

RESEARCH ARTICLE

Context-Dependent Mechanisms of Striated Muscle Dysfunction

Effects of age on intramuscular fascicle kinematics of the medial gastrocnemius muscle of track and field masters athletes

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Abstract

Aging results in a decline in muscle mass and intrinsic mechanical properties, yet its impact on intramuscular force transmission and fascicle kinematics remains poorly understood. We investigated whether age, sex, and habitual high-intensity athletic training modulate medial gastrocnemius (GM) muscle mechanics in 172 competitive masters athletes ($n = 108$ male, $n = 64$ female; aged 35–90 yr). Participants performed ramp plantar flexion to maximum voluntary contraction, whereas GM architecture was assessed via B-mode ultrasound. Fascicle length, pennation angle, fascicle rotation, and strain were quantified at rest and during contraction. Resting pennation angles did not vary with age ($P \geq 0.30$) or sex ($P \geq 0.39$). During contraction, superficial, but not deep fascicle rotation (change in pennation angle) decreased by $6.6 \pm 51.3\%$ per decade ($P = 0.003$), whereas deep fascicle rotation remained stable ($P = 0.27$). Furthermore, resting fascicle length showed a significant age-related decline of $1.8 \pm 13.7\%$ per decade ($P = 0.002$). Finally, Achilles tendon force decreased with age ($-4.3 \pm 16.3\%$ per decade, $P < 0.001$), independent of sex ($P = 0.12$). Exploratory subgroup analyses showed that while athletic specialization (endurance vs. power) did not significantly influence fascicle kinematics, high-performing athletes ($>85\%$ age grade) maintained significantly greater superficial fascicle rotation than lower-performing peers ($P = 0.027$). These findings indicate that while age-related alterations in superficial fascicle kinematics occur even in well-trained individuals, preserved architectural gearing remains a distinct marker of elite athletic performance. In conclusion, our results suggest that aging alters intramuscular force transmission pathways independently of life-long training status, highlighting the limits of exercise in fully mitigating structural neuromuscular aging.

NEW & NOTEWORTHY This study suggests an age-related, nonuniform disruption of fascicle kinematics in the medial gastrocnemius of masters athletes. Although deep fascicle mechanics remain largely preserved ($P = 0.27$), superficial fascicle rotation declines significantly by $6.6\% \pm 51.3\%$ per decade ($P = 0.003$). These findings identify a region-specific decline in “architectural gearing,” suggesting a potential mechanistic hypothesis for the age-related loss of muscle power that persists even in athletes with a long training history.

aging; fascicle kinematics; masters athletes; muscle architecture; ultrasound imaging

INTRODUCTION

Aging is a complex process driven by changes in socioeconomic factors, including occupation, retirement, or changes in social support, which shape aging trajectories. In parallel, interlinked biological factors, such as cellular senescence, inflammation, and maturation profoundly affect skeletal

muscle, with major consequences for health and independence (1, 2). Sarcopenia, defined as the age-related loss of skeletal muscle mass and function (3), is steadily increasing in prevalence (4). This has public health consequences (5), as impaired muscle function is a critical contributor to gait disturbances and falls (6). Frailty and disease can trigger repetitive hospitalizations with prolonged stays, progressively



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increasing morbidity, the need for social care, and ultimately, mortality (7). Muscle mass declines approximately by ~1% per year from middle age, with older adults (e.g., 70–90 yr old) losing ~7% (females) and ~10% (males) of thigh muscle area per decade (8, 9).

Next to muscle mass loss, an age-related decline in muscle quality, termed sarcosthenia, appears to be a major contributor to muscle weakness. Older individuals typically exhibit a disproportionate loss of strength relative to muscle mass (dynapenia). Sarcosthenia specifically describes the component of dynapenia not explained by atrophy, often attributed to neuromuscular and structural factors (10). Importantly, dynapenia is a stronger predictor of adverse clinical outcomes and mortality than muscle mass alone (10, 11). Although the underlying mechanisms remain incompletely understood, age- and activity-related changes in muscle quality encompassing fatty infiltration, mitochondrial dysfunction, fibrosis, and alterations in intramuscular connective tissue are thought to be central to mediating impaired function (12–15).

The majority of human muscles exhibit a pennate architecture, where the axes of the fascicles deviate from the line of action of the tendon. Previous research indicates that age-related muscle loss is associated with smaller pennation angles in the relaxed state and reduced specific force, though fascicle length often remains unaffected (16). The muscle's mechanical kinematics is governed by interactions between contractile and noncontractile tissues. The variable ratio between whole muscle and fiber shortening velocities is termed architectural gearing (17, 18). High gearing facilitates rapid fiber shortening at low forces, whereas low gearing optimizes force transmission during high-force contractions. Although evidence suggests fascicle rotation is impaired in older adults (19), data regarding muscle motility and fascicle kinematics during aging remains scarce.

A consistently observed factor across determinants is the declining engagement of older adults in physical activity (20). Masters athletes, who often remain physically active throughout the lifespan, represent the upper limits of preserved muscle function with aging and therefore provide a unique model to examine aging under conditions of sustained exercise training (21). In this population, age-related declines in aerobic capacity are attenuated by nearly 50% compared with the general population (22), whereas reductions in neuromuscular power during vertical jumping are comparatively moderate (23). Importantly, preservation of macroscopic performance does not necessarily imply maintained intramuscular structure. Rather, functional capacity may be sustained through compensatory neuromuscular and/or architectural adaptations.

However, it remains unclear how sustained exercise training interacts with age-related architectural declines, and whether preservation of macroscopic performance directly mirrors the preservation of internal muscle mechanical properties.

The medial gastrocnemius muscle (GM) serves as an ideal muscle for investigating age-related shifts in muscle mechanics due to its pivotal role in the triceps surae-Achilles tendon complex. Plantar flexion strength and power are fundamental to postural stability and human locomotion, where

the GM functions dynamically, acting predominantly as an actuator during walking and an elastic spring during running (24). This functional versatility, combined with its capacity for architectural gearing, makes the GM a critical unit for evaluating internal muscle behavior.

Based on these considerations, we hypothesized that even competitive masters athletes would exhibit age-related alterations in intramuscular fascicle kinematics, characterized primarily by a significant decline in fascicle motility. In addition to this primary focus, we conducted exploratory analyses to evaluate whether these kinematic patterns are further modulated by sex, training specificity (power- vs. endurance-oriented), or individual performance levels.

MATERIALS AND METHODS

Setting and Participants

Ethical approval was obtained from the ethics committee of the North Rhine medical association, Düsseldorf, Germany (ID: 2018171), as well as the local University research ethical committee in Málaga, Spain. The study was prospectively registered in the German Clinical Trials Register (DRKS identifier: DRKS00015172) before commencement. The investigation was conducted in accordance with the Declaration of Helsinki.

Data were collected during the 23rd World Masters Athletics Championships (WMAC) in 2018 as part of the larger Master Athletic Field Study 2018 (MAFS-18) initiative.

Participants were recruited either via direct invitation by study personnel at the stadium, or by voluntary self-enrollment at the field study information point. Participation was open to all registered WMAC competitors. Sex was determined based on participant self-report. Exclusion criteria included acute or chronic musculoskeletal injuries or disorders affecting calf muscle contractions or vertical jump performance, and use of medication known to directly affect skeletal muscle contractility, metabolism, or neuromuscular control (e.g., muscle relaxants). All participants provided written informed consent prior to participation in the study.

Anthropometric data and medical history were obtained via a standardized questionnaire. Data acquisition was managed using the electronic data capture platform REDCap (Vanderbilt University, Nashville, Tennessee; Version 7.1; 25). A total of 256 athletes consented to participate in the broader field study (26). Of these, 197 individuals completed the specific assessments described herein; ultimately, data from 172 participants were available for final analysis (Fig. 1).

Muscle Model Selection and Rationale

We utilized isometric plantar flexion contractions of the GM as our experimental model, prioritizing it over the lateral head for its substantial contribution to total plantarflexion torque and its favorable anatomical properties for imaging (10, 16, 27). The GM possesses a significantly larger physiological cross-sectional area than the lateral head, establishing it as the primary force generator within the triceps surae. From a technical perspective, the GM's morphology facilitates superior ultrasound image quality and more consistent longitudinal fascicle tracking. Compared with the lateral head, which often exhibits greater curvature and

CONSORT diagram

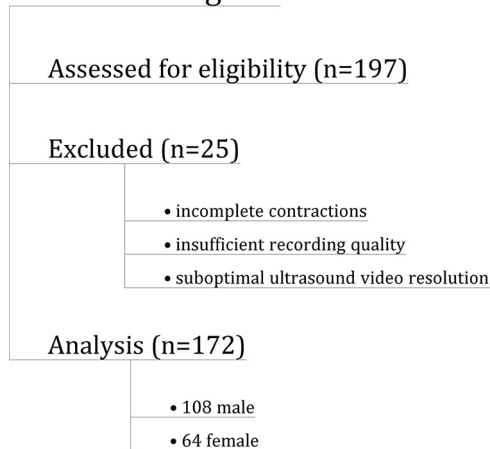


Figure 1. CONSORT diagram of the study.

architectural complexity during contraction, the GM's alignment minimizes parallax error during high-intensity measurements (27, 28).

Anatomical Measurements

Participants were seated on a custom-built dynamometer with the right knee positioned at 90° of anatomical flexion and the ankle in the neutral position (foot at a 90° angle with the tibia). The dynamometer was equipped with an adjustable bar placed above the distal thigh to secure the leg. A force transducer was located under the forefoot, and an adjustable backrest prevented the participant from sliding on the seat (Fig. 2C). The primary aim of the set-up was to record medial gastrocnemius fascicle kinematics using B-mode ultrasound at rest and during isometric contractions. To establish reference points, several anatomical landmarks were identified as follows: the medial malleolus (MM) and the medial knee joint cleft (MKJC) were located by palpation and ultrasound control; the myotendinous junctions of the gastrocnemius (GMJ) and soleus (SOLJ) muscles, the Achilles tendon insertion (ATI) at the calcaneus, and the ultrasound probe position (LPP) over the gastrocnemius mid-belly were determined using ultrasound guidance. The Achilles tendon fulcrum projection (ATFP) relative to the medial malleolus was also marked.

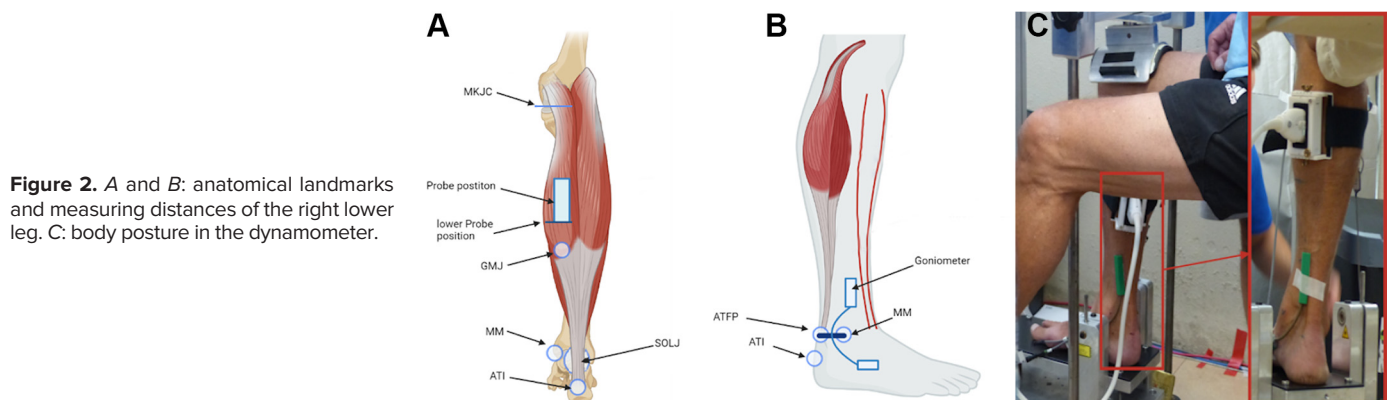
From these landmarks, several linear distances were measured at rest (Fig. 2, A–C): tendon lengths (ATI-GMJ and ATI-SOLJ), the Achilles tendon lever arm (ATLA, distance from MM to ATFP, as an anthropometric approximation), the lower leg length (ATI-MKJC), and the probe position offset (ATI-LPP plus 3 mm clearance to account for the probe bracket).

Ultrasound Acquisition

Ultrasound imaging was conducted using a LOGIQe scanner (GE Healthcare, Chicago, IL) equipped with an L4-12T-RS linear B-mode probe (4.2–13 MHz). To maximize image contrast, the probe was positioned such that the ultrasound beam was as perpendicular as possible to the deep aponeurosis of the GM (29). Probe placement was standardized by 1) aligning the probe with a predefined anatomical landmark along the longitudinal axis of the shank while avoiding large blood vessels in the field of view, 2) adjusting the probe angle in the transverse plane to maximize deep aponeurosis contrast, and 3) rolling the probe so that the superficial and deep aponeuroses appeared as parallel as possible on the B-mode image (Fig. 3). The ultrasound focus was then set midway between the superficial and deep aponeuroses. Next, the probe was affixed with a custom-made probe bracket, and a test contraction was made. Probe placement was reiterated, if required. Throughout the study, all scanner settings were kept constant, except for zoom, gain, and focus zones, which were adjusted manually to account for individual anatomical differences.

Isometric Contraction Protocol

Participants were instructed to perform isometric plantar flexion contractions with the right lower leg, steadily increasing force to reach their maximum voluntary contraction (MVC) within 4 s. They were then asked to maintain this maximal effort for 2–3 s before relaxing gradually. To ensure that participants reached their physiological maximum, standardized verbal encouragement was provided by the investigator during the entire contraction phase. To ensure consistent execution across participants, a visual feedback depicting an idealized force-time curve was displayed, illustrating the gradual ramp-up, sustained plateau, and controlled relaxation phases. Before data collection, each participant completed several submaximal familiarization



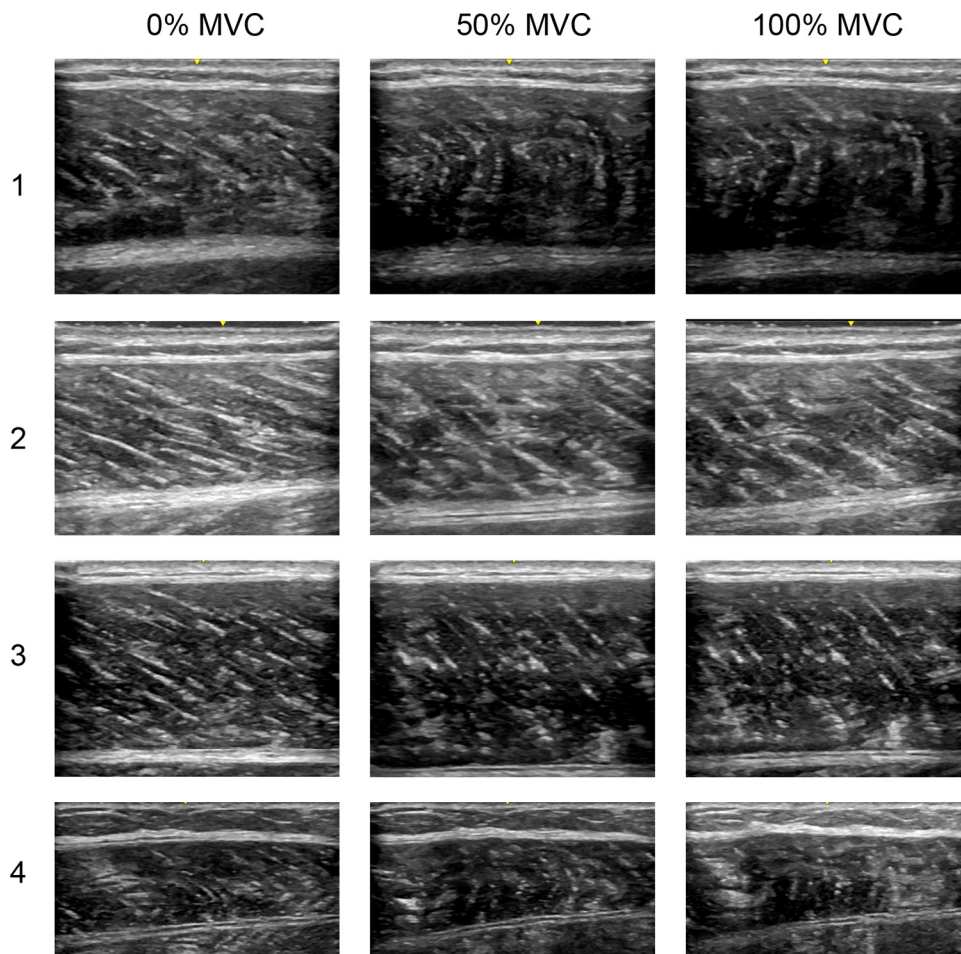


Figure 3. Representative ultrasound images from four different participants (1–4) during isometric plantar flexions contractions at 0%, 50%, and 100% MVC. MVC, maximum voluntary contraction.

trials to practice the task and to ensure proper execution of the task in line with the instructions. During the experiment, we aimed to record three to five contractions that met predefined validity criteria (clear force ramp, stable plateau phase, and acceptable ultrasound image quality; see Fig. 4). For subsequent analysis, ultrasound frames were sampled at 10% increments to 100% MVC. Figure 3 illustrates the dynamic fascicle movement during these contractions; however, quantitative architecture measurements were strictly performed at the aforementioned discrete force intervals. Between trials, participants rested in a seated position for a minimum of 1 min to allow for recovery. All scans were conducted by a single experienced sonographer to maintain methodological consistency. To ensure temporal alignment

between muscle architecture changes and force production, the ultrasound system and the isometric dynamometer were hardware-synchronized. A custom-built synchronization box sent a simultaneous pulse to both the Noraxon data acquisition system and the ultrasound system at the start of each trial. This allowed for the precise identification of the ultrasound frames corresponding to specific force levels, including the 50% MVC target.

Ultrasound Image Analysis and Parameter Extraction

Ultrasound recordings of the GM were analyzed using a custom Python script (IPython version 7.8.0, Windows 10). Contraction sequences (5%–95% MVC in 10% increments) were imported into a graphical interface where the superficial

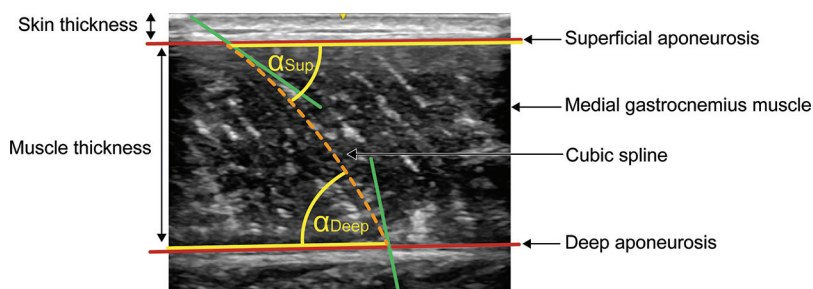


Figure 4. The superficial and deep aponeuroses are delineated by horizontal red lines. A representative fascicle trajectory is represented by a cubic spline (orange dashed line). The pennation angles (α_{Sup} , α_{Deep}) are indicated by the yellow sectors, formed between the aponeurosis and the spline tangents (green lines) at the intersection points. Skin thickness and muscle thickness are indicated by the vertical double-headed arrows.

and deep aponeurosis and a representative fascicle were manually digitized. Skin thickness was calculated as the mean vertical distance between the skin surface and the superficial aponeurosis (Fig. 4).

For curved fascicles, a cubic spline was fitted to digitized points along the trajectory. Curvilinear fascicle length was determined by integrating along the spline between the aponeurotic intersections. Pennation angles (α_{Sup} , α_{Deep}) were defined as the angles between the aponeuroses and the spline tangents at these intersections (Fig. 4). Fascicle curvature (Curv) was approximated using a circular arc sharing the same boundary tangents as the cubic spline. Curvature was calculated as the reciprocal of the radius (r^{-1}), derived from the chord length (d) and the angular displacement (β) between tangents (Fig. 5):

$$\text{Curv [1/m]} = \frac{1}{r[\text{m}]} = \frac{2 \cdot \sin(\beta/2)}{d[\text{m}]}$$

Tissue strains were calculated as the percentage change in length or thickness from rest to 95% MVC. This included transverse strain (y-axis) for skin, adipose, and muscle tissue, as well as longitudinal fascicle strain. Fascicle rotation was quantified as the angular change ($^{\circ}$) from rest to MVC at both aponeurotic insertions. Finally, changes in fascicle curvature were calculated as the absolute change in curvature across the contraction range.

Statistical Analyses

All statistical analyses were conducted in R (version 4.2.1, <https://r-project.org>) using the RStudio environment (version 2022.07.02, <https://rstudio.com>). For variables with a single measurement per participant (e.g., anthropometric data), we used analysis of covariance (ANCOVA) with age, best event type, and sex as fixed factors. For repeated-measures variables (e.g., contraction data), linear mixed-effects models were applied with age, event type, and sex as fixed effects, and participant identity as a random effect. To ensure model stability, primary models focused on main effects, whereas interaction terms were evaluated in separate sensitivity analyses.

Where necessary, dependent variables were Box-Cox transformed to meet the assumptions of homoscedasticity and normality of residuals, verified through residual and quantile-quantile plots. Pearson's correlation coefficient (r) was used to examine inter-dependency of variables, categorized as trivial ($|r| < 0.1$), small ($0.1 < |r| \leq 0.3$), moderate ($0.3 < |r| \leq 0.5$), large ($0.5 < |r| \leq 0.7$), very large ($0.7 < |r| \leq 0.9$), and almost perfect ($|r| > 0.99$) (30). To explore which

dynamometric and fascicle-kinematics parameters might explain age-related changes in performance, we fitted separate linear mixed-effects models with age grade (as detailed in *Computation of age grades and performance metrics*) as the dependent variable and age plus one explanatory variable (Table 4) as predictors. Partial R^2 values were calculated using the *r2beta* function from the *r2glmm* package. In addition, a correlation matrix was generated for dynamometric and fascicle-kinematics parameters (Table 1).

To evaluate the influence of training specificity and performance levels, exploratory subgroup analyses were performed. Athletes were categorized into endurance-oriented and power/sprint-oriented groups ($N = 135$, endurance: $n = 54$ vs. power/sprint: $n = 81$). In addition, performance-based subgroups were created by comparing high-performing athletes (age grade $>85\%$) with lower-performing peers (age grade $<70\%$; 31). Finally, potential interaction effects (Age $\times$ Sex and Age $\times$ Training Specificity) were evaluated in exploratory models to determine if age-related patterns differed by sex or athletic specialization. Sensitivity analyses were also conducted within a restricted age band (50–60 yr) to isolate performance effects from chronological aging effects. The significance threshold (α) was set at 0.05. Results are reported as means $\pm$ standard deviation.

Computation of age grades and performance metrics.

Official competition marks and corresponding age grades for each participant were obtained from World Masters Rankings (<https://mastersrankings.com>). Age grades adjust competition results for age, allowing fairer comparisons between athletes of different ages. They are obtained by first computing age-graded performances (AGP) as $\text{AGP} = f \times m$, where m is the competition mark, and f is a factor specific to age, sex, and event. These factors are the same as those used by WMA to compute point scores in combined events (e.g., decathlon, heptathlon, pentathlon). Second, the age grade is additionally computed from the open standard (S), which represents the benchmark performance for senior (open category) athletes in the respective event. For throwing and jumping events, $100 \times \text{AGP}/S$, and for running events $100 \times S/\text{AGP}$.

For athletes who competed in more than one event, the event with the highest age grade was identified and used to classify participants into one of four primary categories: runner, jumper, thrower, or walker. In the rare case of identical age grades across events, classification was based on the participant's self-reported main discipline. Thus, age grades are also useful for comparing performances across athletic event types. Because age grades are influenced by age-adjustment

Figure 5. Representative B-mode ultrasound image illustrating the geometric model for fascicle curvature. The red lines delineate the superficial and deep aponeuroses. Fascicle curvature is approximated using a circular arc (orange dashed line) sharing common tangents (green lines) with the digitized fascicle trajectory at the aponeurotic intersections. Curvature is defined as the reciprocal of the radius ($1/r$), derived from the chord length (d) and the angular displacement (β).

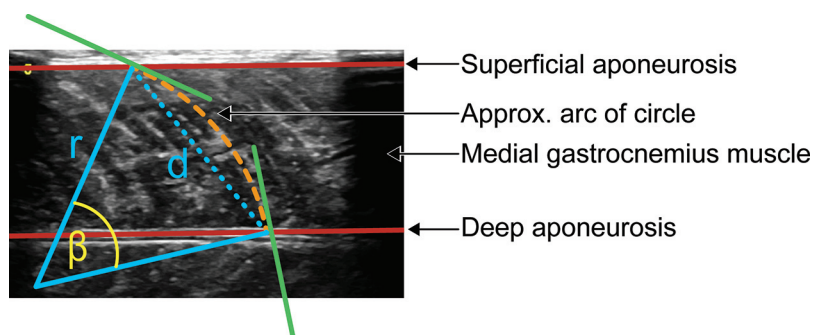


Table 1. Correlation matrix for physiological and architectural endpoints

Muscle Strength	Anatomical Features at Rest										Tissue Deformation					
	gForce, g	Skin Thickness, mm	Muscle Thickness, mm	Deep Penn. Angle, degree	Sup. Penn. Angle, degree	Fascicle Length, mm	Fascicle Curvature, m ⁻¹	Length of the Soleus Tendon, mm	Muscle Tendon Length, mm	Skin and Fat Tissue Strain, %	Muscle Strain, %	Deep Penn. Angle, degree	Change in Penn. Angle, degree	Fascicle Normal Strain, %	Change in Fascicle Curvature, m ⁻¹	
Muscle strength																
gForce, g	-0.198	0.121	-0.088	-0.083	0.261	-0.038	-0.279	-0.181	-0.107	0.035	0.028	0.045	0.136	-0.206	-0.012	
Anatomical features in the relaxed state																
Skin thickness, mm	0.01															
Muscle thickness, mm	0.12	0.8	0.019	0.21	0.179	-0.2	0.111	-0.069	-0.128	-0.044	-0.092	-0.011	0.013	0.106	-0.017	
Deep pen. angle, degree	0.26	0.006	<0.001	0.368	0.41	0.483	0.141	0.315	-0.162	-0.082	0.119	-0.111	0.165	0.217	0.146	
Sup. penn. angle, degree	0.28	0.018	<0.001	<0.001	0.612	-0.483	0.735	0.068	-0.144	0.071	-0.088	-0.048	0.084	-0.052	0.642	
Fascicle length, mm	<0.001	0.008	<0.001	<0.001	<0.001	-0.42	-0.019	0.089	-0.139	-0.023	-0.113	-0.113	0.19	-0.174	0.582	
Fascicle curvature, m ⁻¹	0.63	0.15	0.065	<0.001	0.81	<0.001	0.01	-0.052	0.13	-0.083	0	0.058	-0.028	0.074	-0.121	
ATLA, mm	<0.001	0.37	<0.001	0.38	0.25	0.003	0.89	0.064	0.262	0.555	-0.025	0.136	0.063	-0.044	-0.04	
Length of the soleus tendon, mm	0.019	0.099	0.036	0.064	0.073	0.91	0.51	0.41	0.249	0.205	-0.047	0.045	0.017	-0.1	-0.036	
Length of the GM tendon, mm	0.17	0.57	0.29	0.36	0.76	0.11	0.093	<0.001	0.001	0.42	-0.011	0.15	0.094	0.028	-0.005	
Muscle tendon length, mm	0.6	0.29	<0.001	0.44	0.89	<0.001	0.28	<0.001	0.008	<0.001	-0.023	0.047	-0.034	-0.005	-0.122	
Tissue deformation																
Skin and fat tissue strain, %	0.65	0.23	0.12	0.25	0.14	0.025	1	0.75	0.55	0.88	0.76	-0.151	-0.009	-0.07	-0.03	
Muscle strain, %	0.72	0.88	0.15	0.53	0.14	0.99	0.45	0.08	0.56	0.052	0.048	<0.001	0.378	-0.159	0.205	
Change in deep penn. angle, degree	0.56	0.87	0.031	0.27	0.012	0.2	0.71	0.42	0.83	0.22	0.67	<0.001	0.378	-0.199	0.816	
Change in sup. penn. angle, degree	0.08	0.75	0.52	0.5	0.023	0.36	0.34	0.061	0.36	0.22	0.089	<0.001	<0.001	-0.408	-0.303	
Fascicle-normal strain, %	0.007	0.17	0.004	<0.001	<0.001	<0.001	<0.001	0.57	0.2	0.72	0.95	0.037	0.009	<0.001	0.023	
Change in fascicle curvature, m ⁻¹	0.88	0.83	0.056	0.19	<0.001	0.11	0.2	0.61	0.64	0.95	0.11	0.007	<0.001	<0.001	0.76	

Pearson's correlation coefficients (r) are displayed in the upper right triangle of the matrix, whereas corresponding P values are provided in the lower left triangle. The analysis was conducted for the total cohort ($N = 172$; 108 males and 64 females). Statistically significant correlations ($P < 0.05$) are indicated in bold. According to the criteria by Hinkle et al. (30), correlation strength is interpreted as trivial ($|r| < 0.1$), small ($0.1 < |r| \leq 0.3$), moderate ($0.3 < |r| \leq 0.5$), large ($0.5 < |r| \leq 0.7$), very large ($0.7 < |r| \leq 0.9$), and almost perfect ($|r| > 0.9$). ATLA, Achilles tendon lever arm; gForce, gravitational force equivalent; GM, gastrocnemius medialis; penn., pennation; sup., superficial.

factors, we also calculated mark grades to allow comparisons without adjusting for age. These were computed directly from the recorded mark (32) and the open standard, using the same event-type distinction: $100 \times m/S$ for throwing and jumping events, and as $100 \times S/m$ for running events. This approach ensured that both age-adjusted and raw performance metrics were available for analysis, enabling comparisons across different athletic event types.

Quantification of muscle architecture, tendon mechanics, and tissue strains.

Plantar flexor strength, assessed as peak dynamometric torque, was defined as 100% MVC. Achilles tendon force (F_{AT}) was calculated as plantar flexor strength (F_{PF}) divided by the Achilles-tendon lever arm (ATLA),

$$F_{AT}[N] = \frac{F_{PF}[Nm]}{ATLA[m]}$$

and Achilles tendon g-force was expressed relative to body weight (body mass $\times 9.81 \text{ m/s}^2$).

$$gF_{AT}[g] = \frac{F_{AT}[N]}{m_{body}[kg] \cdot 9.81[m/s^2]}$$

The conversion into a fictive “g-force,” a dimensionless factor comparing a force acting on a body mass to the force acting on the same body mass under static Earth acceleration conditions (1 g), allows to make forces comparable independently of body weight. This is good practice in literature (33, 34).

Skin and muscle thickness were measured along the ultrasound probe alignment as the mean distance between the skin surface and superficial aponeurosis, and between the superficial and deep aponeuroses, respectively. Deep and superficial pennation angles, fascicle length, and fascicle curvature were measured at rest, defined as 5% of MVC.

Strains and angle changes from rest to full contraction (5%–95% MVC) were calculated as follows: skin and fat tissue strain and muscle strain in the vertical direction were expressed as relative changes in length; change in superficial and deep pennation angles as the rotation of the respective angle; fascicle-normal strain as the relative change in fascicle length; and change in fascicle curvature as the difference in curvature.

RESULTS

Study Cohort

The study included 172 participants, comprising 108 males and 64 females (Table 2). As expected, sex differences were observed with regard to anthropometric characteristics, with men being taller, heavier, and having higher body mass index (BMI), as well as longer Achilles tendons and longer tendon lever arms (all $P < 0.001$). In our cohort, female participants were, on average, ~ 5 yr younger than males ($P = 0.007$). Although females reported a slightly higher weekly training volume during the competition season compared with males, this difference did not reach statistical significance ($P = 0.076$). No sex difference was observed in training volume outside of the competition season, strength training frequency, age grade, or mark grade (all $P > 0.20$). Throwers exhibited higher body mass and muscle volume, as well as lower age grades, compared with other athletes, whereas race

walkers were generally shorter and lighter (all $P < 0.001$). No significant difference in training habits was detected between event types ($P > 0.10$).

Sex and Age Differences in Plantar Flexion Strength and Tendon Mechanics

Males achieved greater dynamometer torque than females ($P < 0.001$) and comparable Achilles tendon force ($P = 0.12$), but females had greater Achilles tendon g-force than males ($P = 0.003$) (Table 3). Age was related to all three plantar flexion strength measures (all $P < 0.001$), suggesting declining rates of $-1.8 \pm 7.0\%$, $-4.3 \pm 16.3\%$, and $-3.5 \pm 16.3\%$ per decade of age for dynamometer torque, Achilles tendon force, and Achilles tendon g-force, respectively.

Muscle Anatomical Features in the Relaxed State

Skin and muscle thickness, as well as superficial and deep pennation angles, were unaffected by sex (all $P \geq 0.18$), age (all $P \geq 0.26$), or event type (all $P \geq 0.09$). Across the entire cohort, fascicle length was significantly greater in males than in females ($P = 0.035$) and showed a small age-related decline of -1.8% per decade ($P = 0.002$). No differences in fascicle length were observed between event types ($P = 0.83$). Fascicle curvature at rest differed by event type ($P = 0.033$), with throwers showing lower mean curvature than jumpers, runners, and walkers; however, post hoc pairwise comparisons did not reach statistical significance between specific event groups. Fascicle curvature was not associated with sex ($P = 0.71$) or age ($P = 0.64$).

Tissue Deformation

Skin and fat tissue strain was not affected by sex, event type, or age (all $P > 0.05$). Muscle strain was greater in males than in females ($P = 0.019$) but showed no association with event type ($P = 0.89$) or age ($P = 0.44$). Fascicle rotation yielded an age-related reduction by $-6.6 \pm 51.3\%$ per decade only for superficial ($P = 0.003$) but not for deep fascicle rotation ($P = 0.27$). Neither superficial nor deep fascicle rotation was related to sex or event type (both $P > 0.10$). Fascicle-normal strain averaged approximately -26% and was independent of age ($P = 0.72$), sex ($P = 0.57$), and event type ($P = 0.73$). Similarly, contraction-induced changes in fascicle curvature showed no relationship with any of these variables (all $P > 0.20$).

These findings indicate that fascicle rotation is not simply a result of shortening, as evidenced by the small correlation of fascicle shortening with both superficial and deep fascicle rotation. Instead, two relatively independent modes of fascicle kinematics contribute to muscle-tendon complex shortening: the “shortening-mode” (Fig. 6A), in which relatively straight fascicles at rest (solid black lines) undergo longitudinal shortening and rotation during contraction (dashed red lines), and the “gearing-mode” (Fig. 6B), in which fascicles transition from a linear architecture at rest (solid black lines) to a rotated and curved state during contraction (dashed red lines), concentrating motility in the deep section. Although the gearing-mode typically involves rotation and curving of fascicles to amplify velocity, our data suggest that aging specifically impairs this mechanism in the superficial layer, whereas the stability of the deep section might represent a compensatory or structurally more robust component of the muscle’s architecture.

Table 2. Variables on anthropometrics, training status, and age grade, stratified by sex and event type

Variable	Female	Male	P Value Sex	Jumpers	Runners	Throwers	Walkers	P Value Event Type	Post Hoc
Sample size	64	108		15	129	14	14		
Age, yr	54.5 (11.1)	59.5 (12.2)	0.007	64.1 (13.8)	56.5 (11.2)	54.9 (13.8)	63.7 (12.3)	0.006	
Height, cm	164.1 (6.8)	174.6 (6.8)	<0.001	172.3 (8.6)	170.6 (8)	176.9 (9.7)	163.7 (6.8)	<0.001	Walk-jump ($P = 0.025$), throw-run ($P = 0.014$) and walk-throw ($P < 0.001$)
Body mass, kg	61.2 (9.6)	75.4 (10.8)	<0.001	72.1 (9.4)	68.8 (10.4)	88.5 (18.1)	61.3 (8.2)	<0.001	Throw-jump ($P < 0.001$), throw-run ($P < 0.001$), and walk-throw ($P < 0.001$)
BMI, kg/m ²	22.7 (3.2)	24.7 (2.8)	<0.001	24.4 (3.8)	23.5 (2.5)	28.2 (4.7)	22.8 (2.4)	<0.001	Throw-jump ($P = 0.007$), throw-run ($P < 0.001$), and walk-throw ($P < 0.001$)
Training during season, h/wk	9.5 (6.2)	7.8 (3.8)	0.076	8 (4.6)	8.6 (4.8)	6.3 (3.3)	10.1 (7.2)	0.37	
Training off-season, h/wk	7.9 (5.6)	6.9 (4.6)	0.2	6.6 (4.5)	7.4 (4.8)	5.2 (3.4)	8.4 (7.7)	0.5	
Season length, mo	6.7 (3.4)	6.7 (3.3)	0.99	7 (2.9)	6.5 (3.3)	7.6 (2.9)	7.8 (4.3)	0.41	
Strength training, h/wk	2 (1.8)	2.2 (1.8)	0.48	2.2 (1.6)	2.1 (1.8)	2.2 (1.1)	2 (2.1)	0.59	
Age grade, %	74 (10.9)	74.6 (13.4)	0.4	74.6 (7.4)	76.8 (10.5)	52.8 (14.3)	75.5 (10.4)	<0.001	Throw-jump ($P < 0.001$), throw-run ($P < 0.001$), and walk-throw ($P < 0.001$)
Mark grade, %	62.2 (13.2)	61.8 (13.5)	0.81	54.5 (10.4)	65.5 (11.7)	42.8 (12.4)	59.8 (10.1)	<0.001	
Achilles tendon lever arm, mm	59.3 (6.8)	65.2 (5.8)	<0.001	63.9 (5.2)	63.3 (6.8)	65.8 (5.8)	57.4 (6.3)	0.018	
Length of the soleus tendon, mm	61.8 (25.4)	69.3 (24.7)	0.064	68.9 (22.8)	66 (25.3)	68.7 (27.8)	67.6 (25.6)	0.92	
Length of the GM tendon, mm	184.3 (27.2)	194.2 (22.7)	0.012	200.5 (30.6)	189.5 (25.1)	188.7 (21.7)	190.9 (17.7)	0.36	

Data are presented as means (SD). The total study cohort ($N = 172$) consists of 64 female and 108 male participants. Athletes were classified by event type as jumpers ($n = 15$), runners ($n = 129$), throwers ($n = 14$), and walkers ($n = 14$). Statistical analysis: differences between groups were assessed using analysis of covariance (ANCOVA), with sex and event type as fixed factors and age as a covariate ($n = 172$ for all rows). For significant main effects of event type ($P < 0.05$), pairwise comparisons were performed using Tukey's post hoc tests, with exact P values reported in the final column. Age grades and mark grades represent age-adjusted and raw performance benchmarks, respectively, derived from World Masters Rankings. BMI, body mass index; GM, gastrocnemius medialis.

Interdependency of Muscle Anatomical Features in the Relaxed State

Fascicle curvature showed a strong positive correlation with the deep pennation angle ($r = 0.74$, $P < 0.001$) but was not correlated with the superficial pennation angle ($r = -0.019$, $P = 0.81$). Between the superficial and the deep pennation angles, a strong positive correlation was found ($r = 0.61$, $P < 0.001$). Fascicle length exhibited a positive correlation with muscle thickness ($r = 0.48$, $P < 0.001$) and negative correlations with both deep ($r = -0.48$, $P < 0.001$) and superficial pennation angle ($r = -0.42$, $P < 0.001$). In addition, deep and superficial pennation angle each displayed positive correlations with muscle thickness ($r = 0.37$ and $r = 0.41$, respectively; both $P < 0.001$).

Interdependency of Muscle Anatomical Features in the Contractile State

Change in fascicle curvature showed a positive correlation with deep fascicle rotation ($r = 0.82$, $P < 0.001$), whereas its correlation with superficial fascicle rotation was negative ($r = -0.30$, $P < 0.001$). Fascicle-normal strain

was positively correlated with deep pennation angle ($r = 0.64$, $P < 0.001$), superficial pennation angle ($r = 0.58$, $P < 0.001$), and fascicle curvature at rest ($r = 0.34$, $P < 0.001$). Given that compressive strains are expressed as negative values, these results indicate that greater fascicle curvature and larger pennation angles at rest were associated with reduced fascicle-normal strain during maximal contractions. Achilles tendon g-force displayed only weak or nonsignificant correlations with deep pennation angle ($r = -0.09$, $P = 0.26$), superficial pennation angle ($r = -0.08$, $P = 0.28$), but correlated positively with fascicle length ($r = 0.26$, $P < 0.001$).

Association with Athletic Age Grade

To investigate the influence of muscle strength, architecture, and fascicle kinematics on athletic performance, partial regression models were tested with age and individual muscle parameters as predictors (Table 4). Only dynamometer torque (plantar flexor strength), Achilles tendon force and Achilles tendon g-force, skin and fat tissue thickness, and length of the soleus tendon were significant predictors of age grade (all $P < 0.05$). None of the other architectural or fascicle-kinematic parameters showed significant associations,

Table 3. Results for plantar flexion measurements, anatomical features at rest, and tissue deformation

Variable	Female	Male	P Value	Jumpers	Runners	Throwers	Walkers	P Value Event Type	Post Hoc	Age (% per Decade)	P Value Age
Sample size	64	108		15	129	14	14				
Achilles tendon Force, N	1914.16 (572.91)	2017.45 (592.25)	0.12	2085.38 (524.11)	1968.3 (621.67)	2032.1 (508.07)	1931.65 (453.9)	0.44	-	-4.26 (16.29)	<0.001
Achilles tendon gForce	3.18 (0.89)	2.76 (0.81)	0.003	3 (0.84)	2.92 (0.9)	2.42 (0.61)	3.11 (0.61)	0.061		-3.54 (16.32)	<0.001
Plantar flexor strength, N·m	113.55 (36.87)	131.91 (40.87)	<0.001	133.51 (36.26)	125.58 (42.53)	132.3 (37.58)	112.66 (27.27)	0.31		-1.84 (7.02)	<0.001
<i>Anatomical features in the relaxed state</i>											
Skin + fat tissue thickness, mm	5.45 (2.09)	3.88 (1.8)	0.18	3.88 (1.8)	4.13 (1.55)	6.39 (3.52)	4.69 (1.98)	0.093		n.s	0.29
Muscle thickness, mm	14.83 (2.91)	15.93 (3.15)	0.2	15.28 (3.36)	15.62 (3.02)	16.12 (3.74)	14.96 (2.67)	0.97		n.s	0.26
Deep pennation angle, degree	35.35 (13.6)	35.1 (12.1)	0.9	37.05 (14.73)	34.94 (12.43)	33.5 (11.62)	36.88 (12.08)	0.36		n.s	0.3
Superficial pennation angle, degree	27.22 (8.37)	27.85 (8.08)	0.39	25.99 (6)	27.91 (8.66)	28.07 (7.17)	27.05 (7.42)	0.98		n.s	0.32
Fascicle length, mm	30.03 (6.95)	31.5 (6.45)	0.035	31.26 (8.02)	31.07 (6.71)	32.22 (6.05)	28.89 (4.1)	0.83		-1.83 (13.74)	0.002
Fascicle curvature, m ⁻¹	6.97 (11.68)	6.85 (11.05)	0.71	10.57 (13.74)	6.51 (10.87)	3.38 (10.59)	9.6 (10.05)	0.033	n.s.	n.s	0.64
<i>Tissue deformation</i>											
Skin and fat tissue strain, %	-4.84 (6.62)	-2.24 (13.17)	0.083	-2.86 (8.45)	-3.39 (12.67)	-2.46 (7.82)	-1.49 (8.67)	0.69		n.s	0.49
Muscle strain, %	6.61 (6.7)	9 (6.96)	0.019	7.6 (6.15)	8.3 (6.89)	8.53 (7.08)	8.12 (8.4)	0.89		n.s	0.44
Change in deep pennation angle, degree	25.29 (15.22)	27.34 (14.26)	0.18	25.41 (17.19)	26.8 (14.1)	26.56 (15.95)	27.49 (13.71)	0.96		n.s	0.27
Change in superficial pennation angle, degree	13.14 (9.13)	14.33 (9.49)	0.45	12.53 (6.97)	14.47 (9.63)	12.76 (9.66)	12.84 (9.53)	0.84		-6.57 (51.29)	0.003
Fascicle-normal strain, %	-26.8 (9.18)	-26.03 (9.98)	0.57	-25.84 (8.37)	-26.58 (9.93)	-26.47 (10.2)	-24.11 (9.03)	0.73		n.s	0.72
Change in fascicle curvature, m ⁻¹	11.66 (14.97)	12.78 (15.08)	0.29	11.81 (18.8)	12.03 (14.56)	14.06 (14.83)	14.4 (14.12)	0.83		n.s	0.65

Data are presented as means (SD). The total study cohort ($N = 172$) includes 108 male and 64 female participants, stratified by event type: jumpers ($n = 15$), runners ($n = 129$), throwers ($n = 14$), and walkers ($n = 14$). Statistical analysis: for variables with a single measurement (anatomical features in the relaxed state), an analysis of covariance (ANCOVA) was used. For variables involving contraction data (muscle strength and tissue deformation), linear mixed-effects models were applied with sex, event type, and age as fixed effects and participant identity as a random effect ($n = 172$ for all analyses). The column "Age (% per decade)" reflects the fixed-effect coefficient for age within these models. Significant main effects for event type ($P < 0.05$) were followed by Tukey's post hoc tests. Exact P values for all main effects and age-related changes are provided. GM, gastrocnemius medialis.

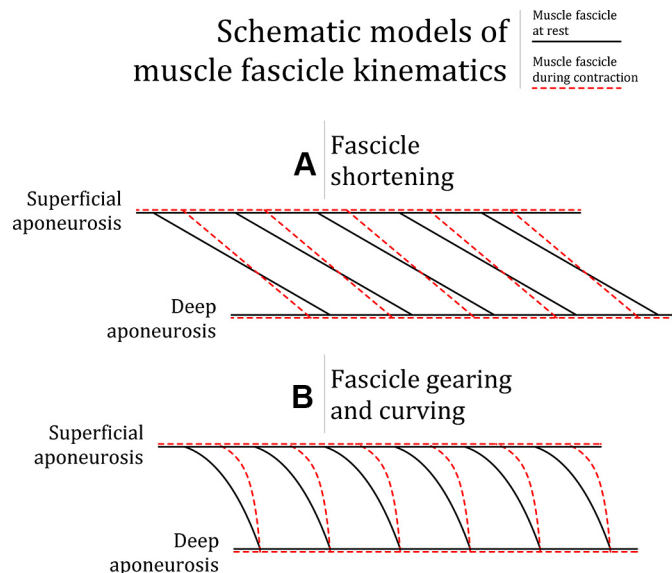


Figure 6. Schematic models of the suggested modes of muscle fascicle kinematics. The resting state is indicated by solid black lines, and the contraction state by dashed red lines. In both models, the superficial aponeurosis elevates during contraction, reflecting the increase in muscle thickness. **A:** fascicle shortening mode: fascicles undergo longitudinal shortening with a concomitant increase in pennation angle. **B:** fascicle gearing and curving mode: fascicles exhibit pronounced curving during contraction, which illustrates the uncoupling of fascicle and muscle-tendon unit kinematics.

with many variables (e.g., deep pennation angle, fascicle length) contributing an R^2 of 0.00. Because fascicle strain and deep fascicle rotation may each contribute independently to mechanical output, an additional partial regression analysis was performed with Achilles tendon g-force as the dependent variable and fascicle strain and deep fascicle rotation as independent variables. The results indicated partial R^2 values of 0.04 (95% CI 0.00–0.12) for fascicle strain and 0.000 (95% CI 0.00–0.03) for deep fascicle rotation. This suggests a contribution of fascicle strain ($r = -0.21$, $P = 0.007$) but no contribution of fascicle rotation ($r = 0.05$, $P = 0.56$) to the mechanical output represented by g-force.

Exploratory Analyses by Training Specificity

To address potential discipline-specific effects, we performed exploratory subgroup analyses comparing endurance-oriented ($n = 54$) and power/sprint-oriented ($n = 81$) athletes (see Supplemental Table S1). After adjusting for age and sex, training specificity did not significantly influence superficial fascicle rotation (β for power/sprint vs. endurance; $\beta = -1.04^\circ$, $P = 0.438$), deep fascicle rotation ($\beta = 0.33^\circ$, $P = 0.879$), or resting fascicle length ($\beta = 0.83$ mm, $P = 0.469$). In contrast, power/sprint-oriented athletes exhibited significantly greater plantar flexor strength ($\beta = 20.33$ N·m, $P = 0.002$) and Achilles tendon force ($\beta = 275.40$ N, $P = 0.006$), whereas Achilles tendon g-force did not differ significantly between groups ($\beta = 0.12$ g, $P = 0.424$). Across all models, age remained a consistent negative predictor for both architectural and functional parameters associated with superficial fascicle rotation ($\beta = -0.11^\circ/\text{year}$, $P = 0.051$), resting fascicle length ($\beta = -0.12$ mm/year, $P = 0.012$),

plantar flexor strength ($\beta = -1.41$ N·m/year, $P < 0.001$), Achilles tendon force ($\beta = -20.19$ N/year, $P < 0.001$), and Achilles tendon g-force ($\beta = -0.025$ g/year, $P < 0.001$).

Exploratory Interaction Analysis of Age and Training Specificity

To examine whether age-related associations differed according to training specificity, we fitted exploratory models including an age $\times$ training specificity interaction term (Supplemental Table S2). These interaction terms were not statistically significant for superficial fascicle rotation ($\beta = 0.031^\circ/\text{year}$, $P = 0.795$), deep fascicle rotation ($\beta = 0.253^\circ/\text{year}$, $P = 0.188$), resting fascicle length ($\beta = -0.097$ mm/year, $P = 0.340$), plantar flexor strength ($\beta = -0.87$ N·m/year, $P = 0.123$), Achilles tendon force ($\beta = -10.56$ N/year, $P = 0.225$), or Achilles tendon g-force ($\beta = -0.017$ g/year, $P = 0.204$). Thus, the age-related patterns did not appear to differ substantially between endurance- and power/sprint-oriented athletes.

Exploratory Analyses by Performance Level

We next compared athletes with high age-graded performance ($>85\%$, $n = 30$) to lower-performing athletes ($<70\%$, $n = 44$), adjusting for age and sex (Supplemental Table S3). Higher-performing athletes exhibited greater superficial fascicle rotation ($\beta = 4.14^\circ$, $P = 0.027$), greater plantar flexor strength ($\beta = 33.29$ N·m, $P < 0.001$), greater Achilles tendon force ($\beta = 474.48$ N, $P < 0.001$), and greater Achilles tendon g-force ($\beta = 1.03$ g, $P < 0.001$). In contrast, no significant difference was found for deep fascicle rotation ($\beta = 0.47^\circ$, $P = 0.892$) or resting fascicle length ($\beta = 2.02$ mm, $P = 0.203$). Within these models, age remained negatively associated with superficial fascicle rotation ($\beta = -0.16^\circ/\text{year}$, $P = 0.039$), resting fascicle length ($\beta = -0.21$ mm/year, $P = 0.003$), plantar flexor strength ($\beta = -1.68$ N·m/year, $P < 0.001$), Achilles tendon force ($\beta = -23.99$ N/year, $P < 0.001$), and Achilles tendon g-force ($\beta = -0.021$ g/year, $P = 0.004$).

Combined Exploratory Analysis of Training Specificity and Performance Level

In an additional model restricted to endurance- and power/sprint-oriented athletes and simultaneously including high/low performers (Supplemental Table S4), the difference in superficial fascicle rotation between high- and low-performing athletes remained borderline significant ($\beta = 4.48^\circ$, $P = 0.050$), whereas a significant difference between training-specific groups was also observed (β for power/sprint vs. endurance = -5.49° , $P = 0.010$). In the same restricted model, high-performing athletes continued to show greater plantar flexor strength ($\beta = 36.48$ N·m, $P = 0.001$), greater Achilles tendon force ($\beta = 550.92$ N, $P = 0.001$), and greater Achilles tendon g-force ($\beta = 1.12$ g, $P < 0.001$), whereas training specificity was not significantly associated with these force-related outcomes after adjustment for age, sex, and performance group (all $P \geq 0.149$).

Sensitivity Analysis in Athletes Aged 50–60 Yr

As a sensitivity analysis, we repeated the endurance-versus-power/sprint comparison within a group with narrower age range of 50–60 yr (Supplemental Table S5, endurance:

Table 4. Partial regression results for variables predicting age-graded competition performance

	Variable	R ² _Model	R ² _Age	R ² _Variable
Muscle strength	Plantar flexor strength, N m	0.255	0.144	0.057
	Achilles tendon force, N	0.261	0.134	0.063
	Achilles tendon gForce	0.312	0.128	0.128
Anatomical features in the relaxed state	Skin + fat tissue thickness, mm	0.379	0.278	0.213
	Muscle thickness, mm	0.211	0.2	0.001
	Deep pennation angle, degree	0.21	0.209	0
	Superficial pennation angle, degree	0.21	0.209	0
	Fascicle length, mm	0.21	0.203	0
	Fascicle curvature, m ⁻¹	0.211	0.209	0.001
	Achilles tendon lever arm, mm	0.212	0.211	0.001
	Length of the soleus tendon, mm	0.232	0.232	0.03
	Length of the GM tendon, mm	0.224	0.22	0.017
	Muscle tendon length, mm	0.22	0.209	0.012
	Skin and fat tissue strain, %	0.211	0.209	0.001
Tissue deformation	Muscle strain, %	0.21	0.209	0
	Change in deep pennation angle, degree	0.21	0.21	0
	Change in superficial pennation angle, degree	0.229	0.196	0.024
	Fascicle-normal strain, %	0.21	0.21	0
	Change in fascicle curvature, m ⁻¹	0.217	0.205	0.009

Linear models (for single measures) or linear mixed-effects models (for repeated measures) were fitted to evaluate the contribution of physiological and architectural parameters to competition performance (expressed as a percentage of the world record). In each model, age and sex were included as fixed covariates to determine their independent contribution to the variance (total $N = 172$; 108 males and 64 females). R^2_{Model} represents the total variance explained by the full model; R^2_{Age} represents the variance explained by age alone; and R^2_{Variable} indicates the unique incremental variance explained by the specific variable after accounting for age and sex, calculated using the $r2\text{beta}$ function. Statistical significance was set at $P < 0.05$. gForce, gravitational force equivalent; GM, gastrocnemius medialis; N, Newtons; N m, Newton meters.

$n = 19$, power/sprint: $n = 29$). In this subset, no significant differences between groups were found for superficial fascicle rotation ($\beta = 1.93^\circ$, $P = 0.412$), deep fascicle rotation ($\beta = 3.77^\circ$, $P = 0.241$), resting fascicle length ($\beta = 1.99$ mm, $P = 0.317$), plantar flexor strength ($\beta = 10.83$ N·m, $P = 0.351$), Achilles tendon force ($\beta = 93.75$ N, $P = 0.603$), or Achilles tendon g-force ($\beta = -0.15$ g, $P = 0.564$).

Exploratory Comparison of High- and Low-Performing Athletes Aged 50–60 Yr

To further examine whether performance level was associated with better preservation of muscle architectural and mechanical characteristics within a narrower age range, we additionally compared high-performing athletes (age grade $>85\%$, $n = 13$) and lower-performing athletes (age grade $<70\%$, $n = 11$) restricted to those aged 50–60 yr (Supplemental Table S6). In this exploratory subset, high-performing athletes showed greater plantar flexor strength ($\beta = 40.98$ N·m, $P = 0.007$), greater Achilles tendon force ($\beta = 565.51$ N, $P = 0.013$), and greater Achilles tendon g-force ($\beta = 1.07$ g, $P = 0.003$). By contrast, no significant differences were observed for superficial fascicle rotation ($\beta = 5.74^\circ$, $P = 0.118$), deep fascicle rotation ($\beta = 3.04^\circ$, $P = 0.495$), or resting fascicle length ($\beta = -0.30$ mm, $P = 0.918$).

Exploratory Interaction Analysis of Age and Sex

As the primary analyses did not include interaction terms, we explored age $\times$ sex interactions for the main outcomes (Supplemental Table S7). None of these interactions were statistically significant, including superficial fascicle rotation ($\beta = -0.067^\circ/\text{year}$, $P = 0.531$), deep fascicle rotation ($\beta = 0.031^\circ/\text{year}$, $P = 0.859$), resting fascicle length ($\beta = -0.044$ mm/year, $P = 0.616$), plantar flexor strength ($\beta = -0.30$ N·m/year, $P = 0.542$), Achilles tendon force

($\beta = 0.48$ N/year, $P = 0.950$), and Achilles tendon g-force ($\beta = 0.009$ g/year, $P = 0.421$).

DISCUSSION

The present study suggests that in a unique cohort of masters athletes, contraction-induced fascicle curvature and rotation in the medial gastrocnemius operate as partially independent kinematic modes, with the superficial region exhibiting a selective vulnerability to aging. Although deep fascicle rotation and overall fascicle strain were largely preserved in masters athletes, superficial fascicle rotation showed a significant age-related decline. These findings extend prior work on fascicle kinematics (27) and are consistent with the idea that aging is associated with region-specific alterations in intramuscular deformation patterns that persist despite long-term athletic training.

Traditionally, fascicle shortening has previously been assumed to directly correspond to rotation, contributing to muscle gearing and velocity modulation (18, 35–37). However, our data reveal a regional decoupling: A key mechanistic observation was a strong positive association between curvature and rotation in the deep medial gastrocnemius, contrasted by a moderate and inverse relationship in the superficial region. This decoupling is consistent with the “non-uniform” model of muscle contraction, where internal rearrangements are not merely a byproduct of fascicle shortening.

Indeed, absolute fascicle strain was not modulated by age, yet superficial rotation declined. This may suggest that within a population of competitive masters athletes, the capacity for fascicle shortening remains remarkably stable across age groups. In contrast, the architectural gearing, specifically the ability of superficial fascicles to rotate during contraction, shows a progressive, age-related impairment.

This dissociation raises the possibility that age-related changes in masters athletes primarily affect the architectural accommodation of internal stresses rather than causing a linear decline in the contractile process itself. Although fascicle curvature and dynamic gearing mechanisms remain present in older muscle (17, 18, 28), the selective reduction in superficial rotation is consistent with a layer-specific age-related vulnerability of muscle kinematics.

Such changes may suggest age-related alterations in intramuscular connective tissue (38, 39) and are consistent with reduced shear mobility between fascicle bundles (40), potentially linked to altered perimysial stiffness. Consistent with this interpretation, muscle thickness increased by ~8% during contraction, with rotation-dominated deformation being slightly more pronounced in males than in females but comparable across athletic specializations. Age-related reductions in resting fascicle length were also observed, whereas resting pennation angles remained unchanged. These observations are consistent with established principles of sarcopenic remodeling (16, 19, 35, 37). Furthermore, the expected declines in muscle quality, including increased intramuscular adipose and extracellular matrix (ECM) infiltration, align with previous reports and represent hallmarks of primary aging processes (9, 14, 15, 41, 42).

Our findings indicate that fascicle rotation remains a major contributor to contraction-induced muscle bulging even in older age, though its regional attenuation may suggest a constraint on optimal architectural gearing. Of note, however, architectural and kinematic variables were not significant predictors of age-graded performance in the current cohort. Consequently, the functional implications of these findings should be interpreted with caution. Furthermore, it must be acknowledged that the observed kinematic patterns may be muscle-specific. Although the medial gastrocnemius is a pivotal locomotor muscle, it may not represent the primary site for observing lifelong training-specific adaptations in power-oriented athletes as compared with larger proximal muscles like the vastus lateralis or hamstrings. Rather than a confirmed explanation for performance decline, the observed regional attenuation of rotation should be viewed as a mechanistic hypothesis that warrants further investigation.

In the present study, the data suggest that even when muscle mass is relatively well preserved, internal mechanical properties may still undergo age-related shifts (8, 12, 13).

The qualitative decline in muscle motility raises the possibility that muscle quantity alone is an insufficient marker of contraction-induced deformation capacity. Although previous literature indicates that masters athletes maintain mass and neuromuscular function better than sedentary age-matched adults (21–23), the absence of a contemporaneous control group in the present study means that these comparisons are indirect and should be interpreted with caution.

Crucially, while neither architectural nor kinematic variables were significant linear predictors of age-graded performance across the entire cohort, our exploratory subgroup analysis provides a more nuanced perspective. These findings must be interpreted with caution given the limited sample sizes in some subgroups; accordingly, they should be considered hypothesis-generating and warrant confirmation in future studies. The observation that high-

performing athletes (>85% age grade) maintain significantly greater superficial fascicle rotation compared with lower-scoring peers ($\beta = 4.14^\circ$, $P = 0.027$; Supplemental Table S3) suggests that preserved architectural gearing may indeed be a hallmark of the elite masters athlete phenotype. This aligns with the hypothesis that high-performing individuals may possess a “younger” biological profile, marked by the preservation of internal muscle mechanical properties. A similar link between high-level performance and biological youth has been demonstrated in masters sprinters, whose performance scores correlated significantly with longer telomere lengths (43).

Sensitivity analysis within the 50–60-yr age range indicated that high performers maintained superior strength and tendon loading capacity. Although the difference in superficial rotation was not statistically significant in this smaller subgroup ($P = 0.118$), the observed trend ($\beta = 5.74^\circ$; Supplemental Table S6) warrants further investigation in larger cohorts. These results further support the hypothesis that loading modality influences intramuscular deformation, as evidenced by the significant difference in superficial rotation between training-specific groups in the combined model ($\beta = -5.49$, $P = 0.010$; Supplemental Table S4).

Consequently, maintained superficial motility may be a prerequisite for achieving higher-level performance in older age, even if global performance is partially sustained through compensatory strategies. This evidence further suggests that neural or tissue property changes, such as altered motor unit recruitment or increased intramuscular connective tissue, may ultimately underlie mechanical decline in this population rather than gross architectural remodeling (44).

Previous work has demonstrated greater variability in fascicle curvature in nonathletic females, underscoring the importance of sex-specific muscle mechanics (27). Although we find that males showed more pronounced rotation-dominated thickness changes, findings were largely comparable across athletic specializations. However, it must be acknowledged that the broad grouping of athletic specializations, particularly the pooling of specific running disciplines (from sprinters to marathoners) into a single category, limits our exploratory scope. This heterogeneity within the runner group may mask discipline-specific adaptations to high-velocity versus high-volume loading.

As runners and jumpers tended to exhibit greater curvature than throwers, the absence of statistically robust post hoc differences may suggest that habitual high-load training promotes broadly similar medial gastrocnemius architecture (24). However, it must be acknowledged that the broad grouping of athletic specializations, particularly the pooling of diverse running disciplines (from sprinters to marathoners) into a single category, limits our exploratory scope. This heterogeneity within the runner group may mask discipline-specific adaptations to high-velocity versus high-volume loading. Future research should specifically target a more balanced comparison between power- and endurance-trained masters athletes to address this limitation.

Importantly, the persistence of superficial kinematic deficits in these competitive masters athletes suggests that certain aspects of age-related mechanical decline may be resistant to the mechanical loading types represented in this cohort.

Although the current data indicate a degree of resistance to lifelong training, the hypothesis that alternative loading modalities could mitigate these declines remains compelling. High-velocity power training specifically targets rapid motor unit recruitment, while eccentric loading may modify the stiffness of intramuscular connective tissue and promote sarcomerogenesis (45). These adaptations could potentially help preserve fascicle rotational dynamics by addressing the qualitative structural shifts that occur with advancing age.

Although our exploratory analyses included a comparison between power-trained and endurance-oriented athletes, the observed age-related patterns were largely consistent across disciplines. This suggests that the training exposures within our cohort were insufficient to fully counteract the age-dependent shift in superficial rotation. Ultimately, this selective reduction in rotation provides a plausible architectural mechanism that may contribute to the disproportionate loss of muscle power relative to isometric strength commonly observed with aging. Whether specifically targeted interventions or different athletic exposures can influence this regional vulnerability remains a subject for future investigation.

Limitations

Although we attribute the age-related decline in superficial fascicle rotation to a disruption in intramuscular force transmission, which may be related to changes in the extracellular matrix (ECM), we did not directly assess connective tissue properties, such as collagen cross-linking or perimysial stiffness. Previous research is consistent with the idea that fibrosis and increased stiffness in noncontractile tissues can impair shear mobility between fascicles (41). Future studies utilizing elastography or histological analysis are required to confirm the biochemical basis of these kinematic shifts.

Experimental posture and task specificity may influence the generalizability of our findings to age-graded performances or daily life mobility. Measurements were obtained at 90° knee flexion, which shortened the gastrocnemius and reduced plantar-flexor torque by ~25% compared with full extension, reflecting significant mechanical constraints and altered motor-unit recruitment (46, 47). Modeling suggests that 100° knee flexion with 3° dorsiflexion approximates the muscle-tendon complex length observed at 60° flexion with 10° plantar flexion, a posture more representative of running (48). Consequently, our measurements likely represent the shorter end of the medial gastrocnemius's physiological range. Furthermore, the results of this ramped isometric task may not translate to the complex, high-velocity, and stretch-shortening cycle movements typical for explosive athletic performance, where fascicle kinematics likely differ from those observed during static movement. Furthermore, the use of two-dimensional B-mode ultrasound and force-based tendon estimates in this study, while reliable for field-based dynamometry, may not capture the complex three-dimensional interactions among fascicles, aponeuroses, and tendons. The field-based setting during international competition precluded the use of high-fidelity laboratory equipment, potentially limiting the detection of subtle architectural differences or causal inferences due to

the study's cross-sectional design. Furthermore, the self-selected nature of the cohort resulted in sex distribution imbalances and lacked a nonathletic control group, thereby restricting direct comparisons to untrained populations. Consequently, these findings on the "optimized" state of aging muscle should be interpreted in relation to existing literature rather than as direct evidence of an athletic protective effect. Although our cohort consisted of competitive athletes with potentially long training history, total daily physical activity levels outside of structured training were not directly assessed in this study. Additional factors such as detailed training and injury histories or direct imaging of tendon material properties were also not addressed and may influence the observed kinematics.

Despite these limitations, this study provides valuable insights into muscle architecture and fascicle kinematics in a unique cohort of highly trained masters athletes across a wide age spectrum. The standardized approach effectively revealed critical distinctions between shortening and rotating mode kinematics. Specifically, the age-related inhibition of superficial fascicle rotation emerged as a robust feature that appears independent of sex and athletic specialization, as evidenced by the lack of significant interaction effects in our exploratory sensitivity analyses. These results suggest that the internal mechanical behavior of the medial gastrocnemius undergoes age-related, region-specific alterations, even when macroscopic performance and exercise training are maintained.

Conclusions

This study provides a detailed characterization of medial gastrocnemius architecture, fascicle kinematics, and tendon loading in a unique cohort of competitive masters athletes. Our findings reveal that sex and event specialization exert minimal influence on muscle architecture, and that the muscle-tendon unit maintains remarkable functional robustness across diverse athletic profiles. However, although global fascicle shortening (strain) is effectively preserved across age groups, aging selectively disrupts superficial fascicle kinematics. This regional impairment in rotation may suggest a progressive and potentially obligatory age-related decline in the mechanical coordination between contractile and non-contractile tissues.

The decoupling of superficial rotation from fascicle shortening raises the possibility that the "architectural gearing" necessary for rapid velocity modulation may be compromised, even when the fundamental contractile machinery remains resilient. However, given the lack of association between these metrics and age-graded performance, these changes should be viewed as structural markers of aging rather than definitive drivers of functional decline. Future research should investigate whether these layer-specific kinematic shifts are driven by age-related alterations in intramuscular connective tissue properties, such as collagen cross-linking, or shifts in regional motor unit recruitment. Ultimately, the selective attenuation of superficial fascicle rotation provides a potential mechanism to explain the disproportionate decline in explosive power relative to isometric strength in aging. These findings underscore that maintaining muscle mass alone may be insufficient to preserve high-level function; rather, the preservation of

internal muscle “motility” and architectural gearing represents a key area for inquiry in understanding functional decline.

Preserving internal muscle motility and gearing in older age may require exercise modalities beyond traditional hypertrophy-oriented protocols. Incorporating high-velocity power training and eccentric loading could be a way to provide the mechanical shear stress necessary to maintain perimysial compliance and prevent the fibrotic constraints that impair fascicle rotation. Clinically, emphasizing movement diversity and full-range-of-motion exercises may mitigate age-related connective tissue stiffening, sustaining the muscle’s capacity for architectural adaptation during contraction.

DATA AVAILABILITY

Data will be made available upon reasonable request.

SUPPLEMENTAL MATERIAL

Supplemental Tables S1–S7: <https://doi.org/10.6084/m9.figshare.33027065>.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author.

AUTHOR CONTRIBUTIONS

S.M., E.M., and J.R. conceived and designed research; S.M. and W.S. performed experiments; U.M., B.A., and J.R. analyzed data; S.M. interpreted results of experiments; S.M. prepared figures; S.M. drafted manuscript; S.M., U.M., E.M., T.V., J.Z., and D.P. edited and revised manuscript; S.M., U.M., E.M., W.S., T.V., J.Z., B.A., and D.P. approved final version of manuscript.

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