Title: Human Perception of Whole-Body Roll Tilt Orientation in a Hypo-Gravity Analog: Underestimation and Adaptation

Running Title: Roll Tilt Underestimation and Adaptation in Hypo-Gravity

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Abstract:

Overestimation of roll tilt in hyper-gravity ("G-Excess" illusion) has been demonstrated, but corresponding sustained hypo-gravic conditions are impossible to create in ground laboratories. Here we describe the first systematic experimental evidence that in a hypo-gravity analog, humans underestimate roll tilt. We studied perception of self-roll tilt in nine subjects, who were supine, but spun on a centrifuge to create a hypo-gravity analog. By varying the centrifuge rotation rate, we modulated the centripetal acceleration (Gc) at the subject's head location (0.5 or 1G), along the body axis. We measured orientation perception using a subjective visual vertical task in which subjects aligned an illuminated bar with their perceived centripetal acceleration direction during tilts (+/-11.5-28.5 degrees). As hypothesized, based on the reduced utricular otolith shearing, subjects initially underestimated roll tilts in the 0.5Gc condition compared to the 1Gc condition (mean perceptual gain change=-0.27, p=0.01). When visual feedback was given after each trial in 0.5Gc, subjects' perceptual gain increased in approximately exponential fashion over time (time constant=16 tilts or 13 minutes) and, after 45 minutes, the perceptual gain was not significantly different from the 1Gc baseline (mean gain difference between 1Gc initial and 0.5Gc final=0.16, p=0.3). Thus, humans modified their interpretation of sensory cues to more correctly report orientation during this hypo-gravity analog. Quantifying the acute orientation perceptual learning in such an altered gravity environment may have implications for human space exploration on the moon or Mars.

New and Noteworthy

Humans systematically overestimate roll tilt in hyper-gravity. However, human perception of orientation in hypo-gravity has not been quantified across a range of tilt angles. Using a centrifuge to create a hypo-gravity centripetal acceleration environment, we found initial underestimation of roll tilt. Providing static visual feedback, perceptual learning reduced underestimation during the hypo-gravity analog. These altered gravity orientation perceptual errors and adaptation may have implications for astronauts.

Introduction:

During launch and landing on Earth or another planet, astronauts experience multiple gravity transitions that can disrupt balance (Kaufman et al. 2001), gait (Bloomberg and Mulavara 2003; Mulavara et al. 2010), visual performance (Clément et al. 2007; Reschke et al. 1999; Reschke and Parker 1987), and motor control (Reschke et al. 1998). Spatial orientation and motion perception are also impacted by gravity transitions (Clément et al. 2001; Clément and Wood 2012; 2014; Harm and Parker 1993; Parker et al. 1985; Young et al. 1984). Nonetheless astronauts must maintain high levels of performance during and immediately after transitions from normal to hyper-gravity (>1 G) to hypo-gravity (<1G) since they also represent the safety-critical phases of flight (Paloski et al. 2008).

Aircraft pilots experience “G-Excess” spatial orientation illusions during hyper-gravic maneuvers (Gilson et al. 1973). Since hypo-gravity environments are difficult to produce (e.g., briefly in parabolic flight, on a centrifuge in orbital flight, or on a body with less mass than the Earth), most experimental studies of altered gravity orientation perception have utilized ground-based centrifuges and addressed hyper-gravic responses. Previous centrifuge experiments demonstrate that in hyper-gravity subjects overestimate their tilt for static roll angles (Colenbrander 1963; Correia et al. 1968; Miller and Graybiel 1966; Schöne 1964). The amount of overestimation varies somewhat among studies, methodologies, and subjects, but for smaller angles (i.e. $\leq$ 40 degrees) on average it is 35% of the actual roll tilt angle per added G (e.g. in 2 G’s, a 20-degree tilt is perceived as 27 degrees, on average). Dynamic roll tilt, when there are rotational cues such as those from the semicircular canals, is also overestimated (Clark et al. 2015b). Static and dynamic overestimation of tilt in hyper-gravity is consistent with the hypothesis that human tilt perception in part depends on the lateral (inter-aural) component of the net gravito-inertial acceleration acting on the inner ear otolith organs (Clark et al. 2015b). Stimulation along this inter-aural axis of the otolith organ is predominantly sensed by the utricular maculae, though the utricle and saccule have complex three-dimensional geometries (Corvera et al. 1958; Curthoys et al. 1999). A mathematical (“Observer”) model incorporating the assumption that utricular cues are weighed differently from saccular cues and the effects of semicircular canal cue integration mimics experimental results for both static and dynamic passively applied body tilts (Clark et al. 2015c). Extending Observer model predictions to hypo-gravity, it predicts an underestimation of tilt (~17.5% underestimation for a 20° static roll tilt in 0.5G) (Clark et al. 2015c), and even more extreme underestimation at Martian (3/8G) and Lunar (1/6G) levels.

Until now there has been only limited experimental data to support or refute this quantitative hypothesis. Two parabolic flight hypo-gravity experiments (de Winkel et al. 2012; Dyde et al. 2009) studied static human roll tilt perception, but only investigated roll tilt angles of 0 degrees (i.e. subject seated upright) and 90 degrees (i.e. subjects lying on their side). Similarly, a centrifuge paradigm varied the magnitude of centripetal acceleration between 0 and 1 G, but did not tilt the subject (i.e. subject aligned with centripetal acceleration) (Harris et al. 2014). During orbital flight, a centrifuge was used to create 0.5 G centripetal acceleration (Clément et al. 2001), but again with the subject always aligned or perpendicular to the resulting g-direction. The underestimation previously predicted in hypo-gravity (Clark et al. 2015c) is specific to smaller roll tilt angles between 0 and 90 degrees. Using parabolic flight to create hypo-gravity (3/8G and 1/6G), we recently showed underestimation of roll tilt angles between 1-48 degrees, consistent with that predicted by a mathematical model (Clark and Young 2017), but only for a single subject.

Parabolic flights (Karmali and Shelhamer 2008) conveniently allow manipulation of the G level, but are expensive and the G level duration is limited. Each hypo-gravity parabola must be immediately followed by a hyper-gravity “pull out”, such that the short term average G level remains near unity. Extended to complete microgravity, perception of “tilt” is highly variable (van Erp and van Veen 2006), since there is no longer any inertial reference (without visual cues) and perception is limited to attempting to integrate rotational cues (e.g., from the semicircular canals). The lack of empirical data on human hypo-gravic tilt perception at angles < 90 degrees motivated the primary aim of the current investigation, to quantify perceptual underestimation in hypo-gravity across a range of tilt angles.

In addition to understanding the expected changes in perception in altered gravity, it is important to assess whether experience in the altered gravity environment causes learning to occur to correct these errors, and also to understand the time course of this learning. While a number of studies have characterized sensorimotor adaptation to transitions in gravity environments (Benson 1987; Benson et al. 1986; Clark et al. 2015a; Clément and Wood 2014; DiZio and Lackner 2002; Mulavara et al. 2010; Newman et al. 1997), fewer studies have characterized perceptual learning (Clark et al. 2015b); these are described in more detail in the Discussion. In particular, the time course of orientation perceptual learning in response to transitions in gravity environments has not been characterized. Thus, a second aim of this study was to quantify perceptual learning and its time constant.

We developed a ground-based method using a specially equipped centrifuge to actuate whole-body tilts while creating a hypo-gravity centripetal acceleration environment. Our hypotheses were that: (1) passive body tilts in 0.5Gc centripetal acceleration will result in underestimation of tilt (assessed via the subjective visual vertical) as compared to the same tilts made with respect to a 1Gc centripetal acceleration environment, indicating reduced perceptual sensitivity to tilt (reduced perceptual “gain”), and (2) Over repeated trials in 0.5Gc with static visual feedback after each tilt report, perceptual learning/adaptation will occur. Eventually, the subjective visual vertical sensitivity will converge to that previously measured in 1Gc. We refer to this process as “perceptual learning,” while noting that this learning/adaptation might involve perceptual, cognitive, or even strategic aspects (see Discussion); we also note that some literature would describe this as “sensorimotor learning,” although we avoid this term because our measures are perceptual rather than motor. Preliminary portions of these findings have been previously presented at a conference (Karmali et al. 2016).

Methods:

Subjects:

The experimental protocol was approved by the Institutional Review Boards at the Massachusetts Institute of Technology and the Massachusetts Eye and Ear Infirmary (MEEI). Ten naïve subjects were recruited, provided informed consent, and went through a multi-step screening process. They completed an online health screen questionnaire (Harris et al. 2009) and had their medical history reviewed by a MEEI otoneurologist. Seven of the subjects performed a vestibular screening clinical exam that included electronystagmogram without calorics, rotational testing, and tests of visual-vestibular interaction, using the same procedures as we have previously used (Grabherr et al. 2008) to ensure subjects have normal vestibular function. Six passed the screening and one did not and was excluded from the study. The three other subjects declined to complete vestibular clinical screening, but another measure of vestibular function (Valko et al. 2012) was used as a proxy: their tilt direction recognition thresholds (upright roll tilt, 0.2 Hz) were within normal limits for their age (Bermudez Rey et al. 2016). The final group of 9 subjects (aged 28.3 ± 6.4 (SD) years, 4 female) were judged to be healthy individuals with no known vestibular disorders.

Centrifugal force stimulus:

Our technique utilized a customized short radius laboratory centrifuge ("Eccentric Rotator", Neurokinetics, Pittsburgh, USA), shown schematically in Figure 1. Subjects lay in a supine, seated position on a chair with their head towards the main axis of rotation, so centrifuge spin produced a footward centrifugal force stimulus to the subject. The subject was positioned with their ear level 0.68 m away from the center of spin, such that the centrifugal force applied to the otoliths was 0.5Gc when the centrifuge was spun at 154 deg/sec and 1Gc when spun at 218 deg/sec. This approach of having a supine subject on a centrifuge to modulate the centrifugal force (including less than 1Gc) is similar to that used by Harris et al. (2014). Centrifuge spin was always in the clockwise direction, as viewed from above. In our paradigm, the chair was separately motorized, so the subject could be passively tilted (head-centered) relative to the centrifugal force direction. We note that the magnitude of the total gravito-inertial force (GIF) at the head was greater than 1 G in each of our experimental conditions, due to the Earth's ever-present gravity (net of 1.12 G for 0.5Gc, 1.41 G net for 1Gc). However, we modulated the centripetal acceleration component, including to hypo-gravic levels, to study perception of roll tilt in the coronal plane. Since the tilts were about an axis parallel to the centrifuge rotation, the tilt stimuli did not induce any vestibular Coriolis cross-coupled illusion (Gray et al. 1961; Graybiel et al. 1960; Melvill Jones 1970), thereby reducing the likelihood of motion sickness. As a result, experimental sessions lasting more than an hour were practical. This approach allowed for the study of tilt perception immediately after G-transitions. It also allowed us to study perceptual learning in response to many more tilt stimuli than would be infeasible in parabolic flight, where hypo-gravity is limited to intermittent periods of less than 30 seconds.

Transitions to each Gc level were achieved by changing the centrifuge spin rate gradually over 60 seconds. Once the desired spin rate was achieved, at least 30 seconds was provided to allow any dynamic spinning sensations to decay. Testing did not begin until the subject reported no spinning sensations. While at a constant spin rate, subjects were roll tilted about a head centered tilt axis to one of 14 possible tilt angles (± 11.5, 15, 18.5, 21, 23.5, 26, 28.5 degrees) relative to the centrifugal force direction. Before each tilt, the chair was aligned with the centrifugal force direction (0 degree tilt) and then was slowly rotated at a constant velocity (1.15, 1.5, 1.85, 2.1, 2.35, 2.6, 2.85 deg/s) to the trial tilt angle over 10 seconds. The tilt time was constant across all tilt angles so that subjects could not correlate tilt time with tilt magnitude. The 10 seconds to tilt was selected to remain near or below threshold for Earth-vertical rotation (Lim et al. 2017). Each tilt was maintained for 35 seconds while subjects reported their perceived tilt using a technique detailed below. The chair was then rotated back to zero degrees at 5.4 deg/s. Tilt stimuli were administered in "tilt blocks" which consisted of a tilt to each of the seven tilt magnitudes. One tilt block consisted of tilts to 18.5, -11.5, 21, -23.5, 15, -28.5, 26 degrees. The other tilt block was the same, but with the tilts in the opposite direction.

Subjects were secured to the chair on the centrifuge with a 5-point harness, shoulder restraints, and a foam-lined adjustable head restraint. Subjects wore noise-cancelling headphones that played white noise throughout the tilt motions to mask chair motor noise and to indicate the start and end of each tilt. A clip-on microphone, along with the headphones, enabled two-way communication with the operators who were located outside of the testing room.

Perceived roll tilt relative to the centripetal acceleration direction:

To report perceived tilt, a subjective visual vertical (SVV) technique (Aubert 1861; Baccini et al. 2014; Vingerhoets et al. 2009) was adapted. Subjects viewed a monitor located approximately 45 cm directly in front of them within the light-tight enclosure. It initially displayed a schematic of brown/blue horizon and two trees within a circular frame (diameter = 20.3cm). The verticality of the schematic was always aligned with the centrifugal force direction. The display was changed to a grey background with black fixation point while the chair rotated to a trial tilt angle. Then, when at the test tilt angle, a 15 cm long black bar replaced the fixation point (Figure 2). Subjects used buttons, one in each hand, to rotate the computer generated SVV indication bar so that it was aligned with the direction of perceived centripetal acceleration. Specific instructions were read to the subjects prior to, during and after training, and repeatedly between testing blocks. They were:

*“Your task is to align the line with where you think the centripetal acceleration vector points. This is also the direction of the main centrifuge rotation arm and the direction you may feel as **down** and we will refer to it as **vertical**”.*

When satisfied with the adjustment, subjects pressed both buttons at the same time causing the bar to disappear, and a new, randomly positioned bar to appear. The subjects then repeated the procedure. The SVV task was self-paced but subjects were encouraged to report three to six times within each 35 second static tilt period.

A training period was provided using only 1Gc centripetal acceleration. This period began with several introductory trials, to familiarize subjects with the task, after which all subjects were able to confidently perform the task and found it intuitive. Subjects then completed a tilt block where SVV data was recorded in 1Gc, but no feedback concerning the magnitude of tilt was provided.

Visual feedback (VFB) was then provided during some tilt blocks (defined in Experimental Protocol below). During VFB ON trials, after completing all SVV reporting and while still tilted, subjects were shown the horizon/tree scene for four seconds just prior to the return to zero tilt. The scene was oriented so it was aligned with the true centrifugal force direction, (just as it was during VFB OFF trials when shown only at 0-degree tilt) and since the subject was tilted, it provided visual feedback of their actual tilt. This VFB did not provide direct feedback about SVV reporting error, since the SVV bar was no longer displayed. Instructions were:

*“While the visual scene is being displayed, please look at it and do your best to make sense of where the horizon is compared to your body. **The horizon is always true and accurate.** Later, when doing the task of aligning the bar to your perceived vertical, please only think about how you feel you are oriented at that instance in time. It is very important that we measure your current perception during each report”.*

The (~65-70 min) training period concluded with 6 blocks of stimuli that included VFB, to obtain control data for perceptual learning in the 1Gc condition. To mitigate fatigue, subjects were then spun down and released for a (~30 min) break. They were free to do as they pleased including going for a walk or eating lunch. Thereafter the "testing period" began, utilizing both 1Gc and 0.5Gc centripetal acceleration stimuli and VFB OFF and VFB ON conditions, as detailed next.

Experimental Protocol

The sequence of experimental conditions is summarized in Figure 3. Manipulations included centripetal acceleration level (1Gc or 0.5Gc), and VFB (ON or OFF). The Testing Period "Phases", 0-4, describe the temporal sequence of conditions compared for purposes of hypothesis testing. In the testing period, subjects experienced one tilt block in 1Gc with VFB ON for refamiliarization and one with VFB OFF to provide a baseline measure. The centrifuge was then spun down so the subjects experienced 0.5Gc stimuli for the first time. They completed one tilt block to measure immediate changes in perception due to the decrease in Gc. VFB was then turned ON for 4 tilt blocks to examine perceptual learning. The testing period ended with one more tilt block with VFB OFF to determine whether changes in perception during 0.5Gc were stable absent visual feedback. After each spin up/down and between each tilt block, subjects remained in the dark, but were given a short break (<1 minute) in which they reported their subjective motion sickness score (MSS) on a scale from 0 to 20 (0 = No motion sickness, 20 = vomiting, (Brown et al. 2002)).

Data analysis and modeling

Data analysis quantified the perceptual "gain" (perceived tilt/actual tilt) allowing us to study the effect of Gc level on over- or underestimation of orientation perception. The reported SVV angles representing the subjects' perceived roll tilt were used as the primary performance metric. Subjects typically reported 3-6 times at each static tilt angle (mean = 4.8). We looked for, but found no significant temporal trends in perception indications during each tilt. Hence all SVV reports for a given tilt were averaged to yield one measure of orientation perception per tilt. This one measure of perceived tilt was hypothesized to relate to the actual tilt using a simple linear gain model: $\theta_{per} = K\theta_{act}$ where K is the "perceptual gain" and can be thought of as tilt perceptual sensitivity, the ratio of perceived tilt/actual tilt. The validity of this simple model of tilt perception is further discussed in the Results and Discussion.

As defined below, perceptual gain from each successive block was fit with a "piecewise" model (Equation 1) for phases 1-4 as a function of tilt number (t). Tilt number was used as the measure of time in our model under the assumption that the tilt motion itself and/or the VFB at the end of each tilt provided the only information to the subject that could drive perceptual learning. Figure 4A shows an example model fit for a single subject (j=1), using Equation 1. The piecewise model has for a constant perceptual gain for the first 7 tilts in 1Gc, $K_{0,j}$ in 1Gc-BL (Phase 1), then allows for another, potentially different perceptual gain for the first 8 tilts in 0.5Gc, $K_{I,j}$ in 0.5Gc-PRE (Phase 2). We hypothesized the VFB, provided in 0.5Gc-VFB (Phase 3), would create an exponential change in the perceptual gain from the initial 0.5Gc gain ($K_{I,j}$) towards a potentially different perceptual gain ($K_{\infty,j}$, the gain after an infinite number of tilts with VFB in 0.5Gc), with some time constant, τ (units of number of tilts with VFB). Finally we hypothesized that without VFB during 0.5Gc-POST (Phase 4) the perceptual gain would remain constant ($K_{F,j}$).

$$K_j(t) = \left\{\begin{array}{lll} K_{0,j} & t < 8 & 1Gc - BL\ (Phase\ 1) \\ K_{I,j} & 8 \geq t < 15 & 0.5Gc - PRE\ (Phase\ 2) \\ \left(K_{I,j} - K_{\infty,j}\right)e^{-(t-15)/\tau} + K_{\infty,j} & 15 \geq t < 43 & 0.5Gc - VFB\ (Phase\ 3) \\ K_{F,j} = K_j(42) & t \geq 43 & 0.5Gc - POST\ \ (Phase\ 4) \end{array}\right. \qquad (1)$$

The model used data from all nine subjects and had 28 free parameters including 27 that were subject-specific (indicated by subscript j) and one that was dependent on the entire group data set. The latter was the adaptation time constant, τ, calculated for the exponential curve fit in 0.5Gc-VFB (Phase 3). In order to model a continuous perceptual response in 0.5Gc (Phases 2-4) and to reduce the number of free parameters, the initial and final gains associated with the exponential curve in 0.5Gc-VFB (Phase 3) were constrained to the fit gains in 0.5Gc-PRE (Phase 2) and 0.5Gc-POST (Phase 4), respectively, for each individual subject (i.e., the perceptual gain in 0.5Gc had no discontinuities). The relationship between the gains in 1Gc-BL (Phase 1) and 0.5Gc-PRE (Phase 2) was not bound in any way (i.e., the gain could have a discontinuity between 1Gc and 0.5Gc representing an instant change in perceptual gain due to the change in centripetal acceleration). Implicit assumptions of our model thus include: (1) no change in perceptual gain across tilts without VFB, (2) no left/right bias in tilt perception (see Table 1 for models that do include bias), (3) a pure gain relating tilt perception to actual tilt (i.e., no small vs. large angle effect on the gain, see Discussion for consideration of this). The model was fit in MATLAB, using the fminsearch.m function, applying the Nelder-Mead simplex algorithm to minimize the sum of square errors between the measured perceived angles and the model predictions of perceived angles. Model residuals met Fisher's requirements of normality and homoscedasticity. In addition to the above model, we also considered several variations, which are listed and quantified in Table 1. All led to similar conclusions. The goodness of fit of these models was compared using the Bayesian information criterion (BIC) and the model in Equation 1 was found to yield the best fit.

Returning to our hypotheses, our two primary scientific questions were (1) does human roll tilt perception change when going from a 1Gc to 0.5Gc environment? and (2) does perception in 0.5Gc change with time spent in the altered gravity environment when VFB is present? To answer these questions, paired t-tests were conducted on the individual fit gains from 1Gc-BL (Phase 1) and 0.5Gc-PRE (Phase 2) (i.e., K_0 vs. K_I) and from 0.5Gc-PRE (Phase 2) and 0.5Gc-POST (Phase 4) (i.e., K_I vs. K_F). Normality was verified by K-S tests.

Results

For one example subject, perceptual gains (circles) for each tilt and the primary model fit (Equation 1) are shown in Figure 4A. The data from this typical subject shows the expected decrease in gain (from K_0 to K_I) upon initial exposure to 0.5Gc (0.5Gc-PRE, Phase 2), representing relative underestimation of static tilts in 0.5Gc. The gain then increased in 0.5Gc with VFB (0.5Gc-VFB Phase 3). Recall that the VFB presented veridical orientation information and was only shown at the end of each tilt, after the subject had reported their perception multiple times. The piecewise function in 0.5Gc-VFB (Phase 3) is defined by individual fit parameters K_I and K_∞ and the group fit exponential time constant, τ. Finally, the estimation of tilt (K_F) remains relatively stable and accurate even when the visual feedback was removed in 0.5Gc-POST (Phase 4).

Change in Perceptual Gain

The fit gains from 1Gc-BL (K_0), 0.5Gc-PRE (K_I), and 0.5Gc-POST (K_F) were compared to determine if there was underestimation upon entry into the hypo-gravity centripetal acceleration environment followed by a recovery to baseline perception, as hypothesized (Figure 4B). Perception reports in 1Gc-BL varied fairly substantially between individual subjects. However, the group mean perceptual gain was not statistically different from one (i.e., accurate tilt perception, mean = 1.11, t(8) = 0.80, p = 0.50, Cohen's d = 0.26).

The fit roll tilt perceptual gains in 0.5Gc-PRE (Phase 2) were significantly less than in 1Gc-BL (Phase 1) (mean diff = -0.27, paired t(8) = -3.21, p = 0.01, Cohen's d = 1.07), showing that subjects underestimated their roll tilts when first put into 0.5Gc compared to 1Gc. Eight out of nine subjects showed this decrease in perceptual gain (Figure 4B). The fit roll tilt perceptual gains in 0.5Gc-POST (Phase 4), were significantly greater than in 0.5Gc-PRE (Phase 2) (mean diff = 0.16, paired t(8) = 2.60, p = 0.016, Cohen's d = 0.87), demonstrating that subjects' estimation of their roll tilts increased after 4 tilt blocks (~ 23 min) in 0.5Gc with VFB, corresponding to perceptual adaptation; 7 out of 9 subjects were consistent with the mean change. The fit roll tilt perceptual gain in 0.5Gc-POST (Phase 4), was not significantly different than in 1Gc-BL (Phase 1) (mean diff = 0.11, paired t(8) = 1.10, p = 0.31, Cohen's d = 0.37), suggesting that after 4 subsequent tilt blocks (~ 23 min) with VFB in 0.5Gc, subjects' gains not only increased, but returned to approximately their 1Gc baseline.

Perceptual learning in 0.5Gc

To quantify the average time or number of trials required for perceptual adaptation in 0.5Gc across subjects, our piecewise model (Equation 1) had one time constant across subjects. We acknowledge that subjects may adapt at different rates (i.e., have different time constants). However, given the variability in the data and the limited sample size, we were unable to reliably fit separate time constants for each subject (See Discussion). Using Model 4 (Equation 1 and Table 1), the fit group time constant was 15.8 tilts (~ 13 min). Models 2-4 estimated slightly higher time constants (see next section), but all were within the number of tilts experienced in the adaptation phase (0.5Gc-VFB) of the testing period (i.e., 28 tilts). The rather short time constants show rapid adaptation in tilt perception in response to changes in Gc level with simple, static visual feedback.

Alternative Models

In addition to our primary model discussed up to this point (Equation 1 and Model 4 in Table 1), we explored multiple additional models and the associated tradeoff between model fit and number of free parameters. We used the BIC as our primary selection criterion, with a lower BIC being preferred (Schwarz 1978). The BIC is a useful aid in model comparison and selection because it rewards improved fitting while penalizing extra free parameters which could result in overfitting of the data.

The simplest model considered (Model 1 in Table 1) had just a single gain (K) that did not change between subjects or phases. This model did not fit the data well as is evident by the large variance in residuals and large BIC, and therefore suggests that gains differ between individuals and/or phases. A model with only nine gains, one for each individual (but not for each phase) was better in terms of BIC, however had residuals that did not met the normality assumptions as determined by a Kolmogorov-Smirnov test. Comparing this model with Model 1 suggests that there were in fact differences in gain between subjects, but also that additional effects of the phase are needed to appropriately explain the data.

To see if the phase had an effect on gain as hypothesized, a model was fit with gains for each subject and each phase, with an exponential fit between 0.5Gc-PRE and 0.5Gc-POST (Model 2 in Table 1). The BIC for this model was dramatically reduced compared to Model 1, suggesting that in fact the gains were dependent on both subject and phase. This model allowed for individual fit time constants of adaptation, τ, in 0.5Gc-VFB (Phase 3). These individually fit τ's had a large range (0.12 – 27.1) and by visual inspection, we determined that the exponential fits to individual data sets were adversely affected by limited data points per individual and inherent variability in perception. We therefore aimed to quantify a group time constant of adaptation, which we believed would be more representative and reliable due to a larger number of total data points included in the exponential fit.

The resulting model was our primary model, (Model 4 in Table 1) in which the gain was allowed to differ between subjects and phases, but the time constant of adaptation was constant across all subjects. This model yielded the lowest BIC indicating an appropriate balance between number of model parameters and model fit.

Studying left/right biases in roll tilt perception and the effect of gravity on these biases was not a primary focus of our study. Nonetheless, inspection of our data showed that some subjects exhibited slight perceptual biases (< 5 degrees). We found no consistent left/right bias across subjects. However, to be thorough, we did attempt models that included a bias term (for all subjects or for each individual subject as separate parameters), but the added parameter(s) was (were) not beneficial (i.e., increased BIC). Interestingly, we did find a significant systematic shift in bias between 1Gc-BL and 0.5Gc-PRE such that regardless of the initial bias in 1Gc, the bias increased upon entering 0.5Gc (comparing 1Gc-BL (Phase 1) and 0.5Gc-PRE (Phases 2): mean difference = 3.44 degrees, $t(8) = 2.85$, $p = 0.02$, Cohen's $d = 0.95$, corresponding to a consistent rightward shift in the bias). In the initial 0.5Gc-PRE phase, the bias was significantly different from zero (mean = 1.86, $t(8) = 2.37$, $p = 0.045$, Cohen's $d = 0.79$). After time spent in 0.5Gc with VFB, the bias significantly decreased (comparing 0.5Gc-PRE and 0.5Gc-POST, Phases 2 and 4: mean difference = 2.54, $t(8) = 3.15$, $p = 0.01$, Cohen's $d = 1.05$), corresponding to a return to near the 1Gc value (no significant difference, mean diff = 0.90, $t(8) = 0.98$, $p = 0.36$, Cohen's $d = 0.24$). In an attempt to incorporate this observed bias shift and for completeness, we fit the data with Model 3 (Table 1) that included individual gains for each phase, a group time constant (τ), and a group bias in 1Gc-BL equal to the group bias in 0.5Gc-POST. As the simplest transition between 0.5Gc-PRE and 0.5Gc-POST, we included a linearly decreasing bias throughout 0.5Gc-VFB. Although this model had slightly less residual variance than our simpler, primary model, it still had a higher BIC due to its two additional free parameters (bias and bias shift). We conclude that our primary model (Model 4 in Table 1, Equation 1) is the most appropriate model of those considered. Furthermore, we highlight that in all models considered, the major conclusions pertaining to the effect of gravity level on perceptual gain was consistent: 1) reduction in perceptual gain between 1Gc-BL and 0.5Gc-PRE and 2) increase in perceptual gain between 0.5Gc-PRE and 0.5Gc-POST with a fairly short time constant of adaptation.

Table 1. A comparison between multiple perception models ranked by BIC

#	Group Parameters	Individual Parameters	BIC	# of Free Parameters	Var. in Residuals	τ (# of trials)	Bias Shift (deg)	0.5Gc transition[1]	0.5Gc adaptation[2]
1	K (single gain for all phases)	--	1893.5	1	72.9	--	--	--	--
2	--	τ, K_0, K_I, K_F	1680.3	36	27.7	0.12 to 27.1	--	8/9, 0.01	9/9, 0.01
3	τ, bias, bias shift	K_0, K_I, K_F	1642.2	30	27.6	41.7	0.95	8/9, 0.02	6/9, 0.04
4	**T**	**K_0, K_I, K_F**	**1632.3**	**28**	**27.7**	**15.8**	**--**	**8/9, 0.01**	**7/9, 0.04**

[1] Number of subjects whose fit gains decreased from 1Gc-BL to 0.5Gc-PRE ($K_0 - K_I > 0$) and associated p-value for a paired t-test between those fit gains (N=9).

[2] Number of subjects whose fit gains increased from 0.5Gc-PRE to 0.5Gc-POST ($K_I - K_F < 0$) and associated p-value for a paired t-test between those fit gains (N=9).

Müller Effect

Previous studies related to visual orientation during roll tilt stimuli have shown evidence of a Müller (E) effect (Müller 1916), or overestimation of roll tilts at small angles and/or an Aubert (A) effect, or underestimation of roll tilt at large angles (Aubert 1861). See (Howard 1982; Howard and Templeton 1966) for a review. The group mean roll tilt perceptual gains in Phases 1, 2, and 4 for each tilt angle (Figure 5) suggest that the Müller (E) effect was present in our data, such that subjects overestimated small roll tilts in 1Gc and initially in 0.5Gc (0.5Gc-PRE). The lack of E effect in Phase 4 suggests that the extended time spent in 0.5Gc with VFB just prior may have trained out the tendency to overestimate small angles. This E effect was not incorporated into our main model. When we fit models that included data from 1) all the angles, or 2) only the largest five angles (eliminating data for smaller angles, ± 10 and 15 degrees, where overestimation was evident in 1 and 0.5Gc) resulted in sets of fit gains (K_0, K_I, K_F) that were not significantly different from each other (two-sample t-tests, $p > 0.05$). With only the large angles included, the fit group time constant of adaptation in 0.5Gc-VFB (Phase 3) was 19.0 tilts (~ 15 min) which is slightly higher, but not substantially different from the group time constant when all angles were included in the model.

No Evidence of Differences Between Genders

While the study, with 4 females and 5 males, was not specifically powered to investigate gender differences, we conducted an exploratory analysis to determine if any differences could be found. There were no significant differences in mean gains K_0, K_I, K_F between females and males (two sample t-test, $p > 0.05$). Additionally, when including only females or only males, the main conclusions remained mostly the same as when including all subjects in a single group. The lone exception is that when considering only the 5 males, there was only a hint of, but no significant, difference between the initial and final phases in 0.5Gc (mean diff = 0.06, paired $t(4) = 1.21$, $p = 0.15$) suggesting less decisive perceptual adaptation.

Motion Sickness

Motion sickness scores were very low throughout all testing, with a maximum score (on a scale of 0 - 20) of four reported by a single subject after one tilt block in 1Gc-VFB. For the remainder of subjects, motion sickness scores did not go above two, and four subjects reported zero motion sickness throughout all testing.

Discussion

Using a novel ground-based altered-gravity paradigm, we investigated the impact of hypo-gravity on human tilt perception. To our knowledge, this is the first study to experimentally measure human perception of moderate self-tilt when placed in a (simulated) hypo-gravity environment. As hypothesized, a 0.5Gc environment (i.e., hypo-gravity analog) caused humans to significantly underestimate their own whole-body roll tilt as compared to their tilt perception in 1Gc. This error in motion perception lessened over time while in 0.5Gc. During this time, visual feedback was given but only after subjects had completed their reports, at the end of each tilt. After 28 tilts (~ 23 min) in 0.5Gc, perceptual gains (perceived angle/actual angle) returned to 1Gc baseline levels, indicating perceptual learning in the hypo-gravity analog environment. Using an exponential model, we quantified a remarkably rapid group time constant of adaptation (i.e. ~16 tilts or ~13 minutes). This study quantified the effect of hypo-gravity on tilt perception *immediately* after a sudden change in gravity magnitude, as compared with post-spaceflight studies that typically begin 1 hour to 1 day post-landing.

Initial Underestimation of Roll Tilt in Hypo-Gravity

Overestimation of roll tilt in hyper-gravity has been shown both empirically (Clark et al. 2015b; Colenbrander 1963; Correia et al. 1965; Schöne 1964) and predicted by modeling efforts (Clark et al. 2015c). This alteration in roll tilt perception is referred to as a "G-Excess" illusion and is often conceptually attributed to a given roll tilt in hyper-gravity causing an increased utricular shear force stimulation. The increased utricular shear leads to perceiving roll tilts as larger than they actually are (i.e. overestimation). This reasoning implicitly assumes that the CNS interprets the GIF stimulation in the utricular plane differently than that to the saccule (i.e. approximately perpendicular to the utricular plane) (Ormsby and Young 1976). Recent work (Clark et al. 2015c) has modified a model of dynamic orientation perception to explain this overestimation by differentially weighting otolith stimulation in the utricular plane vs. perpendicular to the plane (i.e., in the saccular direction).

The modified model predicted an *underestimation* of roll tilt in hypo-gravity. Specifically, the model predicts that in 0.5 G, roll tilt will be underestimated by 17.5% of the actual tilt angle (e.g. a roll tilt of 20 degrees will be perceived as ~16.5 degrees, on average) (Clark et al. 2015c). While the current dataset contains substantial inter-subject variation in the amount of underestimation observed, the subjects as a group appear consistent with this prediction. The percentage of underestimation observed (i.e., $(K_0\text{-}K_I)/K_0$ from Equation 1) had a mean of 23.2% (95% confidence interval: 8.8-37.5%). We note that similarly large inter-subject variability in the change in perceptual gain was observed in our previous *hyper*-gravity experiment (i.e. overestimation gain changes of 8 to 45%, mean=35%, across 8 subjects) (Clark et al. 2015b). Unfortunately there were no subjects in common between the current hypo-gravity and previous hyper-gravity experiments (Clark et al. 2015b), so we cannot yet assess if an individual's susceptibility in terms of gain change correlates across altered gravity levels. Nonetheless, the model predictions, which were calibrated in hyper-gravity, and now directly applied to 0.5 G, appear to be consistent with the group average. In a parabolic flight study with one subject, underestimation of roll tilt in hypo-gravity (at 0.16 and 0.38 G) was also observed and found to be consistent with the model prediction (Clark and Young 2017). This and the current study suggest a similar mechanism to what was proposed in hyper-gravity. Specifically, that the CNS differentially weights the otolith stimulus that is in the utricular shear primary plane, which is increased in hyper-gravity and decreased in hypo-gravity, for a given roll tilt). Therefore, to parallel the "G-Excess" illusion in hyper-gravity, we reiterate the proposal of the "G-Shortage" illusion (Clark and Young 2017) to refer to the underestimation of roll tilt in hypo-gravity. The reduced tilt perception cue in hypo-gravity impairs performance on a manual control task (Rosenberg, et al. 2018, minor revisions).

A recent spaceflight study observed increased variance in orientation perception post-flight (Harris et al. 2017). Unfortunately, our experimental design did not include sufficient replicates to properly calculate the variance of tilt perceptual reports within each gravity condition for each subject. As a preliminary analysis, we calculated the standard deviation of the residuals in each gravity condition (from a simple $\theta_{per} = K\theta_{act}+B$ model) and found no significant differences between 1Gc (mean standard deviation of residuals = 4.1°) and 0.5Gc-PRE (stdev=3.6°) (paired t-test, t(8)=0.91, p=0.39), 1Gc and 0.5Gc-POST (stdev=3.2°) (t(8)=1.1, p=0.31), 0.5Gc-PRE and 0.5Gc-POST (t(8)=0.77, p=0.46). Future investigations of orientation perception in altered gravity should specifically aim to quantify perceptual variability.

Perceptual Learning in Hypo-Gravity Reduces Underestimation

After initial underestimation, subjects demonstrated significant and rapid modification in the perception of roll tilt in 0.5Gc. Specifically, by 0.5Gc-POST (Phase 4, see Figure 4B), 7 of 9 subjects underestimated less than in 0.5Gc-PRE (Phase 2) and the perceptual gain significantly increased across subjects. Various factors could have driven this change in perceptual gain. In 0.5Gc-VFB (Phase 3), at the end of each tilt, subjects received visual feedback consisting of veridical orientation information (Figure 2). Pilot testing without providing any visual feedback (i.e., subjects only viewed the SVV bar or the fixation point in Figure 2), showed that 2 of 3 subjects did not clearly demonstrate an increase in gain over the same time period. As we aimed to study the adaptive response to hypo-gravity, based upon these pilot results, we added the visual feedback to the experiment. While the pilot results are not conclusive, they suggest the importance of the veridical visual feedback in helping drive the change in perceptual gain in 0.5Gc. In addition, other non-visual sensory cues may provide veridical information about tilt perception that could be used to adjust perceptual gain. Specifically, somatosensory cues and even rotational cues from the semicircular canals, if supra-threshold and integrated properly, could provide useful information about roll tilt. Finally, extended exposure to 0.5Gc could have altered the otolith response resulting in less underestimation over time, though we believe this to be unlikely in the relatively short time period (i.e., ~23 minutes) of that phase of the experiment.

Time constants of adaptation due to gravity changes have not been previously quantified for perceptual responses, as was done in this study. Clark et al. (2015b) found evidence of adaptation in hyper-gravity in perceptual responses during passive dynamic rotations, but the study was not designed to quantify the time constant of adaptation. A study of post-flight locomotion function estimated the time for a typical subject to reach 95% recovery as approximately 15 days (Mulavara et al. 2010). The adaptation in orientation perception we observed here occurred over a much more rapid timeframe (i.e., time constant=16 tilts or 13 minutes). There is neural evidence of similarly rapid sensorimotor adaptation during active head movements (Brooks et al. 2015; Carriot et al. 2015), as well as adaptation of saccade eye movements (Shelhamer et al. 2002). Further, Clark et al. (2015a) examined manual control responses to whole body disturbances with hyper-gravity exposure and estimated the time constants of adaptation to be 1.8 min in 1.5 G and 3.6 min in 2 G. A potential explanation for these apparently differing timeframes of sensorimotor adaptation is that single-axis, relatively simple adaptations (e.g., roll tilt perception in hypo-gravity analog, manual control of roll tilt in hyper-gravity, execution of head movements) occur rapidly, while complex reinterpretations (e.g., locomotion through an obstacle course after returning from an environment without gravity) may require additional time to become fully engrained.

We hypothesize that the veridical visual feedback, potentially in combination with other sensory cues, led to a reinterpretation of tilt cues in 0.5Gc causing less perceptual underestimation. However, we cannot entirely rule out the possibility that this change in perceptual gain had a cognitive component (i.e., the subject learned to consciously and purposefully align the SVV bar at an angle greater than their perceived tilt so that their reports would be more likely to match the horizon that would appear afterwards). However, we carefully worded our instructions to try to avoid this type of strategic behavior by emphasizing to subjects that 1) when performing the SVV task they should focus on their "*current perception*" and only "*think about how you feel you are oriented at that instant in time*" and 2) "*while the visual scene is being displayed, please look at it and do your best to make sense of where the horizon is compared to your body.*" Visual feedback was only given *after* SVV reports were completed for a given tilt, so it could not influence the report for that specific tilt angle. Subsequent tilts were different and random so any cognitive adjustment to perceptual reports would have to be generalized and comprehensive.

We propose the following mechanisms to explain the initial underestimation in 0.5Gc followed by the subsequent increase in perceptual gain. Transitioning from 1Gc to 0.5Gc reduces the utricular shear stimulation for a given roll tilt. If the CNS uses the mapping between utricular shear and roll tilt that is appropriate for 1Gc, this will result in initial underestimation in 0.5Gc. However, feedback from the visual scene and potentially other sensory cues that are unaffected by the 0.5Gc environment conflict with this mapping. Over time and with repeated feedback, the CNS reinterprets the modified utricular shear stimulation to better align with the other sensory cues for roll tilt leading to less underestimation.

Perceptual learning changes and adaptation in hypo-gravity are relevant in the context of spaceflight largely because future missions will involve landing and functioning on asteroids or planetary surfaces with less gravity than Earth (e.g. the moon or Mars). Data from the Apollo era of moon missions is limited and since then human space exploration has consisted entirely of transitions between microgravity while in orbit and 1 G here on Earth, with brief hyper-gravity during launch and re-entry. We suspect a similar mechanism occurs when astronauts transition between gravity environments (e.g., landing on the moon or Mars), in which visual and other sensory information unaffected by the altered gravity environment provides sensory feedback to reinterpret modified otolith and other graviceptor cues. While the current study quantifies the acute adaptation in orientation reports upon initial exposure to a hypo-gravity analog, we note several important caveats in applying these results for future exploration of the moon or Mars. First, in our laboratory experiment visual feedback was limited to intermittent, static cues, while astronauts will continuously experience dynamic orientation and rotational cues. Second, to precisely control the roll tilts, only passive motions (i.e., experimenter-controlled) were used and astronauts will experience active motions (e.g., self-locomotion). Third, the short-radius centrifuge paradigm to create a hypo-gravity analog differs from a pure hypo-gravity environment on the moon or Mars in a handful of ways, detailed in the last section. Finally, prior to landing on the moon or Mars, astronauts will experience 3 days to 6 months of microgravity exposure preceding the transition to hypo-gravity. Diminished perceptual ability in an operational hypo-gravity environment (e.g., landing on the moon) could be further worsened by motion sickness drugs (Diaz-Artiles et al. 2017)

Gender Differences

We did not find any substantial differences in roll tilt perception between females and males in our study, although we acknowledge that we are limited by a small sample size. This is consistent with previous studies typically failing to find sex/gender differences in sensorimotor performance of adaptation to altered gravity (Bermudez Rey et al. 2016; Reschke et al. 2014). Inter-individual differences in perceptual gains were relatively large within each phase, including the 1Gc baseline phase (Figure 4B). These differences in perceptual gains between subjects were larger than the changes in perceptual gain between 1Gc and initial exposure to 0.5Gc and between initial and final 0.5Gc phases. Nonetheless, even with these individual differences, our hypothesized changes in perception were seen in the group mean gains as well as in the majority of individual subjects.

Model Fit and Müller Effect

The models discussed in this paper made a number of assumptions. A primary assumption was that there is a linear relationship between actual and perceived angles across the range of angles tested in our experiment. We showed evidence of a Müller effect (Müller 1916) in our data, in that smaller roll tilt angles tended to be overestimated compared to larger angles, particularly in the 1Gc baseline and initial 0.5Gc phases (Figure 5). This would suggest a nonlinear relationship between actual and perceived angles. However, refitting our models excluding the two smallest angles (±10, 15 degrees) resulted in fit gains not different from those fit when all angles were included, suggesting that the overall impact of the Müller Effect was relatively small, and that the assumption of a linear relationship between actual and perceived angles did not confound our conclusion. We also made the assumption in our modeling effort that the change in perception during 0.5Gc-VFB (Phase 3), matched the behavior of an exponential decay curve. There are a number of behaviors associated with adaptation and learning. For example, there could be a sudden discrete shift indicating a change in strategy or consistently gradual changes explained with a linear fit. Although we cannot entirely rule out these alternatives, using an exponential decay curve gave us reasonable model fits with normally distributed and homoscedastic residuals, suggesting that the change in perceptual gain in 0.5Gc-VFB was consistent with exponential decay.

Our study was not meant to focus on changes in perceptual bias due to changes in gravity level, however we did observe a systematic rightward bias shift immediately after the decrease in centripetal acceleration. Specifically, in addition to a reduced gain in 0.5Gc, subjects tended to have a bias towards perceiving the direction of centripetal acceleration slightly to the right of where it actually was. Harris et al. (2014) found a slight (2-3 degrees) leftward bias in "perceptual upright" (PU), using a centrifuge to produce ≤1Gc centripetal acceleration aligned with the body axis (i.e., no tilt). Bias in PU has been attributed to body senses (i.e., idiotropic vector) (Barnett-Cowan et al. 2013). The leftward bias in their study appears similar across a range of hypo-gravic conditions and in 1Gc. This differs from our finding of a rightward bias initially in 0.5Gc and no significant bias in 1Gc, potentially due to different perceptual tasks (PU vs. SVV) or tilt conditions (aligned vs. tilted relative to centripetal acceleration). The centrifuge spin down from 1Gc to 0.5Gc causes a small tangential acceleration which, for our clockwise spin, tilted the net inertial force to the subject's right (consistent with a rightward bias in tilt perception). However, the peak misalignment is only 0.15 degrees (compared to a ~3 degree bias) and subjects do not report until at least 40 seconds after the tangential acceleration ends, making it an unlikely source. The shift in bias we observed in 0.5Gc is intriguing and worthy of further investigation.

Finally, one might reasonably question the validity of a model with 28 free parameters (i.e., model #4 in Table 1). However, recall that 27 of these parameters in the overall fit were just 3 parameters (K_0, K_I, K_F) that were allowed to differ between individual subjects (N=9, such that 3x9=27). For each subject, gravity changes in orientation perception (49 reports per subject) were modeled with just these 3 parameters, plus one (the time constant of perceptual adaptation τ) which was shared across subjects. It seems reasonable that individuals would possess unique values for each of the three perceptual gain parameters (K_0 for the perceptual gain 1Gc, K_I for that initially in 0.5Gc, K_F for that in 0.5Gc-POST). In fact, we hypothesize there are also substantial inter-individual differences in the adaptation time constant (τ); however with our data this yielded a slightly higher BIC (model #2 in Table 1).

Limitations and Advantages of the Hypo-Gravity Paradigm

The use of a short-radius centrifuge to create a hypo-gravity environment has advantages over parabolic flight testing, primarily lower costs, longer possible exposure periods, and lower likelihood of motion sickness. Centrifugation does however introduce a gravity gradient, with gradually higher centrifugal force at the feet than at the head. In our seated configuration, the "gravity force" was 108% and 135% larger at the seat and feet, respectively, than at the head. While the ratio of gravity-gradient was the same between the 0.5Gc and 1Gc conditions, the difference in centripetal acceleration at the feet vs. head was 0.74 G for 0.5Gc and 1.48 G for 1Gc. How these gravity-gradients affected somatogravic cues throughout the body, impacting tilt perception, is unclear.

Additionally, we reiterate that in our 0.5Gc condition differs from to a true hypo-gravity environment (i.e., as would be experienced on a less massive body, such as the moon or Mars) due to the always present background 1 G in the subjects' x-axis. This causes the magnitude of the net gravito-inertial to be greater than 1 G and its direction to pitch relative to the subject. In the 1Gc condition, the net gravito-inertial at the head is 1.41 G ($\sqrt{1^2 + 1^2}$) and pitched 45 degrees ($\tan^{-1}(1/1)$) backwards relative to the subject. In 0.5Gc, it is 1.12 G and pitched back 63 degrees (where just gravity when supine without centrifugation corresponds to pitched back 90 degrees). Subjects did not perform a psychophysical task to quantify their pitch perception, but did not verbally report a confusing sense of pitch tilt. Specifically, subjects were able to successfully report their perception of static roll tilt in the coronal plane without conscious interference of the orthogonal Earth gravity force. On average, subjects perceived their orientation in 1Gc fairly accurately, consistent with previous experiments in which upright subjects were tilted relative to gravity, particularly for the <30 degree angles employed here (De Vrijer et al. 2009). In addition with a small group of subjects (N=5, two of which participated in the primary supine study), we reconfigured our motion device to quantify upright 1G roll tilt perception using the same equipment, SVV task, and procedures. The roll tilt perceptual gain in upright 1G (mean=1.04, 95% CI: 0.80-1.28) was similar to that in the supine 1Gc condition (mean=1.11, 95% CI: 0.76-1.46) and did not statistically differ (two sample t-test, difference in gain=0.07, p=0.58). The inter-subject variability in perceptual gain tended to be lower in the upright 1G condition (sample standard deviation of perceptual gains of 0.17 vs. 0.43 in supine 1Gc), but did not significantly differ (F-test for equality of variances, p=0.09). Lastly, although testing was done in a dark room and in a cab to eliminate external visual cues, proprioceptive and tactile cues could not be completely eliminated, and it is unclear how the brain may have interpreted the varying forces on the body due to the gravity gradient.

Despite these limitations, this hypo-gravity paradigm (i.e., 0.5Gc) provides three substantial benefits. First, spaceflight and suborbital flight can provide microgravity (near 0 G) but not easily G levels between 0 and 1 G, and at relatively high expense. Our paradigm can create any hypo-gravity level relatively easily and inexpensively. Second, our paradigm allowed us to measure alterations to a subject's orientation perception *immediately* after a gravity transition. Particularly, in comparison to tests of adaptation post-spaceflight, upon return to Earth, this represents a substantial improvement (Clément and Wood 2014; Parker et al. 1985; Young et al. 1984). Typically, such tests are only able to gain access to astronauts a few hours to days after landing. For example, a recent study (Clément and Wood 2014) found post-spaceflight (11-15 day Space Shuttle missions) that static roll tilt was overestimated relative to pre-flight. However, dynamic roll tilt perception did not significantly change relative to pre-flight. Such results might be impacted by the fact that testing does not occur until an hour or longer after landing. This uncontrolled exposure to 1 G would presumably drive readaptation prior to experimental measurements begin.

A notable exception is one study that investigated orientation perception in space using a centrifuge to create gravito-inertial stimulation (Clément et al. 2001). Also, the International Microgravity Lab-1 (IML-1) rotator could be configured in either yaw, pitch, or roll with the subjects' head slightly off-axis to produce centripetal acceleration (Reschke 1992). However neither device allowed for providing various tilt angles. Our test paradigm for hypo-gravity exposure allows for orientation perception measurements within one minute of the gravity transition.

A third benefit is that we can study adaptation in perceptual responses from initial exposure over an extended period of time. This is a benefit as compared to previous parabolic flight experiments (Clark and Young 2017; de Winkel et al. 2012; Dyde et al. 2009), which have only 20-30 seconds of hypo-gravity at a time interleaved with ~1.8 G "pull out" maneuvers. Understanding the timing of perceptual adaptation is important for future spaceflight operations that may occur during or immediately after a transition into a new gravity environment, such as piloted landing or emergency vehicle egress.

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Figure Captions:

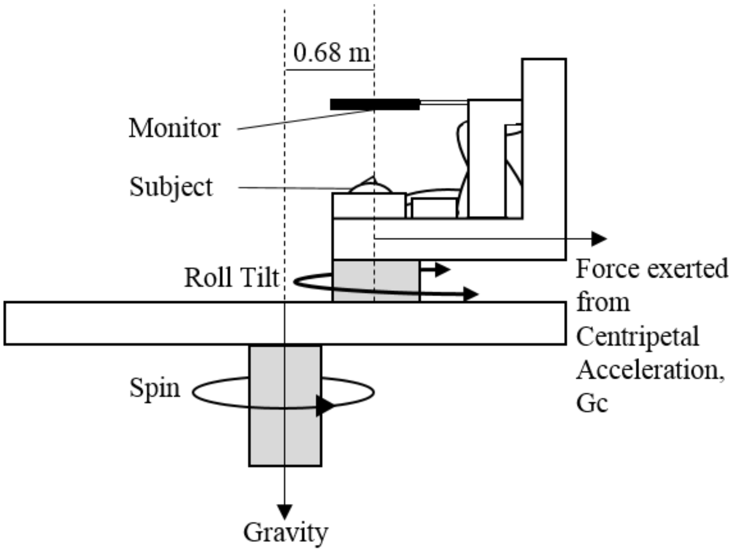

Figure 1. The Eccentric Rotator has a primary spin axis used to create centrifugal force in an Earth horizontal plane, and a servo-controlled subject chair located off the spin axis to independently roll tilt the subject. In each trial, the subject adjusted a luminous line presented on a monitor so it aligned with their perceived direction of the centripetal acceleration. A light-tight enclosure (not shown) around the subject’s head and monitor eliminated Earth-fixed visual and wind cues during testing.

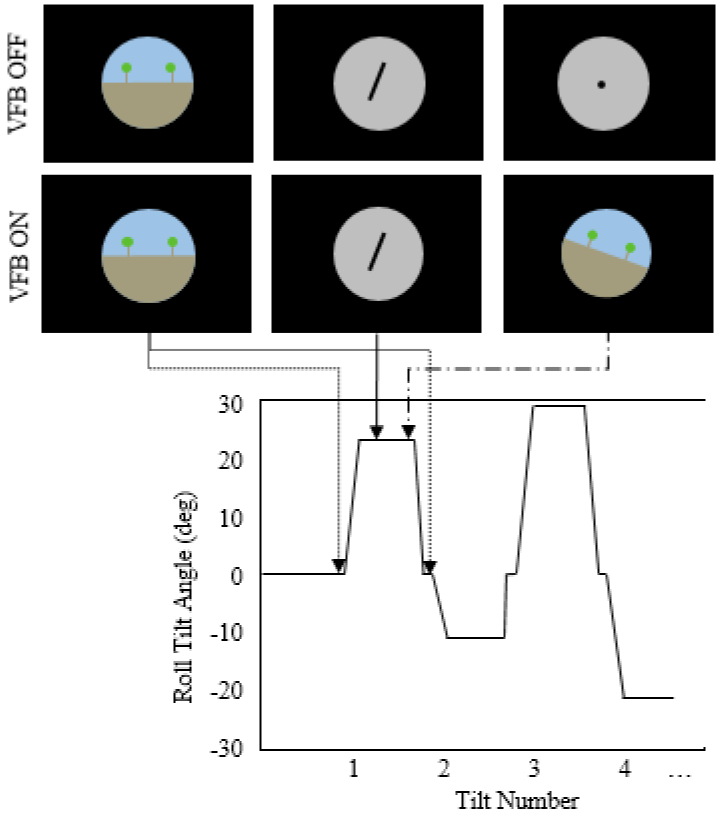

Figure 2. Bottom plot shows roll tilt angle vs. tilt number for four successive static tilts. The display above shows the visual stimulus presented on the monitor in front of the subject at each time point during a tilt. When displayed, the schematic of the brown/blue horizon and trees was always aligned with the centrifugal force direction. The top row shows the sequence of visual stimuli during a Visual Feedback (VFB) OFF tilt, in which the horizon schematic was only shown when upright (providing no feedback regarding tilt). The bottom row shows the visual stimuli provided during a VFB ON tilt, in which the horizon schematic was also shown at the end of each tilt, providing visual feedback. In either case, during the first portion of each tilt the subject performed the SVV task with a black indication bar. Any time the chair was being rolled to a new position, a black center fixation dot (e.g., top right panel) was shown.

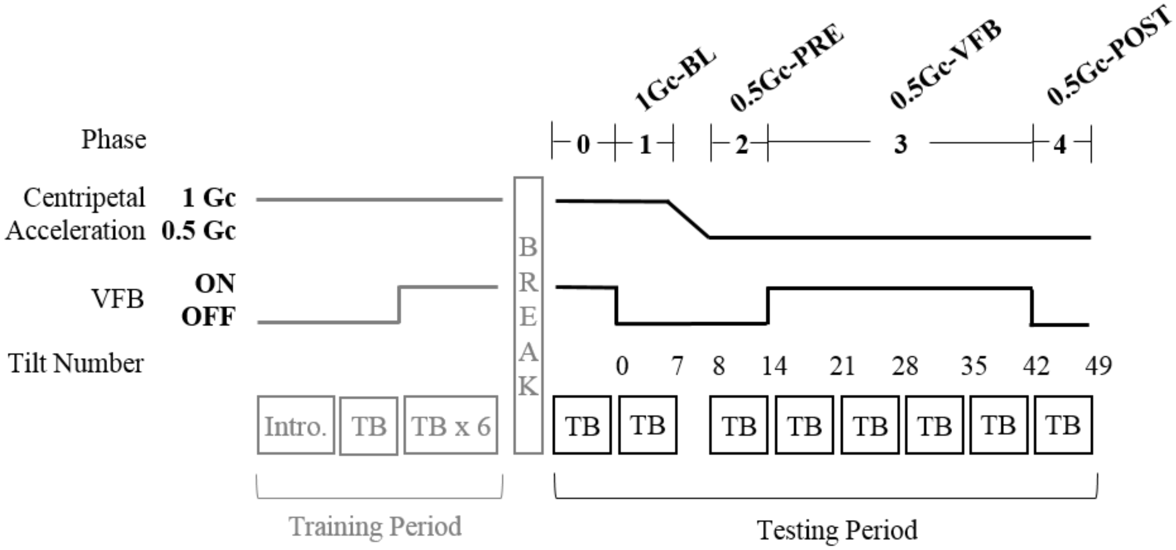

Figure 3. The experimental sequence included training and testing periods made up many tilt blocks (TB), with a break between. The experiment phase, centripetal acceleration, and VFB state are specified for each tilt block completed. The experiment had phases 0-4. Phase 0 refamiliarized the subject, Phase 1 provided a 1Gc baseline (1Gc-BL), Phase 2 transitioned to 0.5Gc (0.5Gc-PRE), Phase 3 then provided visual feedback in 0.5Gc (0.5Gc-VFB), and finally Phase 4 assessed perception at the end after providing visual feedback (0.5Gc-POST). (The gradual centrifuge spin up/down that occurred at the beginning/end of each period is not shown).

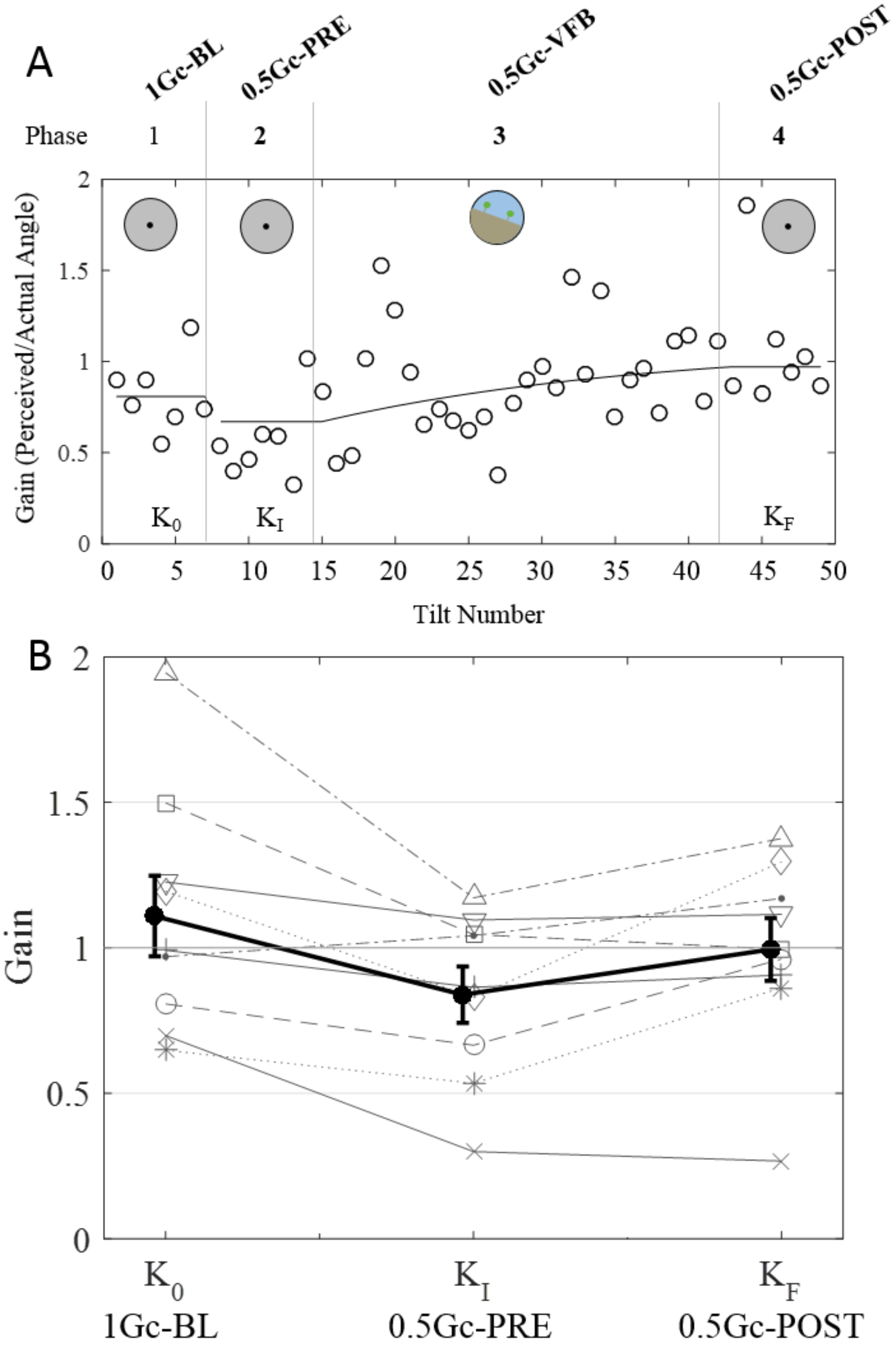

Figure 4. A: Perceptual gains for an example individual subject measured in Phases 1-4 of the Testing Period. Expected perception behavior is exhibited in this subject: a decrease in gain from near unity in 1Gc-BL (Phase 1, $K_0 = 0.81$) when entering 0.5Gc-PRE (Phase 2, $K_I = 0.67$). Then a gradual increase in gain throughout 0.5Gc-VFB (Phase 3) yielding a gain again near unity in 0.5Gc-POST (Phase 4, $K_F = 0.96$). B: Fit gains K_0, K_I, K_F from the model described in Equation 1 in 1Gc-BL (Phase 1), 0.5Gc-PRE (Phase 2), and 0.5Gc-POST (Phase 4), respectively for all subjects (gray shapes). The black circles and error bars represent the group mean gain and standard error (N=9 subjects), shifted horizontally slightly for clarity.

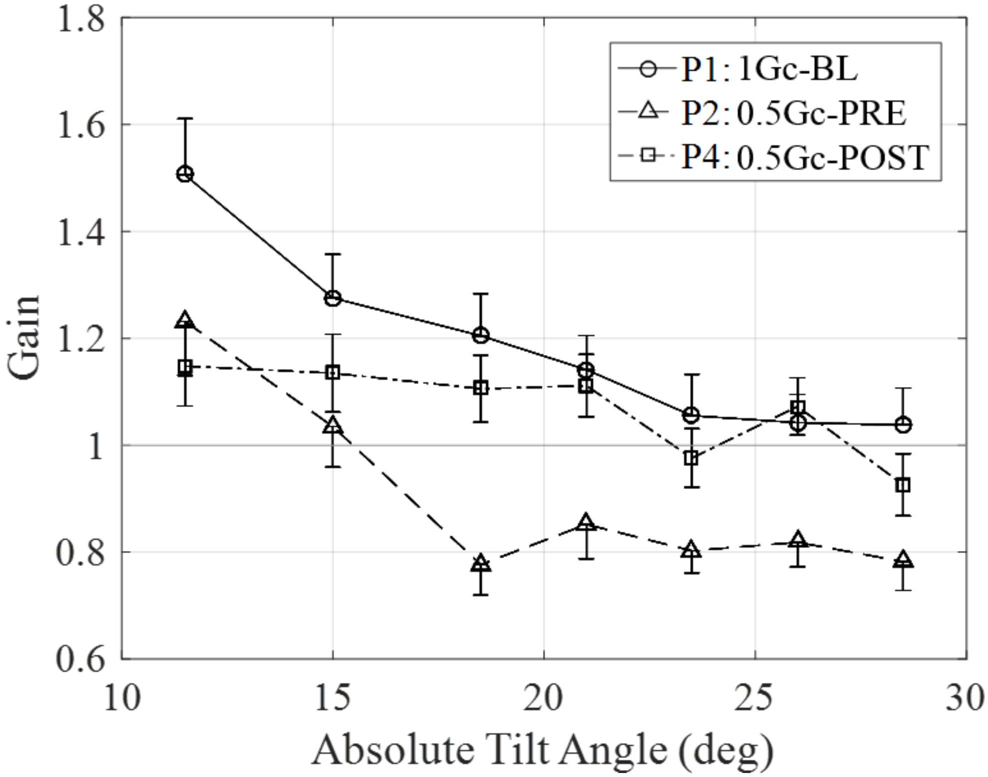

Figure 5. Group mean perceptual gains and standard errors for each static roll tilt angle within Phases 1 (1Gc-BL), 2 (0.5Gc-PRE), and 4 (0.5Gc-POST) (N=9 subjects).