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THERMAL DEPENDENCE OF PASSIVE ELECTRICAL PROPERTIES OF LIZARD MUSCLE FIBRES

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SUMMARY

1. The thermal dependence of passive electrical properties was determined for twitch fibres from the white region of the iliofibularis (IF) muscle of *Anolis cristatellus* (15–35°C) and *Sceloporus occidentalis* (15–40°C), and for twitch fibres from the white (15–45°C) and red (15–40°C) regions of the IF of *Dipsosaurus dorsalis*. These species differ in thermal ecology, with *Anolis* being the least thermophilic and *Dipsosaurus* the most thermophilic.

2. Iliofibularis fibres from the three species reacted similarly to changing temperature. As temperature was increased, input resistance (R_{in}) decreased (average $R_{10} = 0{\cdot}7$), length constant (L) decreased (average $R_{10} = 0{\cdot}9$), time constant (τ) decreased (average $R_{10} = 0{\cdot}8$), sarcoplasmic resistivity (R_s) decreased (average $R_{10} = 0{\cdot}8$) and apparent membrane resistance (R_m) decreased (average $R_{10} = 0{\cdot}7$). In contrast, apparent membrane capacitance (C_m) increased with increasing temperature (average $R_{10} = 1{\cdot}3$).

3. R_{in}, L, τ and apparent R_m were lowest in fibres from *Anolis* (the least thermophilic species) and highest in fibres from *Dipsosaurus* (the most thermophilic species). *Anolis* had the largest and *Dipsosaurus* the smallest diameter fibres (126 and 57 μm, respectively). Apparent C_m was highest in fibres from *Sceloporus*, which had fibres of intermediate diameter (101 μm). R_s did not differ significantly among species.

4. The effect of temperature on the passive electrical properties of these lizard fibres was similar to that reported for muscle fibres from other ectothermic animals (crustaceans, insects, fish and amphibians) but qualitatively different from that reported for some mammalian (cat tenuissimus, goat intercostal) fibres. The changes that occur in the passive electrical properties render the fibres less excitable as temperature increases.

INTRODUCTION

Passive electrical properties are important in determining the excitability of muscle fibres (Bryant & Morales-Aguilera, 1971; Adrian & Bryant, 1974; Jack, Noble & Tsein, 1975). Previous studies have demonstrated significant effects of temperature on the passive electrical properties of muscle fibres from a wide variety of ectothermic

Key words: lizard skeletal muscle, muscle fibres, temperature, cable properties, *Anolis*, *Sceloporus*, *Dipsosaurus*.

animals: membrane resistance (R_m) decreases with increasing temperature in fibres from crab (Fatt & Katz, 1953), crayfish (White, 1983), fish (Klein & Prosser, 1985), frog (del Castillo & Machne, 1953; Hodgkin & Nakajima, 1972), lobster (Coulton & Freeman, 1975) and locust muscle (Kornhuber & Walther, 1987). In contrast, the effects of temperature upon passive electrical properties of mammalian muscle fibres are less uniform: R_m decreases with increasing temperature in rat diaphragm (Palade & Barchi, 1977), but increases with increasing temperature in cat tenuissimus (Boyd & Martin, 1959) and goat intercostal muscle (Lipicky & Bryant, 1972).

Little information is available regarding the passive electrical properties of reptilian muscle fibres (Levine, 1966; Proske & Vaughan, 1968; Ridge, 1971), and the thermal dependence of those properties is unknown. As ectotherms, reptiles must contend with variable environmental and body temperatures and may experience a 20°C range of body temperature during the course of one day (Brattstrom, 1965). The experienced range of body temperatures may include, at its lower end, the activity temperatures of fish and amphibians and, at its upper end, the regulated temperature of mammals. Temperature excursions of this magnitude may significantly affect the passive electrical properties of muscle fibres, and thereby influence muscle excitability and functional capacity.

This study investigated the thermal dependence of passive electrical properties of muscle fibres from three lizard species: *Anolis cristatellus*, *Sceloporus occidentalis* and *Dipsosaurus dorsalis*. These species differ in preferred body temperature (PBT) and upper critical temperature (CT_{max}): *Anolis* has a PBT of 30°C and a CT_{max} of 37°C (Huey, 1983), *Sceloporus* has a PBT of 35°C (Brattstrom, 1965) and a CT_{max} of 44°C (Larson, 1961), and *Dipsosaurus* has a PBT of 40°C and a CT_{max} of 48°C (Norris, 1953; Brattstrom, 1965). The results are compared with those obtained from other studies, and the implications for muscle function are discussed.

MATERIALS AND METHODS

Experimental animals

Anoles (*Anolis cristatellus*, four females, six males; mean body mass $7{\cdot}9 \pm 0{\cdot}39$ g, range 6·0–9·6 g) were collected in Puerto Rico by Dr Paul Hertz (permit no. DRN-84-67). Western fence lizards (*Sceloporus occidentalis*, eight females, seven males; mean body mass $10{\cdot}2 \pm 0{\cdot}64$ g, range 6·3–15·1 g) and desert iguanas (*Dipsosaurus dorsalis*, 14 females, 16 males; mean body mass $46{\cdot}1 \pm 1{\cdot}90$ g, range 27·7–73·6 g) were collected locally in Southern California under California State Fish and Game permits no. 2071 and no. 2141. Lizards were held in glass aquaria, and provided with a photothermal gradient that allowed behavioural thermoregulation. *Anolis* were maintained for several weeks on a diet of crickets. *Sceloporus* were used within several days of capture. *Dipsosaurus* were maintained for several months on a diet of chopped lettuce that was coated with pulverized Purina Puppy Chow and Special-H high vitamin cereal. Access to water was unrestricted for all species.

Muscle preparation

The iliofibularis (IF) muscle was removed with a portion of the ilium attached and pinned at 120% resting length (defined as the *in situ* length with the knee at a 90° angle and the femur perpendicular to the ilium) in a Sylgard-lined chamber. The ranges of *in situ* muscle lengths were 12–15 mm (*Anolis*), 9–12 mm (*Sceloporus*) and 13–20 mm (*Dipsosaurus*). The preparations were superfused with lizard saline (145 mmol l^{-1} NaCl, 4 mmol l^{-1} KCl, 2·5 mmol l^{-1} $CaCl_2$, 20 mmol l^{-1} imidazole buffer, 10 mmol l^{-1} glucose, pH 7·50 at 23°C) throughout the experiments. Imidazole was chosen as the buffer because its pH changes with temperature in a manner very similar to the plasma of a variety of ectothermic vertebrates (Reeves, 1977), including *Dipsosaurus* (Bickler, 1981). Temperature was varied by heating or cooling the saline before it entered the chamber and was recorded with a small thermocouple placed within 1 mm of the muscle. The sequence of temperature exposures was random, except for the highest temperature, which was done last. The preparation was allowed to equilibrate at each newly selected temperature for at least 5 min before measurements were taken.

The iliofibularis of lizards is a parallel-fibred muscle composed of discreet 'white' and 'red' regions. In *Dipsosaurus* the two regions are particularly distinct; the red region contains 69% fast oxidative glycolytic (FOG) fibres and 28% tonic fibres, and the white region contains 2% FOG and 98% fast glycolytic (FG) fibres (Gleeson, Putnam & Bennett, 1980). Data presented here were collected separately from twitch fibres of both the red and white regions of the IF of *Dipsosaurus*; those fibres examined in the white region of the IF are taken to be FG fibres, and those from the red region are considered to be FOG fibres. Fibres having relatively high input resistance (>1 MΩ) and relatively long membrane time constant (>30 ms) were occasionally encountered in the red region of the IF from *Dipsosaurus*; such fibres were presumed to be tonic fibres, and were not included in the analysis.

In the iliofibularis of *Anolis* and *Sceloporus* the red region is not as distinct as in *Dipsosaurus*. Hence, only twitch fibres from the unambiguously 'white' region of the iliofibularis of these species were examined; these fibres had large diameters (80–150 μm), were very transparent, and generated propagated action potentials when stimulated directly *via* an intracellular electrode.

The upper experimental temperature to which muscles from each species were exposed was determined in preliminary experiments to be the highest temperature the preparations could tolerate without obvious deterioration (depolarization of resting potential and decreased transparency). These maximum temperatures were always several degrees cooler than the species' upper critical temperature (CT_{max}).

Determination of passive electrical properties

The passive electrical properties of muscle fibres were determined using hyperpolarizing square pulses, following the procedure of Josephson & Stokes (1982). The preparation was viewed at 50× magnification with transverse illumination; an ocular

micrometer was used to measure distances to the nearest 10 μm. The current-passing electrode (10–20 MΩ, tip filled with 4% Lucifer Yellow solution, back-filled with 3 mol l^{-1} $LiCl_2$) was inserted near the middle of a fibre, and the recording electrode (10–20 MΩ, 3 mol l^{-1} KCl) was inserted in the same fibre 1–2 mm away. For determination of length constant (L), rectangular hyperpolarizing pulses (500 ms duration) of constant magnitude were injected for 3–5 separations of the two electrodes. L was taken as the reciprocal slope of the plot of electrode separation *versus* the natural logarithm of the change in membrane potential.

Input resistance (R_{in}) was determined using a series of 3–6 current injections (500 ms duration) with the electrodes separated by 50–200 μm. Current injections were monitored with a virtual ground circuit connected to the bath *via* a saline–agar bridge. Deviations from resting membrane potential were small (a few millivolts) to avoid membrane 'creep' (Adrian & Freygang, 1962); creep was sometimes present during large hyperpolarizations, and was subtracted from the photographed oscilloscope records before analysis. R_{in} was corrected for electrode separation using the relationship

$$R_{in} = (dV/I)\ (e^{x/L}),$$

where dV is change in membrane potential (mV), I is injected current (nA), e is 2·71, x is electrode separation (μm) and L is the length constant (μm). Membrane time constant was measured with the electrodes close together (within 200 μm), and was corrected for electrode separation using the method described by Josephson & Stokes (1982). Fibres were ionophoretically filled with Lucifer Yellow dye during and following the analysis, viewed at 400× under ultraviolet illumination, and their apparent diameters measured to the nearest 2 μm. Sarcoplasmic resistivity (R_s), apparent membrane resistance (R_m) and apparent membrane capacitance (C_m) were calculated using standard equations for infinite cables (Jack *et al.* 1975).

Data from a given muscle fibre were included in the analysis only if the following criteria were met: (1) the initial resting potential, measured upon first impalement of a fibre with the recording electrode, was at least −70 mV and declined no more than 10 mV during the analysis; (2) voltage offsets in response to constant current pulses were successfully measured at 3–5 electrode separations and (3) current–voltage relationships (I–V plots) were linear and had correlation coefficients of at least 0·95. For any given muscle preparation, several fibres were analysed, each at a different temperature. Fibres from at least five different individuals of each species were examined at each temperature.

Statistical analyses

Data for each species were analysed using one-way analysis of variance (ANOVA) followed by a multiple range test (Student–Neuman–Keuls; SNK). In some cases the data were log-transformed prior to statistical analysis to correct for unequal variance among groups. R_{10} (analogous to Q_{10}; Bennett, 1984) values were calculated

for consecutive 5°C intervals using the mean values for each passive electrical property. Values presented in the text are mean ± S.E.M.

RESULTS

Fibre diameter

There were clear differences in fibre diameter among species, with *Anolis* having the largest and *Dipsosaurus* the smallest diameter fibres (Table 1). In *Dipsosaurus*, FG fibres from the white region of the IF were larger than FOG fibres from the red region. However, within species and within the red and white regions of the IF from *Dipsosaurus*, diameter did not vary significantly among the groups of fibres examined at different temperatures ($P > 0{\cdot}2$; ANOVA). Therefore, all fibres from a species (or region) were combined to calculate average fibre diameters, which were: *Anolis* white IF, $126 \pm 4{\cdot}5\,\mu m$ ($N = 42$ fibres); *Sceloporus* white IF, $101 \pm 3{\cdot}0\,\mu m$ ($N = 46$ fibres); *Dipsosaurus* white IF, $86 \pm 1{\cdot}8\,\mu m$ ($N = 62$ fibres); *Dipsosaurus* red IF, $57 \pm 1{\cdot}3\,\mu m$ ($N = 61$ fibres).

Passive electrical properties

All the passive electrical properties displayed significant thermal dependence (Table 1; Figs 1, 2). The thermal ratios (R_{10} values), calculated for each consecutive temperature interval are shown for each passive electrical property in Table 2.

Input resistance (R_{in}) decreased with increasing temperature (Fig. 1A), and the change was significant in fibres from all three species (Table 1). The absolute value of R_{in} increased in order of decreasing fibre diameter; at any given temperature, R_{in} was lowest in fibres from *Anolis*, intermediate in fibres from *Sceloporus*, and highest in *Dipsosaurus* red IF fibres (Table 1).

Length constant (L) decreased with increasing temperature, except in *Anolis* fibres (Fig. 1B). At 15 and 25°C, length constant was inversely correlated with fibre diameter, being shortest in *Anolis* fibres and longest in *Dipsosaurus* red IF fibres (Table 1).

Time constant (τ) decreased with increasing temperature (Fig. 1C). Time constant tended to be inversely proportional to fibre diameter; it was shortest in *Anolis* fibres and longest in *Dipsosaurus* red IF fibres (Table 1).

Sarcoplasmic resistivity (R_s) decreased with increasing temperature (Fig. 2A). There were no consistent differences in R_s among species, and the value of R_s was not correlated with fibre diameter (Table 1).

Apparent membrane resistance (R_m) decreased with increasing temperature (Fig. 2B). Apparent R_m was inversely related to fibre diameter; fibres from *Anolis* had the lowest apparent R_m and red IF fibres from *Dipsosaurus* had the highest apparent R_m (Table 1).

Apparent membrane capacitance (C_m) increased with increasing temperature (Fig. 2C). Apparent C_m was not strictly correlated with fibre diameter; C_m was greatest in fibres from *Sceloporus* ($101\,\mu m$), next highest in fibres from *Anolis* ($126\,\mu m$), and lowest in fibres from the red IF of *Dipsosaurus* ($57\,\mu m$; Table 1).

Table 1. *Passive electrical properties of lizard muscle fibres, measured at several temperatures*

Temp. (°C)	N	Diameter (μm)	R_m (kΩ)	L (μm)	τ (ms)	R_s (Ωcm)	R_m (Ωcm^2)	C_m ($\mu F\ cm^{-2}$)
Anolis white IF								
15	14	129 ± 7	69 ± 6	842 ± 22	5·1 ± 0·2	212 ± 23	460 ± 38	12·1 ± 1·1
25	14	127 ± 9	78 ± 13	833 ± 25	4·4 ± 0·2*	207 ± 21	462 ± 46	10·3 ± 0·6
35	14	122 ± 7	48 ± 5*	809 ± 31	3·6 ± 0·2*	140 ± 17*	294 ± 33*	13·4 ± 0·9**
Sceloporus white IF								
15	14	97 ± 7	134 ± 12	963 ± 47	9·6 ± 0·4	213 ± 29	755 ± 66	13·8 ± 1·2
25	12	98 ± 6	91 ± 6*	880 ± 29	6·3 ± 0·3*	151 ± 10	476 ± 25*	13·8 ± 1·3
35	13	108 ± 4	64 ± 4*	751 ± 36*	5·4 ± 0·3*	162 ± 18	334 ± 40*	18·2 ± 1·7
40	5	109 ± 9	43 ± 4*	771 ± 48*	5·2 ± 0·4*	106 ± 18*	230 ± 40*	26·1 ± 5·7*
Dipsosaurus white IF								
15	8	80 ± 5	251 ± 18	1181 ± 73	9·4 ± 0·9	217 ± 27	1532 ± 217	6·5 ± 0·4
25	22	85 ± 3	176 ± 12*	1210 ± 44	7·5 ± 0·4*	165 ± 11*	1151 ± 101*	6·9 ± 0·3
40	21	91 ± 3	111 ± 10*	1028 ± 27*	4·7 ± 0·2*	135 ± 9*	629 ± 44*	7·9 ± 0·4
45	9	84 ± 5	86 ± 6*	998 ± 42**	4·6 ± 0·3*	95 ± 10*	440 ± 28*	10·5 ± 0·7*
Dipsosaurus red IF								
15	18	56 ± 3	561 ± 48	1564 ± 46	11·4 ± 0·4	175 ± 16	3026 ± 252	4·3 ± 0·5
25	17	56 ± 2	486 ± 32	1443 ± 69	9·2 ± 0·4*	165 ± 9	2494 ± 215	4·0 ± 0·3
40	26	57 ± 2	247 ± 15*	1034 ± 31*	5·1 ± 0·1*	123 ± 9*	889 ± 52*	6·1 ± 0·3*

Fibres were from the white region of the iliofibularis muscle (IF) of *Anolis cristatellus* (10 individuals) and *Sceloporus occidentalis* (15 individuals), and from the white and red regions of the iliofibularis of *Dipsosaurus dorsalis* (30 individuals).

Values in the table are mean ± S.E.M. N is the number of fibres analysed at each temperature.

* Denotes significant difference from value at 15°C ($P < 0.05$; SNK).

** Denotes significant difference from value at 25°C ($P < 0.05$; SNK).

R_m, input resistance; L, length constant; τ, time constant; R_s, sarcoplasmic resistivity; R_m, apparent membrane resistance; C_m, apparent membrane capacitance.

Table 2. *Thermal ratios (R_{10} values; analogous to Q_{10}) for passive electrical properties, calculated for consecutive temperatures*

	15–25°C	25–35°C	25–40°C	35–40°C	40–45°C
Anolis white IF					
R_{in} (kΩ)	1·1	0·6	—	—	—
L (μm)	1·0	1·0	—	—	—
τ (ms)	0·9	0·8	—	—	—
R_s (Ωcm)	1·0	0·7	—	—	—
R_m (Ωcm^2)	1·0	0·6	—	—	—
C_m ($\mu F\ cm^{-2}$)	0·9	1·3	—	—	—
Sceloporus white IF					
R_{in}	0·7	0·7	—	0·5	—
L	0·9	0·9	—	1·0	—
τ	0·7	0·9	—	0·9	—
R_s	0·7	1·0	—	0·4	—
R_m	0·6	0·7	—	0·5	—
C_m	1·0	1·3	—	2·1	—
Dipsosaurus white IF					
R_{in}	0·7	—	0·7	—	0·6
L	1·0	—	0·9	—	0·9
τ	0·8	—	0·7	—	1·0
R_s	0·8	—	0·9	—	0·5
R_m	0·8	—	0·7	—	0·5
C_m	1·1	—	1·1	—	1·8
Dipsosaurus red IF					
R_{in}	0·9	—	0·6	—	—
L	0·9	—	0·8	—	—
τ	0·8	—	0·7	—	—
R_s	0·9	—	0·8	—	—
R_m	0·8	—	0·5	—	—
C_m	0·9	—	1·0	—	—

For details see Table 1.

DISCUSSION

Fibre diameter

There were significant differences in average fibre diameter among species, and between the red and white IF of *Dipsosaurus* (Table 1). These differences are important because the passive electrical properties depend upon fibre cross-sectional area and the total membrane area available for current flow, and these areas are functions of fibre diameter. Consequently, many of the interspecific and inter-regional differences in passive electrical properties might simply reflect differences in fibre diameter. However, within each species or muscle region, the changes observed in the passive electrical properties are due to temperature variation.

Input resistance

As temperature increased, R_{in} decreased significantly in muscle fibres from all three species (Fig. 1A; Table 1). This result is qualitatively similar to that obtained

in prior studies of muscle fibres from other ectothermic animals, but qualitatively different from results obtained with some mammalian fibres (see section on Membrane resistance below for further discussion).

The thermal dependence of R_{in} (average $R_{10} = 0{\cdot}7$) is similar to that for the aqueous diffusion of ions ($R_{10} = 0{\cdot}67$–$0{\cdot}83$; Hille, 1984). Thus the decline in R_{in} with increasing temperature can be attributed to a purely passive decrease in membrane resistance, due to enhanced conductance of ions through open membrane channels.

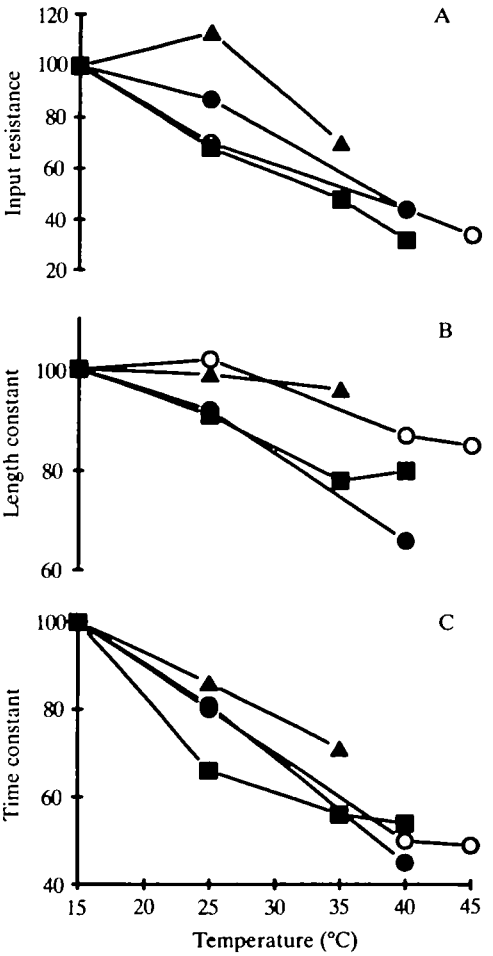

Fig. 1. The effect of temperature on input resistance (A), length constant (B) and membrane time constant (C). All values are expressed as a percentage of the average value at 15°C. (▲), *Anolis cristatellus* white iliofibularis muscle; 10 animals, 14 fibres per temperature. (■), *Sceloporus occidentalis* white iliofibularis muscle; 15 animals, 5–14 fibres per temperature. (○), *Dipsosaurus dorsalis* white iliofibularis muscle; 20 animals, 8–22 fibres per temperature. (●), *Dipsosaurus dorsalis* red iliofibularis muscle; 10 animals, 18–26 fibres per temperature.

Of all the passive electrical properties, R_{in} is perhaps the most important, because it strongly influences the response of a fibre to synaptic current. As temperature increases, R_{in} decreases, and the depolarization in response to a given synaptic current will be less. Temperature-dependent changes in R_{in} have significant effects on the excitability of muscle; the fibres become less excitable as temperature is increased, and require larger depolarizing currents to reach threshold (B. A. Adams, in preparation).

Length constant

Length constant (L) decreased significantly with increasing temperature in all fibres except those from *Anolis* (Fig. 1B). Most previous studies have also found that L decreases with increasing temperature (del Castillo & Machne, 1953; Hodgkin & Nakajima, 1972; White, 1983; Kornhuber & Walther, 1987). The thermal

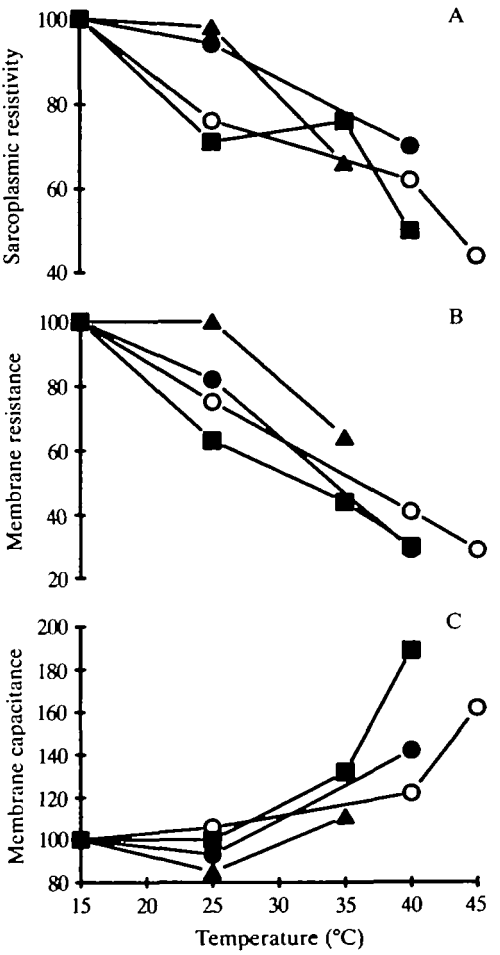

Fig. 2. The effect of temperature on sarcoplasmic resistivity (A), apparent membrane resistance (B) and apparent membrane capacitance (C). All values are expressed as a percentage of the average value at 15°C. Legend as in Fig. 1.

independence of L in *Anolis* fibres is probably caused by the similar temperature-dependences of R_s and R_m. Since L depends upon both R_s and R_m according to the relationship

$$L = (R_m d/4R_s)^{0.5}$$

(where d is fibre diameter) the thermal dependence of L will depend on the interplay between the thermal dependences of R_s and R_m. If R_s and R_m have identical thermal dependences, L will not change with temperature.

Time constant

As temperature increased, τ decreased significantly (Fig. 1C). The thermal dependence of τ was fairly similar in fibres from the different species (range of $R_{10} = 0{\cdot}7$–$1{\cdot}0$; Table 2). Since τ is equal to the product of R_m and C_m, the shortening of τ with increasing temperature must be entirely due to the decrease in R_m, because C_m is either constant or increases with increasing temperature (Table 1; Fig. 2C); increasing C_m would increase, not decrease, τ.

The time constants reported here are within the range reported for lizard scalenus fibres (6–40 ms at 20–25 °C; Proske & Vaughan, 1968) and snake costocutaneus fibres (8–14 ms at 20–23 °C; Ridge, 1971), but are shorter than those reported for turtle retractor capitis fibres (20–40 ms at 15–24 °C; Levine, 1966).

Sarcoplasmic resistivity

R_s decreased with increasing temperature (Fig. 2A), as has been observed in other muscle fibres (del Castillo & Machne, 1953; Fatt & Katz, 1953; Hodgkin & Nakajima, 1972; Klein & Prosser, 1985; Kornhuber & Walther, 1987). The average value of R_s at 25 °C was approximately 180 Ωcm (Table 1), which is in good agreement with the value of 170 Ωcm (20 °C) reported by Hodgkin & Nakajima (1972) for frog fibres, and the value of 150 Ωcm (25 °C) reported by Klein & Prosser (1985) for fish fibres. In previous studies of reptilian fibres, R_s was assumed and not measured, so no comparisons can be made with the present results. The thermal dependence of R_s (average $R_{10} = 0{\cdot}8$) also agrees fairly well with that calculated by earlier authors ($R_{10} = 0{\cdot}72$–$0{\cdot}73$; Hodgkin & Nakajima, 1972; Klein & Prosser, 1985).

There were no consistent differences in either the absolute value or the thermal dependence of R_s among species (Tables 1, 2; Fig. 2A). Therefore, the interspecific differences in passive electrical properties must be solely attributable to differences in the total membrane surface area, and/or the specific membrane resistances of the fibres.

Apparent membrane resistance

As temperature increased, apparent R_m declined significantly (Fig. 2B). This result is qualitatively similar to that reported for muscle fibres from other poikilothermic animals and appears to result from passive changes in membrane conductances. However, the change in R_m is opposite to that observed in some

mammalian muscle fibres; in cat tenuissimus (Boyd & Martin, 1959) and goat intercostal muscle (Lipicky & Bryant, 1972) R_m increases with increasing temperature. This difference in the behaviour of R_m between poikilothermic and mammalian muscle suggests that the resting conductances of mammalian muscle membranes may be actively increased (*via* channel opening) at low temperature and actively decreased (*via* channel closure) at high temperature. Such a response, if it produced changes in Na^+ or K^+ conductances, could influence the activity of Na^+,K^+-ATPase and hence be involved in cellular thermogenesis.

The thermal dependence of apparent R_m (average $R_{10} = 0{\cdot}7$) was indistinguishable from that for the aqueous diffusion of ions ($R_{10} = 0{\cdot}67$–$0{\cdot}83$; Hille, 1984). This similarity suggests that the observed decrease in R_m can be explained by increased single-channel conductance at higher temperatures.

The inverse correlation between fibre diameter and apparent R_m (see Table 1) has also been observed for different sized fibres from a single species (*Rana temporaria*; Hodgkin & Nakajima, 1972), and is based upon the underestimation of true membrane surface area caused by assuming that muscle fibres are simple cylinders; such an assumption ignores the contribution of t-tubular membrane to total fibre surface area.

The clear interspecific differences in apparent R_m (Table 1) could result from differences in true R_m or from differences in total membrane surface area. Unfortunately, true R_m cannot be calculated accurately without measuring the precise membrane area of the fibres, which was not attempted in this study.

Apparent membrane capacitance

In general, C_m did not change significantly over the lower range of temperatures, but then increased at the highest temperatures (Fig. 2C) with R_{10} values as high as 2·1 (*Sceloporus*, Table 2). The average thermal ratio was 1·3. Previous authors (del Castillo & Machne, 1953; Klein & Prosser, 1985; Hodgkin & Nakajima, 1972) have reported smaller increases in apparent C_m as temperature is increased (range of $R_{10} = 1{\cdot}02$–$1{\cdot}10$), but in these studies apparent C_m was not measured at the high temperatures used here. Membrane capacitance should be a function of the area, thickness and dielectric constant of the membrane; temperature must alter one or more of these variables to affect apparent C_m. Possibly the membrane becomes thinner as temperature increases, or perhaps membrane processes such as pinocytosis and exocytosis are greatly increased at the higher temperatures, and more membrane surface area is actually present then.

Apparent membrane capacitance was highest in fibres from *Sceloporus* (mean diameter = 101 μm), and next highest in fibres from *Anolis* (mean diameter = 126 μm). This result suggests a more extensive development of the t-tubular system, and/or a higher specific membrane capacitance in *Sceloporus* than in *Anolis* fibres. Quantitative morphological data, which would provide an estimate of relative t-tubule development, are unfortunately not available for these muscle fibres. Apparent C_m was lowest in the smallest diameter fibres (red IF of *Dipsosaurus*, mean diameter 57 μm). A positive correlation between apparent C_m and fibre diameter has

been previously demonstrated in *Rana* sartorius and semitendinosus fibres (Hodgkin & Nakajima, 1972), and in *Schistocerca* leg muscle fibres (Kornhuber & Walther, 1987).

Functional implications of thermal dependence

The temperature dependence of the passive electrical properties has important implications for muscle function. Because input resistance largely determines the synaptic currents required to depolarize muscle fibres to threshold, decreases in R_{in} will directly increase the excitatory current requirement. Thus, at higher temperatures, larger synaptic currents are necessary to excite the fibres (B. A. Adams, in preparation). Unless the nerve terminal compensates for the decrease in R_{in} by increasing transmitter release, the safety factor for neuromuscular transmission may decline as temperature increases. If safety factor declines enough, or is small to begin with, some fibres may fail to be excited at high temperature; such failure would reduce muscular power output, and would affect locomotor capacity negatively.

At the lower temperatures, R_{in} is relatively high, and the requirement for synaptic current should be reduced. Increased R_{in} would tend to compensate for the decreased transmitter release that may occur at low temperatures (Li & Gouras, 1958; Takeuchi, 1958; Hubbard, Jones & Landau, 1971; Jensen, 1972).

Biological significance of interspecific differences

Although iliofibularis fibres from the three lizard species react similarly to changing temperature, the absolute values of the passive electrical properties differ markedly (Table 1). These differences may be provisionally explained by interspecific differences in fibre diameter. However, it should be noted that the absolute value of the fibre properties is correlated with the thermal ecology of the species. Input resistance, length constant, time constant and apparent membrane resistance were consistently lowest in fibres from *Anolis* ($PBT = 30°C$, $CT_{max} = 37°C$), intermediate in fibres from *Sceloporus* ($PBT = 35°C$, $CT_{max} = 44°C$) and highest in fibres from *Dipsosaurus* ($PBT = 40°C$, $CT_{max} = 48°C$; Table 1). This correlation may indicate a functional basis for the interspecific differences in passive electrical properties.

Since R_{in} is temperature-dependent, and is important in determining whether a given muscle fibre becomes excited, it may be functionally advantageous for species that operate at high temperature (such as *Dipsosaurus*) to maintain R_{in} at relatively higher levels than less thermophilic species (e.g. *Anolis*). High R_{in} would tend to lower the synaptic current required to excite the fibres at all temperatures, and would help to maintain synaptic effectiveness at the unusually high activity temperatures (38–46°C; Norris, 1953) of *Dipsosaurus*. In an evolutionary sense, high R_{in} could be achieved by reducing fibre diameter, decreasing the extent of the t-tubule system, or by increasing specific membrane resistance.

In contrast, species that operate at lower temperatures (such as *Anolis*) may not need to maintain R_{in} at high levels, because they do not normally experience temperatures where muscle fibre excitability or neuromuscular transmission might

fail due to low R_{in}. Low values of R_{in} are not necessarily advantageous at any temperature, but may simply result from the large membrane area and extensive t-tubule development usually found in large-diameter twitch fibres. Consequently, species such as *Anolis* may have more freedom to increase the maximum diameter of their muscle fibres compared with thermophilic species such as *Dipsosaurus*. Large muscle fibres may be more efficient than small muscle fibres during high-speed burst locomotion, because the tension and power generated per nerve impulse would be maximized.

Red versus *white IF fibres from* Dipsosaurus

The red region of the *Dipsosaurus* IF contains approximately 28% tonic fibres (Gleeson *et al.* 1980). However, in the present study only twitch fibres capable of propagating action potentials were examined. Within the IF of *Dipsosaurus*, twitch fibres from the red region had higher R_{in}, L, τ and R_m values than fibres from the white region. These differences in passive electrical properties suggest that twitch fibres from the red region may maintain postsynaptic excitability and effective neuromuscular transmission at higher temperatures than fibres from the white region. This suggestion is in accord with preliminary observations (B. Adams, unpublished data) indicating that red region fibres are more resistant to block by curare than are white region fibres, and appear to possess a greater safety factor for neuromuscular transmission.

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