A Theoretical Basis for Microwave and RF Field Effects on Excitable Cellular Membranes

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***Abstract*—A model of a mechanism for nonthermal interaction of RF or microwave fields with excitable cellular membranes is presented. It may be possible for an oscillating component of membrane potential to change the conductance of the membrane to all ion species which transverse voltage-dependent membrane channels. Some specific effects on squid giant axon predicted by the model are discussed.**

INTRODUCTION

EXCITABLE CELLS are often extremely sensitive to very small changes in the electrostatic field across the cellular membrane. A number of researchers have published somewhat contradictory evidence which supports [1]–[6] and does not support [7]–[10] the hypothesis that RF and microwave fields can affect excitable cells by nonthermal mechanisms. It is the purpose of this paper to provide a theoretical basis for an understanding of how oscillating electromagnetic fields at RF and microwave frequencies might directly affect nerve, muscle, and other electrically excitable tissue.

In what follows, the classical mathematical model formulated by Hodgkin and Huxley [11] for the current-voltage relations in the membrane of the giant axon *Loligo* will provide a framework for further discussion. In the Hodgkin and Huxley (HH) model, certain parameters are nonlinear functions of the instantaneous electric field across the membrane. These nonlinear functions of the electric field provide the basis for a number of possible microwave effects on nerve function.

THE MEMBRANE MODEL

In 1952 Hodgkin and Huxley [11] published a set of equations based on extensive experimental data which expressed the total squid axon membrane current as functions of instantaneous transmembrane potential and time. This highly predictive empirical formulation was a major achievement of quantitative biology. In the HH model, the total membrane current I, written as a function of V is expressed by the following system of coupled equations:

$$I = C_M \frac{dV}{dt} + \bar{g}_K n^4 (V - V_K) + \bar{g}_{Na} m^3 h (V - V_{Na}) + \bar{g}_l (V - V_l) \quad (1)$$

where

$$dn/dt = \alpha_n(1-n) - \beta_n n \quad (2)$$

$$dm/dt = \alpha_m(1-m) - \beta_m m \quad (3)$$

$$dh/dt = \alpha_h(1-h) - \beta_h h \quad (4)$$

and

$$\alpha_n = 0.01(V+10)\Big/\left(\exp\frac{V+10}{10} - 1\right) \quad (5)$$

$$\beta_n = 0.125\exp(V/80) \quad (6)$$

$$\alpha_m = 0.1(V+25)\Big/\left(\exp\frac{V+25}{10} - 1\right) \quad (7)$$

$$\beta_m = 4\exp(V/18) \quad (8)$$

$$\alpha_h = 0.07\exp(V/20) \quad (9)$$

$$\beta_h = 1\Big/\left(\exp\frac{V+30}{10} + 1\right). \quad (10)$$

In these equations V is the displacement of membrane potential from the resting value (depolarization negative). Constants C_M, $\bar{g}_K$, $\bar{g}_{Na}$, $\bar{g}_l$, V_K, V_{Na}, and V_l are explained in detail in [11]. The value of all constants used in the computations which follow are given in Table I.

In (1) $\bar{g}_K n^4$ and $\bar{g}_{Na} m^3 h$ are the potassium and sodium conductances, respectively. The dimensionless dynamical quantities m, n, and h are solutions of the first-order differential equations (2)–(4), respectively, and vary between zero and unity after a change in membrane potential. The α's and β's in these equations depend only on the instantaneous value of membrane potential and are given in (5)–(10).

The proper units for use of the preceding equations are as follows: potentials are expressed in mV, current in $\mu A/cm^2$, conductance in mS/cm^2, capacitance in $\mu F/cm^2$, and t in ms. The expressions for the α's and β's hold only at a temperature of 6.3°C.

THE BASIS FOR MICROWAVE AND RF FIELD EFFECTS

The α and β rate constants were assumed by Hodgkin and Huxley to be functions of the instantaneous electric field across the membrane [11]. We will continue to make this assumption as an alternating field is applied. The total field across the membrane can be expressed as

$$V(t) = V_0 + V_m \cos \omega t \quad (11)$$

where V_0 is the dc displacement of the membrane potential from its resting state and V_m is the peak amplitude of

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TABLE I.
VALUE OF CONSTANTS USED WHEN COMPUTING A SOLUTION TO THE HH EQUATIONS (TAKEN FROM [11])

CONSTANT	VALUE	UNITS
C_M	1.0	$\mu F/cm^2$
V_{Na}	-115	mV
V_K	+ 12	mV
V_l	- 10.6	mV
$\bar{g}_{Na}$	120	mS/cm^2
$\bar{g}_K$	36	mS/cm^2
$\bar{g}_l$	0.3	mS/cm^2

the oscillating component of applied membrane potential. The instantaneous values of the α's and β's are then obtained by replacing V in (5)–(10) by $V(t)$ as given by (11).

For example, when V in (8) is replaced by (11), then β_m becomes a periodic nonnegative function which can be expressed in a Fourier series as

$$\beta_m(\omega t) = \sum_{k=-\infty}^{+\infty} \beta_{m,k} \exp(jk\omega t) \tag{12}$$

where

$$\beta_{m,k} = \frac{1}{2\pi} \int_0^{2\pi} \beta_m(\omega t) \exp(-jk\omega t) d\omega t. \tag{13}$$

The average value of $\beta_m(\omega t)$ is

$$\beta_{m,0} = \frac{1}{2\pi} \int_0^{2\pi} \beta_m(\omega t) d\omega t. \tag{14}$$

The quantity $\beta_{m,0}$ is a nonnegative monotonically increasing function of V_m. Therefore, an oscillating electric field across the membrane can result in a steady (dc) change in all α and β rate constants.

SOME RESULTS

The instantaneous values of $\beta_m(\omega t)$ and $\alpha_m(\omega t)$ when $V_0 = 0$ over a full period and $V_m = 25$ mV are shown in Fig. 1 along with the average values $\beta_{m,0}$ and $\alpha_{m,0}$. The monotonic increase in the average value of all six α and β rate constants as a function of increasing V_m when $V_0 = 0$ is illustrated in Fig. 2. In this figure, all rate constant average values have been normalized so that the constants have unity value when $V_m = 0$.

Fig. 3 is a plot of both α_m and β_m as a function of the dc membrane potential V_0. Note that the average value of both α_m and β_m increases with an increase in V_m.

The α and β rate constants determine both the rate of change in m, n, and h and the final steady-state value of these quantities. The steady-state value reached after a step input is

$$q_\infty = \frac{\alpha_q}{\alpha_q + \beta_q} \tag{15}$$

where q is m, n, or h.

The time constant for $q(t)$ after a step input is

$$\tau_q = \frac{1}{\alpha_q + \beta_q}. \tag{16}$$

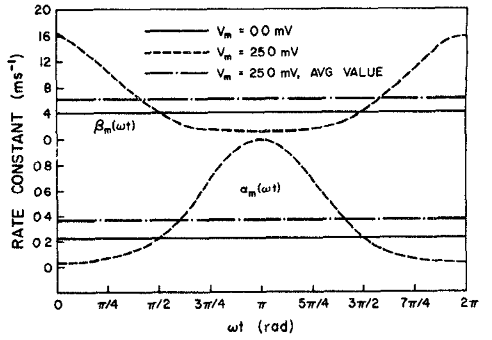

Fig. 1. Instantaneous values of rate constants $\beta_m(\omega t)$ and $\alpha_m(\omega t)$ when $V_0 = 0$ and $V_m = 25$ mV where the membrane potential is $V = V_0 + V_m \cos \omega t$ (– – –); the average values $\beta_{m,0}$ and $\alpha_{m,0}$ when $V_m = 25$ mV and $V_0 = 0$ (—·—); and the rate constants when $V_0 = V_m = 0$ (——).

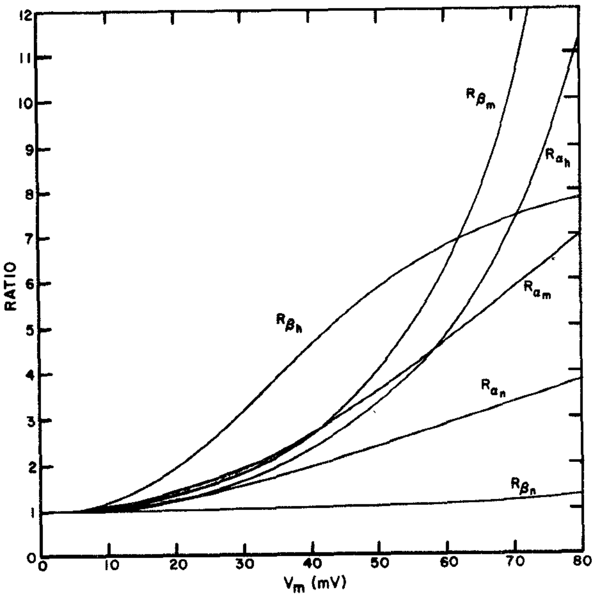

Fig. 2. The normalized average value of all rate constants as a function of increasing V_m when $V_0 = 0$. All average values have been normalized so that the rate constants have unity value when $V_m = 0$, e.g., R_{β_n} is the ratio of $\beta_{n,0}$ when $V_m \neq 0$ to the value of $\beta_{m,0}$ when $V_m = 0$.

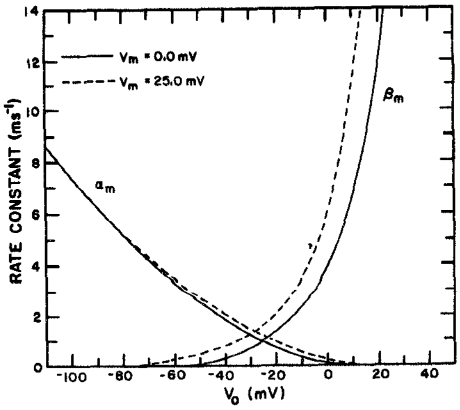

Fig. 3. Average values of rate constants α_m and β_m as a function of V_0 for $V_m = 0$ and $V_m = 25$ mV.

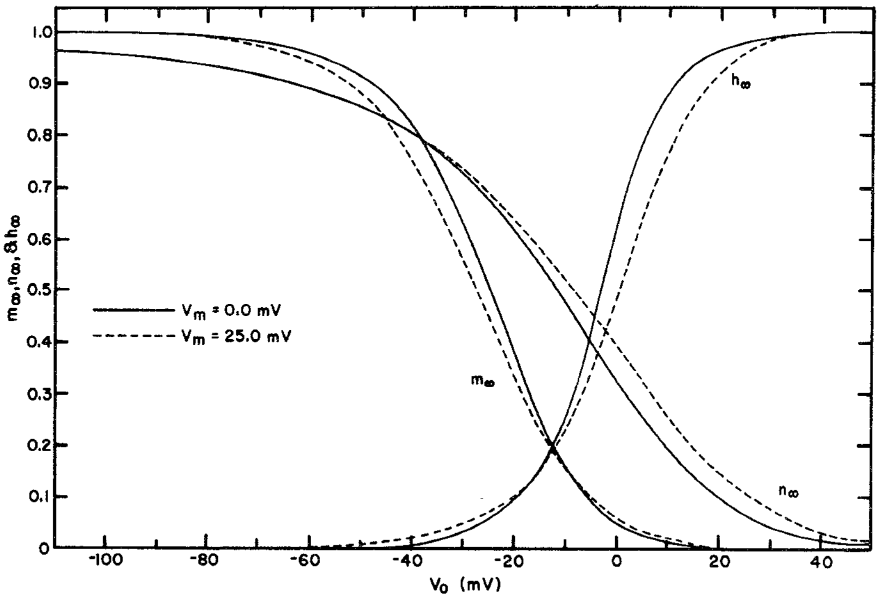

Fig. 4. Steady-state values of m_∞, n_∞, and h_∞ as a function of V_0 for $V_m=0$ and $V_m=25$ mV. m_∞, n_∞, and h_∞ computed from (27) using the numerically computed average values of the α and β rate constants as given by (14).

A plot of m_∞, n_∞, and h_∞ as a function of V_0 with V_m as a parameter is given in Fig. 4.

Let us define the applied potential across the membrane to be

$$V(t) = V_m \cos \omega t [u(t) - u(t - t_0)] \tag{17}$$

where $u(t)$ is the unit step function. Such an applied potential can result if the membrane is irradiated with a microwave or RF pulse beginning at $t=0$ and ending at time t_0. The change in membrane potential in response to this applied ac field can be obtained by numerically solving (1)–(10) with the initial conditions being the resting state values for V, m, n, and h. Since no current flows through the membrane from external sources, I in (1) is set to zero, and the axon is assumed to be irradiated uniformly along the length such that $dV/dx=0$. After each iteration through the HH equations, accurate estimates for the average values of the $\alpha(\omega t)$'s and $\beta(\omega t)$'s are obtained numerically using the appropriate expression analogous to (14). The response of the membrane potential to the pulse of applied oscillating field is shown for one value of V_m in Fig. 5.

The changes in membrane potential shown in Fig. 5 result from changes in both the sodium and potassium conductances. The time course of both these conductances following the pulse of applied ac field (as given in (17)) is also shown in Fig. 5. The conductances were computed after obtaining numerical solutions to the HH equations for $m(t)$, $n(t)$, and $h(t)$ with (17) as the input. Conductances g_K and g_{Na} are then

$$g_K(t) = \bar{g}_K n^4(t) \tag{18}$$

$$g_{Na}(t) = \bar{g}_{Na} m^3(t) h(t). \tag{19}$$

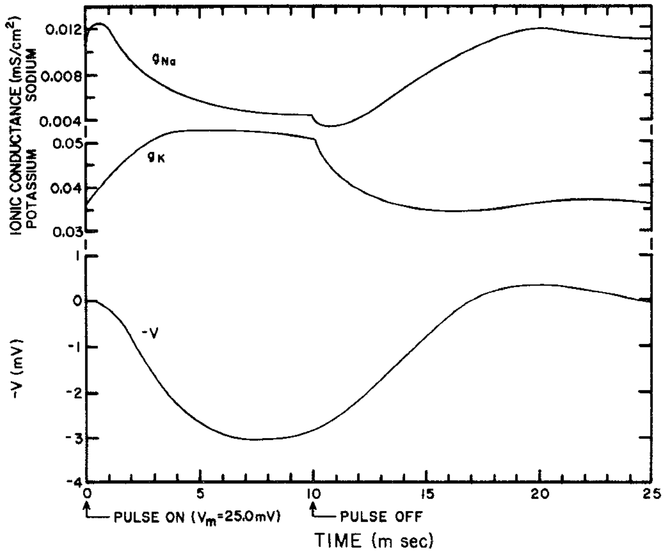

Fig. 5. Response of model axon to a pulsed oscillating component of membrane electric field (10-ms pulse, $V_m=25$ mV). The membrane potential and the sodium and potassium conductances are shown. These curves are solutions of the HH equations (see text).

FIELD WITHIN THE MEMBRANE

In estimating the level of the oscillating component of electric field developed within the membrane, the model discussed by Barnes and Hu [12] was used. Without repeating their formulation, a membrane near the surface in high water content tissue exposed to a 10 mW/cm^2 (194 V/m in air) plane wave would result in an electric field of 980V/m within the nonpolar region of the lipid bilayer (assuming a dielectric constant of 2.1 [13]). This is equivalent to an applied ac membrane potential V_m of 9.8 μV if membrane thickness is 100 Å.

The effects of such a field as predicted by the above model are *not* significant. However, if a pulsed field with a peak intensity of 10 W/cm^2 (194 kV/m in air) is applied, the resulting field across the membrane will be 9.8 mV. This level of applied ac field would cause significant functional changes in the model we have considered. It should be noted that thermal effects of applied fields of this magnitude will be considerable for all but the lowest duty cycle pulsed waveform, e.g., a duty cycle of 0.001 will result in a field thermally equivalent, on the average, to an incident intensity of 10 mW/cm^2. Whether or not such a pulsed waveform would result in significant effect as predicted by the model awaits further analysis.

Because of the large size of the giant squid axon it is possible, using an internal wire electrode, to apply an RF field directly across the membrane (e.g., see Takashima and Schwan [14].) The highly specific predictions of the model presented here may be useful in the design of experiments and the interpretation of results. For example, the effects of directly applied high-frequency fields on membrane conductance as well as static or dc membrane potential should be easily measured. Such experiments may help determine the dielectric relaxation times of the gating dipoles (or charged groups) which compromise the "voltage sensor" for membrane ionic channels (see Discussion). From this kind of information, one might determine the upper limit of frequency for application of the theory presented here.

DISCUSSION

Hodgkin and Huxley pointed out that the steep membrane potential dependence of sodium and potassium permeabilities in squid axon implies the presence in the membrane of polar molecules having large charges or dipole moments [11]. Only through existence of such charged groups acting as "voltage sensors" can the cell be so exquisitely sensitive to small changes in electrostatic potential. Movement of these charged groups (associated with the integral proteins of the voltage sensitive ionic channels) could result in protein conformational changes which open (or close) the "gate" in the ion specific channel. Measuring movement of this charge, recorded as a displacement current, has been the subject of a considerable volume of recent research (see Almers [13] or Hille [15] for excellent reviews).

For a given value of membrane potential, there is an energy barrier separating the fully open and fully closed states of these gating dipoles. From thermodynamic principles [16], it can be shown that the probability of a dipole being in a given state is a highly nonlinear function of the applied potential (a Boltzmann distribution results if certain simplifying assumptions are made [11], [13], [17]). Thus an oscillating field will produce a dc change in the average position of the dipole resulting in a steady shift in the probability of the dipole being in a given state. It is this kind of physical mechanism which could lead to the conductance changes predicted by the modified HH model presented here.

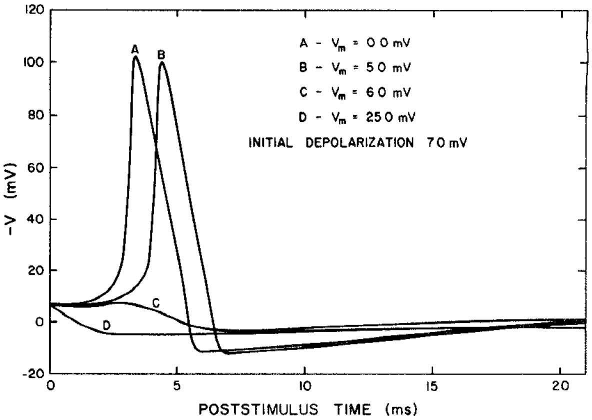

Fig. 6. Computed membrane action potentials in response to an initial membrane depolarization of 7 mV for different values of V_m. Curves are solutions to the HH equations.

It is by no means clear that observed effects of microwave or RF radiation on excitable tissue can always be attributed to a thermal mechanism. In turtle hearts, irradiation with 960 MHz at levels below those which produce general heating can cause bradycardia, while higher microwave intensities and general heating cause tachycardia [2]. In single pacemaker-type neurons of *Aplysia*, a number of observed changes in firing patterns in response to microwave radiation were in the opposite direction to that caused by general heating [3]. Extremely low-frequency electric fields at 6 to 75 Hz, or RF radiation amplitude modulated at these frequencies have been shown to have significant effects on efflux of calcium ions from brain tissue at levels which are thermally insignificant [4]–[6].

The model given in this paper may give a theoretical basis for some of these observed effects. For example, it has been shown that oscillating fields within the membrane of squid axon might effectively open voltage sensitive potassium channels resulting in increased potassium conductance. Furthermore, an oscillating field closes sodium channels in the steady state due to an increase in sodium inactivation. This increase in g_K and steady-state decrease in g_{Na} results in a hyperpolarization of the membrane (Fig. 5) because the potassium equilibrium potential V_K is on the hyperpolarized side of the resting potential. Such a membrane hyperpolarization would have a general inhibitory effect on an irradiated neuron or muscle cell. Thus spontaneously firing cells, e.g., pacemaker cells in neural or cardiac tissue, would be expected to decrease their impulse generating frequency in response to irradiation of sufficient magnitude. This effect is in the opposite direction to generalized heating.

Such an inhibitory effect would decrease the probability of an action potential being generated for a given fixed level of excitory input. This is shown quite graphically in Fig. 6 where the solution to the HH equations is given for a fixed initial membrane depolarization (stimulus) of $V = -7$ mV. The resulting membrane action potential in the absence of an oscillating field across the membrane ($V_m = 0$) is given in trace A. Trace B shows the response to the same stimulus but with $V_m = 5.0$ mV. The peak of the action potential has been delayed by about 1 ms. An oscillating electric field equal to or greater than 6 mV completely quenches the action potential response (traces C and D). The impulses shown in Fig. 6 are membrane action potentials [11]. The effects of an oscillating electric field on propagated action potentials will be discussed in a subsequent paper.

The transitory increase in g_{Na} in response to a pulsed RF or microwave field seen in Fig. 5 is an interesting phenomenon predicted by the model which warrants further discussion. When the membrane is initially at rest ($V=0$), one can see from Fig. 4 that an applied ac field of 25 mV results in a substantial decrease in h and only a slight increase in m. Since $g_{\mathrm{Na}} = m^3 h \bar{g}_{\mathrm{Na}}$, the final steady-state value of g_{Na} will decrease in response to the applied ac field. However, $\tau_h > \tau_m$ so that $m(t)$ reaches its steady-state value before $h(t)$ changes substantially. Thus g_{Na} rapidly increases initially but decreases as $h(t)$ begins to change. In the squid axon, this initial increase in g_{Na} is insufficient to have a significant excitory effect on the membrane. However, in other excitable membranes, a rapid initial increase in g_{Na} of greater magnitude might result in a membrane depolarization sufficient to trigger an action potential. In such a cell, a step of applied ac field might have a phasic excitory effect but a tonic inhibitory effect.

A wide range of other phenomena in response to applied oscillating fields are predicted by the modified HH model of the squid axon and by similar models for other excitable cells. A number of these phenomena and models will be discussed in detail in a subsequent paper.

Since the HH model was published, the equations have been modified to fit a number of situations in the squid axon other than the experimental results which they originally modeled. Modified equations can be used to describe the effects of temperature on the propagated action potential [18], the repetitive firing observed in low-calcium concentrations [18], the prolonged action potentials produced by tetraethylammonium ions [19], [20], and the hyperpolarizing response observed in high potassium solutions [20]. In addition, modified HH-type equations have been applied with some degree of success to model other excitable tissues including myelinated nerve [21]–[23] and cardiac muscle [24], [25]. Modifications of these various mathematical models to account for applied microwave or RF fields might be useful in explaining the RF and microwave field effects on nerve and muscle tissue observed in the laboratory.

SUMMARY

This paper shows that it may be possible for an oscillating component of membrane potential to change the conductance of the membrane to all ion species which traverse voltage-dependent membrane channels. Voltage-sensitive channels for sodium, potassium, calcium, and chloride ions have been demonstrated in a wide range of excitable membranes. Such channels exist in membrane of muscle cells (skeletal, smooth, and cardiac), in nerve cell axon and soma membrane, and even in the membrane of the extensive dendritic branches of some nerve cell types. Modified HH models of the type discussed herein may be useful in predicting the effects of CW, pulsed or amplitude modulated RF and microwave radiation on neural and neural-muscular systems. For example, in the squid giant axon, the model predicts that an oscillating component of membrane potential would increase the membrane potassium conductance and decrease the sodium conductance in the steady state. This would have an inhibitory effect on the axon which is in the direction from effects produced by heating.

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Short Papers

Easy Determination of the Characteristic Impedance of the Coaxial System Consisting of an Inner Regular Polygon Concentric with an Outer Circle

KOICHI TSURUTA AND RYUITI TERAKADO

Abstract—**This paper gives a simple method for the determination of the characteristic impedance of an inner regular polygon concentric with an outer circle. The approach makes use of the method of superposition for plane sheets of charge which were radially disposed in the polygon. The results are in good agreement with those obtained by Laura and Luisoni [2], [3].**

Riblet [1] and Laura and Luisoni [2], [3] have developed interesting techniques for the determination of the charactersitic impedance of the coaxial system consisting of a regular polygon concentric with a circle. This paper gives a simpler method for an inner regular polygon of s apexes concentric with an outer circle.

An infinitely long conducting plane sheet of width $2b$ charged with charge density Q per unit length in the z direction is situated in free space with permittivity ϵ_0, as shown in Fig. 1. Suppose that the reference point for potential is at the conducting sheet whose potential is defined as A. The potential V_P at a point $P(x, y)$ on the z plane can be obtained by conformal mapping of the z plane on a w plane, whose mapping function is

$$Z = \frac{b}{2}\left(w + \frac{1}{w}\right) + (c + ia). \tag{1}$$

By this mapping, equipotential lines on the w plane becomes concentric circles. Therefore, the potential V_P is easily written as follows:

$$V_P = A - \frac{Q}{2\pi\epsilon_0} \ln \left\{ \frac{\sqrt{\left(\frac{x-c}{b} - 1\right)^2 + \left(\frac{y-a}{b}\right)^2} + \sqrt{\left(\frac{x-c}{b} + 1\right)^2 + \left(\frac{y-a}{b}\right)^2}}{2} \right. \\ \left. + \sqrt{\frac{\left(\frac{x-c}{b}\right)^2 + \left(\frac{y-a}{b}\right)^2 - 1 + \sqrt{\left\{\left(\frac{x-c}{b}\right)^2 + \left(\frac{y-a}{b}\right)^2 + 1\right\}^2 - 4\left(\frac{x-c}{b}\right)^2}}{2}} \right\} \tag{2}$$

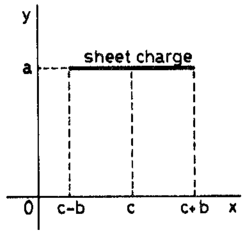

Fig. 1. Dimensions of the plane sheet of charge.

The electric field produced by the conducting sheet charge is derivable as the negative gradient of the potential.

In the proposed method an important supposition is made, that is, the distribution of charge on the conducting sheet invariably remain, even if other conducting sheets are set near it.

Fig. 2 shows the disposition of the sheets of charge for $s = 5$, for example. They were radially disposed between the center and the apexes of the polygon. The potential and the field at any point can be calculated analytically by superposition for these sheets of charge. The potentials at the sides of the polygon and at the outer circle were calculated for $s = 3$, 4, 5, and 6. Table I shows the maximum deviations of the potentials at the sides of the polygon and at the outer circle from the average potentials V_{polygon} and V_{circle}, respectively, expressed as percentages of the average potentials. V_{polygon} was calculated from the potentials at 100 points which were arranged on the half-side $P_1\,P_2$ (Fig. 2) at equal distances and were weighted by the field strength. V_{circle} was calculated in the same manner as V_{polygon} from the potentials on the arc $C_1\,C_2$. R is the radius of the circle and r is the radius of the circumscribed circle of the polygon.

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