Contributions of spatial and temporal control of step length symmetry in the transfer of locomotor adaptation from a motorized to a non-motorized split-belt treadmill

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Running Head: Motorized and non-motorized split-belt walking

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Abstract

The ability to transfer locomotor learning to novel contexts is essential for effective gait rehabilitation. Locomotor adaptation is dependent upon independent processes for spatial and temporal limb control during motorized split-belt walking, where individual belt speeds are fixed with one belt moving faster than the other. Here we investigated the relative contributions of spatial and temporal learning strategies to the transfer of a motorized split-belt adaptation to a non-motorized split-belt treadmill, where each belt is independently user-propelled. In 10 healthy subjects, adaptation of step length symmetry was driven by changes to temporal and spatial motor outputs during motorized split-belt treadmill walking. We found robust after-effects in step length symmetry during transfer to non-motorized split-belt treadmill walking that were driven by changes in temporal motor outputs. We also observed residual after-effects during motorized tied-belt treadmill walking (post-transfer) that were mainly driven by changes in spatial motor outputs. These results suggest independent transfer and de-adaptation of spatial and temporal motor outputs. In addition, our results showed that step length after-effects were mediated by unique patterns of muscle activity during motorized versus non-motorized treadmill walking post-adaptation, suggesting that redundant locomotor outputs are expressed in a context-dependent manner. In sum, this is the first study to show that adaptive learning on a motorized split-belt treadmill is transferable to a non-motorized split-belt treadmill. Future research aims to unravel the independent contributions of spatial and temporal control to gait adaptation and transfer.

Keywords: human gait, interlimb coordination, generalization, electromyography, motor learning

Introduction

Control of human locomotion is highly adaptable. Gait patterns can be altered through motorized treadmill training, even after central nervous system damage. For example, walking on a split-belt treadmill which induces asymmetric step lengths by constraining limbs to move at different speeds is altered over time through an error-based learning process known as motor adaptation (Reisman et al., 2005, 2007). Training on a split-belt treadmill is promising because asymmetric gait patterns can be reduced in hemiparetic walkers (Choi et al., 2009; Reisman et al., 2007). From a clinical perspective, it is desirable to generalize adaptive learning to untrained walking conditions. However, training on a motorized split-belt treadmill is context-dependent and limited in the ability to generalize to over-ground walking or to different modes of locomotion (Choi and Bastian, 2007; Hamzey et al., 2016; Ogawa et al., 2012; Torres-Oviedo and Bastian, 2010, 2012).

Adaptation of symmetric step lengths during motorized split-belt treadmill walking results from changes in both spatial control of foot placement, and temporal control of step timing (Finley et al., 2015; Long et al., 2016; Malone et al., 2012). These spatial and temporal motor outputs reflect distinct neural strategies to overcome the asymmetric belt speeds. Positive asymmetries in foot placement and step timing achieved during adaptation persist during de-adaptation while limb excursions (distance the foot travels during stance) immediately return to tied baseline values. The result is a negative step length asymmetry (i.e. after-effect) which requires time to de-adapt. When given appropriate feedback about foot placement or step length, participants can block adaptation of spatial control of locomotion without affecting temporal control (Long et al., 2016; Malone et al., 2012). What remains to be shown is whether and how spatial and temporal asymmetries used

to reduce step length asymmetry during motorized split-belt treadmill walking transfer to novel contexts.

Changes in muscle activation patterns during adaptation provides further information about feedforward (predictive) and feedback (reactive) mechanisms for gait modifications (Iturralde and Torres-Oviedo, 2019), but have yet to be quantified in a transfer task. Velocity dependent resistance applied to hip and knee movements with an exoskeleton, or increases swing velocity induced with an elastic force-field lead to feedforward adaptation of hamstring muscle activity, evident by post-adaptation after-effects (Blanchette and Bouyer, 2009; Lam et al., 2006). Furthermore, tibialis anterior muscle activity modulates in time with anterior breaking forces during split-belt walking, leading to after-effects during the post-adaptation period (Ogawa et al., 2014). This suggests that transfer of locomotor adaptations would be associated with muscle responses which indicate a mismatch between current and required muscle control for the novel environment.

The current study examined whether locomotor adaptation made during motorized split-belt treadmill walking would transfer to non-motorized treadmill walking, indicated by after-effects in spatial and temporal control, and muscle activity. Non-motorized treadmills have gained in popularity for use in athletic settings and in sports science research; e.g., to measure cost of transport (Smoliga et al., 2015), assess anaerobic performance (Gonzalez et al., 2013), and 5k time trials (Stevens et al., 2015). Non-motorized treadmills have freely moveable belts which are driven by participants pushing against an inclined surface. The user-propelled nature of the non-motorized treadmill allows participants to self-select and express natural variability in gait. However, research utilizing non-motorized treadmills in a clinical setting or for locomotor adaptation is limited (Wang et al., 2017). Here, we developed a non-motorized split-belt treadmill that allows

the user to determine their own walking pace while simultaneously allowing for asymmetric behavior. We hypothesized that due to the contextual similarity between the treadmills, after-effects would be present during transfer. We further hypothesized that after-effects washed out during non-motorized treadmill walking should lead to diminished or absent after-effects during tied motorized treadmill walking. Finally, we hypothesized that leg muscle activity would display adaptive behavior and therefore after-effects during the transfer condition.

Methods

Participants

Ten healthy volunteers (six female, four male; Age 26.5 ± 5.6 years) with the ability to walk on a treadmill for 60 minutes and with no neurological or biomechanical impairments were recruited for this study. All study protocols were approved by the University of Massachusetts, Amherst Institutional Review Board and all subjects provided informed consent prior to enrollment. None of the subjects had prior experience walking on a split-belt treadmill.

Experimental setup

Motorized split-belt treadmill. Subjects walked on an instrumented split-belt treadmill (Bertec Corp, Columbus OH) that has separate left and right belts, each with its own motor and force transducer. Belt speed acceleration was set at 1 m s^{-2}. During motorized treadmill walking, subjects wore a non-weight-bearing safety harness suspended from the ceiling. At the beginning of each trial, subjects were positioned in the middle of the treadmill with one leg on each belt and were instructed to minimize handrail use and walk with normal arm swing as soon as possible during all conditions.

112 *Non-motorized spit-belt treadmill.* We designed and built a user-propelled non-motorized
113 split-belt treadmill (**fig. 1a**). The non-motorized treadmill was fabricated from two commercially
114 available non-motorized treadmills (Inmotion II Manual Treadmill; Stamina, Springfield, MO),
115 which were designed to share a common support structure and minimize spacing between the belts
116 (32 mm). To minimize friction with the belt-deck interface, a sheet of polytetrafluoroethylene
117 (PTFE, 0.30" sheet; ePlastics, San Diego, CA) plastic was secured to the treadmill deck under each
118 belt independently. A ~1kg mass was added to the flywheel of each belt to increase the inertial
119 properties of the belt-flywheel system to ensure that the belt continued to move as the limb
120 transitioned from stance to swing which enabled a smoother transition into the next stance phase.
121 Each belt flywheel was also fitted with a friction tensioner to increase the resistance of the belt to
122 moving, however for this study all subjects used the non-motorized treadmill without the
123 tensioners attached to ensure symmetric resistance on both belts. The treadmill utilizes gravity
124 (~13° incline) and the users body weight to assist subjects driving the symmetrically resisted but
125 independently user-propelled belt speed. During non-motorized treadmill walking, subjects lightly
126 held onto the treadmill handrails throughout baseline and testing conditions and were instructed to
127 minimize handrail use to avoid supporting body weight. Typically, subjects reported only needing
128 the support of the handrails for the first two to three strides, however all subjects were encouraged
129 to maintain minimal contact with the handrail to minimize fall risk.
130
131 *Split-belt adaptation paradigm*
132 All experimental testing was completed in one session lasting approximately two hours.
133 The adaptation paradigm (**fig. 1b**) consisted of walking trials that included motorized tied-belt,
134 motorized split-belt and non-motorized split-belt conditions. Each trial began from a standstill and

subjects were instructed to “walk normally” in all conditions. During all walking conditions, subjects were instructed to maintain a forward gaze and avoid looking at the feet.

During Baseline trials, subjects walked on the motorized treadmill with belts tied at a slow (0.67 m/s), medium (1.0 m/s), and fast (1.34 m/s) speeds for two minutes each. The order of the baseline speeds was randomized across subjects. A Baseline non-motorized treadmill trial was collected at the subject’s preferred walking speed for five minutes. Preferred speed during non-motorized treadmill walking was determined by instructing subjects to “walk as fast as you would to a meeting for which you have adequate time to arrive”. During *Adaptation* trials, subjects walked on the motorized split-belt treadmill at a 2:1 speed ratio (0.67 and 1.34 m/s) for ten minutes. Immediately following adaptation, subjects were instructed to side-step from the motorized treadmill onto the non-motorized treadmill which was located immediately in front of the motorized treadmill. Typically, only two side steps were required to move onto the non-motorized treadmill. Forward stepping was avoided to prevent washout of after-effects. During *Transfer* trials, subjects walked for five minutes on the non-motorized treadmill to assess transfer of the adapted locomotor pattern. Then, subjects returned to the motorized treadmill for the *Washout* period by side-stepping and walked with belts tied at the slow speed (0.67 m/s) for an additional five minutes. Finally, during *Post-adaptation* subjects walked on the non-motorized treadmill to assess any residual after-effects. Subjects were randomly assigned left or right limb to the slow belt during split-belt walking and subsequent references to each respective limb will be as slow or fast limb regardless of the condition.

Data collection

During motorized treadmill walking, lower limb kinematics were recorded at 100 Hz using a 4-camera Oqus system (Qualisys, Sweden). Reflective markers were placed bilaterally over the fifth metatarsal, lateral malleolus, tibial plateau, greater trochanter, and the anterior superior iliac spines. During non-motorized treadmill walking, lower limb kinematics were relegated to use of only the ankle markers for identification of spatio-temporal parameters due to limitations in capture space during data collection.

Electromyographic (EMG) activity was amplified (MA300, Motion Lab Systems, Baton Rouge, LA) and collected using disposable surface electrodes (Ambu, blue sensor N-00-S) placed in a bipolar configuration (inter-electrode distance 2 cm) over the tibialis anterior (TA), medial gastrocnemius (MG), biceps femoris (BF) and the vastus lateralus (VL) according to the Surface Electromyography for the Non-Invasive Assessment of Muscles project (Hermens et al. 2000). System gain was set prior to baseline to ensure adequate signal detection and to prevent clipping. EMG data were sampled at 2000 Hz and synchronized with kinematics data using Qualisys Track Manager 2.11 (Qualisys, Göteborg, Sweden).

Data analysis

Data analysis was performed using custom software written in MATLAB (Mathworks, Natick, MA, v. R2017a). Marker data were low pass filtered at 6 Hz with a second order Butterworth filter. EMG data were high-pass filtered at 45 Hz (3rd order Butterworth), demeaned, rectified, and low-pass filtered at 35 Hz (3rd order Butterworth).

The same method to determined heel contact time during motorized and non-motorized treadmill walking (where ground reaction force data is unavailable) was used. We defined heel

contact time as the instant of peak anterior position of the ankle marker for each step and toe-off as the instant of peak posterior position of the ankle marker for each step.

We used step length difference as our main outcome variable to assess split-belt walking adaptation (Choi et al., 2009; Reisman et al., 2005, 2007; Roemmich and Bastian, 2015). Step length was calculated as the anterior-posterior distance between the ankle markers at time of heel contact. Step length difference was defined as $SL_{fast} - SL_{slow}$, where SL_{fast} is the step length with fast leg leading at heel strike, and SL_{slow} is step length with slow leg leading (**fig. *2a***). We also included double support difference as a secondary outcome (see Supplementary materials).

To quantify the spatial and temporal contribution to step length changes, we applied the following analytical model of step length difference (for derivation, see Finley et al. 2015):

$$SL_{diff} = (\alpha_f - \alpha_s) + \left[\frac{v_s + v_f}{2} * (t_s - t_f)\right] + \left[\frac{t_s + t_f}{2} * (v_s - v_f)\right]$$

where α_f corresponds to where the fast foot is placed relative to the previous slow foot placement, and α_s corresponds to where the slow foot is placed relative to the previous fast foot placement (**fig. *2b,c***). v_f and v_s correspond to the speed of the fast and slow foot, respectively. t_f corresponds to the time between the fast heel strike and the subsequence slow heel strike, and t_s corresponds to the time between the slow heel strike and the subsequence fast heel strike.

Simplifying the equation to

$$SL_{diff} = \Delta\alpha + \bar{v} \cdot \Delta t + \bar{t} \cdot \Delta v$$

gives us an equation for step length difference where the first term is the step position component which represents the difference between the relative positions of the feet at the fast and slow heel strikes , the second term is the step time component which is the difference in slow and fast step times as a function of average foot speed, and the third term is the step velocity component which is the difference in slow and fast foot velocities as a function of the average step time. It is

202 important to note that during motorized treadmill conditions, v_f and v_s are fixed, whereas during
203 non-motorized treadmill walking, the speed of each belt/limb is strictly user defined and becomes
204 a third degree of freedom while walking.

205 To compare EMG across subjects and conditions, EMG amplitude was normalized to the
206 peak averaged EMG during baseline walking at 1 m/s as this was the average walking speed of
207 subjects on the non-motorized treadmill during pilot testing. Stride-by-stride changes in EMG were
208 measured as the mean EMG over a specific phase of the gait cycle for each muscle minus the
209 baseline speed and condition-matched EMG to form an EMG difference to compare changes
210 across Adaptation, Transfer and Washout. The following phases of the gait cycle were selected
211 post-hoc because they showed consistent changes across subjects and represent critical control
212 phases within the gait cycle for each muscle: a time window from the last 5% of the gait cycle (i.e.
213 95-100%) to the first 5% (i.e. 0-5%, early weight transfer) was used for the vastus lateralus and
214 tibialis anterior, referenced as -5:5%; 90-100% of the gait cycle (i.e. terminal swing) was used for
215 the biceps femoris; 15:25% of the gait cycle (i.e. mid-stance) was used for the medial
216 gastrocnemius. Note, these were not the only phases of the gait cycle which showed consistent
217 changes across subjects. However, we limited the analysis to one phase per muscle.

218 While all muscles were normalized to the same condition amplitudes (i.e. baseline medium
219 speed), the EMG differences were calculated relative to the condition and speed matched baseline
220 values across all conditions. During Adaptation, this means that the slow limb differences were
221 calculated relative to the slow limb baseline and the fast limb differences were calculated relative
222 to the fast limb baseline. We justified this with the understanding that, if there were no effects of
223 interlimb coordination, then each limb should individually have the same muscle activation
224 patterns relative to the baseline condition and speed matched counterparts. This assumes that once

225 heel contact occurs for a limb, this limb is now in the reference frame of the belt for which that
226 limb is in contact and therefore references to behavior should be done according to that reference
227 frame. We did this instead of calculating a difference of each curve from the same baseline value
228 (e.g. both limbs from medium speed baseline) to avoid differences in amplitude during the adapted
229 state that would not reflect the adapted state muscle dynamics that are a result of walking on a
230 split-belt treadmill. We are confident that this is a practical way to analyze this data as several
231 muscle activation patterns returned to baseline speed-matched values across the gait cycle by the
232 end of adaptation, specifically the fast VL and the slow MG and TA.
233
234 *Statistical analysis*
235 For each dependent variable, group means were calculated in time bins across the last 10
236 strides for each Baseline trial (motorized slow, motorized medium, motorized fast, and non-
237 motorized preferred) and across the first 5 strides (early) and last 5 strides (late) for Adaptation
238 (AE – early Adaptation, AL – late Adaptation), Transfer (TE – early Transfer, TL – late Transfer)
239 and Washout (WE – early Washout, WL – late Washout) trials. Separate repeated measures
240 ANOVAs were used to test the effects of time on each dependent variable. Post-hoc analyses were
241 performed using independent sample t-tests to compare each dependent variable at each time point
242 to the baseline value and for comparisons between early and late time points (i.e. AE vs AL).
243
244 **Results**
245 To assess the ability to transfer a motorized split-belt treadmill adaptation to non-motorized
246 split-belt treadmill walking, we exposed subjects to a 2:1 motorized split-belt treadmill condition
247 which caused large initial differences in step lengths. Subjects gradually adapted to reduce step

length difference to baseline levels over several minutes of walking. We subsequently tested subjects walking at a preferred pace on the non-motorized split-belt treadmill to assess transfer; adaptation transfer was evidenced by negative after-effects in step length difference. Finally, robust after-effects were again present when we assessed for residual differences in a 1:1 motorized treadmill condition at the slow speed. The group averaged step length data is presented below; double support data is available in the supplementary materials.

Locomotor adaptation on a motorized split-belt treadmill

Repeated measures ANOVA revealed significant effects of time on step length ($F(7,63) = 25.17$, $p < 0.001$, **fig. 3a-5a**). Group averaged step-length differences were not significantly different from zero during baseline tied- slow, medium or fast walking on the motorized split-belt treadmill (all p-values > 0.05). **Figure 3a** shows gradual changes in step length difference (dark grey/black) during the first 100 and last 20 strides in Adaptation. During *early Adaptation*, step length difference showed a large initial change compared to baseline ($p < 0.001$, **fig. 3b,d**). By *late Adaptation*, step length difference was reduced back to baseline levels ($p = 0.58$, **fig. 3b,d**).

As previously reported (Finley et al., 2015; Long et al., 2016; Malone et al., 2012), step length difference can be decomposed into independent step velocity (magenta), step position (red) and step time (blue) contributions (**fig 3c,d)**. The step velocity component, which is largely driven by the difference in belt speeds became increasingly negative over the course of adaptation, reflecting a large negative velocity induced perturbation which required opposition ($p < 0.001$, **fig 3d**). Both the step position and step time components adapted to oppose the step velocity component. During *early Adaptation*, the step position component showed a significant initial asymmetry ($p < 0.001$, **fig. 3d**), however it was not large enough to counter the large negative step

velocity component, as evidenced by a large initial step length difference. The step time component showed more gradual change, with *early Adaptation* values not significantly different from baseline ($p = 0.26$, **fig. 3d**). By *late Adaptation*, the step position and step time components both increased significantly ($p < 0.001$, **fig. 3d**) to cancel the negative step velocity component, resulting in symmetrical step lengths ($p = 0.58$, **fig. 3d**).

Robust transfer of after-effect to non-motorized split-belt treadmill

We found significant transfer of motorized treadmill adaptations to the non-motorized split-belt treadmill. **Figure 4a** shows the after-effect in step length difference during the first 100 and last 20 strides in Transfer. During *early Transfer*, step length difference showed a negative after-effect compared to baseline ($p < 0.001$, **fig. 4b,d**). By *late Adaptation*, step length difference returned to baseline levels ($p = 0.31$).

Figure 4c,d show the contribution of the step velocity, step position and step timing components to the step length after-effects during Transfer. In *early Transfer*, the step velocity component displayed a large positive (i.e. an after-effect) component that was significantly different from baseline ($p = 0.03$, **fig. 4d**, magenta). By *late Transfer*, the step velocity component decreased to a negative value that was significantly different from baseline ($p = 0.02$), indicating that subjects settled on a step velocity difference in the same direction as the initial motorized split-belt perturbation (i.e. a negative velocity difference). The step position component was not significantly different from baseline during *early Transfer* ($p = 0.5$, **fig. 4d**). There were also no significant differences between *early* and *late Transfer* for the step position component ($p = 0.3$). By *late Adaptation,* the step position component was not different from baseline ($p = 0.06$, **fig. 4d**), however, upon inspection of individual data, this result may have been driven by a single

outlier (*late Transfer,* red filled circles). These results indicate that the spatial component did not contribute to the initial after-effects in step length difference. The step time component was significantly different from baseline during *early Transfer* ($p < 0.001$, **fig. 4d**). By *late Transfer*, the step time component decreased back to baseline values ($p = 0.58$), indicating washout of the temporal pattern.

Residual after-effects on return to motorized split-belt treadmill

Despite washout of step length after-effects during non-motorized treadmill walking in the Transfer period, after-effects in step length reappeared during motorized treadmill walking in *early Washout* ($p < 0.001$). Step length difference was significantly different from baseline during early Washout ($p < 0.001$ **fig. 5a**) and returned back to baseline by *late Washout* indicated by significant differences from *early* to *late Washout* ($p < 0.001$) but did not completely return to baseline values ($p = 0.03$, **fig. 5b,d**).

Figure 5c shows the contribution of the step velocity, step position and step timing components to the step length after-effects during the Washout period. The step velocity components were not different from baseline during *early Washout* ($p = 0.72$) or *late Washout* ($p = 0.95$), due to the symmetric belt speeds (**fig. 5c,d**). The step position component displayed significant after-effects during *early Washout*, ($p < 0.001$) that reduced back to baseline by *late Washout* ($p = 0.17$, **fig. 5d**). This is unlike the Transfer period, where the step position component showed no after-effects (see **fig. 4d**, red). The step time component was not significantly different from baseline during *early Washout* ($p = 0.09$) nor *late Washout* ($p = 0.48$, **fig 5d**, blue). Note however that the step time component increased from low initial values during early Washout (0.028m ± 0.03) to greater magnitudes around 6-10 strides into the Washout period (SL: ~0.04m)

317 which later returned to baseline values (**fig. 5c**) indicating a delayed emergence of the temporal
318 component.
319
320 *Unlearning during transfer does not interfere with after-effects during washout*
321 We performed a linear regression analysis to determine whether step length after-effects
322 present during the Transfer condition were the result of unlearning of the motorized treadmill
323 adaptation. We found that step length error magnitude during *early Transfer* did not predict the
324 step length error magnitude during *early Washout* ($p = 0.782$, **fig. 6**). In addition, we ran the linear
325 regression analysis on the individual components to see if there were any interaction effects on the
326 individual components that may not have been captured by the step length after effect. We found
327 no interaction between *early Transfer* and *early Washout* for the step position ($p = 0.132$), step
328 time ($p = 0.451$), nor the velocity components ($p = 0.457$).
329
330 *EMG activity during motorized split-belt adaptation*
331 Changes in EMG activity during Adaptation (left columns), Transfer (middle, gray
332 columns) and Washout (right columns) are illustrated, with the number of subjects analyzed for
333 each muscle indicated, in **figure 7**. Due to issues with EMG acquisition in select subjects, some
334 muscles were omitted from analysis throughout the experiment. Repeated measures ANOVA
335 revealed significant effects of time on both fast (VL: $F(7,35) = 5,75$, $p < 0.001$; BF: $F(7,42) = 6.08$,
336 $p < 0.001$; MG: $F(7,49) = 15.76$, $p < 0.001$; TA: $F(7,42) = 14.59$, $p < 0.001$) and slow limbs (VL:
337 $F(7,35) = 13.24$, $p < 0.001$; BF: $F(7,42) = 24.51$, $p < 0.001$; MG: $F(7,49) = 9.96$, $p < 0.001$; TA:
338 $F(7,42) = 13.85$, $p < 0.001$) (**fig. 7**).

During *early Adaptation* (solid line), muscle activity of the slow VL, BF, and TA (bottom panel, cyan) were significantly greater during terminal swing and weight acceptance relative to slow baseline values ($p < 0.05$, **fig. 7a,b,d**), but not for the MG ($p = 0.65$, **fig. 7c**). By *late Adaptation* (dashed line), the slow VL and TA activation significantly decreased compared to *early Adaptation* ($p < 0.05$) indicating significant modulation of muscle activity, yet did not reach baseline values ($p < 0.05$, **fig. 7a,d**). The slow BF showed a decreasing trend from *early Adaptation* to *late Adaptation* that was not significant ($p = 0.077$) and was still significantly different from baseline during the last five strides ($p = 0.005$, **fig. 7b**). The slow MG did not change from *early Adaptation* to *late Adaptation* ($p = 0.54$) and was not different from baseline during early ($p = 0.65$) or *late Adaptation* ($p = 0.67$, **fig. 7c**). The slow MG during terminal stance (not shown) initially showed a significant increase in activity ($p < 0.001$) during *early Adaptation* which remained slightly greater, albeit significantly, relative to baseline slow ($p = 0.008$) during *late Adaptation*.

In contrast to the slow limb, the VL, BF, and TA of the fast limb (top panel, black) had significantly lower activation during *early Adaptation* compared to the baseline fast condition ($p < 0.05$, **fig. 7a,b,d**). Both the fast VL and TA increased significantly by *late Adaptation* ($p < 0.01$) with no difference from baseline ($p > 0.05$, **fig. 7a,d**) indicating modulation of each muscle's activity during terminal swing and early weight acceptance. The fast BF, however, did not change from *early* to *late Adaptation* during terminal swing ($p = 0.53$, **fig. 7b**). The MG on the fast limb showed similar behavior to that of the VL, BF, and TA of the slow limb with significant increase in activation during *early Adaptation* ($p < 0.001$), a significant decrease by *late Adaptation* ($p = 0.02$), and a persistent difference from baseline values during *late Adaptation* ($p < 0.001$, **fig. 7c**), again, indicating modulation of the muscles activity during this phase of the gait cycle. The fast

362 MG during terminal stance (not shown) was no different during *early Adaptation* relative to
363 baseline fast ($p = 0.85$) and made a non-significant decrease by *late Adaptation* which was
364 significantly lower than baseline ($p < 0.001$).
365
366 *EMG activity during transfer to non-motorized treadmill walking post-adaptation*
367 During *early Transfer*, a significant depression of muscle activity during terminal swing to
368 weight acceptance was found for the slow VL, BF, and TA indicating the presence of after-effects
369 ($p < 0.003$, **fig. 7e,f,h**). The activation of each muscle significantly increased back to baseline
370 values from *early* to *late Transfer* for the slow VL, BF, and TA ($p > 0.05$) and were not different
371 from baseline ($p > 0.05$ **fig. 7e,f,h**). During *early Transfer*, the slow MG displayed early positive
372 differences ($p = 0.03$), which returned to baseline values by *late Transfer* ($p = 0.8$, **fig. 7g**). The
373 slow MG during terminal stance in *early Transfer* was no difference from baseline non-motorized
374 treadmill walking ($p = 0.21$). By *late Transfer* the slow MG during terminal stance was reduced
375 relative to baseline ($p = 0.005$). Of the fast limb muscles, only the BF ($p = 0.008$, **fig. 7f**) and the
376 TA ($p = 0.001$, **fig. 7h**) had a significantly lower activation relative to baseline during *early*
377 *Transfer*, and no muscles were different from baseline by *late Transfer* ($p \geq 0.18$, **fig. 7e-h**). The
378 fast MG during terminal stance in *early Transfer* was elevated relative to baseline ($p = 0.01$), and
379 like the slow MG during terminal stance showed a minor but significant depression ($p < 0.001$).
380 To ensure that suppressed muscle activity during the *early Transfer* period was not just due to
381 lower walking speeds on the slow limb, we compared the average belt velocity during the same
382 period to show that the fast limb was significantly slower than the slow limb (0.662 vs 0.755 m/s,
383 $p = 0.03$, **fig. 8, middle**).
384

385 *EMG activity during washout on motorized treadmill post-transfer*

386 Slow limb muscle activity of the VL, BF, and TA were no different from baseline values
387 ($p \geq 0.13$) and did not change from early to late Washout ($p \geq 0.4$, **fig. 7i,j,l**). The slow MG,
388 however, displayed robust after effects, indicated by a significant increase in muscle activity
389 relative to baseline ($p < 0.001$, **fig. 7k**) that significantly decreased by late Washout ($p < 0.001$)
390 and was not different from baseline values ($p = 0.09$), indicating the pattern washed out. The slow
391 MG during terminal stance showed no difference to baseline throughout the washout period ($p >$
392 0.05). For the fast limb muscles, only the VL had a minor, yet significant increase in activity during
393 the early Washout period ($p = 0.01$, **fig. 7i**). However, a small decrease to late Adaptation occurred,
394 which did not reach significance ($p = 0.05$) and was also not significantly different from baseline
395 ($p = 0.53$).

396

397 *No remaining after-effects during post-washout non-motorized treadmill walking*

398 No residual step length difference after-effects were present once returned to the non-
399 motorized treadmill post-washout ($p > 0.05$, not shown). In addition, there were no asymmetries
400 between any individual component during *early Post-washout* walking ($p > 0.05$). There were
401 significant decreases in muscle activity between *early Post-washout* walking compared to baseline
402 non-motorized treadmill values for bilateral VL ($p < 0.05$), BF ($p < 0.001$), and TA ($p < 0.001$),
403 but not the MG ($p > 0.05$). However, there were no significant differences between limbs for any
404 muscle (all $p > 0.05$). Additionally, no muscle made a significant change between *early* (first 10
405 strides) versus *late* (last 10 strides of a 2-minute period) *Post-washout* ($p > 0.05$), indicating that
406 the amplitude of these muscles was lower throughout the 2-minute *Post-washout* period. Upon
407 further analysis, this appears to be due to a lower average walking speed between *Baseline* non-

408 motorized treadmill walking for both slow and fast limbs (1.0 m/s, **fig. 8, left**) and *early Post-*
409 *washout* non-motorized treadmill walking (0.91 m/s, $p < 0.001$, **fig. 8, right**). To ensure that the
410 lower activation values for the three muscles were not due to residual after-effects, we made sure
411 there were no significant differences between foot velocities during *early Post-washout* ($p = 0.998$,
412 **fig. 8, right**).
413
414 **Discussion**
415 Context has been shown to play a major role in modulating the transfer of sensorimotor
416 adaptations when attempting to apply a motor pattern between environments. Specifically,
417 locomotor adaptation on a split-belt treadmill has repeatedly demonstrated limited transfer to over-
418 ground walking in healthy subjects (Reisman et al., 2009; Torres-Oviedo and Bastian, 2010, 2012).
419 However, patients post-stroke demonstrated greater transfer to over-ground walking, a difference
420 the authors attributed to a limited ability to utilize context cues as a result of cerebral deficits
421 (Reisman et al., 2009). Removal of vision either during training, testing, or both has been shown
422 to substantially improve transfer in healthy walkers, with the greatest transfer present when vision
423 was occluded in both training and transfer conditions (Torres-Oviedo and Bastian, 2010). The
424 removal of vision during transfer of locomotor adaptations is thought to prevent the utilization of
425 visual contextual cues which provide the nervous system with context specific information critical
426 to successful movement (Gordon et al., 1995; Torres-Oviedo and Bastian, 2010).
427 Here we demonstrated large after-effects in a new context (i.e. non-motorized split-belt
428 treadmill walking) after adapting on a motorized split-belt treadmill. In the current study, vision
429 was never occluded, therefore contextual cues about the walking environment were available
430 throughout training, transfer, and washout conditions. The only switch in context between

431 conditions was the treadmill used during walking, which while having several key differences (e.g.
432 incline, propulsion dynamics), still allowed subjects to maintain normal limb and muscle
433 coordination. Our results showed robust after-effects during Transfer, which suggest that the
434 contextual cues available from vision and proprioception were insufficient to block transfer.
435 Instead, consistency of the dynamics or highly overlapping neural networks between the conditions
436 may be more relevant to the ability to transfer newly learned locomotor adaptations to a new
437 context (Choi and Bastian, 2007).

438 We hypothesized that the washout of after-effects during the Transfer period would lead to
439 smaller or no after-effects in the subsequent Washout period (Reisman et al., 2009). However, we
440 found large after-effects in both Transfer and Washout that were driven by asymmetries in step
441 timing and foot placement differences, respectively. We believe this suggests three potential
442 mechanisms. First, if the spatial and temporal parameters were uncoupled, this suggests
443 independent access to the control of spatial and temporal motor outputs, and possibly independent
444 washout of each parameter in consecutive conditions. Second, the apparent uncoupling of spatial
445 and temporal after-effects could be a re-organization of spatial, temporal, and velocity
446 asymmetries resulting from an additional degree of freedom (i.e. belt velocity) when walking on
447 the non-motorized treadmill. This may effectively save the adapted pattern to be later washed out.
448 Last, the persistent after-effects in both Transfer and Washout conditions could be an artifact of
449 walking speed, as this factor has been demonstrated previously to impact after-effect magnitude
450 following a locomotor adaptation (Vasudevan and Bastian, 2010).

451 First, previous work has demonstrated the ability to uncouple spatial and temporal control
452 of locomotor adaptation using feedback during the adaptation period (Long et al., 2016; Malone
453 et al., 2012). Unlike the previous studies, the proposed uncoupling here occurred during the

454 Transfer and Washout periods. On the non-motorized treadmill, visual and tactile cues of the
455 handrail and walking surface may have led to an unintentional restriction of foot placement
456 asymmetry. In line with this idea, there were no significant changes in foot placement differences
457 during transfer as step length after-effects were a result of step time and belt velocity asymmetries.
458 This suggests that by restricting the spatial motor output during Transfer, the temporal motor
459 output was free to vary and likely washed out, leaving the spatial motor output to be washed out
460 later during the Washout condition.

461 Several recent studies indicate that spatial and temporal control of gait may be associated
462 to functionally distinct neural circuitries. Spatial control has been associated with both state-
463 estimation (Maeda et al., 2017), a cerebellar process, and pre-planned cognitive control (i.e.
464 cortical processes) in challenging walking environments (Matthis et al., 2018). In cerebellar lesion
465 patients, double support difference, but not step length symmetry displays adaptive behavior
466 (Morton and Bastian, 2006). Hemispherectomy patients have been shown to adapt step length
467 symmetry, but not double support difference in split-belt walking (Choi et al., 2009). Together,
468 these studies suggest that decoupling and subsequent independent washout of the temporal and
469 spatial components of locomotion is possible if constraints limit access to the neural circuits which
470 are involved in the control of a specific parameter. Our findings here are in line with this idea and
471 suggest that during split-belt treadmill walking, uncoupling of spatial and temporal components
472 are dissociable and can be implicitly and independently accessed.

473 Alternatively, the apparent dissociation between the spatial and temporal components
474 during the Transfer and Washout conditions may be an artifact of having a third degree of freedom
475 (i.e. belt speed) while walking on the non-motorized split-belt treadmill. Close inspection of the
476 individual components during the Transfer condition (**Fig. 4c,d**) might suggest a trade-off in

477 spatial, temporal, and velocity components, which sum to symmetric step lengths. By the end of
478 Transfer, belt speeds were asymmetric in the same direction as during Adaptation, while the spatial
479 component had a positive asymmetry (**Fig. 4d**). Because the context and dynamics of each
480 treadmill were so similar, this would suggest that subjects persisted with their adapted state from
481 the motorized split-belt treadmill to trade-off symmetric step times and lengths with asymmetries
482 in foot placement and step velocity. Consistent with this idea, previous work has demonstrated the
483 high metabolic cost of locomotion with asymmetric step times (Ellis et al., 2013). Further, step
484 length asymmetry alone during split-belt walking does not explain the added cost of asymmetry
485 (Sanchez et al., 2017). This may suggest that subjects preferred temporal symmetry rather than the
486 foot placement or velocity symmetry as a means of reducing metabolic cost. This further suggests
487 that subjects adapted a newly learned motor pattern for a novel condition in a way that was more
488 efficient while meeting the demands of the novel environment without washing out their adapted
489 motor pattern.

490 Partial washout or persistent after-effects during Transfer and Washout could also be
491 caused by after-effects associated with different walking speeds between conditions. The
492 contribution of speed to after-effect size has been demonstrated previously in both over-ground
493 and treadmill walking (Hamzey et al., 2016; Vasudevan and Bastian, 2010). Speeds both faster or
494 slower than the slow speed during adaptation result in diminished after-effects. In the current
495 study, we show robust after-effect magnitudes during both the Transfer and the Washout periods
496 independent of speed; i.e. average walking speed during non-motorized treadmill walking in
497 Transfer was significantly greater than the slow motorized speed (0.8 m/s versus 0.67 m/s, $p <$
498 0.05). Walking at a faster speed in Transfer should have led to smaller after-effect magnitudes,
499 however, this was not the case ($p = 0.26$). Moreover, we demonstrated no association between

500 after-effects in Transfer and Washout, suggesting partial washout did not occur. Therefore, we
501 believe it is unlikely that the persistent after-effects were partial after-effects in each condition as
502 a function of walking speed.

503 Finally, flexible control of walking gait is demonstrated here with dissimilar muscle
504 behavior for similar step length after-effects. Adaptation of muscle activity, but not merely reactive
505 changes, is demonstrated with robust limb- and phase-dependent after-effects in the Transfer
506 condition. Specifically, the slow VL, BF, and TA show large suppressions of muscle activity
507 during late swing and early weight transfer which require substantial time (>25 strides) to recover
508 to baseline non-motorized treadmill walking values. Further, we also show that the suppression of
509 muscle activity during this period is not simply a result of slower limb speeds during the early
510 Transfer period, but instead are suppressed despite faster speeds compared to the fast limb. Tibialis
511 anterior muscle activity has been demonstrated to display after-effects following split-belt
512 treadmill walking, behavior which was correlated with anterior breaking forces (Ogawa et al.,
513 2014). Here we extend these findings to show that the slow limb VL and BF muscles also show
514 similar predictive control around heel strike and weight acceptance which track similar adaptive
515 changes found previously (Iturralde and Torres-Oviedo, 2019; Ogawa et al., 2014). This suggests
516 that muscles of the lower and upper leg participate in predictive control of heel contact and weight
517 acceptance in split-belt walking and are likely subject to formation of, or modification to, an
518 internal model which represents the dynamics of lower limb control (Blanchette and Bouyer, 2009;
519 Lam et al., 2006).

520 In conclusion, we used a novel non-motorized split-belt treadmill in a locomotor transfer
521 paradigm to demonstrate that context and locomotor dynamics influence the ability to transfer a
522 newly learned locomotor adaptation. This study improves on our current understanding of the

transfer of locomotor adaptations and provides further evidence of the adaptability of the human locomotor system for the control of walking gait in novel challenging environments. We believe that the low-cost and portable non-motorized split-belt treadmill may provide a unique and useful tool in gait rehabilitation. Further research is needed to investigate how non-motorized split-belt treadmills can be used in clinical and home settings, and whether training on this device would lead to improved over-ground walking.

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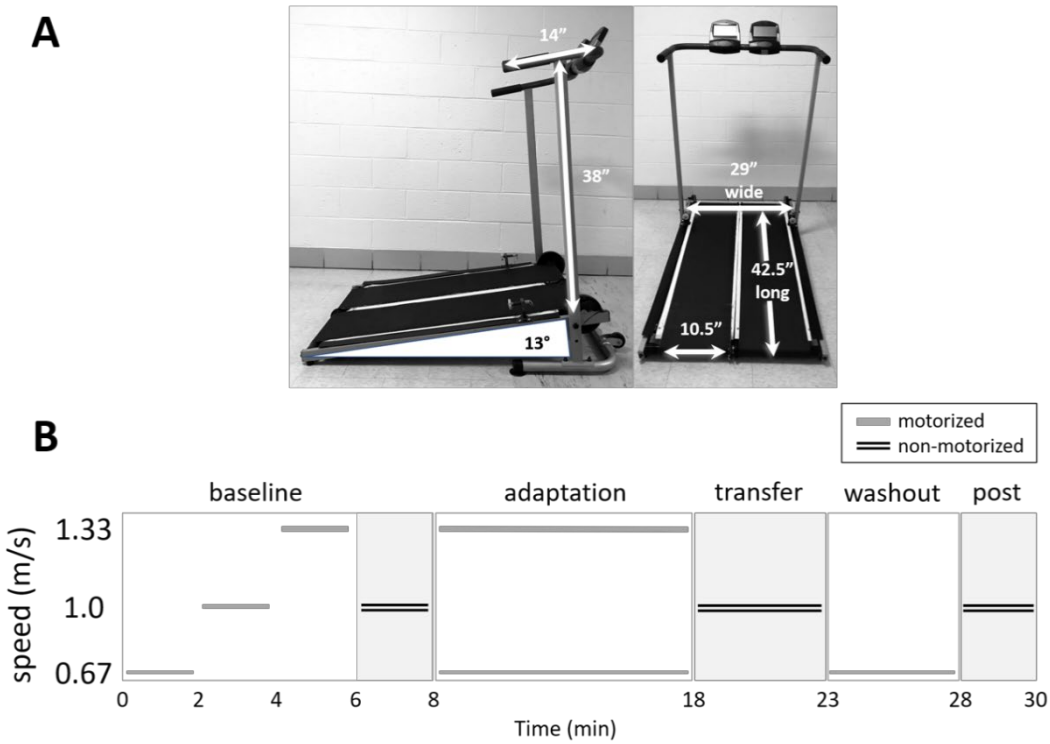

Figure 1. Non-motorized split-belt treadmill and paradigm. ***A.*** Non-motorized treadmill dimensions (inches), *left panel*; handrail height from top of treadmill deck and handle depth, and deck angle in degrees. Non-motorized treadmill dimensions, *right panel*; deck width and length and individual belt widths. ***B.*** Split-belt treadmill trasnfer paradigm. All subjects were recorded in baseline conditions for slow, medium, fast, and non-motorized treadmill (familiarization, not recorded and not shown) conditions in random order. The split-belt adaptation period was always immediately preceded by a second non-motorized treadmill baseline period used for non-motorized treadmill baseline measures. After all baseline periods were completed, all subjects adapted for 10 minutes with one limb on a belt traveling at the slow speed (0.67 m/s) and the other at the fast speed (1.34 m/s). Subjects then moved to the non-motorized treadmill without forward stepping to assess for the transfer to the non-motorized treadmill. Transfer was 5 minutes at preferred speed. Subjects then moved without forward stepping back to the motorized treadmill to assess for residual after-effects specific to the motorized treadmill for an additional 5 minutes. Finally, subjects then returned to the non-motorized once more to ensure all residual after-effects had been washout out for an additional 2 minutes.

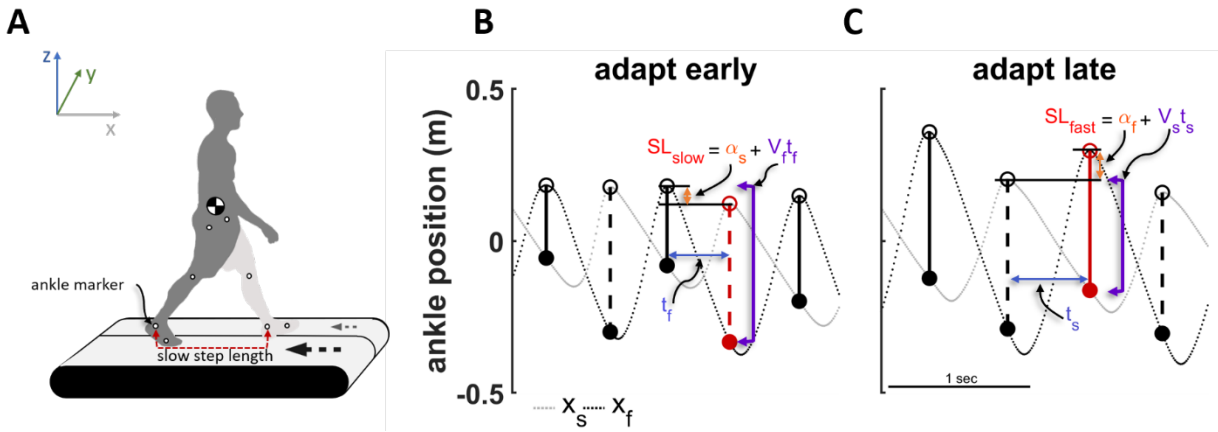

Figure 2. Analytical calculation of step length. Visual representation of walking parameters for the analytical step length derivation. ***A.*** Walker demonstrating the position of the reflective markers on the fifth metatarsal, lateral malleolus, and lateral condyle. Gray crossed circle represents the pelvic centroid used to calculate the reference frame for ankle marker data on the motorized treadmill. Slow instantaneous step length shown (red arrow line) as distance between ankle markers at time of slow limb heel strike. Gray and black arrows indicate belt speeds. ***B.*** Slow step length visualized during early adaptation. Ankle marker trajectories in the pelvic centroid reference frame. Positive values indicate positions in front of the pelvic centroid and negative indicate positions behind the pelvic centroid. Dashed lines indicate individual ankle marker trajectories for the fast (black, x_f), and slow (gray, x_s) limbs. Ankle marker trajectories are plotted with time on the x-axis, therefore distance between dots indciates distance traveled every 10 milliseconds. Open circles indicate the position and time of the respective limbs heel strike. Filled circles indicate the position and time of the trailing limb ankle at the leading limbs heel strike. Solid vertical lines connecting open and closed circles indicate the instantaneous fast step length and the vertical dashed lines connecting open and closed circles indicate the instantaneous slow step length (i.e. SL_{slow}). The slow analytical step length (dashed red line) is the summation of the (negative) spatial component (α_s), and the product of the velocity of the fast limb (v_f) and the fast step time (t_f), the distance traveled by the fast limb from fast heel strike to fast position at slow heel strike. v_f is the difference between the fast limb ankle (x_f) at fast heel strike, and the fast limb ankle at slow limb heel strike, divided by the fast step time (t_f). ***C.*** Fast step length visualized dyring late adaptation. The fast analytical step length (solid red line) is the summation of the spatial component (α_f), and the product of the velocity of the slow limb (v_s) and the slow step time (t_s).

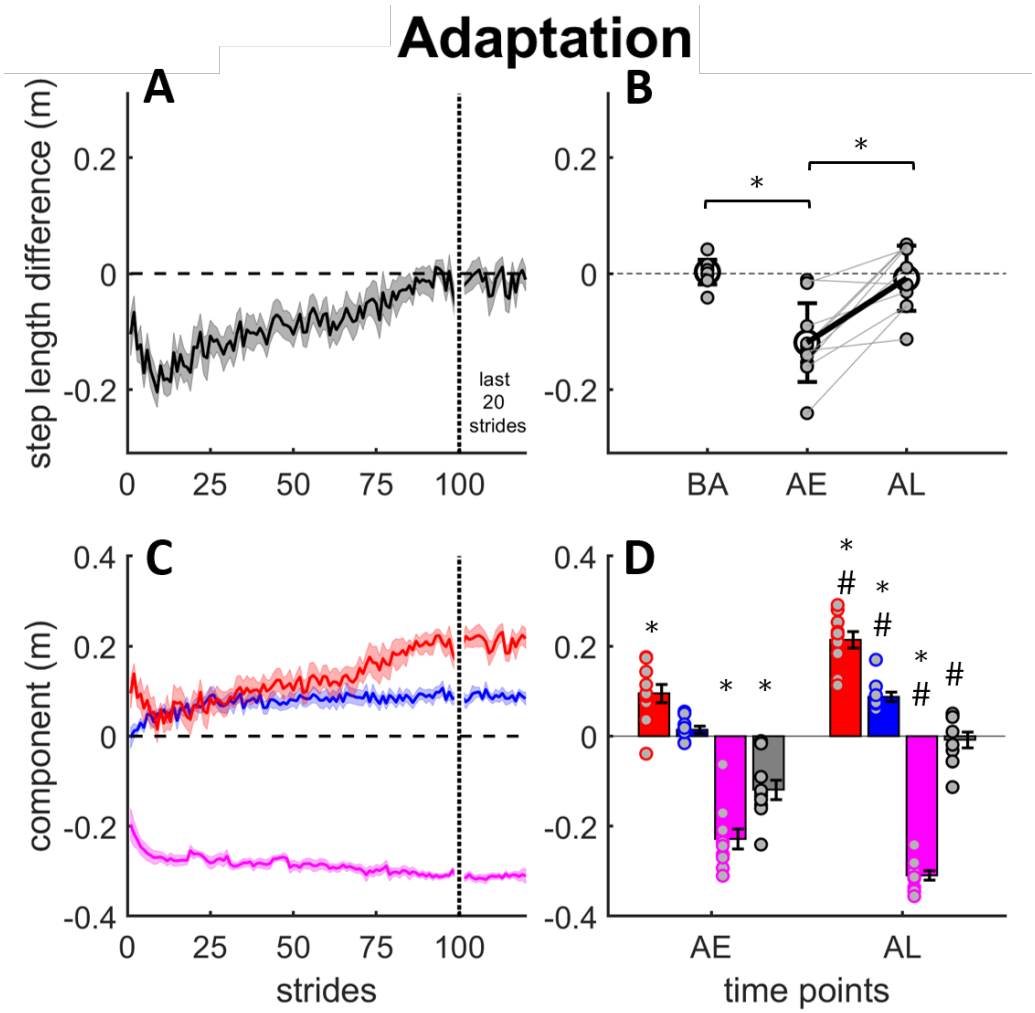

Figure 3. Adaptation; Progression of step length difference and contribution of spatial, temporal, and velocity asymmetries to motorized split-belt treadmill walking during adaptation. ***A.*** Group average step length difference during the first 100 and last 20 strides of the adaptation period. Shaded area represents plus/minus standard error. Negative values indicated the slow step length is larger than the fast step length. ***B.*** Individual subject step length difference data (small gray filled circles) comparing baseline (BA) slow walking to early adapt (AE) and late adapt (AL). Light gray lines connect individual subject data points between AE and AL. Group means are represented by large black circles, error bars are standard deviations. Thick black line connecting AE and AL indicates group change. Horizontal bars with star indicate significant differences between time points ($p < 0.05$). ***C.*** Stride-by-stride changes in individual components for the first 100 and last 20 strides; spatial (red), temporal (blue), and velocity (magenta) differences. Shaded areas are plus/minus standard error. ***D.*** Individual subject component data (gray filled colored circles) comparing AE and AL. Bars are group means, error bars are standard error. "*" indicates significant difference to baseline slow, "#" indicates late time point significantly different from early ($p < 0.05$).

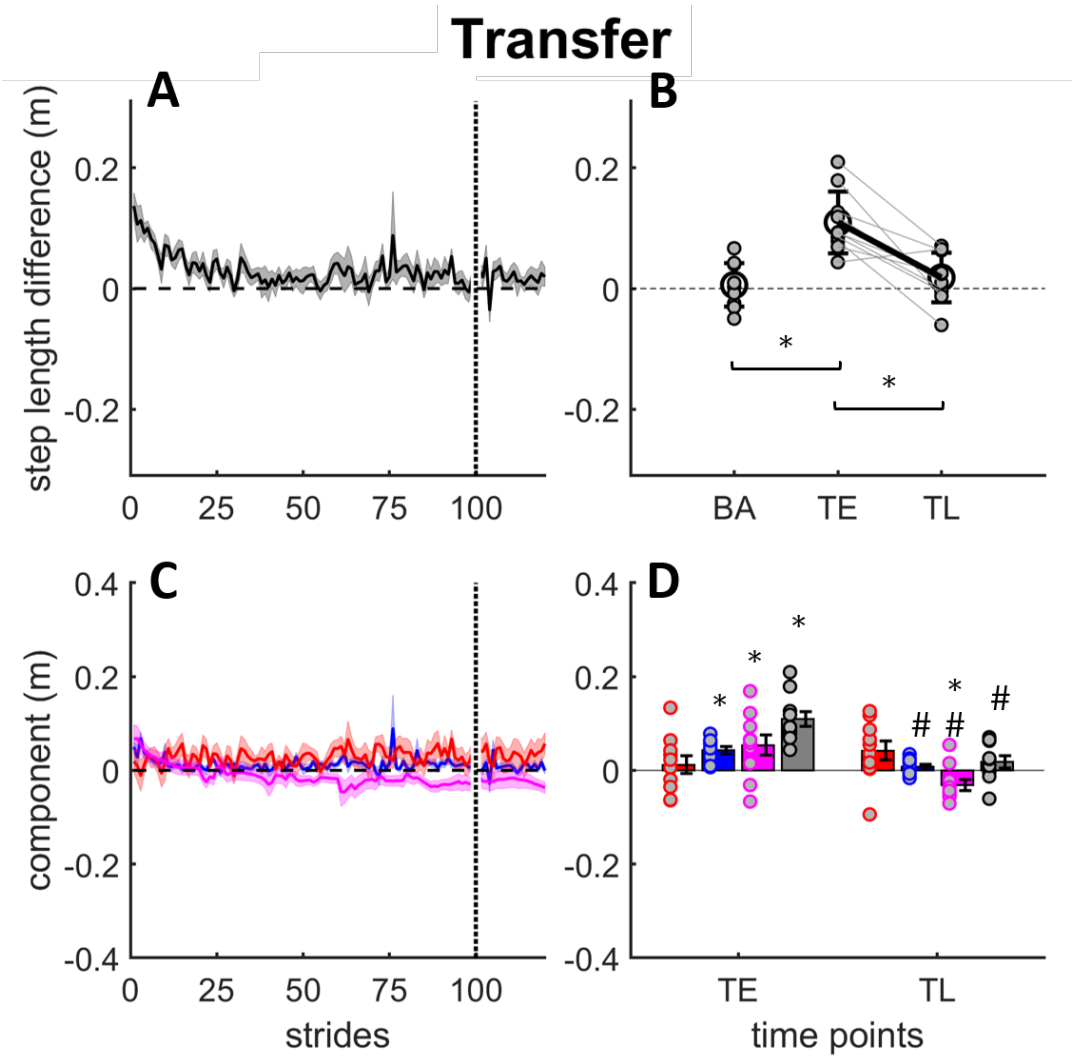

Figure 4. Transfer; Progression of step length difference and contribution of spatial, temporal, and velocity asymmetries to non-motorized split-belt treadmill walking during transfer. ***A.*** Group average step length difference during the first 100 and last 20 strides of the transfer period. Shaded area represents plus/minus standard error. Positive values indicated the fast step length is larger than the slow step length. ***B.*** Individual subject step length difference data (small gray filled circles) comparing baseline (BA) walking to early transfer (TE) and late transfer (TL). Light gray lines connect individual subject data points between TE and TL. Group means are represented by large black circles, error bars are standard deviations. Thick black line connecting TE and TL indicates group change. Horizontal bars with star indicate significant differences between time points ($p < 0.05$). ***C.*** Stride-by-stride changes in individual components for the first 100 and last 20 strides; spatial (red), temporal (blue), and velocity (magenta) differences. Shaded areas are plus/minus standard error. ***D.*** Individual subject component data (gray filled colored circles) comparing TE and TL. Bars are group means, error bars are standard error. "*" indicates significant difference to baseline non-motorized, "#" indicates late time point significantly different from early ($p < 0.05$).

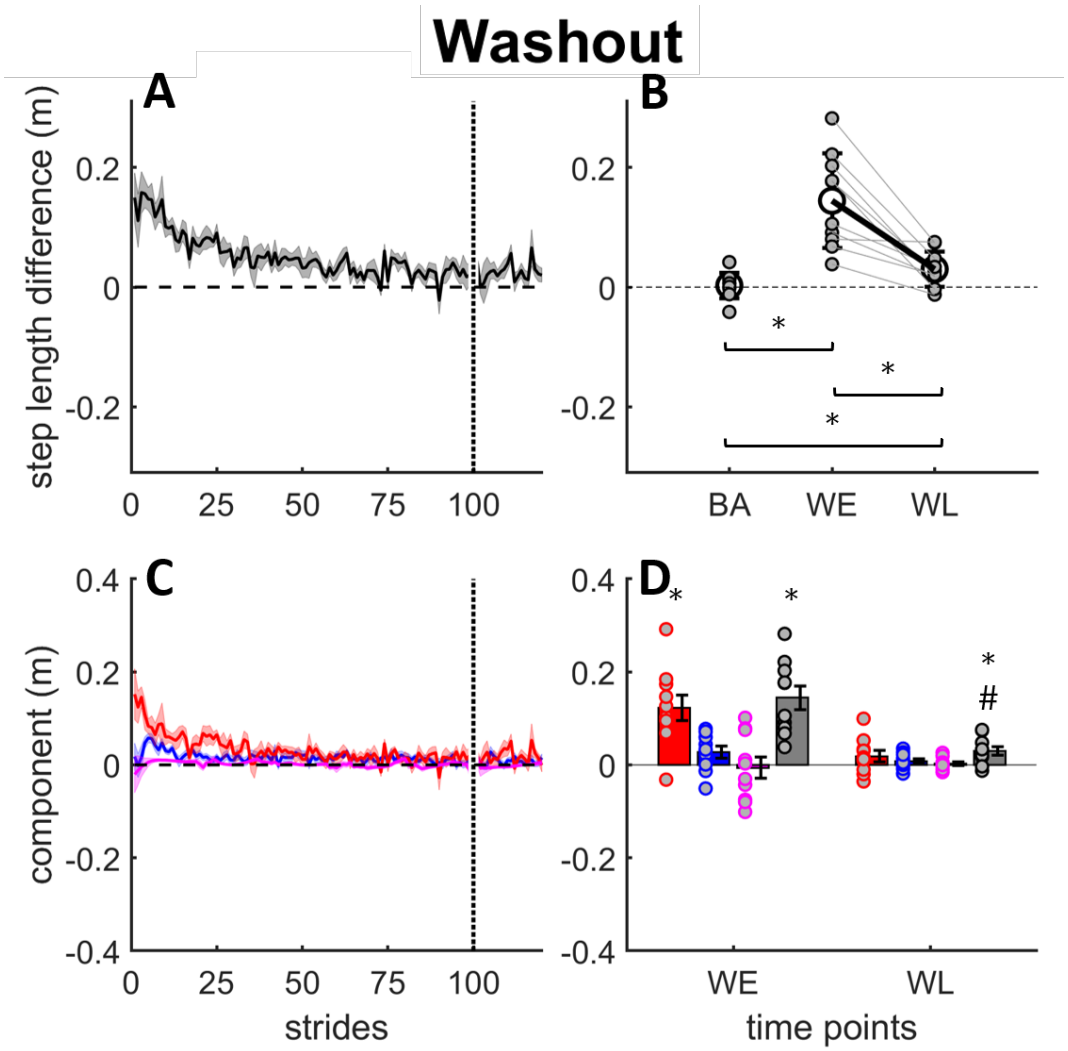

Figure 5. Washout; Progression of step length difference and contribution of spatial, temporal, and velocity asymmetries to motorized treadmill walking during washout. ***A.*** Group average step length difference during the first 100 and last 20 strides of the adaptation period. Shaded area represents plus/minus standard error. Positive values indicated the fast step length is larger than the slow step length. ***B.*** Individual subject step length difference data (small gray filled circles) comparing baseline (BA) slow walking to early washout (WE) and late washout (WL). Light gray lines connect individual subject data points between WE and WL. Group means are represented by large black circles, error bars are standard deviations. Thick black line connecting WE and WL indicates group change. Horizontal bars with star indicate significant differences between time points ($p < 0.05$). ***C.*** Stride-by-stride changes in individual components for the first 100 and last 20 strides; spatial (red), temporal (blue), and velocity (magenta) differences. Shaded areas are plus/minus standard error. ***D.*** Individual subject component data (gray filled colored circles) comparing WE and WL. Bars are group means, error bars are standard error. "*" indicates significant difference to baseline slow, "#" indicates late time point significantly different from early ($p < 0.05$).

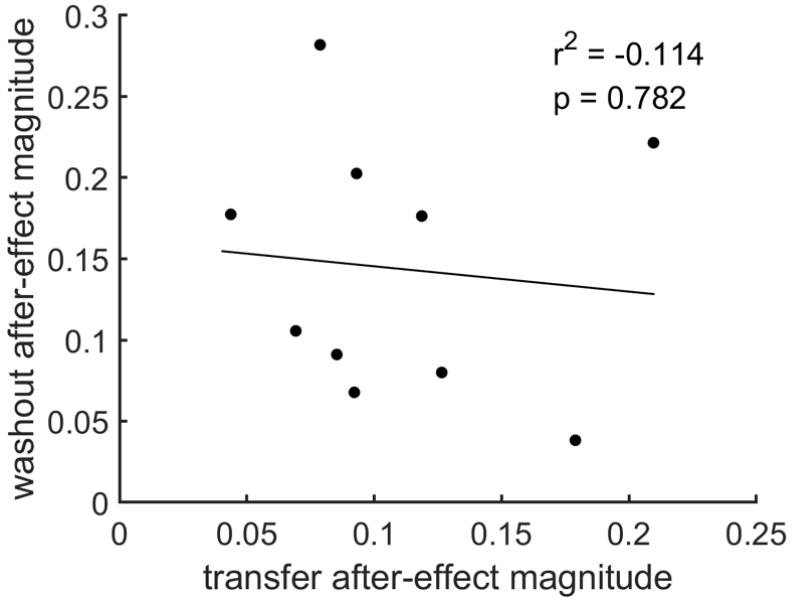

Figure 6. Linear regression to assess interaction between transfer after-effect and washout after-effect magnitude. Data points are individual subject averages from first 5 strides during early transfer (TE) and washout (WE), respectively.

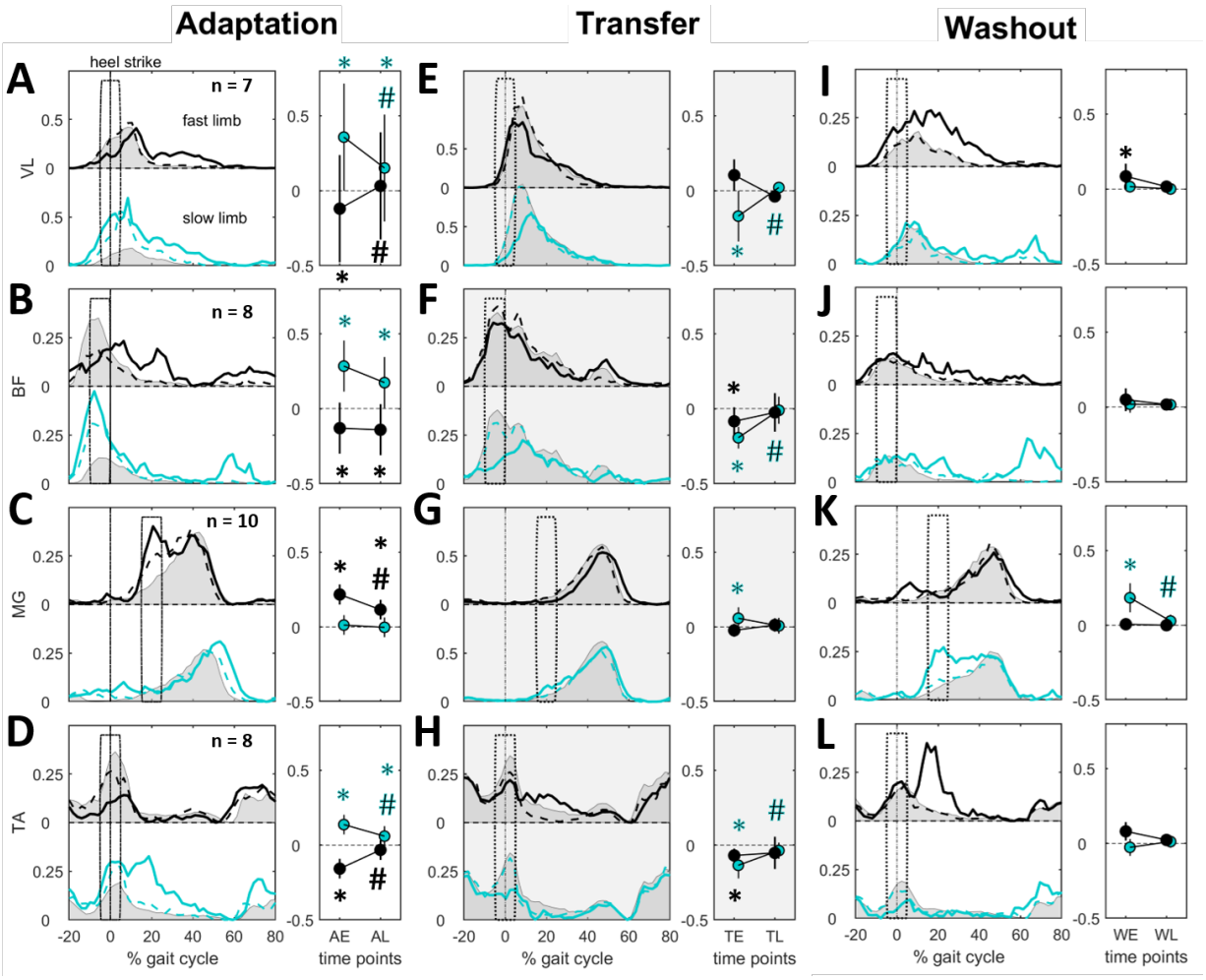

Figure 7. Group averaged muscle activity data during adaptation (first column), transfer (second column, gray), and washout (third column) for the VL (A, E, and I), BF (B, F, and J), MG (C, G, and K) and TA (D, H, and L). Left panels display group average muscle activity tracings during early (solid) and late (dashed line) time points across conditions compared to baseline speed and condition-matched values for each limb (gray shaded area) from -20 to 80% of the gait cycle. Vertical dashed line centered at zero indicates heel strike. Top panels in black are the fast limb with the lower panel in green for the slow limb. Dash-dot boxes within EMG traces indicate area of interest used in statistical analysis. Right panels within the columns are the group average difference curves from condition and speed-matched baseline values. Black dots represent fast limb during early (left) and late (right) time points, green dots are slow limb, and error bars are plus/minus standard deviation. "*" indicates significant difference to baseline, "#" indicates late time point significantly different from early ($p < 0.05$). Several subjects had corrupted EMG activity due to excessive movement artifact, therefore number of remaining subjects for each muscle is indicated with the "n =" in the upper right corner of the first column EMG trace.

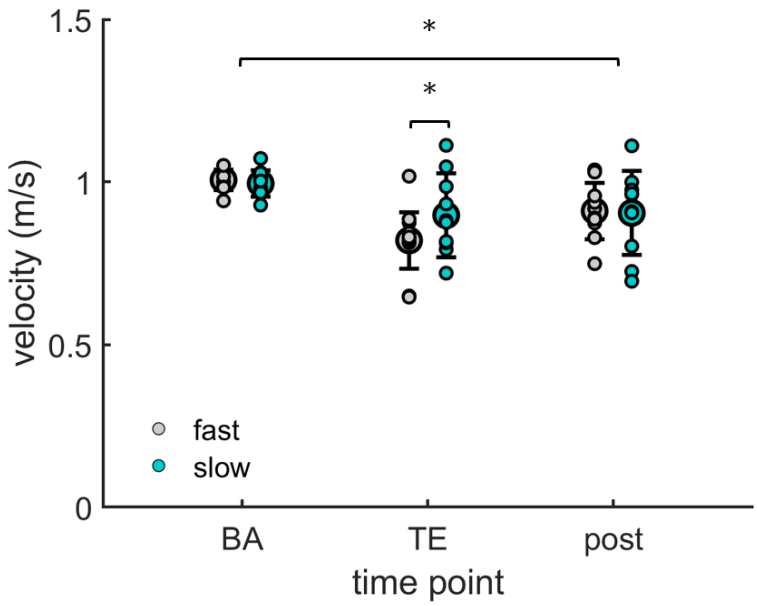

Figure 8. Individual (small cirlces) and group average (large circles, ± sd) non-motorized treadmill belt speeds by limb. Fast limb instantaneous belt velocities are calculated as the instanteanous speed of the ankle marker in the global reference frame for the trailing limb at the instant of the leading limbs heel contact. Time points are during baseline non-motorized treadmill walking, early transfer, and early post-washout. Stars indicated significant difference ($p < 0.05$). Comparison between baseline and post are composite of both fast and slow limbs.