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SHORT COMMUNICATION

Passive muscle tension increases in proportion to intramuscular fluid volume

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ABSTRACT

During extended bouts of exercise, muscle can increase in volume by as much as 20% as vascular fluid moves into the tissue. Recent findings suggest that the fluid content of muscle can influence the mechanics of force production; however, the extent to which natural volume fluctuations should be expected to influence muscle mechanics *in vivo* remains unclear. Here, using osmotic perturbations of bullfrog muscle, we explored the impacts of physiologically relevant volume fluctuations on a fundamental property of muscle: passive force production. We found that passive force and fluid volume were correlated over a 20% increase in muscle volume, with small changes in volume having significant effects on force (e.g. a 5% volume increase results in a >10% passive force increase). A simple physical model of muscle morphology reproduces these effects. These findings suggest that physiologically relevant fluid fluxes could alter passive muscle mechanics *in vivo* and affect organismal performance.

KEY WORDS: Water, Extracellular matrix, Passive tension, Physical model

INTRODUCTION

Over short time scales and individual contractions, skeletal muscle maintains a nearly constant internal fluid volume (Baskin and Paolini, 1967). In accordance with the sliding filament theory of muscle contraction, muscle force generation does not require a change in the fluid volume of muscle or muscle fibers, and consequently, within the field of muscle mechanics, skeletal muscle is typically considered and modeled as an isovolumetric tissue with constant water content and overall volume. However, although muscle volume remains effectively constant over short time scales, increases in the fluid volume of muscle over longer time scales, such as extended bouts of physical exertion, are common and occur naturally *in vivo*. In humans, for example, muscle fluid volume can increase by 1–20% of initial volume during sustained exercise (Sjogaard and Saltin, 1982; Sjogaard et al., 1985). Such increases are driven by a combination of hydrostatic effects resulting from increased blood perfusion, and osmotic effects resulting from accumulation of metabolic breakdown products within muscle fibers, both of which tend to drive water from the vascular system into muscle during prolonged physical activity (Lundvall, 1972). Changes in muscle fluid volume during exercise have long been thought to influence the normal biochemical function of muscle, but the effect of such changes on the mechanics of muscle force production have received less attention.

We recently showed that altering the fluid volume of an isolated muscle alters tension developed during passive stretch (Sleboda and Roberts, 2017), an effect we hypothesize results from the interaction of incompressible, fluid-filled muscle fibers with the collagenous extracellular matrix (ECM) that surrounds them. Experimentally increasing the fluid volume of isolated bullfrog muscle by 40% resulted in a 69% increase in tension produced during passive stretch (Sleboda and Roberts, 2017). This result was taken as evidence that the volume of fluid within muscle fibers and fascicles, through its influence on the geometry of collagen fibers in the ECM, influences the muscle lengths at which collagen contributes to passive muscle tension. It is difficult to know whether this observation of an increase in passive tension with fluid volume might also be relevant to changes in volume that occur physiologically. The increase in passive tension observed in frog muscles was measured after a 40% increase in fluid volume. Such an increase lies outside the range of volume fluctuations that can reasonably be expected to occur in the bodies of living organisms. Whether relatively smaller, physiologically relevant changes should be expected to alter passive muscle tension and muscle performance *in vivo* remains unclear.

Here, we explored the effect of incremental fluid volume changes within a physiologically relevant range of 1–20% on passive muscle tension. Based on conceptual models of fluid volume as a determinant of muscle mechanics (Gindre et al., 2013; Sleboda and Roberts, 2017), we predicted that passive tension and fluid volume should be correlated over this range, with incremental increases in fluid volume resulting in incremental increases in passive tension. To test this, we utilized a graded series of physiological Ringer's solutions to incrementally drive water into isolated bullfrog semimembranosus muscles via osmosis. We report the effect on passive muscle tension and muscle mass (a proxy for fluid volume), and additionally, describe and demonstrate the relationship between muscle fluid volume and passive force using a simple physical model of muscle morphology.

MATERIALS AND METHODS

American bullfrogs [*Rana catesbeiana* (Shaw 1802)] (n=7) were obtained from a breeder and maintained at the Brown University Animal Care Facility. All use was approved by the Brown University Institutional Animal Care and Use Committee. Semimembranosus muscles were isolated from both legs of each animal. Passive tension measurements were recorded from left-leg muscles and mass measurements from right-leg muscles as each soaked in a graded series of physiological Ringer's solutions. Measurements were first made in standard amphibian Ringer's solution isotonic to muscle (115 mmol l^{-1} NaCl, 2.5 mmol l^{-1} KCl, 1.0 mmol l^{-1} $MgSO_4$, 20 mmol l^{-1} imidazole, 1.8 mmol l^{-1} $CaCl_2$, 11 mmol l^{-1} glucose, pH 7.9, 20°C) and then repeated after soaking in three hypotonic solutions of decreasing tonicity [75%, 50% and

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25% solute concentration relative to isotonic (100%)]. Hypotonic solutions provide a net osmotic gradient that favors movement of water into muscle and have been used previously to increase muscle fluid volume (Takemori, 1990; Sleboda and Roberts, 2017). Both left- and right-leg muscles soaked in each graded hypotonic solution for 30 min, after which they either remained in solution (left-leg muscles) or were removed from solution (right-leg muscles) for a period of approximately 60 s to accommodate measurement of tension or mass. Prior to soaking in hypotonic solution, an active length–tension curve was constructed via nerve stimulation of left-leg muscles to determine the length (L_0) at which muscles produced peak isometric force.

All measurements of passive tension were recorded at a length of $1.15L_0$ and normalized to tension at $1.15L_0$ in the isotonic condition. All mass measurements were normalized to the initial mass of muscle in standard isotonic Ringer's solution. Passive and active muscle tensions were measured using a 5 kg load cell (LCM703-5, OMEGA Engineering, Inc.) connected via Kevlar thread knotted about the distal semimembranosus tendon and knee capsule. Muscle length was controlled using a height gage (192-606, Mitutoyo Co.) equipped with a linear displacement transducer (LD621, OMEGA Engineering, Inc.). Muscle mass was measured using a laboratory balance (B 120 S, Sartorius Co.). Muscles were dabbed on paper towel to remove surface water prior to all mass measurements and soaked at slack length to reduce intramuscular hydrostatic pressures that might impede osmosis. Tension and mass in each hypotonic solution was compared with baseline tension and mass measured in isotonic Ringer's solution using paired, two-tailed *t*-tests. Raw muscle tension and raw muscle mass measured in different tonicity solutions are reported in Table S1.

In separate experiments, a simple physical model of muscle morphology was subjected to tensile tests before and after experimentally manipulating its internal fluid volume. The model, modified from another described previously (Sleboda and Roberts, 2017), was composed of a helical sleeve of flexible plastic fibers (Flexo PET, Techflex) representing the collagenous extracellular matrix of muscle, surrounding a compliant water-filled bladder (Trojan ENZ non-lubricated, Church and Dwight Co.) representing an incompressible volume of intramuscular fluid. From slack length, the model was stretched longitudinally until a tensile force of 5 N was achieved. Stretches to 5 N were then repeated at incrementally higher internal fluid volumes. Model tension and length were measured using a 5 kg load cell (LCM703-5, OMEGA Engineering, Inc.) and height gage (192-606, Mitutoyo Co.), respectively. All tension measurements were made at static lengths. Prior to measurements, the model was allowed to sit for a period of at least 1 min to minimize any rate-dependent effects of stretch. Force–length curves from the model were linearized via log transformation and slopes of log-transformed lines were compared using the statistical tool SMATR (Warton et al., 2006).

RESULTS AND DISCUSSION

Isolated muscle experiments

We found that small changes in muscle fluid volume significantly altered passive muscle tension, and that passive tension and muscle fluid volume were correlated over a 20% increase in fluid volume. Soaking muscles in hypotonic solution altered passive tension and mass in a dose-dependent manner, with increasingly dilute solutions yielding increasingly higher tension and mass. Passive tension generated at $1.15L_0$ was significantly increased from baseline (isotonic) in all hypotonic solutions ($P<0.005$ for 75%, 50% and 25% solutions; Fig. 1A). A significant change in muscle mass, an indicator of tissue fluid volume, was also observed in 50% and 25% tonicity solutions, but not in the 75% solution ($P=0.066$ for 75%, $P<0.005$ for 50% and 25%; Fig. 1B). Passive tension and muscle mass were correlated, and their relationship was well described by the exponential function $f(x)=e^{(a+bx)}$ (Fig. 1C). While our previous findings demonstrated that fluid has the potential to influence the mechanical behavior of muscle (Sleboda and Roberts, 2017), the current work suggests that physiological changes in muscle fluid volume can influence passive tension during normal muscle function *in vivo*.

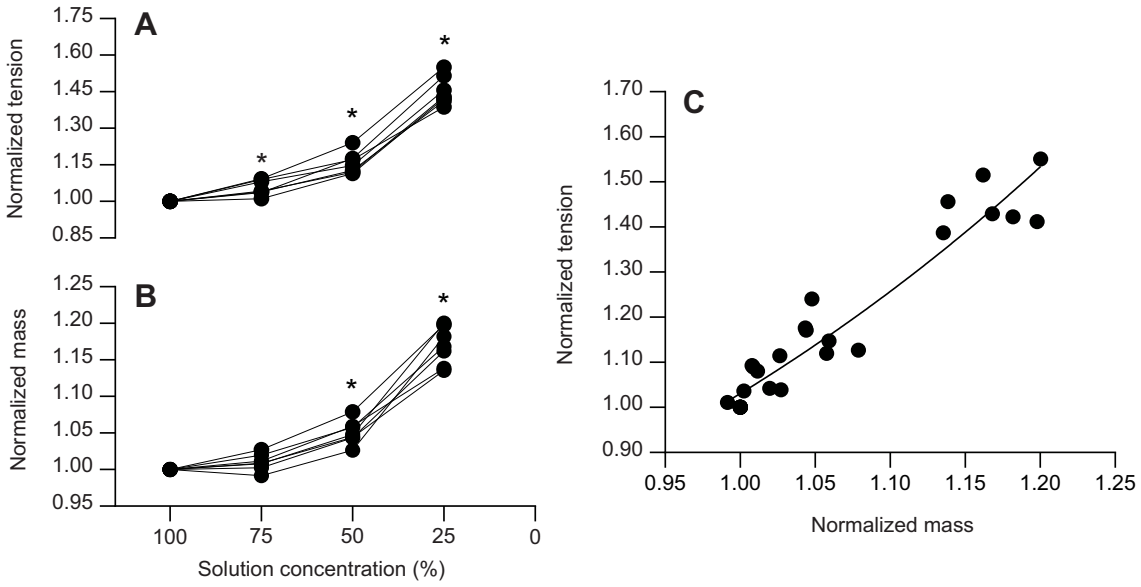

Fig. 1. The effect of solutions of varying tonicity on bullfrog semimembranosus muscle tension and mass (*n*=7). (A) Passive tension (recorded at $1.15L_0$) and (B) muscle mass increased as solution concentration was reduced. Lines between points connect data from individual muscles. Asterisks denote a significant difference from baseline mass or tension. (C) Muscle tension and mass are correlated over a physiologically realistic range of volume changes, and their relationship is well described by the equation $f(x)=e^{(a+bx)}$, which also describes passive muscle tension as a function of length (Otten, 1987).

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As described previously, we hypothesize that increases in passive tension that coincide with volume change result from the interaction of intramuscular fluid with tensile collagen fibers in the ECM of muscle (Sleboda and Roberts, 2017). As muscle is stretched, spatial reorientation of collagen fibers allows the ECM to extend at low force; however, reorientation is inhibited once ECM collagen is drawn taut against the bulk of incompressible fluid contained within muscle fibers (Purslow, 1989; Gindre et al., 2013). We suggest that altering muscle fluid volume shifts the muscle length at which collagen reorientation is inhibited and thus alters the length at which the ECM contributes to passive tension (Sleboda and Roberts, 2017). The current work provides further empirical support for this proposed mechanism by showing that passive muscle tension and fluid volume are correlated, and that successive changes in fluid volume alter tension in a dose-dependent manner.

Effects of muscle fluid variation *in vivo*

During exercise, water diffuses into intracellular, extracellular and capillary fluid spaces within muscle (Sjogaard and Saltin, 1982). Chemical analysis of biopsied muscle from inulin-infused subjects suggests that water content can increase by 1–20% during exercise (Sjogaard and Saltin, 1982; Sjogaard et al., 1985), and similar volume changes are detected in studies of the mass (a proxy for fluid volume) of perfused, isolated muscles before, during and after a period of contractile stimulation (Watson et al., 1993; Ward et al., 1996). Muscle cross-sectional area has been shown to increase during exercise (Nygren et al., 2000) and is correlated with decreases in systematic blood plasma volume (Ploutz-Snyder et al., 1995), providing further evidence that fluid moves from the vascular system into muscle during exercise. Intracellular fluid volume specifically has been shown to increase by as much as 17% during maximal exercise in humans (Sjogaard and Saltin, 1985). Intracellular volume variations may be particularly relevant to passive muscle tension, as intracellular fluid is directly bounded by muscle fiber cell membranes (sarcolemma) and ensheathed by endomysial connective tissue. However, in addition to ensheathing individual muscle fibers, collagenous ECM surrounds and reinforces muscle fascicles, the muscle perimeter and intramuscular blood vessels (Borg and Caulfield, 1980). Thus, it is conceivable that muscle tension is affected not only by movement of fluid into muscle fibers, but also by movement into the extracellular and capillary fluid spaces.

Large increases in passive muscle tension following eccentric exercise have been reported previously and are hypothesized to result from damage to the muscle fiber sarcoplasmic reticulum, resulting in residual cross-bridge activity and increased stiffness (Whitehead et al., 2001). The giant intra-sarcomeric protein titin has also been shown to vary in stiffness in the presence of calcium (Labeit et al., 2003; Joumaa et al., 2008; Leonard and Herzog, 2010) and may influence passive force generated by recently contracted muscle. In accordance with the findings of the present study, we suggest that changes in muscle fluid volume may provide an additional or alternative mechanism by which passive muscle mechanics are transiently modified following exercise. Changes in passive muscle tension that result from fluid volume fluctuations could occur transiently over the course of individual bouts of exercise and should coincide temporally with variations in muscle volume, which occur both during and immediately after exercise (Sjogaard and Saltin, 1982; Sjogaard et al., 1985; Mora-Rodríguez et al., 2015). Passive muscle force contributes to limb movement and body support during walking in humans (Whittington et al., 2008) and likely influences the elastic energy storage capabilities of muscle (Alexander and Bennet-Clark, 1977; Roberts, 2016). Changes in passive muscle tension during exercise should thus influence both the kinematics and energetics of muscle-powered movement.

Though we focus here on exercise, muscle fluid volume is additionally influenced by inflammatory edema associated with muscle damage and disease (Schulze et al., 2009), and by dehydration (Costill et al., 1976). We hypothesize that these and

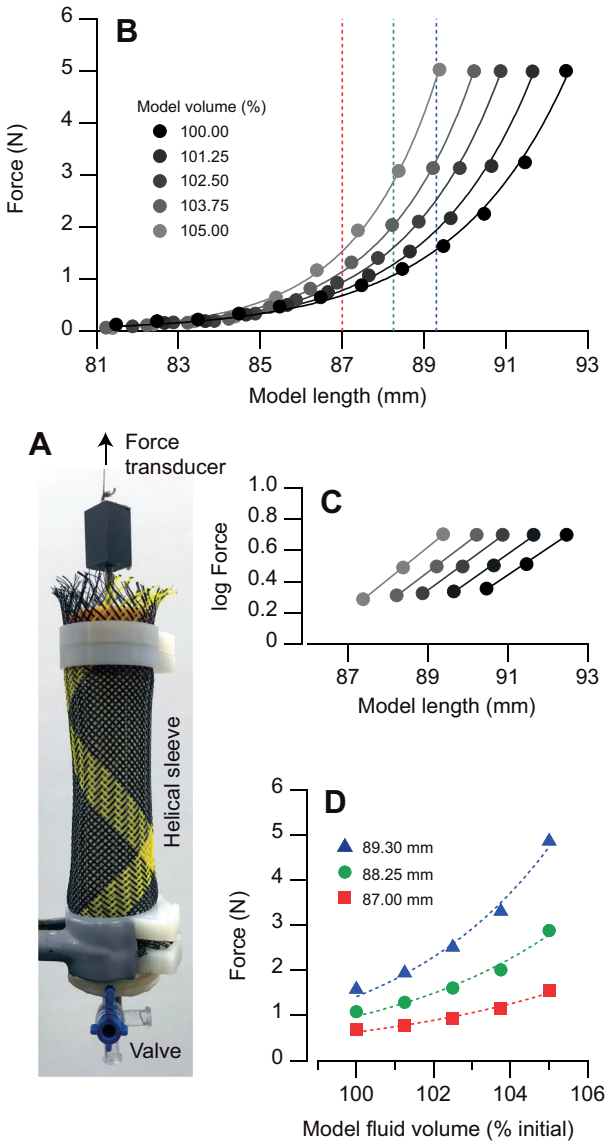

Fig. 2. A simple physical model of muscle morphology demonstrates the effect of sequential increases in fluid volume on tensile force. (A) The model is composed of flexible, helically wound plastic fibers (representing extracellular matrix collagen) surrounding a compliant fluid-filled bladder (representing a volume of incompressible muscle fibers). A watertight valve allows addition or removal of fluid from the internal bladder. (B) At each volume, tension generated by the model increases exponentially with length and is well described by the equation for passive muscle tension, $f(x)=e^{(a+bx)}$. Sequential increases in model fluid volume result in higher tensile force generated at a given length. (C) Slopes of log-transformed force–length curves are not significantly different. (D) Tensile forces measured at three arbitrary model lengths (depicted as dashed lines in B) increase as functions of model volume. The effect of volume change on model tension is smallest at short muscle lengths and greatest at long model lengths. Like the relationship between model force and length, relationships between model force and volume are well described by the equation $f(x)=e^{(a+bx)}$.

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other factors that alter muscle fluid volume have similar potentials to influence muscle mechanics *in vivo*. Additionally, given the structural similarity of vertebrate muscle at the tissue level, we suspect that a relationship between internal fluid volume and passive tension is a property of vertebrate muscle in general, and not one that is specific to the amphibian model used here. Further investigation of the effects of fluid volume variation could provide insight into our understanding of both normal and pathological physiology across vertebrate muscle.

Insights and predictions from the physical model

Our physical model demonstrates an effect of fluid volume on passive tension. At higher internal fluid volumes, the model generated higher tension at a given length (Fig. 2B). Log transformation linearized the model force–length curves, allowing their shapes to be characterized by slope (Fig. 2C). Slopes of log-transformed curves were not significantly different across model volumes (P=0.242), indicating that increasing volume did not alter the shape of model force–length curves, but increased tension by shifting the force–length curve horizontally along the x-axis without changing its form. This same phenomenon is observed in skeletal muscle with experimentally increased fluid volume (Sleboda and Roberts, 2017). Force–length curves from the model were well described by the equation $f(x)=e^{(a+bx)}$, which describes passive tension developed by stretched muscle (Otten, 1987). In both the physical model and muscles, this equation also accurately described the relationship between tension and internal fluid volume (Figs 1C and 2D).

The models demonstrate a mechanism by which the passive force–length curve of muscle dictates the shape of the force–volume curve. Increasing the fluid volume of the model shifts its force–length curve incrementally along the x-axis, such that models with higher volumes generate more tension for a given amount of stretch (Fig. 2B). Because the general forms of model force–length curves are unaffected by volume changes, plotting force as a function of volume at any given model length reproduces the profile of the original force–length curve (Fig. 2D). Fig. 3 provides a graphical demonstration of this phenomenon. A simulated linear force–length curve, duplicated and replotted incrementally along the x-axis and sampled at three arbitrary lengths, produces linear force–volume curves (Fig. 3A). Similarly, simulated exponential and asymptotic force–length curves produce exponential and asymptotic force–volume curves, respectively (Fig. 3B,C). Accordingly, because altering muscle volume shifts the passive force–length curve without altering its general form (Sleboda and Roberts, 2017), we hypothesize that the relationship between passive tension and fluid volume for any given muscle is dictated by the shape of the passive length–tension curve of that muscle. Passive force increases exponentially with length in bullfrog muscle (Bagni et al., 1988), as is typical of vertebrate muscle, and this shape is mirrored in the empirically measured force–volume curve presented in Fig. 1C.

Measuring model force as a function of volume at three arbitrary model lengths showed that the relationship between force and volume is shallowest at short model lengths and steepest at long model lengths (Fig. 2D). Accordingly, we hypothesize that muscle tension should be least affected by volume change at short lengths and most affected at long lengths. All measurements of muscle tension in the present study were made at length $1.15L_0$, which represents a relatively long muscle length on the descending limb of the active length–tension curve of bullfrog semimembranosus muscle. At this length, altering fluid volume over a physiologically relevant range elicited increases in passive muscle tension of over 50% (Fig. 1A,C). *In vivo*, muscles operating on a shallower portion of the passive force–length curve (e.g. closer to the plateau of the active force–length curve) may be less influenced by fluid volume changes; however, a 50% increase in muscle tension remains within the range of tension changes empirically measured following eccentric exercise of skeletal muscle (Whitehead et al., 2001). Additionally, increases in passive torque about the human knee joint following eccentric exercise range from ∼20 to 40% (Whitehead et al., 2001).

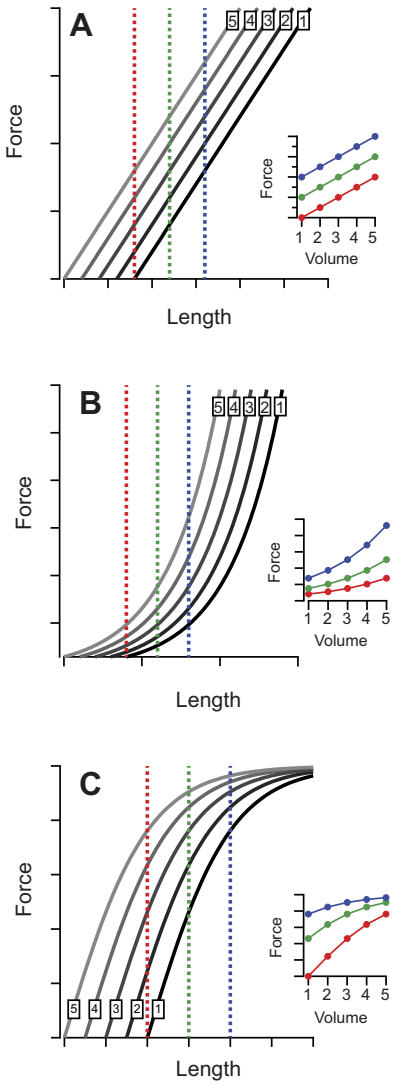

Fig. 3. Conceptual figure (arbitrary units) illustrating similarity between shapes of force–length and force–volume curves. Three simulated force–length profiles are presented: (A) linear, (B) exponential and (C) asymptotic. In each, volume increases are simulated by duplicating an initial curve (volume 1) and replotting at a series of incremental lengths along the x-axis (volumes 2–5). For each profile, force is sampled at three arbitrary lengths (red, green and blue dashed lines) and replotted as a function of volume (insets). The resulting force–volume curves match the profiles of the force–length curves from which they were sampled. Linear force–length curves produce linear force–volume curves, exponential force–length curves produce exponential force–volume curves, and asymptotic force–length curves produce asymptotic force–volume curves.

Fluid may influence many aspects of muscle mechanics

Classic mechanical models of muscle physiology typically do not include fluid as a mechanically relevant component of muscle; however, a growing body of evidence suggests that intramuscular water, through its basic fluid-mechanical properties, can influence

the mechanics of both passively stretched and actively contracting muscle. Computational models that incorporate fluid mechanics accurately predict the mechanical response of muscle to both tension and compression (Purslow, 1989; Gindre et al., 2013; Wheatley et al., 2017). Fluid pressures developed within contracting muscle have been hypothesized to alter the speed and force of active contraction via their influence on dynamic changes in muscle shape (Eng et al., 2018). Intracellular pressure may also directly oppose shortening forces generated by myofibrils and influence the useful work that actively shortening muscles are capable of producing (Azizi et al., 2017). The present study provides an example of how physiologically realistic changes in muscle fluid volume can significantly alter muscle mechanics, providing further evidence that the study of fluid mechanics within muscle may provide important insights into many aspects of muscle physiology.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: D.A.S., T.J.R.; Methodology: D.A.S., T.J.R.; Formal analysis: D.A.S.; Investigation: D.A.S., E.S.W.; Writing - original draft: D.A.S., E.S.W.; Writing - review & editing: D.A.S., E.S.W., T.J.R.; Visualization: D.A.S.; Supervision: T.J.R.; Project administration: T.J.R.; Funding acquisition: T.J.R.

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