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Characterization of the passive mechanical properties of spine muscles across species

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ABSTRACT

Passive mechanical properties differ between muscle groups within a species. Altered functional demands can also shift the passive force-length relationship. The extent that passive mechanical properties differ within a muscle group (e.g. spine extensors) or between homologous muscles of different species is unknown. It was hypothesized that multifidus, believed to specialize in spine stabilization, would generate greater passive tensile stresses under isometric conditions than erector spinae, which have more generalized functions of moving and stabilizing the spine; observing greater multifidus moduli in different species would strengthen this hypothesis. Permeabilized fibre bundles (n = 337) from the multifidus and erector spinae of mice, rats, and rabbits were mechanically tested. A novel logistic function was fit to the experimental data to fully characterize passive stress and modulus. Species had the greatest effect on passive muscle parameters with mice having the largest moduli at all lengths. Rats generated less passive stress than rabbits due to a shift of the passive force-length relationship towards longer muscle lengths. Rat multifidus generated slightly greater stresses than erector spinae, but no differences were observed between mouse muscles. The secondary objective was to determine the parameters required to simulate the passive force-length relationship. Experimental data were compared to the passive muscle model in OpenSim. The default OpenSim model, optimized for hindlimb muscles, did not fit any of the spine muscles tested; however, the model could accurately simulate experimental data after adjusting the input parameters. The optimal parameters for modelling the passive force-length relationships of spine muscles in OpenSim are presented.

1. Introduction

Muscles generate passive tension when strained beyond slack length. At large strains, passive tension within muscles exceeds that generated in maximally activated isometric contractions (Ter Keurs et al., 1978; Winters et al., 2011). These passive forces impact joint stiffness, stability, and dynamic equilibrium in musculoskeletal systems. Passive muscle mechanical properties are related to the structure and composition of myofibrillar (e.g. titin) and especially extracellular matrix (ECM) proteins (Magid and Law, 1985, Prado et al., 2005, Meyer and Lieber, 2018). Importantly, titin isoform size and collagen composition are not believed to correlate with traditional architectural parameters—such as optimal muscle length or physiologic cross-sectional area—used to scale musculotendinous models. This leads to inaccurate predictions of passive muscle force (Winters et al., 2011). It is also known that passive force-length relationships within a species differ amongst functionally different muscle groups (Horowits, 1992; Prado et al., 2005; Winters et al., 2011). As biomechanical models often incorporate data derived from animal models, it would be beneficial to determine the extent to which passive mechanical properties also differ between species, which is currently unknown (Meyer and Lieber, 2018).

Muscle tissues are known to adapt to meet functional demands (Lieber and Ward, 2011). Considering that passive muscle properties vary between muscle groups (Horowits, 1992; Prado et al., 2005; Winters et al., 2011), it is conceivable that two muscles serving different functions may have different passive force-length relationships. Multifidus and erector spinae are spine extensor muscles that are often perceived to perform different primary functions. While the large erector spinae muscles stabilize and move the spine, multifidus is perceived to be preferentially suited for stabilizing intervertebral segments (Donisch and Basmajian, 1972; Richardson and Jull, 1995; Moseley et al., 2002). By

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increasing its ability to generate passive tension, a primarily stabilizing muscle like multifidus would require less energy. Ward et al. (2009) identified that this may be true for spine muscles in surgical patients. The passive moduli of multifidus fibre bundles were ~50% greater than the moduli from erector spinae muscles. Whether passive mechanical differences exist between multifidus and erector spinae in healthy individuals requires further investigation. Observing similar differences in other species would provide strong evidence for fundamental differences in the passive mechanical design of spine muscles.

Despite known differences in the passive mechanical properties, it remains difficult to account for these differences when simulating passive muscle force-length relationships. This is because outcome measures are often not directly related to the input parameters used in existing musculotendinous models. Millard and colleagues created a modifiable passive muscle model in OpenSim based on five input parameters—e_0, e_{ISO}, k_{LOW}, k_{ISO}, and c (for full description see Millard et al. (2012) and OpenSim's doxygen documentation). Default parameters, optimized to simulate rabbit hindlimb muscles, were included. However, it is unknown whether the passive mechanical properties of rabbit hindlimb muscles are similar to those of spine muscles.

The primary purpose of this study was to characterize the passive mechanical differences between spine muscles and amongst species. It was hypothesized that multifidus would generate greater tensile stresses than erector spinae to efficiently stabilize the spine and that differences between muscles would be greater than amongst species. The secondary purpose of this study was to determine the passive muscle parameters required for simulating the passive force-length relationships of spine muscles.

2. Methods

2.1. Muscle experimental testing

Erector spinae and multifidus were harvested from skeletally mature male mice (n = 8), rats (n = 22), and rabbits (n = 8; only multifidus). Muscles were chemically permeabilized in a solution containing (mmol): KPr (170), Na_2ATP (21.2), imidazole (10), $MgCl_2$ (5.3), EGTA (5.0), glutathione (2.5), NaN_3 (1), leupeptin (0.05) and 50% (v/v) glycerol (Wood et al., 1975; Eastwood et al., 1979). Fibre bundles were permeabilized to allow ATP and EGTA to enter the cell and ensure cross-bridge detachment (i.e. passive muscle state). The basement membrane and extracellular matrix are still able to bear load in permeabilized fibres and bundles. Muscles were stored at −20 °C for a minimum of 24 h (maximum of 14 days) before testing. On the day of testing, muscles were immersed in a physiologic relaxing solution, to ensure cross-bridge detachment, containing (mmol): KMSA (86), imidazole (59.4), $Mg(MSA)_2$ (10.8), K_3EGTA (5.5), Na_2ATP (5.1), KH_2PO_4 (1.0), and $Ca(MSA)_2$ (0.13) (Shah and Lieber 2003) and dissected into bundles of 6–10 fibres encased within ECM. Fibre bundles were secured to a force transducer and a high-speed motor (Aurora Scientific, Newmarket, ON) and lengthened until passive tension began to develop, termed slack length. Bundle diameter (average of three locations) was recorded using a microscope reticule and the average sarcomere length as slack length (ℓ_S) was measured using laser diffraction (5-mW laser, beam width ~1.4 mm, wavelength = 635 nm; Lieber et al. 1990). Fibre bundles were rapidly stretched in ~0.2 μm/sarcomere increments. Fibre bundle force (F) and average sarcomere length (ℓ) were recorded after 120 s of stress-relaxation (Linke et al., 1994; Ward et al., 2009). Fibre bundles were sequentially stretched 9–11 times to yield a passive force-sarcomere length relationship.

2.2. Data analysis

Passive muscle stresses are often incorporated into computational models after normalizing to maximal isometric specific tension (P_O) (Zajac, 1989; Millard et al., 2012); P_O for mouse, rat, and rabbit permeabilized fibres are ~70 kPa at an optimal sarcomere length (ℓ_O) of 2.5 μm (D'Antona et al., 2007; Pellegrino et al., 2003). To allow comparisons with previous passive muscle models, tensile forces were converted to stress (σ) as

$$\sigma = \frac{F}{A_S} \times \frac{\ell_O}{\ell_S} \tag{1}$$

assuming a circular cross-sectional area at slack length (A_S) and correcting for the change in area between optimal sarcomere length (ℓ_O) and slack sarcomere length (ℓ_S). This assumes that muscle fibre bundles are isovolumetric when strained longitudinally (Takaza et al., 2013).

The stress-sarcomere length relationship of muscle fibre bundles was observed to follow the integral of a logistic function (Fig. 1). This conceptual model assumes that the modulus ($M = d\sigma/d\ell$ in kPa/μm) increases as a function of sarcomere length (ℓ in μm) following a smooth logistic curve of the form:

$$M(\ell) = \left(\frac{\Delta M}{1 + e^{-k(\ell - t)}} + M_S\right) \times H(\ell - \ell_S) \tag{2}$$

where M_S (kPa/μm) is the modulus at slack length in kPa/μm, ΔM is the change in modulus in kPa/μm, and k (in μm^{-1}) and t (in μm) are rate and length constants governing the change in modulus, respec-

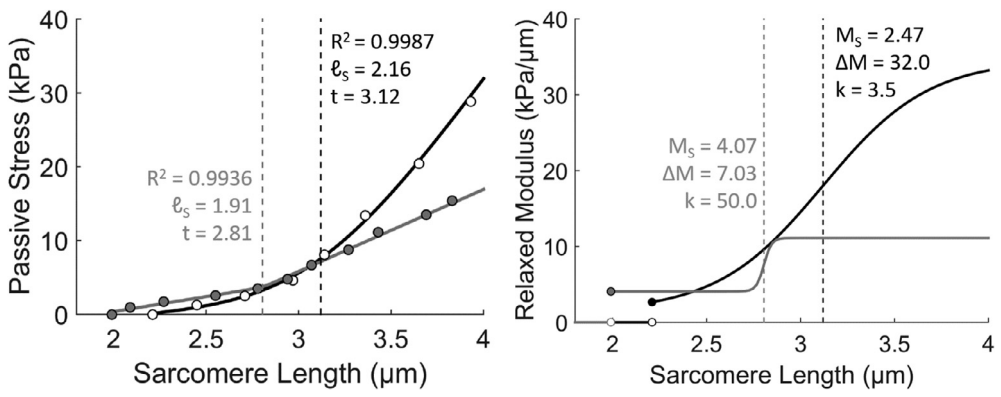

Fig. 1. Two representative experimental tests are depicted in grey and black. (Left) Scatter points are experimental data and solid lines are the predicted fits of the logistic integral. (Right) The corresponding relaxed modulus-sarcomere length relationship for the two tests. The transition between initial and final modulus for the fibre bundle in black is slower (low k-transition rate) and occurs at longer lengths (high t-transition length) than the fibre bundle in grey.

tively. H is the heavyside step function which sets modulus to zero when sarcomere lengths are less than slack length (ℓ_S).

To obtain the coefficients M_S, ΔM, k, and t, experimental stress (σ in kPa) – sarcomere length (ℓ in μm) data were fit with the integral of the logistic function

$$\sigma(\ell) = \frac{\Delta M}{k} ln(1 + e^{k(\ell - t)}) + M_S\ell + C \quad (3)$$

where C is an arbitrary integration constant. Coefficients were determined using a non-linear least square optimizer (MATLAB2014b) and a Trust-Region-Reflective algorithm (Coleman and Li, 1994, 1996). The solver was able to converge on a local minimum for all fibre bundles (specified tolerance of 10^{-6}).

2.3. Statistical analysis

Correlations between fit parameters (slack length, initial modulus, change in modulus, transition length, and transition rate) were tested with Pearson's correlation coefficients. Differences in fit parameters amongst all five muscles (mouse multifidus, mouse erector spinae, rat multifidus, rat erector spinae, and rabbit multifidus) were tested using linear (1) fixed effect and (2) mixed effects models. The mixed effects model treated individual animals as a random effect to account for repeated sampling (Tirrell et al., 2018). Akaike and Baysian Information Criterions and the maximum likelihood test (Akaike, 1998) were used to compare fixed and mixed effects models. A significantly better fit for the mixed effect model indicated that there was a significant random effect of animal. For analysis of the fixed effect of muscle, two contrast statements (customized hypothesis tests on fixed effects coefficients) were used to test for differences between multifidus and erector spinae for mice and rats and two additional contrast statements were used to test for differences amongst species for multifidus and erector spinae. If there was a significant difference in multifidus muscles between mice, rats, and rabbits, then post-hoc tests were applied with a Bonferroni correction factor to test for pair-wise differences. If residuals were not homogenous or normal, then a non-parametric Kruskal-Wallis test for stochastic dominance determined if samples originated from the same distribution.

2.4. Passive muscle modelling

To estimate the whole muscle mechanical response, logistic coefficients were used to predict passive stress and relaxed modulus for each fibre bundle through the physiologic range of muscle lengths. The physiologic range of sarcomere lengths was estimated to be 1.7–4.0 μm based on myofilament lengths of small mammals (μm): myosin (1.7), bare zone (0.2), actin (1.14), and z-disc (0.05) (Walker and Schrodt, 1974; Ringkob et al., 2004). Passive stress values were linearly extrapolated for experimental tests that were terminated (slipping of fibre bundle) before reaching 4.0 μm; constant extrapolation was used for relaxed modulus. Passive muscle stress and relaxed modulus of the whole muscle was predicted as the composite average (±95% confidence in the mean) of all fibre bundles.

Whole muscle computational models were created using the logistic model proposed here and the quintic Bézier curve model used in OpenSim (Millard et al., 2012). Nonlinear constrained optimization was used to find the best fit parameters for each model (fminsearch for logistic parameters and fmincon for Bézier parameters in MATLAB2014b) that minimized the squared difference between the predicted response and the composite average of the relaxed modulus. The Bézier curve model employed in OpenSim predicts passive tension based on muscle length and force normalized to optimal length and maximum isometric active force, respectively. Experimental sarcomere lengths and passive stresses were normalized assuming ℓ_O = 2.5 μm and P_O = 70 kPa (D'Antona et al., 2007; Pellegrino et al., 2003). The default parameters for the quintic Bézier curve model in OpenSim were also used to test whether a generic muscle model accurately predicted the passive mechanical properties of spine muscles.

3. Results

Experimental data were strongly fit by the logistic integral function (mean R^2: 0.99; range 0.73–>0.99). Fit parameters were poorly ($|r| < 0.3$) to moderately ($0.3 < |r| < 0.5$) correlated with each other. The moderate correlations were between initial modulus and change in modulus ($r = 0.40$), initial modulus and transition length ($r = 0.34$), and transition length and transition rate ($r = 0.31$). The linear mixed effect model accounted for a significant random effect of animal for initial modulus and change in modulus. Random effects of animal were not significant for slack length or transition length. The transition rate constants were not fit with a linear effects model because the residuals did not meet the requirements of normality. There was no evidence of stochastic dominance (Kruskal-Wallis: $p = 0.1710$) amongst muscles for the transition rate constant.

Slack lengths were different amongst muscles ($p < 0.0001$), with rabbit multifidus developing passive tension at shorter sarcomere lengths than mice ($p = 0.0077$) and rats ($p = 0.0020$). There was no difference in slack lengths between mouse multifidus and erector spinae ($p = 0.3093$); however, rat erector spinae began bearing passive tension at longer sarcomere lengths than rat multifidus ($p = 0.0001$; Table 1 and Fig. 2).

There was a significant effect of muscle on the initial modulus ($p < 0.0001$; Table 1 and Fig. 2). Mice had greater initial moduli for multifidus ($p < 0.0001$) and erector spinae ($p < 0.0001$) than rats or rabbits. There was no difference between erector spinae and multifidus for rats ($p = 0.5553$) or mice ($p = 0.3680$).

There was a significant effect of muscle on change in modulus ($p = 0.0061$; Table 1 and Fig. 2). The change in modulus was less for rat erector spinae than mouse erector spinae ($p = 0.0003$). Change in modulus was not different amongst species for multifidus ($p = 0.3861$), between mouse muscles ($p = 0.6478$) or between rat muscles ($p = 0.1015$).

There was a significant effect of muscle on transition length ($p = 0.0109$; Table 1 and Fig. 2). Rat erector spinae transitioned to higher moduli at longer lengths than rat multifidus ($p = 0.0391$). No differences in transition length were observed between mouse muscles ($p = 0.4493$), between erector spinae of mice and rats ($p = 0.1462$) or amongst multifidus muscles ($p = 0.2349$).

The whole muscle logistic and quintic Bézier models strongly fit the experimental data (Table 2; Fig. 3). Differences in passive mechanical properties were observed amongst muscles with mouse muscles having greater moduli and larger tensile stresses than rats or rabbits. The default passive muscle model in OpenSim did not fit the experimental data for any of the spine muscles tested. The default model underestimated passive stresses at all muscle lengths and modulus at short lengths. At long muscle lengths the default modulus agreed with experimental values for the mouse muscles but was substantially greater than the moduli of rat and rabbit muscles.

4. Discussion

The primary objective of this study was to determine if there were passive mechanical differences between spine muscles (multifidus and erector spinae) and across species (mouse, rat, and rabbit). Differences between spine muscles and amongst species were

Table 1
Mean (±SE) and 95% confidence in the mean for passive mechanical fit parameters of muscle fibre bundles.

		Slack length (μm)			Initial modulus (kPa/μm)			Change in modulus (kPa/μm)		
		Mean	SE	95% CI	Mean	SE	95% CI	Mean	SE	95% CI
Mouse	Multifidus	2.18	± 0.029	(2.12, 2.24) a	17	± 1.4	(14, 19) a	47	± 6.6	(34, 60)
	Erector Spinae	2.13	± 0.020	(2.09, 2.17)	15	± 2.0	(11, 19)	51	± 5.5	(40, 62)
Rat	Multifidus	2.16	± 0.017	(2.13, 2.20) a	7	± 0.4	(6, 7) b	33	± 2.0	(29, 37)
	Erector Spinae	2.25	± 0.018	(2.22, 2.29) [*,†]	6	± 0.3	(6, 7)[*]	28	± 1.2	(26, 31)[*]
Rabbit	Multifidus	2.04	± 0.019	(2.00, 2.08) b	7	± 0.8	(6, 9) b	33	± 3.9	(25, 40)
		Transition length (μm)			Transition rate (μm^{-1})					
		Mean	SE	95% CI	Mean	SE	95% CI			
Mouse	Multifidus	2.84	± 0.060	(2.72, 2.96)	25	± 4.0	(17, 33)			
	Erector Spinae	2.96	± 0.053	(2.85, 3.06)	19	± 3.2	(13, 25)			
Rat	Multifidus	3.00	± 0.027	(2.94, 3.05)	18	± 1.4	(15, 20)			
	Erector Spinae	3.14	± 0.070	(3.00, 3.27)[†]	17	± 1.5	(14, 20)			
Rabbit	Multifidus	2.80	± 0.029	(2.74, 2.85)	19	± 3.2	(12, 25)			

[†] Mean difference between rat multifidus and erector spinae muscles tested with contrast statement.
[*] Mean difference between mouse and rat erector spinae muscles tested with contrast statement.
Different (a and b) letters indicate mean difference in multifidus muscles amongst species using post-hoc analyses.

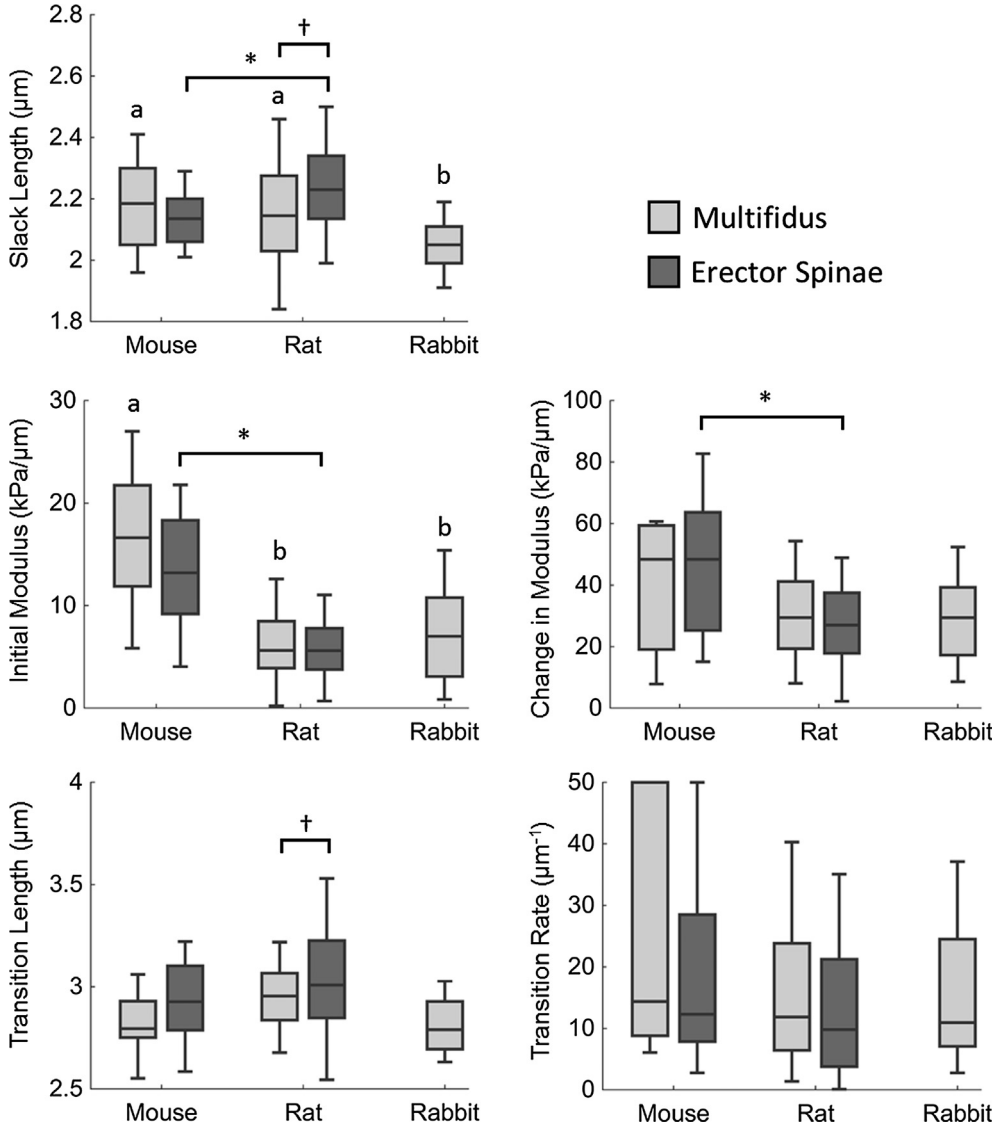

Fig. 2. Distribution of fit parameters for mouse multifidus (n = 24), mouse erector spinae (n = 24), rat multifidus (n = 132), rat erector spinae (n = 132) and rabbit multifidus (n = 25). Boxes extend from 25th to 75th percentile and are bisected by the median. Whiskers extend to the 5th and 95th percentiles. [†] statistical difference between rat muscles. [*] statistical difference between rat and mouse erector spinae muscles. Different letters indicate statistical post-hoc differences amongst species for multifidus ($\alpha = 0.05$).

Table 2
Best fit coefficients for the logistic and quintic Bézier models for predicting whole muscle passive mechanical response.

		Logistic model parameters				
		Slack length (μm)	Initial modulus (kPa/μm)	Change in modulus (kPa/μm)	Transition length (μm)	Transition rate (μm^{-1})
Mouse	Multifidus	2.14	11.55	51.71	2.81	6.55
	Erector Spinae	2.11	11.79	52.65	2.85	6.82
Rat	Multifidus	2.21	6.31	31.93	2.96	7.87
	Erector Spinae	1.88	0.35	33.60	2.88	3.75
Rabbit	Multifidus	2.01	5.44	34.59	2.76	5.78
		Quintic Bézier parameters*				
		e_0	e_{ISO}	k_{LOW}	k_{ISO}	c
Default model		0	0.7	0.2	2.86	0.75
Mouse	Multifidus	−0.61	0.51	0.02	2.28	0.89
	Erector Spinae	−0.73	0.51	0.00	2.33	0.90
Rat	Multifidus	−0.19	0.86	0.18	1.41	0.94
	Erector Spinae	−0.18	0.98	0.20	1.22	0.88
Rabbit	Multifidus	−0.23	0.76	0.25	1.45	0.92

* Quintic Bézier parameters are unitless. e_0 and e_{ISO} are muscle strain where normalized passive force is equal to zero and one, respectively. k_{LOW} and k_{ISO} are normalized stiffness near e_0 and e_{ISO}, respectively. The curviness parameter c adjusts the shape of the passive-force length relationship with values ranging from 0 (slow transition in stiffness) to 1 (sharp transition in stiffness). Muscle lengths are normalized to active optimal length and forces are normalized to maximum isometric (active) muscle force. For a full description of parameters please see Millard et al. (2012).

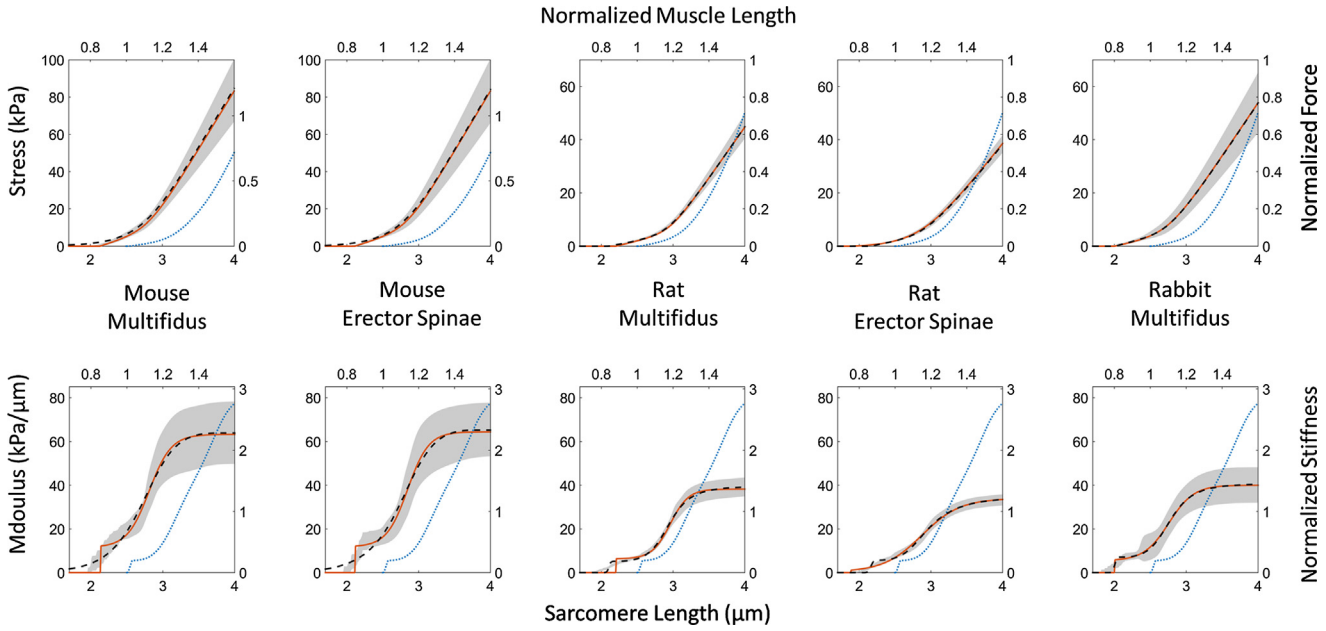

Fig. 3. The grey shading represents the 95% confidence in the mean estimate of passive stress and relaxed modulus for muscle fibre bundles tested across the physiologic range of sarcomere lengths. Minimal differences were observed between the best fit logistic model (orange solid) and the quintic Bézier curve model (dashed). Both models strongly fit the experimental data. The default quintic Bézier curve model (dotted blue; same line for each muscle) did not fit the experimental data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

observed with species having the greater effect. Passive muscle stresses and moduli were greatest in mice and smallest in rats with rabbit multifidus falling between these two extremes. These results were contrary to the original hypothesis that mechanical differences would be greater between multifidus and erector spinae than amongst species.

4.1. Differences amongst species

Bundles of mouse fibres generated the greatest passive stresses at all muscle lengths largely because their initial modulus at slack length was 2.3 to 2.5-fold greater than rats and rabbits. Mouse erectors spinae also had 1.8-fold greater change in modulus compared to rat erector spinae. Differences between mice and rats were not due a horizontal shift of the stress-sarcomere length curve. There was a significant random effect of animal for modulus parameters indicating that muscle moduli vary amongst individual animals; these results support the importance of accounting for repeated sampling from a single individual when investigating differences in relaxed modulus (Tirrell et al., 2018).

The differences between rats and rabbits were subtler than between these animals and mice. There were no differences in modulus values between rats and rabbits. However, the rabbit passive force-length relationship was shifted toward shorter muscle lengths. Rabbits began bearing tensile load and transitioned to the greater modulus ~0.2 μm earlier than rat muscles. This shift led to an 40% increase in passive stress at the longest muscle lengths.

4.2. Differences between erector spinae and multifidus

Multifidus has been described to act primarily as a stabilizer of the spine (Donisch and Basmajian, 1972; Richardson and Jull, 1995; Moseley et al., 2002). It was hypothesized that multifidus would therefore generate greater passive tension to serve this function than the erector spinae which are responsible for both stabilizing and moving the spine. However, evidence for a difference in the passive mechanical characteristics of multifidus and erector spinae in the current study was weak. Differences between muscles were relatively small in rats compared to the differences amongst species and there was no evidence for a difference between mouse muscles. These finding were not inline with the 50% greater modulus in multifidus compared to erector spinae in humans (Ward et al., 2009). This could be due to species differences, which are shown here to be considerable. Additionally, all three animal models tested here were quadruped. Differences in spine loading and stability requirements during bipedal and quadrupedal stance and gait may cause fundamental differences in the passive mechanical characteristics of multifidus and erector spinae. Finally, the findings of Ward and colleagues could also be attributed to muscle remodelling in response to low back pain and injury. Multifidus has been shown to respond to disc injury to increase passive tension (Brown et al., 2011). Further testing is required to determine whether multifidus material properties are better suited for developing passive tension than erector spinae in healthy people. While there were no differences between muscle material properties in the current study, it should be noted that the ability of a muscle to mechanically stabilize a joint via passive strain energy will also depend on musculotendinous length, physiological cross-sectional area, and moment arm (Potvin and Brown, 2005).

4.3. Passive muscle modelling

An important finding of this work is that the mechanical properties of spine muscles are different than a generic passive muscle model would suggest. The default model in OpenSim was optimized to fit experimental observations from rabbit hindlimb muscles. However, for all species tested in the current study, spine muscles developed passive tension at shorter muscle lengths than active optimal length. This observation is consistent with previous findings that axial muscles have shorter titin isoforms and larger amounts of collagen compared to appendicular muscles (Tirrell et al., 2012).

Modelling human muscles based on experimental observation from animals requires a few considerations. First, the current work highlights the importance of considering which animal species is used, as mice, rats, and rabbits all have different passive muscle properties. Ward et al. (2009) mechanically tested human spine muscle biopsies obtained surgically from low back pain individuals and reported moduli ranging between approximately 25 and 45 kPa/μm, values closest to rats and rabbits in our study; however, Ward et al (2009) calculated Young's modulus as the slope of the line on the stress-strain curve between sarcomere lengths ranging from 2.0 and 4.25 μm, and therefore comparisons to our values are not directly possible. Second, spine muscle properties between humans and animals may be affected by functional differences caused by bipedal versus quadrupedal loading and gait patterns. Third, differences in optimal muscle lengths between species should be considered when modelling passive muscle properties. Passive muscle forces are often predicted based on muscle length normalized to optimal length, even though passive muscle properties are not believed to be related to myofilament overlap. This is done simply because sarcomere length data are often unavailable. This has important consequences when modelling human muscles based on data from small rodents. Optimal lengths of human muscles are shifted towards longer sarcomere lengths (2.7–2.8 μm; Gollapudi and Lin, 2009) than small rodents due to longer actin filaments, while slack lengths of human spine muscles (2.0–2.2 μm) are similar to those measured here (Gollapudi and Lin, 2009; Winters et al., 2011). Models predicting passive forces based on normalized muscle lengths should account for the differences in optimal sarcomere lengths.

The goodness-of-fit between the logistic function and the observed experimental data for fibre bundles was very strong. There are two non-exclusive conceptual interpretations for this model: (1) tensile stresses are borne by two different populations of load bearing structures arranged in parallel and/or (2) a single tensile structure undergoes a conformational change at a specific level of strain leading to a change in its stiffness. According to the first interpretation, the first protein structure would be recruited at a sarcomere length of ~2.0–2.2 μm and has a modulus of ~7–17 kPa/μm per area fraction of the bundle occupied by that structure. The second structure is recruited at ~2.8–3.0 μm and has a greater modulus of ~30–50 kPa/μm per area fraction. This conceptual model is supported in the literature by considering the two predominant sources of passive tension—titin and the ECM binding fibres together (Horowits et al, 1986; Prado et al., 2005; Gillies and Lieber, 2011). It is difficult to assign titin and ECM to either structure without knowing the modulus and area fractions of each structure. We suspect that titin and ECM are responsible for the initial stiffness and the change in stiffness, respectively, since elimination of ECM from fibre bundles decreases the modulus by ~75% (Meyer and Lieber, 2011) and mammalian ECM is shown to bear the majority of passive tensile load (Meyer and Lieber, 2018). It should be noted that there is also support for the second conceptual model. Titin has a nonlinear force-displacement relationship in isolated myofibril preparations. The biphasic mechanical response is due to the the poly-Ig region, which is compliant at shorter muscle lengths but becomes stiffer with increasing strain (Linke et al., 1998). These conceptual models are not exclusive, and it is likely that both phenomena contribute to the passive muscle force-length relationship. Further testing is required to differentiate the relative effects of titin non-linearity and ECM.

Both the logistic function and Bézier curves were able to fit the average stress-sarcomere length response of spine muscles. The best fit coefficients for both models are presented for flexibility. The Bézier curve method is incorporated into the equilibrium musculotendon model in OpenSim (Millard et al., 2012) and these coefficients can be supplied to adjust the default passive muscle force-length relationship. However, for those not working in OpenSim, constructing and evaluating Bézier curves is not trivial. The logistic method presented here is simpler to implement and fits the experimental data equally well.

5. Conclusion

Passive mechanical properties differ amongst species and between spine muscles. Differences between multifidus and erector spinae were smaller than the differences amongst species and were only observed in rats. Therefore, there was minimal evidence in small mammals that multifidus is uniquely designed to mechanically stabilize the spine. The results of the current study support a two-structure conceptual model of passive muscle tension. Spine muscles had an initial modulus of ~7–17 kPa/μm and a slack length of 2.0–2.2 μm. Near 2.8–3.1 μm modulus values increased by 30–50 kPa/μm. A logistic function is proposed to allow further investigation into differences in passive mechanical properties between muscles and amongst species.

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Conflict of interest

The authors have no conflicts of interest associated with the work presented in this manuscript.

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