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HUMAN SPATIAL ORIENTATION DURING CENTRIFUGE EXPERIMENTS : NON-LINEAR INTERACTION OF SEMICIRCULAR CANALS AND OTOLITHS

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INTRODUCTION

In order to maintain dynamic human spatial orientation an interaction of otoliths and semicircular canals is necessary. As gravitational and translatory linear acceleration, sensed by the otoliths, can not be measured separately, during and after movements other sources of information must be used to determine the direction of gravity. Without vision the angular velocity sensed by the semicircular canals as well as the knowledge about the constancy of the direction and amount of gravity with respect to earth could help to locate the direction of "up", the subjective zenith (SZ).

When briskly tilted with respect to gravity, a fast change of the direction of gravity as well as the angular velocity of the tilt is sensed by the vestibular system. The perceived direction of the SZ follows without delay quite correctly. This has been shown in [9] in comparison to the "Oculogravic Illusion" experiment (e.g. [4]) performed on a human centrifuge. There a fast change of the direction of the resultant acceleration, the sum of gravity and centrifugal acceleration, when starting the centrifuge run caused the SZ to follow with a time constant of about 20 sec. These results were first interpreted by [5] in a two-dimensional model of otolith-canal interaction as a low-pass filtering of the otolith afferents. Semicircular canals can, due to their sensor dynamics, only measure high-frequency changes of orientation as angular velocity, together with the low-frequency information of the otoliths a dynamic perception of the direction of gravity should therefore be possible.

Several three-dimensional models of human spatial orientation (e.g. [8],[1],[2]) followed, but none of these authors tried to explain the second interesting phenomenon uncovered by the "Oculogravic Illusion" experiment : when stopping the centrifuge rotation, the SZ follows the fast change of acceleration almost without any delay [4]. This is clearly in contrast to the slow increase at the onset of the centrifuge run.

This paper tries to explain the difference between the perception of orientation at the start and the end of "Oculogravic Illusion" experiment, which is reexamined here, by modeling otolith-canal interaction. The model is supported by the results of a second centrifuge experiment presented in which the direction of the resultant acceleration with respect to the subject did not change while the subject was tilted about 60° around the frontal axis with respect to earth.

METHODS

Both experiments described below were performed in a large, computer-controlled human centrifuge (distance been rotation axis and cabin 10m), which could be accelerated and stopped within a few seconds. Subjects (Ss), facing the movement direction of the cabin, were asked to adjust continously a luminous line 40 cm in front of them by remote control to their subjective vertical (SV) during and after the motion stimuli. Line angle and centrifuge frequency were A/D-converted and saved on a micro-computer for further analysis.

1. Centrifuge experiment with fixed cabin ("Oculogravic Illusion" experiment): In the first experiment the cabin was fixed rigidly to the arm of the centrifuge in an upright position. The centrifuge was accelerated to a constant velocity causing a tilt of the resultant acceleration vector relative to the S of 30°. Each of the 7 Ss performed three subsequent runs of 120 sec duration followed by a stop of 60 sec.

2. Centrifuge experiment with free cabin: In the second experiment the movement of the centrifuge cabin was controlled by the main computer to maintain a constant orientation of the subject with respect to the tilting resultant gravito-inertial acceleration. This centrifuge profile is normally used for aircraft pilot training. The centrifuge reached quickly its final velocity causing a g-load of 2g and a cabin tilt of 60° with respect to earth. The head of the Ss was located approximately 0.5 m over the center of cabin rotation. Eight Ss participated and performed at all 12 centrifuge runs (3 Ss 1 run, 4 Ss 2 runs, 1 S 4 runs) adjusting the line 20 sec before the start and during the first 120 sec of each run.

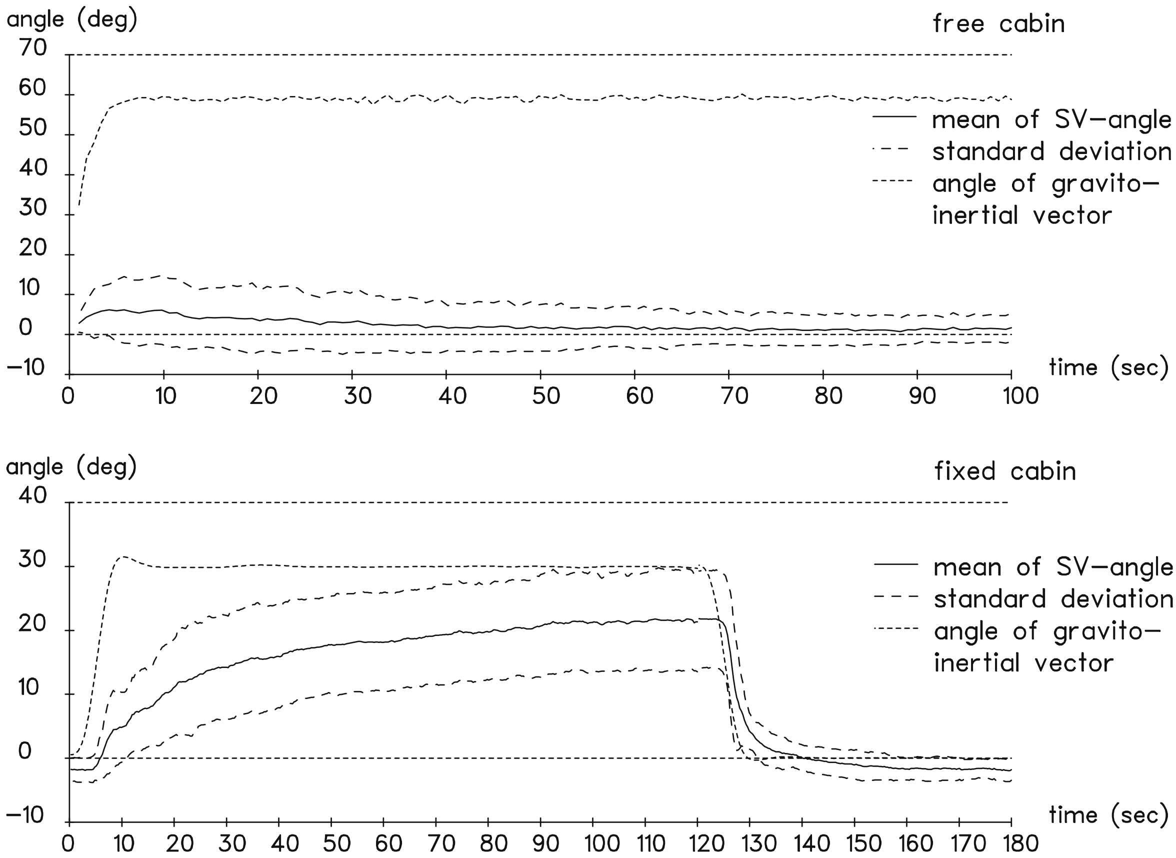

Figure 1 Experimental results of the centrifuge experiments with free cabin (upper part) and fixed cabin (lower part) as means over all Ss and all runs. The angle of the gravito-inertial vector is given with respect to the centrifuge axis to visualize the cabin tilt in the free cabin experiment.

RESULTS

The experiment with fixed cabin showed the same time course as described in [4], the SV increased during and after the start with a time constant of 21.94±0.33 sec (least square fit of a single exponential function) to an inter-individually different static value (mean of all Ss 21.0 deg) and decreased during the stop almost without delay to the initial zero position (see Figure 1 lower part).

In the experiment with the free cabin the stimulation of the semicircular canals equal to a lateral tilt of 60° did not modify at all the perception of the vertical, the SV showed only a small disturbance (mean max. 6.67±8.32 deg) shortly after the start followed by a decrease to its zero level (see Figure 1 upper part).

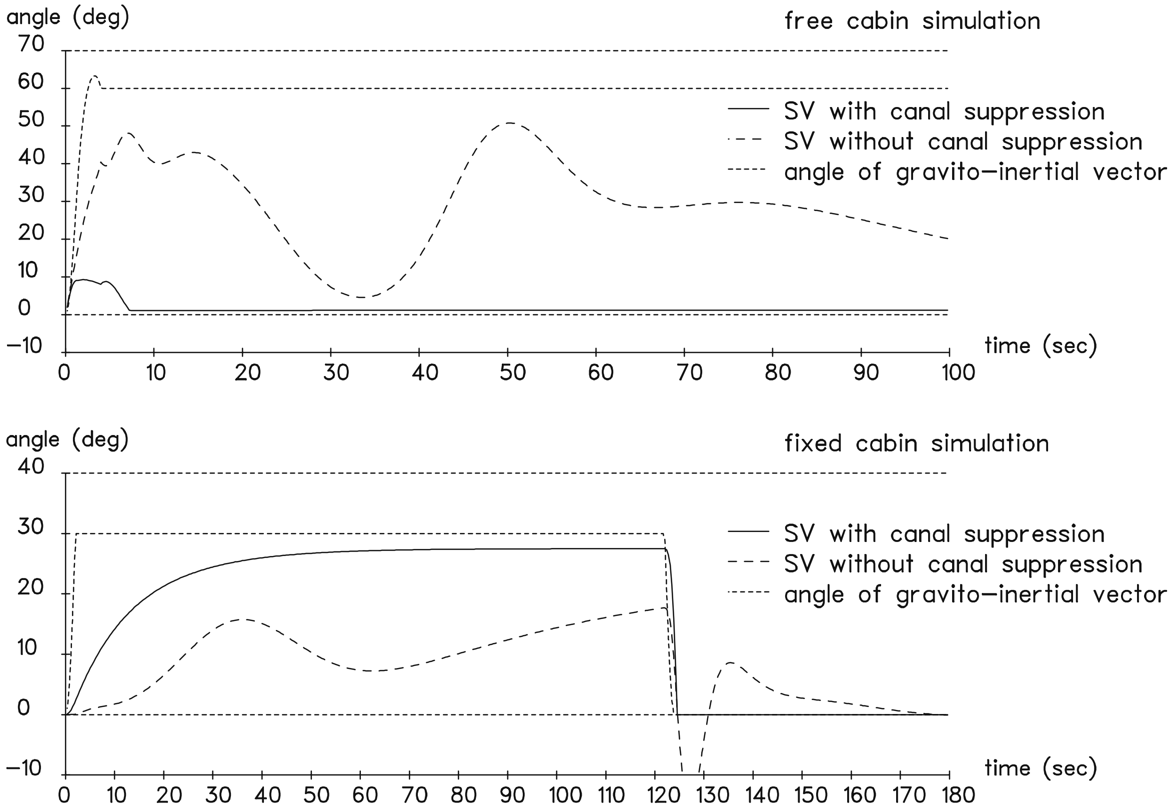

Figure 2 Simulation runs of the fixed cabin (lower part) and free cabin (upper part) experiment. Both the simulations with and without canal signal suppression are shown. Only simulations including suppression of canal signals show correct results, which is evident for the free cabin experiment. In the fixed cabin experiment the time course of the SV results of several effects. During the start a slow increase is produced by the internal low pass filter, whereas during centrifuge stop estimated gravity is rotated by the canal afferents around the body axis. Without canal suppression (lower part, dashed line) this rotation results in an oscillation of the SV time course. Canal suppression (lower part, solid line) stops this rotation exactly when the SV angle is zero as found in the experiment.

MODEL AND SIMULATIONS

A three-dimensional non-linear model of otolith-canal interaction is proposed, which is based on the physical relationship between the angular velocity vector ω (sensed by the semicircular canals) and gravity vector g (sensed by the otoliths) during head rotations
described by the following equation (x 1:vector cross product):

$$\dot{\underline{g}} = -\underline{\omega} \; x \; \underline{g} \qquad (1)$$

In the following a simplified description of the model developed earlier in [3] is given. Sensor dynamics are modelled as linear systems similar to those described in [8]. The otolith afferents a_{ot} and the semicircular canal afferents ω_{rot}, corrected in a non-linear way described below in equation 3, interact centrally according to the following equation to compute the estimated gravity vector g_e:

$$\dot{\underline{g}}_e = -\underline{\omega}_{rot} \; x \; \underline{g}_e + (\underline{a}_{ot} - \underline{g}_e)/\tau \qquad (2)$$

where τ is a time constant of about 20 sec. This equation, being linear with respect to the relation between a_{ot} and g_e, can be interpreted as an optimal linear estimator (steady-state Kalman-Filter) of gravity [3] using the physical relationship given in equation 1.

The experiment with fixed cabin described above suggested that canal afferents are not used to rotate the SZ if the angle between measured acceleration and estimated gravity is increased by this rotation. The following equation describes this statement mathematically by giving the relationship between canal afferents ω_{can} and corrected angular velocity ω_{rot} used in equation 2 ($\circ$: dot product):

$$\underline{\omega}_{rot} = \sigma((\underline{a}_{ot} \times \underline{g}_e) \circ \underline{\omega}_{can}) \cdot \underline{\omega}_{can} \quad (3)$$

where σ is the step function. Thus ω_{can} is unchanged (multiplication by 1) when the argument of σ is positive indicating an decreasing angle between a_{ot} and g_e caused by the rotation and is cancelled (multiplication by 0) if the argument is negative or zero (canal signal suppression).

To model static deviations of the SZ from the objective vertical g_e is normalized an added to an idiotropic vector according to [7].

Simulation runs of the model were performed with and without simulating the suppression of canal signals. For both experiments only simulations including equation 3 showed correct results (see Figure 2). In the fixed cabin experiment the time course of the SV results of several effects (low pass filtering according to equation 2, rotation of the SZ), but can not be reproduced without implementing equation 3. Thus also the asymmetry of the "Oculogravic Illusion" gives evidence for canal signal suppression.

Simulation of tilt experiments around the visual (X-) axis of the head, like described in [9] for a 30° tilt, suggest that this canal signal suppression is necessary to compensate the high pass dynamics of the canals for the perception of the vertical in every-day life. Otherwise these dynamics would cause aftereffects of an oscillating SV lasting several seconds.

CONCLUSION

This information processing structure described above is able to explain both the results found for elementary stimulations like tilting around the X-axis of the head and for more complex experiments like the asymmetry of the "Oculogravic Illusion". Comparison of simulation runs and experimental results suggests that semicircular canal output is only affecting the direction of the SZ if a correction of the SZ in the direction of the acceleration vector measured by the otoliths can be achieved. This non-linear filter cancels implausible canal information and, at the same time, solves the problem of overcoming the high-pass filter characteristics of the semicircular canals.

Recent experiments ([10],[6]) measuring eye movements in fixed centrifuge experiments showed time courses especially of the static component of ocular counterroll similar to that of the SV described above. This suggest that ocular counterroll and perception may share the same estimate of gravity and also the same processing structure. Further experimentation comparing counterroll and perception could verify this possible link between physiological and psychophysical data and improve the knowledge about the underlying canal-otolith interaction.

From the data presented here it can be concluded that the predominance of otolith information, well known for static perception of orientation [7], is maintained as well for dynamic human spatial orientation.

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