Human Perceptual Overestimation of Whole-Body Roll Tilt in Hyper-Gravity

Running title: Roll Perception in Hyper-Gravity

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Abstract

Hyper-gravity provides a unique environment to study human perception of orientation. We utilized a long-radius centrifuge to study perception of both static and dynamic whole-body roll tilt in hyper-gravity, across a range of angles, frequencies, and net gravito-inertial levels (referred to as G-levels). While studies of static tilt perception in hyper-gravity have been published, this is the first to measure dynamic tilt perception (i.e. with time-varying canal stimulation) in hyper-gravity using a continuous matching task. In complete darkness, subjects reported their orientation perception using a haptic task, whereby they attempted to align a hand-held bar with their perceived horizontal. Static roll tilt was overestimated in hyper-gravity, with more overestimation at larger angles and higher G-levels, across the conditions tested (overestimated by ~35% per additional G-level, p<0.001). As our primary contribution, we show that dynamic roll tilt was also consistently overestimated in hyper-gravity (p<0.001) at all angles and frequencies tested, again with more overestimation at higher G-levels. The overestimation was similar to that for static tilts at low angular velocities, but decreased at higher angular velocities (p=0.006), consistent with semicircular canal sensory integration. To match our findings, we propose a modification to a previous Observer-type canal-otolith interaction model. Specifically, our data were better modeled by including the hypothesis that the central nervous system treats otolith stimulation in the utricular plane differently than stimulation out of the utricular plane. This modified model was able to simulate quantitatively both the static and the dynamic roll tilt overestimation in hyper-gravity measured experimentally.

Introduction

Humans normally perceive their own orientation relative to gravity by utilizing a combination of several sensory cues, including vestibular, proprioceptive, tactile, and visual. In this study, we totally eliminate visual cues and focus primarily on rotational cues provided by the semicircular canals and gravito-inertial cues provided by the otolith organs as well as other potential contributors (e.g., tactile, somatosensory).
Hyper-gravity, or an environment of greater than the 1 Earth G normally experienced, provides a
unique stimulus for studying vestibular perceptual function. In hyper-gravity, all graviceptor sensory
signals, such as those from the otolith organs, are altered, while the semicircular canal cues are
presumed unaffected.

Previous studies have utilized a short-radius centrifuge to create a hyper-gravity environment and
then subsequently had subjects report their static roll tilt perceptions with a subjective visual vertical
(SVV) task (Aubert 1861). Using this task, subjective measurements indicated that the subjects
overestimated their roll angle in hyper-gravity when statically tilted (Colenbrander 1963; Correia et al.
1968; Miller and Graybiel 1966; Schöne 1964; Schöne and Parker 1967; Schöne et al. 1967). These
perceptual errors in hyper-gravity contrast with those observed in 1 G, often measured using the SVV
task; one-G errors typically are near veridical for smaller roll tilts, but show underestimation for large
angles (>60 degrees) (De Vrijer et al. 2009; Kaptein and Van Gisbergen 2006; van Beuzekom and

Several more recent investigations have studied hyper-gravity perception (Chelette et al. 1995;
Glasauer and Mittelstaedt 1992; Jarchow et al. 2003; Jia et al. 2002; Merfeld et al. 2005a; Merfeld et
al. 2001) and reported results that are consistent with those reported above. For example, Tribukait
and Eiken have completed a series of studies investigating orientation perception during centrifuge
spin up (Tribukait and Eiken 2012; 2006a; 2005; 2006b). However, studies of perception in sustained
hyper-gravity in the presence of dynamic canal stimulation have been rare (Gilson et al. 1973; Guedry
and Rupert 1991). One of the challenges of studying dynamic perception in hyper-gravity is that
dynamic out of plane head rotations in a fast spinning environment, such as a short-radius centrifuge,
will result in a secondary Coriolis cross-coupled illusion (Graybiel et al. 1960; Guedry and Montague
1961; Melville Jones 1970). (To help minimize any potential confusion, we will use “rotation”
throughout only to refer to the roll rotation experienced during the experimental roll tilt stimuli, we will
use “spin” or “spun” to refer to the planetary motion of the centrifuge.)

In order to produce a hyper-gravity environment with limited angular velocity, and thus less
cross-coupling, a larger radius is required. One technique was to use a high-performance aircraft
performing a coordinated turn to create the hyper-gravity environment (Gilson et al. 1973). Subject made active head tilts within the aircraft and reported illusory motions; however the reports were qualitative and verbal, so it was not possible to quantify the magnitude or dynamics of the illusion. The authors hypothesized that dynamic tilt perception differs from static tilt perception, suggesting this warrants further study.

This was a primary reason for the experimental studies reported herein. More specifically, using a long-radius centrifuge, we sought to quantify both static and dynamic roll tilt perception in hyper-gravity. Measures of static roll tilt perception provided data for direct comparison to the dynamic responses. We hypothesized that both static and dynamic roll tilt would be overestimated in hyper-gravity, with more overestimation at larger angles and higher gravity levels. Furthermore, for dynamic roll tilts, we hypothesized that the amount of overestimation would depend upon the angular velocity, or speed, of the rotation due to the contributions of the semicircular canals.

While the otolith organs are the body’s only sensors specifically focused on transducing gravito-inertial acceleration, other sensory systems might also contribute. Therefore, we specifically note that our studies, like most others (Colenbrander 1963; Correia et al. 1968; Merfeld et al. 2001; Miller and Graybiel 1966; Schöne 1964; Tribukait and Eiken 2006a), cannot directly distinguish gravito-inertial signals provided by the otolith organs from gravito-inertial signals provided by other somatosensors. However, before proceeding, we note two additional facts that suggest a predominant contribution of the otolith organs. First, data show that fully-compensated patients suffering total vestibular loss have tilt thresholds that are on average about twice as big as normal (Valko et al. 2012) – demonstrating that the otolith organs have about twice the precision of all other graviceptor cues combined. Second, as will be presented and discussed in detail later, our findings suggest that cues in the utricular plane are emphasized relative to those out of the utricular plane, which suggests a primary vestibular influence on the processing of gravito-inertial cues.

Several mathematical models have been proposed to explain the overestimation of static roll tilt observed in hyper-gravity. Early on, the utricular shear (Schöne 1964; Schöne and Parker 1967; Schöne et al. 1967) and tangent models (Correia et al. 1968) were proposed to approximate the static
overestimation observed in hyper-gravity by modeling only otolith stimulation. A non-linear model of otolith function was constructed to predict tilt perception over a range of altered gravity levels and orientations (Dai et al. 1989). More recently, a model was developed to predict static orientation perception in altered gravity environments using otolith and tactile cues (Bortolami et al. 2006b).

Mittelstaedt proposed the concept of an “idiotropic vector” (1983a; 1989; 1986), an internal mechanism which drives perceptions in the direction of a person’s own longitudinal axis. By incorporating non-linear otolith transduction (Fernandez and Goldberg 1976b), Mittelstaedt was able to model overestimation in hyper-gravity.

However, none of these models have attempted to predict hyper-gravity perception during dynamic tilts, which is a focus of our study. A variety of dynamic models (MacNeilage et al. 2008) have been proposed for 1 G relating the vestibular system to spatial orientation perception employing physiological and mathematical concepts such as Kalman filters (Borah et al. 1988), extended and unscented Kalman filters (Selva 2009), internal models (Green and Angelaki 2004; Merfeld et al. 1999), particle filters (Karmali and Merfeld 2012; Laurens and Droulez 2007), and three-dimensional rotations (Glasauer 1992; Holly et al. 2011; Holly and McCollum 1996). One of these models is based upon the “observer” concepts from engineering estimation and control theory (Kalman 1960; Kalman and Bucy 1961; Luenburger 1971) that utilize an internal model of a system to evaluate feedback measurements (Oman 1982; 1990). A comparison of the structure of the Observer model to prior Kalman filter models is provided by Selva and Oman (Selva and Oman 2012). This family of Observer models (Merfeld et al. 1993; Merfeld and Zupan 2002; Newman 2009; Rader et al. 2009; Vingerhoets et al. 2009; Vingerhoets et al. 2007; Zupan et al. 2002) can predict a variety of common illusions using only a small set of free parameters.

However, this family of Observer models does not predict the well-established overestimation in hyper-gravity, even for static tilts. In fact, at any hyper-gravity level the Observer model predicts near-veridical perception of static tilt. To our knowledge, a dynamic canal-otolith interaction model has not been proposed that predicts the characteristic overestimation observed for roll tilt perception in hyper-gravity. We modified this previously proposed, relatively well-validated, dynamic model of orientation
perception to mimic the static and dynamic perceptions experimentally observed in hyper-gravity. As
detailed later, we modify the model in accordance with the hypothesis that the central nervous system
differentially weights otolith signals roughly in the plane of the otoliths’ utricular macula versus those
perpendicular to this plane. We acknowledge that the concept of a “utricular plane” is a considerable
simplification since utricular maculae are actually three-dimensional surfaces. However, for simplicity,
we consider only the average plane. As discussed later, the saccule is sensitive to gravito-inertial
stimulation perpendicular to the principle utricular plane and thus is likely a major contributor to
sensing “out of plane” stimulation. Characteristics of afferent neurons for the utricle and saccule
appear to differ (Fernandez and Goldberg 1976b) and there is evidence that both contribute to roll tilt
perception (Rader et al. 2009), potentially in differing amounts (Mittelstaedt 1983a; b).

Methods and Materials

Human subjects reported their perception of static and dynamic roll tilts performed over a range
of actual angles and frequencies, performed at 1, 1.5 and 2 Earth G’s. Subjects reported their roll tilt
perception using a “haptic indicator”, a bar which they could align to the perceived horizontal. They
were trained in its use prior to the experiment. (The perception reporting method we used has
previously been referred to as a “somatosensory task” (Park et al. 2006; Wade and Curthoys 1997).
However to more accurately describe it, we follow the lead of Bortolami et al. (Bortolami et al. 2006a;
Bortolami et al. 2006b) and call it a haptic task.) Since roll rotations on the spinning centrifuge
nominally produce the well-known Coriolis cross-coupled illusion we attempted to reduce the impact
by performing a pre-experimental adaptation protocol. Testing took place over two days. On the first
day, in the following order, the subjects completed the first half of the cross-coupled illusion
adaptation, haptic indicator training, and were introduced to hyper-gravity. The second day consisted
of the second half of the cross-coupled illusion adaptation, refresher training on the haptic task, and
finally all of the hyper-gravity testing sessions.

A previously proposed canal-otolith interaction model for orientation perception (Merfeld et al.
1993; Merfeld and Zupan 2002) was utilized as a starting point for further modification. We modified
the model to incorporate the hypothesis that the CNS weights signals in the utricular plane differently than those out of the utricular plane. The one added free parameter was fit to the static tilt perception observed for a 20 degree tilt in 2 G’s and then the model predictions were compared to the experimentally observed static and dynamic roll tilt perceptions.

**Motion paradigm**

Subjects (N=8) were seated in the cab of the National AeroSpace Training and Research (NASTAR) Center’s ATFS-400 long-radius centrifuge facing tangentially towards the direction of travel (see Figure 1 for motion paradigm). Subjects were restrained with a five-point harness seat-belt. A form-fitting custom head and shoulder support was utilized to restrict roll or yaw head movements and provide support for the torso. Pitch head tilt was also restrained but subjects could actively free their heads in the case of an emergency (e.g. G-force induced loss of consciousness or vomiting). Vacuum cushions provided broad support across the shoulders and upper arms to broadly distribute tactile cues and the interior of the cab was dark to eliminate all 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.

The centrifuge cab was located on the end of the centrifuge arm (7.62 m). The centrifuge was slowly spun up to the desired gravito-inertial force (GIF) level over 60 seconds. During the spin-up 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 (+GZ). 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 the subject’s head level (i.e. within about 5 cm). The gravity gradient along the length of the subject’s body was small due to the large radius of the centrifuge and presumably had a minor impact upon perception. For a 1.83 m (6 foot) tall seated subject, the maximum gradient achieved for the worst-case 2G condition was approximately 0.21 G’s from head to feet and 0.13 G’s from head to buttocks. Once the final G-level was reached, a 60 second wait time...
was provided for the transient effects of the spin-up to subside and to allow for the subjects to become comfortable in the hyper-gravity environment. Subjects then experienced a series of passive, whole-body roll tilts during the testing period. Once complete, the centrifuge was spun-down, also over 60 seconds. Completion of the spin-up, transient wait, testing period, and spin-down took less than 19 minutes.

**Roll tilt profile**

In the hyper-gravity environment, subjects experienced a series of passive cab rotations. The cab rotated about the subject’s body-fixed roll axis (i.e. “x-axis”), with the center of rotation located near the center of the subject’s head. Each rotation went from “upright”, or aligned with the resultant GIF direction, to a specific final angle ($\theta_f$) at a specific frequency ($f$). The rotation profile is given in Equation 1 and was selected because it has no discontinuities in angular acceleration, velocity, or displacement. There is a step in the derivative of acceleration (i.e. jerk) and higher derivatives.

Equation 1

$$\theta(t) = \theta_f \left( ft - \frac{1}{2\pi} \sin(2\pi ft) \right) \quad \text{where} \quad 0 \leq t \leq 1/f$$

The angles tested were 10, 20, and 40 degrees. All of the rotations were to the subject’s left (counterclockwise) except 20 degrees which was also tested to the right (clockwise). This allowed for the evaluation of the hypothesis that there are no directional asymmetries. Leftward tilts were selected as the primary direction because it tilted the cab back towards Earth vertical, leaving the subjects closer to upright if stopped for an emergency.

The frequencies of the changes in roll tilt were 0.0625, 0.125, and 0.25 Hz (or periods of 16, 8 or 4 seconds, respectively). The angles and frequencies were selected to span the region where sensory integration between semicircular canal and otolith cues is believed to occur for dynamic roll tilt (0.1-0.2 Hz) in humans (Merfeld et al. 2005a; Merfeld et al. 2005b; Merfeld et al. 2001; Zupan et al. 2002). The maximum peak angular velocity – just 20 degrees/second for the combination of 40 degrees at 0.25 Hz – does not yield large Coriolis cross-coupled stimulation, which roughly scales with angular velocity as well as net angular displacement. After the cab tilt was completed it remained in the
resulting orientation for 30 seconds and then followed the reverse profile back to “upright” with respect
to the GIF direction. After another 30 second stationary period at upright, the next roll tilt began. An
example complete profile is shown in Figure 3.

Independent variables
Each of the 12 roll tilt combinations (3 frequencies x 4 angles) was presented once per session in
a randomized order. Subjects remained naïve that either specific roll angles or frequencies were
presented and this was confirmed in post-testing debriefs. The 12 roll tilt combinations within a
session were tested at a specific gravity level: either 1, 1.5, and 2 G’s. Each G-level was presented
twice, for a total of six testing sessions. Subjects were removed from the centrifuge cab and had a
break of at least 20 minutes between sessions. The gravity levels for each session were presented in
counterbalanced orders with each gravity level presented in one of the first three sessions and one of
the last three sessions.

Dependent variables
During the 12 roll tilts, subjects reported their perceived roll orientation using a horizontal “haptic
indicator” (Wade and Curthoys 1997). The horizontal haptic task has been well validated in a variety
of other studies, especially those focused on assaying dynamic effects (Merfeld et al. 2001; Park et al.
2006; Rader 2009; Rader et al. 2009; 2011; Wade and Curthoys 1997; Zupan and Merfeld 2003). This
task was selected due to several advantages for our specific goals. First, using a haptic task allowed
us to totally eliminate all visual cues, which we felt was critical to avoid dynamic visual-vestibular
interactions for this quantitative study of dynamic tilt perception in hyper-G. Second, as compared to
visual techniques (i.e. SVV), haptic responses are not potentially contaminated by torsional eye
movements (Betts and Curthoys 1998; Goonetilleke et al. 2008; Wade and Curthoys 1997). This is
especially a potential confound in hyper-gravity where it is well known that ocular counter-rolling is
enhanced (Colenbrander 1963; Miller 1962; Miller and Graybiel 1971; Woellner and Graybiel 1959).
Third, the SVV task is traditionally used for static roll tilt perception, while one of our foci is to study
dynamic perception. Several studies have extended this technique to dynamic tasks using repeated
stimuli presented via an adaptive staircase and forced-choice responses (Kaptein and Van Gisbergen 2006; Vingerhoets et al. 2008; Vingerhoets et al. 2007). However, this method requires many (>10) presentations which was not feasible in hyper-gravity, both for subject comfort, but also because subject responses were likely to adapt with repeated presentations. Fourth, as compared to vertical haptic tasks, typically done with a single hand (Barnett-Cowan and Harris 2008; Bauermeister et al. 1964; Borah and Young 1982), fewer left/right asymmetries are likely to occur for a horizontal task due to its symmetric nature. Fifth, as compared to other discrete tasks (e.g. verbal reports or “perceptual upright” P vs d differentiation (Dyde et al. 2006) it is possible to obtain temporally continuous reports.

The indicator consisted of a 30.5 cm long metal bar, which pivoted at its center point and was connected to a potentiometer (Vishay Spectrol 601HE0000B01 Hall Effect Position Sensor) for recording the response. The bar was located approximately 35 cm from the midriff of the seated subject (Merfeld et al. 2001). Subjects were instructed to hold the indicator at the ends with each hand using their finger tips and were not allowed to move their hands along the length of the bar (Merfeld et al. 2001; Park et al. 2006; Zupan and Merfeld 2003). Subjects attempted to keep the bar aligned with their perceived gravitational-horizontal continuously. At the end of each trial, 10-15 seconds after returning to upright, subjects performed an “indicator reset”, in which they quickly deflected the indicator by at least 40 degrees in each direction several times and then attempted to reset it to horizontal. This action was aimed at making the initial perception for the ensuing trial independent from the final perception of the previous trial. The subject’s perceptions were compared to the actual orientation of the cab with respect to the GIF direction, as recorded from the simulator. The haptic indicator only rotated in roll so any perceived pitching or yawing rotation could not be reported.

The experimental design was fully within-subjects and complete, such that every subject experienced every combination of roll angle, roll frequency, and gravity level. The repeated measures design allowed for fewer total subjects, reducing the time spent completing pre-experimental protocols. The complete design was necessary to study interactions among independent variables.
There were two replications of each treatment level combination in order to test if adaptation was taking place.

**Cross-coupled stimulus adaptation protocol**

As previously described, 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, orthogonal to head roll rotation and centrifuge spin axes. To minimize the impact of the cross-coupled illusion during dynamic rotations on a centrifuge, we utilized both a large radius rotator and a pre-adaptation protocol (Brown et al. 2002; Cheung et al. 2007; Young et al. 2003) prior to hyper-gravity testing on the centrifuge. The following protocol was designed to adapt subjects to this illusion through repeated exposure, such that subjects could effectively report perceptions of roll tilt in hyper-gravity.

In the dark, upright subjects were passively spun in pure yaw. Subjects repeated a series of four active, head-on-body roll tilts, always in the same order: 1) from upright to right ear down, 2) right ear down back to upright, 3) upright to left ear down, and 4) left ear down back to upright. The cross-coupled stimulus adaptation protocol consisted of three phases. In the main (chronologically second) phase, the subject was incrementally adapted to the cross-coupled illusion by manipulation of the spin rate. The spin rate began such that the cross-coupled illusion was near threshold. As the subject adapted and the illusion became sub-threshold the spin rate was increased slightly. This process was repeated for 15 minutes, incrementally adapting the subject to the cross-coupled illusion. The threshold-based adaptation technique was advantageous because subjects were only exposed to near threshold level illusions, making it less provocative of motion sickness than other adaptation protocols (Cheung et al. 2007).

In the first and third phases, pre and post measures of the illusion's intensity were taken to measure the adaptation that took place at a fixed yaw rate of 14.26 rpm (the maximum spin rate of the centrifuge in the hyper-gravity tests). The intensity was reported 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 in the pre-measure phase (Brown et al. 2002; Jarchow and Young 2007; Young et al. 2001). For the pre and post measure phases, subjects performed just one series of the four head tilts. The adaptation protocol was performed twice, once the day before the hyper-gravity testing and again the morning of testing.

The mean illusion intensity across head tilt direction decreased as a result of the adaptation protocol. A two-factor (pre vs. post measure and day 1 vs. 2) repeated measures ANOVA found the mean illusion intensity decreased after each adaptation session (F(1,7)=9.6, p=0.018) and on the second day (F(1,7)=37.2, p<0.0005).

We cannot be certain that the cross-coupled stimulus adaptation protocol could not subsequently impact subjects' perceptions during the experiment; however there are a number of responses to suspect that any such impact was minimal. First, there is evidence that adaptation to the cross-coupled stimulus is specific to the particular adapted axis (Garrick-Bethell et al. 2008), such that the adaptation to the cross-coupled illusion in pitch would not affect roll tilt perception. Second, 1 G roll tilt perceptions after adaptation were similar to those previously reported. Third, an individual subject's roll tilt perception in hyper-gravity did not appear to depend upon how much cross-coupled adaptation took place.

**Training**

While the haptic task was quite intuitive, subjects were provided training in 1G prior to the hyper-G test sessions to ensure adequate performance. Subjects were trained by reporting their perceived orientation with the haptic indicator during a 60 second, pseudorandom sum-of-sines roll tilt profile in 1 G (i.e. no planetary centrifuge spin) in the dark. The motion consisted of three non-phase-locked frequencies (0.061, 0.134, and 0.278 Hz), each with an amplitude of 15 degrees, for a maximum potential roll angle of 45 degrees. The first 10 and last 5 seconds of the profile were scaled such that it began and ended at an upright orientation.

Following each trial, subjects received general feedback on performance (e.g. “You reported angles larger than you were exposed to. Try tilting the bar less aggressively.”). Quantitative
performance scores (e.g. root-mean-square (RMS) error from upright) were provided intermittently
every few trials. Subjects repeated trials until their performance, measured by RMS error, improved to
a steady state. Usually 10-18 trials were presented in the primary training session on the first day. On
the second day, 3-4 additional training trials were presented just prior to testing to ensure
performance had not degraded. Responses from these pseudorandom sum-of-sines training trials
were fit with a simple input-output model incorporating a bias, gain, and time delay. After training,
generally the biases were near 0, the gains near 1, and time delays ranged from 100-350 ms. This
delay is within the range of previously reported vestibular perception response delays (Barnett-Cowan
2013), despite differences in stimuli utilized and the continuous haptic perceptual task we used.
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. Transitions between gravity levels were 1 minute.
During these training sessions, the roll angle of the cab was controlled to always remain aligned with
the net GIF.

**Subjects**

All protocols were approved by the Environmental Tectonics Corporation (ETC)/NASTAR
Center’s Internal Review Board (IRB) and MIT’s Committee on the Use of Humans as Experimental
Subjects (COUHES). Inclusion criteria were defined prior to the start of the study. Subject inclusion
criteria included healthy females and males ages 18-65, with no known vestibular defects or
conditions. 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; 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 and if a
subject responded “YES” to any of the questions, a FAA Class III Physical was required to participate
in the experiment. No subject met any exclusion criterion, likely because of self-selection among those who volunteered. All subjects signed a written informed consent form.

Eight subjects were tested (5M/3F, ages 21-32 y, mean = 26, standard deviation = 3.2). Two subjects had minimal flight experience (< 50 hrs), two had minimal centrifuge experience (< 6 hrs), and the remainder had no prior flight or centrifuge experience. The subjects with prior experiences did not have results that appeared 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 every subject; however no subjects approached vomiting nor asked to stop the experiment. Due to technical issues Subject 1 only completed 4 sessions (omitting the second 1.5 and 2 G tests) and Subject 2 did not complete the last session at 2 G.

Data Analysis

The subjects’ perception was analyzed at specific points during the rotation profile. A measure of upright static perception was taken at the beginning of each test session just before any tilt motions. Even when upright with respect to the gravito-inertial cue, subjects were instructed to keep the indicator aligned with their perception of gravitational-horizontal, reporting upright relative to perceived gravity, not upright relative to their body orientation. Subjects performed an “indicator reset” and then aligned the bar with their perceived horizontal. The average response over the two seconds just prior to the beginning of the first tilt was taken as a measure of upright perception. The metric for static tilt perception was the average haptic indicator response over the two seconds just prior to the beginning of the dynamic return. This was 28-30 seconds after the end of dynamic tilt (see Figure 3). To statistically test the effect of hyper-gravity on static tilt perception, we used the following hierarchical regression:

\[
(\theta_{\text{per}} - \theta)_{ij} = \rho_i + \beta ((G - 1)\theta) + \epsilon_{ij}
\]

The error in perceived roll in degrees \((\theta_{\text{per}} - \theta)\) from the \(j^{th}\) measurement in the \(i^{th}\) subject were a function of the “G-Excess” term \(((G-1)\theta)\), where G is the gravity level (1, 1.5, or 2 G’s), and \(\theta\) is actual...
roll angle in degrees. In addition, the regression has subject-dependent intercepts (i.e. biases) \( \rho_i \), where \( i = 1-8 \) subjects. In the first stage of the regression, the subject's random effects are accounted for \( \rho_i \), accounting for the within-subjects design. In the second stage, the perceptual errors were regressed on the G-Excess term. This analysis is appropriate for the within-subjects design and treats the effects of gravity and angle as linear over the values tested. The “residual” error on the \( i \)th measurement for the \( j \)th subject is denoted \( \epsilon_{ij} \).

To quantify the perception during dynamic rotations (i.e. tilt or return), a metric was used to compare the perceived roll rotation motion to the actual roll rotation motion. A linear fit was applied to the 50% of the dynamic rotation period that was centered temporally, for both the actual roll rotation and the perceptual response. The slope of the perceptual response \( (m_{\text{per}}) \) was normalized by the actual slope \( (m_{\text{act}}) \) and used as the primary metric for the dynamic rotation perception. The metric was selected because it was robust to subject sensorimotor reaction delays and differences in the perceptual response just preceding the dynamic period. From training data, sensorimotor reaction delays were estimated to range from 0.10 to 0.35 seconds and pre-tilt errors were generally within +/-5 degrees from upright on individual trials. While neither the actual dynamic rotation nor the perceptual responses were linear over the entire dynamic period, over the central 50% both were reasonably approximated as linear. Perceptual responses that had \( R^2 \) values < 0.75 were rare and were excluded from the analysis (16 of 532 for tilts, and 18 of 532 for returns). A normalized slope metric of unity indicates accurate dynamic perception. Slopes greater than or less than one correspond to overestimation or underestimation, respectively. While the slope metric measures the rate of change of perceived roll tilt, we do not consider it a direct measure of perceived angular velocity. Subjects were instructed to instantaneously match the indicator position with perceived tilt, as opposed to match indicator rotation rate with perceived angular velocity. This is an important nuance since perceived angular velocity and changes in perceived tilt are often dissociated (e.g. perceived tumbling from the cross-coupled illusion without comparable changes in perceived orientation).

Dynamic perception can be related to static tilt steady-state perception by comparing the normalized slope metric to a ratio of the static tilt perceived angle to the actual angle.
The normalized slope metric was fit with the hierarchical regression in Equation 3. The regression was designed to test if dynamic perception was effected by G-level, if that effect depended upon angular velocity, and if that effect changed between the first and second session in a particular hypergravity level. The regression controls for subject, angle/frequency combination, and direction (i.e. tilt vs. return) in the first three terms of Equation 3.

Equation 3

\[
\frac{m_{\text{per}}}{m_{\text{act}}}_{ijk} = \rho_i + \lambda_j + \tau \text{DIR} + \beta (G - 1) + \kappa (G - 1) \omega_{\text{peak}} + \delta (G > 1) \text{REP} + \epsilon_{ijk}
\]

In Equation 3, \(\rho_i\) is the intercept for subject \(i = 1\)-8, \(\lambda_j\) is the 1 G response for the jth angle and frequency combination (3 angles x 3 frequencies: \(j = 1\)-9), and \(\text{DIR}\) is the dynamic rotation direction and is either 0 for tilts or 1 for returns. The “residual” error on the \(i\)th subject, \(j\)th angle and frequency combination, and \(k\)th trial is \(\epsilon_{ijk}\). The remaining terms all address the effect of hyper-gravity on the dynamic perceptual response, where \(G\) is the gravity level in G’s, \(\omega_{\text{peak}}\) is the magnitude of the peak angular velocity for the rotation, \(\text{REP}\) is either 0 for the first session at a particular hyper-gravity level or 1 for the second session at that hyper-gravity level. The \(\text{REP}\) term is only active for hyper-gravity levels \((G > 1)\). In 1 G this term is omitted, even on the second session, since we expect there to be no adaptation in 1 G responses. In hyper-gravity, however, we hypothesize that sensory conflict may lead to adaptation or learning. The level of significance for all tests was set to \(\alpha = 0.05\).

**Mathematical Modeling**

We modified the most widely validated canal-otolith interaction model, aiming to mimic the dynamic and static perception observed in hyper-gravity. Details of the model are published elsewhere (Merfeld et al. 1993; Merfeld and Zupan 2002; Newman 2009), so we provide just a brief summary here. We utilized the vestibular pathways of the most recent version of the model (Newman 2009), which is shown schematically in Figure 2. In the model, it is assumed that the CNS neural networks have learned the normal relationships between head orientation and motion and the corresponding semicircular canal and otolith afferent responses. These “internal models” compute expected sensory afference signals (e.g. for the canals and otoliths) which are compared to actual
afference. The resulting “sensory conflict” errors are weighted by constant scalar feedback gains used
to “steer” the perception of orientation to values that minimize the errors. There are five feedback
gains which serve as the only free parameters in model and were set according to the values used by
Vingerhoets (2007), who validating entirely on perceptual data (Table 1). The model describes
perceptions resulting from passive, non-self-generated motions, though the frequency content of
active motions typical experienced (e.g. locomotion) presumably influences the model parameters.
Finally, it is essential to note that in the integration of estimated angular velocity to yield the estimated
gravity vector an internal estimate of the magnitude of gravity is applied. Since the majority of our lives
we operate in an environment in which the magnitude of gravity is near 1 G, we assume this internal
magnitude is properly calibrated to 1 G.

We hypothesized that the limitation in the vestibular observer model preventing the expected
overestimation in hyper-gravity was in the otolith pathways. Therefore, the proposed modification was
made in the otolith pathway ($K_a$ pathway in Figure 2), while the canal and canal-otolith interaction
pathways were left unmodified. We hypothesize that the central nervous system (CNS) treats otolith
stimulation in the utricular plane differently than that out of the plane (i.e. in the direction perpendicular
to the utricular plane). In particular, the relative weighting on the otolith sensory conflict signal is not
the same in all directions; signals resulting from the utricular plane are weighted differently than those
out of the plane (i.e. in the direction of saccule primary sensitivity). As discussed later, the proposed
differential weighting could be related to the differences in the number or sensitivity of utricular vs.
saccular afferent neurons or by our roll tilt task that is more sensitive to utricular contributions.

Previous versions of the Observer model (Merfeld et al. 1993; Merfeld and Zupan 2002; Oman
2002) have all utilized scalar feedback gains, implicitly assuming that rotations around and
accelerations along x-, y-, and z-axes are equivalent. Here, we propose using a vector feedback gain,
specifically for the linear acceleration feedback ($K_a$), to allow for different weightings of the linear
acceleration sensory conflict error ($\vec{e}_a$) in the utricular plane ($K_{au}$) versus out of the plane ($K_{au\perp}$). For
simplicity we left the linear acceleration feedback gain on errors out of the utricular plane ($K_{au\perp}$) at the
nominal value of -4.0. The linear acceleration feedback gain on errors in the utricular plane ($K_{au}$) was then adjusted to $K_{au} = -2.0$, to best mimic the average static perception observed for one specific hyper-gravity case (a 20 degree roll tilt in 2 G's). Note that this decrease in sensitivity for the acceleration pathways in the utricular plane yields an effective relative increase in sensitivity for the tilt pathways in the utricular plane, since the model interprets otolith cues as being due to either tilt or translation (acceleration).

The model was implemented in MATLAB – Simulink 2012a (The MathWorks) software suite. The Simulink model was configured with a variable time-step fourth order Runge-Kutta differential equation solver (ode45 Dormand-Prince). The model was simulated with the same motion profiles applied from the experiment (Figure 3), using a 100 Hz sampling rate. Specifically the roll tilt profile from Equation 1 was simulated (see Figure 3B) at different gravity levels. For simulation purposes each desired gravity level was simulated by modifying the magnitude of gravity in the model as opposed to simulating the complex angular velocity and acceleration profiles involved in the centrifugation paradigm. However, we also performed control simulations with the full centrifugation paradigm and found no noticeable impact on roll tilt perception. The static perception can also be calculated as a function of roll tilt angle and gravity level analytically instead of using the full dynamic simulation, albeit a numerical equation solver is required (see Appendix for details). To allow direct comparison, static and dynamic perception metrics for the model predictions were calculated as described above for the experimental analysis.

**Results**

Figure 3A shows the subjects' average perceptual report from the haptic indicator during an example roll tilt profile in each gravity level: the 20 degree roll at 0.125 Hz. Gravity level dramatically altered roll tilt perception. In 1 G, subjects perceived their orientation fairly accurately with only slight delay errors during dynamic tilt, dynamic return, and post-return responses. However, in 1.5 G, subjects overestimated their roll tilt, both in relation to the actual roll angle and the 1 G perception. The perceptual error was even larger in the 2 G case. Figure 3B shows the modified model's
predicted perceptions for the same stimuli. As desired, the model predicts a fairly accurate perception
of the roll tilt profile in 1 G, but yields static and dynamic overestimation in 1.5 G and 2 G. The
predicted time courses mimic those observed experimentally (Figure 3A) across each gravity level
and each phase of the tilt profile.

**Upright static perception**

A repeated measures ANOVA with gravity level as the independent variable found there to be no
evidence that hyper-gravity affected upright roll tilt perception (p = 0.71). Even in hyper-gravity,
reported roll tilt perception was veridical (i.e. upright when untilted). This is consistent with previous
studies using SVV tasks (Colenbrander 1963; Correia et al. 1968; Miller and Graybiel 1966; Schöne
1964; Schöne and Parker 1967; Schöne et al. 1967).

**Static tilt perception**

The static perception of roll angle is plotted versus actual roll angle relative to the GIF in Figure
4A. To more clearly view the effects of the gravity level, the error in perceived angle (perceived minus
actual) is shown in Figure 4B. Here, and throughout, positive errors indicate a perceived roll angle to
the left (counterclockwise) of the actual angle and negative errors correspond to the perceived angle
being to the right (clockwise) of the actual roll. No evidence was found that static tilt steady-state
perception had any learning or adaptation effects (paired t-tests comparing the same presentation in
session 1-3 to that in session 4-6; p = 0.39 for 1 G, p = 0.23 for 1.5 G, p = 0.51 for 2 G), so the two
presentations were pooled. Furthermore, as expected, the static tilt steady-state perception showed
no evidence of being dependent upon dynamic rotation parameters, particularly the roll frequency (p =
0.46). Thus the presentations of specific angle at each of the three frequencies were pooled. Finally,
no evidence was found that static tilt steady-state perception had any left/right asymmetries (paired t-
tests between -20 and 20 degree tilts; p = 0.12 for 1 G, p = 0.80 for 1.5 G, p = 0.80 for 2 G).

In 1 G, on average subjects accurately perceived their roll tilt, though the -20 degree (to the right)
roll angle was perceived as slightly (2-3 degrees) greater, or more to the right, than veridical. In 1.5
and 2 G, systematic perceptual errors were seen. Positive (to the left) angles had positive errors and
negative angles had negative errors, corresponding to subjects overestimating their roll angle in hyper-gravity, increasing with G-level.

The regression fit in Equation 2 was applied to the static tilt perceptions and the results are given in Table 2. The subject intercepts \( \rho_i \) were found to not be consistently different from zero (t-test), further supporting the observation that, when upright, subjects accurately perceive themselves as upright, even in hyper-gravity. The significantly positive \( \beta \) coefficient supports the hypotheses that 1) hyper-gravity causes overestimation of roll angle, 2) there is more overestimation at greater hyper-gravity levels, and 3) there is more overestimation in hyper-gravity at larger roll angles. In hyper-gravity, the perceptual errors in roll tilt were substantial; across the angles tested, the regression indicates that the overestimation was approximately 17% of the actual roll angle in 1.5 G and 35% in 2 G.

The modified model was simulated across the same range of roll tilt angles and hyper-gravity levels as tested experimentally. The model predicted static tilt perception (as above, calculated as the mean perception from 28-30 seconds after the end of the rotation) was directly compared to that measured experimentally. Even though the added free parameters were selected to fit only a single combination of angle and hyper-gravity level (20 degrees and 2 G’s), the modified model produced appropriate static perceptual responses (Figure 4) across each of the combinations of angles and gravity levels tested.

**Dynamic tilt perception**

We hypothesized that the amount of overestimation in hyper-gravity during dynamic tilt and dynamic return would be dependent upon the roll rotation rate, specifically the peak angular velocity. There was no evidence for left/right asymmetries in the dynamic perception and thus the -20 and 20 degree cases were pooled. Figure 5 shows the dynamic perceptions (tilts and returns combined) as a function of gravity level for each of the angle and frequency combinations tested. Recall from Equation 2 and Table 2 that in 1 G static tilts were, on average, perceived accurately (normalized perception not significantly different from 1), in 1.5 G there was \( \sim 17\% \) overestimation (normalized
perception = 1.17) and in 2 G there was ~35% overestimation (normalized perception = 1.35). These benchmarks of static steady-state tilt perception are overlaid on the dynamic perception data for comparison.

The positive trend in dynamic perception with increasing gravity level, shown in each tile of Figure 5, corresponds to overestimation in hyper-gravity that was greater at higher gravity levels. However, the proportional effect of gravity was not the same for every combination of angle and frequency. At small angles and lower frequencies, corresponding to low peak angular velocities (upper left of Figure 5), the trend with increasing gravity was very steep. At 10 degrees and 0.0625 Hz (Figure 5A) the trend is more extreme than for the static steady-state perception (shown via the horizontal lines). Yet, at larger angles and higher frequencies (bottom right of Figure 5), the effect of G-level on perceived dynamic tilt was much smaller and was clearly less than the normalized static overestimation. To statistically test this, the hierarchical regression fit from Equation 3 was applied and the results are given in Table 3.

The significantly positive β and significantly negative κ coefficients indicate that 1) there was significant dynamic tilt overestimation in hyper-gravity, 2) there was more overestimation at higher gravity levels, and 3) the amount of overestimation depended upon the angular velocity of the roll rotation. In particular, there was more overestimation at lower angular velocities and less at higher angular velocities. The significantly negative δ coefficient indicates that on the second repetition of a particular hyper-gravity level, subjects adapted and overestimated the dynamic rotation a little less than on the first repetition. Finally, in all cases, the magnitude of the slope of dynamic returns was perceived as slightly larger than dynamic tilts. However, the effects of hyper-gravity, angular velocity, and adaptation were similar for tilts and returns.

To visualize the dynamic perceptual response in hyper-gravity and the dependence upon angular velocity Figure 6 shows the data for just dynamic tilts in the first session of each gravity level (no adaptation effect). In 1 G, the dynamic tilt perception is fairly consistent across each angular velocity level tested. In hyper-gravity, there is overestimation in dynamic tilt perception, with less overestimation at higher angular velocities. At low angular velocities, the dynamic tilt perception
approaches the amount of overestimation observed for static tilts in hyper-gravity. Perception during dynamic returns and for the second repetition in hyper-gravity exhibited the same characteristic dependence upon angular velocity in hyper-gravity (not shown graphically) as that in Figure 6 for the first repetition of dynamic tilts.

Modeling dynamic tilt perception

For the Observer model modifications to be relevant, the model must also be able to simulate the experimental perceptions observed during dynamic rotation. To evaluate the model, it was simulated with the same roll tilt profiles utilized at 1, 1.5, and 2 G’s. The peak roll tilt angle was held constant at 10 degrees and the dynamic rotation frequency was varied between 0.0625 and 1 Hz to match the peak angular velocities tested (1.25, 2.5, 5, 10, and 20 degrees/second). To allow for direct comparison, the same metric was utilized to quantify the dynamic rotation perception as was employed for the previous experiment: the slope of a linear fit of the simulated perceived roll angle over the central 50% of the dynamic rotation period normalized by that for the actual roll angle. For each simulation, this metric was calculated specifically for dynamic tilts and compared to the mean experimental perception for the first repetition of dynamic tilts, as seen in Figure 6. For comparison, we also include the model’s prediction for normalized static perception (e.g. perceived angle / actual angle) at each gravity level (gray lines in Figure 6).

The modifications to the model allowed it to produce the characteristic responses of dynamic tilt perception in hyper-gravity. Specifically, the model predictions matched the experimental perceptions in terms of 1) near accurate perceptions in 1 G independent of angular velocity, 2) overestimation in hyper-gravity with more overestimation at higher gravity levels, 3) a characteristic dependence of overestimation in hyper-gravity on angular velocity, with less overestimation at higher angular velocities, and 4) across all dynamic conditions, less overestimation than static tilts. The comparison of experimental perceptions and model predictions for dynamic returns were qualitatively similar (not shown).
In Figure 6, the modified model’s dynamic perceptions were validated against experimental measures at frequencies of 0.0625, 0.125, and 0.25 Hz in hyper-gravity. However, the model can be simulated at a much wider range of conditions to more fully understand its predictions. For example, in Figure 7 it was simulated for a 10 degree roll tilt in 2.0 G’s at frequencies ranging over 500 fold, from 0.015625 to 8 Hz. The same metric was utilized (i.e. the ratio of perceived slope to actual slope for linear fits over the central 50% of the rotation period) and compared to the static overestimation from the model and the actual tilt.

As seen in Figure 7, the modified model predicts that the amount of dynamic overestimation in hyper-gravity varies substantially across frequencies. As expected, at very low frequencies (< 0.05 Hz) the predicted dynamic overestimation approaches the static level. At high frequencies (> 5 Hz) the dynamic perception, even in 2 G’s, approaches the actual motion profile (i.e. no overestimation). At middle frequencies, there is a characteristic dependence of the amount of dynamic overestimation inversely depending on frequency. These predictions are consistent with the hypothesis of sensory integration: the CNS combines information from various sensory sources, weighting them by how useful each cue is. The semicircular canal cue is presumed unaffected by altered gravity, but does not provide a veridical measure of angular velocity at lower frequencies. The canal information is veridical at higher frequencies and should therefore be weighted more heavily relative to otolith signals, reducing the amount of overestimation in hyper-gravity. A similar dependence upon frequency can be seen in dynamic tilt perception in 1.5 G’s (not shown).

Discussion

We characterized and quantified subject perceptions of static and dynamic whole-body roll tilt orientation in 1, 1.5, and 2 G environments across a wide range of tilt angles and frequencies. Static roll tilts in hyper-gravity were overestimated. This finding confirms previous reports (Colenbrander 1963; Correia et al. 1968; Miller and Graybiel 1966; Schöne 1964), but is now supported by statistical analyses. Our study is the first to use a haptic task for indication of the subjective horizontal, whereas previous experiments used an SVV task. The close comparison between measures using the two...
techniques helps validate our haptic task, which was essential for the dynamic measures that form the focus of this study. For the first time, we quantified dynamic roll tilt perception and found it was also overestimated in hyper-gravity, with less overestimation at higher angular velocities. We proposed a novel modification to a previous Observer-type dynamic spatial orientation model to allow it to predict the overestimation in roll tilt perception we experimentally quantified. The modification was based upon the hypothesis that the CNS treats otolith stimulation in the utricular plane differently than that out of plane. The modified model quantitatively matched the static and dynamic perceptions across the range of gravity levels, roll tilts, and angular velocities that we studied.

**Upright static perception**

We characterized and quantified subject perceptions of static and dynamic whole-body roll tilt orientation in 1, 1.5, and 2 G environments across a wide range of tilt angles and frequencies. Confirming previous results, when initially upright, subjects perceived themselves as near upright in roll tilt, even in hyper-gravity. Accurate roll tilt perception in hyper-gravity has been previously attributed by the utricular shear theory to the average plane of the utricles being aligned with the Earth horizontal in roll (Corvera et al. 1958; Curthoys et al. 1999; Schöne 1964). Thus when the head is upright (no roll tilt), there is no additional interaural shear force acting on the otolithic membrane of the utricles when the gravity level is increased. While the current experiment was not designed to test this hypothesis, our perceptual data are consistent with it.

There is some evidence of a small leftward bias (3-5 degrees) in roll tilt perception in 1 G using SVV, “perceptual upright”, subjective saccadic vertical, and even vertical haptic tasks (Barnett-Cowan and Harris 2008; Barnett-Cowan et al. 2013; Dyde et al. 2006; Dyde et al. 2009). However our data suggest that if this leftward bias exists when using the horizontal haptic task it is less than 1 degree or it would have been statistically identified. It is possible the symmetric, two-handed task we utilized reduces the biases observed in a one-handed, vertical haptic task which may depend upon which handed is used (Bauermeister et al. 1964).
During static tilt subjects misperceived their orientation in hyper-gravity. Specifically, subjects overestimated their roll tilt, with more overestimation at higher gravity levels and larger angles. At 1.5 G, the static roll angle was overestimated by approximately 17% of the actual roll angle, while at 2 G’s it was overestimated by 35%. The proportional effects of angle and gravity level should only be applied at the range of angles and gravity levels tested (i.e. ≤ 40 degrees and 1-2 G’s). Prior data (Colenbrander 1963; Correia et al. 1968; Miller and Graybiel 1966; Schöne 1964), which match the current data well at up to the 40 degree angles tested, indicate that at angles larger than ~45 degrees the amount of overestimation begins to decrease with increasing angle. Furthermore, while few studies have tested gravity levels much greater than 2 G, we would hypothesize that at more extreme gravity levels the amount of overestimation would be less than proportional to gravity level. In monkeys, at gravity levels greater than approximately 4 G’s the otolith afferent firing rate for some neurons reaches a limit and no longer behaves near linearly with changes in GIF stimulation (Fernandez and Goldberg 1976a; Fernandez and Goldberg 1976b; c).

As in previous studies (Correia et al. 1968; Schöne 1964), we suspect the overestimation of static roll tilt observed in hyper-gravity is primarily due to increased stimulation of the utricular otolith organs. However, there are other sensory cues that are likely to be affected by hyper-gravity and may influence perception. Tactile cues are likely greater in hyper-gravity. We attempted to distribute tactile cues as evenly as possible (hence minimizing their impact) via body-fitting vacuum cushions. In addition, graviceptive somatosensory cues are likely to be affected by the hyper-gravity environment. Unfortunately our study, like most others previously (Chelette 2001; Correia et al. 1968; Gilson et al. 1973; Guedry and Rupert 1991; Jia et al. 2002; Miller and Graybiel 1966; Schöne 1964), is unable to differentially stimulate the otolith sensors from the somatosensory cues. Thus the role of the somatosensory information in overestimation of static roll tilt in hyper-gravity remains uncertain. In one set of studies (Mittelstaedt 1983a; Mittelstaedt and Fricke 1988), a short-radius centrifuge was used to create a gravity gradient along the subject’s body, allowing for the differential stimulation of the otolith organs in the head and somatosensory cues in the body. However, this paradigm by design provides
a substantive gravity gradient. In contrast, given our goals, we minimized gravity gradients by utilizing a long-radius centrifuge. One study (Miller and Graybiel 1966) utilized labyrinthine-defective subjects (presumably without full otolith function, but with somatosensory information) and found highly variable roll tilt perceptions in hyper-gravity that did not follow the characteristic overestimation observed in normal subjects. Furthermore, total vestibular loss patients exhibit tilt thresholds about twice as high as normal (Valko et al. 2012) suggesting the otolith organs are the dominate contributors to tilt perception in the dark. This tentatively suggests the critical role of the otolith organs, but does not rule out the influence of somatosensory or tactile cues.

The modified model was simulated and found to match the experimental results for static tilts. In particular, static roll tilt perception was predicted over the range of angles and gravity levels tested herein. While the added free parameter was fit to the data in one static tilt condition (20 degree tilt in 2 G’s), the fact the model mimicked the experimental static tilt results across the range of conditions tested suggests more generalized functionality.

While our primary interest was in hyper-gravity perception, as a control we also measured roll tilt perception in 1 G. These perceptions are traditionally characterized by slight overestimations for small angles and then underestimation for very large angles (i.e. at least >60 degrees), commonly referred to as E- and A-effects, respectively (Aubert 1861; Muller 1916). Our 1 G perceptions are near accurate and thus do not appear to exhibit these phenomena. However, we tested at relatively small angles where these effects would be small and difficult to observe. Furthermore, A- and E-effects have been primarily studied using the SVV (De Vrijer et al. 2009; van Beuzekom and van Gisbergen 2000; Vingerhoets et al. 2009; Vingerhoets et al. 2008), whereas we used a haptic task which may not have these same systematic errors in 1 G (Schuler et al. 2010). A- and E-effects have been observed using the vertical version of the haptic task (i.e. the subjective tactile vertical), but the results are inconsistent across studies (Barnett-Cowan and Harris 2008; Bauermeister et al. 1964; Bortolami et al. 2006b; Guerraz et al. 2000; Schuler et al. 2010) and the effects are small (~3 degrees peak) at the angles we tested. For the horizontal haptic task we employed, there is not clear evidence for systematic errors in 1 G (Merfeld et al. 2001; Park et al. 2006; Rader 2009; Rader et al. 2009; 2011).
The modified model also does not produce large A- and E-effect perceptual errors in 1 G, which may be considered a weakness. First, as discussed above, these errors are typically only seen using the SVV methodology and are inconsistent or nonexistent when using a haptic task (Barnett-Cowan and Harris 2008; Bauermeister et al. 1964; Guerraz et al. 2000; Schuler et al. 2010). Second, we note that all previous versions of the Observer model also did not produce substantial 1 G errors in roll tilt perception (Haslwanter et al. 2000; Merfeld et al. 1993; Merfeld and Zupan 2002; Vingerhoets et al. 2008; Vingerhoets et al. 2007; Zupan et al. 2002), and the modification proposed herein was aimed solely at extending the model to mimic hyper-gravity perception. Finally, since the perceptual reports we observed in 1 G were near accurate, the model predictions were consistent with the current dataset.

**Dynamic tilt perception**

As the primary focus of this study, we quantified dynamic roll tilt perception in hyper-gravity. Perceptual overestimation was also seen during dynamic tilts and returns in hyper-gravity. The amount of overestimation was generally less than during static rotations, however overestimation persisted across all angles and frequencies tested. The magnitude depended upon the angular velocity of the rotation; at lower angular velocities relatively more overestimation was observed than at higher angular velocities. In particular, at low angular velocities the amount of overestimation tended to approach that observed for static tilts. The angular velocity dependence of the hyper-gravity effect on perception is supportive of the CNS integrating otolith and semicircular canal sensory sources. The hyper-gravity paradigm affects the otolith signal, but presumably has little or no influence on the canal information. However, it is well known that the canal transduction of angular velocity is bandwidth limited, specifically at lower frequencies or angular velocities (Goldberg and Fernandez 1971). Canal-otolith sensory integration is presumably aware of this canal limitation and the relative weighting within the integration process is thus dependent upon rotation angular velocity (Kaptein and Van Gisbergen 2006; Park et al. 2006). Thus, less overestimation in hyper-gravity at higher rotation rates is consistent with the CNS increasing the relative weighting on the canal signal as transduction...
improves. This canal-otolith integration, dependent upon tilt angular velocity (or frequency if the tilt angle is constant), has been previously observed in 1 G testing paradigms (Angelaki et al. 1999; Park et al. 2006; Vingerhoets et al. 2007; Zupan et al. 2000). The hyper-gravity paradigm is convenient for testing canal-otolith sensory integration because, as the gravity level is increased, the otolith cue is modulated while the canal information is presumably unaffected. This creates a canal-otolith sensory conflict, and the resulting perception indicates the CNS’s weighting of the two conflicting cues.

**Effect of cross-coupled stimulus and adaptation**

In this set of experiments, the hyper-gravity environment was created using a centrifuge. While practical for studying hyper-gravity, the methodology comes with a cost. The spinning environment of the centrifuge causes a secondary illusory perception, the Coriolis cross-coupled stimulus, when any rotations out of planetary spin plane are made. In our centrifuge motion paradigm, the roll tilts utilized will cause a cross-coupled illusion during the planetary spin necessary to create hyper-gravity. This secondary cross-coupled illusion is separate from the primary hyper-gravity induced misperceptions and would not occur in a “pure” hyper-gravity environment such as would be experienced on a more massive planet, or approximated in an aircraft making a very large radius constant bank angle turn.

We took several measures to reduce the intensity of the secondary cross-coupled illusion. The illusion’s intensity is roughly proportional to the planetary spin rate, roll angular velocity, and net roll displacement of a tilt. To reduce the planetary spin rate for a desired hyper-gravity level, a long-radius centrifuge was utilized. The roll angles and frequencies selected were selected to remain within reasonable bounds. Furthermore a pre-experimental cross-coupled adaptation protocol was implemented (Cheung et al. 2007) in order to reduce the subjects’ motion sickness and illusion intensities. Despite all of these efforts, the cross-coupled illusion still occurred on at least one roll tilt trial in hyper-gravity for 5 of the 8 subjects. The illusion occurred significantly more often at higher gravity levels and faster angular velocities, so it may have acted as a confounding factor.

However, the illusion intensities reported, even in hyper-gravity, were generally very low.

Furthermore, data from the 3 subjects who did not perceive cross-coupling did not appear to differ
from data from the 5 subjects who did report small cross-coupling effects. In addition, it should be noted that the cross-coupled stimulus in our paradigm provoked an illusory pitching sensation, while the hyper-gravity induced overestimation of interest was in roll. Subjects were only able to report their roll tilt perceptions using the haptic indicator. The cross-coupled illusion from roll tilt to the right versus left would be in opposite pitch directions and thus if it significantly influenced dynamic roll tilt perception might lead to a left versus right asymmetry. However this was not observed, further suggesting roll tilt was not impacted by the Coriolis cross-coupled illusion. The only way to verify that the secondary cross-coupled stimulus issue did not impact hyper-gravity perception is to repeat the experiments in a non-spinning environment. For example, a high performance aircraft performing a coordinated turn could create hyper-gravity environments at such a low planetary angular velocity that the cross-coupled illusion would be sub-threshold.

**Adaptation in perceptual responses**

Evidence of adaptation in the subjects' perceptual response in hyper-gravity was identified for dynamic rotations, but not static tilts. During testing, there was no feedback provided by the experimenters to help drive this adaptation. Sustained sensory conflict between expected and actual afferent signals, as experienced in hyper-gravity, is well known to drive sensorimotor adaptation (Bos and Bles 2004; Edgerton et al. 2001; Gonshor and Melvill Jones 1971; Kornheiser 1976; Lackner and DiZio 2005; Lackner and DiZio 2003; Nooij et al. 2008; Oman et al. 1980; Oman et al. 1986; Pettorossi et al. 2013; Reason 1978; Reason and Benson 1978; Seidler 2005; Welch et al. 1998).

While sensory conflict probably existed for static tilts in hyper-gravity, there was not significant evidence of adaptation either in repetitions between sessions or within a session. The passive rotations and the lack of strong feedback from a secondary veridical sensory source may have limited adaptation. Studying adaptation was not the primary purpose of the current experiment so only two presentations of each stimulus were repeated. Additional or longer sessions in hyper-gravity may result in significant perceptual adaptation for static tilts in hyper-gravity.
On the other hand, there was evidence for adaptation in hyper-gravity for dynamic rotations. During dynamic rotation there is feedback on the gravity-influenced otolith signal from the semicircular canals. While the rotations were still passive, the canal signal may have helped drive adaptation more quickly than for static tilts. Only two sessions were presented for each gravity level so it remains uncertain how dynamic perceptual errors in hyper-gravity may continue to adapt. We hypothesize that with additional sessions, the dynamic perceptual errors in hyper-gravity would continue to decay towards veridical responses.

Modeling dynamic tilt perception

Model simulations of dynamic roll perception showed the characteristic dependence of the amount of overestimation in hyper-gravity on the angular rotation rate. This is an important contribution because alternative previously proposed models (Bortolami et al. 2006b; Correia et al. 1968; Mittelstaedt 1983a; Ormsby and Young 1976; Schöne 1964) for hyper-gravity perception only simulate static tilt perception. The currently proposed model is the first to fit dynamic tilt perception in hyper-gravity or any altered gravity environment. However, one point of difference between the model predictions and experimental perceptions was in 1 G perception. The experimental dynamic tilt perception was on average approximately 90% of the actual roll tilt slope, and while the model predicts normalized dynamic tilt slopes of slightly less than one, the predicted perception was nearly 98% of the actual roll tilt slope (Figure 6). This difference may be explained by the human sensorimotor response time delay which affected the experimental responses, but was absent in the simulation.

Dynamic roll tilt in hyper-gravity was simulated across a wide range of frequencies, beyond those tested herein. The amount of overestimation had strong frequency dependence. Consistent with the concept of sensory integration, the amount of overestimation was reduced at higher frequencies. At very low frequencies (< 0.05 Hz) the predicted overestimation approaches the static level, while at high frequencies (> 5 Hz), where the canal cues dominate, the tilt perception approaches the actual rotation profile. Other well validated 1 G dynamic vestibular motion paradigms, including earth vertical
yaw rotation, linear acceleration, off vertical axis rotation (OVAR), and post-rotation tilt, were relatively
unaffected by the model modifications (simulations not shown).

**Implications of the model modification**

The modification is based on the hypothesis that the linear acceleration feedback error is
weighted differently in and out of the utricular plane. The difference in weighting could be due to a
difference in the quality and characteristics of the otolith signals in and out of the utricular plane. For
example, the resting discharge rate and sensitivity of otolith neurons from the superior nerve (mainly
innervating the utricle) are slightly greater than those from the inferior nerve (mainly innervating the
sacculus, which includes a component perpendicular to the utricle) (Fernandez and Goldberg 1976b).
Given the differences in the characteristics of the otolith neuron signals approximately within and
normal to the utricular plane, it is reasonable to hypothesize that the CNS might weight them
differently. As to how the CNS differentiates between in and out of utricular plane stimulation, we can
only speculate. Presumably the CNS develops an understanding of the directional polarization vector
of each otolith neuron to facilitate its interpretation. In addition, the CNS may interpret the superior
nerve (mainly innervating the utricle) information and inferior nerve (mainly innervating the sacculus)
information differently. Alternatively, for roll tilt the CNS may more heavily weight the neurons that are
most sensitive for tilts about upright (i.e. those in the y-axis). The precise mechanism of how the
apparent differential weighting occurs will require further investigation.

Instead of the difference being in the utricular plane, one could hypothesize that the difference in
CNS processing occurs between the head horizontal (x-y) plane and vertical directions. The current
experiment focused exclusively on whole-body roll tilt perception in hyper-gravity and thus cannot
distinguish the head-horizontal hypothesis from the utricular plane hypothesis (since head y-direction
and the utricular plane y'-direction are aligned). However, hyper-gravity pitch experiments do not
support the head horizontal versus head vertical hypothesis (Cohen 1973; Correia et al. 1968), where
at orientations less than 30 degrees pitched forward (i.e. nose down), increasing hyper-gravity levels
cause subjects to perceive themselves being pitched nose up. These results suggest the importance
of the utricular plane since only when pitched forward by 30 degrees, aligning the utricular plane with
the increasing GIF, does gravity level not have an effect upon perception. The two independent data
sets are in close agreement and another study shows a similar effect of hyper-gravity on static pitch
perception (Schöne 1964), which increases confidence in the utricular plane hypothesis. In Correia et
al. (1968) and Schöne (1964) whole-body tilts were performed, while in Cohen (1973) the tilts were
head-on-body suggesting that proprioception in the neck is not the primary cause of the pitch
perception asymmetry in hyper-gravity.

The concept of differential processing of otolith signals in the utricular vs. the saccular plane has
previously been proposed. The utricular shear model (Schöne 1964), effectively assumes that
stimulation out of the utricular plane is ignored for orientation perception (i.e. weighted by zero).
Mittelstaedt (1983a) proposed stimulation in the saccular direction is weighted 54% as much as
stimulation in the y-axis (utricular shear for roll tilt) direction. Ormsby and Young’s model (1976)
contained non-linear treatment of signals depending on their orientation relative to the utricular and
saccular directions. Finally, differential weighting has been applied in modeling to roll versus pitch and
yaw angular velocity integration (Glasauer and Brandt 2007). Our modified Observer model builds
upon these concepts in two distinct ways: 1) our differential weighting between in and out of utricular
plane is done to the otolith acceleration feedback error, not directly to the transduced afferent signal
(Mittelstaedt 1983a), and 2) the differential weighting is done within the framework of a dynamic
canal-otolith interaction model, providing dynamic as well as static perception predictions in
hyper-gravity.

Limitations of the model modification
While the modifications within the model are able to explain a wide range of hyper-gravity
perceptual responses, there are still limitations. Our modified version, as well as previous Observer
models (Merfeld et al. 1993; Merfeld and Zupan 2002), predict illusory linear acceleration in
hyper-gravity that was not reported by subjects in terms of illusory sensations of linear movement.
The predicted illusory response in hyper-gravity is caused by the internal model of body dynamics
representing the physical relationship between gravity, acceleration, and GIF ($\mathbf{\ddot{f}} = \mathbf{\ddot{g}} - \mathbf{\ddot{a}}$). Since the internal estimate of gravity is assumed to have a magnitude of 1 G, the excess internal estimate of GIF is attributed to acceleration. Even when the subject is simply upright in a hyper-gravity environment, the model predicts an illusory perception of vertical acceleration upward, both in the modified and unmodified versions. The internal estimate of the magnitude of gravity being 1 G is essential to the model mimicking overestimation in hyper-gravity. If in a 2 G simulation for example, the internal magnitude of gravity is adjusted to 2 G as well, the model will no longer predict illusory acceleration, but it also will not predict the expected overestimation.

There are several potential explanations for why experimental subjects did not report illusory translation associated with the predicted acceleration. First, subjects were presumably aware of the motion capabilities of the centrifuge device. Knowledge or expectation that the centrifuge cab cannot enact translations may quench these sensations that may have existed for an unbiased observer (Wertheim et al. 2001). Furthermore, other non-vestibular cues (e.g. proprioceptive, tactile, and somatosensory) may have helped quench illusory translation percepts. We did not attempt to model either the subjects’ expectation of the device’s feasible motions nor non-vestibular pathways. There is evidence (Merfeld et al. 2001) that during centrifugation when the subject’s precept of orientation is not aligned with the GIF (as is the case during roll tilt in hyper-gravity), horizontal vestibular ocular reflex (VOR) eye movements do occur. The horizontal VOR would correspond to the horizontal linear acceleration observed in the model simulations. An expectation in feasible motions or integration of non-vestibular cues could both explain the divergence between reported perceptions and the VOR response.

Other non-otolith graviceptor (e.g. somatosensory) sensors are likely to be influenced by hyper-gravity. However, we did not attempt to include them in the model since our experimental hyper-gravity paradigm is unable to differentiate between otolith and extra-otolith graviceptors. Future modelling efforts will address this issue.
Acknowledgements

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Appendix

We aim to calculate a closed form solution for the perceived roll tilt angle as a function of the actual roll tilt angle and gravity level \( \theta_{\text{per}} = f(\theta, G) \). As will be seen, this is only possible utilizing a numerical equation solver. However, for the case of static roll tilt we will provide the single equation which can be solved numerically, reducing the complexity compared to the full dynamic simulation.

First, the perceived roll tilt angle, from simple geometry, is given as a function of the perceived direction of gravity:

Equation A1:

\[ \theta_{\text{per}} = \arctan(\hat{g}_y/\hat{g}_z) \]

Furthermore, we assumed the internal model of gravity requires its magnitude to be equal to 1 Earth G:

Equation A2:

\[ \hat{g}_y^2 + \hat{g}_z^2 = 1 \]

For roll tilt with no linear acceleration, the applied gravito-inertial force \( f \) is given by:

Equation A3:

\[ f_y = -G\sin(\theta), \quad f_z = -G\cos(\theta) \]
Given these inputs, assuming that the otolith dynamics and internal model of the otolith dynamics can be approximated by identity matrices, and solving for the upper loop of the Observer model yields the following two relationships:

Equation A4:
\[
\hat{a}_y (1 - K_{a_u}) = \hat{g}_y + K_{a_u} G \sin(\theta)
\]

Equation A5:
\[
\hat{a}_z (1 - K_{a_{u\perp}}) = \hat{g}_z + K_{a_{u\perp}} G \cos(\theta)
\]

Finally, the steady-state of static tilt implies that the error in the direction of perceived gravito-inertial force is infinitesimally small:

Equation A6:
\[
|\hat{e}_f| = 0 = \cos\left(\frac{\hat{a}_f}{|\hat{a}_f|} \cdot \frac{\hat{a}_f}{|\hat{a}_f|}\right)
\]

With the applied gravito-inertial force \(f\) in Equation A3 and the assumption that the otolith dynamics are unity, Equation A6 yields the following relationship:

Equation A7:
\[
\hat{a}_{fy}^2 + \hat{a}_{fz}^2 = \left(-\sin(\theta) \hat{a}_{fy} - \cos(\theta) \hat{a}_{fz}\right)^2
\]

Combining Equations A2, A4, A5 and A7 can yield the following relationship for \(\theta \geq 0\) which contains only terms \(\hat{g}_z, \theta, G, K_{a_u}, K_{a_{u\perp}}\):

Equation A8:
\[
0 = \left[\frac{-1}{1 - K_{a_u}} \sqrt{1 - \hat{g}_z^2 + \frac{K_{a_u}}{1 - K_{a_u}} G \sin(\theta)}\right]^2 + \left[\frac{1}{1 - K_{a_{u\perp}}} \hat{g}_z + \frac{K_{a_{u\perp}}}{1 - K_{a_{u\perp}}} G \cos(\theta)\right]^2
\]
\[
- \left[\frac{-1}{1 - K_{a_u}} \sqrt{1 - \hat{g}_z^2 + \frac{K_{a_u}}{1 - K_{a_u}} G \sin(\theta)}\right] \cos(\theta) - \hat{g}_z \left[\frac{1}{1 - K_{a_{u\perp}}} \hat{g}_z + \frac{K_{a_{u\perp}}}{1 - K_{a_{u\perp}}} G \cos(\theta)\right]
\]

Equation A8 cannot be analytically solved for a closed form solution, \(\hat{g}_z = f(\theta, G, K_{a_u}, K_{a_{u\perp}})\).

However, for a given condition \((\theta, G)\) and set of parameters \((K_{a_u}, K_{a_{u\perp}})\), Equation 8 can be solved numerically for \(\hat{g}_z\). Specifically for \(0 \leq \theta < 90\) degrees, the right side of Equation 8 is \(\leq 0\), and at only one
value of $\hat{g}_z$ does it equal or nearly approach 0, so we numerically find the value of $\hat{g}_z$ which maximizes the right hand side of Equation A8. Once $\hat{g}_z$ is determined, $\hat{g}_y$, is calculated from Equation A2, and then finally the perceived roll tilt angle is calculated using Equation A1. A comparison between the steady-state analytic solution and the dynamic Observer model simulation for static roll tilt perception at 2 G’s is given in Figure 8, showing a near identical match.

References


MacNeilage PR, Ganesan N, and Angelaki DE. Computational Approaches to Spatial Orientation: From Transfer Functions to Dynamic Bayesian Inference. *Journal of Neurophysiology* 100: 2981-2996, 2008.


Figure 1: Schematic of Hyper-Gravity Motion Paradigm, in Quasi-Perspective View. The seated subject is inside the closed cab of the centrifuge (dotted box). The centrifuge spins clockwise ($\omega_{\text{cent}}$) about an Earth-vertical axis, creating an Earth-horizontal centripetal acceleration ($a$), which combines with gravity ($g$) to yield the net gravitational-inertial force (GIF). The cab and subject are then tilted relative to the GIF ($\omega_{\text{cab}}$).

Figure 2: The Vestibular Observer Model. The model flows from left to right. On the left the “experimenter” provides actual motion inputs. On the right the model provides predictions of the human perception of those motions. The model functions in a head-fixed right-handed coordinate system such that the x-axis aligns with the naso-occipital axis, the y-axis aligns with the interaural axis, and the z-axis is perpendicular to the x- and y-axes. The positive direction of the x-axis is forward, of the y-axis is left and of the z-axis is cranial. All of the vectors in the model are then three dimensional, with each component representing the signal along the corresponding [x y z] axis. Details on the pathways are in the text. $K_1 = (K_{\omega} + 1)/K_{\omega}$.

Figure 3: Roll tilt perception in each gravity level for an example case: 20 degree roll tilt at 0.125 Hz. Tile A shows the experimental results. The mean across subjects +/- 1 standard error is shown. Tile B shows the modified model predictions for the same roll tilt stimuli. The dynamic tilt, static tilt, and dynamic return periods are highlighted.

Figure 4: Perceived roll angle (A) and error in perceived roll angle (B) across gravity-levels. Error is the perceived minus the actual roll angle. The mean across subjects +/- 1 standard error is shown. Data points are adjusted along the x-axis so as to not overlap, however all conditions were at -20, 10, 20, or 40 degrees of actual tilt. The modified model predictions are overlaid and match the static overestimation experimental observed in hyper-gravity across the range of conditions tested.

Figure 5: Dynamic Rotation Perception as a Function of Gravity Level by Angle and Frequency. Each tile (A-I) shows one combination of angle and frequency. For comparison, the mean normalized static tilt perception is shown for 1 G (solid line), 1.5 G (dashed line), and 2 G (dot-dashed line).

Figure 6: Dynamic Tilt Perception as a Function of Angular Velocity by Gravity Level. Each tile shows one gravity level: (A) 1.0G, (B) 1.5G, (C) 2.0 G. The mean data +/- 1 standard error are shown. The modified model prediction for dynamic perception is overlaid in black. The modified model prediction for static perception is shown in gray.

Figure 7: Modified Model Prediction of Dynamic Roll Tilt Perceptions in Hyper-Gravity across a Range of Frequencies. Predicted dynamic perceptions in 2 G’s (black dashed-dotted line) are compared to predicted static perceptions in 2 G’s (grey dashed-dotted line) and the actual roll tilt (solid black line). The frequencies previously experimentally tested are marked (squares). All simulations were for a 10 degree roll tilt.

Figure 8: Comparison of Analytic Solution to Model Simulation Results. The model was simulated with a 0, 20, 40, 60, and 80 degree roll tilts in 2 G’s, yielding overestimation (grey squares). The analytic solution (see Appendix) with numerical maximization was solved at a range of angles (dotted black line) and compares well with the full dynamic simulation. In both the model simulation and the analytic solution $K_{\omega u} = -2$. 
### Table 1: Modified Model Residual Weighting Parameters

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<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
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<tr>
<td>$K_{\alpha\psi}$</td>
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<td>Unitless</td>
</tr>
<tr>
<td>$K_f$</td>
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</tr>
<tr>
<td>$K_{f\omega}$</td>
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<td>1/seconds</td>
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<td>$K_{\omega\psi}$</td>
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<tr>
<td>$K_{\omega\omega}$</td>
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### Table 2: Static Tilt Statistical Regression Fit

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<th>Estimate</th>
<th>Standard Error</th>
<th>Z value</th>
<th>p-value</th>
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### Table 3: Dynamic Tilt Statistical Regression Fit

<table>
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<th>Coefficient</th>
<th>Units</th>
<th>Estimate</th>
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<th>Z value</th>
<th>p-value</th>
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<tr>
<td>$\tau$</td>
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<td>$\kappa$</td>
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<td>0.029</td>
<td>-2.26</td>
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</tr>
</tbody>
</table>
Normalized Slope of Dynamic Rotations

Gravity Level [G’s]

0.0625 Hz
0.125 Hz
0.250 Hz

A
B
C
D
E
F
G
H
I

10 degrees
20 degrees
40 degrees