

Adaptation of the vestibulo-ocular reflex, subjective tilt, and motion sickness to head movements during short-radius centrifugation

Laurence R. Young*, Kathleen H. Sienko, Lisette E. Lyne, Heiko Hecht and Alan Natapoff
Man-Vehicle Lab Massachusetts Institute of Technology, Cambridge, MA, USA

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Abstract. Head movements made while the whole body is rotating at unusually high angular velocities (here with supine body position about an earth-vertical axis) result in inappropriate eye movements, sensory illusions, disorientation, and frequently motion sickness. We investigated the acquisition and retention of sensory adaptation to cross-coupled components of the vestibulo-ocular reflex (VOR) by asking eight subjects to make headturns while being rotated at 23 rpm on two consecutive days, and again a week later. The dependent measures were inappropriate vertical VOR, subjective tilt, and motion sickness in response to 90° yaw out-of-plane head movements. Motion sickness was evaluated during and following exposure to rotation. Significant adaptation effects were found for the slow phase velocity of vertical nystagmus, the reported magnitude of the subjective tilt experienced during head turns, and motion-sickness scores. Retention of adaptation over a six-day rest period without rotation occurred, but was not complete for all measures. Adaptation of VOR was fully maintained while subjective tilt was only partially maintained and motion-sickness scores continued to decrease. Practical implications of these findings are discussed with particular emphasis on artificial gravity, which could be produced in weightlessness by means of a short-radius (2 m) rotator.

Keywords: Artificial gravity, adaptation, centrifugation, vestibulo-ocular reflex, illusory tilt

1. Introduction

Out-of-plane head movements made during whole-body rotation result in inappropriate semicircular canal stimulation (in planes not typically stimulated) compared to the same head movements made in a stationary environment. The subsequent nystagmus (cross-coupled vestibulo-ocular reflex) is inappropriate for stabilization of any visual field fixed in the rotating environment. Unexpected sensations of self-motion and symptoms of motion sickness often ensue [21]. Such cross-coupled stimulation will be the rule rather than the exception when living in a rotating environment

or when introducing artificial gravity in weightlessness by means of short-radius centrifugation. To function in such a rotating environment [25] astronauts must be able to achieve and retain adaptation. Failure to adapt to intermittent centrifugation could result in repeated episodes of motion sickness. Although brief bouts of motion sickness may be tolerable early in a space mission, it would be unacceptable if these symptoms were to recur each time the astronaut made transitions between different gravito-inertial environments.

The fact that the vestibulo-ocular reflex (VOR) can be adapted in specific ways has been amply demonstrated [6,27]. This holds not only for changes in gain appropriate to magnification of the visual surround, but also for the phase of eye movements relative to head movement [11,15,16,19,21]. The VOR even adapts across axes, so that horizontal head movements can induce vertical or torsional compensatory nystagmus [10,

*Corresponding author: Laurence R. Young, MIT Man-Vehicle Lab, 77 Mass Ave., Bldg. 37-219, Cambridge, MA 02139, USA. Tel.: +1 617 253 7759; Fax: +1 258 8111 617; E-mail: lry@mit.edu.

24]. It is largely unknown, however, how the inappropriate VOR relates to the accompanying illusory sensations and whether all adapt at the same rate. For instance, it is unknown whether the sensory illusion is directly mediated by vestibular output (as measured by slow phase of VOR) or cortically processed. In the latter case, differential adaptation of VOR and tilt illusion are possible.

The present investigation had three goals. First, we wanted to establish if humans can adapt and remain adapted to out-of-plane head movements during short-radius centrifugation at high angular velocity. Second, we sought to measure the relationships among the VOR, subjective illusory tilt, and motion sickness. Finally, we wanted to distinguish between short-lived habituation and more permanent adaptation by testing the retention of the adaptation after a week.

Whenever an observer has to function in multiple environments, context-specific adaptation is desirable, or at least it must be possible to switch environments without suffering from aftereffects. Our ability to switch readily between reading glasses and normal vision or the ease with which we can switch motor programs between wielding a tennis racket and a baseball bat constitute everyday examples of successful context-specific or dual adaptation (for an overview see [26]). In these cases, a context cue apparently triggers the change of the adaptive state. Context-specific changes of adaptive state have recently been demonstrated for the vestibulo-ocular reflex (VOR). For instance, the VOR gain can be conditioned to increase when looking up and to decrease when looking down [23]. Likewise, a particular VOR gain can become associated with a specific orientation of the head with respect to gravity [27]. The present paper investigates adaptation of a similar nature with the notable difference that a pronounced sensory conflict rather than a distortion or a verbal instruction drives the adaptation. VOR adaptation in the presence of compelling vestibulo-visual conflict arises when making head rotations at high angular velocities. In this case, the goal of the adaptation is not limited to changing eye-movement gains, but is directed toward overcoming the debilitating physiological and psychological side effects of the sensory conflict.

Adaptation of this kind becomes increasingly important in environments that necessarily produce unusually large vestibulo-visual conflicts, such as during space travel. For example, on a trip to Mars, astronauts may have to receive regular doses of “artificial gravity” by means of centrifugation to prevent the broad-spectrum physiological deconditioning that accompanies long-

duration space flight. Spacecraft size dictates that any in-flight centrifuge tested in the foreseeable future be of limited radius (on the order 1–3 m). Centripetal accelerations on the order of 1 g (9.8 m/s^2) will therefore require relatively high angular velocities (on the order of 30 rpm). Even with the head near the rotation axis, spinning at these angular velocities will create disruptive sensory effects when the astronaut moves his/her head about any axis other than the centrifuge spin axis [8,22]. The possibility remains that adaptation is specific to the context of head movements while rotating, rather than to the semicircular canal stimulus alone. This “context-specific” explanation has not been proven by the current experiments, and remains a subject for continuing research. Our continuing experiments deal with situations in which the actual cross-coupling stimulus is separated from the subject’s initial perception of whether or not the platform is rotating.

One might argue that during brief centrifugation on a short-radius rotator, the head is best restrained to eliminate disturbances [17]. However, restraining the head limits exercise, recreation and comfort. Movement is mandatory during long-term centrifugation (for example, in a rotating spacecraft) and is desirable for cardiovascular fitness during intermittent centrifugation.

Previous studies suggest that vision plays an important role in facilitating habituation to slow rotating environments [13]. Thus adaptation should be most likely to occur when the conflict between vestibular information and all other sensory modalities, in particular vision, is maximized (for a deliberate test of this hypothesis see [5]). To provide both an effective and simple context for adaptation we presented subjects with a platform-stable visual context and instructed head movements to be 90° yaw turns in the quadrant formed by turning the head from the right-ear-down (RED) to the nose-up (NU) position while the subject was in a supine position on a clockwise-rotating platform. Note that the visual context manipulation is not to be confused with the notion of context-specificity introduced above.

Measures of adaptation included the normalized slow phase vertical velocity component of nystagmus, motion-sickness scores, recovery times from motion sickness, and the magnitude of perceived pitch. A simple model of the semicircular canals (see e.g. [14, 28]) was used to predict the VOR and the direction of illusory tilt.

Cross-coupling and Coriolis effects occur in the semicircular canals as they are re-oriented in a rotating environment. The canals, although signaling angular

velocity, are stimulated by angular acceleration about an axis normal to their planes. If the platform is rotating at constant angular velocity, the stationary canals equilibrate, that is they no longer produce a sensory signal any different from that for null velocity. However, following a head turn, the canal that is moved out of the plane of rotation continues to signal motion for about five to ten seconds. Likewise, the canal that is moved into the plane of rotation picks up the rotator's motion before it equilibrates again. Upon a head turn from RED to NU, the canals signal that the subject has pitched forward (head up, feet down) while also signaling clockwise roll, in the direction of the rotator's motion. The pitch signal causes a vertical nystagmus, as if to compensate for the sensed illusory pitch. The roll signal produces ocular torsion, which we were not able to measure with our equipment. We measured the vertical VOR, which is clearly in an inappropriate direction as long as the visual surround is fixed to the rotating platform. Via the unexpected retinal slip that it creates, one would expect the VOR to decrease by the process of adaptation.

2. Methods

To test for adaptation to the inappropriate vestibular signals we subjected human subjects to sessions on a short-radius rotator that lasted approximately one hour. Baseline measurements were taken while stationary before and after rotation. While rotating, measurements were taken during head movements in the dark (Pretest). Then, internal lights on the rotator provided a stable visual frame of reference during an adaptation phase ensuring maximal conflict between vestibular signals and non-vestibular sensory information. Subjects were asked to make as many head movements as they could tolerate while maintaining a motion sickness score below a set criterion. Another measurement phase followed while still rotating in the dark (Posttest). The whole procedure was repeated a day and a week following the initial session.

2.1. Subjects

Eight healthy MIT students (four males, four females), ranging in age from 19 to 25 years (mean 22.9 yrs. with a standard deviation of ± 2.2 yrs) participated in the study. Their mean height and weight were 173.2 ± 11.8 cm and 68.9 ± 11.7 kg, respectively. Volunteers with histories of vestibular abnormalities, heart condi-

tions, respiratory problems, usage of anti-depressants or barbiturates, extreme susceptibility to motion sickness, or previous artificial gravity experience were excluded from the experiment. Subjects were asked to abstain from caffeine and alcohol 24 and 48 hours preceding the experiment, respectively.

2.2. Equipment

The apparatus consisted of the MIT short-radius centrifuge (2.5 m-long platform), infrared video imaging system, and angular rate sensors. The two-meter radius centrifuge was configured to rotate a supine subject clockwise about a vertical axis just above the head. Subjects rotated at 23 rpm ($138^\circ/\text{s}$) resulting in a centrifugal force of 1 g at the feet of a 1.67 m tall subject. A light-proof canopy covered the subject eliminating external visual and wind cues. An infrared eye imaging system (ISCAN 60 Hz digital image processor) was used to automatically track the center of the subjects' pupils. It computed the vertical and horizontal eye-position based on an initial calibration performed for each subject at the beginning of the testing session. Watson Industries solid-state single-axis angular rate sensors provided an analog output voltage proportional to the angular rate about their sensing axes with respect to inertial space. Two single-axis rate sensors measured head velocity in two planes – yaw (transverse) and pitch (sagittal). To prevent the drift associated with such sensors, regular manual calibrations were performed before converting the output voltage signal into angular velocity. Note that the yaw-axis sensor is not affected by cross-axis motion and did thus provide accurate information about head yaw.

2.3. Procedure

All subjects participated in an identical series of pre-, per-, and post-rotation data collection sessions on Days 1, 2, and 8, while positioned supine with the top of their head placed near the axis of rotation. Each session consisted of eye position recordings during head movements and subjective reporting. Prior to the first session on Day 1 the experimenters issued instructions for reporting illusory tilt and motion-sickness scores/symptoms, obtained the subjects' informed consent, and trained subjects to make 90° yaw head movements of one-second duration. Subjects were instructed to make as many head movements as possible during light adaptation, but to pause and inform the operator when the motion sickness criterion of 15 was reached.

Figure 1 summarizes the 11 phases of each session with the corresponding rotational status of the rotator, lighting conditions, and timing of subjective tests. VOR data collection occurred throughout all 11 phases. With the exception of the light adaptation phase (6), sessions were conducted in the dark. During Phases 1, 2, 10, and 11 the rotator was stationary. Throughout Phases 3–9 the rotator spun at 23 rpm. During Phases 1 and 10 the subject remained still for 30 seconds. Phases 2, 5, 8, and 11 required that the subject make three sets of yaw head movements following the experimenter's instructions. A set of head movements was defined as a $90^\circ/\text{s}$ yaw head turn from "right-ear-down" (RED) to "nose-up" (NU) followed by a 20 second "hold" period in the NU position and a subsequent NU to RED $90^\circ/\text{s}$ yaw head turn back to the starting position.

Subjective evaluations were performed both during and after the experiment to assess the level of motion sickness and magnitude of perceived pitch. Motion sickness was assessed at the end of each session by the Pensacola scoring method [12] with symptom scoring definitions devised by Oman, Rague and Rege [20]. The Pensacola score includes both subjective reports and experimenter impressions of nausea, pallor, sweating, etc. Since the Pensacola assessment requires too much time to be conducted during centrifugation, we also used a simple subjective motion sickness rating 0–20 scale, where a score of 0 represented "I am feeling fine" and 20 represented "I am about to vomit." Subjects reported motion-sickness scores at regular intervals and perceived pitch sensations (in degrees) experienced during specified head movements. If subjects reached a motion-sickness score of 15 or above they were asked to stop making head movements until their score decreased to 12.

The subjects began each phase in the RED position and remained RED throughout the phase unless instructed otherwise. Throughout the entire experiment the rotator always rotated in the clockwise direction. During Phase 3, the rotator underwent constant angular acceleration of $6^\circ/\text{s}^2$ for 23 seconds from 0 rpm to a constant angular velocity of 23 rpm ($138^\circ/\text{s}$). The rotator remained at 23 rpm throughout Phases 4–8 before being decelerated back to 0 rpm at $6^\circ/\text{s}^2$ for 23 seconds during Phase 9. During Phases 5 (Pretest) and 8 (Posttest) the subjects made three sets of yaw head movements in response to the operator's instructions as in Phases 2 and 11, followed by a fourth set of head movements during which subjective reports were collected. Phase 6, the light adaptation phase, was conducted for ten minutes with the interior lights on. The

subjects were able to see the illuminated interior of the canopy and the rotator platform, which appeared stationary to them. The experimenter asked them to report a motion-sickness score every minute. The interior of the canopy provided a sparsely textured stable visual environment. Subjects were not instructed to fixate. Following Phase 11 the Pensacola motion-sickness score was assessed. On completion of the session, subjects were given a post-experiment motion-sickness sheet (using the same 0–20 scale) to fill in every 30 minutes until retiring for bed and once more the following morning.

2.4. Eye movement analysis

ISCAN data (for the 20 sec intervals after each head turn) was filtered using two non-linear order statistic filters and one linear filter. The filtering removed noise in the eye position signal, differentiated the position signal (linear filter), and removed fast-phases in the eye velocity signal. An adaptive asymmetrically trimmed-mean filter analyzed the amplitude distribution of the data samples to determine which of the samples were slow-phase [1,9]. The adaptive filter estimated slow phase velocities (SPV) based on the local statistical properties of the eye-velocity signal and extracted the SPV envelope from the eye-velocity signal resulting in an evenly sampled SPV estimate [9]. Filter output corresponded to relatively smoothed SPV profiles. The decaying SPV eye responses were fit with computer-generated first-order exponential curves¹ (SPV curve fit = $Ae^{-(t/\tau)}$).

Following filtering, slow-phase velocity data (Phase 1) was screened for spontaneous nystagmus and Phase 2 data was screened for any inappropriate non-compensatory responses during yaw head movements while the short-radius rotator was stationary. All eight subjects maintained normal gaze for the 30 seconds of eye data collection during Phase 1 and none exhibited spontaneous nystagmus or VOR abnormalities. Although the video eye imaging system was binocular, only the left eye was used for this analysis because

¹Values for A, the magnitude of the SPV response, and τ , the time for the exponential decaying curve to reach $1/e$, for each head movement were replotted on a semi-log scale and a F-test for simple linear regression was performed. All curve fits associated with head movements conducted in the pre-/post-adaptation phases were significant. Additionally, basic statistics were performed on τ values. The distribution of τ values was fairly normally distributed thereby indicating that the curve-fitting algorithm was consistently fitting curves between subjects and phases.

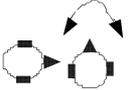
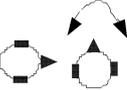
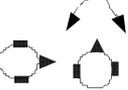
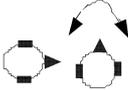
	Pre-Rotation	Ramp-Up	Pretest	Light Adaptation	Posttest	Ramp-Down	Post-Rotation
Centrifuge Velocity	0 rpm		constant	23 rpm constant	constant		0 rpm
Lighting Status	OFF	OFF	OFF	ON	OFF	OFF	OFF
Head Position				Ad lib yaw head movements			
Phase	1 2	3	4 5	6	7 8	9	10 11
Motion Sickness Rating	↑ ↑		↑ ↑	↑ ↑ ↑ ↑ ↑ ↑ ↑	↑ ↑		↑ ↑
Verbal Reports			◇	◇	◇		

Fig. 1. Test session with 11 phases. Vertical VOR caused by yaw head turns was measured in the dark before (Pretest) and after (Posttest) a period of making head turns in the light. Subjects were supine and rotated clockwise with their head close to the axis of rotation.

no systematic differences between the two eyes were observed.

To account for the variability of head turn amplitudes, and to make SPVs comparable across subjects and phases, it was normalized by dividing the magnitude of the SPV-response (A) by the stimulus. The stimulus was composed of the angular extent of the head turn and the platform angular velocity, in $^\circ/s$. Normalized slow phase velocity (NSPV) was determined for each head turn:²

$$NSPV = A / [\sin(\text{magnitude of head movement} * \pi/180) * 138]$$

Vertical cumulative slow phase position was calculated by taking the integral of the SPV curves during centrifuge acceleration and deceleration phases (Phases 3 and 9, respectively). If vertical cumulative slow phase position magnitudes are reduced on Day 2 and 8, vertical VOR suppression during light adaptation generalizes to stimulation of the pitch canal which is induced during the acceleration and deceleration of the platform (the head being RED).

²For any arbitrary head movement the angle of both the starting and final head position would have to be accounted for. However, for our case, the head always either started or ended in the NU position, with the head pitch plane perpendicular to the plane of platform rotation. The sine of either the starting or final angle of the pitch plane relative to the platform was therefore null, and only the magnitude of the head movement was required to calculate the change in angular velocity projected onto the pitch plane by the head movement.

3. Results

The three measures of adaptation, VOR, subjective pitch and motion sickness all showed adaptation, albeit incomplete. The degree of retention of this adaptation varied among the measures. Before presenting the different dependent measures in turn we consider the characteristics of the head movements.

3.1. Head movements

To avoid discomfort and frank nausea we chose not to restrain the head. This led to variability in head movement range and duration and consequently introduced variability of the effective canal stimulus. The magnitude of Pretest and Posttest head movements were generally smaller than the instructed 90° and ranged from 49.2° to 98.7° . The mean magnitude of the head movements conducted during all days was 75.17° (SEM = 0.58°) whereby it increased from one testing day to the next as shown by a repeated measures ANOVA conducted on magnitudes [$F(2, 12) = 5.149, p < 0.029$]. Head movement magnitudes were significantly larger at the beginning of the test (Pretest) compared to the end (Posttest) [$F(1, 6) = 13.184, p < 0.015$]. This difference suggests that subjects either fatigued over the course of the session or responded to increased symptoms of motion sickness by decreasing the head-turn amplitude. To account for this, the SPVs were normal-

ized by introducing a measure (NSPV) that indicates VOR strength regardless of the head turn magnitude.

Peak velocity and duration of the head movements conducted during Pretest and Posttest were $199.8^\circ/\text{s}$ (SEM = 4.3°) and 0.90 s (SEM = 0.02 s) respectively. A separate ANOVA with factors Day (1, 2, and 8), Phase (5, 8), and Repetition (1, 2, 3) was performed on head movement duration. Unlike for magnitude, head movement durations were not significantly different between Pretest and Posttest. No interpretable results for duration were found.

3.2. Eye movements

A repeated measures ANOVA was performed with NSPV as the dependent variable. The independent factors were Day (1, 2, and 8), Phase (5 and 8), Direction of Head Motion (RED to NU versus NU to RED), and Repetition (1, 2, and 3).³ There were significant effects of Day [$F(2, 12) = 14.570$, $p < 0.001$] and Phase [$F(1, 7) = 6.716$, $p < 0.041$], demonstrating that NSPV decreased following adaptation in the light within each Day and across Day. Repetition was significant [$F = 11.075$, $p < 0.015$] although the corresponding univariate analysis was not. The first repetition was associated with significantly higher NSPV values [$F=7.871$, $p < 0.021$] than the average of the second and third repetitions. Direction of Head Motion did not produce a significant effect.

Figure 2 shows exemplar plots of the decrease in magnitude of the inappropriate vertical nystagmus measured in the dark before and after head movements in the light. Average NSPV parameters shown in Fig. 3 illustrate the general decrease both across and within Day. At the end of Day 2, NSPV averaged over eight subjects had decreased by roughly one-third of its initial magnitude. Virtually complete retention of the adaptation was found after six days without exposure to centrifugation (mean NSPV and standard error of the mean (SEM) for Day 2 Phase 8 and Day 8 Phase 5 were $0.287^\circ/\text{s} \pm 0.021$ and $0.292^\circ/\text{s} \pm 0.023$, respectively). No further adaptation occurred on Day 8 following exposure to the light adaptation phase; NSPV values both before and after the light adaptation phase on Day 8 were nearly equal (mean NSPV and SEM for Day 8 Phase 5 and Day 8 Phase 8 were $0.292^\circ/\text{s} \pm 0.023$ and $0.307^\circ/\text{s} \pm 0.019$, respectively).

³On occasion, the corresponding multivariate analysis gave a significant result (which is quoted) when the univariate analysis did not.

Additionally, there was a significant effect of Direction of Head Motion \times Repetition [$F(2,12)=5.807$, $p < 0.017$]. A multivariate analysis showed a significant Day \times Phase [$F=6.260$, $p < 0.044$] effect, though the corresponding univariate analysis did not.

While NSPV provides a good general measure for vestibular output regardless of head turn magnitude, the time constant (τ) of the response decay is another indicator of the nature of the adaptation. As shown in Fig. 4, the time constant was shortened by the adapting head movements made in the light. This was confirmed by a repeated measures ANOVA on τ with factors Day, Phase, and Repetition. Phase was significant [$F(1, 6) = 14.62$, $p < 0.009$]. The trend toward decreasing τ with each day of testing was not significant.⁴ No other effects reached significance.

We computed vertical cumulative slow phase position as a measure of vestibular response during low sustained acceleration and deceleration. It was used to determine whether changes in vertical VOR occurred in the absence of cross-coupling. It was calculated by taking the integral of the SPV curves during the sustained platform acceleration and deceleration phases (Phases 3 and 9, respectively). Because the head was stationary in the RED position during those phases, the vertical semicircular canals were stimulated in the pitch plane. Vertical cumulative slow phase position magnitudes were calculated to reveal whether or not the VOR suppression observed during head rotation was specific to the head movement or generalized to the rotating environment.

The cumulative slow phase vertical position was analyzed by a repeated measures ANOVA on seven subjects (one subject was excluded from the analysis due to equipment failure during the deceleration phase) with factors Day and Phase (3 and 9). The main effect of Day was significant by multivariate analysis [$F = 23.322$, $p < 0.003$], showing a reduction in cumulative eye position with subsequent test days. Phase effects on this measure, although tending toward reduction from the acceleration phase to the subsequent deceleration phase, were not significant. Figure 5 shows the decay of the cumulative slow phase vertical position averaged over seven subjects by Day and Phase (acceleration/deceleration).

If adaptation had generalized even beyond the vertical nystagmus, then horizontal eye movements would

⁴One subject's data could not be used for the ANOVA because in some cases the τ values were not distinguishable from 0.

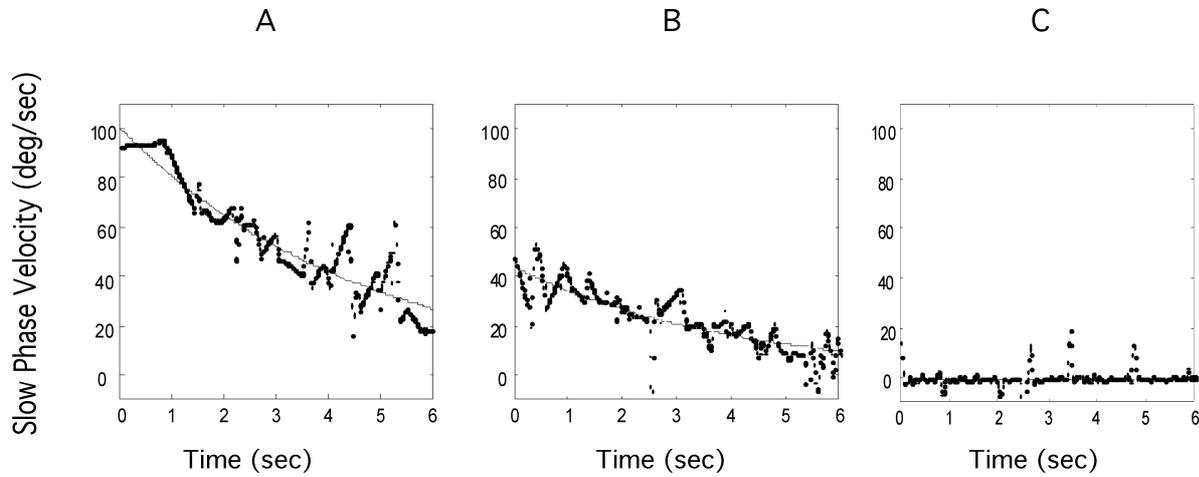


Fig. 2. Exemplary raw slow-phase velocity profiles, in $^{\circ}/s$ for one subject's head turn from RED to NU (Repetition 2). Panel A: before adaptation on Day 1 while rotating (Pretest). Panel B: after adaptation on Day 8 while rotating (Posttest). The fast phases for panels A and B are in the upward direction. Panel C: Before adaptation while making a head turn on a stationary bed.

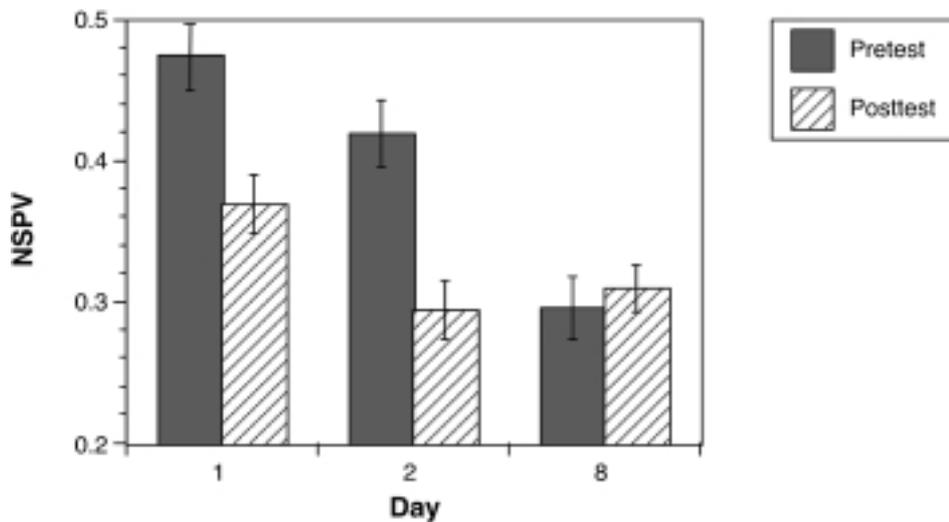


Fig. 3. Mean normalized slow phase velocity (NSPV) measured during Pretest and Posttest by Day (averaged over all subjects for all repetitions). Error bars indicate standard errors of the mean (SEM).

also be affected. This was clearly not the case. Note that the only natural eye response to the yaw head turns in our setup were in horizontal eye movements. These were brief, transitory and entirely appropriate given the fixed visual context. No main effects or interpretable interactions were found. Finally, to investigate possible after-effects of the vertical VOR suppression, we also looked for vertical nystagmus after the rotation had ceased. Following rotation, no significant vertical nystagmus after-effects were found when yaw head-turns were made in the dark.

3.3. Motion sickness

The adaptation process dramatically reduced motion-sickness intensity and duration. Pensacola motion-sickness scores were obtained immediately after rotation for all eight subjects on each day. A non-parametric Page⁵ test showed (Fig. 6) a highly significant decrease in Pensacola motion-sickness scores by Day [ex-

⁵The non-parametric Page test for an increasing (or decreasing) trend in an ordered sequence $A(1), A(2), \dots, A(i), \dots, A(n)$ compares the average of the ranks $R(1), R(2), \dots, R(n)$ of those val-

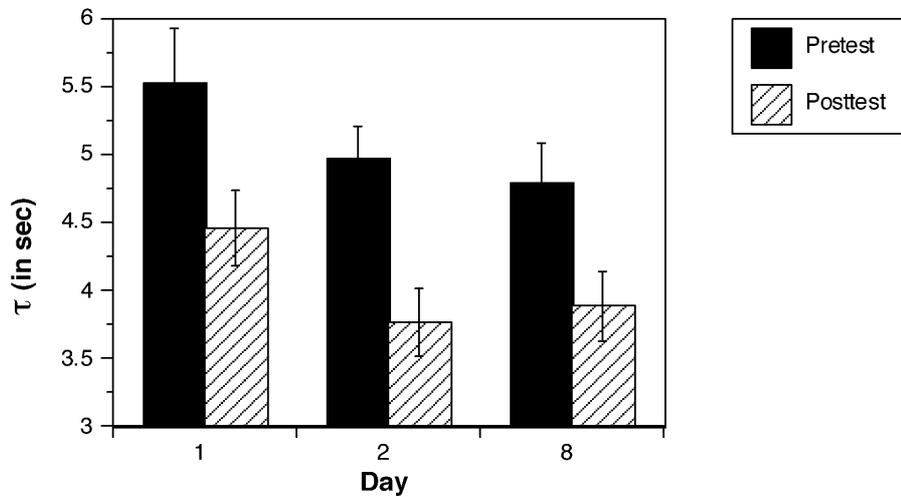


Fig. 4. Mean time constants (τ) for first-order exponential curve fits to the decaying SPV eye responses measured during Pretest and Posttest by Day (averaged over seven subjects for all repetitions). Error bars indicate SEM.

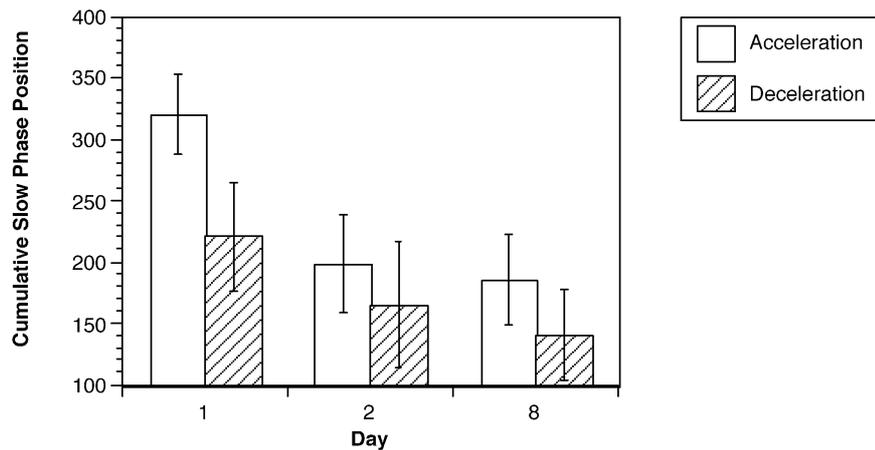


Fig. 5. Averaged cumulative slow phase vertical position measured while the head was stationary in the RED position during Phases 3 and 9 (acceleration and deceleration of the rotator) by Day (averaged over seven subjects). Error bars indicate SEM.

act $p = 0.001$]. The most common motion-sickness symptoms were pallor, drowsiness and nausea.

The recovery time (time taken by a subject to return to a motion-sickness score of 0 following rotation) was extracted or linearly extrapolated from the post-experiment motion-sickness score reports. The median recovery times dropped from about six to two hours or less following the first test day. Of the eight subjects tested, two did not report any post-experimental motion-sickness symptoms, and one subject did not

provide a value for Day 8. They were not included in the analysis. A second Page test showed (Fig. 7) a significant decreasing trend by Day in the time taken to return to a score of 0 [exact $p = 0.009$].

Peak motion-sickness scores recorded during the experiment did show a decreasing trend with Day. However, the results were not significant due to three cases where peak motion sickness increased between Days 1 and 2, and three cases where the same motion sickness score was reported (2 cases between Days 2 and 3 and 1 case between Days 1 and 2). The reports given during rotation maybe less reliable due to subjects having less time to decide on a score. The Pensacola scores taken at the end of the experiment were more thorough

ues $A(i)$ when weighted by their position i in the sequence—i.e., the average of the quantity $i R(i)$ —against its mean value for random sequences (for details see [7, p. 380]).

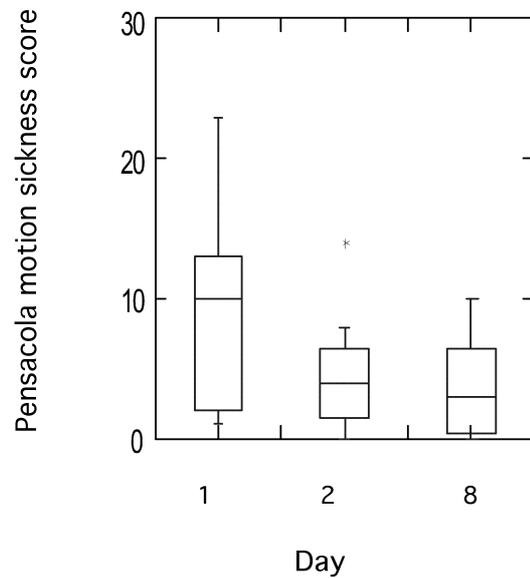


Fig. 6. Box plot of the Pensacola motion-sickness scores by Day (averaged over eight subjects). In the box plots used throughout the paper, the solid line marks the median of the sample. The height of each box shows the range within which the central 50% of the values fall, with the box edges at the first and third quartiles. The whiskers (extended vertical lines) indicate an interval that would include 95% of the distribution if the data were normally distributed. The asterisk represents an outlier.

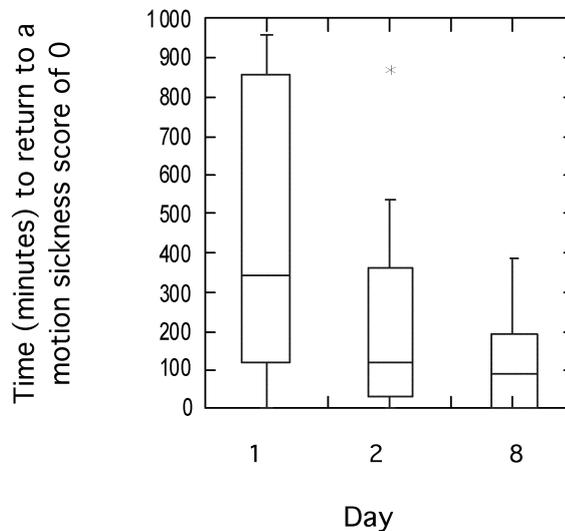


Fig. 7. Time (in minutes) to return to a motion-sickness score of zero by Day (averaged over eight subjects).

and were established together by the experimenter and subject.

3.4. Illusory tilt

All subjects reported illusory tilt sensations, mostly in the body's pitch plane, during head movements. Five subjects reported small-angle pitch, one subject experi-

enced a tumbling pitch sensation of several revolutions, and another experienced damped pitching oscillations. This is consistent with findings by Bockisch, Straumann, and Haslwanter [3] who found that tilt sensations are driven by the canal signal with little or no otolith involvement. The subject who experienced a tumbling sensation reported the number of revolutions which was converted into degrees by the experimenter. The sub-

ject who experienced damped pitching oscillations reported the number of degrees from the equilibrium position (the oscillations were symmetric). One of the eight subjects in the present experiment was unable to quantify the pitch sensation and was omitted from the analysis. In order to account for the large individual differences when reporting the illusory tilt, the data was standardized for each subject to a mean of 1.0 and a standard deviation of 0.3. Figure 8 shows that illusory tilt decreased with repeated stimulation. This is supported by a Page test revealing a significant decreasing trend in Posttest pitch over Day for all head turns (RED to NU [exact $p = 0.008$] and NU to RED [exact $p = 0.008$]). A main effect for Phase was found [$F(1, 6) = 11.89$, $p < 0.014$], reflecting a significant decrease in pitch sensation from Pretest to Posttest. A main effect for Day was also found [$F(2, 12) = 5.91$, $p < 0.016$]. The pitch sensation decreased significantly between Day 1 and 2 [$F(1, 6) = 33.87$, $p < 0.001$]. The decrease was largely maintained for six days; the comparison between pitch reported on Day 1 and 8 gave a marginally significant result [$F(1, 6) = 5.92$, $p < 0.051$]. No interactions were significant. This marginally significant result suggests that retention was less complete for pitch perception than for the other measures.

4. Discussion

4.1. Adaptation

We have obtained clear evidence for adaptation of the vestibulo-ocular reflex in response to repeated head movements about an axis normal to the platform rotation axis. The practical significance of this adaptation, regardless of its mechanism, lies in the demonstration of the possible use of high speed short-radius artificial gravity without long-term consequences of disturbed VOR or sustained motion sickness. We have also demonstrated that this vestibular adaptation to high-speed rotation is mirrored in the adaptation of sensory experience as well as in motion-sickness ratings. Finally, there was an apparent dissociation between the adaptation of the VOR and the illusory sensations. The implications of our data for the presumed cue that triggers a change of adaptive state are discussed in the following sections.

The vestibular adaptation to the unusually strong Coriolis stimulus represents one more example of the ability of the nervous system to use retinal slip as a means of correcting the gain, phase or axis of the VOR.

This is consistent with reports by Guedry [13] who found light necessary for adaptation to Coriolis stimuli (see also [4]).

The vertical compensatory VOR, which was inappropriate for stabilization of the platform-fixed visual field, was reduced with practice not only within a session, but was also retained over days. The subjects did not exhibit notable inappropriate vertical nystagmus following rotation. In this sense the adaptation had no aftereffects. Of course we cannot yet determine whether this finding is because the subject “knew” that the platform was stationary and that no vertical compensation was required, or because there was no stimulus to the vertical canals and therefore no compensation was called for. One might suppose that the adaptation attained during rotation was specific to that rotating context and therefore not brought about when the subject knew or felt that he or she was stationary. On the other hand, the vertical canals were not stimulated during the yaw head movements made while the platform was stationary and therefore, the absence of vertical nystagmus may simply result from the absence of vertical canal stimulation.

The elevated NSPV value for Repetition 1 compared to the average of Repetition 2 and 3 suggests that the sensory conflict resulting from the first head movement conducted within the rotating environment provided feedback necessary for the transition to the appropriate gravito-inertial internal program. This explanation would favor a *stimulus dependent* adaptation, rather than a general *context-dependent* explanation. On the other hand, the unexpected response to the first head movement could simply have provided a heightened arousal level which in turn may have induced an augmented VOR. Therefore, an additional general linear model ANOVA was run on dependent variable NSPV Repetition 1 trials, with independent variables Day, Phase, and Direction of Head Motion. No significant main effects of Day, Phase, or Direction of Head Motion were found for Repetition 1 trials taken alone. This finding supports the *stimulus-dependent* adaptation interpretation.

Thus, subject to the caveat that the adaptation we observed may not be context-specific, we pose two further questions concerning the nature of the cue for switching between states of adaptation. First, we can ask about the *generality of the adaptation*, that is whether the observed reduction in inappropriate vertical eye movements (both within and across Day) was accomplished by a generalized VOR suppression or whether it was specific to the cross-coupling associated with yaw

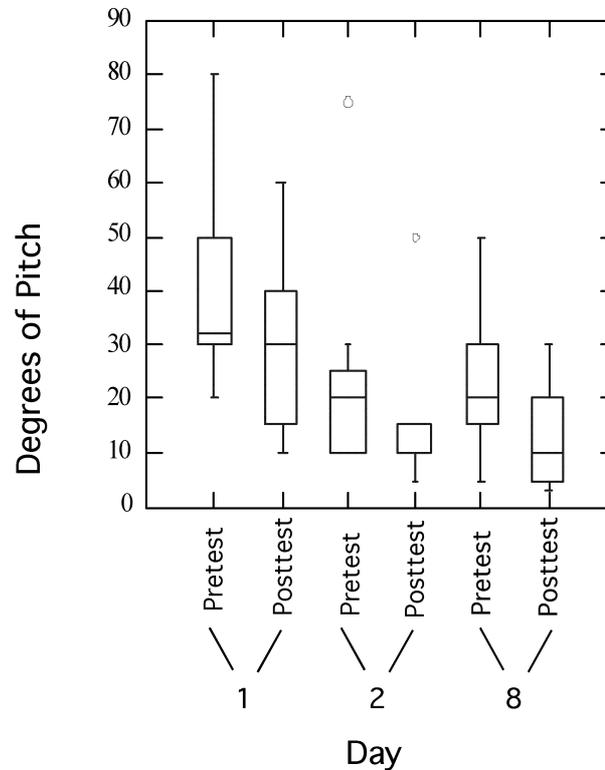


Fig. 8. Reported pitch experienced during Pretest and Posttest after turning the head from RED to NU (averaged over six subjects, one subject who experienced a tumbling sensation has been omitted from the plot for scaling purposes).

head movements during rotation, maybe as a special case of the goal directed VOR modulation introduced by Melvill Jones and Gonshor [18] and elucidated and modeled by many others (for a review of the early work see [15]). Cumulative slow phase velocity components during rotator acceleration (with stationary RED head) were reduced over Day and suggest that, at least in part, a generalized VOR suppression was the case. If the adaptation had been entirely contingent on the type of head movement, then the non-Coriolis vertical VOR elicited by the pitch axis activation during the acceleration of the rotator in the beginning and its deceleration at the end of the experiment (Phase 3 and Phase 9) should be unaffected. This was not the case. Even the non-Coriolis vertical VOR decreased significantly across Day, as measured by the vertical cumulative slow phase position (integral of the slow phase velocity in Phases 3 and 9). Figure 5 shows that the greatest decrease in cumulative slow phase position was achieved between Day 1 Phase 3 (acceleration) and Day 8 Phase 3; the cumulative slow phase position (averaged over seven subjects) decreased to nearly one-third its initial value. Moreover, if suppression were generalized, hor-

izontal VOR should also be affected. This was clearly not the case. Thus, some general suppression seems to be effective side-by-side with head-turn contingent specific adaptation.

The second question relates to the trigger cue that might be used to prepare the subject for the conflicting vestibular signal and activate the suppression mechanism. The platform apparatus itself is not the trigger cue. Subjects did not show any aftereffects while still on the rotator after it had come to a stop. However, a large number of other cues are trigger candidates. They could be external, such as the perceived onset of rotation, the noise of the motor, or the slight vibrations of the rotator. They could also be internal if the experience of a sensory conflict itself serves as trigger. This sensory conflict, in turn, could be of several types. In the current experiment it could be a conflict between the semicircular canal that signals pitch and the visual information that indicates a subject-fixed visual field. Or, it could be between the canal rotation signals and the otolith organs, which failed to confirm any pitch during yaw head movements. Finally, it could be between the canal signals and the internal model that in-

corporates the knowledge that the subject remains lying on a horizontal platform.

The absence of a significant main effect of Day or Phase (5 and 8) on the NSPV Repetition 1 trials taken alone indicates that the subjects potentially required the feedback provided by the first head movement (Repetition 1) to either 1) switch internal programs in order to suppress the non-compensatory vertical eye movements or 2) reroute to an appropriate program. The first head movement conducted in the rotating environment might therefore serve as the cue to activate the suppression mechanism.

One note of caution concerning the comparison of the vertical VOR during Phase 3 (up-beating nystagmus) and Phase 9 (down-beating nystagmus) is important. Typically, stronger upward vertical nystagmus than downward vertical nystagmus in humans has been reported [2]. Throughout the acceleration and deceleration phases, respectively, the subjects were lying supine and remained in the RED position. Clockwise rotation during acceleration produced a compensatory vertical nystagmus with the fast phase in the pitch upward direction (up-beating) while deceleration resulted in down-beating vertical nystagmus. Thus, a decline of the vertical slow phases of the nystagmus between acceleration and deceleration of the rotator could be attributed to habituation or to an up-down asymmetry. However, such an effect was not found. The decrease of this measure over the three testing days is a clear indication that adaptation was, at least partially, generalized VOR suppression. A caveat might be added in that our subjects were younger than the astronaut population, making a replication with an older sample desirable.

4.2. *Are inappropriate eye movements, motion sickness, and illusory tilt congruent measures for adaptation?*

Although we found significant adaptation of all measures, adaptation was not complete. It is entirely possible and desirable from the point of view of artificial gravity as a countermeasure that adaptation should continue with additional duration or intensity of the exposure. The six-day interval between the second and the third day of testing makes it hard to predict such further adaptation. Interestingly, motion sickness was the only measure that continued to decrease on Day 8 despite this interval. This suggests that complete suppression of motion sickness might be attainable and that there is no one-to-one mapping between the measures. Al-

though most subjects showed a continuous decrease in post motion-sickness measures with exposure, there were a few subjects who showed an increase in motion sickness by Day. One subject showed an increase in the Pensacola motion-sickness score from 4 to 7 from Day 2 to 3, one subject showed an increase from 0 to 2 from Day 2 to 3 and one subject showed an increase from 2 to 4 from Day 1 to 2. Likewise, two subjects showed an increase in recovery time from Day 2 to 3. In one subject, the time increase from 60 to 180 minutes and the other subject showed an increase from 90 to 210 minutes. No reasons were identified as to why these subjects did not show continuous adaptation (their values were not the highest of all subjects). The subjects who showed an increase in recovery time between Day 2 and 3 did not show an increase in Pensacola scores between Day 2 and 3.

In particular, it suggests that retinal slip associated with inadequate compensatory eye movements is not primarily responsible for the development of motion sickness. The lower level mechanism of VOR may be more resistant to adaptation than the higher level processes that are involved in the perception of illusory tilt and motion sickness. If the fundamental purpose of vestibular adaptation to artificial gravity is to prevent astronauts from experiencing motion sickness after transitioning to and from the rotating environment, it may not be necessary to expunge inappropriate non-compensatory vertical nystagmus and subjective pitch altogether. It might suffice to reduce them to tolerable levels as long as the inappropriate responses are not accompanied by motion sickness.

It seems obvious that our measures for adaptation (VOR, illusory tilt and motion sickness) are strongly related but at the same time are not equivalent. From a practical point of view, all three are relevant. Motion sickness and illusory tilt are unpleasant at all times, while VOR is not experienced in the dark but it reduces visual tracking ability and acuity in the light. Thus, head movements during centrifugation, which are necessary especially when continuously rotating, require that the astronauts adapt such that all three measures stay within tolerable ranges. The present study has demonstrated that such adaptation is in principle possible at rotation rates much higher than previously reported. However, it may take many training sessions to achieve adaptation that is adequate for a short-radius centrifuge used for space travel.

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