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The Influence of Temperature on the Isometric Characteristics of Fast and Slow Muscle in the Cat

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Abstract. The maximum tetanic tension (initial strength) and the length of time, 20, 40 or 60%, of that initial strength could be maintained (endurance) was assessed in 2 fast twitch muscles (the plantaris and the medial gastrocnemius) and a slow twitch muscle (the soleus) of the cat at muscle temperatures ranging between 22 and 38° C. The results of these experiments showed that the strength of the soleus was constant between muscle temperatures of 38 to 28° C, and then gradually decreased as the muscle was cooled further. Plantaris, on the other hand, showed a reduction in strength at all muscle temperatures less than 38° C; the response of the medial gastrocnemius was between these two extremes. The longest endurance for the soleus muscle was found to be at a muscle temperature of 28° C, the endurance being as much as 3 times higher at this temperature than at muscle temperatures of 22 or 38° C. The medial gastrocnemius showed a similar response but the endurance only doubled when comparing the endurance at a muscle temperature of 28 to 38° C. In contrast, the plantaris maintained a constant endurance over the temperature range of 38 ot 28° C; below this muscle temperature the endurance decreased markedly. The mechanism for this response appeared to be related to the effect of temperature on the contractile characteristics of the muscles.

Key words: Strength – Endurance – Fatigue – Red and white muscle.

Introduction

In man, the resting muscle temperature of the forearm muscles ranges between 30 and 36° C (Barcroft and Edholm 1946; Clarke et al. 1958; Petrofsky and Lind 1975a and b). Although the muscle temperature can be reduced to as low as 27–28° C with little effect on the maximum voluntary strength (Clarke et al. 1958), the endurance for isometric exercise can be as much as three times greater when comparing the endurance at muscle temperatures of 39 to 28° C (Clarke et al. 1958; Petrofsky and Lind 1975a and b). When the muscle is cooled below 28° C, both the maximum voluntary strength and the endurance for sustained isometric contractions is reduced (Clarke et al. 1958; Petrofsky and Lind 1975a and b).

Most muscles in man are comprised of a variable mixture of fast and slow twitch motor units (Dubowitz and Brooke 1974). In the rat, Close and Hoh (1968) have shown that fast twitch motor units, while increasing their twitch tension when cooled from 35 to 20° C, continuously reduced their tetanic tension over this same temperature range. In contrast, slow twitch motor units maintained a constant twitch tension over the muscle temperature range of 35 to 20° C and maintained a constant tetanic tension until the muscle temperature fell below 25° C. On the basis of those observations, it seemed plausible that the influence of the muscle temperature on the endurance for isometric exercise might be different in the two types of muscle as well. It was the purpose of the present investigation to examine this possibility. Three muscles were examined: soleus, a slow twitch muscle; medial gastrocnemius, a fast twitch muscle with a mixed-fiber composition; and plantaris, a nearly pure fast twitch muscle in terms of its physiological characteristics (Ariano et al. 1973; Petrofsky and Lind 1979).

Methods

Female cats weighing an average of 2.9 ± 0.6 kg were used in these experiments. The animals were anesthetized with α-chloralose (75 mg/kg body weight) and maintained with intravenous booster doses as needed.

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A heating pad placed under the cat maintained the rectal temperature within the range of 37 to 39° C. Blood pressure and heart rate were monitored through an arterial cannula inserted into the left carotid artery.

Stimulation

Direct square-wave stimulation (pulse width 0.1 ms) was applied with two needle electrodes at a frequency of 100 Hz. Indirect stimulation was delivered sequentially at sufficient intensity to recruit all motor units through the three bundles of ventral roots dissected as described above, in the manner first described by Rack and Westbury (1969) and later modified (Petrofsky 1978). Distal to the stimulating electrodes, the ventral roots were spread thinly over a second set of electrodes whose purpose was to create an anodal block. The number of active motor units was varied by altering the anodal block voltage (recruitment). This resulted in motor units being recruited by size from the slowest to fastest, respectively (Petrofsky 1978; Petrofsky and Lind 1979). This pattern of recruitment was used in these experiments because it more nearly resembles (than does synchronous stimulation) that which is believed to occur during voluntary contractions (Bigland and Lippold 1954; Wuerker et al. 1965; Olsen et al. 1968; Milner-Brown and Stein 1975).

The anodal block voltage and stimulation frequency were set and maintained by a digital computer (Intel 8080A microprocessor). During fatiguing isometric contractions, the motor unit stimulation frequency was set initially at 10 Hz and the anodal block voltage was reduced until the target tension was achieved. As the muscle began to fatigue, more motor units were recruited to maintain the target tension. Once all the motor units were recruited, the computer increased the stimulation frequency to maintain the target. A complete description of the computer program is given elsewhere (Petrofsky 1978). Once an increase in stimulation frequency was ineffective in maintaining the target, the contraction was terminated; the total length of time the contraction was maintained was called the endurance time.

Estimation of the Number of Active Motor Units

To estimate the number of motor units firing at a given level of electrical stimulation, the anodal block voltage was first applied with sufficient intensity to stop all the impulses generated by the stimulation electrodes (frequency of firing was set at 75 Hz). The block voltage was then gradually removed and the additional recruitment of a motor unit was assessed from a stepwise increase in the tetanic tension developed by the muscle. The block voltages at which this occurred were recorded and from these data the percent of the total number of motor units activated by a given block voltage was estimated.

Surgical Preparation

Each cat was placed in the prone position and the muscle to be tested was exposed and freed from the surrounding muscles. The muscle was attached to a low-displacement isometric strain gauge dynamometer. Liquid paraffin equilibrated initially with a gas mixture of 95% O_2–5% CO_2 was circulated over the muscles to maintain muscle temperature at any of the various temperatures listed under "Procedures".

A dorsal laminectomy exposed the L_6, L_7 and S_1 ventral roots, which were cut proximally to their emergency from the spinal cord, divided surgically and pooled into three groups, each capable of causing the muscle to develop a similar tension following stimulation. Liquid paraffin, maintained at 38° C and oxygenated with a gas mixture consisting of 95% O_2–5% CO_2, superfused the nerve bundles to keep them electrically isolated from each other.

Experimental Procedures

Strength, Endurance and Muscle Temperature

At the beginning of each experiment, the length of the muscle was set at that which allowed the muscle to produce its maximum isometric tension; once this length was determined, the muscle was kept at this length (L_0) for the remainder of the experiments. After a 30 min recovery period, during which the muscles were superfused with 38° C liquid paraffin, the initial strength of the muscle was then recorded as the maximum tension recorded during a 3 s isometric contraction elicited by synchronous electrical stimulation of all of the motor units at a tentanizing frequency (100 Hz). During a subsequent 30 min period, the muscles were superfused with liquid paraffin which was regulated to either 20, 26, 29, or 38° C. The flow rate of the paraffin was adjusted such that the muscle temperature (measured by a thermistor implanted in the tip of a 40 G neddle) was kept at either 22, 28, 32, or 38°C. After this period, the strength (tetanic tension recorded in the fatigued muscle or when the temperature of the muscle was altered) was then recorded again to assess the effect of temperature on the initial strength of the muscle. At 3 min intervals, a series of 3 s contractions were then recorded at different frequencies of stimulation between 10 and 100 Hz to establish the frequency tension relationship. After another 10 min recovery period, a single twitch of all of the motor units was recorded by applying a maximal square wave pulse to the motor nerve followed by a fatiguing contraction sustained at either 20, 40, or 60% of the initial strength of the muscle by the computer program described under "Procedures". In addition, a series of contractions was also conducted at 100% of the strength of the muscle at a given temperature, and the time required for the tension to fall (through fatigue) to 80% of the strength was assessed. These experiments were repeated on each of 8 muscles for each of the 3 tensions and 4 muscle temperature in the 3 types of muscles listed above.

Results

The tetanic tension measured by indirect sequential stimulation of 8 different soleus (○), plantaris (△), and medial gastrocnemius (●) muscles after adjusting the muscle temperatures to either 22, 26, 28, 32, or 38° C and expressed in terms of the initial strength of the muscles is shown in Fig. 1. Each point in this figure shows the respective tension ± the S.D. Soleus, the slow twitch muscle, maintained a constant tetanic tension over the temperature range of 28 to 38° C; the strength of the muscles declined rapidly with temperature when the muscle was cooled further. The medial gastrocnemius, a mixed but fast twitch muscle, showed no reduction in strength as the muscle temperature was reduced from 38 to 32° C. Thereafter, there was a moderate reduction in the strength when the temperature was reduced from 32 to 28°C followed by a rapid reduction in strength when the muscle was cooled further. Plantaris, also a fast twitch muscle, showed a gradual reduction in strength when cooled between 38 to 28° C, with a rapid fall thereafter. A common feature for all 3 muscles was the rapid fall in strength as muscle temperature fell below 28° C, though the proportional fall was greater for the fast twitch muscles.

The frequency-tension relationship was measured at these same muscle temperatures. For convenience of

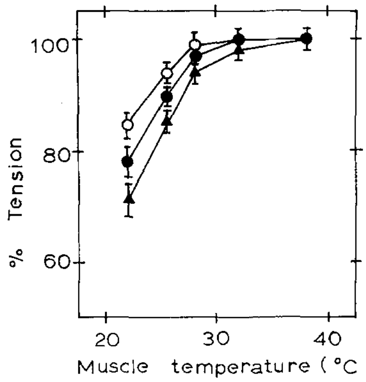

Fig. 1. The tetanic tension developed by 8 soleus (○), medial gastrocnemius (●), and plantaris muscles (△) ± the S.D. after 30 min superfusion with liquid paraffin to adjust the muscle temperature between 22 and 38° C

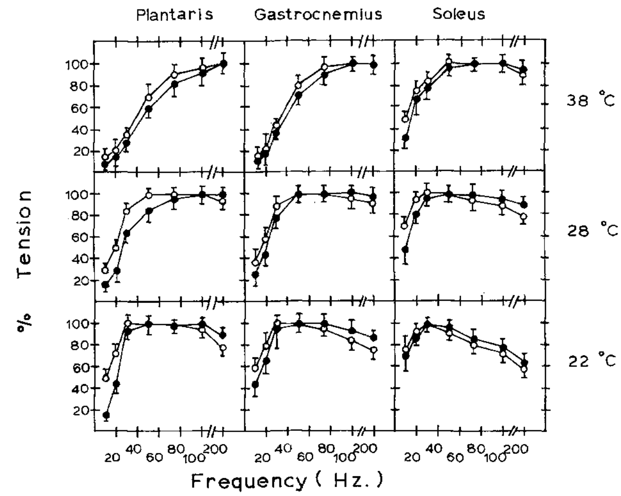

Fig. 2. The tension developed by 4 soleus, medial gastrocnemius, and plantaris muscles ± the S.D. during direct (●) and indirect (○) electrical stimulation at frequencies between 10 and 100 Hz. Muscle temperature was maintained between 28 and 38° C by paraffin superfusion

Table 1. Twitch characteristics of muscles. All values represent the mean ± the S.D.

		Soleus	Medial gastrocnemius	Plantaris
37° C	Twitch rise time (ms)	38.1 ± 6.1	25.1 ± 2.4	19.1 ± 3.4
	Half relaxation time (ms)	44.2 ± 5.1	31.2 ± 4.1	24.3 ± 4.7
	Twitch tetanus ratio	0.26 ± 0.03	0.21 ± 0.02	0.15 ± 0.02
28° C	Twitch rise time (ms)	111.1 ± 9.7	54.3 ± 6.4	38.4 ± 1.3
	Half relaxation time (ms)	122.4 ± 16.3	71.8 ± 6.9	51.2 ± 4.8
	Twitch tetanus ratio	0.27 ± 0.03	0.24 ± 0.02	0.21 ± 0.03
22° C	Twitch rise time (ms)	133.1 ± 11.1	63.7 ± 9.1	45.1 ± 6.3
	Half relaxation time (ms)	156.3 ± 16.4	79.9 ± 7.3	61.2 ± 1.9
	Twitch tetanus ratio	0.38 ± 0.07	0.29 ± 0.06	0.24 ± 0.04

presentation the strength developed by the muscles during electrical stimulation at various frequencies between 10 and 200 Hz is shown in Fig. 2 for all three types of muscle but only at muscles temperatures of 22, 28, and 38° C. Synchronous electrical stimulation was used here to examine the contractile properties of the motor units independent of summation of the tension with other asynchronously firing units as is found with sequential stimulation (Petrofsky 1978; Lind and Petrofsky 1979). Further it is impossible to stimulate the muscle directly by sequential stimulation and ensure electrical isolation of 3 discrete groups of motor units; thereby making the comparison here between direct and indirect stimulation impossible during sequential stimulation. Each point in this figure illustrates the mean of 8 experiments ± the S.D. during both synchronous direct (closed symbols) and synchronous indirect (open symbols) stimulation. The results of these experiments showed that all three types of muscles were able to tetanize at significantly lower frequencies by both direct and indirect stimulation when the muscle was cooled below 38° C. Further, especially in the soleus (slow twitch) muscle, the motor units became refractory to high frequency electrical stimulation when the muscles were cooled below 28° C. Within the normal range of physiological frequencies (< 100 Hz) the maximum tetanic tension of the muscles was the same after both direct and indirect stimulation for the muscle temperatures we examined.

The twitch characteristics of these muscles during indirect synchronous stimulation showed a prolonged rise time of twitch tension and an increase in the half relaxation time (time for the tension to fall to half of the peak value) when the muscle was cooled below 38° C. A

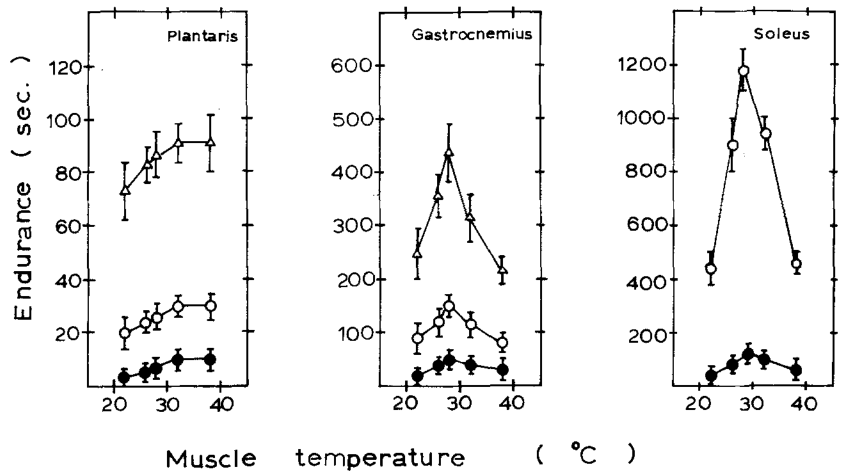

Fig. 3
The isometric endurance for contractions at 20 (△), 40 (○) and 60% (●) of the tetanic tension of the soleus, medial gastrocnemius, and plantaris muscles in 4 cats ± the S.D. after superfusion for 30 min with paraffin at temperatures between 22 and 40° C

summary of the average responses of 4 cats ± the S.D. for twitches recorded at muscle temperatures of 22, 28, and 38° C is shown in Table 1.

The isometric endurance of the three types of muscles at differing muscle temperatures is shown in Fig. 3. Illustrated here are the endurance times for each of the 3 types of muscles for contractions at 20 (△), 40 (○) and 60 (●) of the initial strength recorded after superfusion with the liquid paraffin at 38° C. The endurance times for contractions sustained only at 40 and 60% of the initial strength are shown for the soleus muscle since this muscle did not show any sign of fatigue during contractions at 20% of its initial strength at any of the temperatures reported here even after 4 h of stimulation. The endurance of the soleus muscle, as might be expected from its biochemical makeup, was always longer than that of the other 2 muscles at all muscle temperatures. But for the soleus muscle, the endurance as much as tripled when the muscle temperature was reduced from 38 to 28° C; the enhancement in endurance being more pronounced for the contraction at the lowest tension, 40% of the initial strength. In comparison, the endurance of the medial gastrocnemius doubled, at best, when the muscle was cooled over this same temperature range. Again, the largest enhancement in endurance was found for contractions at the lowest tension. In contrast to these muscles, the plantaris muscles showed a constant endurance at all tension examined over the muscle temperature range of 38° to 28° C and then showed a progressive reduction in endurance as the temperature of the muscle was reduced further.

The time for the muscles to fatigue from 100% to 80% of their initial strength showed a similar pattern of response. Here again, the endurance of soleus was longer than the other 2 muscles. While the endurance for the soleus muscles was increased by reducing the muscle temperature from 38 to 28° C, the endurance of

Table 2. Isometric endurance for sustained maximal efforts (s), where tension fell from 100 to 80% of maximal strength

	Soleus	Medial gastrocnemius	Plantaris
38° C	34 ± 6	13 ± 2	7 ± 1
28° C	53 ± 7	15 ± 3	5 ± 1
22° C	31 ± 3	11 ± 1	4 ± 1

the medial gastrocnemius was affected little by a reduction in its temperature while plantaris showed a reduction in endurance for all temperatures below 38° C.

The pattern of recruitment for contractions at 20, 40, or 60% of the initial strength used by the computer was somewhat different for the 3 types of muscles examined here for contractions at different muscle temperatures. In the soleus, for example, the pattern of recruitment was different for contractions at 29 and 38° C. As an example, the recruitment and frequencies of stimulation throughout a contraction at 40% of the initial strength of the soleus muscles showed that about 80% of the motor units were recruited at the onset of the contractions to maintain a tension of 40% of the initial strength at 38° C, but only about 55% of the motor units were recruited to maintain the same tension at 28° C. Further, the rate of increase of recruitment throughout the contraction was also slower. The recruitment pattern for the plantaris muscle also showed an initially lower recruitment at the onset of contractions below a temperature of 38° C. However, the motor units fatigued rapidly resulting in a more rapid increase in recruitment in the cool than warm muscle. The contractions at 100% of the tetanic strength of the muscles showed similar results as was found for the submaximal contractions. The results of these experiments on 8 cats are listed ± the S.D. in Table 2. Only the results at 3 muscle temperatures are shown for 22, 28, or 38° C.

Discussion

When muscle is cooled from 38° C to 28° C, there is an increase in the duration of the isometric twitch (Close and Hoh 1968; Buller et al. 1966). It is not surprising then, that the muscles were able to tetanize at substantially lower frequencies when their temperature was reduced to 28° C. Further, during these contractions, there is evidence that the motor units are not only able to produce more tension, but are able to produce an absolute tension more efficiently when the temperature was 28 as compared to 38° C. However, the muscles also became refractory to high frequency electrical stimulation when cooled to 28° C. The mechanism of this response may be due to an increase in the absolute refractory period of the sarcolema since Fink and Luttgau (1976) have shown an inverse relationship between the duration of the MUAP and temperature. In man (Humphreys and Lind 1963; Clarke et al. 1958), the blood flow at the onset of a fatiguing isometric contraction is higher for contractions exerted at a muscle temperature of 38 vs 28° C. In addition, Edwards and his colleagues (1972) have shown an increased level of glycolytic intermediates in the resting muscle at 38.6° C (compared to 32.6° C) and an increased rate of ATP utilization during fatiguing contractions in warm muscle. Finally, in the cat medial gastrocnemius (Petrofsky et al. 1979), individual motor units have been shown to use less oxygen to maintain a set tension in the 28° C muscle. Part of the reduction in the ATP utilization may be due to inhibitions of metabolic pathways due to the cold. But part of the reductions in ATP turnover is also probably due to a reduction in myocin ATPase as well. The maximum velocity of shortening of the unloaded muscle (V_{max}) is considered to be an index of myocin ATPase activity. Since V_{max} is reduced with a reduction in muscle temperature (Petrofsky et al. 1980), it can be concluded that ATPase of the myocin is reduced as well. This may cause the cross bridges to become attached longer and thereby enable tension to be held more efficiently. In the soleus muscle, where the tetanic tension was the same over this same range of muscle temperatures, this resulted in less motor units being recruited to maintain a set tension at the onset of a fatiguing contraction. Further, the reduced fatigability of the individual motor units as evidenced by the longer endurance times for contractions at 100% of the initial strength (here all motor units are recruited) resulted in a slower rate of rise of recruitment during the contractions. The total and result, then, was an increase in the endurance of the soleus muscle when cooled to 28° C. When the soleus muscle was cooled below 28° C, the twitch tension and tetanic tension were both reduced and, although each of the motor units developed even more tension when stimulated at a given frequency, the reduction in motor unit strength resulted in more motor units being recruited to maintain a given tension. For this reason, as the muscle was cooled, endurance was reduced as well.

In the plantaris muscle, a muscle comprised of a large proportion of fast twitch motor units, as reported by Close and Hoh (1968), the twitch tension was increased while the rise time of the muscle twitch and the half relaxation time of the muscle twitch were both prolonged when the muscle was cooled below a temperature of 38° C. This resulted in a shift in the frequency-tension relationship to the left such that, here again, the muscles developed more tension at a given frequency of stimulation and tetanized at a lower frequency by either direct or indirect stimulation. However, unlike the soleus muscle, the tetanic tension of the plantaris muscle was reduced as the muscle was cooled below 38° C. Thus although the motor units were able to develop more tension at a given frequency of stimulation, their total strength and their fatigability (as evidenced by the reduction in the duration that a sustained maximal contraction could be maintained) was reduced. Therefore, although the ability of the motor units to tetanize at lower frequencies would initially result in less motor units being recruited to maintain a set tension, their fatigability and reduction in strength would offset this advantage and any increase in endurance when the muscle was cooled. When the muscle was cooled below 28° C, although twitch tension was increased further, strength and fatigability again were reduced and now became the predominant factor, and endurance for sustained submaximal contractions was reduced as well. The response of the medial gastrocnemius muscle, as might be expected from its mixed composition, fell between these extremes.

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