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A Possible Mechanism for the Influence of Electromagnetic Radiation on Neuroelectric Potentials

RONALD J. MACGREGOR

***Abstract*—This paper explores the idea that the electrical component of applied microwave and radiowave radiation might induce transmembrane potentials in nerve cells and, thereby, disturb nervous function and behavior. The paper estimates the transmembrane currents and potentials induced in nerve cells by applied electrical fields and currents. Estimates are made for steady and for oscillating stimulation. The primary conclusion is that intracranial electrical fields associated with low-intensity irradiation in the frequency range of 10^6–10^{10} Hz may induce transmembrane potentials of tenths of millivolts (or more) and that, therefore, such externally applied fields may distrub normal nervous function through this mechanism. The paper also presents a discussion which indicates that the induced transmembrane potential should exhibit a maximum at about 10^8 Hz. Although some researchers suggest that the direct mechanism explored here may not represent the main influence of microwaves and radiowaves on biological tissue, this model together with a recent model by Barnes and Hu [21] suggest that the results so produced may indeed be significant.**

I. Introduction

THERE IS a wide collection of intriguing phenomena concerning the influence of applied fields and currents on nervous function and behavior. Steady electric fields and currents applied to the brain are known to induce a variety of behavioral responses, ranging from hallucinations or the vivid reexperiencing of past events to the performance of coordinated complex motor patterns or the exhibition of rage or fright [1]. Stimulating steady currents are used extensively to activate nerve cells in neurophysiological research [2]. Such experiments are used to investigate basic neuroelectric mechanisms and to examine interconnecting pathways among cells. Less well known in this country is a large body of research carried out in the Soviet Union which indicates that low-intensity electromagnetic radiation may induce insomnia, irritability, loss of memory, fatigue, headache, tremor, hallucinations, automatic disorders, or disturbed sensory sensitivity in humans [3]. These effects seem to occur primarily in the microwave and radiowave region and at mean intensities well below safety standards currently in use for long-term exposure. In this country, Frey has shown that both low-intensity microwave and radiowave radiation applied to the head induces auditory perception in human subjects and neuroelectric potential fluctuations in the brain stem of cats [4]. Reviews of the influence of microwaves and radiowaves on neural function are contained in [3], [5],

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The author is with the Department of Electrical Engineering, University of Colorado, Boulder, CO 80309.

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and [6]. Many recent experimental studies suggest that both micro and radio waves produce nonthermal effects and at least two implicate membranes as the site of the effect [6]–[14].

The mechanisms whereby these and related effects are brought about have not been convincingly demonstrated [15], [16]. With the present state of knowledge, it is possible to know only in general terms how particular neuroelectric events correspond to a behavioral pattern or a subjective experience; detailed understanding of function and activity exists for no entire subsystem of nerve cells. (Many fragments of information exist, however, including recent experimental results which indicate that certain single nerve cells—at least in some invertebrates—seem to act as "triggers" in that their activation elicits a coordinated, seemingly unitary movement pattern.) Moreover, the question of how applied fields and currents affect neuroelectric events is a difficult one and is not resolved. With regard to steady electric fields and currents, it is generally supposed that some portion of current crosses the membrane of a nerve cell (or cells) and thereby activates the cell(s) according to the transmembrane potential it produces. No detailed knowledge concerning how electromagnetic fields influence neuroelectric behavior exists. One hypothesis [3] holds that electromagnetic fields induce a structural change in some key molecule, particularly in the microwave range. This in turn disturbs the normal function of that molecule and thereby disturbs nervous function. Other interpretations include thermal elastic conversion, electrostriction, radiation pressure, membrane disruption, enzymatic changes, and a theory which imputes psychic function to electromagnetic fields in the brains of normal animals and includes in its preview various phenomena from the field of extrasensory perception [17], [18]. The simpler idea that the electrical forces associated with the applied fields may interact directly with basic neuroelectric processes seems to have been largely ignored.

Recent work has indicated that micro and radio wave radiation of 10-mW/cm^2 intensity should produce intracranial electric fields of up to about 200 V/m [9]. This is a considerably stronger field than previous investigators had estimated, and raises the question as to whether there may be direct mechanical interaction of the field with neuroelectric processes. An electric field of 200 V/m is far from negligible compared to some typical values for normal neuroelectric processes: for example, the longitudinal ionic current flow underlying graded potentials in passive dendrites should be typically of approximately the same magnitude; Terzuolo and Bullock [20] found that extracellular voltage gradients as low as 1 V/m could alter firing rates in stretch receptor neurons of crayfish. The electric component of the wave is oscillating at some 10^8 Hz, and it is not immediately clear how valid these comparisons might be. At least two possibilities, however, warrent investigation: the electric field may induce currents which penetrate nerve cell membrane and thereby produce a neuroelectric response, or the field may disturb the normal neural generator currents.

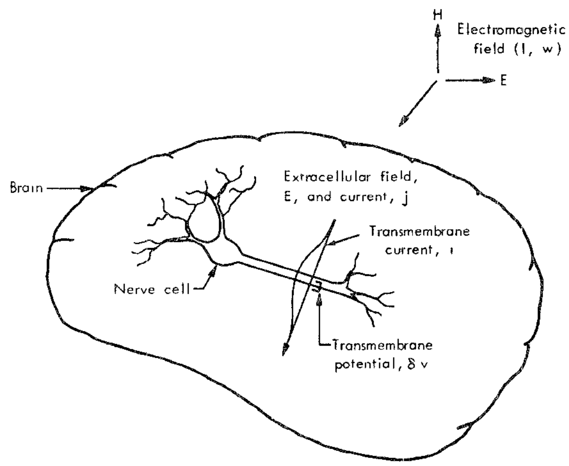

Fig. 1. Illustration of hypothesis.

This paper explores the idea that the electrical component of applied micro and radio wave radiation might induce transmembrane potentials in nerve cells and thereby disturb nervous function and behavior. We present estimates of the magnitude of transmembrane current and potential induced in a single nerve cell by a given extracellular electric field or current, and indicate how appropriate parameters should influence the result. Recently Barnes and Hu have presented a model to estimate possible transmembrane shifts of ions as a result of microwave and radio frequency fields, whose characteristics are quite compatible with those of the model described here [21].

II. Theory

A. Basic Hypothesis and Equations

The physical picture we entertain is illustrated in Fig. 1. We suppose the brain consists of nerve cells and extracellular fluid; that there is an extracellular field E and current j which may be steady or oscillating; and that a certain portion of the current i, depending on appropriate impedances and geometry, penetrates nerve cells and corresponds to a transmembrane potential δV. Our primary concern is to relate i and δV to E and j. To estimate the dependence of induced transmembrane potential δV on frequency for the spectrum of electromagnetic radiation, we relate the intracranial field E to the intensity I, and frequency ω, of an applied external field. We use a very much simplified model to estimate how much of the current penetrates the membrane and suspect that it adequately represents a straight, cylindrical neural element. We deal only with the component of current normal to the process.

This picture can be approximately described by four basic equations. The extracellular current j can be related to the extracellular electric field E, according to

$$j=\sqrt{\sigma^2(\omega)+(\epsilon\omega)^2}\ E. \tag{1}$$

The extracellular fluid is taken as comparable to sea water [15], [16], [22]. The portion of current which penetrates the membrane i is related to the extracellular current j, according to

$$i=\frac{\frac{2}{\pi}\left[1-\frac{d}{\frac{2}{\pi}\times\eta}\right]j}{\sqrt{1+\frac{4\left[\left(\frac{\sigma}{\eta g}\right)^2+\left(\frac{\epsilon\omega}{\eta g}\right)^2\right]+4\left[\frac{\sigma}{\eta g}+\frac{\epsilon c\omega^2}{\eta g^2}\right]}{1+\left(\frac{\omega c}{g}\right)^2}}}. \tag{2}$$

This expression is derived in the next section. It simply splits the current j according to the impedances for the two pathways illustrated in Fig. 1. We have supposed that a unit area of membrane may be represented by a capacitance c and a conductance g in parallel. The geometrical parameters η and x are defined by

$$\eta\equiv\frac{\pi}{2}d\left[1+\frac{1}{x}-x-\frac{\pi}{2}+\frac{2}{\sqrt{1-x^2}}\tan^{-1}\left(\frac{1+x}{\sqrt{1-x^2}}\right)\right]$$
$$x\equiv\frac{l}{d}. \tag{3}$$

As defined more precisely below, d and l represent the diameter of the neural process and the typical intercellular distance, respectively. We have supposed that the intracellular fluid has the same conductivity σ and magnetic permeability μ as the extracellular fluid. The transmembrane potential δV is related to the membrane current i, according to

$$\delta V=\frac{i}{g\sqrt{1+\left(\frac{\omega c}{g}\right)^2}}. \tag{4}$$

Finally, the extracellular electric-field component E is related to the intensity I and frequency ω of an applied electromagnetic wave according to

$$E=\frac{3\left(\frac{\epsilon_0}{\epsilon}\right)\sqrt{\sqrt{\frac{\mu_0}{\epsilon_0}}2I}}{\sqrt{\left[1+2\left(\frac{\epsilon_0}{\epsilon}\right)\right]^2+\left[\frac{\sigma^1}{\epsilon\omega}\right]^2}}. \tag{5}$$

This expression is derived from basic electromagnetic theory [23]–[28]. It represents the mean electric field within a conducting dielectric sphere embedded in a homogeneous medium and subjected to a uniform electromagnetic field. It is probably reasonably accurate up to about 10^8 Hz and is used here to indicate that the induced transmembrane depolarization δV should be particularly marked only in the frequency range of about 10^6–10^{10} Hz. The subscript "0" denotes properties of the external medium and σ' is an effective conductivity for brain tissue as a whole.

Based on (1)–(5), the transmembrane potential δV can be related on extracellular current j, or field E, or to an external electromagnetic wave, according to

$$\delta V=\frac{\frac{2}{\pi}\left[1-\frac{d}{\frac{2}{\pi}\times\eta}\right]\sqrt{\left(\frac{\sigma}{g}\right)^2+\left(\frac{\epsilon\omega}{g}\right)^2}\;E}{\sqrt{\left(\frac{2\sigma}{\eta g}+1\right)^2+\left(\frac{\omega c}{g}+\frac{2\epsilon\omega}{\eta g}\right)^2}}$$

$$\delta V=\frac{\frac{2}{\pi}\left[1-\frac{d}{\frac{2}{\pi}\times\eta}\right]\sqrt{\left(\frac{\sigma}{g}\right)^2+\left(\frac{\epsilon\omega}{g}\right)^2}\;3\left(\frac{\epsilon_0}{\epsilon}\right)\sqrt{\sqrt{\frac{\mu_0}{\epsilon_0}}2I}}{\sqrt{\left[\left(\frac{2\sigma}{\eta g}+1\right)^2+\left(\frac{\omega c}{g}+\frac{2\epsilon\omega}{\eta g}\right)^2\right]\left[\left(1+2\frac{\epsilon_0}{\epsilon}\right)^2+\left(\frac{\sigma^1}{\epsilon\omega}\right)^2\right]}}. \tag{6}$$

B. Evaluation

It is easy to illustrate that the magnitudes of the effects under consideration here are appreciable. Thus an electric field of 200 V/m, oscillating at 10^8 Hz should induce a current of about 36 mA/cm^2 in the intracellular fluid. If we suppose that about one-half of this current penetrates a given nerve cell, a transmembrane potential of about 0.2 mV results. An externally induced potential bias of this magnitude can indeed influence neuroelectric behavior. Moreover, we suspect that higher potentials than this should pertain to many of the microwave effects reported in the literature: most of investigations employ time-varying radiation whose peak intensities may range up to several hundred of milliwatts per square centimeter. For a peak intensity of 1000 mW/cm^2, our estimate would be increased by a factor of 10. We now examine these estimates more closely.

C. Model to Relate Transmembrane Current to Extracellular Current

Fig. 2 illustrates the picture we have used to approximate the percentage of a given extracellular current density j which might be expected to penetrate the membrane of nerve cells. We have represented a section of nervous tissue as comprised of a collection of hollow cylinders (representing neural processes) immersed in a conducting fluid. Moreover, we have approximated the actual tortuous geometric configurations by a uniform distribution of the cylinders as shown in Fig. 2, and supposed that we could approximate the current penetrating a typical process according to a square of side l, also indicated in Fig. 2.

l is the mean distance between the centers of adjacent cylinders when the real situation is replaced by the artificial uniform distribution.[1]

[1] l might be approximated directly from anatomical data or according to $y=\pi r^2/l^2$, where y is that fraction of area in a micrograph which contains nerve cells processes, and r is the mean radius of the processes.

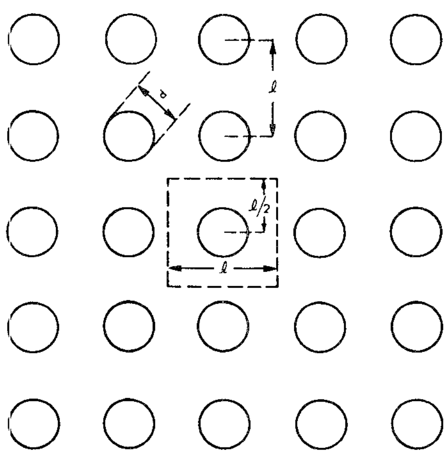

Fig. 2. Representation of nervous tissue for current penetration model.

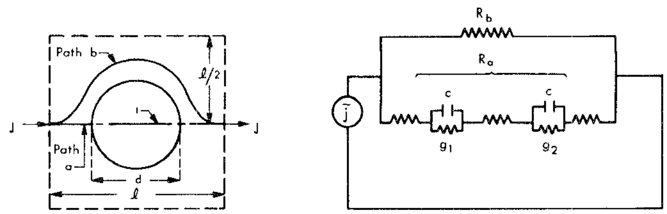

Fig. 3. Alternate pathways for impinging current.

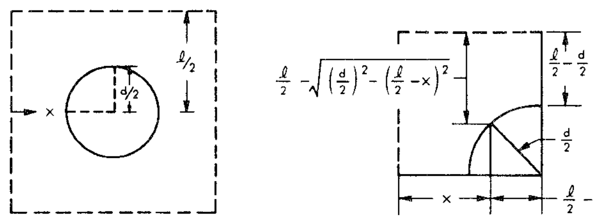

Fig. 4. Method of evaluating impedance for extracellular pathway.

We suppose that a given current density j moves symmetrically through the uniform distribution of cylinders, and that the two pathways may be distinguished as it goes from one side of an elemental square to the other: one pathway penetrates the cell membrane, the other one bypasses the process. Our procedure is simply to estimate, according to the impedances of these two pathways, how much of the current follows the first path. This is illustrated in Fig. 3. R_a represents the impedance of the transmembrane path. The impedance of a unit area of membrane is treated as equivalent to that of a conductance in parallel with a capacitance. The conductance represents pores through which ions may pass, the capacitance is related to lipid molecules within the cell membrane [29], [30].

We suppose that only that current at the square's edge which is on a collision course with the process might penetrate the membrane and that this current has access to all the volume surrounding the process and within the square. This current is denoted by I_T, the total current which penetrates the membrane is denoted by I_M, and finally the transmembrane current density is denoted by i_m. Elementary considerations then lead to the following:

$$I_T = j\,d\delta$$

$$I_M = \frac{R_b}{R_a + R_b} I_T = \frac{R_b}{R_a + R_b} j\,d\delta$$

$$i_m = \frac{I_M}{\frac{\pi d}{2}\delta} = \frac{R_b}{R_a + R_b}\frac{2}{\pi} j. \tag{7}$$

In these expressions, δ is some constant depth. The last of (7) shows that the maximum possible transmembrane current density is $2/\pi j$ which is clearly what it must be for a cylindrical neural component.

It remains, then, only to evaluate R_b and R_a in terms of tissue properties.

R_a can be written from inspection of Fig. 3 as follows:

$$R_a = \frac{l}{(\sigma + J\epsilon\omega) d\delta} + \frac{1}{(g_1 + J\omega c)\frac{\pi d}{2}\delta} + \frac{1}{(g_2 + J\omega c)\frac{\pi d}{2}\delta}. \tag{8}$$

In this expression J is the square root of -1, σ is the conductivity of the extra- and intracellular fluid, ω is the frequency of the stimulating agent, and the other terms are as defined above.[2]

Fig. 4 illustrates our method of evaluating R_b. Equations (9) are written on the basis of this picture.

$$R_b = \int_0^l \frac{dx}{(\sigma + \epsilon\omega)A}$$

$$R_b = \frac{1}{(\sigma + J\epsilon\omega)\delta}\left\{\int_0^{(l-d)/2}\frac{dx}{l/2} + \int_{(l-d)/2}^{l/2}\frac{dx}{\frac{l}{2} - \sqrt{\left(\frac{d}{2}\right)^2 - \left(\frac{l}{2} - x\right)^2}}\right\}. \tag{9}$$

Carrying out the indicated integration results in the following expression for R_b:

$$R_b = \frac{1}{(\sigma + J\epsilon\omega)\delta}\left[\frac{l-d}{l} - \frac{\pi}{2} + \frac{l}{\sqrt{\left(\frac{l}{2}\right)^2 - \left(\frac{d}{2}\right)^2}}\tan^{-1}\left[\frac{\frac{l+d}{2}}{\sqrt{\left(\frac{l}{2}\right)^2 - \left(\frac{d}{2}\right)^2}}\right]\right]. \tag{10}$$

[2] It is reasonable for our purposes to take the conductivities of the intra- and extracellular fluid σ to be equal [22], [29]. The equivalent conductivity of brain tissue σ' differs significantly from σ primarily because of the cellular membranes in the fluid. A more accurate model which differentiated σ with respect to intra- and extracellular fluid would include that differentiation in the expression for R_a.

Comparison of (8) and (10) shows that R_b depends only on the ratio d/l, whereas for a fixed d/l, R_a decreases with increasing d (because the total membrane admittance increases under these conditions.) This is the source of the observation indicated in the text that larger cell processes should be more effective in attracting current.

The final expression for the current i, which is given in (2) is obtained by substituting (8) and (10) in the last of (7) and taking the magnitude of the resulting complex expression.

D. Numerical Evaluation

It is easy to illustrate that the magnitudes of the effects under consideration here are appreciable. Thus an electric field of 200 V/m, oscillating at 10^8 Hz should induce a current of about 36 mA/cm^2 in the intracellular fluid. If we suppose that about one-half of this current penetrates a given nerve cell, a transmembrane potential of about 0.2 mV results. An externally induced potential bias of this magnitude can indeed influence neuroelectric behavior. Moreover, we suspect that higher potentials than this should pertain to many of the microwave effects reported in the literature; most of the investigations employ time-varying radiation whose peak intensities may range up to several hundred milliwatts per square centimeter. For a peak intensity of 1000 mW/cm^2, our estimate would be increased by a factor of 10. We now examine these estimates more closely.

The parameters we need to specify for (1)–(4) are the conductivity of the extracellular fluid σ, the specific membrane properties c and g, and the geometrical parameters d and l. The interstitial fluid can be reasonably treated as sea water. Thus σ can be taken as $1.88/\Omega\cdot m$ at 10^8 Hz {22}. Typical values for c and g are also well known {22}: we can take $c = 10^{-6}\ s/\Omega\cdot cm^2$ and g can be taken as $10^{-3}\ (\Omega\cdot cm^2)^{-1}$ for passive membrane and approximately $1(\Omega\cdot cm^2)^{-1}$ for excited membrane. In normal nervous function g can take on increased ("excited") values when the relevant patch of membrane is the focus of an "all-or-none" spike potential, or when it is the site of an active synapse. These differences will help us specify the regions of nerve cells where induced potentials should be most marked. Thus we will carry out computations for each of three values of g which we suppose correspond to each of three classes of membrane loci: the cases where g is assigned the value for passive membrane should represent neural segments where both sides of the equivalent cylinder are inactive (this should represent passive regions generally and also excitable membrane at points of time when no spikes are being generated); those cases where g is assigned the excited value should correspond to a locus of excitable membrane which is currently active; and a locus of membrane under an active synapse is described here by supposing that the excited value of g applies to one membrane in the current pathway while the passive value corresponds to the other, in this case, we consider the potential across the passive membrane and, therefore, use the passive value of g in (4). The geometrical parameters d and l are interpreted as follows: d is the diameter of the neural process and l is the distance between the centers of adjacent processes ($l \geqslant d$). There is no single set of values for l and d which is representative of nervous tissue generally. Rather, points within an extensive region of l,d combinations are applicable to different neural segments and very large local variations exist. We will map our results over the plane $d,l = 0.01$ to 50 μm and use these comparative results to further aid us in localizing where, within nervous tissue, our predicted effects should be most marked.

TABLE I
MEMBRANE DEPOLARIZATION* FOR ELECTROMAGNETIC RADIATION AT 10^8 Hz

x										
					(a) $g = 0.001$					
0.990	0.0196	0.1462	0.2129	0.2167	0.2178	0.2180	0.2180	0.2180	0.2180	0.21
0.980	0.0132	0.1124	0.2025	0.2101	0.2123	0.2127	0.2127	0.2127	0.2128	0.21
0.950	0.0075	0.0705	0.1773	0.1942	0.1999	0.2008	0.2009	0.2010	0.2010	0.201
0.900	0.0047	0.0456	0.1456	0.1725	0.1831	0.1848	0.1851	0.1852	0.1854	0.18
0.800	0.0028	0.0275	0.1047	0.1377	0.1544	0.1573	0.1579	0.1581	0.1583	0.15
0.700	0.0020	0.0199	0.0805	0.1116	0.1295	0.1329	0.1336	0.1338	0.1340	0.13
0.600	0.0016	0.0158	0.0650	0.0918	0.1080	0.1111	0.1117	0.1119	0.1121	0.11
0.500	0.0013	0.0133	0.0544	0.0761	0.0890	0.0914	0.0919	0.0920	0.0922	0.09
0.400	0.0012	0.0118	0.0464	0.0629	0.0718	0.0734	0.0737	0.0739	0.0740	0.07
0.300	0.0011	0.0108	0.0394	0.0503	0.0555	0.0564	0.0565	0.0566	0.0567	0.05
0.200	0.0010	0.0100	0.0314	0.0368	0.0389	0.0392	0.0393	0.0394	0.0394	0.03
0.100	0.0010	0.0091	0.0194	0.0206	0.0209	0.0209	0.0210	0.0210	0.0210	0.021
0.010	0.0009	0.0022	0.0023	0.0023	0.0023	0.0023	0.0023	0.0023	0.0023	0.00
0.001	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.00
					(b) $g = 1$					
0.990	0.0196	0.1455	0.2124	0.2164	0.2177	0.2179	0.2179	0.2180	0.2180	0.21
0.980	0.0132	0.1118	0.2020	0.2097	0.2122	0.2126	0.2127	0.2127	0.2127	0.21
0.950	0.0075	0.0702	0.1766	0.1937	0.1997	0.2006	0.2008	0.2009	0.2010	0.201
0.900	0.0047	0.0455	0.1449	0.1719	0.1828	0.1846	0.1850	0.1851	0.1853	0.185
0.800	0.0028	0.0275	0.1042	0.1371	0.1541	0.1571	0.1577	0.1580	0.1582	0.15
0.700	0.0020	0.0199	0.0801	0.1111	0.1293	0.1327	0.1334	0.1337	0.1340	0.134
0.600	0.0016	0.0158	0.0647	0.0913	0.1077	0.1109	0.1116	0.1118	0.1121	0.112
0.500	0.0013	0.0133	0.0542	0.0758	0.0888	0.0913	0.0918	0.0920	0.0922	0.092
0.400	0.0012	0.0118	0.0462	0.0626	0.0716	0.0734	0.0737	0.0738	0.0740	0.074
0.300	0.0011	0.0107	0.0392	0.0501	0.0554	0.0563	0.0565	0.0566	0.0567	0.05
0.200	0.0010	0.0100	0.0312	0.0367	0.0389	0.0393	0.0393	0.0394	0.0394	0.039
0.100	0.0010	0.0091	0.0193	0.0205	0.0209	0.0210	0.0210	0.0210	0.0210	0.021
0.010	0.0009	0.0022	0.0023	0.0023	0.0023	0.0023	0.0023	0.0023	0.0023	0.002
0.001	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.000
					(c) $g_1 = 0.001$, $g_2 = 1$					
0.990	0.0196	0.1458	0.2126	0.2166	0.2178	0.2179	0.2180	0.2180	0.2180	0.218
0.980	0.0132	0.1121	0.2023	0.2099	0.2123	0.2126	0.2127	0.2127	0.2128	0.212
0.950	0.0075	0.0703	0.1769	0.1940	0.1998	0.2007	0.2009	0.2010	0.2010	0.201
0.900	0.0047	0.0455	0.1452	0.1722	0.1830	0.1847	0.1851	0.1852	0.1853	0.185
0.800	0.0028	0.0275	0.1045	0.1374	0.1542	0.1572	0.1578	0.1580	0.1583	0.158
0.700	0.0020	0.0199	0.0803	0.1114	0.1294	0.1328	0.1335	0.1338	0.1340	0.134
0.600	0.0016	0.0158	0.0649	0.0916	0.1078	0.1110	0.1116	0.1118	0.1121	0.112
0.500	0.0013	0.0133	0.0543	0.0759	0.0889	0.0913	0.0918	0.0920	0.0922	0.092
0.400	0.0012	0.0118	0.0463	0.0627	0.0717	0.0734	0.0737	0.0738	0.0740	0.074
0.300	0.0011	0.0107	0.0393	0.0502	0.0554	0.0563	0.0565	0.0566	0.0567	0.056
0.200	0.0010	0.0100	0.0313	0.0368	0.0389	0.0393	0.0393	0.0394	0.0394	0.039
0.100	0.0010	0.0091	0.0193	0.0205	0.0210	0.0210	0.0210	0.0210	0.0210	0.021
0.010	0.0009	0.0022	0.0023	0.0023	0.0023	0.0023	0.0023	0.0023	0.0023	0.002
0.001	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.0002	0.000
	0.01	0.10	0.50	1.00	2.50	5.00	7.50	10.00	25.00	50.0

*All entries for δV in this table should be increased by the factor 1.93 in order to give δV millivolts.

Table I shows how the induced transmembrane potential δV for the case of radiation at the frequency 10^8 Hz, depends on the geometric parameters d and x. Table I(a), I(b), and I(c) pertain, respectively, to the cases of passive membrane, excited membrane, and the combination of the two. The values are very nearly the same in all three Tables since at this high frequency almost all the current is associated with the capacitive term.

The values for δV range up to about four-tenths of a millivolt and tend to increase with the packing density x and with the process diameter d. This may be readily understood on the basis of the equations derived above. If

TABLE II
MEMBRANE DEPOLARIZATION* FOR STEADY ELECTRIC STIMULATION

x										
	(a) $g=0.001$									
0.990	0.020	0.198	0.985	1.970	4.926	9.851	14.774	19.697	49.213	98.326
0.980	0.013	0.132	0.662	1.323	3.307	6.614	9.920	13.225	33.050	66.053
0.950	0.008	0.075	0.376	0.752	1.881	3.761	5.641	7.522	18.800	37.584
0.900	0.005	0.047	0.235	0.470	1.175	2.351	3.526	4.701	11.751	23.495
0.800	0.003	0.028	0.140	0.279	0.698	1.396	2.094	2.792	6.980	13.957
0.700	0.002	0.020	0.101	0.201	0.504	1.007	1.510	2.014	5.035	10.069
0.600	0.002	0.016	0.080	0.160	0.399	0.799	1.198	1.597	3.992	7.983
0.500	0.001	0.013	0.067	0.135	0.337	0.674	1.011	1.348	3.368	6.736
0.400	0.001	0.012	0.060	0.119	0.298	0.596	0.894	1.192	2.980	5.958
0.300	0.001	0.011	0.055	0.110	0.274	0.548	0.821	1.095	2.737	5.474
0.200	0.001	0.010	0.052	0.104	0.260	0.519	0.778	1.038	2.594	5.186
0.100	0.001	0.010	0.050	0.101	0.252	0.504	0.756	1.008	2.520	5.037
0.010	0.001	0.010	0.050	0.100	0.250	0.500	0.749	0.998	2.488	4.951
0.001	0.001	0.010	0.050	0.100	0.249	0.494	0.738	0.979	2.379	4.546
	(b) $g=1$									
0.990	0.020	0.196	0.966	1.894	4.472	8.188	11.324	14.008	24.425	32.476
0.980	0.013	0.132	0.652	1.287	3.091	5.803	8.201	10.337	19.460	27.572
0.950	0.008	0.075	0.373	0.740	1.805	3.469	5.010	6.439	13.236	20.422
0.900	0.005	0.047	0.234	0.465	1.143	2.224	3.248	4.220	9.145	14.967
0.800	0.003	0.028	0.139	0.277	0.685	1.343	1.977	2.587	5.826	9.996
0.700	0.002	0.020	0.100	0.200	0.495	0.974	1.438	1.887	4.308	7.528
0.600	0.002	0.016	0.080	0.159	0.393	0.774	1.143	1.501	3.441	6.047
0.500	0.001	0.013	0.067	0.134	0.331	0.652	0.963	1.264	2.893	5.071
0.400	0.001	0.012	0.059	0.118	0.293	0.575	0.848	1.112	2.523	4.375
0.300	0.001	0.010	0.055	0.109	0.268	0.525	0.771	1.008	2.249	3.817
0.200	0.001	0.010	0.052	0.103	0.252	0.490	0.715	0.928	2.002	3.258
0.100	0.001	0.010	0.050	0.099	0.239	0.455	0.651	0.829	1.637	2.424
0.010	0.001	0.010	0.046	0.083	0.167	0.251	0.302	0.335	0.420	0.458
0.001	0.001	0.008	0.025	0.034	0.042	0.046	0.048	0.048	0.050	0.050
	(c) $g_1=0.001$, $g_2=1$									
0.990	0.039	0.394	1.969	3.937	9.841	19.678	29.510	39.339	98.228	196.060
0.980	0.026	0.264	1.322	2.643	6.607	13.212	19.816	26.417	65.987	131.790
0.950	0.015	0.150	0.752	1.503	3.758	7.514	11.271	15.026	37.546	75.030
0.900	0.009	0.094	0.470	0.939	2.348	4.696	7.044	9.392	23.471	46.916
0.800	0.006	0.056	0.279	0.558	1.395	2.790	4.184	5.579	13.943	27.876
0.700	0.004	0.040	0.201	0.402	1.006	2.012	3.018	4.024	10.059	20.111
0.600	0.003	0.032	0.160	0.319	0.798	1.595	2.393	3.190	7.975	15.944
0.500	0.003	0.027	0.135	0.269	0.673	1.346	2.019	2.692	6.729	13.453
0.400	0.002	0.024	0.119	0.238	0.595	1.191	1.786	2.381	5.952	11.900
0.300	0.002	0.022	0.109	0.219	0.547	1.094	1.641	2.188	5.468	10.932
0.200	0.002	0.021	0.104	0.207	0.518	1.037	1.555	2.073	5.181	10.356
0.100	0.002	0.020	0.101	0.202	0.504	1.007	1.511	2.014	5.032	10.054
0.010	0.002	0.020	0.100	0.200	0.499	0.997	1.494	1.990	4.946	9.795
0.001	0.002	0.020	0.100	0.199	0.494	0.978	1.453	1.920	4.542	8.338
	0.01	0.10	0.50	1.00	2.50	5.00	7.50	10.00	25.00	50.00

*All entries for δV in this table should be increased by the factor 2.0 in order to give δV in millivolts.

TABLE III
RELATIVE TRANSMEMBRANE DEPOLARIZATION FOR VARIOUS FREQUENCIES OF INCIDENT ELECTROMAGNETIC RADIATION

Frequency (cps)	Depolarization g = .001	g = 1
10^0	4.28×10^{-7}	4.15×10^{-7}
10^1	3.70×10^{-6}	3.60×10^{-6}
10^2	3.08×10^{-5}	3.00×10^{-5}
10^3	3.08×10^{-4}	3.00×10^{-4}
10^4	2.41×10^{-3}	2.25×10^{-3}
10^5	1.98×10^{-2}	1.93×10^{-2}
10^6	1.85×10^{-1}	1.78×10^{-1}
10^7	1.00×10^{0}	9.60×10^{-1}
10^8	1.00×10^{0}	1.00×10^{0}
10^9	4.32×10^{-1}	4.32×10^{-1}
10^{10}	2.04×10^{-1}	1.83×10^{-1}

TABLE IV
FREQUENCY DEPENDENCE OF PARAMETERS

Frequency (cps)	$\sigma(\frac{1}{\Omega\text{-m}})$	$\sigma'(\frac{1}{\Omega\text{-m}})$	$C(\frac{\mu f}{cm^2})$	$\varepsilon/\varepsilon_0$
10^0	4	.065	1.4	78
10^1	4	.075	1.4	78
10^2	4	.09	1.4	78
10^3	4	.09	1.3	78
10^4	4	.12	.9	78
10^5	4	.14	.9	78
10^6	4	.15	.9	78
10^7	4	.24	.9	78
10^8	1.67	.38	.9	78
10^9	1.88	.38	.9	78
10^{10}	1.88	.38	.9	78

d is held constant, then an increase in x causes relatively little change in the total resistance of the transmembrane pathway, but increases the total resistance in the extracellular pathway. If x is held constant, then an increase in d causes no change in the resistance of the extracellular pathway, but decreases that of the transmembrane pathway by increasing the total quantity of membrane permeability and capacitance. Both of these cases lead to an increase in the percentage of current which penetrates the cell membrane.

As can be seen in Table I, for any given packing density x, there is a value of d beyond which further increase in d causes little increase in δV. For the case shown in Table I, these values are less than about 7.5 μm.

Thus Table I suggests that the induced transmembrane potential should be bigger in more densely packed regions than in sparsely packed regions, should be bigger on larger nerve components than on smaller ones (probably larger on the soma of nerve cells than their dendrites) provided the packing densities are comparable, and should be of the order of tenths of a millivolt for a 200-V/m extracellular field.

Table II (a), (b), and (c) shows comparable results for a steady electric field of 200 V/m. Table II also shows the tendency for δV to increase with increasing x and increasing d. The values of δV for the steady case are roughly an order of magnitude higher than for the microwave case, and for very highpacking densities and large processes exceed tenths of millivolts.

From (5) and the last of (6), one may estimate how the induced transmembrane potential δV varies with the frequency ω of electromagnetic radiation of fixed intensity.

Table III shows such results for both passive and excited membrane for a case where $d=5$ μm and $x=0.6$. These results do indeed show a peak in the response δV in the radio frequency range, specifically at about 10^8 Hz. Physically, our interpretation says that, at lower frequencies, the value of the induced electric field is too small to produce a significant direct neuroelectric effect, and at higher frequencies the ions do not follow the field sufficiently well to produce an effective transmembrane potential.

To get the values shown in Table III, the various parameters have been assigned the frequency dependencies shown in Table IV [22].

The model used for Table III has neglected higher order terms which can result in very large resonance values for E, particularly within the microwave and radiowave region. (Indeed, the value of 200 V/m used in the

TABLE V
GEOMETRIC PARAMETERS

x					η					
0.990	0.3	3.3	16.3	32.5	81.4	162.7	244.1	325.4	813.5	1627.0
0.980	0.2	2.2	11.2	22.4	56.0	111.9	167.9	223.8	559.6	1119.2
0.950	0.1	1.3	6.7	13.5	33.7	67.4	101.0	134.7	336.8	673.5
0.900	0.1	0.9	4.6	9.1	22.9	45.7	68.5	91.3	228.3	456.5
0.800	0.1	0.6	3.2	6.4	15.9	31.8	47.6	63.5	158.8	317.5
0.700	0.1	0.5	2.7	5.4	13.5	27.0	40.6	54.1	135.2	270.4
0.600	0.1	0.5	2.6	5.1	12.8	25.6	38.5	51.3	128.2	256.3
0.500	0.1	0.5	2.6	5.3	13.1	26.3	39.4	52.6	131.5	262.9
0.400	0.1	0.6	2.9	5.8	14.5	29.0	43.5	58.0	145.0	290.0
0.300	0.1	0.7	3.5	7.0	17.4	34.8	52.2	69.6	173.9	347.8
0.200	0.1	0.9	4.7	9.5	23.7	47.4	71.1	94.8	237.1	474.2
0.100	0.2	1.7	8.6	17.3	43.2	86.5	129.7	172.9	432.3	864.6
0.010	1.6	15.9	79.3	158.7	396.6	793.3	1190.0	1586.5	3966.3	7932.5
0.001	15.7	157.2	786.2	1572.4	3930.9	7861.8	11793.0	15724.0	39309.0	78618.0
					$\frac{2}{\pi}\left\{1-\frac{d}{\frac{2}{\pi}x-\eta}\right\}$					
0.990	0.60558	0.60558	0.60558	0.60558	0.60558	0.60558	0.60558	0.60558	0.60558	0.60558
0.980	0.59103	0.59103	0.59103	0.59103	0.59103	0.59103	0.59103	0.59103	0.59103	0.59103
0.950	0.55848	0.55848	0.55848	0.55848	0.55848	0.55848	0.55848	0.55848	0.55848	0.55848
0.900	0.51493	0.51493	0.51493	0.51493	0.51493	0.51493	0.51493	0.51493	0.51493	0.51493
0.800	0.43978	0.43978	0.43978	0.43978	0.43978	0.43978	0.43978	0.43978	0.43978	0.43978
0.700	0.37248	0.37248	0.37248	0.37248	0.37248	0.37248	0.37248	0.37248	0.37248	0.37248
0.600	0.31152	0.31152	0.31152	0.31152	0.31152	0.31152	0.31152	0.31152	0.31152	0.31152
0.500	0.25628	0.25628	0.25628	0.25628	0.25628	0.25628	0.25628	0.25628	0.25628	0.25628
0.400	0.20555	0.20555	0.20555	0.20555	0.20555	0.20555	0.20555	0.20555	0.20555	0.20555
0.300	0.15744	0.15744	0.15744	0.15744	0.15744	0.15744	0.15744	0.15744	0.15744	0.15744
0.200	0.10943	0.10943	0.10943	0.10943	0.10943	0.10943	0.10943	0.10943	0.10943	0.10943
0.100	0.05833	0.05833	0.05833	0.05833	0.05833	0.05833	0.05833	0.05833	0.05833	0.05833
0.010	0.00630	0.00630	0.00630	0.00630	0.00630	0.00630	0.00630	0.00630	0.00630	0.00630
0.001	0.00064	0.00064	0.00064	0.00064	0.00064	0.00064	0.00064	0.00064	0.00064	0.00064
					$\frac{2}{\pi}\left\{1-\frac{d}{\frac{2}{\pi}x-\eta}\right\}\cdot\eta$					
0.990	0.197	1.970	9.853	19.709	49.265	98.530	147.790	197.060	492.650	985.300
0.980	0.132	1.323	6.615	13.230	33.074	66.148	99.222	132.300	330.740	661.480
0.950	0.075	0.752	3.762	7.523	18.808	37.617	56.425	75.233	188.080	376.170
0.900	0.047	0.470	2.351	4.702	11.754	23.509	35.263	47.018	117.540	235.090
0.800	0.028	0.279	1.396	2.793	6.982	13.963	20.945	27.927	69.817	139.630
0.700	0.020	0.201	1.007	2.015	5.036	10.073	15.109	20.145	50.363	100.730
0.600	0.016	0.160	0.799	1.597	3.993	7.983	11.978	15.971	39.927	79.854
0.500	0.013	0.135	0.674	1.348	3.369	6.738	10.107	13.476	33.690	67.380
0.400	0.012	0.119	0.596	1.192	2.980	5.960	8.941	11.921	29.802	59.604
0.300	0.011	0.110	0.548	1.095	2.738	5.476	8.214	10.952	27.381	54.762
0.200	0.010	0.104	0.519	1.038	2.595	5.190	7.784	10.379	25.947	51.895
0.100	0.010	0.101	0.504	1.009	2.521	5.043	7.564	10.086	25.214	50.428
0.010	0.010	0.100	0.500	1.000	2.500	5.000	7.500	10.000	25.000	49.997
0.001	0.010	0.100	0.499	0.9985	2.497	4.993	7.490	9.987	24.963	49.927
	0.01	0.10	0.50	1.00	2.50	5.00	7.50	10.00	25.00	50.00

present paper is just such a case.) However, the effect of these terms should be to accentuate the resonance at 10^8 Hz which our equations have suggested. Thus for frequencies below about 10^8 Hz, (5) should be reasonably accurate for the brain cavity; for frequencies above 10^{10} Hz the neuroelectric mechanisms will not follow the field (this attenuation is very fast); resonances should produce large peaks in the E field within the microwave or radiowave range. These three factors suggest that the peak shown in Table III to occur at about 10^8 Hz, not only should occur in a more detailed analysis, but should be amplified.

Table V shows how some of the geometric parameters involved in (1)–(7) vary with packing density x and diameter d.

III. Discussion

The primary conclusions of this analysis are as follows.

1) Large cell components in regions of high cell density should be most influenced by extracellularly applied currents or fields.

2) The neuroelectric potential induced by electromagnetic radiation should exhibit a maximum at about 10^8 Hz.

3) An electric field of 200 V/m oscillating at 10^8 Hz could produce a neural transmembrane potential of tenths of a millivolt.

And that, therefore,

4) This direct mechanical action of the electric field may very well contribute to the behavioral disturbances associated with low-intensity microwave and radiowave irradiation.

Thus according to this analysis, an incident field of 10 mW/cm^2, which should induce a peak intracranial electric field of some 200 V/m, can in turn lead to transmembrane depolarizations of tenths of a millivolt. Most marked disturbances have been reported in the literature when the incident field exhibits high peaks in intensity well above a low mean level [3], [18]. Thus for example, Frey's auditory hallucinations [5] often incorporate peak intensities close to 100 m/W/cm^2. Our model would predict a depolarization of some 4 or 5 mV for such a case. There is no question but that membrane depolarization of this magnitude can influence ongoing neuroelectric behavior [20], [29], [30].

A main purpose of this paper is to induce experimentation to examine the transmembrane potentials in nerve cells associated with microwave and radiowave radiation. In this context, we echo Frey's observation that "of the sum total of biological experimentation with (radio frequency) energy, however, very little has been concerned with the nervous system," and his call for neuroelectric experimentation [4].

Finally, we should point out that Schwan has argued in personal communication with the present author that, since the cutoff frequency for the membrane potential is in the low-megahertz region, these models probably do not represent the main influence of microwaves or radiowaves on biological tissue. Nonetheless, in our opinion, Schwan's objections to these hypothetical direct nonthermal influences of microwaves may be valid but do not seem necessarily so. Moreover, the balance of the considerable experimental evidence [3]–[14], the apparent plausibility of the mechanisms assumed in both the present model and in the model of Barnes and Hu [21], and the compatibility of these two models seems to strongly encourage us to at least consider them as possibilities, until further experimentation finally resolves the issue.

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