Title: Habitual weekly exercise affects gait adaptation in healthy young adults

Running Title: Exercise and adaptation

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Summary Statement:

Young adults who regularly participate in aerobic exercise respond more quickly to the onset of

a perturbation and continue to search for strategies to reduce energetic cost.

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. Active

(n=19) and Inactive (n=13) young adults 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 timecourse of adaptation between Active and Inactive young adults, and t-tests

compared net work at the end of adaptation between Active and Inactive young adults.

Compared to Inactive young adults, Active young adults initially adapted SLA and positive work

by the fast leg quickly, and continued to gradually adapt them over the duration of split-belt

treadmill walking. There was no effect of exercise on adaptation of negative work by the fast leg

or on net mechanical work. 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 to reduce 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 (Dietz et al., 1994; Reisman et al., 2005). 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 (Brinkerhoff et al., 2021; Gonzalez-Rubio et al.,

2019; Long et al., 2016; Malone and Bastian, 2010; Mariscal et al., 2020). 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 (Darmohray et al., 2019; Mawase et al., 2013;

Roemmich et al., 2016; Sánchez et al., 2021). Recently, Seethapathi and colleagues

computationally posited that the fast component that adapts rapidly is driven by balance

optimization, whereas the slow component that adapts more gradually is driven by energetic

cost optimization (Seethapathi et al., 2021). 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

(Sánchez et al., 2019; Selgrade et al., 2017). As the legs reduce positive work done and

increase negative work done, energetic cost decreases concomitantly (J.M. Donelan et al.,

2002; J M Donelan et al., 2002; Sánchez et al., 2019). This complements the fact that doing

negative work is less energetically costly than doing positive work (Burdett et al., 1983;

Umberger et al., 2003). By reducing work done by the legs, people are likely gradually adapting

towards some lower energetic cost, as computationally determined by Seethapathi et. al.

(Seethapathi et al., 2021) and previously empirically suggested (Buurke et al., 2018; Finley et

al., 2013; Selinger et al., 2015).

The question then arises — do individual factors that affect the ability to reach a

minimum energetic cost 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 (Piercy et al.,

2018). 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

(Cher et al., 2015). Along with an ability to reach an energetic minimum, aerobically trained

adults have a higher maximal oxygen uptake (VO$_2$max) (Jones and Carter, 2000), a better

exercise economy (Jones and Carter, 2000; Morgan et al., 1995), and higher lactate and

ventilatory thresholds (Jones and Carter, 2000). 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 (Cher et al., 2015); conversely, those who engage in

more aerobic exercise may more gradually reach an energetic minimum, due to a higher

tolerance for submaximal exercise (Jones and Carter, 2000; Morgan et al., 1995).

89   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 (Buurke et al., 2018; Finley et al., 2013; Seethapathi et al., 2021;

Selinger et al., 2015) and the well-established effects of exercise on energetics (Cher et al.,

2015; Jones and Carter, 2000; Morgan et al., 1995). Our hypothesis is based on two opposing

mechanisms which we will test here: 1) Active young adults would adapt faster than Inactive

young adults to reach a minimum energetic cost quickly (Cher et al., 2015), evidenced by faster

reduction in SLA and work done by the legs; 2) Active young adults would have a higher

tolerance for the submaximal exercise of treadmill walking than Inactive young adults,

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 Active and Inactive young adults walked on a split-belt treadmill. We

also hypothesized that at the end of adaptation, Active young adults would perform more-

negative net work than Inactive young adults, by reducing positive work done by the legs and

increasing negative work done by the legs in order to reduce overall energetic cost (J.M.

Donelan et al., 2002; J M Donelan et al., 2002; Sánchez et al., 2019). 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: Active (at least 150 minutes per week of exercise for at least the last three months) or Inactive (less than 150 minutes per week of exercise for at least the last three months) (Piercy et al., 2018). 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. For the entirety of treadmill walking, participants held onto side handrails. First, participants determined their typical and their fastest comfortable walking speeds on the treadmill using a modified protocol by Dingwell and Marin (Dingwell and Marin, 2006). 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.

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 (Sánchez et al., 2021, 2019;

Selgrade et al., 2017). In brief, we segmented force data into strides (Selgrade et al., 2017) 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,

subsequently discussed as Work. Finally, we calculated Net Work done by the legs at the end of

adaptation as the time integral of the power over each stride cycle, averaged over the last 100

strides.

Statistical Analysis

181   All statistical analyses were conducted in R (R Core Team, 2020). We used Welch Two

182   Sample t-tests to compare age, height, leg length, mass, and fast-leg belt speed between

183   groups. We also used Pearson's Chi-squared tests with Yates' continuity correction to assess

184   the difference in proportion of males and females in each group, and to assess the difference in

185   proportion of people who walked with the right leg on the fast belt in each group.

186   We analyzed SLA, positive and negative Work by the fast legs, and positive and

negative Work by the slow leg using mixed effects nonlinear regression with the 'nlme' package

in R (Pinhiero et al., 2020). We used multiple candidate models to test our hypotheses and for

each measure the final model that was interpreted corresponded to the simplest, best-fitting

model. 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. We truncated the data for all participants to minimum number of steps taken by a

participant (823 steps) so that participants would weight equally on each step.

194   For each of the four Work outcome measures, we built-up one-exponent models —

assuming that adaptation of the outcome measures occurs over a single timescale — that did

not include a fixed effect for group (eq. 1) and that did include a fixed effect for group (eq. 2).

Here, *c* is the estimated plateau in Work if strides went to infinity; *a* is the initial value of Work;

and *r* is the growth rate of Work adaptation. In the models that included a fixed effect for group,

all three model parameters (*c*, *a*, *r*) were allowed to differ for Active vs. Inactive participants.

$$Work = c + a * e^{-\frac{stride}{r}} + (c|ID) \qquad\qquad 1$$

$$Work = \left(a * e^{-\frac{stride}{r}} + c\right) \sim Group + (c|ID) \qquad\qquad 2$$

203   Then, for the each of the Work outcome measures and for SLA, we built-up two-

exponent models — assuming that adaptation of the outcome measures occurs over two

timescales — that did not include a fixed effect for group (eqs. 2 and 4) and that did include a

fixed effect for group (eqs. 3 and 5). 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. In the models that included a fixed effect for group, all five

model parameters (c, a_f, r_f, a_s, r_s) were allowed to differ for Active vs. Inactive participants.

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$$SLA = c + a_f * e^{-\frac{step}{r_f}} + a_s * e^{-\frac{step}{r_s}} + (c|ID) \qquad\qquad 2$$

212
$$SLA = (c + a_f * e^{-\frac{step}{r_f}} + a_s * e^{-\frac{step}{r_s}}) \sim Group + (c|ID) \qquad\qquad 3$$

213
$$Work = c + a_f * e^{-\frac{stride}{r_f}} + a_s * e^{-\frac{stride}{r_s}} + (c|ID) \qquad\qquad 4$$

214
$$Work = \left(c + a_f * e^{-\frac{stride}{r_f}} + a_s * e^{-\frac{stride}{r_s}} \right) \sim Group + (c|ID) \qquad\qquad 5$$

We then compared the four models (per outcome measure) for fit to the sample data

using the Akaike Information Criterion (AIC) and Bayesian Information Criteria, such that a lower

AIC and BIC and a ΔAIC > 2 indicated a better fit to the data (Burnham and Anderson, 2003;

Lohse et al., 2020). The simplest, best-fitting model to explain each variable was determined as

the final model and was interpreted. 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.

Finally, we used Welch's Two Sample t-test between groups to compare the net work

done 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 Active group and 13 were placed in the Inactive group. The two

groups did not significantly differ by sex, height, mass, leg on the fast belt, or belt speed, but did

significantly differ by age where the Active group was slightly older (Active 22 (SD 4) yrs;

Inactive 20 (SD 1) yrs, $t(21.827)=-2.127$, $p=0.045$). Demographic and belt speed data are

provided in Table 1.

Step Length Asymmetry

The best-fitting model for SLA was the two-exponent model containing a fixed effect for
group (Table 2) indicating that SLA adaptation was affected by exercise. Both candidate SLA
models are shown in Supplemental Table S1. The final model fits to each participant's data are
shown in Supplemental Figure S1.

In summary, compared to Inactive young adults, Active young adults continued to
gradually adapt SLA over the entire trial. All five model-estimated coefficients (plateau, initial
values for both the fast and slow component, and growth rates for both the fast and slow
components) were significantly different from zero, such that the plateau was at a negative SLA,
initial SLA values were negative, and the fast and slow curves were both concave (Fig. 2). The
groups differed in every model-estimated coefficient except for the plateau. Compared to
Inactive young adults, Active young adults' fast component initial SLA was less negative and
slow component initial SLA more negative, resulting in no difference in initial SLA (Active = -
0.144, Inactive = -0.137, $t(28.763)=0.283$, $p=0.779$)). Active young adults adapted the fast
component of SLA significantly quicker than Inactive young adults did (Active r_f = 12 steps,
Inactive r_f = 32 steps), seen in the quicker achievement of the "elbow" by the Active group in
Figure 2. Additionally, Active young adults had a more gradual and more persistent slow
component of SLA adaptation than did Inactive young adults (Active r_s = 396 steps, Inactive r_s =
162 steps), seen in the gradual change in SLA after the elbow in the Active group in Figure 2.

The standard deviation in the SLA plateau due to participant (the random effect) was
0.038 with a 95% CI of [0.029, 0.048]. Compared to the sample mean plateau of 0.040, the
variance due to individual participant was high (95% of the mean). After all model fixed and
random effects were accounted for, the estimated SLA plateau had residual unaccounted-for
variability with a standard deviation of 0.0321 and a 95% CI of [0.0318, 0.0324]. The residual
was also high (80% of the mean).

Positive Work by the Fast Leg

The best-fitting model for the positive Work by the fast leg was the two-exponent model
containing a fixed effect for group (Table 2) indicating that positive Work by the fast leg adapted
over two distinct timescales, and that adaptation of positive Work by the fast leg was affected by
group. The results of all four fast-leg positive Work candidate models are show in Supplemental
Table S1. The final model fits to each participant's data are shown in Supplemental Figure S2.

In summary, compared to Inactive young adults, Active young adults more gradually
adapted the positive Work by the fast leg, and continued to gradually adapt positive Work by the
fast leg over the entire trial. All five model-estimated coefficients (plateau, initial values for both
the fast and slow component, and growth rates for both the fast and slow components) were
significantly different from zero such that the plateau was a positive Work value, initial values
were positive, and the fast and slow curves were both convex for Inactive young adults (Fig.
3A). The groups differed in every model-estimated coefficient except for the fast component
growth rate which corresponds to the proposed balance optimization phase. The results of the
group differences can be seen in Figure 3A. Active young adults had a slightly more-positive
initial fast component and a slightly less-positive initial slow component than did Inactive young
adults, resulting in no difference in initial fast-leg positive Work (Active = 0.044 W/kg, Inactive =
0.039 W/kg, $t(29.429)=-0.898$, $p=0.377$). Active young adults had a more gradual and concave
slow component of fast-leg positive Work adaptation, such that the slope of the fast-leg positive
Work became more negative as strides increased; conversely, the slow component of the fast-
leg positive Work adapted relatively quickly in Inactive young adults, resulting in Inactive young
adults reaching their estimated plateau by about 100 strides (Fig. 3A) (Active r_s = -367 strides,
Inactive r_s = 44 strides). Compared to Inactive young adults, Active young adults' plateau had a
more-positive Work value.
The standard deviation in the fast-leg positive Work plateau due to participant (the
random effect) was 0.009 W/kg with a 95% CI of [0.007, 0.011]. Compared to the sample mean
plateau of 0.020 W/kg, the variance due to individual participant was moderate (35% of the
mean). After all model fixed effects and random were accounted for, the estimated fast-leg
positive Work plateau had residual unaccounted-for variability with a standard deviation of
0.00647 W/kg and a 95% CI of [0.00639, 0.00655]. The residual was also moderate (32% of the
mean).
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Negative Work by the Fast Leg
The best-fitting model for the negative Work by the fast leg was the two-exponent model
containing a fixed effect for group (Table 2) indicating that negative Work by the fast leg
adapted over two distinct timescales, and that negative Work by the fast leg adaptation was
affected by exercise. The results of all four fast-leg negative Work candidate models are shown
in Supplemental Table S1. The final model fits to each participant's data are shown in
Supplemental Figure S3.

In summary, compared to Inactive young adults, Active and Inactive young adults did not

differ in adaptation of the negative Work done by the fast leg. None of the five estimated model-

estimated coefficients (plateau, initial values for both the fast and slow component, and growth

rates for both the fast and slow components) were significantly different from zero for Inactive

young adults (Fig. 4A). For Active young adults, only the fast component initial value was

significantly different from the Inactive group and was more negative but did not result in a

group difference in overall initial fast-leg negative Work (Active = -0.021 W/kg, Inactive = -0.010

W/kg, $t(29.999)=0.999$, $p=0.326$)).

The standard deviation in the fast-leg negative Work plateau due to participant (the

random effect) was 0.010 W/kg with a 95% CI of [0.008, 0.013]. Compared to the sample mean

plateau of -0.014 W/kg, the variance due to individual participant was high (71% of the mean).

After all model fixed effects and random were accounted for, the estimated fast-leg negative

Work plateau had residual unaccounted-for variability with a standard deviation of 0.0073 W/kg

and a 95% CI of [0. 0072, 0. 0074]. The residual was moderate (50% of the mean).

Positive Work by the Slow Leg

The best-fitting model for the positive Work by the slow leg was the two-exponent model

containing a fixed effect for group (Table 2) indicating that positive Work by the slow leg

adapted over two distinct timescales, and that positive Work by the slow leg adaptation was

affected by exercise. The results of all four slow-leg positive Work candidate models are show in

Supplemental Table S1. The final model fits to each participant's data are shown in

Supplemental Figure S4.

In summary, compared to Inactive young adults, Active young adults had a higher initial

positive Work by the slow leg, and adapted positive Work by the slow leg more quickly. Three of

five model-estimated coefficients (plateau, initial value for the slow component, and growth rate

for the slow component) were significantly different from zero. For Inactive young adults, the

slow component had a negative initial value and was slightly concave, and the plateau was

positive (Fig. 3B). Active young adults had a significantly more-positive slow component initial

positive Work and had a significant fast component initial positive Work, resulting in a

significantly more-positive initial slow-leg positive Work (Active = 0.021 W/kg, Inactive = 0.014

W/kg, $t(25.152)=-2.112$, $p=0.045$)). Compared to Inactive young adults, Active young adults had

a significant fast component growth rate such that positive Work by the slow leg initially

decreased (Active r_f = 4 strides, Inactive r_f = -36 strides). Both groups adapted the positive Work

by the slow leg gradually and not differently (Active r_s = 32 strides, Inactive r_s = 48 strides).

Overall, the group differences had small effect sizes, evidenced in Figure 3B; both groups

converged on their plateaus by about 50 strides, and the groups did not differ in their estimated

plateaus.

The standard deviation in the slow-leg positive Work plateau due to participant (the

random effect) was 0.005 W/kg with a 95% CI of [0.004, 0.007]. Compared to the sample mean

plateau of 0.016 W/kg, the variance due to individual participant was moderate (31% of the

mean). After all model fixed effects and random were accounted for, the estimated slow-leg

positive Work plateau had residual unaccounted-for with a standard deviation of 0.00448 W/kg

and a 95% CI of [0.00443, 0.00454]. The residual was also moderate (28% of the mean).

Negative Work by the Slow Leg

The best-fitting model for the negative Work by the slow leg was the two-exponent

model containing a fixed effect for group (Table 2) indicating that the negative Work by the slow

leg adapted over two distinct timescales, and that negative Work by the slow leg adaptation was

affected by exercise. The results of all four slow-leg negative Work models are show in

Supplemental Table S1. The final model fits to each participant's data are shown in

Supplemental Figure S5.

In summary, compared to Inactive young adults, Active young adults adapted the fast

component more quickly. Three of five model-estimated coefficients (plateau, initial value for the

fast component, and growth rate for the fast component) were significantly different from zero.

For Inactive young adults, the plateau was negative, and the fast component had a negative

initial value and was concave (Fig. 4B), while the slow component initial value and growth rate

were not significant. Active young adults had significantly more-negative initial fast and slow

component values, but they did not result in a group difference in overall slow-leg initial negative

Work (Active = -0.034 W/kg, Inactive = -0.025 W/kg, t(29.999)=0.999, p=0.326)). Active young

adults also had a significantly quicker fast component growth rate (Active r_f = 5 strides, Inactive

r_f = 8 strides).

The standard deviation in the slow-leg negative Work plateau due to participant (the

random effect) was 0.005 W/kg with a 95% CI of [0.004, 0.007]. Compared to the sample mean

plateau of -0.014 W/kg, the variance due to individual participant was moderate (36% of the

mean). After all model fixed effects and random were accounted for, the estimated slow-leg

negative Work plateau had residual unaccounted-for variability with a standard deviation of

0.00588 W/kg and a 95% CI of [0.00581, 0.00595]. The residual was also moderate (42% of the

mean).

Net work

The groups did not differ in the total net work performed by the legs (t(28.892) = -.60091,

p = 0.553) (Fig. 5). Active young adults performed 13.62 (SD 9.63) J/kg of net work and Inactive

young adults performed 11.88 (SD 6.46) J/kg of net work at the end of ten minutes of split-belt

walking.

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) Active young adults continued to gradually adapt

SLA and positive work by the fast leg over the entirety of split-belt exposure, 2) Active young

adults initially adapted SLA quicker than Inactive young adults, 3) Neither group adapted the

negative Work by the fast leg, and 4) There was no difference in net work due to exercise

group. The findings from this study support the hypothesis that active young adults have a

higher tolerance for the energetically-challenging asymmetric belt speeds and adapt more

gradually than Inactive young adults.

Active young adults continued to gradually adapt over the entirety of split-belt exposure.

Five minutes of high intensity exercise performed immediately prior to split-belt walking does not

affect the magnitude of gait adaptation nor the rate of adaptation (Helm et al., 2017). While a

short bout of acute exercise may not impact gait adaptation, our results demonstrate that long-

term (at least three months) habitual exercise affects gait adaptation. These current findings

complement the literature. If the gradual component of gait adaptation is driven by energetic

cost optimization (Seethapathi et al., 2021), 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 the reduction in the positive Work by the fast leg. Exercised-

trained adults have an enhanced exercise capacity relative to Inactive individuals, evidenced by

higher maximal oxygen uptake (VO2max) (Jones and Carter, 2000); a better exercise economy

(Jones and Carter, 2000; Morgan et al., 1995); and higher lactate and ventilatory thresholds

(Jones and Carter, 2000). This higher exercise capacity in Active adults would indicate that they

can tolerate submaximal exercise — such as treadmill walking — at a given energetic cost for

longer than Inactive adults can, supporting our results. Active and Inactive young adults can

both reduce positive work by the legs during split-belt adaptation, but Inactive young adults may

have a direr need to do so quickly. Therefore, Inactive young adults would be working at a

higher energetic relative effort, resulting in a stronger incentive to reduce energetic, and

therefore mechanical, (Sánchez et al., 2021, 2019), work than the Active participants. Our
results contradict the potential mechanism that active young adults 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 (Cher et al., 2015) 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.
Active young adults initially adapted SLA quicker than Inactive young adults. 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 (Seethapathi et al.,
2021) more quickly than those who do not exercise habitually. Indeed, athletes have been
shown to have better static balance than non-athletes (Cristina-Elena and Liliana-Elisabeta,
2014). Buurke and colleagues investigated the relationship between mediolateral stability
adaptation and metabolic cost adaptation during 9 minutes of 2:1 split-belt walking (Buurke et
al., 2018). 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 stability (Seethapathi et
al., 2021), all these findings taken together support a nuanced approach to motor skill learning.
Adaptation in balance during early split-belt walking may not relate to the measures during the
task itself (i.e., metabolic cost adaptation), but instead relate to individual aptitude (i.e., a
person's metabolic capacity, affected by exercise training) (Anderson et al., 2021). Future
studies should seek to understand both pre-set individual factors, such as metabolic capacity,
and within-task individual factors, such as metabolic adaptation, that differentially relate to initial
values, growth rates of the early and gradual components of adaptation, and plateau values.
Neither group adapted the negative Work by the fast leg. Negative Work by the fast leg
(and both positive and negative Work by the slow leg) during split-belt adaptation were largely
unaffected by exercise. The small effect sizes of the change in positive and negative Work by
the slow leg support the literature that the majority of change in mechanical work performed
during gait adaptation is done by the fast leg (Sánchez et al., 2021, 2019). However, previous
work reported that over forty-five minutes of adaptation at a 3:1 belt speed ratio, negative Work
by the fast leg increased prior to positive Work by the fast leg decreasing (Sánchez et al., 2021).
Our finding of no adaptation of negative Work by the fast leg, by either group contrasts our
hypothesis that exercise capacity affects metabolic adaptation through increasing the negative

Work 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

by the fast leg in the current study, compared to previous work (Sánchez et al., 2021).

Both Active and Inactive young adults 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 (Sánchez et al., 2021) —

the legs perform net negative work (Sánchez et al., 2019). 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.

It is of note that variability in SLA and work by the fast leg appeared larger in the Active

group than in the Inactive group. Abrams and colleagues determined that during 45 minutes of

3:1 split-belt treadmill walking, along with adaptations in energetic cost and SLA, young adults

reduce the variability in SLA from the start to the end of split-belt treadmill walking (Abram et al.,

2022). If the Active individuals in our sample have a larger tolerance for submaximal exercise

than do Inactive individuals, then they may also have a larger window of tolerance for

movement variability during initial adaptation. To determine if active participants were indeed

more variable than inactive participants, we conducted follow-up analyses of the within-

participant SLA, positive fast-leg Work, and negative fast-leg Work variability (Abram et al.,

2022). We calculated the standard deviation of each measure in the initial 100 strides, middle

100 strides, and final 100 strides. Separate student's two-sample t-tests compared variability of

each measure during the initial, middle, and final epochs of gait adaptation between the active

and inactive groups. There was no difference between groups in variability in any of the

measures during any epoch. Therefore, our sample does not support our theory — informed by

prior work (Abram et al., 2022) — that active young adults employ a more varied hypothesis

testing strategy during early adaptation during ten minutes of split-belt treadmill walking. The

larger variation in the standard error of the active group in SLA, positive fast-leg Work, and

negative fast-leg Work is therefore likely because active young adults' individual responses to

the perturbation is varied, while inactive young adults' individual responses to the perturbation is

more homogenous. Further individual factors that can explain the variation in active individuals'
response should be investigated.

There are some limitations to this study. First, we did not directly measure energetic cost
using expired gas analyses. While it is possible that participants could have modified SLA and
mechanical Work without modifying metabolic cost, the groupings based on aerobic exercise
training allows us to reasonably infer that reported differences between groups would be due to
differences in energetic capacity. Second, we used self-report measures of exercise
participation. Habitual exercise recall has a moderate validity correlation to actual exercise
(0.36) (Sallis and Saelens, 2000) and, despite its drawbacks, is the most common way to
assess physical activity (Castillo-Retamal and Hinckson, 2011; Corder et al., 2009; Ishikawa-
Takata et al., 2008). 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, Active young adults may
require longer time than Inactive young adults 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, Active young adults may
plateau at a more-positive SLA, a more-negative net work done by the legs, and therefore
perhaps a lower energetic cost than Inactive young adults. The current results provide
promising preliminary evidence that Active young adults may be able to accept more assistance
provided by the environment than Inactive young adults, given enough time.

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References

Abram, S.J., Poggensee, K.L., Sánchez, N., Simha, S.N., Finley, J.M., Collins, S.H., Donelan, J.M., 2022. General variability leads to specific adaptation toward optimal movement policies. Curr. Biol. 32, 2222-2232.e5. https://doi.org/10.1016/j.cub.2022.04.015

Anderson, D.I., Lohse, K.R., Lopes, T.C.V., Williams, A.M., 2021. Individual differences in motor skill learning: Past, present and future. Hum. Mov. Sci. 78.

Brinkerhoff, S.A., Monaghan, P.G., Roper, J.A., 2021. Adapting gait with asymmetric visual feedback affects deadaptation but not adaptation in healthy young adults. PLOS ONE 16, e0247706. https://doi.org/10.1371/journal.pone.0247706

Burdett, R.G., Skrinar, G.S., Simon, S.R., 1983. Comparison of mechanical work and metabolic energy consumption during normal gait. J. Orthop. Res. 1, 63–72. https://doi.org/10.1002/jor.1100010109

Burnham, K.P., Anderson, D.R., 2003. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. J. Wildl. Manag. 67, 655. https://doi.org/10.2307/3802723

Buurke, T.J.W., Lamoth, C.J.C., Vervoort, D., 2018. Adaptive control of dynamic balance in human gait on a split-belt treadmill. J. Exp. Biol. 10.

Castillo-Retamal, M., Hinckson, E.A., 2011. Measuring physical activity and sedentary behaviour at work: A review. Work 40, 345–357. https://doi.org/10.3233/WOR-2011-1246

Cher, P.H., Stewart, I.B., Worringham, C.J., 2015. Minimum Cost of Transport in Human Running Is Not Ubiquitous. Med. Sci. Sports Exerc. 47, 307–314. https://doi.org/10.1249/MSS.0000000000000421

Corder, K., van Sluijs, E.M., Wright, A., Whincup, P., Wareham, N.J., Ekelund, U., 2009. Is it possible to assess free-living physical activity and energy expenditure in young people by self-report? Am. J. Clin. Nutr. 89, 862–870. https://doi.org/10.3945/ajcn.2008.26739

Cristina-Elena, M., Liliana-Elisabeta, R., 2014. Aspects Regarding the Level of Coordination Abilities in Both Athletes and Non-athletes. Procedia - Soc. Behav. Sci. 117, 162–166. https://doi.org/10.1016/j.sbspro.2014.02.195

Darmohray, D.M., Jacobs, J.R., Marques, H.G., Carey, M.R., 2019. Spatial and Temporal Locomotor Learning in Mouse Cerebellum. Neuron 102, 217-231.e4. https://doi.org/10.1016/j.neuron.2019.01.038

Dietz, V., Zijlstra, W., Duysens, J., 1994. Human neuronal interlimb coordination during split-belt locomotion. Exp. Brain Res. 101. https://doi.org/10.1007/BF00227344

Dingwell, J.B., Marin, L.C., 2006. Kinematic variability and local dynamic stability of upper body motions when walking at different speeds. J. Biomech. 39, 444–452. https://doi.org/10.1016/j.jbiomech.2004.12.014

Donelan, J.M., Kram, R., Kuo, A.D., 2002. Simultaneous positive and negative external mechanical work in human walking. J. Biomech. 35, 117–124. https://doi.org/10.1016/S0021-9290(01)00169-5

Donelan, J M, Kram, R., Kuo, A.D., 2002. Mechanical work for step-to-step transitions is a major determinant of the metabolic cost of human walking. J. Exp. Biol. 205, 3717–3727.

Finley, J.M., Bastian, A.J., Gottschall, J.S., 2013. Learning to be economical: the energy cost of walking tracks motor adaptation: Split-belt adaptation reduces metabolic power. J. Physiol. 591, 1081–1095. https://doi.org/10.1113/jphysiol.2012.245506

Gonzalez-Rubio, M., Velasquez, N.F., Torres-Oviedo, G., 2019. Explicit Control of Step Timing During Split-Belt Walking Reveals Interdependent Recalibration of Movements in Space and Time. Front. Hum. Neurosci. 13, 207. https://doi.org/10.3389/fnhum.2019.00207

Helm, E.E., Matt, K.S., Kirschner, K.F., Pohlig, R.T., Kohl, D., Reisman, D.S., 2017. The influence of high intensity exercise and the Val66Met polymorphism on circulating BDNF

and locomotor learning. Neurobiol. Learn. Mem. 144, 77–85.
https://doi.org/10.1016/j.nlm.2017.06.003

Ishikawa-Takata, K., Tabata, I., Sasaki, S., Rafamantanantsoa, H.H., Okazaki, H., Okubo, H., Tanaka, S., Yamamoto, S., Shirota, T., Uchida, K., Murata, M., 2008. Physical activity level in healthy free-living Japanese estimated by doubly labelled water method and International Physical Activity Questionnaire. Eur. J. Clin. Nutr. 62, 885–891. https://doi.org/10.1038/sj.ejcn.1602805

Jones, A.M., Carter, H., 2000. The Effect of Endurance Training on Parameters of Aerobic Fitness: Sports Med. 29, 373–386. https://doi.org/10.2165/00007256-200029060-00001

Lohse, K.R., Shen, J., Kozlowski, A.J., 2020. Modeling Longitudinal Outcomes: A Contrast of Two Methods. J. Mot. Learn. Dev. 8, 145–165. https://doi.org/10.1123/jmld.2019-0007

Long, A.W., Roemmich, R.T., Bastian, A.J., 2016. Blocking trial-by-trial error correction does not interfere with motor learning in human walking. J. Neurophysiol. 115, 2341–2348. https://doi.org/10.1152/jn.00941.2015

Malone, L.A., Bastian, A.J., 2010. Thinking About Walking: Effects of Conscious Correction Versus Distraction on Locomotor Adaptation. J. Neurophysiol. 103, 1954–1962. https://doi.org/10.1152/jn.00832.2009

Mariscal, D.M., Iturralde, P.A., Torres-Oviedo, G., 2020. Altering attention to split-belt walking increases the generalization of motor memories across walking contexts. J. Neurophysiol. 123, 11. https://doi.org/10.1152/jn.00509.2019

Mawase, F., Haizler, T., Bar-Haim, S., Karniel, A., 2013. Kinetic adaptation during locomotion on a split-belt treadmill. J. Neurophysiol. 109, 2216–2227. https://doi.org/10.1152/jn.00938.2012

Morgan, D.W., Bransford, D.R., Costill, D.L., Daniels, J.T., Howley, E.T., Krahenbuhl, G.S., 1995. Variation in the aerobic demand of running among trained and untrained subjects: Med. Sci. Sports Exerc. 27, 404???409. https://doi.org/10.1249/00005768-199503000-00017

Piercy, K.L., Troiano, R.P., Ballard, R.M., Carlson, S.A., Fulton, J.E., Galuska, D.A., George, S.M., Olson, R.D., 2018. The Physical Activity Guidelines for Americans. JAMA 320, 2020. https://doi.org/10.1001/jama.2018.14854

Pinhiero, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2020. nlme: Linear and Nonlinear Mixed Effects Models.

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Reisman, D.S., Block, H.J., Bastian, A.J., 2005. Interlimb Coordination During Locomotion: What Can be Adapted and Stored? J. Neurophysiol. 94, 2403–2415. https://doi.org/10.1152/jn.00089.2005

Roemmich, R.T., Long, A.W., Bastian, A.J., 2016. Seeing the Errors You Feel Enhances Locomotor Performance but Not Learning. Curr. Biol. 26, 2707–2716. https://doi.org/10.1016/j.cub.2016.08.012

Sallis, J.F., Saelens, B.E., 2000. Assessment of Physical Activity by Self-Report: Status, Limitations, and Future Directions. Res. Q. Exerc. Sport 71, 1–14. https://doi.org/10.1080/02701367.2000.11082780

Sánchez, N., Simha, S.N., Donelan, J.M., Finley, J.M., 2021. Using asymmetry to your advantage: learning to acquire and accept external assistance during prolonged split-belt walking. J. Neurophysiol. 125, 344–357. https://doi.org/10.1152/jn.00416.2020

Sánchez, N., Simha, S.N., Donelan, J.M., Finley, J.M., 2019. Taking advantage of external mechanical work to reduce metabolic cost: the mechanics and energetics of split-belt treadmill walking. J. Physiol. 597, 4053–4068. https://doi.org/10.1113/JP277725

Seethapathi, N., Clark, B., Srinivasan, M., 2021. Exploration-based learning of a step to step
controller predicts locomotor adaptation (preprint). Neuroscience.
https://doi.org/10.1101/2021.03.18.435986
Selgrade, B.P., Thajchayapong, M., Lee, G.E., Toney, M.E., Chang, Y.-H., 2017. Changes in
mechanical work during neural adaptation to asymmetric locomotion. J. Exp. Biol.
jeb.149450. https://doi.org/10.1242/jeb.149450
Selinger, J.C., O'Connor, S.M., Wong, J.D., Donelan, J.M., 2015. Humans Can Continuously
Optimize Energetic Cost during Walking. Curr. Biol. 25, 2452–2456.
https://doi.org/10.1016/j.cub.2015.08.016
Umberger, B.R., Gerritsen, K.G.M., Martin, P.E., 2003. A Model of Human Muscle Energy
Expenditure. Comput. Methods Biomech. Biomed. Engin. 6, 99–111.
https://doi.org/10.1080/1025584031000091678
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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.

Figure 2. Step length asymmetry adaptation 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=Active group (*n*=19), orange=Inactive group (*n*=13).

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=Active group (*n*=19), orange=Inactive group (*n*=13).

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=Active group (*n*=19), orange=Inactive group (*n*=13).

654 **Figure 5. Net Work done by the legs.** Blue=Active group (*n*=19), orange=Inactive group

655 (*n*=13).

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

	Inactive	Active	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	—

657 Note. Sex: F = female. Type of exercise participated in reflects the exercise modalities of people

658 who participated in any exercise every week (regardless of minutes per week of exercise).

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

660 positive and negative work of the slow leg.

	Coefficient	SLA	Positive Work		Negative Work	
			Fast Leg	Slow Leg	Fast Leg	Slow Leg
Inactive	c (plateau)	-0.043 *** (0.010)	0.019 *** (0.002)	0.016 *** (0.001)	-0.029 (0.061)	-0.013 *** (0.001)
	a (initial value)					
	r (growth rate)					
	a_f (fast component initial value)	-0.097 *** (0.007)	0.014 *** (0.003)	1.611×10^{-8} (9.218×10^{-08})	-0.002 (0.002)	-0.017 *** (0.001)
	r_f (fast component growth rate)	32.465 *** (3.751)	9.319 *** (2.813)	-36.141 (18.525)	7.817 (13.476)	7.534 *** (1.226)
	a_s (slow component initial value)	-0.017 *** (0.008)	0.009 ** (0.003)	-0.002 *** (0.0004)	0.020 (0.060)	-0.001 (.001)
	r_s (slow component growth rate)	162.122 ** (69.910)	43.686 *** (10.347)	48.083 ** (15.930)	1719.919 (5958.438)	91.743 (166.177)
Active	c (plateau)	-0.033 (0.014) p=0.475	0.027 † (0.004) p=0.030	0.016 (0.002) p=0.824	-0.016 (0.061) p=0.822	-0.014 (0.002) p=0.5632
	a (initial value)					
	r (growth rate)					
	a_f (fast component initial value)	-0.078 † (0.009) p=0.032	0.027 † (0.003) p=0.001	0.005 † (0.002) p=0.001	-0.005 † (0.002) p=0.041	-0.028 † (0.002) p<0.001
	r_f (fast component growth rate)	11.628 † (3.929) p<0.001	6.624 (2.855) p=0.345	3.584 † (18.640) p=0.033	21.204 (14.663) p=0.361	4.793 † (1.335) p=0.040
	a_s (slow component initial value)	-0.060 † (0.008) p<0.001	-0.002 † (0.003) p=0.001	0.002 † (0.001) p<0.001	0.0001 (0.060) p=0.743	-0.004 † (0.001) p=0.009
	r_s (slow component	396.341 † (78.306)	-367.291 † (207.016)	32.509 (21.552)	-135.976 (5959.178)	42.971 (166.601)

growth rate)	p=0.003	p=0.047	p=0.470	p=0.756	p=0.7770
AIC	-106168.7	-95499.31	-105208.9	-89994.96	-95676.58
BIC	-106070.6	-95409.44	-105119.1	-89905.39	-95587.01
Log-likelihood	53096.36	47761.65	52616.46	45009.48	47850.29
Number of observations	26336	13216	13216	12896	12896
Number of participants	32	32	32	32	32
SD: ID (*c*)	0.038	0.009	0.005	0.010	0.005
SD: Residual (*c*)	0.032	0.006	0.004	0.007	0.006

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 Active group indicate coefficients

that are significantly different between Active and Inactive, and all group-difference p-values are

shown.