Short communication

Muscle-specific indices to characterise the functional behaviour of human lower-limb muscles during locomotion

Adrian K.M. Lai [a],*, Andrew A. Biewener [b], James M. Wakeling [a]

[a] Department of Biomedical Physiology and Kinesiology, Simon Fraser University, Burnaby, BC, Canada
[b] Department of Organismic and Evolutionary Biology, Concord Field Station, Harvard University, Bedford, MA, USA

ARTICLE INFO

ABSTRACT

The mechanical output of a muscle may be characterised by having distinct functional behaviours, which can shift to satisfy the varying demands of movement, and may vary relative to a proximo-distal gradient in the muscle-tendon architecture (MTU) among lower-limb muscles in humans and other terrestrial vertebrates. We adapted a previous joint-level approach to develop a muscle-specific index-based approach to characterise the functional behaviours of human lower-limb muscles during movement tasks. Using muscle mechanical power and work outputs derived from experimental data and computational simulations of human walking and running, our index-based approach differentiated known distinct functional behaviours with varying mechanical demands, such as greater spring-like function during running compared with walking; with anatomical location, such as greater motor-like function in proximal compared with the distal lower-limb muscles; and with MTU architecture, such as greater strut-like muscles fibre function compared with the MTU in the ankle plantarflexors. The functional indices developed in this study provide distinct quantitative measures of muscle function in the human lower-limb muscles during dynamic movement tasks, which may be beneficial towards tuning the design and control strategies of physiologically-inspired robotic and assistive devices.

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1. Introduction

Muscles generate force and do work to produce body movement. Muscles often contract to generate positive mechanical work and power. However, muscles may also contract isometrically or absorb energy, performing a range of functions across movement tasks and species (Dickinson et al., 2000). These functions can be characterised into four distinct behaviours: (1) a motor that generates positive work; (2) a spring that stores and recovers elastic strain energy; (3) a strut that generates significant force with minimal length change; and (4) a damper that lengthens to absorb energy. These functions depend on a range of factors, from interactions between the external environment and the body to the intrinsic properties of the muscle (Biewener, 2016). One clear example is the change in human ankle plantarflexor work that occurs with a shift in whole body mechanical demands during sprinting (Lai et al., 2016), or in turkey leg extensors during incline running (Roberts et al., 1997; Roberts and Scales, 2004). Other studies have shown that muscle function varies with a proximo-distal gradient of lower-limb muscle organisation (Biewener, 2016), where more distal muscles have been shown to exhibit strut-like, quasi-isometric muscle fibre behaviour favouring force development and spring-like storage of elastic strain energy in humans (e.g. Lai et al., 2015), wallabies (Biewener et al., 1998), and turkeys Roberts et al., 1997). In contrast, more proximal muscles generally favour work modulation (Biewener, 1998; Biewener and Daley, 2007).

Despite our understanding of how muscle function can vary with mechanical demand and anatomical location, there is yet to be a quantitative approach capable of comparing the function of different muscles and how function varies across locomotor demands. Addressing these limitations can assist in tuning the design and control strategies of physiological-inspired robotics and assistive devices that can mimic the diversity of human movement (Grimmer and Seyfarth, 2014). A promising index-based approach was introduced by Qiao and Jindrich (2016) that characterised joint function during locomotion. Our study adapts this approach to define muscle-specific parameters and, based on experimental data and computational simulations, applies the approach to characterise the functional behaviours of the human

* Corresponding author at: Department of Biomedical Physiology and Kinesiology, Simon Fraser 13 University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada.

E-mail address: adrian_lai@sfu.ca (A.K.M. Lai).

lower-limb muscles during locomotion. Using simulations of walking and running, we evaluated the approach by differentiating existing understanding of muscle function, including (1) greater spring-like function during running compared with walking, (2) greater motor-like function in the proximal limb muscles, and (3) greater strut-like function in distal muscle fibres compared with the MTU.

2. Methodology

2.1. Experimental protocol

Experimental data were taken from ten participants (9 males, 1 female; 27 ± 5.6 y.o.; 1.81 ± 0.07 m; 80.2 ± 11.7 kg) who were part of a larger study (Lai et al., 2015). Each participant gave their informed consent and the relevant ethics committees approved the study (University of Queensland ethics #: 2012001215). Marker trajectories and ground reaction forces were extracted during walking and running at steady-state speeds of 1.4 m s^{-1} and 4 m s^{-1}, respectively.

3D trajectories of 36 retro-reflective markers placed on the lower and upper limbs were tracked using an 8-camera, motion analysis system (Qualisys, Gothenburg, Sweden) sampling at 250 Hz. Ground reaction forces were collected using an instrumented treadmill (Tandem Treadmill, AMTI, Watertown, MA) sampling at 1000 Hz. Marker trajectories and ground reaction forces were filtered using a 4th order, low-pass Butterworth filter, both with a cut-off frequency of 15 Hz.

2.2. Musculoskeletal model

The musculoskeletal model consisted of 14 segments and 23 degrees of freedom (Lai et al., 2017). 80 Hill-type muscle-tendon units (MTUs), modelled as a Hill-type actuator with contractile and series elastic elements (Millard et al., 2013), drove the lower-limbs of the model. Tendon compliance of the ankle plantarflexors and knee extensors were set at 10% and 8% at max isometric force (F_o^m), respectively, consistent with averaged literature reported mechanical properties of the Achilles and patellar tendon, respectively (Hansen et al., 2003; Kubo et al., 2001; Lichtwark and Wilson, 2005; Reeves et al., 2003; Stafilidis et al., 2005). Due to limited reported values, tendon compliance of all other muscles were set at 4.9% strain at F_o^m (Millard et al., 2013).

2.3. Computational simulations

Musculoskeletal simulations were performed using OpenSim (v.3.3) (Delp et al., 2007). The generic musculoskeletal model was scaled to each participant's dimensions. Joint kinematics and net joint torques were computed using inverse kinematics and inverse dynamics tools, respectively. A set of smoothed, dynamically consistent kinematics were generated using a residual reduction algorithm (Thelen and Anderson, 2006) and were then used in conjunction with ground reaction forces as inputs to the computed muscle control—an algorithm that used forward integration over a time window (0.015 s)—to predict a set of muscle excitations that drove the simulation to the measured kinematic trajectories (Thelen and Anderson, 2006). Muscle excitations were bounded from 0 (no excitation) to 1 (full excitation).

2.4. MTU and muscle fibre mechanical work and functional indices

MTU, muscle fibre and tendon powers were calculated as the product of each component's force and contraction velocity at each time instant. Negative and positive mechanical work of the MTU,

muscle fibre and tendon, respectively, were calculated as the integral of the negative and positive portions of time-varying power curves.

The functional behaviours of the MTU and muscle fibres were categorised by four dimensionless indices: strut-, spring-, motor- and damper-like, which were calculated relative to each other, such that the cumulative percentage of all four indices was 100%. The functional index with the largest percentage was considered to characterise the "primary" functional role of the MTU and muscle fibres.

Each index is described in detail elsewhere (Qiao and Jindrich, 2016). Briefly, the strut index (I_{strut}) for the MTU and muscle fibres was calculated as follows,

$$I_{strut} = \max\left(1 - \frac{(t_{FS}(n+1) - t_{FS}(n)) \int_{t_{FS(n)}}^{t_{FS(n+1)}} |P_c^m| dt}{l_{cha} \int_{t_{FS(n)}}^{t_{FS(n+1)}} |F_c^m| dt}, 0\right) \times 100\% \tag{1}$$

where t_{FS} and l_{cha} are the time of foot strike and a characteristic length factor, respectively, and P_c^m and F_c^m are the power and force generated, respectively, by each component of the muscle. A high strut index occurs if the MTU and muscle fibres develop high force with minimal length change. A characteristic length factor was required to maintain a dimensionless muscle-specific strut index. To determine a length factor, we assumed that all lower-limb tendons operate as springs during steady-state running (McMahon and Cheng, 1990). Hence, we optimised the length factor to maximize the spring index (see below) of each muscle's tendon relative to its slack length. The optimised length factor was then used to calculate the strut index for the MTU and muscle fibres.

The spring index (I_{spring}) was calculated as follows,

$$I_{spring} = \frac{2 \cdot \min\left(|W_{com}^-|, |W_{gen}^+|\right)}{|W_{tot}^-| + |W_{tot}^+|} \times 100\% - I_{strut} \tag{2}$$

where W_{com}^- is the negative work during the compression phase and W_{gen}^+ is the positive work during the generation phase, W_{tot}^- is total negative work, and W_{tot}^+ is total positive work during the entire gait cycle. A high spring index results from the MTU or the muscle fibres absorbing substantial negative work prior to generating substantial positive work, with net work done being low.

The motor index (I_{motor}) was calculated as follows,

$$I_{motor} = \frac{|W_{tot}^+| - \min\left(|W_{com}^-|, |W_{gen}^+|\right)}{|W_{tot}^-| + |W_{tot}^+|} \times 100\% - I_{strut} \tag{3}$$

A high motor index results from the MTU or muscle fibres generating substantial positive work with little or no negative work during the gait cycle.

Lastly, the damper index (I_{damper}) was calculated as follows,

$$I_{damper} = \frac{|W_{tot}^-| - \min\left(|W_{com}^-|, |W_{gen}^+|\right)}{|W_{tot}^-| + |W_{tot}^+|} \times 100\% - I_{strut} \tag{4}$$

A high damper index indicates that the MTU or muscle fibres generate substantial negative work with little or no positive work during the gait cycle.

2.5. Data analysis

Data were collected for two gait cycles and were time normalised between consecutive foot strikes. The right leg was chosen as the leg of interest for all participants. All data were used to calculate a group mean ± SD values. MTU and muscle fibre mechanical power and work were normalised to body mass.

We selected a subset of lower-limb muscles in which to test the muscle-specific index approach that included gluteus maximus (GMAX), gluteus medius (GMED), rectus femoris (RF), biceps femoris (BF), semimembranosus (SM), vastus lateralis (VL), soleus (SO), medial gastrocnemius (MG), lateral gastrocnemius (LG), and tibialis anterior (TA). These muscles contribute significantly to the force requirements during walking and running (Dorn et al., 2012; Liu et al., 2006). We further grouped the selected muscles based on their locations in the lower-limb with the GMAX, GMED, RF, BF and SM defined as proximal muscles because they all cross the hip joint, and the VL, SO, MG, LG, and TA defined as distal muscles acting about the knee and ankle joints.

To test if the functional indices were capable of differentiating known muscle function during locomotion, we conducted three statistical tests using R (v.3.5) (R-Core-Team, 2018). One-way repeated measures ANOVAs tested for changes in the spring index with gait and changes in the motor index with anatomical location. In addition, for each muscle, one-way repeated measures ANOVA tested for changes in the strut index between the MTU and muscle fibres. A p-value of 0.05 determined statistical significance.

3. Results

The selected muscles generated the majority of total negative (68%) and positive (69%) MTU power and work done by the lower-limb during walking and running (Figs. 1 and 2). Specifically, GMAX, VL, MG, and SO generated substantial MTU and muscle fibre power during the stance phase of walking and running; whereas, bi-articular RF and BF generated substantial negative and positive power during the swing phase of walking and running. The functional indices of the selected muscles varied with mechanical demand and anatomical location (Fig. 3). First, the spring indices of the MTU and muscle fibres averaged 7.2% higher during running compared with walking ($p < 0.001$). Second, the motor indices for the MTU and muscle fibres of proximal muscles averaged 18.4% greater than those of distal muscles across gait

($p < 0.001$). Last, the strut indices of SO, MG and LG muscle fibres averaged 32.1% ($p < 0.001$) and 11.3% ($p < 0.001$) and 18.4% ($p < 0.001$) higher, respectively, than their MTUs across gait.

4. Discussion

A muscle's function is commonly characterised by its mechanical force and work output. We show that the functional index approach introduced here is capable of quantitatively characterising and differentiating functional variations of several human lower-limb muscles across gait-related whole-body mechanical demands, their anatomical location within the limb, and between the MTU and its muscle fibres. For example, our muscle-specific index approach demonstrated the shift to more spring-like muscle function associated with the mass-spring dynamics of running (Blickhan, 1989; McMahon and Cheng, 1990) compared with the inverted-pendulum dynamics of walking (Cavagna et al., 1976).

The index-based approach also identified greater motor-like function of proximal human limb muscles compared with distal muscles during walking and running, consistent with prior suggestions that more proximal limb muscles favour mechanical work modulation (Biewener and Daley, 2007; Carrier et al., 1998; Gregersen et al., 1998). These varying patterns of MTU and muscle fibre function are intrinsically linked to the substantial variation in muscle-tendon architecture that exists in the limbs of humans and other cursorial animals (Biewener and Roberts, 2000). Finally, the greater strut-like function of the human ankle plantarflexors during level steady-state walking and running is consistent with in-vivo studies that have found that the muscle fibres operate quasi-isometrically compared with the MTU, which undergoes spring-like behaviour due to tendon elasticity (Fukunaga et al., 2001; Lichtwark et al., 2007).

Consistent with a recent joint-level study (Farris and Raiteri, 2017), our muscle-specific functional index may have implications for improving the design and control strategies of physiologically-inspired robotics and assistive devices. For example, powered
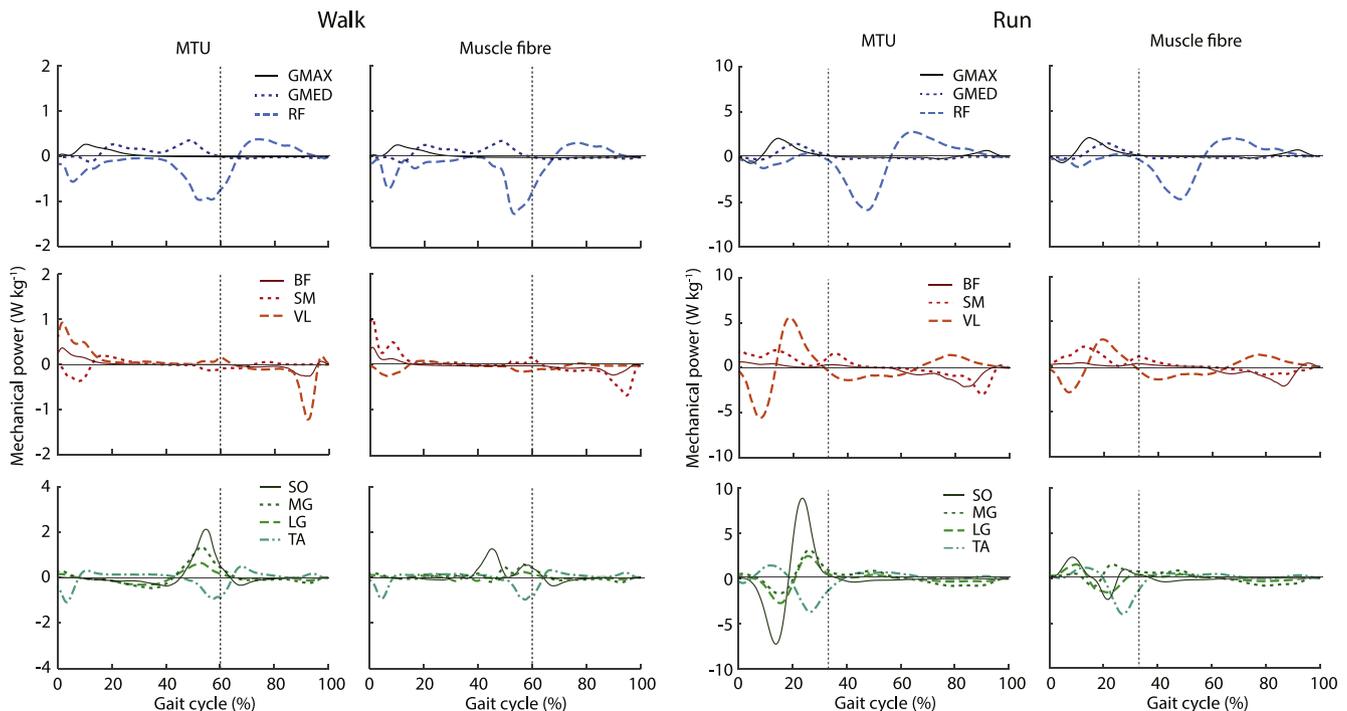
Fig. 1. Mean MTU and muscle fibre power across all participants for the ten selected muscles during walking and running at steady-state speed of 1.4 m s^{-1} and 4 m s^{-1}. Mechanical power was normalised to body mass.
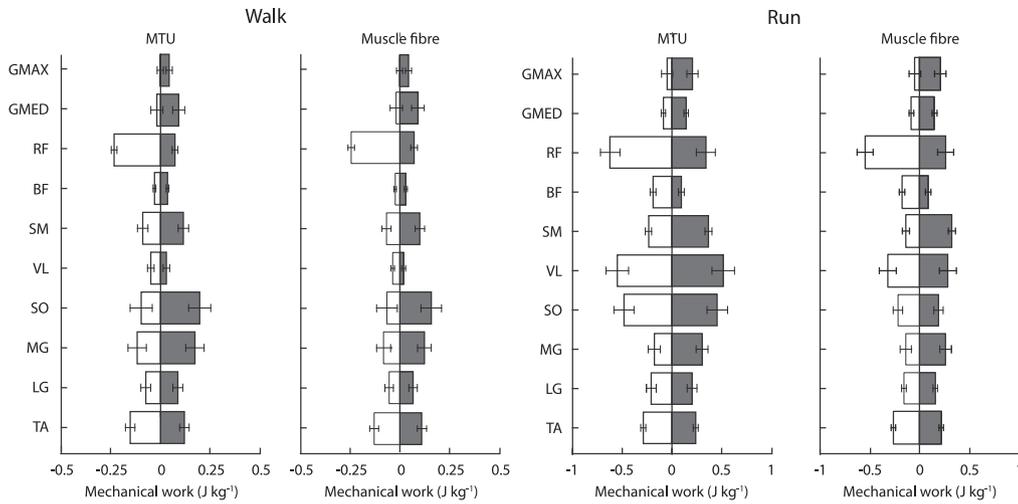
Fig. 2. Positive and negative work done by MTU and muscle fibres for the ten selected muscles during walking and running at steady-state speed of 1.4 m s^{-1} and 4 m s^{-1}. Mechanical work was normalised to body mass.
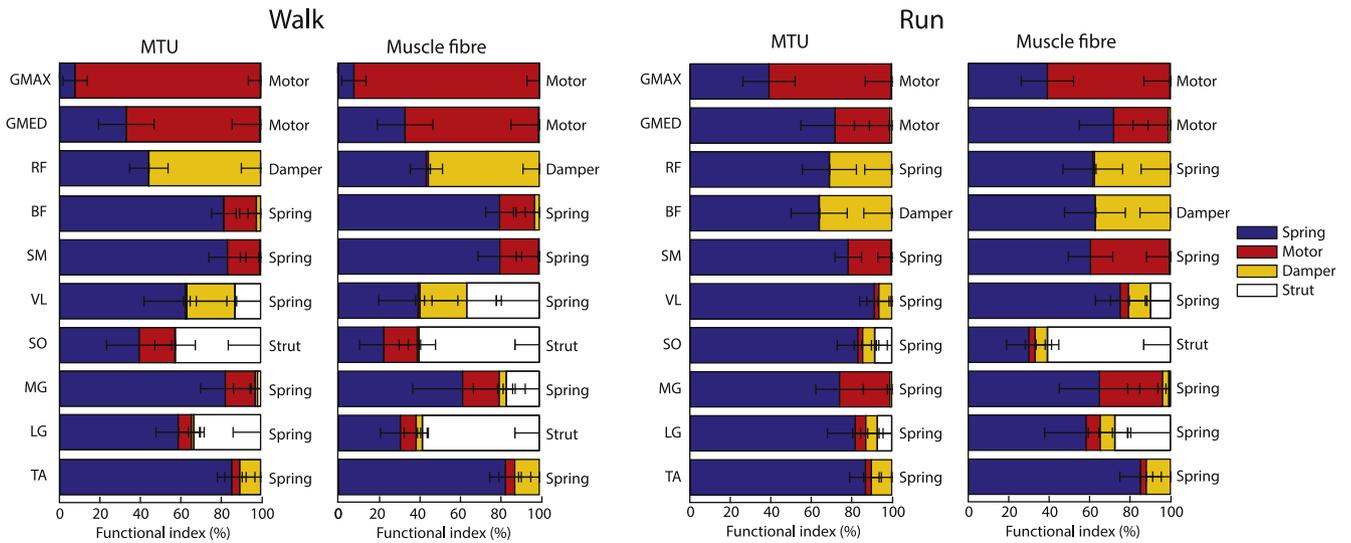
Fig. 3. Functional indices of the MTU and muscle fibres for the ten selected muscles during walking and running at steady-state speed of 1.4 m s^{-1} and 4 m s^{-1}. The indices were dimensionless and calculated relative to each other such that the cumulative percentage was 100%.

actuators designed to mimic the proximal limb muscles have prioritised stiff, high-bandwidth positional control for work modulation while distal actuators have prioritised high force output in series with an elastic element for energy savings (Grimmer and Seyfarth, 2014). Yet, control systems of these actuators such as finite state machines are limited in their ability to adapt to varying mechanical demands (Jiménez-Fabián and Verlinden, 2012). A quantitative index of muscle function, as developed here, could be used as a predictive measure of functional changes in multiple actuators simultaneously when the timing and magnitude of input and position are tuned in real-time. For example, during a change in mechanical demand, an actuator could function more optimally acting in a spring-like compared with a motor-like manner. Thus, the underlying control strategies could be adjusted from prioritising positional control to a strategy for high force output.

While the predicted muscle fibre lengths in more distal limb muscles can be compared with in-vivo measurements during locomotion (Lai et al., 2016), validation of our muscle-index approach is limited by the lack of equivalent in-vivo measure-

ments in more proximal limb muscles such as the GMAX, which limits evaluation of the predicted function of muscle fibres in these muscles and the decoupling effects of tendon compliance. We performed a post-hoc sensitivity analysis by varying the compliance of all muscles to 8% at F_o^m for walking and running simulations of one participant and observed minimal change in muscle fibre length, mechanical work, and functional behaviours of the MTU and muscle fibres. Because the cyclic nature of steady walking and running accentuates a muscle spring index, future studies should consider movements that demand higher power output, such as acceleration and jumping, to explore how changes in mechanical demand may shift the functional roles of different limb muscles.

The muscle-specific functional index developed in this study provides a quantitative approach to characterise the roles of the muscles across different locomotor conditions and was capable of differentiating distinct functional behaviours of the MTU and muscle fibres with varying mechanical demands and anatomical location.

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