

TEMPERATURE AND MUSCLE

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SUMMARY

Rates of force development, contraction and relaxation of vertebrate skeletal muscle are temperature dependent with Q_{10} values of approximately 2. Maximal forces developed have a low or negative thermal dependence. The functional basis of these patterns is poorly understood. Muscle performance generally does not acclimate. There appears to have been some evolutionary adaptation among species and classes to different thermal regimes, such that muscles from cold-adapted species maintain better mechanical performance at low temperatures than do those from warm-adapted animals. However, rate processes remain strongly thermally dependent even in animals with low or variable body temperatures. This thermal dependence of muscle *in vitro* is reflected in behavioural performance: maximal force generation *in vivo* is temperature independent and time-dependent activities are more rapid at higher muscle temperatures.

INTRODUCTION

Mechanical performance of muscle is greatly influenced by temperature, as are most biological processes. Maximal forces developed by muscles and their rates of force generation, contraction, relaxation and power output are all altered when body temperature varies. As these muscular forces and rate processes underlie behavioural capacities, these may also be thermally dependent. Such factors as maximal locomotor speed and reaction rates may change with temperature and be so slow in the cold that effective escape or pursuit by an animal is curtailed. In animals that are subjected to varying or low body temperatures, we might expect to find adaptations which minimize the thermal dependence of muscle performance.

The influence of temperature on the mechanical performance of vertebrate skeletal muscle is reviewed in this paper, first for one species of lizard and then for vertebrates more generally. Adaptations of muscle performance to temperature are examined, underlying mechanisms of thermal dependence are reviewed and implications for behaviour are discussed.

TEMPERATURE AND MECHANICAL PERFORMANCE

First, we will examine the influence of temperature on the contractile performance of muscle from a lizard. Lizards are a particularly useful group of animals for such studies as they may naturally experience a wide range of body temperatures daily. Many species also have very high thermal tolerance. Data are presented here (Fig. 1) on the influence of temperature on several aspects of force generation and contraction of skeletal muscle of the lizard *Dipsosaurus dorsalis* (Marsh & Bennett, 1985). *Dipsosaurus* inhabits the hot desert regions of California and regulates field body temperatures at approximately 40°C. However, it must maintain the capacity to react and move even when its body temperature is far below these diurnal levels. The reported data were measured on the white portion of the iliofibularis muscle of the hind limb. This preparation is composed almost exclusively of fast glycolytic fibres (Gleeson, Putnam & Bennett, 1980), which constitute the large majority of fibres in all the locomotory muscles of this species (Putnam, Gleeson & Bennett, 1980).

All contractile rate processes in this muscle, both isometric and isotonic, are greatly accelerated by increasing temperature, even up to 44°C. In isometric twitch, the rates of both tension development (measured as the inverse of time-to-peak tension, TPT) and relaxation (measured as the inverse of time to return to 50% of maximal twitch tension, 1/2 RT) have Q_{10} values of 2.36 and 2.82, respectively, between 20 and 30°C. Maximal rate of isometric tetanic tension development (dP_0/dt) has a Q_{10} of 2.22 over this range. The maximal velocity of shortening (V_{max}) and maximal power output (\dot{W}_{max}) during isotonic contractions are similarly thermally dependent with Q_{10} values of 1.95 and 2.42, respectively. All these rates have a thermal dependence similar to those of most other biological processes (i.e. $Q_{10} = 2-3$, Precht, Christophersen, Hensel & Larcher, 1973; Prosser, 1973).

In contrast, the temperature dependence of force exerted during isometric contraction is substantially different from that of contractile rate processes. Tetanic tension (P_0) has a significant but very low thermal dependence: its thermal ratio (R_{10} , the ratio of two quantities measured over a 10°C interval, Bennett, 1984) is 1.2 between 20 and 30°C. Maximal P_0 is attained at 40°C. Twitch tension (P_t) is maximal at 15°C, declining at higher temperatures ($R_{10} = 0.62$ between 20 and 30°C).

Force and its rate of development thus have very different thermal sensitivities in this lizard. Nearly maximal muscular performance is obtained at normal field activity temperature (40°C): contraction and relaxation rates are rapid and tetanic force is maximal. Twitch tension is the only factor that is not near its maximal value at this temperature. Exposure to low temperatures greatly retards the speed of muscle contraction in *Dipsosaurus*. This dependence may restrict locomotory responses at low body temperature: the speed of limb movement during burst escape speed in this lizard is limited by the time course of the muscle twitch at 25°C and below (Marsh & Bennett, 1985). Low temperature does not similarly affect force output. Nearly the same tetanic tension can be produced and twitch tension is even increased.

How representative is the thermal dependence of muscle function in *Dipsosaurus*? Q_{10} and R_{10} values measured approximately between 20 and 30°C from all other studies available on vertebrate skeletal muscle are given in Fig. 2. Most of these

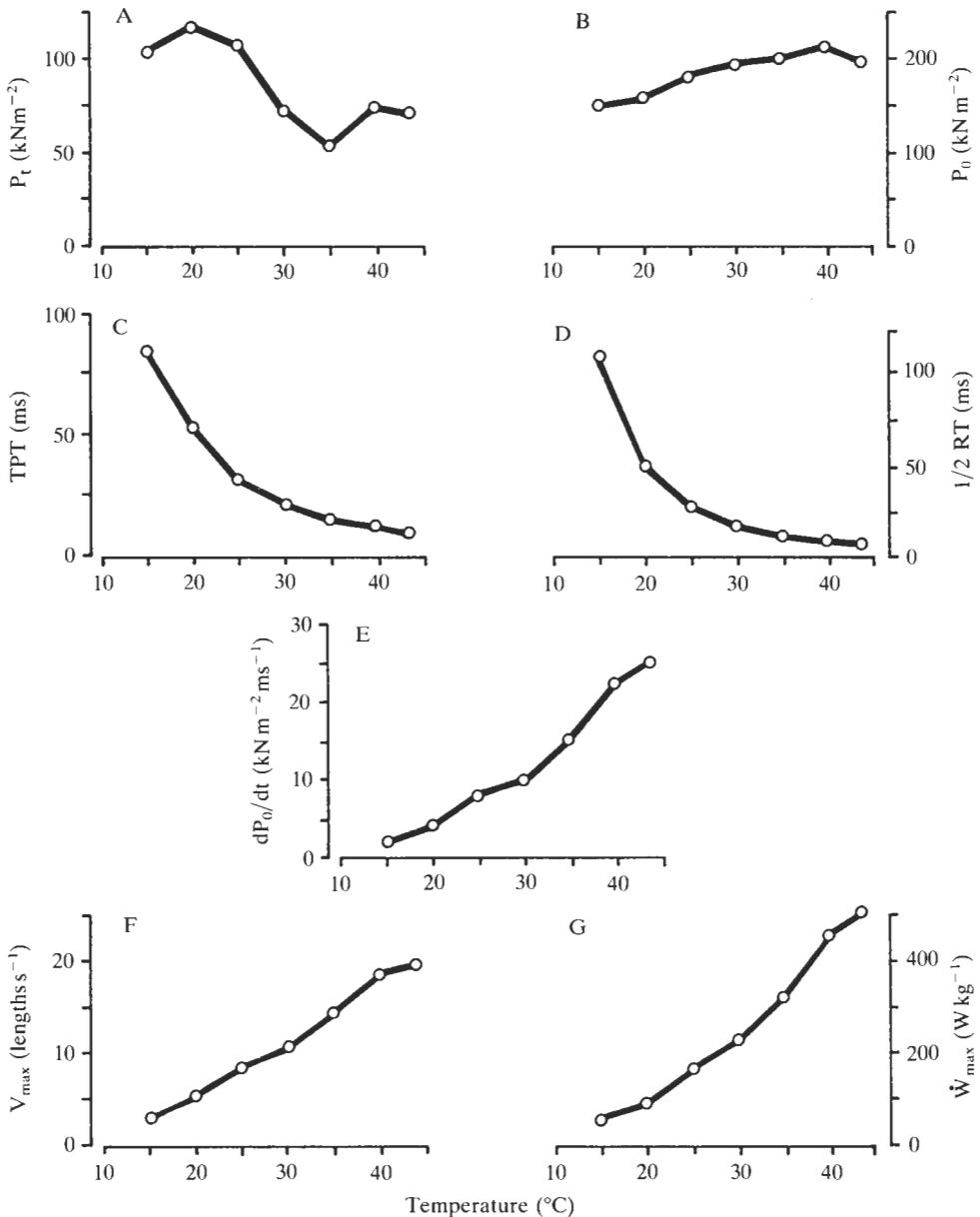


Fig. 1. Contractile performance of the iliofibularis muscle of the lizard *Dipsosaurus dorsalis* as a function of temperature. (A) twitch tension, P_t ; (B) tetanic tension, P_0 ; (C) time-to-peak twitch tension, TPT; (D) time of half relaxation from peak twitch tension, $1/2 RT$; (E) rate of rise of tetanic tension dP_0/dt ; (F) maximal velocity of shortening, V_{\max} ; (G) maximal power output, \dot{W}_{\max} . Data from Marsh & Bennett (1985).

observations were made on amphibian and mammalian muscle. Although the variance in the data is high, due to such factors as the diversity of animals examined, differing fibre type composition of the muscles and different measurement techniques, the pattern is clear. As in the lizard muscle, rate processes in general are thermally dependent with Q_{10} values of approximately 2, tetanic tension has a very low thermal dependence and twitch tension often decreases over this temperature range.

ADAPTATIONS TO TEMPERATURE

This general pattern of high thermal dependence of rate processes might be expected to pose problems for poikilothermic organisms. As muscle temperature changes, so do contractile speeds and possibly reaction rates or locomotor ability. Poikilotherms with low body temperatures might not attain maximal performance of which their muscles are capable due to an extrinsic factor, temperature, rather than an intrinsic structural or biochemical limitation. For example, the lizard *Gerrhonotus multicarinatus* has field active body temperatures of about 25°C, but maximal rates of muscle contraction and burst escape speed at 35–40°C (Bennett, 1980; Putnam & Bennett, 1982), body temperatures far in excess of those encountered under any

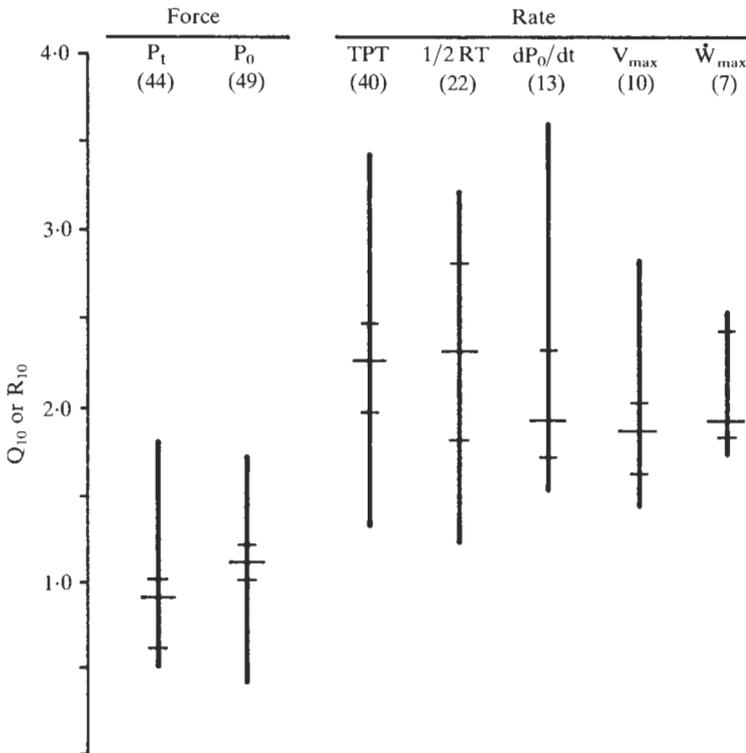


Fig. 2. Thermal dependence of force and rate of contraction of vertebrate skeletal muscle between 20 and 30°C. Wide horizontal bar indicates median value; narrow horizontal bars, 25th and 75th percentile observations; vertical bar, range. Number of observations given in parentheses. Data from summary by Bennett (1984). For details of abbreviations see legend to Fig. 1.

natural conditions. Such a pattern of thermal dependence does not appear particularly adaptive. To what extent has there been adjustment to minimize the thermal perturbation of contractile rate processes in animals with low and/or variable body temperatures? Few data on this topic exist, so no confident generalizations are possible, but the studies available suggest some interesting adaptive patterns.

Acclimation

When an individual animal is exposed to a new thermal regime, it often shows compensatory changes in its physiological reactions (acclimation). Biological rate processes are initially altered in accordance with their Q_{10} upon acute temperature exposure. Over several days or weeks, these rates often return partially or completely to their original levels, even while the new thermal regime is maintained (Precht *et al.* 1973; Prosser, 1973). Several comprehensive studies on the effect of long-term temperature exposure have been done on the mechanical performance of skeletal muscles of anuran amphibians. As illustrated for twitch kinetics (Fig. 3), no acclimation of either force generation (P_t , P_0) or contractile rate (TPT, $1/2 RT$, dP_0/dt , V_{max} , \dot{W}_{max}) has been demonstrated (Renaud & Stevens, 1981*a,b*; Rome, 1983). The initial depression of contraction rates by cold exposure is maintained indefinitely. A similar lack of acclimation occurs in locomotor capacity of these animals (Putnam & Bennett, 1981). In fish, myofibrillar ATPase activity, which should be reflected in V_{max} (Bárány, 1967), has been shown to acclimate in goldfish (Johnston, 1979) but not in killifish (Sidell, Johnston, Moerland & Goldspink, 1983).

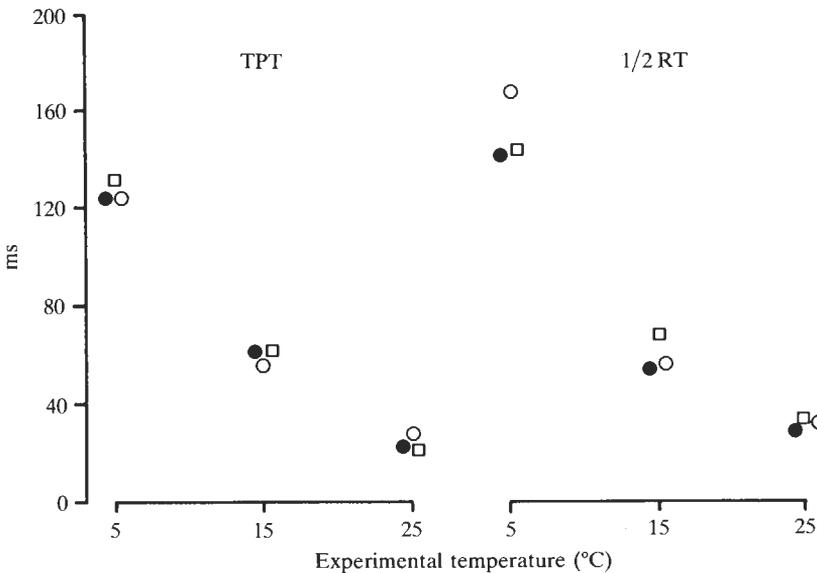


Fig. 3. Mean values of time-to-peak tension (TPT) and half relaxation time ($1/2 RT$) for twitch contractions of the sartorius muscle of *Rana pipiens* acclimated to 5°C (filled circles), 15°C (open circles) and 25°C (squares). The only significant difference among acclimation groups is a longer $1/2 RT$ for 25°C-acclimated frogs measured at 15°C. Data from Renaud & Stevens (1981*a*).

The lack of acclimation of muscle function is a very puzzling result in view of its obvious importance to behavioural capacity and may reflect a constraint on adaptation.

Interspecific comparisons

Studies comparing species naturally exposed to different thermal regimes show a different pattern of adjustment of muscle function over evolutionary time. In lizards, species with lower activity temperatures have lower Q_{10} values for TPT, $1/2 RT$ and dP_0/dt and faster twitch responses measured at any common temperature (Putnam & Bennett, 1982). Maximization of P_t at preferred thermal levels previously reported (Licht, 1964) has not been confirmed (Putnam & Bennett, 1982). The range of temperatures over which lizard muscles can function is clearly affected by their thermal regimes (Ushakov, 1964; Licht, 1964; Putnam & Bennett, 1982): muscles from more thermophilic species lose contractile ability and undergo irreversible heat damage at substantially higher temperatures than do those of more cryophilic animals. In fish, actomyosin ATPases of species from cold environments have both lower Q_{10} values and greater activities at any common temperature than those from warm-adapted fish (Fig. 4) (Johnston, Walesby, Davison & Goldspink, 1977; Johnston & Walesby, 1977, 1979). In both fish and lizards, evolutionary adaptation to temperature has evidently proceeded with both a shift (translation) and rotation of the rate-temperature curve.

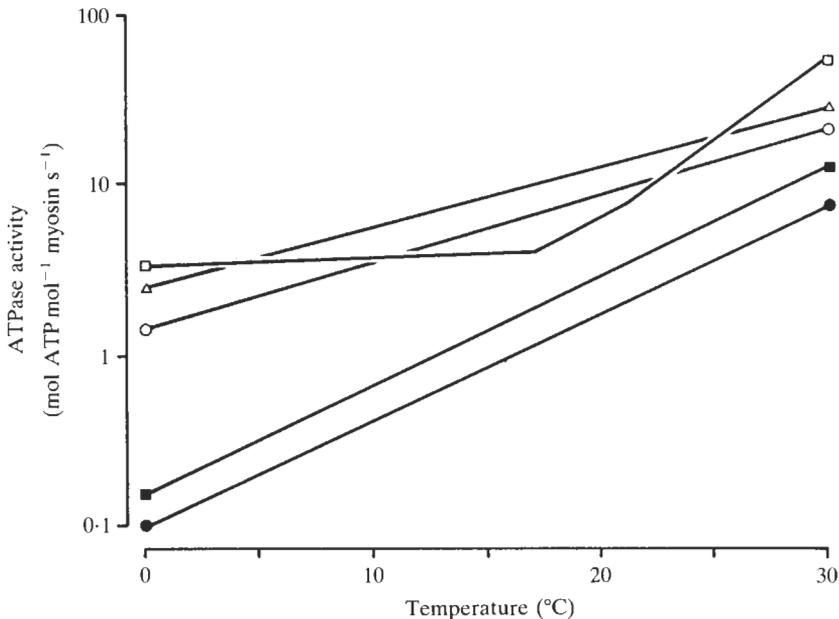


Fig. 4. Activity of Mg^{2+} , Ca^{2+} -activated actomyosin ATPase from teleost fish adapted to different thermal regimes. Cold-adapted species: *Salvelinus alpinus*, arctic (open squares); *Champsocephalus gunnari*, antarctic (open circles); *Cottus bubalis*, North Sea (open triangles). Warm-adapted species: *Dascyllus aruanus* (filled circles) and *Pomatocentrus pulcherrimus* (filled squares), both tropical. Note log axis of enzyme activity. Data from Johnston & Walesby (1979).

It should be emphasized, however, that these interspecific differences are only relative. In absolute terms, rate processes are still very thermally dependent even in cold-adapted species.

Comparison of muscle from homeotherms and poikilotherms

Are there major differences in the thermal dependence of muscle function in homeotherms and poikilotherms? One might anticipate that the latter would show adaptations to minimize thermal dependence and the former would optimize function over a narrow range of high temperatures. It should be noted, however, that even muscles from homeotherms may undergo major temperature changes depending on ambient conditions and work intensity (e.g. Saltin, Gagge & Stolwijk, 1968).

Some functional differences are apparent between muscle from anuran amphibians and mammals (Bennett, 1984). Anuran muscle develops maximal P_t at 0°C; mammalian peak P_t usually occurs at 20°C. Maximal P_0 is maintained at lower temperatures in anurans: P_0 of anuran muscle declines below approximately 15°C, that of mammalian muscle always decreases below 25°C (Fig. 5). The time course of a muscle twitch, both TPT and 1/2 RT, has a lower Q_{10} in anurans than in mammals. Anuran muscle is thus capable of producing maximal tension at lower temperatures than is mammalian muscle and its rate processes are less temperature sensitive, at least in regard to twitch kinetics. However, the distinction between the thermal dependence of saurian and mammalian muscle function is much less clear (Bennett, 1984). Although maximal P_t is developed at lower temperatures in lizard than in mammalian muscle, the thermal dependencies of P_0 and contractile rate processes are almost identical in these groups. The anuran–mammalian differences probably reflect

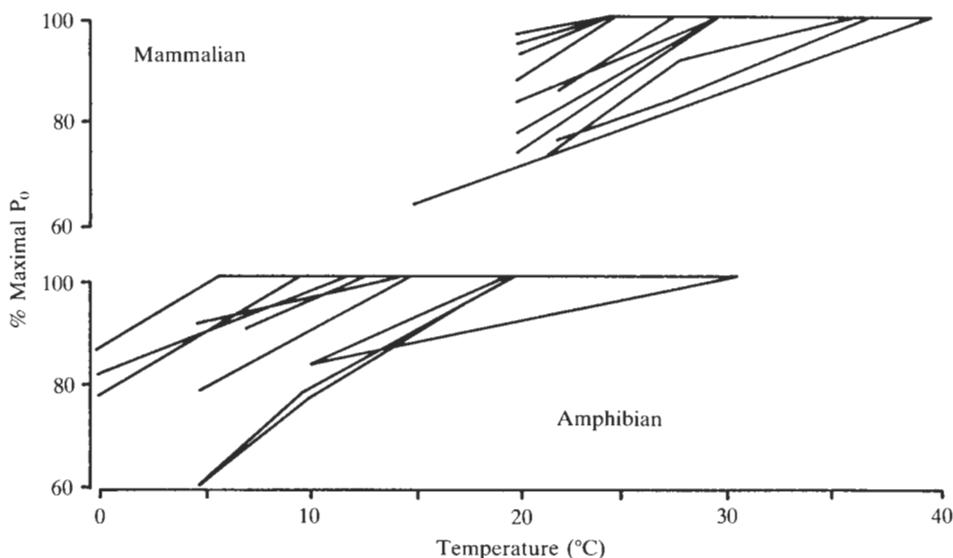


Fig. 5. Thermal dependence of tetanic tension (P_0) in mammalian and anuran amphibian skeletal muscle. Data summarized from the literature by Bennett (1984).

adaptation to very different thermal regimes rather than a dichotomy in the functional capacity of muscle from poikilotherms and homeotherms.

It is apparent from the foregoing that some adjustments of vertebrate skeletal muscle function have evolved with respect to temperature. These adaptations in rate processes, however, have not been substantial. Muscle from poikilotherms still has a marked thermal dependence and rate processes are often faster at temperatures above those normally encountered. Lack of acclimation of these properties in individual animals further points to a lack of plasticity in these systems in regard to temperature adjustment. In view of the small number of studies, it should be evident that more comparative work is required to substantiate or alter these conclusions.

FUNCTIONAL BASIS OF THERMAL DEPENDENCE

The biochemical and functional properties that underlie these patterns of thermal dependence are not well understood. The pronounced thermal dependence of contractile rate processes are expected, as several of the steps underlying contraction and relaxation are enzymatically catalysed and have rates with Q_{10} values of 2.0 or more. For instance, strong thermal dependencies have been demonstrated for the rate of Ca^{2+} release (Blinks, Rüdell & Taylor, 1978; Rall, 1979), the activity of actomyosin ATPase (Bendall, 1964; Hartshorne, Barns, Parker & Fuchs, 1972) and Ca^{2+} uptake by sarcoplasmic reticulum (Yamamoto & Tonomura, 1967; Blinks *et al.* 1978). However, the correspondence between the thermal dependence of contractile events and isolated enzyme systems associated with them is often poor. For example, although actomyosin ATPase is thought to be an important determinant of V_{\max} , the thermal dependence of the former is much greater than that of the latter (Bárány, 1967). An attempt to determine limiting factors of contractile events by comparisons of thermal dependencies would probably be no more successful than previous attempts to elucidate controlling reactions of biochemical pathways by measurement of Arrhenius activation energies.

Twitch tension is generally maximal at 0–20°C, depending on species and muscle type, and declines at higher temperatures. In some sense, the muscle is not as fully activated by a single stimulus at temperatures above 20°C (Ranatunga, 1977). The ratio of P_t/P_0 approaches 1.0 at low temperatures but is less than 0.5 at higher temperatures (Putnam & Bennett, 1982). One possible explanation for this response is insufficient Ca^{2+} release into fibres at higher temperatures. This is evidently not the case, however, as activation heat, which represents the energetic cost of Ca^{2+} release and removal, is thermally independent, indicating no deficiency of release at higher temperatures (Homsher, Mommaerts, Ricchiuti & Wallner, 1972; Rall, 1979). Additionally, measurements with aequorin indicate high levels of Ca^{2+} within the fibre at higher temperatures (Blinks *et al.* 1978). The latter measurements also indicate a much shorter time course for the presence of Ca^{2+} within the fibre at higher temperatures and a consequently shorter period of activation. At high temperatures, insufficient time may be available to attain maximal force. Twitch contraction may be looked upon as a competition between actomyosin ATPase activity and Ca^{2+} removal

by the sarcoplasmic reticulum (Josephson, 1981). These processes evidently have different thermal dependencies, with the latter being more temperature sensitive; the Q_{10} of $1/2 RT$ is generally greater than that of TPT measured on the same muscle (Hill, 1951; Walker, 1960; Bennett, 1984). Thus at low temperatures, greater force can be attained by the contractile proteins, even though their intrinsic contractile velocity is also slowed, before deactivation processes become effective. This explanation of the thermal dependence of P_t , while attractive, has not been critically tested.

Tetanic tension generally has a low but significant thermal dependence below 15–25°C, depending on species (Fig. 5). As the muscle is supposedly completely activated by repetitive stimuli, one might expect P_0 to be thermally independent over the entire temperature range. One explanation for lower P_0 at low temperatures is a smaller number of cross-bridge attachments at those temperatures. However, measurements of instantaneous stiffness, which is dependent upon the number of cross-bridges attached, do not support this hypothesis (Ford, Huxley & Simmons, 1977; Kuhn *et al.* 1979; Bressler, 1981). Instantaneous stiffness is either thermally independent or has a different thermal dependence from that of P_0 . Consequently, the number of cross-bridges attached or a thermally-dependent bridge cycling does not appear to account for the observed pattern. Bressler (1981) suggests that increasing temperature may increase the tension per cross-bridge during tetanus.

It should be clear that further work is required to explain the bases of the thermal dependence of muscle function. Investigations exploiting thermal dependence may well lead to further hypotheses and insights into the nature of the contractile process itself (e.g. Mittenthal, 1975, on the distance of cross-bridge movement). Muscle from animals and/or animal groups with very different thermal histories could be particularly useful in these studies. For example, the different response of P_0 to temperature in anuran and mammalian muscle (Fig. 5) may be helpful to understanding patterns of cross-bridge tension generation and cycling during tetany. Or, the differing thermal dependencies of myofibrillar ATPase from animals adapted to different temperatures (e.g. Fig. 4) may help elucidate their role in determining intrinsic shortening velocities.

THERMAL DEPENDENCE OF MUSCLE PERFORMANCE *IN VIVO*

Is the thermal dependence of muscle function reflected in animal behavioural capacities? On the basis of experiments on isolated muscle, one would expect performance capacity for behaviour involving rates of contraction (e.g. running speed) to improve with increasing temperature. One would also expect performance involving maximal force generation by an animal to be relatively temperature independent.

Physical performance involving rate-dependent factors, such as maximal power output, does improve significantly with increasing muscle temperature (e.g. Asmussen & Bøje, 1945; Binkhorst, Hoofd & Vissers, 1977; Bergh & Ekblom, 1979). Consequently, 'warming up', in the literal sense, does have a positive effect on performance speed, and animals with higher body temperatures do in fact have

greater maximal speeds (Webb, 1978; Bennett, 1980; Putnam & Bennett, 1981). However, the thermal dependence of this performance is distinctly lower than that of rate processes in isolated muscle. For example, in the lizard *Dipsosaurus*, maximal running velocity and limb cycling frequency have Q_{10} values of 1.3–1.4 from 25 to 40°C, while V_{\max} and \dot{W}_{\max} have Q_{10} values of 1.7 and 2.0, respectively (Fig. 6) (Marsh & Bennett, 1985). Similarly low Q_{10} values of 1.0–1.6 have been reported in other studies on rate-dependent performance cited above. This lower thermal dependence of behavioural performance compared to that of isolated muscle function could be attributable to several factors, including storage of energy in elastic structures of low thermal sensitivity (Marsh & Bennett, 1985). However, its basis is unknown at present.

Maximal force generation by muscles *in vivo* is almost independent of muscle temperature from 25 to 40°C (Binkhorst *et al.* 1977; Bergh & Ekblom, 1979; Petrofsky, Burse & Lind, 1981). This pattern accords very well with the observed thermal independence of P_0 over this temperature range. Endurance, measured as the time of maintenance of constant force, is maximal at approximately 30°C in both *in*

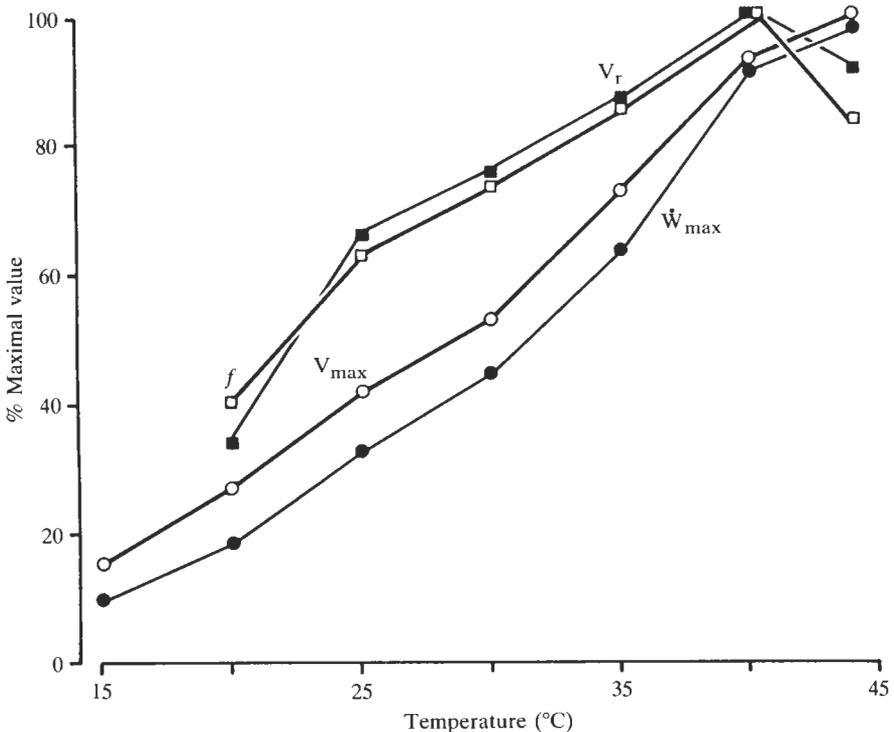


Fig. 6. The thermal dependence of burst locomotory speed and isotonic contractile performance of isolated skeletal muscle of the lizard *Dipsosaurus dorsalis*. V_r , maximal running velocity (filled squares); f , limb cycling frequency (open squares); V_{\max} , maximal velocity of shortening (open circles); \dot{W}_{\max} , maximal power output (filled circles). Data are normalized to maximal value observed ($V_r = 4.3 \text{ m s}^{-1}$; $f = 13.5 \text{ s}^{-1}$; $V_{\max} = 20.1 \text{ lengths s}^{-1}$; $\dot{W}_{\max} = 505 \text{ W kg}^{-1}$). Data from Marsh & Bennett (1985).

in vivo performance (Clarke, Hellon & Lind, 1958; Petrofsky & Lind, 1969; Edwards *et al.* 1972) and in isolated muscle (Petrofsky & Lind, 1981; Segal & Faulkner, 1982). Endurance declines at both higher and lower temperatures.

As the foregoing data indicate, behavioural performance involving both speed and force generation reflects the underlying patterns of thermal dependence of muscle function. Higher muscle temperatures may be expected to result in improved rate performance *in vivo*, although maximal force application may be little affected and endurance may decline.

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