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THE LONGITUDINAL TISSUE IMPEDANCE OF THE SMOOTH MUSCLE OF GUINEA-PIG TAENIA COLI

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SUMMARY

1. The absolute value of the tissue impedance of the guinea-pig taenia coli was measured in the longitudinal direction in air at 36° C. The relation between the tissue impedance and the separation of the recording electrodes indicated that the tissue has cable-like properties. The frequency dependence of the impedance, observed at various distances from the current supplying electrode, showed that the tissue has a capacity component in the longitudinal direction.

2. The tissue impedance in the longitudinal direction was also measured while the tissue was suspended in a narrow tube at 25–28° C. The tissue impedance was calculated on the basis of the difference between the total impedance in Krebs solution and that in Krebs solution containing half the normal Na concentration, knowing the specific resistance of both solutions.

3. The impedance per unit volume of the tissue was 370 Ω cm at 10 c/s and 190 Ω cm at 10 kc/s; at these frequencies the impedance was nearly independent of current frequency. The difference between the impedances (370 − 190 = 180 Ω cm) was taken to be the impedance of the junctions between cells. The possibility of slightly lower values for the actual tissue impedance was discussed. The capacity located at or near the junction was calculated to be 1–3 μF/cm, the time constant of the junctional membrane being about 0·5 msec.

4. Ca ions (0–12·5 mM) and adrenaline (2×10^{-7} g/ml.) had no measurable effect on the longitudinal impedance within 10–15 min. In hyperosmotic solution of twice osmolarity (by adding sucrose), the tissue impedance was increased by about 50 %. When the tissue was immersed in sucrose solution containing no ions, the impedance gradually increased up to nearly 10 times in the course of 1 hr.

INTRODUCTION

Observations on the electrotonic potential produced by large external stimulating electrodes and also on the propagating spike strongly suggest that the smooth muscle of the guinea-pig taenia coli has cable-like properties (Tomita, 1966*a*, *b*; Abe & Tomita, 1968). In order to evaluate the membrane parameters, it is important to know the value of the longitudinal internal resistance of the cells and also that of the junctional resistance between cells.

Jones & Tomita (1967) have measured the longitudinal tissue impedance of the guinea-pig taenia coli in air after the tissue had been immersed for 3 min in isosmotic sucrose solution in order to reduce the shunting by the extracellular fluid. The absolute value of impedance was 320 Ω cm at 10 c/s and 100 Ω cm at frequencies greater than 10 c/s. However, in these measurements the degree of shunting by the extracellular fluid, due to removal of ions from the extracellular space and to leakage of ions from the cells into the extracellular space remained uncertain. Therefore, in the present experiments, the longitudinal tissue impedance was further investigated, and a slightly different method was also employed. Furthermore, effects of osmolarity, of Ca ions and of adrenaline on the longitudinal tissue impedance were studied in connexion with experiments in which the change in the membrane resistance was investigated (Bülbring & Tomita, 1968, 1969).

METHODS

Two different methods were used for measuring the tissue impedance. The first method was mainly used for qualitative information and was the same as that used by Jones & Tomita (1967). In this method, the taenia coli of the guinea-pig (2·5–3 cm) was mounted vertically between two electrodes which were connected with a sine-wave generator or a square-pulse generator as shown schematically in Fig. 1*A*. The bottom electrode was fixed and the movable upper electrode was also connected with a tension recorder through a thread. The lower recording electrode was fixed about 1 mm above the bottom current-supplying electrode. The upper recording electrode was held by a micro-manipulator and could be shifted along the tissue. The recording electrodes were connected to a cathode-follower preamplifier. Current intensity was measured across a 2000 Ω resistor. The voltage and the current were displayed on an oscilloscope and photographed.

After mounting the tissue on the electrodes it was incubated in Krebs solution at 37° C for not less than 30 min before the first impedance measurement was made in air. Since the whole arrangement was placed at the bottom of a heated organ-bath whose wall was kept at 37° C, a reduction of the temperature near the tissue by emptying the bath was less than 1° C. Before each subsequent measurement the tissue was immersed in Krebs solution in which half (61 mM) or all NaCl (122 mM) was replaced with sucrose (112 or 224 mM); or in isosmotic pure sucrose (292 mM) solution; or in hyperosmotic Krebs solution (made by adding 292 mM sucrose to Krebs solution).

The second method was mainly used for quantitative measurements. The taenia coli (3–4 cm) was suspended in a narrow glass tube (length 2·5 cm, cross-section 0·008 cm^2), one

end being fixed, the other being attached to an isometric tension recorder. The glass tube connected an upper and lower chamber which contained two pairs of silver electrodes, one for applying current and the other for recording the potential gradient along the length of tube (Fig. 1*B*). The recording electrodes were insulated by plastic material, except the very tips which were placed near the two ends of the tube.

The test solution was applied from the upper chamber (10 ml.), keeping the level of the solution constant. The rate of flow of solution was about 0·5 ml./min. The test solutions were: (*a*) Krebs solution containing (mM) NaCl 122, KCl 6, $CaCl_2$ 2·5, $MgCl_2$ 1·2, $NaHCO_3$

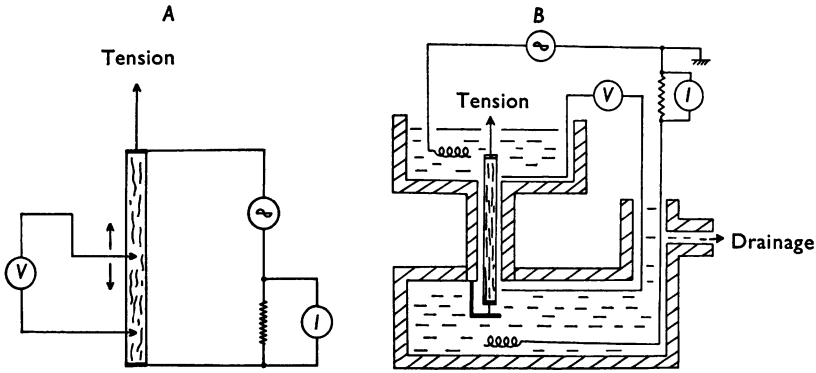

Fig. 1. Arrangements for impedance measurement. A piece of taenia is vertically suspended, one end being fixed and the other end connected to a tension recorder. A sine-wave generator was used as current source and connected to two ends of the tissue through a 2000 Ω resistor for the measurement of current intensity (*I*). The voltage drop along the tissue was measured with a differential amplifier (*V*). *A*, for measurements in air. The upper recording electrode can be shifted along the tissue by a micro-manipulator. *B*, for measurements in solutions in a narrow tube. For further description see text.

15·5, NaH_2PO_4 1·2, glucose 11·5; (*b*) Krebs solution in which half of the NaCl (61 mM) was replaced by sucrose; (*c*) Locke solution containing (mM) NaCl 154, KCl 5·6, $CaCl_2$ 2·2, $NaHCO_3$ 1·8, glucose 5·6; (*d*) Locke solution in which 50% of the NaCl was replaced by sucrose; (*e*) hyperosmotic solutions which were made by adding sucrose (5% and 10% weight per volume).

In order to measure the total impedance across the tube, the absolute value of the voltage was divided by the absolute value of the current intensity. Since the impedance was nearly independent of frequency at 10 c/s and at 10 kc/s, at both these frequencies the impedance could be treated as the resistance for approximation. The tissue impedance (*Z*) per unit volume was calculated on the basis of the equivalent circuits shown in Fig. 2. First, the percentage of the volume occupied by the solution ($1/\alpha$) in the tube was obtained from

$$\frac{1}{\alpha} = \frac{R_1 R_2 (X_2 - X_1)}{X_1 X_2 (R_2 - R_1)}, \tag{1}$$

where R_1 is the specific resistance of solution 1 (Krebs or Locke), R_2 is the specific resistance of solution 2 ($\frac{1}{2}$ Na solution), X_1 is the measured impedance in solution 1 and X_2 is the measured impedance in solution 2. X_1 and X_2 were expressed as impedance per unit volume. The tissue impedance (y) in the tube was calculated from

$$y = \frac{\alpha R_1 X_1}{\alpha R_1 - X_1} \quad \text{or} \quad y = \frac{\alpha R_2 X_2}{\alpha R_2 - X_2}. \tag{2}$$

In this calculation, it was assumed that the volume of the cells and the tissue impedance remained the same in solutions 1 and 2. Then the tissue impedance (Z) per unit volume was obtained by Eqn. (3)

$$Z = [1-(1/\alpha)]y. \tag{3}$$

The phase difference between voltage and current was not measured and hence a proper analysis of the impedance was not attempted. The tension of the tissue was always monitored during the experiments and the temperature was 25–28° C.

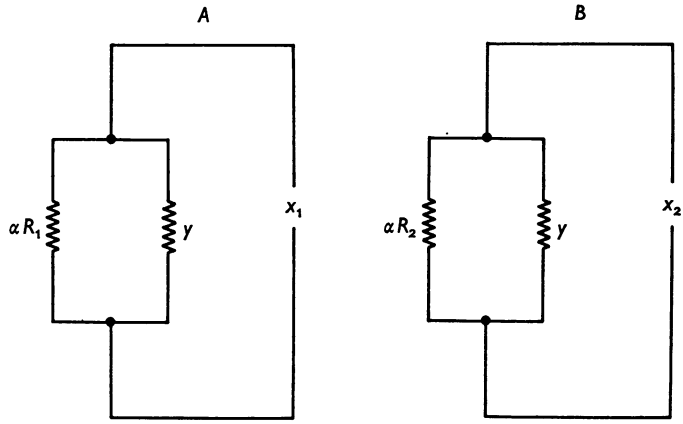

Fig. 2. Equivalent circuits for the impedance measurements in normal Na (A) and 1/2 Na solutions (B). α, a factor determined by the percentage of space in the tube occupied by the solution; R_1 and R_2, the specific resistances (Ω cm) of normal Na and 1/2 Na solution; y, the tissue impedance; x_1 and x_2, the measured impedance (per unit volume, Ω cm) in normal and 1/2 Na solutions.

RESULTS

The impedance measured in air

Impedance and contraction. The tissue was still electrically active and capable of spontaneous contractions in air after draining the Krebs solution. There was no measurable change in the impedance during contraction or relaxation. However, the impedance usually fluctuated a little with time of exposure to air but it was independent of tension. When the impedance was measured in air after the tissue had been equilibrated in Krebs solution in which NaCl had been replaced by sucrose, or in pure solution, or in hyperosmotic Krebs solution, no spontaneous activity was observed.

Impedance and recording distance. From the cable-like properties of the tissue, it would be expected that currents first cross the surface membrane near the current-supplying electrode and then flow longitudinally from cell to cell through the junctions. Therefore, the potential drop recorded along the tissue would be the sum of the potential produced at the surface

membrane and that produced at the longitudinal components (the myoplasm and the junctions). When the potential drop along the tissue is measured at various distances from the current-supplying electrode, the potential drop along the longitudinal component should be proportional to the distance between the two recording electrodes; the potential drop produced by the surface membrane, however, should be independent of the electrode separation except when it is comparable with, or shorter than, the space constant of the tissue (Cole & Hodgkin, 1939).

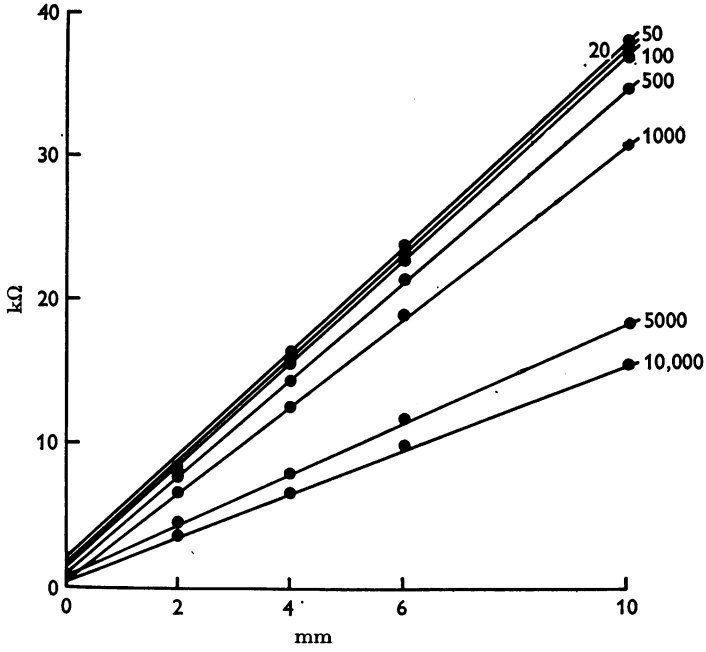

Fig. 3. Relations between impedance (kΩ) and separation of recording electrodes (mm) obtained with various current frequencies (numbered in c/s). Note deviation of lines showing relation at low frequencies from linearity and from the origin.

Figure 3 shows a typical result in which the impedance measured at various frequencies was plotted against electrode separation. In this experiment the tissue was equilibrated in Krebs solution in which half the NaCl was replaced with sucrose in order to reduce the shunting effect of the solution. The relation between the impedance and the recording distance was linear between 4 and 10 mm. Extrapolation of the relation at 20–50 c/s to zero distance usually did not cross the origin but gave some value of the impedance. This deviation was particularly clear when square current pulses (50–100 msec duration) were used instead of sine wave currents. When the frequency was higher than 500 c/s, the lines showing the rela-

tion usually crossed the origin. The deviation at a low frequency is probably due to a potential drop produced at the surface membrane as observed in the squid axon by Cole & Hodgkin (1939), and hence it is further evidence for the cable-like properties of the tissue. When the frequency is higher than 100 c/s, the current will by-pass the membrane through a membrane capacity, so that the deviation disappears. The impedance of the surface membrane actually becomes very low when the frequency is increased to more than 100 c/s (Abe & Tomita, 1968).

It was sometimes difficult to obtain the linear relation due to variations in the impedance, but the tendency for a deviation from the origin at low frequency was usually observed. Even after treatment with hyperosmotic Krebs solution, the deviation at a low frequency could be clearly demonstrated.

The impedance after treatment with the isosmotic sucrose solution. In previous experiments (Jones & Tomita, 1967) the impedance was measured in air after the tissue had been immersed for 3 min in sucrose solution (10 g/100 ml.) containing no ions. It was noticed then that the impedance measured with low frequency gradually declined with time of exposure to air, while that measured with high frequency remained constant or increased only slightly. This change was explained by the redistribution of ions within the tissue. The effect of isosmotic sucrose solution was further investigated. The impedance depended very much on the exposure time to sucrose solution and it gradually increased with time. When the tissue was immersed for about 10 min the impedance measured in air was more than twice that obtained after 3 min immersion, and the reduction of the impedance during exposure to air was much larger.

Frequency response of the impedance. The tissue impedance was frequency-dependent, as observed by Sperelakis & Hoshiko (1961) in cardiac and longitudinal intestinal muscle. Figure 4 shows the impedance measured at different recording electrode separations and at different current frequencies. This measurement was done after the tissue had been equilibrated in Krebs solution in which NaCl had been replaced by sucrose. Results similar to those shown in Fig. 4 were also obtained in the tissue which had been incubated in Krebs solution or in isosmotic sucrose solution.

From Fig. 4 and also from Fig. 3 it is obvious that the reduction of the impedance with increasing frequency was observed at the centre part of the tissue, far from the current-supplying electrodes. Therefore the frequency dependence of the impedance was not due to a property of the surface membrane but due to a property of the longitudinal component. This was also supported by the fact that the reduction of the impedance was sharpest between 500 and 1000 c/s, while the impedance of the surface

membrane was reduced to a very low value at less than 100 c/s (Abe & Tomita, 1968).

In order to reduce the shunting effect of the external solution, the impedance was measured after the tissue had been immersed for 3 min in isosmotic sucrose solution (Fig. 5). It was found that the impedance change was most prominent at frequencies between 100 and 1000 c/s.

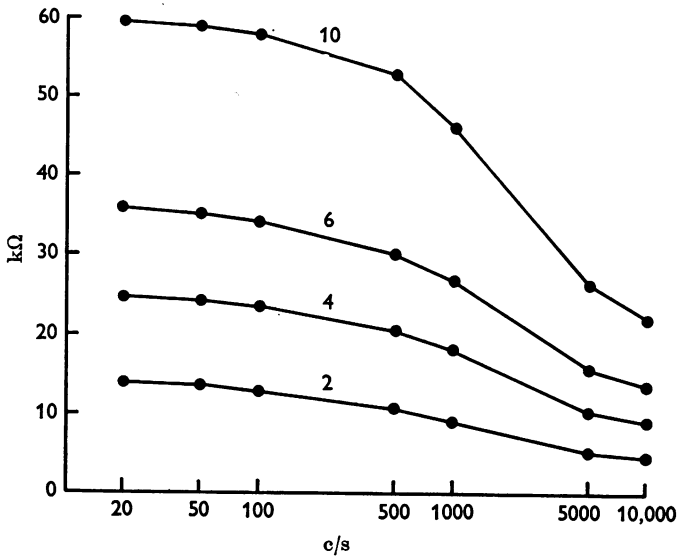

Fig. 4. Frequency response of the impedance measured with different electrode separations (in mm). The impedance was measured in air after the tissue had been immersed for 5 min in Krebs solution in which NaCl was replaced by sucrose.

Since the junctional resistance between cells is probably in parallel with the capacity component located at the junctional membrane and also at the surrounding cell membrane, as shown in the inset of Fig. 5, it is reasonable to assume that the impedance of the junction is decreased with increasing current frequency due to a by-pass of current through the capacity. Therefore the impedance measured at high frequency is probably due to the resistance of the myoplasm, while the impedance which disappeared with increasing frequency might be attributed to the junctional membrane. In most experiments, the absolute value of impedance changed very little between 10 and 100 c/s and between 5 and 10 kc/s. The junctional resistance may be approximately obtained by subtracting the impedance measured at 10 c/s from that at 10 kc/s because at both of these frequencies the impedance was nearly independent of frequency so that it may be assumed that the subtraction involves only the real part of impedance, there being no imaginary part.

A frequency dependency of the tissue impedance would depend on a parallel (shunting) impedance. However, since the parallel impedance was very high compared with the tissue impedance in this particular experiment, the capacity component (C) in the impedance may be calculated from the following equation for a rough approximation, if the equivalent circuit shown in the inset of Fig. 5 is assumed:

$$C = \frac{1}{2\pi f R_j}\sqrt{\frac{(R_j+R_i+Z)(R_j+R_i-Z)}{(Z+R_i)(Z-R_i)}}, \tag{4}$$

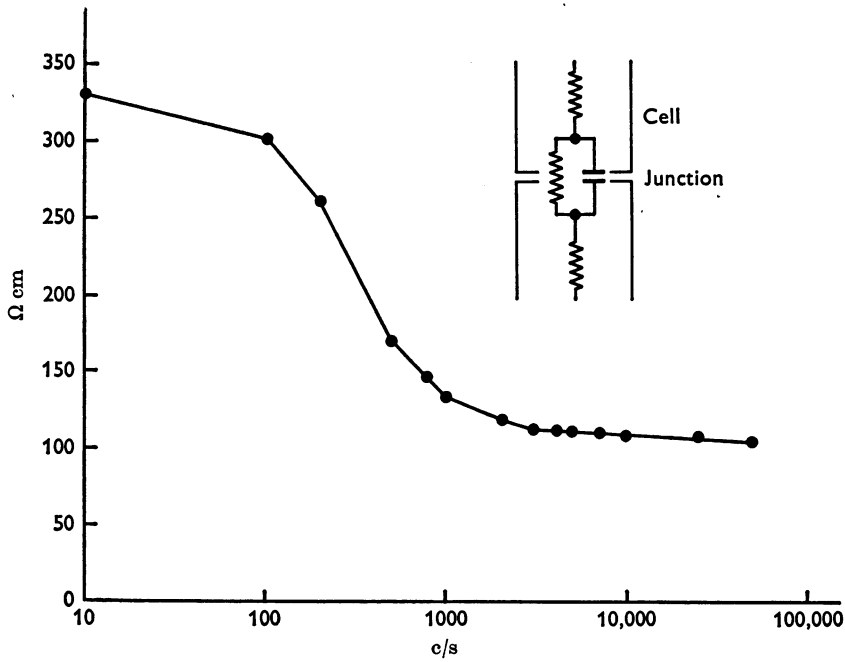

Fig. 5. The tissue impedance (Ω cm) measured at various current frequencies. The impedance was measured in air after the tissue had been immersed for 3 min in sucrose solution. The impedance is expressed as that of unit volume of the tissue excluding the extracellular space. The inset shows the probable equivalent circuit representing the junction between cells.

where R_j is the junctional resistance, R_i the myoplasmic resistance, Z the tissue impedance, and f the current frequency. The capacity was calculated to be between 1 and 3 μF/cm, and the tissue constant of the junctional membrane (the product of the junctional resistance and the capacity) about 0·5 msec. When the tissue was superfused with the sucrose solution the capacity decreased so that, at first, the time constant remained roughly constant even though the impedance was increased. However, the time constant gradually increased to 2–3 msec after more than 30 min superfusion with sucrose solution.

The impedance measured in the narrow tube

The tissue impedance in hyperosmotic solution (5 % *sucrose*). The total impedance of the tube containing the tissue and Krebs (or Locke) solution was lower when the tissue was relaxed than when it was contracted. Since the tension recording was not strictly isometric (the maximum change in length of the tissue was about 0·5 mm), the impedance change seemed to be mainly due to a change in the volume of the tissue in the tube which in turn produced a change in the shunting resistance of the surrounding solution. The impedance accompanying contraction was roughly the same at any frequency of current (10 c/s–10 kc/s).

TABLE 1. The absolute value of specific impedance measured in hyperosmotic solution (5 % sucrose)

	1	2	3	4	5	6	Mean
			Frequency: 10 c/s				
x_1 (Ω cm)	112·0	100·8	90·1	87·5	80·1	92·1	—
x_2 (Ω cm)	186·0	169·0	150·4	166·0	150·0	170·0	—
$1-(1/\alpha)$ (%)	41·5	35·0	27·0	30·5	24·8	36·8	—
Z (Ω cm)	460	356	280	425	337	370	370
			Frequency: 10 kc/s				
x_1 (Ω cm)	100·5	89·7	80·8	79·5	73·9	84·5	—
x_2 (Ω cm)	161·5	142·4	131·0	145·5	132·5	148·8	—
$1-(1/\alpha)$ (%)	38·0	33·5	22·3	26·5	22·5	34·8	—
Z (Ω cm)	260	170	143	210	156	202	190
R_1 (Ω xm)	73·0	72·6	72·0	65·0	64·0	64·7	—
R_2 (Ω cm)	131·0	131·4	128·5	131·0	126·4	130·0	—
t (° C)	26	26	28	25	28	25	—

x_1 Total impedance measured in Krebs (1–3) or Locke (4–6).
x_2 Total impedance measured in 1/2 Na-Krebs (1–3) or 1/2 Na-Locke (4–6).
Z Tissue impedance calculated from Eqns. (1)–(3).
$1-(1/\alpha)$ Percentage of the space occupied by the tissue in the tube.
R_1 Specific resistance of the Krebs (1–3) or Locke (4–6).
R_2 Specific resistance of the 1/2 Na Krebs (1–3) or 1/2 Na Locke (4–6).
t Temperature.

To eliminate this error introduced by the muscle contraction, the mechanical response was abolished by using hyperosmotic solution. For this purpose the addition of sucrose (5 g/100 ml.) to the solution was sufficient. After the tissue had been equilibrated in normal Krebs solution for about 30 min, hyperosmotic Krebs solution was introduced into the chamber. After 15–25 min in hyperosmotic solution the tissue relaxed and the impedance was measured. The solution was then changed to a hyperosmotic solution in which half of the NaCl was replaced by sucrose and the impedance was again measured. The tissue impedance was calculated by Eqns. (1)–(3).

The results obtained in six experiments are shown in Table 1. The tissue

impedance expressed per unit volume was 370 Ω cm at 10 c/s and 190 Ω cm at 10 kc/s. In this calculation it was assumed that the tissue volume remained constant in the two solutions. This was confirmed by the finding that the ratio of (wet weight)/(fresh weight) remained the same (variation 1–3 %) when the tissue was transferred from the hyperosmotic normal to the hyperosmotic 1/2 Na Krebs (or Locke) solution provided that the tissue was first equilibrated for not less than 10 min in the hyperosmotic solution (5 % sucrose Krebs or Locke solution). As described above, the impedance of 190 Ω cm obtained at high frequency would be the myoplasmic resistance per unit volume, and the impedance of 180 Ω cm (370–190) would be the junctional resistance per unit volume of the tissue, if the contribution of the impedance of the surface membrane is neglected. The contribution of the surface membrane seems to be small, probably because of the long tissue length (25 mm), as shown by the small difference between the impedance at 10 and 100 c/s (about 10 Ω cm).

The tissue space calculated from impedance measurements was roughly of the same order of magnitude as that calculated from the fresh weight, the specific weight (1·06) and the extracellular space (35 %, Goodford & Leach, 1966). The percentage of the space occupied by the tissue measured at 10 kc/s was about 10 % smaller than that measured at 10 c/s. This may be due to the current at low frequency not flowing through a small fraction of the extracellular space near the junction.

The effect of Ca ions. The effect of changing the external Ca concentration on the tissue impedance was studied in hyperosmotic 1/2 Na Krebs solution. Removal of Ca had no effect within 10 min.

The effect of excess Ca (12·5 mM) was studied by substituting an equivalent amount of sucrose. The total impedance was decreased by the reduction of the resistance of the solution (from 131 to 116 Ω cm). Any change in the tissue impedance could not have been more than 2 %. It may be concluded that the tisse impedance was insensitive to the external Ca concentrations.

The effect of adrenaline. When adrenaline (2×10^{-7} g/ml.) was added to the normal Krebs solution, the total impedance always decreased. However, this reduction appeared to be due to a decrease in the shunting resistance of the solution since the tissue was relaxed. When the tissue was already relaxed in 1/2 Na solution or in hyperosmotic solution, adrenaline had no measurable effect on the impedance.

Effect of osmolarity. The effect of osmotic pressure on the tissue impedance was measured by adding sucrose (5 g/100 ml. and 10 g/100 ml.). Since adrenaline had no effect on the tissue impedance, it was used for abolishing the tension during the control impedance measurements in isosmotic solutions. In two experiments, shown in Table 2, an increase in the

impedance was observed not only at 10 c/s but also at 10 kc/s. The measurements were made after 15–20 min in the hyperosmotic solution.

In hyperosmotic solutions the tissue weight remained constant when it was transferred from normal Na to 1/2 Na solution. However, in isosmotic solution the tissue weight was decreased by about 5 % within 10–15 min, when transferred to 1/2 Na solution. Since the shrinkage of the tissue increased the shunting by the surrounding solution the tissue impedance had to be corrected to a value higher (10–30 %) than the observed value.

TABLE 2. The absolute value of specific impedance in solutions of different osmolarity

Frequency (c/s)	Osmolarity	1·0 *X*	1·5 *X*	2·0 *X*
		Experiment 1		
10	x_1	78·3	80·1	88·1
	x_2	142·4	150·0	166·0
	$(1-1/\alpha)$	35·0 (32·5)	24·8	18·8
	Z	250 (325)	337	560
10^3	x_1	69·0	73·9	82·8
	x_2	120·0	132·4	150·8
	$(1-1/\alpha)$	30·3 (28·0)	22·5	17·0
	Z	132 (146)	156	215
	R_1	57·2	64·0	73·7
	R_2	115·5	126·4	142·0
		Experiment 2		
10	x_1	89·8	92·1	101·4
	x_2	161·8	170·0	190·4
	$(1-1/\alpha)$	43·5 (41·8)	36·3	30·1
	Z	330 (420)	370	540
10^3	x_1	77·7	84·5	94·3
	x_2	134·0	148·8	173·4
	$(1-1/\alpha)$	38·8 (36·3)	34·8	26·8
	Z	179 (203)	202	330
	R_1	57·3	64·7	75·0
	R_2	116·0	130·0	148·8

Figures in parentheses are corrected values.

Table 2 shows that the tissue impedance remained more or less unchanged in the solution of up to 1·5 times the normal osmolarity, but increased in stronger hyperosmotic solution.

The impedance in the isosmotic sucrose solution. When the tissue was continuously superfused with sucrose solution, it was found that the impedance gradually increased, as shown in Fig. 6. The control value was obtained in Krebs solution containing sucrose (5 g/100 ml.) as described above. The values in pure sucrose solution were obtained by assuming that the tissue volume was constant and the same as in the sucrose Krebs solution and by neglecting the shunting resistance of the sucrose solution which was about 100 times higher than the tissue resistance. The rate of increase in the impedance usually slowed down after 20–30 min in sucrose solution, but

there was still some increase even after 1 hr. When the superfusion was stopped there was an exponential reduction in the impedance, but after 30 min it still remained higher than the original value. The impedance measured at 10 kc/s changed in a similar manner but to a slightly lesser percentage.

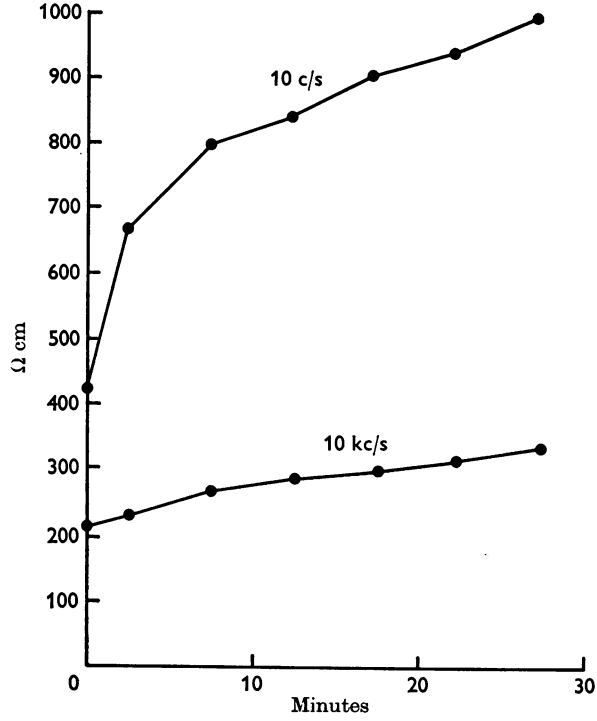

Fig. 6. The change in the tissue impedance (Ω cm) by prolonged superfusion with sucrose solution. The upper curve measured at 10 c/s, the lower curve at 10 kc/s. The impedance is expressed as that of unit volume of the tissue.

DISCUSSION

The method used in the present experiments is not sufficiently accurate to obtain the true tissue impedance in the longitudinal direction. A small error (e.g. 5 %) in the measurement could easily introduce a large error (e.g. 20 %) in the tissue impedance. If the tissue volume and/or the tissue impedance is not the same in the two solutions (normal Na and 1/2 Na), the error would be even greater. Furthermore, there was a difficulty in analysing the tissue impedance by simple division of an observed voltage by a current intensity due to a shunting resistance. Therefore, the values reported here can be taken only as a rough estimation. Nevertheless, the values obtained strongly suggest that the junctional resistance between

cells is quite low and its contribution to the longitudinal tissue resistance is of the same order of magnitude as that of the myoplasmic resistance, supporting the previous conclusion (Jones & Tomita, 1967).

If the impedance measured at a low frequency (10 c/s) contained a component due to the surface membrane, the junctional resistance would be slightly smaller (probably about 10 Ω cm) than 180 Ω cm. In the present experiments, the measurements were done at a low temperature (25–28° C). The temperature coefficient of the tissue impedance is not known, but the true values might be slightly lower than those reported here. Since the smooth muscle cells of the taenia form bundles 20–30 μ wide (Bülbring, 1954) it is possible that the bundles terminate at a certain length. Then the actual tissue impedance within the bundles would be lower than the impedance obtained from the tissue longer than the bundle length.

The internal resistance in Purkinje fibre (which includes the resistance of the intercalated disks) is reported to be 100–150 Ω cm (Weidmann, 1952; Coraboeuf & Weidmann, 1954). Boyd & Martin (1959) obtained a specific resistance of the mammalian myoplasm of 125 Ω cm from a calculation based on the ionic concentration, temperature correction and the value of the frog myoplasm (250 Ω cm, Katz, 1948). These values are not much lower than 190 Ω cm obtained in the present experiments for the taenia. If it were assumed that the true value for the myoplasmic resistance of the taenia was 125 Ω cm instead of 190 Ω cm, and the ratio of the impedance at 10 c/s and 10 kc/s was the same as that measured (370/190), the true total impedance (myoplasmic plus junctional resistance) would be 250 Ω cm.

The cable properties of the smooth muscle are not distorted by the capacity component located at the junction, since the time constant of the junctional membrane is only about 0·5 msec, i.e. 0·5 % of that of the plasma membrane, 105 msec (Abe & Tomita, 1968). According to a model experiment, the time course of the electrotonic potential in a non-uniform cable (short cables of individual cells connected with junctional resistances and capacities located between cells) is little affected by the capacity at the junction when the time constant is less than 5 % of that of the plasma membrane.

When the tissue is superfused with sucrose solution, there is a gradual increase in impedance. This change is probably due to a change in the shunting resistance which is determined by the rate of leakage of ions from the cell and the rate of removal of ions from the extracellular space. It is also possible that sucrose solution (containing no ions) has a direct effect on the junctional resistance. Therefore, prolonged soaking of the tissue in sucrose solution increases the tissue impedance to a value higher than the physiological value, probably mainly by some action on the

junctional resistance and partly by reduction of the internal potassium concentration. This seems to be the reason why Sperelakis & Hoshiko (1961) obtained a rather high value of about 2000 Ω cm for the tissue impedance measured at 10 c/s in the longitudinal intestinal muscle, since they immersed the tissue for 2 hr in sucrose solution containing only one tenth of normal Na concentration.

The increase of the impedance of the junctional membrane may be due to the loss of ions from the junctional region into the superfused solution. The gradual decrease of the impedance when superfusion of sucrose solution is stopped may be the result of reaccumulation of ions near the junction, and also in the bulk of the extracellular space due to ion leakage from the cell, resulting in a reduction of the junctional resistance and an increase in the shunting.

In a solution of twice the normal osmolarity, a block of spike propagation has been observed in cardiac muscle (Barr, Dewey & Berger, 1965) and also in the smooth muscle of the guinea-pig taenia coli (Barr, Berger & Dewey, 1968). They explained this by disruption of the 'nexuses' (the tight junctions). However, Dreifuss, Girardier & Forssmann (1966) reported that in cardiac muscle the block of the spike propagation is not due to separation of the nexus but to the swelling of the sarcotubular system, although they agree with Barr *et al.* (1965) that the nexus is a low-resistance electrical pathway. In the present experiments, the tissue impedance is increased in hyperosmotic solution exceeding 1·5 normal osmolarity, the increase being more at lower frequency than at high frequency. This suggests that there is some effect on the junction. The effect, however, is not dramatic (about 50 % increase in Krebs solution of twice normal osmolarity). After treatment with hyperosmotic solution there is still a deviation of the impedance–distance relation from the origin at a low frequency of currents, and the frequency response curve is very similar to that obtained with isosmotic solution. If disruption of the interconnexions between cells were complete, the line showing the relation would cross the origin, and a change in the frequency response would be expected. Furthermore, the taenia shows proper cable-like properties and spike propagation in twice normal hyperosmotic solution (Tomita, 1966*a*, *b*, 1967; Abe & Tomita, 1968). Therefore the function of the junction seems to be preserved in a solution of up to twice normal osmolarity, at least in the guinea-pig taenia coli.

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