RESEARCH ARTICLE

Learning and long-term retention of dynamic self-stabilization skills

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Abstract

In earlier studies, we had subjects use a joystick to balance themselves when seated in a device programmed to behave like an inverted pendulum. Subjects tested in a vertically oriented roll plane showed rapid learning for dynamically stabilizing themselves about the direction of balance when it corresponded with the direction of gravity. Subjects tested in a horizontally oriented roll plane, unlike the vertical roll plane subjects, did not have gravitational cues to determine their angular positions and showed minimal learning and persistent cyclical drifting. We describe here a training program to enhance learning and performance of dynamic stabilization in the horizontal roll plane based on our previous finding that balance control involves two dissociable components: alignment using gravity-dependent positional cues and alignment using dynamic cues. We hypothesized that teaching subjects to balance in a vertical roll plane to directions of balance that did not correspond with the direction of gravity would enhance the ability to stabilize at the direction of balance in the horizontal roll plane where gravity-dependent cues are absent. All subjects trained in vertical roll later showed greatly improved performance in horizontal plane balance. Control subjects exposed only to horizontal roll plane balancing showed minimal improvements. When retested 4 months later, the training subjects showed further performance improvements during the course of the retest trials whereas the control group showed no further improvement. Our findings indicate that balance control can be enhanced in situations lacking gravitationally dependent position cues as in weightlessness, when initial training occurs with such cues present.

Introduction

In our previous work, subjects showed poor performance and minimal learning when controlling their orientation in conditions lacking gravitational cues about ongoing body position (Panic et al. 2017; Vimal et al. 2017, 2018). The orientation task was a "spaceflight analog" condition involving a multi-axis rotation system (MARS) (see Fig. 1), programmed to behave as an inverted pendulum, in which blindfolded subjects had to balance themselves using a joystick. When subjects dynamically balance in a horizontal roll plane, their performance is degraded relative to vertical roll plane balancing and they collectively show meager learning and characteristic patterns of positional drifting. Because they do not change position in relation to the gravitational vertical they do not have gravity-dependent positional cues about their deviation from the direction of balance (DOB). Instead, they must rely on transient motion cues from their semicircular canals, otolith organs, and somatosensory receptors. In contrast, when balancing in the vertical roll plane subjects have a strong sense of their tilt relative to the upright DOB from the otolith and somatosensory cues they receive as they move in relation to the gravitational vertical. These individuals show rapid and robust learning across many performance measures.

The poor performance of subjects balancing in the horizontal roll plane conflicts with the notion that the direction of balance is a primary determinant of the perceptual "upright", more so even than the direction of gravity (Riccio et al. 1992). That perspective emphasizes the importance of dynamic cues—e.g., semicircular canal signals about body

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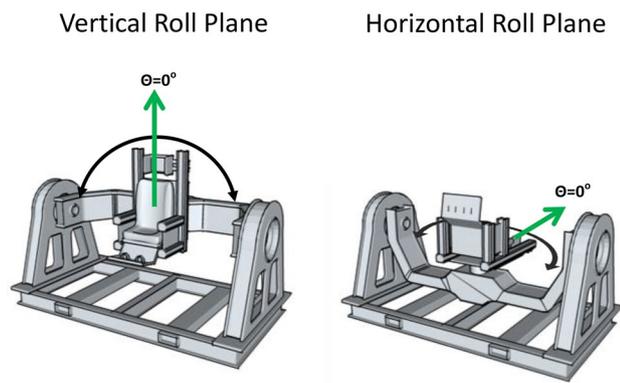3 Department of Psychology, Brandeis University, Waltham, USA

Vertical Roll Plane   Horizontal Roll Plane

Fig. 1 The multi-axis rotation device (MARS) was programmed with inverted pendulum dynamics in the vertical roll plane (left) and the horizontal roll plane (right). Green arrows represent the DOB, which was kept constant in the horizontal roll condition but was offset from the gravitational vertical in the vertical roll condition during training

motion in relation to the direction of balance. Degraded horizontal roll plane performance is also not expected from studies in which blindfolded subjects exposed to single passive angular displacements in yaw are able to estimate accurately their angular displacement (Guedry et al. 1971; Metcalfe and Gresty 1992; Mittelstaedt and Mittelstaedt 1980). Such studies imply that when gravitational cues to positional change are absent, integration of semi-circular canal signals and somatosensory signals should be sufficient for maintaining an accurate estimation of angular position. To determine whether the absence of graviceptive cues or the inexperience of balancing while supine was responsible for the degraded performance and learning in Horizontal Roll, we tested the ability of blindfolded subjects to orient to the direction of balance when exposed to inverted pendulum dynamics about a vertical yaw axis and a horizontal yaw axis (Vimal et al. 2018). Subjects in the vertical yaw axis group showed persistent patterns of cyclical drifting, similar to subjects in the horizontal roll plane. The former can be considered a "helicopter analog" condition and the latter a "spaceflight analog" condition, both of which confine sensory cues to transient semicircular canal and somatosensory cues. Subjects in the horizontal yaw axis group showed rapid performance improvements and were able to sense the DOB. They, like subjects balancing in the vertical roll plane, received gravity-dependent otolithic and somatosensory cues about their ongoing position, in addition to transient cues.

When we examined individual data for the spaceflight and helicopter analog conditions (horizontal roll plane and vertical yaw axis), we found a few subjects who showed learning across several performance parameters, suggesting that dynamic cues alone were helpful when they could be recognized (Vimal et al. 2017, 2018). This made us explore whether we could create a training program to enhance learning for all subjects. Our guiding hypothesis came from

our prior work showing that balance control can involve two dissociable processes: alignment to the gravitational vertical using gravitational cues and dynamic stabilization relative to the direction of balance using only motion cues. We had found this dissociation when we had one group of subjects learn to balance in the vertical roll plane where they had both gravitational and motion cues, and then testing them in the horizontal roll plane where they had motion cues but no relevant gravitational cues. They showed no evidence for transfer of learning. Another group was tested initially in the horizontal roll plane where they showed less evidence of learning, but when they were then tested in the vertical roll plane they showed greatly enhanced performance relative to the group who were initially tested in the vertical roll plane (Vimal et al. 2017). We reasoned that the first group did not transfer learning from the vertical roll plane because they had relied on gravitational cues to align with the gravitational vertical and this strategy was not applicable for the horizontal roll plane. By contrast, the second group showed transfer because when tested in the horizontal roll plane they had only motion cues to focus on and these were also present in the vertical roll plane (Vimal et al. 2017).

These considerations led us to create a training program to teach subjects how to dynamically stabilize about a direction of balance that did not correspond to the gravitational vertical. Our approach was to show subjects how to find the direction of balance in the vertical roll plane by exposing them initially to a situation in which the direction of balance corresponded with that of gravity and then later having them balance to directions of balance that did not correspond with the direction of gravity. This approach decorrelated the graviceptive vertical from the dynamic balance point and placed a premium on transient cues for dynamic balance within the context of gravity-dependent position cues. We found that the subjects in this "Vestibular Training" group showed significant transfer of learning to the horizontal roll plane, whereas a control group, training only in the horizontal roll plane, showed minimal learning. To determine whether the two groups could retain what they learned over long periods of time, we retested them 4 months later and found no deterioration in performance. During the retesting, the vestibular training group showed further improvements in performance. The control group did not.

Methods and materials

Subjects

20 adult subjects (8 females and 12 males, 23.4 ± 5.0 years old) participated in the experiment. Subjects were determined to be healthy based on their responses to a questionnaire that asked about their medical history and they

had no prior experience in the MARS. They gave written consent to the experimental protocol approved by the Brandeis Institutional Review Board. They were randomly assigned to either the control or vestibular training groups. Both groups participated in 2 days of initial exposure and were invited back 4 months later to test for retention. One subject in each group was not available for retention testing.

Apparatus

The multi-axis rotation system (MARS) device was programed with inverted pendulum dynamics about a roll axis through the approximate center of mass of the seated subject (Clauser 1963). The subject could either be seated erect and rolled about a horizontal axis (vertical roll plane) or pitched back 90° (supine) and rolled about a vertical axis (horizontal roll plane). The motion was programmed according to the equation $\ddot{\theta} = k_\mathrm{P} \sin\theta$, where θ is the angular deviation from the direction of balance, DOB (in degrees), and k_P is the pendulum constant. During vertical roll plane motion, the MARS DOB can be offset from the direction of gravity, a dissociation first introduced by Riccio et al. (1992). We used a pendulum constant of 600 deg/s^2 (≈ 0.52 Hz) as in our previous work (Vimal et al. 2016, 2017, 2018) to ensure a difficult task that would require learning. At every time step (~ 50 Hz), a velocity increment proportional to the joystick deflection was added to the MARS velocity and then integrated by a Runge–Kutta RK4 solver (Lambert 1973) to calculate the new MARS angular position and velocity. The latency between joystick deflections and the change in MARS angular velocity was 30 ms up to 1.6 Hz. For higher frequencies, the latency was larger; however, 90% of the MARS spectral power is below 0.75 Hz in the conditions used here. We programmed 'crash' limits to restrict MARS angular range to $\pm 60°$ from the DOB, and we limited angular velocity to ± 300 deg/s, and angular acceleration to ± 180 deg/s^2. Details of the control scheme are available in Panic et al. (2015).

After subjects were familiarized with the experimental protocol described below, they were then blindfolded and secured in the MARS using lateral support plates, a five-point safety harness, a lap belt, and foot straps (Fig. 1). They wore earplugs and noise canceling headphones that played white noise. A padded U-shaped frame attached to the MARS stabilized their head. Subjects grasped a handle on the left arm rest, which had a "kill switch" that could be pressed to stop the experiment. No subject ever used it. Subjects controlled the MARS with their right hand using a Logitech Freedom 2.4 cordless joystick.

Procedure

Subjects were familiarized with the symptoms of motion sickness using the Graybiel Diagnostic Scale (Graybiel 1968). They were informed that the MARS behaved like an inverted pendulum and that they should use the joystick to balance it at the DOB (direction of balance) while also minimizing oscillations. Both groups were told about strategies that good performers in prior experiments had found useful. These strategies included: (1) use small joystick deflections, (2) use intermittent joystick deflections, (3) use smaller joystick deflections when near the DOB compared to when far away from it, and (4) find the DOB by switching from falling in one direction to the other. The control group was shown videos of a person balancing the MARS in the horizontal roll plane and the MARS reaching the "crash boundaries" at $\pm 60°$ from the DOB, and being reset to the DOB. Members of the vestibular training group were shown additional videos of a subject in the MARS balancing to the DOB at the direction of gravity in the vertical roll plane, and to a DOB displaced from the direction of gravity in the vertical roll plane. After signing consent forms, subjects were secured in the MARS, given the blindfold, earplugs, and noise canceling headphones that played white noise.

All trials started with an auditory "begin" command. Whenever subjects allowed the MARS angular position to exceed $\pm 60°$ from the DOB, a "crash", they heard "lost control, resetting" and the MARS automatically reset to the start position at a rate of 5 deg/s. During the reset, the joystick was disabled. Once they reached the start position, subjects heard an auditory "begin" command and the joystick was enabled. Each trial consisted of 100 cumulative seconds of balancing, excluding the reset times after crashes, or after a total elapsed time of 150 s.

Both groups participated on two consecutive days, with 20 trials of balancing on each day. The first four trials on Day 1 and the last four on Day 2 were in the horizontal roll plane to measure baseline and final performance, respectively. The difference in performance between the Day 1 baseline and the Day 2 final trials within groups measured their cumulative improvement. Comparing the final Day 2 trials across groups quantified the relative efficacy of the training program. The control group from trial 5 of Day 1 to trial 16 of Day 2 received additional exposure to horizontal roll plane balancing, where dynamic gravitational cues were absent. The schedule for the vestibular training group was based on pilot studies. It required active self-orientation in the vertical roll plane to a DOB that became increasingly displaced from the gravitational vertical. Table 1 outlines the exposure protocol for each group, and the next paragraph describes the vestibular training in more detail. After every 4 trials, subjects were returned to the upright orientation for a 2 min break and answered

Table 1 Schedules for the control and vestibular training groups

Group	Day	Phase	Trial	Roll plane	DOB	Start at DOB?
Control	1	Baseline	1–4	Horiz	0	Yes
		Training	5–20	Horiz	0	Yes
	2		1–16			
		Final 1	17–20	Horiz	0	Yes
	…4 month gap…					
	3	Retention	1–4	Horiz	0	Yes
		Training	5–16	Horiz	0	Yes
		Final 2	17–20	Horiz	0	Yes
Vestibular Training	1	Baseline	1–4	Horiz	0	Yes
		Training	5–10	Vert	0	Yes
			11–14	Vert	±15	Yes
			15–20	Vert	±15	No
	2		1, 4, 7, 10	Horiz	0	Yes
			2, 3,…, 5, 6, 8, 9,… 11, 12	Vert	±15	No
			13–16	Horiz	0	Yes
		Final 1	17–20	Horiz	0	Yes
	…4 month gap…					
	3	Retention	1–4	Horiz	0	Yes
		Training	5–16	Horiz	0	Yes
		Final 2	17–20	Horiz	0	Yes

DOB = 0 in the vertical roll plane corresponds to the gravitational vertical and in the horizontal roll plane it corresponds to the same angular orientation of the MARS chair relative to its gimbal frame (see Fig. 1)

questions about their performance and whether they were experiencing any symptoms of motion sickness.

Following their 4 baseline horizontal roll plane trials on Day 1, the vestibular training group spent six trials (trials 5–10) in the vertical roll plane attempting to balance themselves at the DOB, which was aligned with the gravitational vertical. In this phase, the MARS start position when trials began and its reset position after crashes were aligned with the upright DOB. Then, for four trials (trials 11–14), they tried to balance at a non-vertical DOB in the vertical roll plane (10°, − 10°, 15°, − 15°). Prior to starting these trials, the subjects were told that the angular location of the DOB and their start and reset positions would always be at the DOB. The last six trials of Day 1 (trials 15–20) showed subjects how to rely on motion cues. Trials were run in pairs, where subjects first had to find and balance at a non-vertical DOB in the vertical roll plane whose location they had not been told, starting away from the DOB. After the trial finished, they were told the correct location of the DOB. In the paired trial, the same DOB and start point were repeated to reinforce how to use motion cues to find the DOB. For the 3 pairs of trials 15–20, the DOBs were 5°, 5°, − 10°, − 10°, 10°, 10°, and the initial start points were 10°, 10°, 0°, 0°, 15°, 15°; however, when subjects crashed, the reset points were randomized ± 15° from the DOB after every crash.

On the second day, the vestibular training group underwent 4 iterations of a triplet of conditions in trials 1–12. The first trial of each triplet involved balancing in the horizontal roll plane with both the DOB and start position at zero, and the last two trials of the triplet were similar to trials 15–20 from Day 1 where the subject had to search for the DOB in the vertical roll plane, with different DOBs and start points. For trials 1–12, the DOBs were 0°, − 10°, − 10°, 0°, 10°, 10°, 0°, 5°, − 5°, 0°, − 10°, 10° and the initial start points were 0°, − 5°, 5°, 0°, 15°, 5°, 0°, 10°, 10°, 0°, 0°, 15°, and the reset points were randomized ± 15° from the DOB after every crash. At the end of each trial, the subject reported verbally the location of the DOB and was given feedback on whether correct or not. The final 8 trials (trials 13–20) consisted of balancing in the horizontal roll plane with both the DOB and start point at zero. To test for retention and further learning of the task, subjects in the control and vestibular training groups came back 4 months later and were tested in the horizontal roll plane for 20 trials.

Data reduction and analysis

MARS angular position and velocity and joystick deflections were sampled at 20.7 ± 1.1 ms (approximately 50 Hz) and filtered using a zero-phase, 5-pole high pass Butterworth filter with a cutoff frequency of 5 Hz. The reset period following a

crash, during which subjects had no control over the MARS, was not included in the data analysis. Each of the measures listed below was calculated for every trial for every subject. All four trials within each baseline and final performance block were averaged for a given subject and compared statistically across all participants.

MARS performance was quantified by calculating the average MARS angular position ($\text{Mean}_{\text{MARS}}$) and the standard deviation of MARS angular position (STD_{MARS}). The frequency of crashes (Crashes) was calculated by counting the number of crashes in a trial and then dividing by the duration of the trial. The average MARS angular deviation from the direction of balance ($|\text{Mag}|_{\text{Pos}}$) and the average magnitudes of MARS velocity ($|\text{Mag}|_{\text{Vel}}$) and acceleration ($|\text{Mag}|_{\text{Accel}}$) were calculated by taking the mean of the absolute value of each measure.

Joystick commands were quantified by calculating the average of the absolute value of joystick deflections ($|\text{Mag}|_{\text{Joy}}$), which could vary from $+1$ to -1 for full deflection. Intermittency of joystick deflections ($\%\text{Zero}_{\text{Joy}}$) was determined by finding the percentage of data points where the joystick deflection was $\leq \pm 1\%$ of its maximum amplitude. Anticipatory joystick deflections (%Anticipatory) were defined as those that removed energy from the MARS by decelerating it while it was moving toward the DOB. We calculated the percentage of anticipatory joystick deflections by finding the number of data points where the MARS angular position and joystick deflection had opposite signs to the MARS angular velocity and then dividing by the total number of data points. To determine where anticipatory joystick deflections were made, we calculated their average phase angle (Mean θ) using the equation, $\tan^{-1}(\dot{\theta}/\theta)$. We subtracted $180°$ from points in the lower right quadrant (IV) of the velocity vs MARS position phase plots (Fig. 2) and averaged them with those in Quadrant II, because both sets represent anticipatory activity, but for approaching the DOB from different directions. Anticipatory joystick deflections at phase angles near $90°$ slow the MARS down near the DOB. Destabilizing joystick deflections were defined as those that add energy to the MARS, accelerating it away from the DOB. We calculated the percentage of destabilizing joystick deflections (%Destab: blue dots, Fig. 2) by finding the number of data points where the MARS angular position, velocity, and joystick deflection all had the same sign and then dividing by the total number of data points.

Stabilogram diffusion functions, as introduced by Collins and De Luca (1993) to the study of postural control, were used to quantify MARS mean-squared displacement (MSD) at different time intervals.

$$\text{MSD} = \left\langle \Delta\theta^2 \right\rangle_{\Delta t} = \frac{\sum_{i=1}^{N-m} \left(\Delta\theta_i \right)^2}{(N-m)}$$

where θ is the MARS angular position, Δt is the time interval, N is the total number of data points, and m is the number of data points for the total time interval. We used the approach of Collins and De Luca (1993) and set the maximum time interval to 10 s and calculated the MSD over time intervals that did not have any crashes.

To examine the motion of the MARS over different time intervals, we calculated the Hurst scaling exponent (H) using the equation:

$$\left\langle \Delta\theta^2 \right\rangle = \Delta t^{2H}$$

H is obtained by plotting the log of MSD versus the log of Δt, calculating its slope, and then dividing by 2. When $H = 0.5 \text{ deg}^2/\text{s}$, the motion is Brownian and the future is not correlated with the past. If $H < 0.5 \text{ deg}^2/\text{s}$, the motion of the MARS is anti-persistent and the past is negatively correlated with the future, such that the direction of MARS movement changes over the time interval Δt. If $H > 0.5 \text{ deg}^2/\text{s}$, the motion is persistent and the past is positively correlated with the future, and the MARS will continue to move in the same direction. The "critical point" occurs when H changes from $> 0.5 \text{ deg}^2/\text{s}$ to < 0.5 and it represents when the transition between the short- and long-term regimes occurs. To quantify positional drifting, we calculated the diffusion coefficient (D) of the SDF, which represents the rate of change of the MSD:

$$\left\langle \Delta\theta^2 \right\rangle = 2\text{D}\Delta t$$

The short-term diffusion coefficient (D_S) is found by taking one-half of the slope between $\Delta t = 0$ s and the critical point on the standard MSD plot. The long-term diffusion coefficient (D_L) is found by taking one-half of the slope between the critical point and $\Delta t = 10$ s. If $D_L > 0 \text{ deg}^2/\text{s}$, it means that the MSD continues to increase in long time intervals, indicating positional drifting. Finally, to quantify the overall energy of the long-term regime (Mean_{MSD}), we calculated the average MSD between the critical point and $\Delta t = 10$ s.

Statistical treatment

Following Collins and De Luca (1995), we first averaged the SDFs across the four trials in each baseline and final block for each subject, after which we calculated the short-term and long-term diffusion coefficients, and the final MSD. We then averaged the values across all participants. For all other measures, we first calculated them in each trial and then averaged them across trials in a baseline or final block and finally averaged them across all subjects. To test for learning within groups, we carried out paired t tests between the baseline trials 1–4 of Day 1 and final performance (trials 17–20) on Day 2. To test the efficacy of vestibular training (searching for the DOB), we compared final performance on
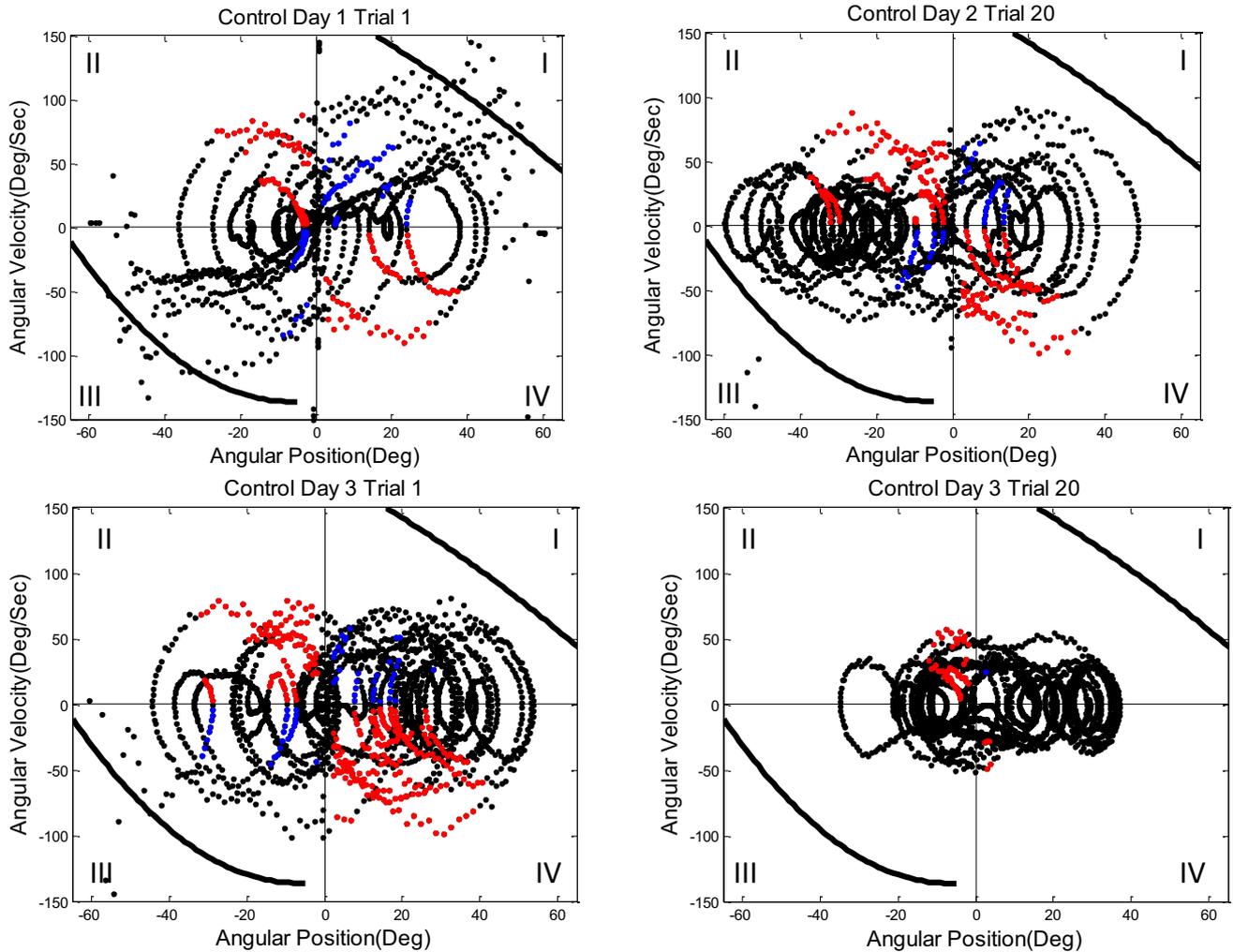
Control Group

Fig. 2 Phase plots of MARS angular velocity against MARS angular position are from representative subjects from the control (top) and vestibular training (bottom) groups. For each group, the first row has phase plots for the same subject comparing Trial 1 on Day 1 (left) to Trial 20 on Day 2 (right), and the second row has phase plots for the same subject comparing Trial 1 (left) and Trial 20 (right) on another experimental day 4 months later. The thick black curves were empirically determined and represent limits after which joystick deflections cannot prevent crashing. The blue points signify the occurrence of destabilizing joystick deflections and the red points are anticipatory joystick deflections

Day 2 between groups with independent t tests. To test for performance retention for the vestibular training and control groups, we conducted t tests between the final four trials of Day 2 and the initial four of Day 3, 4 months later (Fig. 3).

Results

Vestibular training group

Table 2 shows that these subjects had significant learning across most metrics when comparing baseline Day 1 performance to final Day 2 performance (Table 2). In the

MARS Performance category, they were able to decrease the standard deviation of angular position (STD_{MARS}), the frequency of crashes (Crashes) by 20-fold, and the magnitudes of MARS angular position ($|Mag|_{Pos}$), velocity ($|Mag|_{Vel}$), and acceleration ($|Mag|_{Accel}$). In the Joystick Command category, they learned to decrease the magnitude of joystick deflections ($|Mag|_{Joy}$) and the percentage of destabilizing joystick deflections (%Destab); however, they were unable to change the intermittency of joystick deflections (%$Zero_{Joy}$), percentage of anticipatory joystick deflections (%Anticipatory), and the phase angle of anticipatory joystick deflections (Mean θ). In the stabilogram-diffusion function category, subjects significantly
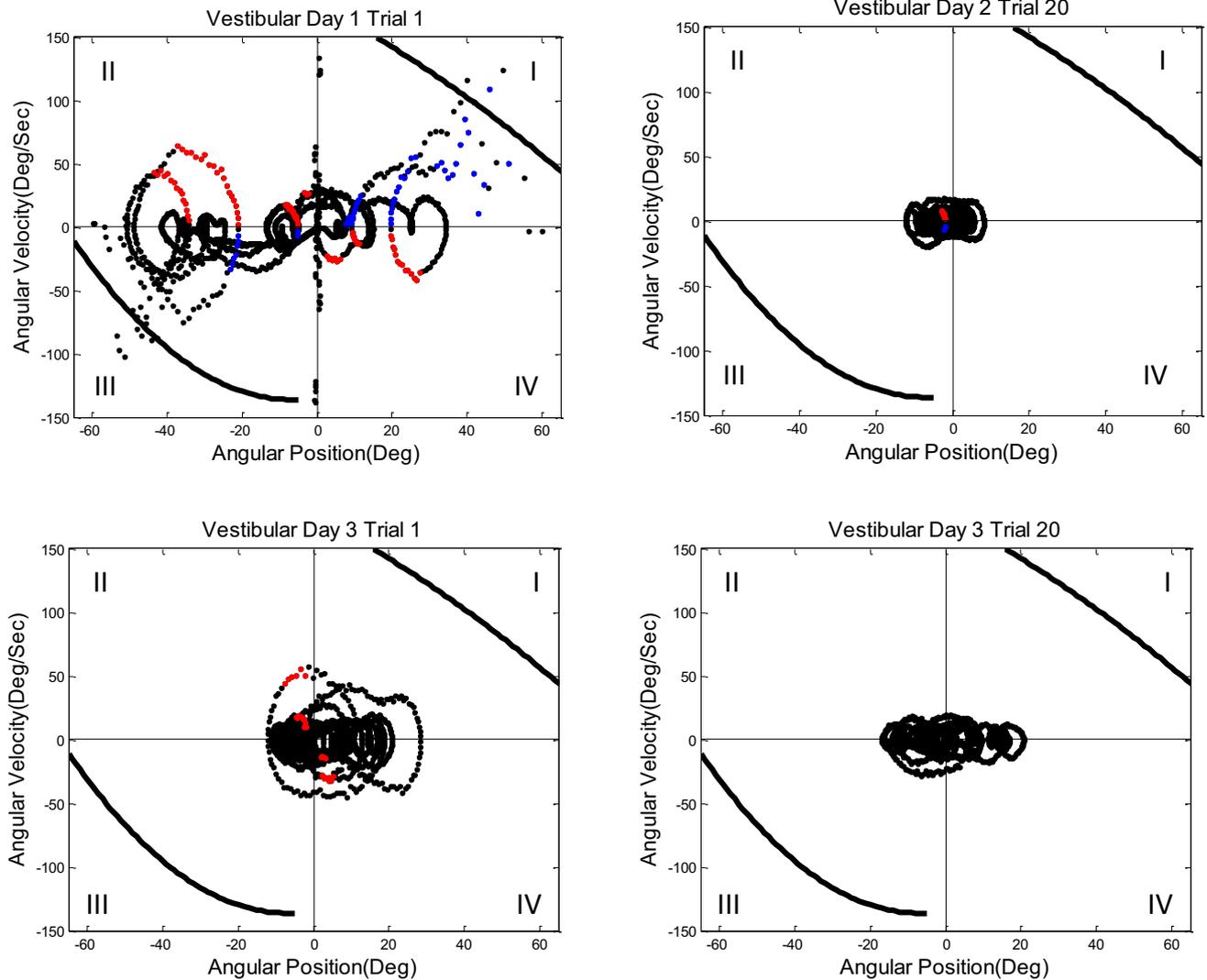
Vestibular Training Group

Fig. 2 (continued)

decreased the short-term diffusion coefficient (D_S), the long-term diffusion coefficient (D_L) and the long-term mean-squared displacement ($Mean_{MSD}$).

Table 3 shows that the vestibular training subjects showed full performance retention across the 4-month break. Paired *t* tests between the ultimate trials on Day 2 and the initial ones on Day 3 (4 months later) revealed no significant differences for any measure. Table 3 also shows that subjects in the vestibular training group exhibited additional learning on Day 3, decreasing the

magnitude of MARS velocity ($|Mag|_{Vel}$) and acceleration ($|Mag|_{Accel}$) from the initial to the final trials.

Control group

Table 2 indicates that the control group, who were tested only in Horizontal Roll, showed minimal learning from the beginning of Day 1 to the end of Day 2. In the MARS Performance category, they only learned to decrease the frequency of crashes (Crashes), but were unable to reduce the standard deviation of angular position (STD_{MARS}) and the
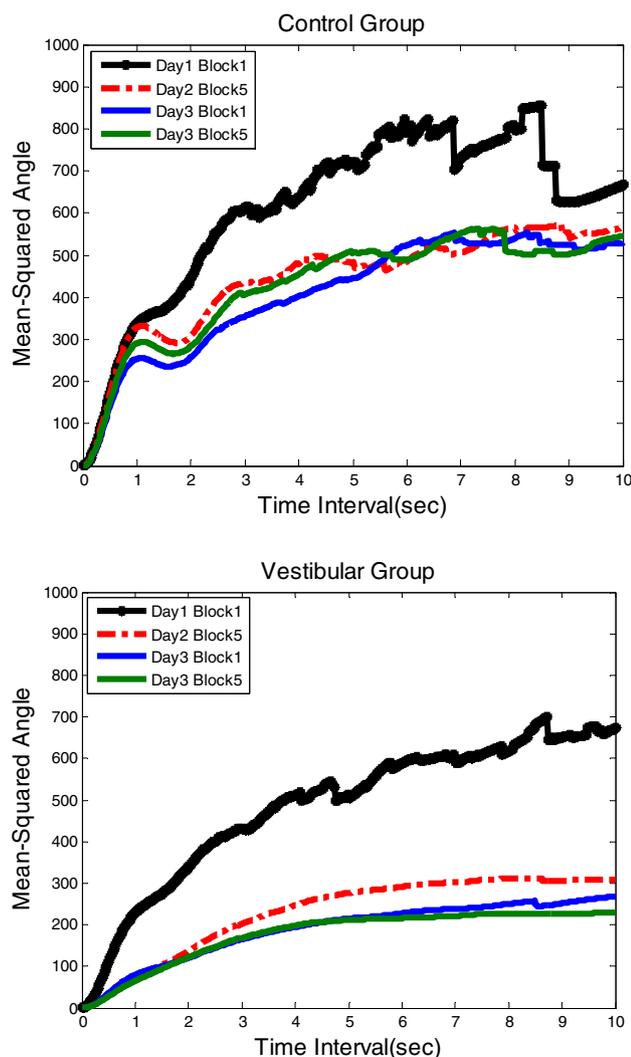
Fig. 3 Stabilogram diffusion functions averaged across all participants in the control (top) and vestibular training (bottom) groups

magnitudes of MARS angular position ($|Mag|_{Pos}$), velocity $|Mag|_{Vel}$, and acceleration $|Mag|_{Accel}$. In the Joystick Command category, subjects learned to decrease destabilizing joystick deflections (%Destab) but were unable to change the magnitude of joystick deflections ($|Mag|_{Joy}$), intermittency of joystick deflections (%$Zero_{Joy}$), percentage of anticipatory joystick deflections (%Anticipatory), and the phase angle of anticipatory joystick deflections (Mean θ). The stabilogram-diffusion function results show that the control subjects were unable to reduce significantly any measure: the short-term diffusion coefficient (D_S), the long-term diffusion coefficient (D_L) and the long-term mean-squared displacement ($Mean_{MSD}$). These results are fully consistent with our earlier studies (Vimal et al. 2017, 2018).

To examine long-term retention, we performed paired *t* tests between final performance on Day 2 and initial performance on Day 3 which took place 4 months later. We found

that no significant change occurred for any measure, meaning that their performance did not significantly improve or decline during the 4 month break. Table 3 also shows that the control subjects did not show any additional learning between the beginning and end of the third and final experimental day.

Control vs vestibular training group

We found statistically significant differences between the control and vestibular training groups when comparing the final trials on Day 2, which represent the ultimate performance levels attained across the two test days. The vestibular group had a 10 times lower crash frequency (Crashes) and 4 times smaller short-term diffusion coefficient (D_S). They also had lower magnitudes of MARS angular velocity ($|Mag|_{Vel}$) and joystick deflection ($|Mag|_{Joy}$). There was a statistical trend showing the vestibular training group to have a smaller standard deviation of angular position (STD_{MARS}, $p = 0.052$), a smaller long-term diffusion coefficient (D_L, $p = 0.057$) and smaller final mean-squared displacement ($Mean_{MSD}$, $p = 0.054$).

Table 3 shows multiple significant differences between the control and vestibular training groups at the end of the tests conducted on test Day 3, 4 months later. The vestibular training group had a mean angular position closer to the balance point ($Mean_{MARS}$), smaller values for the standard deviation of angular position (STD_{MARS}), lower crash frequency (Crashes), smaller magnitude of angular position ($|Mag|_{Pos}$), lower magnitude of angular velocity ($|Mag|_{Vel}$), smaller magnitude of angular acceleration ($|Mag|_{Accel}$), smaller joystick deflections ($|Mag|_{Joy}$), fewer destabilizing joystick deflections (%Destab), fewer anticipatory joystick deflections (%Anticipatory). The short-term diffusion coefficient (D_S), long-term diffusion coefficient (D_L), and final mean-squared displacement ($Mean_{MSD}$) were all significantly lower for the vestibular training group as well.

Effectiveness of vestibular training

A core component of the vestibular training program was the 'searching for the DOB' task. To determine whether subjects learned this task, we averaged the MARS angular deviation from the direction of balance ($|Mag|_{Pos}$) for the first 3 'search for the DOB' trials with different DOBs on Day 1 for the vestibular training group (trials 15, 17, 19) and then used a paired *t* test to compare the last 3 comparable search trials on Day 2 (trials 9, 11, 12). We found that the vestibular training group improved their performance (9.5°–6.4°, $p = 0.02$). To determine whether improvement in the 'search for the DOB' task led to better performance in the horizontal roll plane condition, we calculated for Day 2 the correlation between the last four trials of the 'search for the DOB' task for vestibular training group (trials 8, 9, 11, 12) and the last four trials of the

Table 2 Dynamic balancing on Day 1 and Day 2

Metric	Control ($n = 10$)		Vestibular ($n = 10$)	
	Baseline, Day 1	Final, Day 2	Baseline, Day 1	Final, Day 2
MARS performance				
$Mean_{MARS}$ (°)	− 1.1	− 2.1	− 2.5	− 1.6
STD_{MARS} (°)	21.3	17.6	21.0	11.3***
Crashes (Hz)	0.2	0.05***	0.1	0.005***,#
$|Mag|_{Pos}$ (°)	15.2	14.0	16.1	9.5**
$|Mag|_{Vel}$ (deg/s)	23.9	22.2	19.7	10.3**,#
$|Mag|_{Accel}$ (deg/s^2)	81	83	79	42**
Joystick commands				
$|Mag|_{Joy}$	0.25	0.28	0.23	0.12**,#
$\%Zero_{Joy}$	38	35	36	43
%Destab	3.7	1.6**	2.2	0.44**
%Anticipatory	3.9	5.1	3.9	1.5
Mean θ (°)	117	113	118	121
Stabilogram–diffusion function				
D_s (deg^2/s)	208	211	138	48.0*,#
D_L (deg^2/s)	48.7	24.4	31.0	9.5***
$Mean_{MSD}$ (deg^2)	644	503	533	260**

The '*' represents paired t tests between Baseline Day 1 and Final Day 2 within a group, and the '#' represents independent t tests between the final Day 2 performance of the control and vestibular training groups. A single symbol means $p < 0.5$, two symbols mean $p < 0.01$, and three symbols mean $p < 0.001$

Table 3 Retention of dynamic balancing 4 months after initial training

Metric	Control ($n = 10$)			Vestibular ($n = 10$)		
	Final, Day 2	Initial, Day 3	Final, Day 3	Final, Day 2	Initial, Day 3	Final, Day 3
MARS performance						
$Mean_{MARS}$ (°)	− 2.1	− 1.1	− 1.1	− 1.6	− 0.1	0.9^x
STD_{MARS} (°)	17.6	17.7	16.6	11.3	10.7	9.1^x
Crashes (Hz)	0.05	0.05	0.04	0.005	0.005	0.004^x
$|Mag|_{Pos}$ (°)	14.0	14	13	9.5	8.8	7.2^x
$|Mag|_{Vel}$ (deg/s)	22.2	22	22	10.3	11	8.2*, ^{x}
$|Mag|_{Accel}$ (deg/s^2)	83	87	86	42	45	33*, ^{x}
Joystick commands						
$|Mag|_{Joy}$	0.28	0.28	0.27	0.12	0.13	0.10^x
$\%Zero_{Joy}$	35	30	32	43	43	45
%Destab	1.6	1.7	1.5	0.44	0.32	0.23^x
%Anticipatory	5.1	5.9	5.5	1.5	1.2	0.65^x
Mean θ (deg)	113	114	111	121	103	114
Stabilogram–diffusion function						
D_s (deg^2/s)	211	117	200	48.0	46	36^x
D_L (deg^2/s)	24.4	18.7	21.2	9.5	9.7	5.0^x
$Mean_{MSD}$ (deg^2)	503	446	499	260	210	192^x

The '*' represents paired t tests between the initial and final performance within a group on Day 3, and the 'x' represents independent t tests between the final performance across groups on Day 3. A single symbol means $p < 0.5$, two symbols mean $p < 0.01$, and three symbols mean $p < 0.001$

horizontal roll plane condition (trials 17–20) for the MARS angular deviation from the direction of balance ($|Mag|_{Pos}$). We found a strong positive correlation ($r = 0.97$, $p = 1.5e{-}6$).

Discussion

Our vestibular training procedure enhanced dynamic stabilization skill in the horizontal roll plane, where there are no gravitationally dependent positional cues, by teaching subjects to search for and balance at different directions of balance (DOB) other than the gravitational vertical in the vertical roll plane. The vestibular training protocol was based on our earlier work showing that balance control involves two processes: alignment with the gravitational vertical (using gravitational positional cues) and dynamic stabilization (using motion cues) (Vimal et al. 2017). We had found that these dual processes are dissociable and asymmetric. Therefore, we reasoned that a training procedure that focuses on developing dynamic stabilization in the vertical roll plane independent of aligning with the gravitational vertical could result in better performance on later exposure to the horizontal roll plane. The success of such a training program shows that graviceptive cues available in the vertical roll plane for balancing at DOBs decoupled from the direction of gravity help subjects learn how semicircular canal and transient somatosensory cues are associated with dynamic balancing. In the horizontal roll plane, the dynamic cues are present but cannot be learned effectively because searching for the DOB without the supporting role of graviceptive cues is too erratic to permit internal recalibration of dynamic cues. Having subjects learn to search for and then balance at unknown and changing DOBs in the vertical roll plane devalues information about the direction of gravity and emphasizes reliance upon transient motion cues. For example, subjects could locate the DOB by the transition from falling in one direction to the other.

The training program significantly helped the vestibular group, which showed robust learning across many metrics. They learned to improve MARS performance by reducing the variability of their movements (STD_{MARS}), the frequency of crashes (Crashes) by 20-fold, and the magnitudes of MARS angular position ($|Mag|_{Pos}$), velocity ($|Mag|_{Vel}$), and acceleration ($|Mag|_{Accel}$). They accomplished this, in part, by decreasing the magnitude of joystick deflections ($|Mag|_{Joy}$) and the percentage of destabilizing joystick deflections (%Destab). The stabilogram-diffusion function results were especially striking; the vestibular group was not only able to reduce the final mean-squared displacement ($Mean_{MSD}$) but also both the short (D_S) and long-term diffusion coefficients (D_L). These results are crucial because a characteristic feature of dynamic balancing without relevant gravitational

cues is positional drifting, associated with a large long-term diffusion coefficient, which the vestibular training group was able to significantly reduce.

In prior studies and in the control group here, we found significant individual differences in performance in the horizontal roll plane, where some subjects showed robust learning and others became worse. Our vestibular training paradigm helped all subjects improve regardless of their initial individual performance in the horizontal roll plane. All subjects in the vestibular training group learned to decrease the standard deviation of their angular position by 5% or more over the 2-day training period; however, only half of the subjects in the control group was able to do so. The success of the vestibular training group was due to the novel 'search for the DOB' task and not because they received exposure to the device in the vertical roll plane. Corroborating this, we found that performance improved significantly on the 'search for the DOB' task and that the degree of improvement correlated positively and significantly with the ultimate degree of improvement in horizontal roll plane dynamic balancing. In our prior work, we had found no transfer of learning when subjects were first trained in the vertical roll plane and then tested in the horizontal roll plane (Vimal et al. 2017). In the present study, we gave both the control and vestibular training groups explicit strategies that we had identified from subjects who had performed well in the horizontal roll plane in our earlier studies. However, these strategies
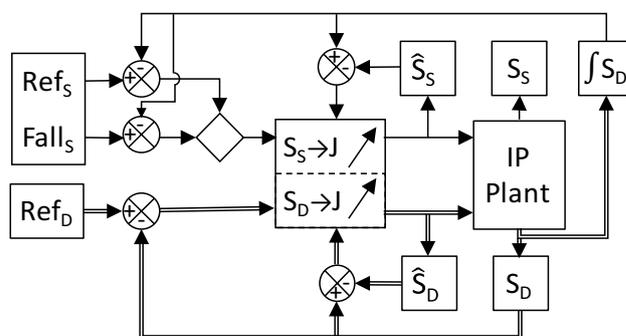

Fig. 4 A model of the dual processes involved in the control and learning of manual self-balancing in the MARS. Alignment with the external gravitational reference frame is presented in single lines of information flow and maintenance of dynamic equilibrium in double lines. Symbols are: *Ref$_S$* reference signal for static target orientation in the external reference frame (direction of gravity = 0°); *Fall$_S$* reference signal for static fall limits in the external reference frame, *Ref$_D$* reference signal for dynamic equilibrium (desired acceleration = 0 deg/s^2) decision process (see text) S_S, S_D—sensory feedback for static orientation/fall avoidance (otolith, somatosensory) and dynamic equilibrium (e.g., semicircular canal, transient somatosensory); $\int S_D$—angular path integration of dynamic orientation feedback; $\hat{S}_S{\to}J\nearrow$ and $S_D{\to}J\nearrow$—variable sensory-joystick maps for orientation/fall avoidance and dynamic equilibrium; $\hat{S}_S$ and $\hat{S}_D$—predicted sensory feedback (internal forward model)

did not enable the control group to perform any better than subjects initially tested in the horizontal roll plane in our earlier work. This implies that training cannot be effectively implemented with exposure only in the horizontal roll plane. When subjects in the vestibular training group were questioned at the end of the experiment, they reported no improvement in their ability to perceive their angular position when in the horizontal roll plane. Instead they had learned strategies to minimize their oscillations and avoid crashes.

Figure 4 depicts the dual static and dynamic orientation sub-systems related to the effectiveness of our training program. The static sub-system compares sensory information to desired reference orientations including the direction of balance and the fall limits. In the vertical roll plane, congruent tilt-dependent stimulation of the otolith organs and somatic mechanoreceptors occurs. As the body is tilted relative to gravity, it is restrained in the apparatus and supported against gravity by all the restraint elements. When the body is parallel with gravity during upright roll plane balancing the distribution of contact cues on the body is basically mirror symmetric about the sagittal plane. As the body is displaced leftward, the distribution of forces on the body changes, leading to changing patterns of somtatosensory pressure and contact cues with greater concentration on the left side of the body and of the head. Tilt stimulates not only cutaneous mechanoreceptors but also produces congruent stresses and strains on limb proprioceptors and visceral interoceptors. Thus, when gravity-dependent directional shear forces are present on the body the otolith organs and proprioceptive-somatosensory systems generate position-dependent signals that are confirmatory and redundant. This is why individuals with absent or impaired vestibular function are virtually as accurate as normal subjects in indicating the postural vertical (Clark and Graybiel 1963).

The dynamic orienting system processes information about motion in relation to the direction of balance. In the horizontal roll plane, dynamic motion is detected by the semicircular canals, otolith organs, and somatosensory receptors. Prior work has shown that vestibular thresholds contribute to an individual's ability to perform in a manual tracking task (Rosenberg et al. 2018). While vestibular thresholds may distinguish individual differences in performance, it is unlikely that our training program results in improved vestibular thresholds that persist for 4 months. It is more likely that subjects learn a mapping between joystick motor commands and the resulting dynamic sensory consequences. Figure 4 schematizes such learning as being driven by a sensory expectation error derived by comparing an internal forward model of the sensory consequences of each command to the actual sensory feedback. Such error-driven sensory-motor learning has been shown to be context specific and long lasting (Bakshi et al. 2019; Lackner and

Lobovits 1977; Todd et al. 2019). The sensory motor map referred to in Fig. 4 is generic, potentially including associations between sensory cues and motor responses (Kawato and Wolpert 1998), refinements of the lag and gain of the controller transfer function (Liao and Jagacinski 2000) and sensory reweighting (Peterka and Loughlin 2004). Our training program likely causes sensory reweighting, placing greater motor reliance on dynamic canal signals that specify motion relative to the balance point. Our training results suggest that dynamic canal and somatosensory signals can be used to estimate deviation from the DOB after they become fine-tuned by comparison with gravitational position cues by exposure in the vertical roll plane. Gravitational position cues in the vertical roll plane provide information about body orientation relative to two statically defined reference orientations—the upright or an intentionally offset orientation and the fall limits.

Our model distinguishes these two reference orientations because in the vertical roll plane both references are necessary to explain the observed anticipatory and corrective joystick commands. For example, when the MARS approaches the upright moving leftward, rightward commands are issued to decelerate and prevent overshooting the upright; and rightward commands are also issued when the MARS approaches the left fall limit. Thus, decisions to make rightward commands require comparing the current MARS state to two separate reference orientations. A decision process is included in Fig. 4 to represent the need for situationally dependent inputs to the command map. Separate static references for the upright and fall limits also accommodate our observations that subjects learned to orient independently to either. For example, in the horizontal roll plane, control group subjects learned to reduce the frequency of crashes significantly without improving any aspect of kinematics, like positional standard deviation. Our vestibular training protocol had subjects search for an unknown DOB in the vertical roll plane while also having position-dependent signals present about the direction of gravity, thereby requiring greater reliance on fine-tuning of the dynamic orientation sub-system. The dynamic reference for the balance point was present in both vertical and horizontal roll, because the DOB of an inverted pendulum is where acceleration equals zero, the sign and magnitude of acceleration are directly related to body deviation from the DOB. This enables learning within the dynamic sensory motor map illustrated in Fig. 4.

Why were subjects in the control group able to show only marginal performance improvements? Prior literature shows that error-based learning of internal models is most effective when there is unambiguous feedback and a target (Tseng et al. 2007). Subjects in the control group experienced the horizontal roll plane for 20 trials on both days and always had ambiguous information about their angular position and only received definitive feedback when they crashed. In

contrast, during training in the vertical roll plane, the experimental group had clear signals of their angular position and unambiguous feedback about their performance accuracy, which allowed them to learn how to fine tune the dynamic component of balance control. Another level of processing illustrated in Fig. 4 is the integration of dynamic semicircular canal signals to create an estimate of self-position (Guedry et al. 1971; Metcalfe and Gresty 1992; Mittelstaedt and Mittelstaedt 1980), which enters the static information processing stream. Improvements in the mapping of this indirect position information to motor commands obtained during vertical roll provide a source of learning applicable later during exposure to Horizontal Roll.

We had no strong expectation about long-term retention of training but found robust effects by retesting subjects in the control group and the vestibular training groups after a 4-month break. When tested initially on Day 3 both groups performed at their prior peak performance level, which had been minimal for the control group. The control group showed no improvement in performance between the beginning and end of Day 3, while subjects in the vestibular training group showed additional improvements by decreasing the magnitudes of both MARS velocity and acceleration. These findings indicate that the vestibular training group continued fine-tuning their learning 4 months later, whereas the control group was unable to do the same.

There is little research on what types of skilled motor learning can be retained over long durations of time. The biological mechanisms are still not well understood because different types of motor learning may involve different processes, such as learning to reach in a rotating environment (sensorimotor adaptation), learning to play the piano (sequence learning) and learning dynamic balancing tasks (Abe et al. 2011; Adams 1987; Dayan and Cohen 2011; Nourrit-Lucas et al. 2013; Park et al. 2013; Park and Sternad 2015; Romano et al. 2010; Sanli and Carnahan 2018). The novelty of our approach is that it provides an exploratory learning environment in a condition where vestibular, somatosensory and sensorimotor signals about body position are fundamentally different from anything experienced in normal life.

Conclusion

Our prior work showed that there are two dissociable components of balance control, one related to using gravitational position cues and the other to using dynamic motion cues. Our current study verified this by successfully implementing a training program providing variable dynamic stabilization requirements in the context of gravitational positional cues, which then led to significant enhancement in balance performance in the horizontal roll plane, a spaceflight analog

task. The pattern of training efficacy reveals a novel form of canal-otolith mutual calibration. We found that after only 2 h of exposure, subjects in the vestibular training group retained all of their learning 4 months later and showed further fine-tuning of skill.

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