THE IMPULSES PRODUCED BY SENSORY NERVE ENDINGS. Part 3. Impulses set up by Touch and Pressure.

BY E. D. ADRIAN AND YNGVE ZOTTERMAN[1].

(*From the Physiological Laboratory, Cambridge.*)

IN Part I of the present series one of us (1) described a method of recording nerve action currents by means of a capillary electrometer and a three-stage amplifier, together with some preliminary observations on the impulses set up in various types of sensory nerve fibres by stimulation of their end organs. In Part II (2) we gave a more detailed analysis of the sensory impulses produced by stretching a muscle, and we were able to show that in a single nerve fibre the impulses usually recurred in a regular series with a frequency depending on the intensity of the stimulus, that the impulses (or rather their action currents) were all of the same intensity and that their frequency was low enough to leave the nerve fibre time for complete recovery between one impulse and the next. As these observations were made on the frog and were confined to one type of sensory ending, we were anxious to extend them to mammals and to some other form of sensation.

The results given in Part I had shown that a cutaneous afferent nerve in the cat (the internal saphenous) usually exhibits a series of action currents and that these increase in number when the skin is pricked or pinched. There is, however, a considerable drawback to the use of such forms of stimulation, since their intensity is not readily measured, and to overcome this difficulty we decided to use moderate pressure as the stimulus in the present research. The end organs sensitive to pressure are not known with certainty, but they are generally supposed to be the touch corpuscles in the skin and the Pacinian and other types of corpuscle in the subcutaneous tissues. Since the latter occur singly or in small groups in the mesentery of the cat, we thought at first that the most suitable preparation would be a single Pacinian corpuscle from the mesentery with its nerve fibre isolated and connected to the electrometer. Unfortunately, we found that various technical difficulties stood in our way. In the living animal it is extremely difficult to detect the

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[1] Travelling Fellow of the Rockefeller Foundation.

course of the nerve fibre which runs to a single corpuscle and the larger nerves usually run with blood-vessels and lymphatics in a band of adipose tissue. Damage to the blood supply might seriously interfere with the functions of the corpuscle and we were rarely successful in producing a preparation in which we felt that both the corpuscle and the nerve could be regarded as normal. In three preparations we were able to record undoubted action currents in the nerve; in two of these the nerve came from a group of corpuscles (three in one experiment and eight in the other), but an irregular series of action currents was present without any stimulation and we could not satisfy ourselves that steady pressure (2–5 grm.) on a small glass plate resting on the corpuscles made any difference to the number of impulses. The highest recorded frequency (with stimulation) was 95 per sec. In the third experiment the nerve was derived from two corpuscles which were stimulated by touching with a glass rod just before the plate was exposed. With stimulation the highest frequency (during a period of ·16 sec.) was just 100 per sec. and no impulses appeared in the absence of stimulation. Although the difficulties in the way of making a good preparation did not seem insuperable, we felt that it would be wiser to leave the organs in the mesentery and to investigate the effects of pressure in some region where organs sensitive to pressure are known to exist and where the sensory nerves are more easily dissected.

Preparation. The region ultimately chosen was the plantar surface of the cat's hind foot. The arrangement of the plantar nerves is shown in Fig. 1 (taken from Langley's diagram, this Journ. 57. p. 434. 1923), and it will be seen that the cushion of the 2nd digit is supplied by the slender medial branch of the internal plantar nerve. It contains from 200–400 fibres and is easily dissected out for a length of 1 cm. or more without interfering with the blood supply. Most of our observations were made on this nerve, though we have sometimes used the other digital nerves. In a few experiments we used cats anæsthetised with urethane but the majority were made with the spinal animal decapitated under chloroform anæsthesia and allowed to remain an hour or more for the effect of the anæsthetic to wear off. The results with urethane narcosis do not differ appreciably from those with the spinal preparation. When the latter was used the hind limbs were immobilised by nerve section.

The animal lies on its belly on an insulated stand inside the iron-walled box which acts as a shield from electromagnetic disturbances (see Part I). The left hind foot is fixed with the plantar surface upper-most on a small platform which carries the electrodes. These are of the Ag, AgCl, NaCl gelatin type and end in small camel-hair brushes curved at the tip so that the nerve can rest on them. The nerve is cut just before its junction with the main trunk of the internal plantar nerve and placed on the electrodes with its proximal end slung by a silk thread from an insulated support. The nerve is constantly irrigated with warm Ringer and the temperature of the foot is maintained by a small carbon lamp placed a few inches away. The lamp is disconnected before an observation is made as it may be a source of artefacts in the amplifier circuit. The stimulating apparatus consists of a glass rod *G* (Fig. 2) ending in a disc 1·1 cm. in diameter which is pressed downwards against the

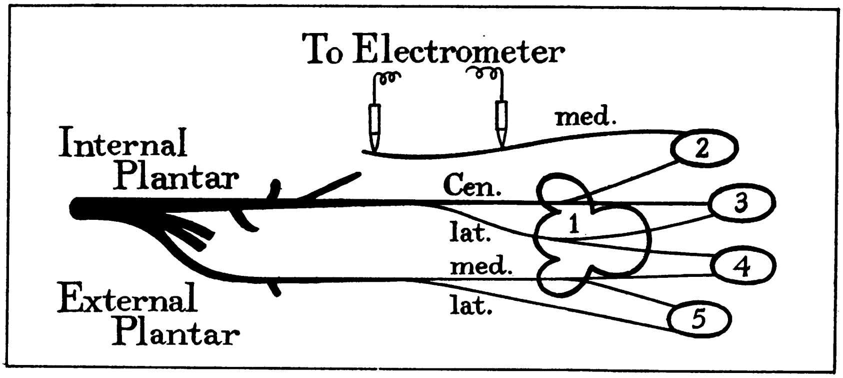


Fig. 1. Digital nerves to plantar surface of cat's hind foot.

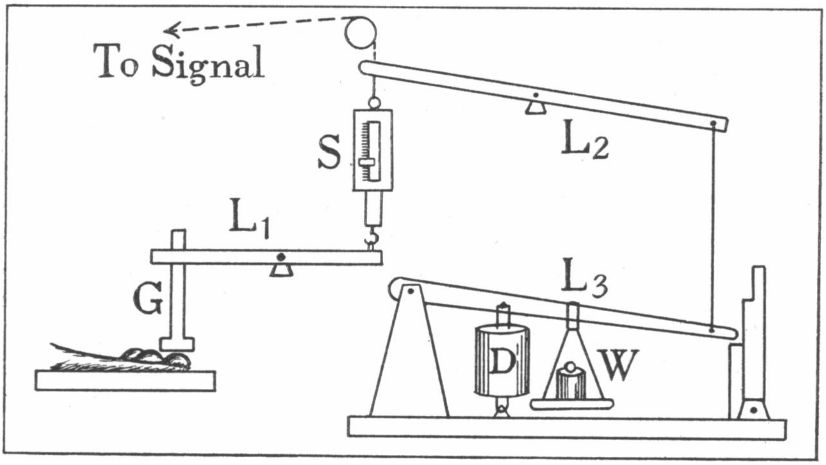


Fig. 2. Stimulating apparatus.

cushion of the pad by a lever L_1. The lever is pivoted at its centre and the far end is attached to the hook of a spring balance *S*, the body of which can be pulled up through varying distances by the movement of the lever L_2. L_2 is connected to a third lever L_3 which is moved downwards at a uniform speed by a weight *W* acting against the dashpot *D*. The rate of movement can be varied by altering the weight; the final value of the pull exerted on L_1 is varied by adjusting the length of the arms of L_2. A light thread attached to L_2 operates a signal lever which moves across the slit of the cinematograph camera and records the increase of pressure on the film.

With this arrangement it is possible to apply a gradually increasing or a steady pressure of any value from 25 to 1500 grm. on the pad under the disc *G*, and to record the pressure simultaneously with the electric responses in the nerve.

RESULTS.

(1) *Touch.*

The contact of the glass disc with the cushion of the toe will presumably stimulate the receptors in the skin which are sensitive to touch and as the pressure increases the receptors in the subcutaneous tissues will be brought into action as well. If there were a continued discharge of impulses from the receptors in the skin as long as the contact was maintained, it might be difficult to measure the added effect of an increase of pressure. Fortunately, the organs concerned all show the phenomenon of adaptation in a high degree. In some preparations with the medial branch of the internal plantar nerve there is a continuous discharge of impulses at a frequency of 20–30 per sec. in the absence of any kind of stimulation; such a discharge is often met with during the first few minutes after the preparation has been set up, but it rarely persists at this rate for more than 5 minutes, and in most preparations the "resting" discharge is not greater than 5–10 per sec. This discharge is not increased under the mere continued exercise of the light contact of the glass disc with the pad. If, however, a record is made as the disc is lowered gently on to the pad a sudden outburst of impulses is seen at the moment of contact lasting for about 1/5 sec. Fig. 3 shows records of this kind. The disc was lowered gently at a speed of 1 cm. per sec. by a lever controlled by an oil dashpot and the weight finally resting on the pad was 5 grm. In the lowest record the signal is moved by hand at what was judged to be the moment of actual contact. For about 1/10 sec.

the impulses recur so rapidly that there is considerable interference, but within 1/5 sec. the discharge has nearly subsided. Evidently the organs for touch become adapted so rapidly to the stimulus that it becomes almost ineffective in 1/5 sec. We cannot therefore assume that the impulses set up by moderate pressure are all derived from the subcutaneous organs, for an increase in pressure might again excite the organs in the skin, but, as will be seen later, the low frequencies obtained with the pressure stimulus make it unlikely that more than a few end organs are excited.

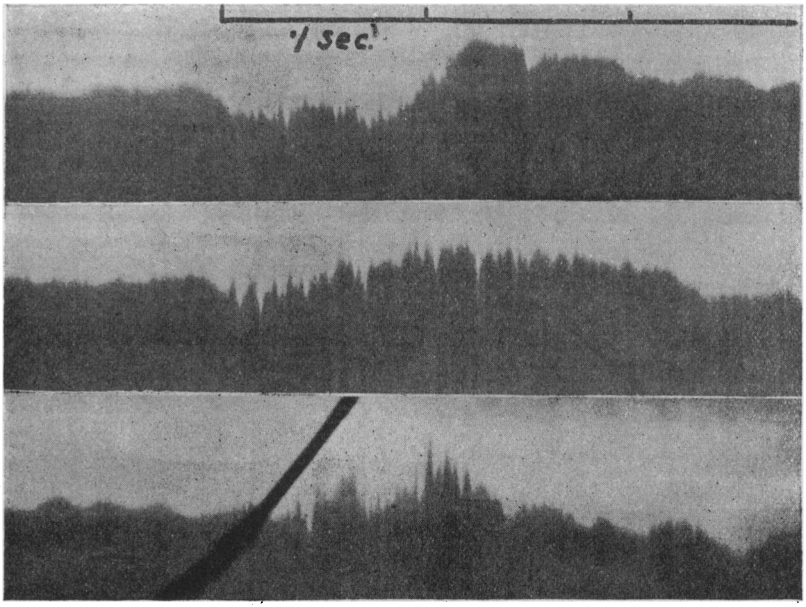


Fig. 3. Film records (enlarged) of impulses due to "Touch." Disc lowered gently on to pad and allowed to remain there. In the middle record the weight resting on the pad was 15 grm. In the others 5 grm. Discharge lasts for ·1 to ·2 sec. at the moment of contact and then subsides.

(2) *Pressure.*

Nature of impulses. In all these experiments the preparation is said to be unstimulated when the disc is resting lightly (weight = 5 grm.) on the pad. It is stimulated by releasing the lever L_3 so that the spring balance is extended and the pressure on the pad increased. The rate of movement could be adjusted so that the full pressure was reached in from $\frac{1}{2}$ to 6 sec. The full pressure was generally made equal to 100 grm.

(·26 grm. per sq. mm.), 250 grm. and 500 grm. and records were made as the pressure was increasing and after it had reached its full value. In every case the discharge of impulses reached its maximum frequency whilst the pressure was increasing and then declined rapidly although the pressure was maintained. The actual frequencies of discharge varied over a wide range from one preparation to another but, fortunately for our purpose, the frequencies were usually low enough to allow the individual impulses to appear in the record. The form of the electric responses as they appear in the electrometer record may be seen from Fig. 4. In *A*, *B* and *C* (Exp. 1) the responses are mostly monophasic, in *D*, *E* and *F* (Exp. 9) they are mostly diphasic. As the nerve was irrigated with Ringer between each record the magnitudes of the

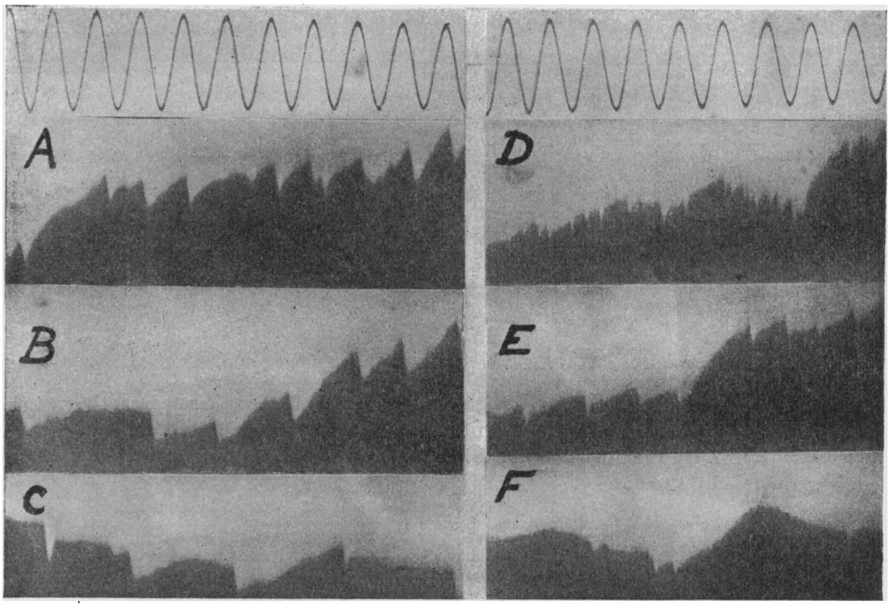


Fig. 4. Plate records of impulses due to pressure. Time marker gives 1/100 sec. periods.

A, B, C. Exp. 1:
- *A.* Slow increase of pressure (100 grm. per sec.). Actual pressure about 350 grm.
- *B.* Steady pressure of 500 grm. for 5 sec.
- *C.* Steady pressure of 100 grm. for 3 sec.

D, E, F. Exp. 9:
- *D.* Slow increase of pressure (100 grm. per sec.). Actual pressure about 450 grm.
- *E.* Steady pressure of 500 grm. for 5 sec.
- *F.* At rest. Disc touching pad.

responses are not strictly comparable but there is evidently no marked variation in size. As in the case of the afferent impulses from the frog's muscle, we have found no indication that a change in the intensity of the stimulus has any effect on the size of the impulses set up; the change is expressed entirely by the altered frequency of the discharge. This point is shown more clearly in Exp. 2 where pressures of 50, 100, 250 and 500 grm. were applied for 5 seconds. The frequencies corresponding to these pressures are < 15, 57, 140 and 170 per sec., and an analysis of a small group of consecutive impulses from each record is given in Fig. 5. Since the impulses are not all derived from the same nerve fibre there is a certain amount of variation in size in each record, but the variation is substantially the same in all three records, and apart from the frequency it would be impossible to say which group of impulses is due to the strong stimulus and which to the weak. We conclude, then, that the all-or-nothing relation between the stimulus and the impulse set up holds good for the mammalian pressure receptor just as it does for the stretch receptors in the frog's muscle.

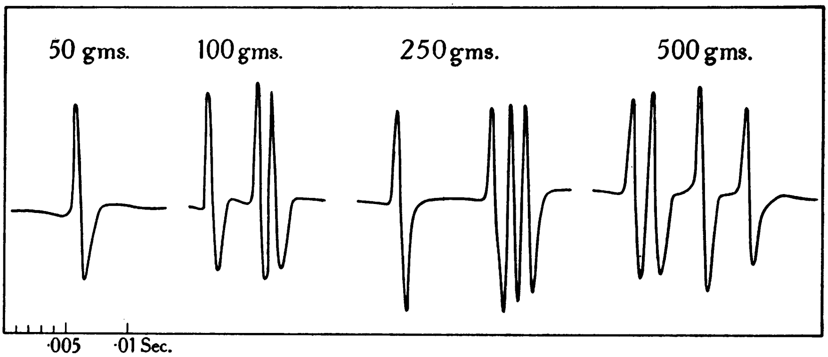


Fig. 5. Analysis of electrometer records, *Exp.* 2, showing that the size of individual impulses does not vary with the stimulus.

Relation between strength of stimulus and frequency of discharge. Owing to the very rapid adaptation which occurs in the end organs, a comparison of the frequencies produced by different stimuli is only valid if the pressure is allowed to act for the same time in each case. Fig. 6 gives the frequencies for various pressures applied for 5 seconds in four experiments. The form of the curve is much the same in each case though the frequency for a load of 500 grm. varies from 50 per sec. in Exp. 5 to 305 per sec. in Exp. 4.

The curves relating frequency to stimulus for a single end organ would not necessarily have the same form, since the stronger stimuli may bring more end organs into action. It may seem remarkable that

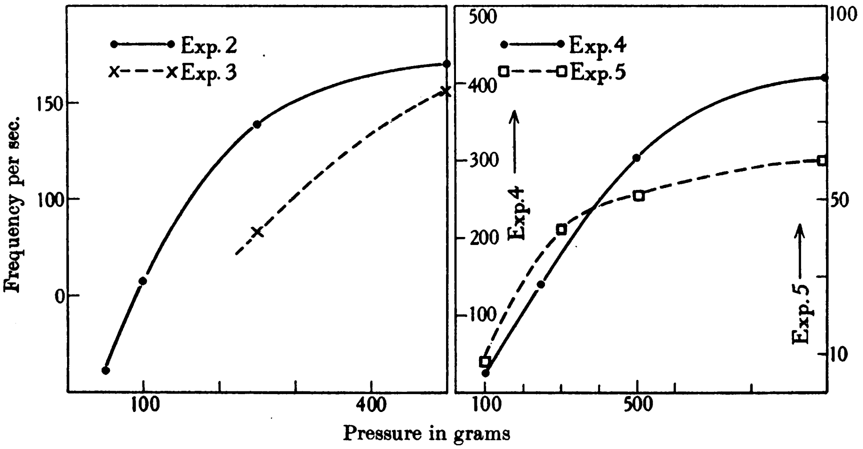


Fig. 6. Relation between stimulus and frequency of discharge. Pressure constant for 5 sec. Every impulse counted.

a load of 1000 grm. does not produce a much greater increase in frequency, for it might be expected to evoke responses from the pain receptors as well as from those of pressure. But considerable pressure may be applied to the cushion of a cat's toe without causing any signs of discomfort and the pad of the human toe is equally insensitive. In one experiment where a load of 2 kilos was applied the curve showed a great rise in frequency between 500 grm. and 2 kilos, and in one a sudden rise occurred between 300 and 500 grm. In both experiments the sudden increase was presumably due to the stimulation of a fresh set of nerve endings.

Adaptation. In the tension receptors of the frog's muscle it was found that if the stimulus was maintained at a constant value, the frequency of discharge fell to half its maximal value in about 10 seconds. In the pressure receptors of the cat's toe the rate of adaptation is much more rapid. This may be seen from the two cinematograph film records given in Fig. 7. In one of these (Exp. 4) the frequency of discharge is always high, and whilst the pressure is increasing the different impulses overlap and produce larger excursions in the electrometer. In the other (Exp. 1) the pressure increases more slowly, the frequency is always lower and there is very little overlapping. In both the frequency reaches its maximum almost as soon as the pressure has begun to increase, and it

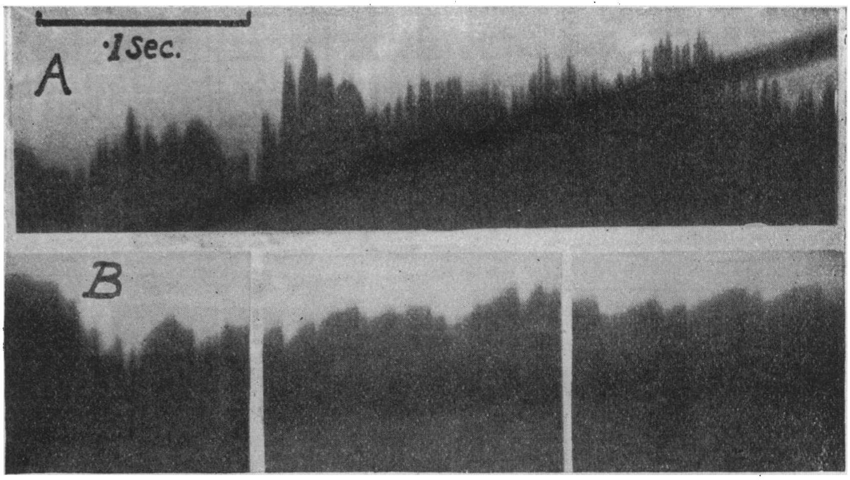


Fig. 7. Film records of response to increasing pressure.

***A. Exp.* 4. Rapid loading (500 grm. in ½ sec.). Interference of impulses as loading begins. Frequency has dropped before maximum pressure is reached. Black line signals increase of pressure.**

***B. Exp.* 1. Slower rise of pressure (500 grm. in 5 sec.). Loading begins in first section, midway in second, maximal in third. Frequency greatest at the beginning.**

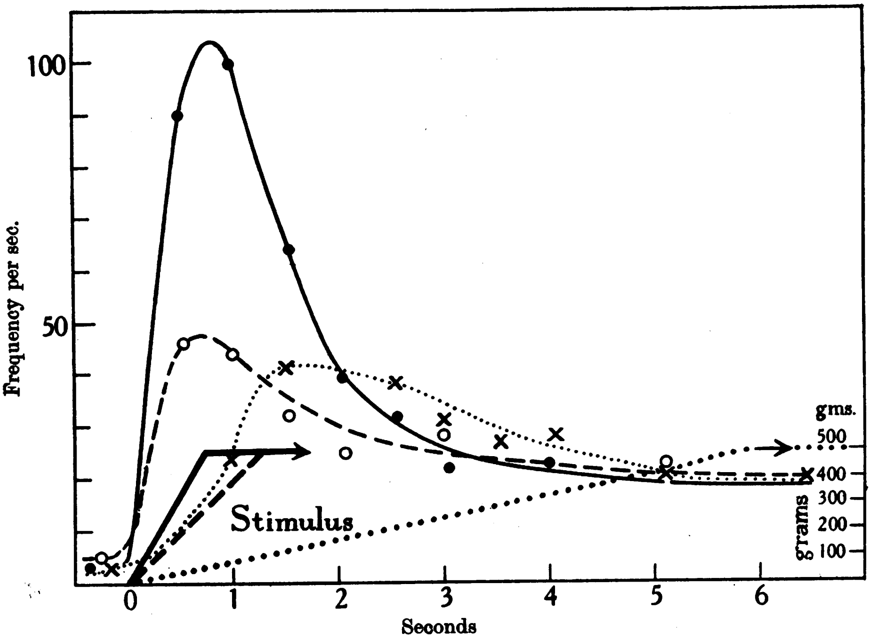


Fig. 8. *Exp.* 6. Frequency with different rates of increase of pressure. Every impulse counted.

has fallen considerably before the full loading is attained. It follows that the maximum frequency will depend much more on the rate of loading than on its final value. The curves in Fig. 8 show an experiment in which the effect of altering the rate of loading was well marked. Fig. 9 shows the effect of an increase in the final pressure in a preparation in which the adaptation was not so rapid. In two other experiments, however, although the maximum frequency was reached before the maximum pressure, it showed very little variation with changes in the rate of loading or in the final pressure. Curves from these experiments are given in Fig. 10 (Exp. 1). As soon as the pressure begins to increase, the frequency rises to a maximum which is much the same in every case. It then falls off rapidly if the final pressure is small, more slowly if the pressure is large. It is possible that our figures for the maximum frequency are at fault and that it is really higher with the more rapid loading. The impulses are certainly difficult to count and there may be more overlapping of impulses in some of the records. We are inclined to think, however, that the true explanation is that the stimulus was maximal in every case. The end organs cannot discharge impulses at more than a certain rate and this rate was already reached with the slow increase of pressure. This conclusion will be discussed in the section dealing with the frequency of discharge from individual end organs.

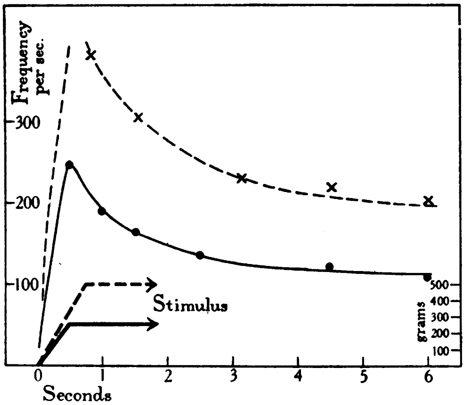


Fig. 9.

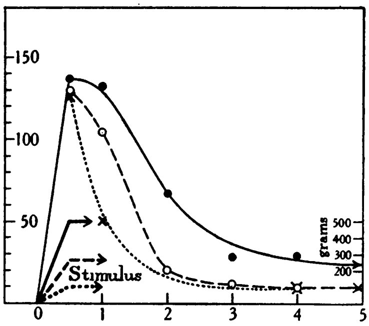
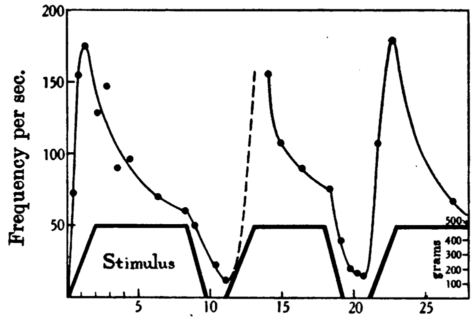


Fig. 10.

Fig. 9. *Exp.* 4. Frequency with different final pressures. Top of upper curve obscured by signal.

Fig. 10. *Exp.* 1. Frequency reaches same (maximal?) value for all stimuli.

Since the rate of adaptation is rapid we might expect to find that the organs would return rapidly to the unadapted condition as soon as the pressure is removed; and we should expect this too from a knowledge of the sensations we experience when the pad of the toe is pressed. If the pressure is removed and applied again immediately, the sensation rises again to somewhere near its initial intensity. In several experiments we have recorded the impulses from the cat's pad when the pressure is released and renewed after a short interval and there is no doubt that the state of adaptation does pass off very rapidly. An experiment of this kind is shown in Fig. 11 (Exp. 7) and it will be seen that when the pressure is renewed after an interval of 2 seconds' rest, the frequency rises very nearly to its initial maximum. Fig. 12 (Exp. 4) shows the effect of a partial removal of the pressure for a short period. Here the state of adaptation persists to some extent since the load is never removed entirely, but each rise of pressure brings about a large increase in frequency. This experiment is interesting because it enables us to form some idea of the nature of the adaptive process. This was discussed in Part II and it was pointed out that it might depend on a change in the rate of recovery of the end organs or on a change in the excitatory disturbance. We might suppose that the intensity of the excitatory disturbance is always proportional to the pressure at any moment, but that the refractory period increases very rapidly with activity and brings about the decline in frequency. The more likely explanation is that with a constant stimulus the excitatory disturbance diminishes rapidly so that the frequency declines, although the rate of recovery of the organs remains unaltered. This explanation is supported



Seconds

Fig. 11.

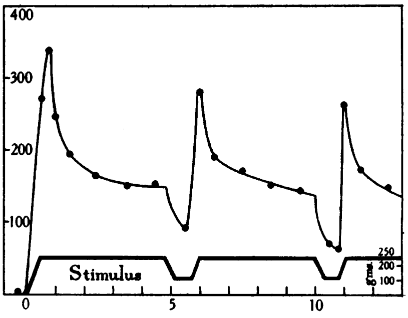


Fig. 12.

Fig. 11. *Exp.* 7. Complete removal of stimulus for short periods. Frequency returns to initial value when stimulus is renewed.

Fig. 12. *Exp.* 4. Partial removal of stimulus. Adaptation persists, but frequency rises again when full load is applied.

by the record in Fig. 12. Here the frequency has fallen to half its initial value in 5 seconds and if the exciting value of the stimulus remains unchanged, the refractory period of the end organs must have been doubled. The drop in the stimulus from 250 to 125 grm. could scarcely restore the end organs to near their resting condition, for the fall in frequency would still have taken place if the stimulus had been 125 grm. throughout. The frequency would rise when the stimulus is increased again to 250 grm. but it would only rise to the value it had just before the load was reduced, whereas in fact it rises a great deal higher. The same difficulty does not occur if we suppose that the adaptation is due to the stimulus becoming less effective[1], for the end organs would then be capable of responding at any time with their original frequency provided that they received a sufficiently intense stimulus. The fall in frequency with a constant pressure stimulus must therefore be due in part at least to a decline in the exciting value of the stimulus apart from any change in the refractory period of the end organs. This agrees with the results obtained from the receptors in the frog's muscle and shows, as they did, that the adaptation of an end organ to a constant stimulus is of much the same nature as the adaptation of a nerve fibre to a constant current.

Frequency of discharge from individual end organs. Although the nerve under investigation has 200–400 fibres, it will be obvious from the data already given that very few of these fibres can be in action when the pad is stimulated by pressure. The total number of impulses passing up the nerve in a second was often less than 50, and even if the frequency of the end organ discharge were as low as 5 per sec., this would mean that only ten organs were in action. However, there is really no reason to credit the cat's toe with a large number of pressure receptors. Owing to its power of responding with 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 as the intensity, but it is not likely that there is a very accurate localisation of pressure within the small area supplied by the nerve (*i.e.* half the plantar surface of one toe).

Of the different types of sensory end organ in the subcutaneous tissue the Pacinian corpuscles are by far the largest, and we have tried several times to dissect out a single corpuscle in the living preparation and record the impulses from it, but in every case we have failed. Damage to the

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[1] The decline in effectiveness of the stimulus may be caused in part by the gradual yielding of the tissues, for this might reduce the extent to which the pressure organs are deformed.

nerve and the end organ is a sufficient explanation of this, though it is conceivable that we were not using the right form of stimulus for this end organ.

The failure to obtain records from preparations with only one end organ need not concern us so much, for those from the intact pad give most of the evidence we need. In the nerve from the frog's muscle (cf. Part II) the afferent impulses fell into several regular series each with a definite rhythm of its own, each series being produced by a single end organ. If the mammalian pressure receptor is built on the same plan we might expect to find evidence of regular rhythms in the present records and these would tell us what was happening in each end organ.

It must be said at once that the discharges cannot always be grouped into perfectly regular sequences. In one record (Exp. 6) we have found a series of four consecutive impulses occurring with perfect regularity at intervals of ·0195 sec. during an increase of pressure of 100 grm. per

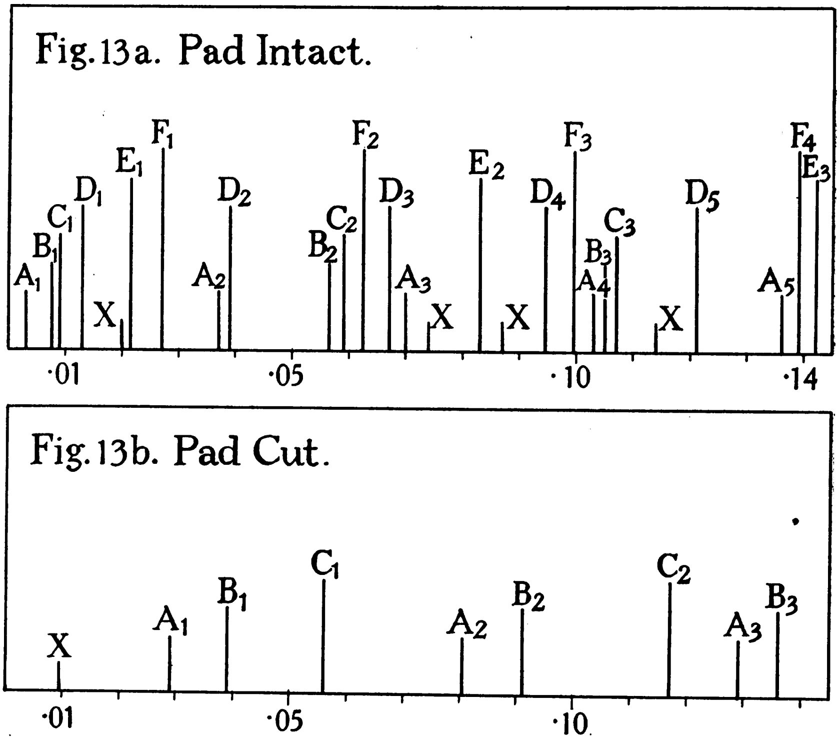

Fig. 13. *Exp.* 2. (*a*) Pressure of 500 grm. for 5 sec. Analysis of impulses into regular rhythms. (*b*) Distal part of pad cut through. Same stimulus.

sec. In other records we can usually detect one or more distinct rhythms with intervals not varying by more than 5 p.c., but most of the impulses will not fit into groups unless we allow a variation of rhythm of at least 10 p.c. during the short space of one record. An example will make this clearer. Fig. 13 gives the moment of occurrence of all the impulses in a particular record. The stimulus was a pressure of 500 grm. applied for 5 seconds. The impulses have been analysed into six groups marked *A–F* and the intervals between the successive impulses in each group are given below in Table I. The four impulses marked *X* which are left out of the scheme may belong to sequences of very slow rhythm. It will be seen that there is a variation of 10 p.c. in the intervals in series *F* and this is well outside the range of experimental error. The impulses may be wrongly grouped and it is conceivable that if 27 impulses had occurred at random during the period of the record, we should have been able to analyse them into groups having the same degree of regularity as those in Table I. But the experiments on the frog and the one record already mentioned (Exp. 6) show that regular discharges are to be expected, and the periods found in Table I agree very well with those from other records.

At a later stage in the same experiment a deep incision was made

TABLE I.

Exp. 2. 500 grm. pressure applied for 5 seconds.

a. Pad intact.

Intervals between impulses in each group

sec.	sec.	sec.	sec.	sec.
$A_1-A_2=\cdot 034$	$B_1-B_2=\cdot 049$	$C_1-C_2=\cdot 050$	$D_1-D_2=\cdot 026$	$E_1-E_2=\cdot 061$
$A_2-A_3=\cdot 033$	$B_2-B_3=\cdot 0485$	$C_2-C_3=\cdot 048$	$D_2-D_3=\cdot 028$	$E_2-E_3=\cdot 059$
$A_3-A_4=\cdot 033$			$D_3-D_4=\cdot 0275$	
$A_4-A_5=\cdot 033$	sec.		$D_4-D_5=\cdot 026$	
	$F_1-F_2=\cdot 0355$			
	$F_2-F_3=\cdot 037$			
	$F_3-F_4=\cdot 039$			

Average frequency:		
	A	30 per sec.
	B	20·5 „
	C	20 „
	D	37 „
	E	17 „
	F	27 „

b. Pad cut across. Same stimulus.

Intervals between impulses in each group

sec.	sec.	sec.
$A_1-A_2=\cdot 0515$	$B_1-B_2=\cdot 052$	$C_1-C_2=\cdot 061$
$A_2-A_3=\cdot 0485$	$B_2-B_3=\cdot 045$	

Average frequency:		
	A	20 per sec.
	B	21 „
	C	16·5 „

across the pad, cutting away the distal two-thirds from connection with the nerve trunk. The responses to the same stimulus are given in Fig. 13 (*b*). They now fall into three instead of six groups, and the periods are given in Table 1 *b*, but there is again a distinct variation in the intervals and a corresponding doubt as to the correct grouping. In other records the variation may be even greater and it becomes quite impossible to group the impulses with any confidence.

In Table II we have collected various regular frequencies found in different experiments. As a criterion of "regular" frequency we take the occurrence of at least four impulses in the record at intervals which vary by less than 10 p.c. When only one frequency is given for a particular record it means that only one could be found to satisfy this criterion. The lower frequencies do not appear in the table, for the rate must be higher than 20 per sec. if four impulses are to appear on the photographic plate.

TABLE II.

Number of experiment	1	5	6	2	7	8
Stimulus	Frequency per second					
Slow increase of pressure 100 grm. per sec.	56	61	52	—	62·5	54
500 grm. constant load for 3½ sec. ...	—	36	—	—	—	—
Do. for 5 sec.	—	—	—	37 30	—	—
Do. for 7 sec.		21	—	—	—	—
Do. for 10 sec.	—	—	—	—	—	26·5 26

The frequencies obtained whilst the pressure was increasing are in remarkably close agreement, and it is unlikely that any higher frequencies can have been overlooked, for in many of the records there are occasional quiet periods lasting as long as ·01–·015 sec. The exact pressure at the moment of exposure was not recorded on the plates and may have varied from 150 to 350 grm., but the curve in Fig. 9 shows that the frequency does not vary much when the pressure is increasing slowly between these values. A more rapid increase of pressure would no doubt give higher rhythms, but before the maximal rate of the end organ is discussed we have to consider why the rhythms we have found are on the whole less regular than they were in the frog.

Irregular responses. In the records from the frog some irregularity was present when the frequency was very low, and whatever was the cause of this may account for the present records also. But there are other possibilities which must be considered. It is unlikely that the more rapid adaptation can account for the lack of regularity, for the total frequency does not fall by more than 2 or 3 p.c. in a period of ·16 sec. (the duration of the record). If the rhythms were all very long, we should not be able to trace them in records lasting only ·16 sec., but we have looked for slow rhythms in the continuous film records and have not found them. A more probable explanation is supplied by the fact that we are dealing with nerve fibres each of which may send branches to several end organs. This arrangement is not found in the case of the muscle spindle and indeed Sherrington(3) has shown that in the cat the converse is often true, one muscle spindle receiving several afferent nerve fibres. Thus, in our records from the frog the possibility of interaction between different end organs did not arise. It must arise, however, when we are concerned with the end organs under the skin, for it is well known that both the Golgi-Mazzoni and the Pacinian corpuscles may occur in groups supplied by a single nerve fibre, and an impulse arising in one corpuscle could scarcely fail to modify the activity of the others[1]. This explanation is supported by the data obtained for the maximal frequency of the response.

Maximal frequency of end organ response. In most of our experiments a rapid rise of pressure (100 grm. in ·1 sec.) gave a total frequency of more than twice the rate given by a slower rise (100 grm. in 1 sec.). Part of this increase in frequency might be due to new organs responding only to a rapidly changing stimulus, but in any case the maximal rate at which the single organ can discharge ought to lie somewhere between 60 and 150 per sec. But in Exp. 1 (Fig. 10) and Exp. 6 (Fig. 9) it will be seen that the total frequency with rapid loading does not exceed 150 per sec. It is unlikely that the stimulus affected only one pressure receptor and the impulses did not form a single regular series, but here, too, we may invoke the fact that several end organs may have a common nerve fibre. An impulse set up in one organ will almost certainly be conducted round as an antidromic impulse to the other organs on the same fibre. If it reaches an organ which is in the refractory state, the antidromic impulse would have no effect, but if the absolute refractory period is over, the impulse might produce a renewed activity of the organ and a renewed refractory period. It does not follow that a fresh centripetal impulse would be set up, for the refractory state of the conducting path would prevent it. Thus the total frequency of the impulses travelling up the nerve fibre from the group of organs might be no greater than the maximal frequency at which any one organ can respond. Since the

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[1] The possibility of interaction of end organs on a common nerve fibre was pointed out by Herring (Brain, 46. p. 209. 1923).

impulses occur irregularly, it is unlikely that one organ can keep all the others permanently out of action, but it is interesting to note that Exp. 6 (one of those with a very low total frequency) gave the record in which four consecutive impulses appeared at perfectly regular intervals. The film records show that this regularity was not maintained, and we must therefore assume that the lead passes from one organ to another. For this to occur we must also assume that the refractory state set up by an antidromic impulse is sometimes shorter than that set up in the organ which originates the impulse.

Since the whole explanation is speculative, it would be useless to discuss in detail the way in which several end organs might interact. It may be pointed out, however, that a disordered rhythm in a nerve fibre attached to several end organs presents a fairly close analogy with the behaviour of the ventricle of a heart in which the rhythm is disturbed by ectopic beats from various parts of the auricle.

Whether this explanation is correct or not, the fact remains that in these two experiments the total number of impulses passing up the nerve in 1 sec. was not greater than 150, and the maximal rate of discharge from the single organ cannot well be higher. There was nothing to indicate that the preparations were in any way abnormal and the regular periods obtained in other experiments are certainly no greater. A maximal frequency of 150 per sec. for a warm-blooded animal is evidently in good agreement with that for the receptors of the frog's muscle, which was reckoned to be 75–100 per sec.

Discussion. The results obtained from the pressure receptors of the cat's foot conform very closely with those for the tension receptor in the frog's muscle. The rate of adaptation is more rapid and the maximal frequency of discharge is probably higher, but there is the same grading of frequency according to the strength of the stimulus and the same all-or-nothing relation between the stimulus and the individual responses in the nerve fibre. We see no reason to doubt that the mode of production of the repeated discharge is the same in both, *i.e.* after each response the refractory state is set up and the excitability returns gradually until it reaches the value at which the stimulus becomes effective again. In both cases the change which would be produced in the end organ by the stimulus is a deformation of its structure. The muscle spindle will elongate when the tension on the muscle is increased, and it will do so whether the muscle is contracting or not, since it is placed as a link between two sections of a contractile fibre. The pressure organ must also be deformed if the stimulus is to be effective, since it is well known that an increase of pressure does not stimulate if it is uniform in all directions, *e.g.* if the limb is placed in water or mercury. The exact process by which the deformation sets up an impulse is, of course, uncertain.

The main difference between the frog records and those from the cat lies in the absence of clear evidence of regular rhythms except in a few cases. This has already been discussed and it has been pointed out that several pressure organs may interfere with one another if they are supplied by a common fibre. In our records from the frog we found that the frequency of discharge from the muscle spindle was always low enough to leave the nerve fibre time for complete recovery between one impulse and the next. This condition would evidently not obtain if a single nerve fibre were to receive impulses from several end organs acting quite independently, but it would be secured if the nerve endings on a common fibre can interact in the way suggested.

If it is true that the activity of one end organ may suppress that of the others on the same nerve fibre, it follows that the multiplication of end organs on a single fibre would merely serve to increase the area upon which the stimulus might take effect. The frequency of discharge would be the same whether all were stimulated or one only, and presumably the intensity of the sensation and its "local sign" would be the same also.

The very rapid adaptation to contact and pressure is surprising at first sight, but it becomes less so when we consider the functional value of these sensations in the cat's toe. In our own toes the sensation due to a steady pressure is very soon over unless it is renewed by a movement, and although we have no objective standard it is fairly clear that the sensation does vary with the intensity and duration of the stimulus according to the same general plan which governs the frequency of discharge of impulses in these experiments.

CONCLUSIONS.

1. Afferent impulses have been recorded in the plantar digital nerves of the cat when the pad of the toe is stimulated by light contact or by pressure.

2. When a glass disc is brought into contact with the pad and rests there lightly, there is a discharge of impulses at a high frequency for a period of about 1/10–1/5 sec. at the moment of contact, but within 1/2 sec. the discharge has ceased almost entirely.

3. When pressure is applied to the disc, a discharge of impulses takes

place which is at a maximum as the pressure is increasing and falls off rapidly when the pressure is maintained at a constant value.

4. The frequency of the impulses varies with the intensity of the stimulus, but the size of the individual action currents does not vary. There is therefore an all-or-none relation between the stimulus and the impulse.

5. The discharges can sometimes be analysed into groups, each occurring with a definite rhythm and each presumably due to a single end organ, but the rhythms are not so regular as in the afferent fibres from the frog's muscle and it is often impossible to trace them. It is suggested that this lack of regularity is due to interaction between several end organs which are supplied by a common nerve fibre.

6. The maximal rate of discharge from the single end organ appears to be about 150 per sec. Frequencies of 20–30 per sec. are commonly found when the pressure has been constant for 5 seconds.

7. These results agree very closely with those obtained from the tension receptors in the frog's muscle and there is little doubt that the activity of the cat's pressure receptors depends in the same way on the development of a refractory state and a return of excitability after each discharge, combined with a slow decline in the exciting value of the stimulus.

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