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Age does not affect the relationship between muscle activation and joint work during incline and decline walking

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ABSTRACT

Older compared with younger adults walk with different configurations of mechanical joint work and greater muscle activation but it is unclear if age, walking speed, and slope would each affect the relationship between muscle activation and net joint work. We hypothesized that a unit increase in positive but not negative net joint work requires greater muscle activation in older compared with younger adults. Healthy younger (age: 22.1 yrs, $n = 19$) and older adults (age: 69.8 yrs, $n = 16$) ascended and descended a 7° ramp at slow (~1.20 m/s) and moderate (~1.50 m/s) walking speeds while lower-extremity marker positions, electromyography, and ground reaction force data were collected. Compared to younger adults, older adults took 11% (incline) and 8% (decline) shorter strides, and performed 21% less positive ankle plantarflexor work (incline) and 19% less negative knee extensor work (decline) (all $p < .05$). However, age did not affect (all $p > .05$) the regression coefficients between the muscle activation integral and positive hip extensor or ankle plantarflexor work during ascent, nor between that and negative knee extensor or ankle dorsiflexor work during descent. With increased walking speed, muscle activation tended to increase in younger but changed little in older adults across ascent ($10 \pm 12\%$ vs. $-1.0 \pm 10\%$) and descent ($3.6 \pm 10.2\%$ vs. $-2.6 \pm 7.7\%$) ($p = .006$, $r = 0.47$). Age does not affect the relationship between muscle activation and net joint work during incline and decline walking at freely-chosen step lengths. The electromechanical cost of joint work production does not underlie the age-related reconfiguration of joint work during walking.

1. Introduction

Healthy aging is accompanied by adjustments in walking mechanics. A functionally relevant adaptation is the 16–30% lower positive ankle plantarflexor (APF) work coupled with 22–82% greater positive hip extensor (HE) and/or flexor (HF) work (DeVita & Hortobagyi, 2000; McGibbon, 2003). Reduced positive APF work is relevant because it correlates with slower walking speed (Uematsu et al., 2018), which predicts mobility disability and falls (Abellan van Kan et al., 2009). In contrast, the distribution of negative work is independent of age during level and decline walking (Waanders et al., 2019), possibly due to the age-related relative maintenance of maximal voluntary eccentric muscle strength (Roig et al., 2010).

This reconfiguration of joint mechanical work may be due to reductions in muscle mass (Tieland et al., 2018) and changes in muscle activation. For example, compared to younger adults, older adults tend to show a smaller increase in APF activation during push-off with increasing walking speed (Schmitz et al., 2009) and inclination (Franz & Kram, 2013), and a larger increase in HE activation with speed (Schmitz et al., 2009) but not incline (Franz & Kram, 2013). In addition, age seems not to affect knee extensor (KE) activation, the primary energy absorbers (Alexander et al., 2017), nor ankle dorsiflexor (ADF) activation during level and decline walking (Franz & Kram, 2013).

To our knowledge, the relationship between muscle activation and mechanical joint work during walking has not been examined but could provide insights into the neural-based mediating effects on the age-

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related joint work redistribution. That is, the increased agonist muscle activation and antagonist co-activation in older vs. younger adults during walking (Hortobágyi et al., 2009; Mian et al., 2006) may lead to greater muscle activation per unit increase in net joint work, i.e. electromechanical cost (Billot et al., 2010). Greater antagonist co-activation is thought to increase joint stability through increased joint stiffness (Hortobágyi & DeVita, 2000), but would also require greater agonist activation to produce a certain amount of net joint work. The emerging picture supporting an age-related increase in electromechanical cost is that the difference in APF activation is less pronounced than the difference in APF positive work (Cofre et al., 2011; DeVita & Hortobagyi, 2000; Franz & Kram, 2013; Schmitz et al., 2009). The potential age effect on electromechanical cost is relevant to determine as it could reinforce the age-related reconfiguration of joint work in order to specifically keep the APF from operating at or near their maximum torque capacity during walking (Beijersbergen et al., 2013; Kulmala et al., 2020; Reeves et al., 2008). Also, muscle activation in turn positively correlates with age-related increases in metabolic cost during level (Hortobagyi et al., 2011) and incline (Ortega & Farley, 2015) walking.

Higher electromechanical costs in older compared with younger adults may be evident only for positive joint work during incline walking and not for negative joint work during decline walking. We make this conjecture because descending involves predominantly lengthening muscle contractions that partially rely on passive forces generated by series elastic structures (Lindstedt et al., 2016), requiring less muscle activation per unit muscle force than shortening muscle contractions predominant while ascending (Bigland-Ritchie & Woods, 1976; Duchateau & Enoka, 2016). Also, decline walking selectively increases muscular demand only on the KE and ADF (Franz & Kram, 2013; Waanders et al., 2019).

In this study, we examined the effects of age and walking speed on the relationship between muscle activation and mechanical joint work during incline and decline walking. We hypothesized that a unit increase in positive but not negative net joint work requires greater muscle activation in older compared with younger adults. We further hypothesized that, compared to younger adults, older adults would exhibit a larger increase in leg muscle activation with faster walking speed during incline but not decline walking.

2. Methods

2.1. Participants

In this cross-sectional study, participants were recruited via word of mouth and flyers distributed at shopping centers and attended one, 2-hour laboratory session. Inclusion criteria were: 18–30 or 65+ years of age and ability to negotiate stairs independently. Exclusion criteria were: any lower-extremity neuromuscular impairment, a history of neurological conditions (dementia, Parkinson's disease, stroke), severe diabetes, asthma, chronic bronchitis, or pregnancy. Before measurements, participants provided written informed consent. The local medical ethics committee at the University Medical Center Groningen, the Netherlands, approved the study (METc no. 2018/622). Younger ($n = 19$) and older adults ($n = 16$) participated in the study who were cognitively healthy (MMSE score ≥ 24, (Folstein et al., 1975)) and had no mobility limitations (SPPB score ≥ 9, (Guralnik et al., 1994)) (Table 1).

2.2. Experimental conditions

Participants ascended and descended a custom-built ramp at two different speeds. Midway embedded in the ramp (6.0 × 1.3 m, 7°, 2-m-long landing surrounded by a railing), was a 0.6 × 0.4 m Bertec force platform (Bertec, Columbus, OH, USA) that was mounted on a solid aluminum frame affixed to the floor. The order of walking speed was block randomized and participants were able to rest between blocks. A minimum of five successful trials per walking condition were collected. A trial was successful when the participant fully stepped on the force platform with the right (incline) or left (decline) foot, because of camera positioning, and when walking speed was within ±5% in the slow (1.20 m/s) and the moderate (1.50 m/s) condition. Participants received verbal feedback on walking speed based on the times measured by a timing system (Minitimer HL 440, TAG Heuer, Switzerland) positioned 0.5 m before and after the force platform.

Table 1
Subject characteristics.

	Younger (10 M, 9F)	Older (8 M, 8F)
Age, years	22.1 (2.6)	69.8 (4.6)
Body height, m	1.78 (0.09)	1.72 (0.07)
Body weight, kg	72.5 (10.1)	73.8 (13.1)
BMI, kg/m^2	22.7 (2.2)	24.9 (3.1)
MMSE score	29.8 (0.4)	28.6 (1.3)
SPPB score	11.9 (0.5)	11.2 (0.8)

Values are in mean (SD). MMSE: Mini-Mental State. Examination, SPPB: Short Physical Performance Battery. M: males, F: females.

2.3. Data collection

During walking, right (incline) and left (decline) leg marker position data were collected at 100 Hz using three Optotrak, active motion-capture units (Northern Digital Inc., Waterloo, Ontario, Canada). Markers were placed on the subjects' anterior and posterior superior iliac spines (plus three tracking markers), lateral thighs (three tracking markers), lateral shanks (three tracking markers), calcanei, and on top of each foot (three tracking markers). The tracking markers served as reference points to define virtual markers with a digital pointer on the greater trochanters, medial and lateral femoral epicondyles, medial and lateral malleoli, and first and fifth metatarsal heads. Ground reaction force (GRF) and moment data in 3D were collected at 1 kHz.

Surface electromyography (EMG) data were collected at 2 kHz using wireless, pre-amplified (909x) parallel-bar sensors (Trigno, Delsys Inc., Natick, MA, USA). These sensors were affixed bilaterally to the following muscles according to SENIAM conventions (Hermens et al., 2000): gluteus maximus (GluMax), semitendinosus (ST), biceps femoris long head (BF), rectus femoris (RF), vastus medialis (VM), gastrocnemius medialis (GaMed), soleus (SOL), and tibialis anterior (TA). Prior to sensor placement, the skin was shaved, abraded with soft sandpaper, and cleaned with alcohol pads. Signal quality for each muscle was visually checked by having participants perform a 3-s long isometric contraction against manual resistance. EMG, force platform, and marker position data were synchronized using an external trigger signal.

2.4. Data analyses

Raw marker position and GRF data were imported into Visual3D (C-Motion Inc., Rockville, Maryland, USA) and low-pass (cut-offs: 6 and 45 Hz, respectively) filtered (4th-order, Butterworth). Marker position data and body height and body mass-based regression equations were used to build a four-segment (pelvis, thigh, shank, foot) rigid-body model. This model and GRF data, with a threshold of 20 N to detect gait events, were used to perform inverse kinematics and dynamics. These analyses produced spatiotemporal measures and lower-extremity joint angles, net joint moments and powers. The data were exported to a custom MATLAB script (Mathworks, Natick, MA, USA) that integrated the body mass normalized joint power-curves over time to obtain the largest energy generation and absorption segments during stance (Waanders et al., 2019). That is, for incline walking, during 0–50% (i.e., heel strike-mid stance) and 50–100% (midstance-toe off) of stance for positive HE work (H1) and for positive APF work (A2), respectively. For decline walking this was during 0–30% (heel strike-peak knee flexion) and 0–20% (heel strike-foot flat) of stance for negative KE work (K1) and for negative ADF work (A0), respectively.

Raw muscle activity signals were band-pass filtered (20–450 Hz) by the Delsys hardware and exported to a custom MATLAB script. After visual inspection of these signals, GluMax data for two participants and VM data for one participant were excluded because of movement artifacts. Further signal processing consisted of offset removal, rectification, and smoothing by calculating the root mean square using a 40 ms moving (step width = 1 unit) window (Basmajian & De Luca, 1985). The signals were then time-normalized (0–100%) with respect to the stance time of each respective trial for each participant in order to compute average muscle activity-curves across the five trials per walking condition. The area under these curves was multiplied by the average non-normalized duration of 1) the 'respective' joint work segment as previously defined and 2) stance to obtain absolute muscle activation integrals (amplitude*duration). These respective segments were as follows: Hamstrings (ST, BF) and GluMax activity-integrals during H1, RF and VM integrals during K1, GaMed and SOL integrals during A2 and the TA integral during A0. The EMG integral was chosen for the EMG analyses rather than the average amplitude (e.g., Nilsson et al., 1985) because the integral incorporates the natural changes in stance time during walking that occur with age, slope, and speed (Waanders et al., 2019). The conclusions based on both methodologies were comparable but the amplitude-based outcomes were also reported (see Supplementary Table and Figure S1) to allow for better comparison with previous literature.

For each muscle, the relative change in activity (i.e., the EMG integral) from slow to moderate walking speed was computed across the respective joint work segment and stance. Relative changes in hamstrings and GluMax activity were pooled to represent HE activity. Similarly, KE (pooled VM and RF), APF (pooled SOL and GaMed), and ADF (TA) activities were calculated. The average change in activity measured during stance across the four muscle groups represented total muscle activation change. Lastly, each muscle's activation was normalized to its mean activation-amplitude during moderate incline walking. These normalized muscle activations were used to determine co-activation indices (CI) from agonist-antagonist muscle pairs at the thigh (RF-ST, RF-BF, VM-ST, VM-BF) and shank (TA-SOL, TA-GaMed), using the following equation (Peterson & Martin, 2010):

$$CI(EMG_1, EMG_2) = 2*\frac{\int \min(EMG_1, EMG_2)}{\int \min(EMG_1, EMG_2) + \int \max(EMG_1, EMG_2)}*100 \tag{1}$$

in which min and max are the minimum and maximum muscle activity curve at each sampled value of the stance phase. Muscle pairs at the thigh and shank were averaged to obtain thigh and shank co-activation, respectively. Averaged thigh and shank co-activation represented total co-activation.

2.5. Statistical analyses

Linear regressions were performed for each muscle group between the relative change in muscle group activation (predictor) and absolute change in joint work (outcome) from slow to moderate speed. These regressions were performed in younger and older adults separately and combined. A dummy-predictor variable 'age' (younger, older) was added to the age-combined data to test for age effects. The regressions met the assumptions of homoscedasticity, independent errors, normal residual distribution, and linearity. A two-way mixed ANOVA (between-participant factor age; within-participant factor slope) was performed on the relative change in total muscle activation from slow to moderate walking speed. Three-way mixed ANOVAs (between-participant factor age; within-participant factors slope and speed) were performed on thigh, shank, and total co-activation. The assumptions of normality (Shapiro-Wilk test) and equal variances (Levene's test) were met. Effect sizes of r = 0.1, r = 0.3, and r = 0.5 represent small, moderate, and large effects, respectively (Cohen, 1992). For all analyses, alpha was set at 5% and IBM SPSS Statistics 26 (SPSS Inc., Chicago, IL, USA) used.

3. Results

3.1. Walking kinematics and kinetics

Table 2 shows that although younger and older adults walked at similar speeds, older adults took 11% ($p < 0.001$) and 8% ($p = 0.001$) shorter strides during incline and decline walking, respectively. Fig. 1 shows age-related lower-extremity joint powers for both slopes and walking speeds. Across incline conditions, older vs. younger adults generated 21% less ($p < 0.001$) APF work and comparable ($p = 0.981$) HE work (Table 2). Across decline conditions, older vs. younger adults generated 19% less ($p = 0.022$) KE work and comparable ($p = 0.157$) ADF work. With faster speed, age did not affect (all $p > 0.05$) the increases in positive HE and APF work, nor the increases in negative KE and ADF work.

3.2. Relationship between muscle activation and net joint work

During incline walking, HE muscle activation predicted (all $p < .05$) 41% (R^2, in younger), 33% (older), and 30% (combined) of the variance in positive HE joint work (Fig. 2). APF muscle activation predicted (all $p < .05$) 48% (younger), 39% (older), and 44% (combined) of the variance in positive APF joint work. Age did not affect the regression coefficient at the hip [$t(32) = 0.68$, $p = .500$] nor the ankle [$t(34) = -0.52$, $p = .605$].

During decline walking, KE muscle activation predicted 20% ($p = .051$, younger), 5% ($p = .444$, older), and 20% ($p = .008$, combined) of the variance in negative KE joint work (Fig. 2). ADF muscle activation predicted (all $p < .05$) 23% (younger), 19% (older), and 22% (combined) of the variance in negative ADF work. Age did not affect the regression coefficient at the knee [$t(33) = 0.19$, $p = .848$] nor the ankle

Table 2
Spatiotemporal measures and net joint work during incline and decline walking.

	Decline		Incline	
	slow	moderate	slow	moderate
Speed, m/s[a]				
younger	1.18 (0.03)	1.49 (0.03)	1.19 (0.04)	1.49 (0.05)
older	1.15 (0.04)	1.47 (0.04)	1.16 (0.06)	1.46 (0.05)
Stride length, m				
younger	1.40 (0.11)	1.62 (0.09)	1.54 (0.10)	1.74 (0.07)
older*	1.31 (0.08)	1.48 (0.10)	1.39 (0.11)	1.54 (0.13)
Stance time, s				
younger	0.74 (0.05)	0.66 (0.04)	0.80 (0.05)	0.71 (0.03)
older	0.72 (0.05)	0.62 (0.06)	0.76 (0.08)	0.65 (0.06)
Stance phase, %				
younger	62.5 (1.5)	60.3 (1.5)	62.7 (1.2)	61.0 (1.0)
older	63.2 (2.0)	60.7 (2.1)	63.8 (1.5)	62.1 (1.6)
Joint work, J/kg				
Hip extensors				
younger			0.09 (0.05)	0.22 (0.08)
older			0.09 (0.05)	0.22 (0.07)
Ankle plantarflexors				
younger			0.53 (0.09)	0.61 (0.09)
older*			0.41 (0.08)	0.49 (0.09)
Knee extensors				
younger	−0.22 (0.06)	−0.36 (0.09)		
older*	−0.18 (0.07)	−0.29 (0.08)		
Ankle dorsiflexors				
younger	−0.04 (0.01)	−0.05 (0.02)		
older	−0.03 (0.02)	−0.04 (0.02)		

Values are in mean (SD). [a]Walking speed when also taking into account the participants' vertical displacement during incline and decline walking. *Age effect ($p < 0.05$).

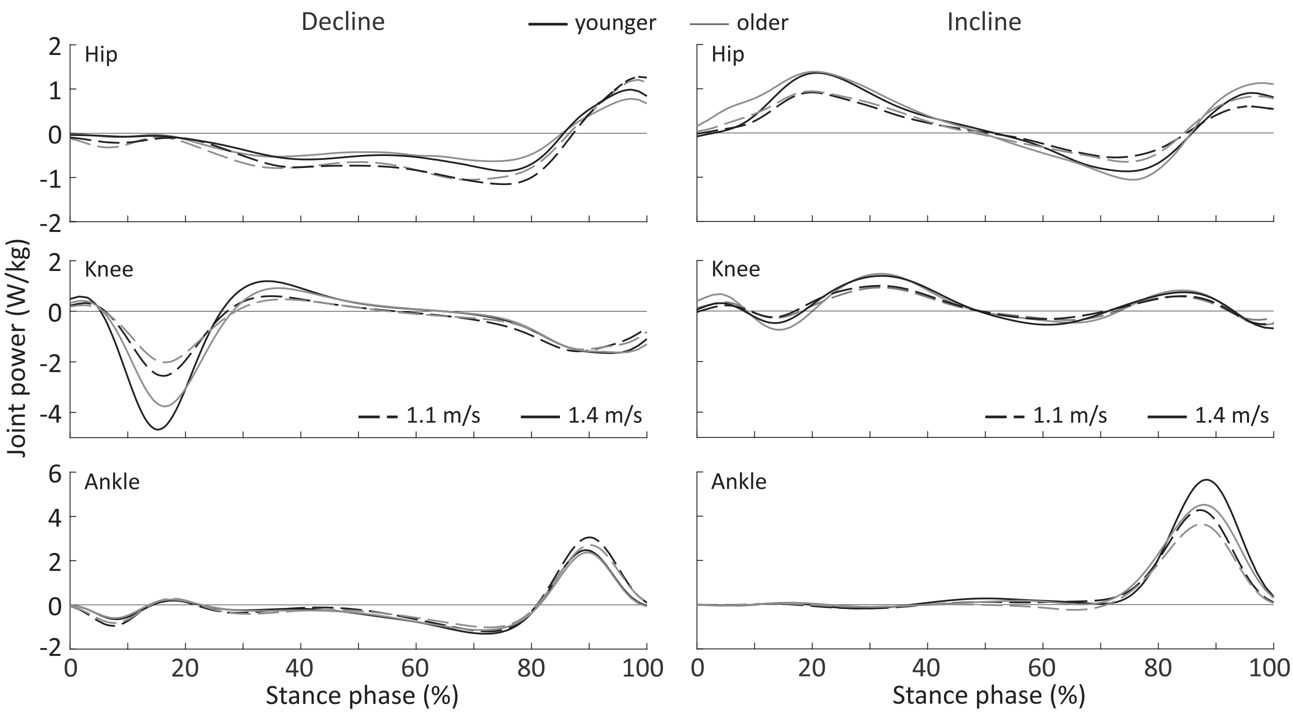

Fig. 1. Group average joint powers during decline and incline walking in younger (black lines) and older adults (grey lines).

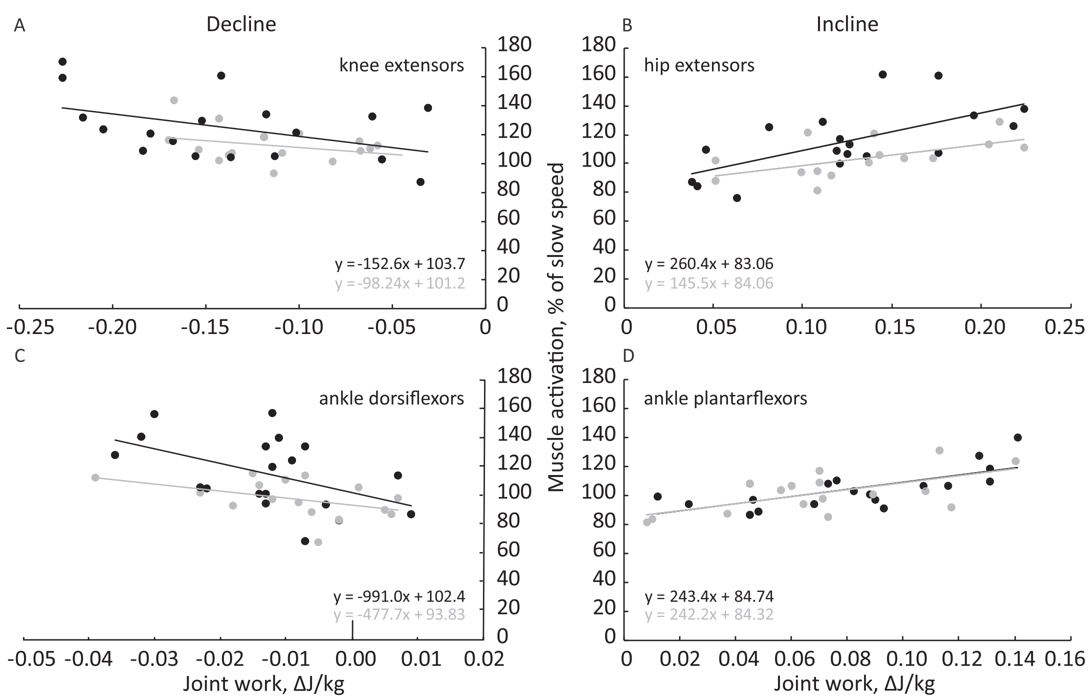

Fig. 2. Regressions of muscle group activation on net joint work at moderate decline (A,C) and incline (B,D) walking speed. Plot A and C show knee extensor and ankle dorsiflexor data, respectively. Plot B and D show hip and ankle extensor data, respectively. Black represents young adults, grey represents older adults. Linear equations are presented in the plots. Age effects were absent (see text). Regression statistics: (**A**) young: $R^2 = 0.21$, $\beta = -0.45$ ($p = .051$); old: $R^2 = 0.05$, $\beta = -0.21$ ($p = .444$); combined: $R^2 = 0.20$, $\beta = -0.45$ ($p = .008$). (**B**) young: $R^2 = 0.41$, $\beta = 0.64$ ($p = .004$); old: $R^2 = 0.33$, $\beta = 0.58$ ($p = .025$); combined: $R^2 = 0.30$, $\beta = 0.55$ ($p = .001$). (**C**) young: $R^2 = 0.23$, $\beta = -0.47$ ($p = .040$); old: $R^2 = 0.19$, $\beta = -0.44$ ($p = .090$); combined: $R^2 = 0.22$, $\beta = -0.47$ ($p = .004$). (**D**) young: $R^2 = 0.48$, $\beta = 0.69$ ($p = .001$); old: $R^2 = 0.39$, $\beta = 0.62$ ($p = .010$); combined: $R^2 = 0.44$, $\beta = 0.66$ ($p < .001$).

[$t(34) = -0.72$, $p = .479$].

3.3. *Total muscle activation*

Table 3 shows age-related muscle activations for slopes and walking speeds. With increased speed, total muscle activation tended to increase in younger but changed little in older adults across incline (10 ± 12% vs. −1.0 ± 10%) and decline (3.6 ± 10.2% vs. −2.6 ± 7.7%) walking [$F(1,31) = 8{,}79$, $p = .006$, $r = 0.47$]. No age × slope interaction on total muscle activation change was observed [$F(1,31) = 1.86$, $p = .183$, $r =$

Table 3
Muscle activation during incline and decline walking.

	Decline				Incline			
	slow[a]		moderate[a]		slow[a]		moderate	
	younger	older	younger	older	younger	older	younger	older
Muscle group, in %							*in μV*	
Hip ext.	33 (10)	40 (14)	39 (12)	35 (16)	92 (21)	104 (12)	16.3 (7.5)	17.7 (6.3)
Knee ext.	111 (42)	101 (28)	115 (42)	100 (26)	86 (19)	98 (12)	14.3 (4.4)	14.7 (5.6)
Ankle PF	31 (5)	37 (11)	32 (6)	33 (7)	100 (8)	98 (8)	35.5 (7.6)	29.9 (7.0)
Ankle DF	58 (22)	70 (22)	61 (15)	71 (15)	81 (15)	104 (20)	28.0 (8.8)	35.9 (13)
Total*	58 (15)	62 (10)	62 (11)	60 (9)	90 (12)	102 (10)	23.5 (4.6)	24.5 (6.1)
Muscle, in %							*in μV*	
GluMax	46 (16)	41 (12)	49 (16)	41 (11)	90 (15)	97 (12)	4.4 (1.8)	5.4 (2.0)
ST	35 (13)	45 (15)	41 (12)	44 (20)	98 (26)	114 (15)	14.4 (7.1)	14.0 (5.2)
BF	32 (12)	37 (17)	40 (16)	35 (18)	85 (21)	99 (16)	14.4 (7.9)	16.4 (8.0)
VM	110 (48)	97 (28)	114 (51)	97 (28)	87 (20)	98 (15)	22.3 (8.3)	21.9 (9.9)
RF	117 (37)	116 (33)	121 (25)	113 (29)	83 (15)	95 (11)	6.4 (2.1)	7.9 (1.7)
SOL	36 (7)	48 (7)	37 (8)	44 (6)	99 (11)	100 (8)	35.9 (7.2)	26.9 (7.8)
GaMed	27 (7)	28 (15)	27 (8)	24 (10)	101 (10)	97 (10)	35.0 (9.1)	32.9 (11)
TA	58 (22)	70 (22)	61 (15)	71 (15)	81 (15)	104 (20)	28.0 (8.8)	35.9 (13)
Coactivation, in %							*in %*	
Thigh	46 (10)	51 (12)	49 (12)	51 (12)	69 (5)	72 (4)	69 (7)	70 (5)
Shank*,#	57 (8)	56 (11)	60 (7)	55 (9)	47 (7)	42 (6)	49 (8)	40 (6)
Total#,γ	52 (7)	53 (10)	54 (9)	53 (9)	58 (5)	57 (5)	59 (6)	55 (5)

Values are in mean (SD). [a]Muscle activation is normalized (in %) to its absolute muscle activation measured during incline walking at moderate speed as presented in the upper and middle part of the last column (*in μV*). Presenting the last column's values in absolute terms merely served for data transparency purposes. *Age effect ($p < 0.05$), #Age-by-walking speed interaction effect ($p < 0.05$), γSlope effect ($p < 0.05$).

0.24].

3.4. Muscle co-activation

Across slopes and speeds, total [F(1,31) = 0.234, p = .632)] and thigh [F(1,31) = 1.55, p = .222] co-activation did not differ with age, but shank co-activation [F(1,31) = 5.02, p = .032] was 5% greater in younger vs. older adults (Table 2). We observed significant age × walking speed interactions for total (younger: 1.5 ± 2.9% vs. older: −1.5 ± 4.7%; [F(1,31) = 6.47, p = .016]) and shank co-activation (younger: 2.2 ± 4.1% vs. older: −1.2 ± 3.2%; [F(1,31) = 5.89, p = .021]), but not thigh co-activation [F(1,31) = 2.13, p = .155]. Finally, total co-activation was 4.2 ± 6.5% greater during incline than decline [F (1,31) = 13.09, p = .001].

4. Discussion

We examined the effects of age and walking speed on the relationship between muscle activation and mechanical joint work during incline and decline walking. Contrary to our first hypothesis, age did not affect the relationship between muscle activation and positive or negative joint work; however, older compared with younger adults did perform less APF work and less KE work. Also, contrary to our second hypothesis, total muscle activation tended to increase in younger but changed little in older adults with faster walking speed independent of slope. These findings may in part be related to older vs. younger adults taking shorter steps. We conclude that the electromechanical cost does not underlie the age-related reconfiguration of joint work during walking.

The separate findings for joint work and agonist muscle activation in the two age groups generally agree with the literature (Franz & Kram, 2013; 2014; Lay et al., 2007). First, the HE and APF were most active during ascent and the KE during descent. This agrees with their function to accelerate the COM forward and upward (HE and APF) and decelerate the COM in early stance (KE) (Pickle et al., 2016; Sadeghi et al., 2001; 2002). Second, the ankle dorsiflexor were most active during ascent, despite the substantial amount of energy absorption during descent (see Supplementary Figure S2). Third, older vs. younger adults performed 21% less APF work and 29% greater (p = 0.024) hip flexor work while the HE work was indifferent to age (Fig. 1). However, the 19% lower negative KE work in older adults contrasts the equal amount of work observed previously between both age groups during treadmill decline walking (Waanders et al., 2019). This discrepancy reflects the inconsistency in age-related changes in knee joint work during walking (Beijersbergen et al., 2013), which may be in part related to differences in stride pattern. Here, older vs. younger adults took 8% shorter strides, instead of showing no difference in stride lengths observed previously. When normalized for stride length, the age-related difference in knee work decreased to 12% (see Supplementary Table S3).

Agonist muscle activation explained between 20 and 44% of variance in joint work in younger and older adults combined (Figure 3), suggesting that agonist activation is a weak-to-moderate predictor (Cohen, 1992) of joint work during sloped walking. The unexplained variance can be primarily attributed to the fact that joint work is the net result of all involved agonist and antagonist muscle–tendon units. Also, agonist activation predicted positive work during incline (R^2 = 30–44%) more accurately than negative work during decline (R^2 = 20–22%) walking. This may partly be due to a higher contribution of elastic structures such as the tendon (Roberts et al., 2016) and active titin (Hessel & Nishikawa, 2017) to negative work production that greatly reduces muscle activation (Bigland-Ritchie & Woods, 1976), and due to differences in the control strategy between tasks. That is, subjects typically show greater movement variability during descent vs. ascent because of increased instability (Dewolf et al., 2020), also supported by a larger co-activation variance during descent (Table 3), which likely contributed to the larger data spread in the muscle activation-negative work relationship.

Contrary to our first hypothesis, younger and older adults showed no difference in electromechanical cost of positive joint work production during incline walking (Fig. 2). That is in part because unlike the age-typical increased antagonist muscle co-activation observed by others (Franz & Kram, 2013; Hortobágyi et al., 2009; Peterson & Martin, 2010), total co-activation was unaffected by age in this study and shank co-activation was actually greater in younger adults. Increased co-activation presumably increases joint stability to compensate for task insecurity and/or impact forces, which could be attenuated by taking shorter strides. Therefore, the present older vs. younger adults did not show greater co-activation possibly because they took 11% shorter strides during incline walking. This argument is supported by Peterson and Martin (2010) who used the same co-activation metric as in this study. In their study, older compared with younger adults had only 2%

shorter strides during level walking, and showed no difference in shank co-activation but greater thigh and total co-activation.

At the same time, older adults performed 21% less APF work and 19% less KE work than younger adults (Table 2), suggesting that the electromechanical cost does not underlie a reconfiguration of joint work. Instead, a decreased neural drive to the soleus muscle during late stance may contribute to the age-related decrease in APF work, also suggested by others (Schmitz et al., 2009). This is based on the 25% and 6% lower soleus and gastrocnemius absolute activation in older vs. younger adults during incline walking, despite that direct comparisons of absolute muscle activation between groups can be biased by several factors such as subcutaneous fat (Kohrt et al., 1992). Although age did not affect the relationship between muscle activation and negative work for the KE, this relationship was not statistically significant in older adults. Whether the age-related increase in active and passive muscle stiffness observed by others (Roig et al., 2010) significantly contributes to negative work production requires further study.

Contrary to our second hypothesis, total activation tended to increase with faster walking speed in younger adults, whereas activation changed little in older adults. Here, the age-related difference in stride length likely also played a critical role as for co-activation discussed above. For example, shorter strides may decrease the magnitude of co-activation and therefore total activation. Furthermore, Ortega & Farley (2007) observed a lower increase in limb mechanical work during stance with faster walking speed in older vs. younger adults, and suggested that this was due to their shorter steps. Smaller increases in mechanical work would presumably require smaller increases in muscle activation. Conversely, perhaps the lower APF work drove the age-related decrease in stride length (Umberger & Martin, 2007). Also, muscle activation was determined by the EMG integral, which limited the increase in activation with faster walking speed more in older than in younger adults. That is because with increasing speed older adults' stance time decreased to a greater extent and consequently also the duration of their muscle activation. Our results at least hint at mechanisms by which age-related differences in stepping strategies with faster walking speed may affect underlying changes in muscle activation.

There are some limitations. First, the present results are limited to sloped walking. Comparisons of sloped walking to level walking could elicit greater inter-condition effects than between the present walking speeds. Second, muscle activation was not also expressed as a percentage of the maximal voluntary contraction (%MVC). This makes comparisons to those studies expressing activation as %MVC activation more difficult. However, MVCs themselves can be difficult to perform and can yield less reliable measurements. Third, we focused on the stance phase, although age-related differences in muscle activation prior to initial contact have been observed (Hortobágyi et al., 2009). Lastly, the effect of step length on the muscle activation-joint work relationship and its implication for the metabolic cost of walking were not systematically examined, which our results suggest may be an important direction for future work.

In conclusion, age did not affect the electromechanical cost of joint work production during sloped walking at freely-chosen step lengths but older compared with younger adults did perform less APF work and less KE work. With faster walking speed, total muscle activation tended to increase in younger but changed little in older adults independent of slope. We conclude that the electromechanical cost does not underlie the age-related reconfiguration of joint work during walking.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jbiomech.2021.110555.

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