Abstract The purpose of the present study was to investigate the effect of muscle temperature on the force/velocity relationship of electrically activated human adductor pollicis muscle. Following immersion of the lower arm for 20 min in water baths of four different temperatures, the calculated muscle temperatures were 37.1, 31.4, 25.6 and 22.2°C. At 22.2°C maximal isometric force was reduced to 79.3±2.9% of the force obtained at 37.1°C. 

Q₁₀ values for the maximal rates of force development and relaxation, and relaxation times, were about 2.0 between 37.1 and 25.6°C and increased to about 3.5 below 25.6°C. The Q₁₀ values of the maximal shortening velocity and the velocity for maximal power production were similar to those of the isometric speed parameters. The Q₁₀ for maximal power production increased from 2.0 above 31.4°C to 6.9 between 25.6 and 22.2°C. Following repetitive isometric contractions maximal power production was reduced to 60.0±1.7 and 90.5±1.0% at 37.1 and 22.2°C respectively. Fatigue decreased with cooling of the muscle over the entire (37.1–22.2°C) temperature range.

Key words Force/velocity relationship · Human · Muscle fatigue · Power · Temperature

Introduction

Skeletal muscle function strongly depends on muscle temperature. It has repeatedly been shown in studies of animal (e.g. [26]) and human (e.g. [19]) muscle that maximal isometric force production and the rates of force development and relaxation (Q₁₀ of about 2), decrease with a decrease of muscle temperature [6, 25]. In many situations, skeletal muscles do not contract isometrically, but shorten while they exert force, hence muscles generate power. The power-producing capacity of muscle is described by the hyperbolic relationship between force and velocity, with the maximum power (P_max) being produced when the muscle operates around 30% of its maximum shortening velocity (V_max). From studies of isolated muscle preparations it is well known that the force/velocity relationship changes with muscle temperature. V_max and P_max have a Q₁₀ of about 2.5 in isolated preparations [6, 22, 25, 28, 31], and, like the Q₁₀ of other contractile parameters, it increases at lower temperatures [6, 28].

It is difficult to extrapolate data obtained from isolated preparations to human muscle, partly because isolated muscles (e.g. frogs and fish) are often studied at relatively low temperatures, but also because the temperature dependency may differ among (type I, IIA, IIX and IIB) muscle fibres [11, 27]. Also, muscles of small mammals such as mice and rats have many type IIB fibres, which are not present in human skeletal muscle. Nevertheless, it is clear that maximal power production in humans decreases at lower temperatures during cycling [4, 13, 34] and jumping [1, 13, 23]. However, detailed information about the effects of temperature on the force/velocity and power/velocity relationships of human muscle is not available. Moreover, the reported Q₁₀ values for V_max [10] and P_max [23, 34] during voluntary effort seem rather low (<1.5) compared to the Q₁₀ values obtained from animal preparations (around 2, e.g. [6]) and compared to the Q₁₀ values for isometric speed parameters in electrically activated human muscle (around 2, e.g. [19]). Recently, more detailed information has become available about the temperature effects on the force/velocity relationship of human muscle but in that study isolated fibres were studied between 12 and 22°C, which is outside their normal physiological temperature range [11]. Given the paucity of data on human muscle, the main objective of the present investigation was to study the effects of muscle temperature on the force/velocity and power/velocity relationships of human skeletal muscle over a broad range of physiological temperatures.
Following repetitive fatiguing contractions both maximal isometric force and $V_{\text{max}}$ are reduced [15, 18]. However, the effects of muscle temperature on these changes of the force/velocity relationship following repetitive activation are unknown. Therefore, the second objective of the present study was to quantify, over a broad range of physiological temperatures, the effects of repetitive isometric muscle activation on the force/velocity and power/velocity relationships. Recently, we have shown that the fatigue-induced decreases in isometric force and the speeds of force development and relaxation of human adductor pollicis are smaller at lower muscle temperatures [19]. Consequently, it was anticipated that the fatigued-induced changes in the force/velocity relationship would also be smaller at lower temperatures.

**Materials and methods**

**Subjects**

The study was approved by the local ethics committee and ten healthy subjects (nine females and one male) took part after giving their informed consent. The subjects (20.7±0.5 years of age) all were right-handed and did not undertake regular exercise of the hand muscles. The subjects visited the laboratory on five different occasions. On their first visit they were familiarized with the procedures and electrical stimulation. The actual measurements were made during the other four visits.

**Force recording and stimulation**

Methods for stimulating the adductor pollicis and force recording are given in detail elsewhere [17]. Briefly, the subject sat in an adjustable chair with the left forearm supinated, the hand was held horizontally and securely fixed with the thumb abducted and in contact with a vertical pin. The pin was attached to a strain gauge mounted below the plane of the hand. The forces reported in the present study are those applied by the thumb at the vertical pin. When the thumb was fully adducted its length axis was parallel with the length axis of the index finger and this position was defined as 0° thumb angle. Because the vertical pin of the force transducer was placed between the thumb and the index finger, the smallest thumb angle at which forces could be measured was 36°. It was possible to increase thumb angle up to 74° (maximal abduction) before anatomical limits were approached. Thus, during shortening contractions, the maximal angular displacement was 38°. The timing and duration of stimulation, onset and speed of motor movement and data sampling frequency (1000 Hz) of the force and length signal were computer controlled.

The adductor pollicis muscle was activated by percutaneous electrical stimulation of the ulnar nerve at the wrist with constant current unidirectional square wave pulses of 100 µs duration (Digitimer, model DS7, Welwyn Garden City, UK) at different frequencies. The current was set 30% above the stimulus that produced maximal isometric tetanic force. Force records of isometric contractions were filtered (fourth-order low-pass digital Butterworth filter, 50 Hz cut-off frequency) and differentiated to obtain the maximal rate of force development and relaxation during each contraction.

**Temperature**

To maintain a constant muscle temperature, the subject’s hand and forearm were immersed in a waterbath for 20 min prior to each of the four tests. During the experiments an infusion bag was placed over the subject’s lower arm and this bag was circulated with water from the bath. Bath temperatures were 17.0, 22.5, 30.5 and 45.0°C. Skin temperature was recorded with a thermocouple (diameter 0.25 mm; Thermo Electric Internationaal, Warmond, The Netherlands) secured with sporting tape over the adductor pollicis muscle. Muscle temperatures were calculated from the measured skin temperatures using the recently established linear relationship between skin and muscle temperature ($T_m = 1.02T_s + 0.89$; where $T_m$ is muscle temperature and $T_s$ is skin temperature, $r^2=0.98$; [19]). Because muscle temperature is the important variable, for clarity the data will be presented in relation to the calculated muscle temperatures.

**Experimental protocol**

Force/velocity curves were constructed using short (duration: 1000–90 ms) isovelocity contractions at seven different angular velocities (0, 76, 153, 229, 306, 382 and 458 °/s) applied in random order as described in detail elsewhere [18]. With this method the muscle starts shortening during the rise phase of isometric force development. Therefore, particularly at the highest speeds, it is important that the muscle reaches its maximum active state as fast as possible. To achieve this, muscles were stimulated at frequencies known to produce the maximum rate of force development at each temperature both in the unfatigued and fatigued muscle [19]. At the highest shortening speeds these stimulation frequencies for 22, 25, 31 and 37°C were respectively 150, 200 and 300 Hz for the unfatigued muscle and 50, 100, 150 and 200 Hz for the fatigued muscle. During the relatively long (1 s) isometric contractions (0 °/s) lower frequencies (50 Hz at 22.2°C and 100 Hz at the other temperatures) were used to prevent activation failure, which could otherwise occur during long stimulation at a high frequency, particularly in fatigued muscle. This procedure guaranteed maximal force (power) production under all circumstances.

The thumb adducted twice at each imposed velocity, once with and once without stimulation of the adductor pollicis (=passive shortening). At each velocity the passive force was subtracted from the total force trace to provide a measure of the active force. Ninety seconds of rest was allowed between contractions. After the measurements from the unfatigued muscle had been completed, the blood supply was occluded by inflation of a cuff placed around the subject’s upper arm. Subsequently the muscle was fatigued with 24 isometric contractions, 1 s duration each, with 1.5 s rest in between contractions. The stimulation frequency during the fatigue test was set to produce approximately 90% of the subject’s maximal isometric force at each temperature: 18.6±3.1, 23.6±3.0, 33.9±3.8 and 38.9±3.8 Hz (means ±SEM, from cold to warm respectively). The fatigue protocol respectively wet tert 100, 150, 200 and 300 Hz for the fatigued muscle and 50, 100, 150 and 200 Hz for the fatigued muscle. During the relatively long (1 s) isovelocity contractions at the seven angular velocities (0, 76, 153, 229, 306, 382 and 458 °/s) applied in random order, with 2 s in between contractions. Only following these measurements was the cuff deflated. Blood flow was occluded to induce fatigue rapidly without the risk of a temperature rise due to an increase of blood flow to the muscle during repetitive contrac- tions. In addition, without blood flow occlusion the measurements from the fatigued muscle would have been affected by oxygen-independent recovery processes such as the resynthesis of phospho-creatine. Please note that the same fatigue protocol was used in a recent study [19]. From that study we knew what changes in the force/stimulation frequency and the rate of force development/stimulation frequency relationships would occur at each temperature and this allowed us to adjust the stimulation frequency and guarantee maximal activation of the muscle under all circumstances.

**Data analysis**

All measurements were performed at a thumb angle of 51°, which is the optimum for force production, although the angle/force rela-