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RESEARCH ARTICLE

Control of Movement

Reduced corticospinal drive and inflexible temporal adaptation during visually guided walking in older adults

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Abstract

Corticospinal drive during walking is reduced in older adults compared with young adults, but it is not clear how this decrease might compromise one's ability to adjust stepping, particularly during visuomotor adaptation. We hypothesize that age-related changes in corticospinal drive could predict differences in older adults' step length and step time adjustments in response to visual perturbations compared with younger adults. Healthy young ($n = 21$; age 18–33 yr) and older adults ($n = 20$; age 68–80 yr) were tested with a treadmill task, incorporating visual feedback of the foot position and stepping targets in real-time. During adaptation, the visuomotor gain was reduced on one side, causing the foot cursor and step targets to move slower on that side of the screen (i.e., split-visuomotor adaptation). Corticospinal drive was quantified by coherence between electromyographic signals in the beta-gamma frequency band (15–45 Hz). The results showed that *1*) older adults adapted to visuomotor perturbations during walking, with a similar reduction in error asymmetry compared with younger adults; *2*) however, older adults showed reduced adaptation in step time symmetry, despite demonstrating similar adaptation in step length asymmetry compared with younger adults; and *3*) smaller overall changes in step time asymmetry was associated with reduced corticospinal drive to the tibialis anterior in the slow leg during split-visuomotor adaptation. These findings suggest that changes in corticospinal drive may affect older adults' control of step timing in response to visual challenges. This could be important for safe navigation when walking in different environments or dealing with unexpected circumstances.

NEW & NOTEWORTHY Corticospinal input is essential for visually guided walking, especially when the walking pattern must be modified to accurately step on safe locations. Age-related changes in corticospinal drive are associated with inflexible step time, which necessitates different locomotor adaptation strategies in older adults.

aging; coherence; electromyography; locomotion; visuomotor

INTRODUCTION

In normal walking, vision plays an essential role in providing the central nervous system with external cues for adjusting our speed, direction, and foot placement (1, 2). Anticipatory locomotor planning based on visual information is dependent on cortical networks including the posterior parietal area, which is important for the integration of visual and proprioceptive signals to estimate the relative location of footfall targets with respect to the body (3, 4). Signals from the motor cortex are integrated into the activity of spinal locomotor circuits to adapt the timing and magnitude of muscle activity, providing precise control of limb trajectory (3, 5). Precision in both timing and positioning is critical, especially when navigating different environments or dealing with unpredictable circumstances [e.g., crowded areas (6), street crossings (7)].

Older adults have more difficulties walking in complex environments that require precise visuomotor coordination and rapid step adjustments, leading to increased fall risks (8–10). When approaching stepping targets or obstacles, older adults exhibit delayed stepping adjustments and prefer more conservative control strategies (e.g., more short steps) compared with young adults (8, 10–14). In addition, visuomotor adaptation may be impaired in older adults (15), diminishing their ability to update leg movements during

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visually guided walking. For example, when walking while wearing prism goggles, older adults demonstrate smaller overall changes and a slower rate of adaptation in angular error compared with young adults (16, 17). When visuomotor adaptation involved precision stepping, older adults performed the movements more slowly but were able to achieve accuracy levels similar to young adults with practice (18). To address these issues and enhance fall prevention strategies for older adults, it is important to understand the neural mechanisms underpinning both the temporal and spatial aspects of gait adaptability during visually guided walking and how these mechanisms change with aging.

Corticospinal drive, which plays an important role in human locomotor control, has been shown to decline with increasing age (19–21). In healthy young adults, electromyography (EMG) recordings from synergistic muscles demonstrate coherence within beta (15–30 Hz) and gamma (30–50 Hz) frequencies during normal walking, suggesting a role of oscillatory inputs in gait (22, 23). This EMG-EMG coherence is linked to corticomuscular coherence within a similar frequency range (∼24–40 Hz), which further suggests that the EMG coupling is driven by corticospinal activity during walking (24).

In older adults, reduced corticospinal drive measured through corticomuscular and intramuscular coherence has been associated with decreased stepping accuracy during precision walking (19). Our previous study also demonstrated that older adults have reduced corticospinal drive compared with younger adults during split-belt treadmill walking and that intramuscular coherence was associated with individual variability in temporal gait adaptation (20, 25). Interestingly, corticospinal drive was associated with temporal adaptation but not spatial adaptation (20), which may indicate that these two processes are independently controlled (26–28). These findings suggest that age-related changes in corticospinal drive may necessitate different control strategies for gait adjustments in older adults in response to visual cues.

The objective of this study was to determine the influence of age and corticospinal drive on temporal and spatial gait strategies during visuomotor locomotor adaptation. Specifically, we examined visuomotor adaptation in a precision stepping task. When visual perturbations were introduced on one side during a target stepping task (i.e., split-visuomotor walking adaptation), healthy young adults gradually adapted both step length and step time symmetry to reduce error in foot placement (29). We hypothesized that *1*) older adults will show reduced visuomotor adaptation and larger errors compared with younger adults; *2*) change in step length and step time will be less or slower in older adults compared with young adults; and *3*) individual variability in change in step time during visuomotor walking adaptation will be associated with the amount of corticospinal drive, based on our previous study in split-belt walking adaptation (20).

METHODS

Participants

Twenty-one healthy young adults and 20 healthy older adults participated in this study (Table 1). Inclusion criteria were no previous history of neurological disorder, no current major medical conditions (including cognitive), no current orthopedic injuries, ability to walk without any walking aids (including ankle-foot orthoses) for at least 10 min, and visual acuity over 20/40. Participants were characterized for physical activity using the Short Physical Performance Battery (SPPB) and the Advanced SPPB (SPPB-A) (30), walking speed (6-m walk test included in SPPB-A), cognitive status using the Telephone Interview for Cognitive Status (TICS), recent subjective experience of fatigue using Fatigue Severity Scale, physical activity levels using the Godin Leisure Time Questionnaire, and leg-dominance using the Waterloo Footedness Questionnaire. All participants gave informed written consent before the study in accordance with the protocol approved by the Institutional Review Board of the University of Florida, Gainesville, FL (Protocol # 202000764).

Table 1. *Participant characteristics*

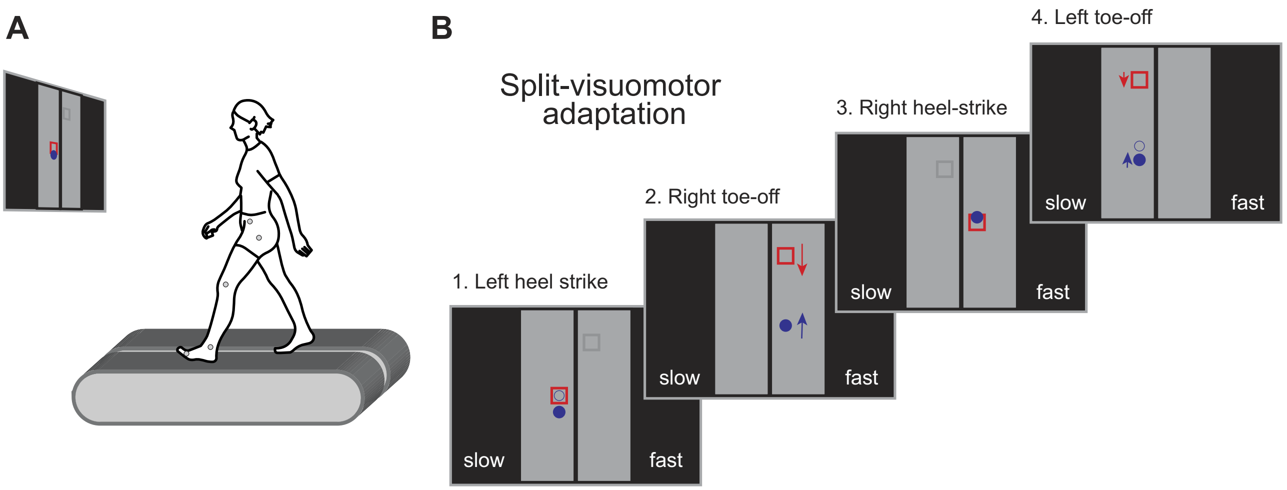
	Young (n = 21)	Old (n = 20)	P Value
Age, yr	23 ± 4.5	75 ± 4.4	< 0.001
Sex (M:F)	9:12	11:9	0.538
Height, cm	169.4 ± 9.5	171.5 ± 9.0	0.425
Weight, kg	67.8 ± 14.2	76.7 ± 16.0	0.055
BMI, kg/m^2	23.5 ± 3.8	26.0 ± 4.9	0.062
SPPB	12.0 ± 0.2	11.5 ± 0.9	0.023
SPPB-A	3.4 ± 0.3	3.0 ± 0.4	0.001
Overground gait speed, m/s	1.8 ± 0.2	1.5 ± 0.3	0.003
FSS	29.0 ± 7.8	28.4 ± 13.3	0.863
Godin	113.2 ± 113.3	188.4 ± 156.8	0.085
Waterloo	0.7 ± 0.6	0.8 ± 0.6	0.922
TICS	36.2 ± 1.7	36.2 ± 2.1	0.988
Treadmill speed, m/s	0.70 ± 0.05	0.70 ± 0.04	0.949

Mean and SD are reported. Independent t tests were used to determine group differences. To assess sex distribution difference, a two-tailed Fischer's exact-test was used. SPPB, short physical performance battery (max score = 12; higher score = higher physical function); SPPB-A, advanced short physical performance battery (max score = 4; higher score = higher physical function). Overground gait speed was measured from a 6-m walking test included in SPPB-A. FSS, fatigue severity scale (max score = 63; higher score = greater fatigue severity); Godin, Godin physical activity questionnaire (higher score = more physical activity); Treadmill speed, treadmill speed based on each participant's leg length; TICS, telephone interview for cognitive status (max score = 41; score greater than 32 = nonimpaired cognitive status); Waterloo, Waterloo footedness questionnaire (2 = strong right dominance, −2 = strong left dominance).

Experimental Setup

Participants walked on an instrumented split-belt treadmill (Bertec, Columbus, OH) while performing a target stepping task projected on a screen in front of the treadmill (Fig. 1*A*). A Miqus camera system (Qualisys, Gothenburg, Sweden) was used for real-time tracking of reflective markers placed on the lower limbs. The screen displayed a dot representing the current y-position (anterior-posterior axis) of the swing foot (i.e., reflective marker on the fifth metatarsal) on the treadmill, where the front of the treadmill is mapped on the top of the screen. Targets were represented by squares on the display. Targets for the left foot and right foot appeared on the left and right side of midline, respectively.

The speed of the treadmill was based on each participant's leg length (Table 1), which was measured from the greater



C

FAM	NO VF	PRE	PRE	VM ADAPTATION	VM POST-ADAPTATION
No VM task	No VM task	Gain = 0.9	Gain = 1.0	Gain =0.9, 1.0	Gain =1.0
5 min	5 min	300 steps	300 steps	600 steps	600 steps

Figure 1. *A*: experimental setup. Reflective markers were placed on: *1*) anterior superior iliac spine (pelvis), *2*) greater trochanter (hip), *3*) joint line of the knee (knee), *4*) lateral malleolus (ankle), and *5*) fifth metatarsal (toe) bilaterally. Stepping target (red box) and a cursor representing the swing foot (blue dot) were displayed in real-time on a screen in front of the treadmill. *B*: visual feedback. During split-visuomotor adaptation, the gain was reduced to 0.9 on the "slow" side and remained at 1.0 on the "fast" side. The text "slow" and "fast" were not visible to the participant. The empty blue circle represents the actual foot position, relative to the seen location (blue dot). The speed of the target and toe (length of the red and blue arrows, respectively) is slower on the side with the lower gain. *C*: split-visuomotor walking adaptation paradigm. Fam, familiarization; no VF, no visual feedback; Pre, baseline conditions; VM, visuomotor.

trochanter to the lateral malleolus for each leg and averaged between limbs. The average step length (i.e., vertical distance between stepping targets for the visuomotor task) was set at two-thirds of the leg length. The speed of the treadmill was set to 1.33 × step length, i.e., speed (m/s) = step length (m) × cadence (90 steps/60 s), which feels comfortable for most participants performing a similar visuomotor walking task (29, 31). Treadmill speed for both young and older adults were well below the overground gait speed assessed with a 6-m walk test during the SPPB-A.

Visuomotor Adaptation Paradigm

Stepping targets were projected on the screen based on the calculated step lengths and speed of the treadmill. Participants were instructed to "step accurately in the target as possible." When the visuomotor gain was set to 1.0, the speed at which the targets moved down was the same as the treadmill speed (equal on both sides). When the visuomotor gain was set to 0.9, the relationship between the screen and treadmill space was distorted in a way that screen space was reduced relative to treadmill space (screen space = treadmill space × 0.9). As a result, when the visuomotor gain is decreased, the target speed decreased on the screen, and the participants needed to alter step timing and/or positioning to hit the target. A supplementary video of the visual feedback display is available from https://figshare.com/s/6c27edb0fa50f49803aa.

The paradigm consisted of six conditions (Fig. 1*C*): *1*) 5 min with no visual feedback for familiarization on the treadmill; *2*) 5 min with no visual feedback for baseline; *3*) 300 steps with symmetrical visuomotor gain set at 0.9:0.9 ("pre-slow"); *4*) 300 steps with symmetrical visuomotor gain set at 1.0:1.0 ("pre-fast"); *5*) 600 steps with split-visuomotor gain for adaptation (0.9:1.0); and *6*) 600 steps with equal visuomotor gain (1.0:1.0) for postadaptation. The leg with visuomotor gain = 1.0 during adaptation (referred to as the "fast leg") and the leg with visuomotor gain = 0.9 (referred to as the "slow leg") were randomized between participants with the same leg dominancy, as leg dominancy may alter the rate of adaptation (32, 33).

Data Collection

Muscle activity in the proximal and distal ends of the tibialis anterior (TAp and TAd, respectively), medial gastrocnemius (MGAS), and soleus (SOL) were collected using surface EMG (MA411 Surface preamplifiers with stainless-steel electrodes connected with an MA300 wired amplifier, Motion Lab System, Baton Rouge, LA). To minimize the risk of cross talk, the proximal and distal EMG electrodes were placed at least 10 cm apart from each other (Fig. 2*A*). Lower limb kinematics were recorded at 100 Hz using an 8-camera Miqus system. Force data from the treadmill and EMG signals were collected at 1,000 Hz and synchronized with kinematics data using Qualisys Track Manager 2.14 (Qualisys, Gothenburg, Sweden).

Kinematic Analysis

Error was calculated as the difference between the location of the toe at heel strike to the center of the target. Step length was calculated as the anterior-posterior distance

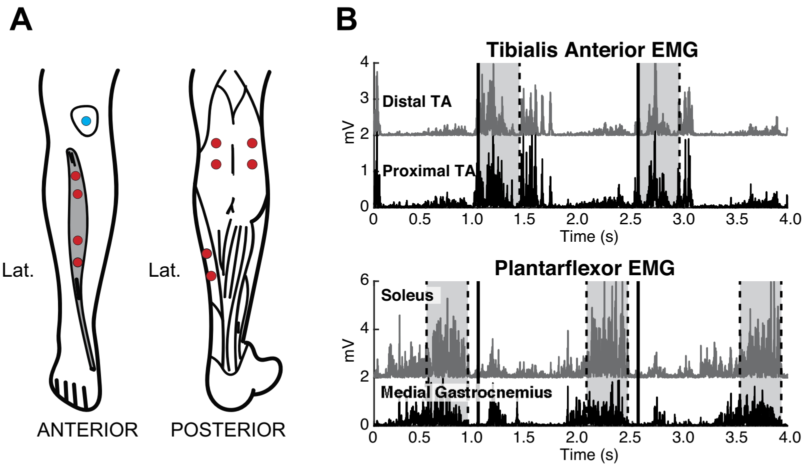


Figure 2. Electromyography. *A*: electrode placement for EMG measurements. *B*: example of processed tibialis anterior (TA) and plantarflexor EMG from a representative participant. To calculate coherence during swing phase, we used EMG signals from the proximal (black) and distal (gray) muscle belly of the tibialis anterior 0–400 ms (shaded area) after toe-off (thick black lines). To calculate coherence during stance phase, we used EMG signals from the medial gastrocnemius (black) and soleus (gray) muscle 500–100 ms (shaded area) before toe-off (thick black line). EMG example is from the fast leg during the split-visuomotor adaptation. Lat., lateral.

between the toe markers at time of heel strike (e.g., Fast step length = distance between toe markers at heel strike when fast leg was the leading leg). Step time was calculated as the time from heel-strike of the nonreference limb to the subsequent heel-strike of the reference limb (e.g., Fast step time = time between slow leg heel strike and subsequent fast leg heel strike).

Step length asymmetry and step time asymmetry were defined as the normalized difference between legs for each stride (*Eq. 1*). Error is already normalized to leg length, so the error asymmetry was defined as the difference between limbs for each stride (fast leg – slow leg).

$$Asymmetry = \frac{Fast\ leg - slow\ leg}{Fast\ leg + slow\ leg} \tag{1}$$

To assess baseline behavior, the first 30 strides were averaged for baseline with no visual feedback, preslow, and prefast conditions. During adaptation and postadaptation, averaged values were calculated over three different time epochs: *1*) initial (mean of first 5 strides), *2*) early adaptation/postadaptation (mean of strides #6–30), and *3*) plateau (mean of last 30 strides) (34). Overall change in adaptation and postadaptation was identified as the asymmetry difference between plateau and initial epochs during split-visuomotor adaptation and postadaptation, respectively. Early change in adaptation and postadaptation was identified as the asymmetry difference between early and initial epochs during split-visuomotor adaptation and postadaptation, respectively.

Coherence Analysis

Coherence between EMG pairs (denoted *x* and *y*) was characterized based on previously described methods and MATLAB functions from NeuroSpec (http://www.neurospec.org). EMG signals were high-pass filtered at 8 Hz, rectified, and normalized to have unit variance (35). Discrete Fourier transformation analysis was applied to short sections of the EMG taken at a fixed offset time to estimate their average autospectras, f_{xx} and f_{yy}, and cross-spectrum f_{xy}. For each Fourier frequency (λ), the resulting coherence value provides a measure of association of the *x* and *y* processes on a scale from 0 to 1 (*Eq. 2*). A coherence value of 0 signifies no synchrony between the two EMG signals and a coherence value of 1 signifies perfect synchrony between the two EMG signals.

$$|R_{xy}(\lambda)|^2 = \frac{|f_{xy}(\lambda)|^2}{f_{xx}(\lambda)f_{yy}(\lambda)} \tag{2}$$

Based on our preliminary data and previous studies with EMG-EMG coherence during walking (20, 25, 36, 37), we used 0–400 ms after toe-off (during swing phase of gait) to calculate TAp-TAd coherence and 500–100 ms before toe-off (during stance phase of gait) to calculate MGAS-SOL (plantarflexor) coherence and MGAS-LGAS (gastrocnemius) coherence (Fig. 2*B*). Coherence was calculated for each leg over the first 100 strides during each baseline condition and over the first and last 100 strides of the adaptation and postadaptation periods. Coherence and cumulant density plots for each participant and each condition were visually checked to verify that there were no signs of cross talk (large and narrow central peak in cumulant density and high coherence > 0.5 for more than most frequencies; 38). The natural logarithm of the cumulative sum of coherence was calculated for the beta-gamma band (15–45 Hz).

Statistical Analysis

Age group differences in baseline kinematic asymmetry and overall and early changes in kinematic adaptation were assessed though independent *t* tests. To assess potential baseline differences in performance, we also assessed "fast" and "slow" limb kinematics for all baseline conditions with a two-way mixed-measures ANOVA to assess age group (Young vs. Old), symmetry (Fast vs. Slow leg), and interaction effects. For kinematic changes that showed significant group differences, we also used an ANCOVA test to test group differences while controlling for physical function (SPPB-A).

Two-way mixed-measures ANOVA was performed to determine the effects of age group (Young vs. Old) and condition (prefast, preslow, early adaptation, late adaptation, early postadaptation, and late postadaptation; for the fast leg, preslow condition was omitted as preslow served as baseline for the slow leg during adaptation only) and interaction effects on each coherence measure. Greenhouse-Geisser corrections were applied when the assumption of sphericity was violated (Mauchly's test: $P < 0.05$). Post hoc pairwise comparisons were conducted with Bonferroni corrections. Effect sizes for paired comparisons were calculated with Cohen's d. Effect sizes were defined as small < 0.499, moderate $= 0.500–0.799$, and large > 0.800.

The relationship between kinematic adaptation (overall and early change) and coherence was assessed through a forward stepwise multiple linear regression. Predictors considered in the model were age groups (1 = Younger adult, 2 = Older adult) and the beta-gamma coherence from both legs during early adaptation (6 coherence values were considered as potential covariates in the model: *1*) fast and *2*) slow leg intramuscular tibialis anterior, *3*) fast and *4*) slow leg intermuscular plantarflexor, and *5*) fast and *6*) slow leg intramuscular gastrocnemius coherence). The strength of the relationships was assessed through root mean square error (RMSE) and coefficient of determination (r^2).

All statistical significance was established with an α level $= 0.05$. Statistical analyses were performed using JASP v0.14.1 (University of Amsterdam, Amsterdam, The Netherlands).

RESULTS

Participants walked with symmetrical error during baseline visually guided walking (preslow and prefast). There was no evidence of age group differences during baseline conditions for target error (Table 2). In the absence of visual feedback, older adults walked with shorter step lengths ($P = 0.007$, d $= -0.212$) and slower step times ($P = 0.006$, d $= -0.879$), reflecting a more "cautious" gait, compared with younger adults. However, there was no age-related difference in error, step lengths, or step times during preslow and prefast suggesting that both young and older adults demonstrated comparable precision stepping during baseline conditions with visual cues. See Supplemental Figs. S1 and S2.

Visuomotor Adaptation during Walking

The capacity for visuomotor adaptation was assessed by the amount of error reduction during adaptation and the aftereffects size in postadaptation (reflecting the updated visuomotor calibration). When the visuomotor gains were split during adaptation, the slow leg undershot while the fast leg overshot the target, so there was a significant increase in error asymmetry during initial and early adaptation (Fig. 3*A*). This error asymmetry was gradually reduced over the course of adaptation. Early change (Δearly− initial) and overall change in error asymmetry during adaptation (Δplateau− initial) were not different between age groups (Fig. 3, *B* and *C*; Table 3; Early Δ: $P = 0.723$, d $= -0.112$; Overall Δ: $P = 0.987$, d $= -0.005$;).

When the visuomotor gains returned to symmetrical during postadaptation, the slow leg overshot while the fast leg undershot the target, so error symmetry became negative in early postadaptation (Fig. 4*A*). This negative aftereffect indicates storage of a new visuomotor calibration, which must be actively washed out. Both overall and early change in error asymmetry during postadaptation was greater in young adults compared with older adults (Fig. 4, *B* and *C*; Early Δ: $P = 0.002$, d $= 1.055$; Overall Δ: $P = 0.037$, d $= 0.677$). This is likely because younger adults had larger aftereffects compared with older adults. After controlling for physical function, overall change in error asymmetry during postadaptation was not different between groups [$F(1,38) = 1.98$, $P = 0.167$]; however, group differences in early change in postadaptation persisted even after controlling for physical function [$F(1,38) = 5.04$, $P = 0.031$]. This suggests that the larger initial aftereffect during initial postadaptation may be driven by differences in physical function between age groups, rather than differences in capacity for visuomotor adaptation.

Step Length Adjustments during Visuomotor Adaptation

Participants walked with symmetrical step lengths and step time during baseline with no visual feedback, preslow, and prefast; there were no evidence of age group differences during baseline conditions (Table 2). Participants took increasingly longer step length on their slow leg compared with the fast leg with split visuomotor gains, so step length asymmetry became more negative over the course of adaptation (Fig. 3*D*). Early and overall change in step length asymmetry during adaptation was not different between age groups (Fig. 3, *E* and *F*; Early Δ: $P = 0.526$, d $= -0.200$; Overall Δ: $P = 0.562$, d $= -0.183$). In the beginning of postadaptation, participants continued walking with a longer step on the slow leg, but this step length asymmetry was gradually reduced and returned to symmetrical values by the end (Fig. 4*D*). Overall change in step length asymmetry during postadaptation was not significantly different between age groups, but early change was greater in young adults

Table 2. *Age group differences in baseline asymmetry*

Baseline Condition	Asymmetry Variables	Young Adults	Older Adults	*P* Value	95% Confidence Interval for Difference in Group Means Lower	95% Confidence Interval for Difference in Group Means Upper	Effect Size
No VF	Step length	0.01 ± 0.04	0.02 ± 0.05	0.445	−0.04	0.02	−0.241
	Step time	0.00 ± 0.02	0.00 ± 0.02	0.925	−0.01	0.01	−0.030
Preslow	Error*	−3.62 ± 14.51	−2.51 ± 29.85	0.881	−16.28	14.04	−0.048
	Step length*	−0.01 ± 0.03	−0.01 ± 0.06	0.894	−0.03	0.03	−0.042
	Step time	0.00 ± 0.03	0.00 ± 0.03	0.998	−0.02	0.02	−0.001
Prefast	Error	0.56 ± 20.74	−0.76 ± 18.32	0.831	−11.07	13.70	0.067
	Step length	0.00 ± 0.03	0.00 ± 0.03	0.929	−0.02	0.02	0.028
	Step time	0.00 ± 0.03	0.00 ± 0.03	0.655	−0.02	0.01	−0.141

Group differences between young ($n = 21$) and older adults ($n = 20$) are analyzed with a Student t test, and effect size is given by Cohen's d. *Levene's test was violated and P value reported is from a Welch test. No VF, no visual feedback.

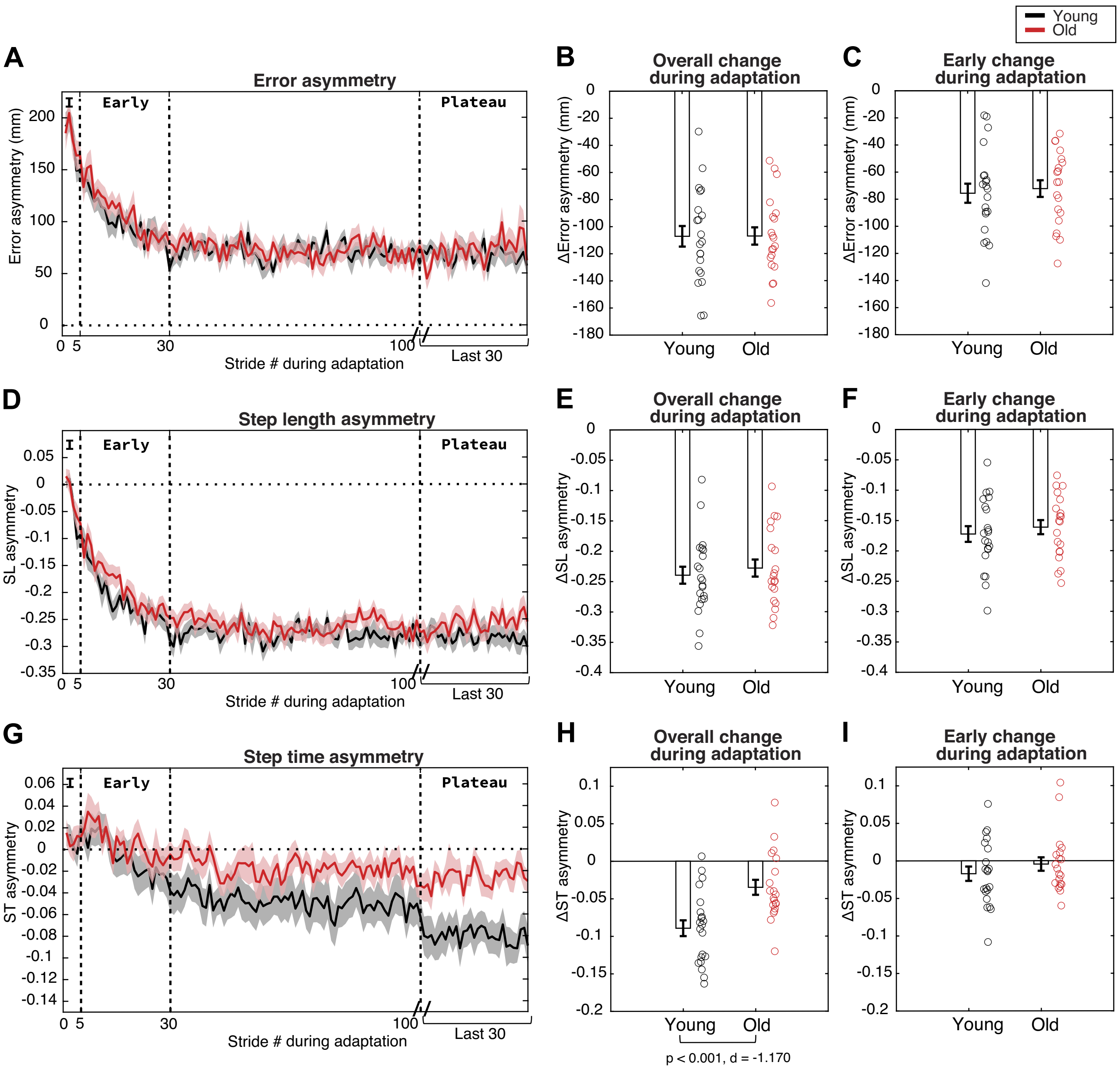


Figure 3. Visuomotor adaptation and gait asymmetry during adaptation. *A*, *D*, and *G*: stride-by-stride changes in error asymmetry, step length asymmetry, and step time asymmetry during adaptation. Shaded areas are standard errors. Initial (I) = Strides #1–5, Early = Strides #6–30, Plateau phase = last 30 strides. Age group means and standard error bars for overall change = Δ plateau phase – initial phase during adaptation (*B, E, H*) and Early change = Δ early phase – initial phase during adaptation (*C, F, I*). Black circles = young participants ($n = 21$); red circles = older participants ($n = 20$). SL, step length; ST, step time.

compared with older adults (Fig. 4, *E* and *F*; Overall Δ: $P = 0.089$, d = 0.545; Early Δ: $P = 0.006$, d = 0.928). This group difference in early change step length asymmetry during postadaptation was still present after controlling for physical function [$F(1,38) = 4.92$, $P = 0.033$].

Reduced Step Time Adjustments during Visuomotor Adaptation in Older Adults

Younger participants gradually adapted their step time during split-visuomotor adaptation so that they took longer step time on their slow leg compared with the fast leg and reached a plateau of negative step time asymmetry (Fig. 3*G*). Early change in step time asymmetry during adaptation was not different between age groups, but overall change in step time asymmetry was greater (i.e., more negative; reached a lower plateau) in young adults compared with older adults (*I* and *I*; Early Δ: $P = 0.337$, d = −0.304; Overall Δ: $P < 0.001$, d = −1.170). This group difference in overall change in step time adaptation was still present after controlling for physical function [$F(1,38) = 16.10$, $P < 0.001$]. During postadaptation, participants gradually deadapted to reach a symmetrical step time (Fig. 4*G*). Early and overall change in step time asymmetry during postadaptation was not significantly different between age groups (Fig. 4, *H* and *I*; Early Δ: $P = 0.164$, d = 0.444; Overall Δ: $P = 0.093$, d = 0.537).

Table 3. *Age group differences in visuomotor adaptation and gait parameters*

				95% Confidence Interval for Difference in Group Means		
Condition	**Asymmetry Variables**	**Difference**	***P* Value**	**Lower**	**Upper**	**Effect Size**
Adaptation	Error	Early change	0.723	−22.33	15.63	−0.112
		Overall change	0.987	−20.32	20.00	−0.005
	Step length	Early change	0.526	−0.05	0.02	−0.200
		Overall change	0.562	−0.05	0.03	−0.183
	Step time	Early change	0.337	−0.04	0.01	−0.304
		Overall change	**<0.001**	−0.08	−0.03	−1.170
Postadaptation	Error	Early change	**0.002**	13.86	55.30	1.055
		Overall change	**0.037**	1.51	44.14	0.677
	Step length	Early change*	**0.006**	0.02	0.11	0.928
		Overall change*	0.089	−0.01	0.08	0.545
	Step time	Early change	0.164	−0.01	0.04	0.444
		Overall change	0.093	−0.00	0.05	0.537

Group differences between young ($n = 21$) and older adults ($n = 20$) are analyzed with a Student t test, and effect size is given by Cohen's d. *Levene's test was violated and P value reported is from a Welch test. Bolded P values are statistically significant differences ($P < 0.05$).

To investigate what component of step time asymmetry adaptation was different between age groups, we examined step time for each leg separately (Fig. 5). Overall change in step time in both the fast and slow leg was different between groups; young adults adjusted to take faster steps on the fast leg and slower steps on the slow leg compared with older adults (Fast leg: $P = 0.002$, d = –1.028; Slow leg: $P < 0.001$, d = 1.178). These group differences were present after controlling for physical function [Fast leg: $F(1,38) = 13.15$, $P < 0.001$; Slow leg: $F(1,38) = 15.53$, $P < 0.001$]. As shown by the stride-by-stride plots and effect size, there were greater differences in the slow leg than the fast leg. This may suggest that older adults have more resistance to adapting to take longer steps.

Older Adults Demonstrate Reduced EMG-EMG Coherence

For all EMG-EMG coherence, older adults demonstrated lower coherence compared with younger adults (Table 4). Beta-gamma-band tibialis anterior coherence in the fast leg during swing phase was different between conditions, but condition × group interaction effect was not significant [Fig. 6*A*, Condition: $F(4, 156) = 5.20$, $P < 0.001$; Condition × group: $F(4, 156) = 1.95$, $P = 0.105$]. Post hoc between-conditions comparisons showed that coherence increased during early adaptation, and it was significantly higher compared with late postadaptation. Coherence during late postadaptation was also lower compared with baseline prefast.

Beta-gamma tibialis anterior coherence in the slow leg during swing phase was different between conditions, but condition × group interaction effect was not significant [Fig. 6*B*, Condition: $F(5, 195) = 4.36$, $P < 0.001$; Condition × group: $F(5, 195) = 1.57$, $P = 0.171$]. Post hoc between-conditions comparisons showed that coherence increased during early adaptation and it was significantly higher compared with late postadaptation. Coherence during late postadaptation was also lower compared with baseline preslow.

Fast leg beta-gamma plantarflexor (MGAS-SOL) coherence during stance phase was different not between conditions, and condition × group interaction effect was not significant [Fig. 6*C*, Condition: $F(4, 156) = 1.39$, $P = 0.240$; Condition × group: $F(4, 156) = 0.56$, $P = 0.696$]. Slow leg plantarflexor coherence was different between conditions, but condition × group interaction effect was not significant [Fig. 6*D*, Condition: $F(3.40, 132.72) = 5.18$, $P = 0.001$; Condition × group: $F(3.40, 132.72) = 0.74$, $P = 0.544$]. Post hoc between-conditions comparisons showed that coherence increased during adaptation compared with baseline prefast and preslow, and coherence during early adaptation was higher compared with late postadaptation.

Fast leg beta-gamma gastrocnemius (MGAS-LGAS) coherence during stance phase was not different between conditions, and condition × group interaction effect was not significant [Fig. 6*E*, Condition: $F(3.05, 118.85) = 0.56$, $P = 0.645$; Condition × group: $F(3.05, 118.85) = 1.41$, $P = 0.244$]. Slow leg gastrocnemius coherence was different between conditions, but condition × group interaction effect was not significant [Fig. 6*F*, Condition: $F(2.91, 113.29) = 2.94$, $P = 0.038$; Condition × group: $F(2.91, 113.29) = 0.87$, $P = 0.457$]. Post hoc between-conditions comparisons showed that coherence was lower during late adaptation compared with baseline prefast.

EMG-EMG Coherence Associated with Step Time Adaptation

A significant regression model was found for the overall change in step time asymmetry during adaptation [$F(1, 39) = 17.60$, $P < 0.001$; $r^2 = 0.311$, RMSE = 0.045]. Higher slow leg intramuscular tibialis anterior beta-gamma coherence during the first 100 strides of adaptation significantly predicted larger overall change (i.e., more negative overall change) in step time asymmetry adaptation, and there was no group interaction effect, suggesting that the association between corticospinal drive and step time adaptation is consistent in young and older adults (Fig. 7; Unstandardized $\beta = -0.040$, Standardized $\beta = -0.558$, $P < 0.001$).

DISCUSSION

In this study, we examined how age-related changes in corticospinal drive impact visuomotor adaptation and gait adaptability during walking in healthy older adults. Our findings suggest that older adults exhibit the capacity for error reduction similar to that of younger adults and the ability to store new visuomotor calibrations during precision walking. However, older adults displayed smaller changes in step

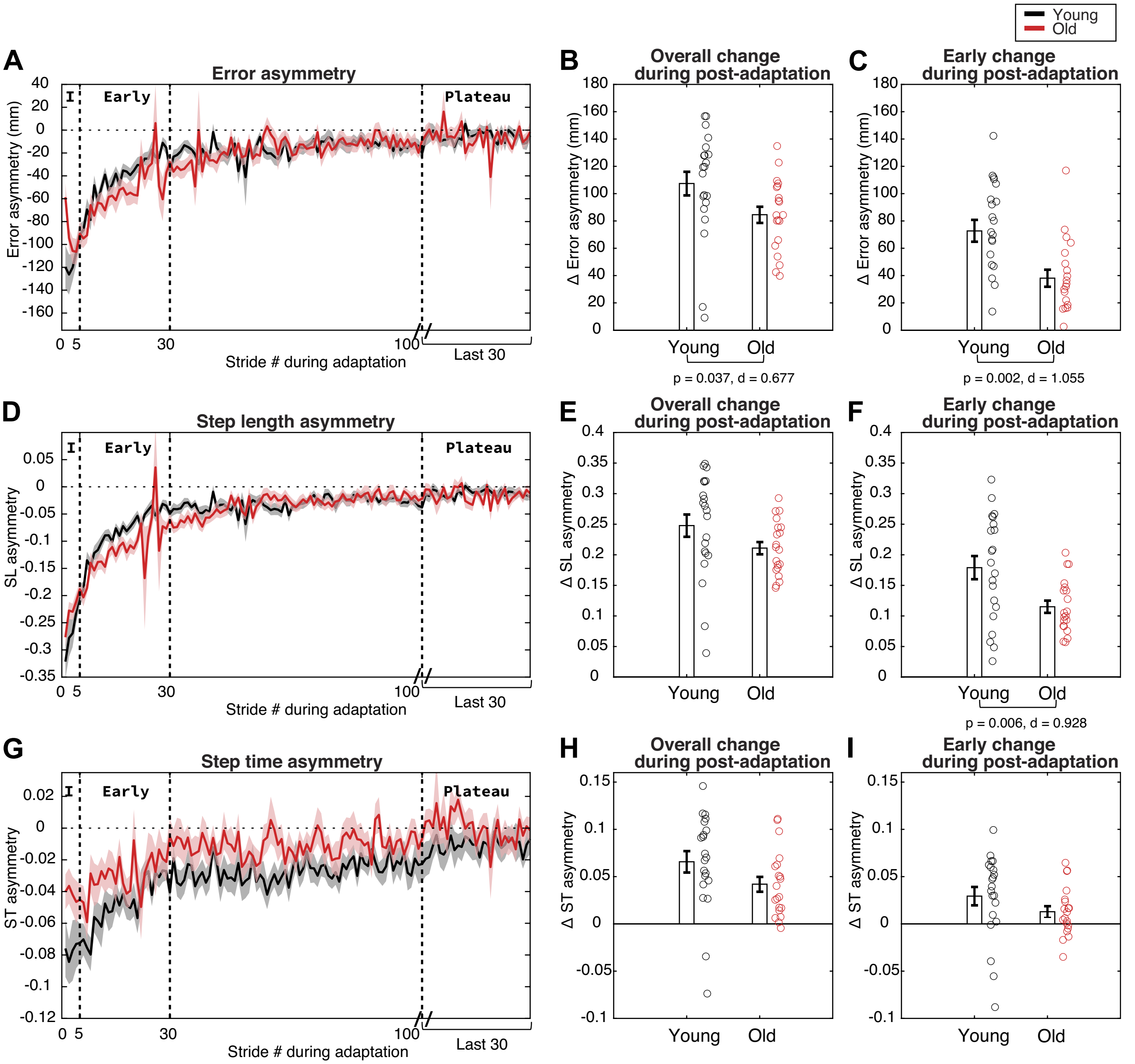


Figure 4. Visuomotor adaptation and gait asymmetry during postadaptation. Stride-by-stride changes in error asymmetry (*A*), step length asymmetry (*D*), and step time asymmetry (*G*) during postadaptation. Initial (I) = Strides #1–5, Early = Strides #6–30, Plateau = last 30 strides. Age group means and standard error bars for overall change during postadaptation (*B, E, H*) and early change during postadaptation (*C, F, I*). Overall change = Δ plateau phase – initial phase; Early change = Δ early phase – initial phase; black circles = young participants (*n* = 21); red circles = older participants (*n* = 20). SL, step length; ST, step time.

timing during visuomotor adaptation compared with young adults. This reduction in overall change in step time asymmetry was associated with the level of corticospinal drive to the tibialis anterior in the slow leg in young and older adults. Our results indicate that age-related changes in corticospinal drive may specifically alter timing control strategies and temporal gait adjustments in response to visual cues.

Adapting and Storing Visuomotor Calibrations in Walking

Visuomotor adaptation is an error-based learning process that involves the recalibration of sensorimotor mappings to maintain movement accuracy (39, 40). Both healthy young and older adults have the capacity to adapt leg movements in response to visual perturbations (16–18, 41, 42). However, previous studies have suggested that aging may impair this ability, leading to slower or small overall error reduction during walking in older adults (16–18, 42). In this study, older adults demonstrated a reduction in foot placement error symmetry that was comparable to younger adults during split-visuomotor adaptation. Another study similarly indicated that when visuomotor adaptation involved precision stepping, older adults achieved error reduction levels comparable to young adults (41). Together, these studies suggest that the capacity for visuomotor adaptation in older adults is "normal" (i.e., comparable to that of younger adults), but could also vary depending on the precision demands of the walking task. Our study further showed that aging did not affect the ability to

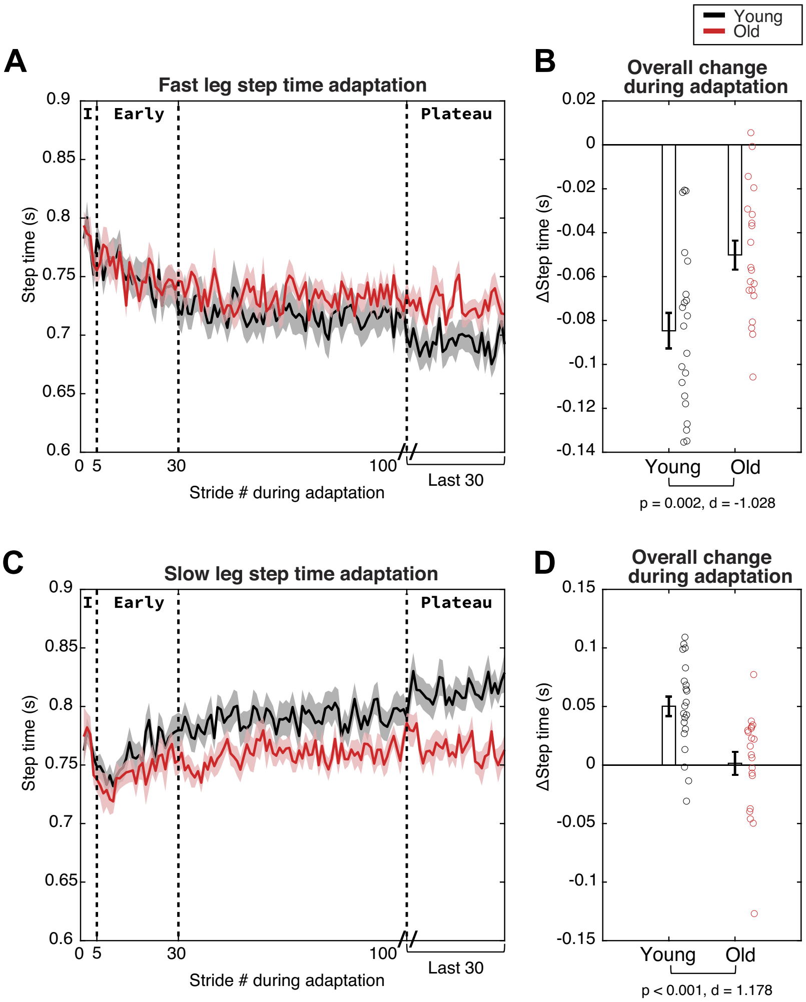


Figure 5. Step time adaptation. Stride-by stride changes in the fast leg (*A*) and slow leg (*C*). Initial (I) = Strides #1–5, Early = Strides #6–30, Plateau = last 30 strides. Age group means and standard error bars for overall change during adaptation in the fast leg (*B*) and slow leg (*D*). Overall change = Δ plateau phase − initial phase. Black circles = young participants (*n* = 21); red circles = older participants (*n* = 20).

retain new visuomotor calibration in walking, as aftereffects in foot placement errors were observed in older adults. These results are consistent with previous studies demonstrating similar aftereffects in young and older adults following visuomotor adaptation (41, 43, 44).

Spatial and Temporal Control of Gait Adaptation with Aging

To reduce foot placement error during the visuomotor adaptation, participants can adjust their step timing and step positioning to minimize error. The initial error arises from a split-visuomotor gain, making the slow foot appear to undershoot the target. The slow target also moves slower, such that the distance to the fast target looks shorter, leading participants to overshoot on the fast leg. By extending step time on the slow leg, participants can wait for the slow target to get closer to reduce error on the slow leg. Participants can also shift the slow limb further forward to minimize the undershoot. Both the timing and positioning strategies would contribute to change step length asymmetry (26). See Supplemental Fig. S3 for detailed kinematics in a typical young adult.

We showed that older adults had reduced overall change in step time in both fast and slow limbs during split-visuomotor adaptation compared with younger adults. Notably, the difference between age groups was larger in the slow limb compared with the fast limb, suggesting that older adults may have resisted extending their step times. Despite these timing differences, older participants took increasingly longer step lengths on their slow leg compared with the fast leg, and their overall change in step length asymmetry was similar to that of young adults. This suggests that older adults may be relying more on a positioning strategy to achieve similar step length symmetry and error reduction. See Supplemental Fig. S4 for kinematics from a typical older adult.

Table 4. *Main effect of age group on coherence*

Coherence	Leg	*P* Value	Cohen's d
Tibialis anterior (TAp-TAd)	Fast leg	**<0.001**	1.588
	Slow leg	**<0.001**	1.771
Plantarflexor (MGAS-SOL)	Fast leg	**<0.001**	1.164
	Slow leg	**0.012**	0.741
Gastrocnemius (MGAS-LGAS)	Fast leg	**<0.001**	1.458
	Slow leg	**<0.001**	1.400

P value is from the main effect of age groups [between young (*n* = 21) and older adults (*n* = 20)] in the mixed-measures ANOVA. Effect size is given by Cohen's d. LGAS, lateral gastrocnemius; MGAS, medial gastrocnemius; SOL, soleus; TAd, distal tibialis anterior; TAp, proximal tibialis anterior. Bolded *P* values are statistically significant differences ($P < 0.05$).

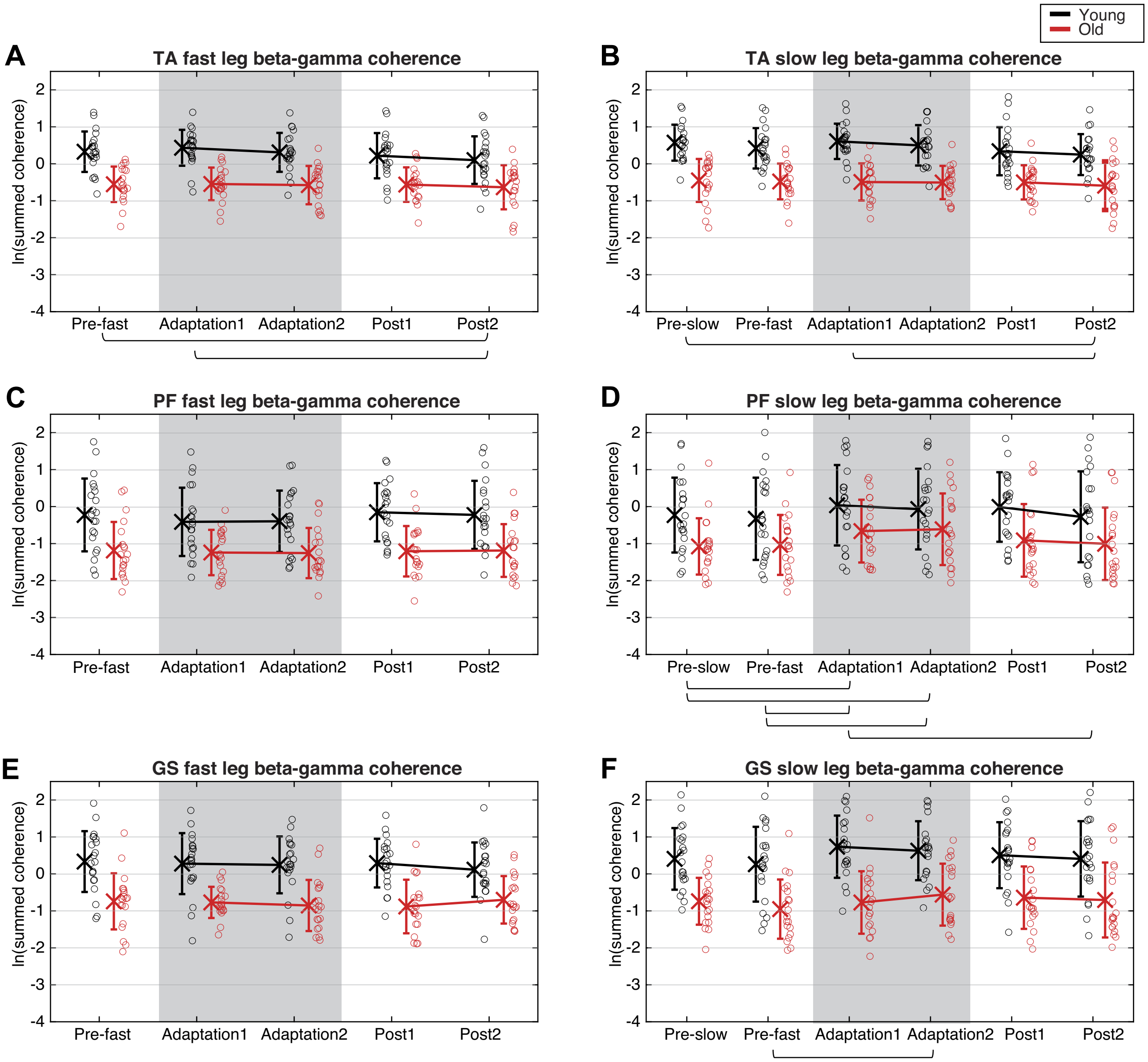


Figure 6. Natural logarithm of cumulative beta-gamma EMG-EMG coherence between the proximal and distal tibialis anterior (*A* and *B*), the medial gastrocnemius and soleus (*C* and *D*), and the medial and lateral gastrocnemius (*E* and *F*) in the fast (*A*, *C*, *E*) and slow leg (*B*, *D*, *F*). Black = young ($n = 21$); red = old ($n = 20$); X = group means; error bars = standard deviation. Gray shaded areas represent adaptation (adaptation 1 = first 100 strides, adaptation 2 = last 100 strides). Brackets indicate between-condition comparisons where $P < 0.05$. All comparisons were corrected for multiple comparisons using the Bonferroni method. GS, gastrocnemius; PF, plantarflexors; TA, tibialis anterior.

Previous studies have suggested the independent control of temporal and spatial aspects of walking adaptation (28, 45, 46). Our results suggest that aging may impact temporal adaptation more compared with spatial adaptation during visuomotor walking adaptation. The differential influence of aging on step time versus step length adaptation could be related to the additional cost of asymmetric step time in walking (46, 47). Walking with asymmetric step times is associated with greater additional metabolic costs compared with walking with asymmetric step lengths (46, 47). Although we did not examine metabolic cost, previous studies have shown that older adults have higher metabolic costs during walking compared with younger adults (48). Therefore, older adults may prioritize maintaining symmetrical step times to decrease metabolic expenditure during split-visuomotor walking adaptation. Note that participants of this study were instructed to "step accurately in the target as possible" without specific guidance on step timing. Therefore, the reduced step time asymmetry in older adults may reflect a more economically efficient strategy compared with younger adults.

Corticospinal Drive and Its Role in Walking Adaptation in Older Adult

Corticospinal drive to leg muscles quantified by beta-gamma coherence was lower in older adults compared with younger adults during walking. This is in agreement with previous studies that examined EMG-EMG coherence in

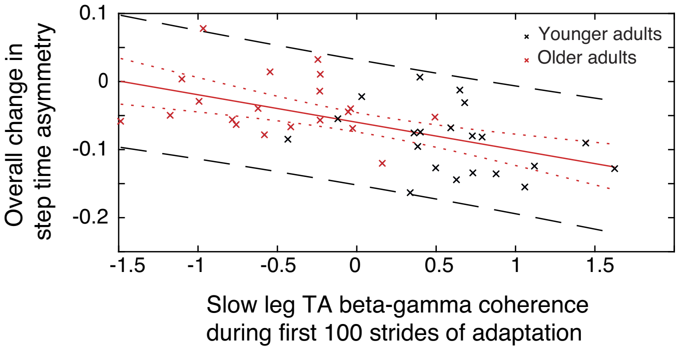


Figure 7. Regression model for overall change in step time asymmetry during adaptation. Black X = young adults (n = 21); red X = older adults (n = 20). TA, tibialis anterior.

older and younger adults during normal and visually guided walking (19, 49) and during split-belt treadmill adaptation (20). These studies suggest that age-related changes in corticospinal drive may alter walking function in older adults.

Specifically, slow leg tibialis anterior beta-gamma coherence was identified as a significant predictor of the overall change in step time asymmetry during split-visuomotor locomotor adaptation. There were no associations between corticospinal drive and step length asymmetry changes nor error asymmetry changes during split-visuomotor adaptation. Previous studies on split-belt locomotor adaptation also showed an association between corticospinal drive and double support asymmetry but not step length asymmetry (20, 25). The relationship between corticospinal drive with temporal but not spatial gait parameters during multiple forms of locomotor adaptation may suggest that corticospinal drive plays a specific role in controlling the timing of gait kinematics.

Note that neither the plantarflexors nor the gastrocnemius coherence during stance was associated with kinematic adaptation during split-visuomotor locomotor adaptation. The lack of relationships between the corticospinal drive to posterior lower leg muscles active during stance suggests that in this task, corticospinal drive may be more important for corrections during swing phase to make appropriate timing adjustments.

Previous studies in people with hemispherectomy indicated that large cerebral lesions do not abolish one's ability to adapt spatial variables, but they demonstrated impaired temporal adaptation in walking (50). This may be due to separate neural mechanisms controlling locomotor cycle timing and cycle pattern (51). In cats, it has been shown that both the motor cortex and the red nucleus have access to circuits controlling the cycle pattern, but only the motor cortex has access to circuits controlling cycle timing (52, 53). The distinct neural mechanisms implies that temporal adjustments may depend more on corticospinal drive to be executed effectively.

It is also documented that older adults overactivate the prefrontal cortex when performing motor and cognitive tasks (54). Functional near-infrared spectroscopy studies have revealed a positive correlation between stride-time variability and activation in the primary motor cortex (55). The relationship between increased cortical activity and decreased corticospinal drive however is not well understood. One hypothesis is that cortical networks may be compensating for the reduced corticospinal drive (56). Further studies using multimodal brain and muscle recordings would be needed to understand their integrated role in gait adaptation with age.

Limitations

There is a challenge in the interpretation of aging outcomes as there are many covariates. Here, we recruited an older sample for our aging cohort (i.e., not middle-aged older adults), as there are fewer studies with older adult cohorts with a group age average >70 yr old (for review see Ref. 57). To facilitate the interpretation and to serve as a reference for future studies, we have included functional assessments that characterized physical and mental status.

Another challenge in the interpretation of kinematics outcomes is the lack of a universal method for quantifying the time course of changes that occur during adaptation. Some studies have quantified the rate by exponential models, or the number of strides to achieve a certain threshold, usually defined by a plateau ± individual variability (58, 59). In this study, we used difference measures to quantify the overall (Δ plateau − initial) versus early (Δ early − initial) changes in kinematic parameters (20), to capture different phases of adaptation and deadaptation.

Our study did not include direct measures of corticomuscular coherence (e.g., EEG-EMG) in parallel with measurements of intramuscular coherence. There may be other neural influence that alters the EMG-EMG coherence, and it would be optimistic to state that the coherence measure quantifies corticospinal drive exclusively. In addition, cross talk between EMG signals can contaminate coherence. To minimize the risk of cross talk between EMG signals, the proximal and distal EMG electrodes were placed at the furthest points in the muscle belly (at least 10 cm apart from each other), and coherence and cumulant density plots were visually examined (38). Based on previous studies (60, 61), the changes in beta-gamma EMG-EMG coherence reported in our study are likely to be largely resultant from the changes in corticospinal activity originating from the motor cortex.

Conclusions

This study provides new insights into the influence of age-related changes in corticospinal drive on visuomotor adaptation and gait adaptability. While older adults can adapt walking patterns to visual perturbations, the underlying neural and gait strategies differ with increased age. We found an age-related reduction in corticospinal drive that is associated with inflexible gait timing. These findings contribute to the literature on how aging affects motor learning and highlight a specific role of corticospinal drive during visuomotor walking adaptation, with potential implications for gait rehabilitation.

DATA AVAILABILITY

Data will be made available upon reasonable request.

SUPPLEMENTAL DATA

Supplemental Video: dx.doi.org/10.6084/m9.figshare.22070123.
Supplemental Fig. S1: dx.doi.org/10.6084/m9.figshare.24412594.
Supplemental Fig. S2: dx.doi.org/10.6084/m9.figshare.24412696.
Supplemental Fig. S3: dx.doi.org/10.6084/m9.figshare.24412705.
Supplemental Fig. S4: dx.doi.org/10.6084/m9.figshare.24412702.

GRANTS

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

S.D.S. and J.T.C. conceived and designed research; S.D.S. performed experiments; S.D.S. analyzed data; S.D.S. and J.T.C. interpreted results of experiments; S.D.S. prepared figures; S.D.S. drafted manuscript; S.D.S. and J.T.C. edited and revised manuscript; S.D.S. and J.T.C. approved final version of manuscript.

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