# PROBLEMS IN THE COMPARATIVE STUDY OF BRAIN WAVES*

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It is the purpose of this discussion to point out certain of the approaches and problems that inhere in the study of that form of nervous activity giving rise to "brain waves," especially as seen from the comparative point of view. Brain waves will be loosely considered as any fluctuating electrical potentials ascribable to the brain or to the highest ganglia of the central nervous system in the absence of apparent external stimulation. It is considered undesirable for the present purpose to attempt an artificial separation of one portion of the frequency spectrum from others by restricting the term to those frequencies that appear as waves instead of spikes at a certain speed of the recording tape. It is not intended to present the results of a finished investigation, but simply to call attention to some significant problems raised by our present knowledge of brain waves in lower animals, supplemented by some new records, and to certain bearings which this knowledge has upon existing interpretations of brain waves.

In the decade and very little more since it became accepted that rhythmic, oscillatory potentials were a valid and constant feature of the normal, apparently unstimulated cerebral cortex of man and higher animals, a large literature has accumulated on the "electroencephalogram" (EEG) under a great variety of circumstances. After a few early attempts at a fundamental explanation of the phenomenon, which served to indicate the difficulty of the problem, attention turned to the establishment of empirical correlations useful in clinical application and it is in this area that the principal body of our knowledge lies. These clinical studies have emphasized the sensitivity and objectivity of this sign of the activity of the brain and at the same time its crudity as compared with signs based on behavior, sensation, and introspection. Thus, the EEG provides clear indications of sleep, of light ether anesthesia, and, under the proper circumstances, of thinking as opposed to the resting state, but it is virtually unaffected by frontal lobotomy (Davis[36]),

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by section of the corpus callosum (Dusser de Barenne and McCulloch[38]), or by decerebration (Bremer,[23] Dusser de Barenne and McCulloch[38]), and in most cases it cannot distinguish a normal from a feeble-minded individual (Davis[35]). But preoccupation with this approach, valuable and fruitful as it has been, has meant that our basic understanding of these potentials has lagged far behind. Little has been done recently on the fundamental nature of brain waves, their physiologic meaning and their relation to other better-known forms of nervous activity.

## *Current concepts*

In the occurrence of these relatively stable, *continuous*, *spontaneous*, *rhythmic* patterns of activity we are presented with an intriguing physiological problem. Perhaps it has ceased to be true that "the general picture of spontaneous activity of the nervous system. . . [is] foreign to the thinking of many neurophysiologists," and that we have still to "enlarge our thinking by assuming a constant background of preexisting, and probably autogenous, activity" (Davis[34]). Perhaps the intensity of the activity has ceased to surprise us as it did the early sceptics on the basis of their experience with recording nerve action currents in situ, shunted by surrounding tissues.[34] But we still have no satisfactory identification of what it is that distinguishes those parts of the nervous system which have such activity from other parts which do not. Nor is there any general agreement on the basis of the observed frequencies of the rhythms, being, as they are, much faster than any familiar changes in state of whole organs or large masses of nervous tissue and much slower than the familiar signs of nervous activity (i.e., nerve impulses).

Some of the questions which early workers naturally asked and which are still unanswered are these: Are the relatively slow (1-50 per sec.) brain waves the envelopes of numerous summed impulses in fibers or cells, or are they some other direct derivative of classical nerve impulses? Or does this kind of activity represent a novel form of nerve cell function, a slow, rhythmical change of state not necessarily involving impulses?

Bartley and Bishop[14] calculated the possibility of deriving the observed potentials from action currents in axons by an analysis of the shunting effect on pieces of peripheral nerve buried at various depths in the cortex. They concluded that brain waves must represent activity of nerve cells and synapses as they could not be accounted for by the summation of impulses as known in peripheral fibers. On the basis of studies of the activity of ganglia in the crustaceans Prosser[89] declared that slow waves are built of summed spikes of at least the same order of time relations as axon action currents. Adrian and Matthews[7] believed that the summation of brief pulsations in nerve cells (not as brief as axon spikes but shorter than the observed waves), synchronized in small groups, could account for the smooth slow waves. Adrian and Moruzzi,[9] in one of the few recent fundamental attacks on the problem, showed very clearly some relations between impulses in the efferent fibers and slow waves in the cortex. A given efferent fiber usually carries a single impulse for each cortical wave but the cortical waves may occur in the absence of impulses. Thus, the waves may bear an intimate relation to spikes but they do not actually represent the spikes or their necessary counterparts in the cortex.

Many authors have expressed the belief that the slow waves are summation products of some direct derivative of impulses (Jasper,[69] Bishop,[17, 18] Prosser,[89] Gibbs,[53] Bremer,[24] Heinbecker and Bartley,[58] Hoefer and Pool,[62] Echlin[42]). But a number of these have felt that some slow process must be involved in the rhythmic excitation or synchronization of the cells though it is not itself the cause of the potentials. Thus Jasper[69] postulated that brain waves are "due in part to a periodic secondary rhythmic change in level of polarization or excitatory state of the tissue." And Prosser[89] admits the necessity of a "blocking mechanism" and a synchronizing mechanism to group the impulse bursts that actually make up the waves. "The slow frequencies are as real as their fast components . . ." and the observed waves are the "sum of responses of many cells" but the modulating frequency is real and distinct (Gibbs[53]).

Opposed to this view, which may perhaps be regarded as the prevalent or majority view, is that represented in various degrees of elaboration by Gerard, Libet, Renshaw, Forbes, Morison, and others. According to these investigators the slow waves are not made up of summed impulse action currents, in cells or fibers, but represent slow rhythmic processes not dependent on and not necessarily causing impulses. Renshaw, Forbes, and Morison[94] found slow waves with micro-electrodes, which pick up from a very restricted area. Under the same conditions it was possible to pick up spikes apparently from a few or single units, but they emphasize the importance "for the interpretation of the slow waves [of the fact] that their contours, even as recorded on the cathode ray oscillograph, show no . . . indications of the participation of fast components in their formation . . ." and that the volume of tissue active in the production of the slow waves is large, quite unlike the situation with respect to unit discharges which their equipment could readily distinguish (see also Forbes[44]).

The idea has been most extensively elaborated by Gerard, who "takes it as probable that an electrically beating cell may discharge a single or a brief volley of impulses down its axon at some regularly repeated phase of the electric variation, but that this does not occur in the majority of cases."[47] Recording typical smooth, slow brain waves from a completely isolated fragment of the frog's olfactory lobe, weighing a fraction of a milligram, Gerard and his co-workers[48, 50, 74] have arrived at the conclusion that the observed wave is due to the summed "beating" of many cells, undergoing simultaneous, rhythmic changes of state. From the facts that nicotine, which blocks at least some central synapses, does not destroy the pattern[73] and that certain waves may actually cross a complete transection of the brain, they conclude that ordinary impulses in established anatomical paths are not involved in the synchronization of the beating cells, but that "electrical, and solely electrical, factors can account for the coordinated beat of cell masses. Potential changes in a small number of cells, which act as pacemakers, are able to play upon other units so as to make their potential changes occur with essential simultaneity (or to make them follow at finite times . . .). Such 'electrotonic' control of the timing of beating cells is foreshadowed in the synchronous discharge of injured nerve fibers (Adrian[1]), in the 'artificial synapse' obtained by partial longitudinal approximation of non-medullated nerves (Jasper and Monnier[70]), in the relation of spinal root discharges to slow cord potential swings (Barron and Matthews,[12] Fessard and Matthews[43]), in the parallelism of nerve after-potentials and spontaneous discharges (Gasser and Grundfest[46]) and the like."[49] Suggesting a similar freedom from synaptic conduction in the mammalian cortex, Heinbecker and Bartley[58] point out that under deep ether anesthesia brain waves disappear long after cortical response to peripheral nerve stimulation, that is, after at least some of the synapses are blocked.

If it be accepted that nerve cells can interact by other than synaptic means* and that brain waves represent a continuous and influential background of activity of nerve cells of a sort distinct from familiar impulses, then a tremendous new area of problems and possibilities is opened for both practical and theoretical neurophysiology. Some of these have been indicated by Gerard.[48] While the concept of such potentials in the brain is still novel, it is not without precedent in simpler centers. Adrian and Matthews[8] showed the presence of slow rhythms which group the impulses in the optic nerve and must mean some interaction of large areas of the retina. Barron and Matthews[11] demonstrated the existence of some form of non-synaptic influence of the surrounding tissue on trains of impulses passing in tracts of the spinal cord, intermittently blocking conduction after the impulses had entered the cord. They believed the explanation lay in electrotonic control by the neighboring gray matter. The same authors[13] showed the crucial importance of slow potentials in permitting or preventing discharge of the ventral horn cells. And Granit[54] and Bernhard[16] among others have analyzed the retinal potentials and the electrotonic potentials in the optic nerve demonstrating that successive slow potential waves precede the discharge of impulses in the nerve and even that "it is probable that inside the retina excitation is carried forwards by electrotonic spread rather than by spike activity between the different layers."[16] Similar retinal potentials as well as maintained rhythms

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* The conclusion of Jasper and Monnier,[70] as a result of studies on transmission of excitation between excised nerves placed in contact, is significant in this connection: "The fact that transmission across the crustacean artificial synapse was observed in our preparations only when the receiving nerve was on the verge of spontaneous discharge may limit this type of transmission to nerve elements possessing the characteristic of autonomous rhythmic activity. Since this is precisely the case with certain neurons in the central gray matter of mammalian nervous systems, and since these neurons are also found to be in very close juxtaposition with no myelin sheath, conduction between adjacent fibers, without the intervention of the classical synaptic ending, may be of considerable importance in the conduction of excitation processeses within the central gray matter. In fact, it is difficult to explain the type of conduction of excitatory processes in the cerebral cortex described by Adrian,[4] i.e., irradiation of waves in all directions at the rate of 25 to 50 cm. per second by the usual conception of impulses following prescribed pathways at a much greater rate of speed with short, synaptic delays. Conduction by juxtaposition with long synaptic delays, as found for crustacean nerves, may account for the nature of the spread and the slow velocity of cortical potential waves."

of slow waves under conditions of steady illumination or darkness have also been described in several invertebrates (Adrian,[5] Jahn and Crescitelli,[31, 32, 33, 63, 64, 65] Jahn and Wulff,[66, 67, 68, 106] Roeder,[96, 97] and Therman[103]).

### *Frequencies involved*

It is now well established that standing or steady state ("D. C.") potentials exist in the nervous system, as elsewhere (Burr,[28] Northrop and Burr,[82] Burr and Harman,[29] Harman,[56] and Libet and Gerard[75]). The question, therefore, naturally arises as to how much of the observed slow waves can be accounted for by fluctuations in these potentials. We are reminded that the basic task of describing brain waves is not finished. Fluctuating brain potentials of real significance probably occupy a continuous frequency spectrum from virtually zero to more than 500 per sec. Yet our knowledge almost exclusively concerns the band from 1 to 50 per sec. An important effect of the great amount of experience accumulated with brain waves studied for clinical purposes has been the freezing of our concept of these waves in a certain pattern largely defined by the arbitrary limits imposed by the conventional technic of recording. A standardized technic has been necessary and has resulted in the development of many highly trained eyes, able to recognize types of records and see variations that are difficult to characterize objectively. But we have come to think of brain waves in the form of these records and it is inevitable that this should mean an emphasis on certain features of the phenomenon and certain parts of the frequency spectrum at the expense of others because these features and frequencies are selected by the recording device used or are favorably shown at the paper speeds used. It suffices to see or to hear the same phenomenon with different apparatus—a cathode ray and loud speaker for example—to be convinced of this. Aside from the matter of special features of the pattern, which is more subtle and complex, it is certainly true that our knowledge of a certain portion of the frequency spectrum is out of proportion to our knowledge of other portions. For very cogent reasons a rather narrow band of the spectrum has been adopted for routine study of brain waves and by keeping amplification down to a value that prevents the largest waves from exceeding the linear excursion of the recording device an effective limitation is made on the amplitude spectrum that is studied. Although difficult to study (not because they are hard to amplify and record, but because of the problem of recognition and elimination of spurious mimicking potentials) significant fluctuations with periods of minutes, hours, and days undoubtedly occur and may well show correlates not revealed by the familiar waves. Thus, Leão[72] has recently demonstrated slowly spreading changes in the electrical properties of the cortex of the order of 1000 times as long as the slowest brain waves. Slowly changing "D. C." accompanying such states is very probable.

Much easier to study on the other hand are the small, fast potentials that are attenuated, compressed, or invisible in the ordinary EEG. Their occurrence, distribution, and correlates are virtually unknown (see, however, Renshaw, Forbes, and Morison[94]). Other descriptive problems which still await satisfactory exploration include the extent and pattern of travelling waves in the normal EEG, the semi-micro distribution of the potentials in the cortex (see Bishop and O'Leary[19, 20, 83]) and the validity of Kornmüller's[71] correlation with cytoarchitectonic areas.

All the problems mentioned above are on the elemental plane. We have not listed the host of more obvious, often more practical, and as yet largely empirical problems dealing with the variations in brain waves in different physiologic and clinical states. This field has long been under active attack and has inevitably shed light on the theoretical questions, but it should profit greatly from extension in some of the directions suggested above and from solution of some of the basic interpretive problems outlined.

### *Brain waves in lower vertebrates*

One approach which would seem to hold promise for the difficult problems of the fundamental meaning of brain waves is the comparative approach. When we consider the variety of organization and range of complexity of the central nervous system of the various vertebrate classes, it might be expected that significant differences in the character of the brain waves are to be found and that they might be interpretable on the basis of known differences in anatomy and physiology. An opportunity for a natural experiment is provided by the existence of animals with simpler projection systems and fewer connections within the cortex and between cortex and basal ganglia, of animals, indeed, with no cortex at all, and those with markedly less complex as well as smaller brains than is that of man. The effect of many anatomical factors may thus be tested, for surely these factors will have significant effects on at least some parameters of the brain waves. The poikilothermous vertebrates also offer opportunities for many experimental procedures based on isolation of the brain or parts of the brain.

Only a few preliminary comparative investigations have been carried out (Adrian and Buytendijk,[6] Shurrager,[100] Gerard,[47] Gerard and Young,[51] Tokaji and Gerard,[104] Libet and Gerard,[74] Bremer, Dow, and Moruzzi,[25] Gerard and Libet,[50] and Swank and Jasper[102]) besides the numerous experimental papers on higher mammals. These have given us at least a first impression of the character of spontaneous electrical activity in the brains of a few representatives of the birds, reptiles, amphibians, and fish. As a result of the work of Gerard and his associates the frog is the best known of these. The outstanding generalization emerging from these studies is that *the brain waves of all vertebrates are strikingly similar.* It is possible that there are real differences and it is probable that much will be learned by systematic comparative surveys among vertebrates, but the astonishing fact remains that the tiny frog brain, without a cortex, exhibits electrical activity essentially like that of man.* Its character is altered little or not at all by isolation of the brain from all connection with sense organs and other parts of the nervous system. Thus, we are presented for consideration the idea that whatever is essential to the production of this particular kind of oscillatory potential exists in a mutilated fragment of the olfactory lobe of a frog, amounting to a tenth of a milligram, resting alone in a glass vessel as well as in the intact brain of man (Fig. 1). It is familiar to many workers that the brain waves of monkeys, cats, rabbits, and rats are significantly alike. The fundamental resemblance is often lost sight of in the strenuous effort to pin down small differences in proportions of frequencies. But when compared with the electrical activity of many other masses of nerve cells (see below) the telencephalon and sometimes other portions of the brains of all vertebrates so far studied show a remarkably uniform pattern.

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* Apparently consistent differences between the activity in parts of the brains of the fish and amphibia studied are in fact already described. This is to be expected and does not in my opinion deprive the generalization, as made, of validity or force. The results of Bremer, Dow, and Moruzzi on the turtle seem to be an exception, but considering the animal and the unanesthetized state in which the recordings were made—from the exposed brain—it is possible that the records represent a highly stimulated (? anxious) nervous system.

It would seem that some significant common element in neural organization in the diverse brains of vertebrates awaits identification to account for this uniformity, and that the phenomenon in which we look for clinical signs of so many delicate maladjustments of the highest nervous functions is based chiefly not on those higher characteristics that distinguish man's brain nor even the innovations that came with the mammalian corticate brain, but on some basic denominator common to the brains of fish and frogs and men.

The idea that brain waves express something primitive and fundamental in the organization of the brain and are not a direct sign of the higher aspects of its functioning is borne out by several lines of experimental results. Dusser de Barenne and co-workers found that the outer four layers of the cortex are not essential for the production of normal-appearing electrical activity, even the fifth layer may be destroyed without abolishing all spontaneous activity provided the preparations are chronic, i.e., some months are allowed to elapse between the thermocoagulation of the cortex and the testing for brain waves. Destruction of the sixth layer permanently and completely abolishes activity of that part of the cortex (see Dusser de Barenne and McCulloch,[37, 38] Murphy and Dusser de Barenne[81]). We may well wonder with Miss Hines[59] "What are the [four] outer layers of the cortex doing? Are they active only when peripheral end organs are definitely stimulated? Was the slow phylogenetic elaboration of the supragranular layers made for the reception of discrete stimuli only?" The supragranular layers may indeed lack spontaneous activity but the evidence is not sufficient to prove it.* We only know that whatever contribution it makes is not indispensable and that brain waves must reflect something very basic in the organization of the cerebrum. This is emphasized further by the facts that brain waves survive removal of the opposite hemisphere, of all the surrounding cortex, of the basal ganglia (Dusser de Barenne and McCulloch[38]), and in some experiments has survived undercutting, i.e., interrupting its connections with the thalamus (Spiegel[101]). That the activity is deeper seated than the cortex is

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* The question might be answered by an extension of the method of Renshaw, Forbes, and Morison[94] with micro-electrodes. It is not certain from their data on the isocortex what layers the electrodes were in but activity which was definitely very local was recorded from depths of as little as 0.3 mm. in the lateral gyrus of the cat. It is of course possible that the superficial layers are active, perhaps driven by the deeper layers, but not essential to the maintenance of the rhythm.

seen in the independence of the subcortical and cortical rhythm and the survival of the former long after the latter has failed in hypoglycemia or under nembutal (Hoagland et al.,[61] Bartley and Heinbecker[15]).

If the study of brain waves in lower vertebrates has disappointed us in not revealing a series of striking differences assignable to correlated evolutionary innovations it has provided a signficant generalization on the neural basis of this type of rhythm and has made available a mass of material for experimental studies which will have the more transference value to man because the phenomena in lower vertebrates and man have so much in common.

### *Electrical activity in the central nervous system of invertebrates*

We should not stop with the exploration of the lower vertebrates; the invertebrates deserve attention—not because there are so many of them but because there are so many kinds of them. They include the great majority of fundamental plans of organization of the nervous system, an impressive diversity in neuron arrangement and function and a great range in levels of complexity. It is difficult to anticipate the character of any spontaneous electrical activity that may occur in the central nervous system of invertebrates—considering (1) the great differences between vertebrates and invertebrates, superimposed on basic common features of nervous organization of all animals, (2) the levels attained by some of the higher invertebrates, and (3) the uniformity we have noted in the vertebrate scale.

Very little work has been done in this area and most of that has concerned other related problems, such as visual rhythms (Crescitelli and Jahn,[31, 32, 33, 63, 64, 65] Adrian,[5] Roeder,[96, 97] Therman,[103] Jahn and Wulff[66, 67, 68, 106]), the physiology of the synapse (Prosser[85, 86, 88, 92]), the effect of drugs (Boruttau,[22] Roeder and Roeder[98]), locomotion (Gray and Lissmann[55]) and the control of the heart (Rijlant,[95] Heinbecker,[57] Bullock,[26] Bullock, Burr, and Nims,[27] Prosser[93]). All of these authors, however, have recorded activity in the central nervous system or ganglia of invertebrates. Somewhat closer to the present point of view are the papers of Adrian,[2, 3] Prosser,[84, 87, 89, 90, 91] Bonnet,[21] and Cardot and Arvanitaki,[30] although most of their records were taken from the lower ganglia rather than from the highest ganglion or "brain" in each species. As will be pointed out, this may make a large difference in the character and therefore in the interpretation of the record. As a result of these studies we can anticipate that spontaneous activity will be found and something of its probable character in the brains of arthropods, but no generalizations beyond this group are possible.

In the course of some preliminary explorations in this territory we have made a number of records from representatives of the major higher invertebrate groups (annelids, arthropods, molluscs) and we have unsuccessfully attempted to obtain them from lower groups (echinoderms and coelenterates). It has been the aim of the technic to obtain records which, in spite of the very different natural history or "biology" of the species used, would be as truly comparable as possible. Complicated as this objective is by the problems (1) of immobilizing an intact animal without producing disturbing stimuli with the restraining devices, (2) of anesthetization to a uniform degree and without grossly affecting the spontaneity, and (3) of surgical exposure or isolation without profound stimulation arising from the trauma of the operation, it might seem that such an aim is futile or naive. Fortunately it has been possible to show in several cases that the activity manifested by the completely isolated brain or ganglion is essentially the same as that in the intact animal in the intervals between gross movement and in the absence of obvious stimulation. It has seemed therefore that the most validly comparable records are those taken from the completely isolated or at least deafferented brain. This remarkable stability of the general pattern of the electrical activity as between the quiet, intact animal and the isolated ganglion corresponds to our own and others' experience with frogs, goldfish, and other vertebrates.

The broad generalization emerging from these various preliminary explorations is that *invertebrate electrical activity is strikingly dissimilar to that of vertebrates.* All of the invertebrates studied agree in exhibiting very complex records, full of "fast" activity and conspicuous spikes. It may appeal to some as remarkable, to others as natural that in essential features the pattern of potentials is the same for animals as diverse as the earthworm, grasshopper, and slug.

Illustrated in the figures are samples of the electrical activity characteristic of the brain or principal ganglion, in the absence of intentional stimulation, of a grasshopper, moth pupa, crayfish, horseshoe crab, earthworm, and slug.

The activity in the grasshopper, *Melanoplus*, is quite consistently a pattern of hundreds of spikes per second, of all sizes up to a maximum but of a rather uniform form and duration resembling in these respects single fiber action potentials in peripheral nerve. These spikes so dominate the record that it is often difficult to see slower components of small amplitude. But in certain situations rhythmic slow waves are conspicuous (Fig. 1). The regular, oscillatory waves shown here are undoubtedly the same as the "visual rhythms" of Adrian, Crescitelli, Jahn and Wulff, who have recorded them by instruments which do not show spike activity. In Fig. 1 the relation between these well-established slow waves and spikes can be seen. The former are not evidently formed by grouped impulse bursts or envelopes of spikes, but would seem to represent an independent slowly fluctuating process. In some experiments it was noted that immediately after traumatic interference with the preparation the spike activity was greatly reduced without appreciably affecting the slow waves.

The crayfish, *Cambarus*, exhibits very similar activity (Fig. 2). However, we have not recorded regular oscillatory slow waves. There are prominent, complex, non-rhythmic waves which fall in the frequency spectrum between simple impulse spikes (500-1200 per sec.) and slow waves (1-40 per sec.). These, especially the slowest components, are more prominent in the anterior ganglia and connectives and may easily be overlooked in posterior levels, as they apparently have been,[89] because their amplitude is usually less than is that of the spikes and at high recording speeds they are stretched out and inconspicuous. Although slow activity is undoubtedly present, spikes dominate the record, in contrast to the vertebrate central nervous system.

The records from the cerebral ganglion and subesophagal mass of *Limulus*, the "horse-shoe crab" (Fig. 3), show a similar complex pattern of fast and intermediate waves. This generally favorable animal, chosen for the present purpose because of its large size, was surprising in that its activity did not usually approach in amplitude any of the other species studied. Whether this is a real peculiarity of the species or a result of the conditions of recording is not clear. It would seem that the factor of operative trauma was ruled out by the experience with most forms, mentioned above, relative to the validity of in vitro records, but it was not possible in this case to control this factor by taking records without operative interference. It was established that the ganglia from which the records were taken were not moribund or failing to initiate nerve impulses, as electrodes on the connectives leaving the ganglionic mass showed vigorous, spiky activity continuing steadily for a long time. In *Limulus*, as elsewhere, it was noted that the activity picked up from ganglionic masses characteristically differs from that in the connectives (like peripheral nerves) leading from the ganglia, in that slow components are much more conspicuous in the former, spikes relatively more dominant in the latter (cf. Adrian[8]).

The records of moth (*Polyphemus* and *Luna*) pupae (Fig. 4) were obtained with a view to demonstrating that the nervous system is spontaneously active even during metamorphosis, when a large number of nerve cells are disappearing, and others differentiating, the organization of the neuronal connections is in process of great change and the organism as a whole is at a low ebb of sensory and motor activity, protected as it is by the cocoon, with no appendages and a very largely dedifferentiated musculature. They were not obtained from the brain but from thoracic ganglia (in situ and isolated) so are not comparable on the same terms as the other records. But the activity of lesser ganglia is typically different from that of the brain in the direction of simplicity, of fewer slow waves and proportionately more simple spikes. So the rather complex pattern obtained from thoracic ganglia probably signifies a still more irregular pattern in the cerebral ganglia of this animal.

A variety of different appearing records were obtained from the earthworm (*Lumbricus*) (Fig. 5). It seemed difficult to standardize the condition of the animals and the state of the preparations so that the degree of spontaneous activity varied between specimens. Some exhibited rather simple activity consisting of fast spikes and little else, others contained a great deal of complex intermediate frequency, non-rhythmic activity, and still others showed regular, rhythmic, slow potentials besides the spikes. An impression that cannot be documented was that there was less difference between cerebral and ventral chain ganglia in this animal than in the others (crayfish and insect especially). This might have its basis in the lesser importance of the brain and in the greater autonomy of the ventral cord known to be true of the earthworm.

Having failed thus far to obtain satisfactory records from a pelecypod and a large shelled gastropod the only records offered representing the molluscs are from *Ariolimax* (Fig. 6), a very suitable terrestrial gastropod ("slug"). While electrodes on the connectives in an isolated cerebral ganglion preparation show vigorous spike activity, electrodes on the ganglia typically reveal a complex of slow and intermediate waves, mostly irregular, with a few spikes superimposed, especially a few regular, very large spikes.

### *The problem of interpretation*

Is there a fundamental dichotomy between vertebrate and invertebrate with respect to this aspect of brain function? How significant is the difference? Can we reconcile the apparently very different potential patterns on the basis of some simple factor such as size, number, or arrangement of cells? Can any of the facts of invertebrate electrical activity be applied to the problem of interpreting human brain waves?

Answers to these questions are today for the most part conjecture and opinion. Yet it would seem that critical thinking on the part of many people about the facts and problems raised by invertebrates will yield important dividends in suggestive hypotheses and critical experiments. The following speculative interpretations do not pretend to comprise an answer, even hypothetical, to these questions but merely provide points of departure for future lines of inquiry.

A simplified statement of the principal differences between vertebrate and invertebrate spontaneous electrical activity would certainly emphasize the prevalence of high frequency components and particularly spikes in the latter and their rarity in the former. It seems likely that many or most of the spikes seen in the latter are either the action potentials of single impulses or of a few well-synchronized impulses. Their simple form and time dimensions recall single fiber action potentials in nerve. It is very possible, further, that much of the complex, irregular, intermediate and high frequency activity represents summated spikes and, therefore, also nerve impulses. Its form recalls the complex records of asynchronous discharges in large peripheral nerves or fiber tracts, and its occurrence and non-occurrence in different preparations and parts of the nervous system suggests the same origin.

The presence of slow waves (duration longer than 20 milliseconds) of relatively simple smooth form and especially when spike activity is light is perhaps significant. The suggestion is strong under these circumstances that the slow waves are not envelopes of spikes or necessarily related directly to impulses but represent rather fluctuations in the standing potential or intercellular or tissue activity with a unit larger than the neuron. This recalls the concept of Gerard with respect to brain waves in the vertebrate. He speaks of masses of neurons "beating" and evidently visualizes a form of activity of nervous tissue distinct from the initiation and propagation of impulses, a slow, synchronous change of state of a considerable mass of gray matter.* Many people (see above) have assumed on the contrary that vertebrate brain waves are the envelopes of many impulses or some other derivative of impulses. It is part of this argument that impulse action currents must be present (cells must be firing) but are not seen because conditions are somehow not suitable for the registration of separate spikes, and that the peaks of the spikes do not rise above the smooth slow waves because those waves are in fact the peaks of many spikes or are summated cell body impulse potentials which under the conditions of pickup are much higher than the spikes. When, then, we discover a ganglion in which conditions permit impulse spikes to rise distinctly above the level of the slow waves and to be separately registered it is perhaps an argument in support of the thesis that the latter are not direct derivatives of impulses but some other form of activity of nerve tissue.

Such slow waves, then, may not be directly related to nerve impulses, that is, a derivative of them, but they may be and in many cases apparently are important in the production of impulses. That is, the slow waves may occur without the occurrence of impulses, but in some cases at least cells will not fire unless slowly changing potentials are at a certain level (see Fig. 7) or phase (Adrian,[3] in the respiratory rhythm of a beetle; Heinbecker,[57] and Bullock, Burr, and Nims[27] in the cardiac ganglion of *Limulus*; Barron and Matthews,[13] in the ventral horn of the spinal cord; Bernhard,[16] in the retina; Adrian and Moruzzi,[9] in the motor cortex; Eccles,[39, 40, 41] in the sympathetic ganglion and spinal cord). And of course the slow waves may be subject to modification by impulses as when incoming discharges from sense organs alter the character of human brain waves.

But if we do decide that some of the slow waves are real and non-dependent on impulses we are still faced with the question: why is the invertebrate record dominated by fast and the vertebrate

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* The slow, rhythmic, oscillatory potentials found in smooth and cardiac muscle pacemakers under certain conditions and distinct from but influencing the initiation of the conducted discharge are suggestive of a similar process (see Bozler[22a]).

record by slow activity? In view of the work of Gerard and his associates on isolated fragments of the frog brain, which we have repeated and confirmed, it does not seem likely that the difference is attributable to size or numbers of cells. Many invertebrate ganglia are larger than the tiny 0.1 mg. piece of olfactory lobe which will exhibit smooth, rhythmic 5-6 per sec. waves like those of the intact brain. On the same evidence it may be said that complexity of organization cannot be the crucial factor, for the cerebral ganglion of the grasshopper or crayfish is probably a more involved structure than is a fragment of the amphibian olfactory lobe.

If the slow waves in the invertebrate record may be regarded as cell body potentials of some kind, whether impulse-forming or not, their poor development relative to the vertebrate may be explained on the basis of the lesser importance of the cell body in invertebrates, as a significant element in the neural mechanism. As is well known the typical nerve cell among all these groups is the unipolar cell with a long common or stem process so that the cell body is removed from the path of conduction, the neuropile, and synaptic field and lies off at the surface of the ganglion playing a chiefly nutritive rôle. If the nerve impulse when it is in the cell body of the typical vertebrate multipolar neuron—or in the thick protoplasmic dendrites peculiar to vertebrates—has a different wave form and if this is a significant element of the vertebrate brain wave then it would be expected that such components would be lacking or little developed in the invertebrate as a consequence of its particular histology. Or if the slow waves of vertebrates represent some rhythmic beating or change of state of nerve cell bodies which has real neural significance then it would at least be expected that such phenomena would be very differently expressed in invertebrates because of the great difference in histology and in the rôle played by the cell body. Perhaps the slow waves of vertebrates are to be regarded as essentially novel developments correlated with some feature of the functional organization of the vertebrate nervous system. They may, for instance, represent a new form of mass activity of nerve cells evolved with the advent of gray matter. This tissue, consisting as it does of a variously organized mixture of multipolar nerve cells, dendrites, axons, synapses, including synapses on cells, and other elements, is entirely or virtually unknown in invertebrates.

But why should spikes be so conspicuous in the one group of animals and so rare or difficult to demonstrate in the other? Bartley and Bishop[14] have given reasons for not expecting the action currents in nerve fibers in the cortex or under it to be recorded except at high amplification. They show, by experiment, the shunting effect of the tissue on a piece of peripheral nerve buried in the cortex and conclude that the recorded brain waves cannot be accounted for as summated spikes. But it is difficult to see why the same shunting effects do not prevent the invertebrate spikes from registering at moderate amplification. A general explanation in terms of ganglion size or proximity of the nerve fibers to the surface does not seem likely. A satisfactory explanation is perhaps easier on the basis of the theory of slow, synchronous cell beats. According to this idea cells need not be firing to contribute to brain waves, i.e., no impulses are necessarily present. Impulse action currents *may* contribute to the pattern if not completely asynchronous, and undoubtedly do so in large or intact or not too deeply anesthetized brains. If sufficiently synchronized they may appear as large spikes as in the cortical response to discrete peripheral stimulation, but ordinarily they are not seen, perhaps because they are too numerous and poorly synchronized. In small masses of cells, as in the isolated frog olfactory lobe, however, where one might expect spikes to appear as they do in invertebrate ganglia, there may conceivably be no continuous spike activity necessary.

From the point of view of distinguishing between the hypotheses (1) of direct dependence of brain waves on impulse potentials in some form and (2) of the independence of brain waves and impulses, two experiments suggest themselves. The first would be a search for evidence that typical brain waves can, in at least some cases, occur when no cells are firing real nerve impulses. This might be done in a suitable preparation by leading off from the fiber tract efferent with respect to the gray mass producing brain waves. The preparation will probably be an isolation one such as the frog olfactory lobe and should be of such simple neural organization that it would be unlikely to have important closed circuits that might be carrying impulses which do not appear in the efferent tract. Such a demonstration has not apparently been made. But the second experiment has been attempted. In this case all possible synchronization by regular neural channels, i.e., by synaptic connections, is prevented by drug action so that even if spontaneous firing were inevitably taking place it would soon cease to be synchronized and could not contribute to the formation of brain waves. Gerard and Libet[49, 73] have used nicotine on the frog brain after showing that in this preparation and under the conditions of their experiment this drug blocked at least certain synapses—all those they could test. Nicotine did not abolish brain waves and only made more regular the large slow waves induced by caffeine. The same authors were able to show that caffeine waves, which they apparently regard as essentially similar to brain waves, will cross a complete anatomical transection of the brain. In the invertebrates no deliberate study of the effect of nicotine on slow waves has been made, but Roeder and Roeder[98] have shown its exciting effect on the initiation of nerve impulses, and in their figure 15 it can be seen that slow waves are present under its action, indeed increased over the prenicotine level. These experiments seem to favor the thesis that the slow vertebrate brain wave and perhaps the slow component of invertebrate activity is due to a form of tissue potential not dependent on nerve impulses though possibly subject to modification by them.

The suggestion that the isolated frog olfactory lobe may not be initiating any impulses is pertinent to another general question raised by the comparative study of brain waves. This is the problem of spontaneity. The occurrence of impulses in the absence of apparent stimulation is now known, as a result of such studies, to be a very widespread phenomenon. It has been found in every group of animals so far studied except the coelenterates and echinoderms where the possibility of its occurrence has not been ruled out. Weiss[105] has expressed the view that "instead of regarding spontaneous activity as an exceptional manifestation of cortex, respiratory center, and insect ganglia, we may have to concede it to all nerve substance," and he apparently regards its absence in many normal centers as a sort of coordination of inhibition. It is not only true of the central nervous system but of some peripheral sensory neurons, such as the lateral line (Hoagland,[60] Löwenstein and Sand[79]), the vestibule (Sand,[99] Löwenstein and Sand[80]), the cochlea (Galambos[45]), and the retina (Granit[54]). It is patently not true of all nerve cells. Is there some general significance in the fact of spontaneity? Why are certain cells active and others not? What is the phylogeny of this property of nerve cells and what are the relations between it and the special cases of closed circuit activity (Lorente de Nó[77, 78]) and pacemakers (Hoagland[60])? Does it have a basis in a threshold to a standing potential between, perhaps, axon and dendrites, so that incoming impulses, metabolic effects, and ion and drug influences act on the same mechanism (potential level, resistance of current path, threshold), so that the same mechanism would account for frequency of spontaneous firing, integration of many unsynchronized incoming impulses into fewer, rhythmic efferent impulses, and central inhibiton (Gerard,[48] Gesell,[52] Lorente de Nó,[76, 78] Bullock, Burr, and Nims[27])? What are these impulses accomplishing in the physiology of the organism? What is the rôle of spontaneous activity which does not take the form of impulses over classical nerve pathways? Such questions provide significant material for speculation and basis for experiment.

## *Summary*

This report constitutes a survey of some of the significant problems raised by our knowledge of brain waves in lower animals, together with some new records and a few speculative interpretations.

Attention is called to the lag in our understanding of the fundamental meaning and nature of spontaneous electrical activity of the brain while clinical experience with certain aspects and frequencies has accumulated. A warped perspective in our interpretations of brain waves seems inevitable. Some directions in which particularly opportune experiments await performance are suggested.

Two principal alternative points of view to be found in the literature with regard to the slow waves of the vertebrate electroencephalogram are pointed out. One assumes the waves to represent classical impulses in some form—summed cell body potentials for example. The other assumes that the waves do not represent impulses, but are some new form of nerve tissue activity involving synchronized fluctuations of state ("beating") of many cell bodies.

Some of the cogent evidence adduced by Gerard for the latter concept is reviewed. The broad significance, for practical and theoretical neurophysiology, of the idea that nerve cells can interact by other means than through established anatomical synaptic pathways is emphasized.

Reasons for expecting the comparative study of lower animals to be rewarding toward a broad, fundamental understanding of brain waves are indicated. The principal generalization that appears to be justified as a result of study of lower vertebrates is that the

telencephalon and often other parts of the brains of all vertebrates exhibit strikingly similar spontaneous electrical activity, regardless of the presence or absence of a cortex, of size, and of deafferentation or even isolation of a small fragment. This, together with other evidence, suggests that brain waves should be looked upon not as a sign of the higher aspects of nervous activity but as a reflection of some basic, primitive, common denominator of the brains of frogs and men.

Special attention is called to the fact that present knowledge of invertebrates indicates a general difference in the character of electrical activity from that of vertebrates. Records are offered representing the principal higher invertebrate groups, and the significant points of agreement among these diverse animals are stressed.

Among others these questions are raised: Why should invertebrates exhibit spikes, as of impulse action potentials, so conspicuously and vertebrates so rarely? What is the meaning of the dominance of rhythmic slow waves in vertebrates and their relatively lesser importance in invertebrates? It is noted, contrary to the impression created by some authors,[89] that slow brain waves do exist in invertebrates and not alone in the visual rhythms. The evidence from invertebrates is considered as compatible with and in some degree supporting the general idea of Gerard that the slow waves represent in large part a form of synchronized activity of nerve cell masses not dependent on nerve impulses though influenced by and influencing them.

The opportunities offered by the comparative approach for the study of these problems as well as of others, such as the evolution of spontaneous activity of nerve cells, are suggested.

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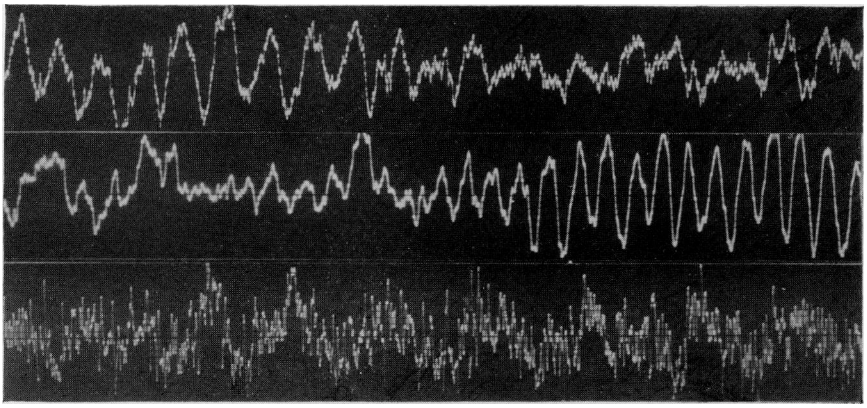


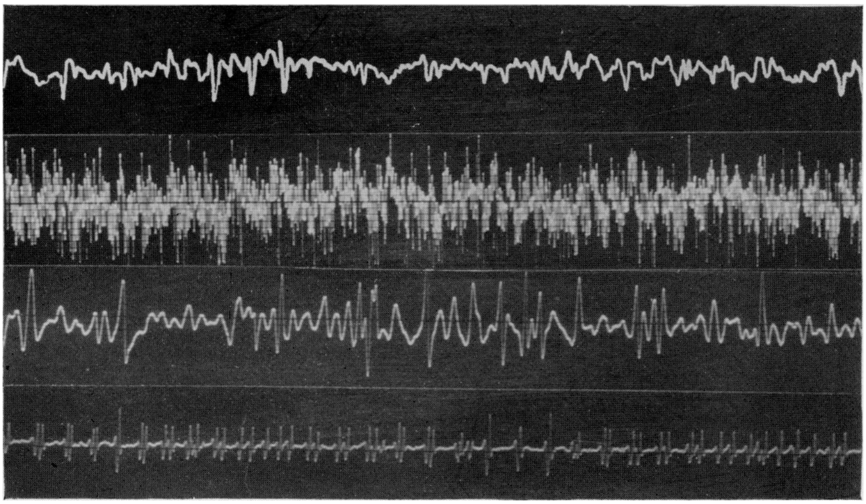
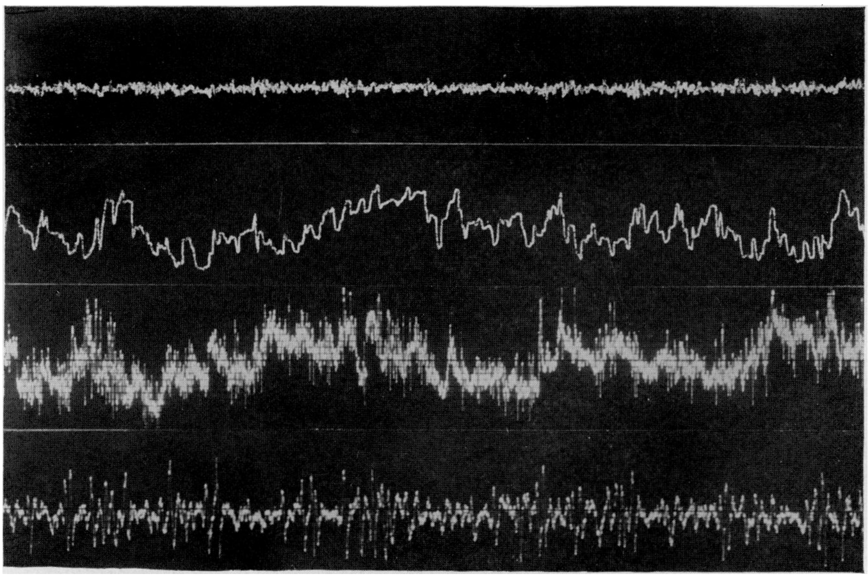


Fig. 1. (Above) Comparison of "spontaneous" electrical activity of the central nervous systems of man, lower vertebrate, and invertebrate. Upper: human brain waves; whole record = 2 seconds; roughness in the line = base line activity. Middle: isolated olfactory lobe of frog; same film speed. Lower: supra-esophagal ganglion of grasshopper, exposed in situ; film speed 4x faster, whole record = 0.5 second. All figures except indicated ink-writer records made with cathode-ray oscillograph; all except Fig. 4 with moving film. Grass amplifier, in high pass filter position ("M1" or "M0") except where noted otherwise. (Filter M represents a time constant of approximately 0.1 second and passes, without much attenuation, frequencies down to 1 cycle per second, as sine waves. The corresponding figures for filter L, used in other records, are approximately 0.5 seconds and 0.5 cps. Filter O passes frequencies up to 10,000 cps. without great attenuation, filter 1 to 2,000 cps., filter 2 to 50 cps., and filter 3 to 40 cps.)

Fig. 2. (Below) Crayfish activity. Upper: ink-writer record of anterior ventral ganglion with filter set to attenuate high frequencies ("L3") and emphasize slow waves, whole record = 5 seconds. Upper middle: cathode ray record of circumesophagal connectives, filter ("M2") reduces height of spikes in proportion to slow waves, whole record = 2 seconds. Lower middle: same, whole record = 0.23 seconds. Bottom: last abdominal ganglion, isolated, with only a few cells active (photoreceptor cells of Prosser) to show simplicity of record in comparison with anterior ganglia, same film speed as preceding.



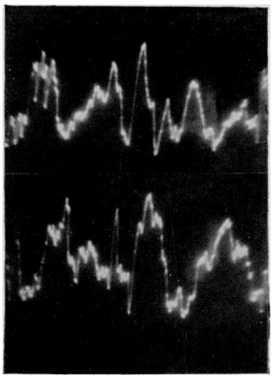
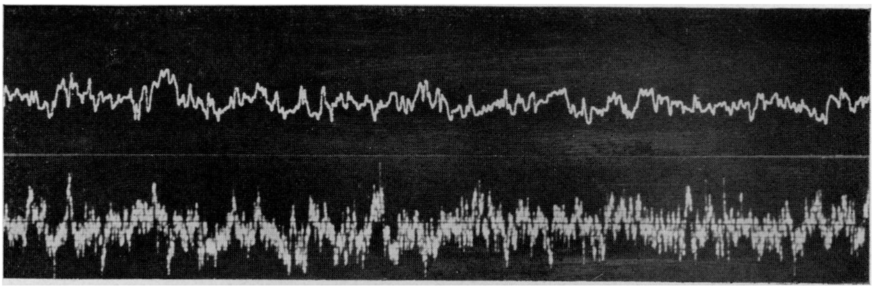
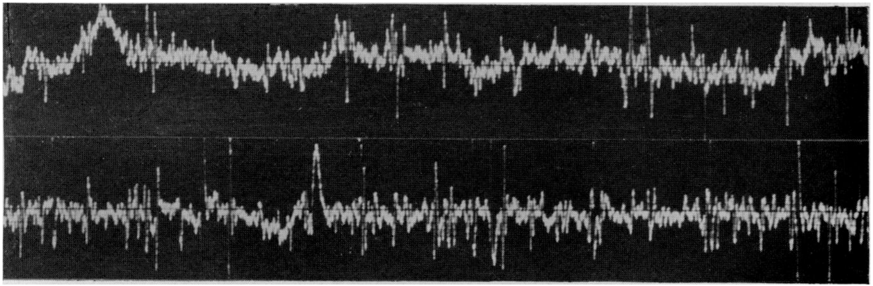


FIG. 3. (Above) *Limulus* activity. Upper: ink-writer record, both electrodes on connective between deafferented cephalothoracic ganglionic mass and first abdominal ganglion, filter ("M0") permits slow activity, if any, to show, as in next record, whole record = 5 seconds. Upper middle: same, one electrode close to cephalothoracic ganglia, filter ("M3") same as preceding wth respect to slow waves but reduces fast activity, same speed. Note greater slow activity from ganglion. Lower middle: as in preceding but filter M0, whole record = 2 seconds, cathode-ray oscillogram. Bottom: cathode-ray oscillogram like top record, showing spikes, but whole record = 0.5 second.

FIG. 4. (Below) *Polyphemus* pupa activity. Both records from isolated ventral chain ganglia, filter M0, whole record = 0.05 seconds (single sweep oscillograms).





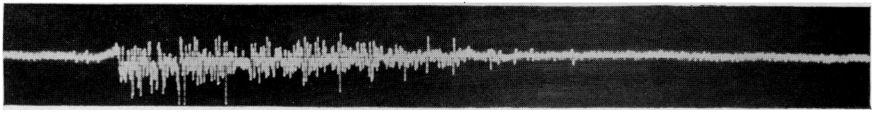


Fig. 5. (Top) Supra-esophagal ganglion activity of earthworm. Upper: ink-writer, M3, 5 seconds, to emphasize slow activity. Lower: cathode-ray, M0, 2 seconds, showing fast and slow activity.

Fig. 6. (Middle) Activity in isolated cerebral ganglion of *Ariolimax.* Records from two preparations taken similarly, filter M0, whole record = 0.5 seconds.

Fig. 7. (Bottom) Activity in cardiac ganglion of *Limulus.* This is the nervous discharge resulting in one heart beat. Note that a slow deflection is the first sign of the beat, not an impulse action spike. Note also the slow wave, on the other side of the base line, on which the first part of the impulse burst is superimposed. Filter = M0, whole record = 2.6 seconds.