The Effect of a Stretch-Shortening Cycle on Muscle Activation and Muscle Oxygen Consumption: A Study of History-Dependence

Kevin E. Caron, Jamie F. Burr, and Geoffrey A. Power

Department of Human Health and Nutritional Sciences, College of Biological Sciences, University of Guelph, Guelph Ontario, Canada

Abstract
Caron, KE, Burr, JF, and Power, GA.. The effect of a stretch-shortening cycle on muscle activation and muscle oxygen consumption: a study of history-dependence. J Strength Cond Res 34(11): 3139–3148, 2020—Stretch-shortening cycles (SSCs) are observed in a variety of human movements and are associated with increases in performance. Few studies have considered the effects of stretch-induced residual force enhancement (rFE) and shortening-induced residual force depression (rFD) during an SSC, and none have considered these properties during voluntary contractions. With force matched via a robotically resisted Smith machine, we hypothesized that in the isometric steady-state following an SSC (a) muscle activation (electromyography) of the knee and hip extensors would be greater and (b) muscle oxygen consumption be higher than the reference isometric condition (ISO), but less than the rFD condition. Subjects (n = 20, male, 24.9 ± 3.9 year) performed a squat exercise over 100–140˚ knee angle and a matched ISO at the top and bottom of the squat. After active shortening, the vastus medialis (VM), vastus lateralis (VL), and gluteus maximus (GM) showed activation increase in the rFD-state compared with ISO (~15%, ~11%, and ~25% respectively). During the isometric steady-state following the SSC, there was no difference in activation as compared with ISO for VM, VL, but GM showed an activation increase of ~15%. VM and VL showed an activation increase in the rFD-state compared with the isometric steady-state following SSC (~16 and ~10% respectively). Muscle oxygen consumption (tissue saturation index) was not different during the isometric steady-states following rFD and SSC compared with ISO. During a voluntary SSC exercise, the activation increase expected in the FD-state was attenuated, with no change in muscle oxygen consumption. The concomitant role of rFE and rFD during a voluntary position-matched SSC seems to counteract shortening-induced activation increase and may optimize movement economy.

Key Words: Electromyography, NIRS, force depression, residual force enhancement, history dependence of force

Introduction
Stretch-shortening cycles (SSCs) are a part of everyday movement and are associated with an increase in performance (19). An SSC involves an active lengthening contraction followed immediately by an active shortening contraction. The isometric steady-state following active lengthening is associated with increased force production, and is referred to as residual force enhancement (rFE) (16). The isometric steady-state following active shortening is associated with decreased force production, and is known as residual force depression (rFD) (16). Both rFE and rFD are observed across all structural levels of the muscle during electrically stimulated and voluntary contractions, and are collectively referred to as the history-dependence of force (3,5,31). There are few studies that measure and take into consideration the concomitant existence of these history-dependent properties during SSCs (9–12,17,22,38) and to our knowledge, none during functional, whole-body exercise, such as a squat.

After active lengthening (stretch), rFE is observed as an increase in force production during the isometric steady-state, compared with a purely isometric contraction at the same muscle length and activation level (16). rFE manifests during the active lengthening phase owing to a Ca2+-dependent stiffening and shortening of the protein titin’s free spring length upon activation, thus increasing the contribution of passive force to total force during and after active lengthening (15). Although rFE is associated with increases in force, if force is matched for the rFE and isometric condition, there is a reduction in muscle activity (i.e., less electromyography [EMG]) referred to as activation reduction (20,26,27,37). This activation reduction is associated with a decrease in the number of active motor units (1,18), and oxygen consumption (29), owing to the greater contribution of passive force to total force production in the rFE state. Paternoster et al. (29) identified with near infrared spectroscopy (NIRS) a significant relationship between activation reduction and muscle oxygen consumption, such that with increasing activation reduction there was lower muscle oxygen consumption on an individual basis. However, at the group level, this relationship was not as clear. Residual force depression is observed as a decrease in force production during the isometric steady-state following active shortening, owing to a stress-induced inhibition of crossbridge attachments (23). If force is matched to a reference isometric contraction, in the rFD state, EMG is increased (4). The increase in muscle activity is referred to as activation increase (20,27,34), and is associated with an increase in the number of active motor units (1). Using NIRS it has been shown that muscle oxygen consumption has a linear relationship with increasing EMG during isometric contractions of the biceps brachii (32); however, whether such an effect occurs in the knee extensors...
during a squat is unknown. There are no reports using NIRS during the rFD state; therefore, it is speculated that an activation increase would result in an increase in muscle oxygen consumption.

Investigation into the history-dependence of force has focused on the effects of rFE and rFD separately; however, most movements occur in a cyclic type pattern (i.e., locomotion) of SSCs, which can be a fast or slower transition, yielding differing mechanisms of performance enhancement (24). Investigation of SSCs and the history-dependence of force for the electrically stimulated thumb adductor pollicis muscle showed that if an SSC occurs with a minimal time delay between stretch and shortening (less than 0.5 seconds), or if shortening occurs quickly, then the stretch-induced enhancements in force can decrease the amount of rFD experienced (10,39). A similar finding was observed with electrically evoked contractions of the plantar flexors, as SSC mitigated the amount of shortening-induced rFD, which demonstrates a performance enhancement in muscles used for locomotion (12). However, it is still unknown whether voluntarily activated muscles demonstrate the same attenuation of rFD following an SSC during a multi-joint movement such as a squat.

The purpose of this study was to investigate the effects of rFE and rFD on EMG amplitude and oxygen consumption during a whole body squat. It was hypothesized that when force and position are matched on a robotically resisted Smith machine (Quantum 1080-Syncro system, 1080 Motion, Inc., Lidingo, Sweden) which measured total work and force over-time in all trials (sampling rate: 333Hz). Subjects were positioned in the 1080-Syncro system so the barbell rested on the upper trapezius, feet were shoulder width apart, and heels placed in front of the zero line (zero line is aligned directly below the barbell). Isometric, shortening (rFD condition), active lengthening (rFE condition), and SSC contractions were performed over knee angles of 100°–140°, where 180° is a straight leg (Figure 1). Two rFE, rFD, and SSC contractions were performed over this 40° range of motion at ~40% (set via metronome) and held isometrically at the end joint angle for 15 seconds (Figure 2).

With verbal encouragement provided by the researchers, 3 maximal voluntary isometric efforts (MVEs) were performed at 140° knee angle, wherein subjects would push up against an unmovable barbell as hard as possible for 5 seconds followed by a 3-minute rest. MVEs were deemed maximal when peak force did not differ by more than 5%, and subjects confirmed they provided a maximal effort. At the end of the testing protocol, subjects performed the 1RM testing again to assess fatigue.

Surface EMG was recorded on the right leg from the vastus lateralis (VL), rectus femoris (RF), vastus medialis (VM), biceps femoris (BF), semitendinosus (ST), lateral gastrocnemius (LG), medial gastrocnemius (MG), and gluteus maximus (GM). A bipolar configuration of silver-silver chloride (Ag/AgCl) electrodes were placed over the muscle of interest in accordance with the Heitz et al. (14), recommendations, with a common ground on the right leg’s patella. Before electrodes were placed, skin was prepared by shaving the area to remove hair and scrubbed vigorously with alcohol. Surface EMG was recorded (2 kHz), amplified (5k) and band-pass filtered (10Hz and 1 kHz) by AMT-8 Bortex (Biomedical Ltd., Calgary, Alberta, Canada).

Near infrared spectroscopy (PortaMon, Artinis Medical Systems, Netherlands) was used to measure (sampling rate: 10 kHz) VL oxygen consumption over the entirety of the testing protocol. This device has 3 optodes that are 30, 35, and 40 mm from the receiver with each optode transmitting 2 wavelengths (760 and 850 nm) (24). The NIRS device was placed on the muscle belly of the VL on the left leg that matched the EMG location of the right leg, secured with tape, covered with a black cloth, and further secured by an elastic sleeve. Changes in oxyhemoglobin (O₂Hb) and deoxyhemoglobin (HHb) were measured and the tissue saturation index percentage (TSI%) was calculated.

\[ TSI = \left[ O_2Hb/(O_2Hb + HHb) \right] \times 100 \]

An AMTI (Advanced Mechanical Technology, Inc., Watertown, MA) force plate (model OR6-5) with amplifier (model SGA6-3) was used to measure ground reaction force (GRF), sheer force, and moments. Ground reaction force were measured in 6 subjects to determine the 30% isotonic load with a 22 kg iso-inertial component (barbell weight). The load at 30% was chosen to ensure sufficient resistance, without excessive resistance during the “isometric hold” at the terminal knee angle to minimize fatigue or task failure.

\[ 1RM = \left( 100 \times \text{weight lifted} \right)/ (48.8 + [53.8 \times e - 0.075 \times \text{repetitions}] ) \]

Subjects performed knee angle position-matched bilateral squats across trials in a robotically resisted Smith machine (Quantum 1080-Syncro system, 1080 Motion, Inc., Lidingo, Sweden) which measured total work and force over-time in all trials (sampling rate: 333Hz). Subjects were positioned in the 1080-Syncro system so the barbell rested on the upper trapezius, feet were shoulder width apart, and heels placed in front of the zero line (zero line is aligned directly below the barbell).

Experimental Approach to the Problem

Subjects performed a voluntarily multi-joint movement (squat) in a robotically resisted smith machine to determine the effect of rFE on rFD during the isometric steady-state after a single SSC contraction at a relatively slow movement velocity (40°/s). Differences in EMG and NIRS were measured and compared across trials to a reference isometric contraction. Trials were pseudo-randomized so that any differences in EMG and NIRS observed were a result of rFE or rFD and not a result of fatigue, as changes in activation and oxygen consumption would have to overcome any fatigue to be observed.

Subjects

Twenty healthy males (Mean ± SD 24.9 ± 3.9 years, 177.6 ± 6.8 cm, 79.0 ± 11.3 kg) volunteered to participate, and data were collected within a single testing session. All subjects were recreationally active, although not systemically training, they were familiar with squat type exercise. Subjects provided informed, written consent before commencement of experimental procedures. This study was approved by the University of Guelph Research Ethics Board and conformed to the Declaration of Helsinki.

Procedures

A calculated 1-repetition maximum (1RM) squat procedure was performed. Using the formula of Wathan (41) and estimated 1RM to
verify that the force the robotically resisted Smith machine applied during the different conditions were matched (Figures 3 and 4).

**Protocol A: Residual Force Depression.** The rFD protocol consisted of 2 shortening contractions with the 30% load from a knee angle of 100° to 140° over 1 second and then held at 140° for 14 seconds (Figure 1A, B). “Shortening contractions” refers to the knee extension phase of the contraction. A metronome set to 60 Hz was used to set the speed of the shortening contraction. The contraction that best matched position and speed was used for further analysis. Subsequently, an isometric contraction was performed at 140° knee angle (Iso_{140}) and held for 15 seconds. Subjects began the contraction seated on a custom-built adjustable drop-seat and received visual feedback on height displacement via laser pointer that was mounted on the barbell which projected onto the wall in front of the subject. The order of these contractions was pseudo-randomized to rFD and then isometric, to ensure that activation increase was not a result of fatigue (28).

**Protocol B: Residual Force Enhancement.** The rFE protocol consisted of 2 active lengthening contractions (140° to 100°) with the 30% load that were preceded by an isometric contraction at 100° (Iso_{100}) (Figure 1C, D). First, an isometric contraction at 100° knee angle was performed and held for 15 seconds. Similar to protocol A, rFE contractions occurred over 1 second, held for 14 seconds at 100° knee angle, the contraction that best matched position and speed was used for further analysis. The adjustable drop-seat was set so the subjects could take the load off their legs and relax their legs before the contraction. Upon initiating the contraction, the seat would drop allowing the subject to take the load and lower themselves down to the knee angle of 100°. The
order of these contractions were pseudo-randomized to isometric and then rFE, to ensure that activation reduction was not a result of fatigue (28).

**Protocol C: Stretch-Shortening Cycle.** The SSC protocol consisted of a lengthening (protocol B) followed immediately by a shortening (protocol A) contraction that matched the previous protocols (Figure 1C through E) with the 30% load. Similar to the other protocols, the ISO140 contractions were completed before and after the 2 SSCs. Subjects performed a 1 second active lengthening followed immediately by a 1 second shortening over the 40˚ knee angle range of motion and held isometrically at 140˚ for 13 seconds.

**Statistical Analyses**

Force and EMG data were converted to a digital signal using a Power Lab (ADInstruments, Inc., Colorado Springs, CO). Force data were run through a calibration matrix to be converted into newtons. The average vertical force (Fz) was calculated over the same window as EMG (5–8 seconds). EMG data were band-passed filtered (10–1,000Hz) and analyzed with Labchart software (Labchart, Pro Modules 2014, version 8). EMGRMS was measured over a 3-second window at 5 seconds from the onset of contraction for all trials (Figures 3 and 4). Percent activation increase and activation reduction were calculated as followed:

\[
\text{Activation Increase} = \frac{(FD - ISO_{140})}{ISO_{140}} \times 100
\]

\[
\text{Activation Reduction} = \frac{(RFE - ISO_{100})}{ISO_{100}} \times 100
\]

Near infrared spectroscopy data were smoothed by a moving Gaussian (average) filter using the Oxysoft program (Artinis Medical Systems, NL) to reduce high-frequency noise. Vastus lateralis TSI% differences were calculated over the same window as force and EMG (5–8 seconds) (Figures 3 and 4). Two subject’s NIRS data were excluded because of instrumental errors (n = 18).

Statistical analysis of all data was completed using SigmaPlot (version 13.0, Systat Software, Inc., San Jose, CA). A Shapiro-Wilk test was performed to test for normal distribution of the data. Paired t tests were used to compare EMG across conditions.
(Iso100 and RFE condition, Iso140 and FD condition, Iso140 and SSC condition, and FD and SSC conditions). If a condition failed normality, a signed ranked paired \( t \)-test was used. A one-way repeated measures analysis of variance was used to analyze the VL TSI% difference of the 3 Iso140 contractions, and for comparing the VL TSI% difference of Iso140, FD condition, and SSC condition. A paired \( t \) test was used to compare VL TSI% difference of Iso100 and RFE condition. An alpha of \( p < 0.05 \) was selected. All descriptive data in text are reported as mean \( \pm SD \), and figures as mean \( \pm SEM \).

**Results**

The average GRF during the MVEs was 3,032 \( \pm 733 \) N. Ground reaction force for Iso140 contractions varied by a maximum of 1.0% of the average MVE force (average Iso140 = 1,397 \( \pm 283 \) N, shortening = 1,427 \( \pm 280 \) N, SSC = 1,402 \( \pm 266 \) N). Similarly, the average GFR between contractions at Iso100 varied by a maximum of 0.18% of the average MVE force (Iso100 = 1,418 \( \pm 286 \) N, stretch = 1,423 \( \pm 294 \) N). These findings demonstrate that force was well-matched during all contractions by the robotically resisted Smith machine. Subjects were successful in matching force across conditions as peak force during active lengthening and lengthening phase of SSC was not different (625 \( \pm 169 \) N & 611 \( \pm 167 \) N, respectively; \( p > 0.05 \)). Total work during shortening (FD) and shortening (SSC) did not differ (179 \( \pm 54 \) J & 184 \( \pm 49 \) J, respectively; \( p > 0.05 \)). All subjects were capable of reaching their 1RM force value at the end of the experimental protocol, indicating there was no effect of fatigue.

**Residual Force Enhancement**

During the rFE protocol, there was no difference in EMG between Iso100 and rFE in any muscle group (\( p > 0.05 \), Figure 5). Similarly, TSI% of the VL did not differ between Iso100 and the rFE condition (\( p > 0.05 \), Figure 7).

**Isometric 140**

Across the 3 Iso140 contractions, there was no significant difference in EMG for any muscle (\( p > 0.05 \)), in either the precontractions or postcontractions. Furthermore, there were no differences in the 3 Iso140 TSI% (\( p > 0.05 \)). As a result, the 3 Iso140 contractions were averaged (termed Iso140avg), and used for all further analysis. This was to account for potential differences and variability in activation during the squat task not detected in the analysis.

**Residual Force Depression**

During the rFD protocol, there was a significant activation increase of 15.1% in VM (\( p = 0.02 \)), 11.6% in VL (\( p = 0.03 \)), and 25.0% in GM (\( p = 0.03 \)) during the isometric steady state following shortening (rFD condition) compared with Iso140avg. There was also a significant activation reduction of 14.5% in BF (\( p = 0.03 \)) during the rFD condition compared with Iso140avg. There was no significant difference in activation for RF, ST, LG, and MG during the rFD condition compared with Iso140avg (\( p > 0.05 \); Figure 6).

**Stretch-Shortening Cycle and Iso140avg**

During the SSC protocol there was a significant activation increase of 15.6% in GM (\( p < 0.001 \)) during the isometric steady-state following SSC compared with Iso140avg. There was no significant difference in EMG for VM, VL, RF, BF, ST, LG, and MG during the SSC condition compared with Iso140avg (\( p > 0.05 \); Figure 6).

**Figure 5.** Group mean percent activation change from isometric 100˚ (Iso100) for the rFE condition, for vastus medialis, rectus femoris (RF), vastus lateralis, gluteus maximus (GM), biceps femoris, semitendinosus, lateral gastrocnemius., and medial gastrocnemius. There was no significant difference in muscle activation during the isometric steady-state following active stretch compared with Iso100 for any muscle measured.
Stretch-Shortening Cycle and Residual Force Depression

When comparing the isometric steady-states following SSC and shortening (rFD condition), “shortening” refers to the knee extension phase of the contraction, there was a significant activation increase of 16.4% in VM (p < 0.001) and 9.9% in VL (p < 0.005) during the rFD condition compared with SSC condition. There was no significant difference in activation between the rFD condition and SSC condition for RF, GM, BF, ST, LG, and MG (p > 0.05); Figure 6). Furthermore, there was no difference in VL TSI% difference between Iso140avg, rFD condition, and SSC (p = 0.07; Figure 7).

Discussion

We investigated the effects of rFE and rFD during an SSC on changes in EMG and NIRS. Our hypotheses were partially confirmed, such that there was significant activation increase for VM (~15%), VL (~11%), and GM (~25%) during the rFD-state compared with the reference isometric (Iso140avg), but no difference in EMG for the RF. After SSC, as compared with the reference isometric (Iso140avg), there was activation increase for the GM, but not for VM, RF, or VL. Furthermore, there was activation increase during the FD-state for VM (~16%), and VL (~10%) compared with the SSC, but not for RF and GM. Regarding muscle oxygen consumption, TSI% was not different for any condition. Therefore, it seems that despite not observing significant activation reduction during the rFE trials, the performance enhancing aspects of rFE attenuated the typical shortening-induced activation increase during an SSC.

We did not observe the typical activation reduction associated with active lengthening-induced rFE. However, on an individual basis, 4 subjects exhibited activation reduction in all of the knee and hip extensors, whereas 3 subjects exhibited no activation reduction for the knee and hip extensors (Figure 8). The other 13 subjects exhibited various activation reduction in 1–3 muscles (Figure 8—individual data). Activation reduction is driven by a net decrease in MU activity that affects both recruitment and rate coding of the MU pool (18). This is owing to the underlying muscular mechanisms causing a neuromechanical coupling of motor unit activation and enhanced force producing capacity. Although the basic mechanisms of rFE are typically attributed to noncontractile elements (i.e., titin), contractile contributions (e.g., decreased cross bridge detachment) cannot be discounted (14). Furthermore, cross bridge cycling is necessary for the engagement of both contractile and noncontractile elements involved in rFE (15). The complex nature of a squat (36), and holding a knee angle position rather than a typical force-matching task commonly used when investigating rFE and rFD (6,20,26,27,37) may have altered activation strategies.
(8), and masked activation reduction, or increased the number of nonresponders (3,38).

When investigating the role of rFE and rFD on SSCs during a complex voluntary movement such as a squat, it is convenient to assume all muscles involved in the task are actively lengthening or shortening during the SSC movement, which is not entirely correct (33). Therefore, some muscles are actively shortened, whereas others may have acted isometrically or lengthened, and based on the mechanisms of rFE/rFD would yield differences in activation (20,28,34,37). Thus, this may explain the high level of variability across subjects and muscles tested, resulting in a high number of nonresponders. Studies using a leg press experimental model would typically match for force (13,30). However, in the present study, during the squat, subjects were required to hold a knee angle constant making this a position-matching task. When comparing task type (position and force), there are distinctly different activation strategies used to perform the task, such that there is rapid recruitment of the motor unit pool for a position task compared with a force-matching task (2,35). Furthermore, when the contraction intensity is below the upper limit of the motor unit recruitment threshold, there is a decrease in the motor unit threshold during a position-matching task, resulting in a shorter time to task failure compared with a force-matching task. However, if the contraction occurs above the upper limit of motor unit recruitment threshold, there is often no difference in the task type for time to failure (25). The VL has been shown to have a maximal recruitment threshold of 95% of MVC (7). Therefore, in the present study which used a 30% load, rapid recruitment of the motor unit pool during the position matching task likely contributed to activation reduction not being observed. Further investigations of activation reduction and position-matching are needed to determine the full effects that task type has on activation reduction and the history-dependence of force.

Figure 8. Absolute root mean square (RMS) electromyography (EMG) for all 20 subjects during the isometric 100° (Iso100) and the isometric steady-state following stretch (rFE cond.) for vastus medialis, rectus femoris (RF), vastus lateralis, gluteus maximus (GM), biceps femoris, semitendinosus, lateral gastrocnemius, and medial gastrocnemius. rFE = residual force enhancement.
There were no differences in NIRS derived muscle oxygen consumption of the VL between the isometric steady state following stretch and reference isometric (Iso(100)) in the overall group. Furthermore, when comparing activation reduction and muscle oxygen consumption on an individual basis, there were no significant relationships in the overall group (r = 0.08), and no relationship in activation reduction responders (r = 0.05). Although it has been shown previously that individuals who demonstrated activation reduction in the MG (with occlusion) had a significant correlation (r = 0.69) between muscle oxygen consumption and activation reduction, there were no differences in the overall group (29). Our current findings align with Pater-noster et al. (29), such that there was no significant activation reduction in the VL during the rFD condition compared with the reference isometric resulting in no difference in muscle oxygen consumption of the VL.

We observed a 15–25% activation increase for the VM, VL, and GM during the rFD state compared with the reference isometric. Previous research investigating rFD of the knee extensors observed a 4% decrease in force during the isometric steady-state after a 40° of shortening compared with the reference isometric (23). However, in the present study, the RF did not demonstrate a significant activation increase (rFD-state), which is likely a result of the movement performed. The multijoint movement used in the present study may have prevented the RF from undergoing substantial shortening or stretch owing to its biarticular function. The RF has been characterized as performing an isometric contraction during a squat as it undergoes a change of length of less than 2% (33). This minimal change in length during the shortening phase of the squat (standing up from seated) would likely be insufficient to result in the elicitation of the rFD-state. Thereby, explaining why there is no significant activation increase for RF in the present study.

During the isometric steady state following an SSC, there was no significant change in EMG for the knee extensors (VM, RF, VL) compared with the reference isometric. However, there was a significant activation increase in VM and VL (10–16%) during the rFD condition compared with the SSC condition. Prior investigations of SSC with regard to rFD have shown that if the amount of stretch was more than that of shortening, rFD could be attenuated or eliminated (39). However, when the amount of stretch was equal to the amount of shortening during an SSC, the magnitude of rFD during the isometric steady-state was not different than the isometric steady-state after pure shortening (39). It was later shown with electrically stimulated thumb adductor pollicis that if shortening occurred with fast velocities and the time-delay between stretch and shortening was less than 0.5 seconds that rFD could be attenuated during the isometric steady state following a SSC when the amount of stretch and shortening were equal (10). Only recently has it been shown that rFD could be attenuated during the isometric steady-state following a SSC in a muscle used for locomotion (plantar flexors during electrical stimulation) (12). In the present study, using a position-matching task during a voluntary contraction, the effects of rFD on activation increase during an SSC was alleviated via the active lengthening phase (i.e., rFE), which is evidenced by no significant activation increase during the isometric steady-state following the SSC.

Muscles of the hip, knee, and ankle have various roles during a squat where activation may not be directly related to the movement being performed, but act as an antagonist and/or a stabilizer (33). The GM was found to have a significant activation increase during the rFD condition (25%) and SSC condition (15.6%) compared with the reference isometric. However, there was no significant difference in GM activation between rFD and SSC conditions. The GM performs multiple actions at the hip (extension, external rotation, and abduction) unlike the VM and VL whose only action is knee extension. Therefore, during a squat, the GM not only acts as an agonist for the movement but also as a stabilizer. The stabilization efforts of the GM may mask the effects of active lengthening during the SSC condition which results in a significant activation increase.

Using NIRS, we demonstrate that the VL TSI% was not significantly different during the rFD and SSC conditions compared with the reference isometric, and between the rFD and SSC conditions. Furthermore, on an individual basis, when comparing activation increase and VL oxygen consumption with rFD and SSC combined, there was no relationship (r = 0.09). However, this result is not surprising when considering the proposed mechanisms of rFD, which is believed to result from decreased cross-bridge formation during the isometric steady-state following shortening, which is associated with lower ATP usage (21). However, when force was matched (which would result in activation increase) during the FD state compared with the reference isometric, relative ATP usage would be similar (21). Because there is no increased need for ATP during the rFD state, there would be no increased need for oxygen consumption, which is in line with the present results. Previous research using NIRS to measure oxygen consumption during the rFE state occluded blood flow (29), which was not performed in the present study. This is a limitation of the present study, as without blood flow restriction, oxygen supply could change between the different conditions. It has been shown that intramuscular blood flow of the knee extensors decreases during an isometric contraction at 10% and is near zero by 50% MVC (40). It is believed that with the 30% load used during the present study, there would be minimal intramuscular blood flow which could affect TSI%. However, because TSI% difference was compared within individuals, such that the resistance load was constant, intramuscular blood flow should have remained the same between the different conditions. Further investigations of rFD with blood flow occlusion should be considered, that eliminate the possibility of a change in oxygen supply.

Extending the measurement of rFE and rFD from well-controlled single-joint movements to a whole-body squat exercise is not without experimental limitations, yet this approach adds considerable ecological validity to these history-dependent properties of muscle in the context of voluntary human movement. Owing to the study design, the NIRS and the EMG data were collected from separate legs, with the NIRS data collected from the VL of the knee extensors. Oxygen consumption values from the VL cannot explain results related to the whole leg, and thus, this should be interpreted cautiously. To gain a fuller appreciation of these SSC findings, the results should be extended to address potential sex-differences, training status, and natural adult aging (26).

In the present study, it was demonstrated that, compared with a reference isometric contraction, activation of the VM & VL was increased in the isometric steady-state following a shortening contraction. In contrast, this activation increase was attenuated during the isometric steady-state following an SSC. Increases in activation occur in the rFD state when force is matched without increases in oxygen consumption, as observed by no significant
change in TSI% difference. Residual force depression was attenuated during an SSC despite no change in oxygen consumption. The present study demonstrates how rFE and rFD interact during a multi-joint movement that is relatable to everyday life to optimize performance.

**Practical Applications**

As a result of a stretch-shortening cycle, stretch-induced rFE can attenuate shortening-induced force depression during a submaximal, multijoint, voluntary movement. This can also be reflected via electromyography as an activation reduction (less EMG for the same force). Force depression was attenuated during an SSC despite no change in oxygen consumption. This improvement in neuromuscular economy (less EMG per unit for force) that occurs as a result of an SSC would be observable in a variety of movements such as lifting and locomotion. Improvements would be most beneficial for endurance type tasks that undergo repetitive SSC at submaximal levels (e.g., marathon running), whereby the energetic cost of movement would be minimized, potentially increasing performance. It has been shown that the amount of force depression after an SSC is inversely related to the amount of rFE that occurs during stretch, where more enhancement results in less force depression. Furthermore, rFE has been shown to be modifiable through concentric and eccentric biased training (4). Therefore, training strategies could be implemented to further improvements in neuromuscular economy at submaximal contractions as well as increase force production during maximal contractions.

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