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Muscle co-contractions are greater in older adults during walking at self-selected speeds over uneven compared to even surfaces

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ABSTRACT

Falls in the aging population are a major public health concern. Outdoor falls in community-dwelling older adults are often triggered by uneven pedestrian walkways. Our understanding of the motor control adaptations to walk over an uneven surface, and the effects of aging on these adaptations is sparse. Here, we study changes in muscle co-contraction, a clinically accepted measure of motor control, due to changes in walking surfaces typically encountered in the outdoor built environment. We address the following research questions: 1) are there walking surface and sex-based differences in muscle co-contractions between young and older adults? and 2) is muscle co-contraction associated with age? We calculated muscle co-contractions from 13 young and 17 older adults during walking at self-selected speeds over even and uneven brick walkways. Muscle co-contraction at the ankle joint was determined from the tibialis anterior and lateral gastrocnemius muscle pair, and at the knee joint from the rectus femoris and semitendinosus muscle pair. Older adults displayed 8–13% greater ankle muscle co-contractions during walking over uneven compared to even surfaces. We found 55–61% (entire gait) and 73–75% (stance phase) greater ankle muscle co-contractions in older females compared to older males during walking over even and uneven surfaces. We found 31–43% greater knee muscle co-contractions in older females compared to older males during the swing phase of walking over even and uneven surfaces. This study underscores the need for determining muscle co-contractions from even and uneven surfaces for quantifying motor control deficits due to aging or neuromuscular disorders.

1. Introduction

Falls are the leading cause of hospital admissions and injury-related deaths among older adults (Li et al., 2006). It is estimated that every year more than a third of community-dwelling older adults in the United States fall (Berg et al., 1997; Campbell et al., 1990), with the total annual cost of related injuries projected to reach $32.4B in 2020 (Centers for Disease Control and Prevention, 2020). Outdoor falls account for more than 50% of falls in community-dwelling older adults (Li et al., 2006). Most outdoor falls (73%) are due to environmental factors, with uneven pedestrian surfaces such as sidewalks, curbs, and streets accounting for 47.6% of these outdoor falls (Li et al., 2006). In addition, walking is the most common (47.3%) fall-related activity (Li et al., 2006).

The biomechanical causes for balance disorders and falls are multifactorial (Horak, 2006). Our understanding of the biomechanical adaptations during walking over uneven surfaces typically encountered in the outdoor built environment, and the effects of aging on these adaptations, is incomplete. Menz et al. evaluated acceleration patterns at the head and pelvis in healthy young and older adults during walking over level and irregular walking surfaces (Menz et al., 2003). They reported that older adults exhibited reduced gait velocity, shorter step length and increased step timing variability compared to young adults; these age-

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based differences were more pronounced when walking over an uneven surface (Menz et al., 2003). In addition to reduced gait velocity and step length, Menant et al. reported decreased cadence, double-support time, heel horizontal velocity at heel strike, as well as greater step width and toe clearance in young and older adults during walking over uneven compared to even surfaces (Menant et al., 2009). Thies et al. measured step width and step time variability in healthy young and older women while walking over even and uneven surfaces and found that surface type significantly affected step width variability, step time, and step time variability (Thies et al., 2005). Recently, Dixon et al. reported differences in joint kinematics and center of mass motion in young and older adults (both males and females) during walking over even and uneven surfaces; these kinematic adaptations were associated with joint strength (Dixon et al., 2018). These previous studies are limited to adaptations in gait parameters; adaptations in muscle co-contraction, a common measure of motor control (Winter, 2005), during walking over uneven compared to even surfaces remain unclear.

Muscle co-contraction, the simultaneous contraction of an agonist and antagonist muscle pair crossing a joint, is an accepted clinical measure to study the effects of deteriorating motor control on gait (Den Otter et al., 2006; Souissi et al., 2017). Muscle co-contraction is theorized to be a form of neuromuscular adaptation to environmental demands (Darainy and Ostry, 2008), with increased muscle co-contraction being a compensatory strategy to counter potential loss of balance and stability when traversing over uneven surfaces. We previously published a study demonstrating greater muscle co-contraction in older compared to young adults during walking over an even surface (Chandran et al., 2019); this study along with other previous studies (Franz and Kram, 2013; Hallal et al., 2013; Hortobagyi et al., 2009; Mian et al., 2006; Nagai et al., 2011; Peterson and Martin, 2010) broaden our understanding of the effects of aging on muscle co-contraction during walking over an even surface. However, studies of increased muscle co-contraction during walking over an uneven compared to an even surface are sparse. Next, our knowledge of sex-based differences in muscle co-contraction during walking is limited. Our rationale for investigating sex-based differences stems from the National Institutes of Health's (NIH) guidelines for scientific rigor and evaluation of biological variables. Biological variables, such as sex, age, weight, and underlying health conditions, are often critical factors affecting health. Sex, in particular, is a biological variable that is frequently ignored in study designs and analyses, leading to an incomplete understanding of the system, disease, or treatment. Mengarelli et al. evaluated sex-based differences in muscle co-contraction at the ankle joint (between the tibialis anterior and gastrocnemius lateralis muscles) during walking over an even surface in terms of onset-offset muscular activation and occurrence frequency (Mengarelli et al., 2015). They used statistical gait analysis, a methodology for characterization of gait by averaging spatiotemporal and EMG parameters over hundreds of strides per subject, and reported sex-based differences in occurrence frequency (number of strides where each co-contraction occurs). We previously reported no sex-based differences in muscle co-contraction at the ankle and knee joints during walking over an even surface and stair use (Chandran et al., 2019). However, sex-based differences in ankle and knee muscle co-contractions during walking over an uneven surface remain unclear.

Accordingly, the objective of this study was to determine the effects of walking surface on ankle and knee muscle co-contractions in healthy male and female young and older adults. We hypothesized that: 1) healthy adults have greater muscle co-contractions at the ankle and knee joints during walking over uneven compared to even surfaces; 2) females have greater muscle co-contractions at the ankle and knee joints compared to males during walking over even and uneven surfaces; 3) significant interaction effects between walking surface and sex will be observed in ankle and knee muscle co-contractions in young and older adults; and 4) muscle co-contractions are associated with age.

2. Methods

2.1. Participant population

Thirty healthy community-dwelling adults were recruited for this study: 13 young and 17 older adults (Table 1). There were no statistically significant differences in height, weight, BMI, or gait speeds between the young and older adults (Table 1). While males were taller and weighed more than females in both the young and older adults groups, there were no statistically significant differences in BMI between males and females within the young and older adult groups (Table 1). There were no statistically significant differences in self-selected gait speeds between males and females in both the young and older adults groups on even and uneven surfaces (Table 1). The participants were screened for neurological impairments, lower-limb musculoskeletal abnormalities (joint replacement, pain, fractures within the last two years), vertigo, dizziness, diabetes, and elevated BMI. Participants were informed on all aspects of the study and provided written consent according to the policies of Harvard University's Institutional Review Board.

2.2. Calculating muscle co-contractions during walking over even and uneven surfaces

We determined muscle co-contractions at the ankle and knee joints during walking at self-selected speeds over even and uneven brick walkways (Dixon et al., 2018). The brick walkways were 8.4 × 2.0 m, with the even surface designed with bricks laid flat (Dixon et al., 2018). The uneven surface comprised bricks randomly tilted medio-laterally or antero-posteriorly via dowels placed beneath the bricks (Dixon et al., 2018). A participant completed all walking trials during a single motion capture session, with simultaneous measurements of muscle electromyography (EMG) activity and three-dimensional marker trajectories (Fig. 1). Subjects wore the same type of basic athletic shoes (Nike Inc., Beaverton, USA) and were tethered to a safety harness. Each subject walked on average 7 (range 5–10) and 8 (range 6–12) times back and forth on the even and uneven surfaces, respectively.

Muscle EMG measurements were obtained using a multi-channel surface EMG system (Trigno™, Delsys Inc., Natick, MA) sampled at 1000 Hz. A single leg was chosen at random for EMG measurements. We measured EMG from tibialis anterior, lateral gastrocnemius, rectus femoris, and semitendinosus muscles using established protocols (Perotto et al., 2005; Rutherford et al., 2011). A participant's mean resting EMG was determined from standing trials with the participant instructed to remain stationary in a neutral pose with their muscles relaxed. The mean resting EMG value was subtracted from his/her raw EMG from walking trials to offset the data to zero. We then filtered the EMG data using a second-order Butterworth bandpass filter (20–400 Hz) to remove motion artifact, full-wave rectified, and filtered with a fourth-order 10 Hz Butterworth low-pass filter (Hallal et al., 2013; Lo et al., 2017). The filtered EMG data were dynamically normalized to muscle-specific maximum activations obtained from all successful trials of walking for each participant (Dixon et al., 2015; Meyer et al., 2017). In other words, for each participant the EMG values from a muscle were normalized to a reference level of activation, which was the maximum EMG value from that muscle from all successful walking trials. A walking trial was determined as successful if there were no obvious tripping or near trips and there were no missing marker data. Each subject had on average 7 successful walking trials on the even (range 4 to 10 trials) and uneven (range 3 to 9 trials) surfaces that were used for further analyses.

Three-dimensional marker trajectories during walking over even and uneven brick walkways were obtained using an 18-camera motion capture system (Motion Analysis Corp., Santa Rosa, CA) sampled at 100 Hz. Retro-reflective markers were placed on a participant according to a modified Plug-in Gait model (Vicon Motion Systems Ltd., Oxford, UK). Three-dimensional marker trajectories were reconstructed, labeled, and gap filled in Cortex (Motion Analysis Corp., Santa Rosa, USA). The

Table 1
Participant demographics and self-selected gait speeds during walking over even and uneven surfaces. Reported *p* values were from two-tailed, unpaired t-tests between the groups.

All participants	Young (n = 13)			Old (n = 17)			*p* value
	Mean	SD	Range	Mean	SD	Range	
Age (years)	28.0	5.1	18.0–35.0	72.7	5.4	65.0–82.0	
Height (meters)	1.70	0.08	1.55–1.83	1.68	0.09	1.57–1.87	0.404
Weight (kgs)	64.5	12.7	52.0–96.5	70.0	13.3	55.0–106.0	0.268
BMI (Kgs/m^2)	22.3	3.9	17.9–30.2	24.8	3.2	20.1–30.3	0.062
Speed even surface (m/s)	1.36	0.14	1.06–1.55	1.32	0.09	1.19–1.53	0.275
Speed on uneven surface (m/s)	1.26	0.14	1.11–1.57	1.35	0.16	1.05–1.57	0.112
Young adults	Males (n = 5)			Females (n = 8)			*p* value
	Mean	SD	Range	Mean	SD	Range	
Age (years)	25.6	5.9	18.0–32.0	29.5	4.3	25.0–35.0	0.194
Height (meters)	1.77	0.05	1.72–1.83	1.66	0.07	1.55–1.75	**0.007**
Weight (kgs)	73.9	14.3	62.0–96.5	58.7	7.7	52.0–72.0	**0.029**
BMI (Kgs/m^2)	23.4	3.9	18.7–28.8	21.6	3.9	17.9–30.3	0.428
Speed on even surface (m/s)	1.33	0.16	1.06–1.48	1.38	0.12	1.23–1.55	0.528
Speed on uneven surface (m/s)	1.23	0.08	1.14–1.33	1.29	0.17	1.11–1.57	0.483
Older adults	Males (n = 7)			Females (n = 10)			*p* value
	Mean	SD	Range	Mean	SD	Range	
Age (years)	74.1	6.3	65.0–82.0	71.7	4.7	65.0–77.0	0.373
Height (meters)	1.73	0.07	1.69–1.87	1.64	0.08	1.57–1.85	**0.021**
Weight (kgs)	79.6	12.9	68.5–106.0	63.3	8.9	55.0–77.5	**0.007**
BMI (Kgs/m^2)	26.3	2.2	23.7–30.3	23.7	3.5	20.1–30.3	0.106
Speed on even surface (m/s)	1.29	0.08	1.19–1.42	1.34	0.09	1.26–1.53	0.214
Speed on uneven surface (m/s)	1.31	0.17	1.05–1.46	1.39	0.15	1.17–1.57	0.316

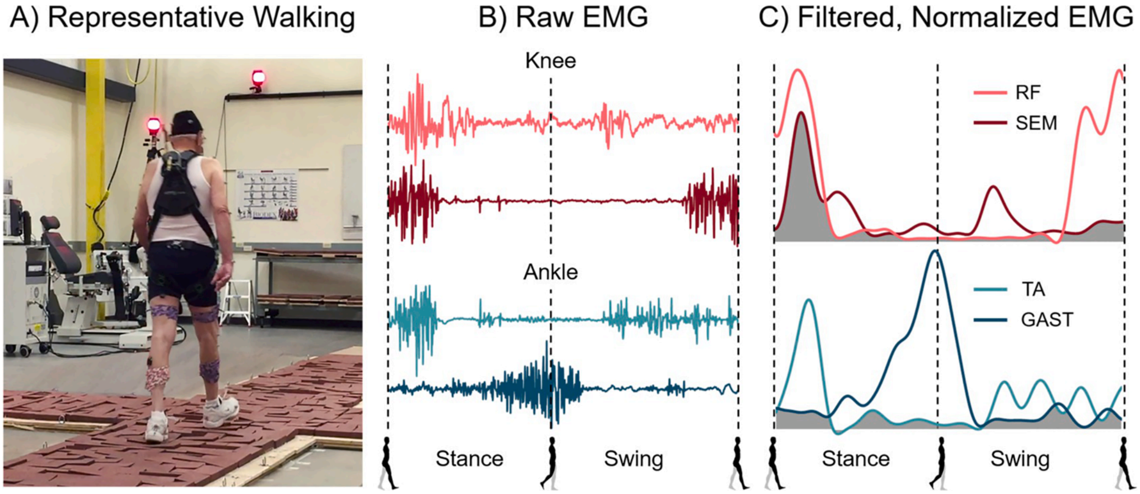

Fig. 1. Determining muscle co-contraction at the knee and ankle joints during (A) a representative walking trial. Raw (B) and filtered and normalized (C) electromyography (EMG) activations of the rectus femoris (RF), semitendinosus (SEM), tibialis anterior (TA), and lateral gastrocnemius (GAST) muscles were synchronized with 3D marker trajectory data to determine the stance and swing phases of a gait cycle. The shaded regions in (C) are the common areas between the muscle pairs. The ratio of the common area of a muscle pair to the sum of the areas under each muscle in that pair represents co-contraction at that joint.

marker data were filtered using a fourth-order low-pass Butterworth filter with a cut-off frequency of 8 Hz (Chiu et al., 2015). Although marker data were collected from both legs, only marker data from the leg used for EMG measurements was included in this study.

The three-dimensional marker data from each gait cycle were labeled manually using three-dimensional displacement plots and visual inspection of the marker trajectories (Fig. 1). Heel strike, the beginning of stance phase, was determined as the frame when the heel marker stopped vertical descent and started plantarflexion rotation. Toe off, the end of stance and beginning of the swing phase, was determined as the frame when the toe marker started its vertical ascent. Gait speeds during walking over even and uneven surfaces were calculated from the C7 marker data.

Muscle co-contractions at the ankle and knee joints were calculated for all complete walking cycles over even and uneven surfaces using a common method (Hesse et al., 2000; Lo et al., 2017; Winter, 2005), given by:

$$\%\text{Muscle co}-\text{contraction} = \frac{2*\text{Common area A\&B}}{(\text{area A} + \text{area B})}*100$$

where A and B are filtered and normalized EMG plots of an agonist/antagonist muscle pair crossing a joint (Fig. 1C). Area A is the area under the EMG plot of muscle A, Area B is the area under the EMG curve of muscle B, and the common area A & B is the intersection of the EMG curves of muscles A & B. The common area is the overlapping region under the EMG curves. The criterion for determining if there was overlap

Table 2

Analysis of variance results for ankle and knee joint muscle co-contraction with the main effects of walking surface and sex for the entire gait cycle, stance phase, and swing phase in healthy young and older adults. * Statistically significant at $p < 0.050$.

Joint	Group	Effects	Entire Gait	Stance	Swing
Ankle	Young	Even vs. uneven	0.824	0.753	0.993
		Males vs. females	0.997	0.944	0.797
		Walking surface × sex	0.471	0.766	0.246
	Older	Even vs. uneven	**0.031***	**0.047***	**0.023**[§]
		Males vs. females	**<0.001***	**<0.001***	0.355 (Even)[#] 0.098 (Uneven)[#]
		Walking surface × sex	0.309	0.504	–
Knee	Young	Even vs. uneven	0.825	0.984	0.909
		Males vs. females	0.119	0.056	0.673
		Walking surface × sex	0.937	0.881	0.516
	Older	Even vs. uneven	0.550	0.798	0.195
		Males vs. females	0.084	0.960	**0.002***
		Walking surface × sex	0.951	0.621	0.404

[§] Repeated measures ANOVA; [#] Welch's F-test. At the ankle joint, the interaction effect for older adults during the swing phase was not evaluated because the corresponding ankle muscle co-contraction data failed Levene's test for homogeneity of variance.

between the two EMG curves was a non-zero value for the intersection of the areas under the two EMG curves over the gait cycle. Any non-zero EMG value added to the area under its curve. Muscle co-contraction at the ankle joint was evaluated between the tibialis anterior and lateral gastrocnemius muscles, while muscle co-contraction at the knee joint was evaluated between the rectus femoris and semitendinosus muscles (Di Nardo et al., 2015; Hortobagyi et al., 2009; Lo et al., 2017; Mengarelli et al., 2015).

2.3. Data analysis and statistical methods

We conducted a statistical power analysis to determine the number of subjects required prior to the beginning of this study. We used statistical software R (RStudio, Boston, MA) to perform our analyses. 2x2 mixed-design analyses of variance (ANOVAs) were performed to evaluate the effects of walking surface and sex on muscle co-contractions in young and older adults (Laerd, 2018; Welkowitz et al., 2012). The independent variables were walking surface (even, uneven) and sex (male, female), and the dependent variable was muscle co-contraction (continuous). Separate ANOVAs were performed on ankle and knee joint muscle co-contractions, for young and older adults, and for the entire gait cycle, the stance phase, and the swing phase. Prior to each 2 × 2 mixed-design ANOVA, we checked a muscle co-contraction dataset for normality (within and between-subject factors) using the Shapiro-Wilk test, and tested for homogeneity of variance using Levene's test (Moder, 2010). In case a muscle co-contraction dataset failed this homogeneity test, sex-based difference (between-subject factor) could not be assessed using a mixed-model (Laerd, 2018). Hence, we evaluated simple main effects, walking surface effect (within-subject factor) by a repeated-measures ANOVA, and sex effects using Welch's F-test (Moder, 2010) for each surface condition separately. A $p < 0.050$ was chosen for testing significance in the main and interaction effects.

Post hoc comparisons were performed for every instance of difference in the main effects from the 2 × 2 mixed-design ANOVA. Prior to each post hoc comparison, we ensured our data passed the normality test. For post hoc comparisons to assess if muscle co-contractions were greater during walking over uneven compared to even surfaces, we used a one-tailed paired samples *t*-test. For post hoc comparisons to assess if muscle co-contractions are greater in females compared to males during walking over even and uneven surfaces, we used a one-tailed independent samples t-tests. We chose $p < 0.050$ for testing significance between the groups and then corrected for multiple comparisons using the Bonferroni correction (three comparisons: entire gait cycle, stance, and swing; $p < 0.017$) (Ranstam, 2016). Finally, we evaluated the relationship between age and muscle co-contraction at the ankle and knee joints during walking over even and uneven surfaces. Linear regression models were used, and a $p < 0.050$ significance level was chosen for testing the linear relationships.

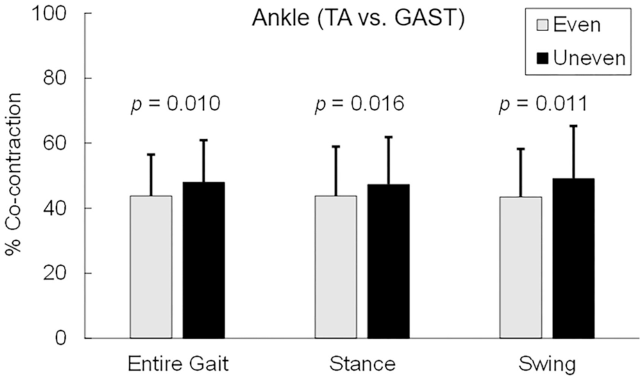

Fig. 2. Post hoc tests to evaluate differences in ankle muscle co-contractions in older adults during walking over even and uneven surfaces. Average (+1 SD) muscle co-contraction values are shown. Ankle muscle co-contractions were evaluated from the tibialis anterior (TA) and lateral gastrocnemius (GAST) muscles. p values are shown for the statistically significant differences ($p < 0.017$ post-Bonferroni correction).

3. Results

3.1. Ankle muscle co-contractions

For ankle muscle co-contractions, the 2x2 mixed-design ANOVAs yielded a significant main effect of walking surface and sex only in older adults with ankle muscle co-contractions being different in older adults during walking over uneven compared to even surfaces for the entire gait cycle ($p = 0.031$), the stance phase ($p = 0.047$), and the swing phase ($p = 0.023$, Table 2). The post hoc comparisons yielded average ankle muscle co-contractions to be 10% ($p = 0.010$), 8% ($p = 0.016$), and 13% ($p = 0.011$) greater for the entire gait cycle, the stance phase, and the swing phase, respectively, in older adults during walking over uneven compared to even surfaces (Fig. 2).

Next, the ANOVA analyses showed that ankle muscle co-contractions were different in older females compared to older males during walking over even and uneven surfaces for the entire gait cycle ($p < 0.001$) and the stance phase ($p < 0.001$, Table 2). The post hoc comparisons indicated that ankle muscle co-contractions were significantly greater in older females compared to older males during the entire gait cycle, with average ankle muscle co-contractions being 55% ($p < 0.001$) and 61%

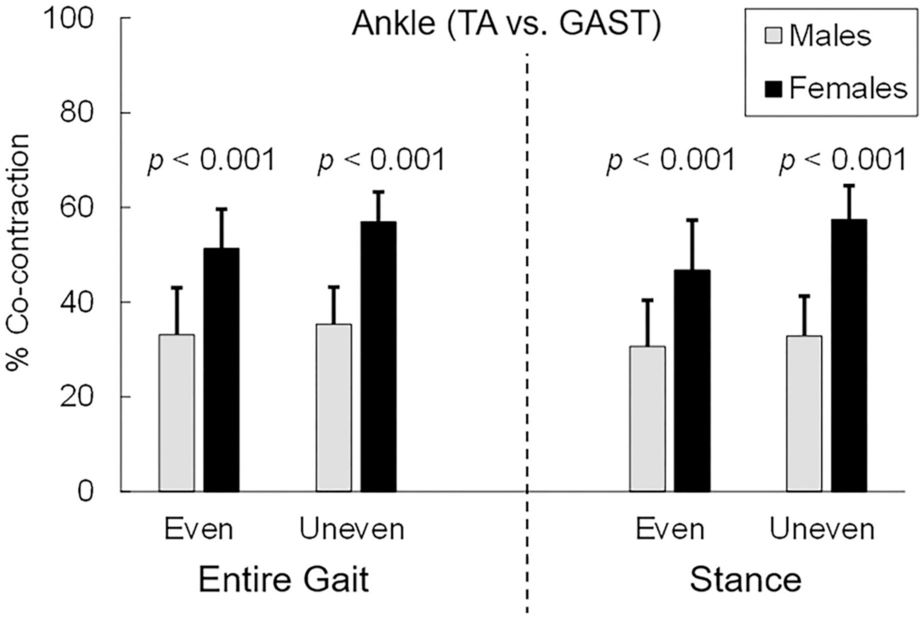

Fig. 3. Post hoc tests to evaluate differences in ankle muscle co-contractions in older females compared to older males during walking over even and uneven surfaces. Average (+1 SD) muscle co-contraction values are shown. Ankle muscle co-contractions were evaluated from the tibialis anterior (TA) and lateral gastrocnemius (GAST) muscles. Post hoc tests were needed only for the entire gait and stance phase of walking. p values are shown for the statistically significant differences (p < 0.017 post-Bonferroni correction).

($p < 0.001$) greater during walking over even and uneven surfaces, respectively (Fig. 3). These sex-based differences in ankle muscle co-contractions were only observed during the stance phase of walking; average ankle muscle co-contractions in older females compared to older males were 73% ($p < 0.001$) and 75% ($p < 0.001$) greater during the stance phase of walking over even and uneven surfaces, respectively (Fig. 3). The ANOVA analyses yielded no interaction effects between walking surface and sex on ankle muscle co-contractions from young or older adults for any phase of the gait cycle (Table 2). Interaction effects in older adults were not evaluated during the swing phase because ankle muscle co-contraction dataset for older adults failed Levene's test for homogeneity of variance. No differences in main walking surface and sex effects on ankle muscle co-contractions were observed in young adults (Table 2).

3.2. *Knee co-contractions*

For knee muscle co-contractions, the 2x2 mixed-design ANOVAs yielded a significant main effect of walking surface and sex only in older adults with knee muscle co-contractions being different in older females compared to older males for only the swing phase ($p < 0.002$, Table 2). The post hoc comparisons indicated that knee muscle co-contractions were significantly greater in older females compared to older males during the swing phase, with average knee muscle co-contractions being 31% ($p = 0.011$) and 43% ($p = 0.006$) greater in older females compared to older males during walking over even and uneven surfaces, respectively (Fig. 4). The ANOVA analyses yielded no differences in older adults walking over uneven compared to even surfaces and no interaction effects between walking surface and sex on knee muscle co-contractions (Table 2). No differences in main walking surface and sex effects on knee muscle co-contractions were observed in young adults (Table 2).

3.3. *Muscle co-contraction and age*

Muscle co-contraction was associated with age only at the ankle joint in older females during walking over an uneven surface (Fig. 5); these linear relationships were significant for the entire gait cycle ($R^2 = 0.65$, $p = 0.005$, Fig. 5B) and the stance phase ($R^2 = 0.55$, $p = 0.014$, Fig. 5D). We found no relationship between age and ankle muscle co-contraction in older males during walking over an uneven surface for the entire gait cycle ($R^2 = 0.09$, $p = 0.512$, Fig. 5B) or the stance phase ($R^2 = 0.42$, $p = 0.12$, Fig. 5D). We found no relationship between age and ankle muscle co-contraction in older adults (males and females grouped together and separately) during walking over an even surface (Fig. 5B, 5D, and 5F). We found no relationship between age and ankle muscle co-contraction in young adults (males and females grouped together and separately) during walking over even and uneven surfaces (Fig. 5A, 5C, and 5E). Finally, we found no relationship between age and knee muscle co-

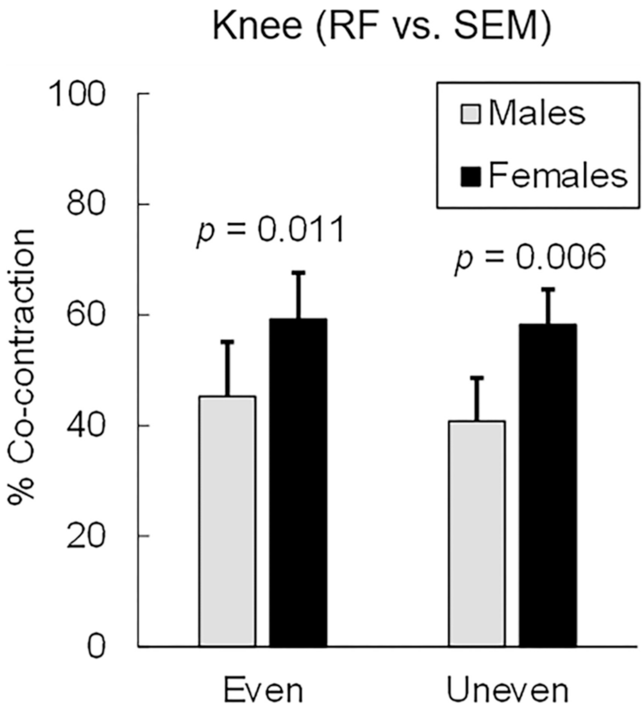

Fig. 4. Post hoc tests to evaluate differences in knee muscle co-contractions in older females compared to older males during the swing phase of walking over even and uneven surfaces. Average (+1 SD) muscle co-contraction values are shown. Knee muscle co-contractions were evaluated from the rectus femoris (RF) and semitendinosus (SEM) muscles. p values are shown for the statistically significant differences (p < 0.017 post-Bonferroni correction).

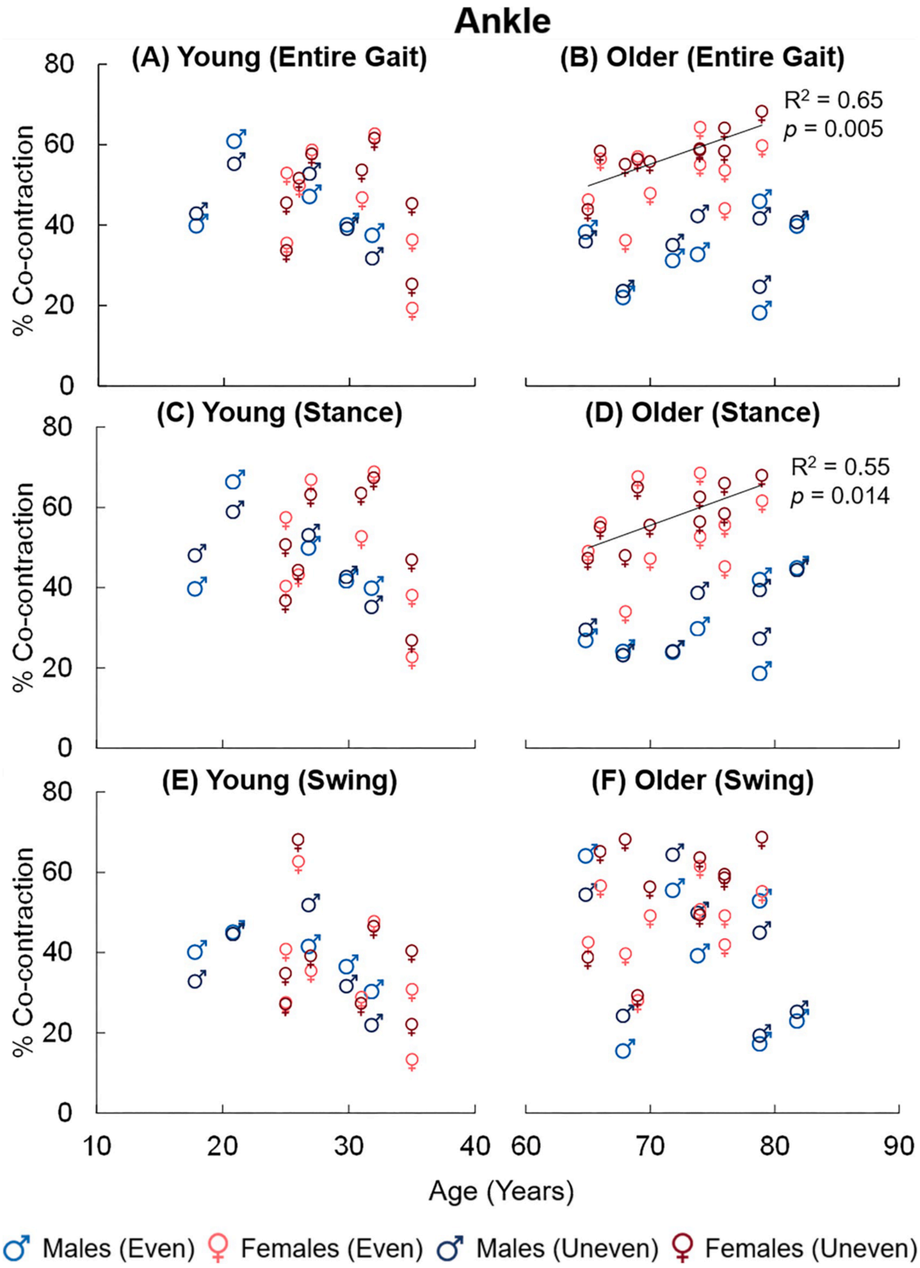

Fig. 5. Relationships between age and ankle muscle co-contraction during walking over even and uneven surfaces from the entire gait cycle (young: A, older: B), the stance phase (young: C, older: D), and the swing phase (young: E, older: F). Ankle muscle co-contractions were evaluated from the tibialis anterior and lateral gastrocnemius muscles. The regression lines represent significant relationships in older females from the entire gait (B) and stance phase (D) of walking over an uneven surface.

contraction during walking over even and uneven surfaces (Fig. 6).

4. Discussion

The objective of this study was to determine the effects of walking surface on ankle and knee muscle co-contractions in healthy young and older adults of both sexes. We proposed four hypotheses. Our first hypothesis was that healthy adults have greater muscle co-contractions at the ankle and knee joints during walking over uneven compared to even surfaces. We found 8–13% greater ankle muscle co-contractions in older adults during walking over uneven compared to even surfaces (Fig. 2). We found no differences in knee muscle co-contractions in older adults during walking over uneven compared to even surfaces. Our second hypothesis was that females have greater muscle co-contractions at the ankle and knee joints compared to males during walking over even and uneven surfaces. We found 55–61% (entire gait) and 73–75% (stance phase) greater ankle muscle co-contractions in older females compared to older males during walking over even and uneven surfaces (Fig. 3). We found 31–43% greater knee muscle co-contractions in older females compared to older males during the swing phase of walking over even and uneven surfaces (Fig. 4). Our third hypothesis was that significant interaction effects between walking surface and sex will be observed in ankle and knee muscle co-contractions in young and older adults. Our analyses yielded no interaction effects between walking surface and sex on muscle co-contractions at the ankle or knee joints (Table 2). Our last hypothesis was that muscle co-contractions are associated with age. Our results suggest that this hypothesis is only true in older females during walking over an uneven surface (Fig. 5).

This study provides new data in support of changes in muscle co-contraction due to changes in walking surface. Previous studies have reported on the protective role of muscle co-contraction in maintaining joint integrity during ballistic activities (Hirokawa et al., 1991; O'Connor, 1993). Studies investigating upper extremity hand reaching movements have documented modulation in muscle co-contraction with motor learning (Darainy and Ostry, 2008; Franklin et al., 2003; Thoroughman and Shadmehr, 1999). Franklin et al. reported an initial

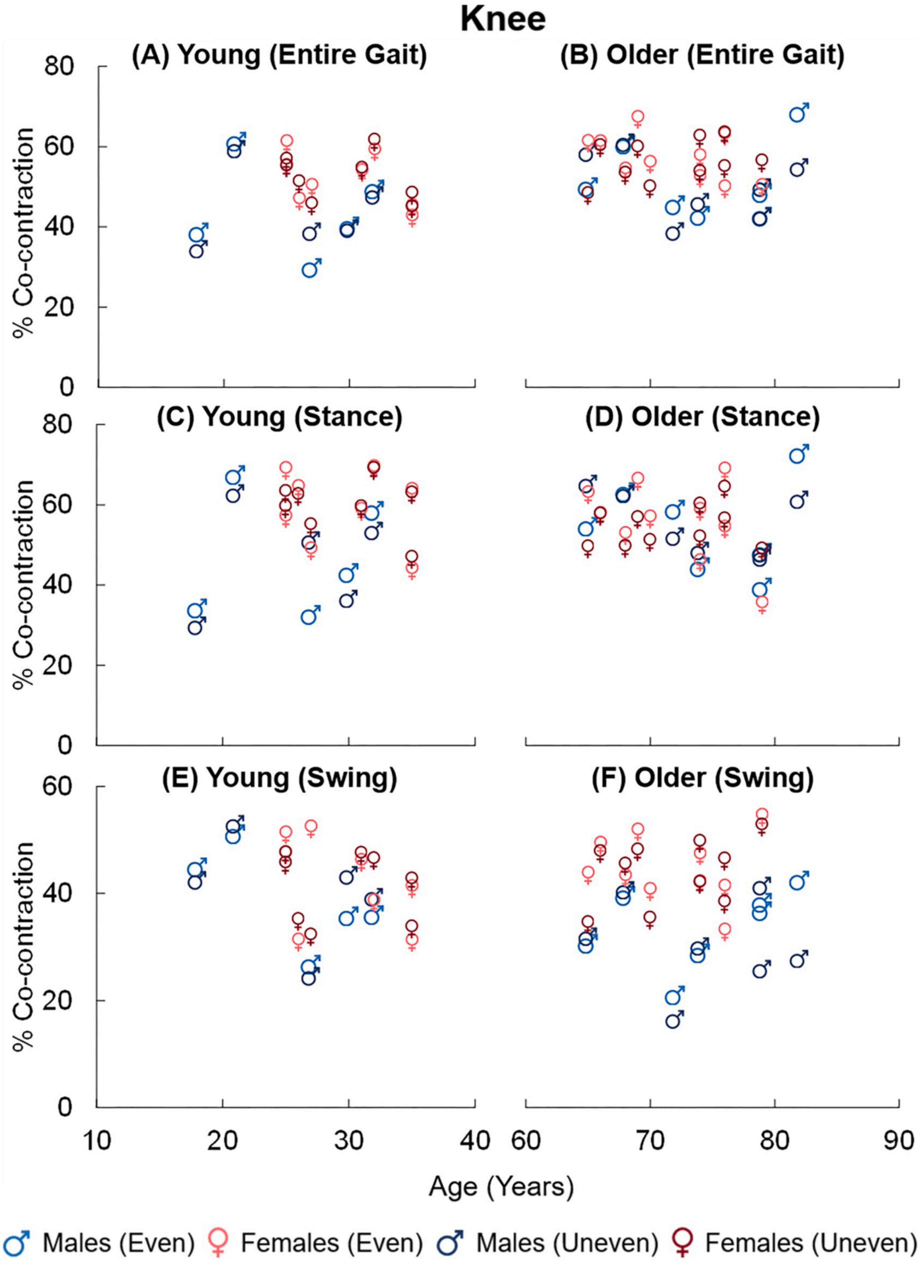

Fig. 6. Relationships between age and knee muscle co-contraction during walking over even and uneven surfaces from the entire gait cycle (young: A, older: B), the stance phase (young: C, older: D), and the swing phase (young: E, older: F). Knee muscle co-contractions were evaluated from the rectus femoris and semitendinosus muscles.

increase followed by a gradual reduction in muscle co-contraction with progression of learning a reaching task under varying force fields (Franklin et al., 2003); these changes in muscle co-contraction with increasing environmental familiarity have been corroborated by other studies (Darainy and Ostry, 2008; Thoroughman and Shadmehr, 1999). However, to the best of our knowledge, this is the first study to report greater muscle co-contractions due to changes in walking surface, namely, an even to an uneven brick surface. Notably, these walking surface-based differences were only observed in older adults (Table 2), adding to the growing literature on diminishing neuromuscular control and efficiency with aging (Benjuya et al., 2004; Hausdorff, 2007; Hortobagyi et al., 2003; Peterson and Martin, 2010; Woollacott, 1993). Next, our results demonstrate greater muscle co-contractions during walking over uneven compared to even surfaces only at the ankle joint, with no increases observed at the knee joint (Table 2). A possible explanation is that the body's neuromuscular adaptations to changes in walking surface may be greater at the distal ankle joint closest to the walking surface. This theory is supported by previous literature related to movement strategies used by older adults to return the body to equilibrium (Horak, 1987; Horak, 2006; McIlroy and Maki, 1996). Horak et al. reported that older adults at risk of falling tend to use hip strategies (the body exerts torque at the hips to quickly move the body center of mass) to return the body to equilibrium (Horak, 2006). In contrast, older adults with low risk of falling use ankle strategies (the ankle is the body's axis of rotation) to maintain postural stability (Horak, 2006). Since our participants were all healthy community-dwelling adults with low risk of falling, it is plausible that they used ankle strategies to maintain postural stability while walking over the uneven surface.

Over the recent years, an interesting approach to study patterns of muscle activations and the underlying motor control of the human system has been the concept of muscle synergies (Bizzi et al., 2008; Bizzi et al., 1991). Muscle synergies, or common activation patterns, are hypothesized to be used by the central nervous system (CNS) for simplifying human motor control by reducing its dimensionality (Bizzi et al., 2008). Using muscle synergies, Santuz et al. demonstrated that the CNS produced more stable signals while walking over an uneven surface (compared to a standard surface) and in older adults (compared to young adults) (Santuz et al., 2019; Santuz et al., 2020). They concluded that in older adults and during locomotion over uneven surface, the CNS produces less complex control signals that are more stable over time, whereas in young adults and easier tasks (walking over standard surface) allow for more unstable and irregular control. These are exciting developments in understanding motor control adaptations during walking over uneven surfaces and the effects of aging, and future work should include understanding the interplay between muscle co-contractions and muscle synergies.

A limitation of this study is that our muscle co-contraction calculations were based on a single muscle pair per joint. We calculated muscle co-contraction at the ankle from the tibialis anterior and lateral gastrocnemius muscle pair, and at the knee from the rectus femoris and semitendinosus muscle pair. Although a more complete approach would include agonist/antagonist muscle activations from all muscles at a joint, muscle co-contractions from a single muscle pair per joint is the norm in the literature (Chandran et al., 2019; Lo et al., 2017; Mengarelli et al., 2015; Souissi et al., 2017). A second potential limitation is that participants walked at their self-selected speeds, suggesting that they would probably choose a speed they felt comfortable and thus their neuromuscular adaptations would be affected.

This study underscores the need for determining muscle co-contraction as part of clinical evaluation for motor control deficits due to aging or neuromuscular disorders. Based on our findings, we recommend these clinical evaluations to incorporate controlled experiments over even and uneven surfaces to tease out underlying motor control and neuromuscular deficits. Next, the substantially greater (55–61% from entire gait and 73–75% from stance phase) ankle muscle co-contractions in older females compared to older males during walking over even and uneven surfaces require further investigation. One plausible explanation is that the older males were physically stronger than the older females and thus more able to control their lower extremity joint accelerations so that neuromuscular control was also better. Mengarelli et al. attributed sex-based differences in muscle co-contraction to “a female tendency for a more complex muscular strategy during gait” (Mengarelli et al., 2015). Future work includes understanding the prevalence and potential causes of sex-based differences in muscle co-contraction during dynamic activities under different environmental demands.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Benjuya, N., Melzer, I., Kaplanski, J., 2004. Aging-induced shifts from a reliance on sensory input to muscle cocontraction during balanced standing. J. Gerontol. A Biol. Sci. Med. Sci. 59 (2), 166–171.

Berg, W.P., Alessio, H.M., Mills, E.M., Tong, C., 1997. Circumstances and consequences of falls in independent community-dwelling older adults. Age Ageing 26 (4), 261–268.

Bizzi, E., Cheung, V.C., d’Avella, A., Saltiel, P., Tresch, M., 2008. Combining modules for movement. Brain Res. Rev. 57 (1), 125–133.

Bizzi, E., Mussa-Ivaldi, F.A., Giszter, S., 1991. Computations underlying the execution of movement: a biological perspective. Science 253 (5017), 287–291.

Campbell, A.J., Borrie, M.J., Spears, G.F., Jackson, S.L., Brown, J.S., Fitzgerald, J.L., 1990. Circumstances and consequences of falls experienced by a community population 70 years and over during a prospective study. Age Ageing 19 (2), 136–141.

Chandran, V.D., Calalo, J.A., Dixon, P.C., Dennerlein, J.T., Schiffman, J.M., Pal, S., 2019. Knee muscle co-contractions are greater in old compared to young adults during walking and stair use. Gait Posture 73, 315–322.

Chiu, S.L., Chang, C.C., Dennerlein, J.T., Xu, X., 2015. Age-related differences in inter-joint coordination during stair walking transitions. Gait Posture 42 (2), 152–157.

Darainy, M., Ostry, D.J., 2008. Muscle cocontraction following dynamics learning. Exp. Brain Res. 190 (2), 153–163.

Den Otter, A.R., Geurts, A.C., Mulder, T., Duysens, J., 2006. Gait recovery is not associated with changes in the temporal patterning of muscle activity during treadmill walking in patients with post-stroke hemiparesis. Clin. Neurophysiol. 117 (1), 4–15.

Di Nardo, F., Mengarelli, A., Maranesi, E., Burattini, L., Fioretti, S., 2015. Assessment of the ankle muscle co-contraction during normal gait: a surface electromyography study. J. Electromyogr. Kinesiol. 25 (2), 347–354.

Dixon, P.C., Jacobs, J.V., Dennerlein, J.T., Schiffman, J.M., 2018. Late-cueing of gait tasks on an uneven brick surface impacts coordination and center of mass control in older adults. Gait Posture 65, 143–148.

Dixon, P.C., Jansen, K., Jonkers, I., Stebbins, J., Theologis, T., Zavatsky, A.B., 2015. Muscle contributions to centre of mass acceleration during turning gait in typically developing children: A simulation study. J. Biomech. 48 (16), 4238–4245.

Franklin, D.W., Osu, R., Burdet, E., Kawato, M., Milner, T.E., 2003. Adaptation to stable and unstable dynamics achieved by combined impedance control and inverse dynamics model. J. Neurophysiol. 90 (5), 3270–3282.

Franz, J.R., Kram, R., 2013. How does age affect leg muscle activity/coactivity during uphill and downhill walking? Gait Posture 37 (3), 378–384.

Hallal, C.Z., Marques, N.R., Spinoso, D.H., Vieira, E.R., Goncalves, M., 2013. Electromyographic patterns of lower limb muscles during apprehensive gait in younger and older female adults. J. Electromyogr. Kinesiol. 23 (5), 1145–1149.

Hausdorff, J.M., 2007. Gait dynamics, fractals and falls: finding meaning in the stride-to-stride fluctuations of human walking. Hum. Mov. Sci. 26 (4), 555–589.

Hesse, S., Brandl-Hesse, B., Seidel, U., Doll, B., Gregoric, M., 2000. Lower limb muscle activity in ambulatory children with cerebral palsy before and after the treatment with Botulinum toxin A. Restor. Neurol. Neurosci. 17 (1), 1–8.

Hirokawa, S., Solomonow, M., Luo, Z., Lu, Y., D’Ambrosia, R., 1991. Muscular co-contraction and control of knee stability. J. Electromyogr. Kinesiol. 1 (3), 199–208.

Horak, F.B., 1987. Clinical measurement of postural control in adults. Phys. Ther. 67 (12), 1881–1885.

Horak, F.B., 2006. Postural orientation and equilibrium: what do we need to know about neural control of balance to prevent falls? Age Ageing 35 Suppl 2, ii7-ii11.

Hortobagyi, T., Mizelle, C., Beam, S., DeVita, P., 2003. Old adults perform activities of daily living near their maximal capabilities. J. Gerontol. A Biol. Sci. Med. Sci. 58 (5), 453–460.

Hortobagyi, T., Solnik, S., Gruber, A., Rider, P., Steinweg, K., Helseth, J., et al., 2009. Interaction between age and gait velocity in the amplitude and timing of antagonist muscle coactivation. Gait Posture 29 (4), 558–564.

Centers for Disease Control and Prevention. 2020. Centers for Disease Control and Prevention Web–Based Injury Statistics Query and Reporting System, https://www.cdc.gov/injury/wisqars/index.html (accessed 07/27/2020).

Laerd, 2018. Mixed ANOVA using SPSS, https://statistics.laerd.com/spss-tutorials/mixed-anova-using-spss-statistics.php (accessed 04/20/2021).

Li, W., Keegan, T.H., Sternfeld, B., Sidney, S., Quesenberry Jr., C.P., Kelsey, J.L., 2006. Outdoor falls among middle-aged and older adults: a neglected public health problem. Am. J. Public Health 96 (7), 1192–1200.

Lo, J., Lo, O.Y., Olson, E.A., Habtemariam, D., Iloputaife, I., Gagnon, M.M., et al., 2017. Functional implications of muscle co-contraction during gait in advanced age. Gait Posture 53, 110–114.

McIlroy, W.E., Maki, B.E., 1996. Age-related changes in compensatory stepping in response to unpredictable perturbations. J. Gerontol. A Biol. Sci. Med. Sci. 51 (6), M289–M296.

Menant, J.C., Steele, J.R., Menz, H.B., Munro, B.J., Lord, S.R., 2009. Effects of walking surfaces and footwear on temporo-spatial gait parameters in young and older people. Gait Posture 29 (3), 392–397.

Mengarelli, A., Maranesi, E., Barone, V., Burattini, L., Fioretti, S., Di Nardo, F., 2015. Evaluation of gender-related differences in co-contraction activity of shank muscles during gait. Conf Proc IEEE Eng Med Biol Soc 2015, 6066–6069.

Menz, H.B., Lord, S.R., Fitzpatrick, R.C., 2003. Age-related differences in walking stability. Age Ageing 32 (2), 137–142.

Meyer, A.J., Patten, C., Fregly, B.J., 2017. Lower extremity EMG-driven modeling of walking with automated adjustment of musculoskeletal geometry. PLoS ONE 12 (7), e0179698.

Mian, O.S., Thom, J.M., Ardigo, L.P., Narici, M.V., Minetti, A.E., 2006. Metabolic cost, mechanical work, and efficiency during walking in young and older men. Acta Physiol (Oxf) 186 (2), 127–139.

Moder, K., 2010. Alternatives to F-test in one way ANOVA in case of heterogeneity of variances (a simulation study). Psychological Test and Assessment Modeling 52 (4), 343–353.

Nagai, K., Yamada, M., Uemura, K., Yamada, Y., Ichihashi, N., Tsuboyama, T., 2011. Differences in muscle coactivation during postural control between healthy older and young adults. Arch. Gerontol. Geriatr. 53 (3), 338–343.

O'Connor, J.J., 1993. Can muscle co-contraction protect knee ligaments after injury or repair? J. Bone Joint Surg. Br. 75 (1), 41–48.

Perotto, A., Delagi, E.F., Iazzetti, J., Morrison, D., 2005. Anatomical Guide for the Electromyographer, 4th ed. Charles C. Thomas, Springfield, IL.

Peterson, D.S., Martin, P.E., 2010. Effects of age and walking speed on coactivation and cost of walking in healthy adults. Gait Posture 31 (3), 355–359.

Ranstam, J., 2016. Multiple P-values and Bonferroni correction. Osteoarthritis Cartilage 24 (5), 763–764.

Rutherford, D.J., Hubley-Kozey, C.L., Stanish, W.D., 2011. Maximal voluntary isometric contraction exercises: a methodological investigation in moderate knee osteoarthritis. J. Electromyogr. Kinesiol. 21 (1), 154–160.

Santuz, A., Brull, L., Ekizos, A., Schroll, A., Eckardt, N., Kibele, A., et al., 2019. Humans exploit robust locomotion by improving the stability of control signals. bioRxiv.

Santuz, A., Brull, L., Ekizos, A., Schroll, A., Eckardt, N., Kibele, A., et al., 2020. Neuromotor Dynamics of Human Locomotion in Challenging Settings. iScience 23 (1), 100796.

Souissi, H., Zory, R., Bredin, J., Gerus, P., 2017. Comparison of methodologies to assess muscle co-contraction during gait. J. Biomech. 57, 141–145.

Thies, S.B., Richardson, J.K., Ashton-Miller, J.A., 2005. Effects of surface irregularity and lighting on step variability during gait: a study in healthy young and older women. Gait Posture 22 (1), 26–31.

Thoroughman, K.A., Shadmehr, R., 1999. Electromyographic correlates of learning an internal model of reaching movements. J. Neurosci. 19 (19), 8573–8588.

Welkowitz, J., Cohen, B.H., Lea, R.B., Welkowitz, 2012. Introductory Statistics for the Behavioral Sciences. John Wiley & Sons, Hoboken, USA.

Winter, D.A., 2005. Biomechanics and motor control of human movement, fourth ed. John Wiley & Sons, New York, NY.

Woollacott, M.H., 1993. Age-related changes in posture and movement. J Gerontol 48, 56–60.