

RESEARCH ARTICLE

Adaptive control of dynamic balance in human gait on a split-belt treadmill

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ABSTRACT

Human bipedal gait is inherently unstable, and staying upright requires adaptive control of dynamic balance. Little is known about adaptive control of dynamic balance in reaction to long-term, continuous perturbations. We examined how dynamic balance control adapts to a continuous perturbation in gait, by letting people walk faster with one leg than the other on a treadmill with two belts (i.e. split-belt walking). In addition, we assessed whether changes in mediolateral dynamic balance control coincide with changes in energy use during split-belt adaptation. In 9 min of split-belt gait, mediolateral margins of stability and mediolateral foot roll-off changed during adaptation to the imposed gait asymmetry, especially on the fast side, and returned to baseline during washout. Interestingly, no changes in mediolateral foot placement (i.e. step width) were found during split-belt adaptation. Furthermore, the initial margin of stability and subsequent mediolateral foot roll-off were strongly coupled to maintain mediolateral dynamic balance throughout the gait cycle. Consistent with previous results, net metabolic power was reduced during split-belt adaptation, but changes in mediolateral dynamic balance control were not correlated with the reduction of net metabolic power during split-belt adaptation. Overall, this study has shown that a complementary mechanism of relative foot positioning and mediolateral foot roll-off adapts to continuously imposed gait asymmetry to maintain dynamic balance in human bipedal gait.

KEY WORDS: Dynamic balance control, Motor learning, Locomotor adaptation, Foot placement, Margin of stability, Metabolic power

INTRODUCTION

Humans are one of few mammals that naturally show bipedal gait. Although human gait is more energy efficient than quadrupedal gait in mammals of equal body weight (Alexander, 2004), maintaining mediolateral (ML) balance is more complex. Active control of balance in human gait is essential to prevent falling (Bauby and Kuo, 2000; Kuo and Donelan, 2010), as the vertical projection of the center of mass (CoM) is outside of the base of support (BoS) for 80% of the gait cycle (Winter, 1991). In order to respond to both external perturbations from the environment (e.g. being pushed or walking on uneven terrain) as well as internal perturbations from the system itself (e.g. controlling the destabilizing effect of the ankle push-off in the stride cycle), the control of balance during gait needs

to be adaptive. By adaptive, we refer to recalibration of motor control in response to perturbations, in order to re-establish reliable and efficient task performance, followed by after-effects once the perturbation is removed, which slowly wash out over time (Krakauer, 2009). A good understanding of dynamic balance control requires knowledge of the adaptability of gait.

The trajectory of the CoM during bipedal human gait can be modeled with the inverted pendulum model (Geursen et al., 1976; Winter, 1995). In this model, the CoM of the human body is described as a single mass on top of an inverted pendulum, in which the pendulum represents the stance leg. Although both can be unstable when perturbed, anteroposterior (AP) balance is largely regulated by passive dynamics in this model, whereas the maintenance of ML balance requires more active control (Kuo and Donelan, 2010). The importance of ML balance control has also been shown by Hilliard et al. (2008), who found that poor ML balance is a key predictor of falls in older adults. Therefore, we study dynamic balance control in the ML direction. In the model, the kinematic state of the CoM can be described with the extrapolated CoM (XCoM) concept, which is the CoM position with the addition of a CoM velocity component (Hof et al., 2005). ML dynamic stability is maintained by active control of the ML position of the XCoM relative to the BoS (Hof et al., 2005) (i.e. relative foot positioning), known as the margin of stability (MoS) (Hof, 2008; Hof et al., 2007). The MoS can thus be regulated by changes in CoM excursion and ML foot placement. A negative ML MoS will result in a loss of balance, necessitating the production of a sidestep to prevent a fall, whereas a positive ML MoS will result in well-balanced and safe gait (Hof, 2008).

Relative foot positioning and ML foot roll-off are sequential in time in a gait cycle. Recently, it has been suggested that relative foot positioning and ML foot roll-off work as a complementary mechanism (e.g. when the foot is positioned too wide relative to the XCoM, the foot will roll-off inwards in the ML direction, and vice versa) that allows for corrective control of the MoS during the stance phase (Reimann et al., 2017). The accuracy of relative foot positioning strongly depends on visual information and in general is not very precise (Hollands et al., 1995; Reynolds and Day, 2005; Smid and den Otter, 2013). However, the aforementioned complementary mechanism can change a small or large ML MoS at contralateral toe-off by rolling the foot inward or outward during stance (i.e. foot roll-off) (Hof et al., 2007), based on real-time afferent information about loading (Duysens et al., 2000; Fouad et al., 2001) or CoM position relative to center of pressure (CoP) position. Because the MoS can be controlled by relative foot positioning and foot roll-off, both variables and the relationship between these variables should be measured when assessing adaptation of dynamic balance control to sustained perturbations.

To gain a better understanding of balance control in gait, ML balance has been challenged experimentally by pushing (Hof et al., 2010; Hof and Duysens, 2013; Vlutters et al., 2016) or pulling the trunk of a participant (IJmker et al., 2014), and by lateral translations

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List of symbols and abbreviations

AP	anteroposterior
BL	baseline
BoS	base of support
CoM	center of mass position
CoP	center of pressure position
CoP _x	anteroposterior center of pressure position
CoP _z	mediolateral center of pressure position
DS	double support time
DSS	double support symmetry
EA	early adaptation
EE	energy expenditure
EE _{gait}	energy expenditure during gait
EE _{net}	net energy expenditure
EE _{rest}	energy expenditure during quiet standing
EP	early post-adaptation
F _y	vertical ground reaction force
<i>g</i>	gravitational acceleration
GRF	ground reaction force
<i>l</i>	leg length
LA	late adaptation
LP	late post-adaptation
<i>m</i>	body mass
<i>M</i>	moment of force
ML	mediolateral
MoS	margin of stability
MP _{net}	net metabolic power
<i>M_x</i>	anteroposterior moment of force
<i>M_z</i>	mediolateral moment of force
RER	respiratory exchange rate
SL	step length
SLS	step length symmetry
SW	step width
<i>v</i> _{CoM}	center of mass velocity
<i>V</i> _{O₂}	oxygen uptake
XCoM	extrapolated center of mass
ΔCoP	change in CoP _z position during stance

of the treadmill (Hak et al., 2012). These experiments focus on reactive balance control (i.e. balance control in reaction to perturbations from which a human recovers within a few steps), while balance control also involves adaptation to more continuous and sustained perturbations in gait (e.g. walking on a rocking ship or walking after a leg amputation). A method to perturb gait directly as well as continuously, and which has gained considerable popularity in recent years, is to let walkers adapt to imposed asymmetric gait on a split-belt treadmill.

Split-belt treadmills have two belts, one under each foot. By setting the speed of one of the belts faster than the other, a participant has to walk faster with one leg than the other, which evokes a temporally and spatially asymmetric gait pattern. Earlier research on split-belt gait in healthy individuals has shown that step lengths and double support times initially show a large asymmetry, but adapt over time to a more symmetrical ratio (Reisman et al., 2005). It has been found that spatiotemporal asymmetry in gait is associated with poor ML balance (Lewek et al., 2014). In addition, recent research in split-belt gait has shown that variability of the frontal inclination angle is reduced during sudden split-belt adaptation (Sawers et al., 2013). Furthermore, ML ground reaction forces (GRF) and fast limb hip moment impulse increased during split-belt adaptation (Roper et al., 2017). Finally, sagittal plane measures of dynamic balance during split-belt adaptation have been previously characterized, showing an increase of AP MoS on the fast compared with the slow belt (Park and Finley, 2017). These studies all show strategies to cope with the

perturbed balance in split-belt gait. Split-belt gait thus provides the opportunity to examine how humans recover their ML balance in reaction to a sustained perturbation.

It has been suggested that the adaptive control of gait serves to decrease energy use (Donelan et al., 2001; Emken et al., 2007; Finley et al., 2013; Sparrow and Newell, 1998; Todorov, 2004; Umberger and Martin, 2007). Recent research has shown that the increase in spatial gait symmetry during split-belt adaptation is related to a decrease in metabolic power (Finley et al., 2013). In addition, it was found that split-belt adaptation leads to an initial increase in mechanical work performed by the legs, followed by a gradual decrease over the adaptation period (Selgrade et al., 2017). Furthermore, research indicates that dynamic balance control and changes in metabolic power might be related (Donelan et al., 2001). To gain insight into processes underlying motor adaptation, we studied this association during split-belt adaptation. We hypothesized that adaptive control of dynamic balance in split-belt gait may be related to the reduction of metabolic power.

The primary aim of this study was to determine the effects of continuous perturbations on ML dynamic balance control, by establishing whether and how dynamic balance control adapts to split-belt gait. We hypothesized that dynamic balance parameters adapt to split-belt walking with a sudden initial increase in MoS and a gradual decrease over time, co-occurring with the adaptation of spatial and temporal gait parameters. Furthermore, we studied whether a complementary mechanism of relative foot positioning and foot roll-off controls ML dynamic balance in split-belt gait. The secondary aim of this study was to assess whether the magnitude of changes in ML dynamic balance control during split-belt adaptation coincides with the magnitude of changes in net metabolic power (MP_{net}). Based on previous research (Donelan et al., 2001; Finley et al., 2013), we expected that a decrease in MoS would be related to a decrease in MP_{net}.

MATERIALS AND METHODS**Participants and ethics statement**

Fourteen healthy young adults (7 males, 7 females, 23.9±1.9 years old, body mass: 74.9±11.7 kg, height: 1.75±0.08 m) volunteered for this study. Participants were excluded from the study if they had any known neurological or orthopedic impairments that affect gait or balance capacity, or if they had any prior experience with split-belt treadmill walking. The procedures of this study were approved by the Ethics Committee of the Center for Human Movement Sciences, University Medical Center Groningen, The Netherlands, and were in accordance with the Declaration of Helsinki (World Medical Association, 2013). All participants gave their written informed consent prior to the experiment.

Instrumentation

Participants walked on an instrumented split-belt treadmill (M-Gait, Motekforce Link, Amsterdam, The Netherlands). Participants were fitted with a harness attached to the ceiling to secure the participants' safety, which did not provide any body weight support or constrain the participants' movements. Two handrails were attached to both sides of the treadmill for safety, but participants were instructed not to touch the handrails other than to prevent a fall. Three-dimensional GRFs (N) and moments of force (N m) were measured using two embedded force plates, one under each belt, and recorded with D-Flow software (Motekforce Link) at a sample frequency of 1000 Hz. The data were analyzed in an XYZ coordinate system with the X-axis along the line of gait progression, the Z-axis positive to the right and the Y-axis pointing upwards, in accordance with International Society

of Biomechanics recommendations (Wu and Cavanagh, 1995). Breath-by-breath respiratory data were measured using a portable K4b2 system (COSMED, Rome, Italy) and synchronized with D-Flow. All data were stored offline on an encrypted external hard drive for further analysis.

Protocol

Participants stood still on the treadmill for 90 s prior to the experiment to measure energy expenditure (EE) during quiet standing. Next, they were exposed to the treadmill protocol as shown in Fig. 1. The treadmill session started with 5 min of warm-up at alternating slow (0.7 m s^{-1}) and fast (1.4 m s^{-1}) tied-belt gait speeds to let the participant adapt to treadmill gait (Matsas et al., 2000). After that, 1 m of slow tied-belt gait (0.7 m s^{-1}) was recorded as a baseline measurement. Fast MoS and fast ML ΔCoP baseline were calculated from data of the last minute of fast tied-belt walking in warm-up. The split-belt adaptation phase lasted 9 min. During the adaptation phase, the left belt speed was set at 1.4 m s^{-1} and right belt speed at 0.7 m s^{-1} (Reisman et al., 2005). Finally, in the post-adaptation phase, both belts were set at 0.7 m s^{-1} for 5 min, to measure washout. This resulted in five experimental phases: baseLine (BL), early adaptation (EA), late adaptation (LA), early post-adaptation (EP) and late post-adaptation (LP). The first (EA, EP) and last (BL, LA, LP) five steps of each phase were used for further analysis. Prior to and during the experiment, no instructions were given regarding the duration of the phases or the changes in gait speed. Participants were instructed to look straight ahead and remain silent for the duration of the protocol so as to not affect respiratory data.

Data analysis

All data were analyzed using custom-made routines in MATLAB (version r2016b; The MathWorks Inc., Natick, MA, USA). GRFs and moments of force were low-pass filtered using a 15 Hz second-order zero-phase Butterworth filter. Gait events were detected by finding the point at which GRF_Y , on either of the force plates, crossed a threshold of 50 N. For the analysis of CoP position, X and Z CoP (m) positions for each force plate were calculated using Eqns 1 and 2:

$$\text{CoP}_X = -\frac{M_Z}{F_Y}, \quad (1)$$

$$\text{CoP}_Z = \frac{M_X}{F_Y}, \quad (2)$$

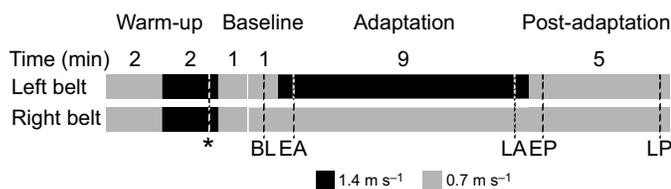


Fig. 1. Split-belt treadmill protocol. The upper bar shows left belt speed and the lower bar shows right belt speed. Phase duration is shown above the bars. Experimental phases [baseline (BL), early adaptation (EA), late adaptation (LA), early post-adaptation (EP) and late post-adaptation (LP)] are shown below the bars. The asterisk indicates BL measurement for the fast margin of stability (MoS) and the fast change in mediolateral center of pressure during stance (ML ΔCoP). Dashed vertical lines visually indicate the point in time at which the first or last five steps for each experimental phase were averaged for further analysis. Warm-up is separated from baseline in this figure to indicate the division between warm-up and baseline; in the actual experiment, the belts continued to run at this point.

in which M is the moment of force (N m) and F the GRF (N). For continuous monitoring of CoP and CoM positions, the data of the two force plates were combined by summing the GRFs. Simulated single force plate CoP position data were calculated by scaling the CoP position of each force plate with the magnitude of its respective GRF (Eqn 3):

$$\text{CoP}_{\text{combined}} = \frac{\text{GRF}_{\text{left}} \times \text{CoP}_{\text{left}} + \text{GRF}_{\text{right}} \times \text{CoP}_{\text{right}}}{\text{GRF}_{\text{left}} + \text{GRF}_{\text{right}}}. \quad (3)$$

Step length symmetry (SLS) and double support time symmetry (DSS) were calculated to monitor spatiotemporal gait symmetry throughout the experiment using Eqns 4 and 5 (Reisman et al., 2005):

$$\text{SLS}(i) = \frac{\text{SL}_{\text{left}}(i) - \text{SL}_{\text{right}}(i)}{\text{SL}_{\text{left}}(i) + \text{SL}_{\text{right}}(i)}, \quad (4)$$

in which SL is step length (m), defined as the difference in CoP_X position between the left and right foot at heel strike. SLS was calculated as a symmetry measure between left and right SL of every stride (i) (Reisman et al., 2005).

The DSS between the first and second DS period was calculated for every stride (i) using Eqn 5:

$$\text{DSS}(i) = \frac{\text{DS}_{\text{first}}(i) - \text{DS}_{\text{second}}(i)}{\text{DS}_{\text{first}}(i) + \text{DS}_{\text{second}}(i)}, \quad (5)$$

in which DS is the double support time (s), defined as the period between heel strike and contralateral toe-off.

Step width (SW) was calculated using Eqn 6 for every step in the gait cycle throughout the experiment:

$$\text{SW}(i) = |\min/\max(\text{CoP}_Z(j)) - \max/\min(\text{CoP}_Z(k))|. \quad (6)$$

SW was defined as the absolute difference between the local minimum/maximum CoP_Z position during ipsilateral single support phase (j) and the local maximum/minimum CoP_Z position during the consecutive contralateral single support phase (k) for each left/right step (i) (adapted from Verkerke et al., 2005).

To determine the ML MoS (m), multiple steps were taken. First, GRF_Z was divided by body mass (kg) to obtain CoM_Z acceleration (m s^{-2}). The CoM_Z acceleration signal was integrated twice to obtain CoM_Z position (m) and high-pass filtered to prevent integration drift. Then, the absolute ML CoM position (m) was calculated by addition of the low-pass filtered CoP_Z signal, and the high-pass filtered CoM_Z position (Schepers et al., 2009). All aforementioned filtering was done using a 0.2 Hz second-order zero-phase Butterworth filter. The ML XCoM position (m) was calculated using Eqn 7 (Hof et al., 2005):

$$\text{XCoM} = \text{CoM} + \frac{v_{\text{CoM}}}{\sqrt{g/l}}, \quad (7)$$

in which v_{CoM} is the ML CoM velocity (m s^{-1}), l is leg length (m) and g is gravitational acceleration (9.81 m s^{-2}). Finally, the MoS was defined as the distance between the CoP_Z position and XCoM $_Z$ position at contralateral toe-off (j) for each step (i) using Eqn 8 (Hof et al., 2005):

$$\text{MoS}(i) = \text{CoP}_Z(j) - \text{XCoM}_Z(j). \quad (8)$$

The fast MoS was calculated for each step with the left limb (which was on the fast belt during split-belt gait), and the slow MoS for each step with the right limb (which was on the slow belt during split-belt gait).

The change in CoP_Z position during single-limb stance (indicating foot roll-off, from this point on referred to as ML ΔCoP) was calculated by subtracting the CoP_Z position at contralateral heel strike from the CoP_Z position at the preceding contralateral toe-off. The ML ΔCoP was calculated for the fast (left) and slow (right) side separately, resulting in fast ML ΔCoP and slow ML ΔCoP . As illustrated in Fig. 2, a positive ML ΔCoP corresponds with an outward ML ΔCoP , and a negative ML ΔCoP with an inward ML ΔCoP .

For the respiratory analysis, first EE (W) was calculated using Eqn 9 (Garby and Astrup, 1987):

$$\text{EE} = (4.940 \times \text{RER} + 16.040) \times \dot{V}_{\text{O}_2}, \quad (9)$$

in which RER is the respiratory exchange rate and \dot{V}_{O_2} is oxygen uptake (1 min^{-1}). Then, net EE (EE_{net} ; W) was calculated by subtracting the mean EE at quiet standing from EE during the experiment. Finally, MP_{net} (W kg^{-1}) was determined by dividing EE_{net} by body mass (m ; kg) (IJmker et al., 2013), as shown in Eqn 10:

$$\text{MP}_{\text{net}} = \frac{(\text{EE}_{\text{gait}} - \text{EE}_{\text{rest}})}{m}. \quad (10)$$

Statistical analysis

The first minute of MP_{net} data of the EA and EP phases was left out of the analyses because of the transient change in the data from one experimental phase to the other (Finley et al., 2013). SLS, DSS, SW, fast MoS, slow MoS, fast ML ΔCoP and slow ML ΔCoP were averaged over the first (EA and EP) or last (BL, LA and LP) five steps of each experimental phase for statistical analysis. MP_{net} was averaged over the first or last 2 min of each experimental phase for statistical analysis, except BL, in which MP_{net} was averaged over the last 1 min of that phase.

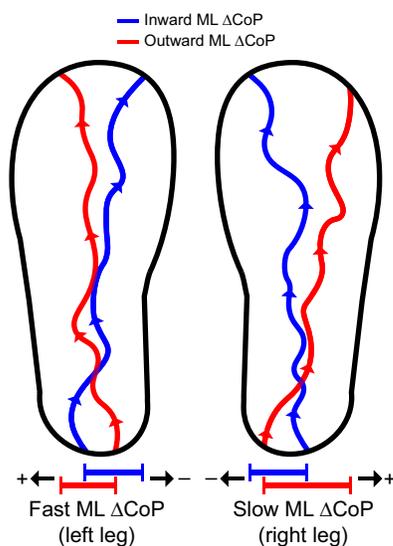


Fig. 2. Visualization of fast (left leg) and slow (right leg) change in mediolateral center of pressure during stance (ML ΔCoP). Red and blue lines indicate hypothetical CoP trajectories. Blue lines indicate inward ML ΔCoP , red lines outward ML ΔCoP . The arrows indicate the direction of the CoP trajectory. A positive ML ΔCoP corresponds with an outward ML ΔCoP , a negative ML ΔCoP with an inward ML ΔCoP . The direction of the ML ΔCoP is mirrored for the left and right foot to make interpretation of the values more intuitive.

To test for differences between the experimental phases, three separate repeated-measures MANOVAs (RM MANOVAs) were performed with SLS, DSS, SW, fast MoS, slow MoS, fast ML ΔCoP , slow ML ΔCoP and MP_{net} as dependent variables. The within-subjects factor 'phase' had two levels in the three respective RM MANOVAs: (1) BL versus EA, (2) EA versus LA and (3) BL versus EP. When multivariate results were found to be significant, univariate results were assessed to find differences between phases. BL versus EA was tested to see whether parameters changed in reaction to split-belt gait, EA versus LA to test whether adaptation to split-belt gait occurred, and BL versus EP to test whether after-effects occurred after returning to tied-belt speeds.

To study the relationship between MoS at contralateral toe-off (from this point on referred to as initial MoS) and subsequent ML ΔCoP , a Pearson correlation coefficient was calculated between those two parameters during baseline, adaptation and post-adaptation and for the fast and slow side. This resulted in six (three experimental phases \times two sides) correlations per participant. To determine whether a relationship between initial MoS and ML ΔCoP existed, Wilcoxon signed rank tests were used to test whether the group median correlation coefficient was different from zero for each of the six conditions.

To study the relationship between change in fast MoS and slow MoS from EA to LA, and the reductions in MP_{net} from EA to LA, linear regression analyses were performed. To test whether changes in spatiotemporal parameters coincided with a reduction in MP_{net} , we also investigated whether changes in SLS and DSS were related to changes in MP_{net} during split-belt adaptation with linear regression analyses, similar to Finley et al. (2013).

Statistical significance was set at a Holm–Bonferroni (Holm, 1979) corrected alpha of 5% for all analyses, to control the family-wise error rate. All statistical analyses were performed using IBM SPSS Statistics for Windows (Version 24, 64-bit edition, IBM Corporation, Armonk, NY, USA).

RESULTS

The group-averaged results of SLS, DSS, SW, fast and slow MoS, fast and slow ML ΔCoP , and MP_{net} are shown in Fig. 3. To determine whether the participants adapted to split-belt gait in the adaptation phase and whether the learned pattern washed out during the post-adaptation phase, symmetry in step lengths (SLS) and double support times (DSS) were measured. As becomes evident from Fig. 3A,B and the results from the RM MANOVAs (Fig. 3G,H and Table 1), participants walked with more asymmetric step lengths and double support times in EA compared with BL, but symmetry increased during split-belt adaptation from EA to LA. During post-adaptation, participants walked with asymmetric step lengths and double support times in EP compared with BL ($P < 0.05$ for all comparisons). The participants thus showed adaptation to split-belt gait in the adaptation phase and after-effects in the post-adaptation phase.

Margin of stability adapts to split-belt gait in an asymmetric fashion

To study adaptive dynamic balance control in gait, we examined whether and how the MoS changed during split-belt adaptation. Fig. 3D,J shows that the fast MoS increased from BL to EA. Subsequently, the fast MoS decreased from EA to LA, indicating adaptation to split-belt gait. All comparisons were significant in the RM MANOVA ($P < 0.05$, Table 1). No significant difference was found in fast MoS in EP compared with BL. Fig. 3D,J shows that the slow MoS increased from BL to EA, and decreased from EA to LA,

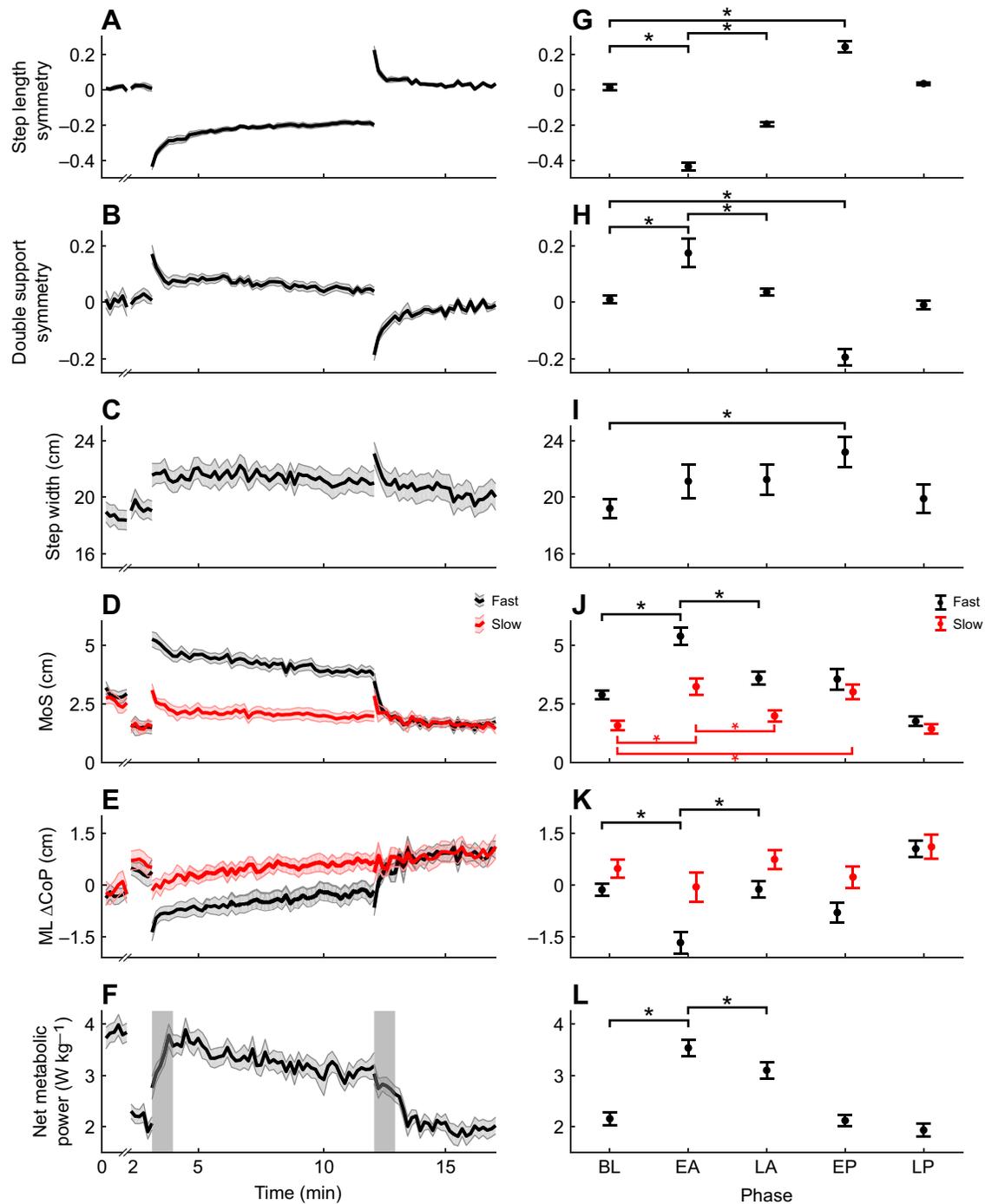


Fig. 3. Group-averaged results (N=14). (A,G and B,H) A value of zero indicates perfect symmetry in step length or double support time for step length symmetry and double support symmetry, respectively. (A–F) Results were averaged within 10 s bins for visualization purposes. Shaded areas around the lines indicate standard error. Gaps (//) in the X-axes indicate the jump in time flow from minute one to two, i.e. from fast to slow tied-belt walking. The vertical grey shaded areas in F indicate the net metabolic power results that have been left out of further analysis. (G–L) Averaged results (means±s.e.m.) and statistics (* $P<0.05$) per experimental phase for the first [early adaptation (EA), early post-adaptation (EP)] or last [baseline (BL), late adaptation (LA), late post-adaptation (LP)] five steps or 2 min (net metabolic power). BL results for the fast margin of stability (MoS) and the fast change in mediolateral center of pressure during stance (ML Δ CoP) correspond with fast tied-belt walking.

indicative of adaptation to split-belt gait. The slow MoS was higher in EP compared with BL, indicative of an after-effect of the learned gait pattern. All comparisons were significant ($P<0.05$; Table 1). Interestingly, the fast MoS was higher than the slow MoS in both EA (group average: 5.4 versus 3.2 cm) and LA (group average: 3.6 versus 2.0 cm), as shown in Fig. 3D,J.

Mediolateral foot roll-off shows adaptation to split-belt gait on one side

The MoS can be adjusted with ML foot roll-off, which is reflected in the change in ML Δ CoP during the stance phase of gait. Fig. 3E,K shows that the fast ML Δ CoP decreased from BL to EA, indicating an inward foot roll-off. During split-belt adaptation, fast ML Δ CoP

Table 1. Differences between the experimental phases – baseline (BL), early adaptation (EA), late adaptation (LA) and early post-adaptation (EP) – for all parameters

Parameter	Phase	F (d.f.)	P
Step length symmetry	BL versus EA	228.5 (1,13)	<0.001*
	EA versus LA	132.7 (1,13)	<0.001*
	BL versus EP	47.8 (1,13)	<0.001*
Double support symmetry	BL versus EA	9.8 (1,13)	0.008*
	EA versus LA	7.6 (1,13)	0.017*
	BL versus EP	49.9 (1,13)	<0.001*
Step width	BL versus EA	2.7 (1,13)	0.124
	EA versus LA	0.0 (1,13)	0.935
	BL versus EP	37.7 (1,13)	<0.001*
Fast margin of stability	BL versus EA	62.8 (1,13)	<0.001*
	EA versus LA	25.1 (1,13)	<0.001*
	BL versus EP	2.0 (1,13)	0.183
Slow margin of stability	BL versus EA	25.3 (1,13)	<0.001*
	EA versus LA	10.4 (1,13)	0.007*
	BL versus EP	27.6 (1,13)	<0.001*
Fast ML Δ CoP	BL versus EA	18.1 (1,13)	0.001*
	EA versus LA	32.3 (1,13)	<0.001*
	BL versus EP	4.1 (1,13)	0.064
Slow ML Δ CoP	BL versus EA	1.6 (1,13)	0.233
	EA versus LA	3.4 (1,13)	0.088
	BL versus EP	0.5 (1,13)	0.476
Net metabolic power	BL versus EA	246.3 (1,13)	<0.001*
	EA versus LA	48.7 (1,13)	<0.001*
	BL versus EP	0.4 (1,13)	0.559

Asterisks indicate statistical significance at a Holm–Bonferroni corrected alpha of 0.05.

increased to a value of almost zero from EA to LA, which indicates no ML foot roll-off. These comparisons were all significant in the RM MANOVA ($P < 0.05$; Table 1). In EP compared with BL, the fast ML Δ CoP showed no significant difference. The slow ML Δ CoP showed no change during the experiment ($P > 0.05$; Table 1). The ML foot roll-off thus showed significant changes and adaptation in response to split-belt gait on the fast side, but not on the slow side.

Relative foot positioning and foot roll-off represent a complementary mechanism in split-belt adaptation

To monitor ML foot placement throughout the experiment, SW was calculated. The group-averaged results for SW are shown in Fig. 3C,I. The RM MANOVA results (Table 1) showed no statistically significant changes from BL to EA, and no change over time during adaptation from EA to LA. However, in EP compared with BL there was a significant increase in SW ($P < 0.05$).

To determine whether the initial MoS and subsequent ML Δ CoP during stance represent a complementary mechanism to maintain a safe MoS during gait, we studied the relationship between these two parameters. A representative example of a single participant's results is shown in Fig. 4 and the group-averaged results are shown in Fig. 5. Fig. 4 shows that there is a strong relationship between the two parameters. When MoS decreases, the ML foot roll-off is directed outward, and when MoS increases, the ML foot roll-off is directed inward. Furthermore, this figure clearly shows the shift from high to low MoS in split-belt adaptation. Also, there was a shift from inward to outward ML Δ CoP (i.e. a change in ML foot roll-off) from EA (blue triangles) to LA (green squares). The relationship between the initial MoS and ML Δ CoP is also apparent in the group data (Fig. 5), as is the shift in MoS and ML Δ CoP from EA (blue ellipses) to LA (green ellipses). The results in Table 2 show that the median correlation coefficient of this relationship was significant for all phases and sides ($P < 0.05$). The group median correlation coefficients

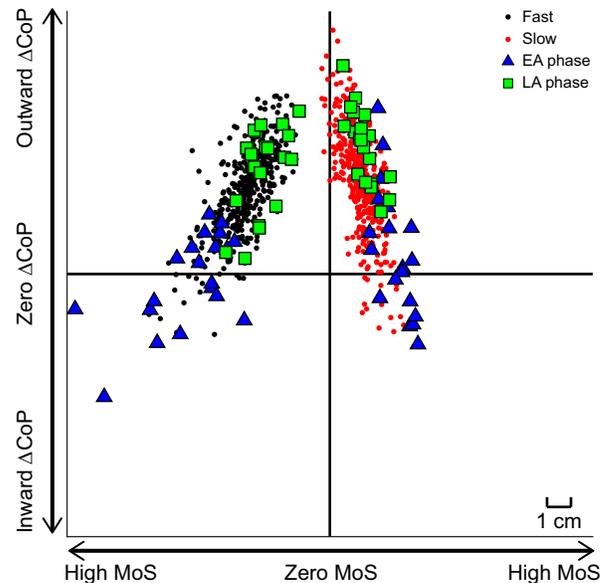


Fig. 4. Representative example of a single participant's initial margin of stability (MoS) versus change in mediolateral center of pressure during stance (ML Δ CoP) during the adaptation phase. Black and red circles represent single steps of the fast and slow leg, respectively. Blue triangles and green squares represent the first/last 20 steps from the early adaptation (EA) and late adaptation (LA) for each side, respectively. Inward ML Δ CoP indicates an inward ML foot roll-off, outward ML Δ CoP an outward ML foot roll-off, zero ML Δ CoP indicates no ML foot roll-off from heel strike to toe-off. Crossing the point of zero, MoS indicates dynamic instability. A high MoS indicates dynamic stability. As this figure illustrates, a low initial MoS is typically followed by an outward foot roll-off (and vice versa) by which dynamic stability is maintained.

for baseline, adaptation and post-adaptation range from 0.54 ± 0.14 to 0.79 ± 0.23 , which indicates a strong relationship between initial MoS and ML Δ CoP in all phases and both sides.

The relationship between adaptive balance control and the reduction of net metabolic power

Fig. 3F,L shows an increase in MP_{net} from BL to EA, and a decrease over time from EA to LA. The gait pattern thus changed from relatively energy costly towards a more energy efficient pattern during split-belt adaptation. RM MANOVAs showed that these changes were statistically significant ($P < 0.05$, Table 1). In EP compared with BL, there was no significant change in MP_{net} (Fig. 3F,L and Table 1). The gait pattern was thus not more energetically costly when the belts returned to symmetrical speeds in comparison to the baseline measurement.

To study whether changes in adaptive balance control and spatiotemporal parameters coincide with a reduction of MP_{net} , we performed four linear regression analyses to test whether changes in SLS (Fig. 6A), DSS (Fig. 6B), fast MoS (Fig. 6C) and slow MoS (Fig. 6D) were related to the reduction in MP_{net} during split-belt adaptation. No significant linear relationship was found between changes in any of the four parameters and the reduction in MP_{net} . Although gait became more efficient during split-belt adaptation, the amount of change in MP_{net} could not be predicted from the amount of change in dynamic balance control or spatiotemporal parameters.

DISCUSSION

Participants adapted metrics of dynamic balance control in response to the imposed gait asymmetry in multiple ways. First, fast and slow

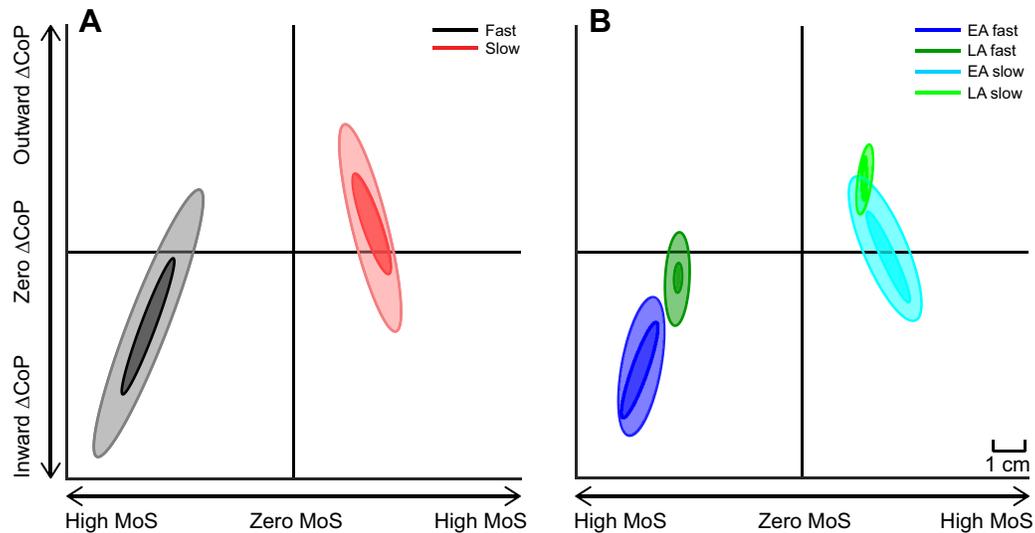


Fig. 5. Group-averaged results ($N=14$) of initial margin of stability (MoS) versus change in mediolateral center of pressure during stance (ML Δ CoP) during the adaptation phase. (A) The black (fast side) or red (slow side) ellipse shows the least squares fit through the group-averaged MoS and ML Δ CoP during the adaptation phase. (B) The blue ellipses show the least squares fit through the group-averaged MoS and ML Δ CoP during early adaptation (EA), the green ellipses during late adaptation (LA) for the fast and slow side. The shaded outer ellipses in A and B show the least squares fit through the group-averaged data plus standard error. The Y-axis is magnified with a factor four with respect to the X-axis. Inward ML Δ CoP indicates an inward ML foot roll-off, outward ML Δ CoP an outward ML foot roll-off, zero ML Δ CoP indicates no ML foot roll-off from heel strike to toe-off. Crossing the point of zero, MoS indicates dynamic instability. A high MoS indicates dynamic stability. As this figure illustrates, a low initial MoS is typically followed by an outward foot roll-off (and vice versa) by which dynamic stability is maintained.

MoS were initially high and decreased over time. This shows that adaptations to sustained perturbations imposed by the split-belt treadmill include adaptations in the control of ML dynamic balance. Second, the fast MoS was larger than the slow MoS during split-belt gait, which indicates an interlimb difference in adaptive dynamic balance control. Third, the initial MoS showed a strong correlation with ML Δ CoP. This shows that a complementary mechanism of relative foot positioning and ML foot roll-off controls ML dynamic balance during split-belt adaptation. The secondary aim of this study was to determine whether changes in MP_{net} during split-belt adaptation are related to changes in dynamic balance control. Contrary to our expectations, the changes in MoS were not related to a decrease in MP_{net} during split-belt adaptation.

Dynamic balance control adapts to imposed spatiotemporal gait asymmetry

Our study is the first to examine the adaptive control of ML dynamic balance in split-belt gait. The observations we made on adaptation of spatial and temporal gait symmetry are comparable to results from previous split-belt gait studies (Bruijn et al., 2012; Malone and Bastian, 2010; Reisman et al., 2005). The present study has shown

that the MoS reflects the adaptive capabilities of dynamic balance control in reaction to sustained perturbations in gait. First, both the fast and slow MoS increased in the early adaptation phase, which reflects the disturbance of ML dynamic balance by split-belt gait. Second, fast and slow MoS adapted to split-belt gait and slow MoS showed after-effects when belts returned to symmetrical speeds. These dynamic balance parameters follow a pattern over time similar to that of the adaptation of spatial (i.e. SLS) and temporal (i.e. DSS) step parameters to split-belt gait, which suggests that these processes occur in parallel and are possibly governed by a common control mechanism.

Adaptive dynamic balance control shows interlimb difference depending on belt speed

A positive ML MoS is a condition for dynamic stability in gait (Hof et al., 2005). In the present study, we found that the MoS was positive during split-belt gait, but also asymmetrical between the fast and the slow side, similar to findings by Park and Finley (2017), who found asymmetry in AP MoS in split-belt gait. This indicates a difference in dynamic balance control dependent on belt speed. This difference could be the result of either active control, or an indirect and more passive consequence of the spatiotemporal changes in split-belt gait.

The MoS can be actively controlled by changes in ML foot placement (Hof et al., 2007). However, in the present study we did not find any changes in SW throughout the experiment, suggesting that the changes in MoS were not caused by altered ML foot placement. Based on the inverted pendulum model of walking, changes in ML MoS can also be caused by changes in stance time (Hof et al., 2007). A shorter stance time results in reduced pendulum swing time; therefore, there is less time for the CoM to move, which results in a larger MoS. The other way around, increased stance time results in increased pendulum swing time, increasing the time for CoM movement, resulting in a smaller MoS. A shorter stance time

Table 2. Relationship between initial margin of stability and mediolateral change in center of pressure during stance for each phase and side

Phase	Side	Median \pm s.d.	Z-score	P
Baseline	Fast	0.79 \pm 0.23	-3.233	0.001*
	Slow	0.66 \pm 0.23	-3.233	0.001*
Adaptation	Fast	0.65 \pm 0.11	-3.296	0.001*
	Slow	0.68 \pm 0.13	-3.296	0.001*
Post-adaptation	Fast	0.54 \pm 0.14	-3.296	0.001*
	Slow	0.69 \pm 0.15	-3.296	0.001*

Asterisks indicate statistical significance at a Holm-Bonferroni corrected alpha of 0.05.

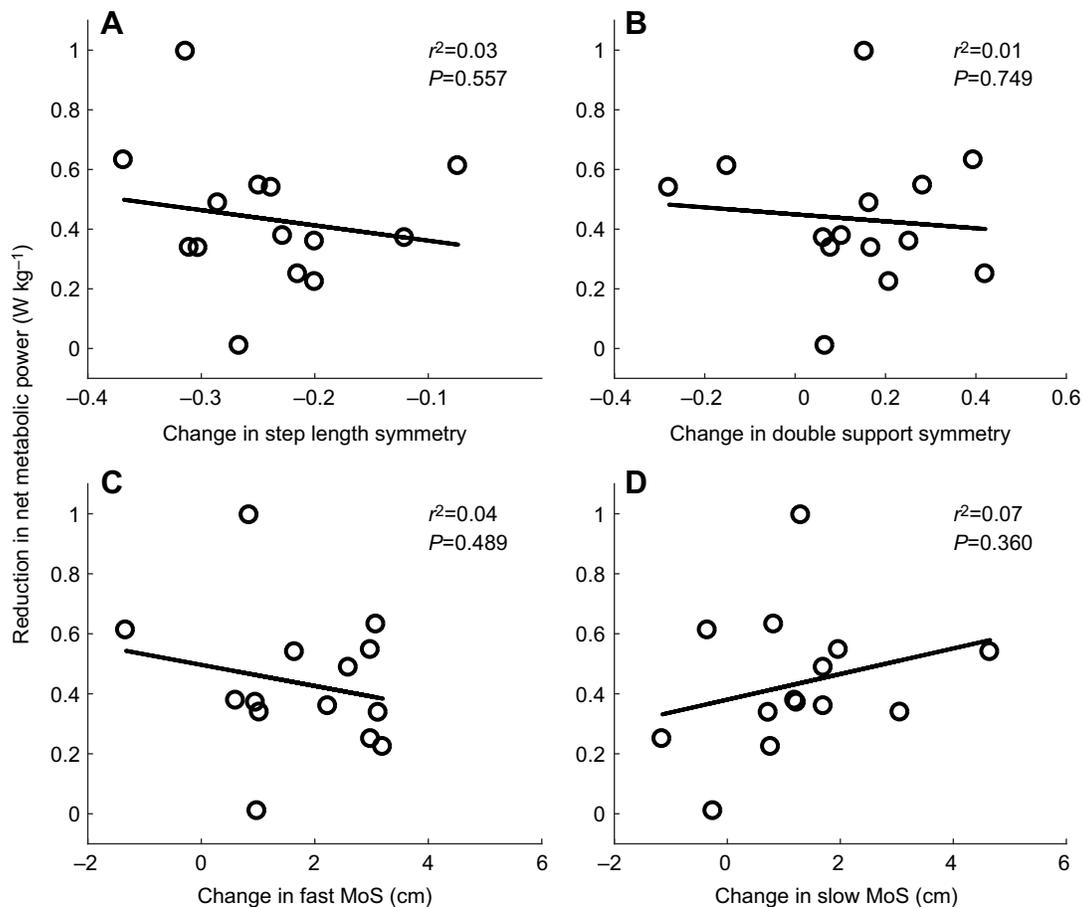


Fig. 6. Group data ($N=14$) for the relationship between the reduction in net metabolic power and step length symmetry, double support symmetry, fast margin of stability (MoS) and slow MoS. Solid lines indicate the linear fit through the group data, open circles indicate results for individual participants.

results in a higher ML MoS (Hak et al., 2013), and as stance time becomes shorter with increased gait speed, the MoS will also increase with belt speed. This leads to the question of whether the observed asymmetry in MoS is a result of active control of dynamic balance, or a passive result of spatiotemporal changes in gait (e.g. changes in stance time). In future research, a more rigorous test is necessary to determine whether the changes and asymmetry in MoS during split-belt gait are the result of active control or the passive dynamics in gait.

A complementary mechanism of relative foot positioning and foot roll-off controls ML dynamic balance during split-belt adaptation

To gain further insight in the control of adaptive dynamic balance, we studied the relationship between initial MoS and ML foot roll-off in the gait cycle. This study has shown that the initial MoS and the subsequent change in ML CoP position were strongly correlated. Recent research (Reimann et al., 2017) suggests that ML foot placement and ML foot roll-off are serially coordinated (i.e. one mechanism responds to changes in the other) in the control of dynamic balance, and that without the possibility of ML foot roll-off, a wider ML foot placement strategy is necessary to maintain upright balance. In line with this, Hof et al. (2007) showed that individuals who walk with an above-knee prosthetic increase their ML MoS on the affected side to compensate for the lack of ML foot roll-off in an above-knee prosthetic leg. The present study shows that a wider ML foot placement strategy is not necessary to cope with imposed

spatiotemporal asymmetry in gait, when ML foot roll-off is available. Furthermore, our results show that the initial MoS and ML foot roll-off are strongly coupled, as shown by the correlational analysis. This complementary mechanism of relative foot positioning and ML foot roll-off showed its flexibility by adapting to split-belt gait. ML foot roll-off is inward in early adaptation, and returned close to baseline values during split-belt adaptation. Although the initial MoS decreased over time during adaptation, the ML Δ CoP increased to maintain stable gait. This shows that a small initial MoS does not necessarily have to result in unstable gait, as the foot roll-off can correct for this. A high initial MoS is followed by an inward foot roll-off. Although this is not necessary to prevent instability, an inward foot roll-off might be necessary to shift the direction of the CoM in time for the next step, or make gait more economical. In short, the complementary mechanism of relative foot positioning and ML foot roll-off presented here represents an active corrective mechanism for maintaining dynamic balance in reaction to sustained perturbations in gait.

Adaptive dynamic balance control is not related to a reduction of metabolic power

The secondary aim of this study was to determine whether adaptive dynamic balance control coincides with a reduction of metabolic power during split-belt adaptation. Dynamic balance control and metabolic power both changed during adaptation to the imposed split-belt perturbation; however, no relationship was found between changes in MoS and changes in MP_{net} . In a recent study (Finley

et al., 2013), a relationship between changes in spatiotemporal step parameters and reduction of metabolic power was found. In contrast, in the present study, we were unable to find this relationship. An explanation for this discrepancy is that different speed ratios were used in Finley et al. (2013) (3:1) and the present study (2:1). A higher split-belt ratio might evoke larger gait asymmetry, which could lead to a more distinct change in metabolic power. Two other possible causes for this discrepancy are: (1) the present study used CoP data to compute step length instead of kinematic data, and (2) the adaptation period in the present study was shorter (9 min) than that in the study by Finley et al. (2013) (12 min). Further research is needed to determine what causes the reduction of metabolic power in split-belt gait and whether this relates to adaptive dynamic balance control.

Implications for adaptive control of human bipedal gait

Human gait is almost unique in its bipedal character and requires control of the distance between ML XCoM and ML foot placement (i.e. relative foot positioning) to maintain dynamic balance. This study has shown a complementary mechanism of relative foot positioning and ML foot roll-off that adapts to a continuously imposed gait asymmetry to maintain dynamic balance. This complementary mechanism shows an asymmetry between the fast and the slow leg in split-belt gait, which suggests that the changes in adaptive dynamic balance control might be the passive result of spatiotemporal changes in gait rather than the active control of balance. Future research should investigate the relationship between dynamic balance control and spatiotemporal control of gait to gain knowledge on adaptive dynamic balance control in human bipedal gait.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: T.J.W.B., C.J.C.L., D.V., L.H.v.d.W., R.d.O.; Methodology: T.J.W.B., C.J.C.L., D.V., L.H.v.d.W., R.d.O.; Software: T.J.W.B., R.d.O.; Validation: T.J.W.B., D.V., R.d.O.; Formal analysis: T.J.W.B., C.J.C.L., D.V., L.H.v.d.W., R.d.O.; Investigation: T.J.W.B., C.J.C.L., D.V., L.H.v.d.W., R.d.O.; Resources: T.J.W.B., R.d.O.; Data curation: T.J.W.B., C.J.C.L., R.d.O.; Writing - original draft: T.J.W.B., C.J.C.L., D.V., L.H.v.d.W., R.d.O.; Writing - review & editing: T.J.W.B., C.J.C.L., D.V., L.H.v.d.W., R.d.O.; Visualization: T.J.W.B., R.d.O.; Supervision: T.J.W.B., C.J.C.L., L.H.v.d.W., R.d.O.; Project administration: T.J.W.B., C.J.C.L., L.H.v.d.W., R.d.O.; Funding acquisition: T.J.W.B., C.J.C.L., L.H.v.d.W., R.d.O.

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