Rhythmic Behavior of the Nervous System

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SINCE THE FAMOUS CONTROVERSY of Galvani and Volta in the last decade of the 18th Century, it has been known that living tissues generate electricity, and in 1848, when this Association was founded, many studies of the electrical properties of nerve and muscle had already been published. By that year, du Bois Reymond had, for example, published a two-volume study of animal electricity, and in 1850 Helmholz measured the rate of propagation of the nerve message for the first time and found it to be absurdly low for conducted electrical action—of the order of 20 meters per second in frog nerve.

It is now established that all living cells are continuous converters of energy, and the form and function of the cell are maintained by dynamic steady states. Only dead cells are in thermodynamic equilibrium with their environments. Within each cell, linked enzyme systems promote in stepwise sequences the degradation of foodstuffs that have entered the cell from its environment of body fluids, of sea water, or of fresh pond water, depending on its habitat.

Membranes separating the protoplasmic contents from the environment are selectively permeable. Due to the asymmetric steady-state flow of substances, including electrolytes, across cell walls, these walls are polarized so that, in most cells, the interior is found to be from 50 to 100 millivolts negative to the exterior. Cells store potential chemical energy, and because they are irritable, this energy can be converted suddenly to other forms. Thus a local decrease in the permeability of a cell membrane, initiated by electrical, chemical, mechanical, or thermal means, permits the cells' own currents to flow through this region of changed permeability from the positively charged outside to the more negatively charged inside and to complete the circuit by flowing back out more diffusely through the adjacent intact membrane. Such a local current in itself may act as an electrical stimulus to release energy from adjacent areas of the cell, so that a wave of electrochemical change is propagated away from the stimulated region as swirling eddies of inwardly and outwardly directed current. In long filamentous cells, such as nerve fibers, the passage of such impulses is detectable with recording apparatus.

Waves of Action in Nerve Tissue

Any study of the behavior of nerve mechanisms becomes a study of waves and rhythms. The impulses in afferent nerve fibers that convey information to the brain and the signals sent out by the brain over motor nerve fibers to muscles are waves of electrochemical change that sweep along the fibers at speeds ranging from a fraction of a meter per second in very small fibers to 120 meters per second in large fibers. Accompanying the passage of impulses in nerve are definite electrical, chemical, and thermal changes.

During the first two decades of this century, primarily through the work of Gotch and of Lucas, it was learned that nerve impulses travel as discrete pulses of energy, and following each pulse or wave, the nerve is refractory to further stimulation for very brief intervals of the order of milliseconds or fractions thereof. Time is required for membrane excitability to be restored by metabolism.

The accelerating development of good electronic devices by physicists and engineers since the middle 1920's has yielded much information about impulses in individual sensory and motor nerve fibers and the ways in which sensory nerves transmit information from the environment to the brain. Adrian and a number of other physiologists have shown that intensity of sensation and strength of muscular contraction are correlated with frequency of nerve impulses, but quality or modality of sensation is not traceable to peripheral nerve impulses but is rather a central phenomenon of the brain.

Impulse conduction across junctions between nerve cells, called synapses, takes place in only one direction. While nonsynaptic nerve nets exist in lower animal forms, such as coelenterates, well-integrated and complex behavior requires effective switching devices as represented by the one-way synapse, where temporal and spatial summation of impulses takes place, permitting control and direction of excitation and inhibition of contiguous cell units.

The nature of waves of action in nerve tissue was well described by A. V. Hill (7) in 1933, when he wrote:

> "Most of the well-known oscillations with which physics is concerned are a consequence of the reaction with one another of properties analogous to inertia and elasticity. A moving or a changing system tends, on the one hand, to continue in its state of motion because it possesses, for example, mass or inductance; even social, economic and intellectual changes are endowed with such characters of inertia which keep them going when they have passed a true position of equilibrium. On the other hand, such

systems, if they are to continue to exist, if they are not merely to be dissipated, must possess converse properties which tend to bring them back once they have overshot their equilibrium: such properties in physics are elasticity and electrical capacity; in finance and politics, fear and conservatism. These exercise a constraining force increasing with the displacement from equilibrium, and ultimately reverse the motion or change and the same oscillation is repeated in the opposite direction.

''There is, however, another type of oscillation, less commonly discussed in physics and mechanics but nonetheless well-known in everyday affairs; that which depends upon a discharge taking place when some limiting potential or intensity is reached. For example, water falling into a tank equipped with a syphon will come out in rushes whenever it rises to a certain level. Or again, a population in which an epidemic of measles cannot start because of the number of people in it who are immune, having had the disease already, will gradually become less immune as time goes on, and finally an epidemic, a wave of measles, will sweep through it. A neon lamp with a parallel condenser in series with a resistance and an electromotive force, will discharge at regular intervals, namely whenever the potential difference across the condenser reaches a certain critical value. This type of oscillation does not depend upon inertia reacting with elasticity. Its essential nature is that (a) some state, some potential, some intensity, is built up by a continuous process, and the condition becomes less and less stable until one is reached in which discharge must take place, and (b) this discharge, once started, forms a path for itself by which (as in a syphon or an electric arc) further discharge is facilitated until what has been built up gradually has been broken down and the process begins again. This type of oscillator (sometimes referred to as a relaxation oscillator) is the one with which we are concerned in physiology.

''Waves may be transmitted on the same principle in a system extended in space. An unstable state is gradually built up at some point, either through an external agency or by some intrinsic process, discharge is begun which starts and facilitates a discharge in neighboring regions which themselves discharge, and so a wave is propagated. Such waves will occur periodically if at some region the potential at which discharge begins is less than that finally attained by the continuous process of charging. They will require, however, an external agency (a 'stimulus') to start them if the unstable condition, the limiting potential, is not attained spontaneously. Models of such waves will occur to all of you; their principle is obvious. I have emphasized it because the waves on which nervous activity is based appear to be of this type. All detailed theories of nervous transmission may well be wrong but this general idea of it, involving a building up and discharge, is almost certainly right.''

All human behavior, whether it be a reflex response to stepping on a tack or the development of a mathematical analysis, depends finally on the organization of messages in the central nervous system. As Johannes Müller stated over a century ago, we do not sense a direct external world but rather properties of this world as interpreted by our nervous system. Since all nerve messages in individual nerve fibers are alike except for differences in timing and voltage, this means that patterns of organization of messages in the brain must be the ultimate basis for the rich quality of our experience, including ideas themselves.

Electrical Brain Waves

In 1929, Hans Berger reported sinusoidal electrical oscillations of a frequency of about 10 per second picked up from electrodes attached to the scalp of relaxed human subjects with closed eyes. Berger's important observations were soon confirmed and in the past 18 years hundreds of studies of electrical activity of the brain, animal and human, have appeared.

The electroencephalogram, or EEG, as the brain wave record is called, usually displays a dominant frequency called the alpha rhythm of 9 to 11 cycles per second at an amplitude of 20 to 50 microvolts, most conspicuous from the occipital region of the head over the region of the brain concerned with visual processes, although it is often manifest all over the head. Exploration of nuclei and tracts in exposed brains of living animals and of man at operation show that all of the brain centers are rhythmically active at frequencies of 2 to 30 cycles per second with different frequencies characteristic of different nuclei but with predominant activity in the range of 8 to 18 cycles per second. Fig. 1, for example, shows cortical and hypothalamic records taken by us from an unanesthetized and contented dog with small electrodes permanently imbedded in the cortex and in the hypothalamus. The cortical records and the ones from the anterior hypothalamus show the same type of waves, although the activity from the posterior hypothalamus displays faster and more irregular fre-

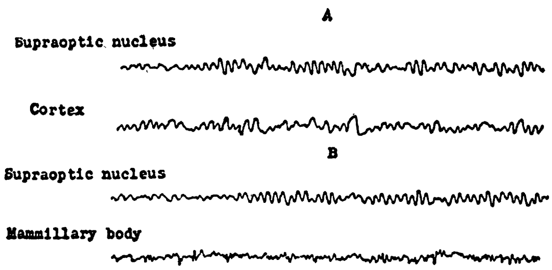

FIG. 1. Two pairs of records from an unanesthetized dog with small leads inserted in the brain. A—Upper from anterior hypothalamus; lower from cortex (simultaneous recording). The dominant rhythms are 14 per sec. B—Upper from anterior hypothalamus; lower from mammillary body (simultaneous recording). From Hoagland, Himwich, Campbell, Fazekas. and Hadidian, *J. Neurophysiol.* 1939, **2**, 276.

quencies. Fig. 2 shows pairs of EEG tracings from each of 5 persons. The upper trace of each pair is from the occipital cortex and the lower trace is from a lead at the roof of the pharynx near the anterior hypothalamus. Somewhat different brain wave patterns characterize each individual, but it is interesting to note the similarity of the records from two such remote brain areas in the same person.

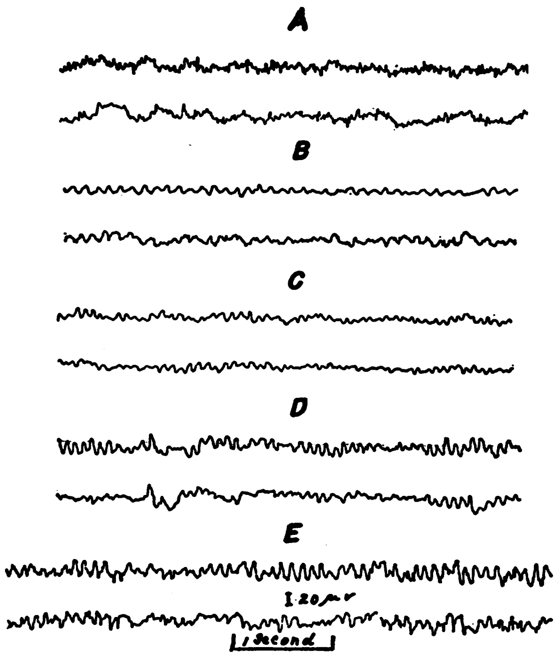

Fig. 2. Pairs of electroencephalographic tracings from five persons. A, B, C, D, and E refer to different individuals. The upper tracing of each pair is from a cortical electroencephalogram, and the lower tracing of each pair is from a recording made simultaneously with a lead inserted in the roof of the pharynx near the anterior hypothalamus. The upper tracings of A, B, and D are from the vertex. The upper tracings of C and E are from the occiput. Note similarities of patterns in a given individual from cortical and basal leads. From Hoagland, Cameron, Rubin, and Tegelberg, *J. gen. Psychol.*, 1938, **19**, 247.

While the EEG is generally characterized by a dominant frequency of around 10 cycles per second, Fourier transforms make it clear that a whole spectrum of waves ranging from 2 to 30 cycles per second is present from any given locus. There is considerable variation in the dominance of components of the frequencies from person to person and studies of identical twins and of family groups in general show a strong tendency for the particular EEG patterns to be inherited. This is also true of abnormal patterns that have proved useful in diagnosing epilepsies.

The brain waves are composed of electrical discharges of many cells firing in synchrony and the sinusoidal pattern appears to be due to the distribution of thresholds of firing of groups of cells. Evidence indicates that reverberating circuits of activity, involving one-way cell-to-cell synaptic conduction between thalamus and cortex and back again, and even between hypothalamus, thalamus and cortex, are involved in the rhythms, since suitably placed lesions in these lower centers may abolish some of the cortical rhythms, apparently by interrupting loops of neurone-to-neurone conduction. But, on the other hand, conduction can take place from cell to cell in oriented

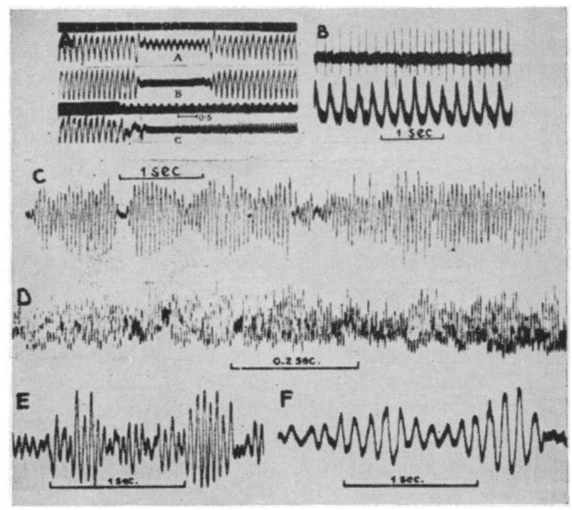

Fig. 3. Waves and rhythms from different central nervous systems as figured by F. Bremer (*J. belge Neurol. Psychiat.*, 1947, **47**, 542). A—Optic ganglion of the beetle *Dystiscus*: effect of light of increasing intensity (A through C) in abolishing the rhythm (from Adrian, 1937). B—Catenary ganglion of the lobster: ganglionic waves (below) and nerve impulses led from an interconnecting nerve trunk (from Bonnet, 1938). C—Gray substance of the anterior horn of the cat spinal cord discharging synchronously after a period of asphyxia (from Bremer, 1941). D—Cat cerebellar cortex: synchronous activity following brief electrical stimulation (from Dow, 1937). E and F—Rhythmic activity in two functional states of the cerebral cortex of the cat after surgical de-afferentiation (from Bremer).

polarized brain cell layers by electrotonic action from active to inactive cells by way of electrical conduction through bathing fluids and independent of synaptic circuits. This phenomenon has been demonstrated by studies from the laboratory of F. Bremer (*2, 3*) of Brussels and in this country by Gerard et al. (*5*) in studies of electrical waves in frog brain and in isolated pieces of frog brain. Moreover, in lobotomy operations, cutting connections of the frontal lobe of the cortex with the thalamus in man does not modify the frontal brain wave patterns. Thus, both synaptic conduction and nonsynaptic electrotonic conduction appear to be involved in the spread of brain waves in central nerve tissue, and work of a number of investigators has shown basic brain wave rhythms to be independent of the arrival of afferent impulses, although such impulses can modify the rhythms. Fig. 3, from a paper of Bremer (*2*), illustrates brain wave rhythms of central nervous tissue from beetles to mammals.

A variety of factors have been found to change the EEG patterns. Thus, the alpha rhythm is characteristic of the subject at rest with eyes closed. Pattern vision with the eyes opened, i.e., focusing visual attention, and even the recall of visual images with the eyes closed, abolishes it although it is not abolished even by strong diffuse illumination through closed lids. Occupation of the visual cortex with pattern discrimination disrupts the synchronized neurone beats.

Sleep and even drowsiness, together with a variety of conditions of impaired consciousness produced by drugs, are accompanied by slowing and disruption of the dominant alpha frequency and its replacement by more or less slow random waves.

One factor determining the basic frequency of the dominant rhythms, other things being equal, seems to be the rate at which the brain burns sugar, its only normal fuel. Thus, there is a progressive slowing of alpha frequency with decreasing sugar or oxygen carried by the blood to the brain or by the administration of inhibitors of the brain's oxidative enzyme systems; conversely, metabolic stimulants increase the frequency. Increasing the alkalinity of the blood slows the frequencies, an effect which is easily demonstrable by rapid deep breathing that blows off carbon dioxide.

Increasing the internal body temperature by fever or by diathermy increases alpha brain wave frequencies and some years ago we found that the Arrhenius equation relating the rates of pace-limiting simple chemical processes to temperature describes this relationship, and gives three values for the activation energy. Two of those values are identified with specific enzyme systems which are known to be present in the brain and which appear to act in the brain's sequence of oxidation steps as rate-limiting chemical pacemakers for the alpha frequencies (*6, 8*).

These metabolic findings are consistent with the view expressed by Hill in our earlier quotation; namely, that nerve cells function as relaxation oscillators that may fire repetitively in response to voltages built up across the cell's membranes by cellular oxidation. This general point of view applies equally well whether the cells are regarded as firing as independent units stimulating neighboring cells to synchrony by electrotonic action or whether the brain waves are due to synchronized reverberating circuits involving, by synaptic conduction, extensive brain regions in loops of activity.

It is of interest in this connection that we have found the human time sense to obey the Arrhenius equation and yield an activation energy similar to that encountered in some studies of cell respiration but different from that for alpha frequencies. The subjective counting of the number of seconds in a minute speeds up with elevated internal body temperature so that more seconds seem to pass per minute and private time therefore appears to drag in comparison with public time accepted as a standard. Our sense of time itself thus seems to be regulated by some as yet unidentified enzyme system, a sort of master chemical clock with an activation energy of 24,000 calories. Fig. 4 demonstrates these data.

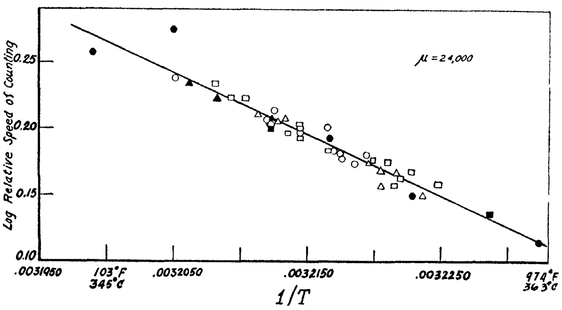

Fig. 4. Arrhenius equation plot showing effect of internal temperature on the rate of estimating time. Different symbols refer to different persons. The absolute rate of counting is not indicated, since the ordinate has been telescoped. From Hoagland, *J. gen. Psychol.*, 1933, 9, 269.

On the clinical side, during the past 15 years electroencephalography has proved to be an important adjunct in diagnosis of epilepsy and in localizing brain lesions for subsequent surgery.

Brain Physiology and Behavior

The discovery of continuous rhythmical electrical activity in the brain has opened new possibilities of interpreting the physiological basis of behavior. Mental processes have a continuity, and consciousness is an enduring affair interrupted at intervals by the sleep rhythm but otherwise normally persisting throughout life. Nothing in the study of classical reflex mechanisms has adequately accounted for learning and the persistence of memory. For a century after Magendie and Bell, the brain was regarded as a complex system of pathways whereby impulses from the periphery reached effector organs to produce behavior in stimulus-response sequences and, while many excellent studies of spinal reflexes shed light on the physiology of these fundamental units of behavior, little progress in correlating brain physiology with higher mental processes was possible so long as the brain was regarded merely as a classical passive telephone-switchboard. Who, after all, plugged in the right connections? Who or what was the operator of this inert switching system? Obviously the brain itself—but how?

Since 1943 several contributions have appeared which shed suggestive light on this problem. Thus, Rosenblueth, Wiener, and Bigelow (*11*); Pitts and McCulloch (*10*); Adrian (*1*); and more recently Northrop (*9*) have considered these matters from refreshingly new angles. It has been my privilege to read in manuscript Norbert Wiener's book *Cybernetics, or control and communication in the animal and the machine* (*13*) and I should now like briefly to consider a few of the matters pertinent to waves and rhythms raised in these studies.

In 1940 Wiener worked out the principles of a machine now in operation for the solution of partial differential equations with more than one variable, and has made interesting comparisons of this machine with the brain. Kenneth Craik in his book *The nature of explanation* (*4*) has made similar comparisons but Wiener's analysis is more extensive. The machine is fed data and proceeds to perform a complicated series of logical operations at a rapid rate through electronic switching devices. The computations are based on a scale of two after the algorithms of Boolian algebra rather than on a scale of ten, and electronic relays which give an on-off or a yes-no answer are the switching devices employed.

All data according to the rules of logic and number are operated upon by the machine in sets of choices between two alternatives, and all the operations on the data take the form of making a set of new choices dependent on a set of earlier choices. The operations are timed by a central clocking device. This clocking may be performed by an actual clock, or its equivalent may be performed by not permitting a process to take place until its antecedents have occurred.

No human interference with the processes takes place from the time of supplying the machine with its initial information until the end of the calculations. Thousands of ordered operations take place at an exceedingly rapid rate, condensing into minutes processes that would require days to complete with ordinary methods of computation.

In such a machine there are devices to retain impulses until it is time for the appropriate circuit to act and relate them to other events in the processes of computation. This may be done in the machine by systems of reverberating circuits and by electronic scanning devices, such as are used in television and also in the form of magnetization patterns of the molecules in iron wire after the manner of the well-known wire recorder. Thus, information can be stored until ready for use, and the machine quite literally possesses a functional memory in the form of patterns of dynamic electrical configurations or of molecular patterns which may be called upon to furnish information by appropriate stimuli arriving as timed pulses from other circuits in the apparatus. It is important to realize that this memory need not be lodged in any one locus in the machine, but belongs to its function as a whole. To ignore this is to commit the fallacy of Descartes in locating the action of mind on matter in the pineal gland.

A basic controlling principle in the integration of patterns of activity in the machine is that of negative feed-back, and evidence clearly indicates that negative feed-back plays a fundamental role in nervous integration. In any system displaying negative feed-back, some of the output of the system returns to limit and control its further output. Thus, Rosenblueth, Wiener, and Bigelow point out that negative feed-back means the behavior of an object is controlled by the margin of error at which the object stands at a given time with reference to a relatively specific goal. A robot-controlled plane may, for example, be directed automatically to seek its target by electromagnetic waves sent out by it and reflected back from the target so as to modify the steering mechanism. The proximity fuse detonates the shell as it approaches the target by the return of electromagnetic waves broadcast from the shell and reflected back to it. Again, the thermostatically controlled house heating system is a more prosaic example of negative feed-back, since as the temperature rises it shuts off the heater and when the house cools off the furnace is turned on again by the thermostat. Engine governors and the steering engines of ships furnish other examples of negative feed-back, and mechanisms so controlled are called servomechanisms.

Nervous system processes are replete with examples of negative feed-back. Thus increasing blood pressure excites stretch receptors in the carotid sinus, which sends to the vasomotor center impulses causing a fall in blood pressure. Homeostatic mechanisms in general that regulate our internal environment use principles of negative feed-back. Breathing movements are examples of control of rhythms of inspiration and expiration by negative feed-back. Another example is the control of movements of the limbs by reciprocal inhibition of antagonistic muscles, producing orderly movement, and Adrian in his *Physical background of perception* (*1*) has discussed a number of such mechanisms familiar to neurophysiologists. The cerebellum is a complex coordinating center for smoothly controlling by way of negative feed-back sensory impulses from the limbs essential to precisely coordinated movements.

Lorente de Nó has demonstrated the action of what he calls reverberating chains of neurones so arranged in closed paths in the central nervous system that each neurone excites the next around the loop, the last finally reexciting the first. With 10 billion neurones in the human central nervous system an appalling number of interacting neurone loops are possible. Action once started in such reverberating circuits can continue indefinitely as long as metabolism supplies the requisite energy.

Suppose now that one or more of the neurones in such a loop is fired by a specific sensory impulse. This loop involving many neurones will correspond to the physiological substratum of that specific sensory event and as McCulloch has put it "A train of impulses in a regenerative loop preserves the form of the fact without reference to the one particular moment when it was experienced." Comparable loops of activity are stored in the electronic calculating machine by use of reverberating systems and principles of electronic scanning.

Wiener also points out that the neurone operates on an on-off basis like an electronic relay. It either fires or not, and the parallel to the machine and its binary scale of operation is thus further borne out in terms of the basic units comprising the brain and the machine. Changing the grid bias of tubes by automatic devices modifies the tube's timing and in like manner negative and positive after-potentials of neurones are important in regulating impulse passage at synapses through modifications of synaptic excitability.

Voluntary acts by their very nature exemplify negative feed-back. Thus when we proceed to pick up an object from a table we do not command a specific sequence of muscular acts. Rather, as Wiener suggests, the controlling factor in the act is the degree to which the act has not been completed. The object may be picked up with either the right or left hand or even by the mouth if the hands are tied. The action ceases when the purpose is realized, after the manner in which servomechanisms control actions and bring them to a stop. Servomechanisms are purposive in nature.

Rosenblueth and Wiener are preparing for publication an experimental study of muscle clonus in spinal and in decerebrate cats. From an anlysis of the clonus frequency based on the theory of servomechanisms, they found good preliminary agreement between calculated and experimental values of the muscle's rhythm of contraction in response to stimulation of its myotatic receptors by stretch.

Form Perception and Memory

Pitts and McCulloch (10) published a paper entitled: "How we know universals, the perception of auditory and visual forms." In this paper they present both anatomical diagrams based on cortical neuroanatomy and a mathematical analysis indicating how a scanning mechanism consisting of waves of impulses sweeping up and down over interlacing nonspecific and associative afferent fibers in the cortex can furnish a basis for the perception and recognition of form when specific afferent stimuli arrive over sensory pathways. In this type of nerve network, form, whether that of a musical chord or a geometrical pattern, is independent of size or position in the field and it is independent of any particular neurone or small neurone group. In this connection it is interesting to recall that Lashley found recognition of patterns and retention of learned acts in rats to be affected to a surprisingly small degree by the surgical removal of specific anatomical brain areas. Retention of learned acts seemed to depend more upon the amount of tissue left than on its locus.

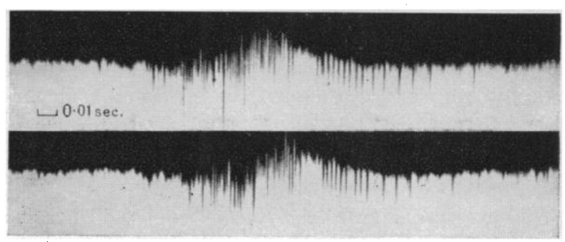

Fig. 5. Complex discharges in several units of the cerebral cortex following the local application of strychnine. Both outbursts are due to sensory stimulation (touching the foot) and show the tendency for the cortex to repeat the same pattern of discharge. From Adrian and Moruzzi, *J. Physiol.*, 1939, **97**, 153.

Pitts and McCulloch write "It is to the nonspecific afferents that modern physiology attributes the well-known rhythmic sweep of a sheet of negativity up and down through the cortex—the alpha rhythm. If our model fits the facts this alpha rhythm performs a temporal 'scanning' of the cortex which thereby gains, at the cost of time, the equivalent of another spatial dimension."

Lashley's experiments with rats indicate that memory traces occupy very extensive cortical areas, since the ablation or transection of a given region does not destroy memory, and he has suggested that signals reaching receiving areas of the cortex may reverberate extensively, affecting patterns of action in innumerable rhythmically acting local circuits. Memory traces would then be more or less stable resonance patterns which might be extensively reduplicated all over the cortex, ready to respond to incoming signals which fitted the pattern of response. Fig. 5, from a paper of Adrian and Moruzzi, shows such a pattern at one point on the cortex set up in response to a specific sensory stimulation of the foot.

But, as Adrian (*1*) has pointed out, it is difficult to see how memories can survive great changes in the over-all patterns of activity of the brain such as occur in normal sleep or in anaesthesia. As Adrian has stated in his lectures on the "Physical Background of Perception," "Clearly if memory traces are patterns they must tend to occur in the same form after a period of inactivity and to bring this about it seems to be necessary to postulate some semipermanent modification as well. A slight change in the exceedingly plastic structure of nerve cells and dendrites would be enough [following activity]." In this connection I would like to suggest by analogy that the storage of information in the wire recorder modifies the wire at a molecular level but not within optically observable microscopic dimensions and information fed by such a wire to scanning circuits can reappear in its original form after a shutdown of the apparatus when its circuits are later reactivated.

Finally, it is worth recalling that both the brain and the machine operate in relation to internal master clocks. In the case of the brain, steady-state enzyme kinetics appear to regulate our time sense.

Philosophical Implications

Northrop, in a paper entitled "The Neurological and Behavioristic Psychological Basis of the Ordering of Society by Means of Ideas" (*9*), has discussed the work of Wiener, Rosenblueth, McCulloch and Pitts against the background of two opposing philosophical views of the role of ideas as determinants of behavior. To the Lockian and Cartesian dualists and to the idealistic German philosophers there are only mechanical causes and no purposes or universals in the biological realm, only particular events and no remembered events with their persistent meanings. According to these classical views, purpose, memory, and the existence of universals establish the reality of nonbiological minds or mental substances and thus lead to the formulation of vitalistic theories. Opposing these views have been the mechanistic biologists and the behavioristic psychologists for whom purpose and mind are mere appearances or epiphenomena, and only stimuli and observed responses are real. Ideas as determinative causes are regarded as mere rationalizations after the fact of behavior.

Northrop dismisses both of these points of view in terms of the light shed by the recent neurophysiological concepts, pointing out that purposeful goal-directed behavior is possible in human neurological

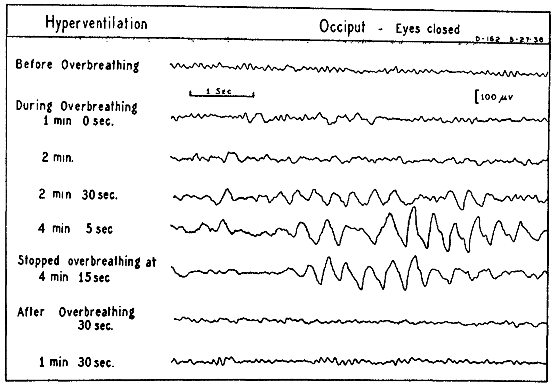

Fig. 6. Effects of hyperventilation on the human electroencephalogram. Note marked slowing accompanying the excessive removal of CO_2 by overbreathing. From Davis and Davis, Res. Publ. Ass. nerv. ment. Dis., 1939, **19**, 50.

systems containing negative feed-back mechanisms and patterns of reverberating circuits which are the epistemic correlates of ideas and which can function causally. Signals from the goal can alter behavior after it has been initiated so that it reaches the goal. This is the requirement for any mechanism in order that it be goal-directed and "a teleological system can

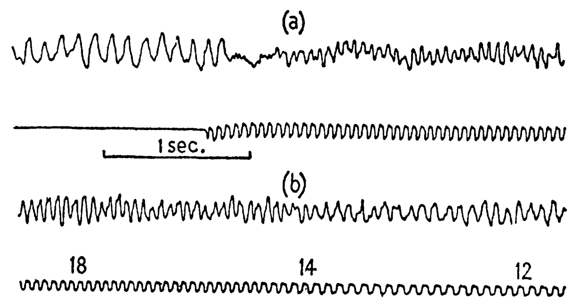

Fig. 7. Records from the occipital region of the head, showing the effect of flickering light. Below the records from the head are tracings from a photoelectric cell indicating the rate of flicker. In the lower record the rate was reduced from 18 to 12 per sec, and the cerebral waves keep in step with the flicker. The cerebral waves are potential changes of the order of 20–30 microvolts. Adrian reports that the alpha frequency here driven at 18 per sec can be driven up to 30 per sec by flickering light. From Adrian, *Lancet*, 10 July, 1943, p. 34.

be—and in the human nervous system it is—a mechanical system. It is a mechanical system in which the behavior of the system is controlled by a negative feed-back over the goal.

"Because overt behavior can be tripped by impulses from reverberating circuits whose activity conforms to universals as well as by impulses coming immediately from an external particular event, the behavior of men can be, and causally is, determined by embodiments of ideas as well as by particular environmental facts."

If brain waves do indeed represent the sweep of cortical scanning circuits it is easy to understand their disappearance in the act of attending to visual experience. Thus attending to sights or even recollecting visual experiences causes them to disappear as the sweep of television scansion is obscured by the formation of pictures. Asynchrony of the nonspecific sweep afferents with the specific sensory circuits might be expected to obscure consciousness and indeed we do find consciousness lost when the brain rhythms show random slow wave activity, or when epileptic discharges take place in the form of abnormally large synchronized bursts of activity. However, it is nonetheless possible to modify profoundly the alpha frequency without appreciable effect on perception or coordinated behavior. This fact is hard to reconcile with the need for precise synchrony of specific afferent patterns of continuous circuits as epistemic correlates of ideas and sweep frequencies of scanning circuits. Thus, hyperventilation can slow the dominant brain wave frequency from 10 cycles per second to 3 and on the other hand flickering light can increase its frequency from 10 to 30 per second without observable modifications of memory, consciousness or of perception in healthy persons (Figs. 6 and 7). However, it is also interesting that both of these procedures can produce seizures in some epileptic patients with attendant loss of consciousness. We might expect modification in the sweep of scansion to produce changes of this kind in everyone, but changes are the exception and not the rule. Failure to modify perception would appear to be possible only if the frequencies of all the reverberating circuits concerned with specific sensory afferents were equally affected by the agents affecting the scanning frequency of the nonspecific associative afferents. But it is hard to see how such uniform synchrony would be possible over wide association areas of the brain, many of which experimentally show different thresholds of susceptibility to chemical agents and which may not be appreciably affected by a stimulus such as a flickering light that drives the neurones concerned with visual reception.

The hypotheses of Wiener and his colleagues are highly suggestive. It will be interesting to observe their impact on experimental physiology during the next decade.

It would be agreed, I am sure, that one of the most significant physiologists of our time is Sir Charles Sherrington and a quotation from his book *Man: on his nature* (*12*) is an appropriate conclusion to a paper on waves and rhythms in the nervous system. In language of singular charm, it pictures the brain asleep and awake. Imagine

> "A scheme of lines and nodal points, gathered together at one end into a great ravelled knot, the brain, and at the other trailing off to a sort of stalk, the spinal cord. Imagine activity in this shown by little points of light. Of these some stationary flash rhythmically, faster or slower. Other are travelling points streaming in serial lines at various speeds. The rhythmic stationary lights lie at the nodes. The nodes are both goals whither converge, and junctions whence diverge, the lines of travelling lights. Suppose we choose the hour of deep sleep. Then only in some sparse and out-of-the-way places are nodes flashing and trains of light points running. The great knotted headpiece lies for the most part quite dark. Occasionally at places in it lighted points flash or move but soon subside.
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> "Should we continue to watch the scheme we should observe after a time an impressive change which suddenly accrues. In the great head end which had been mostly darkness spring myriads of lights, as though activity from one of these local places suddenly spread far and wide. The great topmost sheet of the mass, where hardly a light had twinkled or moved becomes now a sparkling field of rhythmic flashing points with trains of travelling sparks hurrying hither and thither. It is as if the milky way entered upon some cosmic dance. Swiftly the head mass becomes an enchanted loom where millions of flashing shuttles weave a dissolving pattern, always a meaningful pattern though never an abiding one. The brain is waking and with it the mind is returning."

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