

# Mechanical and morphological properties of different muscle–tendon units in the lower extremity and running mechanics: effect of aging and physical activity

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## Summary

The objectives of this work were (i) to investigate whether chronic endurance running is a sufficient stimulus to counteract the age-related changes in the mechanical and morphological properties of human triceps surae (TS) and quadriceps femoris (QF) muscle–tendon units (MTUs) by comparing runners and non-active subjects at different ages (young and old), (ii) to identify adaptational phenomena in running mechanics due to age-related changes in the mechanical and morphological properties of the TS and QF MTUs, and finally (iii) to examine whether chronic endurance-running exercise is associated with adaptational effects on running characteristics in old and young adults.

The investigation was conducted on 30 old and 19 young adult males divided into two subgroups according to their running activity: endurance-runners vs non-active. To analyse the properties of the MTUs, all subjects performed isometric maximal voluntary (MVC) ankle plantarflexion and knee extension contractions at 11 different MTU lengths on a dynamometer. The activation of the TS and QF during MVC was estimated by surface electromyography. The gastrocnemius medialis and the vastus lateralis and their distal aponeuroses were visualized by ultrasonography at rest and during MVC, respectively. Ground reaction forces

and kinematic data were recorded during running trials at  $2.7 \text{ m s}^{-1}$ .

The TS and QF MTU capacities were reduced with aging (lower muscle strength and lower tendon stiffness). Runners and non-active subjects had similar MTU properties, suggesting that chronic endurance-running exercise does not counteract the age-related degeneration of the MTUs. Runners showed a higher mechanical advantage for the QF MTU while running (lower gear ratio) compared to non-active subjects, indicating a task-specific adaptation even at old age. Older adults reacted to the reduced capacities of their MTUs by increasing running safety (higher duty factor, lower flight time) and benefitting from a mechanical advantage for the TS MTU, lower rate of force generation and force generation per meter distance. We suggest that the improvement in running mechanics in the older adults happens due to a perceptual motor recalibration and a feed-forward adaptation of the motor task aimed at decreasing the disparity between the reduced capacity of the MTUs and the running effort.

Key words: age effect, endurance running, skeletal muscle, tendon properties, gear ratio, rate of force generation, human.

## Introduction

In the literature it is well established that intrinsic mechanical and morphological properties of the muscle–tendon unit (MTU) (e.g. tendon stiffness, muscle strength, muscle architecture) determine its function and performance capabilities (Gans and Gaunt, 1991; Zuurbier and Huijing, 1992; Ettema, 1996; Lieber and Friden, 2000; Biewener and Roberts, 2000). Moreover, the mechanical and morphological properties of the MTUs can influence the function and performance of the entire musculoskeletal system during locomotion (De Haan et al., 1986; Biewener and Roberts, 2000; Bobbert, 2001; Hof et al., 2002; Roberts and Marsh, 2003; Biewener et al., 2004). For example, the elastic properties of tendons can enhance muscle performance during stretch–shortening cycle exercises (e.g. running) because

tendon stretch and recoil reduce the muscular work and because the MTU shortens and lengthens at velocities which, without tendons, would be mechanically unfavourable for muscles alone (Biewener and Roberts, 2000; Hof et al., 2002; Roberts and Marsh, 2003).

Past studies provided evidence that the aging process is associated with a loss in muscle strength (Criswell et al., 1997; Frontera et al., 2000; D'Antona et al., 2003; Trappe et al., 2003), changes in the mechanical properties of collagenous tissues (Noyes and Grood, 1976; Vogel, 1980; Blevins et al., 1994; Komatsu et al., 2004; Reeves et al., 2004) and alterations in muscle architecture (Narici et al., 2003; Kubo et al., 2003a,b). Further, it has been shown that the performance capability of the neural system also degenerates with aging (for

a review, see Prince et al., 1997). It is reasonable to assume that the age-related degeneration of the capacities of the biological system will reduce the functional motor performance capacity during daily activities. A clear example is the increased occurrence of falls during daily activities in the older subjects (for a review, see Schultz, 1992). However, humans are able to adapt and to modify their motor task organisation using sensory feedback information (Kagerer et al., 1997; McNay and Willingham, 1998; Pai et al., 2003). This is especially true for repetitive motor tasks, where the central nervous system may use sensory feedback information to update internal models, adjusting the dynamic behaviour of the motor system to achieve a new equilibrium between sensory inputs and motor outputs (Wolpert et al., 1995; Shadmehr, 2004). As the new condition is adapted the human system knows how to behave and so the central nervous system can select and execute an appropriate action in a feed-forward control. Adaptive refinement of motor tasks (motor task reorganization) by humans may be the mediator between changes in the musculoskeletal system (internal changes) and those in the environment (external changes; Mulder et al., 2002). This suggests that changes in the capacities of the musculoskeletal system would lead to motor task adaptations in repetitive tasks like walking and running by continuously updating the internal model, using feedback control. Thus, it is reasonable to hypothesize that older subjects will change their running strategy reflecting the reduction in the capacities of their MTUs (internal changes). This hypothesis is supported by the fact that older subjects do not show deficits in the adaptation level of non-strategic tasks (McNay and Willingham, 1998; Fernández-Ruiz et al., 2000; Buch et al., 2003).

Several studies have documented that exercise with high-magnitude mechanical loads counteracts the age-related degeneration of the capacities of the MTUs (Aagaard et al., 2001; Reeves et al., 2003, 2004). For instance, strength training increases tendon stiffness and muscle strength in older humans (Reeves et al., 2003, 2004). However, several *in vitro* (Viidik, 1969; Kiiskinen, 1977; Woo et al., 1981; Birch et al., 1999) and *in vivo* (Rosager et al., 2002; Hansen et al., 2003) studies have documented that exercise with high total loading volume but relative low loads (e.g. endurance running) does not provide a sufficient stimulus to provoke further adaptational effects on the mechanical properties of high-load-bearing MTUs. Most studies analysing the effect of running exercise on the properties of the MTUs were done with young adult subjects. The influence of chronic running exercise on the age-related degeneration of the mechanical and morphological properties of the MTUs has not been clearly identified. For instance, endurance-running exercise in rooster (Curwin et al., 1988) increases the Achilles tendon collagen deposition and decreases the amount of collagen pyridinoline cross-links, suggesting a greater matrix–collagen turnover, resulting in a reduced maturation of tendon collagen. Therefore, it can be hypothesized that endurance-running exercise is a sufficient stimulus to

counteract the age-related changes in the capacities of the MTUs at the lower extremity.

Further, empirical results show that experience or repeated practice causes a task-specific adaptation (Erni and Dietz, 2001; Pavol et al., 2002; Pai et al., 2003). Most of those studies indicated an improvement in locomotion mechanics. Repeated practise during stepping over an obstacle decreased leg joint trajectory and foot clearance (Erni and Dietz, 2001). Moreover, this so-called ‘use-dependent’ motor learning (Erni and Dietz, 2001) has been described for locomotor movements in young and older subjects (Pavol et al., 2002; Pai et al., 2003). A clear example is that age does not influence the outcome of a slipping perturbation during repeated exposure (Pavol et al., 2002). Chronic exposure to repetitive loading while running increases the risk of injury at the knee joint (e.g. patellofemoral pain syndrome), which is speculated to be caused by the anatomical joint alignment and the internal rotation of the tibia during the stance phase (Messier et al., 1991; Nigg et al., 1993). In general, a certain magnitude of mechanical load and stress is tolerated and even needed for the mechanical adaptation of the musculoskeletal system (for a review, see: Kjaer, 2004; Wang, 2005). However, when the magnitude of the mechanical load or stress exceeds a certain threshold level the biological system will change its control strategy (DeVita et al., 1992; DeVita, 1994; DeVita and Hortobagyi, 2000; Hortobagyi et al., 2003). In other words, the neuromuscular system is flexible and enables humans to change their locomotion strategy, obviously depending on the capacities of the musculoskeletal system and on the functional demand of the task. From a mechanical point of view we hypothesise that running experience will improve running characteristics (kinematics and kinetics). Furthermore, we speculate that running-task-specific adaptations will not be degraded with age.

Therefore, the main purposes of this work were (i) to investigate whether chronic endurance running is a sufficient stimulus to counteract the age-related changes in the mechanical and morphological properties of human triceps surae (TS) and quadriceps femoris (QF) muscle-tendon units (MTUs) by comparing runners and non-active subjects at different ages (young and old), (ii) to identify adaptational phenomena in running mechanics due to age-related changes in the mechanical and morphological properties of the TS and QF MTUs, and finally (iii) to examine whether chronic endurance-running exercise is associated with adaptational effects on running characteristics in old and young adults.

## Materials and methods

### Subjects

The investigation was conducted on 49 male subjects, comprising 30 older adults aged 60–69 years and 19 young adults aged 21–32 years. The subjects were further divided into two subgroups according to their running activity: 29 endurance-runners and 20 non-active individuals. Anthropometric data of the sample are summarized in Table 1.

Table 1. Anthropometric data of the subjects

	Older adults		Young adults	
	Runners	Non-active	Runners	Non-active
Age (years)	64±3	64±2	27±4	29±3
Body mass (kg) <sup>‡</sup>	76±6	81±6	73±5	78±8
Height (cm)**	176±4	174±8	180±4	180±9
Femur length (mm)	449±27	439±34	454±18	450±37
Tibia length (mm)*	413±14	406±25	429±13	430±20

Values are means ± S.D. *N*=20 (older runners), *N*=10 (older, non-active subjects), *N*=9 (younger runners), *N*=10 (younger, non-active subjects).

Asterisks indicate statistically significant differences between older and young adults: \**P*<0.05, \*\**P*<0.01; <sup>‡</sup>significant differences between runners and non-active individuals (*P*<0.05).

There was no age-by-running activity interaction for the analysed parameters (*P*>0.05).

All subjects in the endurance-runners group had performed endurance running at least three times per week over the last 10 years and participated regularly in middle- and long-distance running competitions. One of the subjects in this group was 21 years old and had trained only over the last 7 years. The training distance ranged from 30 to 100 km week<sup>-1</sup>. The criterion for entering the non-active group was no sport-activity except at school.

#### Measurement of maximal isometric ankle and knee joint moment

The subjects performed isometric maximal voluntary ankle plantarflexion and knee extension contractions of their left leg on two separate test days. The warm-up consisted of 2–3 min performing submaximal isometric contractions and three maximal voluntary contractions (MVCs). Afterwards the subjects performed isometric maximal voluntary ankle plantarflexion or knee extension contractions at eleven different ankle–knee and knee–hip joint angle configurations, respectively (Table 2) on a Biodex dynamometer (Biodex Medical Systems, Inc., Shirley, NY, USA). Different joint angle configurations were chosen in order to examine TS and QF muscle force potential over the whole range of achievable MTU lengths. The different joint angle configurations were applied in random order. 3 min rest between contractions were allowed. The subjects were instructed and encouraged to produce a maximal isometric moment and to hold it for about 2–3 s.

The resultant moments at the ankle and knee joints were calculated through inverse dynamics (Arampatzis et al., 2004, 2005a). Kinematic data were recorded using the Vicon 624 system (Vicon Motion Systems, Oxford, UK) with eight cameras operating at 120 Hz. To calculate the lever arm of the ankle joint during ankle plantarflexion the centre of pressure under the foot was determined by means of a flexible pressure distribution insole from Pedar-System (Novel GmbH, Munich, Germany) operating at 99 Hz (Arampatzis et al., 2005a). The

Table 2. Eleven ankle–knee and knee–hip joint angle configurations in degrees used for the isometric maximal voluntary ankle plantarflexion and knee extension contractions

Ankle plantarflexion (degrees)		Knee extension (degrees)	
Ankle joint	Knee joint	Knee joint	Hip joint
120	75	170	90
120	110	170	110
110	100	170	135
120	140	160	120
100	110	160	140
110	150	140	115
90	130	140	140
100	170	110	100
80	130	110	150
90	170	80	110
80	170	80	150

Tibia perpendicular to the foot-sole was defined as 90° ankle angle.

The completely extended trunk and knee were defined as 180° hip and knee joint angles, respectively.

compensation of moments due to gravitational forces was done for all subjects before each ankle plantarflexion or knee extension contraction. The exact method for calculating the resultant joint moments has been previously described (Arampatzis et al., 2004, 2005a).

The moments arising from antagonistic coactivation during the ankle plantarflexion and knee extension efforts were quantified by assuming a linear relationship between surface electromyography (EMG) amplitude of the ankle dorsiflexor or knee flexor muscles and moment (Baratta et al., 1988). This was established by measuring EMG and moment during one relaxed condition and two submaximal ankle dorsiflexion or knee flexion contractions at each joint angle configuration (Mademli et al., 2004). Therefore, in the text below, maximal knee and ankle joint moments refer to the maximal joint moment values considering the effect of gravitational forces, the effect of the joint axis alignment relative to the dynamometer axis and the effect of the antagonistic moment on the moment measured at the dynamometer.

#### Measurement of EMG activity during isometric contractions

Bipolar EMG lead-offs with pre-amplification (analogue RC-filter 10–500 Hz bandwidth; Biovision, Wehrheim, Germany) and adhesive surface electrodes (blue sensor–Medicotest, Ballerup, Denmark) were used to analyse muscle activity. Before placing the electrodes the skin was carefully prepared (shaved and cleaned with ethanol) to reduce skin impedance. The electrodes were positioned above the midpoint of the muscle belly as assessed by palpation, parallel to the presumed direction of the muscle fibres. The inter-electrode distance was 2 cm. The activation of the TS muscle was assessed from the EMGs of the gastrocnemius medialis

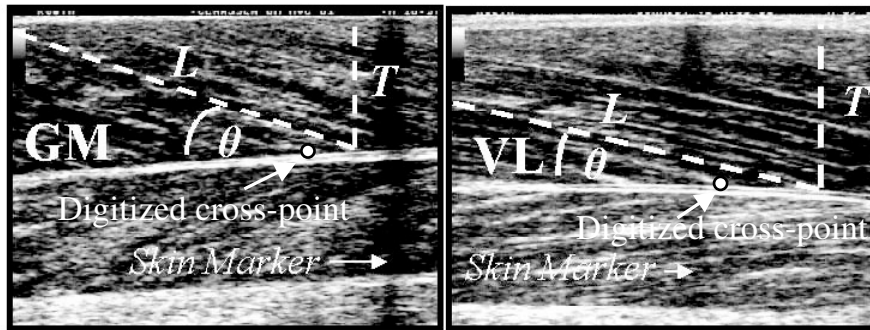


Fig. 1. Ultrasound image of the gastrocnemius medialis (GM, left) and vastus lateralis (VL, right) at rest.  $L$ , fascicle length;  $T$ , muscle thickness;  $\theta$ , pennation angle; digitized cross-point indicates insertion of the fascicle into the deep aponeurosis.

(GM), gastrocnemius lateralis (GL) and soleus (SO). During knee extension the EMG-activities of the vastus lateralis (VL), vastus medialis (VM) and rectus femoris (RF) were analysed. The EMG signals were recorded at 1080 Hz using the Vicon system. Before starting the experiment, tests including submaximal and maximal isometric contractions for each muscle group were undertaken to determine whether an adequate signal was obtained from each muscle and to adjust the amplifier gains. Further, the EMG signal for each muscle was checked online for artifacts due to mechanical causes by passively shaking the leg. The preparation was renewed when such artifacts were observed. All isometric contractions at the knee or the ankle joint were performed within one testing session. No electrode replacement or re-adjusting of the EMG pre-amplification gain were done during the measurements.

The EMG-activity is described by the root mean square (RMS) of the raw signals for a time interval of 1000 ms at peak joint moment. The RMS from each muscle was normalised to the individual maximal RMS value of each muscle for each subject during the eleven isometric contractions. In order to determine the EMG activity of the ankle plantarflexor and knee extensor muscles, the normalised RMS of the examined muscles were averaged and weighted by their physiological cross sectional areas (PCSA). For the TS, a PCSA ratio of 6:2:1 for the SO, GM, GL (Out et al., 1996) and for the QF, a PCSA ratio of 0.92, 1.00 and 0.72 for the RF, VL and VM (Herzog et al., 1987) were used.

#### Measurement of tendon properties

Tendon properties were determined on two additional test days. The subjects performed MVC ankle plantarflexion (ankle joint angle  $90^\circ$ , knee joint angle  $180^\circ$ ) and knee extension (knee joint angle  $115^\circ$ , hip joint angle  $140^\circ$ ) with their left leg on a dynamometer. A 7.5 MHz linear array ultrasound probe (Aloka SSD 4000, Tokyo, Japan; 43 Hz) was used to visualise the distal tendon and aponeurosis of the GM or VL, respectively (Fig. 1). The exact protocol for the analysis of the tendinous tissue elongation during ankle plantarflexion and knee extension is described in detail elsewhere (Arampatzis et al., 2005b; Stafilidis et al., 2005).

Briefly, the effect of inevitable joint angular rotation on the elongation of the tendon and aponeurosis during the loading phase was taken into account by capturing the motion of the tendons and aponeuroses from the GM and VL during a passive motion of the ankle or the knee joint (Muramatsu et al., 2001; Magnusson et al., 2001; Bojsen-Møller et al., 2003). This allowed the correction of the elongation obtained for the tendon and aponeurosis due to joint rotation for each maximal ankle plantarflexion or knee extension trial. The ultrasound images taken during the passive joint motion and during the MVCs were digitised frame by

frame until the maximal calculated tendon force was achieved. The tendon force was calculated by dividing the ankle or knee joint moment by the corresponding tendon moment arm. The tendon moment arms of the Achilles tendon and the patellar tendon were calculated using the data provided by Maganaris et al. (1998) and Herzog and Read (1993), respectively. The insertion of the fascicle into the deep aponeurosis (Fig. 1) was tracked during contraction and during a passive trial to determine the elongation of the tendon and aponeurosis. The resting length of the GM (knee joint angle  $180^\circ$ , ankle joint angle  $110^\circ$ ) and the resting length of the VL (knee joint angle  $130^\circ$ , hip joint angle  $140^\circ$ ) tendon and aponeurosis were identified on the ultrasound images (Arampatzis et al., 2005b; Stafilidis et al., 2005). The specific joint angle configurations were chosen in order to reduce passive joint moments almost to zero (Riener and Edrich, 1999).

The normalised stiffness of the TS and QF tendon and aponeurosis were calculated by the relationship between the tendon force and the strain of the tendon and aponeurosis between 50% and 100% of the maximal tendon force, using a linear regression. The linearity between tendon force and strain was checked using the coefficient of determination ( $r^2$ ). This proved to be reasonably high ( $r^2=0.98-0.99$ ).

#### Measurement of muscle architecture

The muscle architecture of the GM and VL (fascicle length, pennation angle and thickness) were determined by ultrasonography during the same test session as for the analysis of the tendon properties and using the same joint angle configurations (GM: ankle joint angle  $90^\circ$ , knee joint angle  $180^\circ$ ; VL: knee joint angle  $115^\circ$ , hip joint angle  $140^\circ$ ). All measurements were done on the relaxed muscles at the cited positions. The pennation angles of the GM and VL were measured as the angle of insertion of the muscle fascicles into the deep aponeurosis. Fascicle length was defined as the length of the fascicular path between the insertions of the fascicle into the superficial and deeper aponeuroses. The ratios between fascicle length of the GM and tibia length, and between fascicle length of the VL and femur length, were also analysed. Femur length was defined as the distance between the lateral femoral

condyle and the major trochanter, and tibia length as the distance between the lateral malleolus and lateral femoral condyle. Muscle thickness was defined as the distance between the deeper and superficial aponeurosis (Fig. 1).

#### Measurement of running characteristics

On one additional test day, the ground reaction force (GRF) (1080 Hz) and the kinematic data (Vicon 624 system, 12 cameras operating at 120 Hz) were recorded as the subjects ran barefoot at  $2.7 \text{ m s}^{-1}$  on a 16 m track with two force platforms (60 cm  $\times$  90 cm, Kistler, Winterthur, Switzerland) mounted beneath midway of the track. Barefoot running was chosen to exclude any effects of running shoes on the running characteristics. The distance covered by each subject in one trial was about 13 m. The running velocity was chosen to be a normal training and/or marathon competition velocity for the older runners. This running velocity if maintained would result in a time of about 4:20 h to run the marathon, and is the mean marathon time reported for the older runners examined. Running velocity was controlled because running mechanics depend on running velocity (Arampatzis et al., 1999).

All subjects were instructed to run along the track at the designed speed ( $2.7 \text{ m s}^{-1}$ ). Subjects could perform as many practice trials as they wanted (typically 2–3). The running velocity was indicated by a customized electrical adjustable pacemaker stick hanging from the ceiling and running along the whole track in front of the subjects. A trial was successful when the subjects followed the stick at the same distance ( $\sim 50 \text{ cm}$ ) over the whole track and both right and left touch-downs were centred on the corresponding force platforms. Three valid trials were recorded and analysed for each subject. The athletes had a 1–2 min rest between trials. Thirty eight reflective markers (radius 14 mm) were used to track the whole body kinematics. The markers defined the left and right foot, left and right lower legs, left and right thigh, pelvis, thorax, left and right upper arm, left and right forearm, left and right hand and the head. The three-dimensional coordinates were smoothed using a Woltring filter routine (Woltring, 1986) with a minimum mean squared error value of 15. The segmental masses and moments of inertia were calculated basing on the data reported by Dempster et al. (1959).

A whole stride cycle, from foot strike to ipsilateral foot strike, was analysed. One step was defined to be from foot strike to contralateral foot strike. Step length was defined as the anterior displacement of the foot (midpoint of the distance between calcaneus and metatarsal markers) from foot strike to contralateral foot strike. For both legs, the instants of touch-down and take-off were determined from the vertical force data. The threshold for determining touch-down and take-off was set at 20 N. Temporal characteristics, sagittal angular joint angle kinematics and kinetics and GRFs were analysed for both legs. A straight leg was defined as  $180^\circ$  knee joint angle. The tibia being perpendicular to the ground while having the foot flat on it was defined as  $90^\circ$  ankle joint. The limb angle was defined as the angle between the line connecting the centre of

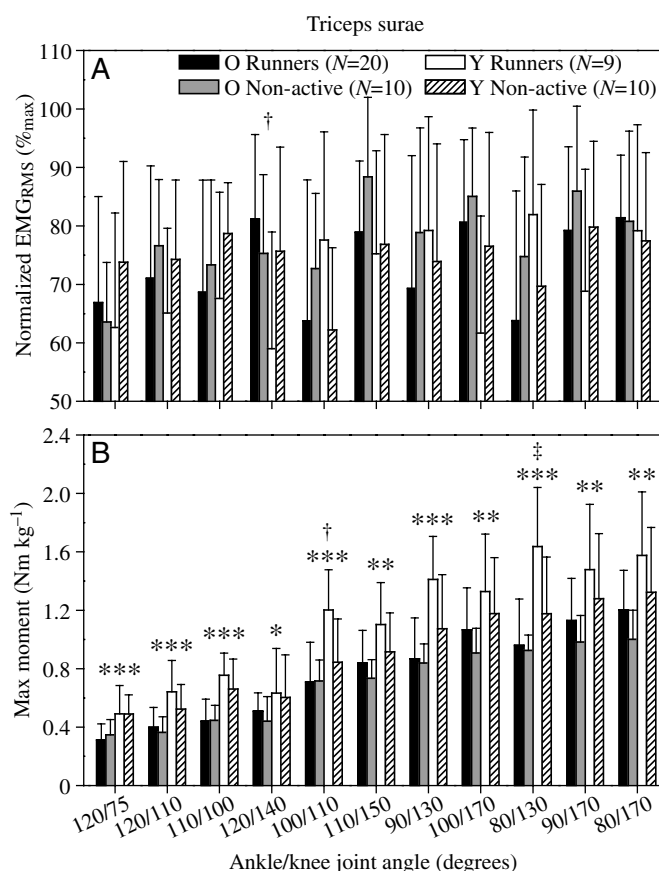


Fig. 2. (A) Normalized RMS values of the EMG signal for the triceps surae muscle (gastrocnemius medialis, gastrocnemius lateralis and soleus) and (B) ankle joint moment during isometric maximal voluntary ankle plantarflexion contraction at 11 different joint angle configurations for the examined groups. Values are means  $\pm$  S.D. RMS values from each subject were normalised to the highest RMS value measured over all joint angle configurations. O, older adults; Y, young adults. Asterisks indicate statistically significant differences between older and young adults: \* $P<0.05$ , \*\* $P<0.01$ , \*\*\* $P<0.001$ ; †significant age-by-running activity interaction ( $P<0.05$ ); ‡significant differences between runners and non-active individuals ( $P<0.05$ ).

mass (COM) and the midpoint of the foot identified by the calcaneus and metatarsal markers and the vertical in the sagittal plane. A posterior or anterior position of the COM relative to the midpoint of the foot in the running direction was defined as a negative or positive limb angle, respectively. The gear ratios of the TS and the QF MTUs were calculated as the ratios ( $R/r$ ) of the moment arm ( $R$ ) of the GRF acting about the joint to the agonist tendon moment arm ( $r$ ) according to Carrier et al. (1994). The moment arms ( $r$ ) of the Achilles tendon and the patellar tendon were calculated using the data provided by Maganaris et al. (1998) and Herzog and Read (1993), respectively. The gear ratio and the moment arm ( $R$ ) of the GRF acting about the joint were determined for the left and right ankle and knee joints for five phases during ground contact (Phase 1: 10–26%; Phase 2: 26–42%; Phase 3: 42–58%; Phase 4: 58–74%; Phase 5: 74–90% of ground

contact). The gear ratio and the moment arm were not determined for the first and last 10% of ground contact because of the low GRF and the consequently unreliable calculation of the moment arm ( $R$ ) of the GRF.

The duty factor (DF) was calculated as the proportion between ground contact duration ( $t_{\text{contact}}$ ) and stride duration ( $t_{\text{stride}}$ ) according to McMahon et al. (1985;  $t_{\text{contact}}$  was calculated as the mean value from both legs). In order to examine the proportion of the COM transport during one stride cycle when the subjects have contact with the ground, we calculated the ratio between anterior COM displacement during ground contact of the left ( $L_{\text{contact,L}}^{\text{COM}}$ ) and right leg ( $L_{\text{contact,R}}^{\text{COM}}$ ) and anterior COM displacement during stride cycle ( $L_{\text{stride}}^{\text{COM}}$ ). This was called ratio displacement (RD):

$$\text{RD} = \frac{L_{\text{contact,L}}^{\text{COM}} + L_{\text{contact,R}}^{\text{COM}}}{L_{\text{stride}}^{\text{COM}}} \quad (1)$$

(Note: a whole stride cycle was from foot strike to ipsilateral foot strike.)

The anterior COM displacement during ground contact and flight phase was calculated as the mean values of the anterior COM displacement during the corresponding phases for the left and right leg. Vertical COM displacement was defined as the difference between the maximum and minimum value of the vertical COM trajectory during the stride cycle. The vertical COM displacement during running was calculated using the kinematic data of the subjects. The joint moments and the corresponding mechanical powers (left and right leg) were calculated through inverse dynamics from the mean values of the left and right leg. For all subjects and parameters the mean values from three trials and both legs were utilised for further analysis. The symmetry and reproducibility of temporal, kinematic and GRF parameters during submaximal running velocity were analysed in previously studies and were reasonably high (Karamanidis et al., 2003, 2004).

### Statistics

We used a two-factor (age-by-running activity) analysis of variance (ANOVA) to detect group differences in (1) isometric maximal voluntary ankle plantarflexion and knee extension moments at different MTU lengths, (2) EMG activity (normalised RMS) of the TS and QF muscle at different MTU lengths, (3) normalised stiffness of the TS and QF tendon and aponeurosis, (4) GM and VL muscle architecture and (5) running mechanics. All significant age-by-running activity interactions are reported. When a significant age-by-running activity interaction was present a Bonferroni *post hoc* test was conducted in order to determine where these differences occurred. The  $F$  ratios were considered significant at  $P < 0.05$ . The Levene Test was used to test the homogeneity of variance across groups ( $P < 0.05$ ). If variances were not equal across samples the  $F$  ratios were considered significant at  $P < 0.01$ . All results in the tables and figures are presented as means  $\pm$  S.D. (standard deviation).

## Results

As shown in Table 1, body height ( $P = 0.003$ ) and tibia length ( $P = 0.045$ ) were significantly lower for the old (body height: runners  $176 \pm 4$  cm, non-active  $174 \pm 8$  cm; tibia length: runners  $413 \pm 14$  mm, non-active  $406 \pm 25$  mm) compared to the young adults (body height: runners  $180 \pm 4$  cm, non-active  $180 \pm 9$  cm; tibia length: runners  $429 \pm 13$  mm, non-active  $430 \pm 20$  mm). Body mass was significantly ( $P = 0.020$ ) lower in runners (old  $76 \pm 6$  kg, young  $73 \pm 5$  kg) compared to non-active individuals (old  $81 \pm 6$  kg, young  $78 \pm 8$  kg).

### Joint moments during maximal isometric contractions

Older adults showed significantly ( $P < 0.05$ ,  $P < 0.01$  and  $P < 0.001$ ) lower maximal isometric ankle plantarflexion moments compared to the young adults at all joint angle configurations (Fig. 2). Conversely, the comparison between runners and non-active subjects revealed significant differences ( $P < 0.05$ ) on maximal isometric ankle plantarflexion moment only for position  $80/130^\circ$  (ankle/knee joint angle), the maximal moment being higher ( $P = 0.020$ ) for runners compared to non-active subjects (Fig. 2). Age-by-running activity interaction ( $P < 0.05$ ) was detected for maximal ankle plantarflexion moment at position  $100/110^\circ$  (ankle/knee joint angle). The *post hoc* analysis revealed a significantly ( $P < 0.05$ ) higher ankle plantarflexion moment for the young runners compared to all other groups (young and old non-active subjects and old runners). As shown in Fig. 3, significant differences ( $P = 0.040$  to  $P < 0.001$ ) between age groups were present for the maximal isometric knee extension moment at positions  $140/115^\circ$ ,  $140/140^\circ$ ,  $110/100^\circ$  and  $110/150^\circ$  (knee/hip joint angle). The young adults were significantly stronger than the old adults. By contrast, there were no significant differences ( $P > 0.05$ ) between runners and non-active subjects on the maximal isometric knee extension moment for any joint angle configuration (Fig. 3).

### EMG-activity during maximal isometric contractions

For the normalised RMS of the TS we found an age-by-running activity interaction ( $P = 0.030$ ) at position  $120/140^\circ$  (Fig. 2). The *post hoc* testing revealed significantly lower normalised RMS values in young runners compared to the old runners ( $P = 0.030$ ). There was a significant ( $P = 0.025$  to  $P = 0.001$ ) age effect on the normalised RMS of the QF muscle at positions  $170/110^\circ$ ,  $170/135^\circ$ ,  $160/120^\circ$ ,  $160/140^\circ$  and  $80/110^\circ$ . The normalised RMS were higher in the older adults compared to the young adults (Fig. 3).

### Tendon stiffness and muscle architecture

The normalised stiffness of the QF was significantly reduced ( $P = 0.001$ ) in the old adults compared to the young adults (Fig. 4). In contrast, no significant differences ( $P > 0.05$ ) was found on the normalised stiffness of the TS tendon and aponeurosis between age groups. No significant differences ( $P > 0.05$ ) between runners and non-active subjects in normalised stiffness of the TS or the QF was detected (Fig. 4). As shown in Table 3, there was almost no group differences

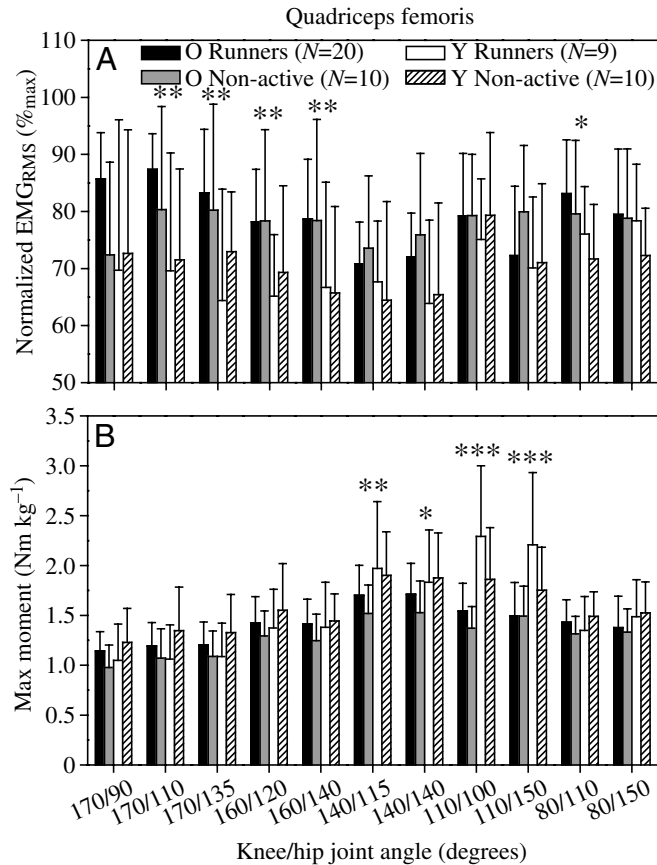


Fig. 3. (A) Normalized RMS values of the EMG signal for quadriceps femoris (vastus lateralis, vastus medialis and rectus femoris) and (B) knee joint moment during isometric maximal voluntary knee extension contraction at 11 different joint angle configurations for the examined groups. Values are means  $\pm$  S.D. RMS values for each subject were normalised to the highest RMS value measured over all joint angle configurations. O, older adults; Y, young adults. Asterisks indicate statistically significant differences between older and young adults: \* $P<0.05$ , \*\* $P<0.01$ , \*\*\* $P<0.001$ ; there was no age-by-running activity interaction for the analysed parameters ( $P>0.05$ ).

on GM or VL muscle architecture. Only the pennation angle of the GM was significantly higher ( $P=0.016$ ) for the runners compared to the non-active subjects.

#### Running characteristics

Fig. 5 displays the sagittal plane angular motion at the ankle and knee joints as well as the limb angle for the left leg during running ( $2.7 \text{ m s}^{-1}$ ) for the examined groups. Fig. 6 shows the ankle and knee joint moments and mechanical powers, and the vertical and anteroposterior horizontal GRFs of the left leg during running. Again, all statistical results regarding the running characteristics are related to the mean values from three trials and both legs for each subject. When running at the same speed as young adults, older adults displayed a significantly higher stride frequency ( $P=0.002$ ), lower step length ( $P=0.021$ ), lower flight time ( $P=0.001$ ), lower anterior COM displacement during flight phase ( $P=0.040$ ), lower

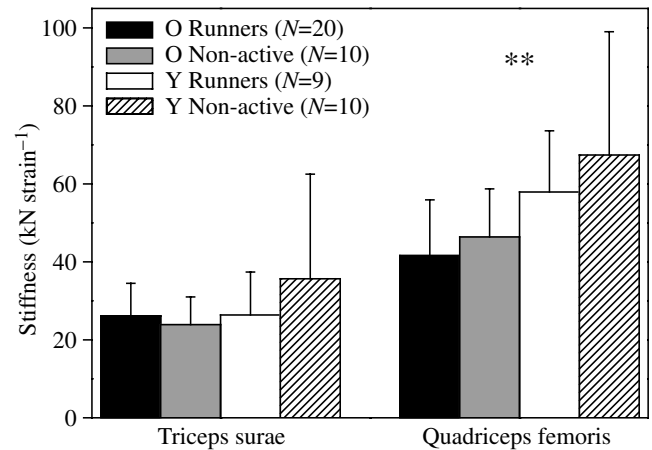


Fig. 4. Normalised stiffness of the triceps surae and quadriceps femoris tendon and aponeurosis for the different groups. Values are means  $\pm$  S.D. O, older adults; Y, young adults. \*\*Statistically significant differences between older and young adults ( $P<0.01$ ); there was no age-by-running activity interaction for the analysed parameters ( $P>0.05$ ).

vertical COM displacement during the stride cycle ( $P=0.007$ ), lower angular displacement at the ankle joint in plantarflexion direction during ground contact ( $P=0.008$ ), higher limb angle at take off ( $P<0.001$ ) and a higher angular displacement of the limb angle during ground contact ( $P=0.001$ ) compared to the young adults (Tables 4, 5 and 6). Furthermore, the duty factor ( $P=0.003$ ) and ratio displacement of the COM ( $P=0.007$ ) were significantly higher for the old adults compared to the young adults (Tables 4 and 5). Runners exhibited a significantly lower step length ( $P=0.032$ ), lower anterior COM displacement during ground contact ( $P=0.039$ ), lower angular displacement at the ankle joint in plantarflexion direction during ground contact ( $P=0.006$ ), lower limb angle at take-off ( $P=0.001$ ) and a lower angular displacement of the limb angle during ground contact ( $P=0.040$ ) compared to the non-active group (Tables 4, 5 and 6). There was a significant ( $P=0.024$ ) age-by-running activity interaction at the angular displacement of the knee joint in knee extension during ground contact (Table 6). The *post hoc* analysis revealed significantly ( $P=0.049$ ) higher values for the young runners compared to the old runners.

For the GRF parameters the average ( $P=0.002$ ) and the maximal values ( $P=0.016$ ) of the vertical force as well as the vertical ( $P=0.002$ ) and horizontal (deceleration phase:  $P=0.009$ ; acceleration phase:  $P=0.028$ ) impulses during ground contact were significantly lower for the old adults compared to the young adults (Table 7). The comparison between runners and non-active subjects revealed significant differences in the horizontal impulse (deceleration phase:  $P=0.043$ ; acceleration phase:  $P=0.010$ ), leading to lower values for the endurance runners compared to the non-active group (Table 7). Significant differences ( $P<0.05$ ) between age groups on joint kinetics were identified at the ankle joint, with virtually no differences ( $P>0.05$ ) at the knee joint (Table 8).

Table 3. Length of the tendon and aponeurosis, pennation angle, fascicle length, ratio (fascicle length/tibia or femur length) and muscle thickness of the gastrocnemius medialis and vastus lateralis for all examined groups at rest

	Older adults		Young adults	
	Runners	Non-active	Runners	Non-active
Resting length GM (cm)	26.8±2.7	27.7±2.5	31.7±9.9	29.3±3.0
Pennation angle GM (°) <sup>‡</sup>	19.6±2.5	18.4±2.6	21.9±2.6	18.9±2.4
Fascicle length GM (cm)	6.18±0.95	6.53±0.63	7.69±2.82	6.34±0.80
Ratio GM (fascicle length/tibia length)	0.150±0.024	0.161±0.015	0.185±0.070	0.152±0.018
Thickness GM (cm)	1.79±0.20	1.73±0.24	2.03±0.52	1.90±0.12
Resting length VL (cm)	33.3±1.7	31.8±2.5	30.6±7.1	32.5±2.0
Pennation angle VL (°)	10.7±2.5	9.8±1.7	10.3±1.6	10.0±2.2
Fascicle length VL (cm)	10.36±3.27	10.61±1.54	10.58±2.59	11.20±2.08
Ratio VL (fascicle length/femur length)	0.231±0.072	0.242±0.038	0.234±0.062	0.248±0.052
Thickness VL (cm)	2.03±0.34	1.78±0.30	2.20±0.19	2.02±0.22

GM, gastrocnemius medialis; VM, vastus lateralis.

Values are means ± S.D.; *N*=20 (older runners), *N*=10 (older non-active subjects), *N*=9 (younger runners), *N*=10 (younger non-active subjects).

The muscle architecture of the GM and the VL was determined at 90/180° (ankle/knee joint) and 140/115° (knee/hip joint), respectively. To determine the resting length of the GM and VL tendon and aponeurosis the joint angles were set at 110/180° (ankle/knee joint) and 130/140° (knee/hip joint) respectively.

<sup>‡</sup>Statistically significant differences between runners and non-active individuals (*P*<0.05).

There was no age-by-running activity interaction for the analysed parameters (*P*>0.05).

The old adults showed a significantly lower maximal ankle plantarflexion moment (*P*=0.017) and mechanical power (*P*=0.005) during ground contact compared to young adults (Table 8). No significant differences (*P*>0.05) in ankle and knee joint kinetics between endurance runners and non-active subjects were found. There was a significant age-by-running activity interaction (*P*=0.010) for the maximal mechanical power at the knee joint (Table 8). The *post hoc* analysis revealed a significantly (*P*<0.05) higher maximal mechanical power at the knee joint for the old non-active subjects compared to the old runners and young non-active subjects (Table 8).

Regarding the gear ratio (*R/r*), older adults showed significantly lower (*P*<0.05) values at the ankle joint from 26% to 58% of the ground contact duration (for phase 2: *P*=0.040 and for phase 3: *P*=0.009) compared to the young adults. This was due to a lower moment arm of the GRF acting about the ankle joint (Fig. 7; for phase 2: *P*=0.048 and for phase 3: *P*=0.009). Conversely, no significant differences between individuals who run regularly and those who do not run in the gear ratio or the moment arm of the GRF at the ankle joint were noted (*P*>0.05). Concerning the knee joint no significant differences (*P*>0.05) between older and young adults in the gear ratio or moment arm of the GRF were detected (Fig. 8). Runners demonstrated a significantly lower gear ratio at the knee joint from 10 to 42% of the ground contact duration (for phase 1: *P*=0.030 and for phase 2: *P*=0.026) compared to the non-active group. This was due to a lower moment arm of the GRF acting about the knee joint (Fig. 8; for phase 1: *P*=0.032 and for phase 2: *P*=0.027).

## Discussion

### Lower extremity muscle–tendon unit properties

Based on the available literature, we hypothesized that endurance-running exercise is a sufficient stimulus to counteract the age-related degeneration of the MTUs. The experimental data do not support this hypothesis. Older adults who run regularly had similar age-related changes in the capacities of their MTUs compared to older adults with no running experience.

The present study shows that age (>60 years) is accompanied by a reduced maximal voluntary isometric ankle and knee joint moment. This is in agreement with previous findings (Klitgaard et al., 1990; Frontera et al., 1991; Kubo et al., 2003c; Savelberg and Meijer, 2004). For the plantarflexion moment at the ankle joint, this age-related reduction was present at all analysed joint angle configurations, which indicates a similar relative contribution of the components of the TS to the total moment developed by this muscle group between age groups. Conversely, for the knee extensor muscles the age-related reduction in maximal moment was present at only some of the studied joint angle configurations. While aging revealed a clear reduction in maximal knee extension moment at intermediate knee joint angles (140° and 110°), there was virtually no age affect at more extended (160° and 170°) or flexed (80°) knee joint positions.

Three potential explanations, all of which are probably contributing to these observations, are suggested. (1) It has been reported that the moment–knee-joint angle relationship of the Vastii describe a parabolic curve having its vertex (maximum value) between 100° and 120°. In contrast, the RF has a rather flat joint moment–length curve (Savelberg and

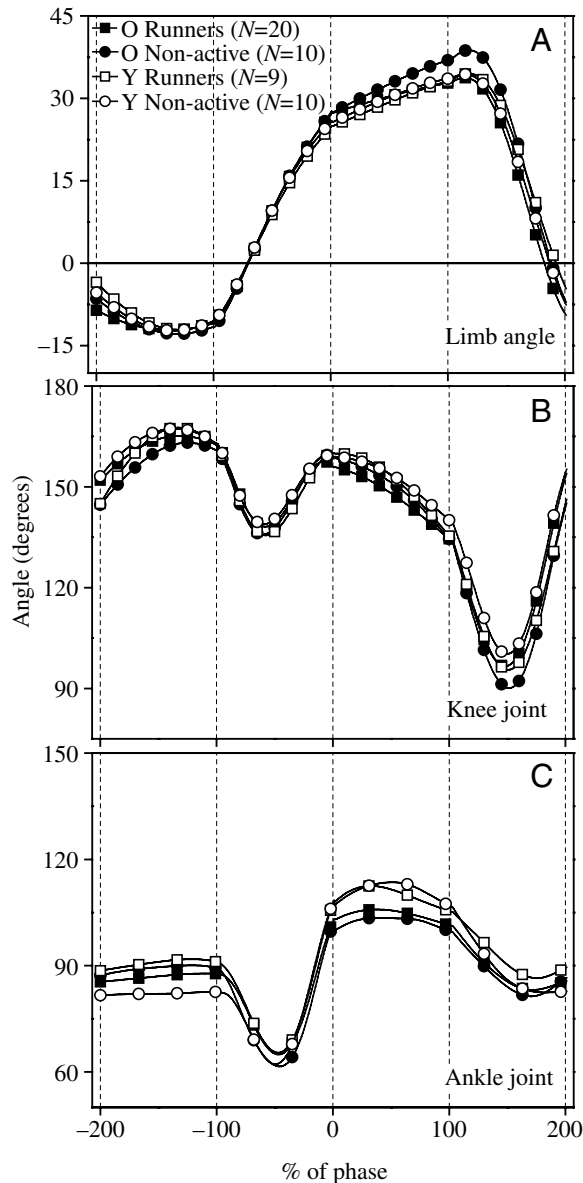


Fig. 5. Average values of the limb angle (A) and sagittal plane angular motion at the knee (B) and ankle (C) joints of the left leg during running ( $2.7 \text{ m s}^{-1}$ ) for the examined groups. O, older adults; Y, young adults. The x-axis was normalised as follows:  $-200\%$  to  $-100\%$ , flight phase before ground contact of the left leg;  $-100\%$  to  $0\%$ , ground contact of the left leg;  $0\%$  to  $100\%$ , flight phase before ground contact of the right leg;  $100\%$  to  $200\%$ , flight phase during ground contact of the right leg. The posterior and anterior position of the COM relative to the midpoint of the foot in vertical direction were defined as negative and positive limb angles, respectively.

Meijer, 2004). This observation would result in a higher relative contribution of the RF to the total knee extension moment at more extended or flexed knee joint positions (Savelberg and Meijer, 2004), where no age effects on QF muscle strength were noted. Recently, it has been reported that the age-related degeneration of the muscle strength at the Vastii is higher than that at the RF (Savelberg and Meijer,

2004). Accordingly, our data might indicate that the age-related reduction in muscle force capacity is distinct within the QF, with a greater decline in monoarticular (Vastii) than biarticular (RF) muscles. (2) At rest (knee/hip joint angle  $115^\circ/140^\circ$ ), the fascicle lengths of the VL were similar for both age groups. This suggests that the working ranges (widths) of the force-length relationship of the Vastii are similar for old and young adults. Consequently, the observed age-related differences in muscle strength of the Vastii would be reduced at short fascicle lengths (extended knee joint) because of the parabolic curve of the force-length relationship of the Vastii (Herzog et al., 1991). (3) Finally, the age-related patterns observed for the knee extension moment at different joint angle configurations might be caused by a modulation of the EMG-activity. Older adults showed an increased QF muscle EMG-activity at more extended ( $160^\circ$  and  $170^\circ$ ) as well as at more flexed ( $80^\circ$ ) knee joint angles in comparison to younger adults. This was not observed at intermediate knee joint angles ( $110^\circ$  and  $140^\circ$ ).

Besides the loss of TS and QF muscle strength we could confirm that aging decreased the stiffness of the QF tendon and aponeurosis. Mechanical changes in collagenous tissues in response to aging have been reported *in vivo* (Reeves et al., 2003; Kubo et al., 2003c) and *in vitro* (Noyes and Grood, 1976; Vogel, 1980; Blevins et al., 1994; Komatsu et al., 2004). The fact that only the TS muscle strength and not the stiffness of the tendon and aponeurosis is affected by aging might indicate that the time courses of tendinous and muscular properties are different (Karpakka et al., 1990; Kubo et al., 2004). Analysing subjects up to the sixth decade revealed no clear age-related changes in the architecture of the GM and VL. However, although not significant, the older adults of the present study showed a tendency towards a reduced pennation angle ( $P=0.08$ ) at the GM and reduced muscle thickness at VL and GM.

Individuals who run regularly and those who do not run displayed no clearly identifiable differences in the mechanical and morphological properties of the TS or the QF MTUs, indicating that chronic endurance-running exercise does not counteract the age-related degeneration of the MTUs. We suggest that the extra stress and strain imposed on the MTUs during endurance running is not a sufficient stimulus to provoke further clear adaptational effects on the capacities of high-load-bearing MTUs. Analysing the effect of endurance-running exercise on the mechanical properties of high-load-bearing MTUs in young adult species led to similar findings (Woo et al., 1981; Birch et al., 1999; Rosager et al., 2002; Hansen et al., 2003). Only the pennation angle of the GM showed higher values in the endurance-runners group compared to the non-active individuals. However, the absolute differences in pennation angle between groups were less than  $1.6^\circ$ , which is probably too low to have any relevant influence on muscle function.

In conclusion, our data indicate that the capacities of the TS and QF MTUs were reduced with aging. In contrast, runners and non-active subjects had no clearly identifiable differences

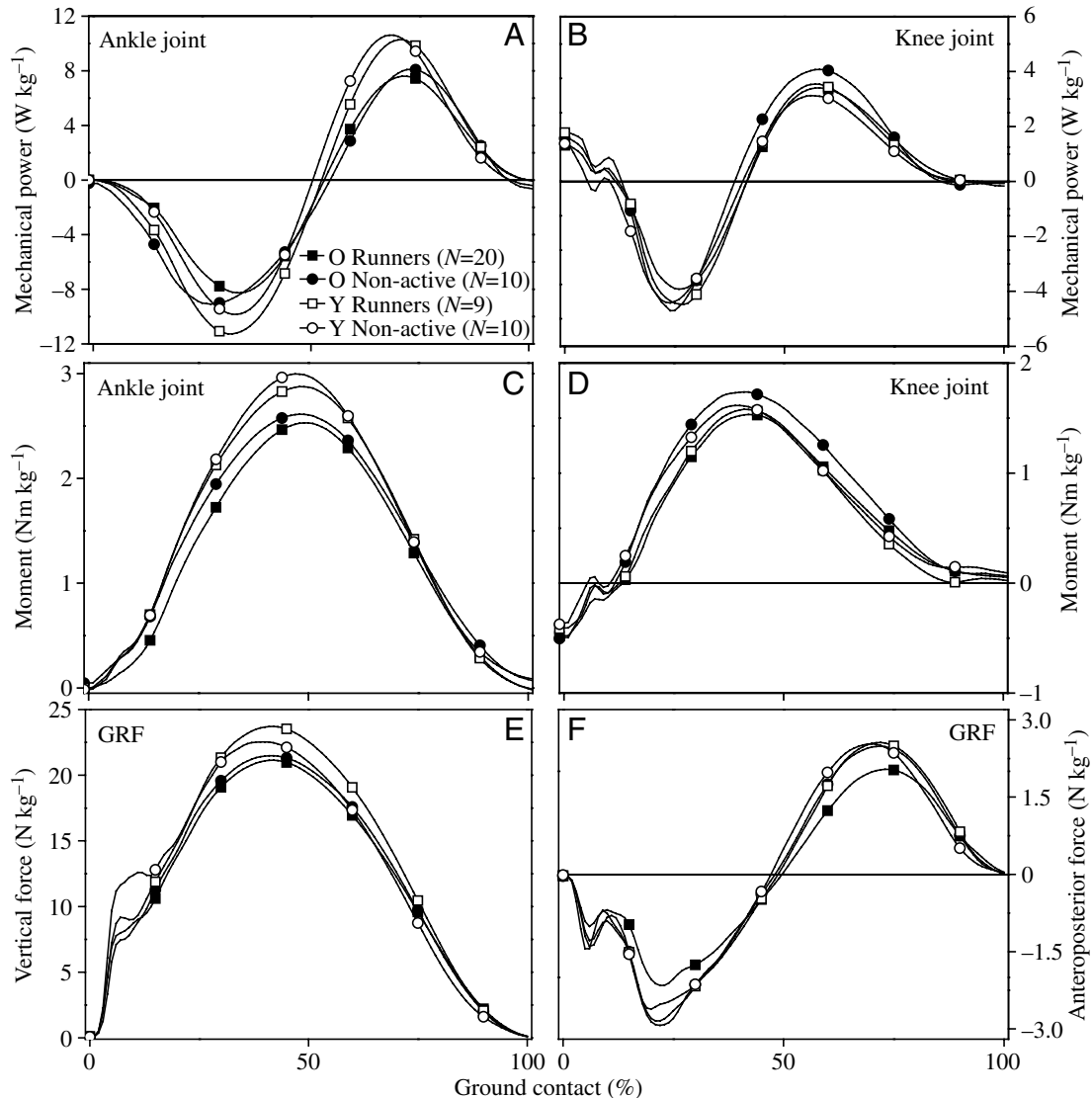


Fig. 6. Mean values of the mechanical power (A,B) and sagittal plane joint moment (C,D) at the ankle (A,C) and knee joint (B,D), and vertical (E) and horizontal (F) ground reaction force (GRF) of the left leg during running ( $2.7 \text{ m s}^{-1}$ ) for the examined groups. O, older adults; Y, young adults. The x-axis was normalised as follows: 0% to 100%, ground contact.

in the mechanical or the morphological properties of the TS or QF MTUs. The relatively low oscillatory load imposed on the QF and TS MTUs during endurance-running exercise is apparently not sufficient to produce measurable changes in the parameters analysed. This is supported by the fact that endurance running does not appear to be able to counteract the influence of aging on the capacities of TS and QF MTUs.

#### *Running mechanics*

##### *Older adults vs young adults*

The second objective of this study was to test the hypothesis that older adults would reveal a differing running strategy from those of young adults, due to a reduction in the capacities of their TS and QF MTUs. The experimental data supported these expectations. When running at the same speed as young adults, older adults selected a different strategy, leading to lower

average and maximum vertical GRF, lower vertical and horizontal (during deceleration and acceleration phase) impulses, a higher duty factor and ratio displacement, a higher stride frequency and consequently lower step length, a lower anterior COM displacement during the flight phase and a lower vertical COM displacement during the stride cycle. However, the ground contact duration and the anterior COM displacement during ground contact did not differ between the older and young adults. The shift towards a higher duty factor and ratio displacement with age probably increased the subjects' safety by increasing the amount of COM transport and time with the foot on the ground while running.

From the mechanical point of view, the above findings indicate that older adults had more advantageous running characteristics than young adults. In the literature, it is generally accepted that there is an inverse relationship between

Table 4. Ground contact time, flight time, step length, stride frequency and duty factor for the different groups

	Older adults		Young adults	
	Runners	Non-active	Runners	Non-active
Contact time (ms)	276±23	284±27	271±023	282±22
Flight time (ms)**	80±25	83±29	112±19	104±21
Step length (cm)*,‡	93.9±7.6	99.1±8.4	99.5±3.0	103.6±6.4
Stride frequency (Hz) **	1.41±0.10	1.38±0.13	1.31±0.08	1.28±0.07
Duty factor (%)**	38.9±3.1	38.8±3.3	35.5±2.3	36.7±2.6

Values are means ± S.D. of both legs; *N*=20 (older runners), *N*=10 (older non-active subjects), *N*=9 (younger runners), *N*=10 (younger non-active subjects).

Step length was defined as the anterior displacement of the foot (midpoint of the distance between calcaneus and metatarsal markers) from heel strike to contralateral heel strike.

Asterisks indicate statistically significant differences between older and young adults: \**P*<0.05, \*\**P*<0.01; ‡significant differences between runners and non-active individuals (*P*<0.05).

There was no age-by-running activity interaction for the analysed parameters (*P*>0.05).

Table 5. Centre of mass parameters for the different groups

	Older adults		Young adults	
	Runners	Non-active	Runners	Non-active
Anterior COM (cm)				
Displacement contact‡	73.6±6.1	78.1±6.7	67.3±10.4	74.3±12.3
Displacement flight*	19.0±6.4	22.1±8.6	26.6±8.9	25.3±9.7
Ratio displacement (%)**	79.6±6.2	78.3±6.9	71.4±4.8	75.3±6.9
Vertical COM (cm)				
Displacement stride)**	7.5±1.2	8.2±1.8	9.3±1.4	9.1±1.3

COM, centre of mass.

Values are means ± S.D. of both legs; *N*=20 (older runners), *N*=10 (older non-active subjects), *N*=9 (younger runners), *N*=10 (younger non-active subjects).

Ratio displacement was calculated as the proportion between anterior COM displacement during ground contact of both legs and anterior COM displacement during stride cycle.

Asterisks indicate statistically significant differences between older and young adults: \**P*<0.05, \*\**P*<0.01; ‡significant differences between runners and non-active individuals (*P*<0.05).

There was no age-by-running activity interaction for the analysed parameters (*P*>0.05).

the rate of energy used for steady state running and the rate of force generation applied to the ground to support the body weight during each stride (Kram and Taylor, 1990; Roberts et al., 1998; Wright and Weyand, 2001; Griffin et al., 2003). To calculate the rate of force generation ( $F_{\text{rate}}$ , in  $\text{N s}^{-1} \text{kg}^{-1}$ ) we divided the average vertical force per kg body weight ( $\bar{F}$ , in  $\text{N kg}^{-1}$ ) by the duration of the ground contact ( $t_{\text{contact}}$ , in s) according to Kram and Taylor (1990):

$$F_{\text{rate}} = \bar{F} / t_{\text{contact}} \quad (2)$$

(Note:  $\bar{F}$  and  $t_{\text{contact}}$  were calculated as mean values from both legs.)

The comparison of the rates of force generation revealed a significant (*P*=0.040) age effect, being lower in older adults than younger adults (Fig. 9). These values show that older adults generated about 9% less force per stride for a given running speed compared to younger adults. Additionally, to calculate the force generation per meter distance ( $F_{\text{trans}}$ ,

$\text{N m}^{-1} \text{kg}^{-1}$ ), we divided the average vertical GRF per kg body weight ( $\bar{F}$ ,  $\text{N kg}^{-1}$ ) by the anterior COM displacement during ground contact ( $L_{\text{contact}}^{\text{COM}}$ , in m) according to Kram and Taylor (1990) ( $L_{\text{contact}}^{\text{COM}}$  was calculated as the mean value from both legs). The results were the same as for the rate of force generation: older adults demonstrated a reduced (*P*=0.004) force generation per meter distance (Fig. 9). Furthermore, the integrals of the horizontal GRF during deceleration and acceleration phase were lower for the older adults compared to the younger adults. Chang and Kram (1999) provided evidence on that an increased generation of horizontal forces (deceleration and acceleration phase) during human running is accompanied by an increased metabolic cost. The above findings (higher duty factor, higher ratio displacement of the COM, lower rate of force generation, lower force generation per meter distance and lower integrals of the horizontal GRF during deceleration and acceleration phase) strongly suggest that older adults demonstrated an improvement in running

Table 6. Range of motion of the ankle, the knee and the limb angle during ground contact phase in degrees for the different groups

	Older adults		Young adults	
	Runners	Non-active	Runners	Non-active
Ankle ROM				
Dorsal in stance	22.7±6.4	25.4±8.6	25.8±5.5	21.2±5.5
Plantar in stance***‡	37.3±6.8	43.3±7.9	43.1±4.8	49.2±7.3
Knee ROM				
Flexion in stance	23.8±3.6	25.5±3.8	26.8±2.8	25.1±3.5
Extension in stance†	18.1±5.9	23.4±8.7	24.7±3.1	21.4±4.9
Limb angle				
Touch-down	-11.2±1.3	-11.8±1.9	-10.6±1.5	-10.8±1.0
Take-off***‡	26.7±2.2	28.6±2.2	24.1±1.4	26.6±1.6
Limb angle ROM (in stance)***‡	37.9±3.1	40.4±3.1	34.7±2.2	36.2±4.4

ROM, range of motion.

Values are means ± S.D. of both legs; *N*=20 (older runners), *N*=10 (older non-active subjects), *N*=9 (younger runners), *N*=10 (younger non-active subjects).

A negative limb angle is defined as posterior position of the COM relative to the midpoint of the foot in horizontal direction and a positive limb angle is defined as anterior position of the COM relative to the midpoint of the foot in horizontal direction.

Asterisks indicate statistically significant differences between older and young adults: \**P*<0.05, \*\**P*<0.01; ‡significant differences between runners and non-active individuals (*P*<0.05); †significant differences between runners and non-active individuals (*P*<0.01); †significant age-by-running activity interaction (*P*<0.05).

Table 7. Ground reaction force parameters for the different groups

	Older adults		Young adults	
	Runners	Non-active	Runners	Non-active
Vertical force (N kg <sup>-1</sup> )				
Maximum*	21.62±1.97	21.78±2.19	23.68±2.45	22.88±1.52
Average**	12.26±0.90	12.54±1.20	13.50±1.01	13.34±0.87
Impulse (N s kg <sup>-1</sup> )				
Vertical**	3.37±0.20	3.54±0.33	3.64±0.14	3.74±0.22
Horizontal deceleration***‡	-0.17±0.03	-0.20±0.04	-0.20±0.02	-0.21±0.03
Horizontal acceleration*‡	0.17±0.03	0.20±0.03	0.19±0.02	0.21±0.04

Values are means ± S.D. of both legs; *N*=20 (older runners), *N*=10 (older non-active subjects), *N*=9 (younger runners), *N*=10 (younger non-active subjects).

Asterisks indicate statistically significant differences between older and young adults: \**P*<0.05, \*\**P*<0.01; ‡significant differences between runners and non-active individuals (*P*<0.05).

There was no age-by-running activity interaction for the analysed parameters (*P*>0.05).

mechanics and increased the safety of their musculoskeletal system while running at a given speed compared to the young adults.

Independent of the above findings we observed an additional age-related strategy that might make running more advantageous and safe. Older adults increased the mechanical advantage (lower gear ratio) for the TS MTU from 26% to 58% of ground contact duration (phases 2 and 3) due to a lower moment arm of the GRF acting about the ankle joint. From experiments done on mammalian tissues, Ker et al. (1988) reported that for the majority of tendons the safety factor (ratio of rupture to functional stress) is about 8, but it is clearly lower for the Achilles tendon. In humans, the Achilles tendon has a

safety factor of about 2.4 during maximal isometric contraction (Magnusson et al., 2001). During the mid-part of the ground contact phase the vertical GRFs while running are high. Thus, the lower moment arm of the GRF acting about the ankle joint during these phases in the older adults might be a beneficial strategy to increase the safety factor of the Achilles tendon by reducing the magnitude of the mechanical load and stress applied to the tendon. The lower maximal ankle joint moment during ground contact in the older adults compared to the young adults strongly supports this suggestion, and results from the product of a reduced moment arm of the GRF acting about the ankle joint and lower GRFs. Thus, besides the lower rate of force generation and higher duty factor, older adults

Table 8. Maximal moment, and minimal and maximal mechanical power of the ankle and knee joint during ground contact for the different groups

	Older adults		Young adults	
	Runners	Non-active	Runners	Non-active
<b>Ankle</b>				
Max. moment (Nm kg <sup>-1</sup> )*	2.63±0.43	2.79±0.55	3.15±0.57	3.05±0.52
Min. power (W kg <sup>-1</sup> )	-8.78±2.90	-10.35±3.48	-12.11±4.00	-10.83±2.33
Max. power (W kg <sup>-1</sup> )**	8.33±2.48	9.54±2.71	10.55±1.93	12.02±2.88
<b>Knee</b>				
Max. moment (Nm kg <sup>-1</sup> )	1.66±0.45	1.88±0.47	1.81±0.37	1.85±0.31
Min. power (W kg <sup>-1</sup> )	-4.63±1.72	-5.91±2.24	-5.26±1.37	-5.70±1.39
Max. power (W kg <sup>-1</sup> )†	4.10±1.19	5.48±1.64	4.44±0.76	3.88±0.88

Values are means ± S.D. of both legs; N=20 (older runners), N=10 (older non-active subjects), N=9 (younger runners), N=10 (younger non-active subjects).

Asterisks indicate statistically significant differences between older and young adults: \**P*<0.05, \*\**P*<0.01; †significant age-by-running activity interaction (*P*<0.01).

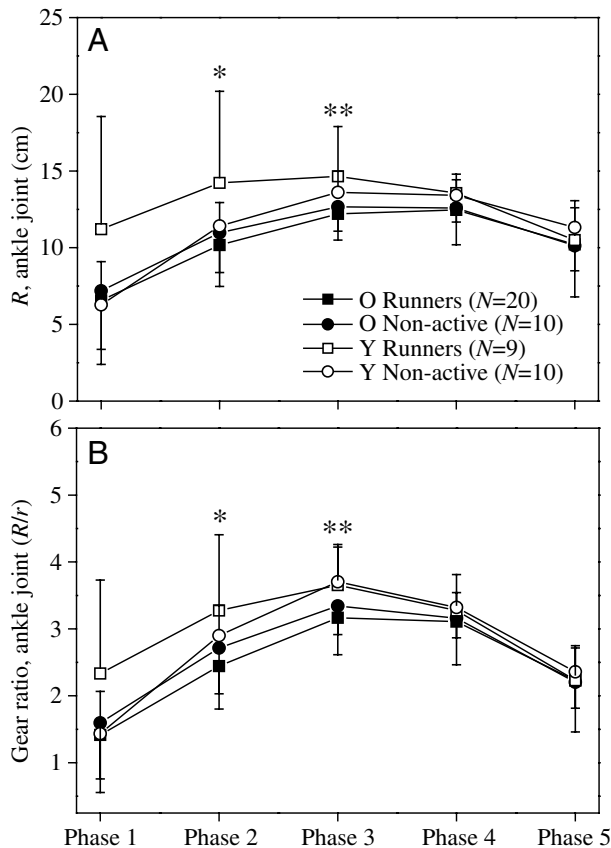


Fig. 7. (A) Moment arm of the ground reaction force (*R*) and (B) gear ratio (*R/r*) acting about the ankle joint during ground contact for the examined groups. Values are means ± S.D. of both legs. O, older adults; Y, young adults. (Phase 1, 10–26%; Phase 2, 26–42%; Phase 3, 42–58%; Phase 4, 58–74%; Phase 5, 74–90% of the period of ground contact). Asterisks indicate statistically significant differences between older and young adults: \**P*<0.05, \*\**P*<0.01; there was no age-by-running activity interaction for the analysed parameters (*P*>0.05).

improved running mechanics and the safety of their musculoskeletal system by increasing the mechanical advantage for the TS MTU during ground contact.

While the ankle joint kinetics altered in the older adults, no clear differences in knee joint kinetics were detected between age groups, even though the age-related decline in maximal joint moment during isometric MVC showed similar relative values at the ankle (25%) and knee joint (20%). A possible explanation could be the lower maximal knee joint moment compared to the maximal ankle joint moment (about 35%) during running and the higher knee extensor muscle strength compared to the plantar flexion muscles (about 60%) by the MVCs.

From a mechanical point of view the results confirm that the older adults adopted a more advantageous running strategy than younger adults, despite the general acceptance of the gradual decrease in the performance capacity of the nervous system with ageing (for a review, see Prince et al., 1997). It seems reasonable to believe that the nervous system of the older subjects was able to recalibrate its motor commands (the act of modifying their internal model that predicts the dynamic behaviour of the motor system) to cope with the running task. Running at submaximal velocities is a periodic (cyclic) motor task, and thus it is possible that the older adults, having had feedback from repeated practice, could update their running strategy and this way decrease the disparity between the reduced capacities of the MTUs and running effort. In the literature it is often reported that older adults show deficits in performing a strategic task but not at the adaptation level of a non-strategic task (McNay and Willingham, 1998; Fernández-Ruiz et al., 2000; Buch et al., 2003). The lower gear ratios at the ankle joint and the consequently increased mechanical advantage for the TS MTU in the older adults at the mid-part of ground contact phase, where the GRF is near its maximal value, support the idea that the observed improvement in the running mechanics is a consequence of proprioceptive feedback from repeated practice to adjust the running effort to the reduced capacity of the MTUs.

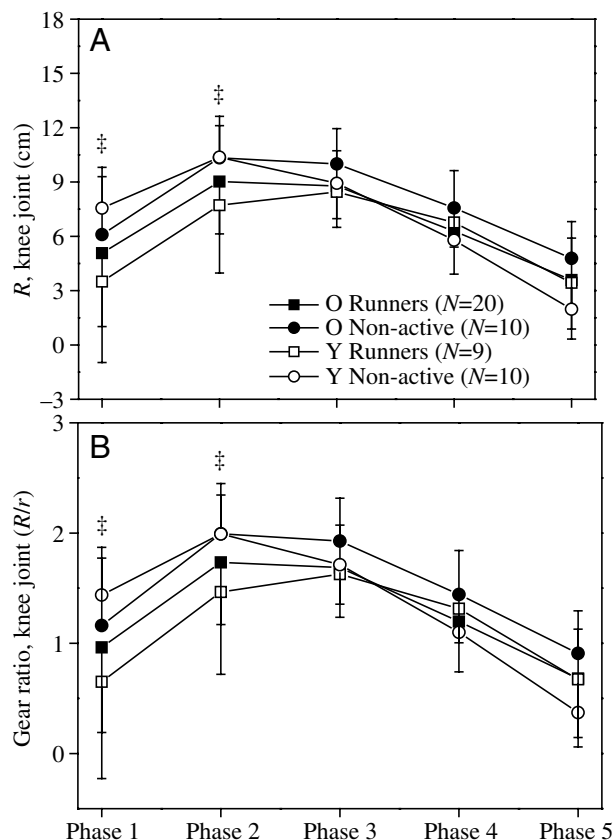


Fig. 8. (A) Moment arm of the ground reaction force ( $R$ ) and (B) gear ratio ( $R/r$ ) acting about the knee joint during ground contact for the examined groups. Values are means  $\pm$  S.D. of both legs. O, older adults; Y, young adults. (Phase 1, 10–26%; Phase 2, 26–42%; Phase 3, 42–58%; Phase 4, 58–74%; Phase 5, 74–90% of ground contact). ‡Significant differences between runners and non-active individuals ( $P < 0.05$ ); there was no age-by-running activity interaction for the analysed parameters ( $P > 0.05$ ).

It would be interesting to identify the main changes in the motor task characteristics leading to the improvement in running mechanics. The changes in the rate of force generation and force generation per meter distance were related to the lower vertical COM displacement during stride cycle, due to aging. A lower vertical COM displacement may also affect the gear ratios during the initial and mid-part of the contact phase, due to a better control of the impact dynamics. The lower maximum of the mechanical power at the ankle joint, and the higher limb angle at take-off for the older adults, seem to be the main causes for the lower vertical COM displacement. Mechanical power at the ankle joint and the limb angle at take-off are parameters located in the second part of the contact phase. The above observations provide evidence that the older adults plan the initial conditions for collision with the ground in the second part of the support phase. In other words, the older adults prepared for the next collision with the ground during the preceding stride, which might indicate a shift from proprioceptive feed-back to a predictive feed-forward running control strategy for the older adults.

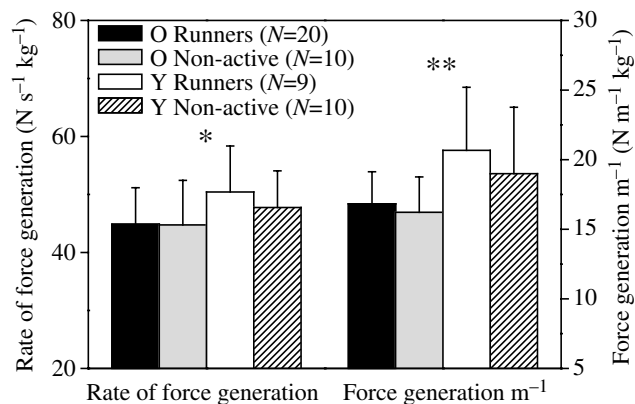


Fig. 9. Rate of force generation and force generation per meter distance during running ( $2.7 \text{ m s}^{-1}$ ) for the examined groups. Values are means  $\pm$  S.D. of both legs. O, older adults; Y, young adults. Asterisks indicate statistically significant differences between older and young adults: \* $P < 0.05$ , \*\* $P < 0.01$ ; there was no age-by-running activity interaction for the analysed parameters ( $P > 0.05$ ).

Based on the present results, however, it is difficult to explain why the non-active older adults (not practiced in running) showed the same changes in running characteristics as the older practiced runners. A possible explanation could be a transfer of motor adaptation from daily activities (e.g. walking) to running. In the literature, a transfer of motor adaptations to different conditions has been reported (van Hedel et al., 2002; Abeele and Bock, 2003; Lam and Dietz, 2004). Moreover the data from Bock (2005) confirmed that there is no evidence of any age-dependence of such transfer and that transfer is not degraded during aging. So, for example, our older adults displaying lower gear ratios at the ankle during running also showed lower gear ratios at the ankle joint during the initial and mid-part of the ground contact during walking (data not presented in this article).

#### Runners vs non-active subjects

The final purpose of this study was to examine the hypothesis that experienced runners would employ a task-specific adaptation in terms of higher advantages in running mechanics compared to non-active subjects, even at old age. The data supported this hypothesis. Although runners and non-active subjects had similar properties of the TS and QF MTUs, running experience decreased the gear ratios at the knee joint during the first 42% of the period of ground contact (phases 1 and 2) to the same extent in the young as in the older adults. This was due to a lower moment arm of the GRF acting about the knee joint. The lower gear ratios due to running activity did not affect the maximal knee joint moment because of its later occurrence during ground contact (at about 50%). However, the higher mechanical advantage for the QF MTU during the initial part of the ground contact indicates that endurance runners have an advantageous running strategy at the beginning of ground contact. A higher mechanical advantage during the initial running phase when an eccentric

QF contraction is necessary to control knee flexion and provide shock absorption, could increase the ability of the knee to attenuate shock and reduce the mechanical load on the knee joint. However, it is not likely that such changes in gear ratio would happen due to reactive corrections, because the available time is too short. Instead, it can be argued that runners use a predictive feed-forward running control strategy. Therefore, as for the older adults vs young adults, it can be suggested that the proprioceptive feed-back information from repeated practice is the mediator of predictive feed-forward motor commands.

Duty factor, ground contact duration, average vertical force and rate of force generation were not different between runners and non-active subjects (Fig. 9). Because the anterior COM displacement during ground contact was lower for active runners we expected force generation per meter distance to be different between runners and non-active individuals. However, no significant ( $P=0.299$ ) differences in the force generation per meter distance were noted between activity groups (Fig. 9). The intra-individual differences within groups might be too high and the effect of the reduced anterior COM displacement during ground contact too low to detect significant differences in the force generation per meter distance between runners and non-active subjects. However, endurance runners showed a lower horizontal impulse during deceleration and acceleration phase compared to the non-active subjects. Thus, besides the higher mechanical advantage at the knee joint during the initial part of the ground contact phase, the lower horizontal forces (deceleration and acceleration phase) in the experienced runners group is a further indicator of an improvement in running mechanics (Chang and Kram, 1999).

### Conclusions

In conclusion, our results show that the capacities of the TS and QF MTUs were reduced during aging. Further, the results suggest that chronic endurance-running exercise did not prevent this age-related degeneration nor provoke any further adaptational effects on the mechanical (tendon stiffness, muscle strength) or morphological (pennation angle, fascicle length, muscle thickness) properties of the high-load bearing MTUs studied in the young adults. However, running experience increases the mechanical advantage for the QF MTU (lower gear ratio at the knee joint) while running even at old age. Older adults react to the reduced capacity of their MTUs by increasing safety during running (higher duty factor, lower flight time) and benefit from a mechanical advantage for the TS MTU (lower gear ratio at the ankle joint), lower rate of force generation and force generation per meter distance. We suppose that the improvement in running mechanics in the older adults happens because of a perceptual motor recalibration and a feed-forward adaptation of the motor task aimed at decreasing the disparity between the reduced capacity of the MTUs and the running effort.

### List of abbreviations

COM	centre of mass
DF	duty factor
EMG	electromyography
$F_{\text{rate}}$	rate of force generation
$F_{\text{trans}}$	force generation per m distance
GL	gastrocnemius lateralis
GM	gastrocnemius medialis
GRF	ground reaction force
$L_{\text{contact,L}}^{\text{COM}}$	anterior COM displacement during ground contact of the left leg
$L_{\text{contact,R}}^{\text{COM}}$	anterior COM displacement during ground contact of the right leg
$L_{\text{stride}}^{\text{COM}}$	anterior COM displacement during stride cycle
MTU	muscle–tendon unit
MVC	maximal voluntary contraction
PCSA	physiological cross sectional area
QF	quadriceps femoris
$R$	moment arm of the GRF acting about a joint
$r$	tendon moment arm
$R/r$	gear ratio
RD	ratio displacement
RF	rectus femoris
RMS	root mean square
SO	soleus
$t_{\text{contact}}$	ground contact duration
TS	triceps surae
$t_{\text{stride}}$	stride duration
VL	vastus lateralis
VM	vastus medialis

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