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CONTRACTIONS OF A HUMAN SKELETAL MUSCLE AT DIFFERENT TEMPERATURES

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SUMMARY

1. Influence of temperature on electrically evoked twitch contractions and maximal voluntary contractions was studied in human first dorsal interosseus muscle. The range of the muscle temperature was 35–12 °C.

2. The maximal twitch tension decreased by about 50% in cooling from 35–12 °C; the tension decrease was more pronounced below 25 °C. The temperature coefficients (Q_{10} values) estimated for muscle temperatures of 35–25 °C were 1·43 for time-to-peak and 1·7 for half-time of relaxation.

3. The maximum voluntary tension remained relatively constant on cooling to 25 °C but decreased by about 30% on cooling to 12–15 °C. The normalized rate of tension rise in voluntary contractions was largely independent of temperature.

4. Results are discussed in relation to previous work on temperature and muscle contraction in humans and in animals.

INTRODUCTION

The influence of temperature on contraction characteristics of skeletal muscle has been examined in detail in a number of vertebrates including at least three mammals, namely the cat, the rat and the mouse (Cullingham, Lind & Morton, 1960; Close & Hoh, 1968; Ranatunga, 1977, 1980, 1984; Stein, Gordon & Shriver, 1982; Buller, Kean, Ranatunga & Smith, 1984). These studies have shown three main features of interest. First, the twitch tension in a fast muscle increased whereas that in a slow muscle decreased when the temperature was lowered from 35–37 °C to 20 °C (Buller Ranatunga & Smith, 1968, 1984; Close & Hoh, 1968). Secondly, the maximum tetanic tension was depressed on cooling in both muscle types and the depression was more pronounced on cooling below 20 °C (Ranatunga & Wylie, 1983). Thirdly, the temperature coefficients (Q_{10} values) obtained for parameters which were related to speed of contraction and relaxation were lower at higher temperatures (35–25 °C) than at lower temperatures (Hill, 1972; Sandow & Zeman, 1979; Stein *et al.* 1982; Ranatunga & Wylie, 1983).

There have been a number of studies on human muscle in which the voluntary contractile performance was examined at altered muscle temperatures (Edwards, Harris, Hultman, Kaijser, Koh & Nordesjo, 1972, and references therein). It has been

shown that the endurance time of sustained, submaximal, voluntary contractions was temperature-dependent (Clarke, Hellon & Lind, 1959), being optimal at intermediate peripheral temperatures of 18–26 °C and that alteration of the rate of muscle metabolism and accumulation of metabolites may be at least partly responsible for muscle fatigue at high temperatures (Edwards *et al.* 1972). Additionally, the maximal voluntary tension was found to be depressed when exposed to temperatures below about 20 °C (at muscle temperatures below 27 °C: Clarke *et al.* 1959). By comparison with the depression of tetanic tension in the cat muscle on cooling, the possibility was raised that this type of depression of voluntary tension on cooling may be due to neuromuscular block and to failure within muscle fibres (Clarke *et al.* 1959; Cullingham *et al.* 1960). Binkhorst, Hooft & Vissers (1977) studied the force–velocity relationship of the handgrip muscles of the forearm using maximal voluntary contractions. They found that within a muscle temperature range of 22–38 °C the maximum force was not significantly altered but the maximum shortening velocity was increased with temperature (Q_{10} 1·2). More recently, Davis, Mecrow & White (1982) reported some observations on the effects of temperature on the contractile properties of the triceps surae muscle. Davies *et al.* (1982) observed that heating and cooling were generally without effect on maximal voluntary tension, although under the coldest conditions (muscle temperature of 24 °C) the tension was significantly reduced. They also reported that the evoked twitch tension was depressed, as was expected from a slow muscle (see above), and the twitch time course lengthened with a Q_{10} of 1·5 under these conditions.

The above studies on human muscle have been made on large, relatively proximal, muscles of the body (muscles of the forearm and the leg). Since changing the temperature in such muscles was difficult, large temperature gradients (in excess of 10 °C) evidently existed between the surface and the muscle interior when exposed to cold conditions (Clarke *et al.* 1959; Davies *et al.* 1982). Therefore, some uncertainty remains as to whether the results can be compared directly with those obtained from small animal muscles. The severity of this uncertainty may be reduced by experimenting on a small peripheral muscle of the body, such as the first dorsal interosseus muscle of the hand. This was the aim of the present study. Additionally, hand muscles may normally become exposed to a range of temperatures and hence our results should also be useful with regard to their normal function.

METHODS

Experiments were done on four subjects and in three of them both left and right first dorsal interosseus muscles were examined in different experiments. The subjects gave their informed consent to taking part in the experiments.

Hand stabilization and tension recording

The first dorsal interosseus muscle produces abduction of the index finger. Evidently the first dorsal interosseus is the only muscle which produces abduction of the first phallanx of the index finger (Milner-Brown, Stein & Yemm, 1973*a*; Desmedt & Godaux, 1978). Therefore, in order to record its contractions isometrically it was necessary to stabilize the whole hand, only allowing free movement of the index finger; the muscle force during contraction could then be monitored indirectly by placing a force transducer against the index finger, preventing its abduction. In early experiments, a Plasticine mould was tried out for stabilizing the hand (Stephens & Taylor, 1972)

but it was not suitable for dealing with different temperatures since the consistency of Plasticine changed. A simple hand clamp was therefore designed and built (see Fig. 1). It consisted of two plywood plates; the basal plate, on which the hand rested, was rigidly bolted to a heavy metal base. The basal plate carried a semicircular aluminium plate for clamping the thumb, and screws for the upper plywood plate which clamped the other fingers except the index finger. A further 'semicircular' aluminium clamp held and stabilized the wrist. The relevant surface of each clamp was padded with sponge. This method of hand stabilization reduced the hand movement sufficiently to obtain reproducible results.

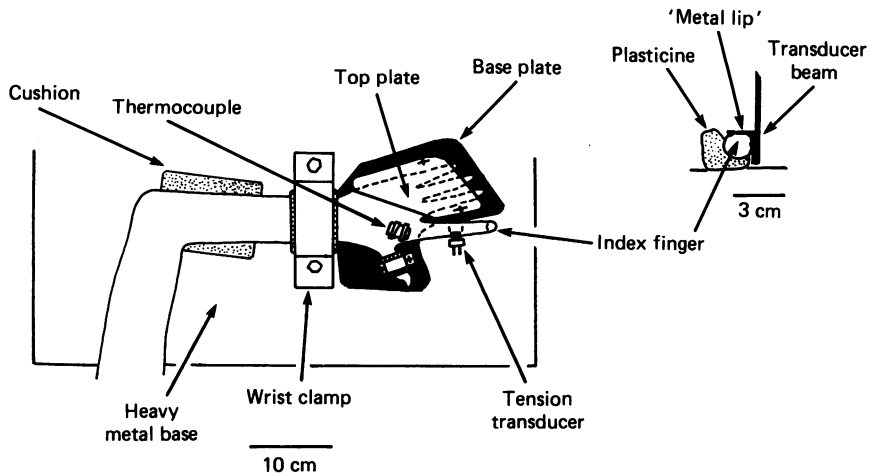

Fig. 1. A diagrammatic representation of the mechanical recording apparatus used in the experiments. The hand was stabilized by clamping between two wooden plates and by a thumb clamp as shown. Contraction of the first dorsal interosseus was recorded by placing the force transducer against the first interphalangeal joint of the index finger (see inset). Cooling and warming was done by placing over the hand a rubber bag through which cold or warm water was circulated. The temperature of the skin overlying the muscle was monitored by a Cr/Al thermocouple connected to a meter.

The index finger was so positioned with a small Plasticine mould that its abduction was resisted solely by the force transducer. The transducer was a brass cantilever beam with a strain gauge element (R. S. Components Ltd.) bonded to each wide side near its base and its resonant frequency was around 500 Hz. The transducer beam was placed vertically against the first interphalangeal joint of index finger, at right angles to the finger axis. The transducer output was examined on two storage oscilloscopes (Telequipment, DM 63).

Temperature variation and measurement

Cooling and warming of the hand was done by using two water baths, one filled with ice and water and the other with water warmed to a required temperature between 25 and 45 °C by means of an electrical, immersion, heating coil. The device used for changing hand temperature consisted of a rubber bag (13 cm × 13 cm) connected to the circulating system of each water bath. A rubber bag was placed on the dorsal surface of the hand over the first dorsal interosseus and also covered much of the metacarpal region of the hand. The bag was held firmly against the subject's hand by a strip of aluminium alloy and water from a water bath was pumped through it to change the temperature.

The temperature of the skin overlying the first dorsal interosseus muscle was monitered by means of a Cr/Al thermocouple connected to a meter. The effective surface area of the thermocouple tip was increased to 1 cm^2 by encasing it in aluminium foil which was placed over the central area of muscle. A cushion of sponge placed upon it insulated it from direct heating or cooling by the rubber bag. The hand temperature (monitored as above) was stable to within 2 °C during contraction recording.

Types of contractions, their measurements and experimental procedures

The experimental results reported in this paper refer to two types of contractions, the rapid voluntary contractions and the twitch contractions evoked by a maximal electrical stimulus to the nerve. In both cases, the contractions were stored on the two oscilloscope screens set at two different sweep speeds, and the corresponding skin temperature was noted.

Twitch contractions were evoked by applying square-wave electrical pulses of 0·5 ms duration and of supramaximal intensity (around 50 V) to the ulnar nerve at the elbow. Stimulation at the wrist and at the muscle's motor point were tried in early experiments but were found to be inconvenient and unsatisfactory for our experiments. The stimulating electrodes were a large metal plate anode strapped to the forearm and a saline-soaked cathode (approximately 1 cm^2 area) placed against the ulnar groove at the elbow. The peak tension, the time-to-peak and the half-time of relaxation were measured from each twitch contraction record stored on the screen.

During voluntary contraction experiments, the subject was instructed to look at the 'slow' oscilloscope screen and to respond, after a certain delay, with a maximal, fast, voluntary abduction of the index finger. Two measurements were made from a voluntary contraction. They were the peak tension and the rate of tension rise at half-peak tension; the linear slope of the tension trace at half-peak tension was calculated (see Fig. 5*B*). In animal muscle experiments, the time-to-peak and time to half-rise to peak tension are measured to monitor the rising phase of a contraction (Ranatunga & Wylie, 1983). It was difficult to make such measurements in a voluntary contraction because of the gradual initial onset of the tension rise.

Either twitch contractions or maximal voluntary contractions were recorded in a given experiment on a subject. Typically, contractions were first recorded at 'resting temperature' (20–25 °C). The hand was then warmed or cooled slowly and contractions were recorded at a new temperature after allowing 5–15 min for equilibration and, in the case of evoked contractions, after checking the adequacy of the stimulus as well; contractions were recorded at 'resting temperature' again, towards the end of an experiment. In a given experiment on one muscle, data were collected in one sitting for eight to fourteen different skin temperatures over a minimum temperature range of 14–36 °C. Five contractions were recorded at each temperature. The coefficient of variation (S.E. of mean as a percentage mean) of such recordings was typically less than 5%, except for the rate of tension rise in voluntary contractions where it was higher (see Results).

Control experiments and general considerations

A number of different types of control experiments were performed to ensure that evoked contractions recorded under the conditions presented here were maximal twitch contractions. These included examination of evoked responses at different stimulus settings. Fig. 2*A* shows six superimposed evoked contractions recorded from one subject as the stimulus intensity was increased from 0 to 50 V. It is seen that the amplitude increased markedly with increase of intensity up to 30 V but, within experimental error, it remained the same at higher intensities. Fig. 2*B* shows four superimposed evoked contractions from another subject, where the stimulus intensity was kept constant at 50 V and its duration was changed from 0·2 to 0·7 ms; the amplitude increased as the duration was lengthened from 0·2 to 0·5 ms, but remained maximal at stimulus widths of 0·5 ms and 0·7 ms. In comparison with animal muscle experiments (Ranatunga & Wylie, 1983) and other human muscle experiments (Ismail & Ranatunga, 1978), the results in Fig. 2*A* and *B* indicate that the evoked contractions we have examined are maximal twitch contractions.

In some mammalian nerve–muscle preparations, application of a single maximal stimulus to the motor nerve results in a brief summated response due to some muscle fibres being excited twice (Merton, 1954*b*; Brown & Matthews, 1960). This is shown to be due to the first muscle action potential ephaptically stimulating nerve terminals which in turn re-excite some muscle fibres. Since presence of such a back-response can alter the twitch time course and tension development inappropriately, we checked for its presence or absence under the conditions adopted here by applying two stimuli to the ulnar nerve, separated by varying short intervals of 1–3 ms. Such experiments done at different temperatures all indicated that if a back-response was present its effect was not very significant in our experiments. Indeed, the original observations of Merton (1954*b*) showed that such back-response effects are not present in human hand muscle when the nerve is stimulated at the elbow.

In a number of experiments we recorded the electromyogram accompanying muscle activation by means of two silver cup electrodes placed over the skin of muscle belly (see Fig. 3*B*). Such

recordings at different temperatures clearly showed that cooling lengthens their duration, thus indicating that the experimental procedures adopted here do lead to changes in muscle temperature.

In all the routine experiments reported in the Results section, muscle contraction characteristics were examined in relation to the skin temperature, measured as described above. There was no convenient way of obtaining the average muscle temperature under the experimental conditions

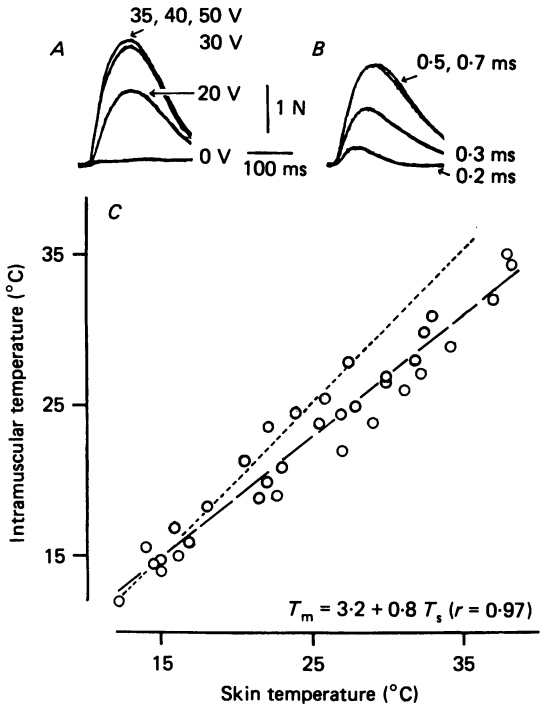

Fig. 2. *A*, superimposed twitch contractions recorded at six different stimulus intensities (given in volts). Stimulus width was 0·5 ms and it was applied to the ulnar nerve at the elbow. Note that the contractions at the three highest intensities are supramaximal (subject C.S.). *B*, four superimposed twitch contractions recorded with different stimulus durations (given near records). Stimulus intensity was 50 V (subject B.S.). *C*, data obtained in two separate experiments on one subject (K. W. R.) to illustrate the correlation between the intramuscular and skin temperatures. The intramuscular temperature was monitored at a depth of 0·5–0·7 cm and the skin temperature was monitored as in routine experiment over a 1 cm^2 area overlying the muscle. In each experiment, data were obtained over the entire temperature range on cooling and warming. The line through the points represents the calculated regression ($r = 0·97$, $n = 34$). The regression equation is $T_m = 3·2\ (\pm 0·9) + 0·8\ (\pm 0·03)\ T_s$, where T_m and T_s are muscle and skin temperatures (in °C); the S.E. of the mean is given in parentheses. Dashed line is the line of identity.

adopted here and we assumed that the skin temperature measured over a relatively large area has a certain direct relation with the average temperature of the muscle lying just beneath the skin. In one subject we carried out two seperate control experiments during which, in addition to the skin temperature, the intramuscular temperature was monitored by means of a fine copper–constantan thermocouple inserted into the muscle. The thermocouple mounted in a hyperdermic needle was pushed about 1·5 cm into the muscle at an oblique angle so that its tip was about 5–7 mm below the skin. Fig. 2*C* shows the data gathered from these experiments correlating the skin temperature and the intramuscular temperature, both measured simultaneously as described above. It is seen that the intramuscular temperature has changed fairly readily under our experimental conditions, but at higher temperature the discrepancy between muscle and skin temperature is greater. The

direct dependence of the intramuscular temperature of a small peripheral muscle on the external temperature was indeed expected from the results of previous workers on larger and more proximal human muscles (muscles of the calf and forearm) (Clarke *et al.* 1959; Binkhorst *et al.* 1977; Davies *et al.* 1982). In these studies the intramuscular temperatures monitored at a depth of up to 1–2 cm were found to vary readily with the applied external temperature. The dashed line in Fig. 2*C* represents the line of identity and the interrupted line drawn through the points represents the calculated regression ($r = 0{\cdot}97$, $n = 34$) according to which the equation relating the intramuscular temperature (T_m) and the skin temperature (T_s) is $T_m = 3{\cdot}2\ (\pm 0{\cdot}9) + 0{\cdot}8\ (\pm 0{\cdot}03)\ T_s$, where the numbers within brackets represent the S.E of the coefficients. The presentation of data in the next section is in the form of scatter diagrams and in relation to skin temperature which is plotted as reciprocal absolute temperature ($10^3 \mathrm{K}/T$). The data for time-to-peak, time to half-relaxation and rate of tension rise are presented as Arrhenius plots, and the temperature coefficients are calculated from the slope of the linear regressions fitted to such data (Ranatunga, 1984); the above equation will be used in the calculation of temperature coefficients based on muscle temperature.

RESULTS

Twitch contractions recorded at two different skin temperatures are shown in Fig. 3*A*. It is seen that cooling has lengthened the contraction and slightly decreased the peak amplitude (tension). The electromyograms shown in Fig. 3*B* show clearly that the duration is increased on cooling. The peak twitch tension data collected from five muscles are shown in Fig. 3*C* where the vertical axis is percentage tension (see below) and the horizontal axis is skin temperature (plotted as the reciprocal of the absolute temperature). From each muscle contractions were recorded over nearly the entire temperature range. Since five muscles developed different tensions, the tensions were represented as percentages of that recorded from each muscle at $37{\cdot}5 \pm 2{\cdot}5$ °C, and a symbol represents the mean calculated on such percentage tensions collected within a 5 °C temperature range. Thus, each symbol denotes the mean of five to fifteen contraction recordings. Despite much scatter, these results show that the twitch tension in the first dorsal interosseus decreases sharply on cooling below about 25 °C, whereas it remains little affected at higher temperatures.

The time-to-peak and the time to half-relaxation data obtained from these experiments are illustrated as Arrhenius plots in Fig. 4*A* and *B* respectively, where each symbol represents the mean from five contractions. The results clearly show that both time-to-peak and time to half-time of relaxation increased with cooling. The mean ($\pm$S.E. of mean) time-to-peak from five muscles was 65 ± 4 ms at 37·5 °C and it was 128 ± 9 ms at a skin temperature of around 12·5 °C. The line drawn through the points represents the calculated regression ($r = 0{\cdot}81$, $P < 0{\cdot}001$) and it corresponds to a Q_{10} value of 1·34 for skin temperatures of 35–25° C. Based on the same regression, the Q_{10} value estimated for muscle temperatures of 35–25 °C (see Methods) was 1·43.

The mean ($\pm$S.E. of mean) half-time to relaxation at 37·5 °C (skin temperature) was 51 ± 3 ms and at 12·5 °C it was 140 ± 10 ms. As in Fig 4*A*, the continuous line through the points is the calculated linear regression ($r = 0{\cdot}88$, $P < 0{\cdot}001$) between the logarithm of the reciprocal of the half-time to relaxation and the reciprocal of the absolute (skin) temperature, $10^3\ \mathrm{K}/T$. The Q_{10} values calculated for 35–25 °C were 1·54 and 1·70, when based on skin temperature and muscle temperature, respectively.

Following the original observations of Hill (1972) on twitch tension relaxation of rat muscle at low temperature, several workers have reported that a number of contraction parameters of isolated mammalian muscle have higher temperature sensitivities at temperatures below about 20–25 °C

than at higher temperatures (see Introduction). An indication of different temperature sensitivities at high and low temperatures is evident on close examination of the pooled data for the half-time to relaxation, shown in Fig. 4*B*. The two dashed lines in Fig. 4*B* are the fitted regressions for skin temperatures higher than and lower than 25 °C (corresponding to a muscle temperature of 23 °C). The regression equation (±S.E. of mean) was log (1/half-time) = 5·48 (±1·07) − 1·30 (±0·326) × 10^3

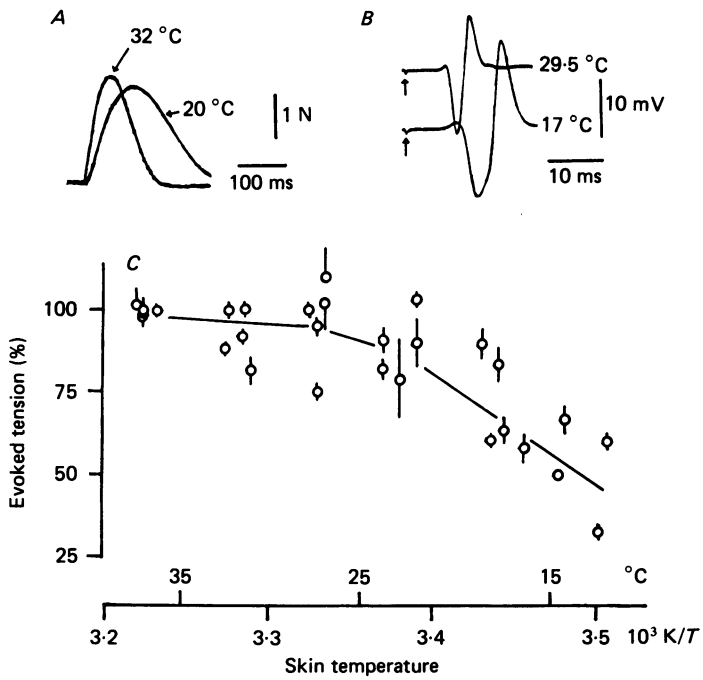

Fig. 3. *A*, two maximal twitch contractions from a subject (K.W.R.) recorded at two different skin temperatures. *B*, two electromyograms recorded at two skin temperatures in response to maximal single stimuli to nerve (subject B.T.). *C*, variation with temperature of the maximal twitch tension. Tensions represented as a percentage of that recorded at 37·5±2·5 °C are plotted on the ordinate and reciprocal skin temperature as 10^3 K/*T* on the abscissa, which is also labelled in °C. Data are from experiments on five muscles, in each of which contractions were recorded at eleven to fourteen different skin temperatures, over a minimum temperature range of 14–36 °C. Each symbol denotes the mean tension from five to fifteen contractions; the vertical bars denote the S.E. of mean associated with the calculations. The line was drawn by eye.

K/*T* for higher temperatures ($r = 0{\cdot}57$, $n = 34$, $P < 0{\cdot}001$) and it was log (1/half-time) = 9·01 (±1·09) − 2·35 (±0·319) × 10^3 K/*T* for the lower temperature range ($r = 0{\cdot}82$, $n = 27$, $P < 0{\cdot}001$). Comparison of these two regressions by covariance analyses (see Snedecor & Cochran, 1967) showed that the residual variance associated with two-regression model was not significantly different from that associated with the pooled, single-regression model (*F* test, $P > 0{\cdot}2$); this indicates that the two-line model does not accommodate the data better than the single-line model. However, comparison of the slopes of the two lines showed that the difference between them was significant ($P < 0{\cdot}03$). Additionally, the Q_{10} value calculated from individual muscle experiments was, in every case, lower for 35–25 °C than for 20–10 °C. The Q_{10} values determined on the basis of the two-line model shown in Fig. 4*B*, were 1·39 and 1·92, respectively for skin temperatures of 35–25 °C and 20–10 °C; they correspond to Q_{10} values of 1·49 and 2·27 when based on muscle temperatures. Similar analyses and considerations made on the time-to-peak data in Fig. 4*A* provided no evidence of a higher temperature sensitivity at the low temperatures. It may be concluded therefore that,

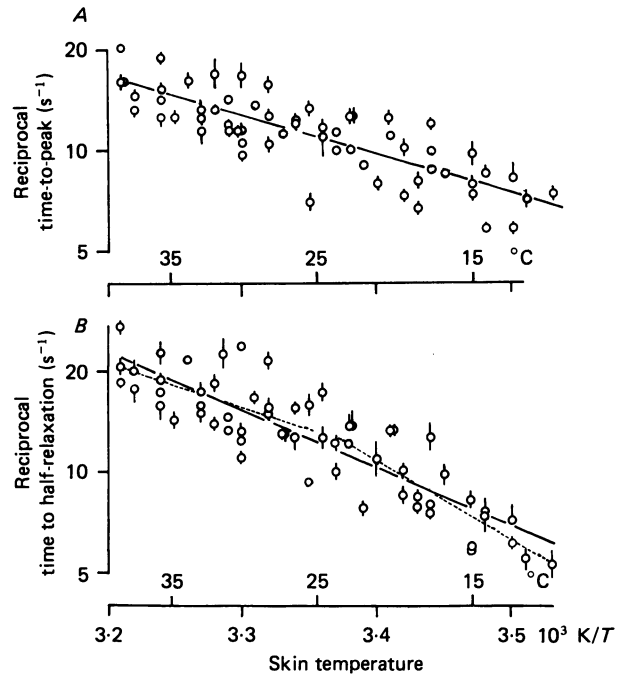

Fig. 4. Data for time-to-peak (A) and for time to half-relaxation (B) measured from maximal twitch contractions. Results are from five muscles and they are presented as Arrhenius plots where the logarithmic ordinate is the reciprocal time measurement and the abscissa is the reciprocal skin temperature, as 10^3 K/T. Each symbol represents the mean of five contractions, and the vertical bars represent $\pm$ S.E. of mean. In symbols without vertical bars, the S.E. was smaller than the width of the symbol. The lines represent the calculated regressions. A, the regression equation was log (1/time-to-peak) = 4·93 ($\pm$0·361) $-$ 1·16 ($\pm$0·108) $\times$ 10^3 K/T, where numbers in parentheses are the S.E. of the coefficients (r = 0·81, n = 61, P < 0·001). The Q_{10} calculated for skin temperatures of 35–25 °C was 1·34 and calculated for muscle temperatures of 35–25 °C was 1·43. B, the continuous line represents the regression calculated from all the data points (as in A); the resulting equation (with S.E. of mean) was log (1/time to half-relaxation) = 6·90 ($\pm$0·418) $-$ 1·73 ($\pm$0·125) $\times$ 10^3 K/T (r = 0·88, n = 61, P < 0·001). The calculated Q_{10} values for 35–25 °C were 1·54 (skin temperature) and 1·70 (muscle temperature). The two dashed lines are regressions fitted for skin temperatures higher than and lower than 25 °C (r > 0·57, n > 26, P < 0·001). See text (small print).

although there is no statistically valid reason for fitting two regression lines to the data in Fig. 4B, the results show that the temperature sensitivity of the rate of tension relaxation may be higher at the low temperatures.

Fig. 5A shows a typical maximal voluntary contraction from a subject. Fig. 5B shows three superimposed contractions recorded at a faster speed so as to estimate the slope of the rising phase (rate of tension rise). The maximum voluntary tensions varied markedly from muscle to muscle and the range obtained from six muscles was 20–90 N. Fig. 5C shows the temperature dependence of voluntary tension in experiments with five muscles, tension is plotted as a percentage of that recorded from each muscle at 37·5 $\pm$ 2·5 °C. Each symbol represents the mean tension from five

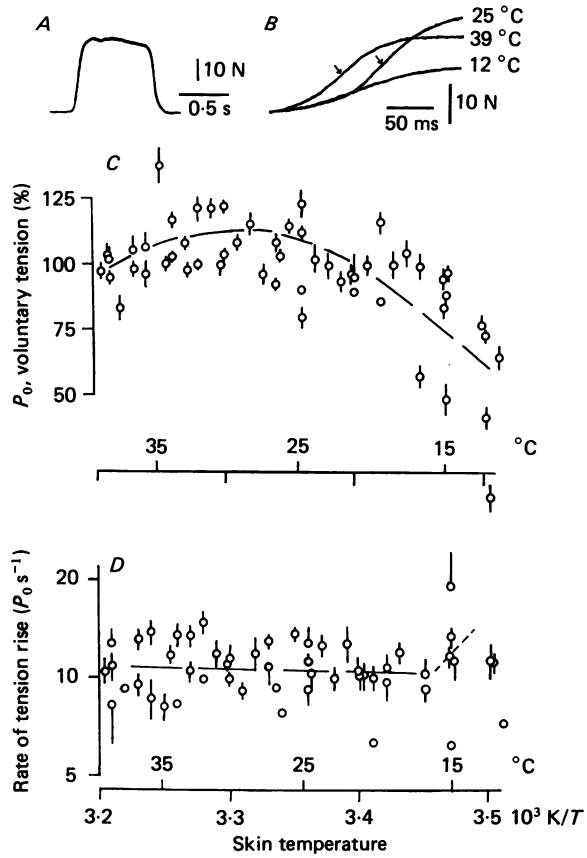

Fig. 5. *A*, a record at slow speed of a rapid maximal voluntary contraction. The maximum tension (P_0) was measured from such records (subject B.T.). *B*, three maximal voluntary contractions at faster speed for estimating rate of tension rise; the slope of the tension record at half-peak tension (arrows) was estimated and represented as a ratio of maximum tension. *C*, data for maximum voluntary tension from five muscles. From each muscle, contractions were recorded in one sitting at eight to eleven different skin temperatures covering a minimum temperature range of 14–36 °C. A symbol represents the mean of five contractions at a temperature and the vertical bar is ± S.E. of mean. The curve through the points was drawn by eye. *D*, temperature dependence of the rate of tension rise in voluntary contractions from experiments on five muscles. Presentation is similar to Fig. 4. Rate of rise was normalized to the tension and plotted on a logarithmic ordinate. Each symbol is the mean of five contractions from a muscle and vertical bar represents ± S.E. of mean. Symbols without error bars were from an experiment in which only the average was recorded.

contractions in one muscle. It is seen that voluntary tension is lower at temperatures below about 20 °C. From a total of seven experiments on six muscles, the mean (± S.E. of mean) tension recorded at 12–15 °C was 72·3 (± 5·2) % of that recorded at 35–39 °C; this is significantly different ($P < 0{\cdot}001$) from 100 %. A decrease of maximum voluntary tension on cooling has been reported by previous workers for other human muscles (Clarke *et al.* 1959; Davies *et al.* 1982). On average, the maximum voluntary tension tended to be a little higher at skin temperatures of around 30 °C.

The mean($\pm$S.E. of mean) tension at temperatures of 25–35 °C was 108 ($\pm$2·9)% and this is also significantly ($P < 0.01$) different from 100%. The rate of tension rise (see Methods) recorded from these contractions is illustrated as an Arrhenius plot in Fig. 5*D*; it was around $10 \times P_0$ s^{-1} (where P_0 is maximum voluntary tension) at 37·5 °C and, within experimental error, it does not appear to change with temperature. The Q_{10} values estimated from pooled data in Fig. 5*D* were 1·01 and 0·9 for high and low temperatures respectively.

It is seen from our results that there is considerable scatter in all the different measurements. Since only twitch contractions or brief voluntary contractions were recorded and voluntary contractions were initiated at infrequent intervals (> 5 min), the scatter in the data is unlikely to be due to muscle fatigue. Indeed, considerably longer voluntary contractions, as well as those initiated successively at shorter intervals, were required in studies on muscle fatigue (Merton, 1954*a*; Clarke *et al.* 1959; Edwards *et al.* 1972; Stephens & Taylor, 1972). Furthermore, circulation to the hand was not arrested by our method of clamping the hand and there was no sign of ischaemic muscle pain during these experimental sessions. It has been shown that rapid temperature alterations can bring about dissociation between the skin temperature and muscle temperature (Clarke *et al.* 1959). Although we avoided rapid cooling and heating, a skin temperature change of 5–10 °C taking 30–40 min, some of the scatter in our results (and in Fig. 2*C*) may be related to such a phenomenon. Other uncertainties may include some contribution from other muscles during contraction recording and imperfections in the mechanical clamping system allowing some movement of the hand during the course of an experimental session. In general, such uncertainties are inherently associated with muscle-contraction recording from intact human subjects and it is assumed in the Discussion below that they did not significantly alter the underlying trends seen in the Results.

DISCUSSION

Our main aim in this study was to examine the temperature dependence of contractions in the first dorsal interosseus muscle of the human hand, adopting an experimental procedure which was basically similar to that used in experiments on isolated mammalian muscle (Ranatunga & Wylie, 1983; Ranatunga, 1984). Thus in a single experimental session on each muscle contractions were recorded at a number of different temperatures (eight to fourteen different skin temperatures) and over a wide temperature range (12–40 °C skin temperatures). On the basis of intramuscular temperature measurements made on larger and more proximal muscles *in situ* (Clarke *et al.* 1959; Binkhorst *et al.* 1977; Davies *et al.* 1982) it was anticipated that the intramuscular temperature of the first dorsal interosseus would vary readily with changes in the environmental temperature. As can be seen from the data in Fig. 2*C*, this was indeed the case. With the particular experimental methods adopted, in which the conductive heat transfer between the hand and the environment was enhanced, the intramuscular temperature was about 4 °C lower than skin temperature at 35 °C and it was within 1 °C of the skin temperature at skin temperatures below 20 °C. Thus the temperature gradients across the experimental muscle were clearly less than those found in previous studies (see Introduction).

The twitch contraction times we have obtained from the first dorsal interosseus muscle (at skin temperatures of around 37 °C) are within the range of values reported from human hand and upper-arm muscles (50–70 ms) (McComas & Thomas, 1968; Desmedt & Godaux, 1978; Ismail & Ranatunga, 1978, 1981; Chapman, Round & Ward, 1984). These are considerably smaller than the values of 100–120 ms recorded from the triceps surae of the lower limb McComas & Thomas, 1968; Desmedt & Godaux, 1978; Davis *et al.* 1982; Chapman *et al.* 1984). Indeed, the first dorsal interosseus has been considered a fast muscle, or a muscle having a predominant fast-twitch component (McComas & Thomas, 1968; Desmedt & Godaux, 1978); 80% of its motor units have been classified as fast units on the basis of contraction-time measurements (Milner-Brown, Stein & Yemm, 1973*b*). It has been shown that cooling of triceps surae muscle results in depression of twitch tension, as expected from a slow muscle (Davies *et al.* 1982). On the other hand, our results show that the first dorsal interosseus does not exhibit a cooling potentiation, as would be expected of a fast muscle (see Introduction). In comparison with animal muscle data (see Ranatunga, 1980; Buller *et al.* 1984), this result suggests that the first dorsal interosseus contains predominantly slow-twitch fibres despite the short contraction time. This is in accordance with the histochemical finding that first dorsal interosseus contains nearly 60% of type 1 (slow) fibres (Johnson, Polgar, Weightman & Appleton, 1973). The temperature coefficients of 1·43 and 1·7 (corrected Q_{10} values for 35–25 °C), obtained for measurements of twitch time course, are considerably lower than those obtained from isolated mammalian muscles (typically higher than 2: Ranatunga, 1980), but they are similar to those reported from human triceps surae (Davies *et al.* 1982) and from cat muscles *in situ* (Buller *et al.* 1984). It remains a possibility that the exact change in muscle temperature is over-estimated in experiments on muscles with intact blood circulation.

Insofar as cooling to low temperatures decreased the maximal voluntary tension, our results are similar to those reported from other human muscles (see Introduction). However, the tension was little affected (or slightly potentiated) on cooling to 25 °C, and cooling depression was clearly evident in lowering the muscle temperature below about 20 °C. In directly stimulated isolated rat muscle the maximum tetanic tension decreased slightly on cooling from 35 to 25 °C but it decreased sharply on cooling below 20 °C, so that the tension at 10 °C was about 60% of that recorded at 35 °C (Ranatunga & Wylie, 1983). This suggests that the depression of voluntary tension by cooling could be due to a direct effect of temperature on muscle fibres and may not be due to failure in neuromuscular transmission. The rate of tetanic tension rise (normalized to tension) in rat muscles has been shown to decrease with cooling (Ranatunga & Wylie, 1983; Elmubarak & Ranatunga, 1984; Ranatunga, 1984). In contrast, the normalized rate of rise of voluntary tension did not show a clear dependence on temperature. In the production of a voluntary contraction, motor units are recruited in an orderly sequence (Milner-Brown *et al.* 1973*b*; Desmedt & Godaux, 1978) and thus one possible explanation of the relative temperature independence of the rising phase of a voluntary contraction is that the motor-unit recruitment order is altered as a consequence of a temperature change. For instance, the particular recruitment sequence may be from slow to fast units at high temperatures whereas it may be from fast to slow motor units at cold temperatures.

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