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A low-dimensional model of coordinated eye and head movements

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Abstract. Eye and head movement data, were recorded under head-fixed and head-free conditions, and compared with theoretical results obtained using a nonlinear model of eye-head coordination. The model explains slow, or pursuit movement correlated closely to target movement, and saccades, or quick phases of eye movement. Eye movement under head-fixed conditions was modeled by an externally forced Duffing equation, whilst properties of head movement are described by a second externally forced Duffing equation with lower eigen frequency. In the more natural, head-free conditions where both eye and head movements are used synergetically to pursue a visual target, the vestibulo-ocular reflex (VOR) is represented by coefficients defining the mutual coupling between these two oscillatory systems. In the present model, the oscillator that models eye movement has an inhibitory influence on head movement; head to eye coupling coefficients are included to model the influence of the VOR mechanism. Individual eye and head movement patterns in different subjects can be adequately modeled by altering the coupling coefficients. In order to adequately simulate those changes introduced by microgravity conditions, the coefficients defining eye-head coordination (mutual coupling) must be changed. It may be hypothesized that such changes in the neurovestibular system could introduce the instability in eye-head coordination, which is known to lead to space sickness.

1 Introduction

Coordinated eye and head movements are employed extensively to direct visual attention during everyday activity. Indeed, the eye may be considered the most active of all human organs, constantly in motion in its task of scanning the visual world. For example, it has been demonstrated that during inspection of a visual scene or picture, the eye scans the available clues to facilitate recognition of objects. Given an identical set of visual clues, each test subject will exhibit his own characteristic sequence of examining any one object, i.e. different cognitive strategies appear to be employed [14]. On the other hand, during

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natural movement in a highly variable physical environment, our impression of the visual world remains stable and coherent. This impression is facilitated through the coordination of accurate eye movements across different head positions and movements. A particularly important role in this coordination is played by the vestibular system which sends to the central nervous system information about every head movement. The main aim of the present contribution is to define a model for eye movements under natural, head-free conditions. The proposed model is also applied to experimental results obtained from eye-head coordination tasks performed during prolonged microgravity, and after return to earthbound, one-G conditions.

The present experiments and model were thus designed to examine the mechanism of the sensory integrative processes involved in human orientation in three-dimensional space, and during vestibular adaptation to altered gravity conditions.

The perception of movement in three-dimensional space involves transduction of three degrees of freedom for rotational, and three degrees of freedom for translational movement. In the vestibular system, this is provided for by the semi-circular canal resp. the otolith receptors. Via the vestibulo-ocular pathways in the brainstem, these six degrees of freedom are utilized synergistically for the purpose of gaze stabilization and are reflected by compensatory eye movements in the three orthogonal planes governed by the extraocular muscle pairs. This mechanism is generally referred to as the vestibulo-ocular reflex (VOR). Thus, any physiological stimulation to the vestibular receptors, either by rotatory or translatory acceleration, or a combination thereof, will potentially elicit a systematic, compensatory eye movement. For a full understanding of the vestibulo-oculomotor system, it is therefore necessary to determine the contributions of the canalicular and otolithic systems to the elicitation of these compensatory reflex eye movements. Whereas much available evidence points to an adaptation in the otolithic system during prolonged microgravity, it has been generally accepted that the G-independent canal function remains unaltered in zero-g conditions [7,8]. Whilst this is most likely correct with regard to the primary transduction mechanisms in the peripheral organs, there is increasing evidence that neuronal mechanisms in the brainstem circuitry are effected by altered gravity conditions by neural modification in the central processing of information from the otolithic receptors and their part in the interaction with the semicircular canal connections [16]. Discordance in this sensory processing during the early days of spaceflight is intimately related to the occurrence of space sickness. In the present experiments, the vestibulo-ocular reflex (VOR) was measured by means of active head rotation under one-G, earthbound and during prolonged microgravity. These results will be interpreted on the basis of a nonlinear model describing interaction between eye and head movements. This model was initially developed for data from experiments involving visual tracking of a moving target under head-free conditions.

2 Methods and Experimental procedure

Measurement and evaluation of eye and head movements was performed exclusively by the video-oculography technique (VOG). The equipment included a lightweight head-mounted assembly, which permits synchronous recording of eye and head movements. Eye movements were recorded from the left eye by miniaturized CCD camera with infrared lighting, mounted in a light-occluding mask. A visual target device was also integrated into this mask, by means of which calibration diodes or a fixation point could be presented to the test subject (right eye). Head movements were recorded by means of angular rate sensors for each of the three axes of rotation, and linear accelerometers for each of the three translational axes. The associated image processing workstation is custom-designed to process the video images of the eye. Essentially, digital image processing software is employed to evaluate the horizontal, vertical and torsional components of eye movement. Measurement resolution is of the order of 0.1 - 0.2 degrees for all three components.The combination of the head-mounted recording package and the portable workstation therefore permit precise eye and head movement measurements and evaluation in almost any experimental situation.

In the first series of experiments, test subjects were required to fixate a sequence of visual targets. For this purpose, an array of light diodes was employed. With the subject in the dark, single diodes were randomly illuminated. The diodes were arranged as a two-dimensional matrix, spaced at 2 deg intervals over the range +/- 20 deg. The switching rate was varied between 0.3 and 2 s with a duty cycle of 1.0. Different random illumination sequences were employed, including one-dimensional, horizontal or vertical, and two-dimensional patterns. Under head-free conditions, the subject was instructed to fixate a sequence of illuminated diodes.

In the second series of experiments, the visual VOR, i.e. with a space/fixed target and head movement in pitch and yaw, was measured during active head oscillations at each of four discrete stimulus frequencies (0.12, 0.32, 0.80, 2.0 Hz). The test subject was cued by a corresponding acoustic metronome signal. A minimum of five head oscillations was performed at each of the frequencies. Visual targets were fixated with the right eye, whilst oculomotor response was measured from the left eye. After initial training, tests were carried out at weekly intervals during the four weeks previous to launch. Inflight testing was performed on days 3, 4, 5 and 6 of mission; postflight measurements were made on day 0, 2, 4, 6 and 10 after returning to terrestrial conditions.

The model is represented by a set (pair) of the nonlinear differential equations - coupled externally forced Duffing oscillators. This was simulated on a Sun Workstation using a modified Dynamical System Toolkit with an Interactive Graphical Interface: dstool [1].

3 Results

3.1 Eye and head movement in response to target motion

An example of eye and head movement recordings in response to horizontal target motion is shown in Fig. 1. The eyes consistently move faster than the head, and both systems also manifested different patterns of movement. This also varied among subjects (compare Fig. 1 left and right panels). In response to the same stimulus, the first subject (Fig. 1 left) exhibited a transient fast dumped eye component. The second subject (Fig. 1 right) showed distinctly larger head movements and more transient, oscillatory eye movements. Similar differences were observed during vertical stimulus and movement sequences.

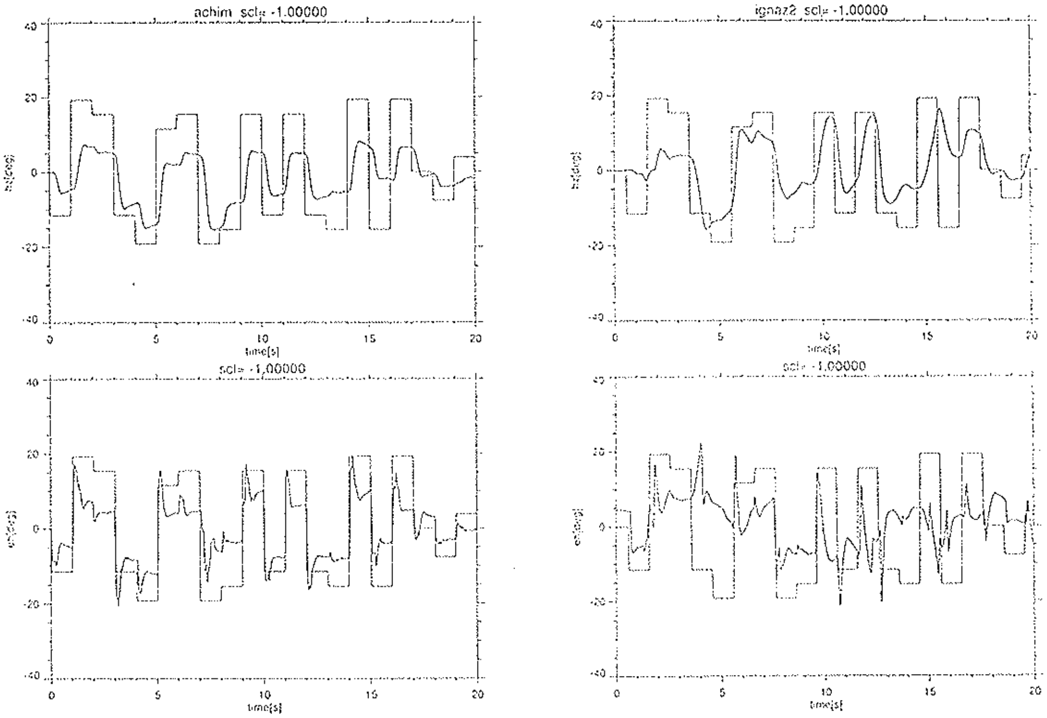
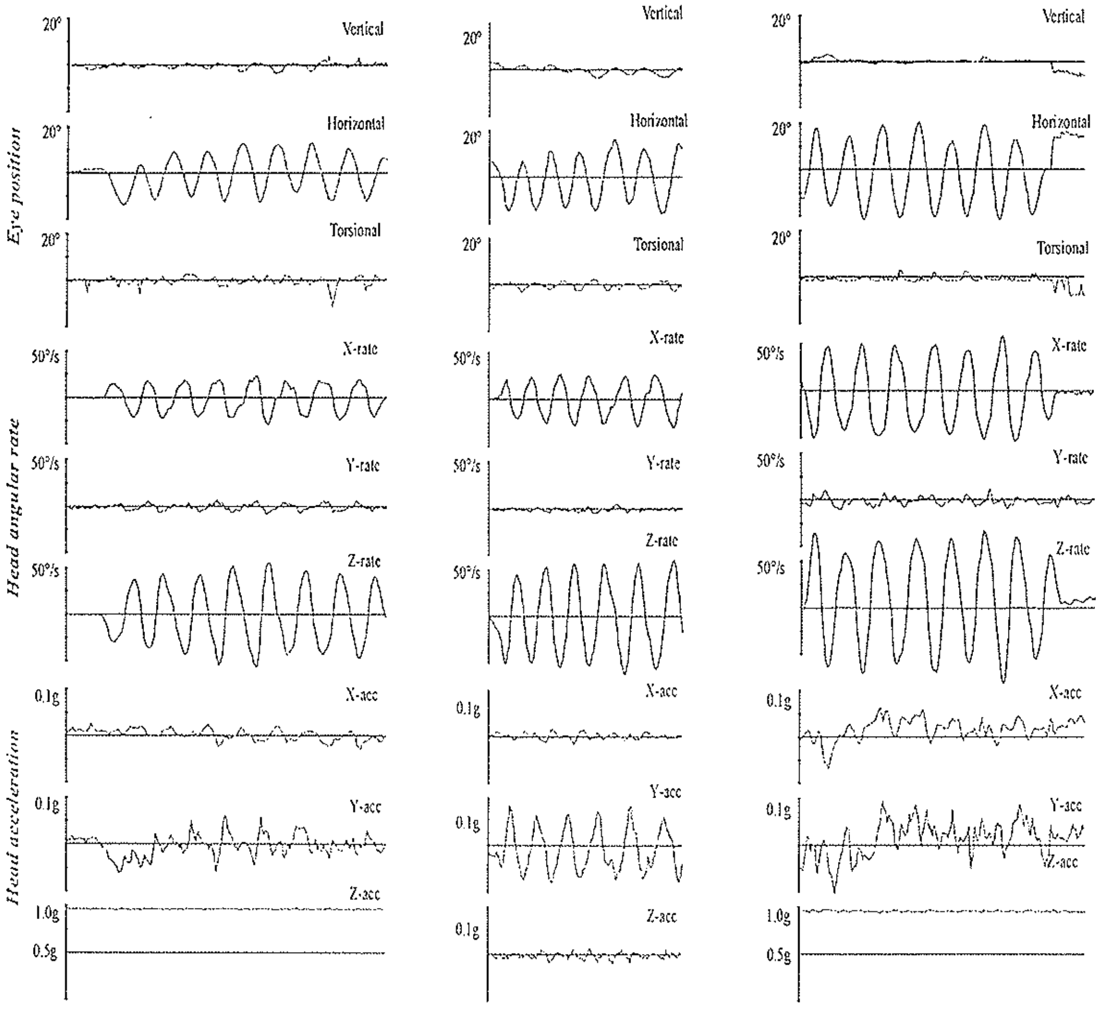


Fig. 1 Horizontal movements of the eye (upper panels) and head (lower panels) in response to the moving target, indicated on each figure by the thin line. The inter individual differences in eye and head movements can be recognized by comparison of the responses to the same random pattern.

3.2 Eye and head movement during active head oscillation

Yaw



Preflight -21 / 0.80 Hz Yaw *Inflight 5 / 0.80 Hz Yaw* *Postflight + 4 / 0.80 Hz Yaw*

Fig. 2 Example of head and eye movements for active yaw during pre-, in- and postflight phases, at 0.8 Hz. From top to bottom are shown: vertical, horizontal and torsional eye position (polarities according to clinical convention - upwards = rightwards); roll (X), pitch (Y) and yaw (Z) axis angular rate of head, anterior-posterior (X), lateral (Y), and rostral-caudal (Z) axis linear acceleration of head (polarities of angular velocities and linear accelerations according to right hand rule).

Pitch

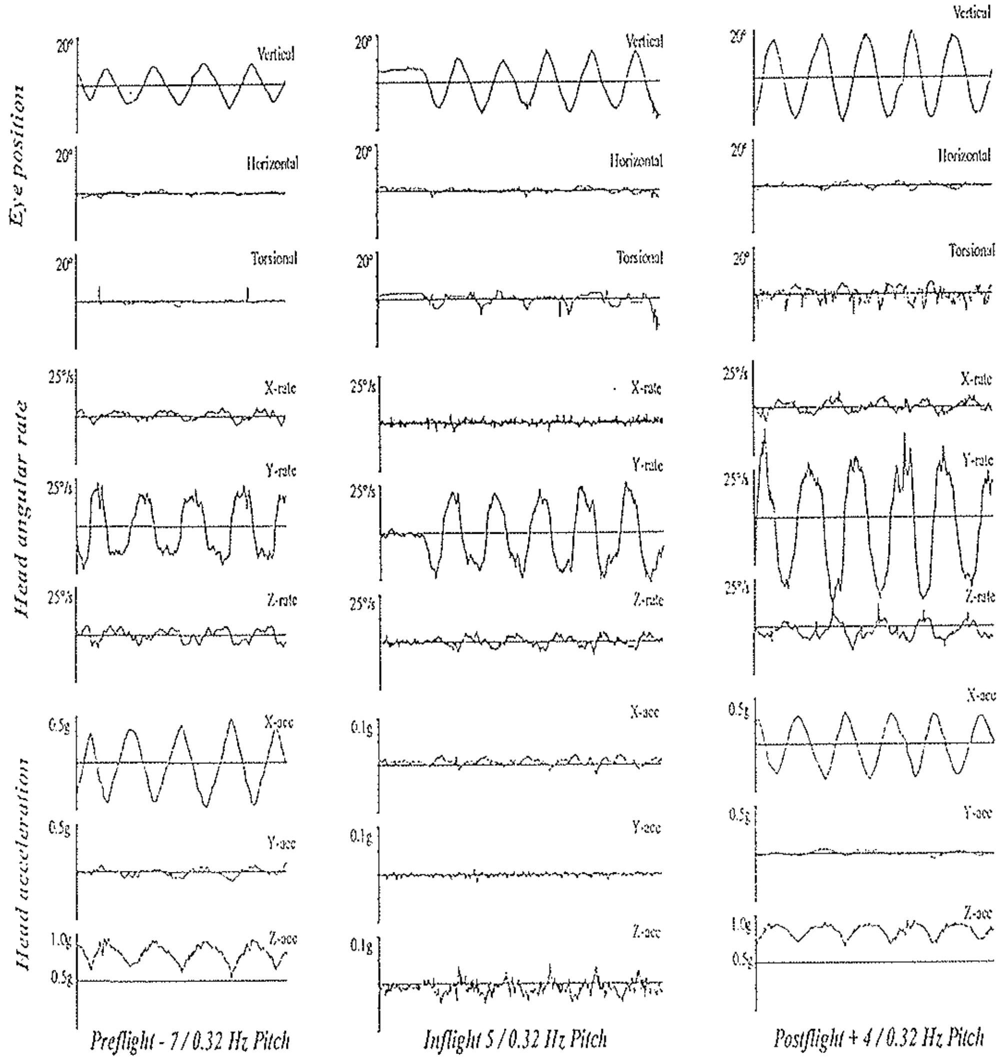


Fig. 3 Example of head and eye movements obtained during pre-, in- and post-flight testing with voluntary head pitch oscillation at 0.32 Hz (nominal). Traces are arranged as in Fig. 2 above.

The vestibulo-oculomotor response during voluntary yaw movement of the head at 0.8 Hz - as performed during preflight (under one-G conditions), inflight (under zero-G conditions), and postflight conditions - is shown in Fig. 2. During this yaw head movement (dominant component around z axis), horizontal components of eye movement correspond primarily to the stimulation of the horizontal canal. The VOR gain (defined below) remains constant over the pre-, in-, and post-flight period. However, a noticeable increase in the amplitude of head movement (4th trace from below) and horizontal eye movement component was recorded. During pitch movement (Fig. 3), the vertical eye movement component is dominant, corresponding to stimulation of the vertical canals and otolith receptors, i.e. angular rate is transduced by the semicircular canals, and head inclination to gravity by the otolith receptors. In the in- and post-flight conditions a significant increase in the amplitude of the head movement (5th trace from below) can be observed. The minor perturbances to be observed on the other rate and acceleration channels reflect the difficulty in performing head movement purely in one plane.

As to be expected the signals from the linear accelerometers are very low in the absence of the one-g gravity vector. The head movements are however reflected clearly by the angular rate sensor signals. Here there appears a more complex pattern than during preflight testing.

The VOR gain is defined for each axis as the ratio of the amplitude of the first harmonic of eye velocity to the first harmonic of head angular rate. This gain factor was calculated for the head oscillations about the yaw and pitch axes at the specified frequencies [Clarke et al. in preparation]. There is a significant increase of the gain during inflight for the pitch but not for yaw movement. The coupled Duffing oscillator model describes the coordination between eye and head movement around one axis. The Duffing oscillator [17] allows for no spontaneous activity, a condition which requires the assumption that no spontaneous eye or head movement occurs when a stationary target is fixated. The first Duffing oscillator describes the head movement, and the second the eye movement. The two oscillators are mutually coupled as follows: the head position provides a negative signal with coefficient β_2 to the eye position, and in turn, the eye position provides negative feedback with coefficient β_1 to the oscillator describing the head position. Further, a positive signal of head velocity (coefficient α_2) is input to the equation describing eye movement. This contributes to the generation of a fast change of an eye position following any change in head position. The equations may be written as follows:

$$\frac{dx_1}{dt} = y_1 \tag{1a}$$

$$\frac{dy_1}{dt} = \omega_1(-x_1 - {x_1}^3/3) + k_1 y_1 + b_1 cos(\omega t) + \beta_1 x_2 \tag{1b}$$

$$\frac{dx_2}{dt} = y_2 \tag{1c}$$

$$\frac{dy_2}{dt} = \omega_2(-x_2 - {x_2}^3/3) + k_2 y_2 + b_2 cos(\omega t) + \beta_2 x_1 + \alpha_2 y_1 \tag{1d}$$

where equations $1a$, $1b$ describe the head movement, and eqs $1c$, $1d$ describe the eye movement; ω_1 (0.5) and are ω_2 (5.2) eigen frequencies for the head and eye; k_1 , k_2 are nonlinearities in equations for the head and eye; ω, $b_1 = b_2$ frequency and amplitude of the visual target (for simplicity, a cosine function is assumed), β_1 describes the influence of the eye position on the head position,and β_2, α_2 the influence of the head position and velocity of the eye position.

3.3 Model of eye and head movement in response to target motion

In the simulation study, visual target frequencies $f = 0.02, 0.05, 0.2$ and $0.1 Hz$ were employed, and the amplitude was varied from $b_1 = b_2 = 1, 4, 6, 8$. This enabled comparison with the experimental results.

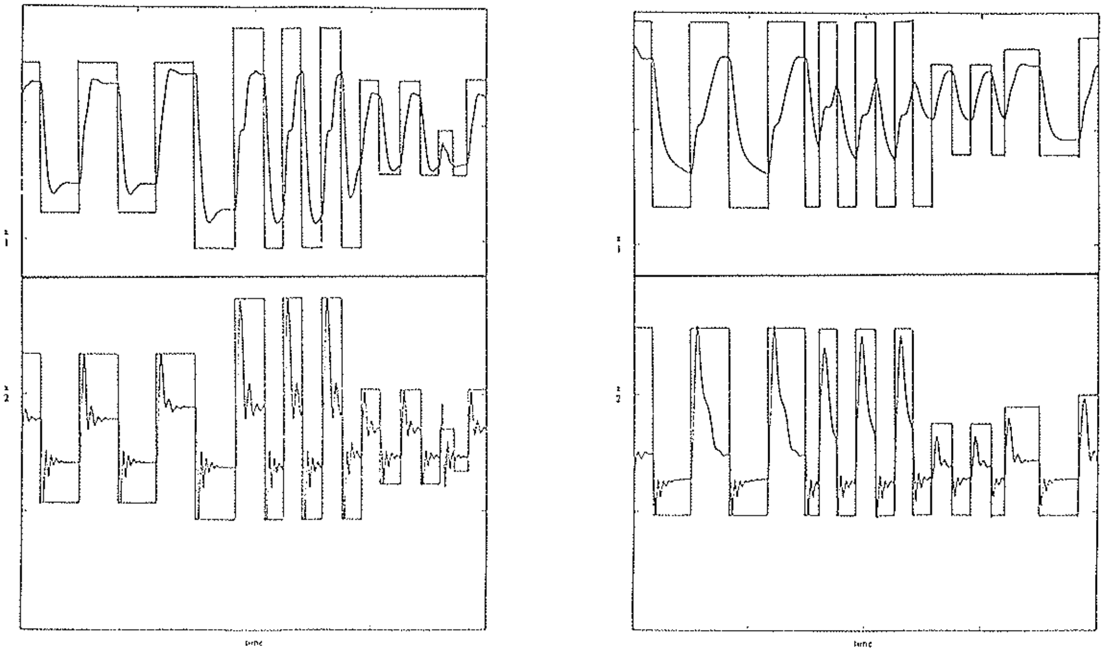


Fig. 4 Example of the simulation for horizontal head (upper parts - x_1 variable) and eye (lower parts - x_2 variable) movements in response to the moving target (represented by the thin dashed line). The individual differences in eye and head movement responses can be observed in the two examples shown .

The experimental results were compared with the simulated data (Duffing equations 1a, 1b) for each of the tested frequencies. It should be noted that the individual patterns of eye and head movement measured in the experimental tests could be accommodated by altering the coupling parameters for the Duffing equations. A subject exhibiting more transients and fast eye movements (Fig. 4 left) tends to produce smaller amplitude head movements. This property was modeled by altering the coefficient β_1 from -2 for the simulation shown on the left -1.2.

3.4 Model of eye and head movement during voluntary head oscillation

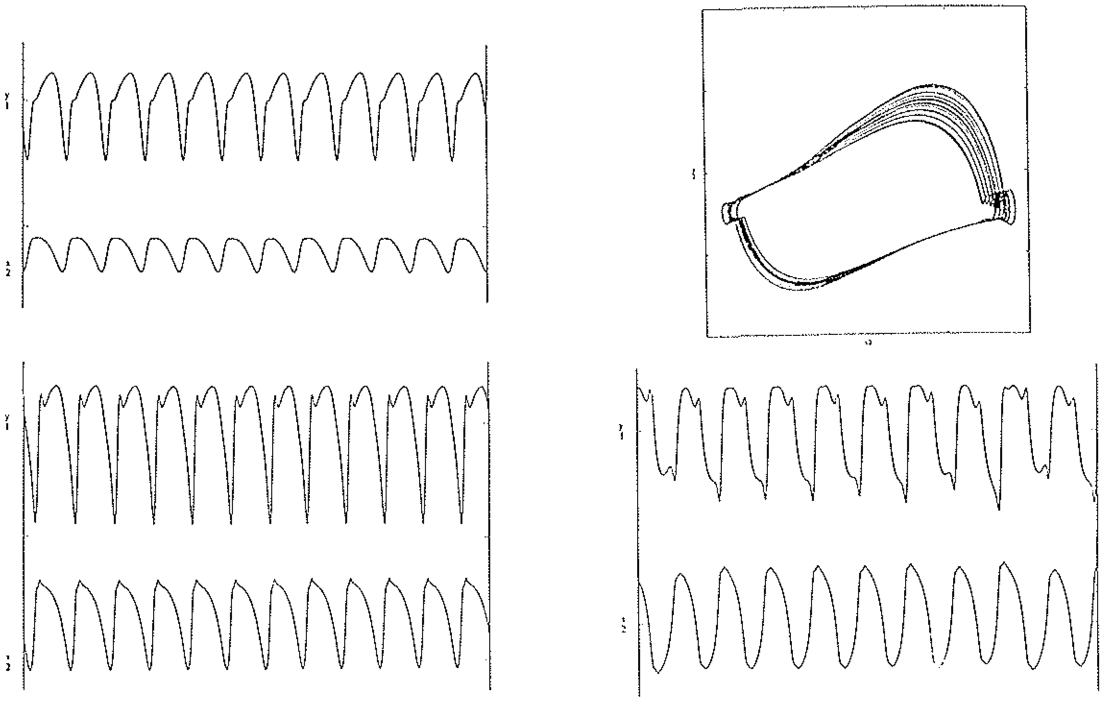


Fig. 5 Example of the simulation of pitch head movements in normal one-G conditions (two upper traces) and in microgravity (zero-G, lower traces). For each simulation the upper trace shows head angular velocity and the lower trace the eye position. On the left, upper panel, the simulation parameters were the same as for subject "achim" (Fig. 1 and 5 left panels) with $b_2 = 0$ - subject fixating an LED. On the left, lower panel, the simulation parameters were changes β_2 from -4 to -2 and α_2 from 3 to 1 to obtain the changes observed in micrograyity (Fig. 3). By small changes in the non-linear properties of the oscillators, one can obtain more complex oscillations (right, lower panel), which are probably chaotic, as can be seen from the trajectory of the eye movements (right, upper panel).

The same model was applied to the experiment with the voluntary head movement. In these experiments the eyes fixated a stationary target, (i.e. were fixed in space), so that in the model , the direct external forced signal to the equation describing eye movement is set to zero amplitude. In order to model the effect of microgravity, the eye - head coupling coefficients were altered. A decrease in the parameter for the influence of head velocity on eye position (β_2 from -4 to -2) does not give large enough changes in the head amplitude and velocity. Furthermore, a separate change of the parameter describing influence of the head position on the eye position (α_2 from 3 to 1) is not adequate. It is necessary to decrease both parameters simultaneously to model the observed experimental changes in pitch response in microgravity.

4 Discussion

The experiments involving fixation of a sequence of illuminated LED targets, indicate that *different strategies are employed by different individuals.* These differences could be accommodated in the simulation model by varying the coefficients defining the mutual influence of head and eye. The properties of our model are related to observations made by others [2, 4, 5, 6]. Bahill et al. [2] simulated recorded saccadic eye overshoots with the second order linear oscillator which they correlated with property of the motoneuronal signal controlling eye movement. Barnes and Lawson [6] observed changes in gain and phase of gaze velocity with the frequency contents of the stimulus, which could be explained with head-fixed pursuit data [4, 5] and frequency-dependent, non-linear visual feed-back mechanisms in gaze control. The properties of the forced nonlinear oscillator could also explain such observations as :
a) effect of changes in the stimulus frequency spectrum on the gain of the eye movements [5], and
b) that a sudden and 'unexpected' change in amplitude and direction of the stimulus waveform cause 'inappropriate' for the current stimulus and and correlated to the preceding sequence in the stimulus, eye movement.
Lauritius and Robinson [13] proposed a complex model utilizing local gaze feedback which agreed with the behavior observed in their experiments when the subjects made self-paced re-fixations between fixed targets. This model could learn to 'recognize' input patterns by producing appropriate outputs. This approach, shown in several papers from Robinson et al. [18, 19, 20], assumes matrix characterization of each structure involved in the head-eye coordination. It is however a static and linear approach. The present model accommodates nonlinear and frequency characteristics with should be find through comparison of the experimental data and simulation. Vieville et al. [21] reported that vertical and horizontal VOR gain dropped during first 4 days of the space-flight and return to normal at 7th day. Matsuo and Cohen [15] in monkey, Baloh et al. [3] in man found asymmetry in velocity storage within the vertical VOR. This asymmetry is clearly related to otolith input since it disappeared in erect position. DiZio and Lackner(parabolic flights) [10] showed that perception of motion and postrotatory nystagmus are shorter in microgravity and longer by 2G conditions. This could be caused by the altered level of stimulation to the otolith organs and, later to the central adaptation processes in the microgravity. The

present findings indicate, however, that the voluntary head movements were not identical in the pre-, in- and postflight intervals. This indicates that the input to the canalicular and otolith organs differ according to different experimental conditions. For example, an increase in the head movement amplitude during postflight test, and altered head pattern movements during the inflight tests were observed. On the basis of our model we suggest that *during the microgravity the same changes in VOR function could give very different responses for different individuals.* Complex chaotic or quasi-periodic oscillations observed in some cases could be the reason of the space sickness. Thus, the present findings point to the use of different "VOR strategies" by different subjects. Assuming that microgravity has an influence on the weighting of VOR parameters, it can be expected that not only changes in gain and time constants [16] but also changes in strategy of eye - head coordination should be observed. Such an effect was observed during performance active roll head movements increasing in frequency over a frequency range from 0.1 to 2.0 Hz. The subject was well trained in performing such roll movements of the head during ground-based studies. However, in microgravity conditions changes in the head movement pattern were observed, although surprisingly, his eye movement pattern was unaltered [9]. In weightlessness, the gravitoinertial forces arising from the inertia of the head mass during active oscillation are minimal, (cf. linear accelerometer signals Fig. 3), so that stimulation to the otolithic organs during such movement can be considered as negligible. The differences observed between pre- and inflight head movements during active roll indicates that in this conditions erroneous motor control does occur. This can be linked to the findings of the sensorimotor tests reported from the recent Russian space mission, which revealed discrepancies in sensorimotor arm control between conditions with and without visual cues. The increase in head movement amplitude observed during the postflight tests further underlines again the influence of the re-calibration of sensorimotor programs during an interval of microgravity. This is reflected, for example, in the well-known, quasi-ataxic. New modes of oscillation could be introduced by large, simultaneous changes to both coefficients. The resulting oscillations can be considered as chaotic, reflecting the complexity of eye-to-head coordination. The question also arises as to how two-dimensional mapping on the retina is related to the three-dimensional velocity information from the vestibular system during head movement. Some implications can be drawn from the report of Hepp et al. [11] in which the preferred on-direction from neurons producing vertical and torsional saccades are not strictly allocated to the saggital and torsional head planes, but rather that they encompass a less specific range involving all three canal planes. In this sense, Ito [12] has reported a zonal organisation in the cortical folia of the vestibulo-cerebellum related to the planes of the semicircular canals.

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