Small Directional Treadmill Perturbations Induce Differential Gait Stability Adaptation

Running title: Gait stability adaptation to small directional perturbations

Jinfeng Li [1,*] and Helen J. Huang [1,2]

[1] Department of Mechanical and Aerospace Engineering, University of Central Florida, Orlando, FL 32816, USA;

[2] Disability, Aging, and Technology (DAT) Cluster, University of Central Florida,

Orlando, FL 32816, USA; hjhuang@ucf.edu

* Correspondence: jinfeng@knights.ucf.edu; Tel.: +1-321-666-0567;

12760 Pegasus Dr., Bldg 40, Room 307, Orlando, FL 32816, USA

Abstract: Introducing unexpected perturbations to challenge gait stability is an effective approach to investigate balance control strategies. Little is known about the extent to which people can respond to small perturbations during walking. This study aimed to determine how subjects adapted gait stability to multidirectional perturbations with small magnitudes applied on a stride-by-stride basis. Ten healthy young subjects walked on a treadmill that either briefly decelerated belt speed ("stick"), accelerated belt speed ("slip"), or shifted the platform medial-laterally at right leg mid-stance. We quantified gait stability adaptation in both anterior-posterior and medial-lateral directions using margin of stability and its components, base of support and extrapolated center of mass. Gait stability was disrupted upon initially experiencing the small perturbations as margin of stability decreased in the stick, slip, and medial shift perturbations and increased in the lateral shift perturbation. Gait stability metrics were generally disrupted more for perturbations in the coincident direction. As subjects adapted their margin of stability using feedback strategies in response to the small perturbations, subjects primarily used base of support (foot placement) control in the stick and lateral shift perturbations and extrapolated center of mass control in the slip and medial shift perturbations. Gait stability metrics adapted to perturbations in both anterior-posterior and medial-lateral directions. These findings provide new knowledge about the extent of gait stability adaptation to small magnitude perturbations applied on a stride-by-stride basis and reveal potential new approaches for balance training interventions to target foot placement and center of mass control.

NEW & NOTEWORTHY Little is known about if and how humans can adapt to small magnitude perturbations experienced on a stride-by-stride basis during walking. Here, we show that even small perturbations disrupted gait stability and that subjects could still adapt their reactive balance control. Depending on the perturbation direction, subjects might prefer adjusting their foot placement over their center of mass and vice versa. These findings could help potentially tune balance training to target specific aspects of balance.

Keywords: gait; adaptation; perturbation; margin of stability; balance

1. Introduction

Perturbations during walking can induce potential losses of balance and elicit corrective locomotor adaptations, which are useful for understanding human balance control (Mansfield et al. 2015; Torres-Oviedo et al. 2011). There are multiple approaches to perturb gait stability, including split-belt walking (Buurke et al. 2018; Torres-Oviedo et al. 2011), visual flow distortions (Franz et al. 2016; O'Connor and Kuo 2009), waist pulling (Hof et al. 2010; Vlutters et al. 2018), platform displacements (Afschrift et al. 2018; McIntosh et al. 2017), and rapid changes in treadmill belt speed (Debelle et al. 2020; Patel and Bhatt 2018). Studies using discrete perturbations such as waist pulling, platform displacements, and changes in treadmill belt speeds often apply the perturbation once out of every 5-20 strides (Afschrift et al. 2018; Debelle et al. 2020; Hof et al. 2010; McIntosh et al. 2017; Patel and Bhatt 2018; Vlutters et al. 2018). These large magnitude perturbations are less frequent and often require recovery steps to regain balance. Recent work has shown that rehabilitation efficiency could improve with frequent repeated locomotor training with high intensity and variability (Hornby et al. 2011, 2019). Based on these findings, applying frequent repeated perturbations with small magnitudes during walking to create small but frequent losses of balance could be an effective approach. Such an approach could be used to increase the amount and variability of perturbations while generating a relatively higher intensity compared to infrequent large discrete perturbations. As such, little is known about the extent to which humans can adapt to small magnitude discrete balance perturbations applied on a stride-by-stride basis during walking. This approach could reveal stride-to-stride adaptation to almost imperceptible perturbations to gait stability, which would provide additional insight about how humans control, maintain, and adapt their stability during walking.

The margin of stability is a well-accepted metric to quantify stability of human walking (Bruijn et al. 2013). The margin of stability is the distance between the edge of the base of support and the extrapolated center of mass (Hof et al. 2005). People tend to maintain a constant margin of stability when walking on different surfaces (Höhne et al. 2011; Rosenblatt and Grabiner 2010). When external conditions in the environment disrupt the steady state of walking and its margin of stability, increasing the base of support is effective for maintaining stability based on the inverted pendulum model (Hof 2008) and has been demonstrated in multiple gait studies (Hak et al. 2013; Hof et al. 2010; Süptitz et al. 2013). After unexpected perturbations during walking, humans reactively adapt their gait by shortening the swing leg time to take fewer recovery steps, which helps them to regain or maintain stability

(McCrum et al. 2018). Additionally, margin of stability revealed that perturbations were more destabilizing for older adults, but both young and older adults scaled their reactive responses with the perturbation intensity (Martelli et al. 2017a).

To date, it remains unknown to what extent humans can control their margin of stability and its components, the base of support and extrapolated center of mass, during walking. How do humans adapt, if at all, to frequent small magnitude perturbations during walking? Are small perturbations in specific directions more disruptive than others? Analyzing the base of support and the extrapolated center of mass components of margin of stability could provide insights on how the body reacts to small perturbations and maintains stability. Controlling foot placement through the swing leg or controlling center of mass through the stance leg are two main balance strategies for perturbed walking (Bruijn and van Dieën 2018; Hof et al. 2010; Reimann et al. 2018). In a slip perturbation study, post-stroke individuals took longer steps and shortened the forward excursion of the extrapolated center of mass to increase their anterior-posterior margin of stability, which was accompanied with decreased medial-lateral margins of stability to recover from the slip perturbations (Buurke et al. 2020). In a waist pulling perturbation study, subjects adjusted the base of support and margin of stability when adapting feedback and feedforward strategies of balance control during walking (Martelli et al. 2017b). Further, older adults primarily adjust the extrapolated center of mass to improve stability of the perturbed leg to maintain and transfer stability to the unperturbed leg (McCrum et al. 2019).

The primary purpose of this study was to determine how subjects adapted margin of stability and its components (base of support and extrapolated center of mass) in response to small treadmill perturbations applied on a stride-by-stride basis. We rapidly accelerated or decelerated treadmill belt speed to create “slip” or “stick” perturbations, respectively. We also rapidly shifted (i.e., translated) the treadmill medially or laterally to create treadmill shift perturbations in the medial or lateral direction, respectively. We applied the treadmill perturbations at right mid-stance of each stride, except for no-perturbation “catch” strides that occurred randomly in each batch of 5 strides. The purpose of the “catch” strides was to probe whether subjects were potentially adopting a feedforward strategy in response to the small magnitude perturbations encountered during perturbed walking. Experimental protocols that apply perturbations trial-by-trial with unexpected catch trials have typically been used in goal-directed arm reaching studies (Huang et al. 2012; Shadmehr and Mussa-Ivaldi 1994). We are extending that

protocol to walking to gain insights on the adaptability of balance control during walking. Because we applied perturbations on a stride-by-stride basis, the strengths of the perturbations were limited to avoid the need for recovery steps, which are often necessary during larger treadmill induced trip and slip perturbations that seek to induce a fall.

The first hypothesis was that when subjects first experienced the small perturbations, their gait stability would be disrupted (i.e., become less stable) and then adapt to regain stability as they gained more experience with the perturbations. As such, we expected margin of stability to decrease upon first experiencing the perturbations and then increase over time with more exposure to the perturbations. The second hypothesis was that subjects would adopt more feedforward strategies as they gained more experience with the perturbations. We expected that as subjects gained more experience with the perturbations, margin of stability, base of support, and extrapolated center of mass during catch strides would deviate more from the averaged levels of the unperturbed strides prior to the perturbed period.

To assess the extent of the expected adaptation, we also sought to determine whether perturbation direction and size affected the responses and adaptation to the perturbations. We hypothesized that the anterior-posterior margin of stability and its components would be more sensitive to the treadmill belt perturbations, which were in the coincident (anterior-posterior) direction and likewise, medial-lateral margin of stability and its components would be more sensitive to the treadmill shift perturbations, which were in the coincident (medial-lateral) direction. We also hypothesized that adaptation of margin of stability and its components would scale with perturbation size.

2. Methods

2.1. Participants, setup and protocol

Ten healthy young subjects (4 males, 6 females; age: 21.7 ± 2.4 years) participated in this study. The Institutional Review Board of the University of Central Florida approved the experimental protocol (SBE-16-12831). The study met all requirements in accordance with the Declaration of Helsinki, and all subjects provided their written informed consent.

Subjects walked on a dual split-belt instrumented treadmill (M-gait, Motekforce Link, Amsterdam, The Netherlands) operating at 300 Hz as we recorded their lower limb kinematics using the 16-marker Conventional

Lower Body Markerset and a passive motion capture system (OptiTrack, NaturalPoint Inc., Corvallis, OR, USA, 13 Prime13W and 9 Prime13 cameras) operating at 240 Hz. The treadmill has independent speed control for each treadmill belt, and the treadmill is mounted on a moveable platform such that the treadmill can rapidly translate side-to-side in real-time. These features were used to produce treadmill perturbations.

We programmed the treadmill (D-Flow, version 3.28.0, Motekforce Link, Amsterdam, The Netherlands) to apply perturbations during mid-stance of the right leg on a stride-by-stride basis. The perturbation onset occurred when the vertical projection of the estimated center of mass (the average of the four pelvis markers) position resided between the right toe (2nd metatarsal) and right heel markers in the anterior-posterior direction and when the left heel marker was at least 5 cm higher than the right toe marker (Fig. 1A). The duration of each perturbation from onset to termination was ~400 ms such that the treadmill could return to the neutral unperturbed position and baseline belt speed (1.0 m/s) prior to or shortly after left heel strike.

Perturbations were applied in four directions: anterior, posterior, medial, and lateral to examine the effects of perturbation directions (Fig. 1A). We also used two perturbation sizes for the anterior and posterior directions, which could be completed in ~400 ms, to examine potential scaling effects with perturbation size (Fig. 1B). The baseline walking speed was 1.0 m/s, and the belt acceleration was set to 12.5 m/s^2. For anterior "stick" perturbations, the right belt speed decreased from 1.0 m/s to the target speed (0.6 m/s and 0.8 m/s; Stick0.4 and Stick0.2, respectively) and then returned to the baseline speed. For posterior "slip" perturbations, the right belt speed increased to the target speed (1.2 m/s and 1.4 m/s; Slip0.2 and Slip0.4, respectively) and then returned to the baseline speed. For medial perturbations, the treadmill shifted 1 cm toward the medial side of the right leg (i.e., to the left) and then returned to the neutral treadmill location (M1). For lateral perturbations, the treadmill shifted 1 cm toward the lateral side of the right leg (i.e., to the right) and then returned to the neutral treadmill location (L1).

Each subject completed six trials, one trial for each perturbation condition. We randomized the order of the six trials and did not inform subjects of the perturbation type, timing, direction, and magnitude. Each trial was 8 minutes long and began with 2 minutes of unperturbed walking (pre). Subjects then experienced 4 minutes of perturbed walking (perturbed) and concluded the trial with another 2 minutes of unperturbed walking (post). During the 4-minute perturbed walking block, no-perturbation "catch" strides occurred randomly 1 out of every 5 strides to

assess whether subjects were anticipating or reacting (Fig. 1C). Subjects wore a safety harness to prevent potential falls during all walking trials.

2.2. Data analysis

We wrote custom MATLAB (version 9.3, R2017b, Mathworks, Natick, MA, USA) scripts to process the kinematic data and calculate the gait stability metrics. We low-pass filtered the three-dimensional coordinates of the markers using a 4th order Butterworth filter with a 12 Hz cut-off frequency, and then extracted the gait events. Heel strike was the instant the vertical position of the heel marker of the foot transitioning from swing to stance was near zero (close to the treadmill) and reached its maximum vertical acceleration (Hreljac and Marshall 2000). Toe off was the instant the toe marker of the foot transitioning from stance to swing reached its maximum vertical acceleration between two consecutive heel strikes (De Witt 2010).

We calculated the margin of stability at every left heel strike as:

$$MoS = BoS - XcoM \tag{1}$$

where MoS is the margin of stability; BoS is the boundary of the base of support; and XcoM is the extrapolated center of mass (Hof et al. 2005). We calculated the extrapolated center of mass using Equation 2, which also accounts for the movement speed of the treadmill surface (Beltran et al. 2014; Süptitz et al. 2012).

$$XcoM = CoM + (V_{CoM} + V_{treadmill})/\sqrt{g/l} \tag{2}$$

CoM is the center of mass position, and V_{CoM} is the center of mass velocity, which was derived as the first derivative of the center of mass position. $V_{treadmill}$ is the belt speed for the anterior-posterior perturbations and the platform speed for the medial-lateral perturbations, respectively. The remaining variables are g, the gravitational constant (9.81 m/s^2) and l, the equivalent pendulum length, which was the distance from the left ankle marker (lateral malleolus) to the center of mass at left heel strike.

We calculated the anterior-posterior margin of stability (MoS_{AP}) as the anterior-posterior distance between the extrapolated center of mass and the left toe marker in the sagittal plane, which defined the anterior-posterior base of support (BoS_{AP}) (Fig. 2A). The anterior-posterior extrapolated center of mass ($XcoM_{AP}$) was the anterior-posterior distance between the extrapolated center of mass and the right toe marker. We calculated the medial-lateral

margin of stability (MoS_{ML}) as the medial-lateral distance between the extrapolated center of mass and the left ankle marker in the frontal plane, which defined the medial-lateral base of support (BoS_{ML}) (Fig. 2B). The medial-lateral extrapolated center of mass ($XcoM_{ML}$) was the medial-lateral distance between the extrapolated center of mass and the right ankle marker.

We quantified margin of stability and its components at different phases throughout the protocol: pre, early perturbed, late perturbed, early catch, late catch, early post, and late post. Pre referred to all strides during the first 2-minute unperturbed walking block except for the first 11 strides during which the treadmill belts were getting up to speed (Finley et al. 2013). Early perturbed and late perturbed referred to the first 3 and last 20 perturbed strides (Finley et al. 2015) during the 4-minute perturbed walking block, respectively. We included the first 3 perturbed strides to minimize the effect of catch stride, as an average of 3 perturbed strides across subjects occurred before the first catch stride. We used 20 strides for late because the behavior had plateaued and averaging over more strides would negate small fluctuations. Early post and late post also referred to the first 3 and last 20 strides during the last 2-minute unperturbed walking block, respectively. Early catch and late catch referred to the first 2 and last 2 catch strides during the 4-minute perturbed walking block, respectively.

2.3. Statistics

We performed statistical procedures using JMP (JMP Pro 12, SAS Institute Inc., Cary, NC, USA) and set the significance level to 0.05. First, we checked and excluded outliers as being beyond 3 standard deviations from the mean for each data set. We also used a Shapiro-Wilk W test and a Levene's test to check for the distribution normality and homogeneity of variance, respectively, of all variables. For the first three hypotheses related to adaptation, using a feedforward strategy, and effects of perturbation directions, we analyzed the anterior (Stick0.4), posterior (Slip0.4), medial (M1), and lateral (L1) perturbation conditions. For the fourth hypothesis related to perturbation size effect, we analyzed the data of the 2 sizes of the anterior (Stick0.4, Stick0.2) and posterior (Slip0.4, Slip0.2) perturbations.

For the first hypothesis regarding adaptation, we performed one-way repeated measures analysis of variance (rANOVA) for the perturbed strides on each metric (MoS_{AP}, MoS_{ML}, BoS_{AP}, BoS_{ML}, $XcoM_{AP}$, and $XcoM_{ML}$) with phase (pre, early perturbed, late perturbed, early post, and late post) as a factor by perturbation condition. When phase was a main effect, we performed post hoc pairwise comparisons using Tukey's Honest Significant Difference

(HSD) tests to account for multiple comparisons for the following apriori comparisons: 1) pre to early perturbed to assess the disruption of gait stability, 2) early to late perturbed to assess adaptation, 3) early to late post to assess de-adaptation. To determine which component of margin of stability contributed more to changes in margin of stability (|ΔMoS|), we compared the magnitudes of the changes of the base of support (|ΔBoS|) and extrapolated center of mass position (|ΔXcoM|) within a phase comparison (pre and early perturbed; early and late perturbed) using paired t-tests (i.e., for pre and early perturbed, $|\Delta BoS| = |BoS_{pre} - BoS_{early_perturbed}|$ versus $|\Delta XcoM| = |XcoM_{pre} - XcoM_{early_perturbed}|$; for early to late perturbed, $|\Delta BoS| = |BoS_{early_perturbed} - BoS_{late_perturbed}|$ versus $|\Delta XcoM| = |XcoM_{early_perturbed} - XcoM_{late_perturbed}|$).

For the second hypothesis regarding whether subjects used a feedforward strategy for adaptation, we performed paired t-tests between the magnitude of the deviation of early catch from the averaged pre level and the magnitude of the deviation of late catch from the averaged pre level for each metric (i.e., |ΔMoS| of pre and early catch versus |ΔMoS| of pre and late catch; |ΔBoS| of pre and early catch versus |ΔBoS| of pre and late catch; |ΔXcoM| of pre and early catch versus |ΔXcoM| of pre and late catch). If subjects were using feedforward strategies, the catch strides would deviate more from pre as adaptation progressed.

For the third hypothesis regarding perturbation direction, we also used a one-way rANOVA for each metric (ΔMoS, ΔBoS, and ΔXcoM for early perturbed minus pre; ΔMoS, ΔBoS, and ΔXcoM for late perturbed minus early perturbed) with perturbation condition as a factor. Here, the direction of the change, not just the magnitude, from pre to early and from early to late was important. We performed post hoc pairwise comparisons using Tukey's HSD if perturbation condition was a main effect.

For the fourth hypothesis regarding a scaling effect, we used a two-way rANOVA on each metric (|ΔMoS|, |ΔBoS|, and |ΔXcoM| for pre to early perturbed; |ΔMoS|, |ΔBoS|, and |ΔXcoM| for early to late perturbed) with perturbation condition (stick, slip) and size (regular, 0.4; half-size, 0.2) as factors. If a significant interaction effect was detected, we performed paired t-tests with Bonferroni correction ($\alpha = 0.025$) to identify differences between sizes for each perturbation condition.

3. Results

3.1. Representative data

Changes of MoS and its components during perturbed walking were evident throughout the gait cycle (Fig. 3). When perturbations first occurred at early perturbed, MoS, BoS, and XcoM at left heel strike all deviated from the pre unperturbed strides, indicating that the perturbations disrupted the subjects. As subjects gained more experience with the perturbations, by late perturbed, MoS at left heel strike generally trended back to pre levels, suggesting adaptation occurred. When the perturbations were removed at the post block, MoS and its components were almost the same as pre, suggesting that subjects returned to pre levels.

3.2. Adaptation to small perturbations applied on a stride-by-stride basis

In the anterior-posterior metrics, subjects were disrupted and destabilized initially and then adapted as they gained more experience with the Stick0.4, Slip0.4, and M1 perturbations (Fig. 4A). Phase had a significant effect on MoS_{AP} for all perturbation conditions (p's < 0.0001). Upon initial exposure to the perturbations, MoS_{AP} decreased significantly by at least 20.9% for all perturbation conditions (p's < 0.0004) except for the L1 perturbation (p = 0.750), indicating destabilization in the anterior-posterior direction. From early to late perturbed, MoS_{AP} increased significantly by at least 26.1% (p's < 0.0007) and trended toward pre levels, indicating adaptation of MoS_{AP} to these perturbations. From early to late perturbed, BoS_{AP} increased with the Stick0.4 and L1 perturbations (p's < 0.003), while $XcoM_{AP}$ decreased with the Slip0.4 and M1 perturbations (p's < 0.006). From early to late post, MoS_{AP} continued trending to pre levels for the Stick0.4 and Slip0.4 perturbations (p's < 0.009).

In the medial-lateral metrics, the Stick0.4, L1, and M1 perturbations were initially disruptive and destabilizing, but subjects adapted with more experience with the medial-lateral perturbations (Fig. 4B). Phase had a significant effect on MoS_{ML} for all perturbation conditions (p's < 0.0003). Upon initial exposure to the Stick0.4 and L1 perturbations, the MoS_{ML} increased significantly by at least 10.3% (p's < 0.019), whereas MoS_{ML} decreased significantly by 36.7% for the M1 perturbation (p < 0.0001), indicating disruption of gait in the medial-lateral direction. From early to late perturbed, MoS_{ML} decreased significantly by 9.9% for the L1 perturbation (p = 0.0006) and increased significantly by 18.2% for the M1 perturbation (p = 0.029), both trending toward their pre levels, indicating that subjects adapted to the medial-lateral perturbations. From early to late perturbed, the BoS_{ML} decreased for the L1 perturbation (p = 0.002), while the $XcoM_{ML}$ did not change significantly for any perturbation condition (p's > 0.176). From early to late post, MoS_{ML} did not change significantly for the medial-lateral

perturbations (p's > 0.075), suggesting that subjects rapidly restored pre levels of margin of stability preferences in the medial-lateral direction during the first few strides of post.

3.3. Which component of margin of stability was affected more by the small perturbations?

Comparing the magnitudes of the changes of BoS and XcoM during disruption (pre to early perturbed) revealed that the perturbations had different effects on the components (Fig. 5A). For the Stick0.4 perturbation, the changes in the BoS were larger than the changes in the XcoM in the anterior-posterior and medial-lateral directions ($|\Delta BoS_{AP}| > |\Delta XcoM_{AP}|$ p = 0.0007; $|\Delta BoS_{ML}| > |\Delta XcoM_{ML}|$ p = 0.014), suggesting that BoS was more disrupted. On the other hand, for the Slip0.4 and M1 perturbations, the change in XcoM was greater than the change in BoS in both directions ($|\Delta XcoM_{AP}| > |\Delta BoS_{AP}|$ p's < 0.003; $|\Delta XcoM_{ML}| > |\Delta BoS_{ML}|$ p's < 0.041), suggesting that XcoM was more disrupted for those perturbations. For the L1 perturbation, there was no difference between the changes in BoS and XcoM in either direction (AP p = 0.272; ML p = 0.414).

3.4 Which component contributed more to the adaptation of margin of stability?

Comparing the magnitudes of the changes of the MoS components during adaptation (early to late perturbed) showed that the component that was the primary contributor to the MoS adaptation varied depending on the perturbation (Fig. 5B). The $|\Delta BoS_{AP}|$ was larger than the $|\Delta XcoM_{AP}|$ for the L1 perturbation (p = 0.007) but was not statistically significant for the Stick0.4 perturbation (p = 0.082). The $|\Delta XcoM_{AP}|$ was greater than the $|\Delta BoS_{AP}|$ (p's < 0.013) for the Slip0.4 and M1 perturbations, suggesting that $XcoM_{AP}$ adapted more during those perturbations. For the medial-lateral metrics, the only significant difference was the larger $|\Delta BoS_{ML}|$ compared to the $|\Delta XcoM_{ML}|$ for the L1 perturbation (p = 0.006), suggesting that BoS_{ML} adapted more in the lateral shift perturbation. There were no significant differences between the $|\Delta BoS_{ML}|$ and $|\Delta XcoM_{ML}|$ in the other perturbations (p's > 0.634).

3.5 Do subjects use more feedforward strategies when adapting to small perturbations applied on a stride-by-stride basis?

Subjects did not use more feedforward strategies based on the responses to the catches (Fig. 6). In the Stick0.4, Slip0.4, and L1 perturbations, the deviation of MoS_{AP} was smaller at late catch compared with early catch (Stick0.4 p = 0.027, Slip0.4 p = 0.053, L1 p = 0.046, Fig. 6A). Despite the presence of differences in the MoS_{AP}, there were

no significant differences between the deviation from pre at early catch compared to late catch in the BoS_{AP} for all perturbation conditions (p's > 0.240) and in the $XcoM_{AP}$ (p's > 0.184) except for the M1 perturbation (p = 0.029) (Fig. 6A). The anterior-posterior metrics did not deviate more from the pre levels as adaptation progressed, which suggests that subjects were reacting more compared to using feedforward strategies in the anterior-posterior direction in general. For the medial-lateral metrics, there were no differences in the MoS_{ML} (p's > 0.073, Fig. 6B). Despite the lack of differences in MoS_{ML}, the deviations of BoS_{ML} and $XcoM_{ML}$ were significantly smaller at late catch compared with early catch in the Stick0.4 and Slip0.4 perturbations (p's < 0.047). Additionally, the $XcoM_{ML}$ was significantly smaller at late catch compared with early catch in the L1 perturbation (p = 0.013). Similar to the anterior-posterior metrics, the medial-lateral metrics did not deviate more from pre levels as adaptation progressed, suggesting that subjects were also reacting in the medial-lateral direction in general.

3.6 Are margin of stability and its components sensitive to directions of small perturbations?

Anterior-posterior metrics were more sensitive to the anterior-posterior perturbations when subjects were disrupted at early perturbed but not during adaptation from early to late perturbed (Fig. 7A). During disruption (pre to early perturbed), perturbation direction had a significant effect on each anterior-posterior metric (p's < 0.0007). All perturbations produced a decrease in MoS_{AP}, during disruption of which, the decreases for the Stick0.4 and Slip0.4 perturbations were significantly larger than the decrease for the L1 perturbation (p's < 0.027). At early perturbed, the BoS_{AP} and $XcoM_{AP}$ had the largest decrease with the Stick0.4 perturbation compared to the decrease with the L1 perturbation (p's < 0.014). On the other hand, the BoS_{AP} and $XcoM_{AP}$ had the largest increase with the Slip0.4 perturbation compared to the increase with the M1 perturbation at early perturbed (p's < 0.0001). During adaptation (early to late perturbed), all perturbations resulted in an increased MoS_{AP} of similar magnitude (p = 0.283). Conversely, perturbation direction had a significant effect on ΔBoS_{AP} and $\Delta XcoM_{AP}$ during adaptation (p's < 0.002), mainly due to differences in sign. The Stick0.4 and L1 perturbations generally resulted in increases of BoS_{AP} and $XcoM_{AP}$, whereas the Slip0.4 and M1 perturbations resulted in decreases of BoS_{AP} and $XcoM_{AP}$ during adaptation.

The medial-lateral metrics, MoS_{ML} and $XcoM_{ML}$, were more sensitive to the medial-lateral perturbations when subjects were disrupted but not during adaptation (Fig. 7B). During disruption (pre to early perturbed), perturbation direction had a significant effect on each medial-lateral metric (p's < 0.006). At early perturbed, the MoS_{ML} had the

largest increase with the L1 perturbation compared to the increase with the Stick0.4 perturbation ($p < 0.0001$), while the MoS_{ML} had the largest decrease with the M1 perturbation compared to the decrease with the Slip0.4 perturbation ($p < 0.0001$). All perturbations produced an increase in BoS_{ML}, during disruption of which, the increase for the M1 perturbation was significantly smaller than the increases for the Slip0.4 and L1 perturbations (p's < 0.020). For the $XcoM_{ML}$ at early perturbed, the increase of $XcoM_{ML}$ in the M1 perturbation was significantly larger than the increase in the Stick0.4 perturbation ($p < 0.0001$), while the decrease of $XcoM_{ML}$ in the L1 perturbation was significantly different than the increases in the Stick0.4 and Slip0.4 perturbations (p's < 0.0001). During adaptation (early to late perturbed), perturbation direction had a significant effect on ΔMoS_{ML} ($p = 0.0002$), largely due to differences in sign. The L1 perturbation resulted in the only decrease of MoS_{ML} whereas all other perturbations resulted in increases of MoS_{ML} during adaptation. For $BoS_{ML}$and $XcoM_{ML}$, nearly all perturbations resulted in a decrease of similar magnitudes during adaptation (p's > 0.168).

3.7 Do responses in margin of stability and its components scale with perturbation size?

Anterior-posterior and medial-lateral metrics both scaled with perturbation size when subjects were disrupted at early perturbed but not during adaptation from early to late perturbed (Fig. 8). Perturbation size had a main effect on the changes during disruption (pre to early perturbed) for each anterior-posterior metric (p's < 0.005, Fig. 8A) and for BoS_{ML} and $XcoM_{ML}$ (p's < 0.031, Fig. 8B). There was a significant interaction effect between perturbation size and perturbation condition for the changes in BoS_{AP} during disruption ($p = 0.026$). Paired t-tests revealed that the half-size perturbations produced significantly smaller magnitude changes in BoS_{AP} than the regular perturbations within each perturbation condition (Stick0.2 vs. Stick0.4 $p = 0.0006$, Slip0.2 vs. Slip0.4 $p = 0.011$, Fig. 8A). These results suggest that subjects scaled BoS_{AP} more in the stick perturbations than slip perturbations at early perturbed. For the changes of each metric during adaptation (early to late perturbed), there was neither a main effect of perturbation size nor a significant interaction effect (p's > 0.150), indicating that all (both anterior-posterior and medial-lateral) metrics did not scale with perturbation size during adaptation.

4. Discussion

We sought to determine how small magnitude multidirectional perturbations affect modulation of margin of stability, base of support, and extrapolated center of mass on a stride-by-stride basis. In the anterior-posterior

direction, subjects primarily modulated BoS_{AP} when adapting MoS_{AP} to the belt deceleration perturbation (Stick0.4), whereas subjects mainly modulated $XcoM_{AP}$ when adapting MoS_{AP} to the belt acceleration (Slip0.4) and medial shift (M1) perturbations. In the medial-lateral direction, subjects primarily modulated BoS_{ML} when adapting MoS_{ML} to the lateral shift (L1) perturbation. Despite the frequent exposure to the perturbations, subjects did not use more feedforward strategies during adaptation. When first experiencing the perturbations at early perturbed, anterior-posterior metrics were more sensitive to perturbations in the coincident anterior-posterior direction, and likewise, MoS_{ML} and $XcoM_{ML}$ were more sensitive to perturbations in the coincident medial-lateral direction. Additionally, all metrics except for MoS_{ML} scaled with perturbation size upon initially responding to the perturbations (at disruption). These findings suggest that applying small perturbations on a stride-by-stride basis led to the adaptation of the margin of stability, providing new insights regarding the extent of locomotor adaptation to small perturbations. Further, perturbation directions could be used to target specific aspects of gait stability control (e.g., primarily modulating base of support or center of mass).

One of the main findings was that small magnitude perturbations altered gait stability, i.e., the margin of stability, in specific directions. For most perturbations, the MoS_{AP} and MoS_{ML} initially decreased before adapting back to pre levels (Fig. 4), suggesting that subjects were destabilized initially before gradually regaining stability during the Stick0.4, Slip0.4, and M1 perturbations. These results are consistent with previous studies that showed that treadmill belt and shift perturbations decreased MoS_{AP} (Debelle et al. 2020; McAndrew Young et al. 2012; McCrum et al. 2018). Adjusting foot placement and BoS is a common approach to modulate MoS (Hof et al. 2010; Süptitz et al. 2013), which was evident in our Stick0.4 perturbation. Other studies demonstrated the importance of center of mass control to modulate MoS (Debelle et al. 2020; McCrum et al. 2019), which was evident in the Slip0.4 and M1 perturbations. MoS did not always decrease in response to perturbations. For the Stick0.4 and L1 perturbation, the MoS_{ML} initially increased, however, instead of decreasing as seen in the other perturbations. This increased MoS_{ML} likely resulted from a combination of a more lateral (leftward) foot placement (i.e., increased BoS_{ML}) and redirected XcoM rightward during the lateral shift perturbation. In another study that applied lateral shift perturbations at early single leg support, people used the gluteus medius of their swing leg to place their subsequent foot more outward (Afschrift et al. 2018) in the direction of the potential fall (Reimann et al. 2018; Wang and Srinivasan 2014), which would help increase the MoS to maintain a more stable body position (Hof et al. 2005). Larger MoS often occurs in response to medial-lateral treadmill shift perturbations (Hak et al. 2012;

McAndrew Young et al. 2012; Onushko et al. 2019), similar to the increased MoS_{ML} in our L1 perturbation. Interestingly, subjects maintained this increased MoS_{ML} for the Stick0.4 perturbation but gradually reduced the MoS_{ML} for the L1 perturbation, suggesting that subjects either could not or did not have a reason to decrease MoS_{ML} while gaining more experience with the Stick0.4 perturbation.

In our study, subjects primarily modulated foot placement compared to the extrapolated center of mass in the belt deceleration and lateral shift perturbations. Researchers are increasingly finding that BoS control is an active neuromechanical balance strategy that is adjusted based on the state of the center of mass during walking (van Leeuwen et al. 2020; O'Connor and Kuo 2009; Reimold et al. 2020; Wang and Srinivasan 2014). Additionally, the central nervous system is actively involved in this foot placement strategy (Bruijn et al. 2015; Sipp et al. 2013). In our study, both the BoS_{AP} and $XcoM_{AP}$ decreased in response to the Stick0.4 perturbation, but subjects primarily adjusted BoS_{AP} by taking shorter steps while adapting to the Stick0.4 perturbation. The reduction and smaller adjustment of $XcoM_{AP}$ compared to the BoS_{AP} was likely a consequence of the rotation and acceleration of the upper body backward relative to the lower body created by the stick perturbations. The significant BoS_{AP} adjustment was likely needed to rapidly interrupt the forward progression of the swing leg to compensate for the interrupted progression of the stance leg caused by the Stick0.4 perturbation (Martelli et al. 2017a). These reactions conform to the theory of stepping in the direction of the potential fall and to the maintenance of forward progression on the treadmill (Reimann et al. 2018; Wang and Srinivasan 2014; Winter 1995). For the lateral shift perturbation, subjects appeared to employ combination of a foot placement strategy through swing leg control that increased the BoS_{ML} (Afschrift et al. 2018), while also using an ankle strategy with the stance leg that decreased $XcoM_{ML}$ by a similar magnitude (Afschrift et al. 2019). Changes in the BoS_{ML} then dominated during adaptation to the L1 perturbation. This aligns with the predominant stepping strategy people often employ, taking shorter and wider steps during medial waist-pull perturbations that produced relative movements of the BoS and XcoM similar to our L1 perturbation (Matjačić et al. 2019).

Our results also showed that subjects primarily modulated the extrapolated center of mass in the belt acceleration and medial shift perturbations. Both the BoS_{AP} and $XcoM_{AP}$ increased in response to our Slip0.4 perturbation, but subjects mainly modulated their $XcoM_{AP}$ while adapting to the Slip0.4 perturbation. The $XcoM_{AP}$ responses were likely related to the decreased hip flexor moment of the right stance leg to reduce the forward

rotation and acceleration of the upper body (Debelle et al. 2020). Even though the BoS_{AP} also changed during adaptation, these changes were smaller than the $XCoM_{AP}$ and were probably a consequence of the facilitated forward swing phase induced by the Slip0.4 perturbation. For the medial shift perturbation, subjects primarily adjusted XcoM, interestingly, in the orthogonal anterior-posterior direction, likely by employing an ankle strategy (Reimann et al. 2018) that incorporated increased tibialis anterior activity of the stance leg (Afschrift et al. 2019). Subjects barely adjusted the BoS_{AP}, likely due to the small magnitude of our M1 perturbation. In other medial-lateral perturbations, subjects often take crossover steps to adjust BoS in the anterior-posterior direction. (Borrelli et al. 2019; Major et al. 2018).

Subjects did not use more feedforward strategies when adapting to small magnitude perturbations applied on a stride-by-stride basis. In response to repeated perturbations, people adapt using feedback (reactive) and feedforward (proactive) control (Bohm et al. 2015; Kuo 2002). Feedback control relies on sensory detection of unexpected disturbances to dynamic stability, whereas feedforward control relies on knowledge about the expected perturbation generated by prior experience (Major et al. 2018; Patla 2003). In our study, subjects apparently used feedback control in response to the treadmill belt and shift perturbations as MoS and its components did not deviate more from the pre levels with more experience with catch strides. Despite the stride-by-stride exposure to the perturbations, subjects did not appear to develop anticipatory responses. The small perturbations in our study likely contributed to the use of feedback control, as mild medial-lateral perturbations reduce feedforward control and facilitate feedback control in the medial-lateral direction (Wu et al. 2017). Additionally, the repetitive fixed magnitude treadmill belt perturbations also likely contributed to the use of feedback control. Unlike overground walking where subjects can control the displacement of their stance foot and the magnitude of a slip perturbation which allows for more proactive responses (Bhatt et al. 2006), subjects are unable to control the displacement of their stance foot during treadmill belt perturbations, resulting in reactive compensatory step lengths and trunk angles responses (Lee et al. 2016).

Perturbations in the coincident direction more strongly affected gait stability after being initially perturbed. As one might expect, the anterior-posterior and medial-lateral perturbations resulted in a stronger effect in their respective directions (Madehkhaksar et al. 2018; Vlutters et al. 2018). In our study, this directional effect was not merely seen in the MoS but was also reflected in its components. Despite the small magnitude, our perturbations

also affected metrics in perpendicular directions, though not as strongly as perturbations in coincident directions. Perturbations in one direction often elicit responses perpendicular to the perturbation direction (Madehkhaksar et al. 2018; Martelli et al. 2016; O'Connor and Kuo 2009; Vlutters et al. 2018) as responses between the sagittal and frontal planes are dynamically coupled (Bauby and Kuo 2000; Buurke et al. 2020). Medial-lateral perturbations are often more challenging than the anterior-posterior perturbations (Madehkhaksar et al. 2018; McIntosh et al. 2017) because medial-lateral balance requires active control during walking (Rankin et al. 2014; Reimold et al. 2020). In our study, medial-lateral perturbations were not more challenging than the anterior-posterior perturbations, which could be related to the magnitude of the shifts. We used 1 cm medial-lateral shift perturbations as opposed to the 12-15 cm shifts that were used in other studies (Madehkhaksar et al. 2018; McIntosh et al. 2017). This suggests that there is a threshold, a medial-lateral shift > 1 cm that is needed to elicit a significant effect on gait stability compared to small anterior-posterior perturbations. We chose relatively small perturbation magnitudes to avoid falls and extra recovery steps as we applied the perturbations on a stride-by-stride basis.

As expected, there was a scaling effect of perturbation magnitude on most of our metrics as people tend to magnify their responses proportionally with perturbation size (Martelli et al. 2016, 2017a; Vlutters et al. 2018). Interestingly, changes in MoS_{ML} were similar between the two treadmill belt perturbations sizes. In our study, the MoS_{ML} did not respond strongly to the anterior-posterior perturbations (Stick0.4 and Slip0.4) so an even smaller half-sized perturbation (Stick0.2 and Slip0.2) would not be likely to elicit a strong response. Based on the interaction effect for BoS_{AP} observed in our anterior-posterior perturbations (Fig. 8A), we found that the stick perturbations had a stronger scaling effect than slip perturbations for the same increment (from 0.2 to 0.4). Backward instability created by belt decelerations (stick perturbations) tend to be more challenging than forward instability created by the belt accelerations (slip perturbations) (Patel and Bhatt 2018; Roeles et al. 2018).

The present study had several limitations. First, the perturbation did not always return to the neutral position or baseline speed before the left heel strike, which likely introduced tiny but extra disturbances. The treadmill system also has a fixed acceleration value for shifting the treadmill platform medial-laterally, which limited the size of the shift perturbation we could use to ≤ 1 cm for our desired time window such that the treadmill could return to its neutral position at or near left heel strike. To control for the time of the perturbation, we set the duration of the anterior-posterior perturbations to be similar to the medial-lateral perturbations, which again limited the magnitude

of the perturbation we could apply. We only applied perturbations to the right leg because to limit the experiment to ~1 hour. We would not have expected a difference between perturbing the left or right stepping limbs during walking or in forward falls (Madigan and Lloyd 2005; Süptitz et al. 2012). Last, we only applied perturbations at one instance of the gait cycle, right leg mid-stance. A recent study applied brief treadmill belt accelerations at push off of each foot on a stride-by-stride basis and that led to sustained increased push-off once the perturbations were removed (Farrens et al. 2020). Applying perturbations at different points of the gait cycle may reveal phase-dependent modulation of margin of stability and its components.

Future directions include studies to determine the muscular and cortical mechanisms involved during adaptation of gait stability in response to small magnitude perturbations during walking. We recently found significant differences in electrocortical activity of the anterior cingulate and motor cortices in response to small magnitude mechanical perturbations applied on a stride-by-stride basis during recumbent stepping using electroencephalography (EEG) and source estimation (Shirazi and Huang 2021). Recording EEG and performing source estimation for subjects experiencing small magnitude perturbations on a stride-by-stride basis during walking may reveal specific cortical networks for modulating foot placement versus center of mass when adapting to perturbations during walking. Currently, EEG gait adaptation studies often use large infrequent perturbations during walking (Peterson and Ferris 2019; Wagner et al. 2016).

5. Conclusions

We investigated how healthy young individuals adjusted their margin of stability, base of support, and extrapolated center of mass in response to small magnitude multidirectional perturbations applied on a stride-by-stride basis. Small magnitude perturbations disrupted gait stability by decreasing the MoS in the belt deceleration (Stick0.4), belt acceleration (Slip0.4), and medial treadmill shift (M1) perturbations, while increasing the MoS in the lateral treadmill shift (L1) perturbation. During adaption, BoS (foot placement) control was primarily used in the Stick0.4 and L1 perturbations, whereas XcoM control was preferred in the Slip0.4 and M1 perturbations. Subjects also primarily used feedback instead of feedforward strategies when adjusting their BoS and XcoM. Moreover, MoS and its components were generally more sensitive to perturbations in the coincident direction and scaled with perturbation size upon initial exposure to the perturbations. Overall, our findings provide insights into inter-stride gait stability and adaptability to small magnitude perturbations experienced on a stride-by-stride basis

and have implications for the development of training interventions that could target specific components of gait stability (e.g., base of support or extrapolated center of mass control) for balance-impaired populations.

ACKNOWLEDGMENTS

The authors thank Alejandro Hurtado, Kevin Graydon, Amy Lebanoff, and Allen Rahrooh for assistance with data collection.

GRANTS

This study was funded by the National Institute on Aging of the National Institutes of Health (NIH), under award number R01AG054621 to H.J.H and a University of Central Florida Office of Research In-House Grant to H.J.H.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

J.L. and H.J.H. conceived and designed research; J.L. performed experiments; J.L. analyzed data; J.L. and H.J.H. interpreted results of experiments; J.L. prepared figures; J.L. drafted manuscript; J.L. and H.J.H. edited and revised manuscript; J.L. and H.J.H. approved final version of manuscript.

ENDNOTE

At the request of the authors, readers are herein alerted to the fact that additional materials related to this manuscript may be found at https://doi.org/10.6084/m9.figshare.c.5285258.v3. These materials are not a part of this manuscript and have not undergone peer review by the American Physiological Society (APS). APS and the journal editors take no responsibility for these materials, for the website address, or for any links to or from it.

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Figure Captions

Fig. 1. Schematic of the perturbations and experimental protocol. **(A)** Perturbation onset occurred at right leg mid-stance (black leg in red outline). There were 4 perturbation directions, and 2 sizes for the anterior-posterior perturbations, for a total of six perturbation conditions. The red arrows are the initial relative surface displacements, and the faded red arrows are the displacements to return to the unperturbed state. **(B)** The left belt speed was fixed at 1.0 m/s (blue dashed line). For the Stick0.2 and Stick0.4 perturbations, the right belt speed (red) decelerated to 0.8 m/s and 0.6 m/s, respectively, and then returned to the tied belt speed. For the Slip0.2 and Slip0.4 perturbations, the right belt speed accelerated to 1.2 m/s and 1.4 m/s, respectively, and then returned to the belt speed. For the L1 and M1 perturbations, the treadmill shifted 1 cm laterally and medially, respectively, and then returned to neutral. The perturbations were ~400 ms in duration. Gait events: right heel strike (RHS), left toe off (LTO), left heel strike (LHS), and right toe off (RTO). **(C)** Blocks of the experimental protocol. Each trial started with a 2-minute unperturbed walking block (pre), followed by a 4-minute perturbed walking block (perturbed), and completed with another 2-minute unperturbed walking block (post). An unperturbed catch stride occurred randomly 1 out of every 5 strides during the perturbed walking block.

Fig. 2. Anterior-posterior and medial-lateral metrics of gait stability at left heel strike. **(A)** The anterior-posterior base of support (BoS_{AP}, orange arrow) was the anterior-posterior distance of the left toe marker relative to the right toe marker. The anterior-posterior extrapolated center of mass ($XcoM_{AP}$, green arrow) was the anterior-posterior distance of XcoM relative to the right toe marker. The anterior-posterior margin of stability (MoS_{AP}, pink arrow) was the BoS_{AP} - $XcoM_{AP}$. **(B)** The medial-lateral base of support (BoS_{ML}) was the medial-lateral distance of the left ankle marker relative to the right ankle marker. The medial-lateral extrapolated center of mass ($XcoM_{ML}$) was the medial-lateral distance of XcoM relative to the right ankle marker. The medial-lateral margin of stability (MoS_{ML}) was the BoS_{ML} - $XcoM_{ML}$.

Fig. 3. Trajectories of the gait stability metrics (MoS, pink; BoS, orange, and XcoM, green) for specific strides of a representative subject for the Stick0.4, Slip0.4, L1, and M1 perturbations (black dotted line: the 2nd to last stride of pre; colored solid line: the 2nd stride of early perturbed; lighted colored line: the 2nd to last stride of late perturbed; and black dashed line: the 2nd to last stride of post). The anterior-posterior MoS, BoS, and XcoM of the Stick0.4 and Slip0.4 perturbations, and medial-lateral MoS, BoS, and XcoM of the L1 and M1 perturbations at left heel strike deviated from pre at early perturbed, then trended back toward the pre trajectory by late perturbed and returned to the pre trajectory by post, shown in the exploded view in the inset circles. Gait events: right heel strike (RHS), left toe off (LTO), left heel strike (LHS), and right toe off (RTO). During single support (between LHS and LTO, RTO and RHS), we used the projection distance of the left toe/heel marker relative to the corresponding markers on the right foot to represent BoS values for a continuous trajectory and the thin faded lines are the corresponding MoS, BoS, and XcoM.

Fig. 4. Group-averaged (n = 10) MoS (pink), BoS (orange), and XcoM (green) batched time courses for the experimental protocol (pre, perturbed, and post) and the mean and standard deviation (thick horizontal lines and one-sided error bar) at pre, early perturbed, late perturbed, early post, and late post for each perturbation, Stick0.4, Slip0.4, L1, and M1 (rows top to bottom). In the batch plots, the thick line is the mean and shaded areas are +/- standard deviation. Circles are individual subjects. **(A)** Anterior-posterior metrics show that subjects were destabilized at early perturbed then adapted by late perturbed during the Stick0.4, Slip0.4, and M1 perturbations. **(B)** Medial-lateral metrics show that subjects were destabilized and adapted during the medial-lateral (L1 and M1) perturbations. *: $p < 0.05$ and color coded for the specific metrics with the significant differences between phases indicated by the brackets.

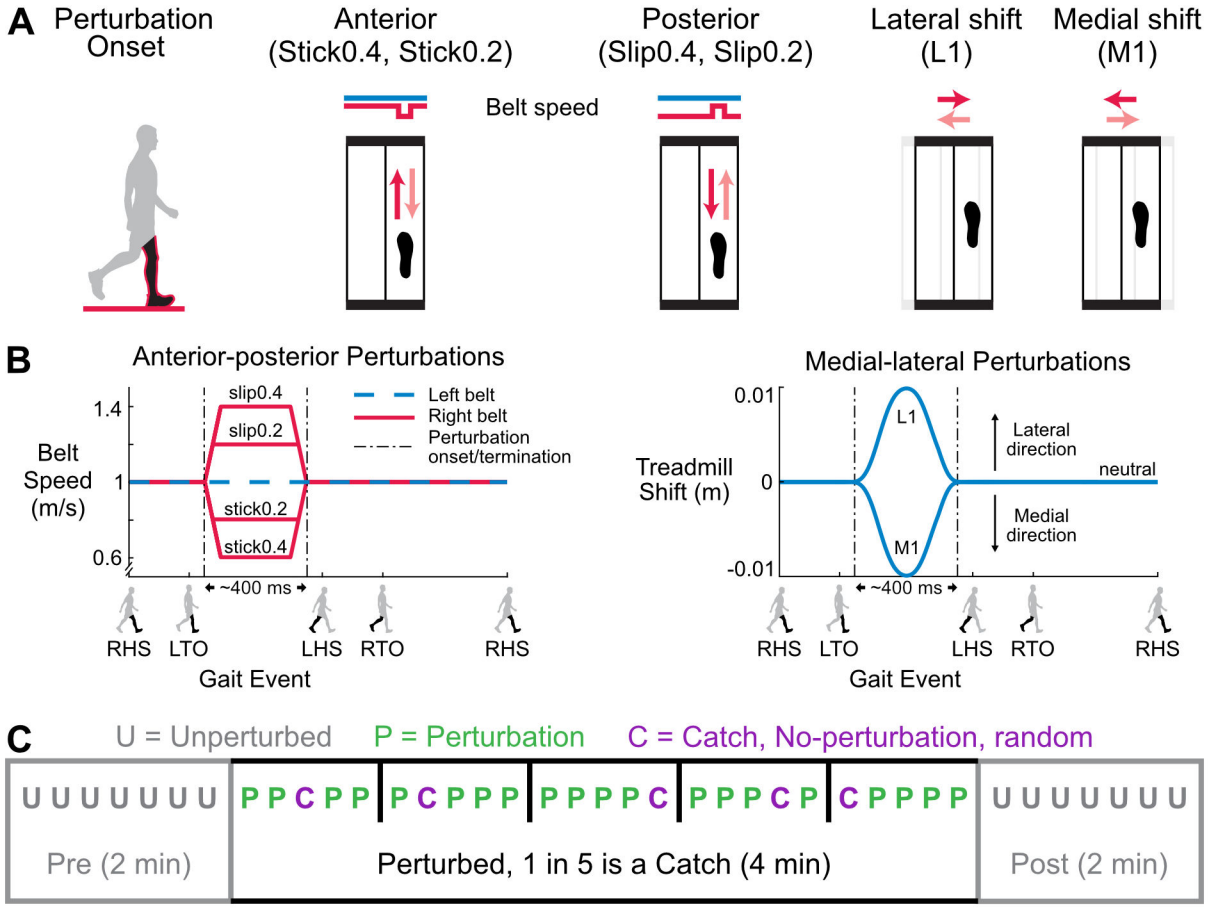
Fig. 5. Group-averaged (mean and standard deviation, n = 10) |ΔBoS| (orange) compared with |ΔXcoM| (green) during disruption (pre to early perturbed) and adaptation (early to late perturbed). Gray lines between bars are individual subjects where solid lines indicate significant changes and dashed lines indicate nonsignificant changes of the corresponding MoS. **(A)** During disruption, BoS was disrupted more by the Stick0.4 perturbation, XcoM was disrupted more by the Slip0.4 and M1 perturbations. **(B)** During adaptation, BoS_{AP} adapted more in the Stick0.4 and L1 perturbations, $XcoM_{AP}$ adapted more in the Slip0.4 and M1 perturbations, BoS_{ML} adapted more in the L1 perturbation. *: $p < 0.05$ and significant differences between |ΔBoS| and |ΔXcoM|.

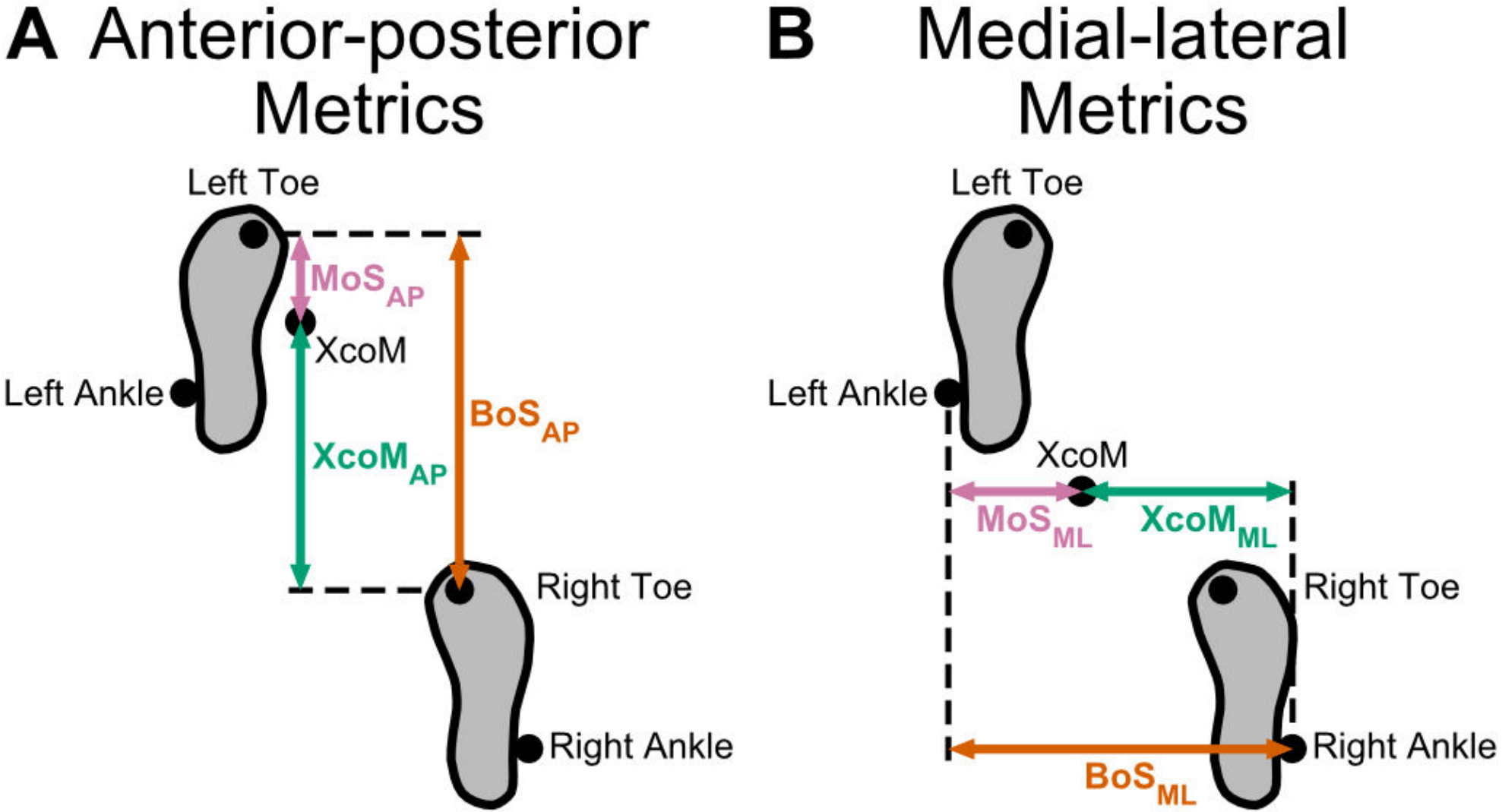
Fig. 6. Group-averaged (n = 10) MoS (pink), BoS (orange), and XcoM (green) batched time courses for the catch strides during minutes 2-6 and the group-averaged deviation from the averaged pre level at early catch (dark bars) compared with late catch (light bars) for each metric (mean and standard deviation). In the batch plot, colored horizontal lines indicate the averaged pre levels. In the bar plots, the colored lines between bars are individual subjects. **(A)** Anterior-posterior metrics and **(B)** Medial-lateral metrics did not deviate more from the pre levels with the progression of the catch strides, indicating that subjects did not use more feedforward strategies as adaptation progressed. *: $p < 0.05$ and color coded for the specific metrics with the significant differences between two deviations indicated by the brackets.

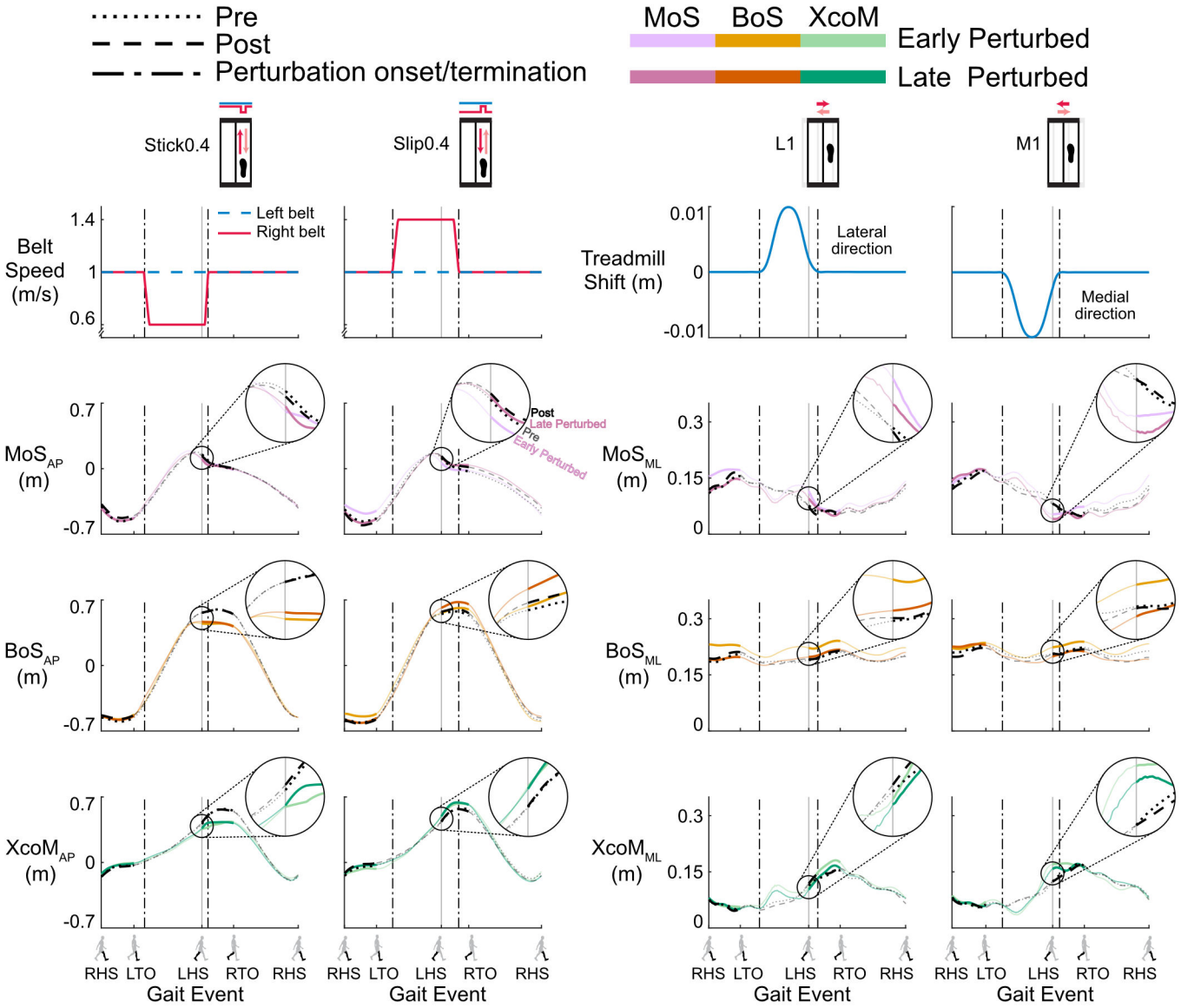
Fig. 7. Group-averaged (mean and standard deviation, n = 10) ΔMoS (pink), ΔBoS (orange), ΔXcoM (green) during disruption (early perturbed minus pre) and adaptation (late minus early perturbed) for the Stick0.4 (black outline), Slip0.4 (gray outline), L1 (white fill), and M1 (gray fill) perturbations. Circles are individual subjects. **(A)** Anterior-posterior metrics were more sensitive to the anterior-posterior perturbations during disruption but not adaptation. **(B)** MoS_{ML} and $XcoM_{ML}$ were more sensitive to the medial-lateral perturbations during disruption but not adaptation. * with thick brackets: $p < 0.05$ and significant same signed differences between two perturbation conditions, * with thin brackets: $p < 0.05$ and significant opposite signed differences between two perturbation conditions.

Fig. 8. Group-averaged (mean and standard deviation, n = 10) |ΔMoS| (pink), |ΔBoS| (orange), |ΔXcoM| (green) during disruption (pre to early perturbed) and adaptation (early to late perturbed) for the anterior-posterior perturbations. Dark bars indicate the

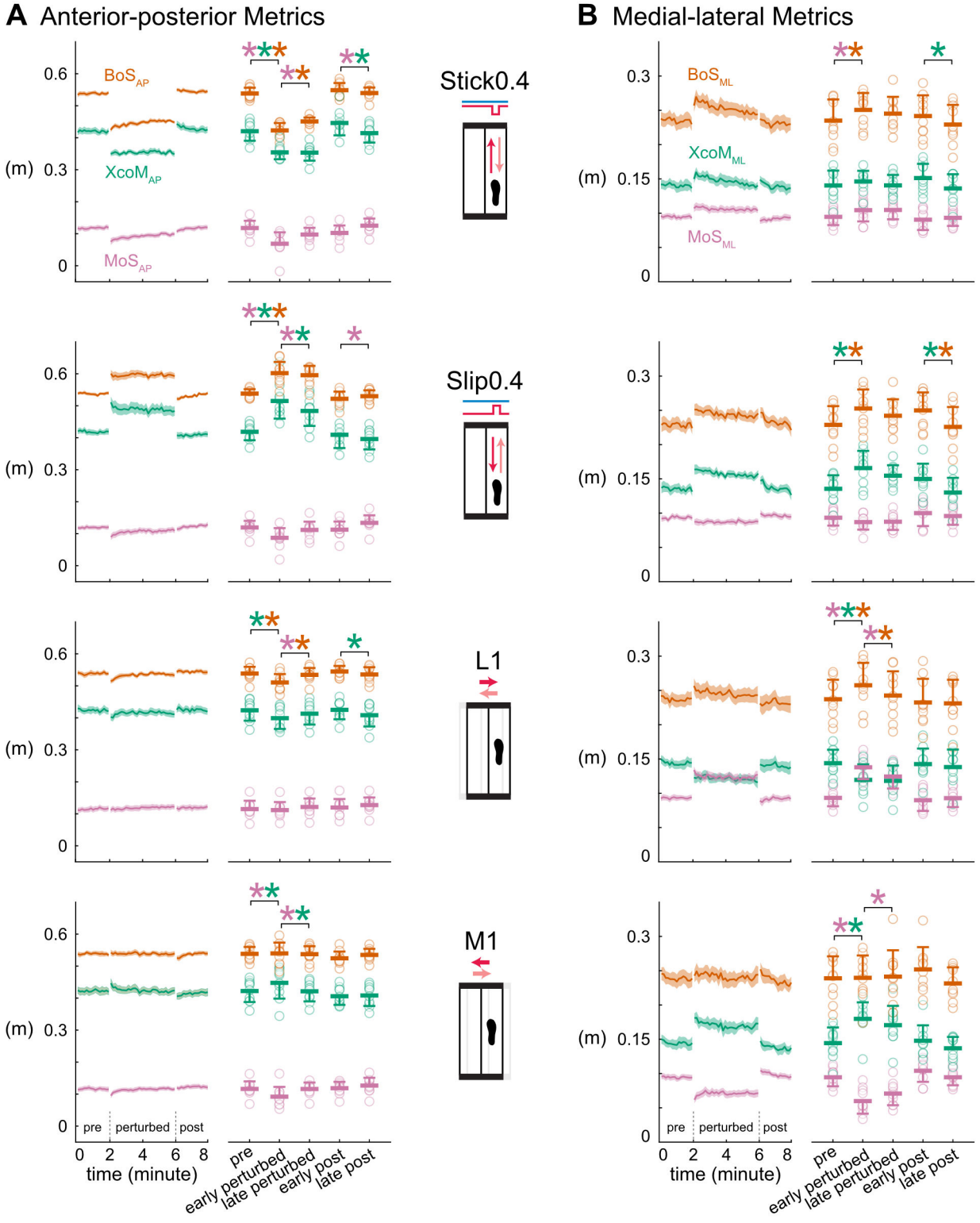
regular size perturbations (Stick0.4 and Slip 0.4) and light bars indicate the half-size perturbations (Stick0.2 and Slip 0.2). Colored lines between bars are individual subjects. **(A)** Anterior-posterior metrics scaled with perturbation size during disruption but not adaptation. **(B)** BoS_{ML} and $XcoM_{ML}$ scaled with perturbation size during disruption but not adaptation. +: $p < 0.05$, perturbation size effect (perturbation condition effect was not reported). #: $p < 0.05$, interaction effect between perturbation size (regular, 0.4; half-size, 0.2) and perturbation condition (stick, slip). *: $p < 0.025$, significant differences between the regular and half-size perturbations of same condition.

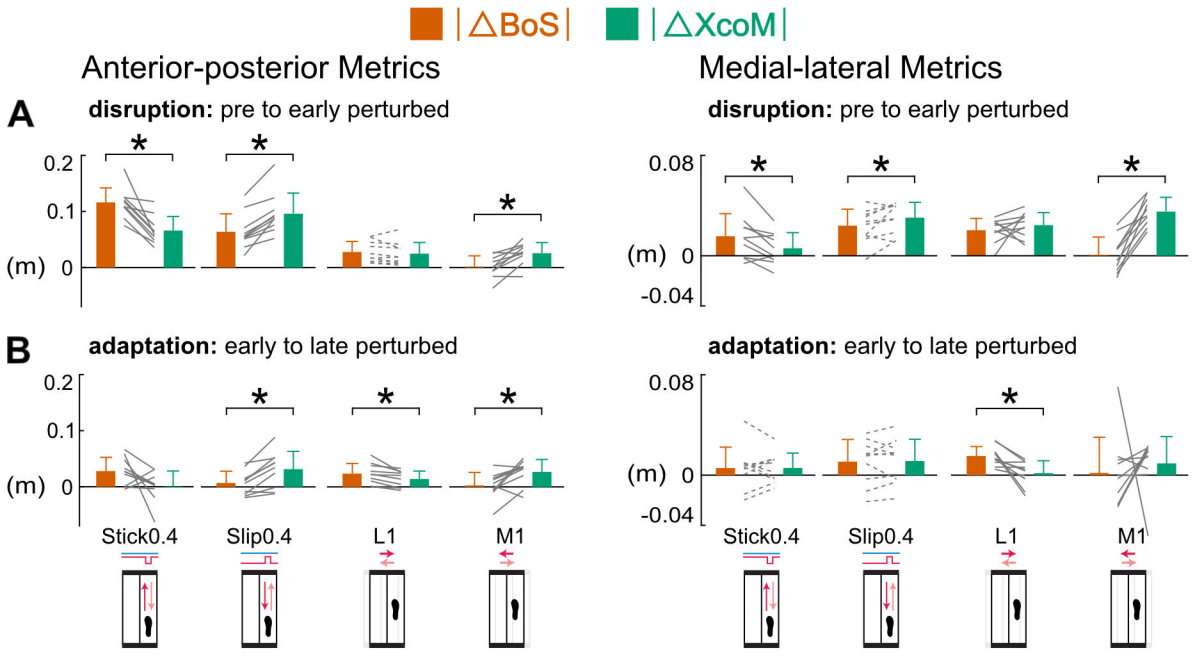

A
Perturbation Onset
Anterior (Stick0.4, Stick0.2)
Posterior (Slip0.4, Slip0.2)
Lateral shift (L1)
Medial shift (M1)
Belt speed
B
Anterior-posterior Perturbations
Belt Speed (m/s)
1.4
1
0.6
slip0.4
slip0.2
stick0.2
stick0.4
Left belt
Right belt
Perturbation onset/termination
~400 ms
RHS
LTO
LHS
RTO
RHS
Gait Event
Medial-lateral Perturbations
Treadmill Shift (m)
0.01
0
-0.01
L1
M1
Lateral direction
neutral
Medial direction
~400 ms
RHS
LTO
LHS
RTO
RHS
Gait Event
C
U = Unperturbed
P = Perturbation
C = Catch, No-perturbation, random
U U U U U U U
Pre (2 min)
P P C P P
P C P P P
P P P P C
P P P C P
C P P P P
Perturbed, 1 in 5 is a Catch (4 min)
U U U U U U U
Post (2 min)

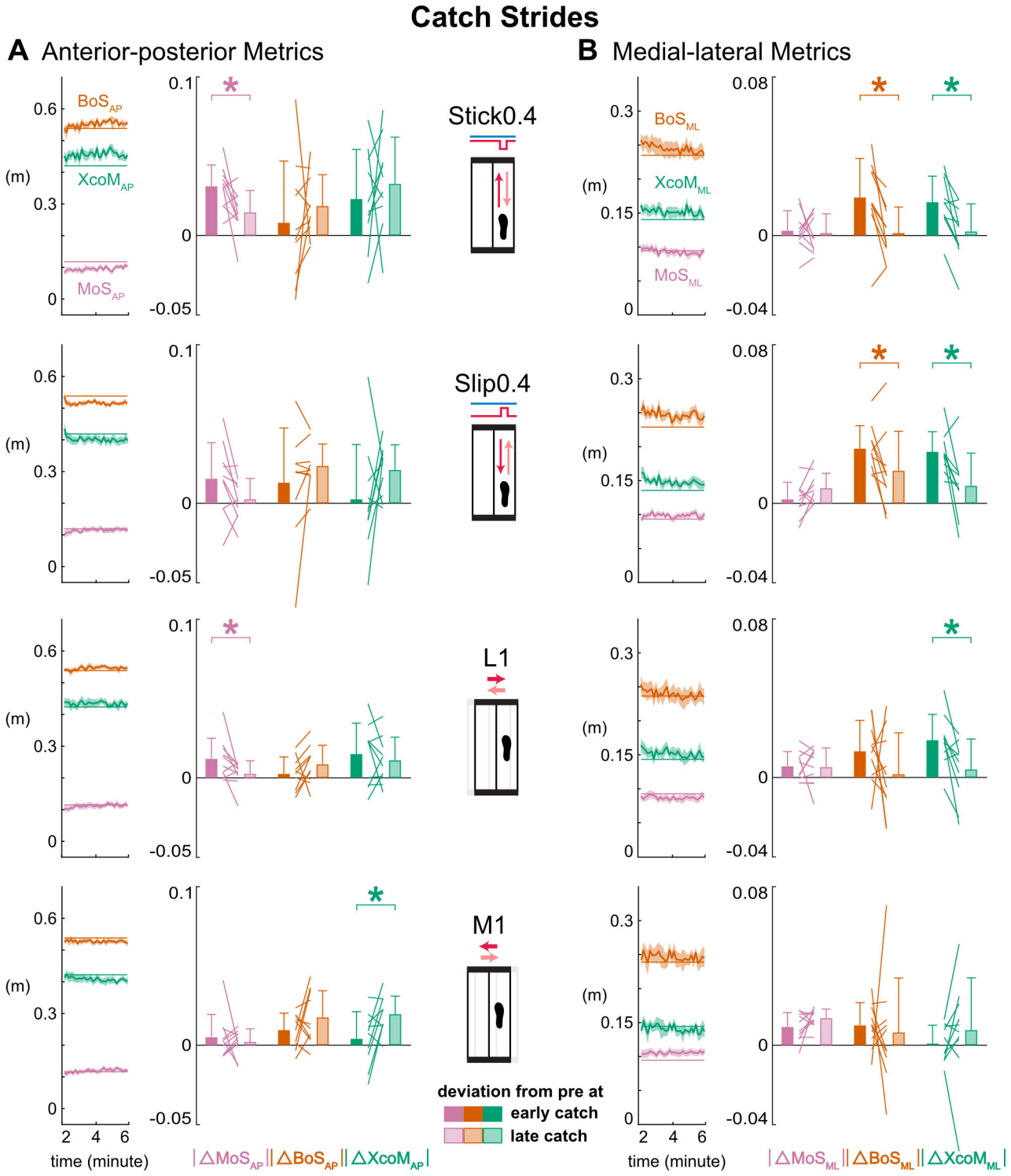

A Anterior-posterior Metrics
Left Toe
MoS AP
XcoM
Left Ankle
BoS AP
XcoM AP
Right Toe
Right Ankle
B Medial-lateral Metrics
Left Toe
Left Ankle
XcoM
MoS ML
XcoM ML
Right Toe
Right Ankle
BoS ML

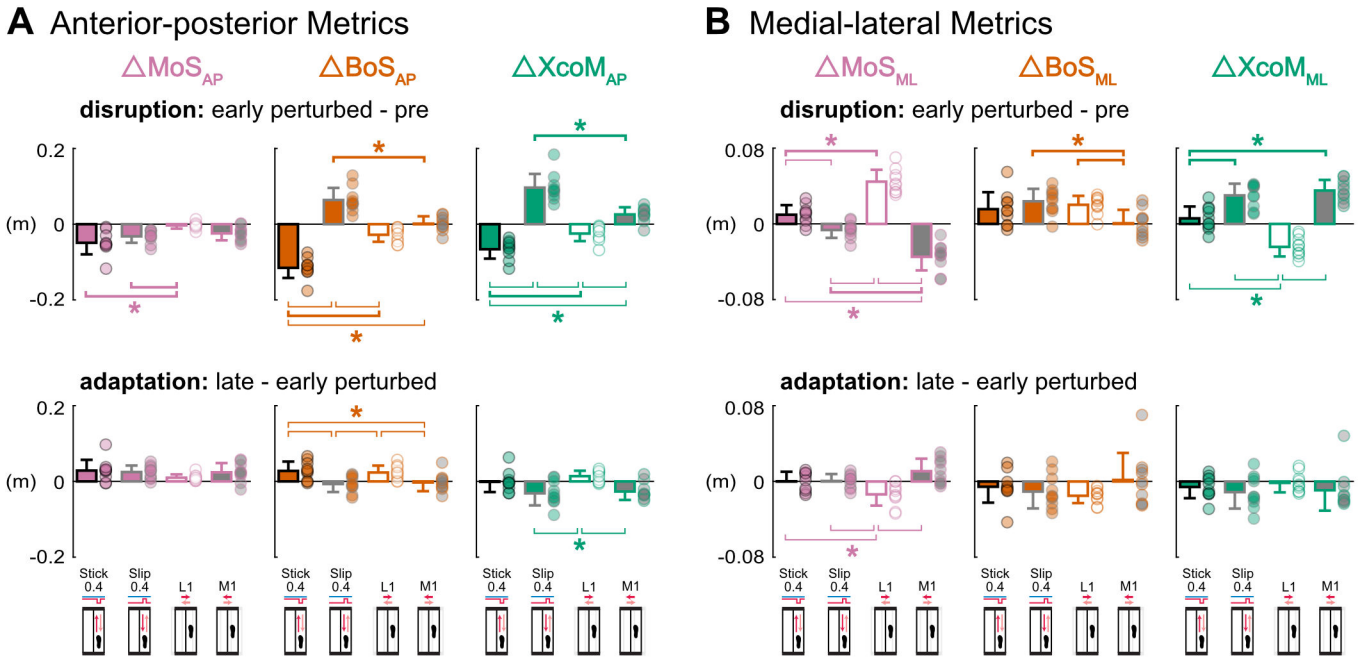

Pre
Post
Perturbation onset/termination
MoS
BoS
XcoM
Early Perturbed
Late Perturbed
Stick0.4
Slip0.4
L1
M1
Left belt
Right belt
Belt Speed (m/s)
1.4
1
0.6
Treadmill Shift (m)
0.01
0
-0.01
Lateral direction
Medial direction
MoS_AP (m)
MoS_ML (m)
BoS_AP (m)
BoS_ML (m)
XcoM_AP (m)
XcoM_ML (m)
0.7
0
-0.7
0.3
0.15
Post
Late Perturbed
Pre
Early Perturbed
RHS LTO LHS RTO RHS
Gait Event

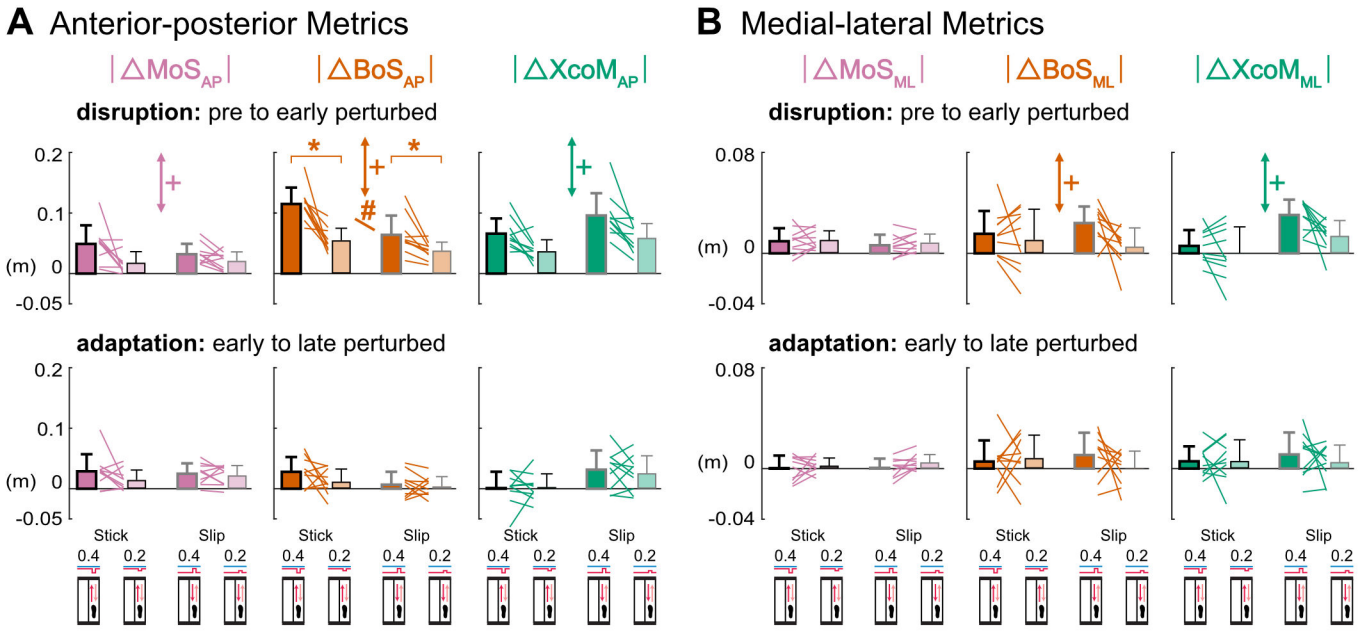
Perturbed Strides




|ΔBoS|
|ΔXcoM|
Anterior-posterior Metrics
Medial-lateral Metrics
A
disruption: pre to early perturbed
disruption: pre to early perturbed
0.2
0.1
(m) 0
0.08
(m) 0
-0.04
B
adaptation: early to late perturbed
adaptation: early to late perturbed
0.2
0.1
(m) 0
0.08
(m) 0
-0.04
Stick0.4
Slip0.4
L1
M1
Stick0.4
Slip0.4
L1
M1


Catch Strides
A Anterior-posterior Metrics
B Medial-lateral Metrics
BoS_AP
XcoM_AP
MoS_AP
BoS_ML
XcoM_ML
MoS_ML
(m)
Stick0.4
Slip0.4
L1
M1
deviation from pre at
early catch
late catch
time (minute)
|ΔMoS_AP| |ΔBoS_AP| |ΔXcoM_AP|
|ΔMoS_ML| |ΔBoS_ML| |ΔXcoM_ML|


A Anterior-posterior Metrics
B Medial-lateral Metrics
ΔMoS_AP
ΔBoS_AP
ΔXcoM_AP
ΔMoS_ML
ΔBoS_ML
ΔXcoM_ML
disruption: early perturbed - pre
adaptation: late - early perturbed
(m)
0.2
0
-0.2
0.08
-0.08
Stick 0.4
Slip 0.4
L1
M1


A Anterior-posterior Metrics
|ΔMoS_AP|
|ΔBoS_AP|
|ΔXcoM_AP|
disruption: pre to early perturbed
adaptation: early to late perturbed
B Medial-lateral Metrics
|ΔMoS_ML|
|ΔBoS_ML|
|ΔXcoM_ML|
disruption: pre to early perturbed
adaptation: early to late perturbed
(m)
Stick
Slip
0.4
0.2