eNeuro

Research Article: New Research

Cognition and Behavior

Context-Specificity of Locomotor Learning Is Developed during Childhood

Dulce M. Mariscal,[1,2] Erin V. L. Vasudevan,[6,7] Laura A. Malone,[4,5,6] Gelsy Torres-Oviedo,[1,2,*] and Amy J. Bastian[3,6,*]

https://doi.org/10.1523/ENEURO.0369-21.2022

[1]Bioengineering Department, University of Pittsburgh, Pittsburgh, PA 15260, [2]Center for Neural Basis of Cognition, University of Pittsburgh, Pittsburgh, PA 15213, [3]Neuroscience Department, Johns Hopkins University, Baltimore, MD, 21205, [4]Neurology Department, Johns Hopkins University, Baltimore, MD, 21205, [5]Physical Medicine, and Rehabilitation Department, Johns Hopkins University, Baltimore, MD, 21205, [6]Kennedy Krieger Institute, Baltimore, MD, 21205, and [7]School of Health Technology and Management, Stony Brook University, Stony Brook, NY, 11794

Abstract

Humans can perform complex movements with speed and agility in the face of constantly changing task demands. To accomplish this, motor plans are adapted to account for errors in our movements because of changes in our body (e.g., growth or injury) or in the environment (e.g., walking on sand vs ice). It has been suggested that adaptation that occurs in response to changes in the state of our body will generalize across different movement contexts and environments, whereas adaptation that occurs with alterations in the external environment will be context-specific. Here, we asked whether the ability to form generalizable versus context-specific motor memories develops during childhood. We performed a cross-sectional study of context-specific locomotor adaptation in 35 children (3–18 years old) and 7 adults (19–31 years old). Subjects first adapted their gait and learned a new walking pattern on a split-belt treadmill, which has two belts that move each leg at a different speed. Then, subjects walked overground to assess the generalization of the adapted walking pattern across different environments. Our results show that the generalization of treadmill after-effects to overground walking decreases as subjects' age increases, indicating that age and experience are critical factors regulating the specificity of motor learning. Our results suggest that although basic locomotor patterns are established by two years of age, brain networks required for context-specific locomotor learning are still being developed throughout youth.

Key words: development; generalization; kinematics; locomotion; motor adaptation; motor control

Significance Statement

The generalization of motor learning from experienced situations to new ones is important for devising optimal rehabilitation programs. Little is known about how the motor system develops the ability to form generalizable versus context-specific motor memories. Here, we find that younger children generalize locomotor patterns to a much greater extent than older children and adults. These results are significant because they demonstrate that the ability to form context-specific locomotor memories develops during childhood.

Introduction

As we interact with the world, we learn how to shape our movements to optimally perform a task in the situation at hand. One form of motor learning is often referred to as adaptation and is driven by movement errors. Through practice, one learns to reduce errors and restore a more optimal movement pattern. When the perturbation is

Received August 10, 2021; accepted February 17, 2022; First published March 28, 2022.
The authors declare no competing financial interests.

Author contributions: E.V.L.V., L.A.M., A.J.B., and G.T.-O. designed research; L.A.M. and G.T.-O. performed research; D.M.M. contributed unpublished reagents/analytic tools; D.M.M. and G.T.-O. analyzed data; D.M.M., E.V.L.V., L.A.M., A.J.B., and G.T.-O. wrote the paper.

removed, people gradually unlearn the adapted movement. It is known that the mature motor system can generalize this type of learning to untrained movements within the same environment. For example, we can learn to counteract predictable visual or force disturbances during reaching and show some generalization to untrained reaches using the other arm (Sainburg and Wang, 2002; Criscimagna-Hemminger et al., 2003; Malfait and Ostry, 2004) or reaching in new directions (Krakauer et al., 2000; Thoroughman and Shadmehr, 2000; Donchin et al., 2003; Day et al., 2016). Generalization is not robust when moving outside of the training environment. This type of learning does not necessarily influence the exact same movement performed in other environments (Cothros et al., 2006; Kluzik et al., 2008). For example, adults adapt their walking on a split-belt treadmill that moves their legs at different speeds but switch back to their original gait (i.e., movements before split-belt adaptation) after a few steps of walking overground (Reisman et al., 2009; Torres-Oviedo and Bastian, 2010, 2012). This motor specificity is possible given contextual information specific to the training situation provided by sensory cues (Krouchev and Kalaska, 2003; Wada et al., 2003; Osu et al., 2004; Ahmed et al., 2008; Cothros et al., 2009; Ingram et al., 2010; Addou et al., 2011; Hirashima and Nozaki, 2012; Howard et al., 2013) or body-state cues (Gandolfo et al., 1996; Langan and Seidler, 2011; Howard et al., 2012, 2013, 2015; Torres-Oviedo and Bastian, 2012). Thus, contextual information about the environment as we acquire new motor patterns contributes to the context-specificity of encoded movements.

The specificity of movements across environments may also depend heavily on the ability to switch actions according to the context. Several studies have shown that healthy aging has an impact on the motor system's ability to transition between different context-specific motor memories (Bock, 2005; Bock and Girgenrath, 2006; Wang et al., 2011; Sombric et al., 2017; Sombric and Torres-Oviedo, 2021). For instance, older adults have greater difficulties switching between the split-belt and the regular walking patterns compared with young adults (Sombric et al., 2017; Sombric and Torres-Oviedo, 2021). Therefore, the generalization from one environment to another can be the by-product of slow switching (i.e., difficulty switching between locomotor patterns on environmental transitions). The ability to rapidly switch actions might require interaction with different environments and thus, it might be developed throughout childhood.

G.T.-O., E.V.L.V., L.A.M., and A.J.B. were supported by the National Institutes of Health (NIH) Grant HD048741; G.T.-O. was supported by the NIH Grant K01 NS092785-01A1; and D.M.M. was supported by the National Science Foundation Grant NSF-GRFP 1747452.

*G.T.-O. and A.J.B. contributed equally to this work.

Correspondence should be addressed to Gelsy Torres-Oviedo at gelsyto@pitt.edu.

https://doi.org/10.1523/ENEURO.0369-21.2022

There are few studies of generalization in young children compared with older children. In these studies, children were tested for generalization of a trained behavior to untrained movements within the same environment. Studies of a learned arm movement show reduced or absent generalization to the other arm in tasks like the Purdue Pegboard Test (De Almeida Batista et al., 2017), target pursuit (Byrd et al., 1986), visuomotor actions (Uehara, 1998), or throwing (Sidaway et al., 2012). In infants, environmental demands learned when crawling do not transfer to walking when performed in exactly the same environment (Kretch and Adolph, 2013). These studies suggest that young children link the learned behavior to the trained effector or action and do not generalize their learning to other movements within the same environment. This type of learning would lead young children to show greater generalization of a motor pattern adapted in one environment (e.g., split-belt treadmill) to a different environment (e.g., overground) compared with older children or adults. A recent study, however, has shown that children can form context-specific memories of the split-belt treadmill that are not degraded by performing the same movement in a different context (Musselman et al., 2016), raising the possibility that age does not impact generalization of walking across different environments. In this work, we explicitly addressed the question of whether human development altered the generalization of locomotor learning.

To test the effect of human development on the generalization of movements, we performed a cross-sectional study in which children walked on a split-belt treadmill or overground after acquiring a new walking pattern on the treadmill. Note that contrary to other developmental studies, we tested the same motor behavior (i.e., children walked in both situations) across environments that had different dynamics (i.e., split-belt treadmill vs overground). We chose to test the generalization of the split-belt learning because it has been shown to develop robust context-specific motor memories in adults (Reisman et al., 2009; Torres-Oviedo and Bastian, 2012) and children can acquire the split-belt walking pattern as young as two years old when they are proficient walkers (Vasudevan et al., 2011; Patrick et al., 2014).

Materials and Methods

Subjects

Thirty-five children (24 males and 11 females; aged 3.1–17.9 years; mean ± SD, 10.6 ± 4.2 years) and seven young adults (four males and three females; aged 19.6–31.5 years; mean ± SD, 25.5 ± 4.0 years) participated in this study. These subjects were divided into six age groups: 3–5, 6–8, 9–11, 12–14, 15–17 years old (y/o), and adults (>18 y/o). Characteristics of each group are shown in Table 1. The experimental protocol was approved by the Institutional Review Board at the Johns Hopkins University, and all subjects and/or their parent or legal guardian gave informed written consent before participating in the study.

Experimental setup and design

Participants adapted their walking pattern on a split-belt treadmill and we tested the transfer of this learning to

Table 1. Age group characteristics

Age group	Number of subjects	Number of females	Age range (years)	Mean ± SD (years)	Mean speeds (m/s; slow, fast)
3–5 y/o	7	2	3.1–5.9	4.7 ± 0.9	(0.49, 0.98)
6–8 y/o	7	2	6.5–9.0	7.9 ± 1.0	(0.79, 1.57)
9–11 y/o	7	2	9.4–11.0	10.5 ± 0.6	(0.75, 1.5)
12–14 y/o	7	2	12.4–14.3	13.3 ± 0.7	(0.88, 1.76)
15–17 y/o	7	3	15.1–17.9	16.3 ± 1.2	(0.95, 1.90)
Young adults (>18 y/o)	7	3	19.6–31.5	25.5 ± 4.0	(0.94, 1.89)

overground walking (i.e., off of the treadmill). Locomotor adaptation was achieved using a split-belt treadmill (Woodway USA) that drove the speed of each leg independently. This paradigm has been demonstrated to induce the storage of a modified walking pattern that is expressed as an aftereffect in "tied-belt" walking (i.e., legs moving at the same speed), and must be de-adapted to return to normal walking (Reisman et al., 2005). Participants were positioned in the middle of the treadmill, with one foot on each belt. A thin wooden panel was placed in between the two belts to ensure subjects would not step on the opposite belt when belts were moving at different speeds (i.e., split-belt condition). Participants of all ages held onto a front handrail adjusted to elbow height and wore a safety harness that did not support their weight during walking. All subjects watched TV while walking.

We recorded the motor behavior of all participants during baseline, adaptation, and postadaptation periods. Baseline and postadaptation were collected off and on the treadmill (Fig. 1*A*). We collected a baseline period before adaptation in which subjects walked with the belts moving together (i.e., "tied-belt" walking) at three different speeds: a slow, a fast, and an intermediate speed for 1 min each. Specifically, the slow speed was set equal to the participant's leg length in m/s, as done before (Vasudevan et al., 2011). Leg length was defined as the distance from the lateral malleolus to the iliac crest (i.e., in Fig. 1*B*, ankle and pelvis marker, respectively). Consequently, the slow speed ranged between 0.4 and 0.98 m/s. The fast speed was

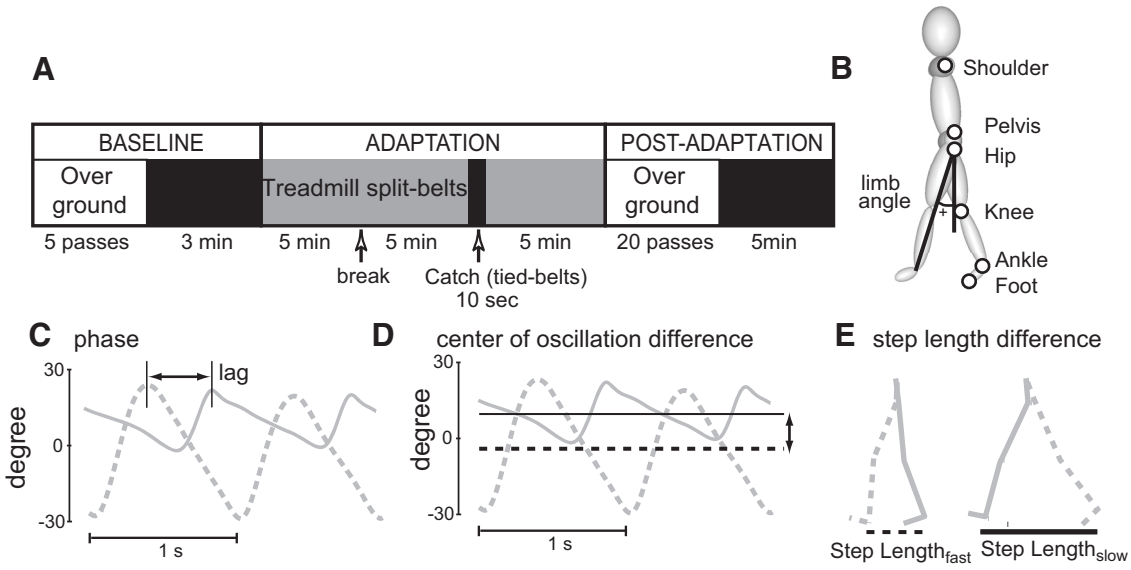

Figure 1. ***A***, Overall paradigm. In all groups, baseline behavior was recorded overground and subsequently on the treadmill. Then subjects were adapted for a total of 15 min divided into three blocks of 5 min each separated by a break. A 10-s catch condition was introduced when subjects had been adapted for 10 min. Aftereffects were also assessed overground after 5 min of re-adaptation to the split condition. Finally, subjects returned to the treadmill where they walked for 5 min to determine the washout of learning specific to the treadmill from the remaining aftereffects. ***B***, Diagram of marker locations. Limb angle convention is shown on the stick figure. ***C***, Limb angle trajectories plotted as a function of time in early split-belt adaptation; two cycles are shown. Limb angles are positive when the limb is in front of the trunk (flexion). Phase quantifies the lag producing the largest cross-correlation between the two legs. When the legs move in anti-phase, the lag of 0.5 leads to the largest cross-correlation. ***D***, Limb angle trajectories are shown in gray and angle axes about which each leg oscillates are shown in black. In this example, slow limb (solid line) oscillates more forward with respect to the vertical axis than the fast limb (dashed line). The center of oscillation quantifies the difference in where the legs oscillate, illustrated by the distance between two black lines. ***E***, An example of kinematic data of two consecutive steps is shown. Kinematic data for every two steps were used to calculate step symmetry, defined as the difference in step lengths normalized by the sum of step lengths.

Figure Contributions: Gelsy Torres-Oviedo created schematics for general paradigm and gait parameters.

equal to two times the slow speed and the intermediate speed was an average of the slow and fast speeds. We scaled walking speeds with this method to ensure subjects from all ages were perturbed similarly during the split-belt condition, when each belt was moving at the calculated slow and fast speeds (Vasudevan et al., 2011).

After baseline walking, subjects walked on the split-belt treadmill, where one belt moved at the slow speed and the other moved at the fast speed, for 15 min. During split-belt adaptation, we stopped the belts every 5 min to allow subjects to rest for ~1 min. After the first two 5-min split-belt treadmill blocks, we collected a 10-s "catch" condition during which both belts were moving together at the slow speed (i.e., slow, tied-belt walking). The recordings during this "catch" condition allowed us to assess storage of the adaptation effects (i.e., aftereffects) on the treadmill. Subjects then walked in the split-belt condition for the final 5 min to re-adapt the walking pattern. The treadmill was stopped and re-started again at every speed transition. After the entire adaptation period, subjects were transported on a wheelchair from the treadmill to a 6-m walkway, to prevent them from taking any steps outside the motion capture area. Subjects walked on the walkway for 20 back-and-forth passes to test for transfer to overground walking of aftereffects because of the split-belt treadmill adaptation. Subjects were asked to avoid stepping outside of the motion capture area so that we could record as many of their initial steps after split-belt treadmill adaptation as possible. The self-selected walking speeds in all subjects ranged between 0.35 and 1.1 m/s. After assessing overground transfer, subjects returned to the treadmill and walked for 5 min in the tied-belts condition at the computed slow speed. This last period allowed us to test for washout of the treadmill aftereffects because of overground walking. We chose to assess aftereffects on the treadmill during catch and washout periods at the slow belt speed since it has been shown to induce the largest aftereffects (Vasudevan and Bastian, 2010). We allowed participants to walk at their preferred overground walking speed since aftereffects during overground walking are minimally affected by speed (Hamzey et al., 2016).

Data collection

During all treadmill and overground walking, kinematic data were collected at 100 Hz using Optotrak (Northern Digital). Infrared-emitting markers were placed bilaterally over the following anatomic landmarks: foot (fifth metatarsal head), ankle (lateral malleolus), knee (lateral femoral epicondyle), hip (greater trochanter), pelvis (iliac crest), and shoulder (acromion process). Marker location is indicated in Figure 1*B*. The times of heel strike and toe-off (i.e., when the foot contacts and lifts off the ground) were recorded by foot-switches placed on the bottom of the shoes or were estimated from the ankle kinematic data. To avoid occlusion of the hip and pelvis markers during overground and treadmill walking because of arm-swing, participants walked with their arms crossed on the treadmill and overground, except for young children (less than six years old) who were unable to consistently maintain their arms crossed while walking. Thus, young children were instructed to walk walking holding a rail with both hand on the treadmill and overground while pushing a light (seven-pound) toy-shopping cart with adjustable rail height. All marker data were rotated to a reference frame centered on the subject's body with the fore-aft axis aligned to the individual's walking direction. This was done because younger children did not walk in a straight path during overground walking, which affected the step lengths' calculation when using the laboratory reference frame. Thus, we estimated each subject's walking direction in every stride as the perpendicular axis to the participant's frontal plane, which was computed using the hip and pelvis markers. We subsequently rotated the fore-aft axis to be aligned to this estimated walking direction. We used the same approach for all individuals and all strides overground and on the treadmill for consistency purposes.

Data analysis

Gait parameters

Temporal and spatial characteristics of gait that are known to adapt during split-belt treadmill walking were assessed (Malone and Bastian, 2010; Vasudevan et al., 2011). We specifically chose to characterize the generalization of gait parameters such as phase shift, center of oscillation, and step asymmetry to compare to prior generalization studies (Torres-Oviedo and Bastian, 2010, 2012) and developmental studies in split-belt walking (Vasudevan et al., 2011; Musselman et al., 2016). To quantify temporal gait features we used phase shift between the two legs. To this end, we computed the cross-correlation between limb angle trajectories during one full step cycle for each leg. Limb angle was defined as the angle between the vertical axis and the vector from hip to ankle on the *x-y* plane (Fig. 1*B*). Phase shift was the lag or lead-time for a maximum correlation between limb angle trajectories (Fig. 1*C*). A phase shift value of 0.5 would indicate that legs are moving in anti-phase. To correct for subjects' biases, we subtracted the phase shift during the baseline period from all other periods. Consequently, a reported value of 0 indicates that legs are moving in anti-phase, positive phase shifts indicate that the fast leg is phase advanced relative to the slow leg, and negative phase shifts indicate that the fast leg is lagging the slow leg.

To quantify spatial gait features we used center of oscillation difference, which is defined as the difference between angles of oscillation of each leg (Fig. 1*D*). The angle of oscillation is defined as the angle between the vertical axis (0° axis in Fig. 1*D*) and the axis about which the leg is oscillating, illustrated by the black dashed and solid lines in Figure 1*D*. A center of oscillation value of 0 would indicate that both legs are oscillating about the same axis, a positive value would indicate that the leg on the fast belt is oscillating about an axis that is forward to the one of the leg on the slow belt, and a negative value would indicate that the leg on the slow belt is oscillating about an axis that is forward to the one of the leg on the fast belt (Vasudevan et al., 2011). We subtracted the center of

oscillation values during the baseline period from all other periods to correct for subjects' biases.

Finally, we also quantified step symmetry which is defined as the difference between step lengths of the two legs, where step length is the distance between two ankle markers at the time of heel strike of the leading leg (Fig. 1*E*). This difference was normalized by the step lengths' sum to account for variations in step length across subjects of different leg lengths. A step length symmetry value of 0 would indicate that step lengths are equal, a positive value would indicate that the leg on the fast belt is taking longer steps, and a negative value would indicate that the leg on the slow belt is taking longer steps. Baseline subjects' biases were removed by subtracting baseline values from all other experimental periods.

Outcome measures

We characterized the subjects' adaptation and postadaptation behavior on the treadmill and overground with six outcome measures corresponding to different time-periods of the experiment: (1) adaptation before overground (Adapt; the difference between the average of first 5 and last 20 strides of the adaptation period); (2) aftereffects on the treadmill during the catch (TM_{catch}; first five strides of catch condition; (3) early overground aftereffects (OG_{early}; first five strides of overground postadaptation); (4) late overground aftereffects (OG_{late}; last 20 strides of overground postadaptation); (5) early treadmill aftereffects (TM_{early}; first five strides of treadmill postadaptation and after overground walking); and (6) late treadmill aftereffects (TM_{late}; last 20 strides of treadmill postadaptation and after overground walking). Note that we quantified aftereffects at the end of the postadaptation periods to determine whether subjects were fully washed out at the end of each postadaptation period.

Statistical analysis

We did a correlation analysis between the participants' age and each of our six outcome measures**:** Adapt, TM_{catch}, OG_{early}, OG_{late}, TM_{early}, and TM_{late}. The correlation analysis between Age and Adapt, or TM_{catch}, respectively, was done to determine whether age affected the extent of adaptation, as quantified by the change in gait parameters during adaptation and by the size of the treadmill aftereffects during the catch condition. Similarly, the correlation analysis between Age and OG_{early} or OG_{late} was done to identify age-related changes on the carryover of recalibrated movements from the treadmill (training context) to overground (testing context). Moreover, the correlation analysis between age and TM_{early} or TM_{late} was done to determine whether age influenced the washout of aftereffects on the treadmill by overground walking. Finally, we evaluated whether the variability in gait asymmetry during baseline was a predictor of the aftereffects overground. This was done with separate correlation between OG_{early} versus baseline variability for each parameter (i.e., phase shift, center of oscillation, or step symmetry). Variability was calculated as the variance during treadmill baseline walking for each measure. We used the steps during treadmill baseline, rather than overground baseline, to have a more robust characterization of each participant's variability given the relatively larger number of steps recorded during treadmill walking compared with overground walking. We also determined the association between age and step variability since these factors could be correlated.

In all correlation analyses, we used a Spearman's rank-order correlation. We used a non-parametric correlation because after testing for normality our outcome measurements fail to pass the Kolmogorov–Smirnov test, $p < 0.05$ as a measure of significance in all correlation.

Power analysis

The primary focus of this study was to test the hypothesis that age influences the generalization of movements from the treadmill to overground. A power analysis based on our previously published data (Sombric et al., 2017; Sombric and Torres-Oviedo, 2021) indicated that an estimated sample size of $n = 11$ would identify a one-sample side correlation coefficient of $r = 0.71$ with a power of 0.8. Thus, $n = 35$ would be sufficient to identify a significant correlation between age and generalization.

Results

All children adapted their gait during split-belt walking

We found that participants of all ages adapted their gait on the split-belt treadmill; however, younger children did so more slowly. Figure 2*A* shows time courses during the adaptation period (split-belt condition) for all age groups. We observed that younger children adapted slower than adults as reported before (Vasudevan et al., 2011). This age-mediated effect is, for example, qualitatively shown by the slower adaptation of 9–11 years old (light green trace) compared with +18 years old (dark green trace). Consistently, younger subjects adapted less over the same period of split-belt walking than young adults. This is indicated by a significant positive association between age and the extent to which participants adjust their gait before overground walking (Adapt) for phase shift (Adapt: $r_s = 0.389, p = 0.014$) and step length asymmetry (Adapt: $r_S = 0.43, p = 0.005$; Fig. 2*B*). On the other hand, we did not observe an age effect in the adaptation of the center of oscillation (Adapt: $r_s = 0.26, p = 0.10$). Of note, we observed negative Adapt indices in a couple of youngest participants because their large step-to-step variability in spatial parameters (step length asymmetry and center of oscillation) made it difficult to quantify their initial adaptation values. Thus, these negative indices represent large step-to-step variability in these youngest subjects, rather than an increment in asymmetric stepping during the adaptation period. In other words, subjects from all ages were able to adapt their gait, but younger individuals did so to a lesser extent before we measured their aftereffects overground.

While all subjects recalibrated their gait similarly, younger children transfer their adapted movements more

Age did not modulate the aftereffects on the treadmill (TM_{catch}) after split-belt walking. This indicates that all subjects, regardless of their age, were able to recalibrate their

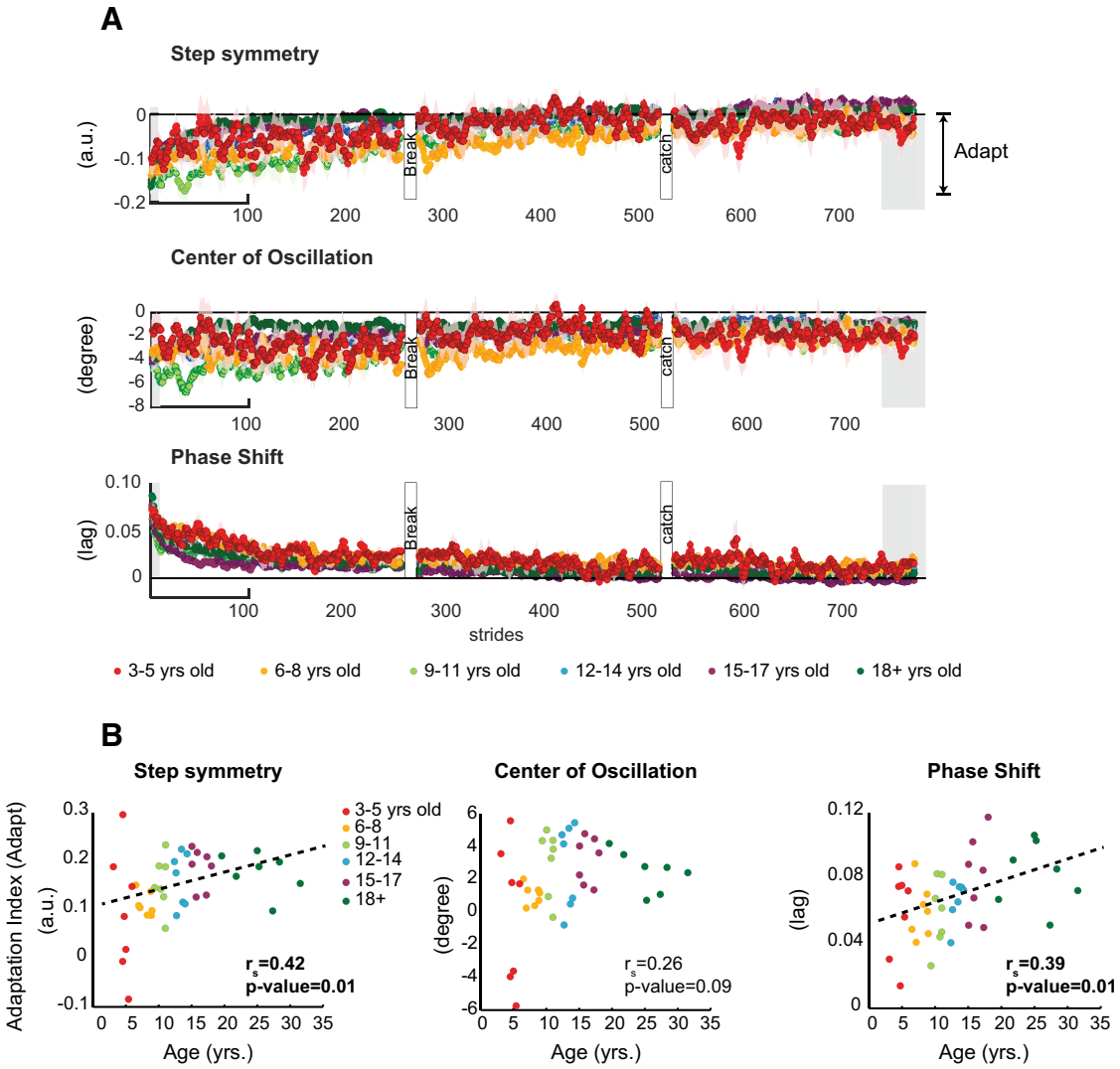

Figure 2. ***A***, Time courses for gait parameters characterizing the behavior during split-belt walking of all age groups. Every dot represents the group average of five strides and color shaded areas indicate standard error (SE). Children adapted their gait more slowly during the split-belt condition. For visualization purposes, gray background indicates the strides used for computing Adapt, used in the scatter plots in panel ***B***. ***B***, Correlation results of Age versus Adapt before overground walking. Adapt quantified the extent to which subjects changed their gait during the adaptation period. Large numbers indicate more adjustments during split-belt walking. Dots indicate individual subjects' data and colors indicate subjects age groups. We found a significant effect of age in phase shift and step length asymmetry, indicating that younger subjects adapted less over the same period of split-belt walking than older children or young adults. This effect is not observed in the center of oscillation, which is a more variable parameter. Dotted line is shown as reference for a linear regression. Arbitrary units (a.u.).
Figure Contributions: Gelsy Torres-Oviedo, Erin Vasudevan, and Laura Malone performed the experiments. Dulce Mariscal and Gelsy Torres-Oviedo analyzed the data.

locomotor pattern on the treadmill. Figure 3*A* shows the time courses of the treadmill aftereffects during the catch for all age groups. Note that all the curves overlap. Accordingly, we found that age was not a strong predictor of individuals' TM_{catch} values for step symmetry ($r_s = 0.02, p = 0.92$), center of oscillation ($r_s = 0.03, p = 0.84$), or phase shift ($r_s = 0.010, p = 0.95$; Fig. 3*B*). Recall that TM_{catch} quantifies the magnitude of aftereffects during the catch condition, and it is used to assess sensorimotor recalibration in the training context. In sum, kids were slower to adapt their gait, but they all experienced similar sensorimotor recalibration, as shown by the similar aftereffects during the catch condition after split-belt walking.

While subjects had similar aftereffects on the treadmill, we found that age strongly modulated the transfer of adapted movements from the treadmill to overground walking. Figure 4*A* shows the time courses of overground aftereffects. The youngest participants (red trace) appear to take a few steps overground before exhibiting large aftereffects in center of oscillation and step length asymmetry. However, this odd transfer pattern should be interpreted with caution since it was driven by two outliers. Figure 4*B* indicates the initial five strides recorded overground for individual subjects of all ages. Note the larger aftereffects in younger subjects for phase shift, which is reflected in the significant relation between age and

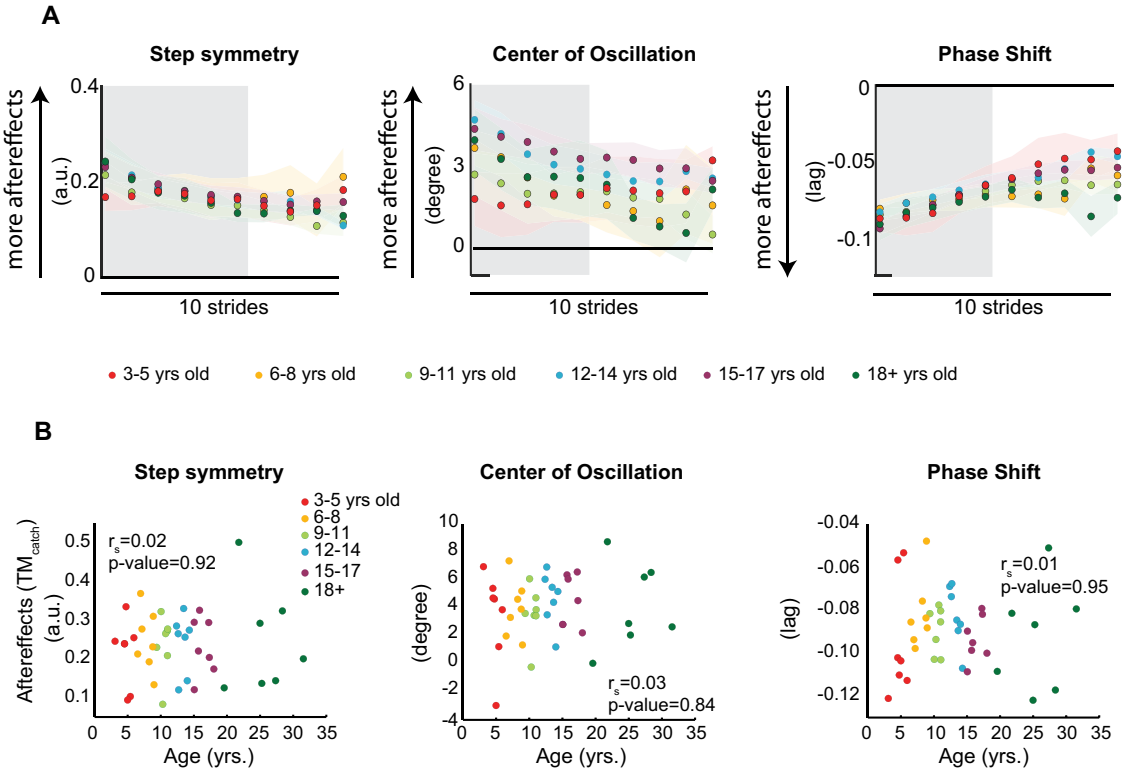

Figure 3. ***A***, Time courses during catch condition for two age groups. Every dot represents the group average of five strides and color shaded areas indicate SE. Gray area indicates the strides used for the regression analysis displayed in panel ***B***. ***B***, Correlations results of Age versus aftereffects on the treadmill during the catch trial (TMcatch); *y*-axis indicates the magnitude of aftereffects on the treadmill TM_{catch} for each individual; *x*-axis indicates the age of each participant at the time of the experiment. Dots indicate individual subjects' data and colors indicate subjects' age group. We did not find an age effect indicating that all individuals recalibrated their movements after split-belt walking. Arbitrary units (a.u.).
Figure Contributions: Gelsy Torres-Oviedo, Erin Vasudevan, and Laura Malone performed the experiments. Dulce Mariscal and Gelsy Torres-Oviedo analyzed the data.

OG_{early} values ($r_s = 0.61, p = 2.3x10 - 5$). This indicates that the transfer of aftereffects across walking environments rapidly decreases as subjects' age increases. This age effect was also observed in step symmetry ($r_S = -0.61, p = 2.9x10 - 5$) and center of oscillation ($r_S = -0.33, p = 0.03$). Interestingly, this effect was maintained after ~200 steps of walking overground on step length asymmetry ($r_s = -0.34, p = 0.03$) and phase shift ($r_s = 0.40, p = 0.01$). The relation between age and aftereffects is not observed during the late steps of center of oscillation ($r_s = -0.24, p = 0.12$; Fig. 4*C*). Thus, age modulated overground aftereffects and young children were still walking with asymmetric step lengths and asymmetric timing between the legs right before they returned to the treadmill.

All children develop a motor memory specific to the treadmill

We also observed an age effect on the washout of treadmill aftereffects by overground walking. Figure 5 shows the magnitude of remaining aftereffects on the treadmill following overground walking (TM_{early}) versus Age for each parameter. Note that aftereffects are larger in younger individuals for step length asymmetry ($r_s = -0.46, p = 0.002$), but not in center of oscillation ($r_s = -0.27, p = 0.08$) or phase shift ($r_s = 0.1, p = 0.52$). Larger persistent aftereffects were are observed during late postadaptation for the younger individuals (TM_{late}; data not shown; step symmetry: $r_S = -0.48, p = 0.001$; phase shift:$r_s = 0.39, p = 0.01$; center of oscillation: $r_s = -0.36, p = 0.02$), indicating that younger adults have not fully de-adapted at the end of the postadaptation period.

Young children that are intrinsically more variable transfer more

We observed that subjects who had more variability in their walking tended to have larger aftereffects during overground walking. Figure 6 shows the observed OG_{early} values as a function of variance in step symmetry (left panel), center of oscillation (center panel), and phase shift (right panel) during baseline for each subject. Our regression analysis indicated that baseline variability was associated with the transfer of adaptation effects in step length symmetry ($r_s = 037, p = 0.03$) and phase shift ($r_s - 0.64, p = 5.17x10 - 5$), but not center of oscillation ($r = 0.17, p = 0.32$). This indicates that individual variability in each participant's asymmetries could regulate the extent to which subjects transfer adapted movements across different environments. Note, however, that younger kids are also more variable than older kids. This is indicated by the

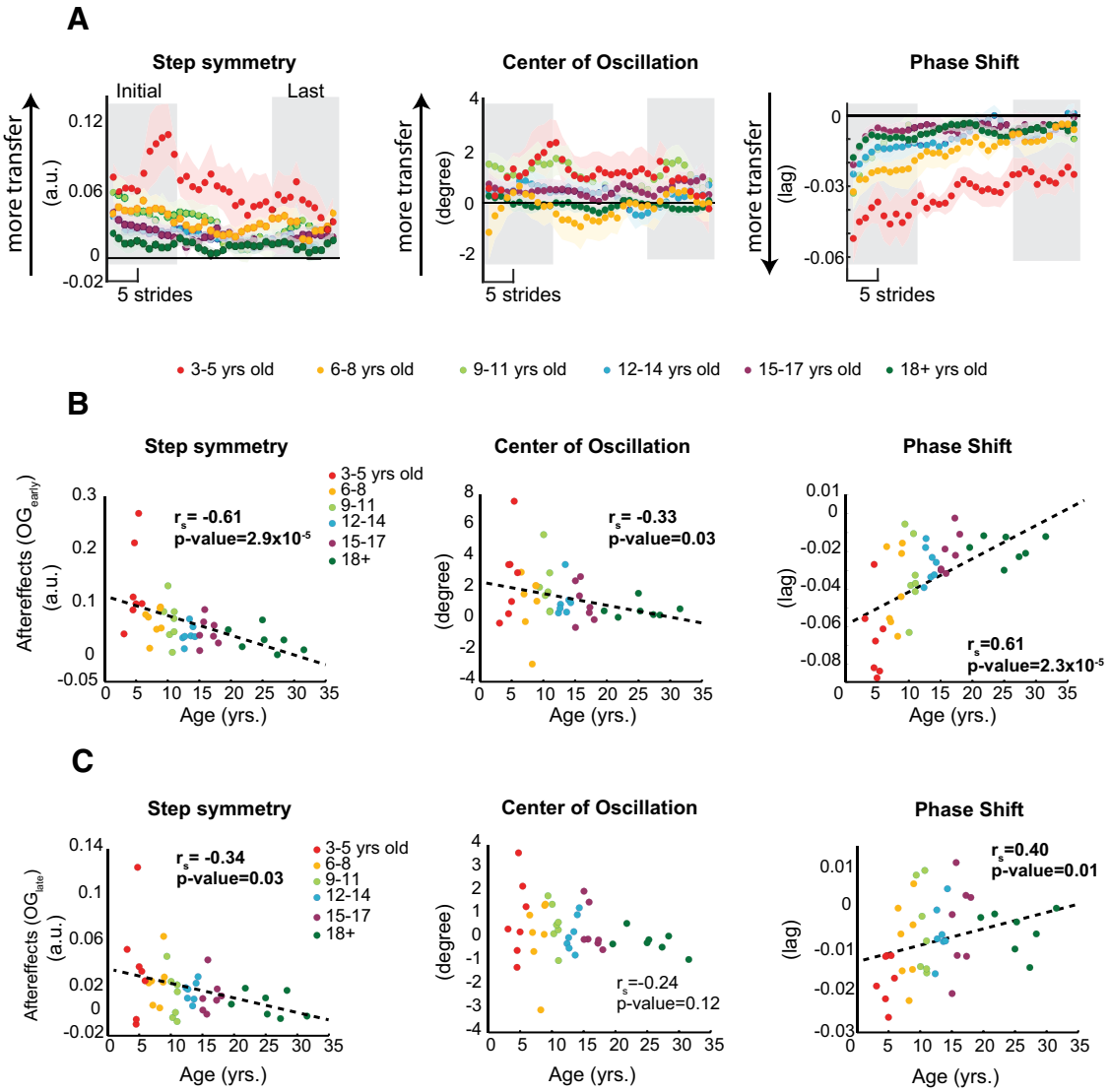

Figure 4. ***A***, Time courses during over ground walking for two age groups. Every dot represents the group average of five strides and color shaded areas indicate SE. Gray area indicates the strides used for the regression analysis displayed in panels ***B***, ***C***. ***B***, ***C***, Regression analyses showing the relation between age and aftereffects during the initial OG_{early} (panel ***B***) and the last OG_{late} (panel ***C***) steps of the post-adaptation period overground in all kinematic parameters. Dots indicate individual subjects' data and colors indicate the different age groups. Age was a significant predictor of OG_{early} and OG_{late} in all step length asymmetry and phase shift, such that younger subjects exhibited greater aftereffects overground than older children and young adults. Dotted line is shown as reference for a linear regression. Arbitrary units (a.u.).

Figure Contributions: Gelsy Torres-Oviedo, Erin Vasudevan, and Laura Malone performed the experiments. Dulce Mariscal and Gelsy Torres-Oviedo analyzed the data.

association between subjects' age and the variability associated with their step symmetry ($r_S = -0.82, p = 2.18x10-7$), center of oscillation ($r_s = -0.86, p = 4.42x10-8$), and phase shift ($r_s = -0.85, p = 7.25x10-8$;Fig. 6*B*). Thus, while motor variability during baseline and transfer appears to be positively related, this association might simply be the by-product of the relation between baseline variability and age.

Discussion

Younger children generalize a newly learned walking pattern from the training environment (i.e., a split-belt treadmill) to an untrained environment (i.e., overground walkway) to a greater extent than older children and adults. We also found that differences in movement variability with age were correlated to differences in generalization, suggesting that movement variability in young subjects might play a role in the generalization of their learning across contexts. Finally, we found larger remaining aftereffects in younger than older children or adults when subjects returned to the treadmill after overground walking. While this was surprising because we would expect that the younger children who generalized more would also wash out more of the learned treadmill pattern, it could be explained by the fact that younger individuals

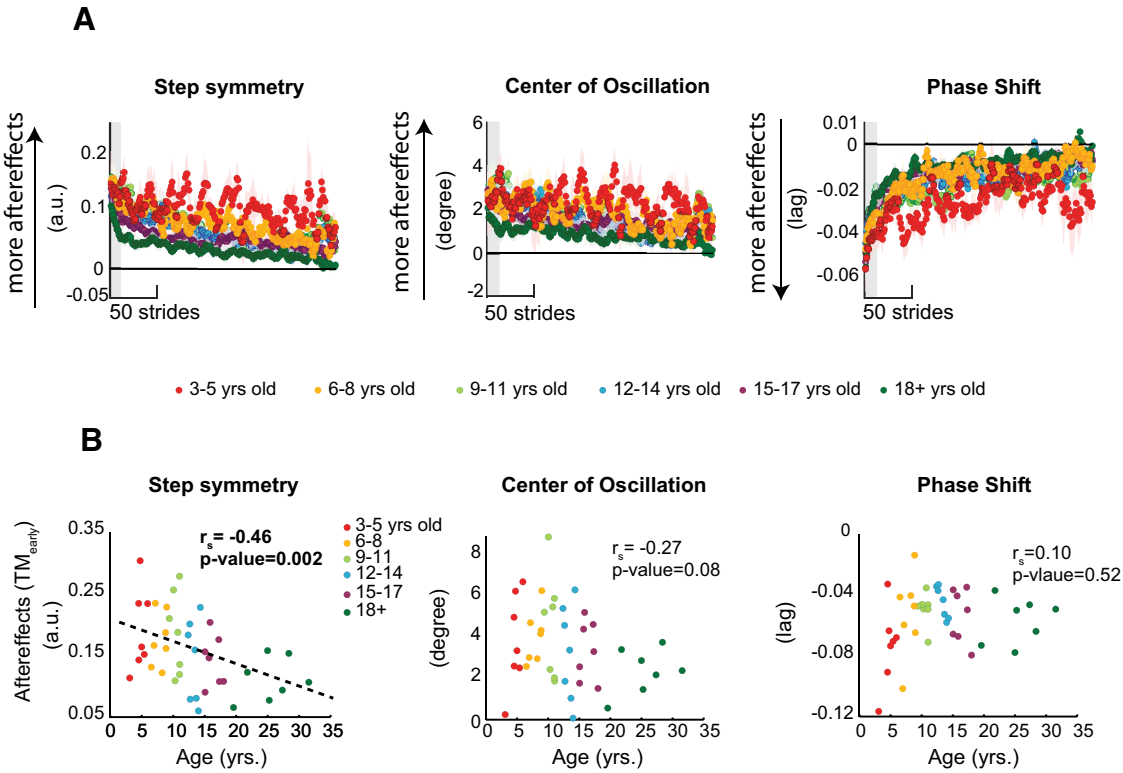

Figure 5. ***A***, Time courses during treadmill walking postadaptation for two age groups. Every dot represents the group average of five strides and color shaded areas indicate SE. Gray area indicates the strides used for the regression analysis displayed in panels ***B***. ***B***, Correlations analyses showing the relation between age and aftereffects during the initial TM_{early} steps of the postadaptation period on the treadmill in all kinematic parameters. Colors indicate the different age groups. Dots indicate individual subjects' data. Age was a significant predictor of TM_{early} in all step length asymmetry, such that younger subjects exhibited greater aftereffects overground than older children and young adults. Dotted line is shown as reference for a linear regression. Arbitrary units (a.u.).
Figure Contributions: Gelsy Torres-Oviedo, Erin Vasudevan, and Laura Malone performed the experiments. Dulce Mariscal and Gelsy Torres-Oviedo analyzed the data.

are not fully de-adapted overground before they returned on the treadmill.

Differences in generalization throughout childhood

Motor adaptation is a form of short-term learning that is induced by movement errors. Through trial-and-error practice, one learns to reduce errors and restore a more optimal movement pattern. One possible explanation for the generalization pattern that we observed following split-belt treadmill adaptation is related to error attribution during learning. Errors (i.e., perturbed movements) experienced in novel situations represent one contextual cue that might mediate the generalization of learning (Berniker and Kording, 2008; Torres-Oviedo and Bastian, 2012). It is thought that the motor system classifies errors as externally-generated or self-generated (Synofzik et al., 2006; Wilke et al., 2013). This classification affects both the extent of learning (Sober and Brainard, 2012; Kelly and Sober, 2014)and pattern of generalization (Berniker and Kording, 2008; Torres-Oviedo and Bastian, 2012). If errors are classified as externally-generated, the motor system associates learned movements to the environment, in this case, the treadmill. Consequently, the learning experience will impact untrained movements within the training environment, but the same motor behavior (e.g., walking) will remain unchanged when performed in other environments. Conversely, if errors are classified as self-generated, the motor system ties these corrections to the trained movement itself; thus, updated movements will generalize to other environments. This framework suggests that the generalization of learning is tightly coupled to the motor systems' ability to recognize externally-generated versus self-generated errors accurately. Therefore, young children might generalize more than older kids or adults because error attribution matures as we develop.

Furthermore, young children's variability might regulate their error attribution. Previous work suggested that people who are naturally more variable will generalize more because more of their errors during training will fall within the larger range of errors they normally experience (Torres-Oviedo and Bastian, 2012). Interestingly, we found greater variability in children's walking behavior, which increases the possibility of attributing errors during split-belt walking to their own faulty movements and therefore generalizing more across different environments. It should also be noted that this idea is not unique to human behavior. For instance, it has been shown that young birds, compared with adult birds, compensate

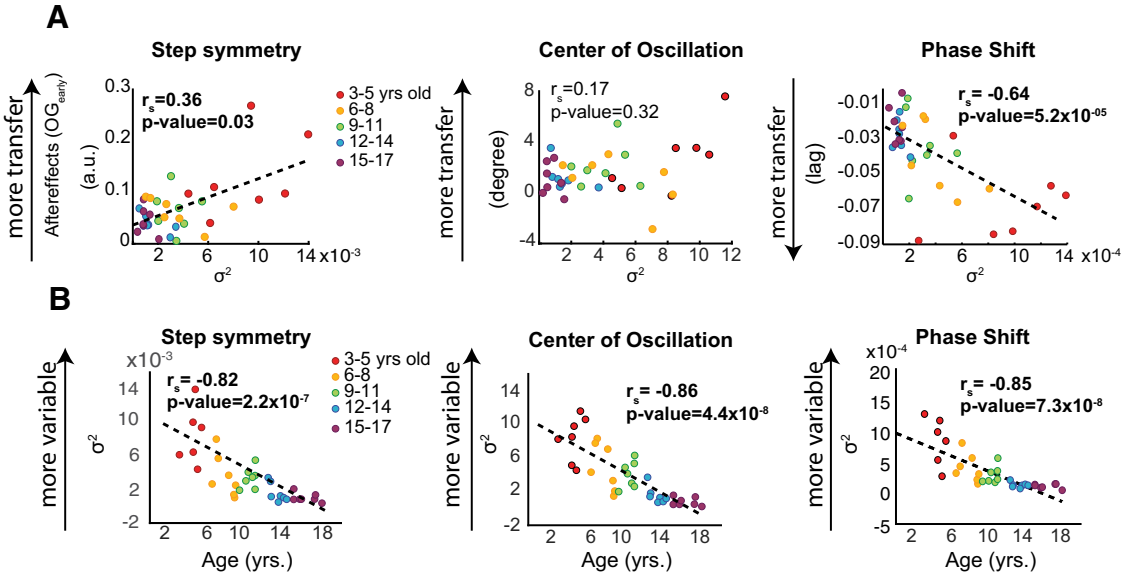

Figure 6. ***A***, Scatter plots showing the relationship between variability in stepping and OG_{early}. Colors indicate the different sensory conditions. Variability in behavior was a significant factor that predicted the transfer of adaptation effects to over ground walking. The magnitude of transfer was positively related to the subjects' behavior variability: the more variable were subjects during adaptation, the more carry-over of aftereffects to over ground. ***B***, Scatter plots showing the correlation between age and baseline variability. There is a significant correlation between age and baseline variability in all gait parameters. These regressions show that children become less variable as in their gait pattern as they develop during childhood. Arbitrary units (a.u.).

Figure Contributions: Gelsy Torres-Oviedo, Erin Vasudevan, and Laura Malone performed the experiments. Dulce Mariscal and Gelsy Torres-Oviedo analyzed the data.

more for external perturbations to their songs when these perturbations fall within the natural range of produced sounds compared with when they fall out of this natural variability (Kelly and Sober, 2014). Here, we suggest that natural variability could also determine the generalization of motor learning across contexts.

The larger extent of generalization in young children could also be explained by ongoing development of neural substrates mediating the ability to disengage context-specific motor actions when switching from one environment to another. We observed younger children continued to perform the motor pattern for split-belt walking in the over ground context. Similar results are observed in adults older than 73 years old (Sombric et al., 2017) and people with stroke (Reisman et al., 2009), which are populations exhibiting either age-related structural decline (Fjell and Walhovd, 2010) or focal lesions to motor areas of the brain. It has been shown that cortical areas necessary for switching between motor programs are still developing during childhood (Wendelken et al., 2012). Therefore, young children might have difficulties disengaging newly learned locomotor patterns when the context changes because cerebral networks underlying action specificity continue to develop throughout youth.

Lastly, the immature executive function needed for task switching could also contribute to young children's persistent motor actions across contexts. Multiple development studies have indicated that executive function, which includes the cognitive flexibility to switch actions, is developed during childhood (Zelazo, 2006; Prencipe et al., 2011) and through adolescence (Wilson et al., 2008). Children younger than five years old have difficulty in task switching: they perseverate in their actions based on rules applicable to a prior context (Zelazo, 2006). A possible explanation for this action perseveration is the inability to use contextual cues to switch actions in a proactive manner (Munakata et al., 2012). It is not until age 8 when the prefrontal cortex has reached the maturity needed for kids to change the course of ongoing actions (Chevalier et al., 2014). Thus, undeveloped cognitive functions in children such as cognitive flexibility might also contribute to children's difficulties in switching locomotor patterns according to the walking condition.

Similarities in learning and context specificity across age groups

While kids are slower learners than young adults (Vasudevan et al., 2011), participants from all ages were able to store new movement calibrations. This was indicated by the lack of age-effect on the treadmill aftereffects on the treadmill (before overground walking). Interestingly, younger participants adjusted their gait less during the split condition (ΔAdapt parameter), which could be explained by the fact that younger individuals adapt more slowly than older children or adults (Vasudevan et al., 2011). Despite the reduced gait changes during adaptation of younger children, they exhibited more aftereffects overground that were more resilient to washout from the overground experience. This suggests that a longer adaptation period on the treadmill for young children might lead to even greater

aftereffects overground since gait changes on the treadmill results in larger aftereffects postadaptation (Sombric et al., 2019; Aucie et al., 2020).

While children from distinct age groups generalize their movements across environments differently, we do not observe differences in washout. Why is this the case? One possible explanation is that younger individuals are not washed out to the same level as older children and adults by the end of the overground period. This is consistent with previous studies showing that younger children take longer to washout the split-belt motor memory compared with older children or adults (Musselman et al., 2016). Thus, a longer washout period might be needed to have the same level of washout across groups. Another possibility might be that younger subjects have a reduced capacity to use contextual cues to transition between the tied and split motor pattern. In other words, older children and adults might learn from the split-to-tied transition during the catch condition to quickly switch to the tied motor pattern, whereas younger children have difficulties doing so. This is consistent with previous work showing that young children can use contextual cues to develop context-specific motor memories (Cox and Smitsman, 2006), but they have difficulties switching between them (Klossek and Dickinson, 2012).

Clinical implications

Promising studies have shown that gait symmetry in adult and pediatric patients with a hemiparesis improves after split-belt walking (Reisman et al., 2013). Since the motor system changes during development, it is important to understand what motor learning mechanisms are available to children to optimize rehabilitation interventions in these patients. Here, we showed that children younger than 12 years are able to transfer more of the movement pattern that they acquired on the treadmill to natural walking compared with older children and adults. This suggests that rehabilitation effects will be conducted more to real life situations if children are trained in their early childhood. In sum, the generalization of motor learning is a mechanism available to children that can be beneficial for improving movements of pediatric populations beyond the clinical setting.

Limitations

We note that arm swing was restricted differently between younger children and all other age groups, which could have led to distinct gait patterns. Namely young children (less than six y/o) walked with their arms extended holding a rail with both hands on the treadmill and overground, whereas older participants (6+ years old) walked with their arms crossed on the treadmill and overground. We had to introduce this methodological difference because young children were unable to maintain their arms crossed to prevent marker occlusion. We believe, however, that age-related differences in generalization are unlikely driven by this methodological distinction for two reasons. First, participants maintained the same arm position across contexts: young children held a rail on the treadmill and overground, whereas older participants crossed their arms on the treadmill and overground. Therefore, arm motion was not contextually different between age groups. Second, there have been other generalization studies in young adults during which arm swing is not constrained on the treadmill or overground, yet generalization patterns remain limited (Sombric et al., 2017; Mariscal et al., 2020) compared with the generalization observed in younger children

References

Addou T, Krouchev N, Kalaska JF (2011) Colored context cues can facilitate the ability to learn and to switch between multiple dynamical force fields. J Neurophysiol 106:163–183.

Ahmed AA, Wolpert DM, Flanagan JR (2008) Flexible representations of dynamics are used in object manipulation. Curr Biol 18:763–768.

Aucie Y, Zhang X, Sargent R, Torres-Oviedo G (2020) Motorized shoes induce robust sensorimotor adaptation in walking. Front Neurosci 14:174.

Berniker M, Kording K (2008) Estimating the sources of motor errors for adaptation and generalization. Nat Neurosci 11:1454–1461.

Bock O (2005) Components of sensorimotor adaptation in young and elderly subjects. Exp Brain Res 160:259–263.

Bock O, Girgenrath M (2006) Relationship between sensorimotor adaptation and cognitive functions in younger and older subjects. Exp Brain Res 169:400–406.

Byrd R, Gibson M, Gleason MH (1986) Bilateral transfer across ages 7 to 17 years. Percept Mot Skills 62:87–90.

Chevalier N, Chatham CH, Munakata Y (2014) The Practice of going helps children to stop: the Importance of context monitoring in inhibitory control. J Exp Psychol Gen 143:959–965.

Cothros N, Wong JD, Gribble PL (2006) Are there distinct neural representations of object and limb dynamics? Exp Brain Res 173:689–697.

Cothros N, Wong J, Gribble PL (2009) Visual cues signaling object grasp reduce interference in motor learning. J Neurophysiol 102:2112–2120.

Cox RFA, Smitsman AW (2006) Action planning in young children's tool use. Dev Sci 9:628–641.

Criscimagna-Hemminger SE, Donchin O, Gazzaniga MS, Shadmehr R (2003) Learned dynamics of reaching movements generalize from dominant to nondominant arm. J Neurophysiol 89:168–176.

Day KA, Roemmich RT, Taylor JA, Bastian AJ (2016) Visuomotor learning generalizes around the intended movement. eNeuro 3: ENEURO.0005-16.2016–12.

De Almeida Batista SR, Rodrigues P, Vasconcelos O (2017) Intermanual transfer of learning in a fine manual skill task. Motriz 23:7–13.

Donchin O, Francis JT, Shadmehr R (2003) Quantifying generalization from trial-by-trial behavior of adaptive systems that learn with basis functions: theory and experiments in human motor control. J Neurosci 23:9032–9045.

Fjell AM, Walhovd KB (2010) Structural brain changes in aging: courses, causes and cognitive consequences. Rev Neurosci 21:187–221.

Gandolfo F, Mussa-Ivaldi F, Bizzi E (1996) Motor learning by field approximation. Proc Natl Acad Sci U S A 93:3843–3846.

Hamzey RJ, Kirk EM, Vasudevan EVL (2016) Gait speed influences aftereffect size following locomotor adaptation, but only in certain environments. Exp Brain Res 234:1479–1490.

Hirashima M, Nozaki D (2012) Distinct motor plans form and retrieve distinct motor memories for physically identical movements. Curr Biol 22:432–436.

Howard IS, Ingram JN, Franklin DW, Wolpert DM (2012) Gone in 0.6 seconds: the encoding of motor memories depends on recent sensorimotor states. J Neurosci 32:12756–12768.

Howard I, Wolpert D, Franklin D (2013) The effect of contextual cues on the encoding of motor memories. J Neurophysiol 109:2632–2644.
Howard IS, Wolpert DM, Franklin DW (2015) The value of the follow-through derives from motor learning depending on future actions. Curr Biol 25:397–401.
Ingram JN, Howard IS, Flanagan JR, Wolpert DM (2010) Multiple grasp-specific representations of tool dynamics mediate skillful manipulation. Curr Biol 20:618–623.
Kelly CW, Sober SJ (2014) A simple computational principle predicts vocal adaptation dynamics across age and error size. Front Integr Neurosci 8:1–9.
Klossek UMH, Dickinson A (2012) Rational action selection in 1 1/2- to 3-year-olds following an extended training experience. J Exp Child Psychol 111:197–211.
Kluzik J, Diedrichsen J, Shadmehr R, Bastian AJ (2008) Reach adaptation: what determines whether we learn an internal model of the tool or adapt the model of our arm? J Neurophysiol 100:1455–1464.
Krakauer JW, Pine ZM, Ghilardi MF, Ghez C (2000) Learning of visuomotor transformations for vectorial planning of reaching trajectories. J Neurosci 20:8916–8924.
Kretch KS, Adolph KE (2013) Cliff or step? Posture-specific learning at the edge of a drop-off. Child Dev 84:226–240.
Krouchev NI, Kalaska JF (2003) Context-dependent anticipation of different task dynamics: rapid recall of appropriate motor skills using visual cues. J Neurophysiol 89:1165–1175.
Langan J, Seidler RD (2011) Age differences in spatial working memory contributions to visuomotor adaptation and transfer. Behav Brain Res 225:160–168.
Malfait N, Ostry DJ (2004) Is interlimb transfer of force-field adaptation a cognitive response to the sudden introduction of load? J Neurosci 24:8084–8089.
Malone LA, Bastian AJ (2010) Thinking about walking: effects of conscious correction versus distraction on locomotor adaptation. J Neurophysiol 103:1954–1962.
Mariscal DM, Iturralde PA, Torres-Oviedo G (2020) Altering attention to split-belt walking increases the generalization of motor memories across walking contexts. J Neurophysiol 123:1838–1848.
Munakata Y, Snyder H, Chatham CH (2012) Developing cognitive control: three key transitions. Curr Dir Psychol Sci 21:71–77.
Musselman KE, Roemmich RT, Garrett B, Bastian AJ (2016) Motor learning in childhood reveals distinct mechanisms for memory retention and re-learning. Learn Mem 23:229–237.
Osu R, Hirai S, Yoshioka T, Kawato M (2004) Random presentation enables subjects to adapt to two opposing forces on the hand. Nat Neurosci 7:111–112.
Patrick SK, Musselman KE, Tajino J, Ou HC, Bastian AJ, Yang JF (2014) Prior experience but not size of error improves motor learning on the split-belt treadmill in young children. PLoS One 9: e93349–12.
Prencipe A, Kesek A, Cohen J, Lamm C, Lewis MD, Zelazo PD (2011) Development of hot and cool executive function during the transition to adolescence. J Exp Child Psychol 108:621–637.
Reisman DS, Block HJ, Bastian AJ (2005) Interlimb coordination during locomotion: what can be adapted and stored? J Neurophysiol 94:2403–2415.
Reisman DS, Wityk R, Silver K, Bastian AJ (2009) Split-belt treadmill adaptation transfers to overground walking in persons poststroke. Neurorehabil Neural Repair 23:735–744.
Reisman DS, McLean H, Keller J, Danks KA, Bastian AJ (2013) Repeated split-belt treadmill training improves poststroke step length asymmetry. Neurorehabil Neural Repair 27:460–468.
Sainburg RL, Wang J (2002) Interlimb transfer of visuomotor rotations: independence of direction and final position information. Exp Brain Res 145:437–447.
Sidaway B, Bates J, Occhiogrosso B, Schlagenhaufer J, Wilkes D (2012) Interaction of feedback frequency and task difficulty in children's motor skill learning. Phys Ther 92:948–957.
Sober SJ, Brainard MS (2012) Vocal learning is constrained by the statistics of sensorimotor experience. Proc Natl Acad Sci U S A 109:21099–21103.
Sombric C, Torres-Oviedo G (2021) Cognitive and motor perseveration are associated in older adults. Front Aging Neurosci 13:1–16.
Sombric CJ, Harker HM, Sparto PJ, Torres-Oviedo G (2017) Explicit action switching interferes with the context-specificity of motor memories in older adults. Front Agining Neurosci 9:40.
Sombric CJ, Calvert JS, Torres-Oviedo G (2019) Large propulsion demands increase locomotor adaptation at the expense of step length symmetry. Front Physiol 10:60.
Synofzik M, Thier P, Lindner A (2006) Internalizing agency of self-action: perception of one's own hand movements depends on an adaptable prediction about the sensory action outcome. J Neurophysiol 96:1592–1601.
Thoroughman KA, Shadmehr R (2000) Learning of action through adaptive combination of motor primitives. Nature 407:742–747.
Torres-Oviedo G, Bastian AJ (2010) Seeing is believing: effects of visual contextual cues on learning and transfer of locomotor adaptation. J Neurosci 30:17015–17022.
Torres-Oviedo G, Bastian AJ (2012) Natural error patterns enable transfer of motor learning to novel contexts. J Neurophysiol 107:346–356.
Uehara I (1998) No transfer of visuomotor learning of button-pressing from right to left hands in right-handed four-year-olds. Percept Mot Skills 87:1427–1440.
Vasudevan EVL, Bastian AJ (2010) Split-belt treadmill adaptation shows different functional networks for fast and slow human walking. J Neurophysiol 103:183–191.
Vasudevan EV, Torres-Oviedo G, Morton SM, Yang JF, Bastian AJ (2011) Younger is not always better: development of locomotor adaptation from childhood to adulthood. J Neurosci 31:3055–3065.
Wada Y, Kawabata Y, Kotosaka S, Yamamoto K, Kitazawa S, Kawato M (2003) Acquisition and contextual switching of multiple internal models for different viscous force fields. Neurosci Res 46:319–331.
Wang J, Joshi M, Lei Y (2011) The extent of interlimb transfer following adaptation to a novel visuomotor condition does not depend on awareness of the condition. J Neurophysiol 106:259–264.
Wendelken C, Munakata Y, Baym C, Souza M, Bunge SA (2012) Flexible rule use: common neural substrates in children and adults. Dev Cogn Neurosci 2:329–339.
Wilke C, Synofzik M, Lindner A (2013) Sensorimotor recalibration depends on attribution of sensory prediction errors to internal causes. PLoS One 8:e54925.
Wilson CM, Christensen BK, King JP, Li Q, Zelazo PD (2008) Decomposing perseverative errors among undergraduates scoring high on the schizotypal personality questionnaire. Schizophr Res 106:3–12.
Zelazo PD (2006) The dimensional change card sort (DCCS): a method of assessing executive function in children. Nat Protoc 1:297–301.