Gravitational and Somatosensory Influences on Control and Perception of Roll Balance

Alexander Sacha Panic; Heather Panic; Paul DiZio; James R. Lackner

INTRODUCTION: Blindfolded subjects used a joystick to orient themselves to the direction of balance in a device programmed to exhibit inverted pendulum behavior in the roll plane; they indicated with a trigger press when they were at that location. Our goal was to determine how otolith and somatosensory information about the gravitational vertical influenced the ability to locate the direction of balance.

METHODS: The subjects ($N = 12$) were tested in each of three orientations of the body roll plane: vertical (Upright), 45° back (45_Degree), and 90° back (Supine), which provided progressively less salient otolith and somatosensory information about roll orientation with regard to the direction of gravity. For each pitch plane, subjects were tested with three directions of balance: 0° (aligned with the gravitational vertical in the Upright condition) and 30° right or left.

RESULTS: The mean achieved and indicated orientations for the Upright and 45_Degree conditions were significantly displaced away from the direction of balance in the direction of gravity, with indicated angles less displaced. In the Supine condition, the mean achieved and indicated angles were closer to the direction of balance, but their within-trial standard deviations were significantly larger than in the Upright and 45_Degree conditions, which did not differ. This greater variability resulted from the frequent side to side "drifting" behavior that was a characteristic feature of the Supine condition only.

DISCUSSION: These findings indicate that in the absence of vision accurate dynamic orientation requires gravity dependent shear forces on the otolith organs and body surface.

KEYWORDS: gravity, otolith organs, somatosensation, orientation, vehicle control.

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Maintaining an "upright" human stance involves aligning the body's long axis with the direction of gravity and, when the body is considered as an inverted pendulum, aligning it with the direction of upright balance. These two orientations are the same under stationary terrestrial conditions, but can become dissociated during locomotion or in a moving vehicle as first shown by Riccio, Martin, and Stoffregen.[19] Their work has demonstrated that when subjects ride in a device that has been programmed to exhibit inverted pendulum behavior in roll with its direction of balance offset from the direction of gravity and attempt to set the device to the "upright," their retrospective judgments of orientation are correlated with their average achieved orientation relative to both the direction of balance and the direction of gravity. We have found[18,21] that when individuals use a joystick to orient to the direction of balance in a device with a direction of balance that is offset from the direction of gravity, they on average set it toward the direction of gravity, but their joystick trigger presses to indicate the direction of balance are more accurate. When asked to orient to the direction of gravity, they set the device slightly past gravity away from the direction of balance, but their trigger presses to the direction of gravity are accurate. These findings show that the direction of gravity and direction of balance can be perceptually distinguished and differentially oriented to depending on instructions. However, they do not show whether gravity dependent otolith and somatosensory cues are playing a

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role. Such cues are critical for orientation to the direction of gravity,[6,10] but it remains to be seen whether they influence settings to the direction of balance. In our previous study and that of Riccio et al.,[19] the locations of the direction of gravity and direction of balance were experimentally offset, but gravity dependent otolith and somatosensory cues about roll position in relation to gravity were always present because the roll plane was always vertical.[18,21] In principle, one could envision that semicircular canal signals per se might allow subjects to distinguish between the direction of balance and direction of gravity and orient to each as instructed, independent of the otolith and somatosensory cues.

To address this possibility, we have now studied whether blindfolded subjects can locate and orient to the direction of balance in the absence of gravity dependent otolith and somatosensory stimulation. Our multiaxis rotator device programed to behave as an inverted pendulum in the roll plane enabled us to: 1) dissociate the direction of balance and direction of gravity, and 2) to manipulate the salience of gravitational and somatosensory cues about roll motion by pitching the roll plane of the apparatus from 0° (vertical upright) to 90° pitch back (supine). This feature allowed gravity dependent otolith and somatosensory stimulation about body orientation in roll to be varied from maximum values at upright to a nearly null contribution when supine. With increasing backward tilt of the roll plane, otolith and somatosensory cues about body position relative to gravity are progressively attenuated and are minimized at 90° tilt back. Regardless of roll plane orientation relative to gravity, attempting to balance at the direction of balance generates multiple transient vestibular and somatosensory cues. When the body is deviated to one side of the direction of balance, it will accelerate in that direction away from the direction of balance and this will activate semicircular canal afferents. In our apparatus, the roll axis is near the subject's center of mass; consequently pendular motion produces tangential, somatosensory pressure cues and radial-lateral otolith stimulation correlated with angular velocity and acceleration. These transient roll plane motion cues are not eliminated by pitch back of the roll plane. Evidence from behavioral[1,16,20] and physiological[5,14] studies supports the integration of transient semicircular canal cues for coding of spatial displacement and heading, though their distinct contribution to dynamic balance is unknown.

We tested individuals in each of three roll plane orientations in pitch—upright, 45° pitch back, and 90° pitch back—and three directions of balance: −30°, 0°, and +30°. The 0° direction of balance corresponded with the direction of gravity when the roll plane was vertical.

METHODS

Subjects

Recruited from students and staff members of Brandeis University were 16 adults, 31 ± 13 yr of age, including 4 women. As explained below, 12 completed the experiment. All but one were right-handed. Five had previous experience in the multi-axis rotation system. None reported any history of balance or sensorimotor problems or injuries. All gave informed written consent to the experimental protocol that had been approved by the Brandeis University Institutional Review Board.

Equipment

A custom-built multi-axis rotation system (MARS) by Neuro Kinetics (Pittsburgh, PA) allowed a seated subject to be rotated in roll about an axis in the midsagittal plane 15 cm above the surface of the chair seat (**Fig. 1A**), coinciding approximately with the body center of mass.[8] The MARS also allowed the roll plane to be fixed upright (Upright), 45° pitched back (45_Degree), or horizontal (Supine). The MARS was programmed to simulate the behavior of an inverted pendulum in the roll plane relative to a specified direction of balance (**Fig. 1B**). When the MARS roll plane is upright and the subject is aligned with gravity, the direction of balance is defined as 0°, and when the roll plane was horizontal the same position in device coordinates was defined as 0°. Roll of the subject to the left was positive. All experimental results are reported in this frame of reference. Any roll angular displacement from the direction of balance (ϕ) would cause the subject to accelerate away from the direction of balance according to the equation $\ddot{\phi} = k_P \sin\varphi$, where k_P is the acceleration constant, which was set to $350° \cdot s^{-12}$ (equivalent to a fundamental frequency of 0.393 Hz). The constant k_P was empirically identified in pilot tests as the largest value at which subjects initially could control the MARS for 3 min while maintaining its roll orientation within ± 90° of the direction of balance. Subjects used a joystick with a ± 30° range of motion (Flightstick Pro, CH Products, Vista, CA) mounted

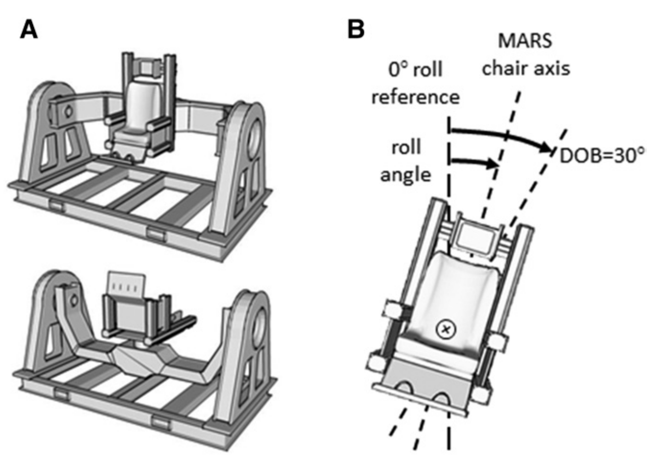

Fig. 1. The multi-axis rotation system (MARS) device and its reference orientations. A) The Upright (top) and Supine (bottom) roll plane MARS configurations are shown. The chair is shown in the 0° reference roll orientation in both panels. The 0° reference roll orientation coincides with the gravitational vertical when the MARS is Upright and is in the same orientation relative to the gimbal in the Supine configuration. The 45_Degree roll plane configuration is midway between the two illustrated conditions. B) The MARS is programmed to mimic inverted pendulum behavior in roll, regardless of pitch orientation. The direction of balance (DOB) represents the unstable equilibrium of the inverted pendulum. The DOB can be offset relative to the 0° roll reference, with positive DOB angles being toward the left ear.

on the right armrest of the MARS to control the MARS motion. The control system algorithms are described in Panic et al.[18]

Procedure

The inverted pendulum dynamics of the MARS were explained to the subjects using the analogy of a pencil balanced on its point and released, and the direction of balance was identified as the orientation at which the MARS would stay with minimal intervention, and that displacements to either side of the direction of balance would result in the MARS falling to that side unless the subject intervened using the joystick. Each subject then completed a 3-min training session while seated at a desk facing the MARS, which was in its upright orientation (Fig. 1A, top panel). Using a desktop joystick, the subject tried to set the MARS to its direction of balance (which was set to the 0° direction, corresponding to the direction of gravity) and pressed the trigger when the MARS was there.

Subjects were familiarized with the cardinal signs and symptoms of motion sickness[11] and told to report immediately during the experiment any symptoms that developed. The subject was then secured in the MARS with a five-point safety harness, side plates restricting their hip and torso motion, a torso restraint strap, foot restraints, and leg straps. The right forearm was loosely restrained with Velcro straps so subjects could manipulate the joystick; the left forearm was tightly strapped down in a configuration that allowed the subject to keep a finger on a kill switch mounted on the armrest (which was never used). The subject then put on noise-cancelling headphones that delivered white noise to mask potential auditory cues. The head was then clamped between lateral plates lined with memory foam contoured to accommodate the entire head, including the headphones. The experimenter and subject interacted over an intercom system that could interrupt the white noise. The subject was blindfolded, and the test chamber was darkened prior to the start of the experiment.

The experiment was divided into six blocks spread over 2 d. A single pitch plane orientation was used for each block: Upright, 45_Degree, or Supine, and all three planes were tested on each test day. Each block began with a single practice trial in which the direction of balance was set to the 0° roll reference. These practice trials were recorded but not analyzed. The remainder of each block included two trials at each of the three directions of balance: −30°, 0°, and +30°. Each subject received each combination of roll plane and direction of balance four times over the 2 test days. The six possible orders of the three pitch orientations were each presented across subjects, and each subject got six trials at 0°, +30°, and −30° in a different order across blocks.

The subject's task was always to set the MARS to the direction of balance and to press the joystick trigger when aligned with it. When the MARS rolled past ± 90° from the direction of balance, the subject was assumed to have lost control and the MARS was automatically moved back at $10° \cdot s^{-1}$ to a random location within ± 4° of the direction of balance. A trial continued until the subject had balanced the MARS for 45 consecutive seconds without losing control. After each block, subjects reported their impressions of its difficulty and their performance and any symptoms of motion sickness they were experiencing.

Statistical Analysis

The MARS roll position, joystick deflections, and trigger presses were sampled and recorded at 48 Hz. Zero-phase, five-pole Butterworth filtering removed high-frequency noise from the data at cutoff frequencies of 5 Hz for MARS and joystick angular deflections. All analyses were done using the filtered data from the 45-s periods of continuous control. A detailed description of the data reduction approach is available in Panic et al.[18] The roll angles during the trial are termed "achieved angles" (see Fig. 1B) and the roll angles at each moment when the joystick trigger was pressed are referred to as "indicated angles." Direction of balance angles and MARS achieved and indicated angles are specified in relation to the 0° reference roll orientation, which is aligned with the direction of gravity in the Upright condition and aligned with the corresponding gimbal direction in the 45_Degree and Supine conditions. For each trial, we calculated the means and within-trial standard deviations of achieved and indicated angles and the mean number of times subjects lost control. Regression slopes and intercepts were calculated from the straight-line fits of these MARS measures vs. direction of balance using all four repetitions for each subject and pitch condition.

The regression coefficients were statistically analyzed with MANOVAs and univariate ANOVAs. Bonferroni-corrected paired *t*-tests were used for all post hoc comparisons. Spectral analysis showed that joystick deflection power was concentrated at low frequencies and trailed off of at higher frequencies. We identified the top of the frequency band that contained 90% of joystick power for each trial and averaged across the direction of balance conditions and repetitions within each pitch condition. Joystick frequency band was analyzed with a one way repeated measures ANOVA and post hoc Bonferroni-corrected *t*-tests.

RESULTS

Four subjects aborted the experiment during their first exposure to the Supine condition because of rapid development of nausea. They had been without symptoms in the Upright and/or the 45_Degree conditions. Three had previously completed other experiments in the MARS in the Upright orientation without developing any symptoms. Their data were excluded from further consideration. A fifth subject reported nausea after completion of the first session, but opted to return the following day for the second session and completed it. The data for the 12 who completed both sessions are reported below. Their impressions were consistent. They found the Supine condition most difficult because it was hard to determine the onset of motion and its direction and amplitude and where the direction of balance was. Some subjects reported that in the Supine condition the direction of balance would seem to drift clockwise or counterclockwise and after losing control and being stopped experienced 360° roll rotation. The stops felt jarring because often no motion was being experienced prior to being stopped.

The number of times that control was lost was affected by pitch condition [$F(2,22) = 8.628$, $P = 0.014$, $\eta^2 = 0.440$, power = 0.762]. Subjects rarely lost control of the MARS in the Upright and 45_Degree conditions, with losses of control occurring on average once every 18 and 21 trials, respectively. Six never lost control, while the subject with the poorest performance lost control five times over the 24 trials. In contrast, in the Supine condition, subjects lost control on average once per trial, and only two never lost control. The subject with the poorest performance lost control 29 times over his 12 trials in the Supine condition.

Fig. 2 shows time series of MARS roll angle for a direction of balance of −30°across pitch conditions for a representative subject's trials. In the Upright and 45_Degree conditions, this subject was able to keep the MARS close to the direction of balance, albeit biased toward the 0° roll reference (the direction of gravity). However, in the Supine condition, the subject was less able to home in on the direction of balance and drifted from one side to the other. This pattern was frequently observed among other subjects and was unique to the Supine condition. The black dots represent the trigger press indications of the direction of balance. There are very few trigger presses in the Supine condition relative to the Upright and the 45_Degree conditions. This pattern was characteristic of all subjects.

Fig. 3 shows histograms of achieved and indicated angles for a single subject across all four repetitions of the three pitch conditions at a roll direction of balance of −30°. Mean achieved angles were closer to the direction of balance in the Supine than in the Upright and 45_Degree conditions. Mean indications of the direction of balance showed the same pattern but were closer to the direction of balance. **Fig. 4** shows that the same patterns are characteristic of all 12 subjects. Every subject reported that the Supine condition was the most difficult and attention demanding.

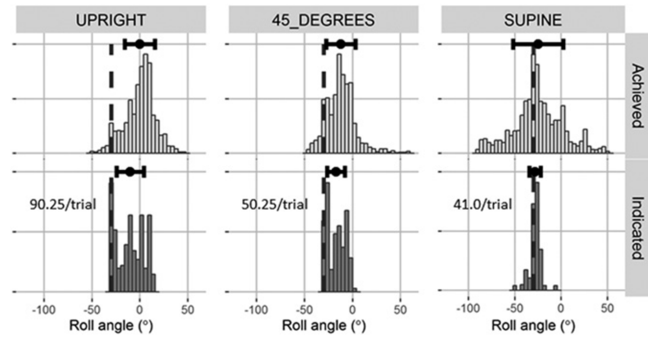

Fig. 3. Histograms of performance across pitch conditions for a single participant at a direction of balance (DOB) of −30°. Achieved angles are plotted in the top row and indicated angles in the bottom row. To accentuate the shapes of the distributions, each histogram is normalized so that the bar for the most frequent angle bin is a standard height. Achieved angle histograms include all samples from all four trial repetitions at a roll DOB of −30° (vertical dashed line), which is constant across pitch conditions. Indicated angle histograms include only the samples where the trigger button was pressed, which varied across pitch conditions; the average number of trigger presses per trial are presented for each pitch condition. The mean and within-trial standard deviations are shown by the black horizontal bars.

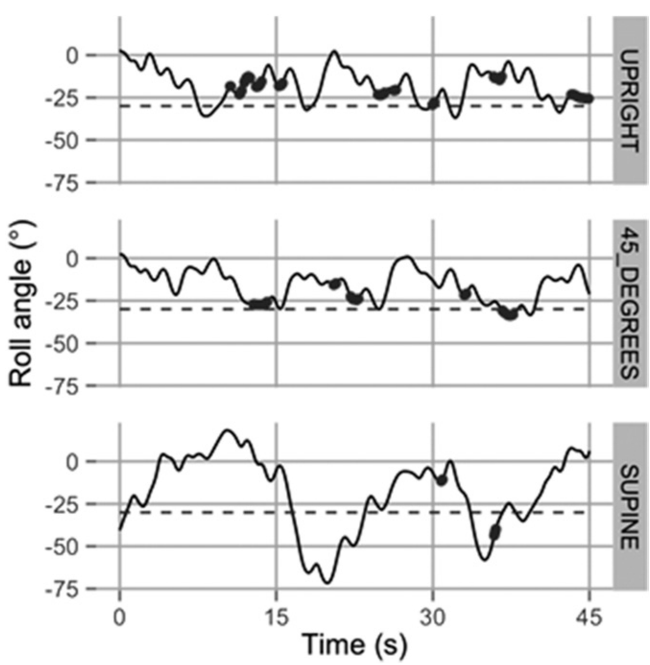

Fig. 2. Time series of trial data across pitch conditions for a single participant at a roll direction of balance (DOB) of −30°. Shown are the DOB (dashed line), achieved roll angles (solid line) in the last 45 s of single trials, and the roll angle at which the participant pressed the joystick trigger to indicate the perceived DOB (dots).

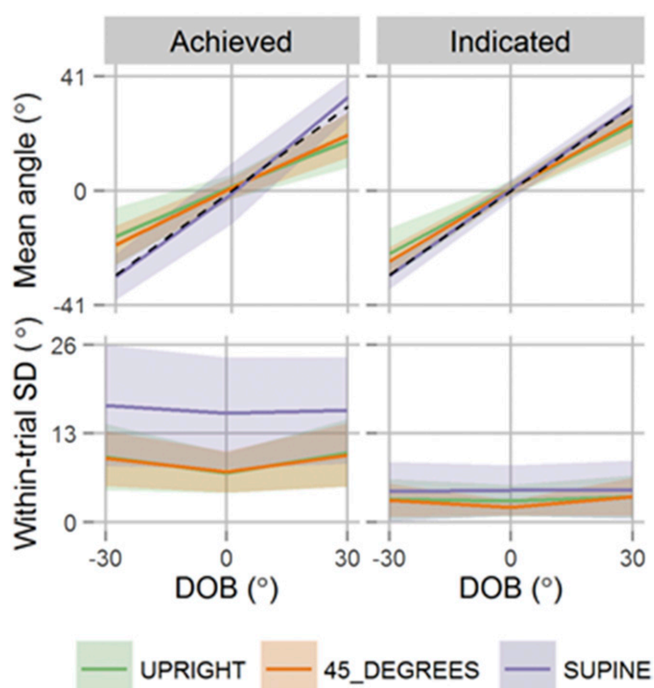

Fig. 4. Mean and within-trial standard deviations across 12 participants of achieved and indicated angles across roll directions of balance (DOBs) and pitch conditions. Top row: mean angles; Bottom row: within-trial SDs. The shaded error bands encompass ± 1 SD.

The top two panels of Fig. 4 present mean achieved and indicated angles as a function of direction of balance for the three conditions. The achieved angle for the 0° direction of balance condition is exact for all three conditions. However, for the −30° and the +30° directions of balance, the mean angles in the Upright and 45_Degree conditions are biased toward the direction of gravity by about 10°. In the Supine condition, the mean achieved angles are closer to the actual directions of balance. Indicated angles are more accurate than achieved, with a bias toward the direction of gravity of only about 3–5° in the Upright and 45_Degree conditions. The mean indications for 0° direction of balance correspond with the direction of balance. For the Supine condition, mean indicated settings correspond closely with the three directions of balance.

To assess the statistical significance of these differences across conditions, a 3 (pitch: Upright, 45_Degree, Supine) × 2 (task: achieved angle, indicated angle) repeated measures MANOVA was performed on the regression slopes and intercepts of mean angle vs. direction of balance. Significant effects of both pitch [$F(4, 44) = 6.250$, $P < 0.001$, $\eta^2 = 0.362$, power = 0.980] and task [$F(2, 10) = 7.786$, $P = 0.009$, $\eta^2 = 0.612$, power = 0.868] were found, as well as an interaction between them [$F(4, 44) = 7.900$, $P < 0.001$, $\eta^2 = 0.410$, power = 0.994]. These results mean that the pitch plane conditions influenced the ability to locate the direction of balance and that the means of achieved angles were more influenced than the means of indicated angles.

Subsequent univariate ANOVAs showed that while regression slopes were affected (all $P < 0.002$), the regression intercepts were not (all $P > 0.411$), indicating that the pitch conditions did not introduce directional biases. Post hoc comparisons of the regression slopes of mean achieved angle vs. direction of balance showed that there was no difference between the Upright and 45_Degree conditions ($P = 0.070$). The Supine condition (mean = 1.07, SD = 0.07) was less biased than both the Upright (mean = 0.57, SD = 0.27) and 45_Degree (mean = 0.65, SD = 0.20) conditions (both $P < 0.001$). The same pattern was present for mean indicated angles: the Supine condition (mean = 1.01, SD = 0.05) was less biased than the Upright (mean = 0.77, SD = 0.17) and 45_Degree (mean = 0.83, SD = 0.15) conditions ($P = 0.002$ and $P = 0.005$, respectively), which did not differ from each other ($P = 0.075$).

The bottom two panels of Fig. 4 present within trial standard deviations for achieved and indicated angles for the three directions of balance and three pitch plane conditions. The plots all have flat slopes with varying intercepts that represent the within-trial standard deviations. The standard deviations for achieved angles show the same patterns for the Upright and 45_Degree condition, being about 9° across the directions of balance. For the Supine condition, the standard deviations of achieved angles are twice as large and virtually flat across directions of balance. The variability of indicated angles was least in the Upright and 45_Degree conditions, being 3 to 4° across the three directions of balance, and for the Supine condition about 5° across directions of balance.

Pitch plane angle had a larger influence on the within-trial variability of the achieved than the indicated settings. This was shown by a repeated measures MANOVA performed on the regression slopes and intercepts of the within-trial standard deviations vs. directions of balance. Significant pitch [$F(4, 44) = 6.839$, $P < 0.001$, $\eta^2 = 0.383$, power = 0.988] and task [$F(2, 10) = 49.398$, $P < 0.001$, $\eta^2 = 0.908$, power = 1.00] effects were found, and an interaction [$F(4, 44) = 7.142$, $P < 0.001$, $\eta^2 = 0.394$, power = 0.991]. Subsequent univariate ANOVAs showed that the regression intercepts (all $P < 0.001$), but not the slopes, were affected by pitch angle, task, and an interaction between them.

Post hoc comparisons showed that performance variability in orienting to and indicating the direction of balance was not affected by being pitched backward 45° from the upright, but was increased by being supine, with a larger increase in variability for achieved ($P < 0.001$) than indicated angles ($P < 0.003$).

Because subjects reported that they found it more difficult to detect the onset, direction, and amplitude of motion in the Supine condition, we expected that the frequency of their joystick inputs would be lower in that condition, and this was the case. A repeated measures ANOVA showed a significant effect of pitch condition [$F(2,22) = 4.161$, $P = 0.029$, $\eta^2 = 0.274$, power = 0.672] and Bonferroni-corrected pairwise *t*-tests showed significantly lower frequency in the Supine (M = 1.21) than the Upright (M = 1.45, $P = 0.038$) and 45_Degree (M = 1.51, $P = 0.005$) conditions.

DISCUSSION

Our experimental findings reveal a relative inability to orient to the direction of roll balance when otolith shear forces and somatosensory pressure distribution asymmetries arising from body orientation relative to gravity are minimized. With gravity dependent cues attenuated in the Supine condition the average achieved orientation to the direction of balance was not biased, but the spatial variance greatly increased, with the MARS undergoing larger displacements in the roll plane. This effect was greater for the achieved than indicated orientations to the direction of balance, but the pattern was the same (Fig. 3).

In the Upright and 45_Degree conditions when subjects oriented to a roll direction of balance that was offset from the direction of the component of gravity in the roll plane, their settings were biased significantly toward the direction of gravity, with slopes for the direction of balance vs. mean achieved orientation functions of 0.57 or 0.67, respectively, and slopes of 0.77 and 0.83 for indicated angles. Such biases were absent in the Supine condition, where slopes were 1.07 and 1.01 for achieved and indicated orientations. These findings replicate and extend our previous study,[18] where we found that subjects can orient to the direction of balance or direction of gravity as instructed. Taken together, the two studies indicate that separable yet overlapping processes underlie orienting to the direction of gravity and direction of balance, and that both are operating in the Upright and 45_Degree conditions. The process underlying orientation to the direction of gravity is highly dependent on gravity dependent otolith and somatosensory cues,[6,10] but the process for orientation to the direction of balance prima facie should not require gravity cues. A synergistic interaction of both processes under normal conditions is consistent with the average bias toward the direction of gravity that our subjects showed when attempting to orient to an offset direction of balance in the Upright and 45_Degree conditions. This synergy assists orientation in static conditions where the direction of balance and direction of gravity coincide, but creates biases in laboratory situations and likely in operational flight conditions. During natural locomotion, the separability of the two processes presumably permits aligning with a direction of balance which does not coincide with the direction of gravity.

With gravity dependent cues attenuated in the Supine condition, overall performance for roll orientation to the direction of balance deteriorated. This deterioration was evident in the increased variances of achieved and indicated orientations and in the 20-fold more frequent loss of control in the Supine compared to the Upright and 45_Degree conditions. The time series for all subjects in the Supine condition reveal oscillations interspersed with automatic resets after losses of control rather than a series of uncontrolled falls (see lower panel Fig. 2 for a typical subject). The degraded performance in the Supine condition is due to the attenuated gravity dependent cues relevant to roll position and not due to lack of experience controlling orientation while lying on the back, because we have found that subjects given 20 consecutive 100-s supine trials never approach the competence seen here in the Upright and 45_Degree conditions. The mean achieved orientations are close to the direction of balance and the greater variance of achieved than indicated settings implies that the ability to identify the direction of balance may not be fully abolished in the Supine condition, but the reason for this requires further investigation. Other research has supported the idea of distinct mechanisms for perceptual and motor orientation.[3,7,15]

In the Supine condition, the roll plane is horizontal and subjects' judgments and settings to the direction of dynamic balance must be derived from semicircular canal signals elicited by roll angular accelerations of the body, transient asymmetric pressure cues exerted by the MARS to displace the individuals in horizontal roll, and transient otolith linear acceleration stimulation resulting because the otolith organs are approximately a meter from the axis of body roll orientation and undergo centrifugal and tangential acceleration during rotation. These patterns of activation in relation to joystick deflection movements provide a potential way of identifying the locus of the direction of balance.

The characteristic increase in variability of MARS angular position in the Supine condition was a consequence of positional drifting. Such drifting was greatly reduced in the 45_Degree and Upright conditions, where significant position dependent otolith and somatosensory cues were available. While some water immersion studies indicate that the otolith organs alone are not sufficient for precise orientation to gravity,[6,10,17] the present results show that otolith and somatosensory cues together are sufficient, as our previous model of 3-dimensional orientation predicts.[4]

When subjects lost control in the Supine condition and the MARS position was reset, they often reported being surprised, not realizing that they were far from the direction of balance. Importantly, when they "crashed," they were automatically repositioned within 4° to one side or the other of the direction of balance. The repositioning was done at a constant velocity so the time to reset provided a potential cue to how far temporally the crash boundaries were from the direction of balance. The question nevertheless arises, why did subjects drift in the Supine condition? The lower frequency of joystick control inputs in the Supine condition is consistent with a higher threshold for detection of drift. Many studies have found that when subjects have to rely on semicircular canal signals to judge their passive angular displacements, they can be quite accurate in physically reproducing their displacement,[1,13,20] estimating verbally their angular displacement, or in making "look back" saccades.[2] These studies typically involve triangular or bell-shaped velocity wave forms, a single brief stimulus that is then followed by a response, then another trial, and another judgment with respect to the start position of the current trial. Put simply the tasks do not require path integration over continuous trials. Studies involving passive rotation generally involve trials of short duration, < 1 s, whereas our trials lasted 45 s. In parabolic flight studies where periods of high acceleration alternate with periods of weightlessness, we have found that semicircular canal signals are accurately integrated in 1 g and 1.8 g background force levels to provide a sense of body spatial displacement in relation to the start position, but in 0 g they are not.[12] It is possible that even small errors in integration could result in the type of drift we observed in the Supine condition over the 45-s period of attempting to orient to the direction of balance.

An unexpected finding was the development of symptoms of motion sickness in the Supine condition so that four subjects had to withdraw from the experiment. Subjects in the Upright and 45_Degree conditions did not develop any significant symptoms. Notably, however, subjects in the Supine condition were exposed to much greater levels of angular acceleration and found their "crashes" to be very provocative. Exposure to repeated patterns of semicircular activation are known to be highly provocative and can be used operationally as a measure of susceptibility to motion sickness.[9]

In conclusion, subjects trying to orient to the direction of balance when supine show an inability to maintain or identify self-position in relation to the direction of balance. The direction of balance in the horizontal plane is not perceptually salient. With the roll plane vertical, the direction of gravity can be distinguished and subjects can both orient to it and indicate it, and, when the direction of balance is offset from the direction of gravity, they can sense that it is offset because the direction of gravity is serving as a positional anchor against which the direction of balance can be judged. Without gravity dependent shear forces providing positional cues it is difficult to resolve one's body direction in relation to the direction of dynamic equilibrium.

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