1 **Title page**

2 **Title of the article**

3 Progressive hyperthermia elicits distinct responses in maximum and rapid torque production.

4 **Author's names**

5 Ralph, J. F. H. Gordon [a]; Christopher, J. Tyler [a]; Federico, Castelli [a]; Ceri, E. Diss [a]; Neale, A. Tillin [a];

6 **Institution and affiliations**

7 [a] Department of Life Sciences, University of Roehampton, Holybourne Avenue, London, SW15 4JD,

8 England, UK.

9 **Corresponding author contact details**

10 Ralph Gordon: gordonr@roehampton.ac.uk

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Abstract

Objectives

To investigate the effect of progressive whole-body hyperthermia on maximal, and rapid voluntary torque production, and their neuromuscular determinants.

Design

Repeated measures, randomised.

Methods

Nine participants performed sets of neuromuscular assessments in HOT conditions (~50°C, ~35% relative humidity) at rectal temperatures (T_{re}) of 37, 38.5 and 39.5°C and in CON conditions (~22°C, ~5% relative humidity) at a T_{re} of ~37°C and pre-determined comparative time-points. Electrically evoked twitch (single impulse) and octet (8 impulses at 300 Hz) responses were measured at rest. Maximum voluntary torque (MVT), surface electromyography (EMG) normalised to maximal M-wave, and voluntary activation (VA) were measured during 3-5 s isometric maximal voluntary contractions. Rate of torque development (RTD) and normalised EMG were measured during rapid voluntary isometric contractions from rest.

Results

All neuromuscular variables were unaffected by time in CON. In HOT, MVT, normalised EMG at MVT and VA were lower at 39.5°C compared to 37°C ($p<0.05$). Early- (0-50 ms) and middle- (50-100 ms) phase voluntary RTD were unaffected by increased T_{re} ($p>0.05$), despite lower normalised EMG at T_{re} 39.5°C ($p<0.05$) in rapid contractions. In contrast, late-phase (100-150 ms) voluntary RTD was lower at 38.5°C and 39.5°C compared to 37°C ($p<0.05$) in HOT. Evoked twitch and octet RTD increased with increased T_{re} ($p<0.05$).

Conclusions

Hyperthermia reduced late-phase voluntary RTD, likely due to reduced neural drive and the reduction in MVT. In contrast, early- and middle-phase voluntary RTD were unaffected by hyperthermia, likely due to the conflicting effects of reduced neural drive but faster intrinsic contractile properties.

Key words

Contractile properties, excitation contraction coupling, heat, muscle contraction, muscle strength, rate of torque development.

Introduction

Whole-body hyperthermia can reduce maximum voluntary torque (MVT) during sustained (>30 s)[1] and brief (3-5 s) maximum voluntary contractions (MVCs)[2-4], and the magnitude of reduction appears proportional to thermal strain up to body temperatures of 39.5°C[2,4,5]. The effects of progressive hyperthermia on voluntary rate of torque development (RTD) are unknown, yet RTD is considered more functionally relevant than MVT for rapid human movements[6]. Knee-extensor voluntary RTD is reduced following tennis match-play in the heat[7]; however, it was unclear if this reduction was due to the effects of hyperthermia or exercise-induced fatigue. Passive heating study models are useful for isolating the effects of hyperthermia on neuromuscular function, from the effects of exercise.

The hyperthermia-induced decline in MVT appears due to an inability of the nervous system to voluntarily drive the muscle's force producing capacity[2-4], with increased thermal strain causing reductions in voluntary activation (VA) at the torque plateau of MVCs[2,4,5]. MVT is an important determinant of voluntary RTD over late phases (0-150 and 100-150 ms) of contraction from rest[8,9], so the hyperthermia-induced declines in MVT may also reduce late-phase voluntary RTD. Early (0-50 ms) and middle (0-100 and 50-100 ms) phases of voluntary RTD are mainly determined by neural drive[8,9] and in the intrinsic capacity of the muscle for RTD (electrically evoked involuntary RTD)[9,10]. It is unknown whether hyperthermia reduces neural drive for RTD in a similar way to that observed at the plateau of an MVC[2,4,5], but if it did, this might reduce early- and middle-phase voluntary RTD. However, increased muscle temperature, which will coincide with hyperthermia, increases involuntary RTD[11,12], and this could negate any detrimental effects of reduced neural drive, thus maintaining or even increasing early- and middle-phase voluntary RTD. It therefore appears the effects of hyperthermia on voluntary RTD will be time-phase dependent.

The aims of this study were to investigate the effects of progressive whole-body hyperthermia on MVT, voluntary RTD, and their neuromuscular determinants. It was hypothesised that (1) early- and middle-phase voluntary RTD would remain unaffected by whole-body hyperthermia, likely due to the counter effects of reduced early-phase neural drive and improved electrically evoked contractile responses; and (2) late-phase voluntary RTD would decline progressively with whole-body hyperthermia, due to the associated declines in neural drive and MVT.

Methods

Participants. Nine healthy, active males (27.7±4.1 years; 80.3±12.0 kg; 180.4±6.6 cm) participated. *A priori* power analysis was performed for sample size estimation using G*Power[13], based on the passive heating VA data from Périard et al., (2014)[5] and a large effect size of d = 1.1. Participants were informed of any risks/discomforts associated with the experiment before giving their informed consent. All procedures were approved by the Ethical Advisory Committee (LSC16/187) and were performed in accordance with the *Declaration of Helsinki*.

Overview. Participants completed a familiarisation session and two, randomly ordered experimental trials in a walk-in environmental chamber (Weiss Technik, Wales, UK). Experimental trials were a thermoneutral (CON; 22.4±0.7°C, 36.7±4.8% relative humidity) and hot (HOT; 48.8±1.1°C, 33.9±5.5% relative humidity) condition. Visits were separated by 5-7 days but completed at the same time of day for each participant. Participants refrained from strenuous exercise and alcohol consumption for 24 h, and caffeine 12 h prior to each session.

In each experimental trial, four sets of the same neuromuscular protocol (Appendix. A) were completed with the knee extensors of the preferred leg. Each set commenced at a pre-determined time-point in CON (5, 50, 83 and 117 min after entering the environmental chamber), and upon reaching a pre-determined rectal temperature (T_{re}) in HOT (37, 38.5, 39.5°C), and at volitional termination or the ethical cut-off limit

of 40.5°C (T_{lim}), which ever occurred first. Participants were immediately removed from the environmental chamber and cooled in the ambient conditions of the laboratory using chilled water (to drink) and an electric fan blowing cool air, if any of the following criteria were met; participant requested to withdraw, participant showed signs of significant distress, discomfort or illness, including but not limited to dyspnoea, nausea, vomiting, rapid declines in either HR or blood pressure, fainting or dizziness, the principle investigator deemed it necessary for any other reason. The pre-determined T_{re} were achieved via a combination of light physical activity and passive heating (*see Protocol below)*. Time-points in CON were chosen to match the estimated times to target T_{re} in HOT, based on an individual data set obtained from pilot testing.

Torque. Participants sat in an isometric strength-testing chair[6] with hip and knee angles fixed at 100º and 105º respectively (full extension: 180°). An ankle strap, in series with a load cell (FSB-1.5kN, Force Logic, Reading, UK) was secured 4 cm proximal to the medial malleolus. The force signal was amplified (x375), sampled at 2000 Hz (Mirco3 1401 and Spike2 v.8; CED, Cambridge, UK), filtered offline (fourth-order low-pass Butterworth, 500 Hz cut-off), corrected for limb weight, and multiplied by the external moment arm[6] to calculate torque.

Surface electromyography (EMG). The skin was prepared by shaving, cleaning (70% ethanol), and lightly abrading. Two separate bi-polar silver-silver-chloride gel-electrode configurations (2 cm diameter, and 2 cm inter-electrode distance; Dual Electrode, Noraxon, Arizona, USA) were placed over the belly of the rectus femoris, vastus lateralis and vastus medialis (6 bi-polar signals in total)[14]. Signals were sampled at 2000 Hz via the same equipment as force, amplified (x500), and transmitted wirelessly to a desktop receiver (TeleMYO DTS, Noraxon, Arizona, USA). Off-line, EMG signals were filtered (fourth-order Butterworth, band-pass, 6-500 Hz) and time-corrected for the 156 ms delay in the Noraxon system.

Electrical stimulation. Square-wave pulses (200 µs duration) were delivered (DS7AH, Digitimer, Hertfordshire, UK) over the femoral nerve to evoke twitch (single pulse), doublet (two pulses at 100 Hz) and octet (eight pulses at 300 Hz) contractions. Electrode location, and determination of supra-maximum

stimulation intensity for twitch responses were established in the familiarisation session by the same investigator, as per Gordon et al., (2020)[15], and remained constant for the experimental trials.

Thermoregulation and perception. A rectal thermistor (REC-U-VL30, Grant Instruments, Cambridge, UK) self-inserted ~10 cm past the anal sphincter, measured T_{re}. Skin thermistors (EUS-U-VL3-0, Grant Instruments, Cambridge, UK) were secured over the skin with a transparent dressing (Tegaderm, 3M, Minnesota, USA) and surgical tape, to assess local skin temperature. Mean weighted skin temperature ($\overline{T}_{sk}$) was calculated[16] from the right-side: suprasternal notch, flexi carpi radials, gastrocnemius and rectus femoris (T_{th}). Heart rate (HR) was recorded with a heart rate monitor (F3, Polar Electro, UK, Ltd). Whole-body thermal sensation (TS) was rated using a 9-point scale from 0 (unbearably cold) to 8 (unbearably hot)[17]. Nude body mass was recorded (Robusta 813, Seca, Birmingham, UK) pre- and post-, and water (non-chilled) was provided *ad libitium* during each experimental trial. Fluid loss was estimated from body mass changes, after correcting for fluid intake and urine output.

Protocol. After instrumentation of thermistors and EMG electrodes, participants put on an impermeable rain jacket, entered the walk-in environmental chamber, and sat in the strength-testing chair. Electrical stimulation electrodes were attached, and the first neuromuscular set (Appendix. A) completed. Next, participants put on impermeable trousers and performed light physical activity on a non-motorised treadmill (Curve 1.5, Woodway, Germany) to facilitate internal heat production without inducing fatigue[18]. Participants started at 6 $km \cdot h^{-1}$, with speed reduced by 1 $km \cdot h^{-1}$ every 5 min for 20 min. Participants then rested (semi-supine or seated) for the remainder of the trial, interspersed by the completion of each neuromuscular set. No further activity was completed on the treadmill. The same physical activity was performed in CON, to control for any effects of exercise-induced fatigue caused by the walking, which would be minimal given the low intensity and long-time course between the end of walking and start on the second neuromuscular set. Each neuromuscular set (Appendix. A) involved two twitch and two octet contractions, followed by 10-15 rapid voluntary contractions in which participants pushed as "fast and hard" as possible for 1.5 s[19]. Next, participants performed 3 MVCs where they pushed as "hard" as possible for

3-5 s. On the second MVC, two doublet stimuli were evoked 2 s apart at the plateau of the force time curve, with a third doublet evoked from rest after the contraction. Strong verbal encouragement was given during all voluntary contractions. Time to complete a neuromuscular set was on average 333±20 s (CON) and 322±28 s (HOT). Each set in HOT commenced at a T_{re} ~0.04°C below the pre-determined temperature, to account for T_{re} increasing throughout the set. The order of measurements in each neuromuscular set was chosen from the least to the most likely activity to cause fatigue or potentiation[20], thus limiting the effects of these factors on our results.

Data analyses. MVT was the greatest voluntary torque recorded in either the rapid contractions or MVCs. Neural drive at MVT (i.e., at MVC plateau) was assessed by: (1) determining VA (VA=[1–superimposed doublet amplitude/resting doublet amplitude]*100) from the MVC involving superimposed doublet (mean of the two superimposed doublets) ; and (2) from EMG RMS amplitude at MVT (EMG_{MVT}; 500 ms epoch), normalised to M_{max}, and averaged across the 6 EMG sites. Using established methods[19], rapid voluntary torque at 50 ms (T_{50}), 100 ms (T_{100}) and 150 ms (T_{150}) from torque onset, and voluntary RTD over three sequential 50 ms time epochs (RTD_{0-50}, RTD_{50-100}, $RTD_{100-150}$), was determined from the rapid contractions. In the same rapid contractions, RMS EMG amplitude was calculated over 0-50 ms (EMG_{0-50}), 0-100 ms (EMG_{0-100}), and 0-150 ms (EMG_{0-150}) from EMG onset, normalised to M_{max}, and averaged across the 6 EMG sites. Voluntary electromechanical delay (EMD) was the time difference between the earliest EMG onset and force onset. Each twitch and octet response was analysed for peak torque (PT), torque at 50 ms (T_{50}), peak RTD (pRTD), time to PT (TPT) and half-relaxation time (HRT). Involuntary EMD during the twitch contractions was the time between M-wave onset and torque onset. Torque and EMG signal onsets (voluntary and evoked) were identified using an established visual identification method[19].

Data are reported as mean±SD. Dependant variables, were assessed via paired samples T-tests (body mass change only) or two-way repeated measures ANOVA (all other variables); the latter assessing main effects of condition (HOTvs.CON) and neuromuscular set (i.e., Set 1=37°C/5 min, Set 2=38.5°C/50 min, and Set 3=39.5°C/83 min). Data were checked for normal distribution, and violations of sphericity were corrected

for using the Greenhouse-Geisser adjustment. Following a significant F-value, pairwise differences were identified using stepwise Bonferroni-corrected paired T-tests within and between conditions. In HOT, only *n*=4 completed a fourth set of the neuromuscular protocol due to the high thermal strain, so Set 4 (i.e., T_{lim}/117 min) data were not included in the ANOVAs but are presented. The alpha was set at $p<0.05$. Statistical analyses were completed using SPSS version 24 (Inc., Chicago, IL).

Results

Data from all the ANOVAs are presented in Appendix. B, and only paired comparisons are reported in the Results.

T_{re} rose more slowly during HOT (0.017 ± 0.003°C·min^{-1}) than estimated thus, times to achieve the target temperatures in HOT (T_{re} 38.5°C=75±15 min, T_{re} 39.5°C=138±32 min and T_{lim}=145±13 min) were longer than the corresponding time points in CON (50, 83 and 117 min).

T_{re}, $\overline{T}_{sk}$, T_{th}, HR and TS all increased in each Set within HOT ($p\leq0.006$; Appendix. C), except HR which was not different at T_{re} 38.5°C and 39.5°C ($p=0.99$). During Set 1, T_{re} was similar ($p=0.480$) between conditions, but $\overline{T}_{sk}$, T_{th}, HR and TS were greater in HOT than CON ($p\leq0.007$). All of these variables were greater in HOT during later sets ($p<0.001$; Appendix. C).

There was no difference in body mass change between conditions ($p=0.095$; HOT, -0.43±0.95%; CON, 0.04±0.48%).

MVT decreased during HOT at T_{re} 38.5°C and 39.5°C by 8% and 12% respectively, compared with T_{re} 37°C ($p\leq0.040$). MVT was 8% greater in HOT than CON in Set 1 ($p=0.004$; Figure. 1). No other within- or between-condition differences in MVT were observed ($p\geq0.105$). While not included in the statistical analysis, MVT was ~4% lower at T_{lim} than T_{re} 39.5°C in *n*=4.

183 $T_{50,}$ T_{100} and T_{150} were unchanged in HOT ($p \geq 0.121$; Figure. 2A-C), as were RTD_{0-50} and RTD_{50-100} ($p > 0.99$;
184 Figure. 2D-E), but $RTD_{100-150}$ decreased by 22% and 30% at T_{re} 38.5°C and T_{re} 39.5°C, respectively,
185 compared with T_{re} 37°C ($p \leq 0.019$; Figure. 2F). Between conditions, $T_{50,}$ T_{100}, T_{150}, and RTD_{0-50} were 7-29%
186 greater in HOT than CON at Set 1 ($p \leq 0.004$), whilst $RTD_{100-150}$ was lower in HOT than CON during Set 2
187 and 3 ($p \leq 0.014$). No other within- or between-condition differences in rapid voluntary torque or RTD were
188 observed ($p \geq 0.067$). While not included in the statistical analysis, $T_{50,}$ T_{100}, and T_{150} were 10-18% lower at
189 T_{lim} than T_{re} 39.5°C in n=4.

190 In HOT, EMG_{MVT} was lower at T_{re} 38.5°C and 39.5°C compared with T_{re} 37°C ($p \leq 0.004$; Figure. 1B),
191 whilst VA was lower at T_{re} 39.5°C than at 37°C and 38.5°C ($p \leq 0.050$; Figure. 1C). Between conditions,
192 EMG_{MVT} was lower in HOT than CON at Sets 2 and 3 ($p \leq 0.004$), whilst VA was lower in HOT than CON
193 at Set 3 ($p = 0.006$). No other within- or between-condition differences in EMG_{MVT} or VA were observed
194 ($p \geq 0.123$).

195 EMG_{0-50}, EMG_{0-100} and EMG_{0-150} were lower at T_{re} 39.5°C than 38.5°C during HOT ($p \leq 0.021$; Figure. 2G-
196 I). Between conditions, EMG_{0-100} and EMG_{0-150} (Figure. 2H-I) were lower in HOT than CON at Sets 2 and
197 3 ($p \leq 0.025$). All other between- and within-condition comparisons for EMG_{0-50}, EMG_{0-100} and EMG_{0-150}
198 were similar ($p \geq 0.114$).

199 Involuntary EMD was shorter within HOT at T_{re} 39.5°C than 37°C ($p = 0.012$), and between conditions, was
200 shorter in HOT than CON at Sets 2 and 3 ($p \leq 0.017$; Appendix. D). Voluntary EMD was shorter in Set 3
201 ($p = 0.043$; Appendix. D) during HOT than CON. There were no other between- or within-condition
202 differences for involuntary of voluntary EMD ($p \geq 0.068$).

203 In HOT, twitch and octet PT, T_{50} and pRTD all increased with increased T_{re} ($p \leq 0.028$; Table 1). Octet TPT
204 shortened with each increase in T_{re} ($p \leq 0.040$), whilst twitch and octet HRT were shorter at T_{re} 38.5°C
205 ($p \leq 0.002$) and 39.5°C ($p \leq 0.005$) compared with 37°C (Table 1). Between conditions, octet T_{50} and pRTD
206 were greater in HOT than CON at Set 1 ($p \leq 0.045$), and at later Sets, twitch, and octet PT, T_{50} and pRTD

were all greater in HOT than CON ($p \leq 0.010$; Table 1), with the exception of octet PT at Set 2 ($p=0.069$). Twitch TPT was faster in HOT than CON at Set 3 ($p=0.013$), whilst twitch and octet HRT were faster in HOT than CON in Sets 2 and 3 ($p \leq 0.015$; Table 1). No other within- or between-condition differences in twitch or octet variables were observed ($p \geq 0.052$).

Discussion

This study investigated the effects of progressive whole-body hyperthermia on maximum and rapid voluntary torque production and found distinct responses in these neuromuscular characteristics. MVT and late-phase RTD ($RTD_{100\text{-}150}$) decreased with increased T_{re}, likely due to decreased neural drive at the MVC torque plateau, evidenced by declines in normalised EMG_{MVT} and VA, thus confirming our second hypothesis. Conversely, early- (0-50 ms) and middle- (50-100 ms) phases of RTD, as well as rapid torque production at all discrete time points, were preserved throughout HOT, despite reduced neural drive during the first 0-100 and 0-150 ms of rapid contraction, confirming our first hypothesis. This preserved rapid voluntary torque was likely due to the faster contractile properties with increased T_{re}, which may have negated the reduced neural drive. A secondary finding was the shortening of involuntary EMD with increased T_{re}.

Progressive hyperthermia reduced MVT, despite an increase in the muscle's intrinsic capacity to produce force, characterised by increased twitch and octet PT. This, coupled with the declines in normalised EMG_{MVT} and VA, suggests the decline in MVT is likely due to a reduced ability of the nervous system to voluntarily utilise the muscle's force capacity. Other studies have passively elicited comparable levels of thermal strain and observed similar declines in MVT and VA during brief MVCs[2,4,5]. Although not included in the statistical analysis, the inclusion of the neuromuscular assessment set at T_{lim} ($n=4$), corresponding to a T_{re} ~40.1°C showed mean MVT further decreased between T_{re} 39.5°C and ~40.1°C, providing preliminary evidence of continued declines in MVT with thermal strain >T_{re} 39.5°C.

Voluntary T_{50} and T_{100}, as well as RTD_{0-50} and RTD_{50-100}, were unaffected by increases in T_{re}, despite evidence of reduced neural drive based on the following two observations. (I) Declines of normalised EMG over all measured time windows (0-50, 0-100 and 0-150 ms). (II) No change in voluntary rapid torque production, despite an increase in maximum RTD capacity, denoted by increased Octet T_{50}, suggesting a decline in the neural ability to utilise the available RTD capacity. Given neural drive is an important determinant of rapid torque, particularly in the early phases of contraction[9,10], it is interesting that voluntary rapid torque measurements did not also decrease with increased T_{re}. However, twitch T_{50}, representative of the force capacity of the muscle at low Ca^{+} concentrations, is also an important determinant of early phase rapid torque[8,9], so the increase in twitch T_{50} with increased T_{re} likely explains the preserved voluntary T_{50} and RTD_{0-50}. Likewise, the increase in octet T_{50} with increased T_{re} likely explains the preserved RTD_{50-100} and voluntary $T_{100,}$ because the maximum RTD capacity elicited during the octets, is an important determinant of middle-phase (50-100 ms) voluntary RTD[9]. Voluntary T_{150} was also preserved with increased T_{re}, which is unexpected given a decrease in $RTD_{100-150}$. However, $RTD_{100-150}$ is influenced by both MVT and prior torques (i.e., T_{50} and T_{100})[9], so variable responses in these prior torques coupled with a systematic decline in MVT could explain a lack of statistical change on T_{150}. Our preliminary evidence suggests T_{150} is eventually reduced with sufficient thermal strain, via the decline in T_{150} at T_{re} ~40°C in the four participants who reached this stage, which is consistent with the further declines in MVT – the main determinant of late-phase rapid torque[9] – in those participants.

The mechanisms for reduced neural drive in hot environmental conditions are not fully understood but may involve a complex interplay between reduced cerebral blood flow[21], cognitive function[22] and cerebral dopamine[23], increased brain temperature[24], and/or inability to increase motor unit rate coding to address faster muscle relaxation rates causing reduced force summation[3]. Whilst reduced neural drive during whole-body hyperthermia have been widely reported at the MVC force plateau[2,4,25], this is the first study to provide evidence of reduced neural drive during the rising torque-time curve of rapid voluntary contractions.

The faster twitch and octet contractile properties (increased involuntary T_{50}, pRTD and HRT) were likely caused by increases in muscle temperature improving excitation contraction-coupling and increasing the rate of myosin-actin attachment during cross-bridge cycling[11,27]. These changes are also likely to explain the shorter octet TPT. In contrast, twitch TPT was unaltered, which is in agreement with some[3] but not all[2,4,5] past literature, and is likely due to the concomitant increases in both twitch PT and pRTD. The increase in twitch PT – which coincided with increases in octet PT – is not always observed with passive hyperthermia[2-4], but was reported by Ross, et al., (2012)[25], who suggested the effect may be due to hyperthermia-induced hyperventilation causing increased blood alkalinity. This mechanism increases tetanic tension via improved calcium handling kinetics[28], and so may explain the increased twitch and octet PT we observed.

A secondary finding was the shortened involuntary EMD with hyperthermia, when we may expect the opposite, given EMD is lengthened by increased compliance of the series elastic elements[29], and series compliance increases with increased muscle temperature[30]. The shortening of involuntary EMD we observed is likely due to an increase in muscle fibre conduction velocity[12] coupled with improved excitation-contraction coupling and rate of myosin-actin cross bridge attachment[11,27]. Shorter EMD and the subsequent reduction of overall motor-response time has important functional benefits during rapid movements.

Conclusion

In conclusion, progressive whole-body hyperthermia reduced MVT and late-phase RTD, likely due to reduced neural drive despite increased intrinsic capacity for force production. In contrast, early and middle-phase RTD were preserved, and EMD shortened, with hyperthermia, likely due to faster intrinsic contractile properties, despite reduced neural drive during the rapid contractions.

Practical implications

- The effects of whole-body hyperthermia on neuromuscular function cannot be inferred from studies only assessing MVT, as RTD is affected differently.
- The preservation of voluntary RTD suggests performance of rapid movements (e.g., sprinting, balance, and joint stabilisation) may be maintained during whole-body hyperthermia.
- The shorter EMD may also help maintain performance of rapid movements when hyperthermic.
- These practical implications are currently limited to a male population, as females were not studied.

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Author contributions

The present investigation was conducted at the Sports and Exercise Science Research Centre physiology laboratory, located on the Whitelands campus at the University of Roehampton. Ralph Gordon, Christopher Tyler, Ceri Diss and Neale Tillin contributed to the conception and design of the study. Ralph Gordon, Christopher Tyler, Federico Castelli, Ceri Diss and Neale Tillin contributed to the acquisition, analysis, and interpretation of the data. Ralph Gordon drafted the manuscript and Christopher Tyler, Federico Castelli, Ceri Diss and Neale Tillin made critical revisions, approved the final version, and agree to be accountable for all aspects of the presented work. All authors qualify for authorship.

Conflict of interest

The authors have no conflicts of interest to disclose.

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Tables

Table 1.

Supramaximal twitch and octet stimuli evoked in the knee extensors, at rest, in two different environmental conditions, HOT (~50˚C, ~35% relative humidity) and CON (~22˚C, ~35% relative humidity). Dependent variables are; peak torque (PT), torque at 50 ms (T_{50}), peak rate of torque development (pRTD), time to peak torque (TPT) and half-relaxation time (HRT).

		Twitch		Octet	
		HOT	CON	HOT	CON
PT (Nm)					
Set 1	(37°C/5 min)	48 ± 9	47 ± 12	202 ± 32	191 ± 41
Set 2	(38.5°C/50 min)	57 ± 12 **	46 ± 13 §§	210 ± 40	189 ± 38
Set 3	(39.5/83 min)	67 ± 14 †	46 ± 14 §§§	219 ± 36 *	189 ± 34 §§
Set 4	(T_{lim}/117 min)	72 ± 27	45 ± 18	198 ± 38	177 ± 36
T_{50} (Nm)					
Set 1	(37°C/5 min)	38 ± 7	37 ± 9	117 ± 18	110 ± 18 §
Set 2	(38.5°C/50 min)	49 ± 10 ***	36 ± 9 §§§	130 ± 20 ***	112 ± 20 §§
Set 3	(39.5/83 min)	58 ± 12 †††	35 ± 10 §§§	136 ± 22 †	111 ± 17 §§§
Set 4	(T_{lim}/117 min)	61 ± 23	36 ± 14	132 ± 27	107 ± 20
pRTD (Nm·s^{-1})					
Set 1	(37°C/5 min)	1153 ± 324	1092 ± 369	3897 ± 721	3592 ± 869 §
Set 2	(38.5°C/50 min)	1466 ± 377 **	1139 ± 358 §§§	4635 ± 879 *	3689 ± 866 §
Set 3	(39.5/83 min)	1888 ± 401 ††	1086 ± 380 §§§	5096 ± 978 ***	3699 ± 578 §§§
Set 4	(T_{lim}/117 min)	2078 ± 868	1114 ± 620	4726 ± 1051	3388 ± 539
TPT (ms)					
Set 1	(37°C/5 min)	81.6 ± 8.9	78.4 ± 7.8	127.9 ± 8.0	129.6 ± 9.8
Set 2	(38.5°C/50 min)	82.6 ± 8.2	83.5 ± 14.7	123.2 ± 7.0 *	127.6 ± 5.0
Set 3	(39.5/83 min)	78.3 ± 7.8	81.2 ± 5.5 §	118.3 ± 7.9 †	128.0 ± 6.5
Set 4	(T_{lim}/117 min)	73.0 ± 5.7	80.1 ± 4.2	114.9 ± 7.0	122.6 ± 5.4
HRT (ms)					
Set 1	(37°C/5 min)	81.8 ± 4.9	85.5 ± 11.1	77.1 ± 19.1	77.1 ± 17.9
Set 2	(38.5°C/50 min)	67.5 ± 6.9 ***	87.2 ± 17.3 §	54.3 ± 11.5 *	72.4 ± 13.7 §§§
Set 3	(39.5/83 min)	64.5 ± 9.0 **	86.0 ± 12.2 §§§	51.3 ± 6.4 **	71.0 ± 15.1 §§§
Set 4	(T_{lim}/117 min)	54.9 ± 3.1	78.6 ± 3.1	41.5 ± 9.3	63.3 ± 11.2

Data are mean±SD for *n*=9 (first three sets).
Within condition, different from Set 1; *, **, ***, for p≤0.05, p≤0.005, p≤0.001.
Within condition, different from Set 1 and 2; †, ††, †††, for p≤0.05, p≤0.005, p≤0.001.
Between condition, different from HOT; §, §§, §§§, for p≤0.05, p≤0.005, p≤0.001.
Data for Set 4 *(n*=4) are presented but not included in the statistical analyses.

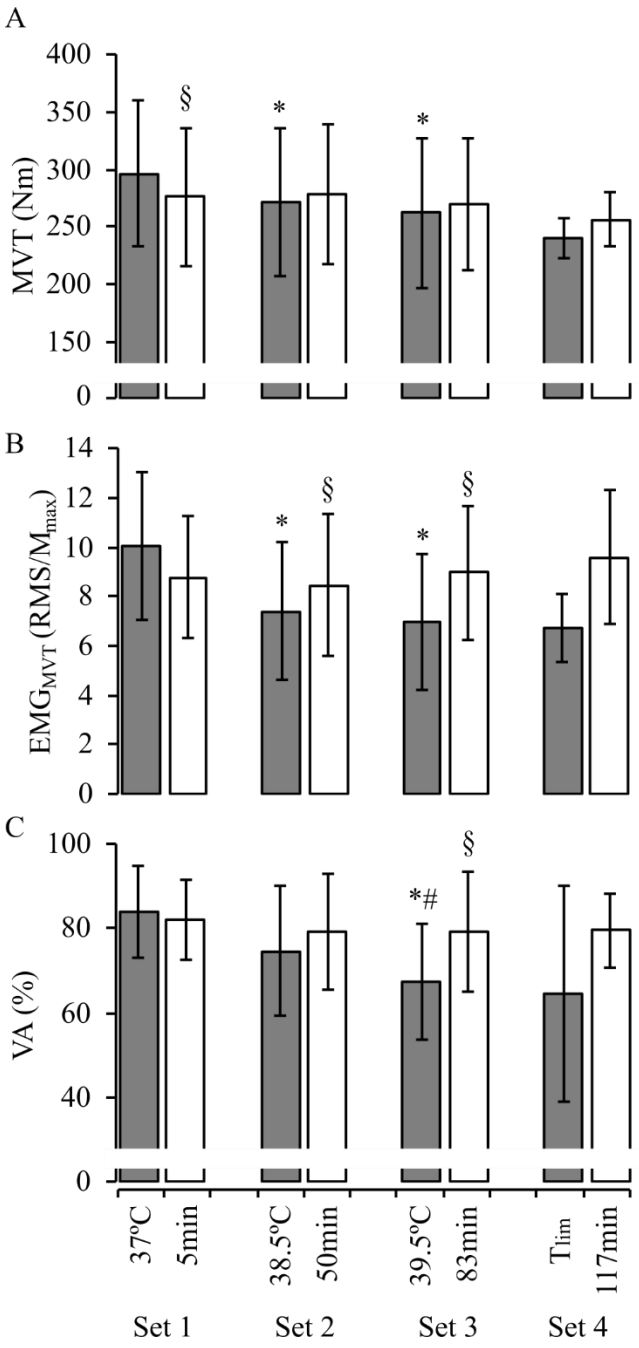


Figure. 1. Maximal voluntary torque (A; MVT), EMG at MVT (B; EMG_{MVT}) and voluntary activation (C; VA) recorded during knee-extensor MVCs in two different conditions; HOT (grey bars) and CON (white bars). Data are mean±SD for *n*=9 (first three sets). Between condition paired differences at corresponding T_{re}/Time points are denoted by: § ($p \leq 0.05$). Within condition paired differences are denoted by: * ($p \leq 0.05$)

different from 37°C; # ($p \leq 0.05$) different from 38.5°C. Data for T_{lim}/117 min (*n*=4) are presented but not included in the statistical analyses.

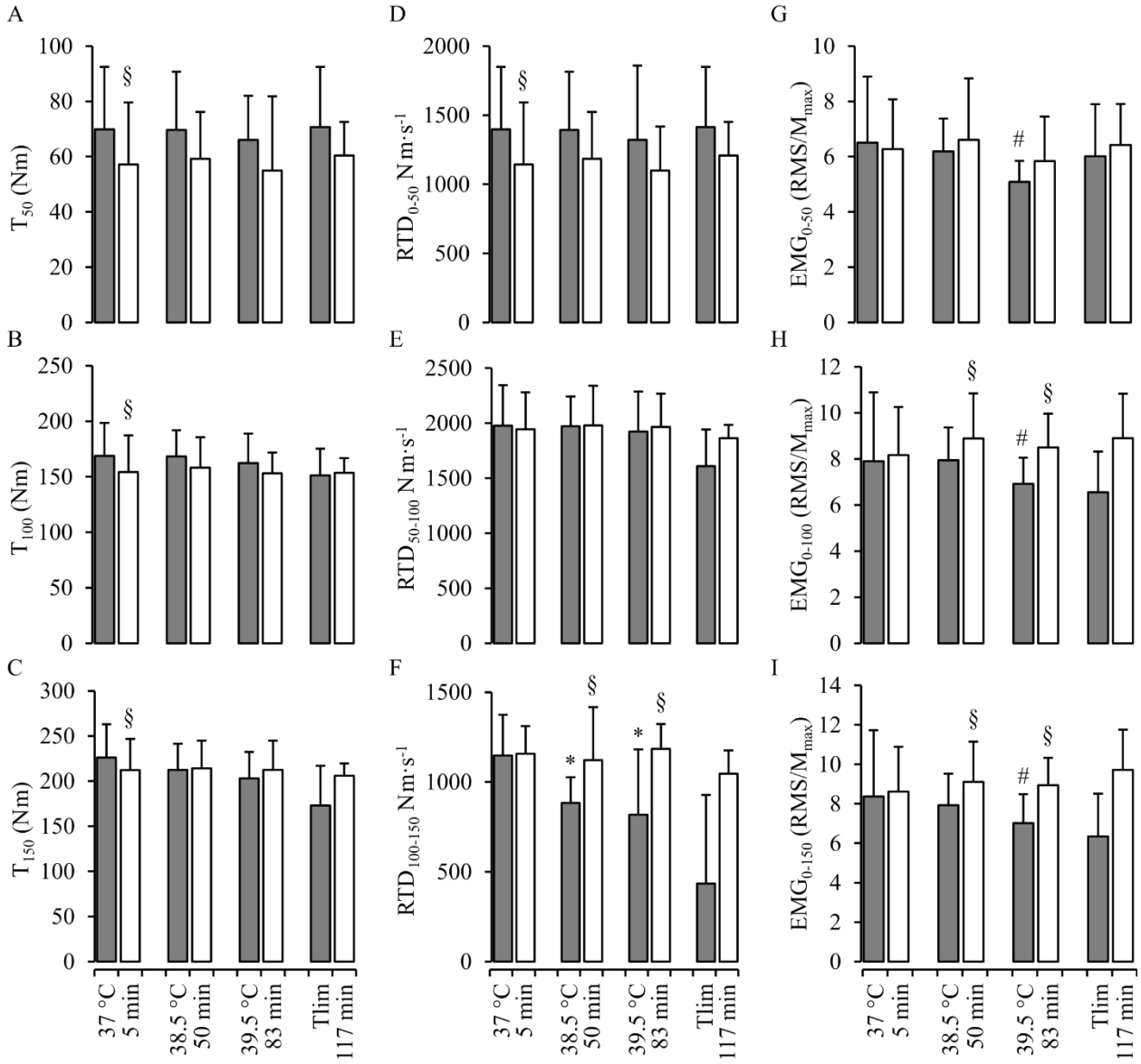


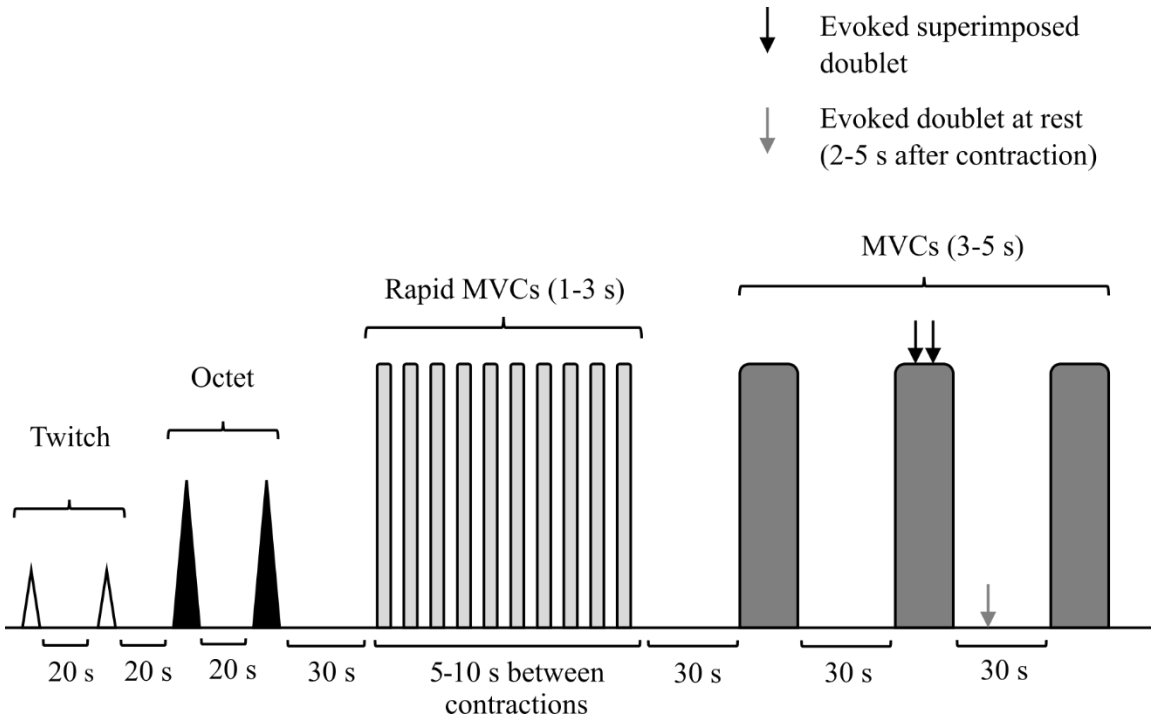
Figure. 2. Dependent variables recorded during rapid voluntary contractions of the knee extensors in two different conditions; HOT (grey bars) and CON (white bars). Variables are: voluntary rapid torque at 50 ms (A; T_{50}), 100 ms (B; T_{100}), and 150 ms (C; T_{150}); rate of torque development (RTD) at sequential time epochs 0-50 ms (D; RTD_{0-50}), 50-100 ms (E; RTD_{50-100}), and 100-15 0ms (F; $RTD_{100-150}$); and EMG normalised to maximal M-wave (M_{max}) at 0-50 ms (G; EMG_{0-50}) 0-100 ms (H; EMG_{0-100}) and 0-150 ms (I; EMG_{0-150}). Data are mean±SD for *n*=9 (first three sets). Between condition paired differences at

corresponding T_{re}/Time points are denoted by: § ($p \leq 0.05$). Within condition paired differences are denoted by: * ($p \leq 0.05$) different from 37°C, : # ($p \leq 0.05$) different from 38.5°C. Data for T_{lim}/117 min (*n*=4) are presented but not included in the statistical analyses.

Supplementary material

Appendix. A

Schematic showing the series of electrically evoked involuntary and voluntary isometric contractions of the knee extensors, comprising a single set of the neuromuscular protocol.



Appendix B

Main effects of condition (HOTvs.CON), neuromuscular set (three sets; T_{re} in HOT and Time in CON) and condition x set interactions for each dependent variable. df, degrees of freedom; MS, mean square; η_p^2, partial eta squared**.**

	Main effect condition					Main effect Time/T_{re}					Condition x Time/T_{re} interaction				
Dependant variable	df	MS	F	p	η_p^2	df	MS	F	p	η_p^2	df	MS	F	p	η_p^2
T_{re}	1	20	421	**<0.001**	.98	2	4	132	**<0.001**	.94	2	7	456	**<0.001**	.98
T_{sk}	1	440	935	**<0.001**	.99	2	14	103	**<0.001**	.92	2	12	84	**<0.001**	.91
T_{th}	1	773	1096	**<0.001**	.99	2	19	51	**<0.001**	.86	2	14	43	**<0.001**	.84
TS	1	117	250	**<0.001**	.96	2	5	49	**<0.001**	.86	2	4	30	**<0.001**	.79
HR	1	26878	216	**<0.001**	.96	2	3412	26	**<0.001**	.76	2	3823	53	**<0.001**	.87
MVT	1	56	0	0.634	.03	2	1827	10	**0.001**	.56	2	1177	8	**0.003**	.52
EMG_{MVT}	1	18	6	**0.036**	.44	2	9	1	0.328	.13	2	20	15	**<0.001**	.66
VA	1	226	3	0.112	.28	2	392	11	**0.001**	.59	2	194	5	**0.013**	.41
T_{50}	1	1722	5	**0.048**	.40	2	71	0	0.637	.05	2	7	0	0.941	.00
T_{100}	1	1688	8	**0.021**	.50	2	221	0	0.418	.09	2	34	0	0.667	.04
T_{150}	1	872	2	0.170	.22	2	526	7	**0.006**	.47	2	245	1	0.194	.18
$EMG_{0\text{-}50}$	1	1	1	0.293	.13	2	5	4	**0.029**	.35	2	1	1	0.230	.16
$EMG_{0\text{-}100}$	1	11	33	**<0.001**	.80	2	2	0	0.408	.10	2	2	1	0.197	.18
$EMG_{0\text{-}150}$	1	16	52	**<0.001**	.86	1.2	2	0	0.472	.07	2	3	2	0.086	.26
$RTD_{0\text{-}50}$	1	706580	5	**0.045**	.41	2	29698	0	0.621	.05	2	2472	0	0.948	.00
$RTD_{50\text{-}100}$	1	317	0	0.953	.00	1.0	8736	0	0.728	.01	2	6055	0	0.670	.04
$RTD_{100\text{-}150}$	1	565084	7	**0.028**	.47	2	137025	6	**0.009**	.44	2	147265	6	**0.011**	.43
Twitch PT	1	1652	35	**<0.001**	.81	2	372	13	**<0.001**	.63	2	431	18	**<0.001**	.69
Twitch T_{50}	1	1875	54	**<0.001**	.87	2	389	24	**<0.001**	.75	2	517	30	**<0.001**	.79
Twitch pRTD	1	21251	59	**<0.001**	.88	2	598233	31	**<0.001**	.79	2	634745	39	**<0.001**	.83
Twitch TPT	1	0	9	**0.017**	.52	2	0	0	0.999	.00	2	2	0	0.520	.07
Twitch HRT	1	0	46	**<0.001**	.85	2	0	4	**0.028**	.36	2	0	3	0.057	.30
Octet PT	1	5642	10	**0.013**	.56	2	273	1	0.191	.18	2	377	1	0.171	.19
Octet T_{50}	1	3773	25	**0.001**	.76	1.1	887	9	**0.012**	.53	2	353	8	**0.003**	.51
Octet pRTD	1	10514943	34	**<0.001**	.81	1.2	3166870	10	**0.007**	.56	1.2	2134563	9	**0.020**	.54
Octet TPT	1	0	3	0.084	.32	2	0	6	**0.007**	.46	2	9	5	**0.019**	.38
Octet HRT	1	0	32	**<0.001**	.80	1.0	0	13	**0.005**	.62	2	0	19	**<0.001**	.70
Voluntary EMD	1	7.0	1	0.271	.14	2	2	0	0.656	.05	2	67	4	**0.034**	.34
Involuntary EMD	1	7.4	30	**0.001**	.79	2	4	6	**0.011**	.43	2	9	1	0.189	.18

Appendix. C

Rectal temperature (**T_{re}**), skin temperature ($\overline{T}_{sk}$), thigh skin temperature (T_{th}), heart rate (HR), and thermal sensation (TS) during HOT and CON. Measurements were taken at the beginning and end of a set and then averaged.

Parameter	T_{re}/Time-point	HOT	CON
T_{re} (°C)			
Set 1	(37°C/5 min)	37.2 ± 0.2	37.3 ± 0.3
Set 2	(38.5°C/50 min)	38.5 ± 0.1 ***	37.2 ± 0.2 §§§
Set 3	(39.5°C/83 min)	39.5 ± 0.0 †††	37.0 ± 0.1 $^{\#§§§}$
Set 4	(T_{lim}/117 min)	40.1 ± 0.1	36.9 ± 0.2
$\overline{T}_{sk}$ (°C)			
Set 1	(37°C/5 min)	35.9 ± 04	32.0 ± 0.5 §§§
Set 2	(38.5°C/50 min)	38.1 ± 0.8 ***	32.1 ± 0.3 §§§
Set 3	(39.5°C/83 min)	39.3 ± 0.4 †††	32.1 ± 0.3 §§§
Set 4	(T_{lim}/117 min)	40.0 ± 0.3	32.4 ± 0.3
T_{th} (°C)			
Set 1	(37°C/5 min)	36.0 ± 0.6	30.2 ± 0.5 §§§
Set 2	(38.5°C/50 min)	38.3 ± 1.2 ***	30.6 ± 0.6 §§§
Set 3	(39.5°C/83 min)	39.8 ± 0.4 †††	30.5 ± 0.7 §§§
Set 4	(T_{lim}/117 min)	40.5 ± 0.8	30.6 ± 0.8
HR (beats·min^{-1})			
Set 1	(37°C/5 min)	91 ± 5	80 ± 9 §
Set 2	(38.5°C/50 min)	140 ± 18 ***	79 ± 12 §§§
Set 3	(39.5°C/83 min)	140 ± 25 ***	78 ± 12 §§§
Set 4	(T_{lim}/117 min)	154 ± 21	80 ± 15
TS			
Set 1	(37°C/5min)	5.8 ± 0.4	3.9 ± 0.8 §§§
Set 2	(38.5°C/50min)	7.2 ± 0.4 ***	4.1 ± 0.4 §§§
Set 3	(39.5°C/83min)	7.8 ± 0.3 ††	4.0 ± 0.5 §§§
Set 4	(T_{lim}/117min)	7.9 ± 0.1	4.2 ± 0.1

Data are mean ± SD for n = 9 (first three sets).
Different from Set 1; *, ***, for $p \leq 0.05$, $p \leq 0.001$.
Different from Set 2; $^{\#}$, for $p \leq 0.05$.
Different from Set 1 and 2; ††, †††, for $p \leq 0.005$, $p \leq 0.001$.
Different from HOT; §, §§§, for $p \leq 0.05$, $p \leq 0.001$.
Data for Set 4 (n=4) are presented but not included in the statistical analyses.

Appendix. D

Voluntary and involuntary electromechanical delay (EMD) in two different environmental conditions.

Parameter	T_{re}/Time-point	HOT	CON
Voluntary EMD (ms)			
Set 1	(37℃/5 min)	17.8 ± 4.5	17.2 ± 3.5
Set 2	(38.5℃/50 min)	15.9 ± 2.9	18.8 ± 3.0
Set 3	(39.5℃/83 min)	14.0 ± 4.2	20.3 ± 4.1 §
Set 4	(T_{lim}/117 min)	10.7 ± 1.4	17.6 ± 3.6
Involuntary EMD (ms)			
Set 1	(37℃/5 min)	7.7 ± 1.4	8.0 ± 1.7
Set 2	(38.5℃/50 min)	6.6 ± 1.8	7.6 ± 1.1 §
Set 3	(39.5℃/83 min)	6.4 ± 1.5 *	7.5 ± 1.5 §
Set 4	(T_{lim}/117 min)	4.4 ± 1.0	6.5 ± 1.7

Data are mean±SD for *n*=9 (first three sets).
Within condition, different from Set 1; *, for $p \leq 0.05$.
Between condition, different from HOT; §, for $p \leq 0.05$.
Data for Set 4 *(n*=4) are presented but not included in the statistical analyses.