Vestibular adaptation to centrifugation does not transfer across planes of head rotation

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Abstract. Out-of-plane head movements performed during fast rotation produce non-compensatory nystagmus, sensations of illusory motion, and often motion sickness. Adaptation to this cross-coupled Coriolis stimulus has previously been demonstrated for head turns made in the yaw (transverse) plane of motion, during supine head-on-axis rotation. An open question, however, is if adaptation to head movements in one plane of motion transfers to head movements performed in a new, unpracticed plane of motion. Evidence of transfer would imply the brain builds up a generalized model of the vestibular sensory-motor system, instead of learning a variety of individual input/output relations separately. To investigate, over two days 9 subjects performed pitch head turns (sagittal plane) while rotating, before and after a series of yaw head turns while rotating. A Control Group of 10 subjects performed only the pitch movements. The vestibulo-ocular reflex (VOR) and sensations of illusory motion were recorded in the dark for all movements. Upon comparing the two groups we failed to find any evidence of transfer from the yaw plane to the pitch plane, suggesting that adaptation to cross-coupled stimuli is specific to the particular plane of head movement. The findings have applications for the use of centrifugation as a possible countermeasure for long duration spaceflight. Adapting astronauts to unconstrained head movements while rotating will likely require exposure to head movements in all planes and directions.

Keywords: Coriolis effects, artificial gravity, dual adaptation, orientation illusions, motion sickness, sensory conflict, vestibulo-ocular reflex

1. Introduction

Artificial gravity produced by short radius centrifugation or by a rotating spacecraft may be required to maintain physical health in microgravity [32]. Unfortunately, for small radii of rotation, high rotation rates are required to produce an equivalent of Earth gravity, which in turn produces a strong Coriolis cross-coupled [1] (CCC) vestibular stimulus when head movements are made outside the plane of rotation. CCC stimulation causes unpleasant sensations of tumbling, non-compensatory nystagmus, heart rate changes, and mo-

tion sickness. If astronauts are to make unconstrained head movements in a rotating environment, they must adapt to these stimuli, preferably before embarking on a mission. One plausible adaptation protocol is to have astronauts adapt to a series of head movements confined to a single plane, with the expectation that adaptation will transfer to other planes of head motion as well. It has been established that humans will adapt to CCC stimulation when making head movements in one plane, as indicated by reductions in illusory motion and motion sickness. In this study we test if this adaptation transfers to another plane of motion.

Several studies with the MIT 2-meter radius centrifuge have shown adaptation to plane-limited head movements during 23 revolution per minute (rpm) head-on-axis rotation [4,15,33,35]. Supine subjects performing yaw (transverse plane) head turns in the

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[1]We use this term following Peters [24].

light have shown significant decreases in the amplitude of the slow phase velocity (SPV) of the non-compensatory vertical vestibular ocular reflex (VOR), the time constant for decay of SPV, sensations of illusory motion, and motion sickness [33]. Changing the visual surround from dark to light results in a decrease in VOR amplitude only in the lighted condition, while the time constant and motion sickness scores are the same for both lighted and dark conditions [4]. These results verify that retinal slip is required to adapt VOR amplitude but not the time constant [11]. Other studies by Adenot et al. [1] have shown that the strength and robustness of adaptation is dependent on the magnitude of the CCC stimulus, i.e. the head angle displacement during habituation.

To date there have been a limited number of studies on transfer of adaptation from one rotational vestibular stimulus to another. Several experiments have focused on stimulating the same pairs of co-planar semicircular canals. For instance, Guedry used a slow rotating room (7.5 rpm) to test the transfer of adaptation to roll (coronal plane) head movements made in one quadrant to roll head movements in the opposite quadrant of the same plane [11,13]. While nystagmus amplitude and subjective illusory ratings declined after habituation in the practiced quadrant, there was little transfer of habituation to the unpracticed quadrant. In the same experiment, the nystagmus of habituated subjects was measured during head-static acceleration and deceleration of the rotating room, but no transfer of the CCC adaptation was observed. Hecht et al. [15] on the other hand, found transfer of adaptation when the direction of the centrifuge was reversed covertly for subjects who had been adapted to yaw head movements while rotating at 23 rpm. These two experiments may suggest that motions involving changes in the direction of gravity relative to the head show no signs of transfer, while those using similar otolith signals do so more readily.

Other studies have assessed the transfer between different environments. Hecht et al. [15] adapted subjects to yaw head movements on the MIT centrifuge, and then relocated them to a slow rotating room at Brandeis University with the same centrifugation rate and subject body position. The adaptation transferred across environments, implying that contextual cues play an insignificant role for the sensory system to identify an adaptive state. In another study, military pilots that were highly susceptible to motion sickness were adapted to tens of thousands of pitch and roll head movements over several months in a rotating room, with rotation rates from 0.25–17 rpm [5]. Each pilot, who had

previously been grounded because of motion sickness, was subsequently able to complete flight training without such symptoms. While this study demonstrates transfer between environments, it does not imply transfer across planes of motion, since the pilots performed turns in all planes.

None of the above studies directly addressed the transfer of adaptation across different semicircular canal planes. Graybiel et al. [10] found that subjects who had habituated in a supine or standing position during rotation in a slow rotating room retained habituation when their posture was changed, as measured by motion sickness, fluid balance, blood levels of catecholamines, corticoids, and cognitive effects. The implications of this study are difficult to assess for our purposes, because no eye movement data were collected, subjects performed head movements in all directions, and only four subjects were studied.

A variety of experiments have assessed the plasticity of adaptation during visual training of the VOR response. Schultheiss and Robinson oscillated upright cats in their pitch plane while exposing them to a visual stimulus rotating in an orthogonal Earth-horizontal plane [14,25]. The cats' VOR responses developed horizontal as well as vertical components that were stable in the dark after training. Similar cat experiments showed that identical rotational semi-circular canal stimulation paired with a right-ear-down or left-ear-down gravity vector yielded two different sets of mixed-axis VOR adaptation, implying that otolith signals are capable of mediating the adaptive state [2, 3]. Dependence of VOR plasticity on otolith stimulation has also been noted in humans and monkeys [9, 23,26], and separate gravity-dependent and gravity-independent components of adaptation have been identified [29–31]. The mixed gravity dependence probably helps stabilize retinal images [31]. All of these experiments demonstrate that VOR adaptation is plastic, i.e. VOR can be trained to correct visual slip in mixed-plane rotating environments. However, these experiments do not show that learning to produce one type of novel VOR response makes the VOR more capable of learning similar responses. That is, transfer or generalization of adaptation from one plane of motion to another has not yet been demonstrated.

In other contexts, evidence for generalization of adaptation is mixed. Work by Welch et al., found generalization for visual motor tasks during prism wear [27], and our own measurements on the MIT centrifuge point to generalization of VOR adaptation. The VOR SPV measured during the ramp-up and ramp-down phases of

centrifugation decreased over consecutive days in subjects that who made additional yaw head turns at constant angular velocity, but not in a Control Group that performed none [35]. The Experimental Group's yaw turns in this study stimulated the yaw and roll planes, whereas ramp-up and ramp-down in the Control Group affected only the pitch plane (the head position was right-ear-down during ramp-up and ramp-down). Other studies have found no evidence of generalization [19, 20,28], including one study on cats [6], suggesting that visual and VOR adaptation is rather stimulus specific. Notably, these experiments differ from our experiment in that they used visual training tasks, and with the exception of the MIT study, involved no CCC stimuli.

Can the brain build up a generalized model of CCC stimulation, and how do gravity cues contribute to generalization of adaptation? Kaufman et al. [18] suggest that the brain is unlikely to build a general response model to changing CCC inputs, and that a global numbing or habituation of the VOR response to different CCC stimuli may be the only adaptive mechanism. Practically speaking, if it is not possible to build a generalized model, it is likely that an astronaut will have to spend more time adapting to the spacecraft centrifugation, depending on the amount of numbing that occurs, if any. In space, however, the lack of otolith signals may permit greater generalization to CCC stimuli. On Earth it is impossible to remove the changing otolith component during CCC stimulation, but this is not a limitation since a test for generalization in this context is required to understand CCC adaptation. Specifically, we examine how habituation and adaptation[2] to yaw head-turns (transverse plane) influences adaptation to pitch turns (sagittal plane), during supine head-on-axis rotation about the Earth-vertical at 23 rpm, Fig. 1.

If adaptation is canal-specific, adaptation to extended CCC stimulation produced by yaw head-turns should not transfer to pitch head-turns. That is, the horizontal nystagmus that is caused by pitch head-turns should be equally strong in a control group that performs only pitch turns, as in an experimental group that makes both yaw and pitch head-turns. However, if the adaptation transfers across planes, then practicing yaw head-turns should in fact reduce the horizontal time constant of subsequent pitch head-turns.

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[2]We define habituation as a desensitization of the VOR response to stimulation during the course of one day, and adaptation as desensitization observed over two days.
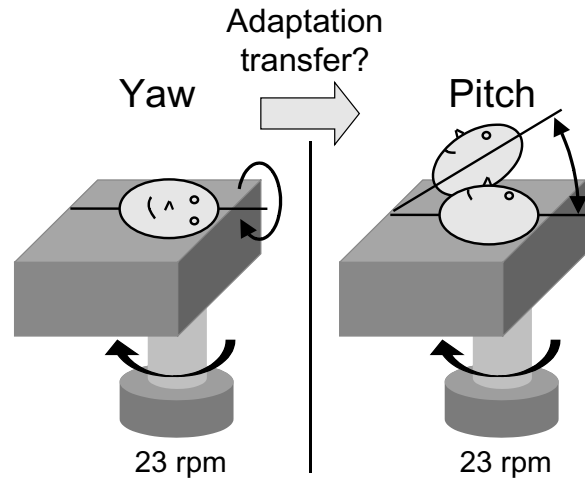

Fig. 1. Illustration of the yaw and pitch head turns that constitute Coriolis cross-coupled stimulation during supine clockwise rotation at 23 rpm.

2. Materials and methods

2.1. Subjects

Informed consent was obtained from 46 subjects free from vestibular problems, heart problems, eye problems, and low blood pressure. Subjects refrained from drug, alcohol, and caffeine use in the 24 hours preceding the experiment. In the Control Group, 3 females and 7 males, ages 19–41, finished the experiment out of 20 subjects who were recruited and started the experiment. In the Experimental Group 6 females and 4 males, ages 18–29, finished out of 24 subjects, which corresponds to a total dropout rate of 57% because of motion sickness. Subjects were assigned to the two groups randomly. One male subject in the Experimental Group was eliminated from analysis due to outlying values. The experiment was approved by MIT's Committee on the Use of Humans as Experimental Subjects.

2.2. Equipment

The centrifuge is a 2 m radius rotating bed that positions a supine subject's head on the axis of rotation (Fig. 1). A clockwise rotation rate of 23 rpm (138°/s) provided a 1.67 m subject with a 1-g load at the feet. An adjustable footplate was used for subjects of different heights so that the actual g-load experienced at the feet varied slightly. During the lights-on portions of the experiment, a stable non-rotating visual surround was presented to the subject. Binocular ISCAN goggles with infrared light sources and miniature off-axis

video cameras record calibrated eye movements in the dark at 60 Hz. A blindfold was worn over the goggles to block out any stray light during the dark portions of the experiment. Yaw head turns were performed freely since it was found that with sufficient training and practice before the experiment, consistent movements were performed [4]. The angle of the pitch head turns was constrained with a head restraint bar positioned above the subject. Subjects wore an aviator cap with a metal rod that made contact with the bar when they reached the maximum angle. A video camera with night vision capabilities is was utilized to ensure compliance with the experiment protocol and to monitor subject well-being.

2.3. Experimental design

Subjects performed all head turns while rotating supine at 23 rpm. One head-turn is defined as a movement of the head in one direction, e.g. for yaw-turns from nose-up (NU) to right-ear-down (RED) and for pitch-turns from NU to nose-forward (NF). On two consecutive days the Experimental and the Control Group performed two blocks of 6 pitch head turns at the beginning and at the end of the session. Between the pitch turns the Experimental Group performed 24 yaw head turns from RED to NU and back to RED, while the Control performed none and was exposed to centrifugation for the same amount of time, Fig. 2. The data collected during the pitch head turns should reveal signs of habituation (within a session, factor phase), as well as signs of adaptation (between the two days, factor day). Head turn Direction was a third factor (NU to RED, RED to NU, NF to NU, and NU to NF). Of the 24 yaw turns of the Experimental Group, the middle 12 were made in the light to maximize retinal slip. Eye movement recordings and illusory motion scores were collected after every head turn in the dark, yielding measurements for a total of 12 yaw turns in the Experimental Group and 2 × 6 pitch turns in both groups on each of the two days.

The number of yaw turns performed was chosen as a compromise between maximal exposure and minimal dropout rates due to motion sickness. We considered a dropout rate of about 50% as manageable. The number of pitch head turns was chosen as a compromise between the risk of adapting the subject to pitch movements simply because of repetition, which could mask the effects of transfer of adaptation, and the need for statistically adequate sample sizes.

2.4. Procedures

Subjects were instructed to use both hands to support the head while performing the pitch head turn to minimize left-right deviation, and to avoid exercising the neck and stomach muscles. The subjects were instructed to perform the pitch forward (from NU to NF until the restraining bar was reached) in 1 second. Almost all subjects were able to pitch forward over 50 degrees, which was more than enough to elicit a strong VOR response. Prior to rotation, each subject rehearsed the pitch movement by making a series of practice turns from NU to NF. After a consistent pattern was achieved, the subject's pitch head angle while at the stop was measured using a line through the bottom of the subject's neck, ear, and top of the head. Yaw movements were then practiced at the maximum rotation angle that was comfortable to the subject, and performed in 1 second. Again, after a consistent pattern of yaw movements was made, the angle of the subject's head was measured at right ear down using the line through the center of the subjects eyes through the back of their head. All yaw head turns were separated by 45 seconds. Pitch forward head turns were held in the NF position for 30 seconds, and upon pitching back the subject waited for 1 minute before pitching up again. All head turns were commanded by the experimenter.

2.5. Measures

While rotating on the MIT-centrifuge, yaw head turns produce vertical non-compensatory nystagmus (VVOR) as semicircular canals are being moved into or out of the plane of rotation (see [16] for a more complete description). Torsional eye movements also accompany yaw turns, but we are unable to measure them. Similarly, pitch turns elicit non-compensatory horizontal nystagmus (HVOR) and torsional eye movements.

The position data of the eyes were filtered and differentiated, and the SPV component was separated with an asymmetrically trimmed-mean order statistic filter (for details see [35]). The decrease of the SPV over time was modeled as an exponential decay of the form $Ae^{(-t/\tau)}$, where A is the maximum amplitude of the SPV and τ is the time constant. A least squares regression routine was used to find the best fit of the function for SPV over a time interval lasting 5–15 seconds for yaw head turns and 20-30 seconds for pitch head turns. Ideally, this function would be modeled as a double exponential, since the central and peripheral cupula time
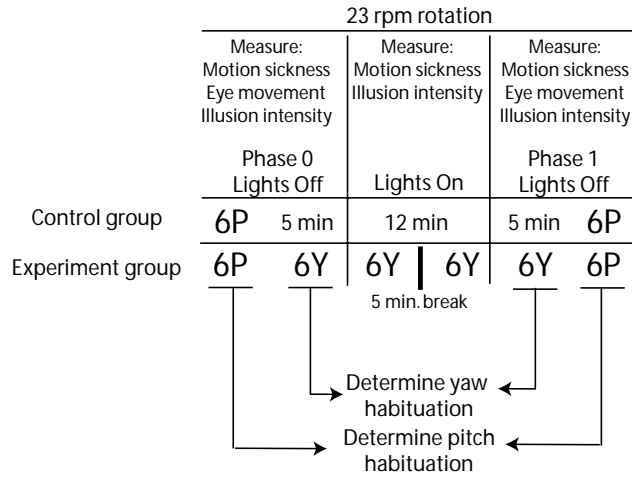
	23 rpm rotation		
	Measure: Motion sickness Eye movement Illusion intensity	Measure: Motion sickness Illusion intensity	Measure: Motion sickness Eye movement Illusion intensity
	Phase 0 Lights Off	Lights On	Phase 1 Lights Off
Control group	6P　　5 min	12 min	5 min　　6P
Experiment group	6P　6Y	6Y ∣ 6Y	6Y　6P

5 min. break

Determine yaw
habituation

Determine pitch
habituation

Fig. 2. Diagram showing the experiment protocol, performed on two consecutive days at 23 rpm. The letters "P" and "Y" indicate blocks of six pitch and yaw head turns. Each head turn represents a head movement in one direction, e.g. nose up to nose forward.

constants contribute to the function [7]. However, we modeled it as a single exponential because evidence of habituation and adaptation is still captured using one exponential.

Normally the gain of VOR eye movement is defined as the ratio of the eye angular velocity to the velocity of the head movement. As described by Adenot et al. [1], an analogous metric was used which defined the equivalent head velocity as the angular velocity component of the rotation rate on the centrifuge. Thus the SPV amplitude A was normalized by ($138°$/sec = 23 rpm) the angle of the head:

NSPV gain = SPV/ ($138°$/sec $\times$ sin(head turn angle)).

An example of pitch turn horizontal VOR NSPV gain data is shown in Fig. 3.

A motion sickness rating (MS) was solicited from the subject at least every minute for the Control Group, and after every head turn for the Experimental Group. Subjects were prompted to report their motion sickness on a scale between 0–20, with 0 being normal, and 20 being about to vomit [4].

During and after each head turn, subjects experienced a tumbling sensation of motion in space. The intensity of this illusory motion for all head turns was reported on a linear scale. The scale was anchored by assigning a value of 10 to the very first pitch head turn of the two-day experiment (e.g. Fig. 7).

3. Results

We performed our statistical analyses on the variables τ, NSPV, MS, and intensity of the tumbling sen-

sations, for both yaw and pitch turns (refer to Fig. 2 for a summary showing when they were collected). All graphs plot mean values with error bars indicating standard errors of the mean, unless otherwise noted.

3.1. Motion sickness

For the Experimental Group, MS generally increased within a day, but declined between the two days. Three subjects suddenly came close to vomiting in the middle of practicing the second set of pitch turns on the first day and dropped out of the experiment. The average of the maximum MS scores per subject achieved within blocks of six head turns (including yaw turns in the light and dark) are plotted for both days in Fig. 4. The Control Group performed only 2 blocks of pitch head turns per day and their values are substantially lower. Generally, it is clear that average MS rose with successive head turns, and did not plateau. For the Experimental Group maximum MS in each phase tended to be lower on the second Day compared with the first, indicating that adaptation had taken place to some extent, but the result was not statistically significant.

3.2. Yaw head turns (*Experimental Group only*)

Individual subjects performed yaw turns that ranged from 65-85 degrees. The yaw τ values of the VVOR were approximately normally distributed with a mean of 4.7 seconds (not shown), comparable to results obtained by Young et al. [35] and Brown et al. [4]. The mean τ-values for each yaw head turn are presented in Fig. 5, which plots the values of τ for all 24 yaw
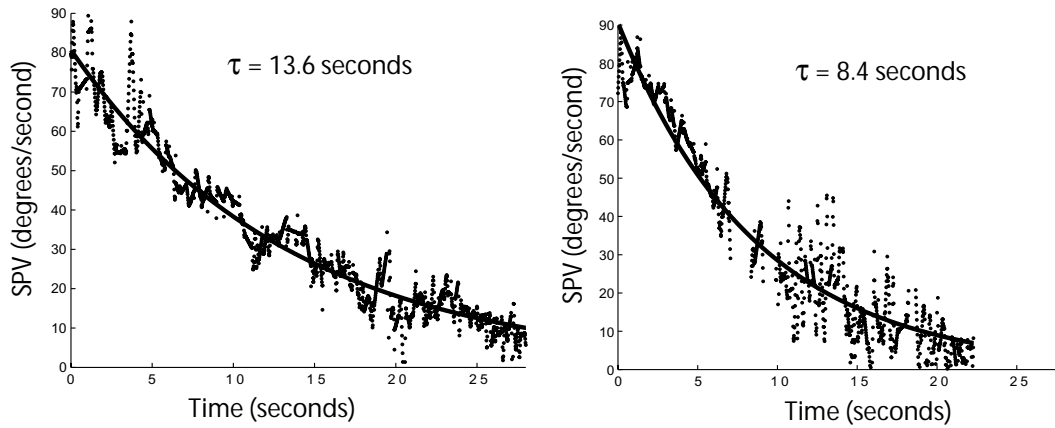
Fig. 3. Example plots of SPV VOR data (unnormalized) for a pitch head turn before (left panel) and after (right panel) the Experimental yaw head turns. The steeper decay on the right is indicative of habituation.
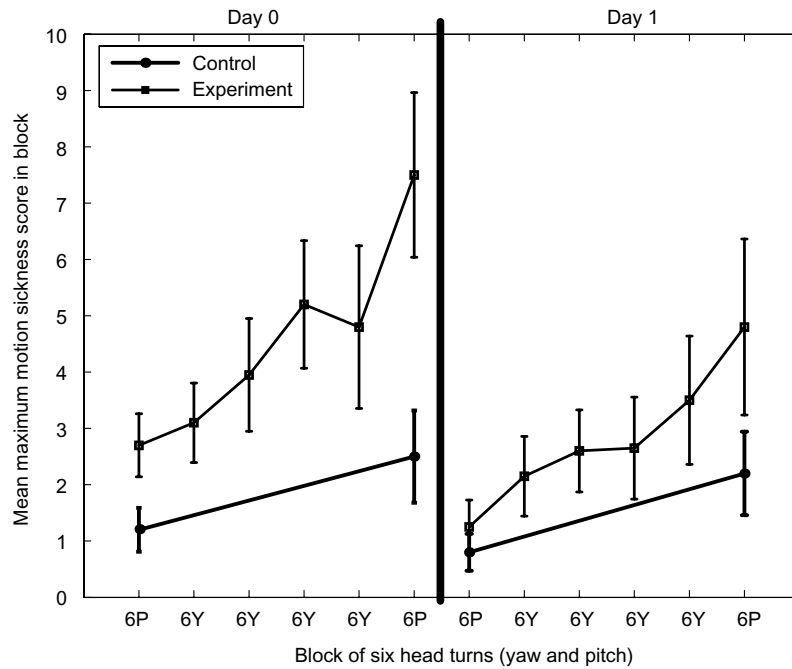

Fig. 4. Mean maximum motion sickness scores achieved in each six-turn block, including yaw turns in light and dark, and pitch turns in the dark, for both Groups. Note that the Control Group performed no yaw head turns.

head turns over day and Phase. A General Linear Model (GLM) univariate repeated measures ANOVA was conducted and the variable τ was transformed to $\log(\tau)$ to meet the ANOVA requirement for uniformity of variances. $\log(\tau)$ decreased significantly both by day ($F(1,7) = 10.04$, $p = 0.016$) and by phase ($F(1,7) = 12.25$, $p = 0.01$). Despite the large variability between subjects, these main effects suggest that both adaptation and habituation of VOR have occurred.

Vertical NSPV gain data were also approximately

normally distributed. Figure 6 shows the course of NSPV gain over the 24 head turns. A GLM ANOVA conducted on log(NSPV) showed significant habituation between phases ($F(1,7) = 84.29$, $p < 0.0005$). There was no significant main effect for day, in agreement with the findings of Brown et al. [4]. The mean NSPV gain values for each turn-direction were not significantly different; for NU to RED NSPV $= 0.3$ ($S_e = 0.013$) and for RED to NU NSPV $= 0.34$ ($S_e = 0.018$). The absolute magnitudes between 0.3 and 0.34 agree
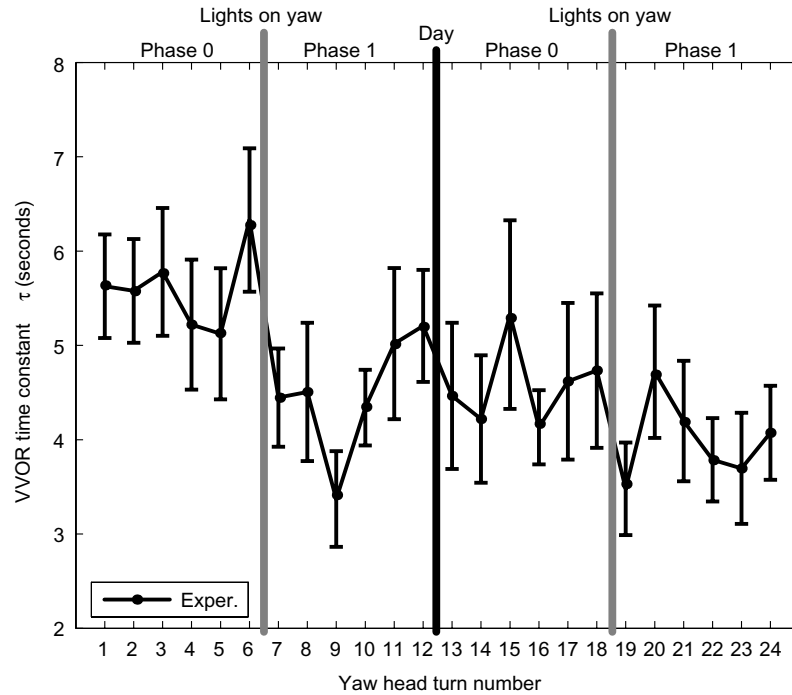
Fig. 5. Mean yaw head turn VVOR time constants (Experimental Group only) measured in darkness. Day 0 and Day 1 are separated by the black vertical line. The gray vertical line indicates where yaw head turns were made in the light.

with the results of Newby [22].

A paired t-test was performed on the subjective scores of illusion intensity because the scores and the logarithm of the scores failed the ANOVA requirement for uniformity of variances. The scores of illusion intensity declined significantly over days (paired t-test, $t(8) = 3.35, p = 0.01$) and nearly so for phases (paired t-test, $t(8) = 2.21, p = 0.059$), as illustrated in Fig. 7. The distinct sawtooth pattern also shows that turns from NU to RED produced less pronounced tumbling sensations than turns to NU (paired t-test, $t(8) = -4.26$, $p = 0.003$). This result agrees with past research [21]. The mean values for the different directions are about 3 rating points apart: NU to RED = 6.9 ($S_e = 0.35$), and RED to NU = 9.9 ($S_e = 0.38$), compared to about a 1.5 point difference observed by [22]. The difference between tumbling sensations on RED and NU turns seems to diminish in the last phase, which was not significant. In sum, the parameters associated with yaw-head turns did habituate and adapt, meeting the necessary condition for any possible transfer to the pitch plan.

3.3. Pitch turns (Experimental and Control Groups)

The complete decay times of the HVOR SPV ranged from about 25–35 seconds, which is consistent with

decay times reported elsewhere [17,34]. The length of the decay was considerably longer for HVOR from pitch head turns than for VVOR from yaw head turns, which is consistent with subjective reports of illusory motion and motion sickness ratings. The HVOR τ values were approximately normally distributed with a mean of 9.0 seconds ($S_e = 0.16$ sec). Reduction of the HVOR time-constant over days can be seen in Fig. 8. Recall that between turns 6 and 7, and between 18 and 19, the Experimental Group performed the entire set of 24 yaw movements. A GLM ANOVA test for signficance was performed using $\log(\tau)$. The values of $\log(\tau)$ were reduced significantly over Day ($F(1,16) = 11.34$, $p = 0.004$) and Phase ($F(1,16) = 57.72$, $p < 0.001$).

Most importantly, no significant main effect in τ was found between Experimental and Control Groups. It may seem from Fig. 8 that the final 6 turns of the Experimental Group dip slightly below the Control Group. However, the difference between the two Groups falls well within the mean standard error of the differences. Additionally, the Experimental Group fluctuates slightly above and below the Control Group line when individual subjects are systematically excluded.

The average HVOR NSPV gain values over all 24 pitch head turns is shown in Fig. 9. The distribution of
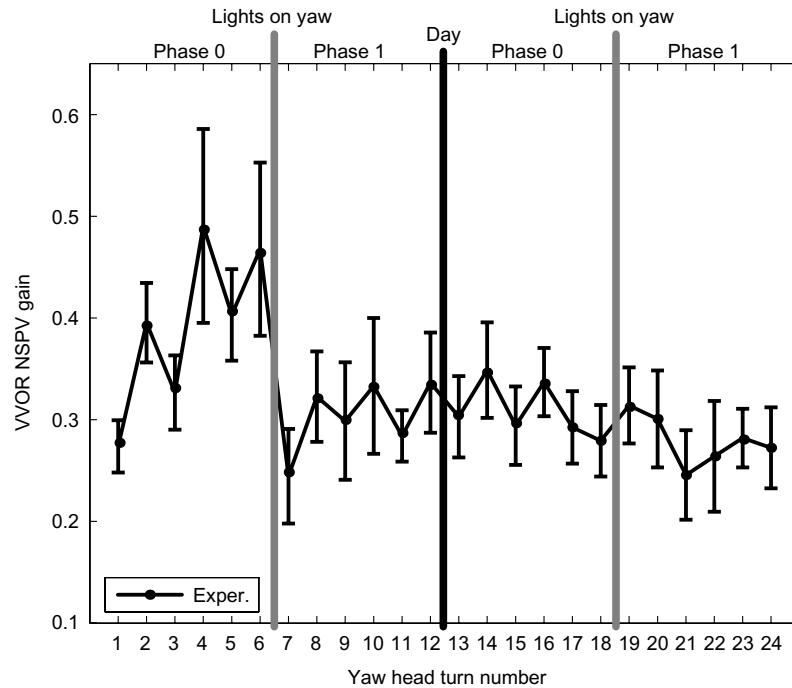
Fig. 6. Mean yaw head turn NSPV gain values (Experimental Group only) measured in darkness. Day 0 and Day 1 are separated by the black vertical line. The gray vertical line indicates where yaw head turns were made in the light.

the Experimental Groups NSPV gain values is not normal (it is skewed strongly to the right), but that of the Control is approximately normal. The skewing can also be seen in the generally higher NSPV gain values for each turn. While the Experimental Group appears to have higher NSPV gain values, and greater variability, there is no clear increasing or decreasing trend over the experiment (presumably because the pitch head turns were conducted in darkness and afforded no opportunity for incorrect horizontal retinal slip to occur [4,11]). The Control Group's NSPV data are remarkably flat, but also less variable from one head turn to the next. There were no significant main or cross effects of day or phase found within either the Control or Experimental Groups. A significant effect of Direction between the Control Group and Experimental Group NSPV gain ($F(1,16) = 9.19$, $p = 0.008$) is clear from the up and down-shifts in Fig. 9. However, this effect is apparent even before the yaw turns begin for the Experimental Group, suggesting that the effect is inherent to the Group itself, and not an effect of the yaw head turns.

The general decrease in the magnitude of tumbling sensations experienced by subjects in both Groups was approximately equal for pitch turns, Fig. 10. The decrease in illusory sensations over Day was significant (paired t-test, $t(18) = 4.00$, $p = 0.001$), but no cross-

Group effects were observed. The Experimental Group appears to generally report slightly lower scores during Phase 0 (the first six measurements of each Day). However, the sensation of illusory motion after the yaw movements (Phase 1) are similar to those during Phase 0 (no effect of Phase was found). Combining both Experimental and Control Groups, the mean score for tumbling sensations from turns from NU to NF is 9.4 ($S_e = 0.21$), and from NF to NU it is 9.2 ($S_e = 0.25$). This lack of NF-NU direction difference contrasts strongly with the difference observed for yaw movements (Fig. 7).

4. Discussion

4.1. Adaptation and habituation

Consistent with other studies (e.g. [35]), for yaw head turns we observed declines in the VVOR τ over days and phases, illusory sensations over days, and NSPV gain over phases. These declines indicate that habituation and adaptation had taken place in the yaw plane and the condition for adaptation transfer was met. In addition, for pitch head turns we observed declines in HVOR τ over days and phases, and declines in sub-
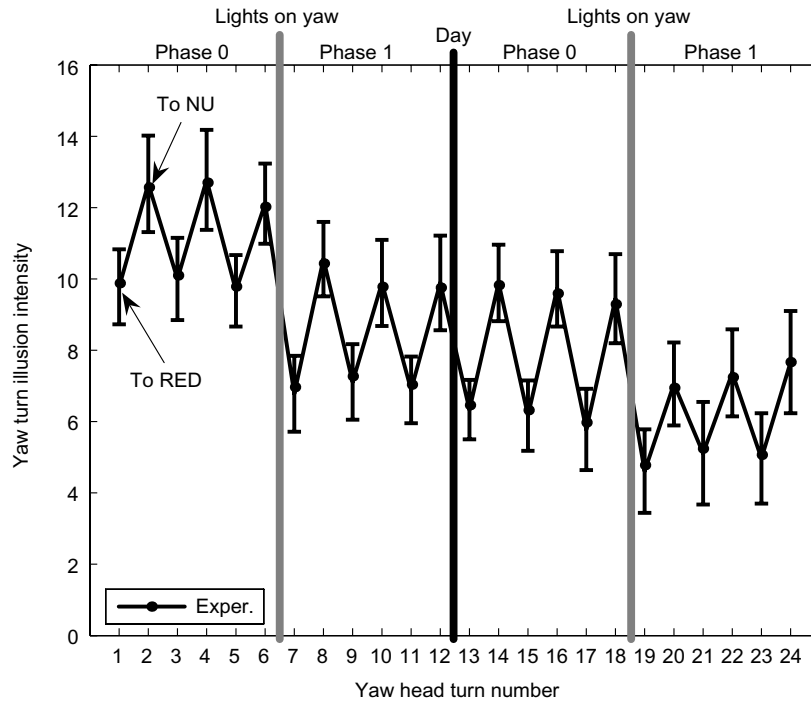
Fig. 7. Mean illusory motion ratings for yaw head turns (Experimental Group only) measured in darkness. The first pitch head turn on Day 0 was anchored to be 10. The gray vertical line indicates where yaw head turns were made in the light.

jective illusory motion scores over days. Evidence of adaptation was thus clearly seen in both groups. However, since the Control Group and Experimental Group showed no significant differences in the temporal evolution of τ, HVOR, or illusory motion, we can conclude that there was no transfer of yaw adaptation to adaptation for pitch movements in these metrics. On the timescale this experiment was conducted, it does not matter if the subject performs pitch turns and yaw turns together or separately.

The three measures, MS, VOR, and illusory motion, differ in their sensitivity to vestibular adaptation. MS is crudest and aggregates over time. The Experimental Group's MS scores appeared to benefit the most from training, but the result is not significant. VOR is a more subtle metric, but the VOR time constant is linked to the generation of motion sickness, and evidence of its reduction over days could be related to reduced motion sickness susceptibility [8]. Additionally, the time constant can be adapted without cues from a visual field, so it is a reasonable measure of adaptation to CCC stimulation.

Interestingly, the τ values associated with pitch head-turns were smaller than hypothetical yaw-canal values typically observed. This may be because pitch head-turns fell short of 90 degrees, and the canals were not

reoriented sufficiently to completely switch their hypothetical plane. Alternatively, a small degree of tilt-dumping could have occurred because the rather strenuous act of holding the head in the NF position could have led to small head movements. This would, however, produce an up-down asymmetry in the τ values, which was not found.

A problem with a null finding is that a lack of sensitivity to a weak measure could fail to reveal an existing effect. However, our measure of illusory motion makes this possibility unlikely. While the illusory motion scores are the most subjective measure, past studies have proven that they may be the most sensitive indicator of adaptation [4]. Even this sensitive measure was unable to reveal a difference between the Experimental and the Control subjects for pitch turns. The nearly identical illusory motion scores of the final six pitch turns (19–24) in the Experimental and Control Groups clearly demonstrates the lack of transfer of adaptation.

4.2. Understanding the lack of transfer

There have been no direct studies of transfer of adaptation during CCC stimulation, but we may discuss the lack of observed transfer in the context of the most
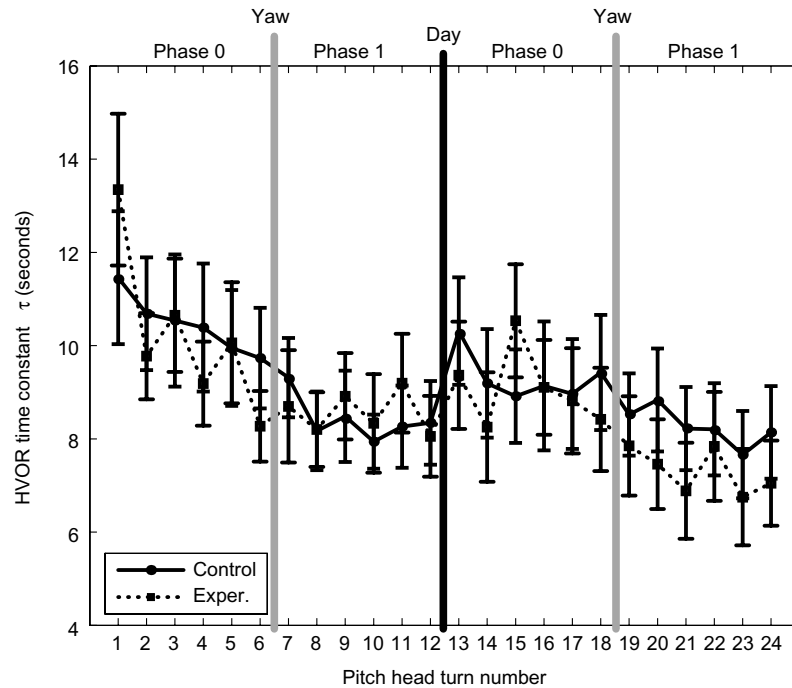
Fig. 8. Mean pitch head turn HVOR time constants (both Groups) measured in darkness. Day 0 and Day 1 are separated by the black vertical line. The gray vertical line indicates where yaw head turns were made in the light (Experimental Group) or the subject rested (Control Group). The downward trend is comparable for both Groups.

closely related studies. Evidence that yaw head-turn adaptation transfers to VOR adaptation during ramp-up of the centrifuge (see Introduction) had suggested that transfer across planes might occur [35]. However, it appears that CCC adaptation is context-specific. This finding is consistent with the notion that otolith cues regulate and limit the plasticity of VOR. For instance in the gravito-inertial force (GIF) resolution paradigm, the central nervous system (CNS) estimates the difference between the actual GIF and the perceived GIF. The CNS uses both the semicircular canals and the otolith organs to make its estimate. Zupan et al. [36] found that the GIF hypothesis accurately predicted the direction of post-rotatory nystagmus in two rotation protocols, confirming the interaction of the otolith cues in orienting VOR. In our experiment, the relative changes in gravity vector are different during motions from NU to RED, and from NU to NF. It is possible that the difference in gravity cues during these motions could curb any transfer of adaptation. Hecht et al. [15] observed successful transfer of adaptation after a change in centrifuge rotation direction, but this experiment did not involve a change in the gravity vector. We note that the role of gravity in the differences between RED and NU yaw head-turns was discussed by Mast et al. [21],

and the cause of differences between pitch and yaw head-turns is still an active area of investigation.

The cross-axis VOR adaptation experiments by Schultheis and colleagues (e.g. [25]) demonstrate the flexibility of the VOR to accommodate complex stimuli, but there are significant differences between those studies and our experiment. Most importantly, cross-axis VOR experiments have tested the maintenance and gating of an adapted VOR response in different environments (e.g. in darkness or in different body axes), while we wish to determine if one adaptive state leads to the more rapid development of adaptation to a different stimulus. Another possible explanation for the lack of cross-plane transfer in our study rests in the fact that our adaptive goal is highly unusual. Because the nystagmus generated during CCC stimulation is non-compensatory, our goal is to remove an undesirable vestibular response rather than creating a positive response. It may just be particularly difficult to remove inappropriate VOR. Therefore, these differences in both our experiment purpose and design suggest that our negative results are not at odds with experiments that demonstrate successful cross-axis VOR training. In fact, our findings are consistent with the negative transfer result reported by Crampton and Brown [6].
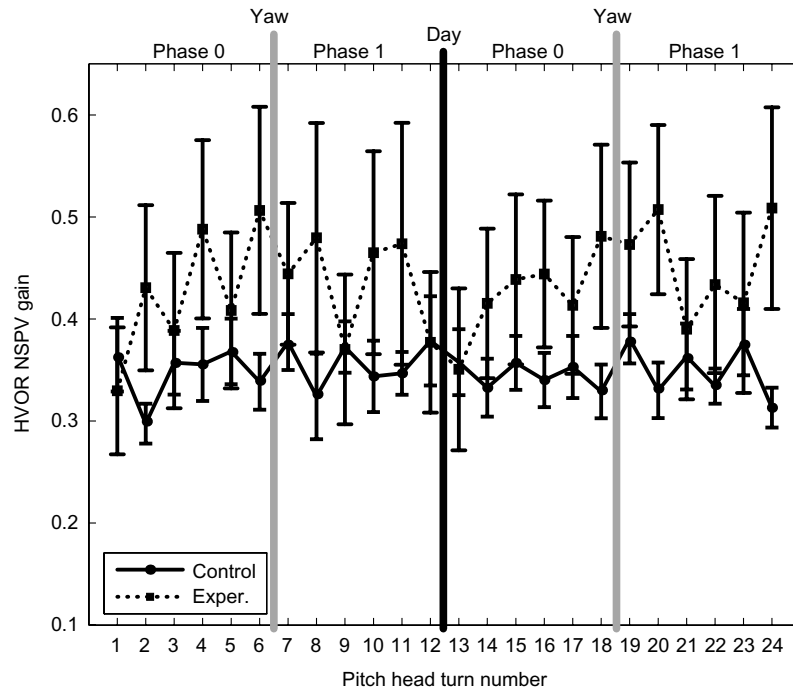
Fig. 9. Mean pitch head turn NSPV gain values (both Groups) measured in darkness. Day 0 and Day 1 are separated by the black vertical line. The gray vertical line indicates where yaw head turns were made in the light (Experimental Group) or the subject rested (Control Group).

In keeping with our results, Kaufman et al. [18] speculate that generalized adaptation to CCC stimulation may be difficult, and the brain may only be amenable to a global vestibular numbing. Evidence of global numbing over two days would have been apparent in our experiment since the Experiment Group performed 48 yaw movements, compared with zero in the Control Group, yet we found no differences between the Groups. The CCC stimulus in our experiment is long lasting compared to most other VOR stimuli [18], and may thus be difficult to generalize. If either global VOR numbing or generalization to CCC stimuli is possible, then it is possible a transfer effect might appear after a longer experiment. Cramer et al. [5] used thousands of head turns to transfer motion sickness tolerance from a rotating chair to a flight environment. It is also possible that the initial impulse from our 6-turn pitch stimulus may have been large, and subsequent pitch turns would have yielded much lower VOR and illusory effects. Guedry et al. [13] did not find evidence for transfer of adaptation during head turns within a quadrant in a rotating room, but they suggest that "not enough post-habituation" measurements may have been made in their study (see also [12]).

Finally, it is worth noting that subjects that dropped out due to motion sickness may have a stronger, possibly more adaptive response to CCC stimulation, and may have shown different transfer results if they could have been included in the study. Similarly, the Experimental Group may have the highest tolerance to motion sickness, since they were able to complete the entire experiment. Therefore, this Group may be expected to behave differently than the average population.

4.3. Implications

At the most basic level it is promising that subjects can adapt to pitch head turns as well as to yaw head turns while rotating. This suggests that astronauts can be adapted to carry out symptom-free head turns in a rotating environment during space flight. However, this is likely to be a more time-consuming process, since the lack of transfer between planes of head motion suggests that each axis of head motion has to be learned separately.

On Earth we cannot turn off the gravitational otolith signal that is present at all times. In space, however, the lack of a consistent otolith signal may permit greater plasticity in adaptation. One might interpret Kaufman et al. [18] to suggest that generalized adaptation to CCC stimulation is unlikely in a terrestrial environment, but once a consistent otolith context is removed, the defin-
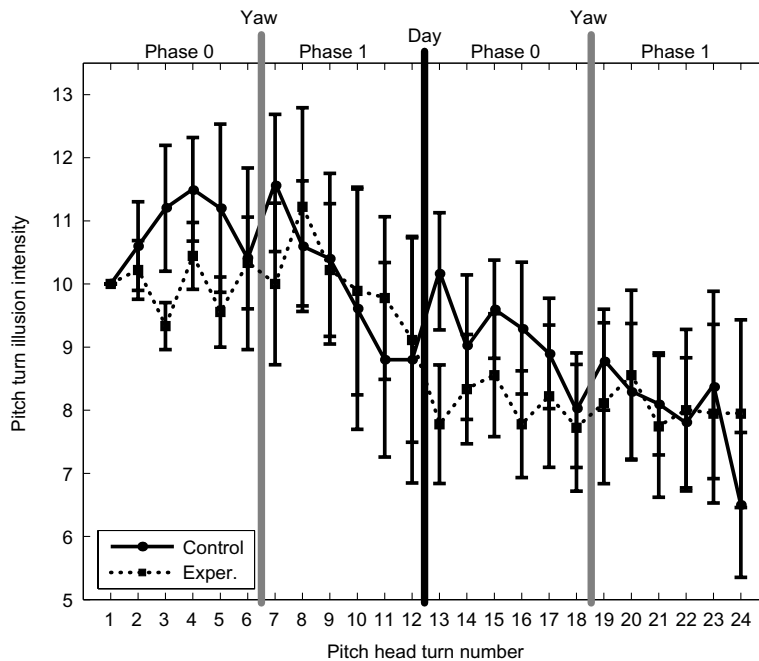
Fig. 10. Mean illusory motion ratings for pitch head turns (both Groups) measured in darkness. The first pitch head turn on Day 0 was anchored to be 10. Day 0 and Day 1 are separated by the black vertical line. The gray vertical line indicates where yaw head turns were made in the light (Experimental Group) or the subject rested (Control Group).

ing cue for a specific body orientation might be removed with it. In other words, transfer of adaptation across planes might be possible in microgravity. However, if this is the case, the influence of otolith cues may also be strong enough to destroy any CCC adaptation gained on Earth once the astronaut enters microgravity.

5. Conclusions

Subjects performing a combination of pitch and yaw head-turns while rotating at 23 rpm showed no statistically significant difference in adaptation to pitch turns, compared to a control group which performed exclusively pitch turns. These results suggest that over the timescale of this experiment, head-turns in just one plane cannot be expected to facilitate generalized multi-plane adaptation to CCC stimulation. Our experiment is unable to distinguish the reason for a lack of generalization, which may include either otolith gating during the different head positions in the two types of head turns, or a general difficulty of the brain in generalizing or desensitizing CCC stimulation. Astronauts using short radius centrifugation may have to adapt separately to head turns in each plane.

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