Knowledge of task duration affects energetic cost during split-belt adaptation and retention of walking patterns during post-adaptation

S.N. Jeffcoat BSc[1], A. Aragon BSc[1], A. Kuch PhD[1], S. Farrokhi DPT, PhD[1], A Hooyman Gstat, PhD[1], N. Sanchez PhD[1,2*]

[1.] Department of Physical Therapy, Crean College of Health and Behavioral Sciences, Chapman University

[2.] Department of Electrical Engineering and Computer Science, Fowler School of Engineering, Chapman University

*Corresponding Author
Natalia Sanchez
sanchezaldana@chapman.edu
9401 Jeronimo Road
Irvine CA 92618

Abstract

Humans continuously adapt locomotor patterns. Whether energetic cost reduction is the primary objective or a by-product of locomotor adaptation is not known. If energetic cost is the primary objective, then manipulating energetic cost will affect the locomotor pattern. Our study aims to determine if information about task duration affects energetic cost and locomotor adaptation during split-belt walking. We hypothesize that information about a longer adaptation duration will result in lower metabolic costs and lower mechanical work. N=52 participants walked for 10 minutes with the belts moving at 1.5 and 0.5 m/s, followed by 6 minutes of walking with both belts at 1.0 m/s. Nineteen participants walked on the split-belt while we provided True information about time remaining every minute (Group T). Nineteen participants received False information that split-belt adaptation duration was around 30 minutes (Group F). Fourteen participants walked on a split-belt with accurate information about task duration, and one update at 5 minutes remaining (Group C). Participants in Groups C and F had a lower rate of change in metabolic cost from baseline ($p=0.002$) and generated less positive work ($p=0.012$) than individuals in Group T. Changes in positive work by the fast leg predicted metabolic cost reductions only in Group F ($R^2=0.18$, $p=0.040$). Participants in Group F showed greater split-belt aftereffects than the C and T groups ($p<0.001$). We conclude that walking biomechanics are adapted to support an energetic cost reduction when maintaining an energetic reserve is needed, as is the case for Group F, but not Group T.

New and Noteworthy

The relationship between walking biomechanics and energetics can be modulated to maintain an energetic reserve during a novel locomotor adaptation task when individuals believe they must sustain a task for a prolonged period. When an energetic reserve is not required, individuals can use more energy than what is required for the task. Planning to sustain the adapted locomotor pattern for a prolonged time increases the aftereffects of locomotor adaptation.

Keywords

Adaptation, locomotion, split-belt, metabolic cost, mechanical work

Introduction

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 dual-belt treadmill in which each belt moves 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 in the field 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). While the kinematic, kinetic, and physiological changes that occur during locomotor adaptation have been thoroughly characterized (11–23), the factors driving split-belt walking adaptation are still under debate. Identifying the factors that impact adaptive locomotor processes can help accelerate adaptation and long-term retention of the newly learned locomotor patterns. A better understanding of how to manipulate these adaptive processes is vital in the retraining of walking behaviors as part of rehabilitation interventions (24, 25).

Empirical studies of split-belt adaptation (26–28), as well as simulation studies of split-belt treadmill walking (29, 30) have shown that the early stages of locomotor adaptation are associated with dynamic balance control, whereas the later stages of locomotor adaptation are associated with reductions in energetic cost. A recent study reported that balance adapts, on average, in less than a minute, whereas metabolic cost and mechanical work adapt on average in ~4-6 minutes (27). An area of interest regarding locomotor adaptation is whether metabolic cost reduction is the driving cost function, or a by-product of the biomechanical changes observed during adaptation. To answer this question, we can manipulate energetic cost reduction during adaptation, which can be done by influencing knowledge of task duration. The anticipatory regulatory model in physiology states that the central nervous system modulates muscle recruitment and power generation depending on expected exercise duration (31, 32), with muscle recruitment and power generation directly influencing energetic consumption (33, 34). 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 (35, 36). An example of this anticipatory regulation can be observed when cyclists increase power generation as the distance to the endpoint decreases (37, 38). More so, if the distance to the

endpoint is unknown, cyclists will keep power generation lower than when these same participants knew the distance to the endpoint (38). 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 (39). Here, we will test if, similarly to higher-effort, well-known tasks such as cycling and running, the information about the duration of a novel split-belt adaptation task could lead to differences in effort production that could result in energetic cost reductions to provide insights into whether energetic cost shapes the locomotor pattern during adaptation.

Split-belt walking can be considered an effortful behavior, where an individual's mechanical work and energetic cost markedly increase during initial exposure to split-belt walking and gradually decrease as individuals adapt to this locomotor task (11, 13, 21, 22, 26). As individuals adapt their walking pattern to the split-belt treadmill, they reduce positive power and positive work generated by their legs (13, 21, 22, 26, 27), which is accompanied by a reduction in metabolic cost (11, 13). Our own work reported that when individuals know they will sustain the split-belt walking task for a prolonged period of 45 minutes without breaks, they can achieve additional metabolic cost reductions from those reported after shorter adaptation (13). Recent studies have shown that energetic optimization is prioritized during a locomotor adaptation task, even when a secondary cognitive task is superimposed (40). Recent studies also showed that fitness level influences adaptation to split-belt walking, with individuals with average fitness showing less adaptation than very fit or very sedentary individuals (26, 27). Studies indicate that walking patterns can change continuously, even for small energetic savings (12, 41), and that individuals can explore different aspects of the walking pattern to identify the specific features that support energetic cost reduction (42). Thus, our working hypothesis is that task duration will influence adaptation of walking behaviors as individuals aim to identify a strategy that allows reducing energetic cost to maintain an energetic reserve needed for a prolonged task duration.

The main goal of our study is to determine if information about task duration affects the adaptation of locomotor patterns to reduce energetic expenditure during split-belt walking. We tested the hypothesis that individuals who believe they will sustain a locomotor adaptation task for a prolonged time (Group F – False task duration knowledge) will have a lower energetic cost compared to individuals who have detailed, minute-by-minute information about task duration (Group T – True task duration knowledge). To assess if the differences between Group T and F are due to a lower cost in Group F or a higher cost in Group T, we also collected a control group

(Group C), who like previous work, was informed about task duration at the beginning of the split-belt adaptation trial and only received one update halfway during adaptation. Previous research has shown that more positive step length asymmetries are associated with lower work by the fast leg and lower energetic cost (12, 13). Thus, we hypothesize that individuals who believe they will sustain the locomotor task for a longer time will adapt towards a more positive asymmetry and reduce positive work by the fast leg compared to individuals with true knowledge of task duration. By confirming our hypotheses, our results will support the role of energetic optimization as a primary goal during the adaptation of locomotor behaviors as opposed to simply being a by-product of the adaptation of walking behaviors.

Materials and Methods

We used data from our previous work for power analyses (13). Since we hypothesized that individuals in Group F would show a greater reduction in metabolic cost from early adaptation to late adaptation, we assessed the effect of detecting a difference in metabolic cost during 10 minutes of adaptation. We obtained metabolic cost measures in N=15 individuals who performed a split-belt walking adaptation protocol for 45 minutes and would need an energetic reserve to perform this task for such a prolonged time (13). 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 time 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 groups T and F, we would have a power of 0.82 to detect a reduction in metabolic cost. We also collected a control group (Group C) of N=14 participants, with a sample size similar to previous studies that showed 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) to assess how the information provided to the T and F groups compares to the traditional approach of informing participants of task duration at the beginning of the task with a halfway update of time remaining.

52 participants between the ages of 18-35 were recruited for this study (N=33 female, N=19 male). Participants were excluded if they had a history of lower extremity surgery or if they had any lower extremity injury 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 previous experience walking on a split-belt treadmill, or had a history of neurological disorders or severe head trauma. The Chapman University Institutional Review Board approved all experimental procedures, with approval number IRB-23-189, and participants provided written, 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 two hours before the experiment. Before each experiment, we calibrated the motion capture system and the metabolic cart per manufacturer specifications. During all walking trials, participants wore a harness to prevent falls, without providing body weight support.

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 6 minutes. Then, participants underwent three walking trials with breaks between each to ensure resting conditions before continuing to the next trial. The first trial, Baseline (Base), had participants walking for 6 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/ (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, 43) and work by the legs (21), while being a short task that all of our healthy young participants can sustain. The third 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. Participants were assigned to either group T or group F via a coin flip to ensure randomization. Group T participants performed the split-belt adaptation trial with true knowledge of how long the trial would last, and they were given an update on the time remaining every minute. Group F participants were given the false instruction: "You will be walking until we obtain the data needed, which can take about 30 minutes". Participants in group F 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 group C were informed that the task would last 10 minutes and given only an update halfway that they had 5 minutes remaining.

Participants were asked to rate their level of exertion via the Borg Rating of Perceived Exertion (RPE) (Borg, 1962) using their fingers 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 5-minute mark. During the Split trial, they were asked to rate their level of exertion at the 1 (early adaptation – EA), 5 (mid-adaptation – MA), and 9-minute (late adaptation – LA) marks. During the tied Post-adaptation trial, participants rated their RPE at the 1 (early post-adaptation – EP) and 5-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 (VO_2) and carbon dioxide production (VCO_2). 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. We estimated the energy consumed using the standard Brockway equation to obtain metabolic rate (Brockway, 1987). We subtracted each participant's standing metabolic rate from each walking trial. Thus, all metabolic rate values presented here are net metabolic rates. Biomechanical data processing was done as in (12, 13). 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:

$$SLA = \frac{SL_{fast} - SL_{slow}}{SL_{fast} + SL_{slow}} \text{ (Eq. 1)}$$

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 (12, 13, 21, 22, 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 (21) 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.

Statistical Analyses

Statistical analyses were run in R version 4.2.2 and MATLAB. 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.

The metabolic power for the Base condition was computed by averaging the power for the last 2 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 split-belt walking 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 1 minute (11, 46). Finally, the metabolic power for post-adaptation 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 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-belt trial (28). For the post-adaptation trial, we averaged the five first and last strides (EP, LP, respectively). These are close to the time points when we obtained RPE and average measures of metabolic cost.

We compared differences during the Base condition between groups using linear models with Group (C, T, F) as a categorical predictor, to ensure no differences during tied-belt baseline walking that influence the adaptation results. As the goal of our analysis is to observe differences within the split and post-adaptation conditions between groups, we ran separate models for these conditions. For the split-belt condition, we used linear models with Time (EA, MA and LA) and Group (C, T, F) 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 (C, T, F) 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. The models had the general form of:

$$x_{Split/Post} \sim Group * Time + x_{Base} * Time + x_{Base} * Group \text{ (Eq. 2)}$$

where x is the scaled value measured during either the split-belt task or during post-adaptation for any of the following outcomes: metabolic cost, heart rate, rating of perceived exertion, step length asymmetry, step width, and positive and negative work by each leg. The reference level for the linear models for Group was set as Group C 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 that they were normally distributed. Post-hoc comparisons were corrected via the false discovery rate. Models for step lengths, limb placement, swing time and net work are included in our Supplementary Materials, which include a detailed R markdown with all analyses.

To determine which biomechanical variables explained the reduction in metabolic cost from EA to LA across groups, we used a linear model of the form:

$$\Delta MetCost \sim Group * \Delta W^{+}_{Fast} + Group * \Delta W^{+}_{Slow} + Group * \Delta SLA \text{ (Eq. 3).}$$

All Δ values were calculated as $EA - LA$ for all variables. We used positive work in our model based on previous work showing that the positive work reductions track metabolic cost reductions (12, 13, 21). We tested for multicollinearity using the variance inflation factor (VIF). All variables were scaled before being input into the model. Post-hoc comparisons were corrected via the false discovery rate. We also assessed individual correlations between metabolic cost, work, step length asymmetry and step lengths. To allow comparison of correlation coefficients for different sample sizes, we used a Fisher transformation of the resulting correlation coefficients.

Results

N = 52 participants volunteered for this study: Group C - N=14, Group T - N=19, Group F - 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 6 participants (three in Group C, one in Group T, and two in Group F) due to Bluetooth connectivity issues. Force data was collected from all participants except one in Group F, for whom force data were corrupted, which hindered performing mechanical calculations. Data for all participants, as available, were included in all analyses.

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

Information about task duration influenced metabolic cost, heart rate, and RPE during split-belt adaptation

We hypothesized that individuals in Group F would have a lower metabolic cost than those in the Group T. 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], $p<0.001$), 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 Group T and baseline metabolic cost ($\beta_{GroupT:BaseMet}$=0.32, 95%CI [0.11, 0.52], $p=0.002$) (adjusted R^2=0.66) . Estimated marginal trends of the slope between

baseline metabolic cost with split-belt metabolic cost by groups show a greater slope in Group T compared to both Group C (slope T = 1.27 vs slope C = 0.62, p=0.007) and Group F (slope F = 0.84, p=0.044), indicating a greater increase relative to their baseline metabolic cost in Group T during split-belt adaptation (Fig. 2A-C). Thus, in agreement with our hypothesis, we observed a lower cost in Group F compared to Group T, but contrary to our hypothesis, this was not due to a reduction in cost in Group F but because of an increased cost in Group T.

The average heart rate was 114 ± 17 bpm during EA , 109 ± 18 during MA, and 113 ± 18 during LA, indicating that the split-belt adaptation task was of moderate cardiovascular intensity. The linear model assessing heart rate as a function of group, time, and baseline heart rate during split-belt adaptation returned a significant intercept (β_0=106, 95%CI [100, 112], p<0.001), a significant main effect of baseline heart rate (β_{Base}=12, 95%CI [7, 16], p<0.001) and a significant main effect of Group T (β_{GroupT}=11, 95%CI [3, 19], p=0.006) and of group F (β_{GroupF}=9, 95%CI [1, 18], p=0.024) indicating higher heart rates in Groups T and F relative to Group C (adjusted R^2=0.66) (Fig. 2D).

The linear model assessing RPE as a function of group, time, and baseline RPE during split-belt adaptation returned a significant intercept (β_0=3.4, 95%CI [3, 4], p<0.001), a significant main effect of baseline RPE (β_{Base}=0.59, 95%CI [0.15, 1], p=0.009) and a significant interaction between Group T and baseline RPE ($\beta_{GroupT:BaseRPE}$=0.70, 95%CI [0.23, 1.16], p=0.003) (Fig. 2E). Estimated marginal trends of the slope between base RPE by groups show a greater slope in Group T compared to both Group C (slope T = 1.32 vs slope C = 0.54, p=0.005) and Group F (slope F = 0.63, p=0.004), indicating a greater increase in RPE relative to baseline in the individuals in Group T who have detailed information about time remaining (adjusted R^2=0.39).

Information about task duration did not influence step length asymmetry during split-belt adaptation

We hypothesized that individuals in Group F would adapt toward more positive asymmetries than the T group. 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 group F (β_{GroupF}=-

0.08, 95%CI [-0.15, 0.01], p=0.036), indicating that group F was slightly more asymmetric but this more negative asymmetry was offset by a marginal interaction between group F and MA ($\beta_{GroupF:TimeMA}$=0.09, 95%CI [-0.01, 0.20], p=0.072) and group F and LA ($\beta_{GroupF:TimeLA}$=0.10, 95%CI [-0.01, 0.20], p=0.068) (adjusted R^2=0.66) (Fig. 3A-B). Contrary to our hypothesis, we observed a similar adaptation of step length asymmetry across groups.

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. 3C), indicating that individuals did not adapt step width (adjusted R^2=0.34). Results for step lengths, swing times, and limb placement matched those for step length asymmetry (Supplementary materials).

Information about task duration influenced work during split-belt adaptation

We hypothesized that individuals in Group F would generate less positive work than the T 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 R^2=0.52). Contrary to our hypothesis, the model points to the fact that all individuals across groups reduced positive work by the fast leg during adaptation similarly (Fig. 4A, C).

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 (β_0=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 Group T (β_T=0.005, SE=0.0018, p=0.012). These results indicate that in Group T, positive work by the slow leg was significantly higher during adaptation than in the C and F groups (adjusted R^2=0.34) (Fig. 4B, D). Thus, in agreement with our hypothesis, we observed lower work in group F, but just like metabolic cost, this was due to an increase in positive work with the slow leg in Group T compared to the C and F groups.

The linear model assessing negative work by the fast leg as a function of group, time and baseline work during split-belt adaptation returned a significant intercept (β_0=-.010, 95%CI [-

0.014, -0.007], p<0.001), a significant interaction between time and baseline negative work indicating that negative work changed proportionally to baseline during adaptation ($\beta_{TimeMA:Base}$=0.0032, 95%CI [0.00, 0.006], p=0.023 and $\beta_{TimeLA:Base}$=0.0038, 95%CI [0.001, 0.007], p=0.006). We also observed a significant interaction between Group T and baseline negative work ($\beta_{GroupT:Base}$=0.0033, 95%CI [0.00, 0.006], p=0.021) indicating that Group T generated less negative work (adjusted R^2=0.18) (Fig. 4A, E). Thus, we observed that individuals in group T generated less negative work with the fast leg, opposite to the strategy shown to allow taking advantage of work from the treadmill to reduce work by the legs and reduce metabolic cost (12, 13).

The linear model assessing negative work by the slow leg as a function of group, time and baseline work during split-belt adaptation returned a significant intercept (β_0=-0.020, 95%CI [-0.022, -0.016], p<0.001), a significant main effect of baseline work by the slow leg (β_{Base}=0.0037, 95%CI [0.001, 0.0006], p=0.002) and a significant effect of time (β_{TImeMA}=0.0097, 95%CI [0.005, 0.014], p<0.001 and β_{TimeLA}=0.011, 95%CI [0.006, 0.016], p<0.001) (adjusted R^2=0.44). This model indicates that overall, all participants decreased negative work by the slow leg during adaptation (Fig. 4B, F).

Information about task 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 Group C (r=-0.55, Fisher transformed r=-0.61, p=0.043) and for Group F (r=-0.51, Fisher transformed r=-0.56, p=0.027). We did not observe an association between metabolic cost and asymmetry in Group T (r=-0.31, Fisher transformed r=-0.32, p=0.203) (Fig. 5A).

We found a significant association between the reduction in positive work by the fast leg and change in metabolic cost for Group F (r=0.67, Fisher transformed r=0.81, p=0.002), but not in the C (r=0.50, Fisher transformed r=0.54, p=0.071) or T (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).

Knowledge of task duration influences split-belt adaptation

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 Group F (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 Group T (r=-0.77, Fisher transformed r=-1.02, p<0.001) (Fig. 5D). We did not observe a significant association between change in step lengths and work in Group C or change in slow step lengths and work in Group T.

There was no multicollinearity in the model predicting the change in metabolic cost during adaptation from the change in step length asymmetry and positive work by the legs (Eq. 3). The linear model assessing change in metabolic cost during adaptation returned a significant intercept (β_0=0.44, SE=0.18, p=0.022), and a significant interaction between group F and the change in positive work by the fast leg ($\beta_{GroupF:W^+_{Fast}}$=0.52, SE=0.25, p=0.040), indicating that the reduction in metabolic cost in Group F was explained by the reduction in work (adjusted R^2=0.19). These results, combined with the correlation analyses, point to a stronger coupling between metabolic cost and positive work in individuals who believed they had to sustain the task longer and who required maintaining an energetic reserve (Group F), providing evidence that in these individuals the biomechanics of locomotor adaptation are adapted to support the energetic cost reduction.

Information about task duration during split-belt adaptation influenced metabolic cost during post-adaptation

The linear model assessing metabolic cost as a function of group, time, and baseline cost during post-adaptation returned a significant intercept (β_0=2.59, 95%CI [2.39, 2.79], p<0.001), a significant main effect of baseline metabolic cost (β_{Base}=0.21, 95%CI [0.06, 0.37], p=0.006), a significant main effect of LP (β_{TimeLP}=-0.34, 95%CI [-0.62, -0.06], p=0.016), and a significant interaction between Group T and baseline metabolic cost ($\beta_{GroupT:BaseMet}$=0.34, 95%CI [0.15, 0.53], p<0.001). Estimated marginal means of the slope by groups show a greater slope in Group T (slope T = 1.1) compared to both Group C (slope C = 0.38, p=0.002) and Group F (slope F = 0.59, p=0.015), indicating a greater increase from baseline metabolic cost during the post-adaptation task in Group T (adjusted R^2=0.52) (Fig. 6A-B).

No differences in heart rate were observed between groups or over time during post-adaptation (Supplementary materials). The RPE did not change over time (β_0=2.25, 95%CI [1.8, 2.7], p<0.001), but Group T showed a significant interaction with baseline ($\beta_{GroupT:BaseRPE}$=0.70, 95%CI [0.07, 1.03], p=0.003). Estimated marginal trends of the slope between base RPE and RPE by groups did not show significant differences between groups (adjusted R^2=0.39)

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

The linear model assessing step length asymmetry as a function of group, time and baseline asymmetry during post-adaptation returned a significant intercept (β_0=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_{TimeLP}=-0.22, 95%CI [-0.28, -0.16], p<0.001), a significant effect of group F (β_{GroupF}=0.12, 95%CI [0.07, 0.18], p<0.001), a significant interaction between group F and LP ($\beta_{GroupF:TimeLP}$=-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 R^2=0.77). Overall, these results indicate a reduction in asymmetry from EP to LP for all groups and a higher asymmetry in Group F compared to C (p<0.001) and Group T (p<0.001) during EP, indicating a greater after-effect of the split-belt for Group F (Fig. 6 C-D).

The after-effect in group F can be explained by changes in the right leg, which was previously on the slow belt. 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 (β_{TimeLP}=157, 95%CI [117, 198], p<0.001), a significant effect of group F (β_{GroupF}=-70, 95%CI [-107, -32], p<0.001), and a significant interaction between group F and LP ($\beta_{GroupF:TimeLP}$=63, 95%CI [10, 116], p=0.043) (adjusted R^2=0.77). Overall, these results indicate that step length on the right leg remains shorter during EP in Group F compared to Group C (p<0.001) and Group T (p<0.001) (Fig. 6E). No differences between groups were observed for the left leg, which was previously on the fast belt (Supplementary Materials).

Information about task duration of split-belt adaptation influenced work during post-adaptation

The linear model assessing positive work by the right leg (previously on the slow belt) as a function of group, time, and baseline work during post-adaptation returned a main effect of baseline work by the right leg (β_{Base}=1.01, 95%CI [0.73, 1.29], p<0.001), and a significant main effect of Group T (β_{GroupT}=0.005, 95%CI [0.0012, 0.008], p=0.009). These results indicate that in Group T, positive work was higher during post-adaptation than in the C and F groups (adjusted R^2=0.38) (Fig. 6F). No differences between groups were observed for positive work by the left leg and negative work by the left and right legs (Supplementary Materials).

Discussion

Studies of motor adaptation have consistently observed reductions in metabolic cost that parallel the biomechanical changes during adaptation (11, 13, 43, 47). However, whether metabolic cost drives these biomechanical changes is still under debate. If energetic cost is the primary objective, then manipulating energetic cost will affect the locomotor pattern. Here, we manipulated the information about task duration during split-belt walking adaptation in neurotypical young adults. Manipulating information about task duration can lead to differences in performance to maintain an energetic reserve (Hampson *et al.*, 2001) and because knowledge of task endpoint is associated with the end spurt phenomenon in which individuals increase effort generation when they know they are close to the endpoint (35, 36). Our results partially supported our hypotheses: we did not find a greater energetic reduction in individuals who received false information about a longer task duration (Group F) relative to a typical adaptation group (Group C). Instead, we found that individuals who had detailed, true information about task duration (Group T) had a greater increase in metabolic cost, higher heart rate, higher RPE, generated more positive work with the slow leg and less negative work with the fast leg. These biomechanical features are the opposite of the strategies used to reduce energetic cost during split-belt walking (13). Thus, our findings indicate that individuals who have detailed information about a short task duration do not prioritize energetic cost reduction.

The differences in the metabolic cost response during adaptation between groups also led to different coupling between biomechanical variables and energetic cost. In individuals who

thought they had to maintain a greater energetic reserve to perform the task for what they believed to be a longer time (Group F), there was a strong coupling between step lengths, work, and metabolic cost. In the typical adaptation group (Group C), who knew the task duration and only received one update about time remaining, we observed a significant association between change in step length asymmetry and change in metabolic cost, but not between change in work and metabolic cost. Finally, in individuals who did not prioritize energy cost (Group T), we did not observe an association between the change in metabolic cost and any of the biomechanical variables assessed. These results support the idea that when energetic cost reduction is a priority, energetic cost drives coordinated gait biomechanics in a way that supports a reduction in energetic cost.

While we observed a strong relationship between gait biomechanics and energetic cost in individuals who believed they would sustain the task longer (Group F), the biomechanic strategies that supported the energetic reduction differed from those hypothesized. We originally hypothesized that we would observe more positive asymmetries due to longer steps with the leg on the fast leg, which also allows for more negative work with the fast leg and less positive work by the fast leg (12, 13). We found that the reduction in metabolic cost in Group F was correlated with step length asymmetry (13), but this correlation was due to changes in step lengths of the slow leg, not the fast leg. That is, the shortening in 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 a group level, there was no change in step lengths by the slow leg 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. Step length adjustments with the slow leg instead of the fast leg may provide a smaller energetic penalty (42), and could supplement other adjustments previously reported (13). Based on this discussion, we assessed the change in step lengths; we observed that both the change in slow leg step length ($r=0.55$, $p=0.017$) and 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 Group F, but not in the C and T groups, supporting the idea that the added slow leg adjustments aim at reducing work during adaptation. Thus, we conclude that when metabolic cost reduction is prioritized in tasks that need to be sustained for a prolonged time, the mechanisms underlying metabolic cost reductions are idiosyncratic and vary between participants.

Another key and surprising finding of our study is the fact 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 (48–50), when adapting using gradual adjustments of the belt speeds and a longer adaptation time (51), or when using visual feedback (17). Here, we found that individuals who received false information about a longer task duration, had a greater aftereffect when the belts were 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 Group F compared to the C and T groups. These shorter steps on the right leg were consistent with the strategy that supported the energetic cost reduction during split-belt walking in Group F. Two potential mechanisms might explain this aftereffect. On the one hand, the increased aftereffect in group F 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 (41). On the other hand, it could be the case that group F, 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 brought to the task compared to Groups T and C; a more implicit adaptation is known to increase retention and transfer of the adapted gait pattern (51, 52).

Based on our results, a question regarding Group T might arise: what was the cost function prioritized during split-belt adaptation in Group T individuals who had detailed information about task duration? Studies have shown that other cost functions can be prioritized over metabolic costs, such as muscle activations (53), comfort (54), time (55), or balance (56). Since the speed of the belts and the duration of the trial are all fixed, there is no strategy that would reduce task duration as in other studies (55). We also did not see an end spurt (35) but instead 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. An alternative explanation is that the cost functions in Group T 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 (27, 30). Based on our results of step width as a proxy for balance (Fig. 3C), while not significant, there seems to be a visually apparent difference in step widths in participants in Group T, with participants in this group showing wider steps than the C and F groups. Thus, it could be the case that the timescales of balance optimization can be extended when energetic cost is not a priority.

Our study has multiple 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/week, we did not exclude sedentary participants or participants who had a history of participation in high performance sports and, as such, cannot determine if either group had different levels of fitness, which has been shown to affect energetic expenditure (57) and adaptation (26). This seems to be the case for the Control group, which had 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 point during the pendular phase when work is generated (21, 22). Our study did not assess if our experimental manipulation affected this pendular work generation. The different contexts created by the different types of instructions in each group may have led to differences in autonomic response. While we measured heart rate, we were not able to obtain measures of heart rate variability to determine sympathetic activation during the task in each group that could explain differences in heart rate and metabolic cost responses (58).

Conclusion

In studies of motor adaptation, reductions in metabolic cost often accompany biomechanical changes during adaptation. To explore whether metabolic cost drives these changes or is a by-product, we manipulated information about task duration during split-belt walking in young adults. We found that when individuals have detailed knowledge about a short task duration, they do not prioritize energetic cost reduction, 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, when individuals do not have detailed knowledge, they prioritize energetic cost. The association between change in energetic cost and change in biomechanics seems to depend on how much individuals prioritize energetic cost reduction, with individuals who believe they must sustain a task for a prolonged time showing a stronger coupling between biomechanics and energetics. These findings suggest that metabolic cost reduction is not merely a by-product of walking patterns but that walking patterns are adjusted to support energetic cost reduction. We also found that information about longer task duration led to greater after-effects during post-adaptation, indicating that planning to sustain a task for longer can influence retention of walking patterns. The simplest implication of our findings is that the metabolic cost associated with a task depends on perceived task duration, and as such, task duration information should be controlled and informed during experimental paradigms of motor

adaptation. Our findings also imply that information about task duration can be manipulated to elicit different efforts, which can have implications for movement interventions in patient populations. Future studies should investigate how feedback about task duration influences adaptation, effort generation, and retention of walking patterns in pathological populations.

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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Table 1

Group	N	Age (yrs)	Height (cm)	Weight (kg)	Sex
Control	14	23.21 ± 3.37	170 ± 10	70.2 ± 12.9	8F/6M
True	19	24.84 ± 3.37	167 ± 8.2	73.0 ± 13.1	13F/6M
False	19	25.74 ± 4.68	167 ± 9.2	67.6 ± 13.6	12F/7M
		p=0.191	p=0.446	p=0.458	p=0.801

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.

Table 2

Group	Metabolic Cost (W)	Heart Rate (bpm)	RPE	Step Length Left (mm)	Step Length Right (mm)	Step Width (mm)
Control	2.26 ± 0.51	100 ± 14	2.0 ± 0.75	514 ± 36	509 ± 46	270 ± 29
True	2.47 ± 0.42	100 ± 12	1.75 ± 1.0	509 ± 28	500 ± 24	252 ± 36
False	2.43 ± 0.51	94 ± 12	2.0 ± 0.92	511 ± 24	508 ± 29	253 ± 30
	p= 0.487	p=0.352	p=0.675	p=0.900	p=0.682	p=0.402

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.

Figure 1.

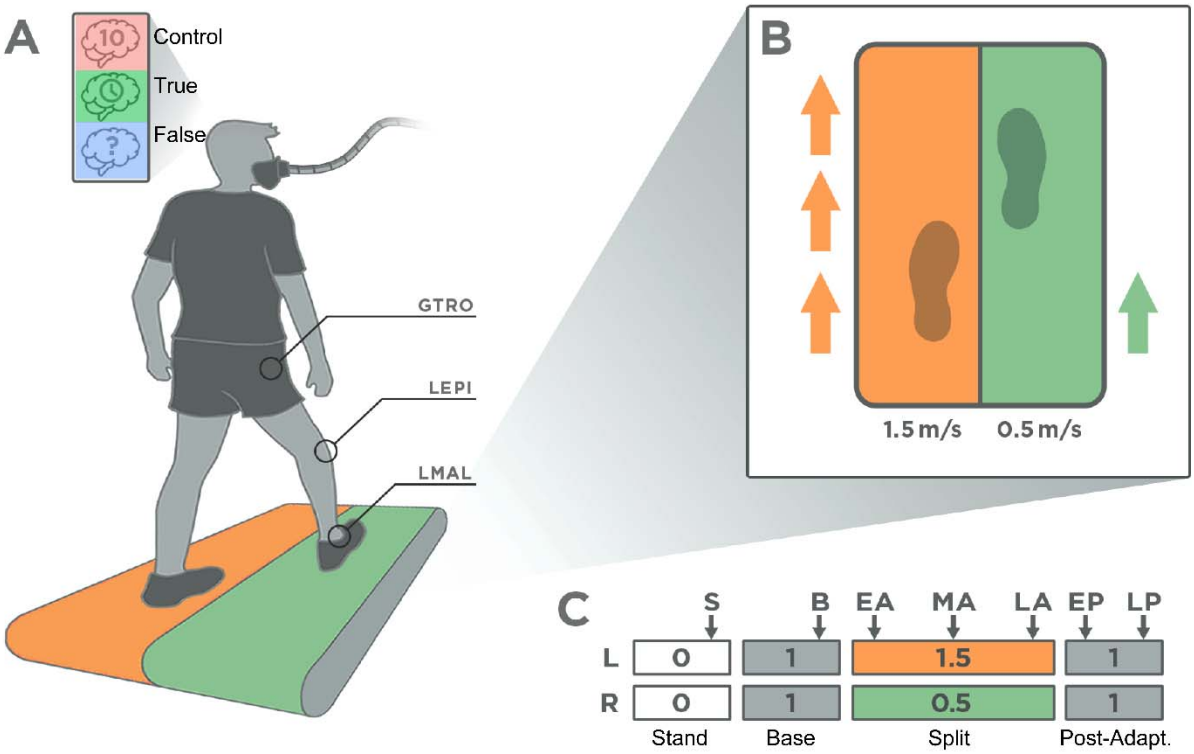

Figure 1. Experimental setup and protocol. A) Experimental setup showing experimental groups, metabolic mask, and marker location to calculate spatiotemporal variables. From top to bottom, the groups are the Control group (red), the True detailed time information group (green), and the False time information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

Figure 2.

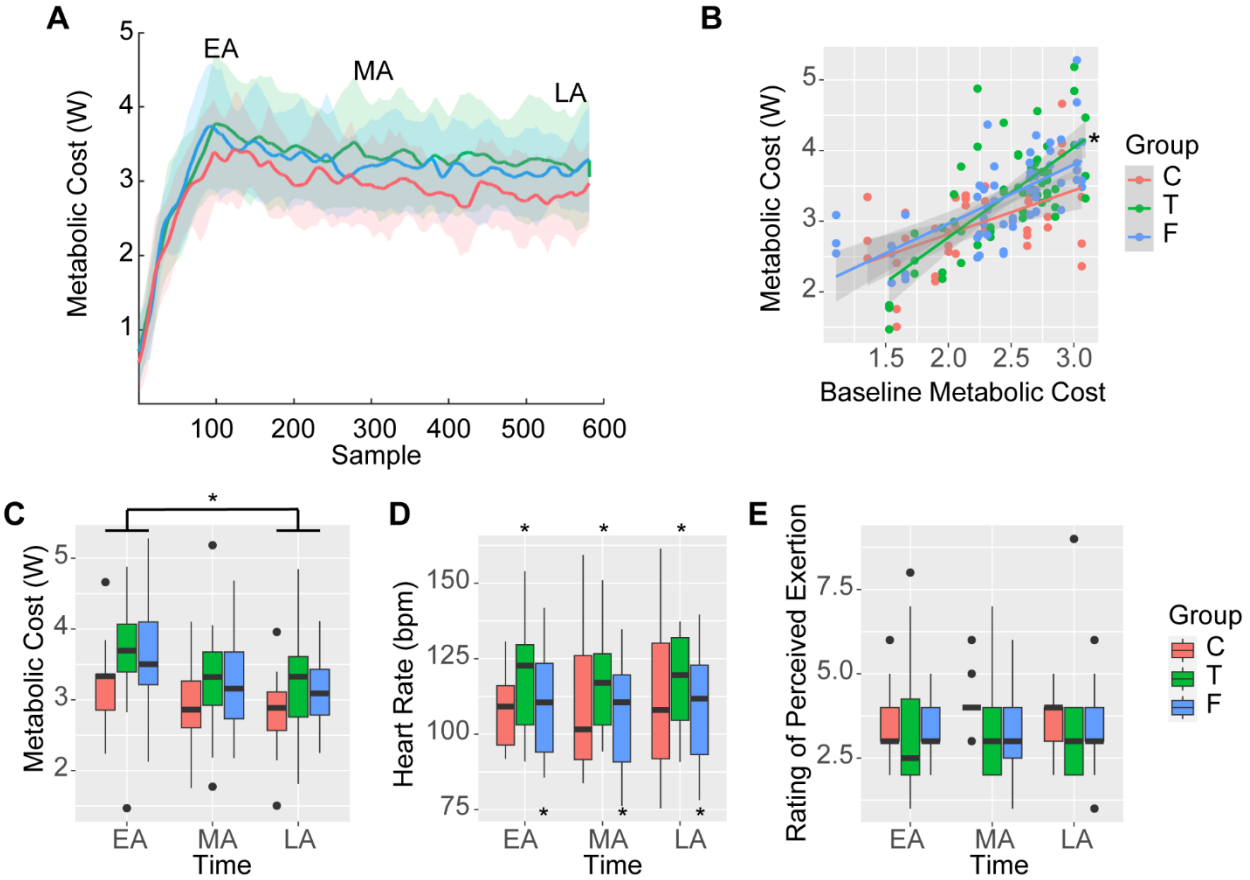

Figure 2. Metabolic cost, heart rate, and perception of effort during split-belt adaptation. A) Net metabolic power timeseries during the split-belt walking between the control (C – red), true knowledge of task duration (T – green) and false knowledge of task duration (F - blue) groups. Time windows 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 Group T compared to both the C and F groups ($p<0.050$). C) Average metabolic cost during EA, MA, and LA. A significant reduction in metabolic cost from EA to LA was observed across groups. D) Average heart rate during EA, MA, and LA. A significantly higher heart rate was seen in Group T relative to C ($p=0.006$) and in Group F relative to C ($p=0.024$). E) Rating of perceived exertion as indicated by participants during EA, MA, and LA. Other abbreviations as in Figure 1 and Table 2.

Figure 3.

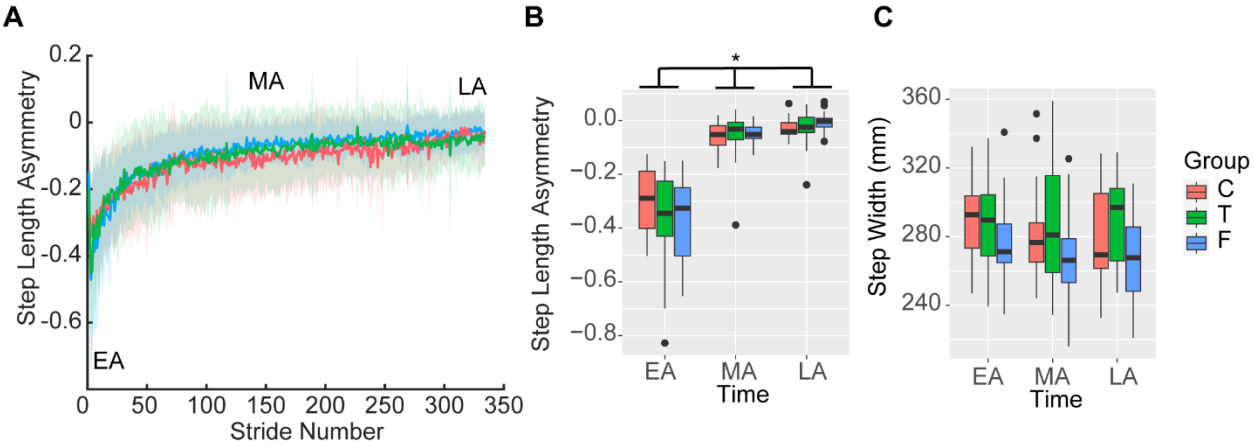

Figure 3. Step length asymmetry and step width during split-belt adaptation. A) Step length asymmetry timeseries during the split-belt walking between the control (C – red), true knowledge of task duration (T – green), and false knowledge of task duration (F - blue) groups. Time windows indicating EA, MA, and LA are indicated in the figure. B) Distribution of average step length asymmetry between groups during the 5 strides corresponding to EA, MA, and LA. Across groups, asymmetry decreased from EA to MA and LA. C) Distribution of average step widths. No differences over time or between groups were observed. Abbreviations as in Figures 1 and 2.

Figure 4.

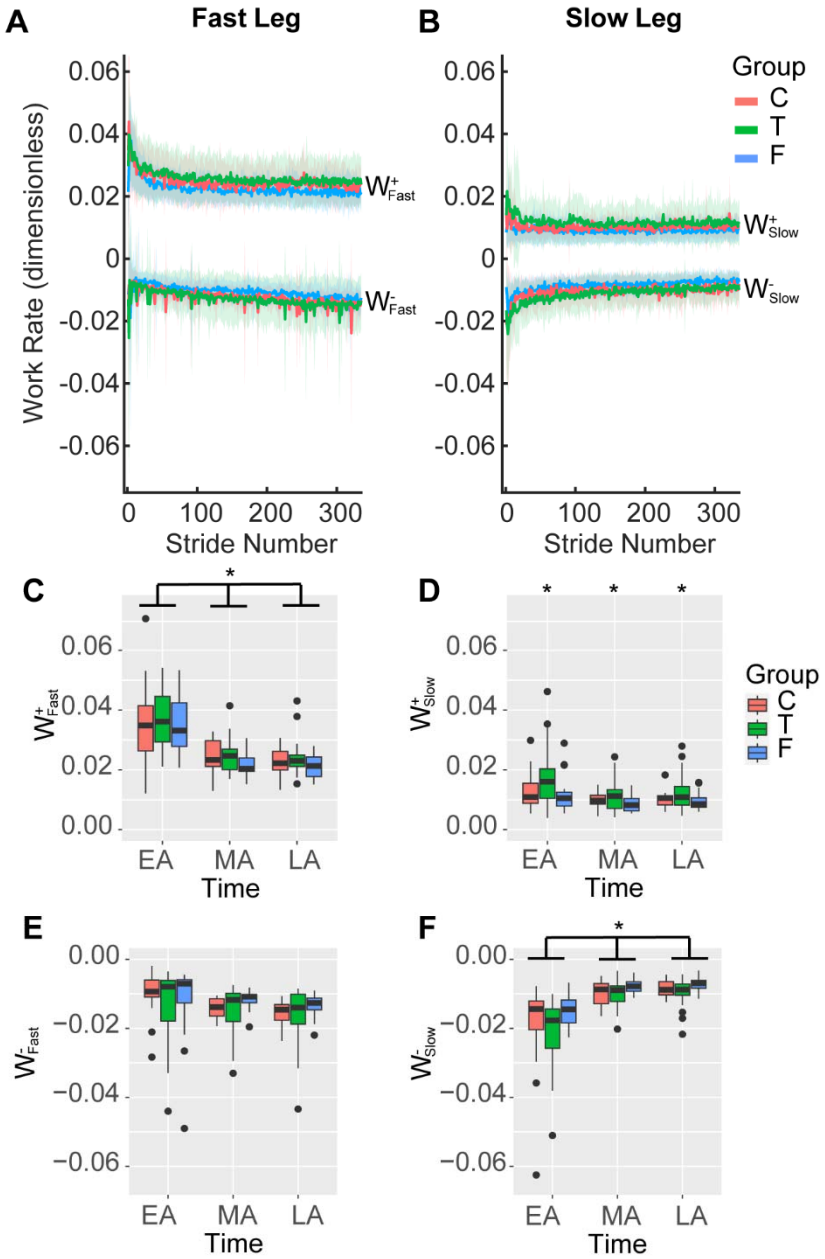

Figure 4. Work by the fast and slow legs during split-belt adaptation. A) Timeseries of work by the fast leg. B) Timeseries of work by the slow leg. C) Distribution of average positive work by the fast leg between groups during the 5 strides corresponding to EA, MA, and LA. We observed a significant 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 5 strides corresponding to EA, MA, and LA. We observed significantly higher work in Group T (p=0.012). E) Distribution of average negative work by the fast leg during the 5 strides corresponding to EA, MA, and LA. F) Distribution of average negative work by the slow leg between groups during the 5 strides

corresponding to EA, MA, and LA. We observed a significant reduction in work from EA to MA and LA across groups. W^+: positive work. W^-: negative work. Other abbreviations as in Figures 1 and 2.

Figure 5

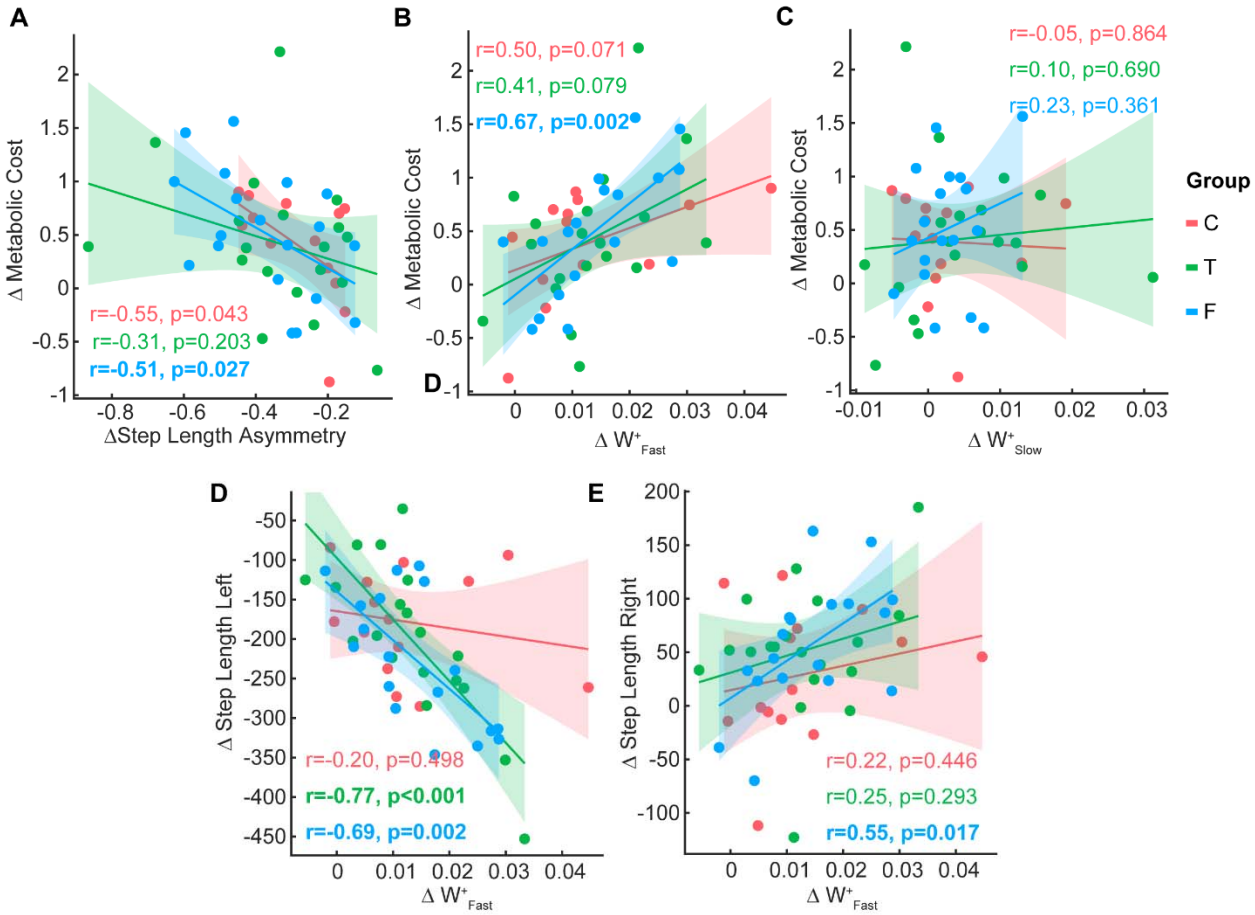

Figure 5. Associations between biomechanical and metabolic measures. A) Association between change in step length asymmetry and change in metabolic cost from EA to LA. B) Association between change in positive work by the fast leg and change in metabolic cost from EA to LA. C) Association between change 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.

Figure 6

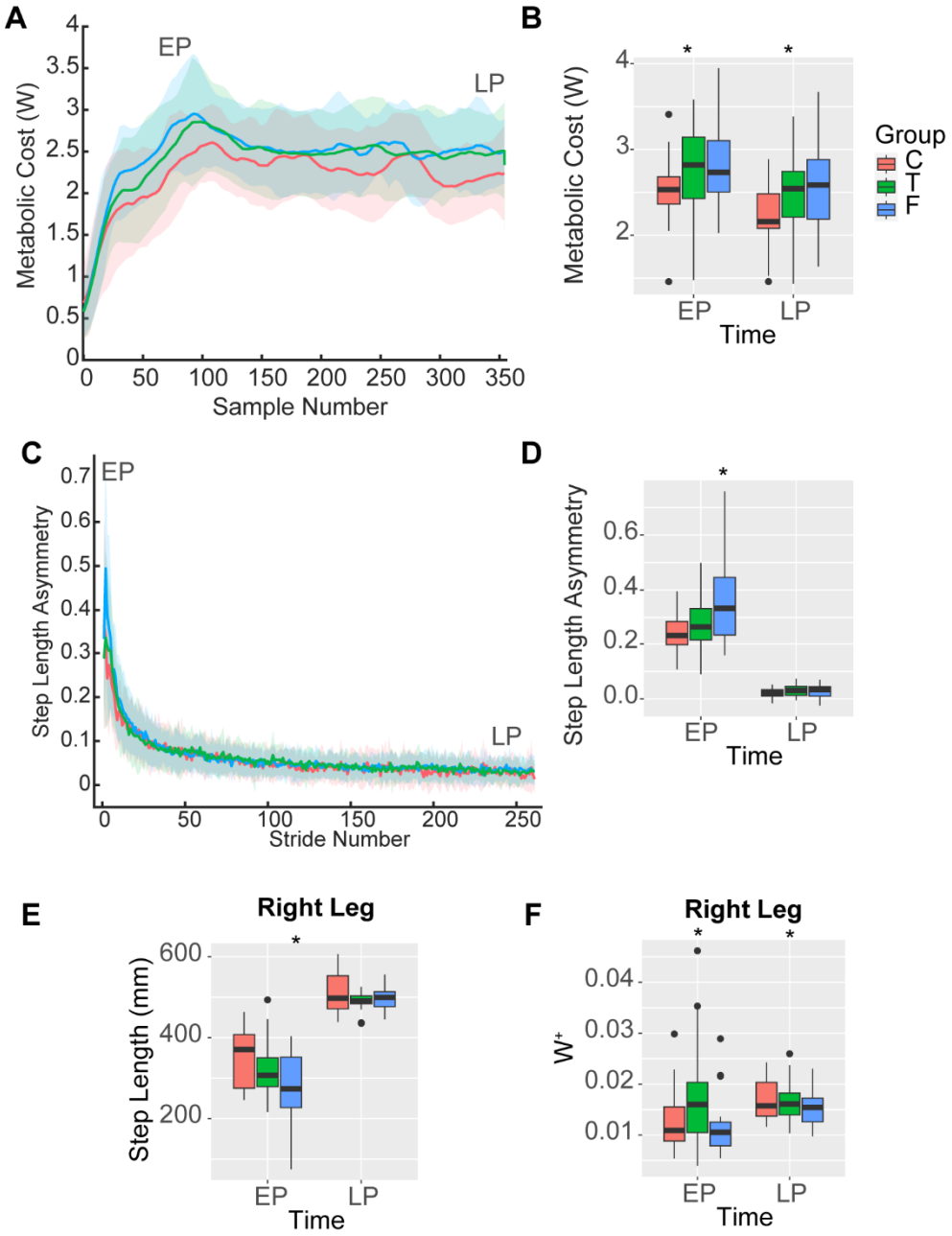

Figure 6. Metabolic cost, step length asymmetry and work during post-adaptation. A) Net metabolic power timeseries during post-adaptation between the control (C – red), true knowledge of task duration (T – green) and false knowledge of task duration (F - blue) groups. Time windows indicating EP, and LP are indicated in the figure. B) Average metabolic cost during EP, and LP. A higher cost was observed in group T ($p<0.050$). C) Step length asymmetry timeseries. D) Average step length asymmetry during EP, and LP. Participants in Group F had a greater asymmetry during EP compared to the C and T groups ($p<0.001$). E) Average step

lengths by the right leg during EP, and LP. Participants in Group F had a shorter step length with the right leg during EP compared to the C and T groups ($p<0.001$). F) Average positive work by the right leg during EP and LP. Participants in group T maintained the higher work with the right leg ($p=0.009$). Abbreviations as in Figures 1 and 2.