The published version of this article can be found on European Journal of Sport Science (https://www.tandfonline.com/toc/tejs20/current)

Title: Effect of environmental temperature change on the neuromechanical function of the quadriceps muscles

Authors: Spillane, P.[1,2] Bampouras, T.M.[1]

Affiliations: [1] Lancaster Medical School, Faculty of Health and Medicine, Lancaster University, Lancaster, UK. [2] Department of Medical and Sport Sciences, University of Cumbria, Lancaster, UK

Corresponding author

Pádraig Spillane (p.spillane@lancaster.ac.uk)

Abstract

This study compared neuromechanical characteristics of voluntary (maximum voluntary contraction (MVC) peak torque, rate of torque development (RTD), voluntary activation (VA)) and electrically stimulated contractions (peak torque, RTD) when performed under the same temperature conditions. Twelve physically active males performed two isometric MVCs of the knee extensors in an isokinetic dynamometer. The MVCs were performed after lower limb submersion for 20 minutes in hot (40 °C) or cold (10 °C) water. A control MVC was performed in ambient room temperature (17 ± 0.7 °C). Electrical twitches were delivered at rest pre-MVC (Unpotentiated), during the plateau phase of the MVC (Superimposed) and post-MVC (Potentiated). Peak torque for MVC, Unpotentiated and Potentiated was recorded. RTD was calculated for the MVC (at 50 ms, 100 ms, 150 ms, 200 ms and peak torque time points), Unpotentiated and Potentiated twitches, while muscle activation capacity (using the central activation ratio method) was calculated. There was no significant change between conditions in MVC peak torque, MVC RTD, muscle activation capacity and (averaged) twitch peak torque ($P > 0.05$). Twitch RTD for the hot condition (1025.0 ± 163.0 N·m ·s^{-1}) was significantly higher ($P = 0.003$) than control (872.3 ± 142.9 N·m ·s^{-1}). In conclusion, environmental temperature changes, in the range examined, do not affect the ability to generate maximum torque or any of the RTD parameters in maximum voluntary isometric contractions. In contrast, increased heat results in higher RTD in electrically stimulated contractions, most likely induced by reduced contraction time. This has practical implications for the use electromyostimulation tools for injury prevention.

Key words

Cooling, heating, maximum voluntary contractions, muscle activation, rate of torque development, post-activation potentiation,

Introduction

Rate of torque development (RTD; the muscles' ability to produce torque over a short time period, in the initial phase of a movement (Maffiuletti et al., 2016)), is a crucial contributor to human movement, whether this is to maintain balance (Pijnappels et al., 2005), contribute to athletic performance (Tillin et al., 2010) or assist in rehabilitation (Cornwall, 1994). Indeed, RTD is more closely related to the performance of everyday tasks (e.g. sit-to-stand, recovery from trips etc.) and sport-specific tasks than maximal strength alone (Pijnappels et al., 2005; Tillin et al., 2013). RTD is an 'overall' reflection of the musculotendinous unit's ability to function to generate torque quickly and as such, it is determined by physiological, mechanical and neural factors (Maffiuletti et al., 2016). These include muscle activation (Folland et al., 2014), muscle fibre type composition (Harridge et al., 1996), myofibrillar mechanisms (Wahr & Rall, 1997), muscle size (Andersen & Aagaard, 2006), muscle architecture (Blazevich et al., 2009), and muscle-tendon unit stiffness (Bampouras et al., 2006).

One of the factors that can affect RTD is temperature. The effect of temperature, however, appears to be inconsistent across various studies. Specifically, in studies that used electrically stimulated *in vivo* muscular contractions in humans, RTD is reported to be significantly increased with heating (from an estimated 31 ºC to 37 ºC) and decreased with cooling (to 22 ºC) (de Ruiter et al., 1999; Gossen et al., 2001). In other studies, however, RTD in voluntary contractions has remained constant across different muscle temperatures of 30 ºC, 34 ºC and 38 ºC (Dewhurst et al., 2010; Ranatunga et al., 1987). Finally, results by Cornwall (1994) and Clarke and Royce (1962) showed that RFD decrease with cooling in 10 ºC, but there was no increase when the limb was heated to 40 ºC.

The discrepancies between studies could have a number of explanations, revolving around the experimental set-up used. For instance, muscle fibre tension has been shown to be significantly temperature-dependant, with slow-twitch muscles tension being lower at lower temperatures but with fast-twitch tension being higher at lower temperatures (Buller et al., 1984). Thus, muscles with different muscle fibre composition would likely produce different RTD results with temperature changes (e.g. Ranatunga et al., 1987). Another potential factor is voluntary activation changes, with voluntary activation affecting both the time to reach a given torque, as well as maximum torque (Maffiuletti et al., 2016). Studies inducing increases in core temperature (but not local muscle temperature changes) would likely see a reduced RTD due to reduced activation (Thomas et al., 2006), something that would not be expected with local temperature changes. It is worth noting here that differences in muscle activation capacity (Behm et al., 2002), calculation method (Bampouras et al., 2006) and the use of un/potentiated resting twitch, which could also be affected by temperature (Moore et al., 1990) for one of the calculation methods (Folland & Williams, 2007) can further complicate the effect of voluntary activation on RTD. Finally, studies are exploring voluntary (e.g. Dewhurst et al., 2010) or electrically stimulated (e.g. de Ruiter et al., 1999) contractions independently, with comparisons then made based on the literature. A direct comparison of contractile properties between voluntary and stimulated contractions, in the same temperature conditions, could provide an explanation for the different effects seen between these two methods.

Therefore, the aim of this study was to investigate the effect of temperature change on the neuromechanical properties of the knee extensors, by comparing them when under the same temperature conditions at the same time. The quadriceps muscles were selected, as both a routinely assessed muscle group in the literature, as well as a crucial actor for locomotion-related movements. Our hypothesis was that a) RTD would remain unaffected by changes in temperature in voluntary contractions, and b) RTD would be reduced with cooling and increased with heating in electrically stimulated contractions.

Methods

Subjects

Fourteen male university students (mean ± SD: age, 20.6 ± 1.4 years; body mass, 71.8 ± 10.6 kg; stature, 1.77 ± 0.06 m; body mass index, 22.9 ± 3.3 kg/m^2) volunteered to take part in the study. The study conformed to the Declaration of Helsinki and subjects were fully informed of the testing procedures before giving their written, informed consent. Institutional ethical approval was obtained.

Subjects had no injuries and no known neuromuscular disorders. All subjects were at least moderately active, defined as meeting current UK physical activity guidelines of at least 150 minutes of moderate intensity exercise per week (Department of Health and Social Care, 2019). Two of the subjects withdrew before completion due to illness and injury, unrelated to the study, and their RTD results solely were excluded.

Experimental design

Subjects attended the laboratory for an initial session to allow familiarisation with the testing procedures, and have their body mass (balance beam scales; Seca 709, Hamburg, Germany), and height (stadiometer; Cranlea & Company, Birmingham, UK) measured. They were instructed to not perform any strenuous physical activity, and to not consume caffeine or alcohol in the 24 hours prior to each testing occasion.

All subjects subsequently visited the laboratory on three different occasions at least 24 hours apart between 09:10h-16:30h and completed testing for the three different experimental conditions (room, cold and hot temperature) in a randomized and counterbalanced order. During each condition, the subject spent 20 min at rest in each experimental condition temperature, before being seated on an isokinetic dynamometer (Biodex Medical Systems, Inc., Shirley, New York, USA) where a maximum voluntary contraction (MVC) and an electrically stimulated contraction (ESC) were performed, allowing measurement of torque and calculations or rate of torque development (RTD_{max}) and voluntary activation (VA). A schematic diagram of testing procedures appears in Figure 1.

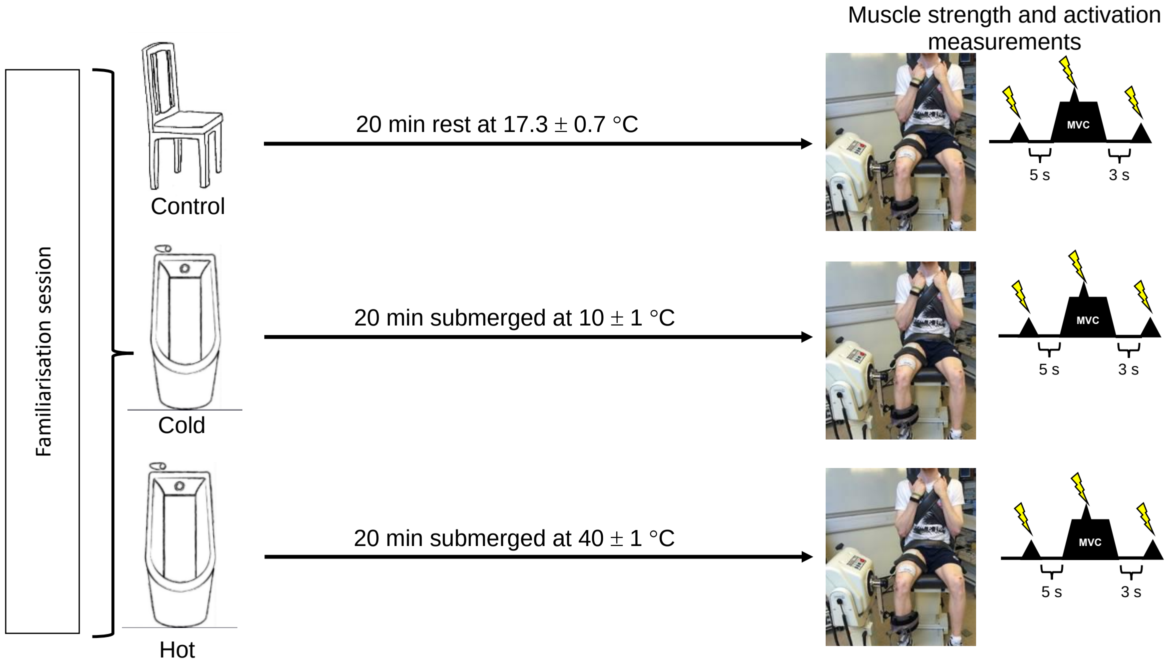

Figure 1. Schematic illustrating experimental conditions and testing procedure

Experimental conditions

For the control condition, subjects in their shorts sat quietly in room temperature of 17.3 ± 0.7°C. For the cold and hot conditions, subjects sat with the lower limbs completely submerged in water, at temperatures of 10 °C and 40 °C, respectively. Water temperature was monitored throughout the 20 minutes and kept to within 1 ºC of the relevant condition. Interaural temperature (InnooCare Forehead and Ear Thermometer, Innoo Tech, Guangdong, China) was monitored throughout the hot and cold conditions for data collection and subject safety. Interaural measurements followed recommendations for thermometer placement, recording from the same ear only and number of measurements (Childs et al., 1999). Whilst moving from the bath to the dynamometer, a rubber water bottle filled with water from the bath was strapped to the right leg over the quadriceps to minimise temperature changes. Skin temperature was measured with a handheld infrared thermometer (H1020, Helect, China) from the distal region of the vastus medialis, 10cm from insertion to the patella, at five-minute intervals during the resting phase, and once seated in the dynamometer to measure temperature changes whilst moving from bath to chair. The time between exiting the bath and commencing the test was <5 min.

Maximum voluntary contraction torque measurements

Strength of the right knee extensor muscles was measured as peak MVC torque from an isokinetic dynamometer with a knee, hip and ankle joint angle of 90°. The centre of rotation of the knee was aligned to the dynamometer’s axis and the subject’s pelvis, trunk and tested leg were firmly strapped to avoid extraneous movement that would affect torque and muscle activation (Bampouras et al., 2017). The dynamometer setup for each subject was recorded during the familiarisation session and used for all subsequent testing. The subjects were asked to exert maximum force against the dynamometer’s arm as fast as possible; 2-minute rest was allowed in between each effort. Verbal encouragement was given for encouraging maximum voluntary activation (Sahaly et al., 2001). Two isometric MVCs were performed, and if there was a coefficient of variation of >5% between the two MVCs peak torque, a third was performed and the mean of two closest MVCs was used for further analysis.

Electrically stimulated contraction torque measurements

With the subjects fixed in the dynamometer (see MVC torque measurements), ESC torque was measured via percutaneous muscle stimulation with the delivery of electrical stimulus to the knee extensors at rest and recording the torque achieved. Two 7.5 x 13-cm self-adhesive electrodes (ValuTrode, Axelgaard Manufacturing, Lystrup, Denmark) were placed at the proximal and distal regions of the quadriceps muscle group. The cathode was connected to the proximal electrode, with electrodes placed horizontally across the largest cross-sectional area of the vastus lateralis and medialis (Pietrosimone et al., 2011). Two stimuli of 200-μs pulse width, 10-ms inter-stimulus gap (doublets) and with the voltage set at 300 V, were generated by a constant current electrical stimulator (model DS7, Digitimer stimulator, Welwyn, Garden City, UK). The stimulation intensity used was that which generated at least one third of the average MVC torque (Bampouras et al., 2012) during rest; this was verified at each test condition. To explore the effect of potentiation on the experimental conditions, the stimulus was delivered to the muscle ~5s prior to the start of (Unpotentiated) and ~3s after the end of (Potentiated) the MVC; only the Unpotentiated and Potentiated twitches of the very first MVC were kept, in order to ensure the Unpotentiated twitch was truly unpotentiated.

Rate of torque development calculation

RTD_{max} was calculated as the torque change from onset of contraction to peak torque, divided by the amount of time needed to attain it. The onset of contraction was defined as 8N·m above baseline (as used by Aagaard et al., 2002) to minimise the impact of unintentional pre-emptive contractions on RTD results. This was done for both MVC and ESC torque. Further, to verify whether any temperature changes did not affect the start gradient of the RTD_{max}, RTD for the first 50 ms (RTD_{50}), 100 ms (RTD_{100}), 150 ms (RTD_{150}) and 200 ms (RTD_{200}) of the MVC were calculated.

Voluntary activation quantification

A stimulus identical to the one described in ‘ESC torque measurements’, was delivered to the muscle during the plateau phase of the MVC (superimposed twitch, SI). To account for any possible changes in the muscle-tendon unit compliance due to temperature changes, the central activation ratio method was used (Bampouras et al., 2006) and VA was calculated as (MVC torque / (MVC torque + SI torque) x 100), with the trial with the highest muscle activation capacity used for analysis. The VA of the two closest MVC trials (please see ‘MVC torque measurements’ earlier) was calculated and the average was kept for further analysis.

Data analysis

Normality of the data was assessed with the Shapiro-Wilks test and was confirmed for all variables. A 1 (variable) x 3 (experimental conditions) repeated measure analysis of variance (ANOVA) was used for examining for differences between the three experimental conditions for MVC torque and VA, followed with pairwise comparisons where differences were seen, with Holm-Bonferroni correction applied. MVC RTD-related variables were examined with 5 (RTD-related variables) x 3 (experimental conditions) repeated measure ANOVA. In addition, a 2 (Un/Potentiated ESC torque) x 3 (experimental conditions) repeated measures ANOVA was used to examine for differences in ESC torque and ESC RTD-related variables. Where differences were found, a univariate analysis followed with subsequent pairwise comparisons (with Holm-Bonferroni correction applied) to identify differences. Hedges’ *g* effect size was calculated for all significant pairwise comparisons and interpreted as small, moderate and large for values of 0.2, 0.5 and 0.8 respectively. Alpha level was set at 0.05 for all tests. Data processing was conducted with commercially available software (SPSS v24, IBM Systems, Chicago, USA).

Results

Following the experimental condition, skin temperature at testing was 19.3 ± 1.5 °C (Cold), 29.0 ± 1.2 °C (Control), 33.4 ± 1.2 °C (Hot). All ESC twitches achieved at least 1/3 of the MVC torque (average 36%, range 33% - 40%).

Maximum voluntary contraction and electrically stimulated contraction torque

There was no difference in MVC torque between the different experimental conditions. ESC peak torque showed a significant interaction between condition and contraction ($f_{2, 22} = 9.119$, $p = 0.006$). Potentiation increased peak torque over unpotentiated in all conditions but this change was reduced in the cold condition (small effect size; see Table 1). Subsequent analysis had no significant main effects for condition ($f_{1.73, 19.00} = 1.633$, $p = 0.222$) but significant main effects for potentiated/unpotentiated ($f_{1, 11} = 42.209$, $p = <0.001$).

Table 1. Peak torque results for both maximum voluntary contractions (MVC) and electrically stimulated contractions (ESC) for all three experimental conditions. Control (17 °C), Hot (40 °C), Cold (10 °C) are the three experimental conditions. Data is presented as mean ± SD. *denotes significant Unpotentiated to Potentiated difference. Hedge's *g* is included in brackets, where a significant difference was identified.

	MVC	**ESC**	
		Unpotentiated	Potentiated
Control (N•m)	264.2 ± 46.4	89.7 ± 10.6	100.2 ± 15.1*(0.80)
Hot (N•m)	266.8 ± 54.5	92.4 ± 12.3	105.6 ± 17.0*(0.89)
Cold (N•m)	268.7 ± 60.6	88.2 ± 20.0	92.6 ± 24.6*(0.20)

Maximum voluntary contraction and electrically stimulated contraction rate of torque development

MVC RTD-related variables showed no significant interaction ($f_{2.2, 24.32} = 0.162$, $p > 0.05$) between condition and time points, while there were no significant main effects of experimental condition on RTD. Significant main effects ($f_{1.19, 13.18} = 32.42$, $p < 0.001$) for RTD time point variables were found (see Table 2 specific differences). For ESC RTD, there was no significant interaction between condition and contraction ($f_{2, 22} = 1.238$, $p = 0.309$). Significant main effects for condition ($f_{2, 22} = 5.664$, $p = 0.010$) Follow up analysis showed that ESC RTD for the Hot condition (1025.0 ± 163.0 $N{\cdot}m \cdot s^{-1}$) was significantly higher ($p = 0.003$, $g = 0.99$) than control (872.3 ± 142.9 $N{\cdot}m \cdot s^{-1}$), but no other comparisons were significant (see Figure 2). Finally, a significant main effect ($f_{1, 11} = 14.260$, $p = 0.003$, $g = 0.59$) for contraction with Potentiated ESC RTD (981.7 ± 223.6 $N{\cdot}m \cdot s^{-1}$) was higher than Unpotentiated ESC RTD (891.7 ± 169.7 $N{\cdot}m \cdot s^{-1}$ (see Figure 2)).

Table 2. Rate of torque development (RTD) results for maximum voluntary contractions (MVC). Data is presented as mean ± SD. 50, 100, 150, 200 and max are time points on the torque-time trace (50ms, 100ms, 150ms, 200ms, and time to reach peak torque, respectively) for RTD calculation. The filled cells (diagonally) include the value of that RTD variable. The top half of the table include the difference (in raw units) between the respective RTD variables. The bottom half of the table includes the significance (p value) and ES (Hedge's *g*) values for each respective comparison.

	RTD_{50}	RTD_{100}	RTD_{150}	RTD_{200}	RTD_{max}
RTD_{50}	1137.7 ± 573.0 $N{\cdot}m{\cdot}s^{-1}$	-105.9 $N{\cdot}m{\cdot}s^{-1}$	-240.9 $N{\cdot}m{\cdot}s^{-1}$	-309.1 $N{\cdot}m{\cdot}s^{-1}$	-884.6 $N{\cdot}m{\cdot}s^{-1}$
RTD_{100}	p = 0.073, *g* = 0.23	1021.8 ± 418.0 $N{\cdot}m\ {\cdot}s^{-1}$	-125.0 $N{\cdot}m{\cdot}s^{-1}$	-193.2 $N{\cdot}m{\cdot}s^{-1}$	-768.7 $N{\cdot}m{\cdot}s^{-1}$
RTD_{150}	p = 0.02, *g* = 0.52	p = 0.012, *g* = 0.34	896.8 ± 310.9 $N{\cdot}m{\cdot}s^{-1}$	-68.2 $N{\cdot}m{\cdot}s^{-1}$	-643.7 $N{\cdot}m{\cdot}s^{-1}$
RTD_{200}	p = 0.02, *g* = 0.69	p = 0.01, *g* = 0.56	p = 0.01, *g* = 0.24	828.6 ± 258.7 $N{\cdot}m\ {\cdot}s^{-1}$	-575.5 $N{\cdot}m{\cdot}s^{-1}$
RTD_{max}	p = 0.009, *g* = 2.2	p = 0.009, *g* = 2.6	p = 0.009, v = 2.9	p = 0.009, *g* = 3.0	253.1 ± 75.0 $N{\cdot}m\ {\cdot}s^{-1}$

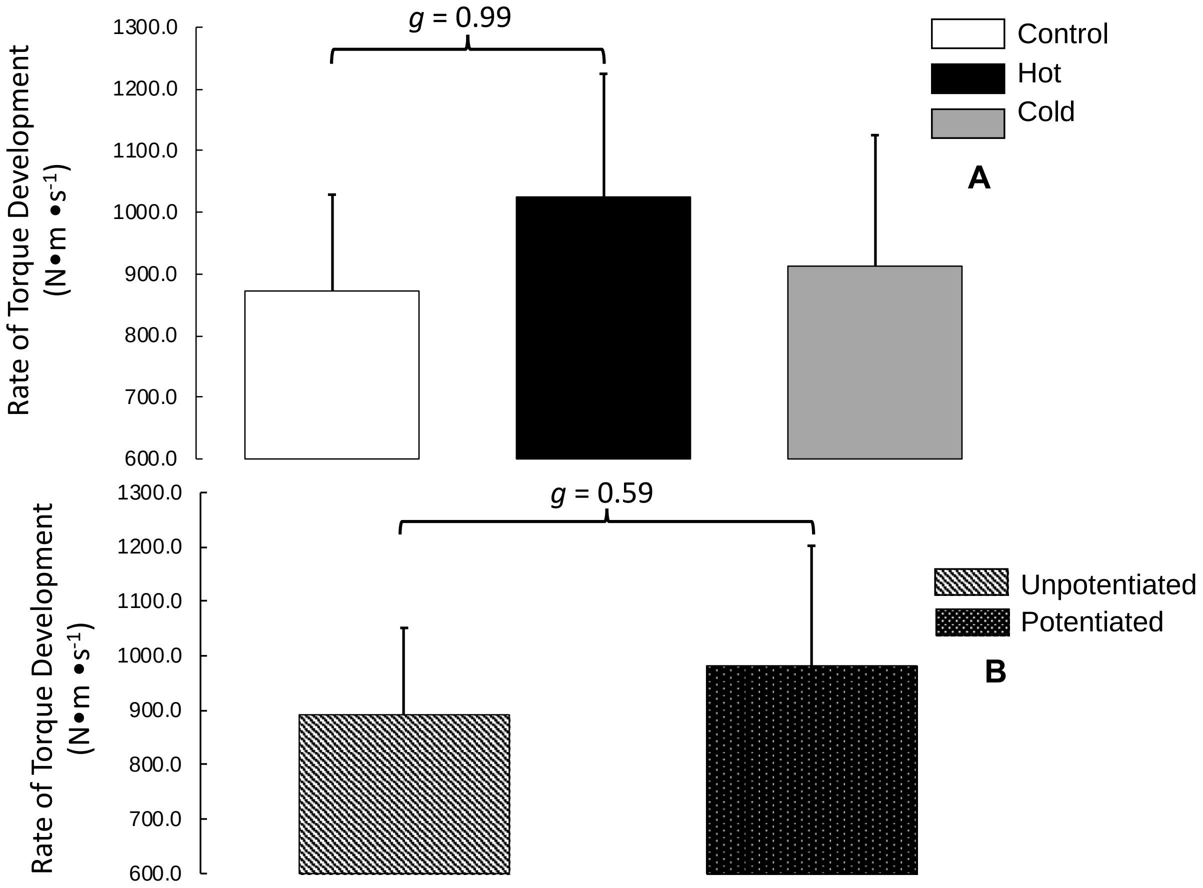

Figure 2. Rate of torque development (RTD) for electrically stimulated contractions (ESC) (Panel A: average of both twitches grouped by condition; Panel B: average of the three conditions grouped by potentiated and unpotentiated twitches). Brackets denote significance ($p < 0.05$). *g* denotes Hedge's *g* effect size.

Voluntary Activation

There was no significant ($p > 0.05$) difference for voluntary activation across the experimental conditions (Cold: 95.6 ± 2.3%, Control: 95.1 ± 4.0%, Hot: 94.2 ± 3.6%).

Discussion

The aim of the present study was to examine neuromechanical parameters relating to quadriceps muscles torque generation from voluntary and electrically stimulated contractions, directly following alterations in temperature conditions. The key findings were:

- None of the MVC-related parameters were affected by the changes in the temperature range examined, as neither MVC torque nor any of the RTD measures were significantly different between temperature conditions, thus confirming the first hypothesis.

- ESC-related parameters, however, only partially followed the same pattern as the MVC, with the ESC torque not affected by the temperature change, at the temperatures used, but the ESC RTD demonstrating a statistically significantly higher value for the Hot condition to the Control condition. Consequently, our second hypothesis was partially confirmed.

It has been shown before that the mechanical and neuromechanical behaviour of the quadriceps muscles differs, with the neural input altering the isometric joint torque generated (Bampouras et al., 2017). In the present study, we utilised the resting twitch (no neural input) to examine the effect of temperature on the mechanical behaviour of the muscle-tendon unit, while the neuromechanical behaviour was examined via an MVC. The difference in the pattern of changes suggests that neural input is affected by the temperature change in order to maintain constant RTD, as the only difference between ESC and MVC is in the Hot condition was the neural aspect present in the MVC. The effect of that input appears to be related to the shortening behaviour of the muscle-tendon unit. As the ESC torque was not different between conditions, the torque part in the RTD equation would remain unaltered, pointing to the time window in which maximum torque was reached as the reason for the change. This finding is probably due to the crossbridge cycling rate (Ball, 2020). Crossbridge cycling rate affects shortening velocity and rate of force development (Fitts et al., 1991), and temperature increases the cycling rate is theorised to lead to greater force generation of attached crossbridges (Ball, 2020; Offer and Ranatunga, 2015). Further, the changes of RTD must also be considered with the structure involved components in mind. The crossbridge cycling rate would increase the rate of force production, i.e. the rate at which the muscle alone could produce force. When the tendon is considered, increased temperature would result in more compliance (Petrofsky et al., 2013), thus having the opposite effect (i.e. reduced RTD). These points taken together suggest the increase in rate of force production due to a rise in temperature was sufficient to counteract the decrease in RTD induced by greater tendon plasticity, thus in total demonstrating an overall faster RTD.

The question then rises as to how, and why, the neural input during the MVC would alter the pattern seen from when the mechanical behaviour was examined in isolation. One possible reason would be via increased VA during the Control and Cold conditions or decreased VA during the Hot condition, as VA is key factor in RTD development (Aagaard et al., 2002; Maffiuletti et al., 2016). Our VA results, however, showed no such differences between conditions. Indeed, our VA findings are in line with suggestions by Thomas et al (2006) that local temperature changes do not affect VA. Another possibility would be the different time within which the MVC and ESC RTD were being measured in. With ESC torque being ~2/3 lower than MVC torque, the time to reach that level would be considerably shorter than the MVC torque. Therefore, the longer time window needed to reach peak torque during MVC, could mask such difference and result in the pattern seen. Nonetheless, our results show that the temperature conditions did not affect any of the RTD measures, regardless of the time window used (50ms, 100ms, 150ms, 200ms or time to maximum torque). Thus, the different time window length is also rejected as a reason for the findings. Consequently, it remains unclear at present why the neuromechanical behaviour at different temperatures is different to the mechanical behaviour. Potentially, one explanation could be offered by Gregory and Bickel (2005) who suggested that electromyostimulation recruits muscle fibres in a non-orderly fashion, in contrast to the Henneman principle. As RTD depends on which muscle fibres are recruited (Maffiuletti et al., 2016), different fibre recruitment (in particular, as MVC and ESC torque levels were considerably different in intensity) would likely result in different RTD values. Unfortunately, the absence of EMG data makes this notion speculative.

Post-activation potentiation is the phenomenon in which previous muscular contractions facilitate increased subsequent force generation (Hodgson et al., 2005), with the more accepted mechanism responsible for it being phosphorylation of myosin regulatory light chains (Requena et al., 2008). Although the effect can still be evident at 10 minutes, it is generally at maximum effect within 10s of the preceding contraction (Requena et al., 2008). The result of this effect could be different torque and / or RTD, depending on whether the twitch examined was unpotentiated or potentiated. To examine this hypothesis, along with the temperature effect, we utilised both an unpotentiated and potentiated twitch. Our results suggest that a) ESC torque is unaffected by temperature, and that b) potentiation from the MVC did occur on the Potentiated ESC torque. With regards to the first point, our results do not match findings by Moore et al (1990), who reported a linear relationship of myosin light chain phosphorylation with temperature. Although the similarity of the three ESC Potentiated torque values is statistically supported, the effect sizes from the pairwise comparison point to an increasing magnitude of effect of temperature. On the other hand, our potentiation results agree with Froyd et al (2013), who reported increased torque and RTD of a stimulated twitch following an MVC. Collectively, the results suggest that the use of a pre- or post-MVC twitch can alter the findings. We posit that such studies should standardise by using the potentiated twitch, as the situation a muscle would be unpotentiated are scarce, given that following an initial previous contraction (e.g. warm-up or conditioning contractions) it is likely to be potentiated.

Similarly to previous studies exploring the rate of force developing over the time period of a given task (e.g. Haff et al., 2015) we found that RTD value was reducing as the time window in which the force was measured in was increasing. The novel finding from the present study is that the temperatures examined did not affect the earlier RTD parameters (RTD_{50}, RTD_{100}, RTD_{150}, RTD_{200}) nor the RTD achieved at MVC (RTD_{max}). Therefore, it provides evidence for future studies to enable comparisons between RTD achieved from different temperature experimental conditions.

Although the study aimed to alter muscle temperature by using the water bath with cold and hot water, the extent to which this was achieved is unknown. As no muscle thermistors or other means (e.g. insulated discs) were available, all temperature references were based on skin temperature, which does not reflect muscle temperature. However, as our subjects were physically active individuals and relatively lean, we are confident that the 20 minutes in the water, with the temperature maintained at the required levels, were sufficient to alter muscle temperature to the experimentally required one (Petrofsky & Laymon, 2009). Sequentially, and while every effort was made to maintain the temperature when subjects came out of the bath, the ice packs and heat blankets are not as effective in maintaining the required temperature (Petrofsky & Laymon, 2009) and skin temperature was not maintained due the heat gradient, resulting in different skin temperatures at testing point than the planned ones. As heat dissipation in the muscle happens at a slower rate than at skin (Jutte et al., 2001), though, it is unlikely the muscle temperature altered away from the experimentally required one as much as the skin one did.

In conclusion, the present study found that environmental temperature changes, at the temperatures examined, do not affect the ability to generate maximum torque or any of the RTD parameters in maximum voluntary isometric contractions. In contrast, increased heat results in higher RTD in electrically stimulated contractions, most likely induced by reduced contraction time. The direct comparison of the voluntary and electrical stimulated contractions and the findings offer insight into the effects of temperature on the neuromechanical muscle function. The present findings can assist in better informing rehabilitation or training, where strategies employ temperature or electromyostimulation. When contrast therapy is being used (e.g. for treatment of exercise induced muscle damage (Bieuzen et al., 2013)), practitioners can be confident that the voluntary RTD, even shortly after the termination of a given temperature exposure, will not be affected and subsequent exercises can be performed safely. On the other hand, in situations where electromyostimulation is utilised without the inclusion of a voluntary contraction (e.g. for spinal cord injury patients (Hamid and Hayek, 2008)), there is potential for higher loading of the relevant structures, which in turn may increase the potential for tissue injury. Finally, the methods employed in the present study provide an avenue for future studies to explore the effects of similar interventions on the mechanical and neuromechanical behaviour of the musculotendinous unit.

Disclosure of Interest

The authors report no conflict of interest.

References

Aagaard, P., Simonsen, E. B., Andersen, J. L., Magnusson, P., & Dyhre-Poulsen, P. (2002). Increased rate of force development and neural drive of human skeletal muscle following resistance training. *Journal of Applied Physiology*, *93*(4), 1318–1326. https://doi.org/10.1152/japplphysiol.00283.2002

Andersen, L. L., & Aagaard, P. (2006). Influence of maximal muscle strength and intrinsic muscle contractile properties on contractile rate of force development. *European Journal of Applied Physiology*, *96*(1), 46–52. https://doi.org/10.1007/s00421-005-0070-z

Ball, D. (2020). Contrasting effects of heat stress on neuromuscular performance. Experimental Physiology, n/a(n/a). https://doi.org/10.1113/EP088191

Bampouras, T. M., Reeves, N. D., Baltzopoulos, V., Jones, D. A., & Maganaris, C. N. (2012). Is maximum stimulation intensity required in the assessment of muscle activation capacity? *Journal of Electromyography and Kinesiology*, *22*(6), 873–877. https://doi.org/10.1016/j.jelekin.2012.02.018

Bampouras, T. M., Reeves, N. D., Baltzopoulos, V., & Maganaris, C. N. (2006). Muscle activation assessment: Effects of method, stimulus number, and joint angle. *Muscle & Nerve*, *34*(6), 740–746. https://doi.org/10.1002/mus.20610

Bampouras, T. M., Reeves, N. D., Baltzopoulos, V., & Maganaris, C. N. (2017). Interplay between body stabilisation and quadriceps muscle activation capacity. *Journal of Electromyography and Kinesiology*, *34*, 44–49. https://doi.org/10.1016/j.jelekin.2017.03.002

Behm, D. G., Whittle, J., Button, D., & Power, K. (2002). Intermuscle differences in activation. *Muscle & Nerve*, *25*(2), 236–243. https://doi.org/10.1002/mus.10008

Bieuzen, F., Bleakley, C. M., & Costello, J. T. (2013). Contrast water therapy and exercise induced muscle damage: a systematic review and meta-analysis. *PloS One*, *8*(4), e62356–e62356. PubMed. https://doi.org/10.1371/journal.pone.0062356

Blazevich, A. J., Cannavan, D., Horne, S., Coleman, D. R., & Aagaard, P. (2009). Changes in muscle force–length properties affect the early rise of force in vivo. *Muscle & Nerve*, *39*(4), 512–520. https://doi.org/10.1002/mus.21259

Buller, A. J., Kean, C. J., Ranatunga, K. W., & Smith, J. M. (1984). Temperature dependence of isometric contractions of cat fast and slow skeletal muscles.

The Journal of Physiology, *355*, 25–31. PubMed. https://doi.org/10.1113/jphysiol.1984.sp015403

Childs, C., Harrison, R., & Hodkinson, C. (1999). Tympanic membrane temperature as a measure of core temperature. *Archives of Disease in Childhood*, *80*(3), 262. https://doi.org/10.1136/adc.80.3.262

Clarke, D. H., & Royce, J. (1962). Rate of muscle tension development and release under extreme temperatures. *Internationale Zeitschrift Für Angewandte Physiologie Einschließlich Arbeitsphysiologie*, *19*(5), 330–336. https://doi.org/10.1007/BF00694275

Cornwall, M. W. (1994). Effect of temperature on muscle force and rate of muscle force production in men and women. *Journal of Orthopaedic & Sports Physical Therapy*, *20*(2), 74–80. https://doi.org/10.2519/jospt.1994.20.2.74

de Ruiter, C. J., Jones, D. A., Sargeant, A. J., & de Haan, A. (1999). Temperature effect on the rates of isometric force development and relaxation in the fresh and fatigued human adductor pollicis muscle. *Experimental Physiology*, 84(6), 1137–1150. https://doi.org/10.1111/j.1469-445X.1999.01895.x

Department of Health and Social Care. (2019). *UK Chief Medical Officers' Physical Activity Guidelines*. https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/832868/uk-chief-medical-officers-physical-activity-guidelines.pdf

Dewhurst, S., Macaluso, A., Gizzi, L., Felici, F., Farina, D., & De Vito, G. (2010). Effects of altered muscle temperature on neuromuscular properties in young and older women. *European Journal of Applied Physiology*, *108*(3), 451–458. https://doi.org/10.1007/s00421-009-1245-9

Fitts, R. H., McDonald, K. S., & Schluter, J. M. (1991). The determinants of skeletal muscle force and power: Their adaptability with changes in activity pattern. *Proceedings of the NASA Symposium on the Influence of Gravity and Activity on Muscle and Bone*, *24*, 111–122. https://doi.org/10.1016/0021-9290(91)90382-W

Folland, J. P., Buckthorpe, M. W., & Hannah, R. (2014). Human capacity for explosive force production: Neural and contractile determinants. *Scandinavian Journal of Medicine & Science in Sports*, *24*(6), 894–906. https://doi.org/10.1111/sms.12131

Folland, J. P., & Williams, A. G. (2007). Methodological issues with the interpolated twitch technique. *Journal of Electromyography and Kinesiology*, *17*(3), 317–327. https://doi.org/10.1016/j.jelekin.2006.04.008

Froyd, C., Beltrami, F. G., Jensen, J., & Noakes, T. D. (2013). Potentiation increases peak twitch torque by enhancing rates of torque development and relaxation. *Journal of Human Kinetics*, *38*, 83–94. PubMed. https://doi.org/10.2478/hukin-2013-0048

Gossen, E. R., Allingham, K., & Sale, D. G. (2001). Effect of temperature on post-tetanic potentiation in human dorsiflexor muscles. *Canadian Journal of Physiology and Pharmacology*, *79*(1), 49–58. https://doi.org/10.1139/y00-107

Gregory, C. M., & Bickel, C. S. (2005). Recruitment patterns in human skeletal muscle during electrical stimulation. *Physical Therapy*, *85*(4), 358–364. https://doi.org/10.1093/ptj/85.4.358

Haff, G. G., Ruben, R. P., Lider, J., Twine, C., & Cormie, P. (2015). A comparison of methods for determining the rate of force development during isometric midthigh clean pulls. *The Journal of Strength & Conditioning Research*, *29*(2). https://journals.lww.com/nsca-jscr/Fulltext/2015/02000/A_Comparison_of_Methods_for_Determining_the_Rate.14.aspx

Harridge, S. D. R., Bottinelli, R., Canepari, M., Pellegrino, M. A., Reggiani, C., Esbjörnsson, M., & Saltin, B. (1996). Whole-muscle and single-fibre contractile properties and myosin heavy chain isoforms in humans. *Pflügers Archiv*, *432*(5), 913–920. https://doi.org/10.1007/s004240050215

Hodgson, M., Docherty, D., & Robbins, D. (2005). Post-activation potentiation. *Sports Medicine*, *35*(7), 585–595. https://doi.org/10.2165/00007256-200535070-00004

Jutte, L. S., Merrick, M. A., Ingersoll, C. D., & Edwards, J. E. (2001). The relationship between intramuscular temperature, skin temperature, and adipose thickness during cryotherapy and rewarming. *Archives of Physical Medicine and Rehabilitation*, *82*(6), 845–850. https://doi.org/10.1053/apmr.2001.23195

Maffiuletti, N. A., Aagaard, P., Blazevich, A. J., Folland, J. P., Tillin, N., & Duchateau, J. (2016). Rate of force development: physiological and methodological considerations. *European Journal of Applied Physiology*, *116*(6), 1091–1116. PubMed. https://doi.org/10.1007/s00421-016-3346-6

Moore, R. L., Palmer, B. M., Williams, S. L., Tanabe, H., Grange, R. W., & Houston, M. E. (1990). Effect of temperature on myosin phosphorylation in mouse skeletal muscle. *American Journal of Physiology-Cell Physiology*, *259*(3), C432–C438. https://doi.org/10.1152/ajpcell.1990.259.3.C432

Offer, G., & Ranatunga, K. W. (2015). The endothermic ATP hydrolysis and crossbridge attachment steps drive the increase of force with temperature in isometric and shortening muscle. *The Journal of Physiology*, *593*(8), 1997–2016. https://doi.org/10.1113/jphysiol.2014.284992

Petrofsky, J. S., & Laymon, M. (2009). Heat transfer to deep tissue: the effect of body fat and heating modality. *Journal of Medical Engineering & Technology*, *33*(5), 337–348. https://doi.org/10.1080/03091900802069547

Petrofsky, J. S., Laymon, M., & Lee, H. (2013). Effect of heat and cold on tendon flexibility and force to flex the human knee. *Medical Science Monitor*, *19*, 661–667. https://doi.org/10.12659/MSM.889145

Pietrosimone, B. G., Selkow, N. M., Ingersoll, C. D., Hart, J. M., & Saliba, S. A. (2011). Electrode type and placement configuration for quadriceps activation evaluation. *Journal of Athletic Training*, *46*(6), 621–628. PubMed. https://doi.org/10.4085/1062-6050-46.6.621

Pijnappels, M., Bobbert, M. F., & van Dieën, J. H. (2005). Control of support limb muscles in recovery after tripping in young and older subjects. *Experimental Brain Research*, *160*(3), 326–333. https://doi.org/10.1007/s00221-004-2014-y

Ranatunga, K. W., Sharpe, B., & Turnbull, B. (1987). Contractions of a human skeletal muscle at different temperatures. *The Journal of Physiology*, *390*, 383–395. PubMed. https://doi.org/10.1113/jphysiol.1987.sp016707

Requena, B., Gapeyeva, H., García, I., Ereline, J., & Pääsuke, M. (2008). Twitch potentiation after voluntary versus electrically induced isometric contractions in human knee extensor muscles. *European Journal of Applied Physiology*, *104*(3), 463. https://doi.org/10.1007/s00421-008-0793-8

Sahaly, R., Vandewalle, H., Driss, T., & Monod, H. (2001). Maximal voluntary force and rate of force development in humans – importance of instruction. *European Journal of Applied Physiology*, *85*(3), 345–350. https://doi.org/10.1007/s004210100451

Thomas, M. M., Cheung, S. S., Elder, G. C., & Sleivert, G. G. (2006). Voluntary muscle activation is impaired by core temperature rather than local muscle temperature. *Journal of Applied Physiology*, *100*(4), 1361–1369. https://doi.org/10.1152/japplphysiol.00945.2005

Tillin, N., Jimenez-Reyes, P., Pain, M. T. G., & Folland, J. P. (2010). Neuromuscular performance of explosive power athletes versus untrained individuals. *Medicine & Science in Sports & Exercise*, *42*(4). https://journals.lww.com/acsm-msse/Fulltext/2010/04000/Neuromuscular_Performance_of_Explosive_Power.21.aspx

Tillin, N., Pain, M. T. G., & Folland, J. P. (2013). Explosive force production during isometric squats correlates with athletic performance in rugby union players. *Journal of Sports Sciences*, *31*(1), 66–76. https://doi.org/10.1080/02640414.2012.720704

Wahr, P. A., & Rall, J. A. (1997). Role of calcium and cross bridges in determining rate of force development in frog muscle fibers. *American Journal of Physiology-Cell Physiology*, *272*(5), C1664–C1671. https://doi.org/10.1152/ajpcell.1997.272.5.C1664