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5

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I feel that my first word must be one of apology for presuming to address you upon the nature of neural processes in the presence of those who can speak on this topic with far more authority than will attach to any remarks of mine.

But, although I can no longer claim to be a professional physiologist, the subject is one to which I have devoted a good deal of thought, approaching it from the point of view of the needs and the problems of the psychologist.

In a series of papers published in *Mind* and in *Brain*, the first of which was written nearly ten years ago, I have propounded, and sought to justify, certain views of the nature of neural processes which in some important respects differ from those more generally accepted by physiologists.

I shall not have time to put before you the whole working scheme, but must confine myself to the exposition of its more fundamental features; i. e. I must deal principally with the nature of nervous excitation and conduction, and must be content to say very little about those more complex nervous functions which Prof. Sherrington, in the volume just published, has so well described as the *integrative functions of the nervous system.* I would, however, say at once that it is the consideration of these integrative functions which, as it seems to me, compels us to regard the more generally accepted views on excitation and conduction as inadequate, and on which the views I am about to put before you in the main depend for support and justification.

I shall not attempt to define the views most commonly held, the more orthodox views, because most of you are no doubt familiar enough with them. I think I may accept as a fair representation of the views most usually put forward the paper of Prof. Marc Verworn, entitled 'Die Vorgänge in den Elementen des Nervensystems,' published in the *Zeitschrift für allgemeine Physiologie* of this year as a *Sammelreferat*. I will merely point out as I go along those features of the scheme I propose in which it differs most markedly from the more generally accepted views, taking Prof. Verworn's view as a type.

First, I would lay claim on behalf of the neurologist to a certain freedom of speculation in treating of the processes of the nervous system. I mean that in forming his hypotheses he should not feel himself bound to give his hypothetical explanations or accounts of neural processes, in terms only of those forms of physical and chemical change which are the familiar concepts of the physicist and the chemist. Let me illustrate my meaning by reminding you of the fact that a number of acute minds among the physiologists, have for some years been striving to show that the conduction of the nervous impulse may be regarded as essentially a process of electrical conduction, such as takes place in a telegraph wire or an electrolytic solution, the process being modified and complicated by the peculiar condition obtaining in the animal body. Now I do not for a moment mean to imply that such attempts ought not to be made. I think it is very important that they should be made, and I wish them all success. But I do not think that it is necessary or desirable that we should await the issue of these attempts before going on to formulate our working hypotheses of neural action. I think biologists are too apt to accept the current conceptions and theories of physics and chemistry as final and unalterable truths, and that by so doing they limit the possibilities of advance in their own territory.

I hold that the biologist should constantly bear in mind that these conceptions of the physicist and chemist have not attained any final and complete form, and that they are in process of change and evolution. This has been rendered very obvious by the recent great discoveries of physicists, the wonders of which are in all men's mouths.

At the present moment the arbitrary theories of transmission of energy seem to be severely shaken, and threatened with a resurrection of their old enemy, the emission theory in a modified form.

Even the distinction between matter and energy seems to have become strangely uncertain and vague, and the attacks of the *Energetikers* led by Prof. Ostwald seem to threaten to destroy matter itself, and to leave us with various forms and collocations of energy only as our basal working conceptions.

It may well be then that the current conceptions of physics are still inadequate, and perhaps for many years to come will be inadequate, for dealing with all the processes of the animal body, especially with the processes of the nervous system which we have reason to regard as the most highly evolved and complex of all material processes.

It may be, e.g., that we shall have to recognize as playing their part in the animal body forms of energy that have not been met with, and perhaps never can be met with outside such bodies, and, in fact, I think we may infer with some confidence that this is the case.

Physiologists should, I think, always bear in mind the great part played by the observations of Galvani, a physiologist, on the legs of a frog, in promoting the growth of the physicists' knowledge of electrical processes, of the galvanic current in particular; and should be emboldened by this example to formulate their hypotheses with some independence.

After these preliminary remarks I will plunge into the midst of my subject, and outline the scheme I have in mind. And first as to the processes within the vital unit the neurone. The substance of the neurone, I hold, is excitable, and capable of conduction of excitement in all its parts, cell-body, dendrons, and axis cylinder process alike. I submit that we have no adequate ground for believing that in regard to these, the essential and specific functions of the nervous tissue, there is any differentiation of the parts of any one neurone; i.e. I suggest that the parts are all excitable and all conduct or transmit the excitement in essentially the same way.

There you have one departure from what is, I think, still the orthodox view, namely that the cell-body plays some very special rôle, beyond its trophic functions, in initiating, augmenting, depressing, or directing the impulse. In this respect the view I advocate carries to its extreme the reaction against the old-fashioned view that the cell-body, or ganglion-cell as it used to be called, is or contains an homunculus endowed with intelligence, choice, and free will, a view which has suffered many severe blows, as, e.g., when Dr. Gaskell showed that the rhythmic beat of the heart is not originated in the nerve-cells, but is independently originated in the muscle-substance.

Now as to the nature of the processes. The view which I am putting before you, and which for the sake of brevity I will speak of as my view—with apologies to any who may have arrived at similar views independently—assumes that on stimulation of any part of the neurone, there takes place in the substance of that part a more or less explosive decomposition of highly complex, unstable molecules rich in potential energy, and that energy of some form is liberated, converted from the chemical potential form to an active form. The most essential part of my view is that the energy thus liberated is not bound down to the place or the substance in which it is thus liberated, but tends like other forms of free energy, like heat and electricity, to diffuse itself through whatever substance is capable of conducting it, flowing from any place of higher potential to all places of lower potential. That is, it diffuses itself evenly through the substance of the neurone from whatever point may be excited. As to the nature of this liberated energy, I do not think we need feel bound to show that this liberated energy is identical in character with electricity, or any other form of energy known outside the body, before we accept its existence. I think we may with advantage attempt to describe it in terms of its own behaviour, allowing our expectations to be guided by our knowledge of those forms of energy with which it seems most nearly analogous.

This conception of the charging of the excited neurone with liberated energy is the central feature of my view. It is, I think, very important clearly to distinguish this liberated energy from the store of potential chemical energy resident in every part of the resting neurone. Hence it is important to have a name for the fixation of this concept, and I have proposed to call it neurin (perhaps unfortunately, in view of the fact that neurine is already the name of one of the waste products of nervous activity). However, I may continue to use this convenient name for this evening at least.

This conception enables us, it seems to me, to give satisfactory explanation of several fundamental facts, for which the current views do not adequately account.

It gives us an insight into the way one neurone plays upon another. We know that there is what is called lost time in the transmission of excitement through a chain of two or more neurones, i.e. that the transmission occupies a considerably longer time than does the passage of the impulse through a nerve-fibre of the same length as the chain of neurones.

There are many good reasons for regarding the synapse, i.e. the place of junction of two neurones, as a place where the process of transmission meets with some special resistance, and that it is at this point that the loss of time is determined.

According to my view, the charge of free energy, or neurin, in the stimulated neurone must reach a certain potential before it can overcome this resistance, and when this potential is reached neurin escapes across the synapse in a rapid series of discharges, each of which acts as a stimulus upon the neurone into which the discharge takes place.

If one neurone thus acts upon another by discharging into it its free energy, what is the process by which the excitement spreads along the length of any one neurone? I suggest that this is not merely the diffusion of the neurin along the length of the neurone, but that in addition to this the explosive decomposition initiated at the spot at which the stimulus is applied, tends to propagate itself through the substance of the neurone from molecule to molecule, much as the chemical change propagates itself when a train of gunpowder is fired.

This has long been considered probable by many physiologists, and the recent demonstration, by Verworn and his pupils, of the fact that a chemical change accompanies the transmission of the impulse in the neurone seems to put this view in a very strong position. Now one special advantage of my view as applied to the processes within the neurone, is that the separation of the process of diffusion and discharge of neurin from the process of transmission of the impulse along the length of the neurone, enables us to explain one of the most important features of nervous processes that has long been a mystery. I mean the fact that stimulation of a sensory nerve produces an amount of change, which, as measured by the effects in consciousness as sensation, e.g. the energy of muscular response, is proportional to the intensity of the stimulus. This quantitative relation between intensity of stimulus and its effects in the nervous system is quite unlike what we observe in the case of all explosive decompositions in inorganic substances; e.g. the train of gunpowder when fired undergoes the same amount of change, namely the maximal amount, whether the stimulus, the spark, applied to it be large or small, very intense or only just intense enough to initiate the change. The change is on the all-or-nothing principle, and if the change in the nervous substance is also an explosive decomposition, it seems that it must necessarily take place in the same way, i.e. that in all the substance, in all that part of the neurone, in which the metabolic change occurs, the maximal amount of change should occur.

My suggestion here is that the nervous substance does conform to the all-or-nothing principle, but that this metabolic change propagates itself through a longer or shorter stretch of the neurone according to the intensity of the stimulus, that is to say, a maximal stimulus applied to an extremity of a neurone causes the change to propagate itself throughout the length of the neurone with liberation of the maximal amount of neurin—while the change initiated by a very feeble, a minimal stimulus, remains confined to the part to which the stimulus is applied with liberation of a minimal amount of neurin, while each stimulus of medium strength initiates a change which propagates itself through a corresponding length of the neurone.

Here another difficulty arises—If the change is of the all-or-nothing type in each part, why does it not propagate itself equally far, no matter how feeble the stimulus? I suggest that this is a matter of quantity of change in unit of time. Even though the change be of the all-or-nothing type it may spread better with a strong stimulus, because at the spot stimulated a greater quantity of substance undergoes the change in the moment of stimulation, in unit of time. Perhaps a train of damp gunpowder affords an analogy. A large amount of heat is applied, and many molecules are exploded in the first moment that the change propagates itself far, whereas when a small spark is applied the explosion dies down, the quantity of change in each unit of time becoming less and less until there is no longer sufficient heat liberated in unit of time to maintain the propagation of the process.

According to my view then, the explosive decomposition propagates itself through the length of the neurone to a distance proportional to the intensity of the stimulus, and thus, although throughout the part of the neurone in which this change takes place it is of the all-or-nothing type, yet the effects in the brain, or on a muscle, of a sensory stimulus, are proportional to the intensity of the stimulus, because the amount of neurin liberated in the sensory neurone and discharged into the high level neurones, or the motor neurones, is proportional to the length of the part affected. It must be proportional to the amount of nervous substance implicated in the metabolic process, and therefore proportional to the length of the part of the sensory neurone through which the process propagates itself.

Now let us consider very briefly two or three other facts which can be well explained in terms of this hypothesis, and hardly at all in terms of the more widely current views.

The summation of subminimal or subliminal stimuli. A stimulus to a sensory nerve too feeble to excite a reflex action or sensation may do so if repeated at brief intervals. On my view this is because the subminimal stimulus liberates a quantity of neurin which is insufficient to raise the potential of the charge in the neurone to discharging point, to such a degree that it may overcome the resistance of the synapse and discharge across it into other neurones. Each repetition of the stimulus then adds to the potential of charge until it suffices to overcome the synapse-resistance.

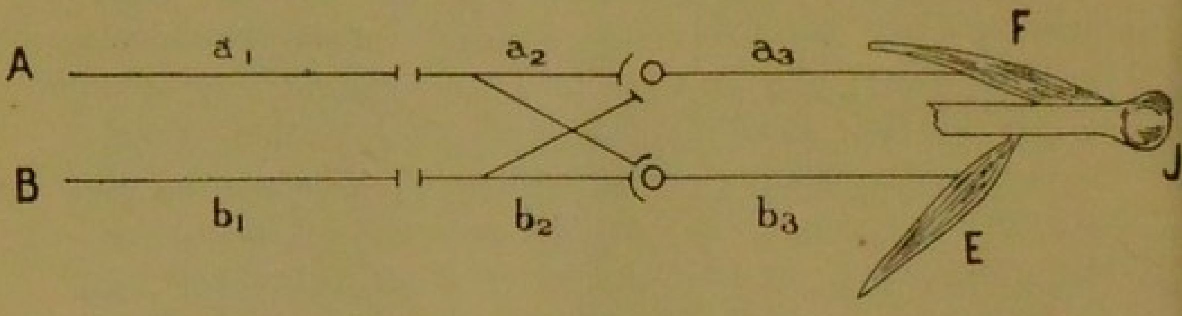
The temporary *facilitation* of the passage of the nervous excitement through a nerve-path, which the Germans (Exner) call *Bahnung*, and which must be carefully distinguished from canalisation (or *Ausschleifung*), the more permanent opening of a pathway resulting from the passage of the excitement; this facilitation is to be regarded as essentially similar to the process of summation of stimuli. It consists in a partial charging of some neurone or group of neurones, so that a smaller stimulus or increase of charge of neurin suffices to bring up its potential to the discharging point.

There are many facts which indicate that any nerve tract that has been active remains for some little time in such a condition that it is more readily thrown into activity again by a new stimulus, than when it is in a resting condition. I need not enumerate these indications. I will only point out that they are especially abundant when one considers the brain processes concerned in such mental operations as association and the reproduction of past impressions or presentations.

This slowly waning condition of increased readiness for action following upon activity of a nerve-tract cannot easily be explained in terms of the current views, while it is exactly what must be expected if my view is adopted. Each neurone must retain some part of the charge of free energy which it acquires under stimulation, so much namely as constitutes a charge of potential just insufficient to overcome the resistance of the synapse, a *residual* charge which may be supposed to leak slowly away if no fresh stimulus comes. Again, there are many facts which indicate that the neurin liberated by chemical changes in one neurone or group of neurones is passed on to other neurones; that the liberated energy does actually flow from the places where it is liberated to other parts of the nervous system, just as the electrical energy set free in a number of chemical cells will flow along conductors to any place at which it is required to undergo transformation into light or heat or molar movement of matter.

Take this fact:—under strong excitement, or by a great effort of will, one can produce a contraction of a group of muscles far stronger than can be produced by way of a simple reflex process, and the force of a maximal voluntary effort seems to vary directly with the degree of general or diffused excitement of the brain. In this case we seem compelled to believe that the energy liberated in a very large number of neurones of the brain is converged upon or flows into the appropriate motor channel, so that the neurones forming this channel transmit much larger quantities of energy than can be directly generated in them.

There are many other facts and considerations which support this view, the view of the vicarious functioning or usage of neurin; i. e. the view that energy liberated in one neurone may be transmitted to, and co-operate in producing effects in, other neurones, and that the efferent neurones especially transmit as stimulus to the muscles, not only the energy liberated by their own metabolic processes, but also serve as conductors for abundant streams of energy liberated in the sensory neurones and in the brain. The last piece of evidence in favour of my view that I will put before you is of an indirect character, but nevertheless, to my mind at least, is very strong. It is that it enables us to form a satisfactory hypothesis as to the nature of inhibitory processes in the nervous system—this is what I have called the *hypothesis of inhibition by drainage.* It assumes that inhibition consists always in a diversion or switching off of a current of energy into some other channel, which is in some way rendered a path of lower resistance; e. g. let A and B be two sensory motor arcs in relation of reciprocal inhibition in enervating the flexor muscles F and the extensor muscles E at the joint J, respectively. Let us imagine them to be connected in the manner indicated in the diagram—



If a feeble stimulus be continuously applied to a_1 it keeps the flexors in a state of tonic contraction. If then a strong stimulus is applied to b_1 the extensors are thrown into contraction, and the flexors relax or are inhibited. We know that this inhibition of F is not brought about by any inhibitory impulse sent down a_3, but consists in the cutting short of the stream of impulses passing down a_3 to maintain the tonus of F.

I suggest that this cutting off of the stream of impulses in a_3 is effected by a diversion of that stream to b_3, the resistance of the synapse b_2—b_3 being reduced by the charging of the neurones b_2 and b_3 to a lower point than the resistance of the synapse a_2—a_3.

Again, if stimuli of moderate strength are continuously applied to both a_1 and b_1, the effect, as Prof. Sherrington has shown, is commonly an alternation of contractions of the flexors and extensors, each being relaxed or inhibited while the other contracts. This alternation is, I suggest, determined by synaptic fatigue. Suppose F to contract first while E remains relaxed,—that means, in terms of the drainage hypothesis of inhibition, that the energy liberated in both a_1 and b_1 is discharged through synapse a_2—a_3. There are many good reasons for believing that the synapse is liable to a fatigue which rapidly comes on and rapidly passes away again, and which expresses itself as a rise of the resistance of the synapse. If that is the case the resistance of synapse a_2—a_3 must very soon increase to such a point that b_2—b_3 becomes the channel of less resistance; both streams of energy, from a_1 and b_1, will then be diverted to b_3, and the flexors will relax while the extensors contract. And this will continue to be the case until increasing fatigue of synapse b_2—b_3 and recovery of synapse a_2—a_3 render a_2—a_3 once more the path of less resistance.

In support of this hypothesis of inhibition by drainage I have produced some positive experimental evidence, and I have also tried to show—

(1) that it explains well all the varieties of inhibition observable or inferrible in the central nervous system, from the spinal cord to the highest levels of the brain;

(2) that no other hypothesis of the nature of inhibition is adequate for the explanation of all the varieties of inhibitory phenomena in the central nervous system.

This involves a long critical argument, which I cannot attempt to put before you in this brief space of time. This inhibitory hypothesis is based upon the assumption of the truth of the view of the nature of the processes within the neurone, which this evening I have spoken of as my view, and therefore, in so far as it proves a satisfactory hypothesis, it strongly supports that view.

In conclusion I would point out that the view I propose makes of the neurone a thoroughly physiological conception, not a merely anatomical conception as it still remains for most authors.

Its chief merit in my eyes is that it provides for the explanation of the processes, which constitute our mental life, a far more satisfactory physiological basis than the more generally accepted views. If time permitted I might go on to show you how well it lends itself to the explanation of the processes of perception, of the formation of the dispositions which are the psychical basis of memory, of the formation of associations, of the reproduction of presentations, and of many of the peculiarities of the spontaneous attention-process.

But I will spare you all this, and will conclude by insisting upon the fact, one which I think some physiologists are liable to forget, that all the immense labours devoted to the elucidation of the nervous processes must aim at, and must find their chief justification in the elucidation of *mental process.*