Unintentional drifts during quiet stance and voluntary body sway

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Abstract

We explored unintentional drifts in voluntary whole-body sway tasks following the removal of visual feedback. The main hypothesis was that the unintentional drifts were produced by drifts of referent coordinates for salient performance variables. Young healthy subjects stood quietly on a force platform and also performed voluntary body sway at 0.5 Hz both in the anterio-posterior and medio-lateral directions. Visual feedback on the center of pressure (COP) coordinate was provided and then turned off. During quiet stance trials, the subjects matched the initial COP coordinate with a target shifted by 3 cm anterior, posterior, left, or right from the coordinate during natural standing, and activated the right tibialis anterior to 30% of its maximal voluntary contraction. During cyclical voluntary sway task, the nominal sway amplitude was always 4 cm while the midpoint was at one of the four mentioned locations. Removing visual feedback caused COP drifts during quiet stance trials that were consistent across trials performed by a subject but could be in opposite directions across subjects; there was a consistent drop in the activation level of tibialis anterior. During voluntary body sway, removing visual feedback caused a consistent increase in the voluntary sway amplitude and a drift of the midpoint that was consistent within but not across subjects. Motor equivalent and non-motor equivalent inter-cycle motion components were quantified within the space of muscle groups (muscle modes) under visual feedback and at the end of the period without visual feedback. Throughout the trial, there were large motor equivalent motion components, and they increased over the period without visual feedback. The results corroborate the idea that referent coordinate drifts at different levels of the control hierarchy can lead to unintentional drifts in performance. It suggests that directions of COP drifts are defined by two main factors, drift of the body referent coordinate toward the actual coordinate (that can lead to fall) and an opposite drift to ensure body motion to a safer location. Analysis of motor equivalence suggests that postural stability is not compromised during unintentional drifts in

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performance in contrast to earlier studies of multi-finger tasks. This may be due to the vital importance of postural stability for everyday actions.

Keywords

posture; sway; drift; motor equivalence; referent coordinate

Introduction

Unintentional drifts in motor performance are seen in young, healthy persons when visual feedback is withdrawn and the subjects are instructed "to continue doing what you have been doing". These phenomena have been described for accurate force production tasks (Slifkin et al. 2000; Vaillancourt and Russell 2002; Shapkova et al. 2008), object holding tasks (Ambike et al. 2014), and multi-joint positional tasks (Zhou et al. 2014, 2015). In particular, if a person is asked to produce a certain force level (e.g., by pressing with a finger on a force sensor) under visual feedback and then the feedback is turned off, a consistent force drift is observed, typically to lower force values (Vaillancourt and Russell 2000; Ambike et al. 2015). These observations were originally interpreted as consequences of limitations of motor memory (Slifkin et al. 2000, Vaillancourt and Russell 2002) supported by brain imaging and clinical studies (Vaillancourt et al. 2001, 2003; Poon et al. 2012). This interpretation has been challenged in recent studies showing that memorizing and reproducing force is not accompanied by force drift to lower magnitudes (Jo et al. 2015; Solnik et al. 2017).

An alternative explanation has been offered recently within the physical approach to the control of movements (reviewed in Latash 2010, 2016). This explanation assumes that the central nervous system produces movements by setting parameters associated with spatial referent coordinates (RC) for the involved effector (RC hypothesis, Feldman 2015). During force production by a finger in isometric conditions along a coordinate X, setting RC_X different from the fingertip coordinate (X_{FT}) produces force proportional to the difference between the RC_X and X_{FT}: $F_X = k(RC_X – X_{FT})$, where k is apparent stiffness, also reflecting spatial RC changes for opposing muscle groups (cf. Latash and Zatsiorsky 1993; Feldman 2015). A drop in force reflects an unintentional RC_X drift toward X_{FT} (drifts in k are also possible but less likely, see Ambike et al. 2017). This interpretation views the documented force drop as a reflection of the natural tendency of physical systems to move toward minimum of potential energy.

Unintentional drifts in performance are also seen during cyclical tasks. For example, during cyclical force production by a finger, a drift in the midpoint of the cycle to lower magnitudes is seen accompanied by a drift of the peak-to-peak force amplitude to higher values (Ambike et al. 2016). Notably, the two drifts occur at significantly different time scales. These observations suggest that there are several factors affecting unintentional drifts in performance that may include the existence of preferred parameters of action (such as preferred peak-to-peak force magnitude in cyclical tasks, cf. Kay et al. 1987; Hatsopoulos and Warren 1996).

In this study, we explored a highly functional task of standing combined with the requirement to produce cyclical patterns of the center of pressure (COP) in the anterior-posterior (AP) or medio-lateral (ML) direction. Note that, if a person is standing quietly while leaning in a certain direction, e.g., forward, from the preferred coordinate, body RC has to be behind the person to produce activation of dorsal muscles counteracting the moment of the gravity force. If RC drifts toward the actual body coordinate, the active force resisting the moment of the gravity force should drop, and the person should lean forward more and more until he or she falls. This prediction sounds rather unlikely given that postural stability and fall prevention are major imperatives that may play a greater role than the assumed drift of RC toward the actual coordinate. On the other hand, if the person is asked not to stand quietly but to sway about a certain coordinate (that deviates from the natural one, but not by too much) with a certain peak-to-peak amplitude, it becomes less obvious, which of the factors would define behavior after the visual feedback on COP(t) has been turned off.

Based on earlier studies with finger force production (Ambike et al. 2016; Reschechtko et al. 2017), we predicted that turning visual feedback off would lead to an increase in the peak-to-peak voluntary body sway amplitude (Hypothesis 1). Note that this hypothesis refers not to spontaneous postural sway, which is known to increase under closed-eye conditions (e.g., Winter 2009), but to a voluntary whole-body action performed while standing. Our second, tentative hypothesis was that both the COP coordinate during quiet standing and the mid-point of the voluntary body sway could show drifts toward the coordinate preferred during natural standing or away from that coordinate in different subjects. Note that all these predictions are drawn assuming that the subject is always trying "to do the same" and is paced by an auditory metronome at a comfortable frequency.

The idea of control with RC suggests that unintentional RC drifts can be observed at different levels of the hierarchy involved in an ongoing motor task. For example, if a muscle is activated to a particular level, not required for performance, turning visual feedback off would lead to a slow drift of the muscle activation level to lower magnitudes. Once again, the subject is asked not to change the activation level of the target muscle. We tested this hypothesis (Hypothesis 3) by asking subjects to perform quiet stance tasks with increased activation level of the tibialis anterior (TA) muscle to a visual target and then removing the target; TA was selected for its obvious role in the control of vertical posture and because its activation can be easily recorded and quantified.

The final purpose of the study was to estimate stability of voluntary whole-body sway and its possible changes during the unintentional drifts. For this purpose, we used the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999) and estimated cycle-to-cycle deviations in the space of activation of muscle groups (muscle modes or M-modes, Krishnamoorthy et al. 2003) before turning the visual feedback off and also at the end of the drift period. These deviations were quantified in two spaces, UCM and ORT. UCM is the space where M-mode deviations have no effect on COP coordinate; deviations within this space are termed motor equivalent (ME; Scholz et al. 2007; Mattos et al. 2011). COP shifts within the ORT space; these are non-motor equivalent (nME) deviations. An earlier study has shown large ME deviations, significantly larger than nME deviations, in the

M-mode space during multi-joint arm movements (Mattos et al. 2013). Hence, we expected ME deviations both prior to and at the end of the drift period that would be at least comparable to task-related nME deviations (Hypothesis 4). Note that ME deviations, by their very definition, are wasteful for task performance, which makes this hypothesis non-trivial.

ME deviations have been interpreted as reflections of stabilization of the salient performance variable (COP coordinate in our study) in the abundant space of M-modes (Mattos et al. 2011, 2013). Based on earlier studies, we expected stability of the drifting variable to become compromised (Parsa et al. 2017a,b) leading to a drop in the ME deviations without a comparable drop, or even an increase, in the nME deviations (Hypothesis 5).

Methods

Participants

Eleven healthy individuals (4 females, 7 males (age 27.5 ± 4.4 years old, height 1.73 ± 0.10 m, body mass 66.4 ± 10.3 kg; mean $\pm$SD) participated in this study. The subjects had normal or corrected to normal vision and no known musculoskeletal or neurological disorders. They signed an informed consent according to the procedures approved by the Office for Research Protections of the Pennsylvania State University.

Apparatus

A force platform (AMTI, OR-6) was used to record the AP, ML and vertical components of the ground reaction force (F_X, F_Y, and F_Z respectively), and also the moments of force around the frontal and sagittal axes (M_Y and M_X, respectively). The force coordinate system was defined with the X-axis pointing anterior, the Y-axis pointing to the right, and the Z-axis pointing downward. Subjects received real-time visual feedback on the trajectory of the COP using a 19″ monitor placed at the eye level about 1.5 m away from the subject. The COP displacement along AP direction (COP_{AP}) caused cursor motion up and down, while the COP displacement along ML direction (COP_{ML}) caused cursor motion right and left.

Surface muscle activation (EMG) signals were recorded using a 16-channel Trigno Wireless System (Delsys Incorporation, Boston, MA, USA). Active electrodes with built-in amplifiers (size: 37×26×15 mm) were attached by two-sided tape to the skin over the bellies of the muscles. Thirteen muscles on the right side of the body were recorded: tibialis anterior (TA), soleus (SOL), gastrocnemius medialis (GM), gastrocnemius lateralis (GL), semitendinosus (ST), biceps femoris (BF), vastus lateralis (VL), vastus medialis (VM), rectus femoris (RF), tensor fasciae latae (TFL), lumbar erector spinae (ESL), thoracic erector spinae (EST), and rectus abdominis (RA). To check the electrode placement, the EMG signals were observed while the subjects performed a set of isomeric contractions and related movements (Kendall et al. 2005). Given the 16-channel system, we opted for recording more muscles on one side of the body only rather than recording fewer muscles bilaterally and potentially missing some important EMG signals. EMG signals were amplified and band-pass filtered (20–450 Hz) before being transmitted to the data collection desktop computer (Dell, Core i7, 2.93 GHz). A customized LabView program (LabView 2014, National Instruments, Austin, TX,

USA) was used to collect and record EMG and force platform signals with the sampling frequency of 1 kHz with the 16-bit resolution data acquisition board (PCI-6225, National Instruments).

Procedure

Each experimental session consisted of 1) Control trials that included quiet standing, standing while holding a load, and rhythmic voluntary body sway; and 2) Main tasks that included steady-state task (quiet standing) in modified initial postures and cyclical voluntary body sway with manipulations of the visual feedback. Control trials were always conducted in a fixed order A, B and C (see below). Then the main tasks (quiet standing and cyclical sway) were performed in a random order. Across all trials, the subject stood barefoot on the force platform, feet in parallel, with the insides of the feet 15 cm apart. The initial foot position was marked on top of the platform and reproduced across all tests. In all trials, except for the trials with standing while holding a load, the subjects stood with the arms crossed on the chest. In the trial with holding the load, the subjects stood with their arms extended as required by the task. Note that the data collected in those trials were used only for EMG normalization.

Control trials

<u>A. Quiet standing:</u> This task was performed to measure the baseline muscle activity, which was used for further EMG normalization. Subjects performed one trial of quiet standing for 30 s without visual feedback, and they were instructed to stand as still as possible and to look at a fixed point on the screen in front of them.

<u>B. Standing while holding a load:</u> In the next two trials, the subjects were instructed to stand quietly, keep vertical posture and grasp a handle bar by pressing with the hands of extended arms on two circular panels at the end of the bar. A 5 kg load (selected based on earlier studies, Danna-dos-Santos et al. 2007; Klous et al. 2011; Piscitelli et al. 2017) was attached to the bar acting either downward or upward (via a pulley system) in different trials. The two load directions were used to provide conditions that required primarily dorsal muscle activation (load acting downward) or ventral muscle activation (load acting upward). The subjects held the bar with the load for 10 s with their arms parallel to the ground. The time interval between the two trials was 30 s. The data from these trials were used for EMG normalization (see Danna-dos-Santos et al. 2007).

<u>C. Voluntary body sway:</u> Further, subjects were instructed to stand in the initial, comfortable position with arms crossed on the chest and fingertips on the shoulders, and perform continuous voluntary body sway between the two targets shown on the monitor. Sways in the AP and ML directions were performed in separate trials. The purpose of this task was to define a low-dimensional set of elemental variables (M-modes, muscle groups with parallel changes in activation levels (Krishnamoorthy et al. 2003a) and to link small changes in M-modes to COP_{AP} shifts (the Jacobian, **J**, Krishnamoorthy et al. 2003b; Danna-dos-Santos 2007). The subjects were asked to sway about the ankle joints while keeping full contact of the feet with the force platform. The target amplitude was set at $\pm$ 3 cm deviation of the COP from the initial position and it was shown on the screen with two lines while the

real-time COP coordinate was displayed as a white circle with 5-mm diameter. Subjects were asked to sway with the auditory metronome (1 Hz) and touch each of the target lines at the metronome beeps. Therefore, one complete cycle was performed in 2 seconds (0.5 Hz). Subjects had two practice trials before data acquisition. Three trials were performed in a row for each sway direction; the duration of each trial was 30 s with a 30-s rest between the trials and one-minute rest between the directions. Subjects were instructed to follow the metronome and do their best to minimize COP deviations in the non-instructed direction. The order of AP and ML directions was randomized.

Main trials

A. Quiet standing with increased TA activation: This test included four conditions that differed in the initial COP coordinate that deviated from the COP coordinates during natural standing: anterior (Ant), posterior (Post), right (Right) and left (Left). First, each subject performed two trials at maximal dorsiflexion of the right foot while seated, and the maximal level of the right TA muscle activation was identified over 3 s during the interval of its maximal activity (MVC_{TA}). The subjects were instructed to move the body to the initial COP coordinate (3 cm from zero-point of CoP) shown on the monitor and simultaneously to contract the TA muscle to reach approximately 30% of MVC_{TA}. The TA EMG feedback was shown as a vertical tank filled up to a level defined by the rectified and low-pass filtered TA EMG signal. There were two horizontal lines on the tank, corresponding to 25% and 35% of MVC_{TA}, and subjects were instructed to hold the TA contraction level between these lines while keeping full foot contact with the force platform and simultaneously holding their COP coordinate at the target. Subjects kept the TA activation level and COP coordinate for 10 s with continuous visual feedback on both variables. Then, they were asked to close the eyes and to "continue doing what you have been doing" for the following 20 s. The four conditions (Ant, Post, Right and Left) were blocked-randomized, and each of them was repeated three times in a row. Before the test, subjects performed one practice trial with open eyes and the feedback on for the whole trial duration (30 s). A 30-s rest between trials and 1-min rest between conditions were applied.

B. Voluntary cyclical sway: This test also included four conditions: Ant, Post, Right and Left. The initial COP coordinate was shown on the monitor for each of the four conditions; it corresponded to the COP shifted by 2 cm from the natural COP coordinate defined as the mean coordinate during quiet standing forward (Ant), backward (Post), to the right, or to the left. Subjects were asked to shift the COP to one of those targets (2 cm away from the natural COP coordinate) and sway rhythmically with ± 2 cm COP deviations for 40 s. In each condition, there were two lines serving as the designated targets on the screen, which were horizontal for the COP_{AP} tasks and vertical for the COP_{ML} tasks. The frequency of the sway was set at 0.5 Hz, paced by the auditory metronome. The metronome was on at all times throughout each trial; so, no drift in the sway frequency was possible. Subjects were instructed to start swaying with visual feedback, close the eyes at 10 s and continue swaying for 30 more seconds with the same voluntary body sway parameters until the end of the trial. The conditions were blocked-randomized with three trials in a row for each condition. Subjects had 30-s rest between trials and 1-minute rest between conditions. Subjects had one practice trial before each condition with open eyes and the feedback on for the whole trial

duration (40 s). Subjects always swayed in the AP direction for the Ant and Post conditions, while they swayed in the ML direction for the Left and Right conditions for a total of 12 experimental trials: 4 conditions $\times$ 3 trials $\times$ 40 s. The total number of trials in the study was 33, and the average duration of the experiment was 90 minutes. There were no reports of fatigue or discomfort during the testing session.

Data analysis

Customized programs in MATLAB 2015b (MathWorks, Natick, MA, USA) were used to process and analyze the data. Signals from the force platform (F_Z, F_X, and M_Y) were filtered with a 5 Hz low-pass, 4th order, zero-lag Butterworth filter before calculating the COP_{AP} and COP_{ML} coordinates with the following equations (Winter et al. 1996):

$$COP_{AP} = -\frac{M_y + (F_x \cdot d_z)}{F_z} \quad (1)$$

$$COP_{ML} = \frac{M_x + (F_y \cdot d_z)}{F_z} \quad (2)$$

where d_z is the distance from the platform origin to the surface, which was 0.043 m in this study. To avoid edge effects, the data were accepted from the (3–27 s) interval only, for each 30-s trial of the voluntary sway task. A cycle was defined as the time between two successive lateral-most COP_{ML} or anterior-most COP_{AP} coordinates. Each subject performed about 12 full cycles within this period in each trial.

Raw EMG signals were full-wave rectified and low-pass filtered using a moving average 100-ms window. EMG data were shifted 50 ms backwards with respect to the force platform data to account for the electro-mechanical delay (Corcos et al. 1992), for computations involving both EMG and mechanical signals. The EMG signals were corrected for background activity and normalized to compare EMG data across subjects (Krishnamoorthy et al. 2003a; Klous et al. 2010):

$$EMG_{norm} = \frac{EMG - EMG_{qs}}{EMG_{ref}} \quad (3)$$

where EMG_{qs} is the average filtered EMG during the quiet standing from the control trial and EMG_{ref} is the average filtered EMG in the middle of standing trials while holding the load. was calculated for the ventral muscles (TA, VM, VL, RF, RA, and TFL) based on the EMG_{ref} data collected during standing while holding the load suspended behind the subject, and for the dorsal muscles (SOL, GL, GM, BF, ST, ESL, and EST) based on the data collected during standing while holding the load suspended in front of the subject.

TA-EMG drifts during the steady-state task—Raw EMG signals were rectified, filtered, and normalized to the value during the MVC test for each subject. The activation level of TA was analyzed for differences across directions and task phases. Two time intervals were selected to test Hypothesis 3: before closing eyes, Phase-1 (8–10 s) and at the

end of the trial, Phase-2 (27–29 s) (see Figure 1 in Results). Further the TA-EMG was integrated over these 2-s time intervals, and its mean magnitude was computed. These values were averaged across the three trials for each subject.

Analysis of the voluntary cyclical sway task—For each cycle, two variables were computed: (1) The sway midpoint of the COP displacement (M_{COP}) as the mean value of the consecutive extrema and (2) Peak-to-peak amplitude (A_{COP}) as the absolute difference between the consecutive extrema. These values (M_{COP} and A_{COP}) were computed starting from two full cycles before closing eyes until the beginning of the last incomplete cycle at the end of the trial. For further processing, the values of M_{COP} and A_{COP} were assigned to the middle of the half-cycle interval between the two extrema. Then, two time intervals were chosen: Phase-1 (the last two full cycles before closing eyes) and Phase-2 (the last two full cycles) (see Figure 3). The averages of M_{COP} and A_{COP} within each phase were calculated and then averaged across three trials in each condition for each subject.

Defining muscle modes—The aim of this step was to define groups of muscles (muscle modes or M-modes, eigenvectors in the muscle activation space, Krishnamoorthy et al. 2003a) that showed parallel changes in their activation levels. These muscle groups are viewed as the elemental variables in the analysis of synergies (Krishnamoorthy et al. 2003b). Principal component analysis (PCA) with Varimax rotation and factor extraction was performed on the correlation matrix of the integrated (50-ms time windows), normalized EMG ($IEMG_{norm}$) data from the sway tasks for each condition and each subject separately (Krishnamoorthy et al. 2003a; Danna-dos-Santos et al. 2007). The first four PCs were selected for each subject to reduce the 13-dimensional muscle activation space to a 4-dimensional factor (M-mode) space. We used the Kaiser criterion confirmed by an infection point on the scree plot after the fourth eigenvalue; in addition, each PC had to contain at least one muscle with a significant loading (with the absolute magnitude over 0.5; Hair et al. 1995). The amount of variance in the muscle activation space was calculated for each M-mode.

Defining the Jacobian matrix—The Jacobian (**J**) matrix was defined to link small changes in M-mode magnitudes (M) to COP displacements (COP_{ML} and COP_{AP}), assuming linear relations between these variables (Krishnamoorthy et al. 2003b; Danna-dos-Santos et al. 2007). M, COP_{ML} and COP_{AP} data were computed from $IEMG_{norm}$ and integrated COP_{ML} and COP_{AP} within 50-ms time windows data from the voluntary body sway task. All M, COP_{ML} and COP_{AP} were filtered with a low-pass, 5-Hz, 4th order, zero-lag Butterworth filter. Separate multiple regression analyses were performed for each subject. Two multiple linear regression analysis without intercept were performed over all selected cycles in the AP and ML directions:

$$\Delta COP_{AP} = k_{AP1}\Delta M_1 + k_{AP2}\Delta M_2 + k_{AP3}\Delta M_3 + k_{AP4}\Delta M_4$$
$$\Delta COP_{ML} = k_{ML1}\Delta M_1 + k_{ML2}\Delta M_2 + k_{ML3}\Delta M_3 + k_{ML4}\Delta M_4.$$

The multiple regression analysis generated sets of coefficients, which formed a matrix, that is the $\mathbf{J}$ matrix: $\mathbf{J_{AP}} = [k_{AP1}\ k_{AP2}\ k_{AP3}\ k_{AP4}]^T$, and $\mathbf{J_{ML}} = [k_{ML1}\ k_{ML2}\ k_{ML3}\ k_{ML4}]^T$, where T is the sign of transpose.

Analysis of motor equivalence—The motor equivalence analysis was performed to quantify the amount of inter-cycle motion in the M-mode space along the uncontrolled manifold (UCM, Scholz and Schöner 1999), estimated as the null-space of the corresponding $\mathbf{J}$ matrix, and along the orthogonal to the UCM space (ORT) computed for the COP_{AP} and COP_{ML} separately. Motion along the UCM will be addressed as motor equivalent (ME) motion, while motion along the ORT subspace will be addressed as non-motor equivalent (nME). M-mode vectors in the 4D space of M-modes were computed for the maximum (Max) and minimum (Min) point in each cycle. Then, we computed the difference between the M-mode vectors at the same phase in consecutive cycles. Finally, the difference vectors were projected onto the UCM and ORT subspaces and the length of each of those projections was computed. These values were further normalized by the square root of the corresponding dimensionality (one and three for the ORT and UCM, respectively; cf. Mattos et al. 2011, 2013) and used as the ME and nME indices. Note that this method computes both ME and nME indices in units of M-mode displacement, which are computed based on changes in the normalized and integrated EMG indices. ME and nME for COP_{AP} and COP_{ML} were computed separately for the Max and Min points in the sway cycles over the whole trial duration, starting with the two cycles in Phase-1 and ending with the two cycles in Phase-2. Further, ME and nME were averaged across trials within each of the two phases for each condition separately and used for further statistical analysis.

Statistical analyses

Data are presented as means and standard errors (SEs). All statistical analyses were performed with SPSS statistical software version 24 (IBM Corporation, Armonk, NY, USA). To test Hypothesis 1, a two-way repeated measures ANOVA on peak-to-peak sway amplitude with factors *Condition-1* (Ant vs. Post) and *Phase* (Phase-1 vs. Phase-2) was performed. A separate two-way ANOVA on peak-to-peak sway amplitude was run with factors *Condition-2* (Rt vs. Lt) and *Phase* (Phase-1 vs. Phase-2). To test the effects of removing visual feedback on midpoint of the sway (Hypothesis 2), the midpoint was subjected to a two-way ANOVA with factors *Condition* (2 levels) and *Phase* (2 levels). A separate two-way ANOVA for COP_{ML} was performed. Hypothesis 3 was tested using a two-way ANOVA on TA activation level with factors *Condition-1* and *Phase*. A separate two-way ANOVA for the ML direction was executed. Lastly, two-way ANOVAs on indices of motor equivalence (ME and nME) were performed with factors *Condition-1* and *Phase* for both Max and Min points. The same analyses were done for the ML direction. In addition, two-way ANOVAs on nME and ME changes from phase-1 to phase-2 in both AP and ML directions were performed. Paired t-test was used to compare percentage of variance and R^2 between AP and ML directions. Significant effects of ANOVA were further explored using pairwise comparisons with Bonferroni corrections. The level of significance was set at $p < 0.05$.

Results

Steady-state task

During steady-state standing without visual feedback, slow unintentional drifts were observed for both task variables, COP coordinate and TA activation level. In particular, in the Ant, Right, and Left conditions, COP on average drifted away from its coordinate observed during natural standing with eyes open. In the Post condition, however, COP drifted toward the coordinate observed during natural standing. In contrast, TA activation level showed a drift toward lower magnitudes across the four conditions. An illustration of the COP and TA activation drifts for the Ant condition performed by a representative subject is shown in Figure 1.

The average COP displacements between Phase-1 (with vision) and Phase-2 (without vision) are presented in Figure 2. For COP_{AP}, there were significant main effects of *Phase* ($F_{(1,10)} = 8.323$; $p < 0.05$) and *Condition* ($F_{(1,10)} = 334.13$; $p < 0.001$) without an interaction reflecting the fact that COP_{AP} shifted forward for both Ant and Post conditions. Note that the forward shift in Ant means a shift away from the natural standing coordinate while the forward shift in Post meant a shift toward that coordinate. For COP_{ML}, there were main effects of *Condition* ($F_{(1,10)} = 1058.711$; $p < 0.001$) and an interaction *Phase* × *Condition* ($F_{(1,10)} = 5.194$; $p < 0.05$) reflecting the fact that in both Right and Left conditions COP_{ML} shifted away from the natural standing coordinate, i.e., in opposite directions.

On average, there was about a 25% drop in the TA activation level in Phase-2 compared to Phase-1. This is illustrated in Figure 2 that shows the averaged across subjects values of the rectified and integrated EMG signal of TA. For the AP direction, the two-way ANOVA revealed a main effect of *Phase* [$F_{(1,10)} = 10.162$; $p < 0.01$] without a main effect of condition or an interaction, whereas no significant effects were found for the ML direction.

Cyclical voluntary body sway task

Closing the eyes during the voluntary sway task led to consistent changes in the peak-to-peak sway amplitude (A_{COP}) and mid-point (M_{COP}). Across all condition, A_{COP} increased while drifts in M_{COP} were condition dependent. Figure 3 illustrates the performance in a typical subject in the Ant condition (the mid-point of the sway was 2 cm anterior to the natural COP coordinate). The open and filled dots represent A_{COP} and M_{COP} respectively computed for consecutive cycles. Note the increase in A_{COP} after the subject closed the eyes (at time = 10 s) with a relatively small, inconsistent drift in M_{COP}. While the drifts in A_{COP} were consistent across subjects (i.e., toward higher magnitudes), changes in M_{COP} could be consistent within-a-subject but in different directions across subjects. Figure 4 displays the blocks of three trials performed by each of four subjects under the Ant and Post conditions. Note that individual subjects could show consistent across trials drifts in M_{COP} toward and away from zero coordinate.

The magnitudes of A_{COP} and M_{COP} averaged across subjects for all conditions are presented in Figure 5 for two time windows corresponding to Phase-1 and Phase-2 (see Methods). Analysis of A_{COP} revealed a main effect of *Phase* [$F_{(1,10)} = 35.235$; $p < 0.001$ for AP and $F_{(1,10)} = 15.004$; $p < 0.005$ for ML] and a *Phase* × *Condition* interaction [$F_{(1,10)} = 16.319$; p

< 0.005] for the AP direction only. Pairwise comparisons confirmed that A_{COP} in Phase-2 was larger than in Phase-1 for both AP and ML sway directions. The interaction reflected the fact that A_{COP} in Phase-1 was larger in the Ant condition ($p < 0.01$) while in Phase-2 it was greater in the Post condition, albeit under the level of significance ($p=0.08$).

The M_{COP} coordinate showed a drift toward the COP coordinate during natural standing (zero coordinate) in the Post and Right conditions, while there was a small drift away from the natural standing coordinate in the Ant and Left conditions (Figure 5). The two-way ANOVA revealed an effect of *Condition* [$F_{(1,10)} = 43.565$; $p < 0.001$], which was due to the different initial M_{COP} across conditions, i.e. positive values in the Ant and Right conditions and negative values in the Post and Left conditions. There was also a main effect of *Phase* [$F_{(1,10)} = 7.944$; $p < 0.05$] and an interaction [$F_{(1,10)} = 5.423$; $p < 0.05$] for the AP sway direction. The interaction revealed a significant decrease in M_{COP} from Phase-1 to Phase-2 in the Post condition only. There was also a main effect of *Phase* [$F_{(1,10)} = 8.288$; $p < 0.05$] for the ML direction corresponding to the overall reduction in the M_{COP} coordinate from Phase-1 to Phase-2.

Muscle modes and the Jacobian

There were consistent patterns of muscle activations at the sway frequency during the cyclical sway task in all the subjects. The PCA with rotation and factor extraction on the integrated indices of muscle activation led to the identification of four M-modes accounting, on average, for $76.59 \pm 5.46\%$ and $61.05 \pm 7.81\%$ of the total variance for the AP and ML sway direction respectively. Paired t-test showed that the amount of variance was higher for the AP direction than for the ML direction ($t_{[10]} = 5.88$, $p < 0.001$). Table 1 presents results of the PCA analysis for a typical subject for both sway directions. There were consistently high loading factors for the dorsal muscles in one of the first two M-modes and ventral muscles in the other M-mode. The third and fourth M-mode were less consistent and could have only one muscle significantly loaded (typically, RA or TFL).

Linear regression analysis between the COP shifts and associated changes in the magnitudes of the M-modes confirmed that each of the four M-modes was a significant predictor of COP shifts in both directions ($p < 0.001$). The average amount of variance accounted for by the regression analysis was $74 \pm 8\%$ and $51 \pm 15\%$ for COP_{AP} and COP_{ML} respectively.

Analysis of motor equivalence

Max points—When displacements between successive cycles in the M-mode space were quantified along the UCM and along the ORT space, ME magnitudes were commonly larger than nME magnitudes, and ME magnitudes increased in Phase-2 compared to Phase-1, whereas nME remained relatively unchanged. ME and nME indices for Phase-1 and Phase-2 are presented in Figure 6. In this Figure, the ME and nME indices are quantified for the peaks (Max) and valleys (Min) of the sway cycle. Note the overall larger ME indices and their trend to increase in Phase-2.

For ME, the two-way ANOVA showed main effects of *Phase* [$F_{(1,10)} = 12.390$; $p < 0.01$] and *Condition* [$F_{(1,10)} = 5.693$; $p < 0.05$] without an interaction for the AP direction, while only

a main effect of *Phase* [$F_{(1,10)}$ = 8.432; $p < 0.05$] was found for the ML direction. Pairwise comparisons showed that the ME in Phase-1 was smaller than in Phase-2 in both AP and ML directions, and also ME was larger in the Post condition compared to the Ant condition.

Analysis of nME showed only a main effect of *Condition* [$F_{(1,10)}$ = 10.730; $p < 0.01$] for the AP direction indicating larger nME for the Post compared to the Ant condition. There were no significant effects for the ML direction.

Min points—Similar to the results of Max points, ME magnitude increased in Phase-2 compared to Phase-1 across all conditions while nME stayed unchanged. The results of two-way ANOVA on ME showed only an interaction of *Phase* × *Condition* [$F_{(1,10)}$ = 9.282; $p < 0.05$] in the AP direction. Post-hoc analysis revealed that ME in Phase-1 was smaller than in Phase-2 in Ant; also ME in Phase-1 was smaller in Ant compared to Post. A main effect of *Phase* [$F_{(1,10)}$ = 6.050; $p < 0.05$] was observed in the ML direction: ME in Phase-1 was smaller than in Phase-2.

There was an interaction *Phase* × *Condition* [$F_{(1,10)}$ = 9.957; $p < 0.01$] for nME in the AP direction, without any effects for nME in the ML direction. Post-hoc analysis showed that nME in Phase-1 was smaller than in Phase-2 only in Ant, and nME in the Ant condition was smaller than in the Post condition in Phase-1 (Figure 6).

Discussion

We observed unintentional drifts in characteristics of voluntary whole-body cyclical sway, caused by turning visual feedback off, that were consistent across subjects and conditions. These included, in particular, an increase in the sway amplitude in support of Hypothesis 1. This result was expected based on earlier studies of unintentional drifts in performance during a very much different task, cyclical finger force production (Ambike et al. 2016, 2017). Drifts of the midpoint of the sway were less consistent across subjects and could show deviations both toward the coordinate seen during natural quiet standing (COP_0) and away from COP_0 (in support of Hypothesis 2; see Figure 6). Note that there were also consistent COP drifts during the quiet stance trials. When the subjects were asked to stand quietly while keeping an increased level of activation of one of the muscles (TA), there was a consistent drift in the TA activation level toward lower magnitudes as predicted by Hypothesis 3. Overall, these findings support the main predictions drawn based on the ideas of postural control with changes in the referent COP coordinate (RC) and of RC drift toward preferred values in the absence of visual feedback (reviewed in Latash 2016).

Our predictions with respect to changes in the motor equivalent (ME) and non-motor equivalent (nME) components of motion in the space of M-modes between consecutive cycles have been confirmed only partly. Indeed, we observed ME deviations that were typically larger than nME deviations both prior to and at the end of the sway drift period in support of Hypothesis 4 (cf. Mattos et al. 2013, 2015). However, there were no signs of a drop in stability of the sway (cf. Parsa et al. 2016, 2017b) during its drift as reflected in an increase in the ME component without a comparable increase in the nME component. These findings refute Hypothesis 5.

Overall, the results have important implications for a range of issues debated recently in the field of the neural control of posture and movement (reviewed in Feldman 2015; Latash 2016, 2017). These include the idea of control with RC, the idea of RC drift as the main cause of unintentional drifts in performance, and the idea of changes in action stability during unintentional drifts in its parameters.

Control of posture and movement with referent coordinates

Two theoretical approaches to the control of posture and movement have been dominating the field recently. The first approach assumes that neural signals within the central nervous system encode desired performance variables (kinetic, kinematic, and/or electromyographic), e.g., with the help of internal models (Wolpert et al. 1998; Kawato 1999; Shadmehr and Wise 2005). This approach assumes computations performed by the central nervous system to predict peripheral effects of planned changes in neural signals given the current and predicted external force field. Within this approach, changes in performance variables have been interpreted as direct reflections of changes in the respective internal models (reviewed in Krakauer and Mazzoni 2011; Yavari et al. 2013).

The alternative approach considers the central nervous system as a physical (physiological) system that behaves according to laws of nature (Latash 2010, 2016; Feldman 2015). According to this approach, the brain uses changes in parameters of those laws to perform motor actions while all the variables recorded in the periphery represent reflections of the time-varying interaction between the body and the environment. This approach started with the equilibrium-point hypothesis (Feldman 1966, 1986) and, more recently, has been generalized for multi-muscle and whole-body actions (Feldman 2015).

Within this approach, any motor action starts with specifying a time change of a low-dimensional RC for salient task-specific variables (RC_{TASK}). A change in RC_{TASK} leads to a chain of events at hierarchically lower levels resulting in higher-dimensional RC changes for individual limbs, digits, joints, and muscles. The few-to-many RC transformations ensure relatively high stability in task-specific salient variables (driven by RC_{TASK}) while allowing freedom of motion at the level of elements in directions that do not affect the salient variables. This idea was formalized within the framework of the UCM hypothesis (Schöner 1995; Scholz and Schöner 1999; reviewed in Latash et al. 2007) leading to two quantitative methods of analysis of stability in the abundant spaces of elements contributing to performance.

The first method quantifies inter-trial (or inter-cycle) variance within the UCM (V_{UCM}) and orthogonal to the UCM (V_{ORT}). The idea is that motion along stable directions is expected to lead to converging trajectories and, consequently, low inter-trial variance. In contrast, motion along unstable directions is expected to lead to diverging trajectories and high inter-trial variance. This method requires collecting multiple trials under the assumption that the subject is reproducing the neural control process at the task level (RC_{TASK}).

An alternative method has been developed recently (Scholz et al. 2007; Mattos et al. 2011), which involves estimation of motion along the UCM and ORT spaces along single trials. Any peripheral or descending input into structures involved in the hypothetical RC

transformations induces motion along all directions, and motion along unstable directions (ME, along the UCM) is expected to be large despite its obvious inefficacy for changing the corresponding salient performance variable. Large ME motion was observed during multi-joint movements and multi-finger force production tasks (Mattos et al. 2011, 2015). In those studies, ME deviations were larger than nME ones, although only nME deviations contributed to changes in salient variables. Our study is the first to document large ME motion in the muscle activation space, larger than nME motion, during voluntary, whole-body tasks (Figure 6).

These observations are very non-trivial suggesting that changes in muscle activation during such tasks are mechanically inefficient since they are mostly inter-compensated leading to ME motion, i.e., no COP shifts required by the task. They speak against theories based on the central nervous system predicting optimal muscle activations with respect to mechanical and/or energetic variables (cf. Nelson 1983, Alexander 2002, Prilutsky and Zatsiorsky 2002). Indeed, changes in muscle activations cause changes in muscle forces and require energy expenditure. Such muscle activation changes lead to an increase in the cost function within any optimization approach based on minimizing a monotonic function of muscle activations, force change magnitudes (e.g., a norm in the muscle force space), or energy expenditure. By definition, they lead to no change in task-specific salient variables; hence, they do not correspond to a minimum of the cost function and, therefore, are not optimal in violation of the assumption that an optimality criterion defines muscle activation patterns. The ME motion is, however, a natural consequence of the physical view on the control of posture and movement, which predicts, in particular, large deviations of any involved systems in directions of low stability

Unintentional drifts during whole-body tasks

Arguably, the best-known example of unintentional performance drifts during whole-body tasks is the postural sway observed during quiet standing. Indeed, even when a person tries to stand as quietly as possible, spontaneous displacements of the COP and center of mass are observed. Adding an explicit visual target for a desired COP coordinate does not help and may even lead to an increase in the sway (Danna-dos-Santos et al. 2008). Traditionally, sway has been seen as a reflection of postural instability (caused by "neural noise"), and indices of sway have been used as proxies of postural stability (Kiemel et al. 2002; Blaszczyk 2016). This assumption is non-trivial given that sway can be reduced in certain groups of patients with pronounced postural instability such as in advanced stages of Parkinson's disease (Horak et al. 1992). It has been criticized and an alternative view on sway has been suggested assuming that it reflects purposeful process such as scanning the environment for stability (Riccio 1993; Riley et al. 1997; Mochizuki et al. 2006).

An approach to sway compatible with the idea of control with RCs was developed by Zatsiorsky and Duarte (1999). According to this approach, sway represents superposition of two processes: migration of an equilibrium point for the body and oscillations about that equilibrium point. The two processes have been referred to as rambling and trembling. Trembling is assumed to reflect peripheral processes defined by the limb/body mechanics and segmental reflexes, while rambling is assumed to reflect purposeful, even if not

intentional, migrations of the equilibrium point. During prolonged standing, large-amplitude changes in rambling may be observed (Duarte and Zatsiorsky 1999, 2000).

Unintentional changes in locomotion have also been reported. In particular, when a person is asked to walk many times toward an obstacle and step over it, the clearance between the foot and the obstacle becomes progressively smaller and, sometimes, the person hits the obstacle (Heijnen et al. 2012, 2014). This happens more frequently with the trailing foot when visual information is less useful for the control of the stepping motion.

Our experiment presents novel examples of performance drifts in whole-body tasks. These involve an increase in the voluntary sway amplitude observed across all conditions. These observations are similar to earlier reports on an increase in the cyclical action amplitude during finger force production tasks (Ambike et al. 2016). Originally, it was assumed that, in such tasks, the amplitude drifted to a preferred magnitude based on reports of preferred amplitudes of cyclical actions (Kay et al. 1987; Hatsopoulos and Warren 1996). A recent study, however, has shown that the increase in the action amplitude persists over a large range of initial amplitude values (Ambike et al. 2017) without a significant change in the magnitude of the increase. This result casts doubt on the mentioned interpretation of the amplitude increase. In the current study, we did not explore a range of initial sway amplitudes to avoid increasing testing time. Hence, our results are compatible with the idea of a drift toward preferred sway amplitude. But this idea has to be checked in future studies using different initial task parameters

Drifts in the mid-point of the sway cycle were much less consistent across subjects and conditions. Originally, we assumed that two factors might define the M_{COP} drifts. One of them is the assumed RC drift toward the actual body coordinate, which was expected to lead to M_{COP} deviations away from the natural COP coordinate (COP_0). As mentioned in the Introduction, this process, if unchecked, could lead to a fall. The other factor is related to standing safety and was expected to lead to a drift of M_{COP} toward COP_0, which represents the most comfortable and safe posture. In two conditions, we observed data compatible with predominance of the second factor: In Post and Right, the subjects moved M_{COP} toward COP_0. In the other two conditions (Ant and Left), however, there was no significant drift in M_{COP}, large inter-subject variability, and on average, a small drift away from COP_0 (Figure 5).

We can only speculate on the origin of the condition-specific findings. The observed directional-specific differences could be related to the biomechanics of the ankle joint and differences in the joint range of motion in different directions. In addition, the difference between the Ant and Post conditions can be explained by the fact that swaying about a position shifted backwards in perceived as more dangerous due to the smaller available range of COP shifts in the posterior direction. Hence, the safety-related factor dominated leading to M_{COP} drift toward COP_0. All, except one, of our subjects were right-leg dominant, which means that they preferred to stand on the left leg while performing quick actions (e.g., kicking a ball) with the right leg. This means that standing with the body weight shifted toward the left leg might be perceived as more safe and stable leading to smaller effects of the safety factor in the Left condition compared to the Right condition.

This interpretation is compatible with the dynamic dominance hypothesis (Sainburg 2002, 2005) and recent observations of higher stability of multi-finger steady-state actions in the left hand of right-handed persons (Park et al. 2012; Jo et al. 2016). On the other hand, several studies reported larger loading of the right leg during quiet standing (Blaszczyk et al. 2000; Haddad et al. 2011). There may be a difference between leg loading in quiet stance and during whole-body motion, such as those required in our study. At this point, we are unaware of any data addressing this point convincingly.

Note that individual subjects could show consistent COP drifts in different directions in conditions where, on average, no significant COP drift was observed (cf. Figure 2). These observations contrast the earlier reports on unintentional force drifts observed without visual feedback (Vaillancourt and Russell 2000; Ambike et al. 2015). In the mentioned studies, forces consistently drifted toward lower magnitudes; drifts to larger magnitudes were only observed for very low initial forces, possibly caused by adaptation of peripheral receptors. Consistent limb drifts were also reported in studies of arm positional tasks in response to transient perturbations (Zhou et al. 2014, 2015). This makes the current observations of drifts in different, subject-specific, directions unusual and implying at least two aforementioned factors that define those drifts, RC-back-coupling and tendency to move to a safer posture.

Drifts in performance: Reflections of natural relaxation processes

According to our main hypothesis, drifts in performance are reflections of natural relaxation processes in the physical (physiological) system involved in movement production (reviewed in Latash 2016, 2017). These processes may happen at different levels of the hierarchy, i.e. they may lead to drifts of RCs for the task-specific salient variables, as well as for RCs at other levels such as those involving individual joints and muscles. Within our task, RC drifts could happen at the task level leading to drifts in the task-specific COP coordinate. They could also happen at the level of M-modes and at the level of individual muscle activations. Note that M-modes may be seen as reflections of elemental RC shifts of the body (see Robert et al. 2008; Latash and Zatsiorsky 2016) that form a frame of reference at an intermediate level between RC_{TASK} and RCs for individual muscles (which are equivalent to threshold of the stretch reflex, λ, see Feldman 1986; 2015).

The consistent drop in the initial TA activation level observed in our study across conditions may be viewed as corroborating this general hypothesis at the muscle level. Note that the subjects could perform the task comfortably with the elevated TA activation, which was not very high and not expected to lead to fatigue over the typical trial duration (about 30 s). The trials with TA activation may be viewed as involving dual-tasking. Indeed, the subjects were required to satisfy requirements related to the initial COP coordinate and to the TA activation level simultaneously. Dual-tasking is known to lead to deterioration of various aspects of performance (reviewed in Fraizer and Mitra 2008; Ruffieux et al. 2015). It is possible that it also led to accentuated TA EMG drifts in our experiment.

The drifts in COP trajectories, which were expected to reflect processes at the task level, were less consistent and involved at least two processes: A drift of the amplitude to higher magnitudes and a drift in the midpoint, which was consistent only in some of the conditions

(see Figure 5). Such complex drift patterns have been described recently in several studies of cyclical force production (Ambike et al. 2016, 2017; Reschechtko et al. 2017). One of the cited papers (Reschechtko et al. 2017) presented a dynamical model able to reproduce such patterns under an assumption of drifts in parameters of the involved dynamical system to their preferred magnitudes. The qualitative similarity of our findings to those reported in the cited studies suggests that the underlying drift processes are robust and can happen across very dissimilar tasks and systems.

Limitations of the study

We would like to acknowledge several limitations of our study that may have implications for generality of the findings and conclusions. First, we recorded and analyzed muscle activation levels (EMGS) on one side of the body only. Effects of limb dominance on motor control are well known and have been formalized recently as the dynamic dominance hypothesis (reviewed in Sainburg 2005). While this hypothesis addresses primarily the control of the upper extremities, it is possible that the M-modes identified in the right lower extremities could not be identical to those in the left lower extremities with implications for other outcome indices. Given the limited number of channels in our system, we opted for recording a larger set of muscles on one side of the body rather than recording eight muscles only on both sides. This is, however, a limitation.

Second, multi-muscle synergies were studied in earlier studies primarily with respect to the control of COP in the anterior-posterior direction (Krishnamoorthy et al. 2003a,b; Danna-dos-Santos et al. 2007). This was partly due to the fact that only a few muscles with strong lateral actions are accessible for reliable surface recording. Studies that tried to analyze multi-muscle synergies with respect to the COP_{ML} coordinate typically reported M-modes accounting for significantly smaller amounts of variance and synergy indices showing large inter-subject variability (e.g., Wang et al. 2005, 2006). As in those studies, most muscles recorded in our study had strong effects on COP_{AP}, and not so strong effects on COP_{ML}. As a result, we also observed much larger amounts of variance in the muscle activation space accounted for by a set of M-modes during analysis related to COP_{AP} as compared to that related to COP_{ML}. Hence, we feel much more confident in our conclusions related to COP_{AP} shifts and less confident in those related to COP_{ML} shifts. This remains a limitation of the study.

Concluding comments

Our main observations included COP drifts seen after removing visual feedback on COP that were consistent across trials performed by individual subjects but could be in opposite directions across subjects. This was true for quiet stance tasks and also for the midpoint of the sway cycle in the cyclical sway tasks. In addition, voluntary sway amplitude increased consistently. Overall, these observations fit the idea of RC drifts as one of the factors that define unintentional drifts in motor performance (Latash 2016). In addition, in tasks involving vertical posture, the safety factor played an important role and could overpower the RC drift effects in some subjects. The observation of TA activation drift confirms that RC drifts can take place at different levels of the control hierarchy, from individual muscles to whole-body. One of the least expected results was the increase in the ME motion during

the drift period without a comparable change in the nME motion. This was confirmed for both peaks and valleys of the sway cycle. These results suggest that postural stability is not compromised during unintentional drifts in performance in contrast to earlier studies of multi-finger tasks (Parsa et al. 2016, 2017b). This may be due to the vital importance of postural stability for everyday actions.

Acknowledgments

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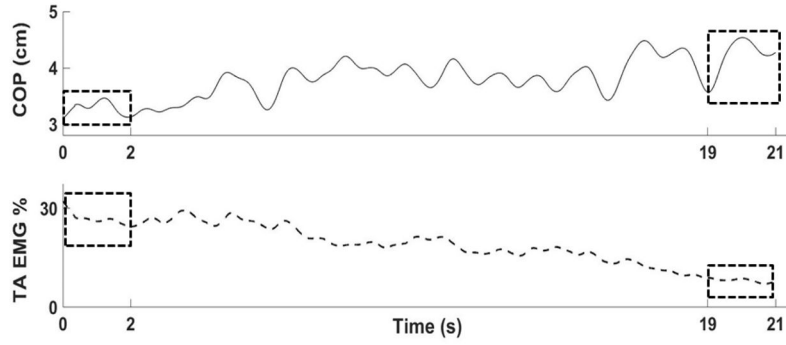
Figure 1.
An illustration of typical behaviors in the quiet stance task from the beginning of Phase-1 to the end of Phase-2. Top: Slow unintentional COP drift for the Ant condition in the AP direction. Bottom: The activation level of TA muscle; the values were normalized to the 30% of MVC of TA EMG. The dashed rectangles denote the time intervals, which were used to obtain the estimates of drifts in the COP and TA EMG from just before closing the eyes (Phase-1) to the end of trial (Phase-2). Note that the first 8 s and the last 1 s are not shown in this figure.
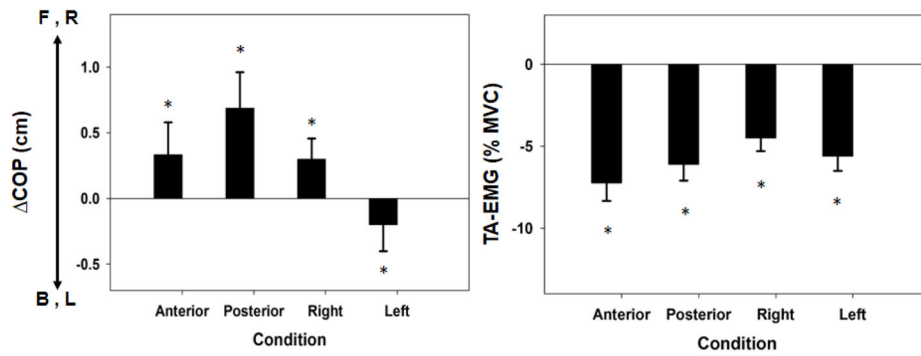
Figure 2.
Left: COP drift from Phase-1 to Phase-2. Right: The change in the activation level of TA from Phase-1 to Phase-2. Averaged across subjects values with standard error bars are shown for each condition. The double-pointed arrow along the Y-axis in the left panel displays "F" (forward), "B" (backward), "R" (right), and "L" (left) COP shifts. * show significant differences.
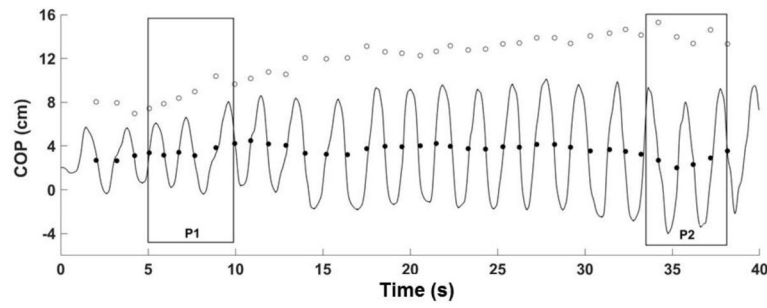
Figure 3.
An illustration of the cyclical sway task (COP_{AP}) for a typical subject in the anterior condition. Open and filled dots show the amplitude (A_{COP}) and midpoint (M_{COP}) time series computed across individual cycles, respectively. The two rectangles represent Phase-1 (P1) and Phase-2 (P2), which included two full cycle before closing eyes and two full cycles at the end of trial.
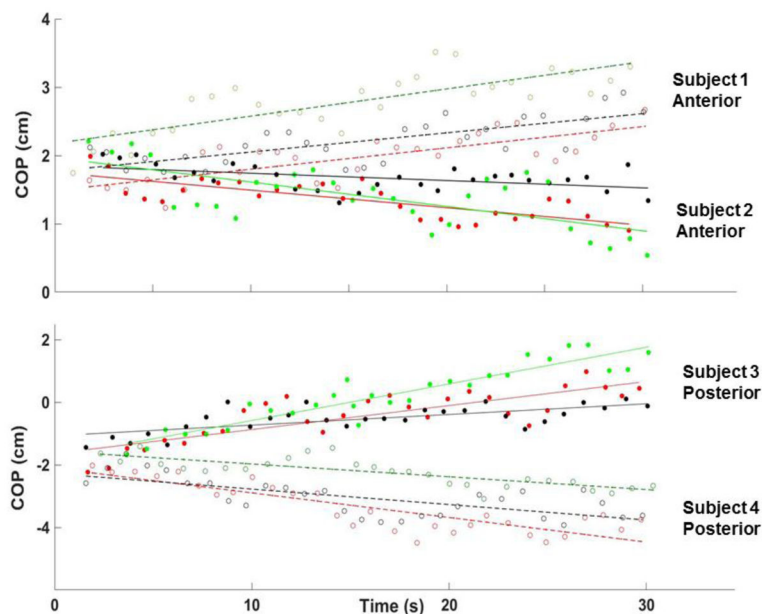
Figure 4.
An illustration of the drift in the midpoints in the cyclical sway task (M_{COP}) for four subjects. Top panel: Ant condition; bottom panel: Post condition. M_{COP} for individual subjects are shown with open and filled dots; linear regression lines are drawn. Note the consistent drifts away from the natural standing COP coordinate (zero) in Subject 1 and Subject 4, and consistent drifts toward zero in Subject 2 and Subject 3.
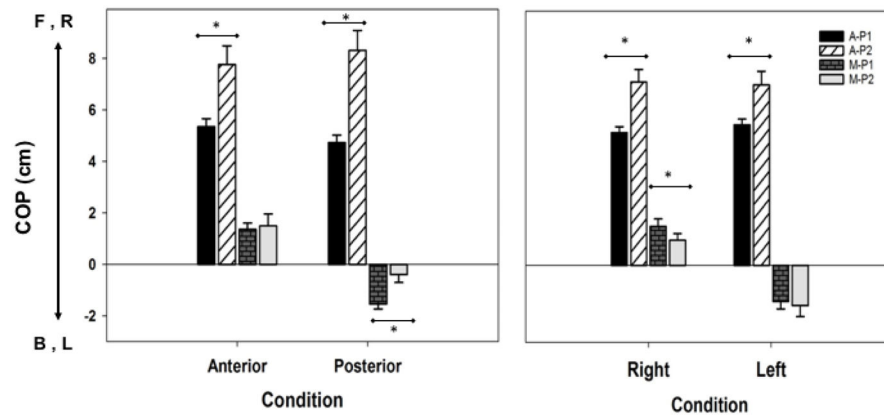
Figure 5.
Averaged across subjects (with standard error bars) peak-to-peak sway amplitude and midpoint before (Phase-1) and after (Phase-2) closing eyes. A_P1: amplitude in Phase-1, A_P2: amplitude in Phase-2; M_P1: midpoint in phase-1, M_P2: midpoint in Phase-2. The double-pointed arrow along the Y-axis in the left panel displays "F" (forward), "B" (backward), "R" (right), and "L" (left) COP shifts. * show significant differences.
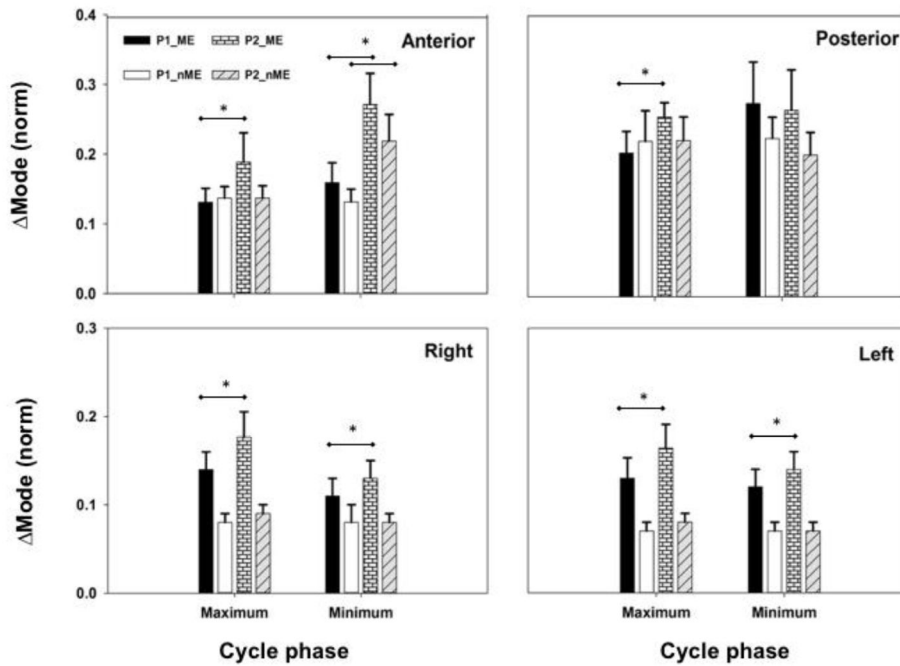
Figure 6.
Averaged across subjects (with standard error bars) normalized magnitudes of the motor equivalent (ME) and non-motor equivalent (nME) motion in Phase-1 and Phase-2 across the four conditions. The indices are shown for both peaks (Max) and valleys (Min) of the cycles. P1_ME: motor equivalent in Phase-1, P1_nME: non-motor equivalent in Phase-1; P2_ME: motor equivalent in Phase-2, P2_nME: non-motor equivalent in Phase-2. * show significant differences.

Table 1

Muscle loadings for the four M-modes

Muscle	AP direction				ML direction			
	M1-mode	M2-mode	M3-mode	M4-mode	M1-mode	M2-mode	M3-mode	M4-mode
TA	**-0.544**	**0.725**	0.034	-0.050	**0.868**	0.204	-0.182	0.019
SOL	**0.790**	-0.307	0.031	0.254	-0.282	**0.765**	-0.158	0.028
GM	**0.842**	-0.359	0.030	0.185	0.163	**0.880**	0.118	0.095
GL	**0.816**	-0.106	0.078	0.310	0.040	**0.671**	-0.107	-0.056
BF	0.309	0.052	-0.085	**0.908**	-0.025	-0.016	**0.867**	-0.049
ST	**0.818**	-0.287	0.054	0.132	0.197	**0.886**	0.103	0.107
VL	-0.403	**0.810**	-0.035	0.096	**0.915**	-0.024	-0.019	0.074
RF	-0.357	**0.820**	-0.022	0.126	**0.928**	-0.125	-0.059	0.043
VM	-0.199	**0.857**	-0.072	-0.010	**0.956**	-0.008	-0.066	0.046
TFL	-0.165	**0.847**	-0.003	-0.129	**0.552**	0.147	**-0.697**	-0.022
RA	0.044	-0.049	**0.991**	-0.067	0.108	0.103	-0.011	**0.983**
EST	**0.831**	-0.349	-0.036	0.028	-0.183	**0.670**	0.478	0.072
ESL	**0.801**	-0.326	-0.023	-0.055	-0.021	**0.555**	**0.600**	0.059

The loading factors for the first four PCs after Varimax rotation and factor extraction are shown for a typical subject. Bold values indicate significant loadings (with the absolute magnitude > 0.5). TA: tibialis anterior, SOL: soleus, GM: gastrocnemius medialis, GL: gastrocnemius lateralis, BF: biceps femoris, ST: semitendinosus, RF: rectus femoris, VL: vastus lateralis, VM: vastus medialis, TFL: tensor fasciae latae, RA: rectus abdominis, EST: thoracic erector spinae, ESL: lumbar erector spinae.