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Orientation illusions and heart-rate changes during short-radius centrifugation

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Abstract: Intermittent short-radius centrifugation is a promising countermeasure against the adverse effects of prolonged weightlessness. To assess the feasibility of this countermeasure, we need to understand the disturbing sensory effects that accompany some movements carried out during rotation. We tested 20 subjects who executed yaw and pitch head movements while rotating at constant angular velocity. They were supine with their main body axis perpendicular to earth gravity. The head was placed at the centrifuge's axis of rotation. Head movements produced a transient elevation of heart-rate. All observers reported head-contingent sensations of body tilt although their bodies remained supine. Mostly, the subjective sensations conform to a model based on semicircular canal responses to angular acceleration. However, some surprising deviations from the model were found. Also, large inter-individual differences in direction, magnitude, and quality of the illusory body tilt were observed. The results have implications for subject screening and prediction of subjective tolerance for centrifugation.

Keywords: Coriolis effects, artificial gravity, orientation illusion, heart rate, perceived motion

1. Introduction

Artificial gravity as created by short-radius centrifugation (SRC) is a potentially effective countermeasure against the adverse effects of prolonged weightlessness. The physiological supportability of the rotation rates required by a centrifuge with a short (2–3 m) radius has been validated [4] for brief periods of exposure. Only with high rotation rates (above 20 rpm) does the gravito-inertial force along the longitudinal body axis created by SRC produce cardiovascular effects that are comparable to those of standing upright in Earth gravity [5]. However, head movements made during centrifugation cause distressing effects of illusory tilt and reflexive eye-movements [e.g. 7,14], as well as cardiovascular responses and motion sickness [e.g. 8]. These disturbing side effects must be better understood and overcome if intermittent artificial gravity is to be implemented with a short-radius centrifuge. In this paper we evaluate illusory body tilt, motion sickness, and heart rate changes induced by head movements in the Coriolis environment of SRC. We do so for a gravito-inertial force direction along the longitudinal body axis, which is a crude approximation of gravity when standing upright. The focus of the present study is on subjective experience caused by the inevitable sensory conflict that accompanies head movements during centrifugation, that is the conflict between erroneous vestibular information and information from vision and kinesthesis. We have also investigated the degree to which the experience is consistent among subjects and predictable based on a model of the semicircular canals. Some surprising inconsistencies were found.

Reason and Graybiel [24] reported large individual differences in subjective tilt caused by head movements when sitting upright in a slow rotating room that rotated counterclockwise. In that study, subjects rolled their heads (down to the left or to the right shoulder and back up again) and reported tilt in the plane of the actual head movements (roll) as well as head-upward and head-downward pitch. Unfortunately, Reason and Graybiel used relatively small head turn angles (30° mostly at 10 rpm) and they did not report the speed of the head turn. Thus, the sensation could have been too faint to be clearly perceived by their subjects.

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In the following, we outline the predictions that can be derived from a simple model of semicircular canal function [see e.g. 33], which assumes an idealized vestibular system with semicircular canals located in planes that coincide with the head pitch-, roll-, and yaw-axes. These canals will be called hypothetical canals. If the subject is supine on a bed that rotates clockwise for more than 30 seconds, with the head at the center of rotation, feet pointing outward, and the centrifuge revolving at constant angular velocity, she no longer feels the rotation. Upon a *counterclockwise yaw head movement* from right-ear-down (RED) to nose-up (NU), the subject should feel a whole body tilt *head-upward* (pitching head up, feet down), and a *clockwise rotation*[1]. This subjective pitch head-upward is induced by the hypothetical pitch canal (with components from the actual posterior and anterior canals). Prior to the head movement, during sustained constant rotation, the cupulae of the vertical canals had equilibrated to their rest position, and subjective motion had disappeared. When those canals are taken out of the centrifuge's plane of rotation by the head turn, as shown in Fig. 1, the endolymph's momentum causes it to continue to rotate slightly and displace the cupula. This signal is interpreted according to the new (NU) position of the head. The hypothetical roll canal (with components also from the actual anterior and posterior canals), which had been perpendicular to the plane of rotation, is now moved into that plane. It is stimulated by sudden exposure to the bed's rotation. This results in a perceived rotation in the same direction as the bed (clockwise roll). The hypothetical yaw canal remains perpendicular to the axis of rotation and does not signal anything except the transient yaw head movement. In summary, assuming that knowledge of head position with respect to the body is retained, the model predicts slowly decaying head-upward body pitch and clockwise body roll sensations for counterclockwise yaw head movements.

Similarly, illusory tilt caused by a *clockwise yaw head-turn* can be predicted. Subjects should experience a downward body pitch combined with a body roll. On the other hand, an actual *pitch head-upward head movement* should produce slowly decaying body sensations of clockwise yaw (to the right) and clockwise roll (feet to the right). Finally, an actual *pitch downward head-turn* should produce a counterclockwise yaw (to the left) combined with clockwise roll (feet to the right). Concurrent experiments showed that cross-coupled vestibular stimulation produced reflexive eye movements as predicted by a semicircular canal model [32]. Here we assessed whether observers consistently experience the illusory body tilts predicted by the same model. We also investigated if illusory motion varies as a function of head movement and how long it persists.

We also investigated the effect of head movements on cardiovascular responses. The vestibular system is known to be involved in the regulation of the cardiovascular system. For instance, Yates [28] proposed that vestibular stimulation provides inhibition of sympathetic discharge to the heart and the vascular smooth muscle, and a sympathetic output to the planchnic organs. In more recent experiments, Wood, Ramsdell, Mullen, Oman, Harm and Paloski [27] have shown a close link between the two systems. Thus, if the vestibular system is involved in regulating blood pressure and heart rate, we expect the same stimulus that creates an illusory sensation of pitching head-upward from the supine position to also trigger an elevation in heart rate to compensate for the expected fluid shift downward. A pitch head-downward sensation should do the opposite. If, on the other hand, the vestibular stimulus causes general arousal, heart rate elevation should follow all head turns. Finally, if the descending influence of the vestibular system is insignificant, we expect no change in heart rate.

Motion sickness was measured and also used as an indicator of whether to continue to perform additional pitch head movements. In the Coriolis environment of the centrifuge the conflict between signals from the otolith organs, semicircular canals and visual and proprioceptive information is thought to cause symptoms of motion sickness [20]. As mentioned before, vestibular stimulation is in conflict with all other sensory information, most of which is veridical (e.g. vision, tactile, and kinesthetic cues). If artificial gravity is to be implemented as a countermeasure, the subjective effects of SRC on illusory tilt, heart-rate, and motion sickness have to be understood and managed.

2. Methods

2.1. Subjects

Twenty healthy human subjects (10 males, 10 females), ranging in age from 18 to 32 years (24 ± 0.8

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[1] Note that this prediction assumes that the representations of head and trunk are not dissociated and that the trunk "knows" how the head is oriented.

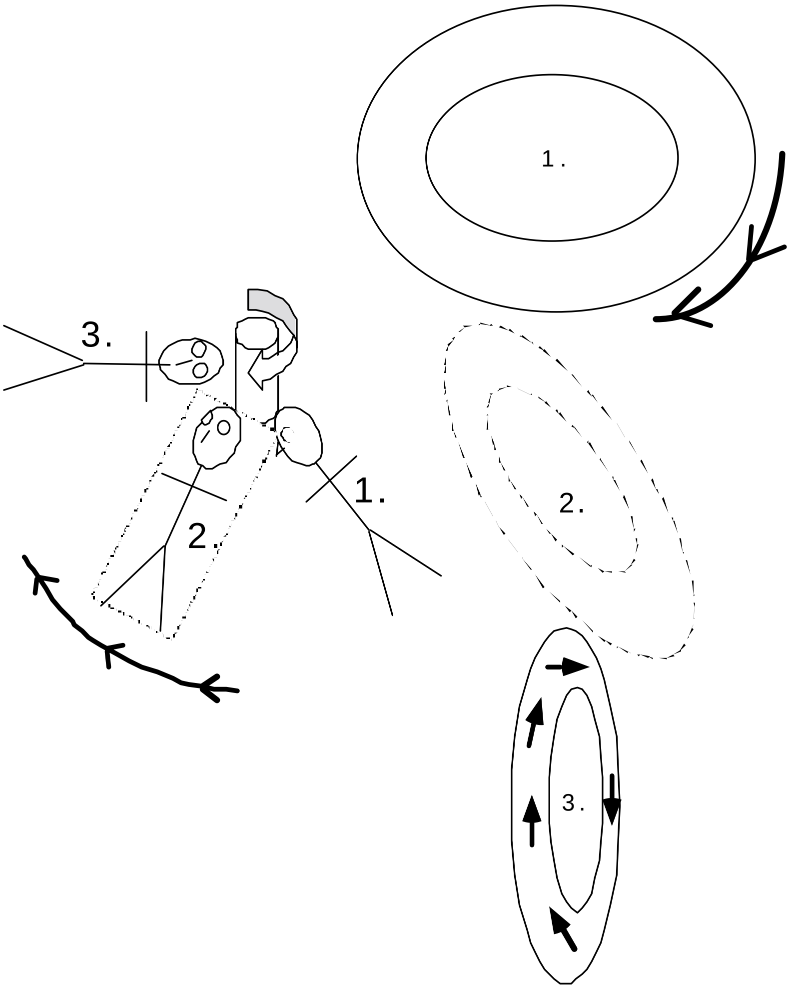

Fig. 1. Schematic of a head-turn from right-ear down (RED) to nose-up (NU) while rotating clockwise. The hypothetical head pitch canal is depicted on the right. In position 1 (RED) the canal is co-planar with the rotating bed. The endolymph is equilibrated, that is, motionless with respect to the canal. After the completed head turn to position 3 (NU), the canal is perpendicular to the bed's rotation plane. Relative inertial motion of the endolymph occurs as indicated by the arrows. Such endolymph motion usually indicates body pitch upward from the supine into the upright position.

years), participated in the experiment. They had no prior experience with centrifuges or other rotating devices in a research environment. Subjects had to testify that they were not taking any medication and had no history of neurological, cardiovascular, respiratory, or ear-related problems. They were required to abstain from alcohol and caffeine for 24 hours prior to the experiment.

2.2. Design

We measured subjective responses first to yaw and then to pitch head movements while the subject lay supine on the clockwise-rotating centrifuge. Also, the starting position of the centrifuge in the laboratory was varied between subjects. The dependent measures were magnitude and direction of experienced body motion, the duration times of these sensations, and heart rate. Additional dependent measures were perceived room orientation while being rotated, body tilt in the absence of head movements, and a verbal motion sickness assessment on a 0–20 rating scale [see 32]. These measures were taken prior to, during, and following centrifugation. Heart rate was monitored throughout the experiment. The initial centrifuge orientation was either with the footplate pointing toward the blackboard at one end of the room or toward the experimenters at the opposite end of the room. Subjects were randomly assigned to these orientations.

2.3. Equipment

The MIT short-radius centrifuge was used [11]. The centrifuge is a 2.8-m long rotating horizontal bed with a subject rotation radius of 2 m. A Browning 1 hp dc motor drove the bed and was controlled by a Browning LWS Series LW second generation DC Motor Controller. The controller produced an input profile providing a constant linear acceleration of $5.5\,°/s^2$ until a constant angular velocity of 138°/s (equal to 23 rpm) was reached. During each trial, the participant lay supine with the top of the head at the axis of rotation. The feet were placed against an adjustable foot plate. At 138°/s, the centrifugal force caused a horizontal gravito-inertial force (GIF) component of 0g at the head and 1 g at the feet of a 168 cm tall participant. Obviously, earth gravity was constantly acting perpendicular to the centrifugal GIF. As shown in Fig. 2, an on-board video camera was used to monitor the subject's well-being and head-movements via a TV monitor for the duration of the experiment. Additionally, an audio tape recorder attached to the bed recorded all verbal responses of the participant. To remove wind cues and external visual stimuli, a light-proof canopy was positioned over the participant's head and torso; however, for purposes of ventilation, the foot of the bed was left open. To eliminate visual cues, subjects wore a blindfold and accordingly all of them reported complete darkness. Subjects were introduced to the safety equipment on board: a power cut-off safety switch, a safety belt, and a motion sickness bag. During the experiment, subjects used wireless communication (Motorola Talk About 250^{TM}) to report their sensations and to answer questions while on the centrifuge.

An Acumen TZ-Max 100^{TM} heart rate monitor was used to measure heart rate. It included a data storage watch, a wireless chest transmitter, and an adjustable elastic strap. Average heart rate was sampled every 5 seconds based on a beat-to-beat measurement from electrocardiograph electrodes. The transmitter was attached to the chest at heart level.

2.4. Procedure

Pre-experiment briefing. The MIT Committee on the Use of Humans as Experimental Subjects had approved the experimental protocol. All subjects underwent a medical examination to ensure normal vestibular function by use of a Rhomberg balance test. Information about handedness and activities that might affect vestibular function, such as flying, diving, or gymnastics, was collected. All subjects were informed about the nature and the general purpose of the experiment as well as the risks involved, particularly the likelihood of motion sickness. All of them read and signed a consent form pointing out the safety features of the centrifuge and the opportunity to abort the experiment at any point should they wish to do so.

Questions to be answered during the test were reviewed beforehand. They comprised subjective ratings of motion sickness, perceived body orientation, and illusory tilt. A pilot study had revealed inherent difficulties in communicating the unusual tilt sensations experienced during out-of-plane head rotations. Thus, to avoid instances of miscommunication subjects were trained using a puppet. Subjective body tilt was categorized into motions about the three body axes: yaw about the body's longitudinal axis (clockwise/counterclockwise), roll (clockwise/counterclockwise), and pitch (head-upward/downward). All motions were to be reported in body axes, rather than head axes. Based on the pilot study, subjective pitch was separated into two distinct motions: tilting for motions where the pitch remained fixed at a distinct angle and tumbling where pitch involved a continuous angular motion sensation of several revolutions.

Subjects were asked to inform the operator if any specific symptoms (e.g. nausea, sweating, feeling hot or cold) were experienced. Several times during the experiment subjects were asked to judge their degree of motion sickness on a scale ranging from 0 ("I feel fine") to 20 ("I am about to vomit"). Before the experiment they were asked if they felt normal and healthy. All of them said so. This state was anchored as a 0. We chose this simple rating scale to assess motion sickness for practical reasons. An objective assessment was not feasible because the experimenter only had visual information via the camera, and a proper scaling as used by Bock and Oman [3] would have required more data points and involved deliberately making subjects motion sick. Fortunately, different methods of assessing motion sickness produce very similar results [13]. Moreover, we have found that the 0–20 scale correlates well with a combined objective and subjective assessment (Pensacola Diagnostic) [32].

Data collection during centrifugation. After subjects strapped on the Acumen heart rate monitor, they mounted the centrifuge such that the top of their head was located on the center of rotation with their nose

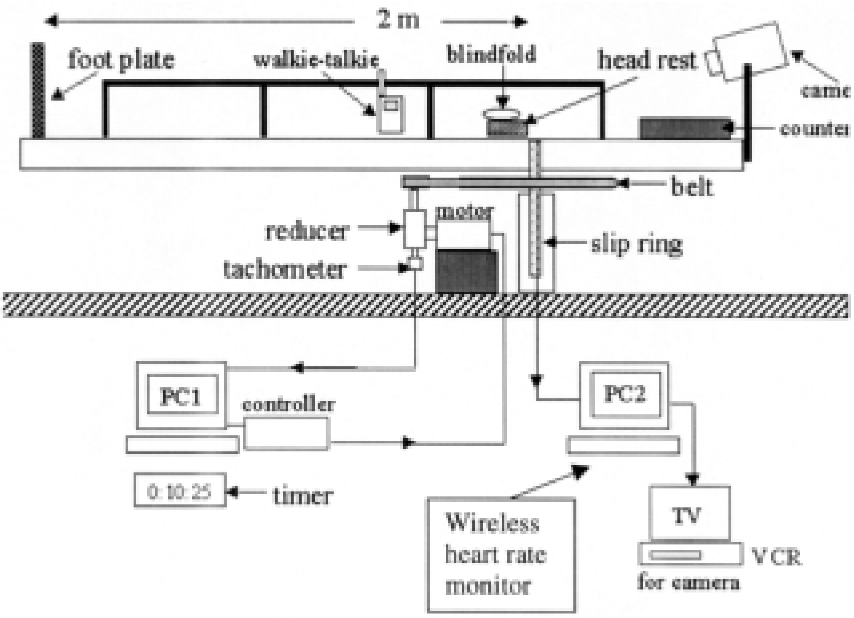

Fig. 2. Schematic of the MIT short-radius centrifuge.

up. The required head movements in the yaw and pitch planes were trained carefully to produce a 90° head turn in 1 second. Then the blindfold was applied. Finally, the experimenter covered the centrifuge with the canopy. Before the bed was rotated, subjects reported their perceived orientation in the room, motion sickness rating, and perceived body tilt. The bed's steady ramp in angular velocity from 0 to 23 rpm took 25 seconds ($5.52^\circ/s^2$). Thirty seconds after achieving constant velocity, subjects again reported orientations. Every participant felt completely still, as expected, since the semicircular canal signals had decayed. At the experimenter's cue the subject made 90-degree head turns. All subjects felt a strong illusory tilt. They had been instructed to say "stop" the moment this illusory motion or tilt ceased. The head was not restrained other than by a flat cushion on which the head rested. The head-turns were monitored by use of a video camera. Very occasionally, the head turns deviated noticeably from the prescribed direction or speed. Those cases were coded as missing values. Twenty seconds after the first head-turn the next head movement had to be made. Subjects made 4 sets of yaw head movements, where each set consisted of a movement from nose-up (NU) to ear-down (ED) and another back to NU. The four sets were initiated to one side and later repeated for the other side. This procedure is summarized in Fig. 3 for yaw head-turns to the right side.

On the fourth set, once a head movement was performed, the participant first reported the direction and magnitude of the illusory motion. All subjects reported strong illusory tilt with each head-turn. When the sensation had subsided and the subject felt stationary again, the experimenter asked whether or not the body had reassumed a level position, and where, if known, the feet pointed in the room.

After the corresponding sets of yaw head movements to the left and to the right were completed, and only if the motion sickness rating was below 4, the participant was asked to make a pitch upward head movement by bringing the chin to the chest. Pitch head movements are very provocative, possibly because the abdominal muscles required to lift the head exert pressure on the diaphragm, and thereby on the stomach, and aggravate motion sickness. Fifteen of the 20 subjects performed pitch head movements. As soon as the illusory motion had disappeared, the participant said, "stop" and pitched the head back onto the bed. Afterward, the subject reported first the perceived motions associated with the pitch upward head movement and then those associated with the pitch downward head movement. Finally, body orientation in the room, body tilt, and motion sickness ratings were given.

While maintaining the NU head position, the centrifuge speed was ramped down linearly to a complete stop in 25 seconds. Then the canopy was removed and follow-up questions were asked while the participant remained on the centrifuge.

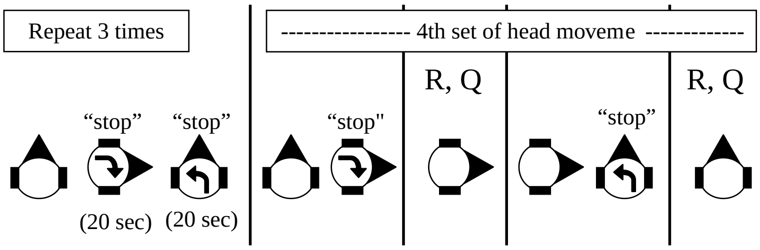

Fig. 3. Three sets of yaw head movements (from nose-up to ear-down and back up) had to be made to one side, then experienced body tilt was recorded on a fourth set. Then the procedure was repeated for the other side. R indicates when motion sickness had to be rated, Q refers to questions regarding illusory body tilt and subjective orientation.

3. Results

3.1. Illusory body tilt

3.1.1. Qualitative assessment of illusory tilt

The on-line visual inspection of the head-turns by the experimenters ascertained that the instructions were followed accurately. Two measures were computed for subjective tilt: illusory motion (magnitude and direction) and duration. Although all 20 subjects made four sets of yaw head movements to each side, only 15 reported motion sickness scores below the criterion (score < 4) to perform additional pitch head movements. The data consisted of audio tape and written recordings of verbal reports while subjects were on the centrifuge. Ambiguous reports were followed-up after the rotation period by asking the subject to demonstrate perceived motion using a puppet.

For *yaw head movements,* the majority of subjects experienced the predicted pitch and roll directions. However, a few subjects perceived illusory motion in the predicted plane but in the opposite direction. This was the case in 13% of all yaw head-turns. This direction inversion was inconsistent insofar as it occurred mostly for illusory pitch. Also, those subjects who reported inverted directions did not do so consistently.

In the case of *pitch head movements,* 40% of the time, the 15 subjects reported an additional body tilt in the direction of the head movement. This is inconsistent with the canal model. Subjects clearly reported a strong full body pitching sensation, which could not have been confused with the comparatively small actual pitch head movement. Tables 1a and 1b summarize the illusory tilt sensations for yaw and pitch head movements respectively and compare them to the predictions of the semicircular canal model.

Table 1a
Yaw head movements: Percentages of reported illusory body motion while rotating in a supine position

Subjective motion	Predicted direction	Opposite direction	Corresponding to actual turn	None
Pitch	76%	13%	–	11%
Roll	60%	13%	–	27%
Yaw	89%*	–	11%	89%*

*Note that illusory pitch and roll body motions are predicted while yaw is not.

Table 1b
Pitch head movements: Percent of illusory motions reported while rotating in a supine position

Subjective motion	Predicted direction	Opposite direction	Corresponding to actual turn	None
Pitch	60%*	0%	40%	60%*
Roll	53%	0%	–	47%
Yaw	43%	7%	–	50%

*Note that illusory pitch body motion is not predicted.

3.1.2. Quantitative assessment of illusory tilt

Yaw head turns: The magnitude of illusory tilt is not easily captured. As mentioned in the introduction, the semicircular canal model predicts subjective pitch and roll caused by yaw head-turns in the clockwise rotating environment. Almost all participants reported the expected roll, but illusory pitch was more ambiguous. About half the observers reported an unambiguous pitch as if the bed had been tilted up. The other half experienced a continuous rotation or tumble in the pitch plane. In both cases, the sensation disappeared after about 10 seconds, such that a pitching or tumbling back to the horizontal position was never experienced. Since about half of the participants reported crisp illusory body tilt between 10° and 120° while the other half reported tumbling for more than 360°, separate data analyses were conducted. They did not yield any significant differences, presumably because the sample sizes were too small. To increase power, we made the tilt reports comparable by arbitrarily choosing to linearly transform all pitch ratings to a mean of 2

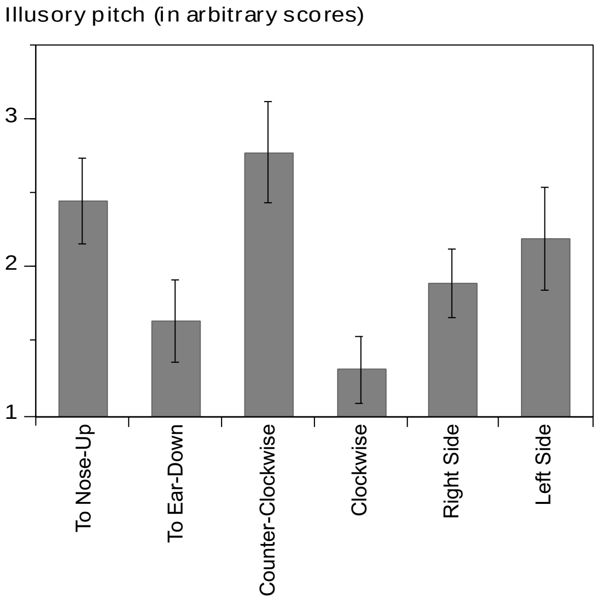

Fig. 4. Yaw head-turns: Illusory tilt in the pitch plane averaged over several yaw head turns. Subjective ratings were normalized to a mean of 2. Error bars indicate standard errors of the mean.

(roughly corresponding to the average of two complete revolutions felt by those who reported tumble).

Figure 4 shows the averaged resulting values, which have to be treated cautiously as relative magnitude estimates of experienced tilt. T-tests, which were performed on the normalized scores, revealed that yaw head-turns to nose-up (NU) produced significantly stronger sensations than turns to ear-down (LED and RED) $(t(19) = 2.70, p = 0.014)$. Also, clockwise head-turns (LED to NU, and NU to RED) produced stronger sensations than counter-clockwise (RED to NU, and NU to LED) head-turns $(t(19) = 4.41, p < 0.001)$. Turns to the right side (NU to RED, and RED to NU) tended to produce weaker illusory tilt than turns to the left side (NU to LED, and LED to NU). However, this tendency did not reach significance.

Pitch head movements: The canal model predicts that our supine subjects experience clockwise yaw when they pitch their head upward (to look at their feet), and a counterclockwise yaw when they pitch the head back down. In both cases, clockwise roll motions should also be experienced. As mentioned above, the predictions of the model were met with the additional experience of movement in the plane of the actual head movement. None of the magnitudes differed significantly between pitch-up versus pitch-down head movements. During pitch-up and down head movements, experienced roll averaged 2.8 and 2.4 revolutions respectively. Illusory yaw averaged .7 and -1.7 revolutions. The unsigned magnitudes were not significantly different because of large variability between subjects.

All participants with the exception of one reported that the illusory motion caused by a pitch-upward head movement was subjectively more disturbing than that caused by pitch-downward turns. Note, however, that by virtue of lying on a solid surface subjects always made the head-upward pitch first and than pitched back. An order effect could have resulted and could fully explain this difference in subjective severity.

Pitching head movements tended to produce stronger experienced roll compared to yaw head turns, but not significantly so. Judged roll was on average 2.46 revolutions for pitch movements and 2.18 revolutions for yaw head turns. A comparison of other magnitude effects between pitch and yaw head movements is not meaningful because only the hypothetical roll canal is activated by both movements.

3.1.3. *Duration of illusory body tilt*

According to a repeated measures ANOVA, the duration of illusory tilt was higher for yaw head movements to the left side than to the right $(F(1, 18) = 7.015, p = 0.018)$. This is consistent with the weak tendency for turns to the left side to produce stronger illusory tilt (see Fig. 4). Also, head turns to NU produced longer lasting sensations than turns to ear-down $(F(1, 18) = 6.066, p = 0.026)$, regardless of whether they were made from the left or the right side. This is consistent with the significant effect of illusion magnitude (Fig. 4). There was no significant difference between the duration of the pitch and roll illusions associated with yaw head movements in the clockwise versus counterclockwise directions. Neither was there an overall difference in duration for yaw and pitch head movements nor between pitch head-upward and pitch downward. The average durations of illusory tilt are shown in Fig. 5. No gender differences were found for qualitative or quantitative measurements of illusory tilt or its experienced duration.

3.2. *Motion sickness scores*

Motion sickness scores were collected three times during the experimental session: after the yaw head movements to the left side, after head turns to the right side, and before ramp-down after the pitch head movements had been completed. Average motion sickness scores are shown in Fig. 6. Five subjects scored higher than 3 on the 0–20 scale after the two sets of yaw head

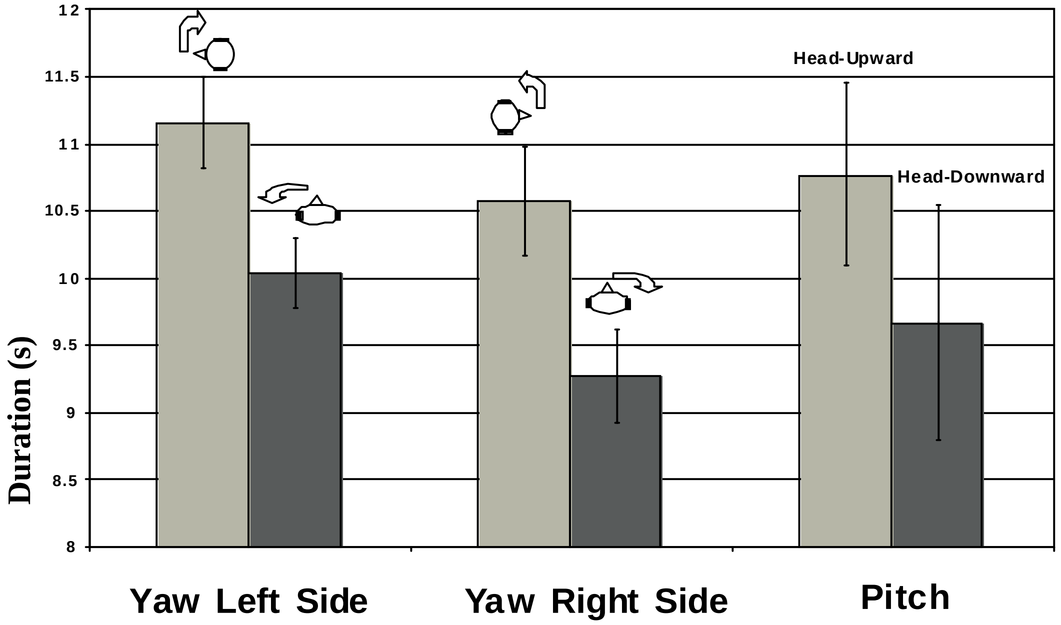

Fig. 5. Durations of illusory body tilt by executed head movement averaged for head movements in six different directions: yaw toward the left side (to ear-down and to nose-up), yaw toward the right side (to ear-down and to nose-up), and pitch (head-upward and back down). Each bar includes all head turns made in the specified direction. Error bars indicate standard errors of the mean.

movements were completed. They were not asked to perform pitch head movements. Their average motion sickness score was 5.0 (median 4.0). Obviously, the motion sickness for those 14 subjects who were selected to continue to perform pitch head movements was significantly lower $(t(1,18) = 3.45, p = 0.003)$. Their mean motion sickness score increased from an average of 1.4 (median 1) before to 9.7 (median 7.5) following pitch head movements. This increase was significant $(t(1,13) = 4.39, p = 0.001)$. In verbal reports 58% of the subjects found yaw turns to the right to be less provocative of motion sickness than yaw turns to the left. No gender differences were found in the motion sickness reports.

3.3. *Orientation in the room*

Our orientation with respect to the environment is normally unambiguous and clearly noticeable if we attend to it. However, on the spinning centrifuge this is no longer so because the subject's orientation changes continuously while at the same time she feels stationary. How does this affect perceived orientation? If orientation were systematically misperceived, this might influence the side effects that accompany head movements. For exploratory purposes only, we collected data on subjective body orientation in the room while subjects were lying still on the rotating centrifuge. 55% of all subjects felt oriented in the room at some point, but this orientation did not remain consistent. Out of this group 45% expressed difficulty indicating the direction. 45% of all subjects were unable to report a specific orientation of where their feet were pointing, but they found this in no way disturbing. Only 10% consistently reported a clear sense of orientation throughout the experiment. For these subjects, the direction of this orientation was not related to the initial orientation of the centrifuge when it was mounted, as had been hypothesized. No pattern in the orientation responses could be related to illusory tilt measures. Thus, the normal sense of body orientation was impaired or lost for 90% of our subjects, but this loss did not appear to have any negative effects.

3.4. *Heart rate*

A repeated measures ANOVA revealed no difference in heart rate between the stationary phase before the bed started rotating and the stationary phase after the bed was ramped back down. However, during the 30 second ramp-up period average heart rate was temporarily elevated from 70 bpm to 76 bpm $(F(5,95) = 6.87, p < 0.001)^2$, as shown for a typical subject in

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[2] P-values are Huyn-Feldt corrected.

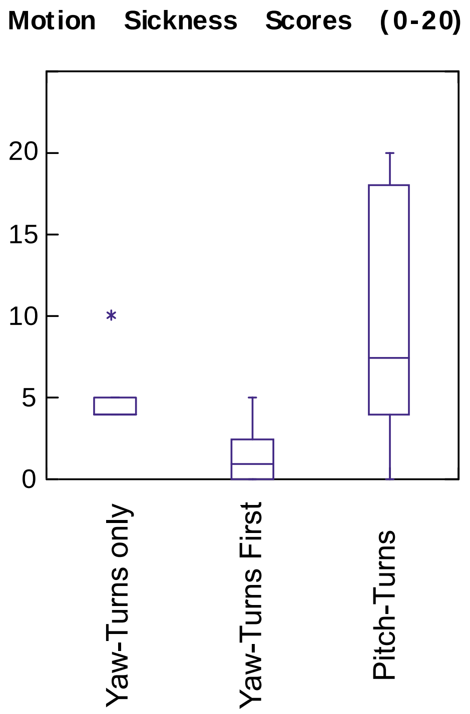

Fig. 6. Box plot of motion sickness scores for subjects who performed yaw head turns only ($N = 5$), and those who performed first yaw and then pitch head movements ($N = 15$). One of the 15 subjects failed to report a motion sickness score after pitch head movements. The box comprises 50% of the values with their median lying at its center (2nd and 3rd quartiles). The asterisk represents an outlier value.

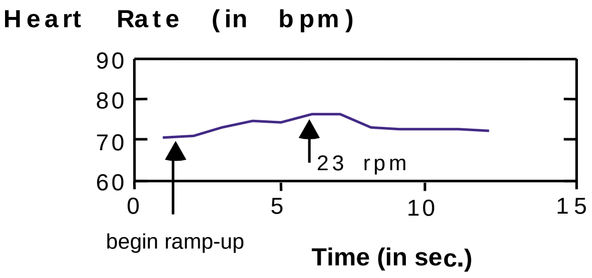

Fig. 7. Heart rate profile during and after ramp-up plotted for one representative subject. Arrows indicate start and end of acceleration from 0 to 23 rpm.

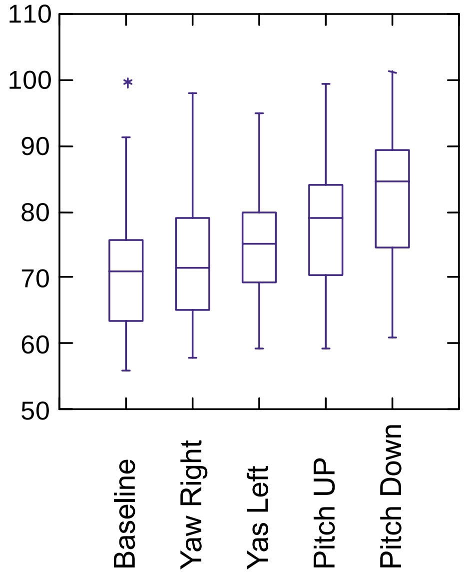

Fig. 8. Box plot of heart rate distributions by head movement type. The box comprises 50% of the values with their median lying at its center (2nd and 3rd quartiles). The asterisk represents an outlier value.

Fig. 7. Five seconds after the bed had reached constant velocity at 23 rpm, heart rate diminished significantly $(F(1,19) = 7.782, p = 0.012)$, and approximately 15 seconds later, it had practically resumed its baseline value (71.5 bpm) $(F(1,19) = 6.332, p = 0.021)$. Similar transient heart rate elevations were found after yaw and pitch head movements. The heart rate increased immediately after the turn, and returned to the baseline within 20 seconds. Distribution plots for heart rate as a function of head movement are presented in Fig. 8. Table 2 shows the ANOVA results for comparisons of average heart rate between each of the head movement conditions. Since 5 subjects were too motion-sick to make pitch head movements, two separate repeated measures ANOVAs were run. Due to equipment malfunctioning and a few noticeably inadequate head turns, some data contained missing values. Separately for yaw and pitch head turns, the entire subject's data was removed from the respective ANOVA whenever such missing data points occurred. Consequently, the first ANOVA ($N = 17$) compared heart rate during yaw head movements to its baseline after ramp up. The second ($N = 11$) compared heart rate during pitch head movements to baseline and to yaw.

Pitch head movements produced significantly higher heart rates (on average 81 bpm) than all yaw turns. In addition, yaw turns to the left side elevated heart rate higher than yaw turns to the right, and pitch-down turns elevated heart rate higher than pitch-up turns. There was no difference between clockwise yaw head movements (about the longitudinal body axis) and counterclockwise yaw head movements. Nor was there any difference in heart rate elevation between head turns that ended in the nose-up position or ear-down position for either left or right yaw turns.

A separate ANOVA was conducted on the individual heart rate variability scores. No significant overall gen-

Table 2

Comparing the different types of head movement with respect to the average heart rates (bpm) associated with them. Averages were computed across all movements of a given type. F-ratios and p-values are provided for each contrast as based on two repeated measures ANOVAs

Average heart rate		Average heart rate		Df	F	p
Baseline	71.5	Yaw right side	73.0	16	11.52	.004
Baseline	71.5	Yaw left side	75.7	16	16.94	.001
Yaw right side	73.0	Yaw left side	75.7	16	11.23	.004
Baseline	71.5	Pitch up	79.1	10	21.89	.001
Baseline	71.5	Pitch down	82.5	10	43.86	<.001
Pitch Up	79.1	Pitch down	82.5	10	10.50	.009
YAW	74.0	PITCH	80.8	10	75.39	<.001

der differences were found. Individual heart rate standard deviations (SD) over the course of the experiment ranged from 3.6 to 13.7 bpm. However, for pitch turns only, males (SD = 17.0, range 56–100 bpm) produced larger SD's than females (SD = 7.5, range 67–92 bpm). There was no chance to test for significance because there were only two data points for pitch per subject.

4. Discussion

When head movements are made during short-radius centrifugation (SRC), observers experience a provocative illusory tilt that is accompanied by a transient increase in heart rate. A typical illusory tilt is characterized by a combined tumbling and rolling illusory motion. For a supine position on the rotating bed, pitch head movements are more provocative than yaw head movements as indicated by motion sickness scores and heart rate increases. The magnitude of experienced body roll also tends to support this conclusion. Considerable individual differences exist with respect to the experienced tilt. A semicircular canal model [33] can explain the majority of tilt sensations but not all of them. In particular, the model predicts tilt experience during yaw head turns fairly well, but it fails to explain why, in 40 % of the pitch head movements, subjects experienced a whole-body pitch rather than the predicted yaw and roll. Also, a substantial minority of subjects experienced body tilt in the predicted plane but in the opposite direction to that predicted by the canal model for cross-coupled stimulation.

Heart rate baselines during centrifugation were the same as during rest, which indicates that there is no main effect of SRC on heart rate and should make centrifugation tolerable even for longer exposures. Second, heart rate elevations that were contingent on head movements only averaged around 10 bpm.

The initial increase of heart rate during and after the ramp-up of the centrifuge is easily explained by general arousal or by a cardiovascular compensation for the fluid shift toward the feet caused by the centrifugal force. Baroreceptors in the carotid sinus and the aorta could have responded and elevated heart rate [8,16]. A similar response can be induced by lower body negative pressure, which causes blood pooling in the lower extremities and elevation of heart rate [1,15]. Since heart rate returned to baseline soon after ramp-up, the gravito-inertial force in the present study (1 g at the feet) did not cause lasting heart-rate changes. This is consistent with findings by Hastreiter and Young [17], who used the same short-arm centrifuge and reported sustained changes in heart rate and blood pressure only for rotation rates that produced more than 1.5 g at the feet.

It is less straightforward to explain why heart rate is elevated as a function of head movement. The exertion involved in turning the head could contribute. The effect could also reflect a cardiovascular response to the experience of being tilted, for example from supine to upright in the case of a counterclockwise yaw head turn [30,31]. This explanation is supported by evidence that monkeys with labyrinthectomy failed to increase heart rate and to maintain stroke volume during centrifugation [25]. Unfortunately, this explanation is inconsistent: If our observed heart rate elevations were vestibularly driven, heart rate should not only increase during counterclockwise yaw head movements, producing a pitch head-upward sensation, but it should decrease during clockwise movements that produce pitch head-downward sensations. Such an asymmetry, however, was not found. However, the generalized heart rate elevation during head movements might still be explained by vestibular responses if one considers the sympathetic inhibition induced by the otolith organs via neural stimulation of the rostal ventrolateral medulla in decerebrated cats [28]. Sympathetic inhibition lowers blood pressure and activates the baroreceptors. This activation, in turn, causes an elevation in heart rate.

Consistent with this explanation, Biaggioni et al. [2] report that vestibular stimulation in animals consistently caused decrease in blood pressure.

A much simpler explanation would be that heart rate elevation is a stress response akin to a startle reflex [9]. This explanation is no longer based on direct vestibular signaling but rather on a mediated perceptual response to that signal. It may explain the relatively strong heart rate effect for pitch head movements, which are more stressful and motion sickness provoking according to the subjective reports of our subjects. Fortunately, if the heart rate changes are a stress response, they should subside with repeated exposure.

The finding that yaw head turns to the right side are associated with smaller heart rate elevation than turns to the left side is peculiar. However, it is consistent with the perceived duration of the illusion. Counterclockwise yaw head movements were associated with longer durations. This is all the more astonishing since all subjects made their first head turns to the right, and the first movements would presumably be the most provocative.

With respect to implementing SRC in space, the present results are encouraging, mainly because the changes in heart rate were so small. Since astronauts seem to suppress the baroreflex to some extent in weightlessness, the heart rate effects during SRC are likely to be even smaller in weightlessness. Moreover, Yates, Aoki, Burchill, Bronstein and Gresty [29] showed no influence of neck receptors on the neural discharge [but see 12]. They question whether vestibular output has any direct effects on heart rate at all (see also Biaggioni et al. [2]). Also, baroreceptor responses of astronauts before and after the STS-27 Shuttle mission suggest that heart rate adapts quickly [12]. The potential conditioning effects obtained through SRC certainly seem to outweigh potential disturbances in heart rate. Pancratz, Bomar and Raddin [23] propose convincing evidence for cardiovascular conditioning using artificial gravity. They produced a mathematical model of the cardiovascular system that calculated the flow and pressure in 40 arterial and venous vascular segments and 10 peripheral capillary bed segments. The results of their simulation showed that space-based SRC in humans should produce similar cardiovascular pressures to those on the ground. They also simulated short radius centrifugation in Earth's 1-g environment and predicted that the only difference with respect to 0-g is higher arterial and venous pressures in the hip region [5]. Moreover, heart rate can be successfully controlled by various methods of biofeedback [18]. Therefore, from a cardiovascular point of view, intermittent exposure to SRC emerges as a candidate countermeasure and now has to be tested for longer exposure times than those used here.

The experiential effects of *illusory* tilt may pose more of a problem. For yaw head turns, a majority of subjects experienced illusory tilt in the predicted planes. Each yaw turn produced a sense of rotation (whole body roll and pitch) for about 10 seconds. The illusory roll is easily explained by the signal of the respective hypothetical canal that is placed into the centrifuge's plane of rotation. The canal which is taken out of the plane of rotation causes subjective body tilt in the pitch plane. The direction depends on the sense of the head turn (clockwise vs. counterclockwise) and is usually felt as predicted. In some cases (13%) the direction was reversed.

Surprisingly, in 11% of the yaw turns and in 40% of the pitch head movements subjects experienced whole body tilt in the same plane and direction as the executed head movement. This experience, which cannot be predicted by a canal model, may reflect the strong conflict between vestibular and other sensory information. While the vestibular stimulus typically dominates the final experience, it seems to falter in the case of pitching head movements, as if the vestibular signal of tilt is reinterpreted with help of the kinesthetic information about how the head has actually moved. One potential explanation for this peculiar tilt sensation for pitch head movements may be due to the head-trunk system closely monitoring how the head has moved with respect to the trunk. We believe that vestibular signals typically get interpreted as trunk tilt regardless of how the head is aligned to the trunk. Note that this is implicitly assumed in the hypothetical canal model that we have used, but we have no direct evidence for the correctness of this assumption. The variability within and between participants may have introduced some noise in the data, but it is unlikely that deviations from the instructed head turn can explain the results – even partially. The head-trunk system might become somewhat dissociated during pitch head movements because the muscular strain is considerable and kinesthetic signals become more prominent. This could explain why our subjects reported pitch head movements to be most provocative. However, Lackner and Graybiel [20] also found pitch head movements to be particularly nauseating in parabolic flight, where the vestibular stimulus is very different.

The shorter *duration of illusory motion* for yaw turns to the right side is consistent with heart rate changes.

Also, the follow-up questions indicated turns to the right to be less provocative. We have no good explanation for this effect. The duration effect (illusory motion for turns from ED to NU lasting longer than the opposite) could be caused by the otolith system. Perhaps the utricular signals, which fail to confirm rotation about the horizontal axis, inhibit the influence of the canal signals when the head is pointing NU. Wall [26] has found evidence for such modulation using earth-horizontal (barbecue-spit) body rotations. On the other hand, it is conceivable that the duration effect was caused by a trivial difference as to when peak head velocity was reached during turns to NU and to ED. The head is stopped at the center of its range in NU turns, presumably just after its peak acceleration. Thus, a later canal response is expected, which translates into experience of longer duration. It is of course easy to test between these two explanations by measuring head velocity or by placing the participant onto the centrifuge facing nose-down and repeating the experiment. Only if the otolith explanation is correct should the duration differences reverse.

We found no gender differences for illusory tilt, its duration, or for motion sickness reports. Average heart rates and their increase after head turns also did not differ between males and females. However, there was an indication that heart rate variability was more pronounced for males when making pitch head movements. This result is consistent with findings that heart rate variability and motion sickness are not related [19].

Individual differences, on the other hand, were remarkably large. Five subjects reached degrees of motion sickness that made the experimenter forego the pitching head movements, while three subjects practically felt no symptoms of motion sickness. Also, the subjective body tilt sensations varied considerably. In particular for yaw head turns about one half of the subjects felt continuous tumble in the pitch plane while the other half felt a fixed body tilt of less than 90°. Some reported a paradoxical combination of continuous tumbling with a steady pitch angle. These alternative motion sensations are reminiscent of the paradoxical vection commonly found in pitch circularvection experiments. It has been explained on the basis of a varying role of the otolith organs in the inhibition of visually induced pitch or roll [33]. However, in the present experiment, the roll sensation, which was induced by the semicircular canal that turned into the plane of rotation was more consistent. It almost always continued for several revolutions. Given the large individual differences, it appears necessary to establish how an astronaut is likely to tolerate prolonged or repeated centrifugation.

Illusory tilt caused by pitch and yaw head movements did not correspond equally well to the model predictions. For yaw about one fifth of our subjects did not feel the predicted directions of tilt, while for pitch head movements almost one half of the subjects deviated from the predictions. This is perhaps due to saccule contribution. The saccules dominate perceived sensation along the longitudinal body axis (z) while the utricles more prominently reflect motion in the lateral and saggital plane (x-y axes) by a ratio of 3:1 [10]. Since the otoliths play a more dominant role in pitch than in yaw, it may mask more of the predicted semicircular canal directions [7]. This is consistent with findings by De Graaf et al. about subjective tilt that was experienced by subjects who did not move during centrifugation [10]. Their subjects sat in a rotating room and oriented their heads differently with respect to the centrifugal force. They experienced greatest tilt while in the pitch-up orientation (z-axis) compared to NU or ED orientations (the y- or x-axes). Further, the NU orientation resulted in slightly larger tilt than the ED orientation in De Graaf's study. Similarly, our subjects experienced greater illusory roll following pitch-up head turns than for yaw head turns. Further, our subjects showed greater sensitivity to yaw turns that ended in the NU orientation (the y-direction) than to those ending in the ED orientation (the x-direction).

In summary, head movements that are made during fast centrifugation produce serious side effects. While heart rate changes were relatively small, all subjects experienced strong illusory tilt and most subjects experienced motion sickness. For a supine body orientation yaw head-turns were less provocative than pitch head movements. Current models based on semicircular canal function are unable to fully explain the illusory effects.

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