Advanced Age Redistributes Positive but Not Negative Leg Joint Work during Walking

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ABSTRACT

WAANDERS, J. B., T. HORTOBÁGYI, A. MURGIA, P. DEVITA, and J. R. FRANZ. Advanced Age Redistributes Positive but Not Negative Leg Joint Work during Walking. *Med. Sci. Sports Exerc.*, Vol. 51, No. 4, pp. 615–623, 2019. **Introduction**: Advanced age brings a distal-to-proximal redistribution of positive joint work during walking that is relevant to walking performance and economy. It is unclear whether negative joint work is similarly redistributed in old age. Negative work can affect positive work through elastic energy return in gait. We determined the effects of age, walking speed, and grade on positive and negative joint work in young and older adults. **Methods**: Bilateral ground reaction force and marker data were collected from healthy young (age = 22.5 yr, $n = 18$) and older (age = 76.0 yr, $n = 22$) adults walking on a split-belt instrumented treadmill at 1.1, 1.4, and 1.7 m·s^{-1} at each of three grades (0%, 10%, and -10%). Subjects also performed maximal voluntary eccentric, isometric, and concentric contractions for the knee extensors (120°·s^{-1}, 90°·s^{-1}, and 0°·s^{-1}) and plantarflexors (90°·s^{-1}, 30°·s^{-1}, and 0°·s^{-1}). **Results**: Compared with young adults, older adults exhibited a distal-to-proximal redistribution of positive leg joint work during level ($P < 0.001$) and uphill ($P < 0.001$) walking, with larger differences at faster walking speeds. However, the distribution of negative joint work was unaffected by age during level ($P = 0.150$) and downhill ($P = 0.350$) walking. Finally, the age-related loss of maximal voluntary knee extensor ($P < 0.001$) and plantarflexor ($P = 0.001$) strength was smaller during an eccentric contraction versus concentric contraction for the knee extensors ($P < 0.001$) but not for the plantarflexors ($P = 0.320$). **Conclusion**: The distal-to-proximal redistribution of positive joint work during level and uphill walking is absent for negative joint work during level and downhill walking. Exercise prescription should focus on improving ankle muscle function while preserving knee muscle function in older adults trying to maintain their independence. **Key Words**: ECCENTRIC, CONCENTRIC, BIOMECHANICS, GAIT, AGING

Advancing age is accompanied by neuromuscular impairments (1–3), which likely contribute to the stereotypical kinematic and kinetic patterns in elderly gait. Kinematic changes include shorter (4) and more variable steps (5), altered posture (6), and slower walking speeds (7). In addition, even when walking at the same speed as young adults, older adults produce 16%–30% less positive plantarflexor work and 22%–82% more positive hip flexor and extensor work (4,8). This age-related distal-to-proximal redistribution in positive leg joint work is a robust phenomenon, evident at various walking speeds (8,9), surface inclines (10), and physical activity histories (11) and in older adults of various physical capacities (12). It is also functionally relevant; reduced plantarflexor work correlates with slower walking speeds (13), and a reliance on positive work performed by the hip musculature can worsen walking economy (14). Some evidence suggests that the plantarflexor muscles operate closer to their maximal capacity for power generation during walking than other leg muscles (15,16). Accordingly, muscle weakness could be at least one factor to explain the disproportionate reduction in plantarflexor positive work in older age.

Compared with our understanding of age-related effects on positive leg joint work, the mechanical behavior of lower-extremity joints with respect to negative work or energy absorption during walking is much less understood. Negative work performed by the leg muscles during walking serves in part to regulate vertical support, to weight transfer

during step-to-step transitions, and to decelerate individual body segments (17–19). As one functionally relevant consequence, inadequate eccentric muscle function can increase the risk of tripping and falling (20,21). In addition, understanding the performance of negative leg joint work during walking may help us explain the age-related redistribution of positive work. Indeed, negative work or energy absorbed during walking can prescribe positive work requirements or even fuel positive work through elastic energy return (22), thereby influencing concentric muscle function, also known as the stretch-shortening cycle. Furthermore, environmental challenges can increase the demand for negative leg joint work. For example, compared with level walking, total negative leg joint work is roughly three times greater during downhill walking, and that increase is largely accommodated by the knee extensor muscles (18).

Compared with that for positive leg joint work, an age-related redistribution of negative leg joint work during walking might be attenuated for several reasons. First, eccentric knee extensor and plantarflexor functions are relatively well maintained in older age. Indeed, older adults exhibit a relative maintenance of maximal voluntary eccentric strength (0%–30% loss) compared with isometric (20%–40% loss) and, in particular, concentric (30%–50% loss) strength for both muscle groups (23–26). Second, based on peak joint moments, the relative demand on hip and knee extensors and ankle plantarflexors to perform negative work during level and downhill walking is lower than that on the plantarflexors to perform positive work during level and uphill walking (18). These findings suggest that leg extensor muscles operate well below their maximal muscle capacity when performing negative work during walking. Functionally, this could minimize the consequences of age-related neuromuscular impairments and, thus, attenuate the need to redistribute negative leg joint work to more proximal leg muscles, for example, during level and downhill walking.

In this study, we hypothesized that an age-related distal-to-proximal redistribution of leg joint work would (i) be evident for positive work during level and uphill walking but (ii) absent for negative work during level and downhill walking. To more comprehensively evaluate the prevalence and functional relevance of these potential age-related adaptations, we also tested those hypotheses across a wide range of walking speeds. Therefore, the aim was to determine the effects of age, walking speed, and grade on positive and negative joint work in young and older adults.

METHODS

Study design. This cross-sectional study consisted of two sessions (dynamometry testing and gait analysis) performed within 14 d for each subject. Subjects were recruited via word of mouth and flyers and screened through a telephone interview. Before any measurement, subjects provided written informed consent approved by the University of North Carolina

Institutional Review Board (IRB no. 16-3217), and subjects were screened again using an extensive health questionnaire.

Subject characteristics. Healthy young (age = 18–35 yr, $n = 18$) and older (age = 65+ yr, $n = 22$) adults participated in this study (Table 1). Subjects were included if they met the age criterion, were able to walk without an assistive device, and could provide informed consent. Exclusion criteria were a current leg fracture or injury, taking medication that causes dizziness, or mild cognitive impairment based on a Mini-Mental State Examination (i.e., score below 24) (27). Subjects were mobility independent based on their performance on the Short Physical Performance Battery (28).

Dynamometry testing session. Before dynamometry testing, subjects warmed up their legs by walking for 5 min on a treadmill at 1.2 m·s^{-1}. We then tested the subjects' right leg maximum voluntary eccentric, isometric, and concentric plantarflexor and knee extensor moment (Biodex System 4 Pro), which we refer to as strength to distinguish from net moments during walking.

For plantarflexor testing, subjects were positioned in the dynamometer with the right leg in 30° of knee flexion (KF), the shank parallel to the floor, and the ankle joint aligned with the rotational axis of the dynamometer head. Straps around the foot and thigh limited movement to dorsal (DF) and plantarflexion (PF). The anatomical zero was set at a neutral ankle angle (i.e., 90° between the shank and the footpad). Subjects performed eccentric and concentric testing at angular velocities of 30°·s^{-1} and 90°·s^{-1} across a range of motion set from 20° PF to 15° DF. Subjects performed isometric testing at 7° DF to compensate for 7° of heel raise common to this test (29) and thereby obtain muscle strength representative of those at a neutral ankle angle. In a *post hoc* analysis, we actually observed 5.2° ± 2.0° of ankle rotation using marker position data on the foot and lower leg.

During knee extensor testing, subjects' right hip was flexed to 85° with the knee joint center aligned with the rotational axis of the dynamometer. Straps above the ankle joint and around the thigh, lap, and trunk limited movement to KF and extension. Anatomical zero was set at full knee extension. Subjects performed eccentric and concentric testing at angular velocities of 90°·s^{-1} and 120°·s^{-1} across a range of motion set from 15° to 90° KF. Subjects performed isometric testing at 65° KF, an angle that typically allows the highest generation of isometric muscle strength (30).

After we performed a gravity correction for each posture, subjects performed several submaximal trials to become

TABLE 1. Subject characteristics.

	Young (9 Males, 9 Females)	Older (9 Males, 13 Females)
Age, yr	22.5 ± 4.1	76.0 ± 5.7
Body height, m	1.78 ± 0.08	1.69 ± 0.09
Body weight, kg	72.3 ± 12.5	69.5 ± 10.5
BMI, kg·m^{-2}	22.8 ± 2.7	24.1 ± 2.8
MMSE score	29.8 ± 0.5	29.5 ± 0.8
SPPB score	11.9 ± 0.2	11.1 ± 0.9

Values are presented as mean ± SD. SPPB, short physical performance battery.

familiarized with the task and then performed two maximal exertions for each muscle group. Here, the contraction type and angular velocities were randomized. Subjects were verbally encouraged during testing, rested at least 1 min between contractions, and, for isokinetic testing, were instructed to generate as much force as quickly as possible. The selected ankle and knee joint angular velocities are similar to those used previously and have been shown to yield good (i.e., ICC 0.75–0.90) to excellent (ICC > 0.90) reliability (23,31).

Treadmill testing session. Before testing, subjects walked on a level, instrumented split-belt treadmill for 5 min at 1.2 m·s^{-1} (Bertec Corp., Columbus, OH). Subjects then walked for 60 s at three speeds (1.1, 1.4, and 1.7 m·s^{-1}) at each of three grades (−10%, 0%, and 10%) for a total of nine experimental conditions. The conditions lasted for 60 s to avoid fatigue during the measurements. Given practical considerations, within each treadmill grade (0%, 10%, and −10%), we fully randomized the walking speeds for each subject. We recorded treadmill ground reaction forces (at 960 Hz) and marker position data (at 120 Hz) from both legs—the latter using an eight-camera passive motion capture system (Vicon, Centennial, CO). Subjects wore 36 markers over specific body/shoe landmarks: posterior superior iliac spines (plus two tracking markers), anterior superior iliac spines, greater trochanters, lateral thighs and shanks (four markers on each segment), lateral and medial femoral condyles, lateral and medial malleoli, calcanei, and first and fifth metatarsal heads. All subjects wore a safety harness and rested as needed between conditions.

Data analysis. We analyzed dynamometer muscle strength data using a custom MATLAB script (Mathworks, Natick, MA) that extracted the peak muscle strength measured from each condition and the muscle strengths were normalized for body height and weight.

Raw ground reaction force and marker position data were imported to Visual3D for analysis (C-Motion, Inc., Germantown, MD). In Visual3D, we applied a fourth-order low-pass Butterworth filter to the ground reaction force (cutoff: 45 Hz) and marker position data (cutoff, 6 Hz). These data, in combination with a rigid body model of the legs and a 20-N threshold in the vertical ground reaction force, were used to obtain step length, duty cycle, and sagittal plane hip, knee, and ankle joint angles, moments, and powers. In MATLAB, crossover walking cycles were removed, and at least 15 walking cycles per condition per subject were averaged, excluding those within the first and last 5 s of every condition. Joint moments and powers were normalized to body height and weight, and all outcomes were averaged bilaterally.

We estimated hip, knee, and ankle joint work by integrating the respective joint power curves with respect to time. We report total positive joint work as the sum of hip extensor work during early stance (32), hip flexor work during late stance, knee extensor work during midstance, and plantarflexor work during late stance. We report total negative joint work as the sum of hip flexor work during midstance, knee extensor work during early and late stance, and plantarflexor work during midstance. Finally, we computed relative contributions from the hip, knee, and ankle joints to total positive and negative joint work as a percentage.

Statistical analysis. First, a mixed three-way factorial ANOVA with between-subject factor age (young and older) and within-subject factors joint (hip, knee, and ankle) and speed (1.1, 1.4, and 1.7 m·s^{-1}) was performed on the relative joint contributions (%) to total positive leg joint work during 1) level walking and 2) uphill walking. The same statistical test was also performed on the relative joint contributions (%) to total negative leg joint work during 3) level walking and 4) downhill walking.

Second, a mixed two-way factorial ANOVA with between-subject factor age (young and older) and within-subject factor joint angular velocity (eccentric fast, eccentric slow, isometric, concentric slow, and concentric fast) was performed on the maximal voluntary muscle strengths of 1) the knee extensors and 2) the plantarflexors. Young adults ($n = 2$) were excluded from this analysis as their peak muscle strengths were consistently (i.e., for six out of eight dynamometry conditions) lower than the older group average, which we deemed to be unrepresentative of their age-group. A Greenhouse–Geisser correction was applied when the assumption of sphericity was violated. Tukey's *post hoc* comparisons were performed for those outcome measures having a significant main effect or interaction. Statistical significance was set at $\alpha = 0.05$. We used IBM SPSS for all statistical testing.

RESULTS

Older adults took shorter steps than young subjects, an effect that was largest, 7.5%, during uphill walking at 1.7 m·s^{-1} and smallest, 4.0%, during downhill walking at 1.7 m·s^{-1} (see Table, Supplemental Digital Content 1, which presents spatiotemporal and kinematic measures across walking grades and speeds, http://links.lww.com/MSS/B435). Figures 1, 2, and 3 report leg joint angles, moments, and powers during walking, respectively (see Table, Supplemental Digital Content 2, which presents the corresponding averaged standard deviation around the group mean time-series, http://links.lww.com/MSS/B436). Here, we note that older subjects generally adopted a more flexed position at their hip and decreased peak ankle plantarflexion than young subjects.

Positive leg joint work. During level walking across the three walking speeds, the largest relative contribution to total positive leg joint work came from the plantarflexors (young, 60.8% ± 4.7%; older, 53.1% ± 7.3%), followed by the hip flexors/extensors (young, 31.9% ± 5.2%; older, 38.4% ± 7.0%), and finally by the knee extensors (young, 7.3% ± 3.2%; older, 8.5% ± 4.9%) (joint: $F_{1.66,63.09} = 498.4$, $P < 0.001$, $\eta_p^2 = 0.93$) (Fig. 4). An age–joint interaction effect ($F_{1.66,63.09} = 10.47$, $P < 0.001$, $\eta_p^2 = 0.21$) for this relative contribution showed that older adults exhibited smaller differences between their plantarflexors and hip flexors/extensors than young adults. Significant joint–speed ($F_{2.09,79.66} = 30.53$,
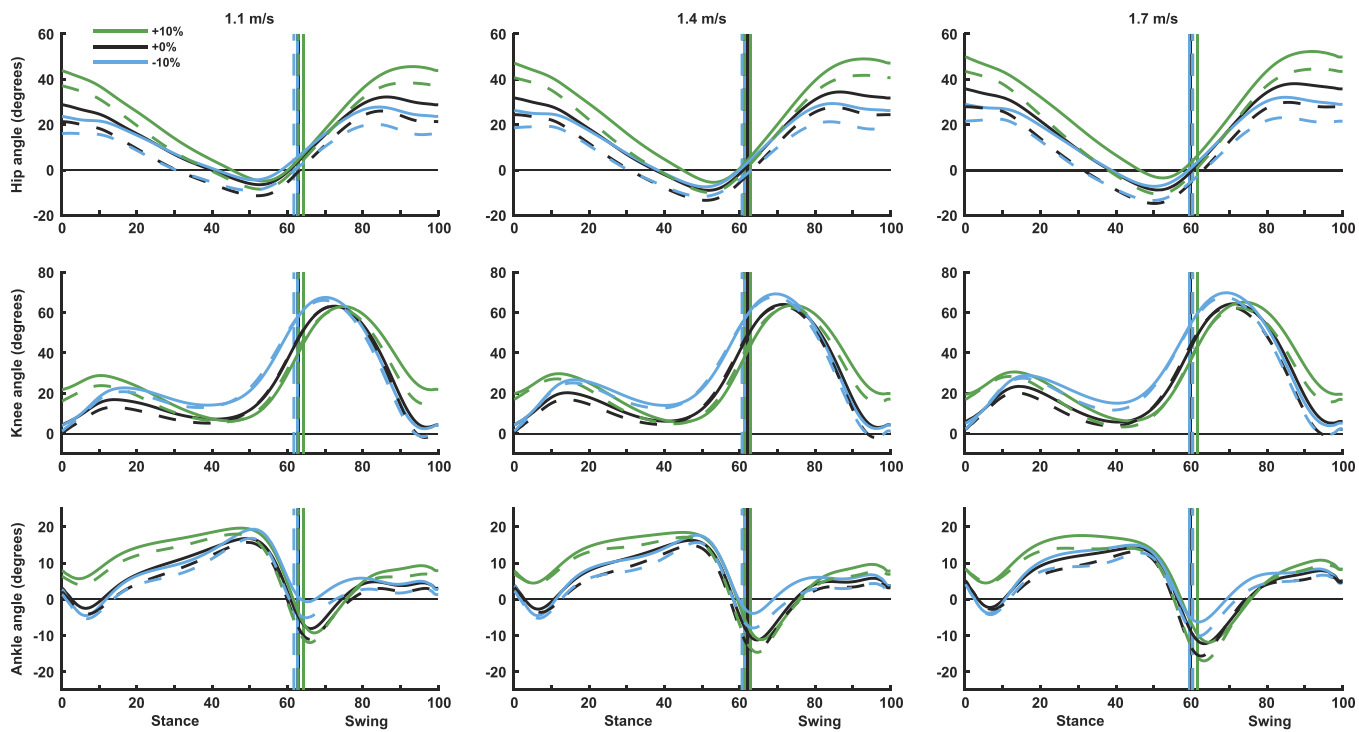
FIGURE 1—Group average hip, knee, and ankle joint angles during level, uphill, and downhill walking at slow, moderate, and fast walking speed in young (*dashed lines*) and older adults (*solid lines*). Positive values represent joint flexion. Vertical lines represent toe-off for the corresponding walking condition and age-group.

$P < 0.001$, $\eta_p^2 = 0.45$) and age–joint–speed ($F_{2.09,79.66} = 5.27$, $P < 0.010$, $\eta_p^2 = 0.12$) interaction effects showed that the difference in this relative contribution between the

plantarflexors and the hip flexors/extensors became smaller with increasing walking speed, an effect that was larger for older than young adults.

FIGURE 2—Group average hip, knee, and ankle joint moments during level, uphill, and downhill walking at slow, moderate, and fast walking speed in young (*dashed lines*) and older adults (*solid lines*). Positive values represent extensor moments. Vertical lines represent toe-off for the corresponding walking condition and age-group.
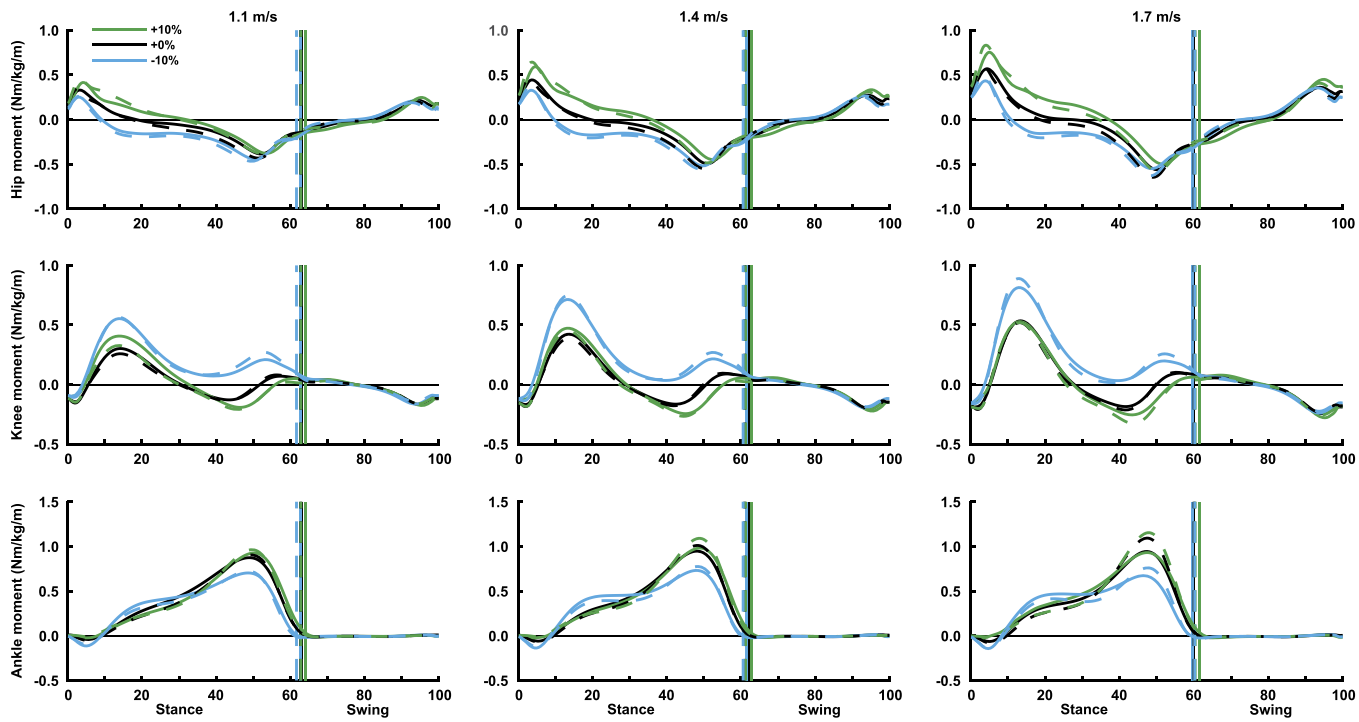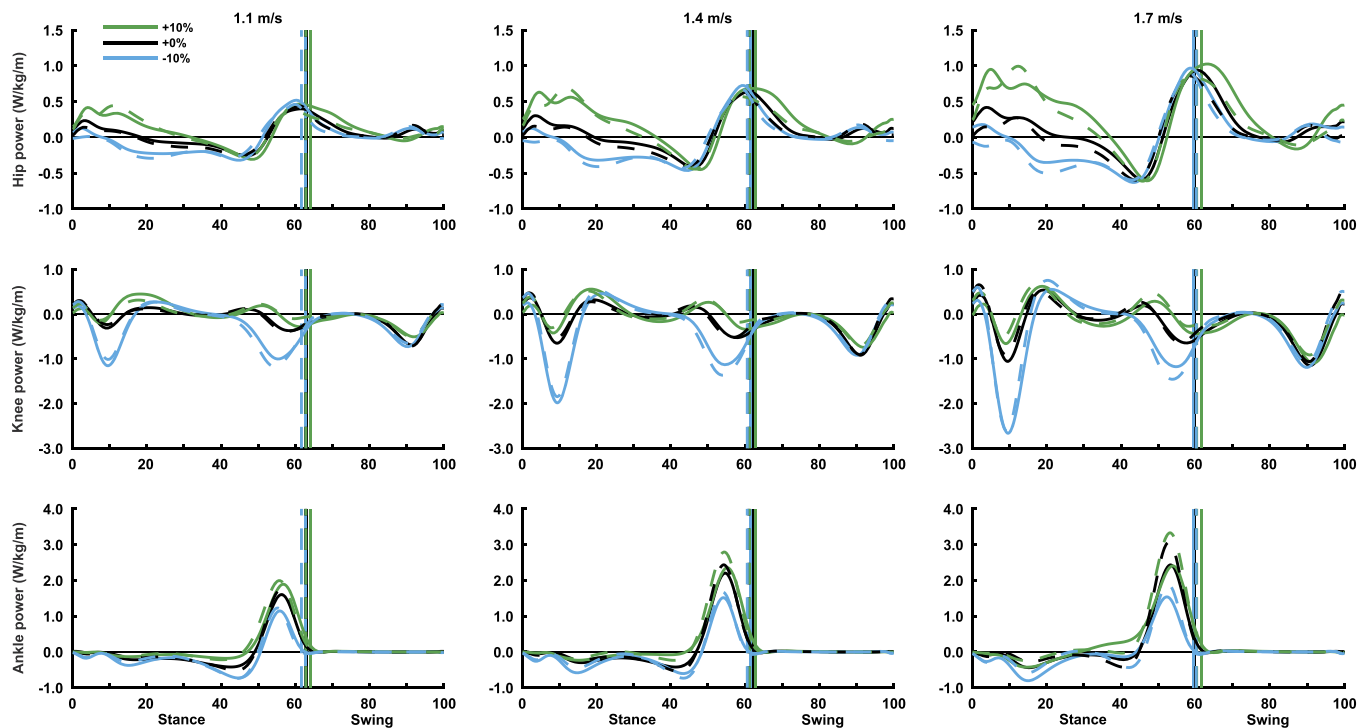
FIGURE 3—Group average hip, knee, and ankle joint powers during level, uphill, and downhill walking at slow, moderate, and fast walking speed in young (*dashed lines*) and older adults (*solid lines*). Positive values represent power generation. Vertical lines represent toe-off for the corresponding walking condition and age-group.

During uphill walking across the three walking speeds, the largest relative contribution to total positive leg joint work in young adults came from the plantarflexors (50.4% ± 6.5%), followed by the hip flexors/extensors (40.2% ± 5.8%), and finally by the knee extensors (9.5% ± 4.7%). By contrast, in older subjects, this relative contribution was largest for the hip flexors/extensors (45.5% ± 6.3%),

followed by the plantarflexors (43.2% ± 5.9%), and finally by the knee extensors (11.3% ± 4.9%) (joint: $F_{1.84,69.98} = 317.7$, $P < 0.001$, $\eta_p^2 = 0.89$). An age–joint interaction effect ($F_{1.84,76} = 8.38$, $P = 0.001$, $\eta_p^2 = 0.18$) for this relative contribution showed that older adults exhibited smaller differences between their plantarflexors and hip flexors/extensors than young adults. The largest relative contribution shifted
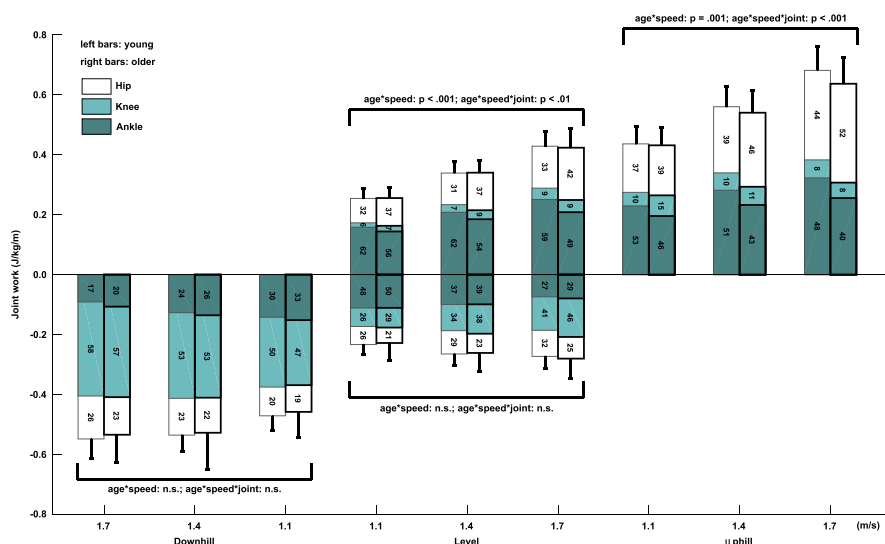

FIGURE 4—Group average relative leg joint contributions to total positive work (level and uphill walking) and negative work (level and downhill walking) across slopes and speeds in young and older adults. Numerical values within each bar represent the group average relative contribution reported as a percentage. n.s. = not significant ($P > 0.050$).

from the plantarflexors to the hip flexors/extensors with increasing walking speed (joint–speed: $F_{2.76,105.0} = 66.94$, $P < 0.001$, $\eta_p^2 = 0.64$). In addition, an age–joint–speed interaction ($F_{2.77,150.08} = 9.72$, $P < 0.001$, $\eta_p^2 = 0.20$) indicated that the difference in this relative contribution between the plantarflexors and the hip flexors/extensors increased more in older adults as walking speed increased from slow to moderate, but more in young adults from moderate to fast speed.

Negative leg joint work. During level walking across the three walking speeds, the largest relative contribution to total negative leg joint work came from the plantarflexors (young, 37.4% ± 7.6%; older, 39.4% ± 10.3%), followed by the knee extensors (young, 33.7% ± 8.8%; older, 37.8% ± 10.8%), and finally by the hip flexors (young, 28.8% ± 10.4%; older, 22.8% ± 10.2%) (joint: $F_{2,76} = 12.01$, $P < 0.001$, $\eta_p^2 = 0.24$) (Fig. 4). The differences in this relative contribution between muscle groups were comparable between older and young adults (age–joint: $F_{2,76} = 1.93$, $P = 0.150$, $\eta_p^2 = 0.18$). The distribution of negative work was also walking speed dependent (joint–speed: $F_{1.63,62.04} = 167.2$, $P < 0.001$, $\eta_p^2 = 0.82$), with a larger relative contribution from the knee extensors and a smaller relative contribution from the plantarflexors with increasing speed. However, those speed effects were unaffected by age (age–joint–speed: $F_{1.63,62.04} = 0.58$, $P = 0.520$, $\eta_p^2 = 0.02$).

During downhill walking across the three walking speeds, the largest relative contribution to the total negative leg joint work came from the knee extensors (young, 53.5% ± 7.6%; older, 52.3% ± 7.7%), followed by the plantarflexors (young, 23.6% ± 3.3%; older, 26.5% ± 5.0%), and finally by the hip flexors (young, 22.9% ± 7.2%; older, 21.2% ± 8.2%) (joint: $F_{1.48,56.3} = 165.7$, $P < 0.001$, $\eta_p^2 = 0.81$). The differences in this relative contribution between muscle groups were comparable between older and young adults (age–joint: $F_{1.48,56.32} = 0.90$, $P = 0.380$, $\eta_p^2 = 0.02$), as were the effects of increasing gait speed (age–joint–speed: $F_{3.11,118.3} = 1.33$, $P = 0.260$, $\eta_p^2 = 0.03$). However, a joint–speed interaction effect ($F_{3.11,118.3} = 158.5$, $P < 0.001$, $\eta_p^2 = 0.81$) revealed a larger relative contribution from the knee extensors and a smaller relative contribution from the plantarflexors with increasing walking speed.

Maximal voluntary strength. Maximal voluntary knee extensor strength was lower in older compared with young adults (age: $F_{1,36} = 28.42$, $P < 0.001$, $\eta_p^2 = 0.44$), but the magnitude of strength loss differed by type of muscle action (age–velocity: $F_{2.42,87.04} = 15.13$, $P < 0.001$, $\eta_p^2 = 0.30$) (Table 2). Specifically, *post hoc* analyses revealed a smaller ($P < 0.050$) difference for eccentric versus concentric muscle actions between young and older adults. Also, maximal voluntary plantarflexor strength was lower in older compared with young adults (age: $F_{1,36} = 13.44$, $P = 0.001$, $\eta_p^2 = 0.27$), independent of muscle action (age–velocity: $F_{2.76,99.42} = 1.17$, $P = 0.320$, $\eta_p^2 = 0.03$).

DISCUSSION

We examined the effects of age, walking speed, and grade on the distribution of positive and negative leg joint work across the hip, knee, and ankle during walking in young and older adults. Positive leg joint work was redistributed from muscles spanning the ankle to muscles spanning the hip in older versus young adults during level and uphill walking, with larger effects at faster walking speeds. Conversely and as hypothesized, we observed no age effects on the distribution of negative leg joint work during level and downhill walking. The results are especially interesting in the context of muscle strength; we observed a relative maintenance of maximal voluntary eccentric compared with concentric muscle strength in older age for the knee extensors but not for the plantarflexors. The findings imply that the age-related redistribution of positive work during walking is likely independent of negative work. We interpret our findings to suggest that exercise prescription for older adults should aim to improve ankle while preserving knee muscle function.

The age-related redistribution of positive mechanical work from the ankle to the hip during level and uphill walking agrees with previous literature and has been extensively discussed elsewhere (4,33). Also, consistent with previous reports, this redistribution became more prominent at faster walking speeds (8,9). Indeed, here, the relative contribution from the hip muscles even overcame that from the plantarflexors in older subjects during moderate and fast uphill walking. Together, these two findings reflect the potential of more challenging walking conditions to amplify hallmark biomechanical differences in elderly gait. This redistribution of positive work is particularly important because lower ankle positive work correlates with slower

TABLE 2. Peak knee extensor and plantarflexor strengths (N·m·kg^{-1}·m^{-1}) in healthy young and older adults.

Knee Extension[a,b]	ECC 120°·s^{-1}	ECC 90°·s^{-1}	ISO	CON 90°·s^{-1}	CON 120°·s^{-1}
Y (*n* = 16)	1.12 ± 0.25	1.14 ± 0.22	1.12 ± 0.13	0.87 ± 0.18	0.76 ± 0.14
O (*n* = 22)	0.95 ± 0.19	1.01 ± 0.21	0.80 ± 0.17	0.51 ± 0.15	0.46 ± 0.15
O % maint.	85 ± 17	88 ± 19	72 ± 15	59 ± 17	61 ± 19
Ankle Plantarflexion[a]	**ECC 90°·s^{-1}**	**ECC 30°·s^{-1}**	**ISO**	**CON 30°·s^{-1}**	**CON 90°·s^{-1}**
Y (*n* = 16)	0.82 ± 0.15	0.92 ± 0.20	0.75 ± 0.18	0.62 ± 0.19	0.40 ± 0.10
O (*n* = 22)	0.66 ± 0.13	0.72 ± 0.16	0.56 ± 0.14	0.43 ± 0.15	0.29 ± 0.14
O % maint.	80 ± 17	78 ± 18	75 ± 19	69 ± 25	72 ± 34

Values are presented as mean ± SD. ECC, eccentric; ISO, isometric; CON, concentric; Y, young; O, older; O % maint., strength maintenance in older relative to young adults in percent.
[a]Peak muscle strength greater in young versus older adults ($P < 0.05$).
[b]Muscle strength loss with aging lower during ECC versus CON.

walking speeds (13) and a greater reliance on hip positive work can reduce walking economy (14). That redistribution is also most likely not explained by shorter steps in older adults; others have observed this phenomenon even in the absence of age-related changes in step length (10,15). We also note here that the relative contribution from the knee extensors to total positive joint work was relatively negligible during level (~8%) and uphill walking (~10%). This finding agrees with previous level walking studies (4,8). Compared with level walking, Franz and Kram (10) observed a substantial increase in the contribution from knee extensor muscles during uphill walking in older adults. Although this differs from our findings, their subjects walked on a steeper, ~16%, ramp, and knee extensor work may increase disproportionately with a greater mechanical demand to raise the body's center of mass.

As the product of joint moment and angular displacement, the age-related reduction in positive ankle joint work during walking arises from a smaller ankle moment and/or range of motion. Consistent with previous work (4,10), we observed 13% and 15% smaller peak ankle moments in older versus young adults during level and uphill walking, respectively. Furthermore, while young adults increased their peak ankle moment by 27% from slow level walking to fast uphill walking, older adults only increased this value by 6%. This difference points to a function-limiting impairment in elderly gait. Indeed, we also observed 25% and 30% losses in maximal voluntary isometric and concentric plantarflexor strength generation in older adults (Table 2). These findings suggest that older subjects may have been less capable of increasing their peak ankle moment compared with young subjects when faced with increasing task demands. One explanation for this could be that the plantarflexor muscles operate closer to their maximal capacity than other leg muscles during walking (15,16). However, and despite subtle reductions in ankle range of motion for older subjects during level (2° less in older) and uphill (1° less in older) walking, older adults increased positive ankle joint work by 77% from slow level to fast uphill walking (vs 104% for young). Accordingly, older subjects appear to meet the ankle positive work demands of walking faster or uphill more by increasing the ankle angular displacement (i.e., plantarflexion) during push-off than by increasing the peak ankle moment. Also, in these conditions, older adults start to push-off slightly earlier, at the expense of the preceding energy absorption phase.

To our knowledge, the present study is the first to show that advanced age is not associated with a redistribution of negative leg joint work during level and downhill walking. As a cyclic functional pair of concentric force generation, eccentric muscle function could help to elucidate the mechanisms underlying the age-related redistribution of positive work. In vitro tests have shown that active muscle lengthening (i.e., eccentric action) before shortening (i.e., concentric action) enhances muscle force production and efficiency during that shortening, largely through the return

of stored elastic energy (34). Ultrasound measurements of plantarflexor muscle–tendon behavior during walking suggest that this enhancement via stretch-shortening cycles also occurs in vivo (22). We would thus interpret our findings to suggest that the well-documented age-related distal-to-proximal redistribution of positive leg joint work is independent of preceding eccentric leg muscle function. Perhaps age adversely affects coupling between eccentric and concentric muscle function in the stretch-shortening cycle. The time duration of and ankle angular velocity at which the plantarflexors performed negative work was similar between young and old adults across level and uphill walking conditions (see Table, Supplemental Digital Content 3, Group averaged time duration of and ankle angular velocity at which the plantarflexors performed negative work prior to push-off across walking grades and speeds, http://links.lww.com/MSS/B437). However, the age-related reduction in tendon stiffness (3) might be one potential structural change that could affect such coupling. Ultrasound measurements during walking or musculoskeletal simulations could provide more definitive insights to these causal links at the individual muscle level.

When walking faster and downhill, the control of energy absorption during KF during early to midstance becomes increasingly important to effectively decelerate the body's center of mass with each step (8,18). Our findings are consistent with this increased mechanical demand. Total negative leg joint work increased by 134% (young) and 135% (older) from slow (1.1 m·s^{-1}) level to fast (1.7 m·s^{-1}) downhill walking, accompanied by similar increases in knee extensor's contribution from 26% to 58% in young and 29% to 57% in older. Eccentric plantarflexor function also assists KF control by decelerating forward rotation of the shank over the stance foot. This specific eccentric action seems more important for controlling downward motion of the center of mass than forward motion; negative ankle joint work increased from level to downhill walking but decreased with faster walking speed. Lastly, eccentric hip flexor function resists hip extension and ultimately assists leg swing through the storage of elastic energy (35). The relative eccentric contribution from muscles spanning the hip remained relatively constant across experimental conditions, although the absolute value mirrored increases in total negative leg joint work. Collectively, our findings underscore the functional importance of preserving adequate knee extensor function in older adults to meet the demands for negative leg joint work, especially when the task or environment requires increasing speed or walking downhill.

In partial agreement with previous studies, we observed a relative maintenance of maximal voluntary eccentric versus concentric muscle function for the knee extensors (23,26) but not the plantarflexors (24). Porter et al. (24) also observed relative eccentric strength maintenance for the plantarflexors, but their sample included females only and older females tend to show a greater eccentric strength maintenance than older males (23,25). The relative

maintenance of eccentric muscle strength is a robust finding, observed in older mice, in healthy and clinical older adult populations, and in both upper and lower-extremity muscles (for a review, see Roig et al. 2010). However, perhaps because eccentric muscle actions have been anecdotally linked to muscle damage and injury, their potential functional benefits are relatively understudied. Notably, older patients can improve their walking speed (36,37), fall risk (36), and balance (36) after eccentric muscle training. However, we previously (26) observed relatively weak associations between self-selected speed during downhill walking or stair decent and eccentric knee extensor strength in healthy older adults. As we elaborate below, our walking data provide important functional context for associations between the type of muscle action and walking condition, with implications for the prescription of targeted, muscle-specific exercise interventions for older adults.

We posit that age had no significant effect on the relative distribution of negative joint work during level and downhill walking because the knee extensors operate well below their maximal available capacity—a stark contrast with the plantarflexors during level and uphill walking. Like other authors, we find that the knee extensors are inherently stronger than the plantarflexors, independent of age (Table 2). We also add that older adults had a relatively high maintenance of maximal voluntary eccentric strength for the knee extensors, which only decreased on average by ~13%. This maintenance is functionally meaningful; an exploratory *post hoc* analysis revealed that maximal eccentric knee extensor strength was significantly and positively correlated with the amount of energy absorbed by those muscles in the early stance phase of downhill walking in older adults ($r^s = 0.52$, $P = 0.014$; see Figure, Supplemental Digital Content 4, which shows data supporting this correlation, http://links. lww.com/MSS/B438). Finally, young and older adults, respectively, increased their peak knee extensor moment by 242% and 170% from slow level to fast downhill walking. Even at its maximum value, peak knee extensor moments in older adults were 17% smaller than their peak ankle moment during uphill walking. Taken together, these findings suggest that the knee extensors operated well below their maximal capacity during level and downhill walking in both age-groups, and perhaps no age-related redistribution in negative joint work was needed. Indeed, others have observed that the knee extensors of older adults operate at only ~30% of their maximum capacity during habitual level walking (16). However, we acknowledge that those values should be interpreted with some caution. Using dynamometry data as a reference for walking can lead to physiologically implausible estimates of the extent to which muscular capacity is used. This is best evidenced by the plantarflexors, for which relative effort in walking often exceeds 100% (15).

This study had several limitations. First, we selected prominent and functionally meaningful phases during the stance phase of walking in which significant total positive and negative leg joint work is known to be performed. Indeed, selecting these phases, a common practice in the literature, accounts for more than 70% of the total positive and negative joint work performed during level walking (8). Second, we only computed joint work in the sagittal plane. Although ~84% of total leg joint work is performed in the sagittal plane during level walking (32), it is unclear whether this contribution changes during uphill and downhill walking. Third, conventional inverse dynamics does not specifically account for coactivation between agonist and antagonist muscles, energy transferred via biarticular muscles, nor for stored elastic energy return. Those factors could influence our interpretations and, thus, our recommendations for exercise prescription. Fourth, we qualitatively evaluated right leg dynamometry outcome measures against gait kinetics averaged across both legs. However, previous literature supports the assumption of bilateral similarity of knee (38) and ankle (39) muscle function in healthy young and older adults. Fifth, the different distribution of males and females between our young and older adult groups may have affected our strength measurement results, as females have larger age-related knee extensor muscle deficits (40). Finally, our results provide only indirect evidence that age adversely affects the coupling between negative and positive joint work in older adults. Future research should focus on discovering age-related neuromuscular changes, e.g., reduced tendon stiffness, that could contribute to decoupling negative and positive joint work during walking.

To conclude, we observed that the distal-to-proximal redistribution of positive leg joint work during level and uphill walking, a hallmark feature of elderly gait, is absent for negative leg joint work during level and downhill walking. Positive joint work may be redistributed away from the plantarflexors in older age because they operate nearer to their maximal capacity than other leg muscles, requiring compensatory increases at muscles spanning the hip. By contrast, the distribution of negative joint work may be unaffected by age because older adults better maintain their eccentric knee extensor strength compared with young, and because the knee extensors operate well below their maximum capacity. On the basis of the present findings, we suggest that the age-related redistribution of positive work during walking is not due to a redistribution of negative work. We also suggest that exercise prescription should focus on improving function of muscles spanning the ankle while preserving function of muscles spanning the knee in older adults trying to maintain their independence in the community.

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