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The Effect of Heating and Cooling on Time Course of Voluntary and Electrically Induced Muscle Force Variation

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Key words: *thermoregulation; muscle fatigue; electrical stimulation; motor variability.*

Summary. *The aim of this study was to investigate the effect of heating and cooling on time course of voluntary and electrically induced muscle force variation.*

Material and Methods. Ten volunteers performed 50 maximal voluntary and electrically induced contractions of the knee extensors at an angle of 120 degrees under the control conditions and after passive lower body heating and cooling in the control, heating, and cooling experiments. Peak torque, torque variation, and half-relaxation time were assessed during the exercise.

Results. Passive lower body heating increased muscle and core temperatures, while cooling lowered muscle temperature, but did not affect core temperature. We observed significantly lower muscle fatigue during voluntary contraction compared with electrically induced contractions. Body heating (opposite to cooling) increased involuntarily induced muscle force, but caused greater electrically induced muscle fatigue. In the middle of the exercise, the coefficient of correlation for electrically induced muscle torque decreased significantly as compared with the beginning of the exercise, while during maximal voluntary contractions, this relation for torque remained significant until the end of the exercise.

Conclusion. It was shown that time course of voluntary contraction was more stable than in electrically induced contractions.

Introduction

It has been established that muscle temperature changes muscle contractile properties; meanwhile, core temperatures can alter the activation pattern from the central nervous system (CNS). Muscle relaxation accelerates at high temperatures, and it might impair force generation as higher motor unit (MU) firing rates would be required to produce the same force compared with the exercise at lower muscle temperatures (1). However, core temperature plays an important role as well (2). The ability to activate skeletal muscles is sensitive to core temperature as passive body heating inhibits the voluntary activation of skeletal muscles during the sustained isometric contraction (1, 3), and it may not always manifest itself during brief maximal isometric contractions (2). It is of interest to note that this inhibition remains significant even when muscle temperature is maintained low by water cooling (3). It might be that muscle temperature plays a special role in voluntary activation of skeletal muscles.

It is thought that force variation depends mainly on the variability of MU firing rates (4). Force variation increases during fatigue in submaximal isometric contractions (5–7), but its behavior during brief electrically induced contractions (EIC) and maximal voluntary contractions (MVC) at different muscle temperatures is less clear. It was shown that a prolonged electrically induced muscle contraction impaired the force development compared with voluntary action. It was suggested that during voluntarily induced contractions, muscle force could be maintained by modulating the firing rates of active motor units, i.e., by recruiting different MUs as those initially recruited become fatigued, and/or activating additional motor units at lower firing frequencies (8). Thus, this recruitment strategy is no longer in operation during electrically induced muscle contractions.

The effect of body heating and cooling on central and peripheral muscle fatigue and on time course of voluntary and electrically induced muscle performance is not, however, clear. Therefore, the main aim of this study was to investigate the effect

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of heating and cooling on time course of voluntary and electrically induced muscle fatigue.

Material and Methods

Subjects. Ten healthy male nonsmokers (age, 21.2±0.1 years; height, 1.82±0.04 m, weight, 78.9±2.1 kg) participated in this study, which was approved by the Human Research Ethics Committee (Lithuanian University of Health Sciences, former Kaunas University of Medicine, Protocol No. 130/2005; BE-2-55, Kaunas, Lithuania). Written informed consent was obtained from the volunteers before their participation in this study. All the volunteers were considered as physically active as they took part in recreational activities two or three times per week. The study consisted of a control experiment (CON experiment) and experiments with passive muscle heating (HT experiment) and cooling (CL experiment). The experiments were performed in random order with at least one week in between experiments.

Body Temperature Measurements. Skin, rectal, and muscle temperatures were measured before and after body temperature manipulations in both HT and CL experiments. Rectal temperature was measured with a thermocouple (Rectal Probe, Ellab, Hvidovre, Denmark) inserted to a depth of 12 cm past the anal sphincter as recommended (9). The intramuscular temperature was measured with a needle microprobe (MKA, Ellab, Hvidovre, Denmark) inserted to a depth of 3 cm under the skin covering *m. vastus lateralis* of the left leg. Skin temperature was measured in the mid-thigh area over *m. vastus lateralis* using a specialized probe (DM852, Ellab, Hvidovre, Denmark).

Isometric Torque and Electrical Stimulation. The equipment and technique used to measure force have been previously described in detail elsewhere (10, 11). Briefly, the subjects were placed in the testing apparatus, i.e., experimental chair. They sat upright in the experimental chair with a vertical back support provided. A strap secured the hips and thighs to minimize uncontrolled movements. The appropriate leg (right or left) was clamped in the force-measuring device (UGO BASILE 7080 type DY 150, Italy) with the knee kept at the angle of 120 (180°, full knee extension). A leather belt 6 cm in width, placed around the leg just proximal to the malleoli, was tightly attached to a linear variable differential transducer. The output of the transducer, proportional to isometric knee extension force, was amplified and digitized at a sampling rate of 1 kHz by a 12-bit analogue-to-digital converter incorporated in a personal computer. The digitized signal was stored on a hard disk for subsequent analysis. The output from the force transducer was also displayed for visual feedback.

The equipment and procedures for electrical stimulation were essentially the same as described previously (10, 12). Direct muscle stimulation was applied using two carbonized rubber electrodes, covered with a thin layer of electrode gel (ECG-EEG Gel, Medigel, Modi'in, Israel). One of the electrodes (0.06×0.11 m) was placed transversely across the width of the proximal portion of the quadriceps femoris. Another electrode (0.06×0.20 m) covered the distal portion of the muscle above the patella. A standard electrical stimulator (MG 440; Medicor, Budapest, Hungary) was used. Electrical stimulation was delivered in square-wave 0.5-ms pulses. The tolerance to electrical stimulation was assessed separately, and only volunteers who showed good compliance with the procedure were recruited for the study. The intensity of electrical stimulation was selected individually by applying single stimuli to the quadriceps muscle. During this procedure, the current was increased until no increment in single twitch torque could be detected.

The half-relaxation time (HRT) was measured in 50-Hz contractions. The half-relaxation time was calculated as the time taken for torque to decline from peak value to the half of that value at the end of 50-Hz contraction.

Control Experiment. The control experiment was carried out at room temperature of 21°C. Firstly, a volunteer performed a 10-min treadmill running session with the intensity corresponding to a heart rate of 120–130 beats/min as monitored by a heart rate monitor (S-625X, Polar Electro, Kempele, Finland). Afterward, the volunteer was positioned in the experimental chair, and the stimulating electrodes were placed on one (left/right) of the randomly selected legs. After a 10-min rest, the force-generating capacity of the quadriceps muscle was assessed by applying 1-s trains of electrical stimuli at 50 Hz. After a 5-min rest, a ~3-s MVC was performed. A 5-min rest period then followed, and the experiment was terminated by a 50×MVC (maximal voluntary contraction time, ~1 s; rest time, ~0.5 s). Within approximately 5 min after the first load, the leg was changed, and involuntary 50×50-Hz electrical pulses were applied to the relaxed quadriceps muscle (stimulus time, 1 s; relaxation time, 0.4 s).

Experiments With Muscle Heating and Cooling. The initial part of heated and cooled experiments was identical to the control experiment. The volunteer performed a 10-min treadmill running session followed by the assessment of the muscle force-generating capacity at 50 Hz followed by MVC. Afterwards, however, the volunteer left the experimental chair, and his body temperature were measured (see section "Body Temperature Measurement"). Then the volunteer spent 45 min sitting immersed up to the waistline in a water bath at approximately 44°C (heating experiment) (13) or 30 min at approximately 15°C (cooling experiment) (14, 15). Immediately after this procedure, the volunteer was toweled dry, and the temperature measurements were repeated again. Within ~3 min after the bath, the volunteer returned to the experimental chair with the stimulating electrodes placed on the randomly selected leg and dressed in the sports wear as in the control experiment. Without delay, the experiment was terminated by 50×MVC. Within ~5 min after MVC load, the leg was changed, and involuntary 50×50-Hz electrical stimulation was applied to the relaxed quadriceps muscle as in the CON experiment.

Statistical Analysis. A 2-way analysis of variance (ANOVA) was used to determine the effects of temperature (control, heating, cooling) and repetition on muscle properties. If a significant effect was found, the post hoc test with the Bonferroni correction was applied to locate the difference. *P* values of the post hoc analyses were adjusted for multiple comparisons and presented at two different levels: <0.05 or <0.001. Data are presented as mean ± standard error (±SE) unless otherwise stated.

The Pearson coefficient of correlation for torque was used to determine the associations with the beginning. Statistical significance was set at $P<0.05$. The coefficient of variation for torque was calculated to determine the variability of muscle performance.

Results

MVC and torque induced by electrostimulation in the CON and HT experiments were significantly greater than in the CL experiment (Fig. 1).

Data on body temperatures in the HT and CL experiments are presented in Table. There were no differences between the experiments comparing temperatures before cooling and before heating. In the HT experiment, the heating procedure significantly increased skin and rectal temperatures. Muscle temperature also increased significantly in all six subjects whose temperatures were measured. On the other hand, the cooling procedure in the CL experiment did not affect rectal temperature, but it reduced skin temperature and muscle temperature in all the subjects studied.

Data on changes in peak torque during 50 maximal voluntary and electrically induced contractions are presented in Fig. 2. From repetition 8 to the end of the exercise, MVC torque decreased (~35%) significantly in all the experiments compared with the beginning ($P<0.001$). These values were not different between the experiments compared ($P>0.05$).

During involuntary muscle contractions evoked by 50×50-Hz electrical stimulation, peak torque started to decrease from repetition 10 and remained significantly lower until the end of the exercise reaching an ~85% decrease ($P<0.001$). The Bonferroni post hoc test revealed that involuntary torque was significantly lower during the HT experiment compared with the other two experiments ($P<0.05$). The temperature-by-repetition interaction did not show any significance ($P<0.001$).

Half-relaxation times of the muscle during 50 electrically induced contractions are presented in Fig. 3. From repetition 8, HRT increased during all the experiments and remained significant until the end of the exercise compared with the beginning ($P<0.001$). The Bonferroni post hoc test revealed that HRT was longer in the CL experiment compared with HT ($P<0.05$), and it did not differ compared with the CON experiment ($P>0.05$). None of the interactions reached significance.

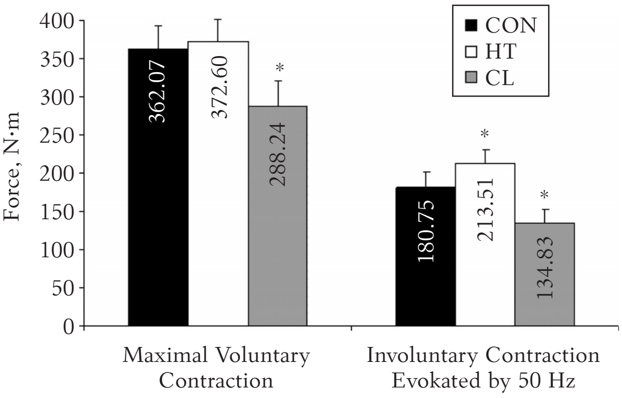

Fig. 1. Baseline values of knee extension torque at 50-Hz electrical stimulation and maximal voluntary contraction torque *$P<0.001$, as compared with control values.

Table. Skin, Rectal, and Muscle Temperatures (t) Before and After Passive Muscle Heating and Cooling During the Heating (HT) and Cooling (CL) Experiments

Temperature	HT Experiment		CL Experiment	
	Before Heating	After Heating	Before Cooling	After Cooling
Muscle t, °C n=6	37.1±0.1	39.7±0.1***	36.8±0.1	34.5±0.2***
Rectal t, °C n=10	37.6±0.1	39.4±0.1***	37.1±0.1	37.3±0.1
Skin t, °C n=10	32.1±0.2	37.4±0.1***	32.4±0.2	25.2±0.2***

Values are mean±SE; n indicates the number of studied volunteers.
***$P<0.001$, as compared with values before heating or before cooling.

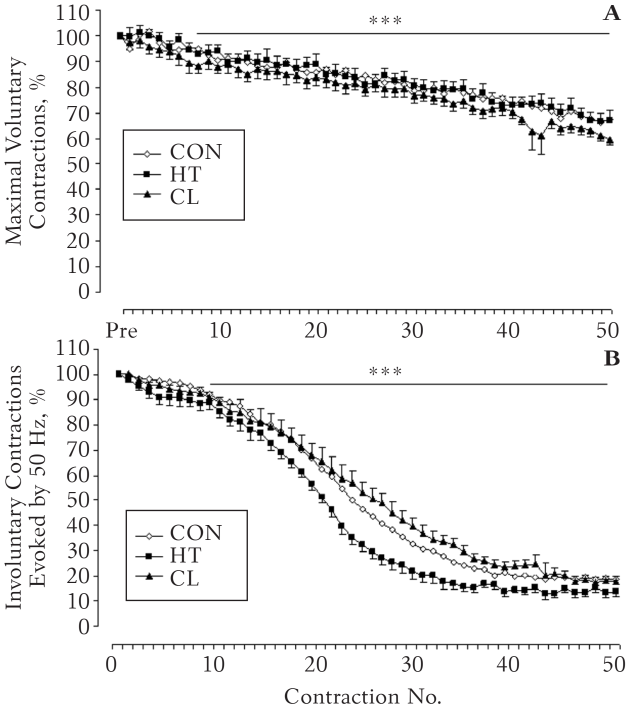

Fig. 2. Peak torque during 50 maximal voluntary (A) and involuntary (B) contractions during the control (CON) experiment and body heating (HT) and cooling (CL) experiments

****P*<0.001, as compared with baseline value.

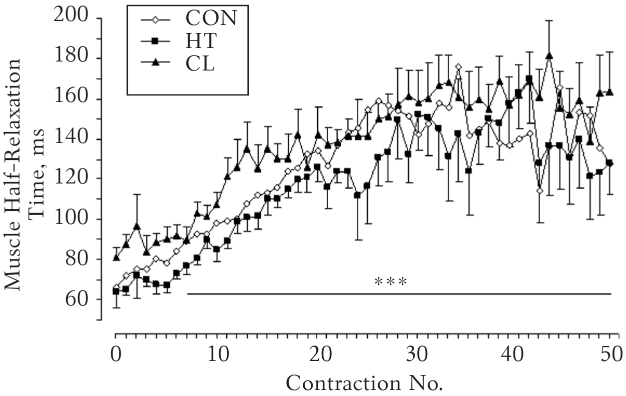

Fig. 3. Muscle half-relaxation time during 50 involuntary contractions during the control (CON) experiment and body heating (HT) and cooling (CL) experiments

****P*<0.001, as compared with baseline value.

Data on changes in the coefficient of correlation for torque as compared to the beginning and coefficient of variation for torque are presented in Fig. 4. As shown in Fig. 4A, during 50-MVC, torque remained in strong correlation with the beginning ($P<0.05$). It was similar during all the experiments. As shown in Fig. 4B, electrically induced torque remained in a strong correlation until repetition ~25 ($P<0.05$) and later on dramatically ranged in

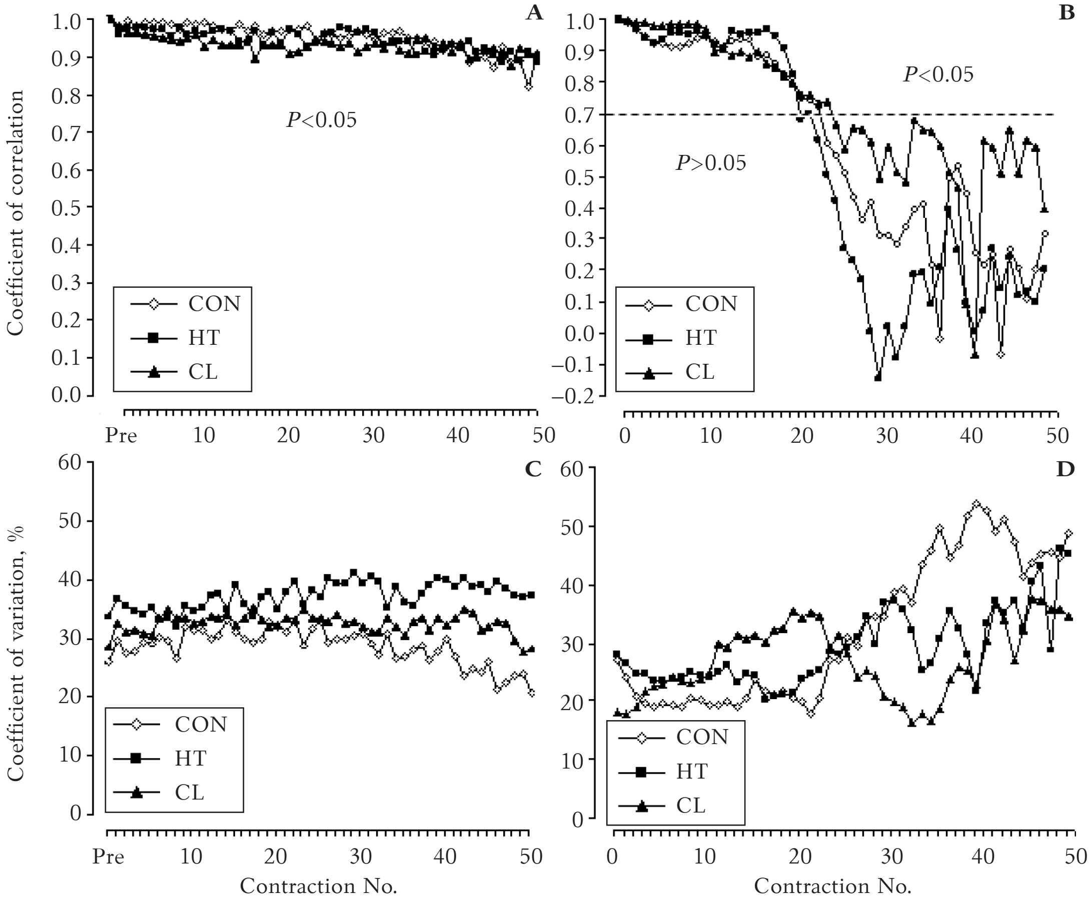

Fig. 4. The coefficients of correlation and variation for torque during 50 maximal voluntary (A, C) and involuntary (B, D) contractions during the control (CON) experiment and body heating (HT) and cooling (CL) experiments

between moderate, weak, or no correlation as compared with the beginning ($P>0.05$).

As shown in Fig. 4C, during 50-MVC, torque variation increased during the HT experiment (9.89%). Besides, torque variation was increased until the middle of the exercise and then decreased during the CL (1.04%) and CON experiments (20.14%). As shown in Fig. 4D, the coefficient of variation increased during 50 involuntary muscle contractions evoked by 50-Hz electrical stimulation during all the experiments: CON (82.23%), HT (39.81%), and CL (44.37%).

Discussion

The main findings of our study are as follows: we observed greater muscle fatigue during electrically induced contractions compared with voluntary contractions. Body heating increased electrically induced muscle fatigue, while it did not affect time course of voluntary contractions. In the middle of the exercise, the coefficient of correlation for electrically induced muscle torque decreased significantly as compared with the beginning, while during maximal voluntary contractions, this relation for torque remained significant until the end of the exercise. It showed that time course of voluntary contraction was more stable than in electrically induced contractions.

The greater torque decrement during EIC compared with MVC is in agreement with the data of other researchers (16–18). For EIC, we observed a ~85% loss of force, while during MVC this loss was only ~35%. It has been established that electrical stimulation recruits MUs in a nonselective, spatially fixed, and temporally synchronous pattern (16). This recruitment pattern contributes to increased muscle fatigue when compared with voluntary actions. Kim et al. (18) have shown a greater reduction in glycogen concentration in all fiber subtypes simultaneously after electrostimulation compared with voluntarily activated muscle. Slow and fast skeletal muscles have been shown to have firing frequencies of approximately 10 and 30 Hz, respectively, during MVCs (19). These frequencies are lower than those applied during our experiment. The frequency of 50 Hz was used during the experiment to ensure tetanic contraction. Thus, the frequency of EIC also may have contributed to fatigability of exercising muscle (16). However, the aim of our study was to investigate whether these changes in EIC and MVC during exercise performance were sensitive to changes in muscle temperature as induced by passive heating and/or cooling. The passive muscle heating resulted in a faster EIC muscle fatigue in the middle of the exercise compared with the CL experiment. Surprisingly, no temperature effect on fatigue was observed during repeated brief MVCs. These results are in contrast to those from the study by Nybo and Nielsen (2). They showed no effect on maximal force development or central activation in hyperthermia when performing brief maximal knee extensions during 40 MVCs. However, the main difference between these two studies is that in our study the time of muscle contraction and interspaced rest time between repetitions was much shorter. This may indicate that although HT condition provokes central fatigue (2), the central nervous system regains the ability to activate the skeletal muscles even when the period of recovery is shorter than that proposed by Nybo and Nielsen (2). Conversely, a relatively (voluntary vs. involuntary muscle activation) greater activation from the CNS to exercising muscle was observed during repeated brief contractions during the HT experiment compared with the CON and CL experiments. As expected, heating caused a decrease in HRT of skeletal muscle compared with CON and CL experiments. Consequently, HT condition may increase the firing frequency necessary to sustain maximal activation of MUs (20), and this may be of minor importance for the activation level during brief contractions, whereas it may inhibit motor activation when the contraction is sustained (21) because it becomes difficult or impossible for the CNS to maintain maximal force (20). It has been suggested that hyperthermia and hypoglycemia may cause central fatigue during the prolonged exercise. However, in both conditions, voluntary force production may be maintained only for a brief period, whereas central activation is reduced if the contraction needs to be sustained for more than a few seconds. Depletion of substrates and metabolic disturbances within the CNS and/or alterations in the release or synaptic levels of certain neurotransmitters are potential mechanisms underlying the decline in central activation during the sustained muscle contraction (22). However, sensory feedback from the contracting muscles could also be a major factor influencing the pattern of CNS activation. Inhibitory feedback from chemoreceptors and metaboreceptors may be of minor importance for the activation level during the initial phase of isometric contractions, whereas it may inhibit motor activation when the contraction is sustained and muscle metabolites accumulate (23). It appears that central activation becomes markedly impaired when hyperthermia is combined with inhibitory signals from skeletal muscles, whereas inhibition from a high brain temperature (24) may be overridden provided inhibitory feedback from chemo- and metaboreceptors is low (25).

Another line of evidence supporting the importance of muscle temperature in exercise performance during EIC and MVC comes from the data on force development variation. A progressive increase in force variation during the submaximal isometric exercise has been linked to muscle fatigue (18). It is, however, known that force variation increases progressively during isometric contractions at 30% MVC, though data at 50–60% MVC are less consistent (5, 18). It appears that force variation depends mainly on variability of MU discharge rate (4). An enhanced peripheral input to spinal motoneurons might contribute to force development variation during fatiguing isometric contractions (18, 26). We failed to find any other study on muscle temperature that described changes in force development variation during brief EIC and MVC at different muscle temperatures. This study found a higher increment in force development variation in EIC during exercise performance compared with MVC. However, during MVC, the force development variation tended to be the largest in heated muscles and the smallest in cooled muscles, while in EIC, the dynamics of force development variation was chaotic. Interestingly, we observed a decreasing correlation as compared with the beginning, which followed after ~20 repetitions of EIC force development, while MVC showed a strong correlation until the end of the exercise. This indicates that during EIC exercise performance, the muscle capacity to maintain the same contractility pattern on force development is limited and lost after ~20 repetitions, while in MVC, this pattern is maintained. Our data support the idea that those changes in associations compared with the beginning or force development variation of EIC were mediated by changes in the HRT of the muscle. However, it was shown that during voluntary actions, muscle force could be maintained by modulating the firing rates of active motor units, i.e., by recruiting different MUs as those initially recruited became fatigued and/or by activating additional motor units at lower firing frequencies (8). Thus, this recruitment strategy is no longer in operation during electrically induced muscle contractions. Recruitment of muscle fibers with electrostimulation is fixed and results in a subsequent drop in force whenever any of the fibers activated during the protocol become fatigued (16). It is likely that loss in correlation and increase in variation during EIC is associated with the inability to alter recruitment patterns and/or the inability to modulate firing frequency.

Conclusions

Warming and cooling did not affect time course of voluntary performance, but changed time course of electrically induced muscle performance. The changes in voluntary performance were more stable than electrically induced ones.

Šildymo ir šaldymo poveikis raumenų valingosios ir elektrostimuliacijos sukeltos jėgos kaitai

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Raktažodžiai: termoreguliacija, raumenų nuovargis, elektrostimuliacija, motorinė kaita.

Santrauka. *Tyrimo tikslas.* Ištirti šildymo ir šaldymo poveikį raumenų valingosios ir elektrostimuliacijos sukeltos jėgos kaitai.

Medžiaga ir metodai. 10 vyrų atliko 50 maksimalių valingų ir elektros impulsų serijos sukeltų raumenų susitraukimo izometrinį krūvį tiesdami koją 120° laipsnių per kelio sąnarį kampu. Tyrimas buvo atliktas įprastinėmis sąlygomis po pasyvaus apatinės kūno dalies šildymo ir šaldymo. Krūvio metu matuotas didžiausios jėgos momentas, jėgos momento kaita ir raumens pusės atsipalaidavimo trukmė.

Rezultatai. Pasyvus šildymas padidino raumenų ir šerdinę temperatūrą, šaldymas priešingai – sumažino raumenų temperatūrą, tačiau nepakeitė šerdinės temperatūros. Nustatėme, kad, maksimaliu intensyvumu atliekant valingus izometrinius susitraukimus, raumenų nuovargis yra statistiškai reikšmingai mažesnis nei atliekant panašų darbą, sukeltą raumenį stimuliuojant elektra. Pasyvus raumens šildymas (priešingai nei šaldymas) padidina nevalingą raumens susitraukimo jėgą, tačiau sumažina elektrostimuliacijos sukeltą raumens atsparumą nuovargiui. Elektrostimuliavimo sukelto darbo viduryje reikšmingai sumažėja raumenų jėgos koreliacija su darbo pradžia, o viso valingo darbo metu šis ryšys išlieka statistiškai reikšmingas.

Išvada. Tai rodo, kad valingi raumens susitraukimai buvo pastovesni (t. y. pasižymėjo mažesne jėgos išvystymo kaita) nei raumenį stimuliuojant elektra.

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