Title: Habitual aerobic exercise evokes fast and persistent adaptation during split-belt walking

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Summary Statement:

Young adults who regularly participate in aerobic exercise respond more quickly to the onset of a split-belt perturbation and continue to adapt their gait pattern throughout the duration of the split-belt exposure.

List of Abbreviations:

SLA = step length asymmetry

Abstract:

Changing movement patterns in response to environmental perturbations is a critical aspect of gait and is related to reducing the energetic cost of the movement. Aerobic exercise improves energetic capacity for submaximal exercise and may affect how people adapt movement to reach an energetic minimum. The purpose of this study was to determine whether differences in recreational aerobic exercise training influence gait adaptation in healthy young adults. Young adults who habitually exercised (n=19) and young adults who did not habitually exercise (n=13) walked on a split-belt treadmill with one belt moving twice the speed of the other belt for 10 minutes. Step length asymmetry (SLA) and mechanical work done by each leg were measured over each stride. Nonlinear mixed effects models compared the time course of adaptation between Habitual Exercisers and Non-exercisers, and *t*-tests compared net work at the end of adaptation between Habitual Exercisers and Non-exercisers. Compared to Non-exercisers, Habitual Exercisers initially adapted SLA and positive work by the fast leg quickly, and continued to modify SLA over the duration of split-belt treadmill walking. Young adults who regularly participate in aerobic exercise respond more quickly to the onset of a perturbation, and throughout the perturbation they continue to explore movement strategies, which might be related to reduction of energetic cost.

Introduction

Adapting walking patterns in response to environmental perturbations is a critical aspect of locomotion. When a person encounters a perturbation — such as when walking on a boat rocking on the water or walking on an icy surface — they must adapt their walking patterns to avoid falling, which can be achieved using different strategies. How individual factors might influence walking adaptation strategies remains to be determined.

A common approach to study walking adaptation is split-belt treadmill walking, in which the belts under each leg move at different speeds (1,2). The changes in the asymmetry between left and right step lengths, or step length asymmetry (SLA) is one measure used to track adaptation. SLA robustly changes during split-belt walking, shows an aftereffect after the split-belt perturbation is removed, is observable with the unaided eye, and is sensitive to experimental manipulations (3–7). In line with upper extremity motor adaptation (8), adaptation of SLA during split-belt walking occurs at two distinct rates – a fast component that adapts rapidly and a slow component that adapts more gradually (9–12). From work in both upper and lower extremity motor tasks, the two timescales of motor adaptation may derive from two separate (but not necessarily independent) processes

Indeed, Seethapathi and colleagues posited that the component that adapts rapidly is driven by balance optimization, whereas the component that adapts more gradually is driven by energetic cost optimization (13). Consistent with these findings, experimental studies have shown that SLA adaptation during split-belt walking occurs in parallel with reductions in the work generated by the legs; gait adaptation results in decreasing positive work and increasing negative work done by the legs, especially the leg on the fast belt (14,15). As the legs reduce positive work done and increase negative work done, energetic cost decreases concomitantly (14,16,17). This complements the fact that doing negative work is less energetically costly than doing positive work (18,19). By reducing work done by the legs, people are likely gradually adapting towards some lower energetic cost, as determined by Seethapathi et. al.(13) and

previously empirically suggested (20–22). Similarly, a study by Park et al showed that during early adaptation to split belt walking, individuals increase whole body angular momentum, which is inversely proportional to balance (23). Therefore, these experimental findings also support the idea of balance and energetic cost as the two distinct processes driving gait adaptation.

The question then arises — do individual factors that affect energy consumption affect the ability to adapt gait during split-belt walking? The multisystem benefits of aerobic exercise are well-known and include improved physical function, cognition, quality of life, and reduced risk of cardiovascular disease and all-cause mortality (24). Moreover, the ability to move at a minimum energetic cost of transport at a given speed is a function of aerobic training experience, such that people with more aerobic training reach a minimum cost of transport while running, but those who engage in less aerobic training do not (25). Along with an ability to reach an energetic minimum, aerobically trained adults have a higher maximal oxygen uptake (VO_2max) (26), a better exercise economy (26,27), and higher lactate and ventilatory thresholds (26). These training-induced adaptations would increase capacity for exercise and enable aerobically trained individuals to tolerate submaximal exercise for longer. If we posit that people adapt to split-belt walking in order to reduce energetic cost, then those who engage in more aerobic exercise may reach an energetic minimum quicker than those who engage in less exercise (25); conversely, those who engage in more aerobic exercise may more gradually reach an energetic minimum, due to a higher tolerance for submaximal exercise (26,27). These two hypotheses indicate that fitness might influence adaptation toward more energetically economical movement patterns.

The purpose of this study was to determine whether differences in weekly amount of exercise influence gait adaptation in healthy young adults. We hypothesized that amount of exercise would affect gait adaptation, and this effect would primarily be driven by differences in the slow component of adaptation, given the role of energetics in shaping the rate of adaptation of the slow component (13,20–22) and the well-established effects of exercise on energetics

(25–27). Our hypothesis is based on two opposing mechanisms which we will test here: 1) Habitual Exercisers would adapt faster than Non-exercisers to reach a minimum energetic cost quickly (25), evidenced by faster reduction in SLA and work done by the legs; 2) Habitual Exercisers would have a higher tolerance for the submaximal exercise of treadmill walking than Non-exercisers, evidenced by more gradual reduction in SLA and work done by the legs. To test these competing mechanisms, we analyzed the adaptation of SLA and the positive and negative work done by each leg while Habitual Exercisers and Non-exercisers walked on a split-belt treadmill. We also hypothesized that at the end of adaptation, Habitual Exercisers would perform more-negative net work than Non-exercisers, by reducing positive work done by the legs and increasing negative work done by the legs in order to reduce overall energetic cost (14,16,17). A significant effect of regular exercise participation on gait adaptation would support the idea that individual factors that influence energetics can also influence walking adaptation. Our findings will provide insights into the multisystem positive effects of exercise, including walking adaptation, and will provide directions for exercise rehabilitation research.

Methods

Participants

We recruited a convenience sample of young adults ages 19-35 for participation in this study. Participants were excluded if they reported cardiovascular, pulmonary, renal, metabolic, vestibular, or neurologic disorders; any lower-extremity injuries or surgeries in the past 12 months; or a prior anterior cruciate ligament injury. The Auburn University Institutional Review Board approved all procedures and all participants completed written informed consent prior to participating (Protocol #18-418 MR 1811). Data were collected in the Locomotor and Movement Control Lab at Auburn University.

Experimental Protocol

Participants first completed a self-report exercise questionnaire. This questionnaire asked how many times per week participants currently exercised at a moderate-to-vigorous intensity, for how many minutes per session, and for how many consecutive weeks. Based on their responses, participants were grouped into one of two groups according to the American College of Sports Medicine Physical Activity Guidelines for Americans: Habitual Exercisers (at least 150 minutes per week of exercise for at least the last three months) or Non-exercisers (less than 150 minutes per week of exercise for at least the last three months) (24). The questionnaire also asked participants which leg they kicked a ball with – the reported kicking leg was determined the dominant leg and was always set on the fast belt during adaptation.

After completing the questionnaire, participants walked on the treadmill. Participants held onto side handrails for the entirety of treadmill walking. The instructions given to participants noted that they should use the handrails for stability, and not to offload bodyweight. First, participants determined their typical and their fastest comfortable walking speeds on the treadmill using a modified protocol by Dingwell and Marin (28). The treadmill was accelerated to a relatively slow speed, and the speed slowly increased until the participant reported that the current speed was their typical walking speed or was their fastest comfortable speed. This was repeated twice for typical walking speed, and twice for fastest comfortable walking speed. The prompt for typical walking speed was, “tell me when you reach your typical walking speed.” The prompt for fastest comfortable speed was, “tell me when you reach the fastest speed that you’d be comfortable walking for ten minutes.” The participant’s fastest comfortable speed was set as the fast belt speed, and half of the fastest comfortable speed was set as the slow belt speed.

The split-belt walking protocol is shown in Figure 1. After finding their preferred typical and fast speeds, participants walked for three minutes at their typical walking speed, followed by three minutes at their fastest comfortable speed, followed by three minutes at half of the fast speed (slow speed). The last tied walking condition — three minutes of walking at the slow speed — was considered the baseline condition for data analysis. Then, participants walked for

ten minutes with the belt speeds split — the belt under the dominant leg moved at participants' fastest comfortable speed, and the belt under the non-dominant leg moved at the slow speed.

Figure 1. Split-belt walking protocol. A) An oblique and birds-eye view of the split-belt treadmill. B) First, the participant walked for 3 minutes at their self-selected typical walking speed. Then, they walked for 3 minutes at their self-selected fastest comfortable walking speed. Then, they walked for 3 minutes at half of their fast speed. Finally, they walked for 10 minutes with the belt under their dominant leg at the fast speed, and the belt under their non-dominant leg at the slow speed.

Data Analysis

Kinematic data were recorded at 100 Hz from reflective markers placed bilaterally on the anterior superior iliac spine and the lateral malleoli of the ankles, using a 17-camera motion capture system (VICON; Vicon Motion Systems Ltd, Oxford, United Kingdom). Kinematic data were lowpass filtered with a 4th order Butterworth filter with a cutoff frequency of 6 Hz. Ground reaction force data were obtained for each individual leg using an instrumented split-belt treadmill, recorded at 1000 Hz from two separate force plates. Force data were lowpass filtered with a 4th order Butterworth filter with a cutoff frequency of 20 Hz.

Step length was calculated as the distance between the ankle markers along the anterior-posterior walking axis at foot strike. SLA was calculated and normalized to stride length as follows:

$$Step\ length\ Asymmetry = \frac{Step\ length_{fast} - Step\ length_{slow}}{Step\ length_{fast} + Step\ length_{slow}}$$

Here, $Step\ Length_{fast}$ is the step length when the leg on the fast belt strikes the belt, and $Step\ Length_{slow}$ is the step length when the leg on the slow belt strikes the belt. A negative SLA

indicates that the leg on the slow belt is taking a longer step than the leg on the fast belt, and an SLA of zero indicates that the legs are taking steps of equal length.

We calculated positive and negative mechanical work generated by the legs using a custom MATLAB program. We used the point-mass model to estimate mechanical work generated by the legs on the treadmill and on the center of mass (12,14,15). In brief, we segmented force data into strides (15) and calculated the center of mass velocities in each direction as the time integral of the center of mass accelerations. Next, we calculated the instantaneous power generated by each leg for each stride as the instantaneous sum of the dot product of the ground reaction force and the center of mass velocity and the dot product of the force applied to the respective belt and the belt speed. We then calculated the total positive and total negative work performed by each leg as the time integral of the positive or negative portion of the total instantaneous power over the stride cycle. We calculated work rate by dividing each work measure by stride duration. Finally, we calculated the net work rate by the legs at the end of adaptation as the time integral of the power divided by stride cycle, averaged over the last 100 strides.

Statistical Analysis

All statistical analyses were conducted in R (29). We used Welch Two Sample t-tests to compare age, height, leg length, mass, and fast-leg belt speed between groups. We also used Pearson's Chi-squared tests with Yates' continuity correction to assess the difference in proportion of males and females in each group, and to assess the difference in proportion of people who walked with the right leg on the fast belt in each group. We analyzed SLA, positive and negative work rate by the fast legs, and positive and negative work rate by the slow leg using mixed effects nonlinear regression models with the ‘nlme’ package in R (30). We truncated the data for all participants to minimum number of steps taken by a participant (823 steps) so that all participants would weight equally on each step.

Detailed description of the statistical models can be found in the supporting information. In brief, for each of the work rate outcome measures and for SLA, we built-up models to two-exponent models — assuming that adaptation of the outcome measures occurred over two timescales — that included a fixed effect for group (eqs. 1 and 2). Here, c is the estimated plateau if strides went to infinity; a_f is the initial value of the fast component of adaptation; r_f is the growth rate of the fast component of adaptation; a_s is the initial value of the slow component of adaptation; r_s is the growth rate of the slow component of adaptation. All five model parameters (c, a_f, r_f, a_s, r_s) were allowed to differ for Habitual Exercisers vs. Non-exercisers.

$$SLA = (c + a_f * e^{-\frac{step}{r_f}} + a_s * e^{-\frac{step}{r_s}}) \sim Group + (c|ID) \quad (1)$$

$$Work\ rate = \left(c + a_f * e^{-\frac{stride}{r_f}} + a_s * e^{-\frac{stride}{r_s}}\right) \sim Group + (c|ID) \quad (2)$$

We compared these two-exponent models with fixed effects for group to models without fixed effects for group, and to one-exponent models assuming adaptation occurs over a single timescale. All models and outcomes can be found in the supporting information. The simplest, best-fitting model for each measure was the final model that we interpreted, such that a lower Akaike Information Criterion (AIC) and Bayesian Information Criteria (BIC) and a ΔAIC > 2 indicated a better fit to the data (31,32). All models were fit with a maximum likelihood estimation and all models contained a random effect such that the outcome measure's estimated plateau was allowed to vary by participant. If the final model included a fixed effect for group, the significance (or lack thereof) of the effect of group on the equation variables in the best-fitting models was evaluated using Welch's t-test with an *a priori* alpha level of 0.05. If the final model included a fixed effect for group, initial adaptation values were calculated for each variable as the average over the first five strides and were compared between group using Welch's Two Sample t-test.

We used Welch's Two Sample t-test between groups to compare the net work rate by the legs at the end of adaptation, to determine if there was a difference between exercise groups in the ability to gain assistance from the treadmill.

Results

Participants

Thirty-two participants completed the study (6 female, age 22 (SD 3) yrs, mass 70.3 (SD 14.6) kg, height 171.82 (SD 9.75) mm). Based on the self-report exercise questionnaire, 19 participants were placed in the Habitual Exercisers group and 13 were placed in the Non-exercisers group. The two groups did not significantly differ by sex, height, mass, leg on the fast belt, or fast belt speed (Habitual Exercisers = 1.49 (0.21) m/s; Non-exercisers = 1.57 (0.16) m/s), but did significantly differ by age where Habitual Exercisers were slightly older (Habitual Exercisers 22 (SD 4) yrs; Non-exercisers 20 (SD 1) yrs, $t(21.827)=-2.127$, $p=0.045$). Demographic and belt speed data are provided in Table 1.

Table 1. Participant demographics in Mean (SD) [range].

	Non-exercisers	Habitual Exercisers	Total
n	*13*	*19*	*32*
Age (yr)	20 (1) [19,22]	22 (4) [19,32]	22 (3) [19,32]
Sex	3 F	3 F	6 F
Height (mm)	1706 (99) [1540,1910]	1727 (98) [1540,1920]	1718 (97) [1540,1920]
Mass (kg)	66.5 (11.9) [48,89]	72.9 (16.0) [50,116]	70.3 (14.6) [48,116]
Fast leg	3 right	3 right	6 right
Fast belt speed (m/s)	1.57 (0.16) [1.25,1.95]	1.49 (0.21) [1.15,1.98]	1.52 (0.20) [1.15,1.98]
Minutes/week exercise	38 (44) [0,120]	268 (157) [150,750]	175 (168) [0,750]
Exercise modality	Run, cycle, basketball, tennis	Run, cycle, basketball, tennis, CrossFit®, dance, boxing	—

Note. Sex: F = female. Type of exercise participated in reflects the exercise modalities of people who participated in any exercise every week (regardless of minutes per week of exercise).

General Timescales of Adaptation

The best-fitting model for each outcome measure was the two-exponent model containing a fixed effect for group (eqs. 1 and 2, Table 2), indicating that SLA and work rate by the legs adapted over two distinct timescales and was affected by exercise. All candidate models for each outcome measure, and the final model fits to each participant's data, can be found in the supporting information.

Table 2. Final mixed effects models for SLA, positive and negative work of the fast leg, and positive and negative work of the slow leg.

	Coefficient	SLA	Positive Work Rate		Negative Work Rate	
			Fast Leg	Slow Leg	Fast Leg	Slow Leg
Non-exercisers	*c* (plateau)	-0.043 *** (0.010)	0.54 *** (0.12)	0.20 (0.17)	-0.28 ** (0.10)	-0.48 ** (0.16)
	a_f (fast component initial value)	-0.097 *** (0.007)	0.38 *** (0.06)	0.28 *** (0.03)	0.02 (0.02)	-0.60 *** (0.06)
	r_f (fast component growth rate)	32.465 *** (3.751)	5.19 *** (1.47)	7.56 *** (1.33)	31.94 (48.41)	6.26 *** (1.18)
	a_s (slow component initial value)	-0.017 *** (0.008)	0.66 ** (0.03)	0.32 * (0.15)	0.03 (0.04)	-0.66 *** (0.03)
	r_s (slow component growth rate)	162.122 ** (69.910)	86.45 *** (5.92)	629.28 (423.13)	1.12 (3.53)	101.41 *** (8.35)
Habitual Exercisers	*c* (plateau)	-0.033 (0.014) *p=0.475*	0.68 (0.16) *p=0.359*	0.36 (0.18) *p=0.362*	-0.24 (0.14) *p=0.754*	-0.68 (0.21) *p=0.341*
	a_f (fast component initial value)	-0.078 † (0.009) *p=0.032*	0.56 † (0.07) *p=0.009*	0.55 † (0.04) *P<0.001*	-0.15 † (0.04) *p<0.001*	-0.831 † (0.07) *p=0.002*
	r_f (fast component growth rate)	11.628 † (3.929) *p<0.001*	6.78 (1.74) *p=0.362*	3.45 † (1.36) *p=0.003*	1.86 (48.41) *p=0.534*	6.76 (1.38) *p=0.718*
	a_s (slow component	-0.060 † (0.008)	0.36 † (0.03)	0.05 (0.15)	0.12 (0.07)	-0.40 † (0.03)

initial value)	*p<0.001*	*p<0.001*	*p=0.064*	*p=0.194*	*p<0.001*
r_s (slow component growth rate)	396.341 † (78.306) *p=0.003*	157.47 † (23.30) *p=0.002*	321.16 (579.39) *p=0.595*	433.6 (304.94) *p=0.157*	156.07 † (23.47) *p=0.20*
AIC	-106168.7	2021.38	-12838.49	-12350.91	4848.64
BIC	-106070.6	2111.25	-12748.6	-12261.04	4938.51
Log-likelihood	53096.36	-998.69	6431.24	6187.46	-2412.32
Number of observations	26336	13216	13216	13216	13216
Number of participants	32	32	32	32	32
SD: ID (*c*)	0.038	0.435	0.231	0.347	0.572
SD: Residual (*c*)	0.032	0.259	0.147	0.150	0.288

Note. The best-fitting model to the data for all five outcome measures was the two-exponent model with a fixed effect on all variables by group. All models contain a random plateau on participant. AIC = Akaike Information Criterion; BIC = Bayesian Information Criterion. Values in parentheses are standard errors of the fixed effects. Asterisks indicate significant effects where *p<0.05, **p<0.01, ***p<0.001. Daggers on coefficients in the Habitual Exercisers group indicate coefficients that are significantly different between Habitual Exercisers and Non-exercisers, and all group-difference p-values are shown.

Step Length Asymmetry

Compared to Non-exercisers, Habitual Exercisers adapted SLA more gradually. The groups differed in every model-estimated coefficient except for SLA plateau. Overall, Habitual Exercisers and Non-exercisers did not differ in initial SLA (Habitual Exercisers = -0.144, Non-exercisers = -0.137, $t(28.763)=0.283$, $p=0.779$)). Habitual Exercisers adapted the fast component of SLA more quickly than Non-exercisers did (Habitual Exercisers r_f = 12 steps, Non-exercisers r_f = 32 steps), seen in the quicker achievement of the “elbow” by Habitual Exercisers in Figure 2. Conversely, Habitual Exercisers adapted the slow component of SLA more slowly than Non-exercisers did (Habitual Exercisers r_s = 396 steps, Non-exercisers r_s = 162 steps), seen in the gradual change in SLA after the elbow in Habitual Exercisers in Figure 2. Notably, the variability in SLA at each step between subjects appeared much larger across Habitual Exercisers than across Non-exercisers (Fig. 2). For better understanding of SLA adaptation, Figure 2B shows the averaged individual step lengths for fast and slow legs.

The model explained some of the variance in SLA plateau (Table 2, SD: Residual (*c*) = 0.032). Variation between participants accounted for a large portion of the variance in SLA plateau (Table 2, SD: ID (*c*) = 0.038).

Figure 2. Step length asymmetry adapts differently over 823 steps of split-belt treadmill walking. (A) Step length asymmetry adaptation. Shaded areas indicate the standard deviation. Solid lines indicate the model fit to the data. Dashed lines indicate the model-estimated plateau for each group. Blue=Habitual Exercisers(*n*=19), orange=Non-exercisers (*n*=13). (B) Average step lengths for the fast and slow legs during adaptation, for each group.

Positive Work Rate by the Fast Leg

Compared to Non-exercisers, Habitual Exercisers continued to gradually adapt positive work rate by the fast leg over the entire trial. The groups differed in the initial values and the slow-component growth rate (Figure 3A). Overall, Habitual Exercisers and Non-exercisers did not differ in initial positive work rate by the fast leg (Habitual Exercisers = 1.44 W/kg, Non-exercisers = 1.45 W/kg, $t(23.484)=0.051$, $p=0.960$). Habitual Exercisers adapted the slow component of positive work rate by the fast leg more slowly than Non-exercisers did (Fig 3A) (Habitual Exercisers r_s = 157 strides, Non-exercisers r_s = 86 strides).

The model explained much of the variance in fast-leg positive work rate plateau (Table 2, SD: Residual (*c*) = 0.259). Variation between participants accounted for a large portion of the variance in fast-leg positive work rate plateau (Table 2, SD: ID (*c*) = 0.435).

Figure 3. Positive work rate by the legs on the fast (A) and slow (B) belts over 823 steps of split-belt treadmill walking. Shaded areas indicate the standard deviation of each group. Solid lines indicate the model fit to the data. Dashed lines indicate the

model-estimated plateau for each group. Blue= Habitual Exercisers (*n*=19), orange=Non-exercisers (*n*=13).

Negative Work Rate by the Fast Leg

Habitual Exercisers and Non-exercisers did not differ in adaptation of the negative work rate by the fast leg. There were no significant adaptation in negative work rate by the fast leg, in either group (Fig 4A).

The model explained much of the variance in fast-leg negative work rate plateau (Table 2, SD: Residual (*c*) = 0.150). Variation between participants accounted for a large portion of the variance in fast-leg negative work rate plateau (Table 2, SD: ID (*c*) = 0.347).

Figure 4. Negative work rate by the legs on the fast (A) and slow (B) belts over 823 steps of split-belt treadmill walking. Shaded areas indicate the standard deviation of each group. Solid lines indicate the model fit to the data. Dashed lines indicate the model-estimated plateau for each group. Blue= Habitual Exercisers (*n*=19), orange=Non-exercisers (*n*=13).

Positive Work Rate by the Slow Leg

Overall, Habitual Exercisers and Non-exercisers did not differ in initial positive work rate by the slow leg (Habitual Exercisers = 0.701 W/kg, Non-exercisers = 0.722 W/kg, $t(23.462)=0.147$, $p=0.885$). Habitual Exercisers adapted the fast component of positive work rate by the slow leg more quickly than Non-exercisers did (Fig 3B) (Habitual Exercisers r_f = 3 strides, Non-exercisers r_f = 8 strides). Both groups converged on a plateau by about 10 strides, and the groups did not differ in their estimated plateaus.

The model explained much of the variance in slow-leg positive work rate plateau (Table 2, SD: Residual (*c*) = 0.147). Variation between participants accounted for a large portion of the variance in slow-leg positive work rate plateau (Table 2, SD: ID (*c*) = 0.231).

Negative Work Rate by the Slow Leg

Compared to Non-exercisers, Habitual Exercisers adapted the slow component of negative work rate by the slow leg more quickly (Figure 4B). Overall, Habitual Exercisers and Non-exercisers did not differ in initial negative work rate by the slow leg (Habitual Exercisers = -1.664 W/kg, Non-exercisers = -1.57 W/kg, $t(23.717)=0.248$, $p=0.806$). Habitual Exercisers adapted the slow component significantly slower (Habitual Exercisers r_s = 156 strides, Non-exercisers r_s = 101 strides). The groups did not differ in their estimated plateaus.

The model explained much of the variance in slow-leg negative work rate plateau (Table 2, SD: Residual (*c*) = 0.288). Variation between participants accounted for a large portion of the variance in slow-leg negative work rate plateau (Table 2, SD: ID (*c*) = 0.572).

Net work rate

The groups did not differ in the total net work rate by the legs ($t(28.549) = -0.774$, $p = 0.445$) (Fig. 5). Habitual Exercisers performed 0.166 (SD 0.072) W/kg and Non-exercisers performed 0.188 (SD 0.085) W/kg at the end of ten minutes of split-belt walking.

Figure 5. Net Work rate by the legs. Orange=Non-exercisers (*n*=13), Blue= Habitual Exercisers (*n*=19).

Discussion

The purpose of this study was to determine the effect of exercise on gait adaptation in healthy young adults. Our main findings are: 1) Compared to Non-exercisers, Habitual

Exercisers more gradually adapted SLA, positive work rate by the fast leg, and negative work rate by the slow leg over the entirety of split-belt exposure, 2) Habitual Exercisers initially adapted SLA and positive work rate by the slow leg quicker than Non-exercisers, 3) Neither group adapted the negative work rate by the fast leg, and 4) There was no effect of exercise on net work done by the legs. The findings from this study support the hypothesis that young adults who habitually exercise have a higher tolerance for the energetically-challenging asymmetric belt speeds and adapt more gradually than those who do not.

Habitual Exercisers continued to gradually adapt over the entirety of split-belt exposure. These current findings complement the literature. If the gradual component of gait adaptation is driven by energetic cost optimization (13), then long-term involvement in regular exercise — affecting exercise capacity — would affect the gradual component of gait adaptation, as seen here in both SLA adaptation, and in the reduction in the positive work rate by the fast leg and negative work rate by the slow leg. Exercise-trained adults have an enhanced exercise capacity relative to non-exercisers, evidenced by higher maximal oxygen uptake (VO2max) (26); a better exercise economy (26,27); and higher lactate and ventilatory thresholds(26). A higher exercise capacity indicates that Habitual Exercisers can tolerate submaximal exercise — such as treadmill walking — at a given energetic cost for longer than Non-exercisers, consistent with our results. Habitual Exercisers and Non-exercisers can both reduce positive work by the fast leg during split-belt adaptation, but Non-exercisers may have a direr need to do so quickly. Therefore, Non-exercisers would be working at a higher energetic relative effort, resulting in a stronger incentive to reduce energetic, and therefore mechanical, (12,14), work than the Habitual Exercisers. Our results contradict the potential mechanism that Habitual Exercisers would be quicker at reducing energetic cost than less active adults. Thus, the fact that adults with more exercise sessions per week and more endurance training reach a minimum cost of transport during running while those with less weekly exercise and less endurance training do not ever reach a minimum cost of transport (25) does not apply to split-belt adaptation.

Therefore, habitual exercise may allow people to have a higher tolerance for the perturbation induced by split-belt walking, allowing them to adapt their gait more gradually.

Habitual Exercisers initially adapted SLA and positive work rate by the slow leg quicker than Non-exercisers. Our findings suggest that young adults who engage in more exercise are quickly able to modify their gait in response to a continuous perturbation, possibly improving stability (13) more quickly than those who do not exercise habitually. Indeed, athletes have been shown to have better static balance than non-athletes (33). Buurke and colleagues investigated the relationship between mediolateral stability adaptation and metabolic cost adaptation during 9 minutes of 2:1 split-belt walking (20). However, they did not find a relationship between mediolateral stability and the reduction in metabolic cost. While their finding seems in contrast to both our findings and the theory that initial rapid gait adaptations are intended to optimize balance (13), all these findings taken together support a nuanced approach to motor skill learning. One explanation, supported by the dual-rate model, is that adults prioritize balance over metabolic cost when first perturbed, to meet the goals of the task (here, the assumed goal being to stay upright and continue walking). Then, once balance is achieved, metabolic cost becomes more relevant.

Neither group adapted the negative work rate by the fast leg. Negative work rate by the fast leg during split-belt adaptation was largely unaffected by exercise. Previous work reported that over forty-five minutes of adaptation at a 3:1 belt speed ratio, negative work rate by the fast leg increased prior to positive work rate by the fast leg decreasing (12). Our finding of no adaptation of negative work rate by the fast leg, by either group contrasts our hypothesis that exercise capacity affects metabolic adaptation through increasing the negative work rate done by the legs. A short adaptation period at a smaller belt speed ratio coupled with high variability across participants could explain the lack of significant change in the negative work rate by the fast leg in the current study, compared to previous work (12).

Both Habitual Exercisers and Non-exercisers performed net positive work by the end of ten minutes of gait adaptation. Sánchez and colleagues reported that, at positive values of step length asymmetry — achieved by enough time spent split-belt walking (12) — the legs perform net negative work (14). This suggests that people are able to reduce overall positive work and increase overall negative work performed. In contrast, our sample performed net positive, not negative, work. The difference in findings between studies is likely due to the shorter adaptation period (ten versus forty-five minutes) and the smaller split-belt speed ratio (2:1 Vs. 3:1) in the current study, leading to negative average values of SLA at the end of adaptation. Given enough time and/or a larger belt speed ratio, our sample would likely have plateaued at positive SLA values and performed net negative work. Future research should explore if exercise affects the ability to perform net negative work over prolonged adaptation periods at more extreme split-belt perturbations.

There are some limitations to this study. First, participants held on to the handrails during treadmill walking, which likely influenced both balance and mechanical work calculations. While handrail holding was kept constant across participants and across groups, future studies should investigate the effect of exercise on gait adaptation without holding on to handrails. Second, we did not directly measure metabolic energetic cost using expired gas analyses. It is possible that Habitual Exercisers may have modified SLA and mechanical work rate through nonmetabolic processes, such as tendon stiffness, without modifying metabolic cost. Our groupings based on aerobic exercise training – and not including resistance-trained adults – reasonably allows us to infer that reported differences between groups would be due to differences in energetic capacity. Future studies examining the metabolic adaptations between Habitual Exercisers and Non-exercisers is a warranted next-step. Third, we standardized belt speeds to participants' fastest comfortable walking speeds, which did not differ between groups. This method of selecting the fast-belt speed has been used previously (34–36), and because there was not a statistical difference between groups in initial SLA, we know that the groups

were not perturbed differently relative to their baseline, despite different belt speeds. Fourth, we used self-report measures of exercise participation. Habitual exercise recall has a moderate validity correlation to actual exercise (0.36) (37) and, despite its drawbacks, is the most common way to assess physical activity (38–40). Additionally, the presence of group differences in the current study suggests that self-report exercise habits were keen enough to separate participants by energetic capacity that would affect gait adaptation. Finally, we did not test retention of the adapted gait pattern, so we cannot comment on whether exercise affects young adults' magnitude or persistence of errors during gait pattern washout.

Habitual exercise affects a young adult's response to a novel perturbation. Our results suggest that people who regularly participate in aerobic exercise respond more quickly to the onset of a perturbation and continue to explore strategies and search for assistance from the environment in order to reduce energetic cost. The effect of aerobic exercise training on movement adaptation likely acts through increasing aerobic capacity, thus reducing relative effort of a given submaximal movement. On a split-belt treadmill, Habitual Exercisers may require longer time than Non-exercisers to fully take advantage of the work done by the treadmill; however, requiring a longer time to adapt is not inherently unfavorable. In fact, if provided enough time to fine-tune their response to the perturbation, Habitual Exercisers may plateau at a more-positive SLA, a more-negative net work done by the legs, and therefore perhaps a lower energetic cost than Non-exercisers. The current results provide preliminary evidence that Habitual Exercisers may be more able than Non-exercisers to use the work done by the treadmill to adapt and reduce positive work done by the legs, given enough time.

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Supporting information captions

Methods S1. A detailed description of the statistical modeling analysis.

Table S2. Model f**its of mixed effects linear models for each outcome measure.**

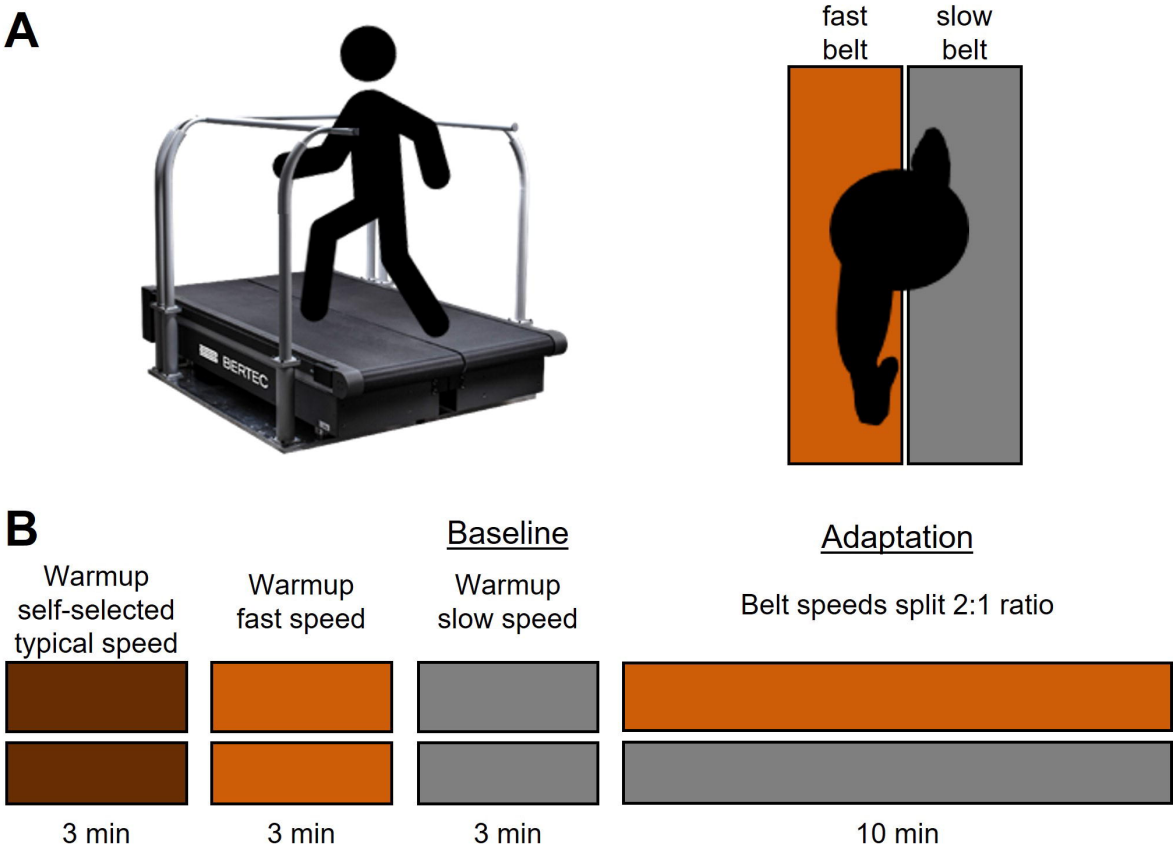
Figure S3. A comparison of the group average model fit (black line) and the individual model fits (blue line) of step length asymmetry adaptation.

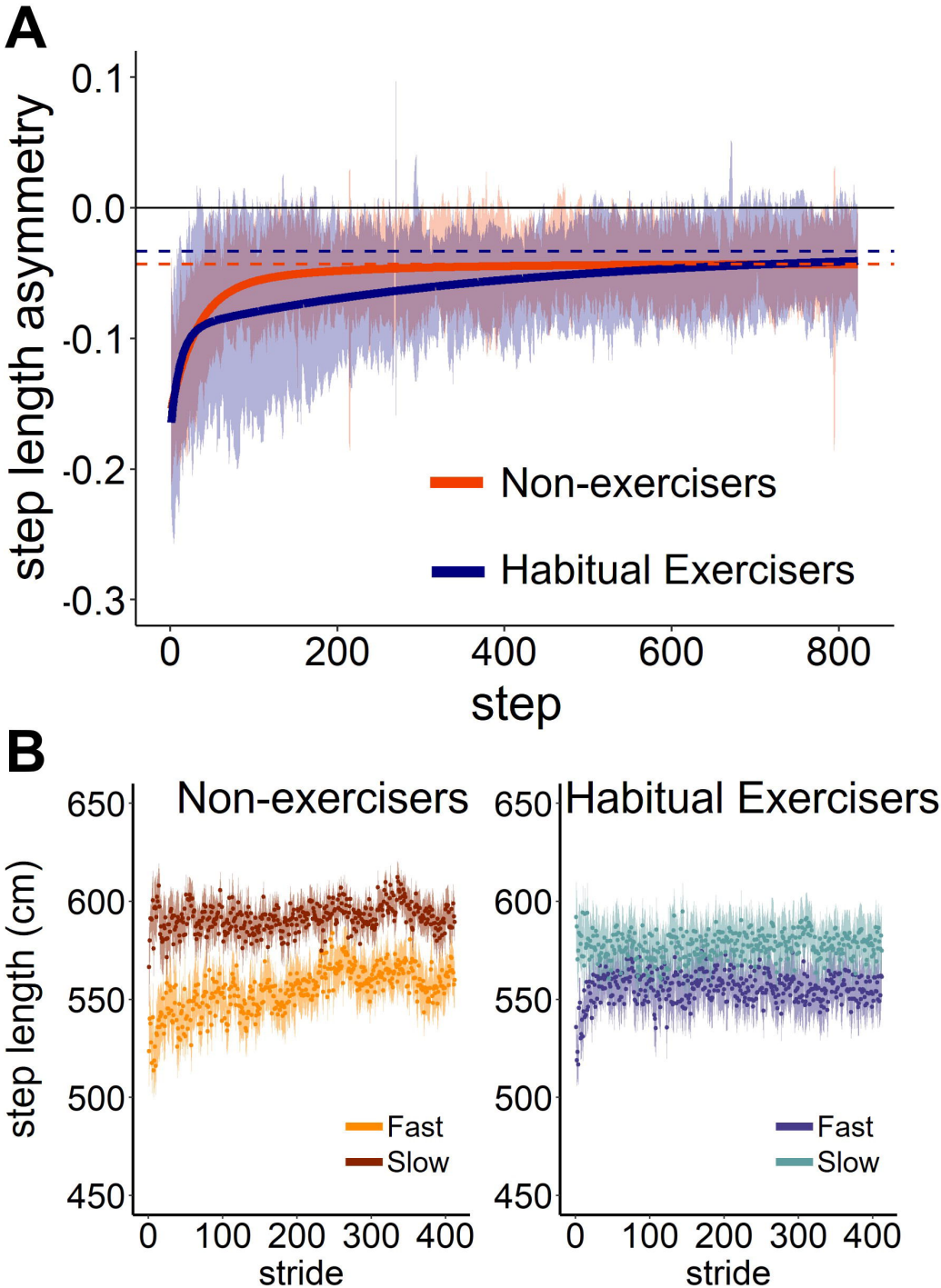
Figure S4. A comparison of the group average model fit (black line) and the individual model fits (blue line) of the adaptation of the positive work rate of the fast leg.

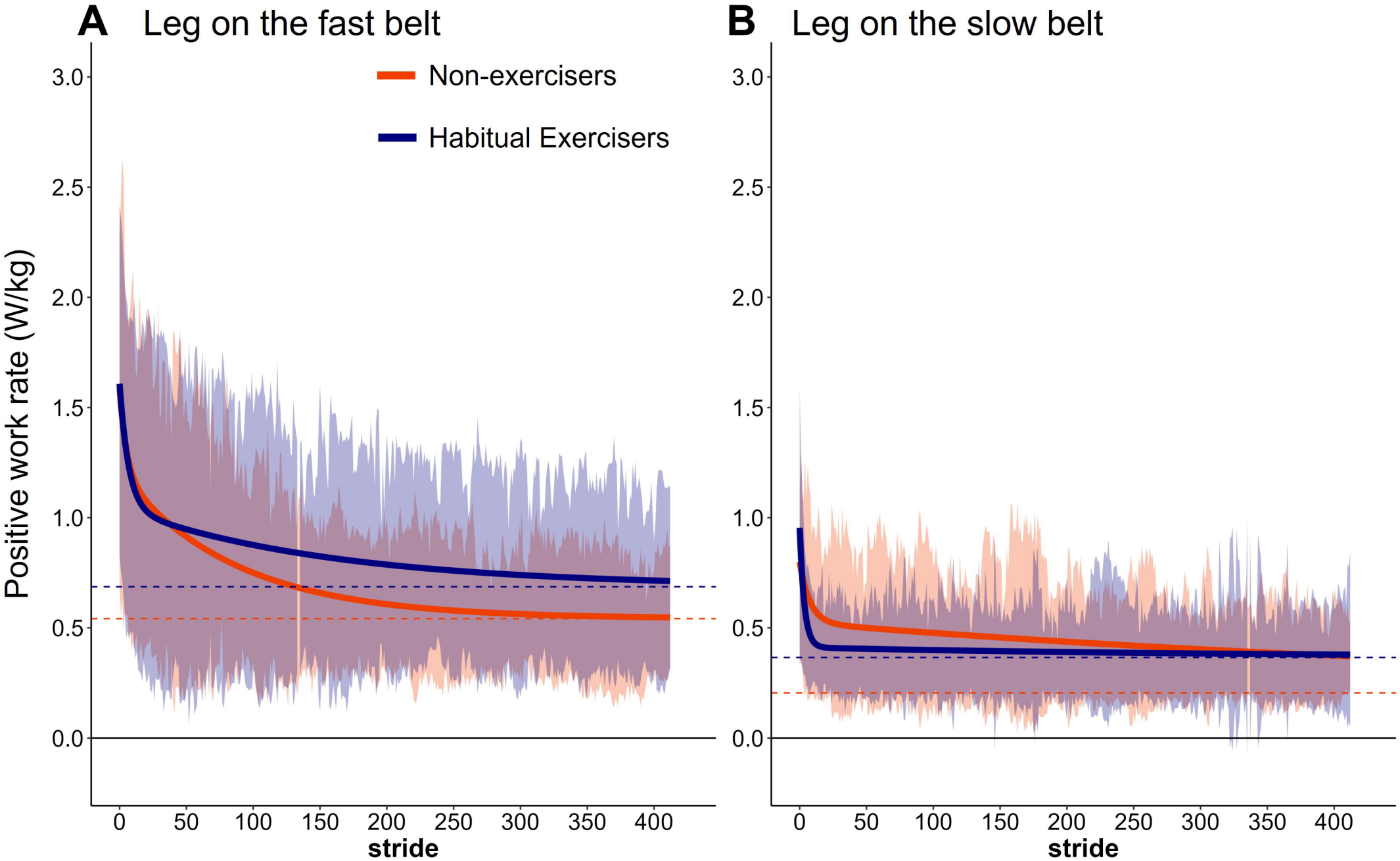
Figure S5. A comparison of the group average model fit (black line) and the individual model fits (blue line) of the adaptation of the negative work rate of the fast leg.

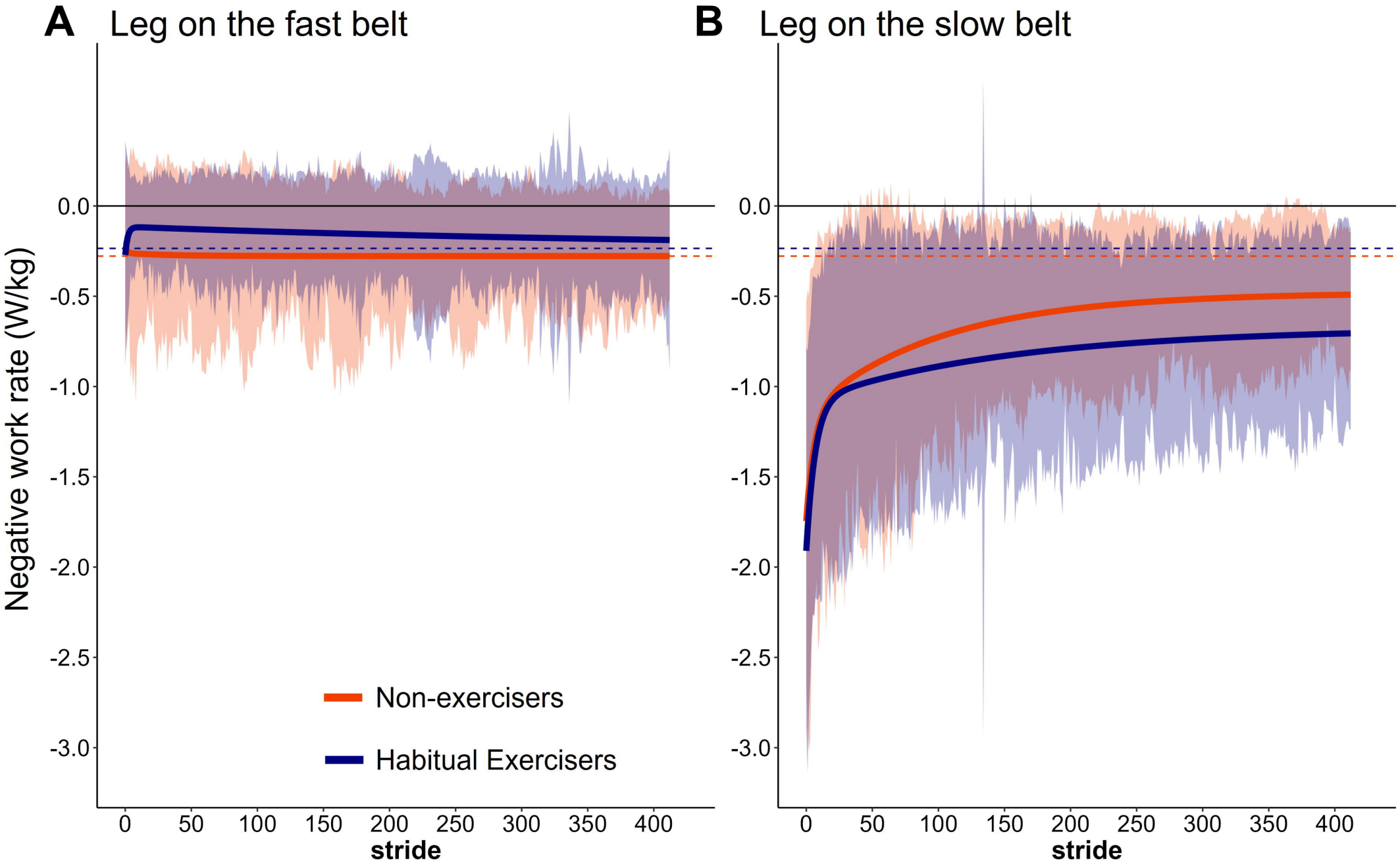
Figure S6. A comparison of the group average model fit (black line) and the individual model fits (blue line) of the adaptation of the positive work rate of the slow leg.

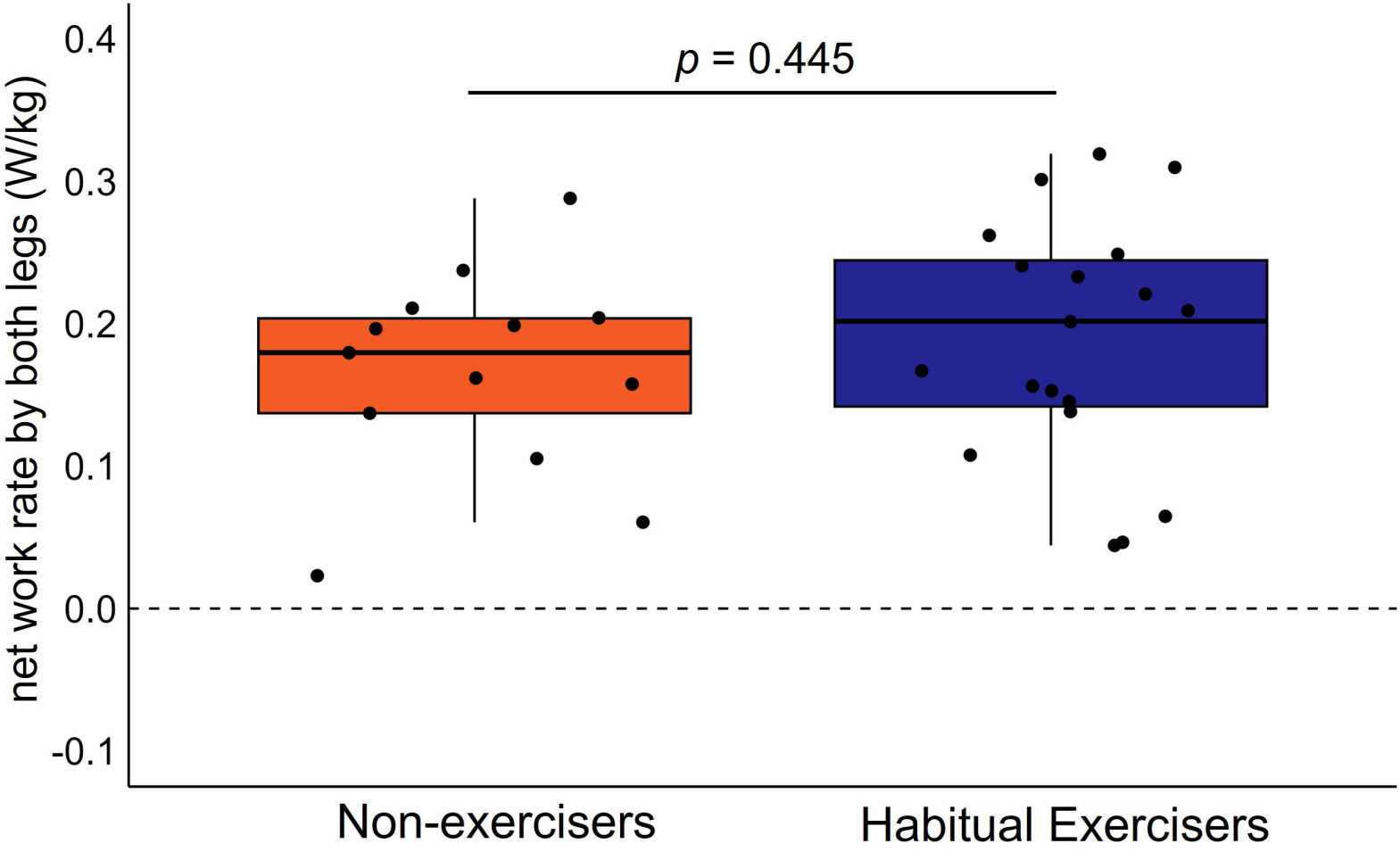
Figure S7. A comparison of the group average model fit (black line) and the individual model fits (blue line) of the adaptation of the positive work rate of the slow leg.


A
BERTEC
fast belt
slow belt
B
Baseline
Adaptation
Warmup self-selected typical speed
Warmup fast speed
Warmup slow speed
Belt speeds split 2:1 ratio
3 min
3 min
3 min
10 min


A
step length asymmetry
0.1
0.0
-0.1
-0.2
-0.3
0
200
400
600
800
step
Non-exercisers
Habitual Exercisers
B
step length (cm)
Non-exercisers
Habitual Exercisers
650
600
550
500
450
0
100
200
300
400
stride
Fast
Slow


A
Leg on the fast belt
B
Leg on the slow belt
Non-exercisers
Habitual Exercisers
Positive work rate (W/kg)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
50
100
150
200
250
300
350
400
stride


A
Leg on the fast belt
B
Leg on the slow belt
Negative work rate (W/kg)
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
-3.0
0
50
100
150
200
250
300
350
400
stride
Non-exercisers
Habitual Exercisers


p = 0.445
net work rate by both legs (W/kg)
0.4
0.3
0.2
0.1
0.0
-0.1
Non-exercisers
Habitual Exercisers