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Learning Dynamic Control of Body Roll Orientation

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Abstract

Our objective was to examine how the control of orientation is learned in a task involving dynamically balancing about an unstable equilibrium point, the gravitational vertical, in the absence of leg reflexes and muscle stiffness. Subjects ($n=10$) used a joystick to set themselves to the gravitational vertical while seated in a multi-axis rotation system device (MARS) programmed with inverted pendulum dynamics. The MARS is driven by powerful servomotors and can faithfully follow joystick commands up to 2.5 Hz with a 30 ms latency. To make the task extremely difficult, the pendulum constant was set to $600^\circ/\text{sec}^2$. Each subject participated in 5 blocks of 4 trials, with a trial ending after a cumulative 100 s of balancing, excluding reset times when a subject lost control. To characterize performance and learning, we used metrics derived from joystick movements, phase portraits (joystick deflections vs MARS position and MARS velocity vs angular position), and stabilogram diffusion functions. We found that as subjects improved their balancing performance they did so by making fewer destabilizing joystick movements and reducing the number and duration of joystick commands. The control strategy they acquired involved making more persistent short-term joystick movements, waiting longer before making changes to ongoing motion, and only intervening intermittently.

Keywords

vehicle control; vestibular system; orientation; dynamic balancing; stabilogram diffusion function; phase portraits; gravitational vertical

Introduction

Control of human orientation and stance rely on multiple sensory systems, including the vestibular, visual, auditory, and somatosensory, as well as motor systems and central integration mechanisms. Many models have been developed to explain how an estimate of the gravitational vertical is obtained from the gravito-inertial acceleration detected by the otolith organs and how the angular acceleration detected by the semicircular canals can help distinguish the gravitational and inertial components (Angelaki et al., 1999; Angelaki and Cullen, 2008; Clark and Graybiel, 1966; Graybiel and Brown, 1951; Graybiel et al., 1979;

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Laurens and Angelaki, 2011; Merfeld et al., 1999; Zupan et al., 2000). The advent of vehicles introduced a variety of conditions outside the normal range of human experience, and current models of estimation of the gravitational vertical and orientation control are not adequate to predict the occurrence of spatial disorientation, which is responsible for many of the fatal mishaps in both civil and military aviation. Current models also fail to help explain why falling becomes such a hazard for the elderly (Gates et al., 2008).

Helicopter control, and even dragonfly flight (Liang and Sun, 2014) requires using active commands to control the orientation of an unstable plant, just as bipedal standing involves using ground reaction forces to control the unstable body. Recently, we have shown that subjects using a joystick to control the roll motion of a device they are seated in can independently control their orientation in relation to either the gravitational vertical or the direction of anti-pendular equilibrium when the two are experimentally dissociated (Panic et al., 2015). This means that estimating the gravitational vertical and self-displacement from it are not the only processes involved in control of orientation in tasks that are dynamically unstable such as helicopter control and standing. Our objective here was to characterize what is learned by the central nervous system in a difficult dynamic balancing task when subjects use only a joystick to orient themselves about an unstable equilibrium direction.

Our approach was to have subjects seated in a Multi-Axis Rotation System (MARS) apparatus that was programmed to behave like an inverted pendulum about the roll axis try to maintain an upright vertical attitude by using a joystick to apply control inputs. We set the balance dynamics of the MARS so that its equilibrium position was very difficult for subjects to maintain, resulting in “falls” and permitting us to evaluate learning. Our apparatus is a multi-axis version of one used by Riccio, Martin and Stoffregen (1992) who studied the relationship between the direction of balance and the perception of the “upright”.

Inverted pendulum dynamics are often used to model human stance (Winter, 1995) and the loss of balance. Substantial research has been devoted to characterizing factors enabling balance control including multi-sensory contributions (Fitzpatrick and McCloskey, 1994) and the role of reflexes and passive stiffness of muscles (Fitzpatrick et al., 1992; Morasso and Schieppati, 1999; Winter, 1995). In a quiet stance balancing task, when a subject deviates from the upright, leg and ankle muscles are stretched, which generates viscoelastic restoring forces and can activate stretch reflexes to restore the subject back toward the upright. Vestibulospinal reflexes can also generate corrective muscle contractions (Wilson and Peterson, 1978).

Central contributions to balance control are not as well understood because it is experimentally difficult to identify control variables and distinguish the contribution of peripheral versus central mechanisms (Hsu et al., 2007; Kiemel et al., 2011; Kuo, 2002). In the experimental paradigm used here, subjects are seated and control their orientation using a joystick, consequently peripheral mechanisms such as segmental reflexes and leg muscle stiffness do not contribute to balance control. In addition, the subjects are blindfolded and wear noise cancelling headphones to prevent visual and auditory feedback. Otolith, semicircular canal and somatosensory cues provide potential signals about roll attitude and angular velocity, and any learning that occurs can be attributed to the CNS relating these

signals to joystick commands that dynamically affect them. Real postural dynamics of standing are more complex than those of a single link inverted pendulum but very likely involve some form of pendular instability, and our paradigm aims to clarify how the CNS learns to manage pendular instability. Our balancing task involves oscillatory behavior with both stochastic and deterministic components, which are the features of a correlated random walk. Consequently, we used the stabilogram diffusion function (SDF) method developed by Collins and DeLuca (1993) to classify two different control regimes: (a) a short term period during which subjects do not make consistent changes to their motion and (b) a longer term period during which subjects make consistent changes. We used phase plots to identify the learning strategies that individuals acquired. This approach enables us to establish how the CNS learns to control dynamic roll orientation in the absence of peripheral stabilizing influences related to the legs.

Materials and Methods

Apparatus

A custom built (Neuro Kinetics) multi-axis rotation system (MARS) was programmed to exhibit inverted pendulum dynamics about the roll axis according to the equation, $\ddot{\phi} = k_p \sin \phi$, where ϕ , measured in degrees, represents the MARS angular deviation from the gravitational vertical and k_p represents the pendulum constant. The MARS pivoted in roll, about an axis in the mid-sagittal plane located 15 cm above the surface of the chair seat, as shown in Figure 1. The subject's head was secured by a compressible, contoured foam restraint. The torso was restrained with lap belts, a Velcro chest belt, lateral support plates and a five-point safety harness, which minimized the subject's movement within the seat. The subject's feet were strapped to a metal plate bolted to the MARS chair. The right and left forearms rested on the chair's arms and the right hand grasped the joystick and the left hand held a rigid post with a "kill switch" to stop the MARS if the subject wanted to abort the trial. No subject ever actually used the kill switch. Subjects controlled the MARS with a Logitech Freedom 2.4 cordless joystick, capable of movement in both the roll and pitch axes, which was attached to the right armrest of the MARS. All subjects began the experiment fully grasping the joystick pistol fashion with their thumb and fingers. Some subjects later reported switching to a control mode in which they tapped the joystick with their thumb and index finger (see Results below). No matter which joystick method subjects used, we were able to extract measures that reflected the amount of intermittency (%Zero_{Joy}). The joystick was spring-loaded towards the central neutral position and had a maximum deflection of $\pm 30^\circ$. Joystick deflections were coded within the range of +1 (maximum leftward deflection) and -1 (maximum rightward deflection). A Runge-Kutta (RK4) solver (Lambert, 1973) integrated the equation to calculate the MARS angular velocity for the next time step every 20.7 ± 1.1 msec. At every time step, the output of the joystick was multiplied by a constant gain (k_j) that was added to the angular velocity of the MARS found by integration. A leftward joystick deflection would result in a leftward (positive) velocity increment of the MARS. The latency between a joystick command and the resulting change in angular velocity was approximately 30 msec and was constant across all joystick input amplitudes and frequencies up to 1.6 Hz. We determined these values by replacing the joystick input with 4 sinusoidal forcing functions ranging from 0.1 to 6.4 Hz

with amplitudes ranging from 1° to 50° . We also found that joystick inputs up to 2.5 Hz were faithfully executed by the MARS. This frequency is double the average joystick frequency (1.2 Hz) subjects actually used (see Results). Safety mechanisms prevented the MARS from exceeding velocities greater than $300^{\circ}/s$ and accelerations greater than $180^{\circ}/s^2$. Further details on the control scheme and system performance are available in a previous publication (Panic et al., 2015).

We conducted a pilot study in which we found that a pendulum constant (k_p) of $600^{\circ}/s^2$ ($10.47 \text{ rad}/s^2$) created a challenging balancing task for subjects. In the pilot study, we increased the k_p until the subjects were unable to balance without multiple falls in a 30 second period. At $k_p=600^{\circ}/s^2$, we found that a joystick gain (k_j) of $19^{\circ}/s$ allowed recovery from large accelerations at large angular positions without causing operator-induced oscillations.

Subjects

Ten healthy adult subjects (24.2 ± 9.8 years old, 4 females and 6 males), without any history of vestibular or sensory-motor problems participated and gave written consent to a protocol approved by the Brandeis IRB. All were without experience in the apparatus or prior knowledge of the experimental paradigm.

Procedure

Subjects were informed that the MARS was programmed to behave like an inverted pendulum. This was illustrated using a pencil balancing on its tip as an example. They were instructed to use the joystick to adjust the MARS so that it remained upright. After being secured in the MARS, they put on noise cancelling headphones that played white noise and were blindfolded. The subjects were not given practice trials prior to the experimental trials.

The experiment included 5 blocks, each block consisting of 4 trials. At the beginning of a trial, subjects were positioned either 10° to the left or right of the vertical. If during a trial a subject's position deviated more than 60° from the vertical, he or she received an auditory message indicating that they had lost control “Crashed”, and the joystick was disabled. The MARS was then automatically reset to the upright position at a rate of $5^{\circ}/s$. After the reset, another auditory message informed them that joystick control was enabled. The trial continued until a cumulative 100s of balance time, excluding resets, was completed. An auditory message announced when a trial was over, and the chair position was then reset to $\pm 10^{\circ}$, and another message announced that a new trial would begin immediately. After every block, subjects received a one minute break and were quizzed about symptoms of motion sickness.

Analysis

Data Reduction—Joystick deflection, MARS angular position and angular velocity were sampled at intervals of 20.7 ± 1.1 msec (approximately 50 Hz). We applied a zero-phase, 5-pole Butterworth filter to all of the data using a cutoff frequency of 5 Hz. In trials where subjects “crashed” (MARS angle exceeded 60° from the vertical), we deleted the data recorded during the period when the MARS was being reset to the upright.

MARS Position—We calculated the average angular position of the MARS ($\text{Mean}_{\text{MARS}}$) in relation to the gravitational vertical and the standard deviation of its angular position (STD_{MARS}) during each trial. We also recorded the number of crashes in each trial. The magnitude of MARS oscillations was derived from phase plots of MARS angular velocity against angular position for each trial, as shown in Figure 2 for a typical subject. The left and right panels plot data from trials 1 and 20, respectively. We calculated the average radius between the origin and every point in the phase space (Rad_{MARS}) as a lumped measure of position and velocity fluctuations. In quadrants I and III of the phase plots the MARS is moving in the same direction as its current tilt, approaching the state where a maximum joystick deflection would not prevent it from reaching the 60° crash limit. We empirically determined the crash limits (black lines in Figure 2), by identifying the angular velocity and position at time points at which a maximum joystick deflection in the correct direction could not prevent the MARS from going past the crash reset point. We then applied a second order polynomial fit that was used to draw the black curves. The significance of the red and blue points in Figure 2 is explained below in the section describing analysis of the MARS-Joystick Dynamic Relationship.

Joystick Control—To assess the magnitude of control commands the subjects made, we calculated the average of the absolute values of joystick deflections ($|\text{Mag}|_{\text{Joy}}$). To evaluate the incidence of joystick inactivity, we calculated the percentage of time the joystick was at zero deflection ($\% \text{Zero}_{\text{Joy}}$). We did this by finding the number of time points where the joystick deflection magnitude was $\pm 1\%$ of the maximum deflection, divided this number by the total number of time points, and multiplied by 100.

MARS-Joystick Dynamic Relationship—Figure 3 shows plots of joystick position against MARS angular position for a typical subject. The left and right panels show data from trials 1 and 20, respectively. To quantify the magnitude of composite variation in MARS tilt and joystick deflection, we calculated the average radius between the origin and every point on the MARS-joystick plot ($\text{Rad}_{\text{M-J}}$). The data points in quadrants I and III indicate when the joystick was deflected in the same direction as the MARS tilt angle. To quantify the percentage of time joystick commands accelerated motion in the same direction as the current MARS tilt, we counted the entries in quadrants I and III and divided by the total number of samples ($\% \text{J=P}$), with the requirement that the MARS angular position was greater than $\pm 2^\circ$ from upright and the joystick deflection was greater than $\pm 0.5\%$ of full deflection. The points in quadrants I and III are shown in blue when the MARS velocity had the same sign as both joystick deflection and MARS angular position (with the requirement that the MARS angular velocity was greater than $\pm 2^\circ/\text{s}$). For these blue points, the joystick commands are “anti-compensatory” in that they accelerate the MARS closer to the fall limits. The points in quadrants I and III are shown in red when MARS velocity was opposite in sign to MARS and joystick positions. In this case, the joystick commands are both “anticipatory” and “compensatory”, decelerating the MARS when it is moving at a high velocity toward the upright position. To find the percentage time spent making “anti-compensatory” joystick commands in the direction of current self-tilt and motion (blue, $\% \text{J=P=V}$) or making “anticipatory and compensatory” joystick commands in the same

direction as self-tilt but not velocity (red, %J=P V), we divided the number of points in each category by the total number of points for that trial and multiplied by 100.

The red and blue points defined above are also shown in Figure 2. The blue, “anti-compensatory” points fell in quadrants I and III and accelerated the MARS toward the nearby crash limits. The red, “anticipatory and compensatory” points decelerated the MARS at phases where it was nearing the upright position. We calculated the average and standard deviation of the phase angle in Figure 2 for red “anticipatory and compensatory” joystick commands ($\text{Mean}\theta_{J=P \text{ V}}$ and $\text{STD}\theta_{J=P \text{ V}}$). Because we were only interested in phase angle relative to the gravitational vertical (position= 0°), we subtracted 180° from all red points in quadrant IV before averaging.

Stabilogram Diffusion Function: Collins and De Luca (1993) used the stabilogram diffusion function (SDF) to model the trajectory of the center of foot pressure during quiet stance as a correlated random walk. We used the same approach to describe the trajectory of the MARS angular position relative to the vertical. The angular mean squared distance (MSD) was calculated where r represents the angle of the MARS, N represents the total number of data points, t represents the time interval, and m represents the number of data points for the maximum time interval of $t = 30$ seconds.

$$\text{MSD} = \langle \Delta r^2 \rangle_{\Delta t} = \frac{\sum_{i=1}^{N-m} (\Delta r_i)^2}{(N - m)}$$

The Hurst scaling exponent (H) of the SDF, is represented by:

$$\langle \Delta r^2 \rangle = \Delta t^{2H}$$

The scaling exponent represents the correlation between past and future movements. If $H > 0.5$, then the past is positively correlated with the future, which means the behavior is persistent and the MARS tends to move in one direction. If $H = 0.5$, the behavior is Brownian motion. If $H < 0.5$, the past is negatively correlated with the future, which means the motion is anti-persistent and corrections are made to change the direction of the MARS. To determine the time interval over which subjects changed from the short term control regime of drifting ($H > 0.5$) to the long term control regime of consistent corrections ($H < 0.5$), we calculated the “critical point” (CP), the first time interval during which H reaches 0.5. H is determined by plotting MSD as a function of time on a log-log scale. The short term scaling exponent (H_s) is calculated by taking the average slope of the function between $t=0$ and the CP and dividing by 2. Similarly, the long term exponent (H_L) is computed by dividing the slope of the function between the CP and $t=30$ s by 2. To determine the energy of the anti-persistent region we averaged the data points of the SDF between CP and $t=30$ (Mean_{MSD}).

Results

The experimental findings for all variables across subjects are presented in Table 1 where trial data are averaged separately for each block of trials. To assess the pattern of learning that occurred we carried out statistical tests to compare the performance changes that occurred across the five blocks of four trials each.

Mars Position was characterized using four factors: the average angular position of the MARS, the standard deviation of the MARS angular position, the number of crashes, and the average radius of the points on the position vs velocity phase plots. A MANOVA showed significant reduction ($p=0.006$) in each variable except MARS average angular position, across blocks. Follow-up univariate ANOVAs showed a reduction ($p<0.01$ at least) of each variable across blocks 1-5. To examine possible learning trends we compared blocks 2,3,4 and 5 with block 1 using t-tests with Bonferroni adjustments for multiple comparisons. Decreases in the standard deviation of MARS angular position (STD_{MARS}) and in average radius (Rad_{MARS}) of position-velocity loci were significant ($p<0.01$) by block 2 and trended lower in subsequent trials. The frequency of crashes (Crashes) was significantly lower from block 3 onward ($p<0.05$). The representative plots of MARS angular position vs velocity for one subject's initial and final trials shown in Figure 2 provide a visual depiction of the magnitude of the learning that occurred.

Joystick Control evolved across blocks as shown by a significant MANOVA ($p=0.00008$) for the magnitude of joystick displacements ($|Mag|_{Joy}$) and the total time for which the joystick deflection was zero ($\%Zero_{Joy}$). Follow-up univariate ANOVAs showed a reduction ($p=0.001$) of each variable across blocks 1-5. By block 2 and all subsequent blocks $|Mag|_{Joy}$ had significantly decreased ($p<0.01$) relative to block 1. By block 3 and the subsequent blocks $\%Zero_{Joy}$ had significantly increased ($p<0.05$ all comparisons). The magnitude of change can be seen in Figure 3 for the typical subject's phase plots for joystick deflection vs MARS angular position.

MARS-Joystick Dynamic Relationship was assessed from phase plots of joystick deflection vs MARS angular position (Figure 3). A MANOVA showed a significant effect across blocks for the six variables listed in Table 1 ($p=0.01$). Follow-up univariate ANOVAs showed a reduction ($p<0.02$ at least) across blocks 1-5 for the five variables discussed next. The average radius, Rad_{M-J} , of the combined joystick deflection and angular offset of the MARS from the vertical (see Figure 3) decreased significantly by block 2 and subsequent blocks ($p<0.01$) for all comparisons indicating overall reductions in flux of control signals and MARS motion. The percentage of joystick deflections in the same direction as the MARS angular deviation from the upright, $\%J=P$, decreased significantly by block 2 and then decreased even further ($p<0.05$, all comparisons), as can be seen by the reduction in the number of points in quadrants I and III of Figure 3 from block 1 to 5. The percentage of blue points in quadrants I and III of Figure 3 that represent when joystick deflections and MARS angular position and velocity all have the same sign, $\%J=P=V$, decrease significantly in number by block 2 ($p<0.05$) and are nearly absent in the subsequent blocks. This means that the incidence of radically destabilizing joystick deflections greatly diminished. The percentage of red data points, $\%J=P \neq V$, in Figures 2 and 3, represents when joystick

deflection and MARS angular position had the same sign but MARS angular velocity had the opposite sign. Significant decreases in percentages of these red points occurred by block 2 and continued in subsequent blocks ($p < 0.05$, all comparisons). A significant change did not occur in $\text{Mean}\theta_{j=p}$, the phase angle relative to the MARS position-velocity space of the red points but the variability of their phase angle, $\text{STD}\theta_{j=p}$, decreased across blocks. This means that anticipatory and compensatory joystick movements became less frequent and more concentrated around a specific phase angle of the MARS.

Stabilogram Diffusion Function

Figure 4 presents summary stabilogram diffusion function (SDF) results across all subjects. Individual SDFs were calculated for every trial of each subject separately for each block of trials. Trials within a block were then averaged for each subject, and then the block means (1-5) were averaged across subjects. Figure 4 shows the results plotted on a linear scale on the left and log-log on the right. A MANOVA showed a significant effect across blocks for H_s , H_L , CP and Mean_{MSD} ($p = 0.0003$). Follow-up univariate ANOVAs showed an increase ($p < 0.002$) of H_s and CP and a decrease of Mean_{MSD} ($p = 0.0001$) but no change in H_L . The short-term Hurst exponent H_s increased significantly across blocks but was always 0.8 deg^2/s or greater. This means that up to the critical point, MARS movements tended to be persistent, i.e. in the same direction. The longterm Hurst exponent, H_L was always 0.01 deg^2/s or less indicating that after the critical point, MARS' motions were predominately compensatory and toward the gravitational vertical. The CP value increased significantly from block 1 to block 2 and continued to increase for the subsequent blocks, indicating that subjects waited longer and made reactive rather than anticipatory corrective movements. The curves for the individual blocks in Figure 4 are symmetric for blocks 1-5 but are displaced downward progressively for the increasing block numbers. This pattern indicates that the overall amplitude of MARS motion decreased across blocks. Mean_{MSD} significantly decreased from blocks 1 to 2 and blocks 2 to 3, which means that subjects learned to decrease the overall energy in the antipersistent region.

Discussion

Our objective was to characterize learning in a dynamic self-balancing task about an unstable equilibrium point, the gravitational vertical, and to examine the contribution of the central nervous system. The paradigm we used minimized the contributions of peripheral mechanisms implicated in balance control under normal conditions of maintaining upright postural stance. Our analysis relied on metrics derived from joystick movements, MARS movements, phase portraits, and the stabilogram diffusion function. We found that subjects rapidly learned to balance themselves about an unstable equilibrium point in that the variability of MARS angular position (STD_{MARS}) decreased over time, fewer losses of control (Crashes) occurred, and the amplitude of MARS combined position and velocity (Rad_{MARS}) decreased. These results point to the CNS being able to play a very active role in balance control.

The decrease in the standard deviation (STD_{MARS}) of MARS angular position and the decrease in crashes (Crashes) show that learning occurs but does not identify the nature of

that learning. However, the joystick-MARS dynamic relations provide insight. All subjects learned to decrease the magnitude of joystick deflections ($|Mag|_{Joy}$), and many commented that adjusting the magnitude of their joystick deflections was a key element in their strategy, allowing them to use smaller magnitude joystick deflections at the appropriate time to keep the MARS upright. They also spontaneously increased the percentage of time they kept the joystick at zero deflection ($\%Zero_{Joy}$). This points to an intermittent control being adopted, in which subjects learn to optimize their use of the joystick and to minimize the magnitude of joystick deflections. Several subjects in post-experiment briefings commented that they switched to ‘a tapping’ method of joystick control as they became more proficient. Interestingly, Loram et al. (2011) who had subjects use a joystick to control a virtual inverted pendulum reported that many subjects found that intermittent “tapping” control was better than continuous control. This suggests that CNS contributions to balance may operate in an intermittent manner, in contrast to the continuous nature of muscle stiffness and postural reflexes in the control of upright stance (Loram et al., 2011). Loram and Lakie (2002) have observed intermittent EMG activity during postural stance and have proposed that intermittent leg muscle control may reduce the adverse effects of neural and motor noise by providing subjects a keener awareness of how their control actions affect body motion in maintaining upright posture. Intermittent control may also be used in manual and virtual stick balancing experiments to overcome neural delays and noise (Cabrera and Milton, 2002; Loram and Lakie, 2002; Milton et al., 2008).

The change from trial 1 to trial 20 in the relationship between MARS angular position and joystick deflection shown in Figure 3 was typical of all subjects and shows that they learned to minimize both joystick and MARS displacement magnitude, Rad_{M-J} (radial distance from the origin of the phase plot). They also learned to minimize joystick deflections that had the same sign as MARS angular position ($\%J=P$), as shown by the reduced proportion of points in quadrants I and III of Figure 3. The blue points, representing destabilizing joystick deflections, ($\%J=P=V$) were virtually eliminated. However, subjects also learned to minimize joystick deflections that are anticipatory and compensatory ($\%J=P \neq V$) where the sign of the MARS angular velocity is opposite to that of the MARS angular position and joystick deflection (the red points in Figures 2 and 3). The fact that the remaining anticipatory and compensatory joystick movements after learning were more concentrated around the same phase angle of the MARS as before learning may indicate CNS attunement to stability conditions of the MARS dynamics. Over blocks of trials, subjects learned to maintain a more anti-phase relationship between joystick deflection and MARS angular position (higher proportion of points in quadrants II and IV of Figure 3 and fewer in quadrants I and III). This means there was a tendency toward more delayed, reactive control commands as subjects became more expert. The tendency toward fewer oscillations and more anti-phase joystick movements is also apparent from the stabilogram diffusion analysis presented next.

The reduction in frankly destabilizing (blue dots in Figures 2 and 3) joystick movements is noteworthy. Such events where subjects throw themselves off balance by their control actions in a postural or vehicle orientation task have not previously been reported to our knowledge. We observe them in a context where we have experimentally removed the biomechanical and reflexive stabilization subjects normally have available and forced them

to attune their CNS to the balance dynamics. This raises the possibility that falling and loss of vehicle control at times might be caused by an improper CNS-generated command rather than a poorly tuned response or a degraded peripheral sensory signal. Our paradigm creates a way to unveil and quantify these risk factors.

Stabilogram Diffusion Function

We used the Stabilogram Diffusion Function (Collins and De Luca, 1993) to characterize learning in our dynamic balancing task. Our results (Table 1 and Figure 4) indicate that the majority of the reduction in the energy of the MARS occurred in the first 3 blocks. Between blocks 1 and 2, Mean_{MSD} decreased by 37% and between blocks 2 and 3 it decreased by 23%. In the final 2 blocks, Mean_{MSD} does not show further changes. In contrast, STD_{MARS} , which represents the total variability of the MARS over both the short and long time intervals, shows improvements into the final block. The decrease of STD_{MARS} in the final two blocks is a result of the increase in duration of short term persistent behavior as shown by the increase in CP, which signifies an increased span of the persistent regime and decreased span of the anti-persistent regime. H_s always remains above 0.5 indicating that in the short term, the past movements of the MARS were positively correlated with its future movements and that with high probability, the MARS's next movement was in the same direction as the previous one. H_s increased over blocks indicating that subjects learned to increase the persistence of short term movements and made fewer corrections to the motion of the MARS. Consistent with this, the percentage of time the joystick was held at zero deflection ($\% \text{Zero}_{\text{Joy}}$) increased. H_L , the long term scaling exponent, always remained below 0.5, indicating that the long term control regime was anti-persistent and subjects made consistent corrections (i.e. there was a higher probability that the next movement would be in the opposite direction to the previous one).

The critical point (CP) of the SDF represents the time at which subjects change from making no consistent corrections to making consistent corrections. We found that the critical point increased with task mastery, meaning that subjects waited longer before making corrections to the motion of the MARS. This is supported by our findings that with learning, short term persistence increased (H_s), and the percentage of time the joystick was at zero increased ($\% \text{Zero}_{\text{Joy}}$). The graphs in Figure 4 show that over subsequent blocks the subjects progressively decreased overall mean squared angular displacement and the MARS was maintained closer to the upright. The increases in CP and H_s across learning blocks are consistent with the lower incidence of joystick deflections and the increase in anti-phase stick movements discussed above. An increase in CP and H_s could occur if the MARS were unable to faithfully execute high frequency joystick deflections. Subjects then would naturally converge to a low bandwidth strategy. However the average joystick frequency was 1.2 Hz which is well below the 2.5 Hz frequency at which the MARS first begins to falter in following joystick commands (see Materials and Methods, Apparatus section). Therefore, the observed trends are a reflection of CNS learning.

Some investigators question whether the SDF represents two different control schemes: a short term open-loop process and a long term closed-loop process. Approaches using a single continuous process are also able to produce an SDF with 2 stages (Newell et al., 1997;

Peterka, 2000) indicating that one cannot conclude with certainty which time intervals are unquestionably open-loop and closed-loop (Delignières et al., 2003). Peterka (2000) has shown that a simple feedback control system representing balance dynamics as an inverted pendulum and using PID control to generate restoring torques can generate SDFs with short-term and long-term regions without any need to postulate open-loop and closed-loop activity. PID control involves a factor proportional to body angle (k_p), a factor proportional to velocity (K_D) and K_I , the integral of sway angle. We can make no conclusions from our data about open-loop or closed-loop control, instead, we have used the SDF as a mathematical tool to determine two different stages of control: no consistent changes to movements versus consistent corrections. It is notable that a detailed analysis of the SDF plots in Figure 4 is compatible with and allows one to infer much of the pattern of joystick control that we identified using the phase-plot analyses of joystick deflections and MARS angular position and velocity.

As Peterka (2000) mentions balance control on a moving surface requires information about body orientation in space and this can be provided by interrelating semi-circular canals signals about rotation and otolith signals about linear acceleration with proprioceptive signals and other graviceptive cues. In our experimental paradigm, muscle spindle and joint receptor information from leg muscles and somatosensory stimulation of the soles of the feet are not available to contribute as they normally do to balance control. While there is feedback from the forearm and wrist, it is not analogous to the role of mechanical stiffness and peripheral reflexes found in the leg muscles. In the future, by running labyrinthine-loss individuals we will be able to dissociate the role of the vestibular system from the somatosensory. Vestibular potentiation is unlikely to be involved in our findings because recent measurements of semicircular canal and otolith afferent responses to naturalistic stimuli in monkeys indicate non-linear responses that remain stationary over the time period our study involved (Schneider et al., 2015).

Differential somatosensory stimulation of the body surface, proprioceptive and vestibular cues were adequate in our experimental situation to allow normal physiological-like SDFs to be generated through CNS relating of these signals to joystick deflections. Our results open the possibility that sensory signals are used not only for estimating and minimizing self-tilt relative to gravity or the ground but also to register and to stabilize purely dynamic variables.

Conclusion

Our objective was to characterize learning of a dynamic balancing task about an unstable equilibrium point and to examine the contribution of the central nervous system in the absence of peripheral mechanisms normally involved in balance control. We found that subjects were able to learn the task and improve their performance as reflected in decreases in MARS angular position variability, the number of crashes, and MARS position and velocity amplitudes. These performance changes indicate that the CNS learns the dynamics of the system being controlled and plays an active role in balance control. As learning proceeded subjects began adopting an anti-phase relationship between joystick deflection and MARS angular position and minimizing both destabilizing and “compensatory and

anticipatory” joystick movements. They did this by allowing more persistent short term movements of the MARS, waiting longer before making changes to its movement, and by decreasing the amplitude of joystick deflections. They also adopted a more intermittent control, which increased the time the joystick was at zero deflection and increased the critical point.

Our experiment combined spatial orientation and vehicle control and is relevant to aviation where spatial disorientation accounts for over 25% of all fatal mishaps. Our experimental approach provides quantitative metrics to describe what the CNS learns when a joystick is used to control an unstable vehicle. Future experiments will examine how we learn to control different unstable dynamics, including those involved in hovering helicopters.

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Figure 1. Subject seated in the MARS (Multi-Axis Rotation System) programmed to behave like an inverted pendulum, used a joystick to try to keep it at the gravitational vertical.

Figure 2.

Phase plots of MARS angular velocity versus angular position for the first and last trials of a session for a typical subject. The solid curved black lines in the perimeter of quadrants I and III, represent the empirically determined limits at which joystick deflections cannot prevent the MARS from going past 60 degrees from the vertical. The blue points represent when the joystick was deflected in the same direction as MARS position and angular velocity. The red points represent when the MARS position and joystick deflection were opposite in direction to the MARS angular velocity.

Figure 3.

Phase plots of joystick deflection versus MARS roll position for the first and last trials of a session for a typical subject. Blue and red dots are explained in the captions for Figure 2 and in the text.

Figure 4. Stabilogram-diffusion functions averaged over all subjects for individual blocks of trials plotted on a linear scale (left) and a log-log scale (right). Details of averaging are presented in the text.

Table 1
Averages and standard deviations of performance parameters across trial blocks, (N=10)

Variable	Block 1	Block 2	Block 3	Block 4	Block 5
MARS Position					
Mean _{MARS} (deg)	-0.88	-0.83	-1.2	-0.67	-0.46
STD _{MARS} (deg)	12.26	9.48**	8.23**	8.25**	8.00*
Crashes	1.4	0.2	0*	0.075*	0.075*
Rad _{MARS}	0.20	0.15**	0.13**	0.13**	0.13**
Joystick Control					
Mag _{Joy}	0.22	0.15**	0.11**	0.11**	0.11**
%Zero _{Joy}	25.7	33.6	38.0**	38.6*	38.0*
MARS-Joystick Dynamic Relationship					
Rad _{M-J} (deg)	0.30	0.21**	0.17**	0.17**	0.16**
%J=P	4.7	2.4*	1.4**	1.4**	1.3**
%J=P=V	0.61	0.19**	0.08**	0.09**	0.09**
%J=P V	4.0	2.1*	1.3**	1.3**	1.1**
Meanθ _{J=P V} (deg)	105.2	103.2	103.5	102.6	102.7
STDθ _{J=P V} (deg)	19.6	16.7	9.0*	12.8	11.4
Stabilogram-Diffusion Function					
MeanMSD (deg ²)	353.7	221.3*	169.9*	174.9	172.5
CP (s)	0.78	0.88**	0.97*	1.00**	1.03**
H _s (deg ² /s)	0.80	0.89*	0.91***	0.90**	0.90**
H _L (deg ² /s)	0.0002	0.01	0.006	0.006	0.01

Asterisks designate significance of change from Block 1 (Bonferroni corrected t tests),
* p<.05,
** p<.01,

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