

RESEARCH ARTICLE

Influence of stretch magnitude on the stretch–shortening cycle in skinned muscle fibres

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ABSTRACT

The mechanical work attained during muscle fibre shortening is increased by prior stretching. Recently, we suggested that residual force enhancement (RFE) may contribute to this enhanced work. RFE can be changed reliably by changing the stretch magnitude. Therefore, the purpose of this study was to examine the effect of stretch magnitude, and by association RFE, on the mechanics of the stretch–shortening cycle (SSC) in skinned skeletal muscle fibres. Three tests were performed using skinned rabbit soleus fibres (N=18). The first test was a pure shortening contraction in which fibres were activated and then shortened from an average sarcomere length of 3.3 µm to 3.0 µm. The second test was a SSC in which fibres were activated and stretched from 3.0 µm to 3.3 µm, and then shortened to 3.0 µm. The third test was a SSC in which fibres were activated and stretched from 2.4 µm to 3.3 µm, and then shortened to 3.0 µm. The mechanical work during shortening and the force maintained 15 s after the end of shortening were determined. The relative increase in mechanical work with respect to the pure shortening condition was greater for the large than for the small stretch condition (P<0.001). Similarly, the relative increase in force 15 s after the end of shortening was greater for the large than for the small stretch condition (P=0.043). We conclude that increasing the magnitude of stretch results in an increase in mechanical work and increased force at steady state following the stretch, probably because of the greater RFE.

KEY WORDS: Elastic energy, Attached cross-bridges, Soleus, Sarcomere, Titin, Residual force enhancement

INTRODUCTION

The mechanical work during a concentric contraction (shortening) phase is increased when shortening is preceded by muscle stretching. This increase in work during a stretch–shortening cycle (SSC) has been called the 'SSC effect' (Bosco et al., 1982; Bosco and Rusko, 1983; Komi, 2000). The SSC effect has been speculated to be caused by enhanced muscle activation (Dietz et al., 1979; Nichols and Houk, 1973), elastic energy utilization (Finni et al., 2001; Kawakami et al., 2002), optimal pre-activation (Bobbert et al., 1996; Bobbert and Casius, 2005), residual force enhancement (RFE) (Edman and Tsuchiya, 1996; Forcinito et al., 1998) and improved cross-bridge kinetics (Cavagna et al., 1986, 1994).

Recently, we examined the influence of RFE on the SSC effect (Fukutani et al., 2017a,b) and found that increased RFE is positively related to the SSC effect. If RFE is the primary contributor to the SSC effect, then an increase in RFE should be associated with an increase in the SSC effect. RFE can readily be manipulated by changing the stretch magnitude, as it is known that increasing stretch magnitude typically results in increased RFE (Bullimore et al., 2007; Edman et al., 1978; Herzog and Leonard, 2005; Schachar et al., 2004). Some previous studies indeed showed that increased stretch magnitude resulted in greater SSC effect (Cavagna et al., 1986, 1994, 1981), while another did not (Lee et al., 2001). These conflicting results may be attributable to the muscle lengths at which the SSCs were performed. It is well accepted that RFE increases when a given stretch is performed at long compared with short muscle lengths (Julian and Morgan, 1979; Morgan et al., 2000; Peterson et al., 2004). Therefore, a RFE-dependent SSC effect would also be expected to be prominent when SSCs are performed at long lengths, whereas it might be negligible when performed at short muscle lengths.

The purpose of this study was to determine whether the SSC effect in skinned single muscle fibres depends on the stretch magnitude. Increasing the stretch magnitude is known to increase RFE reliably (Bullimore et al., 2007; Edman et al., 1978; Herzog and Leonard, 2005; Schachar et al., 2004); thus, we expected a greater SSC effect with increasing stretch magnitude. Tests were performed on the descending limb of the force–length relationship in order to maximize RFE (Edman et al., 1982). We hypothesized that a large stretch preceding shortening in SSCs would result in a large SSC effect, while a small stretch would result in a small SSC effect. All testing was performed in single skinned fibres where activation was controlled and series elasticity was minimal.

MATERIALS AND METHODS

Muscle sample preparation and experimental setup

New Zealand female white rabbits (10–16 weeks) were euthanized according to a protocol approved by the University of Calgary's Life Sciences animal ethics committee. Strips of soleus muscle were harvested and tied to wooden sticks to preserve the *in situ* sarcomere length. The strips were then placed in a 50% rigor and 50% glycerol solution with protease inhibitors (cOmplete™, Roche Diagnostics, Montreal, QC, Canada) to chemically disrupt the muscle membrane. Subsequently, the strips were stored in a freezer at −20°C for 2–4 weeks. On the day of the experiments, a single fibre of the soleus muscle was isolated using fine forceps under a dissecting microscope (SMZ1500, Nikon, Tokyo, Japan). The isolated fibre was transferred to an experimental chamber (Model 802B, Aurora Scientific, Aurora, ON, Canada) containing a relaxing solution with protease inhibitors. One end of the fibre was attached to a force transducer (Model 400A, Aurora Scientific) and the other end was attached to a length controller (Model 308B, Aurora Scientific). Sarcomere length was measured using a He–Ne laser-based diffraction system (1508P-1, JDSU, Milpitas, CA, USA). Fibre length was measured using a microscope (Stemi 2000,

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Zeiss, Oberkochen, Germany). All experiments were performed at room temperature (21.4±1.5°C).

Fibres (n=18) were subjected to three tests: (i) a pure shortening contraction, (ii) a SSC with a small stretch magnitude, and (iii) a SSC with a large stretch magnitude (Fig. 1). For the pure shortening trial (Fig. 1, red line), fibres were isometrically activated at 3.3 µm and then shortened to 3.0 µm in 2 s. For the SSC test with the small stretch condition (Fig. 1, left panel, blue line), fibres were isometrically activated at an average sarcomere length of 3.0 µm, stretched to 3.3 µm in 1 s, and then immediately shortened to 3.0 µm in 2 s. After shortening, the isometric steady-state contraction was sustained for another 15 s. For the SSC test with the large stretch condition (Fig. 1, right panel, blue line), fibres were isometrically activated at 2.4 µm, stretched to 3.3 µm in 3 s, and then immediately shortened to 3.0 µm in 2 s. The isometric steady-state contraction was then sustained for another 15 s at the final length. The pure shortening trials were performed twice, always following the two SSCs. In addition, all tests described above were also performed passively. The order of the small and large stretch SSCs was randomized. Tests were separated by a 2 min rest.

Data were collected at 10 kHz. Active force was obtained by subtracting the passive force from the total force for the corresponding tests. The SSC effect was quantified by the mechanical work during muscle shortening and by the forces at the onset and end of the shortening phase. Mechanical work was calculated as the line integral of the variable force over the entire shortening distance (Fukutani et al., 2017b). Mechanical work and forces in the small and large stretch SSC trials were expressed relative to those obtained in the pure shortening trials. The relative work and force values were compared between the small and large stretch trials. In addition, the steady-state isometric force 15 s after the end of shortening was used as an index of the magnitude of RFE.

Solutions

The relaxing solution contained (in mmol l^{-1}): 170 potassium propionate, 2.5 magnesium acetate, 20 Mops, 5 K_2EGTA and 2.5 ATP, pH 7.0. One tablet of protease inhibitors was added to each 100 ml of relaxing solution. The washing solution contained (in mmol l^{-1}): 185 potassium propionate, 2.5 magnesium acetate, 20 Mops and 2.5 ATP, pH 7.0. The activating solution contained the cross-bridge inhibitor 2,3-butanedione monoxime (BDM) (Herrmann et al., 1992; Higuchi and Takemori, 1989) to attenuate the influence of muscle damage (Bagni et al., 2005); the composition of the solution was (in mmol l^{-1}): 10.0 BDM, 170 potassium propionate, 2.5 magnesium acetate, 10 Mops, 2.5 ATP, and free Ca^{2+} buffered with EGTA (CaEGTA and K_2EGTA mixed to obtain a solution with a pCa value of 4.2), pH 7.0.

Statistics

Paired t-tests (two-tailed) were used for all statistical analyses. The 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

Mechanical work and force enhancement induced by stretch (SSC effect)

The relative increase in mechanical work was greater for the large than for the small stretch condition (P<0.001) (Fig. 2A). Similarly, the relative increase in force at the onset and end of shortening was greater for the large than for the small stretch condition (P=0.006 at the onset, Fig. 2B; P<0.001 at the end of shortening, Fig. 2C).

Steady-state isometric force at 15 s after the end of shortening

The forces at 15 s after the end of shortening were greater for the small stretch (P=0.034) and the large stretch conditions (P=0.001; Fig. 3A) compared with each control condition. In addition, the magnitude of this force enhancement was greater for the large than for the small stretch condition (P=0.043; Fig. 3B).

DISCUSSION

The purpose of this study was to examine the effect of stretch magnitude on the mechanics of the SSC in skinned fibres because it is widely known that RFE is affected by stretch magnitude. We confirmed that the SSC effect, evaluated using the mechanical work during the shortening phase of the SSCs, was greater for the large than for the small stretch condition. As the magnitude of RFE is known to increase with increasing muscle stretch magnitude (Bullimore et al., 2007; Edman et al., 1978; Herzog and Leonard,

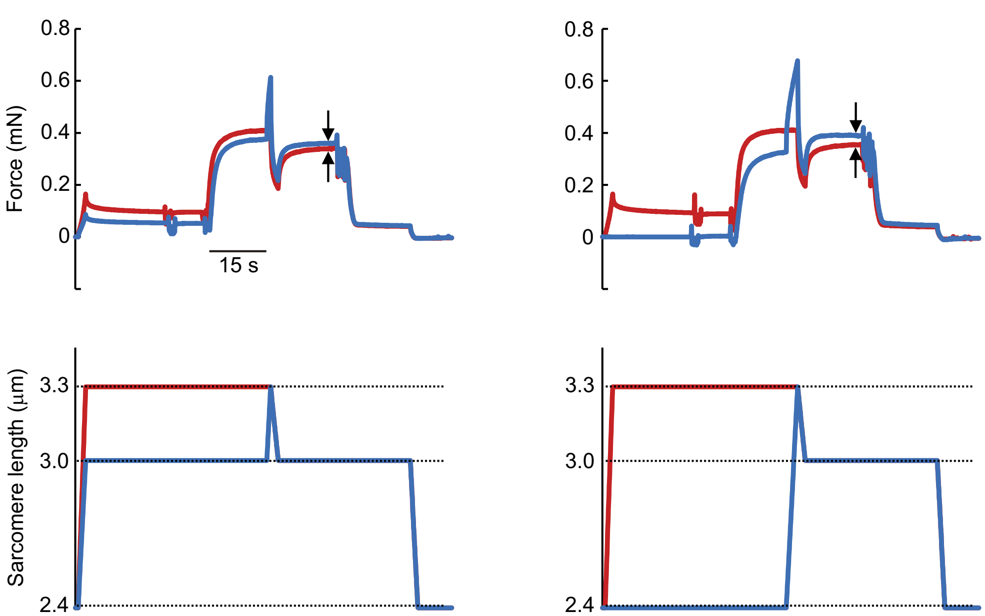

Fig. 1. Typical example of changes in muscle force and muscle length as a function of time. The left panels show the force and sarcomere length responses in the small stretch condition, and the right panels show the force and sarcomere length responses in the large stretch condition. The blue line indicates the stretch–shortening cycle (SSC) trial and the red line indicates the pure shortening trial. Arrows indicate force enhancement relative to the pure shortening trial.

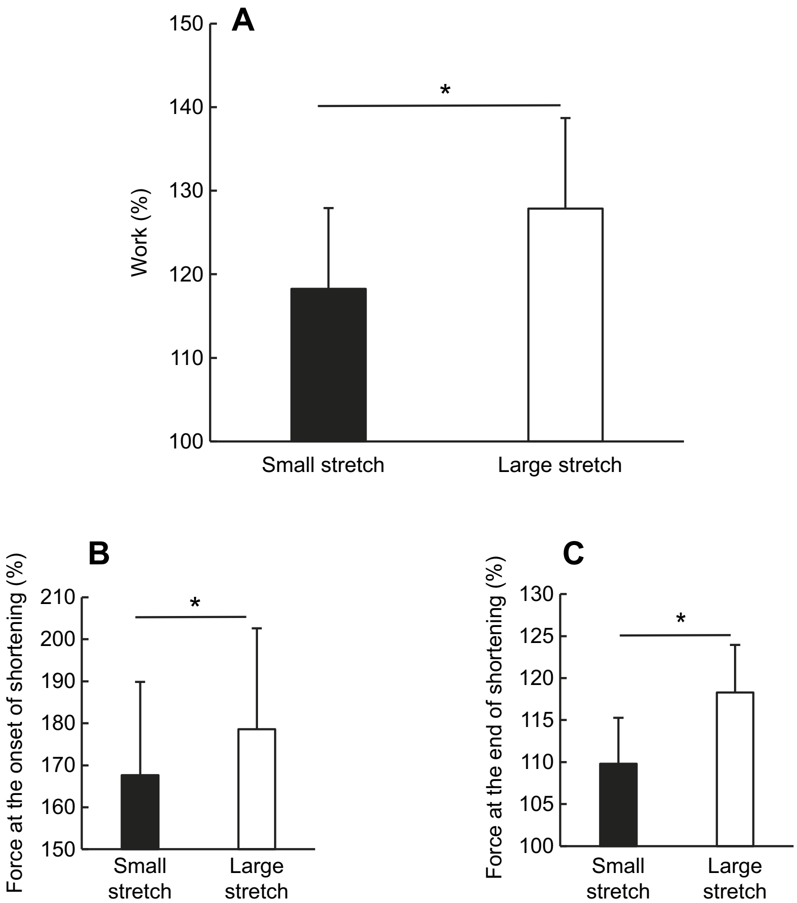

Fig. 2. Mechanical work and force. (A) Increase in mechanical work during shortening for the SSC trials compared with the pure shortening trials. The work is significantly greater for both SSC conditions compared with the pure shortening condition, and is also greater for the large versus the small stretch condition (**P*<0.001) (*N*=18). (B) Increase in force at the onset of shortening for the SSC trials compared with the pure shortening trials. The force at the onset of shortening is significantly greater for both SSC conditions compared with the pure shortening condition, and is also greater for the large compared with the small stretch condition (**P*=0.006) (*N*=18). (C) Increase in force at the end of shortening for the SSC trials compared with the pure shortening trials. The force at the end of shortening is significantly greater for both SSC conditions compared with the pure shortening condition, and is also greater for the large compared with the small stretch condition (**P*<0.001) (*N*=18). All data are shown as means±s.d. relative to the pure shortening condition.

2005; Schachar et al., 2004), the observed difference in the SSC effect may be attributable to RFE. This idea is strengthened by the observed larger steady-state isometric force 15 s after the end of shortening in the large compared with the small stretch condition.

SSC effect and RFE

We examined the effect of stretch magnitude and RFE on the increase in work during SSCs. We confirmed that the steady-state isometric force 15 s after the end of shortening was larger in the

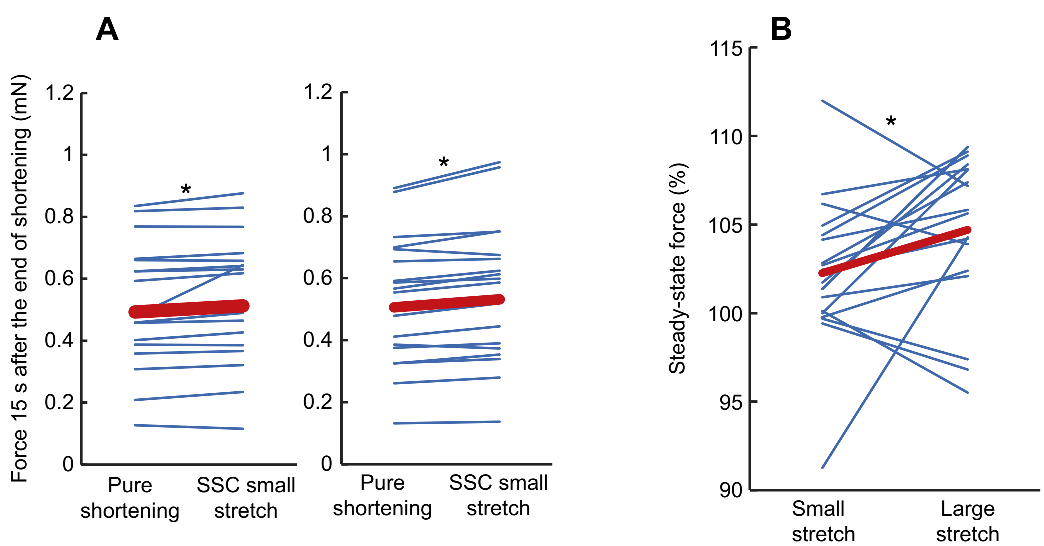

Fig. 3. Force attained 15 s after the end of shortening. (A) Increase in force attained 15 s after the end of shortening for the SSC trials compared with the pure shortening trials. The force attained is significantly greater for both small stretch (left, **P*=0.034) and large stretch (right, **P*=0.001) SSC conditions compared with the pure shortening condition. Blue lines indicate individual values and red lines indicate mean values (*N*=18). (B) Increase in steady-state force attained 15 s after the end of shortening for the SSC trials compared with the pure shortening trials (the index of RFE). The increase in steady-state force is significantly greater for the large compared with the small stretch condition (**P*=0.043). Blue lines indicate individual values and the red line indicates mean values, relative to the pure shortening condition (*N*=18).

SSCs than in the pure shortening tests. We defined this enhanced force as RFE in this study. This result conflicts with some findings from previous studies in which the isometric forces after SSC trials were the same as those obtained for pure shortening contractions, irrespective of the stretch magnitude (Lee et al., 2001). We speculate that this difference may be caused by the muscle length at which the SSCs were performed. While the final length in the Lee et al. (2001) study was on the plateau of the force–length relationship, our study was performed at an average sarcomere length of 3.0 µm, which corresponds to the descending limb of the force–length relationship (de Beer et al., 1988; Herzog et al., 1992; Yuri et al., 1998). It is generally accepted that RFE increases with increasing muscle length (Julian and Morgan, 1979; Morgan et al., 2000; Peterson et al., 2004). In addition, RFE may be offset, at least in part, by the shortening-induced residual force depression (Abbott and Aubert, 1952; Fukutani and Herzog, 2018; Maréchal and Plaghki, 1979) associated with SSCs. These offsetting effects may be the reason for the negligible RFE in the Lee et al. (2001) study. This speculation is partly supported by the observations of Ettema et al. (1990), who found enhanced force following SSCs conducted on the descending limb of the force–length relationship but not when the SSCs were performed on the ascending limb of the force–length relationship. Here, the SSCs were performed on the plateau and descending limb exclusively, thereby maximizing RFE, and thus the SSC effect that may be produced by the RFE.

We confirmed forces at the onset of shortening were greater for the large compared with the small stretch SSC conditions. This result agrees with previous observations reporting that forces at the end of the stretch phase increase with increasing stretch magnitude (Bullimore et al., 2007). In this study, the velocity (0.3 µm s^{-1}) and the final muscle length (3.0 µm) were kept identical, while the stretch magnitude was 0.3 µm for the small and 0.9 µm for the large SSC stretch conditions. From the point of view of the force–length and the force–velocity relationships (Hill, 1938; Gordon et al., 1966), and knowing that the stretch time even for the small stretch magnitude (1 s) was plenty to reach steady-state dynamic conditions, the cross-bridge kinetics at the end of stretching (i.e. the onset of shortening) would be expected to be the same for the small and large stretch SSC trials. Therefore, one would expect the forces at the end of the stretch phase to be the same for the two stretch conditions. Based on these considerations, we feel confident that the large force at the onset and end of shortening in the large stretch SSC conditions are not caused by different cross-bridge kinetics between the two conditions but are reflections of the large magnitude of RFE induced by the large stretch.

As discussed above, the effect of RFE persists even after the completion of the SSCs, and manifests itself as an increased steady-state isometric force after the end of shortening compared with the corresponding force for a purely isometric contraction (Fukutani and Herzog, 2018). Some previous studies reported that the effect of RFE persists throughout and following SSC (Fortuna et al., 2018; Seiberl et al., 2015; Hahn and Riedel, 2018), while others reported contradictory results (Brown and Loeb, 2000; Fukutani et al., 2017a, b; Herzog and Leonard, 2000; Lee et al., 2001). A possible explanation for these contradictory results is the muscle length at which the steady-state isometric force (torque) was measured. Specifically, if muscle length after the SSCs falls on the descending limb of the force–length relationship, the effect of RFE persists throughout the SSCs, presumably because of the prominent effect of RFE on the descending limb (Julian and Morgan, 1979; Morgan et al., 2000; Peterson et al., 2004). Final muscle length may partly explain the contradictory results found in different studies. However, in several studies working at relatively short muscle lengths, increased steady-state isometric forces (torques) have been found after the SSC (Fortuna et al., 2018; Hahn and Riedel, 2018). Knowing that the effect of RFE is small or negligible on the ascending limb of the force–length relationship (Julian and Morgan, 1979; Morgan et al., 2000; Peterson et al., 2004), and that the effect of RFE is attenuated by shortening in SSCs (Fukutani and Herzog, 2018; Herzog et al., 2003), one would not expect a substantial amount of RFE after SSCs on the ascending limb. Regrettably, when, and to what degree, RFE persists following SSCs cannot be fully explained at this point, and should be examined in future studies.

We confirmed that the magnitude of the SSC effect was greater in the long stretch condition. As RFE is known to increase with increasing stretch magnitude (Bullimore et al., 2007; Edman et al., 1978; Herzog and Leonard, 2005; Schachar et al., 2004), our findings support the idea that RFE directly contributes to the SSC effect. We performed our testing at long average sarcomere lengths (up to 3.3 µm) to maximize the RFE, and thus its potential effect on the mechanics of the SSC. As everyday human movements probably occur at shorter average sarcomere lengths, the result obtained here should not be directly translated into *in vivo* physiological conditions. If we had done our testing at shorter average sarcomere lengths corresponding to the plateau or ascending limb of the force–length relationship, the SSC effect would probably have been smaller than that found here (Julian and Morgan, 1979; Morgan et al., 2000; Peterson, et al., 2004). Performing SSC experiments on different segments of the force–length relationship might provide crucial information on the effect of stretch magnitude and RFE on the SSC effect.

Conclusions

We conclude from the results of this study that increasing the magnitude of stretch in SSCs of skinned muscle fibres results in an increase in work in the shortening phase and an increased steady-state force following the shortening phase of the SSC, probably because of the greater RFE achieved with the increased stretch magnitude. Whether this result also holds for *in vivo* SSC cycles (Bosco et al., 1982; Bosco and Rusko, 1983; Komi, 2000) remains to be determined.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

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

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