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Effect of temperature on the contractile properties and muscle power of triceps surae in humans

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DAVIES, C. T. M., AND K. YOUNG. *Effect of temperature on the contractile properties and muscle power of triceps surae in humans.* J. Appl. Physiol.: Respirat. Environ. Exercise Physiol. 55(1): 191–195, 1983.—The effects of heating and cooling on the electrically evoked mechanical and contractile properties of the triceps surae in relation to the maximal dynamic performance of the leg muscles during cycling and vertical jumping have been examined in five healthy male subjects. A mean rise of 3.1°C in muscle temperature (T_m) was associated with a decrease in time to peak tension (TPT) and half-relaxation time ($\frac{1}{2}$ RT) but was without effect on twitch (P_w) and tetanic tension at 20 Hz (P_{o20}) and 40 Hz (P_{o40}) and maximal voluntary contraction (MVC). Reducing T_m by 8.4°C had the opposite effect on TPT and $\frac{1}{2}$ RT and produced a fall in P_w , P_{o40} , and MVC. The peak power output during cycling (\dot{W}_1) and jumping (\dot{W}) was linearly related to T_m as well as negatively associated with TPT. The best single guide to \dot{W} and \dot{W}_1 was given by a ratio of MVC to TPT: \dot{W} (W) = 626.5 + 79.04 (MVC/TPT)(N/ms; $r = +0.82$) and \dot{W}_1 (W) = 1,342 + 84.9 (MVC/TPT)(N/ms; $r = +0.87$). The results underline the importance of the contractile and force generating capacity of human muscle in determining maximal power output and performance during exercise of a few seconds duration.

electrical stimulation; human muscle; isometric exercise; anaerobic power output; force platform; force bicycle

IN A PREVIOUS PAPER (11) we have demonstrated the effects of heating and cooling on the contractile properties and tetanic tensions of the human triceps surae by indirect electrical stimulation. Raising the temperature of the muscle (T_m) to 39°C had little effect on the twitch and tetanic tensions but increased by 20 ms the speed of the contraction of the muscle, whereas reducing T_m to 24°C decreased maximal voluntary contractions (MVC) and tetanic tensions, particularly at high frequencies of stimulation, and increased the time to peak tension (TPT) of the muscle by 61%. Thus the most profound effect of elevating T_m was on contractility, whereas cooling produced not only a marked reduction in speed of contraction but also a loss of the capacity of the muscle to generate force. This result should be compared with the recent findings of Bergh and Ekblom (*Acta. Physiol. Scand.* 107: 33–37, 1979), who investigated the effects of T_m on dynamic strength and short-term muscle power output. They showed that performance in sprinting and jumping was positively related to T_m , the association being due largely to variations in maximal dynamic

strength during knee extension exercise on an isokinetic dynamometer and the maximal power output following heating and cooling being independent of contraction speed over a wide range of movement. To investigate this problem further we have studied the effects of T_m on the responses of five healthy young men to electrical twitch and tetanic stimulation of the triceps surae in relation to maximal short-term cycling on a specially designed ergometer (20) and jumping from a force platform.

MATERIALS AND METHODS

Five healthy young subjects (22.4 ± 1.1 yr; 182 ± 0.05 cm ht; 75.5 ± 6.4 kg wt) took part in the investigation.

Measurement of maximal voluntary dynamic muscle force and power were made during cycling and vertical jumping (12). Each subject was required to make three maximal jumps from a force platform and on different occasions perform maximal work on a force bicycle at various constant velocities. Each jump began with a countermovement as described by Bosco and Komi (4). The force-time data from the platform and the cranks of the bicycle were fed, via an analog-to-digital converter, into a minicomputer system (DEC MINC-11). From the continuous records of force with respect to time the following observations and calculations were made. On the force platform, peak force (P) was taken as the maximal net force (absolute force minus body mass) exerted before take off and on the bicycle as the peak force recorded in a revolution of the cranks. Peak power output on the bicycle was calculated as the product of force \times velocity, velocity being calculated from the formula $2\pi r/t$, where r is the radius of the crank and t is the time of a revolution.

On the platform, instantaneous velocity (V) was calculated by integration of the curve for acceleration (A) with respect to time (t), $V = \int A dt$, and multiplied by instantaneous force to give power. The maximal (instantaneous) power output (\dot{W}) was taken as the highest value recorded before take off. Net impulse (NI) was calculated by integration of the force-time curve and the height (H) of the jump determined from the formula: H (cm) = $\dot{V}_T/2g$, where \dot{V}_T is the take off velocity and g the force of gravity.

The leg dynamometer in which the triceps surae muscle was stimulated has been described by Davies et al. (11). A series of single electrical stimuli of progressively increasing voltage were applied to the triceps surae at

30-s intervals. This was continued to supramaximal stimulation voltages to gain a maximal twitch contraction. In a similar way maximal tetanic tension was reached by increasing the stimulation voltage to supramaximal levels at frequencies of 10, 20, and 40 Hz. Each frequency level lasted 2 s, with the 10-Hz stimulation period being preceded by three single stimuli at 1-s intervals. Total tetanic cycle time was 9 s, and a rest period of 1 min separated each stimulation cycle. Stimulation began at a voltage slightly below the supramaximal level so that the experimental protocol could be kept as short as possible. Subjects were asked to perform two MVCs with 1-min rest between each.

T_m was passively adjusted by immersion of the leg in water at 46 and 0°C. The water level was 5 cm distal to the greater trochanter. The initial immersion period normally lasted 30 min, but this was extended to 45 min in two subjects who possessed large leg muscle bulk. A thermistor needle placed in the upper lateral belly of the gastrocnemius muscle recorded the temperature at a depth of 5 cm below the skin. T_m measurements were taken at rest, immediately following immersion, and during and after stimulation, jumping, and cycling.

Voluntary dynamic forces were measured in the following way. During each visit to the laboratory the subject performed two consecutive jumps on the force platform and one maximal 10-s work load at a preselected pedalling speed on the bicycle ergometer, and then reimmersed his leg in the water bath for a further 10 min to reestablish his previous muscle temperature. The subject then performed two further maximal 10-s work loads at different pedal frequencies on the bicycle ergometer. This procedure was repeated on five separate occasions to minimize the possible accumulative effects of fatigue and to ensure that the required range of pedal frequencies were measured to determine maximal power output (20). In the electrical stimulation experiments the twitch and tetanic data were collected after the 30-min immersion, with the two MVCs following the 10-min reimmersion period. During control measurements the 10-min reimmersion period was substituted for a rest period of an equivalent length of time.

RESULTS

The T_m data are summarized in Table 1. The mean resting T_m for all control experiments was $36.8 \pm 1.6^\circ\text{C}$. Heating effected a 3.1°C rise and cooling an 8.4°C decrease in T_m following water immersion. By carefully reheating or cooling the subjects during the experimental period (see MATERIALS AND METHODS) the postimmersion temperatures were maintained during work on the

TABLE 1. *Effects of heating and cooling on deep (5 cm) muscle temperature*

	Control	Immersion	Force Platform	Force Bicycle	Electrical Stimulation
Heating	36.6 ± 0.7	39.7 ± 0.4	39.5 ± 0.1	39.0 ± 0.5	38.5 ± 0.2
Cooling	36.8 ± 0.3	28.4 ± 1.2	28.5 ± 1.0	28.0 ± 1.4	28.6 ± 1.6

Values are means \pm SD; $n = 5$. Measurements were made immediately following immersion, force platform, force bicycle, and electrical stimulation.

force platform. During cooling this was also true for the experiments involving the bicycle and electrical stimulation; however, following heating there was a reduction in the T_m of 0.7 and 1.2°C , respectively (see Table 1), after both these procedures.

The effects of muscle temperature on the contractile properties of the triceps surae and the various indices of maximal performance on the force platform and bicycle are shown in Tables 2 and 3. Heating significantly ($P < 0.001$) decreased the TPT, $\frac{1}{2}\text{RT}$, and tetanic tension at 10 Hz (P_{010}) but was without effect on tetanic tensions at 20 and 40 Hz, respectively, (P_{020} and P_{040}) and MVC. Cooling had no effect on P_{010} and P_{020} but significantly increased ($P < 0.001$) TPT and $\frac{1}{2}\text{RT}$ and decreased P_{t0} , ($P < 0.01$) P_{040} , and MVC. Thus P_{040} was found to be positively related to MVC: $\text{MVC (N)} = 749 + 0.694 P_{040} \text{ (N)}$ ($r = +0.74$), but changes in TPT and $\frac{1}{2}\text{RT}$ were independent of twitch and tetanic tensions.

On the force platform, H , NI, and average (\bar{W}) and peak (\dot{W}) power output were closely associated with each other and were related to T_m though only cooling produced a significant change in these variables (Table 3). The respective mean changes in H , NI, \bar{W} , and \dot{W} with cooling were 2.38°C , $8.09^\circ\text{N}\cdot\text{s}/^\circ\text{C}$, $21.20^\circ\text{W}/^\circ\text{C}$, and $112.40^\circ\text{W}/^\circ\text{C}$. The changes in \dot{W} on the force platform associated with cooling were due to a decrease in $\dot{V}T$ ($P < 0.001$), the peak forces (P) exerted on the platform before take off were not significantly changed.

On the force bicycle the changes in average (\bar{W}_1) and peak (\dot{W}_1) with temperature were similar to those described for the force platform though both heating and cooling produced less effect. Nevertheless, the peak power outputs of cycling and jumping were closely associated

$$\text{platform } \dot{W} \text{ (W)} = -459 + 0.872 \text{ bicycle } \dot{W}_1 \text{ (W)} \\ (r = +0.89)$$

but the absolute values of \dot{W}_1 were always greater (862–737 W) than those recorded during jumping (Table 3). The reduction in \dot{W}_1 on the bicycle was due to a significant decrease in both the force exerted (P ; $P < 0.05$) and the crank velocity (\dot{V}_{opt} ; $P < 0.05$) at which \dot{W}_1 was measured. \dot{W}_1 was positively associated ($r = +0.86$) with \dot{W}_1 and with \dot{W} ($r = +0.73$) on the force platform.

The peak power outputs on the bicycle and platform

TABLE 2. *Effects of heating and cooling on the contractile properties and twitch and tetanic tensions of human triceps surae*

	TPT, ms	$\frac{1}{2}\text{RT}$, ms	P_{t0} , N	P_{010} , N	P_{020} , N	P_{040} , N	MVC, N
Control	121 ± 18	76 ± 6	137 ± 28	936 ± 162	1,456 ± 164	1,767 ± 246	2,109 ± 480
Heated	92‡ ± 15	59‡ ± 6	126 ± 18	705‡ ± 162	1,349 ± 81	1,716 ± 139	2,098 ± 523
Cooled	167‡ ± 25	147‡ ± 42	94* ± 26	856 ± 187	1,300 ± 316	1,594† ± 355	1,707† ± 545

Values are means \pm SD; $n = 5$. Values are given as time to peak tension (TPT), half relaxation time ($\frac{1}{2}\text{RT}$), supramaximal twitch (P_{t0}) and tetanic (P_0) tensions at 10 Hz, 20 Hz, and 40 Hz and maximal voluntary contraction (MVC). Significantly different from control values: * $P < 0.05$; † $P < 0.01$; ‡ $P < 0.001$.

TABLE 3. Effects of muscle temperature on dynamic performance during work on a force bicycle and platform

	Force Platform						Force Bicycle				
	H, cm	NI, N·s	W, w	\bar{W} , w	P, N	\dot{V}_T , ms. ⁻¹	\dot{W}_1 , w	\bar{W}_1 , w	P ₁ , N	\dot{V}_{opt} , ms. ⁻¹	
Control	31±3	153±15	2,197±278	261±46	1,074±163	2.47±0.14	3,059±430	1,200±208	1,344±112	2.28±0.20	
Heated	34±5	164±19	2,439±329	279±52	1,153±172	2.58±0.21	3,176±458	1,196±123	1,424±177	2.28±0.20	
Cooled	11±2‡	85±13‡	1,253±334†	103±41‡	992±234	1.47±0.15‡	2,096±243*	675±62†	1,110±104*	1.90±0.31*	

Values are means ± SD; *n* = 5. Values are given as height of jump (*H*), net impulse (NI), average (\bar{W} and \bar{W}_1) and peak (\dot{W} and \dot{W}_1) power outputs, peak force (*P*) and take-off velocity (\dot{V}_T) on the force platform and peak force (*P*₁) and velocity (\dot{V}_{opt}) at which \dot{W}_1 was attained on the bicycle. Significantly different from control values: * *P* < 0.05; † *P* < 0.01; ‡ *P* < 0.001.

were negatively associated with the electrically evoked time to peak tension (TPT) of the triceps surae

platform \dot{W} (W) = 3,282 – 10.42 TPT (ms)

$$(r = -0.63)$$

bicycle \dot{W}_1 (W) = 4,043 – 10.00 TPT (ms)

$$(r = -0.59)$$

However, the best single index of peak power output for both the platform and the bicycle was given by the ratio of maximum voluntary contraction (MVC) to TPT (Fig. 1)

platform \dot{W} (W) = 626.5 + 79.04 $\frac{\text{MVC}}{\text{TPT}}$ (N/ms)

$$(r = +0.82)$$

and

bicycle \dot{W}_1 (W) = 1,342 + 84.90 $\frac{\text{MVC}}{\text{TPT}}$ (N/ms)

$$(r = +0.87)$$

DISCUSSION

There have been several previous studies of the effects of muscle temperature on voluntary dynamic performance (1, 2, 13), but no attempt has hitherto been made to relate the changes observed directly to electrically stimulated contractile and force generating properties of the muscle. The present investigation shows that not only does such a relationship exist, but the mechanical and contractile properties of muscle are the main determinants of short-term power output under conditions of passive heating and cooling in vivo experiments in humans.

Under control conditions our electrical stimulation data agree closely with previous work from this laboratory (11). The time to peak tension of the maximal twitch response is 121 ± 18 ms, which is in accord with the data given by Buller et al. (6) and McComas and Thomas (16) for indirect stimulation of human gastrocnemius and soleus muscle. The changes in time to peak tension with heating to 92 ± 15 ms and cooling to 167 ± 25 ms supports our previous work (11) and the investigations of Buller et al. (7), Buchthal and Schmalbruch (5), and Ranatunga (18). The significant (*P* < 0.05) decrease of twitch tension with cooling (Table 2) is in agreement with the work of Ranatunga (18) on rat muscle. Heating and cooling the triceps surae have little effect on the

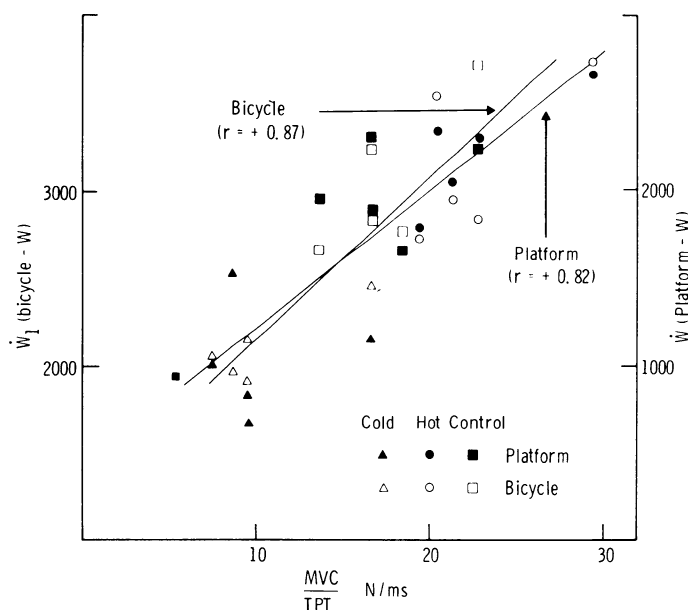


FIG. 1. Relationship of power output on force bicycle (\dot{W}_1) and platform (\dot{W}) to an index (MVC/TPT) of contractile properties of triceps surae.

force-generating capacity of the muscle except at very low-frequency (10 Hz) stimulation in the heat and high-frequency (40 Hz) stimulation in the cold (Table 2). The effects of cooling on electrically stimulated high-frequency and maximal voluntary forces is not surprising in view of our previous work and the investigation of others (5, 7, 18). The *T_m* (even of the superficial layers) of the muscle was always significantly greater than that associated with nerve block (14). Cooling probably interferes directly with the metabolic and force generating mechanisms within the muscle fiber to an extent that it can no longer respond adequately to frequencies of 40 Hz and above. The high-frequency (40-Hz) response was linearly related to MVC (*r* = 0.74), and both variables were affected by cooling (8), but we found no evidence of a reduction in low-frequency forces with decreased *T_m* as previously observed in animal muscle (7, 9, 17). However, this is perhaps not surprising if one considers that the lowest muscle temperature we studied was 28.0°C. The investigation of Cullingham et al. (9) shows that the major loss of tension occurs below this temperature. At 20°C, for instance, they found a 30–35% fall in tetanic force, but over the *T_m* range of 40 to 28°C the tension changed by less than 5%. As we have previously suggested (11), it is probable that the reduced fusion frequency of the muscle as *T_m* is lowered ensures a more

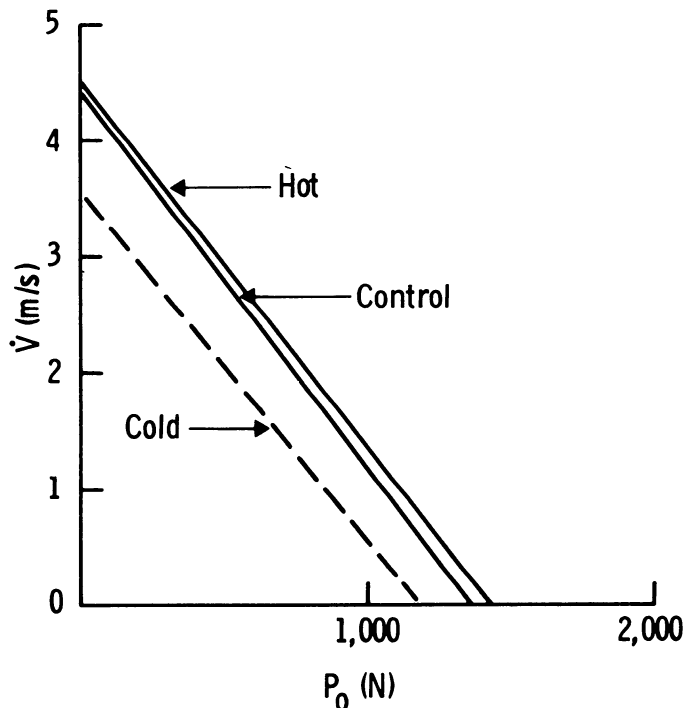


FIG. 2. Effect of heating and cooling on force-velocity relationship (\dot{V}/P_0) during cycling.

complete development of tension and offsets any possible deleterious changes in the underlying contractile and metabolic processes associated with force generation. Equally at a frequency of 10 Hz with heating, where the time interval between stimuli becomes greater than the TPT tetani become incompletely fused, giving rise to a loss of tension (Table 2).

The effects of temperature on dynamic performance reflect the changes in the electrically stimulated contractile properties of the triceps surae, though the association for passively heating is less clear than for cooling. If the increased speed of tension development could be fully utilized during dynamic performance one might expect a 20% increase in power output on the bicycle and platform. In fact the increase in \dot{W} on the force platform is approximately half this value and is the same order of magnitude as found by Bergh and Ekblom (2). The Q_{10} for \dot{W} , NI, and Ht is ~ 1.25 (cf. Ref. (3)). On the bicycle the changes in \dot{W}_1 are negligible (+3.8%) and there is no significant ($P > 0.1$) change in the force/velocity relationship when T_m is increased by $\sim 3^\circ\text{C}$ (Fig. 2). The reason heating has so little effect on \dot{W}_1 , particularly on the bicycle, is not clear. It is possible that optimal tem-

perature for the development of short-term power output (as opposed to isometric force) may extend over the same range as that for prolonged exercise ($37\text{--}39.3^\circ\text{C}$; see Ref. 10). At these temperatures the metabolic reactions and force-generating (Cross-bridge formation) mechanisms are maintained at or near their optimal level. If this is so, then the common athletic practice of prolonged "warm-up" before exercise to improve performance may not be warranted physiologically. The essential factor is that the muscles should not be allowed to cool below their normal physiological range.

Cooling the leg muscles to a T_m of 28.4°C reduces \dot{W} and \dot{W}_1 by 43 and 32%, respectively. The changes in power output during cycling and jumping are associated with the loss of electrically evoked force generation and the contractile capacity of the triceps surae. The Q_{10} for TPT is 1.46, which is of the same order as that found for Ht, NI, and \dot{W} on the force platform and only slightly greater (~ 0.15) than found for the Q_{10} of \dot{W}_1 on the bicycle. The decline of P_{040} , MVC, and increase in TPT is associated with the displacement of the force-velocity relationship during cycling with a lowered T_m (Fig. 2). Thus a loss of power in cycling is due to decrease in both force and velocity, and this parallels the changes in the electrically stimulated properties of the leg muscles. The decreased frequency for optimal force generation (11) and the slowing of chemical reactions which must occur in cooled muscle will inevitably result in delayed cross-bridge formation and effect a decrease in strength and rate at which force can be developed and applied in the dynamic situation.

In practical terms the close association of power output in jumping and cycling with the contractile properties of triceps surae suggest that though it may not be the dominant muscle, it nevertheless contributes to performance in both activities. The relationship of TPT and short-term exercise supports the work of Thorstensson et al. (21) and others (4, 22) who have shown that the ability to sprint and jump is related to the presence of fast-twitch fibers within the muscle. Available evidence would suggest that the fiber composition of muscle is largely an inherent characteristic of humans; at least no study (19) has produced convincing data to show inter-conversion of the two major human fiber types. It would be interesting to know how far the present finding would be affected by training and ageing. Aged muscle is noteworthy for its gradual loss and atrophy of fast-twitch fibers (15).

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