J. Physiol. (1971), **212**, *pp.* 667–683
With 9 text-figures
Printed in Great Britain

BIOPHYSICAL PROPERTIES OF THE LONGITUDINAL SMOOTH MUSCLE OF THE GUINEA-PIG RECTUM

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(*Received 4 June 1970*)

SUMMARY

1. The membrane properties of the longitudinal muscle layer of the guinea-pig rectum were studied in hypertonic solution (twice the normal Krebs by addition of sucrose) by the micro-electrode technique. To produce the electrotonic potential and spike, stimulating partitions were used.

2. Hypertonic solution hyperpolarized the membrane and increased the membrane resistance. However, no change in the space constant was observed before and after treatment with hypertonic solution.

3. The appearance and amplitude of the spike became regular after treatment with hypertonic solution and appearance of the overshoot was consistent.

4. The characteristic constants and the conduction velocity were measured in hypertonic solution.

(i) The space constant of the membrane was 0·81 mm, the time constant of the electrotonic potential was 83·7 msec and the time constant of the foot of the propagated spike was 8·8 msec.

(ii) The conduction velocity of the excitation measured by insertions of the two micro-electrodes was 4·4 cm/sec.

(iii) The chronaxie of the membrane was 71·3 msec.

5. The results obtained from the present experiments were discussed in relation to the cable theory, and it was concluded that the passive properties of the membrane of the rectal smooth muscle could be explained by the cable equations.

6. The specificities of the electrical properties of rectal smooth muscle were compared with muscle from other regions of the alimentary canal.

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INTRODUCTION

The muscle membranes of the longitudinal layers in the guinea-pig alimentary canal, namely fundus and antrum of stomach, jejunum and taenia coli possess cable-like properties (Tomita, 1966*a*, *b*, 1967; Kuriyama, Osa & Toida, 1967; Abe & Tomita, 1968; Kuriyama, Osa & Tasaki, 1970). For example, (i) the electrotonic potentials produced by a given current intensity plotted on a logarithmic scale against the distance from the partition decayed linearly, (ii) the time course of the electrotonic potentials could be simulated from the theoretical time course using the cable equations (Hodgkin & Rushton, 1946), (iii) the relation between distance from the stimulating partition and time to reach the half amplitude of the electrotonic potential was linear, and (iv) the time course of the foot of the propagated spike plotted on a logarithmic scale showed a linear relation with the time course after the onset of the membrane depolarization.

However, the results obtained varied markedly at the different regions of the alimentary canal. For example, the propagation of excitation took place in a non-decremental manner in the jejunum and taenia coli, but decremental conduction of excitation appeared in the fundus of the stomach (H. Kuriyama & T. Osa, personal communication). The propagation of excitation is, of course, not only related to the space constant, the membrane capacitance and radius of the fibres or the functional bundle but also to the capability of spike generation. The electrical property of the longitudinal muscle of the rectum has been investigated in a preliminary way by the microelectrode technique (Kuriyama *et al.* 1967). The present experiments were carried out to investigate in detail the various membrane properties during the resting and active state of the guinea-pig rectum, and the results from the rectum were compared with those from other regions of the alimentary canal of the guinea-pig.

METHODS

Guinea-pigs weighing 250–350 g were stunned and bled. The rectum was removed from the abdomen and was dissected carefully, starting along the long axis. Connective tissue was carefully removed under Krebs solution at room temperature. The longitudinal muscle layer was separated from the mucosal layer and a piece 20–25 mm in length and 4–5 mm in width was prepared. The tissue was mounted in an organ bath through which solution flowed continuously at a temperature of 35–36° C. A modified Krebs solution of the following composition was used (mM): Na^+ 137·4; K^+ 5·9; Mg^{2+} 1·2; Ca^{2+} 2·5; Cl^- 134·0; HCO_3^- 15·5; $H_2PO_4^-$ 1·2; and glucose 11·5; equilibrated with 97 % O_2 and 3 % CO_2. To measure the characteristic constants of the membrane, Krebs solution of twice the normal tonicity (292 mM sucrose in Krebs solution) was used throughout, in order to suppress the spontaneous activity and the muscle movement (Tomita, 1966*a*, 1967, 1969). The arrangement for stimulating and recording is the same as that described and illustrated by Abe & Tomita

(1968). The stimulating electrodes consisted of two silver plates with a small hole (2 mm × 0·88 mm) though which the preparation was passed. One stimulating electrode divided the muscle chamber into stimulating and recording chambers. The interelectrode distance was 10 mm. The piece of rectum was placed in the recording bath and one end was pulled through the hole into the stimulating chamber of 10 mm. Both chambers were independently irrigated with Krebs solution which was sucked away near the partition between the two chambers. The electrical activity was recorded intracellularly using glass capillary micro-electrodes filled with 3 M-KCl. The distances between the stimulating partition electrode and the micro-electrode were measured under the binocular microscope.

RESULTS

The differences between the membrane properties measured in Krebs and in hypertonic Krebs solution

The membrane potential measured in Krebs solution was $-47{\cdot}6 \pm 0{\cdot}8$ mV (S.E., $n = 30$) and the mean amplitude of the monophasic spikes selected from the spontaneous discharges was $44{\cdot}9 \pm 0{\cdot}9$ mV ($n = 30$). The membrane showed spontaneous spike generation. The amplitude of the

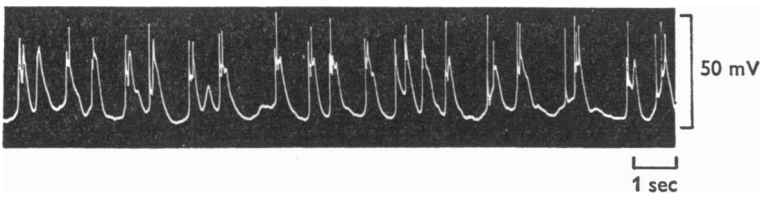


Fig. 1. Spontaneous spike generation of the rectum in Krebs solution.

spike was irregular, and slow depolarization appeared with or without generation of the spike. The amplitude of the slow wave often exceeded more than 20 mV, with a duration of 300–800 msec. The generation of the spike, however, was not consistently related to the generation of the slow wave. Fig. 1 shows the typical pattern of spontaneous spike generation recorded from the longitudinal layer.

When the tissue was perfused with hypertonic Krebs solution, the membrane was hyperpolarized to $-54{\cdot}7 \pm 1{\cdot}2$ mV ($n = 30$), and the spikes elicited by electrical stimulation showed an overshoot. The mean amplitude of the spike was $61{\cdot}0 \pm 1{\cdot}6$ mV ($n = 30$) and the spikes which appeared spontaneously had a constant amplitude with an overshoot. The slow depolarization completely ceased after 30 min of perfusion in the hypertonic solution.

Fig. 2 shows the effects of the hypertonic solution on the spike generation in the rectal smooth muscle. The records were taken simultaneously from two different cells at different times after perfusion in the hypertonic

solution. When the tissue was perfused with hypertonic solution, the spontaneous spike generation ceased within 10 min, but then the ability to generate spontaneous spikes was gradually restored (*a*). The intervals between the spikes were irregular even after 30–120 min (*b*). Finally, the frequency of the spikes became regular and the spike amplitude became nearly constant. During the early stage of replacement with the hypertonic solution spike discharge was in bursts, and no close relation between the appearance of the spike recorded from two different fibres (2·4 mm and 5·8 mm from the partition) was observed. However, as observed in *b* and *c*,

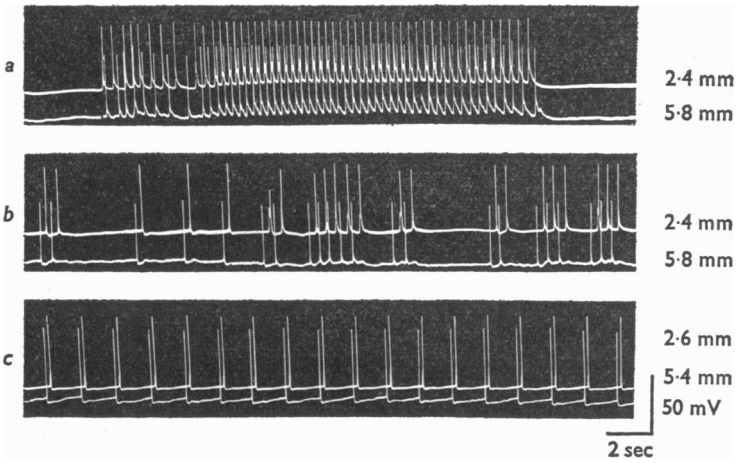


Fig. 2. The changes of the patterns of the spontaneous spike generation in the hypertonic solution recorded from two different sites in the rectum. All records are taken from the same preparation. *a*, after 15 min; *b*, after 90 min; *c*, after 150 min.

well synchronized spike activities could be observed when the spontaneously generated spikes appeared with a low frequency (2·4 mm and 5·8 mm in *b* and 2·6 mm and 5·4 mm in *c* respectively). There was, therefore, a clear difference in the membrane activity in Krebs and hypertonic solution. On the other hand, when the space constant was measured in the same tissue before and after treatment with hypertonic solution, almost no change in the value could be observed as shown in Fig. 3 (0·96 mm in Krebs and 0·93 mm in the hypertonic Krebs), even after 3 hr perfusion.

Fig. 3 shows the decay of the amplitudes of the electrotonic potentials recorded at various distances from the stimulating partition in Krebs and hypertonic solution (after 3 hr). The records were taken from the same tissue. The time constant of the membrane in the hypertonic solution increased to 1·2 times the normal value and the spatial decay of the electrotonic potential in both the conditions were parallel. Therefore, the

similar value of the space constant obtained in both the conditions might indicate an increased internal resistance of the muscle cells which is proportional to the increased membrane resistance in the hypertonic solution. The absence of change of the space constant does not indicate that there was no effect of the hypertonic solution on the muscle, but the similar values of the space constant may be coincidence. It is clear, however, that there are electrical connexions between the fibres, and it might be concluded that the suppression of the motility of the tissue is more important in measuring the passive electrical properties of the membrane than the slight changes of the membrane properties produced by the hypertonic solution.

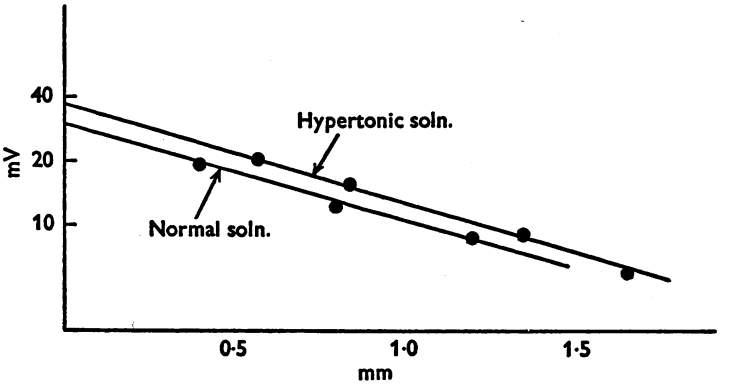


Fig. 3. Spatial decay of the electrotonic potential of the rectum measured in Krebs and hypertonic solution. The applied intensity of the current was the same in both the solutions.

Various electrical parameters of the membrane in the resting state

The membrane properties were measured in the hypertonic Krebs solution.

Fig. 4 shows an example of the current–voltage relation at the steady state of electrotonic potential (pulse duration 500 msec) at four different distances from the stimulating partition (0·48, 0·58, 0·99 and 1·64 mm). Roughly linear relations between the applied inward current intensities and the amplitude of the electrotonic potential at four different places are seen.

Fig. 5*a* shows the relationship between the amplitude of the electrotonic potentials which were produced by a given current intensity and the distance from the partition. The records were taken from the same preparation as those illustrated in Fig. 4. The relationship was linear and this result indicated an exponential decay of the electrotonic potential along the tissue. The average value of the space constant was $0{\cdot}81 \pm 0{\cdot}05$ mm

(n = 11), which was the distance at which the electrotonic potential decayed to 1/e.

Fig. 5*b* shows the relationship between the time to reach the half amplitude of the electrotonic potential against the distance from the stimulating partition. As introduced by Hodgkin & Rushton (1946) and Katz (1948), the above relationship should be linear when the tissue

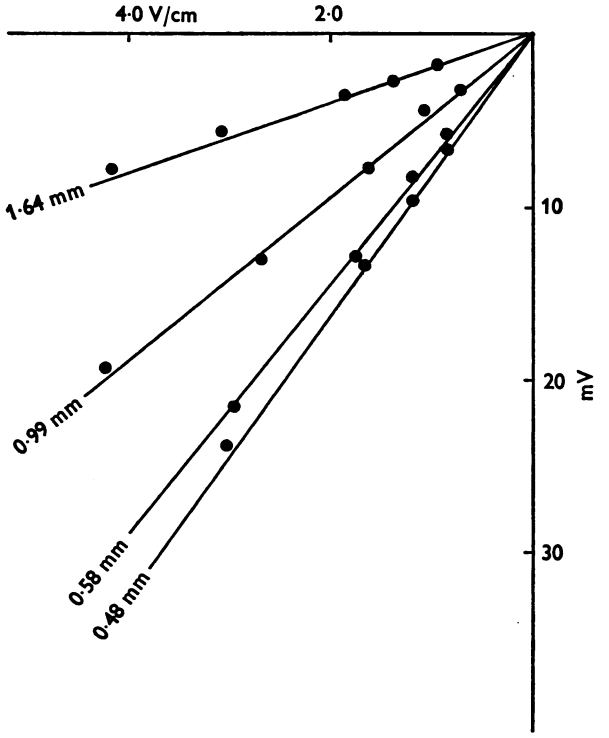


Fig. 4. Current–voltage relations in the rectum obtained at various distances (0·48, 0·58, 0·99 and 1·46 mm) from the stimulating electrode. Ordinate: the amplitude of the electrotonic potential after reaching the steady potential level (mV). Abscissa: current intensity expressed by the potential field (V/cm).

possesses cable properties. The relationship was roughly linear in the rectum as observed previously in the guinea-pig taenia coli (Abe & Tomita, 1968) and stomach (Kuriyama *et al.* 1970). The linear slope is expressed by $\tau/2\lambda$ where τ is the time constant of the membrane (erf 1), and λ is the space constant. From the above relation, the time constant obtained for the membrane was 83·7 $\pm$ 8·9 msec (n = 8). Table 1*a* shows the space constants and time constants of the membranes.

If the longitudinal muscle of the rectum possesses cable properties, it

should be possible to predict the time course of the electrotonic potential at any given distance from the stimulating partition from the theoretical time course using the cable equations described by Hodgkin & Rushton (1946). In fact, in the guinea-pig taenia coli, the time course of electrotonic potentials between the experimental and theoretically traced ones agreed well.

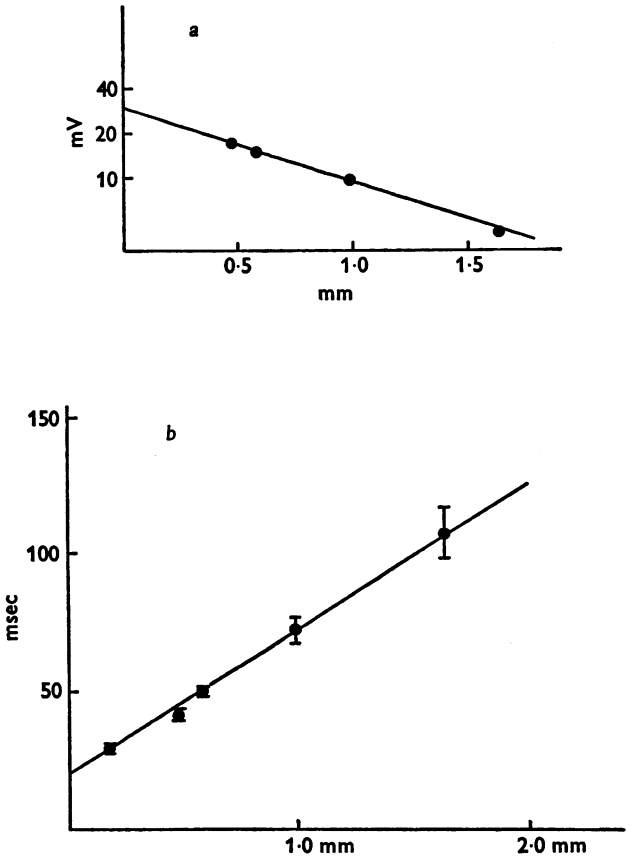


Fig. 5. *a*. The spatial decay of the electrotonic potential of the rectum obtained from current–voltage relations shown in Fig. 4. *b*. Relation between distance from the stimulating electrode and time to reach the half-amplitude of the electrotonic potential.

Fig. 6 shows the electrotonic potentials recorded at 0·58 mm and 0·99 mm distances from the stimulating partition and the theoretical time course of the electrotonic potentials calculated from the cable equations by inserting space constant (λ) = 0·85 mm and the time constant (τ) = 88·0 msec at the distances of 0·58 and 0·99 mm respectively. The time constant

of 88·0 msec was inserted to obtain the best theoretical curve fitting the experimental results. The time constants obtained from the theoretical value using the cable equations and the experimental values showed good agreement.

Properties of the membrane during the active state

In the hypertonic Krebs solution, spontaneous as well as evoked spikes could be recorded. The amplitude of the spikes exceeded the membrane potential as described previously. The maximum rate of rise of the spike was 6·0 V/sec (n = 30). The propagation of excitation was not decremental and propagated with a conduction velocity of $4{\cdot}4 \pm 0{\cdot}3$ cm/sec (n = 12). The foot of a propagating spike rises exponentially and the time

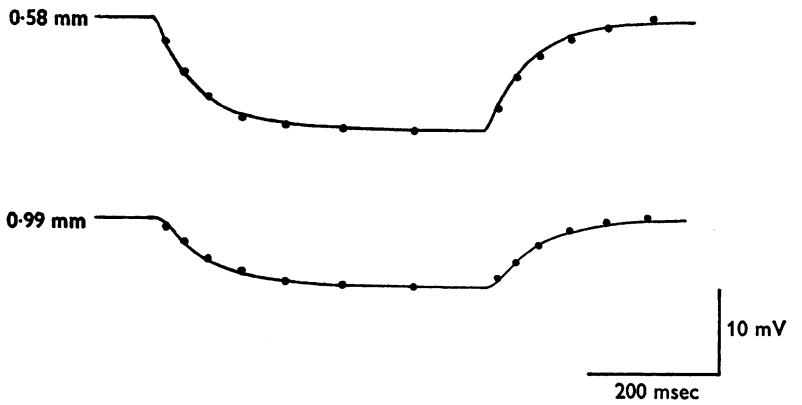


Fig. 6. Tracings of the electrotonic potentials recorded at distances of 0·58 and 0·99 mm from the stimulating electrode. The intensity of applied inward current was the same in both the traces. The points were calculated from the cable equations by inserting λ = 0·85 mm, τ = 88·0 msec and x = 0·58 and 0·99 mm respectively.

constant of the foot is determined by the cable properties of the fibre at rest and also by the conduction velocity (Hodgkin & Rushton, 1946; Tasaki & Hagiwara, 1957; Tomita, 1966*b*; Abe & Tomita, 1968; Kuriyama, 1968; Kuriyama *et al.* 1970).

Fig. 7 shows an example of the relationship between the depolarization of the membrane during the onset of the spike which was plotted on a logarithmic scale and the time. The distance between the stimulating partition and recording electrode was 5·0 mm and the actual action potential recorded for the above measurement is also shown. The time constant of the foot of the propagated spike (T) was $8{\cdot}77 \pm 0{\cdot}24$ msec

(n = 69). From the cable theory, the time constant of the foot of the propagated spike (T) can be expressed by

$$T = \frac{2\lambda^2}{\theta^2\left\{\tau + \sqrt{\left(\tau^2 + \frac{4\lambda^2}{\theta^2}\right)}\right\}},$$

where λ is the space constant (0·81 mm) and θ is the conduction velocity (4·4 cm/sec) and τ is the time constant of the membrane. The calculated time constant of the membrane (τ) was 30 msec. This value was nearly half the value obtained from the electrotonic potential and the theoretically predicted value from the cable equations (83·7 msec and 88 msec respectively).

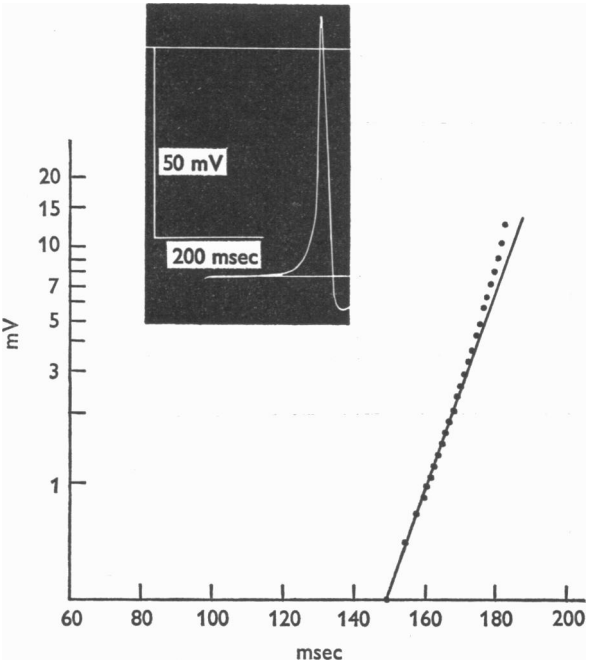


Fig. 7. A spike recorded at 5·0 mm from the stimulating electrode is shown in the insert. The rate of rise of the foot of the propagated spike is plotted on a semilogarithmic scale.

The conduction velocity of excitation was measured by insertion of two micro-electrodes along the long axis of the muscle layer. Fig. 8 shows an example of three different pairs of insertions of the micro-electrodes (0·6 and 1·9 mm, 1·8 and 4·6 mm and 5·0 and 6·6 mm respectively) at three different intensities of the current. As also described by Abe & Tomita (1968) for the taenia coli, the conduction velocity of excitation in the

rectum was widely scattered when the micro-electrodes were inserted within 2 mm from the stimulating partition. However, when the recording electrodes were inserted at a distance of more than 2 mm from the stimulating electrode, the conduction velocity showed a nearly constant value even if the applied current intensity was varied. Table 1*b* shows the interval between the two spikes and the conduction velocity. In these experiments, one electrode was fixed at a distance of 4·7–5·7 mm from the

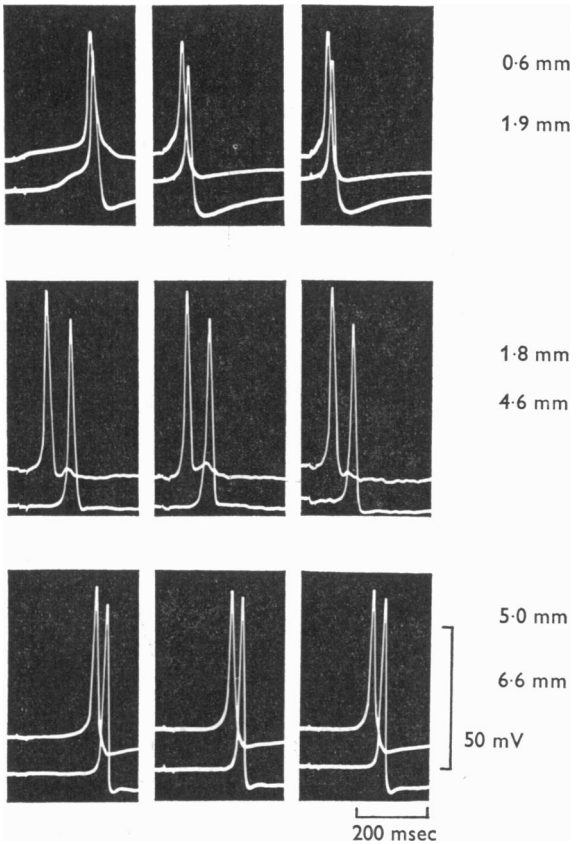


Fig. 8. Examples of the measurement of the interval between the spikes in the rectum by insertions of two electrodes at various distances from the stimulating electrode. Three different intensities of current were used. The distances of the recording electrode from the stimulating electrode are indicated on the right-hand side.

partition and another electrode was inserted into the fibres at two different places successively. The mean value of the conduction velocity was $4{\cdot}44 \pm 0{\cdot}29$ cm/sec ($n = 12$).

The chronaxie of the muscle membrane might also indicate the time

constant of the muscle membrane, since the time constant of the membrane (τ) is a factor that determines the value of chronaxie. From the leaky condenser model the chronaxie could be expressed as $0{\cdot}69\,\tau$, and from the cable model it is $0{\cdot}24\,\tau$ (Hodgkin & Huxley, 1952; Tasaki & Hagiwara, 1957). Fig. 9 shows the strength–duration curve for the spike generation on the longitudinal smooth muscle of rectum. The recording electrode was inserted at a distance of 0·2 mm from the stimulating partition. The mean value of the chronaxie obtained from the above relation was $71{\cdot}3 \pm 2{\cdot}4$ msec ($n = 11$) and the measured individual values were illustrated in Table 1*c*. When the relation between the current intensity and $1/\mathrm{erf}\sqrt{t}$ as a cable model was drawn no linear relation was

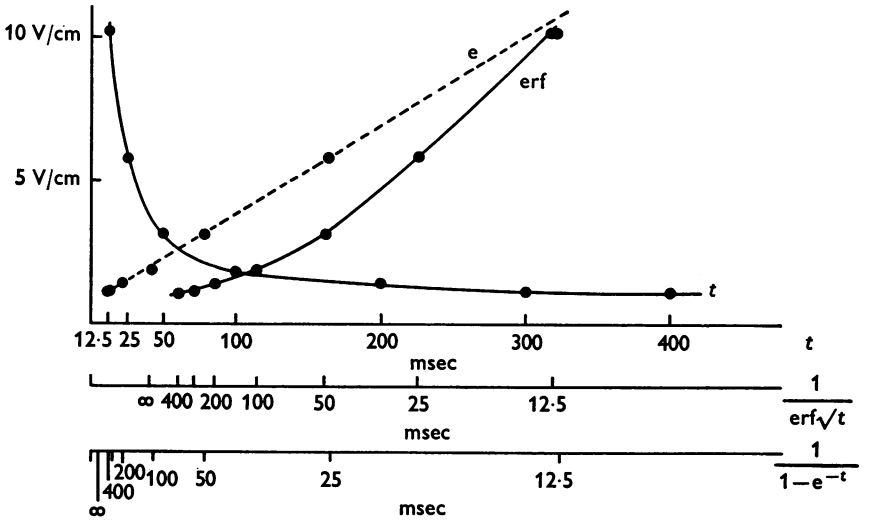


Fig. 9. Relation between the applied current intensity and duration of stimulus for the threshold to evoke the spike. Ordinate: applied current intensity expressed by the potential field (V/sec). Abscissa: the duration of stimulus expressed as t, $1/\mathrm{erf}\sqrt{t}$ and $1/(1-\mathrm{e}^{-t})$. t, ordinal intensity–duration curve; erf, plotted by $1/\mathrm{erf}\sqrt{t}$ (non-linear relation), e, plotted by $1/(1-\mathrm{e}^{-t})$ linear relation.

observed (t is the time to reach the critical firing level after stimulation) (Hodgkin & Rushton, 1946; Hodgkin & Huxley, 1952). On the other hand, when current intensity was plotted against $1/1(1-\mathrm{e}^{-t})$, a linear relation was observed (Lapicque, 1907; Noble & Stein, 1966). The time constant of the membrane, calculated from the chronaxie and the constants predicted from the leaky condenser model or from the cable model, was 103 msec ($n = 11$) and 297 msec ($n = 11$) respectively. The time constant

TABLE 1. Various electrical parameters of the muscle membrane of the rectum. *a*. Space constants and time constants of the membrane calculated from eleven specimens. *b*. The interval between the two spikes recorded at various distances from the stimulating electrode and the calculated conduction velocity of the rectum. Six specimens were used. *c*. Chronaxies of the rectum measured from eleven specimens

a

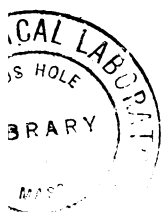
Expt. no.	Space constant (mm)	Time constant (msec)
1	0·74	103·3
2	1·08	—
3	1·10	—
4	0·62	118·9
5	0·72	78·3
6	0·69	55·8
7	0·79	—
8	0·87	108·9
9	0·55	57·9
10	0·93	58·4
11	0·85	88·0
Mean	0·81 ± 0·05	83·7 ± 8·9

b

Expt. no.	Distance from stimulating site (mm)		Conduction time (msec)	Conduction velocity (cm/sec)	Mean
1	4·9	6·5	30·2	5·03	5·69
	4·9	8·6	60·9	6·08	
2	4·9	7·3	55·3	4·34	4·18
	4·9	9·1	102·0	4·02	
3	4·7	7·9	64·6	4·95	4·18
	4·7	9·1	129·1	3·40	
4	4·7	6·9	57·2	3·83	3·65
	4·7	9·3	126·8	3·47	
5	5·0	6·7	30·5	5·57	4·72
	5·0	8·8	98·5	3·86	
6	4·9	6·9	42·0	3·63	4·20
	4·9	9·0	113·0	4·76	
Mean	—	—	—	—	4·44 ± 0·29

c

Expt. no.	Chronaxie (msec)
1	81
2	70
3	65
4	75
5	85
6	68
7	79
8	70
9	64
10	59
11	68
Mean	71·3 ± 2·4



calculated from the chronaxie using the leaky condenser model fitted with the time constant measured from the electrotonic potential better than that predicted by cable property.

DISCUSSION

The membrane potential of the longitudinal smooth muscle of the rectum measured in these experiments was slightly lower than described by Kuriyama *et al.* (1967) of $-55{\cdot}6$ mV. However, it may be said that the membrane potential of the longitudinal muscle of the alimentary canal, namely, stomach, jejunum, ileum, taenia coli and rectum are all within -50 ± 5 mV (Kuriyama *et al.* 1967).

TABLE 2. Various parameters of the electrical properties of the rectum. The specific membrane resistance was calculated assuming that the internal resistance of muscle was 125 Ω cm and 300 Ω cm. The time constants and the capacitance of the membrane were calculated using the cable equations and the equations for the leaky condenser

Space constant	$0{\cdot}81 \pm 0{\cdot}05$ mm ($n = 11$)	
Time constant of the foot of A.P.	$8{\cdot}77 \pm 0{\cdot}24$ msec ($n = 69$)	
Conduction velocity	$4{\cdot}44 \pm 0{\cdot}29$ cm/sec ($n = 6$)	
Chronaxie	$71{\cdot}3 \pm 2{\cdot}4$ msec ($n = 11$)	
Calculated chronaxie		
Leaky condenser model ($0{\cdot}68\,\tau$)	57·8 msec	
Cable model ($0{\cdot}24\,\tau$)	20·1 msec	
Time constant of the membrane	83·7 ± 8·9 msec ($n = 8$) (electrotonic potential)	
	30·0 msec (foot of spike)	
	103·3 msec (obtained from chronaxie using leaky condenser model)	
	297·1 msec (obtained from chronaxie using cable model)	
Taking	$Ri = 125\,\Omega$ cm or $Ri = 300\,\Omega$ cm	
	Radius of fibre	2×10^{-4} cm
Specific resistance	8·2 kΩ cm²	19·7 kΩ cm²
Specific capacitance	10·21 μF/cm²	4·25 μF/cm² (electrotonic potential)
	3·68 μF/cm²	1·6 μF/cm² (foot of spike)
	12·60 μF/cm²	5·24 μF/cm² (chronaxie, leaky)

The passive electrical properties of smooth muscle fibres have been extensively studied by Tomita (1966*a*, *b*, 1967) and Abe & Tomita (1968) using the guinea-pig taenia coli and they concluded that the taenia coli possesses cable-like properties. This conclusion has been confirmed by other investigators using other regions of alimentary smooth muscles of

the guinea-pig (stomach; Kuriyama *et al.* 1970, jejunum; Kuriyama *et al.* 1967). The guinea-pig rectum also shows cable-like properties as concluded from the observation made in the present experiments. In hypertonic solution, the membrane was hyperpolarized and the membrane resistance increased. However, the space constant of the membrane measured before and after treatment with hypertonic solution was the same. Therefore, the internal resistance of the muscle fibre increased in proportion to the increased membrane resistance in the hypertonic solution. The internal resistance of the longitudinal smooth muscle fibres of the rectum was not measured in these experiments. However, Tomita (1969) found that in normal Krebs solution, the impedance of the longitudinal tissue of the guinea-pig coli is 300–400 Ω cm, which is the sum of the junctional resistance about 200 Ω cm, and the myoplasmic resistance, 100–200 Ω cm. Since the impedance is frequency dependent and the value obtained was 320 Ω cm at 10 c/sec and this value was reduced to 100 Ω cm at frequencies greater than 10 kc/sec, the impedance measured at the high frequency was thought to be due to the resistance of the myoplasm while the impedance which disappears with high frequency might be attributed to the junctions between the muscle fibres. When a value of 300 Ω cm for the internal resistance of the muscle was inserted into the equations to obtain the membrane resistance and capacitance of the rectal smooth muscle, the specific membrane resistance could be calculated as 19·7 kΩ cm^2 and the capacitance as 4·25 $\mu F/cm^2$ (Table 2). This value is roughly of the same order as those values obtained for the taenia coli (30–50 kΩ cm^2 and 2–3 $\mu F/cm^2$ respectively).

The time constant of the membrane derived from the conduction velocity of the excitation and the time constant of the foot of the propagated spike was much smaller than that derived from the electrotonic potential (30 msec and 84 msec respectively).

In the skeletal muscle fibre, the membrane may be represented by a circuit with two time constants, one representing that of the plasma membrane and the other that of the tubular system. For instance, the capacity of the frog muscle membrane consists of a small capacity in the plasma membrane (2·6 $\mu F/cm^2$) and a large capacity in the tubular system (3·9 $\mu F/cm^2$) (Falk & Fatt, 1964; Freygang, Rapoport & Peachey, 1967). In the cardiac Purkinje fibre, Noble (1962) also suggested the possibility of two capacity components, and only a small part of the membrane capacity is discharged during the spike and the remaining capacity has a resistance in series so that it is discharged mainly during the plateau (2 $\mu F/cm^2$ and 10 $\mu F/cm^2$ respectively). This idea was confirmed by the observations made by Fozzard (1964, 1966).

If the rectal smooth muscles possess the two capacity components as

observed in the skeletal muscle and the cardiac Purkinje fibre, the different values of the time constant derived from the two different methods could be explained. For example, some part of the muscle membrane, namely, overlapping end parts of the muscle fibre, tight junctions and vesicles distributed along the muscle membrane, might behave electrically in the same way as the tubular structure in the skeletal muscle fibre. Under the above postulations, it is assumed that the capacity of the rectal smooth muscle consists of a small capacity in the plasma membrane (1·6 μF/cm^2 and a large capacity in another part of the membrane which is connected in parallel with the small capacity (2·7 μF/cm^2). Thus the discrepancy of the time constants of the rectal smooth muscle measured by the two different methods might arise if part of the membrane were only accessible via a series resistance. It also might be produced if some of the internal resistance were shunted by a capacity. Histological study of the rectal muscle layer is required to investigate these problems further.

In the rectal smooth muscle, Kuriyama *et al.* (1967) found that the chronaxie obtained experimentally was 5–18 msec and the calculated chronaxie (0·24τ from a cable model) was 4·4–22 msec. Both results agreed well. However, in the present experiments, the chronaxie was 71·3 msec and the theoretical chronaxie at 0·24 τ was 20·1 msec and at 0·68 τ (from a leaky condenser model) was 57·8 msec. The values obtained from the leaky condenser model agree fairly closely with the experimentally observed ones. The earlier experimentally obtained value of 5–18 msec and the present value of 71 msec show quite a large difference in the chronaxie. However, the difference might be mainly due to differences of the experimental methods, since the previous reports were made with an extracellular needle electrode (a point electrode) for stimulation and the rheobase was measured from the propagated spike. On the other hand, in the present experiments, the stimulation was applied to the tissue at the partitions and the recording electrode was inserted at 0·2 mm distance from the partition (the space constant was 0·81 mm). The longitudinal smooth muscle of the rectum is not a simple cylinder like a single skeletal muscle fibre but branches and joins other bundles forming a mesh. Noble & Stein (1966) and Noble (1966) discussed the influence of stimulus and anatomical configuration on excitable properties. They found that one point stimulation along a cable produced a smaller value for the chronaxie than that obtained from uniform stimulation. The present experiments showed that the current density $-1/(1-e^{-t})$ relation was linear and this result agreed with that presented by Lapicque (1907). Presumably, the rectal muscle fibre, where the micro-electrode was inserted, was polarized uniformly with the neighbouring muscle fibres by the stimulation.

The space constant of the longitudinal smooth muscle membrane

measured by application of weak inward current pulses was nearly the same in all the alimentary canal from the stomach to the rectum. However, the spike generation recorded in hypertonic solution was quite different in the various tissues. For example, a spike with overshoot could not be recorded consistently in the stomach antrum; hypertonic solution stabilized the membrane and blocked spontaneous spike generation, in the taenia coli and in the rectum; hypertonic solution stabilized and regularized spike generation, and electrical stimulation could also evoke a full size spike; decremental conduction could be observed in the antral smooth muscle but in neither the taenia coli nor the rectal smooth muscle.

The physiological function of the rectal smooth muscle might be characterized at least by the passive properties of the membrane, and also the ionic conductances during the active state of the membrane. However, *in vivo*, nervous factors might also modify the function of rectal smooth muscle. The nervous factors influencing the membrane activity of the rectal smooth muscle should be investigated to understand the physiological significance of the rectal movement.

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