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RESEARCH ARTICLE

Contribution of the Achilles tendon to force potentiation in a stretch–shortening cycle

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ABSTRACT

Muscle force during concentric contractions is potentiated by a preceding eccentric contraction: a phenomenon known as the stretch–shortening cycle (SSC) effect. Tendon elongation is often considered to be the primary factor for this force potentiation. However, direct examination of the influence of tendon elongation on the SSC effect has not been made. The aim of this study was to evaluate the contribution of tendon elongation to the SSC effect by comparing the magnitude of the SSC effect in the rat soleus with and without the Achilles tendon. The rat soleus was subjected to concentric contractions without pre-activation (CON) and concentric contractions with an eccentric pre-activation (ECC). For the 'with-tendon' condition, the calcaneus was rigidly fixed to a force transducer, while for the 'without-tendon' condition, the soleus was fixed at the muscle–tendon junction. The SSC effect was calculated as the ratio of the mechanical work done during the concentric phase for the ECC and the CON conditions. Substantial and similar (P=0.167) SSC effects were identified for the with-tendon (318±86%) and the without-tendon conditions (271±70%). The contribution of tendon elongation to the SSC effect was negligible for the rat soleus. Other factors, such as pre-activation and residual force enhancement, may cause the large SSC effects and need to be evaluated.

KEY WORDS: Rat, Soleus, Residual force enhancement, Pre-activation, Fascicle length, Sonomicrometry

INTRODUCTION

It is widely known that performance of dynamic movements is augmented by a counter-movement. This phenomenon is called the stretch–shortening cycle (SSC) (Bosco et al., 1982; Komi, 2000). Specifically, muscle force (or mechanical work) attained during concentric contractions is increased by conducting an eccentric contraction immediately preceding the concentric contraction; namely, making a counter-movement (Komi, 1984; Svantesson et al., 1991). Many studies have been undertaken to elucidate the mechanism(s) of force potentiation induced by SSC (i.e. the SSC effect). The following factors have been identified as possibly contributing to the SSC effect: stretch reflex (Dietz et al., 1979; Nichols and Houk, 1973), tendon elongation (Finni et al., 2001; Ishikawa et al., 2006; Kawakami et al., 2002), pre-activation (Bobbert et al., 1996; Bobbert and Casius, 2005; Ettema et al., 1990) and residual force enhancement (Edman et al., 1982; Ettema et al., 1992; Joumaa et al., 2008). Among these factors, tendon elongation has often been considered to be the primary factor contributing to the SSC effect (Kawakami et al., 2002; Kubo et al., 2000).

As tendons are compliant and nearly elastic, they elongate when muscle force increases, thereby storing and releasing elastic energy (Alexander, 2002), which can lead to the enhancement of mechanical work in dynamic movements. In addition, tendon length changes provide another mechanism for optimizing the force-generating capability of muscles, which is known as the muscle–tendon interaction (Ishikawa et al., 2005; Sano et al., 2013). Specifically, for a given muscle–tendon complex length change, tendon length changes affect how much the muscle length changes. Muscle length changes, in turn, directly affect the force-generating capability of muscle as a result of force–length and force–velocity relationships (Gordon et al., 1966; Hill, 1938). Thus, tendon length changes overall directly modify the force-generating capability. Taken together, tendon length changes may have a substantial influence on the performance of dynamic movements. Therefore, many studies have been conducted to clarify the contribution of tendons to the SSC effect as a way to optimize muscle performance and training. For example, Roberts et al. (1997) reported that muscle fascicle length of the lateral gastrocnemius in wild turkeys did not change during stance phase of running although muscle–tendon complex length (i.e. joint angles) did. Based on their results, they speculated that muscle fascicles remained at the same length during a step cycle because the muscle–tendon complex length changes were taken up by elastic elements. Similar results have been confirmed in human studies. Kawakami et al. (2002) reported small muscle fascicle length changes of the medial gastrocnemius during the eccentric contraction phase of dynamic ankle dorsiflexion–plantarflexion movements, indicating that the Achilles tendon length changes contributed to the enhanced mechanical work of the ankle plantar flexors when the concentric phase was preceded by a stretch (i.e. a counter-movement). This body of research supports a primary role for tendon elongation in the SSC effect. However, it is important to note that whole-tendon length changes have not been directly measured in these studies (Kawakami et al., 2002; Roberts et al., 1997). Rather, changes in tendon length were estimated from measured changes in the position of the associated joint and/or length of the muscle–tendon complex and muscle fascicles. Thus, the actual behavior of a tendon during a SSC has not been measured accurately to date. Furthermore, in some studies, it has been suggested that contributions of tendon length changes to the SSC effect are small or negligible, and other factors, such as pre-activation and residual force enhancement (eccentric contraction-induced force potentiation) might have a significant impact on the SSC effect (Bobbert et al., 1996; Zajac, 1993). Given the current state of our knowledge, the precise mechanisms underlying the SSC effect remain unknown and should be further evaluated.

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Therefore, the aim of this study was to compare the magnitude of the SSC effect in two experimental muscle preparations that allowed us to carefully control the contribution of the tendon to the measured SSC effect: a soleus preparation 'with' the Achilles tendon included, and a soleus preparation 'without' inclusion of the Achilles tendon. A possible difference in the magnitude of the SSC effect between these two conditions would provide unique evidence of the contribution of the tendon to the SSC effect. If the magnitude of the measured SSC effect was comparable between the two preparations, the contribution of the tendon would be deemed to be small or negligible. In addition, if a substantial SSC effect was observed in both preparations, the contribution of other factors to the SSC effect – namely, stretch reflex, pre-activation and/or residual force enhancement – should be considered.

MATERIALS AND METHODS

Muscle sample preparation and experimental setup

Male Sprague–Dawley rats (unknown age, mean±s.d. body mass 563±103 g, N=9) were used in this study. The animals were housed according to the guidelines of the Animal Care Services at the University of Calgary. They were fed standard rat chow and provided with water *ad libitum*. The rats were anesthetized with a gas mixture (2–5% isoflurane and O_2) throughout the experiment. After completion of the experimental trials, rats were killed by an injection of sodium pentobarbital (1.5 ml) to the heart. All procedures were approved by the Life and Environmental Sciences Animal Care Committee of the University of Calgary. The soleus was used for all experiments because of its predominant composition of slow-twitch fibers (84%) (Novák et al., 2010), which minimized the effects of fatigue. The soleus of the right leg was exposed and dissected from its surrounding connective tissue, with its blood and nerve supply left intact. Contractions were evoked using a specially designed nerve cuff electrode attached to the sciatic nerve. Changes in muscle fascicle length were measured using 1 mm diameter, spherical ultrasound piezo electric crystals (Sonomicrometry system; Sonometrics Corporation, London, ON, Canada) attached at either end of a muscle fascicle identified by direct surface micro-stimulation. In this procedure, we stimulated the target fascicle at one end with a local electrical stimulus, which allowed us to easily visualize the contracted fascicle and the dimpling of the fascicle at the other (non-stimulated) end. Sonomicrometry crystals were tied to the ends of target muscle fascicle bundles and corresponding aponeurosis tissues using a silk suture. This procedure has been shown to minimize crystal movements (and associated movement artifacts) and guarantees a high signal to noise ratio because of the exclusive transmission of the ultrasound signals through the muscle (rather than air) (Butterfield et al., 2005; Butterfield and Herzog, 2005). Gastrocnemius and plantaris tendons were cut to isolate the soleus tendon with a remnant piece of the calcaneus bone. For trials in which the tendon was part of the muscle system (hereafter referred to as the 'with-tendon' condition; see below), the calcaneus was rigidly attached to the force transducer (LCFA-5, OMEGA Engineering Inc., St-Eustache, QC, Canada) with the motor (Gemini GV6K, Parker Hannifin Corp., Mayfield Heights, OH, USA) (Fig. 1, left). For trials in which the tendon was 'eliminated' from the system (hereafter referred to as the 'without-tendon' condition; see below), the muscle was rigidly attached to the force transducer at the muscle–tendon junction (Fig. 1, right), thereby eliminating the influence of the free tendon from the muscle system. A 0.9% physiological saline solution was applied to the preparation every 2 min to keep the muscle and tendon moist. The rectal temperature was monitored to maintain the animals' body temperature to within 35–37°C using an infrared heat lamp and heating pad. Muscle contractions were evoked by electrical stimulation (S88 Square Pulse Stimulator, Grass Technologies, West Warwick, RI, USA), using square-wave pulses (500 µs for 1 s at 60 Hz). The stimulation voltage was gradually increased until a further increase in voltage did not result in an increase in muscle force. We called this the saturation point. The stimulation voltage for all experiments was set at 1.2 times the saturation voltage to ensure activation of all motor units and a fused tetanic contraction.

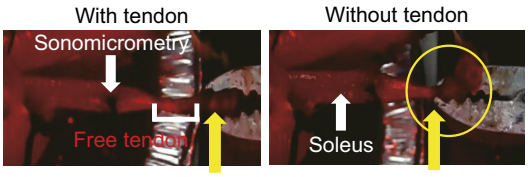

Fig. 1. The experimental set up. Left: the 'with-tendon' condition. The distal end of the Achilles tendon (calcaneus) was rigidly attached to the load cell and motor (yellow arrow). Right: the 'without-tendon' condition. The muscle–tendon junction was rigidly attached to the load cell and motor (yellow arrow).

Experimental design

The following two conditions were used to evaluate the effects of SSCs: (i) SSC trials with the free tendon intact and part of the system (with-tendon condition) and (ii) SSC trials with the free tendon removed from the system (without-tendon condition). For both conditions, three types of contraction were performed (Fig. 2): (i) a concentric contraction without pre-activation (CON); (ii) a concentric contraction that was preceded by an isometric contraction (ISO); and (iii) a concentric contraction that was preceded by an eccentric contraction (ECC). The magnitude of stretch and shortening was 3 mm and occurred at a speed of 6 mm s^{-1} for stretching and 20 mm s^{-1} for shortening. Prior to conducting the experimental trials, the optimal length of the muscle (i.e. the length at which the muscle

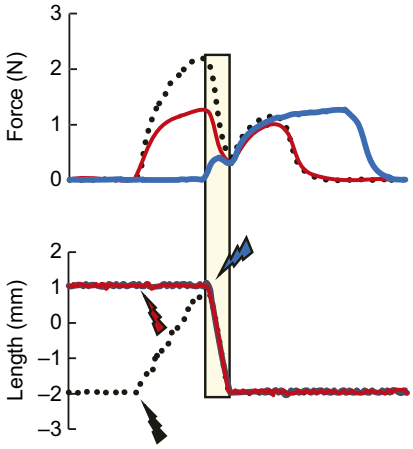

Fig. 2. A representative example of muscle force (upper panel) and muscle length (lower panel) as a function of time. Muscle force is expressed as active force (i.e. net force minus passive force). A muscle length of 0 mm indicates optimal length. The shaded region (i.e. concentric phase) indicates the measurement area for mechanical work (150 ms). The solid blue line shows a trial of a concentric contraction without pre-activation (CON). The solid red line shows a trial of a concentric contraction with an isometric pre-activation phase (ISO). The dotted black line shows a trial of a concentric contraction with an eccentric pre-activation phase (ECC). The colored lightning symbols indicate the onset of stimulation for the corresponding trial (contraction).

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produced the maximal active isometric force) was identified and labeled 0 mm length. Optimal length was determined by measuring passive and active maximal isometric force at different muscle lengths, and subtracting the passive from the total force measured. As the passive forces at optimal length were small and had a shallow slope, shortening of the sarcomeres upon activation was assumed to have a negligible effect on them. Stretching for all conditions started at a length of −2 mm (2 mm shorter than optimal length), and shortening at +1 mm. The sequence of trials was consistent for all animals: CON, ISO and ECC. However, the order of the tendon conditions (with and without tendon) was counter-balanced across animals. To minimize effects of fatigue, a rest interval of >2 min was provided between trials.

Measurements and data analyses

Muscle force and length were recorded at 1000 Hz using data acquisition software (Windaq, DATAQ Instruments Inc., Akron, OH, USA). Mechanical work (calculated from the length change of motor and the muscle force) done during the concentric contraction phase was the primary outcome measure used for evaluating the SSC effect. Although the ISO condition did not include an active stretch, we use the term 'SSC effect' for both ECC and ISO conditions in this paper, as we used pre-activation conditions for both test configurations, and pre-activation has been considered to contribute to the SSC effect (Bobbert et al., 1996; Bobbert and Casius, 2005; Ettema et al., 1990). The SSC effect for the ISO and ECC conditions was expressed relative to the work produced for the CON condition; the greater the value, the greater the SSC effect. In order to evaluate the influence of the tendon on the SSC effect, the work performed during the ECC trials in the with-tendon condition was compared with the work performed in the without-tendon condition. Muscle fascicle lengths were quantified as the linear distance between the two sonomicrometry crystals attached to the ends of an identified muscle fascicle (length resolution was 15 µm based on a transmission velocity of 1540 m s^{-1} and a data sampling rate of 100 MHz), and length changes during the concentric contractions were calculated. Finally, the mechanical work performed during concentric contractions for the CON, ISO and ECC trials in the with- and without-tendon condition was quantified to examine the contribution of pre-activation and eccentric contraction induced-force potentiation to the SSC effect.

Statistics

SSC effects for the with- and without-tendon ECC trials were evaluated using a paired two-tailed *t*-test. Differences in the magnitude of muscle fascicle shortening during the concentric contraction were evaluated using a two-way analysis of variance (ANOVA) with repeated measures, with the main factors tendon condition (with or without tendon) and contraction type (CON, ISO and ECC). Mechanical work performed during muscle shortening was compared between the CON, ISO and ECC conditions using a one-way ANOVA with repeated measures and a Bonferroni correction. The effect size for the ANOVA was calculated as the partial η^2. Statistical analyses were performed using SPSS (version 20, IBM, Tokyo, Japan), with the level of significance set at α=0.05. All values are shown as means±s.d.

RESULTS

There was a substantial SSC effect for the ECC compared with the CON trials for the with-tendon (318±86%) and the without-tendon (271±70%) conditions (Fig. 3), but the effect was comparable between the two tendon conditions (P=0.167). Muscle fascicle shortening during the concentric contractions showed no significant interactions (F=0.793, partial η^2=0.117, P=0.475) (Fig. 4). Subsequent analyses revealed that muscle fascicle shortening was greatest in CON trials, followed by ISO then ECC trials (P=0.001–0.005). However, there was no significant main effect between the tendon conditions (F=0.834, partial η^2=0.122, P=0.396). For the without-tendon condition, mechanical work in the concentric contraction (Fig. 5) was significantly different among CON, ISO and ECC. One-way ANOVA, and subsequent *post hoc* testing revealed that the mechanical work was greatest for ECC, followed by ISO and then CON (P=0.001–0.002).

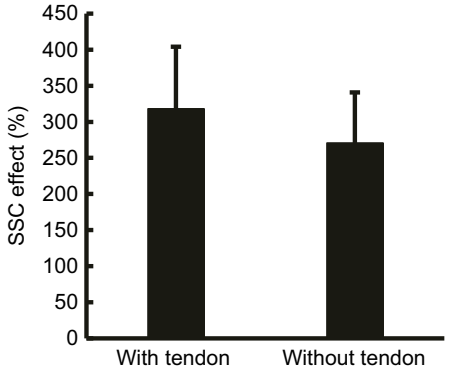

Fig. 3. Comparison of the stretch–shortening cycle (SSC) effect for the with- and without-tendon conditions. The SSC effect was calculated as the value of the mechanical work attained during the concentric phase in the concentric contraction with an eccentric pre-activation phase (ECC) condition relative to the corresponding value obtained in the concentric contraction without pre-activation (CON) condition (N=9; means±s.d.). The difference between the two tendon conditions was non-significant (P=0.167).

DISCUSSION

The aim of this study was to clarify the contribution of the tendon to the SSC effect. In order to achieve this aim, we compared the SSC effect for conditions in which the tendon was part of the system and for conditions where the tendon was eliminated from the muscle system. We report comparable SSC effects for the two tendon conditions, indicating a negligible effect of the tendon on the

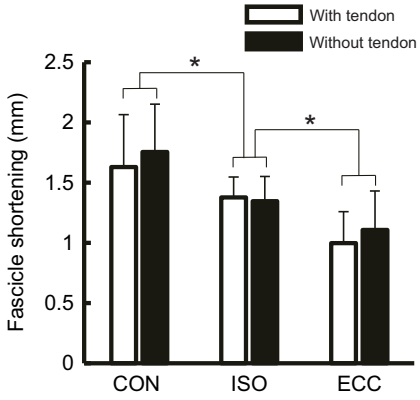

Fig. 4. Muscle fascicle shortening during the concentric contraction phase of the experimental tests. Data are shown for the with-tendon and without-tendon conditions. CON indicates the trial for the concentric contraction without pre-activation. ISO indicates the trial for the concentric contraction with an isometric pre-activation phase. ECC indicates the trial for the concentric contraction with an eccentric pre-activation phase. *Significant difference between CON, ISO and ECC (P<0.05) (N=9; means±s.d.).

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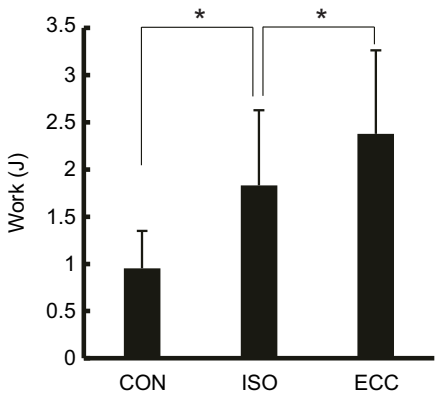

Fig. 5. Mechanical work attained during the concentric phase for the without-tendon condition. CON indicates the trial for the concentric contraction without pre-activation. ISO indicates the trial for the concentric contraction with an isometric pre-activation phase. ECC indicates the trial for the concentric contraction with an eccentric pre-activation phase. *Significant difference between CON, ISO and ECC (P<0.05) (N=9; means±s.d.).

SSC effect in the rat soleus. Thus, we propose that factors other than tendon elongation play a role in the SSC effect. In addition, as the SSC effect was significantly larger with the application of eccentric pre-activation (ECC condition) compared with isometric pre-activation (ISO condition) under both tendon conditions, it is likely that an eccentric contraction-induced force potentiation mechanism contributed to the measured SSC effect. In our experimental preparation, neural activation was carefully controlled by artificial electrical stimulation and was identical across all contraction types. Therefore, a possible influence through the muscle stretch reflex was eliminated in our study. Taken together, muscle pre-activation and residual force enhancement were the likely factors that contributed to the measured SSC effect in the rat soleus.

Because the magnitude of the SSC effect was similar between the with- and without-tendon conditions, the effect of tendon elongation on the SSC effect was negligible, at least for the case of the rat soleus. In addition, the result that a substantial SSC effect was observed in the without-tendon condition indicates that factors other than tendon elongation contributed to the observed SSC effect. The mechanical work attained in the isometric pre-activation condition (ISO) was larger than that attained in the pure shortening condition (CON) (Fig. 5). This result indicates that pre-activation contributed to the SSC effect. This result is consistent with previous studies involving similar experimental tests in human plantar flexors (Fukutani et al., 2015) and human knee extensors (Fukutani et al., 2016). In addition, the mechanical work obtained in the eccentric pre-activation condition (ECC) was larger than that observed for the isometric pre-activation condition (ISO) (Fig. 5). This result indicates that an eccentric contraction-induced force potentiation mechanism(s) does exist. A possible contributing factor could be the residual force enhancement. According to Herzog (2005), residual force enhancement is defined as ‘the steady-state isometric force following active muscle stretch minus the corresponding force obtained in a purely isometric contraction at the same muscle length’. Because we did not compare steady-state isometric forces after eccentric contractions and purely isometric contractions, we do not know the amount of force enhancement that was present following the eccentric contractions preceding the shortening phase in our experiments. However, we compared the mechanical work of the shortening phase for conditions in which the shortening was preceded by an isometric contraction (ISO) or an eccentric contraction (ECC), and observed a significant increase in the mechanical work for the ECC compared with the ISO condition, suggesting that eccentric contraction-induced residual force enhancement might have contributed substantially to the increased work in the ECC experiments. This result agrees with previous studies suggesting that residual force enhancement may contribute to the work enhancement in the SSCs (Cavagna et al., 1968; Fortuna et al., 2017; Fukutani et al., 2017; Fukutani and Herzog, 2018). However, some researchers have argued that the influence of residual force enhancement, produced by a preceding eccentric contraction, disappears quickly at the onset of a concentric contraction (Brown and Loeb, 2000; Herzog and Leonard, 2000). Specifically, the effect of residual force enhancement may be eliminated by shortening, or may be canceled out by residual force depression, which is induced by muscle shortening (Abbott and Aubert, 1952; Maréchal and Plaghki, 1979). These results are inconsistent with a study observing residual force enhancement after SSCs (Seiberl et al., 2015). We showed recently that residual force enhancement was attenuated by shortening following stretch, and that this effect was dependent on the magnitude of shortening (Fukutani and Herzog, 2018). This finding might partly explain the inconsistency regarding residual force enhancement following SSCs. This point should be clarified in the future to elucidate the contribution of residual force enhancement to the SSC effect.

Another possible reason for the observed increase in mechanical work in the shortening phase of SSCs may be the increase in force per cross-bridge, which is caused by the elongation of attached cross-bridges in active muscle stretching (Huxley, 1957; Huxley and Simmons, 1971). This elongation of attached cross-bridges may contribute to the increase in mechanical work in the shortening phase of SSCs. We recently examined the effect of cross-bridge elongation in the eccentric phase of SSCs by adding a pause between the stretch and shortening of SSC testing (Fukutani et al., 2017). When an increase in force per cross-bridge due to cross-bridge elongation was eliminated (by a sufficiently long pause), the mechanical work was still increased compared with control conditions, suggesting that factors other than cross-bridge elongation are responsible for some of the increased work observed in SSCs (Fukutani et al., 2017). We speculate that residual force enhancement may have been the cause of the remainder of the observed SSC effect.

In the concentric contraction phase during SSCs, we observed smaller muscle fascicle shortening in the ECC than in the CON condition for a given magnitude of shortening. Given our results that the muscle fascicle behavior was not different for the with- and without-tendon conditions, we suggest that the smaller muscle fascicle shortening in the ECC compared with the CON condition was not caused by the free tendon. Another possible reason for the reduced muscle fascicle shortening in the ECC compared with the CON condition might be the elimination of any slack in the muscle–tendon complex for the ECC condition. At the onset of shortening in the without-tendon condition, the muscle fascicle length was longer in the CON condition (14.1 mm) than in the ISO (13.7 mm) and ECC (13.3 mm) condition, possibly due to the smaller force at the onset of shortening. Once shortening began, force decreased gradually in the ISO and ECC conditions, while it increased first and then decreased in the CON condition (Fig. 2). Generally speaking, muscle fascicles shorten when muscle force increases and muscle length is constant. Finally, at the end of shortening, muscle fascicles reached similar lengths for the three experimental conditions (12.5 mm for CON, 12.5 mm for ISO, 12.3 mm

for ECC). This greater muscle fascicle shortening in the CON than in the ECC condition would contribute to the condition-dependent force responses. This is because less muscle shortening (i.e. slower muscle shortening) results in greater muscle force as a result of the force–velocity relationship (Hill, 1938).

Another potential reason for the difference in muscle fascicle lengths at the onset of shortening is the difference in length of the aponeurosis at that instant in time. With our experimental design, we could eliminate the effect of the free tendon by eliminating the tendon in the without-tendon condition. However, not only the free tendon but also the aponeurosis can change length, thereby affecting the resulting fascicle lengths, which may contribute to the SSC effect. Length changes in aponeuroses have been observed to occur when muscle length is changed and when muscles are activated or deactivated. These length changes seem to crucially depend on the muscle, and the detailed contractile conditions. For example, Tilp et al. (2007) found that the human tibialis anterior aponeurosis was elongated with muscle activation, while Nigg and Herzog (2007) and Lieber et al. (2000) observed a shortening of aponeuroses in active compared with passive muscles when passive and active forces were matched. As aponeuroses, in contrast to the free tendons of muscles, are not mechanically in series with the contractile elements of muscles, it is hard to estimate how much they might potentially contribute to the storage and release of energy (if at all) in SSCs.

Several issues must be considered when attempting to apply the results of our study to *in vivo* human muscle function. First, geometric differences in the ratio of muscle to tendon length and muscle to tendon cross-sectional area may affect the mechanics of SSCs, including the SSC effect. Specifically, muscles with relatively long tendons compared with muscle fascicles and/or relatively small tendon to muscle cross-sectional area may behave differently from what we observed in the rat soleus muscle. For example, some major hindlimb muscles in kangaroos, which are often used as an example of significant SSC effects caused by tendon elongation (Dawson and Taylor, 1973), have a much greater tendon to muscle fascicle length ratio compared with the major hindlimb muscles in rats and humans. Therefore, comparing the SSC effects across muscles with different geometries would be useful to test whether the results presented here can be generalized to other muscles and species.

Conclusions

In conclusion, our results suggest that tendon elongation does not contribute to the SSC effect substantially in the rat soleus. However, similar experiments should be conducted with muscles whose tendons are long and thin compared with the muscle fascicle length and the muscle's physiological cross-sectional area to evaluate the contribution of tendon elasticity to the SSC effect for a variety of differing muscle–tendon structures and geometries. Furthermore, we conclude that pre-activation and residual force enhancement contribute to the SSC effect. However, the mechanisms underlying these contributions remain to be elucidated.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.F., W.H.; Methodology: A.F., A.S., T.L.; Validation: A.F.; Formal analysis: A.F.; Investigation: A.F., A.S., T.L.; Resources: A.F., W.H.; Data curation: A.F.; Writing - original draft: A.F.; Writing - review & editing: A.F., A.S., T.L., W.H.; Visualization: A.F.; Supervision: W.H.; Project administration: W.H.; Funding acquisition: A.F., W.H.

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