Charting the Sea of Brain Waves

Herbert H. Jasper
Department of Neurology and Neurosurgery, McGill University, and *Montreal Neurological Institute*

WE OF THE AMERICAN ELECTROENCEPHALOGRAPHIC SOCIETY have been brought together, first, by our principal common interest, the electrical activity of the brain. With this as a starting point, we find ourselves led into many related fields concerned with brain function, its anatomy, its metabolism, its circulation, its biophysical properties, and, above all, its functional characteristics, which underlie human thought, experience, and action. We are also led into studies involving the application of electrical recording techniques to other parts of the neuromuscular system, and even the bioelectric properties of the skin have not been neglected by certain members of our Society.

With the development of new and improved techniques by our colleagues, the electronics engineers, the biophysicists, the physical chemists, and the more pure electrophysiologists, the scope of interest of the members of this Society is an ever-broadening one. Our first and foremost interest is—and I hope shall always be—scientific investigation into the basic mechanisms and fundamental properties of nervous system function, with special emphasis on neuronal aggregates.

The gradual development of EEG organizations throughout the world has been a natural evolution. The first society was started in Great Britain with the initiative of Dr. Grey Walter and under the able presidency of Nobel laureate, Prof. E. D. Adrian. This was followed by the Eastern Association of Electroencephalographers and then by the American Electroencephalographic Society, which stimulated the organization of two other sectional groups, the Central Association and the Western Association, on this continent. I have just heard that a Southern Section is in gestation. In Europe there was soon organized a Scandinavian Society under the direction of Drs. Buchthal and Hertz. Recently an EEG Society for French-speaking countries has been organized by Dean Beaudouin and his colleagues in Paris. An Italian Society has also been organized under Drs. Gozzano and Moruzzi.

These various national societies are integrated by an international committee which was formed at the first International Congress held in London in June 1947. This committee, which serves as a federating body for the national societies throughout the world, is under the able chairmanship of Dr. Grey Walter. As an outcome of this organization, an international journal was founded with a representative editorial board from many countries. Considerable progress has already been made in our attempt to bridge political barriers existing between our distant colleagues, including those whose extensive work in this field has been hitherto difficult of access to most of us.

At the first Annual Dinner last year at this time, there were reminiscences of the beginnings of electroencephalography in this country—an historical interlude. At this meeting, I would like to turn your eyes toward the future, "charting the sea of brain waves." Perhaps a better title would be "a theoretical interlude."

The past 15 years have largely exhausted the descriptive phase of this relatively new field of investigation. At this level of exploration we have yet to consolidate our gains by clarifying definitions of terms employed, but there is probably little more to be added to our existing descriptive knowledge of the various rhythms and wave forms to be recorded from the cerebral cortex under a wide variety of conditions, normal and abnormal (*2, 30, 32, 33, 40, 55*). The terms alpha, beta, gamma, delta, and even perhaps theta have a fairly definite meaning to most investigators. Random spikes and sharp waves, rhythmic spike and dome patterns, or sharp and slow wave complexes also have a fairly definite descriptive meaning. The electrical patterns characteristic of sleep, coma, and destructive or degenerative lesions of the brain, as well as those characteristic of increased excitatory states, epileptic activation, and local discharging lesions, are readily recognized. These well-established empirical relationships have made electroencephalography a useful diagnostic aid in neurology, neurosurgery, and psychiatry, but this usefulness will stagnate unless more of our energies are channeled in a different direction during the coming years.

We have made very little progress in our understanding of the fundamental significance of brain

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waves during the past 10 years. The war can be held largely responsible for the lapse in fundamental research in this field, as in many others in which application to the more urgent problems of military medicine seemed remote. There is, however, another reason which is less excusable. Preoccupation and promotion of large-scale, mass-production, brain-wave factories for the clinical use of electroencephalography have left many competent workers little time to contemplate the significance of what they are doing. Instead of representing a stimulus to more intense fundamental investigation, clinical applications have drawn many of us away from basic research. They have lured into this field many more practical-minded men who have neither the background nor the interest to make significant contributions to our understanding of brain function through studies of its electrical activity. The outcome has been a number of pseudoscientific clinical investigations which have served only to burden editors and readers of scientific journals without providing a great attraction to more serious-minded investigators concerned with the fundamental aspects of brain function. However, there are a few glimmers of light in the fog. Some may be beacons to which we may set our course; others may turn out to be warnings of rocks ahead.

What is the functional significance of these slow, rhythmic, potential waves derived from neuron aggregates throughout the nervous system? Compared to the familiar action potential of less than one-millisecond duration which signals the passage of a nerve impulse along a nerve fiber, their duration is of a different order of magnitude, ranging from about 20 to several hundred times as long. Certain of the more prolonged waves may be lengthened by the process of temporal dispersion of a volley of shorter waves not perfectly synchronized in time, but even when recorded with microelectrodes (though we need many more such studies), the rhythmic waves are still many times longer than action potential spikes. Furthermore, they may wax and wane in amplitude, not always showing the explosive "all or none" character of the conducted nerve impulse. Some of this waxing and waning is due to the progressive recruitment and dropping out of nerve units in synchronized mass activity. It is highly probable from the evidence at hand that individual cell potentials also do not always show this "all or none" property. Brain waves cannot be identified, therefore, with aggregates of fiber potential spikes, although such aggregates do produce some of the cortical potential waves recorded under certain circumstances, such as in the evoked potential from the sensory cortex following tactile stimulation.

Electrophysiologists of the "unitarian" school would have us believe that all of the secrets of the electrical activity of neuron aggregates lie hidden in the fundamental properties of single isolated neurons (*26*). This may be true if we add the basic mechanisms of neuronal interaction in synaptic networks or by potential field effects in neuron pools. Rhythmic slow waves have been recorded from isolated axons by many investigators including Monnier and Coppée (*45*), Arvanitaki (*7, 8*), and, more recently, by Lorente de Nó (*41*) in his studies of factors affecting the resting potential of nerve membranes. These fluctuations in membrane potential underlie alterations in the local excitability of the nerve. Slow potential waves are also recorded from sympathetic ganglia and from the spinal cord which are considered to represent polarization changes at the synapse, or synaptic potentials. These also have been shown to be related to excitability changes at the synapse (*10*). Are the spontaneous electrical rhythms of the cortex, then, to be considered of this nature? Do they represent spontaneous rhythmic fluctuations in the local excitability of neuron aggregates in the cortex, a sort of semisynchronized conglomeration of synaptic or cell potentials? Do they affect the excitability of these cells as do changes in the polarization of an isolated axon? This seems a likely working hypothesis (*34*). In its favor are the experiments of Bishop (*16*), showing some form of rhythmic fluctuation in the excitability of the occipital cortex at the frequency of the alpha rhythm in animals, and the experiments of Adrian and Moruzzi (*6*), which indicate that volleys of action potentials may be set off down the pyramidal tract by slow potential waves recorded from the motor cortex. The subjective enhancement of the intensity of light flickering at about 10 per second (the "Bartley effect") gives further evidence in man that rhythmic fluctuation in cortical excitability may accompany the potential changes recorded as the alpha rhythm (*11*). Much more needs to be done, however, before a clear conception of not only the nature but the functional significance of these spontaneous electrical rhythms may be obtained.

Do these electrical brain rhythms represent spontaneous autonomous activity of cortical neurons, or do they depend upon continuous activity maintained by nerve impulses reverberating in closed chains of neurons? Here again, if we turn to the properties of single neurons, we find that they are capable of autonomous rhythmic activity without reverberating reactivation. Isolated mammalian nerves, however, do not show the property of autonomous rhythmicity except under rather special conditions (e.g. decalcification, injury, cathodal polarization). But, there may be certain specialized cells within the cerebral cortex which do have the property of autonomous rhythmicity.

Experimental undercutting of the cortex, or thalamic and possibly also hypothalamic lesions, has been shown to cause a marked reduction or abolition of spontaneous cortical rhythms. This has been interpreted by some to prove that thalamocortical reverberating circuits are necessary for the maintenance of the electrical activity of the cortex. However, the isolated cortex is still capable of sustained rhythmic activity when activated chemically (small amounts of strychnine or acetylcholine) or in response to electrical stimulation. Bremer (*17–20*) has given us the term "tonus corticale" to describe the effect of afferent inflow upon the maintenance of cortical rhythms and does not believe they are dependent upon reverberating circuits. Thalamocortical circuits do serve to enhance and to time or pace the rhythms of the cortex under certain conditions, but spontaneous electrical activity of the cortex is not entirely dependent upon them. This leaves the possibility of short intracortical circuits, which may also play a role, but direct proof is lacking even though the mathematical possibilities as developed by Wiener, McCulloch, and Pitts are most stimulating (*42, 48, 49*).

Another concept which deserves more consideration in our thinking about brain waves is the electrical field effect in contiguous neurons, even when their neuronal interconnections have been completely interrupted. Gerard and his co-workers have shown such effects in the frog's brain after treatment with caffeine (*39*), and Bremer has shown that a similar effect operates in the strychninized spinal cord of the cat (*21*). Monnier and I were able to excite an isolated crustacean axon merely by placing it in close contiguity with another axon of the same type which received an electrical stimulus (*38*). This was called an "artificial synapse," later referred to as "ephaptic conduction" by Arvanitaki (*7, 8*).

Many others have shown that action potentials in contiguous nerve fibers do interact to affect the excitability of adjacent fibers (*44, 50*), even though in uninjured myelinated nerves actual excitation does not occur (though it may occur at a region of injury, as demonstrated by Granit and co-workers, *31*). Arvanitaki showed that when two nerve fibers are firing spontaneously in a rhythmic manner, they begin to fire synchronously at the same frequency when they are placed in close juxtaposition. These field effects must occur not only in the normal brain but especially with the very-high-voltage electrical discharges developed during epileptic activity of the brain. To what extent they may affect the normal integrative function of the brain or contribute to the spread of epileptic discharge has yet to be explored.

The recent revival of interest in automatic frequency analysis by Grey Walter and his associates (*53, 54*) and further studies of photic driving have led to the revival of the analogy of the brain as a series of loosely linked oscillators. According to this view, a given group of nerve cells tends to discharge rhythmically at a relatively fixed frequency, and under normal conditions it cannot be driven much beyond these limits. However, they are not sharply tuned, since adjacent oscillators tend to get into step if left undisturbed, apparently by some form of mutual interaction. Various complex wave forms are thought to be the resultant synthesis of potential patterns from a number of different neuronal aggregates oscillating at a variety of different frequencies. Dawson and Walter (*24*) have been able to synthesize a number of the wave forms common to electroencephalography, including the spike and dome pattern of petit mal, by mixing the right amounts of 9 or 10 different frequencies in an artificial model of the head.

This is a conception which must be continually borne in mind when attempting to understand the underlying structure of brain waves, but its validity needs more direct testing in each case. Even though it may be possible to analyze the complex forms of brain waves into a number of different sine-wave frequencies, this may lead only to what might be termed a "Fourier fallacy," if one assumes *ad hoc* that all of the necessary frequencies actually occur as periodic phenomena in cell groups within the brain. However, frequency analysis, when related at all times to the original recording, is proving to be a useful adjunct to the electroencephalographer's armamentarium, if and when the various spectra thus obtained can receive adequate and valid interpretation.

All of this concerns the possible basic mechanism of brain waves but does not touch the problem of their functional significance. Walter (*52*) has made the intriguing proposal that they represent a perceptual scanning system which oscillates rhythmically when undisturbed by patterns of centripetal impulses. He has constructed an electronic model which reproduces the blocking of the alpha rhythm by visual patterns in a most suggestive manner. This conception may not be incompatible with Bremer's (*23*) view that brain waves represent a tonic background of excitatory activity in nerve centers anywhere, which serves to keep them in a state of readiness to respond (see also Adrian's excellent discussion, *1*).

What, then, of the abnormally slow waves recorded from the cortex during states of apparent inhibition of cortical function—action which seems to produce decreased rather than increased responsiveness? We have the view of Beritoff (*15, 51*) that they represent activation of the "neuropile," which has a special inhibitory function. It seems possible, therefore, that brain waves are related in some obscure manner to the background excitatory and inhibitory states which set the stage for processes of attention to certain aspects of the constant play of afferent impulses as well as a preparation of the readiness to respond.

Berger was the first to recognize the relationship between electrical rhythms of the brain and processes of attention (*13, 14*). He thought that the disappearance of the alpha rhythm with attention represented the general inhibition of cortical activity which must accompany the focusing of attention. Adrian then showed that the disappearance of the alpha rhythm was probably not a true inhibition of cortical activity but a desynchronization of unit discharge (*3–5*). However, Adrian confirmed the close relationship which we have all observed between the alpha rhythm and concentration of attention or to certain types of generalized "tension state." The low-voltage, fast, asynchronous waves which are recorded from the attentive or alerted cortex, the regular alpha rhythm from cortex in wakeful repose, and the very slow waves which characterize the cortex in sleep or coma should give a clue to the functional significance of this constant electrical activity (*9, 25, 28, 29, 35*). If one assumes that these different wave patterns represent different organizations of activity in the same neurons, then the asynchronous pattern of the alerted cortex may indicate a more highly differentiated function of cortical units under these conditions, an essential condition of highly integrative function. The slow waves would then represent the synchronous activity of large masses of neurons, a mechanism which would abolish their differential individual activity, consistent with obvious impairment in the integrative and differential functions of the brain in deep sleep or coma.

It is hardly conceivable that the central mechanism of attention lies in the cortex. Except for certain individuals whose attention seems to be controlled chiefly by the loudest or brightest stimulus presented to them, most persons are able to exert a degree of control over the sounds they hear and the visual impressions they choose to see, or even to become relatively unaware of the outside world when the attention is directed to images or ideas which occupy the central stream of consciousness. There must be some centrally placed integrating center which is capable of a general control, inhibitory and facilitatory, upon the multitude of potentially conscious processes whose patterns of elaboration lie in the cortex. We should probably look for these centers in structures which are most critical to the existence of consciousness itself, namely, certain structures in the general region of the third ventricle.

Morison and Dempsey (*46*) found a centrally placed region of the thalamus, the intralaminar system, which is capable of exerting a widespread control over the electrical rhythms of the brain. With Droogleever-Fortuyn (*36*), we have confirmed and extended these observations to include the reticular nucleus in a thalamic reticular system which may control the electrical rhythms of the entire cortex, or of specific regions alone. We believe that this is a portion of the brain-stem inhibitory and facilitatory system recently brought to light in the brilliant studies of Magoun and Rhines (*43*). From this same system the electrocortical pattern of petit mal epilepsy—a type of seizure which is characterized chiefly by a lapse of consciousness—can also be reproduced. May it not be, therefore, that in this thalamic reticular system are the specific central controlling mechanisms for processes of attention, and that the spontaneous rhythms of the cortex may in some manner reflect the influence this thalamic system exerts upon the function of specific cortical areas involved in the momentary limelight directed here and there in the central stream of consciousness? More generalized diffuse processes affecting the alertness of the cortex as a whole, as in the sleep-wake mechanism, seem to be controlled from subthalamic, hypothalamic, or possibly even upper mesencephalic portions of this central integrating neuronal network, the importance of which, as a regulating center for motor responses, as well as for the control of mental processes, is gradually being clarified.

There are many other important questions in electroencephalography which might be asked and which would receive answers as unsatisfactory as those I have attempted to make. The relations between brain waves and brain metabolism, the influence of electrolytes, hormones, etc. (*27, 47*), is a chapter in itself. It is my hope, however, that the thinking of the members of this Society has been stimulated so that we and our confreres throughout the world shall be able to write the finale on the purely descriptive stage of our development.

We must push ahead during the coming years toward more basic research on the functional significance, as well as on the neurophysiological, anatomical, and physiochemical mechanisms underlying the electrical activity of the brain.

Electroencephalography, properly conceived, is not the study of brain waves per se. It is a recently developed branch of electrophysiology concerned with the functional properties and laws governing the behavior of neuronal aggregates and networks. Attempts have been made to formulate a mathematical basis for the complex interrelationships involved. It is too early to evaluate properly the scope and significance of these developments. Before us lies a new attack on some of the most important problems of human behavior, the neuronal mechanisms underlying processes of awareness, thought, and action.

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