THE EFFECT OF STRETCH ON THE ELECTRICAL CONSTANTS OF MUSCLE FIBRE MEMBRANE

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It is known that by application of stretch to the muscle the heat production and O₂ consumption of the resting muscle is increased (Feng, 1932), the rate of CO₂ production rises (Eddy and Downs, 1921) and the cellular Na diminishes (Harris, 1954). According to Ling and Gerard (1949) the resting potential is not altered by stretch, but recent experiments of Ishiko (1958, 1959) clearly demonstrate a decrease in the resting potential. Martin (1954) reported the conduction velocity of muscle to be unaltered by the application of stretch, while many investigators found an increase in the conduction velocity (Wilska and Varjoranta, 1940; Inoue, 1955; Håkansson, 1957). These experimental results may suggest that the muscle fibre membrane suffers changes in the membrane capacitance and conductance with a change in length. The experiments which will be reported in the present paper, therefore deal with the effect of stretch on the membrane constants of muscle fibres of toads.

METHODS

Material. Sartorius, iliofibular and toe muscles, isolated from Japanese toads (*Bufo vulgaris formosus*), were used. The stretch experiments were carried out on the former two muscles, but not on the latter. The muscle was stretched in a saline bath, its normal length *in situ* being taken as 100%. The membrane constants were measured in several muscle fibres at 100% length, in fibres at 130% length, and finally in muscle fibres relaxed again to 100%. As it was difficult to get a significant difference in experimental results by stretching a muscle step by step, only a 130% stretch was examined.

Experimental procedure and circuits employed. The membrane constants were measured using 'square pulse analysis', by applying to the muscle fibre rectangular anodal currents of about 100 msec duration through a microelectrode filled with 3 M KCl; and recording the electrotonic potential either with another microelectrode inserted into the same fibre or with the same microelectrode. For recording membrane potential change, a d.c. amplifier connected with a cathode follower stage of low grid-current and of reduced grid-to-earth capacity

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was used. The polarizing current through the microelectrode was measured by recording with another d.c. amplifier the potential drop across a resistor inserted between the Ringer bath and the earth.

The first method of passing currents through a microelectrode and of recording membrane potential change at three points of the muscle fibre with another microelectrode was the same as that adopted by Fatt and Katz (1951), and in the present experiment it was employed in measuring the membrane constants of sartorius muscle fibres. Impalement of the muscle fibre was made first with the potential electrode, and the current electrode was inserted into it at distances of about 50–100, 500 and 1000 μ in no fixed order. In some cases, however, the resting potential diminished during successive impalements of the same muscle fibre; and these experiments were discarded. The current strength employed was about 5×10^{-8} A, which is well below the threshold strength of $1-2 \times 10^{-7}$ A, and is of opposite polarity. The distance between the current and potential electrodes on the muscle fibre was measured by a binocular microscope of $48\times$ magnification, and the fibre diameter was similarly measured in order to check the calculated value.

In order to measure the membrane constants of small muscle fibres, it was difficult to adopt the method described above, because these muscle fibres were easily depolarized by impalement with two microelectrodes. Therefore, in the experiments with *M. iliofibularis* and *M. extens. long. digit. IV* the method of employing one and the same microelectrode inserted into a muscle fibre for passing polarizing currents and for recording membrane potential change was used. For this purpose a 'bridge-method' was previously adopted by Koketsu and Nishi (1957); but in the present experiments the circuit designed by Ito (1957) for compensating the potential between the inside of the cell and the earth, and for cancelling the stimulating pulse, was employed. A schematic diagram of the circuit, which was modified by Ito (1958) from his original one, is shown in fig. 1. The potential appearing between the inside of the cell and the earth is compensated with a negative feed-back loop from the output of amplifier (G), and the rectangular pulse from the square pulse generator (E_s) is fed into one of the differential inputs of the G amplifier. For reducing the time constant of the cathode follower stage the negative capacitance method described by MacNichol and Wagner (1954) was used. The circuit described here could not be used for a large cell such as a sartorius muscle fibre, because in this muscle fibre a polarizing current of 5×10^{-8} A is necessary to get a membrane potential change of sufficient magnitude, and with currents of such a strength it is impossible to cancel correctly the polarizing pulse from the pulse generator at the stage of the G amplifier, because of electrode polarization. The currents used for polarizing iliofibular and toe muscles are about 10×10^{-9} A and 6×10^{-9} A, respectively. Microelectrodes of 10–20 $\text{m}\Omega$ resistance were employed in the experiments, because such electrodes do not show a non-linear resistance character with a current of 10×10^{-8} A.

The procedure of the experiments using this compensating circuit is as follows: Before penetrating the muscle fibre with a microelectrode, potentials appearing between the Ringer bath and the earth, *i.e.* electrode potential and

FIG. 1. The schematic diagram of the experimental arrangement with 'one electrode method'. C; voltage calibrator, D.C.I. and D.C.II.; d.c. amplifiers, E_s ; square pulse generator, G; preamplifier of $100 \times$ amplification, g_1 and g_2 ; differential inputs of G amplifier, R; resistor of $10 \text{ K}\Omega$ for recording current strength, R_e ; microelectrode resistance, R_s ; resistor of $100 \text{ M}\Omega$, Y_A and Y_B ; double beam oscilloscope.

FIG. 2. *a*: Oscillograph traces before impaling a muscle fibre with a microelectrode, after potentials from a square pulse generator and from the electrode are compensated. *b*: An electrotonic potential produced in an fibre of *M. extens. long. digiti*. IV with a current of about $7 \times 10^{-9} \text{ A}$. In both records upper traces indicate current recording and lower ones potential recording. Voltage calibration: 10 mV , current calibration: $2.75 \times 10^{-8} \text{ A}$, and time signal: 200 msec .

that due to polarizing currents, were cancelled and the frequency characteristics of the preamplifier was adjusted so that an input time constant of about 100μ sec was obtained (fig. 2 *a*); then the muscle fibre was impaled with a micro-electrode, and a membrane potential change appeared suddenly (fig. 2 *b*). The strength of the polarizing current remained unaltered before and after the penetration.

Method of analysis. The analysis of the electrotonic potential for calculating membrane constants from the electrotonic potentials obtained with the 'one microelectrode method' was the same as that employed by Koketsu and Nishi (1957). The time constant of the membrane (τ_m) was taken as either the time of decline of the electrotonic potential to 15% or that of its 85% rise (Hodgkin and Rushton, 1946; Fatt and Katz, 1951). Actually the time constant of the muscle fibre membrane measured at the rising and falling phases of the electrotonic potentials did not differ significantly (table 1), and therefore their mean values were taken. The diameter (d) of the muscle fibre was measured with a binocular microscope of $48\times$. The myoplasm resistance R_i was calculated by putting t , temperature of the Ringer bath during the experiment, into Tamasige's empirical formula $R_i = 500 (1 - 0.055 t + 0.0009 t^2)$ (Tamasige, 1950), instead of assuming R_i to be 250Ω cm. as adopted conveniently by Fatt and Katz (1951) and Koketsu and Nishi (1957). From d , R_i , τ_m , current strength I and the final value V of the electrotonic potential λ , R_m and C_m were calculated.

TABLE 1. Average Values of Time Constant of Muscle Fibre Membrane at Rising and Falling Phases of Electrotonic Potentials

Muscles		No. of fibres	Time constant (msec.)	
			Rise	Fall
Iliofibularis	A	14	18.8 ± 1.3	19.4 ± 1.2
	B	13	19.9 ± 1.7	19.5 ± 1.6
	C	13	17.9 ± 0.6	16.9 ± 0.3
Extens. long. digit. IV	A	9	13.1 ± 1.1	11.7 ± 1.0
	B	6	15.9 ± 1.8	16.6 ± 0.4
	C	13	17.9 ± 0.6	19.1 ± 0.7

$\pm$ refers to S.E. of the mean.

The analysis of the results on sartorius muscles obtained with the 'two microelectrodes' method is the same as that adopted by Fatt and Katz (1951). τ_m was calculated from the relation between the mean values of half times of rising and falling phases of electrotonic potentials and the distance x . R_i was obtained similarly from Tamasige's formula, and λ and $1/2 (r_m r_i)^{1/2}$ were obtained directly from x , V and I . Other constants including d were calculated from these values.

Ringer's solution. The ionic composition of the Ringer's solution used throughout this experiment was: 111 mM NaCl, 2.5 mM KCl, 1.8 mM CaCl₂ and 2.4 mM NaHCO₃.

The experiments were performed during the spring and summer of 1958.

RESULTS

Membrane constants of muscle fibres of toads. The membrane constants were calculated in 69 muscle fibres from 3 sartorius muscles, in 73 fibres from 3 iliofibular muscles and in 28 fibres from 3 toe muscles. Average values of constants for individual muscles at 100% and 130% lengths are tabulated in tables 2 and 3. The stretch experiment was not carried out on toe muscles; only the constants at a fixed length were measured.

It will be seen in table 2 that the calculated values of d are consistent with those measured directly, indicating that the R_i values calculated from $R_i = 500 (1 - 0.055 t + 0.0009 t^2)$ are correct. If one assumes R_i to be 250 Ω cm., R_i and d in the tables should be multiplied by a factor of $(250/R_i)^{1/2}$, and C_m should be divided by the same factor. For example, calculated d of muscle *B* in table 2 will become 150 μ and 135 μ for 100% and 130% stretch respectively. These agree less well with the observed values. However, Yoshida (1958) reports that the diameter of sartorius muscles of Japanese toads varies between 125 μ and 165 μ , and has its maximum population at 150 μ . Furthermore, when measuring the fibre diameter by microscopic observation, there is in general a tendency to underestimate it. Therefore it cannot be said here whether it is more correct to adopt the R_i value calculated from Tamasige's empirical formula, or 250 Ω cm. as assumed by several investigators (Fatt and Katz, 1951; Koketsu and Nishi, 1957). As it does not seem seriously to affect the comparison of C_m and R_m between relaxed and stretched states, the authors employed Tamasige's empirical formula for calculating R_i .

τ_m and R_m of sartorius muscles *A* and *B* in table 2 show somewhat smaller values than those of sartorius muscle *C* and other muscles. This might be due to the depolarization consequent on the insertion of two microelectrodes

TABLE 2. Average Values of Membrane Constants of Sartorius Muscle Fibres

Temp. Muscle stretch No. of fibres			d (obs.)	$\frac{1}{2} (r_m r_i)^{1/2}$	λ	τ_m	d (calc.)	R_m	R_i	C_m	
°C		%	(μ)	($\times 10^3 \Omega$)	(mm.)	(msec.)	(μ)	($\Omega \cdot \text{cm}^2$.)	($\Omega \cdot \text{cm}$.)	($\mu\text{F}/\text{cm}^2$.)	
19	A	100	7	104 ± 1.3	127 ± 4.6	1.4 ± 0.04	6.7 ± 0.2	98 ± 1.9	1110 ± 21	140	6.6 ± 0.27
		130	7	70 ± 1.0	158 ± 8.5	1.2 ± 0.03	6.5 ± 0.2	86 ± 2.6	870 ± 58		8.9 ± 0.57
26	B	100	11	99 ± 0.6	128 ± 3.8	1.6 ± 0.10	8.5 ± 0.3	89 ± 1.7	1250 ± 28	90	7.1 ± 0.46
		130	11	82 ± 1.0	132 ± 3.6	1.5 ± 0.03	7.9 ± 0.3	81 ± 1.0	1040 ± 36		8.3 ± 0.12
22	C	100	11	86 ± 0.2	301 ± 11.7	1.7 ± 0.05	11.0 ± 0.3	66 ± 1.4	2990 ± 65	115	4.7 ± 0.20
		130	12	66 ± 0.3	420 ± 5.1	1.5 ± 0.03	12.1 ± 0.2	52 ± 0.7	2650 ± 55		4.5 ± 0.20

$\pm$ refers to S.E. of the mean.

TABLE 3. Average Values of Membrane Constants of Ilioibular and toe Muscles

Temp. Muscle No. of Stretch fibres				d	$\frac{1}{2}(\tau_m \tau_i)^{1/2}$	λ	τ_m	R_m	R_i	C_m
°C			%	(μ)	($\times 10^3 \Omega$)	(mm.)	(msec.)	($\Omega \cdot \text{cm}^2$.)	($\Omega \cdot \text{cm}.$)	($\mu\text{F}/\text{cm}^2$.)
M. iliofibularis										
22	A	14	100	59±0.3	384± 9.5	2.0±0.06	19.1±0.1	3190±211	110	9.4±0.38
		13	130	44±0.2	566±11.3	1.6±0.04	21.4±0.5	2910±144		9.3±0.31
26	B	13	100	59±1.1	307± 7.1	1.8±0.01	19.7±0.5	2060± 78	90	10.2±0.18
		10	130	49±0.7	378±13.2	1.6±0.09	22.0±0.8	1990± 86		12.6±0.41
26	C	13	100	62±0.3	278± 4.8	1.9±0.12	17.4±0.1	2170± 86	90	9.6±0.30
		10	130	53±0.3	339± 3.3	1.7±0.06	17.2±0.2	2030±116		11.2±0.54
M. extens. digit. long. IV										
14	A	9		40±0.6	975±35	1.2±0.04	12.5±0.4	3074±184	205	5.7±0.13
14	B	6		44±1.5	991±43	1.5±0.03	16.2±0.6	4300±115	205	5.3±0.26
15	C	13		43±0.1	800±19	1.2±0.09	18.5±0.4	2850±123	190	8.3±0.30

± refers to S.E. of the mean.

into the muscle fibre (Fatt and Katz, 1951; Ishiko, 1957). In general the membrane constants of muscle fibres of toads presented in tables 2 and 3 are very close to those of frogs reported previously (Fatt and Katz, 1951; Koketsu and Nishi, 1957; Frank 1958).

Effect of stretch on the membrane constants. An example of the values of membrane constants of individual muscle fibres at 100% and 130% lengths is presented in table 4, which shows a wide variation among individual fibres, and it may be difficult to draw a conclusion from it. However, average values for each muscle presented in tables 2 and 3 show a tendency for λ and R_m to decrease with an increase in fibre length, but that effective resistance and C_m increase. Although changes in λ and $\frac{1}{2}(r_m r_i)^{1/2}$ are significant, the decrease in R_m is not in most cases statistically significant, and the increase in C_m is statistically significant only in 3 muscles out of 6.

In table 5 the average of C_m and R_m of all muscle fibres for sartorius and ilioibular muscles are calculated. In these collected averages C_m increases by 12–15%, which is highly significant (0.1% level), while the decrease of R_m is significant for sartorius muscle and probably significant for ilioibular muscle.

However, one cannot easily accept the conclusion drawn from this statistical treatment that C_m increases and R_m decreases significantly by application of stretch, because, for evaluating such a small difference of C_m as about 15%, errors involved in the measurements of fibre diameter and of the temperature of Ringer bath, and in the assumption of R_i value are too great.

On the other hand, if one assumes that the muscle fibre consists of the material enveloped by a thin uniform sheet of membrane, the volume of both being independent of the length, the conductance of membrane per unit area

TABLE 4. Membrane Constants of Individual Muscle Fibres of *M. iliofibularis*

Stretch (%)	No. of fibres	d (μ)	$\frac{1}{2} (r_m r_i)^{1/2}$ ($\times 10^3 \Omega$)	λ (mm.)	τ_m (msec.)	r_m ($\times 10^3 \Omega/\text{cm.}$)	r_i ($\times 10^3 \Omega/\text{cm.}$)	R_m ($\Omega \cdot \text{cm}^2$)	C_m ($\mu\text{F}/\text{cm}^2$)
100	13	68	275	2.2	19.9	120	2480	2820	7
		61	264	1.7	20.8	89	3080	1700	12
		65	177	1.3	14.9	46	2720	940	16
		61	263	1.7	17.0	89	3080	1700	10
		54	266	1.3	17.6	77	3940	1300	13.5
		54	228	1.4	16.8	77	3940	1300	13
		65	280	2.1	19.0	120	2720	2450	8
		68	278	2.2	16.6	120	2480	2560	6.5
		61	460	3.0	16.7	277	3080	5300	3
		61	293	1.9	18.0	111	3080	2130	8
		61	293	1.9	16.9	111	3080	2130	8
		68	236	1.5	16.3	56	2480	1200	14
		65	300	2.2	15.8	132	2720	2700	6
Mean		62	278	1.9	17.4	110	2990	2170	9.6
130	10	54	490	2.6	16.6	259	3830	4400	4
		48	490	2.0	13.9	198	4950	3000	5
		54	340	1.8	20.0	124	3830	2100	9.5
		54	303	1.6	19.5	98	3830	1660	12
		54	260	1.4	18.2	77	3830	1300	14
		48	250	1.0	14.2	49	4950	750	19
		51	470	2.1	18.6	194	4400	3100	6
		53	226	1.1	14.6	50	4100	830	19
		58	298	1.8	18.8	104	3400	1900	10
		54	262	1.4	17.7	75	3830	1280	14
		Mean		53	339	1.7	17.2	123	4095

The temperature was 26°C, and R_i is assumed to be 90 $\Omega \text{ cm}$.

TABLE 5. Collected Results

Muscle	Stretch (%)	Number of muscle fibres	R_m ($\Omega \cdot \text{cm}^2$)	C_m ($\mu\text{F}/\text{cm}^2$)
Sartorius	100	29	1879 $\pm$ 57	6.1 $\pm$ 0.09
	130	30	1644 $\pm$ 33	7.0 $\pm$ 0.12
	<i>t</i> -test		$P < 0.01$	$P < 0.001$
Ilioibularis	100	40	2486 $\pm$ 43	9.7 $\pm$ 0.09
	130	33	2365 $\pm$ 36	10.9 $\pm$ 0.14
	<i>t</i> -test		$P < 0.05$	$P < 0.001$
Extens. digit. long. IV		28	3234 $\pm$ 63	6.6 $\pm$ 0.14

$\pm$ S.E. of the mean.

($1/R_m$) will be proportional to the square root of the fibre length (l), or inversely proportional to fibre diameter. Transverse capacitance of membrane per unit area (C_m) is inversely proportional to the membrane thickness (δ). If the membrane is of constant volume, δ will vary as $l^{1/2}$, and therefore C_m is proportional to $l^{1/2}$, or inversely proportional to d . Therefore,

$$R_m(130\%) = \frac{1}{1.14} R_m(100\%) \text{ and } C_m(130\%) = 1.14 C_m(100\%).$$

This calculation shows that by application of 130% stretch on the muscle the increase of C_m and decrease of R_m are only 14%. Although this agrees with the difference of averages of collected results in table 5 (12–15% increase in C_m and 5–12% decrease in R_m), errors involved in the measurement of these constants are too great to warrant the conclusion that C_m increases and R_m decreases by about 14% with a stretch of 130%.

Membrane constants of various muscle fibres of different diameter. In earlier investigations Katz (1948, 1949) obtained 4.5 $\mu\text{F}/\text{cm}^2$ for C_m of the muscle fibres of 45 μ in diameter, 6 $\mu\text{F}/\text{cm}^2$ for those of 75 μ ; and Fatt and Katz (1951) reported 8 $\mu\text{F}/\text{cm}^2$ for C_m of muscle fibres of 137 μ . In table 5 average values of C_m of three muscles do not change according to the diameter of the muscle fibre, although R_m increases with the decrease in diameter. However, this change in R_m may possibly be due to that of the experimental conditions, because (i) the experiments of the toe muscle, which gives the highest R_m value, are carried out under the lowest temperature, and (ii) the experiments on the sartorius muscle, which gives the lowest R_m value, are carried out with the two microelectrodes method, which might have caused a depolarization of the membrane (Fatt and Katz, 1951; Ishiko, 1957) and consequently a smaller R_m value. Therefore from the results shown in table 5 it seems unlikely that there is a systematic change in R_m with the change in the diameter of the muscle fibre when different muscles are compared. However, in order to get a definite conclusion, further accurate experiments to cover a wide range of the diameter of the muscle fibres are necessary.

DISCUSSION

The present experiments do not give conclusive evidence that the membrane capacitance and conductance increase significantly by application of stretch on the muscle fibre, because considerable errors are involved in measuring these constants. However, a tendency for both constants to increase by about 10–15% with 130% stretch, has been observed. Evidence supporting a change of $1/R_m$ with stretch can partly be supplied by Ishiko's experiments (1957, 1958), in which it is shown that the resting potential is reduced by 3–4 mV by stretching the muscle by about 130%. There is at the moment no other definite evidence suggesting the conductance increase of the muscle fibre membrane with stretch, but Harris (1953, 1954) found a decrease in the cellular content of Na and no significant change in K by application of stretch. If a decrease in the Na content of the muscle fibre during stretch indicates the permeability increase of the membrane for sodium ions, this would appear as a reduction in the resting potential and as a rise in the membrane conductance.

Recent experiments with single isolated muscle fibres by Hakansson (1957) have revealed that the conduction velocity remained unaltered up to a stretch of about 50% of the equilibrium length, and that it increased with further

elongation. According to Offner, Weinberg and Young (1940) conduction velocities of similarly constructed non-medullated fibres and muscle fibres, which produce the same inward current density during excitation, are related as $(d/R_i)^{1/2} \times C_m^{-1}$. However, as seen in the present experiments C_m does not change significantly, or changes only by about 12–15% in proportion to $d^{1/2}$. Therefore such a significant change in the conduction velocity as reported by Hakansson cannot be expected merely from a change in C_m . The only possible cause of the increase in the conduction velocity is a decrease in the threshold current of the muscle fibre membrane with stretch, because it is reduced by about 40–50% with a stretch of 130% (Ishiko, 1957), but the magnitude of the action potential does not change.

This reduction of about 50% in the threshold current with a 130% stretch might be explained by both an increase in the effective resistance and an decrease in the resting potential or threshold depolarization potential. For example, if one assumes that the sartorius muscle fibres, having a resting potential of 80 mV, initiate an action potential when they are depolarized by 20 mV, the threshold current should roughly be $20 \times 10^{-3} \text{ V} / 130 \times 10^3 \Omega = 1.5 \times 10^{-7} \text{ A}$ (e.g. muscle A of table 2); when the muscle fibre is stretched to 130% of the normal length, it should initiate an impulse with a depolarization of 16–17 mV, because its resting potential is reduced by 3–4 mV, and therefore its threshold current will become $(16-17) \times 10^{-3} \text{ V} / 160 \times 10^3 \Omega = 1 \times 10^{-7} \text{ A}$. Thus from this approximate calculation it is shown that the threshold current is reduced by about 50% when a muscle fibre is stretched from 100% to 130% length.

SUMMARY

The membrane constants of muscle fibres of toads, in normal and stretched states, were measured by square pulse analysis. A tendency for both C_m and $1/R_m$ to increase by the application of stretch was observed, but the difference of these constants between relaxed and stretched states is so small that it cannot be considered significant by taking into consideration various errors involved in measuring these constants. However, other kinds of experiments on muscle fibres would support the conclusion that C_m and $1/R_m$ increase, although this increase is only about 14%.

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