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Abstract

Hyper-gravity provides a unique environment to study how misperceptions impact control of orientation relative to gravity. Previous studies have found that static and dynamic roll tilts are perceptually overestimated in hyper-gravity. The current investigation quantifies how this influences control of orientation. We utilized a long-radius centrifuge to study manual control performance in hyper-gravity. In the dark, subjects were tasked with nulling out a pseudo-random roll disturbance on the cab of the centrifuge using a rotational hand controller to command their roll rate in order to remain perceptually upright. The task was performed in 1, 1.5, and 2 G's of net gravito-inertial acceleration. Initial performance, in terms of root mean square deviation from upright, degraded in hyper-gravity relative to 1 G performance levels. In 1.5 G, initial performance degraded by 26% and in 2 G, by 45%. With practice, however, performance in hyper-gravity improved to near the 1 G performance level over several minutes. Finally, pre-exposure to one hyper-gravity level reduced initial performance decrements in a different, novel, hyper-gravity level. Perceptual overestimation of roll tilts in hyper-gravity leads to manual control performance errors, which are reduced both with practice and pre-exposure to alternate hyper-gravity stimuli.

Keywords – vestibular – manual control – roll tilt – sensorimotor – adaptation – hyper-gravity

Introduction

Spatial disorientation is common during spaceflight (Young et al. 1984; Paloski et al. 2008) and can also lead to aircraft accidents (Knapp and Johnson 1996; Braithwaite et al. 1997; Curry and McGhee 2007). Specifically, manual control – the ability of pilots to control their vehicle – can be disrupted by spatial disorientation (for a review see (Gillingham and Wolfe 1985)). In this study, we focus on vestibular contributions to a manual control task by performing our task in the dark. Hyper-gravity – an environment having a G-level greater than the 1 Earth G normally experienced – provides a unique paradigm for studying vestibular perception and manual control. In hyper-gravity, the graviceptor sensory signals from the otolith organs are altered, while the semicircular canal cues are presumably unaffected. We study how these altered sensory signals influence the ability to *control* orientation, using a manual control task.

Hyper-gravity affects human perception of orientation. *Static* roll tilt is well known to be overestimated in hyper-gravity (Colenbrander 1963; Schone 1964; Miller and Graybiel 1966; Correia et al. 1968). Qualitatively, *dynamic*, active head tilts in hyper-gravity were shown to result in illusory perceptions (Gilson et al. 1973; Guedry and Rupert 1991). We have recently quantified dynamic roll tilt perception in hyper-gravity, and showed that dynamic roll tilts in hyper-gravity are similarly overestimated, although less so at higher roll rates (Clark et al. 2014). Other studies have focused on how semicircular canal and otolith cues are integrated for orientation perception during a quick spin up of a gondola centrifuge (Tribukait and Eiken 2005; Tribukait and Eiken 2006a; Tribukait and Eiken 2006b). The conflicting vestibular cues in this paradigm can lead to illusory perception of orientation, though there are differences between pilots and non-pilots (Tribukait et al. 2011; Tribukait and Eiken 2012) as well as large inter-individual differences (Tribukait et al. 2013).

How exactly static and dynamic perceptual overestimation in hyper-gravity may impact *control* of orientation remains unclear. Glasauer and Mittelstaedt (1992) studied the effect of gravitational level on pseudo-static perception of orientation using a reporting technique called subjective horizontal body position (SHP). In SHP, subjects lay on their side and adjusted their roll angle on a tilt board until they felt horizontal. Those authors hypothesized that, in addition to vestibular information, subjects use trunk localization information to estimate tilt. Although subjects during SHP manually control body position using feedback, the task is pseudo-static in that subjects adjust their position slowly, then check if they feel horizontal, then re-adjust. How hyper-gravity impacts a dynamic control task, such as attitude control of an airplane, remains an open question.

There has been one investigation of how manual control of orientation is affected by an altered gravity environment (Merfeld 1996). Shortly after returning from 14 days of microgravity exposure on a Shuttle mission, astronaut performance was tested on a manual control nulling task in the dark. Subjects were seated in a flight simulator cabin and physically tilted in roll. They attempted to null a disturbance signal to keep the cabin upright. In the two subjects tested on landing day, post-flight performance was significantly worse than pre-flight baseline performance. This suggests that manual control performance was impaired by the gravity transition back to Earth gravity after 14 days of microgravity exposure and adaptation (Young et al. 1984; Parker et al. 1985; Merfeld 2003; Clement and Wood 2014). Re-adaptation did occur gradually following return to Earth, with performance returning to the pre-flight baseline level 1-2 days after landing.

The effect of hyper-gravity on manual control performance of normal, Earth-adapted subjects has not previously been investigated. We propose the following two hypotheses: 1) hyper-gravity will cause an initial performance decrement relative to 1 G performance and 2) with practice, subjects will adapt their perceptions and control strategies to the hyper-gravity environment and performance will improve.

In other sensorimotor adaptation paradigms, there is evidence that previous experiences adapting to relevant environments can enhance an individual's ability to adapt to novel, but similar, altered environments (a concept often referred to as "learning to learn") (Roller et al. 2001; Roller et al. 2009). For example, pre-exposure to novel locomotion environments can improve subsequent adaptation of gait parameters (Batson et al. 2011) and previous training in random altered visual-motor environments can enhance the learning of future alterations (Turnham et al. 2012). Locomotion in altered visual-motor environments is enhanced by training in multiple altered conditions, more so than training in a single condition (Mulavara et al. 2009). Finally, motor learning (Seidler 2005) is improved in altered visual-motor conditions when pre-training in a similar, but related condition, is provided. The importance of the pre-train and testing environments being related appears to be critical (Bock et al. 2001) for the beneficial effects to be observed. Building upon this literature, we hypothesize that previous exposure to one hyper-gravity level will reduce the initial performance decrement in a subsequent, novel hyper-gravity level.

Methods

Human subjects performed a manual control task at 1, 1.5, and 2 Earth G's. (Here and throughout, G refers to the net gravito-inertial force (GIF), or the combination of gravity and linear acceleration. Since by Einstein's equivalence principle forces of gravity and acceleration are ambiguous, we often refer to the net GIF level as the "gravity level". One-G is equal to the 9.81 m/s^2 of gravitational acceleration regularly experienced on Earth.) A long-radius centrifuge was used to create the hyper-gravity environment. In our task, subjects attempted to null out a pseudo-random roll tilt disturbance using a rotational hand controller (RHC) (e.g. joystick) that controlled cab tilt rate. Subjects were instructed to use the RHC to keep themselves and the cab of the centrifuge "upright" with respect to the GIF. Subjects were extensively trained at the roll tilt manual control task in 1 G prior to testing.

Motion Paradigm

Subjects (N=12) were seated in the cab at the end of the arm of the National AeroSpace Training and Research (NASTAR) Center's ATFS-400 long-radius (7.62 m) centrifuge facing tangentially towards the direction of travel. As the centrifuge was spun up to the desired GIF level, the cab gradually tilted outwards such that the resultant GIF remained aligned with the body axis of the cab and z-axis of the subject ($+G_Z$). Thus from the subject's perspective, the direction of the GIF did not change; it only increased in magnitude to create the hyper-gravity environment. The desired G-level was produced at approximately (i.e. within 5 cm) the subject's ear level.

Subjects were secured with a five-point harness seat-belt. A custom head and shoulder support was utilized to restrict roll or yaw head movements and provide support for the torso. Vacuum cushions provided near-uniform support across the shoulders and upper arms such that tactile cues were evenly distributed and the interior of the cab was darkened to remove any visual cues. Subjects wore a custom-sized helmet with noise cancelling headphones to reduce auditory cues from the mechanical systems of the centrifuge. The headphones were also used for communication between the experimenter and the subject. An infrared camera allowed the experimenters to visually monitor the subject during testing. We did not perform any physiological monitoring (e.g. heart rate) of the subjects, but a trained safety monitor was exclusively tasked with visually monitoring the subject for signs of gravity-induced loss of consciousness or other problems. No subjects experienced any negative effects except minor motion sickness. Once the centrifuge was spun up to provide the desired hyper-gravity environment subjects performed a series of trials of the manual control task.

Roll Tilt Disturbance

The roll tilt motion disturbance was a computer-generated, pseudo-random, zero-mean, sum-of-sines profile. The roll tilt axis was approximately naso-occipetal (x-axis) and aligned within 5 cm of the subject's ear level. Twelve harmonically-independent sinusoids were summed. They ranged in frequency from 0.014 to 0.668 Hz (Table 1). The frequencies and their phase shifts used were identical to a previous pre/post-flight manual control experiment (Merfeld 1996). The amplitudes of each sinusoid, however, were modified to put the majority of the disturbance at the lower frequencies, which was more appropriate for the rate-control task (details below).

Table 1: Sum-of-sines disturbance parameters

Number	Frequency (Hz)	Phase (deg)	Tilt Amplitude (deg)
1	0.014	0	2.6472
2	0.024	37	2.6472
3	0.053	74	2.6472
4	0.083	111	2.6472
5	0.112	148	2.6472
6	0.151	185	2.6472
7	0.200	222	0.2647
8	0.258	259	0.2647
9	0.346	296	0.2647
10	0.434	333	0.2647
11	0.532	19	0.2647
12	0.668	47	0.2647

The same disturbance profile, as shown in Fig. 1, was used for each trial except for an occasional sign change (i.e. left versus right) to prevent subjects from realizing the disturbance was repeated. In post-experiment interviews, it was confirmed that subjects remained naïve to this repetition. (This is not surprising as each subject's feedback control signal made the motion unique for each trial.) The maximum roll tilt of the disturbance was 13.4 degrees and the maximum angular velocity was 7.13 degrees/second. The profile for each trial lasted 214.8 seconds, however the first and last 5 seconds were scaled such that the profile began and ended at upright. These beginning and ending portions were discarded prior to analysis, so the trial length of interest was 204.8 seconds (Merfeld 1996).

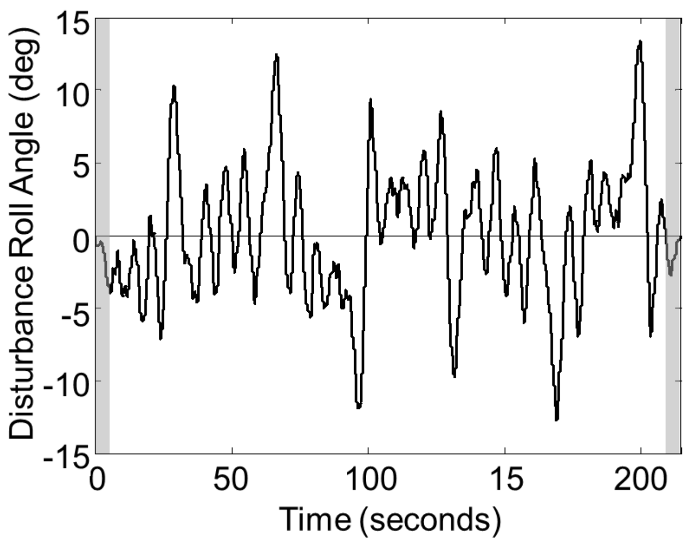

Fig. 1 Roll tilt disturbance profile. The disturbance (defined in Table 1) is a pseudo-random, zero-mean, sum-of-sines profile. The first and last 5 seconds of the profile (shaded grey) are scaled such that the profile begins and ends at upright. These portions are removed prior to analysis

Rotational Hand Controller (RHC)

Subjects were instructed to "keep the cab/vehicle as erect as possible" in response to the roll disturbance using the RHC. The RHC consisted of a 30 cm long vertical rod (2 cm diameter) that rotated about its center point and was located approximately 35 cm from the midriff of the seated subject. Subjects held the RHC at its central rotation axis, such that no large hand or arm displacements were required to make control inputs. Subjects used whichever hand they preferred (i.e., their dominant hand) to operate the controller. The RHC was spring loaded such that the more the stick was deflected from upright the more resistance the subject felt. If released, the spring system would cause the RHC to return to upright (nearly critically damped). The RHC could only rotate in roll and there were mechanical stops to prevent stick deflections of greater than +/- 45 degrees. The RHC orientation was recorded using a potentiometer (Vishay Spectrol 601HE0000B01 Hall Effect Position Sensor) which was then fed into the cab control system.

The vehicle dynamics were rate-control-attitude-hold (RCAH), such that amount of stick deflection was proportional to the commanded roll rate of the cab (0.44 deg/sec of roll rate was commanded per degree of stick deflection, with a maximum commanded roll rate of 20 deg/sec). The roll response dynamics of the cab were rapid, with software and actuation delays (~35 ms) much less than the human sensorimotor delays. Without any disturbance, if the RHC was upright the cab would remain at its current roll orientation. These vehicle dynamics were similar to those of a helicopter or a lunar landing vehicle. First order dynamics (i.e. subject controls roll rate to null out roll angle) are normally relatively easy to control and can be mastered quickly, even by non-pilots (McRuer and Weir 1969). In the software there was a +/- 1 degree deadband about upright in the RHC such that small, unintended stick deflections did not gradually change vehicle orientation. To prevent a subject from commanding an unusual and uncomfortable orientation there were +/- 25 degree roll tilt safety limits in the software. During testing, that limit was reached on only 1 of 144 trials.

Independent Variables

The primary independent variable was the gravity level (1, 1.5 or 2 G's). In addition, to study how performance changed over time, multiple trials were presented at each gravity level. Three consecutive trials at the same gravity level were presented in a session. Each session began with a 60 second spin-up period and a 60 second period for the subject to acclimate prior to testing. (In 1 G there was no spin-up.) Then three 214.8 second long trials were presented with 30 second breaks between trials. During the breaks, the vehicle cab remained aligned with the GIF and the subject remained at the testing gravity level. After the third trial, the centrifuge was spun-down over 60 seconds. During spin-up, acclimation, breaks, and spin-down the RHC was deactivated so any subject control inputs could not influence cab orientation. The total time for each session was less than 15 minutes. At least 20 minute breaks were provided between sessions, in which the subject was removed from the centrifuge, and relaxed in the 1 G environment. Activities during the breaks were uncontrolled. In order to study learning, trial number was considered a second independent variable.

Performance was also studied within individual trials in order to study short term adaptation and learning. During analyses, each trial was split into 6 segments of 34 seconds each. The disturbance profile within each short segment was the same, except for a possible sign change, allowing for performance on any specific segment to be compared across trials and gravity levels.

Dependent Variables

Centrifuge spin rate, disturbance roll tilt, RHC position, and the resulting cab roll tilt were recorded at a 100 Hz sampling rate. The primary performance metric was the root mean square (RMS) deviation of the resulting cab roll tilt away from upright. Smaller RMS values correspond to better manual control performance. Metrics in the frequency domain, such as used by Merfeld (1996), were not considered because the changes in performance observed during trials violated the stationarity assumptions of a Fourier transformation. After each trial, during the 30 second break, subjects reported four items: 1) subjective estimate of performance on a 0-10 scale where 0 corresponds to perfect nulling performance and 10 indicates no nulling was accomplished, 2) subjective mental workload using the modified Bedford scale of spare attention (Roscoe 1984; Roscoe and Ellis 1990), 3) the maximum Coriolis cross-coupled illusion intensity experienced using a subjective scale (detailed in the Pre-Experimental Protocols Section), and 4) motion sickness intensity rating (0-10 scale) (Bos et al. 2010). Subjects remained naïve to the hypotheses of the experiment to minimize biases in their subjective reports.

Experimental Design

As described above, sessions, consisting of three trials each, were presented at each of the gravity levels and subjects experienced each of the three gravity levels. Four distinct orders of gravity level presentation were utilized (Table 2), with each subject randomly assigned to one of the orders, such that the same number of subjects (N=3) was assigned to each order.

Table 2: Four orders of sessions

Order	Session 1	20min break	Session 2	20min break	Session 3	20min break	Session 4
A	1 G		1.5 G		2 G		1 G
B	1.5 G		1 G		2 G		1 G
C	1 G		2 G		1.5 G		1 G
D	2 G		1 G		1.5 G		1 G

Orders A and B both had 1.5 G as the first hyper-gravity level presented, with the only difference between the two orders being the counter-balancing of whether 1 or 1.5 G was presented first. Similarly for orders C and D, except that 2 G was the first hyper-gravity level presented. For all orders, the third session was the other hyper-gravity level that had yet to be presented. The fourth session was a repetition of 1 G to test for learning, fatigue, or whether hyper-gravity testing influenced 1 G performance.

Pre-Experimental Protocols

Prior to the primary experiment, three protocols were completed to prepare the subject. First, subjects were introduced to the Coriolis cross-coupled illusion. When subjects make head rotations in a spinning environment, such as employed here, they will experience an illusory perception of rotation about an unexpected axis, known as the Coriolis cross-coupled illusion (Guedry 1974). For the roll tilt task, the illusory cross-coupled rotation was primarily in pitch. To minimize the impact of the illusion during the manual control task on the centrifuge, we utilized a large radius rotator (r = 7.62 m), permitting slower centrifuge spin rate, and selected the disturbance to avoid excessively large and fast roll rotations, which are more provocative. However, to allow for subjects to report if the illusion was present during testing, it was introduced prior to testing. In the dark, upright subjects were passively spun in pure yaw at 14.26 rpm (the maximum spin rate of the centrifuge in the hyper-gravity tests). Subjects performed four active, head-on-body roll tilts: 1) from upright to right ear down, 2) right ear down to upright, 3) upright to left ear down, and 4) left ear down back to upright. Each head tilt was approximately 40 degrees in roughly 1 second. Each of these head tilts induced the cross-coupled illusion, after which subjects reported the relative intensity of the illusion using the following scale: 0 corresponded to no unusual sensation such as would be experienced during a head tilt in everyday life and a 10 was arbitrarily assigned as the intensity of the first head tilt (Young et al. 2001; Brown et al. 2002; Jarchow and Young 2007). Any cross-coupled illusion experienced during the hyper-gravity experiment was reported using the relative intensity scale developed here.

Next, subjects were extensively trained in 1 G on the manual control task. Subjects were first briefed how the RHC controlled cab roll rate. Then in the ATFS-400, with the centrifuge not spinning (1 G), they were provided practice trials (also 214.8 seconds long) to learn the task, develop a suitable control strategy, and practice to steady-state performance levels. All practice trials were completed in the dark. Following each trial subjects were provided qualitative feedback (e.g. you are controlling too aggressively), and intermittently were provided quantitative feedback (i.e. RMS performance scores on previous trials). After each trial subjects also reported subjective performance and workload scores for practice and to develop consistency in these reports. Training continued until subjects reached a competent and steady-state performance level in terms of RMS error scores. This took between six and 12 trials. Just prior to testing, 1-2 additional training refresher trials were presented to ensure performance levels were maintained. At the end of training, when each subject had settled on a control strategy, they were instructed to maintain that control strategy throughout testing.

Finally, prior to testing subjects were exposed to hyper-gravity to help reduce anxiety and expose them to the physiological effects of hyper-gravity (e.g. increased heart rate). The centrifuge was spun up to 1.5 G's and then 2 G's for 2 minutes each with transitions between gravity levels taking place over 1 minute. The roll angle of the cab remained aligned with the net GIF and subjects had no task to perform. Once the steady-state hyper-gravity level was attained, no tilt of the cab occurred that might have acted to pre-adapt/pre-expose the subjects to the dynamic experimental conditions.

Subjects

All of the protocols were approved by the NASTAR Center's Internal Review Board and the Massachusetts Institute of Technology Committee on the Use of Humans as Experimental Subjects. Subject selection criteria included healthy females and males aged 18-65, with no known vestibular defects. Subjects who were highly susceptible to motion sickness were excluded from the study, as determined by scoring above the 90th percentile on the Motion Sickness Susceptibility Questionnaire (MSSQ) (Golding 1998; Golding 2006). Individuals with no history of any motion sickness (0th percentile on the MSSQ) may not have a normally functioning vestibular system and thus were also excluded from the study. In addition, subjects completed NASTAR Center's medical screening questionnaire. No subjects failed these exclusion criteria, likely due to voluntary self-selection. All subjects signed a written informed consent form.

Twelve subjects were tested (10M/2F, ages 22-38, mean = 27.5, standard deviation = 4.9). Subjects were randomly assigned to one of the four orders (Table 2), such that each order was completed by three subjects. Thus half of the subjects (N=6) experienced 1.5 G as the first hyper-gravity level and half (N=6) experienced 2 G as the first hyper-gravity level. One subject had flight experience (~390 hrs) and four had minimal centrifuge experience (< 2 hrs). These subjects' results did not appear to differ from the remaining subjects. All subjects were able to complete the protocols and experienced no serious adverse effects. Minor motion sickness symptoms occurred for approximately half of the subjects, particularly resulting from the cross-coupled illusion training and the spin down from hyper-gravity during testing sessions; however no subjects approached vomiting nor asked to stop the experiment.

Data Analysis

The RMS error of the nulled cab roll tilt was used as the primary performance metric. As detailed below, the performance in 1 G was consistent across trials and sessions. Thus, for each subject, a 1 G performance baseline was calculated as the mean across repetitions in 1 G. A subject's hyper-gravity performance on each segment was then compared to his or her own 1 G baseline performance for the corresponding segment.

To quantify initial performance and how the effect of hyper-gravity changed over segments within a session, an exponential decay model was fit to the difference in RMS relative to the 1 G baseline as a function of segment number. There was no evidence that the 30 second break between trials impacted performance. Specifically, added free parameters for each trial were not statistically significant. Thus each of the six segments across the three trials in a session were concatenated to yield a total of 18 segments in a session. In this model λ corresponds to the time constant of performance improvement ($\tau = 1/\lambda$, in units of segments), A is the initial difference in RMS deviation between hyper-gravity and 1G, and ε_i is the error in the fit on the ith measurement such that the errors sum to zero.

Equation 1:

$$(RMS_{hyper-G} - RMS_{1G})_i = Ae^{(-\lambda(segment-1))} + \epsilon_i$$

Alternatively, a second model was fit in which the performance in hyper-gravity could approach a different steady-state value than the 1 G baseline. This model, shown in Equation 2, has a non-zero steady-state constant C.

Equation 2:

$$(RMS_{hyper-G} - RMS_{1G})_i = Ae^{(-\lambda(segment-1))} + C + \epsilon_i$$

Since performance in 1.5 and 2 G may be different, we fit the exponential decay model separately to those subjects that experienced 1.5 G as their first hyper-gravity level (orders A and B) versus 2 G (orders C and D).

To analyze the effect of previous roll tilt experience in hyper-gravity (referred to throughout as "pre-exposure"), we compared performance in the subjects who experienced a particular hyper-gravity level first (without pre-exposure) to those that had it as the second hyper-gravity level (with pre-exposure), in a between-subjects test. For example, performance in 1.5 G's was compared between orders A and B (*without* pre-exposure to 2 G's) and orders C and D (*with* pre-exposure to 2 G's). For 2 G performance, orders C and D had no pre-exposure to 1.5 G's and orders A and B did. We hypothesized pre-exposure would reduce the *initial* performance decrement in hyper-gravity, so for this analysis only the segments within the first trial were considered.

There was not significant evidence it made any difference whether the pre-exposure session was the session just before or two sessions prior to the second hyper-gravity session. Thus these orderings were pooled (for example orders C and D were pooled as 1.5 G performance with 2 G pre-exposure).

During testing, one subject made an accidental control reversal that caused the cab to reach the +/- 25 degree hard safety limits. This occurred during the 14^{th} 2 G segment in order C (2 G as the first hyper-gravity level). While the subject was able to recover in ~6 seconds and complete the trial, the mistake caused an uncharacteristically large RMS error during the segment in which it occurred (difference in RMS from 1 G baseline = 7.45 degrees). Thus this segment was removed from the analysis. For all statistical tests, the required level of significance was set to $\alpha = 0.05$.

Results

Performance in 1 G

While there was often substantial improvement in performance during training, performance was fairly consistent in 1 G during testing. Considering only the 1 G trials, a hierarchical regression model with session number (1 or 2), trial number (1, 2, or 3), and order (A, B, C, or D) as independent variables and RMS as the dependent variable found only trial number to be statistically significant ($\beta = 0.13$, $Z(55) = 2.28$, $p = 0.023$). However, the decline in performance (increase in RMS) with repeated trials was primarily due to a decrement on the last trial of the last session which may be attributed to a lack of focus, in expectancy of completing the experiment, or simply fatigue. With the final trial removed from the analysis, the RMS performance was consistent across session number, trial number, and order (i.e. there was not a significant effect of any of these factors in 1 G). The consistent performances across the first 5 trials (3 trials in the first session and first 2 trials in the second session) in 1 G were averaged for each subject to determine that individual's 1 G "baseline" performance. The 1 G baseline RMS errors varied among the 12 subjects (mean = 2.73 degrees, SD = 0.43 degrees, min = 2.05 degrees, max = 3.40 degrees), which represents individual differences in skill level at the manual control task. To account for this, all hyper-gravity performances were calculated as differences from each subject's individual 1 G baseline performance (mean of 5 trials). The consistency in 1 G performance between the first and second session indicates that the recent tests in hyper-gravity do not have a lasting effect that impairs performance on the second 1 G session. However, as will be discussed later, there was an uncontrolled break of at least 20 minutes in 1 G between sessions which may have impacted any temporary impact of hyper-gravity testing on subsequent 1 G performance.

Performance in Hyper-Gravity over Time

Performance in hyper-gravity was first analyzed by considering only the first session in hyper-gravity (for orders A and B, 1.5 G, and for orders C and D it was 2 G). Performance in each hyper-gravity relative to the 1 G performance baseline is shown as a function of segment number in Fig. 2.

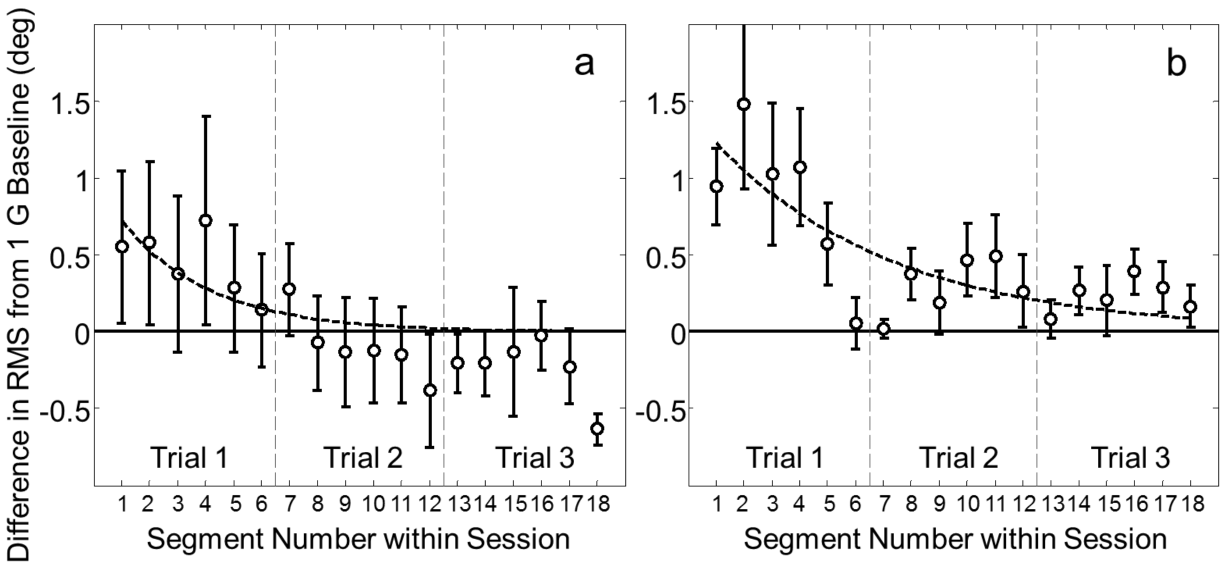

Fig. 2 Effect of hyper-gravity on manual control performance. Panel a shows 1.5 G performance relative to 1 G baseline and panel b shows 2 G relative to baseline. Data are means +/- 1 standard error across subjects (N=6 for each hyper-gravity level). Each segment is 34 seconds in duration resulting in a session of 18 segments being 10 minutes and 12 seconds worth of testing time. RMS values above zero (1 G baseline) correspond to performance decrements in hyper-gravity. Dotted lines show exponential decay fits (Table 3)

In both 1.5 and 2 G's there are two major effects on performance in hyper-gravity: 1) there was an initial performance decrement, with an increased RMS relative to the 1 G performance baseline and 2) across segments the performance then improved to near the 1 G performance level. To quantify these two effects, exponential decay models were fit in the form given in Equation 1 and the results are presented in Table 3. The segment numbers ranged from 1-18 and separate models were fit to the data for those individuals who experienced 1.5 G's first (orders A and B) versus those who had 2 G's as their first hyper-gravity session (orders C and D).

Table 3: Exponential decay fits for hyper-gravity performance versus segment

			95% Confidence Interval	
	Parameter	Estimate	Lower	Upper
1.5 G	A	0.72	0.11	1.33
	λ	0.31	-0.12	0.75
2.0 G	A	1.23	0.86	1.60
	λ	0.16	0.08	0.23

The model fits are shown graphically in Fig. 2. In both 1.5 and 2 G's, the initial difference relative to the 1 G baseline (*A*) was significantly positive, corresponding to an initial performance decrement in hyper-gravity. The estimate of the initial performance decrement was larger in 2 G (1.23 degrees) than in 1.5 G's (0.72 degrees), however this difference was not statistically significant. In the 2 G model, there was a significant exponential decay (improvement in performance) towards the 1 G baseline. In 1.5 G there was also a trend of improvement, but it was not significant ($\lambda = 0.31$, 95% confidence interval [-0.12, 0.75]). The improvement in performance with segment within any hyper-gravity level can be characterized by the time constant ($\tau = 1/\lambda$). The time constant for 1.5 G's was estimated to be 3.23 segments or 110 seconds and that for 2 G's was 6.25 segments (213 seconds). There was not a statistically significant difference between 1.5 and 2 G's in the estimates of the time constants for performance improvement. In 1.5 G, performance appeared to improve to beyond the 1 G baseline. The mean RMS performances on the last 11 segments (nearly all of the last 2 trials) were all lower (better performance) than the 1 G baseline. However, if a steady-state constant *C* was added to the exponential decay model as shown in Equation 2, it was not significantly different from zero ($C = -0.65$, 95% confidence interval [-2.51, 1.20]). In fact, if the model in Equation 2 is fit separately to both the 1.5 G and 2 G data, the steady-state constant *C* is not significantly different between the two hyper-gravity levels.

Effect of Pre-Exposure on Hyper-Gravity Performance

Fig. 3 compares performance in a particular hyper-gravity session with and without pre-exposure to the other hyper-gravity level. Only the performance across the first trial is shown because the performance both with and without pre-exposure approached the 1 G performance baseline after the first trial.

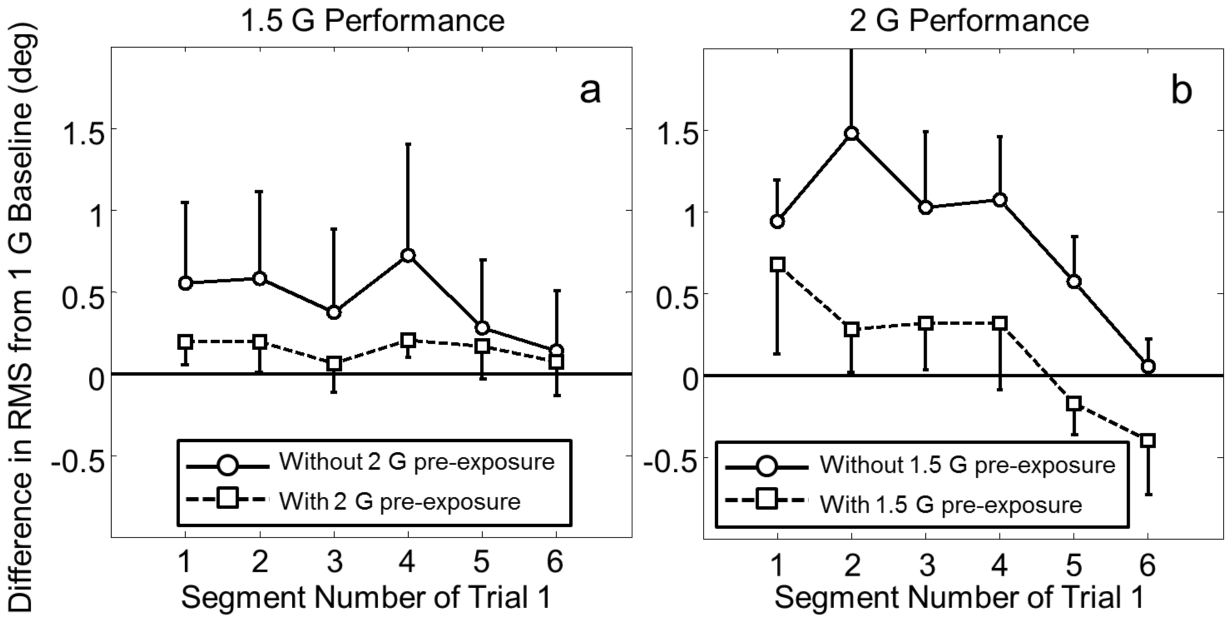

Fig. 3 Effect of pre-exposure on hyper-gravity performance on the first trial. Panel a shows 1.5 G performance relative to 1 G baseline with (dotted line with squares) and without (solid line with circles) pre-exposure to 2 G. Panel b shows 2 G performance with and without pre-exposure to 1.5 G (same labelling for pre-exposure). Data are means +/- 1 standard error across subjects (N=6 within each condition). For graphical purposes only one side of the standard error bars are shown

As previously observed, without pre-exposure, there were large performance decrements initially in hyper-gravity (solid lines in Fig. 3 are the same data from Trial 1, for segments 1-6, in Fig. 2). However, with pre-exposure there were much smaller performance decrements. In 1.5 G (Panel a in Fig. 3) with 2 G pre-exposure, the performance decrements were not significantly different from the 1 G performance baseline throughout the first trial. At 2 G (Panel b in Fig. 3) with 1.5 G pre-exposure, on the first segment there was still a substantial performance decrement. However it was reduced with the pre-exposure and after the second segment the performance was near the 1 G baseline. To test the effect of pre-exposure on performance, an ANCOVA model was constructed with hyper-gravity level (1.5 or 2 G) and pre-exposure ordering (with or without pre-exposure) as factors, segment as the covariate, and the difference in RMS from 1 G baseline as the dependent variable. There was a significant effect of pre-exposure on the difference in RMS from the 1 G baseline after controlling for the effect of segment, $F(1,139) = 11.4$, $p = 0.001$. The covariate, the segment number, was significantly related to the difference in RMS from the 1 G baseline $F(1,139) = 8.11$, $p = 0.005$. Neither the hyper-gravity level nor the cross-effect of hyper-gravity with pre-exposure were statistically significant. This indicates that while all groups adapted by having improved performance with increasing segment number, those with pre-exposure in another hyper-gravity level had smaller initial performance decrements.

Cross-coupled Intensity Reports

During the 30 second breaks between trials, subjects reported the maximum Coriolis cross-coupled illusion intensity they experienced on the previous trial. The reported intensities, for the first session in 1 G and the first session in hyper-gravity (e.g. either 1.5 or 2 G's), are plotted by trial number in Fig. 4.

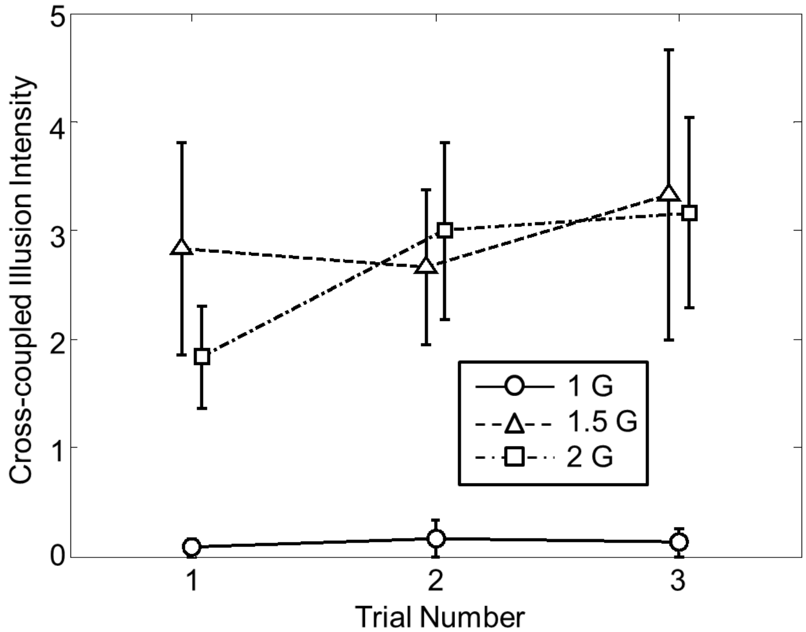

Fig. 4 Cross-coupled illusion intensity reports across trials. Data are the means +/- 1 standard error across subjects (N=6 for 1.5 G and 2 G trials and N=12 for 1 G trials). Data are offset on the x-axis for graphical purposes

As expected there were nearly no reports of the cross-coupled illusion during 1 G testing, since the centrifuge was not spinning. While the centrifuge was spinning, in hyper-gravity, the illusion did occur much more regularly (on 29 of 35 trials in hyper-gravity subjects reported some cross-coupling), though the intensity was generally quite low (e.g. median intensity of 2, mean intensity of 2.8 on the 10-based scale). This is not surprising as the large radius centrifuge, small tilt displacements, and small tilt velocities were all chosen to minimize this side-effect. Somewhat surprisingly, there was no difference in the reported intensities in 1.5 and 2 G's despite the higher centrifuge spin rate in 2 G (14.26 rpm versus 11.46 rpm in 1.5 G). Pooling the hyper-gravity levels together and using a hierarchical regression with subject as the identifier found no effect of trial number on illusion intensity in hyper-gravity. Thus, while hyper-gravity performance showed clear evidence of improvement, we could not demonstrate that the cross-coupled illusion intensity changed across trials.

To further test the impact of the cross-coupled stimulus, we analyzed hyper-gravity performance split between trials in which the subject reported high intensity cross-coupled illusion (greater than the median intensity of 2) versus those trials in which they did not (intensity ≤ 2). A linear regression with performance (difference in RMS error from 1 G) as the dependent variable and trial (1, 2 or 3), G-level (1.5 or 2 G's), and cross-coupled intensity (high or low) as independent variables was developed to test whether the performance decrement was primarily due to high intensity cross-coupled illusions. The effect of cross-coupled intensity was not significant ($p > 0.05$). Trials when subjects reported both low and high cross-coupled intensity reports showed a similar initial performance decrement in hyper-gravity and similar improvement in performance across trials. Since hyper-gravity performance was similar between high and low cross-coupled intensities, this suggests that the side effect of the cross-coupled illusion was not the primary cause of the performance decrements observed in hyper-gravity.

Discussion and Conclusions

Initial Hyper-Gravity Performance

We conclude that hyper-gravity affects a human subject's ability to perform a manual control task, resulting in performance decrements. This finding is consistent with earlier reports that reported tilt illusions during both static (Colenbrander 1963; Schone 1964; Miller and Graybiel 1966; Correia et al. 1968; Chelette et al. 1995) and dynamic (Gilson et al. 1973; Guedry and Rupert 1991; Clark et al. 2014) conditions in hyper-gravity. The initial performance decrements in hyper-gravity were substantial. In terms of RMS, initial performance errors in 1.5 G increased by an estimated 0.72 degrees over the average 2.73 degree 1 G baseline, corresponding to approximately a 26% increase. In 2 G's initial performance was on average 45% worse (1.23 degrees). While it is clear that hyper-gravity is causing the manual control performance decrements, the exact mechanism is unclear. We hypothesize that the initial effect is primarily due to perceptual errors. Specifically, hyper-gravity causes an increased utricular (the portion of the otolith organ most sensitive to roll tilt) shear stimulus compared to the same roll tilt in 1G, yielding an overestimation in roll tilt perception. The influence of the semicircular canals, which are presumably unaffected by hyper-gravity, may help reduce the amount of overestimation for dynamic tilts, but there is still likely some overestimation compared to perceptions in 1 G (Clark et al. 2014). Other non-vestibular cues (e,g. tactile, somatosensory, proprioceptive) likely also contribute to orientation perception. However, it is worth noting that fully-compensated patients suffering total vestibular loss have tilt thresholds that are on average twice as high as normal (Valko et al. 2012) – demonstrating the otolith organs have about twice the precision of all other graviceptor cues combined. In any case, overestimation of roll tilt in hyper-gravity is well documented (Colenbrander 1963;

Schone 1964; Correia et al. 1968; Clark et al. 2014) and may have caused subjects to make too large of inputs to the RHC, resulting in over controlling and pilot induced oscillations (PIO).

However, hyper-gravity has additional effects that could contribute to the manual control performance decrements. First, initial exposure to hyper-gravity may cause physiological (e.g. increased heart rate) and mental (e.g. increased anxiety) effects that would not be present during 1 G testing. To try to reduce the impact of these secondary issues, we exposed subjects to hyper-gravity prior to testing. Here, subjects experienced 1.5 and 2 G's for several minutes without any manual control task to become familiar to the environment and the associated physiological responses. In addition, during testing the spin-up or onset of hyper-gravity was done slowly, over one minute, and another minute was provided in hyper-gravity for subjects to acclimate prior to the initiation of the first trial.

Second, hyper-gravity impacts the accuracy of physical motor responses (Fisk et al. 1993; DiZio and Lackner 2002; Kurtzer et al. 2005; Lackner and DiZio 2005). To minimize the impact of this, we attempted to reduce the amount of physical motor response required in the task by having the rotational axis of the RHC centered in the subject's hand. Only small hand and lower arm rotations were required to make control inputs instead of larger full arm translational movements.

Third, in our motion paradigm where hyper-gravity is produced on a centrifuge, the roll rotations may cause a Coriolis cross-coupled illusion. Since we are not able to produce a "pure" hyper-gravity environment without any cross-coupled illusion, we cannot be certain the cross-coupled illusion did not have some role in the manual control performance decrements observed in hyper-gravity. However, there are several reasons to believe the impact was small. During testing, the reported intensities of the cross-coupled illusion were very low (median of 2 on 0-10 scale). Furthermore, the cross-coupled illusory sensation would be primarily in pitch, which could not be controlled by the subject and was perpendicular to the axis of the roll manual control task. This was confirmed by the hyper-gravity performance not being statistically different between trials in which subjects reported high cross-coupled intensity compared to those where the subjects reported low to no cross-coupling. Finally, while hyper-gravity performance improved across trials the cross-coupled intensities remained constant, further suggesting independence. While hyper-gravity causes altered physiological responses, increased anxiety, altered motor control, and the cross-coupled illusion, each of which may have impacted the manual control performance, we suggest that the perceptual overestimation of roll tilt was the primary cause of the performance decrements observed.

Improvement in Hyper-Gravity Performance

The large initial performance decrements in hyper-gravity were reduced with practice over time. The time frame over which the manual control hyper-gravity improvement occurred was characterized. For an exponential decay of the performance decrements to the 1 G baseline, the time constant for 1.5 G's was estimated to be ~110 seconds and that for 2 G's was ~213 seconds. Thus, with just a little practice, manual control performance in hyper-gravity rapidly returns to baseline levels. On the other hand, for pilots and astronauts, performance during the first 100-200 seconds is often a critical time period for docking or landing tasks. Initial control errors prior to the completion of adaptation may be catastrophic in terms of leading to accidents or aborts. Hence, even the fairly rapid improvements in manual control reported herein leave room for improvement for some tasks.

It should be noted that the majority of our subjects were non-pilots. One might hypothesize that experienced pilots may have less or no initial performance decrement in hyper-gravity or their improvement may be much more rapid than we quantified here. In fact, Tribukait et al. (2011; 2012; 2013) observed differences between pilots and non-pilots in orientation perception over time during a centrifuge spin up paradigm. However, our one subject with piloting experience (~390 hrs) exhibited a similar, if not larger, initial performance decrement in hyper-gravity as compared to the non-pilots and took as long, if not longer, for performance to improve. While further testing with a pilot population is necessary, this tentatively suggests that even trained pilots may experience similar manual control performance decrements in hyper-gravity as quantified here.

The mechanism is unclear for what is causing the reduction over time in the performance decrement in hyper-gravity. The time frame of the improvement (hundreds of seconds) is likely too short for a neural sensory reinterpretation of canal and otolith cues as is hypothesized to occur over several hours to days during spaceflight (Young et al. 1984; Parker et al. 1985; Merfeld 2003). Instead we hypothesize that the improvement is primarily cognitive and is made in an adjustment of the appropriate motor response for a given sensory perception of orientation. In hyper-gravity, static and dynamic roll tilt is overestimated (Colenbrander 1963; Schone 1964; Miller and Graybiel 1966; Correia et al. 1968; Clark et al. 2014). If the same motor response is made as would be appropriate in 1 G for the perceived angle, the overestimation would result in over-controlling in hyper-gravity. However, when successive control errors are made, we hypothesize the CNS adjusts what the appropriate motor response is for a given perceived roll angle. In this fashion, the subject's "gain" of motor response for perceived roll angle is reduced and the performance decrement is reduced. None of the subjects reported consciously making a cognitive change in their control strategy in hyper-gravity (i.e. reducing the response gain); however the adjustment may have been subconscious.

In many adaptation paradigms, adapting to one altered environment will then require a re-adaptation back to the original environment. For example, extended use of prism reversing goggles causes vestibulo-ocular reflex (VOR) changes that require a few hours for VOR phase re-adaptation and 2-3 weeks for VOR gain recovery once the goggles are removed (Gonshor and Melvill Jones 1976). Re-adaptation of arm movement trajectories after being done in a rotating environment is much quicker, requiring only approximately 10 arm reaches to fully recover (Lackner and Dizio 1994). Alternatively, some paradigms require no adaptation time when returning to a previously experienced environment, a concept known as "context-specific" adaptation (Baker et al. 1987; Yakushin et al. 2000; Young et al. 2001; Shelhamer and Clendaniel 2002; Shelhamer et al. 2002; Young 2003; Young et al. 2003). Studying re-adaptation of performance in 1 G after hyper-gravity testing was not the primary focus of this study. Specifically, we provided 20 minute, uncontrolled breaks between sessions in which the subjects were outside of the centrifuge cab in 1 G. During these breaks, re-adaptation after hyper-gravity testing may have occurred without being quantified. Nonetheless, we note that there was not significant evidence that adjustment to hyper-gravity impacted performance on the second 1 G session. However, further experimentation without breaks between sessions is required before concluding manual control adjustments in hyper-gravity are context-specific.

In 1.5 G there was a trend, though not significant, that with sufficient practice, performance could improve beyond the 1 G baseline. One explanation for the potentially enhanced performance in 1.5 G is that there is more utricular shear for a given roll tilt in hyper-gravity, hypothetically increasing sensitivity to roll tilt. If the otolith signal is properly interpreted, hyper-gravity should actually *reduce* a subject's effective roll tilt threshold. If smaller roll tilts can be perceived in hyper-gravity then presumably they could be more effectively nulled out, resulting in super-1 G manual control nulling performance. However, across the three trials tested there was no evidence of this effect occurring in 2 G, where roll tilt sensitivity should be even more enhanced. Note that the potential for a fully adapted subject to exceed 1 G baseline performance in altered gravity should only occur for hyper-gravity. *Hypo*-gravity environments, like on the moon or Mars, would have less utricular shear for a given roll tilt, reducing sensitivity, and hypothetically impairing even fully adapted manual control nulling performance.

Effect of Pre-Exposure on Initial Hyper-Gravity Performance

We found that pre-exposure in one hyper-gravity level reduced the initial performance decrements in another hyper-gravity level. The second hyper-gravity level was completely novel; subjects had never done the task at that level nor had ever made the adaptive adjustment necessary for that level. However, having recently made a similar adjustment to another hyper-gravity level seems to have improved their adaptive capability. The adjustment was similar in that it required an adjustment of the subjects' "gain" of their motor response for a given perceived angle, but different in that the exact magnitude of the adjustment was novel. This finding supports the concept of "metacognition" or "learning to learn" (Bock et al. 2001; Roller et al. 2001; Seidler 2004; Seidler 2005; Mulavara et al. 2009; Roller et al. 2009; Batson et al. 2011; Turnham et al. 2012), in which recent adaptive experiences in relevant environments enhance the capability to adapt to other novel, but similar, environments. This is the first evidence that this effect occurs for manual control adaptation to altered gravity levels.

We only tested scenarios in which the pre-exposure hyper-gravity level preceded the testing level by either a 20 minute break or two 20 minute breaks and a 12 minute 1 G testing session. With only 3 subjects in each of these sub-groups, we could not identify differences in the timing between pre-exposure and testing. However, the effect of timing on the pre-exposure enhancement warrants further research. In order to utilize altered gravity pre-exposure as a countermeasure for astronauts landing on the moon or Mars, the timing separation between pre-exposure training and the critical manual control task would be weeks to months. Here, we have only shown the pre-exposure effect to be retained for less than one hour. While the nuances of adaptive generalization in altered gravity require further study, it is clear that pre-exposure to either a more or less extreme hyper-gravity environment than that used for testing reduces the initial performance decrements.

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