Eur J Appl Physiol (2006) 98:284–298
DOI 10.1007/s00421-006-0277-7

ORIGINAL ARTICLE

Adaptational phenomena and mechanical responses during running: effect of surface, aging and task experience

Kiros Karamanidis · Adamantios Arampatzis · Gert-Peter Brüggemann

Accepted: 13 July 2006 / Published online: 25 August 2006

Abstract The goals of the study were to identify adaptational phenomena in running mechanics over a variety of surfaces due to age related changes in the muscle-tendon units (MTUs) capacities, to examine whether running experience is associated with adaptational effects on running mechanics over a variety of surfaces even at old age, and to investigate whether surface condition affects running mechanics. The investigation was executed on 30 old and 19 young including 29 runners and 20 non-active subjects. In a previous study we documented that the older had lower MTUs capacities. In the present study running mechanics were analysed as the same subjects ran at 2.7 m/s over three surfaces having different compliance. Surface condition did not affect centre of mass trajectory, duty factor or joint kinetics ($P > 0.01$). Older react to the reduced MTUs capacity by increasing duty factor and benefiting from a mechanical advantage for the triceps surae MTU and a lower rate of force generation on all surfaces ($P < 0.01$). Runners displayed lower average horizontal forces and a higher mechanical advantage for the quadriceps femoris MTU for all surfaces ($P < 0.01$). The results provided strong evidence on that running strategy remained essentially unchanged over a variety of surfaces. Adaptive improvements in running mechanics due to task experience were present for all surfaces and did not depend on age. We further concluded that older adults were able to recalibrate their running strategy to adjust the task effort to the reduced MTUs capacities in a feedforward control manner for a variety of mechanical environments.

K. Karamanidis · A. Arampatzis (✉) · G.-P. Brüggemann
Institute for Biomechanics and Orthopaedics,
German Sport University of Cologne,
Carl-Diem-Weg 6, 50933 Cologne, Germany
e-mail: Arampatzis@dshs-koeln.de

Keywords Mechanical environment · Locomotion · Running mechanics · Feedforward control · Recalibration

Introduction

In order to achieve functional locomotion, one must be able to execute the required motor actions over a variety of environmental demands one of which is the mechanical characteristics of the terrain (Ferris et al. 1998, 1999; Marigold and Patla 2002; Pai et al. 2003). A premier concern of the central nervous system is to control the musculoskeletal system by monitoring and interpreting visual, vestibular and proprioceptive information about the different mechanical environments (Patla et al. 1996; Patla 1997; Perry et al. 2001; Sorensen et al. 2002). In the literature it is well documented that the aging process is associated with a gradually decline of the performance capabilities of the cognitive (for a review, see Raz 2000), sensory (for a review, see Wolfson 2001) and musculoskeletal (for a review, see Schultz 1992) system. For example, ankle plantarflexion and knee extension strength decline by up to 3% per year beyond the fifth decade (Aniansson et al. 1986; Frontera et al. 1991; Winegard et al. 1996; Hughes et al. 2001). The age related degeneration of the neural (Stelmach and Worringham 1985; Woollacott et al. 1986; Mulder et al. 2002) and musculoskeletal (Wolfson et al. 1995; DeVita and Hortobagyi 2000; Pavol et al. 2002; Hortobagyi et al. 2003) systems are frequently described as limiting factors for older individuals to execute the required motor responses during different environmental demands. This is especially valid for conditions without prior experience or knowledge of the task (Marigold and Patla 2002; Pavol et al. 2002; van Hedel and Dietz 2004) induced by external (e.g. slippery surface: Pavol et al. 2002) or internal (e.g. restricted vision: van Hedel and Dietz 2004) changes.

The human neuro-motor system can adapt to internal and external changes using sensory feedback information until sensory inputs and motor outputs are again in register (Wolpert et al. 1995; Kagerer et al. 1997; McNay and Willingham 1998; Pai et al. 2003; Shadmehr 2004). As the novel condition is adapted the central nervous system ‘‘knows’’ what to expect and humans can select and execute an appropriate motor action in a feedforward control (Owings et al. 2001; Pai et al. 2003). Moreover, animal (Diamond et al. 1985; Ferchmin and Etorovic 1986) and human (DeVita and Hortobagyi 2000; Erni and Dietz 2001; Pavol et al. 2002; Pai et al. 2003; van Hedel and Dietz 2004) studies revealed that the plasticity of the neural system, which allows the sensorimotor system to adapt to external or internal changes, persist throughout life. For instance, older individuals are able to shift function from weakened muscle groups to those with better function during walking (DeVita and Hortobagyi 2000). Furthermore, humans are able to adjust their leg mechanics to compensate changes in running surface stiffness (Ferris and Farley 1997; Ferris et al. 1998, 1999; Farley et al. 1998). These adjustments in leg mechanics occur rapidly (Ferris et al. 1999) and allow the human system to move in a similar manner despite of large changes in the environmental surface (Ferris and Farley 1997; Ferris et al. 1998, 1999; Farley et al. 1998). Thus, it is reasonable to hypothesize that older adults will reorganize their running strategy in response to the reduced capacities of their musculoskeletal system (internal changes). Moreover, we hypothesized that older adults will show a similar behaviour over a variety of mechanical environments demonstrating a complete running task adaptation. This hypothesis is supported by the fact that older adults 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).

In the literature it is widely accepted that experience or repeated practice causes a task specific adaptation in young (Erni and Dietz 2001; Owings et al. 2001) and older adults (Pavol et al. 2002; Pai et al. 2003; van Hedel and Dietz 2004). From a mechanical point of view, most of those studies reported an improvement in locomotion characteristics and safety for both age groups (Pavol et al. 2002; Pai et al. 2003; van Hedel and Dietz 2004). For instance, repeated slip exposure improved the stability of the centre of mass state (i.e. its velocity and position) with respect to the base of support among older adults (Pai et al. 2003). Chronic exposure to repetitive loading while running increases the risk of injury of the musculoskeletal system such as the structures surrounding the knee joint (Messier et al. 1991; Nigg et al. 1993). In general, a certain magnitude of mechanical load is tolerated and even needed for the mechanical adaptation of the musculoskeletal system (for a review, see Kjaer 2004). However, when the magnitude of the mechanical load exceeds a certain threshold, the biological system will change it is motor task execution (DeVita et al. 1992; DeVita 1994; DeVita and Hortobagyi 2000; Hortobagyi et al. 2003). In other words, the biological system is flexible and enables humans to change their locomotion strategy, obviously depending on their capacities of the musculoskeletal system and on the functional demand of the task. Therefore, it is reasonable to hypothesize that experienced runners will show a mechanical improvement in running task execution (e.g. higher safety of the musculoskeletal system, higher effectiveness of muscle force generation) over a variety of surface conditions independent of their age.

Several studies reported that small environmental changes (e.g. surface or texture of the footwear) can influence the sensory feedback from the feet during gait (Watanabe and Okubo 1981; Nurse et al. 2005). Dixon and co-workers (Dixon et al. 2000) have reported that small alterations in the mechanical properties of running surface (asphalt surface, acrylic sports surface, rubber-modified asphalt surface) can induce changes in human running characteristics. Further, they showed that running motor patterns can vary considerably between individuals due to alteration in surface condition. This happened even though they examined a homogenous subject group comprising young experienced runners (Dixon et al. 2000). Based on the above literature, therefore, we can not obviously conclude whether realistic changes in running surface stiffness influence human running mechanics across age or activity levels.

In a previous study (Karamanidis and Arampatzis 2006) we showed that older subjects had lower capacities of their muscle-tendon units (MTUs) in the lower extremity: between 20 and 25% lower muscle strength at the triceps surae and quadriceps femoris, and lower stiffness of the quadriceps femoris tendon and aponeurosis. Runners and non-active subjects revealed no differences in the mechanical (maximal joint moment, tendon stiffness) or morphological (muscle thickness, pennation angle, fascicle length) properties of the triceps surae and quadriceps femoris MTUs independent subjects age (Karamanidis and Arampatzis 2006). In the present study we analysed running mechanics while running on surfaces of different stiffness at a given speed (2.7 m/s) using the same individuals. The goals of the present work were (a) to identify adaptational phenomena in running mechanics over a variety of surfaces due to age related changes in the capacities of the MTUs in the lower limbs, (b) to examine whether running experience is associated with adaptational effects on running mechanics over a variety of surfaces even at old age, and finally (c) we wanted to investigate whether surface condition affects running mechanics.

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. 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 per week. The criterion for entering the non-active group was no sport-activity at all except at school.

Measurement of running characteristics

The ground reaction force (GRF) (1,080 Hz) and the kinematic data were recorded using the Vicon system (624 system, UK, 12 cameras operating at 120 Hz) as the subjects ran barefoot at 2.7 m/s on a 16 m track with two force platforms (60 cm × 90 cm, Kistler, Winterthur, Switzerland). Barefoot running was chosen to exclude any effects of running shoe on the running characteristics and allowed the controlled variation of surface stiffness by the impacting interface. 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 examined older runners. 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 m/s). Subjects could perform as many practice trial as they required (typically 2–3). The running velocity was indicated by a customized 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 (~50 cm) over the whole track and both right and left touchdowns were centred on the corresponding force platforms. In addition to the normal foot floor (inextensible multiplex material) we used two types of foam to create three different conditions. We cut sections of foam to match the surface area of the force platforms so that the foam surface did not transmit any force off the force platforms. During running trials surface material covered the entire running track. The non-compliant "hard" surface had a stiffness of more than 2,000 kN/m, the "medium" foam (running shoe material "EVA") had a stiffness of 724.56 kN/m and the most compliant "soft" foam (gymnastic mats for children) had a stiffness of 457.94 kN/m. The stiffness of the running surfaces were calculated from the force versus displacement relation between 50 and 100% of the maximal force as determined by a material-testing machine (Zwick, Roell Amsler, Germany; max. force 2,000 N; loading area 5 cm^2; loading velocity 8 mm/s). The thickness of the soft and medium surfaces was 20 mm. The force (2,000 N) was chosen as it is the maximal vertical ground reaction force reported in the literature for the corresponding running velocity (Arampatzis et al. 1999) and body mass of the subjects. Range of surface stiffness was chosen as these values provide a realistic running condition and therefore highlights the interaction between human system and environmental changes usually encountered in daily life.

Three valid trials were recorded and analysed for each subject and surface. The different surface conditions were applied in random order. The subjects had a 1–4 min rest between trials and conditions. 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 recorded by the Vicon system and 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 caput 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° knee joint angle. The tibia being perpendicular to the ground while having the foot flat on it was defined as 90° ankle joint. The linear horizontal and vertical centre of mass (COM) trajectory was calculated using the kinematic data of the subjects. The limb angle was defined as the angle between the line connecting the COM and the midpoint of the foot, calculated from the calcaneal 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 duty factor (DF) was calculated as the proportion between ground contact duration (t_{Contact}) and stride duration (t_{Stride}) according to McMahon et al. (1985) (t_{Contact} was calculated as the mean value from both legs). In order to examine the proportion of the COM transport during one stride cycle whilst the subjects have contact with the ground, we calculated the ratio between anterior COM displacement during ground contact of the left $\left(L^{\text{COM}}_{\text{Contact, Li}}\right)$ and right $\left(L^{\text{COM}}_{\text{Contact, Re}}\right)$ legs and anterior COM displacement during stride cycle $\left(L^{\text{COM}}_{\text{Stride}}\right)$. This was called ratio displacement ($\text{Ratio}_{\text{displ}}$):

$$\text{Ratio}_{\text{displ}} = \frac{L^{\text{COM}}_{\text{Contact, Li}} + L^{\text{COM}}_{\text{Contact, Re}}}{L^{\text{COM}}_{\text{Stride}}}.$$

(Note: A whole stride cycle was defined 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. Further, to calculate the rate of force generation (F_{Rate}, in N/s kg) we divided the average vertical force per kg body mass $\left(\bar{F}, \text{ in N/kg}\right)$ by the duration of the ground contact (t_{Contact}, in s) according to Kram and Taylor (1990):

$$F_{\text{Rate}} = \frac{\bar{F}}{t_{\text{Contact}}}.$$

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

The joint moments of the left and right knee and ankle joint were calculated through inverse dynamics (see: Hof 1992; Arampatzis et al. 1999). We used the Plug-in-Gait model (Oxford Metrics, Oxford, UK) to obtain joint moments calculated about an orthogonal axis system located in the distal segment of a joint. Centre of pressure under the foot during stance phase was calculated from the ground reaction forces. For the calculation of running mechanics we included the relative thin surface thickness (20 mm for the soft and medium surface). This procedure allowed us to limit possible bending moments at the force plate during stance phase and hence provided an accurate estimation of the centre of pressure on the force plate for the different surface foams.

The mean values of both legs were used for further analysis. The gear ratios of the triceps surae and the quadriceps femoris 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 mean values of both legs were used for the statistical analysis. The gear ratio and the moment arm was 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. For all subjects, surfaces 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 previous studies and were reasonably high (Karamanidis et al. 2003, 2004).

Statistics

We used a mixed three-factor [age (young/old) × running activity (endurance runners/non-active) × surface (hard/medium/soft)] analysis of variance (ANOVA) to detect group and surface differences in running characteristics. All significant age-by-running activity, age-by-surface, running activity-by-surface and age-by-running activity-by-surface interactions are reported. When a significant surface effect (hard/medium/soft) or interaction (age-by-running activity, age-by-surface, running activity-by-surface and age-by-running activity-by-surface) was present a post hoc test (Bonferroni) was conducted in order to determine where these differences occurred. Due to the excessive number of statistical comparisons to control for family-wise errors across the analysis, the results were considered significant at the level of $P < 0.01$. All results in the tables and figures are presented as means and standard deviation (SD).

Results

Kinematic characteristics

The anthropometric data of all subjects-groups are provided in Table 1. Body height ($P = 0.003$) was significantly lower for the old compared to the young adults which was on average less than 5 cm. When running at the same speed as young adults, older adults displayed a significantly ($P < 0.01$) lower flight time duration, lower step length, lower vertical COM displacement during the stride cycle, lower amplitude of ankle plantarflexion and knee extension angle during ground contact and higher limb angle at take off compared to the young adults (Tables 2, 3). Further, the duty factor and the ratio displacement of the COM were significantly ($P < 0.01$) higher for the older as compared to the young adults (Table 2). Runners exhibited a significantly ($P < 0.01$) lower ground contact time duration, lower step length, lower amplitude of ankle plantarflexion angle during ground contact and lower limb angle at take off compared to the non-active group (Tables 2, 3). The comparison between surface conditions revealed no significant ($P > 0.01$) surface effect on the analysed temporal parameters (contact and flight time duration, and duty factor), COM trajectory parameters (vertical displacement and ratio displacement) or on sagittal joint angular kinematics (limb angle and knee joint) during ground contact (Tables 2, 3). Ground surface significantly affected ($P < 0.01$) the amplitude of ankle dorsal flexion angle during ground contact (Table 3). The post hoc analysis revealed significantly ($P < 0.01$) lower values for the soft surface compared to the hard and medium surfaces (Table 3). There was a significant ($P < 0.01$) age-by-running activity interaction at the amplitude of knee extension angle during ground contact (Table 3). The post hoc analysis revealed significantly ($P < 0.01$) lower amplitudes of knee extension angle during ground contact for the older runners compared to all other groups (older and young non-active subjects and young runners).

Table 1 Anthropometric data of the subjects (means ± SD)

	Older adults		Young adults	
	Runners	N-active	Runners	N-active
Age (year)	64 ± 3	64 ± 2	27 ± 4	29 ± 3
Body mass (kg)	76 ± 6	81 ± 6	73 ± 5	78 ± 8
Body height (cm)*	176 ± 4	174 ± 8	180 ± 4	180 ± 9

N-active non-active adults

*Statistically significant differences between older and young adults ($P < 0.01$)

Kinetic characteristics

Figures 1, 2 and 3 illustrate the vertical and antero-posterior horizontal GRFs, joint moments and mechanical power at the ankle and knee of the left leg during running on surfaces of different stiffness for all examined groups. For the GRF parameters the average and the maximal values of the vertical force as well as the average values of the horizontal (deceleration and acceleration phases) force were lower ($P < 0.01$) for the older compared to the young adults (Table 4). Further, older adults showed a lower ($P < 0.01$) rate of force generation during the ground contact phase compared to young adults (Table 4). Age-related effects on joint kinetics were identified at the ankle joint with virtually no differences ($P > 0.01$) at the knee joint (Table 4). The older adults showed a significantly ($P < 0.01$) lower maximal ankle joint moment and positive mechanical power at the ankle joint during ground contact as the young adults (Table 4). The comparison between runners and non-active subjects showed that runners had significantly ($P < 0.01$) lower average horizontal forces (deceleration and acceleration phases) and lower positive mechanical power at the ankle joint during ground contact phase (Table 4). The statistical analysis showed also a lower ($P < 0.01$) positive mechanical power at the knee joint during ground contact phase for the runners compared to the non-active group (Table 4). However, there was a

Table 2 Ground contact time, flight time, step length, vertical centre of mass (COM) displacement during stride (Vert $COM_{dis\ stride}$), duty factor and ratio COM displacement (Ratio COM_{dis}) for the examined groups while running (2.7 m/s) on different surfaces (means ± SD of both legs)

	Hard				Medium				Soft			
	Older adults		Young adults		Older adults		Young adults		Older adults		Young adults	
	Runners	N-active	Runners	N-active	Runners	N-active	Runners	N-active	Runners	N-active	Runners	N-active
Contact time (ms)**	276 ± 23	284 ± 27	271 ± 23	287 ± 27	277 ± 23	279 ± 21	266 ± 23	289 ± 28	280 ± 21	295 ± 21	278 ± 29	296 ± 28
Flight time (ms)*	80 ± 25	83 ± 29	112 ± 19	104 ± 21	81 ± 25	86 ± 24	117 ± 20	106 ± 29	78 ± 21	81 ± 34	114 ± 23	106 ± 20
Step length (cm)*,**	93.9 ± 7.6	99.1 ± 8.4	99.5 ± 3.0	103.6 ± 6.4	92.0 ± 11.8	97.7 ± 9.9	98.8 ± 4.8	104.2 ± 7.0	94.1 ± 7.2	101.7 ± 8.9	98.5 ± 7.1	106.3 ± 7.4
Vert $COM_{dis\ stride}$ (cm)*	7.5 ± 1.2	8.2 ± 1.8	9.3 ± 1.4	9.1 ± 1.3	7.5 ± 1.3	8.0 ± 1.6	8.5 ± 2.2	9.6 ± 1.6	7.6 ± 1.3	7.5 ± 1.0	9.6 ± 1.4	10.1 ± 1.6
Duty factor (%)*	38.9 ± 3.1	38.8 ± 3.3	35.5 ± 2.3	36.7 ± 2.6	38.8 ± 3.1	38.3 ± 2.7	34.7 ± 2.6	36.7 ± 3.4	39.2 ± 2.7	39.5 ± 3.9	35.4 ± 2.9	36.8 ± 2.4
Ratio COM_{dis} (%)*	79.6 ± 6.2	78.3 ± 6.9	71.4 ± 4.8	75.3 ± 6.9	79.2 ± 6.3	77.4 ± 5.5	70.1 ± 5.6	73.8 ± 7.6	79.6 ± 5.7	81.6 ± 6.0	71.4 ± 6.1	74.2 ± 5.0

N-active non-active adults

* Statistically significant differences between older and young adults ($P < 0.01$)

** Statistically significant differences between runners and non-active individuals ($P < 0.01$)

significant ($P < 0.01$) age-by-running activity interaction for the positive mechanical power at the knee joint during ground contact (Table 4) and the post hoc analysis revealed significantly ($P < 0.01$) higher values during ground contact only for the older non-active subjects compared to all other groups (older and young runners and young non-active subjects). Running on surfaces of different stiffness had no significant ($P > 0.01$) effect on the analysed GRF parameters, joint moments or mechanical power at the ankle and knee joint (Table 4).

Regarding the gear ratio at the ankle joint older adults showed significantly lower ($P < 0.01$) values from 26 to 58% of the ground contact duration (Phases 2, 3) compared to the young adults (Fig. 4). This was due to a lower moment arm of the GRF acting about the ankle joint during the Phases 2–4 (Fig. 4). Conversely, no significant differences between runners and non-active subjects were detected in the gear ratio or moment arm of the GRF at the ankle joint ($P > 0.01$). Running on surfaces of different stiffness significantly ($P < 0.01$) affected the moment arm of the GRF acting about the ankle joint and the gear ratio at the ankle joint from 42 to 58% (Phase 3) of the ground contact duration (Fig. 4). The post hoc analysis revealed a significantly lower ($P < 0.01$) moment arm of the GRF acting about the ankle joint as well as a lower gear ratio for the soft surface compared to the hard surface for Phase 3. Concerning the gear ratio at the knee joint and the moment arm of the GRF acting about the knee no significant ($P > 0.01$) differences between age groups or surface conditions were found (Fig. 5). Runners demonstrated a significantly ($P < 0.01$) lower gear ratio at the knee joint from 10 to 58% of the ground contact duration (Phases 1–3) in comparison to the non-active group (Fig. 5). This was due to a lower moment arm of the GRF acting about the knee joint during these phases (Fig. 5).

Discussion

Running task reorganisation due to aging

A previous analysis of the same subjects (Karamanidis and Arampatzis 2006) found that the examined older adults had lower capacities of their triceps surae and quadriceps femoris MTUs (between 20 and 25% lower muscle strength and lower tendon stiffness) compared to the examined young adults. The present study analysed running mechanics of the older and young adults while running on surfaces of different stiffness at a given speed (2.7 m/s). We hypothesized that older

Table 3 Range of motion (ROM) of the ankle (A) and the knee (K) joints, and the limb angle (L) during ground contact phase in degrees for the examined groups while running (2.7 m/s) on different surfaces (means ± SD of both legs)

	Hard				Medium				Soft			
	Older adults		Young adults		Older adults		Young adults		Older adults		Young adults	
	Runners	N-active	Runners	N-active	Runners	N-active	Runners	N-active	Runners	N-active	Runners	N-active
$A_{\mathrm{ROM\ dorsal\ in\ stance}}$ ***	22.7 ± 6.4	25.4 ± 8.6	25.8 ± 5.5	21.2 ± 5.5	22.5 ± 6.5	24.7 ± 9.0	25.3 ± 5.3	22.0 ± 6.4	18.3 ± 6.1	17.8 ± 4.7	21.5 ± 5.1	17.4 ± 3.1
$A_{\mathrm{ROM\ plantar\ in\ stance}}$ *,**	37.3 ± 6.8	43.3 ± 7.9	43.1 ± 4.8	49.2 ± 7.3	36.8 ± 6.4	42.0 ± 6.1	40.9 ± 5.7	49.4 ± 5.3	35.9 ± 6.2	41.4 ± 4.5	42.0 ± 4.0	49.1 ± 7.0
$K_{\mathrm{ROM\ flexion\ in\ stance}}$	23.8 ± 3.6	25.5 ± 3.8	26.8 ± 2.8	25.1 ± 3.5	23.8 ± 3.3	25.5 ± 3.4	26.7 ± 2.1	25.5 ± 3.0	24.5 ± 3.9	26.9 ± 2.9	26.5 ± 2.6	27.7 ± 4.7
$K_{\mathrm{ROM\ extension\ in\ stance}}$ *,†	18.1 ± 5.9	23.4 ± 8.7	24.7 ± 3.1	21.4 ± 4.9	18.6 ± 6.0	21.9 ± 10.5	24.1 ± 2.7	22.1 ± 6.6	17.0 ± 5.8	21.7 ± 9.5	23.5 ± 3.4	23.3 ± 6.0
$L_{\mathrm{touch\ down}}$	−11.2 ± 1.3	−11.8 ± 1.9	−10.6 ± 1.5	−10.8 ± 0.9	−11.2 ± 1.5	−11.8 ± 1.4	−10.7 ± 1.4	−11.1 ± 1.5	−11.5 ± 1.4	−13.0 ± 1.6	−10.5 ± 1.8	−11.4 ± 1.4
$L_{\mathrm{take\ off}}$ *,**	26.7 ± 2.2	28.6 ± 2.2	24.1 ± 1.4	26.6 ± 1.6	26.8 ± 2.3	27.9 ± 2.2	23.2 ± 1.7	26.6 ± 1.6	26.5 ± 1.8	28.3 ± 2.0	23.8 ± 1.7	27.2 ± 1.4

A negative limb angle is defined as posterior position of the centre of mass relative to the midpoint of the foot in the sagittal plane and a positive limb angle is defined as anterior position of the centre of mass relative to the midpoint of the foot in the sagittal plane

N-active non-active adults

* Statistically significant differences between older and young adults ($P < 0.01$)

** Statistically significant differences between runners and non-active individuals ($P < 0.01$)

*** Statistically significant ground surface effect ($P < 0.01$)

† Statistically significant age-by-running activity interaction ($P < 0.01$)

individuals would reorganize their running task over a variety of mechanical environments as a consequence of the changes in their MTUs. The present data confirm this hypothesis. When running at the same speed as young adults, older adults selected a different strategy leading to increased safety of the musculoskeletal system (higher duty factor) and benefiting from a mechanical advantage for the triceps surae MTU and a lower rate of force generation on all surfaces.

In the literature it is often reported that the performance capacities of the neural system decrease with aging (for a review, see: Prince et al. 1997; Raz 2000; Wolfson 2001). For instance, the age related decline in peripheral sensory feedback mechanisms, restrict older subjects to improve the accuracy of performance without visual information in a similar way as for the young subjects (van Hedel and Dietz 2004). However, the results of the present study confirm that older adults had more advantageous running mechanics than young adults (lower rate of force generation, lower average horizontal forces during deceleration and acceleration phases, lower gear ratios for the triceps surae MTU). Furthermore, the higher duty factor and ratio displacement of the COM for the older adults (higher amount of COM transport and time with the foot on the ground during stride cycle) are indicators for a higher safety of their musculoskeletal system while running at a given speed in comparison to the young adults. Moreover, the improved running mechanics and safety for the older adults was present for all surface conditions. Thus, the findings show that the functional changes in running strategy (mechanical improvement) in the older adults are stable for different mechanical environments.

Older adults increased the mechanical advantage (lower gear ratios) for the triceps surae from 26 to 58% of the ground contact phase (Phases 2, 3) by means of lowering the moment arm of the GRF acting about the ankle joint. During the mid-part of the ground contact phase the vertical GRF achieves its maximum value. The lower gear ratio at the ankle joint (Phase 3) together with the lower vertical GRF for the older adults are the reason for the lower maximal moment at the ankle joint during ground contact for the older adults compared to the young adults whilst running at the same velocity. The reduction of the maximal moment at the ankle joint for the older adults compared to the young adults was on average about 20%. The relative decrease of the maximal moment at the ankle joint during running is very close to the relative decrease of the maximal plantarflexion moment during isometric contractions found for the older adults compared to

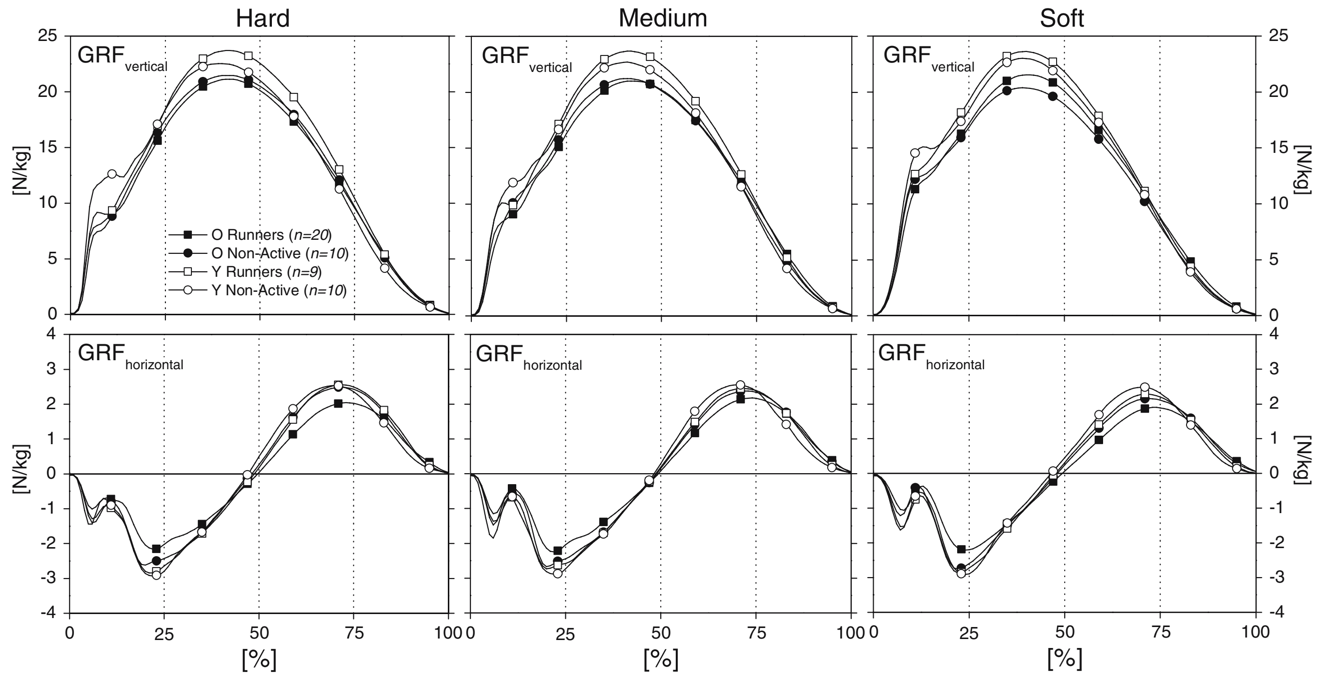

Fig. 1 Average values of the vertical and horizontal ground reaction force (*GRF*) during running (2.7 m/s) on different surfaces for the examined groups (means). *O* older adults; *Y* young adults. The *x*-axis was normalised as follows: 0–100% ground contact duration

the young adults (about 25%; Karamanidis and Arampatzis 2006). These findings suggest that the compensatory changes in the ankle kinetics aim to decrease the discrepancy between the running effort and MTU capacities. Running is a periodic non-strategic motor task and thus, it is possible that the older adults could update their running strategy and adjust the running effort to the reduced MTUs capacities by means of repeated practice. Although significant, the lower moment arm of the GRF during Phase 4 (58–

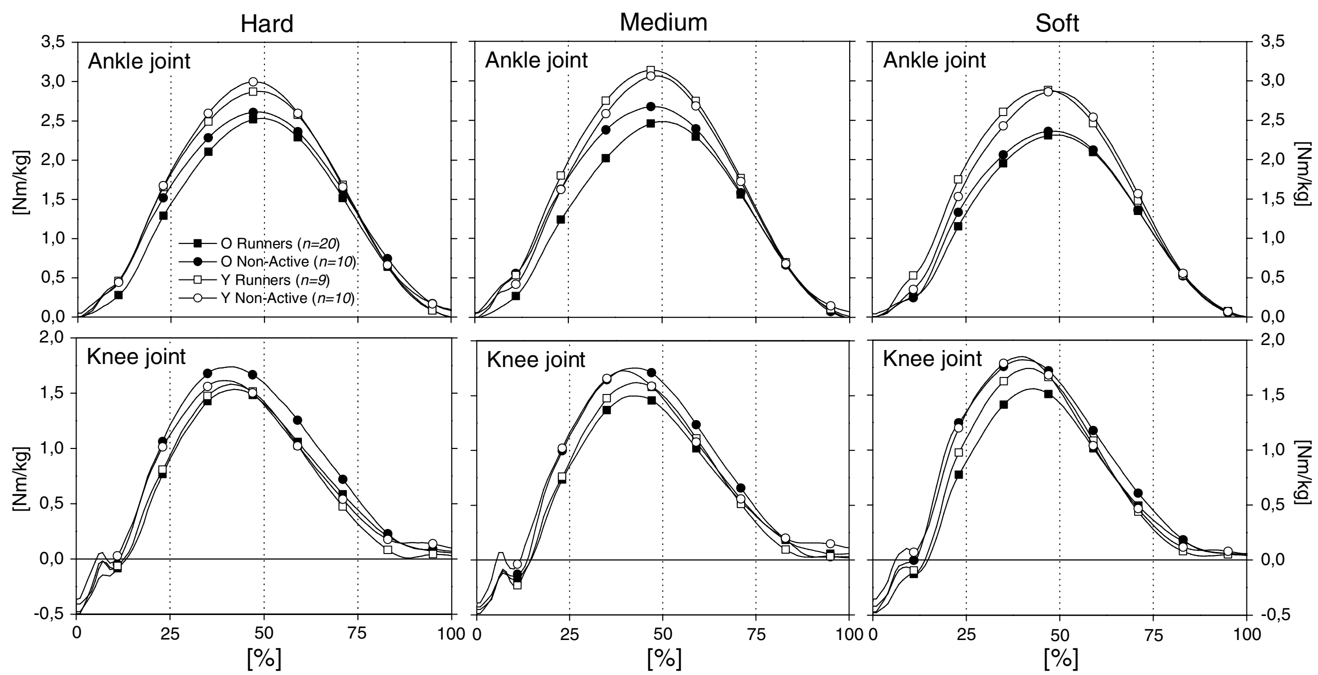

Fig. 2 Average values of the sagittal plane joint moment at the ankle and knee joint during running (2.7 m/s) on different surfaces for the examined groups (means). *O* older adults; *Y* young adults. The *x*-axis was normalised as follows: 0–100% ground contact duration

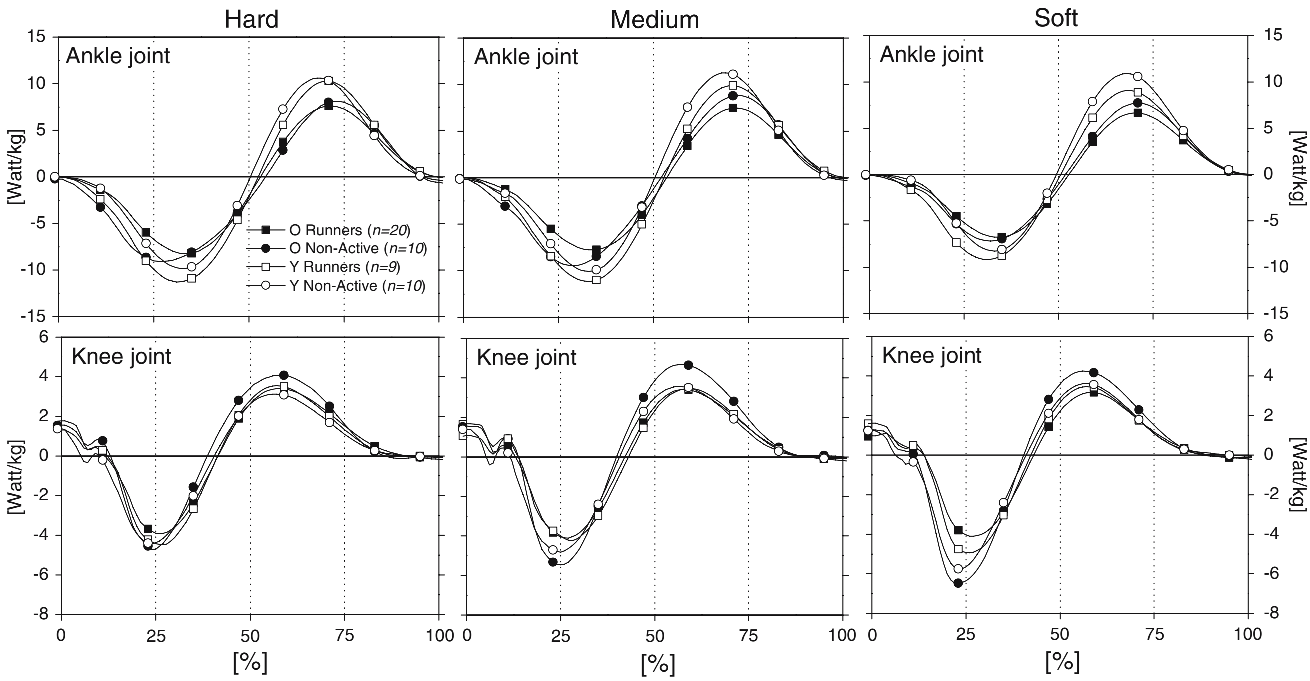

Fig. 3 Average values of the mechanical power at the ankle and knee joint during running (2.7 m/s) on different surfaces for the examined groups (means). *O* older adults; *Y* young adults. The *x*-axis was normalised as follows: 0–100% ground contact duration

74% of the ground contact phase) in the older adults had only a slight effect on the differences in the gear ratio ($P = 0.064$) between age groups during this period. The relative differences in the moment arm of the GRF between age groups might be to low (about 6%) to detect clear changes in the gear ratio.

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 were related to the lower vertical COM displacement during stride cycle for the older adults. A lower vertical COM displacement may also affect the gear ratios during the initial and mid-part of the ground 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. All these changes in running characteristics due to age are observed in the second part of the ground contact phase. The above observations provide evidence that older adults plan the initial conditions for the 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. This phenomenon was again independent from the surface condition. Therefore, the results show that the older subjects were able to recalibrate their running strategy with a mechanical improvement by means of a feedforward adaptation of the motor commands independently of the mechanical environment.

While the ankle joint kinetics were altered in the older adults, no clear differences in knee joint kinetics were detected between age groups. This happened even though the age related decline in maximal joint moment during isometric MVC showed similar relative values at the ankle (about 25%) and knee joint (about 20%; Karamanidis and Arampatzis 2006). 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%; Karamanidis and Arampatzis 2006) at MVC. So it is possible that the threshold for triggering a compensation is not achieved for the knee joint, and the disparity between running effort and reduced quadriceps femoris MTU capacities can be tolerated during submaximal running. One might argue that the choice of running velocity (we used 2.7 m/s which was the preferred running velocity of the older runners) might have influenced our age-related findings because preferred running velocity of younger subjects is usually higher than 2.7 m/s (about 3.6 m/s, Biewener et al. 2004). Based on the data presented by Biewener et al. (2004), however, we do not have evi-

Table 4 Ground reaction force (F) parameters (N/kg) and rate of force generation (N/s·kg), maximal joint moments (Nm/kg) and maximal mechanical power (W/kg) at the ankle ($A_{\text{max Moment}}$, $A_{\text{max Power}}$) and knee ($K_{\text{max Moment}}$, $K_{\text{max Power}}$) joint during ground contact for the examined groups while running (2.7 m/s) on different surfaces (means ± SD of both legs)

	Hard				Medium				Soft			
	Older adults		Young adults		Older adults		Young adults		Older adults		Young adults	
	Runners	N-active	Runners	N-active	Runners	N-active	Runners	N-active	Runners	N-active	Runners	N-active
$F_{\text{max vertical}}$ *	21.62 ± 1.97	21.78 ± 2.19	23.68 ± 2.45	22.88 ± 1.52	21.57 ± 2.11	21.77 ± 2.54	24.06 ± 2.61	23.03 ± 1.78	21.75 ± 1.93	20.46 ± 3.10	23.74 ± 3.15	23.34 ± 1.37
$F_{\text{average vertical}}$ *	12.26 ± 0.90	12.54 ± 1.20	13.50 ± 1.01	13.34 ± 0.87	12.29 ± 1.01	12.54 ± 1.17	13.80 ± 1.03	13.27 ± 1.23	12.26 ± 0.83	12.10 ± 1.37	13.50 ± 1.32	13.18 ± 1.04
$F_{\text{average horiz decel}}$ *,**	–1.23 ± 0.22	–1.39 ± 0.24	–1.46 ± 0.15	–1.57 ± 0.28	–1.18 ± 0.27	–1.39 ± 0.27	–1.40 ± 0.25	–1.48 ± 0.36	–1.24 ± 0.21	–1.38 ± 0.21	–1.39 ± 0.28	–1.46 ± 0.21
$F_{\text{average horiz accel}}$ *,**	1.24 ± 0.18	1.40 ± 0.18	1.41 ± 0.22	1.48 ± 0.23	1.29 ± 0.23	1.42 ± 0.22	1.37 ± 0.20	1.52 ± 0.24	1.20 ± 0.19	1.23 ± 0.15	1.28 ± 0.23	1.47 ± 0.18
$\text{Rate}_{\text{of F generation}}$ *	44.84 ± 6.32	44.76 ± 7.67	50.41 ± 7.95	47.76 ± 6.31	44.90 ± 6.69	45.28 ± 6.83	52.58 ± 8.34	47.22 ± 8.38	44.09 ± 5.76	41.46 ± 7.54	49.50 ± 9.75	45.74 ± 7.20
$A_{\text{max Moment}}$ *	2.63 ± 0.43	2.79 ± 0.55	3.15 ± 0.57	3.05 ± 0.52	2.57 ± 0.53	2.67 ± 0.63	3.19 ± 0.60	3.17 ± 0.53	2.40 ± 0.51	2.40 ± 0.52	2.96 ± 0.67	2.91 ± 0.52
$K_{\text{max Moment}}$	1.66 ± 0.45	1.88 ± 0.47	1.81 ± 0.37	1.85 ± 0.31	1.68 ± 0.37	2.02 ± 0.54	1.75 ± 0.38	1.99 ± 0.34	1.72 ± 0.45	1.84 ± 0.52	1.90 ± 0.42	2.06 ± 0.39
$A_{\text{max Power}}$ *,**	8.33 ± 2.48	9.54 ± 2.71	10.55 ± 1.93	12.02 ± 2.88	8.23 ± 2.30	9.23 ± 2.84	10.35 ± 1.23	12.56 ± 3.09	7.14 ± 2.14	7.79 ± 2.57	9.71 ± 2.38	11.25 ± 2.89
$K_{\text{max Power}}$ **,***	4.10 ± 1.19	5.48 ± 1.64	4.44 ± 0.76	3.88 ± 0.88	4.19 ± 0.98	6.04 ± 2.36	4.32 ± 0.85	4.63 ± 1.52	3.92 ± 1.31	4.91 ± 2.15	4.27 ± 0.95	4.38 ± 1.04

$F_{\text{max vertical}}$ maximal vertical force; $F_{\text{average vertical}}$ average vertical force; $F_{\text{average horiz decel}}$ average horizontal force during the deceleration phase; $F_{\text{average horiz accel}}$ average horizontal force during the acceleration phase; $\text{Rate}_{\text{of F generation}}$ rate of force generation; *N-active* non-active adults

* Statistically significant differences between older and young adults ($P < 0.01$)

**Statistically significant differences between runners and non-active individuals ($P < 0.01$)

***Statistically significant age-by-running activity interaction ($P < 0.01$)

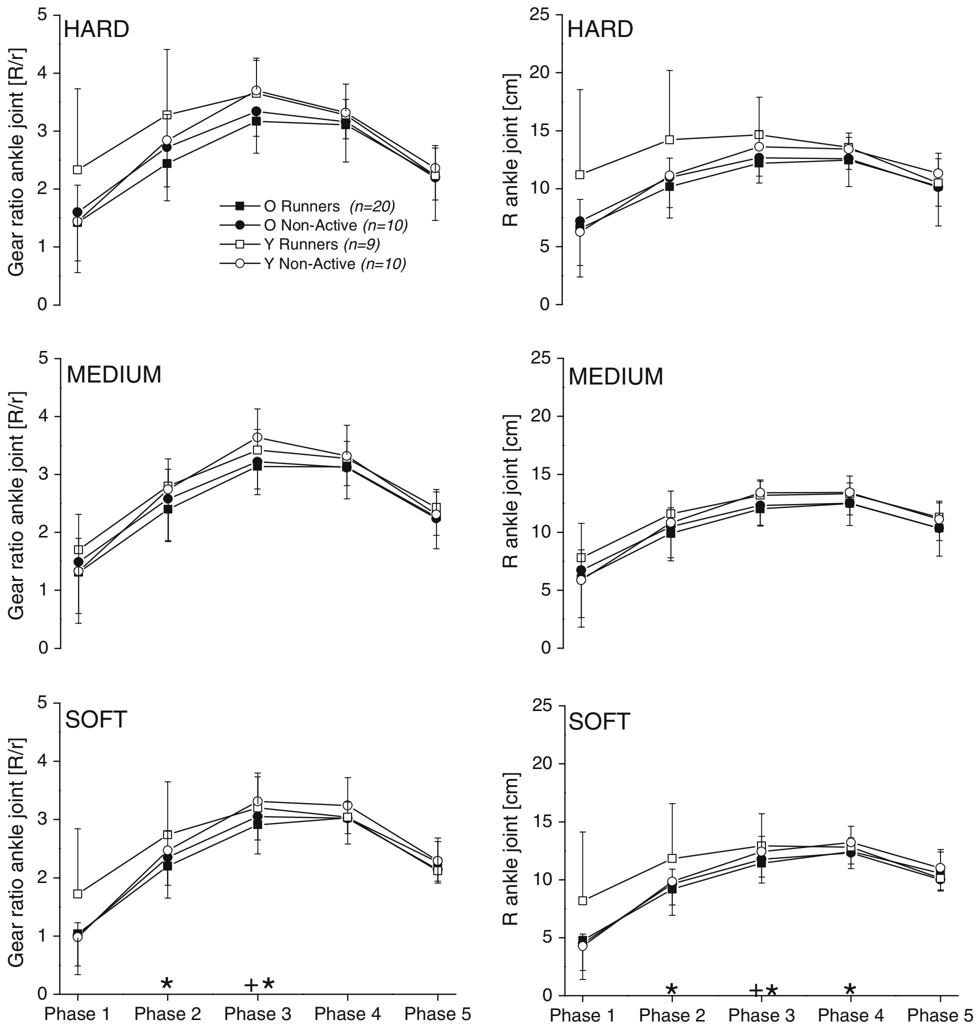

Fig. 4 Moment arm of the ground reaction force (*R*) and gear ratio (*R*/*r*) acting about the ankle joint during ground contact for the examined groups during running (2.7 m/s) on different surfaces (means and SD of both legs). *O* Older adults; *Y* young adults. (Phase 1, 10–26%; Phase 2, 26–42%; Phase 3, 42–58%; Phase 4, 58–74; Phase 5, 74–90% of the period of ground contact duration). *Asterisk* Statistically significant differences between older and young adults ($P < 0.01$). *Plus symbol* statistically significant ground surface effect ($P < 0.01$)

dence to suggest that young subjects change the gearing of their leg extensor MTUs when running at lower than their preferred velocity. We suppose, therefore, that the current age-related findings are not the consequence of running velocity.

Mechanical task adaptation due to running experience

In the literature it is well document that repeated practice of a motor task causes adaptational effects and improvements in locomotion mechanics even in older individuals (Pavol et al. 2002; Pai et al. 2003; van Hedel et al. 2002; van Hedel and Dietz 2004). Therefore, we hypothesized that running experience would improve running mechanics in both age groups. The endurance runners showed a lower average horizontal GRF during the deceleration and acceleration phases compared to the non-active subjects independent from the surface and subjects age. The lower average horizontal GRF during running is a global parameter which shows that running experience might make running more advantageous because it is well accepted that the metabolic cost of the horizontal GRF during human locomotion is more expensive than the metabolic cost of vertical GRF (Chang and Kram 1999; Gottschall and Kram 2003).

In addition to the lower horizontal GRFs runners showed also a joint specific alteration in running mechanics compared to the non-active subjects (lower gear ratio at the knee joint during the first 56% of the period of ground contact, Phases 1–3). This was due to a lower moment arm of the GRF acting about the knee joint. Moreover, these results were again independent of surface and/or age. The knee has been shown to be the most common site of running injuries (Messier et al. 1991; Nigg et al. 1993). The lower gear ratios found for the endurance runners compared to the non-active subjects did not clearly reduce the maximal knee joint moment (there was only a tendency, $P = 0.014$).

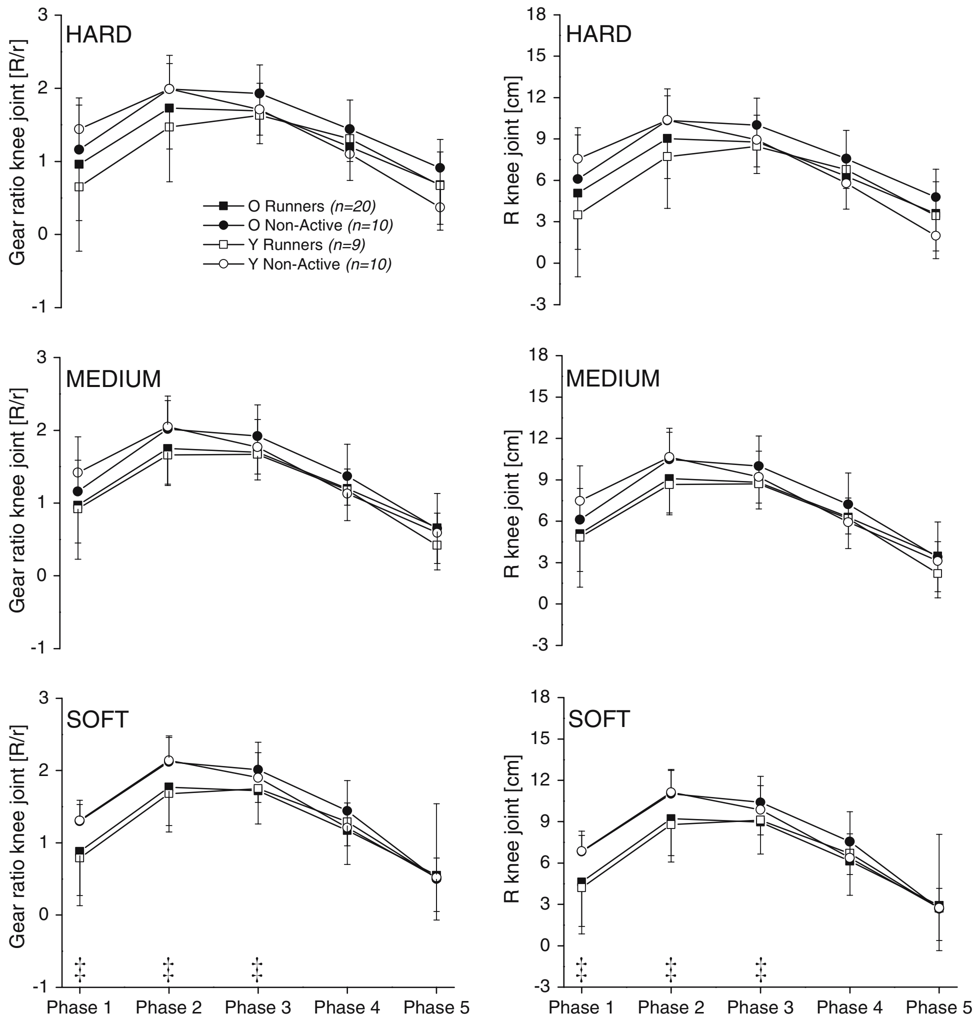

Fig. 5 Moment arm of the ground reaction force (*R*) and gear ratio (*R*/*r*) acting about the knee joint during ground contact for the examined groups during running (2.7 m/s) on different surfaces (means and SD of both legs). *O* Older adults; *Y* young adults (Phase 1, 10–26%; Phase, 2 26–42%; Phase, 3 42–58%; Phase, 4 58–74; Phase 5, 74–90% of ground contact duration). *Double dagger* statistically significant differences between runners and non-active individuals ($P < 0.01$)

The non-clear effect of the lower gear ratios on the maximal knee joint moment can be explained by the relative low difference in the gear ratio at the mid part of the ground contact phase between activity groups (Phase 3: about 9%) where the maximal knee joint moment occurs. However, the higher mechanical advantage [about 32% (Phase 1) and 18% (Phase 2) for the runners compared to the non-active subjects] for the quadriceps femoris MTU during the initial part of the ground contact (Phases 1, 2) indicates that endurance runners have advantages in running mechanics. A higher mechanical advantage during the initial running phase when an eccentric quadriceps femoris 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.

The main question arises how the runners create a running strategy leading to the lower gear ratios at the knee joint during the initial part of the ground contact phase compared to non-active subjects. We cannot suggest that these changes happened due to a correction based on sensory feedback control during the collision with the ground (reactive corrections) because the available time might be to short (for Phase 1, 28–71 ms). Further, the mechanical and morphological properties of the MTUs in the lower extremity showed no specific alterations between runners and non-active subjects. Therefore, we cannot suggest that the capacities of the MTUs are the mediator of the lower gear ratios. We can argue, however, that runners used proprioceptive feedback from repeated practice to improve running mechanics by developing appropriate feedforward motor commands to the expected mechanical load at the knee joint. Moreover the results suggest a complete task adaptation of the experienced old and young runners due to the similar behaviour onto all examined surfaces.

Surface effect on running mechanics

Previous studies reported that changes of the surface or texture of the footwear can influence the sensory feedback from the feet (Watanabe and Okubo 1981; Nurse et al. 2005) and introduce mechanical effects during human walking (Nurse et al. 2005). However, studies analysing the effect of the mechanical environment on running characteristics reported a similar behaviour of the human motor system for a variety of surface conditions (Ferris et al. 1998, 1999; Kerdok et al. 2002) For instance, Kerdok et al. (2002) reported no clear surface effect on ground contact duration, step length, stride frequency, duty factor nor maximal vertical ground reaction force while running. This was done because the runners changed their leg stiffness as well as the vertical displacement of the COM during running on surfaces having different stiffness in order to move in a similar manner on all surfaces (Kerdok et al. 2002). However, if we look at Fig. 4 provided in the work of Kerdok et al. (2002) the values in leg stiffness as well as in the leg compression seem not to be different between the three highest surface stiffness (216.8, 454.2 and 945.7 kN/m) which is the range of the examined surface stiffness of the present study (from 450 to over 2,000 kN/m). Thus, based on our data and the results presented in the literature (Ferris et al. 1998, 1999; Kerdok et al. 2002) it is reasonable to believe that humans use a general running strategy for a wide range of surface conditions. It can be argued that the differences in surface compression at mid stance between surface conditions were to low (approximately 1, 2.5 and 4 mm for the hard, medium and soft surface, respectively) in order to induce clear changes on human running mechanics. Such change in surface compression, however, provide realistic running conditions and highlights the interaction between human system and environmental changes usually encountered in daily life.

An interesting finding of the present study was that the gear ratios were lower at Phase 3 (42–58% of ground contact) during running on soft compared to the hard surface. This was due to a lower moment arm of the GRF acting about the ankle joint. Further, although in Phases 1 and 2 (10–42% of ground contact) we did not identify clear statistically significant ($P > 0.01$) differences, the values of the gear ratios were in tendency lower for the soft compared to the hard surface ($P = 0.020$ and 0.025 for Phase 1 and 2, respectively). It seems that the higher deformation of the soft surface increases the mechanical advantage of the triceps surae in the mid-part of the contact phase. However, during running we did not find any clear surface effect on ankle and knee joint angles as well as on the limb angle, neither at the beginning nor at the end of the ground contact phase. Similarly the mechanical power values at the ankle and knee joints were not influenced by the three examined surfaces. Therefore, an adjustment of the subjects to the different surfaces by means of a feedforward control prior to the collision with the ground is an unlikely explanation. It seems more reasonable to suggest, that the higher deformation of the soft surface and so the modified pressure contribution to the foot sole affect the moment arm of the GRF acting about the ankle joint. The lower amplitude of ankle dorsal flexion angle during ground contact on the soft surface is a consequence of the higher surface deformation (Ferris et al. 1998, 1999; Farley et al. 1998). It is possible that the higher compliance of the soft surface increases the contact area under the foot. This way a translation of the point of force application along the foot towards the ankle joint took place causing a decrease in the moment arm whilst running on the soft surface. However, the above findings indicate that the higher deformation of the soft compared to the hard surface increased the mechanical advantage of the triceps surae muscle to support body weight during each stride.

Conclusions

The results show that the running strategy remained essentially unchanged for a variety of surface conditions independent of subject's age or task experience. Runners compared to non-active subjects had a more advantageous running mechanics (higher mechanical advantage for the quadriceps femoris MTU, lower average horizontal forces) for all surfaces indicating a complete task specific adaptation. Older adults react to the reduced capacity of their MTUs by increasing safety during running (higher duty factor, higher COM transport with the foot on the ground, lower flight time) and benefit from a mechanical advantage for the triceps surae MTU and a lower rate of force generation. Moreover, the improvement in running mechanics and safety of the aged musculoskeletal system while running was present for all surface conditions. We suggest that older adults are able to recalibrate their running strategy to adjust the running effort to their reduced MTUs capacities in a feedforward control manner for a variety of mechanical environments.

Acknowledgment The authors wish to thank G. Morey-Klapsing, S. Stafilidis and G. DeMonte for their help collecting data for this study and for helpful discussions and preparation of the manuscript.

References

Aniansson A, Hedberg M, Henning GB, Grimby G (1986) Muscle morphology, enzymatic activity, and muscle strength in elderly men: a follow-up study. Muscle Nerve 9:585–591

Arampatzis A, Brüggemann G-P, Metzler V (1999) The effect of speed on leg stiffness and joint kinetics in human running. J Biomech 32:1349–1353

Biewener AA, Farley CT, Roberts TJ, Temaner M (2004) Muscle mechanical advantage of human walking and running: implications for energy cost. J Appl Physiol 97:2266–2274

Buch ER, Young S, Contreras-Vidal JL (2003) Visuomotor adaptation in normal aging. Learn Mem 10:55–63

Carrier DR, Heglund NC, Earls KD (1994) Variable gearing during locomotion in the human musculoskeletal system. Science 265:651–653

Chang YH, Kram R (1999) Metabolic cost of generating horizontal forces during human running. J Appl Physiol 86:1657–1662

Dempster WT, Gabel WC, Felts WJ (1959) The anthropometry of the manual work space for the seated subject. Am J Phys Anthropol 17:289–317

DeVita P (1994) The selection of standard convention for analyzing gait data based on the analysis of relevant biomechanical factors. J Biomech 27:501–508

DeVita P, Hortobagyi T (2000) Age causes a redistribution of joint torques and powers during gait. J Appl Physiol 88:1804–1811

DeVita P, Blankenship-Hunter P, Skelly WA (1992) Effects of functional knee brace on the biomechanics of running. Med Sci Sports Exerc 24:797–806

Diamond MC, Johnson RE, Protti AM, Ott C, Kajisa L (1985) Plasticity in the 904-day-old male rat cerebral cortex. Exp Neurol 87:309–317

Dixon SJ, Collop AC, Batt ME (2000) Surface effects on ground reaction forces and lower extremity kinematics in running. Med Sci Sports Exerc 32:1919–1926

Erni T, Dietz V (2001) Obstacle avoidance during human walking: learning rate and cross-modal transfer. J Physiol 534:303–312

Farley CT, Houdijk HH, Van Strien C, Louie M (1998) Mechanism of leg stiffness adjustment for hopping on surfaces of different stiffnesses. J Appl Physiol 85:1044–1055

Ferchmin PA, Eterovic VA (1986) Forty minutes of experience increase the weight and RNA content of cerebral cortex in periadolescent rats. Dev Psychobiol 19:511–519

Fernández-Ruiz J, Hall C, Vergara P, Diiaz R (2000) Prism adaptation in normal aging: slower adaptation rate and larger after effect. Cogn Brain Res 9:223–226

Ferris DP, Farley CT (1997) Interaction of leg stiffness and surfaces stiffness during human hopping. J Appl Physiol 82:15–22

Ferris DP, Louie M, Farley CT (1998) Running in the real world: adjusting leg stiffness for different surfaces. Proc Biol Sci 265:989–994

Ferris DP, Liang K, Farley CT (1999) Runners adjust leg stiffness for their first step on a new running surface. J Biomech 32:787–94

Frontera WR, Hughes VA, Lutz KJ, Evans WJ (1991) A cross-sectional study of muscle strength and mass in 45- to 78-yr-old men and women. J Appl Physiol 71:644–650

Gottschall JS, Kram R (2003) Energy cost and muscular activity required for propulsion during walking. J Appl Physiol 94:1766–1772

Herzog W, Read LJ (1993) Lines of action and moment arms of the major force-carrying structures crossing the human knee joint. J Anat 182:213–230

Hof AL (1992) An explicit expression for the moment in multibody systems. J Biomech 25:1209–1211

Hortobagyi T, Mizelle C, Beam S, DeVita P (2003) Old adults perform activities of daily living near their maximal capabilities. J Gerontol 58:M453–M460

Hughes VA, Frontera WR, Wood M, Evans WJ, Dallal GE, Roubenoff R, Fiatarone Singh MA (2001) Longitudinal muscle strength changes in older adults: influence of muscle mass, physical activity, and health. J Gerontol 56:B209–B217

Kagerer FA, Contreras-Vidal JL, Stelmach GE (1997) Adaptation to gradual as compared with sudden visuo-motor distortions. Exp Brain Res 115:557–561

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

Karamanidis K, Arampatzis A, Brüggemann G-P (2003) Symmetry and reproducibility of kinematic parameters during various running techniques. Med Sci Sports Exerc 35:1009–1016

Karamanidis K, Arampatzis A, Brüggemann G-P (2004) Reproducibility of electromyography and ground reaction force during various running techniques. Gait Posture 19:115–123

Kerdok AE, Biewener AA, McMahon TA, Weyand PG, Herr HM (2002) Energetics and mechanics of human running on surfaces of different stiffnesses. J Appl Physiol 92:469–478

Kjaer M (2004) Role of extracellular matrix in adaptation of tendon and skeletal muscle to mechanical loading. Physiol Rev 84:694–698

Kram R, Taylor CR (1990) Energetics of running: a new perspective. Nature 346:265–267

Maganaris CN, Baltzopoulos V, Sargeant AJ (1998) Changes in Achilles tendon moment arm from rest to maximum isometric plantarflexion: in vivo observations in man. J Physiol 510:977–985

Marigold DS, Patla AE (2002) Strategies for dynamic stability during locomotion on a slippery surface: effects of prior experience and knowledge. J Neurophysiol 88:339–353

McMahon TA (1985) The role of compliance in mammalian running gaits. J Exp Biol 115:263–282

McNay EC, Willingham DB (1998) Deficit in learning of a motor skill requiring strategy, but not of perceptuomotor recalibration, with aging. Learn Mem 4:411–420

Messier SP, Davis SE, Curl WW, Lowery RB, Pack RJ (1991) Etiologic factors associated with patellofemoral pain in runners. Med Sci Sports Exerc 23:1008–1015

Mulder T, Zijlstra W, Geurts A (2002) Assessment of motor recovery and decline. Gait Posture 16:198–210

Nigg BM, Cole GK, Nachbauer W (1993) Effects of arch height of the foot on angular motion of the lower extremities in running. J Biomech 26:909–916

Nurse MA, Hulliger M, Wakeling JM, Nigg BM, Stefanyshyn DJ (2005) Changing the texture of footwear can alter gait patterns. J Electromyogr Kinesiol 15:496–506

Owings TM, Pavol MJ, Grabiner MD (2001) Mechanisms of failed recovery following postural perturbations on a motorized treadmill mimic those associated with an actual forward trip. Clin Biomech 16:813–819

Pai YC, Wening JD, Runtz EF, Iqbal K, Pavol MJ (2003) Role of feedforward control of movement stability in reducing slip-related balance loss and falls among older adults. J Neurophysiol 90:755–762

Patla AE (1997) Understanding the roles of vision in the control of human locomotion. Gait Posture 5:54–69
Patla AE, Adkin A, Martin C, Holden R, Prentice S (1996) Characteristics of voluntary visual sampling of the environment for safe locomotion over different terrains. Exp Brain Res 112:513–522
Pavol MJ, Runtz EF, Edwards BJ, Pai YC (2002) Age influences the outcome of a slipping perturbation during initial but not repeated exposures. J Gerontol 57:M496–M503
Perry SD, Santos LC, Patla AE (2001) Contribution of vision and cutaneous sensation to the control of centre of mass (COM) during gait termination. Brain Res 913:27–34
Prince F, Corriveau H, Hébert R, Winter DA (1997) Gait in the elderly. Gait Posture 5:128–135
Raz N (ed) (2000) Aging of the brain and its impact on cognitive performance: integration of structural and functional findings. Erlbaum, Hillsdale, NJ
Schultz AB (1992) Mobility impairment in the elderly: challenges for biomechanics research. J Biomech 25:519–528
Shadmehr R (2004) Generalization as a behavioral window to the neural mechanisms of learning internal models. Hum Mov Sci 23:543–568
Sorensen KL, Hollands MA, Patla E (2002) The effects of human ankle muscle vibration on posture and balance during adaptive locomotion. Exp Brain Res 143:24–34
Stelmach GE, Worringham CJ (1985) Sensorimotor deficits related to postural stability. Implications for falling in the elderly. Clin Geriatr Med 3:679–694
van Hedel HJ, Dietz V (2004) The influence of age on learning a locomotor task. Clin Neurophysiol 115:2134–2143
van Hedel HJ, Biedermann M, Erni T, Dietz V (2002) Obstacle avoidance during human walking: transfer of motor skill from one leg to the other. J Physiol 543:709–717
Watanabe I, Okubo J (1981) The role of the plantar mechanoreceptor in equilibrium control. Ann N Y Acad Sci 374:855–864
Winegard KJ, Hicks AL, Sale DG, Vandervoort AA (1996) A 12-year follow-up study of ankle muscle function in older adults. J Gerontol 51:B202–B207
Wolfson L (2001) Gait and balance dysfunction: a model of the interaction of age and disease. Neuroscientist 7:178–183
Wolfson L, Judge J, Whipple R, King M (1995) Strength is a major factor in balance, gait, and the occurrence of falls. J Gerontol 50:64–67
Wolpert DM, Ghahramani Z, Jordan MI (1995) An internal model for sensorimotor integration. Science 269:1880–1882
Woltring HJ (1986) A FORTRAN package for generalized, cross-validatory spline smoothing and differentiation. Advances in Engineering Software 8
Woollacott MH, Shumway-Cook A, Nashner LM (1986) Aging and posture control: changes in sensory organization and muscular coordination. Int J Aging Hum Dev 23:97–114