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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23 **Abstract**

24 Background: Locomotor adaptation during motorized split-belt walking depends on independent
25 processes for spatial and temporal control of step length symmetry. The unique mechanics of
26 motorized split-belt walking that constrains two limbs to move at different speeds during double
27 support may limit transfer of step length adaptations to new walking contexts.

28

29 Research question: How do spatial and temporal locomotor outputs contribute to transfer of step
30 length adaptation from constrained motorized split-belt walking to unconstrained non-motorized
31 split-belt walking?

32

33 Methods: We built a non-motorized split-belt treadmill that allows the user to walk at their own
34 pace while simultaneously allowing the two belts to be self-propelled at different speeds. 10 healthy
35 young participants walked on the non-motorized split-belt treadmill after an initial 10-minute
36 adaptation on the motorized split-belt with a 2:1 speed ratio. Foot placement relative to the body
37 and timing between heel strikes were calculated to determine spatial and temporal motor outputs,
38 respectively. Separate repeated measures ANOVAs were used for step length difference and its
39 spatial and temporal components to assess for transfer to the non-motorized treadmill.

40

41 Results: We found robust after-effects in step length difference during transfer to non-motorized
42 split-belt treadmill walking that were primarily driven by changes in temporal motor outputs.
43 Conversely, residual after-effects observed during motorized tied-belt treadmill walking (post-
44 transfer) were driven by changes in spatial motor outputs.

45

46 Significance: Our data showed decoupling of adapted spatial and temporal locomotor outputs
47 during the transfer to non-motorized split-belt walking, raising the new possibility of using a non-
48 motorized split-belt treadmill to target specific spatial or temporal gait deficits.

49 **Keywords:** human gait, interlimb coordination, generalization, motor learning, non-motorized
50 treadmill
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53 Introduction

54 Control of human locomotion is highly adaptable. Gait patterns can be altered through
55 motorized treadmill training, even after central nervous system damage [1]. Walking on a split-belt
56 treadmill induces asymmetric step lengths by constraining limbs to move at different speeds which
57 alters gait through an error-based learning process known as motor adaptation [2], [3]. Adaptation
58 of symmetric step lengths during motorized split-belt treadmill walking results from changes in
59 both spatial control of foot placement, and temporal control of step timing [4]–[6]. These spatial
60 and temporal motor outputs reflect distinct neural strategies to overcome the asymmetric belt
61 speeds. Positive asymmetries in foot placement and step timing achieved during adaptation persist
62 during de-adaptation, while the distance the foot travels during stance immediately returns to tied
63 baseline values [6]. This after-effect during post-adaptation walking reflects the updating of neural
64 control processes for walking and is limited when transferring to over-ground walking or to
65 different modes of locomotion [7]–[11].

66 Step length asymmetry post-stroke is associated with both spatial and temporal
67 abnormalities in gait control [3], [4], [12], [13]. Training on a motorized split-belt treadmill is a
68 promising rehabilitation strategy to reduce asymmetric step length patterns in hemiparetic walkers
69 [3], [14]. After repeated exposure to split-belt adaptation, spatial asymmetries to walking control
70 improve substantially and persist up to three months after an intervention. However, temporal
71 asymmetries such as stance time and double support time remain unchanged both immediately and
72 after 3 months follow up [15]. Further, changing the context of the walking condition substantially
73 reduces or eliminates transfer in both post-stroke [7], and healthy individuals [8]. Potentially
74 limiting transfer of motorized split-belt treadmill adaptations to over-ground walking is the unique
75 mechanics of split-belt treadmills—the constraint to have limbs move at different speeds during
76 the double support period.

77 To address these issues and better understand the capacity to transfer locomotor
78 adaptations, we developed a non-motorized split-belt treadmill that allows the user to determine

79 their own walking pace while simultaneously allowing for asymmetric behavior. In contrast to
 80 motorized treadmills, non-motorized treadmills have freely moveable belts which are driven by
 81 participants pushing against an inclined or concave surface which allow participants to self-select
 82 and express natural gait variability [16]–[18]. Our custom non-motorized split-belt treadmill is also
 83 cheaper, more portable, and safer compared to motorized systems. Prior research on non-motorized
 84 treadmills for locomotor adaptation is limited to single-belt devices [19]. A better understanding of
 85 the generalization between motorized and non-motorized split-belt devices would allow us to
 86 implement split-belt therapy using lower-cost non-motorized systems, and thereby improve the
 87 translational potential of treadmill training to community ambulation.

88 The current study is first to examine (1) whether step length adaptation from motorized
 89 split-belt treadmill walking transfers to non-motorized treadmill walking, and (2) how the separate
 90 spatial and temporal control of step length symmetry contributes to transfer in a novel walking
 91 context. Non-motorized treadmills offer a unique combination of portability and economy which
 92 we believe will provide a valuable bridge between split-belt treadmill and over ground walking.
 93 We hypothesized that after-effects would be present during transfer and would be driven by positive
 94 asymmetries in foot placement and step timing. We further hypothesized that after-effects washed
 95 out during non-motorized treadmill walking should lead to diminished or absent after-effects during
 96 tied motorized treadmill walking.

97

98 **Methods**

99 *Participants*

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

105

106 *Experimental setup*

107 *Motorized split-belt treadmill.* Participants walked on a split-belt treadmill (Bertec Corp,
108 Columbus OH) that has separate left and right belts, each with its own motor. During motorized
109 treadmill walking, participants wore a non-weight-bearing safety harness suspended from the
110 ceiling. Participants were instructed to minimize handrail use, walking with normal arm swing, and
111 to maintain forward gaze.

112 *Non-motorized spit-belt treadmill.* We designed and built a user-propelled non-
113 motorized split-belt treadmill (**fig. 1a**). The non-motorized treadmill was fabricated from two
114 commercially available non-motorized treadmills (Inmotion II Manual Treadmill; Stamina,
115 Springfield, MO), which were designed to share a common support structure and minimize spacing
116 between the belts (32 mm). To minimize friction with the belt-deck interface, a sheet of
117 polytetrafluoroethylene (PTFE, 0.30" sheet; ePlastics, San Diego, CA) plastic was secured each
118 treadmill deck. A ~1kg mass was added to each flywheel to increase the inertial properties of the
119 belt-flywheel system to ensure continuous movement as the limb transitioned from stance to swing,
120 enabling smoother transition into the next stance phase. The treadmill utilizes gravity (~13° incline)
121 and the users body weight to assist driving the symmetrically resisted but independently user-
122 propelled belts. During non-motorized treadmill walking, participants lightly held the handrails and
123 were instructed to avoid supporting body weight.

124

125 *Split-belt adaptation paradigm*

126 The adaptation paradigm (**fig. 1b**) consisted of motorized tied-belt, motorized split-belt and
127 non-motorized split-belt walking conditions. During Baseline, participants walked on the
128 motorized treadmill with belts tied at a slow (0.67 m/s), medium (1.0 m/s), and fast (1.34 m/s)
129 speeds for two minutes each, randomized across participants. A 5-minute non-motorized treadmill

Baseline trial was collected at preferred walking speed. Participants were instructed to “walk as fast as you would to a meeting for which you have adequate time to arrive”. During *Adaptation*, participants walked on the motorized split-belt at a 2:1 speed ratio (0.67 and 1.34 m/s) for ten minutes. These speeds were chosen because the average speed is 1.0 m/s, which was the average preferred walking speed on the non-motorized treadmill during pilot testing. Participants were then instructed to side-step from the motorized treadmill onto the non-motorized treadmill less than 2-feet away. Forward stepping was avoided to prevent washout of after-effects. During *Transfer*, participants walked for 5 minutes on the non-motorized treadmill. Participants returned to the motorized treadmill for the *Washout* period and walked at the slow speed for an additional 5 minutes. During *Post-adaptation*, participants again walked on the non-motorized treadmill for 2 minutes. Participants were randomly assigned left or right limb to the slow belt during split-belt walking and subsequent references to a limb will be as slow or fast regardless of condition.

143 *Data collection*

During motorized treadmill walking, kinematics were recorded at 100 Hz using a 4-camera motion capture 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, kinematics were relegated to use of only ankle markers for identification of spatio-temporal parameters due to limitations in capture space during data collection.

151 *Data analysis*

Data analysis was performed in MATLAB (Mathworks, Natick, MA, v. R2017a). Marker data were low pass filtered at 6 Hz with a second order Butterworth filter. For both motorized and non-motorized treadmill walking, we defined heel contact and toe-off as the time of peak anterior and posterior ankle position for each step, respectively. We used step length difference to assess

split-belt walking adaptation [2], [3], [14], [20], using the anterior-posterior distance between the ankle markers at the 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 and SL_{slow} is with the slow leg leading at heel strike (**fig. 2a**). We also included double support difference as a secondary outcome (see Supplementary materials).

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

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

where the first term (step position) represents the difference between the relative positions of the feet at the fast and slow heel strikes, the second term (step time) is the difference in slow and fast step times as a function of average foot speed, and the third term (step velocity) is the difference in slow and fast foot velocities as a function of the average step time (**fig. 2b,c**). It is important to note that during motorized treadmill conditions, fast and slow speeds are fixed, whereas during non-motorized treadmill walking, the speed of each belt/limb is strictly user controlled and becomes a third degree of freedom while walking.

Statistical analysis

Group means were calculated in bins across the last 10 strides for each Baseline trial (motorized slow, motorized medium, motorized fast, and non-motorized preferred) and the first 5 strides (early) and last 5 strides (late) for Adaptation, Transfer, Washout, and Post trials. Separate repeated measures ANOVAs were used to test the effects of time on each dependent variable. Post-hoc analyses were performed using independent sample t-tests to compare each dependent variable at each time point to the baseline value and for comparisons between early and late time points.

180 Results

181 Adaptation

182 Repeated measures ANOVA revealed significant effects of time on step length ($F(7,63) =$
183 25.17 , $p < 0.001$, **fig. 3a-5a**). Group averaged step-length differences were not significantly
184 different from zero during baseline tied-walking on the motorized treadmill (all p -values > 0.05).
185 **Figure 3a** shows gradual changes in step length difference (dark grey/black) during the first 100
186 and last 20 strides in Adaptation. During *early Adaptation*, step length difference showed a large
187 initial change compared to baseline ($p < 0.001$, **fig. 3b**). By *late Adaptation*, step length difference
188 was reduced back to baseline levels ($p = 0.58$, **fig. 3b**).

189 As previously reported [4]–[6], step length difference can be decomposed into independent
190 step velocity (magenta), step position (red) and step time (blue) contributions (**fig 3c,d**). The step
191 velocity component became increasingly negative over the course of adaptation, reflecting a large
192 negative velocity induced perturbation which required opposition ($p < 0.001$, **fig 3d**). During *early*
193 *Adaptation*, the step position component showed a significant initial asymmetry ($p < 0.001$, **fig.**
194 **3d**). The step time component showed a more gradual change, with *early Adaptation* values not
195 significantly different from baseline ($p = 0.26$, **fig. 3d**). By *late Adaptation*, the step position and
196 step time components both increased significantly ($p < 0.001$, **fig. 3d**) to cancel the negative step
197 velocity component, resulting in symmetrical step lengths ($p = 0.58$, **fig. 3d**).

198

199 Transfer

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

205 **Figure 4c,d** show the contribution of the step velocity, position and step timing
 206 components to the step length after-effects during Transfer. In *early Transfer*, the step velocity
 207 component displayed a large positive (i.e. an after-effect) component that was significantly
 208 different from baseline ($p = 0.03$, **fig. 4d**, magenta). By *late Transfer*, the step velocity component
 209 decreased to a negative value that was significantly different from baseline ($p = 0.02$), indicating
 210 that participants settled on a step velocity difference in the same direction as the initial motorized
 211 split-belt perturbation (i.e. a negative velocity difference). The step position component was not
 212 significantly different from baseline during *early Transfer* ($p = 0.5$, **fig. 4d**). There were also no
 213 significant differences between *early* and *late Transfer* for the step position component ($p = 0.3$).
 214 By *late Adaptation*, the step position component was not different from baseline ($p = 0.06$, **fig. 4d**),
 215 however, upon inspection of individual data, this result may have been driven by a single outlier
 216 (*late Transfer*, red filled circles). These results indicate that the spatial component did not
 217 contribute to the initial after-effects in step length difference. The step time component was
 218 significantly different from baseline during *early Transfer* ($p < 0.001$, **fig. 4d**). By *late Transfer*,
 219 the step time component decreased back to baseline values ($p = 0.58$), indicating washout of the
 220 temporal after-effect.

221

222 *Washout*

223 After-effects in step length reappeared during motorized treadmill walking in *early*
 224 *Washout* ($p < 0.001$). Step length difference was significantly different from baseline during early
 225 Washout ($p < 0.001$ **fig. 5a**) and returned back to baseline by *late Washout* indicated by significant
 226 differences from *early* to *late Washout* ($p < 0.001$) but did not completely return to baseline values
 227 ($p = 0.03$, **fig. 5b**).

228 **Figure 5c** shows the contribution of the step velocity, step position and step timing
 229 components to the step length after-effects during the Washout period. The step velocity
 230 components were not different from baseline during *early Washout* ($p = 0.72$) or *late Washout* (p

231 = 0.95), due to the symmetric belt speeds (**fig. 5c,d**). The step position component displayed
 232 significant after-effects during *early Washout*, ($p < 0.001$) that reduced back to baseline by *late*
 233 *Washout* ($p = 0.17$, **fig. 5d**). The step time component was not significantly different from baseline
 234 during *early Washout* ($p = 0.09$) nor *late Washout* ($p = 0.48$, **fig 5d**, blue).

235

236 *Unlearning interaction*

237 Our linear regression analysis showed that step length error magnitude during *early*
 238 *Transfer* did not predict the step length error magnitude during *early Washout* ($p = 0.782$, **fig. 6**),
 239 suggesting that transfer did not result in unlearning of motorized treadmill adaptation. Linear
 240 regression analysis on the individual components also showed no interaction between *early*
 241 *Transfer* and *early Washout* for the step position ($p = 0.132$), step time ($p = 0.451$), or velocity
 242 components ($p = 0.457$).

243

244 *Post-washout*

245 No residual step length difference after-effects were present once returned to the non-
 246 motorized treadmill post-washout ($p > 0.05$, not shown). In addition, there were no asymmetries
 247 between any individual component during *early Post-washout* walking ($p > 0.05$).

248

249 **Discussion**

250 Effective movement rehabilitation requires the transfer of improvements made in the clinic
 251 to the community. Context is known to play a major role in modulating transfer of sensorimotor
 252 adaptations between different environments. Specifically, locomotor adaptation on a split-belt
 253 treadmill has repeatedly demonstrated limited transfer to over-ground walking in healthy and post-
 254 stroke participants [7], [8], [15], [21]. It is unclear based on previous studies whether spatial and
 255 temporal outputs contribute equally to transfer of split-belt locomotor adaptation. In agreement
 256 with our first hypothesis, we demonstrated transfer of motorized split-belt treadmill adaptation to

257 non-motorized split-belt treadmill walking—a result driven by temporal and velocity but not spatial
258 control asymmetries. These findings are promising and suggest that using a portable, low-cost split-
259 belt treadmill for adaptive training can facilitate transfer from clinical to community walking.

260 Next, we hypothesized that the washout of after-effects during the Transfer period would
261 lead to smaller or no after-effects during the Washout period [7]. However, we found large after-
262 effects in both Transfer and Washout that were driven by asymmetries in step timing and foot
263 placement differences, respectively. We suggest three potential mechanisms contributing to
264 persistent after-effects. First, if the spatial and temporal parameters were uncoupled, this would
265 suggest independent access to the control of spatial and temporal motor outputs and independent
266 washout of each parameter. While previous work has demonstrated uncoupling of spatial and
267 temporal control using feedback during adaptation [5], [6], the proposed uncoupling here occurred
268 during the Transfer and Washout conditions. On the non-motorized treadmill, visual and tactile
269 cues of the handrail and small walking surface may have led to an unintentional restriction of foot
270 placement asymmetry, potentially blocking transfer of the spatial asymmetry. In line with this idea,
271 there were no significant changes in foot placement differences during transfer as step length after-
272 effects were a result of step time and belt velocity asymmetries. This suggests that by restricting
273 spatial control during Transfer, temporal control was free to vary and likely washed out, leaving
274 the spatial motor output to be deadadapted during the Washout condition. Recent studies indicate that
275 spatial and temporal control of gait may be related to functionally distinct neural circuitries. Spatial
276 control has been associated with both state-estimation [22], a cerebellar process, and pre-planned
277 cognitive control (i.e. cortical processes) in challenging walking environments [23]. In cerebellar
278 lesion patients, double support difference, but not step length symmetry displays adaptive behavior
279 [24]. Hemispherectomy patients adapt step lengths, but not double support difference in split-belt
280 walking [14]. Together, these studies suggest that decoupling and subsequent independent washout
281 of the temporal and spatial components of locomotion is possible if constraints limit access to the
282 neural circuits which are involved in the control of a specific parameter. Our findings here are in

283 line with this idea and suggest that uncoupling of spatial and temporal control is dissociable and
284 may be implicitly and independently accessed.

285 Next, the apparent uncoupling of spatial and temporal after-effects could be a re-
286 organization of spatial, temporal, and velocity asymmetries resulting from an additional degree of
287 freedom (i.e. belt velocity) when walking on the non-motorized treadmill. This may effectively
288 save the adapted pattern to be later washed out. Close inspection of the individual components
289 during Transfer (**Fig. 4c,d**) might suggest a trade-off in spatial, temporal, and velocity components,
290 which sum to symmetric step lengths. By late Transfer, belt speeds were asymmetric in the same
291 direction as during Adaptation, while the spatial component had a positive asymmetry (**Fig. 4d**).
292 Because the context and dynamics of each treadmill were similar, this would suggest that
293 participants persisted with their adapted state from the motorized split-belt treadmill to trade-off
294 symmetric step times and lengths with asymmetries in foot placement and step velocity. Consistent
295 with this idea, previous work has demonstrated the high metabolic cost of locomotion with
296 asymmetric step times [25]. Further, step length asymmetry alone during split-belt walking does
297 not explain the added cost of asymmetry [26]. This may suggest that participants preferred temporal
298 symmetry rather than the foot placement or velocity symmetry as a means of reducing metabolic
299 cost. This further suggests that participants adapted a newly learned motor pattern to a novel
300 condition in a way that was more efficient while meeting the demands of the novel environment,
301 all while saving their newly adapted motor pattern for washout during the subsequent condition.

302 Last, partial washout or persistent after-effects during Transfer and Washout could also be
303 caused by after-effects associated with different walking speeds between conditions [27]. The
304 contribution of speed to after-effect size has been demonstrated previously in both over-ground and
305 treadmill walking, with diminishing after-effects at both slower and faster speeds [10], [27]. In the
306 current study, we show robust after-effects during both Transfer and Washout—independent of
307 speed—with walking speed on the non-motorized treadmill being greater than the slow motorized
308 speed (0.8 m/s versus 0.67 m/s, $p < 0.05$). Moreover, we demonstrated no association between

309 Transfer and Washout after-effects, suggesting partial washout did not occur. Therefore, we reject
310 the hypothesis that persistent after-effects were a function of different walking speeds.

311 In conclusion, we demonstrated that temporal (but not spatial) control contributed to the
312 transfer of step length adaptation from motorized to non-motorized split-belt walking. One
313 implication is that the non-motorized system could help translate split-belt training into standard of
314 care because it has the advantage of being low cost, portable, and self-paced. A limitation of this
315 study is that we do not have the data to directly compare after-effects in over-ground transfer.
316 Further research is needed to investigate how non-motorized split-belt treadmills can be used in
317 clinical populations, and whether training on this device would lead to improved over-ground
318 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 transfer 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 indicates 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 during 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.

A **B**

A **B** **C**

Adaptation

Transfer

Washout