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Plantar Flexor Dynamic Contractile Rates Are Not Dependent on Calcaneal Tendon Stiffness

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Abstract

The ability to rapidly generate muscular torque and velocity is important in specialized activities and daily tasks of living. Tendon stiffness is one factor in the neuromuscular system that influences musculoskeletal torque transmission. Previous studies have reported weak-to-moderate correlations between tendon stiffness and rate of torque development (RTD). However, these correlations have been reported only for isometric contractions which may not be relevant to contractions involving joint rotation (i.e., dynamic). The purpose was to investigate the effect of calcaneal tendon stiffness on the dynamic rates of torque (RTD) and velocity (RVD) development in plantar flexor muscles. Young adult males (n=13) and females (n=2) performed prone isometric- and isotonic-mode plantar flexion maximal voluntary contractions (MVC). Ultrasound imaging was used to quantify tendon morphological characteristics to estimate Young's elastic modulus (YM). Maximal voluntary and electrically evoked (300 Hz) isometric- and isotonic-mode (at 10% and 40% MVC loads) contractions were evaluated for RTD and RVD through a 25° ankle joint range of motion. YM was correlated modestly with isometric RTD, but only for evoked contractions ($RTD_{0–50\ ms}$: r=0.54, p=0.02, $RTD_{0–200ms}$: r=0.62, p=0.01). Conversely, YM was not correlated with dynamic RTD (voluntary: r=-0.07–0.41, p=0.06–0.40, evoked: r=-0.2–0.3, p=0.14–0.24) nor RVD (voluntary: r=-0.08–0.24, p=0.27–0.40, evoked: r=0.12– 0.3, p=0.14–0.34). These correlations would indicate that calcaneal tendon stiffness is an important factor for rapid isometric torque development, but a smaller factor for isotonic contractions. The determinants of dynamic contractile rates likely involve more factors than isometric contractions and warrant further study.

Keywords

Dynamic contractile rates, Rate of torque development, Rate of velocity development, Tendon stiffness, Young’s modulus, Ultrasonography, Plantar flexion, Electrically-evoked contractions

Lay Summary

Muscular torque and velocity are two parameters involved in human purposeful movements. The rates of torque and velocity development are important for specialized and daily tasks (e.g., explosive athletic performance and correcting perturbations in balance, respectively). Several factors of the neuromuscular system influence these rates, one of them being the stiffness of the tendon. Stiffer tendons may provide a mechanical advantage as force transmission from the muscle to the bone is optimized. Previous research has shown positive correlations between tendon stiffness and explosive torque development however, the contractions for rate of torque development determination have only been explored in isometric contractions in which there is no joint rotation. Much less is known about these factors in contractions that involve appreciable muscle shortening (i.e., dynamic contractions) during joint movement. Ultrasound imaging was used to gain a measure of tendon elongation so stiffness could be determined during dynamic contractions. These values were plotted against a participant's maximal rate of torque and velocity development at different loads to initiate movement of the dynamometer. We found no significant correlations between tendon stiffness and dynamic rates of torque and velocity development. This indicates that determinants of dynamic contractile rates may differ from isometric contractile rates. Future studies are required to explore additional determinants involved in dynamic contractions that may differ from isometric contractions. Considering torque and velocity are critical for optimal power generation, the opportunity for translational research in this field to improve and understand functional outcomes will be important for continuing studies.

Co-Authorship Statement

Michael T. Paris, Sohum V. Kulkarni, and Charles L. Rice conceptualized and designed the study. Sohum V. Kulkarni and Michael T. Paris participated in data collection and analysis. Sohum V. Kulkarni, Michael T. Paris, and Charles L. Rice participated in interpretation of experimental data.

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List of Abbreviations

Ach – acetylcholine

ADP – adenosine diphosphate

ATP – adenosine triphosphate

[Ca^{2+}] – calcium ionic concentration

E-C – excitation-contraction

ITT – interpolated twitch technique

LG – lateral gastrocnemius

MG – medial gastrocnemius

MyHC-myosin heavy chain

MU – motor unit

MVC – maximal voluntary contraction

N·m – Newton-metre

ROM – range of motion

RTD – rate of torque development

RVD – rate of velocity development

SR – sarcoplasmic reticulum

T-tubules – transverse tubules

VA – voluntary activation

YM – Young’s modulus

Chapter 1

1 Literature Review

1.1 General Introduction

Muscular contractions are at the core of all human movement. Most movements do not require maximal force production but instead rapid purposeful movements of the joint, producing both torque and velocity in a three-dimensional space. These contractile rates are termed the rate of torque development (RTD) and rate of velocity development (RVD). Contractile rates have previously been examined only using isometric contractions. Although the determinants and importance of these rates have been studied, the lack of joint movement in isometric contractions renders them less applicable to dynamic movements involving joint rotation. The determinants of isometric contractile rates may differ from dynamic contractile rates and so examining these differences is important. Dynamic contractile rates have important implications for specialized athletic activities e.g., sprinting, and daily activities like correcting perturbations in balance (Suetta et al., 2004; Tillin et al., 2012).

1.2 Skeletal Muscle

Individual muscle fibres (cells) are bundled into fascicles that comprise whole muscle, with each end affixed to its origin and insertion by tendons. Aponeuroses are connective tissues that maintain structure and localize whole muscle into anatomical compartments. Each muscle fibre is composed of myofibrils containing sarcomeres, the functional unit of the muscular contraction (Rassier, 2010). Sarcomere arrangement determines whether a muscle is better suited for torque or velocity production. Sarcomeres with a more in-series arrangement are optimized for velocity production whereas sarcomeres in parallel arrangement are optimized for force production (Sacks and Roy, 1982). Furthermore, fascicle insertion angle alters force productive capabilities of the muscle. A wider angle of insertion allows for increased packing density of muscle fibres, however, at a proportional loss of force per fibre. The angle of fibre insertion is termed the pennation (pinnation) angle. Muscles with one plane of insertion are termed unipennate and usually

produce less torque and more velocity than muscles with multiple planes of insertion. Bipennate (e.g., rectus femoris) and multipennate muscles (e.g., vastus lateralis) are better equipped for massive force production. However, recent evidence suggests that pennation is more of a packing strategy for short muscle fibres than a muscle feature with great functional significance. Although, the underlying physical principles of force production (e.g., net force decreases as angle of insertion increases) likely still hold fundamental merit (Lieber, 2022).

Muscle fibres are often classified as belonging to one of three distinct subtypes, although there is evidence of fibres displaying multiple subtypes, termed hybrid fibres (Heckman & Enoka, 2012, Stephenson, 2001). They are classified based on their myosin heavy chain (MyHC) isoforms, which alter cross-bridge formation kinetics. The three main types are Type I, Type IIA, and Type IIX. Type I fibres are often called “slow-type” fibres. This is because of their slower contraction velocity (in comparison to other fibre types). Conversely, Type IIX muscle fibres have quicker shortening velocity, while Type IIA offers an intermediary between the two extremes. Type I fibres typically produce less force but are more resistant to fatigue. Type IIX fibres produce more force per unit of ATP, which likely renders them more fatigable (Larsson & Moss, 1993). Task specificity determines what type of fibres will predominate a contraction. A sustained task would likely rely more on Type I fibres whereas a maximal, explosive task would rely more on Type IIA and Type IIX fibres.

1.3 Calcaneal Tendon

Tendons are connective tissues that attach muscles to bony landmarks. Directly following a muscular contraction, tendinous tissue transmits the generated force to the skeleton, resulting in bodily movement. Tendons are primarily composed of densely packed collagen fibrils, fibres, and fascicles that can withstand great tensile forces. Water within the extracellular matrix of the tendon provides viscoelasticity to the tendon. This property confers the ability to store and release kinetic energy for efficient movement (Merry et al., 2022). Tendon composition determines its size and shape, and it is likely best suited for the muscle’s functional capabilities. For example, muscles for power movements (e.g., quadriceps) generally have short, thick tendons while tendons for muscles involved

in finer movements (e.g., intrinsic hand muscles) are generally long and thin (Kjær, 2004), proportionally. The largest, thickest tendon in the body is the calcaneal (Achilles) tendon. As the tendon involved in plantar flexion, it is critical for locomotion. Each of the triceps surae muscles (medial gastrocnemius, lateral gastrocnemius, soleus) insert by three individual subtendons that represent distinct functional properties of the calcaneal tendon (Merry et al., 2022). Throughout the ageing process, tendon composition is altered, and a reduced stiffness and force-generating capacity are seen (Svensson et al., 2016). This is thought to result in increased tendinopathy incidence among aged individuals, further deleteriously impacting their ambulation capacity. Resistance exercise positively remodels the calcaneal tendon, and so further studies are required to explore whether this can be applied throughout the ageing process, maintaining one aspect of optimal neuromuscular function.

1.4 Hill Muscle Model

Archibald Vivian Hill was a British physiologist who developed a model of skeletal muscle that explained how various anatomical structures influence muscular torque production and transmission. Hill's seminal work in 1938 proposed the idea of parallel and series elastic elements that modify the force generated by the contractile element before transmission to the skeleton thereby resulting in movement. Although there has been a greater understanding of muscle contraction since the time of Hill, his model still provides a framework that can be expanded upon. Contemporarily, the contractile element is understood to be comprised of sarcomeres, actin and myosin myofibrils that slide past each other during a muscular contraction and produce torque. The parallel elastic elements of the Hill model are the connective tissue that keep muscles fixed in their place. These include the epimysium surrounding whole muscle, perimysium surrounding individual fascicles, and endomysium surrounding individual muscle fibres, as well as certain sarcomere connective proteins like titin. The series elastic element is primarily comprised of the free tendon, which transmits the force from the contractile element to the skeleton, resulting in movement. Morphological characteristics of these constituent elements (e.g., stiffness) have been shown to influence the rapidity of

isometric muscular torque development (Andersen & Aagaard, 2006; Maffiuletti et al., 2016).

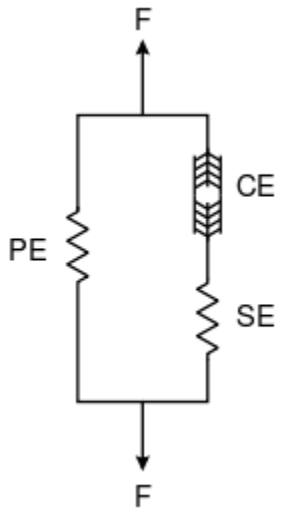

Figure 1. Hill Muscle Model showing the contractile element (CE) as well as the series elastic (SE) and parallel elastic (PE) elements. The elastic elements modify the force (F) generated by the contractile element which is then transmitted to the bone, resulting in movement.

1.5 Motor Units and Excitation-Contraction Coupling

The classical definition of a motor unit is the α-motor neuron and all of the muscle fibres that it innervates. Generally, motor neurons of smaller size innervate slow-twitch fibres and motor neurons of larger size innervate fast-twitch fibres. Elwood Henneman was a neurophysiologist who is often credited with the proposition of orderly recruitment of motor units based on size, which came to be known as the Henneman size principle. Essentially, this means that during a skeletal muscle contraction, motor units of smaller size will be recruited before motor units of larger size. Furthermore, smaller motor units, partially due to their smaller innervation ratios, have lower thresholds of activation than larger fast-twitch units, which may explain their preferential earlier recruitment (Henneman, 1957). Besides motor unit recruitment, the other main mechanism for force modulation at the MU level is motor unit rate coding. This refers to the frequency with

which the α-motor neuron depolarizes and subsequently elicits muscular twitches. Each axonal depolarization results in a single muscular twitch, after a brief (30–100 ms) electromechanical delay (Cavanagh & Komi, 1979). The saltatorial, efferent propagation of action potentials from the axon hillock along a myelinated axon eventually reaches the axon terminal. Here, the local depolarization results in varicosity release of vesicles containing acetylcholine (Ach). These vesicles effuse their acetylcholine into the synaptic cleft, quickly binding to post-synaptic sarcolemmal receptors. The local depolarization travels along the muscle and invades the transverse (T) tubules, causing the voltage-gated dihydropyridine receptors to change conformation and release calcium ions (Ca^{2+}). There is a subsequent interaction with ryanodine receptors on the sarcoplasmic reticulum (SR) membrane, resulting in intracellular Ca^{2+} release (Dulhunty et al., 2002). This calcium binds to Troponin C, which results in a conformational change that pulls tropomyosin off myosin fibres, thereby exposing actin binding sites. After the hydrolysis of adenosine triphosphate (ATP) by intracellular ATPase, the energized myosin binds to actin and after releasing adenosine diphosphate (ADP), undergoes a “power stroke” that “slides” the myofibrils past each other in a ratchet-like fashion, resulting in a muscular contraction. In the absence of further excitation, Ca^{2+} is actively transported back into the SR by Ca^{2+}-ATPase (Stokes & Wagenknecht, 2000).

1.6 Muscle Twitch and Tetanus

Electrically-evoked contractions can be used essentially to bypass or negate the neural influence on muscular contractions; allowing investigators to control the stimulation frequency to the muscle and record its contractile properties. This is done by percutaneous electrical stimulation of the nerve that innervates the muscle of interest. Single pulses can be delivered to characterize the non-physiological muscle twitch. The amplitude and duration of the evoked twitch are dependent on the activation history of the muscle. Evoked twitches can be summated by increasing the stimulation frequency to the muscle which will result in fusion of twitches, and with high frequencies a maximal tetanic (fused) response can be achieved. An unfused tetanus at a lower stimulation frequency would allow time for relaxation between twitches and therefore, incomplete twitch summation. Generally, electrically evoked contractions elicit quicker contractile

rates than voluntary contractions. In fact, de Ruiter and colleagues (2004) reported 300 Hz as the stimulation frequency to elicit maximal muscular contractile rates.

1.7 Plantar Flexors

Plantar flexion involves extending the ankle joint which occurs when one raises their heels to stand on their toes. The main muscle group involved in this action are the triceps surae, which is constituted by the medial gastrocnemius, the lateral gastrocnemius, and the soleus. All three, despite their unique origins, converge into the common calcaneal tendon which inserts on to the calcaneus (Winnicki et al., 2020). The calcaneal tendon is a model tendon for morphological study as its relatively cylindrical, linear shape allows for the application of physical principles like Young's Modulus for stiffness determination. This is in contrast with tendons, for example, of the pectoralis muscles, whose relatively diffuse insertion would render these principles inapplicable. The coordinated action of plantar flexors and dorsiflexors (ankle joint flexors) allows for performances of tasks like standing, walking and running.

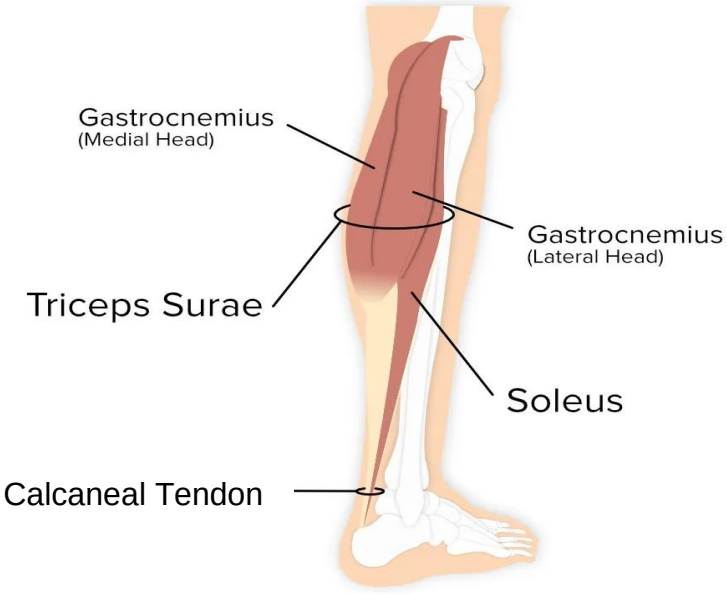

Figure 2. Anatomical illustration of the right plantar flexors and the common calcaneal tendon (Adapted from https://westcoastsci.com/blog/soleus-the-forgotten-muscle-for-runners/)

1.8 Isometric and Concentric Contractions

During isometric contractions, the participant contracts against an immovable force transducer. Ergo, torque is produced by the muscles but the joint angle remains static throughout the contraction, much like pushing against a brick wall. Isometric contractions have utility for morphological measurement and electromyographical studies, as there is generally a greater signal-to-noise ratio in comparison to dynamic contractions. However, most human interactions with the environment involve a change in joint angle. Thus, unlike for isometric contractions, the parameter of angular velocity becomes an important facet of the contraction, considering the product of torque and velocity yields power production. Rapid power production is critical for tasks with limited duration to produce a particular movement (e.g., sprinting off starting blocks, correcting one's gait after a stumble, etc.). Dynamic contractions can be assessed in recording dynamometers using two main modalities, isotonic and isokinetic. Isotonic contractions allow for a particular load (mass) to be moved through a set range of motion in which the velocity of movement can be varied by the participant. Contractions set at low loads can be rapidly moved through the range of motion, and therefore are more velocity-dependent. Conversely, isotonic contractions at high loads are difficult to move through a full range of motion and are therefore more torque-dependent. Isokinetic contractions allow for the constraint of velocity throughout a range of motion. Essentially, the participant can contract as rapidly and as forcefully as possible but the maximal angular velocity of the joint will be maintained at the value set on the dynamometer.

1.9 Rate of Torque Development

Maximal strength is often quantified as the maximal torque or force output measured by a transducer. The time to develop maximal torque is usually ~300 ms. However, the time to develop torque from perturbations in balance have to occur within the first 150 ms of the mechanical perturbation (Suetta et al., 2004). Therefore, rate of torque development has been purported to be more functionally-relevant than a basic measure of maximal voluntary contraction torque.

1.10 Determinants of Contractile Rates

There are several factors within the neuromuscular system that can affect the ability to rapidly generate torque. Among these include muscle fibre type, maximal strength capabilities, rate of neural activation, and musculotendinous stiffness. All of these determinants have been studied in an isometric setting however it is unknown whether these remain the primary determinants of explosive power production in a dynamic setting (Andersen et al., 2010; Maffiuletti et al., 2016). Or, at least, the relative contribution of each of the determinants may be altered when the contraction is performed dynamically.

1.11 Dynamic Contractile Rates

Dynamic rate of torque development (RTD) and rate of velocity development (RVD) are relatively understudied parameters of contractile function. The dynamic RTD informs on how quickly torque can be developed while moving through a range of motion. The RVD quantifies how quickly the angular velocity of the joint is changing throughout the contraction. RVD is known to be affected by joint angle and the range of motion of the contraction (Hinks et al., 2021). Given the length-tension relationship of skeletal muscle, it would follow that certain joint positions are optimal for both explosive torque and velocity development.

1.12 Tendon Stiffness and Ultrasonography

Tendon morphological characteristics (e.g., stiffness) affect the transmission of force from the muscle to the bone. Stiffer tendons may have a mechanical advantage due to reduced recoil of the tendon through multiple loading and relaxation cycles. In this way, the force transmission per tendon length change is increased, meaning augmented skeletal force transmission per unit of tendon elongation. Tendon stiffness has individual variability and is dependent on factors like muscle mass and tendon cross-sectional area. Ageing and disuse have been shown to alter these morphological properties, thereby altering tendon mechanical properties like stiffness (Krupenevich et al., 2022; Winnicki et al., 2020). Tendon stiffness can be defined as the length change of the tendinous structure as a response to the force travelling through it. Ultrasonography is often used to

track tendon elongation throughout a contraction (Hannah & Folland, 2014) to provide a measure of stiffness. Young's modulus is a measure of material stiffness that accounts for individual morphological differences and its principles can be applied to the calcaneal tendon using ultrasonography, given its anatomical shape and accessibility. Young's Modulus relates the elongation ratio of the material (strain) to the force travelling through the material normalized to its cross-sectional area (stress).

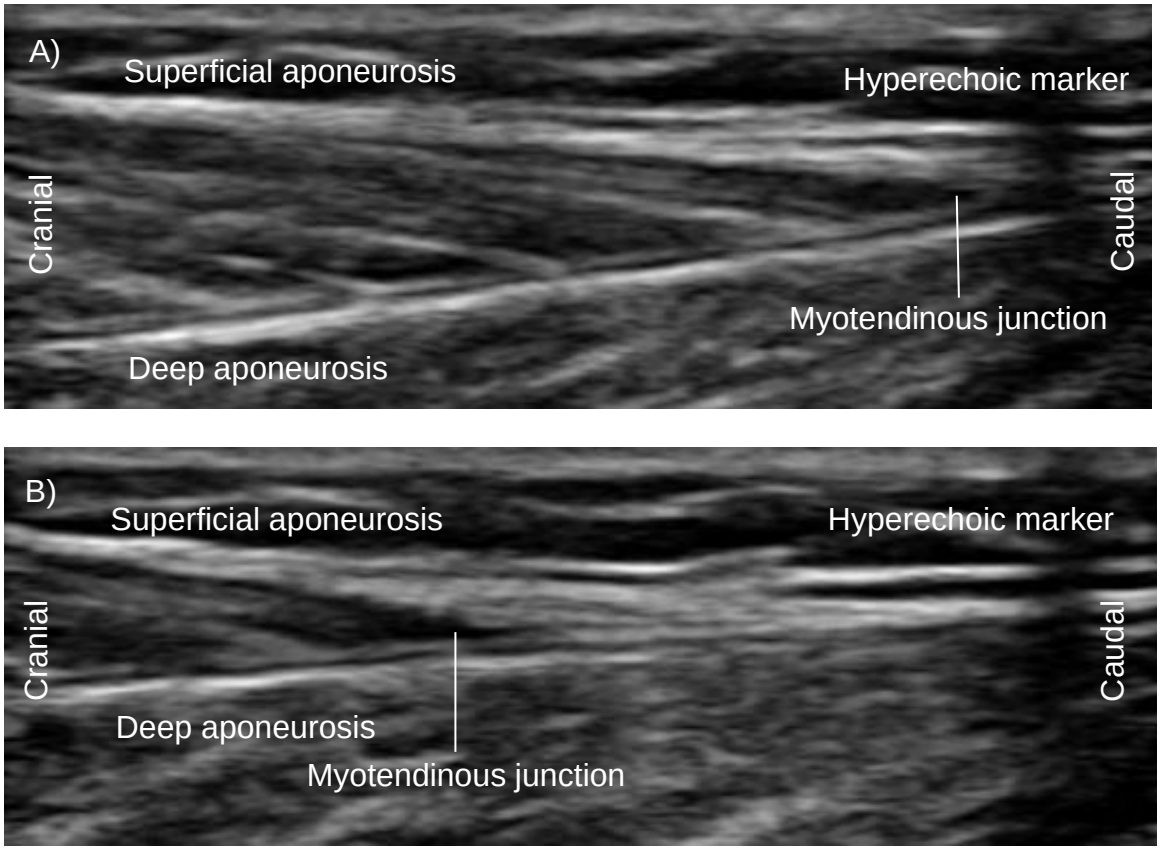

Figure 3. Ultrasonic images of the medial gastrocnemius distal myotendinous junction A) before contracting and B) during maximal contraction. Image was captured at a depth of 3.5 cm.

1.13 Purpose and Hypothesis

The purpose of this project was to investigate the correlations between calcaneal tendon stiffness and dynamic plantar flexor contractile rates. The relationship of these factors, shown to have importance in isometric contractions, have not been explored previously in isotonic dynamic contractions. An overall purpose was to assess whether the modest correlations observed during isometric contractions are also present under a more naturalistic contraction modality. Moreover, electrically-evoked contractions will be used to elicit maximal muscular RTD and RVD to eliminate the various degrees of neural activation across participants and observe any significant correlations. It was hypothesized that individuals with stiffer tendons would also have quicker rates of dynamic torque and velocity development. It was also hypothesized that electrically-evoked dynamic contractile rates would have stronger correlations with calcaneal tendon stiffness than voluntary dynamic contractile rates.

Chapter 2

2 Plantar Flexor Dynamic Contractile Rates Are Not Dependent on Calcaneal Tendon Stiffness

2.1 Introduction

The rates at which muscles generate torque and velocity are important markers of neuromuscular function and may determine successful performance of tasks like walking and correcting aberrant movements (Aagaard et al., 2002, Suetta et al., 2004, Tillin et al., 2012). Central and peripheral factors of the neuromuscular system influence these rates including rate of neural activation of the muscles and intrinsic tendinous properties (Waugh et al., 2013, Folland et al., 2014, Maffiuletti et al., 2016).

In particular, tendon stiffness has shown moderate, positive correlations with the rate of isometric torque development of its respective muscle (Bojsen-Møller et al., 2005, Wang et al., 2012), however, significant correlations are not uniformly observed (Hannah & Folland, 2014). In vivo, tendon stiffness can be defined as the slope of the relationship between tendinous force and elongation during an isometric ramp contraction (Kubo et al., 2001). Massey and colleagues (2018) found significant, weak correlations between quadriceps muscle-tendon unit stiffness and rates of voluntary and electrically evoked (octet) torque development (r=0.3–0.4), although Wang and colleagues (2012) reported stronger correlations in the calcaneal (Achilles) tendon (r=0.6). Tendons, being mechanically in-series with muscle fibres, transmit force from muscle to bone, resulting in torque output (Herzog, 2019). Stiffer tendons are thought to quicken the force transmission process, as there is less “slack” from passive elastic structures for the

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contractile element to take up, as posited by A.V. Hill in 1938. The lessened slack would theoretically allow for quicker tendinous force transmission from muscle to bone and therefore, a quicker rate of torque development (RTD).

Given the many factors that regulate RTD (e.g., rate of neural activation, fibre type composition, muscle strength), accounting for these additional factors will enable more detailed characterizations of the potential effect of tendon stiffness on RTD. For example, innervated muscle that is rapidly activated during a voluntary contraction will summate motor unit twitches quicker and thus, produce a faster RTD. Rate of voluntary activation factors affecting RTD can be removed using electrically evoked contractions, thereby isolating intrinsic musculotendinous properties (Maffiuletti et al., 2016). Evoked contractions at high frequencies (e.g., 300 Hz) will activate the muscle quicker than voluntary contractions to enable assessment of tendon stiffness on very rapid contractions (de Ruiter et al., 2004).

Although most environmental interactions require joint movement (dynamic actions), tendon stiffness correlations have never been investigated when the RTD is assessed dynamically. Furthermore, with dynamic (defined here as isotonic) contractions, angular velocity varies throughout the range of motion, and thus the rate of velocity development (RVD, i.e., acceleration) is critical for achieving a high peak power output (Davidson et al., 2022). Therefore, it is important to examine its relative impact on explosive movements along with RTD, because power (torque $\cdot$ angular velocity) is critical for movement production in dynamic actions. However, the relevance and determinants of RVD are unknown in relation to tendon stiffness.

The purpose of this study was to examine the correlations between calcaneal tendon stiffness and dynamic rates of torque and velocity development of the plantar flexors. More specifically, the voluntary and evoked rates of both torque and velocity development, and their respective correlations with calcaneal tendon stiffness, were evaluated. It was hypothesized that tendon stiffness would have a moderate correlation with dynamic rates of torque and velocity development. Electrically-evoked rates of torque and velocity development were expected to be quicker than voluntary rates and have stronger correlations with tendon stiffness.

2.2 Methods

From the local university, 15 healthy, recreationally-active participants were recruited for this study (13 males and 2 females; aged: 24 ± 2.5 years, height: 175 ± 7.9 cm, mass: 78 ± 11.2 kg) and they visited the laboratory twice with at least one day separating the two visits. This ensured participants became accustomed to activating their plantar flexors to obtain maximal RTDs and RVDs on the second testing day. Exclusion criteria included the presence of any neuromuscular disorders and discomfort lying prone for an extended time. All participants gave informed consent and the protocol was approved by the institutional ethics review board.

Experimental Setup

Torque (N·m), angular velocity (°/s), and ankle joint position (°) were recorded from the plantar flexors. While prone, isometric and isotonic mode contractions were performed with the right foot secured to a footplate and the right lateral malleolus positioned in line with the dynamometer axis of rotation (Cybex HUMAC NORM; CSMI Medical

Solutions, Stoughton, MA). Additional strapping across the torso, lower limbs, and dorsum of the foot were used to secure the participant and minimize extraneous movements. Participants performed contractions using the isometric and isotonic modes. Isometric contractions were performed with the ankle joint angle at 90°. Isotonic mode contractions were performed through a 25° ankle joint range of motion (10° dorsiflexion to 15° plantar flexion). The torque, velocity, and position signals were sampled at 1000 Hz using an external analog-to-digital converter (Power 1401; Cambridge Electronic Design, Cambridge, UK) connected to Spike2 software (version 7.20).

Electrically-evoked Contractions

The stimulation frequency delivered percutaneously to the nerve can be controlled across each participant to assess RTD and RVD. Here, a single stimulus and trains of stimuli at 300 Hz were selected as previous literature has reported this frequency elicits maximal RTD in human participants (de Ruiter et al., 2004). All percutaneous nerve stimulation was delivered to the tibial nerve in the distal popliteal fossa using a bar electrode attached to the Digitimer stimulator (Model DS7A, Digitimer Ltd, Welwyn Garden City, UK) with a pulse width of 100 μs. To obtain maximal responses, the currents for singlet and 300 Hz stimulation were incrementally increased until the torque plateaued. The current was increased a further 10% to ensure maximal stimulation. Singlet currents ranged from 70 mA to 125 mA while currents for 300 Hz stimulation ranged from 25 mA to 90 mA.

Experimental Protocol

During the first visit, tendon cross-sectional area, length, and moment arm were measured using ultrasound (see “Tendon Morphological Measurements” below).

Isometric maximal voluntary contraction (MVC) torque and voluntary activation (using the interpolated twitch technique) were assessed three times with five-minute intervals between assessments. The interpolated twitch technique (ITT) involves delivering a single pulse each before, during, and after an MVC. Percentage of voluntary activation was assessed as previously described (Todd et al., 2004). The highest peak torque for each participant was set as the target torque during the tendon elongation measurements (see "Tendon Stiffness Determination and Heel Lift Correction" below). Isotonic mode contractions were practiced (10–15 contractions) until peak power varied by less than 10%.

During the second visit, MVC isometric torque and voluntary activation were assessed again as described above. Maximal electrically-evoked isometric torque was elicited using 300 Hz percutaneous stimulation. Loads for isotonic mode contractions were set to 10% and 40% of the voluntary (MVC) torque and evoked (300 Hz stimulation) torque for evaluation of maximal voluntary and evoked dynamic contractions, respectively. Participants performed 2 sets of 3 to 5 maximal effort contractions at these loads until peak power output varied by less than 10%. Following 5 minutes of rest, participants performed two testing sequences of isotonic mode contractions (each separated by 5 minutes of rest), which involved two voluntary and one evoked contraction for both the 10% and 40% loads. The loads were randomized for each participant's sets. Participants were instructed to contract "as fast and hard as possible" and were given a verbal "go" cue before each voluntary contraction. All participants received real-time visual feedback from a monitor placed ~1 m away.

Tendon Morphological Measurements

B-mode ultrasound was used to image the calcaneal tendon (Philips Lumify version 4.0). A generous amount of ultrasound gel was applied during imaging to ensure complete visualization of the calcaneal tendon. Cross-sectional area was determined by placing the ultrasound probe in a transverse orientation on the calcaneal tendon, in line with the midpoint of the lateral malleolus (Kruse et al., 2017). The lateral malleolus offers a bony landmark for reliable cross-sectional area determination in participants of various sizes. Regions of interest were digitally placed along the border of the calcaneal tendon to measure cross-sectional area using the polygon tool of ImageJ software (version: Java 1.8.0_172, National Institutes of Health, Bethesda, MD, USA). To calculate calcaneal tendon length, an inelastic measuring tape was fixed to the ultrasound probe and used to image the myotendinous junction of the medial gastrocnemius. The linear distance from the ultrasound probe to the superior aspect of the calcaneal tuberosity was recorded using the fixed measuring tape. The recorded linear distance was corrected for alignment with the myotendinous junction position of the corresponding ultrasound image, as previously described (Arampatzis et al., 2005, Finni et al., 2022). Calcaneal tendon moment arm was determined as the perpendicular distance from the midline of the calcaneal tendon to the centre of the medial malleolus of the ankle (Hashizume et al., 2016; Holzer et al., 2020). The image depth for the calcaneal tendon images was 3 cm.

Tendon Stiffness Determination and Heel Lift Correction

Participants practiced performing 1 to 2 contractions following a torque tracing involving a linear ramp (constant RTD of 25 N·m/s) up to isometric MVC torque output. Given the strain rate sensitivity of a tendon, it is important to standardize this RTD across participants (Clemmer et al., 2010; Massey et al., 2017). Following practice, participants

performed 3 isometric MVCs during ultrasound recording of the medial gastrocnemius myotendinous junction. Between tendon stiffness measurements, participants were given five minutes of rest to allow for the dissipation of any transient thixotropy affecting stiffness properties (Buchtal & Kaiser, 1951; Altman et al., 2015). The probe remained stationary at the myotendinous junction (confirmed with dermal hyperechoic markers). Ultrasound video recordings were synchronised with Spike2 using an external mouse trigger and captured at a frame rate of 24 Hz. Tendon stiffness can be defined as the slope of the tendon force/elongation curve throughout the isometric ramp contraction (Kubo et al., 2001). Tendinous elongation was measured from 20% to 80% MVC in 10% increments by tracking myotendinous junction displacement using ImageJ analysis of ultrasound recordings.

During isometric ramp contractions, participants' heels occasionally lifted from the footplate, despite the inelastic strapping. Heel lift introduces errors in evaluating tendon elongation, as the joint angle changes lead to sizable tendon displacement. To correct for heel lift, a video camera (synchronized with Spike2 using an on-screen marker) was used to record a stationary tape measure placed overtop the calcaneal tendon to measure the amount of vertical lift. The amount of heel lift at each 10% MVC (20 to 80% MVC) increment was determined by frame-by-frame video analysis (VirtualDub Version 1.10.4).

To estimate the degree of joint angle change that occurred due to this heel lift, the lever arm of the foot was measured as the linear distance from the medial malleolus to the head of the first metatarsal and trigonometric ratios were then used to determine the joint angle throughout the isometric contraction. To measure the amount of tendon movement that

occurs with a given joint angle change, tendon displacement was separately imaged using ultrasound during passive joint rotation, during which the dynamometer moved the foot through the range of motion at 5°/second (CPM mode). Linear relationships between passive displacement and joint angle (90°, 92.5°, 95°, 97.5°, 100°, 105°) were obtained for each participant (r=0.95–0.99). At each estimated joint angle (from the heel lift evaluation) during the ramp MVC (i.e., from 20 to 80% MVC) the passive tendon displacement was calculated (Massey et al., 2017). Three passive trials were performed and the tendon displacement values at the various joint angles were averaged and then subtracted from the active elongation values to obtain a corrected calcaneal tendon elongation measurement.

Data Analysis

Isometric maximal torque was evaluated at the peak plateau. Peak torque and velocity of isotonic contractions were taken as the highest instantaneous value recorded. RTDs and RVDs were determined for 0–50 ms (RTD_{50}, RVD_{50}) to represent early onset characteristics and 0–200 ms (RTD_{200}, RVD_{200}) to represent longer duration contractile characteristics. Onset of torque and velocity was marked as the last positive trough of the first derivative of the (torque or velocity) channel, using a 0.01 s time constant. RTDs and RVDs were normalized to the participant's torque and velocity at peak power production. A well-accepted measure of tendon stiffness is the Young's elastic modulus (YM), which relates tendon stress (σ) to tendon strain (ε). Stress is a ratio that relates the force transmitted through a tendon to the cross-sectional area of the tendon (N/m^2, Pa). Strain is a ratio of tendon elongation to tendon length at rest (Winter, 2009). Stress/strain curves were plotted to obtain the slopes of linear regressions, which were YM values for the

participants. These values were plotted against each participant's rates of torque and velocity development and the respective correlations between YM and RTD/RVD were determined.

Statistical Analyses

All statistical tests were performed in IBM Statistical Package for Social Sciences [version: 28.0.1.1 (14)] with α significance set at <0.05. All descriptive statistics are presented as mean ± standard deviation. Pearson correlation coefficients were used to evaluate the relationship between YM and RTD and RVD at early (0–50 ms) and late (0–200 ms) time increments. The assumptions made were that both variables are normally distributed and the relationship is homoscedastic and linear. Correlations are interpreted as weak (r<0.4), moderate (r=0.4–0.7), and strong (r>0.7) (Mukaka, 2012). Paired samples two-tailed t-tests were determined to assess the difference between voluntary and evoked RTDs and RVDs. The assumptions made were that each subject's measurements are independent of other subjects', each paired measurement was obtained from the same subject, and the measured differences are normally distributed.

2.3 Results

Exemplar unprocessed recordings of torque, velocity, and position data during voluntary and evoked contractions are provided in Figure 4. Average plantar flexor isometric MVC torque was 167.6 ± 41.53 N·m with an average voluntary activation of 96.0 ± 0.03% (Table 1). Voluntary RTDs were significantly slower than evoked RTDs for isometric contractions (RTD_{50}: t=-11.09, p=<0.001, RTD_{200}: t=-5.82, p=<0.001). At low loads, dynamic voluntary early RTDs were significantly slower than evoked RTDs (RTD_{50}: t=-

7.5, p=<0.001, RTD_{200}: t=2.4, p=0.3). At high loads, dynamic voluntary RTDs were significantly slower than evoked RTDs (RTD_{50}: t=-19.8, p=<0.001, RTD_{200}: t=-3.4, p=0.01). At low loads, voluntary RVDs were significantly faster than evoked RTDs, but only for RTD_{200} (RTD_{50}: t=1.5, p=0.15, RTD_{200}: t=5.0, p<0.001). At high loads, voluntary RVDs were not significantly lower than evoked RTDs (RTD_{50}: t=-0.22, p=0.83, RTD_{200}: t=0.45, p=0.66)

Calcaneal tendon YM was not significantly correlated with voluntary isometric RTD_{50} (r=-0.23, p=0.16) nor RTD_{200} (r=-0.36, p=0.09) (Fig. 5), but was significantly correlated with evoked isometric RTD_{50} (r=0.54, p=0.02) and RTD_{200} (r=0.62, p=0.01). During isotonic contractions at low loads (10% MVC), calcaneal tendon YM was not significantly correlated with voluntary RTD_{50} (r= 0.15, p=0.30) nor RTD_{200} (r= -0.07, p=0.40) (Fig. 6). Similarly, evoked RTDs at 10% MVC load for RTD_{50} (r=0.26, p=0.18) and RTD_{200} (r=-0.20, p=0.24) were not significantly correlated with calcaneal tendon YM. At higher loads (40% MVC), calcaneal tendon YM was not significantly correlated with voluntary RTDs (RTD_{50} :r=0.09 p=0.30, RTD_{200}: r=0.41, p=0.06) nor evoked RTDs (RTD_{50}: r=0.30, p=0.14, RTD_{200}: r=0.24, p=0.20) (Fig. 6). Similar to correlations between Young's Modulus and RTD, correlations between tendon stiffness and dynamic RTD yielded non-significant correlations (data not shown).

At low loads (10% MVC), calcaneal tendon YM was not significantly correlated with voluntary RVDs (RVD_{50}: r=0.13, p=0.33) (RVD_{200}: r=-0.08, p=0.40) nor evoked RVDs (RVD_{50}: r=0.12, p=0.34) (RVD_{200}: r=0.15, p=0.29) (Fig. 7). Similarly, at higher loads (40% MVC), calcaneal tendon YM was not significantly correlated with voluntary RVDs (RVD_{50}: r=0.24, p=0.19, RVD_{200}: r=0.18, p=0.27) nor evoked RVDs (RVD_{50}: r=0.23,

p=0.21, RVD_{200}: r=0.30, p=0.14) (Fig. 7). Correlations between tendon stiffness and RVD yielded non-significant correlations (data not shown). Average force-elongation (r=0.99) and stress-strain (r=0.99) curves are provided in Figure 8.

Participants	13 males + 2 females
Age, years	23.9 (2.5)
Height, cm	175.8 (8.5)
Mass, kg	77.4 (11.5)
BMI, kg/m^2	25.0 (2.8)
MVC Torque, N m	167.6 (41.5)
VA, %	96.0 (0.03)

Table 1. Anthropometric characteristics. Standard deviation values are provided in parentheses.

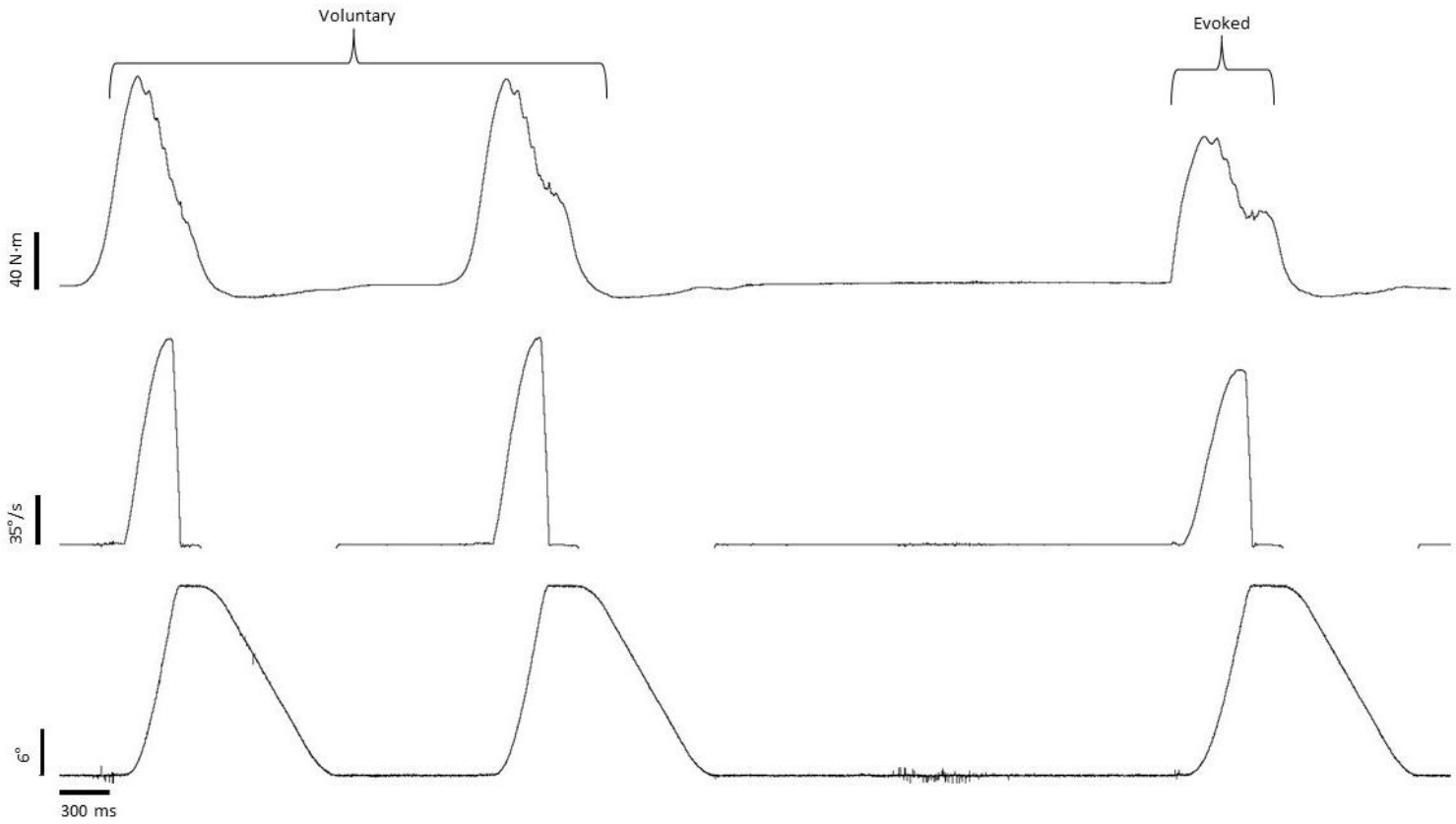

Figure 4. Example tracings of torque, velocity, and ankle joint position change in an isotonic mode contraction with the load set at 40% MVC.

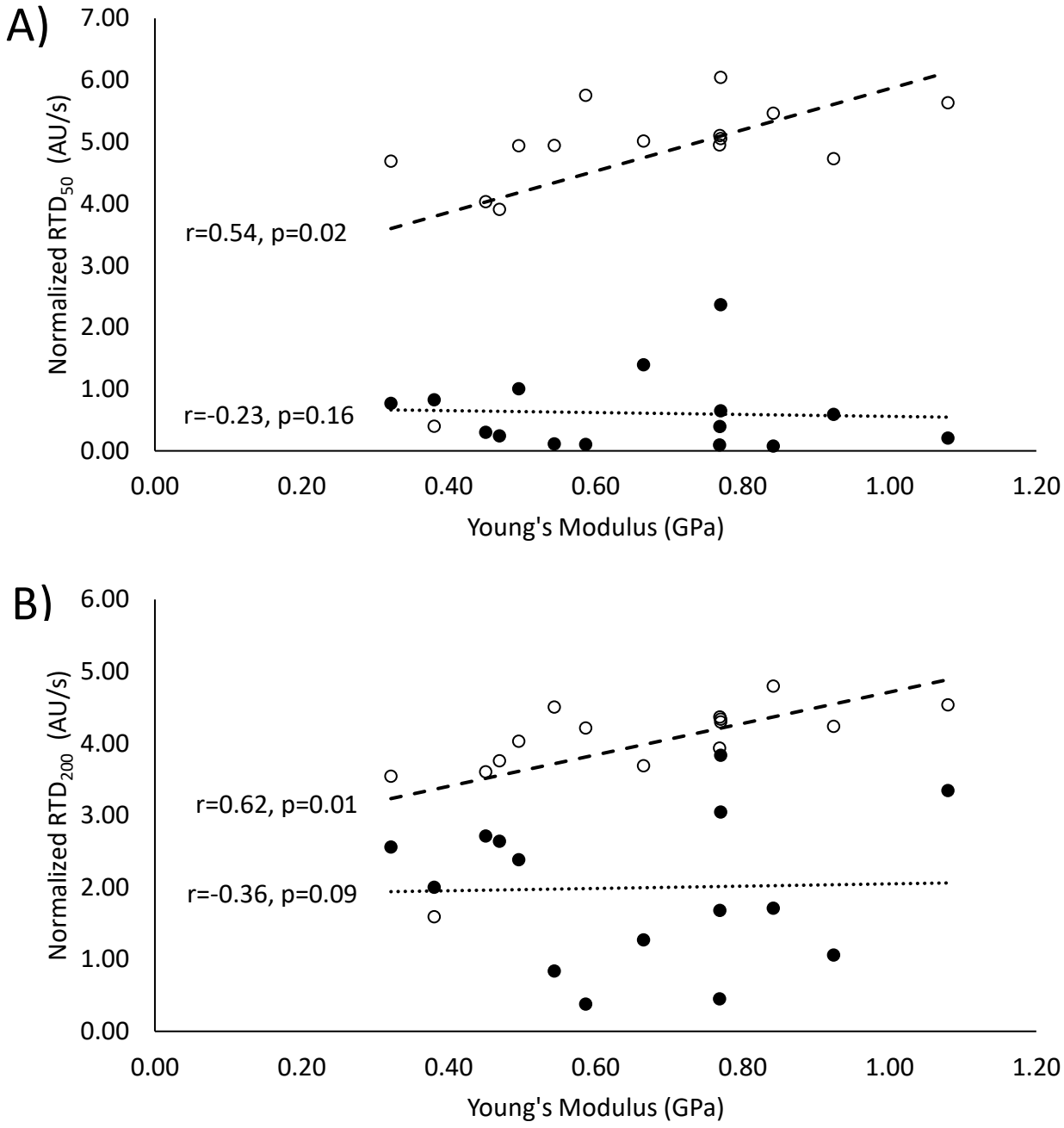

Figure 5. Normalized voluntary (filled circles) and electrically evoked (unfilled circles) rates of isometric torque development versus Young's modulus. Linear best fit regressions (dotted: voluntary, dashed: evoked) for A) 0–50 ms and B) 0–200 ms.

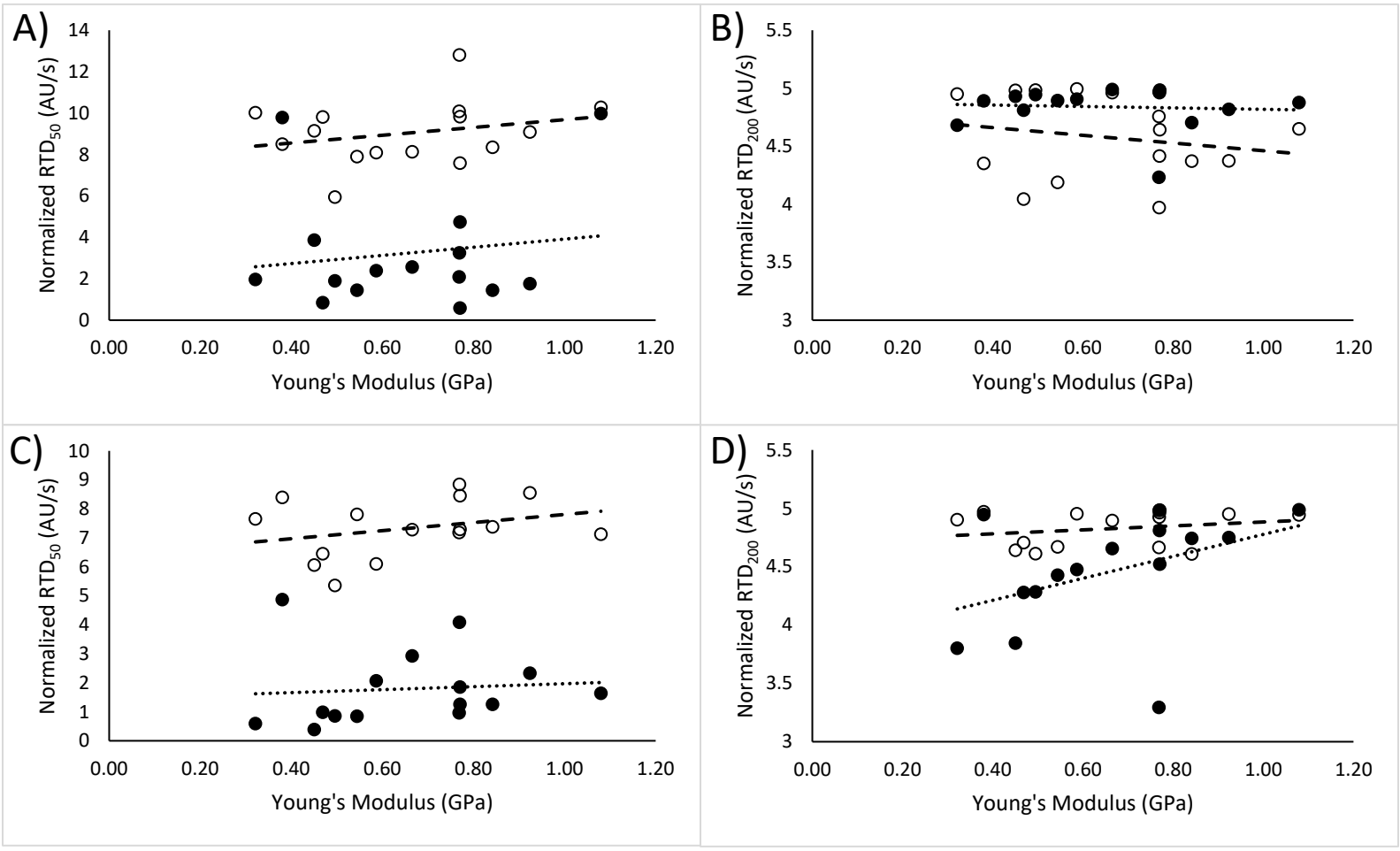

Figure 6. Normalized voluntary (filled circles) and electrically evoked (unfilled circles) rates of dynamic torque development (RTD) versus Young's modulus. Linear best fit regressions (dotted: voluntary, dashed: evoked) for (a) 0–50 ms at 10% MVC load, (b) 0–200 ms at 10% MVC load, (c) 0–50 ms at 40% MVC load, and (d) 0–200 ms at 40% MVC load. There were no significant correlations observed.

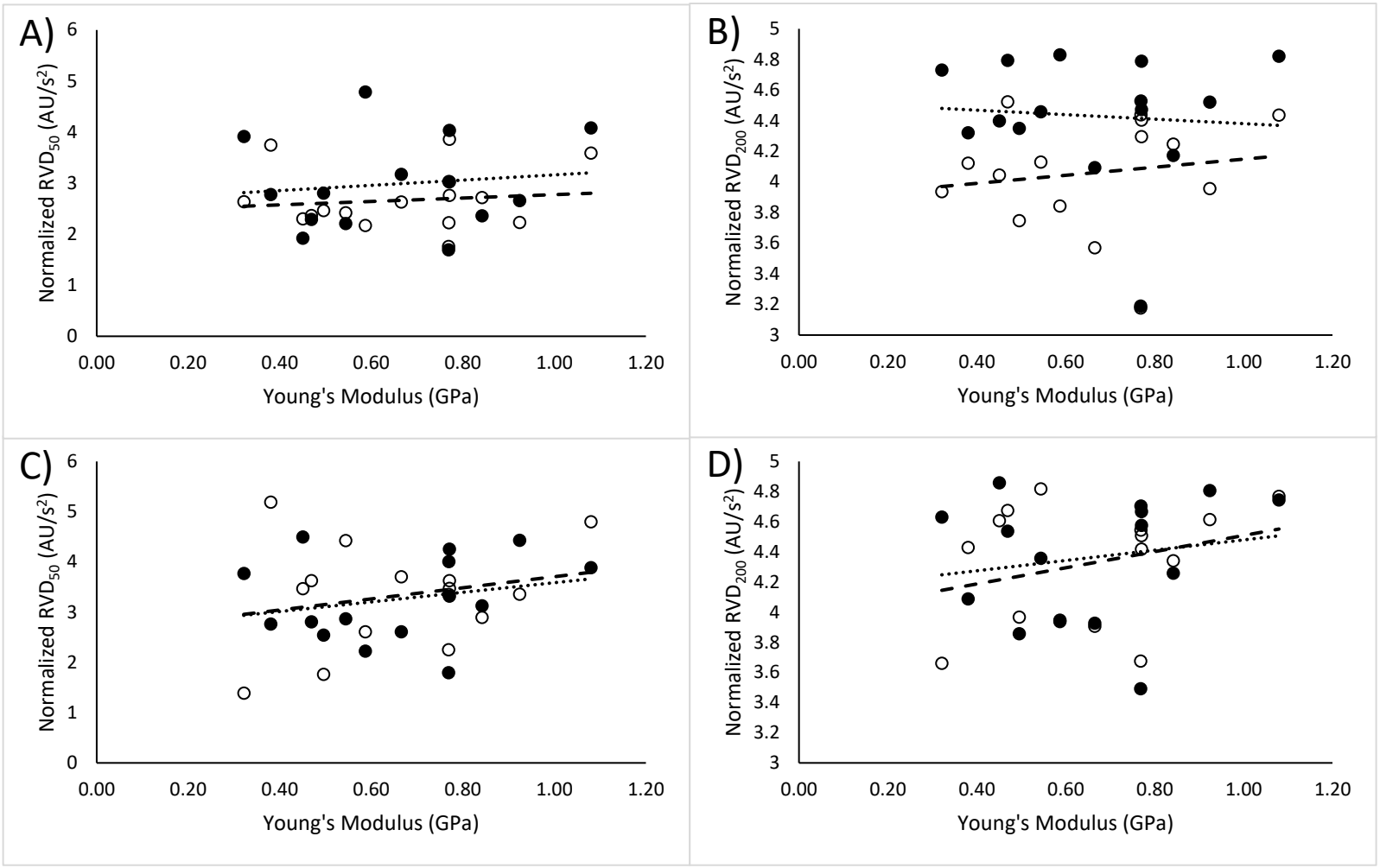

Figure 76. Normalized voluntary (filled circles) and electrically evoked (unfilled circles) rates of velocity development (RVD) versus Young's modulus. Linear best fit regressions (dotted: voluntary, dashed: evoked) from (a) 0–50 ms at 10% MVC load, (b) 0–200 ms at 10% MVC load, (c) 0–50 ms at 40% MVC load, and (d) 0–200 ms at 40% MVC load. There were no significant correlations observed.

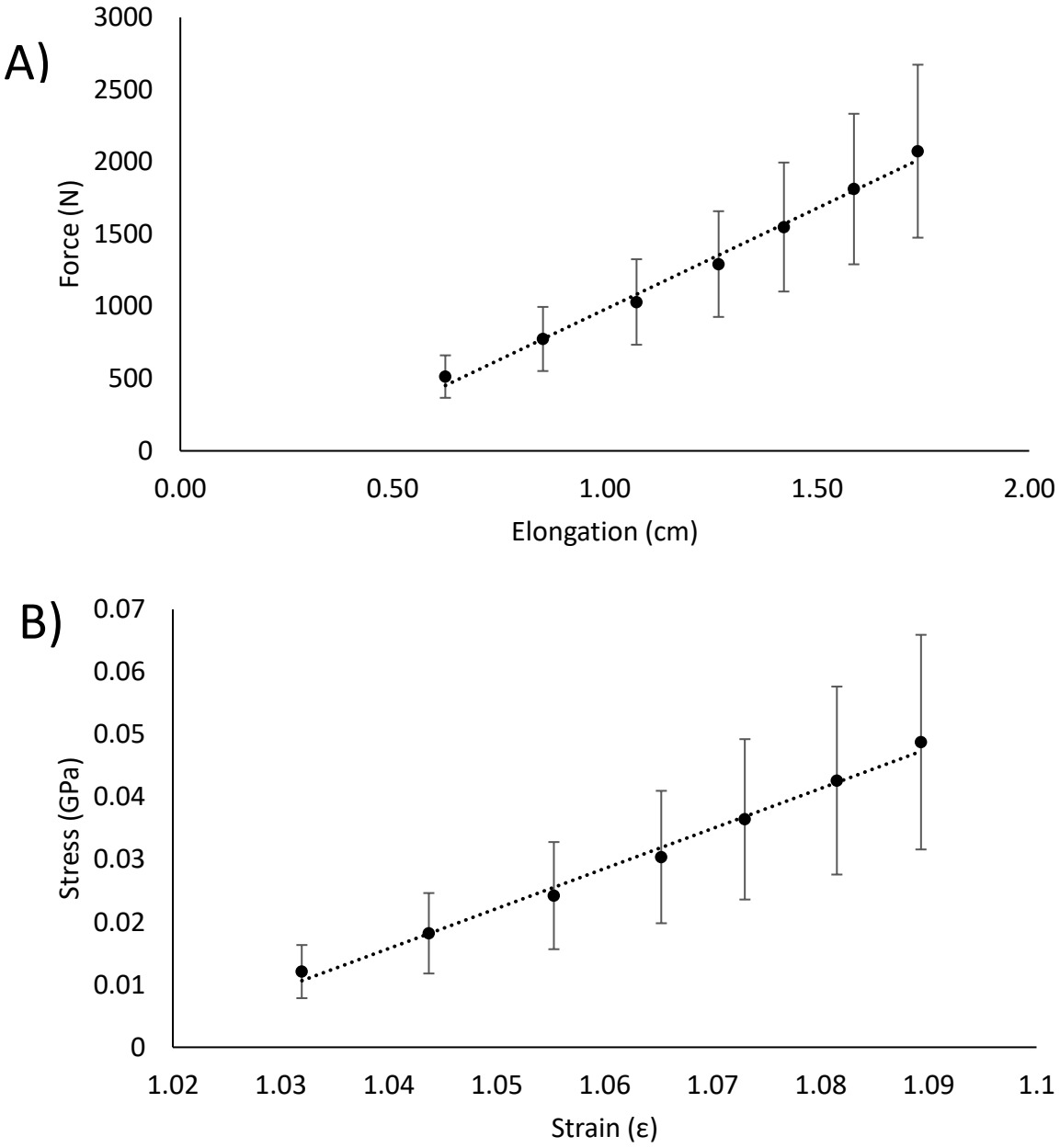

Figure 8. Mean force-elongation (A) and stress-strain (B) curves displaying average participant calcaneal tendon stiffness ($r=0.99$, $p<0.001$) and Young's modulus ($r=0.99$, $p<0.001$), respectively. Values were calculated at 10% MVC increments from 20–80% MVC with their standard deviations.

Chapter 3

3 Discussion and Summary

3.1 Discussion

The present study investigated the relationship between calcaneal tendon stiffness and plantar flexor contractile rates of torque and velocity during isometric and isotonic contractions. Although moderate correlations were observed between YM and evoked RTD during isometric contractions, mostly weak, non-significant correlations were found between both voluntary and electrically evoked dynamic RTD and RVD at low and high loads. These results indicate that tendon stiffness is an important feature of isometric contractile properties but may have limited influence for RTD and RVD during isotonic dynamic contractions (Bojsen-Møller et al., 2005, Monte and Zignoli, 2021, Wang et al., 2012).

In the literature on isometric actions, there are inconsistencies regarding the influence of musculotendinous properties like stiffness on RTD. Several studies have shown significant, positive correlations between tendon stiffness and RTD, but the correlation coefficients have been weak to moderate (r=0.3–0.6), and variable (Bojsen-Møller et al., 2005, Monte and Zignoli, 2021, Wang et al., 2012). The current results for isometric contractions align with previous literature in that evoked RTD was moderately associated with tendon stiffness, and to a greater degree than voluntary RTD (Massey et al., 2017). However, no significant correlations between YM and voluntary isometric RTD were observed. The lack of moderate to strong correlations between YM and isometric RTD has been reported by others (Hannah and Folland, 2014, Massey et al., 2017). When RTDs are normalized to a participant's maximal strength, the correlations between tendon stiffness and RTD are attenuated, suggesting that maximal strength is a better determinant of RTD than tendon stiffness. Because those with greater strength likely would have greater muscle mass with complementary larger tendons, we calculated YM to normalize these differences in morphological tendon properties.

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Although isometric RTD has been used as a critical contractile property for evaluating explosive strength and for functional performance, these contractile properties may not be readily applicable to dynamic contractions, which involve salient changes in joint angle and muscle fascicle shortening. Hence, understanding these tendon properties in relation to dynamic contractile properties is important to understand their role during movement. Unlike the evoked isometric RTD versus YM results, we observed no significant correlations between YM and neither voluntary nor evoked RTD and RVD at either a low (10%) or high (40%) load. For comparisons during dynamic contractions, both RTD and RVD were normalized to peak torque and velocity output during the isotonic contraction, which may attenuate expected correlations, as reported during isometric contractions (Hannah and Folland, 2014). However, neither the evoked nor voluntary contractions provided even moderate correlations, indicating that during maximal effort isotonic contractions, tendon stiffness may have a limited role or relationship in dynamic contractile properties. This would indicate that dynamic contractions may have different determinants of contractile rates than isometric contractions, or at least the relative contributions of these determinants may be altered, but these factors have not been explored.

The greater evoked RTD at 300 Hz stimulation frequency compared to voluntary RTD for both isometric and isotonic contractions agrees with previous literature. The stronger correlations observed with evoked RTD compared to voluntary may be related to the removal of participant differences in the rate of voluntary neural activation, but also could be related to the quicker generation of torque with evoked contractions. Indeed, the influence of tendon stiffness may be more of a factor during the early contraction phase (i.e., 0 to 50 ms) (Folland et al., 2014) compared to later time intervals. Thus, the rapid torque generation of 300 Hz stimulation frequency may be more influenced by the tendon stiffness compared to slower voluntary activation. However, for RVD, no differences were observed between evoked and voluntary contractions. Because the slack within the series elastic elements of the muscle must be removed before the requisite torque is attained to move the load during isotonic contractions, the relative contribution of tendon stiffness during joint rotation may be greatly attenuated, which may explain why we

observed null correlations between RVD and tendon stiffness. Future work exploring isokinetic contractions, which initiate joint rotation upon torque onset, may provide a more applicable model to explore the influence of tendon stiffness on rates of dynamic contractile features.

3.2 Conclusions

Although intrinsic tendinous properties indubitably affect muscular force transmission, the explosiveness of the contraction is likely better related to other neuromuscular factors such as rate of neural activation. Furthermore, dynamic contractions may change the relative contribution of these factors affecting RTD as the influence of tendon stiffness was lessened compared to an isometric state. Compared to RTD, determinants of RVD are relatively understudied factors although the importance of these rates in daily life and in correcting perturbations in balance is well-known.

3.3 Limitations

One potential limitation is that tendon stiffness was determined during a controlled, relatively slow isometric contraction but RTDs and RVDs were evaluated during maximal effort, rapid contractions. This may detract from the relatability of the parameters as tendon stiffness properties are known to be affected by both angular joint rotation and the rate at which they are strained (Arampatzis et al., 2005, Clemmer et al., 2010). Moreover, although both males and females were recruited, we did not have adequate sample size of female participants to explore potential sex-related differences. However, previous work has shown that normalizing RTD to MVC torque can control for possible sex differences in the lower limb (Hannah et al., 2012, Inglis et al., 2017). Using Young's modulus, which accounts for morphological differences across people, may also mitigate any potential sex effect.

3.4 Future directions

The current investigation suggests calcaneal tendon stiffness is not a primary determinant of dynamic RTD nor RVD. Although there are discrepancies in the isometric literature concerning these particular correlations (Hannah & Folland, 2014; Maffiuletti et al.,

2016), there is a relative dearth of literature examining dynamic contractile rates. Considering most environmental interactions require some degree or semblance of joint movement, the co-examination of RTD and RVD and their influence on peak power output warrant further study.

When assessing dynamic contractile rates, the time increments being studied are on the order of hundreds of milliseconds. Given the fleeting nature of these contractions, it is prudent to obtain reliable dynamometer readings for rate determination. Studies using isometric modes have shown poor RTD reliability; the extent of which is dependent on the movement performed (Sleivert & Wenger, 1994). There is currently no research on the reliability of dynamic contractile rate determinants. For dynamic contractions, most commercial dynamometers have the ability to facilitate two main contraction modalities: isotonic and isokinetic. For isotonic contractions, the resistance is fundamentally fixed throughout the range of motion and the angular velocity can vary. Isokinetic contractions involve controlling the maximal velocity of the contraction regardless of contractile effort (Pipes & Wilmore, 1975). Ascertaining the reliability of each dynamic contraction modality will provide insight as to which modality is better suited for assessing dynamic contractile rates.

With the projected rise of the Canadian senior citizen population, research into neuromuscular adaptations that occur with healthy and maladapted ageing continues to grow in relevancy. Studies report a progressive slowing of RTD with ageing (Suetta et al., 2004) which has functional implications like the compromised capacity to generate a corrective movement after a stumble. Understanding the adapted aged state in a dynamic setting may allow for the construction of paradigms that seek to minimize the decline in contractile rates throughout the ageing process.

Movement generation is generally thought to commence in the primary motor cortex. The firing of these neurons is heavily dependent on corticospinal excitability, often assessed using transcranial magnetic stimulation (TMS) (Kalmar, 2018). Baudry & Duchateau (2021) demonstrated that contraction characteristics (including RTD) influence the corticospinal excitability just prior to a contraction. Investigating corticospinal

excitabilities in response to different types of dynamic movements may provide insight into how the most proximal parts of the neuromuscular system facilitate daily tasks that may impact rates of contractile output.

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Appendix

Appendix A. Ethical Approval

Western Research

Date: 9 March 2022

To: Charles Rice

Project ID: 107505

Study Title: Motor neuron and muscle fiber resilience in humans

Application Type: Continuing Ethics Review (CER) Form

Review Type: Delegated

Date Approval Issued: 09/Mar/2022

REB Approval Expiry Date: 07/Mar/2023

***Ethics Approval Lapse:** March 8 - 9, 2022**

Dear Charles Rice,

The Western University Research Ethics Board has reviewed the application. This study, including all currently approved documents, has been re-approved until the expiry date noted above.

REB members involved in the research project do not participate in the review, discussion or decision.

Western University REB operates in compliance with, and is constituted in accordance with, the requirements of the Tri-Council Policy Statement: Ethical Conduct for Research Involving Humans (TCPS 2); the International Conference on Harmonisation Good Clinical Practice Consolidated Guideline (ICH GCP); Part C, Division 5 of the Food and Drug Regulations; Part 4 of the Natural Health Products Regulations; Part 3 of the Medical Devices Regulations and the provisions of the Ontario Personal Health Information Protection Act (PHIPA 2004) and its applicable regulations. The REB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000940.

Please do not hesitate to contact us if you have any questions.

Sincerely,

The Office of Human Research Ethics

Note: This correspondence includes an electronic signature (validation and approval via an online system that is compliant with all regulations).

Curriculum Vitae for Sohum V. Kulkarni

Education

Master of Science
Kinesiology-Integrative Biosciences
The University of Western Ontario
London, ON, Canada
2021-2023

Bachelor of Medical Sciences
Honors Spec. in Interdisciplinary Medical Sciences
The University of Western Ontario
London, ON, Canada
2017-2021

Honors and Awards

Province of Ontario Graduate Scholarship
2022-2023

Undergraduate Summer Research Internship
2020, 2021

Dean's Honor List
2019, 2020

The Western Scholarship of Excellence
2017

Related Work Experience

Graduate Teaching Assistant
The University of Western Ontario
London, ON, Canada
Kinesiology 3335 Leadership in Physical Activity (2021-2023)
Kinesiology 4430F Neuromuscular Physiology (2022)
Kinesiology 1060B Functional Human Gross Anatomy (2023)

Publications

Peer-reviewed Papers

Kulkarni, S. V., Paris, M. T., & Rice, C. L. (2023). Calcaneal tendon stiffness is not associated with dynamic time-dependent contractile output. *Appl. Physiol Nutr. Metab.*, *48*(4), 331–339. https://doi.org/10.1139/apnm-2022-0436

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Published Abstracts

Kulkarni, S.V., Paris, M.T., Rice, C. L. (2022). The effect of calcaneal tendon stiffness on dynamic rates of torque and velocity development. *Appl. Physiol. Nutr. Metab.*, *47*, S76. http://dx.doi.org/10.1139/apnm-2022-0269

Paris, M.T., **Kulkarni, S.V.**, Zero, A.M., Rice, C.L. (2022). Voluntary activation of the knee extensors during isometric and isotonic shortening contractions. *Appl. Physiol. Nutr. Metab.*, 47, S90. http://dx.doi.org/10.1139/apnm-2022-0269

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Conference Presentations

Kulkarni, S.V., Paris, M.T., Rice, C. L. The effect of calcaneal tendon stiffness on dynamic rates of torque and velocity development in plantar flexors. Exercise Neuroscience Group. May 16, 2022. London, ON, Canada. (oral presentation)

Kulkarni, S.V., Paris, M.T., Rice, C. L. The effect of calcaneal tendon stiffness on dynamic rates of torque and velocity development. Canadian Society for Exercise Physiology. November 5, 2022. Fredericton, NB, Canada. (oral presentation)