



Neither total muscle activation nor co-activation explains the youthful walking economy of older runners

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ARTICLE INFO

Keywords:

EMG
Aging
Running
Metabolic rate

ABSTRACT

Background: Older adults (≥ 65 years) exhibit greater metabolic rates during walking (worse walking economy) compared to young adults. Yet, previous research suggests that habitual running, but not habitual walking, exercise mitigates the age-related deterioration of walking economy.

Research question: Does total leg muscle activation and/or agonist-antagonist co-activation explain the superior walking economy of older runners versus older walkers?

Methods: We quantified metabolic power, leg muscle activation, and co-activation in older walkers and older runners during walking at 0.75, 1.25, and 1.75 m/s.

Results: While accounting for multiple comparisons, neither total stride (each speed $p \geq 0.024$), stance- (each speed $p \geq 0.217$), nor swing- (each speed $p \geq 0.170$) phase EMG amplitude differed between older walkers and older runners at 0.75, 1.25, or 1.75 m/s. Stride averaged medial gastrocnemius and biceps femoris activation was lower in older runners than older walkers at 1.25 and 1.75 m/s (all $p \leq 0.025$). We also calculated shank, thigh, and overall (shank and thigh) agonist-antagonist leg muscle co-activation over each stride, and the only difference between groups was a greater shank co-activation in older runners at 0.75 m/s ($p = 0.024$). Across groups, stride, stance-, and swing-phase total muscle activation positively correlated with gross metabolic power ($R^2 = 0.58$ – 0.66 ; all $p < 0.001$). Paradoxically, across groups, stride, stance-, and swing-phase muscle co-activation indices were negatively correlated with gross metabolic power ($R^2 = 0.08$ – 0.29 ; all $p \leq 0.007$).

Significance: Neither total leg muscle activation nor co-activation explains the superior walking economy of older runners versus older walkers.

1. Introduction

Most studies report that older adults (≥ 65 years) select slower preferred walking speeds than young adults (≤ 45 years) [1,2]. Among older adults, a slower preferred walking speed is associated with the loss of functional independence [3] and is a key predictor of mortality [4]. A contributing factor to the reduced preferred walking speeds of older adults compared to young adults may be their 10–25% greater rate of mass-normalized metabolic energy expenditure at a given walking speed (worse walking economy) [1,5]. Due to the implications of reduced walking speeds [3,4], many studies have employed interventions aimed at improving walking economy in older adults [6,7], and in turn, increasing their preferred walking speeds.

Recent cross-sectional [8,9] and longitudinal [7,10] studies indicate

that habitual relatively moderate-to-high intensity aerobic exercise (e.g. swimming, cycling, running) mitigates the age-related deterioration of walking economy. Many studies also indicate that older adults who habitually perform relatively low intensity aerobic exercise (e.g. casual walking), exhibit walking economy that is no better than that of sedentary older adults [6,8]. Collectively, these studies suggest that there is a relative aerobic exercise intensity threshold that older adults need to exercise above to elicit improved walking economy (e.g. $\geq 65\% \dot{V}O_2$ max). Accordingly, older adults who habitually run for exercise (older runners) exhibit better walking economy than older adults who habitually walk for exercise (older walkers) [8]. Yet, the underlying mechanism(s) responsible for the more economical walking of older runners versus older walkers is/are currently unknown.

Leg muscle force generation and mechanical work production

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governs walking biomechanics and economy [11]. For instance, decreased muscle force production [12] and/or positive mechanical muscle work production [13] lowers the metabolic cost of muscle contraction and improves walking economy [11]. Leg muscle activation is a correlate to leg muscle force and positive mechanical work [14], and it is reported to be greater in older adults than young adults [15,16]. Also, agonist-antagonist leg muscle co-activation during walking is greater in older adults compared to young adults [15–19]. Both muscle activation and co-activation positively correlate with worse walking economy [18,19]. Moreover, older adults may co-activate their leg muscles to improve their balance and reduce their risk of falling during walking [20]. Perhaps older runners have a reduced fear of falling compared to older walkers, and therefore, exhibit less antagonist leg muscle activation and co-activation compared during walking. Thus, habitual running, but not habitual walking, exercise may better maintain youthful muscle activation and co-activation patterns in older adults, thereby explaining the superior walking economy of older runners versus older walkers.

In addition to differences in muscle activation, there are other physiological factors that may explain the enhanced walking economy of older runners versus older walkers. For instance, habitual running, but not habitual walking, exercise may attenuate mitochondrial uncoupling with advanced-age and improve muscle efficiency [21]. While considering other factors, improved muscle efficiency (more mechanical work per unit of metabolic energy) improves walking economy. A previous study reported that walking stride kinematics and ground reaction forces were nearly identical for older walkers and older runners, indicating that walking biomechanics do not explain the difference in walking economy between the groups [8]. Yet, it is plausible that subtle differences in leg joint biomechanics and muscle dynamics between older walkers and older runners may relate to cohort walking economy differences by altering leg muscle force and/or mechanical work production.

The aim of our study was to determine whether the superior walking economy of older runners compared to older walkers [8] is related to altered leg muscle activation. We hypothesized that older runners would exhibit less total leg muscle activation and agonist-antagonist leg muscle co-activation compared to older walkers during walking. We also hypothesized that both total leg muscle activation and co-activation would positively correlate with the metabolic cost of walking across participant groups. Further, we compared the activation of select muscles in older walkers and older runners across multiple phases of a stride to reveal whether habitual walking or running exercise affects the activation of select muscles [17].

2. Methods

2.1. Participants

We determined participant sample size by first assuming that *older runners* would exhibit less muscle activation and co-activation than *older walkers*, and would exhibit similar muscle activation to young adults. Next, we used published thigh co-activation data from young adults and older adults (non-runners) during level-ground walking at 1.3 m/s [18]. Based on these published thigh co-activation data of young adults versus older adults [18], the present study needs 11 older walkers and 11 older runners to achieve a statistical power of 80% and an p -value < 0.05 .

Thirty older adults (15 older walkers and 15 older runners) participated (Table 1). Study participants included adults who 1) were ≥ 65 years of age, 2) were apparently free of cardiovascular, neurological, and musculoskeletal disorders, and 3) walked or ran for exercise in ≥ 30 -min bouts, ≥ 3 days per week over the last 6 months. Participants gave informed written consent in accordance with both the Humboldt State University and the University of Colorado Boulder Institutional Review Boards prior to participation.

Table 1

Participant characteristics. An asterisk (*) indicates a significant difference ($p < 0.05$) between participant groups.

Average \pm SD	Older Walkers (4 M, 11 F)	Older Runners (10 M, 5 F)
Age, yrs	68.9 \pm 3.0	68.9 \pm 4.7
Height, m	1.61 \pm 0.09	1.70 \pm 0.09*
Leg length, m	0.83 \pm 0.06	0.88 \pm 0.06
Lean tissue mass, kg	39.2 \pm 7.1	48.6 \pm 9.2*
Body fat, % body mass	31.5 \pm 9.6	23.4 \pm 6.0
VO ₂ peak, ml O ₂ /kg/min	27.7 \pm 3.6	37.3 \pm 5.3*
Standing metabolic rate, W/kg	1.34 \pm 0.21	1.26 \pm 0.14
0.75 m/s, gross metabolic power, W/kg	3.39 \pm 0.33	3.18 \pm 0.31*
1.25 m/s, gross metabolic power, W/kg	4.33 \pm 0.56	3.97 \pm 0.40*
1.75 m/s, gross metabolic power, W/kg	6.33 \pm 0.71	5.95 \pm 0.52*

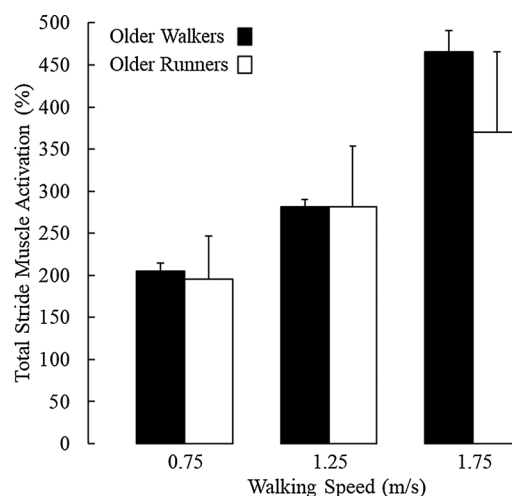


Fig. 1. Total stride muscle activation as a percentage (summed, not averaged, individual muscle activations) for older walkers and older runners across walking speeds. 100% activation represents the average of each muscle's peak activation over 10 strides while walking at 0.75 m/s. Error bars are standard error. Accounting for multiple comparisons, total stride average activation was similar for older walkers and older runners at speed ($p \geq 0.024$).

2.2. Protocol

This protocol was performed concurrent to Ortega et al. [8]. Namely, each participant completed three sessions. For the first session, participants underwent a dual energy x-ray absorptiometry scan (DXA-GE Lunar, Boston, MA, USA) to determine fat versus fat-free mass, as well as a physician supervised graded exercise test incorporating electrocardiography and open-circuit expired gas analysis to determine cardiovascular health (Table 1). During the second session, at least five days following the first session, we further familiarized participants to treadmill walking and the open-circuit expired gas analysis equipment. In this session, participants walked on a dual-belt, force-instrumented treadmill (Bertec Corporation, Columbus, OH, USA) for seven minutes at each speed (0.75, 1.25, and 1.75 m/s) while breathing through a mouthpiece that allowed us to measure their metabolic rates. During the third session, at least two days following familiarization we measured each participant's metabolic rates and muscle activations during standing and during walking on the treadmill at 0.75, 1.25, and 1.75 m/s. Trials from session three were five minutes in duration with at least five minutes of rest between trials.

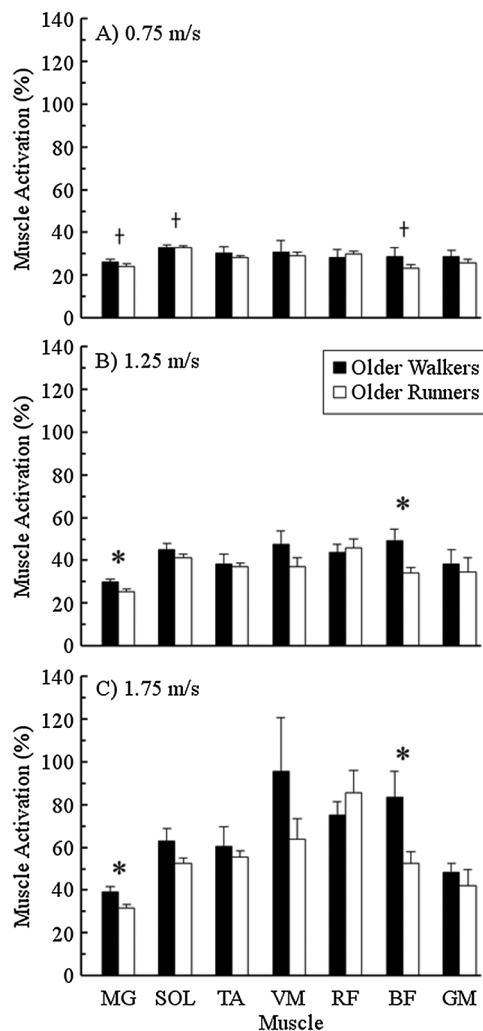


Fig. 2. Normalized stride muscle activation expressed as a percentage of the respective muscle's average peak activation while walking at 0.75 m/s. The panels top to bottom indicate the respective muscle activations while walking at A) 0.75, B) 1.25, and C) 1.75 m/s. The reported muscles are medial gastrocnemius (MG), soleus (SOL), tibialis anterior (TA), vastus medialis (VM), rectus femoris (RF), biceps femoris (BF), and gluteus maximus (GM). A cross (†) indicates a participant group effect (older walkers versus older runners) on muscle activation across speeds. An asterisk (*) indicates a participant group effect at the indicated speed. Walking speed was associated with the activation of each muscle ($p < 0.001$).

2.3. Metabolic rate

Throughout each trial, we measured each participant's rates of oxygen uptake (VO_2) and carbon dioxide production (VCO_2) using open-circuit expired gas analysis (TrueOne 2400, ParvoMedic, Sandy, UT, USA). We averaged VO_2 and VCO_2 during the last two minutes of each trial and used a standard equation [22] to calculate steady-state metabolic power (W). Subsequently, we normalized gross metabolic power by the body mass of the corresponding participant (W/kg).

2.4. Electromyography

We recorded surface EMG signals using the standard procedures of the International Society for Electrophysiology and Kinesiology [23]. Specifically, we shaved and lightly abraded the skin superficial to the medial gastrocnemius (MG), soleus (SOL), tibialis anterior (TA), vastus medialis (VM), rectus femoris (RF), biceps femoris (BF), and gluteus maximus (GM) muscles of each participant's right leg with electrode

preparation gel (NuPrep, Weaver and Co., Aurora, CO) prior to placing bipolar surface electrodes over each muscle belly. We placed the paired surface electrodes (Trigno Bipolar Ag/AgCl, 2 cm IED; Delsys Inc., Natick, MA) superficial to each muscle belly and in the same orientation as the respective muscle fibers. We verified electrode positions and signal quality by visually inspecting the EMG signals while participants contracted each muscle. We collected EMG signals at 1000 Hz and pre-amplified with a gain of 1700 (input impedance $> 100 \text{ M}\Omega$, common mode rejection ratio $> 110 \text{ dB}$ at 60 Hz). Using standard methods [24], we verified that electrode impedance was less than $5000 \text{ }\Omega$ and that the crosstalk between muscles was negligible.

Using Visual 3D software (C-Motion, Germantown, MD), we band-pass filtered (6th order Butterworth) raw EMG data to retain frequencies between 20 and 450 Hz and we full-wave rectified the filtered EMG signals. We then calculated the root mean square (RMS) of the rectified EMG signals with a 40 ms moving window [25]. We synchronized the EMG_{RMS} signals to a stride using the foot strikes and toe offs identified from the treadmill ground reaction forces (2000 Hz) [18]. We filtered ground reaction forces using a 4th order zero-lag low pass Butterworth filter with a 30 Hz cutoff. We used a 20 N threshold to indicate ground contact. We calculated the EMG_{RMS} for 10 consecutive strides (20 steps) during the last minute of each trial and then normalized each muscle's EMG signal relative to the average of each muscle's peak EMG amplitude across 10 strides during the slowest walking trial (0.75 m/s) [26]. Based on visual inspection, we removed 27 EMG signals (out of 210 signals) from our analyses due to poor EMG signal quality (signal-to-noise ratio < 1.2).

We determined the activation of each muscle over the entire stride, stance-, and swing-phase, as well as over each 10% increment of the stride (0–10%, 10–20%, etc. 0% indicates heel strike) [17]. Next, we determined average co-activation of the shank, thigh, and overall leg (average of shank and thigh) per stride, stance-, and swing-phase using a co-activation index (CI) expressed as a percentage [16–18].

$$CI = 2 \times \left(\frac{\int \text{EMG}_{\text{antag}}}{\int \text{EMG}_{\text{ag}} + \int \text{EMG}_{\text{antag}}} \right) \times 100 \quad (1)$$

We calculated stride, stance-, and swing-phase co-activation indices using agonist (EMG_{ag}) and antagonist ($\text{EMG}_{\text{antag}}$) muscle activation. We defined the agonist and antagonist muscles as those with more and less relative activation from the corresponding pair of muscles, respectively [16–18]. We calculated the shank co-activation index (CI_{shank}) as the average co-activation of the TA-SOL and TA-MG. We calculated the thigh co-activation index (CI_{thigh}) as the average co-activation of the RF-BF and VM-BF [17,18]. We averaged CI_{shank} and CI_{thigh} to calculate $\text{CI}_{\text{overall}}$.

2.5. Statistics

We performed two-way repeated-measures ANOVAs to determine the influence of walking speed and participant group 1) on individual muscle activation (MG, SOL, TA, VM, RF, BF, and GM), 2) on total leg muscle activation (summed, not averaged, activation across all muscles [15]), and 3) for each co-activation index (CI_{shank} , CI_{thigh} , and $\text{CI}_{\text{overall}}$), over the stride, stance-, and swing-phase. As warranted, we performed post-hoc ANOVAs to determine the independent effects of walking speed and participant group on the dependent variables. Next, for muscles that did not exhibit a participant group by speed interaction regarding stride phase muscle activation, we performed one-way repeated measures ANOVAs to assess the effect of participant group on individual muscle activation at each 10% interval of the stride across speeds. For muscles that exhibited a participant group by speed interaction regarding stride phase muscle activation, we performed one-way repeated measures ANOVAs to assess the effect of participant group on individual muscle activation at every 10% interval at each walking speed. When assessing individual muscles at every 10% stride interval,

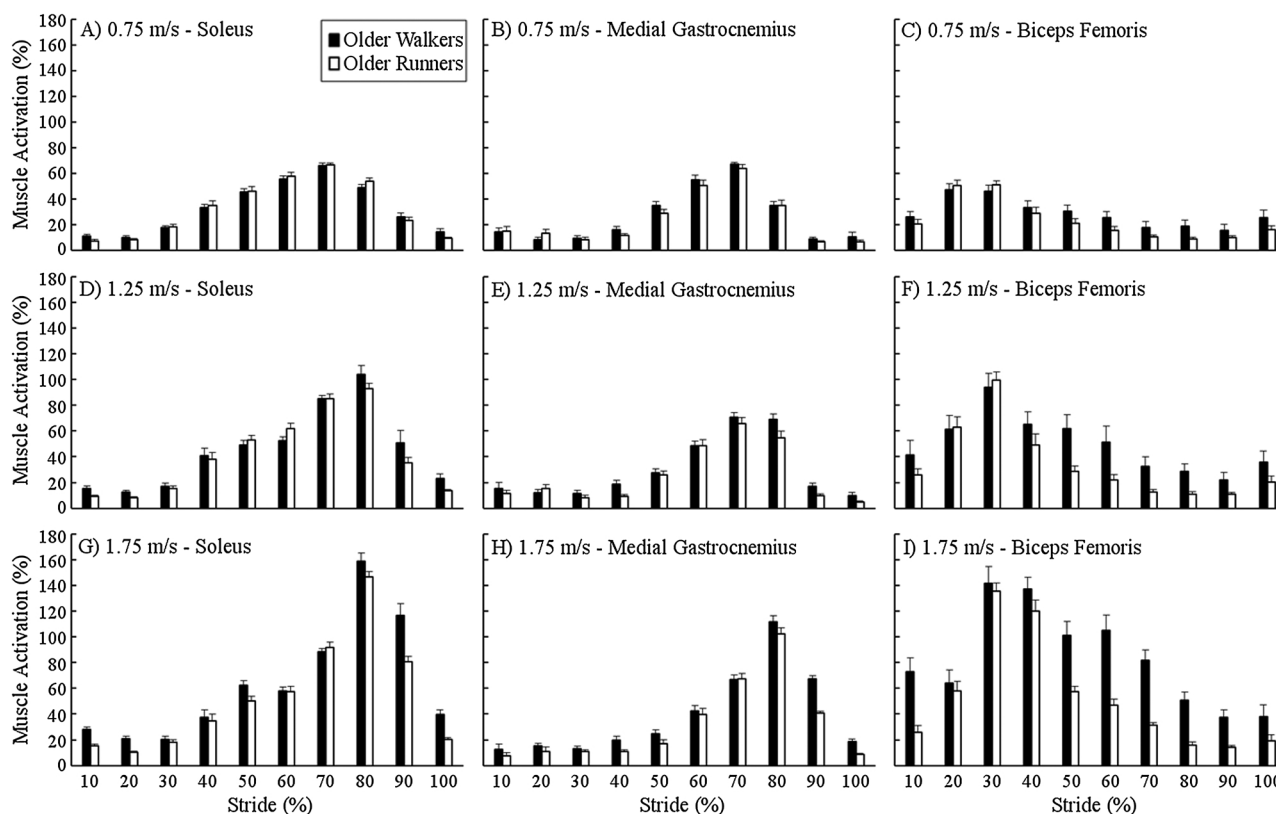


Fig. 3. Muscle activation for every 10% interval of the stride (\pm SE) for the soleus at A) 0.75, D) 1.25, and G) 1.75 m/s, for the medial gastrocnemius at B) 0.75, E) 1.25, and H) 1.75 m/s, and for the biceps femoris at C) 0.75, F) 1.25, and I) 1.75 m/s, of older walkers (black) and older runners (white). There were no significant differences in muscle activation between groups for any muscle over any 10% interval. 0% indicates foot strike.

we accounted for multiple comparisons using a Bonferroni corrected level of significance.

Additionally, we performed independent linear regressions to assess whether total stride, stance-, and swing-phase muscle activation, as well as CI_{shank} , CI_{thigh} , and $CI_{overall}$ correlated with gross metabolic power across all participants. We did not statistically analyze individual agonist-antagonist muscle pairings (e.g. TA-SOL or BF-RF). Furthermore, we performed independent t-tests to compare age, height, leg length, lean body mass, body fat percentage, VO_2 peak, and sub-maximal metabolic rates between older walkers and older runners. We set the level of significance at $p = 0.05$, used a Bonferroni adjusted level of significance when appropriate, and performed statistical analyses using R-studio (Boston, MA, USA).

3. Results

3.1. Muscle activation

Overall, increased walking speed yielded greater total stride, stance-, and swing-phase muscle activation (all $p < 0.001$). While accounting for multiple comparisons, neither total stride (each speed $p \geq 0.024$) (Fig. 1), stance (each speed $p \geq 0.217$), nor swing (each speed $p \geq 0.170$) averaged EMG_{RMS} amplitudes differed between older walkers and older runners at 0.75, 1.25, or 1.75 m/s. Regarding individual muscles, there was a significant participant group by speed interaction for stride, stance-, and swing-phase SOL (all $p \leq 0.033$) and BF (all $p \leq 0.030$) activation. There was also a significant group by speed interaction for stride and stance-phase MG muscle activation ($p \leq 0.049$). No other muscle (TA, VM, RF, and GM) had a group by speed interaction for stride, stance-, or swing-phase muscle activation (all $p \geq 0.056$).

Across speeds, older runners exhibited 15% less swing phase MG

muscle activation compared to older walkers ($p = 0.018$). At 0.75 m/s, all individual stride, stance-, and swing-phase muscle activations did not differ between groups (all $p \geq 0.063$) (Fig. 2). At 1.25 m/s and 1.75 m/s, older runners exhibited less stride, stance-, and swing-phase MG and BF muscle activation than older walkers (all $p \leq 0.040$). At all other speeds, stride, stance-, and swing-phase muscle activation did not differ between groups (all $p \geq 0.070$) (Fig. 2).

3.2. Muscle activation at 10% stride cycle increments

While accounting for multiple comparisons, older walkers and older runners exhibited non-different individual muscle activations at each 10% stride cycle increment (all respective TA, VM, RF, and GM comparisons $p \geq 0.005$; and all respective MG, SOL, and BF group comparisons $p \geq 0.002$) (Fig. 3).

3.3. Co-activation

Swing-phase CI_{thigh} did not change with walking speed ($p = 0.065$). Alternatively, all other shank, thigh, and overall CI 's decreased with faster walking speeds across the stride, stance-, and swing-phase ($p \leq 0.065$). There was a potentially spurious participant group by speed interaction for stride CI_{shank} ($p = 0.024$). At 0.75 m/s, stride CI_{shank} was 16% greater in older runners compared to older walkers ($p = 0.017$). At 1.25 and 1.75 m/s, stride CI_{shank} did not differ between older walkers and older runners ($p \geq 0.665$). No other CI was statistically different between older walkers and older runners (all $p \geq 0.131$).

3.4. Muscle activation and metabolic power

Across all participants, gross metabolic power positively correlated with total leg muscle stride, stance-, and swing-phase activation (all

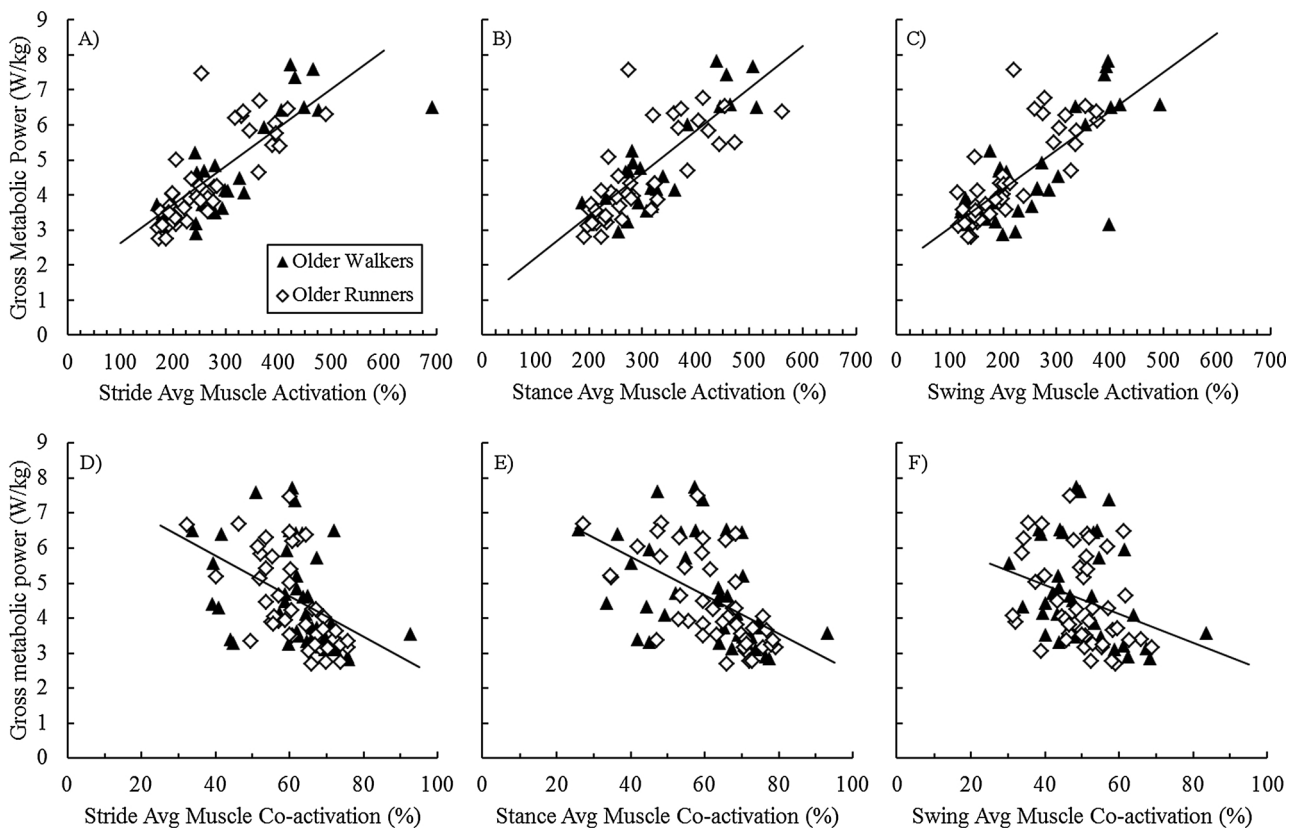


Fig. 4. Across speeds, gross metabolic power (GMP) as a function of total muscle activation (MA) and co-activation indices (CI) over the stride (A and D)), stance- (B and E)), and swing-(C and F)) phase for older walkers (black) and older runners (white). Across speeds, there were no group muscle activation or co-activation differences between older walkers and older runners throughout the stride, stance-, or swing-phases ($p \geq 0.058$). Regression equations are: A) $GMP = 0.011 MA_{stride} + 1.518$, $R^2 = 0.633$, $p < 0.001$; B) $GMP = 0.012 MA_{stance} + 0.954$, $R^2 = 0.654$, $p < 0.001$; C) $GMP = 0.011 MA_{swing} + 1.908$, $R^2 = 0.581$, $p < 0.001$; D) $GMP = -0.058 CI_{overall, stride} + 8.104$, $R^2 = 0.203$; $p < 0.001$; E) $GMP = -0.055 CI_{overall, stance} + 7.934$, $R^2 = 0.288$, $p < 0.001$; F) $GMP = -0.041 CI_{overall, swing} + 6.565$, $R^2 = 0.083$, $p = 0.007$.

Table 2

Correlations between shank, thigh, and overall agonist-antagonist leg (average of shank and thigh) muscle co-activation indices (CI) versus gross metabolic power (GMP).

Correlation	R ²	p-value
$GMP = -0.027 CI_{shank, stride} + 6.584$	0.10	0.004
$GMP = -0.068 CI_{thigh, stride} + 7.614$	0.23	0.001
$GMP = -0.058 CI_{overall, stride} + 8.104$	0.20	0.001
$GMP = -0.026 CI_{shank, stance} + 6.526$	0.15	0.001
$GMP = -0.071 CI_{thigh, stance} + 7.786$	0.33	0.001
$GMP = -0.055 CI_{overall, stance} + 7.934$	0.29	0.001
$GMP = -0.019 CI_{shank, swing} + 5.678$	0.49	0.041
$GMP = -0.043 CI_{thigh, swing} + 6.315$	0.07	0.017
$GMP = -0.041 CI_{overall, swing} + 6.565$	0.08	0.007

$p < 0.001$) (Fig. 4). Conversely, gross metabolic power *negatively* correlated with stride, stance-, and swing-phase $CI_{overall}$ (all $p \leq 0.007$) (Fig. 4 and Table 2).

4. Discussion

The present study’s older walker and older runner metabolic rates, stride kinematics, and ground reaction forces during walking were previously reported by Ortega et al. [8]. Specifically, the older runners exhibited 7–10% better walking economy while using nearly identical stride kinematics and ground reaction forces compared to the older walkers across walking speeds (0.75, 1.25, and 1.75 m/s) [8]. Using the exact same trials from Ortega et al. [8], the present study aimed to uncover whether leg muscle activation explains the difference in older

walker versus older runner walking economy. In the present study, our initial hypothesis was that older runners would exhibit reduced total leg muscle activation and co-activation compared to older walkers. We reject our initial hypothesis because these participant groups exhibited total muscle activation that did not differ during walking (Fig. 1). Further contrasting our hypothesis, older walkers and older runners exhibited non-different agonist-antagonist leg muscle co-activation, apart from shank muscle co-activation at 0.75 m/s, which was greater in older runners than older walkers. Overall, habitual running exercise improves walking economy, but does not change total muscle activation or agonist-antagonist leg muscle co-activation during walking in older adults

In previous studies, at matched speeds older adults exhibited increased agonist-antagonist leg muscle co-activation and poorer walking economy than young adults [15–18]. In the present study, we observed that older runners generally use similar levels of co-activation compared to older walkers while expending less metabolic energy during walking (Fig. 4) [8]. Paradoxically, our participants displayed weak *negative* correlations between gross metabolic power and agonist-antagonist leg muscle co-activation (Fig. 4); accordingly, we reject our second hypothesis. Leg muscle co-activation cannot explain the superior walking economy of older runners versus older walkers. The negative correlations between agonist-antagonist muscle co-activation and gross metabolic power (Fig. 4) were dictated by the influence of walking speed (linear regression: $stride CI_{overall} = -13.8 Spd + 78.1$, $R^2 = 0.30$, $p < 0.001$). This inverse co-activation and walking speed relationship adds to the conflicting literature regarding whether older adult agonist-antagonist leg muscle co-activation correlates negatively (present study), positively [17], or is independent [27,28] of walking

speed.

While increased agonist-antagonist muscle co-activation may contribute to a greater metabolic cost of walking in older adults versus young adults [15–18], we suspect that habitual running exercise delays or prevents other physiological consequences of advanced-age. For example, advanced-age has been associated with reduced muscle efficiency [19,29], attributed to the uncoupling of oxidative phosphorylation in the mitochondria [21]. Conley et al. [21] suggest that habitual aerobic exercise may attenuate mitochondrial uncoupling and improve muscle efficiency in older adults. Therefore, the high relative aerobic intensity attained during running may help maintain youthful muscle efficiency [21] and walking economy in older adults.

It is possible that habitual running exercise does not cause the observed differences in walking economy or muscle activation between older walkers and older runners. Although it seems unlikely, perhaps older runners run because they are more economical in their locomotion than older walkers. We did not screen participants for the total duration that they spent exercising each week, as long as it satisfied our minimum criteria (≥ 30 min per bout, $\geq 3 \times$ per week, during the last 6 months). Also, we did not screen for other modes of exercise (e.g. swimming, cycling, cross-country skiing). Hence, exercise duration and/or additional exercise modes may have contributed to the enhanced walking economy of older runners versus older walkers. Future studies are warranted to quantify the longitudinal effects of running exercise on walking economy and other physiological mechanisms that may relate to the walking economy of older adults, such as muscular efficiency.

5. Conclusions

Compared to older walkers, older runners exhibit reduced medial gastrocnemius and biceps femoris muscle activation during walking at 1.25 and 1.75 m/s. Despite these disparities, neither total leg muscle activation nor co-activation differed between older walkers and older runners. Therefore, total muscle activation and co-activation are not potential mechanisms underlying the 7–10% better walking economy of older runners compared to older walkers.

Conflicts of interest

None.

Funding

CSUPERB Grant #HM531, NIH/NCATS CTSA Grant UL1 TR000154, and the BADER Consortium, a DoD CDMRP cooperative agreement (W81XWH-11-2-0222).

Acknowledgements

We thank Rodger Kram PhD, Jacki Roby DPT, Aria Turney RN, and the staff at the University of Colorado Boulder's Clinical Translational Research Center for their assistance with this study.

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