

Thermal dependence of muscle function

BENNETT, ALBERT F. *Thermal dependence of muscle function*. Am. J. Physiol. 247 (Regulatory Integrative Comp. Physiol. 16): R217-R229, 1984.—Maximal isometric forces during both twitch and tetanus are largely temperature independent in muscles from both endothermic and ectothermic vertebrates. Anuran muscle can develop maximal force at lower temperatures than mammalian muscle. Tetanic tension is maximal at normally experienced body temperatures in a variety of animals, but twitch tension seldom is. Thermal dependence of twitch tension varies with muscle fiber type: tension decreases with increasing temperature in fast-twitch muscles and remains constant in slow-twitch muscles. In contrast to the low temperature dependence of force generation, rates of development of tension (time to peak twitch tension and tetanic rise time) and maximal velocity of shortening and power output are markedly temperature dependent, with average temperature coefficient (Q_{10}) values of 2.0–2.5. Q_{10} values for rate processes of anuran muscle are only slightly lower than those of mammalian muscle. High body temperatures permit rapid rates of muscle contraction; animals active at low body temperatures do not achieve the maximal rate performance their muscles are capable of delivering. Thermal acclimation or hibernation does not appear to result in compensatory adjustments in either force generation or rate processes. In vivo, dynamic processes dependent on contractile rates are positively temperature dependent, although with markedly lower Q_{10} values than those of isolated muscle. Static force application in vivo is nearly temperature independent.

force generation; isometric contraction; isotonic contraction; skeletal muscle; temperature

TEMPERATURE HAS PERVASIVE EFFECTS on the functional properties of biological systems. The influence of the thermal environment on body temperature and on physiological processes is one of the most extensively studied areas of comparative physiology. Biological rate processes commonly decrease by one-half to two-thirds as temperature decreases 10°C (117). Does such a thermal dependence also apply to force generation and contractile rate processes of muscle? If so, activity and behavioral capacities of animals would be greatly influenced by body temperature. Ectotherms that experience wide fluctuations in body temperature, sometimes over the course of a single day, would find their behavioral capacities strongly curtailed by low temperatures. Ectotherms living at low temperatures continuously would have to cope with these effects chronically. Even vertebrate “homeotherms” may experience major changes in muscle temperature, which can vary greatly from regulated core temperature. For example, resting muscle temperatures of humans may be well below core temperature of 37°C: values of 29.4 (56), 31.5 (131), 32.8 (18), and 34°C (128) have been reported for different muscles. Temperature in these same muscles may increase to 40°C during activity (128, 131). Thus human muscle may

experience a thermal range of more than 10°C, depending on activity level and environmental temperature. Even minor changes in muscle temperature, which could occur in either endotherms or ectotherms, have the potential to alter greatly the rates of muscle contraction and power output.

The first reported observations on the influence of temperature on muscle function were made in 1868 by Marey (93) and Schmulewitsch (133). Since then, more than 100 studies have examined the effect of temperature on muscle force generation or shortening velocity. The literature that attempts to examine the biological relevance of these relationships is much smaller. Most studies were directed at the investigation of the mechanism of contraction and used temperature as an analytic variable. Most of these studies were not done in reference to normal body temperatures of the animals investigated, nor were they interpreted within that context. The purpose of this review is to compile and summarize existing information on the influence of temperature on muscle performance and, to the extent possible, formulate general patterns of response of muscle to temperature. The thermal dependence of both force generation (maximal twitch and tetanic tension) and rate processes (time to

peak twitch tension and tetanic rise time, maximal velocity of shortening, and power output) is summarized from literature values. These data are then analyzed to answer questions concerning the adaptive nature of thermally dependent function in different animals. For instance, is the thermal dependence of muscle function fundamentally different in ectotherms and endotherms; is maximal function (e.g., either force-generating capacity or maximal velocity of shortening) achieved at normally experienced body temperature; do these factors acclimate according to recent thermal history? This article concerns itself only with data on contractile properties and not with studies on the thermal dependence of biochemical systems (e.g., myosin ATPase) isolated from muscle. The thermal dependence of these enzymatic systems may be distinct from and is usually greater than that of contractile performance (3, 39). Also the literature on heat damage to muscle tissue is not discussed (see Ref. 144 for a review). The only previous comprehensive review of this topic was done by Walker (148). Close (29) and Faulkner (43) reviewed the influence of temperature on some aspects of mammalian muscle function, and Josephson (71) summarized the literature on thermally dependent function in insect muscle.

To summarize the large amount of information available, the temperature dependence of a rate process is presented as its temperature coefficient (Q_{10}), where $Q_{10} = (R_2/R_1)^{10/(T_2-T_1)}$, in which R_2 and R_1 are rate processes, respectively, at temperatures T_2 and T_1 , and $T_2 > T_1$. $Q_{10} > 1.0$ indicates a positive thermal dependence; $Q_{10} = 1.0$, thermal independence; and $Q_{10} < 1.0$, declining function with increasing temperature. This notation is used in preference to Arrhenius activation energy, because it is easier to interpret directly and because it is descriptive and does not imply a specific biochemical limitation. Because Q_{10} values by definition apply only to rate processes, it is incorrect to calculate Q_{10} values for quantitative variables, such as force, that are not time derivatives (although this is commonly done in the literature on muscle; see Refs. 7, 39, 53, 118, and 136). Consequently the term thermal ratio or R_{10} is defined here as the quotient of a quantity measured at two temperatures and expressed over a 10°C interval: $R_{10} = (S_2/S_1)^{10/(T_2-T_1)}$, in which S_2 and S_1 are quantities measured, respectively, at temperatures T_2 and T_1 , and $T_2 > T_1$. This expression is analogous to Q_{10} .

In Figs. 2-11 summarizing thermal dependence, Q_{10} or R_{10} is calculated and plotted at the midpoint of the observed thermal range. (For data ranges and sources for Figs. 2, 4, 6-8, 10, and 11, see footnote 1). Where functions were measured at more than two temperatures, individual values for each range are plotted. Figures 2, 4, 6-8, 10, and 11 are meant to provide a complete summary of literature values. Because the quality of data may vary considerably between studies and not all points are independent of each other, it would be inappropriate to use

them as more than indications of general thermal trends among different variables. Consequently no statistical analysis is done on these disparate data.

EFFECT OF TEMPERATURE ON ISOMETRIC CONTRACTILE PROPERTIES

Force

Twitch tension. A series of isometric twitch contractions measured at different temperatures is shown in Fig. 1. These data are representative of a general pattern in skeletal muscle tissue. Twitch tension (P_t) is maximal at some intermediate temperature in the thermal range (e.g., 20°C in Fig. 1). Increments above or decrements below this temperature result in declining values of P_t . R_{10} values consequently exceed 1.0 at temperatures below that of peak P_t and are below 1.0 at higher temperatures.

A summary of literature values of the effect of temperature on P_t is given in Fig. 2. The absolute thermal dependence of P_t is low, with almost all observations of $R_{10} = 0.5-1.5$ (avg ~ 0.9). A general trend of declining P_t with increasing temperature has also been reported by other authors who have not cited quantitative observations (16, 21, 25, 38, 60, 127, 147).

Several authors (6, 11, 70, 145), all working with anuran muscle, have emphasized the diversity of thermal

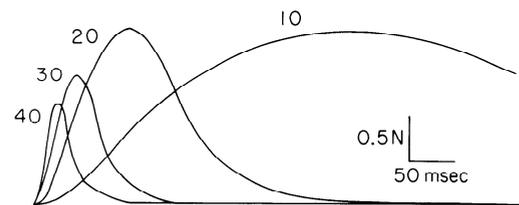


FIG. 1. Force developed during isometric twitch contractions by lizard gastrocnemius muscle at 10, 20, 30, and 40°C. (Data from Ref. 118.)

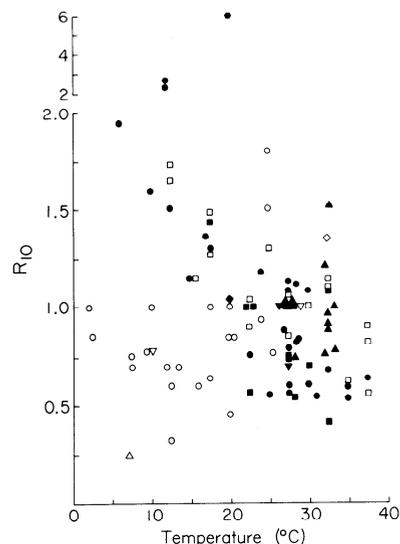


FIG. 2. Thermal dependence of twitch tension. ●, rat; ▲, cat; ▼, hamster; ■, mouse; ◆, bat; ●, pig; ○, anuran; □, lizard; ○, snake; △, fish; ▽, tortoise; ◇, insect. (Data from Refs. 6, 11, 17, 20, 27, 28, 49, 50, 64, 66, 67, 69, 71, 79, 81, 85, 87, 91, 92, 96, 100-102, 106, 112, 115, 118, 119, 121, 122, 125, 135, 140, 143, and 145.)

¹ For individual Q_{10} or R_{10} values for twitch tension, tetanic tension, time to peak twitch tension, twitch relaxation time, tetanic rise time, maximal contractile velocity, and maximal power output data, order NAPS Document 04185 from Microfiche Publications, PO Box 3513, Grand Central Station, New York, NY 10017.

response of P_t within a single group of experimental animals. In one experimental series, P_t of frog gastrocnemius muscle increased between 20 and 30°C in 7 of 16 experiments and decreased in the other 9 (overall range of R_{10} values 0.6–1.4) (6). The average values reported here should consequently be interpreted with some caution.

Isometric P_t is the result of two competing sets of rate processes. One set, including activation and stretching of series elastic components, results in tension development. Another set involves termination of the active state and relaxation of muscle tension. The thermal dependence of P_t reflects a compromise of the thermal dependence of these numerous component rate processes. It is not particularly surprising therefore that the influence of temperature on P_t is so complex and variable.

Different thermal patterns of P_t are apparent among different groups. For mammalian muscle, in studies in which the observed thermal range is sufficiently broad, a peak in P_t occurs at approximately 20°C (38, 49, 69, 100, 139, 140, 143). This is, of course, substantially below normal body temperature. In contrast, peak tension in anuran muscle occurs at very low temperatures, as low as 0°C in some preparations. In all reported observations, except one (5), $R_{10} < 1.0$ for frog or toad muscle. Data on the thermal dependence of P_t in lizard muscle are contradictory. Earlier studies (85, 87) reported species-specific plateaus of maximal P_t of about 5°C, coincident at their upper ends with field-active body temperatures. These observations were not supported by later work (118) on some of the same species, which found instead broad ranges of thermally independent P_t with no consistent relationship between maximal P_t and preferred thermal levels. The previous pattern (85, 87) is more typical of that seen for tetanic tension than twitch tension: because no detailed stimulation protocol was reported, it is possible that these preparations were partially tetanized. As a consequence of the differential thermal dependence of P_t , anuran muscle produces greater levels of P_t (normalized per unit cross-sectional area) than can mammalian or saurian muscle (Table 1). These greater levels of P_t in anuran muscle are attained

at approximately 0°C; P_t is similar in mammalian, saurian, and anuran muscle at 20°C. P_t of insect flight muscle has an average R_{10} of 1.35 at 30–35°C (data for 23 species, summarized in Ref. 71, range 0.4–4.0). Although these values broadly overlap those reported for vertebrate muscle at these temperatures, the greater average value suggests a generally greater thermal dependence.

In mammalian cardiac muscle, maximal P_t is reached at 20–25°C (42, 74) and P_t declines markedly at higher temperatures (40, 42, 74, 82, 90, 97, 153, except see also Ref. 12). This thermal dependence is identical to that of mammalian skeletal muscle. Cardiac muscle of lizards attains peak P_t at low, species-specific temperatures, sometimes as low as 5°C and more than 20°C below field-active body temperatures (34–36, 85, 87). It has consequently been maintained (85, 87) that cardiac muscle of lizards attains maximal P_t at considerably lower temperatures than does skeletal muscle. However, because the thermal pattern of P_t in lizard skeletal muscle is in dispute (see above), this assertion is questionable. The P_t of turtle heart is maximal at 9°C (15). Only scattered and contradictory information is available concerning the effect of temperature on anuran cardiac muscle: all studies (95, 124, 142) agree that P_t decreases with increasing temperature above 20°C, but maximal values have been reported at 0°C with high-frequency stimulation and at 10°C with low-frequency stimulation (142).

Tetanic tension. During repetitive stimulation, muscle undergoes prolonged contraction (tetany) and produces a sustained contractile force (maximal tetanic tension, P_o). The intensity of P_o is dependent on several factors, including stimulation frequency and temperature (see Fig. 3). Either a positive or negative thermal effect can be obtained, depending on stimulation rate. Additionally, very high stimulation frequencies may sometimes depress P_o (the Wedensky effect), particularly at low tem-

TABLE 1. Twitch tension of vertebrate skeletal muscle as a function of temperature

| | T, °C | P_t , kg/cm ² | Muscle | Ref. No. |
|--------|-----------|----------------------------|--------|----------|
| Frog | 0 | 1.42 | Sar | 11 |
| | 0 | 1.61 | Sem | 119 |
| | 2 | 1.42 | Sar | 29 |
| | 20 | 0.85 | Sar | 11 |
| | 20 | 0.58 | Sem | 119 |
| | 20–22 | 0.70 | Sar | 29 |
| Lizard | 25 | 0.4 | Sar | 125 |
| | Max P_t | 0.81–1.16 | G | 118 |
| | Max P_t | 0.49–0.80 | IF | 118 |
| Rat | 20 | 0.5 | Sol | 29 |
| | 20 | 0.51 | Sol | 67 |
| | 20 | 1.0 | EDL | 29 |
| | 20 | 1.03 | EDL | 67 |
| | 20 | 0.65 | Sol | 81 |
| | 22 | 0.60 | Sol | 63 |

T, temperature; P_t , twitch tension; EDL, extensor digitorum longus; G, gastrocnemius; IF, iliofibularis; Sar, sartorius; Sem, semitendinosus; Sol, soleus.

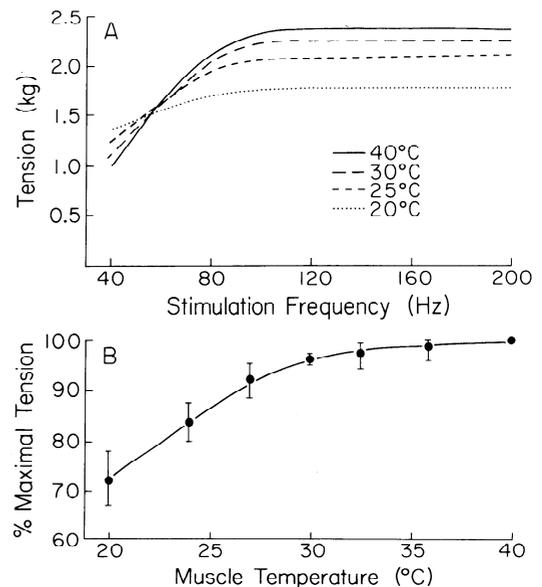


FIG. 3. A and B: effect of temperature and stimulation frequency on tetanic tension (P_o) in cat tibialis anterior muscle (direct muscle stimulation; data from Ref. 33). B: mean maximal P_o and range expressed as percent of values at 40°C.

perature and/or with indirect stimulation via a nerve (33, 115, 143). Consequently care should be taken in the interpretation of reported thermal dependence of P_o , particularly in studies using low stimulation frequencies (see, e.g., Ref. 38 as critiqued in Ref. 143). Ideally a range of frequencies should be used at each temperature to obtain P_o at that temperature.

Literature values of R_{10} for P_o are reported in Fig. 4. The general thermal dependence of this function is low, with average $R_{10} = 1.1$ – 1.2 and most values clustered at 1.09 – 1.3 . Very few studies have reported a decline in P_o with increasing temperature at temperatures below those that irreversibly damage muscle tissue. Nearly all the points in Fig. 4 below $R_{10} = 0.9$ are attributable to studies from a single laboratory (57, 58), and all are substantially below R_{10} values measured by other workers for the same muscles over the same temperature range. There is a trend toward decreasing thermal dependence with increasing temperature across all observations, and this trend is particularly apparent for individual muscles measured at several different temperatures by single investigators. This effect is, however, relatively weak: in most observations, even at muscle temperatures of 10°C or less, $R_{10} < 1.5$. Data on maximal tension in calcium-activated skinned fibers show a thermal dependence similar to that reported for intact muscle fibers (1, 54, 138).

Intergroup comparisons are difficult because the majority of observations are made at nonoverlapping thermal ranges. Most observations on mammalian muscle have been made at temperatures above 20°C and on anuran muscle below 20°C . When data for these groups are normalized to the greatest P_o at any temperature and expressed as a function of muscle temperature (Fig. 5), it is apparent that the thermally independent plateau extends to lower temperatures in anurans. A decline in P_o occurs in all mammalian muscles at temperatures below 25°C ; some anuran muscles maintain maximal P_o

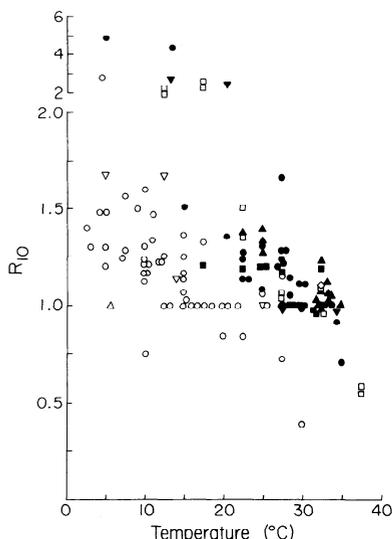


FIG. 4. Thermal dependence of tetanic tension. Symbols as in Fig. 2. (Data from Refs. 6, 11, 15, 17, 20, 23, 24, 27, 28, 32, 33, 37, 39, 44, 47, 49, 50, 57–59, 64, 65, 67–69, 71, 81, 83, 84, 91, 98, 112, 115, 118, 121–123, 125, 126, 129, 130, 135, and 139.)

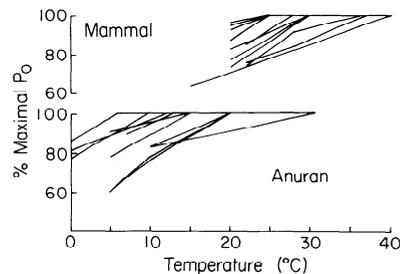


FIG. 5. Thermal range of tetanic tension (P_o) in mammalian and anuran muscle. Data from limb muscles measured at 3 or more temperatures expressed as percent of maximal P_o reported. (Mammalian data from Refs. 28, 33, 81, 115, 121, 123, and 143; anuran data from Refs. 32, 59, 64, 65, 83, 84, 98, 125, 129, and 130.)

to temperatures as low as 6 – 15°C . This maintenance of P_o at low temperature is not a general feature of muscle from ectothermic vertebrates, because the thermal dependence of P_o in lizard muscle (118) is very similar to that reported for mammals: a decrement in P_o is apparent in all species below 25°C . It should be reemphasized, however, that overall thermal dependence of P_o in all groups is low compared with most biological rate processes.

P_o of other muscle types does not show a pattern of thermal dependence similar to that of skeletal muscle. In catch muscle from *Mytilus*, P_o declines with increasing temperature over the entire measured range (0 – 40°C , $R_{10} = 0.7$ – 0.8) (89). This is the only well-documented pattern of negative thermal modulation of P_o . Most studies on mammalian smooth muscle report relatively low R_{10} values (1.0 – 1.2) between 20 and 30°C (52, 53, 136, 141). However, P_o has been reported to increase (31), decrease (141), or remain constant (136) at temperatures greater than 30°C . A high thermal dependence ($R_{10} > 2$) has also been reported at temperatures below 20°C (31, 141). At present it is not clear whether this diversity of responses is real and muscle specific or whether it depends on stimulation technique. In anuran cardiac muscle under potassium contracture, tension is maximal at 20°C and decreases at both higher and lower temperatures (124).

Rate

Time to peak twitch tension. The speed of response of a muscle to a single stimulus eliciting a twitch is generally measured as the time to peak twitch tension (TPT), the time from the first contractile response to maximal P_t . Q_{10} values are calculated on the inverse of TPT and represent the thermal dependence of the average twitch rise time. Maximal rate of development of P_t (dP_t/dt) has also occasionally been measured (49, 62, 92, 96, 120).

The rate of development of P_t increases markedly with increasing temperature (e.g., see Fig. 1). Q_{10} values from the literature are reported in Fig. 6. The average Q_{10} of all observations is about 2.2, with values ranging from 1.3 to 3.9. In each of the three major groups considered (mammals, anurans, and lizards), Q_{10} is clearly a declining function with increasing temperature. That is, TPT is markedly thermally dependent over the entire observed temperature range, but this dependence is lower at higher temperatures. On the basis of available data, it

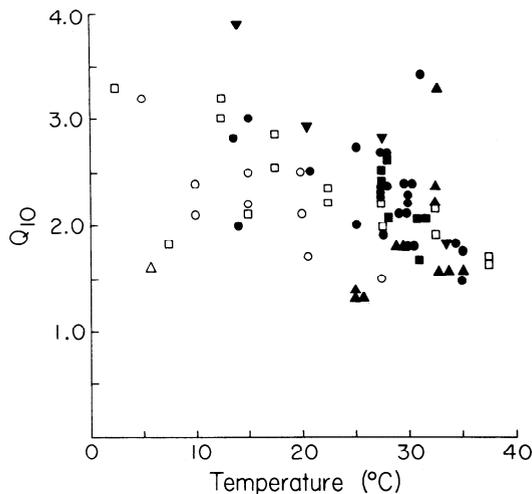


FIG. 6. Thermal dependence of time to peak twitch tension. Symbols as in Fig. 2. (Data from Refs. 11, 17, 20, 27, 28, 43, 55, 60, 67, 81, 91, 96, 100, 101, 108, 115, 118, 120–123, 125, 134, 135, 143, and 145.)

appears that Q_{10} values of anurans are generally lower than those of the other groups, and those of lizards are intermediate between those of anurans and mammals. Stated differently, the mean slope of TPT as a function of temperature is greatest in mammals, intermediate in lizards, and least in anurans.

Absolute TPT is difficult to compare in these different groups, because it is influenced by muscle fiber composition (e.g., 28, 122), temperature, and body size (63a), among other factors. The only observations that achieve some match of these variables are on gastrocnemius muscles measured at 20°C, and these are similar in TPT among different animals: mouse = 42 ms (17), rat = 42 ms (100), lizards = 45–50 ms (118), and frog = 48 ms (108). On the basis of these limited data, there appear to be no striking differences among these different groups or between endotherms and ectotherms in the rate of P_t development.

Insect muscle appears to have a more thermally independent TPT than vertebrate skeletal muscle. Josephson (71) has summarized the thermal dependence of total twitch time (contraction plus relaxation) in flight muscle from 27 species of insects with $Q_{10} = 1.2$ – 1.6 at 30–35°C. The average value is close to the minimum values reported for vertebrate skeletal muscles and indicates a lower thermal dependence.

The thermal dependence of TPT in cardiac muscle is very similar to that in skeletal muscle (12, 42, 82, 95, 97, 153), with $Q_{10} = 2.1$ – 2.8 (avg 2.3) measured at approximately 25–35°C. The dP/dt of rat smooth muscle (portal vein) has a $Q_{10} = 1.8$ between 25 and 37°C (80).

Twitch relaxation time. The rate of twitch relaxation is most often measured as the inverse of the half-relaxation time ($RT_{1/2}$), the time between attainment of peak twitch and return to 50% of peak value. Other measures include the inverse of the total relaxation time (mean rate of relaxation) and maximal rate of tension decline. All these factors have a pronounced thermal dependence (Fig. 7), particularly below 20°C. The range of observed Q_{10} values is very broad and averages about 2.5. Hill (64) asserted that twitch recovery is a process more thermally

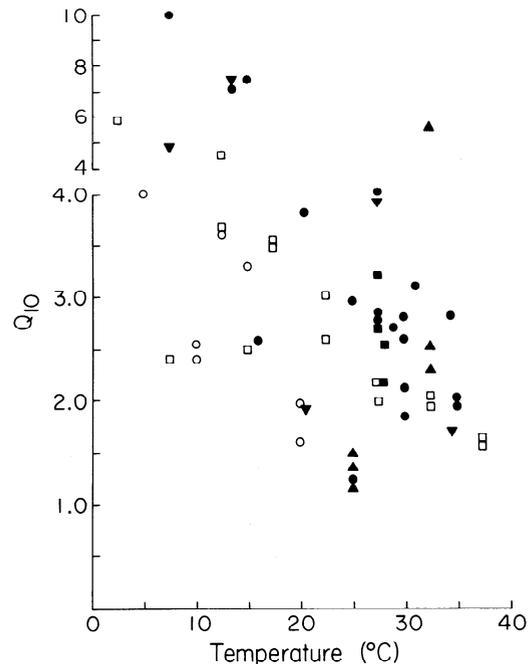


FIG. 7. Thermal dependence of twitch relaxation time. Symbols as in Fig. 2. (Data from Refs. 11, 17, 28, 60, 62, 81, 100, 101, 108, 115, 118, 122, 123, 125, 135, 143, and 145.)

dependent than development of twitch. Although this may be true at low temperatures (< 20°C), this difference is not apparent at higher temperatures (see Figs. 6 and 7), and it cannot be stated that these functions show distinctly different thermal responses. There is a general trend of decreasing Q_{10} with increasing temperature in anurans, lizards, and mammals. As with TPT, there is a differential thermal dependence among the groups: greatest in mammals, intermediate in lizards, and least in anurans. Very high Q_{10} values (3.1–6.4 at 21–29°C) have been reported for twitch relaxation in mammalian cardiac muscle (12, 42, 97).

Development of tetanic tension. The rate of P_o development is measured most commonly as the maximal rate of tension development (dP_o/dt) (e.g., 118, 123) but sometimes is expressed as the total tetanic rise time and its inverse (average rate of P_o development) (e.g., 126). Although the thermal dependence of these functions has not received extensive measurement, existing Q_{10} values (Fig. 8) generally group between 1.5 and 2.4 with an approximate average of 2.0. There is one report of a low thermal dependence of half-rise time for tetanized tortoise muscle (47). There is a general decrease in Q_{10} with increasing temperature in mammalian and saurian muscle, the only groups with sufficiently large data sets, and the thermal dependence of dP_o/dt appears very similar in these animals. The two anuran Q_{10} values are lower than anticipated mammalian or saurian values for this same temperature range. However, the data are too few to permit any further generalizations or intergroup comparisons.

In mammalian smooth muscle, the Q_{10} of $dP_o/dt = 1.7$ – 2.2 between 25 and 37°C (136, 141). Catch muscle from *Mytilus* stimulated with acetylcholine has a dP_o/dt that rises continuously with temperature from 10 to 40°C with $Q_{10} = 1.2$ – 1.7 (89).

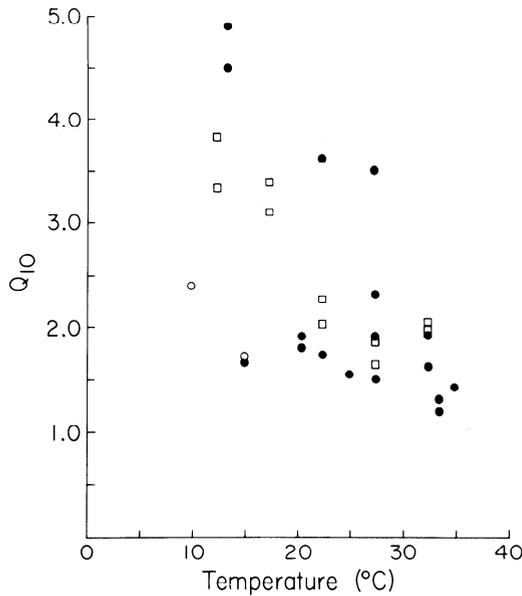


FIG. 8. Thermal dependence of tetanic rise time (dP_o/dt). Symbols as in Fig. 2. (Data from Refs. 99, 118, 123, 126, 135, and 143.)

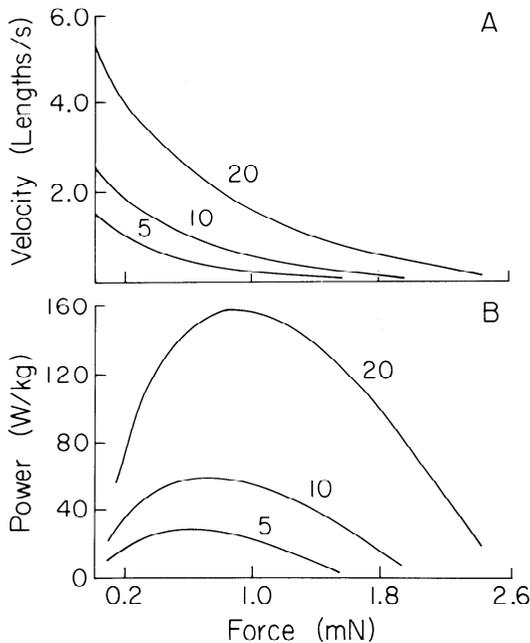


FIG. 9. Contractile speed and power output of iliofibularis muscle of frog at 5, 10, and 20°C. (Data from Ref. 83.)

EFFECT OF TEMPERATURE ON ISOTONIC CONTRACTILE PROPERTIES

Maximal Velocity of Shortening

Isotonic contractile performance is most commonly measured as the velocity of shortening as a function of imposed load. The resulting force-velocity curves are generally described by Hill's characteristic equation (63) or a variant of that equation. The influence of temperature on the force-velocity relation is shown in Fig. 9A. Increasing temperature increases contractile velocity at each imposed load. Such functions permit the estimation of maximal (unloaded) velocity of shortening (V_{max}) and maximal power output during contraction.

The thermal dependence of V_{max} is reported in Fig. 10. The average Q_{10} for all reported values of V_{max} is approximately 2.0. There is a general decline in thermal dependence with increasing temperature in both anurans and mammals. Thermal dependence of V_{max} in anuran muscle may be substantially below that of mammalian muscle measured at the same temperature range. However, no firm conclusions can be based on the present data set, because the observations for these groups are made at nonoverlapping thermal ranges. In lizards and insects, in which the thermal dependence of V_{max} has been measured over the same range as that of mammalian muscle, the thermal dependence is quite similar to that of mammals ($Q_{10} = 1.5-2.0$). Data are not sufficient to permit a comparative analysis of absolute contractile speed in homologous muscles from endotherms and ectotherms at similar temperatures.

The effects of temperature on submaximal contractile speeds under constant imposed loads have been reported for fish muscle, with $Q_{10} = 1.3-1.7$ (0–34°C) (13, 14, 149), but the thermal dependence of P_o makes interpretation of these values difficult.

There is no agreement about the thermal dependence of V_{max} in cardiac muscle. Q_{10} values of 0.6 (rabbit, 23–32°C) (40), 1.5 (frog, 8–23°C) (95), and 2.4 (cat, 23–34°C) (153) have been reported. Velocity is apparently highly dependent on stimulation frequency and technique. Studies on smooth muscle have reported a more consistent thermal dependence with Q_{10} values averaging 2.4 from 15 to 25°C and 1.8 from 25 to 37°C for mammalian muscle (52, 53, 80, 109, 136).

Maximal Power Output

Maximal power output, the greatest rate of work by a contracting muscle, can be calculated from force-velocity relations. Maximal power output is a highly temperature-dependent function, particularly at low temperature (Fig. 9B; see Fig. 11 for summary of literature values). Calculated Q_{10} values of maximal power production range from 1.6 to 4.5 (avg ~2.3). As with V_{max} , thermal dependence

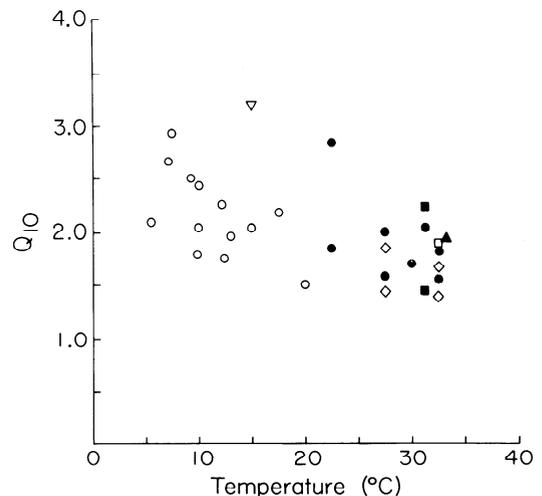


FIG. 10. Thermal dependence of maximal contractile velocity. Symbols as in Fig. 2. (Data from Refs. 19, 24, 27, 39, 43, 44, 72, 73, 77, 78, 83, 84, 94, 116, 123, and 129.)

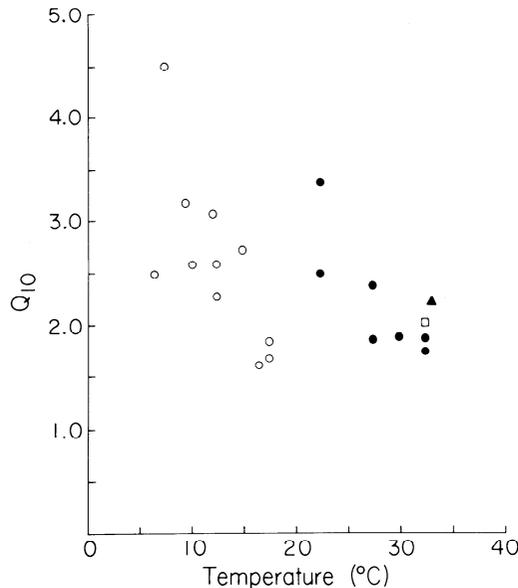


FIG. 11. Thermal dependence of maximal power output. Symbols as in Fig. 2. (Data from Refs. 24, 27, 44, 64, 83, 84, 94, 116, 123, and 129.)

apparently decreases with increasing temperature in both anurans and mammals. There is a clear suggestion that Q_{10} may be greater in mammalian than in anuran muscle if measured at the same temperatures, but lack of data at overlapping temperatures prevents a definitive analysis of these intergroup differences.

Twitch and Tetanic Work

Most of the 19th century observations on the thermal dependence of muscle function involved the measurement of length changes under constant load during either twitch or tetanic stimulation (i.e., twitch work or tetanic work). There was considerable dispute over the temperature dependence of twitch work, with various authors arguing that it was either a decreasing function with increasing temperature (30, 48), independent of temperature (6, 45), or a more complex relation with a minimum at about 20°C (22, 50). Tetanic work was reported to have a generally positive but low thermal dependence ($R_{10} = 1.0$ – 1.6) (6, 50, 57, 133). However, Kaiser (76) demonstrated that observed thermal dependence is a function of imposed load, and any thermal pattern, R_{10} negative or positive, may be obtained by choice of an appropriate load. Because the reported values did not necessarily represent maximal twitch or tetanic work, this literature has now fallen into disuse. Maximal twitch work measured in insect (*Schistocerca*) muscle has an R_{10} of 1.5–1.6 at 10–32°C (see 71).

SUMMARY OF TEMPERATURE EFFECTS

Through the wide range of data reported for each function, two general patterns of response to temperature emerge. Levels of force exerted by muscle tend to be independent of temperature or have a low thermal response. P_t may increase or decrease with a rise in temperature according to taxon, but most observed values fall within $R_{10} = 0.5$ – 1.5 . P_o has a weak positive thermal

dependence ($R_{10} < 1.5$) at low temperatures and a broad zone of thermal independence at higher temperatures.

This pattern is in strong contrast to that of contractile rate processes. All (TPT, $RT_{1/2}$, dP_o/dt , V_{max} , and power output) have a markedly positive thermal dependence with average $Q_{10} = 2.0$ – 2.5 . The accelerating effects of temperature on rates of contraction and relaxation occur up to thermal levels that may damage the contractile apparatus. In general, skeletal muscle thus appears capable of exerting more or less the same force regardless of its temperature, but the rate of development of that force, the rate of work output, and the rate of relaxation from contraction depend very strongly on muscle temperature and are accelerated by increased temperature.

PHYLOGENETIC AND ADAPTIVE CONSIDERATIONS

Intergroup Comparisons

Muscles of ectotherms must function at lower temperatures and over a broader thermal range than those of endotherms. Are there quantitative differences in their thermally dependent processes that might facilitate functioning at different thermal ranges? Two potential patterns of adaptation might be expected. 1) Muscles of ectotherms might have a lower thermal dependence (i.e., lower Q_{10} and R_{10}) than those of endotherms. This lower thermal dependence would promote stability of functional capacity, but low thermal dependence per se would not necessarily indicate high levels of force or velocity over the thermal range in question. An intergroup comparison of absolute levels of force and speed would be required to determine whether thermally independent function was optimized at high performance levels. The possession of muscles capable of delivering high levels of force and rapid contraction rates at all temperatures would presumably be the most desirable condition for ectotherms. 2) If a high thermal dependence (e.g., Q_{10} $R_{10} > 2$) is maintained, adjustments in the muscle might occur such that high levels of performance are attained at low temperatures. This strategy would permit greater functional capacity at any common temperature by the muscles of an ectotherm compared with those of an endotherm. These strategies have properties analogous to rotational and translational thermal acclimation of individual organisms, respectively (117).

The primary difficulty in analyzing such patterns is the restricted phylogenetic range of data available. The amount of mammalian data is reasonable, even if it is largely restricted to rodents and cats. Extensive amphibian data also exist for some functions, but these are almost exclusively derived from observations on a single genus (*Rana*), in addition to a few scattered observations on toad muscle. Further the mammalian and anuran data sets are usually measured over different ranges of temperature. It is thus difficult to distinguish lateral displacement of a function (translation) from a broadened range with a lower thermal dependence (rotation). Data on reptilian muscle have the potential for serving as a biologically relevant comparative base for both groups, because some reptilian species may experience very broad thermal ranges. Existing data on reptiles are not exten-

sive enough to support such an analysis. Data on the influence of temperature on avian muscle are non-existent, and only fragmentary information is available for fish. Thus a truly comprehensive picture cannot be obtained at this time, and we have to be content largely with comparisons of frogs and rats, with an occasional reference to lizards. Further data are required on fish, other amphibian groups, including other anurans and salamanders, reptiles, birds, and all the invertebrate groups. In spite of the phylogenetically limited information available, some tentative patterns emerge.

Anuran muscle is clearly superior to mammalian muscle in its capacity to develop force during twitch contraction at low temperature. High levels of P_t are maintained at temperatures below 20°C in frog muscle, the point at which P_t is maximal in most mammalian muscles. Anuran muscle is thus capable of producing higher levels of P_t over a much broader thermal range. Lizards also apparently have a broader range of thermally independent P_t than do mammals (118). Thus muscle from ectotherms can generally develop P_t at low (< 20°C) temperatures more readily than can muscle from endotherms.

Anuran muscle also develops maximal P_o at temperatures lower (< 25°C) than either mammalian or saurian muscle. It is not possible to conclude positively whether anuran muscle has a broader temperature-independent plateau or whether the P_o -temperature curve is translated to lower temperatures and has an equal width in all groups. This indeterminacy is due to contradictory observations on anuran (e.g., *Rana*) muscle performance at temperatures greater than 25°C. Some authors report a constant or increasing P_o at these temperatures (6, 130, 146), a pattern that would indicate a broader functional plateau. Another investigator (57, 58) reports decreasing P_o values with increasing temperature over this range, a pattern consistent with a translational shift of performance. The former is probably more representative. Because mammals and lizards are very similar in thermal dependence of P_o , the anuran pattern appears to involve adjustments to function at lower temperatures rather than a dichotomy between muscles from ectotherms and endotherms.

Contractile rate processes generally have a lower thermal dependence in ectotherms than in mammals. These patterns are not as clear-cut as would be desirable, primarily because of the lack of anuran data at higher (> 25°C) temperatures. For both TPT and $RT_{1/2}$ measured over the same temperature range, anuran Q_{10} values are lowest, saurian are intermediate, and mammalian are highest. The data on V_{max} and power output are suggestive of a similar differential in anuran and mammalian muscle, but more observations on anuran muscle at higher temperatures are required. It should be reemphasized, however, that these intergroup differences are only relative and that thermal dependence in all groups remains high (i.e., $Q_{10} \geq 2$). Comparisons of shortening velocities in these groups are hampered by the diversity of temperatures, muscle fiber compositions, and body sizes of animals examined. Without this information a definitive statement on translational adaptations cannot

be made. Data on TPT of gastrocnemius muscles cited previously suggest that such adjustments have not taken place, but data are too scanty for more definitive conclusions.

In general, anuran muscle can develop maximal twitch and tetanic force at lower temperatures and has rate processes less affected by changes in temperature than does mammalian muscle. Saurian muscle is intermediate to these groups in most respects, except in its thermal dependence of P_o , which is similar to that of mammalian muscle. It must be recognized that these generalizations are built on a small and phylogenetically restricted data base and may be modified by new information.

Adaptations to Body Temperature

Performance at normal body temperatures. Have muscle properties been adjusted to deliver optimal performance at normally experienced temperatures? There are relatively few comparative studies on different species that bear directly on this question. The most extensive interspecific investigations concern lizards. Earlier studies (85, 87) maintained that P_t is optimized over a narrow thermal range close to field-active temperatures in a number of different species. More recent work (118) has cast doubt on these conclusions (see section on the thermal dependence of P_t). Because vertebrate muscle is not activated in twitch contractions in vivo, optimization of twitch function is not a selectively important feature in any event. The latter study (118) found that P_o is maximal or nearly maximal at field-active temperatures in four different species (generally as part of a larger thermally independent plateau). In this study, there is evidence of a translational shift in contractile rate processes in line with field-active temperatures: species with lower field-active body temperatures (25–35°C) have faster contractile rates (TPT, $RT_{1/2}$, dP_o/dt) measured at any individual temperature than do species with higher field-active body temperatures (40°C). This pattern would tend to equalize intraspecific muscle performance measured at normal active temperatures. However, differences in body size complicate interpretation of these data. Maximal dP_o/dt occurs at field temperatures in three of the four species examined. Data on an Antarctic fish (91) indicate that maximal P_t and P_o occur at –1–4°C, the normal water temperature of this species. Studies on tuna muscle (14) found no difference in the thermal dependence of contraction times in the white muscle of these homeothermic fish and that of poikilothermic fish. It was concluded that tuna muscle possesses no particular adaptations to its unusual thermal regime. Studies of neuromuscular preparations of ghost crabs (*Ocypode*) (46) found maximal P_o at 25°C, close to normally experienced body temperatures of 26–28°C.

No interspecific studies relating temperature to normal thermal levels have been undertaken on mammals or anurans. In mammals, muscle performance would normally be close to maximal at normal body temperature for all functions except P_t , which is greatest at 20°C. P_o , TPT, $RT_{1/2}$, dP_o/dt , V_{max} , and power output are all thermally dependent and would reach maximal values at

high temperatures close to those causing thermal damage. Because mammalian body temperature is typically high and not far from those limits, these functions would be correspondingly great in vivo. In anurans, P_o may be maximal at normal body temperatures, but P_t appears greatest at very low temperatures, below those commonly experienced by active animals. Because rate processes are temperature dependent, as in mammals, they would be maximal at high temperatures. Because amphibians typically have field body temperatures far below critical maximal levels (10), their rate processes would not be maximal under normal thermal conditions.

In general, it appears that P_o is maximal at normally experienced temperatures in a variety of different groups. Maximal P_t does not occur at normal body temperatures. The failure of maximal P_t to correlate with normally experienced temperatures is not particularly surprising, because most muscles (except insect flight muscles) are always tetanized during normal in vivo contractions. Animals with high body temperatures may benefit from the accelerating effects of temperature on rate processes and achieve high levels of muscle performance. Animals living at low temperatures do not achieve similar maximization, although some evolutionary adjustment analogous to temperature acclimation may be possible.

Heterothermy and hibernation. During torpor or hibernation, muscle and core body temperature of mammals may drop to very low levels. Muscular contraction may be required at these temperatures, either during shivering thermogenesis or physical activity. Are there adjustments in the response of muscle from mammalian heterotherms for function over a broad thermal range? Very little attention has been directed at this question. South (135) compared the contractile response of diaphragmatic muscle from hibernating and nonhibernating hamsters and from laboratory rats, which do not undergo torpor. Virtually no differences were found between hibernating and nonhibernating hamsters, suggesting that no specific seasonal or physiological change in the thermal sensitivity of muscle occurs during hibernation. Additionally, very little difference was found between hamsters and rats, at least between 10 and 38°C: the species have a similar thermal sensitivity of P_t , P_o , TPT, and dP_o/dt . Relaxation from twitch or tetanus has a higher Q_{10} value in the rat. The only marked difference among the groups is in cold-blocking temperature of a nerve-muscle preparation, which is greatest in rats and least in hibernating hamsters. Rat skeletal muscle itself retains a contractile response down to very low temperatures (3–5°C) (66, 135, 138). A second study on heterothermic mammals (102) examined the thermal dependence of P_t and twitch duration in muscle from bats, rats, and frogs. It reported that bat muscle is more similar to frog than rat muscle in its thermal dependence, but these conclusions were based on minor differences in cold-blocking temperature, and the study was methodologically flawed. No major differences are apparent in the thermal response of muscle in homeothermic and heterothermic mammals, but clearly more observations are required.

Acclimation. Does recent thermal history alter muscle contractile properties? The effect of temperature accli-

mation on anuran muscle has received a moderate amount of attention. An earlier report (145) commented on differences in twitch performance with season and acclimation state, but these were not quantified. Two studies have reported acclimatory differences in frog muscle performance. Maximal P_o was reported to be achieved at lower temperature in cold-acclimated animals (58), but these differences are not statistically significant. Differences in P_t , under some conditions, and TPT, according to acclimation state, have also been reported (8), with TPT slower in warm-acclimated animals when measured at a common temperature. More recent and comprehensive studies have failed to demonstrate significant acclimation of P_t , P_o , TPT, $RT_{1/2}$, dP_o/dt , V_{max} , or maximal power output (125, 126, 129). Where minor differences among acclimatory groups were observed (125), they often involved inverse compensation. Another study (86) failed to find temperature compensation of P_t in lizard muscle. It appears, contrary to most expectations, that contractile properties of vertebrate muscle do not change according to recent thermal experience of the organism. Some differences in muscle performance have been reported in crustacean muscle as a result of thermal acclimation (61, 137), but these studies are not comprehensive and do not define maximal functional capacity.

Seasonal differences in muscle function remain to be investigated. One study (15) reported seasonal differences in P_o of turtle muscle, with maximal P_o extending to lower temperatures in winter-acclimatized animals.

Response of Different Muscle Fiber Types to Temperature

The effect of temperature on contractile properties of muscles of different fiber composition has been examined extensively in mammals. These studies measure performance in two different muscles from the same animal, usually a "fast"-twitch muscle, such as the extensor digitorum longus, and a "slow"-twitch muscle, such as the soleus. The fiber types in these muscle pairs differ greatly in such factors as twitch kinetics, fatigability, and enzymatic composition. The fiber types also differ in their thermal dependence of P_t . At 27–37°C, P_t of fast-twitch muscle decreases (avg $R_{10} = 0.7$) and that of slow-twitch muscle remains constant (avg $R_{10} = 1.0$) (17, 20, 29, 60, 67, 69, 112, 115, 121, 122). This thermal dependence of fast-twitch muscle is not found in posttetanically potentiated twitches (29). The basis of this differential thermal sensitivity between fiber types is not known. Its functional significance is unclear, particularly because these muscles normally function tetanically in vivo, and none has been suggested. TPT has a similar thermal dependence in both muscle types (at 25–37°C avg fast-twitch $Q_{10} = 2.0$, avg slow-twitch $Q_{10} = 2.2$) (20, 29, 43, 60, 115, 120–123). R_{10} values of P_o are low and almost identical for both muscle types (fast- and slow-twitch $R_{10} = 1.1$ at 25–37°C) (17, 20, 29, 69, 112, 115, 121, 122). V_{max} has been reported to have a greater thermal dependence in fast- ($Q_{10} = 2.1$ – 2.2) than in slow-twitch muscle ($Q_{10} = 1.4$ – 1.6) (43, 123). The thermal dependence

of P_o ($R_{10} = 1.2-1.4$ at $10-20^\circ\text{C}$) and V_{\max} ($Q_{10} = 1.7-1.9$ at $10-15^\circ\text{C}$ and 2.2 at $15-20^\circ\text{C}$) is quite similar in different types of twitch fibers of anuran muscle (84).

Organismic Performance

Are thermal effects on isolated muscle contractility reflected in performance *in vivo*? A large number of studies have been conducted on the effect of body and/or muscle temperature on human performance, largely to determine the benefits of "warming-up" before exercise. To isolate temperature effects *per se*, many of these studies altered muscle temperature with baths or diathermy. In general, the results of these experiments accord with the thermal dependence of related factors in isolated muscle.

Dynamic performance, involving factors that are rate process dependent, such as maximal power output, improves as temperature increases (2, 4, 5, 7, 75, 132, but see also Ref. 51). These increments are significant (and may be particularly important in a sporting contest) and reflect the accelerating effects of temperature on all contractile rate processes. Their thermal dependence, however, is generally low, with $Q_{10} \sim 1.2-1.6$ (2, 7, 132), below those of isolated muscle, which often exceed 2.0. A similar differential in thermal dependence between running performance and muscle kinetics occurs in a lizard, with $Q_{10} = 1.3$ and 2.0 for limb-cycling frequency and maximal muscle power output, respectively, from 25 to 40°C (94). A lower thermal dependence of burst speed than of isolated muscle performance in fish has also been reported (9, 14, 149, 152). The basis of this differential thermal dependence has not been investigated.

In contrast to the accelerating effects of temperature on dynamic performance, *in vivo* static performance may be impaired by increasing temperature. Studies on the time of maintenance of a constant force by human muscles *in vivo* show a maximum endurance at intermediate muscle temperatures of $27-32^\circ\text{C}$ and lower endurance at both higher and lower temperatures (26, 41, 88, 104, 105, 113, 114). This pattern is reflected in endurance of tetanically stimulated mammalian muscle *in vitro*: in both cat (115) and rat (134) muscle, P_o can be maintained longest at $28-30^\circ\text{C}$. At both higher and lower temperatures, the duration of tension maintenance declines. The thermal dependence of maximal tension produced by human muscle *in vivo* is low and has been reported to decrease (107), increase slightly (2, 5), or remain unaffected (7, 111) by increasing temperature above 30°C . This pattern matches the relatively low thermal dependence of P_o of isolated preparations of mammalian muscle.

CONCLUSIONS

The maximal force a muscle can exert is relatively temperature independent. Consequently an animal should be capable of applying an equal force regardless

of its body temperature. This thermally independent capacity would be significant in a number of different static situations, such as standing, crouching, or hanging. During movement, however, the most significant factor is the rate of force application and its removal. Contractile rates are greatly influenced by body temperature in all animals examined. The speed of muscle activity is very much slower at low temperatures. Animals with high body temperatures attain nearly maximal contractile rates and power outputs that their muscles are capable of delivering. This accelerating effect of temperature on contractile performance may have been an important selective factor in the evolution of high activity temperatures in many active groups of ectotherms. Likewise, it may have been a major selective agent in the development of the high temperatures associated with endothermy in both vertebrates and insects.

There is surprisingly little evidence of adaptations that would increase activity performance at low body temperatures in animals that often experience them. The temperature of maximal P_o usually coincides with normally experienced body temperature, but this function has very wide thermally independent plateaus and has a low thermal dependence throughout its range. Contractile rate processes of ectotherms tend to have Q_{10} values lower than those of endotherms (i.e., mammals), but these reflect relatively minor rotational adjustments of rate-temperature curves. The rates in ectotherms are still strongly thermally dependent. There is little evidence of adaptation of rate processes of individual species to activity at low temperatures, either by thermal acclimation or interspecific adjustment to field-active temperatures. Animals active at low temperatures appear to have a lower performance capacity at those temperatures than their muscle systems are physically capable of delivering at higher temperatures.

The need for more data to verify or refute these conclusions should be apparent. Many groups of vertebrates, some with unique thermal circumstances and some that would provide important evidence of developments parallel to those outlined here, remain to be investigated. Apart from the insects, data on the effects of temperature on muscle from invertebrates are almost nonexistent. The utility of these studies would be greatly enhanced if the measurements were made within the context of normally experienced temperatures and organismic performance. This review was undertaken to stimulate such studies.

I thank R. K. Josephson and an anonymous reviewer for helpful comments on the manuscript.

Financial support was provided by National Science Foundation Grant PCM-81-02331 and National Institute of Arthritis, Metabolism, and Digestive and Kidney Diseases Grant K04-AM-00351.

Address reprint requests to A. F. Bennett, School of Biological Sciences, Univ. of California, Irvine, CA 92717.

REFERENCES

1. ASHLEY, C. C., AND D. G. MOISESCU. Effect of changing the composition of the bathing solution upon the isometric tension-pCa relationship in bundles of crustacean myofibrils. *J. Physiol. London* 270: 627-652, 1977.
2. ASMUSSEN, E., AND O. BØJE. Body temperature and capacity for work. *Acta Physiol. Scand.* 10: 1-22, 1945.
3. BÁRÁNY, M. ATPase activity of myosin correlated with speed of muscle shortening. *J. Gen. Physiol.* 50: 197-218, 1967.

4. BERGH, U., E. BLOMSTRAND, B. EKBLUM, AND B. ESSÉN-GUSTAFSSON. Physical performance and muscle metabolites at low muscle temperature (Abstract). *Med. Sci. Sports Exercise* 14: 127, 1982.
5. BERGH, U., AND B. EKBLUM. Influence of muscle temperature on maximal muscle strength and power output in human skeletal muscles. *Acta Physiol. Scand.* 107: 33-37, 1979.
6. BERNSTEIN, J. Zur Thermodynamik der Muskelkontraktion. *Pfluegers Arch.* 122: 129-195, 1908.
7. BINKHORST, R. A., L. HOOFD, AND A. C. A. VISSERS. Temperature and force-velocity relationship of human muscles. *J. Appl. Physiol. Respirat. Environ. Exercise Physiol.* 42: 471-475, 1977.
8. BISHOP, L. G., AND M. S. GORDON. Thermal adaptation of metabolism in anuran amphibians. In: *Molecular Mechanisms of Temperature Adaptation*, edited by C. L. Prosser. New York: Academic, 1967, p. 263-280.
9. BLAXTER, J. H. S., AND W. DICKSON. Observations on the swimming speeds of fish. *J. Cons. Int. Explor. Mer* 24: 472-479, 1959.
10. BRATTSTROM, B. H. A preliminary review of the thermal requirements of amphibians. *Ecology* 44: 238-255, 1963.
11. BRESSLER, B. H. Isometric contractile properties and instantaneous stiffness of amphibian skeletal muscles in the temperature range of 0 to 20°C. *Can. J. Physiol. Pharmacol.* 59: 548-554, 1981.
12. BREWSTER, W. R., JR., J. P. ISSACS, P. A. OSGOOD, A. M. NYLANDER, AND R. Y. W. CHOCK. The effect of thyroid hormones and temperature on the kinetics of contraction and relaxation of ventricular heart muscle. *Bull. Johns Hopkins Hosp.* 103: 157-182, 1958.
13. BRILL, R. W. Temperature effects on speeds of muscle contraction and stasis metabolic rate. In: *The Physiological Ecology of Tunas*, edited by G. D. Sharp and A. E. Dizon. New York: Academic, 1978, p. 277-283.
14. BRILL, R. W., AND A. E. DIZON. Effect of temperature on isometric twitch of white muscle and predicted maximum swimming speeds of skipjack tuna, *Katsuwonus pelamis*. *Environ. Biol. Fish* 4: 199-205, 1979.
15. BROWN, D. E. S. Temperature-pressure relation in muscular contraction. In: *Influence of Temperature on Biological Systems*, edited by F. H. Johnson. Washington, DC: Am. Physiol. Soc., 1957, p. 83-110.
16. BROWN, G. L., E. BÜLBRING, AND B. D. BURNS. The action of adrenalin on mammalian skeletal muscle. *J. Physiol. London* 107: 115-128, 1948.
17. BRUST, M., S. TOBACK, AND J. G. BENTON. Some effects of ultrasound and of temperature on contractions of isolated mammalian skeletal muscle. *Arch. Phys. Med. Rehabil.* 50: 677-694, 1969.
18. BUCHTHAL, F., P. HÖNCKE, AND L. LINDHARD. Temperature measurements in human muscles in situ at rest and during muscular work. *Acta Physiol. Scand.* 8: 230-258, 1944.
19. BUCHTHAL, F., AND E. KAISER. The rheology of the cross-striated muscle fibre with particular reference to isotonic conditions. *Dan. Videnskaberne Selskab Biol. Med.* 21: 1-318, 1951.
20. BULLER, A. J., K. W. RANATUNGA, AND J. M. SMITH. The influence of temperature on the contractile characteristics of mammalian fast and slow twitch skeletal muscles. *J. Physiol. London* 196: 82P, 1968.
21. BULLER, A. J., K. W. RANATUNGA, AND J. SMITH. Influence of temperature on the isometric myograms of cross-innervated mammalian fast twitch and slow twitch skeletal muscles. *Nature London* 218: 877-878, 1968.
22. CARVALLO, J., AND G. WEISS. Influence de la température sur la contraction musculaire de la grenouille. *J. Physiol. Paris* 2: 225-236, 1900.
23. CASELLA, C. Tensile force in total striated muscle, isolated fibre and sarcolemma. *Acta Physiol. Scand.* 21: 380-401, 1950.
24. CECCHI, G., F. COLOMO, AND V. LOMBARDI. Force-velocity relation in normal and nitrate-treated frog single muscle fibres during rise of tension in an isometric tetanus. *J. Physiol. London* 285: 257-273, 1978.
25. CHATFIELD, P. O. Hypothermia and its effects on the sensory and peripheral motor systems. *Ann. NY Acad. Sci.* 80: 445-448, 1959.
26. CLARKE, R. S. J., R. F. HELTON, AND A. R. LIND. The duration of sustained contractions on the human forearm at different muscle temperatures. *J. Physiol. London* 143: 454-473, 1958.
27. CLOSE, R. The relation between intrinsic speed of shortening and duration of the active state of muscle. *J. Physiol. London* 180: 542-559, 1965.
28. CLOSE, R., AND J. F. Y. HOH. Influence of temperature on isometric contractions of rat skeletal muscles. *Nature London* 217: 1179-1180, 1968.
29. CLOSE, R. L. Dynamic properties of mammalian skeletal muscles. *Physiol. Rev.* 52: 129-197, 1972.
30. COLEMAN, A., AND M. POMPILIAN. Influence de la température sur la contraction musculaire des animaux à sang froid: grenouille, écrevisse. *C. R. Soc. Biol.* 48: 696-698, 1896.
31. CSAPO, A. Dependence of isometric tension and isotonic shortening of uterine muscle on temperature and on strength of stimulation. *Am. J. Physiol.* 177: 348-354, 1954.
32. CSAPO, A., AND D. R. WILKIE. The dynamics of the effect of potassium on frog's muscle. *J. Physiol. London* 134: 497-514, 1956.
33. CULLINGHAM, P. J., A. R. LIND, AND R. J. MORTON. The maximal isometric tetanic tension developed by mammalian muscles, *in situ*, at different temperatures. *Q. J. Exp. Physiol.* 45: 142-156, 1960.
34. DAWSON, W. R. Physiological responses to temperature in the lizard *Eumeces obsoletus*. *Physiol. Zool.* 33: 87-103, 1960.
35. DAWSON, W. R., AND G. A. BARTHOLOMEW. Metabolic and cardiac responses to temperature in the lizard *Dipsosaurus dorsalis*. *Physiol. Zool.* 31: 100-111, 1958.
36. DAWSON, W. R., AND T. L. POULSON. Effects of temperature on ventricular contraction in several lizards (Abstract). *Anat. Rec.* 131: 545, 1958.
37. DOI, Y. Studies on muscular contraction. I. The influence of temperature on the mechanical performance of skeletal and heart muscle. *J. Physiol. London* 54: 218-226, 1924.
38. DOUDOUMPOULOS, A. N., AND P. O. CHATFIELD. Effects of temperature on function of mammalian (rat) muscle. *Am. J. Physiol.* 196: 1197-1199, 1959.
39. EDMAN, K. A. P. The velocity of unloaded shortening and its relation to sarcomere length and isometric force in vertebrate muscle fibres. *J. Physiol. London* 291: 143-159, 1979.
40. EDMAN, K. A. P., A. MATTIAZZI, AND E. NILSSON. The influence of temperature on the force-velocity relationship of rabbit papillary muscle. *Acta Physiol. Scand.* 90: 750-756, 1974.
41. EDWARDS, R. H. T., R. C. HARRIS, E. HULTMAN, L. KAUSER, D. KOH, AND L.-O. NORDEJÖ. Effect of temperature on muscle energy metabolism and endurance during successive isometric contractions, sustained to fatigue, of the quadriceps muscle in man. *J. Physiol. London* 220: 335-352, 1972.
42. EKBLUM, B. T., AND O. H. L. BING. Effect of temperature change on the tolerance of isolated contracting cardiac muscle to hypoxia. *Cryobiology* 16: 161-165, 1979.
43. FAULKNER, J. A. Heat and contractile properties of skeletal muscle. In: *Environmental Physiology: Aging, Heat and Altitude*, edited by S. M. Horvath and M. K. Yousef. Amsterdam: Elsevier/North-Holland, 1980, p. 191-203.
44. FENN, W. O., AND B. S. MARSH. Muscular force at different speeds of shortening. *J. Physiol. London* 85: 277-297, 1935.
45. FICK, A. *Mechanische Arbeit und Wärmeentwicklung bei der Muskelthätigkeit*. Leipzig, E. Germany: Brockhaus, 1882.
46. FLOREY, E., AND G. HOYLE. The effects of temperature on a nerve muscle system of the Hawaiian ghost crab, *Ocypode ceratophthalma* (Pallas). *J. Comp. Physiol.* 110: 51-64, 1976.
47. FOWLER, W. S., AND A. CROWE. Effect of temperature on resistance to stretch of tortoise muscle. *Am. J. Physiol.* 231: 1349-1355, 1976.
48. FRÖHLICH, F. W. Über den Einfluss der Temperatur auf den Muskel. *Z. Allg. Physiol.* 7: 461-468, 1907.
49. GABEL, L. P., C. CARSON, AND E. VANCE. Active state of muscle and the second and third derivatives of twitch tension. *Am. J. Physiol.* 214: 1025-1030, 1968.
50. GAD, J., AND J. F. HEYMANS. Ueber den Einfluss der Temperatur auf die Leistungsfähigkeit der Muskelsubstanz. *Arch. Physiol. Bois-Reymond Suppl. Bd.* 59-115, 1890.
51. GENOVELY, H., AND B. A. STAMFORD. Effects of prolonged warm-up exercise above and below anaerobic threshold on maximal performance. *Eur. J. Appl. Physiol.* 48: 323-330, 1982.
52. GIBBS, C. L. Smooth muscle mechanics and energetics: the effect of temperature (Abstract). *Proc. Aust. Physiol. Pharmacol. Soc.* 8: 192P, 1977.

53. GIBBS, C. L., AND D. S. LOISELLE. Effect of temperature on mechanical and myothermic properties of rabbit smooth muscle. *Am. J. Physiol.* 238 (Cell Physiol. 7): C49-C55, 1980.
54. GODT, R. E., AND B. D. LINDLEY. Influence of temperature on contractile activation and isometric force production in mechanically skinned muscle fibers of the frog. *J. Gen. Physiol.* 80: 279-297, 1982.
55. GORDON, G., AND C. G. PHILLIPS. Slow and rapid components in a flexor muscle. *Q. J. Exp. Physiol.* 38: 35-45, 1953.
56. GRANT, R. T., AND R. S. B. PEARSON. The blood circulation in the human limb. Observations on the differences between the proximal and distal parts and remarks on the regulation of body temperature. *Clin. Sci.* 3: 119-139, 1938.
57. HAJDU, S. Behaviour of frog and rat muscle at higher temperatures. *Enzymologia* 14: 187-193, 1951.
58. HAJDU, S. Observations on the temperature dependence of the tension developed by the frog muscle. *Arch. Int. Physiol.* 59: 58-61, 1951.
59. HAJDU, S., AND R. B. O'SULLIVAN. The delta F¹ slope of frog muscle. *Enzymologia* 14: 182-186, 1951.
60. HANSON, J. The effects of repetitive stimulation on the action potential and the twitch of rat muscle. *Acta Physiol. Scand.* 90: 387-400, 1974.
61. HARRI, M., AND E. FLOREY. The effects of acclimation temperature on a neuromuscular system of the crayfish, *Astacus leptodactylus*. *J. Exp. Biol.* 78: 281-293, 1979.
62. HARTREE, W., AND A. V. HILL. The nature of the isometric twitch. *J. Physiol. London* 55: 389-411, 1921.
63. HILL, A. V. The heat of shortening and the dynamic constants of muscle. *Proc. R. Soc. London Ser. B* 126: 136-195, 1938.
- 63a. HILL, A. V. The dimensions of animals and their muscular dynamics. *Sci. Prog.* 38: 209-230, 1950.
64. HILL, A. V. The influence of temperature on the tension developed in an isometric twitch. *Proc. R. Soc. London Ser. B* 138: 349-354, 1951.
65. HILL, A. V. Thermodynamics of muscle. *Nature London* 167: 377-380, 1951.
66. HILL, D. K. Resting tension and the form of the twitch of rat skeletal muscle at low temperature. *J. Physiol. London* 221: 161-171, 1972.
67. HOH, J. F. Y. Neural regulation of muscle activation. *Exp. Neurol.* 45: 241-256, 1974.
68. ISHIZUKA, T., AND M. ENDO. The influence of temperature on tension development of skinned skeletal muscle fibers (Abstract). *Jpn. J. Pharmacol. Suppl.* 31: 214P, 1981.
69. ISSACSON, A., M. J. HINKES, AND S. R. TAYLOR. Contracture and twitch potentiation of fast and slow muscles of the rat at 20° and 37°C. *Am. J. Physiol.* 218: 33-41, 1970.
70. JEWELL, B. R., AND D. R. WILKIE. An analysis of the mechanical components in frog's striated muscle. *J. Physiol. London* 143: 515-540, 1958.
71. JOSEPHSON, R. K. Temperature and the mechanical performance of insect muscle. In: *Insect Thermoregulation*, edited by B. Heinrich. New York: Wiley, 1981, p. 20-44.
72. JOSEPHSON, R. K. Contraction dynamics of flight and stridulatory muscles in tettigoniid insects. *J. Exp. Biol.* In press.
73. JULIAN, F. J., W. D. STEBER, AND M. R. SOLLINS. Force-velocity relations of frog twitch muscle fibers obtained during tetani and at various times in twitches. *Biophys. Soc. Abstr.* 15: 235, 1971.
74. KABARGI, M. D., AND K. W. SCHNEIDER. Effect of temperature and calcium on the diastolic length-tension relationship of rat heart muscle. *Acta Cardiol.* 35: 215-225, 1980.
75. KAIJSER, L. Limiting factors for aerobic muscle performance. *Acta Physiol. Scand. Suppl.* 346: 1-96, 1970.
76. KAISER, K. Zur Analyse der Zuckungcurve des quergestreiften Muskels. *Z. Biol.* 33: 157-177, 1896.
77. KATZ, B. The relation between force and speed in muscular contraction. *J. Physiol. London* 96: 45-64, 1939.
78. KEAN, C., AND E. HOMSHER. The effect of temperature on the maintenance heat rate and maximum shortening velocity of frog skeletal muscle (Abstract). *Federation Proc.* 33: 1334, 1974.
79. KELLY, E., AND W. J. FRY. Isometric twitch tension of frog skeletal muscle as a function of temperature. *Science* 128: 200-202, 1958.
80. KLEMPF, P., AND U. PEIPER. The dynamics of cross-bridge movement in vascular smooth muscle estimated from a single isometric contraction of the portal vein: the influence of temperature and calcium. *Pfluegers Arch.* 378: 31-36, 1978.
81. KRARUP, C. Temperature dependence of enhancement and diminution of tension evoked by staircase and by tetanus in rat muscle. *J. Physiol. London* 331: 373-387, 1981.
82. LANGER, G. A., AND A. J. BRADY. The effects of temperature upon contraction and ionic exchange in rabbit ventricular myocardium. *J. Gen. Physiol.* 52: 682-713, 1968.
83. LÄNNERGREN, J. The force-velocity relation of isolated twitch and slow muscle fibres of *Xenopus laevis*. *J. Physiol. London* 283: 501-521, 1978.
84. LÄNNERGREN, J., P. LINDBLOM, AND B. JOHANSSON. Contractile properties of two varieties of twitch muscle fibers in *Xenopus laevis*. *Acta Physiol. Scand.* 114: 523-535, 1982.
85. LICHT, P. A comparative study of the thermal dependence of contractility in saurian skeletal muscle. *Comp. Biochem. Physiol.* 13: 27-34, 1964.
86. LICHT, P. Thermal adaptation in the enzymes of lizards in relation to preferred body temperature. In: *Molecular Mechanisms of Temperature Adaptation*, edited by C. L. Prosser. New York: Academic, 1967, p. 131-145.
87. LICHT, P., W. R. DAWSON, AND V. H. SHOEMAKER. Thermal adjustments in cardiac and skeletal muscles of lizards. *Z. Vgl. Physiol.* 65: 1-14, 1969.
88. LIND, A. R., AND M. SAMUELOFF. The influence of local temperature on successive sustained contractions. *J. Physiol. London* 136: 12P-13P, 1957.
89. LINEHAN, C. M. The effect of temperature on the tension responses of the anterior byssal retractor muscle (ABRM) of *Mytilus edulis*. *J. Exp. Biol.* 97: 375-384, 1982.
90. LOISELLE, D. S. The effects of temperature on the energetics of rat papillary muscle. *Pfluegers Arch.* 379: 173-180, 1979.
91. MACDONALD, J. A., AND J. C. MONTGOMERY. Thermal limits of neuromuscular function in an Antarctic fish. *J. Comp. Physiol.* 147: 237-250, 1982.
92. MACLAGAN, J., AND E. ZAIMIS. The effect of muscle temperature on twitch and tetanus in the cat. *J. Physiol. London* 137: 89P-90P, 1957.
93. MAREY, E. *J. Du Mouvement dans les Fonctions de la Vie*. Paris: Germer Baillière, 1868.
94. MARSH, R. L., AND A. F. BENNETT. Thermal dependence of isotonic contractile properties of skeletal muscle and sprint performance in a lizard (Abstract). *Physiologist* 24(4): 20, 1981.
95. MASHIMA, H., AND M. MATSUMURA. The effect of temperature on the mechanical properties and action potential of isolated frog ventricle. *Jpn. J. Physiol.* 14: 422-438, 1964.
96. MASHIMA, H., M. MATSUMURA, AND Y. NAKAYAMA. On the coupling relation between action potential and mechanical response during repetitive stimulation in frog sartorius muscle. *Jpn. J. Physiol.* 12: 324-336, 1962.
97. MATTIAZZI, A. R., AND E. NILSSON. The influence of temperature on the time course of the mechanical activity in rabbit papillary muscle. *Acta Physiol. Scand.* 97: 310-318, 1976.
98. MITTENTHAL, J. E. A sliding filament model for skeletal muscle. Dependence of isometric dynamics on temperature and sarcomere length. *J. Theor. Biol.* 51: 1-16, 1975.
99. MITTENTHAL, J. E., AND F. D. CARLSON. Transient phases of the isometric tetanus in frog's striated muscle. *J. Gen. Physiol.* 58: 20-35, 1971.
100. MORI, A. Relation between the muscle temperature and twitch tension of the skeletal muscle. *Nihon Univ. J. Med.* 18: 159-167, 1976.
101. MORRIS, R. W. Effect of temperature on muscle contractility of the eurythermic lizard *Leiopisma zelandica*. *Comp. Biochem. Physiol. A* 71: 635-637, 1982.
102. NELSON, Z. C., J. R. HIRSHFELD, D. O. SCHREIWEIS, AND M. J. O'FARRELL. Flight muscle contraction in relation to ambient temperature in some species of desert bats. *Comp. Biochem. Physiol. A* 56: 31-36, 1977.
103. NEVILLE, A. C., AND T. WEIS-FOGH. The effect of temperature on locust flight muscle. *J. Exp. Biol.* 40: 111-121, 1963.
104. NUKADA, A. Hauttemperatur und Leistungsfähigkeit in Extremitäten bei statischer Haltearbeit. *Int. Z. Angew. Physiol. Einschl. Arbeitsphysiol.* 16: 74-80, 1955.
105. NUKADA, A., AND E. A. MÜLLER. Hauttemperatur und Leistungsfähigkeit in Extremitäten bei dynamischer Arbeit. *Int. Z. Angew.*

- Physiol. Einschl. Arbeitsphysiol.* 16: 61-73, 1955.
106. OETLIKER, H. Influence of low temperature on contractility of single frog muscle fibres. *Experientia* 27: 723, 1971.
 107. OLIVER, R. A., D. J. JOHNSON, W. W. WHEELHOUSE, AND P. P. GRIFFIN. Isometric muscle contraction response during recovery from reduced intramuscular temperature. *Arch. Phys. Med. Rehabil.* 60: 126-129, 1979.
 108. OSGOOD, P. F., AND W. R. BREWSTER, JR. Effect of temperature and continuous stimulation on gastrocnemius of the frog. *Am. J. Physiol.* 205: 1299-1303, 1963.
 109. PEIPER, U., R. LAVEN, AND M. EHL. Force velocity relationships in vascular smooth muscle: the influence of temperature. *Pfluegers Arch.* 356: 33-45, 1975.
 110. PETROFSKY, J. S. The influence of recruitment order and temperature on muscle contraction with special reference to motor unit fatigue. *Eur. J. Appl. Physiol.* 47: 17-25, 1981.
 111. PETROFSKY, J. S., R. L. BURSE, AND A. R. LIND. The effect of deep muscle temperature on the cardiovascular response of man to static effort. *Eur. J. Appl. Physiol.* 47: 7-16, 1981.
 112. PETROFSKY, J. S., A. GUARD, AND A. R. LIND. The influence of muscle temperature on the contractile characteristics of fast and slow muscles in the cat (Abstract). *Physiologist* 21(4): 91, 1978.
 113. PETROFSKY, J. S., AND A. R. LIND. Insulative power of body fat on deep muscle temperatures and isometric endurance. *J. Appl. Physiol.* 39: 639-642, 1969.
 114. PETROFSKY, J. S., AND A. R. LIND. The relationship of body fat content to deep muscle temperature and isometric endurance in man. *Clin. Sci. Mol. Med.* 48: 405-412, 1975.
 115. PETROFSKY, J. S., AND A. R. LIND. The influence of temperature on the isometric characteristics of fast and slow muscle of the cat. *Pfluegers Arch.* 389: 149-154, 1981.
 116. PETROFSKY, J. S., AND C. A. PHILLIPS. The influence of temperature, initial length and electrical activity on the force-velocity relationship of the medial gastrocnemius muscle of the cat. *J. Biomech.* 14: 297-306, 1981.
 117. PROSSER, C. L. *Comparative Animal Physiology*. Philadelphia, PA: Saunders, 1973.
 118. PUTNAM, R. W., AND A. F. BENNETT. Thermal dependence of isometric contractile properties of lizard muscle. *J. Comp. Physiol.* 147: 11-20, 1982.
 119. RALL, J. A. Effects of temperature on tension, tension-dependent heat, and activation heat in twitches of frog skeletal muscle. *J. Physiol. London* 291: 265-275, 1979.
 120. RANATUNGA, K. W. Influence of temperature on the characteristics of summation of isometric mechanical responses of mammalian skeletal muscle. *Exp. Neurol.* 54: 513-532, 1977.
 121. RANATUNGA, K. W. Changes produced by chronic denervation in the temperature-dependent isometric contractile characteristics of rat fast and slow twitch skeletal muscles. *J. Physiol. London* 273: 255-262, 1977.
 122. RANATUNGA, K. W. Influence of temperature on isometric tension development in mouse fast- and slow-twitch skeletal muscles. *Exp. Neurol.* 70: 211-218, 1980.
 123. RANATUNGA, K. W. Temperature-dependence of shortening velocity and rate of isometric tension development in rat skeletal muscle. *J. Physiol. London* 329: 465-483, 1982.
 124. REISER, P. J., AND B. D. LINDLEY. Temperature dependence of tension production by atrial trabeculae (Abstract). *Biophys. J.* 41: 246, 1983.
 125. RENAUD, J. M., AND E. D. STEVENS. Effect of acclimation temperature and pH on contraction of frog sartorius muscle. *Am. J. Physiol.* 240 (Regulatory Integrative Comp. Physiol. 9): R301-R309, 1981.
 126. RENAUD, J. M., AND E. D. STEVENS. The interactive effects of temperature and pH on the isometric contraction of toad sartorius muscle. *J. Comp. Physiol.* 145: 67-71, 1981.
 127. ROBERTS, R. G. D., AND A. H. BRETAG. Effect of temperature on isometric twitch tension in diaphragm muscle of the rat. *Proc. Aust. Physiol. Pharmacol. Soc.* 5: 105-106, 1974.
 128. ROBINSON, S., F. R. MEYER, J. L. NEWTON, C. H. TS'AO, AND L. O. HOLGERSEN. Relations between sweating, cutaneous blood flow, and body temperature at work. *Am. J. Physiol.* 20: 575-582, 1965.
 129. ROME, L. C. The effect of long-term exposure to different temperatures on the mechanical performance of frog muscle. *Physiol. Zool.* 56: 33-40, 1983.
 130. ROME, L. C., AND M. J. KUSHMERICK. Energetics of isometric contractions as a function of muscle temperature. *Am. J. Physiol.* 244 (Cell Physiol. 13): C100-C109, 1983.
 131. SALTIN, B., A. P. GAGGE, AND J. A. J. STOLWIJK. Muscle temperature during submaximal exercise in man. *J. Appl. Physiol.* 25: 679-688, 1968.
 132. SARGEANT, A. J., AND N. L. JONES. Effect of temperature on power output of human muscle during short-term dynamic exercise (Abstract). *Med. Sci. Sports* 10: 39, 1978.
 133. SCHMULEWITSCH, J. Zur Muskelfysiologie und Physik. *Med. Jahrb.* 15: 3-36, 1868.
 134. SEGAL, S. S., AND J. A. FAULKNER. Static endurance of rat skeletal muscles at different temperatures *in vitro* (Abstract). *Med. Sci. Sports Exercise* 14: 106, 1982.
 135. SOUTH, F. E. Phrenic nerve-diaphragm preparations in relation to temperature and hibernation. *Am. J. Physiol.* 200: 565-571, 1961.
 136. STEPHENS, N. L., R. CARDINAL, AND B. SIMMONS. Mechanical properties of tracheal smooth muscle: effects of temperature. *Am. J. Physiol.* 233 (Cell Physiol. 2): C92-C98, 1977.
 137. STEPHENS, P. J., AND H. L. ATWOOD. Thermal acclimation in a crustacean neuromuscular system. *J. Exp. Biol.* 98: 39-47, 1982.
 138. STEPHENSON, D. G., AND D. A. WILLIAMS. Calcium-activated force responses in fast- and slow-twitch skinned muscle fibres of the rat at different temperatures. *J. Physiol. London* 317: 281-302, 1981.
 139. STOVNER, J. The effect of tetraethylammonium (TEA) and temperature on the neuromuscular block produced by magnesium. *Acta Physiol. Scand.* 41: 370-383, 1957.
 140. SULLIVAN, J. S., AND M. A. DENBOROUGH. Temperature dependence of muscle function in malignant hyperpyrexia-susceptible swine. *Br. J. Anaesthesiol.* 53: 1217-1222, 1981.
 141. SUNANO, S., AND E. MIYAZAKI. A comparison of the effects of temperature and metabolic inhibition on the contraction of smooth muscle. *Jpn. J. Physiol.* 31: 445-456, 1981.
 142. SZENT-GYÖRGYI, A. *Chemical Physiology of Contraction in Body and Heart Muscle*. New York: Academic, 1953.
 143. TRUONG, X. T., B. J. WALL, AND S. M. WALKER. Effects of temperature on isometric contraction of rat muscle. *Am. J. Physiol.* 207: 393-396, 1964.
 144. USHAKOV, B. Thermostability of cells and proteins of poikilotherms and its significance in speciation. *Physiol. Rev.* 44: 518-560, 1964.
 145. WALKER, S. M. Potentiation of twitch tension and prolongation of action potential induced by reduction of temperature in rat and frog muscle. *Am. J. Physiol.* 157: 429-435, 1949.
 146. WALKER, S. M. Similarity of the double response and of tetanus in frog and rat skeletal muscle at similar temperatures (Abstract). *Federation Proc.* 10: 142, 1951.
 147. WALKER, S. M. Failure of potentiation in successive, posttetanic, and summated twitches in cooled skeletal muscle of the rat. *Am. J. Physiol.* 166: 480-484, 1951.
 148. WALKER, S. M. The relation of stretch and of temperature to contraction of skeletal muscle. *Am. J. Phys. Med.* 39: 234-258, 1960.
 149. WARDLE, C. S. Limit of fish swimming speed. *Nature London* 255: 725-727, 1975.
 150. WASHINGTON, M. A., M. F. ARRIGHI, S. F. STREET, AND R. W. RAMSEY. Q_{10} of the maximal tetanic tension developed by isolated muscle fibers of the frog. *Science* 121: 445-446, 1955.
 151. WASHIO, H. Effect of external calcium and of temperature on contraction in snake muscle fibers. *J. Gen. Physiol.* 63: 415-431, 1974.
 152. WEBB, P. W. Temperature effects on acceleration of rainbow trout, *Salmo gairdneri*. *J. Fish Res. Board Can.* 35: 1417-1422, 1978.
 153. YEATMAN, L. A., JR., W. W. PARMLEY, AND E. H. SONNENBLICK. Effects of temperature on series elasticity and contractile element motion in heart muscle. *Am. J. Physiol.* 217: 1030-1034, 1969.