



Here we ask whether this critical ability to learn context-specific motor memories and switch between them is a ected by healthy aging.

While it is well established that aging impairs learning of new motor patterns, it is unclear if it also a ects the context-specificity of learned movements. Several studies in motor adaptation have shown that the rate at which people learn (McNay and ; Fernández-Ruiz et al., 2000; Buch et al., 2003; Willingham, 1 Bock, 200; Rodrigue et al., 200; Heuer and Hegele, 200, 2011; Hegele and Heuer, 2010, 2013; Anguera et al., 2011; Bruijn et al., 2012; Trewartha et al., 2014) and the final adapted state they reach are impaired with aging (McNay and Willingham, 1 : Seidler, 200; Langan and Seidler, 2011; Bruijn et al., 2012; Huang and Ahmed, 2014). While there is a consensus that healthy aging impairs subjects' performance during motor adaptation tasks, it is unclear whether aging also a ects transitioning between di erent context-specific motor memories. Previous work has shown that older adults transfer movement patterns learned in one situation to another when it is beneficial to performance (Bock, 200; Bock and Girgenrath, 200 ; Langan and Seidler, 2011; Wang et al., 2011) However, it is unknown if they also transfer information across situations when it is detrimental to do so. Thus, we will test whether older adults can disengage movements learned on a treadmill when they impair their performance in a di erent walking context.

We hypothesize that processes for cognitive switching contribute to motor switching in older adults. This is formulated on the basis of other studies showing that motor performance is influenced by cognitive abilities relevant to the motor task. For example, diminished spatial working memory in older adults decreases the ability to counteract visual (Anguera et al., 2011; Langan and Seidler, 2011) and force perturbations (Trewartha et al., 2014), and to learn spatial motor sequences (Bo et al., 200). In addition, a recent study showed that interventions improving motor switching also improve cognitive switching (Coubard et al., 2011). Thus, we reasoned that cognitive and motor action selection might be related such that the cognitive ability to explicitly switch actions might contribute to transitioning between locomotor patterns when the environment changes. While it is well-known that older adults have limited ability for switching actions in cognitive tasks (Kramer et al., 1 4; Klein et al., 2000; Van Asselen and Ridderinkhof, 2000; Friedman et al., 200 ; Adrover-Roig and Barcelo, 2010), it is unknown if this is correlated with di culties switching patterns in motor tasks. Here we will test the extent to which age-related cognitive impairments for task switching is linked to age-related deficits in motor switching.

In sum, growing evidence indicates that cognitive and motor processes interact in motor learning, but little is known about their relation in action selection and its changes with healthy aging. Thus, we investigated age-related changes in context-specificity of locomotor learning and its correlation to deficits in cognitive switching. We predicted that cognitive switching would contribute to switching locomotor patterns when transitioning across di erent walking contexts. Conversely, we found that cognitive strategies for choosing actions interfered with locomotor switching in older adults. This suggests that cognitive-mediated processes for action selection impair, rather than compensate, for age-related deficits in motor switching.

### Co-ontv as

Two cognitive abilities were evaluated: cognitive switching and processing speed. The assessment of these distinct cognitive abilities allowed us to determine if context-specificity of motor learning was generally related to overall cognitive capacity or to a specific cognitive ability. We tested cognitive switching because we hypothesized it would be correlated to the ability to switch locomotor patterns across walking contexts (i.e., treadmill vs. overground). We also tested processing speed because it has been shown to be correlated to walking performance in older adults (Chen et al., 2012; Odonkor et al., 2013) and motor adaptation in young subjects (Rodrigue et al., 200 ). Cognitive switching was assessed with a Cognitive Switching Task (i.e., a set-shift task) and processing speed was evaluated with a Symbol Digit Coding Task (Figure 1B), as in previous studies characterizing age-related changes in these two cognitive functions switching (Gualtieri and Johnson, 200 ; Klouda et al., 201 ). In the Cognitive Switching Task, subjects had to match two objects based on randomly changing rules that were explicitly given to the subjects (i.e., "Match by color, or "Match by shape,) (**Figure 1B**, left panel). Participants were instructed to answer correctly and as fast as possible. They were given 2-s to answer at every trial during the task. Responses past the 2-s window were considered wrong. Participants performed the Cognitive Switching Task for 0 s, yielding at least 4 trials. In the Symbol Digit Coding Task, subjects had to match symbols to numbers based on a reference

from the analysis because they were performing at chance levels and the cognitive test of one young adult was not recorded due to technical di culties. Thus, our analyses were performed using 2 cognitive data points.

### **Data Collection**

### Loco otor as

Kinematic data were collected to characterize subjects' behaviors. Kinematic data were collected at 100 Hz with a passive motion analysis system (Vicon Motion Systems, Oxford UK). Gaps in raw kinematic data due to marker occlusions were filled with a quintic spline interpolation (Woltring; Vicon Nexus Software, Oxford Uk). Subjects' movements were assessed through passive reflective markers placed bilaterally on bony landmarks at the ankle (i.e., lateral malleolus) and the hip (i.e., greater trochanter). Markers were also placed asymmetrically on shanks and thighs to di erentiate between the legs. Heel strikes, defined as the times when the feet landed on the ground, were identified with kinematic data. This was done to have equivalent event detection on the treadmill and overground as in previous transfer studies (Torres-Oviedo and Bastian, 2010, 2012).

### Co-ontv as

Subjects' cognitive switching and processing speed were assessed with CNS Vital Signs software (CNS Vital Signs, Morrisville, NC). Cognitive switching and processing speed were evaluated with the tasks called "Shifting Attention Test, and "Symbol Digit Coding Test, in the CNS Vital Signs software, respectively. The number of correct and incorrect responses were recorded in both tests. These tests on the CNS Vital Signs software have been validated as compared to conventional neuropsychological tests (Gualtieri and Johnson, 200).

### **Data Analysis**

### Gat ara trs or Loco otor as

We assessed the behavior of spatial and temporal features of gait, which have been shown to adapt (Malone and Bastian, 2010; Malone et al., 2012; Finley et al., 201 ) and transfer di erently (Torres-Oviedo and Bastian, 2010). For a robust measure of adaptation we looked at step length asymmetry (StepAsym). This measure is conventionally used to characterize gait adaptation in split-belt studies (e.g., Reisman et al., 200). StepAsym was defined as the di erence in step lengths when taking a step with one leg vs. the other (where step length was the distance between ankles at heel strike). Thus, a zero value for StepAsym indicated that both steps were the same length. By convention, StepAsym is positive when the step length of the fast (dominant) leg is longer than the one of the slow (nondominant) leg. The adaptation of StepAsym has been shown to be influenced by spatial and temporal gait features (Malone and Bastian, 2010; Malone et al., 2012; Finley et al., 201). Therefore, to more specifically characterize gait adaptation, step length asymmetry was further decomposed into spatial (StepPosition), temporal (StepTime), and velocity (StepVelocity) components for two consecutive steps, as done previously (Finley et al., 201

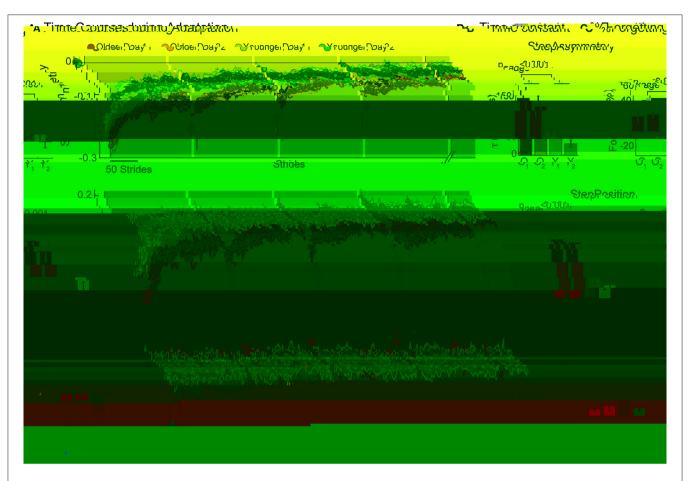
的时候上面的人在自己就是在全国的建筑的时候,就是有非常常的时候,在这个时间,在这个时间,在这个时间,在这个时间,在这个时间,在这个时间,在这个时间,在这个时间,

### TABLE 1 | Locomotor Outcome Measures.

Outcome measure	Meaning	Calculation
Steady State ( )	Steady state of adapted movements at the end of split-belt walking	Mean value of the last 50 strides of split-belt walking
Extent of Adaptation (AdaptExtent)	Extent of adaptation to recover step symmetry in the split-belt environment	$A_{aptExt} nt = a_{sp} - v$
Time Constant (τ)	Rate at which each a gait parameter is adapted	Number of strides to reach 63.2% of steady state
%Forgetting	Average decay of adapted movements due to the passage of time	%For $ttn = \frac{1}{3} \sum_{l=1}^{3} (\frac{F_{l} - I_{l}}{F} \times 100)$
Learning index	After-effects due to newly acquired movements in the split-belt environment	Mean value of first 3 strides of the catch trial following split-belt walking
Transfer index	After-effects due to carry over of adapted movements to overground walking	Mean value of the first 5 strides of overground walking following split-belt walking
%Transfer	After-effects overground expressed as a percent of the extent of adaptation	Transfer index/AdaptExtent
Washout	Remaining after-effects following de-adaptation when walking overground	Mean value of the first 5 strides on the treadmill following overground walking
%Washout	Remaining after-effects expressed as a percent of the extent of adaptation	Washout/ AdaptExtent

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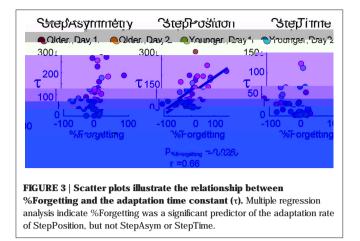
value, as opposed to the learning index, because it is one single value that indicates the maximum adapted state that StepPosition



**FIGURE 2** | **Early Adaptation Behavior. (A)** Stride-by-stride time courses during baseline and adaptation for StepAsym, StepPosition, and StepTime are shown. Shaded gray areas represent the adaptation period. Resting breaks, when subjects were not walking, are indicated by the white regions in between shaded areas. The last 50 strides of the second adaptation block (before subjects walk overground) are also shown. Black arrows indicate the decays in adapted state due to the passage of time during the resting breaks. Colored dots represent the average of 5 consecutive strides and colored shaded regions indicate the standard error for each group. (**B**) Bar plots indicate the mean time constants (i.e.,  $\tau$ ) per group  $\pm$  standard errors and statistical difference lines between groups illustrate significant ANOVA effects of age. Remember that a large  $\tau$  indicates that subjects slowly adapted. Note that, on average, subjects' time constants are <150 strides indicating that they occurred before the first resting break. (**C**) Bar plots indicate the mean %Forgetting per group  $\pm$  standard errors and statistical difference lines between groups illustrate significant ANOVA effects of age.

(Figure 2A bottom panel) did not decay during the restbreaks. The decay of spatial motor memories was quantified by %Forgetting values shown in Figure 2C. We observed that the mean %Forgetting for old groups is significantly higher than for young groups in StepAsym  $[F_{(1,3)} = 1, p < 0.001]$ and Step Position  $[F_{(1,3)} = 13.20, p < 0.001]$ , but not in StepTime  $[F_{(1,3)} = 0.22, p = 0.4]$ . Moreover, these results were maintained with repeated exposures, as indicated by the non-significant exposure e ect across parameters [StepAsym:  $F_{(1,3)} = 0.11, p = 0.4,$  StepPosition:  $F_{(1,3)} = 1.34,$ p = 0.2, and StepTime:  $F_{(1,3)} = 1.0, p = 0.1$ ]. Thus, %Forgetting of adapted spatial gait features in older adults was not reduced with repeated exposures of the locomotor paradigm. Taken together, these results show that older adults "forget the adapted spatial pattern learned on the splitbelt treadmill during rest-breaks, whereas they maintain the temporal one.

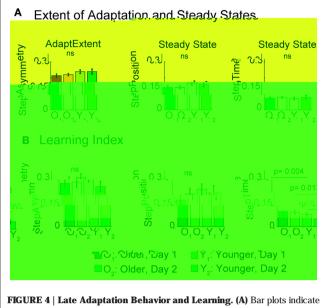
Moreover, forgetting of spatial gait features predicted the rate at which subjects adapted. Figure 3 shows the results from the multiple regression analyses to determine the predictive power of age group, exposure, and %Forgetting on τ. We observed that %Forgetting was a significant predictor (t = 2.32, p = 0.02) of the adaptation rate of StepPosition, quantified by the time constant  $\tau$ . The positive relation between these two measures indicated that as %Forgetting increased, subjects adapted slower-that is, they had a larger time constant  $\tau$  $(\tau_{predicted} = 0.2 \times \% Forgetting - 4.40 \times exposure + .4 \times$  $age + ..., F_{(3, 34)} = ..., 4, p < 0.001, r = 0.$ ). Note that the relation between %Forgetting and  $\tau$  was not observed in StepAsym (t = 1.12, p = 0.2) and StepTime (t = 0.0, p = 0.3). Thus, %Forgetting determined the adaptation rate of StepPosition for all age groups, but not of the other two parameters. It is worth mentioning that out of 11 old subjects reached 3.2% of their spatial adapted state, which was used



to quantify  $\tau$ , after the first rest-break. Therefore, it might be possible that these subjects took longer to reach their steady state because of the decay in adapted spatial gait features occurring during the break. Lastly, age was a significant predictor of StepPosition (t = 2., p = 0.012) and StepAsym (t = 2. 2, p = 0.00), but not StepTime (t = -0., p = 0.4) and exposure was not a predictor for any parameter (StepAsym, t = -1.20, p = 0.24; StepPosition, t = -0.1, p = 0. ; StepTime, t = -0.2, p = 0. 1), which is consistent with results shown in **Figure 2C**. In conclusion, slower adaptation and forgetting of spatial motor memories were related in all age groups.

## Older Adults Adapt and Learn As Much As Young

While older adults adjusted their gait more slowly, they eventually reached a similar adapted state as young. Note in the time courses shown in Figure 2A that young and old reached the same adapted state in all parameters at the end of the adaptation period during both visits. These similarities are indicated in **Figure 4A** by non-significant age  $[F_{(1,3)} = 3, p = 0.0 3]$  and exposure e ects  $[F_{(1,3)} = 0.0, p = 0.]$  on the AdaptExtent of StepAsym. Note that the strong trend of the age factor on the AdaptExtent was not observed when 1 (out of the 11) young subjects was removed from the analysis  $[F_{(1, 34)} = 1, p = 0.22]$ . Thus, while an outlier subject adapted more than the others, in general subjects from all age groups could counteract equally well the split-belt perturbation during both experimental visits. We also observed that young and old groups used similar adaptation strategies, as indicated by the same steady states reached in the adaptation of StepPosition  $[F_{(1,3)} = 3.4, p = 0.0, 2]$  and StepTime  $[F_{(1,3)} = 0.04, p = 0.3]$  across age groups. Again, the strong trend of the age factor was driven by the behavior of the same subject reported above and was not observed if this subject was removed from the analysis  $[F_{(1, 34)} = 1, 2,$ p = 0.23]. Thus, we concluded that age does not have an e ect on adapted steady states even if one subject reached a larger adapted state in StepPosition. Lastly, these similarities in adapted states across age groups were maintained with exposure, as shown by the non-significant exposure e ect on the steady state of StepPosition  $[F_{(1,3)} = 0.0, p = 0.1]$  and StepTime  $[F_{(1,3)} =$ 



**FIGURE 4** [Late Adaptation Behavior and Learning. (A) Bar plots indicate the mean extent of adaptation (AdaptExtent) and adapted steady states per group  $\pm$  standard errors. In general, all subjects reached the same adapted state. (B) Bar plots show the mean learning index per group  $\pm$  standard errors. Recall that the learning index is quantified by the average after-effects on the treadmill during the catch trial, when both belts move at the same speed. We only found an age effect on the Learning Index for StepTime, which was driven by the smaller after-effects of young adults during their second visit compared to other groups ( $\rhoost \ ho \ \rho$ -values and statistical difference lines shown). We believe that this smaller after-effect indicates that young subjects can switch faster between the split and tied StepTime patterns during their second visit.

0. 3, p = 0.43]. Therefore, neither age nor exposure changed the extent of adaptation or the motor strategy used to counteract the split-belt perturbation.

In addition, older adults were able to learn as much as young. Recall that learning was quantified with the magnitude of aftere ects during a catch trial on the treadmill, when the split-belt perturbation was removed. **Figure 4B** indicates that after-e ects on the treadmill were not a ected by subjects' age. Accordingly, age did not have an e ect on the learning index of StepAsym  $[F_{(1,3)} = 0.10, p = 0.]$  or StepPosition alve(1, 3)]TJØR1 3



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new sensorimotor representations of walking, but diminishes the ability to switch temporal stepping patterns on the treadmill based on prior experience.

### Older Adults Transfer More than Younger Adults

Older adults have di culty switching movement patterns when transitioning from walking on the treadmill to walking overground. This was indicated by the larger after-e ects in all parameters observed in older adults walking overground compared to young. Note in Figure 5A that time courses from older groups start from larger initial values compared to younger groups. Consistently, significant age e ects on Transfer were found in all parameters (Figure 5B). Specifically, older adults transferred more than young in StepAsym  $[F_{(1,3)} = .2,$ p = 0.02 ], StepPosition [ $F_{(1,3)} = .23, p = 0.02$  ], and StepTime  $[F_{(1,3)} = .10, p = 0.01]$ . The same results were observed when Transfer was expressed as a percent of AdaptExtent [Figure 5C; StepAsym:  $F_{(1,3)} = ..., p = 0.00$ , StepPosition:  $F_{(1, 3)} = .40, p = 0.02$ , StepTime:  $F_{(1, 3)} = .3$ , p = 0.004]. Moreover, we found that exposure had an e ect on Transfer  $[F_{(1,3)} = .0, p = 0.031]$  and %Transfer of StepAsym  $[F_{(1,3)} = .22, p = 0.01]$ , suggesting that subjects could better disengage the movements learned on the treadmill when walking overground during their second visit. However, post-hoc analysis revealed that this exposure e ect was driven by di erences only in younger subjects. Specifically, younger subjects had less overground after-e ects in StepAsym on their second visit compared to their first one when quantified as Transfer (t = -1., p = 0.0) or %Transfer (t = -2.04, p = 0.04). On the other hand, older subjects did not have statistically di erent Transfer (t = -1.1, p = 0.2) or %Transfer (t = -1.4, p = 0.1) across visits. Thus, younger subjects were able to use the experience switching between walking contexts in their first visit to contextualize movements better during their second visit. Conversely, older adults transferred equally across visits. Taken together, our results indicate that older adults have diminished ability for switching movement patterns across walking situations and, unlike younger adults, this is not improved with prior experiences transitioning between walking contexts.

# Transfer in Older Adults Is Correlated with Cognitive Switching

We observed that older subjects' performance in a cognitive switching task was a predictor of motor switching, which was quantified by movement transfer across walking contexts. Recall that large transfer values indicated that subjects were poor at switching walking patterns when transitioning from the treadmill to overground. Interestingly, cognitive switching was inversely related to motor switching (**Figure 6A**). In

#### A. Time courses overground

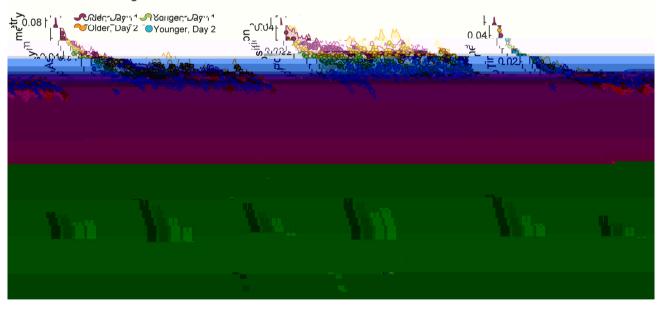
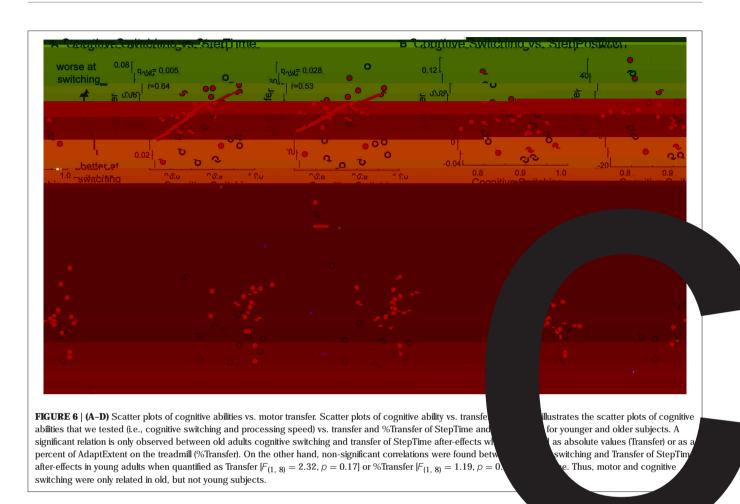


FIGURE 5 | Overground Behavior. (A) Stride-by-stride time courses of StepAsym (left), StepPosition (middle), and StepTime (right) are shown for baseline and post-adaptation overground walking. Colored dots represent the average of 5 consecutive strides and colored shaded regions indicate the standard error for each group. (B) Bar plots indicatet is indicated in the standard error for each index of standard error for each inde





other words, old adults that were better at switching in the cognitive task were worse at switching locomotor patterns in the motor task. Note that this negative correlation was only true for motor switching in the temporal domain when expressed as Transfer  $[F_{(1,1)} = 10., p = 0.00, r = 0.4]$ Transfer =  $0.1 \times CognitiveSwitching - 0.0$ ] or %Transfer  $[F_{(1,1)}] = ..., p = 0.02, r = 0.3,$ %Transfer = 4.2 × CognitiveSwitching - 21. ]. On the other hand, cognitive switching was not related to motor switching in the spatial domain [**Figure 6B**; Transfer:  $F_{(1,1)} = 0$ . 2, p = 0.3, %Transfer:  $F_{(1,1)} = 1.40, p = 0.2$ ]. In addition, motor and cognitive switching were only related in the performance of old, but not young subjects (Figure 6A). This is shown by the non-significant correlation between cognitive switching and motor switching in young adults when quantified as Transfer of StepTime  $[F_{(1, )}] =$ 2.32, p = 0.1 ] and StepPosition [ $F_{(1, )} = 0.13$ , p = 0.3] or %Transfer of StepTime  $[F_{(1, -)} = 1.1, p = 0.20]$  and StepPosition  $[F_{(1, )} = 0.10, p = 0.$ ]. Importantly, this relation between cognition and motor performance was specific to cognitive switching, and not to older adults' cognitive performance in general (Figures 6C,D). This can be observed by the lack of relation between processing speed and motor switching in young and old subjects when expressed as Transfer of StepTime [old group:  $F_{(1, 1)} = 0.0$ , p = 0.1, young group:  $F_{(1, 1)} = 0.3$ , p = 0.3] and StepPosition [old group:  $F_{(1, 1)} = 0.3$ , p = 0.] or %Transfer of StepTime [old group:  $F_{(1, 1)} = 0.0$ , p = 0. 0; young group:  $F_{(1, 1)} = 1.43$ , p = 0.2] and StepPosition [old group:  $F_{(1, 1)} = 1.2$ , p = 0.2; young group:  $F_{(1, )} = 0.30$ , p = 0. 0]. In sum, cognitive switching in older adults interfered with motor switching across walking contexts of temporal gait features.

## Older and Young Adults have Similar Remaining After-Effects When Returning to the Training Context

Neither age nor exposure a ected the magnitude of after-e ects when returning to the treadmill following overground walking. In **Figure 7A** it can be seen that all groups had similar remaining after-e ects when returning to walk on the treadmill after overgroundrwadking. Thus, age did not have an e ect ea1 .1 (nTJIR 4Z.4

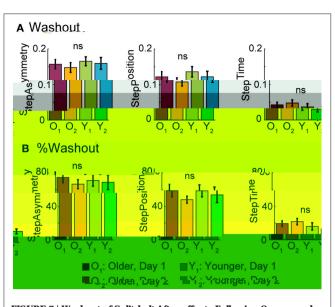


FIGURE 7 | Washout of Split-belt After-effects Following Overground Walking. (A) Bar plots indicate the mean Washout values per group  $\pm$ standard errors. These quantify the initial after-effects when returning to the treadmill after overground walking. (B) Bar plots indicate the mean %Washout values per group  $\pm$  standard errors. %Washout values indicate the amount of remaining after-effects on the treadmill as a percent of AdaptExtent during the split-belt condition. In other words, %Washout values takes into account how well subjects adapted their gait on the treadmill. %Washout values of 100% indicate that the adapted movements on the treadmill remain intact after the overground walking experience.

extent of adaptation (AdaptExtent) on the treadmill (**Figure 7B**). Specifically, age group did not a ect %Washout for StepAsym  $[F_{(1,3)} = 0.03, p = 0.]$ , StepPosition  $[F_{(1,3)} = 0.10, p = 0.]$ , or StepTime  $[F_{(1,3)} = 2.1, p = 0.1]$ . Additionally, exposure did not a ect %Washout for StepAsym  $[F_{(1,3)} = 0., p = 0.4]$ , StepPosition  $[F_{(1,3)} = 1.0, p = 0.30]$ , or StepTime  $[F_{(1,3)} = 0.01, p = 0.4]$ . Therefore, motor memories specific to the treadmill were not washed out by overground walking, regardless of subjects' age or prior experience transitioning between these two walking contexts.

### DISCUSSION

We investigated how healthy aging a ects one's ability to adapt, learn, retain, and switch locomotor patterns across walking contexts and how cognitive action selection impacted motor switching. We found that healthy aging does not alter sensorimotor adaptation, but has a negative impact on the specificity and retention of motor memories acquired during novel situations. Interestingly, cognitive and motor switching were inversely related in older adults. Thus, cognitive action selection hindered, rather than compensated for age-related deficits in motor specificity.

## Older Adults Can Adapt Their Gait and Learn New Walking Patterns

We found that healthy aging does not limit the ability to adapt walking movements in response to sustained changes in the environment. This was indicated by the similarity in adapted behaviors across age groups, as reported before (Malone and Bastian, 201 ). This finding is at odds with previous motor adaptation studies showing limitations in the adapted state reached by old participants in walking (Bruijn et al., 2012) and reaching (e.g., McNay and Willingham, 1 ; Seidler, 200 ; Hegele and Heuer, 2010, 2013; Langan and Seidler, 2011; Huang and Ahmed, 2014). These distinct findings can be explained by the higher instances of large errors occurring after resting breaks, which were present in our protocol unlike the other studies. Notably, it has been shown that learning is facilitated if errors are large (Körding and Wolpert, 2004; Kluzik et al., 200; Wei and Körding, 200 ; Schweighofer et al., 2011; Torres-Oviedo and Bastian, 2012; Pauwels et al., 201 ) and consistent (Korenberg and Ghahramani, 2002; Burge et al., 200 ; Wei and Körding, 2010; Castro et al., 2014). Therefore, old adults can adapt their gait to the same degree as young when they experience multiple instances of large and consistent errors.

Our results also show that healthy aging does not impair the ability to learn new representations of environment dynamics. We observed that after-e ects, which result from adapted and stored representations of the environment, are equally large in old and young subjects before or after the overground walking. This observation is consistent with previous studies showing 200 ), which regulates the sensitivity to errors driving motor adaptation (Criscimagna-Hemminger et al., 2010). Alternatively, older adults are in general risk averse (Albert and Du y, 2012; Tymula et al., 2013) and risk-sensitivity has been shown to influence sensorimotor control (Nagengast et al., 2010; O'Brien and Ahmed, 201 ) and motor adaptation (Trent and Ahmed, 2013). Thus, it is possible that the aged motor system exploits prior experiences rather than exploring new movements to avoid risks such as falling, which have more serious consequences in old than young populations (Talbot et al., 200 ; Mitchell et al., 2010). In sum, older adults need to accumulate a lot of evidence in a new environment before updating their movements possibly due to large sensory and motor noise or their fear of risks associated to movement exploration.

# **Cognition Interferes with Motor Switching in Older Adults**

We observed an unexpected inverse correlation between cognitive and motor switching, which might be explained by the recruitment of cognitive centers compensating for age-related basal ganglia deficits controlling motor switching. It has been shown that the basal ganglia mediates both cognitive (Dreher and Grafman, 2002) and motor switching (Brown and Almeida, 2011; Leunissen et al., 2013; Balser et al., 2014). It has also been shown that cognitive centers are recruited in switching tasks performed by older adults (Coxon et al., 2010) to compensate for age-related functional deficits in the basal ganglia (Bäckman et al., 200 ; Ota et al., 200 ). However, cognitive compensation can worsen the performance of implicitly controlled tasks (Boyd and Winstein, 2004). Thus, we conclude that the recruitment of cognitive resources for switching augments motor switching deficits in older adults instead of e ectively correcting them. This idea is supported by evidence showing that cognitive and motor switching are inversely related in Parkinson patients (Inzelberg et al., 2001) exhibiting stronger functional deficits in the basal ganglia than unimpaired old subjects. Taken together, our findings indicate that utilizing cognitive resources interferes with motor switching instead of compensating for basal ganglia related motor switching deficits in older adults.

## **Older Adults Encode Motor Memories Susceptible to the Passage of Time**

Our results show that aging a ects the retention of movements since older adults exhibit forgetting during resting breaks and naïve-like behavior after repeated exposure of the locomotor task. context. Poor motor switching in older populations might be compensated by recruiting cognitive resources. However, this cognitive mediated compensation interferes with the remaining implicit control of motor switching. Our results are significant because they provide knowledge on how cognition influences motor control in older populations, which could be used to develop more e ective treatments for age-related mobility impairments. Specifically, our findings suggest that reinforcing implicit mechanisms for motor switching would be a more e ective approach for action selection in older adults than using cognitive strategies.

## **ETHICS STATEMENT**

This study was carried out in accordance with the recommendations from the University of Pittsburgh Institutional Review Board with written informed consent from all subjects. All subjects gave written informed consent in accordance with

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