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MEMBRANE CONSTANTS OF MAMMALIAN MUSCLE FIBRES

By I. A. BOYD* and A. R. MARTIN†

From the Department of Biophysics, University College London

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Preliminary estimates of the resistance and capacitance of the mammalian muscle fibre membrane have been reported previously (Boyd & Martin, 1956*b*). In the present paper the results of experiments in which the membrane constants were measured will be presented in greater detail. The constants were determined by the method of 'square pulse analysis' (Hodgkin & Rushton, 1946; Katz, 1948; Weidmann, 1951, 1952; Fatt & Katz, 1951), intracellular electrodes being used to pass current through the membrane and to record the resultant potential changes.

METHODS

The isolated tenuissimus muscle of the cat was used in all experiments and was mounted in a constant-temperature bath containing oxygenated Krebs's solution. The experimental methods have been described in detail in a previous paper (Boyd & Martin, 1956*a*). The electrical arrangement for measuring current and potential across the fibre membrane with two internal electrodes was similar to that described by Fatt & Katz (1951, p. 325, fig. 4).

The two micro-electrodes were inserted into the fibre as close together as possible, and a rectangular current pulse passed through one. The resultant change in membrane potential was recorded by the other (e.g. Fig. 1*a*). The recording electrode was then moved to between 0·5 and 1·0 mm from the current electrode and the procedure repeated (Fig. 1*c*). Finally the recording electrode was returned to an intermediate position and a third set of records obtained (Fig. 1*b*).

Resting potentials ranged from 55 to 70 mV when the records were obtained, generally dropping to about 5 mV below their initial value on insertion of the second micro-electrode, and thereafter decaying slowly. If the resting potential had fallen to below 55 mV when the last record was obtained or if, when the results were plotted as in Fig. 2, the intermediate point did not fall reasonably close to the straight line joining the first two, the measurements were rejected.

RESULTS

In Fig. 1 records are shown of current pulses and electrotonic potentials obtained from one fibre at three different electrode separations. The electrotonic potentials rise in less than 10 msec to a steady value determined for a given

* Present address: Institute of Physiology, University of Glasgow.

† Present address: Department of Physiology, University of Utah College of Medicine, Salt Lake City, Utah, U.S.A.

current by the distance between the electrodes. Applying the cable theory of Hodgkin & Rushton (1946), the potential change, V, produced by a steady current, I, through the membrane is given by the equation

$$V = \tfrac{1}{2}I\sqrt{(r_m r_i)}\exp\left[-x/\sqrt{(r_m/r_i)}\right],$$

where x is the electrode separation, r_m the transverse resistance of a unit length of fibre membrane and r_i the internal longitudinal resistance per unit length of fibre. The term $\sqrt{(r_m/r_i)}$ is the space constant, λ, of the fibre.

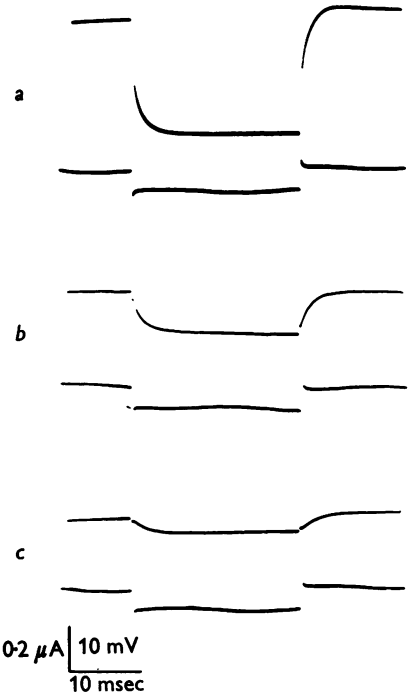

Fig. 1. Electrotonic potentials produced by current pulses with three different electrode separations. Lower record in each case is current pulse. Interelectrode distances were: *a*, 0·05 mm; *b*, 0·60 mm; *c*, 1·10 mm. mV scale applies to electrotonic potentials, μA scale to current pulses. Normal Krebs's solution; 24° C.

The results of four experiments, obtained from records similar to those illustrated in Fig. 1, are shown in Fig. 2. The ratio $V:I$ is plotted on a logarithmic scale against the separation of the micro-electrodes. In each case the experimental points fall on a straight line, as predicted by the theory. λ may be obtained from the slope of the line (being the distance from any point on the fibre over which the electrotonic potential falls to 1/e of its value at that point), and $\frac{1}{2}\sqrt{(r_m r_i)}$ from the point at which the line intersects the vertical axis ($x = 0$). From these two values r_m and r_i can be calculated.

Further calculations require an estimate of the resistivity of the myoplasm

(R_i). This was estimated from the value of 250 Ω cm reported for frog myoplasm (Bozler & Cole, 1935; Katz, 1948), allowing for the higher ionic concentrations in the mammalian muscle and applying a temperature correction. The conductivity ($1/R_i$) was assumed to be proportional to the ionic concentration and to increase with temperature with a Q_{10} of 1·3 (Hartree & Hill, 1921).

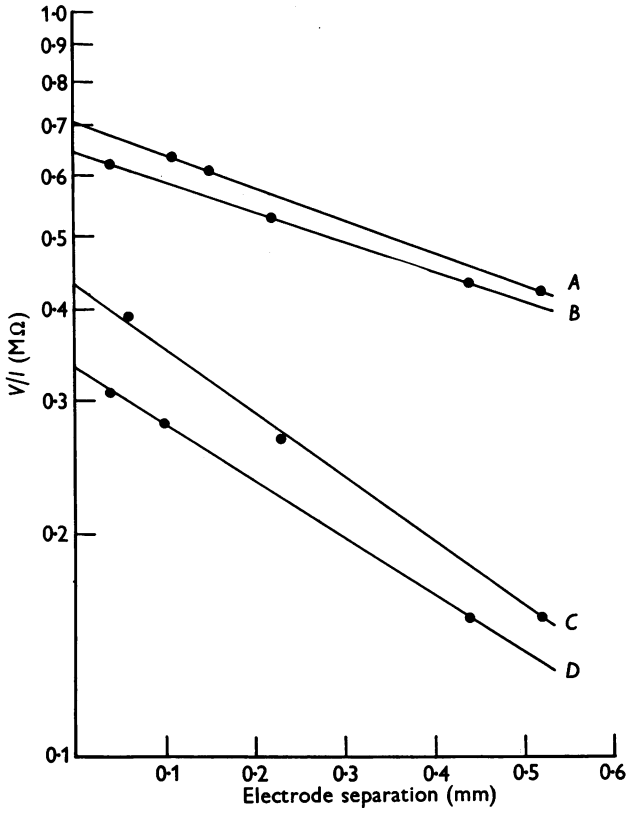

Fig. 2. Spatial decay of electrotonic potentials in four fibres. Ordinate, amplitude of electrotonic potential, when a steady state is reached, divided by amplitude of current pulse; logarithmic scale. Abscissa, separation between current and voltage recording electrodes. Fibres *A* and *B*, 37° C; fibres *C* and *D*, 22° C.

These assumptions result in an estimate of 125 Ω cm for the specific resistance of mammalian myoplasm at 37° C, which is close to the mean value of 105 Ω cm (range 52–190) reported by Weidmann (1952) for the internal resistivity of kid Purkinje fibres. Values used for R_i at other temperatures are based on the same assumptions.

Knowing R_i, the fibre radius, ρ, may be obtained from the relation

$$\rho = \sqrt{(R_i/\pi r_i)}.$$

The transverse resistance of a unit area of membrane is then given by

$$R_m = 2\pi\rho r_m$$

and the membrane capacitance per unit area by

$$C_m = \tau_m / R_m .$$

τ_m, the time constant of the membrane, may be obtained from the rising or falling phase of the electrotonic potential. Two methods were used:

(*a*) τ_m in Tables 1 and 2—the time taken for the potential to rise to 83% of its maximum steady value, with the two electrodes as close together as possible ($x/\lambda = 0{\cdot}1$, Table 1, Hodgkin & Rushton, 1946).

TABLE 1. Data derived from one muscle in which curves were obtained, similar to those in Fig. 2, for five fibres at 37° C and five at 22° C

r_m, transverse resistance of unit length of membrane.
r_i, internal longitudinal resistance per unit length of fibre.
R_i, resistivity of myoplasm.
τ_m, τ_m', membrane time constant by two methods (see text).
λ, fibre space constant (from slope of line as in Fig. 2).
$\frac{1}{2}\sqrt{(r_m r_i)}$, intercept on $V:I$ axis as in Fig. 2.
ρ, fibre radius.
R_m, transverse resistance of unit area of membrane.
C_m, membrane capacitance per unit area.

Fibre	$\frac{1}{2}\sqrt{(r_m r_i)}$ (Ω)	$\lambda = \sqrt{(r_m/r_i)}$ (mm)	τ_m (msec)	τ_m' (msec)	ρ (μ)	R_m (Ω cm²)	C_m (μF/cm²)
			A. 37° C (R_i assumed to be 125 Ω cm)				
I	$6{\cdot}4 \times 10^5$	1·10	5·6	4·1	19	1620	3·5
II	$3{\cdot}7 \times 10^5$	1·10	4·7	4·4	25	1230	3·8
III	$7{\cdot}0 \times 10^5$	1·00	4·5	4·1	17	1490	3·0
IV	$3{\cdot}8 \times 10^5$	1·30	5·0	3·5	26	1600	3·1
V	$4{\cdot}8 \times 10^5$	1·00	4·8	5·7	21	1220	3·9
Mean		1·10	4·9	4·4	22	1430	3·5
			B. 22° C (R_i assumed to be 195 Ω cm)				
I	$3{\cdot}4 \times 10^5$	0·60	1·2	1·3	23	570	2·1
II	$2{\cdot}8 \times 10^5$	0·60	1·7	1·4	26	555	3·1
III	$3{\cdot}7 \times 10^5$	0·75	2·1	2·6	25	872	2·4
IV	$4{\cdot}9 \times 10^5$	0·58	1·6	3·0	19	688	2·3
V	$4{\cdot}5 \times 10^5$	0·50	1·8	2·4	18	506	3·6
Mean		0·61	1·7	2·1	22	638	2·7

(*b*) τ_m' in Table 1—from the velocity of propagation of the half-value of the electrotonic potential following the make of the current pulse (Hodgkin & Rushton, 1946).

The capacitance values given in the tables were obtained using the values of τ_m from method (*a*).

The results of these calculations for ten fibres in one muscle are given in Table 1. Five sets of measurements were made at 37° C and the remainder at 22° C. The mean transverse membrane resistance was 1430 Ω cm² and the capacitance 3·5 μF/cm². At 22° C the membrane resistance was reduced to

about 640 Ωcm^2. In addition to this marked decrease in membrane resistance with temperature there was a decrease in the membrane capacitance to a mean of 2·7 μF/cm^2. The calculated values for the fibre diameters agree with those obtained by direct measurement from histological transverse sections of a tenuissimus muscle. Fibre diameters estimated from photographs ranged from 30 to 60μ.

The results obtained from the muscle of Table 1 and three other muscles are summarized in Table 2. In two of the muscles measurements were made

TABLE 2. Comparison of the mean values of fibre constants at two different temperatures for four muscles. For muscle *A* and *B* fibre radius was calculated from the data; for *C* and *D* fibre radius was assumed to be 25μ. Symbols as in Table 1

Muscle	No. of fibres	Temp. (° C)	ρ (μ)	λ (mm)	τm (msec)	C_m (μF/cm^2)	R_m (Ωcm^2)	Q_{10} of R_m
A	5	37	22	1·1	4·9	3·5	1430	1·71
	5	22	22	0·6	1·7	2·7	638	
B	4	37	18	1·0	4·1	2·8	1475	1·48
	4	22	21	0·7	1·7	2·1	822	
C	4	37	(25)	1·2	4·4	3·1	1400	1·62
	4	24	(25)	0·7	2·6	3·5	750	
D	10	37	(25)	1·2	5·6	4·0	1400	

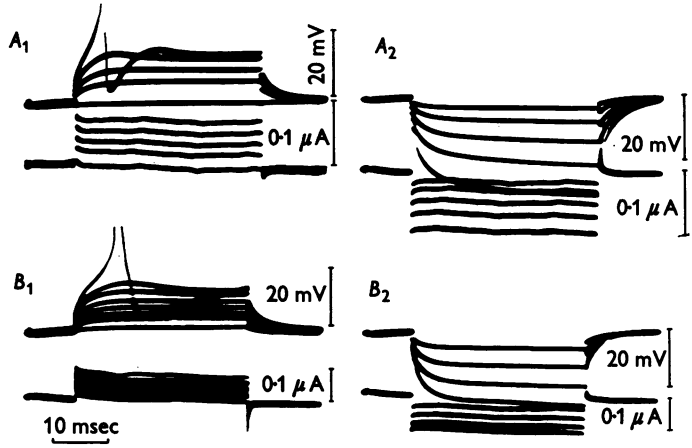

Fig. 3. Variation of membrane potential with applied current in two fibres, *A* at 37° C and *B* at 24° C. A_1, B_1, depolarization; A_2, B_2, hyperpolarization. Zero electrode separation. As depolarizing current pulse is increased a transient 'local response' and then an action potential appears on the electrotonic potential.

only with electrode separation almost zero, and it was necessary to assume a value for the fibre diameter (50μ) in order to obtain values of R_m. However, the results are in good agreement with those obtained from the other two muscles.

Since the theory on which the above analysis is based does not apply to a non-linear system, it is necessary to confirm the implicit assumption that the

transverse resistance is independent of membrane potential. To do this two micro-electrodes were inserted into a muscle fibre as close to one another as possible, and the current and electrotonic potential recorded at various levels of polarization. The records from two fibres, one at 37° C and the other at 24° C, are shown in Fig. 3. The depolarizing current pulses were increased until a transient 'local response' and then an action potential appeared.

Measurements obtained from the records of Fig. 3 are presented graphically in Fig. 4. The amplitude of the electrotonic potentials when a steady state is reached is plotted against the magnitude of the current pulse. The voltage–current relation is linear from about 30 mV hyperpolarization to near threshold depolarization at both temperatures. Similar linear relationships were obtained for six other fibres.

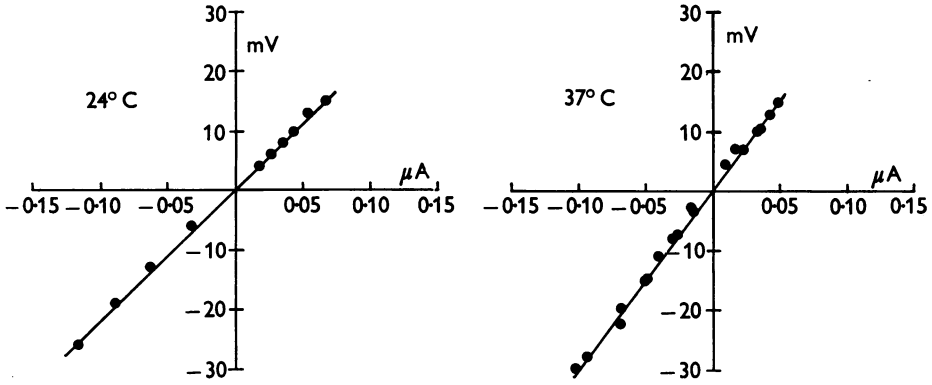

Fig. 4. Voltage-current relation in two fibres, one at 24° C and one at 37° C, plotted from records similar to those shown in Fig. 3. The voltage values represent the amplitude of the electrotonic potential when a steady state is reached, and depolarization is plotted upwards. The relation is linear from about 30 mV hyperpolarization to near threshold depolarization.

DISCUSSION

The results show that the transverse resistance of unit area of mammalian muscle fibre membrane at body temperature is about 1400 Ωcm^2, and the membrane capacitance per unit area between 2 and 4 μF/cm^2. The mean time constant for four muscles, of 4·8 msec at 37° C, is more than twice as large as that obtained from the rate of decay of the end-plate potential (about 2 msec; Boyd & Martin, 1956*b*), although in the present experiments the values obtained by two different methods of calculations are similar (Table 1). The value given for the membrane capacitance is, therefore, only an approximate one.

The calculated mean diameter of the muscle fibres is in good agreement with that found both in the one muscle sectioned in these experiments, and in a series of muscles subsequently examined (Boyd, 1956). In the latter the mean

diameter of the surface fibres in fixed muscles was found to be 35μ; corrected for shrinkage this gives a diameter of about 50μ for fibres accessible to a micro-electrode. This was the value used in the calculations of the constants in muscles *C* and *D* of Table 2. In the muscles in which the mean fibre diameter was calculated, the good agreement between the values obtained at the two temperatures employed (e.g. Table 1) also suggests that the method used was satisfactory.

Lowering the temperature of the preparation by 15° C results in a fall in the transverse resistance to nearly half its value at body temperature (mean Q_{10} = 1·6). This is in contrast to the effect of change in temperature on frog muscle; del Castillo & Machne (1953) obtained a negative temperature coefficient of about 1·35 for the membrane resistance of frog sartorius fibres. The temperature range over which the two series of experiments were carried

TABLE 3. Comparison of the mean values of membrane constants obtained from the tenuissimus muscle of the cat with those obtained from the frog sartorius muscle by del Castillo & Machne (1953)

Temp.	λ (mm)		τ_m (msec)		R_m (Ω cm^2)		C_m (μF/cm^2)	
(°C)	Frog	Cat	Frog	Cat	Frog	Cat	Frog	Cat
3	1·82	—	34	—	3643	—	9·7	—
22	1·59	0·67	22	2·0	2065	730	10·6	2·8
37	—	1·05	—	4·8	—	1453	—	3·4

out was different, however. In two muscles lowering the temperature resulted in a slight fall in membrane capacitance, but in a third there was a slight rise. These changes are not considered to be significant. The results from frog and cat are compared in Table 3, and it will be seen that the values of all the constants are much smaller for the mammalian membrane than for that of the frog, in addition to the fact that the temperature coefficients over the ranges shown are of opposite sign.

Del Castillo & Machne (1953) found that the influence of temperature on the transverse resistance of the frog muscle membrane does not differ significantly from that on the conductivity of a salt solution of about the same ionic concentration as that normally surrounding the muscle fibres. The decrease in membrane resistance in mammalian muscle when the temperature is reduced, however, probably indicates an increase in the permeability of the membrane to one or more of the ions present. It is interesting to note that the values of the resting potential of the mammalian fibre membrane were found to be consistently lower (by about 5–10 mV) when the preparation was at room temperature than when it was maintained at body temperature. No similar change has been reported for frog muscle.

SUMMARY

1. The membrane constants of mammalian skeletal muscle fibres have been measured by 'square pulse analysis'.

2. The transverse resistance of the fibre membrane at 37° C is about 1400 Ω cm^2, and the membrane capacitance lies between 2 and 4 μF/cm^2.

3. The transverse resistance falls with a Q_{10} of 1·6 when the temperature is lowered from 37 to 22° C, while the membrane capacitance is not altered significantly.

4. The results were compared with those obtained by del Castillo & Machne (1953) for frog muscle and the marked differences discussed.

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