

Review article

The Contraction Modalities in a Stretch-Shortening Cycle in Animals and Single Joint Movements in Humans: A Systematic Review

Martin Groeber¹✉, Lena Reinhart^{1,2}, Philipp Kornfeind¹ and Arnold Baca¹

¹ Centre of Sport Science and University Sports, Department of Biomechanics, Kinesiology and Computer Science in Sport, University of Vienna, Vienna, Austria; ² Institute of Sport Science, Technical University of Munich, Munich, Germany

Abstract

A systematic literature search was conducted to review the force-enhancing mechanisms caused by a stretch-shortening cycle (SSC). The review aims to yield an overview of the contraction modalities influencing the SSC performance in animals and single joint movements in humans. The search was executed in common with the PRISMA statement. CINAHL, MEDLINE (via ProQuest), PubMed, ScienceDirect, Scopus and Web of Science databases were used for the systematic search from its inception until February 2019. A quality assessment was conducted with a modified Downs and Black checklist. Twenty-five studies were included. SSC effects, leading to increased force/work during a SSC and a reduced force depression (FD) compared to a pure shortening contraction, are existent on different levels of the muscle, from single fiber experiments to the level of in vivo muscle-tendon complex. Muscle performance is dependent on shortening velocity, shortening distance, stretch distance, the time (transition phase) between stretch and shortening and the active prephase duration. Concerning stretch velocity we found conflicting results. The findings from this systematic review indicate that the mechanisms in the early phase of shortening are associated with pre-activation effects, elastic recoil and stretch reflex. Furthermore, we speculate that residual force enhancement (RFE) is mainly responsible for an increased steady-state force compared to a pure shortening contraction.

Key words: Muscles, contraction, force enhancement, force depression.

Introduction

A stretch-shortening cycle (SSC) is a combination of an eccentric and a concentric muscle action. The lengthening of the muscle is immediately followed by a shortening contraction or may be shortly delayed by a brief transition phase (Komi and Gollhofer, 1997; Komi, 2000). Individually, the two muscle actions have been shown to be history dependent.

An active stretch evokes an enhanced steady-state isometric force compared to a purely isometric contraction at the corresponding muscle length. This increase is also known as the phenomenon of residual force enhancement (RFE). RFE has been observed at different muscle levels; in vitro in single muscle fibres (Edman, 1978), in situ (Abbott and Aubert, 1952; Morgan et al., 2000; Herzog et al., 2003; Bullimore et al., 2007) and in vivo in different muscle groups (Oskouei and Herzog, 2006; Pinniger and Cresswell, 2007; Seiberl et al., 2013). Furthermore, RFE has been observed with electrical stimulation of the muscle and

with voluntary contraction (Lee and Herzog, 2002; Hahn et al., 2010).

RFE increases with rising stretch amplitude (Edman et al., 1982; Sugi and Tsuchiya, 1988); it occurs at all muscle lengths (Rassier et al., 2003) but is independent of stretch velocity (Edman et al., 1982). Nowadays, the mechanisms contributing to RFE are still not completely understood but are associated with the passive element titin upon muscle activation (Herzog and Leonard, 2000; Joumaa et al., 2008; DuVall et al., 2013). The structural protein titin connects the myosin filament distally and actin filaments and the Z-line proximally. Titin is thought to act like a spring and is able to change its stiffness and force upon muscle (sarcomere) stretching (Herzog, 2014).

Contrary to RFE, an active shortening has shown to evoke a force depression (FD) compared to a purely isometric contraction at the corresponding muscle length. FD seems to be dependent on the shortening velocity and FD decreases with increasing shortening speed (Herzog and Leonard, 1997). In accordance with the force-velocity relationship of muscle contraction (Hill, 1938), an increase in shortening speed is associated with a reduction in work and a decrease in FD. Moreover, FD rises with increasing shortening magnitude (Maréchal and Plaghki, 1979; Herzog and Leonard, 1997) and is directly related to the force or work produced during shortening (Herzog et al., 2000).

In daily movements a purely concentric or eccentric muscle action almost never occurs. A combination of these muscle actions, a SSC, can be found in movement patterns like jumping or hopping. With regard to walking and running, a SSC can only be found in the whole muscle-tendon unit, while the muscle fascicles in the triceps surae or vastus lateralis seems to contract mainly isometrically (Bohm et al., 2018). The mechanisms contributing to muscle performance during a SSC remain a matter of debate. Besides the mechanisms contributing to an enhanced state of steady-state force after stretching and a depressed state after shortening, three other mechanisms have been shown to contribute to muscle performance during SSCs: Stretch reflexes, activation dynamics and storage and recoil of elastic energy (van Schenau et al., 1997).

SSC experiments should lead to a better understanding of this muscle action and could furthermore be applicable to training practice in the future. The parameters and mechanisms affecting muscle performance during a SSC are yet to be revealed.

To our knowledge, a systematic review of SSC experiments has not yet been undertaken. Therefore, we are striving to give a systematic overview of in vitro, in situ

and in vivo single joint movement SSC experiments. This review seeks to inform future studies about, which contraction modalities and parameters are necessary to consider in SSC experiments.

Methods

The methodology for the systematic review followed the PRISMA statement.

Literature search

The search for relevant literature was conducted from inception until February 2019. The databases CINAHL, MEDLINE (via ProQuest), ScienceDirect, Scopus and Web of Science were used for the systematic search. First, key words were determined to track the relevant literature (Table 1).

Table 1. Summary of keywords.

stretch-shortening cycle	depression	preactivation
torque	muscle	stretch reflex
force	enhancement	elastic energy
contraction	performance	mechanism

Two authors of this review conducted the search independently of each other. Always two or more keywords were used in different combinations. The Boolean operator “OR” was used within search categories, whilst “AND” was used between search categories. A column in Table 1 represents a search category. Next, the references were imported to the reference management system Citavi 5 and

duplicates were instantly deleted.

Selection criteria

The included studies were identified by title, abstract and full text. The included studies: (1) were experimental (i.e. randomized controlled trials) or quasi-experimental in design (2) measured either mechanical work during the shortening phase, force/torque during the SSC or the steady-state force/torque after a SSC (3) tested on healthy muscle tendon complex units (4) tested on single joint movements for the measurements on humans (i.e. excluding jumps or hops) (5) had the full text journal article available in English (excluding reviews or conference abstracts).

We decided to include only animal studies and single joint movement on humans to elucidate the mechanisms underlying SSCs. Animal experiments can be well controlled and basic muscle properties can be observed. For example, when comparing a countermovement jump (SSC) and squat jump (non-SSC), kinematic variables such as angular velocity and range of motion should be controlled. Activation level is another aspect that can hardly be controlled. Considering these doubts, it is challenging to examine the precise mechanism underlying the SSC in dynamic multi-joint movements.

The title, abstract and full text were scanned by two authors separately and the articles were removed, if the study did not fulfill the previously stated selection criteria. First the title and abstract were scanned for eligibility. A detailed review of the whole text was conducted for the remaining studies (Figure 1), with selection criteria reapplied for the full text and cross-referenced at the end.

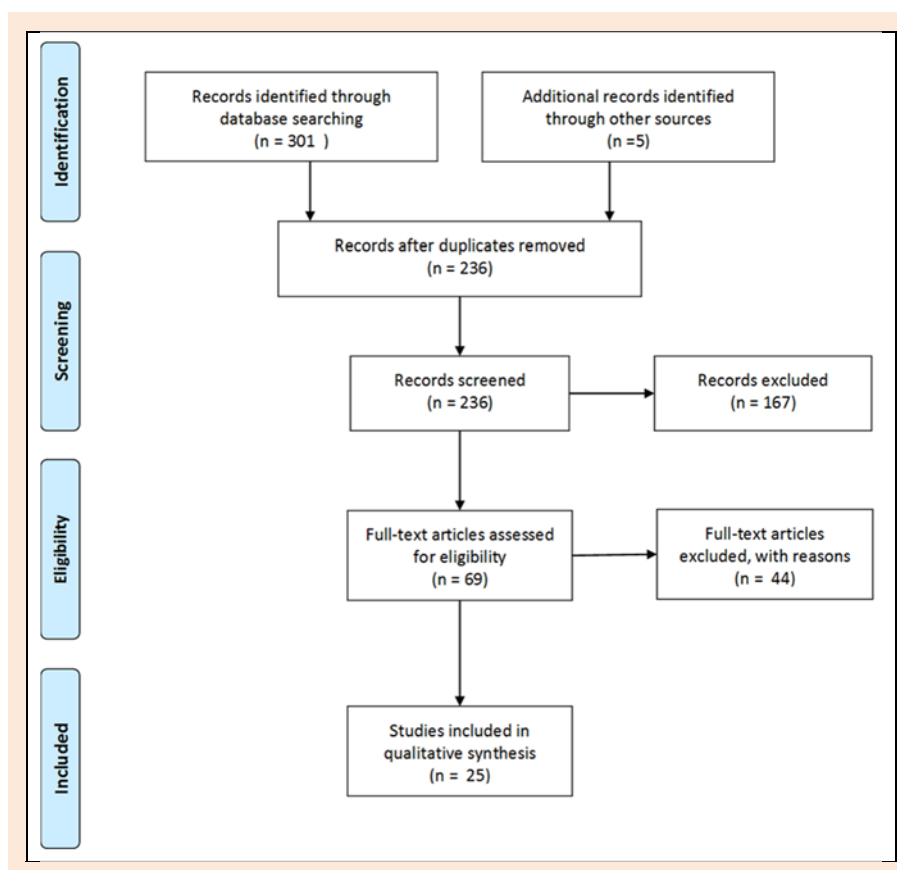


Figure 1. PRISMA flow chart.

Table 2. Modified downs and black checklist.

	Yes	No
1. Is the hypothesis/aim/objective of the study clearly described?	1	0
2. Are the main outcomes to be measured clearly described in the Introduction or Methods section? <i>If the main outcomes are first mentioned in the Result section the question should be answered no.</i>	1	0
3. Are the characteristics of the subjects/animal/specimen included in the study clearly described? <i>Inclusion and/or exclusion criteria should be given.</i>	1	0
4. Are the main findings of the study clearly described? <i>Simple outcome data should be reported for all major findings so that the reader can check the major analyses and conclusions. (This question does not cover statistical tests which are considered below.)</i>	1	0
5. Does the study provide estimates of the random variability in the data for the main outcome? <i>In non-normally distributed data the inter-quartile range of results should be reported. In normally distributed data the standard error, standard deviation or confidence intervals should be reported. If the distribution of the data is not described, it must be assumed that the estimates used were appropriate and the question should be answered yes.</i>	1	0
6. Have actual probability values been reported (e.g. 0.035 rather than <0.05) for the main outcomes except where the probability value is less than 0.001?	1	0
7. If any of the results of the study were based on “data dredging”, was this made clear? <i>Any analyses that had not been planned at the outset of the study should be clearly indicated. If no retrospective unplanned subgroup analyses were reported, then answer yes.</i>	1	0
8. Were the statistical tests used to assess the main outcomes appropriate? <i>The statistical techniques used must be appropriate to the data. For example nonparametric methods should be used for small sample sizes. Where little statistical analysis has been undertaken but where there is no evidence of bias, the question should be answered yes. If the distribution of the data (normal or not) is not described it must be assumed that the estimates used were appropriate and the question should be answered yes.</i>	1	0
9. Were the main outcome measures used accurate (valid and reliable)? <i>For studies where the outcome measures are clearly described, the question should be answered yes. For studies which refer to other work or that demonstrates the outcome measures are accurate, the question should be answered as yes.</i>	1	0
10. Were the control trials from the same population group or were the control trials from other population group? <i>If the reference conditions is from the same subjects/animal/specimen, the question should be answered yes.</i>	1	0
11. Were study subjects measured over the same time period? <i>If the rest time between the single conditions is the same, the question should be answered yes.</i>	1	0
12. Were the trials randomized? <i>If not reported, the question should be answered no.</i>	1	0
13. Did the study have sufficient power to detect an important effect where the probability value for a difference being due to chance is less than 5%? <i>If the necessary sample size was calculated before, the question should be answered yes.</i>	1	0

Quality assessment of the included studies

For a quality assessment of the included studies, the Downs and Black checklist (Downs and Black, 1998) was used. The checklist was modified in a way so that some of the 27 items were not scored (Table 2). Modifications of the original Downs and Black checklist were made due to the fact that some of the items were not convenient for experimental studies. The score for every item on the Downs and Black checklist was either 0 if the criterion was inapplicable or 1 point if the appraised study met the criteria. The Downs and Black checklist was used even though we are aware of this checklist's limitations for assessing experimental studies (Jarde Alexander, Losilla Josep M., and Vives Jaume, 2012). The decision was made to use a quality assessment checklist to provide a relative comparison of the studies. Another review dealing with RFE used the original Downs and Black checklist noting its limitations and yielding proportionally moderate scores (Chapman et al., 2018).

The quality assessment was again made by two authors separately. The interrater variability was calculated by Cohen's Kappa statistics. When the two authors rated the study differently, every single assessment was reviewed. The findings illustrated in the results are the reviewed outcome.

Results

Search result

Once the search of all relevant articles was finished, the first step was to remove duplicates. The initial search yielded 301 studies overall. The duplicates were removed, which left 236 studies for screening. 167 studies were excluded after screening the title and abstract. The full-text of the 69 remaining articles were assessed for eligibility. Five additional studies were identified by reference list, hand checking and citation tracking. After 44 full-text articles were excluded, a total number of 25 studies were included in the review for a qualitative synthesis (Figure 1).

Quality assessment

The quality assessment of the included studies is shown in Table 3 and Table 4. An Interrater variability test of the animal studies revealed a Kappa value of 0.657; the studies with-single joint movements in humans, a Kappa value of 0.693. The results suggest a substantial agreement of both raters (McHugh, 2012).

None of the included publications reached the highest score of 13. The studies ranged overall from a score of 5 to 12 out of a possible score of 13 (Table 3 and Table 4).

Table 3. Animal studies: Itemized scoring of study quality using a modified Downs and Black checklist

First author, year	1	2	3	4	5	6	7	8	9	10	11	12	13	Total	Quality
Bullimore, 2008	1	1	0	1	1	1	1	0	1	1	1	0	0	9	9/13
Cavagna, 1968	1	1	1	1	0	0	1	0	1	1	1	0	0	8	8/13
Cavagna, 1974	1	1	1	1	1	0	1	0	1	1	1	0	0	9	9/13
Cavagna, 1981	1	1	1	1	1	0	1	0	1	1	1	0	0	9	9/13
Cavagna, 1994	1	0	1	1	1	0	1	0	0	1	1	0	0	7	7/13
Ettema, 1992	1	1	1	1	1	0	1	1	1	1	1	0	0	10	10/13
Ettema, 1990	1	1	1	1	1	0	1	1	1	1	1	0	0	10	10/13
Ettema, 1990	1	1	1	1	1	0	1	1	1	1	1	0	0	10	10/13
Fukutani, 2017	1	1	1	1	0	1	1	1	1	1	1	1	0	11	11/13
Fukutani, 2018	1	1	1	1	1	1	1	1	1	1	1	0	0	11	11/13
Herzog, 2000	1	1	1	1	1	0	1	1	1	1	1	0	0	10	10/13
Lee, 2001	1	1	1	1	1	0	1	1	1	1	1	0	0	9	10/13
Sugi (1988)	0	1	0	0	0	0	1	0	1	1	1	0	0	5	5/13
Takarada (1997)	1	1	0	1	0	0	1	1	1	1	1	0	0	8	8/13

Table 4. Human studies: Itemized scoring of study quality using a modified Downs and Black checklist

First author, year	1	2	3	4	5	6	7	8	9	10	11	12	13	Total	Quality
Blanpied, 1995	1	1	1	1	1	0	1	1	1	1	1	0	0	10	10/13
Fortuna, 2017	1	1	1	1	1	0	1	1	1	1	1	1	0	11	11/13
Fortuna, 2018	1	1	1	1	1	1	1	1	1	1	1	1	0	11	12/13
Fukutani, 2015a	1	1	0	1	1	1	1	1	1	1	1	0	0	10	10/13
Fukutani, 2015b	0	1	0	0	0	1	1	1	0	1	1	1	0	7	7/13
Fukutani, 2016	1	1	0	1	0	1	1	1	1	1	1	0	0	9	9/13
Fukutani, 2017	1	1	0	1	1	1	1	1	1	1	1	0	0	10	10/13
Hahn, 2018	1	1	1	1	1	1	1	1	1	1	1	1	0	12	12/13
Seiberl, 2015	1	1	1	1	1	1	1	1	1	1	1	1	0	12	12/13
Svantesson, 1994	1	0	1	1	0	0	1	0	0	1	1	0	0	6	6/13

Description of studies

With the systematic search we found 25 studies, 14 of them investigating SSC effects on animal muscles and the other 11 on single joint movements in humans. The results are divided in two parts. The first section discusses the results of animal studies and the second part the studies on the human muscular system. We especially revisited the mechanical work during the shortening phase, the force/torque during the shortening phase and the steady-state force/torque after the movement.

SSC effects in animal muscles: 14 of the included studies investigated SSC effects in animal muscle. Seven of them tested the frog/toad muscles, three those of rats, two of cats and two of rabbits. Six of the included studies tested on isolated single fibres with a total amount of 135 fibres (Sugi and Tsuchiya, 1988; Cavagna et al., 1994; Takarada et al., 1997; Bullimore et al., 2008; Fukutani et al., 2017b; Fukutani and Herzog, 2018) (two of the included studies did not mention how many fibres they analyzed). The other eight articles did research on 79 muscles (Cavagna et al., 1968; Cavagna and Citterio, 1974; Cavagna et al., 1981; Ettema et al., 1990a; Ettema et al., 1990b; Ettema et al., 1992; Herzog and Leonard, 2000; Lee et al., 2001). The parameters of the included animal studies can be found in Table 5.

Mechanical work

Six studies examined the mechanical work (Table 6) produced during the shortening phase (Cavagna et al., 1968; Cavagna et al., 1981; Ettema et al., 1990b; Ettema et al., 1990a; Cavagna et al., 1994; Takarada et al., 1997; Fukutani et al., 2017a). All of the studies found a significant

increase in the SSC condition compared to a pure shortening contraction.

Force depression/Residual force enhancement: Six of the included articles investigated SSC effects in the post-concentric phase and compared the torque/force values to the isometric reference contraction at the same muscle length or the corresponding pure shortening contraction (Table 7). Two studies reported a statistically lower steady-state force after the movement (Sugi and Tsuchiya, 1988; Lee et al., 2001) whereas two other studies found a small increase compared to the isometric reference contraction (Bullimore et al., 2008; Fukutani and Herzog, 2018). Moreover, two papers found higher force values compared to pure concentric contraction (Ettema et al., 1992; Bullimore et al., 2008), two did not reveal any statistical difference (Herzog et al., 2000; Lee et al., 2001).

One article investigated neither the mechanical work during shortening, nor the steady-state forces after the movement. Cavagna and Citterio (1974) showed, that force after stretch is 50-100% greater in the SSC condition compared to the isometric reference contraction.

SSC effects in human muscles: 11 studies did research on humans, including 223 participants overall ($n = 136$ male and $n = 87$ female subjects). Ten of the included studies investigated healthy young adults (range 17-35 years), whereas only one study considered elderly people (range 70-86 years) (Svantesson and Grimby, 1995). Seven studies examined the triceps surae (Svantesson et al., 1994; Blanpied et al., 1995; Svantesson and Grimby, 1995; Fukutani et al., 2015b; 2015a; Fukutani et al., 2017b; Hahn and Riedel, 2018), three studies the adductor pollicis (Seiberl et al., 2015; Fortuna et al., 2017; Fortuna et al.,

Table 5. Parameters of the included animal studies

First author, Year	n	Animal	Muscle group	Intensity of electrical stimulation	Velocity	Range of Motion Stretch/shortening	Muscle/fibre length at beginning	Notice
Bullimore, 2008	6	Frog (<i>Xenopus laevis</i>)	Lumbrical muscle, single fibres	Slightly less than maximal	Stretch: 0.1 fibre length/s Shortening: maximal possible velocity	0.05 L0 / 0,25,50,75,100,200, 300,400 % of stretch distance	1.15 L0	Delay of 600 ms between stretch and shortening
Cavagna, 1968	5	Frog/Toad (<i>Rana esculenta</i> and <i>Bufo bufo</i>)	Sartorius and gastrocnemius	Slightly less than maximal	3-60 mm/s	3 mm / 3 mm	?	Also on man's forearm flexor
Cavagna, 1974	12	Frog/Toad (<i>Rana esculenta</i> and <i>Bufo bufo</i>)	Gastrocnemius, sartorius and semitendinosus	Supramaximal stimulation	Stretch:3-4mm/s shortening: 190,170 mm/s	5 mm / 5 mm	-2.5mm L0	
Cavagna, 1981	21	Frog (<i>Rana esculanta</i>)	Sartorius	Supramaximal stimulation	Stretch: 1.1 or 22.9mm/s Shortening: 180, 210 or 285mm/s	2 mm / 2 mm	L0	
Cavagna, 1994	37	Frog (<i>Rana temporaria</i>)	Carput laterale and tibialis anterior, single fibres	Supramaximal stimulation	Between 0.5 – 8.6 % of sarcomere strain	0.03 -1.8 sarcomer length/s / isotonic release	?	
Ettema, 1990a	5	Rat (Wistar)	Gastrocnemius medialis	Supramaximal stimulation	Stretch: 5, 10 or 20 mm/s Shortening: 40 mm/s	1.33, 2.5 or 5 mm / 6 mm	L0-1 mm, L0+1.5 mm or L0+2.75 mm	
Ettema, 1990b	5	Rat (Wistar)	Gastrocnemius medialis	Supramaximal stimulation	Stretch: 20mm/s Shortening: ?	4 mm / 4 mm	L0	
Ettema, 1992	7	Rat (Wistar)	Gastrocnemius medialis	Supramaximal stimulation	Stretch:20 mm/s Shortening: 10, 20, 30, 40 or 50 mm/s	5 mm / 5 mm	-2mm L0	
Fukutani, 2017	49	Rabbit (New Zealand white rabbit)	Soleus, Single fibres	Maximal	Stretch: 0.17, 0.3 or 1.2 μ m/s Shortening: 0.3 μ m/s	6 μ m / 6 μ m	2.4 μ m	
Fukutani, 2018	43	Rabbit (New Zealand white rabbit)	Soleus, single fibres	?	Stretch: 0.15 μ m/s Shortening: 48 or 600 μ m/s	3 μ m / 0.024 μ m or 3 μ m	2.724 μ m or 3 μ m	
Herzog, 2000	8	Cat	Soleus	Supramaximal stimulation	Stretch: 4 or 256 mm/s Shortening: 4 mm/s	4 mm / 4 mm	L0	
Lee, 2001	6	Cat	Soleus	Supramaximal stimulation	Stretch: 4, 16 or 64 mm/s Shortening: 4 mm/s	2,4,6 or 8 mm / 4 mm	L0+2 mm, L0, L0-2 mm, L0-4 mm	
Sugi, 1988	?	Frog (<i>Rana japonica</i>)	Tibialis anterior, single fibres	Supramaximal stimulation	Stretch: 0.02 -0.2 of L0/s	5-9% of L0 / 4- 12% of L0	L0	
Takarada, 1997	?	Frog (<i>Rana japonica</i>)	Tibialis anterior, single fibres	Supramaximal stimulation	Stretch: 0.08 -1,0 L0/s Shortening: 1.0L0/s	0.08 L0 / 0.02 L0	?	Also on human elbow flexion

LO: Muscle length in resting tension

2018), and one study the quadriceps femoris (Fukutani et al., 2016). Three of the articles found their results under voluntary muscle contraction, whereas eight studies used electrical stimulation. The electrical stimulation was in the range of 25-60% of MVC (maximal voluntary contraction). All the parameters can be found in Table 8.

Mechanical work: Four of the studies compared the mechanical work during the SSC with the mechanical work of a pure shortening contraction (Seiberl et al., 2015; Fortuna et al., 2017; Fortuna et al., 2018; Hahn and Riedel,

2018). All of the studies found a significant increase of work during shortening in SSCs compared to pure concentric contractions (Table 9). Overall an increase within the range of 9-46% was found in SSC conditions.

Force depression/Residual force enhancement: Four studies investigated force depression in the steady-state after movement (Table 10). Three of the included studies reported a FD for the SSC condition, but less FD compared to the pure shortening contraction (Fortuna et al., 2017; Fortuna et al., 2018; Hahn and Riedel, 2018). Only

one study, dependent on the shortening amplitude, partly reported an increase in the steady-state force compared to the isometric reference condition (Seiberl et al., 2015).

Force/torque during the shortening phase: Seven studies examined the force/torque during the shortening phase (Svantesson et al., 1994; Blanpied et al., 1995; Svantesson and Grimby, 1995; Fukutani et al., 2015b;

2015a; Fukutani et al., 2016; 2017b). They all found a statistical increase for the SSC condition compared to pure shortening contractions. Two of them additionally either reported that the enhancement is diminished at the end of the shortening phase or is quite low compared to the beginning of the shortening (Fukutani et al., 2015b; Fukutani et al., 2016) (Table 11).

Table 6. Mechanical work (animal studies).

First author, year	Mechanical work (SSC condition/pure shortening condition)	Contraction modalities (Conclusion of the article)
Cavagna, 1968	1.3 -1.8 times higher	Dependent on the speed of stretch/shortening and the muscle length
Cavagna, 1981	1.5 -2.3 times higher	Dependent on the speed of stretch
Cavagna, 1994	Significantly higher	Mechanical work increases with stretch amplitude
Ettema, 1990a	Significantly higher	Increase is dependent on active pre-phase duration
Ettema, 1990b	Significantly higher	Increase is dependent on active pre-phase duration
Fukutani, 2017	Significantly higher (Cohen's $d=0.35$)	Is dependent on the time (transitions phase) between stretch and shortening
Takarada, 1997	1.1 -1.5 times higher	In dependent on the peak force developed during stretch

Table 7. Steady-state force after SSC (animal studies).

First author, year	Steady-state force after movement (SSC condition/pure shortening condition; SSC condition/isometric reference condition)	Contraction modalities (Conclusion of the article)
Bullimore, 2008	7.6% \pm 2.3% higher compared to pure shortening 1.4 \pm 1.2% higher compared to isometric reference contraction	Dependent on shortening distance
Ettema, 1992	2% -16% higher compared to pure shortening contraction	Dependent on shortening velocity
Fukutani, 2018	3.5% - 7.1% higher compared to isometric reference contraction	Dependent on shortening distance
Herzog, 2000	No increase compared to pure shortening	Only depressed state compared to isometric reference contraction
Lee, 2001	4-5% lower compared to isometric reference contraction	Independent of stretch speed
Sugi, 1988	Lower compared to isometric reference contraction	Dependent on shortening velocity

Table 8. Parameters of the included human studies.

First author, Year	n	Gender		Muscle group	Intensity (% of MVC)	Speed ($^{\circ}$ /s) Stretch/shortening	Range of Motion ($^{\circ}$) Stretch/shortening	Joint angle at beginning ($^{\circ}$)
		M	F					
Blanpied, 1995	22	0	22	Triceps surae	60 (VC)	50/180, 100/180, 150/180	30/30	10 PF
Fortuna, 2017	16	8	8	Adductor pollicis	50-60 (ES)	30/15, 30/20, 30/30, 30/60	30/30	0
Fortuna, 2018	12	8	4	Adductor pollicis	50-60 (ES)	15/60, 60/60, 120/60	30/30	0
Fukutani, 2015a	12	12	0	Triceps surae	25 (ES)	60/90	30/30	15 PF
Fukutani, 2015b	12	12	0	Triceps surae	25 (ES)	60/30, 60/120	30/30	15 PF
Fukutani, 2016	12	12	0	Quadriceps femoris	25 (ES)	18/90	60/60	80
Fukutani, 2017	12	12	0	Triceps surae	25 (ES)	45/45	30/30	15 PF
Hahn, 2018	14	10	4	Triceps surae	32,9 (ES)	120/120	15/15	5 PF
Seiberl, 2015	14	14	0	Adductor pollicis	50-60 (ES)	103, 152, 170	30/10, 30/20, 30/30	0
Svantesson, 1994	20	0	20	Triceps surae	100 (VC)	120/120, 240/240	47/47	35 PF
Svantesson, 1995	77	48	29	Triceps surae	100 (VC)	120/120, 240/240	40/40	30 PF

ES: Electrical stimulation, VC: Voluntary contraction, PF: Plantar flexion

Table 9. Mechanical work (human studies).

First author, year	Mechanical work (SSC condition/pure shortening condition)	Contraction modalities (Conclusion of the article)
Fortuna, 2017	9% -26% higher compared to pure shortening contraction	Dependent on the shortening velocity and the delay between the stretch and the shortening
Fortuna, 2018	33% -46% higher compared to pure shortening contraction	Independent of stretch velocity
Hahn, 2018	11,6% higher compared to pure shortening contraction	
Seiberl, 2015	36%-39% higher compared to pure shortening contraction	Mechanical work always lower at corresponding pure shortening contraction compared to SSC

Table 10. Steady-state force after SSC (human studies).

First author, year	Steady-state force after movement (SSC condition/pure shortening condition; SSC condition/isometric reference condition)	Contraction modalities (Conclusion of the article)
Fortuna, 2017	13% -21% lower compared to isometric reference contraction Partly higher compared to pure shortening contraction	Dependent on the shortening velocity and the delay between the stretch and the shortening
Fortuna, 2018	17% -19% lower compared to isometric reference contraction Higher compared to pure shortening contraction	Independent of stretch velocity/peak force
Hahn, 2018	8.6% lower compared to isometric reference contraction. Higher compared to pure shortening contraction	RFE related mechanisms contribute to increased performance following SSCs
Seiberl, 2015	4.5% lower - 10.8% higher compared to isometric reference contraction	Dependent on shortening amplitude

Table 11. Force/torque during shortening phase.

First author, year	Force/torque during shortening phase in a SSC	Contraction modalities (Conclusion of the article)
Blanpied, 1995	The average concentric force during shortening is higher for 50°/s stretch compared to 150°/s stretch	Dependent on stretch velocity
Fukutani, 2015a	After 1/4 of shortening: 329%, 1/2 of shortening 159% and 3/4 of shortening 125% higher compared to pure shortening contraction.	
Fukutani, 2015b	Joint torque is increased at any time during the shortening phase for the angular velocity of 150°/s compared to 30°/s.	Dependent on angular velocity
Fukutani, 2016	Joint torque is only increased in the early phase of the concentric contraction in the SSC condition compared to a pure shortening condition.	Pre-activation plays an important role in torque enhancement.
Fukutani; 2017	Joint torque is increased at any time during the shortening phase compared to pure shortening contraction. Compared to a SSC with a delay between stretch and shortening, torque is only increased in the early phase of shortening.	Elastic energy plays an important role in torque enhancement.
Svantesson, 2014	75% -166% higher compared to pure shortening contraction (measurement of torque near to the middle of the shortening phase)	Dependent on angular velocity
Svantesson, 2015	30% -170% higher compared to pure shortening contraction (measurement of torque near to the middle of the shortening phase)	Dependent on angular velocity and sex, no influence of age

Discussion

This systematic review reveals supporting evidence of performance enhancement due to a SSC. This is the first systematic review establishing a connection of the findings from single fiber experiments with the level of in vivo muscle-tendon-complex. The review included both studies on animals testing on single fibres and research on the whole muscle in animals and in humans. The quality assessment was made by two authors independent of each other, but there remains a risk of being partly subjective. McHugh (2012) defined a value for Kappa of between 0.6-0.79 as being moderate level of agreement. The Kappa values of 0.657 and 0.693 indicate adequate agreement for both raters, but there was still disagreement among the raters. This is why every single assessment was reviewed, in cases where the two authors rated an item differently. The basis for exclusion was not the quality assessment. A better interpretation and classification of the results of this systematic review should be helpful. With regard to the scoring of the studies using the Downs and Black checklist, some studies did not satisfy specific criteria because information was not included within the publication. If a study did not explicitly state a certain requested methodology for the item, the item was scored as not satisfying according to the Downs and Black scoring criterion. It is conspicuous that the quality assessment revealed an especially lower score for older studies. The rating criteria that were most frequently not fulfilled in the publications we reviewed were those of randomization and sufficient power. Moreover, the review only focuses on single-joint movements in humans, despite the fact that in most everyday movement patterns we have more complex multi-muscle/multi-joint actions. For the more complex muscle actions further neurophysiological mechanisms can contribute to the SSC like motor coordination and therefore we excluded these articles (Bobbert and Casius, 2005).

A comparison has been made between concentric muscle action and SSCs. The pure concentric muscle action, in comparison to the SSCs, was not preceded by a stretch. The concentric muscle actions are preceded by an isometric contraction. When compared to isometric reference contractions at joint level (without joint rotation),

muscle fascicles can still shorten (Raiteri and Hahn, 2019). Under voluntary contraction, the isometric reference contractions are likely also to be subject to a small FD.

All of the included studies investigating mechanical work during the SSC found an increase in SSCs compared to pure shortening. A comparison of the results should be made with caution, since different studies used different modalities. Some of the studies did not report the extent of increase. Sometimes it was just pointed out, that mechanical work was significantly higher during the SSC condition. Beside this limitation, however, the results indicate that SSC effects on mechanical work can be transferred from single fibres to in vivo experiments.

It was observed that the increase in mechanical work (in the range of 1.1-1.8 times higher) in a SSC is dependent on the shortening amplitude, the shortening velocity, the stretch amplitude, the active pre-phase duration and the time (transition phase) between stretch and shortening. Ettema et al (1990a) reported that the amount of work produced during the shortening is dependent on the active pre-phase duration. One explanation could be a decrease in the elastic energy release after the extended pre-phase duration. For further studies that also reveal the need to match the pre-phase duration when comparing SSC trials with shortening contractions. The elastic energy might get lost after a certain time. Both Takarada et al. (1997) for single fibres experiments and Fortuna et al. (2017) at the adductor pollicis found that the work was reduced in the shortening phase, when there was a delay between the stretch and the shortening. This additionally implies that the influence of elastic energy is lost after a specific amount of time. Moreover, this could also indicate that the elastic energy stored after the stretch phase cannot be the only mechanism contributing to an enhanced performance in the SSC, since there is still an increase in work compared to pure shortening contraction in SSC with a longer transition between stretch and shortening. Conflicting results were found when considering the aspect of stretch velocity. In animal studies it was reported that stretch speed influences the peak forces after the stretch and also the mechanical work produced during the shortening. Fortuna et al. (2017) also found an increase in peak force values for higher stretch velocities, but in contrast to previous studies they did not

find a statistical difference ($p < 0.05$) for the mechanical work during SSCs with different stretch velocities. Interestingly, they also did not find a significant relationship between the steady state isometric force following SSCs and the work performed during shortening, as it is well accepted for pure shortening contractions (Herzog and Leonard, 2000; Kosterina et al., 2009). That could mean that the contractile conditions in a SSC influences the shortening in a way that the previously observed characteristics of pure shortening contractions do not apply to SSC experiments.

Considering the mechanical work done during shortening at in vivo experiments in humans, it is conspicuous that Hahn and Riedel (2018) found a lower increase of work done during the SSC condition compared to the pure shortening conditions. One possible explanation could be the lower intensity (32.9 % of MVC) used by Hahn and Riedel (2018) compared to other studies (50 -60 % of MVC) (Seiberl et al., 2015; Fortuna et al., 2017; Fortuna et al., 2018). The influence of the contraction intensity (level of activation) should be further examined in future studies.

All of the studies found an increase in torque/force during the shortening phase of the SSC compared to pure shortening. The results were found in different muscle groups and under both voluntary contraction and electrical stimulation. The increase seems to be dependent on the angular velocity and the pre-activation.

It was reported that enhancement is higher in the early phase of the shortening. This phenomenon is either explained by the storage and recoil of elastic energy (Fukutani et al., 2017b) since the elastic energy stored in the attached crossbridges would have dissipated over time, or by pre-activation, when there is no isometric pre-activation preceded by the shortening contraction (Fukutani et al., 2016). As previously assumed, that could mean this mechanism does not contribute to an enhanced steady-state isometric force or torque after the SSC. Regarding the force/torque during the shortening phase, two studies revealed a score of 6 out of 13 in the quality assessment (Svantesson et al., 1994; Svantesson and Grimby, 1995). These findings do not stand in contrast to the other studies with regard to their conclusion, that the force/torque during the shortening in a SSC is dependent on the angular velocity. But they additionally reported that the force during the shortening phase in the SSC is dependent on sex, however no influence of age could be found. Therefore, these results should be taken with caution and comparative studies should be made to verify their results regarding sex and age.

Four of the six animal studies, which investigated the steady-state isometric force, found FD after the SSC. Two studies reported a RFE of $7.6 \pm 2.3\%$ ($p = 0.0004$) and $3.5 \pm 2.4\%$ ($p < 0.001$) for a shortening distance equal to the stretch distance (Bullimore et al., 2008; Fukutani and Herzog, 2018). Conflicting results were found, comparing the FD in a SSC with a pure concentric muscle action. Two studies reported a reduced force depression compared to pure shortening, indicating that the stretch mechanism counteracts FD in some way (Ettema et al., 1992; Bullimore et al., 2008). Two other animal studies did not find a significant difference between pure shortening contraction and SSC (Herzog and Leonard, 2000; Lee et al.,

2001).

Herzog and Leonard (2000) and Lee et al. (2001) reported that the effects of RFE are abolished during the concentric phase of the SSC resulting in the same amount of FD as in pure shortening contraction. On the other hand, Seiberl et al. (2015) and Fortuna et al. (2017) observed a contribution of RFE counteracting FD produced during the concentric phase. The quality assessment does also not give a hint which results to trust more, since all of these four mentioned studies reached at least 10 out of 13 points in the quality assessment. The conflicting results may be explained in a time-dependent manner, since Fortuna et al. (2017) reported that FD is not reduced when time between the end of stretching and the end of shortening is long (about 1.5 s or more). This implies that the parameters that contribute to an increased shortening time between the end of stretch and the end of shortening have an effect on the amount of RFE/FD. But this still cannot explain the conflicting results for the studies where the shortening was conducted immediately after the end of stretch. Shortening speed as well as the shortening distance are however also factors influencing the time between the end of stretch and the end of shortening. This would also be in accordance with pure shortening experiments, where an increasing shortening magnitude is associated with increased FD and increased shortening speed with a decreased FD. These results were also shown in SSC experiments in animals (Bullimore et al., 2008; Fukutani and Herzog, 2018) and in humans (Seiberl et al., 2015), where the stretch magnitude remained constant and the shortening magnitude was changed. This also means that the isometric steady-state force after the SSC is highest after great stretch distances (increasing RFE) and small shortening distances (decreasing FD). Another factor influencing RFE and FD is the force-length relationship. FD and RFE are present in all areas of the relationship (Pun et al., 2010), but magnitude of RFE/FD was reported to be greatest on the descending limb of muscle force length curve (Chapman et al., 2018).

Stress-induced inhibition of newly built crossbridge attachments is the primary mechanism suggested for the occurrence of FD (Maréchal and Plaghki, 1979; Lee and Herzog, 2009). The stress-induced inhibition of attached crossbridges is further associated with the work performed during the shortening; the increase of work done during shortening causes a higher FD (Herzog et al., 2000). However, since none of the SSC studies conducted on human muscle could confirm this result of pure shortening contraction experiments, stress-induced inhibition might not apply to SSC contractions in vivo. The results might not be reproducible in human experiments or in SSCs the stress-induced inhibition is displaced by another primary mechanism that ensures a force enhancement in the steady-state compared to pure shortening contraction. Since the elastic recoil, stretch reflexes and pre-activation effects are not long-lasting the latest studies on human musculature indicate that the previously mentioned filament titin might be responsible for the enhanced force/torque after the SSC compared to the shortening contraction (Seiberl et al., 2015). We speculate that in some way the stiffness of the titin changes and counteracts the mechanism that occurs in pure shortening contractions (Labeit et al., 2003; Herzog et

al., 2016).

Groeber et al. (2018) and Hahn and Riedel (2018) found the concept of performance enhancement in the steady-state after a SSC for the human plantar flexor muscle, which is of importance since previous results were obtained only from animal studies or the human thumb adductor pollicis muscle. But also with the long tendon at the human plantar flexor, that is more likely to buffer (storing the elastic energy temporarily, then releasing this energy) the stretch of the muscles (Roberts and Konow, 2013), RFE related mechanisms could be found. This is of importance since such buffering would prevent RFE related mechanisms from contributing to force/torque enhancement (Hahn and Riedel, 2018). Groeber et al. (2018) and Hahn and Riedel (2018) found a significant increase in ankle work of 11.7-17.7% ($p < 0.05$) and 11.6% ($p = .003$) respectively, compared to pure shortening contraction. Furthermore, the FD after the SSC (9.1-10.8% and 8.6% respectively) was significantly ($p < 0.05$) reduced to the pure concentric muscle action.

On the one hand FD in the SSC seems to be dependent on the shortening velocity, the shortening distance and the time (transition phase) between the stretch and the shortening; on the other hand independent of the stretch velocity. The reduction of FD should be further investigated for voluntary contractions. So far, this has only been demonstrated in experiments under voluntary contractions. All of the studies investigating the effects of the steady-state force/torque after the SSC used electrical stimulation. The voluntary contraction would better reflect functional movements but electrical stimulation allows a greater focus on the muscular aspect. For pure shortening contractions Lee et al. (1999) reported that FD is an actual property of skeletal muscle rather than a stimulation artifact.

Since RFE is known to be independent of speed and long lasting (Edman, 1978; Herzog et al., 2003) we suggest that RFE based mechanisms are responsible for the enhanced isometric force/torque in the steady-state condition after the SSC, counteracting the FD produced during shortening. Therefore, it seems likely that RFE is beneficial for performances in human locomotion, whenever a muscle is stretched. One attempt to explain the force enhancement dependent on the contractile history of the muscle/fiber, is the molecular spring titin. Herzog (2001) proposed, that RFE has an active and a passive component and titin might cause the passive force enhancement by changing its stiffness properties.

Beside the mechanical properties neural aspects may play an important role in SSCs. Rousanoglou et al. (2007) showed differences in neuromuscular activation between FD experiments and the corresponding isometric states in human thumb adduction force. Paquin and Power (2018) supported their results, adding that RFE has also altered neuromuscular activation strategies. These results indicate a decreased (FD) and increased (RFE) neuromuscular efficiency, respectively. The interaction of neuromuscular efficiency has to be further assessed for SSC conditions in the future.

Further research is needed to get a better insight into the conditions when the increase in muscle performance in the SSC and during locomotion is present. It should be an

aim to strive for further research in more praxis relevant conditions, resulting in a clarification for when RFE and FD contribute to the SSC in everyday movement patterns and how to improve the muscle performance due to these mechanisms.

Conclusion

Taking all articles together, an enhanced muscle performance can be found on different muscle levels. The review illustrates the contraction modalities and an overview of the research done so far in this field. With this review one should be able to be informed about the actual state of research in this topic. A range of different contraction modalities was investigated, but this review also underlies that the understanding of the mechanism contributing to a performance enhancement in the SSC, especially the role of titin, has to be further investigated with the aim of a transfer to applications in athlete training, rehabilitative medicine or to drive- or movement-engineering.

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Key points

- Reduced force depression at SSC experiments compared to pure shortening contractions.
- Mechanical work in the shortening phase of SSC is dependent on the shortening amplitude, shortening velocity, stretch amplitude, the active prephase duration and the time (transition phase) between stretch and shortening.
- The mechanism contributing to a performance enhancement in the SSC, especially the role of titin, has to be further investigated.

AUTHOR BIOGRAPHY



Martin GROEBER

Employment

PhD candidate, University of Vienna, Department of Biomechanics, Kinesiology and Computer Science in Sport, Austria

Degree

MSc

Research interests

Muscle mechanics, muscle contraction mechanism and motion analysis

E-mail: martin.groeber@univie.ac.at

Lena REINHART

Employment

Technical University of Munich, Institute of Sport Science, Germany

Degree

Bachelor student

Research interests

Biomechanics, Sport medicine

E-mail: leni.reinhart@arcor.de



Philipp KORNFELD

Employment

University of Vienna, Department of Biomechanics, Kinesiology and Computer Science in Sport, Austria

Degree

PhD

Research interests

Biomechanics, Muscle mechanics, Sport equipment technology

E-mail: philipp.kornfeld@univie.ac.at



Arnold BACA

Employment

Professor of Biomechanics, Kinesiology and Computer Science in Sport, Head of Centre of Sport Science and University Sports, University of Vienna, Austria

Degree

PhD

Research interests

Computer Science Applied to Biomechanics, Human Motion and Game Analysis

E-mail: arnold.baca@univie.ac.at

✉ Martin Groeber

Centre of Sport Science and University Sports, Department of Biomechanics, Kinesiology and Computer Science in Sport, University of Vienna, 1150 Vienna, Austria