

THEORETICAL CONSIDERATION OF
A POSSIBLE MECHANISM IN THE CONDUCTION PROCESS
OF THIN-SHEATHED NERVE FIBERS

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The propagation of a transverse disturbance along a tubular membrane enclosing a fluid medium and embedded in another is considered. It is shown that the velocity of propagation of such a disturbance can be identified with the velocity of the conduction process of thin-sheathed nerve fibers. The required values of the associated parameters, tension and pressure, appear not unreasonable. The results obtained indicate that experimental observations on the relation between the conduction velocity and the fiber diameter, as well as the effects of longitudinal stretching and transverse squeezing on the velocity of the conduction process in nerve, may be correlated on such a basis.

We consider the possibility of mechanical motion as a factor in the determination of the velocity of the conduction process in thin-sheathed nerve fibers. As indicated in the literature (Hill and Keynes, 1949; Tobias and Solomon, 1950; Solomon and Tobias, 1950; Tobias, 1950), there exists evidence to support the view that mechanical motion is a concomitant of electrical activity in nerve tissue. A mutual coupling between electrical and mechanical changes can be realized, for example, through a piezoelectric or electrostrictive mechanism.

It will be demonstrated in the succeeding analysis that the velocity of propagation of a transverse disturbance along a cylindrical membrane might be identified with the velocity of propagation of the conduction spike of a thin-sheathed nerve fiber. Numerical values of the requisite parameters are obtained during the course of the analysis. The picture developed is also in accord with other aspects of the conduction process. However, since associated electrical phenomena have not been incorporated into the theory the results should be regarded as suggestive in nature at the present time.

In order to develop a picture in which mechanical disturbances play a major role in the determination of the characteristics of the

conduction process of nerve tissue, it appears necessary to consider disturbances of a type which can be localized or guided along a cylindrical membrane. It does not appear feasible to develop a theory on the basis of longitudinal acoustic waves. Such waves would not be guided either along or inside a tube if the values of the acoustic parameters characterizing the external fluid are close to those of the internal fluid, when the tube has the properties of a thin membrane. Furthermore, the velocity of propagation of longitudinal waves in a liquid medium such as water is about 1500 meters per second. This is of the order of 50 times greater than any observed conduction velocities in invertebrate nerve fibers. Since the density of the material present in the nerve is in the neighborhood of 1 gram/cm³ the compressibility of the medium would have to be very much different from that of water solutions. Assuming that one could surmount these limitations, the variation of the conduction velocity with the radius of the fiber would lead to further complication.

It is possible to free one's self from all the above difficulties by developing a picture on the basis of the transverse vibrations of a

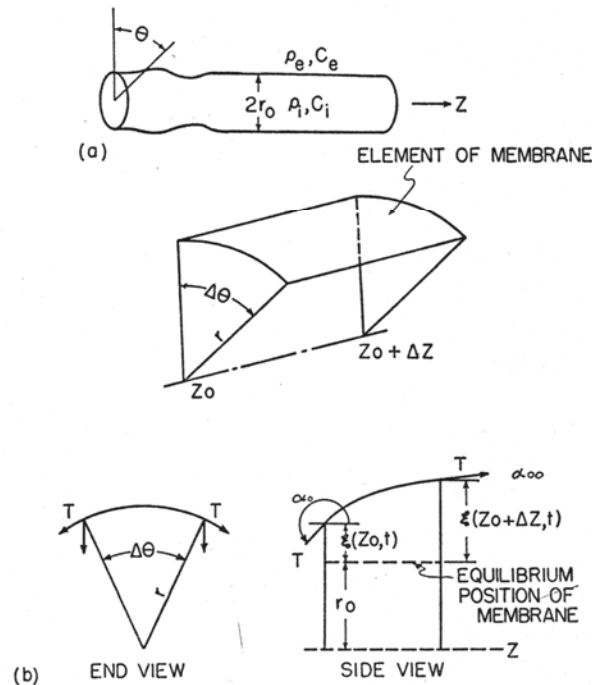


FIGURE 1. (a) A transverse disturbance on a cylindrical membrane of circular cross section. (b) Details indicating forces on an element of the membrane.

tubular membrane enclosing a liquid and embedded in an external fluid medium. A possible role of shear waves in the nerve conduction process has been considered by W. Sutherland (1905, 1906-07, 1908-09). The investigations of O. Frank (1926) on the vibrations of the walls of blood vessels are of interest in this connection, but are not sufficiently general to include the analysis presented here.

We consider a cylindrical membrane of circular cross section as illustrated in Figure 1a. The membrane is under tension, of magnitude T per unit length, perhaps as the result of an excess internal pressure. Its mass per unit area is designated by σ .† The density and acoustic velocity of the internal fluid are represented by ρ_i and c_i , respectively. The symbols ρ_e and c_e designate the corresponding quantities for the external fluid. We are concerned with the equations appropriate for discussing transverse vibrations of small amplitude on such a membrane with the associated disturbances in the surrounding media. It is sufficiently general for our present purpose to restrict the detailed discussion to a symmetrical disturbance, that is, one independent of the angle θ (Fig. 1).

Let us consider a small section of such a membrane as illustrated in Figure 1b. Let ξ represent the displacement of the membrane in the radial direction and let ΔP be the difference between the internal and external pressures, i.e., $\Delta P = P'_{i0} - P'_{e0}$. Then the forces acting on this element in the radial direction are

$$(i) \quad T r_{z_0} \Delta \theta \sin \alpha_0 + T r_{z_0 + \Delta z_0} \Delta \theta \sin \alpha_{00} \approx T \Delta \theta r_0 \left(\frac{\partial^2 \xi}{\partial z^2} \right)_{z_0} \Delta z$$

over the two arcs at z_0 and $z_0 + \Delta z_0$;

$$(ii) \quad -T \Delta z \Delta \theta$$

over the two elements parallel to the z axis, and

$$(iii) \quad \Delta P r_0 \Delta \theta \Delta z = (P'_{i0} - P'_{e0}) r_0 \Delta \theta \Delta z$$

because of the difference in pressure across the membrane. The dynamical equation then follows:

$$\frac{\partial^2 \xi}{\partial z^2} - \frac{1}{r_0} + \frac{P'_{i0} + P'_{e0}}{T} = \frac{\sigma}{T} \frac{\partial^2 \xi}{\partial t^2}. \quad (1)$$

Now the difference $P'_{i0} - P'_{e0}$ can be written as

$$P'_{i0} - P'_{e0} = \Delta P_0 + P_{i0} - P_{e0}, \quad (2)$$

†For list of symbols and their definitions see page 314.

where P_{i0} and P_{e0} are the deviations in pressure from the equilibrium values in the two media at the surface of the membrane caused by the disturbance on the membrane, and ΔP_0 is the pressure difference at equilibrium. The relation between the tension T and the equilibrium pressure difference ΔP_0 is given by

$$T = r_0 \Delta P_0. \quad (3)$$

Expression (1) then reduces to

$$\frac{\partial^2 \xi}{\partial z^2} + \frac{P_{i0} - P_{e0}}{T} = \frac{\sigma}{T} \frac{\partial^2 \xi}{\partial t^2}. \quad (4)$$

The same differential equation (4) is obtained if the tension is maintained by forces other than those arising from a hydrostatic pressure difference. Under the assumption that the displacement of the membrane is small, the equation appropriate for discussing the disturbance in the fluid media is the usual acoustic wave equation. We tabulate it here expressed in the symbols for the internal and external fluids:

$$\begin{aligned} \nabla^2 P_i &= \frac{1}{c_i^2} \frac{\partial^2 P_i}{\partial t^2}; \\ \nabla^2 P_e &= \frac{1}{c_e^2} \frac{\partial^2 P_e}{\partial t^2}, \end{aligned} \quad (5)$$

where P_i and P_e are the pressure deviations from the equilibrium values at any point in the media. The effect of viscosity is neglected. Usually the inclusion of viscous terms affects the expression for velocity only slightly and introduces an amplitude damping factor. An indication of the magnitude of the damping, resulting from viscosity, for small amplitude disturbances of the type discussed might be given by the damping factor of an acoustic disturbance of the same frequency. On the basis of observations at ultrasonic frequencies, it appears that the damping factor for the frequencies and path lengths involved here would be small. Since the membrane is circular in cross section, we express the Laplacian operator in cylindrical coordinates. (See, for example, Morse, p. 296.) It is convenient first to discuss solutions to (4) and (5) which are sinusoidal functions of time. We write

$$\begin{aligned} \xi &= \xi_A e^{j\omega t}; \\ P_i &= P_{iA} e^{j\omega t}; \\ P_e &= P_{eA} e^{j\omega t}. \end{aligned} \quad (6)$$

The expressions (4) and (5) then become

$$\begin{aligned} \frac{d^2 \xi_A}{dz^2} + \omega^2 \frac{\sigma}{T} \xi_A &= -\frac{P_{iA0} - P_{eA0}}{T}; \\ \frac{1}{r} \frac{\partial}{\partial r} \left(r \frac{\partial P_{iA}}{\partial r} \right) + \frac{\partial^2 P_{iA}}{\partial z^2} + \left(\frac{\omega}{c_i} \right)^2 P_{iA} &= 0; \quad (7) \\ \frac{1}{r} \frac{\partial}{\partial r} \left(r \frac{\partial P_{eA}}{\partial r} \right) + \frac{\partial^2 P_{eA}}{\partial z^2} + \left(\frac{\omega}{c_e} \right)^2 P_{eA} &= 0. \end{aligned}$$

A solution to the equations (7) which satisfies the requirements that (a) it approach zero as r approaches infinity and (b) there be no singularity at $r = 0$ is the following:

$$\begin{aligned} \xi_A &= a e^{-jk_z z}, \\ P_{iA} &= A_i I_0[(k_z^2 - (\omega/c_i)^2)^{1/2} r] e^{-jk_z z}, \\ P_{eA} &= A_e K_0[(k_z^2 - (\omega/c_e)^2)^{1/2} r] e^{-jk_z z}, \end{aligned} \quad (8)$$

where a , A_i and A_e are constants to be related to one another through the boundary conditions; I_0 and K_0 are Bessel functions of zero order which are especially suited to the problem since $k_z > \omega/c_i$ or ω/c_e . This latter relation is obtained as follows, $k_z = \omega/V_\omega$ where V_ω is the phase velocity for a sinusoidal disturbance traveling along the membrane. We are interested in phase velocities which are, in general, much smaller than the velocity of sound in the fluid media. This determines the direction of the above inequality.

In order to interrelate the amplitude constants and to determine the propagation constant k_z , we must apply the appropriate boundary conditions at the surface of the membrane, that is, the radial velocities of the fluid media at $r = r_0$ must equal the membrane velocity. Now the relation between the radial velocity, u_r , and the pressure is (see, for example, Morse, 1948, chap. v; note the sign change due to the choice of $e^{-j\omega t}$ in place of $e^{j\omega t}$ of this paper):

$$u_r = \frac{j}{\omega \rho} \frac{\partial P}{\partial r}. \quad (9)$$

We obtain, therefore, the expression

$$\frac{j}{\omega \rho_i} A_i \left(\frac{d I_0}{d r} \right)_{r_0} e^{-jk_z z} = j \omega a e^{-jk_z z} = \frac{j}{\omega \rho_e} A_e \left(\frac{d K_0}{d r} \right)_{r_0} e^{-jk_z z}. \quad (10)$$

Consequently,

$$A_i = \frac{\omega^2 \rho_i a}{\left(\frac{d I_0}{d r}\right)_{r_0}} \quad \text{and} \quad A_e = \frac{\omega^2 \rho_e a}{\left(\frac{d K_0}{d r}\right)_{r_0}}. \quad (11)$$

But (see, for example, Watson, 1944, p. 79)

$$\begin{aligned} \left(\frac{d I_0}{d r}\right)_{r_0} &= (k_z^2 - (\omega/c_i)^2)^{1/2} (I_1)_{r_0} \\ \text{and} \left(\frac{d K_0}{d r}\right)_{r_0} &= - (k_z^2 - (\omega/c_e)^2)^{1/2} (K_1)_{r_0}. \end{aligned}$$

Therefore,

$$P_{iA_0} = \frac{\omega^2 \rho_i}{(k_z^2 - (\omega/c_i)^2)^{1/2}} \left(\frac{I_0}{I_1}\right)_{r_0} \xi_A$$

(12)

and

$$P_{eA_0} = \frac{-\omega^2 \rho_e}{(k_z^2 - (\omega/c_e)^2)^{1/2}} \left(\frac{K_0}{K_1}\right)_{r_0} \xi_A.$$

Upon substituting (12) into the first of equations (7), we obtain

$$\begin{aligned} \frac{d^2 \xi_A}{d z^2} + \omega^2 \left\{ \frac{\sigma}{T} + \frac{\rho_i}{T (k_z^2 - (\omega/c_i)^2)^{1/2}} \left(\frac{I_0}{I_1}\right)_{r_0} \right. \\ \left. + \frac{\rho_e}{T (k_z^2 - (\omega/c_e)^2)^{1/2}} \left(\frac{K_0}{K_1}\right)_{r_0} \right\} \xi_A = 0. \end{aligned} \quad (13)$$

Since the first equation of (8) is a solution of (13), we have the following implicit expression for k_z

$$\begin{aligned} k_z^2 = \omega^2 \left\{ \frac{\sigma}{T} + \frac{\rho_i}{T (k_z^2 - (\omega/c_i)^2)^{1/2}} \left(\frac{I_0}{I_1}\right)_{r_0} \right. \\ \left. + \frac{\rho_e}{T (k_z^2 - (\omega/c_e)^2)^{1/2}} \left(\frac{K_0}{K_1}\right)_{r_0} \right\}. \end{aligned} \quad (14)$$

The phase velocity V_ω can then be expressed implicitly as

$$V_{\omega}^2 = 1 \left\{ \left[\frac{\sigma}{T} + \frac{\rho_i}{T(k_z^2 - (\omega/c_i)^2)^{1/2}} \left(\frac{I_0}{I_1} \right)_{r_0} + \frac{\rho_e}{T(k_z^2 - (\omega/c_e)^2)^{1/2}} \left(\frac{K_0}{K_1} \right)_{r_0} \right] \right\}. \quad (15)$$

As indicated above, we are primarily concerned with phase velocities which are much less than the velocities c_i and c_e . In addition, since $\sigma \ll \rho_i$, we can neglect the first term by comparison with the other two. For such situations, we can write (15) as

$$V_{\omega}^3 = \omega \frac{T}{[\rho_i (I_0/I_1)_{r_0} + \rho_e (K_0/K_1)_{r_0}]}, \quad (16)$$

where the argument of the Bessel functions is $(\omega r_0/V_{\omega})$. Now the magnitude of this argument increases with increasing values of both r_0 and ω . Let us consider, then, relatively large values as follows: $r_0 = 2(10)^{-2}$ cm, $V_{\omega} = 2(10)^3$ cm/sec and $\omega = (10)^5$ sec $^{-1}$. The first value is the approximate radius of a giant squid axon, the second is the conduction velocity in the axon and the third value corresponds to a frequency component $\approx 2(10)^4$. From (16) we then obtain the result that for equal densities of the interior and exterior fluids the value of the second term in the denominator is only about one-third the value of the first term. If the exterior fluid is then replaced by a fluid of very low density (gas) the phase velocity will change by less than 10%. For a value of $\omega = (10)^4$, the phase velocity will change by about 2% for the same exchange. We can thus conclude that the density of the external fluid is of minor importance in determining the velocity of propagation.

If we restrict the range of ω to values such that $\omega \leq (10)^5$, then we can rearrange expression (16) in the following approximate form

$$V_{\omega}^4 = \frac{\omega^2 T r_0}{2 \rho_i}. \quad (17)$$

We see that the phase velocity is proportional to the square root of ω , i.e., the membrane behaves like an anomalously dispersive medium. In other words, the group velocity of a wave packet is greater than the phase velocity of the midfrequency component. In this case $V_g = 2V_{\omega}$. If we substitute from expression (3) for T , we obtain the relation

$$V_{\omega}^4 = \frac{\omega^2 r_0^2 \Delta P_0}{2 \rho_i}. \quad (18)$$

If the tension is the result of a mechanism other than a hydrostatic pressure difference it appears necessary to postulate $T \propto r_0$. The quantity ΔP_0 in (18) is then replaced by a proportionality constant. Now if we assume that the quantity ΔP_0 is constant, i.e., independent of r_0 , the result for the phase velocity is

$$V_\omega = r_0^{1/2} \omega^{1/2} \left(\frac{\Delta P_0}{2\rho_i} \right)^{1/4}. \quad (19)$$

The third equation of (8) indicates that the rapidity with which a disturbance drops off as one moves radially away from the surface of the tube is greater for the larger values of ω . For example, if one inserts the values $r_0 = 2(10)^{-2}$ cm, $V_\omega = 2(10)^3$ cm/sec and $\omega = (10)^5$ sec⁻¹, one computes from the last equation of (8) that at one diameter distance from the membrane the amplitude of the disturbance is only 1/10 the amplitude at the membrane.

For purposes of comparison with experiment, we are, of course, interested in the velocity of propagation of a fairly localized disturbance along the length of the tube. We will show that as long as a signal velocity has a meaning for any particular disturbance, this velocity depends on the radius r_0 in the same way that the phase velocity depends on r_0 . This is shown with the use of the Fourier transform. (See, for example, Guillemin, 1935, chap ii.) We choose an exciting pulse $f(t)$ for the displacement, ξ , of the membrane at $z = 0$. Then this pulse can be represented in terms of sinusoidal functions of time by means of the integral relation

$$f(t_0) = \int_{-\infty}^{+\infty} g(\omega) e^{j\omega t} d\omega, \quad (20)$$

where

$$g(\omega) = \frac{1}{2\pi} \int_{-\infty}^{+\infty} f(t) e^{-j\omega t} dt.$$

From the first of equations (8) we see that the disturbance as a function of time will have the following form at a point z_0 to the right of zero (an identical relation in time is observed at z_0 units to the left of zero)

$$f(t)_{z_0} = \int_{-\infty}^{+\infty} g(\omega) e^{j\omega(t-z_0/\beta\omega^{1/2})} d\omega, \quad (21)$$

where $\beta\omega^{1/2}$ has been inserted for V_ω . The quantity β is a constant. We now refer to equations (17), (18) or (19). If we consider the movement of some point of the disturbance, such as a maximum or

peak value (if this is possible), and define a signal velocity with respect to this point, then, from (21), such a signal velocity, V_s , must satisfy the following relation: $V_s \propto \beta$. We can thus write

$$V_s = br_0^{1/2} \left(\frac{\Delta P_0}{2 \rho_i} \right)^{1/4}, \quad (22)$$

where b is a constant which is to be determined by evaluation of the integral (21). The relation indicated by (22) between the radius r_0 and the velocity V_s is that observed experimentally.

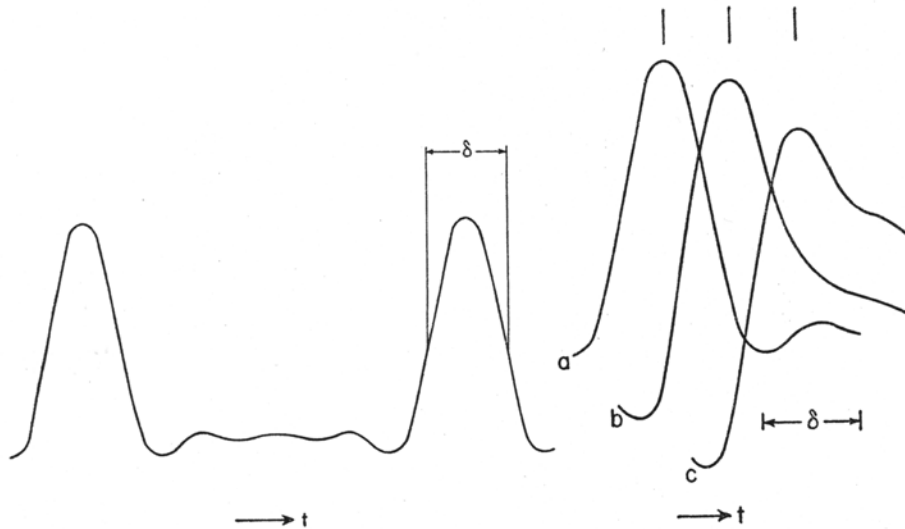


FIGURE 2. (a) Periodic excitation function applied at $z = 0$. (b) The propagated response as a function of position along the tube. The curve labeled a is the exciting function, curve c indicates the response at a point twice as far from the position of excitation as that indicated by curve b .

We have not carried out an exact evaluation of (21) for any pulse shape. However, to obtain a value for the order of magnitude of the signal velocity, we carry out an approximate analysis for a particular exciting function. We assume that the exciting function is a periodic one compounded from four frequencies (multiples of $1/5\delta$) of the form indicated in Figure 2a. Then we obtain for $f(t)$ at the two points to the right of the origin $z_0 = c(\pi\delta/2)^{1/2}$ and $z_{00} = 2c(\pi\delta/2)^{1/2}$, where c is related to the phase velocity of a component corresponding to $\omega = (2\pi/\delta)(0.8)$ by $V_\omega = c[(2\pi/\delta)(0.8)]^{1/2}$, the disturbances labeled (b) and (c) in Figure 2b. It is evident that one can identify a signal velocity if one does not consider points too

far removed from the point of excitation. In this particular case, the signal velocity is equal to about 0.9 of the phase velocity of the highest frequency component present in the exciting function. A calculation based on a value of this order, for a case corresponding to a giant squid axon, yields a value of the required pressure difference, ΔP_0 , of the order of several atmospheres. Pressures of this order of magnitude appear somewhat high. However, from formula (18) we see that a doubling of the value of ω decreases the value of the required pressure by a factor of four. The range of values of ω is suggested by the shape of the spike potential and the membrane conductance change with time (Cole and Curtis, 1939).

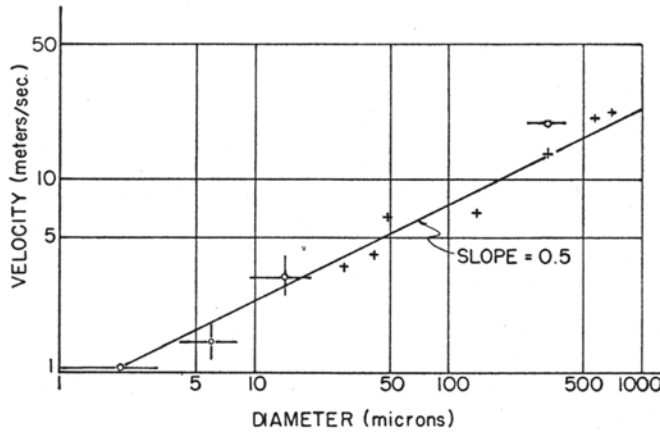


FIGURE 3. Comparison of experimental values for the velocity of conduction versus fiber diameter with the theoretical result.

The graph of Figure 3 indicates a comparison of theoretical results with experiment. The experimental values are from the data tabulated by C. L. Prosser (1946) for crustacea and cephalopod mollusks. The straight line is drawn for a 0.5 power relationship, i.e., the quantity ΔP_0 in (22) is taken constant.

Recent experimental work lends support to the view that mechanical motion coexists with electrical changes taking place in nerve during the conduction process. Dimensional and opacity changes in nerve in the region of electrodes supplying polarizing current have been observed by J. M. Tobias and S. Solomon (1950); Solomon and Tobias (1950) and Tobias (1950). Their results considered with the work of D. K. Hill and R. D. Keynes (1949) on opacity changes accompanying propagated electrical activity suggest the possibility of mechanical motion during activity. The ease of stimulation of nerve tissue by mechanical means also lends support to such a picture

(Blair, 1936).

Investigators (Curtis and Cole, 1942; Hodgkin and Huxley, 1945; Hodgkin and Rushton, 1946) have found useful the concept of an inductive element in the equivalent electrical circuit of nerve. The magnitude of the required inductance is large, of the order of $0.2 H$ cm^2 . It is not necessary that an inductive element as such exist in nerve tissue. Indeed, one of such magnitude would be difficult to accept; mechanical motion, however, would manifest itself in the equivalent electrical circuit of the tissue as a relatively large inductive element.

It is an immediate consequence of (17) and (20) that as the tension varies so does the signal velocity. Experimental results indicate that the conduction velocity may increase when a nerve is longitudinally stretched (Bullock, 1945). Such stretching would increase the tension, T , in relation (17) and thus increase the velocity if the change in radius r_0 does not over-compensate. It would be revealing to check the theory against precise quantitative data on this effect. The experimental evidence that lateral squeezing reduces the conduction velocity (Gasser and Erlanger, 1929) is a direct consequence of (17) since the tension, T , would be reduced in the region of lateral compression. This theory is not inconsistent with the results presented by H. Grundfest (1936) on the effects of hydrostatic pressure. No change in the conduction velocity would be observed on this picture if the difference between internal and external pressures remains constant.

The theory presented in this publication is entirely mechanical. In order to correlate the electrical manifestations of the conduction process of invertebrate nerve with such a picture, it is necessary to postulate an electromechanical coupling mechanism. The mechanical motion might then serve as a sort of trigger for electrical "break-down." In any event, such considerations await further investigation.

It is concluded on the basis of the theory developed herein that mechanical motion may be a primary factor in determining the velocity of propagation of the conduction pulse of thin sheathed nerve fibers.

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LIST OF SYMBOLS

a, A_i, A_e	amplitude constants
c_i, c_e	acoustic velocity of internal and external fluid respectively
k_z	$= \omega/V_\omega$
ΔP	$= P'_{i0} - P'_{e0}$
P_i, P_e	pressure deviations from equilibrium in the respective media
P_{i0}, P_{e0}	deviations in pressure from equilibrium value at surface of membrane in respective media
P'_{i0}, P'_{e0}	pressure at membrane in the respective media
P_{iA}, P_{eA}	pressure displacement amplitudes in respective media
P_{iA0}, P_{eA0}	pressure displacement amplitudes in respective media at the membrane surface
r	radial coordinate
r_0	radius of cylindrical membrane
T	tension per unit length in the membrane
t	time
u_r	radial velocity
V_g	group velocity
V_s	signal velocity
V_ω	phase velocity for sinusoidal disturbance on the membrane
z	coordinate, distance along membrane
I_0, K_0, I_1, K_1	Bessel functions order zero and one, respectively
ω	$2\pi f$ where f is the frequency
δ	width of exciting pulse at half amplitude
θ	angular coordinate
ξ	radial displacement of membrane
ξ_A	radial displacement amplitude of membrane
ρ_i, ρ_e	densities of internal and external media, respectively
σ	mass of membrane per unit area

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