

Electrophysiological Studies of the Smooth Muscle Cell Membrane of the Rabbit Common Carotid Artery

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ABSTRACT The electrical responses of the smooth muscle cells of the rabbit common carotid artery to extracellular stimulation were studied in isotonic and hypertonic solution (1.7 times normal tonicity) with microelectrodes. No spontaneous electrical or mechanical activity was recorded when the tissue was in either isotonic or hypertonic solution. The voltage-current relation of smooth muscle cells in the common carotid artery showed marked rectification in both isotonic and hypertonic solutions. In isotonic and hypertonic solutions mean values for membrane potentials were -44.5 and -51.5 mv, for space constants 1.13 and 1.21 mm, and for time constants 212.2 and 238.2 msec, respectively. Addition of 34.3 mM TEA to the solutions caused spontaneous action potentials in the common carotid artery. The action potentials recorded simultaneously from two microelectrodes showed good synchronization. It was concluded that there is electrical transmission between cells of this artery.

INTRODUCTION

It has been shown, with external current application and intracellular recording, that many visceral smooth muscles have cable-like properties in spite of a complex arrangement of cells in the tissues, suggesting a low resistance pathway between cells (Tomita, 1967; Abe and Tomita, 1968; Kuriyama, Osa, and Tasaki, 1970; Kuriyama and Mekata, 1971). Dewey and Barr (1962) suggested that in smooth muscles nexuses provide the low-resistance pathway for conducted action potentials. It has been reported that in the large elastic arteries of adult animals there are generally no nexuses (Keech, 1960; Karrer, 1961), though in the aorta of newborn rats and with decreasing frequency up to 3 months of age, nexuses may be present (Cliff, 1967). Recently, however, the presence of conducted action potentials in the large arteries produced in response to drugs and ions has been suggested by some workers (Keatinge, 1968). In the present experiments, the cable properties of the smooth muscle cells of the common carotid artery of the adult rabbit were

investigated with microelectrodes and it was concluded that there are electrical connections between the cells of this artery.

METHODS

Adult rabbits, weighing 2.0–2.5 kg, were stunned and bled. The common carotid artery was excised and helical strips, 35–40 mm in length and 2.0–3.0 mm in width, were cut. The tissue was mounted in an organ bath through which solution flowed continuously with a speed of 8 ml/min 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⁺⁺ 1.2; Ca⁺⁺ 2.5; Cl⁻ 134.0; HCO₃⁻ 15.5; H₂PO₄⁻ 1.2, and glucose 11.5; equilibrated with 97% O₂–3% CO₂.

In order to determine whether the common carotid artery has cable-like properties, the spatial decay and time course of the electrotonic potential were measured by the method described and illustrated by Abe and Tomita (1968). The stimulating electrodes consisted of two silver plates with a small hole (2 × 0.7 mm) through which the preparation was passed. One stimulating electrode divided the muscle chamber into stimulating and recording chambers. The interelectrode distance was 8 mm. The piece of the artery was placed into the recording bath and one end was pulled through the hole into the stimulating chamber. Both chambers were independently irrigated with Krebs solution which was sucked away near the partition between the two chambers. For recording the transmembrane potential of the cells conventional 3 M KCl-filled microelectrodes were inserted from the internal surface of the vascular strips. The distances between the stimulating partition and the microelectrode were measured under the binocular microscope. In order to observe the synchronization between membrane activity at different sites the recording electrodes were simultaneously inserted into two different cells. In order to measure the membrane constants and changes in membrane resistance induced by TEA, Krebs solution of about 1.7 times the normal tonicity (204 mM sucrose in Krebs solution) was used throughout in order to abolish muscle movement except during measurement of membrane constants in Krebs solution of normal tonicity. TEA-containing hypertonic solutions were prepared with elimination of equimolar sodium chloride from standard hypertonic Krebs solution.

RESULTS

General Properties of the Membrane

BEHAVIOR OF THE MEMBRANE IN ISOTONIC SOLUTION

If current across the membrane at a point of a cable-like fiber is proportional to the externally applied current, the current-voltage relation corresponds to the input membrane resistance. Fig. 1 A shows the electrotonic potentials of the smooth muscle of the common carotid artery evoked by extracellularly applied depolarizing and hyperpolarizing currents in isotonic solution. The voltage-current relation in the common carotid artery recorded at 0.2–2.5 mm

from the stimulating partition was nearly linear when weak hyperpolarizing currents were applied (Fig. 1 B and Fig. 2). If the hyperpolarization exceeded the resting potential by more than about 10 mv, the membrane resistance increased (Fig. 1 B). With depolarizing currents, the membrane resistance was greatly decreased (Fig. 1 B). Relatively strong depolarizing currents produced a hump in the electrotonic potential, which however never developed into a spike (Fig. 1 A).

Neither spontaneous electrical (number of preparations was 42) nor mechanical activity (number of preparations was 28) could be recorded while the

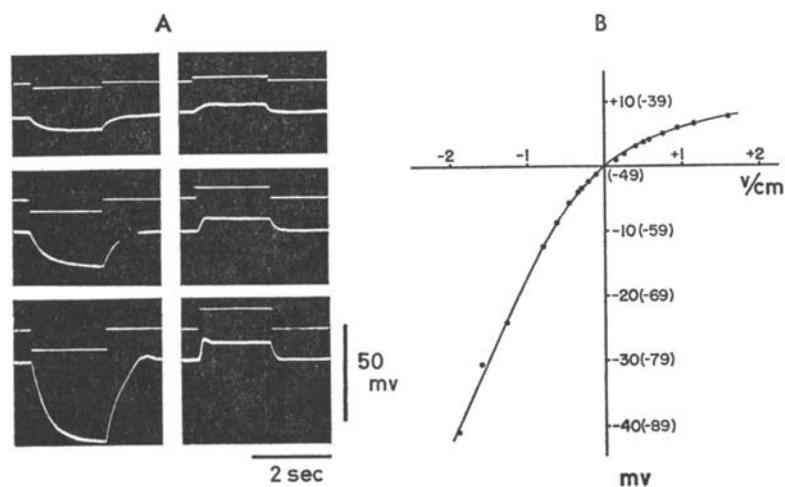


FIGURE 1. Responses of the membrane to external stimulation in isotonic solution. A, intracellular records of electrotonic potentials (lower trace) produced by externally applied anodal and cathodal current of three different intensities (upper trace). B, relation between externally applied current and intracellularly recorded potential shown by solid circles. These were recorded at 0.38 mm from the partition. Depolarization upward, hyperpolarization downward.

arterial strips were in Krebs solution. The resting membrane potential measured from the artery in Krebs solution varied from -36 mv to -59 mv (mean -44.5 mv SD ± 1.4 mv, $n = 30$).

Membrane Constants of the Common Carotid Artery in Isotonic Solution

In some previous reports, measurements of membrane constants of mammalian smooth muscles with external stimulation were not carried out in solutions of normal tonicity because muscle movement prevented the recording of electrotonic potentials from single cells (Tomita, 1966 *a*; Abe and Tomita, 1968; Kuriyama and Mekata, 1971). However, the absence of mechanical activity in this arterial strip made it easy to record the electrotonic potential.

The space and the time constants of the smooth muscle of the common carotid artery were measured in isotonic solution by application of weak anodal current since the membrane resistance increased with strong anodal currents (see Fig. 1). The electrotonic potentials were observed intracellularly at four to five different distances (from 0.10 to 2.50 mm) from the stimulating electrodes, roughly along the middle part of the tissue. The current-voltage relations at the steady state of the electrotonic potentials are shown in Fig. 2

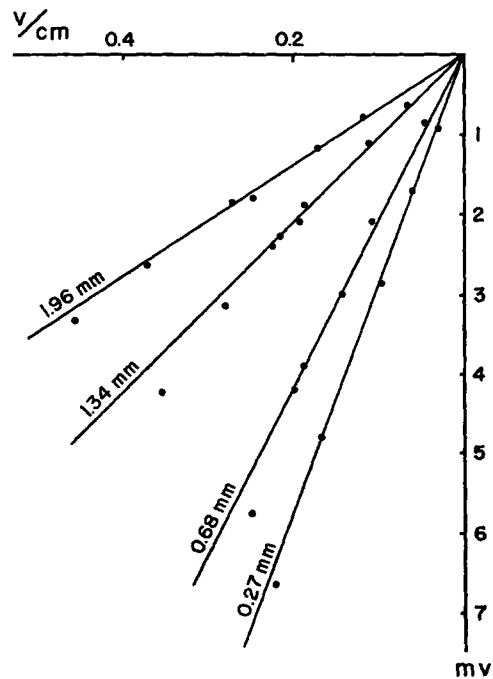


FIGURE 2. Current-voltage relations of the common carotid artery in isotonic solution obtained at various distances (0.27, 0.68, 1.34, and 1.96 mm) from the stimulating site when relatively weak anodal currents were applied. Ordinate, displacement of intracellularly recorded potential. Abscissa, current intensity expressed as the potential field in the stimulating chamber.

for different distances from the insulating partition. The electrotonic potentials produced by a given weak hyperpolarizing current were plotted on a logarithmic scale against the distance from the partition as shown in Fig. 3 A. From the current-voltage relation at the four distances, this relation was linear. The space constant was calculated from the spatial decay of the electrotonic potential, and is the distance at which the electrotonic potential decayed to $1/e$ (37%). The average value of the space constant was 1.13 mm (Table I).

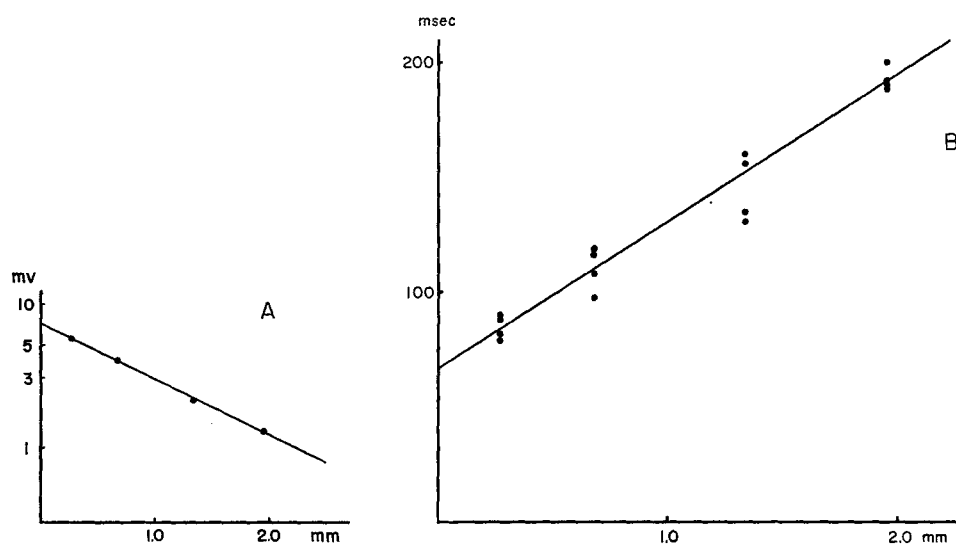


FIGURE 3. A, spatial decay of the electrotonic potential of the common carotid artery in isotonic solution. Points were obtained from the current-voltage relations at a constant current intensity at different distances, as shown in Fig. 2. Ordinate, intracellularly recorded potential on a logarithmic scale. Abscissa, distance from the stimulating site. B, relation between distance from stimulating site (abscissa) and time to reach the half-amplitude of the electrotonic potential (ordinate) in isotonic solution.

TABLE I
MEMBRANE CONSTANTS OF SMOOTH MUSCLE
OF THE COMMON CAROTID ARTERY IN ISOTONIC
AND HYPERTONIC KREBS SOLUTIONS

Experiment No.	Isotonic solution		Hypertonic solution		
	Space constant	Time constant	Space constant	Time constant	
	<i>mm</i>	<i>msec</i>	<i>mm</i>	<i>msec</i>	
1	0.91	196.2	1	1.37	285.0
2	1.35	250.0	2	0.80	181.1
3	1.06	169.6	3	1.10	182.5
4	0.94	176.7	4	1.13	226.0
5	0.96	248.1	5	1.19	235.3
6	1.19	242.8	6	1.64	282.5
7	1.12	215.0	7	1.04	208.0
8	1.52	198.9	8	1.52	252.7
			9	1.03	293.6
			10	1.54	263.3
			11	0.98	210.3
Means	1.13 (sd ± 0.08)	212.2 (sd ± 11.3)	1.21 (sd ± 0.08)	238.2 (sd ± 12.2)	

The time to reach the half-amplitude of the electrotonic potential increased linearly with distance (x) from the stimulating site (Fig. 3 B). As pointed out by Hodgkin and Rushton (1946), the slope of this is expressed by $\tau_m/2\lambda$. The time constant of the membrane was calculated from the slope and the space constant. The mean value of the time constant obtained by this method was 212.2 msec (Table I).

BEHAVIOR OF THE MEMBRANE IN HYPERTONIC SOLUTION

When the tissue was perfused with hypertonic Krebs solution, the membrane was hyperpolarized from -41 to -71 mv (-51 mv SD ± 1.6 mv, $n = 30$).

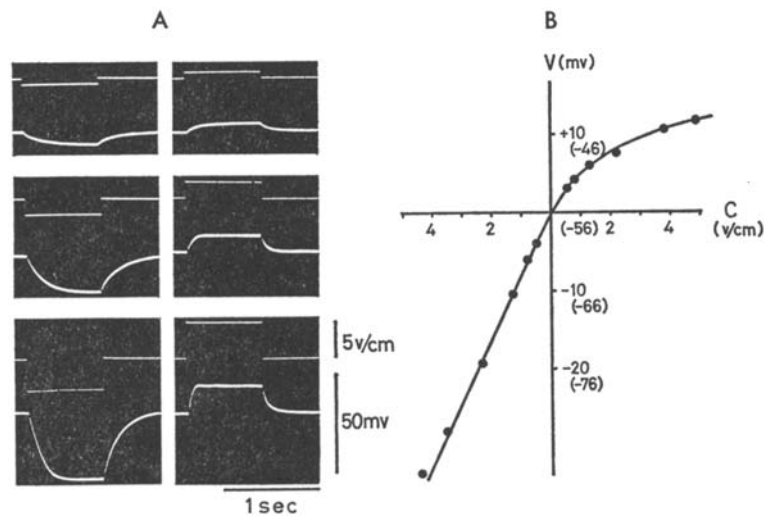


FIGURE 4. Responses of membrane to external stimulation in hypertonic solution. Explanation of the figure is the same as for Fig. 1. These responses were recorded at 0.34 mm from the partition.

Also spontaneous electrical activity was never recorded in hypertonic solution. Fig. 4 shows the voltage-current relation of the smooth muscle of this artery soaked in hypertonic solution. In the hyperpolarizing direction the current-voltage relation was linear even if relatively strong anodal stimulation was applied. In the depolarizing direction as the applied current increased the membrane resistance decreased greatly. The V-I curve in hypertonic solution was similar in shape to the curve in isotonic solution but was displaced along the membrane potential axis. The membrane was never depolarized by more than about 18 mv and action potentials were never triggered even if the recording electrode was placed at a distance of only 0.08 mm from the stimulating electrode and a strong depolarizing current was applied.

Membrane Constants of the Smooth Muscle of the Common Carotid Artery in Hypertonic Solution

In order to compare the membrane constants of the common carotid artery with those of the visceral tracts previously measured in hypertonic solution, measurements of the membrane constants of the common carotid artery were carried out in hypertonic solution by the same methods as described above. The spatial decay of electrotonic potential and the relation between the time to reach the half-amplitude of the electrotonic potential and the distance from the stimulating site are shown in Fig. 5 A and B, respectively. Mean values of the space constant and the time constant were 1.21 mm and 238.2 msec, respectively (Table I).

When the space and time constants were measured in the same tissue before and after treatment with hypertonic solution, almost no change in the space constant (1.52 mm in Krebs and 1.54 mm in hypertonic Krebs solution) and a significant difference in the time constant (198.9 msec in Krebs and 263.3 msec in hypertonic Krebs solution) could be observed. Fig. 6 shows the spatial decay of the amplitude and time to reach half-amplitude of the electrotonic potentials recorded at various distances from the stimulating partition in Krebs and hypertonic Krebs solution (after 2 hr). The space constant in hypertonic solution is similar to that in isotonic solution ($0.01 < P < 0.05$, compared to that in isotonic solution). There was a significant difference between the time constant in isotonic solution and that in hypertonic solution ($P < 0.001$, compared to that in isotonic solution). (P is probability for the correlation coefficient and "Table of normal distribution" was used to obtain the value of P).

Effects of TEA on the Electrical Activity in Hypertonic Solution

It will be reported in detail in another paper that the helical strips of the common carotid artery develop phasic contractions in isotonic Krebs solution containing TEA (34.3 mM) (Mekata, unpublished observation).

When TEA (34.3 mM) was applied in hypertonic Krebs solution, the membrane was depolarized by about 10 mv and action potentials were produced ($n = 10$). This activity started abruptly and consisted of regular discharge with a frequency of 5.3–30.0 action potential/min (mean 13.1 cycle/min, $n = 10$). The amplitude of the action potential was from a few millivolts to 28.0 mv (mean 15.7 mv, $n = 30$). The shapes of the action potentials were of the plateau type or sine waves (Fig. 7). The maximum rates of rise and fall of the action potentials induced with TEA (34.3 mM) were in the ranges of from 69 mv/sec to 982 mv/sec (mean 289 mv/sec, $n = 30$) and from 20.0 mv/sec to 85.1 mv/sec, $n = 30$, respectively. Addition of TEA to give from 4.3 mM to 17.1

mm in hypertonic Krebs solution caused no action potentials though depolarization developed.

Synchronization and conduction velocity of action potentials recorded in the presence of TEA (34.3 mM) were investigated by the insertion of two

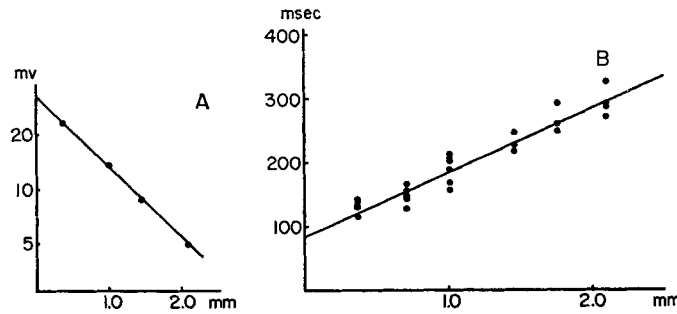


FIGURE 5. A, spatial decay of the electrotonic potential. B, relation between distance from stimulating site (abscissa) and time to reach the half-amplitude of the electrotonic potential (ordinate) in hypertonic solution. Description as for Fig. 3.

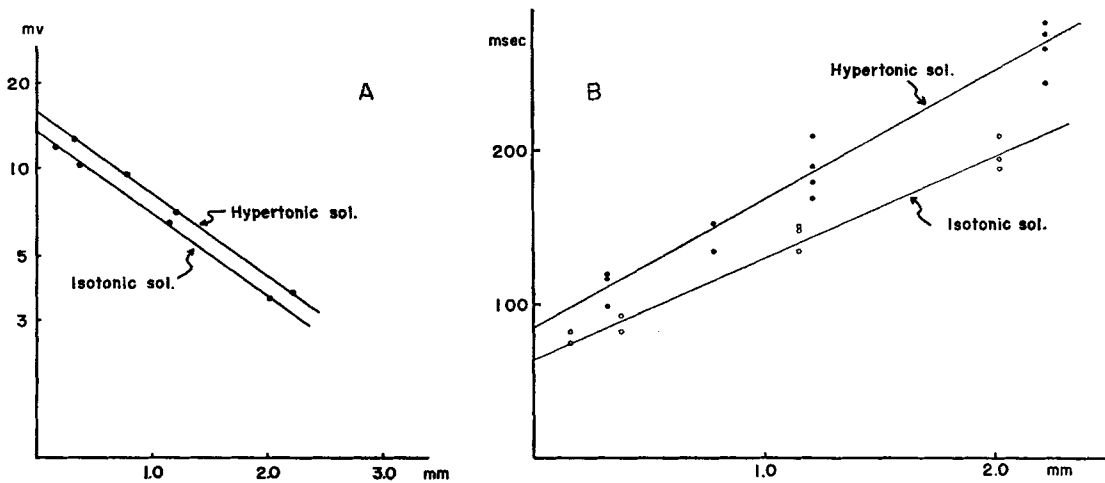


FIGURE 6. Spatial decay of the electrotonic potential (A) and time to reach half-amplitude of the electrotonic potential (B) in one preparation of the common carotid artery in isotonic and hypertonic Krebs solutions. The intensity of the current applied was the same in both solutions.

microelectrodes at various longitudinal distances (2.2–13.0 mm) from each other. Action potentials recorded simultaneously with two electrodes showed good synchronization ($n = 6$) (Fig. 7 B and C). The conduction velocity calculated from the distance between the two recording electrodes and the interval between the action potentials varied greatly from 0.51 cm/sec to 4.03

cm/sec (mean 1.77 cm/sec SD \pm 0.58 cm/sec, $n = 6$). If a pacemaker of the spontaneous action potential exists between the two recording electrodes, the calculated conduction velocity would be greater than the real value. This range was considerably smaller than those observed in the guinea pig taenia coli (Abe and Tomita, 1968) and rectum (Kuriyama and Mekata, 1971) in hypertonic Krebs solution.

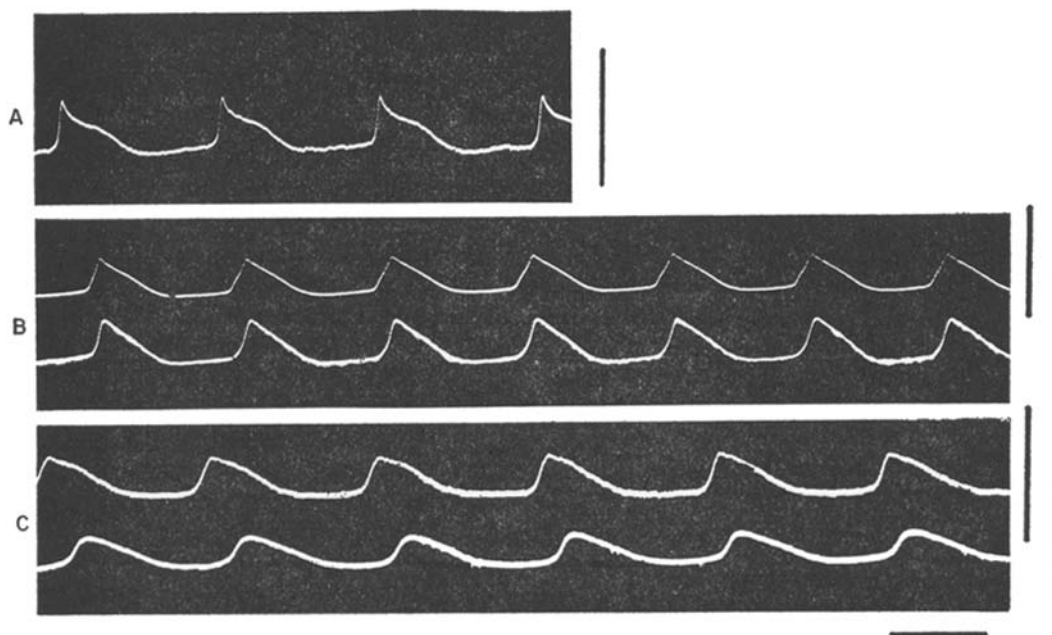


FIGURE 7. Various patterns of the spontaneous action potentials recorded from the rabbit common carotid artery in hypertonic solution containing 34.3 mM TEA and synchronization of TEA-induced action potentials recorded simultaneously from two microelectrodes, which were inserted at different positions on the strip (separated by 2.3 mm (B) and 5.5 mm (C)). Scale, 50 mv and 2 sec.

After the break of a conditioning depolarizing current, action potentials induced with 34.3 mM TEA were temporarily abolished during about 20 sec. At this time external current was applied to the muscle which had been soaked in 34.3 mM TEA and the membrane gave an active response graded according to the intensity of applied current. The voltage-current relation was nearly linear with TEA. The membrane resistance in TEA-containing solution was unchanged or decreased by a few per cent of that in the control solution ($n = 6$). However, the rectifying property of the membrane completely ceased (Fig. 8).

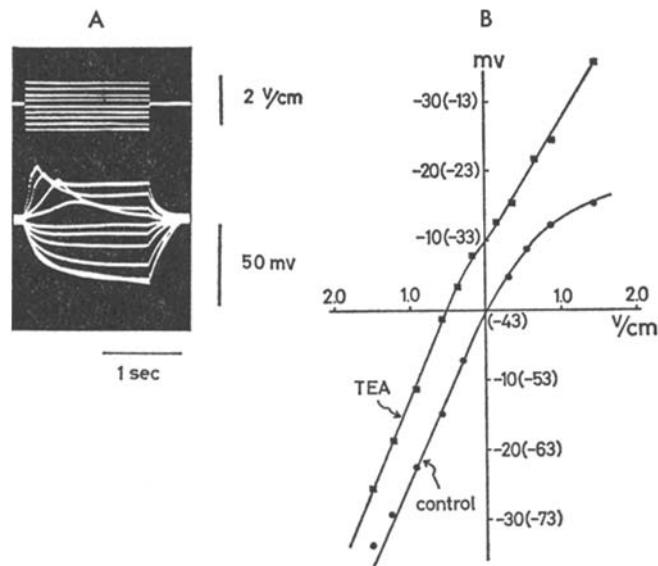


FIGURE 8. A, responses of the common carotid artery in hypertonic solution containing 34.3 mM TEA to polarizing current pulses applied externally. (For description see text.) B, current-voltage relationship in normal hypertonic solution and in 34.3 mM TEA-hypertonic solution.

DISCUSSION

Membrane potential values for the smooth muscle of the common carotid artery were slightly lower than those observed in the guinea pig intestine and stomach (Bülbring and Kuriyama, 1963; Kuriyama, Osa, and Toida, 1967; Kuriyama et al., 1970).

Differences between the smooth muscle of the common carotid artery and that of the intestine or stomach are apparent from the membrane activities and voltage-current relations observed with extracellular stimulation (Abe and Tomita, 1968; Kuriyama et al., 1970). Most visceral smooth muscles have spontaneous spike discharge and moreover action potentials can easily be evoked by external stimulation. No spontaneous action potentials of the common carotid artery were observed and even if strong depolarizing current was applied to the arterial strip, action potentials were never seen. The characteristic absence of action potentials of the common carotid artery might be due to the remarkable rectifying property of this artery which was abolished by TEA. The effects of TEA on the voltage-current relation of the smooth muscle of the artery were similar to those on some other excitable tissues (Tasaki and Hagiwara, 1967; Armstrong, 1967; Stanfield, 1968; Ito, Kuriyama, and Sakamoto, 1970). Crustacean muscle (Fatt and Ginsborg, 1958) and end plate membrane in the nerve-muscle junction of rat sartorius (Katz and

Miledi, 1967) cannot produce the spike during cathodal stimulation in normal physiological solution. However, action potentials of large amplitude are triggered by applied outward current across those membranes in TEA-containing isotonic solution. The response of the smooth muscle of the common carotid artery in TEA solution to a strong outward current was only local depolarization which never developed into a spike. These results suggest that the smooth muscle of this artery has very stable electrical properties. TEA produced remarkable phasic contraction of the artery in isotonic Krebs solution, suggesting production of action potentials not only in hypertonic solution but also in isotonic solution (Mekata, unpublished observation). Sucrose gap or microelectrode records of large arteries stimulated with high potassium (Keatinge, 1968), epinephrine (Keatinge, 1964; Mikata, unpublished observation), norepinephrine (Keatinge, 1964), histamine (Keatinge, 1964), the absence of sodium (Keatinge, 1968), and low calcium (Keatinge, 1968) as well as with TEA (present experiments) have indicated that action potentials can be induced. Further investigations are required in order to understand the mechanism of spontaneous spike discharge of the smooth muscles.

The results obtained by external stimulation in the present experiments strongly suggest that the smooth muscle of the rabbit common carotid artery has cable-like properties. The current applied externally spreads in only one dimension longitudinally, because the fibers run parallel and are polarized to the same extent, so that there is no current flow through the transverse interconnections, while the current applied by an intracellular electrode spreads in three dimensions, since the muscle fibers are electrically interconnected through low resistance pathways (Tomita, 1966 *b*, 1967). Therefore when estimating membrane constants, it is convenient that the tissue can be taken as a simple core when conductor-polarized by external electrodes even though the structure of the tissue is complex as in other smooth muscles. Since both spatial decay of electrotonic potential and the time to reach half-amplitude were linearly related to distance from the partition in the present experiments, it is reasonable that infinite cable equations can be applied to a strip of the artery polarized by the external electrode.

The calculated values of the specific membrane resistance [$R_m = (2/a)R_i \cdot \lambda^2$] and capacitance [$C_m = (\tau_m/R_i) \cdot (a/2\lambda^2)$] are changed by the assumed value of the internal resistance. Therefore, in order to compare the membrane constants of the common carotid artery with those of other excitable cell membranes, R_m/R_i and $R_i C_m$ of this artery should be compared with those of other tissues. R_m/R_i of the common carotid artery, which is about 3.0 cm or 2.0 cm (taking λ as 1.21 mm; radius as 1 μ [Rhodin, 1962] or 1.5 μ [Prosser, Burnstock, and Kahn, 1960]), is similar to those of visceral smooth muscle measured previously. (2.1 cm for guinea pig taenia coli [Abe and Tomita, 1968]; 1.2 and 2.0 cm for the antrum longitudinal muscle and circular muscle of guinea pig

stomach, respectively [Kuriyama et al., 1970]; 0.66 cm for guinea pig rectum [Kuriyama and Mekata, 1971]; 4.4 cm for guinea pig vas deferens [Tomita, 1967].) $R_i C_m$ of this artery was calculated from the space constant of 1.21 mm, the time constant of 238 msec, and the radius of the muscle cell of 1.0 or 1.5 μ . The calculated values were 0.81 msec/cm or 1.22 msec/cm, respectively and are within the range of those of some other smooth muscles (0.49 msec/cm for guinea pig taenia coli [Abe and Tomita, 1968]; 0.23 msec/cm for the guinea pig vas deferens [Tomita, 1967]; and 1.12 msec/cm for the guinea pig rectum [Kuriyama and Mekata, 1971]. The similarity of R_m/R_i and $R_i C_m$ of the smooth muscle of the common carotid artery to those of the visceral smooth muscles may indicate that there is not much difference between the resting biophysical properties of the membrane of the visceral and vascular smooth muscles.

If conduction is brought about by local circuit current in a fiber with cable properties, the conduction velocity (v) is proportional to a factor $v = S' \lambda \sqrt{(R_m)'/R_m/\tau_m}$ (Katz, 1948), where S' is a safety factor, R'_m is the active membrane resistance, R_m is the resting membrane resistance, λ is the space constant, and τ_m is the time constant. If the conduction velocity of the common carotid artery in the presence of TEA is 1.77 cm/sec, this is about one-fourth that of taenia coli. The slow conduction velocity of the common carotid artery may be explained by a large τ_m , which is about twice that of taenia coli, and a low safety factor, which corresponds to the maximum rate of the spike rise (the common carotid artery, 0.29 v/sec; the taenia coli, 7 v/sec). The similar value of the space constant obtained in both the isotonic and hypertonic conditions might indicate an increased internal resistance of the muscle cells which is proportional to the increased membrane resistance in the hypertonic solution. The increased time constant of the membrane and no change of space constant in the hypertonic solution indicate that membrane resistance increases in hypertonic solution.

The nexus which is considered to be the low resistance path for cell-to-cell propagation seems to be absent in the large elastic artery of adult animals (Keech, 1960; Karrer, 1961). However, the very success of the sucrose gap (Keatinge, 1964) methods of electrical recording from large arteries indicates that electrical connections must exist between the muscle cells. The space constant of the tissue (about 1.1–1.4 mm) is much longer than the cell length (30–150 μ) (Rhodin, 1962; Prosser et al., 1960). Good synchronization of action potentials recorded from different positions on the arterial strip further suggested that electrical transmission exists between smooth muscle cells of the rabbit common carotid artery. The absence of conducted spontaneous contractions in the majority of arteries under most circumstances led Bozler (1948) to classify vascular smooth muscle as multiunit smooth muscle. Prosser et al. (1960) have correlated the inability of pig carotid arteries to conduct a

contraction and to respond to stretch with contraction (Burnstock and Prosser, 1960 *a,b*) with the structure of the artery. Both are considered to be properties of multiunit muscles. However, results in the present experiments strongly suggest that the common carotid artery is a smooth muscle of single unit type.

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