Electromechanical Coupling in Tubular Muscle Fibers

II. Resistance and Capacitance of One Transverse Tubule

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ABSTRACT In tubular muscle fibers of the yellow scorpion the transverse tubules are arranged in a radial symmetry. This particular morphology, enables one to derive values for electrical components of one transverse tubule (TT) by treating the TT as a core conductor rather than a complex network. The electrical properties of tubular muscle fibers were completely characterized and analyzed by measuring two independent functions of frequency, i.e., the characteristic impedance and the propagation function. The impedance of a single tubular muscle fiber was determined with microelectrodes over the frequency range 1 Hz to 1.5 kHz. The results were fitted to a possible equivalent circuit model which is based on morphological evidence. The average component values for this model are: $R_\ell = 209 \, \Omega \cdot \text{cm}$, $R_m$, and $R_T = 980 \, \Omega \cdot \text{cm}^2$ (referred to unit area of surface membrane), $C_m$ and $C_T = 0.9 \, \mu \text{F/cm}^2$, and $R_L = 103 \, \Omega \cdot \text{cm}$. Relating the equivalent circuit to ultrastructure shows that the average component values are consistent with the hypothesis that the TT is open to the extracellular medium, the electrical capacity of surface and TT membranes is about $1 \, \mu \text{F/cm}^2$, and the spread of surface depolarization into the TT is attenuated by about 25%.

INTRODUCTION

The electrical properties of the transverse tubules in skeletal muscle fibers, are of great interest since the tubules conduct the activating impulse inward from the surface membrane. In tubular muscle fibers of the scorpion, one of the activating impulses is a small depolarization (Gilai and Parnas, 1970), which presumably spreads passively inward along the membrane of the tubule. Then it is important to know the fractional decline in amplitude of the potential with distance and the velocity of the propagation of a certain threshold potential value for mechanical activation. These parameters depend on space and time constants of the transverse tubules, and therefore attempts were made to determine the values of relevant electrical components, by analyzing the response to
sinusoidal excitation (impedance measurements). The application of impedance measurement techniques to frog muscle fibers was lately reviewed by Valdiosera et al. (1974a). Some of their results are in quantitative disagreement with data of previous studies (Valdiosera et al., 1974c, Table IX). This might have arisen from the complicated structure of frog muscle fibers and the lack of precise morphometric data. Since the approach of impedance measurement was never applied to invertebrate muscle fibers, it was felt that a more simple muscle from a primitive animal would help to elucidate some of the discrepancies.

It is generally accepted that nerve and long muscle fibers have distributed electrical properties (Cole, 1968). That is, the electrical behavior is described by an equivalent circuit model with an infinite number of components distributed uniformly throughout their length. However, a closer look at muscle fibers reveals that only the electrical properties of the surface membrane are distributed along the sarcoplasmic core, and at regular intervals along the fiber, there are discrete “lumped loading points” derived from the transverse tubular system (T system) (Huxley and Taylor, 1958). Thus, different infinitesimal lengths of fiber have different electrical properties and the components involved are not uniformly distributed. If the entire muscle fiber is treated like a distributed core conductor (Falk and Fatt, 1964), then one must treat the properties of the T system as if the tubules are dispersed throughout the entire volume of the fiber (Adrian et al., 1969; Peachey and Adrian, 1973) although the structural evidence shows they are not. Another way to describe a muscle fiber is used here; a fiber is described as a recurrent structure made of many identical sarcomeres. Each of these sarcomeres could be referred to as a four-terminal box and the complete transmission line is therefore made up of a large number of four-terminal networks connected in a chain or cascade. This way of viewing the muscle fiber as a transmission line reduces the long distributed line to a large number of lumped-constant networks. The system as a whole becomes homogeneous and thus enables one to derive a simple consistent analytical method for the determination of the passive electrical constants of the membrane system. A comparative rigorous analysis of the approximation involved in the lumped-constant theory (Gilai 1974) reveals that a muscle fiber can be described as a cascade of lumped networks and an error of about 0.1% is introduced at low frequencies (up to 10 kHz). Lately, Nakajima and Bastian (1974) have reported that it is possible to regard their “artificial node” which is some 180 μm long as a lumped network with an error of 0.1%.

In tubular muscle fibers it is possible to regard the transverse tubular system as a set of known number of cylindrical core conductors which are radially arranged and are continuous with the surface membrane and are open to the extracellular medium (Gilai and Parnas, 1972). This particular morphology greatly simplifies the electrical analysis. The results of the present investigation clearly support the idea that the transverse tubules are open to the extracellular space and that the luminal conductivity of the tubules is comparable with the bathing solution, whereas the conductivity of the sarcoplasm is about twice that of the bathing solution. Moreover, the capacity of the surface and tubular membranes is approximately 1 μF/cm².
THEORY

Fundamental Relations in a Lumped Sarcomere

In order to derive the fundamental relationship between voltage and current in one sarcomere, a few postulates must be dealt with in order to gain some knowledge of the limitations of the theory and the approximations involved in simulating a muscle fiber with electrically cascaded, lumped recurrent networks. There are many types of recurrent networks encountered in communication systems (Shea, 1929). The one which is commonly called "balanced ladder network" (Royal Signals, 1947) requires the fewest assumptions to be made: 

(a) A striated tubular muscle fiber is a uniform cylindrical system consisting of two parallel conductors and composed of repetitive, identical sarcomeres in which the sarcoplasm dimension and cross-section geometry remain fairly constant throughout its length. 

(b) The number of sarcomeres is infinite. This is a reasonable assumption for long skeletal muscle fibers, if one considers that small changes in membrane potential do not produce potential changes at the ends of the fiber. (Tubular fibers [Gilai and Parnas, 1970] are 7 mm long and their space constant is less then 1 mm.) 

(c) The longitudinal and transverse currents in a sarcomere flow perpendicular to each other. The total instantaneous currents in the sarcoplasm and the extracellular fluid are equal in magnitude and flow in opposite directions, provided that the location of the sarcomere is remote from the current source at least a distance which is twice that of the fiber radius (Eisenberg and Johnson, 1970; Table 2). Consequently any transverse section through a sarcomere has a unique value of potential difference between the sarcoplasm and the extracellular fluid. 

(d) The length of a sarcomere \( H \) is short relative to the current wavelength, therefore the electrical behavior of a sarcomere can be described by lumped electric network components which are made up of admittance elements connecting the inside and the outside of a sarcomere and an internal pure resistance path (Mobley et al., 1974). This structure can be represented conveniently by a T-section network. The transmission line resulting from such an arrangement is completely characterized by two independent functions of frequency: the characteristic impedance \( Z_0 \) (ohms) and the propagation function \( \theta \) (Guillemin, 1935; Chap. 4).

Common Inside-Outside Admittance \( Y \)

We have represented a sarcomere of a muscle fiber as a linear lumped network structure. This structure should have all the components necessary to represent the pathways of current passing within a sarcomere. It is generally agreed that there exist two such pathways, namely, longitudinal and transverse. This is essentially the model proposed by Falk and Fatt (1964) and discussed elsewhere (Sandow, 1965; Eisenberg, 1971). The general idea, based on morphological evidence, is that the transverse current is related to the longitudinal current in the sense that they sum up in a common node which is the external medium conductor (Fig. 1).

The longitudinal current is that applied to the muscle fiber which passes along its core before it leaks away through the surface membrane. In other words this current produces a potential drop across the internal resistance \( R \) (ohms) of the sarcoplasm as well as the lumped admittance \( Y_m \) (mhos) of the surface membrane involved. \( Y_m \) consists of a parallel resistance \( r_m \) (ohms) and capacitance \( c_m \) (farads), as represented schematically in Fig. 10. It is convenient to express the components of \( Y_m \) with a complex frequency variable \( s \), thus

\[
Y_m = \frac{1}{r_m} + s c_m. \tag{1}
\]
The transverse current is that current passing along the transverse tubule (TT) which subsequently leaks to the lumen of the TT (which is open to the outside) through the tubular membrane. Thus this current produces a potential drop across a resistance which may be the luminal resistance \( r_L \) (ohms per centimeter)\(^1\) and the tubular membrane admittance \( Y_w \) (mhos per centimeter) (Fig. 1). \( Y_w \) like \( Y_m \), can be regarded as a parallel combination of resistance \( r_f \) (ohm-centimeters) and capacitance \( C_T \) (farads per centimeter).

\[
\tilde{Y}_w = \frac{1}{r_f} + sC_T. \tag{2}
\]

It follows that \( r_f \) and \( Y_w \) are the components which form the input admittance \( \tilde{Y}_f \) (mhos) of the TT.

\[
\tilde{Y}_f = \frac{1}{\sqrt{(r_f Y_w)}}. \tag{3}
\]

This admittance is actually loading the longitudinal pathway in a manner parallel to \( Y_m \), therefore the common inside-outside admittance is given by

\[
Y = Y_m + \tilde{Y}_f \text{ (mhos)}. \tag{4}
\]

In order to simplify the mathematical expressions, all of the muscle fiber components could be expressed by a single function. Using the engineering notation for lumped networks (Van Valkenburg, 1960), the general transfer function \( \mathcal{A} \) is defined as the ratio of driving-point \( z_{12} \) to transfer \( z_{22} \) impedances (see Appendix). Or in terms of the T-network components

\[
\mathcal{A} = \frac{z_{22}}{z_{12}} = \left( \frac{1}{2\sqrt{R}} \right) Y + 1. \tag{5}
\]

**Propagation Function and Characteristic Impedance**

If the number of such T networks connected in a chain is infinite, the impedance at any point along the chain is the complex characteristic impedance \( Z_0 \). A finite chain loaded at its ends with \( Z_0 \) is said to be correctly terminated. Thus, the relation between \( Z_0 \) and the muscle fiber components is given by

\[
Z_0 = \frac{\mathcal{A}}{Y} \tag{6}
\]

(Appendix). The relationship between output and input currents for each network is defined as the propagation function per network

\[
\theta = \ln \left( \mathcal{A} + (\mathcal{A}^2 - 1)^{1/2} \right), \tag{7}
\]

(Guillemin, 1935; equation 417). This propagation function may be referred to as the iterative propagation function to distinguish it from \( y \) (Falk and Fatt, 1964), which is the propagation function per unit length of fiber with distributed components. \( \theta \) (the principal value of the logarithm) is a complex number with real and imaginary parts defined by the relation \( \theta = \alpha + j\beta \) where \( j = \sqrt{-1} \), \( \alpha \), is commonly called the attenuation coefficient,\(^2\) and \( \beta \) is the phase coefficient of a sarcomere. It is important to note that the

\(^1\) The barred letter symbol is used to designate distributed components.

\(^2\) In distributed systems the reciprocal of the attenuation coefficient per unit length is known as the effective AC space constant \( \lambda_0 \) (Falk and Fatt, 1964, equation 4; Schneider, 1970, equation 5; Eisenberg and Johnson, 1970).
propagation function of \( n \) sarcomeres in a cascade equals \( n \) times that per sarcomere and the characteristic impedance is independent of \( n \).

Both \( \theta \) and \( Z_0 \) include the parameter \( \mathcal{A} \). Therefore determination of either one is sufficient for the characterization of membrane properties. However, \( \theta \) was found to be a much more sensitive measure than \( Z_0 \) to small changes in circuit components.

**METHODS**

**Preparation**

The preparation used in these experiments was the long closer muscle (Gilai and Parnas, 1972) of the claw in the yellow scorpion *Leiurus quinquestriatus H.et E.* The closer muscle was exposed after removing the whole femoral cuticle together with nerves, flexor, and extensor muscles of the tibia. The muscle was fixed at its proximal end to the bath, and its distal side was held with a Perspex hook connected to a micromanipulator which controls the length of the muscle fibers. The sarcomere length of the fibers mounted in this way was about 5 \( \mu \)m. Experiments were carried out on single fibers or a group of a few fibers. The bathing solution contains: 150 mM NaCl, 7.7 mM KCl, 5.0 mM CaCl\(_2\), 1.0 mM MgCl\(_2\), and was kept at room temperature at a pH of 7.0.

**Experimental Bath and Optical System**

The bath volume was 0.5–1.0 cm\(^2\) and had a built-in condensor lens with infrared filter. A fine three-dimensional manipulator (10 \( \mu \)m per turn) was attached to the bath enabling a movement of the muscle fibers into the optical field and to control fiber length before the experiment.

The polarization optical system consisted of two parts: (a) a bath stage having a rotating polarizing filter, and a condensor lens which enables dark-field illumination. The stage was mounted with a xenon lamp flash (Carl Zeiss, Inc., New York, Ukatron UN 60) of
short duration for photography and a low voltage tungsten lamp for observation; (b) a compound microscope (J. Swift & Son, London, England) with mounted camera was equipped with a dry long-working distance objective (X40, Vickers Instruments, Inc., Malden, Mass., A.E.I., numerical aperture 0.57) or a luminar objective (Zeiss, 16 mm, numerical aperture 0.2, F/2.5) with a total maximum magnification of ×1,000. The analyzer filter was placed in the real image space of the microscope body. Measurements of electrode separation and fiber diameter were taken from photographs.

**Electrodes**

Two microelectrodes were used, one to pass sinusoidal current into a fiber, the second to record the resulting membrane potential change. The current-passing electrode was filled with 2 M potassium citrate (pH 6), and had a resistance from 5 to 10 MΩ. The electrodes were passing currents of at least ±10 nA, being linear over the frequency range used for both inward and outward currents. The linearity was checked during the experiment by displaying the I-V relation on the oscilloscope. Results showing nonlinearities were rejected. The voltage-monitoring electrodes were filled with 3 M KCl and had a resistance from 5 to 25 MΩ. Both microelectrodes were carefully selected to have a low tip potential. The current and voltage bath electrodes were made with large chlorided silver wires inserted in 3 M Agar KCl and connected to the bath through a 2% Agar Ringer bridge. The voltage electrode resistance ($R_v$) and the current electrode resistance ($R_i$) were measured by connecting a known shunt ($10^{10} \Omega$) to the input of the voltage amplifier and obtaining with a voltage divider 1 mV for 1 MΩ resistance at DC, 2 and 1,500 Hz. Electrode resistance measurements were taken each time before impaling the fiber and after withdrawing the electrodes. Calculations were made using average values of $R_v$ and $R_i$. Results with variation of more than 5% in $R_v$ or in $R_i$ were not analyzed.

**Stimulus and Response Recordings**

The fiber was stimulated with sine wave current obtained from a voltage-controlled sweep generator (Wavetek, San Diego, Calif., model 144). The generator was operated in two different modes either by rectangular voltage pulses which generate successive frequencies from 1 to 1,500 Hz differing by a factor of about 1.4, or by a sweep of frequencies from 2.0 to 1,500 Hz. The duration of the sweep was set at 120 s/sweep, and a DC output proportional to the frequency was connected to the X axis of an x-y recorder (Hewlett-Packard Co., Avondale, Pa., model 7055B). The generator output was fed into a Counterimeter (Monsanto Co., St. Louis, Mo., model 101B) for precise determination of the frequency. The output wave amplitude was displayed on a six-beam oscilloscope (Tektronix, Inc., Beaverton, Ore., 565), and also connected to one terminal of a digital phase meter (AD-YU Electronics, Milwaukee, Wis., type 524A3). The current output of the generator was controlled so that the membrane potentials were kept smaller than 10 mV in order to remain in the linear region of the muscle current-voltage relation.

The circuit for measuring intracellular potential changes (amplifier in Fig. 2), was similar to that proposed by Freygang et al. (1967). Essentially, it contains two stages: (a) A high input impedance operational amplifier (Burr-Brown Research Corp., Tucson, Ariz., 3307/12c) was connected as a voltage follower ($R_v$ to positive input) with about unity gain. The output was connected to the second stage and was also driving the shield. (The shield was connected to the negative input). (b) A frequency-compensated amplifier (Fairchild Industries, Winston-Salem, N. C., A741) supplied the negative feedback to the follower. A circuit was added to this amplifier for DC offset. The output of the amplifier was fed into a differential amplifier with the necessary amplification. The output voltage amplitude ($U_o$) was displayed on the oscilloscope and was also connected to the second terminal of the phase meter (Fig. 2).
The current-monitoring circuit consists of a current to voltage converter similar to that used elsewhere (Moor, 1963; Schneider, 1970). The potentiometer connected to the positive input of the amplifier (Burr-Brown, 3307) serves as a DC voltage source used to offset tip and resting potentials. A calibrator (Bioelectric Instrument Inc., New York, model CA5) was connected to the same terminal to measure current or voltage gain and to calibrate electrode resistances. The output voltage of the current converter ($V_x$) was displayed on the $y$ axis of the oscilloscope to enable continuous observation of the linearity and resistance of the current-passing electrode.

**Compensation for Stray Capacitances**

In experiments employing sine wave currents, amplitude and phase must be accurately determined. Therefore, special measure must be taken to compensate or at least reduce capacitative artifacts produced by stray capacitances around the stimulating and recording systems. The capacity between the voltage and current microelectrodes ($C_4$ in Fig. 14) is critical for accurate measurements. Therefore attempts were made to keep $C_4$ as low as possible by placing a thin shield between the voltage and current electrodes and driving the shield with the output of the follower. A complete neutralization of the interelectrodes' coupling capacity was done by the same method employed by Freygang et al. (1967) and Schneider (1970), i.e., subtracting the input signal (after phase and amplitude correction) from the output signal. Compensation of the effective input capacity of the follower ($C_4$ Fig. 14), was achieved by connecting the voltage microelectrode to the follower with a short coaxial lead whose shield was driven in phase with the signal. The feedback circuit ($R_f$ Fig. 14), reduces the effect of input capacity even further. The capacitances between the microelectrodes and bath ($C_2$ and $C_3$ Fig. 14) are proportional to the depth of electrodes' immersion in the bathing fluid (Nastuk and Hodgkin, 1950), and to the tip potential of the electrodes (Agin, 1969). Therefore the bathing fluid was kept as shallow as possible, and the electrodes were selected to have low tip potential and resistance.

The effectiveness of the compensation procedure was tested just before the current

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**Figure 2.** Block diagram of experimental setup. Further details are given in text.
electrode was inserted into the fiber, by applying a sweep of current at frequencies from 2 to 1,500 Hz, with a greater amplitude than that used after impaling the fiber, and recording the phase shift of $U_o$. It was found that the phase shift in the compensated circuit depends on the distance between current and voltage electrodes. At the shortest distance measured (50 μm) the phase error was about 1° at 1,500 Hz, and negligible at low frequencies. Usually, the interelectrode distance was longer (up to 1,255 μm, see Table I) and a phase error was not detected.3

**Determination of Propagation Function $\theta$ and Characteristic Impedance $Z_o$**

The voltage transfer function $E$ is a complex quantity with a modulus $|U_o/U_i|$ and an angle $\psi$. At a single frequency the function can be represented in the trigonometric form as

$$E = \frac{|U_o|}{|U_i|} (\cos \psi + j \sin \psi).$$ (8)

The value of $E$ was determined for each frequency from photographs of $U_o$ (output voltage) versus $U_i$ (input voltage), and the phase angles ($\psi$) were read from a digital voltmeter (N.L.S. Inc., Del Mar, Calif., Series X3) measuring the output of the phase meter (Fig. 2). $E$ is an exponential function of the number of sarcomeres ($n$) separating the voltage from the current electrodes. By measuring voltage displacement at two different numbers of sarcomere separation ($n_1$ and $n_2$), it is possible to calculate the propagation function. Since $E_1 = ve^{-n_1\theta}$ and $E_2 = ve^{-n_2\theta}$, where $v = (\alpha R_f Z_o)/(R_r(2R_l + Z_o))$ (Eq. 31 in Appendix). Thus, on keeping $v$ constant for each frequency one can obtain $\theta$ (per sarcomere) from the relation $E_1e^{n_1\theta} = E_2e^{n_2\theta}$ or

$$\frac{1}{n_2 - n_1} \ln \left( \frac{E_1}{E_2} \right).$$ (9)

The characteristic impedance was then readily calculated for each frequency using rearrangement of Eq. 30.

$$Z_o = \frac{2R_r R_l E}{\alpha R_f \exp(-n\theta) - ER_r}.$$ (10)

**Determination of Internal Resistance $R$ and the Common Admittance $Y$**

A symmetrical four-terminal network structure is completely characterized by two independent functions of frequency. It should be emphasized that when measurements are taken from muscle fiber at a negligible interelectrode separation (Valdiosera et al., 1974 b), the equivalent network is regarded as one terminal-pair network and a single function of frequency is sufficient to describe the network (Van Valkenburg, 1960).

$Z_o$ and $\theta$ are the observed functions calculated from Eqs. 10 and 9, respectively. These functions are related to the network components by the following equations

$$e^\theta = \mathcal{A} - (\mathcal{A}^2 - 1)^{1/2}; Z_o = (\mathcal{A}^2 - 1)^{1/2}/Y,$$

(Eqs. 7 and 6), where $\mathcal{A}$ is a dimensionless transfer function related to $\theta$ by

$$\cosh \theta = \mathcal{A},$$

using the hyperbolic function identity $\sinh \theta = e^\theta - \cosh \theta$, rearranging and subtracting the above equation gives

3 Lately, Valdiosera et al. (1974 a) have presented a detailed consideration of the experimental measurements necessary to confirm the validity of impedance measurements.
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\[ Y = \frac{\sinh \theta}{Z_0}, \]  

(11)

when \( \theta' \) is expressed explicitly by the network components, i.e., \( \cosh \theta = 1 + \frac{1}{2} RY \) (cf. Appendix) or \( RY = 2 \cosh \theta - 1 \) dividing the last two equations from which

\[ R = 2Z_0 \tanh \frac{\theta}{2}. \]  

(12)

**Fitting Observed Quantities to a Given Model**

The main technique is to find values for a set of unknown circuit parameters in such a way that a set of given equations for the admittance and internal resistance may be satisfied as nearly as possible. A satisfactory solution is taken when the sum of the squares of the deviation between measured and theoretical functions is a minimum. The function minimized was

\[ F = \sum_{M} \left[ \left( Y_{\text{model}} - \frac{\sinh \theta}{Z_0} \right)^2 + \left( R_{\text{model}} - 2Z_0 \tanh \frac{\theta}{2} \right)^2 \right], \]  

(13)

where \( M \) is the number of observations (i.e. frequencies) at which measurements were taken. \( Y_{\text{model}} \) and \( R_{\text{model}} \) are the admittance and the internal resistance of a particular model to be fitted. \( \theta \) and \( Z_0 \) are the observed propagation function and the characteristic impedance.

The computation of the minimized function, i.e. phase angle and absolute value of the term in parentheses, was done by a computer (C.D.C. 6600) using a modified quasi-Newton method. There are other methods for finding the minimum of the phase angle functions (Valdiosera et al., 1974 b; Schneider, 1970). However, this method is one of the variable metric methods (VMM) proposed by Fletcher and Powell (1963), and the original algorithm was modified by Mathews and Davies (1969). It was found suitable for the present analysis since it enables repetition of the fitting routine for each fiber separately in a fast and economical way. Values of phase angle of \( F \) obtained by a double precision are given in Table I. The component values obtained for \( Y_{\text{model}} \) and \( R_{\text{model}} \) were used in Eqs. 5 and 7, in order to demonstrate a satisfactory solution of Eqs. 13 (cf. Fig. 11).

**RESULTS**

**Tubular Muscle Fiber**

The ultrastructure of tubular muscle fibers of scorpion reveals several morphological features which are of great interest for the research of membrane passive electrical properties (Gilai and Parnas, 1972). The fibers have a remarkably symmetrical organization of the surface and transverse membrane system which follows the radial symmetry of the lamellar fibrils. The surface membrane (SM) appears to be simple and smooth, unlike the complicated structural components of the SM, such as the caveolae found in frog fibers (Dulhunty and Franzini-Armstrong, 1974).

A cross section of such a fiber at the region of overlap of the thick and thin filaments shows (Fig. 3), that the TT are straight invaginations of the SM and are open to the extracellular space. The openings are evenly spaced along the fiber circumference. Most of the tubules could be traced down to the central cytoplasmic core (Fig. 4).
TABLE I
EXPERIMENTAL MEASUREMENTS

| Muscle fiber | RP (mV) | Radius (μm) | N1 | N2 | F \times 10^{-9} |
|--------------|---------|-------------|----|----|-----------------|
| 12           | 67      | 32          | 10 | 76 | 3.7             |
| 14           | 64      | 31          | 36 | 98 | 1.8             |
| 15           | 62      | 25          | 52 | 104| 1.4             |
| 17           | 63      | 29          | 14 | 68 | 5.3             |
| 21           | 63      | 31          | 20 | 52 | 12.2            |
| 25           | 66      | 27          | 32 | 251| 2.6             |
| 27           | 65      | 32          | 41 | 85 | 11.2            |
| 30           | 67      | 30          | 25 | 122| 1.0             |
| Mean         | 65 (1)  | 30 (1)      |    |    |                 |

Numbers in parenthesis are ± SEM (n = 8). N1, N2, are the number of sarcomeres between current and voltage microelectrodes. F is phase angle of term in Eq. 13.

Thus, one can look upon the cross section of such a fiber as being built of, or divided into, similar pie-shaped slices (i.e. sectors), each of which is bisected by one transverse tubule (as in Fig. 3). And so the surface membrane of such a fiber is a mosaic of quadrangular areas with a TT opening at approximately the center of each area. The involvement of only one TT in each slice makes it possible to analyze with a high degree of accuracy the component properties of the tubular membrane. Such a sliced cross-sectional aspect immediately implies that the electrical properties of one sarcomere are a simple product of the properties of one slice and the number of slices in a cross section, since all are in parallel. Thus, if Ym (Eq. 1) is regarded as the surface membrane admittance associated with one TT, then Y could be determined using Eq. 4 and the number K of TT in a cross section

\[ Y = K(Y_m + \bar{Y}_T). \]  

The derivation of specific values for the various components is based on the following morphological data:

| Index | Dimension | Mean | ±SE |
|-------|-----------|------|-----|
| H     | Length of sarcomere | μm   | 5.0 | 0.5 |
| K     | Number of TT in cross section | 143 | 16  |
| L     | Length of one TT | μm   | 15  | 5   |
| S     | Surface area of TT | μm² | 10.9| 3.7 |
|       | Cross-section area of TT | μm² | 0.004|

The method of determining the various morphological parameters followed the procedure of Gilai and Parnas, 1972. The only difference is that the results presented here are average measurements from nine tubular muscle fibers, and so the length of TT was found to be somewhat shorter than previously reported. Since the parameters were not measured with a specific technique of structural analysis, it would be difficult to evaluate the errors involved.
FIGURE 3. Cross section of the periphery of tubular muscle fiber at the region of A-I overlap. The SM appears smooth and penetrates into the fiber to form a TT. Note alternate arrangement of diadic structures. × 65,000.

Characteristic Impedance and Propagation Function

The experimental observation presented shows variation of $Z_0$ and $\theta$ with a limited range of frequency. Some difficulty was experienced with such measure-
ments, namely the variation of resting potential over the period while results were being obtained from two different locations in the fiber. It was found that only one-third of the observed fibers showed small variations of resting potential while in the rest of the fibers it sometimes dropped to 50%. Thus recordings of the impedance magnitude were taken only from fibers showing resting potential distortion of up to 10%, the others were rejected. Changes in the resting potential were usually accompanied by a drop in the low frequency impedance magnitude. A straightforward explanation for this was given by Falk and Fatt (1964) referring this distortion to the shunting path and the convergent resistance introduced by damaging the fiber at the point of electrode insertion. It cannot be due to DC current from the oscillator since the backing current was carefully adjusted.

Another difficulty was found in keeping constant the electrode resistances. This condition was found to be important since the impedance magnitude is proportional to the electrode resistances. Therefore recording of the absolute value of these resistances enables one to reject results with more than 5% change in electrode resistance. However, the complete analysis was done only on eight
selected fibers which showed stable electrical properties (measured as the rate of phase drift at one frequency) throughout the course of experiment.

Determination of the complex voltage transfer function $E$ consists of measuring $\psi$ and $|E|$ at different frequencies and number of sarcomeres (Table I). The variation of $\psi$ in one cell at all the measured frequencies is presented in Fig. 5. The rate of change of $\psi$ with the number of cascaded sarcomeres can be evaluated by plotting observed values from different fibers obtained at a frequency of about 1,500 Hz. This is shown in Fig. 6. The rate of change of $\psi$ amounts to 0.8° per sarcomere which is about the same value reported by Schneider (1970, Fig. 5), for measurements in frog fibers. $Z_0$ and $\theta$ are the two independent complex functions of frequency calculated in these experiments. Several functions may be derived from $Z_0$ and $\theta$ to represent their variation with frequency, such as $Z_0 = R_0 + jX_0$ (represented in an $X$-$R$ plot), $\xi = \arctan X_0/R_0$ (phase frequency plot), $|Z_0|$ (magnitude frequency plot) (Falk and Fatt, 1964). Since $\theta$ is a complex quantity ($\theta = \alpha + j\beta$) it can be represented in a similar manner. However, functions derived from $\theta$ were found to be the best because of their direct proportionality to the admittance elements. Thus, variation of $|\theta|$ with frequency shows (Fig. 7) that waves of different frequencies are attenuated with different amounts starting around 30 Hz. The phase frequency plot of the propagation function (Fig. 8) ($\phi = \arctan \alpha/\beta$) was found to be particularly sensitive to small variation in the component of the equivalent circuit model fitted to the observed data. The scatter of points increases with frequency and probably reflects a systematic error in the measurements, the scatter at the highest frequency being about 2°. In order to complete the observed data, values of $|Z_0|$ are plotted against log frequency in Fig. 9.

![Figure 5](image_url)

Figure 5. Plot of phasor transfer-voltage phase angle as a function of the number of sarcomeres separating voltage from current microelectrodes, at various frequencies indicated (in hertzes). Line drawn by eye. Muscle fiber 27.
Figure 6. The variation of transfer-voltage phase angle with the number of sarcomeres. Measurements taken from eight muscle fibers at frequency of about 1,500 Hz. Arrows indicate measurements from fiber 27.

Figure 7. Plot of propagation function magnitude $|\theta|$ against frequency. Muscle fiber indices corresponding to each symbol are as follows: □12, ○14, △15, ▽17, ▲21, ■25, ●27, ◇30.

Fitting Observed $Z_n$ and $\theta$ to a Possible Model

The equivalent circuit model shown in Fig. 10 is based exclusively on anatomical evidence available. That is, the SM is represented by the accepted model of parallel resistance ($r_m$) and capacitance ($c_m$). In this case the elements are lumped and represent the area of SM associated with one TT. Since the average number of TT in a cross section of the muscle fiber is known, the lumped electrical properties of the SM contained in one sarcomere could be determined using Eq.
Figure 8. Plot of phase angle of propagation function $\Phi$ at different frequencies. Symbols correspond to fiber indices as in Fig. 7.

Figure 9. Plot of characteristic impedance magnitude $|Z_\theta|$ at different frequencies for the same observations as in Fig. 7.

1. The TT is treated here as a simple one-dimensional core conductor with membrane components ($r_T$ and $c_T$) distributed along a resistance $(r_L)$ representing the material in the lumen of the tubules (Eqs. 1 and 2). The components of this model could not be simply calculated, since the contribution of $r_T$ to the TT input admittance is negligible even at low frequencies. However, because of the lack of additional information, i.e. ionic conductances of the membranes, the SM and TT membranes were assumed to have similar specific resistances (Adrian et al., 1969). Selecting this particular model for Eq. 13, the values of
Figure 10. Schematic drawing of part of transverse tubule and associated surface membrane, to show the presumptive relation between electrical and morphological structures involved in the paths of current flow. The longitudinal path consists of lumped components $r_m$ (ohms) and $c_m$ (farads), representing the electrical properties of a quadrangular area of surface membrane associated with one transverse tubule. $R$ (ohms) represents the sarcoplasm under this membrane. The transverse path consists of distributed components $g_T$ (ohm-centimeters cm) and $\tilde{g}_T$ (farads per centimeter) representing the membrane of a cylindrical transverse tubule, they are said to be distributed along a resistance $r_L$ (ohms per centimeter) representing the material in the lumen.

Electrical parameters of one TT and the associated surface membrane were calculated and are listed in Table II. The calculated values obtained for each fiber were used for the curve-fitting routine. An example of this procedure is shown in Fig. 11 and the difference between observed and calculated values is also shown. Derivation of specific values for the components in the circuit is based on anatomical measurements taken from EM sections (see Methods), therefore the calculated values should be regarded as approximate. The derived specific values are presented in Table III.

$R_m$ and $C_m$ are values of surface membrane referred to unit area of fiber surface. $C_T$ is the capacity per unit area of TT membrane and $R_L$ is the resistivity of the lumen of the TT. Using these values one can calculate various constants (Table IV) with the definitions listed by Adrian et al. (1969, appendix). $\lambda$ is the
TABLE II
BEST CIRCUIT PARAMETER VALUES OF ONE TRANSVERSE TUBULE
AND ASSOCIATED SURFACE MEMBRANE COMPUTED BY
NEWTON METHOD OF LEAST SQUARES

| Muscle fiber | \( R \) (\( \times 10^6 \)) | \( r_m \) (\( \times 10^3 \)) | \( r_m \) (\( \times 10^4 \)) | \( r_L^* \) (\( \times 10^7 \)) | \( F \) (\( \times 10^{-4} \)) | \( \Omega_m \) (\( \times 10^2 \)) | \( \Omega_m \) (\( \times 10^4 \)) |
|--------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| 12           | 1.63            | 3.17            | 3.07            | 1.12            | 5.10            | 2.67            |
| 14           | 1.74            | 1.65            | 3.04            | 1.30            | 4.69            | 2.54            |
| 15           | 2.67            | 2.51            | 2.43            | 1.28            | 4.77            | 2.55            |
| 17           | 1.98            | 3.07            | 2.79            | 1.21            | 4.89            | 2.60            |
| 21           | 1.74            | 2.04            | 3.01            | 1.29            | 4.68            | 2.50            |
| 25           | 2.30            | 2.25            | 2.63            | 1.30            | 4.75            | 2.61            |
| 27           | 1.61            | 1.51            | 3.20            | 1.58            | 4.76            | 2.63            |
| 30           | 1.86            | 2.12            | 2.92            | 1.28            | 4.70            | 2.56            |
| Mean         | 1.94            | 2.27            | 2.89            | 1.27            | 4.80            | 2.57            |
| ±SEM         | 0.13            | 0.23            | 0.11            | 0.03            | 0.05            | 0.02            |

\( r_L \), \( r_m \), \( r_L^* \) refer to unit length of transverse tubule.
* Calculated assuming similar specific value to \( R_m \).

apparent space constant and the AC propagation constant \( \Gamma \) was taken here as \( 1/\alpha \) at about 1,500 Hz.

DISCUSSION

The analysis of tubular muscle fibers presented here, correlates some expected linear electrical properties with anatomical structures presumably involved in the path of current flow. The electrical and mathematical analysis is based only on a few approximated assumptions and is relatively simple. The distributed electrical properties of muscle fiber could be approximated by a chain or cascade of lumped structures corresponding in their actual size to sarcomeres (Gilai, 1974). In such a treatment the partial differential equations describing the distributed properties are replaced by elementary circuit theory to describe the properties of one sarcomere. In order to analyze measurements of exciting phasor currents and voltage responses taken with two microelectrodes placed together, one must not neglect radial and circumferential effects of current spread (Valdiosera et al., 1974 b). However, if the distance between the electrodes is appreciable, the muscle fiber can be regarded as a one-dimensional cascade of sarcomeres, and the above-mentioned effects become unimportant (Eisenberg and Johnson, 1970). In that case, the large attenuation of potential must be considered by means of a frequency-dependent function such as the propagation function.

In tubular muscle fibers it is possible, due to the symmetry of the transverse tubular system, to divide the fiber cross section into similar imaginary slices and thus to reduce the complexity of the mathematical analysis involved. The approximation of each TT as cylindrical conductor enables the use of the “core conductor theory.” In frog, the T-system morphology is not sufficiently clear, thus approximating the T system with a homogeneous network of one kind or another (Schneider, 1970, Appendix 1; Adrian et al., 1969, appendix) leads to the use of a “disk” or other models which results from the solution of a
differential equation with polar and cylindrical coordinates. In the analysis presented, the TT is treated as an infinitely long distributed cable although it should be more appropriate to treat it as a short cable. As a first approximation the short cable nature of the TT has been ignored. This approximation is necessary because of the considerable complication introduced into the circuit analysis (see Appendix).

The Equivalent Circuit

The problem of evaluating electrical constants of muscle fibers is now limited to design a network model which will simulate with a high degree of precision the observed wave propagation characteristics such as characteristic impedance and propagation function. There are additional requirements for the model which impose restrictions on its nature, these are mainly physical data such as accurate morphometric values for dimensions of various anatomical structures, membrane dielectric composition, temperature dependence, etc. Since detailed figures for the nonpropagating features are not available in tubular fibers, this work is rather less comprehensive, and the resulting model is therefore regarded as an approximation. Despite the reservation, it is possible to outline some of the main features involved.

The equivalent circuit which one might expect from a structure described is shown in Fig. 10. The circuit is divided into two parts: the impedance of the structure associated with the outer surface of the fiber, and the impedance of the
structure associated with the TT. The complete circuit contains more than the minimum number of circuit components necessary to determine its impedance function. In this case the resistance path across the TT membrane is redundant and cannot be evaluated from the impedance measurements presented. Since no information concerning membrane conductances is available, it is possible to eliminate the redundant parameter (Falk and Fatt, 1964) or to assume that both membranes (surface and TT) have similar specific resistances (Adrian et al., 1969). The apparent specific membrane resistance derived in this way (i.e., $R_m = R_T$) is about 1 k$\Omega$-cm$^2$. For comparison, the specific membrane resistance found in frog fibers is 2–3 k$\Omega$-cm$^2$ (Schneider, 1970, Tables II, III; Valdiosera et al., 1974 c).

The sarcoplasmic resistivity ($R_s$) value of 209 $\Omega$-cm (Table III) is somewhat smaller than that reported previously. However, it may be noted that $R_s$ is about twice as high as the resistivity of the extracellular medium (assumed to be about 100 $\Omega$-cm), whereas the resistivity of the lumen of the TT ($R_L = 103$ $\Omega$-cm) is about equal. Hodgkin and Nakajima (1972) have reported, for frog fibers $R_s$ value of 169 $\Omega$-cm (extracellular resistivity 82 $\Omega$-cm) and Schneider (1970) found a much lower value, $R_s = 102$ $\Omega$-cm (in 7.5 mM K$^+$ Ringer). Another discrepancy is found with $R_s$ values in frog fibers, since Valdiosera et al. (1974 c) estimated $R_L$ to be about 190 $\Omega$-cm and Schneider (1970) found a value of about 300 $\Omega$-cm. These results are inconsistent with the hypothesis that the ionic content and mobility of the solution filling the lumen of the tubule is the same as that of the extracellular bathing solution.
It is important to realize that the value of $R_L$ in frog fibers is derived by using morphometric parameters reported by Peachey (1965) and various network factors\(^4\) (Schneider, 1970; Peachey and Adrian, 1973). The uncertainty of these parameters together with the unresolved structure of the mouth of the tubules were lately discussed by Valdiosera et al. (1974\(b\)). Since the analysis of electrical properties in tubular fibers does not depend on assumptions regarding the structure of the mouth of the TT and network factors, the results presented are more reliable.

Thus it is possible to outline various aspects associated with the radial spread of potential (Table IV). For example, assuming that junction potential of about 5 mV propagates electronically down the TT, it would reach the axis of the fiber with about 25% loss in its amplitude. Finally, it is felt that muscle fibers from primitive animals might elucidate some of the unresolved problems in E-C coupling.

APPENDIX

Current-Voltage Relation in One Sarcomere

A sarcomere includes the surface and transverse tubular system membranes existing between two "Z"-band striations. The membranes are represented as passive linear electrical components creating a T-structured four-terminal network (Fig. 12).

In dealing with such a network we are concerned with four quantities: $V_1, V_2, I_1, I_2$. Any two of them may be regarded as applied and the others may be expressed as linear functions of the other two. We are particularly interested in expressing the input quantities ($V_1, I_1$) in terms of the output ($V_2, I_2$). Since the sarcomere is symmetrical, only three of these parameters are independent and there is, thus, one relation between them and three suitable measurements provide all the possible information about the network. Referred to Fig. 12 the transmission equation is

$$I_1 = \frac{1}{z_{12}} V_2 - \frac{z_{22}}{z_{12}} I_2,$$

where $z_{22}$ and $z_{12}$ are driving point impedance and transfer impedance, respectively. If the T network is short-circuited on the output terminals, $V_2$ is zero and the transfer function is given by

$$\frac{I_1}{I_2} \bigg|_{V_2 = 0} = \frac{z_{22}}{z_{12}} = \mathcal{A},$$

(Leon and Wintz, 1970). $\mathcal{A}$ is thus, a complex dimensionless parameter which characterizes the network components. However, regarding the morphology of a sarcomere, the electrical components are: $R$ (ohms) which represents the resistance of sarcoplasm to longitudinal current flow and $Y$ (mhos) which represents the conductance of the leakage current (all referred to one sarcomere). Thus,

$$z_{11} = z_{22} = \frac{1}{2R} + \frac{1}{Y},$$

\(^4\) Mathias et al. (1975) recently modeled the T system of frog fibers as a mesh of miniature transmission lines. With the mesh model the luminal resistivity $R_L$ approximately equals $R_n$, the resistivity of the bathing solution.
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\[ z_{12} = \frac{1}{Y}. \]  

(18)

Substituting in Eq. 16 we get the transfer function in terms of the network components (Eq. 5)

\[ \mathcal{A} = \frac{1}{2} R Y + 1. \]

**Propagation Function**

A portion of a uniform recurrent structure is represented in Fig. 13. The voltages and currents at the junctions are subscripted from \( V_{n=0} \) and \( I_{n=0} \) to \( V_{n=n} \) and \( I_{n=n} \), where \( n \) is the number of sarcomeres. Given the network function \( \mathcal{A} \), the problem is to find analytic expression for current and voltage variations from one sarcomere to another along the structure of the muscle fiber. In the portion of the structure shown, \( I_n \) is considered first as the output of the preceding sarcomere and then as the input to the succeeding one. By the application of appropriate admittance functions to each network, the current at the \( n \)th sarcomere is

\[ I_n = -y_{21} V_{n-1} - y_{22} V_n = y_{11} V_n + y_{12} V_{n+1}. \]  

(19)

Since in symmetrical networks, \( y_{11} = y_{22} \) and \( y_{11}/y_{12} = -\mathcal{A} \) (from Eq. 16), the voltage equilibrium condition can be expressed as a difference equation

\[ V_{n-1} - 2 \mathcal{A} V_n + V_{n+1} = 0. \]  

(20)

A solution of this equation can be assumed to have an exponential form

\[ V_n = V^+ e^{-\theta n} + V^- e^{\theta n}, \]  

(21)

(Jordan, 1965) where \( V^+ \) is a phasor voltage coefficient having a value \( V_o \) when \( n = 0 \), and \( \theta \) is the complex propagation function per sarcomere. \( V^- \) is a voltage coefficient with a

![Figure 12](image12.png)

**Figure 12.** A lumped T network equivalent to one sarcomere. The specifications of phasor output currents \( I_2 \) and voltages \( V_2 \) in terms of input quantities \( I_1, V_1 \) are expressed as two independent functions of frequency, namely, characteristic impedance \( Z_0 \) and propagation function \( \theta \). The network components \( R \) (the internal resistance) and \( Y \) (the common inside-outside admittance) are completely characterized by \( Z_0 \) and \( \theta \).

![Figure 13](image13.png)

**Figure 13.** Part of a muscle fiber treated as an infinite chain of symmetrical four-terminal lumped networks. Each box represents a network of electrical components contained in one sarcomere and is numbered from \( n = 0 \) to \( n = \infty \). Currents \( I \) and voltages \( V \) at the junctions are indicated for each box. The impedance looking into such a chain is the characteristic impedance \( Z_0 \).
value \( V_n \) at \( n = \infty \) and therefore is regarded as \( V^- = 0 \). Substituting the resulting solution into Eq. 20 one finds the solution to be valid under the condition that

\[
V^+ e^{-n\theta} (e^\theta + e^{-\theta} - 2\delta) = 0,
\]

and the propagation function is found after factoring and rearrangement

\[
\cosh \theta = \delta.
\]

The use of hyperbolic identities \((e^\theta = \cosh \theta + \sinh \theta \text{ and } \sinh \theta = (\cosh \theta^2 - 1)^{1/2})\), enables a more explicit form for \( \theta \) which involves the network components

\[
e^\theta = 1 + \frac{1}{2} R Y + \left[(\frac{1}{2} R Y)^2 + R Y\right]^{1/2}.
\]

**Characteristic Impedance**

The input impedance of a recurrent cascade with an infinite number of structures is another definition of the characteristic impedance. Referring to Fig. 12 the input impedance is given by

\[
Z_{in} = \frac{1}{2} R + \frac{1}{Y} \left[\frac{(1/2 R + Z_o)}{1 + (1/2 R + Z_o)}\right],
\]

since \( Z_{in} = Z_o \), rearrangement of Eq. 25 gives

\[
Z_o = \left[(\frac{1}{2} R)^2 + R\right]^{1/2}/Y.
\]

Multiplying both sides by \( Y \) and introducing Eq. 5 gives Eq. 6

\[
Z_o = \frac{3 \delta^2 - 1}{2}^{1/2} Y.
\]

**Error Introduced by Approximating the TT as an Infinitely Long Cable**

When the attenuation coefficient \((\alpha)\) of a cable in consideration is negligible, the cable is not "properly" terminated and there are always reflected waves on the cable. Thus the impedance at every point of the line differs from the characteristic impedance \( Z_o \). The “impedance at every point” means the input impedance of the portion of the line on the terminal load side of the point. It is convenient to write an explicit expression for the normalized input impedance \( Z_{in}/Z_o \) of a length \( L \) of a cable:

\[
Z_{in} = Z_0/\cosh \gamma L = Z_o + \tanh \gamma L / \left[1 + (Z_o/Z_0) \tanh \gamma L\right].
\]

King (1965). Where \( Z_t \) is the terminal load impedance and \( \gamma = \alpha + j \beta \) is the propagation function. If the TT is regarded as an infinitely long cable then \( Z_t = Z_o \) and the formidable equation above reduces to \( Z_{in}/Z_o = 1 \), consistent with the assumptions made previously. The input impedance from the mouth of the TT side when the terminals on the other side are open-circuited (i.e. \( Z_t \) is infinite) is given by Eq. 27 as \( Z_{in} = Z_o \coth \gamma L \). Hence, this is the value of the driving point impedance. The transfer impedance coefficient is the ratio of terminal voltage \((V_t)\) to input current \((I_i)\) when the terminal current \((I_t)\) is zero. Thus the transfer impedance function \( (Z)\) is given by:

\[
Z = \frac{V_t}{I_i} \bigg|_{I_t = 0} = Z_o \frac{V^+ e^{-\gamma L} + (V^-/V^+) e^{\gamma L}}{V^+ (1 - V^-/V^+)}.
\]
(\(V^+\) and \(V^-\) are defined in Eq. 21.) For open circuit termination: \(V^-/V^+ = e^{-\gamma L}\).

The transfer impedance function for an infinitely long cable is given by Falk and Fatt (1964) and Schneider (1970, equation 1).

\[
Z = Z_0 e^{-\gamma L}. \tag{29}
\]

Thus, the error introduced by approximating the TT as an infinitely long cable can be extracted from Eqs. 28 and 29 and with the results obtained. The value of the characteristic input admittance of the TT based on Eq. 29 differed by only 10% from the value based on Eq. 28. About the same figure can be obtained by using the DC equation for short cable (Hodgkin and Nakajima, 1972, equation 8). However, Hodgkin and Nakajima (1972), working on semitendinosus fibers, have reported a deviation of 5% in their results.

**Equivalent Circuit of Experimental Apparatus**

The main parts of the block diagram shown in Fig. 2 are represented as a circuit in Fig. 14. Essentially, the circuit is equivalent to that used by Schneider (1970, Fig. 16 B) with the exception that the present circuit involves the analysis of a cascade of lumped structures terminated with \(Z_0\), rather than part of a distributed structure. The analysis of such a network shows that under the condition of compensation for stray capacitances all terms containing \(C_1\) to \(C_4\) become negligible at frequencies below 1,500 Hz (see Schneider, 1970, equations 39 and 44; Freygang et al., 1967, appendix 1). Lately, Valdiosera et al. (1974 a) have shown that an error of about 1° is introduced to the observed impedance at the frequency mentioned, when measurements are taken with two microelectrodes placed together. In that case a proper correction term should be introduced. However, in the circuit shown in Fig. 14, the separation of electrodes and the compensation procedure enables the following network analysis. For the input (left) side of Fig. 14

\[
U_{n=0} = \frac{U/Z_0}{R_1 + Z_0/2},
\]

![Figure 14](image)

**Figure 14.** A simplified diagram of stimulating and recording circuits. The muscle fiber is represented here as a chain of sarcomeres arranged in tandem and terminated on both sides with \(Z_0\). The number of sarcomeres between the current-passing electrode \(R_1\), and the voltage-recording electrode \(R_v\), is \(n\). The stray capacitances \((C_1-C_4)\) were carefully compensated (see Methods) and therefore have been omitted from the analysis of the network. The voltage-monitoring circuit was similar to that used by Schneider (1970) and Freygang et al. (1967).
and for the output, we first consider the potential at the nth sarcomere
\[ U_n = U_{n-1} e^{-n\theta}. \]

If the operational amplifier open loop gain \((-A)\) is very large, the output potential, is approximately
\[ U_o = U_n \frac{R_j}{R_i}, \]
substitution and rearrangement in the last equation and introducing the overall amplification \(a\) gives the voltage transfer ratio \((E)\)
\[ E = \frac{U_o}{U_i} = \frac{aR_j Z_o e^{-n\theta}}{R_i(2R_i + Z_o)}. \] (30)

At a given frequency, \(E\) varies exponentially with the number of sarcomeres (say \(n_i\), then
\[ E_1 = \frac{aR_j Z_o}{R_i(2R_i + Z_o)} e^{-n_i\theta}. \] (31)

It is a great pleasure to thank Professor I. Parnas for the illuminating discussion and Professor Shigehiro Nakajima for his suggestions and critical reading of the manuscript.

Received for publication 20 March 1975.

REFERENCES

ADRIAN, R. H., W. K. CHANDLER, and A. L. HODGKIN. 1969. The kinetics of mechanical activation in frog muscle. J. Physiol. (Lond.). 204:207.

AGIN, D. P. 1969. Electrochemical properties of glass microelectrodes. In Glass Microelectrodes. M. Lavallee, O. F. Schanne, and W. C. Hebert, editors. John Wiley & Sons, New York.

COLE, K. S. 1968. Membranes, Ions and Impulses. University of California Press, Berkeley, Calif.

DULHUNTY, A. F., and C. FRANZINI-ARMSTRONG. 1974. Caveolae as specialized structural components of the surface membrane of skeletal muscle. Fed. Proc. 33:1074.

EISENBERG, R. S. 1971. The equivalent circuit of frog skeletal muscle fibers. In Contractility of Muscle Cells and Related Processes. R. J. Podolsky, editor. Prentice-Hall, Inc., Englewood Cliffs, N.J. 73.

EISENBERG, R. S., and E. A. JOHNSON. 1970. Three dimensional electrical field problems, in physiology. Progr. Biophys. Mol. Biol. 20.

FALK, G., and P. Fatt. 1964. Linear electrical properties of striated muscle fibers observed with intracellular electrodes. Proc. R. Soc. Lond. B Biol. Sci. 160:69.

FLATCHE, R., and M. J. D. POWELL. 1963. A rapidly convergent descent method for minimization. Comput. J. 6:163.

FREYGANG, W. H., JR., S. J. RAPPORT, and L. D. PEACHEY. 1967. Some relations between changes in the linear electrical properties of striated muscle fiber and changes in ultrastructure. J. Gen. Physiol. 50:2437.

GILAI, A. 1974. Correlation between structure and function of tubular muscle fibers. Ph.D. Thesis. Hebrew University, Jerusalem, Israel.

GILAI, A., and I. PARNAS. 1970. Neuromuscular physiology of the closer muscles in the pedipalp of the scorpion Leiurus quinquestriatus. J. Exp. Biol. 52:325.
Gilai, A., and I. Parnas. 1972. Electromechanical coupling in tubular muscle fibers. I. The organization of tubular muscle fibers in the scorpion Leiurus quinquestriatus. J. Cell Biol. 52:626.

Guillotine, E. A. 1935. Communication Networks. Vol. II. John Wiley & Sons, London, England.

Hodgkin, A. L., and S. Nakajima. 1972. Analysis of the membrane capacity in frog muscle. J. Physiol. (Lond.). 221:121.

Huxley, A. F., and R. E. Taylor. 1958. Local activation of striated muscle fibers. J. Physiol. (Lond.), 144:426.

Jordan, C. 1965. The Calculus of Finite Differences. Chelsea, London, England.

King, R. W. P. 1965. Transmission-Line Theory. Dover Publications, Inc., New York.

Leon, B., and P. Wintz. 1970. Basic Linear Networks for Electrical and Electronics Engineers. Holt, Rinehart and Winston, Inc., New York.

Mathews, A., and D. Davies. 1969. A comparison of modified Newton methods. Comput. J. 14:299.

Mathias, R. T., C. Clausen, and R. S. Eisenberg. 1975. Mesh model of the electrical properties of the tubular system of skeletal muscle. Physiologist, 18(3):310.

Mobley, B. A., I. Leung, and R. S. Eisenberg. 1974. Longitudinal impedance of skinned frog muscle fibers. J. Gen. Physiol. 63:625.

Moor, J. W. 1963. Operational amplifier. In Physical Techniques in Biological Research. W. L. Nastuk, editor. Academic Press, Inc., New York. 6B:77.

Nastuk, W. L., and A. L. Hodgkin. 1950. The electrical activity of single muscle fiber. J. Cell. Comp. Physiol. 35:39.

Nakajima, S., and J. Bastian. 1974. Double sucrose-gap method applied to single muscle fiber of Xenopus laevis. J. Gen. Physiol. 63:235.

Peachey, L. D. 1965. The sarcoplasmic reticulum and transverse tubules of the frog's sartorius. J. Cell. Biol. 25:209.

Peachey, L. D., and R. H. Adrian. 1973. Electrical properties of the transverse tubular system. In Structure and Function of Muscle. G. Bourne, editor. Academic Press, Inc., New York. 2nd edition.

Royal Signals. 1947. Handbook of Line Communication. Her Majesty's Stationary Office, London, England.

Sandow, A. 1965. Excitation-contraction coupling in skeletal muscle. Pharmacol. Rev. 17:265.

Schneider, M. F. 1970. Linear electrical properties of the transverse tubules and surface membrane of skeletal muscle fibers. J. Gen. Physiol. 56:640.

Shea, T. E. 1929. Transmission Network and Wave Filters. D. Van Nostrand Company, Inc., New York.

Valdivosera, R., C. Clausen, and R. S. Eisenberg. 1974 a. The measurement of the impedance of frog skeletal muscle fibers. Biophys. J. 14:295.

Valdivosera, R., C. Clausen, and R. S. Eisenberg. 1974 b. Circuit models of the passive electrical properties of frog skeletal muscle fibers. J. Gen. Physiol. 63:432.

Valdivosera, R., C. Clausen, and R. S. Eisenberg. 1974 c. Impedance of frog skeletal muscle fibers in various solutions. J. Gen. Physiol. 63:460.

Van Valkenburg, M. E. 1960. Network Synthesis. John Wiley & Sons, Inc., New York.