



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

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

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27 **Abstract**

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

42

43 **Introduction**

44 Muscles generate force and do work to produce body movement. Muscles often contract to generate
45 positive mechanical work and power. However, muscles may also contract isometrically or absorb
46 energy, performing a range of functions across movement tasks and species (Dickinson et al., 2000).
47 These functions can be characterised into four distinct behaviours: (1) a motor that generates positive
48 work; (2) a spring that stores and recovers elastic strain energy; (3) a strut that generates significant
49 force with minimal length change; and (4) a damper that lengthens to absorb energy. These functions
50 depend on a range of factors, from interactions between the external environment and the body to the
51 intrinsic properties of the muscle (Biewener, 2016). One clear example is the change in human ankle
52 plantarflexor work that occurs with a shift in whole body mechanical demands during sprinting (Lai et
53 al., 2016), or in turkey leg extensors during incline running (Roberts et al., 1997; Roberts and Scales,
54 2004). Other studies have shown that muscle function varies with a proximo-distal gradient of lower-
55 limb muscle organisation (Biewener, 2016), where more distal muscles have been shown to exhibit
56 strut-like, quasi-isometric muscle fibre behaviour favouring force development and spring-like storage
57 of elastic strain energy in humans (e.g. Lai et al., 2015), wallabies (Biewener et al., 1998), and turkeys
58 Roberts et al., 1997). In contrast, more proximal muscles generally favour work modulation (Biewener,
59 1998; Biewener and Daley, 2007).

60 Despite our understanding of how muscle function can vary with mechanical demand and anatomical
61 location, there is yet to be a quantitative approach capable of comparing the function of different
62 muscles and how function varies across locomotor demands. Addressing these limitations can assist in
63 tuning the design and control strategies of physiological-inspired robotics and assistive devices that can
64 mimic the diversity of human movement (Grimmer and Seyfarth, 2014). A promising index-based
65 approach was introduced by Qiao and Jindrich (2016) that characterised joint function during
66 locomotion. Our study adapts this approach to define muscle-specific parameters and, based on
67 experimental data and computational simulations, applies the approach to characterise the functional
68 behaviours of the human lower-limb muscles during locomotion. Using simulations of walking and
69 running, we evaluated the approach by differentiating existing understanding of muscle function,
70 including (1) greater spring-like function during running compared with walking, (2) greater motor-like
71 function in the proximal limb muscles, and (3) greater strut-like function in distal muscle fibres
72 compared with the MTU.

73 **Methodology**

74 **Experimental protocol**

75 Experimental data were taken from ten participants (9 males, 1 female; 27 ± 5.6 y.o.; 1.81 ± 0.07 m;
76 80.2 ± 11.7 kg) who were part of a larger study (Lai et al., 2015). Each participant gave their informed
77 consent and the relevant ethics committees approved the study (University of Queensland ethics #:

78 2012001215). Marker trajectories and ground reaction forces were extracted during walking and
79 running at steady-state speeds of 1.4 m s^{-1} and 4 m s^{-1} , respectively.

80 3D trajectories of 36 retro-reflective markers placed on the lower and upper limbs were tracked using
81 an 8-camera, motion analysis system (Qualisys, Gothenburg, Sweden) sampling at 250 Hz. Ground
82 reaction forces were collected using an instrumented treadmill (Tandem Treadmill, AMTI, Watertown,
83 MA) sampling at 1000 Hz. Marker trajectories and ground reaction forces were filtered using a 4th order,
84 low-pass Butterworth filter, both with a cut-off frequency of 15 Hz.

85 **Musculoskeletal model**

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

94 **Computational simulations**

95 Musculoskeletal simulations were performed using OpenSim (v.3.3) (Delp et al., 2007). The generic
96 musculoskeletal model was scaled to each participant's dimensions. Joint kinematics and net joint
97 torques were computed using inverse kinematics and inverse dynamics tools, respectively. A set of
98 smoothed, dynamically consistent kinematics were generated using a residual reduction algorithm
99 (Thelen and Anderson, 2006) and were then used in conjunction with ground reaction forces as inputs
100 to the computed muscle control — an algorithm that used forward integration over a time window
101 (0.015 sec) — to predict a set of muscle excitations that drove the simulation to the measured kinematic
102 trajectories (Thelen and Anderson, 2006). Muscle excitations were bounded from 0 (no excitation) to 1
103 (full excitation).

104 **MTU and muscle fibre mechanical work and functional indices**

105 MTU, muscle fibre and tendon powers were calculated as the product of each component's force and
106 contraction velocity at each time instant. Negative and positive mechanical work of the MTU, muscle
107 fibre and tendon, respectively, were calculated as the integral of the negative and positive portions of
108 time-varying power curves.

109 The functional behaviours of the MTU and muscle fibres were categorised by four dimensionless
110 indices: strut-, spring-, motor- and damper-like, which were calculated relative to each other, such that

111 the cumulative percentage of all four indices was 100%. The functional index with the largest
 112 percentage was considered to characterise the “primary” functional role of the MTU and muscle fibres.

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

$$115 \quad I_{strut} = \max \left(1 - \frac{(t_{FS}(n+1) - t_{FS}(n)) \int_{t_{FS}(n)}^{t_{FS}(n+1)} |P_c^m| dt}{l_{cha} \int_{t_{FS}(n)}^{t_{FS}(n+1)} |F_c^m| dt}, 0 \right) \times 100\% \quad (1)$$

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

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

$$125 \quad I_{spring} = \frac{2 \cdot \min(|W_{com}^-|, |W_{gen}^+|)}{|W_{tot}^-| + |W_{tot}^+|} \times 100\% - I_{strut} \quad (2)$$

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

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

$$131 \quad I_{motor} = \frac{|W_{tot}^+| - \min(|W_{com}^-|, |W_{gen}^+|)}{|W_{tot}^-| + |W_{tot}^+|} \times 100\% - I_{strut} \quad (3)$$

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

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

$$135 \quad I_{damper} = \frac{|W_{tot}^-| - \min(|W_{com}^-|, |W_{gen}^+|)}{|W_{tot}^-| + |W_{tot}^+|} \times 100\% - I_{strut} \quad (4)$$

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

138 **Data analysis**

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

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

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

156 **Results**

157 The selected muscles generated the majority of total negative (68%) and positive (69%) MTU power
158 and work done by the lower-limb during walking and running (Figs. 1 and 2). Specifically, GMAX,
159 VL, MG, and SO generated substantial MTU and muscle fibre power during the stance phase of walking
160 and running; whereas, bi-articular RF and BF generated substantial negative and positive power during
161 the swing phase of walking and running. The functional indices of the selected muscles varied with
162 mechanical demand and anatomical location (Fig. 3). First, the spring indices of the MTU and muscle
163 fibres averaged 7.2% higher during running compared with walking ($p < 0.001$). Second, the motor
164 indices for the MTU and muscle fibres of proximal muscles averaged 18.4% greater than those of distal
165 muscles across gait ($p < 0.001$). Last, the strut indices of SO, MG and LG muscle fibres averaged 32.1%
166 ($p < 0.001$) and 11.3% ($p < 0.001$) and 18.4% ($p < 0.001$) higher, respectively, than their MTUs across
167 gait.

168

169 Discussion

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

177 The index-based approach also identified greater motor-like function of proximal human limb muscles
178 compared with distal muscles during walking and running, consistent with prior suggestions that more
179 proximal limb muscles favour mechanical work modulation (Biewener and Daley, 2007; Carrier et al.,
180 1998; Gregersen et al., 1998). These varying patterns of MTU and muscle fibre function are intrinsically
181 linked to the substantial variation in muscle-tendon architecture that exists in the limbs of humans and
182 other cursorial animals (Biewener and Roberts, 2000). Finally, the greater strut-like function of the
183 human ankle plantarflexors during level steady-state walking and running is consistent with in-vivo
184 studies that have found that the muscle fibres operate quasi-isometrically compared with the MTU,
185 which undergoes spring-like behaviour due to tendon elasticity (Fukunaga et al., 2001; Lichtwark et al.,
186 2007).

187 Consistent with a recent joint-level study (Farris and Raiteri, 2017), our muscle-specific functional
188 index may have implications for improving the design and control strategies of physiologically-inspired
189 robotics and assistive devices. For example, powered actuators designed to mimic the proximal limb
190 muscles have prioritised stiff, high-bandwidth positional control for work modulation while distal
191 actuators have prioritised high force output in series with an elastic element for energy savings
192 (Grimmer and Seyfarth, 2014). Yet, control systems of these actuators such as finite state machines are
193 limited in their ability to adapt to varying mechanical demands (Jiménez-Fabián and Verlinden, 2012).
194 A quantitative index of muscle function, as developed here, could be used as a predictive measure of
195 functional changes in multiple actuators simultaneously when the timing and magnitude of input and
196 position are tuned in real-time. For example, during a change in mechanical demand, an actuator could
197 function more optimally acting in a spring-like compared with a motor-like manner. Thus, the
198 underlying control strategies could be adjusted from prioritising positional control to a strategy for high
199 force output.

200 While the predicted muscle fibre lengths in more distal limb muscles can be compared with in-vivo
201 measurements during locomotion (Lai et al., 2016), validation of our muscle-index approach is limited
202 by the lack of equivalent in-vivo measurements in more proximal limb muscles such as the GMAX,
203 which limits evaluation of the predicted function of muscle fibres in these muscles and the decoupling

204 effects of tendon compliance. We performed a post-hoc sensitivity analysis by varying the compliance
 205 of all muscles to 8% at F_0^m for walking and running simulations of one participant and observed minimal
 206 change in muscle fibre length, mechanical work, and functional behaviours of the MTU and muscle
 207 fibres. Because the cyclic nature of steady walking and running accentuates a muscle spring index,
 208 future studies should consider movements that demand higher power output, such as acceleration and
 209 jumping, to explore how changes in mechanical demand may shift the functional roles of different limb
 210 muscles.

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

215 **Conflict of interest statement**

216 There are no conflicts of interest.

217 **Acknowledgements**

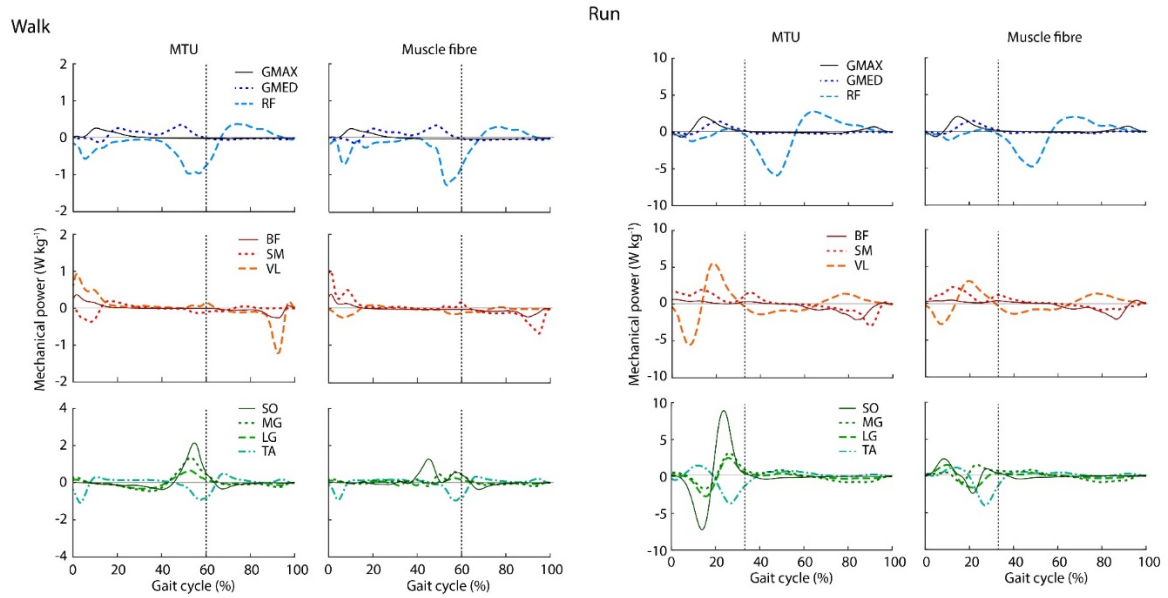
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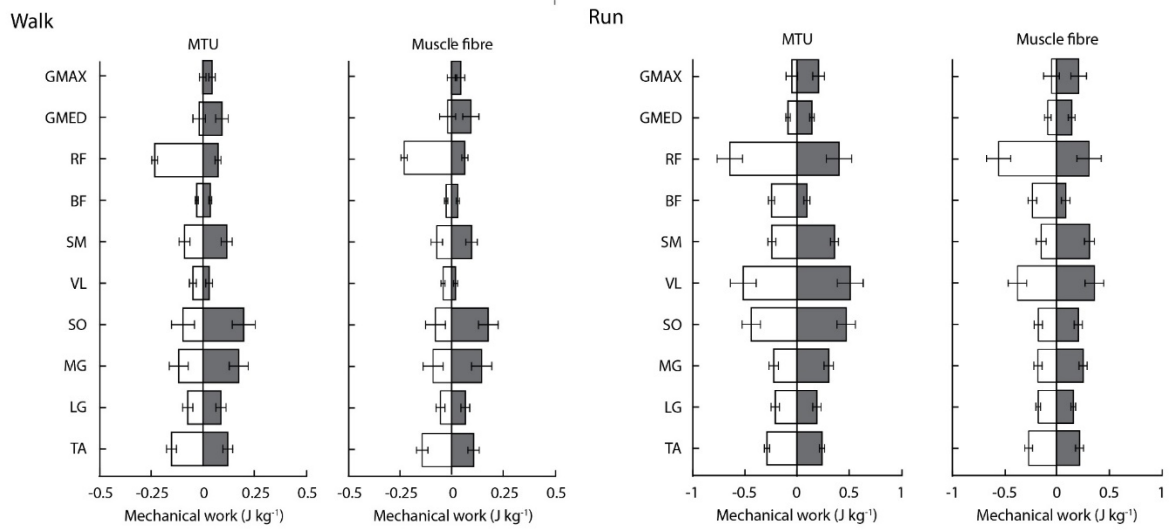
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- 302
- 303

304 **Figures**305 **Figure 1**

306

307 Figure 1: Mean MTU and muscle fibre power across all participants for the ten selected muscles during
 308 walking and running at steady-state speed of 1.4 m s⁻¹ and 4 m s⁻¹. Mechanical power was normalised
 309 to body mass.

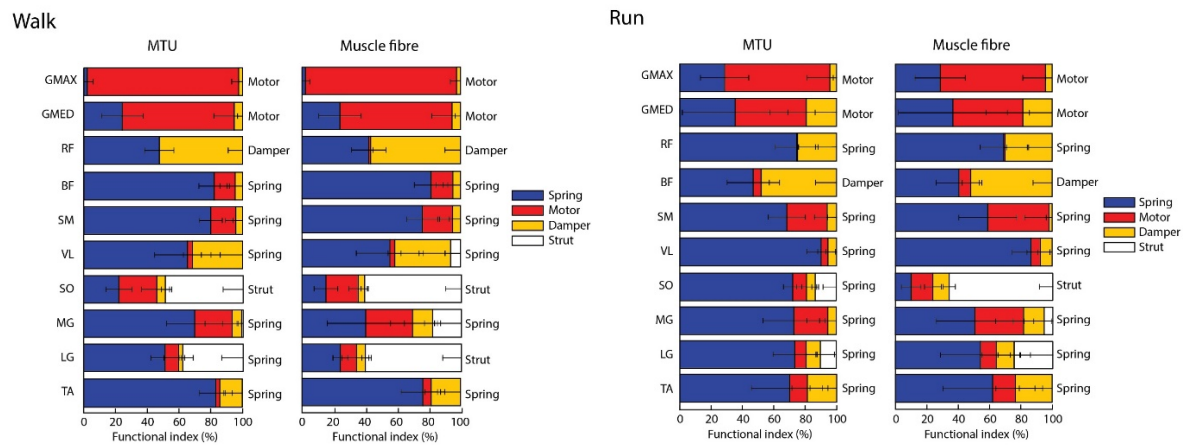
310 **Figure 2**

311

312 Figure 2: Positive and negative work done by MTU and muscle fibres for the ten selected muscles
 313 during walking and running at steady-state speed of 1.4 m s^{-1} and 4 m s^{-1} . Mechanical work was
 314 normalised to body mass.

315

316

317 **Figure 3**

318

319 Figure 3: Functional indices of the MTU and muscle fibres for the ten selected muscles during walking

320 and running at steady-state speed of 1.4 m s⁻¹ and 4 m s⁻¹. The indices were dimensionless and calculated

321 relative to each other such that the cumulative percentage was 100%.

322