cost during split-belt adaptation and retention of

walking patterns post-adaptation

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Abstract

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Studies of locomotor adaptation have shown that adaptation can occur in short bouts and can continue for long bouts or across days. Information about task duration might influence the adaptation of gait features, given that task duration influences the time available to explore and adapt the aspects of gait that reduce energy cost. We hypothesized that information about task duration influences adaptation to split-belt walking based on two competing mechanisms: individuals anticipating a prolonged adaptation period may either (1) extend exploration of energetically suboptimal gait patterns, or (2) adapt toward a more energy-efficient pattern earlier to maintain an energetic reserve to sustain the task longer. We tested three groups: N=19 participants received minute-by-minute updates during a 10-minute adaptation duration (True group), N=19 participants received no updates during a 10-minute adaptation duration and were misled to expect a prolonged 30-minute adaptation duration (False group), and N=14 participants received one update halfway through a 10-minute adaptation duration (Control group). We measured step length asymmetry, leg work, and metabolic cost. Our results partially supported our hypothesis but did not confirm the underlying mechanisms. While step length asymmetry did not differ significantly between groups during adaptation, the True group generated a more effortful gait pattern with a greater increase in metabolic cost (p=0.002) and higher work with the leg on the slow belt (p=0.012). Additionally, the True group showed no association between step length asymmetry and metabolic cost (p=0.203), contrary to the Control (r=-0.55, p=0.043) and False groups (r=-0.51, p=0.027). Finally, we observed that the False group showed greater retention of the split-belt aftereffects than the Control and False groups (p<0.001). Thus, adapted locomotor and energetic patterns are influenced by information about task duration, indicating that Information about task duration should be controlled for, or can be manipulated to elicit different efforts during adaptation.

Introduction

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Humans continuously adapt locomotor patterns in response to environmental conditions, such as changes in walking terrain, footwear, and load carriage [1–3]. In laboratory settings, split-belt treadmills have been used to study locomotor adaptation, where individuals walk on a treadmill with two separate belts (one for the right limb and one for the left limb) that can be independently controlled to move at different speeds [4,5]. Split-belt walking leads to immediate changes in intralimb coordination and gradual changes in interlimb coordination [5], which are attributed to distinct neural control mechanisms [5,6]. A vast amount of literature has shown that the neuromotor system can adapt to the split-belt's asymmetric environment and retain some of the adaptive changes in locomotion in the short and long term [5,7-10]. The kinematic, kinetic, and physiological changes that occur during short locomotor adaptation bouts of 10-15 minutes [11–21], during long adaptation bouts of 45 minutes [22], or during split-belt adaptation across multiple days [23] have been characterized; it is well established that individuals adapt from walking with asymmetric step lengths toward more symmetric step lengths, reduce positive work by the legs, and reduce metabolic cost during adaptation. However, it is not yet known whether these adapted gait patterns are influenced by the information about different adaptation durations. Empirical [24–26], and simulation studies [27,28] have shown that different cost functions are optimized at different points in the adaptation process: the early stages of locomotor adaptation are associated with the regulation of dynamic balance control, whereas the later stages of locomotor adaptation are associated with reductions in energetic cost. A recent study reported that during a 20-minute split-belt walking protocol, measures of balance adapted in less than a minute, whereas metabolic cost and mechanical work adapted in ~4-6 minutes [25]. Our previous work showed that even after 45 minutes of continuous split-belt walking, individuals

continued to adapt their gait pattern and achieve additional reductions in mechanical work and metabolic energy cost [22]. We also estimated from this prolonged adaptation bout that it takes around 1600 strides or close to 30 minutes to adapt step length asymmetry completely [22]. Adaptation has also been studied using exoskeletons [29–33]. A previous study assessing adaptation to an ankle exoskeleton showed that muscle activation patterns adapted faster than step frequency, and that the variability in step frequencies and muscle activation patterns decreased during adaptation [31]. This higher variability when first exposed to a novel locomotor adaptation task is thought to correspond to exploration of different aspects of the walking pattern to identify strategies that support energetic cost reduction [31,32]. Similarly, other studies using exoskeletons showed different timescales of adaptation to different exoskeleton parameters [29]. Thus, given that multiple domains of locomotor adaptation change over different timescales, we propose that task duration will impact the way people adapt to a novel locomotor task.

Since energetic cost is optimized during the later stages of adaptation, information about a longer task duration might influence the adaptation of the aspects of gait underlying this energetic cost reduction. As individuals adapt their walking pattern to the split-belt treadmill, they reduce step length asymmetry, positive mechanical power, and positive mechanical work generated by their legs [11,19,20,22,24,25], which is associated with a reduction in metabolic cost [11,22]. In fact, studies have shown that walking patterns can change continuously, over different timescales, even for small energetic savings [32–34]. Here, we pose that information about task duration may influence the time course of adaptation of different aspects of gait that reduce energy cost.

The main goal of our study was to determine if information about task duration affects the adaptation of locomotor patterns. We tested the hypothesis that individuals provided with

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Since our hypothesis is based on differences in metabolic cost, we assessed the effect size of detecting a difference in metabolic cost after 10 minutes of adaptation. We obtained metabolic cost measures in N=15 individuals from a previous study that assessed split-belt adaptation duration of 45 minutes [22]. We extracted data during split-belt walking between minutes 1-2 (early adaptation) and 9-10 (late adaptation in the experimental protocol used here). We obtained the mean and standard deviation of the metabolic cost at these points to calculate the effect size needed to detect a reduction in metabolic cost for 10 minutes of adaptation. These data provided an effect size of 0.76. With a sample of 16 individuals in the True and False groups, we would have a power of 0.82 to detect a reduction in metabolic cost. To assess differences in the True group and the False group relative to the locomotor pattern described in typical adaptation studies, we also collected a Control group post-hoc, which, like previous work, was informed about a 10-minute task duration at the beginning of the split-belt adaptation trial and only received one update halfway during adaptation. We collected a Control group of N=14 participants, with a sample size similar to previous studies that showed a reduction in energetic cost and mechanical work during adaptation (Buurke et al. 2018 N=14; Finley et al. 2013 N=11; Selgrade et al. 2017a N=14). This group also allowed us to ensure that any potential differences in our True and False groups are due to the misinformation in the False group or minute-by-minute information of task duration in the True group. Participants between the ages of 18-35 were recruited for this study. Participants were excluded if they had a history of lower extremity surgery or if they had any lower extremity injury such as a fracture or sprain in the last two years, performed more than 10 hours of weekly exercise,

reported current cough, cold, congestion, or any respiratory ailment that affected breathing, had

informed consent before testing. All study aspects conformed to the principles described in the

Declaration of Helsinki.

Data were collected at the Gait Behavior Lab at Chapman University's Department of Physical Therapy using a Gait Real-time Analysis Interactive Lab (GRAIL) system (Motek Medical Base.V., Houten, Netherlands). The GRAIL is equipped with 10 motion capture cameras (Vicon Motion Systems Ltd, Oxford, UK), and an instrumented dual-belt treadmill (Motek Medical Base.V). We used a metabolic cart to measure energetic expenditure (TrueOne 2400, Parvomedics, Salt Lake City, UT, USA). Participants were instructed not to eat or have caffeine at least two hours before the experiment. Before each experiment, we calibrated the motion capture system and the metabolic cart per the manufacturer's specifications. During all walking trials, participants wore a harness to prevent falls, without providing body weight support. Participants did not hold on to a handrail at any point in the experiment.

Experimental Protocol

After informed consent, participants were fitted with a mask covering their nose and mouth to measure their breathing (Fig. 1A). First, participants' resting caloric expenditure was measured while standing for six minutes. Then, participants underwent three walking trials with breaks between each trial until metabolic cost reached standing baseline levels to ensure resting conditions before continuing. The first trial, Baseline (Base), had participants walking for six minutes with the belts under each leg moving at 1.0 m/s. The second trial (Split) had participants walking for 10 minutes with the left belt moving at 1.5 m/s (fast) and the right belt at

0.5 m/s (slow) (Fig. 1B, C). We chose 10 minutes of split-belt adaptation as this duration allows us to observe adaptation of spatiotemporal gait measures [5], metabolic cost [11,42], and work by the legs [19]. Participants were assigned to either the True or False groups via a coin flip to ensure randomization. The True group participants performed the split-belt adaptation trial with true information of how long the trial would last, and they were given an update on the time remaining every minute. The False group participants were given the misleading instruction verbatim: "You will be walking until we obtain the data needed, which can take about 30 minutes". Participants in the False group were not given updates on time elapsed or time remaining, and they also walked for 10 minutes. At the end of the 10th minute, we stopped the treadmill and told participants that we had collected all the necessary data. Participants in the Control group were informed that the task would last 10 minutes and only given an update halfway that they had five minutes remaining. The final trial (Post-adaptation) had participants walking again during a post-adaptation trial for 6 minutes with the belts under each leg moving at 1.0 m/s. All participants received the same instructions for the post-adaptation trial, indicating that this was the final trial and that it would last six minutes.

Fig 1. Experimental setup and protocol. A) Experimental setup showing experimental groups, metabolic mask, and marker location to calculate spatiotemporal variables. From top to bottom, the groups are the Control group (red), the True detailed time information group (green), and the False time information group (blue). B) Split-belt configuration.

For all participants, the left belt was set at 1.5 m/s and the right belt at 0.5 m/s. 52 participants reported the right leg as the leg they would use to kick a ball. C)

Experimental protocol. Bars indicate each belt, and numbers indicate belt speed. Bar width indicates the duration of each experimental condition. Participants reported their rate of perceived exertion during the time points identified by the arrows. S: Standing. B: Baseline. EA: Early adaptation. MA: Mid-adaptation. LA: Late adaptation. EP: Early post-

adaptation. LP: Late post-adaptation. GTRO: Greater Trochanter. LEPI: Lateral

Epicondyle. LMAL: Lateral Malleolus.

Participants were asked to rate their level of exertion via the modified Borg Rating of Perceived Exertion (RPE) (Borg, 1962) using their fingers, since they were wearing the metabolic mask, to indicate on a scale of 1-10 which level of the RPE table they perceived. During the Base trial, participants reported RPE at the five minute mark. During the Split trial, they were asked to rate their level of exertion at the one (early adaptation – EA), five (mid-adaptation – MA), and nine minute (late adaptation – LA) marks. During the tied post-adaptation trial, participants rated their RPE at the one (early post-adaptation – EP) and five minute marks (late post-adaptation – LP) (Fig. 1C).

Data Acquisition

We recorded marker data to calculate spatiotemporal variables and force data to calculate work by the legs. The positions of reflective markers located bilaterally on the greater trochanter, lateral epicondyle of the femur, and lateral malleolus were recorded at 100 Hz (Fig.1A). Force plates embedded into the split-belt treadmill recorded the ground reaction forces generated by each leg with a sampling frequency of 1000 Hz. Metabolic cost was recorded by determining the rates of oxygen consumption (VO₂) and carbon dioxide production (VCO₂). We also collected heart rate (HR) as a measure of cardiovascular intensity using a Polar H10 chest strap monitor (Polar Electro Inc., Bethpage, NY, USA), synchronized to the metabolic cart.

Data Processing and Analysis

We used custom-written code in MATLAB R2023b (Mathworks, Natick, MA, USA) for all data processing and analyses as in previous work [22,34]. We estimated the energy consumed using

the standard Brockway equation to obtain metabolic rate [43]. We subtracted each participant's standing metabolic rate from each walking trial. Thus, all metabolic rate values presented here are net metabolic rates. A fourth-order low-pass digital Butterworth filter smoothed marker data and ground reaction force data using cut-off frequencies of 10 Hz and 20 Hz, respectively. We calculated step lengths using marker data, defined as the distance between the lateral malleoli markers at the instance of peak anterior position of the respective marker. Step length asymmetry was then defined as follows:

$$SLA = \frac{SL_{fast} - SL_{slow}}{SL_{fast} + SL_{slow}}$$
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With SL_{fast} representing the step length at heel strike of the fast leg, and SL_{slow} representing the step length at heel strike of the slow leg. We calculated leading and trailing limb placement for each limb as the fore-aft distance of the ankle markers relative to the midpoint between markers placed bilaterally on the greater trochanters.

We estimated the mechanical work performed by the legs using an extension of the individual limbs method [19,20,22,34,44,45]. This method approximates the legs as massless pistons and the entire body as a point mass. We measured individual leg ground reaction forces from the instrumented treadmill, and segmented forces into strides using a vertical ground reaction force threshold of 32 N [19] to identify the beginning and end of each stride. We calculated the mediolateral, fore-aft, and vertical center of mass velocities by integrating the center of mass accelerations. We then calculated mechanical power as the dot product between the center of mass velocity and the ground reaction force from each leg. To determine the total positive and negative work performed by a leg or a belt, we calculated the time integral of the positive or negative portion of the mechanical power over the stride cycle. Work was normalized by leg length and mass to derive unitless mechanical work. We calculated leg length as the distance between the greater trochanter markers and the ground during standing.

We derived variability during adaptation as in a previous study [31]. We determined the variability by applying a high-pass filter with a cut-off frequency of 0.033 steps⁻¹, and then calculated the standard deviation of this filtered signal during the initial, middle, and final minute of the trial. The variability was expressed as a normalized value relative to Base variability. We assessed variability in variables that represent different constructs of adaptation: step length asymmetry, which is used to track adaptation, net work due to its relationship to metabolic cost, and step width as a proxy for balance.

Statistical Analyses

Statistical analyses were run in R version 4.2.2 and MATLAB R2023b. We assessed data for normality using the Shapiro-Wilk test. We compared age, height, and weight between the three experimental groups using one-way ANOVA or Kruskal-Wallis tests for not normally distributed data.

We obtained average values for step length asymmetry, step lengths, step width, and positive and negative work for each leg for the last five strides of the Base trial. For EA, MA, and LA we averaged the first, middle, and last five strides of the Split trial [26]. For the Post trial, we averaged the first five and last five strides (EP, LP, respectively). These are close to the time points when we obtained RPE and average measures of metabolic cost.

The metabolic power for the Base condition was computed by averaging the power for the last two minutes. The metabolic power for EA, MA, and LA was averaged between the second and third minutes, the fifth and sixth minutes, and the ninth and tenth minutes, respectively, of the

Split condition to match the RPE reporting periods (Figure 1C). We used the second instead of the first minute for metabolic data as the average duration to reach peak metabolic power is around one minute [11,46]. Finally, the metabolic power for the Post-adaptation condition was averaged between the second and third minutes and the fifth and sixth minutes of this condition to obtain average values of metabolic cost for EP and LP, respectively.

We tested differences during the Base condition between groups using linear models with group (Control, True, False) as a categorical predictor and all outcome variables as a continuous response, to assess if there are baseline differences between groups that could have influenced our results. As the goal of our analysis was to observe differences within the Split and Post-adaptation conditions between groups, we ran separate models for these conditions. For the Split condition, we used linear models with time (EA, MA and LA) and group (Control, True, False) as categorical variables. We also included the value for the respective outcome measured during Base as a covariate, and its interaction with group and time, given that we observed that the response during the adaptation task depended on baseline walking characteristics. For the Post-adaptation condition, we used linear models with time (EP and LP) and group (Control, True, False) as categorical variables. We also included the value for the respective outcomes measured during Base as a covariate and its interaction with group and time. The models had the general form of:

$$x_{Split/Post} \sim Group * Time + x_{Base} * Time + x_{Base} * Group$$
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where *x* is the scaled value measured during either the split-belt task or post-adaptation for any of the following outcomes: metabolic cost, step length asymmetry, step width, positive and negative work by each leg. Results for heart rate and rating of perceived exertion, step lengths, and step times are included in the Supplementary Materials. The reference level for the linear models for group was set as Control group, and for time was set as EA for the split-belt models and EP for the post-adaptation models. We assessed residual plots for each model to ensure

discovery rate. We also assessed individual correlations between metabolic cost, work, step

length asymmetry and step lengths between groups. To allow comparison of correlation

coefficients for different sample sizes, we used a Fisher transformation of the resulting

correlation coefficients.

To assess differences in variability, which we use here to quantify exploration, we used a linear

model of the form:

$$variability_{x Split/Post} \sim Group * Time$$
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Where *x* is either step length asymmetry, step width or net work. Since the variability data were normalized to Base, we did not use Base as a covariate. The reference level for this model was the Control group during EA.

Results

N = 52 participants volunteered for this study: Control group - N=14, True group - N=19, False group - N=19. No significant differences were observed in participant demographics between groups (Table 1). Metabolic cost and kinematic data were collected for all participants. Heart rate data was missing in six participants due to Bluetooth connectivity issues (three in the Control group, one in the True group, and two in the False group). Force data was collected from all participants except one in the False group, for whom force data were corrupted, which hindered performing mechanical calculations. Data for all participants, as available, were included in all analyses.

Table 1

Group	Control	True	False	
N	14	19	19	
Age (yrs)	23.2 ± 3.4	24.8 ± 3.4	25.7 ± 4.7	p=0.191
Height (cm)	170 ± 10	167 ± 8.2	167 ± 9.2	p=0.446
Weight (kg)	70.2 ± 12.9	73.0 ± 13.1	67.6 ± 13.6	p=0.458

Table 1: Participant demographics for both experimental groups are reported as mean ± standard deviation. P-values for one way ANOVA and for Chi-Square tests show no differences in group demographics.

We did not observe significant differences in any of our outcome variables between groups during the Base condition that could have influenced the Split or Post-adaptation results (p>0.352, Table 2).

Table 2

Group	Control	True	False	
Metabolic Cost (W)	2.26 ± 0.51	2.47 ± 0.42	2.43 ± 0.51	p= 0.487
Heart Rate (bpm)	100 ± 14	100 ± 12	94 ± 12	p=0.352
RPE	2.0 ± 0.75	1.75 ± 1.0	2.0 ± 0.92	p=0.675
Step Length Left (mm)	514 ± 36	509 ± 28	511 ± 24	p=0.900
Step Length Right (mm)	509 ± 46	500 ± 24	508 ± 29	p=0.682

Table 2: Biomechanical and physiological characteristics for participants in the three groups during the Base trial walking with belts tied at 1.0 m/s. Data are reported as means ± standard deviation. P-values for linear models using group as a categorical predictor. bpm: beats per minute. RPE: rating of perceived exertion 1-10 scale.

Information about task duration did not influence step length

asymmetry during split-belt adaptation

We hypothesized different adaptation patterns between groups. The linear model assessing step length asymmetry as a function of group, time and baseline asymmetry during split-belt adaptation returned a significant intercept (β_0 =-0.30, 95%CI [-0,36, -0.25], p<0.001), and a significant main effect of time (β_{TimeMA} =0.24, 95%CI [0.16, 0.32], p<0.001 and β_{TimeLA} =0.28,

95%CI [0.20, 0.36], p<0.001) indicating a reduction in asymmetry during adaptation across groups. We also observed an effect of the False group (β_{GroupF} =-0.08, 95%CI [-0.15, 0.01], p=0.036), indicating that the False group was slightly more asymmetric but this more negative asymmetry was offset by a marginal interaction between the False group and MA ($\beta_{GroupF:TimeMA}$ =0.09, 95%CI [-0.01, 0.20], p=0.072) and the False group and LA ($\beta_{GroupF:TimeLA}$ =0.10, 95%CI [-0.01, 0.20], p=0.068) (adjusted R²=0.66) (Fig. 2A-B). Contrary to our hypothesis, we observed a similar adaptation of step length asymmetry across groups.

Fig 2. Step length asymmetry and step width during split-belt adaptation. A) Step length asymmetry timeseries during the split-belt walking between the control (Control – red), true information about task duration (True – green), and false information of task duration (False - blue) groups. Time windows indicating EA, MA, and LA are indicated in the figure. B) Distribution of average step length asymmetry between groups during the five strides corresponding to EA, MA, and LA. Across groups, asymmetry decreased from EA to MA and LA. (p<0.001) C) Distribution of average step widths. No differences over time or between groups were observed. Abbreviations as in Figures 1 and 2.

The linear model assessing step width as a function of group, time, and baseline asymmetry during split-belt adaptation returned a significant intercept (β_0 =281, 95%CI [267, 294], p<0.001) and a significant effect of baseline step width (β_0 =19, 95%CI [10, 28], p<0.001) but no effect of group or time (Fig. 2C), indicating that individuals did not adapt step width (adjusted R²=0.34). We did not see differences between groups for fast and slow step lengths, swing times, and limb placements (Supplementary Materials).

Information about task duration influenced metabolic cost

during split-belt adaptation

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We hypothesized differences in metabolic cost between groups during adaptation. The linear model assessing metabolic cost as a function of group, time, and baseline cost during split-belt adaptation returned a significant intercept (β_0 =3.30, 95%CI [3.04, 3.96], p<0.001), a significant main effect of baseline metabolic cost (β_{Base}=0.30, 95%CI [0.13, 30.48], p<0.001), and a significant main effect of LA (β_{TimeLA} =-0.39, 95%CI [-0.76, 0.03], p=0.035) indicating that across all groups, participants reduced cost from EA to LA. The model returned a significant interaction between the True group and baseline metabolic cost (β_{GroupT:BaseMet}=0.32, 95%CI [0.11, 0.52], p=0.002) (adjusted R²=0.66). Estimated marginal trends of the slope between baseline metabolic cost with split-belt metabolic cost by groups show a greater slope in the True group compared to both the Control group (slope True = 1.27 vs slope Control = 0.62, p=0.007) and the False group (slope False = 0.84, p=0.044), indicating a greater increase in the True group's metabolic cost relative to baseline metabolic cost during split-belt adaptation (Fig. 3A-C). These results support our hypothesis of different costs between groups. However, these different costs were due to an increased rate of change from baseline metabolic cost in the True group, contrary to our two mechanistic hypotheses. Heart rate and RPE results are presented in the Supplementary Materials (Supplementary Figure 1).

Fig 3. Metabolic cost, heart rate, and perception of effort during split-belt adaptation. A) Net metabolic power timeseries during the split-belt walking between the control (Control – red), true information of task duration (True – green) and false information of task duration (False - blue) groups. Time windows indicating EA, MA, and LA are indicated in the figure. B) Slopes of the relationship between metabolic cost

during baseline and metabolic cost during EA, MA and LA. A significantly greater slope was observed in the True group compared to both the Control and False groups (adjusted p<0.050). C) Average metabolic cost during EA, MA, and LA. A significant reduction in metabolic cost from EA to LA was observed across groups. Other abbreviations as in Figure 1 and Table 2.

Information about task duration influenced positive work

during split-belt adaptation

We hypothesized that less mechanical work would be performed in the less metabolically costly group. The linear model assessing positive work by the fast leg as a function of group, time and baseline work during split-belt adaptation returned a significant intercept (β_0 =0.036, 95%CI [0.032, 0.040], p<0.001), a significant main effect of baseline work by the fast leg (β_{Base} =0.005, 95%CI [0.002, 0.008], p<0.001), an effect of time (β_{TimeMA} =-0.011, 95%CI [-0.017, -0.006], p<0.001 and β_{TimeLA} =-0.013, 95%CI [-0.018, -0.008], p<0.001) but no effect of group (adjusted R²=0.52). Contrary to our hypothesis, the model suggests that all individuals across groups similarly reduced positive work by the fast leg during adaptation (Fig. 4A, C).

Fig 4. Positive work by the fast and slow legs during split-belt adaptation. A)

Timeseries of positive work by the fast leg. B) Timeseries of positive work by the slow leg. C) Distribution of average positive work by the fast leg between groups during the five strides corresponding to EA, MA, and LA. We observed a significant reduction in work from EA to MA and LA across groups. D) Distribution of average positive work by the right leg between groups during the five strides corresponding to EA, MA, and LA.

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We observed significantly higher work in the True group (p=0.012). W⁺: positive work. Other abbreviations as in Figures 1 and 2. The linear model assessing positive work by the slow leg as a function of group, time and baseline work during split-belt adaptation returned a significant intercept (β₀=0.013, SE=0.0014, p<0.001), a significant main effect of baseline work by the slow leg (β_{Base} =0.003, SE=0.0010, p=0.010), and a significant main effect of True group (β_T =0.005, SE=0.0018, p=0.012). These results indicate that positive work by the slow leg in the True group was significantly higher during adaptation than in the Control and False groups (adjusted R²=0.34) (Fig. 4B, D). Thus, supporting our hypothesis, we observed differences in positive work by the slow leg between groups, with the less costly groups (Control and False) generating less positive work. However, consistent with the metabolic cost findings, this was due to increased positive work with the slow leg in the True group. Results for negative work are presented in the Supplementary Materials (Supplementary Figure 2). Information about the duration of split-belt adaptation influenced the association between biomechanical and metabolic changes We found a significant association between the change in step length asymmetry and the

change in metabolic cost for the Control group (r=-0.55, Fisher transformed r=-0.61, p=0.043) and for the False group (r=-0.51, Fisher transformed r=-0.56, p=0.027). We did not observe an association between metabolic cost and asymmetry in the True group (r=-0.31, Fisher transformed r=-0.32, p=0.203) (Fig. 5A).

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group.

Fig 5. Associations between biomechanical and metabolic measures. A) Association between change in step length asymmetry and change in metabolic cost from EA to LA. B) Association between change in positive work by the fast leg and change in metabolic cost from EA to LA. C) Association between change in positive work by the slow leg and change in metabolic cost from EA to LA. D) Association between change in positive work by the fast leg and change in step lengths by the fast leg from EA to LA. E) Association between change in positive work by the slow leg and change in step lengths by the fast leg from EA to LA. Abbreviations as in Figures 1 and 2. We found a significant association between the reduction in positive work by the fast leg and change in metabolic cost for the False group (r=0.67, Fisher transformed r=0.81, p=0.002), but not in the Control (r=0.50, Fisher transformed r=0.54, p=0.071) or True (r=0.41, Fisher transformed r=0.44, p=0.079) groups (Fig. 5B). We did not find an association between the reduction in positive work by the slow leg and change in metabolic cost (Fig. 5C). We found a significant association between the change in step lengths of the fast and slow leg and the change in positive work by the fast leg in the False group (r=-0.69, Fisher transformed r=-0.83, p=0.002 for fast step lengths and r=0.55, Fisher transformed r=0.62, p=0.017, for the slow leg) (Fig. 5D-E). We observed a significant association between the change in step lengths of the fast leg and positive work by the fast leg in the True group (r=-0.77, Fisher transformed r=-1.02, p<0.001) (Fig. 5D). We did not observe a significant association between the change in step lengths and work in the Control group or change in slow step lengths and work in the True

Information about task duration influenced the exploration of

walking patterns during adaptation

The linear model assessing variability in step length asymmetry as a function of group and time returned a significant intercept (β_0 =4.66, 95%CI [3.51, 5.81], p<0.001), a significant effect of time (β_{TimeMA} =-2.52, 95%CI [-4.15, -0.89], p=0.003 and β_{TimeLA} =-2.51, 95%CI [-4.14, -0.88], p=0.003), a significant effect of group (β_{GroupT} =2.40, 95%CI [0.88, 3.91], p=0.002 and β_{GroupE} =2.73, 95%CI [1.22, 4.25], p<0.001) and a significant interaction between time and group ($\beta_{TimeLA:GroupT}$ =-2.42, 95%CI [-4.57, -0.27], p=0.027, $\beta_{TimeMA:GroupT}$ =-3.14, 95%CI [-5.29, -0.99], p=0.004, $\beta_{TimeLA:GroupT}$ =-2.99, 95%CI [-5.13, -0.84], p=0.007) (adjusted R²=0.49). Post-hoc comparisons indicated significantly higher variability, indicating more exploration in the True and False groups during EA compared to the Control group (p<0.005) (Fig. 6A). We did not observe differences between MA and LA in variability as a measure of exploration. Thus, both the True and False groups had more exploration during EA than the Control group, contrary to one of our mechanistic hypotheses that the False group might spend more time exploring suboptimal locomotor patterns. The linear models assessing variability in step widths, and net work identified a significant main effect only of time but not of group, indicating that variability in step width and work decreased from EA to MA and LA similarly across groups (Fig. 6B-C).

Fig 6. Variability of gait features during adaptation. A) We observed significant differences between groups in step length asymmetry variability during EA. Variability significantly decreased during MA and LA. No differences between groups were observed during MA and LA. B) Variability in step widths decreased over timepoints

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across all groups. C) Variability in net work decreased over timepoints across all groups. Abbreviations as in Figures 1 and 2.

Information about task duration during split-belt adaptation influenced step length asymmetry during post-adaptation

We hypothesized no differences during post-adaptation between groups. The linear model assessing step length asymmetry as a function of group, time and baseline asymmetry during post-adaptation returned a significant intercept (β₀=0.24, 95%CI [0.20, 0.28], p<0.001), a significant main effect of baseline asymmetry (β_{Base}=0.05, 95%CI [0.02, 0.08], p=0.003), a significant main effect of LP (β_{Timel P}=-0.22, 95%CI [-0.28, -0.16], p<0.001), a significant effect of False group (β_{GroupF}=0.12, 95%CI [0.07, 0.18], p<0.001), a significant interaction between False group and LP (β_{GroupE:TimeLP}=-0.11, 95%CI [-0.19, -0.03], p=0.006) and a significant interaction between LP and baseline asymmetry ($\beta_{Base:TimeLP}$ =-0.04, 95%CI [-0.07, -0.005], p=0.022) (adjusted R²=0.77). Overall, these results indicate a reduction in asymmetry from EP to LP for all groups. Surprisingly, we found a higher asymmetry in the False group compared to the Control (p<0.001) and True groups (p<0.001) during EP, indicating a greater after-effect of the split-belt (Fig. 7 C-D). This contradicts our hypothesis that the post-adaptation locomotor pattern would be similar between groups. The after-effect in the False group can be explained by changes in the right leg, previously on the slow belt (Fig. 4-5). The linear model assessing right step lengths as a function of group, time, and baseline step lengths during post-adaptation returned a significant intercept (β_0 =347, 95%CI [318, 376], p<0.001), a significant main effect of baseline step lengths (β_{Base}=38, 95%CI [20, 56], p<0.001), a significant main effect of LP $(\beta_{TimeLP}=157, 95\%Cl [117, 198], p<0.001)$, a significant effect of the False group $(\beta_{GroupF}=-70, p=0.001)$ 95%CI [-107, -32], p<0.001), and a significant interaction between the False group and LP

 $(\beta_{GroupF:TimeLP}=63, 95\%CI [10, 116], p=0.043)$ (adjusted R²=0.77). Overall, these results indicate that step length on the right leg remains shorter during EP in the False group compared to the Control group (p<0.001) and the True group (p<0.001) (Fig. 7E). No differences between groups were observed for the left leg, which was previously on the fast belt. Results for metabolic cost and work are included in the Supplementary Materials (Supplementary Figure 3).

Fig 7. Step length asymmetry and work during post-adaptation. A) Step length asymmetry timeseries. B) Average step length asymmetry during EP, and LP. Participants in the False group had a greater asymmetry during EP compared to the Control and True groups (p<0.001). C) Average step lengths by the right leg during EP, and LP. Participants in the False group had a shorter step length with the right leg during EP compared to the Control and True groups (p<0.001). Abbreviations as in Figures 1 and 2.

Discussion

Studies of motor adaptation have shown that adaptation begins within the first minute and continues even after 45 minutes of adaptation to split-belt walking [22–25,29,31,47]. Information about task duration might influence the adaptation of gait features to reduce energy cost, which is considered to be the cost function in the later stages of adaptation [22,27,28,33]. Here, we manipulated the information about task duration during split-belt walking adaptation in neurotypical young adults. Our results partially supported our hypotheses: while we found

differences in adaptation between individuals who knew about a short task duration compared to those who planned to adapt for 30 minutes, the mechanisms underlying these differences contradict our hypotheses. We found that individuals who had detailed, true information about task duration (True group) had a greater increase in metabolic cost from baseline, generated more positive work with the slow leg and less negative work with the fast leg compared to individuals who did not have detailed information about task duration (Control and False groups). The biomechanical strategies adopted in the True group are the opposite of what has been previously reported to reduce energetic cost during split-belt walking [22,34]. These results support the idea that information about task duration influences the adaptation of walking patterns towards patterns with different energetic costs.

We observed a strong relationship between gait biomechanics and energetic cost in individuals who believed they would sustain the task longer (False group), supporting our second mechanistic hypothesis that individuals may adapt toward a lower cost to maintain an energetic reserve [35]. Surprisingly, the biomechanical strategies that supported this energetic reduction differed from those we hypothesized. We originally expected to see more positive asymmetries due to longer steps with the fast leg, which also allows for more negative work and less positive work by the fast leg [22,34]. We found that the reduction in metabolic cost in the False group correlated with step length asymmetry [22], but this correlation stemmed from changes in the step lengths of the slow leg, not the fast leg. Specifically, the shortening of the slow step length during adaptation was proportional to the reduction in metabolic cost. This is an interesting finding since linear models indicated that, at the group level, there was no change in the slow leg's step lengths from EA to LA. It might be the case that the slow leg adjustments are heterogeneous across individuals, such that there is no group-level effect. Adjustments in step length with the slow leg, rather than the fast leg, may result in a smaller energetic penalty [31], and could supplement other adjustments previously reported [22]. Based on this discussion, we

assessed the changes in step lengths; we observed that both the change in slow leg step length (r=0.55, p=0.017) and the change in fast leg step length (r=-0.68, p=0.002) were correlated with the change in positive work by the fast leg in the False group, but not in the Control and True groups, supporting the idea that the added slow leg adjustments aim at reducing work during adaptation.

Our results assessing the exploration of walking patterns were surprising. We observed greater variability in step length asymmetry upon initial split belt exposure in the True and False groups compared to the Control group (Figure 6A). However, this occurred only for step length asymmetry and not for step width or work, indicating that there might be another difference in participant characteristics that potentially influenced these findings. Similar to previous literature [31], we found reductions in variability indicating reductions in exploration across different domains from EA to MA and LA. However, between groups, we found that from MA to LA variability was not different between groups, indicating both similar duration and magnitude of exploration of step length asymmetry over the 10 minutes of adaptation. Thus, our results indicate that information about a longer or shorter task duration did not influence exploration of walking patterns systematically.

Based on our results, a question regarding the True group arises: What cost function was prioritized during split-belt adaptation? Studies have shown that other cost functions can be prioritized over metabolic costs, such as muscle activations [48], comfort [49], time [50], or balance [51]. Since the speed of the belts and the trial duration are fixed, no strategy would reduce task duration as in other studies [50,52,53]. Another potential explanation relates to the anticipatory regulatory model in physiology, which states that the central nervous system modulates muscle recruitment and power generation based on expected exercise duration [35,36], with muscle recruitment and power generation directly influencing energetic

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consumption [54,55]. The idea of an anticipatory regulatory model is supported by a common phenomenon observed in exercise known as the end spurt, where effort generation decreases over time but increases when individuals are informed that the end of the task is approaching [56,57]. An example of this anticipatory regulation can be seen when cyclists increase power generation as the distance to the endpoint decreases [58,59]. Furthermore, if the distance to the endpoint is unknown, cyclists will maintain lower power generation than when these same participants knew the distance to the endpoint [59]. In another study on runners, individuals who believed they would run for longer had lower perceived exertion throughout the task compared to those who were informed of a shorter task duration [59]. While we also did not observe a clear end spurt [56], we saw increased work of the slow leg throughout adaptation, which might indicate that the entire 10-minute task was performed as the end spurt due to the short task duration and moderate effort of the split-belt task. Another alternative explanation is that the cost functions in the True group are the same, mainly balance and energetic cost, but the time during adaptation, where each cost function shapes the gait pattern, differs from what has been previously reported [25,28]. Based on our step width results as a proxy for balance (Fig. 2C), while not significant, there appears to be a visually apparent difference in step widths among participants in the True group, with participants in this group showing wider steps than those in the Control and False groups. Thus, it could be the case that for a short time duration and detailed task information, energetic cost becomes less of a priority, and other cost functions are optimized over a longer timescale.

Another key and surprising finding of our study is that information about task duration influenced the aftereffect of the split-belt walking pattern. Previous work has shown that split-belt aftereffects during post-adaptation can vary in different pathological populations [60–62], when adapting through gradual adjustments of the belt speeds and a longer adaptation time [63], or when using visual feedback [15]. Here, we found that individuals who received false information

about a longer task duration experienced a greater aftereffect when the belts returned to moving at the same speed. This aftereffect was measured as a more positive step length asymmetry during EP, due to the step lengths on the right leg remaining shorter in the False group compared to the Control and True groups. These shorter steps on the right leg were consistent with the strategy that supported energetic cost reduction during split-belt walking in the False group. Two potential mechanisms might explain this aftereffect. On one hand, the increased aftereffect in the False group might indicate an initial selection of a previously experienced more optimal gait pattern, supporting the idea that individuals select these patterns even for small energetic savings [32]. On the other hand, it may be that the False group, who not only received false information at the beginning of the task but also received no updates during the split-belt task, adapted in a more implicit manner, as less awareness was directed to the task compared to the True and Control groups; known to increase retention and transfer of the adapted gait pattern [63,64].

Our study has several limitations. First, we did not systematically assess fitness levels across participants. While our criteria excluded people who, at the time of the experiment, exercised more than 10 hours per week, we did not exclude sedentary participants or those with a prior history of participation in high-performance sports. As such, we cannot determine if either group had different levels of fitness, which has been shown to affect energetic expenditure [65] and adaptation [24]. This seems to be the case for the Control group, which exhibited a lower level of metabolic cost during split-belt adaptation. We controlled for these differences in our statistical analyses by using baseline costs as a covariate. Previous research has shown that the amount of mechanical work reduction during adaptation is influenced by the timing of work generation during the pendular phase of gait [19,20]. Our study did not assess whether our experimental manipulation affected this pendular work generation. The different contexts created by the various types of instructions in each group may have led to differences in

autonomic responses. While we measured heart rate, we were unable to obtain measures of heart rate variability to determine sympathetic activation during the task in each group, which could explain differences in heart rate and metabolic cost responses [66]. Finally, we used step width as a proxy for balance since our marker set did not allow for the assessment of more sensitive measures of balance during adaptation, such as extrapolated center of mass [25,42] or whole body angular momentum [26,67], which may have hindered our ability to measure additional balance adjustments in our protocol.

Conclusion

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Humans continuously adapt their locomotor patterns. Adaptation of kinematics, kinetics, and metabolic cost has been reported during split-belt walking protocols of varying durations. However, it is still unknown whether these adapted gait patterns are influenced by different adaptation durations. We manipulated information about task duration during split-belt walking in young adults. We found that when individuals receive detailed information about a short task duration, they perform the task in an effortful and energetically costly manner, and the changes in energetic cost are not associated with changes in gait biomechanics. In contrast, the strength of the association between changes in energetic cost and changes in biomechanics seems to depend on uncertainty regarding task duration. We also found that information about longer task duration led to greater aftereffects during post-adaptation, indicating that planning to sustain a task for longer can influence the retention of walking patterns. The simplest implication of our findings is that adapted locomotor and energetic patterns are influenced by information about task duration; as such, task duration information should be controlled and clarified during experimental paradigms of motor adaptation. Our findings also imply that information about task duration can be manipulated to elicit different efforts and varying retention of adapted patterns, which can have implications for movement interventions in patient populations, particularly

Data Availability

A detailed R-markdown with statistical models and the data used for statistical analyses for this manuscript are available at: DOI 10.17605/OSF.IO/AW6XK https://osf.io/aw6xk/
Raw data are available upon reasonable request to the corresponding author.

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References

- Marigold DS, Patla AE. Age-related changes in gait for multi-surface terrain. Gait &
 Posture. 2008;27: 689–696. doi:10.1016/j.gaitpost.2007.09.005
- Bruijn SM, van Dieën JH. Control of human gait stability through foot placement. J R Soc Interface. 2018;15: 20170816. doi:10.1098/rsif.2017.0816
- Kowalsky DB, Rebula JR, Ojeda LV, Adamczyk PG, Kuo AD. Human walking in the real
 world: Interactions between terrain type, gait parameters, and energy expenditure. Kao P c, editor. PLoS ONE. 2021;16: e0228682. doi:10.1371/journal.pone.0228682
- 4. Dietz V, Zijlstra W, Duysens J. Human neuronal interlimb coordination during split-belt locomotion. Exp Brain Res. 1994;101: 513–520. doi:10.1007/BF00227344
- Reisman DS, Block HJ, Bastian AJ. Interlimb Coordination During Locomotion: What Can
 be Adapted and Stored? Journal of Neurophysiology. 2005;94: 2403–2415.
 doi:10.1152/jn.00089.2005
- 692 6. Gonzalez-Rubio M, Velasquez NF, Torres-Oviedo G. Explicit Control of Step Timing
 693 During Split-Belt Walking Reveals Interdependent Recalibration of Movements in Space
 694 and Time. Front Hum Neurosci. 2019;13: 207. doi:10.3389/fnhum.2019.00207
- Malone LA, Bastian AJ. Thinking About Walking: Effects of Conscious Correction Versus
 Distraction on Locomotor Adaptation. Journal of Neurophysiology. 2010;103: 1954–1962.
 doi:10.1152/jn.00832.2009
- 8. Malone LA, Bastian AJ. Age-related forgetting in locomotor adaptation. Neurobiology of Learning and Memory. 2016;128: 1–6. doi:10.1016/j.nlm.2015.11.003
- 700 9. Torres-Oviedo G, Bastian AJ. Seeing Is Believing: Effects of Visual Contextual Cues on
 701 Learning and Transfer of Locomotor Adaptation. Journal of Neuroscience. 2010;30:
 702 17015–17022. doi:10.1523/JNEUROSCI.4205-10.2010
- 10. Torres-Oviedo G, Vasudevan E, Malone L, Bastian AJ. Locomotor adaptation. Progress in Brain Research. Elsevier; 2011. pp. 65–74. doi:10.1016/B978-0-444-53752-2.00013-8
- 705 11. Finley JM, Bastian AJ, Gottschall JS. Learning to be economical: the energy cost of walking tracks motor adaptation: Split-belt adaptation reduces metabolic power. The Journal of Physiology. 2013;591: 1081–1095. doi:10.1113/jphysiol.2012.245506
- Hinton DC, Thiel A, Soucy J-P, Bouyer L, Paquette C. Adjusting gait step-by-step: Brain activation during split-belt treadmill walking. NeuroImage. 2019;202: 116095.
 doi:10.1016/j.neuroimage.2019.116095
- 711 13. Stenum J, Choi JT. Step time asymmetry but not step length asymmetry is adapted to 712 optimize energy cost of split-belt treadmill walking. The Journal of Physiology. 2020;598: 713 4063–4078. doi:10.1113/JP279195

- 714 14. Jacobsen NA, Ferris DP. Electrocortical activity correlated with locomotor adaptation
 715 during split-belt treadmill walking. The Journal of Physiology. 2023;601: 3921–3944.
- 716 doi:10.1113/JP284505
- 717 15. Roemmich RT, Long AW, Bastian AJ. Seeing the Errors You Feel Enhances Locomotor 718 Performance but Not Learning. Current Biology. 2016;26: 2707–2716. doi:10.1016/j.cub.2016.08.012
- 720 16. Kambic RE, Roemmich RT, Bastian AJ. Joint-level coordination patterns for split-belt
 721 walking across different speed ratios. Journal of Neurophysiology. 2023;129: 969–983.
 722 doi:10.1152/jn.00323.2021
- 723 17. Roemmich RT, Stegemöller EL, Hass CJ. Lower extremity sagittal joint moment production 724 during split-belt treadmill walking. Journal of Biomechanics. 2012;45: 2817–2821. 725 doi:10.1016/j.jbiomech.2012.08.036
- Mawase F, Haizler T, Bar-Haim S, Karniel A. Kinetic adaptation during locomotion on a split-belt treadmill. Journal of Neurophysiology. 2013;109: 2216–2227.
 doi:10.1152/jn.00938.2012
- 729 19. Selgrade BP, Thajchayapong M, Lee GE, Toney ME, Chang Y-H. Changes in mechanical
 730 work during neural adaptation to asymmetric locomotion. Journal of Experimental Biology.
 731 2017; jeb.149450. doi:10.1242/jeb.149450
- 732 20. Selgrade BP, Toney ME, Chang Y-H. Two biomechanical strategies for locomotor
 733 adaptation to split-belt treadmill walking in subjects with and without transtibial amputation.
 734 Journal of Biomechanics. 2017;53: 136–143. doi:10.1016/j.jbiomech.2017.01.012
- Betschart M, Lauzière S, Miéville C, McFadyen BJ, Nadeau S. Changes in lower limb
 muscle activity after walking on a split-belt treadmill in individuals post-stroke. Journal of
 Electromyography and Kinesiology. 2017;32: 93–100. doi:10.1016/j.jelekin.2016.12.007
- 738 22. Sánchez N, Simha SN, Donelan JM, Finley JM. Using asymmetry to your advantage:
 739 learning to acquire and accept external assistance during prolonged split-belt walking.
 740 Journal of Neurophysiology. 2021;125: 344–357. doi:10.1152/jn.00416.2020
- Z3. Leech KA, Day KA, Roemmich RT, Bastian AJ. Movement and perception recalibrate differently across multiple days of locomotor learning. Journal of Neurophysiology.
 Z018;120: 2130–2137. doi:10.1152/jn.00355.2018
- Prinkerhoff SA, Sánchez N, Roper JA. Habitual exercise evokes fast and persistent
 adaptation during split-belt walking. Pires FO, editor. PLoS ONE. 2023;18: e0286649.
 doi:10.1371/journal.pone.0286649
- 747 25. Brinkerhoff SA, Sánchez N, Culver MN, Murrah WM, Robinson AT, McCullough JD, et al.
 748 The dual timescales of gait adaptation: initial stability adjustments followed by subsequent
 749 energetic cost adjustments. Journal of Experimental Biology. 2024;227: jeb249217.
 750 doi:10.1242/jeb.249217

- 751 26. Park S, Finley JM. Manual stabilization reveals a transient role for balance control during locomotor adaptation. Journal of Neurophysiology. 2022;128: 808–818.
- 753 doi:10.1152/jn.00377.2021
- Price M, Huber ME, Hoogkamer W. Minimum effort simulations of split-belt treadmill
 walking exploit asymmetry to reduce metabolic energy expenditure. Journal of
 Neurophysiology. 2023;129: 900–913. doi:10.1152/jn.00343.2022
- 757 28. Seethapathi N, Clark BC, Srinivasan M. Exploration-based learning of a stabilizing controller predicts locomotor adaptation. Nat Commun. 2024;15: 9498. doi:10.1038/s41467-024-53416-w
- 760 29. Poggensee KL, Collins SH. How adaptation, training, and customization contribute to
 761 benefits from exoskeleton assistance. SCIENCE ROBOTICS. 2021.
 762 doi:10.1126/scirobotics.abf1078
- Gordon KE, Kinnaird CR, Ferris DP. Locomotor adaptation to a soleus EMG-controlled
 antagonistic exoskeleton. Journal of Neurophysiology. 2013;109: 1804–1814.
 doi:10.1152/jn.01128.2011
- 766 31. Abram SJ, Poggensee KL, Sánchez N, Simha SN, Finley JM, Collins SH, et al. General variability leads to specific adaptation toward optimal movement policies. Current Biology. 2022;32: 2222-2232.e5. doi:10.1016/j.cub.2022.04.015
- 769 32. Selinger JC, O'Connor SM, Wong JD, Donelan JM. Humans Can Continuously Optimize
 770 Energetic Cost during Walking. Current Biology. 2015;25: 2452–2456.
 771 doi:10.1016/j.cub.2015.08.016
- 772 33. McAllister MJ, Chen A, Selinger JC. Behavioural energetics in human locomotion: how
 773 energy use influences how we move. Journal of Experimental Biology. 2025;228:
 774 JEB248125. doi:10.1242/jeb.248125
- 34. Sánchez N, Simha SN, Donelan JM, Finley JM. Taking advantage of external mechanical
 work to reduce metabolic cost: the mechanics and energetics of split-belt treadmill walking.
 J Physiol. 2019;597: 4053–4068. doi:10.1113/JP277725
- Hampson DB, Gibson AS, Lambert MI, Noakes TD. The Influence of Sensory Cues on the
 Perception of Exertion During Exercise and Central Regulation of Exercise Performance:
 Sports Medicine. 2001;31: 935–952. doi:10.2165/00007256-200131130-00004
- 781 36. Noakes TD. Time to move beyond a brainless exercise physiology: the evidence for complex regulation of human exercise performance. Appl Physiol Nutr Metab. 2011;36: 23–35. doi:10.1139/H10-082
- 784 37. St Clair Gibson A, Lambert EV, Rauch LHG, Tucker R, Baden DA, Foster C, et al. The
 785 Role of Information Processing Between the Brain and Peripheral Physiological Systems in
 786 Pacing and Perception of Effort: Sports Medicine. 2006;36: 705–722.
- 787 doi:10.2165/00007256-200636080-00006

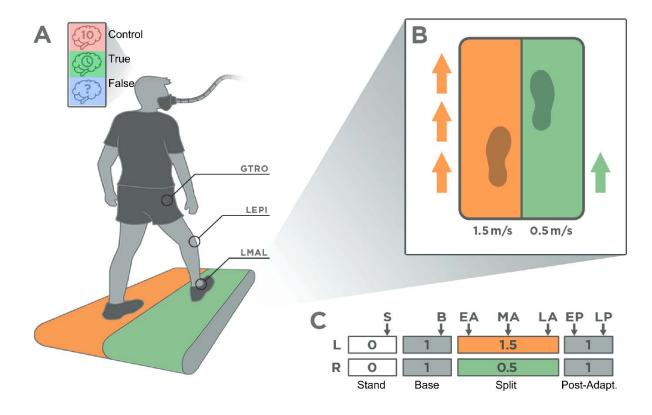
- 788 38. Reisman DS, Bastian AJ, Morton SM. Neurophysiologic and Rehabilitation Insights From 789 the Split-Belt and Other Locomotor Adaptation Paradigms. Physical Therapy. 2010;90: 790 187–195. doi:10.2522/ptj.20090073
- 791 39. Charlton JM, Eng JJ, Li LC, Hunt MA. Learning Gait Modifications for Musculoskeletal 792 Rehabilitation: Applying Motor Learning Principles to Improve Research and Clinical 793 Implementation. Physical Therapy. 2021;101: pzaa207. doi:10.1093/ptj/pzaa207
- 794 40. Sawicki GS, Beck ON, Kang I, Young AJ. The exoskeleton expansion: improving walking
 795 and running economy. J NeuroEngineering Rehabil. 2020;17: 25. doi:10.1186/s12984-020 796 00663-9
- Young AJ, Ferris DP. State of the Art and Future Directions for Lower Limb Robotic
 Exoskeletons. IEEE Trans Neural Syst Rehabil Eng. 2017;25: 171–182.
 doi:10.1109/TNSRE.2016.2521160
- 800 42. Buurke TJW, Lamoth CJC, Vervoort D, Van Der Woude LHV, Den Otter R. Adaptive 801 control of dynamic balance in human gait on a split-belt treadmill. Journal of Experimental 802 Biology. 2018; jeb.174896. doi:10.1242/jeb.174896
- 803 43. Brockway JM. DERIVATION OF FORMULAE USED TO CALCULATE ENERGY 804 EXPENDITURE IN MAN. Human Nutrition: Clinical Nutrition. 1987;41C: 463–471.
- 44. Donelan JM, Kram R, Kuo AD. Mechanical work for step-to-step transitions is a major determinant of the metabolic cost of human walking. Journal of Experimental Biology.
 2002;205: 3717–3727.
- 45. Donelan JM, Kram R, Kuo AD. Simultaneous positive and negative external mechanical work in human walking. Journal of Biomechanics. 2002;35: 117–124. doi:10.1016/S0021-9290(01)00169-5
- 811 46. Bogard AT, Hemmerle MR, Smith AC, Tan AQ. Enhanced motor learning and motor 812 savings after acute intermittent hypoxia are associated with a reduction in metabolic cost. 813 The Journal of Physiology. 2023; JP285425. doi:10.1113/JP285425
- Huang HJ, Ahmed AA. Reductions in muscle coactivation and metabolic cost during visuomotor adaptation. Journal of Neurophysiology. 2014;112: 2264–2274.
 doi:10.1152/jn.00014.2014
- 48. McDonald KA, Cusumano JP, Hieronymi A, Rubenson J. Humans trade off whole-body
 818 energy cost to avoid overburdening muscles while walking. Proceedings of the Royal
 819 Society B: Biological Sciences. 2022;289.
- 49. Yandell MB, Zelik KE. Preferred Barefoot Step Frequency is Influenced by Factors Beyond
 Minimizing Metabolic Rate. Sci Rep. 2016;6: 23243. doi:10.1038/srep23243
- 50. Summerside EM, Kram R, Ahmed AA. Contributions of metabolic and temporal costs to human gait selection. J R Soc Interface. 2018;15: 20180197. doi:10.1098/rsif.2018.0197

Hunter LC, Hendrix EC, Dean JC. The cost of walking downhill: Is the preferred gait energetically optimal? Journal of Biomechanics. 2010;43: 1910–1915.

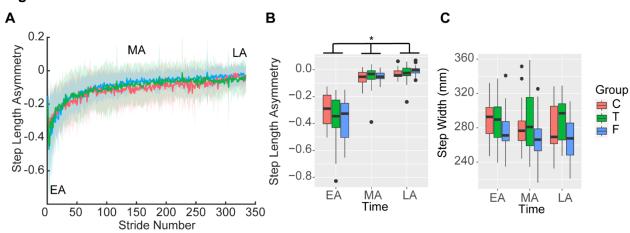
826 doi:10.1016/j.jbiomech.2010.03.030

- 827 52. Rosenbaum DA, Gong L, Potts CA. Pre-Crastination: Hastening Subgoal Completion at the Expense of Extra Physical Effort. Psychol Sci. 2014;25: 1487–1496.
- 829 doi:10.1177/0956797614532657
- 53. Tiew EH, Seethapathi N, Srinivasan M. Pre-crastination: time uncertainty increases walking effort. Physiology; 2020 Jul. doi:10.1101/2020.07.17.208140
- 832 54. Burdett RG, Skrinar GS, Simon SR. Comparison of mechanical work and metabolic energy 833 consumption during normal gait. J Orthop Res. 1983;1: 63–72. 834 doi:10.1002/jor.1100010109
- S5. Gordon AM, Homsher E, Regnier M. Regulation of Contraction in Striated Muscle.
 Physiological Reviews. 2000;80: 853–924. doi:10.1152/physrev.2000.80.2.853
- Lima-Silva A, Correia-Oliveira C, Tenorio L, Melo A, Bertuzzi R, Bishop D. Prior Exercise
 Reduces Fast-Start Duration and End-Spurt Magnitude during Cycling Time-Trial. Int J
 Sports Med. 2013;34: 736–741. doi:10.1055/s-0032-1331258
- Morris MB, Jack Rhodes L, Borghetti L, Haubert A. Vigilance end-spurt patterns in event-related potentials. Brain Research. 2023;1812: 148396.
 doi:10.1016/j.brainres.2023.148396
- 58. Joseph T, Johnson B, Battista RA, Wright G, Dodge C, Porcari JP, et al. Perception of Fatigue during Simulated Competition. Medicine & Science in Sports & Exercise. 2008;40: 381–386. doi:10.1249/mss.0b013e31815a83f6
- Swart J, Lamberts RP, Lambert MI, St Clair Gibson A, Lambert EV, Skowno J, et al.
 Exercising with reserve: evidence that the central nervous system regulates prolonged
 exercise performance. British Journal of Sports Medicine. 2009;43: 782–788.
 doi:10.1136/bjsm.2008.055889
- Hinton DC, Conradsson DM, Paquette C. Understanding Human Neural Control of Short-term Gait Adaptation to the Split-belt Treadmill. Neuroscience. 2020;451: 36–50.
 doi:10.1016/j.neuroscience.2020.09.055
- 853 61. Hoogkamer W, Bruijn SM, Sunaert S, Swinnen SP, Van Calenbergh F, Duysens J.
 854 Adaptation and aftereffects of split-belt walking in cerebellar lesion patients. Journal of
 855 Neurophysiology. 2015;114: 1693–1704. doi:10.1152/jn.00936.2014
- 856 62. Morton SM. Cerebellar Contributions to Locomotor Adaptations during Splitbelt Treadmill Walking. Journal of Neuroscience. 2006;26: 9107–9116. doi:10.1523/JNEUROSCI.2622-858 06.2006
- 859 63. Roemmich RT, Bastian AJ. Two ways to save a newly learned motor pattern. Journal of Neurophysiology. 2015;113: 3519–3530. doi:10.1152/jn.00965.2014

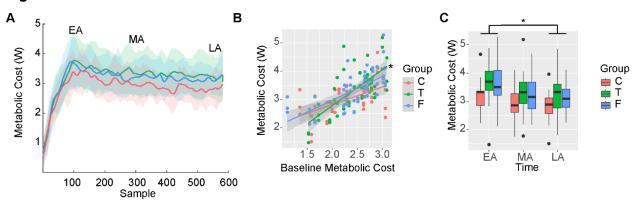
- 864 65. Morgan DW, Bransford DR, Costill DL, Daniels JT, Howley ET, Krahenbuhl GS. Variation 865 in the aerobic demand of running among trained and untrained subjects. Med Sci Sports 866 Exerc. 1995;27: 404–409.
- 66. Stauss HM. Heart rate variability. American Journal of Physiology-Regulatory, Integrative and Comparative Physiology. 2003;285: R927–R931. doi:10.1152/ajpregu.00452.2003
- 869 67. Cornwell T, Novotny R, Finley JM. Associations between asymmetry and reactive balance
 870 control during split-belt walking. Journal of Biomechanics. 2024;172: 112221.
 871 doi:10.1016/j.jbiomech.2024.112221







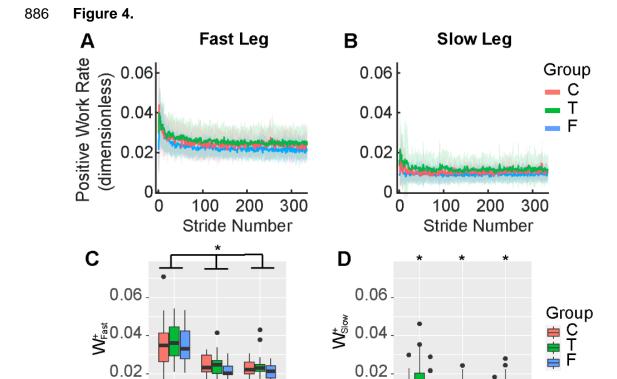




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