

History-dependent perturbation response in limb muscle

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Summary Statement: The response of muscles to rapid, identical strain perturbations is history dependent, but is captured by a viscoelastic model with memory. Muscle function during perturbations therefore depends on locomotor frequency.

12 1 Abstract

13 Muscle mediates movement but movement is typically unsteady and perturbed. Muscle is known
14 to behave non-linearly and with history dependent properties during steady locomotion, but the
15 importance of history dependence in mediating muscles function during perturbations remains less
16 clear. To explore muscle's capacity to mitigate perturbations, we constructed a series of perturba-
17 tions that varied only in kinematic history, keeping instantaneous position, velocity and time from
18 stimulation constant. We discovered that muscle's perturbation response is profoundly history de-
19 pendent, varying by four fold as baseline frequency changes, and dissipating energy equivalent to
20 ~ 6 times the kinetic energy of all the limbs (nearly 2400 W Kg^{-1}). Muscle's energy dissipation
21 during a perturbation is predicted primarily by the force at the onset of the perturbation. This
22 relationship holds across different frequencies and timings of stimulation. This history dependence
23 behaves like a viscoelastic memory producing perturbation responses that vary with the frequency
24 of the underlying movement.

25 2 Introduction

26 Muscle produces, dissipates, stores, returns, and transits mechanical energy to adopt diverse func-
27 tions during locomotion (Dickinson et al., 2000). Even the same muscle can adopt different functions
28 in unsteady or perturbed conditions (Biewener and Daley, 2007; Azizi and Roberts, 2010). A sin-
29 gle muscle in the leg of cockroach normally dissipates energy during steady-state running (Ahn
30 et al., 2006; Full et al., 1998). Yet when the animal is perturbed, neural feedback can categorically
31 switch the muscle's function from one stride to the next (Sponberg, Spence, Mullens and Full,
32 2011). Under unsteady conditions the muscle can dissipate more than ten times the energy that it
33 does in steady state or convert its function to that of non-linear motor (Sponberg, Libby, Mullens
34 and Full, 2011). It remains challenging to predict function from the quasi-static length-tension
35 and force-velocity relationships, especially under unsteady conditions. Nonetheless such conditions
36 likely pose greater performance demands than steady-state.

37 Strain history-dependent muscle properties are well known to affect muscle's stress develop-
38 ment. These properties include force depression during shortening and force enhancement during
39 lengthening. While the specific mechanisms for history dependence remain controversial and are
40 likely multifaceted (Rassier, 2012), there are established consequences for steady, transition, and
41 impulsive behaviors (Josephson, 1999; Roberts and Azizi, 2011; Herzog et al., 2015; Nishikawa,
42 2016). However, muscle function during perturbations during movement is much less explored.
43 Perturbations around steady-state, typically tetanic conditions are ubiquitous and simple material
44 models like a viscoelastic Voigt body or a three component Hill model can typically capture muscle
45 behavior in these cases (*e.g.* (Kirsch et al., 1994; Zajac, 1989; Cannon and Zahalak, 1982). However,
46 dynamic conditions can create unexpected shifts in muscle performance (Robertson and Sawicki,
47 2015). During running, muscle experiences large rapid perturbations against a background strain
48 trajectory where history has the potential to alter function. This modulation could have profound
49 effects on muscle's response to unsteady perturbations encountered during running, including slips
50 or impacts with the substrate. Does history significantly modulate work output during rapid per-
51 turbations to periodic trajectories and can we reconcile any non-linearity with the simple material
52 models that capture perturbations in static conditions?

53 To test these ideas we construct a systematic perturbation to a cockroach limb muscle that can
54 reveal the importance of history on transient behavior and identify simple predictors of function
55 (Fig. 1a). To do this we maintain the same Hill-model contractile properties (stimulation, strain
56 trajectory, and velocity), while changing the strain history leading up to a perturbation. We
57 modify this history by changing the frequency of background strain. We hypothesize that history
58 dependence modulates muscle's mechanical response to rapid perturbations, but that the response

59 will be predictable from the components of an active viscoelastic system. If history dependence has
60 a functionally relevant consequence for rapid mechanical perturbations then muscle work during
61 the perturbation should vary systematically with history. If this history dependence matters for
62 locomotion then the modulation produced should be significant in light of the mechanical power
63 required to alter limb movement.

64 3 Materials and methods

65 Cockroaches (*Blaberus discoidalis*) were housed on a 12:12 light-dark cycle and fed dog chow *ad*
66 *libitum*. We targeted the ventral femoral extensor of the middle leg (muscle 137), which is not the
67 extensor that primarily powers limb extension, but rather a control muscle implicated in pertur-
68 bation responses to locomotion on rough terrain (Full et al., 1998; Ahn and Full, 2002; Sponberg
69 and Full, 2008). Instead of isolated muscle work loops (Josephson, 1985), we used intact joint work
70 loops following previous methods (Fig. 1b, (Sponberg, Libby, Mullens and Full, 2011)). In brief,
71 all motor neurons innervating the middle leg are severed at the mesothoracic ganglion by surgical
72 ablation of Nerves 3, 4, 5, and 6. The limb is then mounted on a custom restraint stage and the
73 coxa immobilized with epoxy. A muscle ergometer (Aurora Scientific 305C) attaches to the femur
74 near the coxa femur joint via a two pin joint that allows for rotation. The femur and more distal
75 segments are removed and the target muscle is activated via implant bipolar silver wire electrodes.
76 The moment arm, pivot point, and linear relationship between joint angle and muscle strain are
77 taken from prior work on this muscle. During steady-state work loop and imposed perturbations,
78 the ergometer prescribed joint trajectories and simultaneously measured force. While this precludes
79 the muscle from dynamically interacting with a load perturbation, it enabled us to use comparable
80 conditions that vary only in history.

81 Besides the advantage of preserving the animals nutrient and oxygen supply to the target
82 muscle, the intact joint work loop allows us to estimate the total passive work done on the joint.
83 Here, muscle work loops are the active component of the work, calculated by measuring a passive
84 work loop under identical strain conditions (including the perturbation) and subtracting the force
85 measured in the passive trial from that of the active trial. The remaining force signal can be
86 converted to muscle force (through the lever arm ratios) or used to calculate muscle work. Prior
87 work (Sponberg, Libby, Mullens and Full, 2011) validated this approach as reflective of the work
88 output and muscle function reported in more traditional partially isolated, muscle work loops with
89 direct neural stimulation (Full et al., 1998; Ahn et al., 2006).

90 Steady-state work loop conditions reflected strain trajectory from *in vivo* 10 Hz running con-
91 ditions and included three muscle potentials (spikes) of stimulation at 10 ms interspike interval
92 and 0.5 ms duration applied at the onset of shortening. Stimulus voltage for each preparation was
93 tuned to the minimum voltage needed to elicit a plateaued twitch response plus one volt. Per-
94 turbations were imposed halfway through shortening (stance) phases. We constructed 10 ms (100
95 Hz) half-sine perturbations of amplitude equal to the stride amplitude. These strain perturbations
96 were not summed with background periodic strain but rather pasted in place, so that kinematics
97 were exactly identical across all history conditions (Fig. 1a). The initial and terminal 1 ms of
98 the perturbation was smoothed into the underlying strain trajectory using a linear ramp filter to
99 prevent discontinuities in velocity.

100 We modified kinematics and timing of stimulus to test the effect of history on perturbation re-
101 sponse. Perturbation kinematics remained constant in all conditions. To preserve Hill determinants
102 during the perturbation, we varied the phase of stimulation so that the spike train always began
103 20 ms before the onset of perturbation (hence the stimulation in these altered conditions did not
104 reflect natural timing). We changed the phase of the background work loop so that perturbations
105 occurred both mid-stance and mid-swing, and we varied cycle frequency from 1 to 13.5 Hz, which
106 was the fastest condition where we could maintain accurate perturbation conditions. To test the

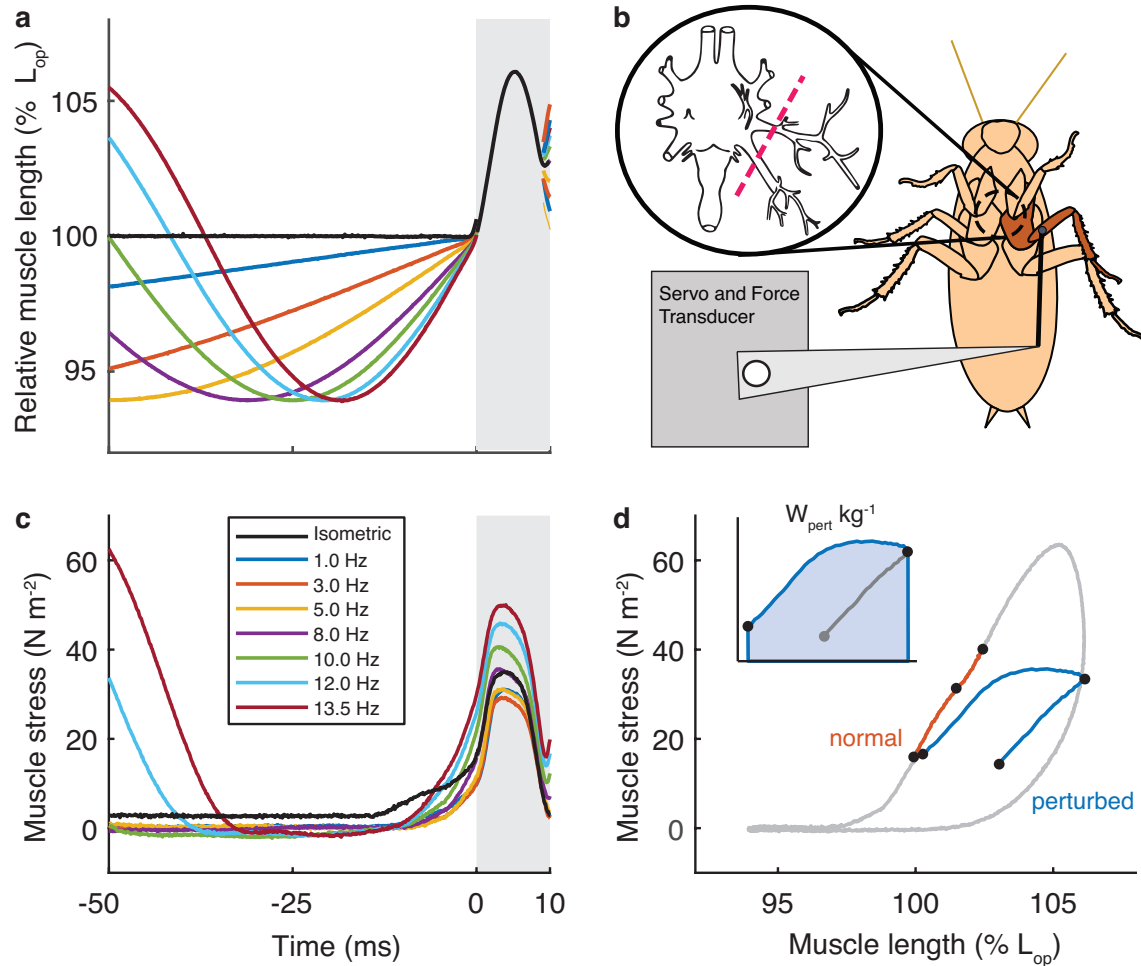


Figure 1: Identical eccentric perturbations (grey region) were applied during sinusoidal strain cycles of 1 Hz to 13.5 Hz (a). The intact joint workloop preparation (b) extracellularly stimulates muscles in the deinnervated limb (inset shows ganglion nerves cut adapted from (Pipa and Cook, 1959)). After subtracting out the passive joint work throughout the cycle (Sponberg, Libby, Mullens and Full, 2011), muscle stress (c) was integrated over strain for the eccentric portion of the perturbation to calculate work, W_{pert} (d).

107 generality of our results, we repeated these conditions at different stimulation timings varying from
 108 10 to 40 ms.

109 4 Results and discussion

110 4.1 Muscle's perturbation response is history-dependent

111 Muscles absorbed energy during all perturbations (Fig. 1c). We characterized the muscle's re-
 112 sponses by the mechanical energy dissipated during the stretch portion of the perturbation (the
 113 area under the force-length curve (Fig. 1d). Muscles absorbed $23.6 \pm 4.6 \text{ Jkg}^{-1}$ during pertur-
 114 bations applied against a 10 Hz pre-lengthened background. A Hill-type contractile unit would
 115 respond with identical force profiles to the perturbation regardless of kinematic history. By con-
 116 trast, we found that active muscle stress and energy dissipation increased strongly as we increased
 117 frequency under pre-lengthened conditions, and decreased with frequency under pre-shortened con-

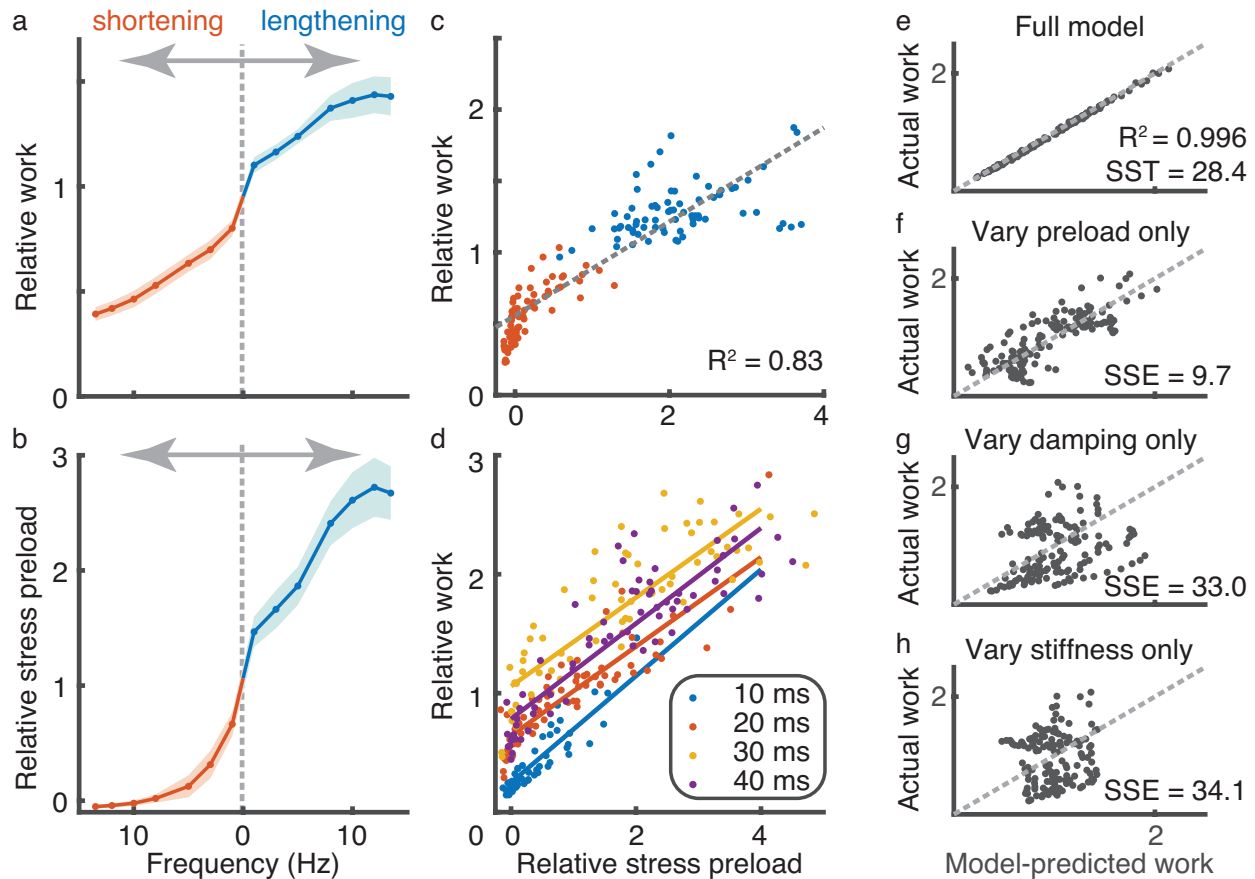


Figure 2: Work during perturbation (a) and preload stress (b) both vary significantly and monotonically with frequency, resulting in a correlated response (c). This relationship persists if stimulation varies by changing how long before the perturbation the muscle is electrically stimulated (d). To normalize across animals, work is taken relative to the average of the two 1 Hz perturbation conditions which most closely approximate the isometric work response. Relative stress is scaled to the isometric response to *in vivo* stimulation conditions (3 spikes, 10 ms interspike interval). Preload refers to stress developed immediately prior to the onset of the perturbation. A 3-parameter viscoelastic model with memory (e) predicts muscle's work during the perturbation (Fig. 1d). While all three parameters contribute to the full model, preload (f) has a predictive effect on its own, unlike damping (g) and stiffness (h). A sum of square errors (SSE) greater than the total sum of squares (SST) indicates a non-predictive model (g & h).

118 ditions (Fig. 2a). Energy absorption varied almost 4-fold over the range of frequencies we tested.
119 At the typical running stride frequency of 10 Hz, dissipation almost tripled if the muscle was
120 perturbed in identical ways during shortening and lengthening.

121 4.2 Force at onset of perturbation determines work

122 If preloading is the primary determinant of the muscle's variable perturbation response, then the
123 force at the onset of the perturbation should parallel the change in dissipative work. Indeed, muscle
124 stress prior to perturbation onset showed a pattern of frequency dependence similar to work (Fig.
125 2b) and the two are highly correlated (Fig. 2c, $R^2 = 0.83$, $p < 10^{-6}$). Despite the sharp deviations
126 from an otherwise monotonic work relationship on pre-stretch at 15 Hz, the stress at onset of these
127 perturbations still recapitulated the changes in absorption. At the fastest shortening velocities (left
128 side of Fig. 2 a,c), work continues to fall off even after preload stress has reached zero likely because
129 of the need to take up slack from the transition of rapid shortening to lengthening.

130 To further test the robustness of this relationship, we repeated the frequency and phase exper-
131 iments while varying the timing of muscle stimulation prior to perturbation. Muscle stress prior
132 to perturbation near static conditions increased almost 10 fold as timing advanced from 10 *ms* to
133 40 *ms*, but both the frequency dependency and the correlation between stress and work persisted
134 across stimulation conditions (Fig. 2d, $R > 0.85$, $p < 10^{-6}$ for all timings).

135 A Hill-type contractile element model fails to predict muscle's perturbation response, even
136 when time scales are quite rapid. Instead we support the hypothesis that history dependence tunes
137 muscle's mechanical response to perturbations. Muscle's response to rapid stretches is known to
138 have viscoelastic properties (Kirsch et al., 1994; Zajac, 1989); here we show that the context in
139 which a perturbation occurs, meaning the muscle's force history, modulates these properties and
140 shapes muscle's function even on short time scales. While Hill-like contractile elements fail to
141 directly predict the functional modulation during the perturbation, they do play a role because the
142 pre-perturbation forces follows a classic force-velocity curve (Fig. 2b), velocity is proportional to
143 frequency). Despite history varying muscle's mechanical work (Fig. 2a), the behavior of muscle is
144 nonetheless predictable. This relationship holds regardless of whether the muscle is pre-shortened
145 or pre-lengthened and across a range of frequencies and stimulation spanning natural running (Fig.
146 2c, d).

147 4.3 A viscoelastic model with memory captures muscle's rapid perturbation 148 response

149 Since muscle force-length behavior during the perturbations appeared viscoelastic (Fig. 1d), we
150 fit a parallel spring-damper (Voigt) model with a variable preload offset to the perturbation data.
151 Changes in dissipative work against history could arise from I) a change in stiffness, II) increased
152 viscous damping, or III) a change in the preload force. The full model fit these parameters separately
153 for each condition (phase and frequency) and strongly predicted observed energy absorption (Fig.
154 2e, $R^2 > 0.99$). To examine which parameters were most predictive, we tested three models
155 which each allowed only one parameter to vary (with the other two set to the average across
156 all frequencies/phases). Doing so reduced the variance accounted for in all cases, but only when
157 preload varied did the model retain any predictive ability (Fig. 2f-h).

158 The model property that best explained the functional variation was preload, rather than stiff-
159 ness or damping. In prior studies with small sinusoid perturbation, muscle stiffness varied with
160 frequency (Cannon and Zahalak, 1982; Kirsch et al., 1994). Here, variable stiffness does not account
161 for the major differences in perturbation work, likely because total strain, velocity and prior stim-
162 ulation were kept the same. During perturbations to steady state conditions, work also varies with
163 pre-perturbation force (Kirsch et al., 1994). We show that this adjustment, equivalent to changing
164 the set point of a viscoelastic model, is the critical feature for dynamic conditions and can account

165 for differences in perturbations responses relevant to locomotion. Our results are consistent with
166 a viscoelastic memory effect, which typically arises from stored energy in elastic structures that
167 cannot relax instantaneously.

168 What are the potential mechanisms for this non-linearity? Series elastic elements (SSEs) can
169 modulate the state of the muscle fibers, contributing to energy storage and return, power ampli-
170 fication, or dissipation (Roberts and Azizi, 2011). Yet SSE's role in rapid perturbations is less
171 explored. Our results might be explained by a contractile element with a series elastic component.
172 However, the viscoelastic properties of insect apodeme and the exoskeletal attachment are typically
173 an order of magnitude stiffer than vertebrate tendon (Bennet-Clark, 1975; Zajac, 1989). They are
174 also short and would require $\sim 60\%$ strain to account for the perturbation if the muscle remained
175 isometric. It is likely that the muscle must be significantly involved in modulating the preloading
176 and hence the work done during the perturbation. Other contributors to series elasticity could also
177 play a role.

178 Nonuniformity in sarcomere strain and force production (Rassier and Herzog, 2004) is a likely
179 contributor to history dependence, but it is unlikely to be the only explanation because history
180 dependence typically manifests in single sarcomeres (Leonard et al., 2010; Rassier, 2012). There is
181 also growing appreciation that components of the muscle lattice other than actin and myosin might
182 contribute to history dependent phenomena (Rassier, 2012; Herzog et al., 2015; Nishikawa, 2016).
183 Titin and other large structural proteins have been implicated in history dependent properties in
184 muscle. Calcium-dependent binding of the N2A domain effectively changes the stiffness and offset
185 of the spring-like PEVK domain (Herzog et al., 2015). Titin also is suggested to have a further role
186 in force generation via active winding of titin around the thin filaments (Nishikawa, 2016; Lindstedt
187 and Nishikawa, 2017). Other components might play a role as well, especially regulatory elements
188 that are strain-dependent like tropomyosin (Tanner et al., 2012; Holt and Williams, 2018).

189 **4.4 Muscle's mechanical behavior during perturbations is significant for loco-** 190 **motion**

191 Regardless of mechanism, the history-dependent modulation of work during a perturbation would
192 only have meaningful consequences for locomotion if the overall change is significant in the context
193 of muscle, joint, limb, and body. Surprisingly this capacity is substantial at all scales even in a
194 relatively small muscle (Table 1). The energy absorbed by the muscle during the perturbation we
195 applied is at least comparable to the kinetic energy of all the limbs (Kram et al., 1997) and at most
196 could absorb the center of mass kinetic energy of a 3 g animal running at 20 cm/s! Despite being
197 about $1/10^{th}$ the mass of the animal's largest femoral extensor, muscle 137 absorbed more energy
198 during a single perturbation at 10 Hz than the larger muscle produces during running (Ahn and
199 Full, 2002). Muscle 137 absorbed about threefold more energy than the entire joint did during the
200 same perturbation.

201 This single cockroach muscle therefore serves as an example of the versatile control role a muscle
202 can adopt. At steady state during running, it typically dissipates a small amount of energy during
203 the swing period of each stride (Full et al., 1998). Its steady-state work is far below its capacity
204 to either dissipate energy or do mechanical work when neural feedback modulates its function
205 during locomotion (Sponberg, Spence, Mullens and Full, 2011). Neural feedback can also turn
206 this muscle into a motor assisting in obstacle traversal or turning (Sponberg, Spence, Mullens and
207 Full, 2011). Our results here indicate another control function: open-loop tuning of the limb's
208 response to disturbances. Cockroaches locomote with stride frequencies that vary over a wide band
209 (at least $1 - 12Hz$); therefore the time available to stabilize perturbations decreases dramatically
210 as running speed increases (Sponberg and Full, 2008). Even with constant timing of stimulation,
211 muscle 137's dissipative capacity during leg swing increases almost 50% over this frequency range.
212 Unlike impulsive behaviors that can do work over a relatively long time (Ilton et al., 2018), both
213 muscle's dissipative power and total work matter for an effective response during perturbations.

| | |
|--|----------------------------------|
| Average reference stress (isometric, 20 ms after first spike) | $17.3 \pm 5.8 \text{ Ncm}^{-2}$ |
| Average reference perturbation work | $-40.2 \pm 8.2 \mu\text{J}$ |
| Perturbation work at 10 Hz (eccentric history) | $-55.8 \pm 11.5 \mu\text{J}$ |
| Passive joint perturbation work | $-17.6 \pm 7.1 \mu\text{J}$ |
| Average specific dissipation power at 10 Hz | $-2360 \pm 798 \text{ Wkg}^{-1}$ |
| Muscle 137 <i>in situ</i> negative work Full et al. (1998) | $-9 \mu\text{J}$ |
| Muscle 137 <i>in situ</i> max positive work, 6 spikes Sponberg, Libby, Mullens and Full (2011) | $25 \mu\text{J}$ |
| Muscle 137 <i>in situ</i> max negative work, 8 spikes Sponberg, Libby, Mullens and Full (2011) | $-45 \mu\text{J}$ |
| Muscle 177c <i>in situ</i> positive work Ahn and Full (2002) | $74 \mu\text{J}$ |
| Peak kinetic energy of all limbs, 20 cm/s running Kram et al. (1997) | $8 \mu\text{J}$ |

Table 1: Selected statistics (means \pm 95% CI) and comparison measures from earlier work. Reference stress/work was used to normalize stress/work across conditions in Fig. 2. Reference work was the average across pre-lengthened -shortened conditions at 1 Hz.

214 But with the capacity to dissipate 2400 W/kg , a muscle need not be large to absorb energy quickly.
215 Rapid movements in animals at many scales challenge sensorimotor bandwidth (More and Donelan,
216 2018). Context-dependent muscle behavior during perturbations could play an important role in
217 stabilizing high-speed movements, especially if the animal can use anticipatory or feedforward
218 control to tune muscle’s perturbation response.

219 Natural perturbations are unlikely to be prescribed kinematic deviations, although rigid ob-
220 stacles such as on rough terrain could produce these. Exploring unsteady muscle function with
221 perturbed work loops coupled to impulsive forces or simulated loads could lead to a more complete
222 picture of perturbation responsiveness in specific muscles (Robertson and Sawicki, 2015). However,
223 our approach of prescribed perturbations imposed at different frequencies isolated the effect of his-
224 tory dependence and showed that stretch enhancement and shortening depression have significant
225 consequences for muscle’s function during perturbations.

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229 6 Competing interests

230 The authors have no competing interests.

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235 8 Data accessibility

236 Data used in this study will be made available through the online repository Dryad upon publica-
237 tion.

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