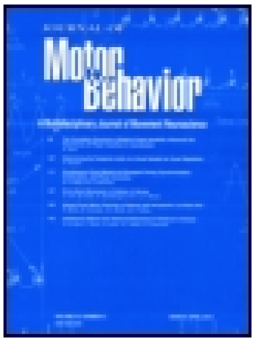

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ARTICLE

Effects of Shank Vibration on Lean After-Effect

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ABSTRACT. Postural adaptability is related to central sensory integration and reweighting efficiency. Incline-interventions lead to lean after-effect (LAE), but it is not fully known how sensory reweighting may affect the magnitude and duration of LAE. We tasked fifteen young and healthy subjects with performing incline-interventions under conditions designed to perturb proprioception during or after the incline-intervention. We found that support surface configuration affected responses to tendon vibration. Additionally, vibration during an incline-intervention did not inhibit LAE, but vibration during an after-effect significantly affected LAE. Results reinforce claims that postural adaptation is based on modifications of central mechanisms of perception, not peripheral shank proprioceptors and improve our understanding of the role of sensory reweighting and sensory integration into postural adaptability.

Keywords: posture, sensory integration, body schema, adaptation, proprioception

Introduction

Postural adaptation involves utilization of vestibular, visual, and somatosensory feedback to update the body schema (Head & Holmes, 1911; Holmes & Spence, 2004). Adaptation of the body schema can be achieved through persistent alteration of sensory feedback or task demands (Gurfinkel et al., 1995). These adaptations represent updates of the preferred reference point which the postural control system strives to maintain. A change in behavior once sensory feedback or task demands return to the original state is called an after-effect, and can be used to infer adaptation of the body schema (Ivanenko & Gurfinkel, 2018; Kluzik et al., 2005). After-effects dissipate over the course of seconds to minutes (Kluzik et al., 2005; Wierzbicka et al., 1998).

The current understanding of motor adaptation is insufficient. The role of cortical structures, such as the posterior parietal cortex (PPC) and of the cerebellum are still being explored (Jayaram et al., 2012; Young et al., 2020). Findings from Jayaram et al. indicate that the cerebellum is crucial in motor adaptation, and that disruption of cerebellar function impaired adaptation (Jayaram et al., 2012). Furthermore, we recently found that inhibition of the PPC decreased postural adaptation and lean after-effect (Young et al., 2020). Previous investigations have suggested that adaptation paradigms can probe relatively long term, or trait, weighting of the vestibular, visual, or proprioceptive system (Chong et al., 2017; Kluzik et al., 2005; Seidler et al., 2015). Adaptability may also serve to identify whether a patient retains sufficient motor plasticity to be successfully rehabilitated over time (Bastian, 2008). Beyond diagnostics, adaptation paradigms have shown promise as therapeutic devices themselves. Stroke patients have exhibited longer term (i.e. five or more days) improvements in function resulting from a single bout of prism adaptation (Rossetti et al., 1998). A line of research has also been performed identifying that adaptation paradigms involving exposure to altered sensory feedback may improve general adaptability in space flight populations, improving performance once the subjects return to gravity (Bloomberg et al., 2015; Seidler, 2004, 2010). The apparent benefits of motor adaptation paradigms as scientific, diagnostic, and even rehabilitative tools demonstrate the need to continue to further our understanding of adaptation of the body schema.

Multiple techniques have been developed to study the adaptation of the body schema by systematically altering task conditions or sensory feedback (Bove et al., 2009; Kluzik et al., 2005). One such method to induce postural adaptation is through an incline-intervention, a bout of stance that occurs on an inclined surface, resulting in ankle dorsiflexion. This intervention has been found to induce a postural after-effect known as lean after-effect (LAE). LAE corresponds with a forward shift in the whole-body center of gravity (COG). After an incline-intervention, there is a global change in the body schema and an alteration of the relationship between preferred orientation and gravitational vertical (Kluzik et al., 2005; 2007). Previous researchers have found high inter-class coefficients (ICC) within subjects upon repeated exposures to incline-interventions for measures of LAE duration (ICC = 0.95) and maximum magnitude (ICC = 0.85) (Kluzik et al., 2005). These findings demonstrate that subjects will respond similarly to incline-interventions with similar parameters, and allow researchers to modify incline-intervention parameters to observe differences in outcome measures between conditions. There is evidence that lean after-effect is dependent on the signal characteristics of the vestibular, visual, and somatosensory systems (Chong et al., 2017; Earhart et al., 2010; Wright, 2011). Chong et al. (2017) showed that healthy individuals differ in response to those with vestibular

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loss (Chong et al., 2017). Chong et al.'s findings demonstrate that one's long-term weighting of sensory signals is related to LAE. In this instance, those with vestibular loss, resulting in increased long-term somatosensory weighting, exhibited greater LAE following an incline-intervention. Earhart et al. systematically altered the presence of visual feedback during LAE. Whenever visual feedback was provided, LAE was immediately extinguished, but when visual feedback was removed, the subjects began to lean forward again (Earhart et al., 2010). Earhart et al.'s (2010) findings demonstrate that dynamic, or state, weighting of sensory signals is also related to LAE. Sway referencing of the support surface has been shown to decrease proprioceptive reliability (Cohen et al., 1996; Ozdemir et al., 2018). Wright (2011) identified that standing on a sway-referenced platform following an incline-intervention did not result in a significant LAE illusion (Wright, 2011). This finding was contrasted with data from subjects who stood on a flat surface resulting in reliable proprioceptive information following the incline-intervention and who demonstrated a large LAE but a quicker return to baseline. These findings support the idea that unreliable proprioceptive information influences the expression of a LAE and can interfere with postural control mechanisms. Mechanical vibration of the shank, which can occur on the Achilles tendon (ATV) or tibialis anterior (TAV), among other sites, has also been shown to induce shifts in body position as well as after-effects, which suggest that vibration induces adaptation of the body schema (Wierzbicka et al., 1998). Mechanical vibration also decreases reliability of proprioceptive sensory feedback, leading to downweighting of the proprioceptive system (Hwang et al., 2014).

As stated previously, both one's longer-term and dynamic sensory weighting are associated with LAE magnitude (Chong et al., 2017; Earhart et al., 2010; Wright, 2011). Therefore, we aimed to identify whether tendon vibration, known to decrease dynamic proprioceptive weighting, would have an impact on the formation of LAE. In order to achieve this goal, we tasked subjects with performing incline-interventions, with or without concurrent ATV or TAV and measured subsequent LAE. Results of the first experiment aid our understanding of how state weighting of the proprioceptive system influences adaptation of the body schema. We hypothesized that because vibration decreases proprioceptive reliability, and proprioceptive reliability is related to LAE, that vibration during inclined stance would decrease the magnitude and duration of LAE regardless of which tendon was vibrated. Next, we aimed to identify whether tendon vibration would influence re-adaptation to flat stance. Subjects performed incline-interventions, and were presented with tendon vibration during the post-test (i.e. lean after-effect period) and compared LAE. Results of the second experiment aid our understanding of how a secondary proprioceptive perturbation can influence a previously established postural adaptation (LAE). We hypothesized that because TAV and ATV both lead to profound postural responses, that TAV following an incline intervention would increase LAE magnitude and duration while ATV would decrease them. Overall, results of these experiments improve our understanding of how dynamic sensory weighting influences adaptation of the body schema. These results may provide insights into future paradigms designed to test sensory reweighting function or adaptability, as well as provide insights to rehabilitation paradigms designed to improve adaptability.

Materials and Methods

Subjects

Fifteen subjects (f = 9) participated in this series of experiments. Subjects ranged from 19-30 years old (23.5 ± 3.7), had an average height of 167 ± 13.5cm, and weight of 77.6 ± 21.1kg. Subjects provided informed consent through a process in accordance with the Helsinki Declaration which was approved by the University of Houston's institutional review board for experimental studies. Subjects were screened to exclude those who were not between 18-35 years of age, or who had a history of neurological or musculoskeletal dysfunctions that may inhibit postural control or sensory feedback.

Protocol

Subjects performed several postural control tasks across two data collection sessions. During the first session, subjects performed a baseline trial of 30s of quiet stance (QS) in order to identify basic postural stability characteristics free of any subsequent intervention, as assessed by COG measures. Subjects also underwent trials of ATV and TAV while standing on a flat surface using a pair of cylindrical model VB115 vibrators vibrating at a frequency of 80Hz and an amplitude of 1.0mm (Technoconcept, France). For both ATV and TAV trials, subjects underwent 5s of QS, followed by 30s of tendon vibration and finally 30 additional seconds of QS. These data are represented in Figure 1a. Following this, spread over the two data collection sessions, subjects performed five conditions of incline-intervention. For each condition, subjects first performed a 30s epoch of QS (E1). The data from this epoch was utilized in order to identify baseline average AP-COG position and calculate LAE characteristics. Next, they stepped onto an inclined surface positioned immediately adjacent to them that was set to an angle of 10 degrees and stood for five minutes (E2). Epoch 3 consisted of stepping off of the incline onto the horizontal surface and standing for five more

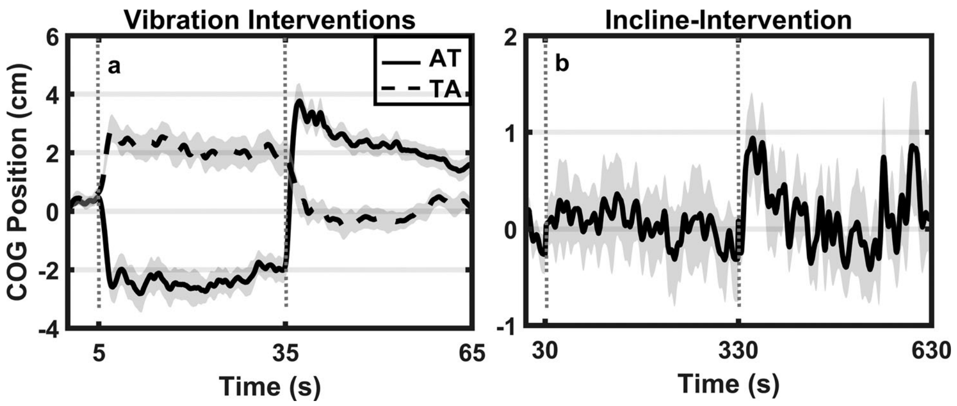

FIGURE 1. a: Mean COG displacement (±1SEM) of responses to AT (solid) and TA (dashed) vibration occurring independent of inclined stance. First and second horizontal bars represent onset and off-set of vibration, respectively. b: Response to C1 incline-intervention without any concurrent vibration intervention. First and second horizontal bars represent onset of E2 and E3, respectively.

minutes (E3). These transitions were practiced several times prior to data collection to minimize the time required to make this movement. Last, they moved back to a horizontal configuration and stood for another five minutes (E3). This protocol has been utilized by our group previously (Young et al., 2020).The five conditions of incline-intervention are reported in Table 1

Conditions were administered in a random order. During the first session, subjects performed baseline testing as well as two randomly assigned conditions of incline-intervention. During the second session, subjects performed the final three randomly assigned conditions of incline-intervention. This stipulation therefore required subjects to attend two data collection sessions. Additionally, between conditions, a 30-minute washout period was performed in order to allow LAE to decay completely. Washout period characteristics have varied in pervious investigations, ranging from as low as five (Wright, 2011) to fifteen minutes (Lee et al., 2017) to as many as one (Earhart et al., 2010) or two (Kluzik et al., 2007) hours. Prior to the start of each protocol, a bout of quiet stance was performed to verify that LAE had completely decayed. For each subject, 30 minutes was sufficient to abolish LAE in each condition. Throughout all components of each task, subjects were instructed to keep their eyes closed and place their arms on their chest. Subjects were also instructed to, "Stand naturally and not to resist any pulls they felt on their body or temptation to lean," and to, "not pay attention to their posture and let their mind wander," which was similar to the instructions Kluzik et al. (2005) provided to their subjects (Kluzik et al., 2005).

Instrumentation

Subjects were measured and outfitted with reflective markers based on the Vicon Plug-in Gait model (Vicon; Oxford Metrics Ltd, Oxford, England) and wore earmuffs to minimize auditory feedback. Incline-interventions took place on a surface set to an incline angle of 10-degrees (ASAHI Corporation, Gifu, Japan). Tape was placed on the floor in order to aid the subject in returning to the same place after the incline-intervention. Throughout the experiment, motion was captured using a 12-camera Vicon Nexus system at a frequency of 100Hz. During trials where vibration was present, vibration occurred at a frequency of 80Hz and an amplitude of 1.0mm.

Data Processing

Kinematic data were collected and exported from Vicon Nexus 1.8.5. Marker trajectories and subject anthropometric measurements were utilized by the Plug-in Gait pipeline in order to compute a whole-body center of mass measurement. This measurement was projected to ground level to calculate center of gravity in the anterior-posterior direction (AP-COG). These data were then imported and analyzed using custom MATLAB scripts (MATLAB 2019a, MathWorks, Inc. Natick, MA). This measure was filtered using multiple techniques. In order to analyze changes in AP-COG position during ATV and TAV trials, a 4th order low-pass Butterworth filter with a cutoff frequency of 5Hz was employed. Then, in order to analyze positional results from C1-C5 Incline-

TABLE 1. Experimental conditions.

Condition	Epoch 1	Epoch 2	Epoch 3
C1	QS 30s	Inclined stance 5m	Flat stance 5m
C2	QS 30s	Inclined stance 5m with concurrent ATV	Flat stance 5m
C3	QS 30s	Inclined stance 5m with concurrent TAV	Flat stance 5m
C4	QS 30s	Inclined stance 5m	Flat stance 5m with concurrent ATV
C5	QS 30s	Inclined stance 5m	Flat stance 5m with concurrent TAV

Interventions, data were low-pass filtered to a cutoff frequency of 0.1Hz. This filter design was previously employed to identify changes in elected positioning while eliminating higher-frequency components of sway (Kluzik et al., 2005). All AP-COG data were also separately band-pass filtered between 0.1 and 5Hz in order to calculate sum of movement in the anterior-posterior direction (AP-Path Length) to serve as a measure of postural sway.

The effects of ATV and TAV trials were quantified by measuring average AP-COG before vibration onset, during vibration, and after vibration offset. These data can be seen in Figure 1 (Figure 1a). AP-Path Length was also quantified during each time period. AP-COG data acquired during E3 for each condition were utilized to calculate two measures which quantified LAE. The first measure, Off-Set Time, identified when the subject ceased leaning forward. Off-Set Time was defined as the first moment in time, following the peak anterior position, in which the subject's AP-COG returned to an average position within two standard deviations of their baseline for a period of 10s (Kluzik et al., 2005). The second measure, Integrated Area, was calculated using measures adapted from previous studies. While previous studies have summed area under a positional curve until subjects reached the Off-Set Time, we summed the area under the curve throughout the entire 300s E3 epoch. This was performed because some E3 data did not exhibit obvious decay over time, and subjects occasionally briefly returned to upright before starting to lean again (Kluzik et al., 2005). Integrated Area was identified as the mathematical summation of the data throughout all points during which the subject's AP-COG was greater than 2SD anterior to their baseline value throughout E3.

Statistical Analysis

In order to assess the effects of vibration on AP-COG position, one-way Repeated Measures Analysis of Variance (RANOVA) tests were used to compare average AP-COG position before, during, and after vibration during flat stance. This process was performed separately for ATV and TAV trials. Next, in order to identify if support surface inclination altered the response to vibration, a Two-Way (Epoch by Configuration) RANOVA was performed to compare the vibration-induced shift in AP-COG position between flat and inclined stance. To accomplish this, we compared AP-COG position pre-and-during vibration on a flat surface to pre-and-during vibration on an inclined surface. This process was again performed separately for ATV and TAV to compare between flat and inclined stance. A similar process was performed to compare the effects of vibration on AP-COG position between flat and post-inclined stance. In order to achieve this, we compared AP-COG position pre-and-during vibration on a flat surface to pre-and during vibration after the incline-intervention. This again was repeated separately for TAV and ATV. Differences in postural sway, indicative of postural stability, were identified by comparing AP-Path length (cm) between no vibration, ATV, and TAV conditions using a One-way RANOVA. We compared no vibration, ATV, and TAV during flat stance (i.e. baseline testing), during inclined stance (i.e. the first 30 seconds of C1-C3) and during post-inclined stance (i.e. the first 30s of C1, C4, and C5).

In order to identify whether there was an effect of vibration during inclined stance (E2) on the formation of LAE, separate One-way RANOVAs were used to compare C1-C3 for the measures of Off-Set Time and Integrated Area. Then, in order to identify the whether there was an effect of vibration during E3 on the re-calibration back to upright (i.e. the extinguishment of LAE), separate One-way RANOVAs were used to compare Off-Set Time and Integrated Area between C1, C4, & C5.

All statistical analyses were carried out using SPSS (SPSS 26, IBM, Chicago, IL). In the case of significant main effect findings, pairwise comparisons were made using a Bonferroni post-hoc adjustment. Greenhouse-Geisser corrections were used in the case of sphericity being violated. Effect sizes derived from partial eta squared (η_p^2) were also derived and presented alongside F statistics in the results. When significant pairwise comparisons were identified, Hedge's G (HG) effect sizes were calculated. For all analyses, significance was identified using an alpha value of $p < 0.05$.

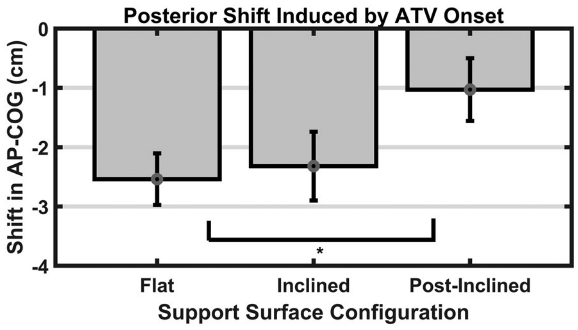

FIGURE 2. Mean change in AP-COG upon onset of ATV (±1SEM). Posterior shift in AP-COG caused by ATV was affected by support surface characteristics. ATV which occurred during post-inclined stance led to significantly less posterior shift than on a flat surface. Asterisks (*) indicate statistical significance with corresponding p value <0.05.

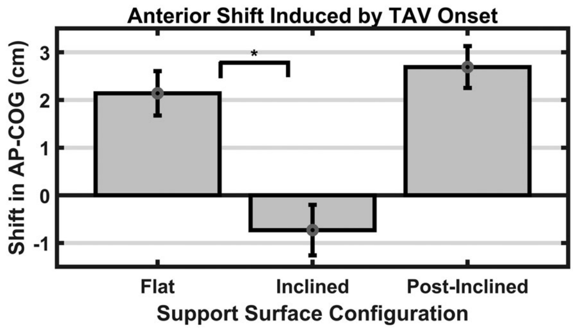

FIGURE 3. Mean change in AP-COG upon onset of TAV (±1SEM). Anterior shift in AP-COG caused by TAV was affected by support surface characteristics. TAV which occurred during inclined stance led to a slight posterior shift in position, differing significantly from the anterior shift which occurred on a flat surface. Asterisks (*) indicate statistical significance with corresponding p value <0.05.

Results

Before identifying whether tendon vibration affected the formation or extinguishment of LAE, we needed to identify the impact of support surface configuration on a subject's response to tendon vibration. When presented on a flat surface, ATV led to significant changes in position throughout the trial ($F_{2,13}$=163 $p < 0.0001$, η_p^2=0.96) (Figure 1a). Post-hoc comparisons using a Bonferroni adjustment revealed a significant posterior shift of −2.54 ± 1.68cm during vibration compared to pre-vibrated stance ($p < 0.0001$ HG = 2.07). The response to ATV was no different when applied on an inclined surface, coinciding with a posterior shift of −2.32 ± 2.48 compared to pre-vibrated stance ($F_{2,13}$=0.089 $p = 0.77$ η_p^2=0.006). Conversely, the posterior shift was significantly reduced when ATV occurred post-incline (i.e. during E3 of the incline-intervention) ($F_{2,13}$=7.39 $p = 0.018$, η_p^2=0.36). During E3, a shift of only −1.03 ± 2.05 was found compared to pre-vibrated stance (Figure 2). On a flat surface, ATV also corresponded with a significant anterior after-effect following vibration, coinciding with a shift of +2.27 ± 1.23 compared to pre-vibrated stance ($p < 0.0001$ HG = 2.08).

On a flat surface, TAV also led to significant changes in position ($F_{2,13}$=16.3 $p < 0.0001$, η_p^2=0.77) overall, with a significant anterior shift of +2.14 ± 1.8cm during vibration compared to pre-vibrated stance ($p < 0.0001$ HG = 1.24) Unlike the response to TAV on a flat surface, when TAV occurred on an inclined surface (i.e. during E2 of the incline-intervention), subjects did not exhibit a corresponding anterior shift in COG, and instead exhibited a slight posterior shift in position of −0.73 ± 2.05cm compared to pre-vibrated stance, differing significantly from the flat surface response ($F_{2,13}$=16.03 $p = 0.001$ η_p^2=0.53). No such differences were found when comparing the typical response to TAV with response to TAV during post-inclined stance. When presented post-incline (E3), TAV corresponded with an anterior shift of +2.69 ± 1.7 compared to pre-vibrated stance ($F_{2,13}$=0.43 $p = 0.52$ η_p^2=0.30) (Figure 3). On a flat surface, unlike ATV, TAV did not result in a significant after-effect compared to baseline. Once TAV ceased, subjects only shifted −0.06 ± 1.18 compared to baseline ($p = 0.31$).

Both ATV and TAV during flat stance led to increased postural sway, as measured by AP-Path Length (cm), compared to non-vibrated baseline quiet stance ($F_{2,13}$=19.3 $p < 0.0001$, η_p^2=0.73; ATV $p < 0.0001$ HG = 1.48; TAV $p < 0.0001$ HG = 1.58). Vibration during the first thirty seconds of inclined stance (i.e. E2) also led to increased postural sway compared inclined stance without vibration ($F_{2,13}$=42 $p < 0.0001$ η_p^2=0.87; ATV $p < 0.0001$ HG = 1.62; TAV $p = 0.012$ HG = 1.35). Conversely, vibration during the first 30 seconds of post-inclined (E3) stance led to no increase in postural sway compared to post-inclined stance with no vibration ($F_{2,13}$=1.38 $p = 0.06$ η_p^2=0.35) (Figure 4).

There were no differences in the magnitude or duration of LAE between C1-C3 (i.e. no-vibration, ATV during E2 and TAV during E2) (Figure 5). No differences were observed in Off-Set Time, indicating the time to calibrate to gravity was not affected ($F_{2,13}$=0.42 $p = 0.64$ η_p^2=0.06). There were also no differences in the measurement of Integrated Area, indicating that the magnitude of LAE was not affected ($F_{2,13}$=0.46 $p = 0.67$ η_p^2=0.06). The minimum off-set time following during

C1 (i.e. no vibration) condition was 11.74s, and three subjects exhibited an off-set time of under 30 seconds (11.74s, 13.5s, 16.15s).

When vibration was presented during E3 (C4 & C5), however, significant changes were observed in Off-Set Time ($F_{2,13}$=9.79 p = 0.003 η_p^2=0.60) (Figure 6). TAV during E3 led to a significantly longer Off-Set Time than the no vibration or ATV conditions (p = 0.009 HG = 0.66, p = 0.002 HG = 1.15, respectively). There was no difference between the ATV and no vibration condition (p = 0.85). Similarly, there were significant differences between conditions in Integrated Area ($F_{2,13}$=9.26 p = 0.003 η_p^2=0.59) TAV during E3 led to significantly greater Integrated Area than ATV (p = 0.002 HG = 1.3). Descriptive data can be found in Table 2. Although subjects exhibited a continuum of responses, all subjects exhibited a significant anterior shift in AP-COG, or LAE, in response to at least one experimental condition. No subject exhibited an off-set time of less than 30s for all conditions (39.15).

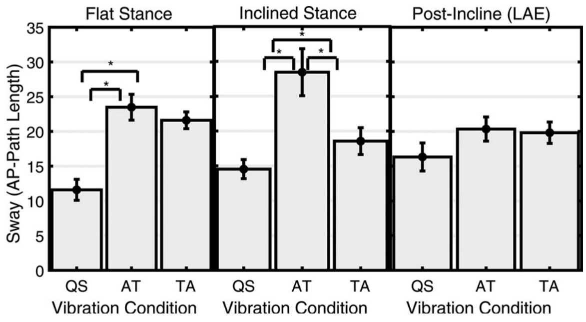

FIGURE 4. Mean path length in anterior-posterior direction (±1SEM) a: on a flat surface b: on an inclined surface c: following inclined stance Asterisks (*) indicate statistical significance with corresponding p value <0.05.

Discussion

In the current investigation, we sought to improve our understanding of postural adaptation and dynamic sensory reweighting by systematically manipulating postural adaptation paradigms. After testing a group of fifteen young and healthy subjects, we found that support surface inclination altered one's response to vibration and that while tendon vibration during inclined stance had no impact on lean after-effect, tendon vibration after inclined stance had a profound impact.

In accordance with previous research, we found that an incline-intervention with no additional perturbation (i.e. C1) led to LAE in our subjects (Figure 1b). These data support the previous understanding that people adapt to changing environmental parameters such as vibration or inclined stance. These data also support the notion that inclined stance alters body schema through the incongruence developed between proprioceptive and vestibular identifiers of verticality, which requires time to be rectified. This incongruence leads to LAE and rectification leads to the extinguishment of LAE (Kluzik et al., 2005). We identified significant LAE in each subject in response to at least one experimental condition. This is in contrast to previous studies, which found a continuum

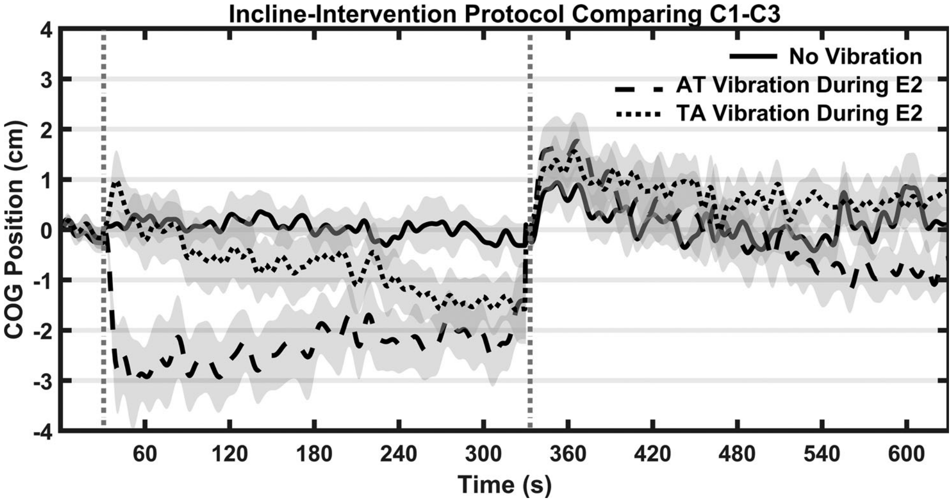

FIGURE 5. Mean COG displacement (±1SEM) throughout the incline-intervention protocol comparing C1-C3. E2 started at 30s and E3 started at 330s (5 minutes and 30 seconds).

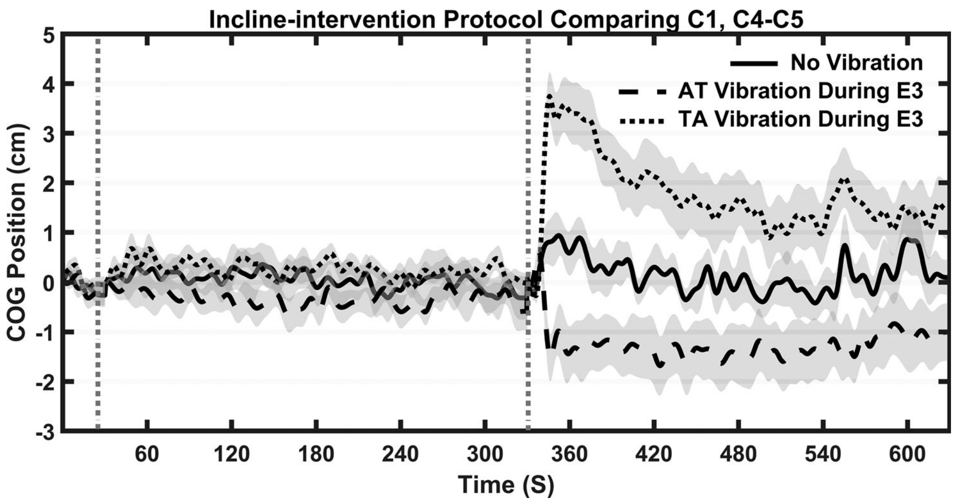

FIGURE 6. Mean COG displacement (±1SEM) throughout the incline-intervention protocol comparing C1, C4, and C5. E2 started at 30s and E3 started at 330s (5 minutes and 30 seconds).

TABLE 2. Lean after-effect descriptive outcomes.

Condition	Off-Set Time	Integrated Area
C1	63 ± 69	11355 ± 8954
C2	85 ± 65	9836 ± 9547
C3	96 ± 107	13071 ± 11840
C4	31 ± 74	5696 ± 8318
C5	172 ± 122	19039 ± 11834

of responses, with some individuals not exhibiting LAE at all. This could be the case for multiple reasons. First, in this experiment we employed an incline angle of 10 degrees and a duration of 5 minutes, both of which are more aggressive than a majority of previous studies (Kluzik et al., 2005; 2007). However, we employed these parameters in another study (Young et al., 2020), and identified that some subjects did not respond, suggesting other potential reasons. The most likely explanation is that the presence of tendon vibration may have led to anterior shifts in situations where LAE was not present, this would be most apparent during C5, where TAV occurred during after-effect period. Also consistent with previous investigations, we found that tendon vibration, when applied on a flat surface, led to increased AP-Path length, suggesting impaired stability (Dettmer et al., 2013).

On a flat surface, TA vibration induced an anterior shift. Conversely, on an inclined surface, TAV induced a slight posterior shift. There are at least two reasonable explanations for this phenomenon. In the current study, inclined stance resulted in increased postural sway compared to flat stance. Ivanenko (1999) has reported that as postural instability increases, the effects of tendon vibration decrease. Ivanenko attributed their findings to proprioceptive downweighting (Ivanenko, 1999). Such downweighting could have also been associated with the effects we report in response to TA vibration during inclined stance. However, the fact that only the effects of TAV, but not ATV were muted suggests that this is unlikely to be the sole reason for our results. Another possible explanation for our findings in response to TAV could be related to lower limb anatomical features. The lack of anterior shift in response to TAV during inclined stance may be due to the increased ankle dorsiflexion inherent to inclined stance. If subjects increased their dorsiflexion to an even greater extent in response to TAV vibration, the additional dorsiflexion may have exceeded the subject's base of support. Instead, subjects may have used an orientation closer to gravitational vertical in order to maintain stability. These constraints were not present in ATV, which leads to more plantarflexion, explaining why response to ATV was not affected. Thus, downweighting of proprioceptive feedback due to vibration was only necessary during TAV due to biomechanical constraints that were not relevant during ATV. Only TAV led to a risk of falling due to extreme dorsiflexion, therefore, only the effects of TAV required suppression.

Following an incline-intervention (i.e. during E3), the posterior shift associated with ATV was decreased compared to ATV independent of an incline-intervention.

These findings show that the anterior bias which results from an incline-intervention (i.e. LAE) can alter the response to vibration. This may suggest a summative effect between the anterior LAE and the posterior shift from ATV. Previous investigations have shown summative effects during two concurrently presented interventions (Kabbaligere et al., 2017). Kabbaligere et al. (2017) found that when presented individually, ATV led to a posterior shift and the visual perturbation they employed led to an anterior shift. When presented together however, the response was close to a mathematical summation of the two perturbations, suggesting a summative or middle ground response (Kabbaligere et al., 2017). To the best of our knowledge, this is the first investigation to show a summative effect of two interventions on postural adaptation that both affected the proprioceptive channel. These results suggest there is a capability of the adapted body schema, as exhibited by LAE, to alter the response to vibration. This finding should reinforce the need for investigators to strictly control their experiments and prevent unintended factors from influencing results of their adaptation paradigm.

Support surface characteristics were related to the increase in postural sway, measured by AP-Path Length, associated with tendon vibration. For both flat and inclined stance, both AT and TA vibration increased sway compared to non-vibrated stance. No such differences were found during E3. The lack of significant stability decrease between the post-inclined conditions may be partially explained by increased 'baseline' sway during E3 compared to regular quiet stance, as previous investigations have found unstable support surfaces decrease the stability loss associated with vibration (Forestier et al., 2015; Lubetzky et al., 2017). Nevertheless, the cost of vibration on postural sway decreased when preceded by an incline-intervention. It is possible that increased adaptive challenges during the incline-intervention were utilized in order to improve the subject's ability to maintain a stable posture during the post-incline period, regardless of the presence of vibration.

No differences were found between conditions C1-C3 for either measure of LAE. Previous studies have identified a positive relationship between proprioceptive weighting and the strength of LAE (Chong et al., 2014; Earhart et al., 2010; Wright, 2011). In one experiment, Chong et al. (2014) increased LAE response in some subjects by adding augmented light touch feedback during the incline-intervention. They argued that providing this feedback increased the weight placed on the somatosensory system in their population, leading to greater LAE. Conversely, in our study, disrupting proprioceptive feedback via tendon vibration during an incline-intervention (i.e. E2) did not affect LAE. These data suggested that despite the system ignoring the noisy signal from shank proprioceptors, relevant proprioceptive information was utilized to create lean after-effect. These results suggest that the formation of LAE is not affected by decreased local reliability of ankle proprioceptors. Kluzik et al. previously identified that LAE is most likely the result of adaptation of the global internal representation of verticality, instead suggesting that the primary somatosensory variable which represents verticality may not be strictly related to the ankle angle, but rather the trunk to support surface relationship (Kluzik et al., 2005; 2007). The current results serve to bolster that argument, as it can be observed that an additional perturbation of the ankle proprioceptors did not inhibit the formation of LAE. Future investigations may consider perturbing trunk sensory feedback to identify if reliable proprioception from spinal extensors is necessary for formation of LAE. Results from this experiment reinforce previous notions that global, rather than local somatosensory weighting is a determining factor of LAE magnitude (Kluzik et al., 2005; Lee et al., 2017). While it is supported that the relative weighting of the somatosensory and vestibular systems are related to LAE magnitude, we did not perform any testing to identify sensory dominance (Chong et al., 2017). The fact that all of our subjects responded to the incline intervention (i.e. exhibited LAE), suggests that no subjects solely utilized their vestibular systems. A greater number of subjects in future studies may allow for correlation between sensory dominance and LAE characteristics.

Comparisons between C1, C4, and C5 demonstrate that LAE can be altered by tendon vibration. Previously, Wright (2011) found that sway-referencing the COP following an incline-intervention quickly led to abolishment of LAE and a return to gravitational vertical (Wright, 2011). Wright argued that this was due to downweighting of the proprioceptive system, which is a well-founded argument (Chong et al., 2014; Clark & Riley, 2007). Despite the decreased proprioceptive reliability associated with tendon vibration, we did not observe a general decrease in LAE following vibration. Instead, we found direction-specific modifications in LAE depending on whether the AT or TA was vibrated. This suggests that the vibration-induced shifts in average position were a more dominant feature when compared to the relative downweighting of the proprioceptive system. The direction specific effects of vibration suggest there is an interactive adaptation which occurs when vibration is performed post-inclined stance. Previous research has found summative adaptations when two sources of stimuli are applied concurrently, while this investigation found an interactive effect when two interventions were performed consecutively (i.e. performing an incline-intervention to form lean after-effect and subsequently performing tendon vibration) (Feldman & Latash, 1982; Kabbaligere et al., 2017; Kavounoudias et al., 1999; Wierzbicka et al., 1998). This finding highlights the possibility of future research to investigate adaptation through more complex and sequential paradigms which may seek to better capture real world contexts.

Results of his investigation improve our general understanding of adaptation of the body schema. Our results demonstrate that the body schema's adaptability is robust even when a concurrent proprioceptive perturbation is performed during the adaptation period. Our results also reinforce previous findings that lean after-effect, and more generally adaptation of the body schema, is primarily the result of central, not peripheral changes (Kluzik et al., 2007). Various mechanoreceptors throughout the shank and foot segments likely sensed an increased stretch during and after inclined stance. Despite these, ascending signals from these receptors were not sufficient to prevent LAE. This again highlights the dominance of the central nervous system and brain centers in motor adaptation despite signal characteristics of specific peripheral sensory organs. It is also possible that these signals would exert greater influence in the event that postural stability was challenged. This can be observed by the lack of after-effects following TAV but not ATV. There is ample evidence that adaptation of the body schema occurs in the CNS. Various brain regions have been studied in this regard, including the cerebellum and posterior parietal cortex (PPC) (Jayaram et al., 2012; Young et al., 2020). Recently, we identified that the PPC is critical in the formation of LAE, which alongside the results of this investigation, reinforce the understanding that postural adaptation is mediated by higher levels of the CNS and not simply by local changes in proprioceptive receptor functioning. These investigations support previous research concluding that impaired adaptability arises due to deficits in the CNS (Mutha et al., 2011; Tseng et al., 2007). The cortical inadequacy may be the inability to effectively integrate sensory information in order to reduce error (Tseng et al., 2007). These cortical inadequacies, leading to ineffective adaptation of the body schema to external changes, may be partially responsible for age-related postural control issues and fall incidence.

This investigation utilized tendon vibration, which is a popular method to investigate dynamic sensory reweighting and postural control. Often, researchers solely utilize ATV. While researchers may consider ATV and TAV to simply be inversions of one another, we found significant after-effects of ATV but not TAV. This result is in contrast to at least one previous study, which showed a majority of subjects exhibited after-effects of shank vibration in both directions (Wierzbicka et al., 1998). While we cannot fully explain this phenomenon, it could be due to the relatively greater limit of stability in the anterior, compared to posterior direction. Subjects may not have felt threatened during the anterior after-effect induced by the offset of ATV, whereas they may have consciously overcame any urge to shift toward the posterior following TAV. The results serve to suggest that future researchers should exercise caution when generalizing the effects of vibration of the AT to other body segments.

In conclusion, we found that altering support surface characteristics impacts the effects of tendon vibration on position. We also found that tendon vibration during inclined stance does not affect the formulation of LAE. Alternatively, tendon vibration during LAE leads to direction-specific responses based on what tendon is vibrated. Last, the increased sway typically observed during vibration is absent during LAE. This information improves our general understanding of sensory integration and reweighting during postural control by expanding our understanding of intrasensory effects of multiple proprioceptive interventions. Results of this investigation may lead to improvements in testing of adaptability in response to multiple perturbations as well as potential improvements in training of adaptability in clinical populations.

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No potential conflict of interest was reported by the author(s).

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