DISCHARGES FROM THE SENSORY ORGANS OF THE CAT'S VIBRISSAE AND THE MODIFICATION IN THEIR ACTIVITY BY IONS

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RECORDS from the cutaneous nerves of the cat, rabbit and guinea-pig [Adrian & Zotterman, 1926; Zotterman, 1939] have given information as to the sensory discharges from the hairs covering the body surface. These discharges are usually of brief duration, occurring only when movement is carried out and ceasing when a steady deflected position is reached. The nerve endings stimulated by hair movement can therefore be described as rapidly adapting, although the short duration of the discharges might be due to mechanical factors, such as the yielding of tissues, rather than to the intrinsic properties of the endings [cf. Dun & Finley, 1938]. But the investigations referred to have been concerned with the covering hairs of the body and limbs; the large vibrissae or tactile hairs of the face have not been specially examined. They might well react differently, since they are supplied by more elaborate nerve endings and have a more definite sensory function than the covering hairs. Indeed, the vibrissae represent a distinct type of organ, absent in man but important in the life of most quadrupeds.

The present work deals primarily with the normal sensory activity of the tactile hairs of the face, studied by the usual technique for recording afferent impulses. In the course of the work it became clear that preparations of these organs gave such consistent results that they could be used for the investigation of problems of more general interest, such as the nature of the adaptation process, its modification by ions, etc. The latter is dealt with in the second part of the paper.

HISTOLOGY

A good description of the tactile hairs and their nerve endings has been given by Ramón y Cajal [1933]. The tactile hairs are quite clearly differentiated from the ordinary hairs by the presence of a large cavernous vascular covering in the connective tissue sheath. They have a rich supply of nerve terminations from the many nerve fibres which coil round the hair bulb and run along the side of the hair sheath as a terminal palisade. Under some epithelial cells beneath the vitreous coat, nerve endings are found in the form of circular menisci or ivy-leaf appendages lying perpendicular to the root. Other club-like endings are found parallel to the hair and situated above the vitreous membrane. The hairs of the eye lashes are thought to be the closest example in man of the tactile hairs of the cat, rat, mouse and other animals.

METHOD

The cat, anaesthetized with dial (Ciba) 0·6 ml./kg., having had a tracheal tube inserted, was laid upon its ventral surface and a screw clamp fixed between the upper jaw and the lower surface of the unwanted eye. The eyelids were removed and the periorbita opened at the reflexion from the eyeball. The eye was quickly removed from the capsule, there being no necessity to ligature the artery accompanying the optic nerve if the eye were removed with sufficient torsion to tear the vessel. The periorbita was then separated from the surrounding fatty tissue and the maxillary, which is the afferent nerve from the vibrissae, exposed lying on the inferior surface of the orbital cavity. The nerve was carefully separated from the accompanying artery and sectioned as close to the brain as possible.

The animal was placed in a heated moist box, the nerve laid upon a thin sheet of ebonite, and dissected with needles. The action currents were recorded with a condenser coupled amplifier and a Matthews oscillograph. The hairs were stimulated either by traction or pressure. The former was provided by a weight attached to a fine silk thread running over a pulley, the thread being tied to the hair by the minimal quantity of sealing wax. The application of the weight by this method was brought about by allowing the weight to drop through a fixed distance without interference. The application of the stimulus could be looked upon as almost immediate. Slower applications could be brought about by allowing the weight to rest upon a lever, the other end of which was attached to a circular disk immersed in a treacle dashpot. For pressure stimulation a cardiac lever was used, a weight being laid on one arm of the lever, the hair being fixed to the other arm. The stimulus here was always applied immediately. It was usually found that the most constant results were to be obtained using the traction method of stimulation but, as will be seen later, this could not be used in every case.

When it was intended to inject solutions into the whisker-bearing area the common carotid artery was selected. The thyroid, internal carotid, occipital and lingual arteries having been tied, a cannula was inserted in a cranial direction. The temperature of injected solutions (all isotonic) was kept at 37°.

PART I

Results

Nature of effective stimulus. Directional effects. When the nerve is subdivided it is found that the tactile hairs supplying each bundle of nerve fibres are distributed in circles around the lower surface of the orbit. When the superior hairs, lying close to the orbit, are examined it is usually found that a much larger afferent discharge is produced by bending the hairs down, towards the mouth, than upward to the eye. For the hairs near the mouth the discharge is greater for bending upward than downwards. For the hairs near the snout, bending aborally is more
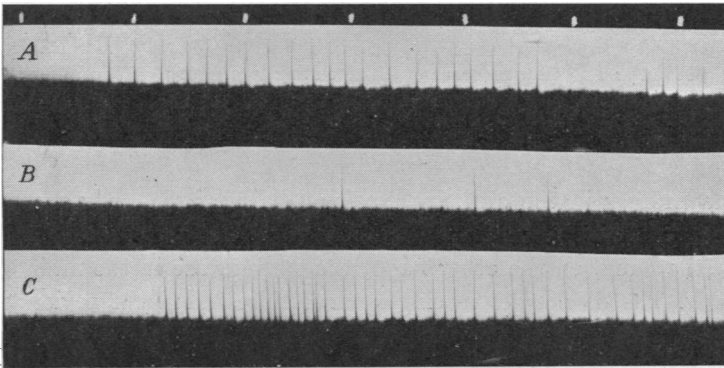

Fig. 1. Different planes of movement stimulating the same nerve ending. A =up, B = back, C =push in. No other movement discharged the ending. Time $\frac{1}{10}$ sec. All records read left to right.

effective than bending orally, and the reverse is true of the hairs lying farther back. In some nerve fibres a discharge can be obtained by bending the hair in one direction only, but it is more usual to find that movement in at least two directions is an effective stimulus, e.g. in either a forward or an upward direction (Fig. 1). Pulling the hair outwards from the skin is never as effective a stimulus as bending it sideways in the optimal direction, and it was unusual to find that the same ending would be stimulated by pushing the hair in towards the skin and by pulling it outwards. It happened on two occasions that the ending which was stimulated by pulling a hair was stimulated by pulling on more than one hair; in one case pulling on four different hairs seemed to stimulate the same endings (Fig. 2).

This directional sensitivity of the tactile hairs has, no doubt, some functional significance, for the results indicate that the hairs are most sensitive to the particular stimulus which they will be the first to meet. Thus an object moving downward relative to the head will bend the superior hairs first, if it moves aborally it will bend the hairs near the snout before any others, and so on.
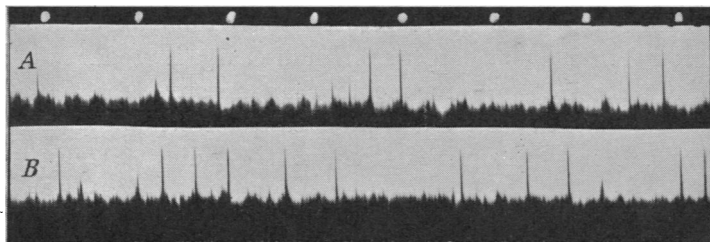

Fig. 2. Both *A* and *B* show response of single ending to stimulating two different hairs. Stimulation of two other hairs also gave responses. Time $\frac{1}{10}$ sec.

Adaptation

The endings in the ordinary covering hairs of the body respond to movement with a discharge which lasts only a fraction of a second. With the tactile hairs, on the other hand, the endings are in the main slowly adapting. The discharges in single nerve fibres from the region of the vibrissae are sometimes very brief, but in most cases it has seemed probable that the endings giving such discharges were attached to the fine hairs surrounding the larger vibrissae. It is true, however, that on occasions the ending was stimulated maximally through the vibrissae so that we must admit the possibility that some of the tactile hair endings are rapidly adapting.

Typical discharge curves from slowly adapting endings are shown in Fig. 3, the endings respond to the stimulus by a moderately high initial frequency, the value reached depending upon the intensity of the stimulus, i.e. the size of the weights used, and the speed of application (Figs. 3, 4).

In constructing the adaptation curves 15 min. rest was always allowed between tests so as to give the endings time for complete recovery. The endings are not as slowly adapting as those found in muscle by Matthews [1931, 1933] but the curves resemble those for the vagal endings in the lung [Adrian, 1933], there being a gradual decline in frequency with complete failure in about 10 min.
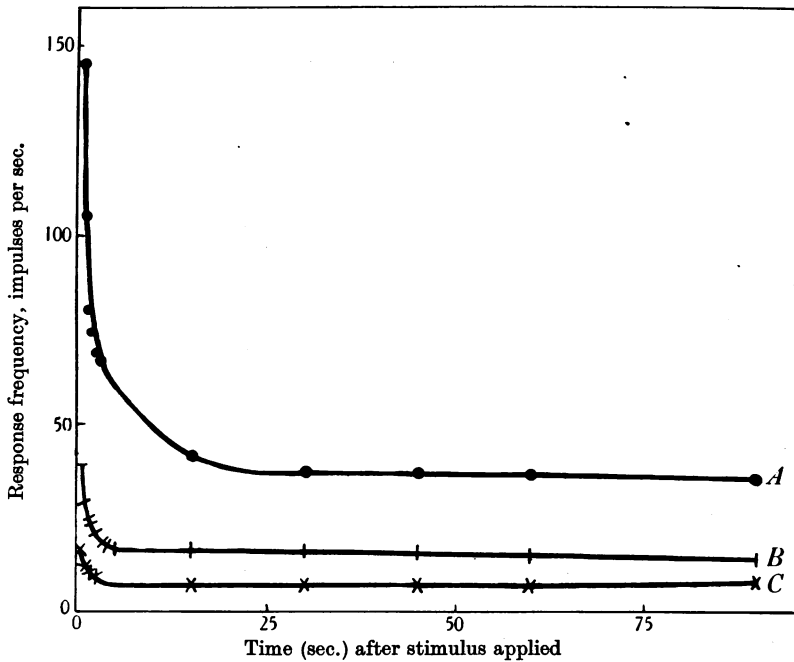
Fig. 3. Effect on discharge curve of varying load. Stimulus applied by traction. $A = 2$ g., $B = 1$ g., $C = 0.5$ g.
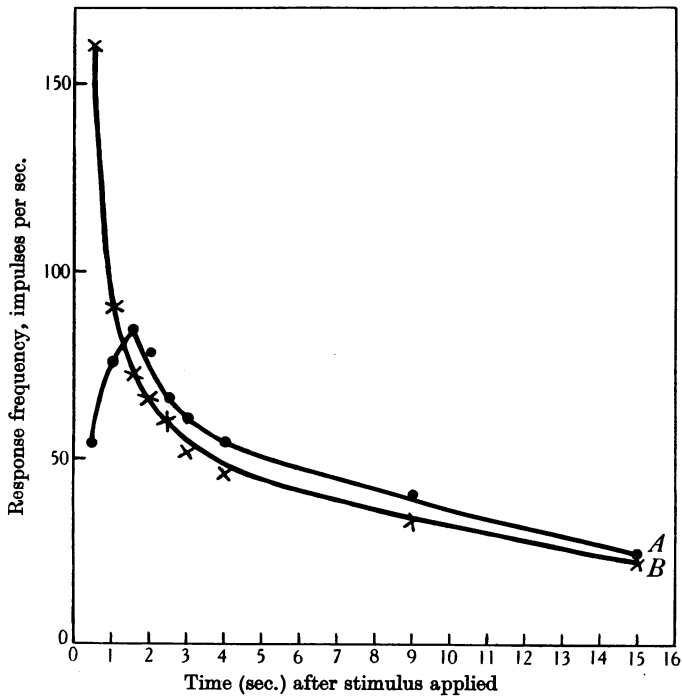

Fig. 4. Effect of different speeds of loading on the discharge curve. Stimulus (2 g.) applied by traction. $A =$ stimulus applied in 1·2 sec. $B =$ stimulus applied in 0·2 sec.

Like the directional sensitivity the slow adaptation of the tactile hairs is probably of value in some of the postural adjustments of the head in relation to solid objects. Although the vibrissae would not be held very long in the bent position, unless the animal were lying down, they might remain distorted for several seconds and it is probably important that there should be very little falling off in the strength of their signals during such a period. Also, by reason of the slow adaptation, a relatively small number of vibrissae can give accurate information of the position of objects in contact with them. Their effectiveness in this respect is shown by Bard's [1938] finding that a blindfolded (but otherwise normal) cat held in the air by the body, reacts to pressure (unilateral or bilateral) of the vibrissae against a solid object by the accurate placing of the forefeet on the object.

Spontaneous discharge

During the course of cutting down a nerve it was nearly always found that out of a bundle of twenty fibres one or two were in a state of spontaneous activity, and one of these could sometimes be isolated. The number of endings giving a spontaneous discharge is small, usually less than 5 % of the total number examined, and the rate of discharge rarely exceeds 40 per sec. It is found that low frequency spontaneous discharges are often more regular than discharges of the same frequency induced by stimulation.

The origin of these spontaneous discharges is of considerable interest, for they have been found with many types of sense organ and their nature has given rise to some speculation. In the present instance the most probable explanation of the discharge is that it is due to a combination of an unusual instability in the ending with an external stimulus which is just above the threshold. The unusual instability is shown by the great regularity at low frequencies (referred to above), and the absence of the usual adaptation, but the second factor, i.e. the intervention of an external stimulus, is strongly suggested by the effects produced by slight movements of the hairs. Thus it is often found that if the hair be moved to the appropriate position all spontaneous activity ceases and does not recur whilst this position of the hair is held. On one occasion it was found that a spontaneous discharge stopped and another ending was stimulated (Fig. 5); when the hair is released the spontaneous discharge recommences with an initial peak in the frequency curve similar to that found normally on stimulation, though of a slighter extent.

Granit [1935] showed the existence of an inhibitory component in a sense organ (the eye). Sand [1937] has described phenomena similar to

those in the present paper of the abolition of a spontaneous discharge and also suggested that they represent an inhibitory process at the sensory nerve ending, comparable to that occurring within the central nervous system. In the present case, at any rate, it seems unnecessary to postulate anything more than the presence or absence of an excitatory stimulus.
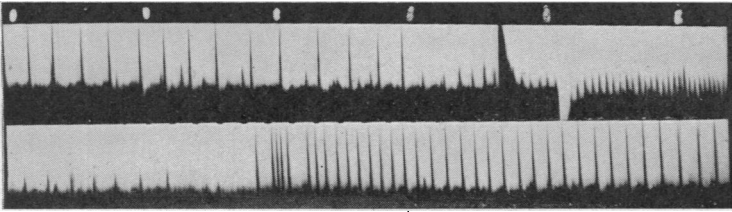

Fig. 5. Spontaneous discharge affected by movement. Upper = spontaneous discharge stopped by hair movement and another ending seen to be discharging. The large excursion is an artefact. Lower = on release of the hair the spontaneous discharge recommences with a slight peak. The other ending stops discharging. Time $\frac{1}{10}$ sec.

The ending is in an abnormally irritable state, a very slight deformation causes a persistent discharge, and the discharge ceases when the stimulus is withdrawn.

The "silent period"

A well-known accompaniment of the spontaneous discharge is the silent period, the temporary failure of the discharge following increased activity. This was described by Adrian & Zotterman [1926] for the stretch receptors of frog muscle, but the factors upon which it depends were not
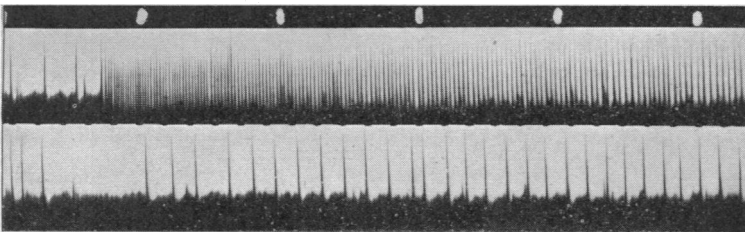

Fig. 6. Spontaneous discharges and the silent period. Upper = stimulation of an ending already spontaneously discharging. Lower = after 1·5 sec. Stimulus is withdrawn resulting in a silent period which is followed by the rebuilding of the spontaneous discharge. Time $\frac{1}{10}$ sec.

investigated. The effect is shown in Fig. 6, which illustrates both the silent period after the stimulus is withdrawn and the gradual rebuilding of the discharge to the original frequency.

In these experiments the length of the "silent period" has been found to depend upon the total activity produced during the period of stimulation. It does not depend upon the particular frequency occurring at the moment when the stimulus is withdrawn, for it may be seen from Fig. 7
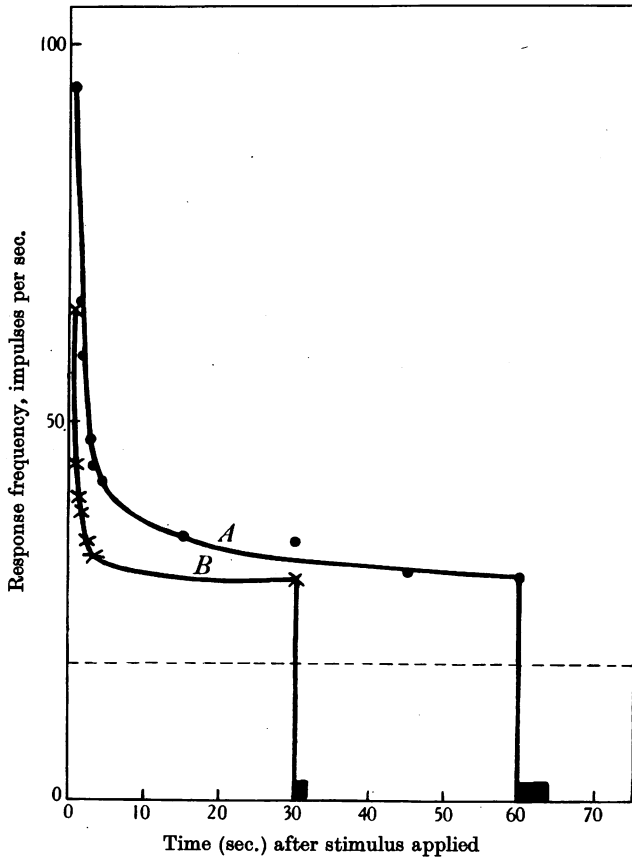

Fig. 7. The greater discharge of the ending leads to greater silent period. Stimulus applied by traction. $A = 17$ g., $B = 7$ g. Blocked out area on base = length of silent period. $A = 1.0$ sec., $B = 3.9$ sec. The intermittent line gives the level of the previous spontaneous discharge.

that similar frequencies at the moment of removal of the stimulus do not lead to similar lengths of silent period. Where stimuli of different intensities were used it was seen that the initial frequency on application of the stimulus was not the sole determining factor, and that the duration of the increased discharge was also important. Finally, in Fig. 7 it will be

seen also that there is a reasonably close relation between the length of the silent period and the total number of impulses set up during the period of stimulation.

After the silent period the spontaneous activity slowly returns along a smooth curve and finally the original frequency of the discharge is again reached. The greater the length of the silent period the more gradual is the curve of recovery, as might well be expected if the failure of the discharge is due to a fall of excitability of the ending, consequent on the period of increased activity.

This gradual return of spontaneous discharge after the silent period is in sharp contrast with the sudden return which takes place when the hair is released from the "no discharge" position (cf. Fig. 5), for then there is an initial peak followed by a decline to a lower level of frequency. In the latter case, presumably, the absence of the discharge was due to the withdrawal of the stimulus which normally maintains it, whereas in the former it was due to a fall of excitability which rendered the stimulus temporarily ineffective; this fall of excitability passes off gradually and allows the stimulus to exert its former effect on the unstable ending.

PART II

In preparations from the frog the influence of changes in the ionic constituents of the surrounding fluid on the activity of the sensory ending is much the same as on skeletal or cardiac muscle. Thus Matthews [1931] has shown that reduction of Ca^{++} leads to a spontaneous discharge of the stretch receptors in frog muscle, and Talaat [1933] has found the same result with endings in frog skin, whilst recently Dun & Finley [1938] have produced very rapid adaptation in the tactile endings of the frog by increasing the Ca^{++}. An increase of K^+ depresses and may abolish the response of these endings. Feng [1933] showed that the K^+ liberated from injured skin was enough to make the endings inexcitable, and it has been suggested by Hoagland [1936a, Summary] that sensory adaptation in general is brought about by the same mechanism, i.e. that it is due to a fall of excitability caused by the liberation of K^+ from cells near the endings.

With the tactile hair preparation it has been possible to extend this study to mammalian endings, for solutions injected headwards into the common carotid artery will bathe the whisker-bearing area, and it is not difficult to rule out the effects of muscular twitching, etc. The results have been of considerable interest; they show that small changes in certain

ions may have a pronounced effect on adaptation rate, but in the case of K+ there is an initial stimulation which is hard to reconcile with Hoagland's theory.

Action of sodium chloride upon the endings

Small quantities of isotonic sodium chloride appeared to have little or no effect upon the endings, but when approximately 15 ml./kg. of isotonic sodium chloride had been injected into the carotid artery there was
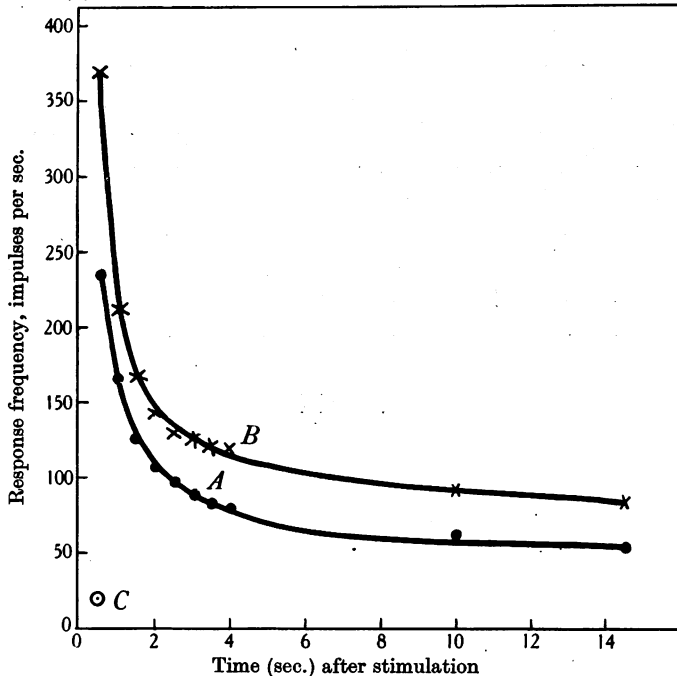

Fig. 8. The increased response of an ending after Na+ injection with the effect of CaCl₂ upon it. The same strength of stimulus was used in both cases. *A* = before injection. *B* = 4 min. after 135 mg./kg. of NaCl. *C* = 3 min. after 40 mg./kg. of CaCl₂ given to same preparation.

usually a development of spontaneous activity. This could be seen when there was no twitching round the facial area. It lasted some minutes or even longer and then the effect gradually disappeared. This stimulating action of the sodium upon spontaneous activity was never as plain as that of sodium citrate or K+ (probably due to the fact that such large or probably variable doses were needed), and was more easily seen when more than one active fibre was present in the nerve bundle. It appeared as if some endings were more easily set into a state of spontaneous

activity than were others. The animal never showed any ill-effects as a result of the injections.

Isotonic sodium chloride in quantities which are sufficient to produce spontaneous discharge from the nerve endings also affect the frequency curve. There is an increased frequency of discharge on stimulation, and the frequency remains at a higher level than normal through the adaptation period (Fig. 8). This effect is quite similar to that found by Matthews [1931] for the muscle spindle of the frog. The stimulating action of Na^+ upon the ending can be rapidly and completely antagonized by Ca^{++} in small doses (Fig. 8). It seems probable that the action of Na^+ is really due to the relative fall in the concentration of the other ions, for large quantities of Na^+ must be injected for an effect; much smaller amounts of K^+ or Ca^{++} having marked effects upon the nerve endings.

Action of potassium chloride upon the endings

As a result of the injection of 1 ml./kg. KCl there is an immediate marked twitching of the facial musculature accompanied by a high-frequency discharge from the nerve endings. This is probably due in part to the hair movement, but when all muscular activity has ceased the ending still continues to discharge spontaneously for at least some minutes. The rate is usually high at first, falling gradually to zero. This is probably due to the washing out of the K^+ by the blood stream. It is essential to inject the KCl very slowly even in quite small quantities (1–2 ml./kg.), for a sudden sharp injection may lead to cardiac failure. After a slow injection there may be some slight signs of cardiac and respiratory effects but these rapidly disappear.

The effect of K^+ injection upon the adaptation rate is interesting, for even 10 mg./kg. KCl injected intra-arterially cause a marked increase in the initial frequency, and the discharge through the period following stimulation is much higher than before the injection (Fig. 9). Spontaneous activity as a result of the injection may have ceased, but this effect persists. The effect is somewhat similar to that which Matthews [1931] found for Na^+ but is the opposite to what he found for K^+. A subsequent injection of more K^+ usually gives a further slight increase in frequency after stimulation, but the maximum increase in initial frequency to a stimulus after the injection has been about 60%.

As can be seen, the level of the discharge remains at a higher frequency all through the period of stimulation. The stimulating action of K^+ upon the endings seems to be followed by depression, but for the development of this depressive action, large quantities (up to 70 mg./kg. of KCl) had to
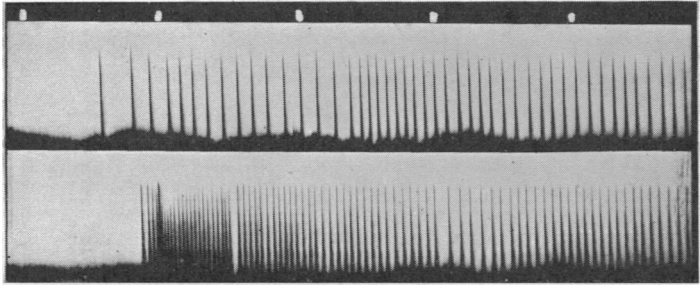
Fig. 9. The modification of the frequency of response by K+. Response to 2 g. traction. Upper = before. Lower = 5 min. after 10 mg./kg. of KCl through the artery. Time $\frac{1}{10}$ sec.
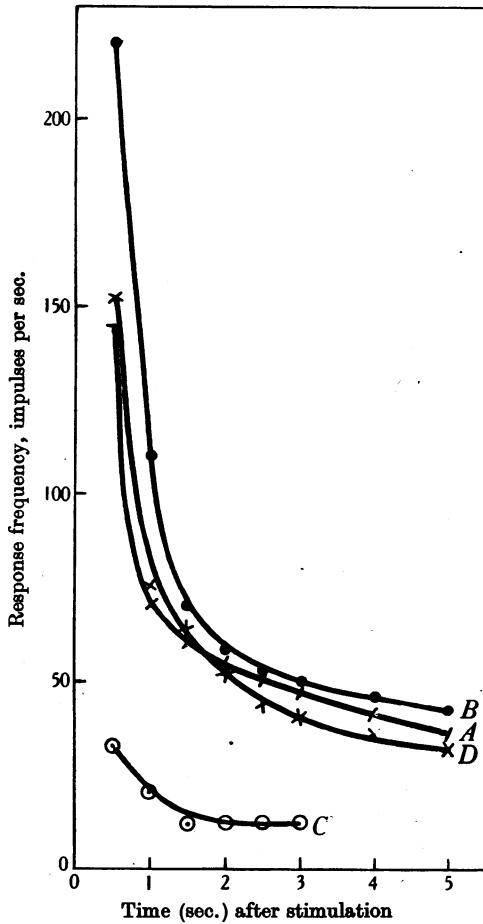

Fig. 10. The stimulating and depressing effects of K+ with the effect of Na+ upon the latter. A = before. B = 2 min. after 10 mg./kg. of KCl. C = 5 min. after total of 50 mg./kg. of KCl. D = 25 min. after 150 mg./kg. of NaCl.

be injected and there was always a prolonged initial increase in the frequency on stimulation before the onset of depression. The chief manifestation of depression was a decreased initial response on stimulation with a markedly increased adaptation rate. If the intra-arterial injection had been given at a sufficiently slow rate this depression was not accompanied by other signs of disturbance in the animal.

The antagonist action of various ions to K^+ is of interest. Na^+ did not appear to have any antagonism to the stimulatory effects of K^+. Ca^{++} in equal doses prevented the occurrence of the spontaneous rhythm and the increased initial response on stimulation. When the depression after excess K^+ had appeared, Ca^{++} in quite small amounts led to an even more marked depression of activity. If more Na^+ were injected, in doses of approximately 15 ml./kg. of isotonic NaCl, there was a gradual return to normal, the ending eventually completely recovering its response to stimulation (Fig. 10). The predominantly depressive action of K^+ found by other workers is possibly due to the fact that they were using frog's tissues and applying the solutions by irrigations and not, as in these experiments, by arterial injection. It must be emphasized that the stimulating effect is not due to the muscular contractions acting on the hairs, for neither slight contraction nor hair movement is observable when the ending is discharging spontaneously. Also, even where there is no further spontaneous activity the frequency response of the ending is much higher than before K^+ injection, showing that the effect is on the ending rather than on the surrounding tissues.

Effect of Ca^{++}

If an ending or a group of endings be discharging spontaneously the injection of a small quantity of $CaCl_2$ (15 mg./kg.) will stop the discharge. This effect can be seen in Fig. 11. Less $CaCl_2$ is required when the injection is a close one through the artery, rather than when the solution is injected through the femoral vein, but larger quantities of $CaCl_2$ (75 mg./kg.) appeared to have no marked toxic action upon the normal animal.

If a quantity of $CaCl_2$ be injected which is sufficient to stop all spontaneous activity it will usually be found that it has some effect upon the adaptation rate, although a more marked effect can be found with larger doses than that required just to stop spontaneous activity. The effect of 40 mg./kg. of $CaCl_2$ is shown in the accompanying Fig. 12. In this case it may be noticed that the $CaCl_2$ solution has been injected through the femoral vein and so the Ca^{++} was distributed through the body fluid before eventually reaching the ending in the hair. Obviously

the effective quantity here was quite small but the effect was a prolonged one. It can be seen clearly in Fig. 12 that there are two distinct effects. The first is not so constantly found and consists in a depression of the initial response. A more constant and possibly more characteristic result is that seen on the adaptation rate, for here the ending is seen to adapt a great deal more quickly than before injection.
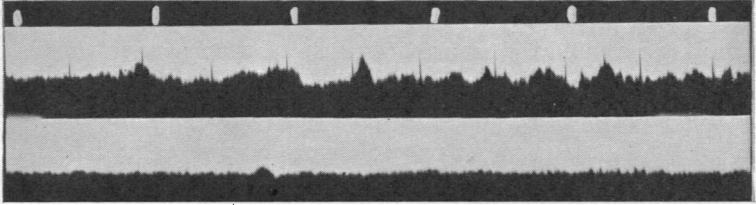

Fig. 11. The effect of Ca^{++} upon a spontaneously discharging ending. Upper = before. Lower = 1 min. after 15 mg./kg. of CaCl$_2$. Time $\frac{1}{10}$ sec.

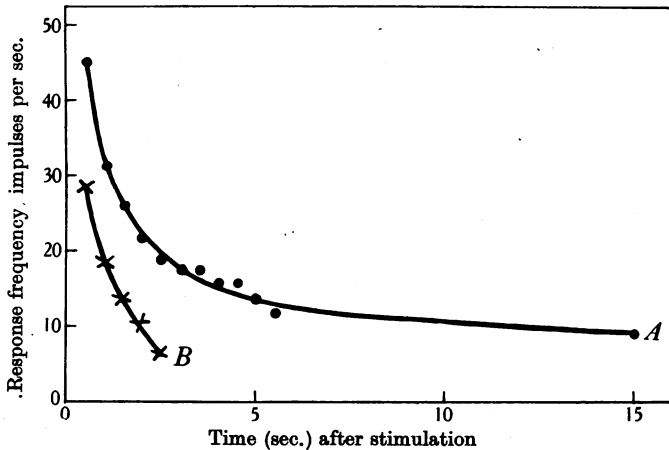Fig. 12. The depressant action of Ca^{++} upon the nerve ending. A = before. B = 5 min. after 30 mg./kg. of CaCl$_2$ through the femoral vein.

The relation of Ca^{++} to other ions is of interest. Na$^+$ in large quantities was capable of reversing the depressant effects of Ca^{++} upon the ending, but not to the extent, as far as was observed, of development of any marked spontaneous activity, the main effect being a return of the adaptation rate to normal. The initial effect of any quantity of K$^+$ is to prevent the depressant action of Ca^{++}. Sodium citrate (3 % isotonic) led to the development of marked spontaneous activity, as it does in frog's skin. The effect of citrate upon the adaptation time was not investigated.

DISCUSSION

In these experiments the ion which is held by some workers to be the cause of rapid adaptation at sensory endings appears to stimulate these in no uncertain fashion. 1 ml./kg. of isotonic KCl, injected into the artery supplying the afferent area, caused a prolonged stimulation of the ending. This quantity of KCl, when distributed in the total body fluids of the animal, would seem to be so small that there is presumably some local concentration effect at the ending on injection, with a gradual disappearance of this effect. This view is supported by the fact that the development of the spontaneous rhythm is almost immediate, and gradually falls off in frequency, with the increased initial response remaining as a more prolonged effect.

In these endings at any rate the speed of adaptation is not affected by quantities of K^+, which cause spontaneous discharge from the ending at the beginning and a more prolonged increased initial response on stimulation. It cannot, therefore, be seriously advanced that a K^+ increase in the external fluid can be a cause of the eventual adaptation of these endings. In the frog's skin the quantities of K^+ used by Hoagland [1936 b] were large (15 times the normal amount) and such quantities might be expected to bring about a rapid depression, the stimulation being quickly overcome (if it were ever present). This view is supported by the fact that Hoagland found that, if the adaptation of an ending (in Hoagland's sense) had been hastened by Ca^{++}, washing with K^+ solution caused a preliminary marked slowing in this adaptation, followed by quickening. Hoagland considered that the depressive action of K^+ was its characteristic effect on the sensory endings of the frog's skin. With these mammalian endings, however, the stimulating action of K^+ seems to be its more pronounced effect, the depressive effect occurring at a later stage. The quantities of K^+ required to produce rapid adaptation would be relatively large and it is doubtful if they could be concentrated at the ending sufficiently quickly.

SUMMARY

1. A method is described for recording sensory nerve impulses from the vibrissae of the cat.

2. The nerve endings are stimulated most effectively by movement of the vibrissae in particular directions, thus downward movement is most effective for the upper vibrissae and upward movement for the lower.

3. The endings are slowly adapting, the frequency of the discharge varying with the extent and rate of development of the main movement.

4. Spontaneous discharges from the endings occur and they appear to be due to an abnormal irritability of the ending, associated with a stimulus which is just above the threshold.

5. In a nerve fibre giving a spontaneous discharge the length of the silent period following stimulation appears to be related to the total number of impulses discharged during stimulation, rather than to either the initial or final discharge frequency.

6. After the silent period the spontaneous discharge returns gradually to its former value. The shorter of two silent periods is followed by a quicker return to the previous level of spontaneous discharge than is the longer.

7. Na^+ in large amounts leads to spontaneous discharges and an increased initial discharge.

8. K^+ in much smaller amounts has a similar effect. In large amounts it has a depressant action upon the spontaneous and the initial discharge, and it also leads to a rapid adaptation of the ending. Citrate produces spontaneous discharge like K^+.

9. Ca^{++} inhibited spontaneous discharges from an ending, decreased the initial response on stimulation, and quickened the rate of adaptation.

10. The result with the above ions does not agree with the view that K^+ can be an agent which would produce rapid adaptation in these endings.

REFERENCES

Adrian, E. D. [1933]. *J. Physiol.* **79**, 332.

Adrian, E. D. & Zotterman, Y. [1926]. *J. Physiol.* **61**, 465.

Bard, P. [1938]. "The neuromuscular and central nervous systems." MacLeod, *Physiology in Modern Medicine.* St Louis: Mosby.

Dun, F. T. & Finley, C. B. [1938]. *J. Physiol.* **94**, 170.

Feng, T. P. [1933]. *J. Physiol.* **79**, 103.

Granit, R. [1935]. *J. Physiol.* **85**, 421.

Hoagland, H. [1936*a*]. *Cold Spr. Harb. Symp.* **4**, 347.

Hoagland, H. [1936*b*]. *J. gen. Physiol.* **19**, 943.

Matthews, B. H. C. [1931]. *J. Physiol.* **71**, 64.

Matthews, B. H. C. [1933]. *J. Physiol.* **78**, 1.

Ramón y Cajal, S. [1933]. *Histology.* London: Baillière, Tindall and Cox.

Sand, A. [1937]. *Proc. Roy. Soc.* B, **123**, 472.

Talaat, M. [1933]. *J. Physiol.* **79**, 500.

Zotterman, Y. [1939]. *J. Physiol.* **95**, 1.