THE BASIS OF SENSATION

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The Action of the Sense Organs

By

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"*Nihil est in intellectu, quod non prius fuit in sensu: nisi ipse intellectus*"

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PREFACE

"THE Basis of Sensation" may seem an ambitious title to a book which makes very little reference to metaphysics or even to psychology. But although it is concerned with such material things as nervous impulses and electric recording instruments, I do not feel that its title really needs an apology. Sensation is aroused by the messages which are transmitted through the nerves from the sense organs to the brain, and this is a description of the nature of the sensory message and the way in which it can be recorded and analysed. It turns out that the messages from our sense organs are all made up of a common vocabulary of the simplest kind. They consist of a series of brief impulses in each nerve fibre; all the impulses are very much alike, whether the message is destined to arouse the sensation of light, of touch, or of pain; if they are crowded closely together the sensation is intense, if they are separated by long intervals the sensation is correspondingly feeble.

To make the account intelligible it has been necessary to say something about the general structure of nerve fibres and sense organs, and in Chapter III some time is spent on a rather theoretical discussion of the formation of the message by the sense organ. The rest is mainly a description of experimental work which has occupied the past two years and is still in progress; I have not tried to give a review of the physiology of the sense organs and little mention has been made of work on other lines. Fortunately there is an admirable excuse for this in the recent publication of Sir John Parsons' *Introduction to the Theory of Perception.*

The final chapter deals briefly and timidly with the relation between the message in the sensory nerve and the sensation aroused in our consciousness; briefly because the relation is simple enough in a way, and timidly because the whole problem of the connection between the brain and the mind is as puzzling to the physiologist as it is to the philosopher. Perhaps some drastic revision of our systems of knowledge will explain how a pattern of nervous impulses can cause a thought, or show that the two events are really the same thing looked at from a different point of view. If such a revision is made I can only hope that I may be able to understand it.

Finally my thanks are due to the University of London for asking me to give a course of lectures which formed the starting-point of this book; to the Royal Society for grants towards the expenses of the experiments, and to my collaborators, Miss Cooper, Mrs. Matthews and Dr. Zotterman, without whom the work would have been impossible.

CAMBRIDGE, E. D. A.
September, 1927.

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THE BASIS OF SENSATION

CHAPTER I

THE FUNCTION OF THE NERVE FIBRE

Introduction—Nerve Fibres and End Organs—The Nervous Impulse: (*a*) Excitation; (*b*) The Impulse; (*c*) The Refractory State of Recovery.

In the nineteenth century most investigations of the sense organs were either anatomical or psychological. The minute structure of the different types of sensory apparatus was worked out in great detail and the relation between the stimulus and the resulting sensation in man was thoroughly explored. The former method seems to have come very near the end of its tether now that microscopical technique has become standardised. As to the latter, there is no doubt that considerable advances can still be made by correlating stimulus and sensation, but the method is bound to leave unexplored what is really the most interesting part of the territory. Whatever our views about the relation of mind and body, we cannot escape the fact that there is an unsatisfactory gap between two such events as the sticking of a pin into my finger and the appearance of a sensation of pain in my consciousness. Part of the gap is obviously made up of events in my sensory nerves and brain, and the psychological method by itself can tell us nothing at all about these events.

With the twentieth century the problem of bridging this gap has taken on a new aspect, in England at least, from the work of four pioneers—Sherrington, Henry Head, Gotch and Keith Lucas. The first two have been mainly concerned with the central nervous system, though their work on the sense organs has been no less important. Sherrington has brought order out of chaos by his work on the simplest reactions of the isolated spinal cord. He has shown how the extremely complex relations which may exist between the stimulus and the response can be analysed into simple reflexes compounded according to definite laws. Head has worked on man, and has determined the effects on sensation of various diseases and injuries of the nervous system. This had been done before often enough, but whereas others were usually content to label the patient's symptoms with a long word—hyperæsthesia or what not—Head has been concerned to assess the exact changes which have taken place in the sensory content of the mind, and from this basis to assign the rôle played by different parts of the central nervous system in linking the mind to the outside world.

The work of Keith Lucas and of his forerunner Gotch seems at first to have much less connection with the problem of stimulus and sensation. Both were electro-physiologists, that is to say their work dealt mainly with the reactions of isolated nerves to electrical stimulation. This branch of physiology is of respectable antiquity, for it starts from the observations of Galvani and Volta and to this extent may claim a common ancestry with a good deal of modern physics. Its justification is that it gives us a means of studying the particular activity of the nerve fibre which makes it the connecting link between the sense organs, the central nervous system and the muscles. When an isolated nerve is stimulated electrically or mechanically, a disturbance is set up which travels rapidly in either direction away from the stimulated point, and reveals itself either by an accompanying electric effect—the action current—or by the twitch of the muscle to which the nerve is attached. The disturbance, called the nervous impulse, is a momentary affair and travels rapidly (about 100 metres a second in a human nerve, i.e., about 220 miles an hour).

The impulse set up by an electric stimulus in a tissue isolated from its normal surroundings might turn out to be a purely artificial effect. It would still be worth investigating, but in reality there is little doubt that it does represent the essential activity of the nerve fibre in the body. Gotch and Keith Lucas, by their analysis of the "refractory period" in nerves, gave us for the first time a clear idea of what may be called the functional value of the nervous impulse. They showed what the nerve fibre can do as a means of communication and what it cannot. Most of these experiments were concerned with motor and not sensory nerve fibres, and there was a remote possibility that the latter would work differently. As it turns out, this possibility may be dismissed. Though some of his conclusions may need modification, the work which ended with Keith Lucas' death in an aeroplane accident in 1916 has given us a picture of the activity of the nerve fibres which is substantially correct. It is of the first importance in the problems of sensation, for it shows what sort of information a sense organ can transmit to the brain and in what form the message must be sent.

These pages make no attempt to review our knowledge of the physiology of sensation or to catalogue all the most recent advances. They are confined to a particular set of researches carried out in Cambridge during the past two years, researches which are the logical outcome of Keith Lucas' work in the same laboratory before the war. With improved technique it is now possible to record the impulses which are set up in sensory nerve fibres by the appropriate stimulation of their sense organs, to determine the actual message transmitted to the brain, and to see how it is related to the stimulus which produces it. If this work is to be intelligible, it must be prefaced by a brief account of what is known of the nature of the impulse and the conditions under which it is set up.

NERVE FIBRES AND END ORGANS

First of all there is the anatomical basis. A nerve is a bundle of separate nerve fibres, each running an uninterrupted course between the central nervous system (the brain and spinal cord) and the periphery (the muscles, sense organs, etc.). The nerve fibre is the conducting unit of the nervous system. Each consists of a long thread of protoplasm called the axis cylinder, attached at one end to the nerve cell and usually enclosed in a tubular "medullary sheath" of a complex fatty substance. This sheath is present in all the nerve fibres which are concerned with the rapid adjustments of the body to its external environment, i.e., all the fibres conveying messages from the sense organs to the central nervous system and from the central nervous system to the muscles which move the body and the limbs. There is another kind of fibre, non-medullated and much slower in its reactions, which serves for the more leisurely adjustments of the viscera, but these need not concern us for the present. The medullated fibres may be a metre or more in length, but their diameter is seldom greater than ·01 mm.

The nerve cell from which the fibre originates is situated in or very close to the spinal cord. Most nerves contain both motor ("efferent") fibres, which connect the central nervous system with the muscles, and sensory "afferent" fibres connecting with the sense organs, but the two kinds of fibre are separated out just before the cord is reached and their cells are differently arranged. The motor nerve cells are within the substance of the cord; the sensory cells are grouped together into small ganglia which form a swelling on each bundle of sensory fibres just before its entrance to the cord. Besides the long axis cylinder which links it to the peripheral structures, the nerve cell sends out other branches which go to form the complex network of connections in the spinal cord, and many of the sensory cells send out very long branches which pass up the cord towards the brain. The whole substance of the brain and spinal cord is built up of similar nerve cells connected by branching threads of protoplasm, but it is believed that the connection between the branches of one cell and another is established, without actual continuity substance, by a specially developed junctional apparatus called the synapse. The structure of the central nervous system is exceedingly delicate, but it is guarded from injury by the bony case formed by the skull and the bony tube formed by the vertebral column.

These facts are summarised in the diagram in Fig. 1, and in this an attempt is made to indicate the structure of some of the sense organs or "receptors" with which we are particularly concerned. Many of the sensory fibres have no end organ at all; the medullary sheath disappears, the naked axis cylinder branches repeatedly and the branches end among the ordinary cells of the skin or connective tissues. As a modification of this, the axis cylinder may form a ring round the base of a hair follicle. Other fibres end in some special structure such as the various "corpuscles" and the muscle spindles and tendon organs. In all of these there is a definite capsule covering the termination of the fibre and usually one or more cells in close contact with the axis cylinder. Considerable doubt exists as to the function of the different types of ending. For instance the Pacinian corpuscle

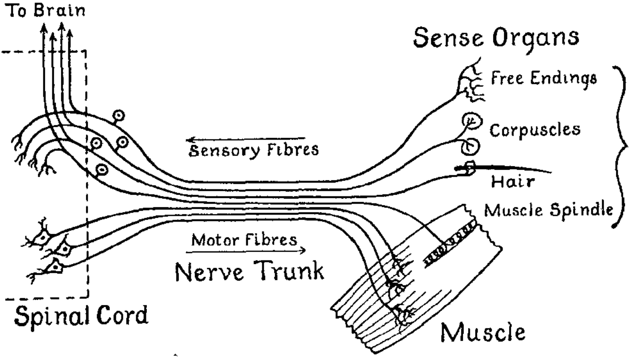

FIG. 1. DIAGRAM TO SHOW THE NERVOUS CONNECTION BETWEEN THE CENTRAL NERVOUS SYSTEM AND THE PERIPHERY (MUSCLES AND SENSE ORGANS).

The mixed nerve trunk is made up of sensory and motor fibres. The cells of the sensory fibres are collected in a ganglion on the nerve root. The motor fibres arise from large polygonal cells in the spinal cord.

(a complex organ as large as a pin's head) is sometimes regarded as a receptor for temperature and sometimes for pressure.

A mixed nerve trunk like the sciatic will contain several thousand fibres, both motor fibres to the various muscles of the leg and sensory from the various receptors in the skin, subcutaneous tissue, muscles, joints, etc. It is with such a nerve trunk that most of the experiments of "muscle nerve" physiology have been made. The nerve, removed from the body and set up in a moist atmosphere, will continue to respond to electric stimulation for many hours. As a rule one of the muscles supplied by the nerve is dissected out as well and its contractions are used as an index of activity. Since the nerve is no longer connected with the central nervous system the preparation remains at rest unless it is artificially stimulated.

THE NERVOUS IMPULSE

(*a*) *Excitation.*—In the following pages we shall have frequent occasion to use the word "stimulus" (it has been used six times already), and since it is a word which may mean a number of different things, it will be as well to start by a definition. We will define a stimulus as any change in the environment of an excitable tissue which, if sufficiently intense, will excite the tissue, i.e., will cause it to display its characteristic activity. The stimulus is thus the external change, and it may be ineffective—the stimulation may not have been intense enough to excite. Now in studying the activity of an isolated nerve or nerve muscle preparation it is the general rule to employ a brief electric current as stimulus, because the intensity and duration of the current can be very accurately controlled, and because such stimulation can be repeated again and again without producing any permanent damage. If the current is very weak, or if its duration is extremely short (less than .00001 sec.), it is unable to excite; no impulses are set up and nothing happens in that part of the nerve which is not traversed by the current. If the stimulus is to be effective it must produce a local change of sufficient intensity in the nerve fibres, and the change appears to be one which takes a certain time to develop. In all probability it consists in the accumulation or segregation of ions in certain parts of the fibre; this accumulation upsets the balance of processes which maintain the fibre in its resting condition, and so leads to the further series of changes which constitute the impulse. The exact train of events need not concern us here, but there is one feature of electrical stimulation which is important, because we shall find the same thing when we have to deal with the natural stimulation of the sense organs. The point concerns the rate at which the current is made to increase. With the usual forms of stimulus the current increases to its maximum value in $\frac{1}{1000}$

sec. or less, but it is possible to arrange for a much slower increase, and it is then found that a current which rises very slowly may attain a relatively enormous intensity without exciting at all. In a frog's sciatic, for instance, if a current of strength x will excite when its full value is reached instantaneously, a current which increases gradually and takes one second to attain the value 40 x will never excite. The stimulus must be a rapid change of conditions, and a gradual change will not do. One way of accounting for this, or rather one way of describing it, is to suppose that the tissue adapts itself fairly rapidly to the change in its environment, so that excitation does not take place unless the change proceeds so rapidly that the tissue is caught unprepared. Another way is to suppose that a rapidly increasing current can produce the necessary accumulation of ions in the nerve fibre, but that this accumulation leaks away almost as soon as it is produced. The process may be compared with the occurrences described in the arithmetic books of our school days, where someone turned on the taps of a bath without taking the precaution of putting in the plug. Whether the bath would ever be filled or not would then depend on the rates of inflow and outflow and on the way in which these rates changed as the cistern emptied and the level in the bath began to rise.

It is convenient to speak of the phenomenon as one of adaptation, though we are quite in the dark as to its real nature. The rule that the effectiveness of the stimulus depends on the rate of change in the environment as well as on its extent applies to mechanical stimuli as well as to electrical, for a gradually increasing pressure on a nerve is far less effective than a sudden blow. As we shall see later, it applies also to the sensory nerve ending under its natural conditions and has an important influence on the nature of the messages which the brain receives from the sense organs.

(*b*) *The Impulse.*—The different fibres of which the nerve trunk is composed behave as independent units, and it is possible to adjust the strength of the stimulus so that some of the fibres are excited and some not. In each excited fibre an impulse is set up, and although the impulses in different fibres do not all travel at precisely the same rate,[1] they keep sufficiently close together to allow us to treat them as a single volley. The arrival of the volley at any point on the nerve is shown by the development of an electrical disturbance. The surface of the active region develops a negative potential with regard to the neighbouring inactive regions, and if electrodes are placed in contact with the active and inactive regions and connected through a galvanometer a current will pass through the circuit towards the active region.

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[1] Erlanger, Bishop & Gasser, *American Journal of Physiology:* vol. 70, p. 624, 1924; vol. 78, p. 537, 1926; vol. 78, p. 574, 1926.

The recording of this "action current" or "electric response" is by far the most sensitive method we have for detecting the passage of an impulse. It is now becoming possible to detect the occurrence of thermal and chemical changes as well, but it is, and must always remain, much easier to detect small alterations of energy if they occur in the form of electrical changes. As the volley of impulses travels down the nerve, the electrically active region shifts with it and comes to lie first under one electrode, A, and then under the other, B (Fig. 2). The result is a diphasic electric response, a current travelling through the external circuit first towards A and then towards B. The activity at any one point lasts at most for a few thousandths of a second, but the active region shifts so rapidly that if the electrodes are close together the

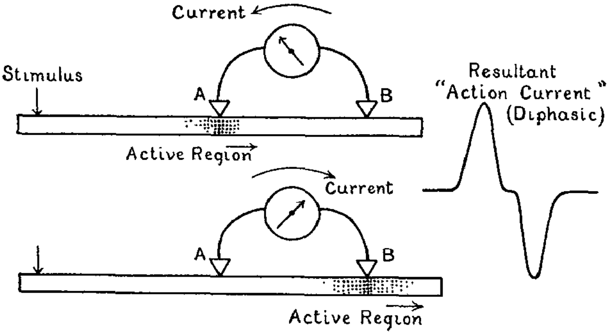

FIG. 2. PRODUCTION OF DIPHASIC "ACTION CURRENT" AS THE ACTIVE REGION TRAVELS DOWN A NERVE FIBRE.

area under the second may have begun to respond before that under the first has ceased. The diphasic current recorded in these circumstances will not give us the time relations of the response at any one point, since it will be a mixture of two responses having opposite effects on the recording instrument. Fortunately we can overcome this difficulty by damaging the nerve under the second electrode. The damaged area behaves as though it were permanently active, giving rise to a steady instead of a momentary negative potential, and its condition remains unchanged when the active region travels towards it. Thus the current will be monophasic and will show the development and decline of the activity under the first electrode alone.

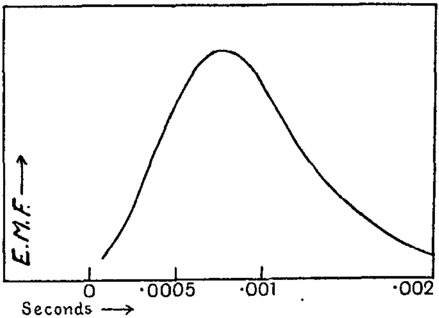

FIG. 3 RISE AND FALL OF ELECTROMOTIVE FORCE IN MONOPHASIC ELECTRIC RESPONSE (ACTION CURRENT) OF FROG'S SCIATIC NERVE AT 13° C.

The form of the monophasic response in a sciatic nerve at 13° C. is given in Fig. 3. It should be understood that this is really the sum of all the responses of the individual fibres in the nerve, but the data obtained from sensory nerves shows that a single fibre would give us very much the same time relations (see p. 51). It will be seen that the outburst of activity is exceedingly brief, for the whole duration of the action current does not exceed a few thousandths of a second.

There is every reason to suppose that the electric response is a true indication of the essential activity of the nerve, that it is not an artificial effect due to our use of an electric stimulus and having no functional importance. The proofs are lengthy, but they may be summarised by saying that there are other ways of detecting the passage of the active state down a nerve, and it is found that this activity is invariably accompanied by the electric charge. The energy involved in the transmission of the impulse is certainly derived from the potential energy present in the resting fibre and not from the stimulus. The exact changes which take place are unknown, but there is no reason to suppose they are unknowable, and it is noteworthy that Lillie has produced a model consisting of an iron wire in nitric acid which, on stimulation, transmits an impulse with properties which are an extraordinarily close copy of those of the impulse in a nerve fibre.

Some time has been spent on the electric response, because it gives the most direct information about the nervous impulse, but the total response of a nerve trunk is not always a sound guide to what is happening in each fibre. For this reason much of our information as to the impulse is derived from experiments in which the contraction of a muscle is used instead of the electric response to signal the arrival of impulses from the nerve. It was by a combination of this method with the recording of electric responses that the phenomena of the refractory state and of recovery have been worked out. These phenomena are so important that they merit a section to themselves.

(*c*) *The Refractory State and Recovery.*—It has been stated that the impulse is a disturbance of very brief duration and the record of the electric response given in Fig. 3 shows a change which is nearly over in .002 sec. It would be natural to associate this with the fact that the stimulus is also very brief when it takes the form of an induction shock. In reality, however, the brief duration of the impulse has a much more fundamental cause, and it is impossible to prolong it by modifying the stimulus. By studying the effects of two stimuli in rapid succession it can be shown that the development of the active state renders the fibre completely inexcitable to a second stimulus, and this refractory state persists until the electric response has subsided. The existence of this refractory period makes it impossible to prolong or enhance the state of activity by further stimulation, and we must regard the impulse as a change which occupies the entire resources of the nerve fibre for the time being.

The ending of the refractory state is a gradual affair. During a period which corresponds fairly closely with the duration of the electric response the refractory state is absolute and a stimulus has no effect, however strong it may be. In a frog's nerve at 15° the absolute refractory period lasts from .002 to .003 sec. It is succeeded by a relative refractory period, during which it is possible to set up a second impulse, but only by a much stronger stimulus than is needed for the resting nerve. The excitability returns gradually, i.e., weaker and weaker stimuli become effective, and within about .02 sec. the excitability has usually returned to within 95% of its resting value, though it may be much longer (.1 sec. or more) before this value is finally reached. This gradual return of excitability is associated with a gradual return of the power of impulse conduction. If two impulses are set up and the second is started during the relative refractory period, the second electric response is much smaller than the first to begin with and is conducted at a slower rate. Owing to the slower conduction the second impulse lags behind the first and comes to travel in regions where the recovery is more advanced, but it seems probable that the normal intensity is not regained until the relative refractory period is completely over.

It is natural to regard the absolute and relative refractory periods as due to the disorganisation produced by activity and the subsequent return to the normal resting state, but the important point is that the process of recovery does not begin until the impulse is over and takes a considerable time before it is complete. We need not discuss the underlying chemical and physical changes, for they are still uncertain. What is certain is that the constitution of the nerve fibre will not allow it to conduct two impulses at less than a definite interval apart—that each impulse is a discrete event and that nothing in the shape of continuous activity is possible.

Thus the development of the refractory state with each impulse imposes a very definite limitation on the working of the nerve fibre. The message which it transmits must consist of a series of impulses which cannot recur at more than a certain frequency. To take an analogy: the nervous message may be likened to a stream of bullets from a machine gun, it cannot be likened to a continuous stream of water from a hose. But there is another and yet more important limitation in the scope of the message, namely, that the intensity of each impulse cannot be made to vary by changing the strength of the stimulus. The likelihood of this was first pointed out by Gotch. Since then many proofs have been advanced, and each of us in turn has claimed that his is the only logical and convincing experiment. But I fancy that most of us, like the generals before Salamis, would award the second place to an experiment carried out by Keith Lucas[1] in 1910. He was really concerned with a different point, but what he did in effect was to stimulate a single nerve fibre which divided into some twenty branches, each supplying a muscle fibre. The contractions of the muscle were recorded and it was found that the twenty muscle fibres behaved as a unit. Either all contracted when the nerve fibre was stimulated or none did, and the force of the contraction did not alter when the stimulus was increased. Thus it was impossible to set up in the nerve fibre an impulse which would be able to pass into some but not all of the attached muscle fibres. This is not a conclusive proof that the impulse does not vary with the strength of the stimulus, but, taken in conjunction with other evidence, it is a reasonably convincing one.

The stimulus, then, may be compared to the pressure on the trigger of a rifle: either it is strong enough to fire the bullet or it is too weak to do anything. The nerve fibre is not the only excitable tissue which reacts in this way, for the same kind of behaviour has been known for many years in the case of the heart muscle. Here, too, the force of the contraction cannot be controlled by altering the strength of the stimulus, and the latter is either completely adequate or completely inadequate. These facts are best expressed by the statement that there is an

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[1] Keith Lucas, *Journal of Physiology*, vol. 38, p. 113, 1909.

"all-or-nothing" relation between the stimulus and the activity which it produces.

The existence of the "all-or-nothing" relation in nerve fibre means that as far as each impulse is concerned there is no possibility of gradation by changing the strength of the stimulus, but it does not mean that the total activity of the fibre cannot be graded, for it is obviously possible to control the total number of impulses which are set up and the frequency with which they recur (up to the limit imposed by the refractory period).

It is also possible to alter the character of an impulse after it has started by altering the condition of different parts of the nerve through which it passes. For instance, if it enters a region at a low temperature it travels more slowly, the electric response is longer, and the maximum electromotive force slightly less than in the warmer regions. But the impulse does not retain these characters when it leaves the cold area and re-enters the warm. They depend on the local conditions in the region through which the impulse is passing and are not affected by the previous history of the impulse, e.g., the nature of the stimulus or the state of the path through which it has travelled. The same thing is true of an impulse travelling in nerve fibre which has not completely recovered from the refractory state. The character of the impulse at any point will depend on the state of recovery of the nerve at that point, i.e., on the interval which has elapsed since the passage of the first impulse, and on this alone. It will be seen that the existence of the refractory period and of the all-or nothing relation both point to the same conclusion, that the impulse is a change which occupies the entire resources of the nerve fibre for the time being. We may liken it, then, to an explosive wave started by the trigger action of the stimulus, and once it is started its character is determined entirely by the local conditions at each point in the fibre through which it passes.

SUMMARY

To summarise what has been said: an effective stimulus implies a certain degree and a certain rate of change in the environment. The stimulus acts merely as a trigger for setting off the impulse and does not contribute the energy needed for its transmission. The impulse is a momentary disturbance which passes down the nerve fibre accompanied by a change of electric potential. The nature of the impulse at any point does not depend on the character or strength of the stimulus which sets it up, but only on the local condition of the fibre at that point. When an impulse reaches any point on the fibre, that point becomes refractory to external stimulation and will not transmit a second impulse until a certain time has elapsed. The result is that the message which a nerve fibre can transmit must consist of one or more discrete impulses and a continuous transmission of the excited state is impossible. In fact the only way in which the message can be made to vary at all is by a variation in the total number of the impulses and in the frequency with which they recur.

CHAPTER II

THE RECORDING OF IMPULSES IN SENSORY NERVE FIBRES

Previous Work—Amplification of Electric Effects—Recording Instruments—Summary.

THE conclusions stated at the end of the last chapter were derived from experiments on isolated motor nerve fibres or on mixed nerve trunks subjected to electrical stimulation. It was, therefore, possible that the sensory fibres would be found to behave differently, and even possible that the motor fibres could transmit a different kind of activity when their connections with the central nervous system were intact. It is still possible that some of them may do so, though there is very little evidence for it, but there is now no doubt that a great deal of the normal activity of the motor nerve fibres does consist in the transmission of impulses of the type described. This has been shown by the analysis of reflex contractions and of the electric responses of motor nerves and muscles excited by way of the central nervous system. For example, Forbes and Gregg[1] recorded the electric response in a motor nerve attached to the central nervous system and activated

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[1] Forbes & Gregg, *American Journal of Physiology*, vol. 39, p. 172, 1915.

by stimulating a sensory nerve and found it to be an action current of typical form. Gasser and Newcomer[1] recorded the response in the phrenic nerve which brings about the rhythmical contractions of the diaphragm in breathing. Each contraction develops slowly and lasts a second or more, and they found that each was associated with a rapid series of action currents in the nerve recurring at a rate of about 70 a second and having the typical diphasic character. Their records are particularly interesting, since they illustrate the discontinuous character of the message which must be employed to evoke a steady period of contraction in the muscle, and show in addition that the different fibres of the phrenic nerve act more or less in unison, the discharge from the central nervous system taking the form of repeated volleys of impulses and not a random fire kept up independently in each fibre.

The question of the timing of the impulses in the different fibres of a nerve trunk has a considerable importance in the case of the sensory nerves, for here the different fibres lead from separate end organs, and it is unlikely that the normal stimulation of a sensory surface would produce a synchronous discharge of impulses from all the different end organs. This means that the electric effects in the nerve will be very hard to detect. If only a few fibres are active at a time, the currents are short-circuited by the

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[1] Gasser & Newcomer, *ibid.*, vol. 57, p. 1, 1921.

inactive tissue and may become too small to detect; and much the same thing will occur if many fibres are acting independently, for there will be a considerable number of inactive fibres at any moment to diminish the potential changes at the electrodes.

For this reason there have been few attempts until recently to record the form of the action currents in sensory nerves. That electric effects do occur in them on stimulation of the end organs had been shown by leading from an intact and a damaged part of the nerve with very sensitive galvanometers of low period. By this method Steinach[1] found them in a cutaneous sensory nerve of the frog, stimulated by tapping the skin surface, and Tschermak and Koster[2] in the cardiac depressor—the main sensory nerve of the heart—when the aorta was distended. The deflections were in the right direction, i.e., the direction we should expect if they were due to the addition of a number of monophasic action currents, but they could not be expected to give any information as to the duration or frequency of the responses in each fibre. Einthoven[3] and Jolly[4] have recorded electric effects in sensory nerves with the string galvanometer, but here too the records merely show an additive effect, since the speed of the recording instrument had to be sacrificed in the interests of greater sensitivity.

[1] Steinach, *Pfluger's Archiv.*, vol. 43, p. 495, 1896.
[2] Tschermak & Koster, *Pfluger's Archiv.*, vol. 93, p. 24, 1903.
[3] Einthoven, *Verh. d. Ges. d. Naturl.*, p. 93, 1911.
[4] Jolly, *Quart. Journ. of Exp. Physiol.*, vol. 4, p. 67, 1911.

The most successful attempts to obtain the true form of the sensory nerve response were made by the sudden excitation of a large number of receptors at once. Buytendyk[1] stimulated the ear of a rabbit with the noise of a pistol shot and found a diphasic or monophasic electric response in the auditory nerve lasting about $\frac{1}{50}$ sec.; this is much longer than the response of a motor nerve, but it is unlikely that the discharge consisted of a single volley of impulses. More recently Forbes[2] investigated the sensory discharge from a contracting muscle. Since this work gave the first clear indication of the nature of the discharge it deserves treating in some detail.

That muscles contain sense organs and sensory nerve fibres was first made clear by Sherrington. The organs belong to the group which he has labelled "Proprioceptors," since they convey information to the central nervous system concerning the movements and posture of the bodily mechanism.[3] Sense organs in muscles, tendons and joints belong to this class, and though their activity has very little obvious effect on the content of our mind it has a very great effect indeed on the working of the body. Without the

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[1] Buytendyk, *Konik. Akad. v. Wetens. te Amst.*, Dec. 8, 1910.

[2] Forbes, Campbell & Williams, *American Journal of Physiology*, vol. 59, p. 283, 1924.

[3] The other groups are the exteroceptors, mainly in the skin, which give information of changes in the immediate environment of the organism. Distance receptors (eyes, ears and nose) for changes in the remote environment, and for the sake of completeness interoceptors for changes within the viscera.

proprioceptors no movement can be accurately performed, for the whole adjustment of the range and force of muscular contraction depends on the information received from them. If this information fails (as in certain diseases, e.g., locomotor ataxy) the movements take on a jerky, fumbling character and may become quite impossible. The patient can compensate to some extent for the failure of his proprioceptor apparatus by watching his limbs to see how their movements are progressing. Information from the eye is then substituted for information from the muscle receptors, but it is a very poor substitute.

Since these organs supply information about the movement and posture of the limbs, we should naturally expect that the particular stimulus which would excite them would be muscular movement or tension. A muscle contracts suddenly and forcibly when it is stimulated electrically, and there was no lack of evidence to show that a sudden contraction of this kind produces a sensory discharge which travels from the muscle to the central nervous system. Hoffmann had already worked out the reflex effects of this sensory discharge in man and de Meyer had called attention to small excursions in string galvanometer records which seemed to indicate the passage of a volley of impulses away from the muscle. Forbes used a mammalian muscle and nerve preparation and stimulated the sense organs in the muscle by pulling on it suddenly with a spring or making it contract by a single shock to the nerve. The electric responses in the nerve were recorded with a string galvanometer, and in some of the experiments the currents were first magnified 50 times by a valve amplifier. The records showed a series of three or four oscillations, which were undoubtedly due to groups of action currents travelling away from the muscle towards the central nervous system. Owing to the fact that the different receptors would not all discharge at exactly the same moment and that each might discharge several times, the composite effect in the record gave no precise information as to the duration of the response in each fibre, but it was certainly very brief and of the same order as the duration of the response in the motor fibre.

Forbes' experiment is doubly interesting from our point of view; taken in conjunction with Buytendyk's it gives the first clear indication that the activity of a sensory nerve evoked by the natural stimulus to its end organ is of the same nature as the activity of a motor nerve stimulated artificially, and in addition it introduces us to a very important improvement in technique. This consists in the use of valve amplification for magnifying very small electric changes.

AMPLIFICATION OF ELECTRIC EFFECTS

A great deal of the difficulty in physiological research is due to the microscopic size of the living cell

—the unit out of which the organism is built. Probably the small size of the cell is essential to its existence, but one result is that all the changes which we wish to investigate are very small too, and experiments, which would be simple enough theoretically, are continually checked by the technical difficulties of work on a minute scale. In dealing with the electric changes in a nerve trunk stimulated artificially this difficulty is overcome to some extent by recording the summed effect of a large number of units, but even so the physiologist has had to devise two special instruments over and above those which he has been able to borrow from the physicist and the engineer. They are Einthoven's string galvanometer and a special form of capillary electrometer. These can give valuable information about the response of an entire nerve trunk where the potential difference between an active and an inactive region is as great as 15 millivolts. They do not react rapidly enough to give a true picture of the rise and decline of a response which last a few thousandths of a second, though the capillary electrometer gives a record from which the true form of the response can be deduced by a fairly simple mathematical analysis. But the changes of potential are very much smaller than 15 millivolts when they are caused by the activity of a few sensory nerve fibres in a large nerve trunk, and neither instrument combines a sufficient sensitivity and a sufficient speed of reaction to deal with these unaided.

Fortunately the detection of very small and very rapid electric changes has recently become a problem not confined to physiology, and our difficulties can be solved by the use of methods devised for wireless communication. When the academic scientist is forced to justify his existence to the man in the street he is inclined to do so by pointing out the essential part played by academic research in the development of our modern comforts. It is only fair, therefore, to point out that in this case the boot is on the other leg and the academic research has depended on the very modern comfort of broadcasting.

As everyone knows, wireless telephony became possible only with the introduction of the three-electrode valve which was developed on a large scale in the war and is now an article as widely advertised as the motor car or the safety razor. Valves are used, in the first place, for producing the electrical oscillations sent out from transmitting stations. These oscillations are made to occur with a frequency of a million or so per second and to wax and wane in strength at the much lower frequencies of audible sound. If the signals are powerful enough they can be detected by means of a crystal rectifier which takes cognisance only of the relatively slow waxing and waning of the oscillations and converts these into sound by means of a telephone. But if the signals come from a long distance the energy picked up by the aerial will be too small to affect a telephone, and it is then necessary to use a receiving set in which valves are used both for rectification and also for amplifying the minute energy changes until they are large enough for conversion into sound. It is this use of the valve for the amplification of very small electric changes which makes it an instrument of physiological research.

The valve acts as an amplifier because it lives up to its name and does act in much the same way as a valve or tap on a water pipe. Very small forces expended in turning a tap will alter the rate of flow of water down a pipe, and so will control the large forces which may be developed in the hydraulic machinery supplied by the pipe. By some such arrangement it would be possible to construct an amplifier which would "receive" very small changes of mechanical force and would deliver a faithful reproduction of these changes magnified a thousandfold or more. The servo-motor which applies the brakes of a racing motor car is a good example of a mechanical amplifier of this type, the essential feature being that the powerful movement of the brakes is produced by an entirely independent source of energy, the output of which is controlled by the relatively weak movement of the brake pedal.

In a valve amplifier the output is a current derived from a high tension battery of 100 volts or so. This current is passed through the valve, where it is carried by a stream of electrons emitted from a filament heated by another (low tension) battery. The electron stream is made to pass through the meshes of a wire grid and the whole operation of the valve lies in the fact that the current which passes through the meshes of the grid varies considerably when the potential of the grid is altered by a small amount. The grid is connected with the input circuit so that its potential is controlled by the small electric changes which are to be amplified, and the result is that the current passed through the valve by the high tension battery is also controlled by these changes, the grid acting in much the same way as the tap on the water pipe in our hydraulic analogy. In effect, then, small changes of potential in the input circuit produce large changes in the output circuit, and the latter follow the former instantaneously because there are no moving parts in the valve (other than the electrons) and therefore no inertia to be overcome. A single valve may produce a 50-fold amplification of the applied change of potential, and greater amplification is obtained by coupling several valves in series with transformers or condensers between each pair to keep the grid potentials at the proper value.

The details of the amplifier used in the present work may be found elsewhere.[1] For the present it is enough to say that it is now a simple matter to con-

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[1] Adrian, *Journal of Physiology*, vol. 61, p. 49, 1926. It follows the design of that used by Gasser and Newcomer and has three valves with resistance capacity coupling and large inter-valve condensers to enable it to follow slow changes of potential.

struct an apparatus which will give us a faithful reproduction amplified to almost any extent of changes of potential as small as a few millionths of a volt occurring with a frequency of many thousands a second.

Valve amplifiers for detecting wireless signals were developed during the war and were applied to physiological research as soon as the war was over by Forbes in America, Daly in this country and Höber in Germany. At first it was not possible to use the amplification from more than one valve, because the amplified electric responses were not much larger than the various irregular oscillations derived from the valves and their attendant batteries and coupling circuits. But the development of the valve and its accessories has proceeded at an enormous rate under the impetus given by broadcasting; in 1923 Gasser and Newcomer used 500-fold amplification to investigate the action currents in the phrenic nerve, and it is now possible to work with 5,000-fold amplification on an input change of a few micro-volts without danger of interference from unsteadiness in the amplifier.

RECORDING INSTRUMENTS

This means that we are no longer bound to use a sensitive recording instrument to detect the action currents in a nerve; all we need is one which reacts rapidly enough to follow the course of the currents without undue lag. At present the most perfect instrument as far as rapidity is concerned is the cathode ray tube. Here the only moving part is a stream of cathode rays which is deflected by applying a potential difference to two plates between which the stream passes. The possibility of using such a tube for recording action currents was suggested by Bernstein as long ago as 1912, but at the time he wrote the possibility was extremely remote, for even with the most sensitive modern tubes the action current of a nerve trunk must be amplified several thousand times if it is to produce a measurable deflection of the cathode ray stream. It has now been used with conspicuous success by Erlanger, Gasser and their co-workers for studying the exact time relations of action currents in the isolated nerve trunk, but there are still certain difficulties in obtaining a permanent record which limit its usefulness.

Most of the work described in these pages has been carried out with the capillary electrometer used in conjunction with a three or four valve amplifier. In this form of electrometer the moving system consists of a column of mercury in a vertical glass tube dipping into sulphuric acid (Fig. 4). The lower part of the tube is drawn out into a very fine conical capillary with an open end, but the mercury does not pour out of the end, and indeed it has to be forced into the narrow part of the tube by air pressure. The reason for this is that any downward movement in the conical part of the tube must cause a reduction in the surface of separation between the mercury and the acid, and this is resisted by the forces of surface tension. Normally, therefore, the lower surface of the mercury comes to rest at a point in the tube where a balance

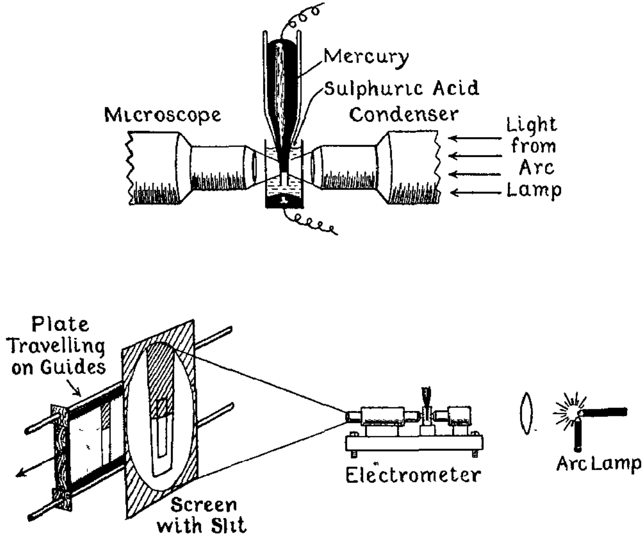

FIG. 4. (*a*) CAPILLARY ELECTROMETER FOR RECORDING VERY RAPID CHANGES OF POTENTIAL. (*b*) OPTICAL SYSTEM FOR PHOTOGRAPHING THE MOVEMENT OF THE MERCURY ON A MOVING PLATE.

is struck between the forces tending to move it downwards (gravity assisted by air pressure) and those tending to move it upwards (surface tension). If a difference of electric potential is set up between the mercury and the acid, the surface forces change and the meniscus moves up or down the tube into a new position of equilibrium. Its movement can be recorded by throwing a beam of light on to the capillary tube so as to cast a shadow of the mercury on to a slit placed in front of a moving photographic plate or strip of film.

In this instrument the restoring and displacing forces are relatively large and the movement is highly damped. For this reason the mass of the moving parts has very little effect on the rate of movement. Owing to the damping the movement is too slow to give an exact reproduction of the electric response of a nerve, but owing to the relative absence of inertia the true form of the response can be deduced by an analysis of the record.

Used in conjunction with an amplifier the capillary electrometer has the great advantage of being relatively fool-proof. If large potentials are applied to it by accident, the worst that can happen is some electrolysis at the surface of the mercury, and as a rule this is easily remedied. At the same time the instrument is elaborate, and the records have to be photographed and developed before we can tell what has happened. Since there is no need for great sensitivity in the recording instrument it may be possible in future to use more amplification and a recording instrument which will write directly on a moving surface. At all events the developments of valve amplification have made it unnecessary to limit ourselves to a particular form of recorder, and provided the reaction is rapid enough we can use whatever type is the most convenient for our particular experiments.

SUMMARY

As far as the motor nerve fibres are concerned there is little doubt that their normal activity in the body consists in the transmitting of impulses of the same type as those which are set up in isolated nerves by electrical stimulation. In the past it has been difficult to investigate the normal activity of sensory nerve fibres since the electrical recording instruments have not been sensitive enough, but the recent developments of valve amplification have now made it possible to detect the smallest electric changes with relatively insensitive recording instruments.

CHAPTER III

THE MECHANISM OF THE END ORGAN

Sensory Impulses in Single Fibres—The Sterno-Cutaneous Preparation—Regular Discharge from End Organ—Production of Repeated Impulses—Nerve Fibres and End Organs.

THE use of an amplifier makes it possible to record the electric response of a single fibre in a large nerve trunk, and this opens up an entirely new field in the investigation of sense organs. If the sensory nerve fibre does transmit impulses of the usual type when the end organ is stimulated, there should be no difficulty in recording these impulses, and in theory at least we shoud be able to determine the exact message transmitted to the brain. This can, in fact, be done in selected cases, though there are various technical difficulties to be faced.

SENSORY IMPULSES IN SINGLE FIBRES

The first step in a research of this kind must be to satisfy ourselves that the message normally tran
mitted by the sensory fibre consists of impulse
the usual type or at any rate of impulses whi
accompanied by measurable electric effect
work of Forbes and others had made this
certain, and preliminary experiments
sensory nerve preparations left no doub

In these experiments and indeed in all the experiments described in these lectures the recording system was a capillary electrometer used in conjunction with a valve amplifier. As a rule three valves were used, and these gave a 1,700–1,800-fold magnification of the electric effects in the nerve. The "preparation," i.e., the nerve and the structures containing the sensory end organs, is set up inside a metal box which screens the input circuit from the small currents which might be induced in it by stray electromagnetic disturbances.

The simplest preparation to use is the ordinary "gastrocnemius-sciatic" preparation of the frog. This consists of the gastrocnemius muscle removed from the body with the sciatic nerve attached to it. The nerve is placed on the two electrodes which lead to the input circuit of the amplifier and the upper end of the muscle is fixed by a clamp on the bone. A thread is tied to the tendon and so arranged that the muscle can be stretched by various weights applied suddenly or gradually. In this way the sense organs in the muscle can be subjected to the natural stimulus of a change of tension or shape in the muscle. The
rog's sciatic nerve contains about 3,000 fibres, and
these only a few are afferent fibres from the
ry end organs in the gastrocnemius. Yet there
ubt about the electric responses in them when
ocnemius is stretched. Records of these are
g. 5. They are photographs of the move-
mercury in the capalliary tube, made on

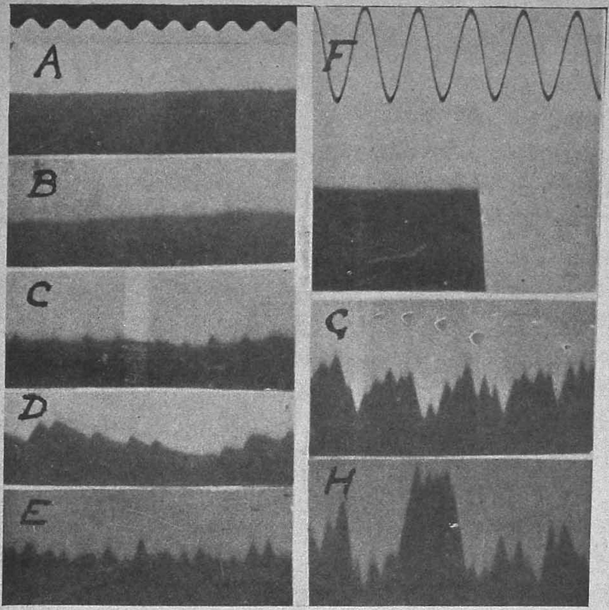

FIG. 5. A–D, G AND H, RECORDS OF ELECTRIC RESPONSES IN FROG'S SCIATIC NERVE WHEN THE GASTROCNEMIUS MUSCLE IS STRETCHED BY A WEIGHT. CAPILLARY ELECTROMETER AND 3-VALVE AMPLIFIER.

A. Control, to show absence of oscillations when the nerve has been crushed near the muscle to prevent the conduction of impulses. The top shadow is that of a tuning fork vibrating 200 times a second.

B. Nerve uninjured but muscle relaxed. No impulses.

C. Muscle stretched with 10 gm. weight applied 10 sec. before record was made. Nerve uninjured. The record shows a succession of diphasic electric responses.

D. 10 gm. weight applied 20 sec. before record was made. Nerve injured under one electrode to show the change in the form of th response, which has now become monophasic.

E. 100 gm. weight in action for 10 sec. Nerve uninjured.

F. Calibration curve, showing response of electrometer to a c of potential of .0001 volt (amplified with 3 valves). The uppe traced by a spring time marker vibrating 100 times a seco record shows the almost complete absence of inertia in the el

G. Another preparation. 40 gm. weight applied for 5

H. Impulses produced by stretching two muscles s gastrocnemius and tibialis anticus. 40 gm. weights.

D

rapidly moving plates by the arrangement shown already (Fig. 4). The shadow of a vibrating tuning fork or spring marks the rate of travel of the plate, which in this case is about 80 cm. per sec. In the top record (A), the nerve has been killed as a control, in B, the nerve is uninjured, but the muscle has no weight on it and the shadow of the mercury does not move; in C and D a weight of 10 gms. is hanging on the muscle and has been there for 10 secs. The records show a succession of small notches, each of which means a very brief change of potential between the two point on the nerve. In E the weight is larger and there are more of these notches, and in G and H there are so many that the shadow is never at rest. The electrometer record has to be submitted to a mathematical analysis before we can obtain the exact potential change at any moment, and Fig. 6 gives the corrected curve for the record shown in in Fig. 5, C, D and E. Some of the excursions are large and obviously complex, but the rest all conform more or less to a standard size and shape, and since there is no evidence of smaller excursions we may assume provisionally that each represents the
sponse of one nerve fibre. If this is so, and if the
nse of the sensory fibre does not differ from that
whole nerve trunk stimulated electrically, we
find a response of the same shape from the
e.

nse of the entire sciatic nerve to an electric shock (recorded without the amplifier) is in fact almost indistinguishable in shape from one of the standard sensory responses of the type shown in Fig. 6. The error involved in the recording and the analysis is fairly large when we are concerned with time intervals of $\frac{1}{1000}$ sec., but we can say quite safely that the normal response of the sensory nerve fibre does not differ considerably from the summed response of all the nerve fibres stimulated artificially.

Very many controls are needed to establish beyond doubt that the electric changes shown in these records are really the action currents of sensory fibres and that they behave like the typical action current of the nerve trunk. They must be changes of potential of the right sign (the active region being negative to the inactive) travelling away from the muscle towards the central nervous system, they must be diphasic if both electrodes are on uninjured nerve, and monophasic if the nerve is injured under one electrode; their duration must alter when the temperature of the nerve is changed and they must only appear when the end organs are stimulated. All these tests have been carried out and none have cast any discredit on the genuine character of the responses.

In Fig. 6, then, we have the sensory message wh
travels to the central nervous system when a m
is stretched, and the message consists of a su
of impulses of the familiar type. The
with which the impulses recur depends on

of the stimulus, but the size of each impulse does not vary; in other words there is the same "all-or-nothing" relation in the sensory fibre as in the motor. In the preliminary experiments other preparations were used as well, and discharges of the same kind were found in the sensory nerves from

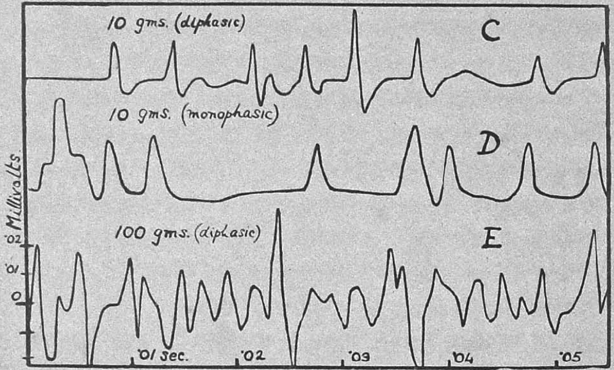

FIG. 6. ANALYSIS OF ELECTROMETER RECORDS IN FIG. 7. C, D AND E GIVING CORRECT FORM OF POTENTIAL CHANGES.

the skin and from the viscera with appropriate stimulation of their end organs.

The next step was obvious. The records showed the total response produced when a number of end organs were stimulated and they showed what were most certainly the individual responses of the
ent sensory fibres. But they gave very little
tion about the sequence of events in any one
, for the number in action was unknown and
othing to distinguish the response of one
om that of another. To investigate the

behaviour of the unit it was evidently necessary to use a preparation in which only one unit was in action. This was done with the co-operation of Dr. Zotterman, who had just arrived from Stockholm.

THE STERNO-CUTANEOUS PREPARATION

The method adopted was suggested at once by the classical researches of Keith Lucas on the "all-or-nothing" response of single muscle fibres. In these experiments it was necessary to use a muscle nerve preparation containing as few units as possible, and Lucas worked on one of the small cutaneous muscles of the frog, which is supplied by a nerve containing only 10 fibres. In a footnote to his paper he stated that another muscle of the same type—the sterno-cutaneous—was found to contain one muscle spindle connected to one sensory nerve fibre.

Ramon y Cajal has given a description of a muscle spindle from the frog's sterno-cutaneous in his book *Textura del Sistema Nervioso* (Madrid, 1899). The organ consists of a modified muscle fibre with a single nerve fibre, which enters and sends long branching processes in either direction. The structure is much simpler than that of a mammalian muscle spindle
where the nerve fibre terminations are wound lik
corkscrew round the modified muscle fibre.
does not say whether more than one spindle
present in the sterno-cutaneous or whether
other types of sensory ending.

The muscle takes origin from the body wall and is inserted into the skin. It is dissected out so that its origin is not interfered with, and a small piece of skin is left attached to the free end so that it can be stretched by weights hanging from a thread tied to the skin.

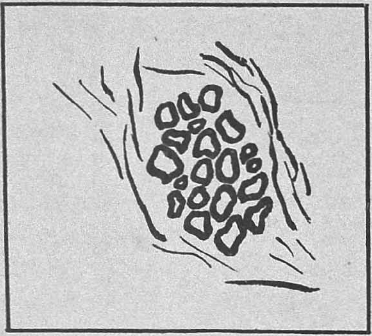

FIG. 7. DRAWING OF TRANSVERSE SECTION OF THE NERVE SUPPLYING THE FROG'S STERNO-CUTANEOUS MUSCLE, STAINED WITH OSMIC ACID.

The myelin sheath of each nerve fibre appears as a black ring; there are 20 fibres, the largest measuring .011 mm. across.

The nerve to the sterno - cutaneous contains from 15 to 25 nerve fibres. A cross-section of the nerve is shown in the drawing in Fig. 7. The slender terminal branch joins a larger nerve trunk with about 500 fibres, and this in turn is ultimately derived from the large brachial nerve which runs through the axillary space. The larger nerve trunk is easily dissected out and arranged on a pair of electrodes connected to he amplifier.

Vith this preparation the sensory action currents uced by stretching the muscle are much larger ose in the sciatic, since they are led off from a erve trunk, and the ratio of active to inactive refore greater. The records showed the same general features as those from the sciatic; most of the responses conformed to a standard size; their frequency, but not their size, varied with the degree of tension on the muscle, and they recurred at irregular intervals with occasional suggestions of regularity. It was obvious, however, that the responses were not all derived from one and the same nerve fibre, for two would often appear with such a short interval between them that the refractory state left by the first would have prevented the development of the second if only one fibre were concerned. Our preparation evidently contained several sensory fibres and not the single one we had hoped for, and we began to consider whether we ought not to try some other muscle. But before we abandoned the sterno-cutaneous Dr. Zotterman suggested that we should try cutting off small strips of muscle in the hope that we should be left in the end with a piece containing only one end organ.

This method was successful and its results can be seen at once in Fig. 8. The record marked A shows the sequence of responses when the whole muscle is extended by a 2 gm. weight. A small strip was cut away, and the same stimulus now gave the record B with fewer action currents and a greater approach to regularity. C was made after another cut, but t
weight was now reduced to 1 gm. to avoid dam
the slender strip of muscle remaining. T
responses are larger is probably due to th
ment of the electrodes between eac

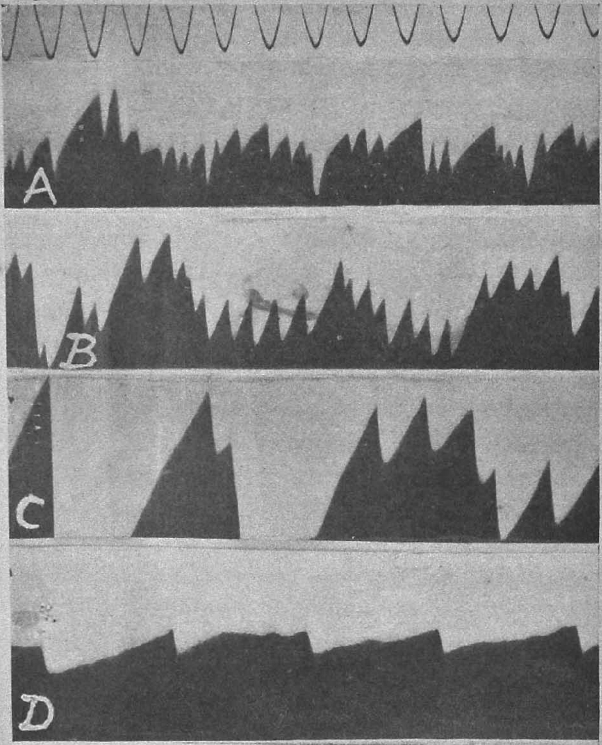

FIG. 8. IMPULSES PRODUCED BY STRETCHING THE STERNO-CUTANEOUS MUSCLE.

The weight has been in action for 10 sec. before each record is made.
Time marker (in A) gives $\frac{1}{100}$ sec. intervals. The responses vary in
n the different records as the preparation is rearranged between
ive observations.

cle intact. 2 gm. weight.
strip of muscle removed. 2 gm. weight.
strip of muscle removed. 1 gm. weight. Impulses in four

of muscle removed. 1 gm. weight. Single regular series.

Since the weight was smaller it is impossible to say whether the reduced frequency was caused by the removal of more end organs, but it is now possible to see (in the original record of which C is only a part) that the responses are arranged in four perfectly regular series recurring at intervals of .035, .042, .045 and .046 sec. respectively. The removal of the next strip gave the record D, one regular series of responses at intervals of .03 sec., and at a later stage in the experiment another strip was removed and the responses vanished completely.

Since two or more sensory end organs acting independently could scarcely give rise to a single regular series of impulses, the preparation used in record D must have contained only one end organ, and this end organ gave a regular series of discharges in response to a constant stimulus. The frequency of the impulses given by preparation D was not invariable; it depended on the weight used as the stimulus and declined gradually as the duration of the stimulation was increased. These relations will be dealt with later. What is of more concern at the moment is to discuss how far this behaviour is peculiar to the frog's muscle spindle or whether it is common to sensory end organs in general.

Regular Discharge from End Organs

If each end organ when stimulated sends out
regular succession of impulses, the responses i

cords from sensory nerves will consist of a number of independent but regular rhythms, and it ought to be possible to trace these by a fairly simple analysis. In the records from the frog's sterno-cutaneous this can nearly always be done, as in Fig. 8 C. In many other experiments from the same muscle, intact or partly cut away, two or three regular rhythms could be traced, though there were occasional impulses which would not fit into a series. These occasional irregularities are more obvious when the stimulus is very weak and the frequency of discharge very slow.

In other forms of sensory ending, however, the regularity is much less. Many records have been made of the sensory nerve impulses produced by moderate pressure on the toe pad of the cat. The nature of the end organs concerned is uncertain, but the number in action cannot have been great, for the total number of impulses per second was often less than 100. An example of these responses is shown in Fig. 9. The difference in the form of the responses from those in Fig. 8 is due to the fact that they are partly diphasic (see p. 22), and their duration is shorter because the preparation is kept at the body temperature of a warm-blooded animal.[1] In these records

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[1] In mammalian preparations the sense organs are not removed from the body, since it is important that they should be supplied with oxy- ated blood. The animal is killed by decapitation under deep chloro- anæsthesia and the circulation is maintained by the surviving he lungs being artificially ventilated.

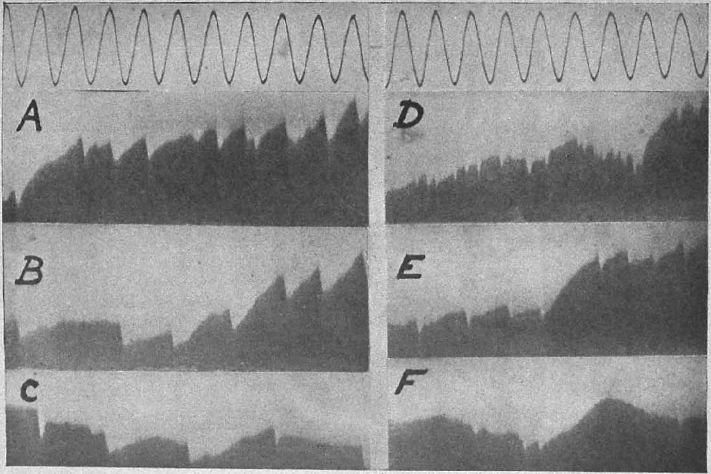

FIG. 9. IMPULSES PRODUCED BY MODERATE PRESSURE ON CAT'S TOE PAD, RECORDED FROM THE CUTANEOUS BRANCH OF THE INTERNAL PLANTAR NERVE. TIME MARKER (A AND D) GIVE $\frac{1}{100}$ SEC. INTERVALS.

A, B and C from one preparation
(monophasic responses).
A. During gradual increase of pressure.
Steady pressure of 500 gm. maintained for 5 sec.
„ „ 100 „ „ 3 „

D, E and F. Another preparation
(diphasic responses).
D. During gradual increase of pressure.
E. Steady pressure of 500 gm. maintained for 5 sec.
F. Disc resting on pad.

there are often one or two regular series of impulses with periods varying from 80–20 per sec., and other series can be made out if it is admitted that the intervals between successive impulses in the series may vary by 5 or 10 per cent. But even so there are many impulses which will not fit into the scheme, and it is very doubtful if the regular rhythms are ever maintained without disturbance for periods of a second or more, as they are in the frog's muscle.

In other types of end organ—those responsive to a light touch on the skin or to the movement of a hair—there is even less regularity than in the pressure organs, though this may be due in part to the fact that the frequency of the discharge declines rapidly. It is clear, then, that a completely regular succession of impulses in the sensory nerve fibre is the exception rather than the rule, though occasional regular sequences of short duration are met with in almost every preparation so far examined.

The explanation of this is probably simple enough. In the sterno-cutaneous preparation it is possible to ensure the condition that only one end organ is present, and therefore the impulses in the nerve fibre must all be derived from that end organ. With other types of end organ it has not been possible to isolate a single one, and the important point is that several end organs are usually connected to a single nerve fibre. e muscle spindle is an exception, for in the mam- n type at least one spindle has several nerve fibres of its own, but other end organs such as the Pacinian corpuscles, the Golgi Mazzoni bodies, etc., are often found in groups of three or four, each organ in the group being supplied by a branch from a common nerve fibre. With such an arrangement the impulses travelling in one nerve fibre are no longer the product of only one end organ, and the sequence of impulses will depend on the way in which the different end organs interact. When a nerve fibre divides, an impulse set up in one of the branches will activate the other branches as well as the parent fibre, and therefore an impulse set up in one end organ can scarcely fail to modify the behaviour of the others connected with it. How it will do so is not certain, but it seems likely that it would give rise to a refractory state in the end organs comparable to that given by the impulses which originate from them. Now if each end organ, when not interfered with, would produce a regular series of impulses, the interaction of three or four might very well produce just such a jumble of regular and irregular intervals as appears in the records. In fact, the sequence of impulses would be comparable to the disordered heart beat when the normal rhythm is disturbed by beats arising from a diseased area. There is, therefore, no reason to suppose that the regular response of the muscle spindle is peculiar to this type of end organ; for we cannot expect to find regular sequences when several end organs are linked together by a common nerve fibre.

Production of Repeated Impulses : Nerve Fibres and End Organs

There is no doubt that the frog's muscle receptor discharges a regular series of impulses when stimulated, and from what has been said above there is a considerable likelihood that other types of end organ would do so too if they were not subject to one another's interference. We are familiar enough with rhythmical activity in living cells, cardiac muscle or ciliated epithelium, for instance, and at first sight the activity of the end organ might seem to be closely related to these. No doubt they are related, but there is also an important distinction which must not be overlooked. In the absence of interference the heart and the cilia beat regularly and continuously, but the muscle spindle is normally at rest and beats only when it is stimulated.

We can best account for this type of rhythmic activity by relating the behaviour of the end organ, not to that of a continuously active tissue like the heart muscle, but to that of the nerve fibre from which the end organ is derived. An ordinary nerve fibre does not send out a rhythmic succession of impulses when it is stimulated, and we can answer the question why the end organ " beats " by asking instead why the nerve fibre does not. The usual stimulus employed to excite a nerve fibre is a very brief electric current, and this has no time to set up more than a single impulse. As the refractory period passes away the excitability of the nerve returns, and in about .02 sec. it is back at its original value, and the nerve can be excited again by a current of no more than threshold strength. The " recovery curve " of a frog's sciatic nerve is given in Fig. 10, and it shows the strength of stimulus needed to set up a second impulse at various intervals after the first. Now if instead of two brief stimulating currents we employed a steady current of the strength shown by the dots, A^1, A^2, etc., in the figure, we might expect that as soon as the recovery of the nerve had reached the proper value a second impulse would be set up and that this would be succeeded after an equal interval by a third and so on as long as the current continued. If the current were weaker the impulses would recur at longer intervals, as at B^1, B^2, etc. But in fact unless the current is very strong indeed, it will never give rise to more than the first impulse of the series. The cause of this failure lies in the very rapid " adaptation " of the nerve to the stimulus. The same process of accommodation or adaptation which makes a slowly-

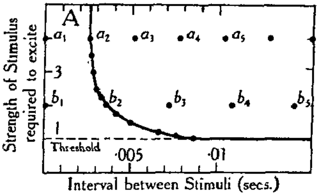

FIG. 10. RECOVERY CURVE OF FROG'S SCIATIC NERVE.

During the absolute refractory period (.002 sec.) a second stimulus, however strong, will not excite. The excitability returns gradually during the next .006 sec. (relative refractory period) and a stimulus applied during this period will excite if strong enough. Threshold strength is that required to excite the resting nerve.

increasing current unable to excite will also cause a rapid decline in the exciting power of a current which is kept at a constant value. Thus by the time the nerve has recovered from the refractory state left by the first impulse the constant current is no longer capable of exciting it again. This state of affairs is represented in the diagram in Fig. 11 A, the evanescent excitatory process being represented by the dotted line. Below this C is a similar diagram showing the rhythmic discharge which would be produced if there were no adaptation and therefore no decline of the excitatory process.

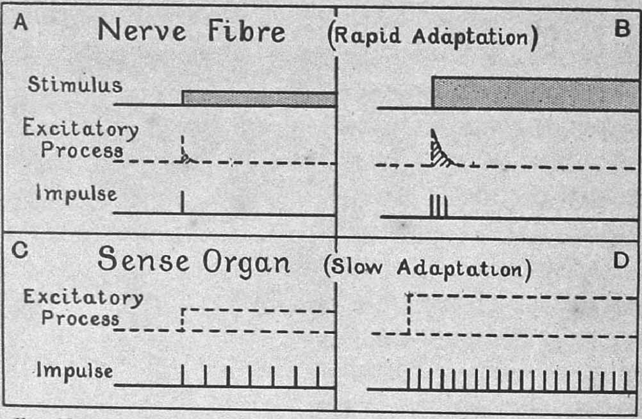

FIG. 11. DIAGRAM TO SHOW EFFECT OF A CONTINUED STIMULUS ON A NERVE FIBRE AND A SENSE ORGAN.

In the nerve fibre the excitatory process declines almost instantaneously, and only one impulse is set up unless the stimulus is very strong. In the sense organ adaptation is much slower and a succession of impulses is produced.

On these lines the frog's muscle spindle may be regarded as a modified nerve fibre without the rapid adaptation which prevents the nerve fibre from responding rhythmically. But the resemblance is really stronger, for the nerve fibre will give a brief series of impulses if the current is strong enough. Fig. 1 B is intended to show this, the excitatory process lasting long enough to produce three or four impulses. In D, where there is no adaptation, the increase in the stimulus leads to a greater frequency of discharge, as indicated already in Fig. 12. But here, too, there is a closer resemblance between the nerve fibre and the end organ than appears in the diagram, for the muscle spindle does show the phenomena of adaptation and other types of end organ show it in a higher degree, some of them becoming adapted almost as rapidly as the nerve fibre.

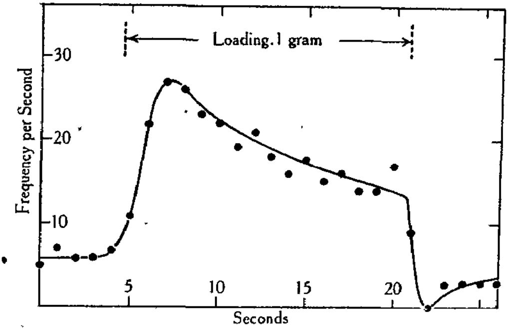

FIG. 12. FROG'S STERNO-CUTANEOUS PREPARATION. CURVES SHOWING THE FREQUENCY OF IMPULSES PER SEC. PRODUCED BY STRETCHING THE MUSCLE.

The bearing of this on the functions of the different end organs is so important that it needs a chapter to itself. Our chief concern at the moment is to relate the behaviour of the end organ to that of the nerve fibre, and for this purpose the muscle spindle will serve as well as any other type. The existence of a process of adaptation comparable to that of the nerve fibre is shown (*a*) by the fact that there is a gradual decline in the frequency of the discharge under a constant stimulus and (*b*) by the fact that a stimulus which increases slowly is less effective than one increasing rapidly to the same final value. The data from several experiments on these points are given in Fig. 12 and 13. In these curves (as in many others to come later) the ordinates give the frequency of the impulses per sec., determined by counting the total number over a short period ($\frac{1}{10}$ to $\frac{1}{5}$ sec.). In Fig. 12 it will be seen that with a constant stimulus the frequency has declined to half its initial value in about 10 sec. In Fig. 13 the tension on the muscle was increased at various rates by stretching an elastic band attached to it, and the frequency is greatest when the stimulus increases most rapidly. Just as in the nerve fibre the rate of increase of the stimulus determines whether it will excite or not, so here the rate of increase determines the frequency of the discharge, i.e., the intensity of the excitation.

Before we can conclude that the adaptation of the end organ is strictly comparable to that of the nerve fibre there is another possibility which ought to be considered. The decline in the frequency of the discharge might perhaps be due to fatigue and not to adaptation. " Fatigue " is a word which can mean so many things that a definition is essential. As used here it means a decline in activity caused by the previous activity of the organ, " adaptation " meaning a decline in excitability caused by the stimulus—the change in the environment—quite apart from the existence of activity. That we have to deal with the latter is shown at once by the curves in Fig. 13. Here the stimulus which increases most rapidly sets up a much greater number of impulses during the first 3–4 sec. than the intermediate stimulus, but the subsequent decline in frequency is the same for both. If the decline were due to fatigue it should evidently be the greater in the case where there has been the greater activity. That true fatigue may occur in the

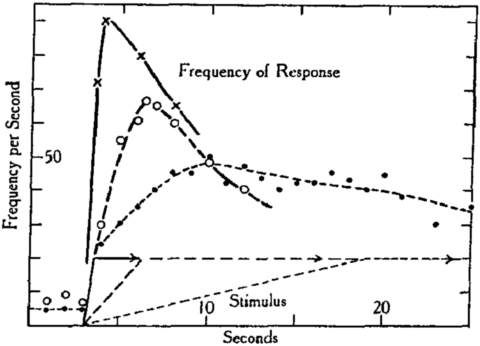

FIG. 13. DECLINE IN FREQUENCY FROM FIG. 13.

The frequency declines as the sense organ becomes adapted to the new conditions.

end organ is a possibility which cannot be altogether ruled out, but there is no doubt that adaptation in the sense defined above is a much more potent factor in causing the decline in frequency.

TIME RELATIONS OF END ORGANS AND NERVE FIBRES

It appears, then, that apart from the nature of the stimulus to which they react, the differences between the end organ and the nerve fibre are mainly quantitative. The greatest quantitative difference is in the rate of adaptation, which is very rapid in the nerve fibre and very slow in an end organ like the muscle spindle. Another difference is in the rate of recovery after an impulse has been set up. In the nerve fibre this is shown by the recovery curve (Fig. 10, page 63), which gives the strength of stimulus needed to set up a second impulse at various intervals after the first. We can construct a similar recovery curve for the end organ by finding the intervals between consecutive impulses with various strengths of stimulus. Curves made in this way for the frog's sciatic and the frog's muscle spindle are given in Fig. 14. Owing to technical difficulties the two curves are not strictly comparable, but there is no doubt that the process of recovery is a much slower affair in the end organ than in the nerve fibre. In the sensory endings of the frog (muscle and skin receptors) the maximum rate of discharge in a single fibre does not exceed 100 a second, whereas the nerve fibre can be made to convey a train of impulses at frequencies of 300–400 a second by repeated stimulation. Again, in the mammalian receptors for pressure, touch and pain, the maximum rate of discharge is almost certainly less than 200 a second and is probably nearer 100–150, though the refractory period of the nerve fibre is less than $\frac{1}{1000}$ sec.

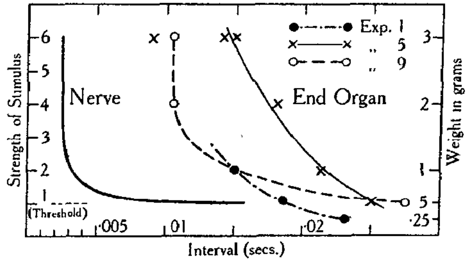

FIG. 14. RECOVERY CURVES FOR NERVE AND END ORGAN COMPARED. The curves for the end organ are constructed from three experiments with the sterno-cutaneous preparation. The nerve recovers its normal excitability much more rapidly.

This difference in time relations is important, for it means that the nerve fibre will never be pushed to the limit of its capacity for conducting impulses. When the frequency of the series is no greater than 100 a second, any point on the nerve fibre will have time to recover completely between the passage of each impulse and the next, and the series will be transmitted to the central nervous system without distortion. In fact the rapid recovery of the nerve fibre makes it practically an aperiodic conducting system as far as the slower end organ is concerned.

There is one other point which deserves mention, and this is that the general range of discharge frequency seems to be very much the same for every type of end organ. It is somewhat higher in mammalian end organs, as would be expected from the higher temperature at which they work, but it is remarkable that such diverse types as the muscle spindle and the receptors in the skin should both give a maximum frequency of about 100 a second. The observations on which this is based are not as numerous or as accurate as could be wished, but there is at least no indication of rhythms of higher frequency in any of the records which have been made.

It seems, then, that the duration of the refractory period and the recovery process is much the same whatever the structure of the end organ and is therefore determined by some factor common to all. What does vary widely from one end organ to another is the duration of the excitatory process or rather its rate of adaptation to a constant stimulus.

SUMMARY

Using a valve amplifier to magnify the electric changes and a capillary electrometer to record them it is possible to detect the action currents of single nerve fibres leading from sense organs in the muscles or the skin. The impulses in sensory fibres are of the same type as those already studied in motor fibres or in the isolated nerve, and there is the same all-or-nothing relation between the stimulus and the impulse. A preparation containing only one end organ can be made from one of the small cutaneous muscles in the frog, and it is found that the impulses produced by stimulating this end organ recur at regular intervals with a frequency in the neighbourhood of 30 a second. The frequency varies with the strength of the stimulus and the time over which it has been in action. In other preparations where several end organs may be connected to a common nerve fibre the discharge of impulses is often irregular, as the different end organs may interfere with one another's rhythm. The production of the rhythmic discharge may be explained by regarding the end organ as a structure having the same properties as the nerve fibre, but differing in its rate of recovery and its rate of adaptation to the stimulus.

CHAPTER IV

SENSORY DISCHARGES FROM VARIOUS TYPES OF RECEPTOR

Pressure—Touch—Hairs—"Postural" and "Phasic" End Organs—Pain.

WHAT may be called the mechanism of the end organ turns out to be closely allied to the mechanism of the nerve fibre. Though we are still a long way from reducing the processes of excitation, recovery, etc., to their precise physical and chemical details, they are, at any rate, of the same nature in the end organ as in other excitable structures.

It is now time to consider how this mechanism works in the different types of end organ and how it enables them to carry out their function as sense receptors.

The most obvious difference between the various types of receptor lies in the nature of the stimulus which excites them, but if we exclude the special sense organs for the present the list of stimuli is not so formidable. The taste buds and similar organs are sensitive to chemical changes, and there are organs which respond to changes of temperature, but for all the rest the stimulus is a mechanical change. There may be specific receptors for a pressure, a touch, tension on a muscle, or the movement of a hair or of a joint surface, but in every case the stimulus is one which will produce some mechanical strain or deformation in the end organ.

A study of the discharge from the chemical receptors might be extremely illuminating, but so far it has not been attempted. I have a few records of sensory discharges produced by changing the temperature of water flowing through a metal tube in contact with the skin, but they show nothing more than the usual rapid succession of action currents. We are left with the mechanical receptors, and of these the only ones studied in any detail are the tension receptors in muscle, the receptors for pressure, pain and touch, and the receptors at the base of the hairs.

The muscle receptors in the frog have been dealt with already. The main features of their response are, first, the very slow adaptation to a constant stimulus and, second, the regular discharge in each nerve fibre. A few experiments made on mammalian muscle have shown the same prolonged discharge under a constant tension, though the analysis of single fibre rhythms has not been attempted.

PRESSURE

The response of the organs sensitive to pressure has been studied in a small cutaneous nerve which supplies one of the toe pads of the cat's hind limb.[1]

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[1] Adrian & Zotterman, *Journal of Physiology*, Vol. 62, p. 465, 1926.

The region supplied by the nerve (half the ventral surface) is free from hairs and is covered by fairly tough skin. The pressure stimulus is produced by a glass disc, 11 mm. in diam., which is held in contact with the pad and to which varying degrees of pressure are applied by the extension of a spring fastened to the other end of the lever which carries the disc. No attempt was made to identify the histological type of end organ which responds to pressure[1] or to restrict the activity to a single nerve fibre. The latter was unnecessary, for the total number of impulses per second was usually below 400, even with pressures of 500 gm. or more on the disc. This must mean that very few nerve fibres are concerned in signalling the pressure changes from this part of the toe, and indeed there is no reason to suppose that many would be required. Owing to its power of responding with

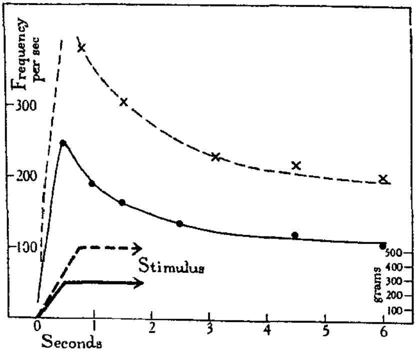

FIG. 15. EVOLUTION OF SENSORY DISCHARGE PRODUCED BY PRESSURE ON CAT'S TOE-PAD, SHOWING THE FREQUENCY OF IMPULSES PER SEC. WITH PRESSURES OF 250 AND 500 GM.

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[1] There are several Pacininian corpuscles in the subcutaneous fat. These are easily dissected out, but we have not succeeded in recording impulses from an isolated corpuscle.

different frequencies one end organ should be enough to signal the intensity of the stimulus. More would be needed if the exact site of stimulation were to be signalled as well, but it is not likely that there is a very accurate localisation of pressure within the small area supplied by the nerve.

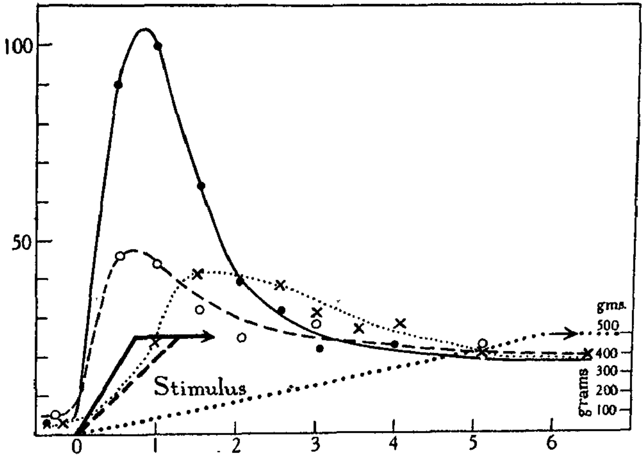
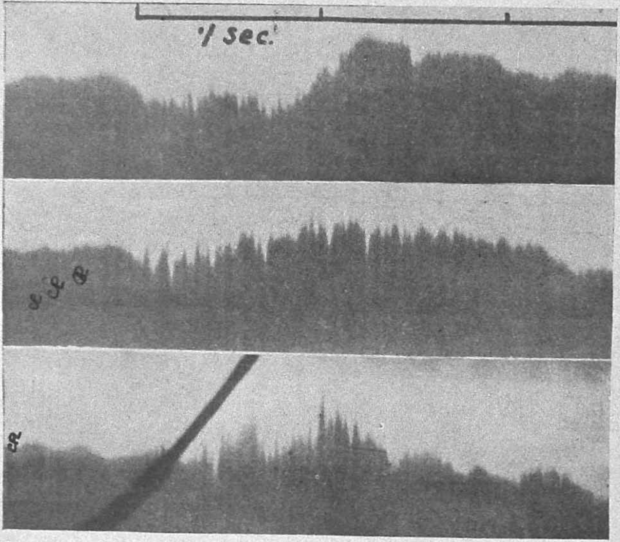


FIG. 16. AS FIG. 15, WITH PRESSURES OF 500 GM. APPLIED RAPIDLY OR SLOWLY.

The stimulus is most effective when the pressure changes rapidly.

The nature of the action currents has been shown already in Fig. 9. They are of the usual type; they follow the usual all-or-nothing rule in that their size does not vary with the intensity of the stimulus, and the records often show several regular rhythms, although the regularity is less than in the frog.

The main feature of the discharge from the pressure organs is summed up in the two figures, Fig. 15 and 16. It will be seen that the frequency of the impulses varies with the rate of increase of the pressure as well as with its actual value at any moment. The frequency declines when the pressure is constant. The rate of decline varies considerably from one preparation to another, but is always more rapid than the rate of decline for the frog's muscle spindle. This is not due entirely to the higher temperature and quicker time relations of the warm-blooded prepara-



Adrian & Zotterman.

FIG. 17. THREE RECORDS OF IMPULSES PRODUCED BY LIGHT TOUCH ON CAT'S TOE-PAD.

A disc (weight 5-15 gm.) is lowered gently on to the pad and allowed to remain there. The discharge lasts for .1 to .2 sec. and then subsides.

tion, for a slower rate of decline is characteristic of the muscle receptors in the cat as well as those in the frog.

TOUCH

A very different kind of discharge is observed if we lower the disc very gently on to the surface of the toe pad instead of pressing it down firmly. When the weight on the disc does not exceed 10 gms. or so there will be very little deformation of the sense organs below the skin, and the sensation which would be aroused would presumably be one of " touch " rather than of " pressure." Three records of the sensory discharge to a light touch of this kind are given in Fig. 17. It should be noted that the recording surface is travelling at a much slower rate than in the previous figures. At the moment of contact there is a sudden, rapid outburst of impulses, but the whole thing is over within a fifth of a second, although the disc is still resting on the skin. Here, then, we have

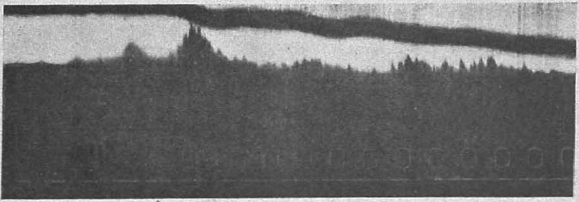


FIG. 18. IMPULSE DISCHARGE PRODUCED BY BENDING A GROUP OF 3-4 HAIRS.

Movement begins at the fall of the signal line. The hairs are held in the bent position, but the discharge subsides within .5 sec. Decerebrate preparation.

an example of adaptation which proceeds so rapidly that it is nearer that of the nerve fibre than that of the muscle spindle.

HAIRS

A brief discharge of the same kind is obtained when a hair is moved. Fig. 18 gives a record made from a small cutaneous nerve in the ear of the cat. At the signal a group of three or four hairs on the external surface of the ear were bent backwards by a small glass hook and held in the bent position. The exact duration of the movement is not recorded, but the discharge evidently ceases very soon after the hairs have reached their final position.

It does not follow that every hair organ becomes adapted so rapidly to a change in the position of the hair. The long vibrissæ on the snout and the guard hairs inside the ear have probably more highly developed sense organs and these may react quite differently, but it is at least clear that a rapid adaptation is characteristic of a great many of the end organs in the skin.

"POSTURAL" AND "PHASIC" END ORGANS

We can summarise these differences in adaptation rate in the diagram given in Fig. 19, and this diagram suggested at once an interesting correlation between the rate of adaptation and the function of the end organ. It is many years since Sherrington first pointed out that the motor activities of the body could be broadly divided into those producing sustained postures and those producing rapid, fluctuating movement. He distinguished the reflexes concerned as "postural" and "phasic," and these words have passed into the accepted vocabulary of the physiologist. The distinction has become so popular of late that one may hesitate to cast the net still wider by including in the same two categories not only the reflexes but the sensory organs which produce them. Yet the distinction is quite as clear on the sensory side as it is on the motor. In the postural reflexes there is a persistent activity of certain muscles, although the

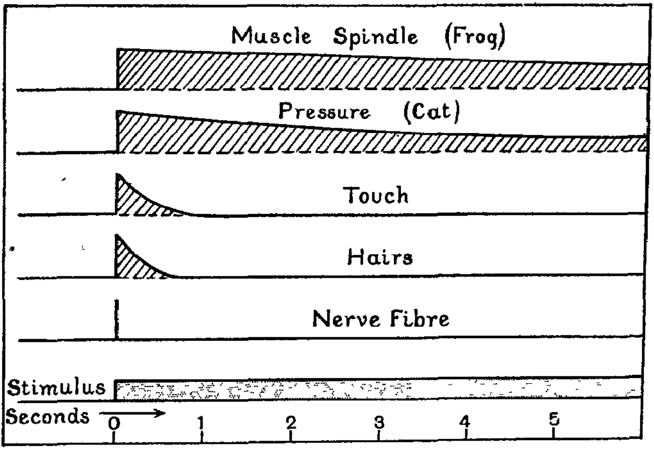


FIG. 19. RESPONSE TO A CONTINUED STIMULUS IN NERVE FIBRE AND DIFFERENT TYPES OF END ORGAN.

Adaptation is most rapid in the nerve fibre and slowest in the sense organs in muscle.

environment remains relatively constant. The persistent activity is known to depend on a persistent inflow of sensory impulses and the receptors concerned must therefore be capable of giving a persistent discharge under a constant stimulation—in other words they must show a very slow rate of adaptation. Many groups of receptors interact to determine the posture of an animal, but the most essential group is that in the muscles themselves, and we have seen that these do in fact adapt themselves very slowly. As long as the muscle is under tension the discharge from the end organs will continue. The frequency declines, but the discharge from a frog's muscle can still be detected, although the tension has remained constant for as long as ten minutes.

Clearly, then, the "postural" end organs must adapt themselves very slowly. The frog's muscle spindle is a good specimen of the class. For the phasic reflexes, on the other hand, a persistent discharge from the end organ would be quite unnecessary. The phasic reflexes are responses to sudden changes in the environment, and the end organs in the skin are quite capable of signalling these. It would, I think, be possible to make out a case for regarding a rapid adaptation rate as a definite advantage in a "phasic" end organ, but it is enough to point out that it is certainly no disadvantage, for the character of the phasic reflexes makes a persistent sensory discharge unnecessary.

The end organs in the skin and at the roots of the hairs may, therefore, be taken as examples of "phasic" end organs with a rapid adaptation rate. The pressure organ comes midway between the two groups, both as regards its adaptation rate and its function. It may serve to illustrate the point that there is no hard and fast line between what is postural and what is phasic, either on the motor side or on the sensory.

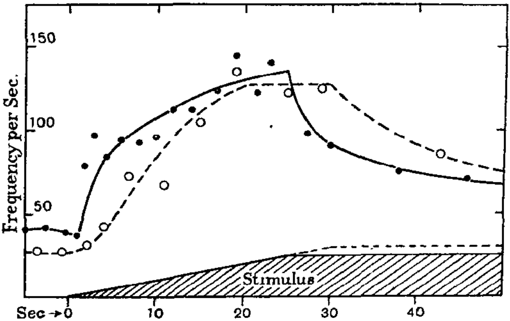


FIG. 20. EVOLUTION OF "PAIN" DISCHARGE WITH NEEDLE GRADUALLY PRESSED THROUGH THE SKIN

Cat's toe-pad and cutaneous nerve. Two experiments. (*cf.* Fig. 21.)

PAIN

If a sharp needle attached to a rigid lever is pressed slowly on to the cat's toe pad there is a discharge of impulses from the sensory nerve which increases in frequency as the needle is driven further and further into the skin. Fig. 20 shows the evolution of the discharge in two experiments, and Fig. 21

gives three portions of a continuous record made in the same way from a sensory nerve supplying the skin of the frog. As the needle ultimately penetrates the skin, there can be no doubt that the sensory discharge is one which would give rise to pain in the cat or the frog if it had been set up in a living animal. Thus an analysis of the impulses should tell us how far, if at all, the message which arouses pain differs from those arousing other forms of sensation.

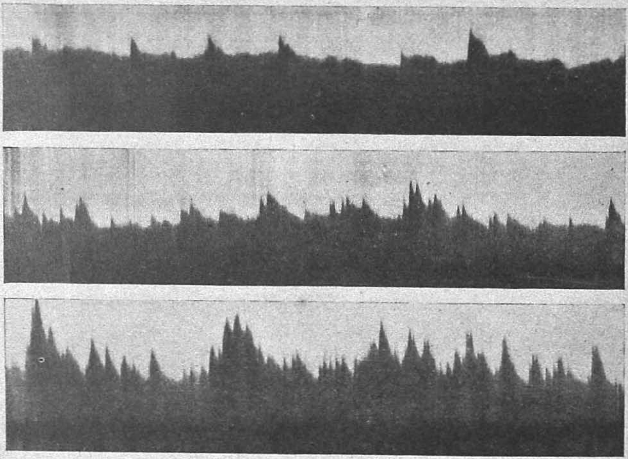


FIG. 21. PREPARATION OF FROG'S SKIN AND CUTANEOUS NERVE. "PAIN" IMPULSES PRODUCED BY FINE NEEDLE POINT SLOWLY PRESSED THROUGH THE SKIN.

Three strips taken from the same record showing the impulses at 4, 12 and 18 sec. after the downward movement of the needle had begun. (*cf.* Fig. 20.)

Many years ago Johannes Müller laid down certain principles which are usually referred to as the

"Doctrine of Specific Nervous Energy." This doctrine is based on the fact that each sense organ or sensory nerve fibre evokes a specific sensation, whether it is excited by the appropriate stimulus or by artificial means, e.g., an electric current.[1] It is often taken to mean that each type of sense organ and nerve fibre transmits a change peculiar to it, a specific form of nervous activity in fact. Müller certainly did not mean this, for he states "We do not know whether the different energies of the sensory nerves are intrinsic in them or in the parts of the brain and cord to which they run."

We have already seen that there is no specific activity in the sensory nerves corresponding to each type of sense organ. The fibres from the various receptors may differ somewhat in their time relations, but the fundamental activity, the nervous impulse, is common to all and is common also to the motor nerve fibre. In the case of the pressure and the muscle receptors the discharges are so much alike that the different quality of sensation aroused must depend on the central connections of the fibres. In the case of pain, however, we have still to determine whether there may not be some specific character in the activity of the nerve fibre.

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[1] "The specific sensations of each sensory nerve can be evoked by different internal and external stimuli." "Sensation is not the transmission to consciousness of a quality or state of an external body, but of the quality, or the state, of a sensory nerve as produced by an extrinsic cause, and these qualities differ in the different sensory nerves."

There is ample reason to look for some difference either in the form of the impulse or in the frequency or grouping of the discharge. The fact that pain is aroused by mechanical, thermal or chemical stimuli of sufficient intensity led originally to the view that it was produced by the excessive stimulation of any cutaneous receptor, but this view was abandoned when it was found that there were definite touch, temperature and pain spots on the skin.[1] It is now believed that there are special receptors and conductors for pain as there are for touch and temperature, but the specific character of pain, its urgency, massiveness, etc., suggest that the receptors and conductors differ considerably from those of other types of cutaneous sensation. For instance Head and Rivers have put forward the view that the sensory nerves have been evolved from two distinct sources, a more primitive "protopathic" system reacting violently to intense stimuli such as pain or extremes of temperature, and a later and more delicate "epicritic" system which reacts to slighter changes in the environment and is able to restrain the activity of the protopathic system. On this theory the nerve fibres concerned with pain must belong to a system phylogenetically distinct from those concerned with touch, and the work of Ranson has added the view that the pain fibres may be non-medullated, i.e., distinct in structure from those concerned with other forms of sensation.

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[1] Cf. von Frey, *Berichte d. k. Sächs, Ges. d. Wiss*, 23, 1896.

So far, however, as the individual impulse is concerned, if any difference exists between the pain impulse and that from a pressure organ or a muscle, it is too small to be detected by the present method. It is true that the magnitude of the action currents in fibres from different receptors cannot be accurately compared, though there is no reason to suspect any considerable difference, but the duration of each response is certainly the same within the limits of error. The recent work of Erlanger and Gasser has shown that the impulses set up in the different sensory fibres of a mixed nerve trunk do not all travel with the same velocity, and it is possible that the pain fibres may conduct at a slower or faster rate than those concerned with touch or pressure. We hope to have some definite evidence on this point before long, but in the meantime there is quite enough to show that there are no radical differences between the impulses which produce the various modes of sensation.

The frequency of the discharge is not characteristic; for in the response to the prick of the needle it varies between the usual limits of about 5–100 a second in each nerve fibre. It is not uniformly high, as it would be if "pain" were due to the excessive stimulation of any kind of receptor. Nor is there any sign of a characteristic grouping of impulses, for there is the usual mixture of regular and irregular rhythms. But there is one fact which is at least suggestive, and that is that the pain discharge is usually one of fairly long duration. This is best seen in another series of experiments in which the skin surface was stimulated by gently lowering a needle point on to it and allowing it to rest there. The needle was carried at the end of a lever counterbalanced so that the force on the needle point varied from a weight of ½ gm. to one of 100 gm. On the human skin the lightest weight gives nothing more than a momentary sensation of contact, but weights above about 20 gm. produce a

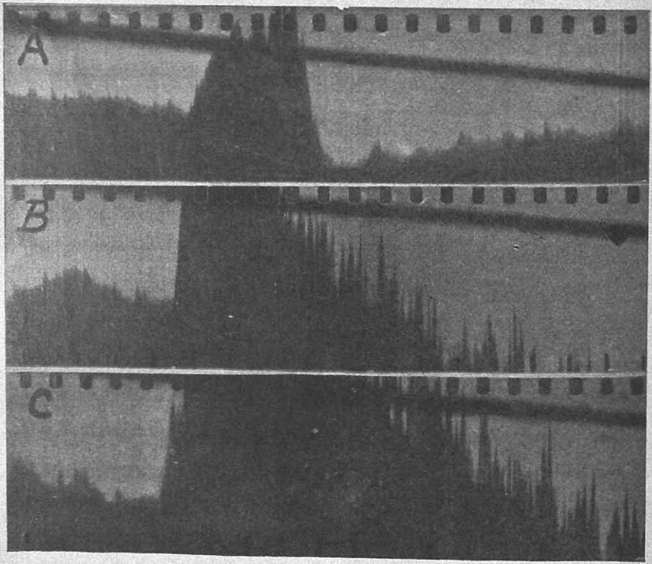

FIG. 22. CAT'S TOE-PAD AND CUTANEOUS NERVE. NEEDLE ON WEIGHED LEVER LOWERED ON TO THE SKIN AND ALLOWED TO REST THERE.

A.	Weight on needle	3 gm.	Very brief discharge.
B.	,, ,,	43 gm.	Continued discharge.
C.	,, ,,	99 gm.	,, ,,

distinct prick, the exact weight at which the transition occurs depending, of course, on the particular skin surface under test. In the cat's toe-pad or the frog's skin the lightest stimulation gives a discharge of impulses lasting for a fifth of a second or less (Fig. 22 A), but if the weight on the needle is above 40 gm. the discharge persists for as long as 20 seconds (Fig. 22 B and C).

In the cat's pad the light contact of the needle point may excite the special touch receptors and the harder contact may excite the pain endings as well, but the real interest of these records lies in the fact that there is very little difference in the initial frequency of the discharge whatever the weight on the needle. This is seen most clearly in the experiments on the frog's skin, where the impulses are easily counted, and records from one experiment are given in Fig. 23. The initial frequency is no higher when the weight is large then when it is very small; it is difficult to avoid the conclusion that no fresh nerve fibres are brought into play by the stronger stimulus and that the same fibres give the brief discharge with the weak stimulus and the persistent discharge with the strong. If this is so, it is possible that a brief discharge in certain nerve fibres may give rise to a momentary sensation of contact and a persistent discharge *in the same fibres* to one of pain.

It is not likely that this is true of all the fibres concerned in signalling light touch and pain. The distribution of "touch spots" and pain spots on the skin implies the existence of specific receptors for the two sensations, and the "touch corpuscles" of

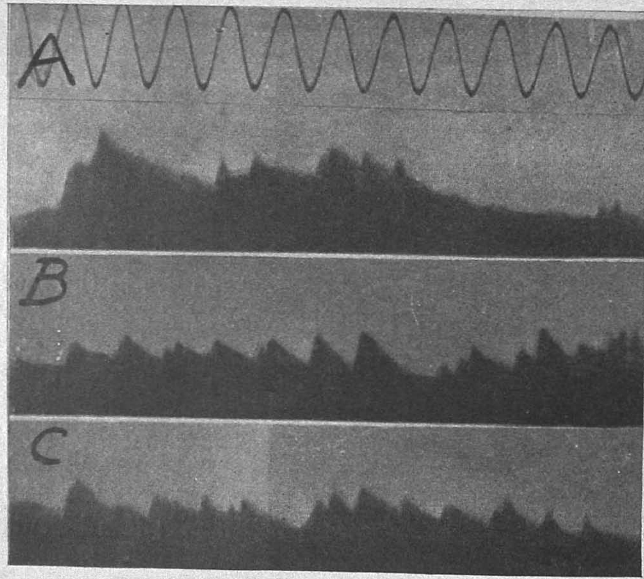

FIG. 23. FROG'S SKIN AND CUTANEOUS NERVE PREPARATION. PLATE RECORDS SHOWING IMPULSES PRODUCED BY NEEDLE POINT RESTING ON THE SKIN WITH DIFFERENT WEIGHTS.

Moment of stimulation coincides approximately with the release of the plate.

A. Weight $\frac{1}{3}$ gm. The record shows almost the entire discharge.
B. ,, 10 gm. Continued discharge.
C. ,, 25 gm. ,, ,,

Meissner are no doubt specific receptors which would not give rise to pain in any circumstances, but there are many regions where the number of specialised end organs does not seem to be enough to account for the number of points which are sensitive to touch. In the frog's skin there are relatively few specialised end organs and the greater part of the skin is supplied by the naked terminations of nerve fibres, ending in connection with the ordinary cells of the epidermis. Sherrington has pointed out that this form of termination would provide a suitable form of pain receptor, since it may be expected to respond like a nerve fibre to any form of stimulus which is sufficiently strong. It would certainly make for economy if one and the same nerve fibre could be used to signal non-painful stimulation by a brief discharge and painful stimulation by a much longer one. The difference in the sensation aroused could be accounted for on the ground that the summated effect of the longer discharge would allow it to break through into parts of the central nervous system which were not accessible to the brief discharge. A long duration of the discharge is evidently not essential, for pain can be aroused by stimulating a nerve trunk by a single induction shock, but the intensity of the pain is much greater when the nerve is large than when it is small, so that here too the number of impulses arriving at the central nervous system seems to determine the intensity of the reaction.

According to this suggestion the main feature of the discharge which causes pain is that it must possess a certain massiveness, and it is possible that some of the naked axis cylinders which act as pain receptors may serve also for signalling milder forms of stimulation which do not give rise to pain. But it is clear that a great deal more will have to be done before we can be certain of this.

SUMMARY

Records have been made of the discharge of sensory impulses produced by the following stimuli: tension on a muscle, pressure, touch, movement of hairs, and pricking with a needle point. With constant stimulation the discharge from the end organs in the skin declines in frequency much more rapidly than that from a muscle or a pressure organ. This difference in the adaptation rate of the end organs corresponds with the different types of reflex action which they produce, and the end organs may be classified, like the reflexes, as "postural" or "phasic."

The impulses produced by a pain stimulus are of the usual type and have the usual range of frequency, but there is some evidence that the discharge must have a certain mass (duration and intensity) if it is to evoke the pain reaction.

CHAPTER V

THE EFFICIENCY OF THE SENSE ORGANS: ADAPTATION

The Relation Between the Sensory Discharge and the Intensity of the Stimulus—Adaptation and Movement—The Eye—Summary

HAVING now some idea of the kind of message which is sent from each receptor, we can discuss what sort of information this message can convey to the central nervous system. Since there is no reason to limit its powers we will assume that the central nervous system is able to get every scrap of information out of the message, or let us say everything that could be learnt by a physiologist who could isolate each nerve fibre and record the impulses in it.

RELATION BETWEEN THE SENSORY DISCHARGE AND THE INTENSITY OF THE STIMULUS

The arrival of a discharge in a particular sensory nerve fibre will mean, of course, that a particular receptor has been excited, and this will imply a particular form of stimulus in a particular locality. The discharge will begin to arrive very soon after the moment of stimulation, for the receptors dealt with so far react almost instantaneously to the change in environment.[1] Thus the nature of the stimulus, the moment of onset and the locality could be determined at once whatever the type of receptor involved. The accuracy of localisation will naturally depend on the number of receptors of the same type in the area which contains the stimulated region—or rather it will depend on the number of nerve fibres which lead from these receptors. If there is much overlapping in the areas supplied by the terminal branches of different fibres it might be possible to localise the stimulus more exactly by comparing the relative intensities of discharge in the different fibres.

This brings us to the most important point, the signalling of different intensities of stimulation. It is here that we find the greatest difference in efficiency between one receptor and another. Suppose first of all that we are dealing with an isolated nerve fibre stimulated electrically; that we can record the impulses and that from our record we have to find out all we can about the intensity of the stimulus. We could tell, of course, whether the stimulus had been strong enough to excite the fibre at all, but we could tell very little more. Unless the stimulus is very strong it will only set up a single impulse and the size of that impulse will be always the same. Thus the stimulus might be varied within wide limits and we

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[1] The interval between a sudden stimulus and the first impulse in the sensory fibre has not been worked out, but it is certainly less than $\frac{1}{20}$ sec. in most cases. In the eye the latent period may be considerably greater.

should be none the wiser. We could tell if it were very strong indeed, for the excitory process might then last long enough to set up two or three impulses, but the discharge would still give only a very rough idea of the intensity of stimulation.

This failure to give a graded discharge to graded stimuli is due to the very rapid adaptation of the nerve fibre to the stimulus and the consequent restriction of the discharge to one or a very few impulses. In a specialised receptor, on the other hand, the rate of adaptation may be much slower, and the discharge will consist of a succession of impulses recurring with a frequency which varies with the strength of the stimulus. Fig. 24 shows the progress of the discharge with different stimuli for the tension receptors in frog's muscle. Fig. 25 gives the relation between impulse frequency and strength of stimulus at a fixed time after the stimulation begins. These curves were not made from preparations with only one end organ, and therefore the increase in frequency

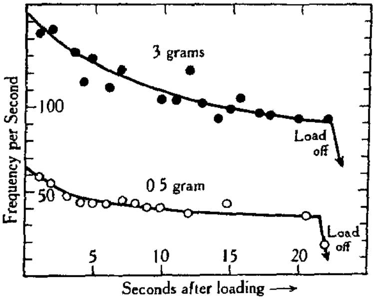

FIG. 24. FREQUENCY OF DISCHARGE PRODUCED BY STRETCHING FROG'S STERNO-CUTANEOUS MUSCLE WITH DIFFERENT WEIGHTS, SHOWING DEPENDENCE OF FREQUENCY ON THE INTENSITY OF THE STIMULUS.

may be due in part to an increase in the number of receptors excited when the stimulus is strong. But an analysis of the regular rhythms shows that a curve of much the same form would be given by a single receptor. Clearly, then, the muscle receptor in virtue of its slow adaptation gives a discharge from which the intensity of the stimulus can be deduced with great accuracy.

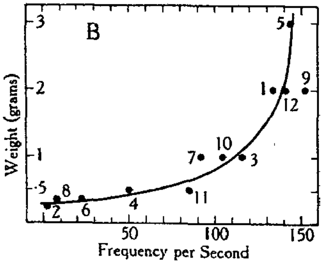

FIG. 25. FROG'S STERNO-CUTANEOUS PREPARATION. RELATION BETWEEN INTENSITY OF STIMULUS (WEIGHT ON MUSCLE) AND FREQUENCY OF DISCHARGE.

The pressure receptors in the cat's toe-pad behave in much the same way, although they become adapted more rapidly. In the skin receptors, however, the rate of adaptation is nearer that of a nerve fibre than that of a muscle spindle and the discharge in a single fibre will give very much less information about the intensity of the stimulus. The frequency of the impulses will still vary with the intensity of the excitation, but as this declines so rapidly we can only compare one stimulus with another by taking the entire evolution of the discharge into account.

Again, with a rapid adaptation in the end organ the effectiveness of the stimulus will depend much more on the rate at which it is applied (i.e., the rate of change of the environment) than on its final value.

For the "phasic" end organs, therefore, it would be impossible to construct a curve like those in Fig. 25, relating the frequency of the discharge to the intensity of the stimulus. The kind of relation which does obtain may be seen from Fig. 26, which gives the discharges produced by stimulating the frog's skin

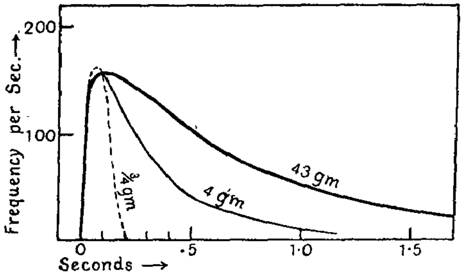

FIG. 26. FROG'S SKIN AND CUTANEOUS NERVE PREPARATION. STIMULATION BY NEEDLE POINT ON THE SKIN.

Duration of discharge depends on intensity of stimulation, but initial frequency does not.

with a needle point. Here, as in the other experiments, there may be several receptors in action, and the discharge from a single one may show less gradation, though the agreement of the initial parts of the curves makes this unlikely (see p. 87). The relatively long discharges obtained with the larger weights on the needle are probably comparable to those which are produced by an extremely strong constant current applied to a nerve fibre. They imply a stimulus which is so intense that it gives rise to pain. When the stimulus is of a non-painful character (touch or hair movement) the duration of the discharge is so short that the possibility of fine gradation is very small. For instance, a discharge which is over in $\frac{1}{10}$ sec. will only contain ten impulses, even if the frequency remains throughout at its maximum value (about 100 a second).

It follows that, as far as the single end organ is concerned, a complex receptor with a slow adaptation rate like the muscle spindle provides a much more efficient signalling mechanism than the simpler end organs which are not far removed from ordinary nerve fibres. Whether complexity of structure and a slow adaptation rate really go hand in hand is certainly doubtful, though it seems to be true for the limited range of end organs which have been investigated.

That end organs can be divided roughly into those which give a finely graded response and those which do not recalls the well-known distinction between epicritic and protopathic receptors drawn by Head and Rivers on the basis of their celebrated nerve regeneration experiment, but it is scarcely possible to relate their classification to the present data, since Head and Rivers were concerned solely with cutaneous sensation (touch, hair movement, pain and temperature) and the receptors for pressure and muscle tension do not enter into their scheme. At the same time it may seem odd that the sensation of touch on the hairless parts of the skin should be classed by Head and Rivers as epicritic and should appear in the present experiments as the product of a receptor which adapts very rapidly and can show very little gradation of response. Here, too, we may be comparing entirely different data, for the touch receptors in the cat's toe may differ from those in the human hand in structure as well as in function, and it would need an investigation of the specialised "touch corpuscles" before we could assert that all "touch" is due to end organs which adapt rapidly. It seems clear that some do not, for Sherrington has pointed out that the sensation aroused by a touch in certain parts of the skin, the alæ of the nose and the inside of the ear, persists long after the stimulus has ceased.

There is, however, another aspect of the question which has not been dealt with. We have been comparing the efficiency of single end organs, but a stimulus will rarely excite only one end organ and the central nervous system will take account of the number of sensory fibres in action as well as of the discharge in each fibre. Unless the receptors are very far apart an intense stimulus will excite more of them than a weak stimulus, and the complete message which reaches the central nervous system may therefore vary with the intensity of the stimulus, even though the message from a single receptor shows no gradation at all. Thus a large number of simple end organs would give as much information as a single complex end organ, and it is true enough that the complex organs, muscle spindles, Pacinian corpuscles, etc., have a very sparse distribution compared with that of the free nerve endings in the epidermis and elsewhere.

We ought, therefore, to think in terms of areas containing many receptors and not in terms of the single receptor when we are trying to estimate what sort of information reaches the central nervous system. But we have still left out what is perhaps the most important factor of all, namely, that the receptors form part of an organism which has the power of movement.

ADAPTATION AND MOVEMENT

If the organism were motionless the phasic receptors would discharge impulses whenever the environment changed, but they would cease to do so as soon as it had settled down to a steady condition. We take advantage of this when we are going to sleep, for the usual method consists in turning out the light, shutting out sounds as far as possible, arranging ourselves in bed so that all the muscles are relaxed, and then keeping quite still. Our consciousness of our body and its environment fades rapidly and sooner or later we go to sleep. This is a good example of the fact that the skin receptors become very rapidly adapted to a constant environment. The pressure receptors and the muscle receptors continue to discharge under constant stimulation, but we stop the latter by relaxing the muscles, and the former as far as we can by lying on a soft mattress, which distributes the pressure evenly. So, if we keep still, we cease to be disturbed by sensations from our limbs because they have ceased to send us any messages. That the absence of sensation is due to the absence of sensory messages and not to a withdrawal of attention from them can be shown by the painful experiment of trying to sleep in a jolting railway carriage or in a boat which pitches so much that we slide up and down in our bunk. The environment is continually changing, the receptors continue to send us messages, and we cannot withdraw our attention from them though we should be very glad to do so. We may be able to divert our attention by giving it a more entertaining message to consider, e.g., by reading a book, and in the end we may go to sleep, because the absence of sensory impulses is a favourable but not an absolutely essential condition.

It is easy to multiply instances of sensations fading owing to the adaptation of the receptors to a constant environment. We cease to be aware that our clothes are touching our bodies almost as soon as we have put them on. This may be due partly to the diversion of our attention to more interesting topics, but even if we try to focus it on the body surface we find that there is little to feel as long as we are careful not to move. But the point is that we have to be careful not to move. If we try to feel the things that are touching us, our clothes, our boots or what not, the natural tendency is to wriggle about so that the receptors are exposed to a changing and not a steady environment. If our attention is focussed on a mobile and sensitive part like the hand it is not at all easy to keep all the muscles completely relaxed when the sensitiveness of the skin is tested. Unless we take pains not to do so we make slight movements, and these keep alive the sensations from the rapidly adapting end organs. The importance of these exploring movements is shown by the fact that the verb to feel is used as often in an active as in a passive sense. We feel the hardness of a surface by pressing our finger against it, just as we feel the shape of an object by moving it about in the hand.

The fact that the receptors can be moved about in relation to the external world enlarges their scope enormously. To gain information about an environment there is no need to wait for it to change, for a motile animal can explore a stationary world by changing the relation of the receptors to the environment. Not only does this counteract the rapid adaptation which takes place in many of the receptors, but it enables us to extract information about the external world, not only from the exteroceptors on the surface of the body, but also from the proprioceptors—the highly efficient sensory apparatus in the muscles and joints. In the normal animal, therefore, both rapidly and slowly adapting end organs will co-operate to build up the complete picture of the external world, and the lack of detail in the message from the simple receptors will be filled in by the messages from the complex "postural" organs which are activated at the same time.

It has been suggested already (page 80) that the rapid adaptation of the "phasic" type of end organ may be an advantage to the organism. It might well be inconvenient if our central nervous system were to be continually flooded with messages from every part of the skin surface, but the main argument has been dealt with by Sherrington in his discussion of the value of reflex fatigue. He points out that the changing activity of the organism, the changing "reflex pattern," is determined, in part at least, by the rapid fatigue of the various reflex paths. In the same way the rapid adaptation of the sense organs will make for an absence of monotony and will allow each new sensory excitation to have its full effect on the central nervous system.

The sensation of pain is on a rather different footing as regards movement and adaptation. If it appears suddenly it is accompanied by violent protective movements, movements which attempt to withdraw the receptors from the sphere of influence of the stimulus, but if these fail our natural tendency is to keep the injured part at rest, even though it is still hurting us. Most pains seem to be due to an abnormal deformation, stretching or tearing, of the tissues, and any movement of the injured part will cause a change in the condition of the pain receptors which may renew or reinforce the excitation. The pulsation of the blood vessels and the oozing of fluids into the injured region may be quite enough to keep up a repeated excitation, even though the part is at rest as far as muscular movements are concerned. From the experiment on the frog's skin it seems that the rate at which the discharge subsides depends on the strength of the stimulus, and it is therefore difficult to compare the rate of adaptation with that of other receptors.

THE EYE

The complexity of the " distance receptors " make them a great deal harder to investigate than the sense organs in the skin and the muscles. But the optic nerve is made of fibres which are much like the ordinary fibres of a peripheral nerve trunk,[1] and it seemed essential to know whether they, too, carry out their function by conducting impulses of the usual discontinuous type. After various false starts, Mrs. Matthews and I found a suitable preparation in the eye and optic nerve of the conger eel. The investigation is still in progress, but it has already given results which are worth stating here, because they fall into line with those already discussed.

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[1] The chief difference is that their myelin sheath is not surrounded by the membraneous " neurilemma," which forms the outermost layer of a peripheral nerve fibre.

The eel was chosen because its optic nerve is long and slender and might, therefore, be expected to give electric responses of reasonable size. The actual number of fibres lies between six and ten thousand, and although this is greater than the number in a large nerve trunk, such as the frog's sciatic (which has about 3,000), it is much smaller than in the optic nerve of an animal whose visual sense is more highly developed. The technique of these experiments does not differ much from those on the simpler sense organs. The eel is killed and the eye and optic nerve are dissected out and set up in a stand with the nerve resting on the electrodes which lead to the amplifier. In front of the eye is an arrangement of diaphragms and lenses so that the image of an opal glass disc of varying size can be focussed on the retina. When a shutter is opened the disc is illuminated from behind by a lamp, adjusted so that the brightness of the surface exposed to the eye is of the same order as that of a piece of white paper held horizontally under a cloudy sky (i.e., about 500 metre candles; the illuminations actually used varied from 20 to 4,000 metre candles).

When the preparation is in the dark there is a complete or almost complete absence of electric responses in the nerve, but on exposure to light there is a discharge of the usual irregular oscillatory character. An analysis of the discharge on rapidly moving plates shows it to be made up of action currents of the usual type, diphasic or monophasic according to the condition of the nerve. The majority seem to conform to a standard size and duration, though there is often so much overlapping that it is difficult to separate the individual action currents. There is no doubt, then, that the discharge in the optic nerve is of the same type as that in other sensory nerves. In Fig. 27, for instance, a record from the eel's optic nerve is set alongside one made from the frog's sciatic. In the former the discharge is produced by allowing light to fall on the eye, in the latter by stretching the gastrocnemius. Apart from the larger size of the action currents in the sciatic (which has fewer fibres) the records are almost indistinguishable.

The production of the optic nerve impulses is a much more complex business than the excitation of a tension receptor in a muscle. The light takes effect on the rod and cone layer of the retina and an elaborate apparatus of nerve cells and branching processes intervenes between this layer and the fibres of the optic nerve. There is an appreciable interval between the moment at which the light falls on the eye and the moment at which the discharge of impulses begins. During this interval a change of electric potential has developed in the retina, and our results suggest that it is this change which is the immediate cause of the optic nerve discharge. It would lead us too far afield to discuss the electric changes in the retina (which have been known for many years) and their relation to the photochemical changes produced by the light. Hecht's analysis of the response of a much simpler type of eye has done a great deal to elucidate the chemical changes which form the actual receptor mechanism, and it is clearly better to study these, as he has done, in a structure less complex than the vertebrate retina. What we are concerned with here is not so much the mechanism of the eye as the way in which it carries out its function as a receptor of visual impressions.

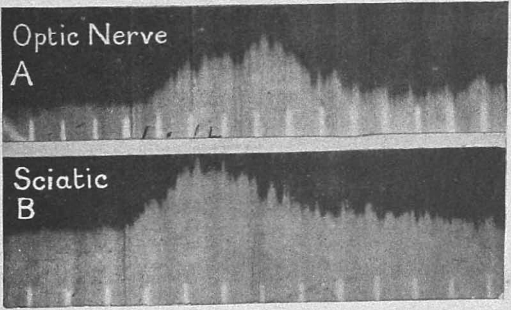

FIG. 27. A. ACTION CURRENTS IN THE OPTIC NERVE OF THE EEL (CONGER VULGARIS) WHEN THE EYE IS EXPOSED TO LIGHT. B. DITTO IN FROG'S SCIATIC NERVE PRODUCED BY TENSION ON THE GASTROCNEMIUS MUSCLE.

We have seen that it signals the appearance of a light by a discharge of impulses of the usual type. The frequency of the discharge in each nerve fibre is doubtful, but it is probably not much higher than 100 a second; thus the message sent from the visual receptor does not differ greatly from that sent by the receptors of the skin, and there is a further likeness in the decline of the discharge with a constant stimulus. The beginning of this decline can be seen in Fig. 27. By constructing the usual frequency curves it is found that the adaptation of the eel's retina to a constant stimulus is on a par with that of the pressure receptor in the cat and rather faster than that of the frog's muscle spindle. Unless the light is very weak or the preparation insensitive the discharge may continue for many seconds under a steady illumination of the retina, but there is always a rapid initial rise to a maximum frequency and then a decline, which is fairly rapid at first, but may be almost imperceptible later on. Whether this decline in rate should be put down to fatigue or adaptation is a matter of definition, but it is evidently related to the process we have called adaptation in the peripheral sense organs. It is not likely that it is a pathological effect, for the rate of decline is not appreciably slower when the circulation through the eye is preserved and there is much the same decline in the discharge of the frog's optic nerve as in that of the eel.

An uncritical examination of our own visual impressions would lead us to suppose that there is no such adaptation in the human eye, that a light of moderate intensity appears equally bright as long as we look at it. But it has been known for a long time that the brightness of an image does, in fact, decline fairly quickly provided that the eye is not moved. It is easy to satisfy oneself of this by looking at something which is faintly visible in a darkened room with one eye closed and the other kept from moving by light pressure with the finger on the lower lid. In twenty seconds or less the object will have disappeared and the whole field will be uniformly dark (not black however). As soon as the eye is moved the object reappears. The eye is a much more important sense organ in man than in the eel, but evidently the rapid adaptation of the eel's retina is shared to some extent by our own.

The existence of adaptation in the visual receptor will have much the same consequences as it has in the peripheral sense organs. Suppose first that the eye is not moved relatively to the visual field. If the latter does not change, there will soon be only a feeble excitation of the retina, and, finally, if the light is weak, there may be none at all. But if a light or a shadow moves across the field there will be an immediate change in the illumination of the different points in the retina. Parts which were shadowed will now be in the light and vice versa, and this will lead at once to a renewed excitation and a renewed discharge of impulses. The great effectiveness of a changing as opposed to a stationary visual field can be seen at once from records of the optic nerve discharge when a large illuminated disc is placed in front of the eye and a shadow is moved across its surface. Whenever the shadow moves there is a great increase in the frequency of the impulses and a rapid decline when the shadow comes to rest.

Thus a moving object will call attention to itself much more effectively than a fixed object, just as the movement of a point over the surface of the skin is a more effective stimulus than a steady contact. This agrees with what is known of the reaction of more primitive types of eye. An eel or a frog will respond to the sudden movement of the hand, but will pay no attention if the hand is kept still, however close it may be, and in these animals there is very little evidence of what is called pattern perception as distinct from perception of movement. In the human eye, too, the visual field for perception of movement is larger than that for perception of form—i.e., there is a region at the periphery of the retina where a steady illumination is quite ineffective, though a changing one can still excite.

But here too, as in the case of the peripheral receptors, it is a mistake to regard the eye as a stationary organ which must wait for the visual field to change. Not only do the eyes move with the head, but in man at least[1] there are constant small movements of the eyes which occur even when we gaze fixedly at an object. It is difficult to say how far these small movements are essential to normal vision, for in cases where there is a complete paralysis of all the external ocular muscles it is unlikely that the optic nerve or its central

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[1] Dodge, *Psychol. Review Monographs*, vol. I, p. 10, 1907.

connections will escape completely, and an impairment of vision might be due to this. In the preparation of the eel's eye, continued oscillatory movement of the eye would evidently have the same effect as an oscillation of the visual field. If the image of a bright disc were thrown on the retina, the regions at the periphery of the image would be continually passing from light to shade and vice versa, and the discharge from these would be constantly renewed, although the discharge from the steadily illuminated points at the centre of the image might have declined almost to vanishing point.

In this way the outlines of the disc would be marked out on the retina by a circle of strongly excited points and the pattern of the motionless visual field would be adequately reproduced. Whether this does occur in an animal like the eel is very doubtful, for so far as I am aware the slight oscillatory movements of the eyeball have only been recorded in man.

The physiology of vision is so vast a subject that it would be very easy to extend this account into many chapters dealing with such matters as dark adaptation, visual discrimination, flicker, latent period, the rod and cone apparatus, and so on. But the evidence we have is still incomplete, and enough has been said to show that the visual apparatus conveys its information to the brain by the same kind of nervous messages which signal a touch or a pin prick. The quality of the sensation aroused by light falling on the retina must depend on the central connections of the optic nerve and not on the quality of the message conveyed by its fibres.

This conclusion has a special interest, because the optic nerve is itself a part of the central nervous system and leads from the complex structure of nerve cells, fibre networks and synapses of the retina to the similar structures of the brain stem. It is not on the same footing as a peripheral sensory nerve fibre, which is the extreme outpost of the nervous system and has no nerve cells beyond it. It seems, then, that the connecting fibres within the central nervous system communicate by impulse discharges of the same type as those in the peripheral fibres. There is nothing very startling in this conclusion, but it is satisfactory to have reached it.

From another point of view it would have been surprising if the eye had shown any marked difference in its method of signalling an excitation. There is no reason to suppose that the optic nerve fibres behave differently from the fibres of a peripheral nerve trunk in regard to the impulses which they conduct, and if this is so the message in the optic nerve fibre must be governed by the same limitations, viz., that the impulses may vary in frequency but not in size, that the interval between consecutive impulses cannot be shorter than the absolute refractory period of the fibre, and must be long enough to allow the complete recovery of the fibre if the latter is to behave as an aperiodic conducting path.

SUMMARY

The information which the central nervous system can derive from a single end organ will depend on the rate at which the end organ becomes adapted to a constant stimulus. When the discharge is very brief it can give little information about the intensity of the stimulus, and for this reason the postural end organ, which becomes adapted very slowly, is a more efficient signalling apparatus than a phasic organ in the skin. In the living organism these differences are outweighed by the much closer distribution of the end organs in the skin and by the fact that the organism has the power of movement. Owing to this the organs in the skin can be continually exposed to a changing environment; and the central nervous system can derive its information from messages from the muscles and joints combined with those from the skin.

The impulse discharge from the eye differs little from that of the simpler sense organs. Owing to the decline in the discharge with a constant stimulus a movement in the visual field will give a stronger excitation than a steady pattern of light and shade, but here, too, the effects of adaptation can be counteracted by movements of the eye.

CHAPTER VI

NERVOUS IMPULSES AND SENSATION

Nervous and Mental Changes—the Relation between the Sensory Discharge and the Intensity of the Sensation—Conclusion

THE previous chapters have discussed the relation between the external stimulus and the message which travels up the sensory nerve fibre. It is now time to consider what the message does when it arrives in the central nervous system, and undoubtedly the most interesting thing it does is to produce a change in the content of our mind.

If we belong to the extreme left wing of the behaviourist school we may deny that the arrival of a sensory message produces anything except a further series of physical and chemical changes in the central nervous system, a complex of excitation and inhibition processes and passages of impulses to and fro, ending in a motor discharge or in the laying down of some kind of pattern in the cortex. If we are on the right wing of the idealists we may hold that nerve fibres and nervous impulses are ideas, and are therefore made of the same stuff as the sensations they produce. But if we have dabbled in metaphysics, but never succeeded in adopting any firm beliefs, we must admit that our sensations are facts to be reckoned with, and that they are facts of such a kind that it is very odd that they should be " caused " by physical and chemical changes in the brain. To many of those whose concern is with the body or with the material world it may not seem odd at all. I have heard Cabanis' statement that " the brain secretes thought after the manner that the liver secretes bile " criticised solely on the ground that the brain cells are not arranged in the usual structure of a secreting gland. There is something to be said for this criticism after all, for the main point is that we can collect the bile from the liver and put it in a bottle, whereas we cannot do this with the thought.

However, it does not matter very much whether we regard the relation of matter to mind as inexplicable or as needing no explanation. There is a relation of some kind between nervous impulses and sensation, and we can discuss this without attempting to decide how, or whether, the one can " cause " the other.

What follows is bound to be speculative to some extent, for all our knowledge of sensation must be derived from man, and we have made no investigation of the impulse discharges from human sense organs. But although we cannot argue from our own sensations to those of the cat and the frog, we are on much safer ground in arguing from their sensory mechanism to our own, for we differ from other animals in the complexity of our brain, but not in the general structure of the sense organs and nerve fibres. Assuming, then, that our own sensory nerve fibres transmit the same kind of message as do those of the cat or frog, when the skin is touched or pricked, the relation which exists between the impulses and the sensation is extremely simple. Provided that there is nothing to distract our attention the intensity of the sensation at any moment turns out to be proportional to the frequency of the impulses in the sensory nerve fibre.

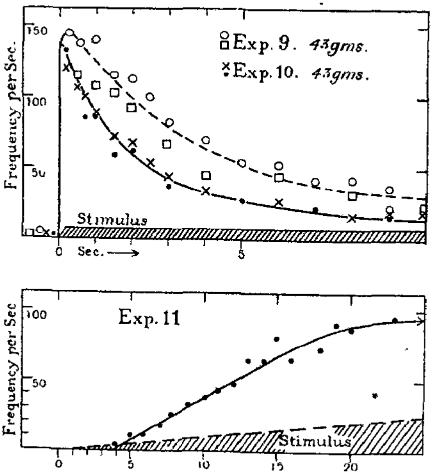

FIG. 28. IMPULSES FROM FROG'S SKIN STIMULATED BY NEEDLE POINT.
In the upper figure the needle rests on the skin with constant weight, in the lower it is pressed slowly through the skin. The intensity of the pain sensation in man follows much the same course.

There are various limitations to this statement; for instance, we have no absolute scale in which to measure intensities of sensation, but the relation is best examined by taking concrete examples. Fig. 28 records the frequency of the impulses in the sensory fibres of a frog's cutaneous nerve excited in the upper record by lowering a weighed needle point on to the skin and allowing it to remain there, and in the lower record by gradually pressing the needle point through the skin. If the same stimuli are applied to the skin of the fore-arm in man, the first produces a sudden sharp pain which declines rapidly at first and then more slowly, and the second gives a pain which increases gradually in intensity as the needle is pressed further and further into the skin. We have no absolute scale of pain, but there seems to be little doubt that the general form of the rise and fall of sensation corresponds with the rise and fall in the frequency of the discharge. Fig. 29 gives another set of frequency curves, this time from experiments with pressure stimuli on the cat's toe-pad. The pressure is removed, or partially removed and renewed again, and at each renewal the frequency rises to somewhere near its

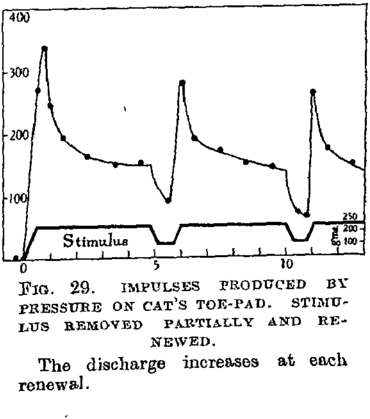

FIG. 29. IMPULSES PRODUCED BY PRESSURE ON CAT'S TOE-PAD. STIMULUS REMOVED PARTIALLY AND RENEWED.

The discharge increases at each renewal.

initial value. The sensation produced by the same stimuli on the human toe goes through a similar rapid decline when the pressure is constant and a similar renewal when the pressure is removed and reapplied. Finally, Fig. 30 gives on the left three curves which show the rise and fall in the brightness of the sensation produced by a flash of light in man. These are taken from Broca and Sulza's experiments with flickering light. On the right of the figure are three more curves showing the rise and fall in the frequency of impulses in the eel's optic nerve when a light is thrown on the eye and allowed to remain

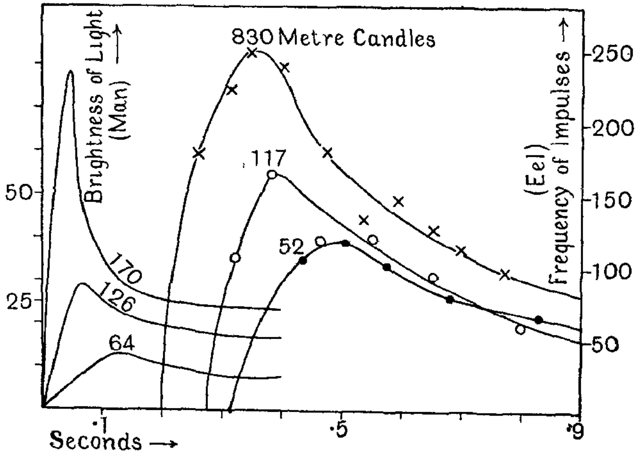

FIG. 30. BRIGHTNESS OF SENSATION PRODUCED BY FLASHES OF LIGHT OF DIFFERENT INTENSITY IN MAN (BROCA AND SULZAR).

there. The curves produced by a flash of light are of the same form, but we have more complete data for the steady exposures.

Comparing the impulse discharge in an eel's optic nerve and the brightness of a visual image in man may be like the comparison of chalk with cheese, but it seems to be justified by the likeness of the two sets of curves. Those from the eel's nerve have much longer time relations, as we should naturally expect in a cold-blooded animal, but the general form with different intensities of light is surprisingly alike in the two cases.

In these experiments the area to which the stimulus is applied is kept constant, and we are concerned only with changes of intensity, not of extensity; moreover, the sensation is supposed to appear against a constant background. The effects of two stimuli presented simultaneously or in rapid succession may be quite different from the sum of effects of each stimulus presented singly. With these reservations, however, the relation between the sensation and the impulse frequency seems clear enough.

The simplicity of the relation is at once very natural and very surprising. It means that our mind receives all the information which can be got out of the messages from those receptors which are in touch with it, but it means also that the mental correlate is a very close copy of the physical events in the sensory nerves. The only kind of distortion which takes place in the transference from body to mind (or in the parallelism of the bodily and mental events) is that the sensations rise and fall smoothly, whereas the nervous message consists of a series of discrete impulses with pauses in between. Somewhere on the way between the two there must be a smoothing process which converts the disconnected impulses into a change of much slower period. If the succession of action currents were recorded by a galvanometer of long period, instead of a capillary electrometer, the mirror would move slowly and its deflection at any moment would be roughly proportional to the frequency of the impulses at that moment. In the same way we can imagine that the impulses are conducted to some part of the nervous apparatus of the brain where the excitatory process rises and declines much more slowly than in the nerve fibre. The existence of such regions has been demonstrated by Liddell and Sherrington in some of the reflex arcs of the spinal cord, where a brief influx of sensory impulses provokes a motor discharge of much more gradual onset and decline. There is, therefore, no need to look outside the central nervous system for the smoothing process which integrates the series of impulses into a quasi-steady effect.

The sequence of events between the stimulus and the mind can be seen most clearly in a diagram (Fig. 31). The stimulus is represented as appearing suddenly and remaining at a constant value. The excitatory process in the receptor declines gradually, and as it declines the intervals between the impulses in the sensory fibre become longer and longer. The impulses are integrated by some central process, and the rise and decline of the sensation is a fairly close copy of the rise and decline of the excitatory process in the receptor. The quality of the sensation seems to depend on the path which the impulses must travel, for apart from this there is little to distinguish the message from different receptors.

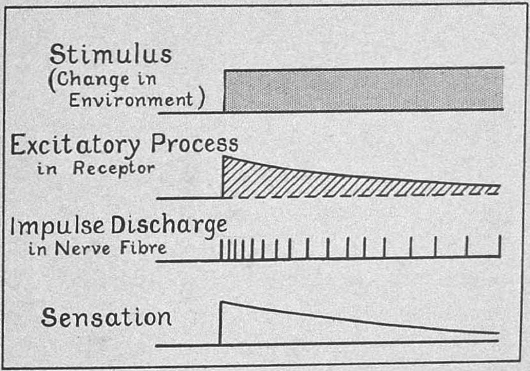

FIG. 31. RELATION BETWEEN STIMULUS, SENSORY MESSAGE AND SENSATION.

Fig. 31 makes a fitting conclusion to this book, for it summarises all that has been said so far about the action of the sense organs. A diagram of this kind is bound to be crude and it is not meant to imply any particular psycho-physical doctrine. It does not bridge the gap between stimulus and sensation, but at least it shows that the gap is a little narrower than it was before.

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