Experimental Brain Research (2019) 237:2345–2352
https://doi.org/10.1007/s00221-019-05570-7

RESEARCH ARTICLE

Effect of knee joint position on triceps surae motor unit recruitment and firing rates

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Received: 31 January 2019 / Accepted: 28 May 2019 / Published online: 10 July 2019

Abstract
Gastrocnemii muscle fibers shorten when the knee joint is in a flexed compared to an extended position. This leads to inhibition of medial gastrocnemius (MG) motor units, however, it is unclear whether this affects motor unit properties of the lateral gastrocnemius (LG) or soleus (SOL). We recorded 171 motor units from the MG (61), LG (39) and SOL (71) at an extended (160°) and flexed (100°) knee joint position with the ankle and hip joints at 90°. Subjects performed isometric ramp plantar flexion contractions at 25, 50 and 100% of the maximal voluntary contraction. MG ($p=0.0002$) and LG ($p=0.02$) motor unit recruitment thresholds (RT) were higher, whereas only MG motor unit firing rates (FR) were lower ($p=0.008$) in the flexed compared to the extended knee joint position. SOL motor unit RT ($p=0.66$) and FR ($p=0.08$) were not statistically different between positions. When comparing properties of the same motor unit followed during contractions at both knee joint positions, RT of ten gastrocnemii motor units were higher ($p=0.0008$) and FR were lower ($p=0.01$) when the knee was flexed. Additionally, in six SOL motor units, RT ($p=0.42$) and FR ($p=0.96$) were not different between the two positions. Thus, MG and LG activation is similarly inhibited during plantar flexion contractions in a flexed compared to an extended knee joint position. Furthermore, our findings indicate that knee joint position changes have no effect on SOL excitability.

Keywords Motor unit · Knee joint position · Triceps surae · Firing rate · Recruitment threshold

Introduction

The triceps surae muscle group is comprised of the soleus (SOL) and the two heads of the gastrocnemii, medial (MG) and lateral (LG). The SOL crosses the ankle joint contributing only to plantar flexion (PF). It is composed of ~85% type I muscle fibers (Johnson et al. 1973) and is engaged chronically during any postural adjustments (Héroux et al. 2014). The gastrocnemii cross both the knee and ankle joints, thus contributing to PF and knee flexion. Both heads are composed of ~50% type I muscle fibers (Johnson et al. 1973) and are predominantly active during fast, explosive movements (Herzog et al. 1993). It has been reported that the heads of the gastrocnemii demonstrate different activation patterns when subjects perform a balancing task, with motor unit recruitment thresholds (RT) of the LG being up to 20 times higher than that of the MG (Héroux et al. 2014). Other compartmentalized muscles such as the flexor digitorum superficialis (Butler et al. 2005) and quadriceps femoris (Kamo 2002) do not show large differences in RT between compartments.

The length–tension relationship of the triceps surae can be manipulated by changing the ankle joint, knee joint, or both. Flexing the knee while maintaining the same ankle joint angle passively shortens the gastrocnemii with no change in SOL length (Kawakami et al. 1998; Lauber et al. 2014). This flexed knee joint position results in a decreased PF isometric maximal voluntary contraction (MVC) torque compared to that in an extended knee joint position (Cresswell et al. 1995; Dalton et al. 2012). In the MG, the decreased ability to produce torque when the knee joint is in a flexed position may lead to a decreased metabolic efficiency of the muscle, ultimately resulting in a decreased neural drive to it (Cresswell

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et al. 1995; Kennedy and Cresswell 2001; Kennedy et al. 2004; Lauber et al. 2014). Specifically, the root mean square (RMS) EMG recorded from the MG using surface electromyography (sEMG) was significantly lower across contraction levels from 10 to 100% MVC when the knee joint was flexed compared to extended (Cresswell et al. 1995; Miaki et al. 1999; Hébert-Losier et al. 2011), whereas that recorded from the LG was found to be significantly lower only at contraction levels of 40% MVC or higher (Cresswell et al. 1995). This lower RMS EMG from the MG was explained by its lower motor unit firing rates (FR) and higher motor unit RT reported in the flexed knee joint position (Kennedy and Cresswell 2001). Despite the differences in motor unit properties between the heads of the gastrocnemii, no studies have reported the effect of knee joint position on LG motor units.

Although the SOL does not cross the knee joint, studies have reported an increase in SOL RMS EMG during PF contractions in a flexed compared to an extended knee joint position (Kennedy and Cresswell 2001; Lauber et al. 2014). When the knee joint was passively rotated through its range of motion while maintaining a 2.5% MVC isometric PF torque. SOL EMG activity increased, whereas MG motor unit FR decreased as the knee progressed towards flexion (Lauber et al. 2014). This was attributed to a reciprocal activation of these muscles; that is, as the MG muscle fibers became shorter, they were less capable of producing torque, and thus an increase in SOL activation was required to compensate (Lauber et al. 2014). Conversely, other investigations using sEMG have reported no changes in SOL activity with knee flexion (Cresswell et al. 1995; Hébert-Losier et al. 2011). These studies have used sEMG (Tamaki et al. 1996; Kennedy and Cresswell 2001) and intramuscular EMG as a global measure of gross neuromuscular activation (Lauber et al. 2014). The sEMG technique does not differentiate motor unit RT and FR (De Luca 1997), and limitations of sEMG (Farina et al. 2014) may help explain prior discordant findings in SOL activation during knee position changes (Cresswell et al. 1995; Kennedy and Cresswell 2001; Hébert-Losier et al. 2011; Lauber et al. 2014). The purpose of this study was to compare MG, LG and SOL motor unit properties (RT and FR) between two different knee joint positions: extended and flexed. Based on previous reports, we hypothesized that during PF contractions with the knee joint in a flexed position (1) MG and LG motor unit RT will be higher and FR will be lower, and (2) SOL motor unit RT will be lower and FR will be higher, compared to the extended knee joint position.

Methods

Eight recreationally active young men (age 26 ± 7 years, body mass 84 ± 11 kg, height 180 ± 6 cm) performed a series of PF contractions at two different knee joint positions. Intramuscular electromyography (EMG) of the MG, LG and SOL was recorded using fine wire electrodes. Exclusion criteria included known neuromuscular and/or orthopedic pathologies of the lower limb, diabetes, and caffeine consumption prior to participation. Consent was obtained both orally and in written format. This study was reviewed and approved by the local University's research ethics board for human experimentation and conforms to the latest revision of the Declaration of Helsinki.

Experimental set-up

Subjects were seated upright on a dynamometer (Cybex HUMAC NORM; CSMi Medical Solutions, Stoughton, MA) with their left (non-dominant) foot fixed on a plate attached to a torque motor. The foot was secured to the footplate using an inelastic strap at the ankle and two other straps across the toes and dorsum of the foot. The ankle joint was aligned with the axis of rotation of the dynamometer. The intervention was repeated at two different knee joint positions: extended (160°) and flexed (100°), in which 180° refers to a fully extended knee. In both conditions, the hip and ankle joints were adjusted to be at a neutral position (90°). Angles were measured using a goniometer. Subjects had a seatbelt tightened around the hip and shoulders to minimize torso movement. Torque was recorded from the dynamometer, analog-to-digitally converted [Power 1401, Cambridge Electronic Design (CED)], calibrated and sampled at 2 kHz (Spike2, CED, Cambridge, UK). Real-time torque production was displayed on a computer screen ~ 2 m away from each participant for visual feedback.

MVC

Isometric PF maximal voluntary contractions (MVC) were performed under each knee joint condition. Each effort was ~ 5 s in duration with 3 min of rest between each attempt until the torque output remained within 5% across two consecutive contractions. Visual feedback and strong verbal encouragement were given during all attempts. The highest value was recorded as MVC torque.

Ramp contractions

Target levels were set at 25, 50 and 100% of MVC torque. Subjects were familiarized with the protocol through multiple attempts at a successful completion of a ramp contraction. The knee joint position at which the subjects performed their contractions first was randomized and subjects remained in the device throughout the whole protocol. Subjects were asked to perform ramp contractions by slowly contracting until the target levels were met (5–10 s), hold the contraction for 5 s and then slowly decrease torque to baseline (5–10 s). Three isometric ramp contractions were performed at each target level with 1–3 min of rest between attempts. Subjects then had ten minutes of rest before beginning ramp contractions in the other knee joint position. Subjects visited the lab 2–4 times to repeat the intervention. During all contractions, single motor unit activity was recorded using custom-made bipolar fine wire electrodes inserted to the muscle belly of the MG and LG, and medial aspect of the SOL. Each electrode contained two stainless steel electrodes (100 µm in diameter; California Fine Wire Company, Grover Beach, California, USA) threaded and hooked at the tip of a 27-gauge hypodermic needle. Prior to insertion, the skin was cleansed using 70% ethanol and the needle was sterilized. The needle was inserted in a slightly different location throughout the multiple visits. Intramuscular EMG was band pass filtered between 10 Hz and 10 kHz (Neurolog, NL844; Digitimer, UK), pre-amplified 200×, analog-to-digital converted (Power 1401, CED) and sampled at 20 kHz (Spike2, CED).

Analysis

Single motor unit analyses were performed offline using Spike2 version 7 (CED, Cambridge, UK). Motor unit action potential trains were identified using a template matching algorithm followed by visual inspection by an experienced operator. For inclusion, each motor unit required the overlay of successive action potentials to have a constant waveform shape with minimal changes in amplitude. Furthermore, the motor unit was required to discharge at least 1 s after recruitment. Doublets were rarely observed but were excluded from analysis. RT was determined as the relative torque (%MVC) at which each motor unit began to discharge. FR was determined from the first 11 successive action potentials (ten inter-spike intervals) after the motor unit was recruited. For each motor unit, a mean RT and FR was determined from all ramp isometric contractions in which the motor unit met the above inclusion criteria.

Statistics

Analysis was performed in R (version 3.4.3). The Δ (delta) values are defined as a change in mean calculated as [(mean in extended position – mean in flexed position)/mean in extended position] × 100%. A two-tailed paired *t* test was used to compare MVC torque values between the two knee joint positions. For all data (171 motor units), RT and FR data were tested for a normal distribution using a Shapiro–Wilk test ($p<0.05$). Following a log transformation, the RT data remained non-normally distributed ($p<0.05$), whereas the FR data followed a normal distribution ($p>0.05$). Each muscle was analyzed separately. A Mann–Whitney *U* test was used to compare motor unit RT between the extended and flexed knee joint position. For multiple linear regression, the *lme4* package (Bates et al. 2012) was used to model the relationship between motor unit FR and knee joint position with the covariates of RT, subject and MVC to minimize variation due to other relevant factors. For a statistical comparison, an analysis of variance (ANOVA) was performed with the likelihood ratio tests of the full model (including knee joint position) in comparison with a reduced model. Effect sizes (Cohen's D) and 95% confidence intervals (95% CI) were calculated for the motor unit FR data. Motor units which were followed during contractions at both knee joint positions (16 motor units) were compared using a two-tailed paired *t* test. The alpha was set at $p<0.05$. A Bonferroni correction factor was used for multiple comparisons. RT data are reported as median and inter-quartile range (IQR) from the 25th to 75th percentile. All other data are reported as mean ± standard deviation.

Results

MVC

PF MVC torque in the flexed (101.8 ± 44.9 Nm) knee joint position was lower than that in the extended (117.1 ± 38.6 Nm) knee joint position ($p<0.05$).

Motor unit firing rate and recruitment threshold

A total of 171 motor units were included in the statistical analysis: 61 from MG, 39 from LG and 71 from SOL (Table 1). MG motor unit RT showed a statistically significant difference with lower motor unit RT in the extended (median = 12.2, IQR = 4.6–24.4%MVC) compared to the flexed (median = 34.4, IQR = 22.3–45.9%MVC) knee joint position ($p=0.0002$). Similarly, LG motor unit RT showed statistically significant differences with lower RT in the extended (median = 17.8, IQR = 8.7–32.8%MVC) compared to the flexed (median = 44.9, IQR = 19–74.5%MVC) knee joint position ($p=0.02$). SOL motor unit RT were not statistically different between the extended (median = 10.8, IQR = 1.5–22.3%MVC) and flexed (median = 9.7, IQR = 3.5–26.3%MVC) knee joint positions ($p=0.66$).

MG motor unit FR showed statistically significant differences between the extended (7.7 ± 1.8 Hz) and flexed (6.4 ± 1.0 Hz) knee joint position ($p=0.008$; $d=0.8$; 95% CI 0.26–1.34), whereas LG motor unit FR were not statistically different between the flexed (7.8 ± 2.3 Hz) and extended (8.6 ± 1.9 Hz) knee joint positions ($p=0.12$; $d=0.5$; 95% CI −0.17 to 1.18). SOL motor unit FR were not statistically different between the extended (8.2 ± 1.9 Hz) and flexed (7.2 ± 2.3 Hz) knee joint position ($p=0.08$; $d=0.5$; 95% CI 0.05–1.01) (Fig. 1).

Table 1 Number of medial gastrocnemius (MG), lateral gastrocnemius (LG) and soleus (SOL) motor units that met the inclusion criteria from each subject in the extended and flexed knee joint positions

Subject	Extended position			Flexed position			Both knee joint positions		
	MG	LG	SOL	MG	LG	SOL	MG	LG	SOL
1	5	2	5	5	2	7	3	2	1
2	8	6	9	5	4	9	1	2	2
3	5	1	5	5	–	2	–	–	1
4	1	8	4	5	4	2	–	–	1
5	7	–	3	3	–	5	1	–	–
6	–	5	6	–	3	3	1	–	–
7	2	2	3	1	2	4	–	–	1
8	4	–	1	3	–	3	–	–	–

Both knee joint positions refers to the number of motor units recorded during contractions at both the flexed and extended knee joint positions

We were able to record and measure 16 motor units during PF contractions at both knee joint positions; MG (6), LG (4) and SOL (6) (Fig. 2). The MG and LG data were aggregated to represent the gastrocnemius motor unit pool. When the knee joint was changed from an extended to a flexed position, the combined gastrocnemii motor unit ΔRT was − 130%, whereas the ΔFR was + 20%. Specifically, the MG motor unit ΔRT was − 250% and motor unit ΔFR was + 20%, whereas LG motor unit ΔRT was − 80% and ΔFR was + 20%. All ten motor units from the gastrocnemii (MG = 6 and LG = 4) demonstrated a statistically significant difference between positions with higher RT ($p = 0.0008$)

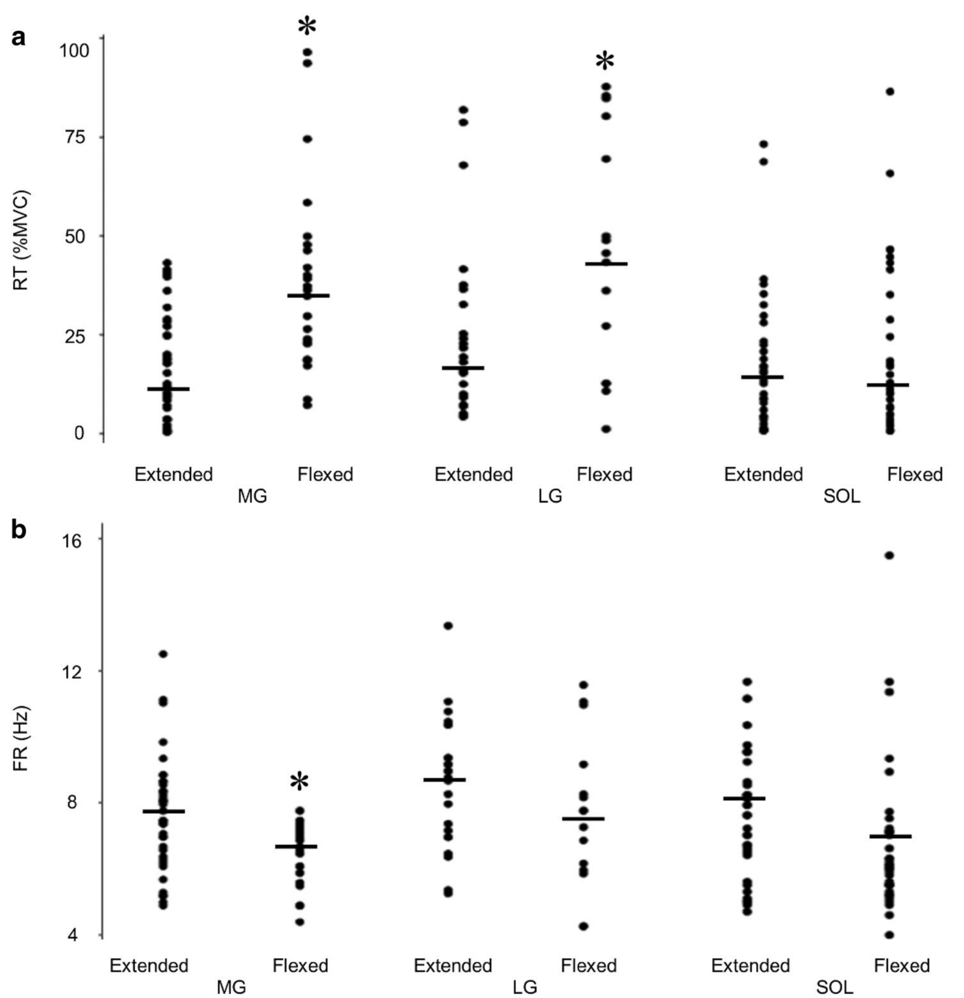


Fig. 1 Motor unit properties are shown for the medial gastrocnemius (MG), lateral gastrocnemius (LG) and soleus (SOL) in both knee joint positions (*x* axis). Each black dot represents an individual motor unit. **a** The *y* axis represents the motor unit RT. The horizontal lines represent the median of the group. **b** The *y* axis represents the motor unit FR. The horizontal lines represent the mean of the group. Asterisk a significant difference compared to the extended knee joint position ($p < 0.05$)

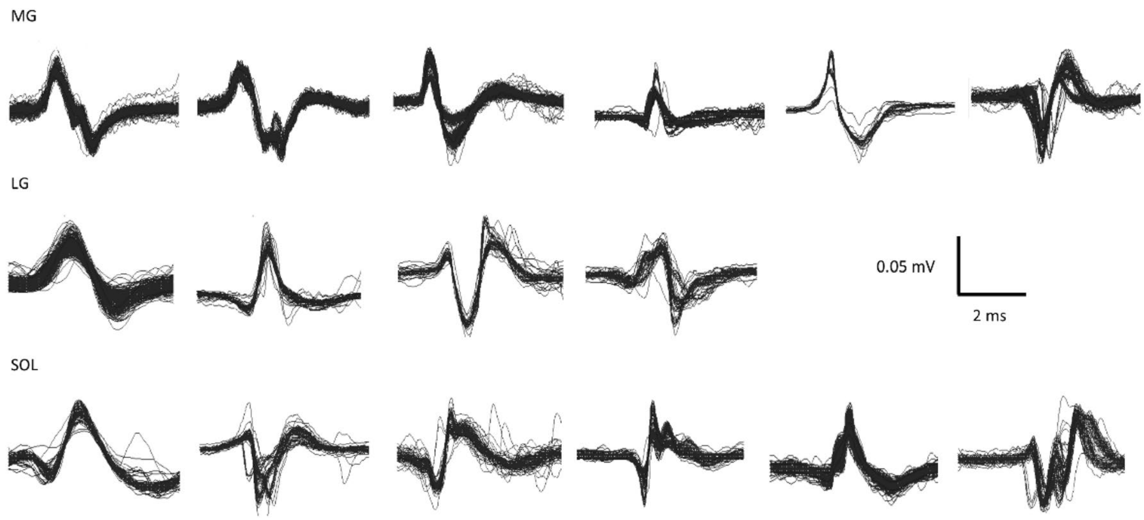


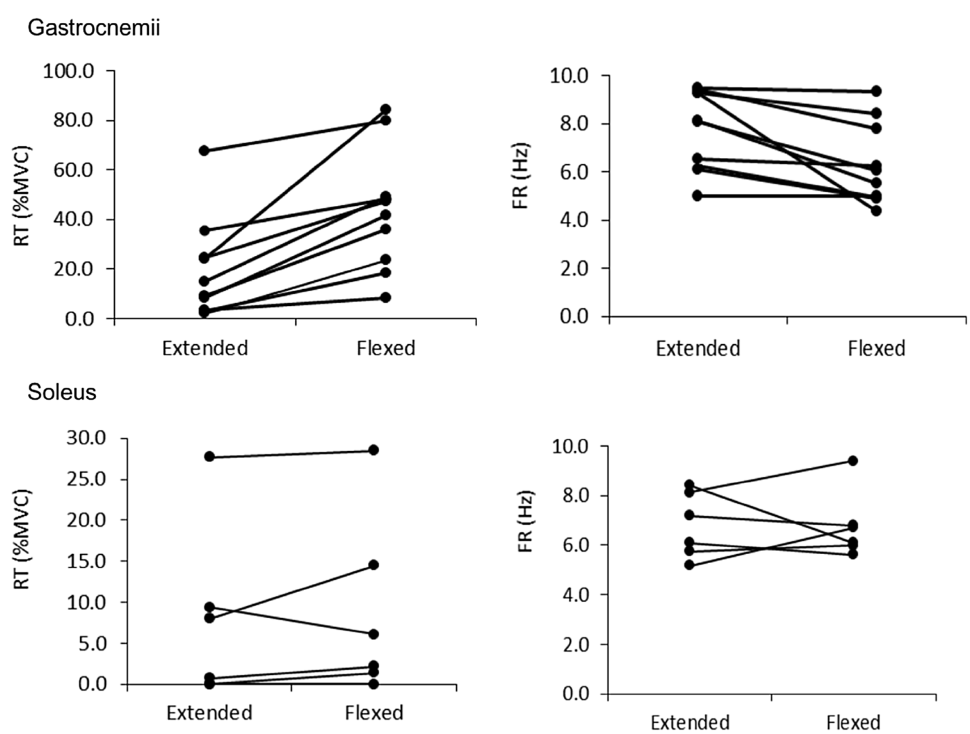
Fig. 2 Each row displays the overlay of action potential spikes for those motor units recorded during contractions in both the extended and flexed knee joint positions. The spike overlays include 50–500 spikes per template. MG, LG and SOL refers to the medial gastrocnemius (six motor units), lateral gastrocnemius (four motor units) and soleus (six motor units), respectively

and lower FR ($p = 0.01$) in the flexed compared to the extended knee joint position. When the knee joint was changed from an extended to a flexed position, SOL motor unit ΔRT was − 10%, whereas ΔFR was 0%. There were no statistically significant differences between SOL motor unit RT ($p = 0.42$) and FR ($p = 0.96$) in the two different knee joint positions (Fig. 3).

Discussion

The present investigation compared MG, LG and SOL motor unit RT and FR during PF contractions between an extended and flexed knee joint position. Consistent with previous literature, our data demonstrate MG inhibition during PF contractions in a flexed compared to an extended knee joint

Fig. 3 Joined dots represent the same motor unit in the extended and flexed knee joint position. The left column represents RT as %MVC. The right column represents FR in Hz



position. The current study provides evidence that motor units from both heads of the gastrocnemii, the MG and LG, are similarly inhibited during PF contractions when the knee is flexed. Additionally, SOL motor unit properties are not affected by the knee joint position, demonstrating that SOL excitability does not increase to compensate for the compromised gastrocnemii.

The triceps surae musculature is responsible for ~ 60% of the PF torque produced at the ankle joint (Murray et al. 1976). In agreement with prior reports (Kawakami et al. 1998; Dalton et al. 2012), our data show a 13% decrease in PF MVC torque when the knee joint is flexed. The decrease in torque in this position has been attributed to a decreased fascicle length and increased pennation angle of the gastrocnemii muscle fibers which together reduce the overall force transmitted to the calcaneal tendon (Kawakami et al. 1998). These architectural changes have been associated with a decrease in neural drive to the gastrocnemius muscle (Cresswell et al. 1995; Kennedy and Cresswell 2001; Kennedy et al. 2004; Lauber et al. 2014). Studies have shown an increase in MG motor unit RT (Kennedy and Cresswell 2001), and a decrease in motor unit FR (Kennedy and Cresswell 2001; Lauber et al. 2014) during isometric (Kennedy and Cresswell 2001) and dynamic (Lauber et al. 2014) PF contractions in a flexed compared to an extended knee joint position. It is important to note that these studies have only recorded motor units under low contraction intensities. Specifically, the average RT torque of MG motor units in the extended knee joint position was 2.97 ± 7.78 Nm, whereas that in the flexed knee joint position was 32.14 ± 10.25 Nm (Kennedy and Cresswell 2001). In a different study, the torque at which subjects were asked to contract at as the knee joint was passively moved through the range of motion was 2.5% MVC (Lauber et al. 2014). This work suggested that there may be a preferential inhibition of lower threshold motor units in the flexed knee joint position (Kennedy and Cresswell 2001). Given the well-established differences between the properties of low and high threshold motor units (Henneman 1957; Henneman et al. 1965; Zajac and Faden 1985), it is important to consider motor units with low and high RT when exploring the effects of length changes in the gastrocnemii. In our study, we recorded MG motor units with RT up to 43% MVC and 96% MVC in the extended and flexed knee joint position, respectively. Our dataset consisting of low and high threshold motor units demonstrated a similar inhibition during PF contractions in a flexed knee joint position as that reported in low threshold motor units (Kennedy and Cresswell 2001; Lauber et al. 2014). Furthermore, we were able to record the same MG motor units ($n = 6$) during contractions in both the extended and flexed knee joint positions. These findings indicate that the lower threshold units recruited in the extended knee joint position are not preferentially inhibited when the gastrocnemii are shortened with knee flexion as previously suggested (Kennedy and Cresswell 2001; Kennedy et al. 2004). Instead, they are recruited at the flexed knee joint position, but at a higher RT.

Despite the many similarities of the heads of the gastrocnemii, it has been shown that the MG and LG have different motor unit (Héroux et al. 2014) and architectural (Antonios and Adds 2008) properties. However, studies have not explored LG motor unit activity with an alteration of knee joint position. The higher motor unit RT in the flexed compared to the extended knee joint position in LG motor units indicate that like the MG, the LG is also inhibited by knee joint flexion (Fig. 1). Similarly, in following all ten motor units from the MG and LG during contractions at both knee joint positions, there was greater inhibition in the flexed compared to the extended knee joint position, as demonstrated by higher RT and lower FR (Fig. 3). These findings thus indicate that the gastrocnemii motor unit pool is inhibited when the knee joint is in a flexed position.

The MG motor unit inhibition in the flexed knee joint position is proposed to be a result of its compromised force producing capacity. This may be caused by altered inputs to the gastrocnemii motor unit pool from various afferent feedback systems (Kennedy and Cresswell 2001; Lauber et al. 2014). By inhibiting functionally insufficient muscle fibers, the central nervous system minimizes the metabolic costs of contractions of a compromised muscle (Kennedy and Cresswell 2001). The present experimental design did not measure afferent feedback, however our results do suggest that a similar strategy is shared between the MG and LG. Studies exploring length changes in other muscles do not report motor unit inhibition when the muscle is shortened. Motor unit FR in the shortened hamstrings (Kirk and Rice 2017) and biceps brachii (Christova et al. 1998) were greater, whereas no change in FR was reported in the shortened tibialis anterior (Bigland-Ritchie et al. 1992) and vastus lateralis (Altenburg et al. 2009) muscles. Reasons behind the discrepancies are not clear, but the muscle may need to reach a functionally insufficient length to cause inhibition as proposed for the MG (Kennedy and Cresswell 2001; Lauber et al. 2014). Alternatively, the change in motor unit properties with length may be muscle specific, which can explain the equivocal findings amongst muscles.

Unlike motor units of the MG and LG, our data show that SOL motor unit properties, both FR and RT, are similar between the extended and flexed knee joint positions (Fig. 1). Furthermore, the motor units followed during contractions in both knee joint positions ($n = 6$) showed no statistical difference in FR or RT (Fig. 3). Thus, changes in knee joint position have no effect on SOL motor unit properties. This finding is supported by previous work (Cresswell et al. 1995; Hébert-Losier et al. 2011). However, other literature reports an increase in SOL excitability during contractions at a flexed knee joint position (Tamaki et al. 1996; Kennedy and Cresswell 2001; Lauber et al. 2014). Given that changing the knee joint position has no effect on SOL length (Kawakami et al. 1998; Lauber et al. 2014), this was attributed to a reciprocal activation between synergists of the triceps surae to compensate for the compromised gastrocnemii in this position (Lauber et al. 2014). Other studies exploring SOL spinal excitability, as reflected by modulations of the SOL H-reflex when the quadriceps muscle is lengthened by knee joint flexion, report conflicting responses of the SOL H-reflex (Misiaszek et al. 1998; Pinniger et al. 2001; Tanabe et al. 2005; Tokuno et al. 2012). However, this change in SOL H-reflex amplitude has been shown to last for up to 8 s following quadriceps stretch (Cheng et al. 1995; Misiaszek et al. 1995). Given that our protocol included a 10 min rest period prior to switching knee joint positions, it is unlikely that the mechanisms involved in SOL H-reflex alterations would have affected SOL excitability in the current study. It seems the discrepancy in the literature, with reports of both an increase (Tamaki et al. 1996; Kennedy and Cresswell 2001; Lauber et al. 2014) and no change (Cresswell et al. 1995; Hébert-Losier et al. 2011) in SOL excitability in the flexed knee joint position, may be explained by a difference in study methodologies and assessment techniques. For example, Kennedy and Cresswell (2001) compared SOL RMS EMG activity during a 20 Nm contraction in both knee joint positions. Given that PF MVC torque decreases when the knee joint is flexed, 20 Nm will be closer to the MVC torque in the flexed compared to the extended knee joint position. As such, it is expected that SOL RMS EMG at this contraction level would be greater, as it is contracting closer to its maximum capacity. Furthermore, all studies showing increased SOL activity when the knee joint is flexed (Tamaki et al. 1996; Kennedy and Cresswell 2001; Lauber et al. 2014) used the same absolute contraction levels in both knee joint positions. However, our data and literature exploring relative contraction levels (Cresswell et al. 1995; Hébert-Losier et al. 2011) indicate that SOL excitability does not change with knee flexion.

Conclusion

This study compared MG, LG and SOL motor unit RT and FR at two knee joint positions. The increased RT and decreased FR reported for the MG and LG demonstrate that the gastrocnemii motor unit pool is inhibited during PF contractions when the knee joint is in a flexed compared to an extended position. SOL motor unit RT and FR were not statistically different between the two knee joint positions. Therefore, increased SOL motor unit excitability as a compensatory mechanism for the compromised gastrocnemii is not supported by the current results.

Funding This research was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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