



universität  
wien

# DISSERTATION / DOCTORAL THESIS

Titel der Dissertation / Title of the Doctoral Thesis

“History-dependent properties in a stretch-shortening cycle: Influence of contraction intensity, rotation magnitude and muscle-tendon unit length”

verfasst von / submitted by

Martin Gröber

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree  
of

Doctor of Philosophy (PhD)

Wien, 2021/ Vienna 2021

Studienkennzahl lt. Studienblatt /  
degree programme code as it appears on the stu-  
dent record sheet:

UA 794 680 481

Dissertationsgebiet lt. Studienblatt /  
field of study as it appears on the student record  
sheet:

Sportwissenschaft

Betreut von / Supervisor:

Univ.-Prof. Dipl.-Ing. Dr. Arnold Baca

## **Acknowledgments**

First of all, I would like to thank you Arnold for giving me the chance to write my PhD thesis in your team. Your supervision has had a profound impact on my research. I have really enjoyed having you as a mentor during this time.

A big thanks to all my colleagues and friends at the department for helping me in the lab and providing critical feedback on my work. Your support through discussions and thousands of coffee chats contributed greatly to my productivity.

I know it was sometimes not very pleasant while participating in my studies, but I would like to thank even more all the volunteers for taking part in my experiments.

To my family for their unconditional support during my academic career. The support I get from all of you helped me immensely during my dissertation.

Last but not least, thank you Linda. You have encouraged me from the beginning of this work. Your love and your faith in me gave me the strength to master this task.

# Table of contents

<b>Zusammenfassung .....</b>	<b>1</b>
<b>Abstract.....</b>	<b>4</b>
<b>List of scientific papers.....</b>	<b>7</b>
<b>1. Introduction .....</b>	<b>8</b>
<b>1.1 Basics of muscle contraction .....</b>	<b>8</b>
1.1.1 Cross-bridge theory .....	8
1.1.2 Force-length relationship .....	10
1.1.3 Force-velocity relationship.....	12
<b>1.2 The stretch-shortening cycle.....</b>	<b>14</b>
1.2.1 SSC theories.....	15
1.2.1.1 <i>Pre-activation</i> .....	15
1.2.1.2 <i>Stretch-reflex</i> .....	16
1.2.1.3 <i>Storage and release of elastic energy</i> .....	17
1.2.1.4 <i>Stretch-induced force enhancing effect within the contractile element of the muscle</i> .....	18
<b>1.3 History-dependent properties.....</b>	<b>18</b>
1.3.1 Residual force enhancement.....	18
1.3.1.1 <i>Phenomenological description of residual force enhancement</i> .....	19
1.3.1.2 <i>Residual force enhancement in humans</i> .....	21
1.3.1.3 <i>Theories on the origin of residual force enhancement</i> .	24
1.3.2 Residual force depression.....	28
1.3.2.1 <i>Phenomenological description of residual force depression</i> .....	28
1.3.2.2 <i>Residual force depression in humans</i> .....	29
1.3.2.3 <i>Theories on the origin of residual force depression</i> .....	30
1.3.3 History-dependent properties in a stretch-shortening cycle .....	33
<b>1.4 Aims.....</b>	<b>33</b>
<b>2. Publications .....</b>	<b>34</b>
<b>2.1 Publication 1: The Contraction Modalities in a Stretch-Shortening Cycle in Animals and Single Joint Movements in Humans: A Systematic Review.....</b>	<b>34</b>
<b>2.2 Publication 2: Contribution of Stretch-Induced Force Enhancement to Increased Performance in Maximal Voluntary and Submaximal Artificially Activated Stretch-Shortening Muscle Action .....</b>	<b>46</b>

2.3 Publication 3: The effect of stretch-shortening magnitude and muscle tendon unit length on performance enhancement in a stretch-shortening cycle .....	60
3. Discussion .....	75
3.1 Summary .....	75
3.2 Limitations .....	75
3.2.1 Participants.....	75
3.2.2 Experimental limitations .....	76
3.2.2.1 <i>Dynamometry</i> .....	76
3.2.2.2 <i>3D-motion analysis</i> .....	77
3.2.2.3 <i>Electrical stimulation</i> .....	78
3.2.2.4 <i>EMG</i> .....	79
3.2.2.5 <i>Ultrasound</i> .....	80
3.2.3 Relevance for everyday movement.....	81
3.3 Outlook.....	81
3.3.1 Non-responder .....	81
3.3.2 Trainability .....	81
3.3.3 Further directions.....	83
4. Abbreviations.....	84
5. Figures .....	85
6. References .....	88
7. Declaration of Authorship.....	102
8. Appendix .....	103

## Zusammenfassung

Die vorliegende Arbeit beschäftigt sich mit dem Dehnungs-Verkürzungszyklus (DVZ), einer kombinierten Muskelaktion bestehend aus einer exzentrischen und konzentrischen Phase. Der DVZ ist Bestandteil von vielen alltäglichen und sportlichen Bewegungsabläufen und ist assoziiert mit einer höheren mechanischen Effizienz gegenüber einer rein konzentrischen Kontraktionsform. Trotz immensen wissenschaftlichen Interesses bleibt weiterhin ungeklärt, welche Mechanismen zu einer/m erhöhten Kraft/Drehmoment/mechanischer Arbeit in der Verkürzungsphase im DVZ beitragen. In der Literatur werden die Speicherung und Freisetzung elastischer Energie, der Dehnreflex und die Voraktivierung der Muskulatur als Gründe genannt. Dieser leistungspotenzierende Effekt konnte allerdings auch an isolierten Muskelfasern ohne Einfluss der zuvor genannten Mechanismen gezeigt werden. Daher muss es einen weiteren Mechanismus geben, der zur Leistungssteigerung im DVZ beiträgt. Ein weiteres Muskelphänomen, das einen positiven Beitrag im DVZ leisten könnte, steht im Zusammenhang mit einer dehnungsinduzierten Steigerung der Kraft innerhalb der kontraktile Elemente der Muskulatur. Eine exzentrische Muskelaktion ist gekennzeichnet durch erhöhte Kräfte/Drehmomente während und nach der Muskelaktion im Vergleich zu einer isometrischen Referenzkontraktion bei gleicher Muskellänge und Aktivierung. Dieses Phänomen wird in der Literatur „(transient) force enhancement (FE)“ beziehungsweise „residual force enhancement (rFE)“ genannt. Im Gegensatz dazu kommt es nach einer reinen konzentrischen Muskelaktion zu einer Verringerung der Kräfte/Drehmomente im Vergleich zu einer isometrischen Referenzkontraktion bei gleicher Muskellänge und Aktivierung („residual force depression, rFD“). Die kontraktile Eigenschaften sind somit nicht nur von den momentanen Bedingungen, sondern auch vom Auftreten vorangegangener Muskelkontraktionen abhängig, was als „history-dependent property“ bezeichnet wird.

Das Phänomen rFE wurde bereits in einer Vielzahl von Studien untersucht, von Untersuchungen bei einem einzelnen Sarkomer bis hin zu mehrgelenkigen Muskelaktionen des Menschen. Die Mehrheit der Studien beschäftigt sich allerdings mit rein exzentrischen Muskelaktionen, welche aber so gut wie nie bei alltagsnahen menschlichen Bewegungen auftreten. Deshalb liegt der Fokus dieser Arbeit auf den Einfluss von rFE im DVZ.

Die erste Publikation gibt eine systematische Übersicht über die aktuelle Literatur. Das Phänomen von rFE im DVZ wird hierbei in vitro, in situ und bei eingelenkigen in vivo Studien untersucht. Hierfür wurde eine systematische Literaturrecherche gemäß dem „PRISMA flow chart“ durchgeführt. 25 Studien wurden inkludiert. Die isometrische Kraft nach einem DVZ unterscheidet sich von der/m isometrischen Kraft/Drehmoment nach einer rein konzentrischen Muskelaktion in Abhängigkeit der Verkürzungsgeschwindigkeit, Verkürzungs- und

Dehnungsamplitude, der Zeit zwischen Dehnung und Verkürzung und der Dauer der Voraktivierung. Unterschiedliche Ergebnisse wurden hinsichtlich der Dehnungsgeschwindigkeit gefunden. Der systematische Review zeigte zudem, dass der positive Effekt von rFE im DVZ eliminiert werden kann und dies ist abhängig von der Zeitdauer der Verkürzungsphase. Die zweite Publikation beschäftigt sich mit dem Einfluss der Kontraktionsintensität auf rFE im DVZ. Ziel dieser Arbeit war zu klären, inwieweit die Intensität der Muskelaktion den Beitrag von rFE zur Leistungssteigerung im DVZ beeinflusst. Hierfür wurde das Phänomen während eingelenkigen Kniebeuge –streck Bewegungen untersucht. 30 gesunde Erwachsene führten rein isometrische (ISO), konzentrische (CON) und DVZ Kontraktionen an einem isokinetischen Dynamometer durch. Maximal willentliche Kontraktionen als auch submaximale elektrisch stimulierte Versuche bei 20%, 35% und 50% der maximal willentlichen Kontraktion wurden untersucht. Die mechanische Arbeit während der Verkürzungsphase war bei allen Kontraktionsintensitäten signifikant erhöht ( $p < 0.05$ ) im Vergleich zur rein konzentrischen Kontraktionsform bei gleicher Intensität (bis zu 21% erhöht). In Bezug auf das isometrische Drehmoment nach der Verkürzungsphase wurden bei allen submaximalen Intensitäten keine signifikanten Unterschiede zwischen der konzentrischen (CON) und DVZ Bedingung gefunden. Im Gegensatz dazu wurde bei willentlich maximaler Kontraktion ein erhöhtes Drehmoment nach der DVZ Bedingung im Vergleich zur CON Bedingung gefunden ( $p = 0.034$ ), ohne signifikante Unterschiede der Kontrollvariablen Kniewinkel, Muskelaktivität des M. vastus medialis und M. rectus femoris und Faszikellänge und Fiederungswinkel des M. vastus lateralis. Aus diesem Ergebnis schlossen wir, dass der Beitrag von rFE im DVZ des Quadriceps femoris von der Kontraktionsintensität und der Art der Aktivierung abhängt.

Die dritte Publikation handelt vom Einfluss der Bewegungsamplitude und unterschiedlichen Muskel-Sehnen-Komplex Längen auf rFE im DVZ. Der Versuchsaufbau war ähnlich wie bei der zweiten Publikation. Wieder wurden 30 Personen am isokinetischen Dynamometer getestet und isometrische (ISO), konzentrische (shortening-hold, SHO) und DVZ Kontraktionsformen verglichen. Die konzentrische Kontraktionsform wurde in Publikation 3 im Reviewprozess von CON nach SHO umbenannt. Es handelt sich dabei um die gleiche Kontraktionsform wie in Publikation 2, wird im weiteren Verlauf dieser Arbeit so genannt wie in der jeweiligen Publikation. Bei der ersten Testung wurde die Bewegungsamplitude verändert (SHO: 50-20°, 80-20° und 110-20°; DVZ: 20-50-20°, 20-80-20° und 20-110-20°) und bei der zweiten Testung die Länge des Muskel-Sehnen-Komplexes (SHO: 50-20°, 80-50° und 110-80°; DVZ: 20-50-20°, 50-80-50° und 80-110-80°; durchgestrecktes Bein = 0°). In Sitzung 1 war die mechanische Arbeit bei allen DVZ Kontraktionen im Vergleich zur entsprechenden SHO Kontraktion signifikant ( $p < 0.05$ ) erhöht, während in der

isometrischen steady-state Phase nach den DVZs bei allen getesteten Bewegungsamplituden keine signifikante rFE gefunden wurde. Bei den Versuchen zum Einfluss der Muskel-Sehnen-Komplex Länge war die mechanische Arbeit bei den DVZ Kontraktionen ebenfalls erhöht, jedoch waren die Werte der mechanischen Rotationsarbeit bei allen Muskel-Sehnen-Komplex Längen nahezu konstant (8.1 - 8.6%). Im steady-state nach der dynamischen Phase fanden wir nur beim DVZ bei der längsten Muskel-Sehnen-Komplex Länge ein signifikant ( $p < 0.05$ ) erhöhtes Drehmoment gegenüber der entsprechenden SHO Bedingung, ohne Unterschiede in der Kniekinematik, dem M. vastus lateralis Fiederungswinkel und der Faszikellänge. Diese Ergebnisse implizieren, dass während DVZ der Kniestrecker der Beitrag von rFE von der Muskel-Sehnen-Komplex-Länge abhängig ist. Dies bedeutet, dass die physiologische Relevanz von rFE in der menschlichen Bewegung besonders bei Bewegungen mit größerer Kniegelenksflexion wichtig ist. Bei kürzeren Muskel-Sehnen-Komplex Längen und bei größeren Bewegungsamplituden wurde der positive rFE Effekt durch die anschließende Verkürzung des Muskels im DVZ abgeschwächt.

## Abstract

The present work deals with the stretch-shortening cycle (SSC), a combined muscle action consisting of a stretch (eccentric phase) directly followed by a shortening (concentric phase) contraction. The SSC is a component of many everyday and athletic movements and is associated with higher mechanical efficiency compared to a pure shortening contraction. Despite immense scientific interest, the mechanisms that contribute to increased force/torque/mechanical work in the shortening phase in the SSC (SSC-effect) remain unresolved. In the literature, the storage and subsequent release of elastic energy, the stretch-reflex, and pre-activation of the muscle are attributed as potential mechanisms. However, the SSC-effect has also been demonstrated in designed studies not related to previously mentioned mechanisms and was present on the muscle fiber level. Therefore, another mechanism must contribute to the SSC-effect. Another muscle phenomenon that could make a positive contribution to the SSC is related to a stretch-induced force enhancing effect within the contractile element of the muscles. An eccentric muscle action is characterized by increased forces/torques during and after the muscle action compared to an isometric reference contraction at the same muscle length and activation level. These phenomena are called (transient) force enhancement (FE) and residual force enhancement (rFE) in the literature. In contrast, after a purely concentric muscle action, there is a reduction in force/torque compared to an isometric reference contraction at the same muscle length and activation level (residual force depression, rFD). The contractile properties are not only dependent on the instantaneous conditions, but also on the occurrence of prior movements, which is called the history-dependent property of muscle action.

The phenomenon rFE has been investigated in a variety of studies, from single sarcomere to multi-joint human muscle actions. However, the majority of studies deal with purely eccentric muscle actions, which almost never occur in everyday human movements. Therefore, the focus of this work is on the influence of rFE in the more relevant SSC.

The first publication provides a systematic review of the current literature. The history-dependent property of rFE in the SSC is investigated in vitro, in situ and in single-joint in vivo studies. For this purpose, a systematic literature search was performed according to the "PRISMA" flow chart. In the systematic review, 25 studies were included. The isometric steady-state force after a SSC differs from the isometric force/torque after a purely concentric muscle action depending on shortening velocity, shortening and stretching magnitude, the time between the stretch and the shortening and the active pre-phase duration. Different results were found regarding the stretch velocity. The systematic review also showed that the positive effect of rFE in the SSC can be eliminated and this might depend on the duration of the shortening phase.



The second publication deals with the influence of the contraction intensity in the SSC. The aim of this work was to clarify to what extent the intensity of the muscle action influences the contribution of rFE to the SSC performance enhancement. The phenomenon was investigated during single-joint knee flexion-extension movements. For this purpose, 30 healthy adults performed pure isometric (ISO), concentric (CON) and SSC contractions at an isokinetic dynamometer. Maximal voluntary contractions (MVC) as well as submaximal electrically stimulated trials at 20%, 35% and 50% of MVC were examined. Mechanical work during the shortening phase was significantly increased ( $p < 0.05$ ) at all contraction intensities compared to the purely concentric contraction form (CON) at the same intensity (up to 21%). With respect to the isometric torque after the shortening phase, no significant differences were found between the CON and SSC condition at all submaximal intensities. In contrast, during MVCs an increased torque was found after the SSC condition compared to the CON condition ( $p=0.034$ ), with no significant differences in the control variables knee angle, muscle activity of m. vastus medialis and m. rectus femoris and fascicle length, and pennation angle of the m. vastus lateralis. From these results, we concluded that the contribution of the potential enhancing factors in SSCs of the m. quadriceps femoris is dependent on the contraction intensity and the type of activation.

The third paper deals with the influence of different SSC-magnitudes and different muscle-tendon unit lengths. The experimental setup was similar to that of the second paper. Again, 30 participants were initially tested at an isokinetic dynamometer. They performed isometric (ISO), concentric (shortening-hold, SHO) and stretch-shortening (SSC) contractions. The concentric contraction was renamed from CON to SHO in Publication 3 during the review process. It is the same form of contraction as in Publication 2, but will be named in the further course of this work as in the respective publication. At the first session, the rotation magnitude was changed (SHO: 50-20°, 80-20°, and 110-20°; SSC: 20-50-20°, 20-80-20°, and 20-110-20°) and at the second session, the muscle-tendon unit length was changed (SHO: 50-20°, 80-50°, and 110-80°; SSC: 20-50-20°, 50-80-50°, and 80-110-80°; straight leg = 0°). In session 1, mechanical work was significantly ( $p < 0.05$ ) increased in all SSC contractions compared to the corresponding SHO contraction, whereas steady-state torque was the same after the SSC and SHO conditions at all tested rotation magnitudes. In session 2, the mechanical work was also enhanced for the SSC contractions, however the enhanced rotational work values were almost constant at all muscle-tendon unit lengths (8.1 - 8.6%). In the steady-state after the dynamic phase, we found only significant ( $p < 0.05$ ) less depressed joint torque in the SSC at the longest muscle-tendon unit length compared to the corresponding SHO condition, without any differences in knee kinematics, m. vastus lateralis pennation angle and fascicle length.

These results implicate that during SSCs of the knee extensors, the extent of the rFE contribution is dependent on the muscle-tendon unit length. This indicates that the physiological relevance of rFE in human movement might be particularly important for movements at greater knee-joint flexion (longer muscle-tendon unit length). At shorter muscle-tendon unit lengths and at greater rotation magnitudes, the stretch-induced force enhancing effects were attenuated by the subsequent shortening of the muscle in a SSC.

## List of scientific papers

1. **Groeber, M.**, Reinhart, L., Kornfeind, P., and Baca, A. (2019). The contraction modalities in a stretch-shortening cycle in animals and single joint movements in humans: A systematic review. *J. Sports Sci. Med.* 18, 604–614.
2. **Groeber, M.**, Stafilidis, S., Seiberl, W., and Baca, A. (2020). Contribution of Stretch-Induced Force Enhancement to Increased Performance in Maximal Voluntary and Submaximal Artificially Activated Stretch-Shortening Muscle Action. *Frontiers in physiology* 11, 592183. doi: 10.3389/fphys.2020.592183.
3. **Groeber, M.**, Safilidis S., and Baca A. (2021). The effect of stretch-shortening magnitude and muscle-tendon unit length on performance enhancement in a stretch-shortening cycle. *Scientific reports* 11, 14605. doi: 10.1038/s41598-021-94046-2.

# **1. Introduction**

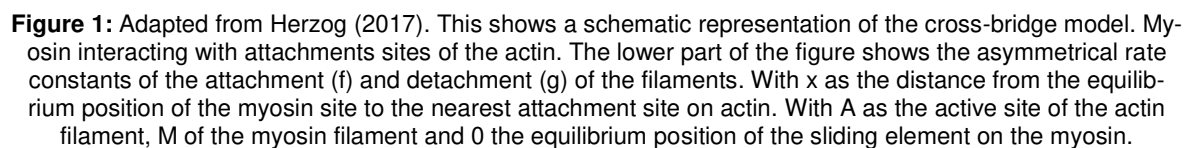
The muscles are often called the “motor” of human movement. The understanding of muscle contraction and force production was completely revolutionized over 60 years ago. Huxley and Niedergerke (1954) and Huxley and Hanson (1954) proposed an interaction of two types of microstructures (actin and myosin filament), which was the birth of the sliding filament theory. According to this theory, the myosin slides past the actin filament during a muscle contraction. This enables the muscle to shorten and thereby generate force. Based on these findings, attempts are still being made today to understand the complexity of muscle contraction. Models are generated to explain the highly complex interaction of various mechanism of human movement. One phenomenon of muscle contraction in particular still raises questions and is the subject of current scientific research. The phenomenon is called the “history dependence of muscle action”. It describes the dependence of force production on the contractile history of muscle action. This phenomenon can be reconciled to the existing theories only to a limited extent. Especially the meaning for everyday movements like the stretch-shortening cycle (SSC) remains unexplained. Therefore, the following thesis deals with the history-dependent properties of muscle action in a stretch-shortening cycle.

In the first subsection (1.1), an introduction to the basic knowledge of muscle contraction is given. Building on this, the basics of a SSC are presented in the next chapter (1.2). Since the history-dependent properties are the focus of this work, three subchapters introduce these phenomena. First, residual force enhancement (rFE) is introduced (1.3); second, residual force depression (rFD) (1.4); and third, the history-dependent properties in a SSC (1.5). In the last subchapter of the introduction, the aims and research questions of this work are presented.

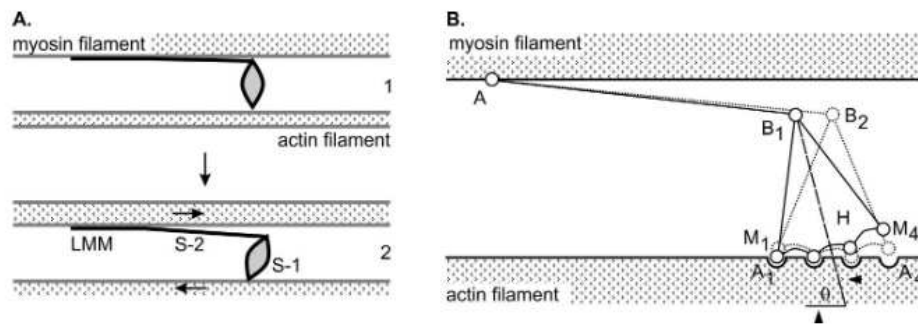
## **1.1 Basics of muscle contraction**

### **1.1.1 Cross-bridge theory**

A first model for muscle contraction was delivered with the cross-bridge theory (Huxley, 1957), which still exists today. In this model, a distinction was initially made between two simple cases. These two conditions are characterized as a connected or disconnected cross-bridge between the actin and myosin filament (Figure 1).



This model has been further developed in the sense that the cross-bridges can take different states (Figure 2). With this extension of the original model, actin and myosin filaments can have different connection states instead of only being attached or not attached (Huxley and Simmons, 1971).



**Figure 2:** Rotating cross-bridge model (Herzog et al., 2012). Complementary to the sliding of actin and myosin filament, a rotation of the cross-bridge head allows for the actin to be pulled past the myosin filament. The left panel represents the model of Huxley (1969), where the different connection states (S) are of varying strength and the right panel of Huxley and Simmons (1971), where the resulting connections (B1 and B2) are of varying strength.

Overall, the cross bridge model has persisted to this day. It captures many experimental properties of the muscle like the force-length relationship (see also chapter 1.1.2) (Gordon et al., 1966). The rate functions of the attachment and detachment can further be adapted to predict also the force-velocity relationship during muscle shortening (see also chapter 1.1.3) (Hill, 1938).

However, the core message and the limitations of the cross-bridge model remain:

**“[...] the cross-bridge theory does not allow for steady-state isometric forces to differ, except if muscle activation or length is different” (Herzog et al., 2008).**

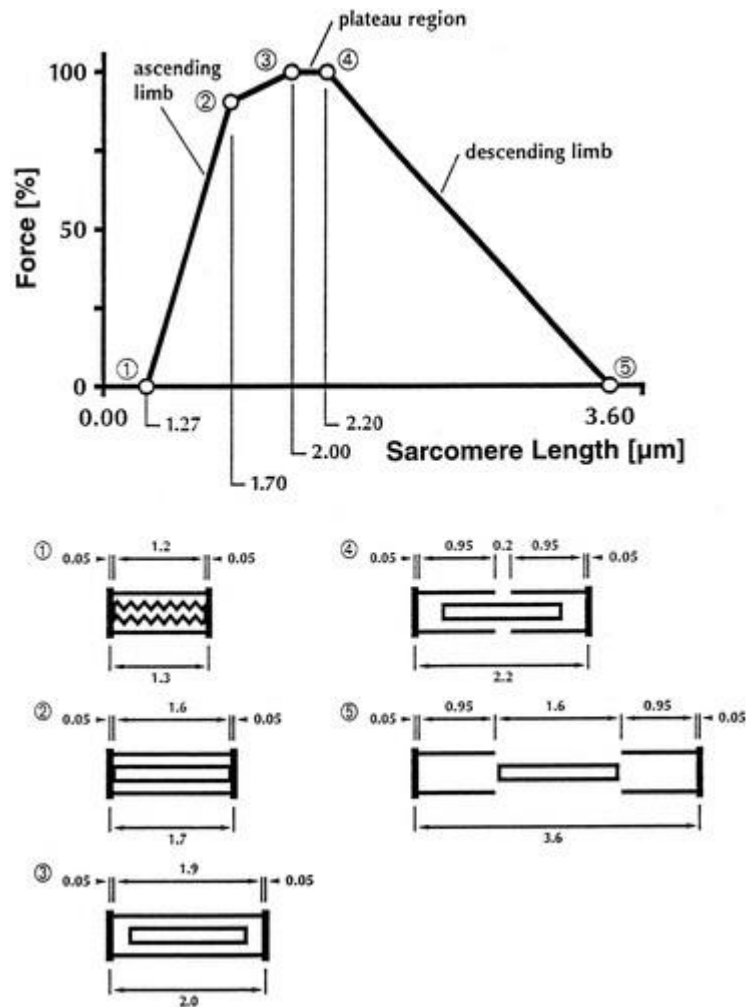
Thus, the cross-bridge theory cannot explain the history-dependent properties of muscle action; neither the phenomenon of rFE, nor rFD (Herzog et al., 2008). This makes it necessary to revise or expand the basic assumptions of the cross-bridge model.

### 1.1.2 Force-length relationship

In order to better understand the history-dependent properties of muscle action and thus the central element of this work, it is necessary to understand the basic biomechanical principles of the musculature. With the assumptions of the cross-bridge theory, the interaction of actin and myosin filaments is responsible for the force development of a muscle. Which further means:

**“...that the maximal isometric force of a sarcomere is linearly related to the amount of actin-myosin overlap” (Rassier et al., 1999).**

Without considering any biochemical, neuronal or coordinative factors, the overlap and therefore the length of the sarcomere are the crucial factor of the potential force. This results in the classic force-length curve of a sarcomere (Figure 3).



**Figure 3:** Adapted from Rassier et al. (1999). Force-length relationship of frog skeletal muscle sarcomere. The representation of the highlighted dots refers to the degree of overlap of actin and myosin filaments as a function of sarcomere length.

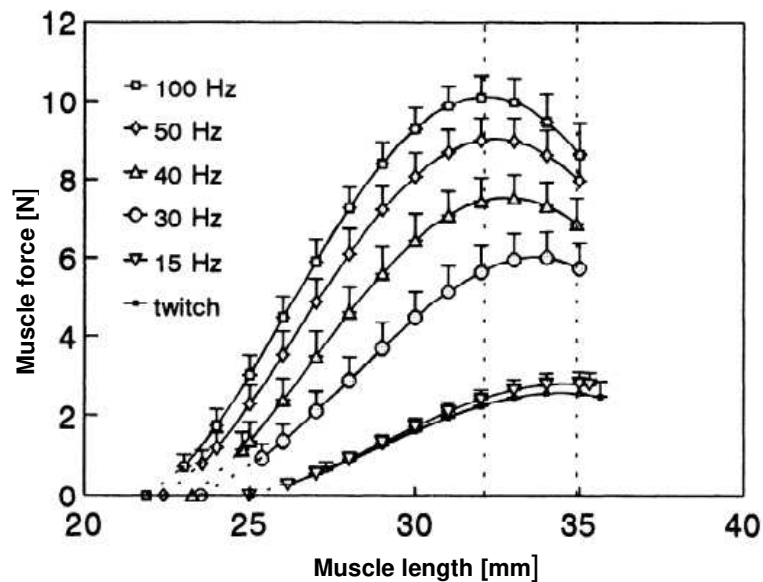
The isometric force generated during maximum activation yields a characteristic curve with a plateau in the middle region, an ascending limb and a descending limb (Figure 3).

Regarding the force-length relationship of the whole muscle-tendon complex a similar characteristic curve can be found, meaning force of the whole muscle-tendon unit is low at very short and very long muscle-tendon unit lengths. However, there are different factors, which provide a variation of the force curve. Different muscles have a different working range, different relative muscle lengths where the passive-elastic forces start to act and the average increase of the passive-elastic force is different depending on the muscle (Wank, 2000). This means the given prerequisites of the individual muscles and the muscle architecture influence the force-length relationship of the whole muscle-tendon unit complex.

Another point that is discussed in literature is the influence of the activation level. Everyday movements are hardly ever performed with maximal activation. Studies investigating the force-length relationship at submaximal levels of activation showed a rightward shift (toward

longer muscle lengths) in single fibers or isolated muscles (Vaz et al., 2012; Rack and Westbury, 1969) (Figure 4). This rightward shift has been associated with an increase in calcium sensitivity with increasing fiber/ muscle length (Rassier et al., 1999).

In contrast to these findings, Brito Fontana and Herzog (2016) reported that the optimal fascicle length of m. vastus lateralis remains constant based on EMG activity and not force, independent of the activation level.

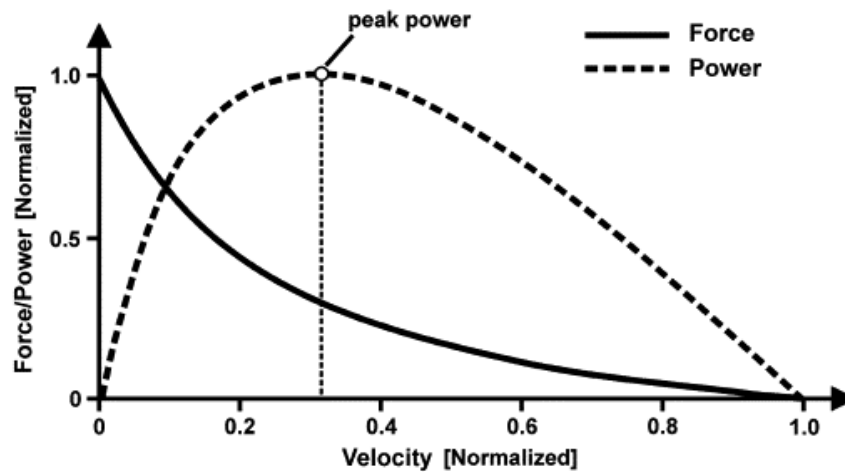


**Figure 4:** Adapted from Roszek et al. (1994). Force-length relationship at different submaximal electrically stimulated stimulation frequencies. The force-length characteristics are from rat m. gastrocnemius medialis.

### 1.1.3 Force-velocity relationship

In addition to the influence of a muscle's length, there is a relationship between the velocity of contraction and the force. Hill (1938) first demonstrated that force and velocity is related in a non-linear way. His work demonstrated a maximum force at the isometric state (velocity = 0) and a loss of force with increasing speed (Figure 5).





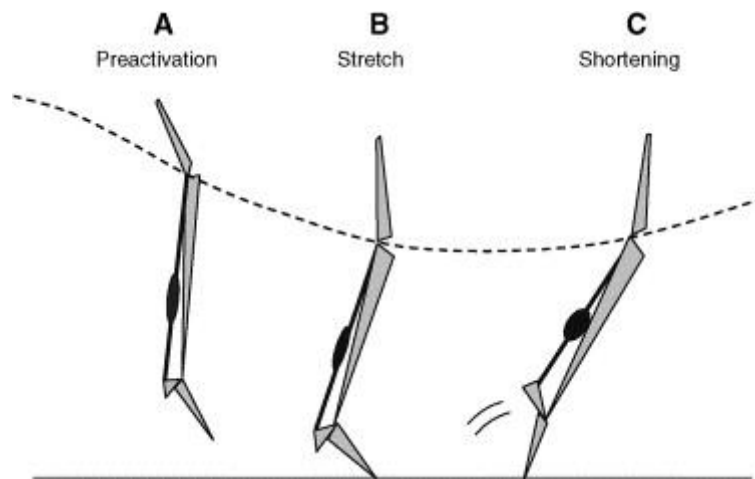
**Figure 5:** Adapted from Herzog (2009). Force-velocity relationship. Normalized force and power as a function of normalized concentric velocity.

These assumptions are based on the fact that the external load is smaller than the isometric maximum force. In cases in which the external load is greater, the attachment and origin of the muscle are moved away from each other, with the result that the muscle is inevitably stretched. The velocity dependence of eccentric muscle action is described in different studies (Edman et al., 1978; Joyce and Rack, 1969; Lombardi and Piazzesi, 1990). This force-velocity relationship during muscle stretching is described as follows:

**“After a certain amount of stretch there is a break in the force record so that the initial sharp rising phase is followed by a plateau or small rise of tension” (Noble, 1992).**

## 1.2 The stretch-shortening cycle

A stretch-shortening cycle (SSC) is a muscle action where a stretch of the muscle (eccentric contraction) is immediately followed by a shortening (concentric) contraction (Figure 6). In contrast to pure stretch and pure shortening muscle action, a SSC occurs in a large number of everyday movements as well as many sporting activities such as running, jumping and throwing (Komi, 2000).



**Figure 6:** Adapted from Komi (2000). Representation of a stretch-shortening cycle. In human movement, impact loads occur when contact is made with the ground. This requires a pre-activation of the lower limb extensor muscle (A) followed by active stretching (B) and then an active shortening (C) immediately afterwards.

The SSC is associated with increased force, torque, mechanical work and power during the shortening phase of the SSC compared to a pure shortening contraction (“SSC-effect”) (Komi and Gollhofer, 1997; Komi, 2000). In addition to this performance-potentiating effect, there is also a higher efficiency in a SSC muscle action (Frick, 1993). Cavagna et al. (1965) were the first to report this greater mechanical efficiency in the shortening phase of a SSC. The authors worked with spiroergometric examination methods and found differences in oxygen consumption during SSC shortening compared to pure shortening muscle action. This result was also confirmed in athletic movements such as jumping with and without a countermovement motion (Thys et al., 1975).

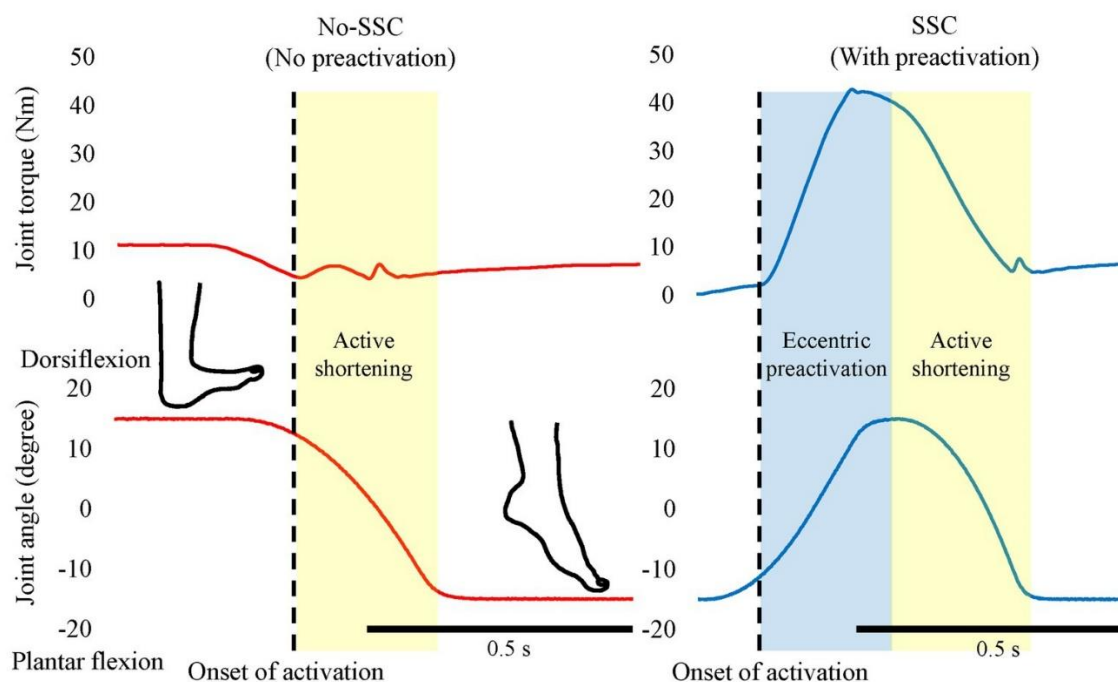
SSCs are consistently observed and represent a central component for optimal performance, thus the SSC-effect has been a central question in sport science for years.

### 1.2.1 SSC theories

There is a variety of proposals for the underlying mechanism of the SSC-effect. The most frequently discussed mechanisms are presented as follows.

#### 1.2.1.1 Pre-activation

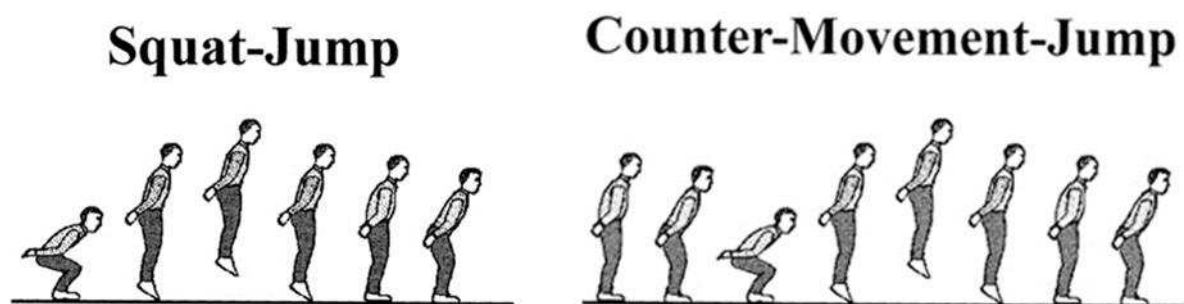
One of the mechanisms attributed to the SSC-effect is the pre-activation of the muscle. Pre-activation means that the muscle is already activated at the onset of muscle shortening. In a pure shortening contraction, a muscle may not be activated prior to the active shortening (Figure 7).



**Figure 7:** Adapted from Fukutani et al. (2020). The left side shows a condition with no pre-activation and the right side shows a SSC (with pre-activation). In the condition without pre-activation, joint torque first increases during muscle shortening, while in the condition with pre-activation the torque continuously decreases. This indicates that joint torque is not fully developed in the early phase of shortening without pre-activation.

In the early phase of pure shortening contractions, activation first needs to increase from zero to “full activation.” This results in much smaller force during the pure shortening compared to the SSC contraction, especially in the early shortening phase (Fukutani et al., 2020). This effect is well described in literature (Bobbert and Casius, 2005; Svantesson et al., 1994; Fukutani et al., 2016). The pre-activation effect plays an especially major role when the shortening phase is short (e.g. small shortening magnitude or high shortening speed), since the time to develop the muscle force is limited (Fukutani et al., 2015b).

In cases where pre-activation is the sole contributor to the SSC-effect, the type of pre-activation would not matter (Fukutani et al., 2020). Therefore, differences in force after an eccentric and an isometric phase before muscle shortening cannot be considered as a pre-activation effect. Therefore, when focusing on other mechanisms, in many experimental studies an isometric fixed-end pre-activation is frequently used before the dynamic contraction (Seiberl et al., 2015b; Hahn and Riedel, 2018; Groeber et al., 2020; Tilp et al., 2011). However, in many athletic exercises pre-activation is an important factor. For example, in a vertical countermovement jump the leg extensor muscles are pre-activated to decelerate and reverse the downward movement, whereas in a squat jump the leg extensor muscles are only slightly pre-activated to generate the joint torque to hold the body in a squatting position (Figure 8).



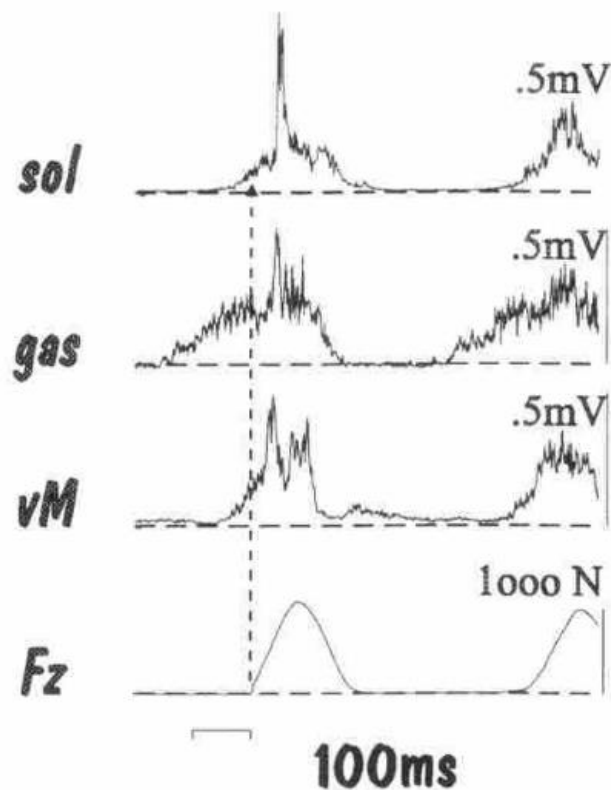
**Figure 8:** Adapted from VBG - Maximalkraft und Schnellkraft (2021). The left panel shows a squat-jump (no SSC), whereas the right panel shows a countermovement jump (SSC).

#### **1.2.1.2 Stretch-reflex**

The SSC-effect is accompanied by enhanced muscle activation, attributed to the stretch-reflex (Dietz et al., 1979). When a muscle is lengthened, the muscle spindle can engage a reflex response to prevent an over-lengthening and reduce the risk of injury. It is thought that this results in an increased number of recruited motor units (Bosco et al., 1981). This would further lead to higher forces (and higher stiffness of the muscle) at the end of the stretch phase in a SSC and can result in a greater SSC-effect.

However, the literature comparing shortening contraction with and without a stretch phase beforehand does not provide convincing evidence for a contribution of a reflex (van Schenau et al., 1997). For example, no difference in the muscle activity of the lower extremity muscles could be detected for volleyball players performing squat jumps and countermovement jumps (Bobbert et al., 1996). Additionally, the SSC-effect was observed in SSC-conditions with electrical stimulation, where no reflex activity should occur (Fukutani et al., 2015a).

Overall, stretch reflexes cannot be solely responsible for the SSC-effect, and are only expected in fast movements with fast muscle lengthening, such as drop-jumps (Figure 9) (Komi and Gollhofer, 1997).



**Figure 9:** Adapted from Komi and Gollhofer (1997). Representation of EMG peaks of m. soleus, m. gastrocnemius and m. vastus medialis in a drop-jump exercise. The sharp EMG reflex peak can best be seen at m. soleus.

### **1.2.1.3 Storage and release of elastic energy**

A very well-accepted mechanism is the storage and release of elastic energy in the muscle-tendon complex (Finni et al., 2001). The elastic energy can be stored during active stretch and can afterwards be used in the shortening phase, resulting in the SSC-effect. Due to the properties of the tendon, they are considered to be the primary site for the storage of elastic energy (Kubo et al., 1999; Lichtwark and Wilson, 2007).

Recent studies also assume that elastic energy is stored in elongated cross-bridges (Tomalka et al., 2020; Fukutani et al., 2020). It was also reported that with higher stretch velocity, more elastic energy can be stored in the cross-bridges, but this energy can be lost when there is a transition time between stretch and shortening (Fukutani et al., 2017a). However, it is speculated that the elastic energy stored in cross-bridges might contribute to the SSC-effect, albeit to a small fraction (Tomalka et al., 2020).

#### ***1.2.1.4 Stretch-induced force enhancing effect within the contractile element of the muscle***

In addition to this previously mentioned mechanism, in current literature residual force enhancement is also associated with the SSC-effect (Seiberl et al., 2015b; Groeber et al., 2019; Fukutani et al., 2020). The reason for this assumption is the presence of the SSC-effect in preparations in which the previously mentioned mechanisms were eliminated (Fukutani et al., 2017a; Fukutani et al., 2017b). This suggested mechanism does not dissipate rapidly; it is still present seconds after the stretch. Therefore, the occurrence of this mechanism is examined in the isometric steady-state after the muscle action. Since this mechanism is the central point of the present work, this history-dependent effect will be discussed in detail in the next chapter.

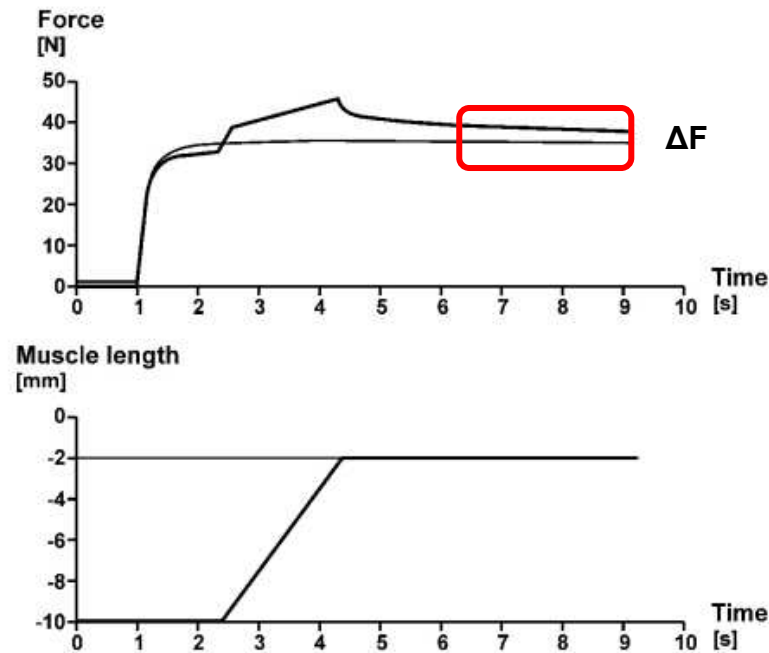
### **1.3 History-dependent properties**

The history-dependent properties of muscle action express the influence of a preceding event on this same muscle action. In this context, a preceding stretch or shortening phase plays a role and can have a force enhancing or depressing effect. Abbott and Aubert (1952) had already described this phenomenon five years before the emergence of the cross-bridge theory. However, such a dependence on the contractile history of muscle action was not included in the cross-bridge theory (Huxley, 1957) and has not yet been incorporated into a unified theory of muscle contraction.

#### **1.3.1 Residual force enhancement**

A unique property of eccentric muscle action is enhanced force/torque during but also following the stretch of the muscle compared to an isometric reference contraction at the same muscle length and activation level. The force/torque response to an active stretch is described to have two components. A transient force enhancement throughout the stretch period (FE) (Edman, 2012), and a long-lasting component which in literature is called residual force enhancement (rFE) (Herzog, 2004) (Figure 10). In literature the terms are often not used in a completely consistent way, some authors name rFE just “FE after muscle stretch” or “FE in the steady-state.” The meaning or definition of this post eccentric force, however, remains the same:

**“Force enhancement is defined here as the absolute (or percent) increase in the steady-state, isometric force following stretch contraction compared to the purely isometric force at the corresponding length” (Herzog, 2001).**

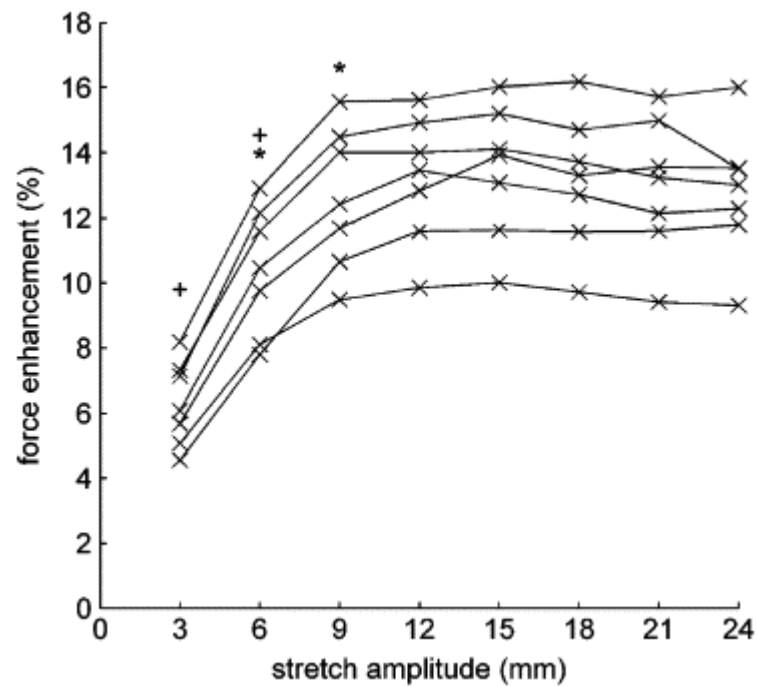


**Figure 10:** Modified from Herzog (2001). Illustration of residual force enhancement. After muscle stretch (unsteady top line), the isometric steady-state force is enhanced ( $\Delta F$ ) compared to the isometric reference contraction at the final reference muscle length.

### ***1.3.1.1 Phenomenological description of residual force enhancement***

Since this phenomenon was first observed by Abbott and Aubert (1952), it was consistently perceived on different structural levels of the muscle. From sarcomere/half-sarcomere level (Rassier and Pavlov, 2012), to single muscle fibers (Edman et al., 1982; Peterson et al., 2004; Rassier et al., 2003) up to whole muscle level (Herzog and Leonard, 2000; Schachar et al., 2004), some basic characteristics concerning rFE have been identified.

First of all, there is the influence of the stretch amplitude. In many studies, the stretch amplitude was varied to determine its influence. Already Abbott and Aubert (1952) worked with a constant speed method and showed that with increasing amplitudes of stretch an increased rFE can be found. This observation was later supported by Sugi (1972), Edman et al. (1982) and confirmed by a study of Bullimore et al. (2007) on a preparation of the m. soleus of the cat. This preparation is very robust and allows for muscle actions at long muscle lengths.



**Figure 11:** Adapted from Bullimore et al. (2007). Residual force enhancement of seven individual m. soleus of the cat. rFE increases up to approximately 9 mm and then levels off.

This study of Bullimore et al. (2007) shows that rFE is at least to a certain extent directly related to the stretch amplitude (Figure 11). With the stretch amplitude, the percentage value of rFE increases relative to the isometric reference contraction.

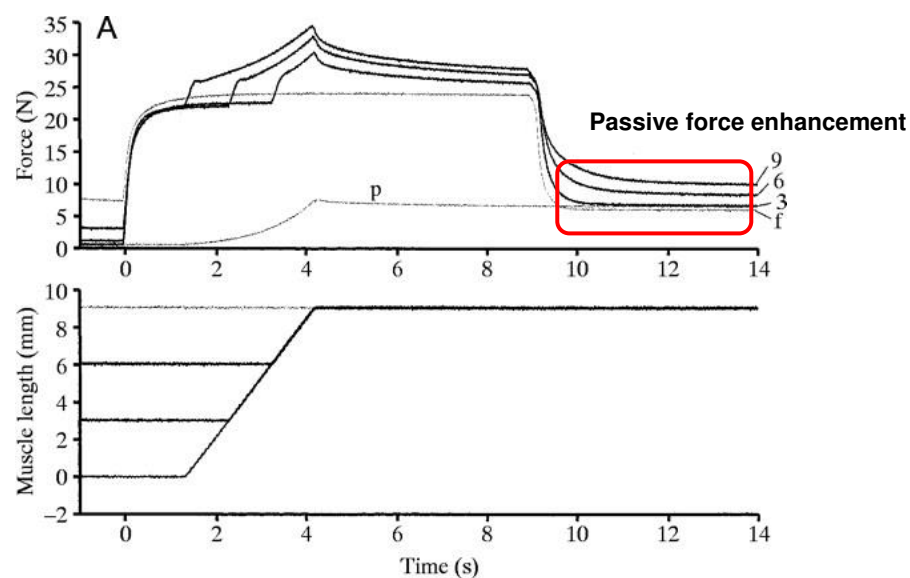
In contrast to the rFE dependency on the stretch amplitude, no correlations between rFE and the stretch velocity could be found (Edman et al., 1978, 1982; Sugi and Tsuchiya, 1988). These earlier findings were supplemented by Fukutani et al. (2019a), which reported an abolishment of rFE at really fast stretch speeds (64 mm/s). They concluded that at fast stretch conditions, a “slippage” (Kuhn, 1978) might explain the abolishment of rFE. “Slippage” refers to the inability of cross-bridges to attach properly to actin at high stretch speeds (Fukutani et al., 2019a).

At the beginning, it was also assumed that rFE only exists in certain areas of the force-length relationship. It was supposed that rFE can only occur on the descending limb of the force-length relationship (Abbott and Aubert, 1952; Edman et al., 1978; Herzog and Leonard, 2000; Julian and Morgan, 1979). Later, rFE could also be found at the ascending limb of the force-length relationship at studies of the whole muscle (Cook and McDonagh, 1995; Ruiters et al., 2000; Herzog and Leonard, 2002). However, there was always some concerns regarding the actual muscle length in preparations of the whole muscle. It might be possible that fibers operate on different parts of the force-length relationship in a whole muscle preparation. Therefore, it would be possible that rFE could be caused by some fibers which act on the descending limb (Lee and Herzog, 2008). Lee and Herzog (2008) also



confirmed rFE on the plateau of the force-length relationship by measuring the average sarcomere lengths in isolated fibers.

Another early observation by Abbott and Aubert (1952) was the “long-lasting” rFE, which lasted up to 30s in their experiment. However, this long-lasting rFE can be immediately eliminated by a deactivation of the muscle. After reactivation, the force potentiation no longer occurs and no difference of force values can be found compared to the isometric reference contraction (Morgan et al., 2000). If the muscle is not reactivated and the passive force is compared to the isometric reference after deactivation, a difference can be observed which is described as passive force enhancement (Figure 12) (Herzog and Leonard, 2002).



**Figure 12:** Modified from Herzog and Leonard (2002). Illustration of passive force enhancement following muscle stretching of 3mm, 6mm and 9mm respectively. Passive force enhancement can be seen after deactivation of the previously stretched muscle compared to the deactivated isometric reference force. Passive force enhancement increases with stretch amplitude.

### 1.3.1.2 Residual force enhancement in humans

The findings described above represent results from animal muscle preparations. In order to draw conclusions about the relevance of rFE in human movements, in vivo studies are also required. In the following, rFE was investigated in a series of experiments in human musculature, with the fundamental question being whether the previous described findings can be transferred to in vivo muscle function in human musculature.

There are two main approaches of in vivo studies which can be characterized by the type of activation: The examination of electrically stimulated contractions and of voluntary contractions. Both approaches have their advantages and disadvantages. Electrically stimulated contractions do not fully represent human muscle contractions. Voluntary contractions

show asynchronous and varied firing frequencies, which is not mirrored in electrically stimulated muscle actions (Lee et al., 1999). Experiments during voluntary contractions can be influenced by possible disturbance factors such as the willingness of the subjects to participate properly. In addition, submaximal contractions are hard to implement under voluntary effort, since torque or EMG feedback controlled trials are impractical and it can only be matched at the isometric state before and after the dynamic phase (Groeber et al., 2020).

The first evidence of rFE in vivo was provided by Cook and McDonagh (1995). They found rFE of 30% after a stretch contraction compared to an isometric reference contraction at the first dorsal interosseous muscle. Later, Ruiter et al. (2000) as well as Lee and Herzog (2002) confirmed the occurrence of rFE in vivo at the m. adductor pollicis. Here the relation to stretch magnitude, but not to stretch velocity was shown for m. adductor pollicis. However, further in vivo measurements showed that rFE only depends on stretch magnitude in some circumstances (dependent on the muscle of interest) (Lee and Herzog, 2002; Hahn et al., 2007; Tilp et al., 2009).

Lee and Herzog (2002) showed that rFE not only exists in electrically stimulated muscle contraction, but also in voluntarily activated muscles. An almost identical rFE was found in both types of activation (voluntarily: 16%, electrically: 17%).

A lot of research on rFE has been done at the m. adductor pollicis (Lee and Herzog, 2002; Oskouei and Herzog, 2005, 2006a, 2006b; Jones et al., 2016). The m. adductor pollicis is an important muscle for hand movements, but for human locomotion it is also necessary to know if rFE appears in the bigger muscles of the lower extremities. The phenomenon rFE could also be found in measurements at the lower leg (m. gastrocnemius or m. tibialis anterior) (Tilp et al., 2009; Tilp et al., 2011; Power et al., 2015; Power et al., 2012a, 2012b; Pinniger and Cresswell, 2007; Fukutani et al., 2019b; Fukutani et al., 2017d) and m. quadriceps femoris (Altenburg et al., 2008; Hahn et al., 2007; Seiberl et al., 2012; Seiberl et al., 2010; Power et al., 2013; Shim and Garner, 2012). Brito Fontana et al. (2018) have also shown that rFE can be found in the elbow flexor. Additionally, rFE has been observed in multi-joint leg extensions (Hahn et al., 2010; Paternoster et al., 2016), which is especially important when considering the presence of rFE in human motion.

Another factor of daily human motion is that muscles are mainly innervated submaximally. Oskouei and Herzog (2006a) compared rFE at different levels of voluntary contraction and found increased rFE with higher intensities at the m. adductor pollicis. Seiberl et al. (2012) could not confirm this result in a feedback-controlled submaximal knee extension protocol. The influence of the contraction intensity (different levels of activation) remains unclear but

has been examined in the frame of one paper included in this dissertation (Groeber et al., 2020).

Another aspect which has been shown regarding rFE is the activation reduction in the steady-state after an eccentric contraction at the same force compared to an isometric reference contraction. Oskouei and Herzog (2005) used a force feedback of 30% of MVC and showed an activation reduction of around 5% after a stretch contraction compared to a pure isometric contraction in the m. adductor pollicis. Also Hahn et al. (2007) found rFE in the form of an activation reduction in the m. quadriceps femoris. This activation reduction means a higher efficiency of the muscle action and is therefore probably an optimization of energetic processes inside the muscle. Joumaa and Herzog (2013) showed for isolated rabbit psoas muscle that ATPase activity per unit of force was reduced by 17% in the isometric steady-state after stretch, compared to the purely isometric contraction. Thus, the basic terminology of rFE has to be completed: rFE can also be seen in the form of reduced activation of an isometric contraction after an active stretch compared to a purely isometric contraction, when using the same amount of force and having the same muscle length.

An unresolved issue during in vivo studies is that non-responders have been identified. Non-responders are human research participants with no or negligible rFE (Power et al., 2020). Various studies have pointed to so-called non-responders (Oskouei and Herzog, 2005; Hahn et al., 2007; Tilp et al., 2009; Seiberl et al., 2010; Seiberl et al., 2012). Various factors like neural inhibition, motor unit recruitment and mechanical factors could probably contribute to the variability of rFE appearance. Oskouei and Herzog (2005) determined with increasing level of activation a higher number of responders (4/12 participants at 10% of MVC and 10/12 participants at 60% of MVC). Lee and Herzog (2002) further showed differences between voluntarily and electrically stimulated rFE at fast-speed lengthening contractions (12% vs. 17%, respectively), which could indicate neural inhibition during fast stretches. Other authors (Chen and Power, 2019) also pointed out a possible neural inhibition during voluntary rFE experiments. They found increased rFE after 4-weeks of concentric resistance training whereas eccentric training decreased rFE for the human ankle dorsiflexors. The decrease in rFE after eccentric training was attributed to increased antagonist muscle co-activation, the increase after concentric training was attributed to the number of responders (11/15 to 15/15). Since the training lasted for just 4-weeks, the adaptations were expected to be predominantly neural, which further indicated a neural contribution to non-responders (Power et al., 2020). Another speculation on the occurrence of the non-responder phenomenon is the different proportion of different fiber types in human muscles. Ramsey et al. (2010) reported greater rFE values for the extensor digitorum longus of rats (mostly type 2 fibers, fast-twitch) compared to the soleus (mostly type 1 fibers, slow-twitch).

In contrast to this study, Pinnell et al. (2019) found no fiber-type difference for rFE. This study was conducted on human single muscle fibers of the m. vastus lateralis.

Overall, this aspect is still not well understood but reveals that this contractile property of muscle always exists during carefully controlled in vitro studies, though the complex neuro-muscular system may not always follow suit (Power et al., 2020). However, the studies on humans are very important for demonstrating the relevance of this phenomenon.

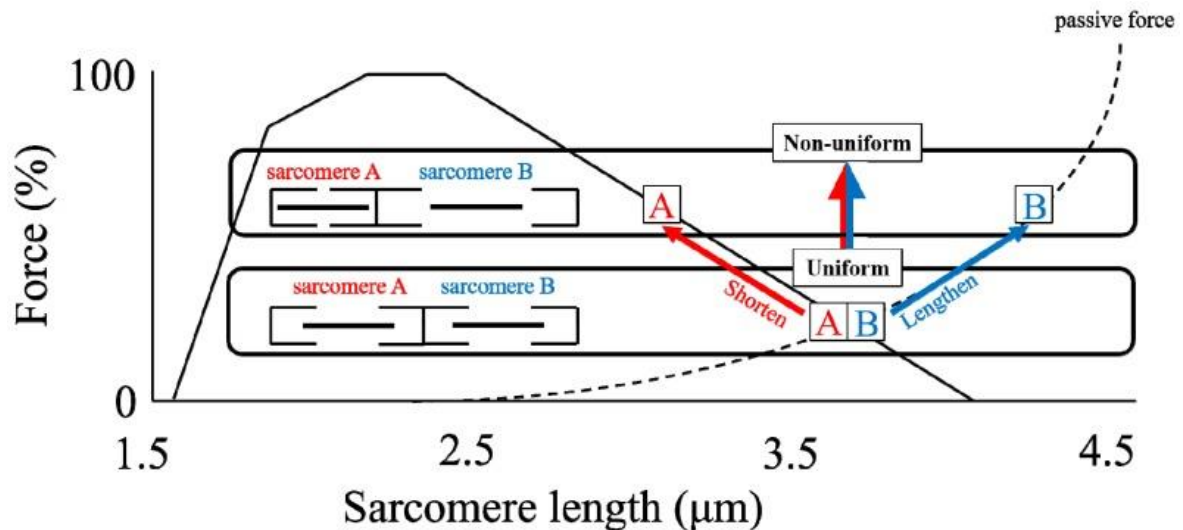
#### ***1.3.1.3 Theories on the origin of residual force enhancement***

In the following section, the mechanism(s) underlying rFE are discussed. To begin with, it should be mentioned that to date, no proposed mechanism is set in stone. The research is characterized by establishing, proving and disproving various hypotheses through experimental studies. It should be mentioned that in the following only the two primary mechanism are discussed. There are also other theories like the increase in the average force per cross-bridge (which is unlikely according to the authors) (Leonard et al., 2010) or the attachment of a second motor domain of myosin head (Brunello et al., 2007).

#### ***Sarcomere length non-uniformity theory***

Maybe the longest-lasting proposal for explaining the origin of rFE is the sarcomere length non-uniformity theory (Julian and Morgan, 1979; Morgan, 1994; Fukutani and Herzog, 2019). This theory assumes that not every single sarcomere is stretched in the same way. Accordingly, this also means that in each sarcomere the overlap of actin and myosin is different - which further means that this results in a different ability to produce force according to the force-length relationship of the sarcomere (Hill, 1953).

To illustrate this, two identical sarcomeres with slightly different lengths can be used as an example. Both sarcomeres are on the descending limb of the force-length relationship. Thus, the shorter sarcomere is stronger and pulls the slightly longer sarcomere. This process lasts until passive forces help the stretched sarcomere to reach a force equilibrium with the previously shorter sarcomere. This non-uniformity at the beginning leads to an equilibrium force greater than the theoretical force at the average sarcomere length (Figure 13) (Fukutani and Herzog, 2019).



**Figure 13:** Adapted from Fukutani and Herzog (2019). Representation of two uniform sarcomeres (lower) and non-uniform sarcomeres (upper) on the descending limb of the force-length relationship. Non-uniform sarcomeres can produce more force at the same average length compared to the uniform condition.

Thus, it is thought that an active stretch can produce rFE, because it is assumed that non-uniformities are established through active muscle stretching while isometric contractions are not (Edman, 2012).

However, it must be mentioned at this point that the sarcomere length non-uniformity theory cannot explain all experimental findings (Herzog, 2001). First, rFE should not be observed on the ascending limb of the force-length curve. Secondly, the maximal isometric force at the plateau of the force-length relationship should not be exceeded. Although in some studies rFE was smaller at the ascending limb, there was still rFE observable on the ascending limb (Peterson et al., 2004; Pun et al., 2010). Concerning the second point, no enhanced forces after stretch should be possible compared to the force of an isometric contraction at optimal muscle length. According to the sarcomere length non-uniformity theory, rFE should come from sarcomeres that produce higher forces than the average sarcomere at the specific length. However, it was shown in experimental studies that an exceeded state is also possible at the optimal muscle length (Lee and Herzog, 2008; Rassier et al., 2003). Another important characteristic of the sarcomere length non-uniformity theory is the fact, that at least two sarcomeres are needed to induce this non-uniformity (Fukutani and Herzog, 2019). Nonetheless, in experiments on isolated single sarcomeres a rFE-state could be found (meaning enhanced forces above the isometric reference contraction) (Leonard et al., 2010; Rassier and Pavlov, 2012). This result is not only important regarding the sarcomere length non-uniformity theory, it also further suggests that the mechanism should be found within a sarcomere. Additionally, the enhanced forces of single sarcomeres also exceeded isometric forces at the plateau of the force-length relationship, which also

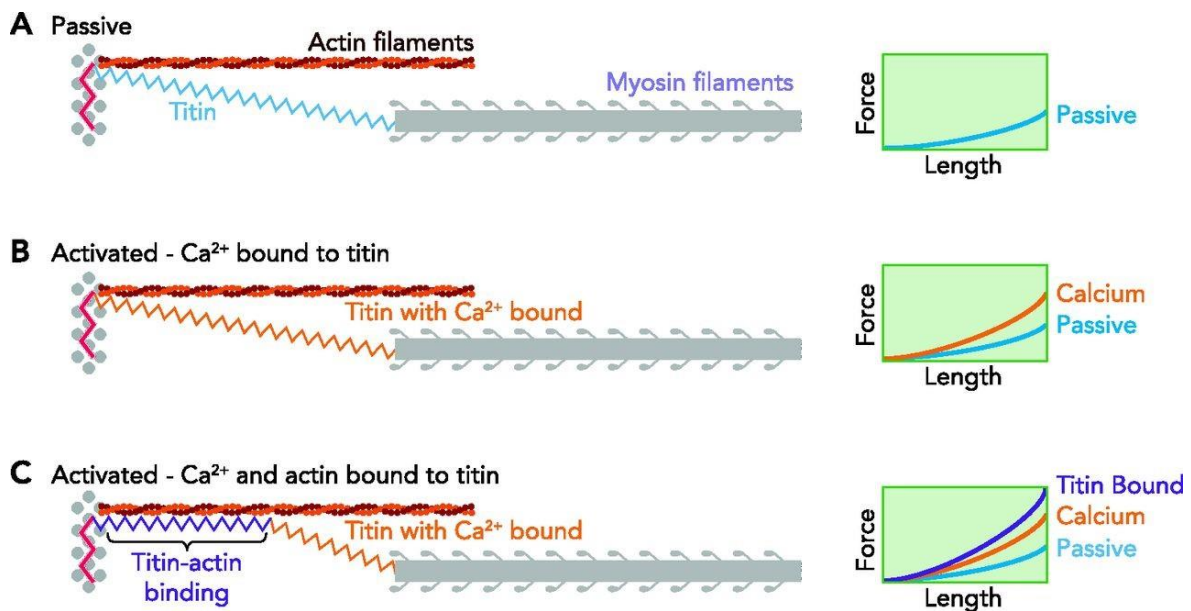
shows that the redistribution cannot be obtained from half sarcomeres (Leonard et al., 2010). The last problem with the sarcomere length non-uniformity theory is that the length of the sarcomeres should be highly non-uniform in the rFE state and essentially uniform in the isometric reference state (Fukutani and Herzog, 2019). Taking this experimental finding together it must be assumed that rFE occurs in the absence of sarcomere length non-uniformity. However, this theory cannot be ruled out entirely; it could be possible that sarcomere length non-uniformity may partly contribute to rFE (Fukutani and Herzog, 2019). With new advances in technology is it also possible to measure single sarcomere lengths in a whole muscle (Moo and Herzog, 2018). It was found that sarcomere length non-uniformity is no different in the isometric state compared to the isometric steady-state after stretch (Johnston et al., 2019), which also makes a partly contribution of non-uniform sarcomere lengths to rFE rather unlikely.

### ***Spring-like molecule titin***

Based on the existence of rFE in single sarcomeres, it is reasonable to assume that proteins within the sarcomere contribute to rFE. It is suggested that the passive structural element titin (at the beginning also called connectin) is responsible for the occurrence of rFE (Herzog et al., 2016). Titin spans from the Z line to the M band and can produce elastic forces when the sarcomere is elongated through an active stretch (Maruyama et al., 1976; Leonard and Herzog, 2010). The protein titin is associated with spring-like properties and might be responsible for rFE beside its more accepted role in passive force production and the stabilization of half-sarcomeres and sarcomeres (Herzog, 2018). There are several theoretical models using titin for the explanation of rFE (Forcinito et al., 1998; Rode et al., 2009; Nishikawa et al., 2012; Schappacher-Tilp et al., 2015). They have slightly different explanations of how exactly titin can be responsible for the development of rFE. However, these theoretical models are not the focus and will therefore not be discussed in detail in this work.

It is thought that titin causes rFE by altering its stiffness (Herzog, 2018; Fukutani and Herzog, 2019). The protein titin binds calcium at specific sites and attaches to actin during an active muscle stretch. This results in a shorter titin length (Figure 14), and the shorter free titin length increases titin stiffness (Fukutani and Herzog, 2019). The force generated by the sarcomere is the sum of cross-bridge forces and the force by parallel elastic components. The force of the parallel elastic components increase with higher titin stiffness with active muscle lengthening, therefore rFE might be achieved without changing cross-bridge induced forces (Fukutani and Herzog, 2019; Rassier, 2012). This could also explain why rFE also occurs on the plateau and the ascending limb of the force-

length curve, because this effect would be in addition to the cross-bridge forces. Additionally, this could also explain the occurrence of rFE in single sarcomeres.



**Figure 14:** Adapted from Herzog et al. (2016). The illustration of force-length diagrams caused by the elongation of titin is represented on the right side. This illustration shows different scenarios: A: Passive stretch with no interaction of titin with actin and no increased stiffness of titin, resulting in pure passive forces (blue line). B: Stretch in the presence of calcium (activation) with no binding of actin with titin. Higher passive forces due to binding of calcium to specific segments of titin and increasing the stiffness of these segments (orange line). C: A “normal” eccentric contraction. Calcium is thought to bind with titin and additionally titin is assumed to bind with actin, thereby shortening the free spring length of titin and therefore increasing its stiffness and forces when muscles are stretched. The force in this situation would be even higher (purple line).

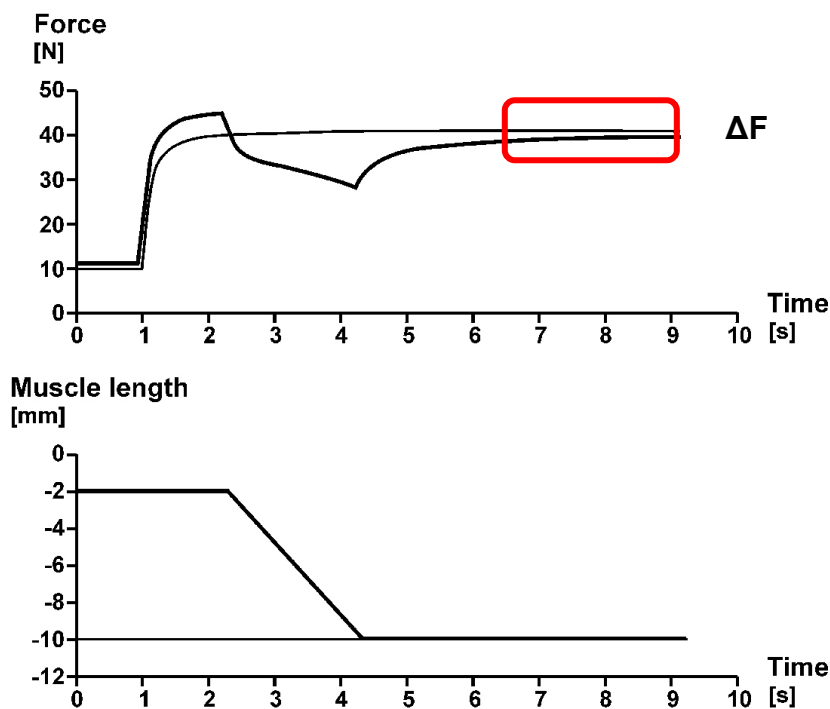
However, it must also be mentioned with the theory that it is simply not yet clear whether titin is actually the decisive factor in the occurrence of rFE. At least, the explanation with the two components of titin ( $\text{Ca}^{2+}$  binding and Titin-actin binding) could still explain observations of rFE for conditions where actin filaments were extracted by gelsolin (Cornachione et al., 2016). An unresolved issue is that it would also be expected for sarcomere stiffness to be enhanced in the force-enhanced state with increased titin stiffness (Fukutani and Herzog, 2019); but different studies found either a decrease (Sugi and Tsuchiya, 1988), no change (Julian and Morgan, 1979) or an increase (Herzog and Leonard, 2000) in sarcomere stiffness in the force-enhanced state compared to the isometric reference contraction.

In future research, it will be necessary to study the exact contribution of titin to rFE, by systematically investigating the influence of “activation-dependent” chemicals on the stiffness of titin. Another aspect to resolve would be the exact deformation and binding of titin during and after active stretch.

### 1.3.2 Residual force depression

In contrast to an active stretch, after a shortening contraction force/torque is depressed compared to an isometric reference contraction at the same muscle length and activation level. In literature, this is called residual force depression (rFD) (Figure 15). However, the term is again not used in a consistent manner; sometimes it is also named “FD after muscle shortening” or “FD in the steady-state.” The meaning or definition of this post-concentric force, however, remains the same:

**“Force depression is defined here as the absolute (or percentage) decrease in the steady-state, isometric force following shortening contraction compared to the purely isometric force at the corresponding length” (Herzog, 2001).**



**Figure 15:** Modified from Herzog (2001). Illustration of residual force depression. After muscle shortening (unsteady lower line), the isometric steady-state force is depressed ( $\Delta F$ ) compared to the isometric reference contraction at the final reference muscle length.

#### 1.3.2.1 Phenomenological description of residual force depression

The phenomenon rFD was first identified by (Abbott and Aubert, 1952). Since then, rFD has been observed in a variety of animal models and functional levels of skeletal muscle (Chen et al., 2019). It is well accepted that rFD is long lasting (Abbott and Aubert, 1952; Herzog and Leonard, 1997), but it can be abolished instantaneously by deactivating the muscle so that the force drops to zero (Abbott and Aubert, 1952; Herzog and Leonard, 1997; Granzier



and Pollack, 1989). Different parameters seem to influence the magnitude of rFD. Firstly, rFD has been shown to increase with the magnitude of shortening (Herzog and Leonard, 1997; Maréchal and Plaghki, 1979) and secondly it depends on the force produced during shortening (Herzog et al., 2000; Kosterina et al., 2008). Previously, it was also reported that the magnitude of rFD depends on the shortening velocity (Kosterina et al., 2008; Maréchal and Plaghki, 1979). The parameter shortening velocity has been recently under discussion and the direct connection between rFD and the shortening velocity has been questioned (Chen and Power, 2019). Taking the influences of mechanical work (force  $\times$  displacement) into account, the velocity dependency of rFD was disproved (Chen and Power, 2019; Herzog et al., 2000). Experiments at the cat soleus showed that rFD was similar for conditions in which the mechanical work during shortening was similar, independent of the velocity of shortening (Herzog et al., 2000). In their experiment, rFD varied significantly at different amounts of mechanical work at constant velocity. This shows that there is a direct dependence of rFD and the mechanical work, and therefore the speed-dependent notion of rFD was initially a wrong assumption (Chen and Power, 2019).

#### ***1.3.2.2 Residual force depression in humans***

The existence of rFD has already been shown in animal preparations a long time ago, finally Ruiter et al. (1998) delivered the proof in human muscle for the first time. Their study was conducted on the m. adductor pollicis under electrical stimulation. Subsequently, this result under electrical stimulation was confirmed on the m. adductor pollicis by other authors (Lee and Herzog, 2003; Fortuna et al., 2017; Fortuna et al., 2018) and the existence of rFD was also confirmed in larger muscle groups such as the plantar flexors (Fukutani et al., 2017c; Hahn and Riedel, 2018). In these studies using electrical stimulation, the dependency of rFD regarding the magnitude of shortening (Ruiter et al., 1998; Lee and Herzog, 2003) and the work performed during shortening (Lee and Herzog, 2003; Fortuna et al., 2017) could be confirmed.

Lee et al. (1999) further showed rFD also under maximal voluntary contraction at the m. quadriceps femoris and demonstrated therefore that rFD is not just an artifact of electrical stimulations, but a property of human skeletal muscle. Later, also during submaximal voluntary contractions the presence of rFD was confirmed (Rousanoglou et al., 2007). When directly comparing electrically with voluntarily activated shortening contractions, no difference in rFD values was found (Ruiter and Haan, 2003; Lee and Herzog, 2003).

Although rFD has been shown in different muscle groups, the direct influence of the size of the examined muscle remains unexplained so far (Chen and Power, 2019). In the literature rFD values between 5-12% for the m. quadriceps femoris (Lee et al., 1999, 2000), 8-21%

for the plantar flexors (Tilp et al., 2009; Tilp et al., 2011) and 8-27% for the m. adductor pollicis (Ruiter and Haan, 2003; Lee and Herzog, 2003) were reported during maximal voluntary contractions.

Additionally, Tilp et al. (2011) and Fukutani et al. (2017c) have also considered the contribution of fascicle behavior on rFD. Neither found any differences in fascicle lengths and pennation angles between isometric reference contractions and shortening contractions, despite significant rFD after the shortening contractions.

### ***1.3.2.3 Theories on the origin of residual force depression***

Over the years, several mechanisms have been proposed to explain the phenomenon of rFD. Similar to rFE previously, the approach has often been to prove/disprove the theories with experimental studies. Four primary mechanisms are discussed in literature (Herzog, 2001). However, the first three of those now-presented theories are unable to explain some experimental results and are therefore considered improbable.

#### ***Sarcomere length non-uniformity theory***

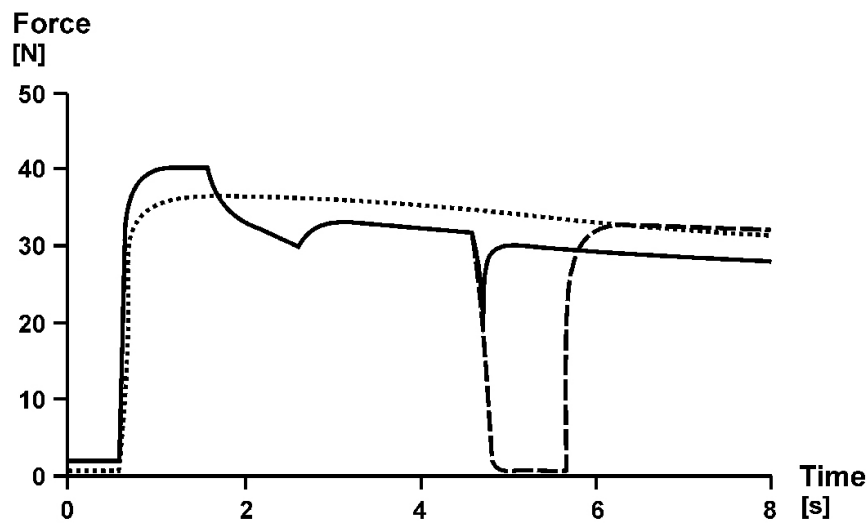
Again, the sarcomere length non-uniformity theory (see chapter 1.3.1.3) is an explanatory approach for the emergence of rFD. However, certain predictions made with this theory contradict experimental study results. Due to the sarcomere length non-uniformity theory, rFD should not occur on the ascending limb of the force-length relationship (Herzog, 2001). Nevertheless, rFD was also found on the ascending limb (Herzog and Leonard, 1997). Additionally, two studies controlled sarcomere length to remain uniform, but they revealed contradictory results: Edman et al. (1993) reported no rFD with uniform sarcomere length, whilst Granzier and Pollack (1989) found the same amount of rFD in conditions where uniformity was artificially enforced compared to non-uniform conditions. Last, due to this theory rFD should be accompanied by an increase in muscle (fiber) stiffness (Morgan et al., 2000; Rassier and Herzog, 2004). Nevertheless, muscle stiffness does not seem to increase in the rFD state; stiffness was equal for purely isometric reference contractions and isometric contractions following shortening (Herzog and Leonard, 2000), or muscle stiffness even slightly decreased (Sugi and Tsuchiya, 1988).

Therefore, it can be asserted here again that the sarcomere length non-uniformity theory cannot (solely) explain the occurrence of rFD.

#### ***Accumulation of protons and phosphates***

An increase in proton and inorganic phosphate concentration during shortening contractions is also suggested as an explanation for rFD (Rassier and Herzog, 2004). It is thought that this increase probably results from ATP consumption (Granzier and Pollack, 1989). The

effect should be similarly long lasting to the fatigue effect. However, in the case of an interruption in muscle activation, rFD is abolished (Figure 16) (Abbott and Aubert, 1952; Herzog and Leonard, 1997). Thus, this theory is very unlikely.



**Figure 16:** Adapted from Herzog (2001). rFD is abolished by an interruption of muscle activation. The dotted line represents the isometric reference contraction at the final muscle length. The solid line represents the shortening contraction and the dashed line the shortening contraction with a short interruption of activation at the final muscle length.

### ***Reduction of calcium affinity***

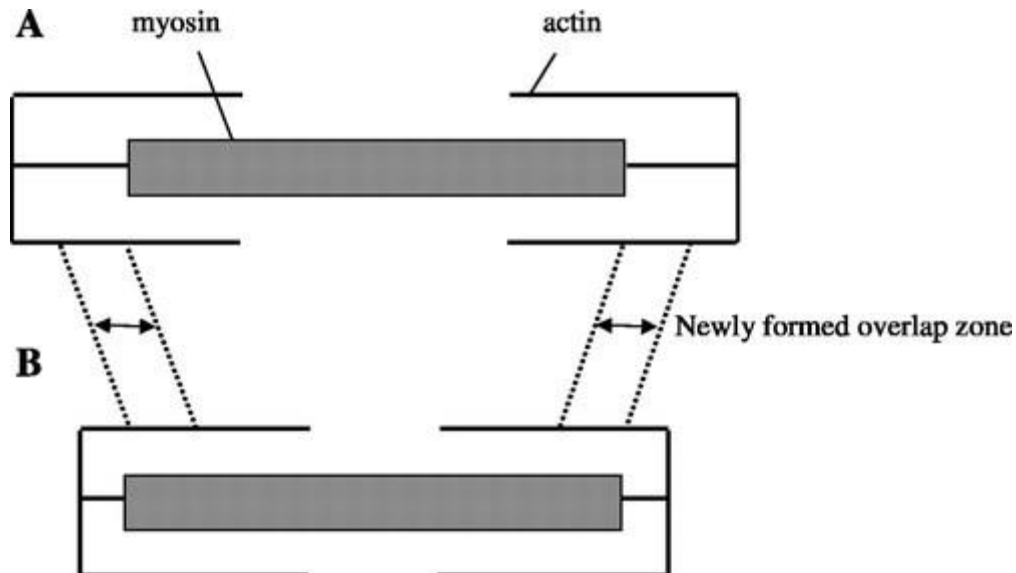
This mechanism is based on the idea that muscle shortening reduces the affinity for calcium at the troponin binding sites on the actin filament (Edman, 1996). According to this theory, the depressed state after shortening should only last about two seconds, because the calcium affinity could be restored in this time interval (Herzog, 2001). Several studies found evidence that rFD is long-lasting (Abbott and Aubert, 1952; Ruiter et al., 1998; Herzog et al., 1998; Maréchal and Plaghki, 1979), which makes this theory unlikely.

### ***Stress-induced inhibition of cross-bridge attachments***

According to this theory, a decrease in cross-bridge attachments in the newly formed actin-myosin overlap zone is responsible for rFD (Figure 17) (Maréchal and Plaghki, 1979). The shortening causes stress-induced angular deformation in the actin filament, which was shown by Joumaa et al. (2018) using X-ray diffraction. During the active shortening, strained and deformed parts of the actin filament are entering the new overlap zone, therefore a formation of new-cross-bridge attachments is inhibited (Joumaa et al., 2012). In contrast to the other theories, there are no experimental studies that refute the stress-induced inhibition of newly build cross-bridge attachments. According to this theory, the following hypotheses can be formulated, all of which have been shown to be correct (Herzog, 2001): rFD increases with the shortening distance (Abbott and Aubert, 1952; Ruiter et al.,

1998; Maréchal and Plaghki, 1979), with the force during shortening (Herzog and Leonard, 1997), and with the amount of mechanical work produced during shortening (Herzog et al., 2000; Lee and Herzog, 2003; Fortuna et al., 2017). Additionally, rFD is long-lasting (Abbott and Aubert, 1952; Herzog et al., 1998) but can be abolished immediately when the muscle is deactivated (Herzog and Leonard, 1997).

Thus, this theory is strongly accepted in the literature and is used to explain the occurrence of rFD. Whether this is the only reason for the occurrence of rFD remain questionable. With the recent findings regarding the titin theory, it is suspected that titin may also contribute to the stress-induced inhibition of newly built cross-bridge attachments (Chen and Power, 2019). For example the “sticky-spring” mechanism suggests, that titin blocks the formation of new cross-bridges (Rode et al., 2009), whereas other authors suggest that titin slackens, which leads to force depression in proportion to the distance shortened (Tahir et al., 2020). A conformational change in titin dependent on the velocity of shortening, could further explain the inversely proportionality of rFD to the shortening velocity (Holt and Williams, 2018), which was unexplained with the theory of the stress-induced deformation of cross-bridges (Nishikawa et al., 2018). Nevertheless, the current literature assumes that a reduction in the number of attached cross-bridges following active shortening is the main factor contributing to rFD (Chen and Power, 2019).



**Figure 17:** Adapted from Rassier and Herzog (2004). Whilst shortening (from A to B), new parts of the actin filaments enter the overlap zone. It is assumed that in the newly formed overlap zone the attachment of cross-bridges is inhibited in a stress-dependent manner. This inhibition on new cross-bridge attachments leads to rFD.

### 1.3.3 History-dependent properties in a stretch-shortening cycle

These mostly independently researched phenomena of rFE and rFD are directly confronted in a SSC. Because pure stretch or pure shortening muscle-tendon unit actions have no high relevance in many athletic movements, it is also necessary to investigate these history-dependent phenomena in the course of a SSC.

### 1.4 Aims

The general aim of this research is to achieve a comprehensive understanding of the history-dependent properties in a SSC. Thereupon this work investigates the parameters by which these properties are influenced in human SSC muscle action.

In the following section, the aim/hypothesis and focus of each paper included is presented.

The **first paper**, “The Contraction Modalities in a Stretch-Shortening Cycle in Animals and Single Joint Movements in Humans: A Systematic review”, was designed to give a holistic overview of in vitro, in situ and in vivo single joint movement of the history-dependent properties in a SSC. A connection between animal models and experiments on human musculature is given. This study was designed to close the gap between the animal and human studies and it seeks to inform future research about which contraction modalities are necessary to consider in SSC experiments.

The aim of the **second paper**, “Contribution of Stretch-Induced Force Enhancement to Increased Performance in Maximal Voluntary and Submaximal Artificially Activated Stretch-Shortening Muscle Action”, was to gain insight into the influence of contraction intensity on performance enhancement in a SSC. We hypothesized that with increasing intensity the SSC-effect is larger due to increased rFE.

“The effect of stretch-shortening magnitude and muscle-tendon unit length on performance enhancement in a stretch-shortening cycle” is the **third paper** of this work. In this study, we sought to investigate the influence of different SSC-magnitudes and muscle-tendon unit lengths on the SSC performance. Firstly, we hypothesized that with greater SSC-magnitude transient FE is enhanced in a SSC compared to an isometric pre-activation of a shortening contraction, which also influences the SSC-effect. However due to greater shortening range at greater SSC-magnitudes, rFE is eliminated by the shortening phase. And secondly, we expected no difference in transient FE, but increased rFE at greater muscle-tendon unit lengths due to increased titin stiffness at longer muscle-tendon unit lengths.

## **2. Publications**

In this chapter, the papers of this cumulative dissertation are presented.

### **2.1 Publication 1: The Contraction Modalities in a Stretch-Shortening Cycle in Animals and Single Joint Movements in Humans: A Systematic Review.**

#### **Authors:**

Martin Groeber, Lena Reinhart, Philipp Kornfeind and Arnold Baca

#### **Status:**

The manuscript was published by the Journal of Sport Science and Medicine on 19 November 2019 (Groeber et al., 2019).

#### **Authors' contribution:**

Martin Groeber and Lena Reinhart carried out the systematic literature search and data collection. Martin Groeber analyzed the data. Martin Groeber, Philipp Kornfeind and Arnold Baca contributed to the interpretation of the data. Martin Groeber wrote the first draft of the manuscript; all authors contributed to the article and approved the submitted manuscript.

Review article

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

Martin Groeber <sup>1</sup>✉, Lena Reinhart <sup>1,2</sup>, Philipp Kornfeind <sup>1</sup> and Arnold Baca <sup>1</sup>

<sup>1</sup> Centre of Sport Science and University Sports, Department of Biomechanics, Kinesiology and Computer Science in Sport, University of Vienna, Vienna, Austria; <sup>2</sup> 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

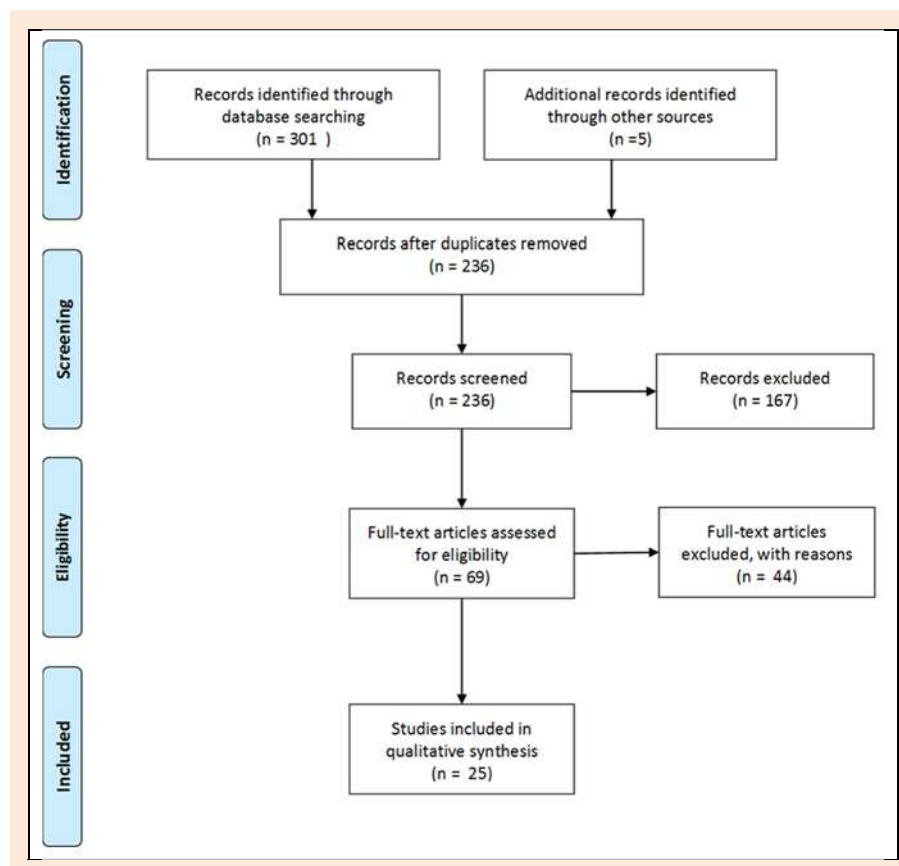
duplicates were instantly deleted.

### 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 esculenta</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 $\mu$ m/s Shortening: 0.3 $\mu$ m/s	6 $\mu$ m / 6 $\mu$ m	2.4 $\mu$ m	
Fukutani, 2018	43	Rabbit (New Zealand white rabbit)	Soleus, single fibres	?	Stretch: 0.15 $\mu$ m/s Shortening: 48 or 600 $\mu$ m/s	3 $\mu$ m / 0.024 $\mu$ m or 3 $\mu$ m	2.724 $\mu$ m or 3 $\mu$ 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 M F	Muscle group	Intensity (% of MVC)	Speed (°/s) Stretch/shortening	Range of Motion (°) Stretch/shortening	Joint angle at beginning (°)
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 ¾ 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.

## Acknowledgements

The reported experiments comply with the current laws of the country in which they were performed. The authors have no conflicts of interests to declare. Open access funding provided by University of Vienna.

## References

- Abbott, B.C. and Aubert, X.M. (1952) The force exerted by active striated muscle during and after change of length. *The Journal of Physiology* **117**(1), 77-86.
- Blanpied, P., Levins, J.A. and Murphy, E. (1995) The effects of different stretch velocities on average force of the shortening phase in the stretch-shorten cycle. *The Journal of Orthopaedic and Sports Physical Therapy* **21**(6), 345-353.
- Bobbert, M.F. and Casius, L.J.R. (2005) Is the Effect of a Countermovement on Jump Height due to Active State Development? *Medicine & Science in Sports & Exercise* **37**(3), 440-446.
- Bohm, S., Marzilger, R., Mersmann, F., Santuz, A. and Arampatzis, A. (2018) Operating length and velocity of human vastus lateralis muscle during walking and running. *Scientific Reports* **8**(1), 5066.
- Bullimore, S.R., Leonard, T.R., Rassier, D.E. and Herzog, W. (2007) History-dependence of isometric muscle force: Effect of prior stretch or shortening amplitude. *Journal of Biomechanics* **40**(7), 1518-1524.
- Bullimore, S.R., MacIntosh, B.R. and Herzog, W. (2008) Is a parallel elastic element responsible for the enhancement of steady-state muscle force following active stretch? *The Journal of Experimental Biology* **211**(18), 3001-3008.
- Cavagna, G., Citterio, G. and Jacini, P. (1981) Effect of speed and extent of stretching on the elastic properties of active frog muscle. *Journal of Experimental Biology* **91**(1), 131-143.
- Cavagna, G.A. and Citterio, G. (1974) Effect of stretching on the elastic characteristics and the contractile component of frog striated muscle. *The Journal of Physiology* **239**(1), 1-14.
- Cavagna, G.A., Dusman, B. and Margaria, R. (1968) Positive work done by a previously stretched muscle. *Journal of Applied Physiology (Bethesda, Md.: 1985)* **24**(1), 21-32.
- Cavagna, G.A., Heglund, N.C., Harry, J.D. and Mantovani, M. (1994) Storage and release of mechanical energy by contracting frog muscle fibres. *The Journal of Physiology* **481**(3), 689-708.
- Chapman, N., Whitting, J., Broadbent, S., Crowley-McHattan, Z. and Meir, R. (2018) Residual Force Enhancement in Humans: A Systematic Review. *Journal of Applied Biomechanics* **34**(3), 240-248.
- Downs, S.H. and Black, N. (1998) The feasibility of creating a checklist for the assessment of the methodological quality both of randomised and non-randomised studies of health care interventions. *Journal of Epidemiology and Community Health* **52**(6), 377-384.
- DuVall, M.M., Gifford, J.L., Amrein, M. and Herzog, W. (2013) Altered mechanical properties of titin immunoglobulin domain 27 in the



- presence of calcium. *European Biophysics Journal* **42**(4), 301-307.
- Edman, K.A. (1978) Maximum velocity of shortening in relation to sarcomere length and degree of activation of frog muscle fibres proceedings. *The Journal of Physiology* **278**, 9-10.
- Edman, K.A., Elzinga, G. and Noble, M.I. (1982) Residual force enhancement after stretch of contracting frog single muscle fibers. *The Journal of General Physiology* **80**(5), 769-784.
- Ettema, G.J., Huijing, P.A. and Haan, A. de (1992) The potentiating effect of prestretch on the contractile performance of rat gastrocnemius medialis muscle during subsequent shortening and isometric contractions. *The Journal of Experimental Biology* **165**, 121-136.
- Ettema, G.J., Huijing, P.A., van Ingen Schenau, G.J. and Haan, A. de (1990a) Effects of prestretch at the onset of stimulation on mechanical work output of rat medial gastrocnemius muscle-tendon complex. *The Journal of Experimental Biology* **152**(1), 333-351.
- Ettema, G.J., van Soest, A.J. and Huijing, P.A. (1990b) The role of series elastic structures in prestretch-induced work enhancement during isotonic and isokinetic contractions. *The Journal of Experimental Biology* **154**(1), 121-136.
- Fortuna, R., Groeber, M., Seiberl, W., Power, G.A. and Herzog, W. (2017) Shortening-induced force depression is modulated in a time- and speed-dependent manner following a stretch-shortening cycle. *Physiological Reports* **5**(12), pii: e13279.
- Fortuna, R., Kirchhübel, H., Seiberl, W., Power, G.A. and Herzog, W. (2018) Force depression following a stretch-shortening cycle is independent of stretch peak force and work performed during shortening. *Scientific Reports* **8**(1), 1534.
- Fukutani, A. and Herzog, W. (2018) Residual Force Enhancement Is Attenuated in a Shortening Magnitude-dependent Manner. *Medicine and Science in Sports And Exercise* **50**(10), 2007-2014.
- Fukutani, A., Joumaa, V. and Herzog, W. (2017a) Influence of residual force enhancement and elongation of attached cross-bridges on stretch-shortening cycle in skinned muscle fibers. *Physiological Reports* **5**(22), pii: e13477.
- Fukutani, A., Kurihara, T. and Isaka, T. (2015a) Factors of force potentiation induced by stretch-shortening cycle in plantarflexors. *PLoS one* **10**(6), e0120579.
- Fukutani, A., Kurihara, T. and Isaka, T. (2015b) Influence of joint angular velocity on electrically evoked concentric force potentiation induced by stretch-shortening cycle in young adults. *SpringerPlus* **4**, 82.
- Fukutani, A., Misaki, J. and Isaka, T. (2017b) Both the elongation of attached crossbridges and residual force enhancement contribute to joint torque enhancement by the stretch-shortening cycle. *Royal Society Open Science* **4**(2), 161036.
- Fukutani, A., Misaki, J. and Isaka, T. (2016) Effect of Preactivation on Torque Enhancement by the Stretch-Shortening Cycle in Knee Extensors. *PLoS one* **11**(7), e0159058.
- Groeber, M., Baca, A. and Seiberl, W. (2018) Influence of different stretch velocities on contraction performance of the human triceps surae during and after stretch-shortening cycles. In: *Book of Abstracts: European College of Sport Science, 4-7 July, 2018*. p. 69.
- Hahn, D. and Riedel, T.N. (2018) Residual force enhancement contributes to increased performance during stretch-shortening cycles of human plantar flexor muscles in vivo. *Journal of Biomechanics* **77**, 190-193.
- Hahn, D., Seiberl, W., Schmidt, S., Schweizer, K. and Schwirtz, A. (2010) Evidence of residual force enhancement for multi-joint leg extension. *Journal of Biomechanics* **43**(8), 1503-1508.
- Herzog W. (2001) The nature of force depression and force enhancement in skeletal muscle contraction. *European Journal of Sport Science* **1**(3), 1-14.
- Herzog, W. (2014) Mechanisms of enhanced force production in lengthening (eccentric) muscle contractions. *Journal of Applied Physiology (Bethesda, Md.: 1985)* **116**(11), 1407-1417.
- Herzog, W. and Leonard, T.R. (2000) The history dependence of force production in mammalian skeletal muscle following stretch-shortening and shortening-stretch cycles. *Journal of Biomechanics* **33**(5), 531-542.
- Herzog, W. and Leonard, T.R. (1997) Depression of cat soleus forces following isokinetic shortening. *Journal of Biomechanics* **30**(9), 865-872.
- Herzog, W., Leonard, T.R. and Wu, J.Z. (2000) The relationship between force depression following shortening and mechanical work in skeletal muscle. *Journal of Biomechanics* **33**(6), 659-668.
- Herzog, W., Schachar, R. and Leonard, T.R. (2003) Characterization of the passive component of force enhancement following active stretching of skeletal muscle. *The Journal of Experimental Biology* **206**(20), 3635-3643.
- Herzog W, Schappacher G, DuVall M, Leonard TR. and Herzog JA. (2016) Residual Force Enhancement Following Eccentric Contractions: A New Mechanism Involving Titin. *Physiology (Bethesda)* **31**(4), 300-312.
- Hill, A.V. (1938) The heat of shortening and the dynamic constants of muscle. *Proceedings of the Royal Society Series B-Biological Sciences* **126**(843), 136-195.
- Jarde A., Losilla J.M. and Vives J. (2012) Suitability of three different tools for the assessment of methodological quality in ex post facto studies. *International Journal of Clinical and Health* **(12)**, 97-108.
- Joumaa, V., Rassier, D.E., Leonard, T.R. and Herzog, W. (2008) The origin of passive force enhancement in skeletal muscle. *American Journal of Physiology. Cell Physiology* **294**(1), C74-78.
- Komi, P.V. (2000) Stretch-shortening cycle: A powerful model to study normal and fatigued muscle. *Journal of Biomechanics* **33**(10), 1197-1206.
- Komi, P.V. and Gollhofer, A. (1997) Stretch Reflexes Can Have an Important Role in Force Enhancement during SSC Exercise. *Journal of Applied Biomechanics* **13**(4), 451-460.
- Kosterina, N., Westerblad, H. and Eriksson, A. (2009) Mechanical work as predictor of force enhancement and force depression. *Journal of Biomechanics* **42**(11), 1628-1634.
- Labeit, D., Watanabe, K. and Witt C. Fujita, H., Wu, Y., Lahmers, S., Funck, T., Labeit, S. and Granzier, H. (2003) Calcium-dependent molecular spring elements in the giant protein titin. *Proceedings of the National Academy of Sciences of the United States of America* **100**(23), 13716-13721.
- Lee, E.-J. and Herzog, W. (2009) Shortening-induced force depression is primarily caused by cross-bridges in strongly bound states. *Journal of Biomechanics* **42**(14), 2336-2340.
- Lee HD, Suter E. and Herzog W. (1999) Force depression in human quadriceps femoris following voluntary shortening contractions. *J Appl Physiol.* **87**(5), 1651-1655.
- Lee, H.D., Herzog, W. and Leonard, T. (2001) Effects of cyclic changes in muscle length on force production in in-situ cat soleus. *Journal of Biomechanics* **34**(8), 979-987.
- Lee, H.-D. and Herzog, W. (2002) Force enhancement following muscle stretch of electrically stimulated and voluntarily activated human adductor pollicis. *The Journal of Physiology* **545**(1), 32-330.
- Maréchal, G. and Plaghki, L. (1979) The deficit of the isometric tetanic tension redeveloped after a release of frog muscle at a constant velocity. *The Journal of General Physiology* **73**(4), 453-467.
- McHugh, M.L. (2012) Interrater reliability: The kappa statistic. *Biochemia Medica* **22**(3), 276-282.
- Morgan, D.L., Whitehead, N.P., Wise, A.K., Gregory, J.E. and Proske, U. (2000) Tension changes in the cat soleus muscle following slow stretch or shortening of the contracting muscle. *The Journal of Physiology* **522**(2), 503-513.
- Oskouei, A.E. and Herzog, W. (2006) The dependence of force enhancement on activation in human adductor pollicis. *European Journal of Applied Physiology* **98**(1), 22-29.
- Paquin J, Power GA. (2018) History dependence of the EMG-torque relationship. *Journal of Electromyography and Kinesiology* **41**, 109-115.
- Pinniger, G.J. and Cresswell, A.G. (2007) Residual force enhancement after lengthening is present during submaximal plantar flexion and dorsiflexion actions in humans. *Journal of Applied Physiology (Bethesda, Md.: 1985)* **102**(1), 18-25.
- Pun, C., Syed, A. and Rassier, D.E. (2010). History-dependent properties of skeletal muscle myofibrils contracting along the ascending limb of the force-length relationship. *Proceeding Biological Sciences* **277**(1680), 475-484.
- Raiteri, B.J. and Hahn, D. (2019) A reduction in compliance or activation level reduces residual force depression in human tibialis anterior. *Acta Physiol (Oxf)* **225**(3), e13198.
- Rassier, D.E., Herzog, W. and Pollack, G.H. (2003) Dynamics of individual sarcomeres during and after stretch in activated single myofibrils. *Proceedings. Biological sciences* **270**(1525), 1735-1740.
- Roberts, T.J. and Konow, N. (2013) How tendons buffer energy dissipation by muscle. *Exercise and Sport Sciences Reviews* **41**(4), 186-



193.

- Rousanoglou EN, Oskouei AE, Herzog W. (2007) Force depression following muscle shortening in sub-maximal voluntary contractions of human adductor pollicis. *Journal of Biomechanics* **40**(1), 1-8.
- Seiberl, W., Paternoster, F., Achatz, F., Schwirtz, A. and Hahn, D. (2013) On the relevance of residual force enhancement for everyday human movement. *Journal of Biomechanics* **46**(12), 1996-2001.
- Seiberl, W., Power, G.A., Herzog, W. and Hahn, D. (2015) The stretch-shortening cycle (SSC) revisited: Residual force enhancement contributes to increased performance during fast SSCs of human m. adductor pollicis. *Physiological Reports* **3**(5), pii: e12401.
- Sugi, H. and Tsuchiya, T. (1988) Stiffness changes during enhancement and deficit of isometric force by slow length changes in frog skeletal muscle fibres. *The Journal of Physiology* **407**, 215-229.
- Svantesson, U. and Grimby, G. (1995) Stretch-shortening cycle during plantar flexion in young and elderly women and men. *European Journal of Applied Physiology and Occupational Physiology* **71**(5), 381-385.
- Svantesson, U., Grimby, G. and Thomeé, R. (1994) Potentiation of concentric plantar flexion torque following eccentric and isometric muscle actions. *Acta Physiologica Scandinavica* **152**(3), 287-293.
- Takarada, Y., Iwamoto, H., Sugi, H., Hirano, Y. and Ishii, N. (1997) Stretch-induced enhancement of mechanical work production in frog single fibers and human muscle. *Journal of applied physiology (Bethesda, Md: 1985)* **83**(5), 1741-1748.
- van Schenau, G.J.I., Bobbert, M.F. and Haan, A. de (1997) Does Elastic Energy Enhance Work and Efficiency in the Stretch-Shortening Cycle? *Journal of Applied Biomechanics* **13**(4), 389-415.

### 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.

## **2.2 Publication 2: Contribution of Stretch-Induced Force Enhancement to Increased Performance in Maximal Voluntary and Submaximal Artificially Activated Stretch-Shortening Muscle Action**

### **Authors:**

Martin Groeber, Savvas Stafilidis, Wolfgang Seiberl and Arnold Baca

### **Status:**

The manuscript was published by Frontiers in Physiology on 12 November 2020 (Groeber et al., 2020).

### **Authors' contribution:**

Martin Groeber, Savvas Stafilidis, and Arnold Baca conceived and designed the experiment. Martin Groeber performed the experiment. Martin Groeber and Savvas Stafilidis analyzed the data. Martin Groeber, Savvas Stafilidis, Wolfgang Seiberl, and Arnold Baca discussed the results, made a substantial contribution to the interpretation of data, and contributed to the elaboration of the manuscript. All authors contributed to the article and approved the submitted version.



# Contribution of Stretch-Induced Force Enhancement to Increased Performance in Maximal Voluntary and Submaximal Artificially Activated Stretch-Shortening Muscle Action

Martin Groeber<sup>1\*</sup>, Savvas Stafilidis<sup>1</sup>, Wolfgang Seiberl<sup>2</sup> and Arnold Baca<sup>1</sup>

<sup>1</sup> Department of Biomechanics, Kinesiology and Computer Science in Sport, Centre for Sport Science and University Sports, University of Vienna, Vienna, Austria, <sup>2</sup> Department of Human Movement Science, Institute of Sport Science, Bundeswehr University Munich, Neubiberg, Germany

## OPEN ACCESS

### Edited by:

Li Zuo,  
The Ohio State University,  
United States

### Reviewed by:

Mark Willems,  
University of Chichester,  
United Kingdom  
Huub Maas,  
Vrije Universiteit Amsterdam,  
Netherlands

### \*Correspondence:

Martin Groeber  
martin.groeber@univie.ac.at

### Specialty section:

This article was submitted to  
Striated Muscle Physiology,  
a section of the journal  
Frontiers in Physiology

**Received:** 06 August 2020

**Accepted:** 19 October 2020

**Published:** 12 November 2020

### Citation:

Groeber M, Stafilidis S, Seiberl W  
and Baca A (2020) Contribution  
of Stretch-Induced Force  
Enhancement to Increased  
Performance in Maximal Voluntary  
and Submaximal Artificially Activated  
Stretch-Shortening Muscle Action.  
Front. Physiol. 11:592183.  
doi: 10.3389/fphys.2020.592183

In everyday muscle action or exercises, a stretch-shortening cycle (SSC) is performed under different levels of intensity. Thereby, compared to a pure shortening contraction, the shortening phase in a SSC shows increased force, work, and power. One mechanism to explain this performance enhancement in the SSC shortening phase is, besides others, referred to the phenomenon of stretch-induced increase in muscle force (known as residual force enhancement; rFE). It is unclear to what extent the intensity of muscle action influences the contribution of rFE to the SSC performance enhancement. Therefore, we examined the knee torque, knee kinematics, m. vastus lateralis fascicle length, and pennation angle changes of 30 healthy adults during isometric, shortening (CON) and stretch-shortening (SSC) conditions of the quadriceps femoris. We conducted maximal voluntary contractions (MVC) and submaximal electrically stimulated contractions at 20%, 35%, and 50% of MVC. Isometric trials were performed at 20° knee flexion (straight leg: 0°), and dynamic trials followed dynamometer-driven ramp profiles of 80°–20° (CON) and 20°–80°–20° (SSC), at an angular velocity set to 60°/s. Joint mechanical work during shortening was significantly ( $p < 0.05$ ) enhanced by up to 21% for all SSC conditions compared to pure CON contractions at the same intensity. Regarding the steady-state torque after the dynamic phase, we found significant torque depression for all submaximal SSCs compared to the isometric reference contractions. There was no difference in the steady-state torque after the shortening phases between CON and SSC conditions at all submaximal intensities, indicating no stretch-induced rFE that persisted throughout the shortening. In contrast, during MVC efforts, the steady-state torque after SSC was significantly less depressed compared to the steady-state torque after the CON condition ( $p = 0.034$ ), without significant differences in the m. vastus lateralis fascicle length and pennation angle. From these results, we concluded that the contribution of the potential enhancing factors in SSCs of the m. quadriceps femoris is dependent on the contraction intensity and the type of activation.

**Keywords:** force enhancement, force depression, elastic energy, electrical stimulation, muscular activation, concentric, eccentric

## INTRODUCTION

A stretch-shortening cycle (SSC) is a muscle action that often occurs in everyday movements or sporting exercises. During a SSC, a lengthening contraction is immediately followed by a shortening contraction. This results in increased performance during the shortening phase compared to pure shortening contractions (“SSC-effect”) (Komi and Gollhofer, 1997; Komi, 2000). The mechanisms attributed to the enhanced force or work during the concentric phase of the SSC are the stretch-reflex (Dietz et al., 1979), the release of stored passive-elastic energy (Finni et al., 2001; Kawakami et al., 2002) and the pre-activation of muscles (Bobbert and Casius, 2005). The reflex motor response can enhance the ongoing contraction and thus stretch reflexes can make a net contribution to muscle stiffness in the SSC (Komi and Gollhofer, 1997). Tendinous tissue can store and recoil passive elastic energy, which can be utilized in a SSC (Finni et al., 2001). Pre-activation describes the time required for force development. In the SSC, the initial stretch allows muscles to build up force before shortening begins (van Schenau et al., 1997). An additional SSC mechanism that has been particularly under discussion in recent literature is related to stretch-induced force enhancing effects within the contractile element of muscles (Seiberl et al., 2015b; Hahn and Riedel, 2018; Tomolka et al., 2020).

It is well accepted that—compared to a length- and activation-matched reference contraction—an eccentric muscle action provides increased force or torque during, but also after, the lengthening phase, when the muscle is kept active in an isometric steady-state. The force or torque response to stretch is described to have two components. First, a velocity-dependent force enhancement (FE) throughout the stretch period (Edman, 2012). And second, the long-lasting component, which is known as the phenomenon of residual force enhancement (rFE) (Herzog, 2004). There is some experimental evidence that mechanisms related to stretch-induced rFE also contribute to enhanced performance in the SSC (Seiberl et al., 2015b; Fortuna et al., 2017; Fukutani et al., 2017a; Hahn and Riedel, 2018; Groeber et al., 2019). Different parameters influence the amount of rFE. For example, with increased stretch amplitude, the amount of rFE rises (Edman, 1978; Sugi and Tsuchiya, 1988), and it occurs at all muscle lengths (Rassier et al., 2003). On the other hand, no influence of stretch velocity could be detected for slow and moderate speeds (Edman et al., 1982; Lee and Herzog, 2002), whereas for fast stretch speeds, no significant rFE could be found (Fukutani et al., 2019a). These findings suggested rFE to be a muscle property which could be observed at different structural muscle levels (Abbott and Aubert, 1952; Edman, 1978; Herzog et al., 2003; Bullimore et al., 2007) and in different muscle groups (Oskouei and Herzog, 2006b; Pinniger and Cresswell, 2007; Seiberl et al., 2013). A very frequently used approach to explain rFE is the protein titin, which is thought to act as a kind of molecular spring. The binding of  $\text{Ca}^{2+}$  might enhance intramolecular attraction and compactness in the PEVK region of titin, which would be expected to increase titin stiffness (Rode et al., 2009; Herzog, 2014; Linke, 2018; Fukutani and Herzog, 2019). However, the exact role of titin is still unclear.

In contrast to an active stretch, the steady-state force or torque after a concentric contraction is reduced compared to an isometric reference contraction at the same muscle length (residual force depression, rFD) (Herzog, 2004). Thereby, an increase in shortening speed is associated with a decrease in rFD (Herzog and Leonard, 2000). In conformity with the force-velocity relationship (Hill, 1938), increased contraction velocities lead to reduced force capacities resulting in reduced work produced during shortening. Thus, the amount of rFD increases with the amount of work during shortening. Accordingly, rFD declines with decreasing shortening magnitude (Maréchal and Plaghki, 1979; Herzog and Leonard, 1997). Stress-induced inhibition of the actin-myosin overlap zone is the primary mechanism suggested for rFD (Herzog, 2004; Joumaa et al., 2017). In addition, the protein titin might bind to actin upon muscle activation. This could lead to an inhibition of cross bridges by less binding sites for myosin on the actin filament due to bound titin (Rode et al., 2009).

These often independently researched phenomena of rFD and rFE are directly confronted in stretch-shortening cycles. If analyzed together in the context of SSCs, conflicting results for the interaction of these force-enhancing and -depressing history-dependent properties are presented in literature. For example, Seiberl et al. (2015b) and Fortuna et al. (2017) reported a contribution of rFE to the SSC performance enhancement by counteracting the development of rFD which is established during the concentric phase. In contrast, Herzog and Leonard (2000) and Lee et al. (2001) reported the same amount of rFD after a SSC as for pure concentric muscle actions. Thus, possible interactions of rFE- and rFD-related mechanisms in SSC, thereby influencing muscle performance, are still not well understood.

The standardized protocols for evaluating the history-dependent properties of muscle action may not adequately represent everyday movements like walking or running, since the operating conditions vary during muscle action with these natural movements (Bohm et al., 2018). However, in some resistance training exercises the magnitude and velocity of the eccentric and concentric phase is kept constant, especially when using lower intensities (Sakamoto and Sinclair, 2006, 2012). Although these parameters are similar in the eccentric and concentric phase, the entire SSC is often performed under different levels of intensity in resistance training exercises in order to regulate training exposure (Wernbom et al., 2007).

Concerning above mentioned mechanisms related to the performance enhancement in SSCs, it can be assumed, that the intensity of muscle action differently affects their contributions to increased force, work or power. For example, it is reported that rFE increases with increasing contraction intensity (Oskouei and Herzog, 2006a). However, this result could not be confirmed in a feedback-controlled submaximal knee extension protocol study (Seiberl et al., 2012). Owing to that, if contraction intensity could influence rFE, it would also influence performance in a SSC. Also, if the proposed mechanism of titin—which spans from the Z line to the M band of the sarcomere (Leonard and Herzog, 2010)—contributes to the enhancing effects, elastic titin forces might increase upon higher muscle activation (Fukutani and Herzog, 2019), meaning elevated  $\text{Ca}^{2+}$  ion concentration in the

environment of the myofibrils (Gehlert et al., 2015). Additionally, tendon elongation should be greater with increasing muscle force (Wang, 2006; Fukutani et al., 2017b), resulting in more elastic energy stored in the tendon during the eccentric phase, which is beneficial in the shortening phase of the SSC, but should not account solely for enhanced performance in a SSC (Seiberl et al., 2015b). Hence, the focus of this work was to examine the influence of contraction intensity on the history-dependent properties of muscle action in a SSC.

We hypothesized that with increasing intensity the SSC-effects are larger; possibly due to increased rFE, which should be observable by enhanced torque compared to a pure concentric (CON) muscle action in the steady-state after the SSC.

## MATERIALS AND METHODS

### Participants

Thirty healthy adults initially participated in this study. Three subjects did not complete the tests, or data was missing; therefore, they were excluded from further analysis. Finally, data were obtained from 12 female and 15 male adults (age:  $26.6 \pm 6.2$  years, height:  $175.4 \pm 8.7$  cm, body mass:  $71.8 \pm 11.3$  kg), they all participated voluntarily and provided written informed consent prior to the study. The suitability of participation was determined with an anamnesis questionnaire to determine the risk factors for physical activity. The participants had no neuromuscular disorders, cardiovascular problems or injury to the right leg. The Ethics Committee of the University of Vienna approved the experimental protocol (reference number: 00364).

### Experimental Setup

Knee joint torque was measured using an isokinetic dynamometer (HUMAC Norm, Model 770; CSMi) at the right leg. We captured all analog signals of the isokinetic dynamometer with the Vicon Nexus A/D card (16 bit) with a sampling frequency of 2 kHz. The upper body was fixed to the dynamometer by straps ( $100^\circ$  seat back angle). The sitting position was precisely adapted to each test person. The lateral femoral condyles of every participant were aligned with the rotation axis of the dynamometer.

Synchronously, kinematic data was recorded with a Vicon Nexus motion-capturing system (Oxford, United Kingdom, 100 Hz) using nine cameras (Vantage V8). Eight reflective markers were captured, fixed at the following positions: trochanter major, the most prominent points of the medial and lateral femoral condyles, medial and lateral malleolus of the right leg. Additionally, we placed one marker at the axis of the dynamometer and two markers on the dynamometer's arm (one of them at the point of force application defining the lever arm as the distance between the line of action of the applied extension force and the dynamometer's axis of rotation).

For all voluntary contractions, the EMG signals of the m. vastus medialis and m. rectus femoris were captured (Delsys, Trigno Wireless EMG System, United States, 2 kHz) and recorded synchronously with the torque and kinematic data. The electrodes were attached following the guidelines of the SENIAM

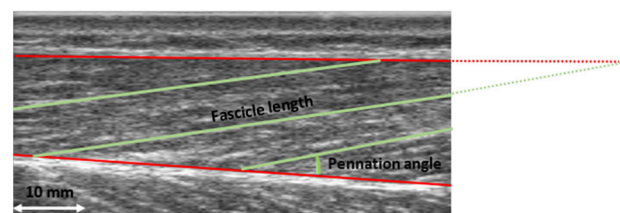
group (Hermens et al., 2000). The sensors had an inter-electrode spacing of 10 mm (Delsys, Trigno Avanti Sensor).

Muscle contractions were evoked at specific intensities by electrical stimulation (Digitimer DS8R, United Kingdom). The areas of the skin were shaved and cleaned with alcohol for the later application of the electrodes. The muscle motor points of m. vastus lateralis and m. vastus medialis were identified by scanning the skin's surface with a motor point pen (COMPEX, United Kingdom). Two electrodes ( $5 \times 5$  cm) were placed precisely on the previously identified motor points (Gobbo et al., 2014). Repetitive 100  $\mu$ s square-wave pulses at 100 Hz were used. The train duration was approximately 6 s long.

For the investigation of history dependent effects in muscle action it is crucial that experimental conditions concerning muscle activity and muscle length are well controlled. Especially muscle length not necessarily follows dynamometer angular settings, what can bias the interpretation of force capacities according to the force-length relationship of the knee extensors. For this reason, we additionally used ultrasonography (Telemed ArtUS EXT-1H, IT, 70 Hz) to determine the underlying fascicle length changes and pennation angle of the m. vastus lateralis (see **Figure 1**). A linear probe (LV8-5N60-A2) with a field of view of 60 mm was used. The probe was fixed to the muscle belly of the m. vastus lateralis with a custom-made bracket. To synchronize the video data with the other data recorded with Vicon Nexus, an analog signal (0–3 V) was generated when the video was started and stopped. This analog signal was captured by the Vicon system.

### Experimental Protocol

On test day, the participants first had a general warm-up (bicycle ergometer, 5 min, between 80 and 90 W), which was followed by a specific warm-up of the quadriceps femoris on the isokinetic dynamometer (several submaximal contractions, 5 min). After the warm-up, the subjects had to perform two maximal voluntary contractions (MVCs) at a  $20^\circ$  dynamometer angle (full knee extension was defined as  $0^\circ$ ). There was no statistical difference (*t*-test paired,  $p = 0.089$ ) between the two MVC contractions (3.8% on average) and the average of peak joint torque of both



**FIGURE 1 |** Ultrasound image of the m. vastus lateralis. Fascicle length and pennation angle were determined for three fascicles. Pennation angle was calculated between the muscle fascicle and the deep aponeurosis. Fascicle length was defined as the distance between the intersection of the upper aponeurosis with the muscle fascicle and the intersection of the lower aponeurosis and muscle fascicle. The mean of the three measured values was used for further analysis.



trials was defined as 100% intensity. As a next step, current was applied and incrementally increased until the desired isometric knee torque was reached (20, 35, and 50% of MVC). Once the desired intensity was reached, the stimulus was maintained for several seconds to ensure a steady torque response. These current intensity settings were used for the entire experiment. The settings were checked again after a pause of one minute. The protocol comprised isometric contraction (ISO), pure shortening contractions (CON) and stretch-shortening cycles (SSC). It should be noted that the term ‘isometric’ is used for simplicity, although it actually refers to a fixed-end muscle-tendon unit contraction, where some muscle shortening at initial activation is likely, even when the joint angle is constant (Fukashiro et al., 1995). The angular velocity was fixed at 60°/s, and a fixed range of motion adjusted by the dynamometer (ISO: 20°, CON: 80°–20°, SSC: 20°–80°–20°) was used. This range of motion refers to the ascending limb of the knee extensor torque-angle relationship (Hahn et al., 2007) and reflects SSC ranges as found in many everyday movements such as walking, running or hopping (Jin and Hahn, 2019). In randomized order, MVC and different submaximal contraction intensities were tested (20, 35, and 50% of MVC) that were triggered through electrical stimulation. For simplified designation, tests under maximal voluntary contraction will be referred to as 100% (Figure 2). Rest between the contractions was two minutes in order to prevent fatigue (Tilp et al., 2011).

Dynamic contractions had an isometric pre-activation period before the dynamic phase (until a plateau was reached) followed by an isometric hold phase (steady-state) after the knee rotation. At the end of the experimental protocol, the subjects had to perform one fixed-end MVC at 20° dynamometer angle.

## Data Processing

Torque and dynamometer angle data were low-pass filtered (zero-delay, fourth-order Butterworth) with a cut-off frequency of 10 Hz. Gravitational forces acting on the dynamometer arm system were corrected for all subjects. Each contraction was repeated twice and mean values were used for further analysis. CON and SSC were compared at T1 (80° dynamometer angle, end of stretch for SSC condition) and at 50° dynamometer angle (midpoint of 80°–20° range, T2) in the shortening phase. ISO,

CON, and SSC were compared at the isometric steady-state, 1–1.5 s after the dynamic phase (T3, 20° dynamometer angle), while at that point the average values of 0.5 s were used (Figure 3).

Additionally, the mechanical work during angular rotation was calculated as the integral of torque during the shortening phase, using a numerical trapezoidal method.

$$W = \int M d\phi = \int M \cdot \omega dt \quad (1)$$

with  $W$  as mechanical work [J],  $M$  as torque [Nm], and  $\omega$  as rotational velocity [rad/s].

Due to difficulties in the standardization of the knee angle range of motion at high torque levels, mechanical work values were additionally adjusted to the respective range of motion in each individual trial (see results section). Different knee angles between CON and SSC at T1 affect the results of the absolute mechanical work during the shortening. Therefore, we decided to adjust mechanical work to the respective range of motion to avoid this problem.

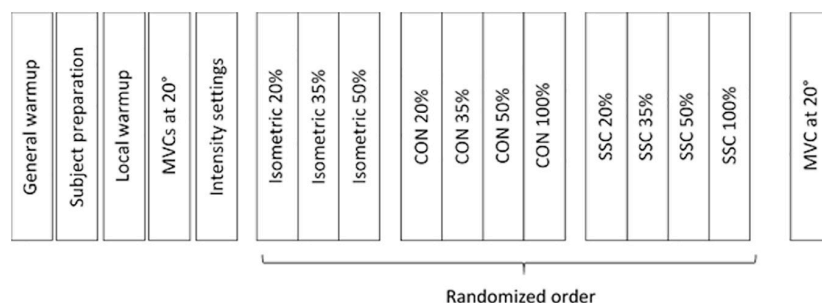
Kinematic data was also low-pass filtered using a cutoff frequency of 10 Hz. Knee-joint angle was compared between conditions at time points T1, T2, and T3. It had been previously shown that due to the compliance of the dynamometer and the tissue deformation, a shift of both knee joint and dynamometer axis occurs, and therefore differences between the measured and the resultant knee joint moments exist. To address this shortcoming, we implemented the inverse dynamic approach proposed by (Arampatzis et al., 2004).

$$M_{res} = M_{Meas} \cdot \frac{d_K}{d_B} \quad (2)$$

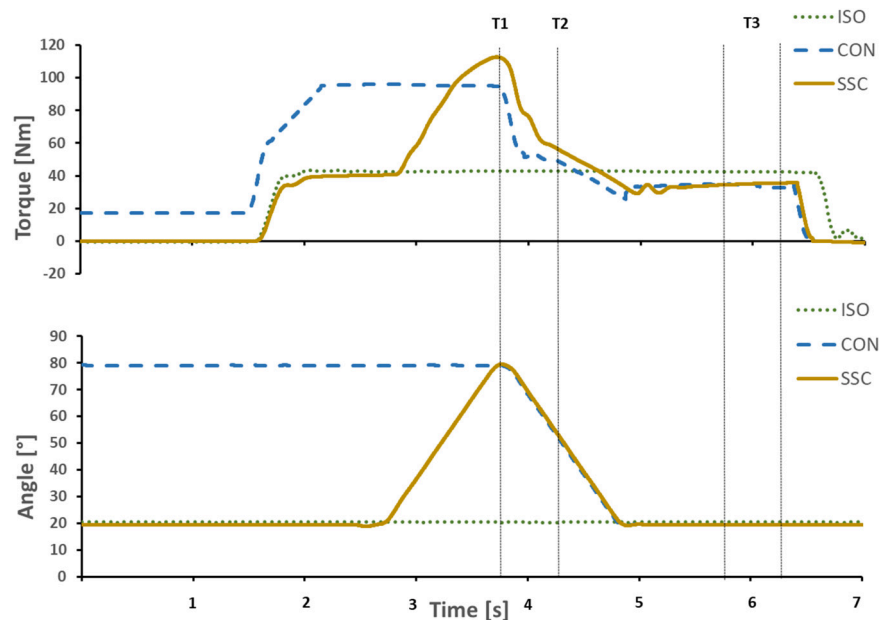
with  $M_{res}$  as the corrected joint moment,  $M_{Meas}$  the initially measured moment,  $d_B$  as the lever arm of the applied force to the dynamometer axis and  $d_K$  as the lever arm of force to the knee joint [according to the free body diagram reported by Arampatzis et al. (2004)].

EMG data were band-pass filtered (10–400 Hz, fourth-order Butterworth), rectified, smoothed (250 ms moving average). Mean difference in m. rectus femoris and m. vastus medialis activity was used for analysis.

Pennation angle was calculated between the muscle fascicle and the deep aponeurosis. Fascicle length was defined as the



**FIGURE 2 |** Experimental protocol work flow. The test protocol comprised maximal voluntary contractions (100%) and submaximal electrical stimulated contractions at 20%, 35%, and 50% of MVC.



**FIGURE 3 |** Exemplary representation of torque-time and angle-time traces. Vertical lines indicate the time point at the end of stretch (T1), midpoint of shortening (T2), and the steady-state interval where the mean steady-state torque was calculated (T3). Continuous yellow line SSC, dotted green line ISO, and dashed blue line CON.

distance between the intersection of the superficial aponeurosis with the muscle fascicle and the intersection of the deep aponeurosis and muscle fascicle. This was always done for three fascicles and the mean value was calculated (see **Figure 1**). If the muscle fascicle was no longer visible on the image section, the point of intersection was calculated by assuming a linear continuation. Trigonometry was used to estimate the part of the fascicle that was not visible. This approach has been widely used before; nevertheless, it should be noted that this linear approach could result in an error. However, it was reported that this error is less than 2.4% (Narici et al., 2003; Reeves and Narici, 2003). Two evaluators digitized the ultrasound image separately for testing on interrater reliability, using open-source software (Tracker, Open Source Physics, Version 5.1.1).

The synchronization of all the data was achieved by use of the ultrasound device's start-stop analog signal.

## Statistical Analysis

Data was tested for normality using a Kolmogorov–Smirnov test. Depending on the number of conditions to be compared, either a paired *t*-test with dependent variables or repeated measures ANOVA was employed. If sphericity was violated, Greenhouse-Geisser correction was used. Two-way ANOVA (within-within subject design) was adopted to examine the interaction (condition  $\times$  intensity) and main effect (condition and intensity) for knee joint torque, mechanical work, knee angle, fascicle length and pennation angle. If the interaction (condition  $\times$  intensity) was significant, subsequent *post hoc* comparisons with Bonferroni adjustments were conducted for comparing CON and SSC at each level of intensity. One-way

ANOVA or paired *t*-test was utilized for EMG. The level of significance was set to  $p < 0.05$ . The effect size was assessed with partial eta squared ( $\eta^2$ ). Interrater reliability for pennation angle and fascicle length measurements was analyzed by calculating the intraclass correlation coefficient (ICC, two-way mixed model; single measures).

By means of a paired *t*-test, the MVC at the end of the test session was compared with the MVC at the beginning to determine possible fatigue. For comparison of ISO, CON, and SSC conditions, the previously described time points (T1–T3) were used. Data are presented as mean  $\pm$  SD.

## RESULTS

### Initial Conditions

The achieved isometric (ISO) joint torque at the specified percentages (20, 35, and 50% of MVC) reached a mean value of  $23.2 \pm 6.0\%$ ,  $36.2 \pm 8.0\%$ , and  $49.3 \pm 9.4\%$ , respectively, at the same dynamometer angle of  $20^\circ$ .

Further, a *t*-test revealed no statistical difference between MVCs at the beginning ( $92.5 \pm 29.9$  Nm) and at the end of the test protocol ( $91.3 \pm 29.2$  Nm), indicating no fatigue.

### Joint Torque and Work Measurements

Two-way ANOVA revealed a significant interaction (condition  $\times$  intensity) of torque after the stretch phase (T1) ( $p = 0.023$ ,  $\eta^2 = 0.159$ ). Main effect of intensity ( $p < 0.001$ ,  $\eta^2 = 0.843$ ) and for condition ( $p < 0.001$ ,  $\eta^2 = 0.501$ ) revealed increased torque with higher intensity and for the SSC condition. For the intensities of 35, 50, and 100%, the torque after the

stretch phase (T1) in SSCs was significantly higher compared to the isometric pre-activation in the CON conditions at the same activation level and the corresponding dynamometer angle (35%:  $p = 0.013$ ; 50%:  $p = 0.001$ , and 100%:  $p = 0.032$ ). This resulted in 13.7, 32.2, and 10.7% FE in the 35, 50, and 100% intensity conditions. No FE could be found for the lowest (20%) activation level ( $p = 0.103$ ) (see **Figure 4** and **Table 1**).

Significant interaction (condition  $\times$  intensity) was found for the range-adjusted mechanical work ( $p = 0.049$ ,  $\eta^2 = 0.123$ ). Main effect of intensity ( $p < 0.001$ ,  $\eta^2 = 0.839$ ) and condition ( $p < 0.001$ ,  $\eta^2 = 0.708$ ) revealed increased mechanical work with higher intensity and for the SSC condition. Range-adjusted mechanical work during shortening was significantly higher for all SSCs compared to CON contractions at the same activation level (20%:  $p < 0.001$ ; 35%:  $p < 0.001$ ; 50%:  $p < 0.001$ ; 100%:  $p = 0.001$ ) (see **Figure 5** and **Table 2**). The absolute mechanical work during shortening was also significantly higher for all SSC conditions compared to the CON conditions at the same intensity ( $p < 0.05$ ). The percentage increase of normalized mechanical work in the SSC compared to CON contraction (referred to as SSC-effect) was 17.4, 17.7, 20.9, and 13.1% for the 20, 35, 50, and 100% intensities, respectively.

Regarding the steady-state torque after the dynamic phase (T3), two-way ANOVA with repeated measures revealed a significant interaction ( $p = 0.004$ ,  $\eta^2 = 0.207$ ). Main effect of intensity ( $p < 0.001$ ,  $\eta^2 = 0.856$ ) and condition ( $p < 0.001$ ,  $\eta^2 = 0.530$ ) was significant. *Post hoc* comparisons revealed significant rFD for all SSCs compared to the isometric reference conditions for all submaximal levels of contractions (20–50%). A significant torque depression of the CON contractions

**TABLE 1** | Mean ( $\pm$ SD;  $n = 27$ ) values of knee joint torque at T1 (onset of shortening) and T3 (steady-state after dynamic phase).

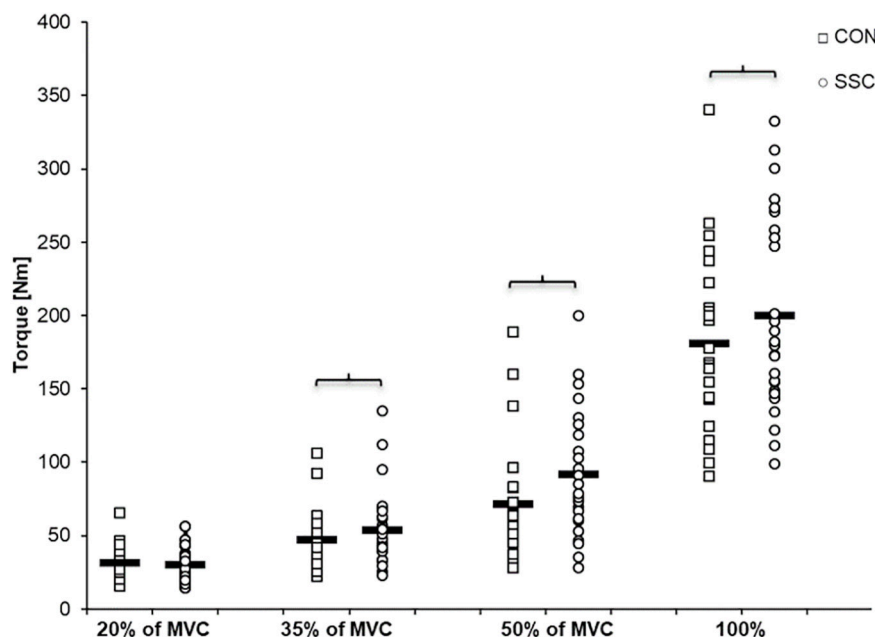
Contraction intensity	Knee joint torque [Nm $\pm$ SD]				
	T1		T3		
	CON	SSC	ISO	CON	SSC
20%	31.1 $\pm$ 10.7	29.8 $\pm$ 10.3	18.2 $\pm$ 4.8	17.1 $\pm$ 4.5	16.7 $\pm$ 3.6*
35%	<b>47.2 <math>\pm</math> 19.6</b>	<b>53.7 <math>\pm</math> 25.8</b>	29.9 $\pm$ 6.9	26.6 $\pm$ 7.0*	25.7 $\pm$ 6.1*
50%	<b>71.6 <math>\pm</math> 37.8</b>	<b>94.7 <math>\pm</math> 50.3</b>	40.4 $\pm$ 9.6	35.3 $\pm$ 10.7*	34.0 $\pm$ 10.1*
100%	<b>180.7 <math>\pm</math> 62.1</b>	<b>200.0 <math>\pm</math> 66.4</b>	76.4 $\pm$ 23.5	<b>67.4 <math>\pm</math> 22.2*</b>	<b>74.1 <math>\pm</math> 25.1</b>

Bold values indicate significant ( $p < 0.05$ ) differences between the shortening (CON) and stretch-shortening (SSC) condition at the respective intensity level and time-point. Asterisks indicate a significant difference of CON or SSC to the isometric reference contraction (ISO) at the respective intensity level and time-point.

(CON\_35%: 11.1%, CON\_50%: 12.7%, CON\_100%: 11.8%) could be found for all activation levels except 20% of MVC (CON\_20%: 6.6%, no significance,  $p = 0.288$ ). The only difference between CON and SSC was found under 100% ( $p = 0.034$ ), where the SSC steady-state torque was significantly less depressed than in the CON condition (see **Figure 6** and **Table 1**).

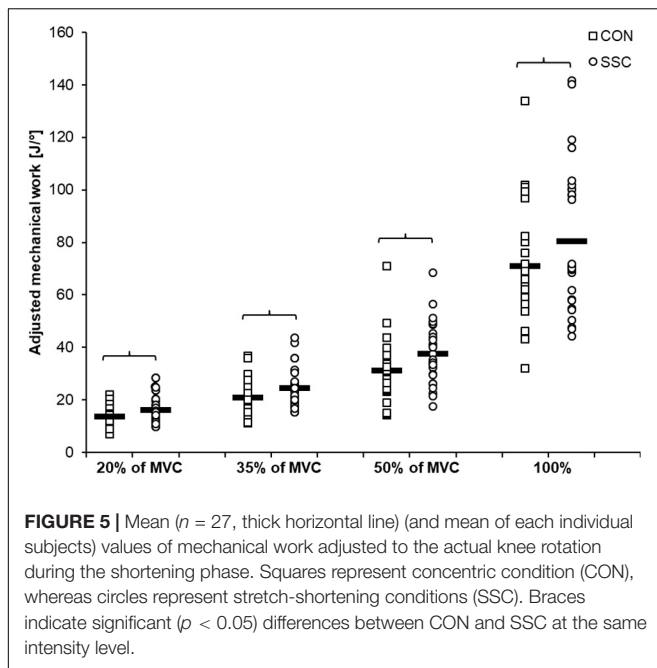
## Knee Angle

For knee angle, no significant interaction (condition  $\times$  intensity) was found at all time points (T1:  $p = 0.251$ ,  $\eta^2 = 0.052$ ; T2:  $p = 0.309$ ,  $\eta^2 = 0.015$ ; T3:  $p = 0.736$ ,  $\eta^2 = 0.012$ ). Main effect of intensity was found at all three time points (T1:  $p < 0.001$ ,  $\eta^2 = 0.800$ ; T2:  $p < 0.001$ ,  $\eta^2 = 0.648$ ; T3:  $p < 0.001$ ,  $\eta^2 = 0.412$ ),



**FIGURE 4** | Mean ( $n = 27$ , thick horizontal line) (and mean of each individual subject) values of joint torque at the onset of shortening (T1). Squares represent concentric condition (CON), whereas circles represent stretch-shortening conditions (SSC). Brackets indicate significant ( $p < 0.05$ ) differences between CON and SSC at the same intensity level.





**FIGURE 5 |** Mean ( $n = 27$ , thick horizontal line) (and mean of each individual subjects) values of mechanical work adjusted to the actual knee rotation during the shortening phase. Squares represent concentric condition (CON), whereas circles represent stretch-shortening conditions (SSC). Braces indicate significant ( $p < 0.05$ ) differences between CON and SSC at the same intensity level.

**TABLE 2 |** Mean ( $\pm$ SD;  $n = 27$ ) values of the absolute mechanical work and the work adjusted to the actual knee rotation during shortening.

Contraction intensity	Absolute mechanical work [J $\pm$ SD]		Adjusted mechanical work [J/m $\pm$ SD]	
	CON	SSC	CON	SSC
20%	<b>763.8 <math>\pm</math> 184.2</b>	<b>869.8 <math>\pm</math> 182.2</b>	<b>13.8 <math>\pm</math> 3.5</b>	<b>16.2 <math>\pm</math> 4.4</b>
35%	<b>1150.0 <math>\pm</math> 321.6</b>	<b>1295.9 <math>\pm</math> 365.3</b>	<b>20.9 <math>\pm</math> 6.9</b>	<b>24.6 <math>\pm</math> 7.6</b>
50%	<b>1648.1 <math>\pm</math> 525.5</b>	<b>1911.6 <math>\pm</math> 558.0</b>	<b>31.1 <math>\pm</math> 11.9</b>	<b>37.6 <math>\pm</math> 11.7</b>
100%	<b>3458.9 <math>\pm</math> 1044.9</b>	<b>3733.6 <math>\pm</math> 1182.6</b>	<b>71.1 <math>\pm</math> 24.0</b>	<b>80.4 <math>\pm</math> 28.6</b>

Bold values indicate significant ( $p < 0.05$ ) differences between the shortening (CON) and stretch-shortening (SSC) condition at the respective intensity.

knee joint flexion angle decreased significantly as the intensity raised. The main effect of condition was only significant at T1 ( $p < 0.001$ ,  $\eta^2 = 0.557$ ), knee joint flexion angle was significantly higher at the CON condition compared to the SSC condition (see Figure 7).

## Muscle Architectural Changes

Analysis of the fascicle length and pennation angle was obtained by two independent investigators. Mean ICC across all measurements was 0.84 (ranging from 0.80 to 0.87 for subjects) for fascicle length and 0.81 (ranging 0.77–0.85 for subjects) for pennation angle, indicating good interrater reliability (Koo and Li, 2016).

The interaction (condition  $\times$  intensity) was not significant for fascicle length at all time points (T1:  $p = 0.667$ ,  $\eta^2 = 0.015$ ; T2:  $p = 0.638$ ,  $\eta^2 = 0.021$ ; T3:  $p = 0.717$ ,  $\eta^2 = 0.021$ ). Main effect of intensity showed significant shorter fascicle length with increased intensity (T1:  $p < 0.001$ ,  $\eta^2 = 0.582$ ; T2:  $p < 0.001$ ,  $\eta^2 = 0.588$ ; T3:  $p < 0.001$ ,  $\eta^2 = 0.456$ ). Main effect of condition

was not significant at all time points (T1:  $p = 0.068$ ,  $\eta^2 = 0.150$ ; T2:  $p = 0.413$ ,  $\eta^2 = 0.032$ ; T3:  $p = 0.257$ ,  $\eta^2 = 0.061$ ) (see Figure 8).

Two-way ANOVA revealed no significant interaction (condition  $\times$  intensity) of pennation angle at all time points (T1:  $p = 0.620$ ,  $\eta^2 = 0.021$ ; T2:  $p = 0.232$ ,  $\eta^2 = 0.067$ ; T3:  $p = 0.742$ ,  $\eta^2 = 0.015$ ). Whereas the main effect of intensity showed, that pennation angle was increased with higher intensity (T1:  $p < 0.001$ ,  $\eta^2 = 0.550$ ; T2:  $p < 0.001$ ,  $\eta^2 = 0.630$ ; T3:  $p < 0.001$ ,  $\eta^2 = 0.452$ ). Pennation angle was significant higher in the CON condition compared to the SSC at T1. No statistical difference could be found at T2 and T3 (T1:  $p = 0.023$ ,  $\eta^2 = 0.224$ ; T2:  $p = 0.392$ ,  $\eta^2 = 0.035$ ; T3:  $p = 0.984$ ,  $\eta^2 < 0.001$ ) (see Figure 9).

## Muscle Activity

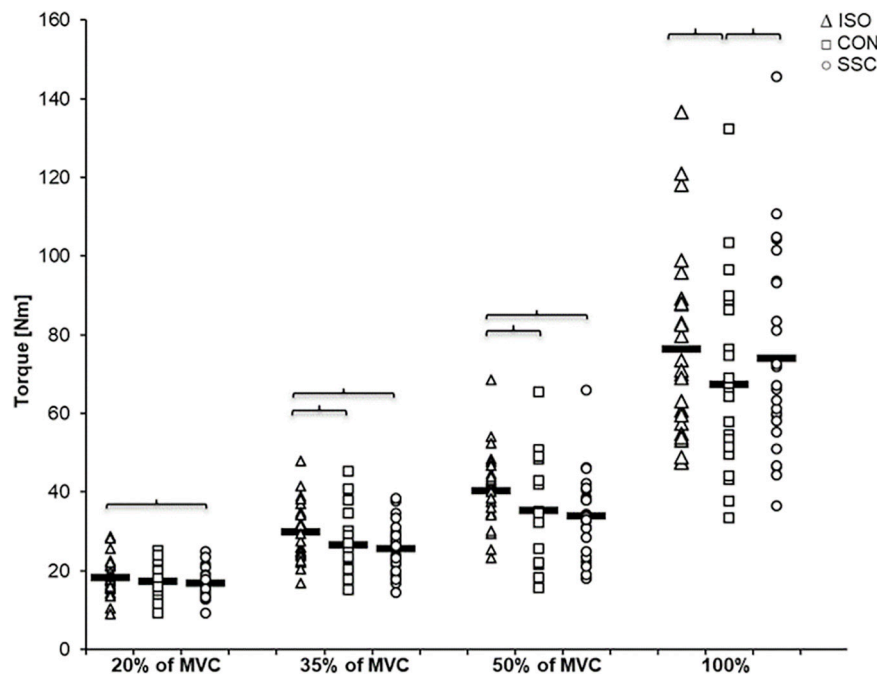
For the comparison of SSC and CON muscle activity, we did not find any differences for all analyzed muscles and time points ( $p > 0.05$ ). Between SSC and CON conditions the mean difference in m. rectus femoris activity was  $3.1 \pm 4.8\%$ ,  $5.5 \pm 5.6\%$ , and  $4.3 \pm 4.0\%$  at T1, T2, and T3, respectively. For m. vastus medialis, the mean difference between SSC and CON activity at T1, T2, and T3 was  $8.6 \pm 9.8\%$ ,  $6.1 \pm 5.0\%$ , and  $2.6 \pm 3.4\%$ .

At T3, in the steady-state phases after shortening, SSC and CON muscle activity was additionally compared to isometric references. Here, m. rectus femoris also did not show any statistical difference between conditions. For m. vastus medialis, compared to the ISO condition we found significantly lower muscle activity for both, the CON ( $22.5 \pm 30.9\%$ ) and the SSC ( $20.6 \pm 30.3\%$ ) condition ( $p < 0.001$ ,  $\eta^2 = 0.36$ ).

## DISCUSSION

The study was designed to investigate the influence of the contraction intensity on stretch-induced performance enhancement in a SSC. We hypothesized that the SSC-effects (enhanced work during shortening phase) are larger with increasing intensity, partly explainable by increased contributions of stretch-induced mechanisms related to rFE. As expected, we found that the average work values were significantly greater for all SSCs compared to the corresponding concentric contractions. The SSC-effect was about 20% in the submaximal electrically stimulated trials, and about 13% in MVCs. Interestingly and against our expectations, despite the clear performance enhancement during SSCs, all shortening phases ended in significant rFD, except for SSCs performed at 100% intensity.

Similar to other studies, we found increased joint torque at the end of stretch compared to the isometric pre-activation in the CON condition (Power et al., 2013; Seiberl et al., 2015b; Hahn and Riedel, 2018), but not for all intensity levels. We did not see a FE at the end of stretches with the lowest activation (20% of MVC), but increasing FE from 13 to 32% with increasing electrical stimulation (Figure 4). Thus, our results indicate that the FE during the stretch phase is intensity dependent—at least during electrical stimulation. During voluntarily maximally activated SSCs, the torque was also significantly enhanced compared with

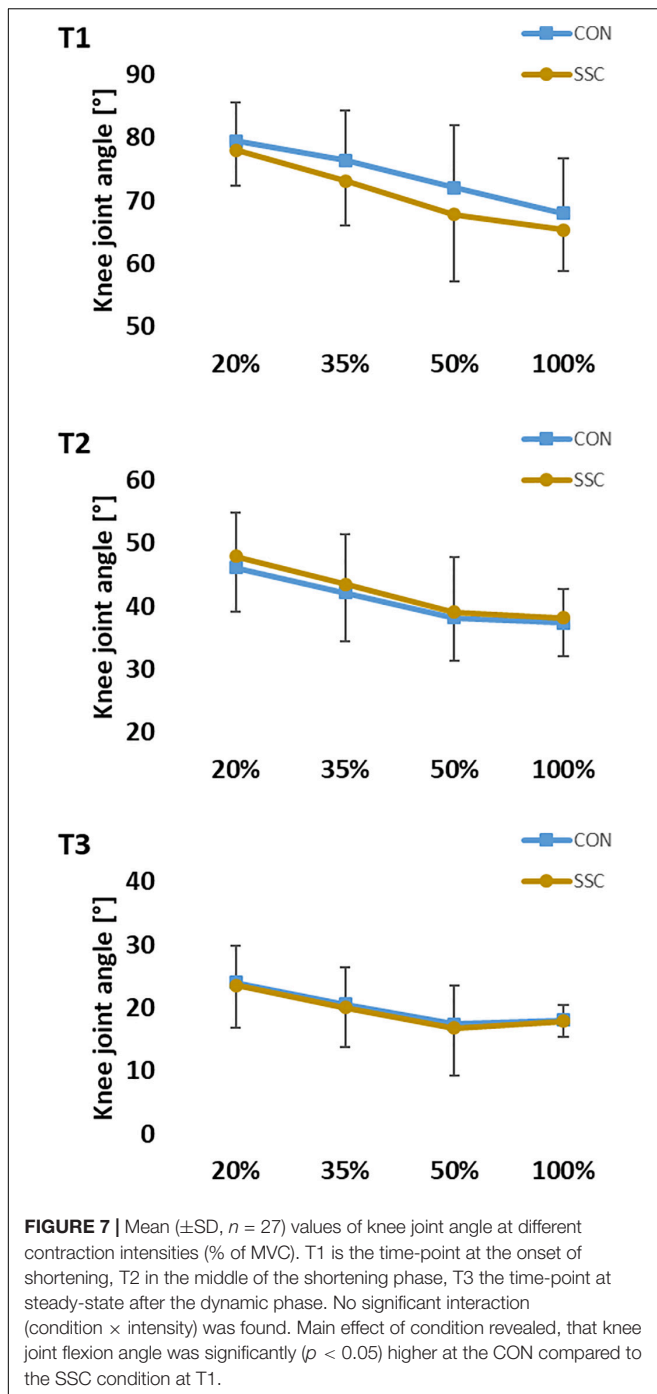


**FIGURE 6 |** Mean ( $n = 27$ , thick horizontal line) (and mean of each individual subject) values of joint torque in the steady-state after the dynamic phase (T3). Triangles represent purely isometric torque at 20° knee flexion (ISO), squares represent concentric condition (CON), whereas circles represent stretch-shortening conditions (SSC). Braces indicate significant ( $p < 0.05$ ) differences between the conditions.

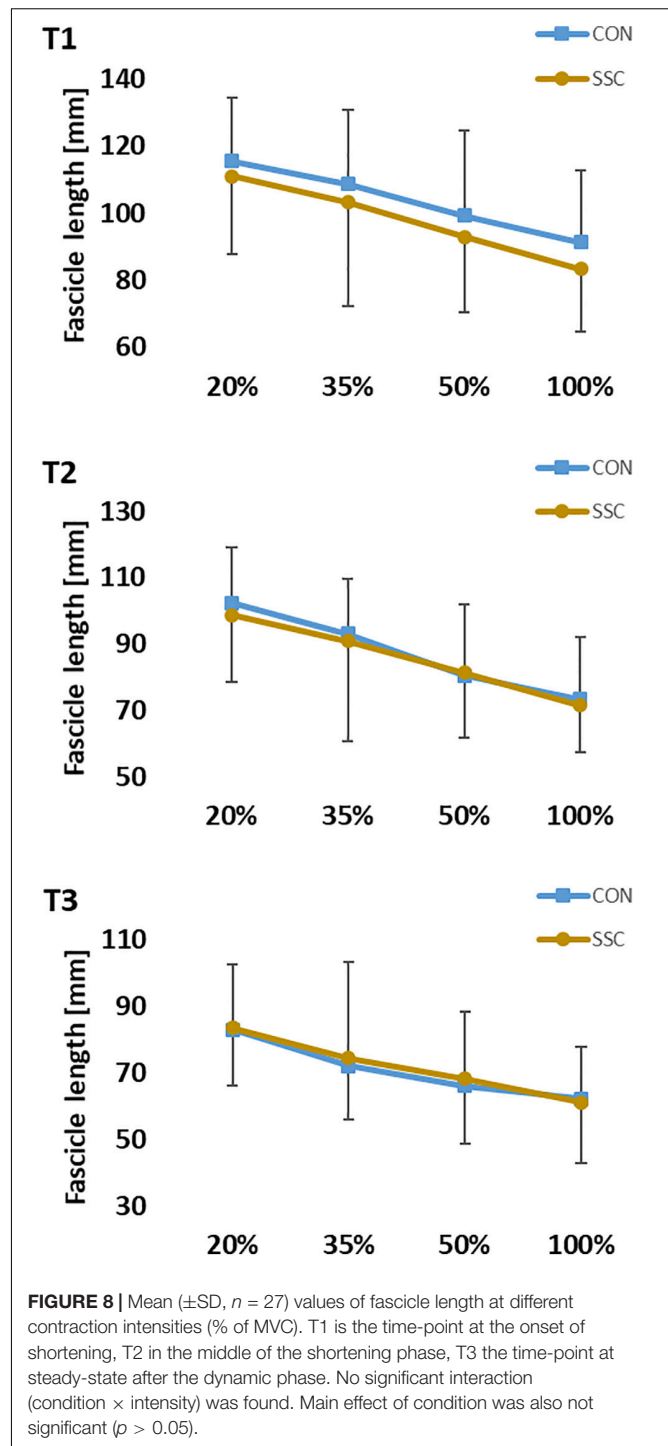
isometric pre-activation of the CON condition; but this FE of about 11% at 100% intensity was slightly lower than the FE at 35% intensity in the electrically stimulated trials. Similar to our study, Lee and Herzog (2002) compared peak forces during eccentric contractions in m. adductor pollicis and also found that slightly less FE was produced under MVC conditions compared to electrically stimulated contractions at an intensity the subjects could comfortably tolerate. A lack of increased force in voluntary eccentric contractions is typically associated with an inhibition of the neural drive (Westing et al., 1990; Webber and Kriellaars, 1997), which could explain the lower relative FE at MVCs compared with the submaximally electrically stimulated trials ( $\geq 35\%$ ). However, examination of the EMG data at the end of the stretch phase in SSCs showed no significant differences ( $p > 0.05$ ) to the CON condition at the respective time point in the isometric pre-activation phase before shortening, which further means that also an inhibition of neural drive cannot explain these results. Our results indicate that relative FE increases with higher submaximal intensities. At the MVC level, the relative FE is smaller than during the electrically stimulated attempts ( $> 35\%$ ).

The kinematic analysis revealed that there was a discrepancy between dynamometer-defined and measured knee angle. In the CON condition, the knee joint angle was significantly more flexed compared to the SSC condition. Although we did not find any statistical interaction (condition  $\times$  intensity), the difference in knee joint angle between the conditions had the tendency to get bigger with increasing intensity. Accordingly, the highest discrepancy was found at the end of the stretch (T1) during MVC stretch-shortening trials, where the highest absolute torques were

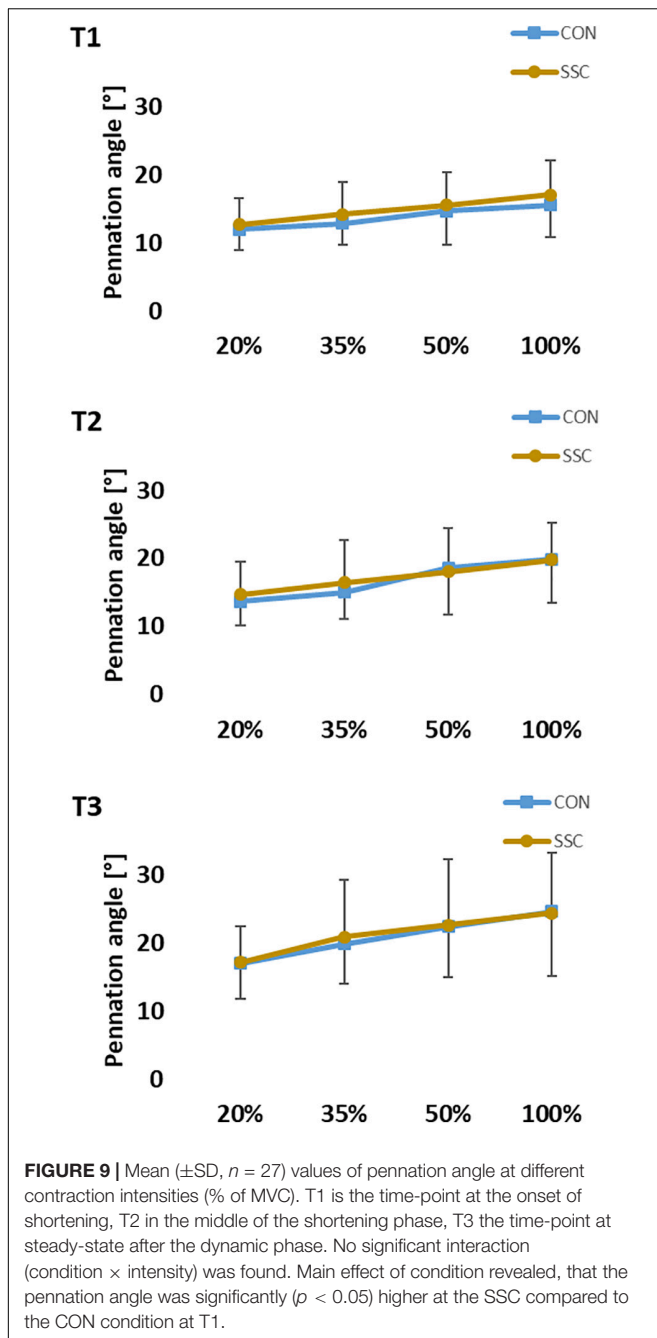
measured. Although the subjects were firmly strapped to the seat of the dynamometer, the high torques during the eccentric phases can lead to a slight elevation of the pelvis, what in turn gives way for the thigh and counteracts exact dynamometer-driven knee flexion. The significantly lower knee joint angles (more extended) at T1 led to architectural differences in pennation angle of m. vastus lateralis in these trials. Although we found no statistical difference in fascicle length (Figure 8), it can be assumed that the differences in knee joint and pennation angle influenced force and torque production according to the force-length and torque-angle relationship of knee extensors. As during this experiment the knee extensors likely worked on the ascending limb of the torque-angle relationship (Marginson and Eston, 2001; Hahn et al., 2007), the standardization difficulties possibly lead to an underestimation of the relative force enhancement at the end of stretch. We assume that a perfectly matched eccentric-concentric turning-point at a greater knee flexion angle would have generated even higher FE. This is also supported by data from the m. vastus lateralis confirming that the presented fascicle lengths in this work can be related to the ascending limb of the respective force-length relationship (Nikolaidou et al., 2017). Therefore, we believe it is safe to assume that there was clear FE in all SSC conditions, except for at the lowest intensities. However, since we did not assess the force-length relationship of each individual subject, the interpretation of an underestimated FE in these cases remains speculative. As already mentioned before, the range of motion was deliberately chosen, since it reflects SSC ranges as found in many everyday movements (Jin and Hahn, 2019). However, it should be noted that the



results could be also different dependent on where the muscle operates on the force-length relationship. Under well controlled conditions *in vitro* or *in situ* studies, eccentric force enhancement during and after stretch is typically greater at longer sarcomeres or fascicle lengths (Granzier et al., 1989; Hisey et al., 2009). However, *in vivo* studies showing greater FE during stretch in multi-joint contractions (Hahn et al., 2014). In contrast to that, Linnamo et al. (2006) reported the same FE at short and long muscle lengths during single joint contractions.



Due to the fact that the knee joint angle at T1 was different between the SSC and CON conditions—which led to a greater angle change in the CON conditions—we adjusted calculations of mechanical work to the actual knee angle range during shortening for better comparability of conditions. The results confirmed that the work performed during shortening is significantly greater for all SSCs compared to the corresponding



CON contractions. Even absolute mechanical work was greater for all SSC contractions, although the knee angle change during shortening, and thus the absolute range, was greater in the CON conditions. In literature, several mechanisms are presented to explain an enhancement of mechanical work during shortening in a SSC. Activation dynamics, i.e., the time required to fully establish muscle activation, can play a major role in movements with or without a counter-movement (Fukutani et al., 2019b). However, muscle activation has no influence on our results of performance enhancement in SSCs, since we always had an isometric pre-activation phase before the dynamic phases. This

means that for every level of intensity, trials for both conditions started with an identical muscle activity. Additionally, the stretch-reflex activity is discussed in order to contribute to increased work in SSCs. However, we consider the relevance of stretch-reflex contributions in our settings to be negligible or even non-existent for two reasons. First, stretch reflexes are expected in fast movements with fast muscle lengthening—such as hopping (Komi and Gollhofer, 1997)—and should not be relevant in our experiment with a movement velocity of  $60^\circ/\text{s}$ . Second, electrical stimulation was used in all submaximal trials, where clear SSC-effects were evident. In addition, by the visual inspection of the EMG data we did not identify any suspicious activation peaks at the onset of stretch. For these reasons, we are confident that the stretch-reflex also has no or negligible influence on our results.

As already mentioned at the beginning of this paper, this leaves two remaining mechanisms that most likely explain the entire SSC performance enhancement found in our work. The lengthening of passive elastic structures leads to the storage of elastic energy that is released during shortening and thereby contributes to enhanced work during shortening in the SSC (Finni et al., 2001). Additionally, tendon elongation can affect changes in muscle length, resulting in enhanced force-generating capability due to the force-velocity relationship (Hill, 1938; Ishikawa et al., 2005). The amount of tendon elongation is dependent on the force applied to the tendon (Reeves et al., 2003), which in our experiment means that with higher intensity, more energy can be stored in the tendon. This is true for the absolute forces and work during SSCs; however, the relative SSC-effect was nearly constant for all submaximal intensities ranging between 17 and 21% increased work, and slightly lower SSC-effects were found during MVCs. Contrary to what we expected, no influence of intensity on the relative mechanical work during shortening in the SSC was found, whereas the type of activation (electrically stimulated vs. voluntary) seems to have an influence on the SSC-effects.

The main question for this experiment was whether, and to what extent, stretch-induced force-enhancing effects within the contractile element of muscles can contribute to enhanced work during the shortening. In contrast to the discussed mechanisms above, a contribution of rFE-related mechanisms to increased work during shortening in SSC should be visible also after the shortening phase (Seiberl et al., 2015b). It was speculated that if rFE-related mechanisms contribute to the SSC-effects, then the increased force/torque should be triggered during the stretch phase, contribute to the performance enhancement during the shortening phase, and should be visible as a history-dependent property in the steady-state phases after the SSC. Joint torque in the steady-state (T3) after the pure CON trials was significantly depressed compared to the ISO reference contraction (range 6.6–12.7%, not significant for 20% intensity), which is in line with previous studies that reported a rFD between 5 and 25% at knee extensions (Lee et al., 1999, 2000; Altenburg et al., 2008; Dargeviciute et al., 2013). No statistical difference of rFD was found for pure CON muscle action and SSC at the same activation level, except for the test under maximal voluntary activation (CON\_100%: rFD of 11.8% and SSC\_100%: rFD of 3.1%), without any difference in m. vastus lateralis fascicle length



and pennation angle. This indicates that mechanisms related to rFE are responsible for the less depressed steady-state torque in our experiment during the maximum voluntary SSC condition, which further means that the intensity of contraction and/or the type of activation in a SSC has an influence on this long-lasting component. Based on this finding, it might be concluded that there is an activation threshold where no significant rFD in the SSC of the m. quadriceps femoris remains. However, one needs to be careful comparing the submaximal and MVC conditions in this work, as there are important differences between voluntary and electrically elicited contractions. Electrically stimulated muscles do not mirror the asynchronous and varied firing frequencies voluntary activation shows (Lee et al., 1999) what likely influences muscle function as well. History-dependent effects show way more variability during voluntary contractions, than what we would expect from the 'facts' derived from animal models and electrically stimulated muscle action (Seiberl et al., 2015a). The reasons are still not well understood. We decided to use electrical stimulation for all submaximal contractions, since torque or EMG feedback-controlled trials are experimentally difficult to implement, and it can be only matched at the isometric state before and after the dynamic phase. This is not the case for MVCs, but extremely high stimulation intensities would be too painful and not tolerable for participants. For this reason, voluntary contractions were used for 100% intensity trials that additionally better represent everyday tasks or exercises like the squat, where we also have a stretch of the m. quadriceps femoris directly followed by a shortening contraction.

In literature, a current approach to explaining rFE is related to a titin-actin interaction (Rode et al., 2009; Herzog et al., 2016; Linke, 2018; Fukutani and Herzog, 2019). Titin stiffness increases with higher muscle activation, which could result in a reduced rFD in our SSC under maximal voluntary contraction. As previously reported, there are conflicting results in literature regarding the effects of rFE in the SSC (Groeber et al., 2019). Some authors reported that any stretch-induced rFE was abolished during the shortening in SSCs (Herzog and Leonard, 2000; Lee et al., 2001; Fukutani et al., 2019b), whereas others observed significantly higher force or torque values in the steady-state after the SSC compared to pure shortening muscle action (Seiberl et al., 2015b; Fortuna et al., 2017; Hahn and Riedel, 2018). Seiberl et al. (2015b) and Hahn and Riedel (2018) used electrical stimulation at 50–60% and 32.9% of MVC respectively, but they both had quite high shortening velocities in their test protocol, which is associated with reduced rFD (Herzog and Leonard, 2000). Additionally, Fortuna et al. (2017) reported that shortening affects rFD in SSC contractions in a time-dependent manner. The authors found that with a longer shortening time, a greater rFD was produced. However, the same authors still reported a reduced rFD after the SSC at an intensity level of 50–60% of MVC when the shortening phase was 1 s in length as was the case in our protocol. Their results come from the m. adductor pollicis, which—compared to the m. quadriceps femoris—is of a smaller size and has a short tendon. Since the mechanism for different rFD values with different muscle group sizes remain unknown (Chen et al., 2019), one can only speculate about the possible influence of muscle size on rFD in a SSC contraction.

## CONCLUSION

To our knowledge, this is the first study considering the steady-state torque after a SSC of the m. quadriceps femoris under maximal voluntary contractions and under different submaximal contraction intensities. We hypothesized that with increasing intensity, the SSC-effects are larger, possibly due to increased rFE.

In conclusion, we observed increased mechanical work during the shortening phase of the SSC for all contraction intensities. Additionally, reduced rFD in the SSC condition compared to CON was only found for 100% intensity. Under reduced activation, the stretch-induced force-enhancing effects were only visible during the shortening phase. Our results indicate that the magnitude of contribution of the potential mechanisms in SSCs of the m. quadriceps femoris changes with the intensity and type of activation. Furthermore, the complete attenuation of rFE in the lower intensities despite greater mechanical work during the shortening phase should be examined in future studies.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Ethics Committee of the University of Vienna. The patients/participants provided their written informed consent to participate in this study.

## AUTHOR CONTRIBUTIONS

MG, SS, and AB conceived and designed the experiment. MG performed the experiment. MG and SS analyzed the data. MG, SS, WS, and AB discussed the results, made a substantial contribution to the interpretation of data, and contributed to the elaboration of the manuscript. All authors contributed to the article and approved the submitted version.

## FUNDING

Open access funding was provided by the University of Vienna, and partial funding was provided by the German Research Foundation (DFG) under the grant number SE 2109/2-1.

## ACKNOWLEDGMENTS

We thank Philipp Kornfeind and Markus Kleinberger for their assistance in the laboratory. We also would like to thank all participants for their time and motivation.

## REFERENCES

- Abbott, B. C., and Aubert, X. M. (1952). The force exerted by active striated muscle during and after change of length. *J. Physiol.* 117, 77–86.
- Altenburg, T. M., de Ruiter, C. J., Verdijk, P. W. L., van Mechelen, W., and de Haan, A. (2008). Vastus lateralis surface and single motor unit EMG following submaximal shortening and lengthening contractions. *Appl. Physiol. Nutr. Metab.* 33, 1086–1095. doi: 10.1139/h08-092
- Arampatzis, A., Karamanidis, K., de Monte, G., Stafilidis, S., Morey-Klapsing, G., and Brüggemann, G.-P. (2004). Differences between measured and resultant joint moments during voluntary and artificially elicited isometric knee extension contractions. *Clin. Biomechan. (Bristol, Avon)* 19, 277–283. doi: 10.1016/j.clinbiomech.2003.11.011
- Bobbert, M. F., and Casius, L. J. R. (2005). Is the effect of a countermovement on jump height due to active state development? *Med. Sci. Sports Exerc.* 37, 440–446. doi: 10.1249/01.MSS.0000155389.34538.97
- Bohm, S., Marzilger, R., Mersmann, F., Santuz, A., and Arampatzis, A. (2018). Operating length and velocity of human vastus lateralis muscle during walking and running. *Sci. Rep.* 8:5066. doi: 10.1038/s41598-018-23376-23375
- Bullimore, S. R., Leonard, T. R., Rassier, D. E., and Herzog, W. (2007). History-dependence of isometric muscle force: effect of prior stretch or shortening amplitude. *J. Biomechan.* 40, 1518–1524. doi: 10.1016/j.jbiomech.2006.06.014
- Chen, J., Hahn, D., and Power, G. A. (2019). Shortening-induced residual force depression in humans. *J. Appl. Physiol.* (1985) 126, 1066–1073. doi: 10.1152/japplphysiol.00931.2018
- Dargeviciute, G., Masiulis, N., Kamandulis, S., Skurvydas, A., and Westerblad, H. (2013). Residual force depression following muscle shortening is exaggerated by prior eccentric drop jump exercise. *J. Appl. Physiol.* (1985) 115, 1191–1195. doi: 10.1152/japplphysiol.00686.2013
- Dietz, V., Schmidtleicher, D., and Noth, J. (1979). Neuronal mechanisms of human locomotion. *J. Neurophys.* 42, 1212–1222. doi: 10.1152/jn.1979.42.5.1212
- Edman, K. A. (1978). Maximum velocity of shortening in relation to sarcomere length and degree of activation of frog muscle fibres. *J. Physiol.* 278, 9–10.
- Edman, K. A., Elzinga, G., and Noble, M. I. (1982). Residual force enhancement after stretch of contracting frog single muscle fibers. *J. General Physiol.* 80, 769–784. doi: 10.1085/jgp.80.5.769
- Edman, K. A. P. (2012). Residual force enhancement after stretch in striated muscle. a consequence of increased myofilament overlap? *J. Physiol.* 590, 1339–1345. doi: 10.1113/jphysiol.2011.222729
- Finni, T., Ikegawa, S., and Komi, P. V. (2001). Concentric force enhancement during human movement. *Acta Physiol. Scand.* 173, 369–377. doi: 10.1046/j.1365-201X.2001.00915.x
- Fortuna, R., Groeber, M., Seiberl, W., Power, G. A., and Herzog, W. (2017). Shortening-induced force depression is modulated in a time- and speed-dependent manner following a stretch-shortening cycle. *Physiol. Rep.* 5:e13279. doi: 10.14814/phy2.13279
- Fukashiro, S., Itoh, M., Ichinose, Y., Kawakami, Y., and Fukunaga, T. (1995). Ultrasonography gives directly but noninvasively elastic characteristic of human tendon in vivo. *Eur. J. Appl. Physiol. Occupat. Physiol.* 71, 555–557. doi: 10.1007/BF00238560
- Fukutani, A., and Herzog, W. (2019). Current understanding of residual force enhancement: cross-bridge component and non-cross-bridge component. *Int. J. Mol. Sci.* 20:5479. doi: 10.3390/ijms20215479
- Fukutani, A., Joumaa, V., and Herzog, W. (2017a). Influence of residual force enhancement and elongation of attached cross-bridges on stretch-shortening cycle in skinned muscle fibers. *Physiol. Rep.* 5:13477. doi: 10.14814/phy2.13477
- Fukutani, A., Misaki, J., and Isaka, T. (2017b). Relationship between joint torque and muscle fascicle shortening at various joint angles and intensities in the plantar flexors. *Sci. Rep.* 7:290. doi: 10.1038/s41598-017-00485-481
- Fukutani, A., Leonard, T., and Herzog, W. (2019a). Does stretching velocity affect residual force enhancement? *J. Biomechan.* 89, 143–147. doi: 10.1016/j.jbiomech.2019.04.033
- Fukutani, A., Shimoho, K., and Isaka, T. (2019b). Pre-activation affects the effect of stretch-shortening cycle by modulating fascicle behavior. *Biol. Open* 8:bio044651. doi: 10.1242/bio.044651
- Gehlert, S., Bloch, W., and Suhr, F. (2015). Ca<sup>2+</sup>-dependent regulations and signaling in skeletal muscle: from electro-mechanical coupling to adaptation. *Int. J. Mol. Sci.* 16, 1066–1095. doi: 10.3390/ijms16011066
- Gobbo, M., Maffiuletti, N. A., Orizio, C., and Minetto, M. A. (2014). Muscle motor point identification is essential for optimizing neuromuscular electrical stimulation use. *J. Neuroeng. Rehabilitation* 11:17. doi: 10.1186/1743-0003-11-17
- Grazier, H. L., Burns, D. H., and Pollack, G. H. (1989). Sarcomere length dependence of the force-velocity relation in single frog muscle fibers. *Biophys. J.* 55, 499–507. doi: 10.1016/S0006-3495(89)82843-7
- Groeber, M., Reinhart, L., Kornfeind, P., and Baca, A. (2019). The contraction modalities in a stretch-shortening cycle in animals and single joint movements in humans: a systematic review. *J. Sports Sci. Med.* 18, 604–614.
- Hahn, D., Herzog, W., and Schwirtz, A. (2014). Interdependence of torque, joint angle, angular velocity and muscle action during human multi-joint leg extension. *Eur. J. Appl. Physiol.* 114, 1691–1702. doi: 10.1007/s00421-014-2899-5
- Hahn, D., and Riedel, T. N. (2018). Residual force enhancement contributes to increased performance during stretch-shortening cycles of human plantar flexor muscles in vivo. *J. Biomechan.* 77, 190–193. doi: 10.1016/j.jbiomech.2018.06.003
- Hahn, D., Seiberl, W., and Schwirtz, A. (2007). Force enhancement during and following muscle stretch of maximal voluntarily activated human quadriceps femoris. *Eur. J. Appl. Physiol.* 100, 701–709. doi: 10.1007/s00421-007-0462-463
- Hermens, H. J., Frieriks, B., Disselhorst-Klug, C., and Rau, G. (2000). Development of recommendations for SEMG sensors and sensor placement procedures. *J. Electromyography Kinesiol.* 10, 361–374. doi: 10.1016/S1050-6411(00)00027-24
- Herzog, W. (2004). History dependence of skeletal muscle force production: implications for movement control. *Hum. Movem. Sci.* 23, 591–604. doi: 10.1016/j.humov.2004.10.003
- Herzog, W. (2014). Mechanisms of enhanced force production in lengthening (eccentric) muscle contractions. *J. Appl. Physiol.* (1985) 116, 1407–1417. doi: 10.1152/japplphysiol.00069.2013
- Herzog, W., and Leonard, T. R. (1997). Depression of cat soleus forces following isokinetic shortening. *J. Biomechan.* 30, 865–872. doi: 10.1016/S0021-9290(97)00046-48
- Herzog, W., and Leonard, T. R. (2000). The history dependence of force production in mammalian skeletal muscle following stretch-shortening and shortening-stretch cycles. *J. Biomechan.* 33, 531–542. doi: 10.1016/s0021-9290(99)00221-223
- Herzog, W., Schachar, R., and Leonard, T. R. (2003). Characterization of the passive component of force enhancement following active stretching of skeletal muscle. *J. Exp. Biol.* 206, 3635–3643. doi: 10.1242/jeb.00645
- Herzog, W., Schappacher, G., DuVall, M., Leonard, T. R., and Herzog, J. A. (2016). Residual force enhancement following eccentric contractions: a new mechanism involving titin. *Physiology (Bethesda, Md.)* 31, 300–312. doi: 10.1152/physiol.00049.2014
- Hill, A. V. (1938). The heat of shortening and the dynamic constants of muscle. *Proc. R. Soc. Lond. B* 126, 136–195. doi: 10.1098/rspb.1938.0050
- Hisey, B., Leonard, T. R., and Herzog, W. (2009). Does residual force enhancement increase with increasing stretch magnitudes? *J. Biomechan.* 42, 1488–1492. doi: 10.1016/j.jbiomech.2009.03.046
- Ishikawa, M., Komi, P. V., Grey, M. J., Lepola, V., and Brüggemann, G.-P. (2005). Muscle-tendon interaction and elastic energy usage in human walking. *J. Appl. Physiol.* (1985) 99, 603–608. doi: 10.1152/japplphysiol.00189.2005
- Jin, L., and Hahn, M. E. (2019). Comparison of lower extremity joint mechanics between healthy active young and middle age people in walking and running gait. *Sci. Rep.* 9:5568. doi: 10.1038/s41598-019-41750-9
- Joumaa, V., Fitzowich, A., and Herzog, W. (2017). Energy cost of isometric force production after active shortening in skinned muscle fibres. *J. Exp. Biol.* 220, 1509–1515. doi: 10.1242/jeb.117622
- Kawakami, Y., Muraoka, T., Ito, S., Kanehisa, H., and Fukunaga, T. (2002). In vivo muscle fibre behaviour during counter-movement exercise in humans reveals a significant role for tendon elasticity. *J. Physiol.* 540, 635–646. doi: 10.1113/jphysiol.2001.013459

- Komi, P. V. (2000). Stretch-shortening cycle: a powerful model to study normal and fatigued muscle. *J. Biomechan.* 33, 1197–1206. doi: 10.1016/S0021-9290(00)00064-66
- Komi, P. V., and Gollhofer, A. (1997). Stretch reflexes can have an important role in force enhancement during SSC exercise. *J. Appl. Biomechan.* 13, 451–460. doi: 10.1123/jab.13.4.451
- Koo, T. K., and Li, M. Y. (2016). A guideline of selecting and reporting intraclass correlation coefficients for reliability research. *J. Chiropractic Med.* 15, 155–163. doi: 10.1016/j.jcm.2016.02.012
- Lee, H.-D., and Herzog, W. (2002). Force enhancement following muscle stretch of electrically stimulated and voluntarily activated human adductor pollicis. *J. Physiol.* 545, 321–330. doi: 10.1113/jphysiol.2002.018010
- Lee, H.-D., Herzog, W., and Leonard, T. (2001). Effects of cyclic changes in muscle length on force production in in-situ cat soleus. *J. Biomechan.* 34, 979–987. doi: 10.1016/S0021-9290(01)00077-x
- Lee, H. D., Suter, E., and Herzog, W. (1999). Force depression in human quadriceps femoris following voluntary shortening contractions. *J. Appl. Physiol.* (1985) 87, 1651–1655. doi: 10.1152/jappl.1999.87.5.1651
- Lee, H.-D., Suter, E., and Herzog, W. (2000). Effects of speed and distance of muscle shortening on force depression during voluntary contractions. *J. Biomechan.* 33, 917–923. doi: 10.1016/S0021-9290(00)00070-71
- Leonard, T. R., and Herzog, W. (2010). Regulation of muscle force in the absence of actin-myosin-based cross-bridge interaction. *Am. J. Physiol. Cell Physiol.* 299, C14–C20. doi: 10.1152/ajpcell.00049.2010
- Linke, W. A. (2018). Titin gene and protein functions in passive and active muscle. *Annu. Rev. Physiol.* 80, 389–411. doi: 10.1146/annurev-physiol-021317-121234
- Linnamo, V., Strojnik, V., and Komi, P. V. (2006). Maximal force during eccentric and isometric actions at different elbow angles. *Eur. J. Appl. Physiol.* 96, 672–678. doi: 10.1007/s00421-005-0129-x
- Maréchal, G., and Plaghki, L. (1979). The deficit of the isometric tetanic tension redeveloped after a release of frog muscle at a constant velocity. *J. General Physiol.* 73, 453–467. doi: 10.1085/jgp.73.4.453
- Marginson, V., and Eston, R. (2001). The relationship between torque and joint angle during knee extension in boys and men. *J. Sports Sci.* 19, 875–880. doi: 10.1080/0264041010753113822
- Narici, M. V., Maganaris, C. N., Reeves, N. D., and Capodaglio, P. (2003). Effect of aging on human muscle architecture. *J. Appl. Physiol.* (1985) 95, 2229–2234. doi: 10.1152/japplphysiol.00433.2003
- Nikolaidou, M. E., Marzilger, R., Bohm, S., Mersmann, F., and Arampatzis, A. (2017). Operating length and velocity of human M. vastus lateralis fascicles during vertical jumping. *R Soc. Open Sci.* 4:170185. doi: 10.1098/rsos.170185
- Oskoue, A. E., and Herzog, W. (2006a). Force enhancement at different levels of voluntary contraction in human adductor pollicis. *Eur. J. Appl. Physiol.* 97, 280–287. doi: 10.1007/s00421-006-0167-z
- Oskoue, A. E., and Herzog, W. (2006b). The dependence of force enhancement on activation in human adductor pollicis. *Eur. J. Appl. Physiol.* 98, 22–29. doi: 10.1007/s00421-006-0170-174
- Pinniger, G. J., and Cresswell, A. G. (2007). Residual force enhancement after lengthening is present during submaximal plantar flexion and dorsiflexion actions in humans. *J. Appl. Physiol.* (1985) 102, 18–25. doi: 10.1152/japplphysiol.00565.2006
- Power, G. A., Makrakos, D. P., Rice, C. L., and Vandervoort, A. A. (2013). Enhanced force production in old age is not a far stretch: an investigation of residual force enhancement and muscle architecture. *Physiol. Rep.* 1:e00004. doi: 10.1002/phy2.4
- Rassier, D. E., Herzog, W., and Pollack, G. H. (2003). Dynamics of individual sarcomeres during and after stretch in activated single myofibrils. *Proc. Biol. Sci.* 270, 1735–1740. doi: 10.1098/rspb.2003.2418
- Reeves, N. D., Maganaris, C. N., and Narici, M. V. (2003). Effect of strength training on human patella tendon mechanical properties of older individuals. *J. Physiol.* 548, 971–981. doi: 10.1111/j.2003.t01-1-00971.x
- Reeves, N. D., and Narici, M. V. (2003). Behavior of human muscle fascicles during shortening and lengthening contractions in vivo. *J. Appl. Physiol.* (1985) 95, 1090–1096. doi: 10.1152/japplphysiol.01046.2002
- Rode, C., Siebert, T., and Blickhan, R. (2009). Titin-induced force enhancement and force depression: a 'sticky-spring' mechanism in muscle contractions? *J. Theoretical Biol.* 259, 350–360. doi: 10.1016/j.jtbi.2009.03.015
- Sakamoto, A., and Sinclair, P. J. (2006). Effect of movement velocity on the relationship between training load and the number of repetitions of bench press. *J. Strength Condition. Res.* 20, 523–527. doi: 10.1519/16794.1
- Sakamoto, A., and Sinclair, P. J. (2012). Muscle activations under varying lifting speeds and intensities during bench press. *Eur. J. Appl. Physiol.* 112, 1015–1025. doi: 10.1007/s00421-011-2059-2050
- Seiberl, W., Hahn, D., Herzog, W., and Schwirtz, A. (2012). Feedback controlled force enhancement and activation reduction of voluntarily activated quadriceps femoris during sub-maximal muscle action. *J. Electromyography Kinesiol.* 22, 117–123. doi: 10.1016/j.jelekin.2011.10.010
- Seiberl, W., Paternoster, F., Achatz, F., Schwirtz, A., and Hahn, D. (2013). On the relevance of residual force enhancement for everyday human movement. *J. Biomechan.* 46, 1996–2001. doi: 10.1016/j.jbiomech.2013.06.014
- Seiberl, W., Power, G. A., and Hahn, D. (2015a). Residual force enhancement in humans: current evidence and unresolved issues: current evidence and unresolved issues. *J. Electromyography Kinesiol.* 25, 571–580. doi: 10.1016/j.jelekin.2015.04.011
- Seiberl, W., Power, G. A., Herzog, W., and Hahn, D. (2015b). The stretch-shortening cycle (SSC) revisited: residual force enhancement contributes to increased performance during fast SSCs of human m. adductor pollicis. *Physiol. Rep.* 3:e12401. doi: 10.14814/phy2.12401
- Sugi, H., and Tsuchiya, T. (1988). Stiffness changes during enhancement and deficit of isometric force by slow length changes in frog skeletal muscle fibres. *J. Physiol.* 407, 215–229. doi: 10.1113/jphysiol.1988.sp017411
- Tilp, M., Steib, S., Schappacher-Tilp, G., and Herzog, W. (2011). Changes in fascicle lengths and pennation angles do not contribute to residual force enhancement/depression in voluntary contractions. *J. Appl. Biomechan.* 27, 64–73. doi: 10.1123/jab.27.1.64
- Tomolka, A., Weidner, S., Hahn, D., Seiberl, W., and Siebert, T. (2020). Cross-bridges and sarcomeric non-cross-bridge structures contribute to increased work in stretch-shortening cycles. *Front. Physiol.* 11:921. doi: 10.3389/fphys.2020.00921
- van Schenau, G. J. I., Bobbert, M. F., Haan, A., and de. (1997). Mechanics and energetics of the stretch-shortening cycle: a stimulating discussion. *J. Appl. Biomechan.* 13, 484–496. doi: 10.1123/jab.13.4.484
- Wang, J. H.-C. (2006). Mechanobiology of tendon. *J. Biomechan.* 39, 1563–1582. doi: 10.1016/j.jbiomech.2005.05.011
- Webber, S., and Kriellaars, D. (1997). Neuromuscular factors contributing to in vivo eccentric moment generation. *J. Appl. Physiol.* (1985) 83, 40–45. doi: 10.1152/jappl.1997.83.1.40
- Wernbom, M., Augustsson, J., and Thomeé, R. (2007). The influence of frequency, intensity, volume and mode of strength training on whole muscle cross-sectional area in humans. *Sports Med. (Auckland, N.Z.)* 37, 225–264. doi: 10.2165/00007256-200737030-200737034
- Westing, S. H., Seger, J. Y., and Thorstensson, A. (1990). Effects of electrical stimulation on eccentric and concentric torque-velocity relationships during knee extension in man. *Acta Physiol. Scand.* 140, 17–22. doi: 10.1111/j.1748-1716.1990.tb08971.x

**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Copyright © 2020 Groeber, Stafiliadis, Seiberl and Baca. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

### **2.3 Publication 3: The effect of stretch-shortening magnitude and muscle tendon unit length on performance enhancement in a stretch-shortening cycle**

#### **Authors:**

Martin Groeber, Savvas Stafilidis and Arnold Baca

#### **Status:**

The manuscript was published by Scientific Reports on 16 July 2021 (Groeber et al., 2021).

#### **Authors' contribution:**

All authors contributed to the study conception and design. Data collection and analysis were performed by Martin Groeber. The first draft of the manuscript was written by Martin Groeber and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.





OPEN

# The effect of stretch–shortening magnitude and muscle–tendon unit length on performance enhancement in a stretch–shortening cycle

Martin Groeber✉, Savvas Staflidis & Arnold Baca

Stretch-induced residual force enhancement (rFE) is associated with increased performance in a stretch–shortening cycle (SSC). Although the influence of different range of motions and muscle–tendon unit lengths has been investigated in pure stretch–hold experiments *in vivo*, the contribution to a SSC movement in human muscles remains unclear. In two sessions, 25 healthy participants performed isometric reference (ISO), shortening hold (SHO) and SSC contractions on an isokinetic dynamometer. We measured the net knee-joint torque, rotational mechanical work, knee kinematics and fascicle behavior (m. vastus lateralis) of the upper right leg. In session 1 the SHO- and SSC-magnitude was changed respectively (SHO: 50°–20°, 80°–20° and 110°–20°; SSC: 20°–50°–20°, 20°–80°–20° and 20°–110°–20°) and in session 2 the muscle–tendon unit length (SHO: 50°–20°, 80°–50° and 110°–80°; SSC: 20°–50°–20°, 50°–80°–50° and 80°–110°–80°; straight leg = 0°). In both sessions, rotational work was significantly ( $p < 0.05$ ) increased in the SSC compared to the SHO contractions (in the range of 8.1–17.9%). No significant difference of joint torque was found in the steady-state for all SSC-magnitudes compared to the corresponding SHO contractions in session 1. In session 2, we found only significantly ( $p < 0.05$ ) less depressed joint torque in the SSC at the longest muscle–tendon unit length compared to the corresponding SHO condition, without any differences in knee kinematics and fascicle behavior. Therefore, the physiological relevance of rFE might be particularly important for movements at greater muscle–tendon unit lengths.

A stretch–shortening cycle (SSC) is a common muscle action during exercise and everyday movement. The SSC is defined as a stretching of the muscle–tendon unit prior to a shortening<sup>1</sup>. It has long been identified that this leads to increased force, torque, mechanical work and power during the shortening phase of the SSC compared to a pure shortening contraction, which is not preceded by active stretching (“SSC-effect”)<sup>2,3</sup>. Despite clear evidence that this phenomenon exists, the associated mechanisms are heavily debated in the literature as none of the mechanisms can entirely explain this SSC-effect<sup>4–6</sup>. The mechanisms attributed to this effect are the pre-activation of the muscle<sup>7</sup>, the stretch-reflex<sup>8</sup> and the release of stored passive-elastic energy in the tendinous tissue<sup>9,10</sup>. Since it was shown that the SSC-effect was also visible in studies not related to the previously mentioned mechanism<sup>6</sup> and the SSC-effect was present on the fiber level (meaning no serial-elastic component such as aponeurosis and tendon)<sup>11</sup>, another mechanism must also play a role in the SSC performance enhancement. The contribution of such an additional mechanism to the SSC performance enhancement should be found within the sarcomere<sup>5,6,11–13</sup>.

In stretch–hold experiments, the force or torque during active stretch but also in the isometric hold phase after active stretch is enhanced compared to a fixed-end reference contraction. This applies when the reference contraction is length-matched and has the same activation level. In literature, the enhancement is described to have a velocity-dependent<sup>14,15</sup> transient force enhancement (FE) throughout the stretch phase<sup>16</sup>. This is characterized by a steep increase in force in the early stretch phase, followed by a slower rise<sup>17,18</sup>. The peak force during stretch is greater with increasing stretch velocity<sup>18</sup>. Followed by a long-lasting component, which is called residual

Department of Biomechanics, Kinesiology and Computer Science in Sport, Centre for Sport Science and University Sports, University of Vienna, Vienna, Austria. ✉email: martin.groeber@univie.ac.at

force enhancement (rFE)<sup>19–21</sup>. It is thought that the protein titin mediates the phenomena of rFE<sup>22,23</sup>. In recent studies, it is proposed that the SSC-effect is also associated with rFE<sup>6,12,24–26</sup>.

The steady-state force or torque is decreased after shortening-hold (SHO) experiments compared to an isometric hold phase of a fixed-end contraction at the same muscle length and activation level. In literature this is called residual force depression (rFD)<sup>19</sup>. The key mechanism attributed to rFD is the stress-induced inhibition of the actin-myosin overlap zone<sup>19,27,28</sup>.

Stretch-hold or shortening-hold experiments do not mirror movements with real everyday significance. To ensure that these history-dependent properties of rFE and rFD are relevant for everyday human movement, controlled in vivo studies<sup>29</sup> investigating SSC muscle action are required. In the context of a SSC, transient FE is increased due to elastic as well as viscoelastic structures<sup>17,30</sup>. Most of the energy storage cannot be explained by cross-bridge mechanism. This was showed in stretch experiments with isolated muscle fibers<sup>17,30</sup> where in the presence of myosin inhibitors the peak non cross-bridge contribution and rFE remain high. Other structures as titin may store and release elastic energy during the stretch and the subsequent shortening phase of the SSC and thereby increasing the SSC-effect<sup>5</sup>.

In stretch-hold or shortening-hold, it was found that the amount of rFE and rFD could be influenced by various factors. In vitro studies show increased transient FE and rFE with higher stretch magnitude<sup>15,20,31,32</sup>. In vivo measurements show that rFE only depends on stretch magnitude in some circumstances (dependent on the muscle of interest)<sup>33–35</sup>. At shortening contractions, rFD increases with the work (force  $\times$  shortening magnitude) performed during shortening in in vivo studies<sup>36–38</sup>.

Additionally, the history dependent properties are also dependent on the location of the muscle action on the force–length relationship. Greater transient FE and rFE occur at long muscle lengths compared to short muscle lengths for in vitro and in situ studies<sup>31,39,40</sup>. In addition to that, a significant larger SSC-effect was reported at relatively long muscle lengths in skinned fibers obtained from rabbit soleus<sup>41</sup>. These results are partially confirmed in in vivo experiments, where mostly increased rFE was found at longer muscle lengths in single joint movements<sup>29,42–44</sup>. However, another study testing the elbow flexor did not show rFE at long or short muscle lengths<sup>45</sup>. Considering rFD, previous studies revealed that the amount of rFD is related to the extent of force development during shortening<sup>38,46</sup>, which should mean that rFD should be larger at muscle lengths where more force can be produced due to the force–length relationship. However, no effect of muscle architecture<sup>47</sup> and angular position<sup>48</sup> on rFD during plantar flexion could be found. The operating length of muscle fascicles determine the force potential of the muscle, therefore it is crucial to measure fascicle behavior to identify if different contraction conditions are comparable. In contrast to the general conception that muscle–tendon unit change is accompanied by major changes in fascicle length, the m. vastus lateralis fascicles act mainly isometrically during the stance phase of running and walking for example<sup>49</sup>.

Based on the literature findings, we sought to investigate the influence of different SSC-magnitudes and muscle–tendon unit lengths on a SSC muscle action of the m. quadriceps femoris in humans. Firstly, we hypothesized that with greater SSC-magnitude transient FE (greater torque at the end of stretch) is enhanced in a SSC compared to an isometric pre-activation of a shortening contraction, which also influences the SSC-effect. But due to greater shortening range at greater SSC-magnitudes, we hypothesized that rFE is eliminated by the shortening phase which will result in a lack of differences in the steady-state isometric torque after the dynamic phase. And secondly, we expected no difference in transient FE<sup>29</sup>, but increased rFE at greater muscle–tendon unit lengths due to increased titin stiffness at longer muscle–tendon unit lengths<sup>23,50</sup>.

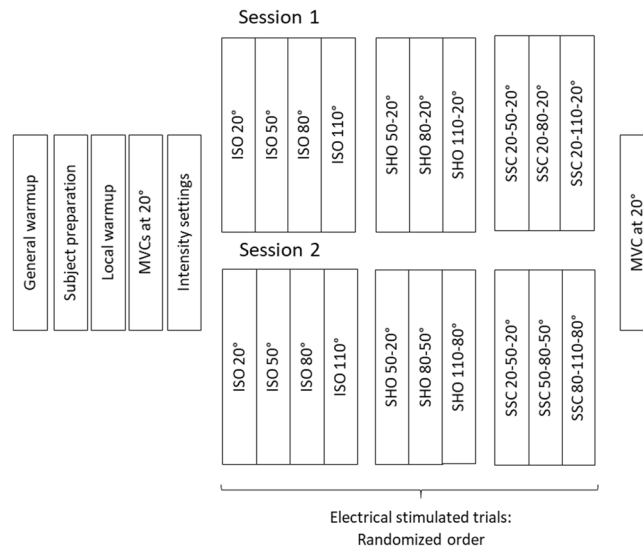
## Materials and methods

**Participants.** 30 healthy adults were recruited for this study. Five subjects did not finish the test protocol or data was missing. Finally, data from 25 participants were obtained (13 male and 12 female adults; age  $26.2 \pm 6.0$  years; body mass  $71.5 \pm 11.7$  kg; height  $175.3 \pm 8.9$  cm). All participants took part in the study voluntarily and provided free written informed consent prior to the study. The participants had no injury to the right leg, neuromuscular disorders or cardiovascular problems. Eligibility for the study was decided with the help of an anamnesis questionnaire to detect the risk factors for physical activity. The experimental protocol was approved by the Ethics Committee of the University of Vienna (Reference Number: 00364).

**Experimental setup.** The setup was configured similarly to a previous study<sup>51</sup>. Experiments were performed with an isokinetic dynamometer (HUMAC Norm Model 770; CSMi, Stoughton, MA, USA) to measure net knee-joint torque of the right leg in a sitting position. The analog signals of the dynamometer were captured with a Vicon Nexus A/D card (16bit) with a sampling frequency of 2 kHz. The seat of the isokinetic dynamometer was precisely adjusted to each participant, so that the rotation axis of the dynamometer was aligned with the lateral femoral condyles. The upper body was tightly fixed to the seat of the dynamometer by inextensible straps.

Kinematic data was recorded synchronously with nine cameras (Vantage V8, Vicon Nexus motion capturing system, Oxford, United Kingdom, 100 Hz). The measured torque was corrected by means of the kinematic data, since tissue deformation and dynamometer padding can result in a misalignment of the joint and dynamometer axes of rotation. Overall, eight reflective surface markers were used. Five were placed at the right leg (medial and lateral malleolus, the most prominent point of the lateral and medial femoral condyles and the trochanter major). Additionally, one marker was placed at the dynamometer's rotation axis and two markers were placed on the dynamometer's arm (one of them at the point of force application to define the distance between the dynamometer's rotation axis and the line of action of the applied extension force).

To ensure a constant muscle contraction, two self-adhering surface electrodes ( $5 \times 5$  cm) were placed on the m. vastus lateralis proximal motor point and m. vastus medialis distal motor point to evoke constant muscle contraction using electrical stimulation (Digitimer DS8R, United Kingdom). The muscle motor points were



**Figure 1.** Experimental protocol. Each subject participated in two test sessions. Both test sessions comprised isometric fixed-end reference contractions (ISO), shortening-hold contractions (SHO) and stretch-shortening contractions (SSC). In session 1 the SHO- and SSC-magnitude and in session 2 the muscle-tendon unit length was modified.

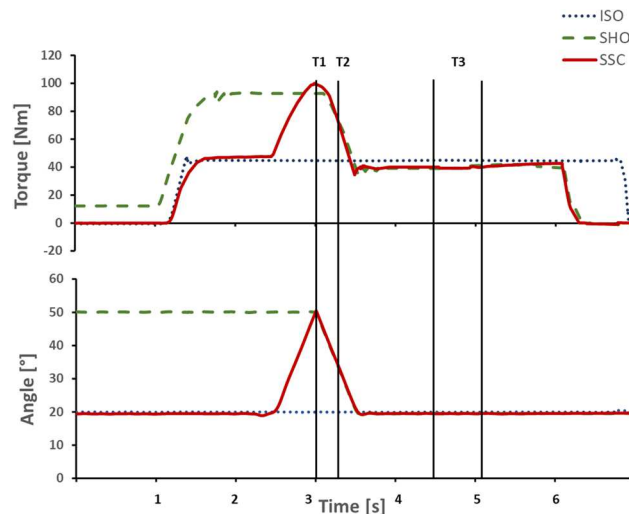
detected by scanning the surface of the skin with a motor point pen (COMPEX, United Kingdom)<sup>52</sup>. Current was increased (100  $\mu$ s square-wave pulses at 100 Hz) until the evoked tetanic torque reached 35% of maximal voluntary contraction (MVC) at a dynamometer angle of 20° (full knee extension was defined as 0°). The reached current was used for the whole experimental protocol. For the electrostimulation, we used an intensity of 35% of the MVC based on a previous study, which examined the history-dependent properties on the m. quadriceps femoris<sup>51</sup>. For that purpose, the current for the m. vastus lateralis and m. vastus medialis was adjusted together.

Fascicle behavior should be well controlled for the examination of the history-dependent properties<sup>36</sup>. Despite identical joint angles, fascicle length changes can be different<sup>29</sup>. Thus, fascicle length, pennation angle and fascicle length changes were determined using ultrasonography (Telemed ArtUS EXT-1H, IT, 70 Hz, Vilnius, Lithuania, EU). A linear probe (LV8-5N60-A2, field of view 60 mm) was tightened to the mid-belly of the m. vastus lateralis<sup>53</sup> with a custom-made bracket. To synchronize the ultrasound data with the kinematic and dynamometer's data, an analog signal (0–3 V) was generated when the ultrasound video was started and stopped, and it was captured by the Vicon system.

To synchronize all data, the analog ultrasound signal was used.

**Experimental protocol.** All participants were familiar with the test setup. The study presented here consisted of two test sessions. Both started with a general warm-up at a bicycle ergometer (5 min, between 80 and 90 W), followed by a specific warm-up of the right leg on the isokinetic dynamometer (5 min, several submaximal contractions). Afterwards, the participants performed two MVCs at a dynamometer angle of 20°. During the MVCs verbal encouragement was provided and the highest developed torque was used for further analysis. Both test sessions comprised electrical stimulated isometric (ISO) at 20°, 50°, 80° and 110° dynamometer angle, shortening-hold (SHO) and stretch-shortening (SSC) muscle actions with different SHO- and SSC-magnitudes (session 1: SHO: 50°–20°, 80°–20° and 110°–20°; SSC: 20°–50°–20°, 20°–80°–20° and 20°–110°–20°) and different muscle-tendon unit lengths (session 2: SHO: 50°–20°, 80°–50° and 110°–80°; SSC: 20°–50°–20°, 50°–80°–50° and 80°–110°–80°) in randomized order (Fig. 1). Each muscle contraction was performed two times. Strictly speaking, the isometric contractions are fixed-end contractions, where muscle shortening can appear even when the joint angle is constant<sup>54</sup>. All ISO, SHO and SSC trials were submaximal, electrically stimulated contractions at 35% of MVC and the angular velocity of the dynamometer was always fixed to 60°/s. All dynamic muscle actions had an isometric pre-activation phase (until a plateau was reached) and an isometric steady-state hold phase for several seconds (3–5 s) after the knee rotation. All ISO, SHO and SSC contractions had a resting phase of two minutes in between to prevent fatigue<sup>47</sup> and to check for fatigue appearance the participants were required to perform a final MVC contraction at 20°.

**Data processing.** The data of the isokinetic dynamometer was filtered with a zero-delay fourth-order Butterworth filter with a cut-off frequency of 10 Hz. Torque values were corrected for gravity for all participants. For each condition the mean values were used for statistical analysis. The different conditions were compared at different instances. At T1, which is defined as the end of stretch in the SSC condition (50°, 80° or 110° dynamometer angle depending on the trial). At T2 which is defined as the midpoint of the shortening range and T3 in the isometric steady-state. At T3, ISO, SHO and SSC condition were compared 1–1.5 s after the knee rotation, while



**Figure 2.** Exemplary representation of torque-time and dynamometer angle-time traces. The dotted blue line represents ISO, the dashed green line SHO and the continuous red line SSC. The vertical lines indicate the timepoint of data analysis, with T1 being end of stretch, T2 midpoint of shortening and T3 the steady-state interval where the mean torque was calculated.

here the average values of the 0.5 s interval window were used (Fig. 2). At T3 all contraction for each participant were visually inspected to assure, that the contractions reached a steady-state.

External rotational work during the shortening was calculated as the integral of knee-joint torque using a numerical trapezoidal method.

$$W = \int M d\varphi = \int M \cdot \omega dt \quad (1)$$

with  $W$  as the mechanical work during the shortening phase [J],  $M$  as torque [Nm] and  $\omega$  as rotational velocity [rad/s].

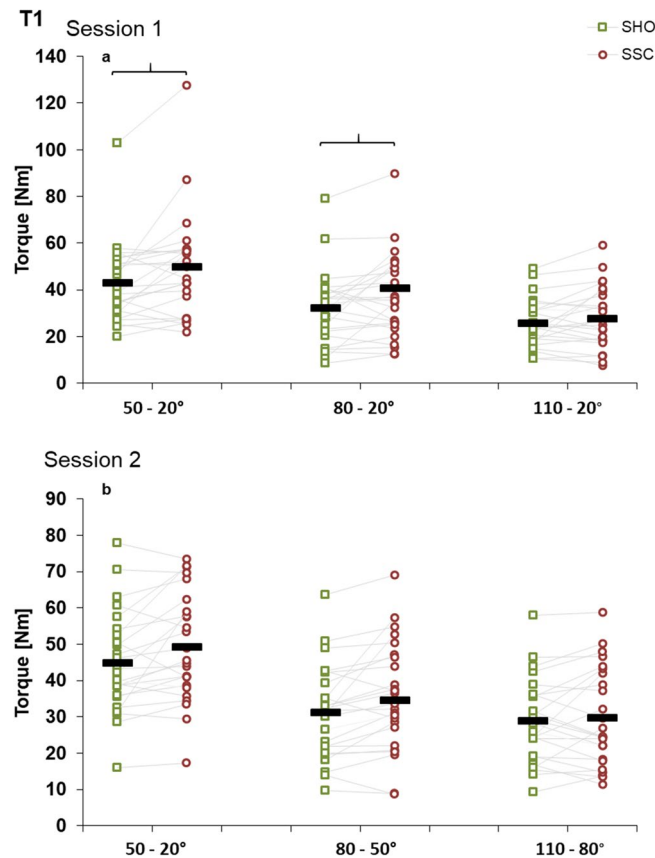
Kinematic data was further processed with a zero-delay fourth-order Butterworth filter with a cutoff frequency of 10 Hz. The knee-joint angles of the different conditions were compared at the previously described instances, because there can be a discrepancy between the measured knee angle and dynamometer-defined angle at higher contraction intensities<sup>51</sup>. Additionally, the kinematic data was used to implement a previously suggested inverse dynamic approach<sup>55</sup>. The measured knee joint torque can deviate from the resultant joint torque up to 4.3%<sup>56</sup>. Due to these differences in the torque measured by the dynamometer and the resultant joint torque, we addressed this shortcoming and implemented the previously mentioned inverse dynamic approach. These differences are triggered by a shift of knee joint axis due to tissue deformation and the compliance of the dynamometer<sup>55</sup>. With this approach, the movement of the segment relative to the dynamometer arm can be corrected. Resultant joint torque was calculated as follows:

$$M_{res} = M_{Meas} \cdot \frac{d_K}{d_B} \quad (2)$$

with  $M_{res}$  as the resultant joint torque,  $M_{Meas}$  the measured torque,  $d_B$  as the lever arm of the applied force to the dynamometer axis and  $d_K$  as the lever arm of force to the knee joint<sup>55</sup>.

The pennation angle was defined as the angle between muscle fascicle and deep aponeurosis, and the fascicle length as the distance between the intersection of the muscle fascicle to the deep and superficial aponeurosis. Fascicle length changes during shortening was defined as the difference of fascicle length at T1 and T3. The average values of three measurements were used for further analysis. In the event that the whole muscle fascicle was not visible on the ultrasound image, a linear continuation was assumed. To measure the non-visible part, trigonometry was used assuming an error of less than 2.4%<sup>57,58</sup>. It was reported that fascicle length values are reliable within the same session, however between sessions the extrapolation method errors cannot be predicted<sup>59</sup>. In our study, the fascicle length was only compared within the same session. Additionally, to test the interrater reliability, two evaluators processed the ultrasound images.

**Statistical analysis.** All data were normally distributed (Shapiro–Wilk test) and therefore a paired t-test with dependent variables or repeated measures ANOVA was used. T-test was used to compare the MVCs at the beginning and at the end of the test session and for the comparison of the same conditions at the two different sessions. Two-way ANOVA (within-within subject design) was used to examine the interaction (session 1: condition  $\times$  magnitude, session 2: condition  $\times$  muscle–tendon unit length) on mechanical work, knee joint torque, knee angle, pennation angle, fascicle length and fascicle length change. If sphericity was violated, Greenhouse–Geisser correction was used. In the case of significant interaction, subsequent post hoc comparisons with Bon-



**Figure 3.** Mean ( $n=25$ , thick horizontal line) (and mean of each individual subject) values of joint torque in session 1 with varying SHO- and SSC-magnitudes (a) and in session 2 with varying muscle-tendon unit length (b) at the onset of shortening (T1). Green squares represent shortening-hold conditions (SHO), whereas red circles represent stretch-shortening conditions (SSC). In the SSC condition the shortening phase was preceded by the corresponding stretch phase. Braces indicate significant ( $p < 0.05$ ) differences between SSC and the corresponding SHO condition.

ferroni adjustments were executed to compare the conditions (ISO, SHO and SSC) at each rotation magnitude (session 1) and muscle-tendon unit length (session 2). The effect size was calculated with partial eta squared ( $\eta^2$ ). Fascicle length and pennation angle measurements were examined for interrater reliability by using the intraclass correlation coefficient (ICC, two-way mixed model, single measures).

**Ethics approval.** Approval was obtained from the ethics committee of the University of Vienna (Reference Number: 00364). The procedures used in this study adhere to the tenets of the Declaration of Helsinki.

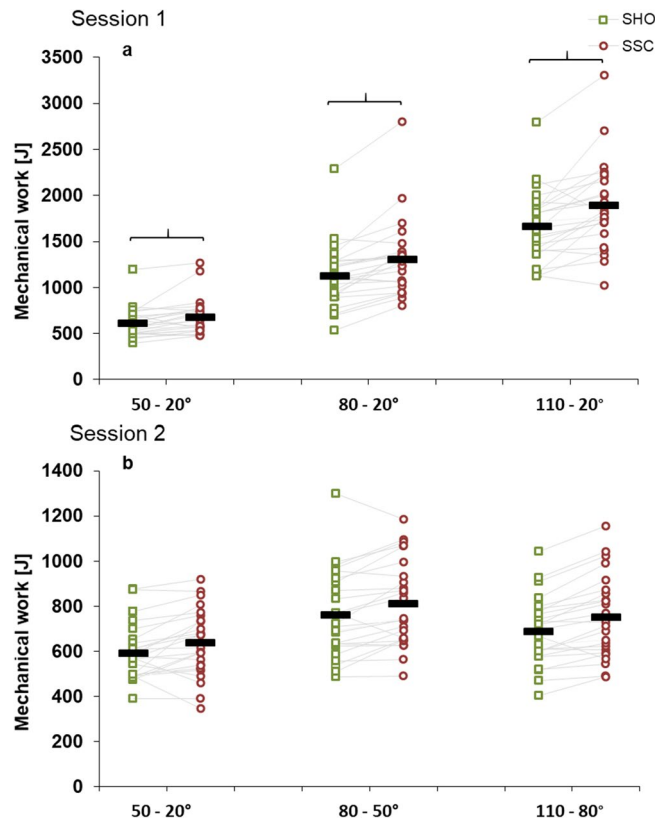
## Results

**Initial conditions.** With the applied current, a mean isometric joint torque of  $32.6 \pm 11.2\%$  at session 1 and  $31.5 \pm 6.6\%$  at session 2 of MVC was achieved at  $20^\circ$  dynamometer angle. Additionally, t-tests revealed no significant differences ( $p > 0.05$ ) between the MVC at the beginning of the test session (session 1:  $97.5 \pm 25.8$  Nm and session 2:  $100.5 \pm 34.0$  Nm) compared to the end of the test session (session 1:  $97.0 \pm 25.4$  Nm and session 2:  $101.4 \pm 33.5$  Nm) and no difference between the sessions ( $p > 0.05$ ), indicating no fatigue and similar conditions at both sessions.

**Joint torque and work measurements.** At T1 in session 1, two-way ANOVA showed a significant interaction (condition  $\times$  magnitude) on knee joint torque ( $p = 0.037$ ,  $\eta^2 = 0.124$ ). Main effect of condition showed increased torque for the SSC compared to SHO condition ( $p = 0.009$ ,  $\eta^2 = 0.240$ ). Post-hoc comparison revealed increased torque at the end of stretch (T1) in the SSC  $20^\circ$ – $50^\circ$ – $20^\circ$  ( $p = 0.008$ ) and  $20^\circ$ – $80^\circ$ – $20^\circ$  ( $p = 0.014$ ) compared to the isometric pre-activation in the SHO condition; no statistical difference could be found after the stretch in the SSC  $20^\circ$ – $110^\circ$ – $20^\circ$  ( $p = 0.252$ ) (Fig. 3a). This resulted in a  $15.4 \pm 15.8\%$  and  $24.4 \pm 17.4\%$  FE, for the SSC conditions at  $20^\circ$ – $50^\circ$ – $20^\circ$  and  $20^\circ$ – $80^\circ$ – $20^\circ$ , respectively. The relative increase at T1 for the SSC  $20^\circ$ – $110^\circ$ – $20^\circ$  was  $8.2 \pm 16.8\%$  (not significant).

In session 1, significant interaction (condition  $\times$  magnitude) was revealed for mechanical work ( $p < 0.001$ ,  $\eta^2 = 0.267$ ). Main effect of rotation magnitude ( $p < 0.001$ ,  $\eta^2 = 0.925$ ) and condition ( $p < 0.001$ ,  $\eta^2 = 0.524$ ) showed increased mechanical work with higher rotation magnitude and for the SSC condition. At all rotation magnitudes,





**Figure 4.** Mean ( $n = 25$ , thick horizontal line) (and mean of each individual subject) values of mechanical work during shortening in session 1 with varying SHO- and SSC-magnitudes (a) and session 2 with varying muscle-tendon unit lengths (b). Green squares represent shortening-hold conditions (SHO), whereas red circles represent stretch-shortening conditions (SSC). In the SSC condition the shortening phase was preceded by the corresponding stretch phase. Braces indicate significant ( $p < 0.05$ ) differences between SSC and the corresponding SHO condition.

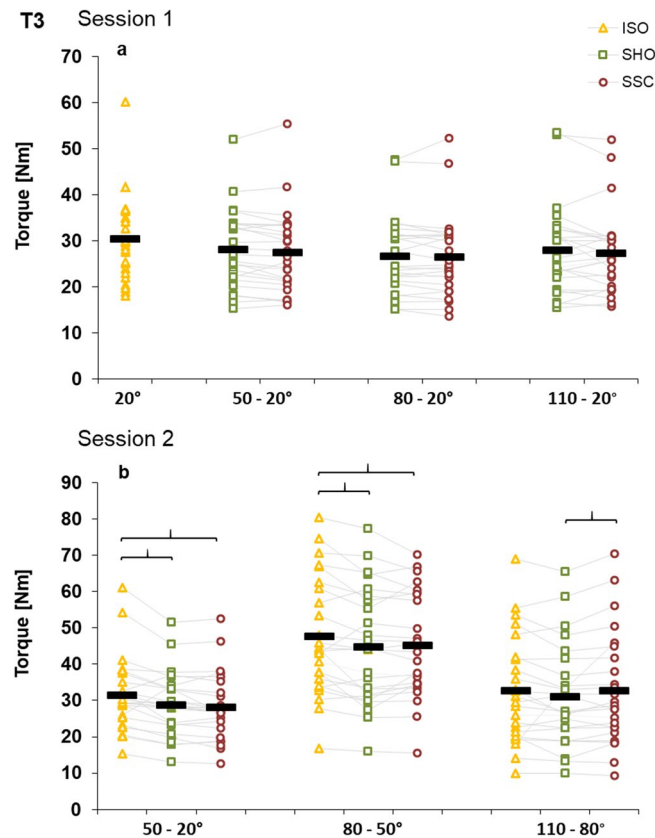
mechanical work was significantly greater during the shortening in the SSC compared to the corresponding SHO condition ( $50^\circ\text{--}20^\circ$ :  $p = 0.003$ ,  $80^\circ\text{--}20^\circ$ :  $p < 0.001$ ,  $110^\circ\text{--}20^\circ$ :  $p < 0.001$ ) (Fig. 4a). The percentage increases of mechanical work in the SSCs (SSC-effect) were  $11.1 \pm 15.1$ ,  $17.9 \pm 16.2$  and  $14.0 \pm 16.0\%$  compared to SHO contraction for the ranges  $50^\circ\text{--}20^\circ$ ,  $80^\circ\text{--}20^\circ$  and  $110^\circ\text{--}20^\circ$ , respectively.

At T3, in the isometric steady-state no significant interaction (condition  $\times$  magnitude) was found ( $p = 0.134$ ,  $\eta^2 = 0.071$ ) in session 1. Main effect of condition revealed significant results ( $p < 0.001$ ,  $\eta^2 = 0.527$ ). Compared to the fixed-end reference condition we found a significant torque depression for SHO ( $p < 0.001$ ) and SSC ( $p < 0.001$ ) and no difference was found between SHO and SSC condition ( $p = 0.296$ ). The main effect of magnitude was significant ( $p = 0.035$ ,  $\eta^2 = 0.126$ ); with increased rotation magnitude we found lower torque at T3, meaning higher torque depression. Compared to the fixed-end reference contraction (ISO) the steady-state torque was depressed in SHO and SSC conditions (SHO:  $50^\circ\text{--}20^\circ$ :  $7.9 \pm 8.0\%$ ,  $80^\circ\text{--}20^\circ$ :  $12.6 \pm 8.1\%$ ,  $110^\circ\text{--}20^\circ$ :  $13.8 \pm 10.9\%$ ; SSC:  $20^\circ\text{--}50^\circ\text{--}20^\circ$ :  $10.0 \pm 10.5\%$ ,  $20^\circ\text{--}80^\circ\text{--}20^\circ$ :  $13.1 \pm 12.6\%$ ,  $20^\circ\text{--}110^\circ\text{--}20^\circ$ :  $15.4 \pm 11.9\%$ ) (Fig. 5a).

A two-way ANOVA showed no significant interaction (condition  $\times$  muscle-tendon unit length) on the joint torque at T1 ( $p = 0.174$ ,  $\eta^2 = 0.70$ ) in session 2. The main effect of condition showed significantly higher torque values at T1 for the SSC condition compared to the SHO condition ( $p = 0.008$ ,  $\eta^2 = 0.257$ ). The main effect for muscle-tendon unit length was also significant ( $p < 0.001$ ,  $\eta^2 = 0.714$ ) (Fig. 3b). The percentage increase in the SSC conditions  $20^\circ\text{--}50^\circ\text{--}20^\circ$ ,  $50^\circ\text{--}80^\circ\text{--}50^\circ$  and  $80^\circ\text{--}110^\circ\text{--}80^\circ$  were  $9.7 \pm 12.3$ ,  $10.9 \pm 12.9$  and  $6.9 \pm 15.2\%$ , respectively (no significant interaction).

For mechanical work in session 2, no significant interaction (condition  $\times$  muscle-tendon unit length) was found ( $p = 0.544$ ,  $\eta^2 = 0.25$ ). The main effect for condition ( $p < 0.001$ ,  $\eta^2 = 0.435$ ) and muscle-tendon unit length ( $p < 0.001$ ,  $\eta^2 = 0.408$ ) showed significantly higher mechanical work with greater muscle-tendon unit length and for the SSC condition (Fig. 4b). The percentage increase of mechanical work (SSC-effect) was almost identical at all different muscle-tendon unit lengths ( $50^\circ\text{--}20^\circ$ :  $8.1 \pm 15.3\%$ ,  $80^\circ\text{--}50^\circ$ :  $8.5 \pm 7.4\%$  and  $110^\circ\text{--}80^\circ$ :  $8.6 \pm 7.8\%$ ).

In the steady-state (T3), a significant interaction (condition  $\times$  muscle-tendon unit length) ( $p = 0.033$ ,  $\eta^2 = 0.127$ ) was identified in session 2. The main effect of muscle-tendon unit length was significant ( $p < 0.001$ ,  $\eta^2 = 0.636$ ), as well as the main effect for condition ( $p < 0.001$ ,  $\eta^2 = 0.296$ ). Further comparison with Bonferroni post hoc correction showed significant higher torque for the SSC condition compared with the SHO condition at the greatest muscle-tendon unit length ( $p = 0.043$ ). No statistical difference was found between SHO:  $50^\circ\text{--}20^\circ$  and SSC:  $20^\circ\text{--}50^\circ\text{--}20^\circ$  ( $p > 0.05$ ) and between SHO:  $80^\circ\text{--}50^\circ$  and SSC:  $50^\circ\text{--}80^\circ\text{--}50^\circ$  ( $p > 0.05$ ). Compared to the



**Figure 5.** Mean ( $n=25$ , thick horizontal line) (and mean of each individual subject) values of torque in the steady-state after knee rotation (T3) in session 1 with varying SHO- and SSC-magnitudes (a) and in session 2 with varying muscle-tendon unit lengths (b). Yellow triangles represent the isometric fixed-end reference conditions at corresponding dynamometer angle (ISO), green squares represent shortening-hold conditions (SHO), whereas red circles represent stretch-shortening conditions (SSC). In the SSC condition the shortening phase was preceded by the corresponding stretch phase.

fixed-end reference contraction torque was significantly depressed ( $p < 0.05$ ), except for the SSC 80°–110°–80° and the SHO 110°–80° condition (SHO: 50°–20°:  $8.1 \pm 11.0\%$ , 80°–50°:  $6.0 \pm 9.9\%$ , 110°–80°:  $4.9 \pm 9.3\%$ ; SSC: 20°–50°–20°:  $10.0 \pm 13.6\%$ , 50°–80°–50°:  $5.3 \pm 8.7\%$ , 80°–110°–80°:  $0 \pm 8.8\%$ ) (Fig. 5b).

Comparing the same conditions in session 1 and 2 revealed no differences between the sessions (T1: SHO: 50°–20°,  $p = 0.626$ ; SSC: 20°–50°–20°,  $p = 0.206$ ; mechanical work: SHO: 50°–20°,  $p = 0.420$ ; SSC: 20°–50°–20°,  $p = 0.168$ ; T3: SHO: 50°–20°,  $p = 0.585$ ; SSC: 20°–50°–20°,  $p = 0.594$ ).

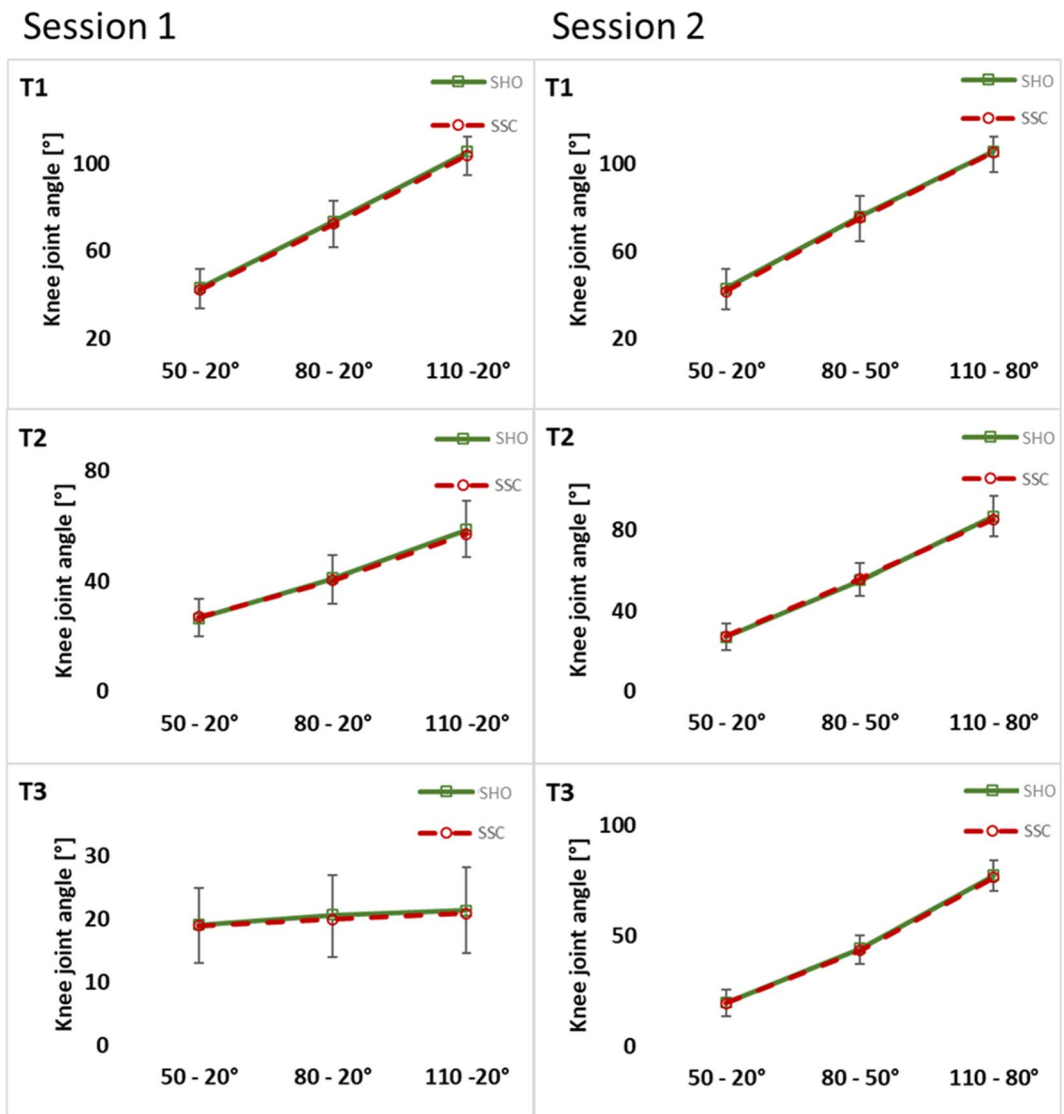
**Knee joint angle.** No significant interaction (condition  $\times$  magnitude) could be found at all instances for the knee joint angle (T1:  $p = 0.843$ ,  $\eta^2 = 0.007$ ; T2:  $p = 0.314$ ,  $\eta^2 = 0.043$ ; T3:  $p = 0.771$ ,  $\eta^2 = 0.010$ ) in session 1. Main effect for condition showed no difference of knee joint angle between SHO and SSC condition (T1:  $p = 0.083$ ,  $\eta^2 = 0.115$ ; T2:  $p = 0.494$ ,  $\eta^2 = 0.019$ ; T3:  $p = 0.215$ ,  $\eta^2 = 0.061$ ) (Fig. 6).

For knee joint angle at session 2, no significant interaction (condition  $\times$  muscle-tendon unit length) was found at all instances (T1:  $p = 0.771$ ,  $\eta^2 = 0.011$ ; T2:  $p = 0.629$ ,  $\eta^2 = 0.019$ ; T3:  $p = 0.418$ ,  $\eta^2 = 0.036$ ). We did not find a significant main effect of condition on knee-joint angle (T1:  $p = 0.062$ ,  $\eta^2 = 0.137$ ; T2:  $p = 0.070$ ,  $\eta^2 = 0.130$ ; T3:  $p = 0.109$ ,  $\eta^2 = 0.103$ ) (Fig. 6).

**Fascicle behavior.** Two independent investigators analyzed fascicle length and pennation angle. For fascicle length, mean ICC across participants for all measurements was 0.87 (ranging from 0.84 to 0.89) and for pennation angle 0.86 (ranging from 0.84 to 0.89). These results indicate a good interrater reliability<sup>60</sup>.

In session 1, statistical analysis of pennation angle revealed no significant interaction (condition  $\times$  magnitude) at T1 ( $p = 0.187$ ,  $\eta^2 = 0.070$ ), T2 ( $p = 0.942$ ,  $\eta^2 = 0.002$ ) and T3 ( $p = 0.201$ ,  $\eta^2 = 0.067$ ) (Fig. 7) and for fascicle length at T1 ( $p = 0.489$ ,  $\eta^2 = 0.035$ ), T2 ( $p = 0.244$ ,  $\eta^2 = 0.065$ ) and T3 ( $p = 0.247$ ,  $\eta^2 = 0.067$ ) (Fig. 8). No significant interaction could be found for fascicle length changes ( $p = 0.849$ ,  $\eta^2 = 0.003$ ).

Further, the main effect of condition showed no significant difference between the SHO and SSC condition for pennation angle (T1:  $p = 0.704$ ,  $\eta^2 = 0.006$ ; T2:  $p = 0.979$ ,  $\eta^2 = 0.001$ ; T3:  $p = 0.408$ ,  $\eta^2 = 0.030$ ) and for fascicle length (T1:  $p = 0.625$ ,  $\eta^2 = 0.012$ ; T2:  $p = 0.100$ ,  $\eta^2 = 0.123$ ; T3:  $p = 0.741$ ,  $\eta^2 = 0.006$ ) is session 1. Main effect of condition showed also no difference between SHO and SSC condition for fascicle length change ( $p = 0.846$ ,  $\eta^2 = 0.002$ ).



**Figure 6.** Mean ( $\pm$ SD,  $n = 25$ ) values of knee-joint angle in both test sessions. T1 is the time point at the onset of shortening, T2 in the middle of the shortening phase, T3 the time point at steady-state after the dynamic phase. No significant interaction (condition  $\times$  magnitude) and (condition  $\times$  muscle–tendon unit length) was found at all instances (T1–T3).

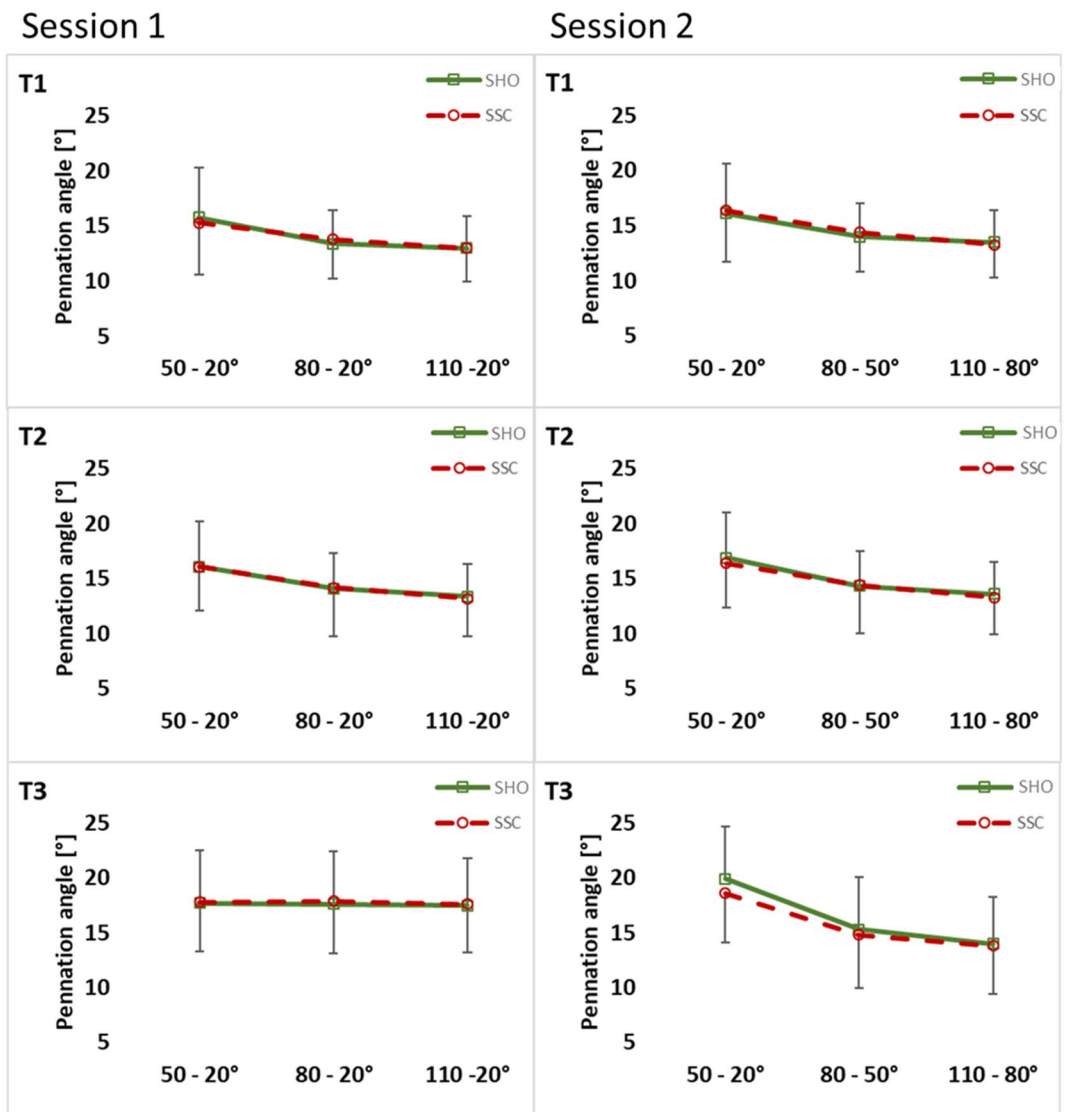
In session 2, no significant interaction (condition  $\times$  muscle–tendon unit length) was found for pennation angle (T1:  $p = 0.053$ ,  $\eta^2 = 0.132$ ; T2:  $p = 0.381$ ,  $\eta^2 = 0.043$ ; T3:  $p = 0.054$ ,  $\eta^2 = 0.136$ ) (Fig. 7) and fascicle length (T1:  $p = 0.981$ ,  $\eta^2 = 0.001$ ; T2:  $p = 0.558$ ,  $\eta^2 = 0.026$ ; T3:  $p = 0.469$ ,  $\eta^2 = 0.033$ ) at all instances (Fig. 8). No significant interaction could be found for fascicle length changes ( $p = 0.913$ ,  $\eta^2 = 0.003$ ).

Also the main effect for condition revealed no difference between SHO and SSC for pennation angle (T1:  $p = 0.088$ ,  $\eta^2 = 0.132$ ; T2:  $p = 0.417$ ,  $\eta^2 = 0.030$ ; T3:  $p = 0.082$ ,  $\eta^2 = 0.143$ ) and fascicle length (T1:  $p = 0.843$ ,  $\eta^2 = 0.002$ ; T2:  $p = 0.928$ ,  $\eta^2 = 0.001$ ; T3:  $p = 0.326$ ,  $\eta^2 = 0.048$ ) in session 2. Main effect of condition also showed no difference between SHO and SSC condition for fascicle length change ( $p = 0.900$ ,  $\eta^2 = 0.001$ ).

## Discussion

The main purpose of this study was to examine the influence of SSC-magnitude and muscle–tendon unit length on the SSC performance, with a special focus on the contribution of the history-dependent properties of muscle contraction. The contribution of rFE was independent of the magnitude, but significantly less rFD was found after the SSC compared to the corresponding pure shortening contraction at the longest muscle–tendon unit length. As expected, the average rotational work values during the concentric phase were significantly greater for all SSCs compared to the corresponding shortening contraction (SHO) at all rotation magnitudes. However, no difference in the SSC-effect with increased rotation magnitude or at different muscle–tendon unit lengths was demonstrated. For all instances (T1–T3) and in both sessions, we could not find any differences for the control





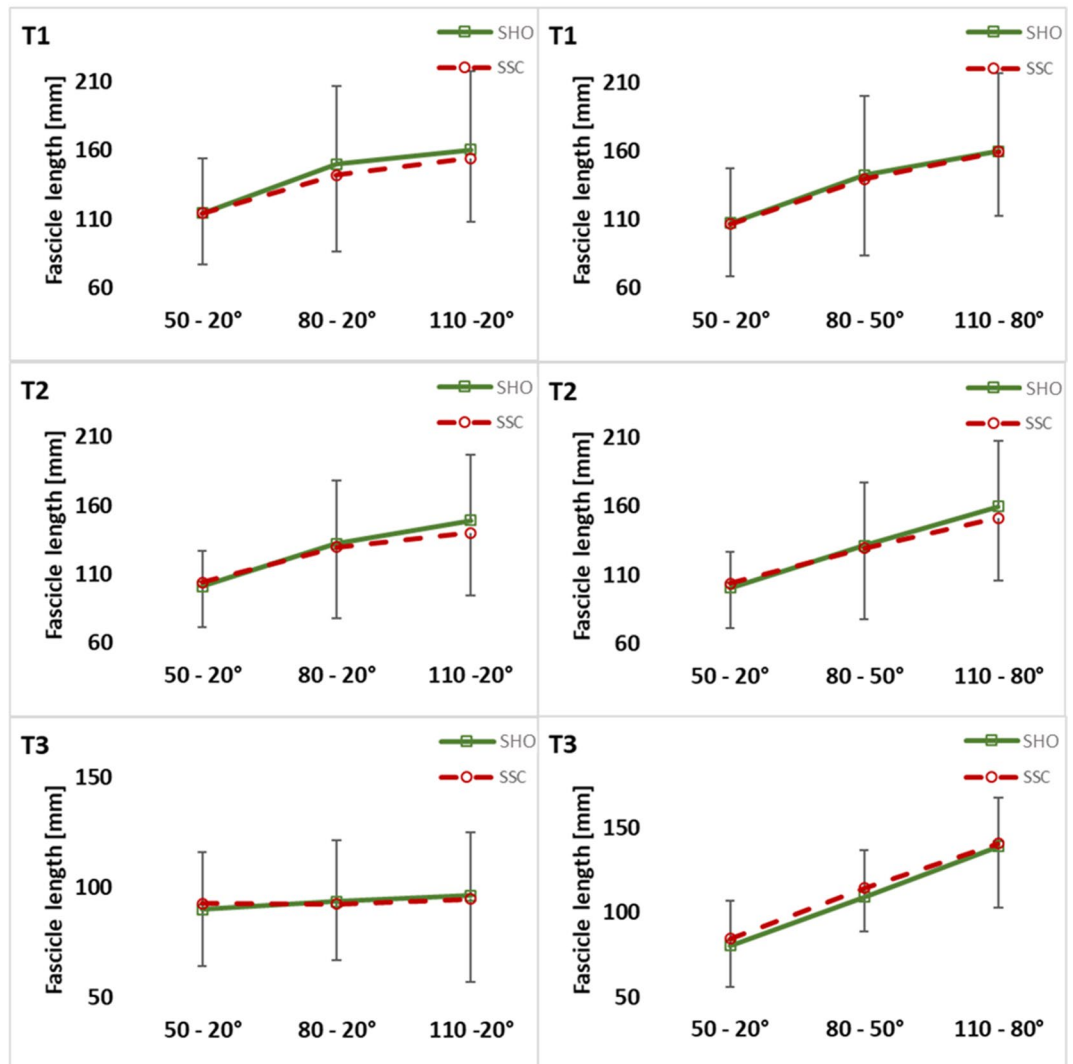
**Figure 7.** Mean ( $\pm$  SD,  $n=25$ ) values of pennation angle in both test sessions. T1 is the time point at the onset of shortening, T2 in the middle of the shortening phase, T3 the time point at steady-state after the dynamic phase. No significant interaction (condition  $\times$  magnitude) and (condition  $\times$  muscle–tendon unit length) was found at all instances (T1–T3).

variables fascicle length, pennation angle, fascicle length change and knee joint angle, meaning the different contraction conditions are very well comparable with each other in our study. In our study, the conditions SHO 50°–20° and SSC 20°–50°–20° were the same in session 1 and 2. The individual comparison by means of t-test revealed no significant differences between the sessions at all instances. This result shows a good repeatability of this experiment, as the identical SHO and SSC conditions, which took place on a different day, showed no differences.

**Effect of stretch–shortening magnitude.** Similarly to other studies<sup>6,43</sup>, increased joint torque at the end of stretch (T1) compared to the isometric pre-activation of the SHO condition was found in session 1. However, contrary to our expectations, we could only find significant transient FE for the smaller SSC-magnitudes and not after the greatest stretch in the SSC 20°–110°–20° condition (FE of 8.2%, not significant) (Fig. 3a). This is in contrast to in vitro studies, which showed higher transient FE with increasing stretch magnitude<sup>15</sup>. In vivo studies reported different results. For example, during or at the end of stretch, the transient FE of adductor pollicis was increased with greater rotation<sup>35</sup>, whereas no difference was reported for larger muscle groups of the lower extremities<sup>33,34</sup>. One explanation of these discrepancies could be the presence of some inhibitory effects during voluntary movement with larger muscle stretches<sup>34</sup>. Similarly to voluntary contractions, in the present study with electrical stimulation we also found no increased transient FE with higher stretch magnitude. One possible

## Session 1

## Session 2



**Figure 8.** Mean ( $\pm$  SD,  $n = 25$ ) values of fascicle length in both test sessions. T1 is the time point at the onset of shortening, T2 in the middle of the shortening phase, T3 the time point at steady-state after the dynamic phase. No significant interaction (condition  $\times$  magnitude) and (condition  $\times$  muscle–tendon unit length) was found at all instances (T1–T3).

explanation of our results could be that at T1 the lowest torque values were observed at 110°, and transient FE seems to be greater at higher absolute force/torque values<sup>51,61</sup>.

The absolute values of mechanical work during shortening increased with greater rotation magnitude (Fig. 4a). Contrary to what we expected, the SSC-effect did not increase with larger rotation magnitude. We expected that due to greater stretch, more elastic energy could be stored and later released by the tendon and increased passive forces would rise caused by the protein titin, which acts in a spring-like manner<sup>62</sup>. The SSC mechanism of different activation dynamics and stretch-reflex activity can be neglected in our study, since we had electro-stimulated contractions and an isometric pre-activation. At the greatest rotation magnitude, the torque at T1 was not statistically different between SHO and SSC, thus it is reasonable to expect that the mechanical work would also be similar. However, relative to the differences at the initial condition (T1), the percentage increase of the mechanical work at the SSC condition 20°–110°–20° compared to the corresponding SHO condition is greater than at the other rotation magnitudes; thus indicating a more “effective” use of the stored elastic energy. Hence, although the enhanced absolute force properties might be eliminated by the subsequent shortening<sup>63</sup>, we possibly observe a relative increase in the mechanical work due to a more “effective” use of stored elastic energy.

In contrast to a positive influence of elastic recoil, stretch-induced force-enhancing effects in the contractile element should be visible in the steady-state after the dynamic phase (T3, Fig. 5a)<sup>6</sup>. At T3, we did not find significant interaction, but the main effect of condition revealed significant torque depression for both SHO and SSC compared to the ISO contraction. Torque depression was between 7.9 and 15.4% in session 1, which is within the range of other quadriceps femoris studies<sup>64–66</sup>. Additionally, the main effect for rotation magnitude (Fig. 5a)

illustrated higher torque depression with greater rotation magnitude. These observations have also been made in shortening-hold experiments; the shortening causes conformational changes to the structure of the actin filament which can inhibit cross bridge attachments and reducing muscle stiffness<sup>67</sup>. Overall, the influence of the rotation magnitude on the history-dependent properties in a SSC shows the same increase of rFD with greater shortening as in SHO contractions. This confirms the assumption that rFE is only stretch-magnitude dependent under specific circumstances, which depend on the muscle of interest<sup>29</sup>. Such a difference might be inhibited by the amount of muscle–tendon compliance<sup>33</sup>. In our experiment all contractions ended at small muscle–tendon unit lengths although most studies investigating rFE at m. quadriceps femoris used relative long muscle–tendon unit lengths<sup>33,68</sup>. The results might be different, when testing different SSC-magnitudes only at long muscle–tendon unit lengths, with a final muscle length at the plateau region or the descending limb of the force–length relationship. However, in human movement the m. quadriceps femoris mostly has a relative short muscle–tendon unit length and based on the results of single muscle fibers rFE should be visible on the ascending limb of the force–length relationship<sup>69</sup>.

**Effect of muscle–tendon unit length.** At T1, we did not find a significant interaction (condition  $\times$  muscle–tendon unit length). We expected to have greater transient FE at longer muscle–tendon unit lengths due to a reduction in myofilament lattice spacing<sup>70</sup> and increased titin stiffness at longer muscle lengths<sup>23</sup>, and inappropriate cross-bridge attachments at shorter muscle–tendon unit lengths<sup>39</sup>. These assumptions could not be confirmed in our study but our findings agree with a previous study, where the authors suggested that at purely eccentric contractions the transient FE is not muscle-length dependent<sup>29</sup>.

Mechanical work during the shortening in the SSCs was significantly higher compared to the SHO conditions in session 2. The SSC-effect was almost constant at all muscle–tendon unit lengths (8.1–8.6%). This result does not correspond to a study in skinned muscle fibers, where a greater SSC-effect was reported at long muscle lengths<sup>41</sup>. As previously stated, two mechanisms most likely can explain the performance enhancement in the SSC found in our study. It is known from the literature that the tendon elongation should increase dependent on the applied force<sup>71</sup>. Since in our experiment we reached the highest torque values at the smaller angular position at T1 (Fig. 3b), more elastic energy should therefore be stored and released in these conditions. In contrast to this mechanism, a contribution of a rFE related mechanism should also be visible in the steady-state (T3)<sup>6</sup>. It was speculated that the contribution of rFE is greater at longer muscle–tendon unit lengths due to greater titin stiffness<sup>23</sup>. We found significant rFD compared to the ISO condition at the smaller angular positions, with no difference between the SHO and SSC condition. The only difference between SHO and SSC was found at the greatest muscle–tendon unit length, whereas significant higher torque values were found for the SSC condition, without any significant differences in pennation angle, fascicle length or fascicle length changes during shortening. This indicates that rFE related mechanisms are responsible for this difference between SHO and SSC at the longest muscle–tendon unit length. This can also be supported by in vivo stretch-hold experiments, which showed that rFE is muscle–tendon unit length dependent<sup>29,44</sup>. Additionally, another study observed rFE at short and long muscle lengths, and also noticed greater rFE at longer muscle lengths<sup>43</sup>. Analogous to the previous stretch experiments, which observed torque values above the fixed-end reference contraction (rFE), we found evidence of rFE in the form of reduced rFD after the stretch–shortening cycle.

In literature, greater rFE at longer muscle length is associated with an increase in titin stiffness<sup>50</sup>. The contribution of such a titin engagement also seems to be greater in our in vivo experiment, but did not lead to any magnification of the SSC-effect.

**Limitations.** The contribution of titin engagement is difficult to identify in in vivo experiments, since muscle tendon unit compliance might change with the muscle length<sup>72</sup>. However, in vitro experiments might give a better understanding of the history dependent effects, but for relevance in human movement such in vivo experiments are necessary<sup>73</sup>.

Participants performed a MVC at the beginning of the test session and at the end of the test session to check for fatigue appearance. This approach has its limitation in estimating the fatigue of the individual sub-muscles from MVC measurements of the whole four-headed muscle group. The relative contribution of the individual sub-muscles is different depending on the amount of the torque and the knee angle<sup>74,75</sup> and the variability in MVC measurements can be large. However, the contractions were fully randomized (condition and stretch–shortening magnitude or muscle–tendon unit length), therefore fatigue would be a systematic error. Additionally, we stimulated with only 35% of MVC and had a resting phase of 2 min between the contractions, therefore it is reasonable to expect no fatigue appearance in our study as also shown by the pre-post MVC control test.

We used electrical stimulation to prevent neural inhibition, which might change depending on rotation magnitude and muscle–tendon unit length. In addition, an unresolved issue is still the potential neural contribution to non-responders to rFE<sup>76</sup>. However, one limitation is that the electrical stimulated contractions we have used in our experiment differ from voluntary contractions with their asynchronous and varied firing frequencies<sup>64</sup>. A previous study investigated the relative contribution of the sub-muscles of m. quadriceps femoris during voluntary activation<sup>74</sup>, however the relative contribution of quadriceps femoris constituents to knee extensor torque during electrical superficial stimulation remains unknown<sup>77</sup>. Another limitation, which concerns relevance during human locomotion, is the examination of a single joint movement where, in natural movements, we have voluntary multi-joint contractions. The motor points for the application of the electrodes for electrical stimulation were identified at a dynamometer angle of 20°. Through the rotation and the large range of motion, the activation might reduce at greater knee flexion angles due to the movement of the motor point relative to the electrodes. This can explain higher torque values at 50° dynamometer angle compared to the 80° dynamometer angle at T1 (Fig. 3). If activation would be constant, higher torque values would be expected at T1 for the SHO

80°–20° and SSC 20°–80°–20° (kinematic data revealed a knee joint angle of ~72°) compared to SHO 50°–20° and SSC 20°–50°–20°, where the measured knee joint angle was approximately 42°. The 72° should be close to plateau region and the 42° should be on the ascending limb of the torque–angle relationship. However, in different studies the greatest torque was also found at different angles in knee extension contractions in the range of 55°–90°<sup>78</sup>. Nevertheless, this is a systematic error and the SHO and SSC can be compared and hence a possible activation reduction at great knee flexion angles would be the same for both contraction conditions.

Ultrasound measurement of only m. vastus lateralis represents a limitation. The measurement only corresponds to the behavior of the individual muscle but not of the entire muscle group. It was reported that fascicle behavior can be different between m. vastus lateralis and the deeper m. vastus intermedius<sup>79</sup>, but the muscle architecture of one superficial muscle is similar to the architecture in another superficial muscle<sup>80</sup>. Thus, we assume in our experiment the measured architectural changes of m. vastus lateralis are also representative for the superficial stimulated m. vastus medialis.

## Conclusion

Overall, we observed a SSC-effect (enhanced mechanical work during the shortening phase) at all SSCs. The contribution of rFE was enhanced with longer muscle–tendon unit length (without a clear relative increase in mechanical work), whereas no influence of rotation magnitude was found. This result indicates that during SSCs in the knee extensors, the magnitude of the contribution of rFE is different depending on the muscle–tendon unit length. At shorter muscle–tendon unit lengths and at greater SSC-magnitudes, the stretch-induced force enhancing effects were attenuated by the subsequent shortening of the muscle. Therefore, the physiological relevance of rFE might be particularly important for movements at greater muscle–tendon unit lengths.

## Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Received: 9 April 2021; Accepted: 6 July 2021

Published online: 16 July 2021

## References

- Nicol, C., Avela, J. & Komi, P. V. The stretch-shortening cycle : a model to study naturally occurring neuromuscular fatigue. *Sports medicine (Auckland, N.Z.)* **36**, 977–999 (2006).
- Komi, P. V. & Gollhofer, A. Stretch reflexes can have an important role in force enhancement during SSC exercise. *J. Appl. Biomech.* **13**, 451–460 (1997).
- Komi, P. V. Stretch-shortening cycle: a powerful model to study normal and fatigued muscle. *J. Biomech.* **33**, 1197–1206 (2000).
- van Schenau, G. J. I., Bobbert, M. F. & Haan, A. de. Does elastic energy enhance work and efficiency in the stretch-shortening cycle? *J. Appl. Biomech.* **13**, 389–415 (1997).
- Tomalka, A., Weidner, S., Hahn, D., Seiberl, W. & Siebert, T. Cross-bridges and sarcomeric non-cross-bridge structures contribute to increased work in stretch-shortening cycles. *Front. Physiol.* **11**, 921 (2020).
- Seiberl, W., Power, G. A., Herzog, W. & Hahn, D. The stretch-shortening cycle (SSC) revisited: residual force enhancement contributes to increased performance during fast SSCs of human m. adductor pollicis. *Physiol. Rep.* **3** (2015).
- Bobbert, M. F. & Casius, L. J. R. Is the effect of a countermovement on jump height due to active state development?. *Med. Sci. Sports Exerc.* **37**, 440–446 (2005).
- Dietz, V., Schmidtbleicher, D. & Noth, J. Neuronal mechanisms of human locomotion. *J. Neurophysiol.* **42**, 1212–1222 (1979).
- Kawakami, Y., Muraoka, T., Ito, S., Kanehisa, H. & Fukunaga, T. In vivo muscle fibre behaviour during counter-movement exercise in humans reveals a significant role for tendon elasticity. *J. Physiol.* **540**, 635–646 (2002).
- Finni, T., Ikegawa, S. & Komi, P. V. Concentric force enhancement during human movement. *Acta Physiol. Scand.* **173**, 369–377 (2001).
- Fukutani, A. & Herzog, W. Influence of stretch magnitude on the stretch-shortening cycle in skinned muscle fibres. *J. Exp. Biol.* **222** (2019).
- Hahn, D. & Riedel, T. N. Residual force enhancement contributes to increased performance during stretch-shortening cycles of human plantar flexor muscles in vivo. *J. Biomech.* **77**, 190–193 (2018).
- Cavagna, G. A., Dusman, B. & Margaria, R. Positive work done by a previously stretched muscle. *J. Appl. Physiol.* **24**, 21–32 (1968).
- Linari, M. *et al.* The mechanism of the force response to stretch in human skinned muscle fibres with different myosin isoforms. *J. Physiol.* **554**, 335–352 (2004).
- Edman, K. A., Elzinga, G. & Noble, M. I. Enhancement of mechanical performance by stretch during tetanic contractions of vertebrate skeletal muscle fibres. *J. Physiol.* **281**, 139–155 (1978).
- Edman, K. A. P. Residual force enhancement after stretch in striated muscle: a consequence of increased myofilament overlap? *J. Physiol.* **590**, 1339–1345 (2012).
- Pinniger, G. J., Ranatunga, K. W. & Offer, G. W. Crossbridge and non-crossbridge contributions to tension in lengthening rat muscle: force-induced reversal of the power stroke. *J. Physiol.* **573**, 627–643 (2006).
- Tomalka, A., Weidner, S., Hahn, D., Seiberl, W. & Siebert, T. Power amplification increases with contraction velocity during stretch-shortening cycles of skinned muscle fibers. *Front. Physiol.* **12**, 644981 (2021).
- Herzog, W. History dependence of skeletal muscle force production: implications for movement control. *Hum. Mov. Sci.* **23**, 591–604 (2004).
- Edman, K. A., Elzinga, G. & Noble, M. I. Residual force enhancement after stretch of contracting frog single muscle fibers. *J. Gen. Physiol.* **80**, 769–784 (1982).
- Abbott, B. C. & Aubert, X. M. The force exerted by active striated muscle during and after change of length. *J. Physiol.* **117**, 77–86 (1952).
- Tomalka, A., Rode, C., Schumacher, J. & Siebert, T. The active force-length relationship is invisible during extensive eccentric contractions in skinned skeletal muscle fibres. *Proc. Biol. Sci.* **284** (2017).
- Herzog, W. The multiple roles of titin in muscle contraction and force production. *Biophys. Rev.* **10**, 1187–1199 (2018).
- Fortuna, R., Groeber, M., Seiberl, W., Power, G. A. & Herzog, W. Shortening-induced force depression is modulated in a time- and speed-dependent manner following a stretch-shortening cycle. *Physiol. Rep.* **5** (2017).

25. Groeber, M., Reinhart, L., Kornfeind, P. & Baca, A. The contraction modalities in a stretch-shortening cycle in animals and single joint movements in humans: a systematic review. *J. Sports Sci. Med.* **18**, 604–614 (2019).
26. Fukutani, A., Joumaa, V. & Herzog, W. Influence of residual force enhancement and elongation of attached cross-bridges on stretch-shortening cycle in skinned muscle fibers. *Physiol. Rep.* **5** (2017).
27. Joumaa, V., Fitzowich, A. & Herzog, W. Energy cost of isometric force production after active shortening in skinned muscle fibres. *J. Exp. Biol.* **220**, 1509–1515 (2017).
28. Maréchal, G. & Plaghki, L. The deficit of the isometric tetanic tension redeveloped after a release of frog muscle at a constant velocity. *J. Gen. Physiol.* **73**, 453–467 (1979).
29. Bakenecker, P., Raiteri, B. J. & Hahn, D. Force enhancement in the human vastus lateralis is muscle-length-dependent following stretch but not during stretch. *Eur. J. Appl. Physiol.* **120**, 2597–2610 (2020).
30. Roots, H., Offer, G. W. & Ranatunga, K. W. Comparison of the tension responses to ramp shortening and lengthening in intact mammalian muscle fibres: crossbridge and non-crossbridge contributions. *J. Muscle Res. Cell Motil.* **28**, 123–139 (2007).
31. Hisey, B., Leonard, T. R. & Herzog, W. Does residual force enhancement increase with increasing stretch magnitudes? *J. Biomech.* **42**, 1488–1492 (2009).
32. Bullimore, S. R., Leonard, T. R., Rassier, D. E. & Herzog, W. History-dependence of isometric muscle force: effect of prior stretch or shortening amplitude. *J. Biomech.* **40**, 1518–1524 (2007).
33. Hahn, D., Seiberl, W. & Schwirtz, A. Force enhancement during and following muscle stretch of maximal voluntarily activated human quadriceps femoris. *Eur. J. Appl. Physiol.* **100**, 701–709 (2007).
34. Tilp, M., Steib, S. & Herzog, W. Force-time history effects in voluntary contractions of human tibialis anterior. *Eur. J. Appl. Physiol.* **106**, 159–166 (2009).
35. Lee, H.-D. & Herzog, W. Force enhancement following muscle stretch of electrically stimulated and voluntarily activated human adductor pollicis. *J. Physiol.* **545**, 321–330 (2002).
36. Chen, J. & Power, G. A. Modifiability of the history dependence of force through chronic eccentric and concentric biased resistance training. *J. Appl. Physiol. (Bethesda, Md. : 1985)* **126**, 647–657 (2019).
37. Lee, H.-D. & Herzog, W. Force depression following muscle shortening of voluntarily activated and electrically stimulated human adductor pollicis. *J. Physiol.* **551**, 993–1003 (2003).
38. de Ruiter, C. J., de Haan, A., Jones, D. A. & Sargeant, A. J. Shortening-induced force depression in human adductor pollicis muscle. *J. Physiol.* **507**(Pt 2), 583–591 (1998).
39. Scott, S. H., Brown, I. E. & Loeb, G. E. Mechanics of feline soleus: I. Effect of fascicle length and velocity on force output. *J. Muscle Res. Cell Motil.* **17**, 207–219 (1996).
40. Granzier, H. L., Burns, D. H. & Pollack, G. H. Sarcomere length dependence of the force-velocity relation in single frog muscle fibers. *Biophys. J.* **55**, 499–507 (1989).
41. Fukutani, A. & Isaka, T. Influence of muscle length on the stretch-shortening cycle in skinned rabbit soleus. *Sci. Rep.* **9**, 18350 (2019).
42. Fukutani, A., Misaki, J. & Isaka, T. Influence of joint angle on residual force enhancement in human plantar flexors. *Front. Physiol.* **8**, 234 (2017).
43. Power, G. A., Makrakos, D. P., Rice, C. L. & Vandervoort, A. A. Enhanced force production in old age is not a far stretch: an investigation of residual force enhancement and muscle architecture. *Physiol. Rep.* **1**, e00004 (2013).
44. Shim, J. & Garner, B. Residual force enhancement during voluntary contractions of knee extensors and flexors at short and long muscle lengths. *J. Biomech.* **45**, 913–918 (2012).
45. de Brito Fontana, H., de Campos, D. & Sakugawa, R. L. Predictors of residual force enhancement in voluntary contractions of elbow flexors. *J. Sport Health Sci.* **7**, 318–325 (2018).
46. Herzog, W. & Leonard, T. R. Depression of cat soleus forces following isokinetic shortening. *J. Biomech.* **30**, 865–872 (1997).
47. Tilp, M., Steib, S., Schappacher-Tilp, G. & Herzog, W. Changes in fascicle lengths and pennation angles do not contribute to residual force enhancement/depression in voluntary contractions. *J. Appl. Biomech.* **27**, 64–73 (2011).
48. Fukutani, A., Misaki, J. & Isaka, T. Force depression in plantar flexors exists equally in plantar flexed and dorsiflexed regions. *Front. Physiol.* **8**, 183 (2017).
49. Bohm, S., Marzilger, R., Mersmann, F., Santuz, A. & Arampatzis, A. Operating length and velocity of human vastus lateralis muscle during walking and running. *Sci. Rep.* **8**, 5066 (2018).
50. Rassier, D. E. & Herzog, W. Relationship between force and stiffness in muscle fibers after stretch. *Journal of applied physiology (Bethesda, Md. : 1985)* **99**, 1769–1775 (2005).
51. Groeber, M., Stafiliadis, S., Seiberl, W. & Baca, A. Contribution of stretch-induced force enhancement to increased performance in maximal voluntary and submaximal artificially activated stretch-shortening muscle action. *Front. Physiol.* **11**, 592183 (2020).
52. Gobbo, M., Maffiuletti, N. A., Orizio, C. & Minetto, M. A. Muscle motor point identification is essential for optimizing neuromuscular electrical stimulation use. *J. Neuroeng. Rehabil.* **11**, 17 (2014).
53. Sharifnezhad, A., Marzilger, R. & Arampatzis, A. Effects of load magnitude, muscle length and velocity during eccentric chronic loading on the longitudinal growth of the vastus lateralis muscle. *J. Exp. Biol.* **217**, 2726–2733 (2014).
54. Fukashiro, S., Itoh, M., Ichinose, Y., Kawakami, Y. & Fukunaga, T. Ultrasonography gives directly but noninvasively elastic characteristic of human tendon in vivo. *Eur. J. Appl. Physiol.* **71**, 555–557 (1995).
55. Arampatzis, A. et al. Differences between measured and resultant joint moments during voluntary and artificially elicited isometric knee extension contractions. *Clin. Biomech. (Bristol, Avon)* **19**, 277–283 (2004).
56. Tsaopoulos, D. E., Baltzopoulos, V., Richards, P. J. & Maganaris, C. N. Mechanical correction of dynamometer moment for the effects of segment motion during isometric knee-extension tests. *J. Appl. Physiol. (Bethesda, Md. : 1985)* **111**, 68–74 (2011).
57. Reeves, N. D. & Narici, M. V. Behavior of human muscle fascicles during shortening and lengthening contractions in vivo. *J. Appl. Physiol. (Bethesda, Md. : 1985)* **95**, 1090–1096 (2003).
58. Narici, M. V., Maganaris, C. N., Reeves, N. D. & Capodaglio, P. Effect of aging on human muscle architecture. *J. Appl. Physiol. (Bethesda, Md. : 1985)* **95**, 2229–2234 (2003).
59. Franchi, M. V., Fitze, D. P., Raiteri, B. J., Hahn, D. & Spörri, J. Ultrasound-derived biceps femoris long head fascicle length: extrapolation pitfalls. *Med. Sci. Sports Exerc.* **52**, 233–243 (2020).
60. Koo, T. K. & Li, M. Y. A guideline of selecting and reporting intraclass correlation coefficients for reliability research. *J. Chiropr. Med.* **15**, 155–163 (2016).
61. Oskouei, A. E. & Herzog, W. Force enhancement at different levels of voluntary contraction in human adductor pollicis. *Eur. J. Appl. Physiol.* **97**, 280–287 (2006).
62. Granzier, H. L. & Labeit, S. The giant muscle protein titin is an adjustable molecular spring. *Exerc. Sport Sci. Rev.* **34**, 50–53 (2006).
63. Lee, H.-D., Herzog, W. & Leonard, T. Effects of cyclic changes in muscle length on force production in in-situ cat soleus. *J. Biomech.* **34**, 979–987 (2001).
64. Lee, H. D., Suter, E. & Herzog, W. Force depression in human quadriceps femoris following voluntary shortening contractions. *J. Appl. Physiol. (Bethesda, Md. : 1985)* **87**, 1651–1655 (1999).
65. Dargeviciute, G., Masiulis, N., Kamandulis, S., Skurvydas, A. & Westerblad, H. Residual force depression following muscle shortening is exaggerated by prior eccentric drop jump exercise. *Journal of applied physiology (Bethesda, Md. : 1985)* **115**, 1191–1195 (2013).



66. Altenburg, T. M., Ruiter, C. J. de, Verdijk, P. W. L., van Mechelen, W. & Haan, A. de. Vastus lateralis surface and single motor unit EMG following submaximal shortening and lengthening contractions. *Appl. Physiol. Nutr. Metab. Physiologie appliquee, nutrition et metabolisme* **33**, 1086–1095 (2008).
67. Joumaa, V. *et al.* Evidence for actin filament structural changes after active shortening in skinned muscle bundles. *Biophys. J.* **114**, 135a (2018).
68. Seiberl, W., Hahn, D., Kreuzpointner, F., Schwirtz, A. & Gastmann, U. Force enhancement of quadriceps femoris in vivo and its dependence on stretch-induced muscle architectural changes. *J. Appl. Biomech.* **26**, 256–264 (2010).
69. Peterson, D. R., Rassier, D. E. & Herzog, W. Force enhancement in single skeletal muscle fibres on the ascending limb of the force-length relationship. *J. Exp. Biol.* **207**, 2787–2791 (2004).
70. Edman, K. A. The force bearing capacity of frog muscle fibres during stretch: its relation to sarcomere length and fibre width. *J. Physiol.* **519**(Pt 2), 515–526 (1999).
71. Reeves, N. D., Maganaris, C. N. & Narici, M. V. Effect of strength training on human patella tendon mechanical properties of older individuals. *J. Physiol.* **548**, 971–981 (2003).
72. Ichinose, Y., Kawakami, Y., Ito, M. & Fukunaga, T. Estimation of active force-length characteristics of human vastus lateralis muscle. *Acta Anat.* **159**, 78–83 (1997).
73. Paternoster, F. K., Seiberl, W., Hahn, D. & Schwirtz, A. Residual force enhancement during multi-joint leg extensions at joint-angle configurations close to natural human motion. *J. Biomech.* **49**, 773–779 (2016).
74. Zhang, L.-Q., Wang, G., Nuber, G. W., Press, J. M. & Koh, J. L. In vivo load sharing among the quadriceps components. *J. Orthop. Res.* **21**, 565–571 (2003).
75. Elias, J. J., Bratton, D. R., Weinstein, D. M. & Cosgarea, A. J. Comparing two estimations of the quadriceps force distribution for use during patellofemoral simulation. *J. Biomech.* **39**, 865–872 (2006).
76. Power, G. A., Hinks, A., Mashouri, P., Contento, V. S. & Chen, J. The long and short of residual force enhancement non-responders. *Eur. J. Appl. Physiol.* **120**, 2565–2567 (2020).
77. Cavalcante, J. G. T. *et al.* The effect of quadriceps muscle length on maximum neuromuscular electrical stimulation evoked contraction, muscle architecture, and Tendon-Aponeurosis Stiffness. *Front. Physiol.* **12**, 633589 (2021).
78. Pincivero, D. M., Salfetnikov, Y., Campy, R. M. & Coelho, A. J. Angle- and gender-specific quadriceps femoris muscle recruitment and knee extensor torque. *J. Biomech.* **37**, 1689–1697 (2004).
79. Ando, R. *et al.* Difference in fascicle behaviors between superficial and deep quadriceps muscles during isometric contractions. *Muscle Nerve* **53**, 797–802 (2016).
80. Blazevich, A. J., Gill, N. D. & Zhou, S. Intra- and intermuscular variation in human quadriceps femoris architecture assessed in vivo. *J. Anat.* **209**, 289–310 (2006).

## Acknowledgements

Open access funding provided by University of Vienna.

## Author contributions

All authors contributed to the study conception and design. Data collection and analysis were performed by MG. The first draft of the manuscript was written by MG and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

## Competing interests

The authors declare no competing interests.

## Additional information

**Correspondence** and requests for materials should be addressed to M.G.

**Reprints and permissions information** is available at [www.nature.com/reprints](http://www.nature.com/reprints).

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2021

### **3. Discussion**

#### **3.1 Summary**

The present work has investigated the history-dependent properties in a stretch-shortening cycle. Firstly, this work gives a systematic overview of performance enhancement in a SSC, establishing a connection of findings from single fiber experiments with the level of in vivo muscle-tendon unit (Groeber et al., 2019).

The experimental findings in SSCs show that the contribution of the potential mechanism change with the intensity of contraction and the type of activation. The influence of rFE is greatest in SSCs of the m. quadriceps femoris during maximal voluntary effort, but no influence of intensity on the SSC-effect was found; whereas the type of activation (stimulated vs. voluntary) seems to have an influence on this SCC-effect (Groeber et al., 2020). The contribution of rFE was also enhanced with longer muscle-tendon unit lengths (without a clear relative increase in mechanical work during shortening), whereas no influence of the rotation magnitude could be found (Groeber et al., 2021).

Therefore, the physiological relevance of the phenomenon rFE is especially important in SSC movements at high contraction intensity and great muscle-tendon unit lengths.

#### **3.2 Limitations**

Following the scientific papers of this cumulative dissertation, some general limitations and weaknesses of the presented experimental studies will be discussed in more detail. These are divided into participants, experimental limitations and the relevance of this study for everyday movements.

##### **3.2.1 Participants**

In the selection of the participants, we included female and male adults between 18 and 40 years. The suitability was determined with an anamnesis questionnaire (see Appendix A). The participants had no injury to the right leg, neuromuscular disorders or cardiovascular problems. Retrospectively, possible influencing factors of the chosen subject group can be discussed.

In our experiments, we had young adults as participants. Age is related to force generating capacity as a consequence of different factors including: The loss of muscle mass (Vandervoort, 2002), muscle architectural changes (Narici and Maffulli, 2010) and decreased neural activation (Aagaard et al., 2010). Previously, Power et al. (2012a) reported greater rFE in older adults (age:  $76.0 \pm 6.5$  years, only men) compared to younger adults (age:  $26.1 \pm 2.7$  years, only men). They speculated that there might be a greater availability of actomyosin binding sites due to age-related decrements in cross-bridge function. This



would allow for a recruitment of weakly bound cross-bridges into strongly bound states. Therefore, during a stretch of the muscle the decline in cross-bridge function in older adults could be modified by an increase in the average force per cross-bridge (Power et al., 2012a). Additionally, it was suggested that increased series elastic stiffness in older adults contribute to enhanced rFE (Ochala et al., 2006). Power et al. (2014) also reported greater rFD after shortening contractions for older adults. Overall, this indicated that older adults are more receptive to history-dependent phenomena compared to younger adults. So far, no study could be found that investigated the history-dependent properties in children. Therefore, with a different age group we might have observed different results regarding the contribution of rFE in the SSC of m. quadriceps femoris.

Regarding the allocation of subjects in terms of gender, slightly less than half were women. As already mentioned in the systematic review (Groeber et al., 2019), only one study showed that young women had a greater SSC-effect than young men (Svantesson and Grimby, 1995). This result was not confirmed in other studies. In our data, we could also find no statistical difference ( $p > 0.05$ ) between men and women regarding the SSC-effect as well as for the steady-state torque after the dynamic phase (not part of the publications). That is why, at least in our measurements, gender did not play a role.

Furthermore, the selection of the participants was not based on the current sporting situation as well as the previous sporting experience of the subjects. However, these factors can lead to sport-specific adaptations in the muscle-tendon unit. The muscles adapt with regard to architecture, fiber-tendon length ratio and fiber type depending on their function (Siebert et al., 2016). In our study, participants were fairly athletic but not top athletes. No special attention was paid to the sport being performed when recruiting participants. At present, we do not expect this to have any effect on the history-dependent properties in a SSC. Siebert et al. (2016) reported that in a weightlifting group (practicing weightlifting competitively), rFE did not increase. This is currently the only study that has investigated the occurrence of rFE in a particular sport. However, based on the existing literature, we cannot exclude an influence of individual athletic performance on the history-dependent properties.

### **3.2.2 Experimental limitations**

#### **3.2.2.1 Dynamometry**

The resultant knee-joint torque was measured with an isokinetic dynamometer (HUMAC Norm, Model 770; CSMi). This method allows for the giving of a constant motion specification and therefore very standardized conditions (Figure 18).



**Figure 18:** Example of the test setup, showing the position and fixation of the subject.

Despite this method being considered the gold standard there are certain limitations. The dynamometer allows the seat to be adjusted (position, rotation, backrest inclination). However, the sitting position was only aligned at the dynamometer angle at the end position (angle in the steady-state isometric hold phase). The rotation axis of the dynamometer was aligned with the lateral femoral condyles of each participant (Arampatzis et al., 2004). During dynamic measurements, this alignment cannot be fully guaranteed. One reason is that the seat is very soft and therefore gives way during the contractions. One idea to compensate for this was to construct a hard shell seat. Since this dynamometer was also used shortly afterwards for measurements of elderly subjects who might have problems sitting on a hard shell seat for a longer period of time, it was decided to record possible movements and changes of sitting posture with a 3D-motion analysis system and correct the measured torque with the kinematic data.

### **3.2.2.2 3D-motion analysis**

For recording 3D kinematics, a marker-based motion analysis system was used (Vicon, Oxford, United Kingdom, 100Hz) using nine cameras (Vantage V8). Due to the compliance of the dynamometer, a shift of knee-joint axis relative to the dynamometer axis would result in over- or underestimated knee-joint torque. Therefore we implemented the inverse dynamic approach proposed by Arampatzis et al. (2004).

In addition, the actual knee angle was measured with the 3D-motion analysis system. Thus, we could determine a further limitation of the isokinetic dynamometer. The actual knee-joint

angle does not correspond to the dynamometer-defined knee-joint angle. We could only find this in publication 2, and observed that the differences in dynamometer-defined and actual knee-joint angle gets bigger with increasing intensity. This explains that we could not identify this discrepancy in publication 3, where the evoked tetanic torque was 35% of MVC. In publication 2, we had also trials with 50% of MVC and MVC contractions. Although the participants were firmly strapped to the seat of the isokinetic dynamometer, high torque values during the eccentric phase can still lead to an elevation of the pelvis (Groeber et al., 2020).

### **3.2.2.3 Electrical stimulation**

For all submaximal contractions, we used electrical stimulation (Digitimer DS8R, United Kingdom). This method has the great advantage that it can cause very constant muscle contractions. Therefore, this method is very often also used in relation to the study of the history-dependent properties of muscle contraction. Indeed, there is a difference between voluntary activation and electrically stimulated activation. Electrically stimulated muscles do not perfectly mirror voluntary activation; it differs in terms of the asynchronous and varied firing frequencies that characterize voluntary activations (Lee et al., 1999; Groeber et al., 2020). As already reported in the introduction (see chapter 1.3.1.2), Lee and Herzog (2002) reported the same rFE for electrically and voluntarily activated stretches. It would have been conceivable to use an EMG/torque feedback. However, it can be only matched at the isometric state before and after the dynamic phase. The change during the dynamic phase cannot be easily controlled with such a feedback. Moreover, this method needs a lot of practice by the participants to be able to hold a specific torque or muscle activity level. Thus, it seemed to be a simpler - as well as the more valid - method to use electrical stimulation for all submaximal trials.

The muscle motor points were identified with a motor point pen (COMPEX, United Kingdom). The procedure was previously reported by Gobbo et al. (2014). The motor points are located by lightly pressing the pen to the specific area. With “surface mapping” of the specific area the presences of mechanical responses (“twitching”) is checked. The level of current intensity is increased when no contraction is observed at all. This procedure is repeated until a twitching can be detected. When using too much current, a twitching response can be also seen when the motor point pen does not exactly face the motor point. This procedure was made at a dynamometer angle of 20° (which in most of the trials was the angle of the isometric steady-state hold phase after dynamic contraction). During dynamic movements while using electrical stimulation a shift of the motor point relative to the electrodes is possible. This could lead to a reduction of the contraction intensity with larger knee flexion angles in our experiments. This might explain the lower torque values at 80° dynamometer

angle compared to the 50° dynamometer angle in publication 3 at T1 (see Figure 3 of publication 3). On the basis of the measured knee angle with the Vicon system, we expected it to be at an optimal muscle-tendon unit length at 80° dynamometer angle and on the ascending limb of the torque-angle relationship at 50° dynamometer angle. The choice of larger electrodes might not have provided this limitation. However, the conditions were always compared at the same dynamometer angle; therefore a possible activation reduction with greater knee flexion angles should occur at any contraction condition. Hence, this can be seen as a systematic error and the statements of the paper are thereby not impaired.

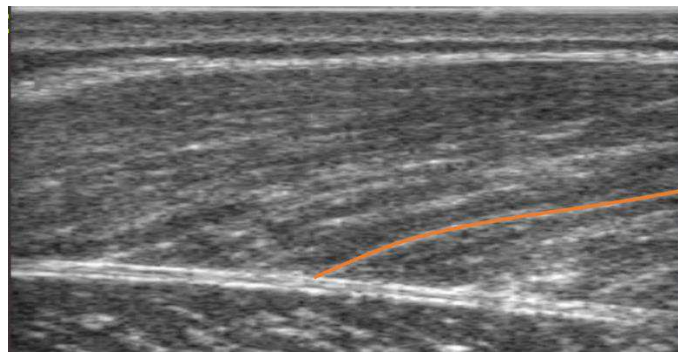
#### **3.2.2.4 EMG**

Muscle activity was measured for all voluntary contractions in publication 2 with EMG (Delsys, Trigno Wireless EMG System, United States, 2 kHz). In the experiment investigating the influence of different contraction intensities (publication 2), we also tested voluntary contractions. During voluntary contractions an activation reduction (at the same force or torque level) could be observed after active stretch compared to an isometric reference contraction (Oskoueï and Herzog, 2005; Altenburg et al., 2008; Seiberl et al., 2012), which could be also confirmed in our SSC contraction. However, no differences could be found between the CON and SSC condition (Groeber et al., 2020). One limitation of our results, however, is that only EMG activity of the m. vastus medialis and m. rectus femoris were measured. The m. quadriceps femoris is actually a four-headed muscle. EMG activity of the m. vastus lateralis could not have been measured because this muscle had already been covered with the ultrasound probe. Although there had been attempts at recording m. vastus intermedius (located deep in the thigh) with surface EMG (Watanabe and Akima, 2011), needle EMG is normally used. Needle EMG has the disadvantage of being invasive, and the needles can be easily displaced during dynamic movements.

Another point that would have been difficult to implement due to the experimental setup would be the measurement of antagonist activity. The participants had a seated position during testing. Previous studies could not find different antagonist activity after active muscle stretching and shortening (Tilp et al., 2009; Grant et al., 2017), but a positive relation between rFD and antagonist co-activation was able to be found (Grant et al., 2017). This indicated that participants with greater antagonist co-activation show a higher rFD value. Based on these studies, it can be assumed that the different conditions in our study can also be compared during voluntary activation. It is expected that the different contraction conditions have similar antagonist co-activation.

### 3.2.2.5 Ultrasound

Ultrasonography (Telemed ArtUS EXT-1H, IT, 70 Hz) was used to determine the fascicle length and pennation angle of m. vastus lateralis. For the ultrasound probe (LV8-5N60-A2, 60 mm), we made a fixation by means of a 3D-printer so that the probe could not move from the muscle belly of the m.vastus lateralis. A linear continuation was assumed for the calculation of fascicle length, although fascicles have a slight curvature (Figure 19). Several factors have been reported to influence the estimation of fascicle length: including the subject's position, where the fascicles are imaged and which fascicles are digitalized, the scanning plane relative to the fascicle plane, the level of pressure and the curvature of the fascicles (Franchi et al., 2020).



**Figure 19:** Example of curvature (orange line) of fascicle of m. vastus lateralis.

The approach of assuming a linear continuation and estimating the non-visible part of the fascicle has been widely used before. With this approach, an error of less than 2.4 % was reported (Narici et al., 2003; Reeves and Narici, 2003). Additionally, Franchi et al. (2020) reported a high reliability within the same session of fascicle length measures. In our studies, we tested for interrater reliability for fascicle length and pennation angle measurements. The intraclass correlation coefficient (ICC, two-way mixed model; single measures) showed good reliability in publication 2 (ICC of 0.84 and 0.81 for fascicle length and pennation angle, respectively) and publication 3 (ICC of 0.87 and 0.86 for fascicle length and pennation angle respectively).

Despite the fact that fascicle length might be under- or overestimated due to the method used, the results of the ICC and the fact that fascicle behavior was only compared within one session indicating valid results. We only compared fascicle behavior of the different contraction conditions within one session.

### **3.2.3 Relevance for everyday movement**

As has already been made clear in this work, there are many studies examining the history-dependent properties in isolated muscle preparations (single sarcomere, single fibers and isolated muscles). These tests under laboratory conditions may not properly reflect conditions occurring during natural human movement or sporting exercises. These experiments are of course needed to get a better understanding of the underlying mechanisms. To gain a better insight during human SSCs, we have tried in this work to create conditions as standardized as possible. This is necessary to understand and elucidate the phenomena of rFE and rFD in a more physiological setting. However, it should be mentioned that such standardized conditions do not occur in everyday human movements. For example, in SSCs during natural human locomotion a multi-joint movement is performed. In future, such investigations will also be necessary in parallel with well-standardized experiments in human musculature and muscle preparations.

## **3.3 Outlook**

### **3.3.1 Non-responder**

As already mentioned in the introduction, a widely discussed topic regarding the history-dependent properties of muscle action is the occurrence of so called non-responders. During voluntary human muscle action it was observed that only a subset of participants showed rFE, while others did not (Seiberl et al., 2015a; Pinnell et al., 2019). Oskoueï and Herzog (2005) determined that the occurrence of non-responders is dependent on the intensity of contraction (the number of non-responders decreased with higher contraction intensity). In our study, we might have observed the same in the case where we would have used voluntary activation in the submaximal trials. This question, and a possible explanation for this non-responder phenomenon, should be addressed in future studies.

### **3.3.2 Trainability**

Especially in the field of sport science, the question is raised of whether training has an influence on these history-dependent properties. So far, there is little research on the trainability. With regards to SSC, it would be an advantage to enhance the beneficial effect of rFE and to reduce the effect of rFD.

According to the previously discussed theory that the protein titin changes its stiffness and therefore rFE appears after an active stretch of the muscle (Herzog et al., 2016), it could be assumed that training should alter titin properties to enhance rFE. There are some studies not directly investigating the effect of training on rFE, but on the expression of titin. Bellafiore et al. (2007) studied the effects of a 6-week endurance training program on titin expression

in the m. gastrocnemius of mice. The endurance training which was characterized by moderate-intensity and continuous and rhythmic exercise revealed an increase in titin expression (% titin immunoreactivity). Additionally, Lindstedt et al. (2001) speculated that titin becomes stiffer in response to eccentric training, which might explain their results of increased vertical jumping height in basketball players after a 6-week high-force eccentric cycle ergometry compared to traditional strength/power resistance training. On the other hand, no change in titin isoforms could be found after 15 weeks of power training (Kyröläinen et al., 2005) and 8-weeks of jump-squat intervention (McGuigan et al., 2003) with human participants using muscle biopsies.

During a comparison of athletes (weight- and powerlifters) with untrained participants, McBride et al. (2003) reported a differential expression of titin isoforms. However, none of these studies directly investigated the effect of training on rFE. It is also difficult to interpret changes in titin isoforms in relation to rFE, since the characteristics and the specific role of titin is still unclear.

Siebert et al. (2016) took up the results of McBride et al. (2003) and hypothesized that the amount of rFE is higher for weightlifters compared to a control group, emphasizing that weightlifters perform many eccentric contractions in their training routine. Against the expectation of the authors, no difference was found between the two groups. However, they mentioned that the functional requirements of the muscular system might be too similar for weightlifters and their control group, as some subjects in the control group performed other sports with many SSCs, thus having many eccentric contractions (e.g. they had volleyball players in their control group) (Siebert et al., 2016).

Hinks et al. (2021) showed that isometric training (8-weeks, 3 days/week) does not alter maximal voluntary rFD and rFE. Chen and Power (2019) further investigated the history-dependent properties after 4-weeks of eccentric or concentric training protocols. They showed that rFE increased with concentric training and decreased with eccentric training; rFD was not affected by the training intervention. Further research is needed to identify the responsible mechanism. However, if the results are confirmed in future studies, concentric training might also enhance the beneficial history-dependent effects in human movements, which are characterized by SSCs. Recently, Chapman et al. (2021) also showed the presence of rFE in a series of consecutive contractions during multiple sets in the hamstring muscle. This means that the effect of rFE does not disappear during a training simulation.



### **3.3.3 Further directions**

Next to the still ongoing experiments to elucidate the mechanisms underlying the history-dependent properties of muscle action, it will also be important to follow more application-oriented approaches. This should be the way to decipher this property of muscle action, so that it can be used in a targeted manner in the future. In sport science, this would implicate the deeper study and contribution of these history-dependent properties in movement action in specific sports. Independently of the experimental design of future studies, the results on the history-dependent properties need to be incorporated into the modeling of human motion.

When then basic mechanisms are clarified, a crossover to other branches of research may become interesting. In many areas, nature has already served as a model for the development of new types of technology. It could also be of interest to use the beneficial effects of the history-dependent properties as a model for developments in bionics or robotics.

#### 4. Abbreviations

ANOVA	Analysis of variance
ATP	Adenosine triphosphate
CON*	Concentric
EMG	Electromyography
FE	Force enhancement
Hz	Hertz
ICC	Intraclass correlation coefficient
ISO	Isometric
M.	Musculus
MVC	Maximal voluntary contraction
rFD	Residual force depression
rFE	Residual force enhancement
SHO*	Shortening-hold
SSC	Stretch-shortening cycle

\* SHO and CON are used for the same kind of contraction. Due to the request of a reviewer, CON was renamed to SHO in publication 3.

## 5. Figures

**Figure 1:** Adapted from Herzog (2017). This shows a schematic representation of the cross-bridge model. Myosin interacting with attachments sites of the actin. The lower part of the figure shows the asymmetrical rate constants of the attachment (f) and detachment (g) of the filaments. With  $x$  as the distance from the equilibrium position of the myosin site to the nearest attachment site on actin. With  $A$  as the active site of the actin filament,  $M$  of the myosin filament and  $0$  the equilibrium position of the sliding element on the myosin. .... 9

**Figure 2:** Rotating cross-bridge model (Herzog et al., 2012). Complementary to the sliding of actin and myosin filament, a rotation of the cross-bridge head allows for the actin to be pulled past the myosin filament. The left panel represents the model of Huxley (1969), where the different connection states (S) are of varying strength and the right panel of Huxley and Simmons (1971), where the resulting connections (B1 and B2) are of varying strength. ... 10

**Figure 3:** Adapted from Rassier et al. (1999). Force-length relationship of frog skeletal muscle sarcomere. The representation of the highlighted dots refers to the degree of overlap of actin and myosin filaments as a function of sarcomere length. .... 11

**Figure 4:** Adapted from Roszek et al. (1994): Force-length relationship at different submaximal electrically stimulated stimulation frequencies. The force-length characteristics are from rat m. gastrocnemius medialis. .... 12

**Figure 5:** Adapted from Herzog (2009). Force-velocity relationship. Normalized force and power as a function of normalized concentric velocity. .... 13

**Figure 6:** Adapted from Komi (2000). Representation of a stretch-shortening cycle. In human movement, impact loads occur when contact is made with the ground. This requires a pre-activation of the lower limb extensor muscle (A) followed by active stretching (B) and then an active shortening (C) immediately afterwards. .... 14

**Figure 7:** Adapted from Fukutani et al. (2020). The left side shows a condition with no pre-activation and the right side shows a SSC (with pre-activation). In the condition without pre-activation, joint torque first increases during muscle shortening, while in the condition with pre-activation the torque continuously decreases. This indicates that joint torque is not fully developed in the early phase of shortening without pre-activation. .... 15

**Figure 8:** Adapted from VBG - Maximalkraft und Schnellkraft (2021). The left panel shows a squat-jump (no SSC), whereas the right panel shows a countermovement jump (SSC).  
.....16

**Figure 9:** Adapted from Komi and Gollhofer (1997). Representation of EMG peaks of m. soleus, m. gastrocnemius and m. vastus medialis in a drop jump exercise. The sharp EMG reflex peak can best be seen at m. soleus. ....17

**Figure 10:** Modified from Herzog (2001). Illustration of residual force enhancement. After muscle stretch (unsteady top line), the isometric steady-state force is enhanced ( $\Delta F$ ) compared to the isometric reference contraction at the final reference muscle length. ....19

**Figure 11:** Adapted from Bullimore et al. (2007). Residual force enhancement of seven individual m. soleus of the cat. rFE increases up to approximately 9 mm and then levels off.  
.....20

**Figure 12:** Modified from Herzog and Leonard (2002). Illustration of passive force enhancement following muscle stretching of 3mm, 6mm and 9mm respectively. Passive force enhancement can be seen after deactivation of the previously stretched muscle compared to the deactivated isometric reference force. Passive force enhancement increases with stretch amplitude. ....21

**Figure 13:** Adapted from Fukutani and Herzog (2019). Representation of two uniform sarcomeres (lower) and non-uniform sarcomeres (upper) on the descending limb of the force-length relationship. Non-uniform sarcomeres can produce more force at the same average length compared to the uniform condition.....25

**Figure 14:** Adapted from Herzog et al. (2016). The illustration of force-length diagrams caused by the elongation of titin is represented on the right side. This illustration shows different scenarios: A: Passive stretch with no interaction of titin with actin and no increased stiffness of titin, resulting in pure passive forces (blue line). B: Stretch in the presence of calcium (activation) with no binding of actin with titin. Higher passive forces due to a binding of calcium to specific segments of titin and increasing the stiffness of these segments (orange line). C: A “normal” eccentric contraction. Calcium is thought to bind with titin and additionally titin is assumed to bind with actin, thereby shortening the free spring length of

titin and therefore increasing its stiffness and forces when muscles are stretched. The force in this situation would be even higher (purple line).....27

**Figure 15:** Modified from Herzog (2001). Illustration of residual force depression. After muscle shortening (unsteady lower line), the isometric steady-state force is depressed ( $\Delta F$ ) compared to the isometric reference contraction at the final reference muscle length. ....28

**Figure 16:** Adapted from Herzog (2001). rFD is abolished by an interruption of muscle activation. The dotted line represents the isometric reference contraction at the final muscle length. The solid line represents the shortening contraction and the dashed line the shortening contraction with a short interruption of activation at the final muscle length. ...31

**Figure 17:** Adapted from Rassier and Herzog (2004). Whilst shortening (from A to B), new parts of the actin filaments enter the overlap zone. It is assumed that in the newly formed overlap zone the attachment of cross-bridges is inhibited in a stress-dependent manner. This inhibition on new cross-bridge attachments leads to rFD.....32

**Figure 18:** Example of the test setup, showing the position and fixation of the subject....77

**Figure 19:** Example of curvature (orange line) of fascicle of m. vastus lateralis.....80

## 6. References

- Aagaard, P., Suetta, C., Caserotti, P., Magnusson, S. P., and Kjaer, M. (2010). Role of the nervous system in sarcopenia and muscle atrophy with aging: strength training as a countermeasure. *Scandinavian journal of medicine & science in sports* 20, 49–64. doi: 10.1111/j.1600-0838.2009.01084.x.
- Abbott, B. C., and Aubert, X. M. (1952). The force exerted by active striated muscle during and after change of length. *The Journal of Physiology* 117, 77–86.
- Altenburg, T. M., Ruiter, C. J. de, Verdijk, P. W. L., van Mechelen, W., and Haan, A. de (2008). Vastus lateralis surface and single motor unit EMG following submaximal shortening and lengthening contractions. *Applied physiology, nutrition, and metabolism = Physiologie appliquee, nutrition et metabolisme* 33, 1086–1095. doi: 10.1139/H08-092.
- Arampatzis, A., Karamanidis, K., Monte, G. de, Stafilidis, S., Morey-Klapsing, G., and Brüggemann, G.-P. (2004). Differences between measured and resultant joint moments during voluntary and artificially elicited isometric knee extension contractions. *Clinical biomechanics (Bristol, Avon)* 19, 277–283. doi: 10.1016/j.clinbiomech.2003.11.011.
- Bellafiore, M., Cappello, F., Palumbo, D., Macaluso, F., Bianco, A., Palma, A. et al. (2007). Increased expression of titin in mouse gastrocnemius muscle in response to an endurance-training program. *European journal of histochemistry : EJH* 51, 119–124.
- Bobbert, M. F., and Casius, L. J. R. (2005). Is the effect of a countermovement on jump height due to active state development? *Medicine and science in sports and exercise* 37, 440–446. doi: 10.1249/01.mss.0000155389.34538.97.
- Bobbert, M. F., Gerritsen, K. G., Litjens, M. C., and van Soest, A. J. (1996). Why is countermovement jump height greater than squat jump height? *Medicine and science in sports and exercise* 28, 1402–1412. doi: 10.1097/00005768-199611000-00009.
- Bosco, C., Komi, P. V., and Ito, A. (1981). Prestretch potentiation of human skeletal muscle during ballistic movement. *Acta physiologica Scandinavica* 111, 135–140. doi: 10.1111/j.1748-1716.1981.tb06716.x.
- Brito Fontana, H. de, Campos, D. de, and Sakugawa, R. L. (2018). Predictors of residual force enhancement in voluntary contractions of elbow flexors. *Journal of sport and health science* 7, 318–325. doi: 10.1016/j.jshs.2018.06.001.
- Brito Fontana, H. de, and Herzog, W. (2016). Vastus lateralis maximum force-generating potential occurs at optimal fascicle length regardless of activation level. *European journal of applied physiology* 116, 1267–1277. doi: 10.1007/s00421-016-3381-3.
- Brunello, E., Reconditi, M., Elangovan, R., Linari, M., Sun, Y.-B., Narayanan, T. et al. (2007). Skeletal muscle resists stretch by rapid binding of the second motor domain of

- myosin to actin. *Proceedings of the National Academy of Sciences of the United States of America* 104, 20114–20119. doi: 10.1073/pnas.0707626104.
- Bullimore, S. R., Leonard, T. R., Rassier, D. E., and Herzog, W. (2007). History-dependence of isometric muscle force: effect of prior stretch or shortening amplitude. *Journal of biomechanics* 40, 1518–1524. doi: 10.1016/j.jbiomech.2006.06.014.
- Cavagna, G. A., Saibene, F. P., and Margaria, R. (1965). Effect of negative work on the amount of positive work performed by an isolated muscle. *Journal of applied physiology* 20, 157–158. doi: 10.1152/jappl.1965.20.1.157.
- Chapman, N. D., Whitting, J. W., Broadbent, S., Crowley-McHattan, Z. J., and Meir, R. (2021). Residual Force Enhancement Is Present in Consecutive Post-Stretch Isometric Contractions of the Hamstrings during a Training Simulation. *International journal of environmental research and public health* 18. doi: 10.3390/ijerph18031154.
- Chen, J., Hahn, D., and Power, G. A. (2019). Shortening-induced residual force depression in humans. *Journal of applied physiology (Bethesda, Md. : 1985)* 126, 1066–1073. doi: 10.1152/japplphysiol.00931.2018.
- Chen, J., and Power, G. A. (2019). Modifiability of the history dependence of force through chronic eccentric and concentric biased resistance training. *Journal of applied physiology (Bethesda, Md. : 1985)* 126, 647–657. doi: 10.1152/japplphysiol.00928.2018.
- Cook, C. S., and McDonagh, M. J. (1995). Force responses to controlled stretches of electrically stimulated human muscle-tendon complex. *Experimental physiology* 80, 477–490. doi: 10.1113/expphysiol.1995.sp003862.
- Cornachione, A. S., Leite, F., Bagni, M. A., and Rassier, D. E. (2016). The increase in non-cross-bridge forces after stretch of activated striated muscle is related to titin isoforms. *American journal of physiology. Cell physiology* 310, C19-26. doi: 10.1152/ajpcell.00156.2015.
- Dietz, V., Schmidtbleicher, D., and Noth, J. (1979). Neuronal mechanisms of human locomotion. *Journal of neurophysiology* 42, 1212–1222. doi: 10.1152/jn.1979.42.5.1212.
- Edman, K. A. (1996). Fatigue vs. shortening-induced deactivation in striated muscle. *Acta physiologica Scandinavica* 156, 183–192. doi: 10.1046/j.1365-201X.1996.t01-1-198000.x.
- Edman, K. A., Caputo, C., and Lou, F. (1993). Depression of tetanic force induced by loaded shortening of frog muscle fibres. *The Journal of Physiology* 466, 535–552.
- Edman, K. A., Elzinga, G., and Noble, M. I. (1978). Enhancement of mechanical performance by stretch during tetanic contractions of vertebrate skeletal muscle fibres. *The Journal of Physiology* 281, 139–155. doi: 10.1113/jphysiol.1978.sp012413.



- Edman, K. A., Elzinga, G., and Noble, M. I. (1982). Residual force enhancement after stretch of contracting frog single muscle fibers. *The Journal of general physiology* 80, 769–784. doi: 10.1085/jgp.80.5.769.
- Edman, K. A. P. (2012). Residual force enhancement after stretch in striated muscle. A consequence of increased myofilament overlap? *The Journal of Physiology* 590, 1339–1345. doi: 10.1113/jphysiol.2011.222729.
- Finni, T., Ikegawa, S., and Komi, P. V. (2001). Concentric force enhancement during human movement. *Acta physiologica Scandinavica* 173, 369–377. doi: 10.1046/j.1365-201x.2001.00915.x.
- Forcinito, M., Epstein, M., and Herzog, W. (1998). Can a rheological muscle model predict force depression/enhancement? *Journal of biomechanics* 31, 1093–1099. doi: 10.1016/S0021-9290(98)00132-8.
- Fortuna, R., Groeber, M., Seiberl, W., Power, G. A., and Herzog, W. (2017). Shortening-induced force depression is modulated in a time- and speed-dependent manner following a stretch-shortening cycle. *Physiological reports* 5. doi: 10.14814/phy2.13279.
- Fortuna, R., Kirchhübel, H., Seiberl, W., Power, G. A., and Herzog, W. (2018). Force depression following a stretch-shortening cycle is independent of stretch peak force and work performed during shortening. *Scientific reports* 8, 1534. doi: 10.1038/s41598-018-19657-8.
- Franchi, M. V., Fitze, D. P., Raiteri, B. J., Hahn, D., and Spörri, J. (2020). Ultrasound-derived Biceps Femoris Long Head Fascicle Length: Extrapolation Pitfalls. *Medicine and science in sports and exercise* 52, 233–243. doi: 10.1249/MSS.0000000000002123.
- Frick, U. (1993). *Kraftausdauerverhalten im Dehnungs-Verkürzungs-Zyklus*. 1. Aufl. Köln: Sport und Buch Strauß Ed. Sport.
- Fukutani, A., and Herzog, W. (2019). Current Understanding of Residual Force Enhancement: Cross-Bridge Component and Non-Cross-Bridge Component. *International journal of molecular sciences* 20. doi: 10.3390/ijms20215479.
- Fukutani, A., Isaka, T., and Herzog, W. (2020). Evidence for Muscle Cell-Based Mechanisms of Enhanced Performance in Stretch-Shortening Cycle in Skeletal Muscle. *Frontiers in physiology* 11, 609553. doi: 10.3389/fphys.2020.609553.
- Fukutani, A., Joumaa, V., and Herzog, W. (2017a). Influence of residual force enhancement and elongation of attached cross-bridges on stretch-shortening cycle in skinned muscle fibers. *Physiological reports* 5. doi: 10.14814/phy2.13477.
- Fukutani, A., Kurihara, T., and Isaka, T. (2015a). Factors of force potentiation induced by stretch-shortening cycle in plantarflexors. *PloS one* 10, e0120579. doi: 10.1371/journal.pone.0120579.

- Fukutani, A., Kurihara, T., and Isaka, T. (2015b). Influence of joint angular velocity on electrically evoked concentric force potentiation induced by stretch-shortening cycle in young adults. *SpringerPlus* 4, 82. doi: 10.1186/s40064-015-0875-0.
- Fukutani, A., Leonard, T., and Herzog, W. (2019a). Does stretching velocity affect residual force enhancement? *Journal of biomechanics* 89, 143–147. doi: 10.1016/j.jbiomech.2019.04.033.
- Fukutani, A., Misaki, J., and Isaka, T. (2016). Effect of Preactivation on Torque Enhancement by the Stretch-Shortening Cycle in Knee Extensors. *PloS one* 11, e0159058. doi: 10.1371/journal.pone.0159058.
- Fukutani, A., Misaki, J., and Isaka, T. (2017b). Both the elongation of attached crossbridges and residual force enhancement contribute to joint torque enhancement by the stretch-shortening cycle. *Royal Society open science* 4, 161036. doi: 10.1098/rsos.161036.
- Fukutani, A., Misaki, J., and Isaka, T. (2017c). Force Depression in Plantar Flexors Exists Equally in Plantar Flexed and Dorsiflexed Regions. *Frontiers in physiology* 8, 183. doi: 10.3389/fphys.2017.00183.
- Fukutani, A., Misaki, J., and Isaka, T. (2017d). Influence of Joint Angle on Residual Force Enhancement in Human Plantar Flexors. *Frontiers in physiology* 8, 234. doi: 10.3389/fphys.2017.00234.
- Fukutani, A., Shimoho, K., and Isaka, T. (2019b). Isometric preactivation before active lengthening increases residual force enhancement. *Scandinavian journal of medicine & science in sports* 29, 1153–1160. doi: 10.1111/sms.13454.
- Gobbo, M., Maffiuletti, N. A., Orizio, C., and Minetto, M. A. (2014). Muscle motor point identification is essential for optimizing neuromuscular electrical stimulation use. *J NEUROENG REHABIL* 11, 17. doi: 10.1186/1743-0003-11-17.
- Gordon, A. M., Huxley, A. F., and Julian, F. J. (1966). The variation in isometric tension with sarcomere length in vertebrate muscle fibres. *The Journal of Physiology* 184, 170–192. doi: 10.1113/jphysiol.1966.sp007909.
- Grant, J., McNeil, C. J., Bent, L. R., and Power, G. A. (2017). Torque depression following active shortening is associated with a modulation of cortical and spinal excitation: a history-dependent study. *Physiological reports* 5. doi: 10.14814/phy2.13367.
- Granzier, H. L., and Pollack, G. H. (1989). Effect of active pre-shortening on isometric and isotonic performance of single frog muscle fibres. *The Journal of Physiology* 415, 299–327. doi: 10.1113/jphysiol.1989.sp017723.
- Groeber, M., Reinhart, L., Kornfeind, P., and Baca, A. (2019). The Contraction Modalities in a Stretch-Shortening Cycle in Animals and Single Joint Movements in Humans: A Systematic Review. *Journal of sports science & medicine* 18, 604–614.

- Groeber, M., Stafilidis, S., Seiberl, W., and Baca, A. (2020). Contribution of Stretch-Induced Force Enhancement to Increased Performance in Maximal Voluntary and Submaximal Artificially Activated Stretch-Shortening Muscle Action. *Frontiers in physiology* 11, 592183. doi: 10.3389/fphys.2020.592183.
- Groeber, M., Stafilidis, S., and Baca, A. (2021). The effect of stretch-shortening magnitude and muscle-tendon unit length on performance enhancement in a stretch-shortening cycle. *Scientific reports* 11, 14605. doi: 10.1038/s41598-021-94046-2.
- Hahn, D., and Riedel, T. N. (2018). Residual force enhancement contributes to increased performance during stretch-shortening cycles of human plantar flexor muscles in vivo. *Journal of biomechanics* 77, 190–193. doi: 10.1016/j.jbiomech.2018.06.003.
- Hahn, D., Seiberl, W., Schmidt, S., Schweizer, K., and Schwirtz, A. (2010). Evidence of residual force enhancement for multi-joint leg extension. *Journal of biomechanics* 43, 1503–1508. doi: 10.1016/j.jbiomech.2010.01.041.
- Hahn, D., Seiberl, W., and Schwirtz, A. (2007). Force enhancement during and following muscle stretch of maximal voluntarily activated human quadriceps femoris. *European journal of applied physiology* 100, 701–709. doi: 10.1007/s00421-007-0462-3.
- Herzog, W. (2001). The nature of force depression and force enhancement in skeletal muscle contraction. *European Journal of Sport Science* 1, 1–14. doi: 10.1080/17461390100071301.
- Herzog, W. (2004). History dependence of skeletal muscle force production: implications for movement control. *Human movement science* 23, 591–604. doi: 10.1016/j.humov.2004.10.003.
- Herzog, W. (2009). The biomechanics of muscle contraction: optimizing sport performance. *Sport-Orthopädie - Sport-Traumatologie - Sports Orthopaedics and Traumatology* 25, 286–293. doi: 10.1016/j.orthtr.2009.10.001.
- Herzog, W. (2017). Skeletal muscle mechanics: questions, problems and possible solutions. *J NEUROENG REHABIL* 14, 98. doi: 10.1186/s12984-017-0310-6.
- Herzog, W. (2018). The multiple roles of titin in muscle contraction and force production. *Biophysical reviews* 10, 1187–1199. doi: 10.1007/s12551-017-0395-y.
- Herzog, W., Leonard, T., Joumaa, V., DuVall, M., and Panchangam, A. (2012). The three filament model of skeletal muscle stability and force production. *Molecular & cellular biomechanics : MCB* 9, 175–191.
- Herzog, W., and Leonard, T. R. (1997). Depression of cat soleus forces following isokinetic shortening. *Journal of biomechanics* 30, 865–872. doi: 10.1016/s0021-9290(97)00046-8.

- Herzog, W., and Leonard, T. R. (2000). The history dependence of force production in mammalian skeletal muscle following stretch-shortening and shortening-stretch cycles. *Journal of biomechanics* 33, 531–542. doi: 10.1016/s0021-9290(99)00221-3.
- Herzog, W., and Leonard, T. R. (2002). Force enhancement following stretching of skeletal muscle: a new mechanism. *The Journal of experimental biology* 205, 1275–1283.
- Herzog, W., Leonard, T. R., Joumaa, V., and Mehta, A. (2008). Mysteries of muscle contraction. *Journal of applied biomechanics* 24, 1–13. doi: 10.1123/jab.24.1.1.
- Herzog, W., Leonard, T. R., and Wu, J. Z. (1998). Force depression following skeletal muscle shortening is long lasting. *Journal of biomechanics* 31, 1163–1168. doi: 10.1016/s0021-9290(98)00126-2.
- Herzog, W., Leonard, T. R., and Wu, J. Z. (2000). The relationship between force depression following shortening and mechanical work in skeletal muscle. *Journal of biomechanics* 33, 659–668. doi: 10.1016/S0021-9290(00)00008-7.
- Herzog, W., Schappacher, G., DuVall, M., Leonard, T. R., and Herzog, J. A. (2016). Residual Force Enhancement Following Eccentric Contractions: A New Mechanism Involving Titin. *Physiology (Bethesda, Md.)* 31, 300–312. doi: 10.1152/physiol.00049.2014.
- Hill, A. V. (1938). The heat of shortening and the dynamic constants of muscle. *Proc. R. Soc. Lond. B* 126, 136–195. doi: 10.1098/rspb.1938.0050.
- Hill, A. V. (1953). The mechanics of active muscle. *Proceedings of the Royal Society of London. Series B, Biological sciences* 141, 104–117. doi: 10.1098/rspb.1953.0027.
- Hinks, A., Davidson, B., Akagi, R., and Power, G. A. (2021) Influence of isometric training at short and long muscle-tendon unit lengths on the history-dependence of force. *Scandinavian journal of medicine & science in sports* 31, 325–338. doi:10.1111/sms.13842.
- Holt, N. C., and Williams, C. D. (2018). Can Strain Dependent Inhibition of Cross-Bridge Binding Explain Shifts in Optimum Muscle Length? *Integrative and comparative biology* 58, 174–185. doi: 10.1093/icb/icy050.
- Huxley, A. F. (1957). Muscle structure and theories of contraction. *Progress in biophysics and biophysical chemistry* 7, 255–318.
- Huxley, A. F., and Niedergerke, R. (1954). Structural changes in muscle during contraction; interference microscopy of living muscle fibres. *Nature* 173, 971–973. doi: 10.1038/173971a0.
- Huxley, A. F., and Simmons, R. M. (1971). Proposed mechanism of force generation in striated muscle. *Nature* 233, 533–538. doi: 10.1038/233533a0.
- Huxley, H., and Hanson, J. (1954). Changes in the cross-striations of muscle during contraction and stretch and their structural interpretation. *Nature* 173, 973–976. doi: 10.1038/173973a0.
- Huxley, H. E. (1969). The mechanism of muscular contraction. *Science (New York, N.Y.)* 164, 1356–1365. doi: 10.1126/science.164.3886.1356.

- Johnston, K., Moo, E. K., Jinha, A., and Herzog, W. (2019). On sarcomere length stability during isometric contractions before and after active stretching. *The Journal of experimental biology* 222. doi: 10.1242/jeb.209924.
- Jones, A. A., Power, G. A., and Herzog, W. (2016). History dependence of the electromyogram: Implications for isometric steady-state EMG parameters following a lengthening or shortening contraction. *Journal of electromyography and kinesiology : official journal of the International Society of Electrophysiological Kinesiology* 27, 30–38. doi: 10.1016/j.jelekin.2016.01.008.
- Joumaa, V., Curtis Smith, I., Fakutani, A., Leonard, T., Ma, W., Irving, T. et al. (2018). Evidence for Actin Filament Structural Changes after Active Shortening in Skinned Muscle Bundles. *Biophysical Journal* 114, 135a. doi: 10.1016/j.bpj.2017.11.765.
- Joumaa, V., and Herzog, W. (2013). Energy cost of force production is reduced after active stretch in skinned muscle fibres. *Journal of biomechanics* 46, 1135–1139. doi: 10.1016/j.jbiomech.2013.01.008.
- Joumaa, V., Macintosh, B. R., and Herzog, W. (2012). New insights into force depression in skeletal muscle. *The Journal of experimental biology* 215, 2135–2140. doi: 10.1242/jeb.060863.
- Joyce, G. C., and Rack, P. M. (1969). Isotonic lengthening and shortening movements of cat soleus muscle. *The Journal of Physiology* 204, 475–491. doi: 10.1113/jphysiol.1969.sp008925.
- Julian, F. J., and Morgan, D. L. (1979). The effect on tension of non-uniform distribution of length changes applied to frog muscle fibres. *The Journal of Physiology* 293, 379–392. doi: 10.1113/jphysiol.1979.sp012895.
- Komi, P. V. (2000). Stretch-shortening cycle: a powerful model to study normal and fatigued muscle. *Journal of biomechanics* 33, 1197–1206. doi: 10.1016/S0021-9290(00)00064-6.
- Komi, P. V., and Gollhofer, A. (1997). Stretch Reflexes Can Have an Important Role in Force Enhancement during SSC Exercise. *Journal of applied biomechanics* 13, 451–460. doi: 10.1123/jab.13.4.451.
- Kosterina, N., Westerblad, H., Lännergren, J., and Eriksson, A. (2008). Muscular force production after concentric contraction. *Journal of biomechanics* 41, 2422–2429. doi: 10.1016/j.jbiomech.2008.05.019.
- Kubo, K., Kawakami, Y., and Fukunaga, T. (1999). Influence of elastic properties of tendon structures on jump performance in humans. *Journal of applied physiology (Bethesda, Md. : 1985)* 87, 2090–2096. doi: 10.1152/jappl.1999.87.6.2090.

- Kuhn, H. J. (1978). Cross bridge slippage induced by the ATP analogue AMP-PNP and stretch in glycerol-extracted fibrillar muscle fibres. *Biophys. Struct. Mechanism* 4, 159–168. doi: 10.1007/BF00539229.
- Kyröläinen, H., Avela, J., McBride, J. M., Koskinen, S., Andersen, J. L., Sipilä, S. et al. (2005). Effects of power training on muscle structure and neuromuscular performance. *Scandinavian journal of medicine & science in sports* 15, 58–64. doi: 10.1111/j.1600-0838.2004.00390.x.
- Lee, E.-J., and Herzog, W. (2008). Residual force enhancement exceeds the isometric force at optimal sarcomere length for optimized stretch conditions. *Journal of applied physiology (Bethesda, Md. : 1985)* 105, 457–462. doi: 10.1152/jappphysiol.01109.2006.
- Lee, H. D., Suter, E., and Herzog, W. (1999). Force depression in human quadriceps femoris following voluntary shortening contractions. *Journal of applied physiology (Bethesda, Md. : 1985)* 87, 1651–1655. doi: 10.1152/jappl.1999.87.5.1651.
- Lee, H. D., Suter, E., and Herzog, W. (2000). Effects of speed and distance of muscle shortening on force depression during voluntary contractions. *Journal of biomechanics* 33, 917–923. doi: 10.1016/s0021-9290(00)00070-1.
- Lee, H.-D., and Herzog, W. (2002). Force enhancement following muscle stretch of electrically stimulated and voluntarily activated human adductor pollicis. *The Journal of Physiology* 545, 321–330. doi: 10.1113/jphysiol.2002.018010.
- Lee, H.-D., and Herzog, W. (2003). Force depression following muscle shortening of voluntarily activated and electrically stimulated human adductor pollicis. *The Journal of Physiology* 551, 993–1003. doi: 10.1113/jphysiol.2002.037333.
- Leonard, T. R., DuVall, M., and Herzog, W. (2010). Force enhancement following stretch in a single sarcomere. *American journal of physiology. Cell physiology* 299, C1398-401. doi: 10.1152/ajpcell.00222.2010.
- Leonard, T. R., and Herzog, W. (2010). Regulation of muscle force in the absence of actin-myosin-based cross-bridge interaction. *American journal of physiology. Cell physiology* 299, C14-20. doi: 10.1152/ajpcell.00049.2010.
- Lichtwark, G. A., and Wilson, A. M. (2007). Is Achilles tendon compliance optimised for maximum muscle efficiency during locomotion? *Journal of biomechanics* 40, 1768–1775. doi: 10.1016/j.jbiomech.2006.07.025.
- Lindstedt, S. L., LaStayo, P. C., and Reich, T. E. (2001). When active muscles lengthen: properties and consequences of eccentric contractions. *News in physiological sciences : an international journal of physiology produced jointly by the International Union of Physiological Sciences and the American Physiological Society* 16, 256–261. doi: 10.1152/physiologyonline.2001.16.6.256.

- Lombardi, V., and Piazzesi, G. (1990). The contractile response during steady lengthening of stimulated frog muscle fibres. *The Journal of Physiology* 431, 141–171. doi: 10.1113/jphysiol.1990.sp018324.
- Maréchal, G., and Plaghki, L. (1979). The deficit of the isometric tetanic tension redeveloped after a release of frog muscle at a constant velocity. *The Journal of general physiology* 73, 453–467. doi: 10.1085/jgp.73.4.453.
- Maruyama, K., Natori, R., and Nonomura, Y. (1976). New elastic protein from muscle. *Nature* 262, 58–60. doi: 10.1038/262058a0.
- McBride, J. M., Triplett-McBride, T., Davie, A. J., Abernethy, P. J., and Newton, R. U. (2003). Characteristics of titin in strength and power athletes. *European journal of applied physiology* 88, 553–557. doi: 10.1007/s00421-002-0733-y.
- McGuigan, M. R., Sharman, M. J., Newton, R. U., Davie, A. J., Murphy, A. J., and McBride, J. M. (2003). Effect of explosive resistance training on titin and myosin heavy chain isoforms in trained subjects. *Journal of strength and conditioning research* 17, 645–651. doi: 10.1519/1533-4287(2003)017<0645:eoerto>2.0.co;2.
- Moo, E. K., and Herzog, W. (2018). Single sarcomere contraction dynamics in a whole muscle. *Scientific reports* 8, 15235. doi: 10.1038/s41598-018-33658-7.
- Morgan, D. L. (1994). An explanation for residual increased tension in striated muscle after stretch during contraction. *Experimental physiology* 79, 831–838. doi: 10.1113/expphysiol.1994.sp003811.
- Morgan, D. L., Whitehead, N. P., Wise, A. K., Gregory, J. E., and Proske, U. (2000). Tension changes in the cat soleus muscle following slow stretch or shortening of the contracting muscle. *The Journal of Physiology* 522 Pt 3, 503–513. doi: 10.1111/j.1469-7793.2000.t01-2-00503.x.
- Narici, M. V., and Maffulli, N. (2010). Sarcopenia: characteristics, mechanisms and functional significance. *Br Med Bull* 95, 139–159. doi: 10.1093/bmb/ldq008.
- Narici, M. V., Maganaris, C. N., Reeves, N. D., and Capodaglio, P. (2003). Effect of aging on human muscle architecture. *Journal of applied physiology (Bethesda, Md. : 1985)* 95, 2229–2234. doi: 10.1152/japplphysiol.00433.2003.
- Nishikawa, K. C., Monroy, J. A., and Tahir, U. (2018). Muscle Function from Organisms to Molecules. *Integrative and comparative biology* 58, 194–206. doi: 10.1093/icb/icy023.
- Nishikawa, K. C., Monroy, J. A., Uyeno, T. E., Yeo, S. H., Pai, D. K., and Lindstedt, S. L. (2012). Is titin a ‘winding filament’? A new twist on muscle contraction. *Proceedings. Biological sciences* 279, 981–990. doi: 10.1098/rspb.2011.1304.
- Noble, M. I. (1992). Enhancement of mechanical performance of striated muscle by stretch during contraction. *Experimental physiology* 77, 539–552. doi: 10.1113/expphysiol.1992.sp003618.



- Ochala, J., Dorer, D. J., Frontera, W. R., and Krivickas, L. S. (2006). Single skeletal muscle fiber behavior after a quick stretch in young and older men: a possible explanation of the relative preservation of eccentric force in old age. *Pflugers Archiv : European journal of physiology* 452, 464–470. doi: 10.1007/s00424-006-0065-6.
- Oskouei, A. E., and Herzog, W. (2005). Observations on force enhancement in submaximal voluntary contractions of human adductor pollicis muscle. *Journal of applied physiology (Bethesda, Md. : 1985)* 98, 2087–2095. doi: 10.1152/japplphysiol.01217.2004.
- Oskouei, A. E., and Herzog, W. (2006a). Force enhancement at different levels of voluntary contraction in human adductor pollicis. *European journal of applied physiology* 97, 280–287. doi: 10.1007/s00421-006-0167-z.
- Oskouei, A. E., and Herzog, W. (2006b). The dependence of force enhancement on activation in human adductor pollicis. *European journal of applied physiology* 98, 22–29. doi: 10.1007/s00421-006-0170-4.
- Paternoster, F. K., Seiberl, W., Hahn, D., and Schwirtz, A. (2016). Residual force enhancement during multi-joint leg extensions at joint- angle configurations close to natural human motion. *Journal of biomechanics* 49, 773–779. doi: 10.1016/j.jbiomech.2016.02.015.
- Peterson, D. R., Rassier, D. E., and Herzog, W. (2004). Force enhancement in single skeletal muscle fibres on the ascending limb of the force-length relationship. *The Journal of experimental biology* 207, 2787–2791. doi: 10.1242/jeb.01095.
- Pinnell, R. A. M., Mashouri, P., Mazara, N., Weersink, E., Brown, S. H. M., and Power, G. A. (2019). Residual force enhancement and force depression in human single muscle fibres. *Journal of biomechanics* 91, 164–169. doi: 10.1016/j.jbiomech.2019.05.025.
- Pinniger, G. J., and Cresswell, A. G. (2007). Residual force enhancement after lengthening is present during submaximal plantar flexion and dorsiflexion actions in humans. *Journal of applied physiology (Bethesda, Md. : 1985)* 102, 18–25. doi: 10.1152/japplphysiol.00565.2006.
- Power, G. A., Hinks, A., Mashouri, P., Contento, V. S., and Chen, J. (2020). The long and short of residual force enhancement non-responders. *European journal of applied physiology* 120, 2565–2567. doi: 10.1007/s00421-020-04511-5.
- Power, G. A., Makrakov, D. P., Rice, C. L., and Vandervoort, A. A. (2013). Enhanced force production in old age is not a far stretch: an investigation of residual force enhancement and muscle architecture. *Physiological reports* 1, e00004. doi: 10.1002/phy2.4.
- Power, G. A., Makrakov, D. P., Stevens, D. E., Herzog, W., Rice, C. L., and Vandervoort, A. A. (2014). Shortening-induced torque depression in old men: implications for age-related power loss. *Experimental gerontology* 57, 75–80. doi: 10.1016/j.exger.2014.05.004.

- Power, G. A., Makrakos, D. P., Stevens, D. E., Rice, C. L., and Vandervoort, A. A. (2015). Velocity dependence of eccentric strength in young and old men: the need for speed! *Applied physiology, nutrition, and metabolism = Physiologie appliquee, nutrition et metabolisme* 40, 703–710. doi: 10.1139/apnm-2014-0543.
- Power, G. A., Rice, C. L., and Vandervoort, A. A. (2012a). Increased residual force enhancement in older adults is associated with a maintenance of eccentric strength. *PloS one* 7, e48044. doi: 10.1371/journal.pone.0048044.
- Power, G. A., Rice, C. L., and Vandervoort, A. A. (2012b). Residual force enhancement following eccentric induced muscle damage. *Journal of biomechanics* 45, 1835–1841. doi: 10.1016/j.jbiomech.2012.04.006.
- Pun, C., Syed, A., and Rassier, D. E. (2010). History-dependent properties of skeletal muscle myofibrils contracting along the ascending limb of the force-length relationship. *Proceedings. Biological sciences* 277, 475–484. doi: 10.1098/rspb.2009.1579.
- Rack, P. M., and Westbury, D. R. (1969). The effects of length and stimulus rate on tension in the isometric cat soleus muscle. *The Journal of Physiology* 204, 443–460. doi: 10.1113/jphysiol.1969.sp008923.
- Ramsey, K. A., Bakker, A. J., and Pinniger, G. J. (2010). Fiber-type dependence of stretch-induced force enhancement in rat skeletal muscle. *Muscle & nerve* 42, 769–777. doi: 10.1002/mus.21744.
- Rassier, D. E. (2012). Residual force enhancement in skeletal muscles: one sarcomere after the other. *Journal of muscle research and cell motility* 33, 155–165. doi: 10.1007/s10974-012-9308-7.
- Rassier, D. E., and Herzog, W. (2004). Considerations on the history dependence of muscle contraction. *Journal of applied physiology (Bethesda, Md. : 1985)* 96, 419–427. doi: 10.1152/japplphysiol.00653.2003.
- Rassier, D. E., Herzog, W., Wakeling, J., and Syme, D. A. (2003). Stretch-induced, steady-state force enhancement in single skeletal muscle fibers exceeds the isometric force at optimum fiber length. *Journal of biomechanics* 36, 1309–1316. doi: 10.1016/s0021-9290(03)00155-6.
- Rassier, D. E., MacIntosh, B. R., and Herzog, W. (1999). Length dependence of active force production in skeletal muscle. *Journal of applied physiology (Bethesda, Md. : 1985)* 86, 1445–1457. doi: 10.1152/jappl.1999.86.5.1445.
- Rassier, D. E., and Pavlov, I. (2012). Force produced by isolated sarcomeres and half-sarcomeres after an imposed stretch. *American journal of physiology. Cell physiology* 302, C240-8. doi: 10.1152/ajpcell.00208.2011.

- Reeves, N. D., and Narici, M. V. (2003). Behavior of human muscle fascicles during shortening and lengthening contractions in vivo. *Journal of applied physiology (Bethesda, Md. : 1985)* 95, 1090–1096. doi: 10.1152/japplphysiol.01046.2002.
- Rode, C., Siebert, T., and Blickhan, R. (2009). Titin-induced force enhancement and force depression: a ‘sticky-spring’ mechanism in muscle contractions? *Journal of theoretical biology* 259, 350–360. doi: 10.1016/j.jtbi.2009.03.015.
- Roszek, B., Baan, G. C., and Huijing, P. A. (1994). Decreasing stimulation frequency-dependent length-force characteristics of rat muscle. *Journal of applied physiology (Bethesda, Md. : 1985)* 77, 2115–2124. doi: 10.1152/jappl.1994.77.5.2115.
- Rousanoglou, E. N., Oskouei, A. E., and Herzog, W. (2007). Force depression following muscle shortening in sub-maximal voluntary contractions of human adductor pollicis. *Journal of biomechanics* 40, 1–8. doi: 10.1016/j.jbiomech.2005.12.002.
- Ruiter, C. J., Didden, W. J., Jones, D. A., and Haan, A. D. (2000). The force-velocity relationship of human adductor pollicis muscle during stretch and the effects of fatigue. *The Journal of Physiology* 526 Pt 3, 671–681. doi: 10.1111/j.1469-7793.2000.00671.x.
- Ruiter, C. J. de, and Haan, A. de (2003). Shortening-induced depression of voluntary force in unfatigued and fatigued human adductor pollicis muscle. *Journal of applied physiology (Bethesda, Md. : 1985)* 94, 69–74. doi: 10.1152/japplphysiol.00672.2002.
- Ruiter, C. J. de, Haan, A. de, Jones, D. A., and Sargeant, A. J. (1998). Shortening-induced force depression in human adductor pollicis muscle. *The Journal of Physiology* 507 (Pt 2), 583–591. doi: 10.1111/j.1469-7793.1998.583bt.x.
- Schachar, R., Herzog, W., and Leonard, T. R. (2004). The effects of muscle stretching and shortening on isometric forces on the descending limb of the force-length relationship. *Journal of biomechanics* 37, 917–926. doi: 10.1016/j.jbiomech.2003.10.006.
- Schappacher-Tilp, G., Leonard, T., Desch, G., and Herzog, W. (2015). A novel three-filament model of force generation in eccentric contraction of skeletal muscles. *PloS one* 10, e0117634. doi: 10.1371/journal.pone.0117634.
- Seiberl, W., Hahn, D., Herzog, W., and Schwirtz, A. (2012). Feedback controlled force enhancement and activation reduction of voluntarily activated quadriceps femoris during sub-maximal muscle action. *Journal of electromyography and kinesiology : official journal of the International Society of Electrophysiological Kinesiology* 22, 117–123. doi: 10.1016/j.jelekin.2011.10.010.
- Seiberl, W., Hahn, D., Kreuzpointner, F., Schwirtz, A., and Gastmann, U. (2010). Force enhancement of quadriceps femoris in vivo and its dependence on stretch-induced muscle architectural changes. *Journal of applied biomechanics* 26, 256–264. doi: 10.1123/jab.26.3.256.

- Seiberl, W., Power, G. A., and Hahn, D. (2015a). Residual force enhancement in humans: Current evidence and unresolved issues. *Journal of electromyography and kinesiology : official journal of the International Society of Electrophysiological Kinesiology* 25, 571–580. doi: 10.1016/j.jelekin.2015.04.011.
- Seiberl, W., Power, G. A., Herzog, W., and Hahn, D. (2015b). The stretch-shortening cycle (SSC) revisited: residual force enhancement contributes to increased performance during fast SSCs of human m. adductor pollicis. *Physiological reports* 3. doi: 10.14814/phy2.12401.
- Shim, J., and Garner, B. (2012). Residual force enhancement during voluntary contractions of knee extensors and flexors at short and long muscle lengths. *Journal of biomechanics* 45, 913–918. doi: 10.1016/j.jbiomech.2012.01.026.
- Siebert, T., Kurch, D., Blickhan, R., and Stutzig, N. (2016). Does weightlifting increase residual force enhancement? *Journal of biomechanics* 49, 2047–2052. doi: 10.1016/j.jbiomech.2016.05.017.
- Sugi, H. (1972). Tension changes during and after stretch in frog muscle fibres. *The Journal of Physiology* 225, 237–253. doi: 10.1113/jphysiol.1972.sp009935.
- Sugi, H., and Tsuchiya, T. (1988). Stiffness changes during enhancement and deficit of isometric force by slow length changes in frog skeletal muscle fibres. *The Journal of Physiology* 407, 215–229. doi: 10.1113/jphysiol.1988.sp017411.
- Svantesson, U., and Grimby, G. (1995). Stretch-shortening cycle during plantar flexion in young and elderly women and men. *European journal of applied physiology and occupational physiology* 71, 381–385. doi: 10.1007/bf00635870.
- Svantesson, U., Grimby, G., and Thomeé, R. (1994). Potentiation of concentric plantar flexion torque following eccentric and isometric muscle actions. *Acta physiologica Scandinavica* 152, 287–293. doi: 10.1111/j.1748-1716.1994.tb09808.x.
- Tahir, U., Monroy, J. A., Rice, N. A., and Nishikawa, K. C. (2020). Effects of a titin mutation on force enhancement and force depression in mouse soleus muscles. *The Journal of experimental biology* 223. doi: 10.1242/jeb.197038.
- Thys, H., Cavagna, G. A., and Margaria, R. (1975). The role played by elasticity in an exercise involving movements of small amplitude. *Pflügers Archiv : European journal of physiology* 354, 281–286. doi: 10.1007/BF00584651.
- Tilp, M., Steib, S., and Herzog, W. (2009). Force-time history effects in voluntary contractions of human tibialis anterior. *European journal of applied physiology* 106, 159–166. doi: 10.1007/s00421-009-1006-9.

- Tilp, M., Steib, S., Schappacher-Tilp, G., and Herzog, W. (2011). Changes in fascicle lengths and pennation angles do not contribute to residual force enhancement/depression in voluntary contractions. *Journal of applied biomechanics* 27, 64–73. doi: 10.1123/jab.27.1.64.
- Tomalka, A., Weidner, S., Hahn, D., Seiberl, W., and Siebert, T. (2020). Cross-Bridges and Sarcomeric Non-cross-bridge Structures Contribute to Increased Work in Stretch-Shortening Cycles. *Frontiers in physiology* 11, 921. doi: 10.3389/fphys.2020.00921.
- van Schenau, G. J. I., Bobbert, M. F., and Haan, A. de (1997). Does Elastic Energy Enhance Work and Efficiency in the Stretch-Shortening Cycle? *Journal of applied biomechanics* 13, 389–415. doi: 10.1123/JAB.13.4.389.
- Vandervoort, A. A. (2002). Aging of the human neuromuscular system. *Muscle & nerve* 25, 17–25. doi: 10.1002/mus.1215.
- Vaz, M. A., La Rocha Freitas, C. de, Leonard, T., and Herzog, W. (2012). The force-length relationship of the cat soleus muscle. *Muscles, ligaments and tendons journal* 2, 79–84.
- “VBG - Maximalkraft und Schnellkraft,” (2021). Accessed April 22, 2021. [https://www.vbg.de/DE/3\\_Praevention\\_und\\_Arbeitshilfen/1\\_Branchen/11\\_Sport/02\\_HANDBALL/2\\_Diagnostik\\_Versorgung/01\\_Funktionelle\\_Tests/01\\_Schwerpunkt\\_Beinachse/Schwerpunkt\\_Maximal\\_Schnellkraft\\_node.html](https://www.vbg.de/DE/3_Praevention_und_Arbeitshilfen/1_Branchen/11_Sport/02_HANDBALL/2_Diagnostik_Versorgung/01_Funktionelle_Tests/01_Schwerpunkt_Beinachse/Schwerpunkt_Maximal_Schnellkraft_node.html).
- Wank, V. (2000). *Aufbau und Anwendung von Muskel-Skelett-Modellen zur Bestimmung biomechanischer Muskelparameter: Habilitationsschrift*: Institut für Sportwissenschaft. Jena. Friedrich-Schiller-Universität.
- Watanabe, K., and Akima, H. (2011). Validity of surface electromyography for vastus intermedius muscle assessed by needle electromyography. *Journal of neuroscience methods* 198, 332–335. doi: 10.1016/j.jneumeth.2011.03.014.

## 7. Declaration of Authorship

I hereby certify that I have written this work independently and have not used any sources or aids other than those indicated. All direct or indirect sources used are acknowledged as references.

The work has not been submitted previously to qualify for any other academic degree. The content is the result of work since the official commencement date of the PhD program.



---

Martin Gröber

## 8. Appendix

### Appendix A: Anamnesis questionnaire to determine the risk factors for physical activity

#### Anamnesebogen zur Erhebung der Risikofaktoren bei körperlicher Aktivität

**Studientitel:** Vergleich der abgeschätzten maximalen Arbeit über der kritischen Leistung und der tatsächlichen maximalen Arbeit über der kritischen Leistung

Name \_\_\_\_\_ Größe (cm) \_\_\_\_\_

Geburtsdatum \_\_\_\_\_ Gewicht (kg) \_\_\_\_\_

Bitte beantworten Sie die folgenden Fragen nach bestem Wissen. Sollten Sie Schwierigkeiten bei der Beantwortung einer Frage haben, kontaktieren Sie bitte die für die Untersuchung verantwortliche Person. Die Fragen sind ausschließlich dazu bestimmt, um Ihre Eignung für die geplanten körperlichen Aktivitäten festzustellen. Ihre Daten werden strikt geheim behandelt und nicht an dritte Personen weitergegeben.

	ja	nein
1a Waren Sie während der letzten 6 Monate in ärztlicher Behandlung?	<input type="checkbox"/>	<input type="checkbox"/>
1b Ist aufgrund dieser ärztlichen Behandlung eine Genesung erfolgt?	<input type="checkbox"/>	<input type="checkbox"/>
2 Wurden bei Ihnen jemals Herzbeschwerden festgestellt?	<input type="checkbox"/>	<input type="checkbox"/>
3 Nehmen Sie regelmäßige Medikamente gegen Herzbeschwerden ein?	<input type="checkbox"/>	<input type="checkbox"/>
4 Haben Sie während körperlicher Belastung Beschwerden im Brustkorb?	<input type="checkbox"/>	<input type="checkbox"/>
5 Wurde bei Ihnen jemals Bluthochdruck diagnostiziert?	<input type="checkbox"/>	<input type="checkbox"/>
6 Hatten Sie jemals unbegründete Atemnot?	<input type="checkbox"/>	<input type="checkbox"/>
7 Hatten Sie jemals Schwindel- oder Ohnmachtsanfälle?	<input type="checkbox"/>	<input type="checkbox"/>
8 Wurde bei Ihnen jemals Epilepsie diagnostiziert?	<input type="checkbox"/>	<input type="checkbox"/>
9 Wurde bei Ihnen jemals Diabetes (Zuckerkrankheit) diagnostiziert?	<input type="checkbox"/>	<input type="checkbox"/>
10 Wurde bei Ihnen jemals Asthma oder eine andere Lungenkrankheit diagnostiziert?	<input type="checkbox"/>	<input type="checkbox"/>
11 Nehmen Sie im Moment Medikamente ein?	<input type="checkbox"/>	<input type="checkbox"/>
12 Haben Sie im Moment Muskel- oder Gelenksbeschwerden, die durch körperliche Aktivität verschlimmert werden könnten?	<input type="checkbox"/>	<input type="checkbox"/>
13 Haben Sie im Moment akute Verletzungen?	<input type="checkbox"/>	<input type="checkbox"/>
14 Nur für Frauen: Sind Sie schwanger?	<input type="checkbox"/>	<input type="checkbox"/>
15 Besteht Ihrer Meinung nach ein Grund warum Sie nicht körperlich aktiv sein sollten?	<input type="checkbox"/>	<input type="checkbox"/>

Wenn Sie eine der Fragen 2-15 mit "Ja" beantwortet haben, wird vor Beginn einer körperlichen Belastung eine genauere Befragung vorgenommen.

Kardiovaskuläre Risikofaktor	1 für Ja oder 0 für Nein
16 Aktueller Blutdruck systolisch > 140 mm Hg oder diastolisch > 90 mm Hg, wenn systolisch > 160 mm Hg oder diastolisch > 100 mm Hg nicht testen! (wird vor Ort gemessen)	<input type="text"/>
17 BMI > 30 oder Taillenumfang > 102 cm (Männer) oder > 88 cm (Frauen) (wird vor Ort gemessen)	<input type="text"/>
18 Hatte einer Ihrer Angehörigen (Vater, Mutter, Schwester und/oder Bruder) einen Herzinfarkt?	<input type="text"/>
19 Rauchen Sie oder haben Sie innerhalb der letzten 6 Monate zu rauchen aufgehört?	<input type="text"/>
20 Sind Sie an weniger als 3 Tagen pro Woche 30 Minuten körperlich aktiv?	<input type="text"/>
Summe der kardiovaskulären Risikofaktoren (Fragen 16-20)	Summe <input type="text"/>

- 21 Seit welchem Lebensjahr trainieren sie regelmäßig (d.h. zumindest 3x wöchentlich)?
- 22 Wieviele Stunden trainierten sie im Schnitt im letzten Trainingsjahr?


Ich habe die vorliegenden Fragen nach bestem Wissen beantwortet. Es ist mir klar, dass unrichtige Angaben ein Gesundheitsrisiko darstellen können. Ich wurde darüber informiert, dass im Rahmen dieser Untersuchungen mein Gesundheits- und Fitnessstatus erhoben wird. Ich wurde darüber informiert, dass die Belastungsuntersuchungen eine intensive körperliche Beanspruchung darstellen können. Während diesen Untersuchungen kann es zu Übelkeit, Ohnmacht oder muskulären Beschwerden kommen. Diese Risiken werden durch entsprechende Maßnahmen wie Auf- und Abwärmen sowie Anleitung in die Zielübung minimiert. Bei Auftreten von ungewöhnlichen Beschwerden werde ich den Testleiter umgehend darauf aufmerksam machen. Ich habe das Recht, jederzeit ohne Angabe von Gründen die Untersuchung zu beenden, ohne dass mir dadurch ein Nachteil entsteht. Alle im Rahmen dieser Untersuchungen erhobenen Daten werden ausschließlich in anonymer Form zu Studienzwecken verwendet und nicht an Dritte weitergegeben.

\_\_\_\_\_  
Datum

\_\_\_\_\_  
Unterschrift des Teilnehmenden

#### Interpretation des Risikofaktoren Gesamtscores (Fragen 16-20)

- Als Personen mit **geringem Risiko** werden asymptomatische Männer bis zum 45. Lebensjahr und Frauen bis zum 55. Lebensjahr eingestuft, deren Gesamtscore nicht mehr als 1 beträgt. Solche Personen können einem maximalen Belastungstest ausgesetzt werden und ein regelmäßiges und intensives Training durchführen.
- Als Personen mit **moderatem Risiko** werden asymptomatische Männer ab dem 45. Lebensjahr und Frauen ab dem 55. Lebensjahr eingestuft und - unabhängig vom Alter - solche Personen deren Gesamtscore 2 oder mehr beträgt. Solche Personen können einem sub-maximalen Belastungstest ausgesetzt werden und ein Training mit moderater Intensität durchführen. Vor dem Beginn eines intensiven Trainings oder einer maximalen Belastung sollte eine medizinische Untersuchung erfolgen.
- Als Personen mit **hohem Risiko** gelten solche, die Symptome von akuten oder chronischen Krankheiten aufweisen ("Ja" Fragen 2-15). Solche Personen sollten einen Arzt aufsuchen bevor sie einem Belastungstest ausgesetzt werden oder mit einem regelmäßigen Training beginnen.

American College of Sports Medicine. *ACSM's Guidelines for Exercise Testing and Prescription*. 8th ed. Baltimore: Lippincott Williams & Wilkins, 2010.

Deutsche Gesellschaft für Sportmedizin. *S1 - Leitlinie Vorsorgeuntersuchung im Sport*. DGSP, 2007.



## Appendix B: Decision of the Ethics Committee

<b>Beschluss der Ethikkommission</b> Decision of the Ethics Committee	 universität wien Ethikkommission
--	--

Antragsteller/Applicant: **Martin Gröber, BSc MSc**  
Bearbeitungsnummer/Reference Number: **00364**  
Projekttitel/Title of Project: **Muskuläre Leistungssteigerung im Dehnungs-Verkürzungs-Zyklus.  
Einfluss von Bewegungsamplituden und Belastungsintensitäten.**

Die Stellungnahme der Ethikkommission erfolgt aufgrund folgender eingereichter Unterlagen/ The decision of the Ethics Committee is based on the following documents:

04.06.2018

- Antragsformular\_Martin\_Groeber
- TeilnehmerInneninformation\_Martin\_Groeber

10.07.2018

- Antrag\_Martin\_Groeber\_neu
- Begleitschreiben Wiedereinreichung
- TeilnehmerInneninformation\_Martin\_Groeber\_neu

Die Kommission fasst folgenden Beschluss (mit X markiert)/The Ethics Committee has made the following decision (marked with an X):

☒ Zustimmung: Es besteht kein ethischer Einwand gegen die Durchführung der Studien/ Consent: There is no ethical objection to conduct the study as proposed

☐ Negative Beurteilung: Der Antrag wird von der Ethikkommission abgelehnt /Negative evaluation: The proposal is rejected by the Ethics Committee

Unterschrift/Signature



Datum/Date  
23.07.2018

Stellvertretende Vorsitzende der Ethikkommission/Deputy Chair of the Ethics Committee  
ao. Univ.-Prof. MMag. Dr. Sylvia Kirchengast