

Sensorimotor aspects of high-speed artificial gravity: I. Sensory conflict in vestibular adaptation

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Abstract. Short-radius centrifugation offers a promising and affordable countermeasure to the adverse effects of prolonged weightlessness. However, head movements made in a fast rotating environment elicit Coriolis effects, which seriously compromise sensory and motor processes. We found that participants can adapt to these Coriolis effects when exposed intermittently to high rotation rates and, at the same time, can maintain their perceptual-motor coordination in stationary environments. In this paper, we explore the role of inter-sensory conflict in this adaptation process. Different measures (vertical nystagmus, illusory body tilt, motion sickness) react differently to visual-vestibular conflict and adapt differently. In particular, proprioceptive-vestibular conflict sufficed to adapt subjective parameters and the time constant of nystagmus decay, while retinal slip was required for VOR gain adaptation. A simple correlation between the strength of intersensory conflict and the efficacy of adaptation fails to explain the data. Implications of these findings, which differ from existing data for low rotation rates, are discussed.

Keywords: Coriolis effects, artificial gravity, orientation illusions, motion sickness, classical conditioning, control theory, sensory conflict, space sickness, vestibulo-ocular reflex

1. Introduction

Sensorimotor functioning in rapidly rotating environments poses numerous challenges to our understanding of sensory psychophysics as well as motor learning. The three papers that follow examine the sensory and motor consequences that arise when humans have to operate in the unfamiliar environment of high-speed rotation. We consider artificial gravity (AG) by means of high-speed rotation to be the most promising method for preventing serious deconditioning effects associated with prolonged exposure to weightlessness. We define high-speed rotation as those rotation rates

necessary to administer AG equivalent to 1-g within the confines of a small spacecraft (rotation radius not exceeding 3 m). This amounts to angular velocities in the neighborhood of 20 rpm, or 100°/sec or more. Such a system may in fact be feasible. Not only can humans tolerate the cardiovascular effects of high-speed AG [2, 3, 14], they can also adapt their basic motor actions up to at least 20 rpm (DiZio & Lackner, in this volume), and they can adapt to the provocative effects caused by head movements made in the rotating environment [37]. The central issue in the current three papers further explores adaptive changes caused by the unexpected Coriolis forces on the arm, head, and vestibular system associated with movement in a rotating environment.

The present paper, Part I of our investigation, is concerned with the role of sensory conflict in vestibular adaptation. Economic factors suggest that AG may be

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best implemented as short-radius intermittent centrifugation at high rotation rates for limited daily exposures. This would require frequent state transitions between 1-g on the ground, 0-g during flight, 0.38- or 1-ag when on the centrifuge during flight, and non-rotational 0.38-g on the surface of Mars. Ideally, such transitions need to be made rapidly and without any after-effects. We know this is possible in principle [38], but we do not yet understand the mechanism by which the transitions are made or what specific roles the various sensory modalities play in the adaptation. We report empirical test results on the relative contributions of visual, kinesthetic, and vestibular inputs to both physiological and subjective adaptation.

Part II of the investigation examines the effects of gravitational cues on head movements made in high-speed rotational environments. In particular, experimental data concerning the semicircular canal, otolith, and neck proprioceptive contributions to orientation illusions will be presented. Finally, it has been questioned whether limb movements can adapt to the effects of particularly strong Coriolis forces that arise with high-speed rotation. The feasibility of such sensorimotor adaptation as a function of rotation speed is demonstrated in Part III.

1.1. Adaptation at higher speeds

Research on AG was plentiful after the first moon landings, and researchers were aware of the vestibular and motor consequences for AG (e.g. [9,10]). It was generally thought then that a large rotating habitat providing AG day and night was the likely solution [8, 33], and this architecture has remained the benchmark for AG. Rotation rates of 6 rpm were perceived as the tolerance barrier beyond which side effects might not be surmountable, and such large devices would stay safely within that barrier [7,11,20]. Current constraints, however, press the issue of using smaller, more rapidly rotating devices for use onboard existing spacecraft. In addition to questions regarding the effectiveness such of a short-radius centrifuge (SRC) as a countermeasure, the main vestibular issue is how humans adapt to the severe sensorimotor changes that accompany rotation rates around 20 or even 30 rpm. Moreover, the adaptation must be achieved while subjects maintain their perceptual-motor abilities in the stationary environment. In this sense, adaptation to high-speed rotation has to be context-specific, or at least free of after-effects. It would be unacceptable for an astro-

naut to suffer disorientation and motion sickness with each transition into or out of AG.

When moving the head in a high-speed rotating environment, vestibular Coriolis effects are very provocative because they generate nystagmus, illusory body rotation or tilt sensations, and motion sickness. Fortunately, all of these Coriolis effects adapt away with repeated exposure. Moreover, while Coriolis effects adapt during repeated centrifugation, no after-effects have been identified when making head turns back in the stationary environment [37]. This contrasts sharply with the recalibration that accompanies motor adaptation [18], implying that the mechanisms underlying motor recalibration and vestibular adaptation are likely very different. Successful Coriolis adaptation can thus be thought of as state-dependent learning with the ability to switch almost instantaneously into and out of the adaptive state required for the given environment. We investigated how this adaptive state is learned and what role different sensory modalities play in the learning process.

1.2. Visual-vestibular conflict

A tentative conflict model of sensory adaptation suggests that adaptation is driven by the conflict between semicircular canal afferents on the one hand, and most other sensory modalities as well as the efference copy on the other hand. By this paradigm, the sensory apparatus would attempt to reduce the conflict by first determining which signal is the veridical one, and then systematically suppressing the output of dissenting sensory modalities. An immediate consequence of this assumption is that the greater the sensory counterevidence against the dissenting modality, the quicker adaptation, that is suppression of the dissenter, should be. We hypothesize that whenever different sensory channels are in disagreement the resultant outcome should be a weighted (probably non-linear) sum of all inputs, with vision receiving the largest weight followed by the canal signal. This weighting can be deduced from visual-vestibular interactions in the generation ofvection [36,39].

In the context of head turns made in a rotating environment with a centrifuge-fixed field of view, the following sensory conflict arises: Semicircular canal information is erroneous because changing their orientation with respect to the platform's plane of rotation creates a false sense of body rotation. Vision, tactile information, kinesthesia, efference copies of the motor commands, and somatosensory and proprioceptive in-

formation provide information that the subject is stationary. Moreover, sound and wind cues remain constant, indicating that no changes other than the head turn have been made. The otolith signals assume a special role here because, depending on the subject's orientation, they can provide accurate or erroneous information about the state of rotation. We chose to minimize otolith conflict signals by rotating subjects with their heads at the axis of rotation. This pits vestibular canal information against all other sensory and cognitive information. According to the assumptions above, this maximal conflict should lead to maximal adaptation. As sources of veridical sensory input are removed (e.g. turn off the lights, disrupt tactile afferents, etc.) the relative strength of the erroneous vestibular information should increase and consequently adaptation should be slower and/or less thorough. We term this the conflict model of sensory adaptation, and the experiment detailed herein focuses on the role of vision.

The model's logic is supported at least indirectly by adaptation studies. For instance, Kornheiser [15] surmises that adaptation is a learning process designed to reduce intermodal sensory conflict. He arrived at this conclusion while studying adaptation to laterally displaced vision, finding that the more sensory and motor evidence was available to show that vision was non-veridical, the quicker adaptation occurred. The conflict model of sensory adaptation has close relatives in the conflict models devised by Reason [27,28], Oman [24], and others to explain motion sickness. They hypothesize that onset of symptoms is triggered by a conflict between sensory input and the expected sensations, as determined by prior experience and/or the efference copy of the motor signal. Persistent conflict leads to an updated model and adaptation to the stimulus. However, these particular models examine only non-conflicting sensory inputs. Dichgans and Brandt [5], and Bles [1] applied the idea of a conflict model to inter-sensory disagreements between multiple end organ or cognitive inputs. They showed that stronger inter-sensory conflicts drive stronger illusory sensations of self-motion. If the conflict gets too strong, however, this relationship might break down [31].

In this paper, we examine the interaction between inter-sensory disagreement and conflict with the efference copy by testing the hypothesis that maximal adaptation accompanies maximal conflict. That is, we hypothesize that erroneous vestibular output leads to adaptation as a function of the strength of all other sensory input, including efference copy information. While numerous studies have shown that repeated head

turns orthogonal to the prevailing rotation lead to adaptation of motion sickness and sensory illusions, this study examines the particular role of varying sensory conflict in mediating these responses at high rotation speeds.

When spun at constant velocity, the semicircular canal signals decay and subjects typically do not experience sustained rotation. The only continuing rotational cues are provided by ambient sounds of the centrifuge, tactile wind cues, and cognitive knowledge. However, once an out-of-plane head movement is made, a strong sense of body rotation (illusory motion) is reported and nystagmus is observed. Eyeson-Annan, Peterken, Brown and Atchison [6] found that, when rotated at 10 rpm, the visual-vestibular conflict provided by veridical visual information about rotation caused more severe motion sickness than the canal-otolith conflict of normal Coriolis illusions, suggesting that the visual-vestibular conflict is more salient than the contribution of the other sensory modalities. Thus, in order to better understand the relative roles of these two sensory inputs in the process of adaptation to high-speed rotation, we built upon a previously successful adaptation paradigm [38], and varied the degree of visual-vestibular conflict. In pilot work we found that vestibular adaptation can be maintained over months. To rule out such learning effects with certainty we chose a between-subjects design, rather than a within-subject design, randomly assigning subjects without prior centrifuge experience to each of the groups.

2. Methods

2.1. Experimental design

We tested three groups to examine the hypothesis that adaptation to a Coriolis stimulus is optimal when maximizing the conflict between opposing sensory inputs. The first test group (STABLE), identical to the original design in [38], viewed a platform-fixed visual surround. Thus, constant rate rotation with a platform-fixed visual world placed vision, the strongest sensory modality, in direct opposition to the erroneous canal signal that ensues when making a head turn in a rotating environment. The second group (EXTERNAL) received veridical visual input. They could see the external laboratory through a clear plastic canopy. Thus, when looking at the ceiling, appropriate torsional nystagmus was induced and when looking to the side, vertical nystagmus ensued. Finally, the third group (DARK)

received no visual information at all. Based on our conflict model of sensory adaptation, we hypothesized that removing the input of the strongest modality in this paradigm should dramatically reduce conflict, and thereby, adaptation, as measured by reductions in motion sickness scores, inappropriate vertical nystagmus, and magnitude and duration of illusory tilt.

All three groups of subjects (factor Condition) were exposed to repeated single-quadrant lateral head turns during adaptation sessions on three consecutive days (factor Day) (see Fig. 1). Rotation in this experiment was at 23-rpm, such that the level of centrifugal acceleration at the feet was approximately equal to 1-g. Subjects were supine with the crown of the head aligned with the axis of rotation. Otolith input due to centripetal accelerations was minimal (approx. 0.07-g). The adaptive stimulus consisted of 18 directed yaw head turns plus 6 minutes of turns made by the subject at ad lib intervals. Test phases before (pre-exposure) and after (post-exposure) this adaptation consisted of 3 pairs of yaw head turns performed in the dark at approximately 30 sec intervals, for which vertical nystagmus, and magnitude and duration of illusory tilt were measured (factor Phase). Except for one condition discussed later, any vertical nystagmus in these conditions was inappropriate and did not serve to stabilize the retinal image. Changes in motion sickness were monitored throughout the experiment. All of the subjects were presented with the same set of stimuli, excepting the visual stimulation that they received during their adaptation phase. The measures of interest to us were always taken in the dark, on three consecutive days, before and after adaptation.

2.2. Subjects

Informed consent was obtained from 44 subjects according to a protocol approved by the MIT Committee of the Use of Humans as Experimental Subjects. Eleven subjects chose to abort the experiment during the adaptation phase due to excessive motion sickness on the first day. One more dropped out in the latter half of the final day. His data up to that point is included for analysis. 13 had irrecoverable gaps in their physiological data sets when the eye-tracking software was unable to determine eye position, mostly because of high blink rates or slippage of the eye goggles. Among the remaining data, if only one in a set of three consecutive head turns in the same direction had flawed data, we replaced that value with the average of the other two if they were roughly equal. This was done for 4% of all

vestibulo-ocular reflex (VOR) sequences. We thereby obtained complete data for 19 subjects (6 DARK, 6 STABLE, 7 EXTERNAL).

Study participants were healthy young adult volunteers recruited predominantly from the MIT community. Subjects were between the ages of 18 and 31, 5'0" to 6'1" in height, and weighed between 110 and 190 lbs. All subjects verified that they performed some form of exercise more than 2 hours a week and had no prior exposure to experimental centrifugation. They were asked to abstain from consuming caffeine and alcohol from 24 hours preceding the start of the 3-day experiment until they had completed the study.

2.3. Equipment

MIT's 2-meter radius SRC provided the rotating platform for this experiment. This 1-hp "rotating bed" supported the subject supine with the crown of the head on-axis, while an adjustable foot plate provides support in the radial direction (for details see [13,37]). A clear plastic canopy was placed over the length of the bed to minimize rotational cues provided by directional air flow, and an opaque cover was utilized to block visual cues from the surrounding room when desired. Three on-board lights provided a fixed visual frame of reference for STABLE subjects, and a SonyTM digital video camera with infrared NightShotTM capabilities allowed constant monitoring in all lighting conditions.

Vertical eye movements were collected and analyzed from all subjects utilizing an infrared miniature eye tracking system (ISCANTM). Eye movements were sampled at 60 Hz, spatial range was 40° horizontally and vertically. Spatial resolution was typically better than 0.3°. Head movements were tracked by a six-degrees-of-freedom Shooting StarTM goniometer, also sampled at 60 Hz. Three potentiometers encoded head position in roll, pitch, and yaw throughout the experiment to an accuracy of approximately $\pm 5^\circ$. The end of the goniometer arm proximal to the subject's head was mounted to a stiff plastic plate on the crown of a soft aviation cap.

2.4. Procedure

Prior to the start of the experiment, subjects were briefed on the basic protocol and potential hazards of the study. Simple gaze tracking and Rhomberg tests were administered to check for normal ocular and vestibular function, and standing blood pressure was taken using an automated arm cuff.

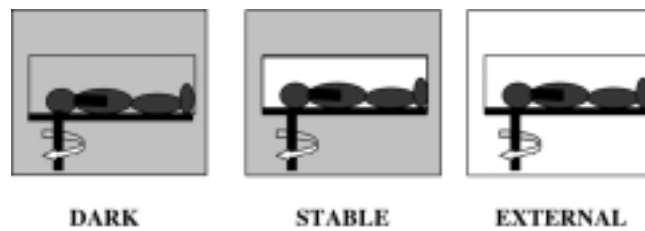


Fig. 1. Stimulus conditions used for the three experimental groups. All groups received pre-exposure and post-exposure testing while rotating in the dark. The groups only differed with respect to the lighting during adaptation. The DARK condition creates a vestibular-proprioceptive conflict. The STABLE condition adds visual information that is consistent with proprioception and in conflict with vestibular information. The EXTERNAL condition is the only condition that provides visual information about the rotation.

A pre-experiment briefing described the data reporting techniques to be used for subjective estimations of motion sickness, as well as illusory self-motion direction, intensity, magnitude, and duration. With the help of a toy astronaut as a visual aid, subjects were introduced to the concepts of body pitch, roll, and yaw that they would use to describe their illusory motion sensations. All coordinates were described with respect to a platform-fixed frame of reference. During the course of the experiment, subjects were instructed to keep their eyes wide open during periods of data collection, particularly during head turns and for the 20 seconds that immediately followed.

During pre-exposure and post-exposure testing, subjects were instructed to make 6 yaw head turns in the right quadrant, 3 to nose-up (NU) and 3 returning to right-ear down (RED). Head turns were made at a nominal speed of $90^\circ/\text{sec}$ at 30 second intervals. Typically a subject reached a comfortable turn angle, somewhat less than 90° , and maintained it.

The ISCAN apparatus was calibrated at the beginning of each experimental session by instructing observers to fix their gaze on a series of dots subtending 10° up, down, left and right with respect to a central fixation point. The centrifugation session each day lasted approximately 40 minutes and consisted of three main Phases: Pre-exposure in the dark, an Adaptation phase with lighting condition selected according to the group, and a Post-exposure in the dark. The centrifuge was rotated with a trapezoidal velocity profile with ramp accelerations of $6^\circ/\text{s}^2$ for 23 seconds. During ramp-up and ramp down subjects were instructed to remain right ear down and to stare at an imaginary point in the dark in front of them. This provided a pure head pitch plane stimulation during bed acceleration and deceleration. Throughout the experiment a steady-state velocity of 23-rpm ($138^\circ/\text{sec}$) was maintained, such that the level of centrifugal acceleration at the subjects' feet was approximately equal to 1-g.

2.5. Dependent measures

1. *Motion Sickness*: The intensity and time-course of motion sickness development throughout the experimental period provided a subjective measure of overall discomfort. Motion sickness was determined by periodically prompting subjects for a rating between 0 and 20, where 0 represented "I feel fine" and 20 represented "I am about to vomit." On each day, 22 such estimates were made during the course of the experiment. If motion sickness levels reached a score of 15 or higher and the subject opted to continue the experiment, further head turns were delayed until the malaise dropped back to a score of 12 or below. Subjects were also asked to track the post-rotation time-course of their motion sickness by recording a score every half hour until bedtime, as well as one additional data point the following morning.

As a second measure, the modified Pensacola Motion Sickness Scoring System developed by Oman, Rague and Rege [25] and utilized in our own work [37] was used as a diagnostic immediately following each day's rotation. This scale quantified the severity of subjective and objective motion sickness symptoms (headache, nausea, pallor, etc.) to provide a detailed snapshot of the peak nausea experienced by a subject on a given day.

2. *Number of head turns*: During the adaptation phase, subjects were encouraged to make as many head turns as they could tolerate comfortably. This simple count of head turns has previously been used successfully as a measure of adaptation (e.g. [19]).

3. *Illusory Tilt*: During the head turns made while the platform was rotating, subjects experienced illusory feelings of tumbling or tilt as their equilibrated semi-circular canals were brought into or out of the plane of rotation (for a model regarding the quality and cause of these tilt illusions, see [13]). Intensity ratings and duration of this illusory tilt were used as measures of

the subjective experience. A simple hand-held button was used to indicate duration of illusory motion associated with each head turn. Subjective estimation of the illusion's intensity was anchored at a score of 0, corresponding to a feeling equivalent to a head turn in a stationary environment. At the high end, the scale was anchored with a score of 10, corresponding to the intensity associated with the first head turn made during rotation on the first day. The intensity measure was used to capture the overall strength of the illusory sensation for each directed head turn, and to provide a common measure for relative adaptation between subjects. More detailed verbal descriptions at the end of each phase of head turns captured the magnitude (in degrees) and direction of illusory motion.

4. *Vestibulo-ocular reflex (VOR)*: The 1 sec duration yaw head turns made by the subjects are rapid enough to be modeled as a step change in head angular velocity as the head rotates relative to the spinning SRC. This step change induces reflexive eye movements (vertical and torsional) that slowly decay following the head turn. Vertical eye position data was collected with the IS-CAN goggles (equipment is not capable of determining torsion). To eliminate eye blink artifacts, saccades, and noise from the slip ring, the position data was subjected to a series of linear and non-linear filters (for details see [38]). Eye position signals were then differentiated to produce velocity traces. An adaptive asymmetrically trimmed-mean filter extracted the fast phases of the nystagmus from this signal and concatenated the remaining slow phases to produce a continuous trace of Slow Phase Velocity (SPV).

The SPV response to a step change in head angular velocity was approximated as a simple exponential decay, $Ae^{-t/\tau}$, where A is the maximum slow phase velocity and τ is the dominant time constant of decay calculated by a MATLAB least squares exponential fit routine. The use of SPV as measure of VOR adaptation assumes that the angular extent of the head turns remained constant across the experiment. However, to prevent injury, subjects were not mechanically restrained in the excursion or timing of their head turns. Thus, potential variability between and within subjects (e.g. due to fatigue or motion sickness) had to be accounted for. This was accomplished by normalizing SPV relative to the turn angle for each individual head turn. Head position data was collected from the goniometer. The position data about the head yaw axis was isolated and the duration, magnitude, and average position of each turn were calculated. We can approximate the stimulus to the vertical semicircular canals

as $\omega \sin \theta$, where ω is the angular velocity of the platform in degrees/sec, and θ is the angle of the yaw head turn [37]. We therefore normalized our SPV fitted amplitude (A) to the magnitude of the stimulus to remove the effects of head turn variations¹

$$\text{NSPV} = A/\omega \sin \theta$$

The angle of yaw head turns was approximately normally distributed about 57° ($\sigma = 12^\circ$). Note that this value contains 10% remedied data, where equipment malfunctioned and values were replaced by the average of head turns in the same direction on the remaining two days. Subjects made significantly slower head turns to RED (46.7 ± 20.0 °/sec) than to NU (55.7 ± 21.6 °/sec) ($p < 0.0005$, $F(1, 16) = 22.121$). Also, from day to day, head velocity increased significantly ($p < 0.0005$, $F(2, 32) = 9.743$), presumably as subjects became less motion sick and more accustomed to the environment.

3. Results

3.1. Motion sickness

All 11 subjects who could not finish the experiment due to excessive nausea dropped out during the first day of testing (drop out rate was 25%). These dropouts were distributed fairly evenly across both gender and experimental condition (6M, 5F; 3 DARK, 4 STABLE, 4 EXTERNAL). The remaining subjects reached a motion sickness plateau mid-way through the adaptation phase and stabilized there or showed improvement.

On average, subjects reported maximum motion sickness scores that were nearly 200% higher on day 1 than day 2, and 35% higher on day 2 than day 3. There was also a significant Gender effect. Peak scores were nearly 3 times as high for men than for women ($p = 0.002$, $F(1, 26) = 12.211$). No significant differences in motion sickness scores were found between groups. There were no significant main (or cross-) effects of Condition used during adaptation. Thus, the visual field had no effect on motion sickness adaptation. STABLE subjects exhibited the lowest scores on Day 1 of the experiment, as shown in Fig. 2, however, we believe that this non-significant difference is likely

¹It should be noted here that while this parameter accounts for differences in stimulus magnitude, it does not take stimulus duration or velocity into account. It is assumed that all head turns made in this study can be considered a velocity step change.

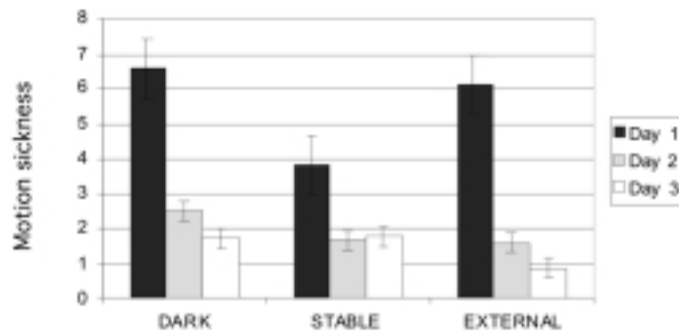


Fig. 2. Maximum motion sickness scores per Day by Condition. Scores were assessed once a minute during adaptation periods. The scale ranged from 0–20 with a score of 0 corresponding to “I feel fine”, and a score of 20 corresponding to “I am about to vomit”.

to be a group difference unrelated to the experimental condition.

The average motion sickness ratings, the daily peak scores and the Pensacola assessments were all highly correlated (Pearson correlation coefficients between $r = 0.81$ and $r = 0.94$). Post-experiment surveys indicated that all of the subjects in all conditions experienced at least some subjective adaptation to the stimulus over the course of the three days. In fact, by the end of day 3 many subjects were reporting neither illusory motion nor motion sickness, even after repeated head turns.

3.2. Number of head turns

The number of head turns made during the adaptation phases of the experiment provides another measure of resistance to motion sickness. It showed a significant daily increase ($p < 0.0005$, $F(2, 54) = 17.322$). The EXTERNAL group showed significantly larger increases from one day to the next than did the other groups (day*Condition effect: $p = 0.002$, $F(4, 54) = 4.847$; see Fig. 3).

3.3. Illusory self-motion

The *subjective intensity* of illusory self-motion showed a clear pattern of adaptation over days and habituation within each day as shown in Fig. 4 (for days 1 and 3 only). A repeated measures ANOVA revealed an effect of day ($p < 0.0005$, $F(2, 38) = 46.250$) and Phase (i.e. pre-exposure vs. post-exposure: $p < 0.0005$, $F(1, 19) = 82.212$). The first head movement in a given direction within a phase was stronger than the last of the three repetitions (Repetition effect: $p < 0.0005$, $F(2, 38) = 10.787$). An asymmetry based on Turn Direction resulted in significantly higher

intensity scores ($p < 0.0005$, $F(1, 19) = 38.329$) for yaw head turns made to Nose-Up (NU) than those made to Right-Ear-Down (RED). Student's t-tests verified the asymmetry at $p < 0.001$ for each adaptation condition. Condition had no effect: no significant difference in illusory tilt estimates was found between the three groups. Neither main effects nor interactions were found for the visual condition used during adaptation.

The *durations* of illusory sensations of self-motion mirror the intensity ratings. An ANOVA found no significant differences in duration between groups. Significantly longer durations were observed for turns to NU than to RED ($p = 0.04$, $F(1, 21) = 4.815$), matching the asymmetry seen in illusory motion intensity above.

Likewise, the absolute *magnitude* of illusory pitch (how many degrees subjects felt their body had tilted) mirrored intensity and duration. Magnitude decreased significantly within ($p < 0.0005$, $F(1, 17) = 20.429$) and across days ($p = 0.001$, $F(2, 34) = 9.483$). Only 21 subjects had clear enough sensations to produce a value for this measure. A significant ($p = 0.015$, $F(2, 17) = 5.406$) cross effect of Condition*Phase on illusory pitch magnitude was observed. The magnitudes of illusory pitch and its adaptation were largest for subjects who adapted in the DARK.

3.4. VOR: Normalized slow phase eye velocity (NSPV)

Overall, NSPV adapted for the STABLE and EXTERNAL subjects but not for the DARK condition. We therefore find a dissociation between vertical VOR gain and other adaptation measures which showed clear adaptation for all three groups. Figure 5 shows the average NSPV values by Phase for the first and last days of the experiment.

Examining the groups one at a time using a repeated measures ANOVA, we found no significant adaptation

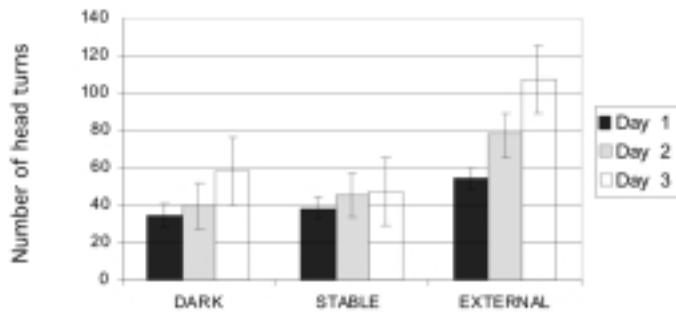


Fig. 3. Number of voluntary head turns made during adaptation periods by Day and Condition. Subjects were encouraged to make as many head turns as they comfortably could.

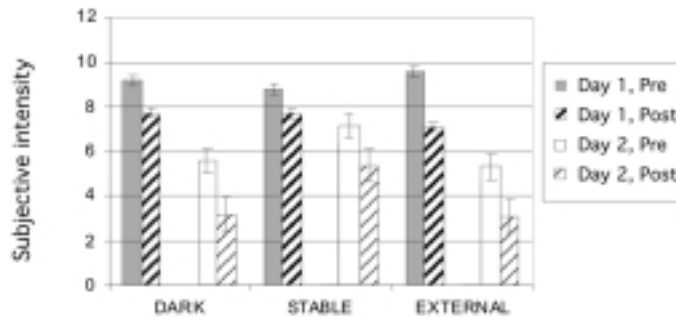


Fig. 4. Pre-exposure and Post-exposure averages of subjective intensity ratings by Condition for Day 1 and Day 3. Participants made 6 head turns while rotating in the dark before and after each adaptation session. The intensity of the illusion encountered upon making the very first Coriolis head-turn was anchored as a 10. A normal stationary head turn was assigned a 0. Error bars indicate standard errors of the mean.

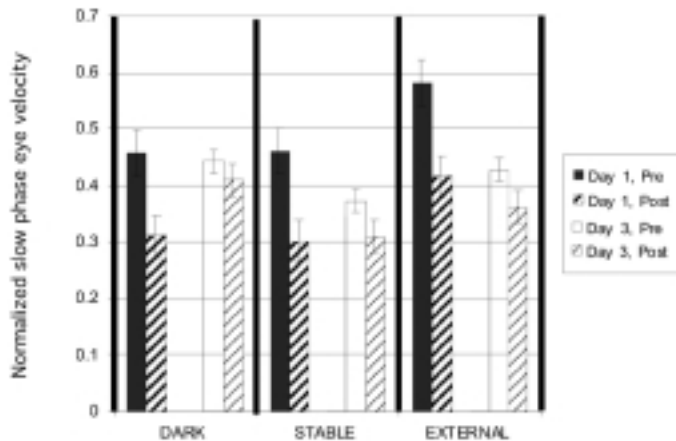


Fig. 5. Average normalized slow phase eye velocity (NSPV) for vertical nystagmus measured following yaw head turns while rotating clockwise in the dark. Results for pre- and post-exposure measures are plotted by Condition for Day 1 and Day 3.

occurring across days in the DARK group ($p = 0.584$, $F(2, 8) = 0.576$). The STABLE and EXTERNAL groups, on the other hand, showed signs of adaptation as seen in Fig. 5. However, they failed to reach significance ($p = 0.101$, $F(2, 8) = 3.093$, and $p = 0.335$, $F(2, 10) = 1.187$, respectively), probably because too

many outliers had been removed. A non-parametric Friedman test showed significant adaptation effects for both the STABLE visual field group ($p = 0.006$, assuming χ^2 with 35 df) and the EXTERNAL visual field group ($p < 0.0005$, assuming χ^2 with 35 df). The DARK group showed no such effect ($p = 0.254$, as-

suming χ^2 with 35 df).

There was also a distinct turn direction asymmetry for the EXTERNAL group only. While DARK and STABLE subjects showed no difference in NSPV for turns to RED vs. those to NU, EXTERNAL subjects produced significantly larger NSPV on turns to RED than on turns to NU ($p = 0.018$, $F(1, 15) = 7.089$), opposing the trend in subjective measures of intensity and duration.

3.5. VOR: Time constant of decay, τ

As opposed to the NSPV data, which showed no significant reduction in vertical VOR gain for subjects adapted in the dark, a repeated measures ANOVA on the dominant time constants of the slow phase eye-movements showed a significant decrease in the dominant time constant (τ) of the vertical SPV decay across days ($p = 0.001$, $F(2, 32) = 8.483$) and between pre-exposure and post-exposure testing ($p < 0.001$, $F(1, 16) = 24.32$). No effect for Condition was found. When running separate ANOVAS for all three experimental Conditions, comparable adaptation effects for Day and Phase (pre/post-exposure) were found for all groups, albeit with marginal significance due to the relatively small number of subjects in each Condition (DARK: $p = 0.021$, $F(2, 16) = 4.99$; EXTERNAL: $p = 0.029$, $F(2, 22) = 4.17$; STABLE: $p = 0.066$, $F(2, 14) = 3.33$). Figure 6 shows the average τ values by Phase for the first and last days of the experiment.

As with NSPV and subjective intensity ratings, the time constants showed a significant asymmetry between head turns to NU and those to RED ($p = 0.033$, $F(1, 26) = 5.09$). The down-beating nystagmus that accompanied turns to NU was more prolonged. On average, time constants were 5.23 sec and 4.95 sec respectively for turns to NU and to RED on Day 1. The values decreased to 4.97 and 4.73 on Day 2 and 4.55 and 4.05 on Day 3. This main effect of turn direction did not interact with Day or Condition.

4. Discussion

The fact that not all our dependent measures behaved similarly is very revealing and of practical importance for adaptation. VOR time constants and all parameters measuring subjective experience, including metrics of motion sickness and illusory self-motion, showed adaptation across days, regardless of the visual condition.

Normalized slow phase eye velocity (NSPV), however, showed no significant adaptation in the DARK, while visual stimulation (STABLE and EXTERNAL) caused NSPV to adapt. Visual inputs were required to adapt eye movement amplitudes but were irrelevant for the adaptation of subjective experience and eye movement time constants.

Thus, the predictions of our conflict model of sensory adaptation were met for VOR gain adaptation only. The model is not valid for all measures. Adapting the slow phase magnitude of the VOR requires retinal slip, while vestibular and proprioceptive input provide sufficient conflict to drive reduction of illusory tilt, motion sickness, and the time constant of VOR decay.

This dissociation between subjective and physiological measures of adaptation shows that VOR gain adaptation in its entirety is not a precondition for the adaptation of other sensory responses. Neither is the sensation of illusory tilt yoked to VOR gain. The fact that the two typically co-occur is deceptive; there is no evidence for a functional relation between the two responses. Instead, adaptation seems to occur along separate parallel paths in response to a given environment. On the other hand, the reduction in the dominant time constant of the VOR is correlated with a reduction in motion sickness and is presumably reflective of a central adaptive phenomenon.

These findings rule out the possibility that repeated sensory conflict exclusively suppresses the dissenting modality at its root, for instance the afferents at the level of the vestibular nucleus. If this was the case, then adaptation of all subjective and VOR measures should have been synchronized.

Our finding that VOR time constants adapt in all groups while reduction in VOR amplitudes require retinal slip is consistent with evidence that the two are based on different neural substrates. Time constant habituation has been linked to the nodulus and uvula while gain adaptation is under cerebellar (flocculus) control [4]. The latter requires a visual-vestibular mismatch. We may speculate then that the tilt illusion, which we found adapted in the dark, is fed by the same mechanism responsible for velocity storage. This storage mechanism is turned off as soon as the system senses vestibular conflict of any sort (for a related idea see [29]). These findings are consistent with results reported by Guedry [9] for subjects seated in the Pensacola Slow Rotating Room: 20 adult males rotated for several hours at 7.5-rpm either in the dark or with normal lighting inside the rotating room. Testing periods in darkness preceded and followed an adaptive

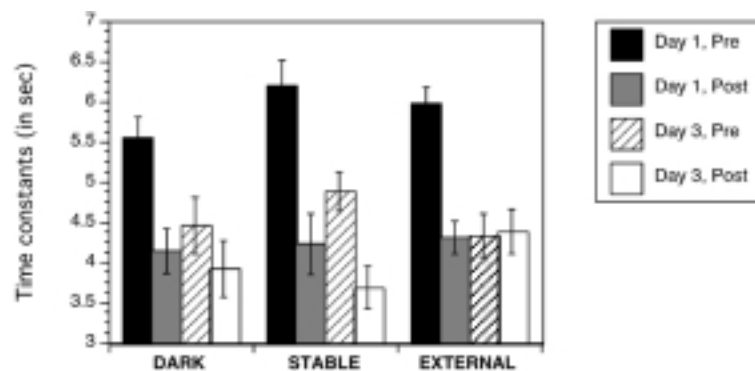


Fig. 6. Average time constants for decay of vertical slow phase eye velocity measured following yaw head turns while rotating in the dark. Results for pre- and post-exposure measures are plotted by Condition for Day 1 and Day 3.

period of single quadrant head turns. Subjects habituated in the light exhibited pronounced reductions in nystagmus and subjective effects to head turns in the dark, but those who had spent the whole test period in darkness demonstrated no similar reduction. However, the case has also been argued from the opposite perspective by Clément, Flandrin, and Courjon [3]. Using cats, they found that 5 days of velocity step training in the dark reduced both the amplitude and duration of the VOR to less than 50% of their original values. Training sessions spread over multiple days showed retention of this response. They argue that nystagmus seen in darkness is “parasitic,” and that because it serves no functional purpose, the eye movements should be generally suppressed. Likewise, Melvill Jones, Berthoz and Segal [22] found that the mental effort involved in imagining a head-fixed target while making head turns on a rotator sufficed to achieve VOR gain reduction. Large differences between the studies make direct comparison between these conflicting results difficult. However, rotation rates for the experiment reported here are much higher than those used in earlier studies, and for these higher rates, our data shows that retinal slip is indispensable for gain adaptation.

For all three experimental groups, head turns made to RED elicited less intense sensations of illusory motion than turns made to NU. This finding replicates results obtained by Hecht et al. [13] and is explored in greater detail in Part II of the current investigation by Mast, Newby and Young (in this volume). For groups adapted in the DARK or with a STABLE visual field, this asymmetry was not replicated in the elicited VOR. However, our subjects adapted with a view of the EXTERNAL world actually experienced VOR asymmetry that opposed their subjective sensations. That is, the NSPV was significantly higher for turns to RED than to

NU. This unexpected effect may be explained by close examination of the nature of the visual stimulation: for a STABLE subject, the visual scene is essentially static and it is at the same close accommodative distance, regardless of head position. In this condition, VOR adaptation is needed to prevent excessive retinal slip. For a subject with a view of the EXTERNAL world, however, a turn to the RED position provides a downward pitching visual stimulus of the passing room, such that the vestibular counterclockwise torsional component of nystagmus is inappropriate, but the up-beating nystagmus caused by the change in pitch plane canal velocity is compensatory. In other words, during those head turns the compensatory slow phase of the VOR is down, as is the direction of slip of the room walls. Thus, for EXTERNAL subjects, it would not be adaptive to eliminate these functionally useful eye movements.

Given the need for repeated stimuli in an adaptation experiment, learning effects cannot be entirely ruled out. However, the intensity rating scale was anchored at the high end with the intensity of the first head turn, and at the low end with a score of zero, equivalent to a normal head turn in a static environment. The adaptation achieved with repeated exposure prohibited providing the standard more than once. Thus, the scale can be considered firmly anchored only at the bottom. It is conceivable that the memory for the initial head turn faded over the three days of the experiment. However, to explain the results described above, such fading would have had to increase with time. Such a phenomenon seems unlikely, particularly given the reliable metric used for the lower anchor.

As a general note, those cases where we did not find significant differences between groups need to be evaluated with caution given the relatively small number of subjects used in the between-subjects design. More-

over, the high drop-out rate because of motion sickness might have selected more or less highly adaptable subjects than representative for the general population. A replication of those results, perhaps within an incremental adaptation paradigm is, of course, highly desirable.

From a countermeasure point of view, the results of our experiment suggest that DARK, STABLE, and EXTERNAL visual surrounds all provide nearly equivalent adaptation of the illusions and nausea that previously provided a barrier to SRC countermeasures. This suggests that the choice between the three conditions should be driven predominantly by the need for a stable visual field and reduced VOR gain. By rotating astronauts in the DARK, changes in VOR gain will be limited to simple habituation and the effects upon return to a non-rotating environment will be minimized. This is desirable in principle but might not be feasible in an operational spacecraft. To make economical use of the astronaut's time, visual stimulation and head movements may be desirable during centrifugation. If visual stimulation is provided, a full view of the spacecraft interior, as used by the EXTERNAL group, can offer valuable information to an astronaut on board the SRC in an emergency (situational awareness), although the challenge of making sense of the rapidly spinning surround may be formidable. A STABLE visual surround, on the other hand, would offer a number of other conveniences and benefits, such as reading or operating a computer, which could be safely carried out on board the SRC.

5. Conclusion

It was thought until recently that AG could be implemented only by using large radius rotating spacecraft. We have further challenged the assumption that 4–6 rpm is a natural barrier beyond which adaptation becomes unattainable [11]. Fast-spinning small rotational devices are a practical alternative. Our experiment has shown that different physiological and subjective responses to Coriolis stimulation adapt in different ways. Augmented visual-vestibular conflict did not facilitate adaptation uniformly. While strong conflict involving retinal slip is required to adapt VOR gain; illusory tilt, motion sickness, and dominant VOR time constants also adapt effectively in the reduced sensory conflict provided by Coriolis stimulation in the dark.

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