RESEARCH ARTICLE

Intrinsic foot muscles contribute to elastic energy storage and return in the human foot

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Kelly LA, Farris DJ, Cresswell AG, Lichtwark GA. Intrinsic foot muscles contribute to elastic energy storage and return in the human foot. *J Appl Physiol* 126: 231–238, 2019. First published November 21, 2018; doi:10.1152/japplphysiol.00736.2018.—The human foot is uniquely stiff to enable forward propulsion, yet also possesses sufficient elasticity to act as an energy store, recycling mechanical energy during locomotion. Historically, this dichotomous function has been attributed to the passive contribution of the plantar aponeurosis. However, recent evidence highlights the potential for muscles to modulate the energetic function of the foot actively. Here, we test the hypothesis that the central nervous system can actively control the foot's energetic function, via activation of the muscles within the foot's longitudinal arch. We used a custom-built loading apparatus to deliver cyclical loads to human feet in vivo, to deform the arch in a manner similar to that observed in locomotion. We recorded foot motion and forces, alongside muscle activation and ultrasound images from flexor digitorum brevis (FDB), an intrinsic foot muscle that spans the arch. When active, the FDB muscle fascicles contracted in an isometric manner, facilitating elastic energy storage in the tendon, in addition to the energy stored within the plantar aponeurosis. We propose that the human foot is akin to an active suspension system for the human body, with mechanical and energetic properties that can be actively controlled by the central nervous system.

NEW & NOTEWORTHY The human foot is renowned for its ability to recycle mechanical energy during locomotion, contributing up to 17% of the energy required to power a stride. This mechanism has long been considered passive in nature, facilitated by the elastic ligaments within the arch of the foot. In this paper, we present the first direct evidence that the intrinsic foot muscles also contribute to elastic energy storage and return within the human foot. Isometric contraction of the flexor digitorum brevis muscle tissue facilitates tendon stretch and recoil during controlled loading of the foot. The significance of these muscles has been greatly debated by evolutionary biologists seeking to understand the origins of upright posture and gait, as well as applied and clinical scientists. The data we present here show a potential function for these muscles in contributing to the energetic function of the human foot.

flexor digitorum brevis; foot biomechanics; longitudinal arch; muscle fascicle; ultrasound

INTRODUCTION

The human foot is a mechanical paradox. Compared with other nonhuman primates, the foot is uniquely stiff, enabling

forward propulsion (2, 7). Yet, the foot is also renowned for compliance, possessing spring-like qualities that allow mechanical energy to be stored and returned during each step, substantially improving the economy of locomotion (22, 31). This unique interplay of mechanical function is considered to have played an important role in the evolution to habitual upright locomotion (4).

The plantar aponeurosis and plantar ligaments have been attributed much of the credit for determining human foot function. These ligamentous structures provide a means to store and return mechanical energy via elastic stretch and recoil (22), while also passively increasing foot stiffness to facilitate forward propulsion via the windlass mechanism (14). The spring-like function of the foot is considered a vital element in economical human locomotion, providing a means to recycle mechanical energy without the added metabolic cost of activating muscles (22). However, the model of the foot as a passive structure does not explain the capacity for the foot to adapt to the varied mechanical requirements of locomotion with constantly varying speeds and substrates, while still facilitating effective foot-ground force transmission (2, 6, 21). If the foot spring mechanism were purely passive in nature, the magnitude of energy stored and returned within the foot would be directly dependent on the magnitude of strain produced in the plantar aponeurosis and ligaments. In contrast to this assertion, it has recently been shown that the magnitude of negative and positive work performed at the foot can vary considerably with locomotion requirements, independently of the magnitude of plantar aponeurosis strain (16, 18, 29). This suggests that structures other than the ligamentous tissues of the foot may also be contributing to the energetic function of the foot, and importantly, the foot spring may not be an entirely passive mechanism.

The plantar intrinsic foot muscles are a group of muscles located within the longitudinal arch (LA). They have muscle tendon units (MTUs) that course a parallel anatomical pathway to the plantar aponeurosis, spanning from the calcaneus to the toes (24, 27), and therefore generate torques about the LA in the same direction as the plantar aponeurosis. The plantar intrinsic muscles display similar activation patterns to that of the triceps surae (calf) muscles, with recruitment occurring before foot-ground contact and de-activation occurring through late stance, during propulsion (20). We have estimated in previous experiments that the MTUs of the largest intrinsic foot muscles, flexor digitorum brevis (FDB) and abductor hallucis (AH) actively lengthen and shorten during stance phase of locomotion, highlighting the potential for these muscles to perform

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negative and positive work at the foot, in addition to that performed by the plantar aponeurosis (20).

In a similar anatomical arrangement to the ankle plantar flexor muscles and Achilles tendon, the FDB and AH muscles have very short muscle fibers (<25 mm) attached to long tendons (~100 mm) (24, 27, 35), making them candidates for significant storage and return of elastic energy during a stretch-shorten cycle (3, 36) (3, 36). The plantar flexors have been shown to operate near isometrically during the stance phase of walking and running (13, 25, 28), allowing energy to be recycled through stretch and shorten of the elastic tendon. Given the structure and function of the intrinsic foot muscles, it is certainly feasible that a quasi-isometric function of the contractile tissue may actually facilitate elastic energy storage within the tendons of these muscles. This function may act to modulate the foot's energy storage capacity, in addition to the contribution of the plantar aponeurosis.

Here we explored whether the foot-spring mechanism is actively modulated by the central nervous system (CNS), via the function of the intrinsic foot muscles. Specifically, we tested the hypothesis that FDB muscle would produce force in a quasi-isometric manner, facilitating storage and return of elastic energy within the tendinous tissue during compression and recoil of the foot's arch, providing additional scope for recycling of energy within the foot.

METHODS

Participants

Ten healthy participants (1 woman and 9 men, age 27 ± 7 yr; height: 179 ± 7 cm; mass: 76 ± 10 kg) with no diagnosed history of lower limb injury in the previous 6 mo or known neurological impairment volunteered to participate in the study. Written informed consent was obtained from each subject. The study protocol was approved by the institutional human research ethics committee of The University of Queensland and conducted in accordance with the Declaration of Helsinki.

Experimental Set-Up

Each participant was seated with their right forefoot placed on a rigid supporting platform that was secured to a force plate (AMTI OR6-7-1000, AMTI, MA). The ankle was orientated in ~10° of dorsiflexion, and the thigh was parallel to the floor. A magnetically driven, servo-controlled actuator, connected to a computer with real time control of force output (Linmot PS10-70x400U-BL-QJ, NTI AG Linmot, Switzerland) was positioned such that loads of up to 150% of body weight could be delivered in a downwards direction to the distal aspect of thigh at controlled speeds, using a custom-built loading apparatus (Fig. 1). The heel was positioned on a horizontal plane with the forefoot when unloaded and could move freely during each loading cycle. The loading apparatus was positioned over the thigh such that the resultant ground reaction force vector was located anterior to the ankle joint axis, similar to where it is located during mid- to late-stance in locomotion. This experimental set-up was designed to best replicate the gravitational and muscular forces acting on the lower limb during locomotion, in a tightly controlled manner.

Experimental Protocol

The actuator induced five compression cycles of the foot, delivered sequentially with ~10 s between each cycle. The time between each foot compression cycle was varied by ± 2 s, to prevent preparatory activation before loading. Foot compression cycles were performed at three loads; low (50% body wt), moderate (100% body wt), and high (150% body wt), reflecting the vertical ground reactions forces in bipedal stance (low), unipedal stance (medium), and walking (high). The rate of loading and unloading delivered by the actuator was programmed to remain constant across all conditions, with total cycle duration of 2 s. During the foot compression cycles, participants were instructed to maintain their heel at the same height as their forefoot through active plantar flexion of the ankle. This was achieved by activating the ankle plantar flexors to generate an internal ankle plantar flexion torque, countering the torque at the ankle created by the actuator. Verbal feedback was given to participants during and after each trial regarding their capacity to keep the heel in a relatively constant position. This experimental approach was chosen to produce sufficient force in the Achilles tendon, which is required to induce

Fig. 1. Experimental set-up to apply cyclic compression of the longitudinal arch (LA). An actuator delivers and downward force over the knee and anterior to the ankle joint (*left*). The ankle plantar flexors are activated to counter the downward force applied by the actuator, with this force couple producing deformation of the LA. B-mode ultrasound images (*top right*) were collected from the flexor digitorum brevis muscle during the foot compression cycles (*right*).
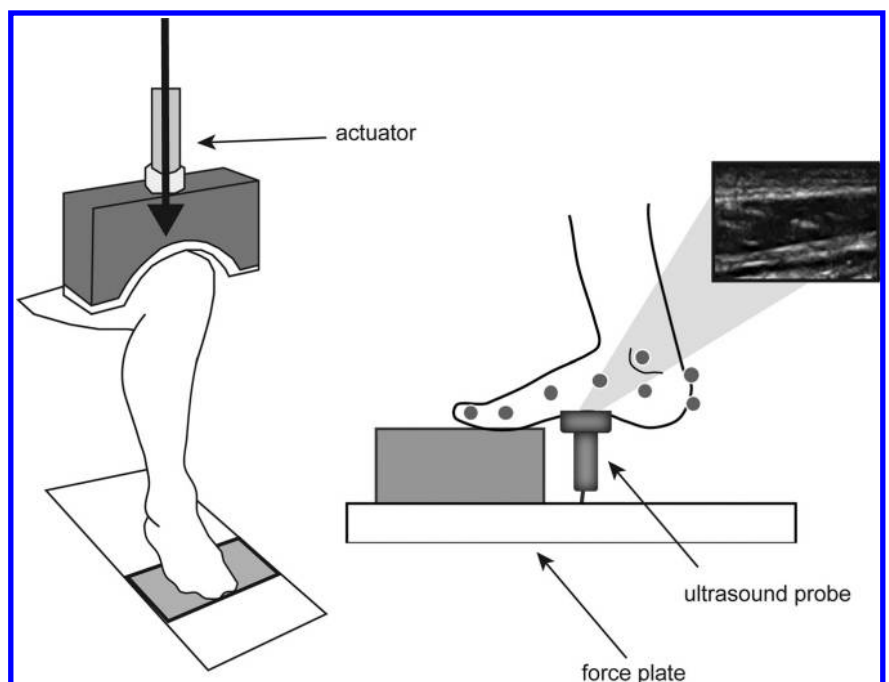
compression of the LA in a similar manner to that observed during locomotion (11) (Fig. 1).

Data Acquisition

Kinematic and kinetic measurements. Motion data were captured at 200 Hz using a six-camera three-dimensional optoelectronic motion capture system (Oqus, Qualysis, Gothenburg, Sweden). Ground reaction force (GRF) and electromyography (EMG) data were synchronously captured with the motion data at 4 kHz using a 14-bit analog to digital converter using and the Qualisys Track Management software (Qualisys, Gothenburg, Sweden). Fourteen retro-reflective markers (diameter 9.0 mm) were placed on the skin of the right foot and ankle according to a multisegment foot model developed to describe rear-, mid- and forefoot motion (26). Two additional markers were applied to the skin over the second and fourth toes, at the level of the middle phalanx, to track the movement of the lesser toes. Three markers were placed on the shank and a marker placed on the medial and lateral femoral condyles to track the position of the shank segment (20).

Muscle activation measurements. Fine-wire intramuscular EMG data were collected from the right foot of each participant in accordance with previously described methods (20). All EMG signals were amplified 1,000 times and hardware filtered with a bandwidth of 30 to 1,000 Hz (MA300, Motion Laboratories, LA). Surface EMG electrodes were also placed over the muscle belly of soleus (SOL). To prevent movement artefacts, the fine-wire electrodes, connectors, cabling, and preamplifiers were secured with cohesive bandage around the distal part of the shank. A surface ground electrode (Ag–AgCl electrode, 24 mm diameter; Tyco Healthcare Group) was secured to the skin overlying the medial malleolus.

Ultrasound measurements. Muscle fascicle length for the FDB in the loaded foot was measured using B-mode ultrasound imaging. A 128-element linear array ultrasound transducer (SonixTouch, Ultrasonix, BC, Canada) was placed under the foot such that it imaged the muscle tissue of the FDB at an orientation where the fascicles of the midbelly could be visualized throughout the muscle. The transducer was bandaged securely to the foot to hold it in place during the loading cycles (Fig. 1). Ultrasound images were sampled at 26 Hz.

Data Analysis

Kinetic, kinematic, and EMG data files were exported to Visual3D (C-Motion, Inc., Germantown, MD) for analysis. Analogue signals from the force plate were digitally filtered with a 35-Hz recursive second order Butterworth filter. A force onset-offset threshold was defined at 10% above the baseline vertical GRF (e.g., 10% more than the mass of the leg and foot). The start of the loading cycle was determined as the time-point when the rising edge of the vertical GRF rose above the onset-offset threshold, whereas the end of the loading cycle was determined as the time-point when the falling edge of the vertical GRF fell below this threshold. Subsequently the peak vertical GRF was calculated during each loading cycle and normalized to body weight.

Kinematic and kinetic data. Marker trajectories were digitally filtered with a 10-Hz recursive second-order low-pass Butterworth filter. Assumed rigid segments were created in accordance with a previously described multisegment foot model (26), including the shank, foot, calcaneus, and metatarsals. Ankle angle was defined as the rotation of the calcaneus segment relative the shank segment, in the sagittal plane, with ankle dorsiflexion represented as positive rotations. The midfoot angle was defined as the sagittal plane rotation of the metatarsals relative to the calcaneus, with midfoot dorsiflexion being positive (15). Under this definition, an increase in midfoot angle is indicative of a reduction in LA height. Ankle and midfoot angles were offset to a static unloaded trial, such that the unloaded angles are 0°. For each loading condition, LA compression was calculated by subtracting the midfoot angle at the start of the loading cycle from the

peak midfoot angle recorded during the ensuing cycle. Mean LA compression was calculated for each loading condition by averaging LA compression occurring across all loading cycles for each loading condition.

Net joint moments generated about the midfoot during each loading cycle were calculated by applying an inverse dynamic analysis within Visual 3D software (C-Motion, Inc.) in accordance with previously described techniques (5, 18). Midfoot moments were represented as internal joint moments in the proximal segment's coordinate system. Mean peak midfoot plantar-flexion moment was calculated at each load by averaging the peak values calculated during each foot compression cycle for a given condition.

Foot power analysis. We applied a unified deformable foot model to quantify the instantaneous power of the foot during the foot compression cycles (34). This approach [described in detailed elsewhere (32–34)] represents the power because of the six degree of freedom movement between the calcaneus and the ground, providing an estimate of combined power from all structures within the foot distal to the calcaneus.

MTU length. The length of the FDB MTU was calculated based on multisegment foot motion, using a previously described geometric model (20). Briefly, the MTU length was defined as the straight-line distance from the muscle origin at the calcaneus, to the insertion at the toes, via a tether point at the metatarso-phalangeal joint. Change in MTU length was calculated by subtracting the resting unloaded MTU length from the MTU length during each loading cycle. The resting MTU length was calculated during a static unloaded trial, with the foot in the experimental position. Subsequently, MTU strain was calculated by dividing the change in MTU length by the resting MTU length. The shortening and lengthening velocity of the FDB MTU was calculated as the first derivative of the MTU length with respect to time, during each loading cycle.

Muscle activation. All EMG signals were high-pass filtered using a recursive second-order Butterworth filter at 35 Hz to remove any unwanted low-frequency movement artefact. Following DC-offset removal, a root mean square (RMS) signal amplitude was calculated using a moving window of 50 ms to generate an EMG envelope. The EMG envelope for the FDB and SOL muscles was normalized to the peak RMS amplitude found across all conditions for the respective muscle. Subsequently, the magnitude of activation for each loading condition was determined by calculating an average of the mean EMG RMS envelope amplitude during each compression cycle, for each muscle.

Muscle fascicle length. Length changes of FDB muscle fascicles were assessed from the B-mode ultrasound images recorded during each loading cycle. A previously described semiautomated tracking algorithm was used to track fascicle length throughout each trial (8, 12). Briefly, an area of interest within the FDB muscle and a representative muscle fascicle was defined at the first frame of the ultrasound data. Subsequently, the ultrasound image sequence was processed using the Ultra-Track software (12), which tracks the end points of fascicles in a frame-to-frame, iterative fashion. Once the image processing was complete, instantaneous muscle fascicle length was produced as an output. Change in FDB fascicle length was calculated by subtracting the resting unloaded fascicle length from the fascicle length during each foot compression cycle. The resting fascicle length was calculated during a static, unloaded trial, with the foot in the experimental position. Muscle fascicle strain was calculated by dividing the change in fascicle length by the resting fascicle length. Shortening and lengthening velocity of the FDB fascicles were calculated as the first derivative of their lengths with respect to time, during each foot compression cycle.

Statistics

A one-way repeated measures ANOVA was used to describe the effects of loading condition (low/medium/high) on midfoot angular

displacement, peak midfoot moment, FDB MTU and fascicle length changes, and average muscle activation. Post hoc multiple comparison tests, including Bonferroni corrections were performed between each loading condition. Statistical differences were established at $P \leq 0.05$. Results are presented as mean difference + standard deviation unless otherwise stated. Effect sizes (ES) were calculated using partial ETA squared. Midfoot motion and midfoot moment data were obtained from nine participants, with one participant excluded because of issues with marker reconstruction.

RESULTS

During each foot compression cycle, vertical GRF increased (peak GRF 0.7 ± 0.1 body wt at low, 1.1 ± 0.07 body wt at medium, and 1.5 ± 0.2 body wt at high, $P \leq 0.05$, ES = 0.94, Fig. 2) as downward force was applied by the actuator (loading phase), subsequently declining as the force from the actuator was removed (unloading phase). Loading cycle duration remained relatively constant across all conditions (1.85 ± 0.40 s at low, 1.78 ± 0.35 s at medium, and 1.77 ± 0.35 s at high).

Ankle Mechanics

The ankle remained in a relatively constant orientation across all conditions, even though a small increase in ankle
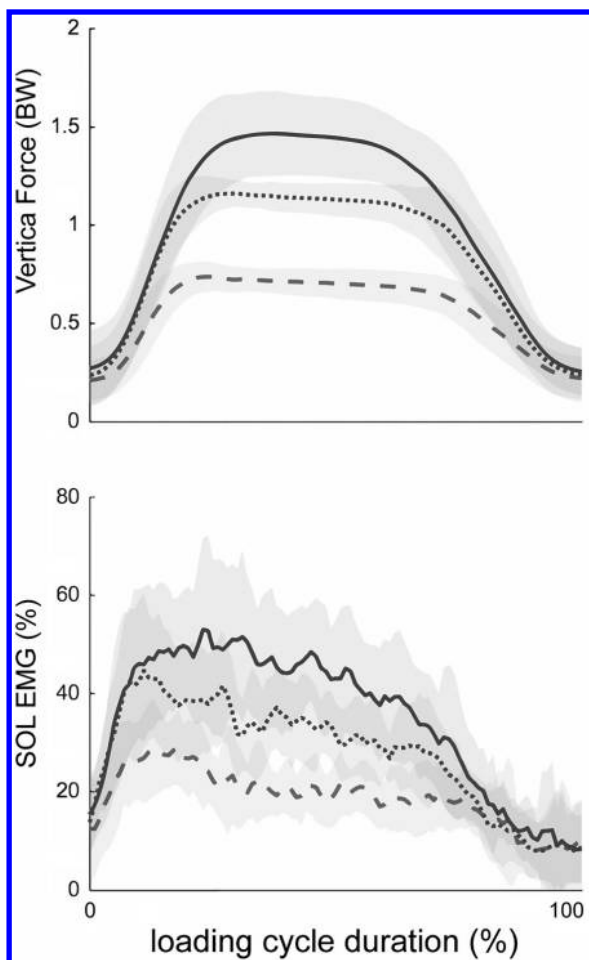

Fig. 2. Group mean ensemble data for vertical ground reaction force (*top*) and soleus electromyography (EMG) data (*bottom*) recorded during foot compression cycles at low (dash), medium (dots), and high (full line) loading conditions. *Significant difference between all conditions. BW, body weight; SOL, soleus muscle.

joint dorsiflexion was observed between the 0.5 body wt and 1.5 body wt conditions (Δ angle of $1.0 \pm 0.5°$ at low, $2.2 \pm 0.8°$ at medium, and $2.5 \pm 1.4°$ at high, $P \leq 0.05$, ES = 0.53). Average SOL muscle activation increased substantially with increasing foot compression force ($19.0 \pm 4.6\%$ at low, $27.8 \pm 5.4\%$ at medium, and $35.0 \pm 7.4\%$ at high, $P \leq 0.05$, ES = 0.81, Fig. 2).

Foot Mechanics

The LA compressed as force was applied to the leg by the actuator (loading phase) and subsequently recoiled as the force was removed (unloading phase), in a similar manner to that observed during locomotion (Fig. 3). The magnitude of LA compression increased with increasing foot compression force ($3.0 \pm 1.2°$ at low, $4.3 \pm 1.2°$ at medium, and $5.0 \pm 1.6°$ at high, $P \leq 0.05$, ES = 0.85). Midfoot plantar flexion moment increased substantially as compression force increased (-0.27 ± 0.08 Nm/kg at low, -0.45 ± 0.17 Nm/kg at medium and -0.59 ± 0.20 Nm/kg at high, $P \leq 0.05$, ES = 0.81).

The foot absorbed energy during the loading phase of the foot compression cycle and subsequently returned/generated mechanical energy during the unloading phase (Fig. 3). The magnitude of negative work (-0.03 ± 0.01 J/kg at low, -0.06 ± 0.02 J.kg^{-1} at medium, and -0.10 ± 0.04 J/kg at high, $P \leq 0.05$, ES = 0.80) and positive work (0.03 ± 0.01 J/kg at low, 0.07 ± 0.01 J/kg at medium, and 0.10 ± 0.03 J/kg at high, $P \leq 0.05$, ES = 0.85) increased with compression force. However, the net work performed by the foot remained constant and was always close to zero (0.002 ± 0.005 J/kg at low, 0.004 ± 0.02 J/kg at medium, and 0.002 ± 0.02 J/kg at high, $P = 0.67$, ES = 0.04).

FDB Function

The FDB MTU (unloaded length of 231 ± 11 mm) lengthened during the loading phase and shortened during the unloading phase of the foot compression cycles. The magnitude of FDB MTU stretch increased with load (4 ± 1 mm at low, 5 ± 1 mm at medium, and 6 ± 1 mm at high, $P \leq 0.05$, ES = 0.82). For all loading conditions, the MTU displayed a positive (lengthening) velocity during the loading phase and negative (shortening) velocity during the unloading phase of the compression cycle (Fig. 4). There was a significant group effect of load on peak MTU lengthening velocity (17.1 ± 6.3 mm/s at low, 21.0 ± 4.8 mm/s at medium, and 22.3 ± 7.4 mm/s at high, $P \leq 0.05$, ES = 0.32). However, post hoc analysis indicated that only the low and high conditions were significantly different ($P \leq 0.05$), whereas the medium condition was no different to either the low or high conditions (0.5 body wt vs. 1.0 body wt, $P = 0.21$ and 1.0 body wt vs. 1.5 body wt, $P = 0.90$). Peak MTU shortening velocity significantly increased between each loading condition (-10.3 ± 6.4 mm/s at low, -14.5 ± 6.9 mm/s at medium, and -18.0 ± 9.2 mm/s at high, $P \leq 0.05$, ES = 0.50).

The FDB muscle fascicles were ~10% of the unloaded MTU length (unloaded fascicle length of 22.0 ± 0.4 mm). Generally, the fascicle length changes during the foot compression cycles were small (<1 mm). Across all conditions, the fascicles displayed an initial stretch at the start of the compression cycle (0.2–0.4 mm, Fig. 4). Subsequent to this initial stretch, the muscle fascicles displayed a divergent behavior between load-
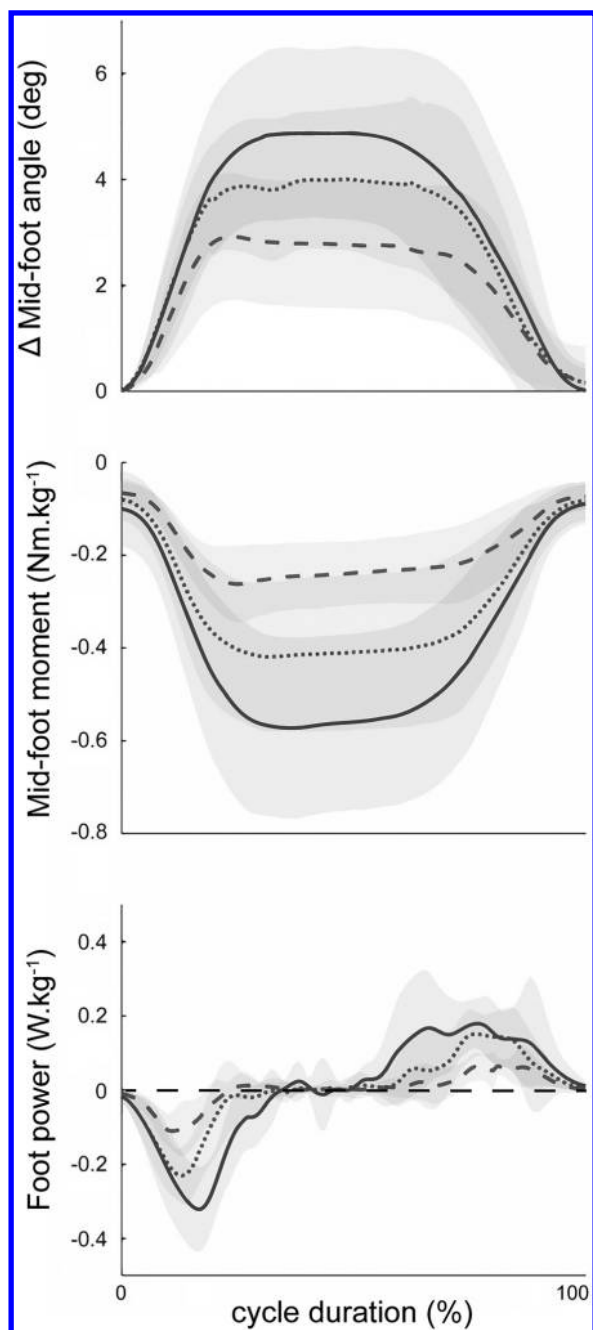
Fig. 3. Group mean ensemble data for midfoot angle (*top*), midfoot moment (*middle*), and foot power (*bottom*) recorded during foot compression cycles at low (dash), medium (dots), and high (full line) loading conditions. *Significant difference between all conditions.

ing conditions, depending on the magnitude of muscle activation with activation increasing with compression force ($P \leq 0.05$, ES = 0.60). During the low load condition, very little FDB activation was observed ($7.5 \pm 4.0\%$ max). Accordingly, the muscle fascicles continued to lengthen (net length change of 0.8 ± 0.3 mm) until peak vertical force, then shortening during the unloading phase. In the medium load condition, an increase in FDB activation was observed ($16.3 \pm 7.6\%$ max) and the fascicles shortened slightly, after the initial stretch, with a net length change of -0.4 ± 0.4 mm from the unloaded fascicle length. In the high load condition, a marked increase in

FDB activation was observed ($24.0 \pm 10.5\%$), and fascicles shortened following the initial stretch with a net length change of -0.6 ± 0.4 mm from the unloaded fascicle length. Subsequently, the fascicles lengthened back to the unloaded length as the compression force declined.

Despite considerable differences in the temporal patterns of fascicle lengthening and shortening during the foot compression cycles, the magnitude of fascicle shortening velocity (-2.7 ± 1.8 mm/s at low, -3.2 ± 1.8 mm/s at medium, and -3.6 ± 2.7 mm/s at high, $P = 0.35$, ES = 0.11) and lengthening velocity (3.4 ± 1.4 mm/s at low, 3.6 ± 1.7 mm/s at medium, and 3.5 ± 1.4 mm/s at high, $P = 0.86$, ES = 0.02) was similar between loading conditions.

DISCUSSION

This study provides novel evidence for active contributions to the foot-spring mechanism. Compared with the overall length changes observed in the FDB MTU, the muscle fascicles contracted in a relatively isometric nature, facilitating storage and return of strain energy in the elastic tendon in conjunction with the plantar aponeurosis. The capacity both to increase energy absorbed at the foot with muscle activation and to increase power generated via recoil of tendon rather than muscle provides the foot with an adaptive mechanism to deal with changes in locomotion requirements. This may be of considerable importance during tasks that require acceleration, deceleration, or change of direction.

The parallel anatomical arrangement of the FDB muscle and the plantar aponeurosis provides a unique mechanism for the CNS to utilize both passive and active structures to modulate the energetic function of the foot. During tasks such as bipedal standing and slow walking, when loading forces are low, the intrinsic foot muscles remain relatively inactive unless there is a significant perturbation to the center of mass (19, 20). Presumably, under these loading scenarios, the foot can effectively operate as a passive spring-like structure. However, during tasks that require larger magnitudes of energy to be absorbed or generated, the intrinsic foot muscles can provide additional energetic capacity for the foot. Our data show that when active, the contractile element of the FDB MTU remained at a relatively constant length, with the tendon (in parallel with the plantar aponeurosis) undergoing all of the stretch imposed on the MTU. The force produced by the muscle increased the mechanical energy stored within the in-series (tendon), adding to that stored in parallel (plantar aponeurosis) elastic components. This interaction between passive and active elastic elements within the foot helps to explain how large magnitudes of mechanical energy [12–24 J when running (16)] can be stored within a structure with such marked stiffness.

The FDB muscle has relatively short fibers, and therefore, the contractile element of the MTU is limited in its capacity to generate mechanical power (3, 36). Based on FDB MTU length changes and ground contact times reported in a previous experiment (20), we estimate that the shortening velocity of this muscle approaches 8–10 fascicle lengths per second during running. This is approaching the maximum shortening velocity predicted from the muscle fibers (15). Thus, the power generating capacity of FDB would be almost completely diminished if muscle fibers were required to add power alone.
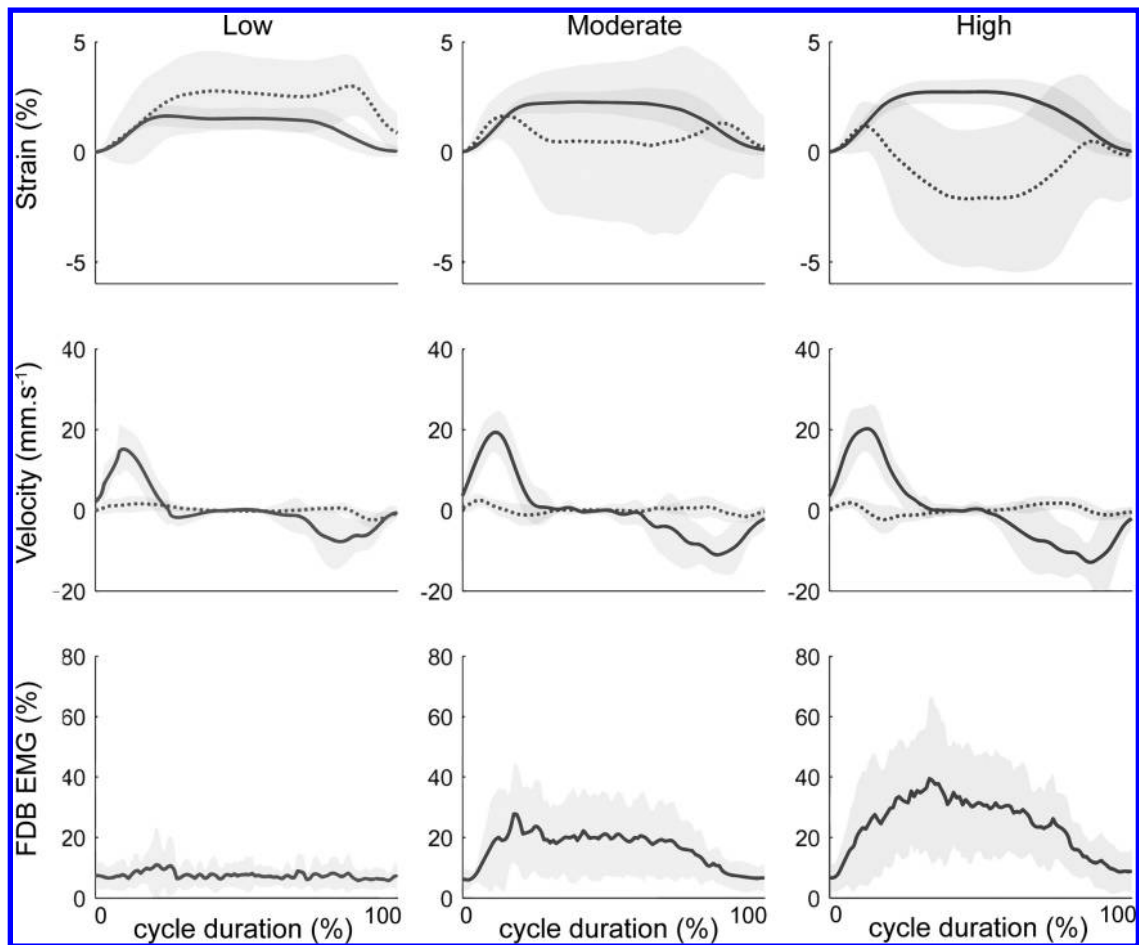
Fig. 4. Group mean ensemble data for flexor digitorum brevis (FDB) muscle tendon unit (full lines) and fascicle (dots) strain (*top*), velocity (*middle*), and muscle activation (*bottom*) during foot compression cycles at low (*left*), medium (*middle*), and high (*right*) loading conditions. EMG, electromyography.

However, the attachment of an elastic tendon allows the muscle to operate near isometrically, which is more favorable for force production and facilitates energy storage in the tendon as the LA compresses. This stored energy can be returned to the body as a burst of positive power as the LA recoils in late stance, to aid forward propulsion. The tendon may also act as a buffer to attenuate some of the energy associated with foot-ground collision, protecting the muscle fibers from excessive stretch (23, 30) and potentially vibration (37).

An additional benefit of actively controlling the energetic function of the human foot is the potential to transform the foot from an energy conserving structure to that of an energy damper or motor, when locomotion requirements change. For example, active lengthening of the FDB muscle fascicles during a rapid deceleration may help to dampen oscillations associated with foot-ground contact (1), aiding in deceleration of the body's center of mass. Recent in vivo data suggests that the foot functions more like a spring-damper during locomotion, with a significant proportion of absorbed mechanical energy not being returned to the body (34). It has been hypothesized that muscles within the foot may act to dissipate some of this energy (34). Within the current experiment, the foot performed close to zero mechanical work. This is probably because of the mechanical constraints of our experimental set-up, with the mechanical

actuator programed to perform external work on the foot in a sinusoidal manner, with net zero mechanical work. Despite the foot performing zero mechanical work and a predominantly isometric function of the FDB, periods of active fascicle shortening and lengthening were observed. This suggests a potential for these muscles to generate or dissipate mechanical energy, to adapt the foot energetic function during locomotion. Although, it must be highlighted that any length change and the associated lengthening (or shortening) velocity in the FDB fascicles is very small (see Fig. 4) compared with that of the entire MTU. Therefore, the magnitude of energy that can be dissipated or generated by the contractile element of these muscles may be limited.

The underlying neurophysiology governing the control of this active tuning mechanism is of considerable interest but remains largely unknown. We have previously observed that the intrinsic foot muscles remain relatively inactive until loads exceeding body mass are encumbered on the foot, despite considerable deformation of the LA and MTU stretch (17). Within the current experiment, we observed similar behavior in the low-load condition, with the FDB muscle remaining inactive, despite considerable MTU and fascicle stretch during the loading phase of the foot compression cycle. This finding suggests the presence of inhibitory inputs on the motoneuron

pool of the FDB muscle. Indeed, this notion is supported by a relatively small range of modulation in H-reflex amplitude in the FDB muscle, compared with other lower limb muscles (10). Increased inhibitory drive on the FDB motoneuron pool may be an important element in the control of foot mechanics. For example, overly responsive foot muscles may lead to unnecessary activation, which could potentially increase the metabolic cost of locomotion. The close relationship between SOL muscle activation and FDB activation observed in this study highlights the potential for heteronymous facilitation between these muscles. Functionally, shared excitatory drive would make sense, as tasks that require a large power output from the ankle plantar flexors appear also to require a concurrent increase in power output from the foot (18, 38). Further research is required to explore the underlying control of the foot's mechanical and energetic function.

The findings of this study need to be acknowledged in the context of a number of experimental limitations. The primary limitation of this study is that it was performed using an external actuator to apply compressive loading cycles on the foot. This experimental paradigm was designed to consistently replicate the loading about the LA in locomotion, while allowing evaluation of the mechanical behavior of muscles deep within the arch of the foot. We believe that the data presented here are an adequate representation of the mechanical function of the intrinsic foot muscles during locomotion. However, it is possible that this function may differ slightly because of differences the magnitude of torques produced about the midfoot and also the lack of a true foot-ground collision or need to generate propulsive impulses. The observed torque production and LA deformation within the current experiment (0.6 Nm/kg, 5° deformation) are lower than that produced during walking (1 Nm/kg, 7° deformation) (5, 9, 20) and running (1.5 Nm/kg, 10° deformation) (18). Therefore, it is likely that the observed FDB activation may actually be greater during locomotion than those reported within this study. We have shown that the FDB MTU contributes to elastic energy storage within the foot. Because of its similar anatomical pathway, it is likely that the plantar aponeurosis was also stretched more as loading increased and shared some of the increased energy storage and return with the FDB tendons. However, within the current experiment, we were unable to parse out the relative contribution to energy storage of the plantar aponeurosis and FDB MTU or indeed other tissues within the foot. Further research is required to explore the capacity of the intrinsic foot muscles to modulate the energetic function of the human foot.

This study provides novel evidence that the CNS utilizes the parallel anatomical arrangement of the intrinsic foot muscles and plantar aponeurosis to control the spring-like behavior of the human foot actively. It appears that considerable excitatory neural drive is required to activate the intrinsic foot muscles, allowing the foot to function as a relatively passive structure during tasks that require low forces to be generated. When active, the isometric function of the FDB muscle fascicles facilitates energy storage and return from the FDB tendon, in parallel to the energy stored within the plantar aponeurosis. This mechanism may enhance the versatility of the human foot during locomotion.

DISCLOSURES

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

AUTHOR CONTRIBUTIONS

L.A.K. conceived and designed of research; L.A.K. and D.J.F. performed experiments; L.A.K. analyzed data; L.A.K., D.J.F., A.G.C., and G.A.L. interpreted results of experiments; L.A.K. prepared figures; L.A.K., D.J.F., A.G.C., and G.A.L. drafted manuscript; L.A.K., D.J.F., A.G.C., and G.A.L. edited and revised manuscript; L.A.K., D.J.F., A.G.C., and G.A.L. approved final version of manuscript.

ENDNOTE

At the request of the authors, readers are herein alerted to the fact that additional materials related to this manuscript may be found at the institutional website of one of the authors, which at the time of publication they indicate is: https://www.drop-box.com/sh/okbsab120jsc2az/AAD05Q1dtaY6MLdi_dkaqUjsa?dl=0. These materials are not a part of this manuscript, and have not undergone peer review by the American Physiological Society (APS). APS and the journal editors take no responsibility for these materials, for the website address, or for any links to or from it. Data Availability.

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