

Tissue Interactions With Nonionizing Electromagnetic Fields

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In several parts of this treatise an attempt has been made to explain electromagnetic phenomena by means of mechanical action transmitted from one body to another by means of a medium occupying the space between them. The undulatory theory of light assumes the existence of a medium. . . . To fill all space with a new medium whenever any new phenomenon is to be explained is by no means philosophical, but if the study of two branches of science has independently suggested the idea of a medium, and if the properties which must be attributed to the medium in order to account for electromagnetic phenomena are of the same kind as we attribute to the luminiferous medium in order to account for the phenomena of light, the evidence for the physical existence of the medium will be considerably strengthened.

James Clerk Maxwell (286)

I. INTRODUCTION

Life on earth has evolved in the presence of an unceasing flux of natural electromagnetic fields. These arise mostly from solar radiation, supplemented substantially at some frequencies by terrestrial electromagnetic disturbances.

including thunderstorms. In the last 50 years there has been an exponential growth of man-made electromagnetic fields, associated with communication systems that now blanket the earth and with a vast and ever-increasing network of electric power distribution systems (317). It is therefore curious that although many of the most important fundamental observations on physical effects of light and other nonionizing electromagnetic radiations were made more than 100 years ago, knowledge of their biological effects has remained minimal (215). It is only recently that selective imposition of these fields at radio and microwave frequencies has been recognized as a possibly unique tool in understanding aspects of the molecular biology of normal and abnormal growth (150, 175), cell-mediated immune responses (423), and in intrinsic processes of communication between brain cells (4). At the same time, heightened public awareness of potentially hazardous aspects of domestic and industrial sources of these fields has only served to underline the biologist's meager understanding of physical and chemical substrates of bioeffects other than those induced by strong thermal interactions. It has been commonly held that field interactions occur only with a thermal perturbation that directly increases cell metabolic levels (299). This would preclude the occurrence of so-called "nonthermal" effects, now widely reported in experiments with tissue dosimetric controls lacking a decade ago. The question of adequate controls in experiments with low-level electromagnetic fields, particularly in some pioneering studies two decades ago, is often difficult to evaluate. Therefore much of the earlier research is now being repeated, with careful attention to absorbed tissue dosage; to the possibilities of focal "hot spots" attributable to structural phase discontinuities within organ systems (258) and to the organism's physical geometry with respect to wavelength and polarization of the imposed field (82, 154); and to time-dependent aspects (116, 196, 278) of biological responses to a virtually infinite matrix of field intensity, frequency, and modulation parameters.

Research in this field began with the clear desire to better understand physical processes underlying biological interactions with natural and artificial electromagnetic (EM) fields (378). This continues to be a major and substantially uncompleted task. There is a new awareness, however, that manipulation of the EM environment of tissues with nonionizing energy sources has disclosed new classes of molecular events of fundamental importance in broad areas of cell biology (373). These are cooperative processes, characterized by extreme nonlinearity in the often-catastrophic level of response elicited by a far weaker stimulus. Transductive coupling of weak EM stimuli at the neuronal membrane surface (238) or at the lymphocyte surface (118) may involve these processes. It is in the essence of cooperativity that nonequilibrium processes are involved, with energy exchanges circumscribed within relatively narrow intensity and frequency bands. Familiar biological doctrines of excitatory processes based on ionic shifts toward or away from equilibrium conditions do not pertain in these models (144, 148, 149, 172, 173, 207, 221), even though the sequence of excitatory events beyond the first transductive coupling can be so described.

So far this research field has remained outside the general interest of biologists. Only recently have sufficient experimental data accumulated on interactions with the nervous system to permit even a qualitative approach to models of observed "nonthermal" interactions. Quantitative models that can be evaluated in rigorous experimental testing must await future research. This is an important point, emphasizing that biological observations, biophysical concepts, and engineering methodologies are all at an early stage in a common approach to understanding the molecular basis of electromagnetic (EM) bioeffects.

This review emphasizes EM field interactions with nervous tissue. It draws significantly on recent research in the molecular biology of immunology, hematology, and oncology, where related EM field research has helped to develop unifying concepts (92, 191, 216, 430, 435). The cumulative evidence suggests that the brain and certain other regions of the nervous system may be more sensitive than other major organ systems, certainly in the context of short-term, reversible interactions. At the same time, these nervous interactions with low-level fields have stimulated a search for comparable sensitivities in other systems.

II. BIOPHYSICAL CONSIDERATIONS

The natural EM environment covers a very wide frequency spectrum, from essentially steady-state electric and magnetic fields to very energetic γ -rays of extraterrestrial origin at frequencies of 10^{23} Hz. The higher frequencies of X rays and γ -radiation can disrupt atomic structure with release of charged and uncharged subatomic particles. These bands of frequencies are thus sources of ionizing radiation, a property that can also be interpreted in terms of particle theories of EM radiation as an attribute of high photon energies. At lower frequencies (and longer wavelengths), atomic destruction does not occur, and modes of energy transfer are modeled on a variety of frequency-dependent processes in molecules and portions of molecules. Again, in the idiom of particle theories of radiation, these lower frequencies have lower photon energies than in an ionizing field (316). This review considers bioeffects of nonionizing electromagnetic fields in the spectrum from zero frequency to the far infrared. Our knowledge of the physical electrodynamics of these interactions rests on the monumental studies of Maxwell (286), who ascribed properties of both particles and waves to propagating EM waves. Feynman et al. (132) have remarked that "from a long view of the history of mankind—seen from, say, ten thousand years from now—there can be little doubt that the most significant event of the 19th century will be judged as Maxwell's discovery of the laws of electrodynamics. The American Civil War will pale into provincial insignificance in comparison with this important scientific event of the same decade."

A. Concepts of Steady-State Electromagnetic Fields

The basis of an electric field in association with unequal spatial distribution of electric charges is a familiar intuitive concept. An electric field is said to exist in a region of space if a charge at rest experiences a force of electrical origin. A moving charged particle produces a magnetic field at right angles to its direction of motion.

Electric fields alter molecular and atomic configurations in dielectric substances. All atoms polarize when placed in an electric field. If we envisage the atom as a positive nucleus at the center of a spherical cloud of negative charges, the center of this cloud is coincident with the nucleus, and there is no net negative charge at points outside the atom. In the presence of an electric field, however, the atom of a dielectric substance is polarized, with the positive nucleus and the negative electron cloud now slightly displaced by the impressed field. The atom thus behaves as a dipole. Molecules may have permanent dipoles between their constituent atoms, and external electric fields then exert a torque on these dipoles. To the extent that thermal motion allows, they will then align themselves with the impressed field. Whereas this polarization of the electron cloud-nucleus system is essentially temperature independent, this is not the case for polarization of molecules with permanent dipoles. Thermal motion causes them to remain more or less randomly oriented, in the high- T limit.

Magnetic properties of matter can be traced to charge motion, whether over long distances, as in the flow of conduction electrons, or in charge motions close to or within an atom or molecule (65). Each orbital electron can be considered as providing its own magnetic moment to the atom. An orbital electron also possesses an intrinsic magnetic moment, since it can be considered as a charge spinning about its axis. The nuclei of most atoms also have magnetic moments, which are about one-thousandth as large as the orbital and spin magnetic moments. The magnetic moment of an atom as a whole is the sum of these three moments. An imposed magnetic field tends to cause the magnetic loops within each atom and molecule to align with the imposed field. This paramagnetic effect of alignment in the presence of an external magnetic field is therefore greater at low temperatures. On the other hand, thermal motion tends to disalign them. Normally dipole moments are exactly opposite between orbital electron pairs, so that there is no paramagnetic effect from this source in atoms with an even number of electrons. Atoms with an odd number of electrons do not have exact cancellation. For most nonferromagnetic substances, their presence in a magnetic field changes the imposed magnetic field as a result of alignment of moving charges by only 1 part in 10^5 . By contrast, the transition elements, including iron, nickel, and cobalt, have a complex arrangement of electrons in two incompletely filled outer shells. The usual cancellation of electron spin magnetic moments does not occur, and these atoms therefore have unusually large magnetic dipole moments. They become aligned in small regions (domains) with magnetic moments all in the same direction. They belong to the class of diamagnetic substances.

*

The preponderance of paramagnetic material in living tissues therefore minimizes interactions between stationary objects and steady magnetic fields. The situation changes sharply for moving objects, particularly in the presence of artificial fields that may be 10^5 times the earth's natural field. Whereas this background level is about 0.00003 T, steady magnetic fields in projected public transportation systems would expose the public to fields in the range of 0.05 T. Projected electric power storage in toroidal superconducting magnets would have leakage fields as high as 8.0 T in their immediate vicinity. A migrating bird flying diagonally in the horizontal component of the earth's magnetic field at a speed of 20 m/s would induce a gradient of only 10^{-7} V/cm in its tissues. Even this small gradient appears to provide cues for navigation and spatial orientation (241-243, 246, 411). Far bigger fields in the vicinity of superconducting magnets induce gradients as large as 10^{-3} V/cm with normal body movement and lead to sensory nervous effects and changes in vector cardiogram and aortic blood flow (47).

B. Concepts of Oscillating Electric and Magnetic Fields

It is convenient to consider electric and magnetic fields separately in their effects on objects located in them when the fields are static or oscillating at very low frequencies. This is justified for these fields since little or no energy is lost from the system by radiation. Inefficiency of radiation from artificial generators at these frequencies is related to the extremely long wavelengths involved. A 10-Hz oscillation has a wavelength of 30,000 km. According to the Maxwell equations, an efficient radiator should approach a half wave in length at the frequency of excitation. Only the longest overhead power lines excited at 60 Hz, for example, even begin to approach these dimensions. In conductors substantially shorter than a half wave, as current rises and falls in the conductor, surrounding electric and magnetic fields collapse back into it. Energy is not lost from the conductor by radiation but is transmitted along it (403). The importance of this concept can be seen in the proposed U.S. Navy Seafarer submarine communication system. With a buried antenna grid covering more than 10,000 km² and an input power of megawatts at 76 Hz, the actual radiated power would be less than 100 W. Also characteristic phase relations are preserved between electric and magnetic fields in a radiated wave, with propagating electric and magnetic fields displaced 90° with respect to each other. These relations are difficult to define in the near field extending from 10 to 50 wavelengths from a radiating antenna. We consider effects of a conducting body on an electric field surrounding it and current flow induced by this field in that body.

1. Distortion of an electric field surrounding a conducting body

A body in an otherwise uniform electric field distorts the field so that electric gradients at the surface of the body are markedly increased.

For humans in the erect position close to the ground in a vertically oriented field, this enhancement is maximal around the head (104, 105). Thus the body presents an equivalent area at the head substantially larger than its physical cross section. This is associated with an increase in the displacement charge per unit area in the field surrounding the head. The capacitance to ground is maximized when the person stands on the ground and minimized when he is suspended far from the ground. In the latter situation, a solution of Laplace's equation describes potential distribution about the body surface (31, 403). Electrical gradients at the body surface are determined by the capacitance to free space, which is a function of the body's size and shape. For a spheroidal model of radius r (31), this capacitance (C) far from ground is

$$C = 4\pi\epsilon_0 r$$

where ϵ_0 is the dielectric permittivity of free space. This gives a capacitance of about 50 pF for $r = 0.5$ m. A third situation is that of the linesman working in actual contact with a live high-voltage transmission line at a distance above ground.

2. Current induced in a body exposed to an oscillating electric field

Sheppard and Eisenbud (403) have modeled current flowing in the body in the three situations described above. Close to the ground, total current I is determined by field strength E , body capacitance C , and effective height above ground h . The product $E \cdot h$ gives the potential V_0 to which the body current is

$$I = \omega V_0 C$$

where ω is the angular frequency of the field. For a man standing on the ground in a 10-kV/m, 60-Hz external field, the induced current would be about 200 μ A, or an approximate current density of 1.0 mA/m² through the trunk, and an internal electric field of 8.0 mV/m, assuming an internal resistivity of 5 $\Omega \cdot \text{cm}^{-1}$. For a man suspended in the same field, the total current drops to 65 μ A, with a current density through the trunk of 0.52 mA/m² and an internal electric field of 2.6 mV/m. For a person in contact with a conductor at 200 kV and 60 Hz, the total current is about 3 mA (31).

3. Dielectric behavior of tissue elements

The cellular nature of tissues establishes a vast number of dielectric partitions that separate strongly conducting intracellular and extracellular compartments. Thus cells are enclosed by poorly conducting membranes with a typical resistance of 5,000 $\Omega \cdot \text{cm}^{-2}$ (89) and lie within an extracellular space

with a specific resistance as low as $4 \Omega \cdot \text{cm}^{-1}$ (322). In this respect, tissues may be modeled in accordance with Maxwell's experiment with nonconducting sea urchin eggs as the dispersed phase in a bucket of seawater (88). Membrane structures contribute complexly to the observed dielectric behavior of tissues, and water itself is an important additional factor.

The dielectric properties of tissues, cell suspensions, and macromolecules have been extensively studied (378-384). The dielectric properties of tissues indicate that polarization from induced charges exceeds contributions from permanent dipoles. Dielectric dispersion studies indicate that most tissue water is in the free state. Schwan (378, 381) has identified three major dispersions: α , β , and γ . Each dispersion is fairly well defined by either a single relaxation time or a small spectrum of relaxation times:

1) α -Dispersion: dielectric relaxation of free water (frequency near 20 GHz, dielectric constant 10-50).

2) β -Dispersion: Maxwell-Wagner type of relaxation resulting from the charging of cell membranes (frequency near 1.0 MHz, dielectric constant of $10^2 - 10^4$).

3) γ -Dispersion: variability with frequency of the apparent outer cell membrane capacitance (frequency near 100 Hz, dielectric constant around 10^3). Schwan suggests that this frequency dependence of membrane capacitance may result from several causes: a frequency-dependent access to inner membrane structures that connect with the outer membrane (130); a frequency-dependent surface admittance, tangential to the cell membrane caused by counterion displacement from fixed-charge sites on membrane surface macromolecules; a capacitance related to the boundary potential and in series with the membrane capacitance; and a frequency-dependent intrinsic membrane capacitance arising in ionic gating currents (378, 425, 428).

Secondary dispersions may result from Maxwell-Wagner relaxation effects in membranes of organelles, from Debye-type relaxations caused by polar moments in proteins, and in relaxation of protein-bound water (164, 345, 382). Interactions of oscillating electric fields with biological macromolecules have been extensively studied (333, 426). Calculation of dispersions of dielectric constants of ice, protein-bound water, and free water shows that ice relaxes at audio frequencies, bound water between 100 and 1,000 MHz, and free water near 20 GHz (385). These data have been interpreted as indicating that the major fraction of all biopolymers is surrounded by nonstructured or free water. The measurements have been made with tissue field levels that provide an excellent model for an understanding of tissue heating induced by these fields. However, the techniques may not be adequate to reveal small amounts of structured bound water, as, for example, in intimate contact with the surface of macromolecules (272). From measurements at 10 MHz, Grant (165) concluded that hemoglobin may have such a layer of "highly viscous" water at its surface. Though difficult to detect, the existence of water in this special relationship to macromolecular substrates (114) may be important in the transductive coupling of weak EM fields. For example, binding of calcium

to macromolecular charge sites may occur directly to carboxyl groups, whereas *O*-sulfate groups offer a looser electrostatic attraction through an atmosphere of water molecules (346).

C. Models of Electromagnetic Radiation

The strong interdependence of electric and magnetic fields in conductors is easy to envisage phenomenologically where the current flowing in a conducting element is either flowing steadily in one direction or oscillating at low frequencies under 1 kHz. More complex situations may exist at frequencies beyond 10 or 20 kHz. This change may be attributed to the length of the conductor with respect to the wavelength of the electric oscillation. For metallic conductors, the wavelength of the flowing current may approximate a wavelength in free space. In body fluids and tissues, ionic conduction substantially replaces an electron flow, and the velocity factor is substantially less than in a metallic conductor. In a metallic conductor, the velocity of the current is a significant fraction of the velocity of light.

When the conductor is a significant fraction of a wavelength of the alternating current, the behavior of the electric and magnetic fields surrounding the conductor is modified substantially. Electric and magnetic fields around a conductor carrying a steadily flowing current or a low-frequency alternating current have energy levels that closely follow the changing current. As the flow declines from each maximum, the energies of these fields are returned to the conductor essentially without loss. "Long" conductors behave quite differently, because much of the energy surrounding electric and magnetic fields does not return to the conductor with declining current flow in it. Energy now moves away from the conductor as a propagated wave at the velocity of light. Its amplitude decreases linearly with distance from the conductor. Descriptively, the electric field around such a long conductor is impeded in its collapse by the simultaneous presence of a magnetic field, which is also collapsing toward the conductor, but relatively slowly. Portions of the field remote from the conductor do not collapse into it. Instead they propagate into the surrounding medium. Energy is lost from the conductor as a radiated wave. Maximum radiating efficiency occurs when the conductor is one or more half waves in length. These models and their experimental proof were intensively investigated in theoretical formulations by Maxwell (286) and in observations by Hertz (193) and Popov (353). There are few more exciting monographs in all science than the delightful account by Hertz of standing waves in a field reflected from a sheet of zinc suspended among the gas pipes at the end of the physics lecture room, from which he had removed the chandeliers and other metal objects to avoid "objectional effects."

Maxwell was the first to draw together in a coherent way earlier studies by Gauss and Faraday in four mathematical statements now known as Maxwell's equations. They include Gauss's law describing the electric charge on a body as the integral flux lines emerging from a dielectric volume containing

the body, Gauss's law showing that the algebraic sum of the number of magnetic flux lines emerging from the surface of a volume must be zero, Faraday's law on electromagnetic induction, and a modification of Ampère's law describing magnetic fields around a current-carrying conductor. Maxwell's elaboration of Ampère's law is known as the wave equation and remains the basis for all computations involving electromagnetic waves. His models allowed prediction of the velocity of light, are cornerstones in understanding biophysical interactions of electromagnetic fields with tissues, and have had tremendous importance in the physical and engineering sciences.

D. *Electromagnetic Radiation in the Environment*

The spectrum of natural EM radiations runs a gamut from γ -rays with frequencies of 10^{23} Hz and wavelengths of 10^{-14} m to frequencies below 10 Hz and wavelengths of 10^7 m. In the progression to shorter wavelengths, atomic disruption with production of ionized particles first occurs with longer X rays that overlap with ultraviolet fields at frequencies around 10^{16} Hz and wavelengths of 10^{-8} m. Nonionizing interactions occur at all lower frequencies. This review focuses on the region that includes the far infrared, microwave, radio, and extremely-low-frequency portions of the spectrum. There are a number of arbitrary classifications of these bands. The following scheme is used here:

DC-300 Hz	Extremely low frequency (ELF)
300 Hz-10 kHz	Very low frequency (VLF)
10 kHz-1 MHz	Low frequency (LF)
1 MHz-30 MHz	High frequency (HF)
30 MHz-300 MHz	Very high frequency (VHF)
300 MHz-1,000 MHz (1 GHz)	Ultrahigh frequency (UHF)
1 GHz-3,000 GHz	Microwave (MW)

1. *Natural environmental fields*

The natural sources of these radiations are galactic, solar, and terrestrial. Detectable components of extraterrestrial sources at radio and microwave frequencies are extremely weak, around 10^{-20} $W \cdot m^{-2} \cdot Hz^{-1}$ from a typical radio star, so that the possibility of bioeffects are negligible. Even the sun cannot be considered a strong source of energy in the nonionizing spectral region. In terms of possible direct interaction with central nervous tissue, terrestrial components of solar flux at 10 Hz do not exceed about 1 m V/m, with expected tissue gradients around 10^{-9} V/cm. It should be emphasized that at 10 Hz a wavelength is 3×10^7 m long. In the light of the preceding discussion of Maxwell's models, the human head is an extremely small fraction of a wavelength at electroencephalogram (EEG) frequencies and incapable of significant radiation.

TABLE 1. *USSR standards for civilian microwave exposure*

Frequency Range	Maximum Allowable Level (Domestic Exposure)
Long wave, 30-300 kHz	20 V/m
Medium wave, 0.3-3.0 MHz	10 V/m
Short wave, 3-30 MHz	4 V/m
Ultra short wave, 30-300 MHz	2 V/m
Microwaves (24-h exposure), 300 MHz-300 GHz	5 μ W/cm ²

Based on Shandala (401).

The models appear to offer no basis for telepathy, on a head-to-head basis. On the other hand, there is evidence for central nervous system (CNS) interactions with much stronger artificial fields at these frequencies (9).

There is a continuous spectrum of natural environmental EM fields of terrestrial origin from DC to about 3 kHz (252). Some change markedly with altered weather patterns. Others are related to the earth's geomagnetic field (352). This is influenced by particle radiation reaching the ionosphere from solar flares during years of high sunspot activity in the 11-yr solar cycle (97). In fair weather, the steady atmospheric electric field is about 150 V/m (432) but may increase to 10 kV/m in thunderstorms (112). The amplitude of natural oscillating electric gradients decreases logarithmically at frequencies up to 3 kHz, averaging 10^{-2} V/m at 1 Hz and 10^{-6} V/m at 3 kHz (253). Thunderstorm activity and ground currents associated with disturbed geomagnetic fields produce electric field oscillations as high as 10^{-2} V/m at frequencies between 1 and 10 Hz. The earth's magnetic field of 0.5 G may be increased severalfold during these storms, particularly at high latitudes. There is a series of resonances in this background spectrum at frequencies between 8 and 32 Hz. These Schumann (377) resonances arise as a cavity resonance between the earth's surface and the concentric conducting shell of ionospheric particles at heights between 80 and 200 km (240, 352).

2. *Man-made EM fields*

Background levels in urban domestic and industrial environments have increased exponentially in the last half century with the advent of electric power and EM communication systems. Ambient 60-Hz field levels of 1-10 V/m and levels as high as 250 V/m in the vicinity of electric blankets are typical in American homes (436). Hair dryers, electric shavers, and electric hand tools may expose the user to 60-Hz magnetic fields of 5-25 G, 20-75 times above natural DC background levels. High-voltage DC and 60-Hz overhead power lines have electric gradients of 10 kV/m to ground under them. These fields induce big charges on large ungrounded metal objects, such as trucks and vans, in their vicinity. Short-circuit currents between these objects and ground range from 1 to 5 mA. Accidental contact by a human subject produces painful shock.

Rapid growth of radio, television, and radar sources has raised issues of public health and environmental quality associated with current exposure guidelines. Current occupational standards for microwave frequencies permit an incident field of 10 mW/cm² for 0.1 h in any 1 h and a maximum continuous exposure of 1.0 mW/cm². (The significance of these units in relation to linear electric gradients used so far in this review is discussed below.) Existing standards for civilian microwave exposure in most Soviet bloc countries currently permit only 0.01 mW/cm², and a further downward revision is proposed to 0.005 mW/cm² for the USSR, based on animal models with immunological, hematological, and reproductive end points (401).

Surveys in the United States by the Environmental Protection Agency have shown that for a population group representing 18% of the total U. S. population, there is a median exposure of 0.000005 mW/cm² time-averaged power density. Less than 1% of the population are potentially exposed to levels above 0.001 mW/cm² (1 μW/cm²) (431). At least 99% of the population are not exposed to levels above the very stringent safety standards proposed for the USSR in 1974 (161). The FM radio broadcast service (88–108 MHz) is responsible for most of the continuous illumination of the general population (212).

3. Concepts of incident field power density and correlated environmental and tissue electric gradients

The amplitude of a radiated EM field decreases linearly with distance from the source. In the context of the introductory quotation from Maxwell, this decrement might be interpreted in terms of an "ether" that would fill all space and thus offer an impedance to EM wave propagation. The concept of an ether, which so vexed the modeling of Maxwell and Hertz and their contemporaries, has long been discarded. However, there is a residual concept, *the characteristic impedance of free space*, that addresses the same general problem. From it we may also derive the electric gradient associated with a particular incident field density.

The electric vector E and magnetic vector H may be expressed in terms of the electrical permittivity ϵ_0 and magnetic permeability μ_0 for an electromagnetic field propagating in a vacuum

$$E/H \pm \sqrt{\mu_0/\epsilon_0}$$

The electric and magnetic fields are therefore in a constant ratio to one another. On numerical substitution

$$E/H = 377 \Omega$$

This is the characteristic impedance of free space. It is the impedance of each 1.0 m of medium traversed by the incident field. For an incident field of 1.0

mW/cm² (10 W/m²), the electric gradient E may be expressed in terms of the power density W and the characteristic impedance R

$$E = \sqrt{W \cdot R}$$

Thus the electric gradient in a vacuum for an incident field of 1.0 mW/cm² is 61.4 V/m, and values in dry air will be similar.

The electric gradient induced in tissue by an environmental oscillating field will be determined by the electrical coupling of the organism to its surroundings. As discussed above in connection with the distortion a body causes in an environmental field, the electric gradients at the body surface are determined by its capacitance to free space. This is a function of the body's size and shape. For a body of fixed size, induced tissue currents will therefore increase as the field frequency increases below the condition of whole-body resonance, since the capacitive reactance ($1/C_{\omega}$) decreases linearly with frequency and capacitance. As discussed below, energy absorption is proportional to the square of frequency or higher for radio frequencies close to but below body resonance. Measured gradients for a 7-Hz 10-V/m field in a phantom monkey head are around 10^{-7} V/cm (437), whereas a 10-V/m field at 450 MHz induces a measured gradient of about 10^{-2} V/cm in the brain of a cat (34). The actual level at a particular locus will be determined by additional factors, including skin effects that limit depth of field penetration and local "hot spots" resulting from resonances arising in the physical geometry of the organism. These are discussed below (176, 258).

E. Nature of Interactions of Nonionizing Electromagnetic Fields With Biomolecular Systems

I. Molecular

In a recent comprehensive review, Illinger (208) has evaluated the collisional basis of molecular interactions with microwave and far-infrared fields. Crucial to the form of the dielectric response function (complex permittivity) of a molecule at the field frequency in the presence of collisional perturbations, and to the attenuation function that describes interaction with the field, is the duration of the collisional perturbation in relation to the period of the field (142, 439). Where the collisional perturbations are very brief for one period of the impressed EM field, every collision is effective in interrupting the absorption-emission process. In a fluid with many collisions per unit time, a collision-broadened relaxation-type spectrum results (206). Conversely, where collisional perturbations are very long compared to the period of the EM field, there is a resonant-type spectrum, even in a fluid where there are numerous collisions per unit time. Since the duration of a typical collision in a molecular fluid is fixed at a given temperature and pressure,

the field frequency determines whether there is a relaxation or resonance spectrum. Illinger concludes that no compelling evidence exists for resonant adsorption in ordinary molecular fluids below 3,000 GHz (163, 208). On these general grounds, the dielectric response function, as expressed in the complex permittivity, would be expected to have a relaxation spectrum from zero frequency to the far-infrared region. Attenuation of microwave fields in biological fluids is dominated by the ubiquitous distribution of water. Gaps in these data for the millimeter-wave region have recently been filled by measurements with a high-loss traveling-wave technique at 70 GHz (165). Accurate spectroscopy at these frequencies taxes current electromechanical technology. The broad attenuation due to water at these frequencies also shields other possible biomolecular absorption processes, including quasi-lattice vibrations in biopolymers and the vibrations of hydrogen-bonded bridgeheads (207).

Structural water, as opposed to free water in the bulk space, plays an important role in the stability of biopolymers and in their tertiary conformation changes (346, 373). Structural water is closely related to phase transitions in biopolymers that are known to be cooperative processes (391), as discussed below. The EM field interactions with brain tissue have been ascribed to cooperative transitions in transductive coupling to neuronal membranes (9).

2. Interaction of weak EM fields with biomolecular systems

It is clear from the preceding section that enhanced sensitivities of biomolecular systems through resonant interactions with EM fields at frequencies below 3,000 GHz in the far infrared are unlikely. On the other hand, there is unequivocal experimental evidence (cited below) that fields from ELF to UHF (10 Hz–450 MHz) interact directly with brain tissue. A striking feature of some of these observed interactions with weak radio-frequency (RF) fields is their relationship to modulation frequencies in the ELF range and not to the radio carrier frequency. This suggests the importance of a search for uniquely organized macromolecular systems as substrates for cooperative processes.

a) Possible biomolecular substrates of interactions with weak EM fields. Prior to later detailed consideration, it is desirable to set out the known or probable levels of induced tissue electric gradients associated with confirmed physiological or behavioral effects and to compare these with gradients associated with cellular events in excitation. The disparities emphasize the importance of understanding molecular mechanisms in transductive coupling of weak extracellular fields. Thus ELF fields in the range of the order of 10^{-7} V/cm are used in orientation, navigation, and prey attack in marine vertebrates (66, 227–230, 273, 274), in bird navigation (241–243, 245, 246, 410, 413–416), and in mammalian biorhythms (157, 159, 448, 454). Similar ELF fields modify calcium binding in cat and chick cerebral tissue (38). At higher tissue gradients around 100 mV/cm induced by RF fields with low-frequency

modulation, there are altered patterns in "spontaneous" ELF field potentials (400), in EEG wave trains evoked as conditional responses (40), and in the release of calcium from cerebral tissue (39, 41, 42, 58). By contrast, the gradient of typical membrane potentials is about 10^5 V/cm and membrane depolarization associated with synaptic excitation shifts the membrane potential by about 10^3 V/cm. The EEG gradient in extracellular fluid at cellular dimensions is only 20–50 mV/cm (124). Moreover, because of differential conductivities, transmembrane derivatives of extracellular current flow will be smaller by about 3 orders of magnitude. Thus without specialized molecular organization having an amplification mechanism, cellular sensing of the weak intrinsic EEG field or of imposed environmental fields of similar magnitude appears unlikely.

There is much evidence that the molecular organization in biological systems needed to perform this sensing of weak stimuli, whether thermal, chemical, or electrical, may reside in joint functions of molecular assemblies or subsets of these assemblies (238). Katchalsky (236) has reviewed the historic development from the time of Heraclitus (540–480 B.C.) of concepts of dynamic patterns that develop in a population of elements as a result of their complex flow patterns. These flow patterns can undergo sudden transitions to new self-maintaining arrangements that will be relatively stable over time. Transformation of complex flow patterns into larger hierarchical patterns is saltatory, as in the appearance of large crystals from small ones in a supersaturated solution (396). Because these dynamic patterns are initiated and sustained by continuing inputs of energy, they are classed as "dissipative" processes. For this reason they occur far from equilibrium with respect to at least one important parameter in the system (237). As nonequilibrium processes, they may be characterized by resonant or windowed phenomena, an important aspect of their occurrence in cerebral tissue interactions with weak EM fields (4, 10). Also two or more quite distinct mechanisms can give rise to the same dynamic pattern. A given pattern therefore need not relate to a unique mechanism; conversely, different mechanisms may generate a common pattern (337–339). To neurobiologists accustomed from their earliest training to consider cellular excitatory phenomena in terms of equilibrium processes, these concepts, though quite old in some areas of modern physics and chemistry (366), offer interesting new insights on possible substrates for initial events in excitatory transductive coupling.

b) Concepts of cooperative processes. A strong theme running through many of these functional linkages between participating elements of a dynamic pattern is *cooperativity*, defined here as the ways in which components of a macromolecule, or a system of macromolecules, act together to switch from one stable state of a molecule to another. These joint actions frequently involve phase transitions, hysteresis, and avalanche effects in input-output relationships (373, 462, 463). Trigger signals to cooperative processes may be weak and the amplified response orders of magnitude larger, as in the large generation of cyclic AMP by glucagon binding to plasma membrane receptors (368).

in the amplification of the immune response (119), and in swimming behavior of bacteria elicited by a small concentration gradient of an attractant (21, 254). The sharply nonlinear release of $^{45}\text{Ca}^{2+}$ from binding sites in cerebral tissue by added Ca ions (222) strongly suggests a cooperative interaction. Dense interactions of neurons in some brain centers have led to concepts of domains of cooperative neural activity (135). Detection of weak electrical fields by the brain is also consistent with highly cooperative effects (4).

Amplification effects in cooperative events raise questions about thresholds and the minimum size of an effective triggering stimulus. In studies of cooperativity in biological systems, attention is usually focused on the effect of a change in an external parameter on the equilibrium constant for a given reaction (391). Although the sharp transition from one highly stable state to another such state that is characteristic of a cooperative process can also be achieved by noncooperative means, much larger transition energies would be required and the transition would occur more slowly. Sharp and fast cooperative transitions characteristic of many biological systems thus involve cooperative interactions, such as the individually weak forces in a series of hydrogen bonds or hydrophobic reactions (128, 389, 392, 394). In considering possible cooperativity in electrical excitation of nerve membranes, Schwarz (391) points out that application of an electric field of strength E to a cooperative system alters the equilibrium constant according to Van't Hoff's relationship

$$\frac{\partial \ln s}{\partial E} = \frac{\Delta M}{RT}$$

where s is the stability constant (the equilibrium constant for $A \rightleftharpoons B$ when half the nearest neighbors are in *state A*, half in *state B*), and ΔM is the difference in the partial molar electrical moments (parallel to E) of reaction products and reactants (53, 387). A change of $\ln s$ therefore occurs when an electric field is applied to a biological macromolecule. A much higher electric field than can be reached in biological systems would be required to induce a transition in a noncooperative system, but a much weaker field will be adequate in a highly cooperative system. Compared with tissue electric gradients induced by environmental EM fields, the requisite gradient for some known cooperative macromolecular transitions are very large. The helix-coil conformational change in poly(γ -benzyl L-glutamate) can be induced as cooperative transition by a gradient of 260 kV/cm (395). Long-lasting conformational changes occur in poly(A)·2 poly(U) and in ribosomal RNA with pulsed electric field of 20 kV/cm and with a decay time of 10 μs (320). They are viewed as a model nerve excitability (321).

Therefore observed EM field interactions with brain and behavioral processes based on tissue gradients between 10^{-7} and 10^{-1} V/cm noted above clearly would involve degrees of cooperativity many orders of magnitude greater than envisaged in the examples just cited. A most important factor in determining the threshold for a low-level coherent oscillation to elicit a

cooperative response is the thermal Boltzmann (kT) noise in the system. This is 0.02 eV at room temperature and is the basis of molecular collisional interactions already discussed. Simply stated, the sensing of a gradient of 10^{-7} V/cm would require a cooperative molecular system extending over a distance of 300 m. The abundant evidence that extracellular electric gradients from 10^{-4} V/cm down to this level can be biologically significant in systems of cellular dimensions is a salutary reminder of the importance of better understanding molecular and morphological substrates of this transductive coupling. A hypothesis as yet untested suggests that the cell surface may act as an extremely narrow-bandwidth low-pass filter in the transfer of thermal noise along the surface of micron-sized spheres and tubes (38), thus enhancing the signal-to-noise ratio of ELF oscillations in the pass band of such a filtering system.

3. Quantum mechanical models of long-range interactions

There has been growing interest in models for predictive evaluation of these unexpected biological sensitivities. These models have considered two of the more baffling problems of these bioeffects: sensitivity to low incident field energy and possible bases for molecular interactions in the ELF spectrum below 100 Hz. There are at least four major groups of models. They have emphasized phase transitions at ELF, charge "pumping," and Volterra models of charge population transitions, limit-cycle phenomena, and possible tunneling effects.

a) *Models of macromolecular phase transitions at ELF.* No known mechanisms explain ELF bioeffects on the basis of direct interactions with component dipoles of molecular systems oscillating at these low frequencies. Therefore a structural and functional basis must reside in properties of molecular systems. Grodsky (172-174) has hypothesized that excitable membranes are energetically equivalent to sheets of giant dipoles bathed in controlled external electric fields. Grodsky's formulation envisaged the outer layer of phospholipid polar heads as a two-dimensional crystal mosaic of multipolar charge sites (p-sites), sprinkled with islands of glycoproteins with cationic binding sites (c-sites), in accordance with "greater-membrane" and "fluid-mosaic" models (372, 406) discussed below. Grodsky hypothesized that with the addition of an external low-frequency electric field to the system, when the frequency of an allowed mode of oscillation reaches zero, the system should then become a macroscopic quantum amplification device and would exhibit long-range order phase changes that generate energy into the zero-frequency mode (Einstein-Bose condensation). His model considers these long-range cooperative processes in latticed mosaic systems of the type first proposed by Ising (209) to explain mechanisms of ferromagnetism. The model has merit in seeking a basis in membrane ultrastructure but necessarily rests on the severe constraint of a rigidly ordered, spatially symmetric lattice having certain minimal dimensions. A structural counterpart of such a highly ordered lattice remains to be detected in biological membranes. It is applicable to chemically nonreactive systems. In

other applications of a linear Ising model to the kinetics of conformational changes in linear biopolymers (120, 388, 393), as many as four relaxation spectra have been found, but only one of them had a finite amplitude for a conformational transition having a strong degree of cooperativity (390). Moreover recent reappraisal of the possibilities of an Einstein-Bose phase transition as the basis for sensitivities at very low frequencies indicates that it would not occur with the particular formulation initially proposed by Grodsky (I. T. Grodsky and H. Fröhlich, personal communications).

b) *Charge "pumping" and Volterra models of charge population transitions.* Sensitivity of some biological systems to weak EM fields suggests that these systems can store signal energy and thus overcome thermal noise. These systems should require relatively small activation energies but be protected from thermal fluctuations. From an evolutionary viewpoint, the biological membrane can be considered as one of the most elemental of dissipative systems (324), and membrane properties have been defined in terms of nonequilibrium thermodynamics (62). The biological membrane may be considered as a chemically pumped, open, steady-state system (208), with energy provided for the membrane system from a sequence of feedback loops linking the steady-state concentrations of oscillatory biochemical reactions (328). Illinger (207) proposes that these dissipative processes in a membrane subsystem composed of biopolymers, structural water, and ions may elicit complex and novel interactions, as developed in the Fröhlich model (143, 144, 146, 148, 149).

Fröhlich has hypothesized that ELF electric oscillations in the brain may be connected with such a system requiring relatively small activation energies but protected from thermal fluctuations. These oscillations cannot arise from a collective mode based on interactions of various molecular groups, since enormous volumes of tissue would necessarily be involved to overcome their thermal noise. Fröhlich has instead applied a general theory of coherent vibrations in biological systems (55, 143, 144, 146, 224, 225) for which there is some experimental evidence (106, 147, 148, 284). Fröhlich envisages collective chemical oscillations in which globular proteins and the surrounding ions and structural water behave as an entity and oscillate between a strongly electrically polar excited state and a weakly polar ground state. A slow chemical oscillation is thus connected with a corresponding electrical vibration. The strong electrical interaction between the highly polar states in conjunction with strong damping of electric currents then imposes limit-cycle conditions on these polar systems, making the oscillations highly sensitive to external electrical and chemical influences, as described by Kaczmarek (220) and discussed below.

Fröhlich's theory of long-range coherence in biological macromolecules describes coherent electric vibrations in the frequency region of 10^{11} Hz when energy is supplied to these molecules above a threshold level. These excitations can cause far-reaching long-range interactions not seen with static or slowly oscillating electric charges, where they are screened at much shorter

range by small ions. Application of this model to enzymatic reactions (145, 166) suggests a possible basis for collective enzymatic reactions, with strong polarization of the activated state reducing activation energies and coherent vibrations causing long-range selective interactions with other systems.

In the context of field interactions with membrane surface enzymes that might form part of a "greater membrane," Fröhlich (149) has considered a population of enzymes, of which N are in the excited polar state and Z are not excited, interacting with substrate molecules S . All three presumably show long-range selective interactions that tend to increase their number by influx or excitation. The ratio of increase of activated enzymes would be proportional to their concentration N , to the concentration of inactive enzymes Z , and to the number of substrate molecules S (expressed in the function αNZS). Chemical destruction of substrate occurs with each transition from nonpolar to polar state. Spontaneous transitions from excited to ground states may also occur. Nonlinear differential equations describe this model

$$dN/dt = \alpha NZS - \beta N \quad (1)$$

$$dS/dt = \alpha NZS + \gamma S \quad (2)$$

$$dZ/dt = \alpha NZS + \beta N - \gamma(Z - A) \quad (3)$$

where γS and $\lambda(Z - A)$ result from the long-range interaction, $Z = A$ in the absence of enzymatic activity ($N = 0, S = 0$), λ is the rate of long-range substrate attraction, and β is the rate at which an excited enzyme returns to its ground state.

If the equilibrium of nonexcited enzyme concentration is reached very fast (i.e., Z can be considered time independent), the equilibrium values N_0 and S_0 are given by

$$\begin{aligned} N_0 &= \gamma/\alpha Z \\ S_0 &= \beta/\alpha Z \end{aligned} \quad (4)$$

Equation 3 may then be discarded, and Equations 1 and 2 are the Lotka-Volterra equations describing cyclic behavior of populations, as in predator-prey relationships. For a system close to equilibrium, the concentrations N and S may be written

$$\begin{aligned} N &= N_0 + \nu \\ S &= S_0 + \sigma \end{aligned} \quad (5)$$

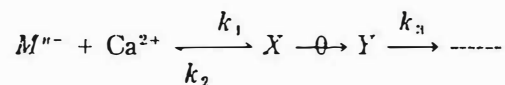
If ν and σ are small, the product $\nu\sigma$ may be ignored and

$$\begin{aligned} d\nu/dt &= \gamma\sigma \\ d\sigma/dt &= -\beta\nu \end{aligned} \quad (6)$$

In this approximation the periodic enzyme reaction oscillates around the steady-state equilibrium at a circular frequency of $\sqrt{\beta\gamma}$ as a limit-cycle phenomenon of the type proposed by Kaczmarek (220, 221). Fröhlich's model differs from that of Grodsky in envisaging nonlinear dissipative interactions in biochemically reacting systems, rather than in nonreactive systems discussed by Grodsky. Both consider dissipative processes as essential in cell regulatory mechanisms.

c) *Limit-cycle models.* Turing (433) predicted that a system of chemical reactions and diffusion may develop a dynamically maintained temporal and/or spatial pattern from an initially steady-state homogeneous system of matter [for review, see Katchalsky et al. (239)]. Temporal patterns in chemical reactions are well known. Belousov (49) continuously stirred potassium bromate, ceric sulfate, and citric acid in dilute sulfuric acid and noted oscillations in the ratio of ceric (yellow) to cerous (colorless) ions, producing a recurring temporal pattern. Zhabotinsky (467) substituted malonic acid for citric acid and noted similar oscillations. Spatial organization maintained by these dynamic systems of chemical reactions occurs if the Belousov-Zhabotinsky reactions are not stirred, alternating stripes of oxidized and reduced forms of the indicator then propagating through the medium (67). Viewed as a dissipative structure (192, 359, 360, 361), the spatial patterning of the Belousov-Zhabotinsky reaction behaves in two ways from its initial instability. It develops a limit-cycle oscillation for its chemical constituents, having a defined period and a temporal pattern independent of the initial perturbation. In response to a space-dependent perturbation it also develops a spatial organization or "dissipative structure" distinct from the conventional structure found only in systems at dynamic equilibrium. This link between limit-cycle oscillation and dissipative structure may be related to the dynamics of neural populations (220, 221).

Kaczmarek (220, 221) has considered the possible occurrence of resonant phenomena in chemical reactions analyzed as linear systems (205, 334). A simple model of calcium binding to anionic membrane binding sites suggests this possibility



Calcium ions bind to the anionic membrane component M^n to form the calcium complex X . The calcium complex may exist in two forms, X and Y . The individual complexes are linked through conformational coupling so that the presence of Y favors the transition $X \rightarrow Y$. The rate of such a process may be approximated by a "molecular-field" approach in which the rate constant is set equal to $\beta e^{n\psi}$ (62). The third step of the reaction scheme provides for removal of Y , as in its utilization for release of transmitter substances at synapses. The kinetic equations describing the system are

$$dx/dt = k_1[M^{n-}][Ca^{2+}] - k_2X - \beta e^{n\psi}X$$

$$dy/dt = \beta e^{n\psi}X - k_3Y$$

For appropriate values of the kinetic constants and the extent of cooperativity n , this scheme can display multiple steady states, limit-cycle behavior, or both (220). In the limit of a very weak field, the effect of an oscillating EM field on the rate constants for the initial binding of Ca^{2+} to the membrane may be represented by

$$k_1 = k_{10}[1 + \alpha \sin(\omega t + \phi)] \alpha \ll 1$$

In computer simulations, the dynamics of the system were very sensitive to the frequency of perturbation ω when the system was in the limit-cycle mode. Kaczmarek (221) points out that if calcium binding in neural membranes can exhibit limit-cycle behavior due to reaction steps being maintained far from chemical equilibrium, weak external perturbations could easily disrupt the electrochemical balance. The narrow range of ELF frequencies evidenced in weak field interactions with brain tissue (discussed below) does not support a molecular or dipole moment interaction at, or close to, equilibrium.

d) Tunneling models. There is a possibility, as yet untested, that long-range interactions between membrane surface fixed-charge sites may occur at the boundary between zones of fixed charges exhibiting coherence and incoherence. This boundary would be an energy barrier for charge movement between the zones. Coherence of charge sites has been observed along the surface of macromolecular biopolymers. From studies of relaxation times in the binding of acridine dyes to poly-L-glutamic acid, Schwarz (387) postulated a condition of identical energy levels at adjoining fixed-charge sites in the length of the biopolymer sheet. This coherent condition persisted for periods approaching a millisecond. The dimensions of such a coherent "patch" have not been determined.

The possibility of biological tunneling has been considered for excitatory processes (90) and for the hemoglobin molecule in binding oxygen (197, 198). It has been proposed that the "window" phenomena noted in several types of EM field interactions with tissues (38, 42, 58) may arise in charge tunneling across an energy barrier (8, 10, 39). Most previous schemes have envisaged electrons as the charge carriers in tissue tunneling in conformity with classic observations at semiconductor junctions (129). Hopfield (198) points out that the separation between linking sites in biological sites for electron tunneling may be limited to 8–10 Å. Experiments and related models on the role of hydrogen ions in EM field interactions suggest that protons may offer a basis for tunneling interactions along cell surfaces in brain tissue (10, 39).

4. Tissue interactions with strong EM fields

Absorption of EM energy increases the kinetic energy of molecular constituents of the absorption medium. We associate increased rates and energies of collisional events with raised temperature (418). In tissues of intact

multicellular organisms, particularly those possessing cardiovascular and respiratory systems capable of efficient thermal exchange with the environment, the observed rise in temperature at a particular locus within the body may be substantially below the expected increment in an equivalent volume of nonliving material. On the other hand, enhanced field levels may occur in resonant interactions with body segments or with the whole body as a function of the relationship between body geometry and the wavelength of the imposed field. These relationships are important in induction of hyperthermic states for therapeutic purposes.

a) Whole-body resonance at radio- and microwave frequencies. The wavelength of a 3,000-MHz signal is 10 cm and is closely related to the length of mice or rats, making "hot spots" inevitable at some point along the body (14, 177). A hot spot for a mouse or rat may occur near the tip of the tail and frequently along the neck. For the human head, simulated as a sphere 15 cm in diameter with three layers representing brain, fat, and skin, a 2,450-MHz microwave beam is rapidly absorbed at the surface of the head. There is a maximum specific absorption rate (SAR) for energy of 2.0 W/kg in the outer 1.0 cm of the phantom for an incident power density of 1.0 mW/cm², although the average heating for the whole head is only 0.121 W/kg. In a small zone in the center of the head, curvature and a high tissue refractive index produces an SAR of 0.2 W/kg for the monkey head (258). This picture for humans is sharply changed at a lower frequency of 918 MHz, where energy absorption at the center of the head for an incident field of 1.0 mW/cm² is 0.45 W/kg, which is significantly greater than the 0.20 W/kg calculated at the surface. The human head may behave resonantly at frequencies between 400 and 500 MHz (154), whereas in the long axis of the body, maximum absorption occurs at frequencies around 35 MHz for the grounded subject and closer to the free-space resonant frequency of 70 MHz for man standing on or above a perfectly conducting ground plane. In the transverse and anteroposterior axes, maximum absorption occurs at frequencies from 135 to 165 MHz (153). Whole-body rates of energy absorption for models of humans and for animals subjected to incident fields of 10 mW/cm² (the maximum permitted for 0.1 h in any 1 h under current U. S. occupational safety standards at microwave frequencies) show that rates of energy deposition at resonant frequencies in the presence of a ground plane or a reflector are markedly increased (155). With grounding and reflection combined, "they are truly staggering" (156). Energy deposition rates for models of humans subjected to fields at a power density of 10 mW/cm² predict SAR values as high as 35-70 times the basal metabolic rate for adults at resonant frequencies. The time-to-time convulsion of 100-g rats exposed to power densities of 3-20 mW/cm² confirms some of these predictions of enhanced absorption in the presence of reflecting surfaces.

b) Focal thermal effects. The preceding section emphasized anisotropy of thermal effects in whole organisms arising in geometric factors. This thermal anisotropy merits further discussion for the whole organism and also at the ultrastructural level. We have discussed EM wave propagation as a "bootstrap"

operation in which the electric field accompanies the magnetic field through the transmission medium.

Electromagnetic radiation has a kinetic energy that is transferred to any particle encountered by the propagating field. At 300°K, the thermal kT energy has a wavelength of about 200 cm^{-1} or 6,000 GHz; hence the energy of an electromagnetic wave below the far-infrared region is substantially below kT , whereas fields of higher frequencies (wavelengths shorter than 200 cm^{-1}) have energies above kT . However, it will induce movements of charged particles, including ions and electrons. Currents generated by their movement lead to two phenomena (276). They may be dissipated as "eddy" currents, producing heat. Also their movement as a current generates a magnetic field that interacts with the intrinsic field of the EM wave, resisting changes in the applied magnetic field by generation of a local field of opposite sign (Lenz's law). Penetration of an EM wave into a conducting material will therefore be limited to a depth (δ) that is a function of the frequency of the wave (ν) and the conductivity of the material (σ)

$$\delta = 1/\sqrt{\nu \cdot \sigma}$$

Electromagnetic waves therefore exhibit "skin effects" in remaining near the surface of most conducting materials. For the microwave spectrum, maximum tissue absorption occurs near the surface and decreases sharply at increasing depth (417). This frequency-dependent penetration and preponderant energy deposition at superficial levels is important in evaluating prospects for successful therapeutic utilization of millimetric microwaves in oncology, even where tumor-specific absorption bands may exist at these frequencies (150). It should be emphasized that the existence of such bands in the millimetric-wave region has not been established.

On the other hand, general tissue heating that can be induced by microwave fields at frequencies below about 3.0 GHz (218, 424) is likely to be associated with differential tumor heating (74, 107) because of the limited vascularity of neoplastic tissue. This impaired heat exchange can inhibit tumor growth or produce necrosis (108-110, 181, 340, 341, 419, 422, 424).

Focal thermal effects may also occur in the vicinity of metallic objects implanted in tissues, as, for example, in the vicinity of brain electrodes or surrounding orthopedic nails, screws, or plates. This enhancement is greater at microwave frequencies, where the metallic object approaches dimensions of a wavelength, and in the near field of the generator, where very strong magnetic coupling exists (370). In these conditions, absorbed dose rate in a cadaver may be 2 orders of magnitude higher than the energy level of the unperturbed incident field for small volumes of tissue surrounding the electrode (176). The phenomenon is all too familiar to those who may have attempted to heat food in a metal container in a microwave oven.

There remains the far more difficult problem of possible thermal microdomains in which local molecular ultrastructure may enhance field sensitivity.

The numerous structural phase partitions with strong dielectric properties suggest this possibility, but appropriate models and experimental data are scanty. Little (275, 276) points out that ringlike structures, such as benzene, which are diamagnetic, do not have significant interactions with EM fields. If tissue molecules were organized as in a liquid crystal, however, the van der Waals' forces would be strong enough to couple molecules to one another, producing a "swarmlike" structure. Possessing only three degrees of freedom, and because of the coupling forces, the whole system will move in one direction at the same time. In this case the energy of interaction with the EM wave would be directly proportional to the number of molecules in the "crystal." This sensitivity would probably be less in nematic crystals with a planar organization than in smectic systems having both planar and lamellar organization. For smectic crystals, the susceptibility of a "swarm" to an EM field can be large with respect to kT due to strong coupling of the molecules. In such a system, very weak magnetic fields (such as the earth's magnetic field) could interact with matter. A biological system with molecular "swarming" properties could act as an information-processing device, sensing the forces of an electric field in the length of a neuron or allowing one neuron to influence the excitability of its neighbors (277).

F. Effects of Magnetic Fields

It is possible to construct ELF facilities that provide only a magnetic field without a concomitant electric component (102). At microwave frequencies, this is also possible for small specimens by placing them in a wave-guide section at a current antinode (268). In most exposures to oscillating environmental EM fields, this virtual suppression of the electric component is uncommon. However, continuous environmental magnetic fields range in intensity from the earth's natural field (0.00003 T) to extremely powerful fields in the vicinity of superconducting cryogenic magnets with fields between 10 and 100 T.

The magnetic component of an EM wave possibly could interact with the magnetic component of spinning atomic nuclei discussed above. Even for a field of 1.0 T (10,000 G), however, the energy of interaction would be of the order of 1°K and far below kT , and the coupling of this field with brain tissue would be very small. The nuclear coupling energy in the earth's magnetic field would be of the order of 10^{-8} °K for typical ring molecules oriented with the magnetic field (276), so that this appears a quite unlikely model for detection of the earth's magnetic field in bird navigation (241-243, 246). Rather, the improbability of direct transduction of weak environmental magnetic fields at atomic levels in nervous tissue emphasizes the likelihood that observed bio-effects arise in ionic eddy currents and concomitant long-range macromolecular interactions associated with movement of the tissue through the magnetic field (4, 5, 38, 86, 250).

Effects of magnetic fields on the nervous system have been reviewed by Kholodov (247, 248). Because of the ability to penetrate uniformly through the

entire cranial cavity from suitably oriented pole pieces, sensory and other effects attributable to central stimulation have long been known. The magnetophosphene was discovered by d'Arsonval (96), elicited as a subjective flashing light by a magnetic field oscillating at 10–100 Hz. The optimal stimulation range is 20–30 Hz at an intensity of 0.004 T. Kholodov points out that although initial explanations rested on an induced EMF causing stimulation of retinal receptors, later research has cast doubt on this model, since the induced EMF may be 3–4 orders of magnitude weaker than the electric gradient necessary to produce an electrophosphene, and the threshold for the electrophosphene is influenced by the duration of exposure to a steady magnetic field, suggesting that the biophysical basis for these interactions requires further study.

III. OBSERVED BIOLOGICAL EFFECTS

There are difficulties in arriving at a historical perspective on major developments in this field over the past 25 years. The problems are of sufficient import to the newcomer seeking a basis for his own critical participation and so broad in their physical, biological, and social implications that it should be emphasized that no single reviewer can authoritatively evaluate the entire gamut of bioeffects attributed to environmental EM fields. Until recently, deep differences in research priorities and methodologies have tended to separate Eastern and Western investigators. East European studies have emphasized effects of "nonthermal" exposures, based in part on long-term exposures of a type rarely, if ever, performed in the West (until very recently). Western critics have often argued that results of these studies have been poorly documented statistically and in the physics of the exposure environments; that such studies may still be credible at an observational level has been lost all too often in sociopolitical differences.

At least the onus for repetition of many important but controversial East European studies is now accepted in a joint USA-USSR study program under the Nixon-Brezhnev agreement in 1973. As a case in point, American investigators have recently attempted to "replicate Soviet findings" by exposing rats to a weak (0.5 mW/cm^2) 2,450-MHz field for 7 h/day for 3 mo (278). Altered blood cholinesterase and glutathione activity, significant shifts in sodium, potassium, and carbon dioxide, and altered behavior were in partial agreement with Soviet findings and "clearly suggest a need for further low-level microwave chronic exposure protocols." On the other hand, there has been a preponderant Western opinion that the effects of microwave and radiofrequency fields are attributable only to the heating mechanism of those fields at power densities in excess of 10 mW/cm^2 . As recently as 1976, reviewers stated that " 10 mW/cm^2 is approximately one-tenth the level calculated to cause significant heating in human tissues, and agrees with physiologic and metabolic calculations" (160), despite earlier impressive evidence noted above that significant heating can occur at levels below 10 mW/cm^2 (176). In terms of nonthermal or "micro-

thermal" effects, a representative U. S. view of that period stated that "there is no evidence thus far presented to indicate the existence of nonthermal effects at the molecular or cellular level" (383). In the past 3 years, the impetus of collaborative endeavors between East and West and bioengineering collaboration on exposure techniques and tissue dosimetry have validated some earlier findings and given credibility to certain new observations.

A. Dosimetry of Tissue Field Levels

Devices for measuring tissue components of impressed fields must function without distorting field levels in adjacent tissue. This imposes severe constraints on the size of any metallic conducting elements in tissue probes and equally severe requirements on connecting devices inside and outside the tissues. There has also been considerable use of phantoms that simulate whole bodies or appendages, with appropriate laminar structure to simulate skin, fat, and bone. For humans, small mannikins have been used at radio and microwave frequencies with appropriate upward sealing of the frequency of the imposed radiation. Theoretical techniques have been used to relate measures of absorbed energy in humans and animals to the power density of incident radiation.

1. Instrumentation for tissue dosimetry

In situ tissue electric gradients can be measured at radio and microwave frequencies without distortion of the induced field by a triaxial array of small diodes that rectify the electric vector along mutually orthogonal axes (34, 78). To avoid antenna effects on leads to external devices, connections can be made either by thin, high-resistance film leads or, by first converting the rectified signal to a pulse train that activates a light-emitting diode, through a fiber-optic system. Calibration of these dipole-diode arrays depends on the dielectric constant of the medium in which they are implanted, the dimensions of the dipole antenna, and the thickness of the insulating material surrounding the antenna. Both dimensions must be small compared to the wavelength of the field in the biological medium. A typical dipole is 2.5 mm long and the diode 0.25 mm wide. These systems are small enough to be inserted between cerebral hemispheres of small mammals and are sensitive enough for accurate field measurements with incident energies well below 1.0 mW/cm² and in the absence of significant tissue heating (42).

Measurement of tissue gradients induced by ELF fields is far more difficult because of the far weaker coupling of the low-frequency field to tissues. In an ingenious approach, Valentino (437) has used a phantom of the head of a small mammal, such as a monkey, with measurement of the total current induced in the phantom by the external field. Thus for a 10-V/m, 7-Hz field, the measured total current is 0.9 nA. Obviously electric gradients established within the multitude of tissue planes within the head will not be uniform and

cannot be measured by this technique. Order-of-magnitude calculations are possible, however, from a knowledge of the total induced current. They indicate a general gradient of 10^{-7} V/cm for the 10-V/m, 7-Hz field.

Thermometry with small liquid-crystal devices is accompanied by minimal tissue damage from their implantation (214). Fiber optics transmit information to and from a sensor tip about 1.0 mm in diameter formed of a liquid-crystal thin film. In the temperature range 20–40°C, these sensors will reliably resolve a temperature shift of 0.1°C. Pyroelectric probes that also sense temperature shifts in lossy crystalline material can be used in the far field (201). Although too large for implantation, they respond to changing temperature in tissue with which they are in contact. They are fabricated from pyroelectric crystals, such as triglycine sulfate, so named because they lack a center of symmetry and exhibit spontaneous polarization with alignment of electric dipoles within crystal domains. This polarization is modified by heating. The optical birefringence of lithium titanate and lithium niobate has also been used to produce a 1.0-mm-diameter sensor with a temperature resolution of 0.1°C at 30°C (35, 75, 76). Microthermometers with a thermodilatable liquid in a small glass capillary are also feasible (99). A viscometric thermometer that senses changing pressure in a fluid with strongly temperature-dependent viscosity flowing through a capillary constriction offers a potential advantage that such probes may be not just nonabsorbing but nonperturbing, in that their contents may be closely matched to electrical properties of tissue (68).

Calorimetric measurements of energy absorbed in tissue have been successful. They assume that all absorbed energy is converted to heat within a short period and is not stored or dissipated in another form. Earlier workers used heating and cooling curves (32, 211, 288, 289). The method has been extended to utilize data from the entire heating and cooling curves in a non-steady state procedure that avoids use of approximations (15, 57). However, the method has weaknesses for *in vivo* experiments where animals regulate body temperature and where energy deposition within the subject is not uniform.

Just as distortion of a microwave field within tissues occurs in the presence of a metallic sensor or in the vicinity of any dielectric material substantially different from tissue, so too is a free field modified by the presence of humans or other biota (48). This is important in assessing field effects on a group of subjects in changing proximity to each other. Measurements on humans at frequencies from 1 to 12 GHz indicate substantial perturbations in front of the subjects, with body reflections producing a series of standing waves. Sharp field enhancement occurs at antinodes in this wave pattern. The findings are clearly important where objects are to be simultaneously irradiated or where the object may be close to test equipment.

2. *Dosimetric models of absorbed energy*

Considerable effort has recently been expended to provide the link between biological effects of radiofrequency fields observed in irradiated animals and cor-

responding effects that might occur in humans. A handbook has been compiled describing theoretical methods relating measures of absorbed energy in humans and animals to the power density of incident radiation (213). The traditional approach with models that use homogeneous spheres has been replaced by prolate-spheroid and ellipsoidal models. These offer great advantages over the spherical model in quantitation and in the prediction of resonant behavior and effects of orientation. The technique enables the user to estimate the SAR—the mass-normalized rate of energy absorption of W/kg—in humans at a given frequency as a function of the incident power density, or of strengths of E and H fields, and to extrapolate animal studies to humans. Theoretical techniques to obtain SAR data include a perturbation method for the lower frequencies, an extended-boundary-condition method for higher frequencies to the region of resonance and beyond, and the geometrical-optics method for yet higher frequencies. Findings are that the SAR is proportional to f^2 for body lengths less than 0.05 wavelength; the SAR increases at a rate greater than f^2 near, but below, resonance; the SAR decreases at a rate less than f^2 at frequencies beyond resonance; for E polarization, resonance occurs when the long dimension of the body is approximately 0.4 wavelength; below and at resonance, the SAR is greatest for E polarization (E vector along the model's longest axis), intermediate for K polarization (vector of propagation along the model's longest axis), and least for H polarization (H vector along the model's longest axis).

Caution is desirable, however, in evaluating recent use of the SAR in terms of averaged values and in attempting its application to "nonthermal" tissue interactions with weak fields. Averages for very simple models, such as prolate spheroids and ellipsoids, may have limited relevance to the complex geometry and changing posture of the human subject, for example. Also the absorbed energy has a spatial distribution over any real mammalian body that is quite sensitive to the layering of skin, fat, muscle, and bone. This layering is associated with a resonance for three-dimensional bodies that is quite distinct from the geometrical resonance. Calculations for a multilayered prolate spheroidal model of humans predicted a whole-body layering resonance at 1.8 GHz with a power absorption 34% greater than that predicted by a homogeneous model (29). A related model for a specific skin-fat-muscle cylindrical model of humans predicted a layering resonance frequency of 1.2 GHz, with an "averaged" SAR double that calculated for the corresponding homogeneous model. The layering resonance frequency was the same for incident waves polarized parallel and perpendicular to the cylinder axis. The energy deposited in different body layers will clearly be different, and further modeling of this differential distribution has been attempted by modeling the human body as a series of small "blocks" (184). Even here, these differentials have been submerged in the further calculation of a "whole-body SAR."

At issue here is the vitally important question of the levels of energy deposition at interfaces represented by tissue discontinuities. These may be structurally gross and macroscopic, as at an interface between muscle and

bone. They may also occur in a microcosm of molecular dimensions, as at the margins of macromolecular domains on membrane surfaces, or on the surface of intracellular organelles. In either case, they might be expected to be the site of enhanced energy deposition, not effectively modeled in the general SAR concept and even less in the "averaged SAR." Local electrical fields up to 100 times larger than average fields can be induced around microscopic wedge-shaped boundaries between regions with different dielectric constants likely to be present in the human body (326). Nor can field effects that might arise in "non-thermal" interactions be appropriately described simply as a small fraction of the total absorbed energy, since cellular sensitivity may change profoundly with time as a result of intercurrent humoral factors. The development of national safety standards for human exposure must therefore await needed knowledge of the biophysical mechanisms of these low-level interactions.

B. Bacteria and Invertebrates

The small size of bacteria and unicellular organisms such as protozoa inherently limits the total magnitude of any electromagnetic gradient induced in them. There is an analogous situation in the transductive coupling of chemotactic processes in bacteria. "a formidable task for an organism only 2 μm in length" (254). For bacteria, the evidence favors a comparison of concentrations at different locations in a temporal sequence, rather than by instantaneous spatial sensing through receptors at head and tail that would make an instantaneous comparison of attractant concentrations at head and tail. Viewed as a prototypic sensory system, this bacterial chemotaxis comprises distinct chemoreceptor proteins, including the Mg^{2+} - and Ca^{2+} -dependent adenosine triphosphatase that is responsible for interconversion of the energized membrane state to adenosine triphosphate and is also the receptor for divalent metal ions in bacterial chemotaxis (468). A central role for proton and cation gradients in energy transduction processes in microorganisms and higher species is proposed in the chemiosmotic hypothesis of Mitchell (308, 309).

1. Magnetosensitivity in bacteria

While microscopically examining marine and freshwater muds collected from the Woods Hole area, Blakemore (60) observed that several forms of anaerobic and microaerophilic bacteria (as yet unnamed) consistently swim to the north when separated from the sediments. Their direction of swimming was readily altered when a small bar magnet approached the microscope slide, and they were observed to contain iron-rich particles. Kalmijn and Blakemore (233) found a reversal of this north-seeking tendency on reversing the ambient magnetic field with Helmholtz coils. When exposed to strong, brief monophasic magnetic pulses, the internal permanent magnetic dipole movement was reversed, and the bacteria instantly turned around and from then on continued

to swim in a southerly direction. Depending on the strength of the imposed magnetic pulse, the bacteria either remained northbound or became southbound. None were completely depolarized. In this respect they exhibit single-domain properties.

Magnetosensitive bacteria include cocci, spirilla, and rods. Killed cells orient to the imposed field but do not swim. Some show chains of crystals that stain with phosphotungstic acid, with typically two chains per cell. These chains may show nascent particles with zones of incipient crystallization. Energy-dispersive X-ray analysis shows a predominance of iron in the crystals, with significant amounts of magnesium, phosphorus, sulfur, and calcium. Clones of bacterial cells that lack these crystals show no magnetosensitivity. Strains containing crystals may lose them after about six divisions in culture. Cloned nonmagnetic bacteria may regain their sensitivity. For sensitive bacteria, the axis of motility and the axis of magnetization coincide. Kalmijn (231) points out that this responsiveness fades out at magnetic field levels below the natural fields and also disappears at levels about 100 times higher, which is strongly indicative of a "window" phenomenon common to this and other bioeffects of EM fields discussed below. These bacteria, live and killed, orient in uniform magnetic fields of about 0.1 G (10^{-5} T) (134).

The strongly ferromagnetic characteristics of these intracellular crystalline chains provide a physical basis for the bacterial orientation. Biopolymers, such as the polysaccharide agarose, can exhibit a much weaker diamagnetism. Agarose aligns its major molecular axes parallel to an applied magnetic field. This alignment can be evaluated by measuring gelation temperature as a function of magnetic field intensity (234). Gelation temperature of aqueous 1.4% agarose solution increases linearly from 37.4°C at 0.0 T to 38.8°C at 1.0 T. Electrophoretic mobility of high-molecular-weight bacterial DNA is 7% faster through 1.4% agarose gels allowed to solidify in a 1.0 T field than in an 0.0 T field, suggesting that selective orientation of other polymers may be a basis for biomagnetic effects.

2. Mutagenic and growth changes in bacteria exposed to EM fields

There is evidence that strong DC electric fields may increase bacterial mutation rates. The Ames *Salmonella* strain TA 98, which mutates by frameshift, failed to show significant mutation frequencies after exposure to DC fields with gradients as high as 800 kV/m. On the other hand, *Salmonella* strain TA 100, which mutates by base exchange, showed significantly increased frequencies when exposed to DC fields of 250–750 kV/m (202). Under similar conditions, *Photobacterium fisheri* showed significantly increased frequencies of colonies resistant to tetracycline.

Slowed mitotic nuclear division has been reported in the myxomycete slime mold *Physarum polycephalum* continuously exposed to weak (2.0-G, 0.7-V/m) 75-, 60-, and 45-Hz fields (169). The effects appear to depend on field frequency.

The slime mold *Physarum* produces a plasmodium up to 5 cm in diameter in 24 h under laboratory conditions. The entire plasmodium contains about 10^6 individual nuclei, all of which undergo a mitotic division simultaneously, dividing within seconds of one another. The time for two cell cycles (normally 14–16 h) was increased by 1–2 h after 90–120 days of exposure at 75 Hz and after shorter exposure times at 60 and 45 Hz. If cultures showing the delay were removed from the fields, the mitotic delay slowly diminished, becoming indistinguishable from the control after about 30 days. No effects were noted on fertile-spore formation or encystment. Evidence for a threshold was noted in the absence of a mitotic delay in cultures exposed to 0.4-G, 0.15-V/m, 75-Hz fields.

These microbiological studies on growth and division during EM field exposure have been limited. They exemplify the need for much further work to corroborate and extend initial evidence for certain positive effects. Many laboratory and field tests have failed to show growth or reproductive effects in bacteria or simple invertebrate organisms after prolonged exposure to ELF and microwave fields. Continuous-wave 2.45-GHz microwave exposure of *E. coli* in the far field at power densities of 10 and 50 mW/cm² (SAR 15 and 70 W/kg, respectively) did not cause mutagenic effects (59). Similar studies in the near field at 1.70 GHz were also without effect. After 6 years of exposure to earth currents of a simulated ELF long-range communication system at 45 and 75 Hz, population counts and species ratios of mites, *Collembola*, earthworms, slugs, and woodlice were unchanged (168). Typical gradients attributable to this field in exposed populations were 0.1 V/m and 0.2 G. No changes were detected in oxygen consumption or respiratory quotient, and there was no evidence of abnormal behavior, habitat selection, or altered external features or pigmentation.

3. Effect on reproduction, growth, and development

Bacterial growth and development may be modified by low-level microwave fields at millimetric wavelengths. Fine changes in frequency around 42 GHz sharply altered growth of yeast (*Saccharomyces cerevisiae*) cultures, with both raised and lowered growth rates occurring reproducibly (175) in incident fields of 1.1–2.7 mW/cm² that caused temperature shifts of 0.4°C or less. The magnitude of effects and their change in sign with frequency appeared to preclude a simple temperature relationship, suggesting instead a direct macromolecular interaction at these field frequencies, as proposed in the Fröhlich model discussed above. Responses of *E. coli* in media containing either glucose and amino acids or glucose and NH₄⁺ have been examined for protein synthesis, DNA and RNA synthesis, and growth rates in microwave fields at frequencies from 59 to 143 GHz and incident energies from 10 to 50 mW/cm² (445). No measurements of temperature increments were reported, but two sets of frequencies were noted that affected these metabolic processes, one separated by integral multiples of 7 GHz and the other by 5 GHz. Interpretation of these findings as due to rotational

transitions associated with biopolymers at microwave frequencies has not won general acceptance. Also there are major technical difficulties in exposures at these frequencies, with geometry of exposure chambers requiring careful consideration to avoid spurious frequency dependence from problems of multipath and internal reflection. Another study of possible effects on growth of *Escherichia coli* at these frequencies has been negative (194), emphasizing that seemingly minor aspects of technique may be critical in replication of these experiments (56). Effects of long-term exposure to 45-, 60-, and 75-Hz electric fields on reproductive cycling in *Physarum polycephalum* have been discussed above (169). Research to date on ELF field effects on bacterial growth has been limited, with mostly negative findings (167). Myxovirus multiplication and oxidative metabolism were increased in cell cultures exposed to a 3-GHz, 5-mW/cm² microwave field, without evidence of cell damage from the exposure, but actual energy deposition in these experiments could not be measured (423). Reduced virus multiplication and clear evidence of irreversible cell damage occurred with irradiation at 20 mW/cm².

C. *Marine Vertebrates*

Sensitivity of fish to environmental electric fields was first described for the catfish (342). The blindfolded catfish is remarkably sensitive to metal rods in water in its vicinity. A glass rod elicits no response. When a long metal segment is introduced into the tank, the fish may swim away from it but then often approach and nibble at a short segment of the metal. Parker and van Heusen (342) also noted that nibbling responses were elicited by a total current of approximately 1.0 μ A between two electrodes about 2.0 cm apart. Avoidance reactions occurred with stronger currents.

1. *Orientation, navigation, and predation by electrosensing in marine vertebrates*

Weak electric fish (*Gymnarchus*) emit a continuous train of pulses at rates between 300 and 1,000 Hz. Lissman (274) proposed that these pulses are essential in locating environmental objects by an electrosensory mechanism and that weak electric fish have evolved from a preelectric fish lacking specialized electric organs but already sensitive to electric fields. This first electrosensitivity might detect tissue potentials arising in surrounding animals, including predators and prey, as well as within the animal's own body. This capacity exists in catfish and sharks. They are both very sensitive to electric fields but lack electric organs.

In 1962, Dijkgraaf (111) first reported escape reactions in blindfolded sharks when a piece of steel wire came within several centimeters of the body. Escape reactions occurred with local DC fields of 1–10 mV/cm. Square-wave 5.0-Hz fields elicited the same response and also caused eyelid contraction.

These square-wave fields altered respiration of rays that had settled to the bottom of a tank where the gradient was only $0.1 \mu\text{V}/\text{cm}$ ($10^{-6} \text{ V}/\text{m}$) (227). Kalmijn (228) evaluated the biological significance of this electrical sensitivity in the shark, first examining its feeding responses toward flatfish that form part of its natural diet. The flatfish buried itself in sand at the bottom of the tank. At first the sharks approached randomly to within 10–15 cm of the flatfish and then made well-aimed dives at the prey, uncovering it from the sand and eating it voraciously. The flatfish was then placed in an agar chamber in sand on the floor of the tank and sustained by a flow of aerated seawater. The agar chamber concealed the flatfish visually, chemically, and mechanically but did not change the animal's bioelectric field. Both sharks and rays continued well-aimed attacks from the same distance in the same frenzied fashion as with unscreened prey. As a further control on possible odor leakage from the agar roof of the chamber (1 cm thick), pieces of dead fish substituted for the live flatfish failed to evoke a directed response from either sharks or rays. Finally a polyethylene film only $10 \mu\text{m}$ thick over the agar container eliminated all responses.

Rays can be trained in a circular tank to seek a food reward concealed in one of two identical buckets, symmetrically placed with respect to the earth's magnetic field (at 9:00 and 3:00 o'clock) against the walls of the tank (231, 232). Thus the earth's magnetic field became an essential cue and determined the direction in which the animal circled the tank to reach the bucket. When the tank was rotated 180° with respect to the earth's magnetic field, the rays reversed their direction of circling to reach the food reinforcement. Calculated tissue electric gradients based on the rate of the animal's movement through the natural magnetic field were $0.5 \mu\text{V}/\text{cm}$. These responses faded out with magnetic fields weaker than the natural levels and were not observed with imposed fields 2 orders of magnitude greater, suggesting an intensity "window."

There are substantial differences between the electrosensitivity of ordinary and electroreceptive fish to weak electric fields from DC to 1.0 kHz in marine and freshwater environments (66). Three criteria of responsiveness in ordinary fish included a first reaction, a galvanotaxic response, and further responses that involved modified heart rates in certain species, all at much higher thresholds than those of electroreceptive fish. The first reaction is a threshold response with slight twitching of the body or its appendages. These thresholds are substantially lower in fish with electrogenic organs than in ordinary fish, typically about $10^4 \mu\text{V}/\text{cm}$ in ordinary fish and about $1 \mu\text{V}/\text{cm}$ in the electroreceptive fish for frequencies between 0 and 10 Hz. Electric gradient sensitivities for behavioral responses may be as low as $0.2 \mu\text{V}/\text{cm}$ in weak electric fish with organ discharges between 300 and 1,000 Hz. This first reaction is more sensitive in marine than in freshwater fish. The latter typically have a high skin resistance and a high internal conductivity, whereas marine fish attain a much less perfect isopotential interior. The second criterion of galvanotaxic responses includes swimming or turning movements with a definite orientation to the applied field. They are classed as "forced movements," arising from involuntary muscular contractions through direct nervous or muscular stimula-

tion. Their high thresholds do not suggest a relationship to effects of natural environmental fields. Open-circuit signals of the order of 1 V produced by weak electric fish fall quickly to millivolt levels in the vicinity of the fish, so that object detection is only possible for distances of a few centimeters.

2. *Electroreceptive sensing organs and systems in marine vertebrates*

There are fascinating characteristics of electroreceptive sensing organs in relation to the animal as a whole. The system behaves as a voltmeter without significant shunting of the imposed field. Its dynamic range is low, not more than 20–30 dB, so that range has been sacrificed in favor of sensitivity, a characteristic shared with the olfactory system (1).

Two types of electroreceptors have been described, ampullary and tuberous. Ampullae of Lorenzini occur in both electric and nonelectric fish and detect low fields originating externally, but they may also respond to certain nonelectric organ fields generated by the animals themselves. The ampullary electroreceptor opens on the skin surface by a minute pore connected to a subcutaneous jelly-filled canal with a terminal swelling, the ampulla proper. Sensing cells lie in the wall of this ampulla proper. Their outer surfaces face the lumen of the ampulla and thus appear to be connected to the external aqueous environment. Their inner surfaces synapse with afferent nerve fibers. Ampullary receptors are clustered along the snout region of the shark. Tuberous receptors are found exclusively in electric fish, are sensitive only to high frequencies, and seem to be specialized for detecting electric organ discharges (371). Discharges in this high-frequency receptor system are often synchronized with the electric organ discharge, with frequencies from 300 to 1,000 Hz. There appear to be thousands of receptor sites on the body. Each may oscillate at its own rate, not necessarily tuned to the electric organ frequency, although this is typical in organs with a higher frequency discharge (51, 52).

Because the ampullary canal has an extremely high wall resistance but a relatively low core resistance within the central canal and at the blind ampullary end, it exhibits almost ideal cable properties at DC and for low-frequency electric oscillations. Typically the wall resistance may be $6 \text{ M}\Omega/\text{cm}^2$, whereas core resistivity may be as low as $31 \Omega \cdot \text{cm}^{-1}$. The high wall capacity per unit length rapidly attenuates coupling of high-frequency oscillations in the length of the tube (443). Thus a canal 10 cm long and 0.12 cm in diameter would have a calculated space constant of 74 cm, several times the canal length. The low-pass frequency characteristic of the ampullary system gives it an effective upper frequency limit of about 10 Hz. Its sensitivity may be high for frequencies as low as 0.1 Hz, but it shows adaptation to DC fields. At frequencies between 0 and 10 Hz, the threshold for the first reaction of slight twitches in the body or appendages is about $1 \mu\text{V}/\text{cm}$ in fish with electrogenic organs and $10^4 \text{ V}/\text{cm}$ in ordinary fish. Weak electric fish with organ discharges between 300 and 1,000 Hz have sensitivities for behavioral responses as low as $0.2 \mu\text{V}/\text{cm}$. Kalmijn (230)

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for either ferromagnetic particles within sensory cells or electric charge displacement by movement through the field. Other insects, including termites (44-46) and beetles (19), are also sensitive to steady magnetic fields (374-376).

Evidence for insect sensitivities to electric fields is less substantial and the findings are somewhat contradictory. Bee colonies exposed to 50-Hz high-voltage fields (3-5 kV/vm) have higher metabolic rates than controls (16), with higher food intake and activity and reduced life-span of worker bees. Other reports confirm restless and aggressive behavior in bees exposed to AC power lines carrying 220-kV, 50-Hz current (204, 447). Controls and data in these studies are difficult to evaluate, and the picture is further complicated by reported effects in plastic hives that are absent in wooden hives (444).

2. Bird navigation and orientation

Many early studies of bird orientation to natural and artificial magnetic fields have been questioned on theoretical grounds, or for lack of statistical validation, or because of difficulties in reproducibility. Yeagley (464) first reported that pigeons carrying a magnet became disoriented, but this was not confirmed in his later study (465), and his hypothesis that interactions take place between the geomagnetic field and Coriolis forces was abandoned. More recent studies of bird migration and homing have correlated physiological, ecological, and behavioral evidence that sheds new light on mechanisms underlying avian migratory abilities (54, 113, 126, 152, 170, 244).

There is now substantive evidence that birds may use a variety of cues in the course of migratory flight, including landmark recognition, sun altitude, azimuth, a precise time sense, star patterns, and the wind and weather. According to Keeton (242), a possible role for the geomagnetic field was first suggested by Middendorf in 1855. Since that time, experiments have tested models based on a comparison of field intensities, travel along a magnetic contour, and movement up or down a gradient (245). The results have been conflicting, partly because of difficulties in designing experiments that are unequivocal in evaluation of perception and response to signals that humans may not perceive (7).

a) *Conditioned responses to environmental magnetic fields.* Conditioning experiments aimed at testing the ability of birds to detect steady or oscillating magnetic fields have produced various results (126). No evidence was found that pigeons can discriminate between a series of closely graded differences in steady magnetic field intensity between 0.582 and 1.000 G (297). Changed heart rate as a nociceptive conditional response to an oscillating 0.8-G, 300- to 500-Hz field was reported in pigeons (367), with similar but weaker responses to a continuous 0.8-G field oriented 120° away from the earth's field and also to a field oscillating slowly at 0.5 Hz. These findings were not confirmed by Beaugrand (43) and Kreithen and Keeton (257), who concluded that detection of these conditioned autonomic responses may require long-duration stimuli combined with motion, if indeed the pigeon does possess this ability. Emlen (126) and

Gavalas-Medici (158) have both stressed the necessity of pairing a particular conditioned stimulus with an appropriate behavioral response. Unless both elements of a stimulus-response pair are known, prediction of the missing one may be difficult or impossible, particularly if the conditioning time scale is expanded from seconds to hours. It may be hypothesized that transduction of magnetic information is a slow process requiring these longer time scales, and therefore experiments designed to test temporal discrimination, EM field detection, and preferences in pigeons and rats briefly exposed to fields of 45, 60, and 75 Hz; 2 G; and 100 V/m (282) would fail to show reliable reinforcement or altered temporal discrimination.

By contrast, there have been statistically significant results from experiments in which discrimination behavior in the magnetic environment was associated with unrestrained movement (63). Pigeons were trained in a flight tunnel 3 m long to discriminate between a simulated field 0.5 G and a field reduced to 0.02 G at paired feeding stations at the termination of the tunnel. Birds were trained to travel the length of the tunnel for 2 wk to permit stimulus-reward association and were tested in mated pairs, since they showed greater activity in the chamber than single birds. Discrimination was statistically significant in trials associated with "fluttering," defined as more than 3 s of jumping, hovering, or flight. "No-flutter" trials yielded random responses.

b) Orienting in confined birds during seasonal migratory restlessness. With lengthening of days in spring and shortening in the fall, nocturnal migratory birds exhibit migratory restlessness (*Zugunruhe*). When confined, they show sharply increased nightly locomotor activity, with the body pointed in the direction of intended migratory flight. This tendency to directional movement within the cage has been used to evaluate magnetic and other cues that might be used in navigation. Imposition of weak fields (0.6–1.7 G) during this restlessness raised locomotor activity 2–4 times in 85% of all subjects in five species tested (123). Russian workers have also reported a two- to threefold increase in this activity in birds transferred from their home site to the center of the Kursk magnetic anomaly, where the geomagnetic field is increased and its horizontal component shifted 60° (404).

The ring-billed gull inhabiting the shores of Lake Huron leaves the colony in a generally southeasterly direction at the onset of the fall migration (411). Young birds on their first migration show this tendency (410, 413). Chicks 2–3 days old placed in a nonmagnetic cage near the colony site showed a statistically significant preference for walking or flying in a southeasterly direction during periods of both clear and overcast skies, provided that the geomagnetic field was stable with a k index of geomagnetic disturbance of less than 3 (deviation less than 4×10^{-6} G). Under disturbed geomagnetic conditions, with the daily k index in the range 4–7 (with field perturbations in the range of 4 – $>20 \times 10^{-6}$ G), headings were widely scattered and became statistically random. Related studies with European robins in an octagonal cage with radial perches showed spontaneous orientation in the direction of intended migration. When the geomagnetic field was reduced from 0.41 to 0.14 G by placing the cage

inside a steel screen, movements became random (151, 292-295, 458). Changing direction (but not intensity) of the field with Helmholtz coils caused an equivalent change in nocturnal activity. Moreover, with reduction of the magnetic field to 0.14 G or when it was approximately doubled, the birds became disoriented, a finding consistent with "windowed" behavioral, neurophysiological, and neurochemical data discussed elsewhere in this review. Interestingly, when housed in the weak test field (0.14 G) for 3 days or more, the birds showed adaptation and oriented correctly to the axis of the imposed field when tested at 0.14, 0.30, and 0.41 G. They also became accustomed to magnetic fields greater than ambient levels (460). Apparently these birds may not detect the north direction simply from the polarity of the magnetic field. Rather it is derived from interpreting the inclination of the axial direction of the magnetic field lines in relation to the gravity vector, with north perceived as the direction where the magnetic field lines and the gravity vector form the smallest angle. In these experiments the vertical component of the field was manipulated independently of the horizontal. The robins were disoriented in an artificial field with a normal horizontal component but lacking a vertical. In a field with a normal horizontal vector but with the vertical component reversed, they reversed the preferred direction (461). A similar function is ascribed to the angle of declination in setting direction of migration in the European garden warbler (459). Laboratory experiments with the indigo bunting confirmed their sensitivity to rotation of the horizontal component of an artificial field similar in strength to the geomagnetic field and support the view that this information helps finalize the appropriate seasonal direction of migration (127). Related experiments with a modified design were not successful (199), but duplication of the robin experiments yielded similar findings (441).

c) Bird homing and migratory responses. Migratory and homing flight appear to depend on multiple cues (discussed above). The evidence suggests redundancy between sun and magnetic cues in the pigeon's orienting mechanism (241-243). Pigeons with either a magnet bar or an identical bar of brass at the base of the neck were released alternately at a site remote from the home location. The magnet strength was 255 G at the poles and 0.45 G at the bird's head. They were tossed in random directions and the compass bearing of the vanishing point and the time to disappearance were both noted. Under clear skies, experienced pigeons, released at both familiar and unfamiliar sites, were able to orient correctly, although vanishing times were longer and speeds slower than in control animals for birds released at an unfamiliar site 85 km from home. By contrast, experienced pigeons released from unfamiliar sites under total overcast with magnets attached failed to orient homeward, and vanishing and homing speeds were again slower than in control birds. These two tests were taken to indicate that the attached magnets have no appreciable effects in experienced birds released at unfamiliar sites when the sun is visible and that experienced subjects may use these cues interchangeably. Magnets attached to young birds interfere with learning of orientation. Fledglings equipped with either magnet or brass bars were trained in release trials close to home. The

bars were then removed and the birds were released at a remote site under overcast conditions. In three test releases, birds trained with magnets took significantly longer to vanish than controls ($p = 0.046, 0.035, \text{ and } 0.014$). Untrained young birds released on their first flight under sunny conditions were disoriented when carrying magnets, suggesting that fledglings orient correctly only under good environmental conditions and require both sun and magnetic cues. Birds raised without sunlight do not develop a "sun compass" but use only a "magnetic compass" (245).

The extreme sensitivity to small differential changes in ambient magnetic field levels has been a striking aspect of these avian studies and a consistent finding among many of them. Minor fluctuations of 10^1 – 10^5 G associated with perturbations in solar particle fluxes are detected by homing pigeons (246). Orienting by the European robin becomes random after a sudden change in the magnetic field strength by 0.1–0.2 G but may resume its directed character after adaptation over several days. Translated into expected levels of induced tissue gradients at flight velocities of tens of meters per second, these would probably not exceed 10^{-7} V/cm and might be several orders of magnitude lower for delta functions attributable to geomagnetic perturbations. Birds also exhibit a sensitivity to weak oscillating low-frequency electric fields, with good evidence of a shortened intrinsic diurnal cycle (450). In the absence of environmental electric fields, the intrinsic diurnal cycle was observed to be 24.8 h, but this shortened sharply to 23.9 h during periods of continuous exposure to a 10-Hz, 2.5-V/m square-wave field for 10–20 days. Again the presumptive tissue gradients would not be expected to exceed 10^{-7} V/cm.

Studies of avian sensitivities to radio and microwave EM fields have produced conflicting reports, ranging from "the insouciant sparrows of Constantinov" exposed to kilovolt-per-meter fields (50) to radar tracking of birds migrating through other potentially distracting EM fields of high-powered ELF radio transmitters (263, 457). The sparrows of Constantinov in Poland actually built a nest and raised their young within the pseudocoaxial feedline of a 2.0-MW, 277-kHz broadcast transmitter, making frequent transits through fields that ranged from microvolts to kilovolts per meter. The hatchling sparrows constantly stretched their necks into the high-level field between inner and outer conductors but grew to maturity without apparent ill effects. Flight patterns of large nocturnal migratory birds, presumably geese, were tracked over the cruciform antenna site of a 76-Hz ELF transmitter of the U.S. Navy's Seafarer navigation experiment with a low-powered tracking radar operating at 30 pulses/s. Flight direction changed significantly more often with the ELF antenna on than off and even more often if the transmission mode was changing during the flight (powering-up or powering-down). The north-south antenna tended to deviate flight paths, but the east-west antenna did not ($P < 0.01$). Although the investigators concluded that the radar itself probably had no effect on observed flight paths, this assumption may be unwarranted, since pulse or other amplitude-modulation characteristics at low

frequencies have marked effects on central nervous functions not seen with unmodulated RF fields of the same average strength (40, 41, 58, 336, 400). Perhaps the absence of a major ELF modulation component in the huge fields experienced by the sparrows of Constantinov may have been a factor in their apparent insouciance. Unlike marine vertebrates, no specialized electroreceptors are known in peripheral or central nervous tissue of birds. The data therefore suggest that observed sensitivities may reflect a direct transductive coupling in central nervous tissue.

*E. Responses of Mammalian Organisms to Weak ("Nonthermal")
Electromagnetic Field Stimulation*

Scientific and public interest in possible adverse effects of power-line, RF, and microwave fields has increased sharply in recent years. Separation of these tissue responses into "thermal" and "athermal" classes clearly is not based on strict physical considerations. Any absorption of EM energy is associated with increased thermal energy. The term "athermal" has been widely applied to bioeffects of RF and microwave fields where the rise in tissue temperature does not exceed a fraction of a degree and is too small to offer a simple explanation for these responses. On the other hand, temperature shifts of several degrees offer an adequate explanation for many field-induced physiological responses. Even for these higher field levels, not all effects have been replicated by identical thermal shifts produced by other means (100, 397, 398). The rise in temperature during irradiation will depend on the specific absorption rate of EM energy and the rate at which this burden of absorbed energy is removed from the tissue. In mammals, vascular mechanisms effectively minimize tissue temperature changes. For these reasons, SARs measured in phantoms and cadavers (176, 215) do not indicate temperature changes likely to occur in the living organism, where other factors such as environmental temperature (255, 310, 325), states of consciousness [including anesthesia (87, 219)], and immobilization with curarizing agents (11) may all play a part.

Field-induced temperature increments will cross many thresholds of important tissue responses. Shifts of a few millidegrees may alter firing rates in hypothalamic cells (315), and microwave hearing effects may relate to sudden temperature shifts of a few microdegrees (84, 136, 180, 265). On the other hand, brain temperature changes in the range 0.1–2.0°C are regular concomitants of exercise and environmental thermal stress (22, 23) and are not associated with shifts in cortical neuron membrane potentials of more than 1–2 mV/°C (3, 311). Rats exposed to a 2,450-MHz microwave field at power densities as low as 1 mW/cm² for 1–2 h showed small but significant colonic temperature shifts in the range of 0.3–0.5°C. Circadian temperature cycling may also be a factor in the observed shifts at the lower intensity, however, and none of the averaged rectal temperatures reliably exceeded those of sham-irradiated rats after 8 h of exposure (280). The transient character of these shifts emphasized the

importance of homeothermic adaptive mechanisms in the mammal. With incident microwave field intensities above 5 mW/cm^2 for the human head, and expected SAR values of 5 W/kg or more, the absorbed energy is about one-sixth to one-half the metabolic heat production and may be associated with a progressive rise in brain temperature (178). Similar relationships may exist with incident power densities above $2.5\text{--}5.0 \text{ mW/cm}^2$ for the cat and above $0.5\text{--}1.0 \text{ mW/cm}^2$ for small mammals and birds.

Responses in *Aplysia* pacemaker neurons to pulsed and continuous-wave (CW) microwave fields support these generalizations and also indicate specific effects of pulsed fields not seen with CW fields of the same average power (398). For CW fields at 1.5 or 2.45 GHz, threshold energy absorptions for a change in firing rate were at SARs around 7.0 W/kg tissue at temperatures of $21\text{--}26^\circ\text{C}$. At threshold SAR levels, the firing rate changed slowly, reaching a new steady value with a time constant of about 1 min. Over the entire population of cells tested, 87% responded with slowed firing. With fields pulsed at 5,000/s (pulse duration $0.5 \mu\text{s}$), rapid changes were also seen at the onset of irradiation, with faster firing beginning in the first interspike interval and lasting less than 25 s. This effect occurred at an SAR as low as 1.0 W/kg . It was better defined for pulsed fields than for CW radiation and tended to occur at smaller averaged SARs for pulsed radiation. The slow response is attributed to a thermal interaction, with a change in temperature at equilibrium of about $0.02^\circ\text{C} \cdot \text{W}^{-1} \cdot \text{kg}^{-1}$ (corresponding to a temperature shift of 0.14°C at threshold for changed firing rate). The rapid changes in firing rate cannot be readily attributed to a thermal mechanism and may be related to a direct action of the EM field on the neuron.

Popular accounts of injuries or impaired quality of life (64) from deliberate or inadvertent exposure have all too frequently been based on an inadequate understanding of either radiation biophysics or potential pathophysiology. For low-level fields, design and performance of experiments that would credibly evaluate possible effects, particularly those of long-term exposures, have been difficult. Reliable data have been acquired slowly and corroborative studies have been limited. For RF and microwave fields with incident energies below 10 mW/cm^2 , separate observations of developmental, hemopoietic, neuroendocrine, neurohumoral, and immunological responses collectively are in general agreement with some aspects of physiological and biochemical data gathered in central nervous tissue. Many of these effects in other tissues appear related to membrane transductive functions and may therefore be relevant by extrapolation to excitable membranes in nervous tissue. They are briefly summarized below.

1. Effects on reproduction, growth, and development

Studies of possible effects of low-level radio and microwave fields on mammalian growth and development have yielded a spectrum of findings including "windowed" interactions. The possibility that fetal death and

teratoma development may be related to factors other than simple heating is suggested by higher mortality and resorption rates of fetuses exposed to microwave (2.45 GHz, SAR 31 W/kg) and infrared fields that produced identical increments (3.5°C) in colonic temperature (77). Soviet investigators have hypothesized that some actions of microwaves may be modeled as "nonthermal" but progressing against a background of tissue heating (210, 355-357). In later stages of pregnancy in the rat (*days 13* and *14*) exposure to thermalizing 27-MHz fields produces many more malformations, possibly due to heat accumulation in the amniotic sac (108). Soviet investigations have reported decreased fecundity and litter size and premature cessation of reproductive function in mice exposed for 4 h daily for 48 wk to microwave fields of only 250-500 $\mu\text{W}/\text{cm}^2$ (161), but details are lacking on possible dose enhancement that might be due to the particular carrier frequencies used and from field interactions between simultaneously exposed subjects. Nevertheless the findings emphasize the importance of further studies of possible effects of chronic low-level exposures. On the other hand, quail eggs incubated under controlled conditions that prevented a temperature rise during a daily 4-h exposure to a 2.45-GHz field (absorbed power 14 mW/g) during the first 5 days of hatching showed no gross malformations, altered body weight, or hematological effects (290), suggesting that at this much higher incident field intensity, there is not a specific microwave effect on development.

Osteogenesis may be influenced by direct and pulsed current via implanted electrodes and by induced electric fields (351). Pulsed low-frequency magnetic fields inductively coupled to tissues augment bone repair (36) and offer surgical advantages in avoiding disruption of skin integrity (37). Typical field parameters in bone-regeneration studies use pulse rates around 70 Hz, with pulse durations of 325 μs , peak intensities of 35 G, current densities around 1.0 $\mu\text{A}/\text{cm}^2$, and electric gradients, of 1-10 mV/cm. A second technique uses 5-ms bursts of 3-kHz pulses, with the bursts repeating at 15/s. When cultures of a clonal line of osteoblast cells were exposed to the 70-Hz magnetic field described above, there was a 90-99% inhibition of the adenylyl cyclase response to parathyroid hormone (PTH). At the same time, PTH-specific decreases in collagen synthesis and alkaline phosphatase release did not occur. Fluoride-activated adenylyl cyclase formation was unchanged, suggesting that the magnetic field blocked PTH action either by modification of the PTH receptor on the membrane or by altered coupling between the receptor and the enzyme adenylyl cyclase inside the membrane (281). Bone cell cultures from fetal rat calvaria responded to similar magnetic fields with significantly increased DNA synthesis, but the response depended on pulse wave form and culture techniques (327). The expected transmembrane current components of these extracellular fields would be on the order of 10^{-8} A/cm², 5 orders of magnitude less than the typical threshold for excitation based on a Hodgkin-Huxley model, implying the occurrence of a powerful amplification process in transduction of these exceedingly weak electrochemical triggers.

2. Hematology and immunology

Positive findings have included transient, reversible, and dose-dependent changes in rates of blastic transformation of unstimulated hamster lymphocytes irradiated for 15 min daily for five consecutive days with a 2.45-GHz CW field at power densities from 0 to 45 mW/cm² (200). Blood was removed 1 h after sham or microwave irradiation and cultured. Rate of transformation was maximum at a power density of 30 mW/cm², associated with a postirradiation body temperature of 39.3°C. However, both enhancement of transformation and inhibition of mitosis occurred with a 5-mW/cm² field where the mean control temperature of 38.2°C was increased by only 0.2°C, and autoradiography showed no evidence of radiation-related DNA repair. There was an inverted U-shaped functional relationship between transformation index and power density, with a reliable effect at 5.0 mW/cm², a maximum at 30 mW/cm², and a small effect at 45 mW/cm² intermediate between rates for controls and those exposed to 5.0 mW/cm². The investigators suggest that this may be yet another microwave sensitivity window described below for central nervous effects that include athermal energy levels. Further studies are necessary to decide whether this window relates to averaged strength of the tissue fields per se or simply to tissue heating, since each of three independent variables—power density, temperature increase, and postexposure rectal temperature—predicts with equal accuracy the percentage of transformation. "Whatever the source, the existence of such a window across a range of body temperatures of less than 2°C is of signal importance" (200). Czerski and his colleagues (25, 26, 94) have studied effects of long-term, low-dose microwave exposure of rabbits in producing slight alterations in erythroblast maturation and mitotic indices and mitotic aberrations in lymphocytes. Incident fields were 2,950 MHz, 3.0 mW/cm², for 2 h daily. Sensitivities were higher to pulsed (1,200 Hz, 1 μs) than CW fields of the same average intensity. Granulocyte precursors were unaffected, but mitoses in stem cells of erythroblasts, early granulocyte precursors, and lymphocytes showed markedly abnormal circadian rhythms.

Weak microwave fields may also influence the responses of immunocompetent lymphocytes. Immune responses were measured by the number of antibody-forming cells found in lymph nodes of young adult mice treated daily for 6 wk with 2-h exposures to a 2.95-GHz pulsed field (1,200/s, 1 μs, 0.5 mW/cm²) and then immunized against sheep erythrocytes (94). Irradiation increased the numbers of lymphoblasts in the lymph nodes, but no alterations in plasmocyte counts were seen in control or irradiated nonimmunized mice. Mice irradiated for 6 wk showed significantly higher numbers of antibody-producing cells and serum hemagglutinins than controls, but those exposed for 12 wk did not suggesting an adaptation similar to that described in temperature responses of dogs subjected to whole-body microwave exposure (298). Comparable *in vitro* experiments on mouse lymphocytes have not yielded positive findings (407).

Immunological effects of microwave fields are currently the subject of many investigations. These studies have been presented mainly in three symposia that await extended publication (URSI Symposium, Amherst, MA, 1976; URSI Symposium, Airlie House, VA, 1977; URSI Symposium, Helsinki, 1978). A wide range of field parameters are under investigation, including comparisons of pulsed and CW radiations and of field intensities from $50 \mu\text{W}$ to more than 10 mW/cm^2 . There is no consensus in these preliminary reports of a potentially high sensitivity of immunologic responses to nonionizing radiation, although it remains for future research to demonstrate an unequivocal modification of cell-mediated immunity *in vivo* by microwave field exposure. Fetal rats exposed *in utero* and for 40 days after birth to 2.45-GHz CW fields at 10 mW/cm^2 (SAR 1–5 W/kg) for 4 h daily show increased responses of lymph node cells to T and B mitogens and increased responses of blood lymphocytes to T-cell mitogens (408). Rabbits and guinea pigs exposed to a 3.1-GHz, 1-mW/cm^2 field for 320 h in an anechoic chamber showed decreased uptake of colloidal gold by liver Kupffer cells, and increased mitotic indices in spleen, thymus, and lymph node cells, with increased serum γ -globulins (307). Decreased antibody production to T-lymphocyte-dependent and -independent antigens and increased numbers of IgM-secreting cells have been reported after exposure of nonimmunized mice to a 2.45-GHz field (SAR 12 W/kg) for 30 min/day for 3 days (456). At much lower field levels (2.375 GHz, $50 \mu\text{W/cm}^2$ for 30 days) rats and guinea pigs show decreased T-cell responses, with suppression of phagocytosis. In the same study, field levels at and above $500 \mu\text{W/cm}^2$ evoked an autoimmune disease, with production of antibrain and antiliver antibodies (402). Negative findings have also been reported, including absence of changes in segmented polymorphonuclear leukocytes, circulating lymphocytes and γ -globulins of rats and mice exposed to 2.45-GHz, 5-mW/cm^2 fields 5 h/day for 6–12 wk (362, 421). Increased bone marrow cellularity occurred in mice exposed to a 2.88-GHz, 5-mW/cm^2 field (SAR 2.3 W/kg) for 80–400 h, but not at 10 mW/cm^2 (SAR 6.3 W/kg), suggesting a windowed response (362). More exact determination of thresholds and an elucidation of inconsistencies in these immunogenic and immunosuppressive responses must await further studies.

Diurnal rhythms in the production of hemopoietic stem cells respond sensitively to weak microwave field exposures (26, 92). Guinea pigs were exposed 4 h daily to a 2.95-GHz pulsed field with an averaged power density of 1 mW/cm^2 . Daily exposures began at either 0800 or 2000 h. Circadian rhythms of bone marrow mitoses showed major phase shifts in the times of maximum proliferation of early normoblasts, myeloblasts, and lymphoblasts. No effects were noted in granulocyte precursors. Similar diurnal phase shifts were noted in mice exposed to a weaker 2.95-GHz, 0.5-mW/cm^2 pulsed field that did not significantly raise body temperature over the 4-h exposure period, even though mice show a whole-body resonance at this frequency. Sensitivity of human and avian circadian rhythms in sleep, wakefulness, and metabolic cycles (448, 454) to far weaker 10-Hz ELF fields is discussed below.

3. Central nervous system

Environmental EM fields influence behavioral, neurophysiological, and chemical responses in the mammalian CNS. An evaluation of all possible modes of interaction is not yet possible. Indeed the matrix of possible physical parameters that might be tested is obviously so vast that it has been necessary from pragmatic fiscal considerations, as well as for economy in scientific effort, to first examine the effects of those fields deemed most likely to interact with central nervous tissue. Thus there has been a clustering of studies utilizing ELF fields in the spectrum from DC to 100 Hz, with evaluation of fields at power-line frequencies of 50 and 60 Hz and at proposed U.S. Navy long-range communication frequencies of 45 and 76 Hz, as well as intense research into the spectrum from 1 to 35 Hz associated with intrinsic oscillations in central nervous tissue. For RF and microwave fields, a broad spectrum of carrier frequencies has been tested with essentially no evidence of effects attributable to the carrier frequency per se for fields below thermalizing levels, but again a clustering has been noted of apparently higher sensitivities to fields amplitude-modulated at frequencies between 1 and about 40 Hz. There is also evidence of interactions with radio and microwave fields pulse-modulated at higher frequencies from 500 to 1,500 Hz and an absence of similar effects with CW fields of the same average power density at the same carrier frequency. As in certain hematological and immunological responses and in interactions with nervous systems of marine vertebrates, windowed amplitude sensitivities have also been detected. Merely to unravel the more important elements of this complex matrix, each of the three classes of bioeffects is treated separately.

a) *Biological rhythms and endocrine mechanisms.* Human circadian rhythms arise endogenously (20). Even without time cues in a constant environment, they deviate only slightly from 24 h, with most autonomous human rhythms approximating 25 h. Typically, oscillators governing different physiological and psychological variables are coupled and run synchronously (453) but may run asynchronously in "internal desynchronization."

Human and avian circadian rhythms have been modified in an underground isolation unit shielded against natural electric and magnetic fields. They also appear sensitive to 10-Hz, 2.5-V/m square-wave fields imposed in this shielded environment (448, 450-454). Dual identical chambers, one shielded and the other unshielded, allowed simultaneous testing of field-exposed and control subjects who were not aware of differences between the units. Circadian periodicity was measured by sleep-wakefulness and rectal temperature periodicities in initial experiments. In the unshielded unit, subjects had free-running circadian periods shorter on the average by 20 min, the interindividual differences around the means were smaller by about 50%, and internal desynchronization was less likely than in the shielded facility (unshielded unit: $n = 57$, mean free-running period 24.87 ± 0.45 h, internal desynchronization in 4 subjects; shielded unit: $n = 80$, mean, free-running period 25.21 ± 0.80 h, internal desynchronization in 28 subjects). All these differences were significant

at $P < 0.01$ or lower when considered separately. Wever (449) therefore hypothesized that the differences were due to natural EM fields present only in the unshielded unit. Initial tests with DC electric fields (600 V/m) and magnetic fields (1.5 Oe) were without effect. Subjects were then exposed to a 2.5-V/m, 10-Hz square-wave electric field, usually in the shielded unit, first in the absence of the artificial field for 1 or 2 wk. The field was then applied continuously for 1 or 2 wk, followed in some cases by a further control period without fields. In 10 subjects, the period was shorter during field exposure than without it by an average of 1.3 ± 0.7 h ($P < 0.001$). The shortening was greater for those subjects with the longest circadian cycles in the absence of the field. In some subjects internal desynchronization occurred immediately after the field was switched off; in others it ceased immediately after the field was switched on. Reducing field exposure to 12 h on and 12 h off did not eliminate its *Zeitgeber* effect in temporarily restoring a 24.0-h rhythm in 10 subjects with free-running rhythms between 23.5 and 26 h. Wever (449, 452) interpreted these results as indicating a significant *Zeitgeber* capacity of the 10-Hz field even when imposed intermittently. Shortened circadian rhythms were also seen in birds exposed to the same 10-Hz, 2.5-V/m square-wave fields (450). In the European green finch, continuous field exposure for 10–20 days sharply shortened the circadian period from 24.8 to 23.9 h. Nocturnal restlessness in the European brambling associated with seasonal migration was enhanced by a 10-Hz field that illuminated certain perches for which the birds exhibited a preference over unexposed perches in the same row. No differences were detected during the day (454). Further evaluation of Wever's experiments requires more information on spontaneous drifts in the periods of circadian oscillations. Analysis of these data by linear regression should be approached with caution, since differences between control and test phases may be significantly influenced by the number of cycles included in each phase. In view of Wever's strong emphasis on the role of natural electric fields in entrainment of the normal circadian rhythms, further information is needed on residual natural and artificial fields in his test chambers. Although altered circadian rhythms provide indirect evidence on the chronobiology of endocrine rhythms (405), only a few studies have directly evaluated possible endocrine effects of EM field exposure. Mice exposed to 75-Hz electric fields (1–10 V/m) and magnetic fields (0.5–2.0 G), singly and in combination, showed no effects on circadian rhythms, body temperature, food consumption, estrus, or survival rates (185). Although these data present "no persuasive evidence of adverse effects of ELF fields," only cautious comparisons can be made between these studies at 75 Hz and effects reported at field frequencies below 20 Hz, in view of frequency-selective behavioral and neurophysiological interactions at these lower frequencies.

Pulsed microwave fields of low power density imposed on guinea pigs and mice at various times of day cause abnormal circadian rhythms of bone marrow cell mitoses (94, 96). Exposure involved a pulsed field of 2.95 GHz (1,200 Hz, 1 μ s) and 1 mW/cm² for 4 h daily. Two groups of animals were irradiated,

beginning at either 1:00 A.M. or 2:00 P.M. for 14 days. Observed effects depended both on the time of day at which exposure occurred and on the cell series. Granulocyte precursor mitoses were unaffected, erythroblast cell line mitoses showed slight disorders of circadian rhythms, and bone marrow stem cells (early erythroblasts, myeloblasts, hemopoietic stem cells, and probably lymphocytes) showed changes in amplitude and phase of circadian rhythms in animals irradiated in the evening or in the morning compared with each and with controls. Because of the short observation period and small number of animals tested, the investigators confirmed their initial observations in a further study with over 200 mice, divided into four groups. These syngeneic mice were subjected to a single 4-h exposure (either A.M. or P.M.) to the same pulsed 2.95-GHz field at a lower incident energy of 0.5 mW/cm² and examined during three consecutive days, beginning 28 h after the end of irradiation. Expectations were confirmed that if microwave exposure induced changes in the circadian rhythm of marrow cell mitoses, a disturbance resembling a decaying oscillation would occur, with altered amplitude and phase of the mitotic rhythm of stem cells. Differences were noted in iron metabolism studies between CW and pulsed microwave effects at the same wavelength and average power density in strictly comparable exposure conditions, "stressing the importance of taking to account the physiologic properties of cells, tissues and organs when investigating microwave bioeffects, and the dangers of generalizations" (95). At much higher field levels (2.45 GHz, 20 mW/cm²) associated with increased body temperature in rats, no alteration in rhythmicity of serum corticosterone was observed (280). At far lower intensities (5 and 10 μ W/cm²), 50-MHz, 2.5-GHz, and 10-GHz fields have been reported by Soviet workers to increase urinary ketosteroids in 24-h specimens with statistically significant differences ($P < 0.05$) at 30, 90, and 120 days for the microwave exposure (116). The 50-MHz fields were imposed for 10–12 h daily and the microwave fields for 8 h. This study used both CW and pulsed fields, with rates of 1,000 and 20/s for the pulsed fields. The authors give no indication of possible differences in effects of pulsed and CW exposure regimens, nor are there data on possible changes in diurnal rhythmicity of steroid excretion.

A Soviet study of metabolic indices in rats chronically exposed to "nonthermal intensity" RF fields showed changed excretion of sodium, potassium, and chlorides compared with controls (103). One experiment was conducted with a 69.7-MHz, 150-V/m field with exposures of 1 h daily for 3 mo. A second test used a 14.8-MHz, 70-V/m field with exposures of 4 h daily. Urine output and Na/K ratios decreased in the first 2 wk, but by the end of the irradiation the excretion of water, nitrogen, and electrolytes rose sharply, with Na concentration increasing more than threefold. Adrenal weights and thyroid follicular epithelium dimensions were significantly increased. Demokidova (103) concluded that the RF field acted as a nonspecific stress in activating hypothalamohypophyseal adrenal systems. Mikolajczyk (305) reached the same conclusion for rats exposed to thermalizing microwave fields (2.88 GHz, 10 mW/cm²).

b) *Behavioral effects.* There are numerous reports—probably more than in any other area of claimed bioeffects of weak environmental EM fields—of subtle behavioral changes in situations lacking necessary rigor in experimental design, often defective in control procedures, with inadequate evaluation of intercurrent stimuli, and plagued by experimental data so noisy that even statistical evaluation does little to establish credibility for claimed interactions. A special problem is the fact that most reported effects have not been independently confirmed. From the complex spatiotemporal character of perineuronal fields in central nervous tissue (125), there is good evidence that they remain essentially independent and incoherent in most behavioral states, creating myriad intrinsic fields, each with unique spatial and frequency characteristics (2). Imposed environmental fields, which may reproduce with varying accuracy dominant frequency components of these intrinsic fields, would not be expected to duplicate the endless complexities of these spatial patterns. In this respect, the imposed field would remain a weak manipulandum, and the ensuing behavioral effects would be only a subtle modification of some basic state. Even this level of behavioral effect can be anticipated only in terms of cellular transductive coupling mechanisms that transcend by orders of magnitude typical synaptic mechanisms of excitation.

1) **BEHAVIORAL EFFECTS OF ELF FIELDS.** Behavioral correlates have been sought with natural and artificial ELF fields. Reaction times in humans have been reported as slowed at times of high natural activity between 3 and 6 Hz, with a converse effect at times of 10-Hz peaks (253). These natural oscillations are believed to arise in the Schumann resonance discussed above, with typical amplitudes of 1-2 V/m. Further studies from the same group with artificial fields at frequencies of 5-10 Hz and strengths of 0.3-5.0 V/m again showed trends consistent with effects of natural fields, but these trends were not amenable to statistical analysis. Other tests of human reaction times in ELF fields of 1-20 Hz have suggested that reaction time is inversely related to field frequency (186-188), but the statistical significance of these results has been questioned (318). No changes in reaction time were seen in three squirrel monkeys tested for 1 h daily before, during, and after exposure to a 45-Hz, 10-G magnetic field for 42 days (171). Changes were small in those reaction times where positive effects were reported, typically less than 5%. "If a psychophysiological effect exists, it is probably quite subtle, and will therefore require a broad range of very sensitive experiments to evaluate properly the long-term effects of the ELF environment" (171). The influence of ELF fields on subjective estimates of the passage of time by monkeys has been examined in two laboratories. Monkeys were required to estimate a time interval of 5.0 s in the absence of behavioral cues. Results were conflicting, but may be related to seemingly minor differences in test procedures. In two separate studies, Gavalas-Medici and colleagues (157, 159) studied subjective time estimation in pigtail macaque monkeys to fields of 7, 45, 60, and 75 Hz at intensities of 1-100 V/m. At 7 Hz and 10 V/m, the mean time estimate was 5-10% shorter than in no-field conditions. There was an apparent threshold for the 7-Hz fields between 1 and 10 V/m.

At 45 and 75 Hz, fields of 56 V/m produced smaller changes. At 100 V/m, no consistent effects were noted at any test frequency. No effects were observed in tests at 60 Hz. These experiments included monkeys with and without implanted cerebral electrodes. Implanted and unimplanted animals showed similar sensitivities. Measurements of total current (0.9 nA) induced in a phantom monkey head (437) by a 10-Hz, 10-V/m field in this exposure chamber indicated expected extracellular electric gradients of 10^{-7} V/cm enhanced to 10^{-4} V/m in the vicinity of the electrode tips. The implanted electrodes were not believed to be associated with significant "antenna" effects, since the transmembrane components of these induced extracellular currents would be less than 1.0% of the total flow and would change membrane potentials by far less than the 10^3 V/cm associated with synaptic depolarization. This conclusion is supported by analyses of electroencephalogram (EEG) records during field exposure (see below) and invites consideration of transductive mechanisms at the neuronal surface, which are preliminary to later transmembrane events in the sequence of excitation.

In a similar study on rhesus monkeys exposed to weak (8.2–9.3 G) 15- and 45-Hz magnetic fields, deLorge (101, 102) interpreted the findings as equivocal. Three of four subjects showed shorter interresponse times with the first series of exposures but not to the second. A test of the distributions was highly significant (Kalmogorov-Smirnov test, $P < 0.001$). However, means of interresponse times (IRTs) were not altered by field exposure. One monkey had shorter IRTs with both 45-Hz exposures ($P < 0.001$). In the 15-Hz fields, one monkey was significantly faster ($P < 0.05$), one was significantly slower ($P < 0.001$), and two were unaltered. Differing conclusions in studies that appear so similar may be related to details of the test procedures. Gavalas-Medici used a daily exposure schedule of 4 h. In some subjects, larger-field/no-field differences in IRTs occurred in the 3rd and 4th h than in the 2nd h of exposure. DeLorge used situations with either one or two different behavioral tasks. The IRT schedule was imposed three or six times in a 2-h session, but for only 15 min for each task. If the findings of Gavalas-Medici validly indicate a gradual onset of altered subjective time estimation over several hours, there is a need for further studies of long-term exposure, particularly since investigator intervention was sometimes required in the later hours of the experiment to stimulate performance. A relatively slow onset of altered reaction time was noted in 20 human subjects exposed to 50-Hz electric fields of 1,000 and 15,000 V/m (189). An attempt to replicate these studies was unsuccessful (122).

Altered feeding and drinking behaviors have been reported in the adult offspring of rats exposed to rotating magnetic fields of 0.5–3.0 G at 0.5 Hz during pregnancy (347) or after exposure of the offspring during postnatal days 1–4. However, appropriate statistical analyses are not possible from published data.

II) BEHAVIORAL EFFECTS OF WEAK RADIOFREQUENCY AND MICROWAVE FIELDS. There is an extensive literature from Eastern European research on behavioral effects of long-term exposure to weak RF and microwave fields. Much is

related to industrial exposure in man presumed to produce a "vegetative dysfunction," with symptoms of hyperhidrosis, enhanced pilomotor reflexes, and anomalies of thermoregulation, manifested as the "asthenic syndrome" (226), with fatigue, impotence, and loss of appetite. A similar syndrome has not been reported as a widespread concomitant of industrial exposure in Western microwave-exposed workers. On the other hand, sensitive behavioral measures in animal experiments in Eastern and Western laboratories are now providing some convergent evidence of effects of chronic low-level exposure. Dumanskiy and Shandala (116) and their colleagues at Kiev first reported altered conditioned reflex activity in rabbits and rats chronically exposed to extremely low levels of VHF and microwave fields. They used either 50-MHz or 2.5-GHz CW fields or 10-GHz fields with 1- μ s pulses at repetition frequencies of 1,000 or 20, with daily exposures of 10–12 h at 50 MHz and 8 h with the microwave fields, and found statistically significant effects with field intensities between 1.9 and 2.0 μ W/cm². In each experiment the animals were irradiated for 120 days, with a 60-day follow-up. For the first 10 days of irradiation the animals were "somewhat excited" and reacted to onset of field exposure. Thereafter responses to conditional stimuli had a longer latency, with weaker responses to positive stimuli and more numerous missed responses, leading to "pathologic stagnation and inertia." In a counterpart experiment, Lovely et al. (278) exposed rats for 7 h daily for 3 mo to a 500- μ W/cm², 2.45-GHz CW microwave field. Findings suggested significant differences between control and irradiated groups in monthly testing of behavioral sensitivity to electric shock and in terminal tests of open-field activity and shuttle-box avoidance. These behavioral effects disappeared after a 1-mo recovery period. There has been a tendency in Western countries to discount evidence of an asthenic syndrome among workers in electrical switchyards and microwave industries because of the vagueness of the symptomatology and absence of defined endocrine or autonomic disorders that would characterize the syndrome uniquely, reliably separating it from functional disorders attributable to a stressful work environment. Available data cannot yet resolve this question, but there is evidence from these animal models of subtle behavioral effects that could be the counterpart of elements of the asthenic syndrome in microwave-exposed workers.

c) Entrainment of central nervous electrical rhythms by ELF fields and by RF fields amplitude-modulated at ELF. Both entrainment of brain electrical rhythms at the frequency of an imposed environmental field (where that field is at or close to the frequency of an intrinsic rhythm or EEG "burst" in a particular cerebral structure) and changes over a much broader EEG spectral range have been reported. Some of these changes have persisted beyond the period of field exposure. Newer techniques for intracerebral recording are compatible with environmental field exposure by the use of nonmetallic electrode materials (81, 140, 434). Most earlier studies at radio or microwave frequencies must be cautiously interpreted, although the observed interactions should not be dismissed as artifactual or simply due to enhanced electrical gradients in the vicinity of these metal electrodes, as discussed above (215).

Indeed, special tests, such as spectral analyses of EEG records over extended exposure periods, appear to preclude an origin for the EEG entrainment in a simple electrochemical basis, such as demodulation of the impressed field at an electrode-tissue interface. Monkeys exposed to 7- or 10-Hz, 7-V/m peak-to-peak fields for 4-h periods showed changes toward the end of the test time for EEG periods associated with predominantly incorrect responses in a subjective time-estimation test (157). The animals were trained to estimate a 5-s interval without external cues, and were rewarded with apple juice for responses within ± 1.25 s of the 5-s interval. The EEG records from hippocampi, amygdalae, nucleus centrum medianum, midbrain reticular formation, and visual and motor cortices were examined by auto- and cross-spectral analyses, including coherence calculations and by use of a "peak-quotient" estimator that evaluated deviations of the spectral contour from a logarithmic contour that might be attributable to EEG entrainment at the field frequency or at its harmonics. Interresponse times were significantly faster with 7-Hz fields (159). Peak quotients were compared for fields-on versus fields-off conditions and showed significant differences in hippocampi, amygdalae, and nucleus centrum medianum for both 7- and 10-Hz conditions ($P < 0.01$). Coherence between the 7-Hz sinusoidal field wave form and the responsive EEG structures were always higher for fields-on than for fields-off conditions, but coherence levels between responsive brain structures showed no consistent patterns of change. Although not detectable on visual inspection of EEG records, discriminant analyses of spectral data showed strong driving (increased intensity and increased coherences) at harmonics of the field frequency. Although such harmonic response is entirely compatible with biological transduction (438, 442), its occurrence does not preclude artifactual transduction. This is unlikely, since the EEG electric gradients were orders of magnitude larger than tissue components of the fundamental of the imposed 7- to 56-V/m ELF fields, which were estimated at around 10^{-7} V/cm, based on induced current measurements in phantom heads (437).

Because RF fields are more strongly coupled to tissues than ELF fields, they induce much larger tissue electric gradients with similar levels of environmental electric gradients. Thus RF fields at around 100 MHz can be expected to induce an EEG-level tissue gradient (10–100 mV/cm) with an incident energy around 1.0 mW/cm² (61 V/m), subject to variations attributable to body resonance effects noted above. Persistent EEG changes occurred for several days in rabbits after exposure for 2 h daily for 4–8 wk to a 5.0-MHz field amplitude-modulated at 14–16 Hz (427). Fields with amplitudes of 90–150 V/m enhanced EEG activity at 10–15 Hz, and 500-V/m fields enhanced 4- to 5-Hz waves. No brain heating occurred during these exposures. "Bursts" of EEG waves occurring in various brain nuclei of the awake cat as conditional responses to a flash of light (and thus constituting a learned response) were tested for interactions with a 147-MHz, 0.8-mW/cm² field, amplitude-modulated at the dominant frequency of the selected transient EEG pattern (40). The irradiated animals were superior to a control group in the rate of

performance, accuracy (in terms of bandwidth of the EEG spectrum during the learned response), and resistance to extinction (minimum of 50 days vs. 10 days). The specificity of the frequency of the modulation was tested on another group of untrained animals where spontaneous transient patterns were used to trigger for short periods (20 s after every burst), the VHF fields amplitude-modulated at various frequencies. The fields acted as reinforcers (increasing the rate of occurrence of the spontaneous rhythms) only when modulated at frequencies close to the biologically dominant frequency of the selected intrinsic EEG rhythmic episodes. Although this study used metal brain electrodes, spectral analysis of EEG records between wave "bursts" disclosed no artifactual rectification of imposed fields at brain-electrode interfaces.

A persistent component in rat EEG spectral analyses at the pulse-repetition frequency of a microwave field after irradiation has been reported (400). With a 3.0-GHz field at 500–600 pulses/s (1.0- μ s pulse duration, average power density 5.0 mW/cm²), exposure for 10 days was followed by a distinct EEG peak at the pulse-repetition frequency that waxed and waned in cycles lasting several minutes. The high frequency of the entrained spectral peak reported in this study may indicate a transductive mechanism distinct from that underlying EEG entrainment, where dendrites of cerebral neurons are the presumed locus of interaction for natural dominant frequencies typically below 50 Hz.

d) "Windowed" responses of calcium ion binding in brain tissue to ELF, VHF, and UHF fields. Calcium ions are essential in transductive coupling of a wide range of immunological, endocrinological, and neurological events at cell membrane surfaces. Whereas the typical extracellular calcium concentration is around 2.0 mM, concentrations in the general cytoplasm within cells are far lower, around 10^{-7} M (267). Calcium efflux from cerebral tissue is extremely sensitive to weak electrical stimulation and to certain weak environmental EM fields. There is evidence that these field effects occur at binding sites on cell membrane surfaces (39). Calcium ions trigger their own release from intact cat cerebral cortex in a highly nonlinear fashion, strongly suggestive of a cooperative process (222). A 0.5-mM increment in Ca²⁺ concentration in superfusing fluid elicited an increased efflux of 1.25 ± 0.08 , whereas an increment of 20 mM Ca²⁺ caused an efflux 1.61 ± 0.15 greater than in control experiments. There was a parallel and similarly nonlinear increase in [³H] γ -aminobutyric acid ([³H]GABA) efflux. Electrical stimulation of cat cortex with 200/s, 1.0-ms pulses through cylindrical agar electrodes that produced an essentially uniform electrical field of 20–60 mV/cm from cortical surface to basal diencephalon increased ⁴⁵Ca²⁺ efflux 1.29 \pm 0.06-fold and [³H]GABA efflux by 1.21 \pm 0.04-fold. These changes may reflect much larger shifts in rates of binding and release in the tissue (219). For a synaptic terminal 0.5 μ m in diameter the extracellular gradient imposed by these fields is at most 1–2 μ V. It is unclear how such a weak stimulus may affect the transmembrane potential of 50 mV to influence transmitter release. Similar considerations apply to effects of the fields on postsynaptic excitability. In this case a transmembrane potential of several millivolts is required to induce altered activity

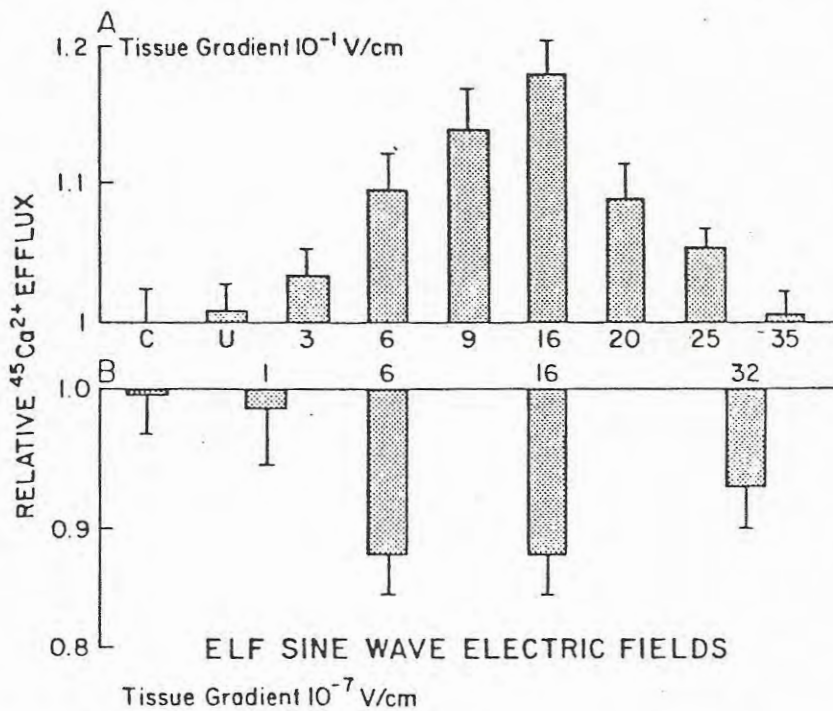


FIG. 1. A: $^{45}\text{Ca}^{2+}$ efflux from freshly isolated chick cerebral hemispheres exposed to a weak radio-frequency field (147 MHz, 0.8 mW/cm^2), amplitude-modulated at low frequencies. B: $^{45}\text{Ca}^{2+}$ efflux changes from exposure to far weaker electric fields (56 V/m) in the same frequency spectrum from 1 to 32 Hz. Peak magnitude of efflux change is similar for the 2 fields but opposite in direction. For radio-frequency field in A, the unmodulated carrier wave U had no effect when compared with controls C. Field gradients differ by about 6 orders of magnitude between A and B. [Adapted from Bawin and Adey (38) and Bawin, Kaczmarek, and Adey (41).]

(117). This change is equivalent to a gradient of 1 kV/cm across the membrane and exceeds the extracellular applied gradients by almost 10^5 . There is a further question about the extent to which the extracellular field generated by one cortical neuron may influence a nearby cell. Extracellular gradients generated by spinal motoneurons exceed 50 mV/cm (319, 363), and even larger EEG gradients have been recorded in the absence of seizures across a dipole of only $30 \mu\text{m}$ (124). Thus these imposed experimental fields are in the range of naturally occurring gradients and the findings support the possibility of electrical interaction between cortical cells.

Freshly isolated chick and cat cerebral tissues exposed to sinusoidal electric fields at 1, 16, 32, or 75 Hz with electric gradients in air of 5, 10, 56, and 100 V/m exhibit a general trend toward a reduction in release of preincubated $^{45}\text{Ca}^{2+}$ (38). Tissues were bathed in Ringer solution at 36°C . After 30 min of incubation with $^{45}\text{Ca}^{2+}$, each sample was immersed in fresh solution and exposed to the field for 20 min. Efflux of $^{45}\text{Ca}^{2+}$ was then measured and com-

pared with unexposed controls. Maximum decreases of 12–15% occurred at 6 and 16 Hz, with thresholds around 10 V/m for chick ($P < 0.01$) and 56 V/m for cat cortex ($P < 0.05$ at 6 Hz and $P < 0.01$ at 16 Hz), with estimated tissue gradients of the order of $0.1 \mu\text{V}/\text{cm}$. Similar but nonsignificant trends occurred during other field exposures at 5 and 100 V/m. Thus the field effect on $^{45}\text{Ca}^{2+}$ efflux was "windowed" in both frequency and amplitude domains (Fig. 1B).

Similar frequency and amplitude windows have been observed in chick cerebral tissue exposed to VHF and UHF fields with ELF amplitude modulation. Neonatal chick cerebral hemispheres were first incubated in a physiological medium containing $^{45}\text{Ca}^{2+}$ and then immersed in a nonradioactive solution. They were then irradiated in a 147-MHz, $0.8\text{-mW}/\text{cm}^2$ field, sinusoidally amplitude-modulated at a depth of 80–90% at frequencies from 0.5 to 35 Hz (41). Unmodulated fields and modulation frequencies of 0.5 and 3 Hz did not induce a significant change in $^{45}\text{Ca}^{2+}$ efflux. By contrast there was a progressive increase in efflux at 6 Hz (10.1%, $P < 0.05$), 9 Hz (14.3%, $P < 0.05$), 11 Hz (16%, $P < 0.01$), and 16 Hz (18.5%, $P < 0.01$). The response decreased progressively at modulation frequencies from 20 to 35 Hz (Fig. 1A). Brains treated with 10^{-4} M sodium cyanide prior to $^{45}\text{Ca}^{2+}$ incubation and irradiation responded identically to unpoisoned tissue, indicating that the response did not depend on integrity of cytochrome respiratory enzyme systems. These experiments have been repeated independently with 147-MHz fields and have confirmed the existence of this modulation-frequency window between 9 and 16 Hz (58). The latter study also disclosed statistically significant effects at incident power densities around $1.0\text{ mW}/\text{cm}^2$. This power window has also been observed for chick cerebral tissue exposed to a 450-MHz field, sinusoidally modulated at 16 Hz (42). Increased efflux of $^{45}\text{Ca}^{2+}$ occurred only at 0.1 and $1.0\text{ mW}/\text{cm}^2$ ($P < 0.01$) and not at 0.05 and $5.0\text{ mW}/\text{cm}^2$. Dosimetry measurements showed tissue gradients of the order of $100\text{ mV}/\text{cm}$ with incident fields of $1.0\text{ mW}/\text{cm}^2$.

Efflux studies have further elucidated the role of H^+ and HCO_3^- ions in controlling the $^{45}\text{Ca}^{2+}$ movements in cerebral tissue and have more accurately identified the probable site of tissue coupling of the EM field (39). Addition of H^+ ions sharply enhanced $^{45}\text{Ca}^{2+}$ efflux in the presence of the 450-MHz, $0.75\text{-mW}/\text{cm}^2$, 16-Hz modulated field but had no effect on the nonstimulated efflux, suggesting a role for H^+ ion binding in these field effects, perhaps in accordance with the model of competitive H^+ - Ca^{2+} binding on cell membrane surface macromolecules originally proposed in Pauling's laboratory (33), or perhaps in terms of proton tunneling across phase boundaries at the margins of cell surface fixed-charge domain (8). This decrease is unlikely to be due to inhibition of movement of Ca^{2+} ions into mitochondria and other cell organelles (24, 314), because the HCO_3^- concentration was only 2.4 mM in the control medium (70, 249). Nor can the reduced efflux be explained by increased calcium entry into the cell, because the effect persisted in the presence of 0.5 mM La^{3+} and was enhanced at a higher concentration of the ion. On the other hand, inhibition of inward Ca^{2+} currents in the absence of HCO_3^- ions could result in decreased

transmembrane calcium exchange, followed by a reduction of intracellular $^{45}\text{Ca}^{2+}$ efflux (323). This model would not explain evidence from the same study that responses to the field occurred in lanthanum-treated tissue, with the response probably mediated in the extracellular compartment.

Treatment of chick cerebral tissue in these experiments with lanthanum prior to testing 450-MHz field effects on $^{45}\text{Ca}^{2+}$ efflux indicates that at least one major class of these field interactions probably occurs at cell membrane surfaces (39). Since La^{3+} ions block movement of Ca^{2+} ions both inward and outward across the cell membrane, field effects of $^{45}\text{Ca}^{2+}$ efflux that persist after La^{3+} may be presumed to occur in the fluid surrounding cerebral cells. Addition of La^{3+} to the HCO_3^- -free solution described above restored sensitivity to the 6-Hz-modulated, 450-MHz field, but the stimulation decreased instead of increasing $^{45}\text{Ca}^{2+}$ efflux. This response exhibited the same windowed specificity to field intensity seen in tissues in normal physiological solutions (38, 41). Here the stimulated decrease occurred only at field intensities around 0.75 mW/cm² and vanished at higher and lower field intensities. The consistency of the effect in all experiments (10–15% change in efflux), together with the exquisite sensitivity of the system to narrow windows in frequency and amplitude, supports the hypothesis that a limited number of cationic binding sites are involved in the transduction of weak, low-frequency extracellular electric gradients and may constitute a specific class of binding sites, normally occupied by calcium ions and susceptible to competitive hydrogen ion binding.

e) Sensitivity of the blood-brain barrier to microwave fields. The selective permeability of the blood-brain barrier for small, lipid-soluble molecules, including glucose and for certain amino acids, purines, and nucleosides appears to depend on carrier proteins with a high affinity for specific molecules (331, 332, 365). A wide variety of drugs, including barbiturates and other anesthetic agents, modify this permeability. It is also susceptible to physical agents, such as cold stress, electroconvulsive shock, cerebral concussion, and ionizing radiation.

Microwave irradiation at 2.45 GHz sufficiently intense to raise brain temperature to 40°C in rats increases uptake of horseradish peroxidase as a strong correlation with the time-intensity product (420). Rats made hypothermic at 30°C prior to exposure showed longer latencies to increased uptake than normothermic animals. They also had a lower mortality when their heads were selectively exposed to high thermalizing fields. However, this difference may be related to continued lower temperatures in medullary respiratory centers during irradiation of precooled subjects. Subsequent studies have attempted evaluation of much weaker fields and the possibility of differential effects of pulsed and CW fields. The picture remains confused, with insufficient attention to important variables such as use of anesthetic agents and concurrent hypothermia in studies that purport to be replications of paradigms involving awake subjects. Furthermore, thermalizing levels of field exposure are very likely to be associated with altered cerebral blood flow. Assessment of changed barrier permeability by the Oldendorf (332) dual-indicator technique requires that cerebral blood flow be kept constant, whereas

the dual-compartment technique of Rapoport (365) measures and controls for changes in blood flow. All these considerations are important in evaluating recent research.

Relatively weak 1.2-GHz fields (2.4 mW/cm² CW; or pulsed at 1,000/s, 0.5- μ s pulse duration, with peak power density of 2.0 mW/cm² and average density of 0.2 mW/cm²) increased uptake of fluorescein sodium in anesthetized rats after 30 min of exposure (139). Dye uptake was evaluated in brain slices viewed with UV light. Pulsed radiation was 2.5 times more effective than CW, even though the average power density of the CW field was an order of magnitude greater than the pulsed field. No dye leakage was detected in control samples from any brain region. Such a categoric separation is unexpected, since there is good evidence that the blood-brain barrier is poorly developed or absent in the pineal gland, median eminence, area postrema, and the wall of the optic recess (12). Considerable fluorescence in normal brain tissue activated with UV light has led to use of the Oldendorf (329, 330) double-indicator technique for barrier studies in brains of rats exposed to pulsed or CW 1.3-GHz radiation for 20 min (336). Uptake of polar molecules was compared with movement of tritiated water. Three studies were performed, two with anesthetized and one with unanesthetized rats. Uptake of D-[1-¹⁴C]mannitol was slightly but consistently greater in hypothalamus, hippocampus, and neocortex of irradiated anesthetized rats than in sham-irradiated subjects. Again there was evidence of a windowed sensitivity for pulse frequency, with 10- μ s pulses at 50/s (average power density 0.3 mW/cm²) consistently more effective in increasing uptake than 10- μ s pulses at 1,000/s (average power density 2.0 mW/cm²). A second study, also with anesthetized rats, compared uptake of [¹⁴C]mannitol, [¹⁴C]inulin, and [¹⁴C]dextran in control subjects and in animals exposed to the 1.3-GHz field with 0.5- μ s, 1,000/s pulses (average power density 0.3 mW/cm²). Increased uptake of mannitol and inulin followed a regional pattern similar to that seen in the first study, but very little effect was noted on uptake of larger dextran molecules. In unanesthetized rats, uptake of mannitol was elevated by 50–100% in the hypothalamus, cerebellum, and medulla 8 min and 4 h after irradiation, but after 24 h only the medulla showed a significant increase of 20%. There was a windowed response in medullary tissue to changing power density for both CW and pulsed fields, with a maximal ninefold increase occurring in CW fields around 1.0 mW/cm². For pulsed fields, a 7.5-fold increase occurred with field densities around 0.5 mW/cm², but a sevenfold increase occurred after 20 min of exposure to 10-ms pulses at a much slower rate of 5/s and an average power density of only 30 μ W/cm². This slower rate is reminiscent of windowed modulation-frequency sensitivities between 6 and 20 Hz in brain tissue discussed above. Light and electron microscopy of the barrier with horseradish peroxidase injections has confirmed its sensitivity to microwave exposure in regions of rat and hamster brains normally showing permeability (12, 13, 336).

Despite the apparent congruity of these studies in anatomical localization and differential sensitivities to microwave field characteristics, there have been negative results in three attempted replications at the same and higher carrier

frequencies (296, 335, 358). In two of these studies with anesthetized animals (296, 358) concomitant hypothermia was not separately evaluated. So far these studies have identified several separate modes of possible interaction between microwave fields and the blood-brain barrier. There is evidence that low-level pulsed fields may selectively increase permeability at field densities below those significantly raising brain temperatures. At higher field levels that raise brain temperature, increased cerebral blood flow may alter barrier permeability. There is a third possibility that raised brain temperature directly alters barrier permeability. The observed effects of thermalizing fields would then depend on brain temperature at the onset of irradiation, since barrier permeability shows a U-shaped function as power density of a 2.45-GHz CW field is increased from 0.3 to 30 mW/cm² (358). No dosimetric data are available so far on energy absorption from microwave fields in blood-brain barrier experiments.

*F. Responses of Mammalian Organisms to Strong ("Thermal")
Electromagnetic Field Stimulation*

In general physiological responses to tissue heating by EM fields are identical to effects of raising temperatures by other means. Many effects of microwaves on the CNS are attributable to heating (61, 279, 301). Neurophysiological responses to raised local tissue temperature are basically twofold: 1) direct effects on nervous tissue functions and 2) reflex effects operating through sensors or transducers of these thermal changes and then through effector mechanisms in the central nervous system. Skin thermal receptors can respond to temperature changes of a few thousandths of a degree in a second. Hypothalamic sensitivity to direct thermal stimulation exhibits thresholds for local temperature increases of 0.5–0.6°C. This central sensitivity is consistent with induction of altered circulating pituitary hormone levels (280, 301) as discussed below. A recent Russian review has criticized thermal models of these endocrine responses, however, on the grounds of higher lethality of microwaves over identical intensities of infrared radiation (210), and has proposed that microwave fields produce "nonthermal" effects that progress against a background of tissue heating (355, 356). Again, it should be emphasized that any evaluation of apparent differences between microwave heating and other thermalizing factors must consider specific absorption rates of energy at the hypothesized locus of interaction, including possible frequency-dependent resonant effects discussed above.

1. Thermal effects on central and peripheral nervous functions

a) *Intracranial absorption of electromagnetic energy.* Electromagnetic energy absorption within the cranial cavity shows hot spots. A model of lossy spheres simulating brain tissue shows that these occur inside spheres with radii

8 cm $< r >$ 0.1 cm for frequencies between 300 MHz and 12.0 GHz (259). At lower frequencies and at much higher frequencies, heating occurs primarily at the surface of the sphere facing the field source. Small animals may also exhibit high focal microwave energy absorption at the craniocervical junction, where body size approaches a significant fraction of a wavelength at the field frequency (82, 179). Kritikos and Schwan (261) have recently modeled conduction and convection from a hot spot in central brain structures, with inclusion of a factor for blood flow. For a spherical "head" 10 cm in diameter exposed to a 1.0-GHz, 10-mW/cm² field with a central hot spot 2 cm in diameter, the expected temperature rise would be 0.5°C with normal blood flow and heat conduction. In this model, heat conduction and normal blood flow appear to contribute equally to heat removal from the hot spot. For a given incident field flux, the heating potential in the hot spot decreases rapidly with increasing head radius (258-260), and for humans the expected temperature elevations in the center of the head would be much lower at this 1.0-GHz field frequency. Although these models may establish general levels of expected temperature rise in relation to head size and incident field levels, they do not account for important differentials in focal cerebral thermal gradients. There is normally a gradient of about 0.5°C between central diencephalic zones and the cortical surface in the monkey (190). There are strong differentials in convective capacities between cerebral gray and white matter, attributable to substantially different densities of capillary beds (364). Moreover, the physiological significance of raising cerebral temperatures by 1-2°C is not known. General, as distinct from focal, increments in brain temperature up to 2°C occur in normal subjects during exercise and in moderate heat stress, without evidence of major alterations in higher nervous functions (23).

b) Effects of intracranial heating on sensory evoked potentials. Microwave heating of the cat's brain shortens latency of auditory and somatic evoked potentials in primary thalamic relay nuclei (182) during exposure to a 918-MHz field, with a maximum SAR between 2.5 and 5 W/kg at the center of the brain. The temperature rise at threshold for shortened latency was 0.2°C. Extrapolating to the human head, a plane-wave power density of 10-25 mW/cm² would be necessary to produce the same SAR in central brain structures. Microwave hyperthermia in guinea pigs (41°C) is followed by decreasing latency in cortical visual evoked responses as body temperature returns to 39.5°C, suggesting that "temperature for optimal visual processing may be 1-2°C above resting 'norms'" (217).

c) Microwave hearing. The phenomenon of "RF hearing," with a sensation of a click elicited by pulsed RF energy, was first described by Frey (136). The threshold incident energy density for hearing was 1.6 μ J/cm² for a 1.31 GHz pulse and 5.0 μ J/cm² for 3.0-GHz pulses. A patient with conduction deafness perceived the pulses at the same thresholds as in normal subjects. Frey postulated a mechanism of direct neural stimulation. There is now much evidence favoring a thermoelastic expansion of inner ear structures by the absorbed pulse, but some aspects of the phenomenon do not support this model.

The hypothesis of radiation pressure (409) was discounted by Frey (137). More studies have examined the physical parameters of the field for a threshold at which the sound is first perceived. Sound perception depends primarily on peak power and also on pulse width (141). For 15- μ s pulses at a 5/s repetition rate, a threshold between 2.3 and 20 μ J/cm² for each pulse has been reported (69). The incident energy density for pulse-perception thresholds in humans is 40 μ J/cm² and a specific energy absorption density of 16 mJ/kg, for all pulse widths less than 30 μ s (180). The threshold energy can increase tissue temperature by only 5×10^{-4} °C. Nevertheless there is a cochlear microphonic associated with absorption of these threshold pulses, indicating displacement of the basilar membrane (79, 83, 84). A pressure wave generated by a microwave pulse in distilled water is inverted between 0 and 4°C, disappears at 4°C, and reappears at higher temperatures, in good agreement with the temperature-dependent density of water (133). Pulsed 915-MHz microwave stimulation evokes responses in single auditory nerve fibers (265, 266) and in the medial geniculate body (429). These data indicate that thermal expansion is the most probable mechanism for auditory responses (269), but this thermoelastic model remains controversial. Lebovitz (264) reviewed alternative possibilities and suggested that pulsed microwaves might produce highly localized field gradients in the inner ear and elicit generator potentials. Using holography techniques, Frey and Coren (138) were unable to detect skull movements that would be predicted in a thermoelastic model. Tyazhelov et al. (434) have examined interactions between acoustic and microwave pulse trains and found only partial support for a thermoelastic model. For pulses longer than 100 μ s, their subjects reported a qualitatively different sensation (an apparent lowering of pitch) and a shift in the apparent site of the sound source in space. Suppression of the sensitivity to a 5-kHz RF signal by simultaneous acoustic stimulation at 10-kHz is "at variance with the simplest principles of the thermoacoustic hypothesis, which can hardly explain a number of observed peculiarities of auditory sensation near threshold."

d) Effects on peripheral nerve and muscle. Altered conduction velocity and excitability have been widely reported for peripheral nerves, mostly preparations of frog sciatic nerve, during CW and pulse microwave exposure (98, 235, 369). Molluscan giant neurons show increased permeability to Na⁺ and K⁺ when exposed for 1 h to a 2.45-GHz field at an SAR of 15.5 W/kg. The neurons hyperpolarized because of activation of a sodium pump mechanism (18). Aplysia ganglion cells exposed to 1.5- or 2.45-GHz microwave fields showed a threshold for a slow change in firing rate at an SAR of 7 W/kg and an SAR of 10 W/kg for a rapid change (398, 440). Exposure of isolated frog sciatic nerves to a 2.45-GHz CW field at an SAR of 10 W/kg consistently lowers their survival time to stimulation at high repetition rates (50 pulse pairs/s). The time course of loss of excitability resembles blockade of active transport of Na⁺ and K⁺ by ouabain. Microwave exposure of ouabain-treated nerves did not further reduce survival times, lending support to the view that relative loss of excitability in microwave-exposed nerves may be related to an interference with,

or counteracting of, the $\text{Na}^+\text{-K}^+$ pump (291). There is good evidence that these effects on frog sciatic nerves, cat saphenous nerves, rabbit vagi, and superior cervical ganglia result solely from thermal effects, since their exposure to 2.45-GHz fields in a temperature-controlled wave guide or in a constant-temperature bath was without effect at SARs as high as 1.5-kW/kg CW and 220-kW/kg pulsed field (82, 262). Exposure of isolated frog sartorius muscle to a 2.88-GHz, 10-mW/cm² field for 2 h causes reversible changes in membrane resistance, capacitance, ionic conductance, action-potential velocity, water permeability, and action-potential configuration. Differences were also noted between sensitivities of summer and winter frog muscles (345). Reports of effects on intestinal smooth muscle are conflicting. Increased peristalsis in isolated segments of postpyloric rat gut has been reported during exposure to 960-MHz fields at an SAR of 1.5–5.5 W/kg, possibly mediated by release of transmitter substances (287), but no effects were seen in a replication at 1.0 GHz (455).

2. *Thermoregulatory, cardiovascular, and endocrine responses*

With the advent of techniques for measuring energy absorption in tissues during microwave exposure (203), there has been a careful evaluation of thermoregulatory and related responses to high-intensity fields. Rats tolerate a 2.45-GHz microwave radiation intensity producing energy absorption at a rate of 22.5 mW/kg for as long as 20 min before succumbing to hyperthermia (348). This rate of energy absorption in a 400-g rat represents about 544 J/min, or about 5 times the basal metabolic rate reported for rats this size (251). The threshold dose for death during prolonged exposure, typically lasting 4–6 h, is about 2.5–3 times the basal metabolic rate (349). Rats exposed to 2.45-GHz microwaves for 30 min at an absorbed energy rate of 116 J/min showed an initial rise in colonic and skin temperature, but O_2 consumption, CO_2 production, and heart rate were unaltered. At a dose rate of 168 J/min, colonic and skin temperatures immediately after radiation were even higher but then dropped to below normal for about 3 h, with metabolic rates also reduced below normal during the same period. Bradycardia developed within 20 min after exposure and also persisted for about 3 h. At a dose rate of 285 J/min for 30 min, responses were similar to those at 168 J/min, but changes were more severe and lasted longer. In this group, bradycardia developed abruptly about 20 min after exposure, accompanied by an irregular heartbeat. Incomplete heart block occurred in many subjects in this high-dose group, but not at lower dose rates, and developed 7–30 min after exposure. Complete recovery from heart block occurred within 60 min after the end of exposure (349). The investigators attribute the irregular heart rhythm to a central nervous action of the microwave field, possibly due to enhanced intracranial absorption of microwave energy in rats at a 2.45-GHz field frequency (215). On the other hand, the incomplete heart block may arise in peripheral rather than central mech-

anisms, including direct damage to cardiac conduction mechanisms, toxic agents released from heat-injured tissues, from changes in cellular Na^+ - K^+ balance, or from myocardial ischemia. Altered S-T segments have been reported in the dog exposed to pulsed 2.8-GHz microwaves at 165 mW/cm^2 . This could result from myocardial ischemia (303).

Endocrinological functions are modified in rats by protracted irradiation with 2.45-GHz fields that raise body temperatures (280). Michaelson has also hypothesized that long-term, low-level effects of microwave radiation may be related to the general adaptation syndrome (399) through responses in three neuroendocrine systems, the hypothalamic-hypophyseal-adrenocortical system (HHA), the hypothalamic-hypophyseal-thyroidal system (HHT), and the sympathoadrenal-medullary system (300). Responses in HHA and HHT may be critical in secretion of the trophic hormones (115). It has also been proposed that different hypothalamic mechanisms controlling the release of growth and thyrotropic hormones are activated by temperature changes (312). In Michaelson's studies, rats were exposed without anesthesia at power densities from 1 to 20 mW/cm^2 for 1, 2, 4, or 8 h. After exposure, rectal temperatures were higher than in sham-irradiated subjects after 4-hr in a 1.0 mW/cm^2 field, after 1 and 2 h at 5.0 mW/cm^2 , after 2 and 4 h at 10 mW/cm^2 , and at 20 mW/cm^2 for all durations of exposure. Except for rats exposed at 20 mW/cm^2 for 4 and 8 h, however, none of the averaged rectal temperatures reliably exceeded those of sham-irradiated rats after 8 h of exposure. Exposure at power densities below 10 mW/cm^2 accelerated the appearance of the peak rectal temperature. Serum corticosteroid levels were significantly lower in rats exposed at 20 mW/cm^2 for 8 h than in sham-exposed subjects. There was also a significant correlation between rectal temperature and corticosteroid level in the sham-exposed rats, but this became dissociated with certain combinations of exposure duration and intensity of exposure that raised colonic temperature without increasing corticosteroid levels. Serum thyroxine levels decreased in rats exposed to 20 mW/cm^2 for 4 or 8 h. Thyroid function was transiently stimulated by exposures at 1.0 mW/cm^2 for 4 h. Growth hormone levels were unchanged. Polish workers have also reported thyroid stimulation in male rabbits exposed to 3.0-GHz fields at power densities below 5 mW/cm^2 for 3 h daily for 3 mo (28). Their results were interpreted as being caused by an extrathermal mechanism, but the evidence cited above points to thermogenic effects in rats at incident power densities as low as 1 mW/cm^2 . Differences in microwave frequencies and animal subjects and lack of tissue dosimetry in these studies mandate further research to evaluate possible extrathermal mechanisms.

Conflicting results in many neuroendocrine studies of microwave effects may arise in their essentially adaptive nature to a stress that can vary in type, magnitude, and rate. For example, gonadotropic hormone levels in rats exposed to a 3.0-GHz field at 10 mW/cm^2 at first increased and then decreased 18 h after exposure to either single or repeated 1-h doses. Growth hormone concentrations were not altered at this field level, but under other irradiation conditions, its release was either stimulated or suppressed (304). Both de-

creased (343) and increased (302) thyroid activity have been reported after microwave exposure. A decrease of 23% in protein-bound iodine and a 55% decrease in serum thyroxine followed exposure to 2.45-GHz CW microwaves at 15 mW/cm² for 60 h. Dogs exposed to 1.24-GHz pulsed fields at 50 mW/cm² averaged power for 6 h daily for 6 days showed increased radioiodine uptake. With 100-mW/cm² fields, there was increased uptake 4 years after exposure, suggesting irreversible thyroid dysfunction. At much lower levels, rabbits repeatedly exposed to 3.0-GHz CW fields at 5 mW/cm² showed increased radioiodine uptake, with histological evidence of thyroid hyperplasia (28). On the other hand, rats continuously exposed to 2.45-GHz CW fields at 1.0 mW/cm² for 8 wk or for 8 h/day at 10 mW/cm² for 8 wk showed no histological changes except those directly attributable to heat stress (306). The role of adaptation to microwave exposure through hypothalamic-hypophyseal mechanisms is exemplified in the longer survival of hypophysectomized rats over controls when exposed to 2.86- to 2.88-GHz, 120-mW/cm² fields. Raised corticosterone levels after exposure to 10-mW/cm² fields did not occur if the animals were allowed to habituate to the test situation for 2 wk prior to exposure (305).

3. Cataractogenesis

No aspect of inadvertent exposure to high-intensity microwave fields has aroused greater public concern than ocular damage, particularly the possibility of cataract formation. The subject is controversial. It is difficult to extrapolate from studies in anesthetized (and often hypothermic) animals to findings in radar-exposed workers and others who may be occupationally exposed at low levels on a daily basis, with possible infrequent exposures to intense fields that would be frankly thermalizing. Questions arise concerning possible cumulative effects of repeated exposure. There is also the possibility that microwave cataracts may constitute a pathological entity, morphologically distinct from those induced by X rays or by longer wavelengths of nonionizing radiation.

The histopathological sequence in development of microwave cataracts in animals from a single exposure first involves lens fibers in the posterior subcapsular cortex (71), which are slightly swollen with small vesicles during the first 2 days. On the 4th day, epithelial cells migrate posteriorly under the lens capsule from the equatorial region and show active mitosis. Over the next week, swollen "balloon" cells appear at the equator or in the posterior cortex of the lens and may indicate abortive attempts to form lens fibers. From 15 to 30 days after irradiation, the posterior cortex shows nucleated cells, lens fibers, and cysts containing protein aggregates and cellular debris. These changes are said not to occur in lens damage resulting from heating by nonmicrowave sources (71).

Cataracts appear after exposure of anesthetized rabbits to 2.45-GHz fields in the range 100-300 mW/cm². At 100 mW/cm² the minimal effect on lens structure is a milky band in the posterior cortex immediately adjacent to the

posterior capsule. Fields of higher intensity produce permanent changes with lens banding and vaculation. The posterior cortical opacity may then extend to the anterior subcapsular cortex (183).

For single exposures, induction of lens opacities in the rabbit as a function of a time-intensity product suggests a thermal effect (183). More interesting as models of human cataract induction are the effects of repeated subthreshold exposure. Opacities occurred in 1 of 11 unanesthetized rabbits exposed to 20–24 times for 1 h to a 2.45-GHz field of 80 mW/cm² and opacities appeared in 4 of 10 animals exposed to 100-mW/cm² fields. At 120 mW/cm², 8 of 10 rabbits showed opacities after repeated exposure, even though a single 1-h exposure at this intensity caused no opacities (72), but small central opacities did occur with 4- or 4.5-h exposures. However, other studies have not found evidence of cumulative effects (17). At a lower intensity, unanesthetized rabbits exposed to far-field 2.45-GHz CW radiation at 10 mW/cm² for 8 h/day for 5 consecutive days a week for 8–17 weeks showed no abnormalities 6 mo after exposure (131). For single acute near-field exposures, the apparent temperature threshold for lens opacities in the rabbit is around 41°C beyond a certain minimal duration of exposure. However, opacities also occur from repeated exposures at lower intensities, depending on duration and number of exposures. This suggests a cumulative component of microwave-induced lens damage that depends on the time-temperature history of the exposed tissue. Also comparison of lens temperature shifts produced by means other than radiation suggests that microwave radiation “appears to exert a unique component of thermal stress in the induction of opacification in the mammalian lens” (85). Opacities did not occur in rabbits subjected to local or whole-body hyperthermia at 42°C for 30 min (256); nor did they occur in rabbit eyes exposed to localized heating at the same rate to the same temperature for the same duration as in cataractogenic microwave exposures (73). Thus microwave cataractogenesis does not appear to be solely a thermal effect. Only limited data are available on microwave cataract induction in humans. Although some of these studies involved exposures at levels similar to those used in animal experiments, others may have involved exposures from microwave oven leakage around 1 mW/cm², with levels around 90 mW/cm² with the door open (466), but the causative role of microwaves in the latter cases remains controversial.

IV. REVIEW OF MODELS OF TISSUE INTERACTIONS WITH ELECTROMAGNETIC FIELDS

The molecular biology of interactions with EM fields reviewed above points to phase partitions at membranes of cells and organelles as probable sites of transductive coupling. Evidence that membrane surface glycoproteins with a polyanionic structure might function as sensing sites for weak fields is also discussed. These concepts have provided avenues for evaluation of low-level interactions in the brain. The same precepts may apply in other tissues.

If we consider further the possible sequence of events in the coupling to cells of weak EM fields in the fluid surrounding them, and ways in which they may be effective as triggers to excitatory or metabolic processes, our speculative options narrow rapidly. Intrinsic oscillating gradients of the order of 100 mV/cm in extracellular fluid, typical of slowly oscillating gradients in brain and other tissues, are clearly unlikely to be effective in directly influencing the normal transmembrane potential of 10^5 V/cm that exists over approximately 40 Å in the transverse dimension of a plasma membrane. Therefore, we may anticipate effective coupling of these weak fields only through one or more mechanisms capable of "amplifying" the initial triggering gradient. If these mechanisms exist, they must be sought in the hierarchical organization of membrane ultrastructure, probably beyond the level of individual macromolecules and certainly within the vista of the separate but interrelated structural entities that constitute phase boundaries on and within cell membranes. Membrane surface glycoproteins behave as a longitudinally organized (though imperfect) biopolymer sheet that encodes the membrane in length and in area (118). This contrasts with ionic transport channels organized in a transmembrane axis (313). Both structural entities are characterized by polyanionic charge sites involved in cationic bindings. Each has been assigned a unique role in models that purport to explain aspects of low-level field interactions at "athermal" energy levels. We have reviewed mechanisms at the molecular level known to be the basis of cooperative processes, including coherent states between macromolecular fixed-charge sites (387). For cerebral tissue these also include molecular mechanisms suspected of involvement in the genesis and transduction of low-frequency electrical oscillations at cell surfaces, phase transitions in dipole organization of charges on glycoproteins (173), or through limit-cycle phenomena (149, 220). Partly as pointers to future research, it is now appropriate to consider experimental models that rest on somewhat higher levels of cellular morphology, while retaining essential aspects of the molecular organization discussed above.

Preliminary models of some "nonthermal" transmembrane effects of radio and microwave fields have considered effects on equilibrium concentration of ions on opposite sides of the membrane (30, 350), estimating by the use of the nonlinear Boltzmann equation shifts in ion concentration and magnitude of current flow resulting from membrane rectification. In such a system, where charged-particle concentrations vary in space, and if there is no net current, the field-driven drift current must balance the diffusion current, so that a potential barrier is formed to maintain the concentration difference. Where an oscillating field is superimposed on this steady potential at equilibrium, even small values of this alternating field will shift the equilibrium concentrations. Numerical substitution in this model shows that an incident field of 10 mW/cm² produced a gradient of 4.4 V/cm across a membrane enclosed in an aqueous dielectric medium. This corresponds to an electric gradient of 9 μV across a 200-Å membrane, with a concentration shift of 1 part in 10⁶ and a flow of 400 ions/s for a cell with a surface area of 10⁻⁶ cm². Proponents of these models emphasize

that it is difficult to estimate the biological significance of such small currents but that "these nonlinearities provide a mechanism for possible biological change," particularly where cumulative ionic shifts may result from modulation of the microwave carrier wave at a low frequency (30). However, participation of such weak transmembrane gradients in excitatory processes must be reviewed less optimistically when considered in terms of energy of interaction between ion and membrane. The membrane poses an energetic barrier to ions in the adjacent solutions and modulation of this barrier is the primary means by which a membrane controls ionic flow. Parsegian (344) points out the tendency to consider the interaction only as one imposed by the membrane on the ion, rather than a mutual interaction that might also act to perturb the structure of the membrane. The ion-membrane interaction arises in the coulomb field that emanates from the ionic charge. A single ionic charge ($e = 4.8 \times 10^{-10}$ stat-coulombs) in a lipid medium (dielectric constant $\epsilon = 2$) has an electric field equal to or greater than 6×10^5 V out to a distance of 35 Å from the ionic charge ($e/\epsilon r^2 \leq -6 \times 10^{-5}$ V/cm, $r \leq 35$ Å). This suggests that when an ion is crossing a 50-Å membrane, one or both faces of the membrane experience an electric field from the ion greater than the known breakdown voltage. The pull on an ion at a distance of 10 Å from the interface is about 3×10^{-6} dynes. The stress on the interface is more than 200 atm nearest to the ion, and the local field at that part of the membrane is about 14×10^6 V/cm. An expected consequence of the electric stress is pinching of the membrane at the point of traverse. In a thin membrane, the reach of the electric field from an ion exceeds the thickness of the membrane, so that in this respect the membrane would not constitute a separate phase. Peptides that facilitate ion transport lower the energetic barrier to ion flow, but their efficacy in lowering transport energies is not known. Questions as yet unanswered include the possibility that these peptides might move as a mobile unit with an attached cation, if the width of the lipid layers exceeds the length of the peptide molecule (38 Å for gramicidin A, for example). However, Parsegian's (344) model requires a transmembrane driving gradient of the order of 100–200 mV for this phenomenon. Mitchell's (309) Nobel award-winning observations and models of chemiosmotic coupling in oxidative and photosynthetic phosphorylation systems address much higher energy levels in membrane transductive systems. Stepwise translocation of protons occurs from one side of the membrane to the other along a thermodynamic gradient, with "symporter" and "antiporter" systems associated with proton-motive forces of 200–300 mV between aqueous proton-conducting forces on either side, thus catalyzing the sym- and anticoupled translocation of chemically and sterically unrelated solutes. However, the bonding prescribing these translocations should provide free energies of activation of exchange or dissociation that are large compared with kT , so that thermally activated dissociation or exchange is minimized (195, 309). Behavioral evidence cited above for fish (227), birds (242, 448), and mammals (159, 448, 454) favors far higher sensitivities at certain frequencies with tissue gradients in the range 10^{-7} – 10^{-8} V/cm.

Thus the sum of observations and theoretical constraints does not favor a direct transductive coupling of such weak extracellular fields across the plasma membrane, with its extremely high electric gradient probably 12 orders of magnitude greater than these extracellular fields. Some form of amplification of the initial transductive steps appears essential. We may also presume that if this occurs at an extracellular location, it involves systems capable of integrating the weak field over some distance and would thus occur in the length and area of the membrane surface, rather than in a transmembrane axis (5). Einolf and Carstensen (121) addressed this problem in a study of the behavior of micron-sized resin particles considered as porous particles with uniformly distributed fixed-charge sites. Their model extends an earlier formulation by Schwarz (386) that considered the movement of ions along the surface of solid (rather than porous) colloid particles. At the surface of the particle, the boundary region is characterized by a very large, radially directed static field with a corresponding radial variation in the distribution of mobile ions. Maintaining this distribution has the effect of requiring the ions in the boundary layer to move in a path tangent to the surface of the particle. Porous charged particles are characterized by a low-frequency dielectric relaxation leading to large static dielectric constants. A final result is polarization of the ionic atmosphere at the surface of the particle in the presence of an external electric field. This produces an additional "apparent" dielectric constant of the particle, exceeding the actual dielectric constant by several orders of magnitude at low frequencies. The magnitude of the low-frequency dielectric constant is proportional to the size of the particle and the square root of the fixed-charge concentration in the porous material. The relaxation frequency depends directly on counterion mobility and is inversely proportional to the square of the particle size. The effective dielectric constants of micron-sized ion-exchange resin particles are as high as 10^6 at frequencies below 1 kHz (121). Similar properties may be expected at the surface of tubular structures with diameters in the micron range, including dendrites with polyanionic glycoprotein surface layers.

This model provides an avenue for future research into the bioeffects cited above in which it appears that thermal noise at normal tissue temperature is substantially larger than the tissue components of the imposed electric fields. For typical conductors in the biological temperature range, the Boltzmann kT noise is of the order of 0.02 eV. This expression, however, gives little concept of the extent to which electric gradients in tissue may be established by thermal atomic or molecular perturbations, nor of the way in which components of this noise may be transferred to distant sites within tissue. In metallic conductors, the transfer function for this noise energy has an essentially infinite bandwidth, a condition that does not exist in tissue. The transfer function of thermoelectric noise in tissue has yet to be studied. However, a tentative model does offer interesting points of resemblance to observed neurochemical and behavioral thresholds (38). Data from the study of Einolf and Carstensen (121)

indicate that ionic conductance along a membrane surface in the counterion layer exhibits an inverse frequency dependence and limited bandwidth, due to the very high dispersion dielectric constant in this zone. The Boltzmann equation may be written in terms that model the tissue in this region as a low-pass filter

$$e^2 = 4 kTBR$$

where the transfer function for the root-mean-square noise voltage e is a function of the frequency bandwidth B and the specific resistance of the noise pathway R . With a specific resistance for brain tissue of the order of $300 \Omega \cdot \text{cm}^{-1}$ and an effective frequency bandwidth from 0 to 100 Hz, the equivalent noise voltage gradient would be of the order of 10^{-6} V/cm. This closely agrees with observed sensitivities in marine vertebrates, birds, and mammals for certain low-frequency fields, and these thresholds are consistent with a thermal "floor" as the limiting factor.

Future research on tissue interactions with weak EM fields may take account of these and related models. The disclosure of the "windowed" character of many important interactions, particularly those with central nervous tissue, argues in favor of system transductive properties that are cooperative and thus nonequilibrium in character. No clear basis has yet been established structurally or functionally for either the frequency or amplitude characteristics of these windows—whether, for example, it lies in phase transitions or limit-cycle phenomena as substrates for the observed frequency sensitivities or in proton or electron tunneling phenomena that might be the basis for restricted-amplitude windows. Whatever basis may be found for these specific interactions, current research increasingly emphasizes the importance of amplitude-modulation characteristics of radiowave and microwave fields in determining patterns of tissue interactions. Without modulation at frequencies below 1 kHz, and for the central nervous system below 20 Hz, biological sensitivity to these fields drops sharply, and virtually all observed effects of unmodulated fields at these frequencies appear to have a thermal basis. As predicted from physical considerations, it is only in the millimetric-microwave and far-infrared regions that direct molecular resonances are now being detected. Disclosure of sensitivities to modulation patterns may also offer valuable new tools for understanding system aspects of molecular biology and membrane ultrastructure. With increasing public awareness of the exponential increase in environmental levels of nonionizing EM radiation, it is urgent that an understanding of biophysical substrates of these tissue interactions be reflected in a rational approach to public health and safety standards. It must also be remembered that premature imposition of restrictive regulatory measures not well founded in scientific observations may unreasonably impede development of valuable therapeutic applications.

Many tissue interactions with weak EM fields discussed here are consistent with highly cooperative processes. Manipulation of these fields in the fluid sur-

rounding cellular elements has shown this technique to be of value in a first approach to the baffling problem of cell-to-cell communication. For some cells, effective electrochemical oscillations are weaker by orders of magnitude than those necessary to depolarize the cell membrane potential by a direct influence on equilibrium phenomena that maintain it. Future research will doubtless determine the full significance of cell membrane surface glycoproteins in sensitive nonequilibrium processes that mediate some forms of communication between adjoining cells.

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