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Which muscles compromise human locomotor performance with age?

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Ageing leads to a progressive decline in human locomotor performance. However, it is not known whether this decline results from reduced joint moment and power generation of all lower limb muscle groups or just some of them. To further our understanding of age-related locomotor decline, we compare the amounts of joint moments and powers generated by lower limb muscles during walking (self-selected), running ($4\ \mathrm{m\,s^{-1}}$) and sprinting (maximal speed) among young, middle-aged and old adults. We find that age-related deficit in ankle plantarflexor moment and power generation becomes more severe as locomotion change from walking to running to sprinting. As a result, old adults generate more power at the knee and hip extensors than their younger counterparts when walking and running at the same speed. During maximal sprinting, young adults with faster top speeds demonstrate greater moments and powers from the ankle and hip joints, but interestingly, not from the knee joint when compared with the middle-aged and old adults. These findings indicate that propulsive deficit of ankle contributes most to the age-related locomotor decline. In addition, reduced muscular output from the hip rather than from knee limits the sprinting performance in older age.

1. Introduction

It is clearly evident that human locomotor performance declines with age. This phenomenon is largely owing to age-related attenuation of the locomotor system function [1], which predisposes to compromised movement patterns [2] and substantially limits the amount of ground reaction forces (GRFs) that can be applied by lower limb muscles to support and move the body forward [3]. However, although the biomechanics of human locomotion is well studied, there is still a substantial lack of knowledge regarding whether age-related decline in locomotor performance results from reduced muscular output of all lower limb muscle groups or just some of them. This information is essential for further understanding the underlying mechanisms behind age-related locomotor decline and would provide important insights for preventing performance impairments in older age.

Previous studies examining age-related changes in lower limb joint kinetics during walking have revealed that older adults exhibit a reduction in ankle plantarflexor power generation, but instead demonstrate more power generation from the hip and/or knee extensors [4–7]. This so-called distal-to-proximal shift in joint powers in walking is suggested to be a compensation strategy for old people to accommodate diminished force generation capacity of the lower limbs [2].

As humans switch from walking to running, more than two times greater GRF must be generated by lower limb muscles [8], which likely pose even greater challenges for ageing humans. Previous research of age-related changes in running mechanics has focused mainly on GRF, stride parameters and kinematics. These studies have demonstrated that at a given speed, older runners exhibit lower GRF and take shorter steps at a higher frequency compared with younger runners [9,10]. Other findings include a larger knee flexion angle observed at initial ground contact, but reduction in the knee flexion excursion during the first half of the stance phase in older population [9,11]. As runners increase speed, greater GRF

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Table 1. Subject parameters of young, middle-aged and old groups.

parameters	young	middle-aged	old
number of subjects	13	13	13
age (year)	$26 \pm 6^{***}$	$61 \pm 5^{\#\#\#}$	$78 \pm 4^{+++}$
height (cm)	$181 \pm 4^{**}$	178 ± 6	$172 \pm 6^{+}$
body weight (kg)	73.3 ± 8.0	79.6 ± 9.6	$69.7 \pm 7.8^{+}$
body mass index (kg $\times$ m^{-2})	22.5 ± 2.1	$25.0 \pm 2.1^{\#}$	23.7 ± 2.0

$^{*,\#,+}$Statistical significance between young and old, young and middle-aged, and middle-aged and old, respectively.
$^{*,\#,+}p < 0.05$; $^{**,\#\#,++}p < 0.01$; $^{***,\#\#\#,+++}p < 0.001$.

generation is required to support and propel the body [8,12]. Comparison of older and young sprinters has shown that reduced GRF generation, decreased step length and increased ground contact time limits sprinting performance with age [3].

To date, we have encountered only two studies in which lower limb joint kinetics have been compared between older and young runners [13,14]. The results of these studies show that older runners exhibit lower ankle plantarflexor moment and power generation, but exhibit no differences in the kinetics of the knee and hip joints when running at 2.7 m s^{-1}. These findings suggest that running at speed below approximately 3 m s^{-1} may be not enough to trigger kinetic changes in the knee and hip joints. So far, however, no studies have quantified the effects of ageing on lower limb joint kinetics at greater running speeds where higher moment and power output from all lower limb muscle groups are required [15,16].

The purpose of this study was to examine age-related changes in lower limb joint kinetics across different modes and intensity of locomotion. Specifically, we compared the amounts of joint moments and powers generated by the lower limb muscles among three age-groups as they changed locomotion from walking to more intensive running and then to maximal sprinting. We hypothesized that during walking and running the older adults would demonstrate distal-to-proximal shift in joint powers to compensate reduced moment and power output of the ankle joint. In addition, we predicted that during sprinting older adults would demonstrate reduced moment and power output of the ankle, knee and hip joints.

2. Material and methods

2.1. Participants

Three different age groups of competitive healthy male athletes (sprinters, long jumpers) with several years of training background participated in this study. Each group consisted of 13 participants with a mean age of 26 ± 6 (young group), 61 ± 5 (middle-aged group) and 78 ± 4 (old group) years, respectively (table 1). At the beginning of the study, all participants provided informed consent and confirmed that they did not have a previous history of any musculoskeletal problems, such as a recent injury or surgery, which could have an effect on the locomotion pattern of the subject. We included athletes if they were injury and symptom-free at the onset of the study. The study was approved by the ethical committee of the central Finland healthcare district and was performed in the accordance with the Declaration of Helsinki.

2.2. Biomechanical analysis

Biomechanical measurements were conducted in an indoor sports hall. After a warm-up, subjects performed three walking trials at a self-selected speed, three running trials at 4.0 ± 0.2 m s^{-1} and two 60 m sprinting trials at maximal effort. The speed was monitored with photocells between 30 and 40 m section of the runway, which was also used as the capture area for the motion analysis. Subjects used their own running shoes during walking and their own track shoes during running and sprinting.

An eight-camera system (Vicon T40, Oxford, UK) and five force platforms (total length 5.7 m, AMTI, Watertown, MA) were used to record marker positions and GRF data synchronously at 300 and 1500 Hz, respectively. Anthropometric measurements (height, weight, leg length and knee and ankle diameters) and bilateral placement of 22 retroreflective markers (on the shoe over the second metatarsal head and over the posterior calcaneus, lateral malleolus, lateral shank, lateral knee, lateral thigh, anterior superior iliac spine, posterior superior iliac spine, clavicula, sternum, seventh cervical vertebra, 10th thoracic vertebra) were carried out according to plug in gait full body model (Vicon).

Kinematic and kinetic analyses were performed using the standard plug in gait model (Vicon Nexus v. 1.7, Oxford, UK). Marker trajectories and GRF data were low-pass filtered using a fourth-order Butterworth filter with cut-off frequency of 18 Hz to avoid impact artefacts [17,18]. Step frequency, contact time and step length were determined using foot contact and toe-off events based on the 20 N GRF threshold level. Foot strike angle during initial ground contact was determined according to Altman & Davis [19]. Net joint moments and powers determined by inverse dynamics were normalized to body weight (Nm kg^{-1}). Kinematic and kinetic data during the stance phase were then time normalized (0–100%) and averaged across several ground contacts. In order to avoid muscle fatigue, only two maximal sprinting trials were collected per subject. Therefore, the leg that exhibited more successful force place contacts on any of the five force plates during two sprinting trials was selected for the analysis. The total number of analysed contacts per subject varied from three to four during walking and running and two to four contacts during sprinting.

2.3. Statistical analysis

Primary parameters of interest were peak net joint moments and powers during the stance phase. Secondary parameters including peak vertical and anterior–posterior GRF and selected spatio-temporal and joint angle parameters were also analysed. Univariate differences between three age-groups were compared using one-way ANOVA with Bonferroni adjustment (SPSS 18.0, SPSS, Chicago, IL). p-Values less than 0.05 were considered significant.

3. Results

3.1. Walking

No differences were found between age groups in the spatio-temporal and GRF parameters (table 3 and electronic supplementary material, figure S1). Lower limb kinetics

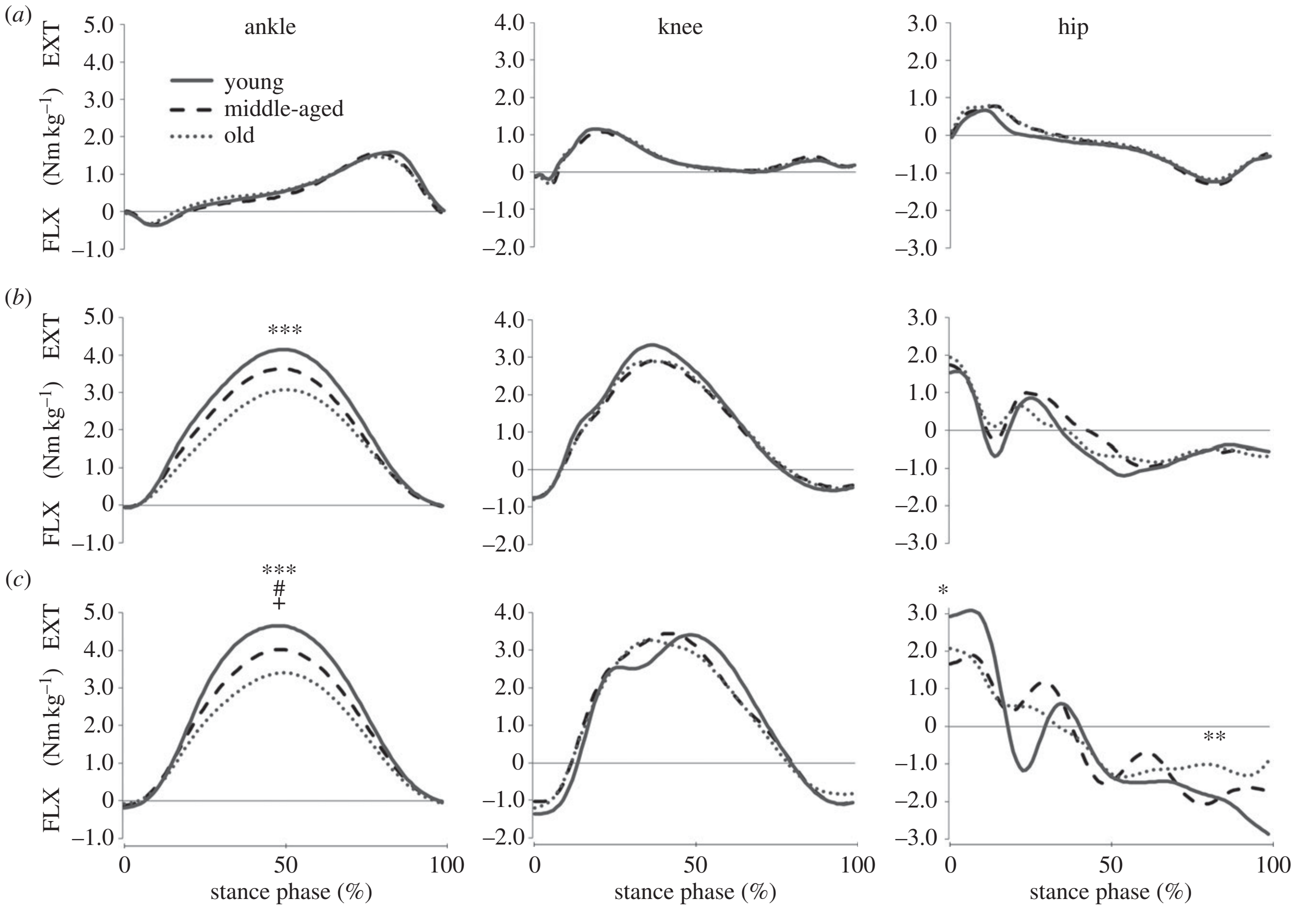

Figure 1. Mean joint moments for the young, middle-aged and old groups during (*a*) walking, (*b*) running and (*c*) sprinting.

showed no differences in joint moments (figure 1*a*), but in joint powers, the old group demonstrated 22% less power generation of the ankle plantarflexors ($p < 0.05$) and 31% more power absorption of the knee extensors ($p < 0.05$) compared with the young group (figure 2*a* and table 3). In addition, the athletes in the middle-aged and old groups showed trends towards lower ankle plantarflexor moments (5% and 10%, respectively) but higher hip extensor moments (16% and 22%) and power (27% and 41%) than the athletes in young group (figure 1*a* and table 3). Results of kinematic analysis showed that during the first half of the stance, the old athletes flexed at the knee more compared with the young ($p < 0.01$) and middle-aged ($p < 0.05$) athletes. Additionally, the old group demonstrated more hip flexion than the young group ($p < 0.05$; figure 3*a* and table 3).

3.2. Running

The running speed and contact time did not differ between groups, but the athletes in the old group had shorter step length and higher step frequency compared with the young ($p < 0.001$, $p < 0.001$) and middle-aged ($p < 0.05$, $p < 0.001$) groups (table 2). GRF comparisons showed that the young and middle-aged athletes produced 17% ($p < 0.001$) and 10% ($p < 0.05$) higher vertical force than the old athletes, respectively (table 3 and electronic supplementary material, figure S1). In addition, the propulsion force of the young group was 25% higher compared with the old group ($p < 0.001$, table 3 and electronic supplementary material, figure S1). Joint kinetics differed between groups at the ankle joint level where the young group demonstrated 25% higher ankle plantarflexor moment ($p < 0.001$, figure 1*b* and table 3) and 31% more power absorption ($p < 0.05$, figure 2*b* and table 3) than the old group. Furthermore, the ankle joint power generation was 41% ($p < 0.001$) and 22% ($p < 0.001$) greater in the young and middle-aged athletes, respectively, compared with the old athletes (figure 2*b* and table 3). In the knee kinetics and kinematics, there were no significant group differences. At the hip joint level, the athletes in the old group showed more flexion compared with the young ($p < 0.01$) and middle-aged ($p < 0.05$) athletes (figure 2*b* and table 3). In addition, the middle-aged and old groups showed a tendency towards greater hip kinetics, with significant differences observed in the hip extensor power, where the old athletes had 41% higher values compared with the young athletes ($p < 0.05$, figure 2*b* and table 3).

3.3. Sprinting

The young group (9.3 m s^{-1}) had higher maximum sprinting speed compared with the middle-aged (7.9 m s^{-1}, $p < 0.001$) and old (6.6 m s^{-1}, $p < 0.001$) groups. The athletes in the old and middle-aged groups showed shorter step length ($p < 0.01$, $p < 0.001$), greater contact time ($p < 0.001$, $p < 0.001$) and lower step frequency ($p < 0.001$, $p < 0.001$; table 2) than athletes in the young group. GRF comparison revealed an age-related decline in both vertical and horizontal force (table 3 and electronic supplementary material, figure S1). Peak vertical GRF of the young and middle-aged groups were 19% ($p < 0.001$) and 12% ($p < 0.001$) higher than in the old group, respectively. The young group showed 20% greater propulsion force compared with the middle-aged

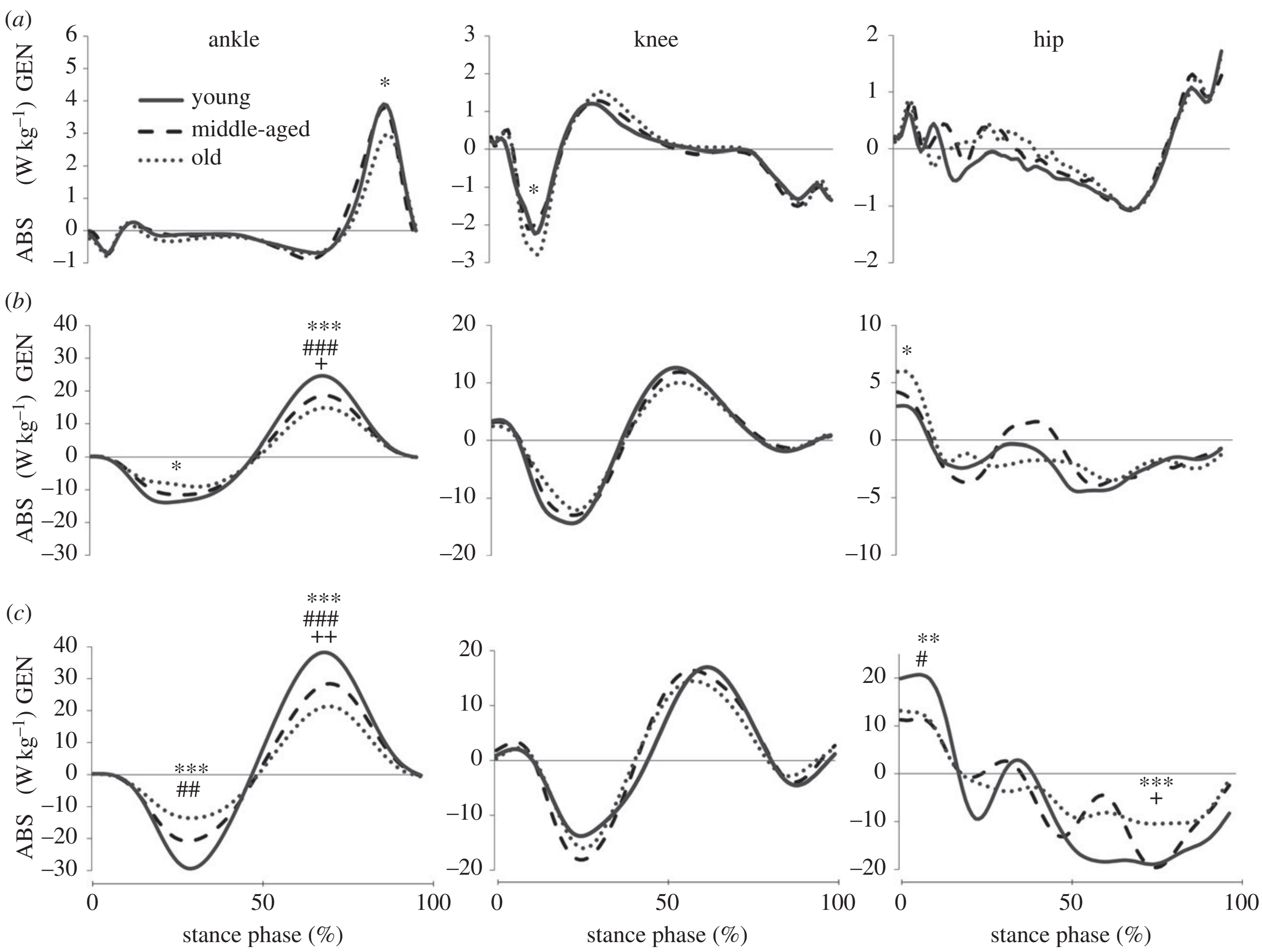

Figure 2. Mean joint powers for the young, middle-aged and old groups during (*a*) walking, (*b*) running and (*c*) sprinting.

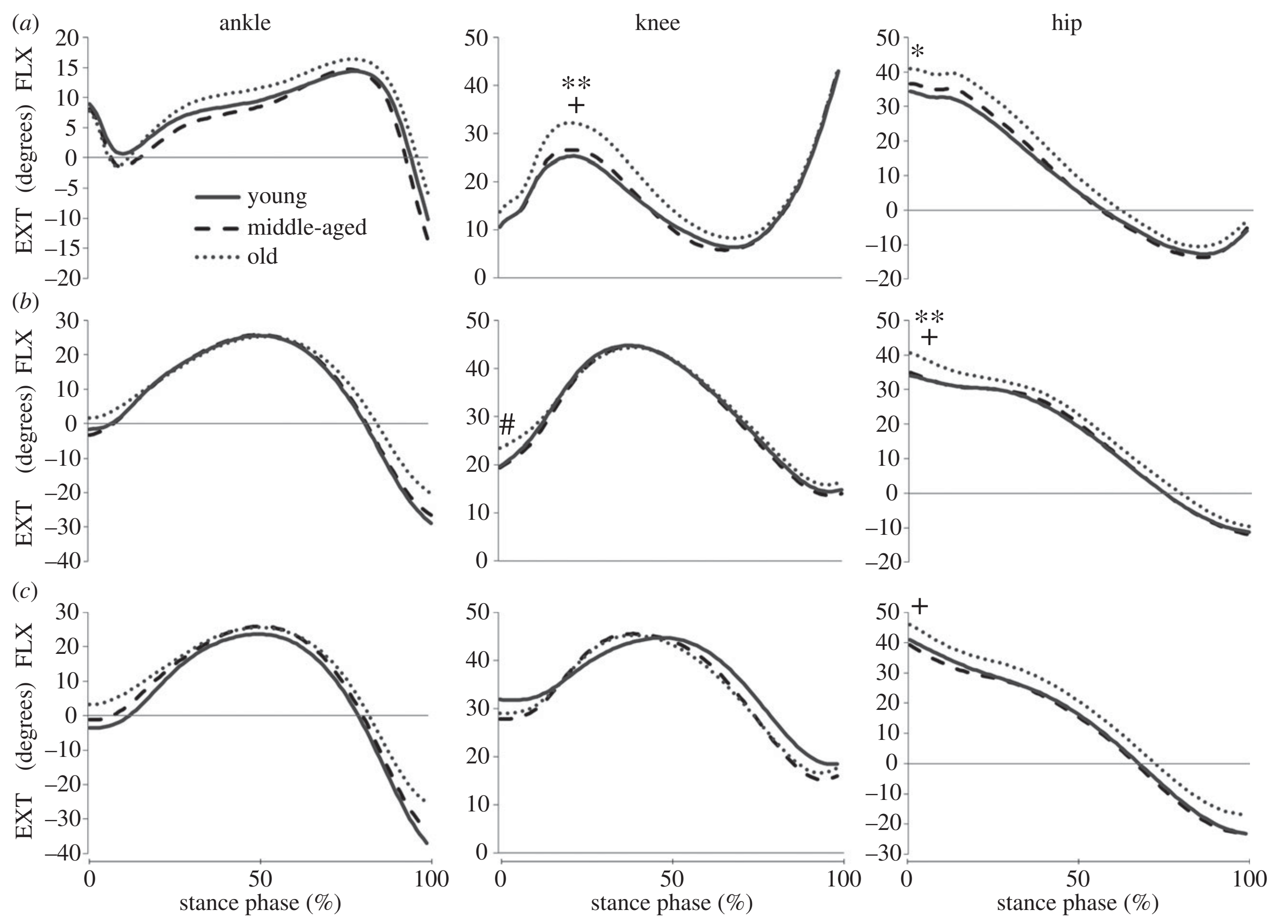

Figure 3. Mean joint angles for the young, middle-aged and old groups during (*a*) walking, (*b*) running and (*c*) sprinting.

Table 2. Spatio-temporal parameters of young, middle-aged and old groups during walking, running and sprinting. Data shown as mean $\pm$ s.d.; BW, body weight; power generation 1, first half of the stance; power generation 2, second half of the stance during walking.

parameters	walking			running			sprinting		
	young	middle-aged	old	young	middle-aged	old	young	middle-aged	old
spatio-temporal parameters									
speed (m s^{-1})	1.6 ± 0.1	1.6 ± 0.2	1.6 ± 0.2	4.1 ± 0.2	4.0 ± 0.2	4.0 ± 0.2	$9.3 \pm 0.4^{***}$	$7.9 \pm 0.5^{\#\#\#}$	$6.6 \pm 0.7^{+++}$
step length (m)	0.81 ± 0.04	0.85 ± 0.08	0.81 ± 0.07	$1.49 \pm 0.13^{***}$	1.45 ± 0.10	$1.32 \pm 0.10^{+}$	$2.09 \pm 0.10^{***}$	$1.94 \pm 0.13^{\#\#}$	$1.67 \pm 0.12^{+++}$
contact time (ms)	633 ± 20	647 ± 50	624 ± 50	207 ± 17	212 ± 22	210 ± 16	$118 \pm 13^{***}$	$140 \pm 10^{\#\#\#}$	$156 \pm 17^{+}$
swing/flight time (ms)	109 ± 11	110 ± 11	100 ± 10	$162 \pm 25^{***}$	145 ± 27	$117 \pm 19^{++}$	109 ± 11	113 ± 15	102 ± 7
step frequency (steps per min)	115 ± 4	111 ± 7	115 ± 7	$163 \pm 10^{***}$	168 ± 11	$184 \pm 7^{+++}$	$265 \pm 15^{***}$	$237 \pm 10^{\#\#\#}$	234 ± 16

$^{*,\#,+}$Statistical significance between young and old, young and middle-aged, and middle-aged and old, respectively. $^{*,\#,+}p < 0.05$; $^{**,\#\#,++}p < 0.01$; $^{***,\#\#\#,+++}p < 0.001$.

group ($p < 0.001$) and 28% and 36% greater braking and propulsion GRF than the old group ($p < 0.001$, $p < 0.001$). Lower limb kinetics differed significantly between groups at the ankle and hip joints, but not at the knee joint. The young athletes produced 14% and 27% more ankle plantarflexor moment compared with the middle-aged ($p < 0.05$) and old ($p < 0.001$) athletes (figure 1*c* and table 3). Ankle power absorption of the young group was 32% ($p < 0.01$) and 53% ($p < 0.001$) greater and power generation 30% ($p < 0.001$) and 47% ($p < 0.001$) greater compared with the middle-aged and old groups, respectively (figure 2*c* and table 3). At the hip joint level, the young group demonstrated 25% greater extensor moment and 34% greater flexor moment than the old group (figure 1*c* and table 3). Hip power generation of the athletes in the young group was 31% and 38% greater compared with middle-aged ($p < 0.01$) and old ($p < 0.001$) athletes, respectively (figure 2*c* and table 3). Hip power absorption of the young and middle-aged groups was 38% ($p < 0.001$) and 29% ($p < 0.05$) higher compared with the old group, respectively (figure 2*c* and table 3). Kinematic comparison showed more hip flexion in the old compared with the middle-aged athletes ($p < 0.05$, figure 3*c* and table 3). In addition, the old athletes demonstrated higher foot strike angle when compared with the young group ($p < 0.05$, table 3).

4. Discussion

This is the first study, to the best of knowledge, to describe which lower limb muscles are mainly responsible for the age-related deterioration seen in human locomotor performance. Our findings demonstrate that age-related propulsive deficit of ankle plantarflexors becomes more severe as humans switch from walking to running to sprinting. As a result, old athletes exhibit significantly higher muscular output of the more proximal lower limb muscles than their younger counterparts when walking and running at the same speed. During maximal sprinting, reduced muscular output of the hip extensors and flexors in older athletes also contribute to the declines seen in performance, whereas no age-related effects were present in the muscular output of the knee joint.

4.1. Walking

Consistent with the recent investigations in physically active older men [4,5], we found that competitive older athletes demonstrated changes in lower limb kinetics during walking but maintained similar preferred speeds as their younger counterparts. The alteration in gait was largest among the old group who demonstrated 22% lower ankle power generation compared with the young group. Furthermore, there was a trend towards lower ankle plantarflexor moment among the middle-aged and old athletes who exhibited 5% and 10% lower values compared with young athletes. An almost similar age-related decline in the ankle plantarflexor moment during walking was recently reported by Boyer *et al.* [5], who observed 7% difference between young and physically active older adults when a similar speed (1.6 m s^{-1}) was used. As a compensatory action for reduced ankle kinetics during walking, we observed increased knee flexion angle and eccentric power in the old group and a trend towards higher hip extensor moment and power in both the middle-aged

Table 3. Ground reaction force and joint kinematic and kinetic parameters of young, middle-aged and old groups during walking, running and sprinting. Data shown as mean ± s.d.; BW, body weight; power generation 1, first half of the stance; power generation 2, second half of the stance during walking.

	walking			running			sprinting		
parameters	young	middle-aged	old	young	middle-aged	old	young	middle-aged	old
ground reaction forces									
peak braking (% BW)	−24 ± 3	−25 ± 3	−24 ± 4	−38 ± 4	−33 ± 6	−33 ± 5	−58 ± 11***	−51 ± 5	−42 ± 7^{+}
average braking (% BW)	−11 ± 2	−12 ± 2	−12 ± 2	−23 ± 2**	−20 ± 3$^{\#}$	−19 ± 3	−33 ± 4***	−31 ± 3	−26 ± 3^{++}
peak propulsion (% BW)	25 ± 3	23 ± 3	23 ± 4	44 ± 4***	39 ± 7	33 ± 5	70 ± 5***	56 ± 6$^{\#\#\#}$	45 ± 6^{+++}
average propulsion (% BW)	11 ± 1	11 ± 2	11 ± 2	26 ± 3***	22 ± 4	19 ± 3	41 ± 3***	34 ± 4$^{\#\#\#}$	27 ± 4^{+++}
peak vertical (% BW)	124 ± 7	127 ± 10	126 ± 9	319 ± 33***	295 ± 31	266 ± 19^{+}	337 ± 33***	313 ± 40	274 ± 15^{++}
average vertical (% BW)	83 ± 2	82 ± 3	83 ± 3	177 ± 14***	164 ± 14	154 ± 11	188 ± 11***	178 ± 13	163 ± 7^{++}
ankle									
foot strike angle (°)	25.8 ± 4.3	27.1 ± 4.4	24.5 ± 5.6	1.6 ± 11.0	1.8 ± 7.7	5.4 ± 13.2	−1.7 ± 7.9*	3.7 ± 7.3	7.4 ± 9.8
angle at initial contact (°)	9.0 ± 3.4	8.1 ± 4.1	7.8 ± 4.4	−1.6 ± 8.9	−3.3 ± 6.6	1.5 ± 11.3	−3.4 ± 5.9	−1.2 ± 7.6	3.2 ± 8.4
plantarflexor moment (Nm kg^{-1})	1.66 ± 0.31	1.57 ± 0.16	1.49 ± 0.17	4.17 ± 0.70***	3.66 ± 0.63	3.11 ± 0.40	4.69 ± 0.65***	4.05 ± 0.59$^{\#}$	3.42 ± 0.28^{+}
power absorption (W kg^{-1})	−1.0 ± 0.4	−1.1 ± 0.4	−1.3 ± 0.4	−15.0 ± 4.9*	−12.9 ± 3.7	−10.3 ± 2.6	−31.9 ± 8.6***	−21.6 ± 8.2$^{\#\#}$	−15.0 ± 3.9
power generation (W kg^{-1})	4.1 ± 0.7*	3.9 ± 0.8	3.2 ± 0.8	25.3 ± 4.1***	19.2 ± 3.9$^{\#\#\#}$	15.0 ± 3.2^{+}	41.0 ± 4.6***	29.0 ± 4.9$^{\#\#\#}$	21.8 ± 4.9^{++}
knee									
angle at initial contact (°)	10.5 ± 3.7	10.5 ± 4.9	13.8 ± 4.8	19.6 ± 4.3	19.4 ± 3.7	23.5 ± 5.4	31.9 ± 6.0	27.8 ± 4.9	29.0 ± 4.4
flexion excursion (°)	25.4 ± 4.6*	27.0 ± 5.6	32.4 ± 4.5^{+}	25.3 ± 4.3	25.7 ± 5.8	21.1 ± 6.5	13.2 ± 6.2	18.6 ± 6.0	16.6 ± 4.7
extensor moment (Nm kg^{-1})	1.22 ± 0.22	1.13 ± 0.32	1.21 ± 0.27	3.35 ± 0.50	2.95 ± 0.59	2.99 ± 0.56	3.59 ± 0.96	3.58 ± 0.50	3.42 ± 0.50
power absorption (W kg^{-1})	−2.4 ± 0.7*	−2.6 ± 0.8	−3.5 ± 1.4	−15.5 ± 6.5	−14.8 ± 5.5	−12.7 ± 5.7	−13.9 ± 10.0	−19.3 ± 6.9	−16.0 ± 5.8
power generation (W kg^{-1})	1.2 ± 0.3	1.5 ± 0.6	1.7 ± 0.5	12.4 ± 3.5	12.3 ± 3.3	10.2 ± 2.9	17.6 ± 8.2	18.2 ± 6.0	14.2 ± 3.2
hip									
angle at initial contact (°)	34.3 ± 6.0*	36.6 ± 3.6	41.0 ± 7.3	34.0 ± 5.7**	34.9 ± 5.7	40.6 ± 4.1^{+}	40.9 ± 7.1	39.2 ± 7.4	46.0 ± 5.7^{+}
extensor moment (Nm kg^{-1})	1.30 ± 0.34	1.54 ± 0.47	1.66 ± 0.49	1.85 ± 0.53	2.28 ± 0.79	2.11 ± 0.39	3.44 ± 0.70*	3.10 ± 0.91	2.59 ± 0.73
flexor moment (Nm kg^{-1})	−1.31 ± 0.21	−1.41 ± 0.21	−1.26 ± 0.18	−1.57 ± 0.52	−1.58 ± 0.43	−1.33 ± 0.51	−3.36 ± 1.03**	−2.99 ± 0.82	−2.21 ± 0.70
power generation 1 (W kg^{-1})	1.0 ± 0.8	1.6 ± 0.7	1.7 ± 0.7	4.1 ± 1.5*	5.6 ± 1.9	6.9 ± 3.0	25.1 ± 10.3**	17.2 ± 5.2$^{\#\#}$	15.5 ± 6.8
power absorption (W kg^{-1})	−1.3 ± 0.5	−1.3 ± 0.4	−1.3 ± 0.4	−7.8 ± 4.1	−8.2 ± 2.0	−7.3 ± 4.3	−29.6 ± 7.7***	−25.8 ± 8.1	−18.3 ± 5.1^{+}
power generation 2 (W kg^{-1})	1.7 ± 0.4	1.8 ± 0.5	1.8 ± 0.9	—	—	—	—	—	—

$^{*,\#,+}$Statistical significance between young and old, young and middle-aged, and middle-aged and old, respectively.

$^{*,\#,+}p < 0.05$; $^{**,\#\#,++}p < 0.01$; $^{***,\#\#\#,+++}p < 0.001$.

and old groups. In addition, there was an age-related tendency towards higher hip flexion. These findings generally agree with the literature [4–7] suggesting that during walking old adults rely less on ankle plantarflexors and more on knee and/or hip extensors than young adults.

4.2. Running and sprinting

Because ankle plantarflexors are shown to contribute most to the generation of the support and propulsion forces during walking [20–22], and running [15,23,24], we hypothesized that older subjects would demonstrate a progressive deficit in the ankle plantarflexor moment and power generation as the mode of locomotion changed from walking to running to sprinting. Our results partially supported this hypothesis, in that during running, we observed 12% and 25% lower ankle plantarflexor moment among the middle-aged and old athletes, respectively. However, during sprinting, the deficit remained roughly the same showing only slightly greater decline (15% and 27%) compared with the young athletes. A previous study [14] with slower running speed (2.7 $m\ s^{-1}$) found 13% decrease in the ankle plantarflexor moment among the older adults (mean age 64 year), which is similar to the middle-aged group (mean age 61 year) in this study despite the different running speeds (4 $m\ s^{-1}$ and maximum speed). Therefore, these findings suggest that age-related decline in the ankle plantarflexor moment is more related to ageing than running speed. However, the same was not true in the ankle power absorption and generation, where between-group differences were much larger during sprinting than during running. This most likely results from remarkably shorter ground contact time in the young group compared with the middle-aged and old groups, which require more rapid muscular force generation reflected by increased peak muscle power rather than by peak muscle moments [23]. Furthermore, because ageing seems to have a greater effect on rapid force generation than peak force of the muscles in untrained [25–27] and also in speed- and power-trained older adults [3], larger age-related reduction in the ankle plantarflexor power during locomotion may therefore be expected. Because the majority of the ankle plantarflexors' (soleus and gastrocnemius) muscle–tendon unit power generation during walking and running results from recoil of in-series elastic structures [28,29], less efficient utilization of the stored elastic energy may be one key mechanism to explain impaired ankle propulsion among older adults during locomotion [30]. However, further research of age-related changes in muscle–tendon interaction during walking and running is required to evaluate this hypothesis.

During running, we found that older athletes tended to compensate reduced ankle contribution by increasing effort of the hip extensors. Although older people are known to demonstrate a redistribution of power output to more proximal muscles during walking to maintain similar speed with their younger counterparts [4–7], to the best of our knowledge, this compensation strategy has not been demonstrated before in running. A distal-to-proximal shift in joint kinetics was found especially in the old group which exhibited reduction in the ankle kinetics, but instead, increased hip extensor power during the stance phase of running when compared with the young athletes. The old group showed also a tendency towards higher foot strike angle during both running and sprinting which suggests the presence of a rearfoot running pattern [19]. It is possible that alteration in the landing strategy among old athletes can be a mechanism to shift contribution from ankle plantarflexors to the more proximal muscles such as knee extensors by changing lower limb alignment in relation to GRF vector (reduction of the ankle but increase of the knee joint distance in relation to the GRF vector) [31]. In addition, the old group demonstrated more flexed hip joint across all measured activities. Previously an age-related shift towards hip flexion has been observed during walking [4,6,7], but the findings of the current study suggest that altered hip movement is present in running and sprinting as well. However, it remains unclear whether more flexed hip joint during the whole stance phase results from age-related reduction in the hip range of motion as suggest by previous studies [32,33], or alternatively, is it an adaptation strategy that may help older people to optimize their force generation over the period of ground contact.

We further hypothesized, that during maximal sprinting, the middle-aged and old athletes would demonstrate reduced muscle moments and powers at the knee and hip joints. However, the results show that the reduction in the joint moments and powers was present only at the hip joint, but, surprisingly, not at the knee joint. This novel finding suggests that, besides ankle plantarflexors, an age-related decline in the muscular output during sprinting occurs in the hip extensors and flexors, whereas the contributions of the knee extensors remain essentially similar. Therefore, the knee extensors capacity may not be a limiting factor of the sprinting performance in older age. Such a result may be explained by the findings that, in contrast to ankle and hip joints, the kinetics of the knee joint during the stance phase of sprinting appears to change very little as running speed increases from 5 to 9 $m\ s^{-1}$ [23], and thereafter with higher speeds, the extensor moment of the knee may even decrease [34,35]. In line with these findings, a recent computer simulation study suggests that the contribution of the ankle plantarflexor to GRF generation increases whereas knee extensors decreases during sprinting with greater speeds than 7.0 $m\ s^{-1}$ [24]. Because, in this study, the young adults reached remarkably higher sprinting speeds (9.3 $m\ s^{-1}$) than the middle-aged (7.9 $m\ s^{-1}$) and old athletes (6.6 $m\ s^{-1}$), the need for a larger knee extensor moment or power generation among the young group may be diminished.

4.3. Mechanisms of age-related locomotor decline

The majority of the research to date examining age-related locomotion ability and muscular force capacities has focused on the proximal lower limb muscles such as knee extensors rather than on ankle plantarflexors [36–38]. The findings of these experiments generally suggest a strong link between walking ability and knee extensor strength. However, in this study, we found age-related deficit in the ankle moment and power generation during locomotion, whereas no deterioration was present at the knee moment or power. This suggests that the force generation capacity of the ankle plantarflexors rather than knee extensors may play a critical role in maintaining locomotor performance in older age. The fact that the age-related declines in force generation capacity occur similarly in different lower limb muscle groups [25,39], may be an explanation for the strong association between walking ability and knee extensor capacity in previous studies [36–38], even though it may not be the limiting factor of walking performance.

Because age-related loss of muscle force generation capacity occurs similarly in different lower limb muscle groups [25,39], one might ask why the reduction in the lower limb joint moments and powers during locomotion take place mainly at the level of ankle plantarflexors instead of knee and hip muscles. One possible explanation for this question is a recent notion that a much greater percentage of the maximal force generation capacity is required from the ankle plantarflexors than knee and hip muscles to drive the motion during walking gait [2]. By expressing joint moments during walking in relation to the maximal available effort of each joint, the researchers [2] pointed out that old adults walk near the maximal capacity of the ankle plantarflexors, whereas the knee and hip muscles operate at much lower relative effort. Furthermore, the results of a previous modelling study, where researchers progressively weakened all lower limb muscle groups in gait simulation suggest, that walking gait is remarkably robust to weakness of the knee and hip extensors but very sensitive to weakness of the ankle plantarflexors [40]. These findings together with the current results show that age-related decline in muscular capacity first challenges the normal function of ankle plantarflexors during locomotion, thus leading to compensatory actions such as shorter steps and shift of the joint kinetics from ankle towards more proximal joints.

4.4. Future studies and limitations

Because propulsive deficit of ankle plantarflexors seems to be a key factor behind locomotor decline in older age, it seems reasonable to assume that exercise interventions designed to slow down or even restore age-related attenuation in locomotion should focus on improving ankle plantarflexor capacity. However, although several studies have already revealed the positive effects of resistance training [36,38,41] or almost any kind of physical activity [5,42,43] on locomotion ability, the underlying biomechanical mechanisms behind these improvements appear to be unclear [2]. For example, a previous study [42] comparing walking mechanics of young versus old adults with active (running background) and inactive training backgrounds found that both groups of old adults had a similar propulsive deficit of the ankle plantarflexors when compared with the younger adults. However, the active old adults exhibited significantly higher hip joint kinetics than their inactive counterparts, suggesting a distal-to-proximal shift in joint kinetics. This finding is somewhat surprising with respect to general expectation that high physical loading of the ankle plantarflexors, as occurs in running, would lead to similar locomotion mechanics between older and young individuals. These observations highlight the need for further investigations to better understand how physical exercise affects locomotion mechanics in older age.

Our results regarding age-related changes in GRF, stride characteristics and kinematics during running and sprinting agree well with previous studies [3,9–11] suggesting that old adults generate less vertical and propulsion GRF, take shorter steps at a higher frequency and demonstrate larger knee flexion angle at heel strike, but reduce the knee flexion excursion during the first half of the stance phase of running (table 2). These observations indicate that the general running mechanics of old adults in this study are in line with those reported earlier. However, there are certain limitations associated with this study that should be considered when interpreting its findings. This study investigated only sagittal plane mechanics during the stance phase of locomotion. However, because both the swing phase [44] and secondary plane mechanics [45] can also affect locomotion performance, the role of these should be considered in future studies in different age groups. In addition, the participants in this study were males in excellent physical condition. Because of certain sex-related differences in walking [46] and running [47] mechanics, caution should be exercised in generalizing these results to females and persons with limited neuromuscular capacities. In this study, joint kinetics determined by inverse dynamics approach reflects the net product of the all muscles crossing the joint. However, this does not necessarily represent the true actions of the individual muscles, because the inverse dynamics analysis is unable to account for the effects of in-series elastics structures and energy transport via two-joint muscles from one joint to another [48,49]. Finally, we did not compare muscle force production capacities or other functional properties such as joint range of motions between different age groups. Future work examining lower limb mechanics together with these factors will provide more detailed insights into the mechanisms behind age-related locomotor decline.

5. Conclusion

This study examined which lower limb muscles are mainly responsible for age-related deterioration in human locomotor performance. We found that the most prominent age-related deficit in the joint moment and power generation occurred at the level of ankle joint across different modes and intensity of locomotion. Old adults compensated impaired ankle propulsion by demonstrating higher muscular efforts of the more proximal lower limb muscles than their younger counterparts when walking and running at the same speed. During sprinting, the middle-aged and old adults generated less muscle moments and powers from the ankle and hip joints, but surprisingly, not from the knee joint when compared with the young adults. These findings highlight the importance of the ankle plantarflexors in locomotion and provide new insights for preventing performance impairments among older adults.

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References

1. Korhonen MT, Cristea A, Alen M, Hakkinen K, Sipila S, Mero A, Viitasalo JT, Larsson L, Suominen H. 2006 Aging, muscle fiber type, and contractile function in sprint-trained athletes. *J. Appl. Physiol.* (*1985*) **101**, 906–917. (doi:10.1152/japplphysiol.00299.2006)

2. Beijersbergen CMI, Granacher U, Vandervoort AA, DeVita P, Hortobágyi T. 2013 The biomechanical mechanism of how strength and power training

improves walking speed in old adults remains unknown. *Ageing Res. Rev.* **12**, 618–627. (doi:10.1016/j.arr.2013.03.001)

3. Korhonen MT, Mero AA, Alen M, Sipila S, Hakkinen K, Liikavainio T, Viitasalo JT, Haverinen MT, Suominen H. 2009 Biomechanical and skeletal muscle determinants of maximum running speed with aging. *Med. Sci. Sports Exerc.* **41**, 844–856. (doi:10.1249/MSS.0b013e3181998366)
4. Cofre LE, Lythgo N, Morgan D, Galea MP. 2011 Aging modifies joint power and work when gait speeds are matched. *Gait Posture* **33**, 484–489. (doi:10.1016/j.gaitpost.2010.12.030)
5. Boyer KA, Andriacchi TP, Beaupre GS. 2012 The role of physical activity in changes in walking mechanics with age. *Gait Posture* **36**, 149–153. (doi:10.1016/j.gaitpost.2012.02.007)
6. Monaco V, Rinaldi LA, Macri G, Micera S. 2009 During walking elders increase efforts at proximal joints and keep low kinetics at the ankle. *Clin. Biomech.* (*Bristol, Avon*). **24**, 493–498. (doi:10.1016/j.clinbiomech.2009.04.004)
7. DeVita P, Hortobagyi T. 2000 Age causes a redistribution of joint torques and powers during gait. *J. Appl. Physiol.* **88**, 1804–1811.
8. Keller T, Weisberger A, Ray J, Hasan S, Shiavi R, Spengler D. 1996 Relationship between vertical ground reaction force and speed during walking, slow jogging, and running. *Clin. Biomech.* **11**, 253–259. (doi:10.1016/0268-0033(95)00068-2)
9. Bus SA. 2003 Ground reaction forces and kinematics in distance running in older-aged men. *Med. Sci. Sports Exerc.* **35**, 1167–1175. (doi:10.1249/01.MSS.0000074441.55707.D1)
10. Cavagna GA, Legramandi MA, Peyre-Tartaruga LA. 2008 Old men running: mechanical work and elastic bounce. *Proc. R. Soc. B* **275**, 411–418. (doi:10.1098/rspb.2007.1288)
11. Fukuchi RK, Duarte M. 2008 Comparison of three-dimensional lower extremity running kinematics of young adult and elderly runners. *J. Sports Sci.* **26**, 1447–1454. (doi:10.1080/02640410802209018)
12. Weyand PG, Sternlight DB, Bellizzi MJ, Wright S. 2000 Faster top running speeds are achieved with greater ground forces not more rapid leg movements. *J. Appl. Physiol.* **89**, 1991–1999.
13. Fukuchi RK, Stefanyshyn DJ, Stirling L, Duarte M, Ferber R. 2013 Flexibility, muscle strength and running biomechanical adaptations in older runners. *Clin. Biomech.* (*Bristol, Avon*) **29**, 304–310. (doi:10.1016/j.clinbiomech.2013.12.007)
14. Karamanidis K, Arampatzis A, Bruggemann GP. 2006 Adaptational phenomena and mechanical responses during running: effect of surface, aging and task experience. *Eur. J. Appl. Physiol.* **98**, 284–298. (doi:10.1007/s00421-006-0277-7)
15. Hamner SR, Delp SL. 2013 Muscle contributions to fore–aft and vertical body mass center accelerations over a range of running speeds. *J. Biomech.* **46**, 780–787. (doi:10.1016/j.jbiomech.2012.11.024)
16. Arampatzis A, Bruggemann GP, Metzler V. 1999 The effect of speed on leg stiffness and joint kinetics in human running. *J. Biomech.* **32**, 1349–1353. (doi:10.1016/S0021-9290(99)00133-5)
17. Bisseling RW, Hof AL. 2006 Handling of impact forces in inverse dynamics. *J. Biomech.* **39**, 2438–2444. (doi:10.1016/j.jbiomech.2005.07.021)
18. Bezodis NE, Salo AI, Trewartha G. 2013 Excessive fluctuations in knee joint moments during early stance in sprinting are caused by digital filtering procedures. *Gait Posture* **38**, 653–657. (doi:10.1016/j.gaitpost.2013.02.015)
19. Altman AR, Davis IS. 2012 A kinematic method for footstrike pattern detection in barefoot and shod runners. *Gait Posture* **35**, 298–300. (doi:10.1016/j.gaitpost.2011.09.104)
20. Liu MQ, Anderson FC, Pandy MG, Delp SL. 2006 Muscles that support the body also modulate forward progression during walking. *J. Biomech.* **39**, 2623–2630. (doi:10.1016/j.jbiomech.2005.08.017)
21. Kepple TM, Siegel KL, Stanhope SJ. 1997 Relative contributions of the lower extremity joint moments to forward progression and support during gait. *Gait Posture* **6**, 1–8. (doi:10.1016/S0966-6362(96)01094-6)
22. Neptune RR, Kautz SA, Zajac FE. 2001 Contributions of the individual ankle plantar flexors to support, forward progression and swing initiation during walking. *J. Biomech.* **34**, 1387–1398. (doi:10.1016/S0021-9290(01)00105-1)
23. Schache AG, Blanch PD, Dorn TW, Brown NA, Rosemond D, Pandy MG. 2011 Effect of running speed on lower limb joint kinetics. *Med. Sci. Sports Exerc.* **43**, 1260–1271. (doi:10.1249/MSS.0b013e3182084929)
24. Dorn TW, Schache AG, Pandy MG. 2012 Muscular strategy shift in human running: dependence of running speed on hip and ankle muscle performance. *J. Exp. Biol.* **215**, 1944–1956. (doi:10.1242/jeb.064527)
25. Candow DG, Chilibeck PD. 2005 Differences in size, strength, and power of upper and lower body muscle groups in young and older men. *J. Gerontol. A, Biol. Sci. Med. Sci.* **60**, 148–156. (doi:10.1093/gerona/60.2.148)
26. Hakkinen K, Kraemer WJ, Newton RU. 1997 Muscle activation and force production during bilateral and unilateral concentric and isometric contractions of the knee extensors in men and women at different ages. *Electromyogr. Clin. Neurophysiol.* **37**, 131–142.
27. Piirainen JM, Avela J, Sippola N, Linnamo V. 2010 Age dependency of neuromuscular function and dynamic balance control. *Eur. J. Sport Sci.* **10**, 69–79. (doi:10.1080/17461390903100254)
28. Farris DJ, Sawicki GS. 2012 Human medial gastrocnemius force–velocity behavior shifts with locomotion speed and gait. *Proc. Natl Acad. Sci. USA* **109**, 977–982. (doi:10.1073/pnas.1107972109)
29. Ishikawa M, Komi PV, Grey MJ, Lepola V, Bruggemann GP. 2005 Muscle–tendon interaction and elastic energy usage in human walking. *J. Appl. Physiol.* (*1985*) **99**, 603–608. (doi:10.1152/japplphysiol.00189.2005)
30. Hoffren M, Ishikawa M, Komi PV. 2007 Age-related neuromuscular function during drop jumps. *J. Appl. Physiol.* (*1985*) **103**, 1276–1283. (doi:10.1152/japplphysiol.00430.2007)
31. Kulmala JP, Avela J, Pasanen K, Parkkari J. 2013 Forefoot strikers exhibit lower running-induced knee loading than rearfoot strikers. *Med. Sci. Sports Exerc.* **45**, 2306–2313. (doi:10.1249/MSS.0b013e31829efcf7)
32. Kerrigan DC, Todd MK, Della Croce U, Lipsitz LA, Collins JJ. 1998 Biomechanical gait alterations independent of speed in the healthy elderly: evidence for specific limiting impairments. *Arch. Phys. Med. Rehabil.* **79**, 317–322. (doi:10.1016/S0003-9993(98)90013-2)
33. Kerrigan DC, Xenopoulos-Oddsson A, Sullivan MJ, Lelas JJ, Riley PO. 2003 Effect of a hip flexor–stretching program on gait in the elderly. *Arch. Phys. Med. Rehabil.* **84**, 1–6. (doi:10.1053/apmr.2003.50056)
34. Kuitunen S, Komi PV, Kyrolainen H. 2002 Knee and ankle joint stiffness in sprint running. *Med. Sci. Sports Exerc.* **34**, 166–173. (doi:10.1097/00005768-200201000-00025)
35. Bezodis IN, Kerwin DG, Salo AI. 2008 Lower-limb mechanics during the support phase of maximum-velocity sprint running. *Med. Sci. Sports Exerc.* **40**, 707–715. (doi:10.1249/MSS.0b013e318162d162)
36. Liu CJ, Latham NK. 2009 Progressive resistance strength training for improving physical function in older adults. *Cochrane Database Syst. Rev.* CD002759. (doi:10.1002/14651858.CD002759.pub2)
37. Hairi NN, Cumming RG, Naganathan V, Handelsman DJ, Le Couteur DG, Creasey H, Waite LM, Seibel MJ, Sambrook PN. 2010 Loss of muscle strength, mass (sarcopenia), and quality (specific force) and its relationship with functional limitation and physical disability: the Concord Health and Ageing in Men Project. *J. Am. Geriatr. Soc.* **58**, 2055–2062. (doi:10.1111/j.1532-5415.2010.03145.x)
38. Geirsdottir OG, Arnarson A, Briem K, Ramel A, Jonsson PV, Thorsdottir I. 2012 Effect of 12-week resistance exercise program on body composition, muscle strength, physical function, and glucose metabolism in healthy, insulin-resistant, and diabetic elderly Icelanders. *J. Gerontol. A, Biol. Sci. Med. Sci.* **67**, 1259–1265. (doi:10.1093/gerona/gls096)
39. Karamanidis K, Arampatzis A. 2006 Mechanical and morphological properties of human quadriceps femoris and triceps surae muscle–tendon unit in relation to aging and running. *J. Biomech.* **39**, 406–417. (doi:10.1016/j.jbiomech.2004.12.017)
40. van der Krogt MM, Delp SL, Schwartz MH. 2012 How robust is human gait to muscle weakness? *Gait Posture* **36**, 113–119. (doi:10.1016/j.gaitpost.2012.01.017)
41. Holviala J, Kraemer WJ, Sillanpaa E, Karppinen H, Avela J, Kauhanen A, Hakkinen A, Hakkinen K. 2012 Effects of strength, endurance and combined training on muscle strength, walking speed and dynamic balance in aging men. *Eur. J. Appl. Physiol.* **112**, 1335–1347. (doi:10.1007/s00421-011-2089-7)
42. Savelberg HHCM, Verdijk LB, Willems PJB, Meijer K. 2007 The robustness of age-related gait

adaptations: can running counterbalance the consequences of ageing? *Gait Posture* **25**, 259–266. (doi:10.1016/j.gaitpost.2006.04.006)

43. Krebs DE, Scarborough DM, McGibbon CA. 2007 Functional vs. strength training in disabled elderly outpatients. *Am. J. Phys. Med. Rehabil.* **86**, 93–103. (doi:10.1097/PHM.0b013e31802ede64)
44. Clark KP, Ryan LJ, Weyand PG. 2014 Foot speed, foot-strike and footwear: linking gait mechanics and running ground reaction forces. *J. Exp. Biol.* **217**, 2037–2040. (doi:10.1242/jeb.099523)
45. Winter D. 1995 Human balance and posture control during standing and walking. *Gait Posture* **3**, 193–214. (doi:10.1016/0966-6362(96)82849-9)
46. Boyer KA, Beaupre GS, Andriacchi TP. 2008 Gender differences exist in the hip joint moments of healthy older walkers. *J. Biomech.* **41**, 3360–3365. (doi:10.1016/j.jbiomech.2008.09.030)
47. Ferber R, Davis IM, Williams III DS. 2003 Gender differences in lower extremity mechanics during running. *Clin. Biomech.* (*Bristol, Avon*). **18**, 350–357. (doi:10.1016/S0268-0033(03)00025-1)
48. Cronin NJ, Prilutsky BI, Lichtwark GA, Maas H. 2013 Does ankle joint power reflect type of muscle action of soleus and gastrocnemius during walking in cats and humans? *J. Biomech.* **46**, 1383–1386. (doi:10.1016/j.jbiomech.2013.02.023)
49. van Ingen Schenau GJ. 1989 From rotation to translation: constraints on multi-joint movements and the unique action of bi-articular muscles. *Hum. Mov. Sci.* **8**, 301–337. (doi:10.1016/0167-9457(89)90037-7)