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TEMPERATURE DEPENDENCE OF ISOMETRIC CONTRACTIONS OF CAT FAST AND SLOW SKELETAL MUSCLES

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SUMMARY

1. The influence of temperature (range 38–20 °C) on the isometric contractions of flexor digitorum longus (fast-twitch) and soleus (slow-twitch) muscles of the cat hind leg was examined *in situ* and with supramaximal nerve stimulation.

2. The maximum tetanic tension decreased by 5–7 % on cooling from 38 to 27 °C and by about 17 % on further cooling to 20 °C. The results were similar between the two muscles.

3. The twitch tension increased by 100 % in flexor digitorum longus and decreased by about 40 % in soleus when the temperature was lowered from 38 to 20–24 °C.

4. The results are compared with those reported for fast- and slow-twitch muscles of the rat.

INTRODUCTION

Following the observations of Buller, Ranatunga & Smith (1968*a*, *b*) in the cat and Close & Hoh (1968) in the rat, it is known that the isometric twitch tension of the mammalian fast- and slow-twitch muscles vary differently when the temperature is lowered from 35–37 °C. Whereas the twitch tension of slow-twitch muscle decreases, that of fast-twitch muscle increases with cooling. The temperature dependence of several contraction parameters of rat extensor digitorum longus (fast-twitch) and soleus (slow-twitch) muscles has been examined in much greater detail in our subsequent studies (Ranatunga, 1982; Ranatunga & Wylie, 1983).

This paper is a report of the effects of temperature on the isometric tension development in the flexor digitorum longus (fast-twitch) and the soleus (slow-twitch) muscles of the cat hind limb and it extends our original observations, which were only briefly reported (Buller *et al.* 1968*a*, *b*). The results from cat soleus muscle in particular should be of interest, since – in comparison with rat soleus muscle – it is known to be a more homogeneous slow-twitch muscle (see Close, 1972).

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METHODS

Cats weighing 1·7–2·5 kg were used under pentobarbitone sodium (40 mg/kg body weight) anaesthesia. Dissection of the hind leg muscles with their motor nerves and setting them up for isometric recording was done essentially as described by Buller & Lewis (1965*a*). Most of the experiments were done on the soleus (slow-twitch) and the flexor digitorum longus (fast-twitch) muscles. The animal was mounted on a conventional cat frame and the exposed muscles of the calf region and their motor nerves lay in a pool of paraffin made by sewing the skin flaps. Special care was taken to ensure that the muscle's blood vessels in the leg were well exposed to the paraffin.

Temperature control and variation

The cat's body temperature was kept at 37–38 °C by a thermostatically controlled electric blanket wrapped round the animal. The temperature of the pool of paraffin was maintained at 37–38 °C by an electric heating lamp. Cooling of the pool to 27–28 °C was done typically by switching off the lamp. Further cooling to around 20 °C was done by immersing in the pool a (flat) coil of glass tubing and passing cool water through it. About 20 min was allowed for equilibration of muscle temperature, before recording was made at a new temperature.

Both the oral temperature and the pool temperature were monitored continuously by means of thermistors. In the results presented here, temperature refers to paraffin pool temperature measured close to the muscle. In one experiment where internal muscle temperature was measured by means of a fine thermocouple inserted into the muscle belly, the muscle interior was found to be within 1 °C of that of the pool temperatures in the range 38–28 °C. In two experiments, in which the cat's body temperature was lowered to around 30 °C and the pool temperature varied between 38 and 28 °C, the variation of muscle contractile properties was found to follow changes in the pool temperatures.

Stimulation and tension recording

The muscles were stimulated through their individual motor nerves which were divided centrally, and placed on bipolar platinum or silver wire electrodes. Square-wave electrical pulses of 0·1–0·2 ms duration were used (from Type Mk IV, Devices) and the intensity was adjusted to be three or four times the minimal value that produced the maximal twitch tension.

Tension recording was done by means of resistance-bridge tension transducers (Statham Instruments). They were mounted on micrometers which enabled adjustment of initial muscle length. A number of tension transducers having different tension maxima were used during this study. Their unloaded resonant frequencies ranged between 600 Hz and 1·2 kHz, and they were linear within $\pm 2\%$ over their entire tension range. The tension transducer output was amplified by a Fenlow d.c. bridge-balance amplifier (Type ZA2, Fenlow Electronics). The amplifier output was analysed by using electronic circuitry built as described by Buller & Lewis (1965*b*) to obtain such characteristics as resting tension, active tension, time to peak tension, and rate of rise of tension. Using a data logger (Solartron Electronic Group Ltd.), these values were obtained as a typewriter print-out during each cycle of stimulation. A small digital computer (PDP 8/I with AX08, Digital Equipment Corporation) was available for later experiments. The computer was programmed to carry out stimulation, gain adjustment etc., on-line, and also provide the characteristics of the myogram as a teletype print-out and/or as an alpha-numeric CRO display (Ranatunga, 1972).

Procedure

Typically, a muscle was set up for recording at 37–38 °C. The stimulus parameters and the initial length of muscle were adjusted to obtain maximal twitch tension. Evidence was always sought by a double stimulus pulse technique for the presence of a back response (Brown & Matthews, 1960), and the few muscles which showed a back response were excluded from the study. The same procedure was adopted when temperature was lowered to 27–28 °C and to 20–22 °C. Muscles were stimulated once every 20 or 30 s whether or not the responses were recorded. This cycle of stimulation was discontinued while cooling in some experiments. The stimulation frequencies used in recording maximum tetanic tension were around 200 and 80–100 Hz at 37–38 °C, and 60–90 and 25–50 Hz at 20–24 °C, respectively for flexor digitorum longus and soleus muscles. The duration of a stimulus train ranged from 0·5 to 1·0 s. Experiments on six flexor digitorum longus and seven soleus muscles were done primarily to obtain the maximum rate of tetanic tension development at 37–38 °C and at 27–28 °C. In these experiments, a series of about ten short tetanic contractions were recorded at each temperature, in order to ascertain the true fusion frequency. The differentiated tension record was smooth and the rate of tension rise was highest at this frequency (Buller & Lewis, 1965*a*). The true fusion frequencies at 37–38 °C were around 500 Hz for flexor digitorum longus and 300 Hz for soleus; at 27–28 °C, they were 250–350 Hz for flexor digitorum longus and 150–200 Hz for soleus.

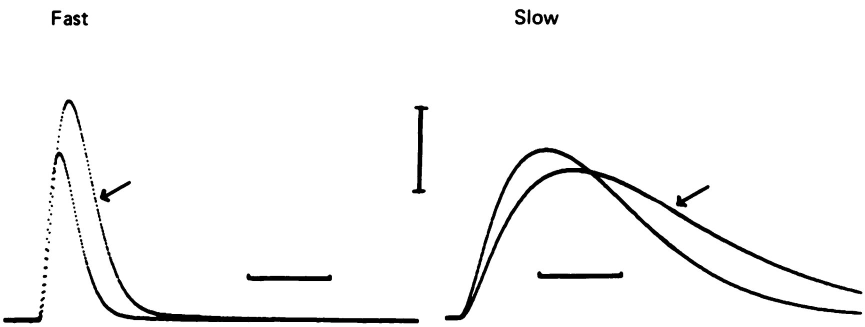

Fig. 1. Isometric twitch myograms from a flexor digitorum longus (left) and a soleus (right) muscle of cat recorded using, on-line, the PDP 8/I computer (Ranatunga, 1972). From each muscle the twitch myogram recorded at 29 °C (indicated by arrow) is superimposed on that recorded at 37 °C. The horizontal bars represent 70 ms and the vertical bar represents 1 N.

The recovery of the muscle responses following rewarming back to 37–38 °C was examined in most cases. The maximum tetanic tension after rewarming did not differ by more than 10 % from that recorded before cooling.

RESULTS

Isometric twitch myograms recorded from a flexor digitorum longus and a soleus muscle of a cat are shown in Fig. 1. These were recorded using a PDP 8/I computer on-line. From each muscle, the myogram recorded at 29 °C (marked by arrow) has been superimposed on that recorded at 37 °C. These records illustrate the basic observation reported by Buller *et al.* (1968*a*). Whereas the twitch tension in the fast-twitch muscle is higher at 29 °C, that in the slow-twitch muscle is lower at 29 °C than at 37 °C.

Fig. 2 illustrates results from four flexor digitorum longus muscles and four soleus muscles in which twitch tensions were recorded while the muscles were cooled from and rewarmed back to 38 °C. The twitch tensions are normalized to that recorded at 37–38 °C before cooling and are plotted on the ordinate. It may be seen that the twitch tension in flexor digitorum longus increases sharply as the temperature is lowered from 38 °C; the highest tension development occurs at temperatures around 20–22 °C. In soleus, on the other hand, the twitch tension decreases with cooling from 38 °C. The mean normalized twitch tensions for three different temperature ranges are given in Table 1. The mean twitch tension is 100 % higher in flexor digitorum longus muscle at 20–22 °C, whereas it is around 40 % lower in soleus muscle at 20–24 °C, when compared with their twitch tensions recorded at 37–38 °C.

Both muscles developed lower tetanic tensions at lower temperatures and the relative decrease in tension with temperature was similar between the two muscles (see Table 1). The tetanic tension is decreased by about 5–7 % in cooling to 27 °C, and by 17 % in cooling to 20 °C. The cooling depression of tetanic tension is apparently more pronounced below about 27 °C. In both muscles the maximum rate of tension

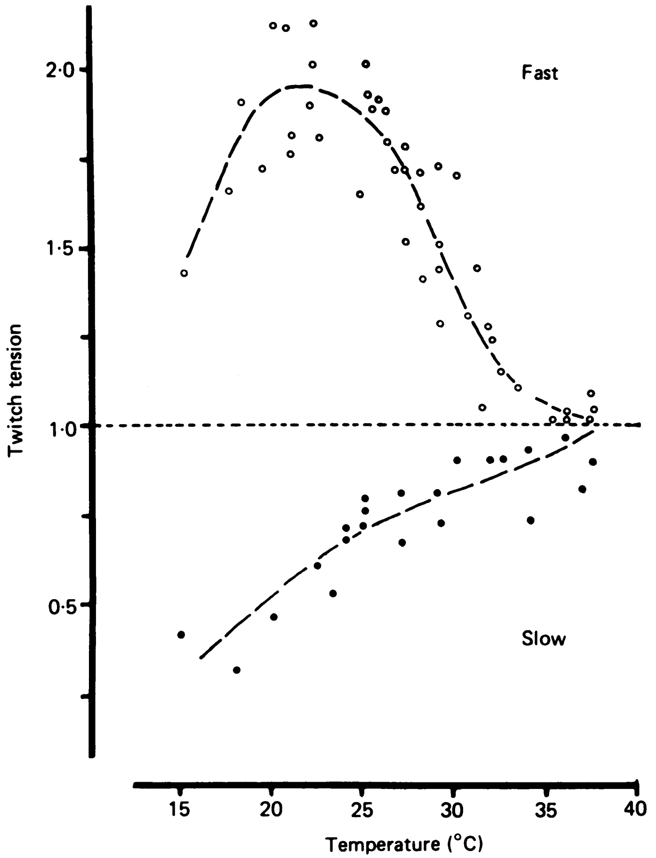

Fig. 2. Variation with pool temperature of the twitch tension in flexor digitorum longus (○) and soleus (●) muscles. Results are from four flexor digitorum longus and four soleus muscles, in which pool temperature was lowered and raised (see Methods). Twitch tension is plotted, along the vertical axis, as a ratio of that recorded at 37–38 °C before cooling, against the pool temperature in °C. Results include those obtained during cooling and rewarming. The interrupted lines through the data points were fitted by eye.

development in a fused tetanus also decreased in lowering the temperature (see Table 1) from 38 to 27 °C. The relative decrease in the rate of tension development, however, was significantly higher in the slow-twitch muscle. The mean decrease was 35 % in soleus as compared with about 12 % in flexor digitorum longus muscle.

When, in flexor digitorum longus, the twitch tension recorded 10–20 s after a tetanus was compared with the pretetanic twitch tension at the same temperature, it was found to be 75 % higher at 37–38 °C. The extent of this post-tetanic

TABLE 1. Summary of results for three different temperature ranges from sixteen flexor digitorum longus (fast-twitch) and thirteen soleus (slow-twitch) muscles of the cat

	Flexor digitorum longus data		
	37–38 °C	27–28 °C	20–22 °C
Time to peak twitch (ms)	19·8 ± 0·5 18 (10)	30·3 ± 1·1 14 (9)	44·6 ± 1·7 8 (8)
Twitch/tetanic tension ratio	0·16 ± 0·01 14 (8)	0·26 ± 0·02 9 (7)	0·33 ± 0·03 6 (6)
Post-tetanic potentiation	1·75 ± 0·1 13 (8)	1·20 ± 0·05 8 (7)	1·09 ± 0·03 6 (6)
Twitch tension	1·00 ± 0·01 19 (10)	1·48 ± 0·05 16 (10)	2·00 ± 0·07 8 (8)
Tetanic tension	0·99 ± 0·01 14 (8)	0·95 ± 0·01 9 (7)	0·82 ± 0·03 6 (6)
Rate of tension rise	0·98 ± 0·01 11 (6)	0·87 ± 0·04 7 (6)	— —
	Soleus data		
	37–38 °C	27–28 °C	20–24 °C
Time to peak twitch (ms)	78·1 ± 2·7 12 (6)	133·0 ± 7·8 8 (5)	182·0 ± 17 5 (5)
Twitch/tetanic tension ratio	0·24 ± 0·01 12 (6)	0·23 ± 0·02 7 (5)	0·16 ± 0·03 5 (5)
Twitch tension	0·97 ± 0·02 12 (6)	0·80 ± 0·02 9 (5)	0·57 ± 0·02 5 (5)
Tetanic tension	1·00 ± 0·01 12 (6)	0·93 ± 0·02 7 (5)	0·83 ± 0·04 5 (5)
Rate of tension rise	1·00 ± 0·01 13 (7)	0·65 ± 0·03 8 (7)	— —

Each value gives the mean ± S.E. of mean, the number of observations and, within parentheses, the number of muscles. The data include those obtained in cooling and rewarming. The twitch tension, the tetanic tension and the rate of tension rise (in a tetanus) were normalized to those recorded before cooling at 37–38 °C. Post-tetanic potentiation gives the ratio of post-tetanic/pretetanic twitch tension.

potentiation of twitch tension decreased with cooling. As seen from the data in Table 1, the post-tetanic potentiation was only 9 % at 20 °C.

DISCUSSION

Results we have reported here from cat muscles differ in one important respect from those reported for rat muscles. It is seen from our data that the twitch tension in the cat slow-twitch muscle (soleus) decreased by about 40 % when cooled from 38 to 20–24 °C. This is very much higher than that reported from rat slow-twitch muscle. The percentage decrease in twitch tension in rat soleus was less than 20 % when cooled from 35 to 20 °C, with either direct stimulation (Close & Hoh, 1968; Ranatunga, 1977) or with nerve stimulation (Hoh, 1974). Cooling to only 27–28 °C was sufficient to obtain a twitch tension depression of that magnitude in cat soleus muscle (see Table 1). Moreover, in order to obtain a 40 % depression (as seen in cat soleus), the rat soleus muscle had to be exposed to very low temperatures of 10–11 °C (K. W. Ranatunga & S. R. Wylie, unpublished observations). It is known that the cat soleus is a homogeneous muscle consisting only of slow-twitch motor units (Henneman, Macphedran & Wuerker, 1965; Burke, 1967) having the same histochemical definition (Henneman & Olson, 1965). The rat soleus, on the other hand, contains, both on the basis of histochemistry and motor unit types, a mixture of slow-twitch and intermediate muscle fibres (Close, 1967; Stein & Padykula, 1962). The difference between cat soleus and rat soleus data may be at least partly accounted for on the basis of this difference in their muscle fibre composition. The extent of cooling potentiation and post-tetanic potentiation seen in cat flexor digitorum longus muscle appears to be within the range obtained for rat fast muscle (Hoh, 1974; Krarup, 1981).

Cooling depression of tetanic tension in cat muscles is essentially similar to that obtained for rat muscles (see Ranatunga & Wylie, 1983). It is of interest to note, however, that the maximum rate of tetanic tension development in the cat slow-twitch muscle is clearly more temperature sensitive than that of the fast-twitch muscle. An indication of such a difference was noted between rat slow and fast muscles (Ranatunga, 1982; Ranatunga & Wylie, 1983).

In general, these findings from cat muscles suggest that the differences between mammalian fast-twitch and slow-twitch muscle fibres – with respect to the temperature dependence of their contractile characteristics – may be more pronounced than was indicated in rat muscle experiments.

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