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# SENSORY DISCHARGES IN SINGLE CUTANEOUS NERVE FIBRES.

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SEVERAL investigations have dealt with the sensory impulses produced in the cutaneous nerves of the frog by stimulating the skin [Adrian, 1926; Bronk, 1929; Matthews, 1929], but until recently there was no certain method of restricting the discharge to a single nerve fibre. Sharp localization of the stimulus goes some way towards this, but there is so much overlapping in the areas of distribution of the sensory fibres that we can rarely be sure of confining the excitation to one of them. Section of all but one of the fibres might be tried, but owing to the arrangement of the connective tissue in the nerves of the frog it would be exceedingly difficult to carry out. This lack of a convenient method of observing the discharge in single fibres has made it impossible in the past to investigate the cutaneous receptors with anything like the accuracy obtainable in the case of the muscle receptors, but a method has now been found for the end-organs responding to touch, and in this paper we give some preliminary results obtained by its use.

The method was discovered by chance in an investigation of the impulses in sympathetic fibres [Adrian, 1930 *a*]. In the spinal frog if one of the dorsal cutaneous nerves is cut where it enters the skin and suspended on electrodes it is found that sympathetic discharges take place when various parts of the body surface are rubbed or pinched. The impulses are easily recognizable by their slow time relations, and they cease when either the spinal cord or the sympathetic ganglion chain is destroyed[3]. But in some animals stimulation of the body surface gives

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[3] In many preparations a light touch on almost any part of the body surface gives an immediate reflex discharge in the sympathetic fibres. The impulses cease when the stimulus is withdrawn, but with stronger stimulation (pinching) there is often a long after-discharge. Pinching the leg of a spinal frog produces a considerable secretion from the mucous glands of the skin and presumably the sympathetic reflexes are chiefly concerned with skin secretion.

in addition a discharge of impulses of quick time relations indistinguishable from those in the medullated sensory fibres (Fig. 1). As the impulses travel centrifugally (the peripheral connection of the nerve having been cut) it was thought at first that they were reflex discharges in efferent fibres, but this is ruled out by the fact that they can still be obtained by touching the skin after destruction both of the spinal cord and of the sympathetic chain. The only remaining possibility is that the discharge is an "axon reflex" in cutaneous sensory fibres which branch near the cord, and in agreement with this it is found that it can only be elicited by stimulation of a small and sharply defined skin area.

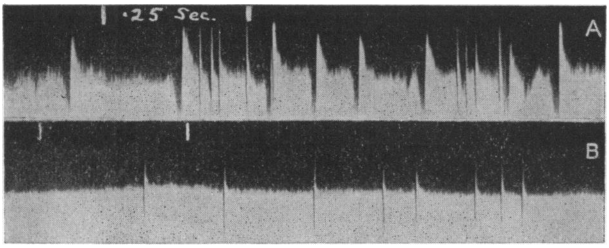

Fig. 1. Efferent sympathetic impulses and antidromic sensory impulses. Spinal frog. Electrodes 7 mm. apart on dorsal cutaneous nerve, cut peripherally.

A. Sympathetic ganglia intact. Discharge produced by rubbing the skin of the abdomen. The slow waves (sympathetic) may be due to several fibres acting more or less in unison. The rapid waves are due to antidromic conduction in branching sensory fibres.

B. Discharge produced after destruction of the sympathetic ganglion chain. The sensitivity of the recording system has been reduced by one-half.

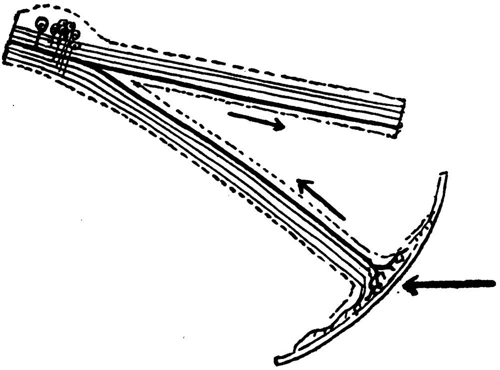

Fig. 2. Arrangement of nerve fibres giving the antidromic discharge.

The discharge is, therefore, an antidromic effect depending on the kind of arrangement shown in Fig. 2.

The arrangement is convenient for our purpose because it is relatively uncommon. The dorsal cutaneous nerves contain some fifty medullated fibres apiece; several hundred nerves have been examined, and about half of them have contained no fibres with branches in other nerves; in the remainder antidromic discharges are obtained. These are usually produced by stimulating a single small skin area, and the simplicity of the discharge indicates that it occurs in only one fibre. Occasionally the impulses are arranged in a way which shows that more than one nerve fibre is in action and sometimes discharges are produced from two areas with each area giving the single fibre type of discharge. It will be seen that the nerves in which the antidromic discharges occur give an almost ideal preparation for the study of the touch receptors, for by recording the impulses in one nerve we can tell what is happening in a single fibre of another nerve when its end-organs are stimulated; the central connections of the receptive skin area may be left intact and the operative interference may be confined to regions some distance away from it. There is, as a rule, no doubt about the number of fibres concerned in the discharge; the uniform size and regular spacing of the impulses and the absence of any interference or summation show when we are dealing with only one fibre, and the findings with regard to adaptation (reported in the following paper) make it clear that discharges of this type are in fact produced by a single unit.

When we use one branch of a nerve fibre to sample the discharge which passes up the other branch we are assuming that for every ascending impulse in the one there will be a corresponding antidromic impulse in the other. Kuhne's gracilis experiment and many others of the same kind show that an impulse can travel freely into the side branch of an axon whether it is ascending or descending in the parent fibre. For sensory fibres the most complete proof is provided by the grouped discharges which occur in injured mammalian nerves [Adrian, 1930 *b*]. The impulses in each group have a characteristic spacing, and similar groups are repeated at regular intervals. Since the discharge often arises from the side branch of a fibre it is possible to compare the groups which travel up the main axon and those which travel down the other terminal branches. No difference can be detected, and as the impulses in the groups are often very closely spaced there can be no appreciable difference in the refractory periods as between the ascending and descending pathways.

In the experiments to be described the antidromic preparation has been used to study the area supplied with tactile endings by a single afferent fibre and to see whether this area remains constant under varying conditions. We have also made observations on the maximum frequency of the sensory impulses and on the reactions of the animal to sensory discharges of high frequency.

## METHOD OF EXPERIMENT.

We have used only the dorsal cutaneous nerves (rami cutanei dorsi mediales) of the frog exposed by a median incision. If it was desired to record impulses coming directly from a skin area, the central end of the nerve was tied with silk thread and cut close to its entrance into the dorsal muscles, while for antidromic impulses the nerve was tied and cut near its entrance to the skin. In either case the free end of the nerve trunk was drawn into a short piece of glass tubing containing silver-silver chloride leads, while the other extremity was left attached to the animal. Action potentials were recorded by means of a Matthews oscillograph and valve amplifier. A few of the experiments were made with the apparatus usually employed by one of us (E. D. A.), but for the majority we used an alternative system which has been set up in a room of its own. The amplifier is of the standard pattern supplied by the Clifton Instrument Company, and records are made on a bromide paper camera which is combined with a rotating mirror of the type described by Forbes [1924] by means of which the individual impulses can be viewed on a screen. The rotating mirror is mounted directly above the camera on a level with the eye, and part of the light from the oscillograph mirror is deflected on to it by a train of prisms. Both camera and mirror are driven by an electric gramophone motor which runs at a constant speed and can be engaged with the camera mechanism by a friction pulley. With this arrangement the experimenter can observe the impulses as they would appear if recorded on a surface moving at 2 m. a sec. and can make permanent records at speeds up to 20 cm. a sec. Provision has been made for fitting a second camera below the first for high speed recording, but this has not yet been added. As a further aid to the study of the nerve discharge the amplified potential waves were also converted into sound (cf. Adrian and Bronk [1929]).

For mapping the areas supplied by a given sensory nerve light strokes with a feather were used to stimulate the skin endings. It was desired, however, to employ a method by means of which repeated stimuli of definite intensity and frequency could be applied. In a few of the earlier experiments repeated stimulation was secured through a light bristle attached to a tuning fork, but this was soon discarded in favour of an interrupted air blast. Preliminary trials showed the latter to be an adequate stimulus to the end-organs of the frog's skin, the rate of discharge following the frequency of interruption over a wide range. The same principle has been employed by Allen and Hollenberg [1924] in a study of human sensory preception.

The air jet was formed by passing air at a pressure between 500 and 800 mm. of mercury through a glass nozzle having a diameter at the tip of approximately 0·2 mm., and in most of the experiments placed 15 mm. from the surface of the skin. For interrupting the jet of air celluloid discs containing slots were revolved in front of the nozzle. For this purpose an ordinary dental drill was employed, the slotted discs being substituted for the grinding surfaces employed by the dentist. These discs were 26 mm. in diameter with notches cut at the periphery immediately behind which the air nozzle was mounted. The intensity of the stimulus can be controlled by changing the distance between the nozzle and the preparation or by altering the air pressure, and the frequency of stimulation can be altered by changing the speed of rotation or by varying the number of slots contained in the disc. The duration of the individual stimuli (air blasts) is controlled by the width of the slots in the disc and by its rate of rotation. In the present experiments we have employed frequencies of stimulation up to 400 per sec. The apparatus should be capable of giving higher rates, though at high speeds of rotation the vibration of the moving parts may be troublesome.

In the earlier experiments the air was saturated with moisture to prevent drying, but later the skin was painted with liquid paraffin which rendered this precaution unnecessary.

### *Area supplied by the dorsal cutaneous nerves.*

The number of dorsal cutaneous nerves on each side is usually between six and eight, though occasionally there are as few as four. The distribution of the tactile endings connected with each nerve can be outlined by stroking the skin with a feather and recording the nerve impulses with a loud speaker. The results of a typical experiment are shown in Fig. 3. In general one of these nerves supplies a portion of skin on the dorsal surface having an area of between 0·5 and 2·0 sq. cm., but varying greatly in different preparations. These areas extend well over the dorsal median line, and to the mid-lateral region in an irregular band. There is also extensive overlapping of the areas supplied by adjacent dorsal nerves, so that usually any point on a major portion of the skin in the dorsal region gives sensory fibres to two or more dorsal nerves. Since there are also endings connected with the dorsal fibres on the other side and presumably with the lateral cutaneous branches on the same side, it is safe to conclude that sensory stimulation of any area results in the passage of impulses to the central nervous system through a variety of peripheral pathways.

There is always a central portion in the area supplied by a nerve in which a given stimulus produces a maximal discharge indicating the involvement of a large number of sensory fibres. Towards the periphery the number of endings thins out, and at the margins the electrical response shows that only a very few nerve fibres are responding.

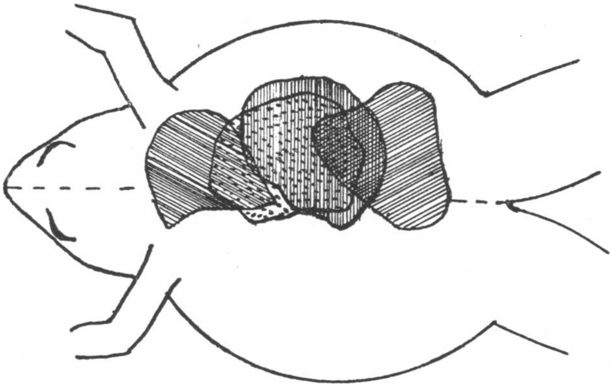

Fig. 3. Distribution of tactile endings supplied by four dorsal cutaneous nerves in a typical experiment.

### *Area supplied by single sensory nerve fibres.*

After placing leads on the central portion of one of the dorsal cutaneous nerves cut near the skin the whole skin surface is systematically explored with a feather. If a receptor is stimulated whose fibre gives off a branch to the nerve under examination it will, of course, be apparent by the action potentials. In certain frogs every dorsal nerve has given an antidromic discharge in response to the stimulation of some skin area, while in others every nerve has failed to respond. In roughly 10 p.c. of the nerves giving antidromic discharges these have been produced by stimulating two distinct areas, but the impulses from each area form a single series and are presumably conducted by a single fibre. An example of this arrangement is shown in Fig. 4.

The position of the area giving rise to antidromic impulses in any nerve bears a definite relationship to that nerve. It is always on the same side of the animal and usually at approximately the same spinal level as the main area supplied by the nerve under observation. At this level the areas appear in three chief locations as follows: (1) in the region of the thickened line marking the attachment of the dorsal septum; (2) on the ventral surface 2–8 mm. from the median line; and (3) less frequently in the mid-lateral region. The size of the area supplied by a single nerve fibre is exceedingly variable, but in most of the preparations examined it falls between 4 and 100 sq. mm. Its shape is irregular but usually elongated in an anterior-posterior direction. When located in the dorsal region it usually occupies a strip about 3 mm. wide and 8–14 mm. long along the line marking the attachment of the dorsal septum. In addition to this the same sensory nerve fibre also supplies an area in the dorsal region, through the axon branch in the dorsal nerve from which the action potentials are recorded. This last area is of course indeterminate, owing to the nerve containing this branch having been cut peripherally.

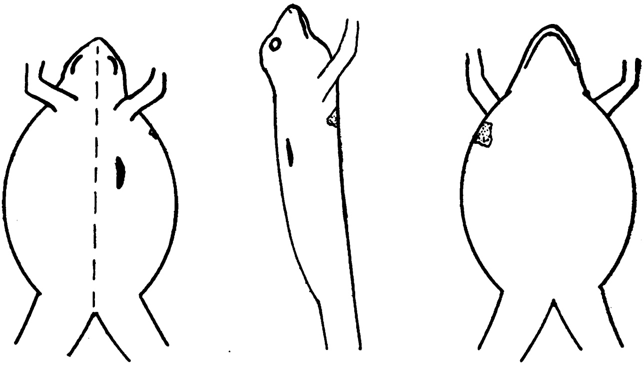

Fig. 4. Areas giving an antidromic discharge in a dorsal cutaneous nerve in one experiment. Each area shows the distribution of tactile endings from a single nerve fibre.

The position of the areas giving antidromic impulses in a particular nerve trunk suggests that the branching fibres do not supply regions outside the area of distribution of a single spinal nerve. Cutting the other dorsal cutaneous nerves does not interfere with the discharge, and in all probability the branches are confined to the various medial and lateral rami of the spinal nerve. It should be recorded, however, that out of several hundred preparations three have been observed in which the areas giving antidromic impulses did not correspond to this distribution. In one of these the discharge ceased when the cord was pithed, and its exact nature is uncertain.

There is no reason to suppose that the widespread distribution of the sensory endings of a single fibre will necessarily interfere with the exact localization of a stimulus. Owing to the overlapping of the area of distribution of different fibres the stimulation of any point on the skin will cause impulse discharges in several fibres, and the particular combination of fibres in action, together with the relative intensity of the discharge in each, would supply all the data needed for localization.

### *Constancy of areas.*

In view of the evidence brought forward by Waterston [1923] and by Allen and his collaborators, indicating a fluctuation of activity of the sensory endings in the skin of man under various conditions, there was a remote possibility that the receptive areas in the frog's skin might vary from time to time according to the state of the animal.

In a number of decerebrate frogs areas supplied both by a single nerve trunk and also by single nerve fibres have been observed from time to time over a period of several hours. In no instance has any change been discovered. By using the antidromic response it is possible to leave intact all efferent connections to the area under investigation, and it can be subjected to a reflex discharge of sympathetic impulses by stimulating other skin areas or by pinching the legs, but these procedures, and also the subcutaneous injection of adrenaline, have been without influence on the area responding to stimulation.

In several of the earlier experiments what seemed to be a definite increase in area occurred when the spinal cord was destroyed. Efforts to verify this observation in a series of about twenty frogs have not been successful, or have at most resulted in but a slight increase in the area responding to stimulation. The earlier observations are still unexplained, but we are inclined to account for them through an accidental change in the position of the leads on the nerve such that an additional nerve fibre has been included. The slight spreading of the area occasionally observed after pithing is probably associated with the general relaxation of the underlying muscles, resulting in a more readily movable skin and an apparent increase in excitability. This point is considered further in the paper on adaptation which follows.

Our methods are inadequate to detect slight changes in the sensitivity of the skin, and these might well follow from the mechanical effects resulting from sympathetic discharges to blood vessels and skin glands and possibly from a direct effect of the sympathetic discharge on the sensory endings, but we have no doubt that the nerve endings responding to touch are grouped into a series of distinct areas each supplied by a single nerve fibre. The areas overlap one another, but each area is perfectly definite and is determined presumably by the anatomical distribution of the nerve fibre terminations. For the touch receptors there is no indication of a peripheral network intervening between the sense organs and the sensory fibres and directing the sensory discharge now along one fibre and now along another according to the functional state of the network.

### *Frequency of discharges.*

In earlier work on the skin receptors [Adrian and Zotterman, etc.] the maximum frequency of the impulse discharge in a single fibre was left uncertain, but it was thought that it would not exceed the figure obtained for the tension receptors in frog's muscle, namely 100–150 a sec. This figure was based on an extrapolation which Matthews [1931] has now shown to be unjustified, for he finds that rapid extension of a muscle will give discharge frequencies as high as 250 a sec. in a single fibre, *i.e.* frequencies which are very near the maximum carrying capacity of the fibre. The present technique makes it possible to obtain accurate values for the frequency of discharge from the cutaneous receptors, and we find that they too can be made to give frequencies up to the limiting capacity of the nerve fibre. An example of a high frequency discharge is given in Fig. 5 from a record made with the antidromic preparation and photographed with a high speed camera. The skin was stimulated by rubbing with a camel hair paint brush, and a group of impulses is shown evenly spaced at a frequency of 200 a sec. As this method of stimulation is naturally incapable of accurate control a further study was made by stimulating with air currents produced in the way described on p. 381.

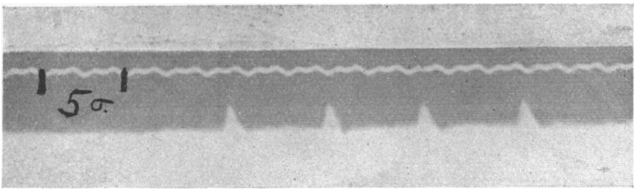

**Fig. 5.** Antidromic preparation. Receptive area stimulated by touching with a brush. The record shows a group of impulses at a frequency just under 200 a sec.

### *Response to air currents.*

(*a*) *Continuous air blast.* It was known that the touch receptors become very rapidly adapted to a constant stimulus, and it was therefore to be expected that a continuous air blast would call forth but few impulses. Actually it was found that when the air was turned on by opening the stopcock, cessation of activity occurred in less than one-fifth of a second and the discharge consisted of only from four to twelve impulses. In this case the application of the stimulus was not instantaneous because of the time required to open the stopcock and develop the full pressure at the tip of the nozzle. When the air was applied by quick removal of a screen from in front of the air jet the number of impulses was reduced to three or less, and usually to only one. In Fig. 6 is given a record from a preparation responding to a continuous blast of air with the greatest number of impulses we have ever observed. The lower record shows the reduction in the number of impulses which occurs when the air was applied suddenly by turning a wide-slotted disc before the air jet. These observations indicate that impulses are set up only during the actual period of movement of the skin although the air pressure is great enough to cause a visible pitting of the skin to a depth of several millimetres during its application. It will be seen that the

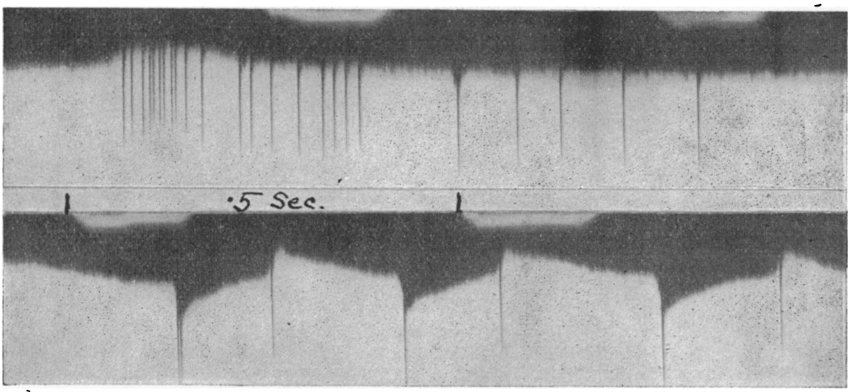

**Fig. 6. Antidromic preparation. Records showing how the response depends on the rate of development of the stimulus.**

***Above.*** **Continuous stream of air applied by opening stopcock.**

***Below.*** **Same air current applied three times by turning a disc with wide slots in front of the air jet. The shift in the base line (slow upward movement) marks the duration of each period of stimulation.**

cutaneous regions adapt so rapidly that their reactions to mechanical stimulation are comparable with those of a nerve fibre to an electric current. There is a further likeness in the fact that a certain abruptness is essential to stimulation. With a nerve fibre it is well known that the rate of increase of the current must exceed a certain "liminal gradient" if it is to excite, and with the cutaneous receptors we find that if the air current is turned on gradually over a period of several seconds it can be made to rise to its full intensity without the production of a single impulse. In the cat the sensory endings activated by movement of the hairs behave in the same way; *i.e.* impulses are only set up during the actual movement of hairs and a very slow movement may be without effect.

(*b*) *Intermittent air blast.* With repeated air blasts of short duration produced by the rotation of the slotted disc in front of the air jet a series of antidromic impulses are set up in the single nerve fibre preparation, and these may follow the rate of interruption for long periods if the frequency is not too high. When it is very high the frequency of the discharge does not keep pace with that of the stimulation except at the outset. The conditions which determine this decline are described in the following paper, and for the present it is enough to state that for short periods the frequency may be made as high as 250–300 a sec. by stimulating at these rates. This approaches very closely to the maximum frequency which can be obtained by repeated electrical stimulation of a frog's nerve, and in the following paper it will be shown that the skin receptors can be made to set up two impulses spaced so closely that the second is greatly reduced in size compared with the first owing to the incomplete recovery of the nerve fibre. An example of a high frequency discharge produced by the intermittent stimulus is given in Fig. 7.

It is clear then that the cutaneous receptors, like the muscle receptors, can discharge at a higher frequency than that originally suggested as the maximum value. It is clear too that the receptors themselves are capable of intermittent activity at these high frequencies. Matthews has pointed out that in the stretch receptors of the frog's muscle high frequency discharges might perhaps be caused by a continuous active state in the end-organ which would set up intermittent activity in the nerve fibre at a rate depending on its refractory period. In the cutaneous receptors, however, when the stimulus is intermittent the activity of the receptors must also be intermittent, since the frequency of the discharge agrees with that of the stimulus. Thus the cutaneous receptors must react as rapidly or almost as rapidly as the nerve fibre itself, and we must abandon the view that the absolute refractory period of end-organs is in general longer than that of their nerve fibres.

### *Effects of high frequency sensory discharge.*

The interrupted air blast gives us a means of producing discharges of very high frequency in certain cutaneous nerve fibres, and although there is a progressive decline the discharge can be maintained for several seconds at frequencies in the neighbourhood of 150 a sec. The afferent mechanism producing painful sensation (or a corresponding response) has been the subject of much discussion, and one suggestion which has been advanced is that such effects are caused by long continued or high rates of discharge in fibres which can also produce non-painful sensation when the discharge is not so great. This suggestion can evidently be tested as far as concerns the particular nerve fibres which discharge when the skin is stimulated by the air blast.

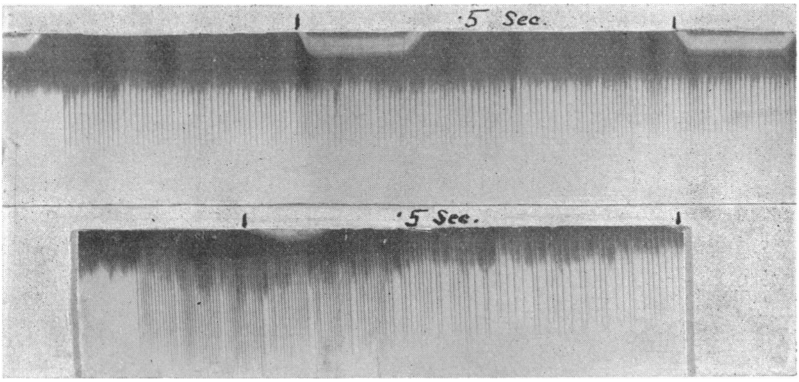

**Fig. 7.** Antidromic preparations. High frequency discharges produced by intermittent air current. In the upper record the frequency averages 140 per sec. for the first half second, in the lower it is 310 for the first fifth of a second. The irregularities in the rhythm may be due to unsteady running of the stimulating apparatus.

When an intact and active frog is placed beneath the nozzle a single blast of air does not elicit a response, a result which harmonizes with the fact that this stimulus causes but very few afferent impulses. An interrupted blast which, judging from experiments on decerebrate preparations, causes discharges in a number of sensory fibres, each at a rate up to two or three hundred a second, frequently causes minor movements of the eyes and limbs, and occasionally general movements effectively removing the animal from the source of stimulation. More often, however, the frog continues to sit quietly after perhaps initially making a few small movements and remains thus indefinitely during the application of the high frequency series of stimuli. In striking contrast is the vigorous response evoked by a slight pin prick.

It follows that the nerve fibres connected with the tactile endings do not produce pain, although they are made to conduct a discharge of long duration at a frequency not much below the maximum which the fibre can tolerate. This result is, of course, in agreement with the views which are generally held as to the specific functions of different fibres and end-organs. The nerve fibres concerned are most probably the larger medullated fibres, for Matthews [1929] has shown that in the nerves of the frog's leg the impulses from tactile receptors travel at a rate of about 15 m. a sec. at 15° C. This corresponds with the rate of conduction of the $\beta$ fibres in Erlanger and Gasser's group A [Erlanger and Gasser, 1930]. The end-organs seem to be confined to the epidermis, for if this is scraped away with a sharp knife the usual tactile discharge is no longer obtainable[1]. But we might expect that such treatment would produce pain, and it is interesting to find that scraping the skin, although it destroys the mechanism of the normal tactile response, results in a persistent discharge of small waves travelling at a much slower rate.

Slow waves have been noticed in earlier work on skin discharges, and one of us has found that they are regularly produced by applying weak acid to the frog's skin [Adrian, 1930 *a*]. We can now add that they are produced by scraping, crushing or burning the skin as well as by chemical irritants. The great difference between these slow potential waves and the large, rapid waves of the tactile discharge may be seen in Fig. 8. A limited area of the epidermis was removed with a knife a few minutes before the record was made, and at the moment of recording an undamaged part of the receptive field was touched with a brush to produce the tactile impulses. Owing to the high amplification the base line shows the usual small, irregular fluctuations which are caused by the unsteady emission of the first valve, but the slow waves can be clearly distinguished by their uniform size and shape. They are diphasic, but owing, probably, to the varying cross-section of the nerve, the first phase is less prominent than the second. In the rapid waves the two phases follow one another so closely that each response appears as a narrow vertical line, but the deflection is very much larger in spite

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[1] If the epidermis is completely removed and the corium exposed the normal tactile response does not return, but if only the surface layers are destroyed the response ceases for a time, but eventually some points in the damaged area regain their excitability.

of the interference of the effects at the two electrodes. The great difference in time relations suggests that the fibres responsible for the slow waves belong to the C group of Erlanger and Gasser. As they have shown, the fibres of this group have many of the properties which we should expect to find in a system concerned with pain, though it is unlikely that it is the only system concerned, since there is evidence that some pain reactions are evoked by fibres which conduct more rapidly [Piéron, 1929; Adrian, 1930 *b*].

These results raise many further points on which the experimental data are still incomplete and a more detailed discussion of the pain mechanism or mechanisms would go beyond the scope of this paper. For the present the only conclusion which we can safely draw is that a high frequency and a long duration of the discharge from the skin does not alone suffice to cause pain.

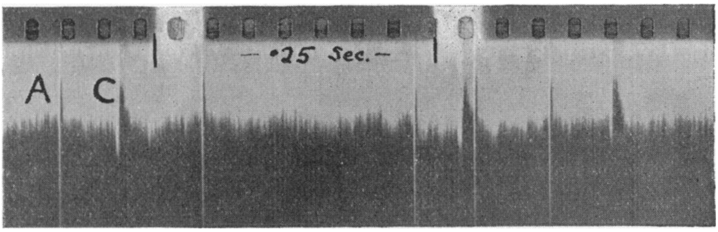

Fig. 8. Slow impulses due to injury and rapid impulses due to tactile receptors. Electrodes 5 mm. apart on dorsal cutaneous nerve cut proximally. Epidermis scraped away from part of the receptive area. The rapid impulses are produced by touching the intact skin. The first rapid impulse is marked A and the first slow impulse C. The base line shows small, irregular movements due to the amplifier.

## SUMMARY.

1. The impulse discharges in single nerve fibres from the tactile receptors can be studied in the dorsal cutaneous nerves of the frog. Many of these nerves contain a single fibre which has divided near the cord and sent branches into two nerve trunks. On stimulation of the receptive skin area supplied by one branch, antidromic impulses pass down the other branch and can be recorded in the nerve trunk in which it runs.

2. The skin area supplied by a single fibre of the dorsal cutaneous nerves varies from 4 to 100 sq. mm., but in a given preparation the area remains constant despite various physiological changes induced in the frog. There is considerable overlapping of the areas supplied by different fibres, but no evidence of a peripheral network common to several fibres.

3. The tactile endings become adapted very rapidly: impulses are only set up during the actual movement of the skin and a very slow movement may fail to excite. Skin vibration caused by an intermittent air blast produces discharges of long duration and high frequency.

4. The frequency of discharge in a single nerve fibre may be as high as 200–300 a sec. This approaches the maximum frequency which the fibre can carry. The view, put forward previously, that the sensory endings have a longer absolute refractory period than their nerve fibres is incorrect.

5. Stimulation with an air blast interrupted at a high frequency does not give rise to pain reactions in an intact or decerebrate frog in spite of the maximal discharge which would be set up in the sensory fibres. Thus the endings responding to this form of stimulation do not produce pain when the discharge frequency is very high.

6. The endings in question are situated in the epidermis, for the discharge can no longer be obtained after this has been scraped away. This treatment sets up a continued discharge of slow impulses indistinguishable from those produced by acid on the skin.

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