Perception of task duration influences metabolic cost during split-belt adaptation and biomechanics during both adaptation and post-adaptation

S.N. Jeffcoat[1], A. Aragon[2], A. Kuch[1], S. Farrokhi[1], N. Sanchez[1,3*]

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

[2.] Department of Applied Human Physiology, Crean College of Health and Behavioral Sciences, Chapman University

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

* Corresponding Author
Natalia Sánchez, PhD
sanchezaldana@chapman.edu
9401 Jeronimo Road
Irvine CA 92618

Abstract

Humans continuously adapt locomotor patterns. In laboratory settings, split-belt treadmills have been used to study locomotor adaptation. Whether metabolic cost reduction is the primary objective or a by-product of the observed biomechanical changes during adaptation is not known. The main goal of our study is to determine if perception of task duration affects the adaptation of locomotor patterns to reduce energetic cost. We tested the hypothesis that individuals who believe they will sustain a split-belt adaptation task for a prolonged time will adapt toward a walking pattern associated with lower cost. N=14 participants adapted for 10 minutes with knowledge of time remaining (group K), while N=15 participants adapted under the assumption that they would walk for 30 minutes with no knowledge of time elapsed or time remaining (group U). Both groups adapted for 10 minutes. We observed a significant main effect of Time ($p<0.001$, observed power 1.0) and the interaction of Time×Group ($p=0.004$, observed power 0.84) on metabolic cost. The K group did not reduce metabolic cost during adaptation. The U group reduced metabolic cost during adaptation to a cost 12% lower than the K group. We observed a significant effect of Time×Group ($p<0.050$) on step lengths and work by the right/slow leg during adaptation and post-adaptation. Our results indicate that metabolic cost reduction has a primary role in tasks that need to be sustained for a prolonged time, and this reduction occurs through a combination of biomechanical changes small in magnitude and a marked influence of non-biomechanical factors.

New and Noteworthy

Individuals can markedly reduce the metabolic cost of split-belt adaptation if they believe they must sustain the task for a prolonged time. The variables typically used to track adaptation do not track the reductions in metabolic cost observed in our study. Believing that the adaptation task will be sustained over a prolonged time also influenced retention of locomotor patterns. Non-biomechanical strategies have a marked effect on metabolic costs during split-belt adaptation.

Keywords

Adaptation, locomotion, split-belt, metabolic cost

Introduction

Humans continuously adapt locomotor patterns in response to environmental conditions, such as changes in walking terrain, footwear, and load carriage (Bruijn and van Dieën 2018; Kowalsky et al. 2021; Marigold and Patla 2008). In laboratory settings, split-belt treadmills have been successfully used to study locomotor adaptation, where individuals walk on a dual-belt treadmill in which each belt moves at different speeds (Dietz et al. 1994; Reisman et al. 2005). Split-belt walking leads to immediate changes in intralimb coordination and gradual changes in interlimb coordination (Reisman et al. 2005), which are attributed to distinct neural control mechanisms (Gonzalez-Rubio et al. 2019; Reisman et al. 2005). 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 (Malone and Bastian 2010, 2016; Reisman et al. 2005; Torres-Oviedo et al. 2011; Torres-Oviedo and Bastian 2010). While the kinematic, kinetic, and physiological changes that occur during locomotor adaptation have been thoroughly characterized (Betschart et al. 2017; Finley et al. 2013; Hinton et al. 2019; Jacobsen and Ferris 2023; Kambic et al. 2023; Mawase et al. 2013; Roemmich et al. 2012, 2016; Sánchez et al. 2019, 2021; Selgrade et al. 2017a, 2017b; Stenum and Choi 2020), the factors driving split-belt walking adaptation are still under debate. Identifying the factors that shape adaptive locomotor processes allows manipulating them to accelerate adaptation and long-term retention of the newly learned locomotor patterns, and this information is vital in the retraining of walking behaviors as part of rehabilitation interventions (Charlton et al. 2021; Reisman et al. 2010).

Empirical studies of split-belt adaptation (Brinkerhoff et al. 2023; Park and Finley 2022), as well as simulation studies of split-belt treadmill walking (Price et al. 2023; Seethapathi et al. 2021) have shown that the early stages of locomotor adaptation are associated with an increase in balance control, whereas the later stages of locomotor adaptation are associated with reductions in energetic cost. An area of interest regarding locomotor adaptation is whether metabolic cost reduction is the driving cost function or a by-product of the observed biomechanical changes (Sparrow and Newell 1994, 1998). Studies in cycling have provided evidence for energetic cost shaping motor behaviors: cyclists generate power proportionally to the distance to the endpoint (Joseph et al. 2008; Swart et al. 2009). These findings indicate that the central nervous system uses efferent feedback and modulates central commands to couple the metabolic and biomechanical limits of the body to the demands of physical tasks in a

feedforward process that allows individuals to complete a task while maintaining a reserve capacity (Hampson et al. 2001). Thus, individuals can modify effortful motor tasks to maintain the task for prolonged time. What remains to be determined is whether maintaining an energetic reserve is also prioritized when performing a novel task, such as adapting to a split-belt treadmill, and how maintaining an energetic reserve might shape locomotor 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 (Brinkerhoff et al. 2023; Finley et al. 2013; Sánchez et al. 2021; Selgrade et al. 2017a, 2017b). As individuals adapt their walking pattern to the split-belt treadmill, they reduce positive power and positive work generated by their legs (Brinkerhoff et al. 2023; Sánchez et al. 2021; Selgrade et al. 2017a, 2017b), which is accompanied by a reduction in metabolic cost (Finley et al. 2013; Sánchez et al. 2021). Recent studies have shown that energetic optimization is prioritized during a locomotor adaptation task, even when a secondary cognitive task is superimposed (McAllister et al. 2021). Also, a recent study showed that fitness level influences adaptation to split-belt walking, with fitter individuals adapting the kinematics related to energetic cost reduction at a slower rate than sedentary individuals (Brinkerhoff et al. 2023). Given that walking patterns can change continuously, even for small energetic savings (Sánchez et al. 2019; Selinger et al. 2015), our working hypothesis is that task duration will influence walking behavior during locomotor adaptation as individuals aim to maintain an energetic reserve, further supporting the role of energetics in driving adaptation of locomotor behaviors.

The main goal of our study is to determine if perception of 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, will have a lower energy cost. Previous research has shown that more positive step length asymmetries are associated with lower work by the fast leg and lower energetic cost (Sánchez et al. 2019, 2021). Thus, we hypothesize that individuals who believe they will sustain the locomotor task for a longer time will adapt faster towards a more positive asymmetry and reduce positive work by the fast leg. By confirming our hypotheses, our results will support the role of energetic optimization in being 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 recruited 29 participants between the ages of 18-35. Participants were excluded if they had a history of lower extremity surgery at any point in their lives or 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 B.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 B.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 (B), had participants walking for 6 minutes with the belts under each leg moving at 1 m/s. The second trial had participants walking for 10 minutes with the left/fast belt moving at 1.5 m/s and the right/slow belt at 0.5 m/s (Fig. 1B, C). The third trial had participants walking again for 6 minutes with the belts under each leg moving at 1 m/s. Participants were assigned to either the knowledge group (K) or the uncertainty group (U) via a coin flip to ensure randomization. Group K participants performed the split-belt adaptation trial with knowledge of how long the trial would last, and they were given an update on the time remaining every minute. Group U

participants were given the instruction: “You will be walking until we obtain the data needed, which can take about 30 minutes”. Participants in the U group were given no 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 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 baseline walking trial (B), participants reported RPE at the 5-minute mark. During the split-belt 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

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 as follows (Brockway, 1987):

$$E_{met,gross} = \left(16.48 \frac{J}{ml\ O_2} VO_2 \times 1000\right) + \left(4.48 \frac{J}{ml\ CO_2} VCO_2 \times 1000\right) \quad \text{(Eq. 1)}$$

From here, we divided by the exact duration (T) over which it was calculated to obtain an estimate of the gross metabolic rate measured in Watts. We subtracted each participant’s standing metabolic rate from each walking trial. Thus, all metabolic rate values presented here are net metabolic rates.

Data processing was done as in (Sánchez et al. 2019, 2021). 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:

$$SLA = \frac{SL_{fast} - SL_{slow}}{SL_{fast} + SL_{slow}} \quad \text{(Eq. 2)}$$

With SL_{fast} representing the step length at heel strike on the fast belt and SL_{slow} representing the step length at heel strike on the slow belt. Negative SLA values correspond to longer steps with the right/slow leg and positive SLA values correspond to longer steps with the left/fast leg. Step lengths are the product of adjusting the leading and trailing limb placement at heel strike and toe-off, respectively. Limb placement will affect the fore-aft component of the ground reaction force and the amount of work the legs must generate. Therefore, 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 (Donelan et al. 2002a, 2002b; Sánchez et al. 2019, 2021; Selgrade et al. 2017a, 2017b). 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 (Selgrade et al. 2017a) 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.

Statistical Analyses

Statistical analyses were run in SPSS version 29 (IBM, Armonk, NY, USA) and MATLAB R2023b. We assessed data for normality using the Shapiro-Wilk test. We compared age, height, and weight between the two experimental groups using independent samples t-tests or

Wilcoxon Signed Rank test for not normally distributed data. All summary statistics are reported as mean ± standard deviation unless otherwise specified.

The metabolic power for the B condition was computed by averaging the power for the last 2 minutes. The metabolic power for EA, MA, and LA was averaged for 30 seconds after the first and fifth, and before the ten-minute marks, respectively, of split-belt walking (Figure 2). We used the data after the one-minute mark for EA as the average duration to reach peak metabolic power is around 1 minute (Bogard et al. 2023; Finley et al. 2013). Finally, the metabolic power for post-adaptation was averaged for 30 seconds after the first minute mark and 30 seconds before the end of the trial to obtain average values of metabolic cost for EP and LP, respectively. The average heart rate was collected at the same timepoints.

We obtained average values for step length asymmetry, step lengths, leading and trailing limb placement, double support time, swing time, step width, and positive and negative work for the left/fast and right/slow legs for the last five strides of the B trial. For EA, MA, and LA we averaged the first, middle, and last five strides of the split-belt trial (Park and Finley 2022). For the post-adaptation trial, we averaged the five first and last strides (EP, LP respectively). These are close to the timepoints when we obtained RPE and average measures of metabolic cost.

We compared differences between both groups for all average variables via 2×6 Mixed ANOVAs with group (U or K) being the between-subjects effect and timepoint (B, EA, MA, LA, EP, LP) being the within-subjects effect. Data were tested for sphericity using Mauchly's test. If the sphericity assumption was not fulfilled, we used the Huyn-Feldt corrected p-values to assess for significant effects or interaction effects. We obtained the post-hoc estimated statistical power for each significant effect in the mixed ANOVA and effect size estimates using partial eta-squared, with values of .01, .06, and .14 to indicate small, medium, or large effect sizes, respectively (Cohen 1988; Richardson 2011). We ran multiple comparisons using LSD-adjusted confidence intervals for significant effects in the ANOVA.

To assess the rate of adaptation and post-adaptation we modeled individual step length asymmetry (Mawase *et al.*, 2013; Roemmich *et al.*, 2016; Sánchez *et al.*, 2021) using the sum of two exponentials (Equation 3):

$$y(s) = a_{fast} \times e^{-s/b_{fast}} + a_{slow} \times e^{-s/b_{slow}} \quad \text{(Eq. 3)}$$

In the two-exponential model, a_{fast} and a_{slow} are the initial values of the fast and slow exponentials and b_{fast} and b_{slow} are the fast and slow rate constants. We obtained the model coefficients for each participant and compared the distribution of each coefficient between the K and U groups using independent samples t-tests or non-parametric Wilcoxon signed rank tests if the data were not normally distributed.

To determine whether the observed differences in metabolic cost during LA were due to group-specific differences in gait biomechanics during EA, MA, and LA, we ran correlation analyses between biomechanical variables and metabolic cost for each group and between biomechanical variables. We also used linear regression models of the form: $MetCost \sim W^{+}_{Fast} + W^{+}_{Slow} + Group$ during LA and $\Delta MetCost \sim \Delta W^{+}_{Fast} + \Delta W^{+}_{Slow} + Group$. We used positive work in our model based on previous work showing that the positive work reductions track metabolic cost reductions (Sánchez et al. 2019, 2021; Selgrade et al. 2017a).

Results

N = 29 participants volunteered for this study, age 25.86 ± 3.98 years, height 166.9 ± 8.8 cm, mass 67.11 ± 12.76 kg. No significant differences were observed in participant demographics between groups (Table 1). Metabolic cost and kinematic data were collected for all participants. Force data was collected in all participants except one participant in the U group for whom force data were corrupted, which hindered performing mechanical calculations. Metabolic and kinematic data for this participant were included in all other analyses.

Perception of task duration influenced metabolic cost during adaptation

We observed a significant main effect of Time ($p<0.001$, observed power 1.0, partial eta-squared 0.714) and the interaction of Time×Group ($p=0.004$, observed power 0.84, partial eta-squared 0.141) on metabolic power (Fig. 2A, 2B). We did not observe a main effect of Group ($p=0.580$). Both groups significantly increased their metabolic cost when the belts were split ($p<0.001$ for EA compared to B). Contrary to previous studies (Buurke et al. 2018; Finley et al. 2013), participants in the K group did not significantly decrease their metabolic cost during adaptation (post-hoc $p=0.233$ between EA and MA, and $p=0.092$ between EA and LA). In contrast, participants in the U group significantly decreased their metabolic cost during adaptation (post-hoc $p<0.001$ between EA and MA and $p=0.005$ between EA and LA). The

metabolic cost during EA was 3.806 ± 0.647 Watts for the K group and 3.646 ± 0.647 for the U group. The metabolic cost during MA was 3.657 ± 0.702 Watts for the K group and 3.204 ± 0.564 for the U group. The metabolic cost during LA was 3.533 ± 0.698 Watts for the K group and 3.182 ± 0.583 for the U group.

For heart rate, we observed a significant main effect of Time ($p<0.001$, observed power 1.0, partial eta-squared 0.703) and the interaction of Time×Group ($p=0.024$, observed power 0.69, partial eta-squared 0.109) but no main effect of Group ($p=0.206$) (Fig. 2C). We did not observe significant post-hoc differences between the K and U groups during the different timepoints.

Despite differences in metabolic cost and heart rate in the U group compared to the K group, participants' perception of exertion was not significantly different between groups. We observed a significant main effect of Time ($p<0.001$, observed power 1.0, partial eta-squared 0.572). We did not observe a significant main effect of Group or for the interaction of Time×Group ($p=0.369$ and $p=0.165$ respectively) (Fig. 2D).

We did not observe any differences between groups during post-adaptation in metabolic cost, heart rate or RPE ($p>0.050$).

Perception of task duration affected step lengths during adaptation and post-adaptation

We observed a significant main effect of Time ($p<0.001$, observed power 1.0, partial eta-squared 0.896) but no significant effect of Group ($p=0.191$) or the interaction of Time×Group ($p=0.170$) on step length asymmetry (Fig. 3A-B). Step length asymmetry during LA was -0.035 ± 0.089 for the K group and 0.004 ± 0.041 for the U group. Step length asymmetry during EP was 0.313 ± 0.080 for the K group and 0.413 ± 0.136 for the U group.

Step length asymmetry is a combination of right/slow and left/fast step lengths. No significant differences between groups were observed for the left/fast step length (main effect of Time $p<0.001$, observed power 1.0, no effect of the interaction of Time×Group, $p=0.976$ or Group, $p=0.403$) (Fig. 3C). In contrast, we observed significant differences in the right/slow leg step lengths (Fig. 3D). We observed a significant main effect of Time ($p<0.001$, observed power 1.0, partial eta-squared 0.845) and the interaction of Time×Group ($p=0.031$, observed power 0.73, partial eta-squared 0.098) and no significant effect of Group ($p=0.591$) on step lengths of the

right/slow leg. The step lengths with the right/slow leg were shorter in the U group during LA compared to B (p=0.002) but not in the K group compared to B (p=0.437). Step lengths for the right/slow leg during LA were 491 ± 59 mm for group K and 463 ± 46 mm for group U (p=0.166). Step lengths for the right/slow leg during EP were 296 ± 75 mm for group K and 247 ± 56 mm for group U (p=0.095).

The distribution of parameter estimates for our samples for the two exponential models did not differ between groups during adaptation (Supplementary Fig. 1). We observed no differences between the distribution of a_{fast} (p=0.917), a_{slow} (p=0.780), b_{fast} (p=0.561) and b_{slow} (p=0.310) between groups. As the distribution of each parameter was not normal, we report summary models using medians. The summary model for the K group was:

$$SLA_{Adapt_K}(s) = -0.31 \times e^{-\frac{s}{27}} - 0.08 \times e^{-\frac{s}{292}}$$

and the summary model for the U group was:

$$SLA_{Adapt_U}(s) = -0.27 \times e^{-\frac{s}{21}} - 0.12 \times e^{-\frac{s}{203}}.$$

For the models during post-adaptation (Supplementary Fig. 2), we observed no differences between the distribution of a_{fast} (p=0.054), a_{slow} (p=0.290), b_{fast} (p=0.621) and b_{slow} (p=0.294) between groups. We report summary models using medians. The summary model for the K group was:

$$SLA_{Deadapt_K}(s) = 0.33 \times e^{-\frac{s}{7}} + 0.08 \times e^{-\frac{s}{228}}$$

and the summary model for the U group was:

$$SLA_{Dedapt_U}(s) = 0.41 \times e^{-\frac{s}{8}} + 0.08 \times e^{-\frac{s}{303}}.$$

Perception of task duration did not systematically influence other spatiotemporal variables during adaptation and post-adaptation

We observed a significant main effect of Time (p<0.001), but not of Group (p>0.500) or the interaction of Time×Group (p>0.100) on double support times, swing times, leading and trailing limb placement, and step widths for the left/fast or right/slow leg. We did not observe significant differences in cadence between the groups during split-belt walking (p=0.660), which could explain the differences in metabolic cost.

Perception of task duration influenced work by the right/slow leg during adaptation

Contrary to our hypothesis, we did not observe any significant differences between groups in work by the left/fast leg during adaptation or post-adaptation (Fig. 4A, 5C): we observed a significant main effect of Time ($p<0.001$, observed power 1.0) but not for the interaction of Time×Group ($p=0.652$) or the main effect of Group ($p=0.278$). For negative work by the left/fast leg (Fig. 4E), we observed a significant main effect of Time ($p<0.001$, observed power 1.0) but not for the interaction of Time×Group ($p=0.573$) or the main effect of Group ($p=0.802$).

Contrary to our hypothesis, we observed a significant main effect of Time ($p<0.001$, observed power 1.0, partial eta-squared 0.690) and the interaction of Time×Group ($p=0.031$, observed power 0.69, partial eta-squared 0.111) and no significant effect of Group ($p=0.597$) on the positive work by the right/slow leg (Fig. 4B, 4D). Participants in the U group generated marginally less positive work with the right/slow leg during EA compared to B ($p=0.052$), and significantly less work during MA, LA compared to B ($p<0.005$). In contrast, participants in the K group generated work that was significantly lower than B only during MA ($p=0.017$) (Fig. 4D). For negative work by the right/slow leg (Fig. 4F), we observed a significant main effect of Time ($p<0.001$, observed power 1.0) but not for the interaction of Time×Group ($p=0.462$) or the main effect of Group ($p=0.419$).

For net work, which is the sum of positive and negative work by both legs, we observed a significant main effect of Time ($p<0.001$, observed power 1.0) but not for the interaction of Time×Group ($p=0.320$) or the main effect of Group ($p=0.185$).

Lack of association between metabolic cost and gait biomechanics during adaptation

We assessed correlations between the change in metabolic cost from EA to LA and the change in biomechanical variables (Fig. 5). Contrary to previous studies (Bogard et al. 2024; Finley et al. 2013; Sánchez et al. 2021), the change in metabolic cost during adaptation was not associated with a change in step length asymmetry in the K group ($r=-0.257$, $p=0.370$) or in the U group ($r=-0.175$, $p=0.534$) (Fig. 5A). The change in metabolic cost was not correlated with the change in positive work by the left/fast leg in the K group ($r=0.449$, $p=0.107$) or in the U group ($r=0.328$, $p=0.252$) (Fig. 5B). The change in metabolic cost was marginally correlated with the

change in positive work by the right/slow leg in the U group (r=0.552, p=0.054) but not in the K group (r=0.029, p=0.920) (Fig. 5C). The change in net work by the legs was not correlated with the change in metabolic cost (p=0.113 for the K group and p=0.947 for the U group) (Fig. 5D).

Regarding the association between gait biomechanics, we found a significant association between change in step length asymmetry and change in positive work by the left/fast leg (r=-0.580, p=0.030 for the K group, and r=-0.905, p<0.001 for the U group) (Fig. 5E), but no association between change in step length asymmetry and change in positive work by the right/slow leg (Fig. 5F).

The model using work to predict metabolic cost during LA was not significant (p=0.751). None of the biomechanical variables measured were significantly associated with metabolic cost (p>0.100) during LA. The model using change in work from EA to LA to predict change in metabolic cost from EA to LA was also not significant (p=0.235).

Comparison to previous studies of split-belt adaptation indicates both an increase in cost for known time duration and a reduction in cost for unknown time duration

To determine whether we observed a reduction in energy cost in the U group or an increase in energy cost of the K group that led to the observed metabolic cost differences, we compared the energy cost at 10 minutes of adaptation (LA) to previous studies using the same 3:1 split-belt ratio at similar timepoints during adaptation. We report results as mean ± standard errors in this section to match previous studies (Finley et al. 2013). The metabolic cost during LA for the K group in our study was 3.53 ± 0.19 W/kg and for the U group was 2.91 ± 0.14 W/kg. Finley *et al.*, 2013 measured a metabolic cost of 3.05 ± 0.24 W/kg at 12 minutes of adaptation. Sánchez *et al.*, 2021 measured a metabolic cost of 2.37 ± 0.17 W/kg at 10 minutes of a 45-minute adaptation trial.

Using previous data by the authors (Sánchez et al. 2021), we ran a one-way ANOVA with group as the independent variable and metabolic cost at minute 10 as the dependent variable (Sánchez 2021 data and U group N=15, K group N=14) and found that the cost reported in Sánchez 2021 was significantly lower than the K and U groups: one way ANOVA p<0.001, post-hoc p<0.001 Sanchez 2021 compared to K, p=0.025 Sanchez 2021 compared to U and p=0.013 for K compared to the U group. The comparison of all these studies indicates both an

increased cost in participants who have detailed knowledge of task duration (K group) relative to Finley 2013, and a reduction in cost in individuals who plan to maintain the task for a prolonged time (U group and Sanchez 2021).

We also compared step length asymmetry across the three groups. We did not observe significant differences in step length asymmetry between Sanchez 2021 and participants in the U or K groups (one-way ANOVA p=0.208).

Discussion

While studies of motor adaptation have consistently observed reductions in metabolic cost that parallel the kinematic and kinetic changes during adaptation (Finley et al. 2013; Huang et al. 2012; Sánchez et al. 2021), whether metabolic cost drives these biomechanical changes is still under debate. To test whether metabolic cost indeed shapes the adaptation of locomotor behaviors or is a byproduct of adaptation, we manipulated the perception of task duration during split-belt walking adaptation in neurotypical young adults. Manipulating perception of task duration can lead to differences in performance between individuals in order to maintain an energetic reserve (Hampson *et al.*, 2001). Here, participants were assigned to either a group that had detailed knowledge of task duration and received updates of time remaining while walking on a spilt-belt for 10 minutes (Knowledge – K), or a group that believed they would walk until we collected the data of interest, which could take around 30 minutes, and received no updates on time remaining (Uncertainty – U). Our results support the idea that when participants believe they have to sustain a task for a prolonged time, they prioritize energy reduction and markedly reduce metabolic cost. When participants know they must sustain a task for a short time, they do not reduce metabolic cost. These differences in metabolic cost are not associated with clear differences in walking biomechanics. Step length asymmetry did not track the reductions in metabolic cost, nor did it track the changes in the biomechanical variables that explain the metabolic cost reductions observed. Step length by the right/slow leg differed between the groups, pointing at this variable potentially contributing to the energetic cost reduction. In fact, the marginal association between work and metabolic cost points to energy reduction being a multidimensional process. We also observed more consistent behaviors across individuals who believed they would sustain the task for a longer time, pointing at the

idea that these individuals avoided any movement strategies associated with potential energetic penalties. Thus, we conclude that metabolic cost reduction is prioritized in tasks that need to be sustained for a prolonged time, yet the mechanisms underlying metabolic cost reductions are idiosyncratic and vary between participants, and can include both biomechanical and non-biomechanical strategies to reduce energy cost.

During adaptation, we observed different metabolic costs between groups such that by the end of adaptation, the metabolic cost in the U group was ~12% lower than in the K group. Note that this difference in metabolic cost is well above the 5% energetic savings that have been reported to lead to walking adjustments in order to reduce energetic cost (Selinger et al. 2015). The lack of reduction in metabolic cost for the K group might indicate that for a relatively short task of 10 minutes, our population of healthy young adults might not prioritize metabolic cost reduction, consistent with recent studies showing prioritization of other cost functions over metabolic cost (McDonald et al. 2022). Note that the split-belt adaptation task duration is comparable to that used in (Finley et al. 2013) of 12 minutes, and (Buurke et al. 2018) of 9 minutes, where they observed significant reductions in metabolic cost during adaptation. The only difference in our study is the added updates about remaining time, which potentially provided contextual cues that led to an increased sympathetic response in the K group (Gordan et al. 2015) as indicated by the higher heart rate and metabolic cost. In contrast, the 12% reduction in cost in the U group indicates that for a perceived task duration three times longer than the actual task duration, metabolic cost reduction to maintain an energetic reserve is a priority and is achieved via multidimensional strategies as opposed to changes in a single biomechanical variable. Our findings are similar to studies of motor adaptation during reaching, where they observed continued metabolic power reductions even when kinematics and muscle activation patterns had already reached stable behaviors (Huang et al. 2012; Huang and Ahmed 2014). These findings during reaching adaptation, in combination with our results point at additional mechanisms that might explain metabolic cost, beyond the cost of reaching or walking, such as autonomic response associated with the different contexts (walking for 10 min or the instruction to walk “around 30 minutes”) (Robinson *et al.*, 1966; Lay *et al.*, 2002), differences in neural activity during the task between groups as they received regular updates vs. no information (Hasenstaub et al. 2010), value placed on task duration (Summerside et al. 2018), postural demands and comfort during the task between groups (Rosenbaum et al. 1995) among others. Overall, our findings show that metabolic cost during adaptation can be significantly reduced

without being able to attribute these changes to specific biomechanical changes of similar magnitude to the metabolic cost reduction.

While step length asymmetry has been consistently used as a metric to track adaptation (Leech et al. 2018; Reisman et al. 2005; Roemmich et al. 2016; Roemmich and Bastian 2015; Sánchez et al. 2019), our study shows that it cannot serve as a proxy to track adaptation when the goal prioritized is metabolic cost. Despite no differences in step length asymmetry, we observed marked differences in metabolic cost between groups. We also observe a lack of association between step length asymmetry and positive work by the right/slow leg, the latter being marginally associated with metabolic cost reduction. While step length asymmetry provides a simple measure that is easily observable and easily quantified, it is also a global measure that involves both limbs and might not be sensitive enough to detect smaller adjustments during adaptation. This is also supported by our results showing that while step length asymmetry did not show differences between groups, the right/slow step lengths did differ between groups. Thus, research should quantify step length asymmetry and the underlying factors that produce this asymmetry to further understand locomotor adaptation.

Participants in our study did not perceive a reduced effort that aligned with the differences in metabolic cost between groups. Our previous work has also indicated that people's perception of effort does not necessarily reflect their actual metabolic expenditure (Sánchez et al. 2017). In a prior study, participants used visual feedback to adjust their foot placements, leading to varying levels of step length asymmetry and metabolic costs (Sánchez et al. 2017). Interestingly, we found that participants reported similar ratings of perceived exertion (RPE) even when there was a substantial difference in metabolic cost of about 30% (Sánchez et al. 2017). These findings suggest that the perception of effort is influenced by factors beyond just energy expenditure and may be related to the perceived difficulty of the task (Sparrow and Newell 1998), which might relate to both physiological and psychological factors associated with an unknown task duration (Morgan 1994) and have a greater influence on metabolic cost than what we observed in previous studies.

Consistent with our previous work, we observed a strong correlation between work by the left/fast leg and step length asymmetry (Sánchez et al. 2019, 2021). Contrary to previous studies, the reduction in positive work by the left/fast leg here was not associated with the reduction in metabolic cost (Sánchez et al. 2021). Also, surprisingly, here, the reduction in work

seemed to be associated with the reduction in work by the slow leg, but only in participants in the U group, also contrary to previous work (Sánchez et al. 2019, 2021). Based on our previous studies, it might be the case that any change in work by the left/fast leg might incur a large energetic penalty, such that individuals in the U group modify the work in the right/slow leg to avoid energetic penalties when modifying the larger work generated by the fast leg (Sánchez et al. 2021). What is also interesting is the narrower variability in the U group, as evidenced by the smaller standard deviations of the biomechanical variables. This also supports the idea of the U group avoiding metabolic penalties by keeping a more consistent behavior (Abram et al. 2022).

Participants in the U group, who believed they would walk for a longer time, showed a greater magnitude of retention of split-belt aftereffects. We observed shorter step lengths with the right/slow leg and more asymmetry in the U group during EP, indicative of greater aftereffects in this group. Previous research has observed that adding a distraction improves the retention of split-belt patterns (Malone and Bastian 2010). Research has also shown that the slow component of adaptation has greater retention (Huang and Shadmehr 2009; Smith et al. 2006). Our results conflict with some of these findings since during adaptation, the median values of the slow component of adaptation were faster for individuals in the U group, yet the U group had greater retention. An alternative is that participants who are more symmetric at the end of adaptation are more asymmetric during early post-adaptation (Bruijn et al. 2012), but we did not observe differences in asymmetry during LA between groups to support this idea. Another alternative explanation is that the lower metabolic cost during adaptation led to the selection of this pattern when starting the next trial, which can be supported by studies showing that individuals chose more economical patterns after experiencing gaits with different metabolic costs (Sánchez et al. 2019; Selinger et al. 2015). A recent study showed that virtual reality manipulations can induce perceived threats such as falls, and influence walking adaptation in a feedforward manner (Ellmers et al. 2024). This study also observed that adapted behaviors associated with a greater perceived threat showed greater aftereffects after the threat was removed (Ellmers et al. 2024). Another study showed greater transfer and generalization of walking patterns when the patterns are learned with adverse consequences when making errors in foot placement (Bakkum and Marigold 2022). In an analogous manner, participants in the U group might avoid metabolic penalties to maintain an energetic reserve, which is the perceived threat or adverse consequence equivalent to the Ellmers or Bakkum studies. In this way, the greater aftereffect in the U group indicates that they prioritized energy and selected the pattern

that reduced energy, even when the threat, which in this case is both the uncertainty and the split-belt perturbation, had been removed.

Our study has multiple limitations. First, we did not systematically assess fitness levels across participants. While our criteria excluded people who exercised more than 10 hours/week, we did not exclude sedentary participants and, as such, cannot determine if either group had different levels of fitness, which has been shown to affect energy expenditure (Morgan et al. 1995) and adaptation (Brinkerhoff et al. 2023). As previously mentioned, the different contexts created by the instructions provided between groups 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 (Stauss 2003). It might also be the case that the metabolic cost differences observed between groups are due to differences in muscle coactivation during adaptation, detected using electromyography of both lower extremity and postural muscles, which cannot be detected using the biomechanical variables we measured. Finally, our results indicate that metabolic cost reduction is not attributed to a single biomechanical variable but necessitates significant coordination of gait biomechanics. While we are well-powered to measure differences in metabolic cost between groups (post-hoc power 0.84), the changes in gait biomechanics that occur during our adaptation protocol that might explain metabolic cost reduction are small in magnitude and might involve a combination of kinematic, kinetic, and temporal changes. There are multiple aspects of gait that individuals can adapt to reduce metabolic cost, including limb power, positive and negative work by each leg, and the timing of power and work generation during the gait cycle (Selgrade et al. 2017a). As such, a lack of consistency in strategies to reduce energy costs among participants might have hindered us from detecting a specific strategy in our sample. It could be that we can predict metabolic cost using a multidimensional model with interactions between multiple biomechanical terms, which would require a larger sample size than the one used here.

Conclusion

We observed significant differences in the metabolic cost of split-belt walking in individuals who were uncertain of task duration compared to individuals who had definitive information about task duration without clear differences in biomechanical variables that explained metabolic cost reduction. We also observed greater aftereffects in individuals uncertain about task duration and with a less costly gait, indicating persistence and potential preference for a less costly pattern.

Our findings indicate that metabolic cost reduction is not a by-product of the walking pattern; metabolic cost reduction is prioritized during movements that need to be sustained over a prolonged time to maintain an energetic reserve, and this metabolic cost reduction can occur using a combination of biomechanical, physiological, and psychological factors. 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. Our findings also imply that information about task duration can be manipulated to elicit different cardiopulmonary and metabolic responses, which can have implications for movement interventions that require achieving different levels of cardiovascular intensity or aim to prevent fatigue in patient populations. Additionally, perceived task duration can influence the retention of adapted patterns and might be used as a tool in movement retraining interventions to manipulate task retention. Future work should assess how the perception of task duration might affect locomotor learning, metabolic cost, and cardiovascular responses in pathological populations.

Data Availability

Data used for analyses in this manuscript are available at:
https://github.com/GaitBehaviorLab/TimeUncertaintyData/tree/d0437e6242c050fdbc35f4aafad1ff7b3a0f8d1c

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Table 1

Group	N	Age (yrs)	Height (cm)	Weight (kg)	Sex
K	14	25.71	165.82	67.67	9F/5M
U	15	26.00	167.91	66.59	9F/6M
		p=0.851	p=0.532	p=0.824	p=0.999

Participant demographics for both experimental groups. P-values for independent samples t-tests and for Chi-Square tests show no differences in group demographics.

Figure 1.

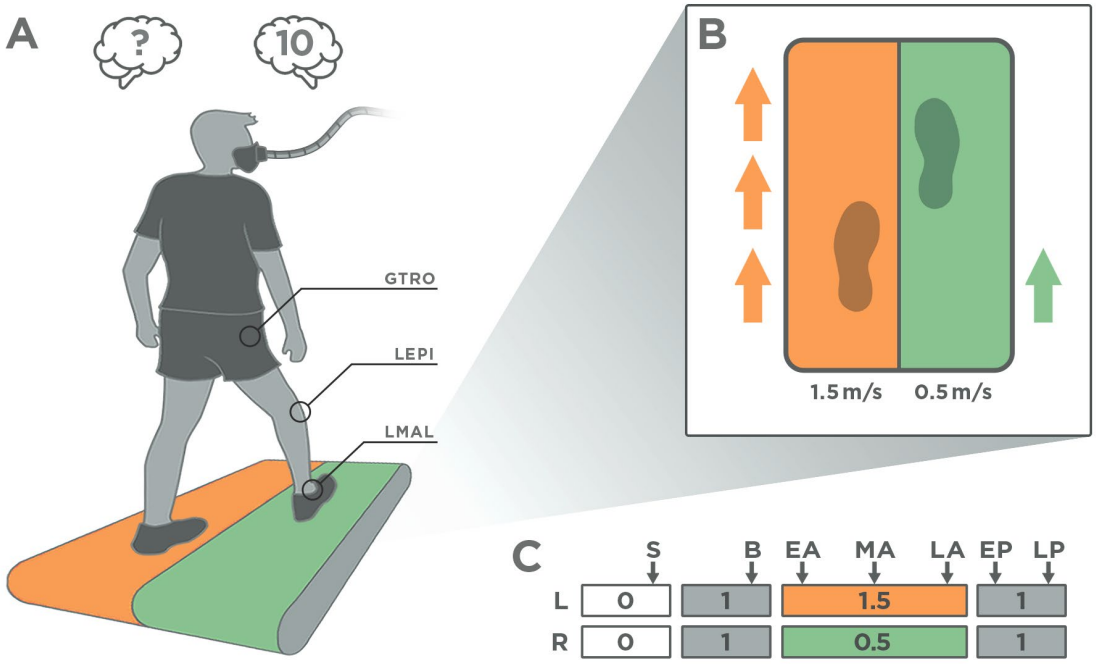


Figure 1. Experimental setup and protocol. A) Experimental setup showing experimental groups, metabolic mask, and marker location to calculate spatiotemporal variables. B) Split-belt configuration. For all participants, the left belt was set at 1.5 m/s and the right belt at 0.5 m/s. 27 participants reported 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 timepoints 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.

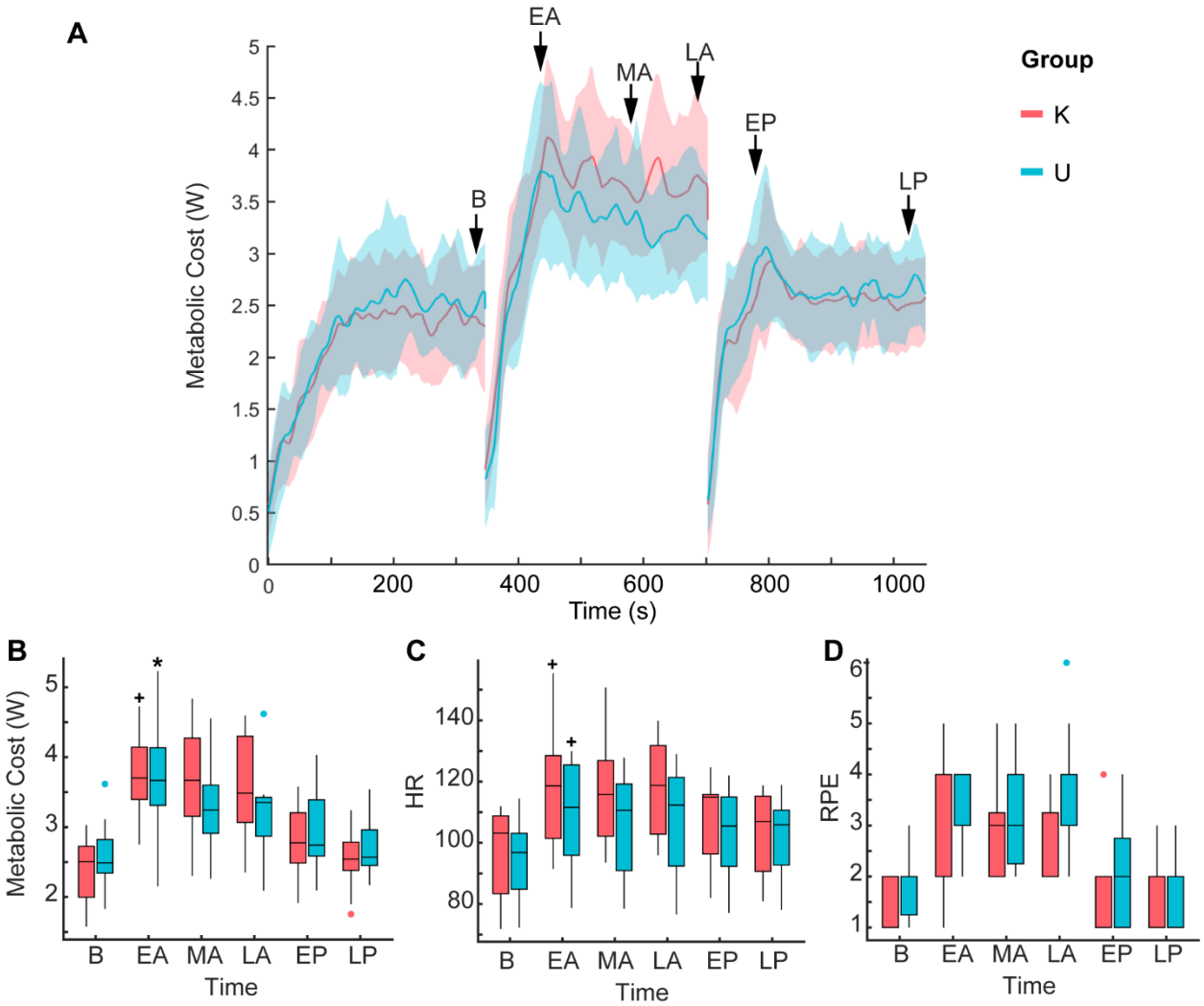


Figure 2. Metabolic cost, heart rate, and perception of effort. A) Net metabolic power timeseries during the experiment between the Knowledge (Red) and Uncertainty (Blue) groups. Time windows indicating B, EA, MA, LA, EP, and LP are indicated in the figure. We observed a significant effect of Time ($p<0.001$) and the interaction of Time×Group ($p=0.007$) but not of Group ($p=0.580$) on metabolic cost. B) Average metabolic cost between groups during 30 seconds corresponding to B, EA, MA, LA, EP, and LP. Across groups, the metabolic cost during EA ($p<0.001$), MA ($p<0.001$), LA ($p<0.001$), and EP ($p<0.001$) was significantly different from B. In the U group, metabolic cost during EA was higher than MA ($p<0.001$) and LA ($p<0.001$). C) Average heart rate between groups during 30 seconds corresponding to B, EA, MA, LA, EP and LP. We observed a significant effect of Time ($p<0.001$) and the interaction of Time×Group ($p=0.041$) on HR. Across groups, heart rate during EA ($p<0.001$), MA ($p=0.003$), EP ($p<0.001$), and LP ($p<0.001$) was significantly different from B. D) Rating of perceived exertion as indicated

by participants during B, EA, MA, LA, EP, and LP. We observed a significant effect of Time ($p<0.001$) but not of Time×Group ($p=0.369$) or Group ($p=0.165$) on RPE. Across groups, RPE during EA ($p<0.001$), MA ($p<0.001$), and LA ($p<0.001$) was significantly different from B. +: Significant differences between EA compared to all tied belt conditions: B, EP and LP ($p<0.001$). *: Significant differences between EA and all other timepoints ($p<0.005$). K: Knowledge. U: Uncertainty. HR: Heart Rate. RPE: Rating of Perceived Exertion. Other abbreviations as in Figure 1.

Figure 3.

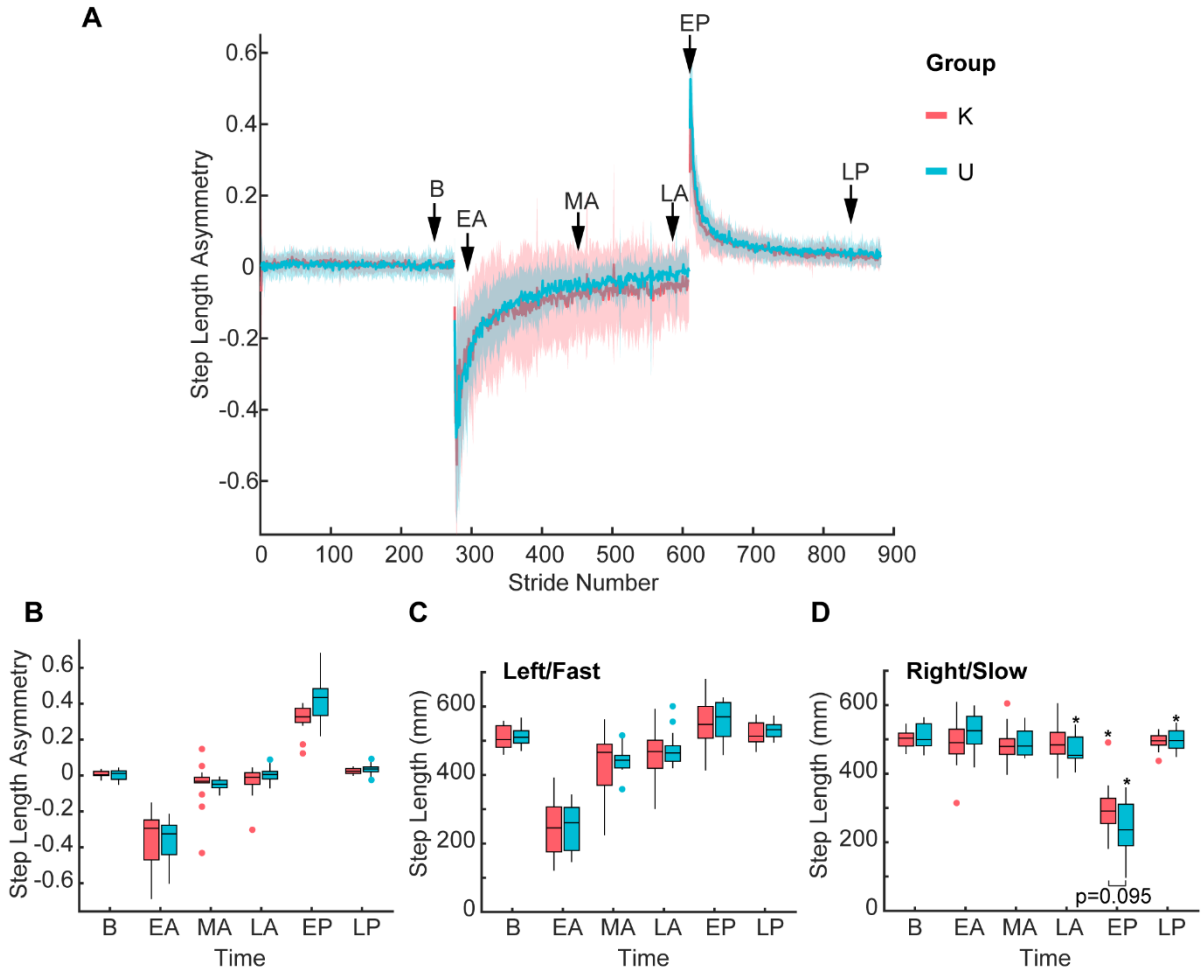


Figure 3. Step length asymmetry and step lengths. A) Step length asymmetry during the experiment between the Knowledge (Red) and Uncertainty (Blue) groups. Time windows indicating B, EA, MA, LA, EP, and LP are indicated in the figure. We observed a significant effect of Time ($p<0.001$) but not for the interaction of Time×Group ($p=0.170$) or Group ($p=0.191$) on step length asymmetry. B) Distribution of average step length asymmetry between groups during the 5 strides corresponding to B, EA, MA, LA, EP, and LP. Across groups, step length asymmetry during EA ($p<0.001$), MA ($p=0.003$), EP ($p<0.001$), and LP ($p<0.001$) was significantly different from the B condition. C) Distribution of average step lengths for the left/fast leg between groups during the 5 strides corresponding to B, EA, MA, LA, EP, and LP. We observed a significant effect of Time ($p<0.001$) but not for the interaction of Time×Group ($p=0.991$) or Group ($p=0.649$) on step lengths with the left/fast leg. Across groups, step lengths during EA ($p<0.001$), MA ($p<0.001$), LA ($p<0.001$), EP ($p<0.001$) and LP ($p<0.001$) were

significantly different from the B condition. D) Distribution of average step lengths for the right/slow leg between groups during the 5 strides corresponding to B, EA, MA, LA, EP, and LP. We observed a significant effect of Time ($p<0.001$) and the interaction of Time×Group ($p=0.031$) but not Group ($p=0.591$) on step lengths with the right/slow leg. Across groups, step lengths during MA ($p=0.031$), LA ($p=0.007$), EP ($p<0.001$), and LP ($p=0.005$) were significantly different from B. The step lengths with the right/slow leg were shorter in the U group during LA compared to B ($p=0.002$) but not in the K group ($p=0.437$). During post-adaptation, the step lengths in the U group remained 11 ± 4 mm shorter than B during LP ($p=0.015$) but not in the K group ($p=0.095$). *$p<0.050$ significant differences from the B condition. Abbreviations as in Figures 1 and 2.

Figure 4.

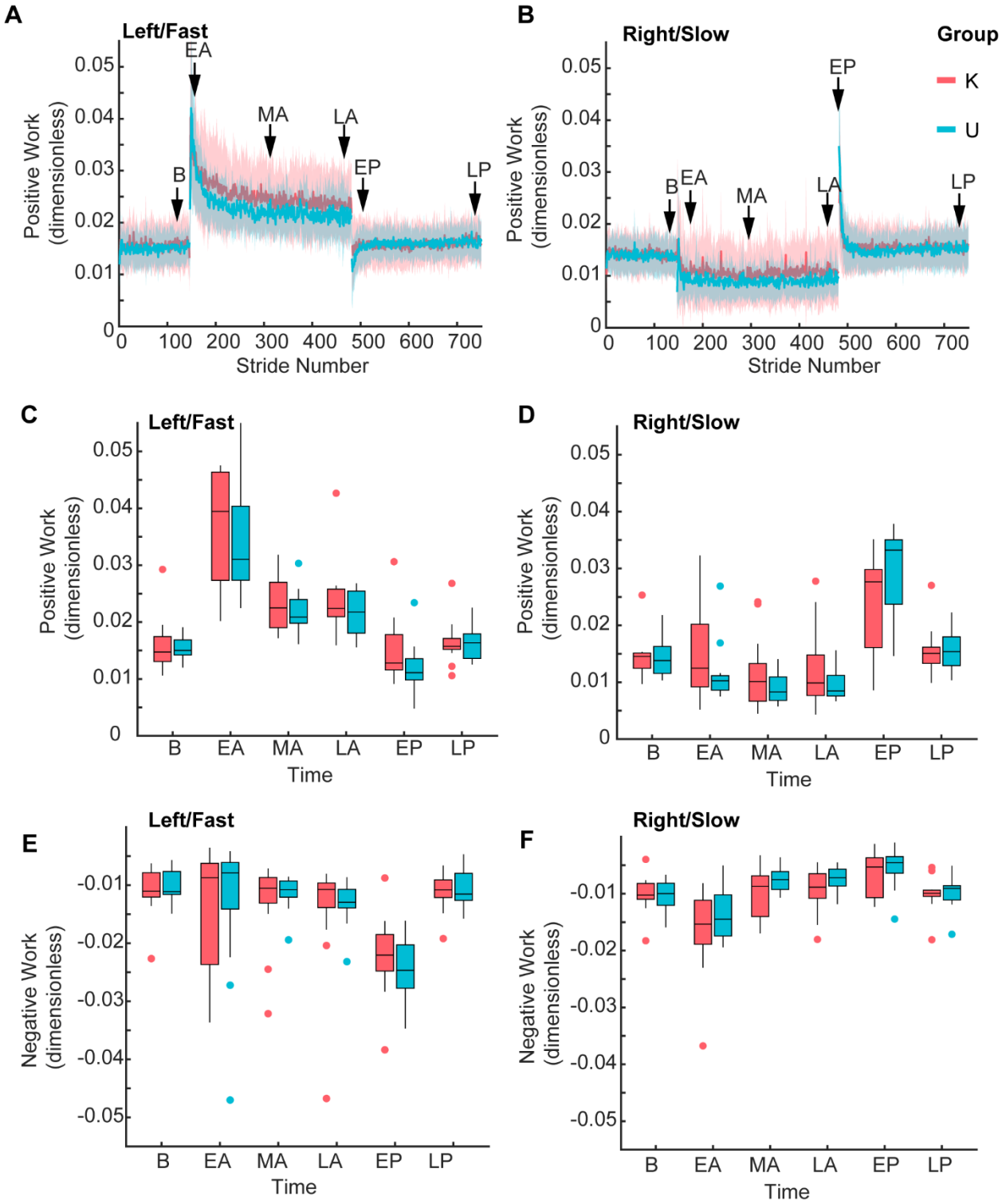


Figure 4. Work by the fast and slow legs. A) Positive work by the fast leg during the experiment between the Knowledge (Red) and Uncertainty (Blue) groups. Time windows indicating B, EA, MA, LA, EP and LP are indicated in the figure. We observed a significant effect

of Time ($p<0.001$) but not for the interaction of Time×Group ($p=0.652$) or Group ($p=0.278$) on positive work by the fast leg. B) Positive work by the slow leg during the experiment between the Knowledge (Red) and Uncertainty (Blue) groups. We observed a significant main effect of Time ($p<0.001$) and the interaction of Time×Group ($p=0.031$) but not of Group ($p=0.597$) on positive work by the slow leg. C) Distribution of average positive work by the left/fast leg between groups during the 5 strides corresponding to B, EA, MA, LA, EP, and LP. Across groups, work during EA ($p<0.001$), MA ($p<0.001$), LA ($p<0.001$), EP ($p=0.007$), and LP ($p=0.017$) was significantly different from the B condition. D) Distribution of average positive work by the right/slow leg between groups during the 5 strides corresponding to B, EA, MA, LA, EP, and LP. Across groups, work during MA ($p<0.001$), LA ($p=0.002$), EP ($p<0.001$), and LP ($p=0.001$) was significantly different from the B condition. For the U group, work during MA ($p<0.001$) and LA ($p=0.002$) was significantly lower than the B condition. E) Distribution of average negative work by the fast leg between groups during the 5 strides corresponding to B, EA, MA, LA, EP, and LP. Across groups, work during EA ($p<0.001$), MA ($p<0.001$), LA ($p<0.001$), EP ($p=0.007$), and LP ($p=0.017$) was significantly more negative than the B condition. F) Distribution of average negative work by the slow leg between groups during the 5 strides corresponding to B, EA, MA, LA, EP, and LP. Across groups, work during EA ($p<0.001$), MA ($p<0.001$), LA ($p<0.001$), EP ($p=0.007$) was significantly different than B. Abbreviations as in Figures 1 and 2.

Figure 5

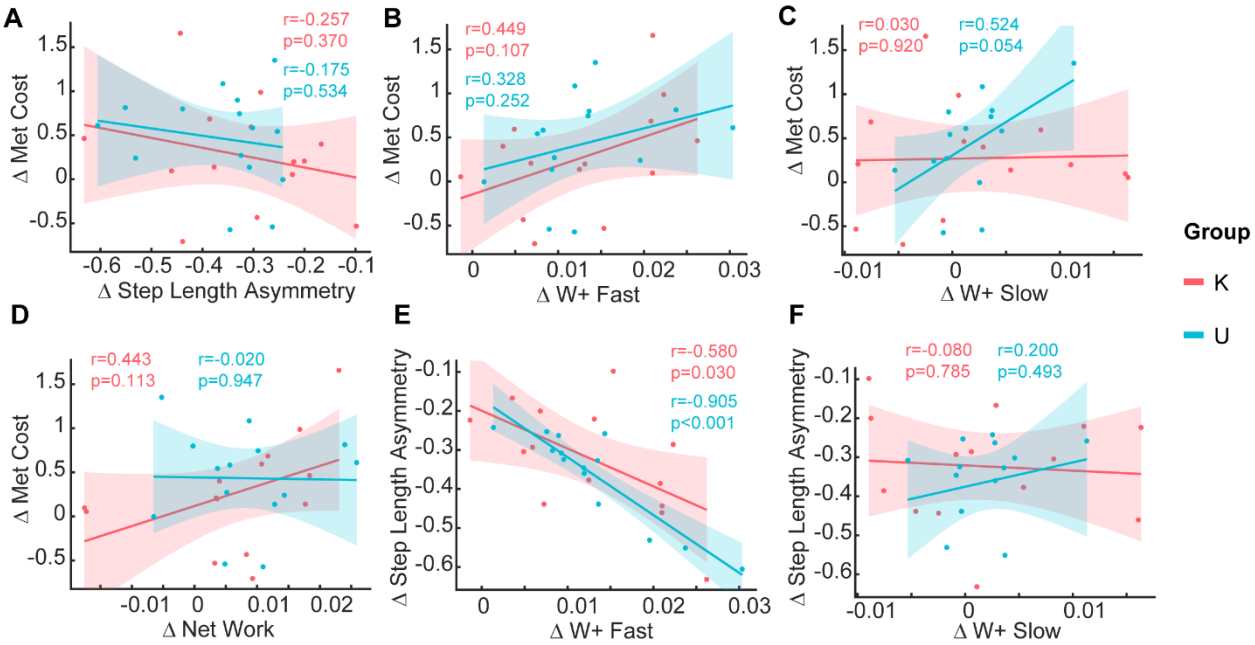
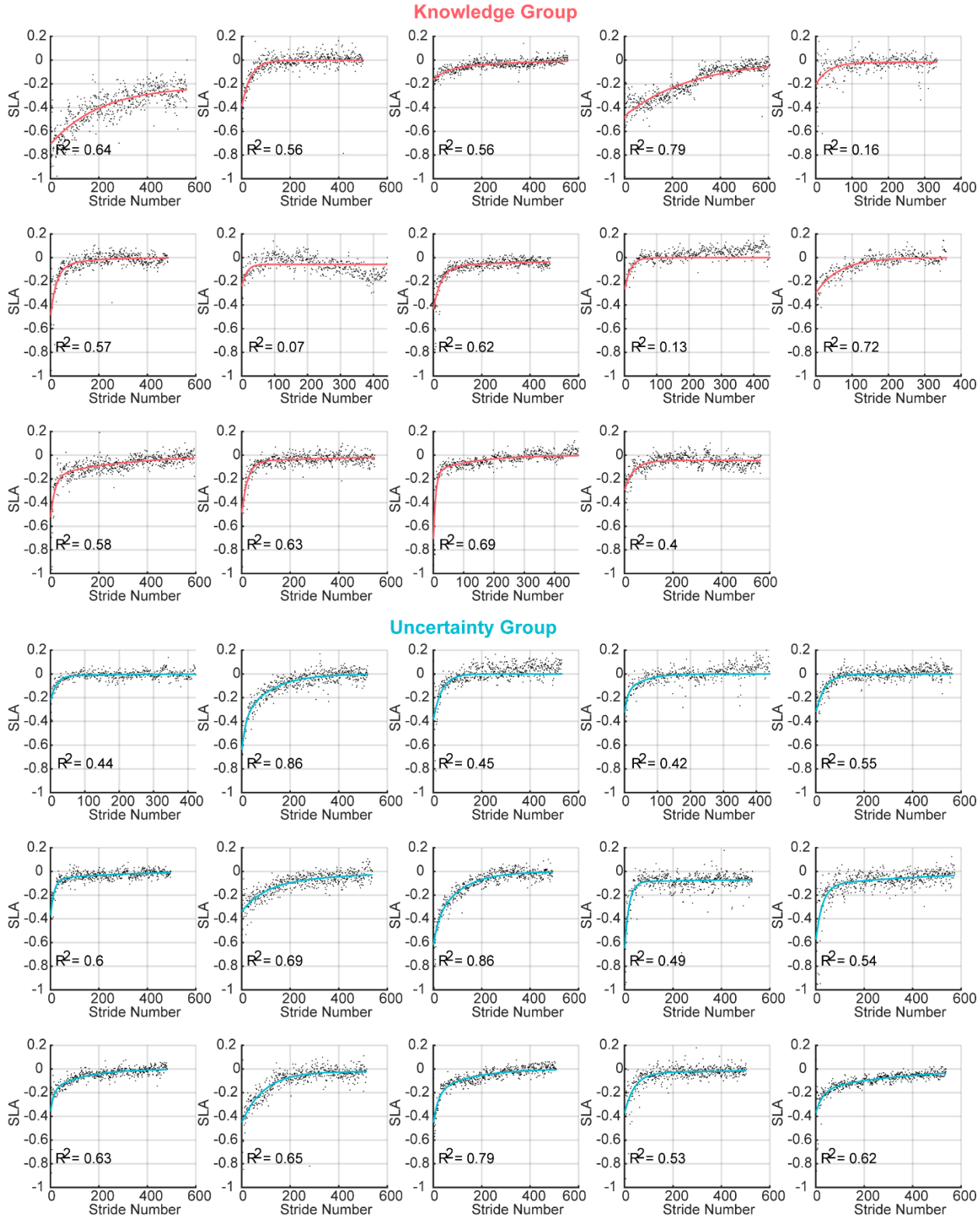


Figure 5. Associations between biomechanical and metabolic measures. A) Association between change in step length asymmetry and change in metabolic cost from EA to LA. B) Association between change in positive work by the left/fast leg and change in metabolic cost from EA to LA. C) Association between change in positive work by the right/slow leg and change in metabolic cost from EA to LA. D) Association between change in net work and change in metabolic cost from EA to LA. E) Association between change in positive work by the left/fast leg and change in step length asymmetry from EA to LA. F) Association between change in positive work by the right/slow leg and change in step length asymmetry from EA to LA.

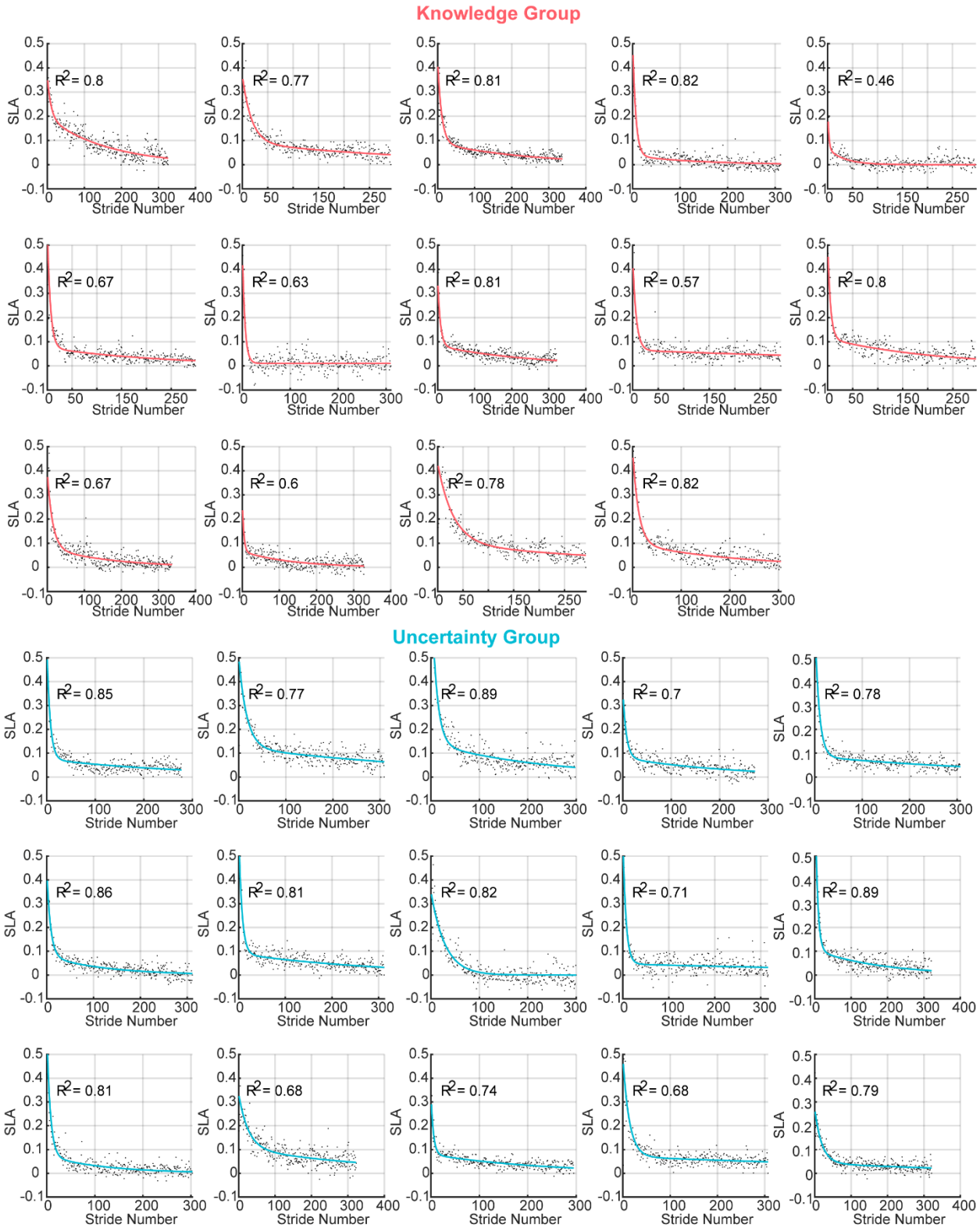
Supplementary Figure 1



Supplementary Figure 1. Individual step length asymmetry data and two-exponential fits during split-belt adaptation. N=14 participants in the Knowledge group and N=15 participants

in the uncertainty group. Coefficients of determination (R^2) for the two exponential models are indicated for each participant. Based on the Akaike Information Criterion (AIC), a two-exponential model provided the best fit to the data for all participants in the K group. Based on the Akaike Information Criterion (AIC), a two-exponential model provided the best fit to the data in N=13 participants in the U group. For participants 3 and 5, in the U group, a one-exponential model provided the best fit to the data (a two-exponential model was used).

Supplementary Figure 2



Supplementary Figure 2. Individual step length asymmetry data and two-exponential fits during post-adaptation. N=14 participants in the Knowledge group and N=15 participants in

the uncertainty group. Coefficients of determination (R^2) for the two exponential models are indicated for each participant. Based on the Akaike Information Criterion (AIC), a two-exponential model provided the best fit to the data for all participants in the K and U groups.