Enduring motor memory of walking on a split-belt treadmill in young children and adults

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Abstract

Background: Adults and children modify their motor program to accommodate persistent changes in movement conditions, called motor adaptation. We studied motor adaptation using a split-belt treadmill, with the belts for each leg at different speeds. A memory trace is reflected when reintroduction of the previously novel condition results in a smaller initial error in comparison to the first exposure. To date, retention of motor adaptation on a split-belt treadmill is only known for a 24 hour period.

Research question: We wondered if retention of split-belt adaptation extends over days and weeks, and whether it varies as a function of age.

Methods: We studied the persistence of the memory trace over 24 hours, one week, and two weeks, in young children (3-6 yr old), younger adults (20-30 yr old) and older adults (50-70 yr old).

Results: We found that retention of the memory trace declines with the interval duration, but was evident up to 2 weeks after initial exposure in all age groups. Retention of the motor memory in children and younger adults was better than older adults. Further, only older adults demonstrated forgetting between trials on a single day when a short break was introduced, but this forgetting was diminished with repeated trials.

Significance: The results indicate that long term memory of motor adaptation is affected by age, but it may be possible to enhance the memory in older adults by repeated exposure. For clinical practice, this may mean that older adults need more repetition when learning walking-related motor skills.

Keywords: motor adaptation, locomotion, human

Introduction

Motor memory from skills mastered during childhood, such as riding a bicycle, endure a life-time, even when the skills are rarely re-experienced in adulthood. In contrast, new motor learning is less enduring in older adults, such as with sequence learning in a serial reaction time test (1-3), visuomotor tracking (4), and in a ballistic task (5).

Motor adaptation, a form of motor learning that modifies a well learned motor program to persistent changes in the environment (6), is also affected by age. Children adapt at a slower rate than younger adults (7-9), which may confer children with better retention (10). Older compared to younger adults had more variable adaptation rates (11-17). Interestingly, the slower rate of adaptation in older adults has been linked to a decline in cognitive resources (17, 18), and reduced volume in the striatum, prefrontal and sensorimotor cortical areas (19).

Motor adaptation involves a number of memory processes, including modification of an internal model (20), and other model-free processes (21, 22). Memory of motor adaptation has been quantified in two ways – retention and savings. Retention is defined as a smaller movement error when exposed to a previously learned adaptation (23, 24), while savings is a faster rate of relearning after a period of washout (25). Interestingly, retention is evident by the age of 6 years, whereas savings is not seen until 12 years (26). Savings, but not retention, has also been linked to 'model free' mechanisms of motor memory (21, 22).

Here, we focus on age-related retention of split-belt adaptation over days and weeks, in young children, younger and older adults. Long-term retention of motor adaptation has not been documented, and is relevant to its usefulness in motor rehabilitation (27). We used the split-belt paradigm, because it is a novel task for adults and children alike, and it is not dependent on visual acuity or muscle strength, both of which may vary with age.

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MATERIALS AND METHODS

Participants

Participants had no known health problems that would interfere with motor learning, and were naïve to split-belt walking. Children (3-6 yo), young adults (20-30 yo) and older adults (50-70 yo) were recruited. We chose young children because their slow time course of learning may offer an advantage for retention (24), young adults because their adaptation is well known, and older adults because there is evidence for within-session forgetting (17). The small age range for children was to minimize the variability associated with development (9). Adult participants and a parent/guardian of children gave informed, written consent. Verbal assent was obtained from the children at the time of the experiments. The Health Research Ethics Board, University of Alberta, approved the study (Pro00043622). There was no prior information regarding possible differences between groups. Thus, sample size was based on a prior publication of age-related differences in split-belt walking (9).

Experimental Protocol

Participants were tested on 2 days, separated by 24 hours, 1 week or 2 weeks (Figure 1). The allocation of participants to intervals was partly determined by participant availability, but was otherwise random.   On Day 1, two tied-belt trials (belts at the same speed) were followed by 5 split-belt trials (speed ratio 2:1) (Figure 1). Trials were 3 min, separated by a 1 min standing break. The trial length was to accommodate children, who were more amenable to multiple short bouts rather than continuous walking. Because some adults exhibit surprise when first exposed to split-belt walking, resulting in an exaggerated initial error (25), a 'surprise' trial of no more than 5 seconds was inserted between the two tied-belt trials (25). Children do not display 'surprise', so this was not inserted for them (8, 9). On Day 2, participants started with 5 split-

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belt trials to determine their retention of the adaptation, followed by 2 tied-belt trials to quantify the aftereffect.

A Woodway split-belt treadmill (Woodway USA Inc., Waukesha, WI) was used. Adults used a tied-belt speed of 0.7m/s, and split-belt speeds of 1.4 m/s and 0.7 m/s. The speed of the tied-belt trials was set according to leg length for children, with the distance from the greater trochanter to the lateral malleolus (meters) providing the speed in meters/s (9); the speed ratio was 2:1 for the split-belt trials. The leg on the fast belt was chosen randomly on the first day, and then held constant for subsequent measures.

For safety, all participants held a front handrail and an adult spotter stood behind the children. All participants watched a movie of their choice during walked. Adults were instructed not to think about their walking, while children were asked questions about the movie to divert their attention from walking.

Instrumentation

Infrared emitting markers (Northern Digital Inc., Waterloo, ON) were positioned bilaterally at the top of the pelvis directly above the hip, the greater trochanter, the knee joint line, the lateral malleolus, and the head of the 5th metatarsal. Two 3-D Investigator motion sensors on each side of the treadmill captured the positions of the markers using NDI First Principles software. In addition, all trials were recorded with a video camera for quality control. A timer synchronized the video image with the marker data.

Data Analysis

Video recordings were used to exclude steps in which the participant was not stepping with one foot on each belt. We focused on step length symmetry, because step length is a global

measure of spatial and temporal adaptation on the split-belt treadmill (9). Custom MatLab (The Mathworks Inc., Natick, MA) code was used to analyze the data. Step length was defined as the antero-posterior distance between the ankle markers of each leg at the time of heel strike of the slow (SL_s) and fast (SL_f) leg, respectively. Step symmetry (SS) was the normalized difference between the fast and slow step length:

$$SS = \frac{SL_f - SL_s}{SL_f + SL_s} \quad \text{...... (1)}$$

A negative step symmetry means the slow step was longer than the fast step. Participant data were smoothed using epochs of 9-step averages, arbitrarily chosen as a compromise between the fast and slow time courses of learning in adults and children, respectively. The data were then averaged across participants within each age group and time gap.

Since 3 to 6 years old children do not always show adaptation (9), we first determined if there was evidence of adaptation in each child. A standard t-test was used for Day 1 data to determine if the average step symmetry of the last split-belt trial was significantly more positive than the first split-belt trial ($p<0.05$). The same test was used on the adult trials for comparison. In addition, presence of an after-effect on Day 2 was confirmed by the average step symmetry of the first 10 steps on the tied-belt being more positive than the last 30 steps on the split-belt (standard t-test). If both of the above comparisons showed no differences, indicating absence of learning, the child was removed from further analysis.

The differences in the time course of adaptation on Day 1 between the age groups were determined by collapsing the data across the 3 gap durations for each age group. This was justified since there were no significant differences in age between the participants with different gap periods.

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Step symmetry during specific times were of interest. Baseline symmetry was the average from all steps in the second tied-belt trial on Day 1, reflecting walking symmetry prior to the split-belt trials. The initial error on the split-belt for Day 1 (IE_1) was the average of the first 9 steps on the split-belt. The final error on Day 1 (FE_1) was the average of the last 30 steps on the split-belt (25). Initial error on Day 2 (IE_2) was the average of the first 9 steps on the split-belt. Forgetting between Day 1 to Day 2 was the difference between the initial error on Day 2 and the final error on Day 1, with negative values indicating forgetting (Forgetting = IE_2 - FE_1). The aftereffect (AE_2) was the average of the first 9 steps of the tied-belt on Day 2 immediately following the split-belt trials.

Forgetting between trials on Day 1 was the difference between the average of the 9 steps just before and just after a break. Only the adults were considered in this comparison, as the variability in children is likely to mask any real differences between trials.

Statistical Analysis

One-way ANOVAs were used to compare the ages between participant groups within the same gap interval. Because there were no age differences within each age group, the time course of adaption on Day 1 was collapsed across different gap durations within each age group. This data were then modeled by a mixed, linear regression model to compare participants in the different age groups using the log likelihood ratio test. In addition, we used the Akaike Information Criteria (28) to determine if a linear or exponential model provided a better fit of the time course for each age group.

Two-way ANOVAs (factors: age group and gap interval) determined the differences between the groups in: 1) baseline stepping symmetry, 2) initial error when first exposed to the split-belt (IE_1), 3) after-effect (AE) in Day 2, and 4) forgetting between Day 1 and Day 2.

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Within-day forgetting for Day 1 was compared between the younger adults and older adults using a mixed model ANOVA (between-subject factor: age group, and within-subject factor: breaks). Within-day forgetting for Day 2 was analyzed in the same way. A significant difference was set at $p<0.1$ for all comparisons to avoid Type II errors with the small number of participants per group.

Results

Seventy-four volunteers (31 children, 21 younger adults, 22 older adults) participated in the study. Data from one child were eliminated from analysis because of an absences of motor adaption. See Table 1 for participant numbers, sex and age in each group.

All participants completed the trials except for one child, who did not want to continue after 4 split-belt trials on Day 1; this same child completed all trials on Day 2. This child's data was included for analysis.

Similarities between the groups

The age of the participants within each age group were not different from each other (Table 2, Age). Symmetry of walking with tied-belts on Day 1 was the same for all 9 groups (Table 2, Baseline step symmetry). Initial error on the split-belt on Day 1 was the same between groups (Table 2, SB Initial error), indicating all groups were equally perturbed by the split-belt.

Time course of adaptation and overall learning

The time course of adaptation during split-belt walking on Day 1 for each age groups shows the effect of age on the initial adaptation (Figure 2). The time course is truncated at the lowest number of total steps obtained (i.e., the number of steps from the child who completed 4 instead of 5 split-belt trials). All groups showed a reduction in step asymmetry over time, with

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the children showing a slower time course and more variability compared to the adults. The best fitting model for all age groups was a linear model. The age groups were significantly different from each other, with children being different from younger adults [log ratio(LR) chi2 (62)=462.65, prob=0.0000] and older adults [LR chi2(62)=180.36, prob=0.0000], but younger and older adults were not different from each other [LR Chi2(62)=-282.29, prob=1.000]. The aftereffect on Day 2, a reflection of overall learning over the two days, was the same across all age groups and time gaps (Table 2, Day 2, Aftereffect).

Forgetting between Day 1 and Day 2

The time course of split-belt adaptation is superimposed for each of the groups on Day 1 and Day 2 in Figure 3. All groups showed evidence of retention on Day 2, as reflected by the starting steps on Day 2 (orange) being less asymmetric than the starting steps on Day 1 (blue). The smaller initial error on Day 2 led to all groups achieving symmetric walking sooner on Day 2 compared to Day 1. The forgetting between days is shown in bar graph form (Figure 3, bar graph),

Statistical tests of forgetting were not significantly different for the age x gap interaction (Table 2, Forgetting, Day 1 to Day 2). Thus, 1-way ANOVAs were used to examine the main effect of age collapsed across gap durations, and main effect of gap duration collapsed across age. Only a significant effect for age was observed (Table 2, Forgetting, Day 1 to Day 2).

Forgetting between trials within a day

Data from younger and older adults of different gap durations on Day 1 were combined to examine the effect of age, since Day 1 was the same for everyone. Figure 4 shows the step symmetry before and after each break, together with the initial 9 steps on the split-belt. Statistical comparison of the forgetting within Day 1, represented by the difference between the

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average of the 9 steps immediately after a break minus the average of the 9 steps immediately before the break, showed older adults forgot significantly more than the younger adults (mixed model ANOVA with repeated-measures over breaks, and between-subject factor of age). There was no interaction, but a significant main effect of age (Table 2, Forgetting, Within Day 1). Post-hoc test using one-way repeated measures ANOVA for each age group indicated the older adults showed a significant effect of breaks, whereas the younger adults did not (Table 2, Forgetting, Within Day 1, post-hoc). Further pairwise comparisons for the older adults using paired t-tests indicated the differences were between the first break and all the others (p=0.052, 0.023, 0.023, for Break 1 vs Breaks 2, 3 and 4, respectively), whereas Break 2 through 4 were not different from each other (p=0.857, 0.140, 0.171, for Breaks 2 vs 3, 2 vs 4 and 3 vs 4, respectively). Forgetting between trials was not examined for Day 2 because of the low statistical power resulting from the smaller number of participants in each group.

DISCUSSION

The novel findings are retention remains strong for children and younger adults after a 1- and 2-week interval from the first exposure, whereas older adults had forgotten significantly more. Further, within the first day of split-belt adaptation, older adults forgot more than younger adults between trials, but this within-day forgetting was short-lived, and only evident between the first and second trial on Day 1. Contrary to our original expectation, young children were no better than younger adults at retention, at least up to a 2-week interval after first exposure.

Characteristics of adaptation in children

The rate of adaptation on Day 1 was considerably slower in children compared to adults, confirming previous reports for split-belt adaptation (8, 9) and other forms of adaptation (7). The slower time course of split-belt adaptation may be related to the absence of a 'cognitive

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component' of learning, seen in adults (21, 22), since the fast time course of split-belt

adaptation can be interfered with by a concurrent cognitive task, especially in older adults (17).

Further, the fact that young children did not exhibit 'savings' 24 hours later (26) is also

consistent with an immature cognitive component of motor learning, since savings in other

forms of adaptation may result from a cognitive process of motor selection or retrieval (22, 29).

Endurance of the memory in all age groups

There was a trend for the greatest difference in memory between age groups to appear at 1-

week after initial exposure (Figure 3, bar graph). By 2 weeks, all groups have forgotten a

considerable amount, but still far from completely forgotten. We estimated the proportion of

forgetting by dividing the average initial asymmetry on the split-belt on Day 2 by the average

initial error on the split-belt treadmill on Day 1. Average forgetting at 2 weeks was 42%, 52%

and 67% for children, younger and older adults, respectively.

Forgetting in older adults

The forgetting in older adults within the first day of exposure confirms the earlier findings of

Malone and Bastian (17) that older adults forget between trials on the first day of exposure.

Some procedural differences between the two studies include the duration of each split-belt

trial, and the rest period between trials, both of which were considerably shorter in our study.

Thus, instead of five 3-min split-belt trials with 1 min rest between trials here, Malone and

Bastian used three 5-min trials with 5 min rest between trials. With the short rest between

trials and more repeated trials in our study, forgetting was only evident between the first and

second trials in older adults, whereas it was evident between both rest periods in the earlier

study. This suggests that with repeated exposure and shorter breaks, older adults may be able

to retain the learning better.   Indeed, retention of split-belt adaptation in adult participants

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after stroke, over 12 sessions of repeated practice, has shown about half of the participants can retain the learning, resulting in their over ground walking becoming more symmetric (27). Many of the participants in that study were over 50 years old, and whether a participant responded to the intervention did not appear to be age-related, although the number of participants was small. Overall, repeated practice may be one way to improve retention in older adults.

Limited evidence suggests acute, aerobic exercise may enhance subsequent motor learning and memory in persons with stroke (30) and Parkinson's disease (31). Finally, neuromodulation with non-invasive brain stimulation may also hold promise for improving certain types of motor adaptation in older adults (32), but its influence on motor memory remains to be seen.

Conflict of interest statement

All authors disclose no conflicts.

Tables

Table 1. **Participant numbers and ages from each experimental groups.**

Gap duration		24 hours	1 week	2 weeks
Kids	N (f)	12(6)	9(3)	9(3)
	Age (yr)	4.6±0.9	4.9±0.9	4.4±0.5
Young adults	N (f)	7(4)	7(2)	7(4)
	Age (yr)	23.5±3.7	24.0±2.0	25.6±2.3
Old adults	N (f)	7(4)	8(6)	7(4)
	Age (yr)	62.1±8.6	59.7±5.7	59.7±7.1

N is the number of participants contributing data in the group with the number of female (f) participants in parentheses. Age is represented by years (yr) with mean ± 1 SD.

Table 2. Statistical results.

Measure	Statistic	Results	Post-hoc
Age	1-way ANOVA	Gap: F=0.891, p=0.422 (children) Gap: F=1.110, p=0.351 (YA) Gap: F=0.267, p=0.769 (OA)	
Baseline step symmetry	2-way ANOVA	Age: F=0.92, p=0.274 Gap: 0.462, p=0.632 Interaction: 1.314, p=0.274	
Day 1			
SB Initial error	2-way ANOVA	Age: F=0.243, p=0.785 Gap: F=0.731, p=0.485 Interaction: F=1.326, p=0.270	
Day 2			
Aftereffect	2-way ANOVA	Age: F= 1.186, p=0.312 Gap: F=1.472, p=0.237 Interaction: F=1.550, p=0.198	
Forgetting			
Day 1 to Day 2	2-way ANOVA	Age: F=2.357, p=0.103 Gap: F= 0.203, p=0.817	1-way main effect age: F=2.645, p=0.078*

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		Interaction: F=0.543, p=0.705	1-way main effect gap: F=0.280, p=0.757
Within Day 1	Mixed model ANOVA	Age: F=2.978, p=0.092* Interaction: F=1.964, p=0.123	1-way RM ANOVA: YA: F=0.311, p=0.817 OA: F=4.524, p=0.006*

The results from all statistical comparisons are listed here. The measures included: Age measured in years, Baseline step symmetry was the average of step symmetry (see equation in **MATERIALS and METHODS, Data Analysis**) from all steps in the second tied-belt trial on Day 1. SB Initial error was the average of the first 9 steps of split-belt walking on Day 1. Aftereffect was the average of the first 9 steps of tied-belt walking on Day 2. Day 1 to Day 2 Forgetting was the difference in step symmetry between the first 9 steps of split-belt walking on Day 2 minus the SB Final error on Day 1. Within Day Forgetting was the difference in step symmetry between the first 9 steps after a break minus the last 9 steps before the break.
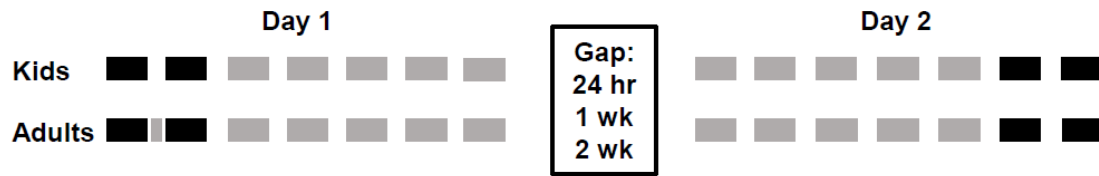
Figures

Figure 1. Experimental sequence. Each walking trial is represented by the solid horizontal bars. Black bars represent tied-belt trials and gray represent split-belt trials. All trials were 3 min long except the surprise trial of 5 strides, 5 seconds long, short gray bar between 2 tied-belt trials on Day 1. All participants experienced the same sequence of trials, with the exception of the surprise trial for adults only. Three gap durations between Day 1 and Day 2 were used for each of the age groups.
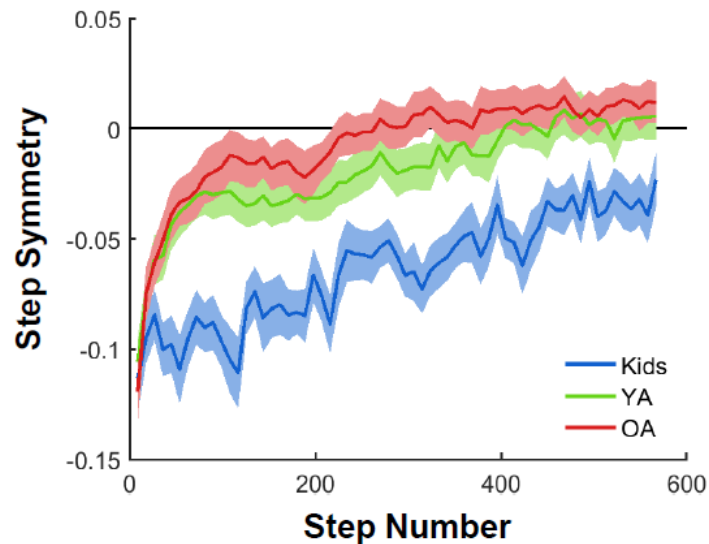

Figure 2. Time course of split-belt adaptation on Day 1. Average (9-step average) step symmetry is shown for the 3 age groups over the adaptation period of ~15 min. The age groups each contain data from n=30 for young children (Kids), n=21 for younger adults (YA), and n=22 for older adults (OA).
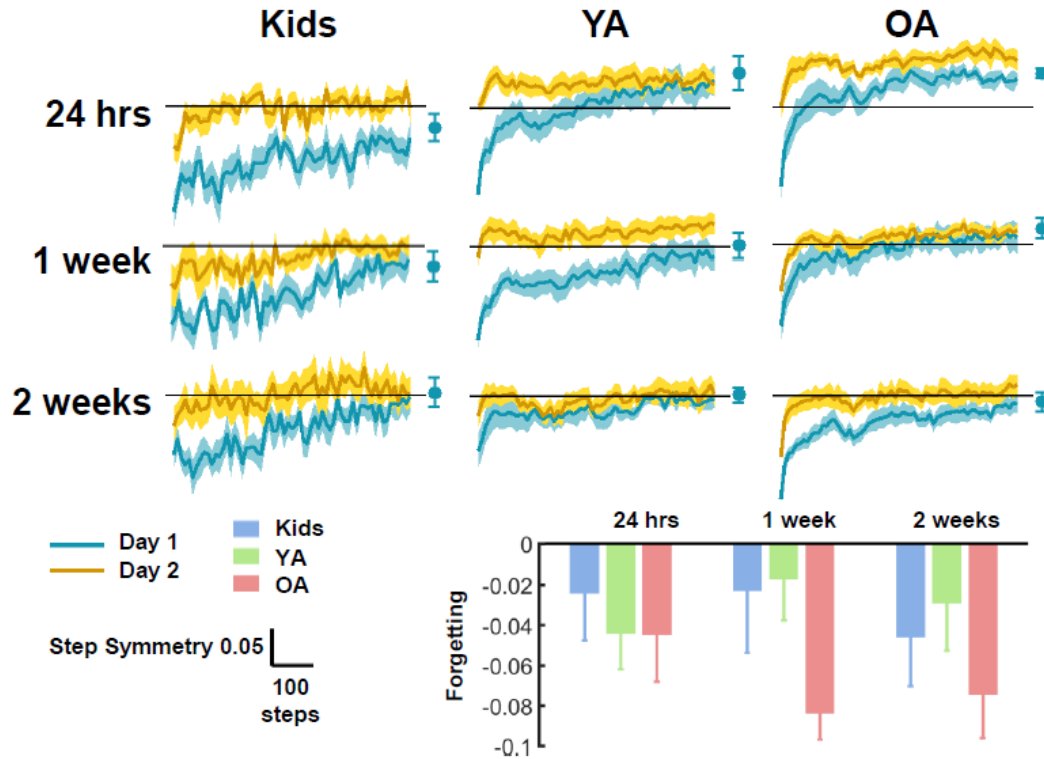
Figure 3. Average split-belt adaptation on Day 1 and Day 2 for each age group and gap durations. Adaptation is shown for 9 step averages across 567 steps, with the final step symmetry on Day 1 (average of last 30 steps, final error) shown as a blue symbol with ±1 SEM. The bar graph (bottom) shows the forgetting between the Initial Error on Day 2 minus the Final Error on Day 1. Means and 1 SEM are shown. Older adults (OA) showed more forgetting compared to the younger age groups (Kids and younger adults – YA). Abbreviations: Kids - children 3-6 y.o.; YA - younger adults, OA - older adults.
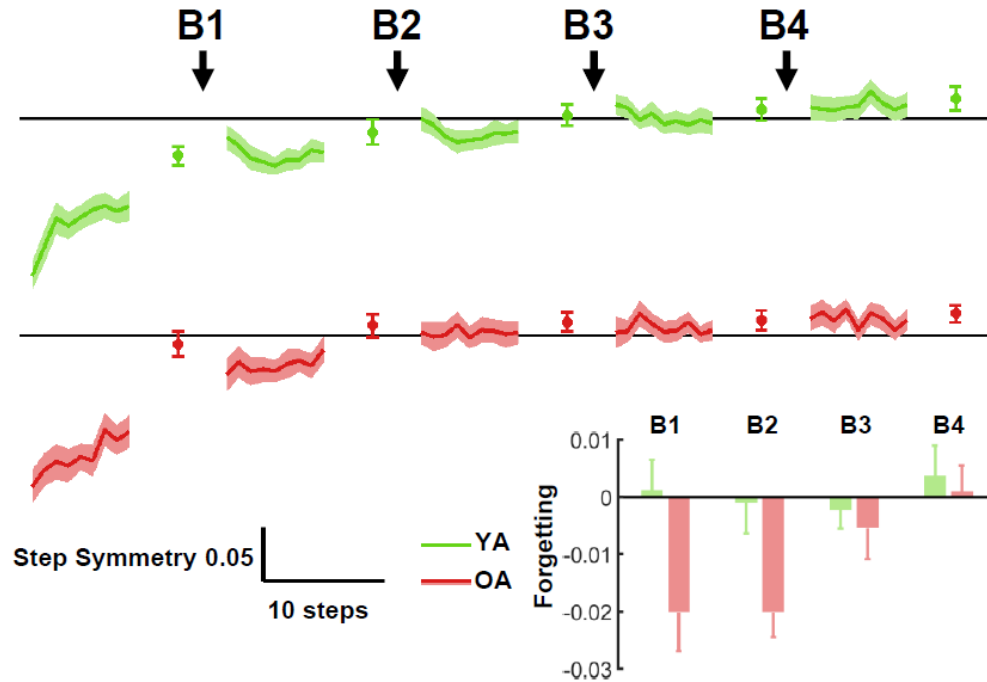
Figure 4. Forgetting between trials on Day 1. The step-by-step average step symmetry for each age group is shown for the first 9 steps on the split-belt treadmill, then the overall average of the last 9 steps before the breaks (B) and the step-by-step average of the first 9 steps right after the breaks, averaged across participants in each adult age group. The bar graph represents the quantified difference in forgetting between trials (forgetting = average of first 9 steps after break – average of last 9 steps before break). YA- younger adults, OA – older adults.

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