946) postural stability is affected when looking at a picture hung 15° askew. Kitahara and Uno (1967) report that postural stability is slightly affected when standing on

a sinusoidally tilting platform with stationary visual surroundings but that stability decreases when the visual surround tilts together with the platform . They state that the latter condition causes severe motion sickness ; they observed that even a stationary tilted room could induce symptoms similar to motion sickness. This last finding was confirmed by de Wit (1972) and Kapteyn (1973) but only when the subjects were walking in a stationary tilted room. In stabilometric recordings of subjects standing on a horizontal platform in a room tilted over 20° Kapteyn did not find a decrease of stability when compared to normal circumstances. Stabilometric data of de Wit (1972, 1973) revealed that upright stance is influenced by a vertical illuminated bar that slowly tilts around a horizontal axis at ankle height just in front of the subject : in some cases a slight tendency to follow the movements of the bar could be observed.
The experiments described in this chapter are in fact an extension of those performed by the Wit and Kapteyn. Since peripheral vision is of special importance for dynamic spatial orientation (Brandt et al., 1973) the bar was replaced by a three-dimensional tilting room. With this device in combination with a tilting platform the postural and perceptual consequences of static and dynamic tilt of the room and/or platform were investigated. This chapter deals with the reactions of healthy subjects whereas in chapter 6 the influence of tilting surroundings on patients is discussed.

4.2. APPARATUS AND METHODS

4.2.1. Tilting Room I

Tilting Room I was a motor driven device, tilting laterally from the base. The front side was open. The back wall (3m x 2m) was painted with alternating black and white vertical stripes, each 1.5 cm wide. The subject stood in front of the room toward the open front side at a distance of 1.5 m from the back wall. The side walls, floor and ceiling were of such dimensions that the entire visual field was covered. The room was illuminated by two lamps of 75 W each, mounted on the back wall ; the laboratory itself was completely dark during the tests.

The tilt could be varied up to 15° to the right or to the left. A sinusoidally varying tilt could be generated in the frequency range from 1/60–1/3 Hz. By means of a potentiometer the tilt of the room was recorded during the sinusoidal tilt experiments with a view to further data handling. For the static tilt experiments the tilt of the room was read from a protractor (accuracy ± 0.02°). At the back wall a rotatable test-bar (length : 50 cm ; rotating axis at eye-level) was attached by which the subject indicated his subjective vertical (subjective vertical (SV) = direction of gravity as perceived by the subject). In some experiments a Békésy-like method was used as long as a button was pressed , the bar rotated to the right (CW) , when released the bar rotated to the left (CCW). The angular velocity of the rod was 6°/sec. The subject was instructed to press the button the moment the bar was in accordance with his SV, and to release the button after a few seconds. In this way about every 5 sec an estimation of the SV was obtained. The position of the bar was recorded by a potentiometer and the exact SV indications were determined by a computer program. In each test condition the median of these SV estimates was taken to represent the SV of the subject for that particular condition.
In another experiment the subject could, by means of a position servo, adjust the bar to his SV by turning a potentiometer adjustment method. These adjustments were read directly from a protractor (accuracy ± 0.02°).

4.2.2. Tilting Room II

Tilting Room II (manufactured by Tönnies, Freiburg im Breisgau) was constructed in order to have more stimulation facilities than with Tilting Room I. Again the tilting is done from the base. The device (2.5m x 2.5m x 2m) is completely closed, except for a hole in the floor, and has two doors in two adjacent walls. Depending on the stimulus mode (lateral or foreaft) one of the doors is open. Two ceiling-lights (75 W each) illuminate the room.
A tilting platform is mounted just under floor-level with its tilting axis coaxial to the tilting axis of the room. This platform is constructed in such a way that the tilting axis is at ankle height of the subject standing on the stabilometer on the platform. Several methods of operation can be chosen :

(1) platform in fixed position (12° to the left up to 12° to the right) free from the tilting room which is driven by the motor (12° to the left up to 12° to the right) ;
(2) platform mechanically coupled to the room, both driven by the motor (12° to the left up to 12° to the right) ;
(3) room in fixed position (12° to the left up to 12° to the right) free from the platform which is driven by the motor (12° to the left up to 12° to the right).

Sinusoidal tilt of maximum 12° can be realized up to 1/6 Hz, and of maximum 2° up to 1 Hz. The tilts of the room and the platform are servo-controlled (position feedback). With this construction the experimenter or the observer can easily manipulate the tilt of the room or of the platform by turning a potentiometer. In the static and semi-static conditions the tilt of the platform was read directly from a protractor (accuracy ± 0.02°) whereas the room tilt was obtained via a potentiometer and a digital voltmeter (accuracy ± 0.01°).

During lateral room tilt the SV was measured with the "Fan"-method. A fan-shaped cord construction was fixed at the back wall of the room with its centre at the tilt axis. These cords were stretched at 0.5° distance of each other, covering a range of 15° to each side. By numbering the cords in random order (which order was changed as much as necessary for each subject) it was possible to use this fixed construction for SV indication without introduction of unwanted cues : the subject was asked to indicate the cord which was in line with his SV.
In case of foreaft room tilt the perceptual space transformations were investigated by measuring the SH (=subjective horizon). For this purpose a linear vertical scale was fixed on the wall opposite to the subject. The subject was requested to indicate the scale number corresponding to his eye-level, after which the deviation of the SH from the OH (objective horizon = plane perpendicular to gravity at eye-level) was calculated, taking into account the changes in distance between the eyes and the wall of the tilted room and the length of the subjects.

4.2.3. Stabilometer

The stabilometer used in these experiments has already been described in 2.2.4.

4.2.4. Hydraulic Tilting Platform

A hydraulically driven tilting platform (constructed by Technische Dienst, AZVU) was, in combination with Tilting Room I, very useful in those test conditions in which the subjects, standing on the (tilted) platform were requested to adjust the platform to a subjectively horizontal position. The tilt velocity of the platform was 1.5°/sec ; the maximal tilt 5° to each side. By means of a valve system the experimenter or the observer could set the platform to each desired tilt. The tilt of the platform was determined by means of an adapted waterlevel (accuracy $\pm 0.02^{\circ}$).

4.2.5. Data Processing

All analogous signals were registered by a strip chart recorder (Siemens EM 81.80) and stored on a magnetic tape recorder (Philips Analog-7) for further data processing by the PDP-8I computer system. The data analyses are described for each experiment separately.

4.3. EXPERIMENTS AND RESULTS

The series of experiments on postural and perceptual consequences in tilting environments was started with Tilting Room I, and continued with Tilting Room II which was constructed later. This means that there is some overlap between the experiments performed with the two rooms.

4.3.1. (Semi-)static Room Tilt

4.3.1.1. Subjective vertical and lateral body sway as a function of static lateral room tilt

The aim of this experiment was to investigate the influence of static lateral room tilt (a) on the SV, (b) on the position of the centre of gravity of the body in the lateral plane and (c) on the stability of the lateral body sway of a subject standing on the stabilometer in fixed horizontal position. Room tilts (Tilting Room I) of 0, 0.5, 1, 1.5, 2, 3, 4, 5, 7 and 10° to each side were used. The stabilometer was used with and without one layer of foamrubber (see 3.2.2.) in order to make the somatosensory information from the ankle joints less effective. The conditions were presented in random order for one minute each in short subseries.
The tilt of the room was pre-set when the subject had his eyes closed. The subject was requested to stand upright, relaxed, and after opening his eyes his task was to indicate his SV by means of the Békésy-like method described in 4.2.1. The SV data were used from the whole one-minute recording whereas the stabilogram of only the last 30 sec was used for analysis in order to exclude possible transients.
Six healthy subjects (4 male, 2 female ; age 22-31) participated.

An analysis of variance has been performed on the SV data (Table 4.I.). This statistical technique determines which parameters are responsible for the variance among the data.
The room tilt is found to influence the SV indication significantly (48.6% of the variance). The subjects show significantly interindividual differences, but, this accounts only for a small percentage of the total variance (3.5%). Furthermore the parameter foamrubber is not contributing to the variance as a main effect but the first order interaction between subjects and foamrubber is highly significant and contributing to the variance to a considerable extent (11.4%), indicating that foamrubber results in a disturbance of the SV indication for each subject in a different way. In Fig. 4.1. the SV data obtained in the conditions with and without foamrubber are plotted as a function of room tilt. The linear behaviour over the entire range of room tilt investigated is noteworthy.

Source of variance	Sum of squares	df	F-ratio	Variance %	Significance %
T(tilt angle)	1762	18	26.1	48.6	< 0.001
F(foamrubber x S(subjects)	369.5	5	9.99	11.4	0.001
S	138.6	5	3.75	3.5	< 0.5
F x T	177.5	18	1.33	1.3	n.s.

Table 4.1. Results of an analysis of variance of the SV values as a function of room tilt and the use of foamrubber measured for six subjects.

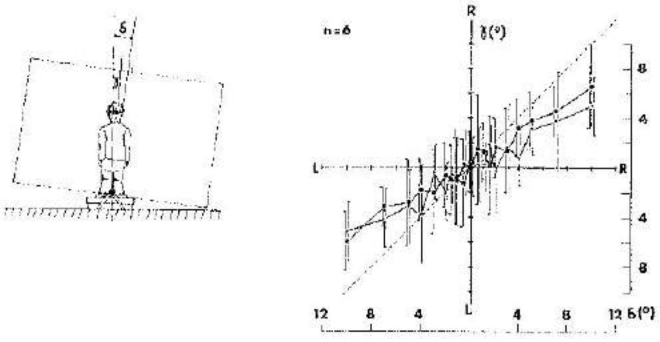

Fig. 4.1. Deviation (γ) of SV from direction of gravity (mean value ± 1 σ) as a function of lateral room tilt (δ) obtained with the Békésy-like method in Tilting Room 1 from six subjects who were standing on the platform which was in fixed horizontal position (+: without, ● : with foamrubber).

The left/right stabilograms have been analysed in order to obtain an indication of the postural stability during room tilt. As measures of stability the RMS and the Total Sway Path have been computed because these two

measures both reflect stability of the stabilogram rather well (Kapteyn and Bles, 1976). On these data an analysis of variance has been carried out as well. As was to be expected the conditions with and without foamrubber are statistically significantly different from each other. The interindividual differences are also contributing considerably to the variance, but no dependence upon room tilt was found.

From the left/right stabilograms also the median position was determined in order to detect a possible shift of the centre of gravity in relation to the room tilt. An analysis of variance did not reveal a statistically significant relation, although visual inspection of the data indicated a slight relation. This discrepancy was probably due to saturation of the effect at room tilt of more than about 3° in which case the analysis of variance is not the adequate analysing technique. Therefore these data were handled in a different way by determining the Spearman rank correlation coefficient for each subject separately and Kendall's concordance coefficient for the data together. This analysis showed that there is some influence of room tilt on the position of the centre of gravity indeed : the subjects are shifting their centre of gravity into the direction of room tilt, but only to an extent of a few mm, both with and without foamrubber ($p < 0.05$).

The result of this experiment indicates that the spontaneous movements of the centre of gravity are too large to reveal the minor postural effects induced by static room tilt very clearly by means of stabilometry : the S/N ratio is too bad. It is also possible that the subjects made use of knowing that the stabilometer was positioned horizontally, although it is impossible to determine the extent to which this cue was used. Therefore another strategy has been chosen and worked out in experiment 4.3.1.3.
The SV-adjustments (Fig.4.1.) show a linear behaviour up to a room tilt of 10°. The aim of experiment 2 was to extend this range and to obtain more accurate SV-values by means of the position servo (4.2.1.) since the Békésy-like method introduced rather large standard deviations (Fig.4.1.)

4.3.1.2. SV and Static Room Tilt

With the adjustment method of the position servo in Tilting Room I the SV was determined for room tilts up to 15°. The room tilts investigated were 0, 1, 2, 3, 6, 9, 12 and 15° to both sides presented in random order. In order to prevent the subject from using the possible cue of the horizontal foot support, the hydraulic tilting platform was used which was given a tilt of 0, 1, 2, 3 or 4° to each side, also in random order. The subject stood on the platform with his eyes closed after which the room and the platform were given the required tilt (the platform after some irregular tilting to both sides). Then the subject was asked to open his eyes, to wait for 20 sec and to adjust the bar, which was initially in a vertical position relative to the room, to his SV.

Four healthy subjects (1 male, 3 female ; age 18-22) participated. The conditions were presented in subseries of nine conditions each.

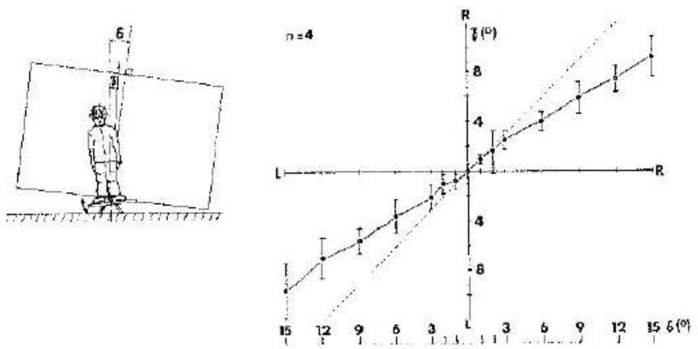

Fig. 4.2. Deviation (γ) of SV from direction of gravity (mean value ± 1 σ) as a function of lateral room tilt (δ), obtained with the adjustment method in Tilting Room I from four subjects who were standing on the tilting platform. Each condition was measured under nine different tilt angles (up to 4° to each side) of the tilting platform.

The resulting SV adjustments as a function of room tilt are shown in Fig. 4.2. The relationship between room tilt and SV values is seen to be linear

over the entire range investigated. Linear regression shows direction coefficients of 0.56, 0.61, 0.64 and 0.69 for the subjects respectively. The increasing standard deviations with increasing tilt angle are due to these differences : the standard deviations for the subjects spread around 1°. Analysis of variance showed that the SV adjustment was independent of the platform tilt.

The SV has been measured once more in Tilting Room II with the "Fan"-method, described in 4.2.2., under static lateral room tilt of 4, 8 and 12° to each side. This experiment was done with each subject

(A) standing on the platform which was in fixed horizontal position.
(B) standing on the platform which was coupled to the room and
(C) sitting on a chair with support of the head, on the platform in fixed horizontal position.

The subject had his eyes closed when the room was given the desired tilt and had to wait for 20 sec before indicating the cord parallel to his SV. Six healthy subjects participated (3 male, 3 female : age 18-38). The test conditions were randomized as much as possible and each test condition was presented twice.

The results are shown in Fig. 4.3.
The results for only five subjects are shown because the sixth subject had severe problems with this particular SV measuring method and was not able to indicate the SV properly. The direction coefficients for these five subjects are for condition
(A) : 0.62, 0.62, 0.60, 0.59, 0.65 respectively, for condition
(B) : 0.62, 0.71, 0.65, 0.60, 0.65 and for condition
(C) : 0.41, 0.78, 0.66, 0.59 and 0.59.
No statistically significant differences among the SV values in conditions (A), (B) and (C) were found indicating that the SV, at least for this range is not determined by the somatosensory system and is therefore the result of an interaction between vision and the vestibular (utricular) system. This is in good agreement with the experiment with foamrubber described in 4.3.1.1.

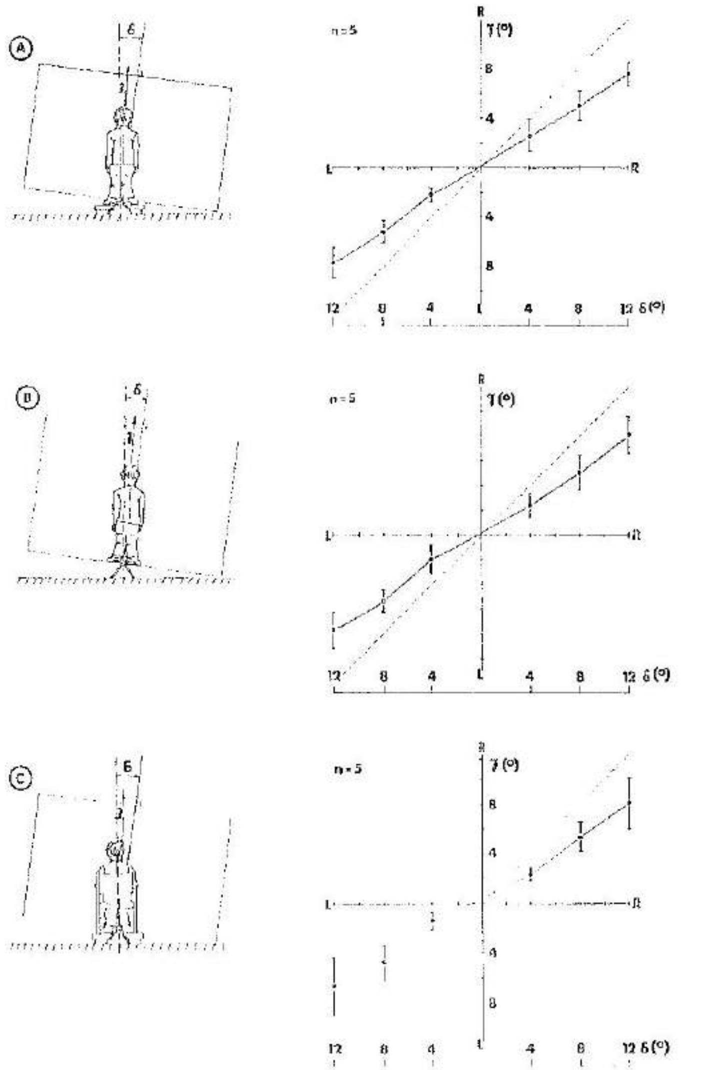

Fig. 4.3. Deviation (γ) of SV from direction of gravity (mean value $\pm$ 1σ) as a function of lateral room tilt (δ), obtained with the "Fan" method in Tilting Room II from five subjects (tested twice) (A) standing on the platform which was in fixed horizontal position, (B) standing on the platform which was mechanically coupled to the room, and (C) sitting on a chair (with support of the head) on the platform in fixed horizontal position.

The influence of static foreaft room tilt on the perception of the horizon has been investigated in Tilting Room II with the subjects standing on the platform in fixed horizontal position. 16 Subjects (5 male, 11 female ; age 18-32) participated in this experiment.

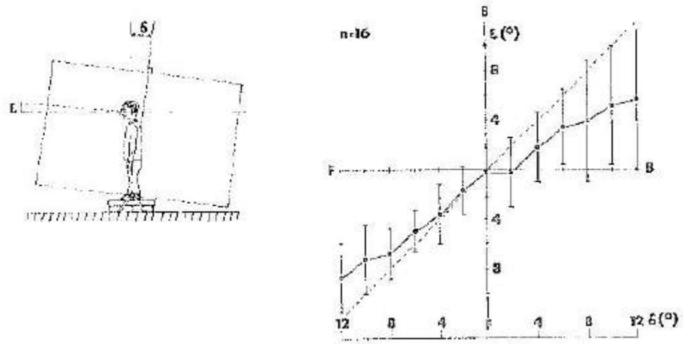

Fig. 4.4. Deviation (ε) of SH from OH (mean value $\pm$ 1 σ) as a function of foreaft room tilt (δ), obtained in Tilting Room II from sixteen subjects who were standing on the platform which was in fixed horizontal position.

The results of this test, analysed with the method described in 4.2.2. are shown in Fig. 4.4. The magnitude of the effect is of the same order as found for the deviation of the SV at lateral room tilt.

The experiments on the perception of verticality in tilting surroundings can be summarized as follows:
With free standing subjects static lateral room tilt induces a deviation of the SV from the direction of gravity toward the direction of room tilt. At least up to 15° of room tilt a linear relationship has been found between the deviation of the SV from gravity (γ) and the room tilt (δ):

$\gamma = m.\delta$ $\quad$ ($\bar{m}$ = .62 , σ = 0.07)

This relationship is independent of the position or rigidity of the supporting surface on which the subject is standing, but shows interindividual differences. Foreaft tilt induces similar perceptual space transformations.

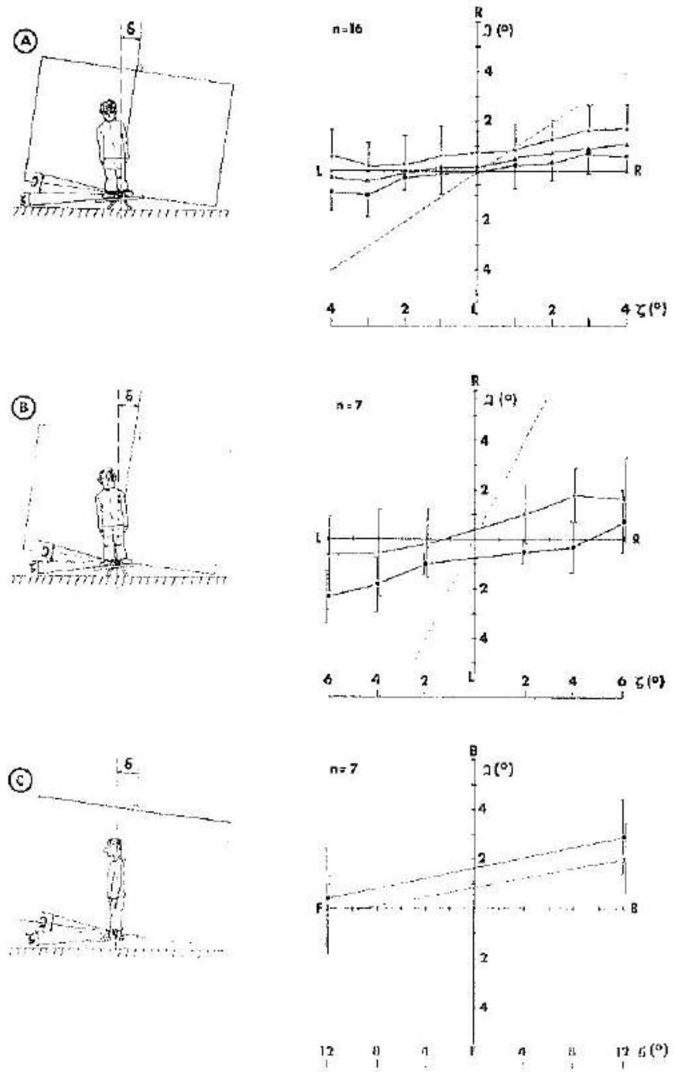

Fig. 4.5. Deviation (ϑ) of subjectively horizontal platform from OH (mean value ± 1 σ) as a function of initial lateral platform tilt (ζ), obtained in Tilting Room I under lateral tilt conditions (+: δ = 15° → R, Δ: δ = 0°, o: δ = 15° → L) from sixteen subjects (A) and in Tilting Room II (+: δ = 12° → R, ●: δ = 12° → L) from seven subjects (B) ; (C) shows the deviation (ϑ) of the subjectively horizontal platform from OH as a function of initial foreaft platform tilt (ζ) under foreaft room tilt conditions (+: δ = 12° forward, ●: δ = 12° backward) from the same seven subjects.

4.3.1.3. Posture and Static Room Tilt

In order to prevent the difficulties in studying the influence of static lateral room tilt on posture as described in 4.3.1.1., the hydraulically tilting platform (see 4.2.4.) was used in this test. The subject, standing on the tilting platform placed in front of Tilting Room I, was requested to adjust the platform to normal the (earth-horizontal) position. Deviations angles from the objective horizon were determined by use of a waterlevel. The initial tilt of the platform was 0, 1, 2, 3 or 4° to each side whereas the room tilt was 0, 15° to the left or 15° to the right. The subject stood on the platform with his eyes closed after which the room and the platform were given the required tilt (the platform after some irregular tilting to both sides). Then the subject opened his eyes and after 20 sec adjusted the platform to a subjectively horizontal position. His feet were in the normal ("ten to two") position but he was allowed to move his body and the platform to both sides as long as necessary to obtain the desired position. The experimenter then determined the platform tilt. The experimental conditions were randomized as much as possible, an the experiment for each subject was performed within half an hour. 16 Healthy subjects (9 male, 7 female ; age 20-32) participated.

The results are shown in Fig. 4.5.A. It is easily seen that both the initial platform tilt and the room tilt have an ipsiversive influence on the adjustments. The adjustments of the platform under both 15° tilt conditions are significantly different from each other ($p < 0.01$).

This experiment was repeated with Tilting Room II and its accessory tilting platform (for description see 4.2.2.). The room tilt was either 12° to the left or 12° to the right and the initial platform tilt was 4, 8 or 12° to each side. The procedure was the same as described for the previous experiment. Seven healthy subjects (5 male, 2 female ; age 18-32) participated.

The results are shown in Fig. 4.5.B. The differences in the adjustments during tilt to the left and to the right are statistically significant

($p < 0.01$). The results are in agreement with the findings of the previous experiment.

The same seven subjects also participated in the next experiment. This test was performed in order to reveal the influence of foreaft room tilt (12^0) on the adjustment of the platform into the horizontal position from initial forward or backward tilt of 12^0.

The results are shown in Fig. 4.5.C., indicating that the same effects are present for foreaft tilt as for lateral tilt with the same order of magnitude. The subjects apparently set the platform tilted backward on the average which might be due to the fact that one is apt to shift the centre of gravity forward in case of postural instability (cf. forward shift during optokinetic stimulation in Fig. 2.2.).

In the next experiment three conditions were compared in which the visual stimulus was not stationary or absent :

(A) adjustment of the platform to the horizontal position in the absence of visual information ;
(B) adjustment of the platform into the horizontal position with the room coupled to the platform (tilt of room and platform the same) ;
(C) adjustment of the room into the normal (vertical) position while standing on the platform fixed in horizontal position.

The platform and/or room tilt was 4, 8 or 12^0 to each side.
The experimental procedure was similar to the previously described experiments.
Six healthy subjects participated in this experiment (3 male, 3 female ; age 18–38).
The conditions were randomized and each condition was presented twice.

The results are shown in Fig. 4.6. It is seen that the values obtained in the eyes-closed condition (A) are situated in between the values obtained with the 12^0 room tilt to the left and to the right (Fig.4.5.B.).
In Fig. 4.6. again the dependence on the degree of initial platform tilt

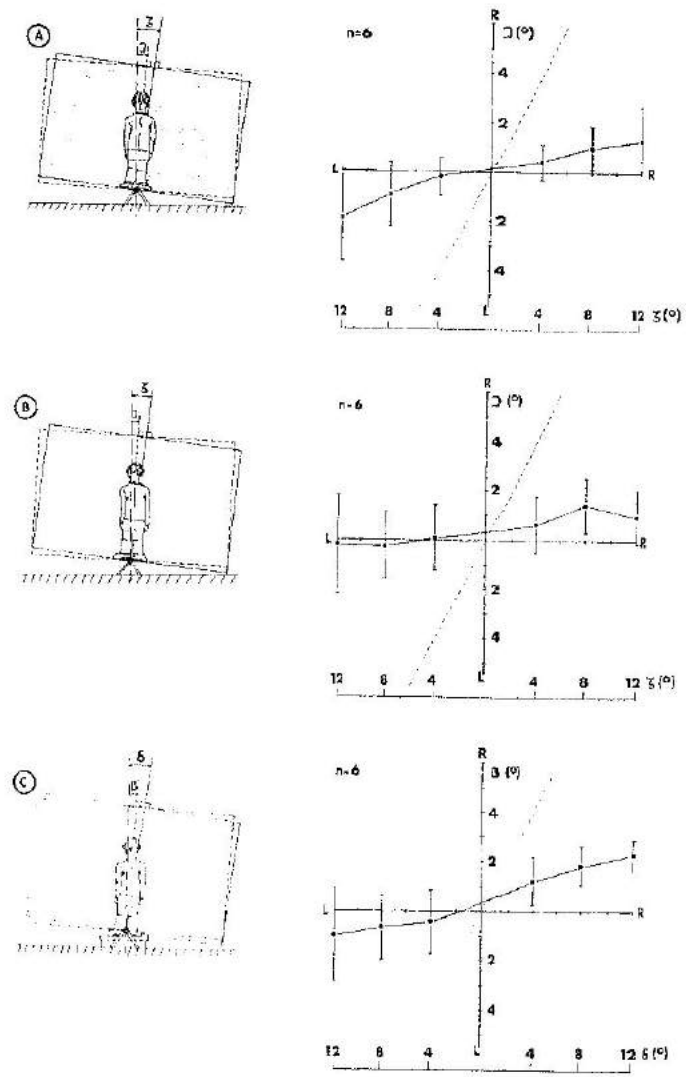

Fig. 4.6. Deviation (θ) of the subjectively vertical room from the direction of gravity as a function of initial room tilt (ξ), obtained from six subjects under the conditions (A) standing on the platform which was coupled to the room, light off ; (B) standing on the platform which was coupled to the room, light on ; (C) standing on the platform which was in fixed horizontal position.

is seen. This dependence is less clear when the room was coupled to the platform (B), although the initial tilt direction is still the direction of the final deviation of the settings. It is interesting to note that coherent disturbance of the room and the platform is handled slightly better than the disturbance of the room or platform separately.

Summarizing these experiments on stationary tilting surroundings and posture, we may conclude that a tilting surround induces a shift of the body in the same direction. This has been revealed by the adjustments of the supporting surface into the normal position. Another feature of interest is the dependence upon the initial platform tilt (final deviation in the same direction as the initial deviation). Similar effects were obtained when adjusting the room into the vertical position (which is in fact SV indication).

4.3.2. DISCUSSION

The tilting rooms, and especially Tilting Room II, are in fact ideal optic stimuli since the whole visual field is used which is of importance because of the dominant role of the retinal periphery in spatial orientation (Brandt et al., 1973). Furthermore Tilting Room II is a "natural scene" with clear directional cues which has been shown to provoke the strongest directional induction effects on the SV (see Bischof, 1974).
The influence of lateral tilt of both rooms on the SV has been found to be :

$$\gamma = m \cdot \delta \qquad (1)$$

$(\bar{m} = 0.62 \; ; \; \sigma = 0.07)$

γ = deviation of SV from direction of gravity

δ = room tilt. $\delta \leq 15^{0}$.

The three methods used to determine the SV have all shown to yield this relation. However, the Békésy-like tracking method (4.2.1.) introduced rather much dispersion and some subjects experienced difficulties with the "Fan" method (4.2.2.).

In literature only few data are available directly comparable with the

present findings. Experiments concerning SV measurements mostly deal with body tilt (sitting or lying subjects) and optic tilt at the same time, and the tilt angles are rather large in those experiments. However, Witkin and Asch (1948) reported on an experiment with their rod and frame construction (see 3.4.) which was performed with standing subjects. In their experiment the frame was initially tilted over 15, 30 or 60^{0} to the left. The mean deviations of the SV from gravity were found to be 8.6, 9.3 and 5.9^{0} respectively in the direction of frame tilt. The SV deviation (γ) at the 15^{0} tilt condition is in close agreement with the present findings. Equation (1) supposes for a room tilt of 30^{0} a γ which is twice as large as found by Witkin and Asch. The explanation for this rather small deviation given by Witkin and Asch is that at this tilt angle the natural redundancy expectations about the vertical and the horizontal are ambiguous : with the Witkin frame tilted at 45^{0} the visual system has no cues as to which side is base or altitude, so it is likely that the directional induction reduces, decreasing the SV deviation. In Tilting Room I and II this ambiguity is not present of course, but it is sure that the deviation of the SV from gravity has a limit at a certain room tilt. For technical reasons the tilt of the rooms was restricted to 15 and 12^{0}, respectively, and unfortunately at 15^{0} the maximum was not yet reached. Determination of this maximum would have been interesting since this maximal deviation is considered to be an index of the visuo-vestibular weight-ratio according to Bischof and Scheerer (1970) but it is not obvious that this deviation is the same for sitting and standing subjects.
The parameter m in equation (1) can be seen as an index for the weight ratio as well. Such a definition of the index is, in a certain sense, similar to the definition of von Holst (1950). In the present experiments this parameter m was found to be subject dependent indeed (see also 6.3.) , but the question of whether this factor is the determinant of the visuo-vestibular weight vertigo also for other visuo-vestibular interactions has not been solved yet.

Somatosensory information has been demonstrated to influence the perception of verticality. Steinleitner (1975) demonstrated this by keeping the position of the otoliths constant but varying the body position. For the present experiments it has been shown that the somatosensory system involved in standing is not involved in the determination of the SV since the SV values were found to be neither dependent on the platform tilt, nor on the rigidity of the foot support. Moreover, it was found that the SV values were the same for sitting and standing subjects. This implies that equation (1) should be in agreement with the model proposed by Bischof and Scheerer. Since in the present study the spatial position of the otoliths was kept rather constant and the room tilt limited, this is seen to be the case indeed.

Considering the findings of the SV, the influence of a static tilting surround on posture is remarkably small. Only with considerable difficulty the misleading visual information can be shown to be involved in postural stabilization. This is in agreement with findings of Kapteyn (1973). So, apparently, for postural stabilization the correct proprioceptive information is given a greater weight than the visual information.

The experimental results of the platform adjustments suggest a strong adaptation of the somatosensory system involved in standing, since the amount of initial platform tilt appears to be of considerable influence on the final adjustments. Similar adaptation effects have been reported for seated subjects (reviewed by Howard and Templeton, 1966). In the present study the subjects always believed that they had stood upright so in view of the rather large range of platform tilts, this points to an integration within the somatosensory system. This explains also why with stabilometry the influence of static room tilt on posture was so difficult to objectify. However, the fact that the final deviation of the platform remains on the same side as the initial deviation is not necessarily adaptation alone.

It might be a consequence of some uncertainty within the somatosensory system itself.

This concept will be illustrated with an experiment dealing with visual adaptation. It is known that, when a tilting frame is put back into the subjective vertical position, the final position deviates from gravity in the same direction as the initial tilt (Witkin and Asch, see also 4.3.1.3.). This effect is probably related to the concept of verticallity : the vertical refers to only one position, so, if a certain tilt of the

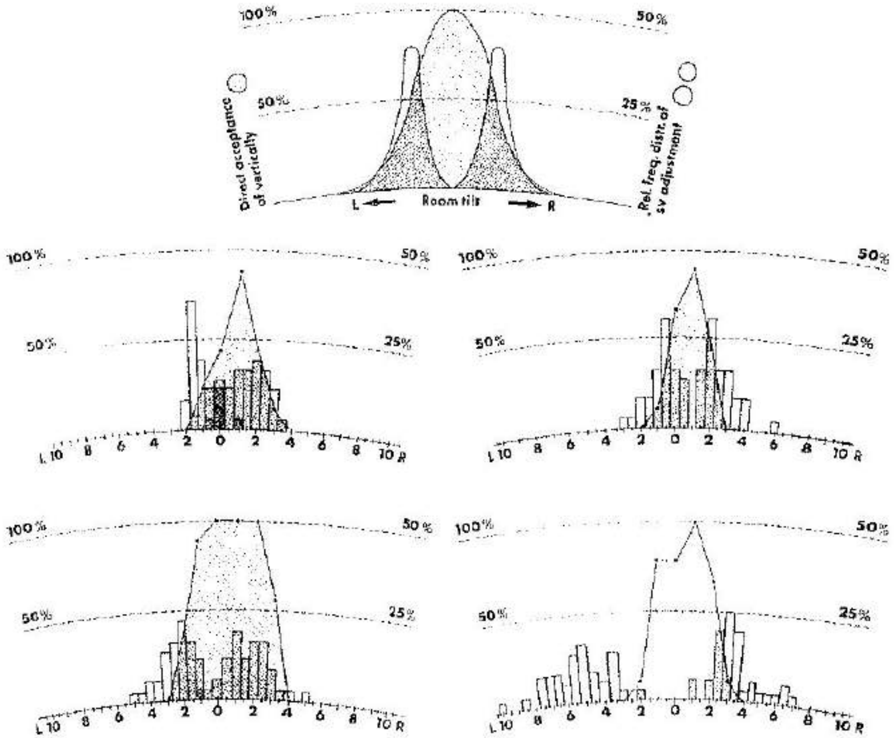

Fig. 4.7. Theoretically expected and experimentally found SV indications. For explanation see text.

frame is perceived as vertical by the subject, he will not make futher corrections since another position of the room cannot be "more" vertical. Suppose that a subject has his eyes closed and is, when opening his eyes, confronted with a tilted room : because of the proprioceptive information during the eyes closed period he is able to estimate whether the room is tilted or not. This can be repeated for several tilt angles and the result is a histram indicating the tilt which is accepted directly as vertical (Fig. 4.7.). When asked to set the tilted room (large tilt angle) repeatedly back into vertical position, it is to be expected that a distribution of these adjustments is obtained around the 50% points of the area of "direct acceptance" at the same side of the initial tilt. The results of such a test, done with Tilting Room I with four subjects, are shown in Fig. 4.7. too. The initial room tilt was 0, 1, 2, 3, 6, 9, 12 or 15° to both sides. The histogram of "direct acceptance of room tilt as vertical" is seen to be different for the subjects and most sharply defined for subject 1 and 3. In view of the results of the adjustment (only from initial room tilt of 6° or more is shown) subject 1 fits in with the concept (no adaptation), subjects 2 and 3 also show a visual adaptation (their distributions are skewed which can be explained only in terms of visual induction of the otolith information), whereas subject 4 shows predominantly adaptation.

| Subject 4 demonstrated after the experiment that she was quite able to minimize the deviation by closing the eyes for some seconds each time she perceived the room as vertical : apparently in the eyes-closed period the utricular information was reset resulting in recognition of the room tilt after opening the eyes again. |

A similar explanation can be given for the fact that the initial and final platform tilt remain in the same direction relative to gravity. Such an induced modification of the utricular information by optic tilt (corresponding to an apparent change in direction of the gravitational vector) should be analogous to the physiological mechanism for circular movements as described in chapter 1. Visual induction of otolith information transfering units in the vestibular nuclei of a cat has been reported by Daunton and Thomsen (1976), who demonstrated that the majority of units which responded to linear acceleration in a given direction also responded to the visual stimulation which simulated actual movement of the cat in the same direction.

4.3.3. Sinusoidally Tilting Surroundings and Posture

Sinusoidal tilt of the surroundings was induced by means of Tilting Room I ; the amplitude of the sinusoidal tilt was 5^0 for eight frequencies in the range of 0.016-0.22 Hz.

The stabilometer was in a fixed horizontal position in front of the tilting room and was used both without and with a layer of foamrubber (see 3.2.). From each frequency the stabilograms over at least five periods were recorded, except for the lowest frequency of 0.016 Hz in which case only three periods were taken in order to avoid a too long period of standing upright (especially standing on foamrubber is rather tiresome). Care was taken to avoid the presence of possible transients by presenting the stimulus at least for another half period before the sinusoids which were used for analysis.

The subjects (the same as participated in 4.3.1.1.) had to stand upright and relaxed, and were given a task (SV indication by means of Békésy-like method). The mean amplitude of the induced lateral body sway ("Optic Sway" ; according to de Wit, 1972) was computed as well as the phase angle between stimulus and body sway. The results are summarized in Fig. 4.8. The upper diagram shows that upright stance is more affected by low than by high frequencies, most clearly in the conditions with foamrubber. Furthermore it is seen that with foamrubber the Optic Sway is increased because by the reduction of the somatosensory information the sensory weight of vision is

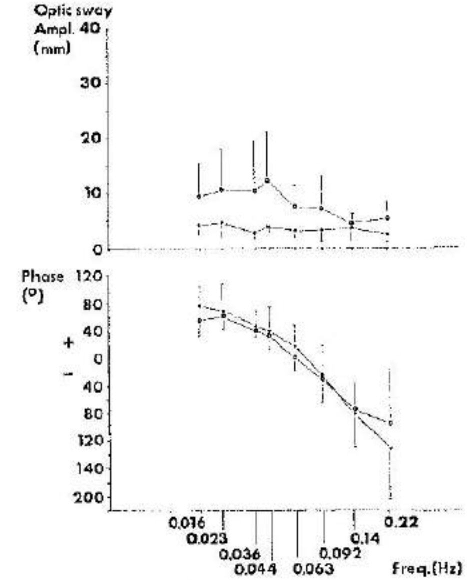

Fig. 4.8. Amplitude of lateral Optic Sway (mean value ± 1 σ) as a function of the frequency of the sinusoidally moving Tilting Room I (ampl. 5^0). The six subjects were tested both with (o) and without (x) a layer of foamrubber on top of the stabilometer. The phase angle between stimulus and Optic Sway is also shown.

enhanced. The phase angle shows the same behaviour, with and without foamrubber, indicating a phase lead at low frequencies and a phase lag at high frequencies. An important finding is that the subjects appeared to be unaware op the Optic Sway in conditions without foamrubber and in most of the conditions with foamrubber : they believed to have stood upright, uninfluenced by the room tilt.

With Tilting Room I also the effect of the tilt amplitude has been investigated (1, 3.5., 5 and 10^0) at a fixed frequency of 1/45 Hz. This experiment was part of the study on eye-object distances and posture, and will be discussed in 5.3.2. Since in that study the propriocpetive interference was under investigation, the subjects were tested without, with one and with two layers of foamrubber. The foamrubber was always covered with the rigid plate (see 3.2.2.).

The data here have been handled differently by computing the average amplitude and phase angle in the same way as in the previous experiment.

Six subjects (4 male, 2 female ; age 21-24) participated. They were given no specific task but to stand upright.

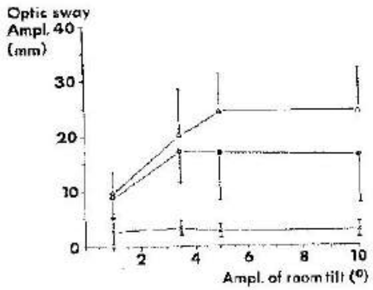

Fig. 4.9. Amplitude of lateral Optic Sway (mean value + 1 σ) as a function of the amplitude of the sinusoidally moving Tilting Room I (freq. 1/45 Hz). The six subjects were tested without (x), with one layer (o) and with two layers (Δ) of foamrubber on top of the stabilometer.

The results of this experiment are shown in Fig. 4.9. The amplitudes of the induced Optic Sway in the conditions without foamrubber are not dependent on the tilt amplitudes. The use of a single layer of foamrubber results in a saturated Optic Sway at tilt amplitudes beyond 3.5°. With two layers of foamrubber a larger Optic Sway is found, but again a saturation can be seen. With three subjects standing without foamrubber the stimulus did not result in an Optic Sway. With foamrubber induction always took place. The average phase lead was 61.3 ± 21.4°, which is in agreement with the previous experiment.

Tilting Room II offered the possibility to stimulate with foreaft tilt of the surroundings as well. In order to compare the foreaft tilt to the lateral tilt the next experiment was carried out. The stimulus was a sinusoidal movement with an amplitude of 2, 4, 8 or 12° with frequencies of 1/40, 1/20,

1/10 or 1/5 Hz, both for foreaft and lateral tilt (the stimulus with amplitude 12° and 1/5 Hz resulted in a distorted sinusoid and was therefore not used). In order to enhance the sensory weight of vision, the subjects were tested on a single layer of foamrubber as well (same construction as described under 3.2.2.). In the original experimental design also conditions with two layers of foamrubber were incorporated but it turned out that the

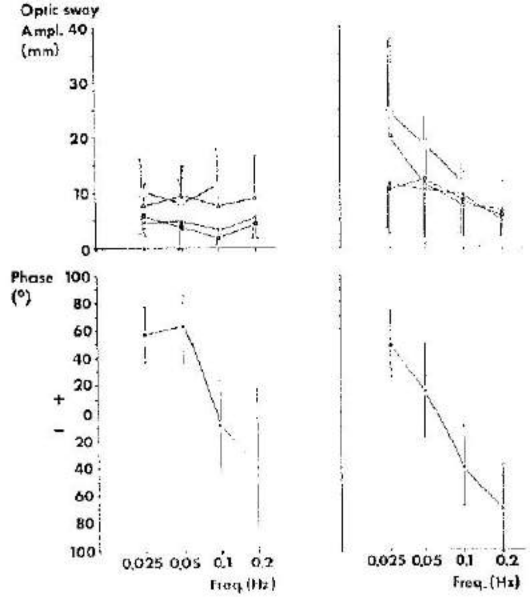

Fig. 4.10. Amplitude and phase of lateral (le) and foreaft (ri) Optic Sway (mean value + 1 σ) as a function of the frequency of the sinusoidally moving Tilting Room II (lateral and foreaft tilt respectively, ampl. x: 2°, o: 4°, Δ: 8° and □: 12°). The six subjects were tested with one layer of foamrubber on top of the stabilometer.

subjects could not remain standing upright on two layers during sinusoidal room tilt. Six healthy subjects participated (4 male, 2 female ; age 18-42). They were requested to stand upright, relaxed as much as possible, and were given no specific task. The conditions were counterbalanced as much as possible. The Optic Sway was measured with the stabilometer in fixed

horizontal position ; the recordings and analyses were performed in the same way as described in the foregoing experiments.
The experimental results for the foamrubber conditions are shown in Fig. 4.10. By comparing Fig. 4.10 with Fig. 4.9. it is seen that the induced lateral Optic Sway on a single layer of foamrubber is smaller in the present experiment. This is partly due to the fact that especially under the small amplitude conditions, an Optic Sway is not always induced. This is noteworthy since all subjects in this experiment, even those without Optic Sway, preferred to have assistance available because they felt uncertain and sometimes experienced vertigo, which was not the case in the previous experiment. As mentioned already, these subjects could not perform the test on two layers of foamrubber. Without foamrubber the subjects were found to be quite able to resist the stimulus : an induced Optic Sway was hardly found. This was also the case with foreaft room tilt, but the induced foreaft Optic Sway under the conditions with foamrubber is seen to be larger than the lateral Optic Sway.

Summarizing the experiments on sinusoidally tilting surroundings and posture, we may conclude that :
sinusoidal lateral or foreaft tilt of the seen environment may induce a sinusoidal body sway (Optic Sway). Without foamrubber the amplitude of the Optic Sway is independent of the amplitude of the room tilt and does not exceed 1 cm.
Reduction of the somatosensory information by standing on foamrubber was. found to enhance the sensory weight of vision, so to enhance the Optic Sway. Induced foreaft sway was found to be larger than lateral sway. With stimulus-frequencies up to about 0.06 Hz a phase lead is seen and at higher frequencies a phase lag.

4.3.4. DISCUSSION

Artificial movement of the seen environment may induce an apparent self-motion in the opposite direction followed by a postural reaction with a tendency to fall into the direction of pattern motion. Such destabilizing

effects on posture have been demonstrated in several experiments with circular surround movement (Kapteyn and Bles, 1977 ; Koitcheva et al., 1976; Miyoshi et al., 1978 ; cf. chapter 2), with optic roll stimuli (Dichgans et al., 1976 ; cf. also chapter 3) and with linear surround movement (Lee and Lishman, 1975 ; Lestienne et al., 1976, 1977).
The problems with an optic roll stimulus with rotation axis at eye-level have been discussed in 3.4. ; for linear surround movement similar difficulties concerning the destabilizing and stabilizing role of vision can be supposed. With the tilting rooms these difficulties are not present since motion is around an axis at ankle height. However, with the above mentioned stimuli a clear apparent motion is induced, which is not the case with the tilting room : the subjects, standing on the rigid horizontal platform during sinusoidal room tilt, reported neither roll vection nor a sensation of body tilt, in spite of the fact that the SV is tilting to a considerable extent and an Optic Sway is induced. When standing on foamrubber mostly the Optic Sway is perceived and not an apparent movement against the stimulus direction. Only by patients the tilting room has been perceived as stationary (meaning that a pure roll vection was experienced) which was accompanied with a considerable Optic Sway (cf. chapter 6).
The amplitude of the Optic Sway in healthy subjects is found to be of the same order of magnitude (< 10 mm) as the visual influence on the platform adjustments during static room tilt (a shift of the centre of gravity of ∿ 17 mm corresponds to a tilt of 1°). The amplitude of the induced Optic Sway is restricted because of proprioceptive interference and also by the inertia of the body. This can be seen by the phase lead at low frequency stimuli (proprioceptive interference) and a phase lag at higher frequencies (inertia). Foamrubber diminishes the effectiviness of the somatoreceptors resulting in a shift in the level of the proprioceptive interference. This explains the increased amplitudes of the Optic Sway at the lower frequencies and, because of the inertia of the body, the relatively smaller increase at the higher frequencies.

The perceptual and postural consequences of the static and sinusoidal room tilt are known from the experiments described so far. The question as to the mechanism behind these effects is still open. Further research is required to reveal which parameters are of importance. At least three parameters may be involved, (1) the presence of directional structures in the visual stimulus field, (2) retinal image shift, and (3) stimulus area as will be shown by two pilot investigations :

In the tilting room a white sheet was suspended which was covered with a randomized pattern of circular dots of various sizes and colours. The subjects viewed this pattern from a distance of 65 cm through an inverted funnel,attached to the head, which restricted the visual field to 75° in order to prevent the subjects from looking at the (vertical) side walls during tilt. The pattern of the dots did not contain direction cues since stationary lateral room tilt of 7° to either side did not affect the direction of the SV. In order to illustrate the possible effect as clear as possible, foam-rubber was used. The stimulus was a sinusoidal movement with an amplitude of 7° and a frequency of 0.05 Hz. The results were compared to those obtained under the condition in which the sheet was removed, the subjects viewing the back wall of the room containing the horizontal and vertical structures. In order to show the influence of peripheral vision, this condition was followed by a third condition, in which the subjects did not use the funnel, so with complete visual field. Eight healthy subjects (all female, age 18-32) of small body weight participated.
The original recordings are shown in Fig. 4.11. From inspection of the curves it is seen that (a) tilting of visual surroundings without directional structures may induce an Optic Sway, that (c) the Optic Sway is enhanched if these surroundings contain a clear optic vertical e.g. horizontal, and that (c) this Optic Sway is enhances still more if the visual field is not restricted to 75°.
It must be noticed, however, that the subjects did not experience a roll vection.

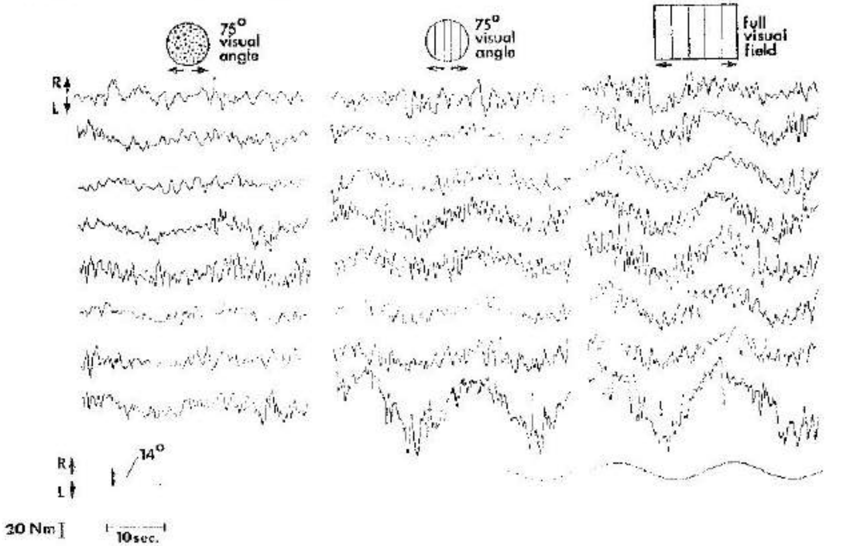

Fig. 4.11. Original recordings of the lateral Optic Sway of eight subjects standing on one piece of foamrubber in Tilting Room II under the conditions (1) no directional cues in visual field which is restricted to 75° visual angle, (2) vertical and horizontal directional cues in visual field which is restricted to 75° visual angle and (3) vertical and horizontal directional cues with full visual field.

The retinal image shift is not necessarely a continuous shift because with flicker illumination of the room an Optic Sway can be induced as well.

In a pilot-study the influence of sinusoidal room tilt (ampl. 5° ; freq.0.05 and 0.1 Hz) on standing upright during flicker illumination (rep. rate 1, 2, 3 and 4 Hz) was recorded for two subjects. These subjects were standing on foamrubber in order to enhance a possible effect.
The original curves are shown in Fig. 4.12. No doubt that even at the repetition rate of 1 Hz an Optic Sway is induced, be it with a reduced amplitude.

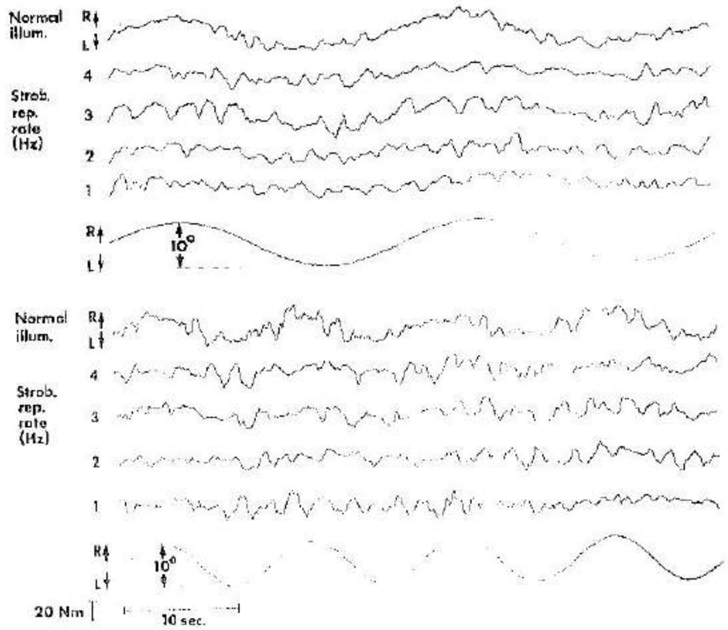

Fig. 4.12. Original recordings or lateral Optic Sway of a subject standing on one piece of foamrubber under the conditions of normally illuminated room and of flicker illumination with a repetition rate of 1, 2, 3 and 4 Hz.

It may be derived from this experiment that the directional structures are very important although an integration of the intermittent images by the CNS into a perception of a sinusoidally moving room is possible. The results of the latter test are not in agreement with the findings of Amblard and Crémieux (1976) that flicker illumination with a repetition rate of at least 6 Hz is a necessary condition for visual stabilization of posture.

According to Baron (1967) a movement of the eyes sidewards should be accompanied with an ipsiversive body shift, due to stimulation of the proprioceptors in the oculomotor muscles.
This could account for the Optic Sway since in the first experiment described in 4.3.3.1. the subjects were looking continuously at the SV bar fixed at eye-level on the (moving) backwall. It does not explain, however, why the amplitude of the Optic Sway remains the same with subjects keeping their eyes fixed at a light spot projected on the backwall by a flashlight attached to their heads, because in that case no eye movements are made (unpublished data).

CHAPTER 5

EYE-OBJECT DISTANCE AND HUMAN POSTURE *

Summary

Because of the limited spatial resolution of the retina self-motion is not perceived visually when the eye-object distance is sufficiently large. A series of experiments is described in which the eye-object distance has been varied from 0.5 to 200 m. It is shown that vision does not contribute to postural stability when the eye-object distance exceeds 5 m. The subjects were tested also in the tilting rooms in order to compare postural behaviour under both circumstances. The influence of head tilt on postural stability as well as the presence of nearby stationary contrasts in the periphery of the visual field, both of importance under conditions where height vertigo might occur, have also been investigated.

5.1. INTRODUCTION.

In the experiments described in the previous chapters intersensory conflicts have been induced by stimulation of the sensory systems, separately or in combination.
Since the resolution of the retina is limited it is argued by Brandt (1976) that self-motion is not visually perceived when the eye-object distance exceeds a certain value, leading to an intersensory conflict between the visual information (signaling no body sway) and the proprioceptive information (signaling body sway). Such an intersensory conflict could account for a postural imbalance with physiological height vertigo (not to be confused with acrophobia : with height vertigo is meant the sensation of instability or desorientation, the sensation of being pushed forward ; in fact height vertigo may be seen as the first stage of acrophobia).

* This chapter was part of a study on the mechanism of physiological height vertigo which was performed in close cooperation with Dr. Brandt and Dr. Arnold, Krupp Krankenanstalten, Essen, F.R.G. Publications on this subject are found in the reference list under Brandt and under Bles.

In order to verify the above hypothesis the central theme of this chapter is the influence of vision on postural stability as a function of eye-object distance.

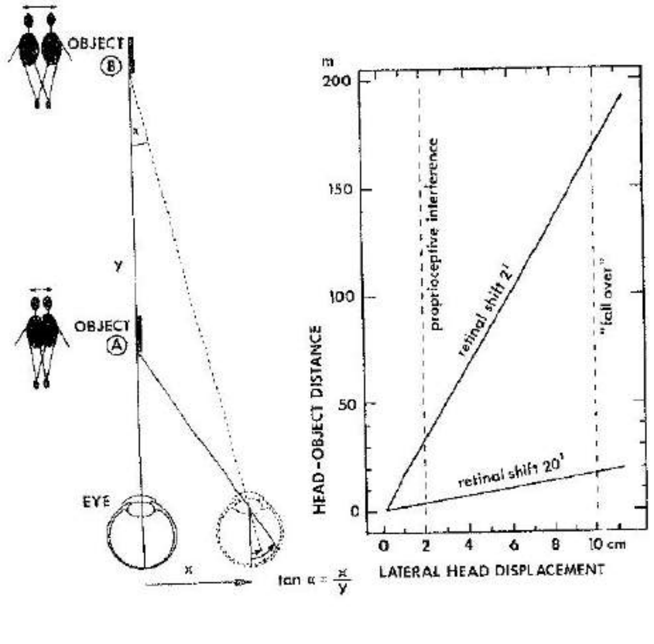

Fig. 5.1. Angular displacement α on the retina, caused by a lateral head displacement X, is smaller the greater the eye-object distance Y is. The diagram shows for which eye-object distances lateral head displacement can be detected visually assuming a retinal movement detection threshold of either 2 or 20 minutes of arc.

Increasing eye-object distances might lead to postural instability due to the limited resolution Δ of the retina (about 2' for the foveal parts and about 20' for the paracentral and peripheral parts (Aubert, 1886 and Leibowitz, 1955)). The retinal shift α of a viewed stationary object in the environment depends on the lateral head displacement Y and on the eye-object distance X (Fig. 5.1). A head or eye displacement Y is not perceived for $\alpha < \Delta$. In this situation there is no visual cue that could be used for

postural compensation of this movement. The lack of a visual cue should result in larger, disinhibited sway amplitudes at greater eye-object distances. However, vision is not the only system which regulates posture : the proprioceptive system (including labyrinths and somatoreceptors) is active too. So it cannot be expected that the sway increases linearly with increasing eye-object distance but rather should behave non-linearly and should be limited because of proprioceptive interference. The hypothesis was originally developed for the lateral body sway since the lateral sway is horizontal over several centimeters (parallel shift) because of the mechanical relationship of the lower limbs, pelvis and vertebral column (Kapteyn, 1973). A similar line of reasoning can be developed for foreaft body sway (Brandt et al., 1979). Involvement of eye countertorsion (in which the retinal shift is independent from the eye-object distance) can be consequential for posture in case of great lateral (rotational) sway amplitudes only.

It seems reasonable that the displacement angle on the retina, dependent as it is upon distance, cannot be the only determinant of the net compensatory sway. Higher order depth constancy mechanisms must be involved, similar to those for size and motion constancy. This is evident in a normally structured surround when the body sways in front of stationary objects at different distances. Here monocular and binocular depth cues, as well as motion parallax, may be used to stabilize posture. The gain of the motor action in reaction to a visually sensed sway requires a precise intersensory calibration based on all mechanisms subserving self-motion perception.

For the validation of the hypothesis it must be shown that its consequences fit in with the concept. The postural consequences are :

(1) The body sway should increase with increasing eye-object distances.
(2) At larger eye-object distances nearby stationary structures in the periphery should re-establish postural stability because it is especially the retinal periphery which contributes to postural balance.
(3) Head tilt (by which the otoliths are brought out of their optimal

working range) or additional disturbances of the somatosensors (foam-rubber) should enhance the swaying of the body because the "false" visual signal should be given a disproportionally greater influence.

As already indicated in 5.1. it is not to be expected that the body sway increases linearly with increasing eye-object distance because of proprioceptive interference. In chapter 4 it has been shown that increasing the tilt amplitude of the tilting rooms does not imply an increasing body sway, also indicating a proprioceptive interference. In the tilting rooms, however, the subjects were aware of the misleading character of the visual stimulus which is not the case with the visual stimulation at larger eye-object distances. Therefore the subjects participating in the experiments with the varying eye-object distances have been tested also in the tilting rooms (low frequencies) in order to compare the proprioceptive interference under both stimulus conditions.

5.2. APPARATUS AND RESULTS

5.2.1 Experimental Set-up

The experimental set-up concerning the tilting rooms has been described in 4.2. In experiment 5.a with Tilting Room I (freq. 1/45 Hz ; ampl. 1, 3.5, 5 and 10°) and in experiment 5.b with Tilting Room II (freq. 1/40 Hz ; ampl. 2, 4, 8 and 12°) the stimulus lasted for at least three periods. The stabilometer has been described in 2.2.4. In the experiments to be described also single and double layers of foamrubber (height 10 cm, s.g. 40 kg/m^3) were used, mounted on top of the stabilometer and covered by a rigid plate. Creation of various visual surroundings in which the only varying parameter should be the distance, is very difficult. In the present experiments the various eye-object distances were obtained by a suitable choice of the balconies of a high building (Experiment 5.a) and in a university lecture hall by appropriate illumination and restricted visual field (experiment 5.b). In each condition the stabilograms were recorded for one minute.

5.2.2 Analysing Methods

Kapteyn (1973) classified his clinical material from direct observation of the stabilograms. His findings were confirmed by a routine computerized analysis using the Root Mean Square (RMS) as a measure of stability (Kapteyn and Bles, 1976). Since that study mainly concerned patients suffering from vestibular dysfunctions, the stabilograms showed predominantly low frequency components with high amplitudes. According to the hypothesis developed in 5.1, one would also expect to find a low frequency, high amplitude body sway in conditions with considerable eye-object distances. This makes the choice of the RMS as a measure of stability in the following experiments acceptable. Of course, the RMS of the stabilograms is an avarage value over a certain period. This makes it impossible to relate the RMS directly to the movements of the head which means that the resolution Δ of the retina cannot be determined. However, if it is to be shown that the movements of the head increase, it will be clear that this can be concluded if an increase in the RMS is found.
The RMS was computed from the last 45 seconds of the one-minute recordings in Experiment 5.a and from the last 40 seconds in Experiment 5.b. From the stabilograms obtained in the tilting rooms the RMS was computed during the second period in order to avoid possible transients.

5.3. EXPERIMENTS AND RESULTS

5.3.1 Pilot Experiment : Effects of vision, eye-object distance and head position on stability

Stabilometry was performed at free stance on a balcony (fourth floor) under four different visual stimulus conditions which were presented at random : (a) eyes closed ; (b) eyes open, eye-object distance 2 m ; (c) eyes open, eye-object distance ∿ 200 m, restriction of the visual field to 75° by use of an inverted funnel attached to the head ; (d) eyes open, eye-object distance ∿ 200 m, full visual field with stationary contrasts in the nearby periphery (walls, ceiling and balustrade).

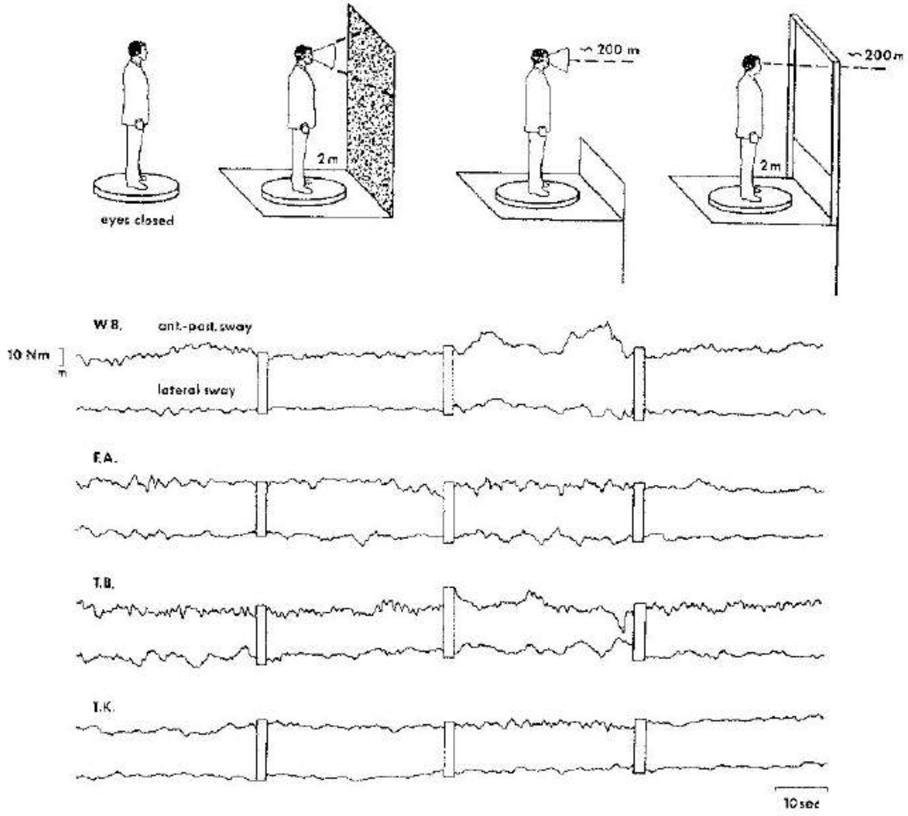

Fig. 5.2. Stabilograms of four subjects under the stimulus conditions (a) eyes closed ; (b) eyes open, eye-object distance 2 m ; (c) eyes open, eye-object distance ~ 200 m, restriction of the visual field to 75° by use of a funnel attached to the head ; (d) eyes open, eye-object distance ~ 200 m, full visual field with stationary contours in the nearby periphery.

The four observers were not aware of differences in their body sway under the four conditions. From inspection of the stabilograms in Fig. 5.2 it can be seen that in condition (c) postural stability is worse than in (b) or (d). The fact that condition (c) is less stable than (b) supports the hypothesis that instability increases with increasing eye-object distance. The fact that (d) is more stable than (c) must be the result of the contribution of peripheral vision, when nearby stationary objects serve as a frame for spatial orientation. However, in condition (c) subjects sometimes reported anxiety to fall over (probably because the stabilometer was placed just behind the balustrade), which makes it difficult to separate the visual factors from possible psychological factors that influence postural stabilization. Therefore, in the other experiments care was taken to avoid these unwanted influences as much as possible by positioning the stabilometer 1.5 m behind the balustrade.

Another point of interest are the rather marked interindividual differences.

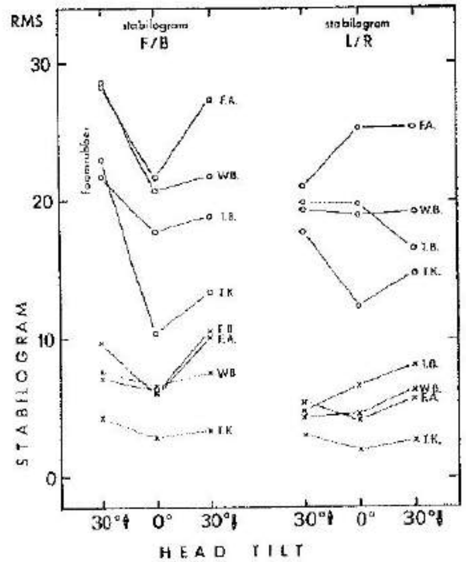

Fig. 5.3. Root-Mean-Square values of lateral and foreaft stabilograms recorded during upward or downward inclination of the head 30° out of the normal position (normal head position : ~ 15° tilted forward). The four subjects were standing with the eyes closed both without (x) and with one layer (o) of foam-rubber on top of the stabilometer.

The influence of the head position relative to the gravitational vector was measured with eyes closed because with eyes open effects are contaminated by additional changes of visual cues.
As can be seen in Fig. 5.3 upward or downward inclination of the head approximately 30° out of the normal position affects the body sway at least in the foreaft direction. Stabilization is best with the otoliths in their normal working position (normal head position : ∿ 15° tilted forward).

5.3.2 Experiment 5.a : Lateral body sway at various eye-object distances (0.5 to 200 m), influence of peripheral vision and proprioceptive interference

Six healthy subjects (4 male, 2 female, age 21-24) participated in this

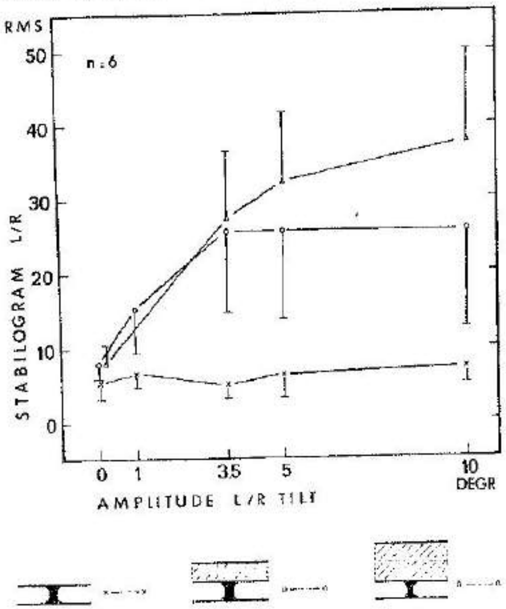

Fig. 5.4. Mean Root-Mean-Square values (arbitrary units, ± 1σ) of the lateral stabilogram recorded during sinusoidal lateral movement of Tilting Room I (ampl. 1, 3.5, 5 and 10° ; freq. 1/45 Hz). The six subjects were standing without (x), with one layer (o) and with two layers (Δ) of foamrubber on top of the stabilometer.

experiment. They first were tested in Tilting Room I while standing both with and without foamrubber, to check the proprioceptive interference during visual destabilization (tilt freq. 1/45 Hz ; ampl. 1, 3.5, 5 and 10°). All subjects completed the tests, including the conditions with two layers of foamrubber.

The results in Fig. 5.4 show that instability of the left/right stabilogram without foamrubber is not increasing very much despite the increasing amplitude of the room tilt. With foamrubber a certain level of the RMS value (indicating proprioceptive interference) is reached already at an amplitude of 3.5° of room tilt. With two layers of foamrubber this occurs at a higher level, as was to be expected. The rather large standard deviations are partly a result of the interindividual differences which will be discussed later. The fact that the RMS asymptotes a certain level despite the increase of the amplitude of Tilting Room I, must be explained

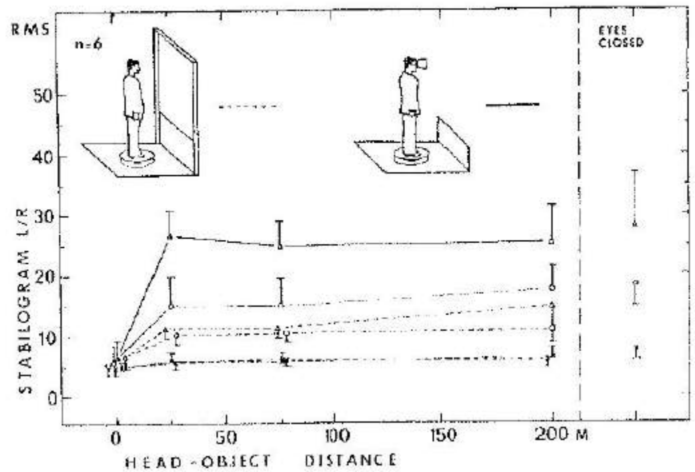

Fig. 5.5. Mean Root-Mean-Square values (arbitrary units, ± 1σ) of lateral stabilograms recorded at different eye-object distances (0.5, 25, 75 and 200 m) without (——) and with (----) the presence of nearby stationary contours in the periphery of the visual field. The six subjects were tested without (x), with one layer (o) and with two layers (Δ) of foamrubber on top of the stabilometer. The RMS values of the eyes-closed conditions are also shown.

by the interference of the proprioceptive system.

Subsequently by positioning the stabilometer on the balconies of a high building, it was possible to vary the distance between the eye and the visible surroundings from 0.5, 25, 75 to 200 m if the subjects had a funnel (restricting visual field to 75°) attached to their head. In each condition six stabilograms were recorded (no, one or two layers of foamrubber on the stabilometer ; with or without funnel). A stabilogram of the subjects having their eyes closed was measured as well. It must be emphasized that the experimental conditions were not optimal because the visual scenery was different under the four test conditions, and, although the measurements were performed on a sunny afternoon, there was a gentle breeze all the time.

It can be seen in Fig. 5.5 that the instability is already maximal at an eye-object distance of 25 m. No significant difference between the RMS values for the different test conditions obtained at 25, 75 and 200 m could be established. This is also the case when peripheral vision is present. However, the RMS levels of instability obtained with peripheral vision (under the conditions with foamrubber) are below the levels found without peripheral vision ($p < 0.01$). This implies that the influence of peripheral vision on postural balance is very important : the influence of the proprioceptive system must be playing a role of minor importance relative to vision in these conditions because the instability under these conditions increases with exclusion of peripheral vision. Without foamrubber no difference between the conditions with or without the presence of nearby stationary contours in the periphery of the visual field could be established which implies that there the proprioceptive system is adequate to keep proper balance although the visual information is misleading.
The RMS of the stabilogram obtained in the "Eyes-closed" condition is of the same order of magnitude as the RMS obtained with eye-object distances of at least 25 m without peripheral vision.

The rather large standard deviations are partly result of the interindividual differences. Ranking the subjects according to the RMS in both the balcony and tilting room experiments gives a coefficient of rank correlation of 0.82 indicating that the role of vision in postural stabilization is subject dependent.

This experiment leaves some problems unsolved. One might ask whether the instability at eye-object distances of more than 25 m may be the result of wind or perhaps height-fear although the subjects were unaware of it since no height vertigo was reported.
Another point to be noted is that the instability is already maximal at 25 m but the exact saturation point has not been found. Apart from these points no tilting room data about the foreaft sway are available which leaves open the question as to whether the hypothesis is also true for the foreaft body sway.

5.3.3 Experiment 5.b. Lateral and foreaft body sway at various distances (0.5 to 25 m) and proprioceptive interference

Six healthy subjects (4 male, 2 female, age 20-42) participated in this experiment.
First they were tested with foreaft and lateral optic tilt in Tilting Room II both with and without foamrubber. These tests were presented in random order.
The results are shown in Fig. 5.6. It is interesting to note that the subjects are much more sensitive to the foreaft than to the lateral tilt. There is a remarkable discrepancy with the results of Experiment 5.a. Although the RMS of the stabilograms obtained with one layer of foamrubber with Tilting Room II is less than that found in Experiment 5.a, the subjects could not perform the test on double foamrubber. Most of the subjects preferred to have some assistance available even with one layer of foamrubber because they felt uncertain and sometimes experienced vertigo. An explanation might be that in Tilting Room II the subjects could not just get off the stabilometer as with Tilting Room I because in Tilting Room II they

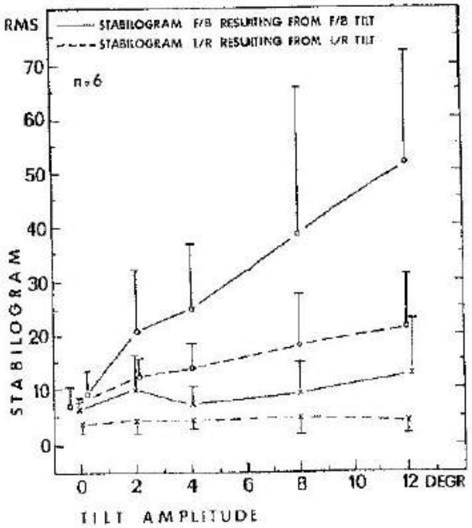

Fig. 5.6. Mean Root-Mean-Square values (arbitrary units ± 1σ) of lateral and foreaft stabilograms. Both the lateral and the foreaft stabilograms were recorded during lateral and foreaft sinusoidal movement respectively of Tilting Room II (ampl. 2, 4, 8 and 12^0 ; freq. 1/40 Hz). The six subjects were standing both without (x) and with (o) foamrubber on top of the stabilometer.

would not step down on the stable floor but rather onto the floor of the tilting device itself which certainly would not facilitate stability. There is no reason to suppose a difference between the two groups of subjects. The most likely explanation is that Tilting Room II is much more "real" which causes a shift in the sensory weight in favour of vision.

The Tilting Room II experiment was followed by a more natural stimulus situation for testing the influence of the distance below 25 m under "static" conditions. In this experiment a university lecture hall was used to provide different eye-object distances, thus eliminating the possibility of wind influencing the results. By a suitable choice of the illumination (illuminated backwall) and the use of an adapted funnel the eye-object distance could be varied up to 25 m. The distances in the lecture hall at which the stabilograms were recorded were 0.5, 2.5, 5, 10, 15, 20 and 25 m in the sequence 15, 10, 5, 2.5, 0.5, 25, 20 m, and 15 m once more as a check. The eyes-closed condition was tested as well. These measurements

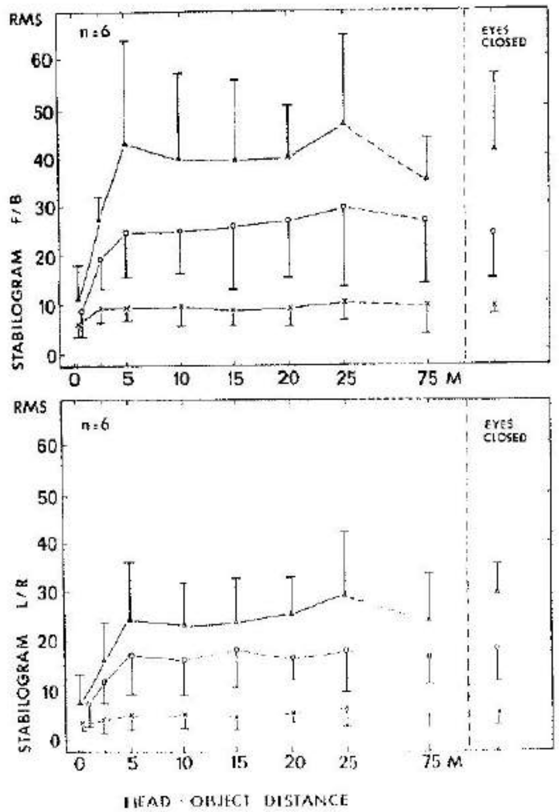

Fig. 5.7. Mean Root-Mean-Square values (arbitrary units, ± 1σ) of lateral and foreaft stabilograms recorded at different eye-object distances (0.5, 2.5, 5, 10, 15, 20, 25 and 75 m) without (x), with one layer (o) and with two layers (A) of foamrubber on top of the stabilometer. The six subjects had a restricted visual field of 75^0 by means of a funnel attached to the head. The RMS values of the eyes-closed conditions are shown as well.

were performed with the stabilometer without, with single and with double foamrubber layers. As a check these six subjects were also tested at the 75 m condition of Experiment 5.a.

Fig. 5.7 shows the results. Here too it is found that the instability of the foreaft sway is greater than of the left-right sway. The results

confirm the findings of Experiment 5.a because the RMS of the stabilograms in the lecture hall at an eye-object distance of at least 5 m is of the same order of magnitude as the RMS obtained at the 75 m condition on the balcony.
It is noteworthy that postural instability was found to be maximal at a distance of only 5 m. This means that at larger distances vision does not contribute to postural stabilization. However, it does not play a really destabilizing role because the RMS obtained under the eyes-closed condition has about the same value as those obtained under conditions with eye-object distances exceeding 5 m. Furthermore the results of Experiment 5.b confirm those of Experiment 5.a concerning the order of magnitude of the RMS in the left-right stabilogram.

5.4 DISCUSSION

The results of Experiment 5.a with Tilting Room I reveal a level of proprioceptive interference which is relatively independent of the increasing amplitude of the sinusoidal tilt. No vertigo was experienced by the subjects indicating that these stimulus conditions were not particularly stressful. It must be emphasized that despite the fact that the subjects knew about the tilting of the room, the body sway is influenced by the stimulus, most clearly when the subjects are standing on foamrubber.
Experiment 5.b using foamrubber in Tilting Room II did not reveal a clear level of proprioceptive interference. However, in this experiment some of the subjects reported vertigo. It happened several times that a complete loss of orientation occurred inducing a sudden onset of vasovegetative symptoms, lasting for several seconds. All subjects reported that this part of the experiment was exerting and rather unpleasant. The behaviour of these subjects on foamrubber is in fact the same as that patients with vestibular lesions or post-concussional dizziness showed with Tilting Room I without foamrubber (Bles et al., 1977 ; Bles, 1977 ; cf. chapter 6), although to a lesser extent. With these patients having difficulties with integration of the sensory information it was found that the greatest sensory weight was placed on vision and not on proprioception. The

conclusion to be drawn from the tilting room experiments is that the more natural the optic stimulus, the more sensory weight is given to vision. This explains why the subjects had to exert themselves under the conditions without and with single foamrubber and could not perform the test on double foamrubber. So when the integration is difficult, either as a result of strong conflicting sensory information or as a result of pathology, most sensory weight is attributed to vision. This conclusion also fits in with earlier results obtained with the slanting ships cabin (de Wit, 1973) and the behaviour of the subjects living in a tilting environment (Kitahara and Uno, 1967)- see also Bischof (1974).

The experiments 5.a and 5.b support the hypothesis that increasing eye-object distances are associated with a measurable postural imbalance. With eye-object distances of more than 5 m vision does not play a role in postural stabilization. The "static" stimulus conditions of large eye-object distances will not destabilize posture to falling per se because of the redundancy in the control system. The lack of appropriate visual input is widely compensated for by the somatoreceptors and labyrinths.

The experiments described so far may explain the physiological mechanism of height vertigo. If, for any reason, much sensory weight is attributed to vision, this may result in serious problems in maintaining the upright position under conditions where height vertigo might occur because the visual information under those conditions is in fact false. Therefore patients with vestibular or somatosensory dysfunctions (e.g. polyneuropathy) are subjected to a particularly greater risk when exposed to such situations. Because the postural behaviour in the tilting room experiments and in the experiments with the varying eye-object distances was subject dependent, it is expected that subjects experiencing difficulties in the tilting room, will also have difficulties in stabilizing posture when the critical eye-object distance is exceeded.
As already indicated this would also be true for subjects with vestibular lesions and this therefore explains why Pogány (1958) found so many of such subjects among his population of sufferers from height vertigo.

It is also possible that height vertigo in healthy subjects is induced too by the intersensory conflict between vision and proprioceptive system at large eye-object distance. A necessary condition in that case is that most sensory weight is contributed by vision. As has been found in the experiments this is not the case: vision does not destabilize posture; the proprioceptive system interferes adequately. However, several arguments can be put forward that in height vertigo circumstances a shift of the sensory weight in favour of vision occurs indeed.

(1) In height vertigo circumstances the subject usually looks downward with tilted head. From the pilot experiment it is seen that this influences stability. Moreover, if the otoliths are not in the ideal position, because of head tilt, the sensory weight of the otoliths decreases in favour of vision as found by Dichgans et al. (1974).
(2) It has been argued in discussing the results of the tilting room experiments that the natural character of the optic stimulus leads to an increase of the sensory weight contributed by vision, but this certainly holds for height vertigo circumstances; for in that case the optic stimulus is far from artificial.
(3) Additional disturbances like wind or an unstable foot support may also result in a shift in favour of vision. Subjects are apt to use especially the visual information in problematic circumstances.

If the argument is true that height vertigo is based on a visual destabilization of free stance when the eye-object distance becomes critically large, the perceptual consequences must fit in with the concept as well. These consequences are :

(1) The occurrence of height vertigo should be related to body position. Height vertigo should be maximal with upright stance (because the head sway is maximal in that position so just then the conflict can be induced) and minimal in lying position (minimal head movement; no conflict). This was found to be the case indeed (Brandt et al., 1978) and although the results might have been contaminated by height fear, the results are not conflicting with the hypothesis.
(2) Height vertigo should be induced by downward or upward gaze (identical visual condition) because it should be the distance rather than the gaze direction that is critical.
Evidence was obtained that this is the case indeed (Brandt et al., 1979).
(3) Height vertigo should appear at a distance of about 5 m, should increase with increasing distance (Fig. 5.1), and saturate at a height below 15-20 m.
Using a magnitude estimation technique it was found that the subjective height vertigo was not significantly different at heights of 20, 60 or 100 m respectively (Brandt et al., 1979).

The present posturographic data suggest that induction of height vertigo can be minimized by :

(1) Adjustment of the head to the gravitational vector when looking down, since head tilt reduces postural stability as found in the pilot study.
(2) Providing visible nearby cues in the periphery of the visual field, since nearby stationary contours provide peripheral vision with the necessary information to stabilize posture. This is shown in experiment 5.a in which the RMS levels determined in the "peripheral vision-foamrubber" conditions are the levels of visual interference. This is true because with exclusion of peripheral vision the instability increases significantly up to the level of proprioceptive interference.
Without foamrubber no difference in stability could be established indicating that the level of the proprioceptive interference here is lower than that of peripheral vision. In the conditions without foamrubber and with peripheral vision there is no chance that a perceptual conflict arises because, with the nearby stationary contours in the visible periphery, body movement is detected by both proprioception and vision.
(3) Avoiding of free stance under conditions where height vertigo might occur as the vertigo is primarily due to the induced body sway. If the subject is lying down incongruity of the proprioceptive and visual information cannot be induced.

CHAPTER 6

THE TILTING ROOM AS A CLINICAL TOOL

Summary

It is found that with patients suffering from post-concussional dizziness the sensory weight attributed by vision in spatial orientation is exceptionally large, resulting in an Optic Sway of large amplitudes. It is discussed that the tilting room might be a suitable device to objectify the subjective post-concussional syndrom. It is also shown that in spatial orientation and postural control patients devoid of vestibular function rely to a far greater extent on vision instead of on the somatosensory information.

6.1. INTRODUCTION

In the experiments described so far only healthy subjects participated. It was the well functioning central nervous system which had to cope with experimentally induced incongruity of the sensory information. The question of how an improperly functioning CNS, which is probable with patients suffering from post-concussional dizziness, deals with incongruent sensory information will be discussed in 6.2.
The question of how, with patients devoid of vestibular function, in case of incongruity of the sensory information, the CNS relies on vision and the somatosensory system will be discussed in 6.3.

6.2. Post-Concussional Dizziness and the Tilting Room

People who suffer from the after effects of a concussion sometimes complain about dizziness for a long time (about 6% according to van 't Hooft, [illegible]) even when no vestibular dysfunction can be shown. This complaint continues even in the case that other symptoms like headache and vasovegetative instability have disappeared or have lessened considerably. Usually these

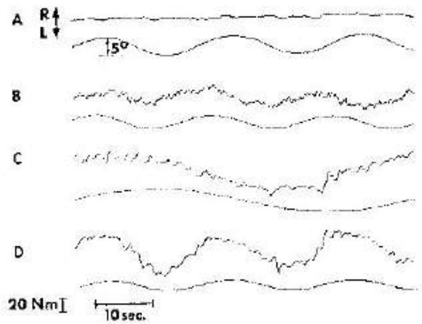

Fig. 6.1. Representative examples of Optic Sway recordings.
A. Healthy subject without foamrubber on top of the stabilometer.
B. Healthy subject with foamrubber on top of the stabilometer.
C. Patient devoid of vestibular functioning, without foamrubber.
D. Patient suffering from post-concussional dizziness, without foamrubber.

complaints about dizziness are most serious when there are severe and abrupt changes in the scenery of the patient's surroundings, e.g. when he is walking in a busy street. Dizziness also occurs if the equilibrium system is greatly strained, e.g. when climbing a winding staircase.
Stabilometric investigations revealed that sufferers from post-concussional dizziness as a group show a significantly greater instability than a control group of healthy subjects (Kapteyn, 1973 ; Kapteyn and Bles, 1976), but this instability was not of such magnitude that it was possible to use the routine stabilogram as a decisive factor for the diagnosis. Obviously, these patients have adapted to every-day situations in which the sensory information of the different sensory systems can be handled reasonably well.

There was an opportunity to examine ten patients suffering from post-concussional dizziness in the tilting rooms. They were examined more than half a year after the concussion took place. Even without foamrubber with these patients sinusoidal movement of the room (ampl. 5° ; freq. 1/60-1/5 Hz) resulted in large Optic Sways with amplitudes exceeding 20 mm.
Several times, however, the subjects had to be supported during the tests which makes a computer analysis not meaningfull. Moreover, sometimes the test

had to be stopped prematurily because of the induced vasovegetative instability.
Three patients reported to have stood upright although they showed an Optic Sway with amplitudes of over 20 mm, which is rather large as compared with the amplitudes shown by healthy subjects. Three other patients experienced pure roll vection, reporting that instead of the room the platform was moving, which resulted in Optic Sways of such amplitudes that they sometimes needed support. The other four patients had a mixed experience (both platform and room moving) resulting in large Optic Sways. A recording of the lateral stabilogram of a patient experiencing roll vection is shown in Fig. 6.1. These findings make clear that these patients mainly rely too much on vision, indicating that the sensory weight of vision in the integration of the sensory information is dominant over the sensory weight of the somatosensory system.

Of course, it is impossible to relate the postural behaviour of these particular patients to specific lesions in the central neural structures since the lesions in these patients are not known. But, in view of the findings of Amphoux and Sevin (1975) that it is especially the brainstem which is very vulnerable in case of concussion, it is highly probable that this aberrant postural behaviour is due to an integration problem, so to a lesion in the brainstem regions. This would confirm the findings of Vedrenne and Chodkiewicz (1975) who, with autopsies after skull injuries, found in the brainstem macroscopic lesions in 65% and microscopic lesions in 99% of all (187) cases.

6.3. Vestibular Deficiency and the Tilting Room

There was a possibility to examine in the tilting rooms two patients devoid of labyrinthine function caused by a basal meningitis. They showed no response to caloric irrigation and rotatory movement. They also showed no Coriolis-effect and it turned out to be impossible to induce Pseudo-Coriolis effects either (in accordance with the findings of Dichgans and Brandt (1973).

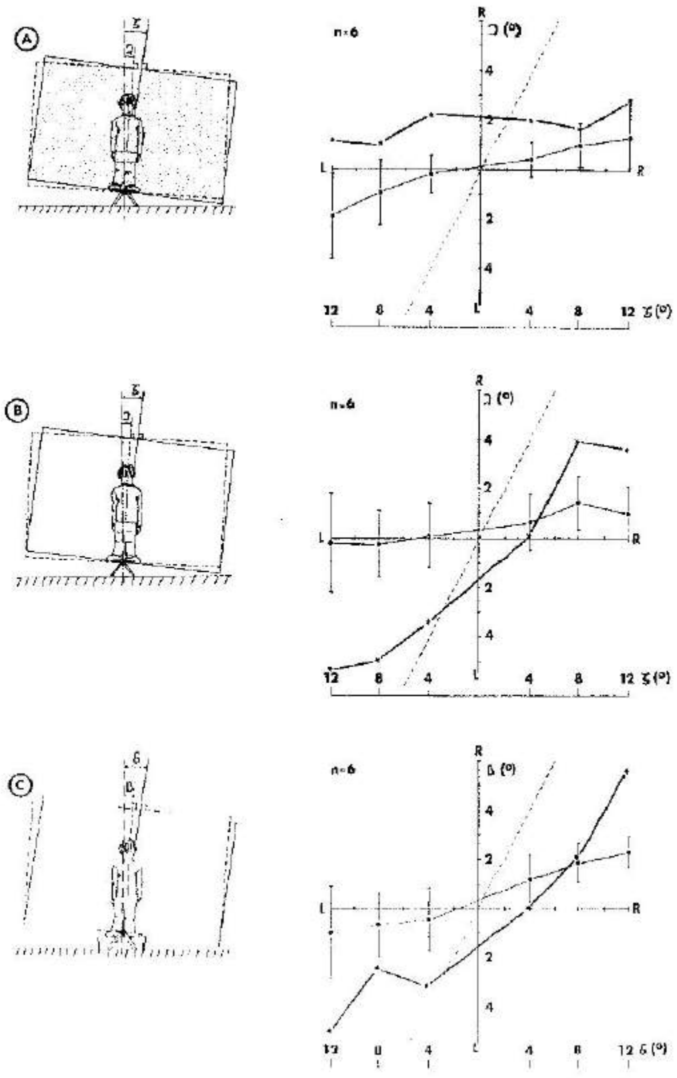

Fig. 6.2. Patient devoid of vestibular functioning in comparison with healthy subjects. For legend see Fig. 4.6.

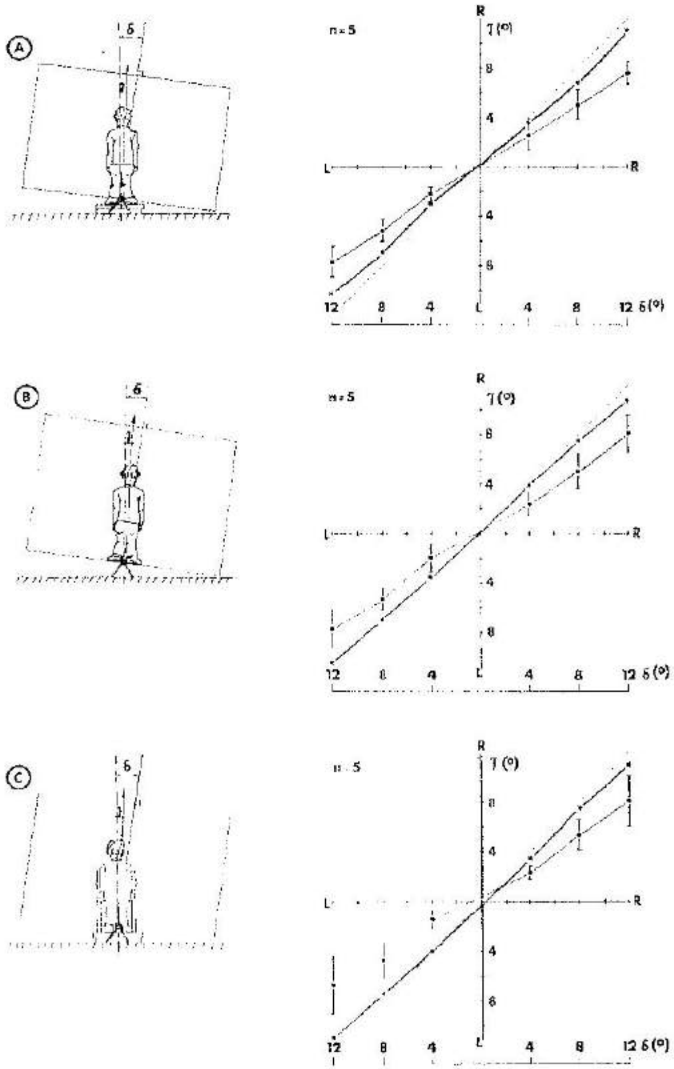

Fig. 6.3. Patient devoid of vestibular functioning in comparison with healthy subjects . For legend see Fig. 4.3.

Submitted to the sinusoidally moving tilting room they experienced a pure roll vection ('the platform is moving'). When convinced that the platform was stationary and that it was only the room that moved, they still could not resist the induced Optic Sway although the magnitude was not equally impressive (see Fig. 6.1.). However, by abruptly changing the frequency of the sinusoidal movement, it appeared to be easy to overthrow these patients. Apparently they have serious problems in maintaining balance in the tilting room because they rely too much on vision instead of on the somatoreceptors. The predominance of vision over the somatosensory system is shown in the (semi-)static tests as well by one of these two subjects in Tilting Room II (from the other patient unfortunately no data are available). Fig. 6.1A. shows that the somatosensory information itself is adequate for adjusting the platform to the horizontal position (which is done remarkably well, compared to the performance of the healthy subjects), whereas vision over-rules the somatosensory information completely (Fig. 6.2. B and C).
The SV indication in the static tilt experiment is also shown to be heavily dependent on vision (Fig. 6.3.). This last test reveals that the parameter m (see equation (1) in 4.4.) could be a visuo-vestibular weight ratio indeed.

6.4. Conclusion

A patient suffering from post-concussional dizziness is in many cases, because of his dizziness, not fit to resume his work. Many times such a patient is suspect of aggravation especially when he is found to have normally functioning vestibular apparatus and when no further objective phenomena are present that could explain his dizziness.
Perhaps the above described "Optic Sway Test", an examination of especially the integrator of the sensory information, can be used to objectify their complaints.

Concerning the patients devoid of labyrinthine functioning, it should be noticed that the "Optic Sway Test" is of course not the appropriate examination method of the vestibular function per se : for that purpose the vestibulo-ocular examination methods as developed and propagated by a.o. Jongkees (1969, 1974) and Oosterveld et al. (1972) should be used. However, posturography in combination with the tilting room is an effective tool to objectify the troubles a patient with vestibular deficiency will experience when confronted with misleading sensory information.

An important result of the "Optic Sway Test" described above is the large sensory weight contributed by vision, even when the patients are aware of the fact that the optic stimulus is misleading. As stated already in 5.4. these patients are subjected to a higher risk when exposed to situations in which they are not aware of the misleading character of the optic stimulus (cf. the discussion about height vertigo in 5.4.).

SUMMARY AND CONCLUSIONS

SUMMARY

"... Als prinzipielle Voraussetzung für das Studium vestibularer Effekte gehören passive Rotationen. Alle aktiven Drehbewegungen sind glatt zu verwerfen....". In the present study this statement from Fischer and Wodak (1924) is literally trodden under feet.
It is true indeed that by stepping around (active rotation) the vestibular reflexes and sensations differ from reactions induced by passive rotations. In chapter 1 it has been tried to explain these discrepancies by experiments which show that the somatosensory system involved in stepping around plays a role similar to vision. Rotation of the visible surroundings around a stationary subject invariably leads to a sensation of self-motion ; a similar sensation can be induced by apparent stepping around (which is possible by stepping around in darkness on a rotating platform in such a way that the spatial position does not change). The sensation induced by apparent stepping around cannot be distinguished from the sensation induced by real stepping around. It also turned out to be possible to induce nystagmus and Coriolis-like effects during apparent stepping around suggesting that the somatosensory-vestibular interactions are analogous to the visuo-vestibular interactions.
In chapter 2 the influence on posture is discussed of semicircular canal stimulation (by means of caloric irrigation and by active or passive rotation) and corresponding visual stimulation. It is found that there exists a relation between body torsion and sensation of rotation on the one hand and lateropulsion and nystagmus on the other hand. Here too the somatosensory information is important because the direction of the nystagmus and the sensation of rotation were sometimes found to be different, for instance during caloric irrigation of standing subjects.
Apart from the sensory interactions during rotations, similar interactions

are known for linear movements (e.g. the apparent departure of the own train when the neighbouring train leaves). In this case, however, the otoliths are also involved.

In the present study the interactions between vision and otoliths are studied by varying the optical vertical relative to the direction of the gravitational vector by means of a tilting room. In chapter 4 the influence of stationary tilt of the tilting room on the perception of the vertical and on standing upright has been under investigation. It appears that the subjective vertical in subjects standing upright is mainly determined by the visual and vestibular information being independent of the position or rigidity of the foot support. Static room tilt has a slight influence on posture, but stability is not affected. With a sinusoidal movement of the tilting room (lateral or foreaft) a sinusoidal body movement is induced (to be called "Optic Sway"), without the subject being aware of this. When the somatosensory system is made less effective by positioning the subjects on foamrubber, the sensory weight given to vision is enhanced considerably resulting in an increase of the Optic Sway. The Optic Sway as a function of amplitude and frequency of the sinusoidally moving tilting room has been investigated systematically.

As a prelude to these investigations an experiment has been described in chapter 3 with continuous roll motion of the visual surround about a sagittal axis at eye-level.

Visual detection of head displacement is dependent on the distance between the eyes and stationary objects in the visible surround because of the limited resolution of the retina. By means of stabilometry the postural stability as a function of the eye-object distance has been investigated. It has been found that at eye-object distances of over 5 m vision does no longer contribute to postural stabilization. These experiments, together with the possible consequences for the height vertigo mechanism, are discussed in chapter 5.

Finally in chapter 6 the results are given of preliminary experiments done in the tilting room with patients suffering from post-concussional dizzeness and patients devoid of the vestibular function. It appeared in these tests that these patients rely to a considerable extent on vision.

Also as a result of this study it can be said that as an auxiliary to the classical vestibular examination methods posturography can be applied in the clinic (Kapteyn and de Wit, 1972 ; Folkerts et al., 1973 ; Gagey, 1977).

Because hardly ever the same subjects participated in the different experiments of this study, the various aspects of sensory interactions are not synthesized into one model. With a view to the interindividual differences measured under the various test conditions and to the systematically divergent behaviour of certain patients it would seem recommendable to lay in further studies more weight on the inter-relations between the various tests so as to obtain a better insight into the physiology and pathophysiology of the equilibrium mechanism as a whole.

CONCLUSION

In the present study it is shown that the information of the vestibular system, the visual system as well as the somatosenory system is equally significant for keeping balance and keeping a proper orientation. For an adequate spatial orientation it is of primary importance that the information of these three sensors is weighed and integrated properly.

Dizziness being due to a dysfunction in this integration, either by an unadequately functioning of the sensors or by a dysfunction of the integration centre itself, the following suggestion presents itself. With patients with dizziness complaints (including height vertigo and motion sickness) it could be of advantage if in addition to the classical examination of the vestibular system attention is paid also to the functioning of the entire equilibrium system. Suitable tests for this purpose are presented in this study.

SAMENVATTING EN CONCLUSIES

SAMENVATTING

"... Als prinzipielle Voraussetzung für das Studium vestibularer Effekte gehören passive Rotationen. Alle aktiven Drehbewegungen sind glatt zu verwerfen...". Deze opvatting van Fischer en Wodak (1924) wordt in de onderhavige studie letterlijk met voeten getreden.
Inderdaad blijken door rondstappen (aktieve rotatie) de vestibulaire reflexen en sensaties af te wijken van door passieve rotatie geïnduceerde reacties.
In hoofdstuk 1 wordt een verklaring voor deze discrepanties gezocht door middel van experimenten die laten zien dat het somatosensorische systeem geïnvolveerd in rondstappen een rol speelt analoog aan die van het visuele systeem. Draaien van de zichtbare omgeving rond een zich niet bewegend persoon induceert onveranderlijk een sensatie van zelf te draaien ; dit blijkt ook het geval te zijn bij stimulatie van uitsluitend de somatosensoren door schijnbaar rond te stappen (hetgeen gebeurt door in het donker op een draaiend platform te lopen zonder dat de ruimtelijke positie zich wijzigt). De op deze wijze opgeroepen bewegingssensatie blijkt niet te verschillen van de sensatie die optreedt bij echt rondstappen. Tijdens schijnbaar rondstappen blijken ook nystagmus en Coriolisachtige effecten geïnduceerd te kunnen worden hetgeen pleit voor interacties tussen het somatosensorische en het vestibulaire systeem analoog aan die van het visuele en het vestibulaire systeem.
In hoofdstuk 2 wordt de invloed van stimulatie van de horizontale halfcirkelvormige kanalen (d.m.v calorisatie en aktieve en passieve rotatie) en overeenkomstige visuele stimulatie op het houdingsevenwicht besproken. Het blijkt dat de torsie van het lichaam en de draaisensatie als ook de lateropulsie en de nystagmus aan elkaar gekoppeld zijn. Dat ook bij deze proeven de somatosensorische informatie een rol speelt blijkt b.v. uit het verschil in richting van de draaisensatie bij calorisatie tijdens staan of zitten.

Behalve de boven beschreven interacties bij rotaties, treden soortgelijke interacties ook op bij rechtlijnige bewegingen (b.v. het vermeende vertrek van de eigen trein wanneer een ernaast staande trein vertrekt). Hierbij zullen echter ook de otolieten een rol spelen.
In de huidige studie worden de interacties van de otolieten en het visuele systeem bestudeerd met een andere methodiek nl. het wijzigen van de optische vertikaal ten opzichte van de zwaartekracht door middel van een kantelkamer.
In hoofdstuk 4 wordt de invloed van stationaire scheefstand van de kantelkamer op de waarneming van de vertikaal en op het houdingsevenwicht onderzocht. Het blijkt dat de subjectieve vertikaal bepaald wordt door de visuele en vestibulaire informatie en onafhankelijk is van de positie of de stijfheid van het grondvlak waar de proefpersonen op staan. Stationaire scheefstand heeft een geringe invloed op de houding, maar de stabiliteit wordt niet aangetast. Wanneer de kamer sinusvormig beweegt (voor-achterwaarts of zijwaarts) dan wordt een sinusvormige beweging van het lichaam geïnduceerd (zgn. "Optic Sway") zonder dat de proefpersoon zich dat bewust is. Wordt de somatosensorische informatie minder effectief gemaakt door de proefpersoon op schuimrubber te plaatsen dan blijkt de invloed van de visuele informatie op de Optic Sway aanzienlijk groter te zijn. De Optic Sway als functie van amplitude en frequentie van de sinusvormig kantelende kamer is systematisch onderzocht.
Als preludium op deze experimenten wordt in hoofdstuk 3 een experiment beschreven waarbij de visuele omgeving volledig draaide om een sagittale as op ooghoogte.
Wanneer de afstand van de ogen tot stationaire objecten in de visuele omgeving toeneemt, zal, ten gevolge van het begrensde oplossend vermogen van de retina, de verplaatsing van het hoofd steeds groter moeten worden om deze verplaatsing ook visueel waar te nemen. De invloed van toenemende oog-object afstand op het houdings-evenwicht is d.m.v. de stabilometrie onderzocht waarbij gevonden werd dat bij afstanden van meer dan 5 meter het visuele systeem geen bijdrage meer levert aan het houdings-evenwicht. Deze experimenten, samen met de mogelijke consequenties op het gebied van de hoogtevrees, worden bediscussieerd in hoofdstuk 5.

Tenslotte worden in hoofdstuk 6 enige resultaten besproken van experimenten in de kantelkamer met patienten lijdend aan post-commotionele duizeligheid en patienten zonder vestibulaire functie. Het opvallende bij deze tests was dat deze patienten zeer veel waarde hechten aan de visuele informatie. Mede op grond van deze studie kunnen we stellen dat naast evenwichtsonderzoek met de klassieke methodieken (Oosterveld et al., 1972) ook van de posturografie nuttig gebruik gemaakt kan worden in de kliniek (Kapteyn en de Wit, 1972 ; Folkerts et al., 1973 ; Gagey, 1977). Aangezien meestal met verschillende proefpersonen gewerkt werd voor de verschillende onderdelen van deze studie is een modelmatige benadering van alle beschreven aspecten van zintuigelijke interacties tesamen niet toegepast. Gezien de interindividuele verschillen gemeten in de diverse testcondities en het systematisch afwijkende gedrag van bepaalde patienten, verdient het de aanbeveling in een verdere studie meer nadruk op de dwarsverbanden tussen de verschillende tests te leggen teneinde meer inzicht te krijgen in de fysiologie en de pathofysiologie van het evenwichtsmechanisme in zijn totaliteit.

CONCLUSIES

Uit de onderhavige studie blijkt dat zowel voor wat betreft het bewaren van het houdingsevenwicht als ook voor wat betreft de ruimtelijke waarneming, de informatie zowel van het somatosensorische, het visuele als het vestibulaire systeem van grote betekenis is. Voor een adequate ruimtelijke orientatie is het derhalve van wezenlijk belang dat de informatie uit te verschillende kanalen op de juiste wijze gewogen en geïntegreerd wordt.
Aangezien duizeligheid wijst op een dysfunctie van deze integratie ōf doordat de receptoren niet adequaat functioneren (dat wel misleidende informatie aangeboden krijgen) ōf doordat het integratiesysteem zelf gestoord is, zal men bij patienten met duizeligheidsklachten (met inbegrip van bewegingsziekten en hoogtevrees) naast het klassieke vestibulaire onderzoek ook zijn voordeel kunnen doen met onderzoek dat meer gericht is op de samenwerking van deze zintuigsystemen. Hiertoe geeigende tests zijn in deze studie beschreven.

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