A Case Study of Human Roll Tilt Perception in Hypogravity

Torin K. Clark; Laurence R. Young

BACKGROUND: Increased gravito-inertial acceleration, or hypergravity, such as produced in a centrifuge or in an aircraft coordinated turn, causes humans to systematically overestimate their roll tilt in the dark. This is known as the "G-excess" illusion. We have previously modified a mathematical observer model of dynamic orientation perception to replicate these illusory tilt perceptions. This modified model also made a novel, previously untested, prediction that humans would underestimate acute roll tilt in reduced gravitational environments (hypogravity).

CASE REPORT: In the current study, we used aircraft parabolic flight to test this prediction in a single subject. Roll tilt perception was reported using a subjective visual vertical task in which the subject aligned an illuminated line, presented in a head mounted display, with their perceived direction of down. The same subject made reports during hypogravity parabolas (0.165 G and 0.38 G, corresponding to lunar and Martian gravity, respectively), hypergravity maneuvers (1.6 G during a pull out maneuver and 1.2 G during a coordinated turn), and 1-G control conditions (both on the ground and in straight and level flight). As hypothesized, the subject significantly underestimated roll tilt in the hypogravity environments by approximately 40% compared to 1-G reports while overestimating roll tilt in the hypergravity environments.

DISCUSSION: The amount of underestimation observed was quantitatively consistent with that predicted a priori by the modified observer model. We propose the term "G-shortage" illusion for the underestimation of roll tilt in hypogravity. This illusion may have implications for aircraft pilots and astronauts.

KEYWORDS: observer model, orientation perception, parabolic flight, vestibular, otolith, spatial disorientation.

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At least for smaller angles ($< 45°$), normal human subjects tend to perceive their roll tilt orientation fairly accurately in the normal Earth gravity environment.[1] However, in hypergravity environments (i.e., greater than 1 Earth G, such as would be experienced on a more massive planet, on a centrifuge, or during a coordinated turn in an aircraft), it is well known that humans systematically misperceive their orientation. These misperceptions, known as the "G-excess" illusion,[7] are often characterized by overestimating roll tilt. We recently found subjects overestimated their roll tilt by approximately 35% for each additional G beyond 1 Earth G.[5] The linearity of this effect appears to only be maintained for smaller angles ($< 45°$), beyond which the amount of overestimation tends to decrease.[12]

To model this G-excess illusion, we modified a previous mathematical model of spatial orientation, known as the observer model.[10] The model includes components for the semicircular canals and otoliths (both the utricular and saccular maculae) of the vestibular system and has been validated across a wide range of experimental paradigms.[10] The modified model[6] predicted perception of both roll and pitch tilt in hypergravity for both static tilts and, uniquely, also for dynamic tilts. However, the model made another interesting prediction: roll tilt in hypogravity (i.e., less than 1 G) would be underestimated. It further makes quantitative predictions of how much underestimation depending upon the hypogravity level.

To our knowledge there have been two published studies aimed at quantifying static roll perception in hypogravity,[8,9] but

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both only tested at 0 or 90° (upright and lying on one's side). The model only predicts underestimation at acute roll tilt angles, which has not been experimentally evaluated. In the current study, we aimed to quantify roll tilt ($< 45°$) perception in hypogravity using parabolic flight. In accordance with the modified observer model predictions, we hypothesized subjects would underestimate their roll tilt angle in hypogravity.

CASE REPORT

The hypogravity environment was created using parabolic flight. For the purposes of our experiment, the parabolas of interest were intended to be 0.38 G (Mars) and 0.165 G (lunar). Correspondingly, at the bottom of the parabolas, the passengers experience hypergravity. Orientation perception was reported while experiencing these various altered gravity environments [1 G on the ground, 1 G on the airplane (early), 0.38-G parabolas, 0.16-G parabolas, 1.6 G during a pullout, 1.2 G during a coordinated turn, and 1 G on the airplane again (late)].

We measured subjective tilt using a modified version of the well-established subjective visual vertical (SVV) task[7] with a head mounted display (eMagin Z800 3DVisor) using the Pscyhophysics Toolbox[2] in Matlab. The subject was seated upright (**Fig. 1A**) and, for flight tests, was secured with a strap across the knees. The subject would tilt his head relative to his body in primarily a roll axis, to random tilt angles, both left ear down and right ear down. Once tilted at a specific angle, the subject maintained that head position, then pressed a keyboard button, causing a black line to appear at a random angle against a gray background (**Fig. 1C**). The subject could then press one of two other buttons to rotate the line clockwise or counterclockwise, attempting to align it with their perceived vertical. Once aligned to their satisfaction, the subject pressed a fourth button to record their response, at which point the line disappeared and was replaced with a black fixation point. The subject would then tilt his head to another random angle and repeat the task. Due to the short duration of the hypogravity parabolas (~23–38s), the subject was instructed to make reports as quickly as possible without sacrificing accuracy. There were 7 to 11 reports made during each parabola.

Actual head orientation relative to gravity and the magnitude of the gravito-inertial acceleration (G level) was recorded by an accelerometer unit (APDM Wearable Technologies "Opal" device), which was mounted to the head-mounted display unit (**Fig. 1B**). A light-tight shroud covered the remaining portions of the subject's field of view to remove any externally fixed visual cues (Fig. 1B).

The subject was a healthy, 29-yr-old man who passed a clinical vestibular diagnostic exam to screen for undiagnosed vestibular disorders. The subject had no previous experience in parabolic flight and was a nonpilot, but had experience in hypergravity on a centrifuge. The subject also had extensive experience reporting orientation perception and was well trained on the SVV task. On his own accord 30 min prior to the parabolic flight, the subject orally took the over-the-counter antiemetic dimenhydrinate (Dramamine). Informed consent was obtained from the subject. The study was approved by the Massachusetts Institute of Technology's Committee on the Use of Humans as Experimental Subjects.

The subject's perception of roll tilt, obtained from SVV reports, was compared to actual head roll tilt, calculated from the accelerometer unit recording. While some previous studies have observed angle-dependent effects (i.e., A and E effects[12]), we could not clearly identify any nonlinearity in orientation perception as a function of angle (**Fig. 2**), potentially due to the limited number of reports. Therefore, we fit simple, linear models of perceived roll tilt (θ_{per}) as a function of actual roll tilt (θ_{act}). Two free parameters were estimated: 1) the "gain" of perception (K), and 2) left/right perceptual "bias" (B):

$$\theta_{per} = K\,\theta_{act} + B \qquad \text{Eq. 1}$$

For a small bias, a "gain" equal to one corresponds to "accurate" perception of roll tilt, while greater than one corresponds to overestimation (as hypothesized and previously observed in

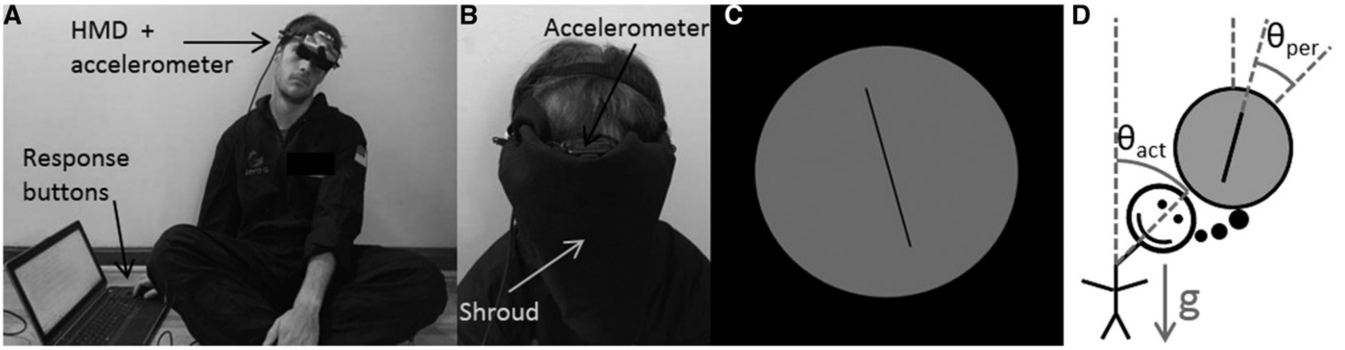
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Fig. 1. Methods and materials of the parabolic flight orientation perception experiment. A) The subject wore a head mounted display (HMD) with an accelerometer unit mounted to it to record the direction and magnitude of the gravito-inertial acceleration (G level) relative to the head and was seated upright. B) A shroud was worn to obscure any external visual references. C) The HMD presented a line which the subject was tasked with aligning to their perceived vertical (subjective visual vertical – SVV task). D) Each actual head roll tilt (θ_{act}) was compared to the perceived roll tilt (θ_{per}), defined by the orientation of the SVV line in the HMD. In the example shown, the subject has aligned the SVV line such that it is tilted relative to the subject's head slightly less than the subject's head is tilted relative to the gravitational vertical ($\theta_{per} < \theta_{act}$), corresponding to underestimation of roll tilt.

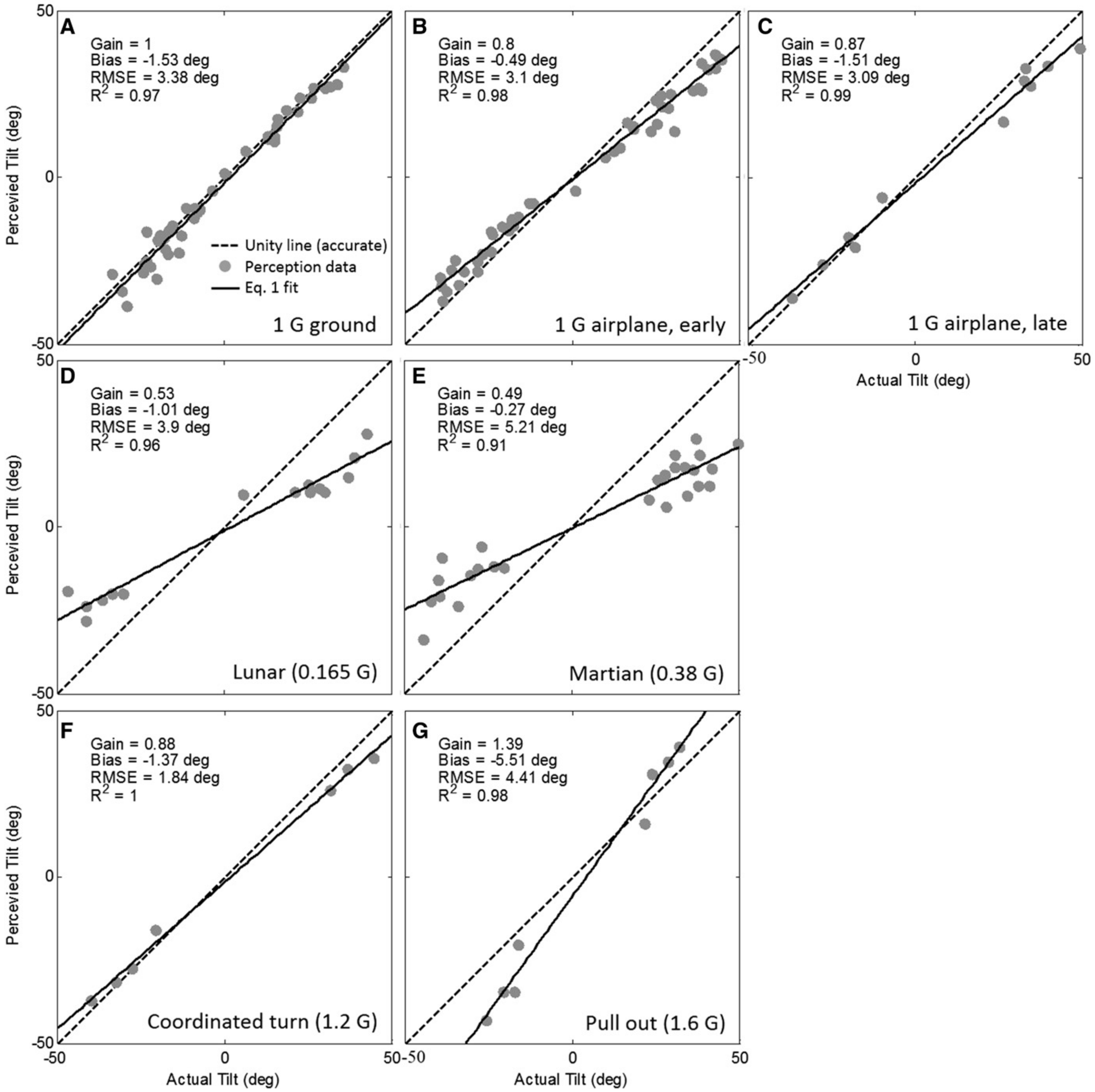

Fig. 2. Perceived roll tilt as a function of actual roll tilt by gravitational condition. Each panel shows the perceived roll tilt reports plotted vs. actual roll tilt angle (grey circles) for one condition, pooled across blocks of the same type. The top row is for each of the 1-G control conditions: A) on the ground, B) at the beginning of the flight, and C) near the end of the flight. The second row shows each of the hypogravity conditions: D) lunar gravity and E) Martian gravity. The bottom row has each of the hypergravity conditions: F) a coordinated turn of 1.2 G and G) a pull-out maneuver of 1.6 G. In each panel the unity slope line (i.e., accurate perception) is shown as a dotted line. The simple linear fit of Eq. 1 is shown as the solid line. The parameters of this fit are inset. A gain $\approx$ 1 corresponds to accurate perception, $<$ 1 indicates underestimation, and $>$ 1 corresponds to overestimation. A positive bias indicates a tendency to perceive each tilt to the right of the actual tilt (negative $=$ left). Root mean square error (RMSE) and R^2 values were calculated to quantify goodness of fit.

hypergravity[7]), and less than one indicates underestimation (as hypothesized in hypogravity).

Details can be found elsewhere on the observer model[10] and the modification made to explain the observed overestimation of roll tilt in hypergravity. Here, we simulated the model to predict static roll tilt perception in hypogravity. The proportionality of the effect of G level when simulating small angles (i.e., $<$ 45°, see Figs. 2 and 5A in Clark et al.[6]) allowed us to calculate a predicted "gain" (predicted perceived roll angle divided by actual roll angle) that would represent the effect across that range of small roll tilt angles. To focus on the relative effect of gravitational level, the observer model predicted gains were normalized to match that observed in the subject's 1-G reports on the airplane (pooled across early and late blocks).

This adjustment has no impact upon the observer's predicted relative effect of gravity; instead it simply corrects the 1-G gain to match that of the subject. A range of predictions is provided based upon the eight subjects in a previous centrifuge experiment.[5] Specifically, the amount of overestimation observed in 2 Gs ranged from 13 to 48% across subjects (average of 35% of the actual roll tilt angle), corresponding to the model parameter K_{au}, ranging from -3.2 to -1.4 (average of -2). Simulating the model with this range of parameters yields a range of predictions (gray shading in **Fig. 3B**).

We fit the linear model in Eq. 1 to the reports made in each gravitational condition, pooled across parabolas. As hypothesized, G level had a dramatic impact upon the "gain" of the subject's roll tilt perception, as observed by the differing slopes of the solid lines in Fig. 2. In the 1-G conditions (Fig. 2A–C), the gain was near one, remarkably so for the ground-based reports (Fig. 2A), indicating fairly accurate roll tilt perception. However, in the hypogravity conditions (Fig. 2D–E), the perceptual gain was much less than one, corresponding to an underestimation of roll tilt. Finally, in the hypergravity pull-out condition (1.6 G), the gain is greater than one (overestimation), consistent with previous centrifuge hypergravity experiments.[3]

The linear model fits yielded generally small left/right biases ($< 2°$) across conditions, with the exception of the hypergravity pull-out case (bias $= -5.5°$). The typically small root mean square error values and R^2 values near 1 (always > 0.9) suggest the linear model fits are appropriate and the subject maintains fairly consistent reports within each gravitational condition. However, we note the gravitational conditions farther from 1 G (e.g., lunar, Martian, and 1.6 G) tend to have higher root mean square error values, potentially indicating more variability or less certainty in these perceptual reports.

To directly compare perceptual "gains" across gravitational conditions, Fig. 3 plots the estimated coefficients (K in Equation 1) with 95% confidence intervals. First, we note that, somewhat unexpectedly, the roll tilt perception gains in the 1-G ground and "1-G airplane, early" conditions statistically differ [$t(44) = 6.5$, $P < 0.001$]. While the explanation is unclear (see Discussion), we compared the remaining gravitational conditions (hypo- and hypergravity) to the "1-G airplane, early" condition, such that these comparisons controlled for any possible influence of being tested in the airplane. There was not a statistically significant difference in gains between the "1-G airplane, early" and "1-G airplane, late" conditions [$t(12) = 1.98$, $P = 0.07$], suggesting the subject maintained consistent reports in 1 G while in the airplane.

As our main new finding, both the Martian (0.38 G) [$t(37) = 9.2$, $P < 0.001$] and lunar (0.165 G) [$t(18) = 7.5$, $P < 0.001$] hypogravity conditions reduced perceptual gains compared to the "1-G airplane, early" condition, corresponding to relative underestimation. While the gain in lunar G might be expected to be slightly less than Martian G, there was not a significant difference between these two conditions [$t(32) = 1.1$, $P = 0.28$].

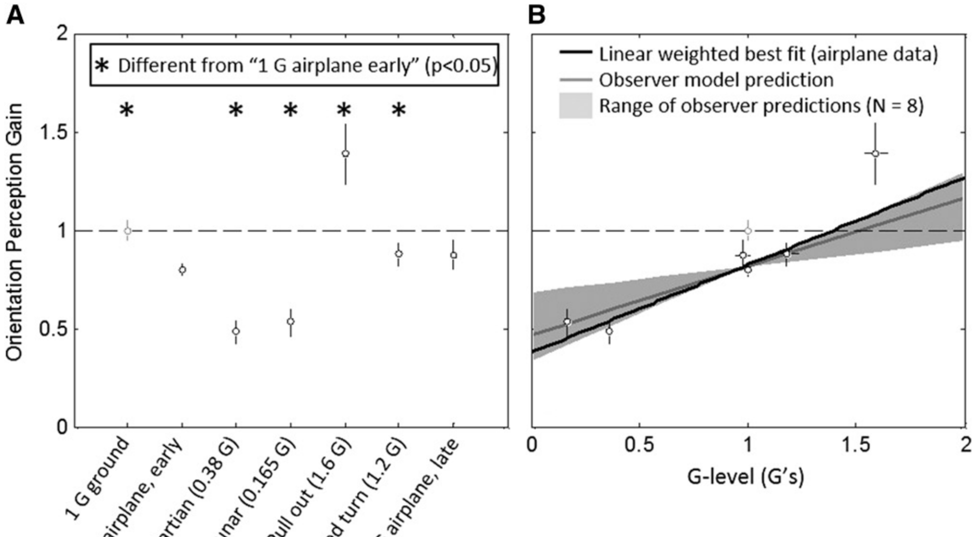

Fig. 3. Gain of roll tilt perception by gravitational condition. Data points represent the best fit "gains" using Eq. 1 (values provided in the insets of Fig. 2). Tests performed on the ground are shown in gray. The vertical error bars correspond to the 95% confidence intervals of the estimated fit parameter (gain). There were different numbers of reports for each condition (see Fig. 2), which contributed to differently sized confidence intervals. A) The data in each condition as it was collected chronologically. *Statistically significant differences (*t*-tests, $P < 0.05$) between the "1-G airplane, early" condition and each other condition. B) The same data as a function of G level now compared to observer model predictions. The horizontal error bars indicate 95% confidence intervals of the actual G level across reports in each condition. In some cases, the error bars are small and are often hidden by the shapes. The linear best fit (weighted by the standard error of the gain estimate for each condition) to the data collected on the airplane (i.e., excluding the 1-G ground condition) is shown as the solid black line. The observer model prediction for static tilt perception is provided by the gray line. The range (minimum to maximum) of gain vs. G level relationships predicted by the observer, when fit individually for each of eight subjects in a previous hypergravity centrifuge experiment,[5] is shown as the gray shaded area. Observer model predictions are adjusted so the gain in 1 G matches that for the subject in 1 G on the airplane.

In the hypergravity conditions, as previously found,[12] the subject overestimated roll tilt relative to the "1-G airplane, early" condition. Specifically, the gain was higher in both the pull-out (1.6 G) condition [$t(7) = 8.6$, $P < 0.001$] and the coordinated turn (1.2 G) case [$t(8) = 2.7$, $P = 0.026$] than when compared to "1-G airplane, early."

In Fig. 3B, a linear best fit was applied to data collected on the airplane (solid black line in Fig. 3B). The slope of this fit was +0.45 (95% confidence interval: 0.27–0.62) units of gain per G. The linear fit seemed to fit each of the airplane conditions quite well except the pull-out (1.6-G) condition, which seems to be somewhat of an outlier. Excluding this case yields a fitted slope of +0.40 (95% confidence interval: 0.27–0.53) units of gain per G (not shown in Fig. 3B). This indicates increasing G levels cause a relative increase in gain (i.e., overestimation), while, as a new empirical finding, decreasing G levels below 1 Earth G cause a relative decrease in gain (i.e., underestimation).

The effect of G level on perceptual gain observed empirically is quantitatively consistent with that predicted by the observer model. The model predicts a change of +0.35 units gain per G level, which compares well with the empirical best fit slopes provided in the previous paragraph. Furthermore, the observed hypogravity responses (lunar and Martian G levels) fit within a reasonable range of observer predictions (gray shaded area in Fig. 3B). This suggests that the modification to the observer model aimed at explaining roll tilt perception in hypergravity on a centrifuge was able to quantitatively predict the roll tilt perceptual underestimation observed here in hypogravity.

DISCUSSION

Our results show a human subject underestimates acute roll tilt angles in hypogravity environments in the dark (Figs. 2–3). Several previous studies have observed the characteristic overestimation of roll tilt in hypergravity, called the G-excess illusion.[3] In contrast, the underestimation of roll tilt observed in hypogravity might be termed the G-shortage illusion. This result was quantitatively predicted by the modified observer model, widely applicable to human spatial orientation, and, in particular, previously aimed at explaining the overestimation of roll tilt observed in hypergravity. The finding that this modification also appears to quantitatively predict the amount of underestimation of roll tilt observed in hypogravity suggests a similar mechanism as that which yields overestimation in hypergravity. While other mechanisms cannot be ruled out, the central nervous system differentially weighting otolith signals in the utricular plane and perpendicular to it (i.e., in the saccular direction), as implemented in the observer model, appears to be a consistent with the current data. We note that this was an a priori prediction in the sense that the observer model was not further altered or refit to match the hypogravity perception data (Fig. 3B). These predictions for the modified observer model for roll tilt in hypogravity were published[6] prior to the initiation of the current experiment.

We had a few unexpected experimental results which warrant further discussion. First, we found the 1-G gain measured on the airplane during straight and level flight to be statistically less than that measured on the ground. We aimed to replicate the conditions as best as possible (e.g., subject sat in the same posture, used the same hardware, similar reporting rates, and head tilt angles), but other aspects did vary. On the airplane, the G level was less precisely controlled due to turbulence, there was much higher background noise levels, a strap was worn across the knees to secure the subject during G transitions (not used on the ground, altering tactile cues), and, finally, there may have been an order effect as the ground measurements occurred first. We would not expect these differences to significantly impact tilt perception, but they cannot be ruled out. Given that the 1-G airplane condition most fully controlled for the hypo- and hypergravity conditions collected on the airplane, it was used as our 1-G "control" condition for further comparative analyses. However, if the 1-G ground condition was used instead for comparisons, it would not impact our primary conclusion: that the subject underestimated roll tilt in hypogravity (i.e., the perceptual gains in lunar and Martian G levels were also significantly less than the 1-G ground case).

Also, while we hypothesized that the roll tilt perception gain in 0.16 G would be slightly less than that in 0.38 G, we were not able to statistically distinguish between these conditions. This is likely due to the expected small effect size (the observer model predicts a relative difference in gains of only 0.075) and the limited number of trials and resulting large confidence intervals associated with these measures.

The primary limitation of this study is that only a single subject was tested. Extending these conclusions to the broader population of humans requires caution. There are, however, some reasons to suggest the results might be representative. In our previous centrifuge experiment,[5] the subjects showed a wide range of variation, but all eight subjects significantly overestimated roll tilt in hypergravity. Given how the effects observed in the single subject in hypogravity were consistent with the predictions derived from hypergravity data, combined with the fact each subject overestimated in hypergravity, suggests the conclusion that roll tilt is underestimated in hypogravity might be generalizable.

Our finding that roll tilt in hypogravity is underestimated may have important implications for aircraft pilots, as well as astronauts. Spatial disorientation during aircraft maneuvers, including hypogravity, can lead to manual control errors and even vertigo. However, our current experiment tested, and the modified observer model assumes, a subject with normal vestibular function (i.e., is adapted to the 1 Earth G environment). Yet astronauts in microgravity undergo sensorimotor adaptation (see Paloski et al.[11] for a review) during the 3 d (lunar) to 6 mo (Mars) of transit. The range of data from the current experiment, previous hypergravity studies, and studies on astronauts returning to Earth after extended microgravity exposure[11] suggest there will be systematic errors in orientation perception initially following a transition to any novel gravitational environment. Furthermore, such orientation perception errors are likely to impact mission critical tasks, such as vehicle manual control.[4] Future studies should aim to further quantify these impacts of altered gravity on sensorimotor function.

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