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Original article

Residual force enhancement due to active muscle lengthening allows similar reductions in neuromuscular activation during position- and force-control tasks

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Abstract

Background: Residual torque enhancement (rTE) is the increase in torque observed during the isometric steady state following active muscle lengthening when compared with a fixed-end isometric contraction at the same muscle length and level of neuromuscular activation. In the rTE state, owing to an elevated contribution of passive force to total force production, less active force is required, and there is a subsequent reduction in activation. *In vivo* studies of rTE reporting an activation reduction are often performed using a dynamometer, where participants contract against a rigid restraint, resisting a torque motor. rTE has yet to be investigated during a position task, which involves the displacement of an inertial load with positional control.

Methods: A total of 12 participants (6 males, 6 females; age = 22.8 ± 1.1 years, height = 174.7 ± 8.6 cm, mass = 82.1 ± 37.7 kg; mean ± SD) completed torque- and position-matching tasks at 60% maximum voluntary contraction for a fixed-end isometric contraction and an isometric contraction following active lengthening of the ankle dorsiflexors.

Results: There were no significant differences in activation between torque- and position-matching tasks ($p = 0.743$), with ~27% activation reduction following active lengthening for both task types ($p < 0.001$).

Conclusion: These results indicate that rTE is a feature of voluntary, position-controlled contractions. These findings support and extend previous findings of isometric torque-control conditions to position-controlled contractions that represent different tasks of daily living.

Keywords: Eccentric; Electromyography; History dependence of force; Position tasks; Residual force enhancement

1. Introduction

The contractile history of a muscle, termed the "history dependence of force", is known to increase a muscle's force-producing capacity following active lengthening (residual torque enhancement; rTE) compared with a fixed-end isometric contraction at the same muscle length and level of activation.[1] Following active muscle lengthening, a given submaximal isometric force can be achieved with less neuromuscular activation than before the lengthening stimulus.[2–4] This activation reduction during submaximal contractions ranges from 7%–25%[2] and has been observed across multiple muscles and muscle groups, such as the adductor policis brevis,[3,5,6] tibialis anterior,[4,7] plantar flexors,[8–10] knee extensors,[11] and elbow flexors.[12] Some studies have reported differences in the control of isometric force between conditions that require the subject either to hold a rigid load or to hold an equivalent inertial load in the same anatomical position (i.e., position task) but in free space.[13] We were interested in investigating how this task-dependency may carry over to isometric tasks following active lengthening. Despite marked differences in neuromuscular activation during these tasks,[13] the implications of rTE during position tasks has not yet been explored.

The history dependence of force was first observed by Abbott and Aubert,[1] and since then it has been observed from the single sarcomere,[14] at the single-fiber level in humans,[15] and up to *in vivo* studies of human voluntary muscle contraction.[2,16] Despite these observations, the mechanisms of the history dependence of force are still under debate, and the implications on voluntary control of force are not fully understood. The magnitude of rTE has been shown to be dependent

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on the amplitude of muscle lengthening and is thought to involve 2 components: a cross-bridge-based component[17] and a passive component related to the giant molecular spring, titin. Titin contributes to an increase in passive force following active lengthening.[18,19] Following active lengthening, in the rTE state, an increased contribution from passive force to total force allows for reduced neuromuscular activation (i.e., activation reduction) through less motor unit recruitment and a lower firing rate.[2,4,5,20,21]

In vivo studies of activation reduction in the rTE state use a dynamometer to control the joint excursion and presumed rate of stretching that a muscle is subjected to during the protocol. The participant contracts against a rigid restraint, receiving torque feedback in order to match torque between the rTE and isometric states. To date, rTE has not been studied during a position task that requires the participant to hold an inertial load in the same anatomical position as a rigid load (i.e., position-matching task) but with unconstrained movement. Position-matching tasks are known to differ from torque-matching tasks in activation strategies of the motor neuron pool[22–25] in that position-matching tasks are associated with decreased presynaptic inhibition[23] and increased muscle spindle sensitivity compared with torque-matching tasks.[24] During eccentric contractions, there is a distinction to be made between the 2 separate actions of displacing a load during a position-matching task and resisting a torque motor in a torque-matching task,[26] which lead to different control strategies during dynamic contractions.[27,28] During eccentric contractions, lowering an inertial load involves a reduction in corticospinal excitability and a reduction in motor unit discharge rates compared with resisting a torque motor.[26] It has been proposed that increased gain in stretch reflex is, in part, responsible for these differences in motor unit discharge rates.[27]

Therefore, the purpose of the present study was to determine whether activation reduction is present following active lengthening of the ankle dorsiflexors for a position-matching task. Based on reports of rTE and activation reduction in previous *in vivo* studies, we hypothesized that activation reduction would still occur during position-matching tasks.

2. Methods

A total of 14 healthy adults (7 males, 7 females; age = 23.4 ± 2.6 years; height = 175.5 ± 8.3 cm; mass = 81.9 ± 35.1 kg; mean ± SD) participated in a single data-collection session. Participants were free of neurological, orthopedic, or cardiovascular conditions. Participants gave written informed consent prior to testing. All procedures involving human subjects were approved by the Research Ethics Board of the University of Guelph (15NV008) and, with the exception of registration in a database, conformed to the Declaration of Helsinki.

2.1. Experimental arrangement

Participants were seated in a HUMAC NORM dynamometer (CSMi Medical Solutions, Stoughton, MA, USA), which recorded all torque, angular velocity, and position (joint angle) data. Participants were seated with a hip angle of 110˚, a knee angle of 130˚ (relative to 180˚ as full extension), and an ankle angle of 130˚ of plantarflexion (from 90˚ as neutral). The knee was supported by a padded cushion and immobilized by a strap. The right foot was fixed to the dynamometer foot plate with one strap placed over the ankle and one strap placed at the mid-distal portion of the metatarsals (for experimental set up, see Fig. 1).

Electromyography (EMG) was recorded from the tibialis anterior (TA) and soleus muscles using silver−silver chloride (Ag/AgCl) electrodes (1.5 cm × 1.0 cm) (Kendall, Mansfield, MA, USA). Prior to electrode placement, the skin was shaved and cleaned with alcohol. A common ground electrode was placed on the patella; an electrode was placed 7 cm inferior, 2 cm lateral to the tibial tuberosity over the muscle belly of the TA near the TA motor point; and an electrode was placed distally over the tendon of the TA with an inter-electrode distance of ∼8 cm. The tendon of the TA was located by palpating the

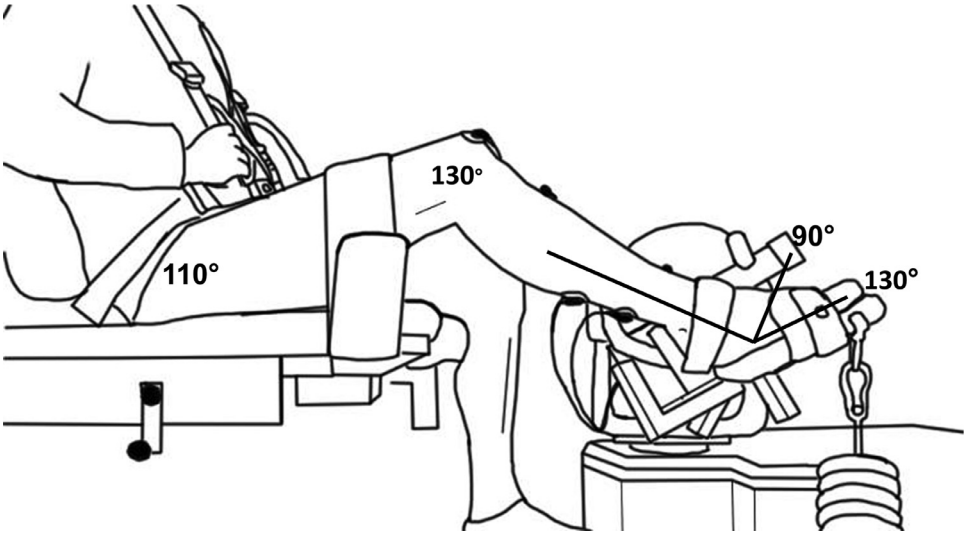

Fig. 1. Depiction of the experimental set-up on the HUMAC NORM dynamometer. Participants sat on the dynamometer with a hip angle of 110˚ and a knee and ankle angle of 130˚. Active lengthening occurred through a 40˚ range of motion about the ankle joint. For position tasks, a load equivalent to 60% maximum voluntary contraction at a joint angle of 130˚, corresponding to 40˚ plantarflexion, was hung from the dynamometer foot plate.

ankle and instructing participants to dorsiflex against the strap. A large electrode distance was used to optimize evoked potentials. Two more electrodes were placed on the soleus, one being placed 2 cm inferior to the midline of the gastrocnemii and one being placed on the calcaneal tendon.

Torque, angular position, and stimulus trigger data were sampled at 1000 Hz using a 12-bit analog-to-digital converter (PowerLab System 16/35; ADInstruments, Bella Vista, Australia). EMG data were sampled at 2000 Hz and bandpass-filtered online between 10 Hz and 1000 Hz. All data were analyzed using Labchart (Labchart, Pro Modules 2014, Version 8; ADInstruments) software.

2.2. Experimental protocol

In order to normalize EMG root mean square (EMG_{RMS}), maximal compound action potentials (M-max) were recorded from the TA and soleus muscles by stimulating the deep fibular and tibial nerves, respectively. A standard 30-mm clinical bar electrode (Chalgren Enterprises, Gilroy, CA, USA) was placed over the nerve, and stimuli were delivered with a single pulse from a constant-current high-voltage stimulator (Model DS7AH, Digitimer, Welwyn Garden City, Hertfordshire, UK). Voltage was set to 400 V and pulse width to 200 μs. Current was increased incrementally until a plateau in peak-to-peak M-wave amplitude was reached. To ensure consistent activation, this current was increased to 120% of the current required to generate M-max.

Participants performed up to 3 (a minimum of 2) maximum isometric voluntary contractions (MVC) and were instructed to perform ankle dorsiflexion as hard and as fast as possible. For each MVC, participants received visual feedback, provided as a torque trace on a computer monitor, as well as strong verbal encouragement from the researcher. Each MVC was separated by 5 min of rest. The first MVC was used as a practice trial. Subsequent MVCs involved the use of the interpolated twitch technique (ITT) to ensure ≥ 95% voluntary activation (VA).[29] All participants were capable of ≥ 95% VA. After ≥ 95% VA was achieved, participants performed a 10-s maximum effort fixed-end isometric contraction. Torque was obtained and averaged from 8.0 s to 8.5 s of this contraction. This time point was used because it corresponded to the isometric steady state of the rTE contractions. A total of 60% of this value was used as the target load for both the position- and torque-matching tasks. All tasks were completed twice, with 5 min of rest in between each task. All participants were familiar with these experiments and had participated in similar experiments before; therefore, we did not expect an ordered learning effect. The order of contractions was chosen to minimize the effects of fatigue and bias our results toward lower rTE values. The isometric contraction was performed first, followed by the rTE contraction. With this approach, we can be fully confident that any effect of active lengthening on subsequent activation reduction was, indeed, due to the history-dependent properties of the muscle and not to some extraneous factor.

The position-matching tasks were performed first to ensure the load would be matched during the isometric steady state of both the position and torque tasks. With the foot plate set to 130° plantarflexion, a load consisting of 0.1 kg, 0.5 kg, and 1.0 kg plates was hung from the foot plate until 60% MVC was reached. Once 60% MVC load was attached to the foot plate, the dynamometer's angular velocity was unrestricted to ensure free movement, and the range of motion was increased from approximately 85° to 133° to ensure that the participant could lower to 130° unhindered. Because the load was suspended from the dynamometer, and the participant was actively holding the load, the torque value, which the load cell registers, would essentially be 0 N·m. Therefore, during the position tasks, the participant matched angular position. The participant was given position feedback for both the isometric position-matching task and the rTE position-matching task as a prescribed angle shown as a line on the computer monitor. For the isometric task, the participant's foot was moved to 130°, and the participant was instructed to "take the weight" to initiate contraction, holding the position at the joint angle that matched the position guideline. For the rTE position-matching task, the researcher moved the participant's foot to 90°, and the participant was instructed to "take the weight" to initiate contraction in the 90° position and then carefully control the lowering of the foot to the 130° guideline over 3 s. It should be noted that, because the weight stack was hung from the foot plate, the moment arm and, thus, the load imposed on the ankle dorsiflexors would vary throughout the range of motion during the active lengthening contraction. To obtain an isometric steady state, the participant held this contraction for at least 5 s following the active lengthening.

Torque-matching tasks were performed following position-matching tasks. The participant received torque feedback during the isometric and rTE torque tasks. To ensure tasks were controlled for torque within-participants, the torque-matching guidelines were matched to the inertial load used during the position task. During the isometric torque task, the foot plate was set to an ankle angle of 130°. The participant was instructed to match the torque guideline for 10 s. During the rTE torque task, the participant initiated the contraction at 90° and actively lengthened, at 13°/s over ∼3 s, to 130°, and was instructed to maintain a constant effort while matching the target torque guideline. The participant held the contraction for 5 s thereafter. We make the assumption that torque reaches an isometric steady state following the dissipation of torque transients. Therefore, for both position and torque tasks, torque and EMG data from the tibialis anterior and soleus muscles were taken from 8.0 s to 8.5 s and averaged for data analysis.

Following 2 trials for each task, the participant performed a final MVC with ITT to ensure that the participant was not fatigued and was capable of near maximal activation. For a depiction of the experiment's time line, see Fig. 2.

2.3. Data and statistical analyses

Of 14 participants tested, 12 were used in analysis. Two participants were excluded because the post-MVC was reduced > 15%, indicating fatigue. The 15% value was chosen as a cut-off point owing to a *post hoc* analysis of torque declines following

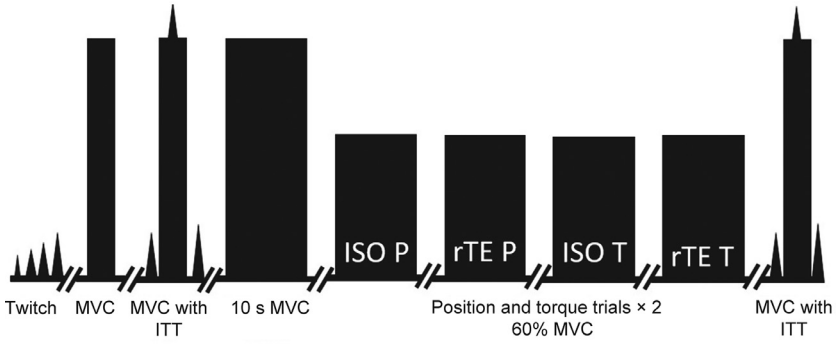

Fig. 2. Depiction of the experiment's time line. The protocol began with twitch determination so that MVCs could be completed with the interpolated twitch technique. One 10-s MVC was completed, where 60% MVC was taken from the 8.0 s to 8.5 s steady-state time epoch. All tasks were performed twice at an intensity of 60% MVC with 3 min of rest, culminating with a final MVC to monitor any strength loss throughout the protocol. ISO = isometric contraction; ITT = interpolated twitch technique; MVC = maximum voluntary contraction; P = position matching task; rTE = residual torque enhancement; T = torque matching task.

the task. Indeed, there was some variability, but most participants declined < 10%, and only 2 participants declined > 15%. Of the 12 participants used in analysis (6 males, 6 females; age = 22.8 ± 1.1 years, height = 174.7 ± 8.6 cm, mass = 82.1 ± 37.7 kg; mean ± SD), a single trial that best matched 60% MVC (e.g., < ± 5% deviation from the target trace) from each task was used in analysis. Position trials were not used if the participant's ankle angle movement went past the target ankle angle; this limited corrective muscle shortening to avoid any confounding factors of shortening-induced torque depression (for a review, see Chen et al.[30]) on rTE. Time-matched data during the isometric steady state of contraction, between 8.0 s and 8.5 s or 9.0 s and 9.5 s, was analyzed for mean torque, mean TA, and soleus EMG_{RMS}. Activation reduction of the TA was calculated as a percent from EMG_{RMS} as follows:

$$((\text{rTE}-\text{ISO})/\text{ISO}) \times 100\%.$$

Neuromuscular economy was also used to assess torque per unit of EMG_{RMS} during rTE tasks. This measure eliminates differences and variability in the EMG values that may occur due to difficulties in matching torque.[3] Antagonist coactivation was determined by normalizing soleus EMG during dorsiflexion to the resting Mmax; this value was then divided into the normalized agonist activation to account for the presumed greater activation (and cross-talk) in the isometric condition *vs.* the rTE condition. All data were analyzed using Labchart (Labchart, Pro Modules 2014, Version 8; ADInstruments), Excel (Microsoft , Redmond, WA, USA), and SPSS Version 26.0 software (IBM Corp., Armonk, NY, USA). *t* tests were used to analyze differences in strength, as well as voluntary activation pre- and post-protocol. There are no reports of a sex difference for the history-dependence of force; however, a one-way analysis of variance (ANOVA) was used to assess any differences owing to sex, before collapsing across sex. A two-way ANOVA with repeated measures was used to assess differences in activation reduction, neuromuscular economy, and soleus coactivation (history dependence × task). Effect size was calculated as partial eta squared (η_p^2). All data in the text are reported as mean ± SD and are reported in the figures as mean ± SEM. Significance was set to $p \leq 0.05$. For a depiction of one participant's raw data traces, see Fig. 3.

3. Results

3.1. Peak torque and voluntary activation

Voluntary activation was not different between males (99.6% ± 0.9%) and females (99.2% ± 0.9%) ($p = 0.157$) during the initial MVC (99.4% ± 0.9%) and final MVC (99.3% ± 0.8%) ($p = 0.659$). Males were stronger than females ($p = 0.050$). There was no difference ($p = 0.926$) in torque generation from the initial to final MVC for males (24.6 ± 7.5 N·m to 20.9 ± 6.7 N·m) and females (17.3 ± 2.0 N·m to 20.7 ± 5.5 N·m).

3.2. Activation reduction and neuromuscular economy

Activation reduction did not differ between males and females ($p = 0.113$, $\eta_p^2 = 0.232$) and was, thus, collapsed across sex. There was no interaction between history dependence and task ($p = 0.882$, $\eta_p^2 = 0.002$). However, there was a main effect of activation reduction between isometric and rTE states in that activation reduction was present in both the position-matching (26.9% ± 14.3%) and torque-matching (27.1% ± 9.4%) tasks ($p < 0.001$, $\eta_p^2 = 0.704$); however, the magnitude of activation reduction did not differ between the position- and torque-matching tasks ($p = 0.743$, $\eta_p^2 = 0.010$) (Fig. 4). For neuromuscular economy, there was no interaction between history dependence and task ($p = 0.199$, $\eta_p^2 = 0.145$). Neuromuscular economy increased similarly for both tasks ($p = 0.047$, $\eta_p^2 = 0.312$), from 2.8 ± 1.5 during the isometric to 3.4 ± 2.1 in the rTE state for the position tasks, and from 2.9 ± 1.2 during the isometric to 3.4 ± 1.5 in the rTE state during the torque tasks, with no difference observed between tasks ($p = 0.971$, $\eta_p^2 = 0.000$).

3.3. Soleus coactivation

For antagonist coactivation, there was no interaction between history dependence and task ($p = 0.892$, $\eta_p^2 = 0.000$). There was an effect of history dependence ($p = 0.006$, $\eta_p^2 = 0.048$), in that soleus coactivation was increased from 22.6% ± 11.6% in

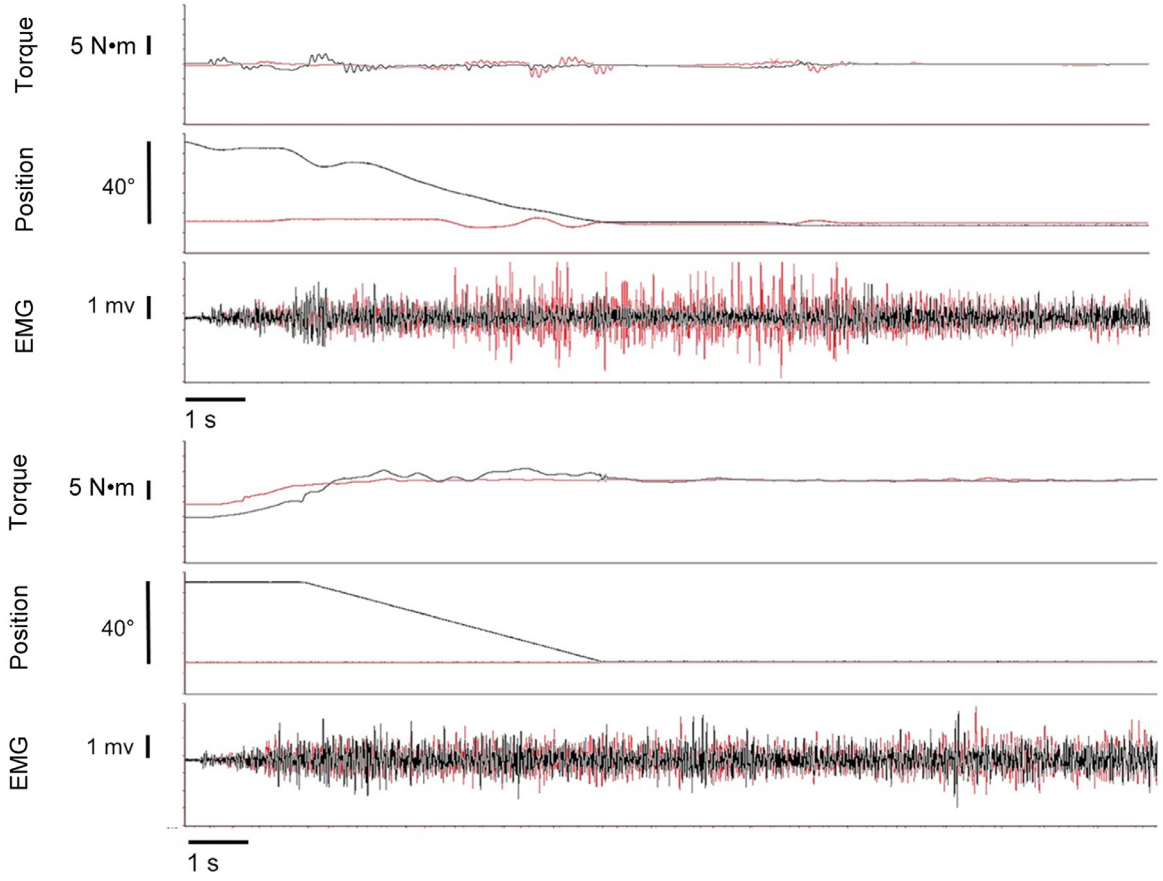

Fig. 3. Raw data traces displaying torque, position, and electromyography (EMG) for position (top) and torque (bottom) tasks. Residual torque enhancement (rTE) is overlaid in black over fixed-end isometric conditions in red. rTE conditions involved an isometric contraction, followed by active lengthening to a subsequent isometric contraction. Please note that other than some minor adjustments, the load during the position-matching task registers as 0, owing to the participant's holding and matching the load.

isometric to 29.0% ± 17.2% in the rTE state during the position tasks and from 21.0% ± 10.4% in isometric to 26.4% ± 14.4% in the rTE state during the torque tasks. There was no significant difference between tasks ($p = 0.591$, $\eta_p^2 = 0.007$).

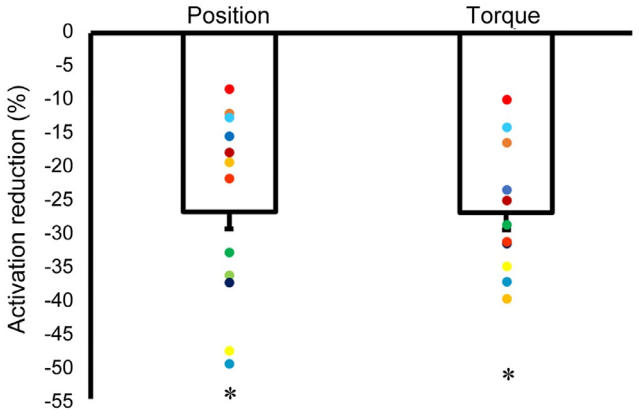

Fig. 4. Activation reduction during position and torque tasks. Bars represent the mean and standard error. Individual circles represent individual participants. Activation was reduced in both position and torque tasks (* $p < 0.001$) but was not different between tasks ($p = 0.743$).

4. Discussion

The purpose of the present study was to determine the relevance of rTE as it relates to a position-matching task with the use of an inertial load in the same anatomic position (i.e., position task) as compared with a static rigid load. Our hypothesis was confirmed, because activation reduction occurred in both tasks, with no differences observed between the position- and torque-matching tasks. There was a ∼27% reduction in EMG activity between the isometric contraction and isometric steady states following active lengthening for both position tasks and torque tasks. Thus, rTE is a feature of controlling a positional contraction (i.e., position-matching task), which supports and extends previous findings of isometric torque control conditions to position matching that represent various tasks of daily living.

When studying the effects of prior lengthening contractions on torque, an activation or torque-matching task may be imposed, resulting in a subsequent increase in torque or reduction in activation, respectively. Thus, activation reduction can serve as a proxy for rTE. Activation reduction observed in this study is not different from rTE (range: 7%−25%) observed in previous studies of the ankle dorsiflexors. Power and others[31,32] observed 7%−25% and 10%−25% rTE during maximal

dorsiflexion contractions. Previous studies of rTE in the ankle dorsiflexors found a 7%−15% increase in torque following active lengthening.[8,33] Neuromuscular economy, the amount of torque produced per unit of EMG, is a measure that accounts for variability in torque and EMG when attempting to match a target torque. In both position and torque tasks, neuromuscular economy was enhanced in the rTE state following active lengthening, indicating that less neuromuscular activity was required to produce the same amount of torque.

In the present study, all participants displayed rTE, indicating that our participant pool had no nonresponders. When investigating rTE in humans, there is often an incidence of nonresponders, or participants who do not exhibit increased torque following active lengthening. Our lack of nonresponders could, in part, be due to our study design. Our study involved a high load of 60% MVC, and it appears that the incidence of nonresponders is reduced with increasing contraction intensity.[4,5,16] However, the mechanism for increased responders during higher contraction intensities is currently not fully understood.[2] Another factor that may affect the responder/nonresponder phenomenon is the magnitude of active muscle fiber lengthening. The range of motion of 40° in our study was likely large enough to induce sufficient active muscle fiber lengthening and take advantage of the passive component relating to rTE.[1,2,16] An important consideration when investigating rTE in humans is controlling for the amount of muscle fiber versus tendon lengthening, which is ultimately governed by the amount of in-series compliance of the musculotendinous unit.[34,35] This, in turn, affects the magnitude of active muscle lengthening during the protocol by each participant. By having a large range of motion, some differences in tendon compliance that may affect rTE can, it is hoped, be attenuated.

During the position task, because lowering the load was completed by the participant, angular velocity was at times variable, while terminal angle was consistent across participants. It should also be noted that the load imposed on the ankle dorsiflexors varied throughout the range of motion owing to a changing moment arm during the active lengthening contractions. This variability is, in part, a limitation, but it is also an aspect of task differences that can occur with position-controlled movement, and it adds further ecological validity to the relevance of rTE during position-controlled tasks. Despite some potential variability in torque during the eccentric phase of the tasks, there were no significant differences in activation reduction during position and torque tasks. The lack of differences in activation reduction, despite some variability in tasks, is likely because rTE is velocity independent.[36] Another factor to consider in this study is the use of only surface EMG to observe activation strategies during position- and torque-matching tasks. Surface EMG is relevant for the study of rTE; however, specific neuromuscular-activation differences in position and torque tasks are better observed at the motor unit level.[37] If differences exist between position- and torque-matching tasks during dynamic contraction, surface EMG may not be sensitive enough to detect them.[38,21] Motor unit recordings could better determine whether any differences exist in motor neuron output between position and torque tasks during rTE protocols. As well, to investigate the adaptability of the neuromuscular system,[39] future studies should investigate activation reduction and potential changes to muscle energetics[40] following lengthening contractions in older adults.

5. Conclusion

Activation reduction in the isometric steady state following active lengthening is a feature of both torque-matching and position-matching tasks. Until the present study, the history dependence of force in humans has been investigated via electricity-stimulated or voluntary contractions, with the active lengthening component controlled by a dynamometer motor, which is represented by our torque-matching experiments. Positon-matching tasks are inherently more complex owing to their unconstrained nature. Given that activation reduction was still present during the position-matching task, the data from our study provide us with further insight into the relevance of rTE in tasks that better represent voluntary human movement.

Data accessibility

Individual values of all supporting data are available upon request.

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Author contributions

GAP and RM contributed equally. Both authors have read and approved the final version of the manuscript, and agree with the order of presentation of the authors.

Competing interests

The authors declare that they have no competing interests.

References

1. Abbott BC, Aubert XM. The force exerted by active striated muscle during and after change of length. *J Physiol* 1952;**117**:77–86.
2. Seiberl W, Power GA, Hahn D. Residual force enhancement in humans: current evidence and unresolved issues. *J Electromyogr Kinesiol* 2015;**25**:571–80.
3. Jones AA, Power GA, Herzog W. History dependence of the electromyogram: implications for isometric steady-state EMG parameters following a lengthening or shortening contraction. *J Electromyogr Kinesiol* 2016;**27**:30–8.
4. Paquin J, Power GA. History dependence of the EMG-torque relationship. *J Electromyogr Kinesiol* 2018;**41**:109–15.
5. Oskouei AE, Herzog W. Force enhancement at different levels of voluntary contraction in human adductor pollicis. *Eur J Appl Physiol* 2006;**97**:280–7.
6. Oskouei AE, Herzog W. Activation-induced force enhancement in human adductor pollicis. *J Electromyogr Kinesiol* 2009;**19**:821–8.
7. Chen J, Power GA. Modifiability of the history dependence of force through chronic eccentric and concentric biased resistance training. *J Appl Physiol (1985)* 2019;**126**:647–57.

8. Pinniger GJ, Cresswell AG. Residual force enhancement after lengthening is present during submaximal plantar flexion and dorsiflexion actions in humans. *J Appl Physiol (1985)* 2007;**102**:18–25.
9. Dalton BH, Contento VS, Power GA. Residual force enhancement during submaximal and maximal effort contractions of the plantar flexors across knee angle. *J Biomech* 2018;**78**:70–6.
10. Mazara N, Hess AJ, Chen J, Power GA. Activation reduction following an eccentric contraction impairs torque steadiness in the isometric steady-state. *J Sport Health Sci* 2018;**7**:310–7.
11. Seiberl W, Hahn D, Herzog W, Schwirtz A. Feedback controlled force enhancement and activation reduction of voluntarily activated quadriceps femoris during sub-maximal muscle action. *J Electromyogr Kinesiol* 2012;**22**:117–23.
12. MacDonald GZ, Mazara N, Herzog W, Power GA. Mitigating the bilateral deficit: reducing neural deficits through residual force enhancement and activation reduction. *Eur J Appl Physiol* 2018;**118**:1911–9.
13. Hunter SK, Yoon T, Farinella J, Griffith EE, Ng AV. Time to task failure and muscle activation vary with load type for a submaximal fatiguing contraction with the lower leg. *J Appl Physiol (1985)* 2008;**105**:463–72.
14. Leonard TR, DuVall M, Herzog W. Force enhancement following stretch in a single sarcomere. *Am J Physiol Cell Physiol* 2010;**299**:C1398–401.
15. Pinnell RAM, Mashouri P, Mazara N, Weersink E, Brown SHM, Power GA. Residual force enhancement and force depression in human single muscle fibres. *J Biomech* 2019;**91**:164–9.
16. Chapman N, Whitting J, Broadbent S, Crowley-McHattan Z, Meir R. Residual force enhancement in humans: a systematic review. *J Appl Biomech* 2018;**34**:240–8.
17. Mehta A, Herzog W. Cross-bridge induced force enhancement. *J Biomech* 2008;**41**:1611–5.
18. Powers K, Nishikawa K, Joumaa V, Herzog W. Decreased force enhancement in skeletal muscle sarcomeres with a deletion in titin. *J Exp Biol* 2018;**219**:1311–6.
19. Fukatani A, Herzog W. Current understanding of residual force enhancement: cross-bridge component and non-cross-bridge component. *Int J Mol Sci* 2019;**20**:5479. doi:10.3390/ijms20215479.
20. Altenburg TM, de Ruiter CJ, Verdijk PWL, van Mechelen W, de Haan A. Vastus lateralis surface and single motor unit EMG following submaximal shortening and lengthening contractions. *Appl Physiol Nutr Metab* 2008;**33**:1086–95.
21. Jakobi JM, Kuzyk SL, McNeil CJ, Dalton BH, Power GA. Motor unit contributions to activation reduction and torque steadiness following active lengthening: a study of residual torque enhancement. *J Neurophysiol* 2020;**123**:2209–16.
22. Akazawa K, Milner TE, Stein RB. Modulation of reflex EMG and stiffness in response to stretch of human finger muscle. *J Neurophysiol* 1983;**49**:16–27.
23. Baudry S, Jordan K, Enoka RM. Heteronymous reflex responses in a hand muscle when maintaining constant finger force or position at different contraction intensities. *Clin Neurophysiol* 2008;**120**:210–7.
24. Baudry S, Enoka RM. Influence of load type on presynaptic modulation of Ia afferent input onto two synergist muscles. *Exp Brain Res* 2009;**199**:83–8.
25. Rudroff T, Jordan K, Enoka JA, Matthews SD, Baudry S, Enoka RM. Discharge of biceps brachii motor units is modulated by load compliance and forearm posture. *Exp Brain Res* 2009;**202**:111–20.
26. Duchateau J, Enoka RM. Neural control of shortening and lengthening contractions: influence of task constraints. *J Physiol* 2008;**586**:5853–64.
27. Doemges F, Rack PM. Changes in the stretch reflex of the human first dorsal interosseous muscle during different tasks. *J Physiol* 1992;**447**:563–73.
28. Christou EA, Shinohara M, Enoka RM. Fluctuations in acceleration during voluntary contractions lead to greater impairment of movement accuracy in older adults. *J Appl Physiol (1985)* 2003;**95**:373–84.
29. Power GA, Makrakos DP, Stevens DE, Herzog W, Rice CL, Vandervoort AA. Shortening-induced torque depression in old men: implications for age-related power loss. *Exp Gerontol* 2014;**57**:75–80.
30. Chen J, Hahn D, Power GA. Shortening-induced residual force depression in humans. *J Appl Physiol (1985)* 2019;**126**:1066–73.
31. Power GA, Rice CL, Vandervoort AA. Increased residual force enhancement in older adults is associated with a maintenance of eccentric strength. *PLoS One* 2012;**7**:e48044. doi:10.1371/journal.pone.0048044.
32. Power GA, Rice CL, Vandervoort AA. Residual force enhancement following eccentric induced muscle damage. *J Biomech* 2012;**45**:1835–41.
33. Tilp M, Steib S, Herzog W. Force-time history effects in voluntary contractions of human tibialis anterior. *Eur J Appl Physiol* 2009;**106**:159–66.
34. Seiberl W, Hahn D, Kreuzpointner F, Schwirtz A, Gastmann U. Force enhancement of quadriceps femoris *in vivo* and dependence of stretch-induced muscle architectural changes. *J Appl Biomech* 2010;**26**:256–64.
35. Raiteri BJ, Hahn D. A reduction in compliance or activation level reduces force depression in human tibialis anterior. *Acta Physiol (Oxf)* 2019;**225**:e13198. doi:10.1111/apha.13198.
36. Edman KA, Elzinga G, Noble MI. Residual force enhancement after stretch of contracting frog single muscle fibers. *J Gen Physiol* 1982;**80**:769–84.
37. Rudroff T, Justice JN, Matthews S, Zuo R, Enoka RM. Muscle activity differs with load compliance during fatiguing contractions with the knee extensor muscles. *Exp Brain Res* 2010;**203**:307–16.
38. Mottram CJ, Christou EA, Meyer FG, Enoka RM. Frequency modulation of motor unit discharge has task-dependent effects on fluctuations in motor output. *J Neurophysiol* 2005;**94**:2878–87.
39. Power GA, Dalton BH, Rice CL. Human neuromuscular structure and function in old age: a brief review. *J Sport Health Sci* 2013;**2**:215–26.
40. Herzog W. Why are muscles strong, and why do they require little energy in eccentric action. *J Sport Health Sci* 2018;**7**:255–64.