17 April 1959, Volume 129, Number 3355 SCIENCE

CURRENT PROBLEMS IN RESEARCH

Neuron Doctrine and Electrophysiology

A quiet revolution has been taking place in our concepts of how the nerve cells act alone and in concert.

Theodore Holmes Bullock

The neuron doctrine, which we chiefly owe to Cajal (*1*), was unquestionably a giant stride forward in the understanding of the substratum of nervous function. It forms the basis of all modern work on the nervous system. It asserts that the nerve cell and its processes, together called the neuron, form the cellular units of the nervous system which are directly involved in nervous function; that all nerve fibers are neuronal processes; that the neuron and all its extensions develop embryologically from a single neuroblast; and that the neuron is a trophic unit, all its processes being dependent upon the nucleated cell body for their maintenance and regeneration. Although this is not inherent in the original anatomical concept, the neuron has classically come to be regarded as a functional unit, and it is here that newer information forces a reappraisal.

We can appreciate the significance of the neuron doctrine more fully by visualizing the alternative concepts historically available (*2*). In various forms, these alternatives, as formulated by Gerlach in the '70's and by Golgi, Meynert, Weigert, Held, Apathy, Bethe, and Nissl, among others, during several subsequent decades, assumed a diffuse reticulum of anastomosing dendritic and axonal processes. The "reticularists," as this heterogeneous group came to be called, were united mainly in their conviction that anatomical continuity of fibers and branches was the prevalent condition in the nervous system. But without assuming some kind of discontinuity and a useful, noncapricious lability it was extremely difficult, to say the least, to analyze, in a functionally meaningful way, pathways, connections, and the processing of discrete responses through complex centers, and this difficulty became more acute after the discovery of propagating all-or-none nerve impulses.

Early Evidence of Independent Neurons

Actually, the idea that nerve fibers are the greatly elongated extensions of nerve cells, though by no means generally accepted until after the time Harrison observed the outgrowth of processes in tissue culture (1907), had been clearly stated by workers in the first half of the last century (Kölliker, Wagner, and Remak). The individuality of the nerve cell in degenerative as well as in embryological processes was strongly indicated by the works of Forel and His in the '80's. But a convincing illustration of these principles and of the fact that *axons generally terminate among dendritic ramifications*—but freely and without forming a reticulum—awaited that scientific stellar nova, Santiago Ramon y Cajal. It is one of the ironies of history that his start and all his early work were based on the exploitation of a remarkable silver impregnation method discovered by the Italian Camillio Golgi in 1873 but virtually unknown until 14 years later when Cajal, among others (including the Norwegian Fridtjof Nansen, the future polar explorer), began to use it. Golgi shared with Cajal the Nobel prize of 1906 because of the crucial role his method had played in the 20 formative years of the neuron doctrine. But even at that date he had not given up his reticularism and regarded Cajal as an adversary. Flurries of controversy continued for years, but of all the contributions of neurohistologists none has stood the test of time as well as those of Cajal, as amazing for their quality as for their quantity (*3*).

As a subsidiary doctrine, Cajal made the brilliant inference from the anatomical arrangement of sensory, motor, and internuncial neurons that they are all *dynamically polarized,* usually in such a way that excitation can only be transmitted from the axon of one neuron to dendrites or soma of the next and, within a neuron, must normally spread from dendritic to axonal poles (Fig. 1).

Convergence of Physiology and Anatomy

The parallel strides made in electrophysiology during much of the same period, from the time of Helmholz in the middle of the last century to the period just before and after World War I, and the work especially of Keith Lucas, E. D. Adrian, Herbert Gasser, and Joseph Erlanger led to the discovery of the change in electrical potential with action which, in the single nerve fiber, came to be called the nerve impulse. This was found to be an all-or-none event of the order of 1 millisecond in duration and capable of following a preceding impulse only after a short interval. Thus, the concept of a quantum of activity or a *unit of function* came to be emphasized, and the nervous system

---

Dr. Bullock is a member of the staff of the department of zoology, University of California, Los Angeles.

came to be regarded as a kind of digital computer with a binary—that is, yes-or-no—response. Some would prefer to call it a pulse-coded device, since the intervals between pulses are graded and can introduce noise. We can now recognize four basic tenets which grew out of the impact of electrophysiology on the neuron doctrine during this classical period of the '20's and '30's (classical from the standpoint of present-day textbooks) and which still dominate much of the thinking in the field.

1) We came to think that the all-or-none impulse was synonymous with the neuron in action—that is, that the impulse together with its afterpotentials was the only form of truly nervous activity.

2) We thought that when any part of the neuron was excited this excitation spread to all parts of the neuron as a propagated nerve impulse.

3) We thought that Cajal's doctrine of the dynamic polarity of neurons meant that dendrites propagate impulses toward the cell body.

4) We have thought for many years that the secret of all labile functions must lie in the properties of a junction between neurons. This locus, called the synapse, was supposed to be the only seat of selection, evaluation, fatigue, and facilitation and perhaps of long-persistent changes as well.

Four Main Revisions

The evidence of the last few years has significantly altered all four of these tenets.

1) We now believe that the neuron is a functional unit somewhat in the same sense that a person is in society, in that it speaks with one voice at a time. At least so long as the neuron has but one output path (in terms of the textbook vertebrate neuron, one axon), it will speak with one voice at a time in the all-or-none pulsed code output essential for long-distance propagation. But we know that some neurons have two axons and can deliver two nonidentical pulse-coded outputs at the same time in different directions (*4*). More important, we believe that this pulsed form of activity—the nerve impulse or *spike*—is only characteristic of a specialized portion of the neuron, the axon, as is explained further below.

2) We now believe that the responses of many or most parts of the neuron to impinging excitation do not spread to become impulses directly but help determine the firing of impulses at some critical region such as the base of the axon—somewhat in the same manner as the impinging sights and sounds act upon the trigger finger of a man with a pistol. These responses we will call *prepotentials* or subthreshold processes, and some of them are enumerated below.

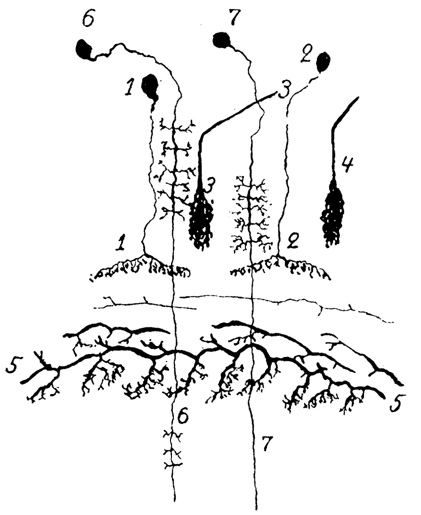


Fig. 1. Neurons of the optic ganglia (medulla externa) of a crab stained by the Golgi silver impregnation method. Since the eye is above and the brain is below, it is reasonable to assume that most transmission is downward—therefore, from terminals like 3 and 4 to upper (dendritic) processes of 6 and 7. But it is not so easy to say what direction transmission takes in the purely local neurons (1 and 2) or the coarse horizontal fibers (5). [From Hanström (*11*)]

3) We now believe that many parts of the neuron cannot respond in an all-or-none manner and therefore cannot propagate without decrement. The establishment of the conduction of the nerve impulse without decrement was one of the achievements of the '20's and early '30's but apparently applies only to a special portion of the neuron—the axon. *Decremental conduction* is probably characteristic of the great bulk of neuronal surface membrane—that is to say, the cell membrane of the extensive ramifications of dendrites making up much of the gray matter of higher animals and the neuropiles of lower. Decremental conduction requires that all such membranes be within shouting distance of the locus of spike initiation—in other words, within the distance of electrotonic spread—in order to be able to exert a physiological influence on the generation of all-or-none events by the neuron. Many dendrites are so short that we can easily believe this condition is met, but some are so long and fine that it remains seriously open to question whether they can directly influence to any significant degree the initiation of spikes by the cell or whether their main role is quite another one (Fig. 2). In this paragraph we have been traversing a no man's land from areas of more general agreement to areas of less and less agreement, and here we pass definitely into the area of personal speculation. But it has been suggested that much of the activity of dendrites has its significance in an influence upon other neurons, even though the activity is local, graded, and small in amplitude. It seems likely that brain waves are the synchronized subthreshold dendritic potentials of many neurons summed and, further, are perhaps more than a mere by-product like the noise of a car, but are a physiologically significant causal agent (*5*).

4) We now believe that labile and integrative processes, insofar as they are localizable to the single unit level, are not confined to the synapse but occur as well at other places in the sequence of events preceding the initiation of the propagated spike (*6*). There may be as many as four or five *different kinds of circumscribed loci* in various parts of the neuron, each of which is integrative in the sense that it does not pass on whatever comes to it in a one-to-one relation but exercises some labile evaluative action (Fig. 3).

These changes in viewpoint add up to a quiet but sweeping revolution. They renew the old hope that we may one day be able to explain complex behavior in terms of neurons—of their patterns and properties. In my opinion that day is still far away. But now, in contrast to a decade ago, our models do not lack degrees of freedom at the level of the physiology of the single neuron. On the contrary, the permutations of the half dozen integrative processes now known within the neuron permit so much complexity that we need rather to know what restrictions to place upon the models. However, I think we are getting closer to an explanation of one of the most basic features of the neuronal basis of behavior—namely, the mechanism of origin of *temporally patterned impulse sequences*. Such patterns are the coded commands or output of every neuron, high or low, and the problem of how the characteristic sequences within and among neurons of a group are formulated has hardly been investigated heretofore. "Characteristic" means recurrent, and if we state the problem in terms of the mechanism of formulating a meaningful pattern and then retaining or stabilizing that mechanism, we have essentially stated in one form the basic problem of the neuronal basis of instinct as well as of learning.

Capillary Ultramicroelectrode

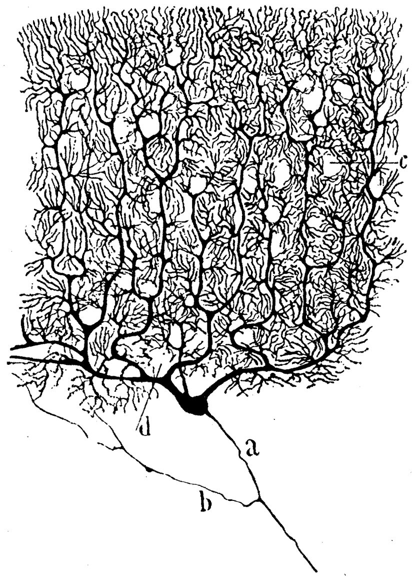
These drastic changes in viewpoint are almost entirely due to the technical advances made possible by the intracellular electrode, a device introduced by Ling and Gerard in 1949 (*7*) and perfected by a number of other workers, which makes it possible to record from inside the larger neurons many of the events that occur prior to the initiation of the all-or-none impulse, with but very slight damage. The electrode is a glass capillary tube drawn out to submicroscopic dimensions, of the order of a few tenths of a micron in outside diameter, filled with an appropriate salt solution as conductor and inserted into the cell to measure the electrical potential difference between the inside and a second electrode outside the cell.

The technique is not extraordinarily difficult, but under the best of conditions it presents problems. The electrodes are of high resistance—from several to many tens of megohms—and require special circuits for reasonable fidelity of recording of rapid events. They introduce many microvolts of noise. The capillary pipettes have to be drawn again and again to the same shape, carefully filled, and frequently replaced, for they break not only under the stress of a little connective tissue but of their own accord, presumably from internal stresses. While the tips are quite visible in air, they are beyond the limits of ordinary microscopy under water, and in most experiments the penetration is made blindly. A rather satisfactory sign that the tip has penetrated into a cell is provided by the sudden appearance of a negative potential of several score millivolts. The main limitation, however, aside from uncertainty about exactly where the tip is located, is the intolerance of small cells and processes—below about 10 microns—of even the finest electrodes thus far produced. Our knowledge is based on sampling from a rather small number of types of large neurons, and even here only from the axon, the cell body, and perhaps the bases of the larger dendrites.

Let us now look a little more closely at the major evidence for the main conclusions stated above.

Subthreshold Activity

Every neuron so far penetrated gives at least one output of all-or-none spikes, and a few have been encountered which can give two different rhythms of spikes and which have two axons or major processes going in different directions (*4*). But it would probably occasion less surprise today than ever before were someone to find a neuron which gave no all-or-none impulses but whose axon carried only graded and decrementally spreading activity. This may well be the primitive property, and it may well be retained in the many very short axoned neurons in the highest centers of both invertebrates and vertebrates. This is to say that the possibility remains with us that in the most complex and finely textured higher centers, made up largely of very small neurons, perhaps much of the normal functioning is carried out *without nerve impulses*—that is without all-or-none, propagated spikes but by means of graded and decrementally spreading activity. Perhaps the first direct demonstration that subthreshold events in one neuron can increase the activity in another neuron has recently been supplied by experiments of Watanabe and myself on the nine-celled ganglion of the lobster heart (*8*). Here, relatively long-lasting pulses of current repeatedly applied through the intracellular electrode into one of the five large anterior cells increased the pace of firing of small posterior cells many millimeters away, even when the applied currents were below threshold or were in the wrong polarity for spike production. (The internally anodal



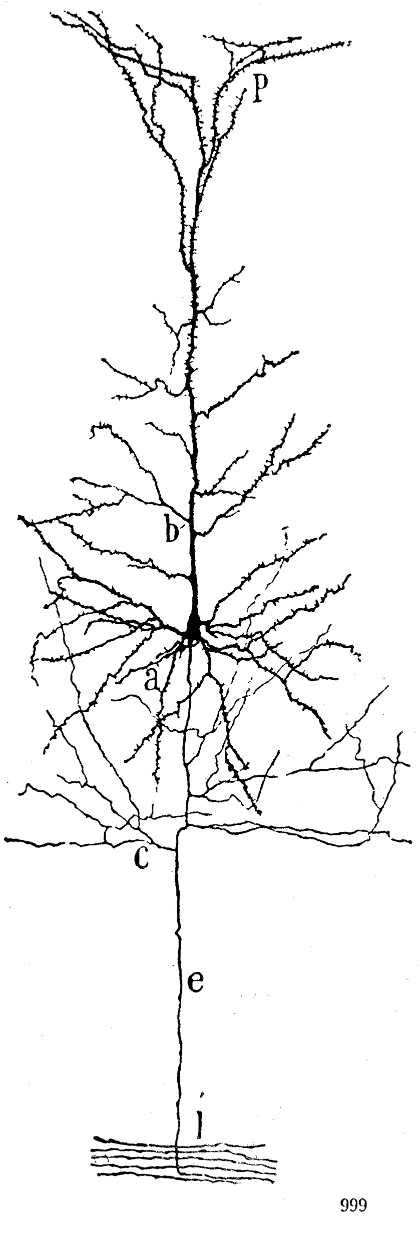


Fig. 2. (Above) Purkinje cell of the cerebellar cortex of man. (Right) Pyramidal cell of the cerebral cortex of man. Both are shown incompletely; the axon actually extends a long distance downward. (Golgi stain.) The great arborization of dendrites probably does not conduct impulses, and even electrotonic influence from the farthest ones must be very weak in the spike-initiating region, be that soma, or base of the larger dendrites, or axon. [From Cajal, *Histologie du Système Nerveux de l'Homme et des Vertébrés* (*12*)]

stimuli caused the distant small cells to tend to fire during the long pulse, while the internally cathodal currents caused the small cells to tend to fire their impulses just after termination of the current.) These effects, obtained without the intervention of nerve impulses, are not due to escape of current but occur only if the stimulated cell is penetrated.

The Several Forms of Activity

Like the multiplication of the fundamental particles of physics, the known forms of activity of nerve cells have multiplied from a single one—the all-or-none impulse or spike—which was all that was known up to 1938. In that year Hodgkin, using the giant fiber of the squid, and very soon thereafter Katz, using the sciatic nerve of the frog, discovered the local potential, which can be graded and which spreads essentially passively—"electrotonically"—declining to half amplitude about every millimeter. Later work has shown several more kinds, the exact number depending on the distinctions one wishes to make.

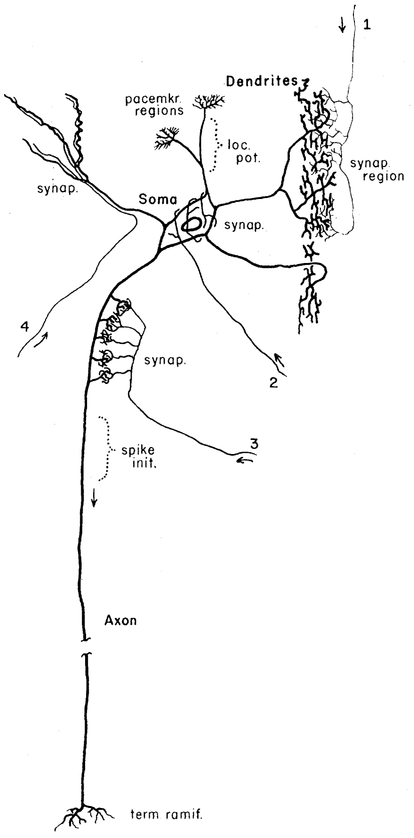


Fig. 3. Schematic representation of a neuron from the cardiac ganglion of a crab. There are several presynaptic pathways converging from diverse sources—inhibiting, exciting (other followers and pacemakers), accelerating (1, 2, 3, 4). These produce synaptic potentials in their several special loci. Restricted regions also initiate spontaneous activity ("pacemaker" regions, shown purely diagrammatically); local potentials (only labeled in one place but perhaps repeated elsewhere); and propagated impulses ("spike init.," also located arbitrarily). Only the axon supports all-or-none activity. Terminal ramifications are presumed to act by graded, local potentials. Integration occurs at each of the sites of confluence or transition from one event to the next. [Modified from Alexandrowicz (*13*)]

The scheme proposed in Fig. 4 indicates the relations between most of these. The first two, the *spike* potential and the *local* potential, are regarded as responses to antecedent activity within the same cell (when physiologically activated, not artificially stimulated); both are mediated by the local electric currents across the membrane as the result of the change in resistance of the already active regions and the standing "batteries" or electromotive forces between the two sides of the membrane. The one is regenerative, all-or-none, and propagated; the other is graded and decremental. In contrast, *generator* potentials of receptor neurons and *synaptic* potentials are responses of cells to impinging external events of specific kinds—sensory stimuli and junctional transmitters. There are two subdivisions of each of these categories based on the polarity of the response. On the basis of other differences, further subdivisions can be defined. There are also prepotentials resulting from no impinging environmental change but occurring under normal steady-state conditions and therefore properly called *spontaneous.* These can be manifested in more than one form: one is more or less sinusoidal (the time course is relatively independent of the occurrence of spikes); another is more or less saw-tooth-like (the time course is dependent on the intervention of a spike or local potential to reset the starting condition; a relaxation oscillation).

It is highly probable that some if not all of these different kinds of activity represent specialized kinds of cell surface membranes (*9*). This is suggested by the striking differences in properties and by the localization of each of these processes to restricted regions of the neuron. The circumscribed loci may recur at more than one site on the surface of a given neuron. Any one of the prepotentials is probably capable of causing spike initiation, at the restricted locus where this occurs, but commonly two or more prepotentials will act in sequence to this end. Perhaps any of the potentials can interact with any of the others to alter its rate of development or amplitude. But besides these sources of complexity a still more important source may prove to be the anatomical distribution of these different kinds of cell membrane over the neuron, their spatial separation, and the possibilities of interaction, of attenuation, and of invasion by the explosive all-or-none spike process. Only some regions of the cell are capable of supporting such a process, and perhaps it is just those which cannot support it that are most integrative.

Changes of State Not Visible in Potential

But this does not exhaust the list of separate processes within the neuron which contribute to the determination of firing. Besides the processes reflected in the membrane potential, there are others whose occurrence may give no sign in the membrane potential.

For example, many junctions manifest the property known as *facilitation.* This means that successively arriving impulses in the presynaptic pathway cause larger and larger synaptic potentials in the postsynaptic neuron. The excitability of the postsynaptic membrane may be said to have increased—although there may be no change whatever in the level of membrane potential after one synaptic potential has passed off and before the next has begun—from the corresponding level at an earlier stage, when the excitability was lower. Another junction upon the same neuron may under the same conditions manifest the opposite property, which may be called *diminution;* that is to say, successive responses are smaller (Fig. 5).

Aftereffects provide still other indications of differences in excitability not predictable from the membrane potential. Some cells under certain conditions continue to fire for a considerable time after the input has ceased; others show the opposite response—namely, a prompt rebound or overshooting return after input has ceased. Thus, if the response to the input is an increase in the level of activity, then there may occur after the cessation of this input a continued afterdischarge—a maintained high level of activity for some time; or there may occur a rebound, which would mean in this case a period of decreased activity even below the previous background level. If on the other hand, the given input has for its effect an inhibition of ongoing activity, upon its cessation there may continue for a period an afterinhibition, or there may occur a rebound increase in activity above the previous ongoing level.

Whereas the classical concept of the neuron has recognized the importance of excitability, this has been measured or thought of in terms of the spike threshold. The spike threshold is certainly important, although only at one point in the neuron—namely, the point where spikes are initiated. After this initiation has occurred, the spike excitability elsewhere is relatively unimportant, because the margin of safety is usually quite large for the activation of each successive point along the axon. What the newer knowledge has added is understanding that prior to initiation of the spike there are critical forms of excitability not measured by thresholds, because they determine the responses of subthreshold, graded and local events as a function of what came before them.

Spontaneity

Still further increasing the complexity of the combination of processes possible is the tendency to spontaneous activity in some neurons. By means of penetrating microelectrodes, spontaneity has now been examined from within in a number of cells—central neurons, receptors, and pacemakers of the heart. The observed voltages are enormously greater than in the usual arrangement of two electrodes outside the cell shunted by extracellular fluids, and this has permitted new insight into the intimate events that occur prior to each spontaneous discharge.

As a consequence, we can see the *continual change of state* at the subthreshold level, at least insofar as it is reflected in the potential of the cell body and nearby cell membrane (Fig. 6). We can infer also from the observations that the tendency to spontaneous change of state inheres in certain restricted regions of the neuron (the pacemaker loci), which influence the rest in turn indirectly. Furthermore, there is evidence that, at least in some neurons, more than one locus of spontaneity can exist at the same time in different parts of the cell, each with a different rate of change of state. The continual change of state of parts of the neuron under steady conditions of its environment may have significance not only in generating spontaneous activity but also in altering the responsiveness of the cell to any input impinging upon it. In addition, the spontaneous subthreshold potential changes of one neuron may influence other neurons, perhaps by electrotonic spread over short processes and perhaps by less specific mass field effects —for example, when many cells "beat" in unison, as in brain waves (*10*).

Conclusion

In sum, anatomically the neuron doctrine has never been more firm. The classical controversy gradually focused upon the issue of protoplasmic or neurofibrillar continuity between neurons. Today, while a number of exceptional cases of nerve cell syncytia are commonly ac-

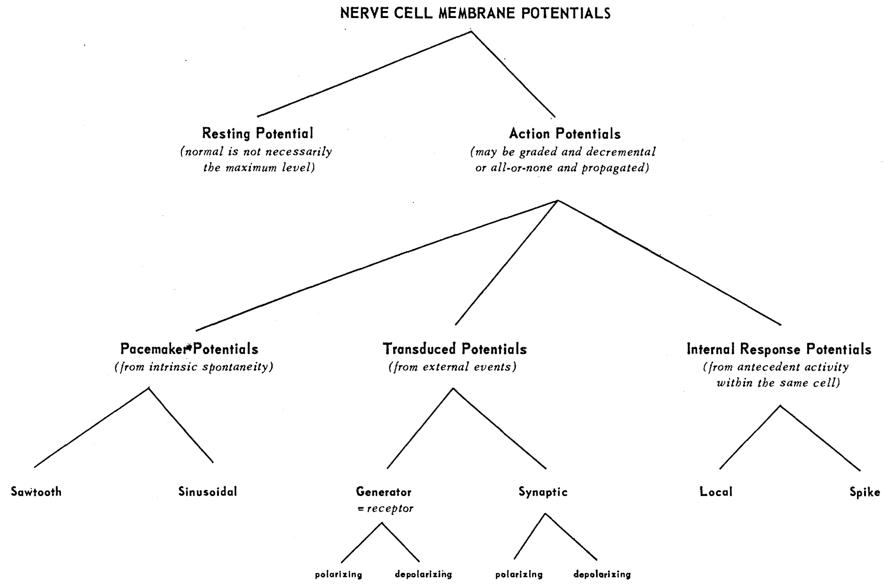


Fig. 4. The types of nerve cell membrane potentials.

Fig. 5. Facilitation and diminution. An ultramicroelectrode inside a nerve cell (of the cardiac ganglion of a lobster) recorded first the synaptic potentials resulting from a burst of five arriving impulses from one presynaptic pathway (from posterior small cells) and then those responding to a series of impulses arriving in another pathway (from the central nervous system). The former responses show diminution—the amplitude declines; the latter show facilitation—the amplitude grows. (Calibration, 100 msec, 21 mv.) [Courtesy of Dr. Carlo Terzuolo]

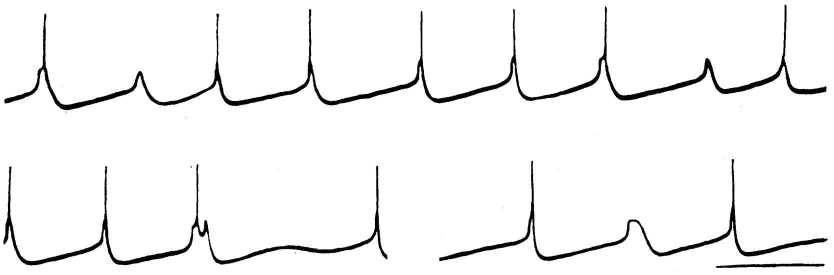


Fig. 6. Spontaneous activity in a ganglion cell as revealed by an electrode inside the soma (nerve cell body). The spikes are about 10 mv here (electrotonically spread from the axon) and are followed by a repolarization, then a gradual depolarization—the pacemaker potential, which at a critical level sets off a local potential. This, in turn, usually rises high enough to trigger a spike but is seen here several times by itself. Once (in the first half of the bottom row) the local potential fails to be set off. (Time, 0.5 second.) [Courtesy of Dr. Carlo Terzuolo]

cepted (for example, giant fibers of earthworm and squid), the weight of evidence from silver impregnation and, especially in recent years, from electron microscopy is against any such continuity. Physiologically, however, we have a new appreciation of the complexity-within-unity of the neuron. Like a person, it is truly a functional unit, but it is composed of parts of very different function not only with respect to metabolism and maintenance but also in the realms of processing diverse input and determining output—that is, of integration. The impulse is not the only form of nerve cell activity; excitation of one part of the neuron does not necessarily involve the whole neuron; many dendrites may not propagate impulses at all; and the synapse is not the only locus of selection, evaluation, fatigue, and persistent change. Several forms of graded activity—for example, pacemaker, synaptic, and local potentials—each confined to a circumscribed region or repeating regions of the neuron, can separately or sequentially integrate arriving events, with the history and milieu, to determine output in the restricted region where spikes are initiated. The size, number, and distribution over the neuron of these functionally differentiated regions and the labile coupling functions between the successive processes that eventually determine what information is transferred to the next neuron provide an enormous range of possible complexity within this single cellular unit.

In the face of this gradual but sweeping change in functional concepts, any statement but the most diffuse about expectations for the future must be very dangerous. Nevertheless I will venture to suggest that in the near future we will gain significant new insight at this unitary level of neurophysiology with respect to the functions and differentiations among dendrites, the chemical and perhaps ultramicroscopic specification of different kinds of surface membrane, additional labile processes, sites of possible persistent change, and the normal functional significance of intercellular reactions mediated by graded activity without the intervention of all-or-none impulses.

References and Notes

1. S. Ramon y Cajal, *Neuron Theory or Reticular Theory?* (Consejo Superior de Investigaciones Cientificas, Madrid, 1954), English translation.
2. A. T. Rasmussen, *Some Trends in Neuroanatomy* (Brown, Dubuque, Iowa, 1947).
3. For a complete bibliography, see S. Ramon y Cajal, *Recollections of My Life*; English translation by E. H. Craigie, *Mem. Am. Phil. Soc.* 8 (1937).
4. T. H. Bullock and C. A. Terzuolo, *J. Physiol. (London)* 138, 341 (1957).
5. F. Bremer, *Physiol. Revs.* 38, 357 (1958).
6. T. H. Bullock, *Revs. Modern Phys.*, in press; *Exptl. Cell Research* 5, suppl. 323 (1958).
7. G. Ling and R. W. Gerard, *J. Cellular Comp. Physiol.* 34, 383 (1949).
8. The study by Watanabe and Bullock was aided by a grant from the National Institute of Neurological Diseases and Blindness, National Institutes of Health, and by a contract (NR 101-454) between the Office of Naval Research, Department of the Navy, and the University of California.
9. H. Grundfest, *Physiol. Revs.* 37, 337 (1957).
10. See further: *Ciba Foundation Symposium, Neurological Basis of Behavior* (Churchill, London, 1958); J. C. Eccles, *The Physiology of Nerve Cells* (Johns Hopkins Press, Baltimore, Md., 1957); H. Fernandez-Moran and R. Brown, *Exptl. Cell Research* 5, suppl. (1958); A. Fessard, *Proc. Intern. Physiol. Congr. 20th Congr. Brussels* (1956).
11. B. Hanström, *Arkiv. Zool.* 16, 10 (1924).
12. S. Ramon y Cajal, *Histologie du Système Nerveux de l'Homme et des Vertébrés* (Maloine, Paris, 1909–11).
13. J. S. Alexandrowicz, *Quart J. Microscop. Sci.* 75, 182 (1932).

CURRENT PROBLEMS IN RESEARCH

Rock Magnetism

The magnetization of ancient rocks bears on the questions of polar wandering and continental drift.

S. K. Runcorn

Polar wandering, as a geological hypothesis, seems to have been first mentioned in correspondence between Halley and Hooke. It is interesting that it was then invoked as an explanation of the occurrence of marine fossils in sedimentary rocks well above sea level! In the early days of geology, Buffon and the "catastrophic school" were advocates of the shifting pole hypothesis as an essential element in the evolution of the earth's crust. Apparently Francis Bacon first suggested that continental drift had occurred when he noticed the similarity of the Atlantic coast lines of South Africa and South America.

Wegener gave the first thorough discussion of these hypotheses, opening a lively geological and geophysical discussion which reached its height in the 1920's. Of late, these important hypotheses have been discounted, partly because the geological data were complicated and by no means conclusively in favor of them and partly for the less legitimate reason that a tenable explanation of the supposed phenomena had not been put forward. Darwin's famous paper on polar wandering was thought to have disposed of the possibility. The suggested explanations of continental drift were shown by Jeffreys and others to be incompatible with the inferences successfully drawn by geophysists on the strength of the earth's interior. Yet Wegener's book, though dated, makes a strong case for continental drift. Later writers, such as Du Toit, amassed a great deal of information from structural geology and paleontology which, by its nature, could hardly appear decisive to the scientists in other fields and which perhaps unintentionally obscures some of the simpler and very persuasive reasons for serious consideration of continental drift. Moreover, these arguments are essentially qualitative, and their various presuppositions are open to criticism. They were therefore, perhaps unfortunately, not widely considered.

Recently, renewed interest in the problem of polar wandering and continental drift has resulted from paleomagnetic measurements. The directions of the permanent magnetization of certain sedimentary and igneous rocks of many ages from various parts of the world have now been determined. Most of the rocks studied have been well-bedded red sandstones

---

Dr. Runcorn is director of the department of physics, King's College, University of Durham, Newcastle upon Tyne, England.